

Evaluating drivers of spatiotemporal individual condition of a bottom-associated marine fish

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Abstract

A fish's body condition is described by its 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 or even survival of the population. Several hypotheses have been proposed (e.g., competition, hypoxia, lack of prey) and evaluated temporally using averages over large spatial scales (basin or population level). However, as these variables operate at local spatial scales and are heterogenous in space, it is important to evaluate the link between body condition and covariates on local scales as well. By applying a geostatistical model that includes spatially and spatiotemporally correlated random effects using Gaussian Markov random fields, we analyze the body condition of cod in the autumn (main feeding season) in relation to biotic and abiotic covariates at different spatial scales and their spatiotemporal dynamics. We find that body condition declined over the whole domain until 2008, after which a plateau was reached. Oxygen, sprat biomass (at the subdivision level), haul-level temperature, and the biomass of the benthic isopod *Saduria entomon* (to a lesser extent) were positively related to condition, whereas the haul-level density of cod and depth were negatively associated with condition. However, the effect sizes of these variables were small, such that even though cod are now found in deeper and less-oxygenated waters, this could not alone explain the steep decline that occurred between 1993–2008. In fact, latent spatial and spatiotemporal variation was several times larger in magnitude than any single covariate's coefficient, and spatial and spatiotemporal random effects explained 6.5 times more variation than all fixed effects. However, body condition is a complicated trait to analyze as it builds up over a long time period. Hence, observational analysis of condition data should be complemented with e.g., tagging studies or otoliths analyses, before mechanistic links between condition and covariates can be determined. Understanding the drivers of spatiotemporal variation in body condition is

critical for identifying impacts of environmental change and for the management of marine fish and fisheries.

Introduction

Body condition is a morphometric index that describes the “plumpness” of an organism, or its weight relative to its length (Nash *et al.*, 2006; Thorson, 2015). It is related to food intake rates and metabolic activity, and is 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). Condition has also been linked to environmental variables, (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 (often resulting in the 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;

Sampaio *et al.*, 2021). As both environmental and biological variables can affect condition, it is important to study their relative contribution to 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 have 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 package ‘INLA’ (Rue *et al.*, 2009; Lindgren *et al.*, 2011). 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 density 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 (hereafter referred to as cod), 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 benthic prey *Saduria entomon* (Haase *et al.*, 2020; Neuenfeldt *et al.*, 2020), the flounder complex (European flounder *Platichthys flesus* and Baltic Flounder *Platichthys solemdali*) (Orio *et al.*, 2017), as well as an increase in abundance of its main pelagic prey species (sprat *Sprattus sprattus* and herring *Clupea harengus*) in northern areas where cod are scarce (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). It is also one of the fastest warming regional seas (Belkin, 2009; Reusch *et al.*, 2018). Previous studies have linked changes in mean condition of cod over large spatial scales to single or some combination of ecosystem drivers (Casini *et al.*, 2016a, 2021; Orio *et al.*, 2020). However, in previous studies, within-population variability in condition have been neglected and the effects of environmental and biotic covariates have not been studied on local scales. Moreover, the effect of all the above-mentioned covariates on cod condition have not been analyzed in a common framework.

In this study, we apply geostatistical GLMMs to characterize the spatiotemporal variation in body condition and distribution of cod in the south-eastern Baltic Sea. We use data from the scientific surveys between 1993–2019, which corresponds to a period of initially high but then deteriorating cod condition (Casini *et al.*, 2016a). We then seek to (1) identify which set of covariates (biomass densities of flounder, cod, and *S. entomon* (benthic prey) and biomass of sprat and herring (pelagic prey), 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 the International Council for the Exploration of the Sea (ICES) subdivisions 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 kg/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 (mid October to mid December), which corresponds to the main growing and feeding season of cod (Aro, 1989) and also the quarter in which the Baltic International Acoustic Survey (BIAS) is conducted, meaning sprat and herring biomass 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 using a spatiotemporal version of Le Cren’s relative condition index (K_{rel}). This index is defined as the ratio between the observed weight for individual fish i , caught in time t at space s , and the predicted weight. The predicted weight, was given by the relationship $\bar{w} = al^b$, where parameters a and b were estimated in a non-spatial model with all years pooled, to represent the average weight prediction, \bar{w} . 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 assess the ability of covariates (see section *Covariates* below) to explain variation in condition, we fit a geostatistical GLMM to the spatiotemporal Le Cren index, assuming Student-t distributed residuals (with the degrees of freedom parameter set to 5) due to the presence of extreme values:

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

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

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

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

$$\omega \sim \text{MVNormal}(\mathbf{0}, \Sigma_\omega) \quad (5)$$

$$\delta_{t=1} \sim \text{MVNormal}(\mathbf{0}, \Sigma_\epsilon) \quad (6)$$

$$\delta_{t>1} = \rho \delta_{t-1} + \sqrt{1 - \rho^2} \epsilon_t, \epsilon_t \sim \text{MVNormal}(\mathbf{0}, \Sigma_\epsilon), \quad (7)$$

Where K_{rel} represents the Le Cren condition factor at space 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 (Eqns. 2-4) 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 x_k represents a vector of the k -th covariate (biomass densities of flounder and cod, biomass of sprat, herring and *Saduria entomon*, depth, oxygen concentration and temperature) and β_k is its effect. The parameter ω_s (Eq. 5) represents spatial random effects. The parameter $\epsilon_{s,t}$ (Eqns. 6-7) represents spatiotemporal random effects, and we assume it follows a stationary AR1 process, where ρ represents the correlation between subsequent spatiotemporal random fields. Spatial and spatiotemporal random effects were

assumed to be drawn from Gaussian random fields (Lindgren *et al.*, 2011; Cressie and Wikle, 2015) with covariance matrices Σ_ω and Σ_ϵ . The covariance ($\Phi(s, s')$) between spatial points s and s' in all random fields is given by a Matérn function.

Density models

We fit spatiotemporal GLMMs to biomass density data in a similar fashion as for condition to 1) evaluate how the depth distribution of cod, as well as oxygen and temperature conditions experienced by cod have changed and 2) 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 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):

$$y_{s,t} \sim \text{Tweedie}(\mu_{s,t}, p, \phi), 1 < p < 2 \quad (8)$$

$$\mu_{s,t} = \exp\left(\gamma_t + \sum_{k=1}^{n_k} f_k(x_k) + \omega_s + \epsilon_{s,t}\right) \quad (9)$$

where $y_{s,t}$ represents density (kg/km²) at space s and time t , μ is the mean density, p and ϕ represents the power and dispersion parameters, respectively. The parameters γ_t represent independent means for each year, f_k is a penalized smooth function for covariate x_k and ω_s and $\epsilon_{s,t}$ represent spatial and spatiotemporal random effects. ω_s and $\epsilon_{s,t}$ have the same definition as in the condition model (Eq. 5-7).

Covariates

For both models (condition and density), covariates were chosen to reflect hypothesized drivers based on published literature. For the condition model, we included covariates at spatial scales

that roughly reflect the habitats cod would have been exposed to during the seasonal 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', *SI Appendix Fig. S1*) (Hüssy *et al.*, 2020). Therefore, we included environmental and biological demersal covariates (sea bottom temperature [°C], sea bottom oxygen [ml/L], depth [m], and biomass density of cod and flounder [kg/km²] and *S. entomon* [mg/m²]) at the haul and the median over the ICES rectangle-level, and the pelagic covariates at the ICES rectangle- and subdivision-level (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>). Monthly predictions for sea bottom temperature and sea bottom concentration of dissolved oxygen were extracted at the haul locations from the ocean model NEMO-Nordic-SCOBI (Eilola *et al.*, 2009; Almroth-Rosell *et al.*, 2011; Hordoir *et al.*, 2019) and averaged for October–December (approximately 14%, 76% and 10% of the hauls were conducted in October, November and December, respectively). Depth 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 density of *S. entomon* was extracted from a habitat distribution model using the modelled hydrographical data from the regional coupled ocean biogeochemical model ERGOM (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 (fourth quarter BITS). We used predicted densities from GLMMs (described above) 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 used to evaluate changes in the average depth, oxygen concentration and temperature experienced, we used these variables as

covariates. For the cod and flounder models that were used to predict covariates for the condition model, the only covariate used was depth.

Following Thorson (2015) and 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 marginal 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 from stepwise selection (e.g., Whittingham *et al.*, 2006) and because initial analyses suggested the model was not overfit (see *SI Appendix*, Fig. S2 for Pearson correlation coefficients across variables).

Model fitting

For computational efficiency, we fit all models 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, S12), 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. After initial exploration, we chose 200 knots for this application. We fit the models using ‘TMB’ (Kristensen *et al.*, 2016) via the R-package ‘sdmTMB’ (version 0.0.21.9006) (Anderson *et al.*, 2022) with maximum marginal likelihood and the Laplace approximation to integrate over random effects. We assessed convergence by confirming that the maximum absolute gradient with respect to all fixed effects was < 0.01 and

that the Hessian matrix was positive-definite. Model residuals are shown the *SI Appendix* (Figs. S4-S8 and S13-S16). We used packages in the ‘tidyverse’ (Wickham *et al.*, 2019) for data processing and plotting.

Results

The condition model revealed a mean decline in the Le Cren condition factor of 14% [17%, 11%] (values in brackets are the 2.5% and 97.5% quantiles from 500 draws from the joint precision matrix). It declined from approximately 1.11 to 0.95 between 1993 and 2019 (the decline leveled off in around 2008) and the whole distribution of condition values in the population exhibited a shift to lower values (Fig. 1). The condition factor declined the most in the northern subdivisions (i.e., 27 and 28) and the least in the south-western subdivision 24 (Fig. 1B). The spatial predictions from the condition model illustrate the presence of consistent “low spots” of body condition in deep and low-oxygen areas, and that the condition factor declined in the whole area over time (Fig. 2, *SI Appendix*, Fig. S9).

The covariates with the largest positive standardized effect sizes on the condition factor were temperature at the haul level (0.009 [0.004, 0.014]) (values in brackets indicate 95% confidence interval), median depth of the ICES rectangle (0.01 [0.004, 0.02]), oxygen concentration at the ICES rectangle level (0.01 [0.002, 0.016]), and biomass of sprat at the ICES subdivision level (0.007 [0.002, 0.013]) (Fig. 3). Depth at the haul level was negatively associated with condition (-0.023 [-0.027, -0.02]) (see *SI Appendix*, Fig. S10, for marginal effects plots). The biomass density of cod, flounder and *S. entomon*, and the biomass of herring did not affect the condition of cod at any scale (Fig. 3). The magnitude of any individual covariate effect size was generally small. In fact, these effect sizes were several times smaller than the magnitude of latent spatiotemporal and spatial variation (Fig. 3). Using the approach proposed in Nakagawa and Schielzeth (2013), we calculated marginal R^2 for fixed and random

effects, and found that fixed effects had a marginal R^2 of 0.039, while random effects had a marginal R^2 of 0.27 (of which the time-varying intercepts, spatial random effects and spatiotemporal random effects contributed with 0.06, 0.07 and 0.14, respectively). This suggests considerable variation in space and time due to latent factors, as well as changes of spatial variation through time, that cannot be explained by the covariates used.

We conducted a sensitivity analysis by fitting the condition model to different parts of the data. The different models where only cod above 30 cm, only cod below 30 cm, omitting subdivision 24 (the mixing zone with western Baltic cod), and including only grid-points with cod above a certain threshold when calculating median variables across the ICES rectangle. (*SI Appendix*, Fig. S11). However, the model coefficients were similar across all models.

The median cod depth and oxygen experienced by cod (depth and oxygen in the environment weighted by the predicted biomass density of cod at location, respectively, Fig. 4C) got deeper and declined, respectively, throughout the time period (Fig. 5C-D), though the population again occupied slightly shallower waters in the last 3 years of the time series (see *SI Appendix*, Fig. S19-S21 for results split by subdivision, Fig. S24 for the corresponding analysis on temperature, and Fig. S18 for a marginal effects plot of the biomass density model).

The standardized effect size for oxygen was 0.0035, meaning that for each unit increase in the standardized oxygen variable (i.e., 1 standard deviation or 1.85 ml/L), the Le Cren condition factor increased by 0.35%. 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. 5C–D). The biomass-weighted oxygen concentration declined more steadily (approximately 1 ml/L between 1993 and 2019) (*SI Appendix*, Fig. S19-S21).

Discussion

The body condition of fish depends on previous energy accumulation and is therefore largely shaped by the quality of the habitat the fish has occupied. By using a spatially explicit condition model, we can link the condition of Eastern Baltic cod to covariates at different ecologically relevant spatial scales. Our model reveals that the Le Cren condition factor declined on average by 14%, in 1993–2019, with the majority of this decline occurring 1993–2008. Moreover, while there are persistent low-spots of body condition (in the deep and low-oxygen areas), the condition declined in the whole area, which suggests that there are drivers acting on large spatial scales. While we identify changes in the spatiotemporal distribution of cod that could have led to poorer environments experienced by cod (deeper areas with less oxygen), effect sizes of single covariates are overall small and latent spatial and spatiotemporal variation is several times larger in magnitude and explain more variation in the condition factor.

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 in the past three decades. Direct effects here refer to mild hypoxia reducing the appetite and food consumption (Chabot and Dutil, 1999) and by extension also their condition, as their ability to accumulate energy reserves reduces. We find that Baltic cod experienced oxygen concentrations at around 7.2 ml/L on average in 1993 (1st and 3rd quartile are 5.8 and 7.7) and are currently experiencing oxygen concentrations at around 6.3 ml/L on average (1st and 3rd quartile are 4.5 and 7.2). In subdivision 25 (the core area of cod currently) we estimate it to be around 6.5 in 2019 (*SI Appendix*, Fig. S19). This is higher than recent estimates of 4–4.5 ml/L as an average oxygen concentration based on oxygen levels at the mean depth of the cod population in the recent years (Brander, 2020; Casini *et al.*, 2021). The difference in our estimate compared to previous studies is likely because we, instead of calculating average oxygen at the mean depth of cod, weighted the sea bottom oxygen in the

environment (from the ocean model NEMO-Nordic-SCOBI) by the predicted densities from the cod density model. Hence, our approach overcomes the issue that oxygen concentrations span a large range for any given depth and avoids the assumptions that cod depth occupancy is independent of the oxygen concentration.

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). Despite the median oxygen concentrations experienced by the population in our study is above this threshold, 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 higher oxygen being correlated with richer habitats that feature higher food availability, or if there are direct physiological impacts at a lower threshold in the wild. The effect of oxygen could also be larger for small cod (i.e., a higher threshold), that currently dominate the Baltic population, as discussed in Casini *et al.* (2021).

However, despite this positive association between oxygen experienced and condition, the trends per subdivision are mixed. For instance, the experienced oxygen concentrations were stable in subdivision 27 and 28, despite declines in in the environment (Fig. S19-S20). By contrast, the oxygen in the environment was more stable in subdivision 25. However, when considering changes in the distribution of cod, the oxygen concentration experienced by cod in subdivision 25 declined with 1.5 ml/L over the study period, partly due to the fact that cod moved to deeper waters, as found in Casini *et al.* (2021). This highlights the need to incorporate changes in the distribution when assessing changes in the environmental conditions that cod experience. An indirect effect of declining oxygen is the potential amplification of competition with other cod and/or flounder for shared benthic prey species, such as the isopod *S. entomon*, due to habitat contraction caused by the expansion of “dead

zones” avoided by cod (Casini *et al.*, 2016a, 2021; Orio *et al.*, 2019; Haase *et al.*, 2020). To address the potential effects of changes in intra- and inter-specific competition, we used predicted density of flounder and cod at the haul- and at the ICES rectangle-level, as well as *S. entomon* densities as covariates. We detected a negative effect of cod haul-level density, also in line with predictions (Svedäng and Hornborg, 2014), though the effect is uncertain and very minor compared to the other predictors. We did not detect an effect of flounder density at any scale. The effect of *S. entomon* was positive, but uncertain and very minor. These lack of clear signals of competition could be because biomass density is not a direct measure of competition; areas with higher densities of cod and flounder could simply also have more food. It could also be because the biomass of both cod and flounder have been at relatively low levels during the past three decades from a historical perspective (Tomczak *et al.*, 2022).

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; Neuenfeldt *et al.*, 2020). In our study, using spatially resolved data, we also found positive effects of sprat biomass on cod condition at the ICES subdivision level, which was not observed for herring. The biomass of sprat generally declined from the levels in the early 90’s, and this decline is more accentuated in the northern subdivisions analyzed, where also cod condition declined the most. However, despite the decline, sprat has been most abundant in subdivision 28, while cod biomass in subdivisions 27 and 28 has been very low during the study period, suggesting that further analyses should be made to infer whether the decline in sprat drove the decline in condition. Overall, the fact that cod condition has declined in all areas—also in areas where high abundance of prey remains—indicates that several variables and driving processes have been involved, including variables operating on a large spatial scale

In conclusion, our study illustrates fine-scale spatiotemporal development of body condition in the eastern Baltic cod, and population-level changes in depth distribution and oxygen concentrations. The small effect sizes of the single covariates we used based on existing literature, analyzed for the first time in a common framework using individual-level data, suggest that multiple factors are responsible for the observed spatiotemporal changes in cod condition during the past 25 years. The small effect size of the covariates found in our models might also be explained by the fact that condition is shaped over a long time period, while trawl data and correspondent environmental predictors reveal snapshots in time. We therefore argue that analysis of condition data from surveys conducted with low temporal resolution should be complemented with e.g., tagging studies (as suggested also by Thorson 2015), or using “life-time recorders” such as otoliths (Limburg and Casini, 2019), before mechanistic links between condition and covariates can be determined. However, the explanatory power of latent variables (time-varying intercepts and spatial and spatiotemporal terms) in the models suggests that other factors, not explicitly included in our analyses, can also play an important role in the decline of cod condition during the past three decades. It is also possible that the mechanisms that initiated the body condition decline are not the same ones that have kept cod in a poor physiological state in the last 10 years (Tomczak *et al.*, 2022). Liver parasites are for instance numerous now, but likely did not cause the decline (Ryberg *et al.*, 2020). Evaluating factors associated with condition hotspots would help understand the role of food availability for condition. The Eastern Baltic cod stock is not predicted to grow even in the absence of fishing mortality (ICES, 2021a). This makes it crucial to understand how environment and species interactions affect the body condition of cod (Eero *et al.*, 2020) since body condition is a key biological trait determining mortality and reproductive output.

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Author Contributions

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

Data and code availability

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

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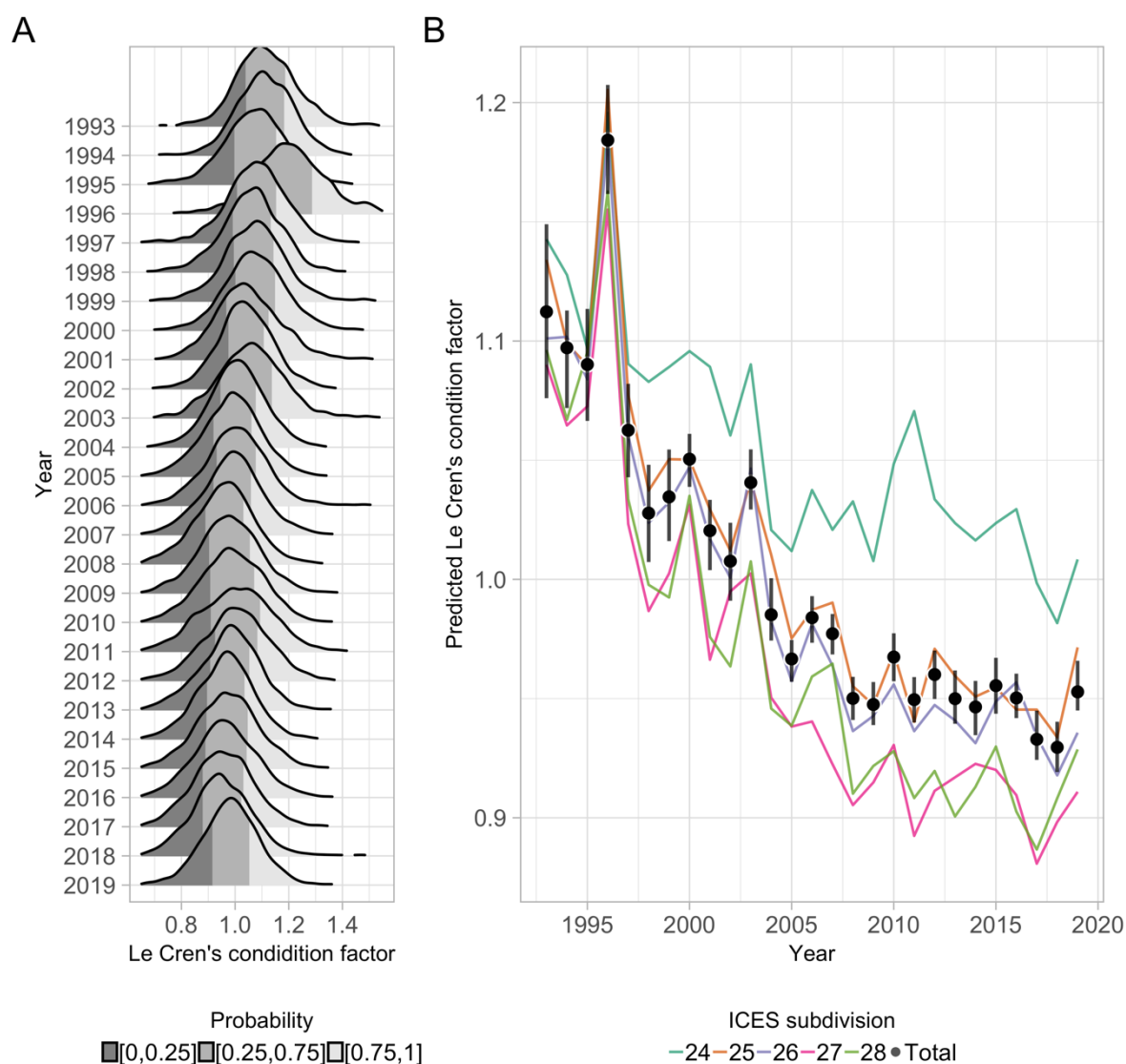


Fig. 1. A) Density plots of condition data by year. B) Predicted Le Cren condition factor of cod condition factor over the period 1993-2019 in the Baltic Sea (total as well as by each ICES subdivisions), acquired by predicting from the spatiotemporal condition model over a grid with spatially varying covariates set to their true values (ICES rectangles with missing pelagic data were given the subdivision median when predicting but not fitting, see *SI Appendix*, Fig. S23). Vertical lines depict 95% confidence intervals.

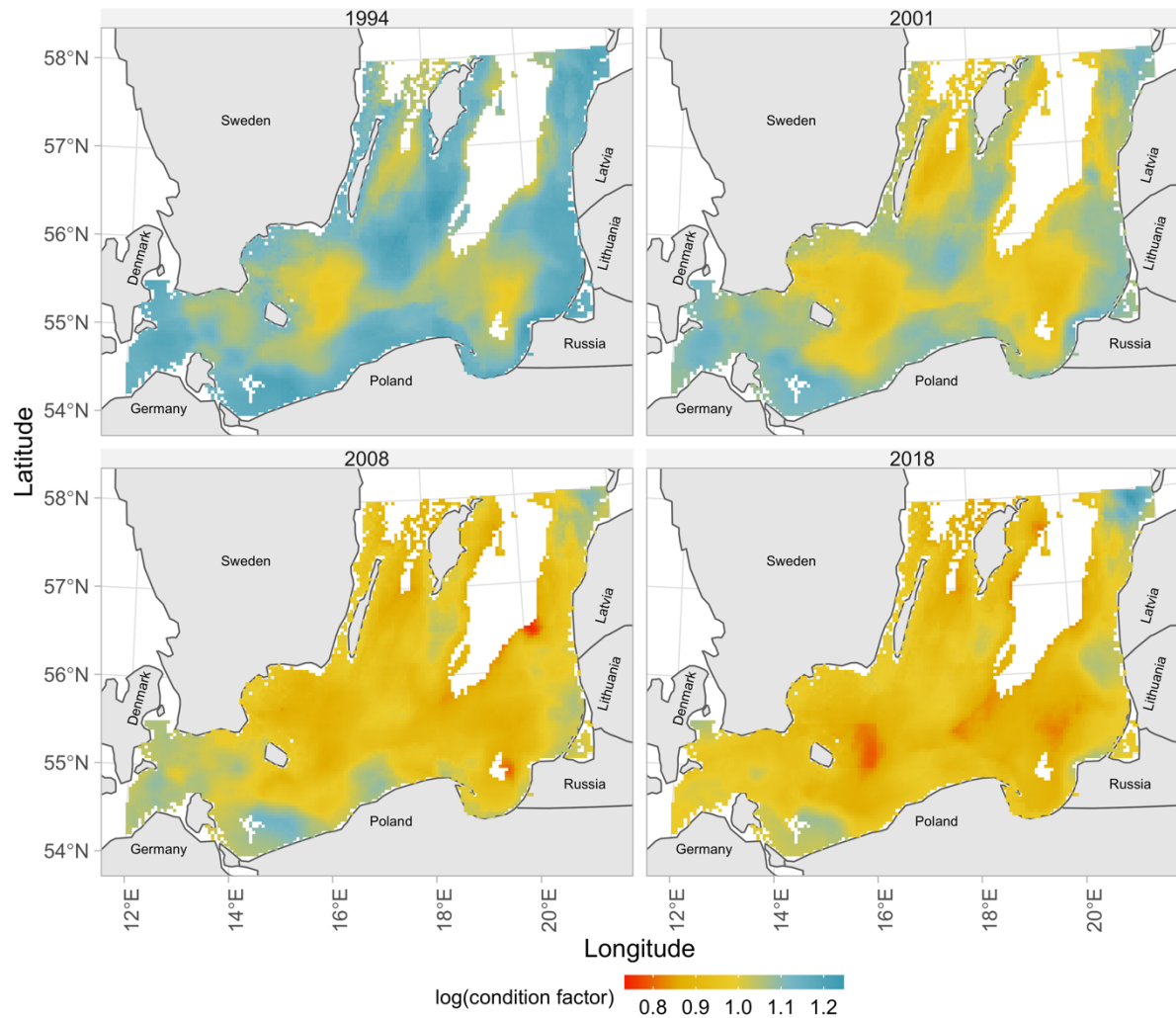


Fig. 2. Predicted log condition factor with spatially varying covariates set to their true values (ICES rectangles with missing pelagic data were given the subdivision mean, see *SI Appendix*, Fig. S23). Included in the plot are years 1994, 2001, 2008, 2018. Only grid cells with depths between 10m and 120m are included in the plot. For all years in the series, see *SI Appendix*, Fig. S9.

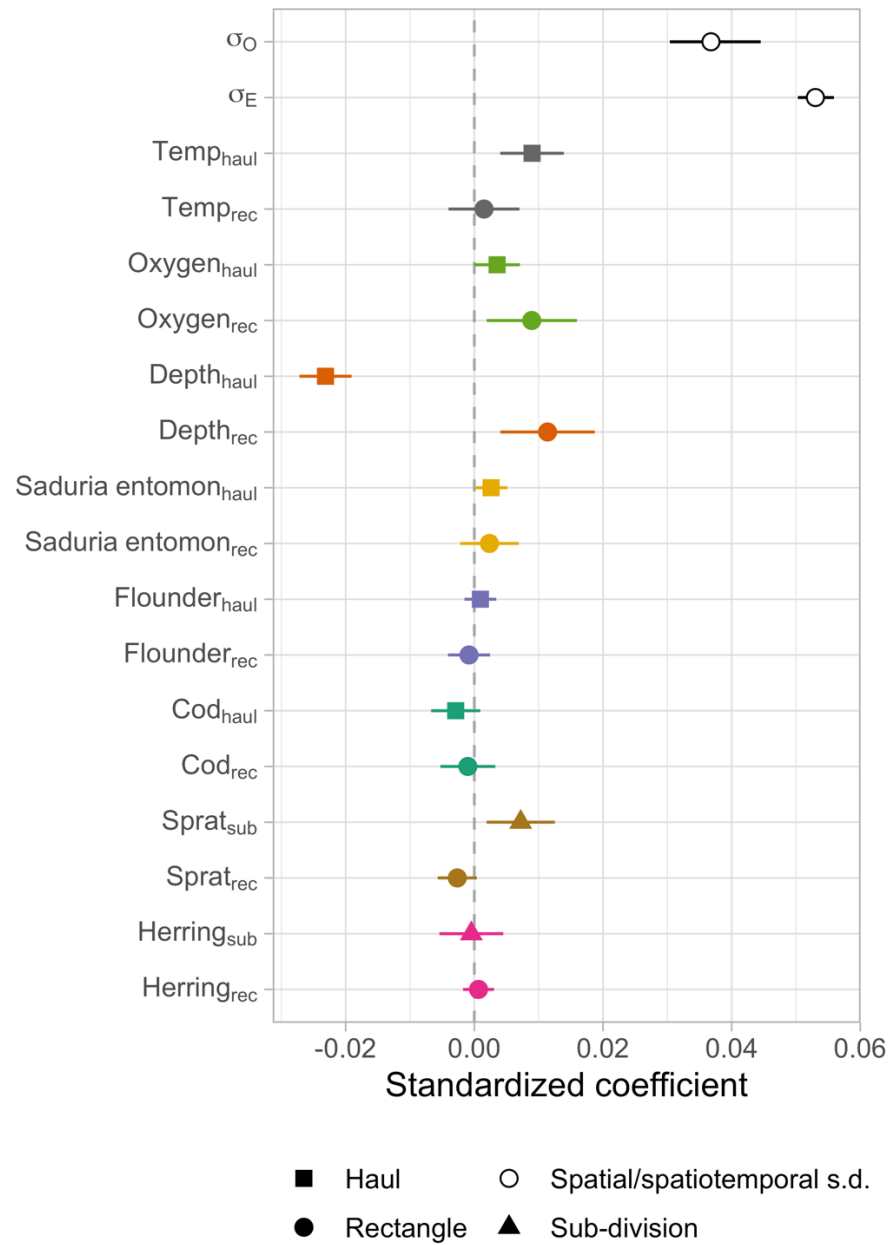


Fig. 3. Mean and 95% confidence interval of standardized coefficients (effect sizes) for covariates and spatial and spatiotemporal standard deviation (σ_E and σ_O , respectively) in the condition model. The subscript *haul* refers to covariates estimated at the location of the haul, *rec* refers to covariates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

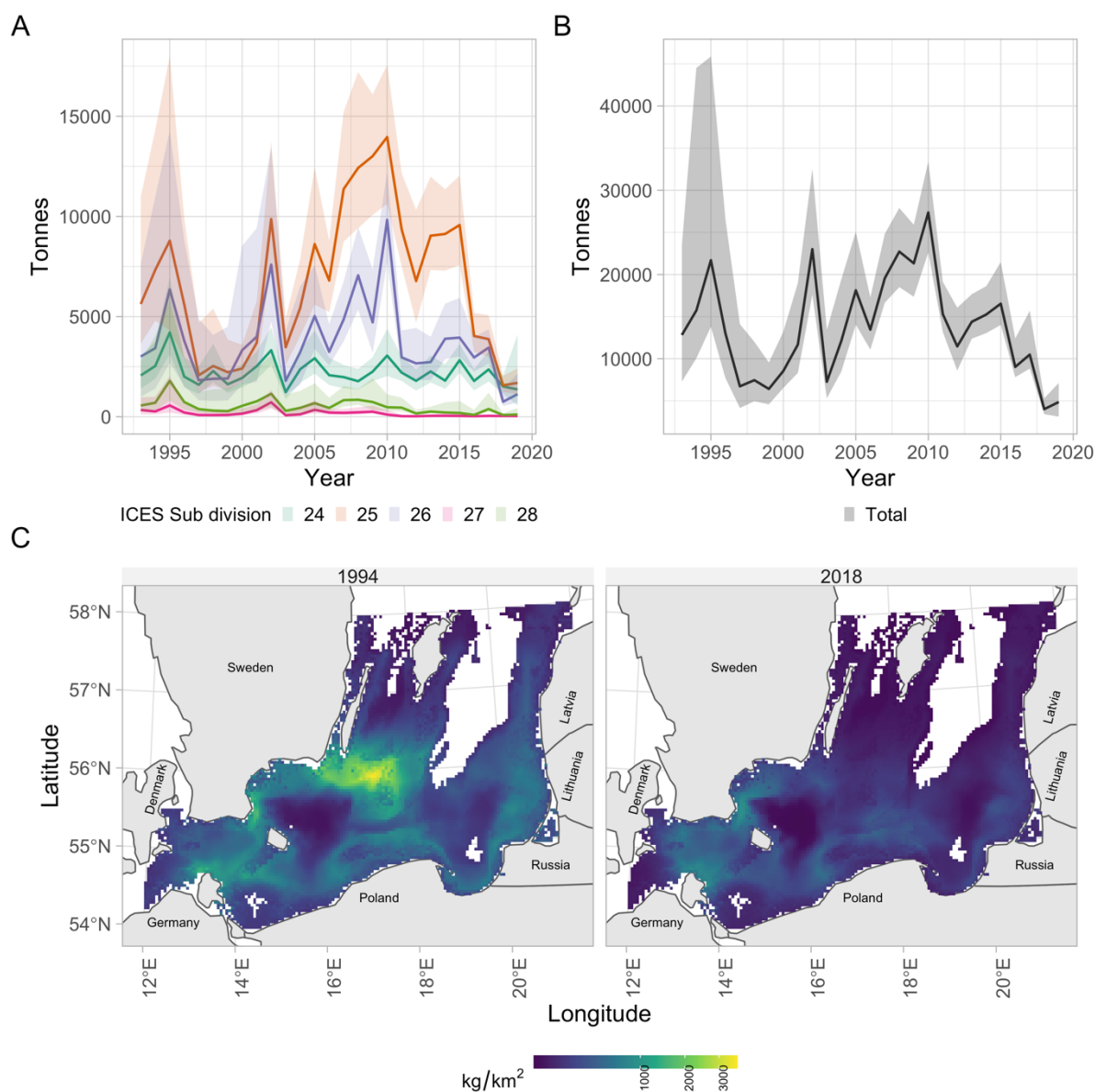


Fig. 4. A) Predicted biomass from the spatiotemporal CPUE model (Eq. 10–11) by ICES subdivision (B) and total across all subdivisions. C) Predicted density (kg/km²) in select years (1995 and 2017) (for all years in the series, see *SI Appendix*, Fig. S17). Only grid cells with depths between 10 and 120 are included in the plot.

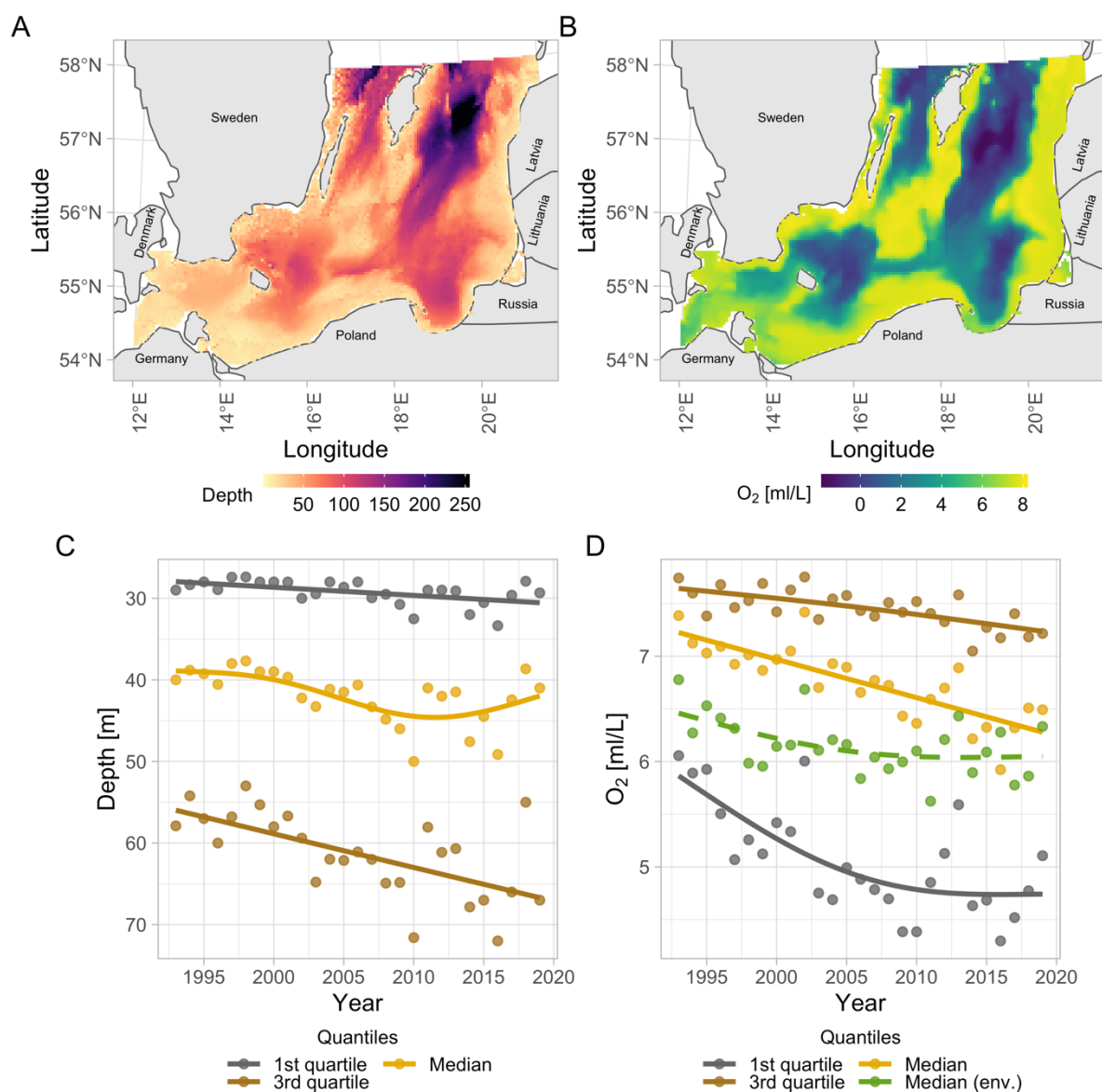


Fig. 5. (A) Bathymetry and (B) oxygen concentration (exemplified using year 1999) in the study area. Panels (C) and (D) illustrate depth and oxygen weighted by predicted cod density, respectively. Colors indicate quantiles (1st quartile, median and 3rd quartile). Lines depict generalized additive model (GAM) fits ($k=4$).