

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

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Commented [SA2]: Who is 'd'? Michele?

Commented [MOU3R2]: Yes! Thanks

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21 **Key Words**

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

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## 25 Abstract

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

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**Commented [SA4]:** To be fair, this is compared to any one covariate, not the combined explained variance

**Commented [MOU5R4]:** Yes, that's a good point, Michele said something along those lines too!

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## 71 Introduction

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

81 Because of the link to food consumption, interannual variation in condition is often  
82 associated with changes in the strength of competition for food, via changes in density of the  
83 population, competitors, or prey species (Cardinale and Arrhenius, 2000; Casini *et al.*, 2006;  
84 Thorson, 2015; Grüss *et al.*, 2020). It has also been linked to environmental conditions, (e.g.,  
85 temperature, salinity) affecting ecosystem productivity and local habitat quality (Möllmann *et*  
86 *al.*, 2003; Morgan *et al.*, 2010; Thorson, 2015; Grüss *et al.*, 2020). More recently, studies have  
87 found a link between declining body condition and deoxygenation (expansion of dead zones  
88 causing habitat degradation and compression) (Casini *et al.*, 2016a, 2021), fueled by warming  
89 and nutrient enrichment (Diaz, 2001; Breitburg, 2002; Diaz and Rosenberg, 2008; Carstensen  
90 *et al.*, 2014). However, reduced oxygen concentrations also cause lower food intake rates due  
91 to lower metabolic rates, which can occur even during milder hypoxia (Kramer, 1987; Chabot  
92 and Dutil, 1999; Claireaux *et al.*, 2000; Hryciuk *et al.*, 2017; Brander, 2020; Sampaio *et al.*,  
93 2021). As both environmental and biological variables can affect condition, it is important to  
94 study their relative contribution to variation in condition in a common framework.

Commented [MC6]: Casini et al. "a" as is the first to be mentioned.

Commented [MOU7R6]: Hmm yeah I don't know why Zotero calls it b here actually. I won't change it manually do until the very last end because if I do it becomes unconnected.

Commented [MOU8R6]: ok so it is alphabetized by title to determine which is "a" and which is "b.", did not know that!

Commented [MOU9]: Mich, you asked for more non-Baltic references here. I have a few of those (Grüss, Thorson, Kramer, Chabot, Claireaux, Hryciuk), but if you know of more please let me know :)

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Commented [MOU11R10]: I tried to shorten it instead, since I think they fit together topic-wise

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Deleted: are both indirect and direct. Hypoxia, or low dissolved oxygen, can cause habitat compression and thus force organisms to occupy sub-optimal habitats, which may enhance density dependence (Diaz and Rosenberg, 2008; Orio *et al.*, 2019; Gogina *et al.*, 2020). Direct effects include metabolic constraints on organisms, manifested as lowered

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

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

Commented [MC12]: This likely because there were other parameters, other than density and temperature, influencing condition. Or you mean noise?

Commented [MOU13R12]: Yes that's true, and the author authors point is that these represent variables that are constant or varying in space that are not explicitly accounted for, unlike the covariates.

Commented [SA14]: Something is off here

Commented [MOU15R14]: fixed!

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134 the flounder complex (European flounder *Platichthys flesus* and Baltic Flounder *Platichthys*  
 135 *solemdali*) (Orio *et al.*, 2017), and in the distribution of its main pelagic prey species (sprat  
 136 *Sprattus sprattus* and herring *Clupea harengus*) (Casini *et al.*, 2011; Eero *et al.*, 2012; ICES,  
 137 2021a). Lastly, the irregular inflows of saline and oxygenated water from the North Sea  
 138 together with a long residence time (25–30 years) are features that have contributed to making  
 139 the Baltic Sea the largest anthropogenically induced hypoxic area in the world (Carstensen *et*  
 140 *al.*, 2014), and it is also one of the fastest warming regional seas (Belkin, 2009; Reusch *et al.*,  
 141 2018). However, it remains unknown what the relative importance of these variables are, since  
 142 they have not been analyzed directly in a single framework, and not on different spatial scales.

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

## 152 Materials and methods

### 153 Data

154 To model the spatiotemporal development of cod condition and distribution, we acquired  
 155 weight and length data, as well as catch per unit effort data (CPUE, numbers/hour) of cod by  
 156 10-mm length class from the Baltic International Trawl Survey (BITS) between the years 1993–  
 157 2019 and in ICES sub-divisions 24–28 (SI Appendix, Fig. S1). CPUE data were standardized  
 158 based on gear dimensions and towing speed following Orio *et al.* (2017) to the unit kg/km<sup>2</sup>

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Deleted: (Momigliano *et al.*, 2018)

Commented [MC16]: But you speak also about inflows, that can be also due to “natural” variations?

Commented [MOU17R16]: Yes, I (& they) probably mean that these features make it extra sensitive to hypoxia. Added “are features that [...]”

Commented [SA18]: Sorry, leave as is if you’d like

Commented [MC19]: I think this is what we should aim at.

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Commented [MOU20]: I switched place between the model descriptions and the covariate section. This was because cod and flounder covariates are predictions from the models we describe in that section. So instead of saying “see below” it is now in a more natural order in my view at least. Note though this whole section (M&Ms) has been edited a lot, but it’s not tracked because it would recognise moving the whole section as a move... I accepted the change for readability.

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170 using a TVL trawl with 75 m sweeps (note that compared to Orio *et al.* (2017), we further  
 171 express density in kg/km<sup>2</sup> instead of kg ~~in~~ 1 h trawling sweeping an area of 0.45 km<sup>2</sup> by  
 172 dividing by 0.45). Abundance density was converted to biomass density by fitting annual  
 173 weight-length regressions. We used only data from the fourth quarter, which corresponds to  
 174 the main growing and feeding season (Aro, 1989) and also the quarter in which the Baltic  
 175 International Acoustic Survey (BIAS) is conducted, meaning sprat and herring abundance can  
 176 be used as covariates. The BITS data can be downloaded from [https://www.ices.dk/data/data-](https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx)  
 177 [portals/Pages/DATRAS.aspx](https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx).

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## 179 *Estimating spatiotemporal development of body condition and biomass density*

### 180 *Condition model*

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

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

$$192 \quad \log(w_{s,t}) \sim \text{Student-t}(\mu_{s,t}, \phi, \nu) \quad (1)$$

$$193 \quad \mu_{s,t} = \alpha_t + \beta_l \log(l) + \sum_{k=1}^{n_k} \beta_k x + \omega_s + \epsilon_{s,t} \quad (2)$$

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

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

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

$$\epsilon_t \sim \text{MVNormal}(\mathbf{0}, \Sigma_\epsilon) \quad (6)$$

where  $w_{s,t}$  represents the weight at space  $s$  (a vector of two UTM zone 33 coordinates) and time  $t$ ,  $\mu$  represents the mean weight and  $\phi$  represents the scale parameter. The parameter  $\alpha_t$  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  $\sigma_\alpha^2$  for subsequent values. The parameter  $\beta_l$  represents the length-coefficient (corresponding to the allometric exponent  $b$ ), and  $x_k$  represents a vector of the  $k$ -th additional covariate and  $\beta_k$  is its effect. The parameters  $\omega_s$  and  $\epsilon_{s,t}$  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  $\Sigma_\omega$  and  $\Sigma_\epsilon$ . The covariance  $(\Phi(s, s'))$  between spatial points  $s$  and  $s'$  in all random fields is given by a Matérn function:

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

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:

$$\delta_{t=1} \sim \text{MVNormal}(\mathbf{0}, \Sigma_\epsilon) \quad (8)$$

$$\delta_{t>1} = \rho \delta_{t-1} + \sqrt{1 - \rho^2} \epsilon_t, \epsilon_t \sim \text{MVNormal}(\mathbf{0}, \Sigma_\epsilon) \quad (9)$$

Commented [SA21]: Yes?

Commented [MOU22R21]: yes!

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Commented [SA23]: Maybe Lindgren 2011

Commented [MOU24R23]: done

Commented [SA25]: This is fine, but I think you could also drop the Matern equation if you want.

Commented [MOU26R25]: ok! might as well keep it

where  $\rho$  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  $\log(\text{length}) = 0$ .

#### 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, oxygen conditions experienced by cod, as well as overlap with saduria and sprat 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  $s$  and time  $t$  as weights when calculating the annual average depth, temperature, and oxygen concentration. For the overlap with saduria and sprat, we used a biomass-weighted overlap index (Carroll *et al.*, 2019), calculate by year as:

$$\frac{\sum_i^n \left( \frac{\text{pred}_i}{\max(\text{pred})} \times \frac{\text{prey}_i}{\max(\text{prey})} \right)}{\sum_i^n \frac{\text{prey}_i}{\max(\text{prey})}} \quad (10)$$

where  $\text{pred}_i$  (cod) and  $\text{prey}_i$  (saduria or sprat) are densities of predator and prey in each area (grid-level predictions for saduria and ICES rectangle for sprat). This overlap index is useful where relative biomass of predator and prey is of interest (Carroll *et al.*, 2019).

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

$$y_{s,t} \sim \text{Tweedie}(\mu_{s,t}, p, \phi), 1 < p < 2 \quad (11)$$

$$\mu_{s,t} = \exp \left( \alpha_t + \sum_{k=1}^{n_k} f_k(x_k) + \omega_s + \epsilon_{s,t} \right) \quad (12)$$

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Deleted: , as well as overlap with sprat and saduria. The latter overlap was

Deleted: defined by the

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249 where  $y_{s,t}$  represents density [kg/km<sup>2</sup>] at space  $s$  and time  $t$ ,  $\mu$  is the mean density,  $p$  and  $\phi$   
 250 represents the power and dispersion parameters, respectively. The parameters  $\alpha_t$  represent  
 251 independent means for each year,  $f_k$  is a smooth function for covariate  $x_k$  and  $\omega_s$  and  $\epsilon_{s,t}$   
 252 represent spatial and spatiotemporal random effects and have the same definition as in the  
 253 condition model (Eqns. 5–6).

254

### 255 *Model fitting*

256 For computational efficiency, we fit the model in a “predictive process” modelling framework  
 257 (Latimer *et al.*, 2009; Anderson and Ward, 2019), where spatial and spatiotemporal random  
 258 fields are approximated using a triangulated mesh and the SPDE approximation (Lindgren *et al.*,  
 259 2011) (*SI Appendix*, Fig. S2, S12), created using the R-package ‘R-INLA’ (Rue *et al.*,  
 260 2009). The random effects are estimated at the vertices (“knots”) of this mesh. The locations  
 261 of the knots were chosen using a  $k$ -means clustering algorithm (with a fixed seed for  
 262 reproducibility), which minimizes the total distance between data points and knots. As the knot  
 263 random effects are projected to the locations of the observations, more knots generally increase  
 264 accuracy at the cost of computational time, up to a threshold (REF). After initial exploration,  
 265 we chose 200 knots for this application. The models were fit using ‘TMB’ (Kristensen *et al.*,  
 266 2016) via the R-package ‘sdmTMB’ (version 0.0.18.9001) (Anderson *et al.*, 2019, 2021). We  
 267 checked the models were consistent with convergence by confirming the maximum absolute  
 268 gradient was  $< 0.005$  and that the Hessian matrix was positive-definitive. We used packages in  
 269 the ‘tidyverse’ (Wickham *et al.*, 2019) for data processing and plotting.

270

### 271 *Covariates*

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

**Commented [SA27]:** Bizarrely not usually the case past some threshold! High resolution meshes often let the GMRF overfit the data. Eric and I are working on a paper highlighting that fact.

**Commented [MOU28R27]:** Interesting! I added “up to a threshold” in case your paper would come out first, else we can rewrite to something like “is generally though to” or “can” or something weaker.

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**Commented [MOU29]:** I’m not sure about which threshold is used normally! At this point I know the models don’t give me a warning (can check what my values are soon!)

**Commented [SA30]:** This seems fine. People use all sorts of thresholds. Generally if everything else is fine and this is pretty small, it’s just a matter of how long you want to run the optimizer to crunch this down further.

**Commented [MOU31R30]:** Ok I see! I do not get any warnings about the maximum absolute gradient, so it must be above the threshold for that warning message (which I couldn’t find the value of!)

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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 were extracted from the ICES WGBIFS database for the BIAS survey data (<https://www.ices.dk/community/groups/pages/WGBIFS.aspx>). Sea bottom temperature and sea bottom concentration of dissolved oxygen in the fourth quarter were extracted from the ocean model NEMO-Nordic-SCOB (Eilola *et al.*, 2009; Almroth-Rosell *et al.*, 2011; Hordoir *et al.*, 2019). 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 densities of *Saduria entomon* 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 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

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Deleted: of covariates were chosen to reflect the local conditions (i.e., haul-level covariates for environmental effects, larger scale covariates for mobile pelagic species etc.) (Hüssy *et al.*, 2020). The covariates for the condition model were abundance

Deleted: , which are important prey species for cod (Gårdmark *et al.*, 2015; Haase *et al.*, 2020), available on a ICES rectangle (1° by 30') and ICES sub-division level

Deleted: (Casini *et al.*, 2016a, 2021; Limburg and Casini, 2019; Brander, 2020)

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Commented [MOU38]: Removing the interactions made it easier to get better convergence when playing around with models with different scales of covariates... so I didn't put them back in

Deleted: ), interactions between oxygen and depth, temperature, and depth, and lastly oxygen and temperature were also included on a haul-level

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Deleted: with respect to gear dimensions, and we did not want to remove condition data, flounder and cod covariates were predicted local densities from GLMMs (described below) fitted to density data. Flounder data were standardized in the same way as cod data (described above)

Deleted: For the density model we included depth, oxygen, and temperature as covariates, using the same sources mentioned above.

Commented [MOU39]: Mich pointed out that it might be problematic to use the same variables here, so for the model that we use to predict densities onto the condition data, I just used depth as a covariate.

[https://github.com/maxlindmark/cod\\_condition/blob/master/R/clean\\_data/cod\\_fle\\_density\\_models\\_as\\_covars.Rmd#L121-L156](https://github.com/maxlindmark/cod_condition/blob/master/R/clean_data/cod_fle_density_models_as_covars.Rmd#L121-L156)

different units and allows for comparison between the estimated coefficients and the standard deviation of spatial ( $\sigma_O$ ) and spatiotemporal ( $\sigma_E$ ) 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 2008, after which the decline leveled off (Fig. 1A). This corresponds to a 1.5% [1.7%, 1.1%] decline in log weight for a cod of any length. 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 1<sup>st</sup> and 9<sup>th</sup> 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

**Commented [SA40]:** I think it's a bit confusing how this is currently worded. Do we need to fit the minimal model for this test? Is the comparison on the 20% vs. the 80% or how the 80 to 20 compare for the 2 models (minimal and full)?

I'm thinking that reasonable out-of-sample prediction with the full model is sufficient.

Honestly, given the dataset size, I don't think anyone would think the full model is unreasonable. The penalty for too many covariates is larger CIs.

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**Commented [SA41]:** Round both to 1 decimal?

**Commented [MOU42R41]:** Or two for both perhaps?

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**Commented [SA43]:** If you want an easy way to get uncertainty on this, you can use the MVN simulation option... `predict(... sims = 500)` or `sdmTMB::spread_sims()` to get parameter draws themselves. Then do your calculation on the draws and summarize.

**Commented [MOU44R43]:** Very cool! This is what I do now (see e-mail comment about the condition factor). This is the code I use to calculate these summaries:

[https://github.com/maxlindmark/cod\\_condition/blob/master/R/analysis/condition\\_model.Rmd#L468-L556](https://github.com/maxlindmark/cod_condition/blob/master/R/analysis/condition_model.Rmd#L468-L556)

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**Deleted:** As the condition factor declines (Fig. 1A), the coefficient of variation (standard deviation of Le Cren's condition index over the mean) increased, indicating that the variation did not decline as steadily as the mean and that the relative variation is now larger than in the beginning of the time series

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**Deleted:** (Fig. 1C). We also find the different conditions deciles (1<sup>st</sup>, 5<sup>th</sup> and 9<sup>th</sup>) declined at the same rate over time (SI Appendix, Fig. S11). This means

381 Öland and Gotland) (Fig. 2, *SI Appendix*, Fig. S1), and that the condition factor declines in  
 382 the whole area over time (Fig. 2, *SI Appendix*, Fig. S8, S10).

383 The covariates with the largest positive standardized effect sizes are temperature at the  
 384 haul (0.009 [0.004, 0.014]) (values in brackets indicate 95% confidence interval), median  
 385 depth (0.01 [0.004, 0.02]) and oxygen concentration at the ICES rectangle level (0.01  
 386 [0.002, 0.016]), and biomass of sprat in the ICES sub-division (Fig. 3). Depth at the haul is  
 387 negatively associated with condition (-0.023 [-0.028, -0.02]) (weight) (Fig. 3) (see *SI*  
 388 *Appendix*, Fig. S9, for marginal effects plots). The biomass density of flounder and the  
 389 biomass of herring did not affect the weight of cod at any scale (Fig. 3). The magnitude of  
 390 single covariate effect sizes are generally small. In fact, several times smaller than residual  
 391 spatiotemporal and spatial variation. This means there is considerable variation in space,  
 392 and variation in space that changes through time, that the covariates cannot explain.

393 The median depth and oxygen (depth and oxygen in the environment weighted by the  
 394 predicted biomass density of cod), as well as the biomass-weighted overlap with saduria and  
 395 sprat got deeper or decline throughout the time period (Fig. 5). However, their contribution  
 396 to the decline over time is likely quite minor. For instance, the standardized effect size for  
 397 oxygen is 0.0034 [95% confidence interval: -0.0002, 0.0070], meaning that for each unit  
 398 increase in the standardized oxygen variable (i.e., 1 standard deviation or 1.85 ml/L), log  
 399 weight increases by 0.34% (corresponding to a 2% increase in weight for a cod weighing  
 400 380g, which is the median weight in the data). As a comparison, the average oxygen  
 401 concentration in the environment declined by approximately 0.65 ml/L between 1993 and  
 402 the lowest in 2006 (Fig. 5C-D. The biomass-weighted oxygen concentration declined more  
 403 steadily (approximately 1 ml/L between 1993 and 2019), but still, the contribution to the  
 404 3.6% decline in the log condition factor is likely minor, as the change in experienced oxygen  
 405 only corresponds to a change that is slightly larger than half a standard deviation in change,

Commented [MOU45]: surprisingly this is pretty positive

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Moved down [2]: However, the magnitude of covariate effect sizes is several times smaller than residual spatiotemporal and spatial variation. This means there is considerable variation in space, and variation in space that changes through time, that the covariates cannot explain.

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Commented [MC46]: Or condition?

Commented [MOU47R46]: Technically weight so maybe we stick with that.

Commented [ML48]: <https://stats.stackexchange.com/questions/2142/linear-regression-effect-sizes-when-using-transformed-variables>

Commented [MC49]: maybe good to say also the % in non-transformed units.

Commented [MOU50R49]: Ok! I used 380g as an example because it is the median weight and is even enough :)

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Deleted: (Neuenfeldt *et al.*, 2020b; Casini *et al.*, 2021)), which is less than half a standard deviation. Since cod are not evenly distributed in space, we also calculated the biomass-weighted median oxygen concentration for cod (Fig. 4-5C-D). The mean oxygen concentration experienced by cod (... [1]

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454 and oxygen trends vary in space whereas condition declined everywhere (*SI Appendix*, Fig.  
455 S10, SX).

456 ~~Being based on the empirical weight-length relationship, Le Cren's condition index does~~  
457 ~~not scale with length itself if weight is not proportional to the cube of length. However, accurate~~  
458 ~~estimates of the weight-length relationships require a large enough range of weights and~~  
459 ~~lengths. However, some covariates related to competition or food availability (such as cod and~~  
460 ~~flounder density, or sprat and herring abundance) could be relevant for only specific size-~~  
461 ~~classes of cod. Therefore, we also fit the same condition model to cod above and below 30 cm~~  
462 ~~(where cod below 30 cm are more likely to compete with flounder and other cod for benthic~~  
463 ~~resources (Haase *et al.*, 2020), and cod above 30 are able to feed on the entire size-distribution~~  
464 ~~of the herring (Niiranen *et al.*, 2019) (*SI Appendix*, Fig. SX). These results showed that the~~  
465 ~~neither the parameter estimates nor the trends over time changed drastically.~~

## 467 Discussion

468 Using a fine-scale spatiotemporal condition model, we show that the log cod weight for a given  
469 length in the Baltic Sea declined by 15%, primarily between the years 1993–2008. While there  
470 are persistent low-spots of body condition (deep and low-oxygen areas), the condition declined  
471 in the whole area. While we identify changes in the spatiotemporal distribution of cod that  
472 could have led to poorer environments for condition (deeper areas with less oxygen and overlap  
473 with prey), effect sizes of single covariates are overall small and residual spatial and  
474 spatiotemporal variation is several times larger in magnitude.

475 Previous studies have suggested both direct (Limburg and Casini, 2019; Brander, 2020) and  
476 indirect (Neuenfeldt *et al.*, 2020a; Orio *et al.*, 2020) effects of oxygen as a cause for the  
477 declining body condition of cod. Direct effects here refer to mild hypoxia reducing the appetite  
478 and food consumption (Chabot and Dutil, 1999) and by extension also their condition, as they

**Commented [MOU51]:** I think we can make the point here with oxygen as an example (i.e. the calculations based on effect sizes and the change in biomass-weighted population values)

**Deleted:** This is comparable to the change in depth distribution, which is likely contributing to the change in experience oxygen (the median density-weighted depth changed from 40 m in 1993 to 45 m in 2019. Between these depths, the difference in average oxygen concentration is approximately -0.25 ml/L). The effect size of depth is -0.02, corresponding to a change in -2% when depth increase with a standard deviation (22 m, which can be compared to the median increase in depth of 5 m). Temperature is positively related to condition (Fig. 3), and this is likely a spatial (rather than temporal) effect, reflecting higher body condition in shallower and warmer waters. Hence, there is probably limited support for covariates to explain the change over time, as opposed to e.g., over space (the 1<sup>st</sup> and 9<sup>th</sup> density-weighted decile of depth and oxygen are approximately 20 and 85, and 3.8 and 7.5, respectively – which are considerably larger ranges than the change over time).

**Moved up [3]:** The local (haul-level) density flounder and the sub-division abundance of herring did not have any effects on the weight of cod. Sub-division abundance of sprat abundance had a slightly more clear, positive effect than flounder and sprat, but it is still a small effect (0.003 [95% confidence interval: -0.0012, 0.0083]).

**Deleted:** To estimate body condition without it scaling with length, we first estimated empirical

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**Deleted:** are likely mostly important for specific size-ranges of the cod population, rather than all sizes of cod

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**Deleted:** we identify a complex picture regarding the cause of the decline in body condition, with changes in the environmental variables (such as deepening and reduced oxygen) having the largest, but still relatively modest

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are not able to accumulate as large energy reserves. First, we find that the Baltic cod are currently experiencing oxygen concentrations at around 6.4 ml/L on average (1<sup>st</sup> and 9<sup>th</sup> decile are 3.6 and 7.5). This is higher than a recent estimate of 4.5 ml/L as the average oxygen concentration in recent years (for the eastern Baltic cod) (Brander, 2020; Casini *et al.*, 2021). 4.5 ml/L has also been proposed as a threshold for negative but sub-lethal physiological impacts, including, but not limited to, reduced feeding rates (Hrycik *et al.*, 2017). The difference in the estimated average oxygen concentration could be because we estimate the average oxygen across the prediction grid (populated with sea bottom oxygen concentration from the ocean model NEMO-Nordic-SCOB1), and then calculate the average experienced oxygen by weighting the average oxygen per grid cell by the predicted densities from the density model. This should be a more precise approach; oxygen concentrations span a large range for any given depth. Moreover, we see that the 1<sup>st</sup> decile of the density-weighted oxygen concentration reached an all-time low (approximately 3.5 ml/L in 2005), and then steadily increased, suggesting the average decline in oxygen concentration is not driven by a decline in the lowest oxygen concentrations. Interestingly, we still find a positive effect of oxygen, though 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 and the progressive deepening of the cod stock 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. Instead, we use predicted density of flounder and cod at the haul and at the ICES rectangle-level to include “crowding” effects. Population-level density has previously been

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Commented [MC52]: It could be, but also not, since it as many assumptions too. I suggest to delete it.

Commented [MOU53R52]: Hmm, wouldn't it have fewer assumptions though?

In the depth-based approach, it is implicitly assumed that cod in a certain depth experience the average oxygen concentration at that depth in the whole sd.

I can rephrase: “This approach therefore takes into account that cod are distributed in areas with higher-than-average oxygen conditions for a particular depth”

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551 linked to fishery-induced size truncation causing higher intraspecific competition among  
552 smaller sized fish who primarily feed on benthic prey (Svedäng and Hornborg, 2014). We  
553 detected negative effects of local (haul) density of cod, but not flounder. However, biomass  
554 density is not a direct measure of competition; areas with higher densities of cod and flounder  
555 could simply also have more food. Hence, we cannot rule out that that competition occurring,  
556 only that cod are not skinnier in areas with high density of flounder. To properly test for  
557 competition, we would need data of the benthic invertebrate community, which does not exist  
558 on this spatial and temporal resolution. Moreover, the proportion of *Saduria entomon* in the  
559 diet declined more (from average 0.18 to 0.09 across size all groups) in 2007-2013 relative to  
560 1989-2006 than the decline in 1989-2006 relative to 1974-1988 (from 0.3 to 0.18) (Kulatska  
561 *et al.*, 2019). This is **notable** because we find a stable (but low) condition in 2007-2013, when  
562 the proportion declined fastest. More studies need to be done to evaluate if the lasting low  
563 feeding rates of *Saduria entomon* in recent years are due to the high flounder densities and  
564 therefore to competition with flounder.

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

573 The last piece of evidence (although indirect) against a food-shortage for the decline in  
574 condition is that our model predicts a decline in condition for cod of all sizes. Hence, for the  
575 decline to still be related to competition or food availability, all food sources used by cod over

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Commented [MC56]: Add also Haase et al 2020, MEPS and what they say.

Commented [MOU57R56]: It's difficult to make the same kind of comparison because their data starts in 2006, i.e., after the plateau

Commented [MC58]: True, but we should then also see the effect of hypoxia in different SDs. Condition declined everywhere, but oxygen changed in different ways in different SDs.

Commented [MOU59R58]: Yes that's true. I can make an appendix plot showing time trends of oxygen by SD.



577 ontogeny ought to have declined in synchrony, or that poor condition starts early in life due  
578 a shortage of a specific resource and that cod cannot compensate for that later in life. Even  
579 if that is possible, Neuenfeldt *et al.*, (2020a) showed that the feeding levels of cod where  
580 relatively high in the period 1995-2004 when the decline in condition was the most rapid,  
581 and the growth rates had not yet declined to the lowest in seven decades (Mion *et al.*, 2021).  
582 Hence, a decade of deteriorating condition under normal feeding- and growth rates preceded  
583 the poor growth in recent years. That low feeding levels was not limiting cod in the mid 90's  
584 in the midst of the steep decline in condition is in line with a recent finding that feeding rates  
585 may actually have increased, based on the N-content of otoliths (Svedäng *et al.*, 2020).  
586 Increased feeding rates could be an attempt to compensate for declines in the quality rather  
587 than quantity of food (Svedäng *et al.*, 2020).

588 In conclusion, our study illustrates the fine-scale spatiotemporal development of body  
589 condition in the eastern Baltic cod, and the population-level changes in depth distribution  
590 and oxygen concentrations. We show, in line with Casini *et al.*, (2016a) that the decline in  
591 body condition started in the early 1990's and reached a bottom in the mid 2000s, and that  
592 condition has declined for all sizes and in all areas. These two features, together with small  
593 effect sizes of covariates in relation to several times larger magnitude of residual  
594 spatiotemporal and spatial variation, suggest that food limitation likely has not driven the  
595 decline in body condition of the stocks. However, it is possible these factors (food  
596 availability, density dependence, and environmental condition) still limit a "physiological"  
597 recovery of cod in more recent years (Haase *et al.*, 2020). I.e., the mechanisms that caused  
598 the decline in body condition may not be the ones that have kept cod in a poor physiological  
599 state in the last 15 years. More research is needed to understand the role of fine-scale food  
600 availability for condition, e.g., by evaluating factors associated with hotspots in condition  
601 in recent years. The Eastern Baltic cod stock are not predicted to grow even in the absence

Commented [SA60]: Missing a word or two

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Commented [SA61]: Can we say this any other way? Maybe flip it around. Evaluating factors associated... would enable us to understand...



603 of fishing mortality (ICES, 2021a). This makes it crucial to understand the role of environment  
604 and species interactions for the body condition of cod (Eero *et al.*, 2020), as body condition is  
605 a key biological trait determining mortality and reproductive output.

Commented [SA62]: Should ref come after this or is it not about cod?

## 607 Acknowledgements

608 We are very grateful for help from Alessandro Orio for standardization survey data used in the  
609 density models, Federico Maioli for helpful modelling discussion, Hagen Radtke and Ivan  
610 Kuznetsov for assistance in acquiring predictions of saduria densities, Martin Hansson and Elin  
611 Almroth Rosell at SMHI for assistance with environmental data, and Olavi Kaljuste for  
612 providing pelagic data. We thank staff involved in the scientific sampling and analysis of  
613 biological data.

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## 615 Author Contributions

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

Commented [MOU63]: How does this sound? Let me know if you have other ideas on how to write this! (e.g., different topics or words for contribution).

## 621 Data and code availability

622 All code and data are publicly available at [https://github.com/maxlindmark/cod\\_condition](https://github.com/maxlindmark/cod_condition) and  
623 will be deposited on Zenodo upon publication.

Commented [MC64]: I cannot promise we can do this. In many journals it is ok to say "Data can be requested".

Commented [MOU65R64]: I prefer to keep it together with the code now and when we publish © I have checked with Olavi for the pelagic data, ICES for Datas and Copernicus for environmental data, and they all ok'ed!

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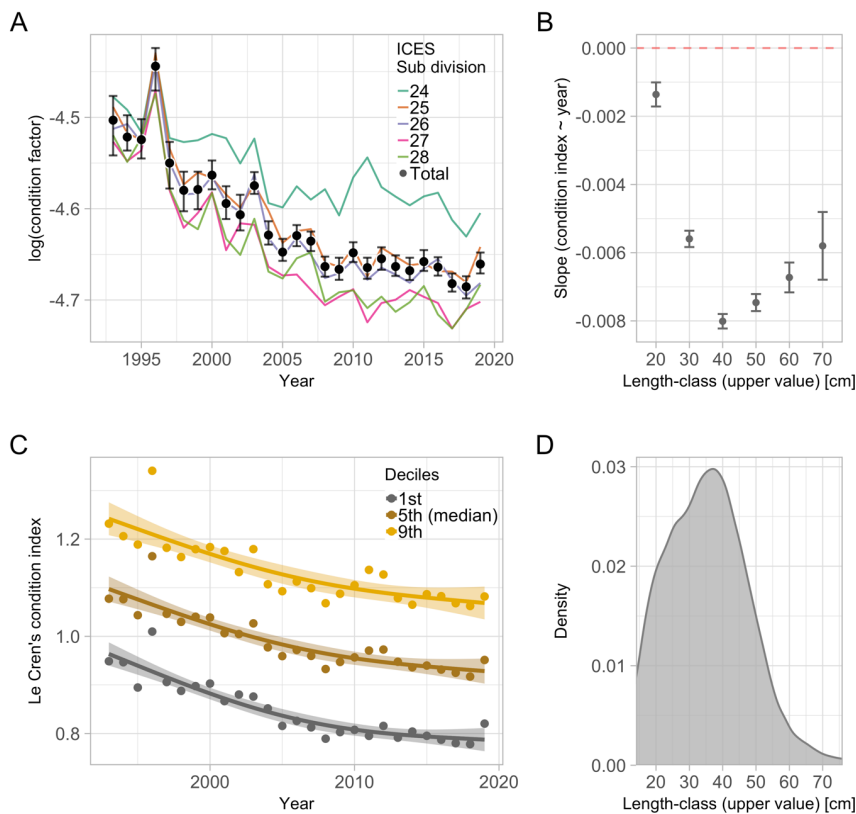
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875 **Figures**



**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. SX). 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) Deciles of the Le Cren condition index as a function of year (shaded band corresponding to the 95% confidence interval) 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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Commented [SA66]: Is what I wrote correct?

Commented [MOU67R66]: it was at that point but not anymore! see comment below

Commented [SA68]: Is this simpler to just state this is alpha? I know this is technically true, but this made me think this was spatially projected and summed... or am I wrong?

Commented [MOU69R68]: see e-mail

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Deleted: with all covariates held at zero (i.e., their means)

Commented [SA70]: This is cool

Commented [SA71]: Yes?

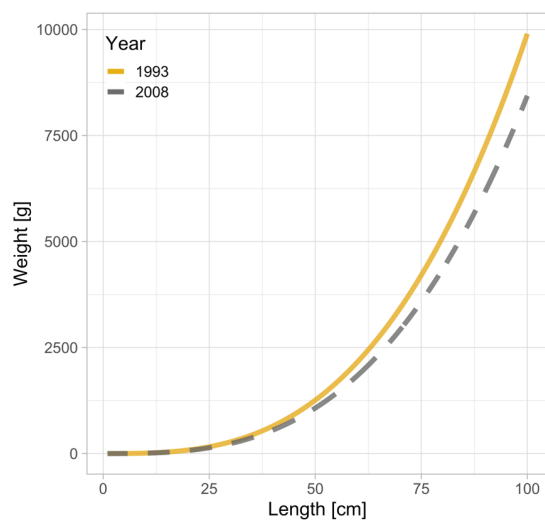
Commented [MOU72R71]: yes! I use credible intervals in other papers i'm working on so I mixed them up

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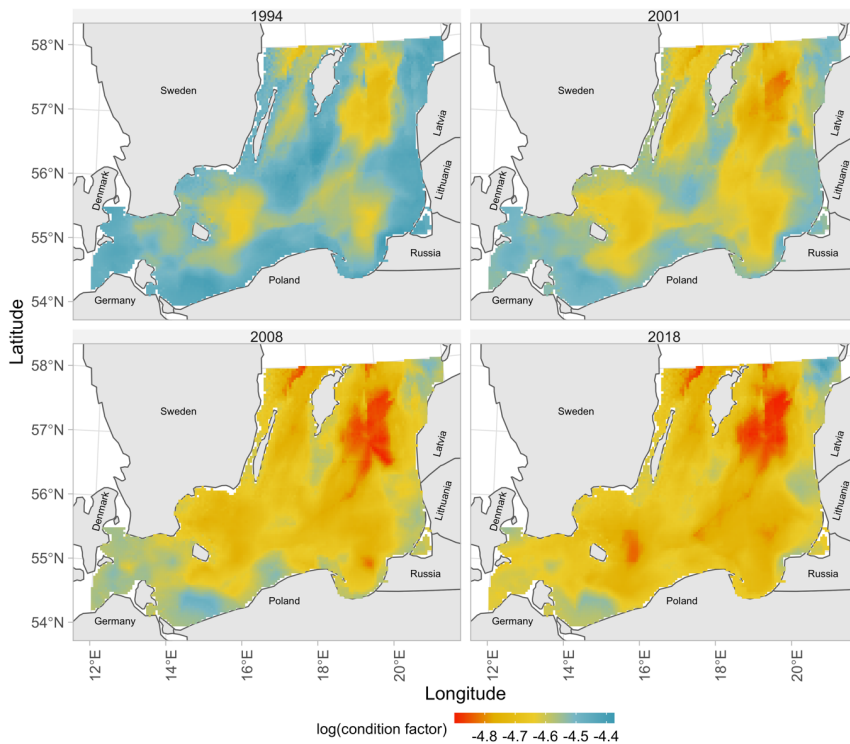
Commented [MOU73]: See e-mail for why I prefer this over the former CV sub panel

Commented [SA74]: Yes?





**Fig. 2.** Change in weight-at-length given  $\beta_t$  and the estimated  $\alpha_t$  for years 1993 and 2008.



**Fig. 2.** Predicted **log condition factor** 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. SX*), such that the prediction corresponds to the depth, temperature, and oxygen-dependent log-condition factor for years **1994, 2001, 2008, 2018**. For all years in the series, see *SI Appendix, Fig. S8*.

**Commented [SA75]:** Is it possible to extend the land polygons a bit so they aren't all cut off? Not a big deal. Also, get those nice country labels on the first map?

**Commented [MOU76R75]:** like this you mean?

**Commented [SA77]:** Is what I wrote correct?

**Commented [MOU78R77]:** it was at that point but not anymore! see comment below

**Deleted:** all other non-spatially varying

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**Commented [SA79]:** Shouldn't things that vary spatially that we don't want to standardize for spatially (e.g., depth) be set to their 'true' values, not means?

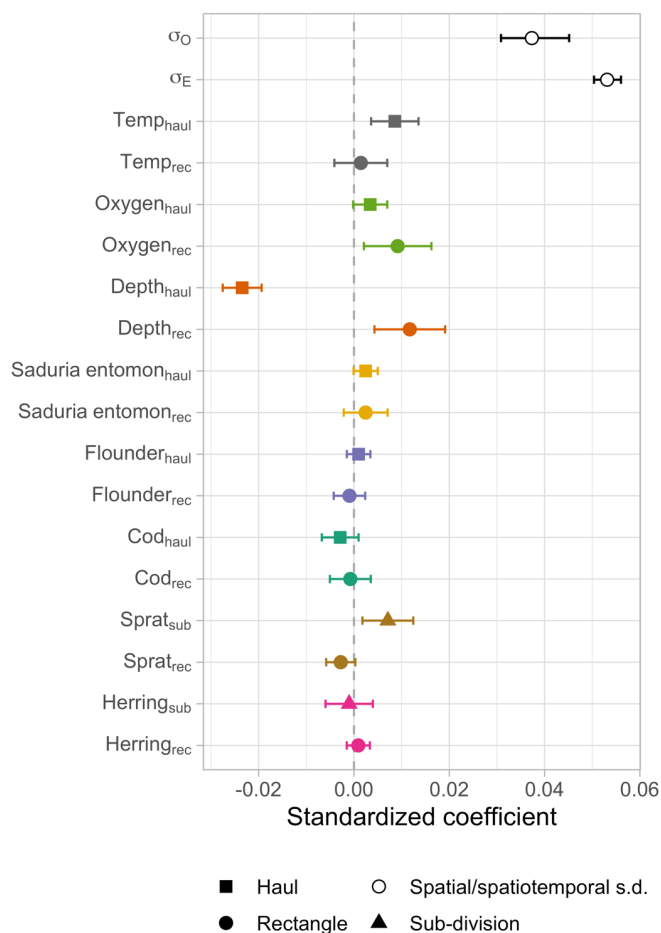
**Commented [MOU80R79]:** yes, I updated the prediction grid now so that it has all covariates at each location and time (before it was only the environmental covariates).

So this prediction is with all covariates at their true value. Except for sprat and herring - in some years information is missing for some ices-rectangles. To avoid having holes in the map I replaced those missing values with the average value in the sub-division (only for the map prediction though, not in the data used for fitting!)

That's why I use 1994 now, because 1993 had the most missing pelagic data.

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**Fig. 3.** Mean and 95% confidence interval of the standardized coefficients and the spatial and spatiotemporal standard deviation ( $\sigma_E$  and  $\sigma_O$ , respectively) in the condition model. The subscript *haul* refers to a covariate estimated at the location of the haul, *rec* refers to a covariate that is averaged by ICES statistical rectangle and *sd* refers to a covariate that is averaged over ICES subdivision (SI Appendix, Fig. S1).

**Commented [SA81]:** Is sigmaE really bigger than sigmaO!? Perhaps because you have so many fixed effects that are helping spatially.

**Commented [MOU82R81]:** Yes! I had not thought about it, but basically you expect spatial variation to be larger than the spatiotemporal one? It seems actually that James Thorson found slightly larger sigma\_E than sigma\_O in this 2015 paper: <https://doi.org/10.3354/meps11204>

**Commented [MOU83]:** New layout! I don't order them by effect size anymore, but grouped by "variable". I thought this made more sense now that we have several variables at different scales.

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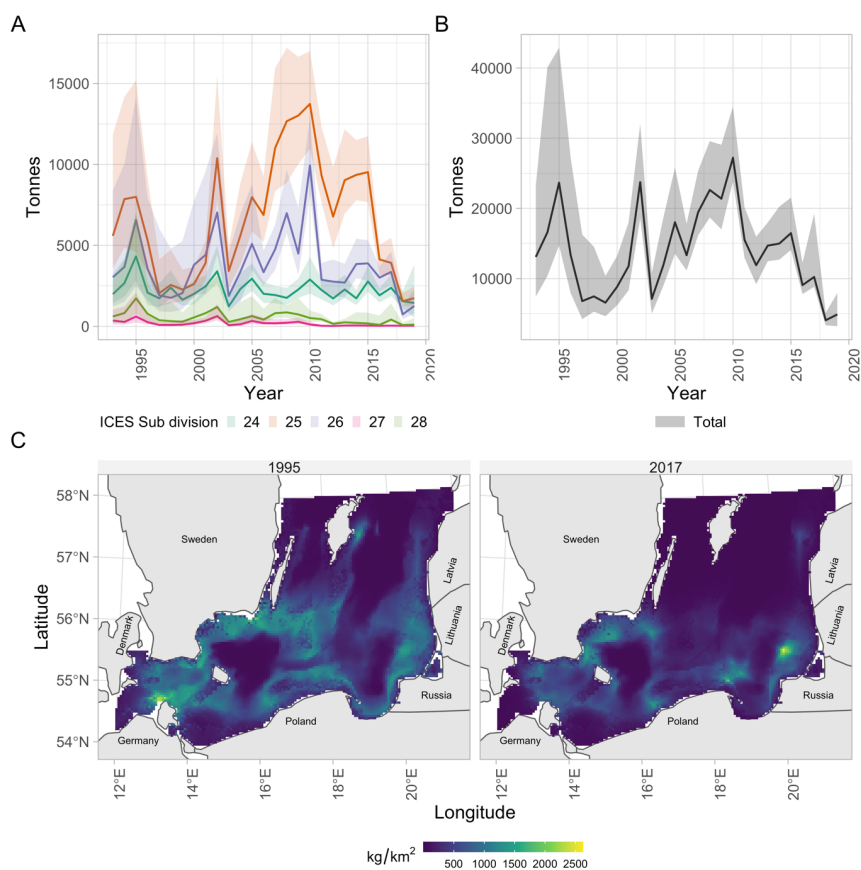
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**Commented [SA84]:** Can we do anything but 'sd' since people will read as standard deviation? Maybe 'sub'?

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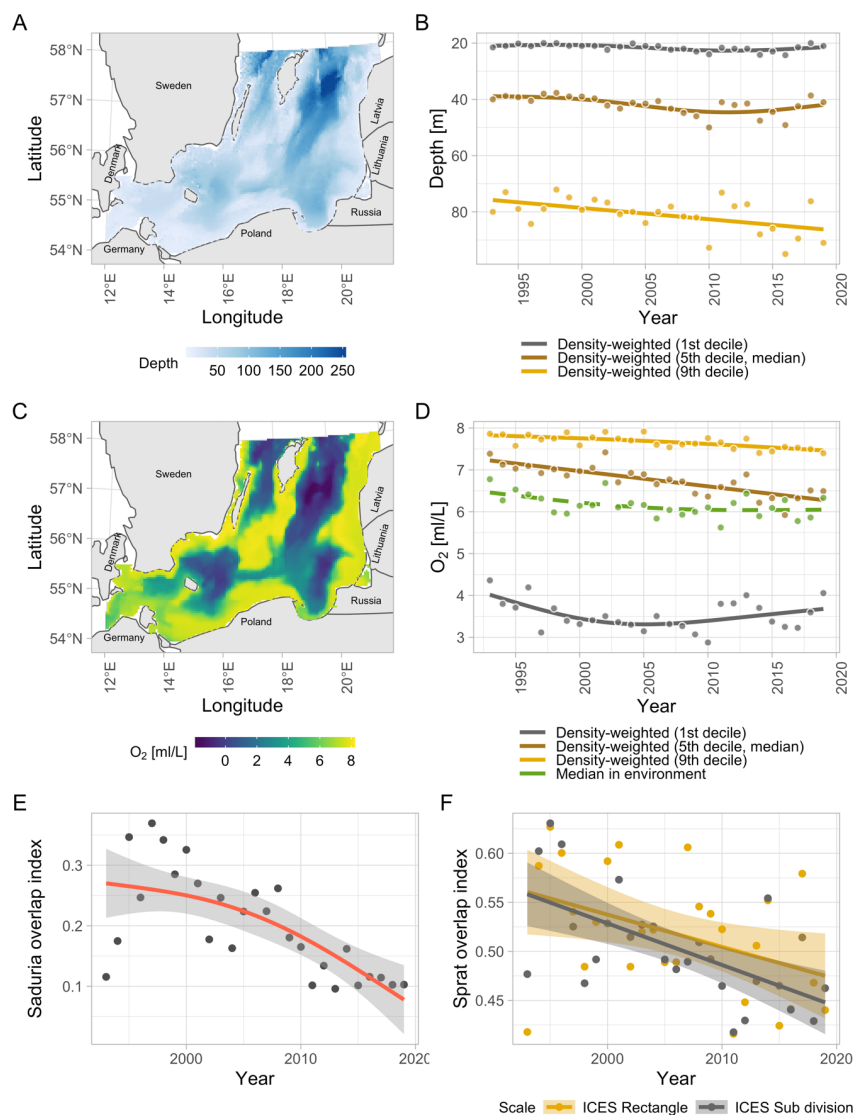
**Fig. 4.** A) Predicted biomass (tonnes) from the spatiotemporal CPUE model (Eq. 10-11), (B) Predicted density [kg/km<sup>2</sup>] in select years 1995 and 2017 (for all years in the series, see *SI Appendix*, Fig. S17), with oxygen, depth, and temperature covariates.

Commented [SA85]: Is this bias corrected? If not, see `sdmTMB::get_index_sims()` as a way that appears to work well but be much faster.

Commented [MOU86R85]: It was not actually. Wow thanks! This was so much faster... and minimal difference.

Commented [SA87]: This is super pretty!

Commented [MOU88R87]: Thanks :)



939

940 **Fig. 5.** A) Bathymetry of the study area, B) depth weighted by predicted cod density. Lines

941 correspond to the 1<sup>st</sup>, 5<sup>th</sup> (i.e., median) and 9<sup>th</sup> decile. C) Oxygen concentration in space (using

Commented [MOU89]: I should change legends to decile instead

Maybe change palette for right column since I use that for sub-divisions

Commented [SA90R89]: Quantile seems fine too. Maybe flip the y-axis so deep is down?

Commented [MOU91R89]: Already done! And good idea, Mich though the same

942 year 1999 as an example) (D) oxygen concentration weighted by predicted cod density. Points  
943 | correspond to the 1<sup>st</sup>, 5<sup>th</sup> and 9<sup>th</sup> decile and lines depict GAM fits ( $k=4$ ) fits.  
944

Commented [SA92]: Loess? GAM? ...?

Commented [MOU93R92]: GAM!

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