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

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**Key Words**

Le Cren’s condition factor, Spatial analysis, Spatio-temporal models, Density dependence, Deoxygenation, Species distribution models

**Abstract**

An organism’s body condition describes its mass given its length and is often positively associated with fitness. The condition of Atlantic cod (*Gadus morhua*) in the Baltic Sea has declined dramatically since the early 1990s, possibly due to increased competition for food and hypoxia. However, the effect of biotic and abiotic variables on body condition have not been evaluated at local scales, which is important given spatial heterogeneity. We evaluate changes in distribution, experienced environmental conditions, and individual-level condition of cod in relation to covariates at different spatial scales using geostatistical models with spatial and spatiotemporal random effects. Sprat biomass, *Saduria entomon* biomass density, temperature and oxygen were positively related to condition, and depth negatively associated. However, the effect sizes of explanatory variables were small—spatial and spatiotemporal latent variables explained 5 times more variation than all covariates together. Weighting environmental oxygen concentrations and spatiotemporal condition predictions with local biomass densities reveal both lower values and steeper trends compared to unweighted values in the population. Understanding the drivers of spatiotemporal variation in body condition is critical for predicting responses to environmental change and to effective fishery management; yet low explanatory power of covariates on individual condition constitutes a major challenge.

**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 (Bolger and Connolly, 1989; Morgan *et al.*, 2010). 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 abiotic 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). Moreover, laboratory experiments have shown that warming is associated with lower condition unless fish have food in excess (Cui and Wootton, 1988). This suggests effects of deoxygenation and warming could be synergistic, as reduced oxygen concentrations also cause lower food intake rates (even during milder hypoxia). As both environmental and biological variables can affect condition, it is important to study their relative contribution to condition in a common framework.

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 since the collapse of the stock in the early 1990s (Casini *et al.*, 2016a; Mion *et al.*, 2021). This has compromised the stock’s 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 and distribution of both cod and its potential competitors for the benthic prey *Saduria entomon* (Haase *et al.*, 2020; Neuenfeldt *et al.*, 2020)—the flounder species complex (European flounder *Platichthys flesus* and Baltic Flounder *Platichthys solemdali*) (Orio *et al.*, 2017), and its main pelagic prey species (sprat *Sprattus sprattus* and herring *Clupea harengus*) (Casini *et al.*, 2011; Eero *et al.*, 2012; ICES, 2021a). Also increased intraspecific competition has been linked to the low growth rates of the stock (Svedäng and Hornborg, 2014). Lastly, the irregular inflows of saline and oxygenated water from the North Sea together combined with a slow water exchange (a residence time of 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 models to characterize the spatiotemporal variation in individual body condition and distribution of cod in the south-eastern Baltic Sea. We use data from scientific surveys between 1993–2019, which corresponds to a period of initially high but then deteriorating cod condition (Casini *et al.*, 2016a). We then address three aims: (1) Identify which covariates (biomass densities of flounder and cod (representing competition), *S. entomon* (benthic prey), biomass of sprat and herring (pelagic prey), as well as depth, oxygen concentration and temperature), at different spatial scales (from haul-location to ices rectangle and for pelagic fishes, also basin-level), can explain observed variation in condition; (2) Develop a spatiotemporally standardized, biomass-weighted condition index for cod in the eastern Baltic Sea that takes into account the heterogenous and temporally varying distribution of cod; (3) Explore how the spatiotemporal distribution of cod impacts the environmental conditions experienced and their implications on trends body condition.

**Materials and methods**

***Data***

To model the spatiotemporal development of cod condition and distribution, we acquired weight and length data for 94295 individual cod, 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 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 (TVL trawl with 75 m sweeps at 3 knots), following Orio *et al.* (2017). Kg/h was then converted to the unit kg/km2 by multiplying with haul duration and dividing with swept area in the given time (0.45 km2). Abundance density was converted to biomass density by fitting annual weight-length regressions (*SI Appendix* Fig. S2). 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 cod condition using a spatiotemporal version of Le Cren’s relative condition factor () (note we reserve the term “condition index” to the annual, model-based index, see *Spatiotemporal predictions* below). This factor is defined as the ratio between the observed weight for individual fish , caught in time at space , and the predicted weight. The predicted weight was given by the relationship , where parameters and were estimated in a non-spatial model with all years pooled, to represent the average weight prediction, based on observed lengths *l*. An individual cod with a thus has the average condition across years and space in the domain. Unlike Fulton’s K, Le Cren’s relative condition factor does not rely on the assumption that growth is isometric (), which, if violated, leads to bias when comparing condition of different lengths as the condition factor scales in proportion to (Le Cren, 1951). Spatially autocorrelation was accounted for with spatial random effects through Gaussian random fields. This approach to modelling spatiotemporal data is an increasingly popular method for explicitly accounting for spatial and spatiotemporal variation 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 open source software such as the R package ‘INLA’ (Rue *et al.*, 2009; Lindgren *et al.*, 2011).

To assess the ability of covariates (see section *Covariates* below) to explain variation in condition, we fit a geostatistical generalized linear mixed-effects model (GLMM) to the natural log of the Le Cren condition factor (in location and time ), assuming - distributed residuals with the degrees of freedom parameter [set to 5 due to the presence of extreme values:

where represents the Le Cren condition factor at space (a vector of two UTM zone 33 coordinates) and time , represents the mean weight, and represents the scale parameter. is the design matrix, with the following covariates: year (as a factor), biomass densities of flounder and cod, biomass of sprat, herring, and *S. entomon*, depth, oxygen concentration and temperature) at different scales (from local to large scale), and is a vector of fixed effect coefficients. The parameters and (Eq. 3-4) represent spatial and spatiotemporal random effects, respectively. 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 and . The spatiotemporal random fields are assumed independent for each year. The covariance () between spatial points and 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; and 1) use predicted local densities of cod and flounder as covariates in the condition model, 2) and acquire local biomass weights to weight the spatiotemporal predictions of condition with local biomass density when calculating the annual condition index (see *Spatiotemporal predictions* below) 3) evaluate how the depth distribution of cod, as well as oxygen and temperature conditions experienced by cod, have changed. For the third task, we used the predicted density at space and time as weights when calculating the annual median (and interquartile range) depth, temperature, and oxygen concentration.

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

where represents density (kg/km2) at space and time , is the mean density, and and represent power and dispersion parameters, respectively. We use year as a factor and the remaining covariates (see section *Covariates* below) were modelled with smooth functions, implemented as penalized splines. The parameters and have the same definition as in the condition model (Eq. 3), but the spatiotemporal random effectsare here assumed to follow a stationary AR1-process where represents the correlation between subsequent spatiotemporal random fields. This is because in contrast to the condition model, the confidence intervals of do not overlap 0.

*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 (Mion *et al.*, 2022). However, within the feeding season, stationary cod move roughly over an area corresponding to an ICES rectangle ( degree cells, *SI Appendix* Fig. S1) (Hüssy *et al.*, 2020). Therefore, we included environmental and biological demersal covariates (sea bottom temperature [], sea bottom oxygen [ml/L], depth [m], and biomass density of *S. entomon* [mg/m2]), cod and flounder [kg/km2] and at the haul level and the median over the ICES rectangle-level. Oxygen and temperature covariates at the ICES rectangle-level were also lagged 1 quarter (which was not possible for biotic data), as these large-scale variables are introduced to capture past exposure affecting current condition. Pelagic fish covariates were included at the ICES rectangle- and subdivision-level (as pelagic species are highly mobile) (see *SI Appendix*, Fig. S1 for the spatial units ICES rectangle and subdivision).

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 BITS hauls were conducted in October, November and December, respectively). We also conducted preliminary analysis to determine if oxygen should be modelled with a linear (as depicted in Eq. 6), or a linear threshold effect, as suggested in experimental studies (Chabot and Dutil, 1999; Hrycik *et al.*, 2017). This showed that the model with a linear effect was favored in terms of Akaike Information Criterion (AIC) (*SI Appendix*, Table S1). 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 coupled with modelled hydrographical data from the regional coupled ocean biogeochemical model ERGOM (Gogina *et al.*, 2020; Neumann *et al.*, 2021). The model was trained to the time period 1981–2019 and predicted for the time period 1993–2019 to match the condition data (but note this prediction is constant over time and therefore more represents *S. entomon* habitats and not temporal variation in biomass density). All raster-derived covariates (oxygen, temperature, depth, and *S. entomon*) were linked to spatial points using bilinear interpolation (values for a spatial point interpolated from the four nearest raster cells). We used predicted densities of cod and flounder (kg/km2) 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 and flounder models that were used to provide covariates for the condition model and weights to the body condition predictions, the only fixed effects were year as a factor variable and a smooth effect of depth. For the cod density models used to evaluate effects of changes in the average depth, oxygen concentration and temperature, we included also smooth effects of temperature and oxygen as covariates.

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 () and spatiotemporal () 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. S3 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. S5, S16), created using the R-package ‘R-INLA’ (Rue *et al.*, 2009). The random effects were estimated at the vertices (“knots”) of this mesh and bilinearly interpolated to the data locations. The locations of the knots were chosen using a -means clustering algorithm, 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 100 knots for the condition model and 200 knots for the density models. We fit the models using ‘TMB’ (Kristensen *et al.*, 2016) via the R-package ‘sdmTMB’ (version 0.1.4.9004) (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 < 0.001 and that the Hessian matrix was positive-definite. Model residuals are shown the *SI Appendix* Figs. S6–S8 and S17–S18, conditional effects in *SI Appendix* Figs. S13, S22, and spatial and spatiotemporal random effects are show in *SI Appendix* Figs. S9–S10 and S19–S20. We used packages in the ‘tidyverse’ (Wickham *et al.*, 2019) for data processing and plotting.

*Spatiotemporal predictions*

We predicted body condition and biomass density of cod onto a 44 km prediction grid with covariates to visualize spatiotemporal variation and to calculate random-field model-based indices of condition and relative biomass (Shelton *et al.*, 2014; Thorson *et al.*, 2015a). Annual condition and biomass indices were calculated from 500 draws from the joint precision matrix and model predictions on the grid. Predicted condition in each grid cell was weighted with the predicted biomass density of cod in the same grid cell, to account for the heterogenous and temporally varying distribution of biomass in the domain (*SI Appendix* Fig. S4) (Grüss *et al.*, 2020; Indivero *et al.*, 2023). The final, annual condition index was acquired by dividing the index by the sum of weights (cod biomass densities) by year.

# **Results**

The condition model revealed a mean decline in the spatiotemporal biomass-weighted Le Cren condition index by 15% [12%, 19%], from approximately 1.12 [1.07, 1.17] to 0.95 [0.94, 0.95], between 1993 and 2019 (the decline leveled off around 2008) (Fig. 1A). The values are medians of 500 draws from the joint precision matrix, and values in brackets are in 2.5% and 97.5% quantiles. The year effect is important for the decline in condition index over time; the index based on predictions only including biotic and abiotic covariates over space and time (omitting the estimated annual means in condition) only show a very weak decline over time, and some tendency for an increase in the last years (Fig. 1A). The condition factor declined in synchrony across subdivisions and in space (*SI Appendix*, Fig. S12), but the condition index plateaued at a slightly higher value in subdivision 24 (Fig. 1B). There was in general high agreement with the simple empirical mean of condition and the spatiotemporally standardized and biomass-weighted predicted condition index, but in some years the empirical mean was outside the confidence interval of the model-based index (Fig. 1). The spatial predictions from the condition model illustrate the presence of consistent “low spots” of body condition. These largely occur in the deep, low-oxygen areas (see e.g., Fig. 5C–D), creating a horizontal dumbbell shape of low-condition spots in the center of the study area.

The covariates with the largest positive standardized effect sizes on the condition factor were biomass of sprat at the ICES subdivision level (0.008 [0.002, 0.013]) (values in brackets indicate 95% confidence interval), biomass density of *S. entomon* at the rectangle level (0.007 [0.0026, 0.012]), temperature at the haul and rectangle level (0.007 [0.0025, 0.01] and 0.007 [0.0019, 0.012], respectively), haul-407. The effects of median depth, median oxygen and herring biomass at the rectangle-level, and flounder and cod biomass density at the haul-level were positive but with confidence intervals overlapping 0. The covariates with the largest negative effects were depth at the haul-level (-0.021 [-0.024, -0.018]), sub-division level biomass of herring (-0.05 [-0.01, -0.001]), biomass of sprat at the ices rectangle level (-0.04 [-0.006, -0.001]). Haul-level biomass density of *S. entomon*, and rectangle-level median biomass density of cod and flounder were also negatively associated with condition, but with confidence intervals overlapping 0. See also *SI Appendix*, Fig. S13 for conditional effects plots of selected variables.

The effect sizes of fixed effects were several times smaller than the magnitude of latent spatiotemporal and spatial variation (Fig. 3). The average random effect magnitude was 10 times larger than the average magnitude of individual fixed effects (excluding the year effects) (Fig. 3). To address the collective explanatory power of many but small individual fixed effects, we used the approach proposed in Nakagawa and Schielzeth (2013) to calculate marginal for fixed and random effects. We found that fixed effects had a marginal of 0.14, while random effects had a marginal of 0.22 75 Of the 0.14 marginal for the fixed effects, 0.094 constitutes the fixed year effects, and 0.043 for the remaining covariates. Hence, the ratio of for spatial and spatiotemporal random effects to biotic and abiotic covariates (i.e., omitting the annual means) is 5.

We conducted several sensitivity analyses with respect to the fixed effects. First, we refit the condition model to different parts of the data. The different models were only cod above 30 cm, only cod below 30 cm, omitting subdivision 24 (the mixing zone with western Baltic cod (Mion *et al.*, 2022)), and including only grid-points with cod above a certain threshold when calculating median variables across the ICES rectangle. We also explored alternative ways to define the raster-derived large-scale variables. Specifically, instead of using the rectangle average, we aggregated the raster file to resolutions approximate to the area of an ICES rectangle, and then extracted the aggregated value with bilinear interpolation. We also explored different lags for the abiotic covariates (not shown). However, across all additional models, model coefficients were similar and so was the ratio of spatiotemporal magnitude and coefficients (*SI Appendix,* Figs. S14–S15).

The median depth and oxygen experienced by cod (depth and oxygen weighted by the predicted biomass density of cod at location, respectively, Fig. 4C) got deeper and declined, respectively, throughout the time period (Fig. 5). However, the population again occupied slightly shallower waters in the last 3 years of the time series (Fig. 5C; see *SI Appendix*, Fig. S24 for results split by subdivision). The trends in experienced oxygen were steeper than the average oxygen in the environment at depths corresponding to the interquartile range of cod (Fig. 5C–D). The average oxygen concentration in the environment declined by approximately 0.6 ml/L between 1993 and the lowest in 2006, while the biomass-weighted oxygen concentration declined more steadily (approximately 1 ml/L between 1993 and 2019) (*SI Appendix*, Fig. S23 for estimates split by subdivision). The lower quartile of weighed oxygen plateaued around year 2000. However, while the biomass-weighted oxygen concentration declined between 1993 and 2019) (Fig. 5D), the corresponding effect on condition given the effect size of oxygen at the haul was small (*SI Appendix*, Fig. S13). The standardized effect size for oxygen of 0.004 means that for each unit increase in the variable (i.e., 1 standard deviation or 1.8 ml/L), the Le Cren condition factor increases by 0.4%. This can be compared to the 1 ml/L decline in the oxygen concentration and 17% decline in the condition factor between 1993–2019. This result also holds when considering all covariates; i.e., while there are covariates with statistically clear effects, and changes in these over time in the environment, the magnitude of changes in covariates are not large enough for the condition factor to decline over time (Fig. 1A).

# **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 15%, in 1993–2019, with most 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. We identify shifts in the spatiotemporal distribution of cod that could have contributed to a decline in cod condition (deeper areas with less oxygen, as in also Casini *et al*., (2020)). However, effect sizes of single covariates were overall small, and latent spatial and spatiotemporal variation was several times larger in magnitude and explained more variation in condition, a pattern also found in in the California Current groundfishes (Thorson, 2015).

Previous studies have suggested both direct (Limburg and Casini, 2019; Brander, 2020) and indirect (Brander, 2020, 2022; 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. Indirect effects refer to due to increased competition for benthic prey, as both habitat area and quality is reduced with de-oxygenation. We found that Baltic cod experienced oxygen concentrations at around 7.4 [6.1–7.4] in 1993 (interquartile range in brackets) ml/L on average (biomass-weighted median) and are currently experiencing oxygen concentrations at around 6.5 [5.15–7.2] ml/L. In subdivision 25 (the core area of cod, currently) we estimate it to be on average 6.4 [4.9–7.3] ml/L between the years 2015–2019 (*SI Appendix,* Fig. S23). This is higher than recent estimates of an average oxygen concentration of 4–4.5 ml/L, based on oxygen levels at the mean depth of the cod population in the recent years (Brander, 2020; Casini *et al.*, 2021).

One reason for the difference in our estimate compared to previous studies is because instead of calculating average oxygen at the mean depth of cod, we weighted the sea bottom oxygen in the environment (from the ocean model NEMO-Nordic-SCOBI) by the predicted densities from the cod density model. This approach overcomes the issue that oxygen concentrations span a large range for any given depth and avoids the assumption that cod depth occupancy is independent of oxygen concentration. Our finding that trends in weighted and unweighted oxygen differ suggests that it is important to account for species’ heterogenous distribution. This is evident in subdivisions 25 and 27, where the oxygen trends in the environment have been stable since 2005, as in (63), but the experienced oxygen by cod continued to decline (in subdivision 27 the pattern is the opposite and the weighted median is stable over time) (*SI Appendix*, Fig. S23). Another reason for differences between previous estimates of experienced oxygen could be due to different oxygen models being used. For example, the model developed by Lehmann et al. (2002, 2014) (the “GEOMAR” model) and used in Casini et al. 2021 (Casini *et al.*, 2021) and Orio et al. (Orio *et al.*, 2019), results in weighted oxygen concentrations 0.5–1 ml/L lower on average, but a less steep decline than the NEMO-Nordic-SCOBI model between 1993–2016 in subdivision 25 (*SI Appendix,* Fig. S27). Also the unweighted estimates differ approximately 0.5–1 ml/L between the models at depths between 29–61 m. Although explaining the differences between the models is outside the scope of this paper, care should be taken when interpreting absolute values of oxygen concentrations.

In an experiment by Chabot & Dutil (1999), 5 ml/L (converted from 73% O2 saturation at 10, 28, and 1013.25 ) was estimated to be a critical value concentration below which negative effects on growth and condition were observed on cod. This value is higher than a meta-analytic estimate across fishes of a 3.15 ml/L threshold, below which negative effects on fish growth occur (Hrycik *et al.*, 2017). However, despite our data spanning oxygen levels above and below these values, we do not find support for a threshold in the relationship between condition and oxygen, in contrast to Casini *et al.*, (2021). That oxygen is positively associated with condition is however in line with both Limburg and Casini (2019) and Casini *et al.*, (2021), despite differences in methodological approaches. However, we can only speculate if the positive association is due to higher oxygen being correlated with richer habitats that feature higher food availability, if there are direct physiological impacts at a higher threshold in the wild, or if behavioral responses (e.g., movement between high and low oxygen area) essentially remove any measurable thresholds in natural systems.

An indirect effect of declining oxygen on condition is the potential amplification of intra- and interspecific competition with flounder for shared benthic prey species, such as the isopod *S. entomon*, due to habitat contraction of cod caused by the expansion of “dead zones” (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 did not detect a negative effect of cod density on cod condition, in contrast to previous studies suggesting density-dependent effects on growth (Svedäng and Hornborg, 2014). Flounder density was also not clearly linked to condition at any scale. That said, growth is not the same as condition and 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). We do find statistically clear positive effects of *S. entomon* biomass density at the rectangle level. This is interesting, because Neuenfeldt *et al.*, (2020) found that cod had more saduria in stomachs in the years 1963–1988 compared to 1994–2014. However, the time period 1963–1988 contains years with both low and high body growth and condition in cod (Casini *et al.*, 2016a; Mion *et al.*, 2021). Moreover, Svedäng et al. (Svedäng *et al.*, 2022) recently showed that benthic food availability has not changed dramatically over the time period in the southern Baltic Sea. More studies are needed to determine why cod seem to feed less on *S. entomon* and if it is related to competition.

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 (but a negative association on finer scales, possibly because it is a too fine scale for a pelagic and mobile species). 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 cod are relatively scarce (Fig. S25–26). In the main distribution area of cod (subdivisions 24–26), sprat biomass declined from 1993 until around 2010 (where condition plateaued at low values), but after that it increased again to levels close to those in the early 2000’s. However, condition did not, which suggests that further analyses should be made to understand the link between biomass of pelagic fish and the condition of cod, possibly accounting condition and size-structure of pelagic species.

We interpret environmental covariates to explain little variation in condition, compared to previous studies using population or basin-level averages of body condition as the response variable (e.g., Casini *et al.*, 2016a). A potential explanation for this difference is our use of individual-level data, as there is large variation in condition among individual cod. For instance, the average condition is lower in deep, low-oxygen, low sprat areas, yet we still observe cod in good condition there, which may dilute effects compared to if using averages. The benefit of using individual-level data is more data becomes available, one can account for uncertainty associated with individual-level, and it allows for using covariates on different scales (from local to large scale). However, using individual data also requires accounting for spatial and spatiotemporal autocorrelation (e.g., with latent variables), which if not accounted for, can introduce a false sense confidence due to reducing residual correlation. It also allows us to conclude that other factors, not explicitly included in our analyses, may have also played an important role in the decline of condition (since the magnitude of spatial and spatiotemporal variation is large). For instance, the mechanisms that initiated the body condition decline may not the same ones that have kept cod in a poor physiological (Tomczak *et al.*, 2022). As an example, liver parasites, are numerous now that cod are in poor condition, but likely did not cause the decline as cod in good condition are not as susceptible to parasite infection (Ryberg *et al.*, 2020).

It is also difficult to know how to integrate covariates over time. While we include lagged and current covariates on large and local scales (respectively), we do not find a clear difference in explanatory power between these. This may suggest environmental effects do explain little variation in condition, or that covariates need to be integrated over longer time periods, e.g., average lifetime exposure. To further increase our understanding of how the environment shapes spatiotemporal variation in body condition, we suggest 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 as done in Limburg and Casini (Limburg and Casini, 2019).

In conclusion, the small effect sizes of single covariates, and the high synchrony in temporal trends of biomass-weighted average condition across basins (subdivisions) despite large variation in environmental conditions, suggest that multiple factors, and factors acting on large spatial scales, are responsible for the observed spatiotemporal changes in cod condition during the past 25 years. The fact that also the condition of herring and sprat started to decline in the late 1980’s early 1990’s (Casini *et al.*, 2011) suggests there could be ecosystem-level drivers, possibly related to productivity (but it could also be a spurios correlation since clupeid condition has been linked to density dependent processes, see Casini et al., (2006)). Moreover, in line with Thorson *et al.*, (2017) this study shows that it is important to consider the proportion of variance explained by covariates for understanding how ecosystem changes and management interventions (Bryhn *et al.*, 2022) aiming to improve habitat quality may affect the productivity of fish stocks via condition. Lastly, since the overall productivity (of which body condition is a critical component), is so low that the stock is not predicted to grow even in the absence of fishing mortality (ICES, 2021a), it is crucial to gain a broader understanding of the drivers of the decline in condition of eastern Baltic cod.

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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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**Figures**

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**Fig. 1.** Trends in Le Cren’s condition factor between 1993–2019 in the Baltic Sea. In the top row, the empirical mean (green) is depicted with the spatiotemporal model-predicted and biomass-weighted Le Cren condition index for the full prediction (blue) and the predictions with only biotic and abiotic fixed effects included (i.e., omitting spatial and spatiotemporal random effects and the factor year effect). Hence, the latter represents the predicted index given changes in only environmental conditions. Model-based indices were acquired by simulating 500 draws from the joint precision matrix and 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. S26. Solid lines depict the mean, the shaded area is the 95% confidence interval and single, thin lines are example draws (n=25) from the join precision matrix. In the bottom row, the index (from the full prediction) is split by ICES subdivision (indicated by color).

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**Fig. 2.** Predicted Le Cren’s 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. S26). Included in the plot are years 1994, 2001, 2008, 2018. Only grid cells with depths between 10m and 110m are included in the plot. For all years in the series, see *SI Appendix*, Fig. S11.



**Fig. 3.** Mean and 95% confidence interval of standardized coefficients (effect sizes) for covariates and spatial and spatiotemporal standard deviation ( and , 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 subdivisions (*SI Appendix*, Fig. S1). Colors indicate covariate-groups and shapes indicate scale.



**Fig. 4.** Biomass index from the spatiotemporal density model by ICES subdivision (A) and total across all subdivisions (B). Panel C depicts predicted biomass density (kg/km2) in select years (1994 and 2018). For all years in the series, see *SI Appendix*, Fig. S21. Only grid cells with depths between 10 and 110 are included in the plot.



**Fig. 5.** Bathymetry (A), oxygen concentration (B), and temperature (C) (B-C exemplified using year 2006) in the study area. Panels D-F illustrate depth, oxygen, and temperature, respectively, weighted by predicted cod density. Colors indicate biomass-weighted quantiles (1st quartile, median and 3rd quartile), as well as the un-weighted average (green dashed line) at depths corresponding to the average interquartile range (29–61 m). Lines depict generalized additive model (GAM) fits (=4).