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

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Le Cren condition factor, Weight at length, Spatial analysis, Spatio-temporal models, Density dependence, Deoxygenation

**Abstract**

The body condition of a fish describes the weight given its length and is often positively associated with fitness. Atlantic cod (*Gadus morhua*) in the south-eastern Baltic Sea has experienced a drastic deterioration of its physiological status since the early 1990s to levels that compromise the growth of the population. Several variables have been attributed to the decline in body condition, including increased intra- and interspecific competition for benthic resources, lack of pelagic food, and increased hypoxia in the Baltic. However, despite operating on small spatial scales, these variables have only been evaluated on large spatial scales (Baltic Sea basin- or population level), and the relative importance of these covariates has not been evaluated in a common framework. By applying a geostatistical model that includes spatially and spatiotemporally correlated random effects using Gaussian Markov random fields, we analyze changes in condition and spatiotemporal distribution in relation to fine-scale habitat variables. We find that the body condition declined until 2008, after which a plateau was reached, and the decline occurred for cod of all sizes. Oxygen, sprat abundance at the sub-division level, and temperature where positively related to condition, whereas density of cod and depth were negatively associated with condition. However, despite the deepening and declines in experienced oxygen of the population, the effects sizes of these variables were small, and could not explain the steep decline that occurred between 1993–2008. In fact, residual spatial and spatiotemporal variation were several times larger in magnitude than any single covariate’s coefficient, suggesting there is still considerable variation unexplained by covariates and likely many underlying causes behind the decline in body condition. Understanding the drivers of spatiotemporal variation in body condition, which affects mortality and reproduction, is important for understanding the impacts of environmental change and for the management marine fishes.

**Introduction**

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

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; Grüss *et al.*, 2020). It has also been linked to environmental conditions, (e.g., temperature, salinity) affecting ecosystem productivity and local habitat quality (Möllmann *et al.*, 2003; Morgan *et al.*, 2010; Grüss *et al.*, 2020). More recently, studies have found a link between declining body condition and global deoxygenation (declines in dissolved oxygen and the expansion of dead zones) (Casini *et al.*, 2016a, 2021), fueled by warming and nutrient enrichment (Diaz, 2001; Breitburg, 2002; Diaz and Rosenberg, 2008; Carstensen *et al.*, 2014).

The underlying mechanisms 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 food intake rates, which can occur even during milder hypoxia (Kramer, 1987; Chabot and Dutil, 1999; Claireaux *et al.*, 2000; Hrycik *et al.*, 2017; Brander, 2020; Sampaio *et al.*, 2021). As both environmental and biological variables can affect condition, it is important to study their relative contribution to variation in condition in a common framework.

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

The Baltic Sea constitutes an interesting case study for disentangling ecosystem drivers affecting body condition (Reusch *et al.*, 2018). First, in the Eastern Baltic Sea cod stock, the average body growth and body condition has declined in the time post the collapse of the stock in the early 1990s (Casini *et al.*, 2016a; Mion *et al.*, 2021). This has compromised the stock productivity to the extent that population biomass is expected to remain below safe limits despite the ban of targeted cod fisheries in 2019 (ICES, 2021a, 2021b). Second, the Baltic ecosystem has seen a major change in the abundance of both cod and its potential competitors for the important prey the isopod *Saduria entomon* (Neuenfeldt *et al.*, 2020) the European and Baltic Flounder (*Platichthys flesus* and *Platichthys solemdali,* respectively) (Momigliano *et al.*, 2018), and in the distribution of its main pelagic prey species (sprat *Sprattus sprattus* and herring *Clupea harengus*). Lastly, the irregular inflows of saline and oxygenated water from the North Sea together with a long residence time (25–30 years) are features that have contributed to making the Baltic Sea the largest anthropogenically induced hypoxic area in the world (Carstensen *et al.*, 2014), and it is also one of the fastest warming regional seas (Belkin, 2009; Reusch *et al.*, 2018). However, it remains unknown what the relative importance of these variables are, since they have not been analyzed directly in a single framework, and not on different spatial scales.

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

**Materials and methods**

***Data***

*Survey data*

To model the spatiotemporal development of cod condition and distribution, we acquired weight and length data, as well as catch per unit effort data (CPUE, numbers/hour) of cod by 10-mm length class from the Baltic International Trawl Survey (BITS) between the years 1993-2019 and in ICES sub-divisions 24-28 (*SI Appendix*, Fig. S1). CPUE data were standardized based on gear dimensions and towing speed following Orio *et al.* (2017) to the unit using a TVL trawl with 75 m sweeps (note that compared to Orio *et al.* (2017), we further express density in instead of after 1 trawling sweeping an area of 0.45 by dividing by 0.45). Abundance density was converted to biomass density by fitting annual weight-length regressions. We used only data from the fourth quarter, which corresponds to the main growing and feeding season (Aro, 1989) and also the quarter in which the Baltic International Acoustic Survey (BIAS) is conducted, meaning sprat and herring abundance can be used as covariates. The BITS data can be downloaded from <https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx>.

*Covariates*

For both models (condition and density model), covariates were chosen to reflect hypothesized drivers based on published literature. As cod are mobile species, we included covariates at different spatial scales that we assumed best reflected the environment they were exposed to when building energy reserves after spawning in winter/spring. 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 (Hüssy *et al.*, 2020). Therefore, we included environmental covariates (temperature, oxygen, depth) at the haul- and median over the ICES rectangle level, benthic biomass density variables (cod, flounder and saduria) at the haul-, ICES rectangle- and ICES sub division level (the sub division level is to reflect that both predator and prey move, in contrast to the environmental variables), and the pelagic covariates at the ICES rectangle- and sub division-level (not including haul-level densities as pelagic species are highly mobile).

(i.e., haul-, ICES rectangle- and ICES sub-division [roughly corresponding to basins]). This is to account for the fact that cod are mobile species (Hüssy *et al.*, 2020) and thus likely have been exposed to nearby environments during the time frame relevant for the body condition at catch. The covariates for the condition model were biomass of sprat and herring, which are important prey species for cod (Gårdmark *et al.*, 2015; Haase *et al.*, 2020) (for the pelagic covariates, ICES rectangle (1° by 30') is the smallest scale available, not haul). Sea bottom temperature and sea bottom concentration of dissolved oxygen in the fourth quarter (Casini *et al.*, 2016a, 2021; Limburg and Casini, 2019; Brander, 2020) were derived from the ocean model NEMO-Nordic-SCOBI (Eilola *et al.*, 2009; Almroth-Rosell *et al.*, 2011; Hordoir *et al.*, 2019) and included on a haul-level. 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 *Saduria entomon* was extracted from a habitat distribution forced to a a regional coupled ocean biogeochemical model (Gogina *et al.*, 2020). Biomass density of cod and flounder were taken from the same scientific survey as the condition data (BITS) and represent intra- and interspecific competition for mainly benthic food resources (Svedäng and Hornborg, 2014; Orio *et al.*, 2019; Neuenfeldt *et al.*, 2020). However, as not all CPUE (density) data could be standardized 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 biomass density data. Flounder data were standardized in the same way as cod data (described above).

Following (Thorson, 2015; Grüss *et al.*, 2020), we rescaled all covariates to have a mean of 0 and a standard deviation of 1. This facilitates comparison between covariates of different units and allows for comparison between the estimated coefficients and the standard deviation of spatial () and spatiotemporal () 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.

***Estimating spatiotemporal development of body condition and catch-per-unit-effort***

*Condition model*

We modelled condition by assuming weight is related to length as , where is weight in grams, is length in cm, is the allometric length exponent and is the condition factor in unit (Froese *et al.*, 2014). In addition to estimating the condition factor, we used this relationship to calculate Le Cren’s relative condition factor for each individual fish (). Unlike Fulton’s K, this relative condition factor does not rely on the assumption that growth is isometric (), which if violated leads to bias when comparing condition of cod of different lengths as the condition factor scales in proportion to (Le Cren, 1951).

To acquire a spatiotemporal condition factor, we fit a geostatistical GLMM to the weight-length relationship on - scale, assuming - distributed residuals (with 5 degrees of freedom) due to the presence of extreme values:

where represents the weight at space (a vector of two UTM zone 33 coordinates) and time , represents the mean weight and represents the scale parameter. The parameter (corresponding to the log condition factor) 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 for subsequent values. The parameter represents the length-coefficient (corresponding to the allometric exponent ), and represents a vector of the -th additional covariate and is its effect. The parameters and 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 and . The covariance () between spatial points and in all random fields is given by a Matérn function:

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:

where 𝜌 represents the correlation between subsequent spatiotemporal random fields.

*Density models*

We fit a spatiotemporal models to biomass density data in a similar fashion as for condition for two reasons: 1) to evaluate how the depth distribution, temperature and oxygen conditions 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 and time as weights when calculating the annual average depth, temperature, and oxygen concentration, as well as overlap with sprat and saduria. The latter overlap was defined by the biomass-weighted overlap index:

, which 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):

where represents density [] at space and time , is the mean density, and represents the power and dispersion parameters, respectively. The parameters represent independent means for each year, is a smooth function for covariate and and represent spatial and spatiotemporal random effects and have the same definition as in the condition model (Eqns. 5–6).

*Model fitting*

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

# **Results**

The spatiotemporal condition model revealed a decline in the log condition factor (i.e., , the log weight when all covariates are zero) of 3.3%, from approximately -4.5 to -4.65 between 1993 and 2008, after which a plateau was reached (Fig. 1A). This corresponds to a 14% decline in 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 10-20cm was more modest (-0.012 annual decline) (Fig. 1C). 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 (Fig. 1C). We also find the different conditions deciles (1st, 5th and 9th) declined at the same rate over time (*SI Appendix*, Fig. S11). This means the decline in the condition factor was not solely driven by a decrease of fish in good condition or a worsening of condition of cod already in poor condition, but a more general decline.

Predictions from the condition model illustrate the presence of consistent “low spots” of body condition in deep and low-oxygen areas (east of Bornholm, south of Gotland and between Öland and Gotland) (Fig. 2, *SI Appendix*, Fig. S1), and that the condition factor declines in the whole area over time (Fig. 2, *SI Appendix*, Fig. S8, S10).

The covariates with the largest positive standardized effect sizes are temperature, oxygen, the interaction between depth and temperature and sub-division level sprat abundance (Fig. 3). Depth and cod density are both negatively associated with condition (weight) (Fig. 3) (see *SI Appendix*, Fig. S9, for marginal effects plots). 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.

Cod at the end of the time series are found in deeper and less oxygenated areas (Fig. 5). However, their contribution to the decline over time is likely quite minor. For instance, the standardized effect size for oxygen is 0.0044 [95% confidence interval: 0.00042, 0.0084], meaning that for each unit increase in the standardized oxygen variable (i.e., 1 standard deviation or 1.85 ml/L), log weight increases by 0.44%. As a comparison, the average oxygen concentration in the environment declined by approximately 0.65 ml/L between 1993 and the lowest in 2006 (Fig. 5C-D), 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 was not only considerably larger than the average in the environment, but it also declined more continuously than in the environment, with approximately 1 ml/L between 1993 and 2019 (Fig. 5C-D). Still, the contribution to the 3.3% decline in the condition factor is likely minor, as the change in experienced oxygen only corresponds to a change that is slightly larger than half a standard deviation in change, and oxygen trends vary in space whereas condition declined everywhere (*SI Appendix*, Fig. S10, SX). 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 1st and 9th 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).

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]). To estimate body condition without it scaling with length, we first estimated empirical weight-length relationships using the whole size-range of the cod population. However, the covariates related to competition or food availability (such as cod and flounder density, or sprat and herring abundance) are likely mostly important for specific size-ranges of the cod population, rather than all sizes of cod. Therefore, we also fit the same condition model to cod above and below 30 cm (where cod below 30 cm are more likely to compete with flounder and other cod for benthic resources (Haase *et al.*, 2020), and cod above 30 are able to feed on the entire size-distribution of the herring (Niiranen *et al.*, 2019) (*SI Appendix*, Fig. SX). These results showed that the neither the parameter estimates nor the trends over time changed drastically.

# **Discussion**

Using a fine-scale spatiotemporal condition model, we show that the cod weight for a given length in the Baltic Sea has declined by 16%, primarily between the years 1993–2008, that there are persistent low-spots of body condition (deep and low-oxygen areas), and that condition has declined in the whole area. Furthermore, 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 effect sizes and overall, residual spatial and spatiotemporal variation having several time larger magnitude effects than covariates.

Previous studies have suggested both direct (Limburg and Casini, 2019; Brander, 2020) and indirect (Neuenfeldt *et al.*, 2020; Orio *et al.*, 2020) effects of oxygen as a cause for the declining body condition of cod. Direct effects here refer to mild hypoxia reducing the appetite and food consumption (Chabot and Dutil, 1999) and by extension also their condition, as they are not able to accumulate as large energy reserves. First, we find that the Baltic cod are currently experiencing oxygen concentrations at around 6 ml/L on average (1st and 9th decile are 3.8 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-SCOBI), 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 1st 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” cascond (Orio *et al.*, 2019; Haase *et al.*, 2020). We did not include the extent of hypoxic areas not spatial overlap as 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 linked to fishery-induced size truncation causing higher intraspecific competition among smaller sized fished who primarily feed on benthic prey (Svedäng and Hornborg, 2014). We detected negative effects of local (haul) density of cod, but not flounder. However, biomass density is not a direct measure of competition; areas with higher densities of cod and flounder could simply also have more food. Hence, we cannot rule out that that competition occurring, only that cod are not skinnier in areas with high density of flounder. To properly test for competition, we would need data of the benthic invertebrate community, which does not exist on this spatial and temporal resolution. Moreover, the proportion of *Saduria entomon* in the diet declined more (from average 0.18 to 0.09 across size all groups) in 2007-2013 relative to 1989-2006 than the decline in 1989-2006 relative to 1974-1988 (from 0.3 to 0.18) (Kulatska *et al.*, 2019). This is interesting because we find a stable (but low) condition in 2007-2013, when the proportion declined fastest. More studies need to be done to evaluate if the lasting low feeding rates of *Saduria entomon* in recent years are due to the high flounder densities and therefore to competition with flounder.

A reduced availability of sprat and herring (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 cascond (Gårdmark *et al.*, 2015). We found positive effects of sprat abundance at the ICES subdivision level, but not for herring. It is however unclear if the decline in sprat drove the decline in condition. Even though the spawning stock biomass of sprat declined from 1.9 million tonnes in the whole Baltic in 1994 to 1.05 million tonnes in 2006, most of the decline occurred in subdivision 26-28 whereas the condition of cod on the other hand has declined in the whole Baltic.

The last piece of evidence (although indirect) against a food-shortage for the decline in condition is that our model predicts a decline in condition for cod of all sizes. Hence, for the decline to still be related to competition or food availability, all food sources used by cod over ontogeny ought to have declined in synchrony, or that poor condition starts early in life due a shortage of a specific resource and that cod cannot compensate for that later in life. Even if that is possible, Neuenfeldt *et al.*, (2020) showed that the feeding levels of cod where relatively high in the period 1995-2004 when the decline in condition was the most rapid, and the growth rates had not yet declined to the lowest in seven decades (Mion *et al.*, 2021). Hence, a decade of deteriorating condition under normal feeding- and growth rates preceded the poor growth in recent years. That low feeding levels was not limiting cod in the mid 90’s in the midst of the steep decline in condition is in line with a recent finding that feeding rates may actually have increased, based on the N-content of otoliths (Svedäng *et al.*, 2020). This, to compensate for declines in the quality rather than quantity of food (Svedäng *et al.*, 2020).

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

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# **Author Contributions**

All authors contributed to the manuscript. Specifically, M.C. coordinated the study, M.L. prepared the raw data, M.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**

Chart, scatter chart

Description automatically generated

**Fig. 1.** A) Logarithm of the condition factor ( in Eq. 2) survey domain for years 1993-2019, acquired by predicting from the spatiotemporal condition model with all covariates held at zero (i.e., their means). 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) Coefficient of variation in Le Cren’s 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).

Chart, surface chart

Description automatically generated

**Fig. 2.** Predicted condition with all other non-spatially varying covariates set to zero (i.e., their means), such that the prediction corresponds to the depth, temperature, and oxygen-dependent log-condition factor for years 1993, 2001, 2008, 2018. For all years in the series, see *SI Appendix*, Fig. S8.

Table

Description automatically generated with low confidence

**Fig. 3.** Mean and 95% confidence interval of the standardized coefficients and the spatial and spatiotemporal standard deviation ( and , 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).

Chart

Description automatically generated

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

**Graphical user interface, diagram, application

Description automatically generated**

**Fig. 5.** A) Bathymetry of the study area, B) depth weighted by predicted cod density. Lines correspond to the 1st, 5th (i.e., median) and 9th decile. C) Oxygen concentration in space (using year 1999 as an example) (D) oxygen concentration weighted by predicted cod density. Lines correspond to the 1st, 5th, and 9th decile.