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

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**Abstract**

The body condition of fishes 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 1990’s, 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 spatial and spatiotemporal predictive-process GLMM that explicitly accounts for spatiotemporal autocorrelation with Gaussian Markov random fields, we analyse changes in condition and spatiotemporal distribution in relation to fine-scale habitat variables. We find that the body condition declined until 2006, after which a plateau was reached, and this occurred for both mature and immature cod. Environmental variables (oxygen, depth, temperature) had stronger effects on condition than ecological variables (density of cod and flounder reflecting competition, and pelagic prey such as sprat and herring). Moreover, cod appear to have moved into deeper and less oxygenated areas, which likely has contributed to the decline in condition over time as oxygen is positively associated with condition. Understanding the drivers of spatiotemporal variation in body condition is important for understanding the impacts of climate change and the role of species interactions on productivity and resilience of marine fishes.

**Key Words**

Condition, Spatio-temporal models, Density dependence, Deoxygenation

**Introduction**

The body condition describes the “plumpness” of an individual, or its weight relative to its length. It 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 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 to a link between declining body condition and global deoxygenation (declines in dissolved oxygen and the expansion of dead zones), fuelled 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 environmental and ecological variables can affect condition it is important to study their relative contribution to variation in condition in a common framework.

Furthermore, since modelling fine scale ecological data (such as variables affecting body condition, i.e., food availability and local environmental conditions) tends to result in correlated residuals, as these data are spatially and temporally correlated. Relatively recently have 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 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 on range shifts (Thorson *et al.*, 2015a) and density (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, respectively) explained more variation than density and temperature covariates in the California current ecosystem. Studies like these reveal the importance of accounting for spatial and spatiotemporal variation in condition for clarifying the sources of variation in body condition in relation to unmeasured variation and independent variables.

The Baltic Sea constitutes an interesting case study for disentangling ecosystem drivers affecting body condition. First, in the Eastern Baltic Sea cod stock, there has been negative trend in both body growth and body condition since the collapse of stock and the subsequent regime shift in the early 1990’s (Casini *et al.*, 2009; Möllmann *et al.*, 2009; Gårdmark *et al.*, 2015). This has compromised the stocks growth potential such that it is estimated to remain below the limit reference point where recruitment may be at risk – even in the absence of fishing (Mion *et al.*, 2018; Eero *et al.*, 2020). Second, the ecosystem has seen a major change in the abundance of both cod and its potential competitor European Flounder (*Platichthys flesus*), and in the distribution of its main pelagic prey species (sprat and herring). Lastly, the irregular inflows of saline and oxygenated water from the North Sea together with a long residence time (25-30 years) (Carstensen *et al.*, 2014) have contributed to it containing the largest anthropogenically induced hypoxic area in the world (Carstensen *et al.*, 2014). However, it remains unknown what the relative importance of these variables are, since they have not been analysed directly in a single framework, and not on a fine spatial scale.

In this study, we apply spatiotemporal predictive-process GLMMs to characterize spatiotemporal variation in body condition of cod in the Baltic Sea. We use data from the Baltic International Trawl Survey between 1991-2020, 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 (density of flounder, cod, availability of pelagic prey or oxygen concentration) provide a parsimonious fit to weight-length and (2) estimate the variation explained by these covariates and contrast that to variation explained by spatial and spatiotemporal variation.

**Materials and methods**

***Model description***

*Condition model*

We model condition by assuming weight varies log-normally around an average allometric function of length: , where is weight in grams, is length in cm, is the allometric length exponent and is the condition factor that we are seeking, in unit (Froese *et al.*, 2014). The condition factor is a better measure of condition than the commonly used Fulton condition factor as growth tends to be allometric (Ricker, 1975; Nash *et al.*, 2006; Froese *et al.*, 2014) rather than isometric (). If isometric growth is assumed but , the condition factor itself scales with size in proportion to (Le Cren, 1951). This can lead to bias if the size-distribution in the population has changed, which it has as in the Baltic Sea.

We fit this model as a spatiotemporal GLMM after taking the log on both sides:

(1)

(2)

where the degrees of freedom, , are set to 2 and is the standard deviation. We modelled the response (log of weight) using a Student-t distribution (eq. 1), because of the presence of extreme values. is a time-varying intercept (log condition factor):

(3)

and represent spatial and spatiotemporal random effects, respectively. is a vector of the k-th additional covariate and is its effect. is the length-coefficient, corresponding to the allometric exponent . Eq. 1 can be viewed as an approximation of Le Cren’s condition index (Thorson, 2015; Grüss *et al.*, 2020), as the log of the condition factor, i.e., or the constant in the allometric relationship, can be defined as:

(4)

Thus, eq. 2 is a model for a spatially and temporally varying condition factor.

*CPUE model*

In order to estimate the biomass-weighted average depth and oxygen concentration experienced by cod in the survey area, we fitted a spatiotemporal model to scientific catch data. As the data are in unit kg/h and hence positive and continuous, we assumed a Tweedie-distribution for the response variable:

(5)

(6)

where is a log-link function and the inverse link, is an independent mean for each year, is a smooth function for covariate and and represent spatial and spatiotemporal random effects, respectively.

*Spatiotemporal random effects*

The spatial and spatiotemporal random effects are drawn from Gaussian Markow random fields (Cressie and Wikle, 2015) with covariance matrices and :

(4)

. (5)

We further assume the spatiotemporal random effects to follow an AR1 process:

(6)

. (7)

The covariance () between spatial points and in all random fields is given by a Matérn function:

(8)

where is the spatial or spatiotemporal (marginal) variance.

*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 (Lindgren *et al.*, 2011) (Fig. S2), created using the R-package ’R-INLA’ (Rue *et al.*, 2009). We accounted for barriers (islands) in the survey area by implementing a barrier mesh, such that the correlation is lower over islands (Bakka *et al.*, 2019). 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 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’ (Andersen *et al.*, 2019; Anderson *et al.*, 2021). All code and data are publicly available at <https://github.com/maxlindmark/cod_condition> and will be deposited on Zenodo upon publication.

***Data***

To model the spatiotemporal development of cod condition and distribution, we acquired weight-at-length data and catch per unit effort data (CPUE) by length class, respectively, from the Baltic International Trawl Survey (BITS) between the years 1993-2019. Abundance data were converted to biomass (kg) in the CPUE model using the catch at length, and the estimated weight-length relationship from the (mean of all years) and coefficients in the condition model (eq. 2). Hauls in the Kattegat (west coast of Sweden) were excluded due to inconsistent coverage in the data. 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) survey is conducted, meaning sprat and herring abundance can be used as covariates. These data can be downloaded from <https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx>.

For both models (condition and CPUE model), covariates were chosen to reflect hypothesised drivers based on published literature. For the CPUE model we included depth, oxygen and temperature as covariates. The covariates for the condition model were (1) abundance of sprat and herring (Gårdmark *et al.*, 2015; Casini *et al.*, 2016a), available on a ICES rectangle (1° by 30') and ICES sub-division level; (2) haul- and ICES rectangle density of cod and flounder (abundance per trawled hour), representing intra- and interspecific competition for mainly benthic food resources (Svedäng and Hornborg, 2014; Orio *et al.*, 2019; Neuenfeldt *et al.*, 2020a); and (3) average sea bottom temperature and sea bottom concentration of dissolved oxygen in the fourth quarter, at the location of the haul (Casini *et al.*, 2016a, 2021; Limburg and Casini, 2019; Brander, 2020), derived from the ocean model NEMO-Nordic-SCOBI (Eilola *et al.*, 2009; Almroth-Rosell *et al.*, 2011; Hordoir *et al.*, 2019). In addition, we include depth, interactions between oxygen and depth, temperature and depth, and lastly oxygen and temperature as predictor variables. Depth data was 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.

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 of 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 variable selection because we judged the condition model was not more overfit than a model without any additional covariates. 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 model fit 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 () from -4.5 to -4.65 between 1993 and 2006, after which a plateau was reached (Fig. 1). This corresponds to a 16% decline in weight for a given length. Predictions from the condition model illustrate the presence of consistent “low spots” of condition in the deep areas of the eastern Baltic Sea (east of Bornholm, south of Gotland and between Öland and Gotland) (Fig. 2), but that the condition factor declines in whole area over time. The poor condition of cod in eastern deep areas could be due to the lower diversity and abundance of benthic food items and the lower concentrations of dissolved oxygen (Fig. 3). The covariates with the largest positive standardized effect sizes are oxygen, sub-division level sprat abundance and temperature (positive). Depth, interactions between oxygen and temperature, depth and temperature and depth and oxygen, and lastly sub-division abundance of herring are all negatively associated with condition (weight) (Fig. 3).

The standardized effect size for oxygen is 0.01, meaning for each unit increase in the standardized oxygen variable (i.e., 1 standard deviation or 1.8 ml/L), log weight increases by 1%. The average oxygen concentration in the environment (see Fig. 2 for a map) declined by approximately 0.18 ml/L or 0.007 ml/L year-1 between 1993 and 2019 (Fig. 4C). However, the average oxygen concentration experienced by the cod, calculated as oxygen concentration weighted by cod density as estimated from the CPUE model, declined by 0.7 ml/L or 0.027 ml/L year-1 on average) (Fig. 4C; see Fig. S4 for sub-division separately). This change alone is predicted to result in a decline in the log condition factor by 0.4% (which can be compared to the total decline in the log condition factor by about 3.2%). The faster decline in the experienced oxygen concentration is likely partially driven by the progressive deepening of the cod, going from an average of 46 m in 1993 to 51 m in 2019 – depths where there the difference in oxygen concentration is approximately 0.3 ml/L). Moreover, the negative interaction coefficient between depth and oxygen suggests that the negative effect of depth decreases for every unit decrease in oxygen, again highlighting the detrimental combination of deep areas poor in oxygen for condition.

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. Interestingly, the experienced temperature by the cod closely follows the trend in the environment (Fig. 4D), despite the deepening of the populations, suggesting the potential “cooling” from the deepening is offset by the general warming.

The abundance of sprat is positively related to body condition (Fig. 3), in line with the hypothesis that a lack of pelagic food has driven the decline in body condition. However, while the abundance of sprat has declined in abundance from the peak in the mid 1990’s overall in the entire Baltic Sea, the trends vary by sub-division (ICES; Fig. S5). Moreover, the density of cod has also declined (as also indicated by the CPUE model, Fig. 4A), and therefore there is no clear relationship between the ratio of cod to sprat over time (Fig. S6). Herring abundance on a sub-division level is estimated to have a negative effect on the weight of a cod given its length, meaning there is no support for lack of herring being the cause of the decline in body condition. This result did not change when fitting the same condition model to cod above 30 cm, a size group that is able to feed on the entire size-distribution of the herring (Niiranen *et al.*, 2019). In fact, most parameter estimates did not change considerably when fitting the condition model to cod below or above what is approximately maturation size (30 cm) (Fig. S7-8), and neither is there a clear relationship between model residuals and length (Fig. S3). This suggests the length-weight model is appropriate for all lengths of cod, the changes in the size-distribution of cod are accounted for and that the condition factor has declined within the whole cod population.

All variables related to density (catch per unit effort of cod and flounder by haul and ICES rectangle) had small effect sizes and confidence intervals overlapping 0. This suggests density-dependence or competition for food resources has had little effect on the decline of the cod condition. Fitting the model to fish below 30 cm (sizes believed to be more prone to competing for benthic resources with flounder) had only a small effect on the coefficients, with the flounder coefficient being more negative, but still with a small effect size and confidence intervals crossing zero.

Chart, histogram

Description automatically generated

**Fig. 1.** Predicted logarithm of the average condition factor ( in eq. 4) for years 1993-2020 from the spatiotemporal condition model while holding all covariates at 0. Vertical lines show the 95% confidence interval.

Calendar

Description automatically generated

**Fig. 2.** Spatial variation in the logarithm of the average condition factor ( in eq. 4) for years 1993-2020.

Table

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**Fig. 3.** Mean and 95% confidence interval of the standardized coefficients in the condition model.

Chart, scatter chart

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**Fig. 4.** Predicted average CPUE (kg/hour) from the spatiotemporal CPUE model (eq. 5-6) (A), CPUE-weighted average depth of cod in the Baltic Sea between 1993-2019 (B), CPUE-weighted average oxygen experienced by cod (C) and CPUE-weighted average temperature experienced by cod (D).

# **Discussion**

Using a fine-scale spatiotemporal condition model, we show that the weight given its length of cod in the Baltic Sea has declined by 16%, primarily between the years 1993-2006. Our analysis reveals 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. Furthermore, in contrast to recently proposed hypotheses (Svedäng and Hornborg, 2014; Neuenfeldt *et al.*, 2020a; Orio *et al.*, 2020), we were unable to detect clear effects food limitation in driving the changes in condition. These findings are discussed in more detail below.

Previous studies have suggested both direct (Limburg and Casini, 2019; Brander, 2020) and indirect effects (Neuenfeldt *et al.*, 2020a; Orio *et al.*, 2020) 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 experiencing oxygen concentrations at around 6 ml/L on average. This is higher than a recent estimate of 4.5 ml/L in recent years (for the eastern Baltic cod) (Brander, 2020; Casini *et al.*, 2021), which has also been proposed as a threshold for negative but sub-lethal physiological impacts (including reduced feeding rates) (Hrycik *et al.*, 2017). Our estimate did not differ when fitting the CPUE model to the eastern Baltic cod stock (subdivisions 24-32) separately (Fig. S9). This difference could be due to previous studies estimating oxygen levels indirectly, by calculating the average depths and then average oxygen at those depths. By contrast, 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 CPUE model. This should be a more precise approach, since the relationship between oxygen and depth is very variable. 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 levels is 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 European flounder for shared benthic prey species, such as the isopod *Saduria entomon*, due to the habitat contraction caused by the expansion of “dead zones” (Orio *et al.*, 2019; Haase *et al.*, 2020; Neuenfeldt *et al.*, 2020b). We did not include the extent of hypoxic areas not spatial overlap as covariate. Instead, we use the average density (CPUE) or flounder and cod at the haul and at the ICES rectangle-level to include “crowding” effects. Increased density dependence has also been linked to lower growth rates, though not via shrinking habitats, but fishery-induced size truncation causing higher intraspecific competition among smaller sized fished who primarily feed on benthic prey (Svedäng and Hornborg, 2014). We could not detect any effects of cod or flounder density for body condition (at neither scale), meaning cod are not skinnier in areas with higher density of cod or flounder. It does not, however, mean that competition is not occurring, because food levels relative to cod and flounder density could be more or less constant in space. To properly test for competition, we would need data of the benthic community, which does not exist on this spatial and temporal resolution. That said, it does not seem likely that the flounder has caused the decline in condition via competition, since the flounder population in subdivisions 24 and 25 declined steeply in the years where condition decline (mainly 1993-2006) (Orio *et al.*, 2017). 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 low feeding rates of *Saduria entomon* in recent years are due 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 (Gårdmark *et al.*, 2015; Casini *et al.*, 2016a). We find positive effects of sprat density at the ICES subdivision level, but it is 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 and the ratio of cod to sprat has remained stable in the time series (Fig. S6). 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 (as indicated from the model residuals; Fig. S3). Hence, in order for the decline to still be related to competition or food availability, all food sources utilized by cod over ontogeny ought to have declined more or less in synchrony. Even if that is possible, (Neuenfeldt *et al.*, 2020a) showed that the feeding levels of cod where relatively high in the period 1995-2004 when condition declined, and the growth rates had not yet declined to the lowest in seven decades (Mion *et al.*, 2021). Hence, a decade of declining condition under normal feeding- and growth rates preceded the poor growth we see today. That food limitation 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 provides new estimates for the development of the body condition of Baltic cod that can account for potential biases associated with the Fulton condition factor when there are simultaneous changes in size-structure and the length-weight exponent is not 3. We show, in line with (Casini *et al.*, 2016b), that the decline in body condition started in the early 1990’s and reached a bottom in the mid 2000’s, and that condition has declined for all sizes. These two features, together with analysis of covariates and recent studies reveal that food limitation likely has not driven the decline in body condition that preceded the decline in growth and the poor physiological status of the stocks. However, these factors can still limit a “physiological” recovery of cod in more recent years. 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 in recent years, when condition and growth rates are low, and mortality is high. The Eastern Baltic cod stock are not predicted to grow even in the absence of fishing mortality. This makes it even more important to understand the role of interactions between species for the development of the stock (Eero *et al.*, 2020).

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