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 environmental variables (oxygen, depth, temperature) have 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 move 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. They body condition of fishes is related to food intake rates and metabolic acticity, 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, oxygen and salinity) affecting ecosystem productivity and local habitat quality (Möllmann *et al.*, 2003; Morgan *et al.*, 2010; Grüss *et al.*, 2020). More recently, studies have pointed 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). Because of these multiple and sometimes interacting effects, it is important to further study their relative contribution variation in condition in order to make predictions on changes in condition from ecosystem changes (warming, species on the move etc.)

Variables affecting body condition (local environmental conditions, food availability) operate on a fine scale, yet they have often been analysed on a larger spatial scale. Modelling body condition on a fine scale however leads to spatially residual patterns, as the processes governing condition (local environmental conditions and food availability) are spatially and temporally correlated. Only 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) as well as estimates of 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.

In this study, we apply spatiotemporal predictive-process GLMMs to characterize spatiotemporal variation in body condition of cod in the Baltic Sea. Baltic Sea cod 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). Second, the ecosystem has seen a major change in the abundance of both cod and its potential competitor (European Flounder), 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). 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. End with a fitting concluding sentence.

**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 modeled 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 matricies 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. SX), 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 verticies (”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.*, 2020); 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 () of 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), as well as a consistently deteriorating average condition factor across 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), weight increases by 1%. The average oxygen concentration in the environment (see Fig. 2 for a map) declined by approximately 0.25 ml/L or 0.01 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 0.027 ml/L year-1 vs, respectively) (Fig. 4C; see Fig. SX-SX in appendix for sub-division separately). The faster decline in the experienced oxygen concentration is likely due to 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). Over the course of the time series, the average oxygen concentration declined by 0.7 ml/L. 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%). 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. The effect of oxygen did not change considerable when fitting the condition model to data east of 14° longitude (Fig. SX), corresponding to areas more exposed to de-oxygenation because of the deep basins.

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. This interpretation is based on the lack of relationship between the annual condition factor and the average annual temperature) (Fig. SX). Moreover, while the temperature has increased since 1993, the effect size is quite small. 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. 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. SX). Hence, the density of sprat likely has not contributed to the steep decline in body condition between 1993-2006.

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 responsible for 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 maturation size (Fig. SX), and neither is there a clear relationship between model residuals and length. 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.

Chart, histogram

Description automatically generated

**Fig. 1.**

Calendar

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**Fig. 2.**

Table

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**Fig. 3.**

Chart, scatter chart

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**Fig. 4.**

# **Discussion**

HELLO

Despite the concurrent de-oxygenation of coastal ecosystems and the known effects from experimental studies, support for effects of dissolved oxygen on fish condition in field conditions is limited (Chabot and Dutil, 1999). For instance, (Cavraro *et al.*, 2019) found no significant effect of dissolved oxygen on the body condition in the sand smelt *Atherina boyeri* in the Mediterranean, while expansion of hypoxic zones has been linked to the decline in the body condition of Atlantic cod (*Gadus morhua*) in the Baltic Sea (Casini *et al.*, 2016a, 2021; Limburg and Casini, 2019). Hence, it is critical to understand the impacts of global deoxygenation on the fitness of aquatic organisms.

Why deepening?

Stock population biology

While variables related to the extent of hypoxic areas correlate with a decline in body condition, the story in the Baltic Sea is more complicated than that. In fact, several interlinked density-dependent hypotheses have been put forward to explain the negative trend in body condition and growth starting after the collapse of the Eastern Baltic cod stock in the early 1990’s and the following regime shift (Casini *et al.*, 2009; Möllmann *et al.*, 2009; Gårdmark *et al.*, 2015). These include increased intra- and intraspecific competition for benthic prey, such as the isopod *Saduria entomon*, and lack of pelagic prey caused by changes in the spatial distribution of sprat (*Sprattus sprattus*). The former has been linked to fishery-induced size truncation of the cod stock increasing intraspecific competition (Svedäng and Hornborg, 2014), and a hypoxia-driven spatial range contraction causing an increased spatial overlap with the potential competitor European flounder (*Platichtys flesus*) (Casini *et al.*, 2016a; Orio *et al.*, 2019; Neuenfeldt *et al.*, 2020). Hypoxia has also been suggested to lower the condition of cod directly via physiological stress, including increased ventilation costs and lower food intake rates (Limburg and Casini, 2019; Brander, 2020).

Discussion points:

1. Using a new model, we show that the condition factor of cod in the Baltic Sea has declined with 10%. Of all the considered variables, declines in ambient dissolved oxygen conditions via deoxygenation and deepening explains most of the change in condition through time, though it explains not all of the effects. It seems that the positive effect of sprat is a spatial result, because over time, yes the sprat has moved but the cod has also declined, so the sprat per cod is relatively stable over time.
2. We also calculate the population average ambient oxygen levels (first look at population average experienced oxygen concentration, instead of looking at depth interval and then looking at oxygen at that depth as in Brander, 2020). We find that the ambient levels at the end of the time period (now) are very close to what has been found to impact their physiology and likely many cod do experience oxygen levels below 4.5 ml/l, which has experimental research has shown impacts their physiological performance. We also know that since 2010, the decline in oxygen in ICES sub-division 25 in the Baltic is 2 ml/l per decade! Hence, it seems that they are at the physiological edge in that sub-area, especially considering that oxygen solubility in water decreases (Benson and Krause, 1984), whereas fish metabolism increases (Fry, 1971), and the Baltic Sea is one of the fastest warming ocean regions (Belkin 2009)
3. Our approach reveals spatial structure in the body condition and change in body condition over time.
4. How do our findings relate to other studies (mostly on growth, so also need to explain that difference?

**Svedäng** 2020: They eat a lot still, so maybe it’s some kind of vitamin deficiency?

**Overgård**: If we feed them herring they growth really well

**Engelhart**: Tiamin def, but no time series

East-west difference in growth: **McQueen** (2020)

Long term changes in tagged cod growth: **Mion** (soon)

**Parasites**: Horbowy and/or Ryberg (see if any interesting there)

**Neuenfeldt**: If they would be scarce (and limiting), we should find that areas with little more sprat gives higher condition, and less flounder e.g. We also know that they undergo strong ontogenetic shifts in diet, so if it was down to a specific prey that should come out as a size-signal.

**Chabot, Neuenfeldt & Brander**: Neuen get stuck on extrapolating the specific, missing the overall effects of hypoxia (can’t extrapolate from these different ecosystems exact numbers). Further, if competition, we should see negative effects of density (or the rescaled variable). Moreover, we do not find a clear size-based difference, because there’s no pattern in the residuals (indicating it’s not related to ontogenetic niche shift). Could be a result stemming from NOT using Fultons, but Neuendfeldt uses growth though. This is in line with Mion (et al) in prep, which show negative declines for all sizes.

**Haase:** even in the title we see flounder stealing food…

**Saduria?** In discussion point: assuming they haven’t changed their distribution (tough assumption but we can’t overcome it right now), we can extract the raster value for saduria from Gogina each year, and see if the average overlap has changed. For that we would need a cod-distribution map, which we could easily do. Then the question is: can we assume saduria hasn’t changed their distribution? Not really… Without invoking all this, we can use the verbal argument that cod are now in deeper areas and there there’s no flounder nor saduria (AND THE POINT ABOUT NOT BLAMING FLOUNDER! IDENTIFY THAT AS A KNOWLEDGE GAP… BASICALLY; SPATIOTEMPORAL HAASE MODEL). SUMMARY: can we use the Gogina map as a raster to see how much cod has moved into average saduria habitat?

Re. Saduria data. We don’t really know if it even has decreased… The master’s thesis used BITS data, which aren’t reliable before 2013 (pers comm mich). So not really sampled properly. That data are also available on ICES ecosystem services. SMHI has too few sample stations per year, and the data from Mattias Sköld is only coastal basically. One option is to ask about the Gogina paper. BUT! Saduria doesn’t exsist in the Western Baltic Sea - too salty! So, if we can get a hold of Saduria, that would mean we should probably focus our efforts on that part (also remove barrier spde). But if we find similar declines in condition also there, that implies the Saduria-effect isn’t likely the main effect!

1. Management implications? Could mean that suggest spatial fisheries of sprat and herring would be limited in effect (Eero & Cardinale open for that). Could cite Mion and Casini 2016 on inclusion of biological knowledge for assessment.
2. Implications and outloot: it’s not looking great from physiological standpoint (oxygen and temperature) with the ongoing climate change.

Read how oxygen affects metabolism, e.g. here: <https://www.sciencedirect.com/science/article/pii/S1546509808000101>

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