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, these variables have only been evaluated on large spatial scales (Baltic Sea basin- or population level), even though they operate on smaller scales. 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 and food), and that cod are moving to deeper and less oxygenated areas, which can explain the decline in condition over time. Understanding the drivers of spatiotemporal variation in body condition is important for understanding the impacts of climate change on productivity and resilience of marine fishes.

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# **Introduction**

Global warming and nutrient enrichment have contributed to a reduction in dissolved oxygen levels and the expansion of dead zones in coastal marine ecosystems worldwide (Diaz, 2001; Breitburg, 2002; Diaz and Rosenberg, 2008; Carstensen *et al.*, 2014). Extreme hypoxia (low dissolved oxygen) leads to a direct loss of fauna from increased mortality (Diaz and Rosenberg, 1995; Sampaio *et al.*, 2021), and causes habitat compression, which forces organisms to occupy sub-optimal habitats and suffer effects of density dependence (Diaz and Rosenberg, 2008; Orio *et al.*, 2019; Gogina *et al.*, 2020). Even milder hypoxia can alter individual physiology by imposing metabolic constraints on organisms (Kramer, 1987; Chabot and Dutil, 1999; Claireaux *et al.*, 2000; Hrycik *et al.*, 2017; Sampaio *et al.*, 2021). Hence, it is critical to understand the impacts of global deoxygenation on the fitness of aquatic organisms.

Experimental studies show that fishes lower their food intake rates during hypoxic conditions. This is likely to avoid overshooting the oxygen budget when processing food, which can lead to declines in growth rates (Chabot and Dutil, 1999; Thetmeyer *et al.*, 1999; Pichavant *et al.*, 2001) and body condition. The body condition describes the “plumpness” of an individual and reflects accumulated energy reserves (Beverton and Holt, 1957; Ricker, 1975; Nash *et al.*, 2006). Hence, condition is often positively associated with fitness (Morgan *et al.*, 2010; Thorson, 2015), and individuals with high condition have greater reproductive success (Hislop *et al.*, 1978; Marshall and Frank, 1999). 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). Therefore, it is important to study the effects of the ongoing de-oxygenation of marine coastal areas on body condition of fishes.

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). The Baltic Sea constitutes an interesting case study for studying the impacts of hypoxia, because it is a semi-enclosed brackish arm of the Atlantic Ocean that contains the largest anthropogenically induced hypoxic area in the world (Carstensen *et al.*, 2014). Factors that make the Baltic Sea exposed to hypoxia is 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).

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).

The association between these covariates and body condition has previously been analysed using average values over large spatial scales (basin level), despite that these hypothesised density-dependent processes operate on a finer 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 Eastern Baltic cod. 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.

***Model selection and comparison***

We conducted exploratory analysis without the main covariates to decide on a candidate baseline model. This was done in three steps: (1) deciding on an appropriate distribution for the residuals (2) compare models with different number of “knots” to ensure model convergence and that the spatial processes were accurately captured and (3) whether or not to include year as a fixed effect or a spatial random field of slopes of year effects, as well as including an independent spatiotemporal field for each year or if there is support for a spatiotemporal field following an AR1 process.

Next we evaluated the ability of covariates to explain spatial variation in condition.

***Data***

To model the spatiotemporal development of cod condition, we acquired weight-at-length data from the Baltic International Trawl Survey (BITS) between the years 1993-2019. 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.

***Covariates***

Covariates were carefully selected to represent a hypothesized driver of variation in condition, and is likely to explain at least some variation (Table 1). Following (Thorson, 2015; Grüss *et al.*, 2020), we rescale all covariates to have a mean of 0 and a standard deviation of 1, which allows for comparison between the estimated coefficients and the standard deviation of spatial () and spatiotemporal variation ().

*Table 1. Summary of covariates and the corresponding hypothesized effect on cod condition.*

|  |  |  |  |
| --- | --- | --- | --- |
| **Covariate** | **Driver/Hypothesis** | **Reference** | **Source** |
| Cod catch-per-unit effort by haul (#/h) | Increases intraspecific competition | (Svedäng and Hornborg, 2014) | BITS |
| Flounder catch-per-unit effort by haul (#/h) | Increases interspecific competition for benthic food sources | (Orio *et al.*, 2019; Neuenfeldt *et al.*, 2020) | BITS |
| Oxygen concentration | Affects spatial extent of habitat thus inter- and intraspecific competition; direct effect on physiological processes; direct effect on benthic food availability (e.g. Saduria) | (Casini *et al.*, 2016a) | CMEMS (NEMO-Nordic-SCOBI) |
| Sprat abundance per ICES rectangle of haul (#/1° by 30' rectangle) | Increases food levels for piscivorous cod | (Gårdmark *et al.*, 2015; Casini *et al.*, 2016a) | BIAS |
| Herring abundance per ICES rectangle of haul (#/1° by 30' rectangle) | Increases food levels for piscivorous cod | (Casini *et al.*, 2016a) | BIAS |

# **Results**

# **Discussion**

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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