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

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**Abstract**

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# **Introduction**

The relationship between length and weight has a long tradition in fisheries science. From it, body condition indices can be calculated (Beverton and Holt, 1957; Ricker, 1975; Nash *et al.*, 2006), which describe the “plumpness” of an individual, or its weight relative to its length. Hence, condition is related to accumulated energy reserves and often positively associated with fitness (Morgan *et al.*, 2010; Thorson, 2015). For instance, 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). Because of the link between condition and physiological status, and the availability of length-weight data, body condition constitutes a valuable index for evaluating changes in productivity of fish stocks (Thorson, 2015; Grüss *et al.*, 2020).

Being related to energy reserves, condition can vary seasonally due to maturation, migration, reproduction and overwintering (Bromley, 2000; Dutil and Lambert, 2000; Yaragina and Marshall, 2000). Interannual variation in condition is affected by both density dependent, such as variation in population density, affecting intra- and interspecific competition for a limiting food source (Cardinale and Arrhenius, 2000; Casini *et al.*, 2006; Grüss *et al.*, 2020), and density independent factors, such as environmental conditions (e.g. temperature and salinity) determining productivity and local habitat quality (food availability) (Möllmann *et al.*, 2003; Morgan *et al.*, 2010; Grüss *et al.*, 2020). In both cases, variation in condition is attributed to changes in food availability. Moreover, plankton, benthic organisms and small pelagic fish, are patchily distributed (Omori and Hamner, 1982; Bergström *et al.*, 2002; Boyd *et al.*, 2015; Greer *et al.*, 2015), and local densities can be governed by species interactions (Bergström *et al.*, 2002). Hence, spatially correlated density dependent and independent factors can lead to spatially correlated variation in condition. However only relatively recently have spatiotemporal models been applied to study variation in condition (Thorson, 2015; Grüss *et al.*, 2020).

By including spatial random effects through Gaussian random fields in a GLMM framework, spatially correlated residual variation can be accounted for, and the magnitude of spatial or spatiotemporal variation can be directly compared to other covariates (Thorson, 2015; Grüss *et al.*, 2020). In the first such application, (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. Moreover, these covariates did not have consistent effects across species. Using a similar modelling approach, but where condition and density were simultaneously estimated in a multivariate framework, (Grüss *et al.*, 2020) showed that spatial variation in temperature had positive associations with condition in general in the Eastern Bering Sea and density negative. These studies reveal the importance of accounting for spatial and spatiotemporal variation in condition, and clarify the sources of variation in body condition.

The growth and body condition of Eastern Baltic cod (*Gadus morhua*) has declined steadily since the early 1990’s, which corresponds to a period after the collapse of the cod stock and a regime shift (Casini *et al.*, 2009; Möllmann *et al.*, 2009; Gårdmark *et al.*, 2015). Several hypotheses have been put forward to explain this trend. A growth bottleneck has been proposed to be induced by increasingly size selective fishing pressure on large cod during the rebuilding of stock after its collapse in the early 1990s, causing a size-truncation of the population and increased intraspecific competition among individuals below maturation size (Svedäng and Hornborg, 2014). It has also been linked to changes in the spatial distribution of species. A range contraction of the cod population driven by an increase in hypoxic areas, has been hypothesized to cause an increased competition with European flounder (*Platichtys flesus*) for benthic prey, such as the isopod *Saduria entomon* (Casini *et al.*, 2016a; Neuenfeldt *et al.*, 2019; Orio *et al.*, 2019). Oxygen also modulates several physiological processes that could affect body condition, including increased ventilation costs and lower food intake rates (). Reduced spatial overlap with pelagic prey (sprat, *Sprattus sprattus*) has also been suggested to cause declines in food availability and by extension, condition (Casini *et al.*, 2016a). However, the effects of these covariates on condition have previously been evaluated on larger spatial scales (e.g. averages over sub-division or in across short time scales) and the variation explained by these variables have not been compared directly on a fine spatial scale.

In this study, we apply spatiotemporal predictive-process GLMMs to characterize spatiotemporal variation in body condition of Eastern Baltic cod. We use Le Cren’s condition index (Le Cren, 1951), which defines condition as the residuals from a fitted length-weight regression. Hence, it allows for allometric growth, i.e. a length-exponent slightly larger than 3 (as is often observed in fishes) (Froese *et al.*, 2014), in contrast to Fulton’s condition factor which assumes isometric growth (weight being related to the length cubed) (Ricker, 1975; Nash *et al.*, 2006). 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**

*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 1991-2020. Hauls north of 58° and west of 12.5° and in the Kattegat (west coast of Sweden) were excluded due to inconsistent coverage in the data and because they represent a different cod stock with no mixing with the Eastern Baltic cod, as in (Orio *et al.*, 2019). We used only data from the fourth quarter, which corresponds to the main growing and feeding season (Aro, 1989) and the quarter in which the Baltic International Acoustic Survey (BIAS) survey is conducted and therefore biomass estimates of pelagic fish used as covariates are available, following (Casini *et al.*, 2016a).

*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 | (Neuenfeldt *et al.*, 2019; Orio *et al.*, 2019) | BITS |
| Oxygen concentration | Affects spatial extent of habitat thus inter- and intraspecific competition; direct effect on physiological processes | (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 |

*Model description*

In fishes, weight is typically assumed to vary 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 in unit (Froese *et al.*, 2014). Typically this relationship is linearized by taking logs on both sides: . Le Cren’s condition index is defined as the residuals from this length-weight relationship. We model this individual-level relationship with a spatiotemporal GLMM of the form:

(1)

Where is the female condition factor, is the offset for males and for unsexed individuals. and represent spatial and spatiotemporal random effects, respectively. is a matrix of measured *additional* covariates and is the effect of the -th additional covariate. is the length-coefficient, corresponding to the allometric exponent. The spatial random effects are assumed to be drawn from a multivariate normal distribution:

(2)

the spatiotemporal random effects to be drawn from a multivariate normal distribution following an AR1 process:

(3)

In the spatial and spatiotemporal random fields, and are covariance matricies, where the covariance between spatial points and is given by a Matérn function:

where is the spatial (marginal) variance. This model (Eq. 1) can be viewed as an approximation of Le Cren’s condition index (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. 1 is a model for a spatially and temporally varying condition factor.

*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.

*Model fitting*

We fit GLMMs with the R-package ‘*sdmTMB’* <https://github.com/pbs-assess/sdmTMB>, which utilises Template Model Builder ([TMB](https://github.com/kaskr/adcomp)), [R-INLA](http://www.r-inla.org/), and Gaussian Markov random fields for representing spatial and spatiotemporal random effects.

Code for reproducing data processing and model fitting is publicly available at <https://github.com/maxlindmark/cod_condition> and will be deposited on Zenodo upon publication. Data can be sent on request or downloaded directly from DATRAS <https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx> and processed as described in the available code.

# **Results**

# **Discussion**

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