Evaluating drivers of spatiotemporal changes in fine scale individual condition of a bottom-associated marine fish

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**Key Words**

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

**Abstract**

A fish’s body condition is described by its 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 or even survival of the population. Several hypotheses have been proposed (e.g., competition, hypoxia, lack of prey) and evaluated temporally using averages over large spatial scales (basin or population level). However, as these variables operate at local spatial scales and are heterogenous in space, it is important to evaluate the link between body condition and covariates on local scales as well. By applying a geostatistical model that includes spatially and spatiotemporally correlated random effects using Gaussian Markov random fields, we analyze the body condition of cod in the autumn (main feeding season) in relation to biotic and abiotic covariates at different scales and their spatiotemporal dynamics. We find that body condition declined over the whole domain until 2008, after which a plateau was reached. Oxygen, sprat biomass (at the subdivision level), haul-level temperature, and the biomass of the benthic isopod *Saduria entomon* (to a lesser extent) where positively related to condition, whereas the haul-level density of cod and depth were negatively associated with condition. However, the effect sizes of these variables were small, such that even though cod are now found in deeper and less-oxygenated waters, this could not alone explain the steep decline that occurred between 1993–2008. In fact, latent spatial and spatiotemporal variation was several times larger in magnitude than any single covariate’s coefficient. Moreover, spatial and spatiotemporal random effects explained 6.5 times more variation than all fixed effects, suggesting there are still missing latent factors. Understanding the drivers of spatiotemporal variation in body condition, which affects mortality and reproduction, is critical for understanding the impacts of environmental change and for the management of marine fish and fisheries.

**Introduction**

Body condition is a morphometric index that describes the “plumpness” of an organism, or its weight relative to its length (Nash *et al.*, 2006; Thorson, 2015). It is related to food intake rates and metabolic activity, and is 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).

Because of the link to food consumption, 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; Thorson, 2015; Grüss *et al.*, 2020). Condition has also been linked to environmental variables, (e.g., temperature, salinity) affecting ecosystem productivity and local habitat quality (Möllmann *et al.*, 2003; Morgan *et al.*, 2010; Thorson, 2015; Grüss *et al.*, 2020). More recently, studies have found a link between declining body condition and deoxygenation (often resulting in the expansion of dead zones causing habitat degradation and compression) (Casini *et al.*, 2016a, 2021), fueled by warming and nutrient enrichment (Diaz, 2001; Breitburg, 2002; Diaz and Rosenberg, 2008; Carstensen *et al.*, 2014). However, reduced oxygen concentrations also cause lower food intake rates due to lower metabolic rates, which can occur even during milder hypoxia (Kramer, 1987; Chabot and Dutil, 1999; Claireaux *et al.*, 2000; Hrycik *et al.*, 2017; Sampaio *et al.*, 2021). As both environmental and biological variables can affect condition, it is important to study their relative contribution to 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 fish 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’ (Rue *et al.*, 2009; Lindgren *et al.*, 2011). 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 density 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 (hereafter referred to as cod), 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 benthic prey *Saduria entomon* (Haase *et al.*, 2020; Neuenfeldt *et al.*, 2020), the flounder complex (European flounder *Platichthys flesus* and Baltic Flounder *Platichthys solemdali*) (Orio *et al.*, 2017), as well as an increase in abundance of its main pelagic prey species (sprat *Sprattus sprattus* and herring *Clupea harengus*) in northern areas where cod are scarce (Casini *et al.*, 2011; Eero *et al.*, 2012; ICES, 2021a). 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). It is also one of the fastest warming regional seas (Belkin, 2009; Reusch *et al.*, 2018). Previous studies have linked changes in mean condition of cod over large spatial scales to single or multiple ecosystem drivers (Casini *et al.*, 2016a, 2021; Orio *et al.*, 2020). However, the effects of environmental and biotic covariates have not been studied on local scales, and effect sizes of covariates have not been compared in a standardized manner.

In this study, we apply geostatistical GLMMs to characterize the spatiotemporal variation in body condition and distribution of cod in the south-eastern Baltic Sea. We use data from the Baltic International Trawl Survey between 1993–2019, which corresponds to a period of initially high but then deteriorating cod condition (Casini *et al.*, 2016a). We then seek to (1) identify which set of covariates (biomass densities of flounder, cod, and *S. entomon* (benthic prey) and biomass of sprat and herring (pelagic prey), as well as depth, oxygen concentration and temperature) can explain variation in weight given length and (2) explore the role of changes in the spatiotemporal distribution for the trends in body condition.

**Materials and methods**

***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 the International Council for the Exploration of the Sea (ICES) subdivisions 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 kg/km2 using a TVL trawl with 75 m sweeps (note that compared to Orio *et al.* (2017), we further express density in kg/km2 instead of kg in 1 trawling, sweeping an area of 0.45 kg/km2 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 (mid October to mid December), 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>.

***Estimating spatiotemporal development of body condition and biomass density***

*Condition model*

We modelled condition using a spatiotemporal version of Le Cren’s relative condition index (). This is defined as the ratio between the observed weight for individual fish , caught in time at space , and the predicted weight. The predicted weight was given by the relationship , where parameters and were estimated in a non-spatial model with all years pooled, tro represent the average weight prediction. Unlike Fulton’s K, this relative condition index does not rely on the assumption that growth is isometric (), which, if violated, leads to bias when comparing condition of different lengths as the condition index scales in proportion to (Le Cren, 1951).

To assess the ability of covariates to explain variation in condition, we fit a geostatistical GLMM to the spatiotemporal Le Cren index, assuming - distributed residuals (with 5 degrees of freedom) due to the presence of extreme values:

where represents the Le Cren condition factor at space (a vector of two UTM zone 33 coordinates) and time , represents the mean weight, and represents the scale parameter. The parameter (Eqns. 2-4) 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. represents a vector of the -th additional covariate (biomass densities of flounder and cod, biomass of sprat, herring and *Saduria entomon*, depth, oxygen concentration and temperature) and is its effect. The parameter (Eq. 5) represents spatial random effects. (Eqns. 6-7) represents spatiotemporal random effects, and we assume it follows a stationary AR1 process, where 𝜌 represents the correlation between subsequent spatiotemporal random fields. Spatial and spatiotemporal random effects 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.

*Density models*

We fit spatiotemporal GLMMs to biomass density data in a similar fashion as for condition to 1) evaluate how the depth distribution, temperature and oxygen conditions experienced by cod have changed of the Baltic cod and 2) 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.

We modelled densities using a Tweedie distribution, as density is both continuous and contains 0 values (Tweedie, 1984; Shono, 2008; Anderson *et al.*, 2019):

where represents density (kg/km2) 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 penalized smooth function for covariate and and represent spatial and spatiotemporal random effects. and have the same definition as in the condition model (Eq. 5-7).

***Covariates***

For both models (condition and density model), covariates were chosen to reflect hypothesized drivers based on published literature. For the condition model, we included covariates at spatial scales that roughly reflect the habitats cod would have been exposed to during the seasonal build-up of energy reserves. 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 (1° by 30', *SI Appendix* Fig. S1) (Hüssy *et al.*, 2020). Therefore, we included environmental and biological demersal covariates (sea bottom temperature [], sea bottom oxygen [ml/L], depth [m], and biomass density of cod and flounder [kg/km2] and *S. entomon* [mg/m2]) at the haul and the median over the ICES rectangle-level, and the pelagic covariates at the ICES rectangle- and subdivision-level (as pelagic species are highly mobile). Biomass of sprat and herring (tonnes) were extracted from the ICES WGBIFS database for the BIAS survey data (https://www.ices.dk/community/groups/pages/WGBIFS.aspx). Monthly predictions for sea bottom temperature and sea bottom concentration of dissolved oxygen where extracted at the haul locations from the ocean model NEMO-Nordic-SCOBI (Eilola *et al.*, 2009; Almroth-Rosell *et al.*, 2011; Hordoir *et al.*, 2019) and averaged for October–December. 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 *S. entomon* were extracted from a habitat distribution model using the modelled hydrographical data from the regional coupled ocean biogeochemical model ERGOM (Gogina *et al.*, 2020; Neumann *et al.*, 2021). Biomass densities of cod and flounder (kg/km2) were taken from the same scientific survey as the condition data (BITS). We used predicted densities from GLMMs (described above) as covariates, since not all hauls in the CPUE (density) data could be standardized and joined with the condition data. For the cod density models used to evaluate changes in the average depth, oxygen concentration and temperature, we used these variables as covariates. For the cod and flounder models that were used to predict covariates for the condition model, the only covariate was depth.

Following Thorson (2015) and 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 marginal 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 from stepwise selection (e.g., Whittingham *et al.*, 2006) and because initial analyses suggested the model was not overfit (see *SI Appendix,* Fig. S2 for Pearson correlation coefficients across variables).

*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. S3, 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. We fit the models using ‘TMB’ (Kristensen *et al.*, 2016) via the R-package ‘sdmTMB’ (version 0.0.21.9006) (Anderson *et al.*, 2019, 2021, 2022) with maximum marginal likelihood and the Laplace approximation to integrate over random effects. We assessed convergence by confirming that the maximum absolute gradient with respect to all fixed effects was < 0.01 and that the Hessian matrix was positive-definitive. Model residuals are shown the *SI Appendix* (Figs. S4-S8 and S13-S16). We used packages in the ‘tidyverse’ (Wickham *et al.*, 2019) for data processing and plotting.

# **Results**

The condition model revealed a decline in the Le Cren condition factor of 14% [17%, 11%] (values in brackets are the 2.5% and 97.5% quantiles from 500 draws from the joint precision matrix). It declined from approximately 1.11 to 0.95 between 1993 and 2019 (the decline leveled off in around 2008) (Fig. 1B). The condition factor declined the most in the northern subdivisions (i.e., 27 and 28) and the least in the south-western subdivision 24. The median Le Cren’s condition index declined at the same rate as the 1st and 9th decile (Fig. 1A), meaning that the decline in the condition index 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. The spatial predictions from the condition model illustrate the presence of consistent “low spots” of body condition in deep and low-oxygen areas, and that the condition factor declined in the whole area over time (Fig. 2, *SI Appendix*, Fig. S9).

The covariates with the largest positive standardized effect sizes on condition factor were temperature at the haul level (0.009 [0.004, 0.014]) (values in brackets indicate 95% confidence interval), median depth of the ICES rectangle (0.01 [0.004, 0.02]), oxygen concentration at the ICES rectangle level (0.01 [0.002, 0.016]), and biomass of sprat at the ICES subdivision level (0.007 [0.002, 0.013]) (Fig. 3). Depth at the haul level was negatively associated with condition (-0.023 [-0.027, -0.02]) (see *SI Appendix*, Fig. S10, for marginal effects plots). The biomass density of cod and flounder, and the biomass of herring did not affect the condition of cod at any scale (Fig. 3). The magnitude of any individual covariate effect size was generally small. In fact, these effect sizes were several times smaller than the magnitude of latent spatiotemporal and spatial variation (Fig. 3). Using the approach proposed in Nakagawa and Schielzeth (2013), we calculated marginal for fixed and random effects, and found that fixed effects had a marginal of 0.039, while random effects had a marginal of 0.27 (of which the time-varying intercepts, spatial random effects and spatiotemporal random effects contributed with 0.06, 0.07 and 0.14, respectively). This suggests considerable variation in space and time due to latent factors, as well as changes of spatial variation through time, that cannot be explained by available covariates.

We conducted a sensitivity analysis by fitting the condition model to different parts of the data. The different models where: only cod above 30 cm, below 30 cm, omitting subdivision 24 (the mixing zone with western Baltic cod), and including only grid-points with cod above a certain threshold when calculating median variables across the ICES rectangle. (*SI Appendix,* Fig. S11). However, the model coefficients were similar across all models.

The median depth and oxygen (depth and oxygen in the environment weighted by the predicted biomass density of cod at location, Fig. 4C) got deeper or declined throughout the time period (Fig. 5C-D), though the population again occupied slightly shallower waters in the last 3 years of the time series (see *SI Appendix*, Fig. S19-S21 for results split by subdivision, Fig. S24 for the corresponding analysis on temperature, and Fig. S18 for a marginal effects plot of the biomass density model).

The standardized effect size for oxygen was 0.0035, meaning that for each unit increase in the standardized oxygen variable (i.e., 1 standard deviation or 1.85 ml/L), the Le Cren condition factor increased by 0.35%. 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. The biomass-weighted oxygen concentration declined more steadily (approximately 1 ml/L between 1993 and 2019). The change in experienced oxygen corresponds to a change in condition slightly larger than half a standard deviation, and oxygen trends vary in space whereas condition declined everywhere (*SI Appendix*, Fig. S9, S19-S20).

# **Discussion**

The body condition of fish depends on recent energy accumulation and is therefore largely shaped by the quality of the habitat the fish has occupied. By using a spatially explicit condition model, we can link the condition of Eastern Baltic cod to covariates at different ecologically relevant spatial scales. Our model reveals that the Le Cren condition factor declined by 14%, in 1993–2019, with the majority of this decline occurring 1993–2008. Moreover, while there are persistent low-spots of body condition (in the deep and low-oxygen areas), the condition declined in the whole area, which suggests there are drivers acting on large spatial scales. While we identify changes in the spatiotemporal distribution of cod that could have led to poorer environments experienced by cod (deeper areas with less oxygen), effect sizes of single covariates are overall small and latent spatial and spatiotemporal variation is several times larger in magnitude and explain more variation in the condition factor.

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 their ability to accumulate energy reserves reduces. First, we find that the Baltic cod are currently experiencing oxygen concentrations at around 6.3 ml/L on average (1st and 3rd quartile are 4.5 and 7.2). In subdivision 25 we estimate it to be around 6.5 (*SI Appendix,* Fig. S19). This is higher than recent estimates of 4–4.5 ml/L as an average oxygen concentration based on oxygen levels at the mean depth of the cod population in the recent years (Brander, 2020; Casini *et al.*, 2021). 4.3 ml/L has been proposed as a threshold for negative but sub-lethal physiological impacts, including, but not limited to, reduced feeding rates (Chabot and Dutil, 1999; Hrycik *et al.*, 2017). The difference in our estimate compared to previous studies are because we use oxygen concentration from the ocean model NEMO-Nordic-SCOBI which is sea bottom oxygen, and instead of calculating average oxygen at the mean depth of cod, we weight the oxygen in the environment by the predicted densities from the density model. This approach overcomes the issue that oxygen concentrations span a large range for any given depth. Moreover, the decline in oxygen in subdivisions 25 and 26 is relatively stable over time, while the condition declined considerably there. This result is in accordance with Svedäng *et al.* (2022), who found that the area of well-oxygenated sea floor remained stable in core distribution area of cod in the time period of a rapid decline in condition. We also note that the 1st quartile of the density-weighted oxygen concentration reached an all-time minimum (approximately 4.5 ml/L in 2007), and then increased, suggesting the average decline in oxygen concentration is not driven by the cod experiencing the lowest oxygen concentrations. Despite the median oxygen concentrations experienced by the population being above the proposed thresholds, we still find a positive effect of oxygen, in line with previous studies showing that exposure to low-oxygen areas is associated with low condition (Limburg and Casini, 2019; Casini *et al.*, 2021). However, we can only speculate if this is due to oxygen being correlated with richer habitats that feature higher food availability, or if there are direct physiological impacts at lower threshold in the wild.

An indirect effect of declining oxygen is the potential amplification of competition with other cod and/or flounder for shared benthic prey species, such as the isopod *S. entomon*, due to habitat contraction caused by the expansion of “dead zones” (Casini *et al.*, 2016a; Orio *et al.*, 2019; Haase *et al.*, 2020). To address the potential effects of changes in intra- and inter-specific competition, we used predicted density of flounder and cod at the haul- and at the ICES rectangle-level as direct effects of density. 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 a weak negative effect of cod haul-level density, but not for flounder at any scale. The lack of clear signals of competition could be because the biomass of both cod and flounder being at relatively low levels, from a historical perspective (Tomczak *et al.*, 2022). However, biomass density is not a direct measure of competition; areas with higher densities of cod and flounder could simply also have more food. Lastly, we did not find strong effects of *S. entomon* density on condition. Even without strong evidence of benthic competition as a driver of cod condition overall, it could still be important on local scales, i.e., in habitats with *S. entomon* and flounder. Future studies could investigate the effect of benthic competition for local differences in condition—ideally in combination with benthic prey biomass estimates.

A reduced availability of sprat (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). In our study, using spatially resolved data, we also found positive effects of sprat biomass on cod condition at the ICES subdivision level, which was not observed for herring. It is however unclear if the decline in sprat drove the decline in condition. Even though the spawning stock biomass of sprat generally declined from the levels in the early 90’s, both the abundance and steepness of the decline differ between subdivisions. For instance, while the decline in sprat was steepest in subdivisions 27 and 28, sprat is still most abundant in subdivision 28, while cod biomass in 27 and 28 is very low (Fig. 4; *SI Appendix*, Fig. S22).

The fact that cod condition has declined in all areas—even though prey densities (e.g., *S. entomon*) vary geographically and condition has also declined in regions where high abundance of prey remains—suggests that several variables and driving processes have been involved. The decline could still be related to competition or food availability, of multiple prey. However, Neuenfeldt *et al.*, (2020) showed that the feeding levels of cod between 21–30 cm where relatively high in 1995–2004, when the decline in condition was the most rapid. The growth rates in that period, however did not yet reach the observed minimum (Mion *et al.*, 2021). That low feeding levels were not limiting cod in the mid 90’s during 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). Those increased feeding rates could be an attempt to compensate for declines in the quality rather than quantity of food (Svedäng *et al.*, 2020).

In conclusion, our study illustrates fine-scale spatiotemporal development of body condition in the eastern Baltic cod, and population-level changes in depth distribution and oxygen concentrations. We show, in line with Casini *et al*., (2016a), that the decline in body condition started in the early 1990s and reached a low in the mid 2000s, and that condition has declined in all areas. The small effect sizes of the single covariates we used based on existing literature, analyzed for the first time in a common framework, suggest that multiple factors are responsible for the observed spatiotemporal changes in cod condition during the past 25 years. It is also possible that the mechanisms that initiated the body condition decline are not the same ones that have kept cod in a poor physiological state in the last 10 years (Tomczak *et al.*, 2022). Evaluating factors associated with condition hotspots would help understand the role of fine-scale food availability for condition. The Eastern Baltic cod stock is not predicted to grow even in the absence of fishing mortality (ICES, 2021a). This makes it crucial to understand how environment–and species interactions affect the body condition of cod (Eero *et al.*, 2020) since 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.G. provided *S. entomon* 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.

# **Literature cited**

Almroth-Rosell, E., Eilola, K., Hordoir, R., Meier, H. E. M., and Hall, P. O. J. 2011. Transport of fresh and resuspended particulate organic material in the Baltic Sea — a model study. Journal of Marine Systems, 87: 1–12.

Anderson, S. C., Keppel, E. A., and Edwards, A. M. 2019. A reproducible data synopsis for over 100 species of British Columbia groundfish. Doc. 2019/041. DFO Can. Sci. Advis. Sec. Res. <www.dfo-mpo.gc.ca/csas-sccs/Publications/ResDocs-DocRech/2019/2019\_041-eng.html>.

Anderson, S. C., and Ward, E. J. 2019. Black swans in space: modeling spatiotemporal processes with extremes. Ecology, 100: e02403.

Anderson, S. C., Ward, E. J., Barnett, L. A. K., and English, P. A. 2021. sdmTMB: spatiotemporal species distribution GLMMs with ‘TMB’. https://pbs-assess.github.io/sdmTMB/index.html.

Anderson, S. C., Ward, E. J., English, P. A., and Barnett, L. A. K. 2022, March 27. sdmTMB: an R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. bioRxiv. https://www.biorxiv.org/content/10.1101/2022.03.24.485545v1 (Accessed 27 March 2022).

Aro, E. 1989. A review of fish migration patterns in the Baltic. Rap. Proc.-verb. Re. Cons. Int. Explor. Mer, 190: 72–96.

Belkin, I. M. 2009. Rapid warming of large marine ecosystems. Progress in Oceanography, 81: 207–213.

Brander, K. 2020. Reduced growth in Baltic Sea cod may be due to mild hypoxia. ICES Journal of Marine Science, 77: 2003–2005. Oxford Academic.

Breitburg, D. 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. Estuaries, 25: 767–781.

Cardinale, M., and Arrhenius, F. 2000. Decreasing weight-at-age of Atlantic herring (Clupea harengus) from the Baltic Sea between 1986 and 1996: a statistical analysis. ICES Journal of Marine Science, 57: 882–893. Oxford Academic.

Carstensen, J., Andersen, J. H., Gustafsson, B. G., and Conley, D. J. 2014. Deoxygenation of the Baltic Sea during the last century. Proceedings of the National Academy of Sciences, 111: 5628–5633. National Academy of Sciences.

Casini, M., Cardinale, M., and Hjelm, J. 2006. Inter-annual variation in herring, Clupea harengus, and sprat, Sprattus sprattus, condition in the central Baltic Sea: what gives the tune? Oikos, 112: 638–650.

Casini, M., Kornilovs, G., Cardinale, M., Möllmann, C., Grygiel, W., Jonsson, P., Raid, T., *et al.* 2011. Spatial and temporal density dependence regulates the condition of central Baltic Sea clupeids: compelling evidence using an extensive international acoustic survey. Population Ecology, 53: 511–523.

Casini, M., Käll, F., Hansson, M., Plikshs, M., Baranova, T., Karlsson, O., Lundström, K., *et al.* 2016a. Hypoxic areas, density-dependence and food limitation drive the body condition of a heavily exploited marine fish predator. Royal Society Open Science, 3: 160416.

Casini, M., Eero, M., Carlshamre, S., and Lövgren, J. 2016b. Using alternative biological information in stock assessment: condition-corrected natural mortality of Eastern Baltic cod. ICES Journal of Marine Science, 73: 2625–2631. Oxford Academic.

Casini, M., Hansson, M., Orio, A., and Limburg, K. 2021. Changes in population depth distribution and oxygen stratification are involved in the current low condition of the eastern Baltic Sea cod (*Gadus morhua*). Biogeosciences, 18: 1321–1331. Copernicus GmbH.

Chabot, D., and Dutil, J.-D. 1999. Reduced growth of Atlantic cod in non-lethal hypoxic conditions. Journal of Fish Biology, 55: 472–491.

Claireaux, G., Webber, D. M., Lagardère, J.-P., and Kerr, S. R. 2000. Influence of water temperature and oxygenation on the aerobic metabolic scope of Atlantic cod (Gadus morhua). Journal of Sea Research, 44: 257–265.

Cressie, N., and Wikle, C. K. 2015. Statistics for Spatio-Temporal Data. John Wiley & Sons. 612 pp.

Diaz, R. J. 2001. Overview of Hypoxia around the World. Journal of Environmental Quality, 30: 275–281.

Diaz, R. J., and Rosenberg, R. 2008. Spreading Dead Zones and Consequences for Marine Ecosystems. Science, 321: 926–929. American Association for the Advancement of Science.

Dutil, J.-D., and Lambert, Y. 2000. Natural mortality from poor condition in Atlantic cod (Gadus morhua). Canadian Journal of Fisheries and Aquatic Sciences. NRC Research Press Ottawa, Canada. https://cdnsciencepub.com/doi/abs/10.1139/f00-023 (Accessed 8 October 2020).

Eero, M., Vinther, M., Haslob, H., Huwer, B., Casini, M., Storr-Paulsen, M., and Köster, F. W. 2012. Spatial management of marine resources can enhance the recovery of predators and avoid local depletion of forage fish. Conservation Letters, 5: 486–492.

Eero, M., Cardinale, M., and Storr-Paulsen, M. 2020. Emerging challenges for resource management under ecosystem change: Example of cod in the Baltic Sea. Ocean & Coastal Management, 198: 105314.

Eilola, K., Meier, H. E. M., and Almroth, E. 2009. On the dynamics of oxygen, phosphorus and cyanobacteria in the Baltic Sea; A model study. Journal of Marine Systems, 75: 163–184.

Gårdmark, A., Casini, M., Huss, M., van Leeuwen, A., Hjelm, J., Persson, L., and de Roos, A. M. 2015. Regime shifts in exploited marine food webs: detecting mechanisms underlying alternative stable states using size-structured community dynamics theory. Philosophical Transactions of the Royal Society B: Biological Sciences, 370: 20130262.

Gogina, M., Zettler, M. L., Wåhlström, I., Andersson, H., Radtke, H., Kuznetsov, I., and MacKenzie, B. R. 2020. A combination of species distribution and ocean-biogeochemical models suggests that climate change overrides eutrophication as the driver of future distributions of a key benthic crustacean in the estuarine ecosystem of the Baltic Sea. ICES Journal of Marine Science, 77: 2089–2105.

Grüss, A., Gao, J., Thorson, J., Rooper, C., Thompson, G., Boldt, J., and Lauth, R. 2020. Estimating synchronous changes in condition and density in eastern Bering Sea fishes. Marine Ecology Progress Series, 635: 169–185.

Haase, K., Orio, A., Pawlak, J., Pachur, M., and Casini, M. 2020. Diet of dominant demersal fish species in the Baltic Sea: Is flounder stealing benthic food from cod? Marine Ecology Progress Series, 645: 159–170.

Hislop, J. R. G., Robb, A. P., and Gauld, J. A. 1978. Observations on effects of feeding level on growth and reproduction in haddock, Melanogrammus aeglefinus (L.) in captivity. Journal of Fish Biology, 13: 85–98.

Hordoir, R., Axell, L., Höglund, A., Dieterich, C., Fransner, F., Gröger, M., Liu, Y., *et al.* 2019. Nemo-Nordic 1.0: a NEMO-based ocean model for the Baltic and North seas – research and operational applications. Geoscientific Model Development, 12: 363–386. Copernicus GmbH.

Hrycik, A. R., Almeida, L. Z., and Höök, T. O. 2017. Sub-lethal effects on fish provide insight into a biologically-relevant threshold of hypoxia. Oikos, 126: 307–317.

Hüssy, K., Casini, M., Haase, S., Hilvarsson, A., Horbowy, J., Krüger-Johnsen, M., Krumme, U., *et al.* 2020. Tagging Baltic Cod – TABACOD. Eastern Baltic cod: Solving the ageing and stock assessment problems with combined state-of-the-art tagging me-thods. DTU Aqua Report, 368–2020. National Institute of Aquatic Resources, Kemitorvet, 2800 Kgs. Lyngby, Den-mark.

ICES. 2021a. Cod *(Gadus morhua)* in subdivisions 24-32, eastern Baltic stock (eastern Baltic Sea). *In* Report of the ICES Advisory Committee. ICES ADVICE 2021 cod.27.24-32. https://doi.org/10.17895/ices.advice.7745.

ICES. 2021b. Report of the Baltic Fisheries Assessment Working Group (WGBFAS). 3:53. https://doi.org/10.17895/ices.pub.8187.

Jørgensen, C., Ernande, B., Fiksen, Ø., and Dieckmann, U. 2006. The logic of skipped spawning in fish. Canadian Journal of Fisheries and Aquatic Sciences, 63: 200–211. NRC Research Press.

Kramer, D. L. 1987. Dissolved oxygen and fish behavior. Environmental Biology of Fishes, 18: 81–92.

Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., and Bell, B. M. 2016. TMB: Automatic Differentiation and Laplace Approximation. Journal of Statistical Software, 70: 1–21.

Latimer, A. M., Banerjee, S., Jr, H. S., Mosher, E. S., and Jr, J. A. S. 2009. Hierarchical models facilitate spatial analysis of large data sets: a case study on invasive plant species in the northeastern United States. Ecology Letters, 12: 144–154.

Le Cren, E. D. 1951. The Length-Weight Relationship and Seasonal Cycle in Gonad Weight and Condition in the Perch (Perca fluviatilis). Journal of Animal Ecology, 20: 201–219. [Wiley, British Ecological Society].

Limburg, K. E., and Casini, M. 2019. Otolith chemistry indicates recent worsened Baltic cod condition is linked to hypoxia exposure. Biology Letters, 15: 20190352. Royal Society.

Lindgren, F., Rue, H., and Lindström, J. 2011. An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach. Journal of the Royal Statistical Society: Series B (Statistical Methodology), 73: 423–498.

Marshall, C. T., and Frank, K. T. 1999. The effect of interannual variation in growth and condition on haddock recruitment. Canadian Journal of Fisheries and Aquatic Sciences, 56: 347–355. NRC Research Press.

Mion, M., Thorsen, A., Vitale, F., Dierking, J., Herrmann, J. P., Huwer, B., von Dewitz, B., *et al.* 2018. Effect of fish length and nutritional condition on the fecundity of distressed Atlantic cod *Gadus morhua* from the Baltic Sea: POTENTIAL FECUNDITY OF BALTIC *G. MORHUA*. Journal of Fish Biology, 92: 1016–1034.

Mion, M., Haase, S., Hemmer‐Hansen, J., Hilvarsson, A., Hüssy, K., Krüger‐Johnsen, M., Krumme, U., *et al.* 2021. Multidecadal changes in fish growth rates estimated from tagging data: A case study from the Eastern Baltic cod (Gadus morhua, Gadidae). Fish and Fisheries, 22: 413–427.

Möllmann, C., Kornilovs, G., Fetter, M., Köster, F. W., and Hinrichsen, H.-H. 2003. The marine copepod, Pseudocalanus elongatus, as a mediator between climate variability and fisheries in the Central Baltic Sea. Fisheries Oceanography, 12: 360–368.

Morgan, M. J., Rideout, R. M., and Colbourne, E. B. 2010. Impact of environmental temperature on Atlantic cod Gadus morhua energy allocation to growth, condition and reproduction. Marine Ecology Progress Series, 404: 185–195.

Nakagawa, S., and Schielzeth, H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution, 4: 133–142.

Nash, R., Valencia, A., and Geffen, A. 2006. The origin of fulton’s condition factor : Setting the record straight. Fisheries, 31: 236–238.

Neuenfeldt, S., Bartolino, V., Orio, A., Andersen, K. H., Andersen, N. G., Niiranen, S., Bergström, U., *et al.* 2020. Feeding and growth of Atlantic cod (*Gadus morhua* L.) in the eastern Baltic Sea under environmental change. ICES Journal of Marine Science, 77: 624–632.

Neumann, T., Koponen, S., Attila, J., Brockmann, C., Kallio, K., Kervinen, M., Mazeran, C., *et al.* 2021. Optical model for the Baltic Sea with an explicit CDOM state variable: a case study with Model ERGOM (version 1.2). Geoscientific Model Development, 14: 5049–5062. Copernicus GmbH.

Orio, A., Florin, A.-B., Bergström, U., Šics, I., Baranova, T., and Casini, M. 2017. Modelling indices of abundance and size-based indicators of cod and flounder stocks in the Baltic Sea using newly standardized trawl survey data. ICES Journal of Marine Science, 74: 1322–1333. Oxford Academic.

Orio, A., Bergström, U., Florin, A.-B., Lehmann, A., Šics, I., and Casini, M. 2019. Spatial contraction of demersal fish populations in a large marine ecosystem. Journal of Biogeography, 46: 633–645. John Wiley & Sons, Ltd.

Orio, A., Bergström, U., Florin, A.-B., Šics, I., and Casini, M. 2020. Long-term changes in spatial overlap betweeninteracting cod and flounder in the Baltic Sea. Hydrobiologia, 847: 2541–2553.

Reusch, T. B. H., Dierking, J., Andersson, H. C., Bonsdorff, E., Carstensen, J., Casini, M., Czajkowski, M., *et al.* 2018. The Baltic Sea as a time machine for the future coastal ocean. Science Advances. American Association for the Advancement of Science. https://www.science.org/doi/abs/10.1126/sciadv.aar8195 (Accessed 1 September 2021).

Rue, H., Martino, S., and Chopin, N. 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. Journal of the Royal Statistical Society: Series B (Statistical Methodology), 71: 319–392.

Sampaio, E., Santos, C., Rosa, I. C., Ferreira, V., Pörtner, H.-O., Duarte, C. M., Levin, L. A., *et al.* 2021. Impacts of hypoxic events surpass those of future ocean warming and acidification. Nature Ecology & Evolution: 1–11. Nature Publishing Group.

Shono, H. 2008. Application of the Tweedie distribution to zero-catch data in CPUE analysis. Fisheries Research, 93: 154–162.

Svedäng, H., and Hornborg, S. 2014. Selective fishing induces density-dependent growth. Nature Communications, 5: 4152.

Svedäng, H., Thunell, V., Pålsson, A., Wikström, S. A., and Whitehouse, M. J. 2020. Compensatory Feeding in Eastern Baltic Cod (Gadus morhua): Recent Shifts in Otolith Growth and Nitrogen Content Suggest Unprecedented Metabolic Changes. Frontiers in Marine Science, 7. Frontiers. https://www.frontiersin.org/articles/10.3389/fmars.2020.00565/full (Accessed 8 July 2020).

Svedäng, H., Savchuk, O., Villnäs, A., Norkko, A., Gustafsson, B. G., Wikström, S. A., and Humborg, C. 2022. Re-thinking the “ecological envelope” of Eastern Baltic cod (Gadus morhua): conditions for productivity, reproduction, and feeding over time. ICES Journal of Marine Science: fsac017.

Thorson, J. T. 2015. Spatio-temporal variation in fish condition is not consistently explained by density, temperature, or season for California Current groundfishes. Marine Ecology Progress Series, 526: 101–112.

Thorson, J. T., Shelton, A. O., Ward, E. J., and Skaug, H. J. 2015a. Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for West Coast groundfishes. ICES Journal of Marine Science, 72: 1297–1310. Oxford Academic.

Thorson, J. T., Scheuerell, M. D., Shelton, A. O., See, K. E., Skaug, H. J., and Kristensen, K. 2015b. Spatial factor analysis: a new tool for estimating joint species distributions and correlations in species range. Methods in Ecology and Evolution, 6: 627–637. John Wiley & Sons, Ltd.

Tomczak, M. T., Müller-Karulis, B., Blenckner, T., Ehrnsten, E., Eero, M., Gustafsson, B., Norkko, A., *et al.* 2022. Reference state, structure, regime shifts, and regulatory drivers in a coastal sea over the last century: The Central Baltic Sea case. Limnology and Oceanography, 67: S266–S284.

Tweedie, M. C. 1984. An index which distinguishes between some important exponential families. *In* Statistics: Applications and new directions: Proc. Indian statistical institute golden Jubilee International conference, pp. 579–604.

Whittingham, M. J., Stephens, P. A., Bradbury, R. B., and Freckleton, R. P. 2006. Why do we still use stepwise modelling in ecology and behaviour? Journal of Animal Ecology, 75: 1182–1189.

Wickham, H., Averick, M., Bryan, J., Chang, W., D’Agostino McGowan, L., François, R., Grolemund, G., *et al.* 2019. Welcome to the tidyverse: 1686.

# **Figures**

**Chart, histogram

Description automatically generated**

**Fig. 1.** A) Density plots of condition data by year. B) Predicted Le Cren condition factor of cod condition factor over the period 1993-2019 in the Baltic Sea (total as well as by each ICES subdivisions), acquired by predicting from the spatiotemporal condition model over a grid with spatially varying covariates set to their true values (ICES rectangles with missing pelagic data were given the subdivision median when predicting but not fitting, see *SI Appendix*, Fig. S23). Vertical lines depict the 95% confidence interval.

Map

Description automatically generated

**Fig. 2.** Predicted log condition factor with spatially varying covariates set to their true values (ICES rectangles with missing pelagic data were given the subdivision mean, see *SI Appendix*, Fig. S23). Included in the plot are years 1994, 2001, 2008, 2018. Only grid cells with depths between 10m and 120m are included in the plot. For all years in the series, see *SI Appendix*, Fig. S9.

Chart, scatter chart

Description automatically generated

**Fig. 3.** Mean and 95% confidence interval of standardized coefficients (effect sizes) for covariates and spatial and spatiotemporal standard deviation ( and , respectively) in the condition model. The subscript *haul* refers to covariates estimated at the location of the haul, *rec* refers to covariates at the ICES statistical rectangle and *sub* refers to covariates over ICES subdivision (*SI Appendix*, Fig. S1). Colors indicate covariate-groups and shapes indicate scale.

Calendar

Description automatically generated with low confidence

**Fig. 4.** A) Predicted biomass (tonnes) from the spatiotemporal CPUE model (Eq. 10–11) by ICES subdivision (B) and total across all subdivisions. C) Predicted density (kg/km2) in select years (1995 and 2017) (for all years in the series, see *SI Appendix*, Fig. S17). Only grid cells with depths between 10 and 120 are included in the plot.

Graphical user interface, chart

Description automatically generated

**Fig. 5.** (A) Bathymetry and (B) oxygen concentration (exemplified using year 1999) in the study area. Panels (C) and (D) illustrate depth and oxygen weighted by predicted cod density, respectively. Colors indicate quantiles (1st quartile, median and 3rd quartile). Lines depict GAM fits (=4).