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

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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). However, despite operating on small spatial scales, processes attributed to each of these hypotheses have only been evaluated temporally on large spatial scales and using condition averages, therefore missing variability of this trait in the population (basin or population level). By applying a geostatistical model that includes spatially and spatiotemporally correlated random effects using Gaussian Markov random fields, we analyze changes in cod condition in relation to biotic and abiotic covariates at different scales and their spatiotemporal variation in autumn. We find that body condition declined over the whole domain until 2008, after which a plateau was reached. The decline occurred for cod of all sizes, although more in large cod, and upper and lower quantiles of the distribution of Le Cren’s condition indices declined at the same rate. Oxygen, sprat biomass (at the subdivision level), temperature, and the biomass of the benthic isopod *Saduria entomon* (to a lesser extent) where positively related to condition, whereas density of cod and depth-at-catch were negatively associated with condition. However, even though cod are now found, on average, in deeper and less-oxygenated waters, the effect sizes of these variables were small, and could not alone explain the steep decline that occurred between 1993–2008. In fact, residual spatial and spatiotemporal variation was several times larger in magnitude than any single covariate’s coefficient, suggesting there is still considerable unexplained variation. 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). Body condition 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 circumstances, (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; Brander, 2020; Sampaio *et al.*, 2021; Casini *et al*., 2021). As both environmental and biological variables can affect condition, it is important to study their relative contribution to variation in 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’ (REF?) or ‘TMB’ (REF) or interfaces such as ‘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) 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* (Neuenfeldt *et al.*, 2020; Haase *et al*. 2020), the flounder complex (European flounder *Platichthys flesus* and Baltic Flounder *Platichthys solemdali*) (Orio *et al.*, 2017), as well as in the distribution of its main pelagic prey species (sprat *Sprattus sprattus* and herring *Clupea harengus*) (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). In literature there are studies relating changes in cod condition to single or multiple ecosystem drivers (Casini *et al*., 2016a, 2021; Orio et al. 2020), However, the relative importance of these ecosystem drivers on cod conditions is still not fully understood, since they have not all been analyzed in a single framework, and not on an individual level with covariates on different spatial scales.

In this study, we apply spatiotemporal predictive-process GLMMs to characterize the spatiotemporal variation in body condition and density 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 and cod, biomass of pelagic (sprat and herring) and benthic (*S. entomon*) 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 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 (October-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 by assuming weight is related to length as , where is weight in grams, is length in cm, is the allometric length exponent and is the condition factor in units (Froese *et al.*, 2014). In addition to estimating the condition factor, we calculated Le Cren’s relative condition index for each individual fish : (). 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 acquire a spatiotemporal condition factor and to assess the ability of covariates to explain variation in condition, we fit a geostatistical GLMM to the weight-length relationship on - scale, assuming - distributed residuals (with 5 degrees of freedom) due to the presence of extreme values:

where represents the weight at space (a vector of two UTM zone 33 coordinates) and time , represents the mean weight, and represents the scale parameter. The parameter 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. The parameter represents the length-coefficient (corresponding to the allometric exponent ), and represents a vector of the -th additional covariate and is its effect. The parameters and represent spatial and spatiotemporal random effects, respectively. These 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:

where Γ is a gamma process, κ controls the spatial scale, 𝜏 controls the variance, and ν is fixed at ν = 1 to use the Stochastic Partial Differential Equation (SPDE) approximation to the GMRF (Lindgren *et al.*, 2011). Lastly, we assumed the spatiotemporal random effects to follow a stationary AR1 process:

where 𝜌 represents the correlation between subsequent spatiotemporal random fields. In summary, a log spatiotemporal condition factor can be defined as: , i.e., Eq. 2 with . When calculating Le Cren’s condition index over time, we use and the average across all (1993 to 2019) to calculate the predicted weight, from which Le Cren’s condition index are the residuals in log space.

*Density models*

We fit spatiotemporal models 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 (Eqns. 5–6).

*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, S13), 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 sdmTMB\_0.0.20.9, sim2 branch) (Anderson *et al.*, 2019, 2021) 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 < 0.005 and that the Hessian matrix was positive-definitive. We used packages in the ‘tidyverse’ (Wickham *et al.*, 2019) for data processing and plotting.

***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', Fig…) (Hüssy *et al.*, 2020). Therefore, we included environmental and biological demersal covariates (temperature, oxygen, depth, cod density, flounder density and *S. entomon* density) 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). Sea bottom temperature (°C) and sea bottom concentration of dissolved oxygen (ml/L) in the fourth quarter were extracted from the ocean model NEMO-Nordic-SCOBI (Eilola *et al.*, 2009; Almroth-Rosell *et al.*, 2011; Hordoir *et al.*, 2019). Depth (m) 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 densities of *S. entomon* (g/m2) 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, we used depth, temperature, and oxygen 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; 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). 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 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 condition model revealed a decline in the log condition factor (i.e., the spatiotemporal prediction when ) of 3.6% [2.6%, 4.2%] (values in brackets are the 2.5% and 97.5% quantiles from 500 draws from the joint precision matrix). It declined from approximately -4.50 to -4.66 between 1993 and 2019 (the decline leveled off in around 2008) (Fig. 1A). This corresponds to a 15% [11%, 17%] decline in weight for cod of median length (35 cm) (see *SI Appendix,* Fig. S10 for changes in weight-at-length on the arithmetic and log scale given and the estimated for years 1993 and 2019). The condition factor declined the most in the northern subdivisions (i.e. 27 and 28) and the least in the south-western subdivision 24 Le Cren’s condition index calculated change over time for discrete 10 cm length classes using the spatiotemporal length-weight model showed a decline for size-classes 30–70 cm (upper boundary) with approximately -0.007 annually between 1993-2019. The decline for cod in the size-class 10–20 cm and 20-30 cm was more modest (-0.0015 and 0.0057 annual decline, respectively) (Fig. 1B). The median Le Cren’s condition index declined at the same rate as the 1st and 9th decile (Fig. 1C), 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 (east of Bornholm, south of Gotland and between Öland and Gotland) (Fig. 2, *SI Appendix*, Fig. S1), and that the condition factor declined in the whole area over time (Fig. 2, *SI Appendix*, Fig. S9).

The significant 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 (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 (Fig. 3). Depth at the haul level was negatively associated with condition (-0.023 [-0.028, -0.02]) (weight) (Fig. 3) (see *SI Appendix*, Fig. S11, for marginal effects plots). The biomass density of cod, flounder, and the biomass of herring did not affect the weight 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 residual spatiotemporal and spatial variation. To ensure that this was not due to covariates not being spatially (i.e. ecologically) matched properly with condition data (i.e., due to the scale differences, or due to the use of the entire cod population for model fitting, even though feeding interactions and competition are size-dependent), we conducted a sensitivity analysis by fitting the condition model to different parts of the data (only juvenile or adult cod, omitting the mixing zone with western Baltic cod e.g. subdivision 24, etc. (*SI Appendix,* Fig. S12). However, the model coefficients were similar across all models. This suggests considerable variation in space due to latent factors, as well as changes of spatial variation through time, that cannot be explained by available covariates.

The median depth of cod occurrence and oxygen (depth and oxygen in the environment weighted by the predicted biomass density of cod, Fig. 4) got deeper or declined throughout the time period (Fig. 5), though the population again occupied slightly shallowed waters in the last 3 years of the time series. However, the contribution of depth and oxygen changes to the decline over time was likely minor. For instance, the standardized effect size for oxygen was 0.0034 [95% confidence interval: -0.0002, 0.0070], meaning that for each unit increase in the standardized oxygen variable (i.e., 1 standard deviation or 1.85 ml/L), log weight increased by 0.34% (corresponding to a 1.2% increase in weight for a cod of median length (35cm). 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), but still, the contribution to the 3.6% decline in the condition factor is likely low, as the change in experienced oxygen only corresponds to condition change slightly larger than half a standard deviation, and oxygen trends vary in space whereas condition declined everywhere (*SI Appendix*, Fig. S9, S11).

# **Discussion**

The body condition of fish depends on recent energy accumulation and is therefore largely shaped by the quality of the habitat where fish have dwelled. By using a fine-scale spatiotemporal condition model, we can link the condition of Eastern Baltic cod to covariates at different ecologically relevant spatial scales. Our model reveals that the weight of a median-length cod (xxx cm) declined by 15%, in 1993–2019, with the majority of this decline occurring 1993–2008. Moreover, while there are persistent low-spots of body condition (i.e. in the deep and low-oxygen areas), the condition declined in the whole area, suggesting several factors are responsible for the decline in condition. 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 residual spatial and spatiotemporal variation is several times larger in magnitude.

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 9th decile are 3.6 and 7.5). In subdivision 25 we estimate it to be around 6.4 (*SI Appendix,* Fig. S20). 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 the estimated average oxygen concentration could occur because we estimate the values as average sea bottom oxygen concentration from the ocean model NEMO-Nordic-SCOBI weighted 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, we see that the 1st decile of the density-weighted oxygen concentration reached an all-time minimum (approximately 3.5 ml/L in 2010), and then increased, suggesting the average decline in oxygen concentration is not driven by the decline in 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 habitats that feature higher food availability, or if there are direct physiological impacts at lower threshold in the wild. Either way, the declined oxygen concentrations have likely contributed to the deteriorated body condition of cod.

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 its habitat contraction caused by the expansion of “dead zones” (Casini *et al.*, 2016a; Orio *et al.*, 2019; Haase *et al.*, 2020). We did not include the extent of anoxic areas as a covariate representing suitable habitat area. 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 a direct density effects. 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. However, biomass density is not a direct measure of competition; areas with higher densities of cod and flounder could simply also have more food. However, 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—potentially in combination with benthic prey biomass.

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. The relation between sprat biomass on cod condition, resulted from the statistical modeling of our study, is also evidenced by the fact that the decline in cod condition has been stronger in the subdivisions where the sprat biomass has declined the most (Fig. S21).

The fact that cod condition has declined for all sizes and 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 remain—suggests that several variables and driving processes have been involved. The decline could still be related to competition or food availability, but if it was the only important effect, all food sources used by cod over ontogeny ought to have declined in synchrony, or, possibly, poor condition would start early in life due a shortage of a specific resource and cod could not compensate for that later in life. Even though it is possible, 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, although with differences, for all sizes and in all areas. The small effect sizes of the single covariates we used based on existing literature, analysed for the first time in a common framework, suggest that multiple factors are responsible for the observed spatio-temporal 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. For example, the increased abundance of flounder, facilitated by the almost disappearance of the large predatory cod individuals (Orio et al. 2000), could lock the system in a low-cod state due to the potentially increased competition for food and space with flounder, as suggested for other species in other studies (……). 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.

# **Acknowledgements**

We are very grateful for help from Alessandro Orio for standardization of survey data used in the density models, Federico Maioli for helpful modelling discussion, Hagen Radtke and Ivan Kuznetsov for assistance in acquiring predictions of *S. entomon* densities, Martin Hansson and Elin Almroth Rosell at SMHI for assistance with environmental data, and Olavi Kaljuste for providing pelagic data. We thank the staff involved in the scientific sampling and analysis of biological data. The study was financed by the Swedish Research Council Formas (grant no. 2018-00775 to M.C.).

# **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.

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# **Figures**

**Chart

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**Fig. 1.** A) Dynamic of the cod condition factor (log-transformed) over the period 1993-2019 in the Baltic Sea (total as well as by each of the considered 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, see *SI Appendix*, Fig. S22). Here and below, vertical lines depict the 95% confidence interval. B) Slope of the linear regression relating Le Cren’s condition index and year by 10 cm cod length-classes. C) Le Cren’s condition index as function of year (points indicate median, large light grey shaded area show the range of the 10th and 90th percentile). Line depicts the GAM fit (=4) and the narrow dark grey shaded band corresponds to the 95% confidence interval of the median). D) Density-plot of the size (length-classes) distribution (all years pooled) of cod (note that it has the same x-axis as panel B).

Map

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**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. S22). Included in the plot are years 1994, 2001, 2008, 2018. For all years in the series, see *SI Appendix*, Fig. S9.

Chart, scatter chart

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**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.

Diagram

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**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. S18).

Chart, diagram

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**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. The shaded areas correspond to the range of weighted depths and oxygen concentrations (1st and 9th deciles). Lines depict GAM fits (=4).