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

Max Lindmarka,1, Sean C. Andersonb,c, Mayya Gogina, Michele Casinia,d

a Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Marine Research, Turistgatan 5, 453 30 Lysekil, Sweden

b Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, BC, Canada

c Department of Mathematics, Simon Fraser University, Burnaby, BC, Canada

d Leibniz Institute for Baltic Sea Research, Seestraße 15, 18119 Rostock, Germany

e University of Bologna, Department of Biological, Geological and Environmental Sciences, Via Selmi 3, 40126 Bologna, Italy

1 Author to whom correspondence should be addressed. Current address:

Max Lindmark, Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Marine Research, Turistgatan 5, 453 30 Lysekil, Sweden, Tel.: +46(0)104784137, email: max.lindmark@slu.se

**Key Words**

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

**Abstract**

The body condition of a fish describes the weight given its length and is often positively associated with fitness. Atlantic cod (*Gadus morhua*) in the south-eastern Baltic Sea has experienced a drastic deterioration of its physiological status since the early 1990s to levels that compromise the growth of the population. Several hypotheses have been proposed in the literature (competition, hypoxia, lack of prey), however, despite operating on small spatial scales, these variables have only been evaluated temporally on large spatial scales (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 distribution. We find that the body condition declined in the whole domain until 2008, after which a plateau was reached. The decline occurred for cod of all sizes, and upper and lower quantiles of the distribution of Le Cren’s condition indices declined at the same rate. Oxygen, sprat biomass (at the sub-division level), temperature and saduria biomass (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 the biomass-weighted overlap with sprat and have decreased over time, and cod are now on average at deeper and less oxygenated waters, the effects 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 were several times larger in magnitude than any single covariate’s coefficient, suggesting there is still considerable variation unexplained by covariates. Understanding the drivers of spatiotemporal variation in body condition, which affects mortality and reproduction, is important for understanding the impacts of environmental change and for the management marine fishes.

**Introduction**

The body condition is a morphometric index that describes the “plumpness” of an organism, or its weight relative to its length. Body condition is related to food intake rates and metabolic activity, and 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). It has also been linked to environmental conditions, (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 (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). 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’, ‘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 demersal CPUE 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, 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 prey the isopod *Saduria entomon* (Neuenfeldt *et al.*, 2020a) the flounder complex (European flounder *Platichthys flesus* and Baltic Flounder *Platichthys solemdali*) (Orio *et al.*, 2017), and 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), and it is also one of the fastest warming regional seas (Belkin, 2009; Reusch *et al.*, 2018). However, it remains unknown what the relative importance of these variables are, since they have not been analyzed directly in a single framework, and not on different spatial scales.

In this study, we apply spatiotemporal predictive-process GLMMs to characterize spatiotemporal variation in body condition of cod in the south-eastern Baltic Sea, as well as their spatiotemporal distribution. We use data from the Baltic International Trawl Survey between 1993–2019, 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 (biomass densities of saduria, flounder and cod, biomass of pelagic prey (sprat and herring), 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 ICES sub-divisions 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 using a TVL trawl with 75 m sweeps (note that compared to Orio *et al.* (2017), we further express density in instead of in 1 trawling sweeping an area of 0.45 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, 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 unit (Froese *et al.*, 2014). In addition to estimating the condition factor, we used this relationship to calculate 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 kappa controls the spatial scale, tau controls the variance, and nu is fixed at nu = 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 .

*Density models*

We fit spatiotemporal models to biomass density data in a similar fashion as for condition for two reasons: 1) to evaluate how the depth distribution, temperature, oxygen conditions experienced by cod, as well as overlap with saduria and sprat have changed of the Baltic cod and 2) to 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. For the overlap with saduria and sprat, we used a biomass-weighted overlap index (Carroll *et al.*, 2019), calculate by year as:

where (cod) and (saduria or sprat) are densities of predator and prey in each area (grid-level predictions for saduria and ICES rectangle for sprat). This overlap index is useful where relative biomass of predator and prey is of interest (Carroll *et al.*, 2019).

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

where represents density [] 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 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. S2, 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, up to a threshold (REF). After initial exploration, we chose 200 knots for this application. The models where fit using ‘TMB’ (Kristensen *et al.*, 2016) via the R-package ‘sdmTMB’ (version 0.0.18.9001) (Anderson *et al.*, 2019, 2021). We checked the models were consistent with convergence by confirming the maximum absolute gradient 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 different spatial scales that roughly reflect the habitats cod would have been exposed to during the 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') (Hüssy *et al.*, 2020). Therefore, we included environmental and demersal covariates (temperature, oxygen, depth, cod, flounder and saduria) at the haul and the median over the ICES rectangle-level, and the pelagic covariates at the ICES rectangle- and sub division-level (not including haul-level densities as pelagic species are highly mobile). Biomass of sprat and herring were extracted from the ICES WGBIFS database for the BIAS survey data (https://www.ices.dk/community/groups/pages/WGBIFS.aspx). Sea bottom temperature and sea bottom concentration of dissolved oxygen 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 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 *Saduria entomon* were extracted from a habitat distribution forced to a regional coupled ocean biogeochemical model (Gogina *et al.*, 2020; Neumann *et al.*, 2021). Biomass densities of cod and flounder were taken from the same scientific survey as the condition data (BITS). We used predicted densities from GLMMs (described below) fitted to cod and flounder density 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, and only depth as a covariate for the cod and flounder models that were used to predict covariates for the condition model.

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 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 stepwise selection (e.g., Whittingham *et al.*, 2006) and because initial analyses suggested the model was not overfit. 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 spatiotemporal 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 2008, after which the decline leveled off (Fig. 1A). This corresponds to a 15% [17%, 11%] decline in log weight for a cod of any length. Calculating change over time in Le Cren’s condition index for discrete 10 cm length classes using the spatiotemporal length-weight model shows that the condition index declined for size-classes 20-70 cm (upper boundary) with approximately -0.007 annually. The decline for cod in the size-class 10-20 cm was more modest (-0.015 annual decline) (Fig. 1C). The median Le Cren’s condition index declined at the same rate as the 1st and 9th decile, meaning the decline in the condition factor 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.

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 declines in the whole area over time (Fig. 2, *SI Appendix*, Fig. S8, S10).

The covariates with the largest positive standardized effect sizes are temperature at the haul (0.009 [0.004, 0.014]) (values in brackets indicate 95% confidence interval), median depth (0.01 [0.004, 0.02]) and oxygen concentration at the ICES rectangle level (0.01 [0.002, 0.016]), and biomass of sprat in the ICES sub-division (Fig. 3). Depth at the haul is negatively associated with condition (-0.023 [-0.028, -0.02]) (weight) (Fig. 3) (see *SI Appendix*, Fig. S9, for marginal effects plots). biomass of and the biomass of herring did not a at any scale (Fig. 3). The magnitude of single covariate effect sizes are generally small. In fact, several times smaller than residual spatiotemporal and spatial variation. This means there is considerable variation in space, and variation in space that changes through time, that the covariates cannot explain.

The median depth and oxygen (depth and oxygen in the environment weighted by the predicted biomass density of cod), as well as the biomass-weighted overlap with saduria and sprat got deeper or decline throughout the time period (Fig. 5). However, their contribution to the decline over time is likely quite minor For instance, the standardized effect size for oxygen is 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 increases by 0.34% (corresponding to a 2% increase in weight for a cod weighing 380g, which is the median weight in the data). 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 minor, as the change in experienced oxygen only corresponds to a change that is slightly larger than half a standard deviation in change, and oxygen trends vary in space whereas condition declined everywhere (*SI Appendix*, Fig. S10, SX).

Being based on the empirical weight-length relationship, Le Cren’s condition index does not scale with length itself if weight is not proportional to the cube of length. However, accurate estimates of the weight-length relationships require a large enough range of weights and lengths. However, some covariates related to competition or food availability (such as cod and flounder density, or sprat and herring abundance) could be relevant for only specific size-classes of cod. Therefore, we also fit the same condition model to cod above and below 30 cm (where cod below 30 cm are more likely to compete with flounder and other cod for benthic resources (Haase *et al.*, 2020), and cod above 30 are able to feed on the entire size-distribution of the herring (Niiranen *et al.*, 2019) (*SI Appendix*, Fig. SX). These results showed that the neither the parameter estimates nor the trends over time changed drastically.

# **Discussion**

Using a fine-scale spatiotemporal condition model, we show that the log cod weight for a given length in the Baltic Sea declined by 15%, primarily between the years 1993–2008. While there are persistent low-spots of body condition (deep and low-oxygen areas), the condition declined in the whole area. While we identify changes in the spatiotemporal distribution of cod that could have led to poorer environments for condition (deeper areas with less oxygen and overlap with prey), 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.*, 2020a; 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 they are not able to accumulate as large energy reserves. First, we find that the Baltic cod are currently experiencing oxygen concentrations at around 6.4 ml/L on average (1st and 9th decile are 3.6 and 7.5). This is higher than a recent estimate of 4.5 ml/L as the average oxygen concentration in recent years (for the eastern Baltic cod) (Brander, 2020; Casini *et al.*, 2021). 4.5 ml/L has also been proposed as a threshold for negative but sub-lethal physiological impacts, including, but not limited to, reduced feeding rates (Hrycik *et al.*, 2017). The difference in the estimated average oxygen concentration could be because we estimate the average oxygen across the prediction grid (populated with sea bottom oxygen concentration from the ocean model NEMO-Nordic-SCOBI), and then calculate the average experienced oxygen by weighting the average oxygen per grid cell by the predicted densities from the density model. This should be a more precise approach; 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 low (approximately 3.5 ml/L in 2005), and then steadily increased, suggesting the average decline in oxygen concentration is not driven by a decline in the lowest oxygen concentrations. Interestingly, we still find a positive effect of oxygen, though we can only speculate if this is due to oxygen being correlated with richer habitats or if there are direct physiological impacts at lower threshold in the wild. Either way, the current trend of declining oxygen and the progressive deepening of the cod stock will likely contribute to further deteriorating body condition of cod.

An indirect effect of declining oxygen is a potentially intensified competition with other cod and/or flounder for shared benthic prey species, such as the isopod *Saduria entomon*, due to the 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 hypoxic areas as a covariate. Instead, we use predicted density of flounder and cod at the haul and at the ICES rectangle-level to include “crowding” 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 negative effects of local (haul) density of cod, but not flounder. However, biomass density is not a direct measure of competition; areas with higher densities of cod and flounder could simply also have more food. Hence, we cannot rule out that that competition occurring, only that cod are not skinnier in areas with high density of flounder. To properly test for competition, we would need data of the benthic invertebrate community, which does not exist on this spatial and temporal resolution. Moreover, the proportion of *Saduria entomon* in the diet declined more (from average 0.18 to 0.09 across size all groups) in 2007-2013 relative to 1989-2006 than the decline in 1989-2006 relative to 1974-1988 (from 0.3 to 0.18) (Kulatska *et al.*, 2019). This is notable because we find a stable (but low) condition in 2007-2013, when the proportion declined fastest. More studies need to be done to evaluate if the lasting low feeding rates of *Saduria entomon* in recent years are due to the high flounder densities and therefore to competition with flounder.

A reduced availability of sprat and herring (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). We found positive effects of sprat abundance at the ICES subdivision level, but not for herring. It is however unclear if the decline in sprat drove the decline in condition. Even though the spawning stock biomass of sprat declined from 1.9 million tonnes in the whole Baltic in 1994 to 1.05 million tonnes in 2006, most of the decline occurred in subdivision 26-28 whereas the condition of cod on the other hand has declined in the whole Baltic.

The last piece of evidence (although indirect) against a food-shortage for the decline in condition is that our model predicts a decline in condition for cod of all sizes. Hence, for the decline to still be related to competition or food availability, all food sources used by cod over ontogeny ought to have declined in synchrony, or that poor condition starts early in life due a shortage of a specific resource and that cod cannot compensate for that later in life. Even if that is possible, Neuenfeldt *et al.*, (2020a) showed that the feeding levels of cod where relatively high in the period 1995-2004 when the decline in condition was the most rapid, and the growth rates had not yet declined to the lowest in seven decades (Mion *et al.*, 2021). Hence, a decade of deteriorating condition under normal feeding- and growth rates preceded the poor growth in recent years. That low feeding levels was not limiting cod in the mid 90’s in the midst of 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). 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 the fine-scale spatiotemporal development of body condition in the eastern Baltic cod, and the 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 1990’s and reached a bottom in the mid 2000s, and that condition has declined for all sizes and in all areas. These two features, together with small effect sizes of covariates in relation to several times larger magnitude of residual spatiotemporal and spatial variation, suggest that food limitation likely has not driven the decline in body condition of the stocks. However, it is possible these factors (food availability, density dependence, and environmental condition) still limit a “physiological” recovery of cod in more recent years (Haase *et al.*, 2020). I.e., the mechanisms that caused the decline in body condition may not be the ones that have kept cod in a poor physiological state in the last 15 years. More research is needed to understand the role of fine-scale food availability for condition, e.g., by evaluating factors associated with hotspots in condition in recent years. The Eastern Baltic cod stock are not predicted to grow even in the absence of fishing mortality (ICES, 2021a). This makes it crucial to understand the role of environment and species interactions for the body condition of cod (Eero *et al.*, 2020), as body condition is a key biological trait determining mortality and reproductive output.

# **Acknowledgements**

We are very grateful for help from Alessandro Orio for standardization survey data used in the density models, Federico Maioli for helpful modelling discussion, Hagen Radtke and Ivan Kuznetsov for assistance in acquiring predictions of saduria densities, Martin Hansson and Elin Almroth Rosell at SMHI for assistance with environmental data, and Olavi Kaljuste for providing pelagic data. We thank staff involved in the scientific sampling and analysis of biological data.

# **Author Contributions**

All authors contributed to the manuscript. Specifically, M.C. coordinated the study, M.L. prepared the raw data, M.G. provided saduria 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., and Ward, E. J. 2019. Black swans in space: modeling spatiotemporal processes with extremes. Ecology, 100: e02403.

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., 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.

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

Barnett, L. A. K., Ward, E. J., and Anderson, S. C. 2021. Improving estimates of species distribution change by incorporating local trends. Ecography, 44: 427–439.

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.

Carroll, G., Holsman, K. K., Brodie, S., Thorson, J. T., Hazen, E. L., Bograd, S. J., Haltuch, M. A., *et al.* 2019. A review of methods for quantifying spatial predator–prey overlap. Global Ecology and Biogeography, 28: 1561–1577.

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.

Froese, R., Thorson, J. T., and Reyes, R. B. 2014. A Bayesian approach for estimating length-weight relationships in fishes. Journal of Applied Ichthyology, 30: 78–85.

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.

Kulatska, N., Neuenfeldt, S., Beier, U., Elvarsson, B. Þ., Wennhage, H., Stefansson, G., and Bartolino, V. 2019. Understanding ontogenetic and temporal variability of Eastern Baltic cod diet using a multispecies model and stomach data. Fisheries Research, 211: 338–349.

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.

Neuenfeldt, S., Bartolino, V., Orio, A., Andersen, K. H., Andersen, N. G., Niiranen, S., Bergström, U., *et al.* 2020a. 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.

Neuenfeldt, S., Bartolino, V., Orio, A., Andersen, K. H., Andersen, N. G., Niiranen, S., Bergström, U., *et al.* 2020b. Reply to “Reduced growth in Baltic Sea cod may be due to mild hypoxia”—a comment to Neuenfeldt et al. (2020). ICES Journal of Marine Science, 77: 2006–2008. Oxford Academic.

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.

Niiranen, S., Orio, A., Bartolino, V., Bergström, U., Kallasvuo, M., Neuenfeldt, S., Ustups, D., *et al.* 2019. Predator-prey body size relationships of cod in a low-diversity marine system. Marine Ecology Progress Series, 627: 201–206.

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).

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.

Thorson, J. T. 2019. Guidance for decisions using the Vector Autoregressive Spatio-Temporal (VAST) package in stock, ecosystem, habitat and climate assessments. Fisheries Research, 210: 143–161.

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

Description automatically generatedFig. 1.** A) Logarithm of the condition factor survey domain for years 1993-2019, total and by ICES sub division, 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 sub division mean, see *SI Appendix*, Fig. SX). Vertical lines depict the 95% confidence interval. B) Slope of the linear regression relating Le Cren’s condition index and year by 10 cm length-classes (vertical lines depict the 95% confidence interval). C) Deciles of the Le Cren condition index as a function of year (shaded band corresponding to the 95% confidence interval) and D) Density-plot of the size-distribution (all years pooled) of cod (note it has the same x-axis as panel B).

Chart, line chart

Description automatically generated

**Fig. 2.** Change in weight-at-length given and the estimated for years 1993 and 2008.

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 sub division mean, see *SI Appendix*, Fig. SX), such that the prediction corresponds to the depth, temperature, and oxygen-dependent log-condition factor for years 1994, 2001, 2008, 2018. For all years in the series, see *SI Appendix*, Fig. S8.

Chart, scatter chart

Description automatically generated

**Fig. 3.** Mean and 95% confidence interval of the standardized coefficients and the spatial and spatiotemporal standard deviation ( and , respectively) in the condition model. The subscript *haul* refers to a covariate estimated at the location of the haul, *rec* refers to a covariate that is averaged by ICES statistical rectangle and *sd* refers to a covariate that is averaged over ICES subdivision (*SI Appendix*, Fig. S1).

Diagram

Description automatically generated

**Fig. 4.** A) Predicted biomass (tonnes) from the spatiotemporal CPUE model (Eq. 10-11), (B) Predicted density [] in select years 1995 and 2017 (for all years in the series, see *SI Appendix*, Fig. S17), with oxygen, depth, and temperature covariates.

**Graphical user interface, diagram, application

Description automatically generated**

**Fig. 5.** A) Bathymetry of the study area, B) depth weighted by predicted cod density. Lines correspond to the 1st, 5th (i.e., median) and 9th decile. C) Oxygen concentration in space (using year 1999 as an example) (D) oxygen concentration weighted by predicted cod density. Points correspond to the 1st, 5th, and 9th decile and lines depict GAM fits (=4) fits .