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

Max Lindmarka,1, Sean C. Andersonb, Michele Casinia

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 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

**Abstract**

The body condition of fishes describes the weight given its length and is often positively associated with fitness. Atlantic cod (*Gadus morhua*) in the south-eastern Baltic Sea has experienced a drastic deterioration of its physiological status since the early 1990’s, to levels that compromise the growth of the population. Several variables have been attributed to the decline in body condition, including increased intra- and interspecific competition for benthic resources, lack of pelagic food and increased hypoxia in the Baltic. However, despite operating on small spatial scales, these variables have only been evaluated on large spatial scales (Baltic Sea basin- or population level), and the relative importance of these covariates has not been evaluated in a common framework. By applying a spatial and spatiotemporal predictive-process GLMM that explicitly accounts for spatiotemporal autocorrelation with Gaussian Markov random fields, we analyse changes in condition and spatiotemporal distribution in relation to fine-scale habitat variables. We find that the body condition declined until 2006, after which a plateau was reached, and this occurred for both mature and immature cod. Environmental variables (oxygen, depth, temperature) had stronger effects on condition than ecological variables (density of cod and flounder reflecting competition, and herring), except sprat abundance which had similar effect size as the environmental variables. Moreover, cod appear to have moved into deeper and less oxygenated areas, which likely has contributed to the decline in condition over time as oxygen is positively associated with condition. Understanding the drivers of spatiotemporal variation in body condition is important for understanding the impacts of climate change and the role of species interactions on productivity and resilience of marine fishes.

**Key Words**

Condition, Spatio-temporal models, Density dependence, Deoxygenation

**Introduction**

The body condition is a morphometric index that describes the “plumpness” of a organism, or its weight relative to its length. It 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).

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; 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; Grüss *et al.*, 2020). More recently, studies have found a link between declining body condition and global deoxygenation (declines in dissolved oxygen and the expansion of dead zones) (Casini *et al.*, 2016a, 2021), fuelled by warming and nutrient enrichment (Diaz, 2001; Breitburg, 2002; Diaz and Rosenberg, 2008; Carstensen *et al.*, 2014). The underlying mechanisms are both indirect and direct. Hypoxia, or low dissolved oxygen, can cause habitat compression and thus force organisms to occupy sub-optimal habitats, which may enhance density dependence (Diaz and Rosenberg, 2008; Orio *et al.*, 2019; Gogina *et al.*, 2020). Direct effects include metabolic constraints on organisms, manifested as lowered food intake 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.

Furthermore, modelling fine scale ecological data tends to result in correlated residuals, as these data are spatially and temporally correlated. Relatively recently have spatiotemporal models been applied to study variation in condition (Thorson, 2015; Grüss *et al.*, 2020). In these studies, spatially correlated residual variation was accounted for with spatial random effects through Gaussian random fields in a GLMM framework. This approach to model spatiotemporal data is an increasingly popular method for explicitly accounting for spatial and spatiotemporal variation – likely due to its ability to improve predictions 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 like these reveal the importance of accounting for spatial and spatiotemporal variation in condition for clarifying its sources of variation in relation to unmeasured variation and independent variables.

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 population biomass is expected to remain below safe limits despite banning 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 the European and Baltic Flounder (*Platichthys flesus* and *Platichthys solemdali,* respectively) (Momigliano *et al.*, 2018), and in the distribution of its main pelagic prey species (sprat *Sprattus sprattus* and herring *Clupea harengus*). 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 analysed 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 1991-2020, which corresponds to a period of initially high but deteriorating condition (Casini *et al.*, 2016a). We then seek to (1) identify which set of covariates (catch-per-unit-effort of flounder and cod, availability of pelagic prey or oxygen concentration and temperature) can explain variation in weight given length and (2) explore how the average depth and average oxygen experienced by the Baltic cod has changed over time.

**Materials and methods**

***Data***

*Survey data*

To model the spatiotemporal development of cod condition and distribution, we acquired weight-at-length data and catch per unit effort data (CPUE, numbers/hour) by 10-mm length class from the Baltic International Trawl Survey (BITS) between the years 1993-2019 and in ICES sub-divisions 24-28 (Supporting information). Abundance data were converted to biomass (kg/hour) in the CPUE model using the length-specific CPUE and the weight-length relationship estimated in this study. 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>.

*Covariates*

For both models (condition and CPUE model), covariates were chosen to reflect hypothesised drivers based on published literature. For the CPUE model we included depth, oxygen, and temperature as covariates. The covariates for the condition model were abundance of sprat and herring (Gårdmark *et al.*, 2015; Casini *et al.*, 2016a), available on a ICES rectangle (1° by 30') and ICES sub-division level, CPUE of cod and flounder on a haul and average per ICES rectangle), representing intra- and interspecific competition for mainly benthic food resources (Svedäng and Hornborg, 2014; Orio *et al.*, 2019; Neuenfeldt *et al.*, 2020), haul-level sea bottom temperature and sea bottom concentration of dissolved oxygen in the fourth quarter (Casini *et al.*, 2016a, 2021; Limburg and Casini, 2019; Brander, 2020). The latter covariates were derived from the ocean model NEMO-Nordic-SCOBI (Eilola *et al.*, 2009; Almroth-Rosell *et al.*, 2011; Hordoir *et al.*, 2019). In addition, we include depth, interactions between oxygen and depth, temperature, and depth, and lastly oxygen and temperature as covariates. Depth data 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.

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 variable selection because initial model exploration we judged the condition model to be not more overfit than a model without any additional covariates. 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 model fit 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.

***Estimating spatiotemporal development of body condition and catch-per-unit-effort***

*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, used this relationship to calculate Le Cren’s relative condition factor for each individual fish (). Unlike Fulton’s K, this relative condition factor does not rely on the assumption that growth is isometric (), which if violated leads to bias when comparing condition of cod of different lengths as the condition factor scales in proportion to (Le Cren, 1951).

To acquire a spatiotemporal condition factor, we fit a GLMM to the weight-length relationship on log-log scale, assuming Student-t distributed residuals (with 2 degrees of freedom) due to the presence of extreme values:

where represents the weigth at space and time , represents the mean weight and represents the scale parameter. The parameter (corresponding to the log condition factor) 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 the length-coefficient (corresponding to the allometric exponent ), and represents a vector of the -th additional covariate and is its effect. and represent spatial and spatiotemporal random effects, respectively. These were assumed to be drawn from Gaussian Markow random fields (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 is the spatial or spatiotemporal (marginal) variance. Lastly, we assumed the spatiotemporal random effects to follow an AR1 process:

where 𝜌 represents the correlation between subsequent spatiotemporal random fields.

*CPUE model*

We fit a spatiotemporal model to CPUE (biomass density, []) data in a similar fashion as for condition to evaluate how the depth distribution, temperature and oxygen conditions have changed of the Baltic cod. This model was then used to predicted density at space and time , and these were used as weights when calculating the average depth, temperature, and oxygen concentration. 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 CPUE at space and time , is the mean CPUE, and represents the power and dispersion parameters, respectively. is an independent mean 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 (Lindgren *et al.*, 2011) (Supporting Information Fig. S2), 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 increase accuracy at the cost of computational time. After initial exploration we chose 200 knots for this application. The models where fit using ‘TMB’ (Kristensen *et al.*, 2016) via the R-package ‘sdmTMB’ (version 0.0.18.9001) (Anderson *et al.*, 2019, 2021). We checked the models had converged 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. All code and data are publicly available at <https://github.com/maxlindmark/cod_condition> and will be deposited on Zenodo upon publication.

# 

# **Results**

The spatiotemporal condition model revealed a decline in the log condition factor () from approximately -4.5 to -4.65 between 1993 and 2006, after which a plateau was reached (Fig. 1A). This corresponds to a 16% decline in weight for a cod of mean length (mean of lengths on a natural log scale). Calculating change over time in Le Cren’s condition index for discrete 10cm 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 10-20cm was more modest (-0.012 annual decline) (Fig. 1C). As the condition factor declines (Fig. 1A), the coefficient of variation (standard deviation of Le Cren’s condition index over the mean increased), indicating that the variation did not decline as steadily as the mean and that the relative variation is now larger than in the beginning of the time series (Fig. 1C).

D Predictions from the condition model illustrate the presence of consistent “low spots” of condition in the condition index decline for deep areas of the eastern Baltic Sea (east of Bornholm, south of Gotland and between Öland and Gotland) (Fig. 2, Fig. SX, Supporting Information), but that the condition factor declines in whole area over time. The poor condition of cod in eastern deep areas could be due to the lower diversity and abundance of benthic food items and the lower concentrations of dissolved oxygen (Fig. 3). The covariates with the largest positive standardized effect sizes are oxygen, sub-division level sprat abundance and temperature (Fig. 3). Depth, interactions between oxygen and temperature, depth and temperature and depth and oxygen, and lastly sub-division abundance of herring are all negatively associated with condition (weight) (Fig. 3).

The standardized effect size for oxygen is 0.01, meaning for each unit increase in the standardized oxygen variable (i.e., 1 standard deviation or 1.8 ml/L), log weight increases by 1%. The average oxygen concentration in the environment declined by approximately 0.18 ml/L or 0.007 ml/L year-1 on average between 1993 and 2019 (Fig. 4C). However, the average oxygen concentration experienced by the cod, calculated as oxygen concentration weighted by estimated CPUE of cod, declined by 0.7 ml/L or 0.027 ml/L year-1 on average) (Fig. 4C; see Supporting Information Fig. S4 for sub-division separately). This change alone is predicted to result in a decline in the log condition factor by 0.4% during the study period (which can be compared to the total decline in the log condition factor by about 3.2%). The faster decline in the experienced oxygen concentration is likely partially driven by the progressive deepening of the cod, going from an average of 46 m in 1993 to 51 m in 2019 – depths where there the difference in oxygen concentration is approximately 0.3 ml/L). Moreover, the negative interaction coefficient between depth and oxygen suggests that the negative effect of depth decreases for every unit decrease in oxygen, again highlighting the detrimental combination of deep areas poor in oxygen for condition.

Temperature is positively related to condition (Fig. 3), and this is likely a spatial (rather than temporal) effect, reflecting higher body condition in shallower and warmer waters. Interestingly, the experienced temperature by the cod closely follows the trend in the environment (Fig. 4D), despite the deepening of the populations, suggesting the potential “cooling” from the deepening is offset by the general warming of the waters.

The abundance of sprat is positively related to body condition at the spatial resolution of the sub-divisions (Fig. 3), in line with the hypothesis that a lack of pelagic food has driven the decline in body condition. However, while the abundance of sprat has declined in abundance from the peak in the mid 1990’s overall in the entire Baltic Sea, the trends vary by sub-division (Supporting Information Fig. S5). Moreover, the CPUE of cod has also declined (as also indicated by the CPUE model, Fig. 4A), and therefore there is no clear relationship between the ratio of cod to sprat over time (Supporting Information Fig. S6). Herring abundance on a sub-division level is estimated to have a negative effect on the weight of a cod given its length, meaning there is no support for lack of herring being the cause of the decline in body condition. This result did not change when fitting the same condition model to cod above 30 cm, a size group that is able to feed on the entire size-distribution of the herring (Niiranen *et al.*, 2019). In fact, most parameter estimates did not change considerably when fitting the condition model to cod below or above what is approximately maturation size (30 cm) (Supporting Information Fig. S7-8), and neither is there a clear relationship between model residuals and length (Supporting Information Fig. S3). This suggests the length-weight model is appropriate for all lengths of cod, the changes in the size-distribution of cod are accounted for and that the condition factor has declined within the whole cod population.

All variables related to CPUE of cod and flounder had small effect sizes and confidence intervals overlapping 0. This suggests density-dependence or competition for food resources has had little effect on the decline of the cod condition. Fitting the model to cod below 30 cm (sizes believed to be more prone to competing for benthic resources with flounder) had only a small effect on the coefficients, with the flounder coefficient being more negative, but still with a small effect size and confidence intervals crossing zero.

# **Discussion**

Using a fine-scale spatiotemporal condition model, we show that the weight given its length of cod in the Baltic Sea has declined by 16%, primarily between the years 1993-2006. Our analysis reveals a complex picture regarding the cause of the decline in body condition, with changes in the environmental variables (such as deepening and reduced oxygen) having the largest, but still relatively modest effect sizes. Furthermore, in contrast to recently proposed hypotheses (Svedäng and Hornborg, 2014; Neuenfeldt *et al.*, 2020; Orio *et al.*, 2020), we were unable to detect clear effects of food limitation in driving the changes in condition. These findings are discussed in more detail below.

Previous studies have suggested both direct (Limburg and Casini, 2019; Brander, 2020) and indirect effects (Neuenfeldt *et al.*, 2020; Orio *et al.*, 2020) 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 ml/L on average. This is higher than a recent estimate of 4.5 ml/L in recent years (for the eastern Baltic cod) (Brander, 2020; Casini *et al.*, 2021), which has also been proposed as a threshold for negative but sub-lethal physiological impacts (including reduced feeding rates) (Hrycik *et al.*, 2017). Our estimate did not differ when fitting the CPUE model to the eastern Baltic cod stock (subdivisions 24-32) separately (Supporting Information Fig. S9). This difference could be due to previous studies estimating oxygen levels indirectly, by calculating the average depths and then average oxygen at those depths. By contrast, 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 CPUE model. This should be a more precise approach, since the relationship between oxygen and depth is very variable. 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 levels is 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 European 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 not spatial overlap as covariate. Instead, we use the average CPUE or flounder and cod at the haul and at the ICES rectangle-level to include “crowding” effects. Increased density dependence has also been linked to lower growth rates, though not via shrinking habitats, but fishery-induced size truncation causing higher intraspecific competition among smaller sized fished who primarily feed on benthic prey (Svedäng and Hornborg, 2014). We could not detect any effects of cod or flounder CPUE for body condition (at neither scale), meaning cod are not skinnier in areas with higher catches of cod or flounder. It does not, however, mean that competition is not occurring, because there may simply be more cod and flounder where there is high abundance of food. To properly test for competition, we would need data of the benthic community, which does not exist on this spatial and temporal resolution. That said, it does not seem likely that the flounder has caused the decline in condition via competition, since the flounder population in subdivisions 24 and 25 declined steeply in the years where condition decline (mainly 1993-2006) (Orio *et al.*, 2017). 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 interesting 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 find positive effects of sprat abundnace at the ICES subdivision level, but it is 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 and the ratio of cod to sprat has remained stable in the time series (Supporting Information Fig. S6). 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 (as indicated from the model residuals; Supporting Information Fig. S3). Hence, in order for the decline to still be related to competition or food availability, all food sources utilized by cod over ontogeny ought to have declined more or less in synchrony. Even if that is possible, (Neuenfeldt *et al.*, 2020) showed that the feeding levels of cod where relatively high in the period 1995-2004 when condition declined, and the growth rates had not yet declined to the lowest in seven decades (Mion *et al.*, 2021). Hence, a decade of declining condition under normal feeding- and growth rates preceded the poor growth we see today. That food limitation 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). This, to compensate for declines in the quality rather than quantity of food (Svedäng *et al.*, 2020).

In conclusion, our study provides new estimates of the body condition of Baltic cod and the population-level changes in depth distribution and average oxygen condition that account spatiotemporal variation. We show, in line with (Casini *et al.*, 2016b), that the decline in body condition started in the early 1990’s and reached a bottom in the mid 2000’s, and that condition has declined for all sizes. These two features, together with analysis of covariates and recent studies reveal that food limitation likely has not driven the decline in body condition that preceded the decline in growth and the poor physiological status of the stocks. However, it is possible these factors can still limit a “physiological” recovery of cod in more recent years. 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 in recent years, when condition and growth rates are low, and mortality is high. The Eastern Baltic cod stock are not predicted to grow even in the absence of fishing mortality. This makes it even more important to understand the role of interactions between species for the development of the stock (Eero *et al.*, 2020).

# **Acknowledgements**

Ale Orio, Federico. James Thorson, Martin Hansson and Elin Almroth Rosell at SMHI, Olavi Kaljuste for providing pelagic data, staff involved in sampling

# **Figures**

Chart, scatter chart

Description automatically generated

**Fig. 1.** A) Logarithm of the condition factor ( in Eq. 2) survey domain for years 1993-2019, acquired by predicting from the spatiotemporal condition model with all covariates held at zero (i.e., their means). 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% credible interval). C) Coefficient of variation in Le Cren’s condition index as a function of yead (shaded band corresponding to the 95% credible 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, surface chart

Description automatically generated

**Fig. 2.** Predicted condition with all co-variates set to zero (i.e., their means), such that the prediction corresponds to the depth, temperature, and oxygen-dependent log-condition factor for years 1993, 2001, 2008, 2018. For all years in the series, see Fig. SX, Supporting information.

Table

Description automatically generated with low confidence

**Fig. 3.** Mean and 95% confidence interval of the standardized coefficients and the spatial and spatiotemporal standard deviation ( and , respectively) in the condition model.

Chart

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 Fig. SX, Supporting information), 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 (all years pooled) (D) oxygen concentration weighted by predicted cod density. Lines correspond to the 1st, 5th and 9th decile.

# **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.

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., 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., 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.

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.

Momigliano, P., Denys, G. P. J., Jokinen, H., and Merilä, J. 2018. Platichthys solemdali sp. nov. (Actinopterygii, Pleuronectiformes): A New Flounder Species From the Baltic Sea. Frontiers in Marine Science, 5: 225.

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.* 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.

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.

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