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

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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, these variables have only been evaluated on large spatial scales (Baltic Sea basin- or population level), even though they operate on smaller scales. 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 environmental variables (oxygen, depth, temperature) have stronger effects on condition than ecological variables (density and food), and that cod are moving to deeper and less oxygenated areas, which can explain the decline in condition over time. Understanding the drivers of spatiotemporal variation in body condition is important for understanding the impacts of climate change on productivity and resilience of marine fishes.

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# **Introduction**

The relationship between length and weight has a long tradition in fisheries science. From it, body condition indices can be calculated (Beverton and Holt, 1957; Ricker, 1975; Nash *et al.*, 2006), which describes the “plumpness” of an individual, or its weight relative to its length. Hence, condition is related to accumulated energy reserves and often positively associated with fitness (Morgan *et al.*, 2010; Thorson, 2015). For instance, individuals with high condition have greater reproductive success (Hislop *et al.*, 1978; Marshall and Frank, 1999), and poor condition increases the likelihood of skipped spawning (Jørgensen *et al.*, 2006; Mion *et al.*, 2018) and can lower chances of survival (Dutil and Lambert, 2000; Casini *et al.*, 2016b). Because of the link between condition and physiological status, and the availability of length-weight data, body condition constitutes a valuable index for evaluating changes in productivity of fish stocks (Thorson, 2015; Grüss *et al.*, 2020).

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

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

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

In this study, we apply spatiotemporal predictive-process GLMMs to characterize spatiotemporal variation in body condition of Eastern Baltic cod. We use Le Cren’s condition index (Le Cren, 1951), which defines condition as the residuals from a fitted length-weight regression. Hence, it allows for allometric growth, i.e. a length-exponent slightly larger than 3 (as is often observed in fishes) (Froese *et al.*, 2014), in contrast to Fulton’s condition factor which assumes isometric growth (weight being related to the length cubed) (Ricker, 1975; Nash *et al.*, 2006). We use data from the Baltic International Trawl Survey between 1991-2020, which corresponds to a period of initially high but deteriorating condition (Casini *et al.*, 2016a). We then seek to (1) identify which set of covariates (density of flounder, cod, availability of pelagic prey or oxygen concentration) provide a parsimonious fit to weight-length and (2) estimate the variation explained by these covariates and contrast that to variation explained by spatial and spatiotemporal variation.

**Materials and methods**

*Data*

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

*Covariates*

Covariates were carefully selected to represent a hypothesized driver of variation in condition, and is likely to explain at least some variation (Table 1). Following (Thorson, 2015; Grüss *et al.*, 2020), we rescale all covariates to have a mean of 0 and a standard deviation of 1, which allows for comparison between the estimated coefficients and the standard deviation of spatial () and spatiotemporal variation ().

*Table 1. Summary of covariates and the corresponding hypothesized effect on cod condition.*

|  |  |  |  |
| --- | --- | --- | --- |
| **Covariate** | **Driver/Hypothesis** | **Reference** | **Source** |
| Cod catch-per-unit effort by haul (#/h) | Increases intraspecific competition | (Svedäng and Hornborg, 2014) | BITS |
| Flounder catch-per-unit effort by haul (#/h) | Increases interspecific competition for benthic food sources | (Neuenfeldt *et al.*, 2019; Orio *et al.*, 2019) | BITS |
| Oxygen concentration | Affects spatial extent of habitat thus inter- and intraspecific competition; direct effect on physiological processes; direct effect on benthic food availability (e.g. Saduria) | (Casini *et al.*, 2016a) | CMEMS (NEMO-Nordic-SCOBI) |
| Sprat abundance per ICES rectangle of haul (#/1° by 30' rectangle) | Increases food levels for piscivorous cod | (Gårdmark *et al.*, 2015; Casini *et al.*, 2016a) | BIAS |
| Herring abundance per ICES rectangle of haul (#/1° by 30' rectangle) | Increases food levels for piscivorous cod | (Casini *et al.*, 2016a) | BIAS |

*Model description*

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

(1)

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

(2)

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

(3)

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

where is the spatial (marginal) variance. This model (Eq. 1) can be viewed as an approximation of Le Cren’s condition index (Grüss *et al.*, 2020), as the log of the condition factor, i.e. or the constant in the allometric relationship, can be defined as:

(4)

Thus, Eq. 1 is a model for a spatially and temporally varying condition factor.

*Model selection and comparison*

We conducted exploratory analysis without the main covariates to decide on a candidate baseline model. This was done in three steps: (1) deciding on an appropriate distribution for the residuals (2) compare models with different number of “knots” to ensure model convergence and that the spatial processes were accurately captured and (3) whether or not to include year as a fixed effect or a spatial random field of slopes of year effects, as well as including an independent spatiotemporal field for each year or if there is support for a spatiotemporal field following an AR1 process.

Next we evaluated the ability of covariates to explain spatial variation in condition.

*Model fitting*

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

All code and data reproducing data processing and model fitting is publicly available at <https://github.com/maxlindmark/cod_condition> and will be deposited on Zenodo upon publication.

***Points I would like to stress:***

1) no one has so far look at the food-availability or oxygen explicitly across space and time and related that to condition. Instead, we tend to have used averages across space (e.g. sub-divisions, stock. Find a paper that doesn’t discretise!) or discrete time periods. However, oxygen can affect habitat quality already before there is an oxygen deficit, and competitors (flounder, cod) and prey are not evenly distributed in space across time. Hence, there is a need to explore fine scale spatiotemporal dynamics. (After accounting for that, we still find large residual variation, which suggests… other factors e.g. metabolism)

# **Results**

# **Discussion**

Discussion points:

Growth =/= condition… need to get that out there in order to compare the papers below.

Our approach reveals spatial structure in the body condition and change in body condition over time.

Sum what we know: cod experience less oxygen – less oxygen means lower feeding, metabolism and growth – we don’t find a positive effect of food density or negative effect of crowding, which we would do had it been limiting – we know from otholits that they experience more mild hypoxia (Limburg) and that either metabolism goes down or growth up (Svedäng) - i.e. down because we know growth goes down.

**Svedäng** 2020: They eat a lot still, so maybe it’s some kind of vitamin deficiency?

**Overgård**: If we feed them herring they growth really well

**Engelhart**: Tiamin def, but no time series

East-west difference in growth: **McQueen** (2020)

Long term changes in tagged cod growth: **Mion** (soon)

**Parasites**: Horbowy and/or Ryberg (see if any interesting there)

**Neuenfeldt**: If they would be scarce (and limiting), we should find that areas with little more sprat gives higher condition, and less flounder e.g. We also know that they undergo strong ontogenetic shifts in diet, so if it was down to a specific prey that should come out as a size-signal. Yet our model does not have that size-trend in the residuals

Read how oxygen affects metabolism, e.g. here: <https://www.sciencedirect.com/science/article/pii/S1546509808000101> . Can also ask phys science twitter

**Chabot, Neuenfeldt & Brander**: Neuen get stuck on extrapolating the specific, missing the overall effects of hypoxia (can’t extrapolate from these different ecosystems exact numbers). Further, if competition, we should see negative effects of density (or the rescaled variable). Moreover, we do not find a clear size-based difference, because there’s no pattern in the residuals. This is in line with Mion (et al) in prep, which show negative declines for all sizes.

**Haase:** even in the title we see flounder stealing food…

Also discuss the change in maturity size?

* Management implications? Could mean that suggest spatial fisheries of sprat and herring would be limited in effect (Eero & Cardinale open for that)

In discussion point: assuming they haven’t changed their distribution (tough assumption but we can’t overcome it right now), we can extract the raster value for saduria from Gogina each year, and see if the average overlap has changed. For that we would need a cod-distribution map, which we could easily do. Then the question is: can we assume saduria hasn’t changed their distribution? Not really… Without invoking all this, we can use the verbal argument that cod are now in deeper areas and there there’s no flounder nor saduria (AND THE POINT ABOUT NOT BLAMING FLOUNDER! IDENTIFY THAT AS A KNOWLEDGE GAP… BASICALLY; SPATIOTEMPORAL HAASE MODEL). SUMMARY: can we use the Gogina map as a raster to see how much cod has moved into average saduria habitat?

Re. Saduria data. We don’t really know if it even has decreased… The master’s thesis used BITS data, which aren’t reliable before 2013 (pers comm mich). So not really sampled properly. That data are also available on ICES ecosystem services. SMHI has too few sample stations per year, and the data from Mattias Sköld is only coastal basically. One option is to ask about the Gogina paper. BUT! Saduria doesn’t exsist in the Western Baltic Sea - too salty! So, if we can get a hold of Saduria, that would mean we should probably focus our efforts on that part (also remove barrier spde). But if we find similar declines in condition also there, that implies the Saduria-effect isn’t likely the main effect!

Pattern is stable over time, hotshots. So discuss why they are moving there in increasibg numbers cite ale.

Also discuss implications for e.g. assessment as thorson

No size effect? Because the length-weight regression fits OK for all sizes? Plot diff between pred and obs by size or have i done that?

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# **Literature cited**

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

Bergström, U., Englund, G., and Bonsdorff, E. 2002. Small-scale spatial structure of Baltic Sea zoobenthos—inferring processes from patterns. Journal of Experimental Marine Biology and Ecology, 281: 123–136.

Beverton, R. J. H., and Holt, S. J. 1957. On the Dynamics of Exploited Fish Populations. Fishery Investigations London Series 2, Volume 19.

Boyd, C., Woillez, M., Bertrand, S., Castillo, R., Bertrand, A., Punt, A. E., and Trenkel, V. 2015. Bayesian posterior prediction of the patchy spatial distributions of small pelagic fish in regions of suitable habitat. Canadian Journal of Fisheries and Aquatic Sciences, 72: 290–303.

Bromley, P. J. 2000. Growth, sexual maturation and spawning in central North Sea plaice (Pleuronectes platessa L.), and the generation of maturity ogives from commercial catch data. Journal of Sea Research, 44: 27–43.

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.

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., Hjelm, J., Molinero, J.-C., Lövgren, J., Cardinale, M., Bartolino, V., Belgrano, A., *et al.* 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. Proceedings of the National Academy of Sciences, USA, 106: 197–202.

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.

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).

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.

Greer, A. T., Cowen, R. K., Guigand, C. M., and Hare, J. A. 2015. Fine-scale planktonic habitat partitioning at a shelf-slope front revealed by a high-resolution imaging system. Journal of Marine Systems, 142: 111–125.

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.

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.

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.

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].

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.

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.

Möllmann, C., Diekmann, R., Müller‐Karulis, B., Kornilovs, G., Plikshs, M., and Axe, P. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. Global Change Biology, 15: 1377–1393.

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.

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

Neuenfeldt, S., Bartolino, V., Orio, A., Andersen, K. H., Andersen, N. G., Niiranen, S., Bergström, U., *et al.* 2019. Feeding and growth of Atlantic cod (Gadus morhua L.) in the eastern Baltic Sea under environmental change. ICES Journal of Marine Science: fsz224.

Omori, M., and Hamner, W. M. 1982. Patchy distribution of zooplankton: Behavior, population assessment and sampling problems. Marine Biology, 72: 193–200.

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.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada, 191: 1–382.

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

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.

Yaragina, N. A., and Marshall, C. T. 2000. Trophic influences on interannual and seasonal variation in the liver condition index of Northeast Arctic cod (Gadus morhua). ICES Journal of Marine Science, 57: 42–55. Oxford Academic.