01-Dec-2022  
  
Dear Mr Lindmark,  
  
Manuscript ID ICESJMS-2022-442 entitled "Evaluating drivers of spatiotemporal individual condition of a bottom-associated marine fish" which you submitted to the ICES Journal of Marine Science, has been reviewed.  The comments of the three reviewers are included at the bottom of this letter.  
  
The reviewers have recommended publication only after major revisions to your manuscript. Therefore, I invite you to respond to the reviewers' comments and revise your manuscript. Please note that one of the major concerns (Rev. 3) was weak (or even absent) statistical links between the environmental variables considered and cod individual body condition. The reviewer proposes a few very helpful ways on how to address this concern via additional/different analysis. Also, there are several important comments related primarily to the ecology of the cod (Rev. 2) with explicitly associated methodological implications (on either already performed analysis or recommendations for additioanl test).  
  
Please submit your revision by 1 March 2023.  
  
Kind regards,  
Dr Henn Ojaveer  
Editor, ICES Journal of Marine Science  
[henn.ojaveer@ut.ee](mailto:henn.ojaveer@ut.ee)

Summary of revision

* Add it here
* Added numbers to reviewer comments by #1
* Many minor edits to figures
* Overhaul of discussion to add text on random vs fixed effects,

Reviewer(s)' Comments to Author:  
  
Reviewer: 1  
  
Comments to the Author  
General comments  
This work uses an interesting case study of Atlantic cod body condition (an ecologically relevant and management-applicable indicator of fish productivity) and applies a comprehensive model structure to advance understanding of how to evaluate drivers of change across space and time. It combines a comprehensive suite of possible environmental (depth, oxygen, and temperature) and ecological (prey, competition) covariates as well as latent spatial and spatiotemporal effects into a single model framework. It also demonstrates an approach to evaluate the environmental conditions experienced by a fish population by weighting environmental measurements by fish density. As the paper mentions, determining what changes can be tied to specific environmental and biological covariates, versus latent spatial and spatio-temporal effects, is a challenge. This work extends the body of literature on how to address this challenge and would be relevant to other systems, species, and fish population demographics. The model structure used is very clearly explained and well-suited for the data and questions. The results are well presented and easy to follow. I just have minor suggestions (below) for points in the paper that the authors could clarify:  
  
Minor Comments  
1. L34-35: Should this say “each fixed effect”? To me, this wording makes it seem like it means all fixed effects combined  
- We do in fact mean all fixed effects combined (excluding the factor year effect). We have clarified this in the text in response to comment #11 because it was ambiguous how we calculated those R2 ratios.

2. L36: Just a typo: “lover” should be “lower”  
- Corrected

3. L67-69: Authors mentions that reduced oxygen concentrations lower food intake because of lower metabolic rates in L67—69; it might be worth adding a citation here. Also, I would consider also addressing that increased temperatures (which cod have experienced) can increase metabolic rates (and consequently demands on body reserves and possible decline in body condition)  
- For the combined (potential) effect of temperature and oxygen, see reply to comment #16 below. We also agree that in theory, based on experimental studies, warming could have negative impacts on condition if food is limited. However, while we find that cod do experience higher temperatures now and condition has declined, we also find the temperature has a clear positive (albeit small) effect on condition. We can only speculate why that is (potentially due to condition being higher in shallow, warmer areas in general).

4. L100: I would clarify what is meant by scales by saying “at different spatial scales”, or add in the “ecologically relevant spatial scales” phrase from L296-297

- We agree (see edits on L106-107)  
  
5. L101-102: I found the wording of goal 2 to be vague, especially compared to 1, and I had a difficult time determining which section of the methods addressed this goal. I’m assuming this refers to L160-161 in the Methods, about “evaluate how the depth distribution of cod, as well as oxygen and temperature conditions experienced by cod, have changed”. Is that correct? If so, it would be more clear to make the statement for specific, for instance something like: “Explore how the spatiotemporal distribution of cod impacts the environmental conditions experienced by cod and explore the implications on body condition”. Weighting environmental measurements by fish density to evaluate environmental conditions experienced by the fish is a really interesting and important piece of this paper, and I suggest making this statement more specific and clear to highlight and emphasize it.

- We agree with this comment and think we use the suggested edit (with minor edit).

6. L108: I might have missed this somewhere else in the paper, but what is the number of observations for weight and length data from BITS? It might be helpful to include to get a sense of how much data was used in the condition model.

- Good idea, 94190 individuals for condition (added at L177)

7. L127-128: I understand why a non-spatial model and pooled years were used to estimate a and b for the predicted weight from length, but I would be curious to see if there was any change in relationship between weight and length over different time periods or spatial regions. Or, even just showing in the Supplement the annual weight-length regressions used to convert abundance density to biomass density mentioned in L114-115.

- We have added a supplementary figure showing the parameter estimates used for converting between abundance density to biomass density, by year and species (we include also flounder in this plot). This figure shows 1) a clear negative correlation between the trends in a and b over time and 2) the trend over time (larger a and smaller b) is similar for both cod and flounder. This leads to fish smaller than 20 cm being weighing more in 2020 relative to 1993, and fish larger than 20 cm weighing less now than in 1993. We do not know if these patterns are due to changes in the size-distribution, body shape, or condition over time (and potentially space), but it does not matter here since the aim of these was to get appropriate conversation from numbers to biomass for each year. It does show the core issues with condition factors, i.e., the comparison between individuals/groups/populations given the dependence of the condition factor on the regression parameters (Cone, 1989; Le Cren, 1951), and the correlation between the regression parameters (Froese et al., 2006). Therefore, we chose the approach we did, i.e., to consider eastern Baltic cod between 1993-2019 as a sample and use Le Cren’s relative condition factor to assess the condition of individuals independent of their lengths (Froese et al., 2006; Le Cren, 1951).

8. L152-154 & L175-177: It was not clear to me why spatiotemporal random effects were assumed to follow an autoregressive process only for the density model, not the condition model. It might be helpful to just add a brief explanation for why this was done.

- We initially had the same structure for the spatiotemporal random effect in both models, but the correlation parameter in the AR1 field had estimates overlapping with 0 (0.069 [-0.039, 0.176]) in the condition model, in contrast to the density model 0 (0.622 [0.475, 0.735]), hence we opted for omitting it. We have clarified this in the text (L171 and L194)

9. L242: I am curious if the authors considered also density-weighting the condition factor as another way to evaluate the mean condition?

- It did cross our minds but in the end it was not included. However, we agree it is a very good idea. The condition index then accounts for uneven and changing spatial distribution of cod which should better reflect the population-level average condition, given the spatial variation we observe in both condition and biomass density. We have now updated Fig. 1 (which now also includes a raw mean series of data to contrast with the index), added a supporting figure showing the (uneven) spatial distribution condition samples, and updated the text with a specific paragraph on the index standardization (e.g., L260-267). The raw data mean shows a slightly larger mean condition and a slightly smaller decline over time, compared to the index (now calculated on gridded predictions using cells between depths 10-110.

10. L248-250: It could help highlight this point by describing more specifically some of the patterns observed in Figure 2; for instance, that the consistent low spots of body condition are in the upper northeast corner and lower southwest near 14 E, 54N, there is a dumbbell-shaped area in the middle of the area that seems to be persistently lower than the surrounding area, etc. The spatiotemporal, local-scale differences in body condition are an interesting and unique part of this study, and more elaboration on these patterns could help emphasize this.

- Good advice, we added some text (L265-267), and added a reference to Fig. 5C-D where we show the bathymetry and oxygen maps, so that it’s clearer that the low spots largely correspond to these.  
  
11. L263-268: I understood how each estimated effect size was several times smaller than the random effects after looking at Figure 3, but when I initially read this section in the Results I was unclear how the marginal R2 of 0.153 for the fixed effects compared to the R2 of 0.218 for random effects fit into this claim, since 0.218 is not even double 0.153. This section of the results (showing the effect sizes of fixed effects vs latent spatial/spatio-temporal variation) is a huge piece and really interesting part of the paper, so it might be worth clarifying and emphasizing this more. For instance, there could be more elaboration about how each individual fixed effect size was several times smaller, and that the overall combined effect, as shown by the R2, was X% less.

- We see how those numbers could be mixed up. 0.218 and 0.153 correspond to the marginal R2 of all random effects (spatial and spatiotemporal) and fixed effects–including the factor years. However, two thirds of the fixed effect R2 is made up of the factor year effect. When we talk about the 4.5 times higher R2 for random effects we use the R2 omitting these and include only the remaining 16 biotic and abiotic covariates. We have clarified this in the abstract, and on L314-318. For the other point, that each individual fixed effect is several times smaller, we have also clarified that in the text. Specifically, on average, the effect size of fixed effects (omitting year) is 0.002, while that of random effects is 0.049. Hence, the ratio is ~44, which is much larger than the ratio of R2’s (because while the average effect is small, they are(Bolger and Connolly, 1989; Morgan *et al.*, 2010; Thorson, 2015) also many, as you point out). This has also been clarified in the text (L312)

12. L298: Authors could consider including some broader context on how the decline in body condition of cod in this study compares to changes in body condition in other fish populations.  
- Good idea. On line 438 we have added a reference to the somewhat synchronous change in the condition of sprat and herring in the Baltic Sea. We have not added any discussion on general trends in condition across ecosystems, because our understanding of the literature (mainly studies using similar modelling approaches as we do), is that the trends are very heterogeneous among species and in species’ associations with specific covariates.

13. L301-302: Were the shifts in spatial distribution of cod over time to deeper areas, with lower oxygen, also to cooler environments? Or do those deeper, less-oxygenated areas have higher prey density? If cod were moving into deeper areas, but there was less oxygen in those environments, could it have been to seek cooler temperatures or more prey at those deeper depths? It might be worth further elaborating here on possible reasons or mechanisms for the shift in spatial distribution.

- It’s a bit puzzling to us why cod have shifted their distribution to deeper and less oxygenated habitats (which also have lower diversity of benthic prey). Our conditional effect plots for the density model shows a monotonically increasing density with our smooth temperature effect (which could indicate they are not seeking cooler temperatures to stay near their optimum temperature). We are unsure therefore on if we should expand too much on this topic in the discission, given that we also have added a new paragraph.

14. L302-304: It could be helpful to include context on the magnitude of random effects vs fixed effects of the authors’ model compared to other similar studies using GLLM’s with fixed environmental covariates and random spatial fields (e.g. Thorson et al. 2017 <https://onlinelibrary.wiley.com/doi/abs/10.1111/faf.12225>).  
- Thanks for the suggestion. We now cite this in the discussion, where we have added a sentence of the importance of first estimating the variance explained by covariates (L482), and we also cite Thorson (2015) on line 371, on the relative importance of fixed vs random effects.

15. L304-307: It was not readily apparent to me what the mechanism for this would be. Are the authors saying that using individual-level body condition rather than average condition adds variation in the data that makes an effect harder to see when fitting the model, and therefore that the low effect sizes in this model compared to the random spatial fields are an artefact of the data type used? If this is what they’re suggesting, is there a recommendation for what the best approach would be for future work? Or was there a different mechanism for why using individual-level body condition vs. average condition caused less strong relationships? I suggest more specifically explaining this statement.  
- Thanks for the suggestion. We have written a new paragraph in the discussion on this topic (L455-475). Here we imply that one of the reasons we conclude smaller effects of environmental covariates compared to previous studies (though they are not entirely comparable), is that we use individual level data, and that there is large variation in condition among cod. (I.e., variation in condition of individuals caught in similar locations is very high, and therefore relationships between environmental variables and this contributes to their estimates being small/uncertain). We also discuss the use of individual-level data in combination with latent variables for quantifying condition and avoiding false sense of effects from covariates, and in identifying sources of explained vs unexplained variation.

16. L348-L351: Similar to comment about L67-69, consider adding in some references and discussion about how increased temperatures increase metabolic demand, so that even if food is available, there may still be a decline in condition, and that decreased oxygen and increased temperature can have synergistic effect on metabolic demand (and consequently condition).

- This is an interesting point. We have added a sentence on how the effects of temperature and oxygen can be synergistic (higher metabolism, lower food intake rates), and provide a reference (L68-L70)

17. L394-397: This point—about the strength of latent variables compared to the fixed effects—could be emphasized even more strongly by elaborating on how including only environmental covariates, and not considering latent spatial and spatiotemporal effects, in models may lead to false confidence in the explanatory power of an environmental variable. I suggest more clearly describing what they consider best practices or recommendations for future studies.  
- We agree—we merged this feedback with the one in comment #15

18. L650 Figure 1A: Typo in the x-axis label

- Thank you, this has now been correct in this figure and in the marginal effects plots (Fig. SX)

19. L692 Figure 5: I think it would clarify this section to include the weighted temperature in this main figure in the paper, rather than putting it in the supplement. Since the temperature, oxygen, and depth cod experience are all related to each other, and it’s really helpful to see them all side-by-side.  
- The temperature panel is now included in Fig. 5

**References**

Cone RS. 1989. The Need to Reconsider the Use of Condition Indices in Fishery Science. *Transactions of the American Fisheries Society* **118**:510–514. doi:[10.1577/1548-8659(1989)118<0511:TNTRTU>2.3.CO;2](https://doi.org/10.1577/1548-8659(1989)118%3c0511:TNTRTU%3e2.3.CO;2)

Froese R. 2006. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology* **22**:241–253. doi:[10.1111/j.1439-0426.2006.00805.x](https://doi.org/10.1111/j.1439-0426.2006.00805.x)

Le Cren ED. 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. doi:10.2307/1540

Reviewer: 2  
  
Comments to the Author  
The authors present a thorough spatio-temporal analysis of cod condition. The text is very well written, the time span for the analyses is well chosen, representing the crash of cod condition after the early 1990s. The analysis performed is methodologically new to the Baltic Sea. While several authors have treated the cod condition problem from different angles (mainly statistically and bioenergetically), the major novel results of this study (to me) is, that latent spatial and spatio-temporal variability show about 5-times higher effect sizes than the ‘usual suspects’- abiotic and biotic conditions in the respective regions. This made me curious, and I would have appreciated more discussion on this topic.

Before I propose potential improvements for the discussion, I would like to address the only (possible) shortcoming in the methods: I had a quick check on the BITS survey, and more than 80% of the stations are at depts greater than 40 m. By far the most stations are below the halocline. Does this create a bias in the representation of cod condition? The results maps seem to cover a great deal of water with depths < 40 m. So, either the authors should limit the depth range in their maps, or explain that the two very different habitats above and below the halocline have been treated in a way that avoids bias in the results due to under-representation of the habitat above the halocline.  
As aforementioned, it is interesting that latent variability explains much more than the variable effects. This topic should be elaborated on in the discussion. Please note that e.g., the liver worms also are spatially heterogeneous.

- The data we use range between 10-190 m (but note the 99% percentile is 108m, so the 190 is an outlier in this case). When we visualize predictions in space, we use the range 10-120m, which corresponds to the range used to fit the model and estimate the effect of depth. We do not see the need to limit the range for prediction to an even smaller range than used for fitting (which seems to be the suggestion here).

We have conducted sensitivity analysis (not shown) with respect to also trimming the prediction grid to 10-120m when calculating the index, but since it showed virtually no difference, we kept the full prediction grid in the first submitted version. However, we have now chosen to use the trimmed prediction so that it better matches the spatial plot. We have also added a section in the methods on the spatiotemporal prediction and index calculation.

On a related note, we picked up the idea brought up by Reviewer #1 and have now weighted the annual condition index by the predicted local density of cod. In summary, our index is based on spatial predictions within the depth ranges used to estimate the effect of depth, and density weights at location, such that spatial predictions in high-density areas get more weight when calculating the total, population index for each year.

I would appreciate a more in-depth discussion of possible reasons for this dominance of latent variability in a well-preformed spatial model. Immediately, I thought that there might be sub-systems (the different basins) that each have different factors limiting cod growth. Hence, if aggregated the effects might appear blurred? I would appreciate, if the authors could repeat the analysis on a basin (ICES Sub-division level). Is the relation between variable and latent effects on this spatial scale the same as for the whole Baltic Sea? This would be important, because if not, the Baltic Sea-scale latent effects can be explained by basin-differences, but if yes, there is something going on we were not aware of, yet.  
  
- This is an interesting idea. But, a few things: the condition index declines in a very synchronous way between subdivisions (basins). Even more so after density weighting as brought up by Reviewer #1. This is interesting because the subdivisions vary tremendously in sprat biomass (orders of magnitude) and the trend in sprat biomass over time (Fig. SX), and in oxygen (also here the both the value and the trend over time). This pattern likely also exists for other covariates with some effect on condition, such as temperature. Despite this, the condition trends are synchronized. For that to occur in the presence of subdivision/basin-specific relationships between condition and covariates, they would need to cancel each other out in a way that just doesn’t seem likely. Another point we wish to add is that we in general do not see the merit in splitting up the data based on somewhat arbitrary spatial units and fitting separate regressions to there. In doing so, we lose both the range of covariates and sample size, which would make it harder to disentangle each covariate’s effect. Lastly, by splitting the data into smaller units (such as subdivision), we would need to change the mesh and it would make the spatial random effects difficult to compare.

As an example, however, we have refitted the main model with interactions between Saduria biomass density, oxygen concentration, cod biomass density, and sprat biomass (all at the ICES rectangle average scale), and subdivision. This allows effects to vary between basins. We find that the spatial and spatiotemporal standard deviations are unchanged from the original model to the model including interactions (from 0.0425 to 0.0419, and 0.0544 to 0.0540, respectively). Below is a figure showing the coefficients for these variables (and how they do not change much between subdivisions, except for saduria, (note coefficients and error bars have been changed from a difference to estimate subdivision 24 to the actual slope):

Table

Description automatically generated with low confidence

Reviewer: 3  
  
Comments to the Author  
The manuscript investigates biotic and abiotic environment of cod could determine individual body condition index variability. Despite many studies already existing on cod body condition in this area, I acknowledge the novelty of this study by considering individual values. I really appreciated to read this study, but several comments about the potential explanation of the lack of significant results raised and are detailed below.  
  
My main concern is about the weak (or even absent) statistical links between the environmental variables considered and cod individual body condition. If I understand well, you used cod samples from October to December and environmental variables during the same period. But you never try to test a relationship between cod body condition and environmental variables averaged on the 2 or 3 months preceding the sampling. I mean that fish body condition is an integrative index that do not necessarily reflect the environmental conditions experienced by the individual at the sampling moment. I am aware that for sprat and other fish biomass, this could be difficult, but I really think that testing environmental variables such as oxygen and temperature averaged on 2 or 3 months or with a lag could improve the results.

- We agree with these points. In the previous version, we addressed this uncertainty in experienced environmental conditions (that is due to unknown movement before catch) by averaging environmental covariates on larger scales (note also these were averaged for the entire q4, so some shorter lag is inherent in that variable).

As per your suggestion, we have added a lag to oxygen and temperature (the only ones we are able to lag within a year, as you note). Note that we only lag the large scales variables (ices rectangle averages), because they are meant to reflect previous exposure, not the ones at the catch location. The choice to use the average in quarter 3 is somewhat arbitrary. We do not know what time is the most appropriate or how to best weight the average to give more weight to values closer in time (and closer to the catch location). Our new analysis show there is a correlation between the ICES rectangle averages between q3 and q4, see figure below), and, importantly, the parameter estimates are essentially unchanged, see table below (but note these exact parameter estimates may not perfectly match the manuscript since they were extracted before we switched to bilinear extrapolation when extracting point values from rasters, see also reply to your next comment). We include only the lagged variables in the main analyses in the revised manuscript since it better reflects what it is supposed to represent (environmental conditions back in time).

|  |  |  |
| --- | --- | --- |
| Quarter | Temperature | Oxygen |
| 3 | 0.0064 (0.0016, 0.0113) | 0.0068 (0.0018, 0.0119) |
| 4 | 0.0079 (0.0034, 0.0125) | 0.0067 (0.0012, 0.0122) |

Chart, scatter chart

Description automatically generated

Relationship between temperature (left) and oxygen (right) in quarter three (y-axis) and four (x-axis).

I also wonder how the match between individuals body condition and environmental conditions is done for individuals sampled near the edge of an ICES rectangle or subdivisions. For these individuals, even if cod is probably a resident fish, they may have moved just before sampling and be assigned to wrong environmental conditions. Could you for these individuals (caught close to the edge between areas) compute an average of two areas? I guess that environmental condition between two adjacent areas are probably really close, but the case of these individuals deserve to try something.

- This is an interesting point that is somewhat difficult to assess and overcome, because it is inherent in using aggregated variables that it will not be the most representative value for all individuals within the large-scale spatial unit. But on average it might make sense. You are also correct in that the covariates we consider here are quite autocorrelated in space (see e.g., spatial plots of depth, oxygen and temperature in Fig.5, and the ICES rectangle level biomass of sprat (Fig. S26). Given these patterns, individuals near the edge of a larger scale spatial unit are likely not assigned environmental conditions that differ dramatically from what they experienced when caught or in the months before they were caught.

Moreover, we do not think it is really feasible to match individuals within those larger scale spatial units depending on how close they are to the center of the spatial unit (we would also have to then define what is close enough to a border etc.). However, we did add a sensitivity analysis (Fig. S15). Here, instead of calculating the median covariate value within the ICES rectangle (as in the main analysis), we aggregated the raster files such that each cell approximately had the area of an ICES rectangle. Then we extracted the covariate value at location using bilinear interpolation (i.e., a weighted mean based on the four nearest surrounding cells). We did this for temperature, oxygen, depth and *Saduria entomon* because those are our raster-derived covariates. The estimates for *S. entomon* and depth were very similar but for oxygen and temperature, the raster-resampling approach led to slightly larger (positive) estimates (but the effect of depth was estimated to be less negative, so this approach did not lead to larger magnitude of estimates in general). The ratio of covariates effect sizes to spatiotemporal standard deviation was consistent between the models.

Finally, we opted to use bilinear interpolation as a standard method for extracting raster-derived covariates (i.e., also the haul-level covariates) to smoothen out the surfaces we link to each haul with condition data. This change did not have any big effects on the pattern of explanatory power of fixed vs random effects, nor the sign of estimates, however, it did lead to *S. entomon* having a larger positive effect and cod density to have a weaker effect, and we have updated the text to reflect that.

Minor comments:  
Regarding the references used, especially in the introduction, I recommend to authors to use more general studies. For example, line 50 and 52, they use Thorson et al., 2015 to justify very broad statements about fish body condition. I really think that studies or books like Lloret et al., 2013 and Bolger and Connelly 1989 should be used instead of references on one species and/or one area. This comment is also valid for many references used in the introduction and discussion.

- Thank you, we have added the Bolger and Connelly 1989 reference to L57.

Line 299: Is ‘poor body condition spot’ better than ‘low-spot’?  
- Thank you for the suggestion, but of the two options we prefer “low-spot”

References used:  
Bolger, T., & Connolly, P. L. (1989). The selection of suitable indices for the measurement and analysis of fish condition. Journal of Fish Biology, 34(2), 171-182.  
Lloret, J., Shulman, G., & Love, R. M. (2013). Condition and health indicators of exploited marine fishes. John Wiley & Sons.