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

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  
L34-35: Should this say “each fixed effect”? To me, this wording makes it seem like it means all fixed effects combined  
- That’s what is meant yes (explain better)

L36: Just a typo: “lover” should be “lower”  
- Yes…

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)  
- Will add a citation

- Yes, that’s true (higher metabolism and higher demands on body reserves). The effect on condition however should ultimately depend on the relative temperature dependence of food intake rate in relation to metabolism (all else constant, but see comment further down on a related question).

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

- I agree, clarify, since it’s a key spot (last paragraph of the intro)  
  
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.

- I agree with this comment and think we can use the suggested edit

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.

- Will do!  
  
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 can do both (because that’s what we did in previous versions). Basically, our approach now (modelling residuals as a response variable) is very much the same as looking at the intercept from a length-weight regression. (Explain/show why).

- I could show that too, but perhaps it’s confusing because there I estimate both a and b (w=aL^b) per year using a simple lm(), whereas in the paper, we keep b fixed because to compare changes over time in weight relative to length, we need to keep the length-weight exponent constant, else we would compare apples and pears between years.

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.

- Because the diagnostics (and AIC, though we don’t really use AIC to decide these things) were better. Unfortunately I don’t recall which and I didn’t specify it either in the e-mail from July when I told you about it, hmm.

L242: I am curious if the authors considered also density-weighting the condition factor as another way to evaluate the mean condition?  
- Interesting, and yes this has been considered (see attachment in e-mail, co-authors)

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.

- Agreed we can do this (around line 250)  
  
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 can clarify this, and I need to check that the latest numbers are in the text. That said, the value 0.153 includes the factor year effect, which is why it’s so big in relation to the random effects. The X% that we want to present (whichever the final number is) is the fixed effects without factor year in relation to the random effects.

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.  
- Let’s think about it and see if we can find studies we can compare (R3 provides some references)

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.

- That I do not now. I guess we can fit a simple density model with a spatial trend random field, or calculate the spatial trend manually (might do this actually) from the prediction grid, and then compare that with a) the distribution of temperatures and b) bathymetry. But it will be difficult to address.

- Prey density is likely much lower (at least less diverse) in those areas.

- We can discuss that yes (in the literature temperature and predation has been suggested)   
  
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>).  
- Great, we’ll have a look. And we should again cite Thorson (2015) for this (that’s his condition paper, and somehow that specific citation for that paper was lost some version ago). Can also check Grüss et al (2020), also on condition but with a multivariate condition/density model.

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.  
- I would say yes to the first sentence: 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. However, on average over space, there is a clear decline over time, also for e.g., oxygen and sprat. But some of this can also be spurious correlations, because for instance the condition is highest and declines least in subdivision 24, which is also the subdivision with least sprat and smallest change (magnitude of difference depends on weighting though)

- We can clarify this a bit, that it boils down to: do you want to estimate the relationships between conditions and covariates on finer scales (closer to the environmental conditions they experience), then you likely need to use individual level data, and then you also need to account for residual spatiotemporal correlation.

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).

- We can add the synergistic part, that’s interesting.

- I would have guessed that condition doesn’t necessarily decline with higher metabolism because it depends on if their feeding rates can match that (simplified)

- I went to check Cui & Wotton (1988, J Fish Bio), and they actually find that condition is not temperature dependent when there’s enough food, only when rations are reduced. I don’t know if the reduced ration treatments are close to what cod experience now, but we can discuss this.

- Also, temperature is positively associated with condition. I think this could partly be because it’s warmer in subdivision 24 and colder in the deepest parts, but it could also be other things.

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.  
- This is interesting, I think… Feels like it’s related to the previous comment on scale. I’d say (and let me know if you agree or not) the main thing one must decide when taking on a similar study: do you want to link fish-traits to the environments they experience? Then you need to go down to scales where you’ll likely also get spatiotemporal residual patterns. Or are you OK with the assumptions and “loss” of uncertainty due to loss of variation that comes with modelling the average condition over a large area with the average change in environmental conditions?

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

- Will fix!

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.  
- Can bring it back from the appendix and merge it again with Fig. 5

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.

- I suspect the reviewer mean a bias in the condition factor INDEX, because it’s averaged over the whole area, whereas data do not come from the shallowest (or the deepest) areas. Below is a figure of the simulated index on the full grid, and the grid with depths between 20 and 120 meters.

Chart, line chart

Description automatically generated

Below is the same figure for depths between 40-120 (I think 40 sounds excessive though–we do have a depth covariate). Mainly it’s a different in magnitude though, not trends.

Chart

Description automatically generated

- It’s also possible this is not what the reviewer meant… Ideally, we would have more data in shallow areas, but, we do have some and we estimate the effect of depth (the 20-40 m depth range is not extrapolation). I’m also hesitant of trimming the prediction grid too much because certain areas haven’t been sampled, because the idea of this model-based index is to estimate effects and interpolate, right? If we start trimming by depth, why not other variables? Or remove grid cells that never have a data point close to them, or where do we stop this (and ultimately, when is it no longer spatiotemporally standardized index?).

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.  
  
- I suppose we could do that but I’m leaning towards not doing it (or at least not including it. I can check it out though just for curiosity, but mainly I’m not sure what we do with it, irrespective of what the results show).

- My spontaneous thought is that it seems unlikely that a difference in the effect covariates between subdivision would lead to so clearly synchronized trends in condition (not growth). E.g., oxygen in sd 27 and sprat in sd 25 limiting condition the same amount, but when pooled the effect would disappear.

- I’m also sceptical of splitting the data too much. If we wanted to estimate the effect of X on Y in a simpler regression, would we split the data into 5 chunks and run the regression on those? Not without a good motivation, and I don’t think we have that in this case (that the covariates should have different effects in each subdivision)

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.

- Do this (and consider if this shouldn’t be the main version of the model. But do we know of any references? Or is 2-3 months ok?)

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.  
- I think this is the hardest question to address and I’d appreciate your thoughts on this!

- It seems very tricky/difficult/not so nice to find individuals near edges and assign averages to them because how close should they be for this to kick in?

- I think in that case, it’s better is to use two buffer zones that extend similar distances to the area of an ices rectangle and a subdivision. This seems doable (the environmental covariates + saduria are rasters, and the cod and flounder biomass are predicitons), but will be trickier for the pelagics. In those cases, it might be better to maybe use all surrounding ices rectangles when calculating an average (maybe weighted to give more weight to the one they were in). But what about the subdivision values?

- BUT! How will this work in the prediction grid… Should we keep the same? I.e., the variable at the location, the average ices rectangle average for that point and the same with subdivision? I guess so, but how does that work with the models being fitted with slightly different variables?

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.  
Line 299: Is ‘poor body condition spot’ better than ‘low-spot’?  
- I can check out those reference

- “poor body condition” spot sounds a bit strange to me!

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.