Decision: **Major revision**  
Date of decision: 2025-01-10  
Decision email title: Decision: Major revision  
Decision email text: Manuscript: MEPS-2024-09-002- Blue mussels Mytilus edulis L. and M. trossulus Gould in sympatry: assessment of ecological niche divergence using species distribution modeling  
Author(s): Vadim Khaitov (Corresponding Author), Paul Safonov (Co-author), Alisa Zaichikova (Co-author), Marina Katolikova (Co-author), Mikhail Ivanov (Co-author), Petr Strelkov (Co-author)  
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Dear Dr. Khaitov,  
  
Thank you very much for submitting the above manuscript to Marine Ecology Progress Series.  
  
The handling Editor Dr. Seitz has now assessed your manuscript and the 3 reviewer comments (see below for detailed comments) and asks that you prepare a major revision.  
  
A decision on the acceptability of your manuscript will most likely be made after another round of review. Therefore, please make sure to follow the instructions below, as this will facilitate the evaluation of your revision.  
  
When submitting your revision, please include these 3 files:  
  
(1) a revision showing edits made in this revision (preferably use the track-changes function in Word; please upload the file as PDF [this avoids technical problems when viewed on a different computer system]), file name: Manuscript showing edits  
(2) a revision with all changes accepted ('clean' file, in Word doc format), file name: Manuscript  
(3) a response letter, file name: Response letter  
  
Your submission should contain a complete set of files related to your manuscript, i.e. in addition to the 3 above-mentioned files, include any files relevant to your submission (e.g. supplementary files), even if they did not require editing.  
  
Your response letter should list all review comments along with either an explicit description of what changes you have made in response (refer to line numbers in the tracked-changes document whenever possible) or convincing arguments why you disagree with a comment.  
  
Please make sure to not only answer questions in the response letter but also make appropriate changes in the manuscript text, since other readers would likely have the same questions.  
  
We look forward to receiving your revision as soon as possible, but within 3 months at the latest. Please contact us ahead of time if you require an extension.  
  
Thank you for your patience with the evaluation process and for choosing Marine Ecology Progress Series as an outlet for your work.  
  
In case of questions, please reply to this email to reach the Editorial Office.  
  
  
Sincerely,  
Mae Rose  
  
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Mae Rose Rossteuscher  
Assistant Editor  
Marine Ecology Progress Series  
  
  
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Contributing Editor comments:  
  
I have received three reviews of your manuscript. As you will see from the comments made by the reviewers, there are some serious concerns about your manuscript, which may require major revisions. I agree with the reviewers' assessment, but because of the potential interest of your study, I am recommending major revision. Specifically, this paper was unclear in many places, which made it difficult to get through. There are some issues with the English language, and the ms lacks structure in the Intro and Discussion that develops the general need for this type of work beyond just monitoring mussels in the particular locations studied. In addition, there are methodological aspects that require further clarification. A decision on the acceptability of your manuscript will most likely be made after another round of review.  
  
Thank you for your patience with the evaluation process and for choosing 'Marine Ecology Progress Series' as an outlet for your work.  
  
In case of questions, please reply to this email to reach the Editorial Office.  
  
Regards,  
Rochelle Seitz  
Contributing Editor  
Marine Ecology Progress Series  
  
  
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Reviewer 1 report:  
  
Review of Kaitov et al 2024  
  
Major concern.  
  
For the insights gained from the manuscript I feel the reader must do too much work to make sense of the outcomes. To make things worse, there are several incorrect references to figures etc (outlined below, in minor concerns below).

We have checked and corrected the figure references

Several of the parameters are not accurate measurements of environmental factors:  
- Salinity was measured at low tide, and may not represent the salinity experienced by intertidal mussels. (The authors acknowledge this, but do not have a solution.)

Water in the White Sea often has a layered structure with a freshened surface layer, which varies in thickness from a few cm to several meters, and an underlying layer with normal for the White Sea salinity (about 24 psu). We specifically emphasized that by the term “salinity” we mean salinity at low tide. This salinity characterizes the upper layer of water. If this layer is desalinated, then at low time, desalination will affect littoral animals, although at full water they may be at normal salinity. Thus, the value we used rather characterizes the impact of low salinity (if any) during low water. This is exactly the water that will be in the mantle cavity of the clams during drying period. If this water is desalinated, the mussels will be exposed to desalination for several hours. Accordingly, this value could be more important as salinity during the rest of the tidal cycle.

Additionally more adequate measurement of the salinity regime at a particular site is virtually impossible because the salinity regime could be very stochastic and depends on many parameters (e.g., wind speed affecting the redistribution of water layers). Therefore, we introduced two more characteristics to estimate the salinity regime: the distance to the nearest river and the size of the nearest river. These two values are proxies for estimating the “chronic” salinity at a given location.

- Because 80% of MT have the dark, prismatic strip, up to 20% of MT may be misidentified.

This is true, but only if we are assessing the species identity of a particular specimen. We used a different approach. As shown earlier (Khaitov et al 2021) the value of Ptros, which characterizes the taxonomic structure of the population, i.e. the proportion of M.trossulus, is highly correlated with PT, which we define by the frequency of T-morphotype. With this approach, the mentioned problem of misidentification of individuals is leveled out.

Several of the results may impact the interpretation of the study, but their relevance is lost because their context is left for the reader to interpret, e.g. Lines 287-306 : many suigniuficannt patterns are listed, but their relevance is left open.

Странное замечание. Не знаю что отвечать. Очевидно же, что статистически значимая связь с каки-то предиктором что-то значит. Не писать же, что мидии осмоконформеры и поэтому для них низкая соленость это плохо.

Minor concerns  
Line 58 “In THE North Atlantic”

Corrected  
  
Although mussels were taken from the “fucoid belt to minimize differences in depth” the fucoid belt could vary from location to location depending on wave exposure, salinity etc.

Thanks for the comment. We have removed the reference to the choice of the fucoid belt as a way to standardize depth.   
  
Line 190 : The breakdown of the equation doesn’t make sense, the text states “where PT – proportion of T-morphotype.” Is the “-“ here supposed to be “=”.

Corrected

Line 270: Instead of “(Fig 1B)” it looks like it should be “(Fig 1C)”.

Corrected

Line 305: “Fig. 1 C, D” is mislabeled and should be “Fig. 1 D, E”.

Corrected

Also if PC2 explains only 20% of the variation in ME distribution, can it really be considered a “proxy”?

The transition from initial abundances to PC is a technical trick that allows us to avoid the problem of predictor collinearity. The principal components obtained are just new coordinates that are characterized by the fraction of explained variance of the initial data. How much percentage of the variance describes the PCs is not important at all. What is important is that PCs are highly correlated with T-morphotype (PC1) and E-morphotype (PC2) abundance, both on algae and bottom. This correlation means that it is possible to translate PC values into mussel abundance of a particular morphotype with a high degree of accuracy. This is what was done in the visualization (see red and blue gradient stripes in Fig. 3 B, C).  
  
The Introduction and Discussion are way too long.

We have shortened these parts of the article.  
  
Line 470: How do the authors know that hybrids are rare in the Kola zone? Is there a citation they can provide?

We have inserted appropriated references.  
  
Line 721: the arrows in Fig 1 are very hard to see when printed in black, white and gray.

We have repainted the arrows to make them more contrast for BW-printing.  
  
Line 752: Not clear where the solid lines are and what they delineate. There are solid lines at 0.50 and 0.25/0.75 but these are just grid markers…

We have changed the caption of the figure to make it clearer.  
  
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Reviewer 2 report:  
  
In this paper, the authors use joint species distribution models to evaluate coexistence of two species of blue mussels. The dataset they have is impressive. The paper could use substantial work to improve clarity and to broaden out the topic to more general ecological principles.  
  
General comments  
  
The introduction is extremely long and unclear. The background information could be much more direct and succinct. For example, Table 1 summarizing the potential drivers that are considered in this paper could be referenced in the introduction; it wasn’t until this table was referenced in line 196 that I was able to understand the main categories relevant to this study. I think a statement that several factors (Table 1) have been hypothesized to drive distributions would suffice, and the authors could eliminate a lot of the text describing each individual driver. In Table 1, adding a literature reference or two identifying a previous study that looked at each driver would help organize the parameters tested in the context of past research. There is also a tone in the Introduction that a lot of separate drivers have been looked at in the past, but there’s no consensus, or there’s not a single driver that comes out as being more important. Yet, the findings of this paper are that many drivers are important (lines 325). So the Introduction sets up a false expectation that the single most important driver is going to be identified because of the extensive dataset used here, but it does not deliver on this expectation. The authors should also be made clear from the start (probably in the Introduction itself) that the relative influence of the different drivers is not going to be identified in this paper (as stated in line 484-485).

Здесь не очень понятно, что ответить  
  
The results would benefit from some summary statements to help a reader know what the main findings were. For example, in line 273, what does this mean? That all parameters were thus retained in further analyses? Or the paragraph starting with line 275 could include a more general take home point such as: Substrate type substantially influenced distributions of Ptros. The importance of the curvilinear finding stated in line 289 is not clearly summarized.  
  
Возможно надо вставить в текст фразу

In contrast, the Effective degrees of freedom in the case of Salinity was 2.4 indicating the curvilinear dependency of Ptros on this predictor (Table 2).

It is not clear how some decisions for analysis were made. For example, in line 274 all correlations are stated as being low, but the thresholds for what counts as low vs high are never defined (or citations included to justify those decisions).

The correlation data for continuous predictors are given only for the general characterization of their relationships. To test for multicollinearity of predictors, we focused on the variance inflation factor (VIF).

The use of quotations is odd (especially in lines 423-440). I’d suggest just stating what you mean, rather than using quotations. Quotations imply (whether intentionally or not) that you’re using some proxy rather than saying directly what the finding is.

We removed quotation marks where it wasn't necessary.

Line by line comments  
  
Line 3: suggest making mussel singular rather than plural in the running head

We changed running head  
  
Line 20: suggest taking out the “no conclusion has been made” because it’s likely that individual papers have in fact drawn conclusions, even if there is no general consensus.  
  
Line 29: can the authors provide some more information about what they conclude about usefulness of this outside of the White Sea, instead of saying that they are going to do that, just say what they found  
  
Line 33-41: The value of using SDMs to address ecological or conservation questions would help this paper broaden out to a wider audience. Why do we need to know which environmental parameters related to species occurrence more generally, and why do we need to know about species diversity more broadly?  
  
Line 42: remove quotations and the valuation statement and just say they are applied to morphologically distinct species  
  
Line 43: I’m not sure what involved means. Does that mean sampled? And level of ease is relative…most monitoring programs are actually quite difficult!  
  
Line 46: citations about coexistence are needed here  
  
Line 54: can more information be provided here, how many species exist, typically how many coexist  
  
Line 59: can you provide the correlates specifically? Is salinity included in this, since it becomes important later on?  
  
Line 84: suggest adding “a” before the word mosaic  
  
Line 100: definite conclusions in ecology are rare and maybe shouldn’t be expected in the first place…suggest rewording  
  
Line 108: suggest replacing “is” with “may be” because you’re trying to suggest that using cryptic diversity might help understand these patterns better, but you don’t know for sure  
  
Line 119: not sure the see also above is needed, or what it specifically refers to  
  
Line 126: can more information be provided on where the Ptros name comes from? Is it an acronym? I’m not able to figure out where that nomenclature is derived from. It’s even difficult to follow in the methods (line 188)  
  
Line 120-128: this reads like methods and breaks up the flow of the introduction  
  
Line 189: is this a minus sign after the PT? If not, I’d suggest replacing the dash with the word “is”  
  
Line 267: the authors might mean variable here rather than mosaic  
  
Line 273: what would be considered high in this correlation analysis? It would be worth adding thresholds to the methods section to demonstrate the level at which correlation was considered happening and subsequently some parameters thrown out.  
  
Line 288: I think In contrast would be better here than on the contrary  
  
Line 295: I think In addition would be better here than besides  
  
Line 317: “fit well” might be better here than “good”  
  
Line 320: The plots for Tyuva look very poorly fit. However, I think the authors are suggesting here that they fit fairly well. Could some more context be provided? What would be considered a poor fit? All of those points are far off the 1:1 line, so it’s not clear how the data are being evaluated here. There is some discussion of this in lines 409-420, but the tone of that paragraph in the discussion doesn’t match how the results are reported here.  
  
Line 324: I think the authors mean dataset instead of material  
  
Line 330-335: Instead of saying what you’re going to do in the discussion, I'd suggest stating directly what you found. This first paragraph would benefit from being rewritten to reiterate the findings just presented in the results and then a statement or two about the importance of this work more broadly.  
  
Line 351: Needs some clarification. Which important factors? If salinity is the important factor, I don’t quite follow how it can be masked. If there’s something else masking it, isn’t that other factor the important factor then?  
  
Line 351-352: provide a reasonable range for each location to emphasize the point being made  
  
Line 359: Needs some clarification. Opportunistic in what sense? In feeding? In colonization? Perhaps the authors mean generalist rather than opportunistic?  
  
Line 478-479: What are the predictors that were ignored. These should be included in Table 1 as a separate category to accurately represent the possible drivers, distinguished from the subset of drivers the authors chose to study.  
  
Line 486: This topic deserves broadening out. Multiple stressors, context dependency, etc. in the ecological literature more generally makes this point.  
  
  
Table 2 doesn’t define the ref abbreviation  
  
Line 715: suggest adding “red” box since there’s also a black box outlining the inset  
  
Figure 1: I’d suggest stating that white is ocean and grey is land. The anchors and asterisk labeling is confusing. As written it sounds like there are two separate ports identified, one by an anchor and one by an asterisk. I think the wording just needs to be adjusted to something like “Anchors with names mark ports. Asterisks identify whether the port is currently abandoned.” I’d suggest changing the color of the arrows in (c) since the yellow matches the legend. Can you also add numbers within the arrows to match to numbers in Table S1? Please add units for the metrics fetch and salinity.  
  
Line 722: I think it should read by the GAM fit  
  
Line 725: wiggling sounds very informal. Is there a more formal way to describe why the dotted lines are needed and what they show?  
  
Line 727: I might be missing it, but I don’t see any information here on substrate (bottom vs algae)  
  
Figure 3: I don’t think the grey shading or bolding in the insets of panels b and c are defined.  
Line 734: It would help to have Diff somewhere on the panel itself, maybe as an axis title  
Line 735: I don’t see a D panel, I think this might be a typo.  
  
Figure S1: can statistics be provided here (r values?)  
  
Table S2: what is the red text?  
  
Table S3: the heading/table legend is cut off.  
  
Table S4: the heading/table legend is cut off.  
  
  
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Reviewer 3 report:  
  
General comments  
In the context of increasing invasions by alien species, it is crucial to better understand how these species overlap with the ecological niches of endemic species, especially in the case of cryptic species. This paper investigates the ecological niche differentiation between two conspecific mussel species, Mytilus edulis (ME) and Mytilus trossulus (MT), in sympatry within a so-called contact zone using a Generalized Additive Model (GAM) approach. By applying a relative proportion index (Ptros) based on mussel morphotype abundance, the authors find that M. edulis (ME) and M. trossulus (MT) dominate in distinct environmental conditions. The authors also explore potential competition mechanisms in structuring the intertidal community by investigating whether the segregation pattern across substrate types is dependent on species abundance.  
The study was conducted rigorously well illustrated, but some methodological aspects require further clarification. A key point to address is why the authors chose to focus on the relative proportions of MT species, which provide less informative insights compared to directly analyzing morphotype abundance. For instance, examining only proportions does not indicate whether mussels of each morphotype are more abundant in certain environments relative to others, which may offer more insights on species niche differences. Additionally, in cases of low abundance, it cannot be excluded that the dominance of some mussel morphotypes may occur by chance. As a suggestion, developing morphotype/species-specific SDMs based on abundance (either with or without including the abundance of other species as an independent variable to account for potential competition effects) could provide a clearer comparison of ecological niches. The use of species abundance would also enable the use of other niche comparison methods, such as those proposed by Broennimann et al. (2012) and Guisan et al. (2014). Otherwise, the reason for using Ptros to explore niche divergence needs to be explicitly specify.  
Broennimann, O., Fitzpatrick, M. C., Pearman, P. B., Petitpierre, B., Pellissier, L., Yoccoz, N. G., et al. (2012). Measuring ecological niche overlap from occurrence and spatial environmental data: Measuring niche overlap. Global Ecology and Biogeography, 21(4), 481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x  
Guisan, A., Petitpierre, B., Broennimann, O., Daehler, C., & Kueffer, C. (2014). Unifying niche shift studies: insights from biological invasions. Trends in Ecology & Evolution, 29(5), 260–269. https://doi.org/10.1016/j.tree.2014.02.009  
  
Another point that requires clarification, as highlighted by the authors, is the potential presence of confounding variables in the models. While collinearity between continuous variables and multicollinearity have been addressed, it would be useful to examine any potential dependencies between categorical and continuous variables. Additionally, although the authors confirm the structural impact of water temperature on mussel species distribution, the absence of this variable from the study is regrettable, especially given that no justification for its exclusion is provided.  
While the paper is generally well-written, it contains numerous imprecisions and stylistic issues, particularly in the introduction and discussion sections, which hinder a clear understanding of the proposal (see specific comments below). For example, the introduction is somewhat confusing and should be revised to improve clarity and conciseness. Specifically, the first few paragraphs discussing jSDM in the context of cryptic species could be simplified, as this is not the central focus of your work.  
Section-specific comments and suggestions  
Abstract  
-line 24. The term "normal" is not appropriate. It would be better to refer to values that are consistent with the averages found in the White Sea.  
Introduction  
-line 38-39: jSDM is only a particular case of multispecies modelling framework which also include the correlative analysis of residuals. However, there is different way to produce community models (for instance see (Caradima et al. 2019)  
Caradima, B., Schuwirth, N., & Reichert, P. (2019). From individual to joint species distribution models: A comparison of model complexity and predictive performance. Journal of Biogeography, 46(10), 2260–2274. https://doi.org/10.1111/jbi.13668  
  
-line 43: The term "Good species" is too imprecise. Please modify it  
-line 64: "Dating back to the Pliocene" - Is there a reference for this claim?  
Line 85: "At the local scale" – Could you clarify what you mean by "local scale"? Are you referring to centimeters, meters, or hundreds of meters?  
-line 93: "On the bottom" – Do you mean "bare bottom"? Please clarify this term here and consistently throughout the paper.  
-lines 102-103: This sentence is crucial for the paper's objective. It would be better placed earlier in the manuscript, when describing the known dependencies of ME and MT distributions across different basins.  
-lines 111-113: The meaning here is unclear. Since SDM approaches were successfully applied, as mentioned in the following sentence, please clarify what you are trying to convey.  
-line 129: space is lacking  
Method  
-line 148: Please remove “ppt,” as it is no longer commonly used in scientific literature.  
  
-line 149: The term "normal salinity" is still confusing here and elsewhere. Please rephrase for clarity.  
  
-line 165: Did you control for the different years of sampling in your models? This aspect must be discussed at least. Additionally, it is unclear if all sampling sessions were conducted in the same season. Please clarify.  
  
-lines 171-174: The methodology and surface used to estimate the abundance of mussels on bare substrate (bottom samples) and on fucoid canopy were different. Is there any justification for this? What is the potential impact on abundance estimation?  
  
-lines 203-204: As the authors explained, the drivers of mussel community structure vary between spatial locations. To help readers better interpret the limitations of model transferability (i.e., the relatively poor performance in new environments), I suggest indicating the different samples associated with your training and testing datasets on the map (Fig. 1).  
  
-line 195: Why didn’t you include variables describing temperature, given that it plays a structural role in mussel species distribution (lines 59, 118)? In my opinion, incorporating this fundamental parameter could improve overall model performance. If not included, you should provide a justification.  
  
-line 169: It is unclear if the bare bottom samples (bottom samples) were collected at the same depth (parallel to the seafloor) as the corresponding algal samples. If not, the distinction between algal and bottom categories may confound the effect of depth. Please clarify.  
  
-line 170: Is there a specific reason for using different frames for the “algal” and “bottom” samples?  
  
-line 192: From which salinity values does the formula lead to false positive identifications? Please provide more details.  
  
-line 226: Technically, your approach is more aligned with a generalized additive mixed model (GAMM) since you included a random effect.  
-line 234: Could you clarify the thresholds you used with VIF and Pearson’s r correlation to detect collinearity?  
  
-line 257: It is unclear why you chose to test classification performance using AUC on binarized values instead of testing regression performance on Ptros values (as shown in Fig. 4) to assess model transferability. In my opinion, using performance metrics applied to your continuous predictions (predicted Ptros values) would provide a more accurate evaluation of your model transferability.  
Result  
-line 266: This sentence would be more appropriate in the Materials and Methods section and should be relocated there.  
  
-line 273: Based on the violin plot in S1, there appears to be a difference in salinity between small and large rivers. If this is the case, the estimated effect of salinity may at least partially reflect differences between river categories, and vice versa. Additionally, have you checked for any dependencies between your categorical variables (e.g., river size and port status) or between categorical and continuous variables (e.g., distance to port and port status)? Please verify.  
  
-line 279: The formulation of this sentence could be improved for better readability. Are you referring to the absence of a clear spatial pattern?  
  
-line 284: Please remove the unnecessary phrase “In our opinion.”  
  
-line 294: Replace the term “normal” with “moderate.”  
  
-line 297: This point has already been mentioned and is not necessary to repeat.  
  
-lines 300-305: From a methodological point of view, I question the necessity of using PCA scores instead of the mean total abundance of ME and MT on both substrates, especially since the PCA axes seem to clearly describe the mean species abundance.  
Discussion  
-line 350: I agree with this point, but could you specify some relevant factors that were not considered in your study?  
-lines 374-380: Alternatively, since Fucus distribution is strongly influenced by surf levels, it could also be argued that the effect of surf on mussel distribution operates indirectly through its impact on substrate availability.  
-line 407: You are correct. As a suggestion, it would be interesting, if feasible, to exclude subtidal data (sorted by algae group) to assess the transferability of your model under comparable shore height conditions.  
-line 416: Considering the possibility that the increase in Ptros could be attributed to the failure of the morphotype test under high salinity conditions ~30), could the high rate of false positive predictions be caused by the higher salinity observed in the Barents Sea?  
-line 496: This sentence appears to overstate the transferability performance of your model in the Barents Sea. While there is no universally accepted standard for interpreting AUC values, scores below 0.75 are often considered indicative of poor performance. Additionally, your performance plot shows that the comparison between observed and predicted Ptros does not reveal a clear relationship, further suggesting limited transferability. Please revise this sentence accordingly.  
-line 420: In the context of global warming, could variations in water temperature have influenced the observed Ptros? Since temperature was not included as a parameter in your model, might this explain some of the observed patterns?  
-line 425: I am unsure if two functionally similar species necessarily imply a similarity in their fundamental niches, as suggested by your statement (“and therefore”). Please modify this assertion or provide a justification.  
-lines 427-440: This section is unclear. Are you proposing that, contrary to previous assumptions, the two species have conserved their fundamental niches across zones? Please revise and clarify this part for better readability.  
-lines 441-448: To support your argument, you could consult global occurrence databases (e.g., MT: https://obis.org/taxon/140482 and ME: https://obis.org/taxon/140480). These databases indicate differences in salinity affinity, with the global distribution showing that MT is typically found in lower salinity ranges (0–5) compared to ME.  
-lines 449-450: The phrases “no non-random relationship” and “significant predictors” seem circular. Please rephrase for clarity.  
-lines 453-455: This sentence is overly complex and difficult to follow, which may hinder the reader’s understanding. It also appears to contradict your intended argument. Please clarify and simplify it.  
-lines 459-461: This point would be more appropriately placed in a conclusive section. Please consider moving it there?  
-lines 466-467: Why does the morphotype test not provide a reliable estimation of species abundance in your framework? What about the values shown in Table S3? Please clarify.  
-lines 478-479: As a suggestion, have you considered incorporating proxies of site productivity, such as chlorophyll-a or, to a lesser extent, turbidity? These proxies, which are available at relatively fine resolutions, are known to significantly influence the distribution of filter-feeding species. Additionally, what about including temperature?  
-line 482: It is recommended to use the more commonly recognized terms “high tide” and “low tide” for better clarity.  
-line 484: As an informative comment, although it depends on the sampling strategy and data quality, methods like random forest variable importance could be used to rank the most influential factors.  
-line 499: To my knowledge, including biotic effects in SDM models is currently more challenging than incorporating other important abiotic factors not considered in this study, such as water temperature, turbidity, or better control for depth.  
-line 504: Please remove the additional space in this line.