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.

We are grateful to you and the three reviewers who provided extremely valuable comments and suggestions, which we have taken advantage of. We have substantially revised the text, shortening it where possible.

We are grateful to you and the three reviewers who provided extremely valuable comments and suggestions, most of which we agreed with.  
  
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

We have corrected the references to figures, thank you for pointing this out.

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.

Ptros (taxonomic structure) varies with salinity at low tide, as well as with distance to the nearest river. These are our results and we are confident that they are robustly validated. We mentioned that it would be useful to see how Ptros is affected by salinity at high water (L), but we have not studied this ourselves.

- 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.

This is a misunderstanding. Since the marker is semi-diagnostic, it is not possible to accurately assign individuals to species, you are right. But we do not perform individual assignments; we simply determine the proportion of species in the samples using a robust procedure from Khaitov et al. 2021.

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.

We have rewritten the Discussion and hope that our interpretations of the patterns identified have become clearer.

Minor concerns  
Line 58 “In THE North Atlantic”

Corrected (L?)  
  
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.

Thanks for the comment. Please note that mussels live from the upper littoral to a depth of 30 meters, relative to this range variability of the depth of the fucoid belt is small. We have removed the reference to the choice of the fucoid belt as a way to standardize depth from Materials and Methods.

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 (L?)

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

Corrected (L?)

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

Corrected (L?)

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 of the variance describes the PCs is not important for the aim of our analysis. 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).~~ This means that we can accurately translate PC values into mussel abundance of a particular morphotype (as illustrated at Fig. 3 B, C).

The Introduction and Discussion are way too long.

We have shortened these parts of the article.

We tried to keep the Introduction and Discussion as short as possible, but we had to take into account the recommendations of other reviewers.

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.

We provide references to studies in which this has been proven (L?).  
  
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.

We apologize for this design flaw. Corrected  
  
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.

We apologize for this design flaw. Corrected  
  
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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

In the introduction, we describe the views presented in the literature on the factors governing species distributions. Further on in the text of our paper, we specifically explain to the reader that there is no single leading factor regulating distribution of both species.

We sincerely appreciate your advice that allowed us to improve both illustrations and the text.

We have rewritten and shortened the text of the Introduction as much as possible following your instructions, but we had to add new phrases at the request of reviewers.

We do not think that the hypothesis that there is no single major predictor explaining M. edulis and M. trossulus species distribution in any contact zone has been formally tested by anyone before us.

Table 1 summarizes the predictors we studied directly; we did not find space in the table to report the results of published studies.

A statement that the SDM we used does not directly assess the relative or absolute significance of factors is now included in Materials and Methods (L ???).

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.

All results of the modeling are presented in standard form, see Table ? and Figures +++, We hope the statistical conclusions are articulated more clearly in the new edition of the Results.

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).

All data on correlations between predictors are needed for assessment of their collinearity. The correlation coefficients 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). This metric takes into account not only pairwais as Pearson correlation does, but assesses the dependence of a given predictor on a set of all predictors included in the model. Using VIF we did not find predictor's collinearity (Line +++).

When judging the multicollinearity of predictors, we focused on the variance inflation factor (VIF). This metric takes into account not only pairwise relationships, like Pearson correlation, but also estimates the dependence of a given predictor on the set of all predictors included in the model. Using VIF, we found no collinearity between predictors. Pearson correlation coefficients between continuous predictors are given only for the general characterization of their relationships (Line +++).That the correlation coefficients were low seems expected in light of the above.

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.

Thank you for the advice. Corrected.

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

We have changed our running head.

Corrected. Now “Mussel species niche divergence”   
  
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.

We have rephrased this sentence

OK (L?)  
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

We have rephrased this sentence

OK(L?)  
  
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?

Thank you for this valuable advice. In particular we now refer to the experience of studying invasive species, following suggestions of another Reviewer (L?)

We decided not to change the general structure of the introduction in order not to depart from the central question concerning the divergence of the niches of the two mussel species.

Line 42: remove quotations and the valuation statement and just say they are applied to morphologically distinct species

OK( L?)

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!

We have rephrased this sentence to make it clearer. … distinguished in in routine biodiversity assessment studies (L?)

Line 46: citations about coexistence are needed here

The citations are provided now (L?)  
  
Line 54: can more information be provided here, how many species exist, typically how many coexist

We have changed the sentence and added reference

We have written six species and cited references to papers that reveal details (L?). Out of brackets: in Western Norway, mixed settlements may contain purebreds of M. edulis, M. trossulus and M. galloprovincialis together with all possible their hybrids (Simon et al. 2020).

Line 59: can you provide the correlates specifically? Is salinity included in this, since it becomes important later on?

We have added explanations of the correlates of temperature: ice extent and primary production (L ?)

We have explained what is meant by temperature correlates: ice extent and primary production (L ?)

Line 84: suggest adding “a” before the word mosaic

We have rephrased this sentence (L ?)

Line 100: definite conclusions in ecology are rare and maybe shouldn’t be expected in the first place…suggest rewording

We removed this text to avoid confusion (L ?)   
  
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

We have reworked the paragraph (L ?) .  
  
Line 119: not sure the see also above is needed, or what it specifically refers to

We have reworked the paragraph (L ?) .

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)

We have removed this sentence and explained the term “Ptros” in the “Material and Methods” section.

The Ptros was introduced before, reference to Khaitov et al, 2021 was provided. Please notice that Ptros is introduced in “Materials and Methods” section (L?)

Line 120-128: this reads like methods and breaks up the flow of the introduction

We have reworked this paragraf.

Agree, see L??

Line 189: is this a minus sign after the PT? If not, I’d suggest replacing the dash with the word “is”

We have changed this part to remove the confusion.

OK (L??)

Line 267: the authors might mean variable here rather than mosaic

We replaced “mosaic” by “variable”

OK (L??)  
  
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.

When analyzing the relationships between the predictors, we focused on the VIF value, on which the conclusion about the collinearity of the predictors is based. The values of correlations are given for general information only.

УВАЖИТЕЛЬНО БЫЛО БЫ ДОБАВИТЬ ЭТО ОБЪЯСНЕНИЕ ПОСЛЕ СТРОЧКИ 346 - ОН КАК ЗДОРОВЫЙ ЭМПИРИЧЕСКИЙ ЧЕЛОВЕК НЕ ВЕРИТ “МОДЕЛИ” И ХОЧЕТ ЧТО ТО ПОНЯТЬ ИЗ КОРРЕЛЯЦИЙ…

Please see our reply above.   
  
Line 288: I think In contrast would be better here than on the contrary

We have changed the sentence as you proposed.

OK (L?)

Line 295: I think In addition would be better here than besides

We have changed the sentence as you proposed.

OK (L?)

Line 317: “fit well” might be better here than “good”

We've accepted your offer.

OK (L?)

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.

Yes, we agree that there is no perfect match (as we write about in the discussion). However, it would be difficult to expect full correspondence. However, since the problems of transferability of SDM built on one data to another material will inevitably be acute in the development of the proposed approach, we felt it necessary to consider such a case in our paper. We considered AUC more greater or equal to 0.7 as acceptable discrimination (Hosmer et al., 2013). We have somewhat reduced the pathos of the text when we considered the predictive power of our model.

You may be right. However, an AUC greater than or equal to 0.7 is considered acceptable discrimination (Hosmer et al., 2013). We no longer insist that Model 1 works well in the Barents Sea. Thank goodness it works well in the White Sea.

Line 324: I think the authors mean dataset instead of material

We’ve changed “materials” to “data”.

ОК (L?)

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.

We have removed this paragraph entirely. We have summarized our results in the previous paragraph.

We have shortened the introductory paragraphs of the Discussion according to your recommendations.(L?)

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?

We’ve removed the word “important” to reduce categorical statement about salinity as an the most important factor.

We rewrote the sentence. We hope it is now clear what factors we are talking about. (L?)

Line 351-352: provide a reasonable range for each location to emphasize the point being made

We have rewritten this paragraph, the range of salinity in the two seas is no longer discussed. (L?)

Line 359: Needs some clarification. Opportunistic in what sense? In feeding? In colonization? Perhaps the authors mean generalist rather than opportunistic?

We removed references to opportunistic strategy so as not to cause unnecessary cannotations.

We have rewritten this paragraph, opportunism is no longer discussed. (L?)

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.

We suppose this is unnecessary, as the need to include any additional predictors is a task for future research. Table 1 is self-sufficient, as it describes exactly those predictors that were included in our models.

We have rewritten the phrase. We hope it is now clear which predictors we mean. Unfortunately, we cannot agree with your suggestion to engage in a meta-analysis of the literature and use a table from Materials and methods for this purpose.

Line 486: This topic deserves broadening out. Multiple stressors, context dependency, etc. in the ecological literature more generally makes this point.

In this part of the paper, we rather talk about the methodological limitations of the applied approach (i.e. morphotype test as a way to describe the taxonomic structure of mixed settlement, and GAM as a modeling technique).

This is an interesting suggestion, but the Editor and other reviewers say that the Discussion is too long as it is.

Table 2 doesn’t define the ref abbreviation

Corrected (L?)  
  
Line 715: suggest adding “red” box since there’s also a black box outlining the inset

We see no need to introduce unnecessary entities, since the description of the box is given in the subscript section of Figure 1 A.

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.

Здесь надо что-то сделать с подписями к рсункам. Лучше обсудить.

We've modified the Figure following your instructions. We believe that numbering the river mouths in the figure would make the figure too complex and make it difficult to understand other information. We remind you that the coordinates of the river mouths are given in the ESM.

Line 722: I think it should read by the GAM fit

We've completely redesigned this Figure and its caption.

Line 725: wiggling sounds very informal. Is there a more formal way to describe why the dotted lines are needed and what they show?

We've changed the caption and removed “wiggling”.

Line 727: I might be missing it, but I don’t see any information here on substrate (bottom vs algae)

This information is presented in the new version of the figure (L?)  
  
Figure 3: I don’t think the grey shading or bolding in the insets of panels b and c are defined.

Надо добавить в подпись рисунка про то, что болдом выделены наиболее высокие коррелции.

Line 734: It would help to have Diff somewhere on the panel itself, maybe as an axis title

This doesn't make much sense, since all three panels of the figure say about Diff.

Line 735: I don’t see a D panel, I think this might be a typo.

Yes, that was a typo, we have completely redone this drawing and corrected that typo.

УБЕРИ БОЛДShading is now explained while bolding eliminated.D panel was a typo, we are sorry for that.

Figure S1: can statistics be provided here (r values?)

This is not necessary, since we used VIF as a value describing the collinearity of the predictors.

Statistics are provided in the main text: VIF as a measure of predictors collinearity.

Table S2: what is the red text?

It was used to mark samples taken from Katolikova et al., 2016, but you are right that it is not necessary to use color.

Table S3: the heading/table legend is cut off.

Не понимаю, что ответить

Sorry, we do not understand you. The heading is present.

Table S4: the heading/table legend is cut off.  
  
Не понимаю, что ответить

Sorry, we do not understand you. The heading is present.  
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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

Yes, you are right - ultimately the SDMs should predict species abundance. Also, niche divergence must somehow translate into differences in species abundance along ecological gradients. When we started this work we were oriented towards this as well, which forced us to do quantitative samples. The latter was not easy, because it was impossible to take into account the abundance of mussels on the bottom surface (actually on a plane) and on fucoids (a three-dimensional structure) using comparable methods. Therefore, we focused on relative abundances (Ptros). The latter usually underlie the analysis in a paradigm of genetic studies of hybrid zones. (????) Therefore, we focused on the study of Ptros. At the same time, however, we considered your comments to be significant and we have extended the paper to include morphotype abundance data in the analysis as well (we cannot speak of species in this case). The results obtained fully coincided with the results of the study of Ptros.

Thank you for your detailed and friendly review, for which we are very grateful.

We focused on species proportion (Ptros) rather than morphotype abundance A) in order to make the analysis more simple and B) because samples were collected in different ways on different substrates. But we were happy to supplement the study by morphotype abundance data analysis (Model 2).

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.

Using the variance inflation factor (VIF, it was calculated by function vif() from R-package 'car') as a measure of collinearity, we also estimated potential collinearity for discrete predictors. All VIF values were within the acceptable range (less than 2). In addition, we presented a correlation table for continuous predictors (Table S5) and Figure S2 for one discrete predictor that can be discussed in the context of collinearity (RiverSize). Other discrete predictors (Substrate and PortStatus) are not needed to be involved in this context.

Using the variance inflation factor (VIF, calculated by function vif() from R-package 'car') as a measure of collinearity, we estimated potential collinearity for both continuous and discrete predictors. All VIF values were within the acceptable range (less than 2).

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.

The inclusion of temperature in our model makes no sense, as this value does not vary practically on such a small geographic scale. In the latitudinal direction, the distance between the northernmost and southernmost collection points is only about 100 km. All points were located in more or less similar conditions of the fucoid belt. Yes, it makes sense to discuss the influence of local temperature, which can vary greatly within a site and potentially depend on exposure and substrate properties, but this is a task for further research.

At the scale of thousands of kilometers, temperature affects species distribution, about a more local scale (we have a maximum distance between sites of 100 km) no one has checked. Unfortunately, we have not monitored temperature in the study sites and have nowhere to get it from.

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.

Yes, we reworked the Introduction removing confounding positions.

We have rewritten the introduction and discussion following your suggestions and those of other reviewers.

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.

We changed text as you recommended.

OK (L?)

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

Thanks for the useful reference! We have reworked text and cited the recommended source.

Thanks for the useful reference! Added (L?)

-line 43: The term "Good species" is too imprecise. Please modify it

We have changed text.

Morphologically distinct species (L?)

-line 64: "Dating back to the Pliocene" - Is there a reference for this claim?

We rearranged text to join this sentence with appropriated references.

Yes (L?)

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?

We have changed sentence to clarify it.

From dozens of kilometers to tens of centimeters (L?).

-line 93: "On the bottom" – Do you mean "bare bottom"? Please clarify this term here and consistently throughout the paper.

We hope changing the sentence we were able to point that under “bottom” substrates we understood “directly on the bottom of substrates such as mud, sand, stones and gravel”.

We know that the expression “bare bottom” does occur in marine science, more often in Scandinavian authors. But please notice that in English it has an obscene figurative meaning. We haven't had a problem with “bottom substrate” before. In the text we added “directly on the bottom of substrates such as mud, sand, stones and gravel”.

-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.

Не очень понятно, что тут написать

Agree. See L?

-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.

We reworked the paragraph, L. ?.

-line 129: space is lacking

?

Method  
-line 148: Please remove “ppt,” as it is no longer commonly used in scientific literature.

Replaced by “PSU”

OK (L?)

-line 149: The term "normal salinity" is still confusing here and elsewhere. Please rephrase for clarity.

We replaced “normal salinity” by “average salinity”

We changed “normal salinity” to “average salinity” (L?)  
  
-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.

We pointed out that samples were made in summer months. Additionally we add the special part in “statisitc” section where we describe the checking for spatial and temporal patterns in the model’s residuals. We did not find any significant pattern in residuals in association with the sampling year.

We pointed out that all samples were taken in summer (L?). Additionally we checked for spatial and temporal patterns in the Model 1 residuals. We did not find any significant pattern in residuals in association with sampling year (L?).  
-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?

The principles of organization of mussel settlements on fucoids (three-dimensional structure) and on the bottom (settlements o a plane) are significantly different. We cannot describe these two types of settlements using the same methods, for example by simply collecting samples with the same sampler. This is why a special technique was developed to quantify mussel on fucoids.

For using Ptros as the dependent variable, differences in quantification techniques are not crucial. However, if one is engaged in modeling mussel abundance, differences in collection techniques can be crucial for comparing abundance on algae and on the bottom. Because of these differences, we do not attempt anywhere in our models to compare mussel abundance on these two substrates. For this reason, we had to drop the Substrate as a predictor in Model 2, in which the dependent variable was the abundance of mussels.

Mussel settlements on fucoids (three-dimensional substrate) and on the bottom (flat substrate) are very different. Therefore, different techniques were used to quantify mussel abundance on different substrates. To use Ptros as the dependent variable, differences in sampling techniques are not fundamentally important. However, this makes it difficult to compare abundance on algae and on the bottom. Because of these difficulties, we did not attempt to compare mussel abundance on the two substrates anywhere in our models. In particular, we excluded substrate as a predictor in Model 2 (added at your suggestion), in which mussel abundance was the dependent variable.

-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).

We decided not to complicate the already complicated Figure 1. We have introduced Figure S1 in Appendix 2, where we show the location of the test sample collection points in the White Sea. The test data from the Barents Sea are described in detail in the original paper (Marchenko et al., 2023) from which the data were taken.

We feel that Figure 1 is already too complicated and we do not want to complicate it further. In Appendix 2 we now provide a map (Figure S1), which shows the location of sampling sites in the testing data from White Sea. The test data from the Barents Sea are described in detail in the original study (Marchenko et al., 2023) from which they were taken.

-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.

Sea above

Unfortunately, we do not have such data and reliable data cannot be obtained from external sources (see also above)

-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.

Мы это не прояснили

Approximately at the same depth (L?)

-line 170: Is there a specific reason for using different frames for the “algal” and “bottom” samples?

Sea above

Please see explanation above

-line 192: From which salinity values does the formula lead to false positive identifications? Please provide more details.

We have added needed information.

“However, as studies in the Barents Sea have shown, this equation may overestimate Ptros at higher salinities, e.g. up to 20% at salinity around 30 psu (Khaitov et al. 2021, Marchenko et al. 2023)”. (L?)

-line 226: Technically, your approach is more aligned with a generalized additive mixed model (GAMM) since you included a random effect.

Agree! It was corrected for the Model 1 which is really GAMM, but Model 2 and Model 3 are not (they are referred to as GAM).

-line 234: Could you clarify the thresholds you used with VIF and Pearson’s r correlation to detect collinearity?

We have included the information about threshold values for VIF (3.5). We also pointed out that correlations between predictors are given only for general information about their relationships.

-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.

We disagree for the following reasons. First, the data from the test sample from the Barents Sea, although close in essence to our training dataset, are collected in a completely different way. Therefore, a complete match between the model prediction and the observed data is not to be expected. Unfortunately, we have not found a more suitable dataset collected outside the White Sea. Second, if someone were to use our modeling approach, it would be important for them to understand whether MT or ME is present at a given location in meaningful quantities. Looking at MT-dominated VS ME-dominated in discrete categories gives an easier-to-understand picture. Third, the predictor values for the test sample in Tyuva Bay vary in narrow range, making the model predictions very crude (note the numerous very close predictions in Figure 4). In such a situation, estimates of the predictive power of the model would be quite crude. This makes it impossible to apply the metrics accepted in machine learning for continuous values. And finally, ROC analysis is accepted in this kind of assessment and many recommend it (we provide references in the paper).

If you mean Pearson correlations, we have added them in Fig. 4 to give additional possibility to compare observed and predicted Ptros values. We disagree with you for the following reasons. First, samples from the Barents Sea were collected using different methods. Therefore, a complete match between the model prediction and the observed data is not to be expected. Unfortunately, we have no other datasets from outside the White Sea but the Tyuva one.

Second, the question we answer - what species dominate the site is scientifically sound. Third, the predictors vary in a narrow range in a small Tyuva Inlet (note the very close predictions in Figure 4). In such a situation, estimates of the predictive power of the model would be crude. Further, this complicates application of metrics used in machine learning for continuous predictors. And finally, ROC analysis is accepted in this kind of assessment and many recommend it (references are provided, L?).

Result  
-line 266: This sentence would be more appropriate in the Materials and Methods section and should be relocated there.

We disagree. This table explains the nature of predictors (ecological axes) and patterns of their variation. This is also the subject of the analysis.

Sorry, but these are the results of the study.

-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.

All relationships between predictors were controlled using VIF (see above). However, you are right, salinity is somehow related to the status of the nearest river. This overlap between the predictors is deliberate because salinity measured at low tide may not be a reliable characterization of the salinity regime at a given location. We therefore additionally estimate the salinity regime using two proxies: the status of the nearest river and the distance to the nearest river. Given the acceptable level of VIF these three predictors can be considered as relatively independent.

Relationships between all predictors were controlled using VIF (see above).

-line 279: The formulation of this sentence could be improved for better readability. Are you referring to the absence of a clear spatial pattern?

We have rewritten the end of this paragraph.

We have rewritten the paragraph. Hope it is more understandable now (L?)

-line 284: Please remove the unnecessary phrase “In our opinion.”

Removed

OK  
  
-line 294: Replace the term “normal” with “moderate.”

We have changed the sentence.

OK (L?)

-line 297: This point has already been mentioned and is not necessary to repeat.

Removed

OK (L?)  
  
-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.

In the first versions of the analysis, we attempted to use mean values of mussel morphotype abundance on both substrates as predictors in this model. However, the high collinearity of these values VIF >> 3 made this model not valid. In such situations, PCA based on a predictor matrix is recommended with further use of principal components as complex features that are known to be orthogonal, i.e. not collinear (Quinn, G. P., & Keough, M. J. (2002). Experimental design and data analysis for biologists. Cambridge university press. Chapter 6.1.11). Which we have done. The obtained components themselves are easily interpreted by analyzing correlations with the original values: PC1 mainly characterizes the variation of T-morphotype abundance, and PC2 characterizes the abundance of E-morphotype.

Assessing the dependence of Diff on PtrosSite, we could not directly operate with densities of morphotypes because they were collinear on different substrates (VIF >> 3). In such situations, PCA based on a predictor matrix is recommended with further use of principal components as complex features that are known to be orthogonal, i.e. not collinear (Quinn, G. P., & Keough, M. J. (2002). Experimental design and data analysis for biologists. Cambridge university press. Chapter 6.1.11). We followed these recommendations…

Discussion  
-line 350: I agree with this point, but could you specify some relevant factors that were not considered in your study?

First of all, distance to ports (L?)

-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.

Мы по этому поводу ничего не дописывали в этот раздел

You may be true. Unfortunately we did not control fucoid abundance as well as species composition. What we know is that in the studied area fucoids are ubiquitous (noticed at L?).

-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.

This is exactly what we did, intentionally dividing the dataset from the Tyuva Bay into a littoral part (comparable to our main material) and a sublittoral one.

This is exactly what we did, by analysing data from Tyuva littoral and sublittoral separately.

-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?

We disagree with this objection. This would be true if we used PT (T-morphotype ptoportion) as the dependent variable in Model 1 and then converted the predicted PT value into Ptros. Using the Model 1, however, we predict Ptros. We compare the predicted Ptros values to the observed value in Tyuva Bay, which was already obtained by taking into account the particularities of the morphotype test used in conditions of higher salinity. In this case, we cannot attribute the high number of false positive predictions to performance of the morphotype test in the case of high salinity in Tyuva Bay.

Not. We now explain that Ptros for Tyuva was predicted either by direct genotyping or from morphotype frequencies using the formula derived for local populations existing under salinities higher than in the White Sea (Marchenko et al. 2023). (L?)

-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.

We have rewritten this part and reinforced doubts about the transferability of the model.

OK (L?)

-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?

Given the cold-loving nature of MT, global warming is unlikely to explain its establishment in the waters of Tyuva Bay. More complex dynamics is observed here, which is probably related to temperature anomalies. However, this is a material for a special study. We continue to monitor mussels in the Kola Bay and plan to publish a special work about mussel population long-term dynamics.

Yes and no. Published data from 2004-2018 can be interpreted this way (Marchenko et al. 2023), but we continue to monitor mussels in the Kola Bay and know that Ptros has grown there since then despite rising temperatures.

-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.

We have modified this.

We modified the sentence. May have overlapping niches (L?).

-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.

We have reworked this section. Hopefully it is clearer now.

-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.

In general, OBIS shows the same association of MT and ME with those factors that are considered in this database. However, our experience in genetic studies of mussels makes us skeptical about the mentioned database. For MT, this database is substantially incomplete, with no data on MT settlements in Greenland, Scotland, Hudson Bay, Norway and the White Sea.

This database captures the state of knowledge 30 years ago, when cryptic mussel species research was in its infancy. It does not report MT from Greenland, Scotland, Hudson Bay, Scotland, Norway, and the White Sea. This makes it useless unfortunately.

-lines 449-450: The phrases “no non-random relationship” and “significant predictors” seem circular. Please rephrase for clarity.

We have rephrased the begin of the section

Done (L?).

-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.

We have reworked the sentence

Done (L?).

-lines 459-461: This point would be more appropriately placed in a conclusive section. Please consider moving it there?

We have moved this phrase below to reinforce its meaning.

Thank you for this suggestion. Moved to the end of the Discussion.

-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.

The main problem with the application of the morphotype test is that it does not allow for an assessment of the abundance of hybrids. Since the proportion of hybrids can be different in different contact zones this does not allow for a reliable estimate of the abundance of “pure” species using the morphotype test.

The text states that the morphotype test cannot account for hybrids, which may be abundant in blue mussel contact zones (but not in the White Sea)...

-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?

You are right but for our study area these proxies are unavailable at needed resolution.

We have reworked the begin of this section adding some references and considering temperature as well.

In addition, we would like to emphasize once again that we are not against the inclusion of temperature in the SDM. This will certainly have to be done when building the model in the future, but on our data we cannot assess the influence of temperature on mussel species distribution.

-line 482: It is recommended to use the more commonly recognized terms “high tide” and “low tide” for better clarity.

Changed.

Thank you for your advice. Done.

-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.

Yes, it is. But given the non-linearity of the relationships we came across, GAM was favored. Perhaps the involvement of modern methods of SDM construction, which appear recently ("sdm" R-package for example), will give additional tools to identify significant factors. However, this is again a task for future research, when it will be possible to combine data from different contact zones with broader variation of predictors.

Thank you for your advice. Perhaps the recent methods of SDM construction like "sdm" R-package will also give additional tools to identify significant 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.

Yes, we too believe that introducing biotic components into SDM can be difficult and may give contradictory results. However, some biotic factors, such as the presence of fucoids as a factor of niche partitioning, enabling two species to coexist in common biotope, seems to be very productive. We have completely reworked this paragraph, removing confusing positions.

We excluded mentioning of biotic components

-line 504: Please remove the additional space in this line.

Done

OK