May 2023

Dear Dr. HunterunterH and reviewers,

Thank you very much for the positive comments you gave in response to our paper on our MerMADE case study on lesser sandeel patch depletion; we were very happy to receive your feedback.

For line-level edits and simple suggested changes, we have implemented these and will not list them all here in the interest of efficiency. Where more detail or explanation is needed, please see our responses to your comments below. Line numbers correspond to the “Manuscript showing edits” document to see insertions and replacements.

One point which all reviewers and the editor mentioned was the availability of the software. We apologise this was not uploaded to the github repository, this was an oversight. It has now been made available at this github location: <https://github.com/MerMADEsoftware>. This contains data for running the example shown in the article published on bioRxiv as well as the simulations presented here. We have also included reference in the paper to the preprint article introducing MerMADE that can be found on bioRxiv. Reviewer 2 commented that the description of demography for MerMADE was insufficient. The manuscript uploaded onto bioRxiv was formatted as a software note (and is under review for journal publication at present) and therefore had very limited space available for such detail. However, the github repository that is linked above contains a user manual that describes in great detail how demography is incorporated into the model. As the current article’s purpose is to present a case study, we only present the demographic and dispersal parameters for the types of functionality used for this species. Hopefully the link to the user manual will satisfy the request for more demographic information to underpin what is presented here. We have included a link to the github repository on line 139 which will redirect readers to both the software and its documentation.

Terminology

Reviewer 1 pointed out we use in-and out-degree centrality interchangeably with destination- and origin-centrality, respectively, and that the latter was more intuitive. We agree and have kept the use of in- and out-degree centrality to the description of the methods, as they are established calculations in network theory. For the remainder of the paper, we use the terms origin- and destination-centrality to avoid any further confusion. We have also clarified the definitions of these terms. We have edited the line 112-117 to be number of patches, not number of individuals. It now reads: “using patches as nodes and movement of successful dispersers as weighted edges, to calculate the in- and out-degree centrality measures – the number of patches supplying dispersers to and being supplied by a particular patch, respectively – to identify both important and vulnerable patches within the system”. We introduce the terms origin- and destination-centrality in line 281, as suggested. It now reads: “Therefore, for the remainder of this paper, we will refer to these centralities as origin- and destination-centrality measures to avoid confusion.” We have removed reference to in- and out-degree centrality for the rest of the paper.

The use of the term “extinction” has likewise been amended following Reviewer 1’s comments that “depletion” is more accurate. Since a disturbance event in our simulations introduced a 95% mortality rate and not a 100% mortality rate, “patch depletion” is more descriptive. We have amended the language throughout the paper.

Hydrodynamics

Both reviewers requested more explanation regarding the use of dynamic seascapes and why the years 2004,6,8,10,12,14 were used and not every year. There was also some confusion about what exactly was cycled so we have edited this section to read: “Every other year of the 50-year simulation, MerMADE read in new hydrodynamic data taken from the time period 2004-2014. Though not every year was included, because the differences in hydrodynamics in the space of a single year are minimal, we still captured larger-scale changes over a decade, which we then cycled for the remainder of the 50-year simulation. We acknowledge that this makes assumptions about the predictability and variability of hydrodynamics in this area, but as interannual differences in the connectivity matrix were small, we deemed this a reasonable compromise for increased computational efficiency in not reading in new data every yearly timestep of the model.” (L195)

We also added in justification as to why March was chosen on L207: “The month of March was chosen as sandeel eggs hatch between February and May with a peak usually in March (Regnier et al. 2017) and therefore the hydrodynamics would largely match what the larvae experience in their first few weeks of dispersal.”

Figures

Figure 1: the Editor requested a change in format in the figure, which we have applied. The land is now grey and the Stock Assessment Area 4 is defined in the legend. We have split the figure into parts A and B. Part A holds the closed areas and defines the stock assessment area and Part B shows the sandbank patches. We did this because filling in colour into the sandbank patches made the figure harder to read. We hope this satisfies the editor’s requests as well as Reviewer 2’s comment that the patches were not recognisable. All other figures have been edited to conform to the ‘grey land’ format requested.

Figure 2: We have redone this figure on a 2D map instead of the 3D representation as this hopefully makes it clearer where patches are located. The labels for Patch 26 and Patch 8 were only there to help the reader notice the side panel had been rotated (for easier view of the movement track) so hopefully this change satisfies Reviewer’s 2 comment as well. We have removed one of the panels as the addition of Figure1B has already given the reader context for where the patches are located. Figure2B now has an example track that works better on the map where the upwards and downwards movements can be seen clearly.

Figure 3: Reviewer 2 commented on the use of the term “volume” and that it should be normalised by patch size, affecting Fig 4 and 5 too. We don’t feel this would change our results presented here. In Figure 3, the width of the arrows shows the number of super-individuals moving, regardless of size of patch. Having it show number of individuals/km of patch size would still have proportionately the same arrow width. In Figure 4, self-recruitment is a proportion, therefore constrained between 0 and 1. Normalising by patch size would not affect this calculation. For Figure 5, centrality is calculated by the number of patches giving or receiving dispersers from a target patch. The number of individuals isn’t taken into account in this calculation beyond determining if there was at least one individual making this journey. Therefore, we respectfully do not incorporate this comment.

Figure 6: Both reviewers commented that this Figure didn’t seem to add much to the paper and could be removed or moved to the Appendix. The results section for Figure 5 already covers the spatial pattern created and the link with local hydrodynamics, therefore we have removed Figure 6 completely.

Figure 7 (which, because of the removal of the previous figure is now Figure 6): Reviewer 2 commented that the quality was too low to see all six patches. We have increased the resolution so hopefully this is clearer now. We have edited the caption to clearly state what the dashed vertical lines represent (occurrence of a depletion event).

*Comments from Reviewer 1:*

Further referencing of general statements in paragraphs 2+3 of the introduction: We have added referencing here and expanded on the area of management methods to include more specific references there.

A sentence or two stating how the software is an advance on alternatives. We have added a few lines to L131: “This makes it uniquely suited to asking how dispersal and population dynamics are linked for marine species. Contemporary models for aquatic environments tend to focus solely on the dispersal phase and do not track impacts over generations (i.e. CMS (Paris et al. 2013), Icthyop (Lett et al. 2008)), and terrestrial counterparts, though more inclusive where population dynamics and evolution are concerned (i.e. RangeShifter (Bocedi et al. 2021)), lack the 3D, hydrodynamically forced environment.”

Line 231: question on 97% dispersal mortality. For clarification, we have added this to L268: “This is applied as a per-step mortality rate during the transfer phase of dispersal as it by proxy captures factors such as predation in transit.” We have also added a comment in the legend of Table 1 as requested, L964: “ Note that the 97% dispersal mortality is not included in this matrix as it is applied per-step during dispersal.”

Line 511-14 confusion on incorporating pre-settlement dispersal factors in stock assessments: We have made the following edit at L575 to clarify: “Most stock assessments, where the current state of the stock is evaluated by estimating population size and fishing mortality, do not explicitly incorporate pre-settlement dispersal, nor other spatial processes, which can lead to biased stock estimates (Cadrin 2020).”

Table 2/3: patch sizes would be more intuitive in km2. We have added in columns representing the patches in both cells and km2. We have also changed the origin- and destination-centrality terminology here.

The first two paragraphs in the discussion are too wordy. We have removed the majority of the first two paragraphs of the discussion, keeping the critical points to focus more solidly on the implications of the results.

Suggesting other methods to validate conclusions: We have added a section at the end of the Discussion (L645) suggesting otolith chemistry and abundance time series data to validate findings from MerMADE simulations.

*Comments from Reviewer 2:*

Line 170: why was 21 million chosen as the ratio for superindividuals? We have added a line of clarification at L179, it reads: “This number is biologically arbitrary but simply represented the ratio that made these simulations computationally feasible.” Reducing the ratio meant the simulation slowed down considerably and while we acknowledge the assumptions made when using super-individuals (which we address in the paper), we still modelled hundreds of thousands of individuals and therefore thought 1:21million an adequate balance between computational load and ecological relevance. Work is ongoing to try and reduce the demographic stochasticity of using super-individuals.

Line 228: more information needed on swimming implemented in the model. We have added this additional detail to Line 261: “Their orientation therefore may vary from the direction of the current, giving them more freedom to explore the seabed for suitable sandbanks for settlement. If they detect suitable habitat, they will bias their travel in that direction, though the force of the current continues to act on them.”

Line 259-260 was unclear as to what was being increased, so we have edited it to read: “To investigate the effect of repeated local depletion events, we introduced these once every other year for the duration of the 50-year simulation.” (L303) We hope this is clearer now.

Request for more information on estimation of parameters without cited literature in Table A1. We have added a section in the Appendix underneath Table A1 giving justification of estimation of these parameters. It is not uncommon for some parameter values to be missing and therefore estimated. We give our reasoning in the Appendix instead of the Methods as we feel this explanation would somewhat slow the flow of the Methods section.

Not clear to the reader why there would be limited dispersal between stock assessment areas. The 2010 stock boundaries were based on limited larval exchange from a biophysical model and we have now made this clear in line 76 of the introduction “where average annual exchange across stock boundaries was <5% (Christensen et al., 2008 )”. We have added a few lines to make it clear that this is how the fishery is managed. L155: “We make this assumption as this is the way this fishery is managed: as discrete stocks contained within delineated assessment areas”. We have not added a map as we don’t feel this would add any clarity, since it is not only geographic location that determines connectivity and our results show at a later point in the paper that individuals are moving out of SA4 into a neighbouring stock assessment area.

Addressing metapopulation theory: We have added a section at Line 471 addressing how our findings are relevant to the discussion on metapopulation theory.

Finally, we discovered a slight inaccuracy in the analysis R script (also found at the github location) that led to a small change in origin and destination centrality measures. Qualitatively, the patterns remained largely unchanged and the analysis of the effect of depletion simulations were completely unaffected. Figures 4 and 5 have been updated as well as Tables 2 and 3. Additionally, the patterns shown in Figure A1 in the appendix became even more prominent and we have therefore moved it into the main text because we feel it is an important pattern to highlight. Reference to the new Figure 8 can be found at L525.

Thank you again to the editor and reviewers for their comments and feedback, which we feel have helped improve this manuscript.

Kind regards,

Rebekka Allgayer

Paul Fernandes

Justin Travis

Peter Wright