

Herring spawned poleward following fishery induced collective memory loss

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This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Referee #1

(Remarks to the Author)

A. Summary of the key results

Survey, catch data and tagging data for NSS Atlantic herring are synthesized to evaluate how a particularly strong year-class (2016) disrupted spatial distribution patterns (catch and survey data) and migration patterns (tagging data). Large changes in distributions and recaptures attended the influx of this year-class, which the authors attributed to disruption of traditional migration circuits that had been established through learned behaviors. Alternative hypotheses were evaluated through examination of macroscale changes in flow (bioenergetics) and temperature (prey distributions). These failed to show the same episodic change shown by distribution data.

B. Originality and significance: if not novel, please include reference

C. Data & methodology: validity of approach, quality of data, quality of presentation

D. Appropriate use of statistics and treatment of uncertainties

E. Conclusions: robustness, validity, reliability

Adoption of migration behaviors is poorly understood in marine fishes (say, in comparisons to birds) and learned behaviors is a key theoretical construct that arguably has not been given its due. Genetics data is amenable to establishing patterns of inherited migrations by lineage (philopatry, natal homing), but adopted migration is behavioral and difficult to observe in a mechanistic manner. The result has been a series of case studies particularly on herring (McQuinn, I.H., 1997. Metapopulations and the Atlantic herring. Reviews in Fish Biology and Fisheries, 7: 297-329; Corten, A., 2001. The role of "conservatism" in herring migrations. Reviews in Fish Biology and Fisheries, 11(4): 339-361.; Huse, G., Ferno, A., Holst, J.C., Establishment of new wintering areas in herring co-occurs with peaks in the 'first time/repeat spawner' ratio. Marine Ecology-Progress Series, 409: 189-198) but other species – see Petitgas, P., Secor, D.H., McQuinn, I., Huse, G., Lo, N., 2010. Stock collapses and their recovery: mechanisms that establish and maintain life-cycle closure in space and time. ICES Journal of Marine Science, 67(9): 1841-1848, and Bakun's school trap hypothesis - Bakun, A., 2001. 'School-mix feedback': a different way to think about low frequency variability in large mobile fish populations. Progress in Oceanography, 49(1-4): 485-511.

The current paper builds on new interest and modeling related to adopted migration in marine fishes, yet fundamentally is a case study in the natural history of Atlantic herring, presenting strong circumstantial evidence that builds on past case studies. For this field to develop further empirically, I think what is needed is some kind of a priori hypothesis testing to subject this and other case studies, perhaps built from models of adopted migration so that we might test what is the probability of adopted migration? Can we understand how much memory transfer must be loss to destabilize distributions? What is the threshold between conserved and disrupted migration circuits? I think the next steps in this field will have to quantitative tests of new metrics of learning and conservatism to get us beyond natural history and case studies.

Having said this, I would like to see this published in Nature or elsewhere. This is a wonderful synthesis important to capture and provide data and questions for those interested in adopted migration in marine fishes. The authors are to be commended on very careful and comprehensive treatment of available data.

F. Suggested improvements: experiments, data for possible revision

G. References: appropriate credit to previous work?

H. Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

The style of narrative was not consistently empirically driven but rather driven by the overarching thesis. In this manner there was sometimes the assertion of repeat spawners leading to adopted migration (e.g., lines 110. 179) where references were not specific to this phenomenon but to the role of memory and learning in migration in theory and modeling. Again, I am not sure if this style of narrative is suitable for Nature portfolio journals, but would be well suited for other journals that feature review or thesis driven essays.

(Remarks on code availability)

None

Referee #2

(Remarks to the Author)

I have reviewed the manuscript "Herring spawned poleward following fishery-induced collective memory loss" by Slotte et al. as submitted to Nature.

The manuscript provides a range of evidence supporting the hypothesis that large-scale movements in herring are regulated by group formation processes where individual preferences are pooled together to determine the migration dynamics of the fish schools. Hence, a strong cohort with a preference for a different migration strategy can drive major shifts in the distribution of the entire population. This seems coherent with theoretical results of De Luca et al. 2014 demonstrating that three factors can regulate long-distance migratory dynamics in fish: habitat quality, numerical dominance, and the "sociality" (probability of being in a school relative to individual navigation).

I found the paper original and significant since, differently than in terrestrial animals, the effect of social dynamics in regulating fish migrations is an often overlooked process in ecology, despite its critical influence on population distribution and ecosystem stability. Traditional studies on fish migration have primarily focused on environmental factors such as water temperature, salinity, and food availability, as well as physiological cues like growth and reproductive cycles. While these factors undoubtedly play significant roles, the social behaviors within fish populations can profoundly impact migratory patterns in ways that are not entirely understood. This paper is one of the very few presenting robust observations to disentangle those processes providing convincing arguments supporting the hypothesis that rapid shifts in habitat utilization of fish populations are regulated by social interactions.

The manuscript presents the case of a poleward shift in the spawning of Norwegian spring spawning herring. This population has recently disappeared from historical breeding grounds in the south of Norway, shifting its distribution further North. Climate and bioenergetic arguments cannot entirely explain this rapid shift. While, on the other hand, individual preferences and social interactions (aka. collective memory) can be used to describe how the loss of experienced individuals due to overfishing can disrupt traditional migratory pathways, leading to the entire schools adopting new routes based on the dominant preferences of remaining members.

This seems to be the case for the 2016 cohort of herring. Several indicators are presented in the manuscript to describe the numerical dominance of this group over time and the corresponding shifts in catches and spawning behavior of the population. Similarly, different methods are used to analyze the role of climate, food, and energetic constraints in migrations. The Authors then conclude that fishery-induced collective memory loss is the major factor driving the observed changes in migrations.

I think the manuscript is interesting and well written. It provides convincing quantification of the above processes, which are inherently very difficult to quantify. The analysis for the world's largest herring population offers clear advantages in obtaining quality observations that are not generally available for other fish groups.

I have no major objections to having it published in Nature. However, I provide below specific remarks and suggestions for improvements that can be used in the revision of the paper.

Bioenergy model: The method used to simulate migrations and estimate bioenergetic demands can be improved to reduce the number of assumptions and better estimate uncertainties. I would suggest performing Lagrangian simulations of larvae dispersion using standard individual based modeling (as for example in Gabellini et al. 2023 <https://www.frontiersin.org/articles/10.3389/fmars.2023.1141726/full> see supplementary materials), with a better description of ocean currents (as for example extracted from numerical models under Marine Copernicus) and a range of directional swimming velocities to assess year-to-year variability as well as estimate the actual swimming speed that should be used to reproduce the observed patterns. The method used assumes averaged geostrophic currents as representative of the actual conditions which I think is an unnecessary simplification that prevents to estimate uncertainties.

Spatial analyses: There are few places where information on the spatial distribution is lacking. Figure 1 shows that since 2011 the catches in Q1 and Q2 are substantially reduced relatively to previous periods. This is despite the spawning stock biomass (Figure 2c) is above the precautionary reference point. It would be nice to have some text to explain those patterns. Also, what is the hypothesis on why the 2016 cohort did not move south of Røst as first-time spawners (ref. page 6 lines 195-197)? Also, it would help the reader to have a detailed description of the herring migration process already in the introduction part with indication of wintering, feeding, spawning areas as well as the area where the shift in migration has

occurred.

Specific comments:

Page 3 line 110-111. This sentence is more an hypothesis and the references there do not really have data for the herring supporting it

Page 6 line 215. "...north easternmost wintering area..." it would be better to add the location in one of the map of figure 1

Page 7 line 243-245. You could strengthen this statement linking it to the results in De Luca et al 2014. In that paper is the product between density of informed individual and individual preference for a given location that produce the group bias towards the selected location.

Page 7. Line 243. "... that that..." please correct

Page 7 line 255 "...faction" or fraction?

Page 8 line 280-281. "...2026-cohort in 2023 was smaller than...." I cannot really see it in Figure 2i

Page 9 line 327 "...ocean warming instead indirectly...." unclear

Figure 6. I would consider showing Figure b and c as anomalies relative to a given baseline (e.g., 1988-2000) and compare those to Figure 2a for the shift in landings.

Figure 6 caption. It needs some revision I think d,c,e and d,e,f have been mixed up.

Page 21. Extended Data Fig 1 and Fig 2 do not really add much to the text. Either explain it better or just remove

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(Remarks on code availability)

I have open the GitHub repository and checked some of the R-code. I have not tried to install but only looked at the code.

Referee #3

(Remarks to the Author)

Slotte et al. 2024 - Herring spawned poleward following fishery induced collective memory loss

I appreciated the opportunity to review this manuscript. The subject is very timely and interesting given the rapidly changing marine environment. I felt there were still a few missing pieces in the story that made it hard for me to recommend the manuscript for publication. For example, in Figure 1 the northward migration of catch seems largely driven by a lack of southern catch rather than a movement of the northward edge. It may be helpful to include leading and trailing edge statistics alongside center of gravity. There is catch in the northernmost area (and even further north) in 1995-200 and 2001-2005 for example. I appreciated the bioenergetic model and the climate change scenario explored, and found most helpful Figure 6 on zooplankton prey. The later zooplankton bloom timing in the north does offer potential for the match-mismatch hypothesis but that also assumes that food is limiting. If the population is a fraction of where it was in earlier decades, there is the potential that there is simply sufficient food in the north thus the lack of migration southward. All this to say, I think the collective memory loss is a valid hypothesis and a very enticing one, but I do not find the evidence presented convincing enough that it is due solely to lack of group memory (as the authors repeatedly claim). I would like to have seen a figure that provides an overview of herring migration in the study area including prevailing currents, and then the suite of potential hypotheses that could have resulted in the observed pattern of catch and population dynamics with the corresponding approaches taken to disprove those hypotheses. The authors present the sole hypothesis from the first paragraph of the introduction rather than presenting the potential mechanisms from the broader field of fisheries ecology that could result in similar patterns of distribution. Including larval herring data (or spawn surveys) to show the potential for reduced dispersal would have also been really valuable. For example, what about the hypothesis simply that smaller population sizes contract their range (and forego migration) due to an abundance of food available? Providing a more holistic view of migratory coastal pelagic life history (beyond NA Herring) and the mechanisms that drive distribution would make the manuscript much more approachable and interesting to a broad audience. I have no argument with the findings that the population COG is more northern in recent years, but I would encourage the authors to be more inclusive of multiple potential drivers and why collective migration is the best here. Some detailed comments follow as well.

L48-50 – this is a very valid hypothesis but far from the only one here. See comment above that migratory behavior may be lost simply due to the lack of competition due to small population sizes.

L56-57 – see the work of Stier et al and Okamoto et al. <https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.3283> and <https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/eap.2051> that document loss of portfolio effects and potential for loss of collective migration. Also, see the example from Pacific herring that shows range contraction as a result of overfishing as an alternative hypothesis to collective memory loss (<https://cdnsiencepub.com/doi/full/10.1139/cjfas-2021-0047>).

L110-111 – these citations vary from a book on collective migration to terrestrial mammals and whales. They do not support the sentence here which is focused on herring. I would like to see more support for herring "adopt(ing) the migration culture of the population."

L127 – "Different explanations for this dramatic change have been explored" – it would be valuable for the reader to know the potential explanations here (e.g. at least cite the relevant manuscripts).

L133 – “the increased fishing pressure with age” – figure 2f shows that in boom years (1998, 2010) older fish are harvested more. Why did these two periods of intense fishing not lead to this hypothesized loss in memory? The same argument could be made about figure 2c and the plummet in catch of <2002 cohort?

L181-182 – again the authors cite these 5 manuscripts which do not all support the point being made. I would encourage the authors to be selective about their citations as many of these are theoretical or review papers discussion the potential role of social behavior but it does not direct back to the sentence as written.

L247-263 – this is one of the most valuable paragraphs of the manuscript and should be explored earlier and in more detail. You discuss climate below but I would argue that this is the first population decline that coincided with the warmer (>2005) climate the authors present. This suggests there could be an interplay (or at least the alternative hypothesis) between warmer waters.

L265-298 – I found this section much less useful than the rest of the manuscript. Specifically the authors have made the claim that social behavior is the driver here and have created a null model without social behavior that shows a different pattern (e.g. persistent migrations). I would have liked to see a model that includes social behavior + bioenergetics + climate (e.g. IBM + collective behavior + multiple copepod regimes) and shows that social behavior is the dominant factor resulting in the observed pattern. As described, this exercise belongs largely in the supplement with a few sentences in the text to the point that bioenergetics alone does not explain the lack of migration.

L296-298 – see my comment above, but I do not see how this exercise offer insight into transfer of migration culture. It just shows (in my naïve reading) that migration is supported by the bioenergetics.

L340 – “which contributed to the unsuccessful transfer of traditional migration culture” – this should at least be written, which could have contributed... but as mentioned above, there is the potential that the warming + large 2016 year class following heavy depletion could simply be a climate+fishing signal (e.g. Essington et al. 2015 PNAS) rather than collective memory. The authors need to do more to convince the reader that their hypothesis is the most parsimonious which the current manuscript simply does not do.

L385-386 – is there evidence in the literature from other locations around the world for this? And you mention centuries here but is there data showing that this northward trend has not happened previously over the past centuries scale?

L390-392 – I apologize that I keep harping on this, but your study presents a valid hypothesis but does not reveal the disrupted migration culture.

L397-398 – also the portfolio effects in Stier et al. There is much more research on forage fish management than is presented here.

L562-564 – do you need individual landings to calculate COG? Having a longer time series would help bolster your hypothesis.

L579-581 – this hypothesis (alongside alternatives) would be valuable in the introduction.

L650 – do you think alternative tagging locations (e.g. not just the northern portion of the range) would have provided a different result? If not, why not?

L680 – did you include actual measurements of prey distribution (e.g. Fig 6) or scenarios of prey distribution? I also would be curious to know the bioenergetic considerations of not migrating as far south since that seems to be a newly observed behavior and might be energetically more efficient.

Version 1:

Reviewer comments:

Referee #1

(Remarks to the Author)

In my past review, I signaled through provision of past literature on the entrainment concept that the current study represents another, albeit important case study in support for socially-determined migration behaviors. The authors in response provided additional context related to collective mechanisms and memory thresholds. Further, they have better structured the counter-hypotheses related to climate change and bioenergetic determinants. My point of the work being a phenomenological case study that contributes to an existing body of similarly structured studies on entrainment did not warrant concern by the Editor in terms of the paper's impact. Thus, as the science is quite sound in this integrative study, I recommend that it be accepted.

Referee #2

(Remarks to the Author)

I have reviewed the revised version of the paper "Herring spawned poleward following fishery-induced collective memory loss" by Slotte et al., submitted to Nature.

In my initial review, I provided three specific remarks all of which have been addressed in this revised version.

Below, I provide feedback on each point and some additional remarks on the revised overall structure of the paper:

1. Introduction: The introduction has been expanded to include an initial description of the current understanding of the NSS herring migration process.

I find this revision adequate. However, I have additional comments regarding the general structure of the paper (detailed below).

2. Bioenergetic Model: The authors have not modified the bioenergetic model, arguing that additional complexity is unnecessary for the scope of the study.

While I agree that this may hold true for a fully individual-based model, I still recommend that Authors should assess the uncertainties associated with their use of geostrophic currents - instead of using the available surface currents for specific years (e.g., from marine copernicus data).

Although geostrophic currents and surface currents are closely related in open-ocean, this assumption requires formal validation in coastal settings, where the use of geostrophic currents could result in significant underestimation of the currents experienced by the herring and, consequently, significant changes in the respiration costs reported in this study.

3. Spatial Processes: The spatial processes illustrated in the previous Figure 1 have been clarified, and the corresponding text is now much easier to follow. Nonetheless, I have additional remarks on the use of figures (see below).

The revised version of the manuscript introduces a substantially different structure compared to the previous submission.

While these changes appear to respond to comments from other reviewers, I have a few critical observations regarding this new version:

4. Introduction: The introduction now includes a schematic detailing the migration process, strategies, currents, prey availability, etc.

In my view, this section includes excessive details now that dilute the paper's core message. Much of the detailed information on NSS herring migration is well-explained in cited references. I suggest reducing the text on page 2, lines 57–77 to keep only the essential required to correctly follow the analyses performed in this study. For example, the discussion of *Calanus finmarchicus* transport seems to me an extra that is better addressed in other sources.

5. Figure 1 and schematics: I recommend either a complete revision or removal of Figure 1 in its current form. It is overly complex, with excessive text that reduces readability and clarity.

The schematics of ocean currents and *C. finmarchicus* are superfluous and approximations at best. If a schematic figure is deemed necessary by the Authors, it should focus solely on simplified monthly migration patterns from 1988 to 2024, identification of the localities while avoiding unnecessary symbols and text. For instance, depth could only show the 250 m bathymetry and similarly to illustrate migration processes a reduced number of arrows and text could be used, maybe with different colours for the different regimes.

6. Extended Data Figure 1: This figure should be moved back to the main text, as in the previous version, given its centrality to the paper's narrative and its role in explaining shifts in distribution patterns.

The figure is very useful to illustrate various factors such as species distribution, fishing practices, and year-to-year or seasonal variability. Additionally, I suggest replacing "Røst" with "Lofoten" in the text for consistency and maybe provide in the caption (or graphically if possible) notations to underline the change in fishing strategy (rather than availability) after 2011 (which is now well explained in the text).

7. Terminology: The manuscript occasionally refers to concepts like optimality and the maximisation of lifetime fitness in relation to habitat selection and NSS herring ecology. These are assumptions rather than verified conclusions, as they are not entirely supported by existing data. To avoid misinterpretation, I recommend revising this terminology and using for example "suitable" habitats instead of "optimal." For instance, the text on page 1, lines 13–18, could be revised accordingly.

Overall, I remain supportive of the publication of this paper in Nature or a related journal. However, addressing the comments above could enhance the clarity, focus, and scientific robustness of the manuscript.

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(Remarks on code availability)

The code is available at the link provided but I have not reviewed it.

Referee #3

(Remarks to the Author)

Slotte et al. 2024 revision - Herring spawned poleward following fishery induced collective memory loss

I appreciated the opportunity to re-review this manuscript. The subject remains very timely and interesting given the rapidly changing marine environment. I feel it also is much improved but I will re-iterate some of the comments I made previously that still persist in this draft. The authors have proposed and I would argue support a very clear hypothesis that loss of memory is influencing spawning behavior but, they have not disproven or even attempted to disprove the alternative hypothesis. Line 161 "Memory loss explains the new migration" is just another example of overstating the confidence. This should say "Memory loss could explain this new migration." I think the authors have a great story here that supports their hypothesis but I remain unconvinced that it's the only plausible hypothesis. I have not provided line edits for this reason.

Version 2:

Reviewer comments:

Referee #2

(Remarks to the Author)

This is my third review of the manuscript. All remarks provided in my previous revisions have been satisfactorily addressed by the Authors, and I do not have any further remarks. Clarity, focus, and robustness of the scientific results have been largely improved in this version of the manuscript.

As a minor comment, I have noticed that in several places the Authors have chosen to replace the term "fraction" with "proportion". I am not a native speaker, and while I recognise the value of proportion in the context of mapping acoustically derived quantities, fraction feels more appropriate when referring to numerical dominance and cohort distributions. However it is ultimately up to the Authors to decide on what to use.

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Response to reviewers

This is a response to three constructive reviews on our manuscript **Herring spawned poleward following fishery-induced collective memory loss** submitted to Nature. We were encouraged by the positive feedback from Reviewers 1 and 2, who were supportive of our findings.

On the other hand, we find that main criticisms raised by Reviewer 3, particularly the proposed alternative explanation for our observations, were not sufficiently substantiated. However, in response to this critical review we made considerable revisions that in our opinion improved the manuscript.

Below, is our point-by-point response to reviewers.

Reviewer 1:

Reviewer 1 provides a thorough summary of the literature that supports our study, recognizing the novelty of our work. We are also commended for the careful and comprehensive treatment of our data, and the reviewer express hope that the study will be published in Nature or elsewhere. However, two main points are raised, related to the manuscript's narrative style and suggested directions for future research, which we have addressed in our revision.

1. Narrative and Style:

While Reviewer 1 described the manuscript's style as resembling a "synopsis," we respectfully disagree with this characterization. Our study follows the format of a conventional scientific investigation, with clearly stated hypotheses, well-documented methodologies, and results presented in the context of relevant literature.

However, we acknowledge that the merged "Results and Discussion" section may have contributed to this perception. This format was chosen to ensure a more cohesive flow to the narrative and is an approach permitted by Nature.

We recognize that placing the section "A conservative migration culture" after the objectives in the original manuscript may have contributed and impression of a synopsis. This section is now condensed into 3rd paragraph of introduction. Note also that the print version of Nature omits the Methods section at the end of our manuscript, so we took care to integrate essential details of our methods into the main text to ensure clarity for all readers.

2. Suggested Future Research:

We fully agree with Reviewer 1's insightful suggestion regarding future work to explore the threshold of memory needed to preserve migration culture. The reviewer points to the need for theoretical models to integrate empirical data in this area, and we have emphasized this in our revision of text. We point to this threshold in abstract, intro, results and discussion. We have also introduced a new section titled "Memory threshold preserving culture," which includes a specific discussion on this topic.

We want to emphasize that our empirical data, which addresses social learning processes at the school level in a spatiotemporal context in relation disrupted migration culture, sets our study apart from other case studies working more at the population level. We believe these findings will be of particular interest to the large community of theoretical modelers studying animal behavior, as they demonstrate that more complex dynamics in time and space must be considered in future models.

Moreover, we find that such empirical case studies are critical, not only for advancing scientific understanding but also for raising awareness among the broader public, researchers, and policymakers. It often takes real-world events, like those we document here, to spur theoretical insights into practical action, especially when it comes to revising management strategies for migratory species.

3. Use of references:

Reviewer 1 found some places we had used theoretical references for a specific phenomenon. We have taken this into account in the revised MS.

Reviewer 2:

We are pleased that the non-anonymous Reviewer 2 supports our manuscript's publication in Nature, describing it as interesting and well written. He emphasizes the study's originality, highlighting the often-overlooked role of social dynamics in regulating fish migrations, which critically influence population distribution and ecosystem stability. He also commends our quantification of these difficult-to-measure processes, using the world's largest herring population as a valuable case study.

In agreement with Reviewer 2 we are concerned with the number of studies relating changes in fish distributions to environmental condition without showing interest in age and size structure. With age the experience increases and with size the migration potential increases. On top of that social learning adds a third dimension. We appreciate that Reviewer 2 finds that NSS herring may serve as a good quantitative example pointing on the role of social dynamics in regulating fish migrations.

Below, we address two constructive suggestions from Reviewer 2 to improve the introduction and bioenergetic migration model.

Improving the Introduction

The reviewer suggests including a detailed description of the herring migration process in the introduction, specifying wintering, feeding, and spawning areas, along with the region where the shift in migration occurred.

We agree this is an excellent suggestion. We have condensed the section “A conservative migration culture” from the original manuscript and moved it to the third paragraph of the introduction, positioning it before the objectives. This adjustment enhances the manuscript's focus while maintaining necessary background information.

Improving the Bioenergetic Migration Model

The reviewer suggests that our model, which assumes averaged geostrophic currents for spawning migration, oversimplifies the conditions faced by NSS herring. He recommends using Lagrangian simulations with individual-based modeling and a range of directional swimming velocities, derived from ocean current models (e.g., Marine Copernicus), to better capture year-to-year variability.

While his suggestion is interesting, we believe it introduces a level of complexity that is not necessary for the scope of our study. More advanced models, as the one suggested, could offer a representation of variability, but they also introduce significant uncertainty due to the increased number of assumptions needed to parameterize both the biological and oceanographic models. Our simpler approach provides a reliable and robust framework for addressing our research question. By using averaged currents, we still capture the key oceanographic drivers influencing migration patterns, while avoiding unnecessary complexity that could obscure, rather than clarify, the bioenergetic dynamics we are modelling.

Minor comments:

- *“Figure 1 shows that since 2011 the catches in Q1 and Q2 are substantially reduced relatively to previous periods. This is despite the spawning stock biomass (Figure 2c) is above the precautionary reference point. It would be nice to have some text to explain those patterns”.* - We have added text, this reflects a change in fishing strategy not availability.
- *“What is the hypothesis on why the 2016 cohort did not move south as first-time spawners?”* - This is linked to two processes, one is the size dependent migration as showed under the bioenergetic migration model, but the main explanation is the lack of spatial overlap with the elders feeding and wintering farther southwest, i.e. lack of leadership also linked to the threshold we are discussing. It is normal for first time spawners to start spawning farther north, but they follow older fish south when migration potential increase with growth and the threshold of determined leaders is well established.
- *“Page 3 line 110-111. This sentence is more an hypothesis and the references there do not really have data for the herring supporting it”.* - This is rewritten, and we have used the one specific reference on NSS herring supporting that social transfer of migration culture is essential: Huse, G., Fernö, A. &

Holst, J. C. Establishment of new wintering areas in herring co-occurs with peaks in the ‘first time/repeat spawner’ ratio. Mar. Ecol. Prog. Ser. 409, 189–198 (2010). <https://doi.org/10.3354/meps08620>

- “Page 6 line 215. “..north easternmost wintering area...” it would be better to add the location in one of the map of figure 1”. - We now refer to (Fig. 4c, and the new Fig. 1) for this location.
- “Page 7 line 243-245. You could strengthen this statement linking it to the results in De Luca et al 2014. In that paper is the product between density of informed individual and individual preference for a given location that produce the group bias towards the selected location.” - We had added this reference here. In addition we have added the reference in the introductory text and results/discussion to support the same statement, and we added also there the third factor suggested in de Luca et al; “intensity of social interaction” in introduction.
- “Page 7. Line 243. “... that that...” please correct.” - Fixed now
- “Page 7 line 255 “...faction” or fraction?” - Text is changed
- “Page 8 line 280-281. “...2026-cohort in 2023 was smaller than....” I cannot really see it in Figure 2i” - It is Fig. 2h that shows body length not Fig. 2i that is condition factor. Perhaps ‘smaller’ is not best word, we have rephrased to “shorter”.
- “Page 9 line 327 “...ocean warming instead indirectly....” Unclear”. - We revised sentence to: We propose that ocean warming instead indirectly influenced the abrupt poleward shift in NSS herring spawning by affecting spatial overlap between recruits and elders.
- “Figure 6. I would consider showing Figure b and c as anomalies relative to a given baseline (e.g., 1988-2000) and compare those to Figure 2a for the shift in landings.” - This figure is replaced by predictions from GAM models
- “Figure 6 caption. It needs some revision I think d,c,e and d,e,f have been mixed up.”. - Same as above, new Fig. 6, so not relevant.
- “Page 21. Extended Data Fig 1 and Fig 2 do not really add much to the text. Either explain it better or just remove”. - We have rephrased this to “measuring density distributions during early (April-June, Extended data Fig. 2) and late (July-August, Extended data Fig.3) in revised MS. We wanted to have these Extended Data Figs in the manuscript as they are an addition to the data we show on proportion of 2016 year class in samples from surveys. Readers may want to see also density distributions from where we have sampled the fish. But we can remove them if Editors suggests that it is not essential and there is no need to write much more details.

Reviewer 3:

While Reviewer 3 also agrees that collective memory loss is a valid hypothesis for the poleward shift in NSS herring spawning, the evidence presented was apparently insufficiently convincing. The reviewer argues that there may be alternative explanations and suggest that this may simply be a spatial contraction due to a smaller population and abundance of prey in the north. This hypothesis appears influenced by research on Pacific herring (*Clupea pallasii*) based on three suggested references. There is a specific request for an overview figure that outlines herring migrations and oceanographical conditions in the study area, along with rationale behind potential hypotheses and approaches used to examine them.

Although we tend to disagree with Reviewer 3’s most critical points, we really appreciate this detailed and constructive review. It made us acknowledge that our initial presentation of the NSS herring life history strategies in a dynamic environment and the basis for our hypotheses may have been unclear. In response, we have revised the manuscript significantly, incorporating new analyses and figures, while also forwarding our arguments of disagreement where we find that appropriate. Below, we outline our revisions and rationale.

New conceptual overview (Fig. 1):

We are thankful for this suggestion; it most certainly is a great idea. We have developed a new conceptual figure illustrating how size dependent migration strategies of NSS herring likely have evolved as an adaptation to spatiotemporal dynamics in its main prey, *Calanus finmarchicus*, including the importance of social interactions for preserving migration culture. The figure demonstrates the triangular migration framework and life history from larvae to recruitment and transfer to adult life. We also highlight the poleward shift in

spawning from Møre to Lofoten (note we use Lofoten the region instead of Røst the location in revised MS) and the three hypotheses explored (memory loss, migration constraints, or climate change) as explanations. This figure replaces the original Fig. 1 with spatiotemporal dynamics in the fishery, which is now moved to Extended Data Fig. 1, and should give readers a good overview of both background, rationale and objectives even without reading introduction.

We have also revised the abstract and introductory text accordingly. Introduction now includes a new general reference on the coevolution of genetics and culture, which likely have shaped the NSS herring's long-established strategy of spawning at Møre. We have added one new reference better showing the tight spatiotemporal link between *C.finmarchicus* production and phytoplankton spring bloom dynamics propagating northward and westward, in addition to a reference suggesting that the tradition of NSS herring spawning at Møre is upheld because the region is the main area for cross shelf transport of *C.finmarchicus*, both results marked in Fig. 1.

Clarifying research questions:

It appears from some comments by Reviewer 3 that objectives have not been clear enough in our introduction. We have therefor expanded the objectives section to link the three suggested hypotheses more directly with specific research questions.

For instance, the climate change hypothesis now includes a clear objective to investigate whether biotic and abiotic environmental changes have made Møre suboptimal for spawning, contributing to the abrupt poleward shift. We also raise questions about potential indirect effects, such as altered feeding migrations of elders contributing to lack of overlap with recruits, which again might disrupt the social transfer of migration knowledge, as opposed to directly affecting suitability of a spawning area.

New Analyses on Zooplankton and Temperature Trends:

Reviewer 3 captured interest in our Fig. 6 on zooplankton trends, with interpretations of prey levels in the north that we did not fully understand. We must admit that our intention with the figure simply was to give readers a rough overview of zooplankton and temperature relevant for adult spawners and their offspring, demonstrate trend over season and latitudes fitting with the strategy of NSS herring southward spawning migration. These data are not collected at same time every year across the different cross sections and monitoring stations, so we grouped data in 5-year intervals just to make sure there was data from each area at every interval and month shown. Given Reviewer 3's interpretation we acknowledge that this way of presenting data was not the best.

We have reanalyzed the zooplankton and temperature data, extending the time series to cover 30 years (1995–2024) and using GAM models to predict spatiotemporal development in prey availability and ambient temperatures from onset of spawning migration until metamorphosis of the offspring. We have been much more careful in filtering data to represent ambient conditions of adult spawners and their offspring. This revision is considered a significant improvement to the original analysis giving a more correct overview of dynamics relevant for evaluation of the climate change hypothesis.

The new Fig. 6 summarizes these predictions, while the GAM model diagnostics appear in Extended Data Figs. 6–8. The new results do not indicate that Møre has become suboptimal for spawning, rather they confirm that despite fluctuations in the conditions it remains the most optimal spawning area in terms of growth conditions for the larvae. We also must stress that the larvae hatching at Møre start drifting in the best growth conditions, while they match with conditions developing over spring during northward drift. Our analyses just support previous studies describing this adaptation to the latitudinal trend along the Norwegian coast.

The revised section, now titled "Influence of Climate Change," reflects these updates. We have also added some new references here on the stable phenology of spring phytoplankton blooms over climate change, and delayed summer-autumn blooms over same period. The first is important for the spawning strategy, the latter for the feeding opportunities of elders, given the link to *C.finmarchicus* production. It appears day length, which is unaffected by climate, is the main driver for spring blooms, causing a delayed production at higher latitudes. We have added a reference that NSS herring spawning in fact is regulated by photoperiod, likely evolved as an adaptation for match between first feeding larvae and their prey. These processes are also highlighted in the new Fig. 1.

Why Pacific herring dynamics may not apply to NSS herring:

Reviewer 3 points to Pacific herring for other explanations to the abrupt poleward shift in NSS herring. We believe that factors driving erosion in the portfolio of Pacific herring populations have limited relevance to the dynamics observed in NSS herring. There is a considerable difference in life history strategies where Pacific herring spawn in shallow waters on seaweed and are less migratory than NSS herring that spawn at hard substrates in much deeper and more stable environments. It is to be expected that Pacific herring may be more susceptible to climate change.

Moreover, Pacific herring consist of a complex metapopulation structure of smaller populations presumably connected to their natal areas. NSS herring is one large single population inhabiting large areas with no evidence of natal homing but having a strategy to maximize lifetime fitness by optimizing spawning migrations. We must acknowledge all the relevant research developed over last 100 years in both Pacific and Atlantic herring, and that factors driving dynamics in one population may not apply to the other.

However, Pacific herring is relevant as an example where spatial management is very important, and spatial management is perhaps the way forward if we want to protect older fish from being plummeted to a level surpassing the threshold of memory required for preserving migration culture. We have therefore added a paragraph under “Consequences for Management,” noting lessons from Pacific herring spatial management, adding one suggested reference from Reviewers 3. Additionally, we reference two studies on Pacific herring that are directly relevant for integration of social learning in management. Simulations have shown that if Pacific herring is managed with optimal fishing pressure under the concept of natal homing, while the recruits instead just follow the elders proportional to their abundance, there is a high risk of losing spawning sites, as we now have for NSS herring.

Why spatial contraction at lower biomass and abundant prey is not a valid explanation

Reviewer 3 suggests the that the poleward shift simply is spatial contraction linked to a smaller population and abundant prey in the north. Here we must stress again what we have stated clearly in our study, that NSS herring has used Møre as its primary spawning ground for 70 years while the population has fluctuated significantly in size. During the stock collapse it was down at spawners biomass levels around 200-500.000 t. Still, it wintered in northern fjord, spawned at Møre but had a narrow and more coastal feeding distribution. Now the spawners biomass is smaller than it was before, but still a very large population above 3 million t, being widely distributed over the feeding season as we also document in our study.

We see no evolutionary rationale for a sudden northward shift at the current population size as long as southern spawning remains optimal. We do not understand how the population suddenly should predict that there will be enough prey for their offspring if spawning north during time of poleward shift. We have argued that these strategies of spawning south are something that must have evolved over a long time as an adaptation the biotic and abiotic environment, and as a coevolution of genetics and culture.

The condition along the Norwegian coast fluctuates considerably and in some years the recruitment success is very high, likely across many spawning sites, but on the long run higher in the south than in the north. The way NSS herring has utilized spawning sites over history does not reflect a population that simply adjust its spawning migrations to interannual environmental fluctuations on a latitudinal scale. It rather reflects a population that maintain a clear strategy of going south.

Minor comments:

- *“Figure 1 the northward migration of catch seems largely driven by a lack of southern catch rather than a movement of the northward edge. It may be helpful to include leading and trailing edge statistics alongside center of gravity. There is catch in the northernmost area (and even further north) in 1995-200 and 2001-2005 for example.”* - Møre has not only been the main spawning ground, but the main fishing ground over spawning season, before the herring abandoned the area. Our point with both the original Figure 1 (now Extended Data Fig. 1) and Fig. 2a on latitudinal COG has been to demonstrate this shift in distribution through the fisheries, while at the same time demonstrating the quarterly trends in distribution reflecting dynamics in the triangular migrations between spawning, feeding and wintering areas. The feeding and wintering areas have been dynamic, but Møre has remained the main

spawning area as we show in Extended Data Fig.1 and mark in new Fig. 1. We still feel these figures describe these processes well and see no need for adjustments.

- “L48-50 – *this is a very valid hypothesis but far from the only one here. See comment above that migratory behavior may be lost simply due to the lack of competition due to small population sizes*”. - We have argued against this hypothesis above, it simply does not fit for this population although we clearly acknowledge it fits well for Pacific herring. We also think our revised introduction including new Fig.1 and more specified objectives under the three hypotheses should make things a bit clearer to the readers.
- “L56-57 – *see the work of Stier et al and Okamoto et al* <https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.3283> and <https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/eap.2051> *that document loss of portfolio effects and potential for loss of collective migration.* (<https://cdnsiencepub.com/doi/full/10.1139/cjfas-2021-0047>) *Multi-decadal shifts in the distribution and timing of Pacific herring (Clupea pallasii) spawning in Prince William Sound, Alaska*”. - Although we find all these studies interesting, we have argued above that that NSS herring is not directly comparable, but we have included one reference and refer to two references on Pacific herring we find especially relevant in one paragraph under last section on consequences for management.
- L110-111 – *these citations vary from a book on collective migration to terrestrial mammals and whales. They do not support the sentence here which is focused on herring. I would like to see more support for herring “adopt(ing) the migration culture of the population.”* - We agree, and this was also pointed out by Reviewer 2. This is rewritten and we have used the one specific reference on NSS herring supporting that social transfer of migration culture is essential: Huse, G., Fernö, A. & Holst, J. C. Establishment of new wintering areas in herring co-occurs with peaks in the ‘first time/repeat spawner’ ratio. Mar. Ecol. Prog. Ser. 409, 189–198 (2010). <https://doi.org/10.3354/meps08620>
- L127 – *“Different explanations for this dramatic change have been explored” – it would be valuable for the reader to know the potential explanations here (e.g. at least cite the relevant manuscripts).* - We agree, this was unclear, the sentence has been removed in the revised MS
- L133 – *“the increased fishing pressure with age” – figure 2f shows that in boom years (1998, 2010) older fish are harvested more. Why did these two periods of intense fishing not lead to this hypothesized loss in memory? The same argument could be made about figure 2c and the plummet in catch of <2002 cohort?* - We explained this also in the original MS, but have even more focus on it in the revised MS under the new section “Memory threshold preserving culture”. We use here the 2002 cohort as an example to demonstrate how we interpret migration culture is preserved under more normal conditions. By normal conditions we mean that a cohort leaving the Barent Sea over 2-3 year mix properly with elders when it enters the Norwegian Sea and the threshold of memory required for successful transfer of culture is present. Slow-growing fish from a cohort recruiting 1-2 years after the fast-growing fish could also follow repeat spawners from same cohort, not just the older fish. We make a point out of the fact that 2016 was born 12 years after the last large 2004 cohort, and did not overlap properly with older fish when entering the Norwegian Sea, so it was allowed to establish its own pattern. Hence, over centuries shifts in spawning distribution may have occurred naturally when there are long periods with recruitment failure before a bursting cohort, and there is little overlap between the new and old generations. As we also highlight migration constraints and climate change may affect this process with mixing and overlap in the Norwegian Sea. So in the case of the 2016 cohort several circumstances contributed to the dynamics, but the main explanation is fishery induced memory loss. We believe that if we did not fish millions of tons of elders, it is unlikely that this poleward shift in spawning would have happened.
- L181-182 – *again the authors cite these 5 manuscripts which do not all support the point being made. I would encourage the authors to be selective about their citations as many of these are theoretical or review papers discussion the potential role of social behavior but it does not direct back to the sentence as written.* We have kept three citations we believe support our point
- L247-263 – *this is one of the most valuable paragraphs of the manuscript and should be explored earlier and in more detail. You discuss climate below but I would argue that this is the first population decline that coincided with the warmer (>2005) climate the authors present. This suggests there could*

be an interplay (or at least the alternative hypothesis) between warmer waters. This section is extended in the revised MS, we still suggest that the main climate effect is on the feeding conditions, contributing to the lack of overlap between older generations and the 2016 cohort entering the Norwegian Sea.

- L265-298 – I found this section much less useful than the rest of the manuscript. Specifically the authors have made the claim that social behavior is the driver here and have created a null model without social behavior that shows a different pattern (e.g. persistent migrations). I would have liked to see a model that includes social behavior + bioenergetics + climate (e.g. IBM + collective behavior + multiple copepod regimes) and shows that social behavior is the dominant factor resulting in the observed pattern. As described, this exercise belongs largely in the supplement with a few sentences in the text to the point that bioenergetics alone does not explain the lack of migration.* - The first paragraph under this section has been rewritten to improve clarity in the revised MS. Throughout the MS we have highlighted that heterogeneity in a population, such as diverging age (experience) and size (migration potential) may contribute to failed transfer of migration culture. In schooling fish this is likely of high importance, especially in migratory populations like NSS herring where the size dependencies are significant. In NSS herring it is also important to consider energy reserves as it does not feed over winter and spawning season. We find it highly relevant to explore if migration constrains could explain or partly explain the shortened spawning migration. In our view the best way to test this in addition to exploring biological data, was to use a simplified bioenergetic model. We do, however, agree that the suggested complex model to study all factors at the same time would have been wonderful. We do have such a model under development, Norwecom.e2e [Ecosystem model | Institute of Marine Research \(hi.no\)](#). In fact our co-author Erik Mousing was invited to contribute in our study as the developer of the IMB part of the model predicting herring migrations. However, this model is not at a level where the suggested simulations can be run, this is for the future, we instead chose to build the simpler bioenergetic migration model. Else see comment to Reviewer 2 on the bioenergetic model.
- L296-298 – see my comment above, but I do not see how this exercise offer insight into transfer of migration culture. It just shows (in my naïve reading) that migration is supported by the bioenergetics.* Perhaps the rewritten first paragraph of this section has improved clarity. It should be clear from text before this section that the 2016 cohort did not overlap well with elders until it had established its own migration pattern. It did not have the threshold of leaders to follow southwards for spawning during the recruitment process. However, the section on bioenergetics prove that it did have the potential to follow them if conditions were similar like for the 2002-year class, which we consider as more normal conditions. So, migration potential was not the explanation why it maintained spawning north.
- L340 – “which contributed to the unsuccessful transfer of traditional migration culture” – this should at least be written, which could have contributed... but as mentioned above, there is the potential that the warming + large 2016 year class following heavy depletion could simply be a climate+fishing signal (e.g. Essington et al. 2015 PNAS) rather than collective memory. The authors need to do more to convince the reader that their hypothesis is the most parsimonious which the current manuscript simply does not do.* - The whole section on climate change is revised considerably as replied further up in this response, where we also have rephrased this sentence to “which ultimately may have hindered the successful transmission of traditional migration culture”. Else regarding effects of climate / size of population etc, we have replied to this further up.
- L385-386 – is there evidence in the literature from other locations around the world for this? And you mention centuries here but is there data showing that this northward trend has not happened previously over the past centuries scale?* We have not looked at other places in the world where millions of tons have shifted spawning location and potential effects for bird colonies. There is a limited amount of 50 references, and we do not see that this is a major issue. It is, however, a major issue for the bird colonies in Norway. We do not have data to demonstrate that such an abrupt northward shift in spawning has not happened in past centuries. Of course, detailed data were not available centuries ago and fisheries were small scale close to shore. In this regard we have rephased text under last section of “Consequences for management”, where we write that NSS herring has spawned off southern Norway for centuries interspersed with periods of absence under climate change. This is the only thing history

tells. We then suggest that the mechanism is these long periods with climate related recruitment failure ending with a burst recruitment, and disrupted migration culture. This is opposed the alternative explanation that spawning sites in the south become unsuitable for spawning or less optimal under climate change. We can argue for this because of how we believe this population has evolved over time with strategic adaptations to the dynamic environment, and that we do not have scientific proof of shifts in spawning sites related to change in the environment.

- *L390-392 – I apologize that I keep harping on this, but your study presents a valid hypothesis but does not reveal the disrupted migration culture. Our study reveals that 391 the age-selective fishery targeting NSS herring can alter the demographic balance within the 392 population and lead to a disrupted migration culture* – This section is considerably revised, the sentence is not there. But we still stand for the result that fishing millions of tons of elders, may have caused an unbalanced demography, again leading to unsuccessful transfer of migration culture to the bursting 2016 cohort.
- *L397-398 – also the portfolio effects in Stier et al. There is much more research on forage fish management than is presented here.* – Again, this section is revised, and we do refer to Stier et al, while also highlighting two studies on Pacific herring we find relevant because of the direct link to potential effect of managing schooling fish not accounting for social transfer of culture, if this in fact is happening instead of homing to natal areas.
- *L562-564 – do you need individual landings to calculate COG? Having a longer time series would help bolster your hypothesis.* – We do not need individual landing data, but data on daily basis and for smaller rectangles. Unfortunately, the official data before 2000 is not available at this detailed level, else we would have prolonged this time series.
- *L579-581 – this hypothesis (alongside alternatives) would be valuable in the introduction.-* In the revised MS research questions are formulated alongside the hypotheses in a better way.
- *L650 – do you think alternative tagging locations (e.g. not just the northern portion of the range) would have provided a different result? If not, why not?* Unfortunately, weather conditions during wintering does not allow us to tag herring in the southwestern oceanic winter area occupied by the elders when the 2016 cohort recruited. But if we did, it should have shown more recaptures southward along the coast during spawning season as we know they consistently migrated south to spawn, yet of course the same poleward shift after 2020. We would also have expected to see tagged fish shifting to the northeastern wintering area when mixing more with the 2016 cohort.
- *L680 – did you include actual measurements of prey distribution (e.g. Fig 6) or scenarios of prey distribution? I also would be curious to know the bioenergetic considerations of not migrating as far south since that seems to be a newly observed behavior and might be energetically more efficient.-* There seems to be a misunderstanding here related to our choice of wording “energy consumption”. We have rephased sentences here to “NSS herring do not feeding during spawning migration, they rely on stored reserves²⁶. The energy used during the spawning....” Of course, it is energetically more efficient to just spawn close to the wintering in the north, but as we have argued the investment in migrating south pays of in higher survival probabilities of larvae. The background info here should be very clear from revised abstract, intro, including the new suggested Fig. 1.

Response to reviewers and editor

We thank the reviewers and editor for their constructive feedback on the revised manuscript “Herring spawned poleward following fishery induced collective memory loss” submitted to Nature. We appreciate that the reviewers find the manuscript much improved and more acceptable for publication, yet with some further suggestions for revision.

We trust that our second revision of the manuscript aligns with both the scientific rigor and editorial requirements of Nature. This condensed (20 %) version keeps all arguments intact while hopefully making the language more concise, polished, and professional. Let us know if further refinement is needed.

Below, we address reviewer comments while at the same time adhering to the editorial guidance.

Editorial instructions

We acknowledge the clear instructions provided by the editor for this second revision and have made the following changes accordingly:

- 1. Manuscript structure:**

Text and display items have now been separated into the specified order: Main text, References, Figure legends, Methods, Method references, and Extended Data Figure Legends. All figures, including Extended Data Figures, have been uploaded as individual files in requested formats. We have uploaded both a clean version of the manuscript and a version with track changes for evaluation.

- 2. Introduction:**

We were instructed to reduce the introduction to a maximum 500 words. It has been reduced from 880 to <500 words. This reduction specifically involved condensing background information on Norwegian spring-spawning herring and our research objectives. We retained all key references, and to our understanding no critical content was lost.

- 3. Display items:**

The number of main display items was reduced to five, per editorial instructions. Original Fig. 6 (GAM models on zooplankton and temperature data) has been moved to Extended Data Fig 5. This decision was discussed with the editor. While this adjustment reduces content in the print edition, all material will remain accessible in the online version. We also followed the guidelines and reduced the size of main display items when possible.

4. **Word limit:**

We followed the editorial instructions about making our story as brief as possible, given the size of our main display items. The main text including summary was further condensed to 3400 words (20 % reduction from the original ~4300), with minor adjustments throughout the manuscript without losing critical content. We trust this now will fit 8 pages in Nature.

Note that a significant reduction (40 %) was made in the "Influence of climate change" section. We removed methodological details in GAM model setups already described under Methods. We also deleted some detailed descriptions of GAM model predictions visible from Extended Data Fig. 5, which were not critical to have in the main text. Note that we also changed the order of condensed paragraphs under this section, and order of references accordingly.

Other minor revisions and clarifications

During final edits, we made some minor revisions to improve language and clarity throughout the manuscript, which all are visible in the tracked changes version along with the other revisions. Additionally, we replaced two ecological references with recent review studies (2025) under "Consequences for management" to highlight the relevance of longevity conservation, also supporting that our study providing extensive empirical data behind the theory is timely and of general interest:

- Kopf, R. K. et al. *Loss of Earth's old, wise, and large animals*. Science 387, eado2705 (2025). <https://doi.org/10.1126/science.ado2705>
- Wilson, J. A., Giske, J. & Brown, C. *Overfishing social fish*. Fish Fish. (2025). <https://doi.org/10.1111/faf.12880>

Responses to reviewer comments

Reviewer 1

We are pleased that Reviewer 1 now recommends our manuscript for publication and hope that this second revision will reinforce that conclusion.

Reviewer 2

We thank Reviewer 2 for supporting the publication of our manuscript, and for the thoughtful suggestions to final adjustments to enhance the manuscript's clarity, focus, and scientific robustness. Below, we address each comment:

1. Bioenergetic model:

I was recommended using surface currents (e.g., Copernicus data) instead of geostrophic currents to refine our bioenergetic model. In response, we incorporated surface velocities from the ORAS5 global ocean reanalysis, which uses a 3D model constrained by observations. The results, while comparable to those with satellite geostrophic currents, show slightly stronger currents and shorter swimming distances. Methods and Fig. 5 have been updated, and a new reference to the data product has been added. However, the main text remains the same, as the original description of results still fits well with the updated Fig. 5. In fact, the difference between 2020 and subsequent years in terms of migrations constraints is reinforced with the updated data on surface velocities.

2. Introduction:

We followed the suggestion to streamline the introduction, reducing background details on NSS herring migration and description of objectives substantially. This also aligns with the editor's instruction to limit the introduction to 500 words while retaining essential content and references.

3. Figure 1 and schematics:

It was recommended to remove or significantly simplify schematic elements of Fig. 1. Among other things it was suggested to remove the schematic overview of ocean currents. To show currents overlapping with herring migration patterns was originally a suggestion from Reviewer 3, which we supported as informative for our story. Reviewer 2 also suggested moving Extended Data Fig. 1 on spatiotemporal fishery dynamics into the Main text again. Given space limitations, and some disagreements between Reviewer 2 and 3 and us authors, we here reached a compromise. We decided to combine spatiotemporal fishery dynamics with simplified schematics of localities, currents and migration patterns into a new Fig. 1. Note that revised Fig. 1 merges Q2–Q3 landing data to reduce complexity as well as space, while maintaining a clear overview of feeding migration. We believe revised Fig. 1 now aligns with both Reviewer 2's and Reviewer 3's feedback as well as our own preferences. We hope Reviewer 2 finds this new version acceptable. We find that the combination of schematics and empirical data to describe herring migrations in a dynamic environment as an improvement.

4. Terminology:

Reviewer 2 suggested revising terms such as "optimality" and "lifetime fitness". We have removed or adjusted these terms throughout the manuscript.

Reviewer 3

We are encouraged by Reviewer 3's positive view of our study as timely and much improved after the revision. We are happy that the reviewer finds that the data presented support our hypothesis of memory loss, while we acknowledge the continued skepticism about this being the sole explanation for the observed shift.

We do not claim memory loss is the only hypothesis. Instead, we propose it as the primary mechanism behind the disrupted culture, alongside contributions from migration constraints and climate change. We have previously forwarded our arguments against another alternative hypothesis suggested by Reviewer 3, which we maintain. Given that our arguments were not met with counter arguments at this stage of revision, we trust that our current version can be acceptable despite some disagreements.

However, regarding Reviewer 3's concern about overstated confidence, we fully agree. Hence, we have revised the heading "Memory loss explains the new migration" to "Why memory loss could explain the shift" (we need to stick to 40-character limit) and softened the language throughout the manuscript with terms such as could, may, likely, probably and proposed. We hope these changes adequately address Reviewer 3's concerns.

Sincerely, Aril Slotte

A handwritten signature in blue ink that reads "Aril Slotte". The signature is written in a cursive, flowing style.

Bergen, 31. January 2025