

To the editorial board at the Philosophical Transactions of the Royal Society B,

Please find attached our revised manuscript *Eco-evolutionary dynamics, density dependent dispersal, and collective behavior: implications for salmon metapopulation robustness* (RSTB-2017-0018.R2), which we resubmit for a themed issue in Philosophical Transactions of the Royal Society B. We would like to thank the editorial team as well as the two reviewers for again providing a detailed set of comments and suggestions aimed at improving the quality of our submission. We note that all of the comments and suggestions were oriented towards more accurately communicating the results of our model. We have addressed all of the comments and thoughts below, and believe that our edited contribution has clearly benefited from the review process, and hope that it satisfies the concerns raised by both the editor as well as the two reviewers. We will be happy to address any additional concerns as they arise. Thank you again for the opportunity to resubmit to PTRSB.

Sincerely,

Justin Yeakel
Jean Philippe Gibert
Thilo Gross
Peter Westley
Jonathan Moore

[Editors comments/Author's responses](#)

[1. Perhaps define CV at its first use.](#)

Thank you. We have included the definition in the revised manuscript.

[2. Reference \[18\] \(Berdahl et al Evolution\) does not include any collective behaviour, so I do not think it belongs the two places it is currently cited. It is about the evolutionary interplay between dispersal and local adaptation, and given your model includes both dispersal and local adaptation, I think that it is important for this introduction and I would be happy if it were included. It might fit better in the sentence starting on line 37, or on its own. If you wanted to expand on it at all, another relevant would be \[Kisdi É.](#)

Dispersal: risk spreading versus local adaptation. *The American Naturalist*. 2002 Jun;159(6):579-96.], which is similar, but has a two-site model, much like your own.

Thank you for catching this. We have removed the reference from that section.

3. Line 119: "According to Berdahl et al..." I would be a little more comfortable with something like 'Following[As in] Berdahl et al., we assume...', since I don't think that we claimed that that is necessarily THE relationship, it was just a simple functional form we felt captured the trends.

Thank you. We have amended the sentence as suggested.

4. What is y-axis of the inset of Fig 1? Asymmetry? I assume that the x-axis is m , but it might be good to make that explicit. It did help me understand the main figure, but I was confused by what it was showing. I understand that it is a cartoon, but please be as explicit as you can.

Thank you for pointing this out. We have clarified the axes in the inset to Figure 1, and modified the caption to better describe the depiction of the stable and unstable fixed points.

5. What are the vertical lines in Fig 1? I would expect these transitions to not be continuous.

The editor is correct in pointing out that the vertical lines should not suggest a continuous transition (and instead where a graphics artifact). We have modified the figure so that these vertical lines are no longer present.

6. Is the word 'time' missing from the following sentence?

"It should be noted that when there is no straying ($m = 0$), recovery from extinction is infinite and these values are not shown." If not, what does recovery being infinite mean?

Thank you. This has been corrected.

7. What are the vertical/diagonal green lines in insets of Fig 3?

We have clarified in the figure caption that the vertical lines link the dominant and subordinate steady states in asymmetric cases.

8. In several places you should use \log_{10} instead of \log_{10} .

Thank you. We have corrected this mistake.

9. Fig 4: Consider inverting the colours. This is completely subjective, but it seems like red=bad/danger and a long recovery time is 'bad', right?

Thank you for the suggestion. We agree that this would be helpful for interpreting the figures and have made the adjustment.

10. Fig 4: The y-axis is labeled on one panel only, but the x-axis is on all four.

Thank you for catching this. We have amended the figure.

11. Fig 5: Why are the different panels different shapes? I like that they have consistent x- and y-ranges, but giving them the same aspect ratio and size would facilitate comparison. Can they all be like panel a, arranged in a row?

We were attempting to save space, however are happy to align them in a row.

12. Fig 5: The x-axis labels (m) do not match the caption's description (m_0).

Thank you for catching this. We have fixed the axes labels.

13. Is C really the strength of collective navigation? I see what you mean (and I humbly apologise if we called it that!), but I would point out that very high and very low values of C give a nearly constant $m(N)$ relationship. Yes, when $C \sim 0$ it is highly non-linear at very low values of N , but, if you for example set $C=1$ in a population where N^* is of the order on 100s or 1,000 (or more) $m(N)$ will be effectively constant (at $m=0$). I wonder then, if rather than finding certain results at intermediate ranges of collective navigation, you are really finding them at the extreme values, it is just that collective navigation is not a simple monotonic function of C . Another consideration the value of m_0 also sets the 'strength' of collective navigation. m_0 sets the potential to which collective navigation can improve things, such that if m_0 is low, then it matters less what C is.

You are of course correct that the 'strength' depends on both C and m_0 . In the Berdahl et al. paper, it is described as the half saturation point, which is a general description and does not in itself communicate biological meaning. However, for a given m_0 , an increased C reduces the effect of group size on straying (lowering the 'strength' of

collective behavior), and decreasing C increases the effect. Accordingly, we think that it is a useful proxy, and would prefer to use it as it emphasizes what is being changed in a biological sense as C is increased or decreased, though we acknowledge that it is not a perfect descriptor.

In the case that is described above, where C is low, and N^* is high, we would argue that in this case the ‘strength’ of collective behavior is still large, in that straying is reduced at very low population sizes, regardless of the fact that it then asymptotes as the population size grows... in a biological sense, it took a very small group size to ‘correct’ the mistakes of its constituent individuals, and this is what we mean by saying the effects of collective behavior are ‘strong’.

To clarify our use of the term, and to acknowledge its limitations, we have included the following text:

“Henceforth, we refer to C as determining the strength of collective behaviour: as $C \rightarrow \infty$, the effect of collective behaviour becomes weaker, such that the size of the population has no impact on straying, and $m(t) \rightarrow m_0$. In contrast, if $C \ll \infty$, the effect of collective behaviour is strong, and smaller populations reduce $m(t)$. Although the strength of collective behaviour depends both on C as well as the probability that an individual strays m_0 , for a specific value of m_0 , a lower C reduces straying for smaller population sizes, increasing the strength of collective behaviour. We acknowledge that the strength of collective behaviour is not exclusively determined by C , but suggest that it is an effective proxy for the role of collective navigation in this model.

”

14. Repeated period, '.', on the second line of page 4.

Thank you. This has been fixed..

Referee reports:

Referee: 1

Comments to Author(s)

Main comments

(1) The definition of recovery time (lines 145-148) is unclear. N^*_T is a random variable (its expectation and variance is used elsewhere). What is then N^*_T plus-minus SD? N^*_T is not a number. Moreover, if T goes to infinity, the random process N^*_T will get out of plus-minus SD simply due to the random term in eq 3.

Thank you. We have clarified that it is the expectation +/- the standard deviation that is used to evaluate recovery times. T is set at a value less than infinity ($T=10000$ for all simulations, and this is reported in the table).

Further, how was recovery time measured if the system returns to an alternative steady state, not the one that was disturbed? "Robustness" is an ill-defined word in this case, is a system "robust" if it quickly settles to a very different steady state? The authors should discuss how they use recovery time in case of multiple attractors. Minor comments to this paragraph: eigenvalues do show the speed of convergence also for dampened oscillations (contrary to line 144), and different eigenvalues show speeds of convergence in different directions (akin to what line 149 describes as more nuanced perspective). But of course for large perturbations, one has to use numerical methods.

Thank you. We have now clarified that if the system is pushed into an alternative steady state, the recovery time is measured with respect to the new steady state. Given that we apply perturbations that are larger than infinitesimal, we rely on a numerical approach.

(2) The description of the equilibria in lines 158-181 neglects that the asymmetric equilibria (both the stable equilibria and the unstable equilibria) come in symmetric pairs. For example, in regime I, there are three stable equilibria: one symmetric and two asymmetric, the latter two form a symmetric pair having the same two values of population densities but in opposite arrangement (one where N_1 is the high density and N_2 is low, one where N_1 is low and N_2 is high). The same holds for the unstable asymmetric equilibria. Due to the symmetry of the model, there are two fold bifurcations occurring at the same value of m (not one, as said in line 159). Throughout this text, the asymmetric equilibria should be in plural as there are always two of them, even though they are mirror images of each other and therefore qualitatively the same.

We have followed the Reviewer's recommendation and have revised the text accordingly. The first section of the Results now accurately describes changes in equilibria and bifurcations.

Further, the inset of fig 1 does not show any separatrix, only the unstable equilibria (correct both the text and the figure legend). The separatrix is a line in the N_1 - N_2 plane (and the equilibrium is a point on it). In continuous-time systems, it would be straightforward that such a separatrix exists and contains the unstable equilibrium. But in the present discrete-time system, the basins of attraction could have a fractal structure (see Hastings 1993, Ecology). Therefore the authors should make it clear how they investigated the basins of attraction.

We thank the Reviewer for pointing this out. Indeed the bracket "(dashed line)" was misplaced. It should have stood behind "fixed point" but ended up behind separatrix. Our experience with the system, as well as theoretical arguments consistently points to the basin boundary being a smooth separatrix formed by the stable manifold of the unstable state. However, we feel that including these discussions in the paper would draw too much attention to technical points and distract from our intended message about the role of collective behaviour on eco-evolutionary dynamics. To avoid confusing the reader we have instead removed the statements regarding the separatrix, as they did not contribute to the biological results.

Lastly, the Ricker model is well known to show period-doubling bifurcations and periodic orbits. The authors should state whether these occur with the parameters used (or when would they occur).

We do not encounter a Flip (period doubling) bifurcation in the parameter space that we investigate and therefore do not include a discussion of this in the manuscript.

(3) I could not interpret figure 2a and the corresponding text. Initially I thought that the grey/black lines in regime 1 refer to the symmetric/asymmetric attractors. But the text talks about portfolio effects for near-collapse and single extinction scenarios. This makes no sense: the portfolio effect was defined at steady-state, not during a transient after perturbation.

The portfolio effects are calculated with respect to the alternative steady states that the system is pushed into following a perturbation, which are measurably different than cases where an alternative steady state is not encountered following a disturbance. We have clarified that portfolio effects are measured with respect to the post-perturbation steady state in both the text and the caption to the figure.

(4) The bifurcation shown in the middle inset of fig 3 is unclear. If the asymmetric equilibrium appears through a fold bifurcation as in fig 1, then the symmetric equilibrium should not lose stability exactly at the same point (just as it does not do in fig 1).

We have now corrected the figure to show all steady states in both Regimes I and II (and do this as well for Figure 1).

(5) In figure 4, the most conspicuous features are the sharp changes in recovery times. Presumably these follow the bifurcations shown in figure 5. The text should comment on this.

Thank you. We now describe these sharp changes in the text.

(6) I found it difficult to follow the discussion in lines 321-344. Previously, I came to believe that region I is detrimental for metapopulation robustness because of the low-density attractor. For small C , region I dominates in fig 5, so why does small C provide increased robustness? Contrary to lines 339-344, the difference of densities of the dominant and subordinate populations are the highest when m_0 is low (as in fig 1). And how can the range of m_0 depend on the value of m_0 ?

We have now clarified this paragraph. We emphasize that recovery time is measured with respect to the aggregate (the dominant + subordinate population densities). We deem a system to be more robust if the aggregate recovers to its steady state faster, regardless of the densities of its constituent populations. Although regime I dominates at low C (which in one sense is bad), it leads to a relatively faster recovery time, which could be seen as good. The message that we aim to convey here is that the effects of straying and collective behavior on robustness are not straightforward, and in some sense depends on the observer's priorities. We have revised the text to emphasize these qualifications.

(7) I appreciate the authors' effort in the supplementary material, but since the equation they derive in the SM is not used, I think it is not necessary to include this derivation.

Although we agree that it is a diversion, we prefer to leave this exploration in the SM because we think that it a) aids our reasoning for the Gaussian approximation that is used and b) provides context as well as a 'stepping-off' point for a more rigorous analysis of mixed trait distributions through time that may be helpful to the interested reader wanting to expand on our approach.

Detailed comments

- The Introduction confounds diversity and asynchrony. Monomorphic metapopulations can very well exhibit asynchrony over habitat patches; likewise, diverse populations can be synchronous.

We agree that the diversity/stability/asynchrony link is not exclusive and have modified the sentence to emphasize this. We now state that the “diversity-stability link [can arise] when there are asynchronous population dynamics...”

- The MS rightly criticizes the portfolio effect as a not-so suitable statistic for measuring robustness. But even if one tries to use the portfolio effect, one needs to distinguish between continuous small perturbations (in the present model, P_i in eq 3) from occasional large disturbances. The portfolio effect is calculated under the former, and cannot predict robustness with respect to the latter (line 24).

We agree, though note that there is a strong relationship between our measure of robustness (e.g. recovery time) and statistical measures such as PE, which we show in Figure S3.

- line 34, how could phenotype-independent dispersal sort in space? (The next sentence correctly states that dispersal homogenizes, not sorts.)

We are simply stating that phenotypes can sort in space via dispersal. We have attempted to clarify this statement in the revised draft.

- line 70, I doubt that evolutionary rescue plays a role in this model. The immigrants are always less adapted than the local population. Introducing maladapted genes is not the sort of variation that helps to adapt.

We have modified this to emphasize only demographic rescue in this context.

- top of page 4, what "In this sense" means in "In this sense, both populations serve simultaneously..."

We have deleted this sentence for clarity.

- eq 3 middle line: what the authors denote with "pr" is not a probability but a probability density function (a usual notation for which is f, but it needs to be spelled out in the explanation).

This is now fixed.

- In my reading, the model assumes that after dispersal, the parents mate, reproduce, and die; selection acts on the offspring. In line 96, the statement that the dispersers' rate of recruitment is diminished can be misinterpreted; they mate and produce offspring as anyone else, although their offspring carry locally less adapted genes (as part of the Gaussian distribution assumed for simplicity).

The Reviewer is correct in stating how this mixing process would occur in nature. However, as is described in the text, we assume that individuals from both populations mix, that this mixed distribution can be approximated by a single Gaussian distribution, and that it is this (approximate) Gaussian distribution that determines the rate of recruitment, giving rise to the next generation of individuals. Selection occurs during the recruitment phase. We clarify this point in both the main text as well as the supplement.

- line 102, Gaussian after, not before reproduction. Before reproduction, the distribution is clearly not Gaussian, but local random mating takes it closer to Gaussian.

See response to prior comment.

- line 103 the correct notation is $E(X_i)$ instead of $E(g(x_i))$ (and X_i is distributed according to g).

Thank you. We have fixed this.

- line 109, ref 11 used the hypergeometric model to check the robustness of their quantitative genetic model. The hypergeometric model has since been shown to lack robustness, so this part of ref 11 is dated.

We thank the reviewer for pointing this out and are interested in learning more about this. The justification of our approach based on the work done by Ref. 11 rests on the fact that they did not observe differences in their results based on these two approaches. Because our models are nearly identical, this justification should hold even if the hypergeometric model lack robustness in other contexts.

- line 148, the value of T used in the numerics should be given.

The value of T is given in the table.

- I am not sure whether the "low density state" in line 268 is the symmetric equilibrium or not. Also, it is unclear whether the black line in the left of figure 1 shows total density (in which case it is a "low density state") or density in one habitat such that total density is twice this (in which case it is not low density).

We now refer to this as the asymmetric low-density state.

- line 269 this is not a cusp bifurcation

We do not cite a cusp bifurcation here, but a general cusp point. We can see where this confusion may have arisen given the previous versions of this manuscript, but hope that a reader unfamiliar with those versions will not see this to mean a cusp bifurcation.

- line 326, Allee's name should be capitalized

Thank you. This has been fixed.

- line 344 says that the portfolio effect is "interestingly" high near bifurcations. In fact, this is more an undesirable property than a useful indication, see lines 208-215.

We agree and point to 'alternative perspectives on robustness'.

- fig 1 the inset should have axis titles and scales. I found the vertical lines in the main panel disturbing, the equilibria do not connect. The legend could mention that asymmetric equilibria are in pairs (see above).

Thank you. This has been fixed.

- fig 3 explain the dotted lines connecting branches of equilibria. Describe exactly how averaging over low and high values of m was done.

Thank you. We have included a description of the lines linking equilibria in the caption.

- fig 4 panel letters (a) (b) etc are missing; vertical axis title is missing in the lower panels.

Thank you for catching this. This has been addressed.

- In the legends of fig 4 and 5, log₁₀ is misspelt

Thank you. This has been fixed.

- the legend of figure S3 should specify how the data points shown in the figure were obtained (including the parameter values used)

Thank you. We have included this information in the caption to figure S3.

Referee: 3

Comments to Author(s)

From what I can piece together, I am reasonably sure that the original discussion of the bifurcations was wrong and I think the current one in the beginning of the results section is probably right. I say "reasonably sure" and "probably" because to be completely certain one would have to do a complete mathematical bifurcation analysis (perhaps up to actually computing normal forms in detail, depending on what the initial analysis showed), and to even be almost certain would require a very careful numerical analysis. However, doing such a detailed analysis would probably require what would amount to a separate paper which would be more suitable for an applied math or mathematical biology journal. To be more specific, I think it is quite unlikely that the system has a cusp bifurcation, and a claim that it did would cause me to raise questions as it seems to have done with the referees, but it is quite plausible that it has fold and pitchfork bifurcations. I should note, however, that on line 268-269 the paper still says "As the strength of collective behaviour increases, regime I appears at a cusp" which may be left over from the previous version.

I must admit that the manuscript is somewhat confusing, in particular, it is not specified explicitly, which difference equations completely define the discrete-time dynamical system.

In the main Fig.1 related to the bifurcation analysis, the inset does not correspond to the figure itself. While the inset is clearly and correctly described in the text, the main drawing does not show any fold bifurcations, but rather some vertical lines, not present in the inset. Moreover, the symmetric fixed point is not always shown. Such inconsistencies are not acceptable for publication.

We thank the Reviewer for catching some of the terminology that we did not sufficiently describe in the detail required. We have amended the text that describes the bifurcations, as well as figure 1 and the inset to figure 1 to more accurately explain and show the equilibria.

Another concern is that the terminology from the bifurcation theory of deterministic discrete-time dynamical systems is naively applied to a system with noise.

We verified that the noise intensity is sufficiently low such that the system behaves deterministically. In particular, typical noise induced phenomena, do not occur. We have added an extra sentence that points this out to the reader.

Regarding symmetry, I think a .1 fold change is suggestive, but not necessarily completely convincing, depending on details of the parameterization of the system. In the text and figure caption the authors say that the asymmetry does not affect the qualitative dynamics. To support that claim, I would suggest replacing the scatter plot in the SI (Fig.S2), with a series panels in the style of Fig.1, but with increasing values of asymmetry, well beyond 0.1. It is OK if the pattern breaks down, but it would be helpful for the reader to know when that happens.

Given the complexities of the model we have not computed the normal form coefficients which could prove this beyond doubt, but instead conjecture the bifurcation type based on the overall structure of the diagram and the Jacobian eigenvalues, both of which point to a fold. We have phrased the corresponding sentence more carefully and now use the verb "conjecture", to make clear to the reader that we have not proved the bifurcations occurring at this point are indeed folds.

We have remade Figure S2. We have also removed the process error in the model so that there is no 'scatter', and the influence of asymmetry in vital rates is more easily observed. We have also made a second panel where asymmetry is increased. Although there are no qualitative changes in the dynamics when asymmetry is high, the bifurcation occurs at values of $m < 0$, such that the system always exists in dominant/subordinate states at lower values of m .