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

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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 comforatble with something like 'Following[/As in] Berdahl et al., we assume...', since I don't think that we claimed that that is nessesarily 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? Asymetry? 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.

Thank you. We have corrected this mistake.

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

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

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

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

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..

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Referee reports:

Referee: 1

(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-min SD? N^*_T is not a number. Moreover, if T goes to infinity, the random process N^*_T will get out of plus-min 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.

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.

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.

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.

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).

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

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.

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.

- 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.

This is now fixed.

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.

See response to prior comment.

Thank you. We have fixed this.

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.

The value of T is given in the table.

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

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.

Thank you. This has been fixed.

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

Thank you. This has been fixed.

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

Thank you for catching this. This has been addressed.

- In the legends of fig 4 and 5, log_10 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 begining 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 no 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 diagramm 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.