

Genetic growth potential, rather than phenotypic size, predicts migration phenotype in Atlantic salmon

Paul V. Debes, Nikolai Piavchenko, Jaakko Erkinaro and Craig R. Primmer

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Review timeline

Original submission: 16 April 2020
Revised submission: 17 June 2020
Final acceptance: 29 June 2020

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSPB-2020-0867.R0 (Original submission)

Review form: Reviewer 1

Recommendation

Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?

Good

General interest: Is the paper of sufficient general interest?

Good

Quality of the paper: Is the overall quality of the paper suitable?

Excellent

Is the length of the paper justified?

Yes

Should the paper be seen by a specialist statistical reviewer?

No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.

No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?

N/A

Is it clear?

N/A

Is it adequate?

N/A

Do you have any ethical concerns with this paper?

No

Comments to the Author

The objective of the experiment was to seek a greater understanding of the genetic and environmental basis of the often previously studied Atlantic salmon juvenile developmental transition towards age-specific smolt migration phenotypes including a demonstration here of its strong thermal stability. The study principally confirms the findings of previous investigations that showed that parr length observed in the summer is highly correlated with the age of smolt migration in the following spring(s), but moreover, importantly, in addition to the previous studies, reports a very high heritable genetic component, which is remarkably stable under differing temperature conditions. The study considered the contribution of a number of additional environmental (temperature, feeding regime), life history (male maturation) and genetic (variation at VGLL-3) variables, and found no evidence for them having any effect on the migration phenotype.

This was a very robust experiment, with solid experimental design and from which the data obtained are thoroughly and expertly analysed. The authors were probably expecting more from the VGLL-3, where there has been significant progress in elucidating the genomic basis of variation in sea age of maturity. Nevertheless that VGLL-3 does not have a role in the determining the timing of the migration decision is very valuable. The discussion, is excellent and provides much food for thought.

The authors might also be interested to consider some of the papers listed below, which while exploring the genetic and environmental basis for a different migratory life history transition in brown trout, the approach is similar in some ways to that reported here and might be of some benefit for comparative purposes.

I am happy to recommend the paper for publication in PRSB and believe the report represents a valuable contribution to research in the area.

Ferguson, A., Reed, T.E., Cross, T.F., McGinnity, P. and Prodöhl, P.A., 2019. Anadromy, potamodromy and residency in brown trout *Salmo trutta*: the role of genes and the environment. *Journal of fish biology*, 95(3), pp.692-718.

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Review form: Reviewer 2

Recommendation

Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?

Good

General interest: Is the paper of sufficient general interest?

Good

Quality of the paper: Is the overall quality of the paper suitable?

Good

Is the length of the paper justified?

Yes

Should the paper be seen by a specialist statistical reviewer?

No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.

No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?

Yes

Is it clear?

Yes

Is it adequate?

Yes

Do you have any ethical concerns with this paper?

No

Comments to the Author

In this study, Debes et al. investigate the genetic and environmental determinants of migration probability in Atlantic salmon during the second spring. The study focuses in particular on the accuracy of using body size at the end of the first summer as liability proxy for migration the next spring. The authors use an impressive longitudinal common-garden experiment and different models to assess the impact of temperature and body length on migration probability, as well as assess the heritability of migration probability and length under different temperatures. Overall, this study finds that migration probability and body length are strongly correlated, and that migration probably more strongly depends on the genetic growth potential rather than realised body length at the end of the first summer. These findings have stark implications for the study of migration probability in salmonids, suggesting that body length is a rather conservative proxy for migration probability.

Main comments: The study is very well executed, and the authors describe and discuss the results

thoroughly. I don't have any major concerns regarding this study. However, I found it difficult to follow the results at times, particularly toward the end of the results section, as some of the descriptions are very technical and many different results are presented at the same time (e.g. L272 - 286). Here the authors first talk about tank effects on length, then differences between models regarding MIG heritability and then again about length. Some minor restructuring might, and potentially summary sentences, make it easier to follow the results. Furthermore, the discussion is very thorough, but it might be easier to follow if the authors link the discussion more closely to their results e.g. by referring to figures in the discussion.

Minor comments:

L.243: word missing '...dependent ON the size...'

L.380 - 383: Maybe make clear here for the reader what that means and what the implications are, as this section is very technical.

Decision letter (RSPB-2020-0867.R0)

08-Jun-2020

Dear Dr Debes:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into <http://mc.manuscriptcentral.com/prsb> and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" - in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

When revising your manuscript you should also ensure that it adheres to our editorial policies (<https://royalsociety.org/journals/ethics-policies/>). You should pay particular attention to the following:

Research ethics:

If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

Use of animals and field studies:

If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

Data accessibility and data citation:

It is a condition of publication that you make available the data and research materials supporting the results in the article. Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (<https://royalsociety.org/journals/ethics-policies/data-sharing-mining/>). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

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If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

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All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Dr Daniel Costa

mailto:proceedingsb@royalsociety.org

Associate Editor

Board Member: 1

Comments to Author:

This study has now been reviewed by two expert Referees and I have read the study myself. As can be gauged by the reviews, both Referees were impressed with the robust longitudinal common-garden experimental design to assess the heritability and impact of temperature and body length on migration probability, finding that migration probability and body length are strongly correlated, but that migration depends on the genetic growth potential rather than realised body length in Atlantic Salmon. The result has significant implications for the study of migration in salmonids and the conclusions are well supported by the data. Both Referees make thoughtful suggestions how to improve the clarity of the study, hence my recommendation of Revise to improve the paper.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

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I am happy to recommend the paper for publication in PRSB and believe the report represents a valuable contribution to research in the area.

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Archer, L.C., Hutton, S.A., Harman, L., O'Grady, M.N., Kerry, J.P., Poole, W.R., Gargan, P., McGinnity, P. and Reed, T.E., 2019. The interplay between extrinsic and intrinsic factors in determining migration decisions in brown trout (*Salmo trutta*): an experimental study. *Frontiers in Ecology and Evolution*, 7, pp.1-18.

Archer, L.C., Hutton, S.A., Harman, L., McCormick, S.D., O'Grady, M.N., Kerry, J.P., Poole, W.R., Gargan, P., McGinnity, P. and Reed, T.E., 2020. Food and temperature stressors have opposing effects in determining flexible migration decisions in brown trout (*Salmo trutta*). *Global Change Biology*, 26(5), pp.2878-2896.

Referee: 2

Comments to the Author(s)

In this study, Debes et al. investigate the genetic and environmental determinants of migration probability in Atlantic salmon during the second spring. The study focuses in particular on the accuracy of using body size at the end of the first summer as liability proxy for migration the next spring. The authors use an impressive longitudinal common-garden experiment and different models to assess the impact of temperature and body length on migration probability, as well as assess the heritability of migration probability and length under different temperatures. Overall, this study finds that migration probability and body length are strongly correlated, and that migration probably more strongly depends on the genetic growth potential rather than realised body length at the end of the first summer. These findings have stark implications for the study of migration probability in salmonids, suggesting that body length is a rather conservative proxy for migration probability.

Main comments: The study is very well executed, and the authors describe and discuss the results thoroughly. I don't have any major concerns regarding this study. However, I found it difficult to follow the results at times, particularly toward the end of the results section, as some of the descriptions are very technical and many different results are presented at the same time (e.g. L272 - 286). Here the authors first talk about tank effects on length, then differences between models regarding MIG heritability and then again about length. Some minor restructuring might, and potentially summary sentences, make it easier to follow the results. Furthermore, the discussion is very thorough, but it might be easier to follow if the authors link the discussion more closely to their results e.g. by referring to figures in the discussion.

Minor comments:

L.243: word missing '...dependent ON the size...'

L.380 - 383: Maybe make clear here for the reader what that means and what the implications are, as this section is very technical.

Author's Response to Decision Letter for (RSPB-2020-0867.R0)

See Appendix A.

Decision letter (RSPB-2020-0867.R1)

29-Jun-2020

Dear Dr Debes

I am pleased to inform you that your manuscript entitled "Genetic growth potential, rather than phenotypic size, predicts migration phenotype in Atlantic salmon" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

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All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,

Dr Daniel Costa

Editor, Proceedings B

<mailto:proceedingsb@royalsociety.org>

Associate Editor:

Board Member

Comments to Author:

The authors have satisfactorily address what were minor revisions in an already strong manuscript. The revisions improve the clarity of the study and the significance of the findings. I recommend acceptance - the study will be of broad interest to readers of PRSB.

Appendix A

Responses to the associate editor and referees

We would like to thank Daniel Costa as associate editor and both referees for their time and work in reviewing the manuscript and the valuable and constructive contributions these reviews have yielded. We now provide a revised version of the manuscript, for which we took an account of the comments and suggestions. We inserted a response (in bold and blue) below each raised concern or suggestion of improvement and also provide a Word version of the revised manuscript with tracked changes.

With best wishes on behalf of the authors,

Paul Debes

Associate Editor

Board Member: 1

Comments to Author:

This study has now been reviewed by two expert Referees and I have read the study myself. As can be gauged by the reviews, both Referees were impressed with the robust longitudinal common-garden experimental design to assess the heritability and impact of temperature and body length on migration probability, finding that migration probability and body length are strongly correlated, but that migration depends on the genetic growth potential rather than realised body length in Atlantic Salmon. The result has significant implications for the study of migration in salmonids and the conclusions are well supported by the data. Both Referees make thoughtful suggestions how to improve the clarity of the study, hence my recommendation of Revise to improve the paper.

RESPONSE: Thank you for your contributions!

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

The objective of the experiment was to seek a greater understanding of the genetic and environmental basis of the often previously studied Atlantic salmon juvenile developmental transition towards age-specific smolt migration phenotypes including a demonstration here of its strong thermal stability. The study principally confirms the findings of previous investigations that showed that parr length observed in the summer is highly correlated with the age of smolt migration in the following spring(s), but moreover, importantly, in addition to the previous studies, reports a very high heritable genetic component, which is remarkably stable under differing temperature conditions. The study considered the contribution of a number of additional environmental (temperature, feeding regime), life history (male maturation) and genetic (variation at VGLL-3) variables, and found no evidence for them having any effect on the migration phenotype.

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there has been significant progress in elucidating the genomic basis of variation in sea age of maturity. Nevertheless that VGLL-3 does not have a role in the determining the timing of the migration decision is very valuable. The discussion, is excellent and provides much food for thought.

RESPONSE: Thank you!

The authors might also be interested to consider some of the papers listed below, which while exploring the genetic and environmental basis for a different migratory life history transition in brown trout, the approach is similar in some ways to that reported here and might be of some benefit for comparative purposes.

RESPONSE: We now refer to Ferguson, Reed [1] in both the introduction (to emphasize similarity in suggested methodology) and the discussion (to discuss the therein suggested possibilities in brown trout of 1. maternal effects on migrant probability and 2. that it remains unclear whether male maturation conflicts with migration).

I am happy to recommend the paper for publication in PRSB and believe the report represents a valuable contribution to research in the area.

Ferguson, A., Reed, T.E., Cross, T.F., McGinnity, P. and Prodöhl, P.A., 2019. Anadromy, potamodromy and residency in brown trout *Salmo trutta*: the role of genes and the environment. *Journal of fish biology*, 95(3), pp.692-718.

Archer, L.C., Hutton, S.A., Harman, L., O'Grady, M.N., Kerry, J.P., Poole, W.R., Gargan, P., McGinnity, P. and Reed, T.E., 2019. The interplay between extrinsic and intrinsic factors in determining migration decisions in brown trout (*Salmo trutta*): an experimental study. *Frontiers in Ecology and Evolution*, 7, pp.1-18.

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Referee: 2

Comments to the Author(s)

In this study, Debes et al. investigate the genetic and environmental determinants of migration probability in Atlantic salmon during the second spring. The study focuses in particular on the accuracy of using body size at the end of the first summer as liability proxy for migration the next spring. The authors use an impressive longitudinal common-garden experiment and different models to assess the impact of temperature and body length on migration probability, as well as assess the heritability of migration probability and length under different temperatures. Overall, this study finds that migration probability and body length are strongly correlated, and that migration probably more strongly depends on the genetic growth potential rather than realised body length at the end of the first summer. These findings have stark implications for the study of migration probability in salmonids, suggesting that body

length is a rather conservative proxy for migration probability.

Main comments: The study is very well executed, and the authors describe and discuss the results thoroughly. I don't have any major concerns regarding this study.

RESPONSE: Thank you!

However, I found it difficult to follow the results at times, particularly toward the end of the results section, as some of the descriptions are very technical and many different results are presented at the same time (e.g. L272 – 286). Here the authors first talk about tank effects on length, then differences between models regarding MIG heritability and then again about length. Some minor restructuring might, and potentially summary sentences, make it easier to follow the results.

RESPONSE: Following the recommendation, we have done our best to improve the named sections. Specifically:

- **We have moved the reporting of tank effects on length from the beginning of the third to the end of the second paragraph of results section c), where we first mention results on length (and where the reporting of tank effects probably fits better).**
- **We also made some minor text modifications to paragraph 2, where the reported results change from dealing with MIG to dealing with LEN, to make this change clear from the beginning.**
- **To further facilitate comprehension, we also added the suggested summary sentences to the last two paragraphs of the results section c) (paragraphs 4 and 5), like we did in section b) and paragraph 2 of section c).**

Furthermore, the discussion is very thorough, but it might be easier to follow if the authors link the discussion more closely to their results e.g. by referring to figures in the discussion.

RESPONSE: Following the recommendation, we have now added references to figures in the discussion.

Minor comments:

L.243: word missing '...dependent ON the size...'

RESPONSE: "on" has now been added.

L.380 – 383: Maybe make clear here for the reader what that means and what the implications are, as this section is very technical.

RESPONSE: We now make it clearer what we refer to, include the major implication, and added a clear remark to where the reader can find a recent discussion of the topic:

“However, it is important to remember that heritabilities on the liability scale (and also heritabilities for liability proxy traits) do not relate linearly to the probability scale across many factors, including the - environmentally governed - overall probability [2]. This effect was here exemplified by disparate heritability differences between temperature environments on the liability (more similar) vs. the proportional scale (less similar). As recently discussed by de Villemereuil, Schielzeth [3], predicting the responses to selection for migration phenotypes may follow standard assumptions if based on liability-scale heritability, but less so on proportional-scale heritability.”

1. Ferguson A., Reed T.E., Cross T.F., McGinnity P., Prodohl P.A. 2019 Anadromy, potamodromy and residency in brown trout *Salmo trutta*: the role of genes and the environment. *J Fish Biol* **95**(3), 692-718. (doi:10.1111/jfb.14005).
2. Dempster E.R., Lerner I.M. 1950 Heritability of threshold characters. *Genetics* **35**(2), 212-236.
3. de Villemereuil P., Schielzeth H., Nakagawa S., Morrissey M. 2016 General methods for evolutionary quantitative genetic inference from generalized mixed models. *Genetics* **204**(3), 1281-1294. (doi:10.1534/genetics.115.186536).