Peer Community In Ecology

Why are trout getting smaller?

Aleksandra Walczyńska *based on peer reviews by* ***Jan Kozlowski*** *and 1 anonymous reviewer*

Quentin Josset, Laurent Beaulaton, Atso Romakkaniemi, Marie Nevoux (2024) Changes in length-at-first return of a sea trout (*Salmo trutta*) population in northern France. bioRxiv, ver. 4, peer-reviewed and recommended by Peer Community in Ecology.
https://doi.org/10.1101/2023.11.21.568009

Submitted: 24 November 2023, Recommended: 28 March 2024

Cite this recommendation as:
Walczyńska, A. (2024) Why are trout getting smaller?. *Peer Community in Ecology*, 100599. 10.24072/pci.ecology.100599

Published: 28 March 2024

Decline in body size over time have been widely observed in fish (but see Solokas et al. 2023), and the ecological consequences of this pattern can be severe (e.g., Audzijonyte et al. 2013, Oke et al. 2020). Therefore, studying the interrelationships between life history traits to understand the causal mechanisms of this pattern is timely and valuable.

This phenomenon was the subject of a study by Josset et al. (2024), in which the authors analysed data from 39 years of trout trapping in the Bresle River in France. The authors focused mainly on the length of trout on their first return from the sea.

The most important results of the study were the decrease in fish length-at-first return and the change in the age structure of first-returning trout towards younger (and earlier) returning fish. It seems then that the smaller size of trout is caused by a shorter time spent in the sea rather than a change in a growth pattern, as length-at-age remained relatively constant, at least for those returning earlier. Fish returning after two years spent in the sea had a relatively smaller length-at-age. The authors suggest this may be due to local changes in conditions during fish's stay in the sea, although there is limited environmental data to confirm the causal effect. Another question is why there are fewer of these older fish. The authors point to possible increased mortality from disease and/or overfishing.

These results may suggest that the situation may be getting worse, as another study finding was that "the more growth seasons an individual spent at sea, the greater was its length-at-first return." The consequences may be the loss of the oldest and largest individuals, whose disproportionately high reproductive contribution to the population is only now understood (Barneche et al. 2018, Marshall and White 2019).

References

Audzijonyte, A. et al. 2013. Ecological consequences of body size decline in harvested fish species: positive feedback loops in trophic interactions amplify human impact. Biol Lett 9, 20121103. https://doi.org/10.1

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Barneche, D. R. et al. 2018. Fish reproductive-energy output increases disproportionately with body size. Science Vol 360, 642-645. https://doi.org/10.1126/science.aao6868

Josset, Q. et al. 2024. Changes in length-at-first return of a sea trout (Salmo trutta) population in northern France. bioRxiv, 2023.11.21.568009, ver 4, Peer-reviewed and recommended by PCI Ecology. https://doi.org/10.1101/2023.11.21.568009

Marshall, D. J. and White, C. R. 2019. Have we outgrown the existing models of growth? Trends in Ecology & Evolution, 34, 102-111. https://doi.org/10.1016/j.tree.2018.10.005

Oke, K. B. et al. 2020. Recent declines in salmon body size impact ecosystems and fisheries. Nature Communications, 11, 4155. https://doi.org/10.1038/s41467-020-17726-z

Solokas, M. A. et al. 2023. Shrinking body size and climate warming: many freshwater salmonids do not follow the rule. Global Change Biology, 29, 2478-2492. https://doi.org/10.1111/gcb.16626

Reviews

Evaluation round #2

DOI or URL of the preprint: https://www.biorxiv.org/content/10.1101/2023.11.21.568009v3
Version of the preprint: 3

Authors' reply, 20 March 2024

Eu, March 19th 2024
To: PCI Ecology Recommender: Aleksandra Walczyńska

Dear Recommender and Reviewers,
We thank you again for this round of comments. You will find hereafter the changes that were made accordingly.
With kind regards,
Quentin Josset, on behalf of the authors.

Download author's reply

Decision by Aleksandra Walczyńska, posted 29 February 2024, validated 01 March 2024

Minor revision required

Dear Authors,

The reviewers are satisfied with how their concerns have been addressed, and so am I. As the reviewers suggest some minor changes, please address their comments and revise the manuscript accordingly.

With kind regards,

Aleksandra Walczyńska

Reviewed by Jan Kozlowski, 28 February 2024

The paper is much improved. I recommend it after the minor corrections listed below.

Lines 281-287

"At the same time, the percentage of 0SW individuals increased in recent years to up to 60% (in 2018) of all first returning sea trout. The percentage of 1SW individuals in the population remained predominant and stable over time (mean = 82.3%; SD = 11.5%). This pattern indicates a decrease in the mean sea age at first return of the Bresle sea trout population: 1.06 years (SD = 0.4) from 1984-1988, but 0.80 years (SD = 0.4) from 2018-2022. The age structure differed greatly in 2001, when only 1SW individual was captured due to extreme flooding that disrupted trapping and thus decreased its efficiency greatly."

The year 2001 should be removed from Figure 4, or at least the message about the flooding should be added to the caption. Certainly this year should not be included in the calculation of averages.

Caption to Figure 3.

"Top panel: qualitative predictors, as well as qualitative by qualitative interactions"

Qualitative by qualitative interactions is not a proper wording. It couldn't be better: Top panel "the effects of qualitative predictors and their interactions"; middle panel "the effects of quantitative predictors and interactions between quantitative and qualitative predictors"; bottom panel:". I don't understand the bottom panel: is this the effect of, say, ctrAvgDOY in 1984, 2000, etc.?

The text starting on line 317 should continue on line 312. Figure 4 is now in between. Please read the text between lines 317 and 321 carefully. Is everything correct?

Line 354. "relatively stable for 1FW, but slightly increased over time for 2FW and 3FW" Should read: relatively stable for FW1, but slightly increased over time for FW2 and FW3. Also correct the symbols in the rest of this paragraph. Same in lines 467-475 and other places. Check this automatically, as the symbols should be consistent.

In Figure 5, I see the pattern described in lines 356-360, but I don't see the pattern described in lines 353-355.

Line 485: Kozlowski, not Koslowski.

Lines 495-499. When discussing seal predation, it is important to note that salmonids have not been found in their diet. If they were found, the increased seal population would be sufficient to reduce the optimal age for first reproduction. Selectivity is not required, as you quoted above. There are many more papers showing that non-selective predation (or fishing) is not necessary for such a decline, but that increased pressure is sufficient. You have cited two papers and that seems sufficient in this context. However, I recommend removing "Furthermore, most seal predation on salmonids appears to be opportunistic, with no evidence of length-dependent selection for larger fish (Suuronen and Lehtonen, 2012; Thomas et al., 2017)" unless you have information that the seal population has not increased (under stable predation pressure, selectivity may have the same effect).

I'm glad you changed the shape of figure 5. It is much clearer now.

Jan Kozłowski

Download the review

Reviewed by anonymous reviewer 1, 27 February 2024

The authors have done a large amount of work to address the reviewer and editor comments; I have no further comments to add. Just one observation for Figure 3 - Should the middle axis label read 0% rather than 100% change?

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/2023.11.21.568009

Version of the preprint: 2

Authors' reply, 06 February 2024

Oulu, February 6th 2024

To: PCI Ecology Recommender: Aleksandra Walczyńska

Dear Recommender and Reviewers,

We thank you for your thorough reading and constructive commenting of our manuscript. You will find here a revised version taking into account your comments, with additional point-by-point precisions below on the changes that were made.

With kind regards,

Quentin Josset, on behalf of the authors.

Download author's reply

Download tracked changes file

Decision by Aleksandra Walczyńska, posted 22 December 2023, validated 22 December 2023

Dear Authors

I am impressed by the huge amount of the work done by the authors in this study. However, I was somewhat overwhelmed by the complexity of the description of the methods, especially the statistical analyses. In consequence, the most important part of the manuscript, the addressing of the hypotheses, was rather diluted. Apparently, the reviewers had a similar impression. The reviewers clearly pointed out the strengths and weaknesses of the manuscript, which the authors should take into consideration.

Two additional points for consideration on my part are as follows:

- the question of the possible effect of rising temperatures on the results obtained - there is considerable discussion on the influence of global warming on ectotherm shrinkage, an important part of which is devoted to fish. Do the authors have any data to comment on this? It would be ideal if the authors could include the temperature factor in their analyses.

- " Consequently, management actions could be aimed at alleviating pressures on juveniles" - not necessarily. There is a growing body of research that shows that for species that experience very high mortality at the earliest stages of development, the most effective way to protect them is to protect the adults (e.g. https://apcz.umk.pl/EQ/article/view/v10090-009-0006-z). I know that such data are also available for fish, though I am not able to give an example right now.

With kind regards,

Aleksandra Walczyńska

Reviewed by Jan Kozlowski, 19 December 2023

Download the review

Reviewed by anonymous reviewer 1, 19 December 2023

Josset et al. Changes in length-at-first return of a sea trout (Salmo trutta) population in northern France

Summary

This study quantified temporal changes in the body length of sea trout returning to rivers, and described the body length of first-time returning sea trout individuals as a function of age, life history characteristics (time spent in freshwater and at sea) and migration phenology (date of return) using a dataset spanning nearly 40 years. They found that body length of sea trout had decreased over time, and that variation in the body length of first-time returners was likely driven by a decrease in the age of first-returns, rather than an influence of sea sojourn duration or growth conditions in the river or at sea. This is an interesting study which

contributes knowledge of a comparatively understudied salmonid species and life stage. I have a couple of major comments on the paper but mostly minor comments; I hope these are clear and helpful.

L127-128. How is the sub-sample of fish aged determined? For example, is the sampling protocol random and/or stratified by length classes?

L133-134. There is inconsistency in the description of data used for the testing of a temporal trend in mean length. The introduction (e.g. L92-93) and results (e.g. 232-235) suggest that this first investigation focused on all fish captured in the trap (not just first-time returns), whereas the methods here (and abstract L27) seem to suggest that only data for first-time migrants was used. Please clarify in the text the data that were used. This also raises the question for me, why look at the temporal trend in length of all fish, and then attempt to describe length of first-time returns only? I think this could be potentially misleading and I recommend to either limit the first investigation to first-time returns only, or include this analysis alongside the existing linear model fit to all the fish data, and make it very clear which dataset is used for subsequent analyses. Currently, the study is linking the decrease in average body length of all fish over time to the findings of the analyses specific to first-time returns only, and I do not think this is correct.

L142. Typo “no spawning mark” rather than “no a spawning mark”

L146. Is the subsample with age assessed the same number as reported on L143 (n = 11,844)? Please clarify.

L184-186. Perhaps the authors could add how they hypothesised number of years spent in the river to influence length-at-first return, i.e direction of the effect.

L194-195. A reference that could be useful support to the assumption that timing of smolt migration to sea has remained unchanged over time: de Eyto et al. 2022. https://doi.org/10.3389/fevo.2022.915854

L230. A general comment on the results section is that I feel more could be done with presenting the best fitting model results, e.g. partialized model fits of each main effect/interaction and move figures describing explanatory variables to the methods section, and present tables or values in text of average coefficient estimates. Also, I do not see the effect of kype detailed in the results section, even though it is retained in the best fitting models.

L233. “On average” ?

Figure 2. As in my previous comment, I think this should be either limited to first-time returns only (as the relevant response variable for the subsequent analyses) or additionally done for first-time returns. Otherwise, it is a bit misleading to present this figure which might not be representative of the pattern or variation in first-time return length data.

L256-257. Do you mean that the effect size for sea age on length-at-first return was the strongest (relative to other explanatory variables), or that the variable was retained in the best fitting models more frequently? Reference to a table or figure here would be helpful (perhaps, Table 1 and Figure 4), or reporting the mean coefficient estimate for sea age. I can see from Table 1 that the addition of the sea age variable greatly increases the average explained deviance, but there are not any other 2-variable models to compare this with (e.g. Kype + River age or Kype + deltaDOY, etc).

L259-260 and Figure 3. Temporal change in mean sea age, while an interesting finding, was not part of the original study hypotheses. I consider Figure 3 to be more appropriate in the methods and it would be beneficial to combine this with figure panels describing all of the other explanatory variables, e.g. proportions of freshwater age structure, presence of kype, numbers of returns per year, and histograms for timing of return migration. Additionally, given the low proportion of 2SW fish (as shown in Figure 3), it would be beneficial to state how many data points this was, especially for the interpretation of any interaction effects.

L283-288. It appears from Figure 4 that river age has an effect on length for 0SW fish only. Would it be fair to say that some of the effects shown in Figure 4 are simply representative of the overall age of the fish? For example, there is a large difference between the average length of 0SW and 1FW fish (age 1 year) to that of 0SW and 2FW and 3FW fish (ages 2 and 3 years). As the time spent at sea increases, the influence of time spent in freshwater (and total age) decreases, which is a more interesting result, I think. Furthermore, for 1SW and 2SW fish, there appears to be no statistical difference in the average length with confidence intervals completely

overlapping, so this result is really limited to that of 0SW fish (hence the retained interaction effect).

L296-297. Again, average coefficient estimates would be beneficial to report here to be able to compare with the other included explanatory variables. It would be also be interesting to visualise these model fits given the interesting interaction effect with sea age. Do the authors consider the low sample of 2SW fish to influence its opposing directional effect relative to 0SW and 1SW fish?

L306-309. Another example of a result that I don't think was in the original hypotheses, but rather relates to the description of the explanatory variable of day of return. It could instead be described in the methods, or added as a study hypothesis to test for changes in day of return over time (in addition to the effect of day of return on length at first return).

L332-333. Wasn't the temporal trend based on all returns and not just first-time returns? If this is correct, this sentence needs to be amended as currently it is linking two analyses based on different data and thus, inferences should not be linked.

L341. This is a nice paragraph to include. Do the authors consider any influence of measurement error in their results, for example, any differences in the error in measurement by size-class, i.e. are large fish more difficult to measure accurately?

L343. Slight typo, suggest rewording to "to maintain constant sampling effort"

L354. I thought a log-normal Gaussian distribution was used (i.e. L170-171) but here the authors describe a Gamma distribution (and indeed, describe it as a quasi-normal distribution on L252), could they clarify and be consistent with the terms to help readers understand what was done.

L374-355. Does this finding come from Milner et al. 2017? It is not immediately clear, so suggest to link the sentences together, for example "Consistent with our results, structural changes in the age at return of sea trout have been previously been reported by Milner et al., (2017), who found a change in the proportion…"

L378-380. But only an effect of river age on 0SW? I think this is the main finding and should be reported upfront and then compared to the literature. Also, I don't agree that river age "indicates that the increase in length acquired in the river had long-term consequences until the first return to the river", as the variable, river age, was a three-level categorical variable and not a measure of an individual's length at seaward migration, which could be highly variable within freshwater age structure. In general, I think this discussion section could benefit from further work as there are a lot of other studies cited but the results of all of these studies are not coherently brought together with the findings of this paper, and I find it hard to follow the message that the authors want to state. Furthermore, a lot of the references relate to smolt length, which is not the explanatory variable used here and I think this is an important point. I appreciate the amount of research done, but I would find it clearer to read a few well thought out links to other studies rather than an exhaustive list of many (including those which are not particularly comparable and have their associated caveats listed, e.g. Jonsson and Bohlin 2006). I hope these comments make sense and are helpful.

L389-390. Slower growth rates "in this study" instead of "there"? If this is correct.

L400-401. Could the authors offer some suggestions as to what they think could be driving this observation?

L409-410. Suggest clarifying this sentence, do the authors mean that temporal variations in the return date had little influence on length, despite major changes in the return dates of sea-age classes 0SW and 1SW, which arrived earlier by 53 and 47 days, respectively – compared to return dates of 2SW, the average return date, or over the timeframe of the study so earlier by 53 and 47 days in 2022 compared with 1984? The following sentence suggests it is describing a temporal variation in average return date and if so, there is a considerable difference in the change of average return dates between this study and Legrand et al. 2021 – could the authors offer some suggestions as to why there is such a large difference?

L415-416. I don't see this finding in the results? Looking at Figure 5, there appears to be little effect of the interaction between sea age and day of return. Could the authors please clarify?

L420-437. Nice paragraph.