Author's reply:

Oulu, February 5th 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.

Decision for round #1 : Revision needed

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.

Answer: Yes, this is a valid point. As temperature at sea change, it is expected to modulate both resources availability, quality and quantity, as well as intrinsic metabolic rates. Some authors have included the sea surface temperature in their analysis, with varying success in their ability to explain some of the variability in the focused phenotypic traits. To test the hypothesis of a direct or indirect effect of marine temperature on sea trout size at return, it is a prerequisite to know where sea trout are located during their marine life. The Channel and North Sea are characterized by strong currents and highly contrasted temperatures over small spatial scales but we have unfortunately very little evidence of marine habitat use for our study population. The lack of biological support in defining potential temperature variables may lead to spurious correlation between any temperature variable and sea trout size at return.

- " 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.

Answer: Along the slow-fast continuum of life histories, the contribution of the fecundity rate to the population growth rate increased with increasing clutch size and decreasing adult survival rate, while the greatest contribution of adult survival rate occurred among long-lived species that matured late and laid few eggs (Saether & Bakke, 2000). Populations at the slow end of the continuum are characterised by high adult survival and a high elasticity of population growth rate to adult survival. This is the case of the above mentioned study on a population of pond turtle, where the adult survival of the pond turtle was set to 0.8 and the conservation of the population maximised when adult survival is maximised. Salmonid species occupy an intermediate position along this continuum of life histories and the difference in elasticity between traits is generally less clearly cut. Using a size-structured population model for 12 trout populations, Carim et al. (2017) showed that population growth rate was by far more sensitive to the size-specific maturation probability than to adult survival. In trout species where the expected number of reproduction is low, being able to reproduce just one year earlier likely has a large impact on the reproductive success of individuals, and therefore on population growth.

Carim, K. J., Vindenes, Y., Eby, L. A., Barfoot, C., & Vøllestad, L. A. (2017). Life history, population viability, and the potential for local adaptation in isolated trout populations. *Global Ecology and Conservation*, *10*, 93–102. https://doi.org/10.1016/j.gecco.2017.02.001
Sæther, B.-E., & Bakke, Ø. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, *81*(3), 642–653.

With kind regards,

Aleksandra Walczyńska
by Aleksandra Walczyńska, 22 Dec 2023 12:31
Manuscript: https://doi.org/10.1101/2023.11.21.568009
version: 2

Review by Jan Kozlowski, 19 Dec 2023 14:26

First of all, I have to say that I'm not an expert in fish biology and ecology. I'm a theorist in the field of life history evolution.

The manuscript is based on a large data set covering the period 1984-2022. The results clearly show that the length-at-first-return of salmon from the sea to the studied river decreases with time. If this result has not yet been published, it is worth doing so. However, this result is not the main theme of the paper, which focuses on explaining the mechanism of this decrease in length. The statistical analysis is complex because several factors are studied with an even higher number of interactions. In addition, the coverage of such a long period is not uniform, which is understandable. To deal with this non-uniformity, the authors use bootstrapping on subsamples that are more uniform. I have no objections to this part of the paper. Unfortunately, only the most complex models, with all variables and all interactions considered, proved to be the best according to the Akaike criterion. This does not make further analysis easy. The paper seems to be overloaded with statistics in relation to results that are not entirely clear, partly because some variables are not independent. For example, the time spent in a river affects the size of the smolt, and the size of a smolt is functionally the initial size for growth at sea, and so must affect the growth curve at sea. Here the relationship is similar to a complex life cycle. It is not surprising that the interaction between sea age and river age is significant for reasons other than "effects of latent intrinsic differences between individuals depending on their life history". I suggest that the section "Statistical analysis" be omitted and that the appropriate parts be placed immediately before the presentation of subsections of relevant results. This will make the paper much easier to follow.

Lines 123-124. Different measures of length were used in different years. Fork length is presented in Figure 2 and presumably in the analysis. I could not find information on how total length was converted to fork length.

Answer: Indeed, this is confusing. Total length only were collected from 1981 to 1983 but these data were not used in the present study, which focuses on data collected as part of a consolidated protocol starting in 1984, using fork length as a standard. The reference to "total length" was removed to improve clarity and prevent confusion.

Lines 216-217. "Collinearity between variables was tested using Pearson correlation coefficients, and only variables with $|r| \leq 0.7$ were kept". There is nothing in the text about correlations between variables and the elimination of any variable. In fact, I would not be happy with such elimination and would expect an explanation of such high correlations instead. The matrix of correlations, perhaps in the supplementary information, might be helpful in understanding the causal system.

Answer: The sentence was rewritten to clarify that no variables were actually removed and that all correlation coefficients remained under the 0.7 threshold. A correlation plot is now given in Appendix 3.

I am not sure whether it is worth showing Table 1. It would be sufficient to describe the two winners (models 19 and 21). On the other hand, it is striking that, with the exception of model 2, the average explained deviance is very similar, especially starting from model 5. Together with Figure 5, this suggests that only sea-age, river-age and their interaction are important, and such detailed analysis of other factors and their interactions could be placed in supplementary information to make the text more reader friendly.

Answer: Table 1 illustrates the respective deviance explained by the addition/removal of each variable. In particular, it highlights that i) only a small number of variables explain most of the variance in the data, and ii) the variables that changed the most over time (e.g. timing of return) are not the variables that explain most of the variance in length at return. For this reason, we want to keep Table 1 in the main part of the ms.

Figure 4 is terrible. It looks like a jumble of lines, most of which are horizontal or almost horizontal. It would be better to explain everything in words.

Answer: We split figure 4 in 3 panels, for each river age and reduced the thickness of the outline of the confidence intervals. This way, there is no overlap between lines and confidence intervals, which we think, improved the readability of both river and sea age signals.

There is no clear description of how the results of the analysis based on Table 1 were 'translated' into Figure 5, which is crucial for interpreting the results. Presumably such a description is present in lines 166-174, but it is completely abstract before the variables are defined. I would suggest a sentence or two before this figure is presented. The caption to this figure reads: "Mean estimated effects of each predictor modality...", but there is no indication of what this effect is (difference in length in cm, percentage change). Figures should be as self-explanatory as possible, because we usually look at figures before deciding whether to read a paper or not.

Answer: We described l225-228 that from the estimates of the 1000 best models we computed mean estimates and 95% confidence intervals. As indicated in figure 5 (now figure 3), the reference used in the model was a FW1-SW1 individual with a kype, returned on the average day of its sea age class (ctrAvgDOY and deltaDOY =0). Mean estimates are then computed in comparison with this reference individual, but they are given in the response scale and as such, should be multiplied. These should be read as percentage of increase/decrease, with effects <1 meaning the individual should be smaller than the reference fish (or larger if effect is >1).

We tried to improve the clarity of the message carried by figure 3, by displaying the extent of the minimum and maximum effects of the variables and their interactions. Indeed, several variables have effect that are extremely small for a 1 unit increase and appear to be very close to 0. However, when minimum and maximum effects are displayed, we visualize the actual extent of change that can be brought by a given variable or interaction.

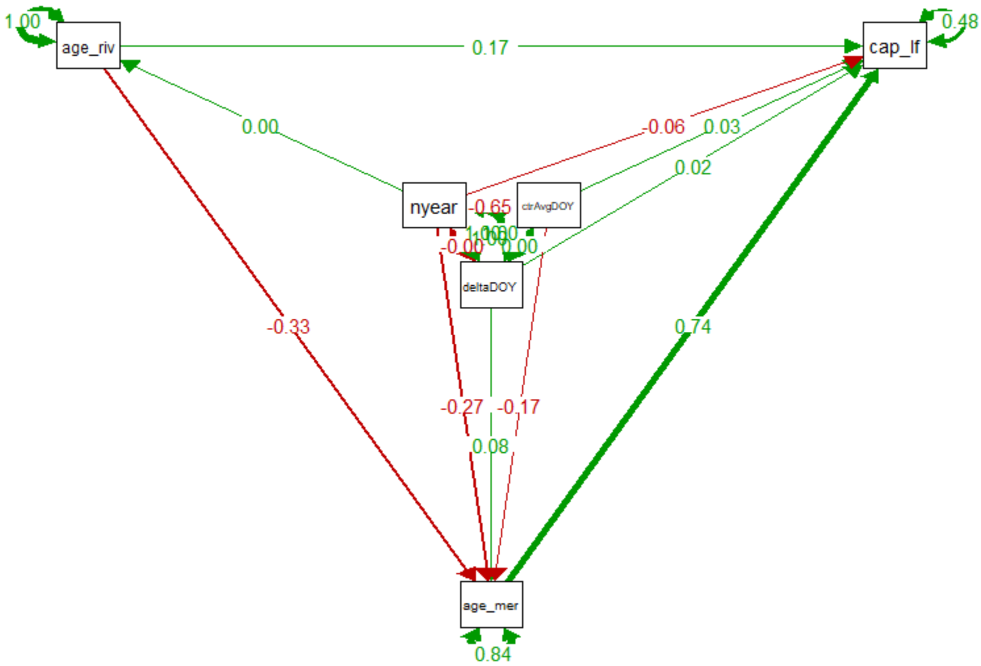
I suggest using path analysis to study the causal system. Of course, I'm not sure that such an analysis will give a clear picture, but why not try? The model could look like this

```
model<-'
length-at-first-return~sea-age+river-age+ctrAvgDOY+deltaDOY+year
sea-age~river-age+ctrAvgDOY+deltaDoy+year
river-age~year
'
fit <- cfa(model, data = ...)
semPaths(fit, ...)
```

My guess is that the effects of ctrAvgDOY and deltaDOY will be negligible, and so can be excluded from the plot in semPath by setting minimum to some small number; strong effects will be present from year to sea-age and from sea-age to length-at-first-return, and mild effects from river-age to length-at-first-return. Perhaps there will be some mild effects from year directly to length-at-first-return and to river age. If this analysis is successful, it could provide a more direct argument for the change in sea-age as the main driver of the decline in length-at-first-return, which is an important message of the paper.

Answer: We thank you for this suggestion, which is an interesting way to investigate the causal relationship between variables. We ran the lines of code you suggested on a single balanced dataset and you will find the graph below. It offers a nice visualisation of the model, highlighting that river (age_riv), sea age (age_mer) and their interaction are indeed the main explanatory variables for length at first return (cap_lf). However, as you will see, the timing variable ctrAvgDOY does not appear to be so unimportant, with a weak correlation with the sea age and a rather strong negative correlation with year.

On the other hand, this analysis does not offer the same resolution than ours. For instance, it does not inform on the effects of variables for each of their respective levels. As such, it would not allow to observe the different temporal evolution in size-at-age by sea age (quite flat in SW0 and 1, but slightly decreasing in SW2) or the fading influence over time of the river age on length-at-first-return. Therefore, we think the analysis described in the MS offers a broader understanding of the role of *each explanatory variables in our study population.*



The discussion is too long and contains some unnecessary elements. For example, the entire subsection "Strengths and limitations of long-term datasets" could be omitted. On the contrary, "An additional case study of decreasing average length of salmonids" could list other cases outside salmonids, after changing the title of the subsection.

Answer: We think the subsection on strengths and limitations of long-term datasets is useful as it illustrates some of the key difficulties inherent with working with such data. It is also an appropriate place to discuss about the question of the violation of the residuals normality, which is one of the key assumptions in linear modelling, a point about which we would be likely to be blamed if we would not have discussed it.
References outside of the salmonid family were included as advised in the relevant subsection. We also did our best to revise and shorten the discussion where we deemed it possible.

The weakest point of the paper is its inadequate reference to life history theory. This is best illustrated by two sentences: (i) “The age-specific decrease in length-at-first return may have been due to length-specific selective pressure that targeted mainly larger individuals” and (ii) “Furthermore, most seal predation on salmonids seems to be opportunistic, with no indication of length-dependent selection for larger fish”. Both statements invoke the false paradigm that mortality must be size selective to select for reduced (or increased) age at maturity and hence size at maturity. This paradigm is only correct in two cases: when population growth is unconstrained, or when density dependence acts by increasing mortality with density equally for all age classes. Clearly neither case is typical of fish. Here I must refer to my own work on the subject. I recommend starting with the introductory one Kozlowski (2006). Then there are three papers related to fish life history: the oldest Kozłowski and Uchmański (1987), the easiest to understand Kozlowski (1996) and the most difficult because of the mathematics, but also the most general Kozłowski and Teriokhin (1999). It follows from these papers that the increase in size- and age-independent mortality is a strong selective pressure for earlier maturation and smaller size. Thus, increased fishing pressure and increased seal predation may explain the pattern described in this paper.

Answer:
This is a good point, thank you for highlighting this. We do recognize that reproductive output must scale with time to maturation in order to compensate for increased risk of death during a longer juvenile phase. As such, a length (and age) independent mortality alone can induce smaller size at maturation and earlier age maturation. This could certainly be an explanation to the decrease of the mean sea age observed in this study.
The text was revised to clarify the message that we are not actually limiting our hypothesis to size-dependent mortality. Moreover, possible influence of an increased length-independent mortality on age-at-maturation was acknowledged.

Line 334. Contrasted variation? Do you mean "related variation"?

Answer: We meant here, that the response differ between the sea-age classes as we only detect a declining trend in the SW2 while the length of SW0 and SW1 remained relatively stable over time.

Lines 359-360. "Considering the very high within strategy length variation that can be observed in sea trout, it is likely to be a major factor here". What is likely to be a major factor?

Answer: The high heterogeneity in the response between individuals is likely to be a major factor responsible for deviation from normality. This point was reworded.

Lines 378-382. "We found that river age had a significant effect on length-at-first return, which indicates that the increase in length acquired in the river had long-term consequences until the first return to the river. This effect could have major implications for individuals' future life history, such as the timing of maturation and duration of the sea sojourn, as length can strongly influence when smolt reach key thresholds that drive life history transition." I don't understand the logic of the second sentence starting with "as length...".

Answer: This whole section has been revised to try to clarify the message that if there is a carry-over effect of the length of the smolts until the first return, then it may lead to an earlier reaching of key length-dependent maturation thresholds.

Lines 383-387. Is it compensatory growth or lengthening of the sea phase of life?

Answer: These studies are referring indeed to compensatory growth. For instance, Marco-Rius et al. (2012) compared individuals of different length within a single age-class using growth increments as recorded in scales. In order to shorten the discussion, this point was dropped.

Lines 502-505. Here papers on hyperallometry of reproduction should be cited (Barneche et al. 2018; Marshall & White 2019)

Answer: Thank you for these useful references. Included.

In summary, the paper can be published in a journal on fish biology and ecology after some relatively minor changes. To make it more interesting for a wide range of readers, it needs to be shortened and simplified by moving some material to supplementary information and, more importantly, it needs to be better related to life history theory.

Jan Kozłowski, 19th December 2023.

1. Barneche, D.R., Robertson, D.R., White, C.R. & Marshall, D.J. (2018). Fish reproductive-energy output increases disproportionately with body size. Science, 360, 642-645.
2. Kozlowski, J. (1996). Optimal allocation of resources explains interspecific life-history patterns in animals with indeterminate growth. Proceedings of the Royal Society B, 263, 559-566.
3. Kozlowski, J. (2006). Why life histories are diverse. Polish Journal of Ecology, 54, 585-605.
4. Kozłowski, J. & Teriokhin, A.T. (1999). Allocation of energy between growth and reproduction: The Pontryagin Maximum Principle solution for the case of age- and season-dependent mortality. Evolutionary Ecology Research, 1, 423-441.
5. Kozłowski, J. & Uchmański, J. (1987). Optimal individual growth and reproduction in perennial species with indeterminate growth. Evolutionary Ecology, 1, 214-230.
6. Marshall, D.J. & White, C.R. (2019). Have we outgrown the existing models of growth? Trends in Ecology & Evolution, 34, 102-111.

Review by anonymous reviewer 1, 19 Dec 2023 15:39

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?

Answer: The process is two-fold, first the scale sampling, second, the reading, at each step some selection may have occurred and both changed over time. It is now described in the text.

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.

Answer: The idea was first to have a look at the trend in the general population and secondly to focus on the first-returns, a more homogeneous subset of individuals having experienced the decision-making process for the return most recently. But indeed, we acknowledge this was misleading. The temporal regression on the mean length was reproduced on first-returns alone, so that all analysis presented in the MS are focused on this subset of fish. Results indicates a sharper decline in first-returns, with -1.73mm (SD = 0.08) per year, instead of -1.18mm (SD = 0.03).

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

Answer: Thank you for spotting this. Corrected.

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

Answer: No, this was in fact referring to the 15,730 individuals sampled and whose scales were examined. We revised the text and hope it is clearer now.

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.

Answer: We expected a similar positive influence of longer river sojourn on size, as more years spend in the river offer more time for growth and thus length increment. However, we expected its effect to be of a lesser extent than the effect of years at sea, due to lower growth rate in the river than at sea. Clarified in the text.

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

Answer: Thank you for this useful reference. Included.

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.

Answer: We stated in a more consistent way the numerical effects of each variable and interaction (Figure 3) in the results. Figures describing the explanatory variables have been produced and presented in appendix 1. Effect of the presence or absence of a kype was detailed in the results.

L233. “On average” ?

Answer: Thank you for spotting this. Corrected.

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.

Answer: As indicated above, this analysis and graph was reproduced on first-returns alone.

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).

Answer: The idea here was indeed to indicate that the sea age was the most influential variable on the length at first return, as it lead to the highest gain in explained deviance. Table 1 was referenced, the text was clarified and a "kype + river age" was included in the list of models to help to differentiate the respective explanatory power of river and sea age.

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.

Answer: We clarified hypothesis 2 to make it more explicit that the duration of the sea sojourn was actually one of the main point of interest here, as it is indeed likely to be of major importance as an important part of the length at return is achieved at sea. Number of 2SW (averaged over the 1000 datasets) is now given in the text. As indicated above, figures presenting the other explanatory variables are presented in Appendix 1.

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).

Answer: This is correct; the effect of the river age is especially detectable for the 0SW and tends to decrease as time at sea increases; this was discussed on lines 310-313. However, this is not only true for SW0, but also for SW1-FW1 and SW1-FW2, as predicted length for these strategies are distinct and well separated. The wide confidence interval for SW1-FW3 comes from the fact that few individuals are represented in this specific strategy. We clarified the sentence dealing with this result.

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 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?

Answer: Average coefficient estimates are reported in Figure 3, but as the model is parameterized with a log link, effects are multiplicative and as such, should be read as percentage of increase (effect > 1) or decrease (effect < 1). In order to clarify the reading of effects from figure 3, minimum and maximum values of the quantitative effects and interactions for the reference age-class (SW1) appear now respectively as downward red triangles and upward green triangles. The ctrAvgDOY by Year interaction presented in a discretized way are represented by blue diamonds, i.e. only one value of ctrAvgDOY for the SW1 age-class per year.
We do not expect the low numbers of 2SW individuals to affect the direction of the effect, most likely however, it could affect the precision around the estimates.

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).

Answer: We mentioned in our third hypothesis on l96 "iii) a shorter growing season at sea and an advanced date of return". So we tested accordingly 1) whether timing influenced the length at first return and 2) whether timing of return had indeed been advanced, leading to a possibly shorter growth season.

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.

Answer: As indicated above, temporal regression on the mean length is now only on first-returns.

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?

Answer: Thank you for your positive appreciation. No we did not consider this, as we do not have the data to actually evaluate this. However, we do not expect that large fish would be more difficult to measure accurately, as all fish are well anesthetized before any handling and the measuring boards are designed for the restraint of a large range of fish lengths.

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

Answer: Thank you for this suggestion. Corrected.

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.

Answer: The sentence lacked clarity: the Gamma distribution was only tested, but did not improve the results of the normality tests and as such, the Gaussian distribution with a log-link was kept. We tried to make it more explicit in the text.

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…"

Answer: Thank you for this suggestion. Modified.

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.

Answer: As answered above, the effect of the river age is not only perceptible for SW0, but also to some extent on the SW1 individuals. As our study did not have access to individual measurements of the length at smoltification, here we relied on river age and used it as a proxy of the length of the smolt. We rewrote this part of the discussion to improve the clarity of our message.

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

Answer: To shorten the discussion, this point was dropped.

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

Answer: The text has been revised to provide an explanation: "Our results suggest that the effect of river age on length differences at return are most visible in 0SW and tend to decrease as time at sea increases, likely as a consequence of high individual heterogeneity in marine growths."

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?

Answer: The comparison was indeed with the respective average return dates for each age class in 1984, this was detailed in the text. We think the difference with Legrand et al. may come from the fact that their study covered a broad geographical range, averaging effects over populations that may have contrasted, or even opposite, temporal trends. This may be accentuated by the fact that the Bresle observatory was the northernmost one and as such may exhibit trends more pronounced than in southern France. Lastly, Legrand et al. are presenting results at the scale of the species and we are presenting ours by age classes, which may lead as well to more contrasted differences.

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?

Answer: This is stated on l322-324. The interaction effect is stronger for the SW0 strategy and even negative for SW2.

L420-437. Nice paragraph.

Answer: Thank you for your positive appreciation.