Response to reviewer’s comments

* First, we would like to thank the reviewers and the Editor for the very helpful and insightful comments. The suggestions and revisions are discussed in the point-by-point reply.

Editor's Comments to the Author:

Subject Editor: 1

Comments to Author :

Both reviewers recognize the importance of the research and findings from this manuscript. They indicated some specific aspects that can help improve the manuscript. I look forward to seeing a revised manuscript.

Reviewer(s)' Comments to Author:

**Reviewer: 1**

Comments to the Author

I think this is an outstanding piece of work and is exactly what the field needs. I don't have any major suggestions but this shouldn't be interpreted as a lack of engagement. I've read the work carefully and while I don't agree with everything in it, I think it's a very important paper.

My only suggestion is this:

The authors note that scalings in one context will not match scalings in another. I agree entirely. But on line 262, the authors state: :It is, however, typically found and assumed that standard metabolic rate and natural feeding levels are proportional to routine metabolic rate and maximum consumption rate, respectively, and thus exhibit the same mass-scaling relationships (Kitchell et al. 1977; Neuenfeldt et al. 2020)."

I accept that all we have is maximum consumption rates but I would argue that assuming proportionality between those and wild consumption rates is profoundly fraught and as I'm sure the authors are well aware, the tests of the tests of proportionality upon which these assumptions lie are meagre to non-existent. I don't know, but I suspect that older/larger fish are much more likely to forage more effectively than smaller/younger fish within a species - if only because of their differential sensitivity to predation themselves. I think the authors should strongly consider what level of disproportionality between max. and wild consumption rates would render these results moot. I'm not saying they are moot at all, in fact I strongly suspect that they are close to what is really happening. But still - the whole point of this paper is to show that we shouldn't assume things work in a certain way, that slight differences in allometries yield major differences in outcomes. Wouldn't it be good to retain that guiding principal with regards to all of the key components? A sensitivity analysis would go a long way to showing what the assumption of proportionality of max assumption to wild conumption does. It may even encourage folk to go out and actually measure consumption rates in the wild and how they change with body size - the incentive to do so won't exist unless we point out we really don't know.

Great work on a fantastic paper!

Dustin

* We agree that it is very important to question common assumptions about bioenergetic processes (which, as the reviewer identifies, was one of our main motivations to write this manuscript). We also agree that the reference we make in the discussion with respect to previous work “*typically found and assumed that standard metabolic rate and natural feeding levels are proportional to routine metabolic rate and maximum consumption rate, respectively, and thus exhibit the same mass-scaling relationships*” could be discussed further.
* The first of the papers we cite, Kitchell et al., 1977) is a seminal bioenergetics modelling paper, in which proportionality is assumed (realized feeding rate is a proportion of maximum consumption rate). This is not a statistical proof of proportionality, rather this constant is a free parameter that can be tuned to adjust intake to fit empirical growth data. Interestingly, Kitchell et al., (1997) already 44 years ago (!) identified this parameter as a high priority parameter for understanding and modelling empirical growth rates.
* The second paper we cite is Neuenfeldt et al., 2020, which uses a gastric evacuation rate model to estimate consumption and expresses the consumption as a proportion of maximum consumption rate (i.e., the feeding level). While in some decades the feeding levels tend to vary with size, overall, it seems to be close to 0.4 (their Fig. 4). This is very close to the values used in Kitchell et al., (1977) [0.25, 0.4].
* These two papers represent to two main approaches to account for that natural feeding rates are lower in the wild. The first is essentially introduces a free parameter for fitting, and the latter is based on sub-models representing the size-dependence of gastric evacuation. Hence, none of them are assessments of proportionality of consumption in the wild and maximum consumption rates, and to the best of our knowledge, these studies do not exist.
* Therefore, we decided to do the following changes to the manuscript:
  1. Added a citation to Messmer et al., (Global Change Biology) for their results showing that maximum metabolic rate and standard metabolic rate had similar mass-scaling exponents.
  2. We also broadened the discussion about proportionality in consumption rates to acknowledge how the prediction of optimum growth temperature declining with body size depends on – the unknown – scaling of consumption rates in the wild:
     + From:
       - *“It is, however, typically found and assumed that standard metabolic rate and natural feeding levels are proportional to routine metabolic rate and maximum consumption rate, respectively, and thus exhibit the same mass-scaling relationships (Kitchell et al. 1977; Neuenfeldt et al. 2020).”*
     + To:
       - “*It is, however, typically found that standard metabolic rate is proportional to routine metabolic rate (exhibit the same mass-scaling relationships (Kitchell et al., 1977; Messmer et al., 2017)). This assumption is very common also for the relationship between consumption rates in the wild and maximum consumption rates (i.e., they are related via a constant). It seems to fit data well (Kitchell et al., 1977), and is supported by the recent study on Atlantic cod showing relative stable feeding levels (consumption/maximum consumption) over size (Neuenfeldt et al., 2020). However, it has to our knowledge not been tested thoroughly, even though Kitchell et al. 44 years ago identified this as a highly important parameter that needed more research (Kitchell et al., 1977)*”.
  3. Instead of using the median estimates in Fig. 3 (one line per rate and size-class), we now simulate 500 draws from the posterior distribution of the mass-exponents for metabolism and consumption. We do this to illustrate uncertainty around the negative relationship between optimum growth temperature and body mass as predicted from the simple growth model. However, we cannot attribute this uncertainty to uncertainty regarding the proportionality between standard metabolic rates and natural average metabolic rates, and consumption rates in the wild and maximum consumption rates measured in laboratory settings, simply because we do not have these estimates from natural conditions. Instead, it reflects uncertainty in our estimates, which may or may not be of the same magnitude and direction as maximum vs natural average rates.
* References:
  1. Kitchell, James F., Donald J. Stewart, and David Weininger. "Applications of a bioenergetics model to yellow perch (Perca flavescens) and walleye (Stizostedion vitreum vitreum)." *Journal of the Fisheries Board of Canada* 34.10 (1977): 1922-1935.
  2. Neuenfeldt, Stefan, et al. "Feeding and growth of Atlantic cod (Gadus morhua L.) in the eastern Baltic Sea under environmental change." *ICES Journal of Marine Science* 77.2 (2020): 624-632.
  3. Messmer, Vanessa, et al. "Global warming may disproportionately affect larger adults in a predatory coral reef fish." *Global Change Biology* 23.6 (2017): 2230-2240.

**Diagram

Description automatically generated**

New idea for Fig. 3. Basically, I find it difficult to address the sensitivity related to translating from maximum consumption rates to wild consumption rates, because I’m not aware of any study that looks into that specifically (i.e., if/how these allometries differ). We could however address uncertainty in the parameters we estimate. Instead of using the median of the posteriors to make 1 average line per rate and size, I now do 500. Because the specific question was about the mass-scaling, I here kept all the other parameters at their medians, like before, but the mass-scaling exponents were 500 draws from the normal distribution that is their posterior (i.e., our mean and estimated sd from the posterior samples). I then added a new panel, which shows the distribution of the optimum temperatures (that was previously a single arrow, note the arrows are replaced by rugs and that is what the new panel c shows). Plotting the distributions rather than medians side-by-side gives a completely different impression, I think. First, they are clearly different, second, the uncertainty is much larger the bigger they are with the additional variation, and lastly, in the previous plot, it was a bit difficult to see exactly where the arrows were on x since we had to compare across plots (not in the same plot).

Now, of course we cannot address this uncertainty to different allometries of natural vs maximum feeding rates, but maybe that’s impossible if we don’t have anything to base that sensitivity analysis on? And either way, I think I prefer this over the old one!

**Reviewer: 2**

Comments to the Author

Using intraspecific data of fish, the authors found that maximum consumption rates and metabolic rate scales positively with body size but the former with a lower slope. Considering that optimal maximum consumptions rates are unimodal over the full temperature range the authors predict that optimum growth rate should scale negatively with size. This prediction is supported with an independent dataset. These results certainty improve our understanding of the adaptive mechanism behind adult fish-size-reduction under warmer temperatures. I only have a few suggestions and questions, that might help to improve the clarity of the working hypothesis/prediction and the scope of the study.

Lines 93-117. This section points to a novel relationship between growth rate, body mass, and temperature, only when evaluated at the intraspecific level. However, there is no information or a logical argument to expect such novel relationships. I think the authors should include, if possible, the logical argument that allows them to make predictions about the relationship (including the different slopes) between maximum consumption and size, and the relationship between metabolic rate and size, at the intraspecific level. This logical explanation should include, as a consequence, the predicted relationship between optimum growth rate and body size. Preferably, these expectations should be supported with a figure. This can help the general readers of Global Change Biology to understand the biological basis of the study.

* We would like to clarify that we in this paragraph do not claim these relationships are novel. Rather, we briefly review some of the differences between intra- and interspecific relationships, mainly the unimodal relationship between a rate and temperature due to de-activation and the number of studies showing deviations from the predicted ¾ mass exponent (which seem to fit interspecific, but not intraspecific, data well). We do not make any explicit predictions based on the literature we cite here. We also wish to clarify that our study is purely empirically driven – the predictions about the slopes of consumption and metabolism vs mass are entirely driven by data and our estimates.

Lines 95-97. Why do the authors not expect an interspecific relationship between optimum growth temperature and body mass? In other words, why bigger fish should not have lower optimum growth temperatures?

* The context of this sentence (and the expectation) is that we wished to highlight one of the key differences between intra- and interspecific data, it is not an expectation that affects our analysis.

We share the view of Marshall & White (2019), that body size as a trait (at a given location and time) on a species level is the result of multiple tradeoffs to maximize fitness. For instance, some of the largest marine fishes, such as whale sharks (*Rhincodon typus*), sunfishes (*Mola* genus) and bluefin tuna (*Thunnus thynnus*), all occupy warm waters (tropical to temperate oceans) and have lifestyles and adaptations that allow them the grow to big sizes in warm waters (e.g., low activity and feeding on small prey, or large mass-exponents of relative gill surface area) (Pauly, 2021). Thus, all the different tradeoffs that shape the size of a species could make it challenging to find a signal of optimum growth temperature and species’ body size, if there even is one.

To clarify our reasoning, we have revised the text to “are not aware of” (line 86), and to “want to confound that effect with any relationship that might occur across species that have different asymptotic sizes” (on line 426).

* References:
  + Marshall, Dustin J., and Craig R. White. "Aquatic life history trajectories are shaped by selection, not oxygen limitation." *Trends in ecology & evolution* 34.3 (2019): 182-184.
  + Pauly, Daniel. "The gill-oxygen limitation theory (GOLT) and its critics." *Science advances* 7.2 (2021): eabc6050.

Line 179. Why do the authors consider the 92% of negative slopes as statistical evidence for an effect of size on optimum growth temperature? What is the criterion to use such a threshold?

* We do not mean to say that 92% is a threshold for a strong effect. In fact, we aim to avoid using arbitrary thresholds that are based on convenience (e.g., 95% confidence interval). The role of an interval is to communicate the width of a distribution (which is why we use more than one interval in our figures, 80% and 95%). In this specific case, where we want to communicate the probability that optimum growth temperature declines with size (i.e., that the slope is smaller than zero), we believe it is much more informative to use the widest interval that does not include zero (McElreath, 2018), rather than an arbitrary interval (e.g., 95%) that may cross the value a little bit. We also think that a 92% chance that the slope is indeed smaller than 0 is a clear statistical signal, given the relatively small sample size of different species.
* References:
  + McElreath, Richard. *Statistical rethinking: A Bayesian course with examples in R and Stan*. Chapman and Hall/CRC, 2018.

Discussion. A recent article written by Peralta-Maraver & Rezende (2021) demonstrates that smaller ectotherms (including fish) can maintain higher body temperatures than larger ones but for shorter times. The article also demonstrates that, with increasing size, thermal death occurs at lower metabolic rates. Like the manuscript submitted by the authors, the article of Peralta-Maraver & Rezende reveals important mechanisms behind the pattern of size reduction under warming. I think the authors should discuss whether the findings of Peralta-Maraver & Rezende support, complement, or contradict their results.

* As we write on line 73, the underlying mechanisms behind the TSR are not well understood. TSR describes the change in size-at-age or life stage with warming and is one of several rules/patterns that could partly explain why ectotherm populations are predicted to shrink (usually, what is meant is a decline in mean or adult size). The paper by Peralta-Maraver & Rezende shows that size-dependent heat tolerance could contribute to changes in size-distribution (and hence the broader question about shrinking). But, this is an abundance-at-size change, rather than the size-at-age change that we focus on. Even though the finding is very interesting, we find it hard to motivate including this paper and a discussion around it since we already have an extensive bibliography (111 references), and it concerns a slightly different topic.

Peralta-Maraver, T. & Rezende, E., L. Heat tolerance in ectotherms scales predictably

with body size. Nature Climate Change. 11, 58–63. 2021.

Jorge Avaria Llautureo.

* Additional changes:
  + On line 149, we also provide the estimate for the intercept for maximum consumption rate (instead of only for metabolic rate)