

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 consumption 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 consumption rates in the wild and their size-scaling is a key. They are, however, unknown. Thus, we cannot test their effect in a sensitivity analyses. Instead we now account for uncertainty in the growth prediction, and acknowledge the issue in the discussion.
- On line 265, the first paper we cite is Kitchell et al. (1977), which is a seminal bioenergetics modelling paper where proportionality is assumed (realized feeding rate is a proportion between 0.25 and 0.4 of maximum consumption rate). The second paper we cite is Neuenfeldt et al., 2020, which uses a gastric evacuation rate model to estimate consumption. The proportion of consumption to maximum consumption varies around 0.4 for cod of different sizes.
- However, these studies are not assessments of proportionality between consumption in the wild and maximum consumption rates, rather they reflect common approaches and assumptions in the literature. To the best of our knowledge, such studies do not exist.
- Therefore, we made the following changes to the manuscript:
 1. We 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. See changes on lines 265-273 (we also added “often” to line 285).
 2. Added uncertainty to Fig. 3 showing the prediction that optimum growth temperature declines with size. We now sample 50 values of the exponents from the posterior distributions. This illustrates uncertainty around the negative relationship between optimum growth temperature and body mass as predicted from the simple growth model. We cannot, however, quantify any 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.
 3. 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.
- 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.

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 consumption 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 certainly 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 of the rate, and the number of studies showing deviations from the predicted $\frac{3}{4}$ mass exponent (which seems 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?

We share the view of Marshall & White (2019), that body size as a trait (at a given location and time) at the 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 to 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, the different tradeoffs that shape the size of a species could make it challenging to find a relationship between optimum growth temperature and body size at the interspecific level, if there even is one.

To clarify our reasoning, we have revised the text to “are not aware of” (line 96), and to “want to confound that effect with any relationship that might occur across species that have different asymptotic sizes” (on line 438).

- 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 that value (zero in this case) (McElreath, 2018), rather than an arbitrary interval (e.g., 95%) that may cross the value a little bit. In line with this reasoning, we removed “strong” from line 181 in the manuscript to more focus on the 92% probability instead of a categorical qualifier.
- 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.

- Thanks for the suggestion. 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). We added a reference to this paper on line 298, where we discuss that larger individuals in a population tend to exhibit higher mortality. However, we do not discuss it further, since mortality is an abundance-at-size change, rather than the size-at-age change that we focus on in this study.

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.

- We also made the follow minor changes for clarification.
 - Line 483: Provided the conversion factor between ml/L O₂ to g/day (it was only described how it was calculated).

- Line 860 (Figure 1): added “on the centered data” to clarify what the equation intercept refers to.
- Added a missing parenthesis to Fig. 1A
- Changed sub panel annotation from a, b, c to A, B, C in Fig. 1
- Line 39 (abstract): changed to “...and body size. Small individuals of a given population may therefore...” to avoid repeating “within species”.
- On line 150, we now also provide the estimate for the intercept for maximum consumption rate (and not only for metabolic rate)
- Line 33: changed from 59 to 52 studies. This is the total number of unique studies across all rates accounting for studies appearing for more than one rate
- Line 85: removed “which”
- Line 91: added “body” before growth to avoid confusion with population growth
- Line 121: switched the order of rates and # species per rate to follow the rest of the paper (consumption, metabolism, growth)
- Line 108: replaced “and” with comma
- Line 195: removed “data of fish from temperature experiments”
- Line 199: replaced “, also” with “and is”
- Line 231: replaced “the average intraspecific predictions for the activation” with “the predicted average intraspecific activation energy”
- Line 245: added “itself”
- Line 262: added “they”
- Line 273: made the new sentence a start for a new paragraph, because it became quite long with the additional text in response to reviewer #1
- Line 327: added “(below peak temperatures)” to clarify what n referred to
- Line 350: added “for species-size group combinations” to clarify what n referred to, and added how many data points were below peak, for consistency
- Line 366: fixed math notation , ... ,
- Line 387: changed phrasing to “and allow intercepts and slopes”
- Line 415: added “, note it is on centered scale” to clarify how temperature can be -10.
- Line 415: added “frequentist”
- Line 851: clarified that the models were fitted to centered data, but for easier interpretation the x-axes in Fig. 1 show the non-centered masses.
- Line 859: clarified how the results presented in Fig. 1C correspond to the coefficients in Eq. 2.
- We removed supplementary figures and analysis of growth rate data below peak temperatures (not to be confused with the analysis of optimum growth temperature, based on the same dataset). This analysis has received progressively less attention in the paper in previous versions, and in the submitted version these analyses were not cited in the main text. We therefore feel it is best to remove these analyses to make the paper more clear and concise. Thus, we made the following changes:
 - Line 35: replaced “these three processes” with “maximum consumption and metabolic rate”
 - Line 188: replaced “maximum consumption, metabolism and growth rate” with “maximum consumption and metabolic rate”
 - Line 119: added “, and how optimum growth temperature scales with size”
 - Line 378: removed growth from subheading

- Line 382: removed growth from text
- Line 389: removed growth from text
- Line 389: removed growth from text
- SI text: removed first paragraph of heading “*Supplementary methods and analysis*”
- Removed Fig. S4, Fig. S20-23
- Table S3: removed “growth”
- Table S4: removed column “growth”