

Gill area explains deviations from body size–metabolic rate relationship in teleost fishes

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Funding information

Horizon 2020 Framework Programme, Grant/Award Number: 770884; Natural Sciences and Engineering Research Council of Canada; European Research Council; the Natural Sciences and Engineering Research Council of Canada; Academy of Finland; Saint Mary's University

Abstract

Whether gill area constrains fish metabolism through oxygen limitation is a debated topic. Here, the authors provide insights into this question by analysing mass-specific metabolic rates across 44 teleost fishes extracted from FishBase. They explore whether species deviations from metabolic rates predicted by body mass can be explained by species gill area. They show that the gill area explains c. 26%–28% of species-level deviations from mass-specific metabolic rates. Their findings suggest that gill area might indeed be one of the factors limiting metabolic rate in fishes.

KEYWORDS

body size, gill area, meta-analyses, metabolism, oxygen consumption, teleost fish

Body size is a well-established proxy of an organism's metabolic rate across taxa (e.g., Makarieva *et al.*, 2008). In fishes the gill surface area (GSA) has been suggested as an additional correlate as it regulates the amount of oxygen intake and may ultimately constrain the fish metabolic rate (Pauly, 1981). Whether such a constraint ultimately determines fish body size has been intensively discussed over recent years (e.g., Marshall & White, 2019; Pauly, 2021; Pauly & Cheung, 2018). Therefore, the role of GSA on fish metabolic rate is intriguing, but analysing this is difficult due to many confounding morphological and behavioural properties (Killen *et al.*, 2016). If GSA had no constraining role in fish metabolism, one would hypothesize that metabolic rates standardized by body size do not systematically differ among species with differing GSAs. To test this, and to provide data-driven insights into the ongoing discussion about the role of GSA in fish metabolism, here the authors review data on metabolic rate (approximated through oxygen consumption; Verberk *et al.*, 2011), body size and gill area of teleost fishes. The focal question is whether species-level

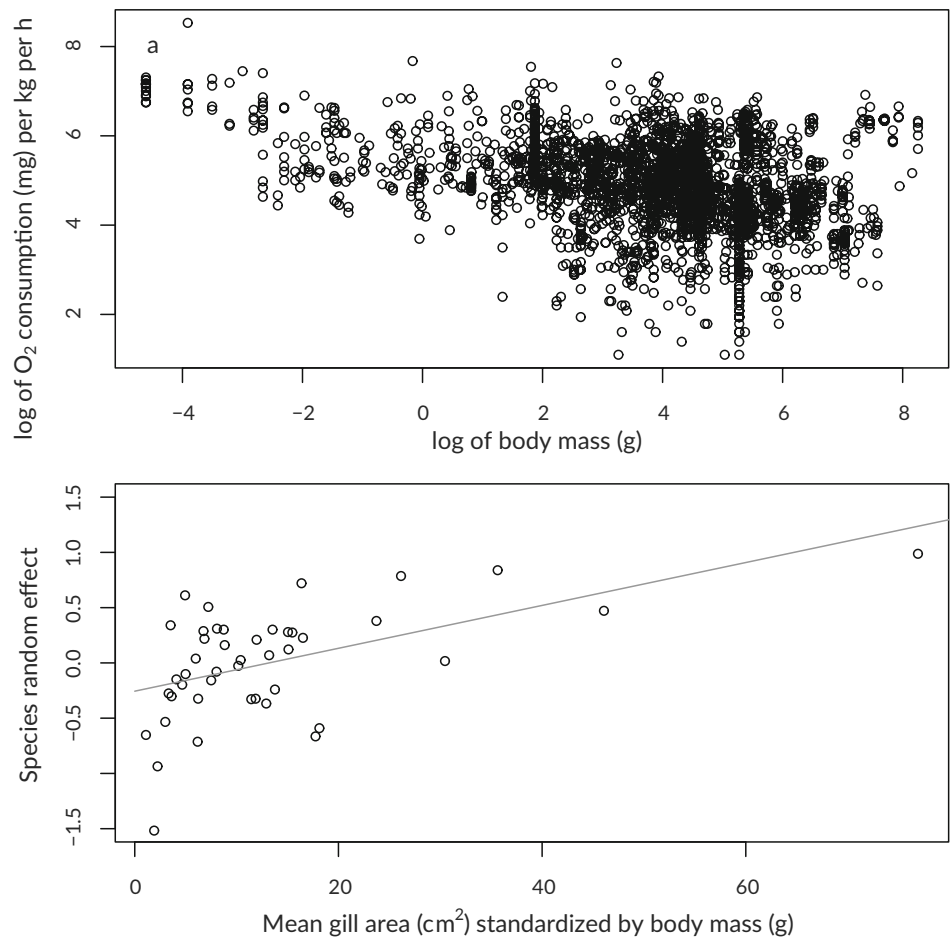
deviations from the body size–metabolic rate relationship can be explained by differences in species gill area with respect to body size.

In the analyses, the authors focused on teleost fishes for which observations on oxygen consumption, gill area and body mass were available in FishBase (www.fishbase.org; Froese & Pauly, 2008). For these species, they extracted pairs of observations on body mass and hourly oxygen consumption standardized by body mass. In total, they analysed 2645 observations from 44 fish species, representing 30 different families (for species list, see Supporting Information Table TABLE S1). The species covered 11 marine species, 25 freshwater species and 11 species that use both marine and freshwater habitats; species environments ranged from polar (1) to temperate (14), subtropical (16) and tropical (13) (Supporting Information Table TABLE S1). A scatterplot of this data is shown in Figure 1a. Next, they similarly extracted pairs of observations for GSA and body mass for each fish species, i.e., 167 observations. Given that larger fish tend to have larger gills, they standardized GSA by body mass by calculating $GSA/(M^{0.8})$ as suggested by Pauly and Cheung (2017).

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FIGURE 1 (a) Log-transformed body masses and log-transformed hourly oxygen consumption of 2770 observations reported in FishBase (www.fishbase.org; Froese & Pauly, 2008) for 44 teleost fish species. (b) Species random effects (Supporting Information, TABLE S1) plotted against species-specific averages of gill area divided by body mass to the power of 0.8 (see main text for details) and a linear regression line illustrating the relationship among the variables. The regression suggests that about 26%–28% of among-species variation in oxygen consumption can be explained by species-specific variation in gill area standardized by body mass



Then, they calculated an average of this “GSA standardized by body mass” index for each species.

As metabolic rate x is known to scale with body mass M exponentially, *i.e.*, $x \propto M^A$ (*e.g.*, Brose *et al.*, 2006), authors' analyses focused on log-transformed oxygen consumption and log-transformed body mass to linearize the relationship. The analyses were conducted in two steps. First, they modelled log-transformed oxygen consumption as a function of log-transformed body mass, temperature, activity and salinity as fixed effects (to control for potential variation in metabolism caused by these available covariates) and species as a random intercept. All the covariates turned significant (P -values < 0.01), and therefore, no model reductions were needed. Normality and homogeneity of the model residuals were inspected. Model fitting was performed using the `lmer` function within the `lme4` library in R (R Development Core Team, 2021). Variation in oxygen consumption associated among observations within species was 56.8%, whereas variation among species was 43.2%. The key product of this first set of analyses was the random intercepts, *i.e.*, species-level deviations from average metabolic rates based on body size and other covariates. The values of the random intercepts are given in Supporting Information Table TABLE S1.

In the second step of the analyses, the species-level random effects were extracted and plotted against species-specific “GSA standardized by body mass” indices (Figure 1b). Correlation among the two variables was estimated and found to be positive with a Pearson's

correlation coefficient of 0.526 ($t = 4.00$, $df = 42$, $P < 0.01$). Finally, a linear model describing the correlation between these variables was fitted (multiple $R^2 = 0.277$; adjusted $R^2 = 0.259$) to illustrate the pattern in the data (Figure 1b). Residuals of the regression model were inspected for normality and homogeneity.

The robustness of these results was explored in two ways. (a) In addition to species-level random intercepts, species-level random slopes were considered. Nonetheless, the results were analogous as the variation associated to species-level random slopes was negligible (0.02%). (b) In the correlation analyses, the authors considered log-transformed averages of GSA standardized by body mass, which resulted in higher Pearson's correlation coefficient of 0.606 ($t = 4.94$, $df = 42$, $P < 0.01$). Regression results were similar but with higher R^2 values (0.352–0.367). The applied data and the analyses codes can be found in the Supporting Information.

In summary, authors' analyses illustrate that once body mass-related variation in oxygen consumption (Figure 1a) is controlled for, variation in oxygen consumption that remains among species can be to some extent (*c.* 26%–28%) explained by the species-specific variation in GSA standardized by body mass (Figure 1b). In practice, this observation implies that even though body mass is a well-established predictor of oxygen consumption (*e.g.*, Clarke & Johnston, 1999) and a predictor of the metabolic rate (Brose *et al.*, 2006), the prediction can be improved by accounting for GSA. Naturally, many other abiotic and biotic variables than those included in authors' data set, such as stress,

affect oxygen consumption as well (Clarke & Johnston, 1999; Killen *et al.*, 2010). The authors included available covariates in the present analyses to control for the variation that might affect the item of focal interest here: the body size–metabolic rate relationship. Nonetheless, the data used in their meta-analyses included a large amount of random noise, as they were gathered in numerous experiments conducted with varying methods. As a result, their finding about the GSA effect is conservative, and its emergence, despite residual variation and limited amount of GSA data available, is an interesting outcome of authors' meta-analyses. Given that the correlation between species deviations from mass-specific metabolic rates and the GSA is positive, the results also suggest that GSA might indeed be one of the processes constraining metabolism in teleost fishes, particularly in larger active fish in warmer waters (Rubalcaba *et al.*, 2020). While in their meta-analyses, Killen *et al.* (2016) reported ambiguous evidence on the direct effect of GSA on metabolic rates, they detected across a continuum of teleost fish types (in terms of their life history, behaviour and physiology) that large GSA are generally associated with high metabolic rates. Thus, their findings are in line with the results of the present study.

It should be noted that the correlation detected in the present study is purely empirical (*i.e.*, it provides no information on the causal mechanisms) and stems from the data available in FishBase (www.fishbase.org; Froese & Pauly, 2008), which may be biased towards species of most commercial interest. Furthermore, the analyses are limited to 44 species for which the required data was available, thus covering merely *c.* 0.13% of all teleost fishes. Thus, authors' analyses do not provide very strong nor conclusive evidence across teleost fishes. Nonetheless, one can speculate the practical consequences of such a correlation. Global warming is predicted to reduce the amounts of dissolved oxygen in marine and freshwater habitats (*e.g.*, Breitburg *et al.*, 2018). Assuming that fish with large GSA relative to their body size require a greater oxygen consumption, reductions in oxygen level might reduce species feeding activity and metabolism and thereby reduce growth and body condition (Cheung *et al.*, 2012; Pauly & Cheung, 2017). In addition, some previously occupied habitats might become unsuitable for such species. On a broad scale, this might lead to changes in fish community structure and altered conservational status on species with certain morphologies. Correlations, such as the one detected in the present meta-analyses, can be useful in directing future research and conservation efforts towards species that might be particularly vulnerable to projected changes in abiotic environmental conditions.

AUTHOR CONTRIBUTIONS

D.G. edited the data and performed literature search, J.A.H. and A.K. designed the analyses and A.K. performed the analyses and compiled the first draft of the manuscript. D.G. and A.K. jointly finalized the first version of the manuscript, and A.K. revised it twice.

ACKNOWLEDGEMENTS

We are extremely saddened by the sudden loss of our co-author Jeffrey Hutchings during the article writing process. We thank Patrick White

(Saint Mary's University, Halifax, Canada) for the extraction of the data from www.FishBase.org. We are grateful to Daniel Pauly for helpful comments on an earlier version of the manuscript. This study was funded by the Academy of Finland (project grant no.: 317495 to A.K.), the Natural Sciences and Engineering Research Council of Canada (NSERC; Discovery Grants to A.K. and J.A.H.) and the European Research Council (COMPLEX-FISH 770884 to A.K.). The present study reflects only the authors' view, and the European Research Council is not responsible for any use that may be made of the information it contains.

ETHICAL STATEMENT

The present study collected no new data but utilized data previously published in FishBase (www.fishbase.org).

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REFERENCES

- Breitburg, D., Levin, L., Oschlies, A., Grégoire, M., Chavez, F., Conley, D., ... Zhang, J. (2018). Declining oxygen in the global ocean and coastal waters. *Science*, 359, 6371.
- Brose, U., Williams, R. J., & Martinez, N. D. (2006). Allometric scaling enhances stability in complex food webs. *Ecology Letters*, 9, 1228–1236.
- Cheung, W. W., Sarmiento, J. L., Dunne, J., Frölicher, T. L., Lam, V. W., Deng Palomares, M. L., ... Pauly, D. (2012). Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, 3, 254–258.
- Clarke, A., & Johnston, N. M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, 68, 893–905.
- Froese, R., & Pauly, D. (2008) FishBase. <http://www.fishbase.org>
- Killen, S. S., Atkinson, D., & Glazier, D. S. (2010). The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. *Ecology Letters*, 13, 184–193.
- Killen, S. S., Glazier, D. S., Rezende, E. L., Clark, T. D., Atkinson, D., Willener, A. S. T., & Halsey, L. G. (2016). Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. *The American Naturalist*, 187, 592–606.
- Makarieva, A. M., Gorshkov, V. G., Li, B., Chown, S. L., Reich, P. B., & Gavrilov, V. M. (2008). Mean mass-specific metabolic rates are strikingly similar across life's major domains: Evidence for life's metabolic optimum. *Proceedings of the National Academy of Sciences of the USA*, 105, 16994–16999.
- Marshall, D. J., & White, C. R. (2019). Aquatic life history trajectories are shaped by selection, not oxygen limitation. *Trends in Ecology & Evolution*, 34, 182–184.
- Pauly, D. (1981). The relationships between gill surface area and growth performance in fish: A generalization of von Bertalanffy's theory of growth. *Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung*, 28, 251–282.
- Pauly, D., & Cheung, W. W. (2017). Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. *Global Change Biology*, 24, 1–12.
- Pauly, D., & Cheung, W. W. (2018). On confusing cause and effect in the oxygen limitation of fish. *Global Change Biology*, 24, e743–e744.
- Pauly, D. (2021). The gill-oxygen limitation theory (GOLT) and its critics. *Science Advances*, 7, eabc6050.

- R Core Team. (2021). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Rubalcaba, J. G., Verberk, W. C. E. P., Hendriks, A. J., Saris, B., & Woods, H. A. (2020). Oxygen limitation may affect the temperature and size dependence of metabolism in aquatic ectotherms. *Proceedings of the National Academy of Sciences of the USA*, 117, 31963–31968.
- Verberk, W. C. E. P., Bilton, D. T., Calosi, P., & Spicer, J. I. (2011). Oxygen supply in aquatic ectotherms: Partial pressure and solubility together explain biodiversity and size patterns. *Ecology*, 92, 1565–1572.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Kuparinen, A., Gielewski, D., & Hutchings, J. A. (2022). Gill area explains deviations from body size–metabolic rate relationship in teleost fishes. *Journal of Fish Biology*, 101(1), 308–311. <https://doi.org/10.1111/jfb.15084>