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Cite this article: Wong S, Bigman JS, Dulvy NK. 2021 The metabolic pace of life histories across fishes. *Proc. R. Soc. B* **288**: 20210910. <https://doi.org/10.1098/rspb.2021.0910>

Received: 18 April 2021

Accepted: 24 May 2021

Subject Category:

Ecology

Subject Areas:

physiology, ecology, theoretical biology

Keywords:

allometry, Bergmann's rule, gill oxygen limitation theory, metabolic theory of ecology, temperature-size rule

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Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5448709>.

The metabolic pace of life histories across fishes

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All life acquires energy through metabolic processes and that energy is subsequently allocated to life-sustaining functions such as survival, growth and reproduction. Thus, it has long been assumed that metabolic rate is related to the life history of an organism. Indeed, metabolic rate is commonly believed to set the pace of life by determining where an organism is situated along a fast–slow life-history continuum. However, empirical evidence of a direct interspecific relationship between metabolic rate and life histories is lacking, especially for ectothermic organisms. Here, we ask whether three life-history traits—maximum body mass, generation length and growth performance—explain variation in resting metabolic rate (RMR) across fishes. We found that growth rate and maximum body size, explained variation in RMR, yet maximum body mass and generation length did not. Our results suggest that measures of life history that encompass trade-offs between life-history traits, rather than traits in isolation, explain variation in RMR across fishes. Ultimately, understanding the relationship between metabolic rate and life history is crucial to metabolic ecology and has the potential to improve prediction of the ecological risk of data-poor species.

1. Introduction

Metabolism is the process by which all living organisms transform external resources into available energy and, in turn, allocate this energy among competing life-history processes, such as survival, growth and reproduction [1–3]. Metabolic rate scales reliably with body mass and temperature, and these mathematical relationships are used to predict ecological phenomena across scales, ranging from life-history traits to ecosystem functioning (e.g. [4,5]). However, predictions of many higher-order ecological phenomena are based on the underlying assumption that metabolic rate underpins life history. Despite a long history of studies examining the connection between life histories and metabolism, there are surprisingly few interspecific, empirical tests of whether life histories are directly related to metabolic rate, particularly for aquatic ectotherms [6–9]. Interspecific studies that incorporate both metabolic rate and life-history traits in the same analysis, rather than studies that focus on similarities in how these traits scale with body mass, are needed as they provide a powerful and distinct complement to intraspecific and experimental work and illustrate generalizability across species. If this putative relationship between metabolic rate and life histories exists, the idea that there is an organismal physiological basis underlying conservation and global-change-related phenomena, such as overfishing, climate change responses and extinction risk may prove to be a reality [2,10–12]. Thus, exploring the connections between metabolic rate and life histories may increase our understanding of the diversity of life histories and offer simple, trait-based approaches to support the development of ecological risk analyses [2,13].

Life-history traits are optimized through natural selection to maximize fitness [2,3,10]. Trade-offs among life-history traits arise as individuals have finite resources to allocate to the competing processes related to survival, growth and reproduction [2,14,15]. For example, there is a trade-off between

maximum body size and growth rate whereby fishes either grow fast to a small size or grow slower to a larger size [16,17]. In turn, these trade-offs and the environment provide the framework for the evolution of life-history traits [2,10]. Specifically, in response to selection imposed by a particular environment, suites of life-history traits commonly co-evolve, clustering together along a fast–slow axis, with organisms that grow slower, mature later, live longer and have a larger maximum body size on the ‘slow’ end of the continuum, and organisms with the opposite suite of traits on the fast end [2,14,18,19]. Thus, life-history traits characterize an organism’s pace of life, as they describe where an organism is situated along this fast–slow continuum of life history [14]. Metabolic ecology assumes that metabolic rate sets this pace of life and that organisms with a higher metabolic rate will sit towards the ‘faster’ end of the life-history continuum, since allocation of resources to growth and reproduction is powered by a faster metabolism [4]. Yet, the relationships between metabolic rate and life histories have rarely been examined across species, and when they have, it has yielded conflicting results. For endotherms (birds and mammals), it is still unclear whether age-related life-history traits such as age at first reproduction and maximum age are related to metabolic rate, even after controlling for body mass and evolutionary history [7,9,20]. Conflicting results have also been found in studies of growth rate. While growth rate has been found to be a strong, positive predictor of resting metabolic rate (RMR) across vertebrates and has also been found to positively correlate with metabolic rate in nestling songbirds, no relationship has been found between growth rate and metabolic rate in other interspecific studies of birds and mammals [7,8,21,22]. Furthermore, we know little about relationships between metabolic rate and life histories for ectotherms. Fishes present a unique opportunity to examine this relationship in ectotherms, as they are the most speciose group of ectotherms, constitute one of the most taxonomically and metabolically diverse radiations of vertebrates, and exhibit a wide range of life histories [23–25]. Thus, examining whether metabolic rate and life-history traits are related across fishes allows us to test a fundamental premise of metabolic ecology in ectotherms.

Here, we ask whether life-history traits explain interspecific variation in metabolic rate across teleost and cartilaginous fishes, after accounting for shared evolutionary history and the effects of body mass and temperature. Specifically, we examined whether three life-history traits—maximum body mass, generation length and growth performance—were related to RMR across 104 fish species using a phylogenetic generalized least-squares regression framework [26]. We hypothesized that all three life-history traits would explain variation in RMR, but that growth performance would explain the most variation in RMR because it encapsulates a life-history trade-off (between growth and maximum body size) and thus may better characterize organisms’ life histories and the energetic trade-offs associated with the allocation of finite resources between processes related to survival, growth and reproduction, whereas maximum body mass and generation length do not encapsulate trade-offs. Specifically, we predicted that species with a high metabolic rate for their body mass would have the characteristics of a ‘faster’ life history—a smaller maximum body mass, a shorter generation length and a higher growth performance.

2. Material and methods

(a) Metabolic rate data collation and selection

RMR, measurement temperature (i.e. the temperature associated with the metabolic rate measurement) and measurement body mass (i.e. the wet body mass associated with the metabolic rate measurement) were collated from the literature. For our analysis, we only used estimates of metabolic rate from rates of oxygen consumption where the study noted that fishes were resting and post-absorptive. Obtaining estimates of RMR only from peer-reviewed studies allowed us to categorize the type of metabolic rate (e.g. RMR) measured in each study with a high degree of confidence and avoid propagating potentially erroneous metabolic rate estimates. We collated raw metabolic rate data (i.e. separate estimates for individuals of the same species), if available, although in most cases only a species mean was published. Thus, for our analyses, we averaged raw estimates of RMR and measurement body mass at a given measurement temperature, resulting in a species-specific mean RMR, measurement temperature and mean measurement body mass. If more than one study reported RMR for the same species, we chose only one study to include in our dataset to avoid biasing our results towards species that were represented by multiple studies, following Killen *et al.* [23]. To ensure that our choice of which study for a given species to include in our dataset did not affect the results, we conducted all analyses on three separate datasets (the ‘sample size dataset’, the ‘mass dataset’ and ‘the temperature dataset’) resulting from the following inclusion criteria: (i) based on the largest sample size, as presented in the main manuscript, (ii) based on the largest average measurement body mass and (iii) based on which study’s measurement temperature was within the natural temperature range of the species but closest to 20°C to minimize the range of temperatures included in the dataset following Gillooly *et al.* [27] and Killen *et al.* [23]. If a study measured RMR at multiple measurement temperatures, we also used selection criteria to determine which RMR data to include. For more detail on data collation and our selection criteria see electronic supplementary material, Methods, section 1.

(b) Life-history data collation, selection and aggregation at the species level

To assess if life-history traits explain variation in RMR, we collated maximum body mass, generation length and the von Bertalanffy growth coefficient (k) and asymptotic length (L_{∞} , for estimation of growth performance, here ϕ') collected from peer-reviewed studies and grey literature (hereafter ‘life-history study’) using literature searches and FishBase [17,28]. These life-history traits were chosen because they are available for many species and are widely used to describe fishes’ life histories [16,17,29]. Maximum body mass was collated from the literature or derived from maximum body length using species-specific length-weight conversions (for more detail, see electronic supplementary material, Methods, section 2.1). Generation length and growth performance are both life-history traits that are calculated from other life-history traits (i.e. they are both ‘composite’ life-history traits). Generation length was calculated as $T_{\text{mat}} + (T_{\text{max}} - T_{\text{mat}}) \times z$, where T_{mat} is age at maturity, T_{max} is the maximum age recorded for the species and z is a constant that depends on survivorship and the relative fecundity of young versus old individuals in the population [30,31]. We used a conservative value of $z = 0.5$ that is consistent with IUCN guidelines to account for the truncation of age structure in many fish populations by overfishing (electronic supplementary material, Methods, section 2.2) [30,32]. Growth performance is a composite life-history trait that allows for the comparison of growth rates

across species that differ in maximum size, and thus accounts for the trade-off between growth rate and maximum body size [33,34]. Growth performance is often calculated as ϕ' , $\phi' = \log_{10}(k) + 2 \times \log_{10}(L_{\infty})$, where L_{∞} is the asymptotic length, or the mean body length that individuals in the population would reach if they were to grow indefinitely, and k (yr^{-1}) expresses the rate at which the asymptotic length is approached [33,34]. We also calculated growth performance using asymptotic weight rather than asymptotic length, yet our analysis was largely insensitive to this choice (electronic supplementary material, Methods, section 2.3). Finally, for 28 of the 104 fish species, not all life-history traits were available and thus life-history trait values from closely related species (here, 'proxy species') were used. To ensure that our results were not sensitive to the inclusion of data from proxy species, we reran analyses while excluding all species for which life-history trait data from proxy species was used, and compared results (electronic supplementary material, Methods, section 2.4).

(c) Statistical analyses

We included a phylogenetic random effect in all models to account for phylogenetic non-independence among residuals using a phylogenetic generalized least squares (PGLS) framework as implemented in the *caper* package [26,35]. We constructed a supertree from two sources: (i) the teleost Fish Tree of Life [24], and (ii) a molecular phylogeny for chondrichthyans [25] using the R package *phytools* [36]. All statistical analyses were conducted in R v. 3.6.1 [37].

(i) Do life-history traits explain variation in RMR across fishes?

To test whether life-history traits explain variation in RMR across fishes, we parameterized and compared four models—one for each of the three life-history traits (i.e. maximum body mass, generation length or growth performance), and a 'null model'. The 'null model' included only measurement body mass and measurement temperature as explanatory variables. For each life-history model, RMR was the response variable, and measurement body mass, measurement temperature and the respective life-history trait were the explanatory variables. For all models, measurement body mass was converted to grams, measurement temperature was converted to inverse temperature, $1/(\text{temperature} \times K)$, where K = Boltzmann's constant and temperature is in Kelvin following Gillooly *et al.* [27], and then standardized, and RMR was converted to watts following Grady *et al.* [22]. All variables, other than inverse measurement temperature and growth performance, were \log_{10} -transformed for all models. It should be noted that growth performance is already on a \log_{10} scale by nature of its calculation. Comparisons of the four candidate models were then made using the Akaike information criterion (AICc), which penalizes models for their number of estimated parameters, with smaller AICc values indicating a better model fit [38]. Of the candidate models, the weight of evidence for any given model was measured by its Akaike weight (w_i), the relative likelihood of the model divided by the sum of the likelihoods of all other models. Finally, as generation length and growth performance are composite life-history traits, we parameterized four additional models—two with the components of generation length (i.e. age at maturity and maximum age) and two with the components of growth performance (i.e. k and L_{∞}) as explanatory variables—to ensure that no one component of these composite traits was driving the relationship with RMR.

(ii) What is the relative importance of each life-history trait in explaining variation in RMR across fishes?

To assess the relative importance of maximum body mass, generation length and growth performance in explaining variation

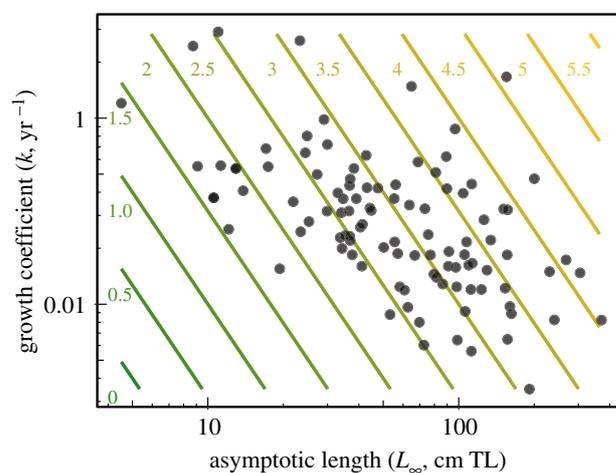


Figure 1. Contour plot of the inverse relationship between asymptotic length and growth coefficient. Each point represents a species, and the lines denote high (yellow) to low (dark green) growth performances values. (Online version in colour.)

in RMR across fishes, we fitted one additional PGLS model that included measurement body mass, measurement temperature, maximum body mass, generation length and growth performance as explanatory variables (hereafter, 'global model'). Collinearity between variables was checked using variance inflation factors (VIFs) and all VIFs were less than five indicating that explanatory variables were not strongly linearly related [39] (electronic supplementary material, figure S1). All explanatory variables were centred and scaled by subtracting the mean and dividing by twice the standard deviation (hereafter 'standardized') so that effect sizes could be interpreted relative to each other and compared in terms of units of standard deviations [26,40].

3. Results

(a) Do life-history traits explain variation in RMR across fishes?

Overall, we found that the only life-history trait which explained variation in RMR across fishes was growth performance, which encompasses a life-history trade-off (figures 1 and 2a). The best overall model (AICc = 16.84, $w_i = 0.989$; electronic supplementary material, table S1) described RMR as a function of measurement body mass, measurement temperature and growth performance. Growth performance explained variation in RMR even after accounting for the effects of measurement body mass and measurement temperature (electronic supplementary material, figure S2A), with species with a high metabolic rate for their measurement body mass also having a high growth performance ($\beta = 0.24$, 95% confidence interval (CI): 0.12–0.36; electronic supplementary material, table S2). On the other hand, the other life-history traits did not explain variation in RMR despite our prediction that species with a high metabolic rate for their measurement body mass would have a smaller maximum body mass and a shorter generation length. Specifically, a null model with only measurement body mass and measurement temperature had similar relative support (AICc = 27.47, $w_i = 0.005$) to the models containing either maximum body mass (AICc = 27.80, $w_i = 0.004$), or generation length (AICc = 29.58, $w_i = 0.002$; electronic supplementary material, table S1). Thus, maximum body mass (figure 2b) did not explain

variation in RMR after accounting for the effects of measurement body mass and measurement temperature (electronic supplementary material, figure S2B) and generation length (figure 2c) did not explain variation in RMR after accounting for the effects of measurement body mass and measurement temperature (electronic supplementary material, figure S2C). Similarly, none of the component traits used to calculate the composite traits of generation length and growth performance—age at maturity, maximum age, k or L_{∞} —explained variation in RMR on their own, as the 95% CI of their effect sizes crossed zero (electronic supplementary material, table S2).

(b) What is the relative importance of each life-history trait in explaining variation in RMR across fishes?

Only growth performance, measurement body mass and measurement temperature explained variation in RMR, as evidenced by their relative effects in the global model with standardized explanatory variables (electronic supplementary material, figure S3) [40]. Growth performance had over a four-fold larger effect on RMR compared to maximum body mass, and a 34-fold larger effect on RMR compared to generation length (electronic supplementary material, figure S3).

(c) Sensitivity analyses

Our findings were robust to the three different data inclusion criteria (electronic supplementary material, Results and table S3), another measure of growth performance (electronic supplementary material, tables S4 and S5), and the use of traits from related proxy species to in-fill data gaps (electronic supplementary material, table S6). Finally, the residuals from all models had a phylogenetic signal (λ) of 0.56 or greater, indicating that including a random effect of phylogeny is necessary when examining metabolic rate across species (electronic supplementary material, table S1).

4. Discussion

Our study directly tests whether life history explains variation in RMR across fishes, and our findings help reconcile the conflicting results of previous work relating metabolic rate and life histories across species. We find that the connection between metabolic rate and life histories across fishes only exists when accounting for life-history trade-offs, such as that between growth rate and maximum body size, and that neither maximum body mass nor generation length explained variation in RMR after accounting for measurement body mass, measurement temperature and evolutionary history. First, we compare the relationships among various measures of life history and RMR and discuss these results in the context of life-history trade-offs. Second, we consider the utility of this and other studies for explaining broad life-history patterns and the implications for metabolic ecology. Finally, we highlight future directions for furthering our understanding of the relationships between metabolic rate and life histories.

We found that of the life-history traits examined, only growth performance explained variation in RMR across fishes. We hypothesized that growth performance would explain this variation because it incorporates a trade-off between life-history traits (i.e. between maximum body size, L_{∞} and growth rate, k) and thus may better characterize a fishes' life-history strategy [14,17,33,41]. By contrast, when

the components of growth performance (k and L_{∞}) were examined in isolation, they did not explain variation in RMR, emphasizing the need to examine composite indices that encompass trade-offs when investigating the relationship between RMR and life history. Although all life-history traits are likely correlated due to trade-offs between them, these relationships must be explicitly captured in models, and are not captured when a single life-history trait is studied in isolation [42]. However, some composite traits may not fully capture life-history trade-offs among competing processes. For example, generation length is also a composite measure of life history that combines age at maturity and maximum age, yet it did not explain variation in RMR, likely because it does not capture a life-history trade-off. As age at maturity increases, so does maximum age, so there is a positive, rather than negative relationship between these components of generation length which does not capture the fact that organisms that mature earlier are potentially reducing their future growth and thus body size and fecundity [10,17]. The lack of relationship between RMR and maximum body mass in our study was also notable because maximum body mass is widely used as an indicator of an organism's position along the fast-slow life-history continuum and is often used in assessments of extinction risk in ectothermic species [17,29]. Instead, the size-dependency of metabolic rate may be mostly captured by measurement body mass, leaving little variation to be explained by maximum body mass, despite the differences in these two measures. Consequently, empirical tests of the foundations of metabolic ecology should explicitly consider life-history trade-offs in fishes, and potentially other ectotherms, rather than individual life-history traits in isolation.

Testing the assumption that metabolic rate sets the pace of life histories is a first step before using metabolic ecology in its intended predictive capacity. A clearer understanding of whether life history explains variation in metabolic rate across taxa is necessary before metabolic ecology can be reliably used to predict life histories. If future studies find that life histories explain variation in metabolic rate for both endotherms and ectotherms, we will then be set with the challenge of determining whether: (i) metabolic rate does indeed dictate and drive life history; (ii) life history drives metabolic rate; (iii) metabolic rate and life history are co-adjusted with each other, affecting each other in a reciprocal manner; or (iv) both life history and metabolism are indirectly related to additional factors [43]. These studies will not only require correlative approaches as executed here, but selection and common-garden experiments to uncover mechanistic drivers.

Other measures of metabolic rate, life-history trade-offs, and statistical approaches may help clarify the relationship between metabolic rate and life history in the future. First, RMR, while the most commonly reported measure of metabolic rate, only reflects energy use and availability at rest, and does not describe the scope for processes such as activity, growth or reproduction [1]. Field metabolic rate, for example, is likely a more accurate measure of day-to-day energy expenditure than RMR and thus could be more closely linked to life-history strategy than RMR [1]. Second, while our results indicate that a measure of life history that accounts for a trade-off explains variation in RMR, there are other life-history trade-offs, popularized as Beverton's dimensionless ratios or Charnov's life-history invariants [44,45]. For example, natural mortality rate (M) has been found to be positively

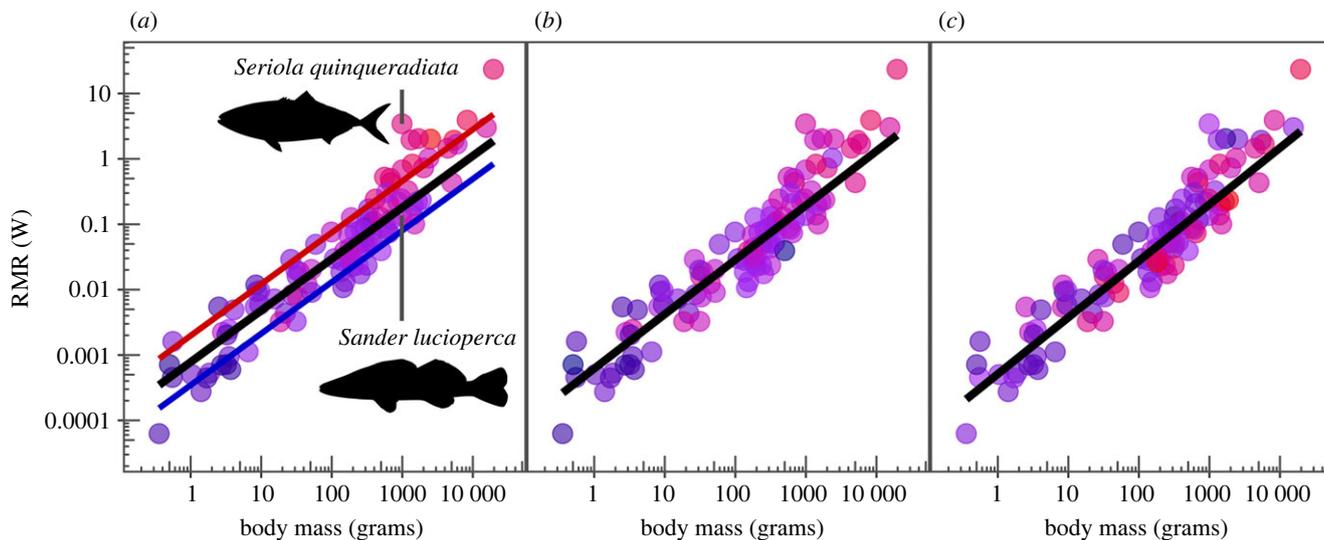


Figure 2. Relationships between resting metabolic rate (RMR), measurement body mass and life-history across fishes. Points are coloured by growth performance (a), maximum body mass (b) and generation length (c), where red denotes larger values and blue denotes smaller values. The black fitted regression line in all three panels is the estimated RMR across the body sizes of all species in the dataset, while incorporating temperature, evolutionary history and the relevant life-history trait (maximum body mass, generation length or growth performance). Growth performance was the only life-history trait to explain variation in RMR, as illustrated by the red and blue lines in (a) which show the estimated RMR for species with high (e.g. Japanese amberjack, *Seriola quinqueradiata*) and low (e.g. zander, *Sander lucioperca*) values of growth performance while accounting for temperature and evolutionary history. (Online version in colour.)

related to k from the von Bertalanffy growth function and negatively related to age at maturity, so testing whether invariants such as M/k and $T_{\text{mat}} \times M$ also explain variation in metabolic rate may be a fruitful avenue for future research, especially in taxa for which reliable estimates of mortality rate are available (e.g. phytoplankton or birds [44,45]). Third, new statistical approaches that explicitly account for trade-offs and correlations between life-history traits may help us reconstruct life-history strategies for species and populations that are data-poor by estimating difficult-to-measure life-history traits, such as fecundity [42,46].

Environmental and ecological factors such as activity level, predation risk, food availability and environmental temperature may obscure relationships between metabolic rate and life-history traits, particularly in ectotherms, thus future studies that account for such factors could further elucidate these relationships [6,23,47,48]. Fish species with a high metabolic rate for their body mass have a high growth performance, but they may also have high activity levels [23,33]. For example, Japanese amberjack (*Seriola quinqueradiata*) had a higher RMR than zander (*Sander lucioperca*), though metabolic rates of both species were measured on individuals of similar body masses and at similar measurement temperatures (figure 2a). This difference in RMR may be because Japanese amberjack had a higher growth performance than zander, but activity level may also play a role. Metabolic rate is strongly correlated with activity level, confounding studies of the relationship between metabolic rate and activity level [49]. Thus, future studies should investigate the interrelationships between activity level, metabolic rate and life history by using morphological proxies of activity such as the caudal fin aspect ratio ($= [\text{height of the caudal fin}]^2 / [\text{surface area of the fin}]$) [23,47]. For example, the caudal fin morphology of the Japanese amberjack is strongly lunate, suggesting that this species is more active compared to the zander with its rounded tail (figure 2a). Additionally, predation risk, environmental stability and food availability, while sometimes experimentally tractable, are difficult to

tease apart, let alone account for in macroecological analyses, despite probably influencing both metabolic rate and life history. However, if realistic approximations of predation risk can be attained, dynamic state variable models may provide an avenue for future investigation by featuring the trade-offs associated with life history and factors such as predation risk and food availability within a dynamic behavioural context to determine fitness [13]. Finally, while measurement temperature greatly affects metabolic rate, environmental temperature may have an evolutionary effect on both metabolic rate and life histories through thermal constraints on production or thermal effects on survival as illustrated by broad patterns such as the temperature-size rule [27,50].

In conclusion, our analyses show that growth performance, but not maximum body mass or generation length, explains variation in RMR across a diverse set of 104 fish species. To our knowledge, this is the most comprehensive study to date that tests whether empirical measures of life history explain variation in metabolic rate across fishes. Our findings revealed that a measure of life history that incorporates a trade-off between life-history traits is strongly associated with RMR and therefore provides some support for the assumption that metabolic rate sets the pace of life across species. If this assumption is to be more broadly accepted, studies *first* need to demonstrate that metabolic rate and life history are related, as indicated by the results in this study, and *then* must demonstrate that metabolic rate dictates and drives life history (a task for future studies that incorporate experimental work). Insight into the links between physiology and life histories has the potential to inform ecological risk assessments, particularly for data-poor species, because life histories are closely related to risk of overfishing and extinction risk [16,19,29].

Data accessibility. The data and code necessary to reproduce the results in this study are archived in Figshare (data: doi:10.6084/m9.figshare.13076267; code: doi:10.6084/m9.figshare.13076285).

Authors' contributions. S.W.: Conceptualization, data curation, formal analysis, investigation, methodology; J.S.B.: conceptualization,

investigation, methodology; N.K.D.: conceptualization, funding acquisition, methodology, project administration.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. The authors declare no competing interests.

Funding. This study was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Canada Research Chairs Program.

Acknowledgements. The authors thank Dr John Reynolds and the Dulvy lab at SFU for feedback on the study.

References

- Clarke A. 2017 *Principles of thermal ecology: temperature, energy and life*, pp. 267–280. Oxford, UK: Oxford University Press.
- Reynolds JD. 2003 Life histories and extinction risk. In *Macroecology* (eds TM Blackburn, KJ Gaston), pp. 195–217. Oxford, UK: Blackwell Publishing.
- Sibly RM. 2012 Life history. In *Metabolic ecology: a scaling approach* (eds RM Sibly, JH Brown, A Kodric-Brown), pp. 57–66. London, UK: John Wiley & Sons.
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004 Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789. (doi:10.1890/03-9000)
- Gillooly JF, Charnov EL, West GB, Savage VM, Brown JH. 2002 Effects of size and temperature on developmental time. *Nature* **417**, 70–73. (doi:10.1038/417070a)
- Barneche DR, Allen AP. 2018 The energetics of fish growth and how it constrains food-web trophic structure. *Ecol. Lett.* **21**, 836–844. (doi:10.1111/ele.12947)
- Lovegrove BG. 2009 Age at first reproduction and growth rate are independent of basal metabolic rate in mammals. *J. Comp. Physiol. B: Biochem. Syst. Environ. Physiol.* **179**, 391–401. (doi:10.1007/s00360-008-0322-4)
- Ton R, Martin TE. 2016 Metabolism correlates with variation in post-natal growth rate among songbirds at three latitudes. *Funct. Ecol.* **30**, 743–748. (doi:10.1111/1365-2435.12548)
- White CR, Seymour RS. 2004 Does basal metabolic rate contain a useful signal? Mammalian BMR allometry and correlations with a selection of physiological, ecological, and life-history variables. *Physiol. Biochem. Zool.* **77**, 929–941. (doi:10.1086/425186)
- Hutchings JA. 2002 Life histories of fish. In *Handbook of fish biology and fisheries* (eds PJB Hart, JD Reynolds), pp. 150–174. Blackwell Publishing.
- Reynolds JD, Dulvy NK, Goodwin NB, Hutchings JA. 2005 Biology of extinction risk in marine fishes. *Proc. R. Soc. B* **272**, 2337–2344. (doi:10.1098/rspb.2005.3281)
- Sunday JM, Bates AE, Dulvy NK. 2011 Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B* **278**, 1823–1830. (doi:10.1098/rspb.2010.1295)
- Thygesen UH, Farnsworth KD, Andersen KH, Beyer JE. 2005 How optimal life history changes with the community size-spectrum. *Proc. R. Soc. B* **272**, 1323–1331. (doi:10.1098/rspb.2005.3094)
- Healy K, Ezard THG, Jones OR, Salguero-Gómez R, Buckley YM. 2019 Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. *Nat. Ecol. Evol.* **3**, 1217–1224. (doi:10.1038/s41559-019-0938-7)
- Stearns ASC. 1989 Trade-offs in life-history evolution. *Funct. Ecol.* **3**, 259–268. (doi:10.2307/2389364)
- Jennings S, Greenstreet SPR, Reynolds JD. 1999 Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *J. Anim. Ecol.* **68**, 617–627. (doi:10.1046/j.1365-2656.1999.00312.x)
- Juan-Jordá MJ, Mosqueira I, Freire J, Dulvy NK. 2013 Life in 3-D: life history strategies in tunas, mackerels and bonitos. *Rev. Fish Biol. Fish.* **23**, 135–155. (doi:10.1007/s11160-012-9284-4)
- Bielby J, Mace GM, Bininda-Emonds ORP, Cardillo M, Gittleman JL, Jones KE, Orme CDL, Purvis A. 2007 The fast-slow continuum in mammalian life history: an empirical reevaluation. *Am. Nat.* **169**, 748–757. (doi:10.1086/516847)
- Juan-Jordá MJ, Mosqueira I, Freire J, Dulvy NK. 2015 Population declines of tuna and relatives depend on their speed of life. *Proc. Biol. Sci.* **282**, 20150322–20150322. (doi:10.1098/rspb.2015.0322)
- Furness LJ, Speakman JR. 2008 Energetics and longevity in birds. *Age* **30**, 75–87. (doi:10.1007/s11357-008-9054-3)
- Trevelyan AR, Harvey PH, Pagel MD, Ecology SF. 1990 Metabolic rates and life histories in birds. *Funct. Ecol.* **4**, 135–141. (doi:10.2307/2389332)
- Grady JM, Enquist BJ, Dettweiler-Robinson E, Wright NA, Smith FA. 2014 Evidence for mesothermy in dinosaurs. *Science* **344**, 1268–1272. (doi:10.1126/science.1253143)
- Killen SS, Glazier DS, Rezende EL, Clark TD, Atkinson D, Willener AST, Halsey LG. 2016 Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. *Am. Nat.* **187**, 592–606. (doi:10.1086/685893)
- Rabosky DL *et al.* 2018 An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* **559**, 392–395. (doi:10.1038/s41586-018-0273-1)
- Stein RW, Mull CG, Kuhn TS, Aschliman NC, Davidson LNK, Joy JB, Smith GJ, Dulvy NK, Mooers AO. 2018 Global priorities for conserving the evolutionary history of sharks, rays and chimaeras. *Nat. Ecol. Evol.* **2**, 288–298. (doi:10.1038/s41559-017-0448-4)
- Garamszegi LZ ed. 2014 *Modern phylogenetic comparative methods and their application in evolutionary biology: concepts and practice*. Berlin, Germany: Springer.
- Gillooly JF, Brown JH, West GB, Savage V, Charnov EL. 2001 Effects of size and temperature on metabolic rate. *Science* **293**, 2248–2251. (doi:10.1126/science.1061967)
- Froese R, Pauly D eds. 2019 FishBase. See www.fishbase.org (December 2019)
- Dulvy NK *et al.* 2014 Extinction risk and conservation of the world's sharks and rays. *Elife* **3**, e00590–e00590. (doi:10.7554/eLife.00590)
- IUCN Standards and Petitions Committee. 2019 Guidelines for using the IUCN Red list categories and criteria. Version 14. See <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>.
- Pacifici M, Santini L, Di Marco M, Baisero D, Francucci L, Grottollo Marasini G, Visconti P, Rondinini C. 2013 Generation length for mammals. *Nat. Conserv.* **5**, 89–94. (doi:10.3897/natureconservation.5.5734)
- Barnett LAK, Branch TA, Ranasinghe RA, Essington TE. 2017 Old-growth fishes become scarce under fishing. *Curr. Biol.* **27**, 2843–2848. (doi:10.1016/j.cub.2017.07.069)
- Pauly D. 2010 Gasping fish and panting squids: oxygen, temperature and the growth or water-breathing animals. In *Excellence in ecology series*, vol. 22. (ed. O Kinne). Oldendorf, Germany: International Ecology Institute.
- Pauly D, Munro JL. 1984 Once more on the comparison of growth in fish and invertebrates. *Fishbyte* **2**, 1–21.
- Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2018 caper: comparative analyses of phylogenetics and evolution in R. R package version 1.0.1. See <https://CRAN.R-project.org/package=caper>.
- Revell LJ. 2012 phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**, 217–223. (doi:10.1111/j.2041-210X.2011.00169.x)
- Core Team R. 2019 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <https://www.R-project.org/>.
- Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. New York, NY: Springer Science + Business Media.
- Quinn GP, Keough MJ. 2002 *Experimental design and data analysis for biologists*. Cambridge, UK: Cambridge University Press.
- Gelman A, Hill J. 2007 *Data analysis using regression and multilevel/hierarchical models*. Cambridge, UK: Cambridge University Press.

41. 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.
42. Horswill C, Kindsvater HK, Juan-Jordá MJ, Dulvy NK, Mangel M, Matthiopoulos J. 2019 Global reconstruction of life-history strategies: a case study using tunas. *J. Appl. Ecol.* **56**, 855–865. (doi:10.1111/1365-2664.13327)
43. Glazier DS. 2015 Is metabolic rate a universal 'pacemaker' for biological processes? *Biol. Rev.* **90**, 377–407. (doi:10.1111/brv.12115)
44. Charnov EL, Gislason H, Pope JG. 2013 Evolutionary assembly rules for fish life histories: natural mortality in fish life-history evolution. *Fish Fish.* **14**, 213–224. (doi:10.1111/j.1467-2979.2012.00467.x)
45. Gislason H, Daan N, Rice JC, Pope JG. 2010 Size, growth, temperature and the natural mortality of marine fish: natural mortality and size. *Fish Fish.* **11**, 149–158. (doi:10.1111/j.1467-2979.2009.00350.x)
46. Thorson JT, Munch SB, Cope JM, Gao J. 2017 Predicting life history parameters for all fishes worldwide. *Ecol. Appl.* **27**, 2262–2276. (doi:10.1002/eap.1606)
47. Bigman JS, Pardo SA, Prinzing TS, Dando M, Wegner NC, Dulvy NK. 2018 Ecological lifestyles and the scaling of shark gill surface area. *J. Morphol.* **279**, 1716–1724. (doi:10.1002/jmor.20879)
48. Forster J, Hirst AG, Atkinson D. 2012 Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proc. Natl Acad. Sci. USA* **109**, 19 310–19 314. (doi:10.1073/pnas.1210460109)
49. De Jager S, Dekkers WJ. 1975 Relations between gill structure and activity in fish. *Neth. J. Zool.* **25**, 276–308. (doi:10.1163/002829675X00290)
50. Angilletta MJ, Steury TD, Sears MW. 2004 Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integr. Comp. Biol.* **44**, 498–509. (doi:10.1093/icb/44.6.498)