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ORIGINAL ARTICLE

Metabolism, population growth, and the fast-slow life history continuum of marine fishes

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Abstract

The maximum intrinsic rate of population increase (r_{max}) represents a population's maximum capacity to replace itself and is central to fisheries management and conservation. Species with lower r_{max} typically have slower life histories compared to species with faster life histories and higher r_{max}. Here, we posit that metabolic rate is related to the fast–slow life history continuum and the connection may be stronger for maximum metabolic rate and aerobic scope compared to resting metabolic rate. Specifically, we ask whether variation in r_{max} or any of its component life-history traits – age-at-maturity, maximum age, and annual reproductive output – explain variation in resting and maximum metabolic rates and aerobic scope across 84 shark and teleost species, while accounting for the effects of measurement temperature, measurement body mass, ecological lifestyle, and evolutionary history. Overall, we find a strong connection between metabolic rate and the fast-slow life history continuum, such that species with faster population growth (higher r_{max}) generally have higher maximum metabolic rates and broader aerobic scopes. Specifically, r_{max} is more important in explaining variation in maximum metabolic rate and aerobic scope compared to resting metabolic rate, which is best explained by age-at-maturity (out of the life history traits examined). In conclusion, teleosts and sharks share a common fast–slow physiology/life history continuum, with teleosts generally at the faster end and sharks at the slower end, yet with considerable overlap. Our work improves our understanding of the diversity of fish life histories and may ultimately improve our understanding of intrinsic sensitivity to overfishing.

KEYWORDS
Bayesian phylogenetic regression, information theory, life-history theory, metabolic ecology, oxygen demand, population dynamics

1 | INTRODUCTION

Marine fishes exhibit a vast range of life histories resulting in considerable variation in their sensitivities to global-change-related phenomena (Hutchings, 2021; Kindsvater et al., 2016). Under the selective pressures of a given environment, life histories evolve depending on the partitioning of resources among survival, growth, and reproduction, resulting in traits that underlie population dynamics (Hutchings, 2021; Stearns, 1992). Consequently, these traits tend to co-evolve and cluster along at least three axes of life history variation: size-related traits (e.g., body length or mass, length-at-maturity), time-related traits (e.g., maximum age, age-at-maturity), and reproductive allocation (Juan-Jordá et al., 2013). In general, species with faster life histories exhibit faster growth, earlier maturity, smaller maximum body size, shorter lifespans, and invest proportionally more of their resources towards annual reproductive output (i.e., the number of female offspring produced per year; hereafter, 'reproductive output'; Denney et al., 2002; Hutchings, 2021). Therefore, species on the fast end of the continuum have faster population growth rates than species on the slower end of the continuum (Juan-Jordá et al., 2013; Reynolds, 2003). One such measure of population growth, the maximum intrinsic rate of population increase, r_{max}, is the average annual number of female spawners produced per female spawner at low population density (i.e., in the absence of density dependence) and, hence, is directly related to a species' inherent sensitivity to overfishing (Myers et al., 1997; Myers & Worm, 2005; Pardo et al., 2016).

Population growth rates (including r_{max}) generally vary with temperature and maximum body size (and, hence, depth and latitude) across marine fishes. Generally, populations and species in warmer (tropical and/or shallow) habitats have faster life histories and higher r_{max} compared to their deeper or higher-latitude relatives in cooler waters (Barrowclift et al., 2023; Drazen & Haedrich, 2012). However, r_{max} also decreases with depth independently of temperature in fishes (Drazen & Haedrich, 2012; Pardo & Dulvy, 2022). Population growth rate tends to be lower in larger species, although the strength of the negative relationship of r_{max} with maximum body size weakens at cooler temperatures in sharks (Pardo & Dulvy, 2022). These spatial patterns suggest an underlying connection to metabolic rate, which also varies with body size and temperature (Brown et al., 2004; Savage et al., 2004).

Metabolism reflects the rates of resource uptake, transformation into available energy, and allocation of that energy to survival, growth, and reproduction (Brown et al., 2004). In addition to varying with body size and temperature across species, metabolic rate relates to life histories and population dynamics (Brown et al., 2004; Savage et al., 2004; White et al., 2022). However, not all life history traits relate to metabolic rate equally, and recent work suggests that time-related and integrative traits (i.e., those that account for a trade-off between life history traits) relate more strongly to metabolic rate (Pettersen et al., 2016; Wong et al., 2021). For example, growth performance is a trait that integrates the trade-off between somatic growth rate and maximum body size and explains more variation in resting metabolic rates (RMRs) across fishes than these 'component' traits alone (Wong et al., 2021). Similar to growth performance, r_{max} can be considered an integrative, time-related trait as it is calculated using age-at-maturity, maximum age, and reproductive output and, therefore, encompasses the trade-off between reproductive investment and survival (Hutchings, 2021). Indeed, variation in r_{max} among determinate-growing vertebrates, including mammals, is linked to metabolic rate (Duncan et al., 2007; Savage et al., 2004). However, it remains to be determined whether there is a broadscale,

interspecific relationship between metabolic rate and r_{max} in fishes, which grow indeterminately throughout their life.

The RMR of an organism is the basal energetic cost required for survival and maintenance functions (i.e., not including activity, growth, and reproduction) and is typically measured by oxygen consumption via respirometry (Chabot et al., 2016; Prinzing et al., 2021). Although RMR is the default measure used in metabolic theory and comparative life history analyses due to its widespread availability, other measures of metabolic rate that include energetic costs above maintenance may relate more strongly to life histories and population dynamics (Arnold et al., 2021; Brown et al., 2004; White & Kearney, 2013). Indeed, previous work has identified that maximum metabolic rate (MMR) and aerobic scope (the difference between maximum and resting metabolic rate, AS) are more related to life history when compared to RMR (Auer et al., 2017; Clavijo-Baque & Bozinovic, 2012; Norin & Clark, 2016). Relatively few studies have examined the interrelationships among life histories, population dynamics, and metabolic rates other than RMR, including MMR and AS (Auer et al., 2017; Clark et al., 2013; Killen et al., 2016).

Here, we examine whether variation in RMR, MMR, and AS relates to variation in r_{max} and its component life history traits (i.e., age-at-maturity, maximum age, and reproductive output) across 84 marine fishes, comprising 47 teleosts and 37 chondrichthyans (24 sharks, 12 rays, and one chimaera, hereafter referred to as 'sharks'), whilst accounting for the effects of body mass, temperature, and evolutionary history. Additionally, we account for the effect of 'ecological lifestyle', where species are categorised in descending order of activity level as pelagic, benthopelagic, or benthic (Bigman et al., 2018; Killen et al., 2016). Specifically, we ask three questions: (1) do fishes with lower metabolic rates have slower life histories (later maturation, longer lifespan, and lower reproductive output), and (2) do fishes with lower metabolic rates have lower r_{max} (a composite of these life history traits), and (3) is maximum metabolic rate (and aerobic scope) more strongly related to r_{max} when compared to RMR?

2 | METHODS

2.1 | Data collation

We collated metabolic rate (resting, maximum, and aerobic scope) and the life history data required to calculate r_{max} (age-at-maturity, maximum age, and reproductive output) for marine fish species to assess whether life history traits and r_{max} explain variation in metabolic rate. As we needed species-means of metabolic rates to match the level of life history trait data (i.e., at the species level), we developed inclusion criteria for retaining studies for both metabolic rate and life history traits, which we detail below. We only included one study per species and focused on matching the metabolic rate and life history data to a geographic region to minimize variability across populations. For anadromous and brackish species, we only retained data if the individuals measured were collected from the marine environment.

For the metabolic rate data, we supplemented published datasets of resting and maximum metabolic rate (RMR and MMR) (Auer et al., 2017; Killen et al., 2017; Wong et al., 2021) with literature searches on Google Scholar. Our search terms were: 'fish' followed by 'maximum'/'active' or 'resting'/'standard' AND 'metabolic rate', 'oxygen uptake', or 'oxygen consumption', OR other keywords such as 'energetics' and 'respirometry'. After ensuring that life history data was also available for that species in the same geographic region, we prioritised studies for inclusion that (1) reported measurement body mass and measurement temperature (if only a range of masses or temperatures were given, the median was used), (2) contained older life stages (no embryos or larvae), and (3) adhered to standard conditions for measuring a given metabolic rate type (e.g. if a study reported RMR, data must have been collected in the absence of stressors and in undisturbed, quiescent, and fasted fish displaying little to no movement; Chabot et al., 2016).

For the life history data, we collated age-at-maturity, maximum age, and reproductive output from the literature and online databases such as the RAM Legacy Stock Assessment Database (hereafter RAM, 2018; Ricard et al., 2012), the IUCN Red List of Threatened Species (Dulvy et al., 2021; IUCN, 2022), FishBase (Froese & Pauly, 2019), and Sharkipedia (Mull, Pacoureau, et al., 2022). Age-at-maturity is the age at which 50% of the individuals have reached maturity. Maximum age is the maximum observed (validated) age, or the theoretical maximum age when the validated maximum age was unavailable (see section '*Theoretical maximum age*' in the 'Supplementary Information S1'). Reproductive output is the number of female offspring produced per year (see below for further detail and how it is calculated). We also collated stock-recruitment time series (age of recruitment is the first censused age class in the stock-recruitment relationship), length-weight regressions, and von Bertalanffy growth parameters required for the calculation of r_{max} from the RAM database when available, otherwise, from stock assessments, the primary literature, or databases (IUCN Red List and FishBase). We prioritised data from (1) the same geographic region as that measured for metabolic rate, (2) females, and studies with (3) larger sample sizes and (4) larger body size ranges. Please see the SI for more information regarding data collation.

2.2 | Calculation of the maximum intrinsic rate of population increase r_{max}

We calculate r_{max} following established methods in Pardo et al. (2016) and Cortés (2016) for sharks and Myers et al. (1997), Denney et al. (2002), and Goodwin et al. (2006) for teleosts in our dataset (those species that have life history data on reproductive output, maximum age, age-at-maturity, and natural mortality). The estimation of reproductive output varies between the lower fecundity oviparous and viviparous sharks and higher fecundity broadcast spawning teleosts and thus, r_{max} is calculated slightly differently for each group (Hutchings et al., 2012; Pardo et al., 2016). Briefly, for sharks, r_{max} is calculated from age-at-maturity (a_{mat}), maximum age (a_{max}), and reproductive output (b). For teleosts, r_{max} is calculated

from age-at-maturity (a_{mat}), maximum age (a_{max}), stock-recruitment data, and any required conversion relationships (e.g., length-weight and von Bertalanffy equations). The key difference in the methods is how is calculated, which is the number of daughters produced per female that survive to a reproductive age in the absence of density-dependent processes (i.e., the maximum spawners per spawner). For sharks this is calculated by discounting reproductive output (b) using instantaneous natural mortality (M). For teleosts, this is calculated from the slope at the origin of the stock-recruitment relationship while accounting for the growth and mortality of larvae to maturity. For more details, please see the '*The calculation of* r_{max}' section in the Methods S1.

To verify the comparability of the shark and teleost r_{max} calculation methods, we compared r_{max} values calculated using the shark r_{max} method (where $\tilde{\alpha}$ is calculated from reproductive traits from the literature) and the teleost r_{max} method (where $\tilde{\alpha}$ is calculated from stock-recruitment time series) for five shark species with stock-recruitment time series in RAM. We find that both methods generate similar r_{max} values for the five species (see '*The comparison of shark and teleost* r_{max} *methods*' section in the Results S1 and Figure S1).

2.3 | Statistical analyses

For analysis, we created two datasets as sample size and measurement temperature of metabolic rate varied across studies. The first dataset was based on studies where metabolic rate was measured at a temperature closest to 15°C ('temperature dataset'), while the second was based on studies with the largest sample size for metabolic rate measurements ('sample size dataset'). Our findings were not sensitive to the choice of dataset, and therefore, we present the results based on the 'sample size dataset' (see Tables S2–S4 in the SI for results from the 'temperature dataset'). We also fit all models with a fixed effect of taxon (e.g., shark or teleost) but found that this effect did not provide a better fit for any model (see Tables S5 for more detail); thus, we present the results without the fixed effect of taxon. Because five tuna and lamnid shark species in our dataset are regionally endothermic (Skipjack Tuna *Katsuwonus pelamis*, Scombridae; Yellowfin Tuna *Thunnus albacares*, Scombridae; Pacific Bluefin Tuna *Thunnus orientalis*, Scombridae; Bigeye Tuna *Thunnus obesus*, Scombridae; and Shortfin Mako Shark *Isurus oxyrinchus*, Lamnidae) and, thus, their metabolic rates will be greater for a given size compared to ectothermic fishes, we fit the most supported models for each metabolic rate type (from Tables 1 and 2) without the inclusion of these five species. The model results did not differ with and without the inclusion of these species (see Table S6).

We used a phylogenetic Bayesian modeling framework and an information-theoretic approach to assess whether life histories and r_{max} explained variation in metabolic rate across marine fishes. For all models, metabolic rate data were converted to whole-organism (if not already) Watts [Joules·s^{-1}] following Grady et al. (2014), aerobic scope was calculated as MMR minus RMR if not reported directly (Clark et al., 2013; Killen et al., 2016), measurement body mass was converted to grams, and measurement temperature was converted to inverse temperature. The inverse temperature was parameterised as the Boltzmann-Arrhenius formulation, $-E/kT$, following Gillooly et al. (2001), where E is the activation energy, k is the Boltzmann constant (8.617×10^{-5} eV), and T is the temperature in Kelvin. All covariates (with the exception of temperature) and the response variable (metabolic rate) were natural log-transformed, following which all covariates were centered and scaled (i.e., standardised) using the function *scale* in R v.4.0.5. All models included a phylogenetic random effect to account for phylogenetic non-independence among residuals because of the evolutionary relatedness between species. For this random effect, we constructed a supertree from a molecular chondrichthyan tree (Stein et al., 2018) and a teleost tree from the Fish Tree of Life (Rabosky et al., 2018). Only species present in the resulting phylogeny were included in our analyses. All models were fitted in Stan using the *brms* package v.2.14.4 (Bürkner, 2017) in R v.4.0.5 (R Core Team, 2021).

2.3.1 | Do fishes with lower metabolic rates have slower life histories?

We tested whether variation in metabolic rate was explained by any of the life history trait components of r_{max} (age-at-maturity, maximum age, and reproductive output), to which end we fitted 12 models ('life history models'). Models were parameterised building on the relationship among metabolic rate, body mass, temperature, and ecological lifestyle, hereafter the 'null model' (e.g., following Bigman et al., 2018; Brown et al., 2004; Gillooly et al., 2001). We then added in either age-at-maturity, maximum age, or reproductive output. For example, the response variable was either RMR, MMR, or AS and the covariates were measurement body mass, measurement temperature, ecological lifestyle (benthic, benthopelagic, pelagic), and one life history trait.

We then used Pareto-smoothing leave-one-out cross validation (PSIS-LOO) to identify the model(s) with the most support for each metabolic rate type (RMR, MMR, and AS; Vehtari et al., 2017). Specifically, we used the LOO information criterion value (*looic*) implemented in the *loo* package (Vehtari et al., 2017), where all models within *looic* <2 of the top-ranked model (lowest *looic* value) have similar support.

2.3.2 | Do fishes with lower metabolic rates have lower r_{max} (a composite of these life history traits)?

We fitted three additional models to examine whether r_{max} explained variation in metabolic rate (for RMR, MMR, and AS). As above, models were parameterised building on the null model and then adding in r_{max}. To assess whether r_{max} better explained variation in metabolic rate compared to its composite life history traits (or null model, if top model), we compared these models (with r_{max}) to the model(s)

TABLE 1 Comparison of life history models for (a) resting metabolic rate (RMR), (b) maximum metabolic rate (MMR), and (c) absolute aerobic scope (AS; MMR − RMR).

Life history models		p_{loo}	Looic	$elpd_{loo}$	se_elpd_{loo}	$elpd_{diff}$	Weight
	(a) RMR ~ (*n* fish species = 82)						
RMR_null	body mass + temperature + lifestyle (null model)	20.0	167.8	−83.9	13.0	−1.4	0.012
RMR_amat	**body mass + temperature + age at maturity + lifestyle**	18.0	165.1	−82.6	12.9	0.0	0.964
RMR_amax	body mass + temperature + maximum age + lifestyle	18.9	167.3	−83.7	13.5	−1.1	0.023
RMR_RO	body mass + temperature + reproductive output + lifestyle	19.7	169.8	−84.9	13.0	−2.3	0.000
	(b) MMR ~ (*n* fish species = 49)						
MMR_null	**body mass + temperature + lifestyle** (null model)	30.7	46.4	−23.2	3.9	0.0	0.929
MMR_amat	body mass + temperature + age at maturity + lifestyle	15.3	51.9	−26.0	4.5	−2.8	0.071
MMR_amax	body mass + temperature + maximum age + lifestyle	27.8	51.9	−25.9	4.5	−2.8	0.000
MMR_RO	body mass + temperature + reproductive output + lifestyle	30.0	50.1	−25.1	4.0	−1.9	0.000
	(c) AS ~ (*n* fish species = 45)						
AS_null	body mass + temperature + lifestyle (null model)	17.8	77.0	−38.5	7.1	−0.9	0.246
AS_amat	**body mass + temperature + age at maturity + lifestyle**	12.4	75.3	−37.6	3.9	0.0	0.754
AS_amax	body mass + temperature + maximum age + lifestyle	17.8	79.3	−39.6	7.6	−2.0	0.100
AS_RO	body mass + temperature + reproductive output + lifestyle	18.0	78.8	−39.4	6.8	−1.8	0.000

Note: Values reported are LOO information criterion value (*looic*, similar to Akaike Information Criterion [AIC]), the effective number of parameters (p_{loo}), the expected log predictive density ($elpd_{loo}$), the standard error of the expected log predictive density (se_elpd_{loo}), the difference in the expected log predictive density ($elpd_{diff}$), and the Bayesian stacking weight (similar to Akaike weight). The model with the lowest *looic* has the most support and is emboldened and any model(s) within 2 looic of the top model is highlighted in grey.

Abbreviations: amat, age-at-maturity; amax, maximum age; RO, reproductive output.

TABLE 2 Comparison of r_{max} models for (a) resting metabolic rate (RMR), (b) maximum metabolic rate (MMR) and (c) absolute aerobic scope (AS; MMR − RMR).

r_{max} models		p_{loo}	Looic	$elpd_{loo}$	se_elpd_{loo}	$elpd_{diff}$	Weight
	(a) RMR ~ (*n* fish species = 82)						
RMR_rmax	body mass + temperature + r_{max} + lifestyle	19.7	168.3	−84.2	13.3	−1.6	0.006
RMR_amat	**body mass + temperature + age at maturity + lifestyle**	**18.0**	**165.1**	**−82.6**	**12.9**	**0.0**	**0.994**
	(b) MMR ~ (n fish species = 49)						
MMR_null	body mass + temperature + lifestyle(null model)	30.7	46.4	−23.2	3.9	−4.8	0.206
MMR_rmax	**body mass + temperature + r_{max} + lifestyle**	**21.7**	**36.7**	**−18.4**	**5.3**	**0.0**	**0.794**
	(c) AS ~ (n fish species = 45)						
AS_null	body mass + temperature + lifestyle (null model)	17.8	77.0	−38.5	7.1	−6.2	0.000
AS_amat	body mass + temperature + age at maturity + lifestyle	12.4	75.3	−37.6	3.9	−5.4	0.000
AS_rmax	**body mass + temperature + r_{max} + lifestyle**	**14.3**	**64.5**	**−32.3**	**6.1**	**0.0**	**1.000**

Note: Values reported are the same as in Table 1. The model with the lowest *looic* has the most support and is emboldened and any model(s) within 2 looic of the top model is highlighted in grey. Abbreviations are the same as in Table 1.

[Correction added on 19 January 2024, after first online publication: The variable(temperature) was included in MMR_rmax equation in this version.]

with the most support for each metabolic rate type from the previous question.

2.3.3 | Is maximum metabolic rate (and aerobic scope) more strongly related to r_{max} compared to resting metabolic rate?

To assess which type of metabolic rate, RMR, MMR, or AS, more strongly related to life histories and r_{max} across fishes, we again compared whether r_{max} or its composite life history traits better explained variation in the different metabolic rate types as in the previous question.

3 | RESULTS

We compiled population-specific metabolic rate and life history data required for the calculation of r_{max} for 84 marine fish species (37 sharks and 47 teleosts). r_{max} ranges from 0.04 to 0.57 $year^{-1}$

in sharks (in the Greenland Shark, *Somniosus microcephalus*, and the Nursehound, *Scyliorhinus stellaris*, respectively) and 0.04–2.25 $year^{-1}$ in teleosts (in the Bigeye Tuna, *Thunnus obesus*, and the Lesser Sandeel, *Ammodytes tobianus*, respectively). Typically, the r_{max} of sharks is less than half that of teleosts (median for sharks = 0.29 $year^{-1}$ ±0.03 [standard error of the median]; teleosts = 0.61 $year^{-1}$ ±0.07). Although there are inevitable differences in the methods by which r_{max} is calculated for sharks and teleosts (highlighted in the Methods S1), the lower r_{max} in sharks relative to teleosts may be due to their later age-at-maturity (median for sharks = 7.5 years ±0.73; teleosts = 2.9 years ±0.19), greater maximum age (median for sharks = 20 years ±1.80; teleosts = 17 years ±1.73), and lower reproductive output (median for sharks = 3 daughters ±0.46; teleosts = 18.7 daughters ±3.74).

3.1 | Do fishes with lower metabolic rates have slower life histories?

Overall, metabolic rates are better explained by time-related traits compared to reproductive output, where species with lower metabolic rates are relatively later-maturing and longer-lived (Figure 1). For RMR, the model with age-at-maturity ranks highest (*looic* = 152.0, Table 1a, Figure 1a), further evidenced by a negative slope of −0.25 (95% BCI: −0.47 to −0.02, 100% of the posterior distribution <0; Table S1, Figure 2a), after accounting for measurement body mass, measurement temperature, ecological lifestyle, and phylogenetic relatedness. For MMR, no model with a single life history trait explains more variation than the null model (Table 1b). Although it is worth noting the considerable (negative) effect size

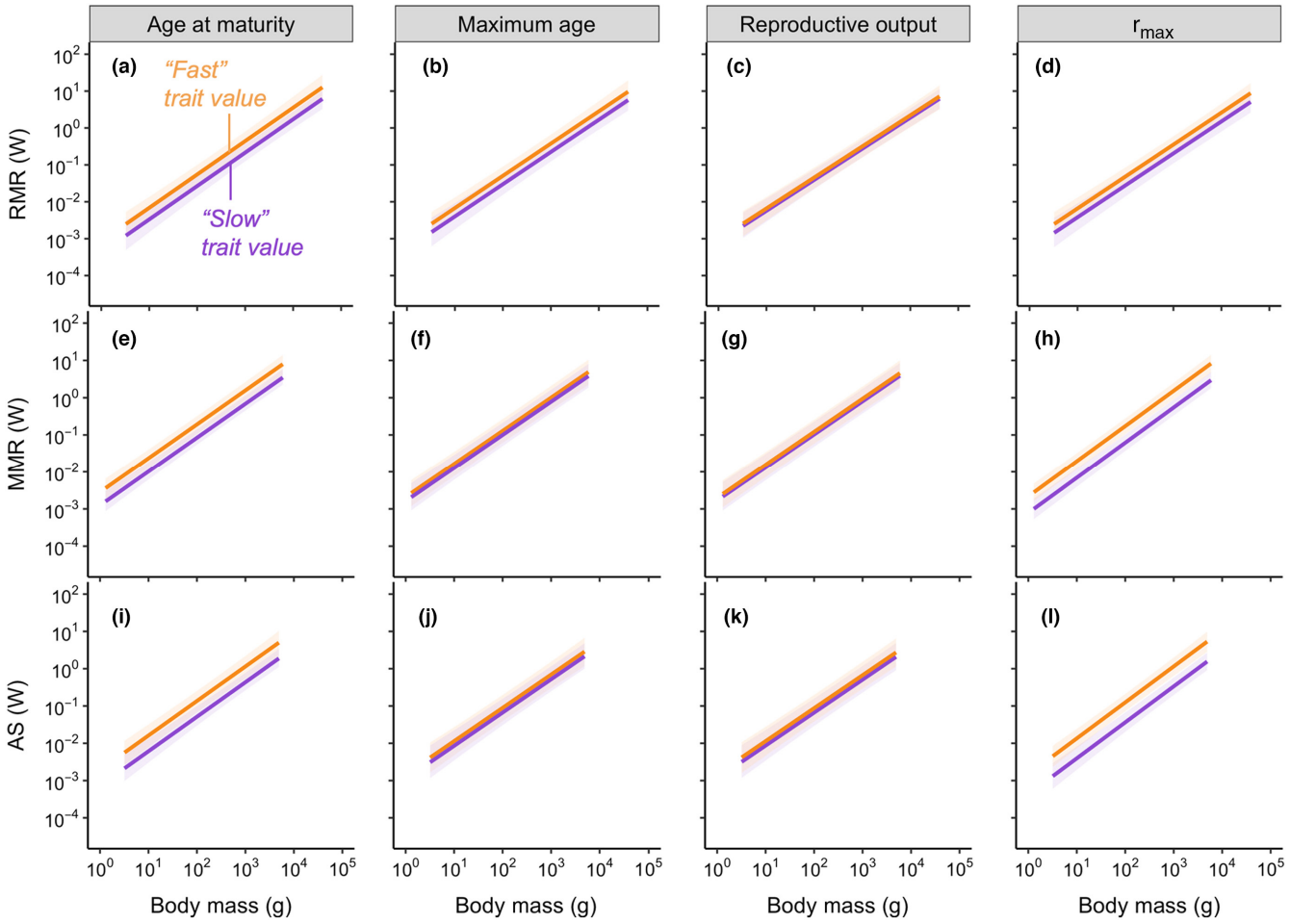

FIGURE 1 Time-related traits are overall better related to metabolic rates compared to reproductive output. Relationships between resting metabolic rate 'RMR' ($N = 82$), maximum metabolic rate 'MMR' ($N = 49$), or aerobic scope 'AS' ($N = 45$) and any single one of the component life history traits of r_{max} – age-at-maturity (a, e, i), maximum age (b, f, j), or reproductive output (c, g, k) – or with r_{max} itself (d, h, l). The purple and orange fitted regression lines in all panels are the estimated metabolic rate (in Watts) scaling with body mass (in grams), fit to relatively high (95th percentile) or relatively low (5th percentile) values of the life history trait in the dataset, characteristic of either a faster or slower life history. Models fit to 'fast' values of the trait are shown in orange (e.g. low age-at-maturity, low maximum age, high reproductive output, high r_{max}), while lines fit to 'slow' trait values are in purple (e.g., high age-at-maturity, high maximum age, low reproductive output, low r_{max}). All models also accounted for the effects of temperature, ecological lifestyle, and evolutionary history. r_{max} explained the most variation in MMR and AS, while the model with age-at-maturity is preferred in the case of RMR (see Tables 1 and 2, S1–S3). Metabolic rates and all covariates were natural log transformed, except for measurement temperature which was taken as the inverse temperature (see 'Section 2'). All covariates were standardised.

of age-at-maturity on MMR (mean slope = −0.32, 95% BCI: −0.52 to −0.10, 100% of the posterior distribution <0; Table S1, Figures 1e and 2a), the inclusion of this trait appears to reduce the amount of variation explained by temperature and is less parsimonious than the null model (Table 1b). Similarly, AS scales with age-at-maturity with a negative slope of −0.38 (95% BCI: −0.63 to −0.10, 100% of the posterior distribution <0; Table S1, Figures 1i and 2a). Although the AS model with age-at-maturity ranks higher (*looic* = 75.3) than the null model (*looic* = 77.0), the null model is the more parsimonious of the two (Table 1c).

3.2 | Do fishes with lower metabolic rates have lower r_{max}?

Species with lower maximum metabolic rates (MMR) and narrower aerobic scopes (AS) also have slower population growth rates (lower r_{max} values) after accounting for measurement body mass, measurement temperature, ecological lifestyle, and phylogenetic relatedness (Figures 1d,h,l and 2b). For example, the benthopelagic Pacific Spiny Dogfish, *Squalus suckleyi*, has relatively lower r_{max} and MMR than the similarly-sized pelagic Skipjack Tuna, *Katsuwonus pelamis*, even after accounting for differences in measurement body mass, measurement temperature, and ecological lifestyle (Figure 3). Similarly, at the smaller end of the body size range, the r_{max} and MMR of the benthic Epaulette Shark, *Hemiscyllium ocellatum*, is lower than that of the similarly-sized pelagic Peruvian Anchoveta, *Engraulis ringens*, after accounting for the effects of measurement body mass, measurement temperature, and ecological lifestyle (Figure 3). Overall, the model with measurement body mass, measurement temperature, and r_{max} is the highest-ranking model for both MMR and AS (Table 2b,c, Figure 1h,l). Specifically, the MMR model with r_{max} has significantly more support (*looic* = 36.7) than the null model (*looic* = 46.4; Table 2b), evidenced by a positive slope of 0.43 (95% BCI: 0.26–0.60, 100% of the posterior distribution >0; Table S1, Figure 2b). Similarly, the AS model including r_{max} has more overall support (*looic* = 64.5) than the models without (*looic* = 77.0 and 75.3 for the null and age-at-maturity models, respectively; Table 2c), where AS increases with r_{max} exhibiting a positive slope of 0.51 (95% BCI: 0.28 to 0.73, 100% of the posterior distribution >0; Table S1, Figure 2b). For RMR, there is considerable support for a positive relationship with r_{max}, as 96% of the posterior distribution is greater than zero (mean slope = 0.16, 95% BCI: −0.02 to 0.33; Table S1, Figure 2b). However, the model with age-at-maturity has slightly more support (*looic* = 165.1) than the model with r_{max} (*looic* = 168.3; Table 2a).

3.3 | Is maximum metabolic rate (and aerobic scope) more strongly related to r_{max} compared to resting metabolic rate?

Both MMR and AS are better explained by r_{max} compared to its composite traits (Table 2). This is in contrast to RMR, for which age-at-maturity is the life history trait that best explains variation in this metabolic rate type.

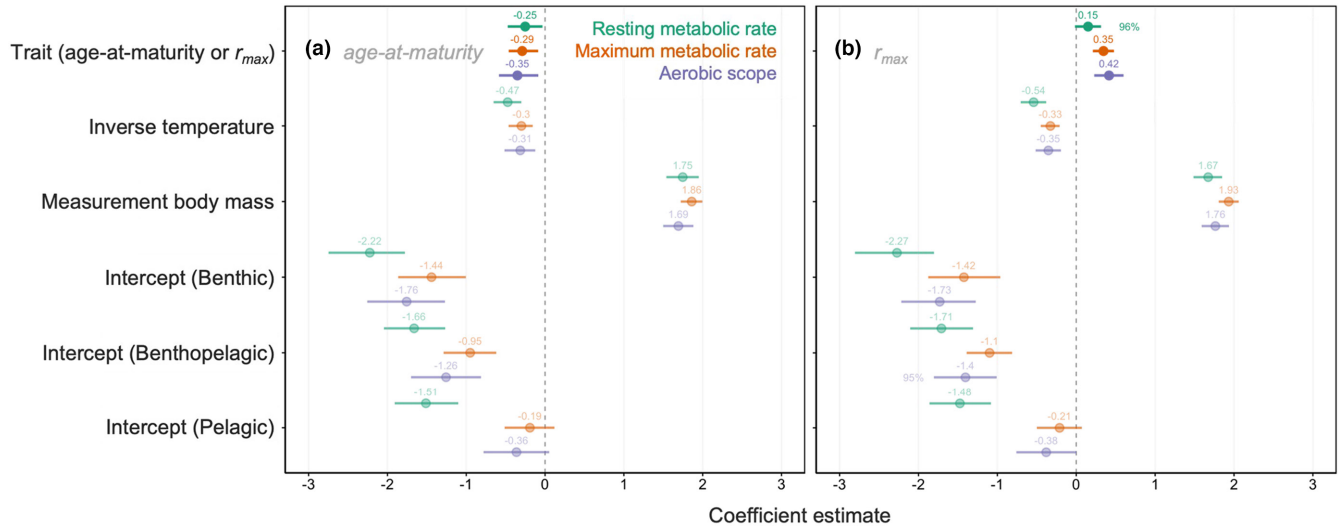

FIGURE 2 Age-at-maturity and r_{max} are related to metabolic rate across marine fishes. Coefficients plot of the effects of age-at-maturity or r_{max}, measurement body mass, measurement temperature, and ecological lifestyle (with respective intercepts for 'Benthic', 'Benthopelagic', and 'Pelagic' species) on resting metabolic rate 'RMR' (in green, $N = 82$), maximum metabolic rate 'MMR' (in orange, $N = 49$), and aerobic scope 'AS' (in purple, $N = 45$). For inverse temperature, a steeper (more negative) effect size indicates a more strongly positive relationship between temperature and metabolic rate. The intercepts correspond to the metabolic rates of 'Benthic', 'Benthopelagic', or 'Pelagic' species at the mean body mass, temperature, and the time-related trait (either age-at-maturity or r_{max}), where more negative value indicates a lower metabolic rate level. Metabolic rate and all covariates were natural log-transformed, except for measurement temperature, which was taken as the inverse temperature. All covariates are standardised (centered and scaled) to allow for comparisons amongst standard effect sizes.

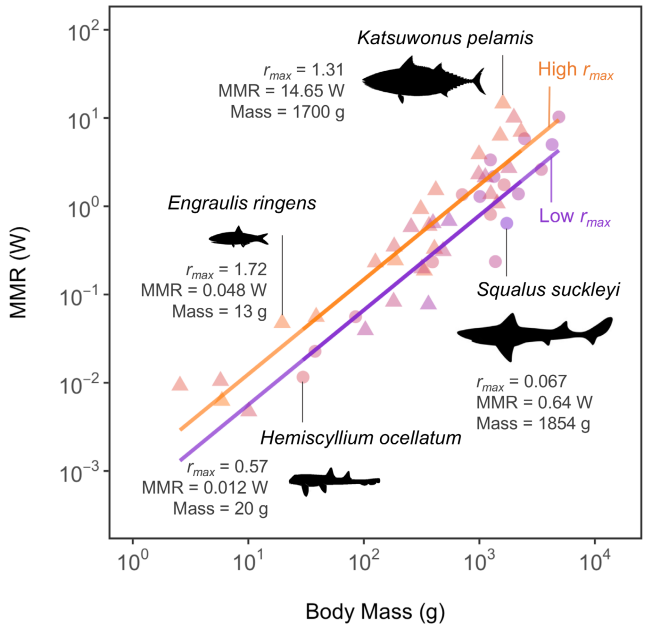

FIGURE 3 Species with higher r_{max} have higher maximum metabolic rates for their measurement body size and temperature. Mean whole-organism maximum metabolic rate (Watts) plotted against mean measurement body mass (grams) for 49 marine fish species. Triangles symbolize teleost fishes, while circles symbolize sharks. Overall, teleosts and sharks had similar metabolic rates for a given body size and temperature (see 'Section 2.3'). Points are coloured by the value of r_{max}, where orange indicates species with higher values of r_{max} and purple indicates species with lower values of r_{max}. The relationship between MMR and r_{max} is not fully apparent when comparing the high–low MMR values (shown by their elevation along the y-axis) and high–low r_{max} values (shown by the colour of the data points). However, once the effects of temperature and ecological lifestyle on MMR are accounted for, we observed a clear (positive) relationship between MMR and r_{max}. Lines show the estimated maximum metabolic rate (controlling for the effect of mass, temperature, and evolutionary history) for species with relatively high (95th percentile, orange line) versus relatively low (5th percentile, purple line) values of r_{max}.

4 | DISCUSSION

Overall, we find that across fishes, species with slower life histories (with lower r_{max} and late age-at-maturity) had lower metabolic rates. Second, we find that the connection between life histories and metabolic rates is much stronger for maximum metabolic rate (and absolute aerobic scope). Specifically, maximum metabolic rate (MMR) and absolute aerobic scope (AS) are positively related to r_{max}, while resting metabolic rate (RMR) is less strongly (but positively) related to r_{max}. In addition to being strongly related to r_{max}, metabolic rates are negatively related to age-at-maturity. Next, we consider (1) why metabolic rates are better explained by time-related traits (age-at-maturity and, particularly, the integrative trait r_{max}) compared to reproductive output, (2) how metabolism and life histories are intertwined, and (3) the evolutionary convergence of sharks and teleosts along the fast-slow life history continuum.

4.1 | Why metabolic rates are better explained by time-related and integrative traits (age-at-maturity and r_{max}) compared to reproductive output

Vertebrate life histories have largely been reduced into three axes: body size allometry, fast-slow continuum, and reproductive allocation (Beukhof et al., 2019; Healy et al., 2019; Juan-Jordá et al., 2013). The body-size dimension of life histories and associated allometric patterns in metabolism are well understood and have profound consequences for individuals, populations, species, and ecosystems (Andersen et al., 2016; Brown et al., 2004; Jennings et al., 2008). Once size-related effects are controlled or accounted for, the fast-slow continuum is apparent (Bielby et al., 2007; Healy et al., 2019; Juan-Jordá et al., 2013). Recently, the fast-slow continuum of tunas and their relatives was revealed by isolating the size-related effects using Principal Components Analysis to reveal a second axis of life history variation characterised by time-related traits, such as age-at-maturity and maximum age, as well as time-dependent biological rates, notably somatic growth rate (von Bertalanffy K year^{-1}) and instantaneous natural mortality rate (M year^{-1}) (Juan-Jordá et al., 2013). Given that r_{max}, like somatic growth and mortality, is a rate with units year^{-1}, the expectation is that this is the leading measure of the speed of life and determines a species position along the fast-slow continuum. Our findings are consistent with the expectation that species with slower life histories (e.g., later maturity, longer lifespan, slower population growth) have slower metabolic rates (Auer et al., 2018; Pettersen et al., 2016; Wong et al., 2021). Specifically, once the measurement body mass and measurement temperature of experimental subjects are accounted for, their metabolic rates are more closely related to time-related traits (r_{max} and age-at-maturity) than reproductive traits (this study) and maximum size (Wong et al., 2021). Indeed, metabolic rate is itself viewed as the most fundamental biological rate in ecology and is often described as the 'pace of life' or 'speed of life' (Auer et al., 2018; Brown et al., 2004, 2022). Next, we consider the integrative nature of r_{max} and its relationship to three types of metabolic rate.

Recent work has identified integrative traits (i.e., traits that are a composite of one or more life history traits which lie on either side of a trade-off) as being most representative of the life history continuum, and hence, more strongly related to metabolic rate (Pettersen et al., 2016). Metabolism is an emergent property and reflects the sum of anabolic and catabolic reactions underlying the biological processes which make up a life history (Uyeda et al., 2017). Metabolic rates and life histories evolve in parallel under selective pressures from environmental and ecological factors such as predation risk, resource supply, and environmental variability (Auer et al., 2018). As such factors may place stronger selection on some traits than others, integrative traits may better capture the range of the selective influences acting synergistically on species. Consequently, the relationship between metabolism and integrative life history traits may produce a stronger evolutionary signal that can be more easily detected in interspecific analyses (Arnold et al., 2021; Pettersen et al., 2016; Wong et al., 2021). In addition

to being a time-related trait, r_{max} is an integrative trait that incorporates the life history trade-off between survival and the timing of reproduction (age-at-maturity and maximum age) (Hutchings, 2021; Kindsvater et al., 2018; Stearns, 1992). Thus, it is unsurprising that metabolic rate is more strongly related to r_{max} than its component life history traits (Arnold et al., 2021; Juan-Jordá et al., 2013; Pettersen et al., 2016). We found this to be especially true for MMR and AS but not for RMR, which is slightly better related to age-at-maturity.

Our findings suggest that MMR and AS are more strongly related to r_{max} than RMR across fishes (Table 2, Figure 1), a pattern that has also been observed in rodents (Clavijo-Baque & Bozinovic, 2012). The evolutionary advantages of an elevated RMR are less apparent than increases in MMR and, consequently, AS (Clark et al., 2013; Eliason et al., 2011; Pörtner, 2012). Indeed, selection upon daily energy expenditure will increase MMR and may 'pull-up' RMR, while broadening AS (Auer et al., 2017; Killen et al., 2016). For example, we found that species with higher MMR (such as pelagic species) also had wider AS, despite the heightened maintenance costs (RMR) required to achieve such high MMR. Our results suggest that macroecological studies of metabolic rate and population dynamics would greatly benefit from the incorporation of MMR and AS (in addition to RMR) as these data become more available.

4.2 | The physiology/life history nexus of fishes: How metabolic rates and life histories are intertwined

The bigger question is how metabolism and life history are intertwined. Insights into this cross-species comparative relationship between metabolic rate and the fast–slow life history continuum (Figure 3) can be derived from common-garden experiments, the evolutionary effects of fishing, and optimality modeling (e.g., Auer et al., 2017; Waples & Audzijonyte, 2016; White et al., 2022). A unique selection experiment on Trinidadian Guppy (*Poecilla reticulata*), a classic model of evolutionary change in the wild, has previously revealed how the pattern of mortality shapes the fast-slow continuum of life histories (Reznick, 1990; Reznick et al., 1996). Guppies in 'high predation' streams are exposed to a cichlid (*Crenicichla alta*), which predates larger guppies leading to faster growth, earlier maturation, and reproductive output (more, smaller offspring) than populations in 'low predation' streams populated with Killifish (*Rivulus harti*), which consume only the smallest-sized guppies (Reznick, 1990; Reznick et al., 1996). Hence, guppy populations have a faster pace of life when adults are subjected to higher predation than guppies subjected to lower rates of predation, primarily on smaller size classes.

This pattern of mortality has also been shown to drive metabolism, such that populations with faster life histories have higher standard metabolic rates than 'low predation' populations with slower life histories (Auer et al., 2018). This connection between metabolic rate and pace of life is apparent across streams with different predators but also in reciprocal transplant experiments. Shifting individuals from an ancestral high predation stream to a low predation stream results not only in slower life history but also a concomitant reduction in metabolic rate (Auer et al., 2018). Hence, metabolism and the pace of life history are inextricably intertwined, such that high predation drives earlier maturation, presumably through the faster growth and greater reproductive allocation made possible only by a faster metabolic rate (Auer et al., 2018; White et al., 2022). Selection for early maturation ensures reproduction prior to an individual reaching a size vulnerable to predation. This requires fast growth, considering the amount of resources allocated to reproduction is size dependent in fishes (Auer et al., 2018; Barneche et al., 2018).

These common-garden experiments on guppy life history evolution are consistent with large-scale natural experiments of the evolutionary effects of fishing on fish life histories and optimality theory (Parker & Smith, 1990). The additional fishing mortality imposed on the larger, older size classes has led to reductions in the age-at-maturity across a range of commercially exploited fishes and is particularly apparent in those with long time series such as Atlantic Cod (*Gadus morhua*) and Pacific salmon (*Onchyrhynchus* spp.) (Hard et al., 2008; Kuparinen & Merilä, 2007; Olsen et al., 2008).

Taken together with recent compelling evidence for the *age-specific mortality hypothesis* of life histories (Healy et al., 2019), it appears that the distribution of mortality across the life cycle shapes the pattern of maturation, metabolic rate, and overall pace of life. Life histories have long been understood to be driven by mortality, and comparative patterns show the landscape of life histories can be partitioned by patterns of mortality (i.e., Type I-III survivorship curves), with profound consequences for maturation and patterns of reproductive allocation (Healy et al., 2019; Kindsvater et al., 2016; Winemiller & Rose, 1992). These patterns of reproductive investment and consequent juvenile and adult survival rates arise from the relative benefits depending on the survival of offspring of various sizes (resulting in the trade-off between offspring size and number). Further, the interconnection of metabolic rate and life histories has been generalised through optimization modeling, which predicts that metabolic level (the intercept or 'height' of metabolic allometry) is positively related to growth rate and annual reproductive output (White et al., 2022). Our comparative findings complement other lines of evidence of a fast-slow continuum in birds (Ricklefs & Wikelski, 2002), supporting a similar physiology/life history nexus across fishes.

4.3 | The evolutionary convergence of sharks and teleosts along the fast-slow life history continuum

Sharks and teleosts, particularly broadcast spawning teleosts, could not differ more in life histories, yet despite their differences we show they have converged upon a common fast–slow physiology/life history continuum. While there can be considerable overlap in patterns of growth, mortality, and ages of maturity and longevity across fishes, the greatest differences lie in their physiology and reproduction (Andersen, 2019; Speers-Roesch & Treberg, 2010).

Sharks are the oldest evolutionary radiation of vertebrates (Stein et al., 2018) and have distinct respiratory systems and energy metabolism compared to teleosts and other vertebrates. Sharks (and rays) possess distinct plate-like gills, befitting the translation of the name of their subclass, Elasmobranchii. Shark gills exhibit differences from those of teleosts, both in their gross morphology (teleost operculum vs. elasmobranch gill slits) and fine-scale anatomy (the arrangement of gill filaments on gill arches) that have functional consequences for oxygen uptake and may impose an upper limit on MMR (Wegner, 2011; Wegner et al., 2012). For example, shark gill filaments are backed by a plate-like 'septum' that increases the water resistance between the oxygen-absorbing lamellae, which are stacked upon the gill filaments. Thus, high-performance tunas, for a given size, have up to double the lamellar density and twice the gill surface area compared to the ecologically similar Shortfin Mako Shark (Wegner et al., 2012). It has been suggested that such limitations may not apply exclusively to high-performance fishes, as sharks generally have a narrower range of gill surface areas compared to teleosts (Bigman et al., 2018; Wegner, 2011). Thus, differences in metabolic rates (after body size has been considered) between sharks and teleosts may be related to differences in gill morphology. Gill surface area is upstream of – and related to – the emergent property of metabolic rate, and recent work has shown that respiratory surface area explains a surprising amount of variation in metabolic rate across vertebrates (Bigman et al., 2021; Killen et al., 2016).

Further more, sharks have profoundly different energy metabolism, resulting in part from their osmoregulation (Speers-Roesch & Treberg, 2010). Sharks have high concentrations of urea in their plasma to match the osmolality of seawater and, hence, are iso-osmotic, unlike teleosts which are hypo-osmotic. Sharks use amino acids, along with ketone bodies, as an oxidative fuel for energy metabolism, as well as a nitrogen donor for urea synthesis (Speers-Roesch & Treberg, 2010; Watanabe & Payne, 2023). By contrast, teleosts (and mammals) mobilize and metabolize fatty acids from adipose tissues. These differences in metabolic substrate are hypothesized to underlie differences in the temperature sensitivity of RMR between elasmobranchs and teleosts, with consequences for the diversity of elasmobranchs at higher latitudes (and, presumably, greater depths) (Watanabe & Payne, 2023).

The most obvious difference between teleosts and sharks, in terms of their life histories, lies along the third axis. Reproductive allocation in terms of offspring size and number is profoundly different between teleosts and sharks (Andersen, 2019; Goodwin et al., 2002). Broadcast spawning teleosts have numerous, similar-sized small eggs, each with relatively low likelihood of survival (Duarte & Alcaraz, 1989). Such a strategy is thought to be advantageous when primary production is high but patchy in space and time, as typified by the mosaic of zooplankton patches that larval fishes need to sustain them through development following yolk absorption (Winemiller & Rose, 1993). By contrast, sharks and rays (and chimaeras) either lay large, well-provisioned benthic eggs or give birth to live young, provisioning from very large ova or more direct forms of matrotrophy, such as placentotrophy (Goodwin et al., 2002; Mull, Pennell, et al., 2022; Wourms & Lombardi, 1992). Notwithstanding these profound differences in respiration, metabolism, and reproductive allocation, our results show no difference in the intercept of the allometric relationship of metabolic rate for sharks and teleosts (e.g., see Figure 3). This finding suggests that differences in life histories between sharks and teleosts may be driven primarily by body size, where both lineages are convergent upon a common fast-slow continuum at the nexus of physiology and life histories (Andersen, 2019; Wong et al., 2021).

Many papers written on chondrichthyans, particularly in relation to the risk of overfishing, begin by highlighting that sharks and rays have slow life histories characterised by slow growth, low reproductive capacity, and high sensitivity to overfishing. Our findings that teleosts and sharks are aligned and interwoven along a common physiology/life history continuum suggests that we should use comparative language that reflects this shared continuum of variation. Concomitantly, we should instead introduce papers with terminology such as, 'sharks and rays have slower life histories characterized by slower growth, lower reproductive output, and higher sensitivity to overfishing', to reflect that the differences between lineages are *relative* rather than *absolute*, and that there are sharks with fast life histories, such as Epaulette Shark, with higher r_{max} compared to many teleosts with very low r_{max} such as the Bigeye Tuna (0.04), which appears to have an r_{max} more like a Greenland Shark (0.04) (Kulka et al., 2020; VanderWright et al., 2021).

5 | CONCLUSION

To the best of our knowledge, this is the first extensive study of r_{max} and metabolic rate (RMR, MMR, and AS) across fishes. Here, we find that the integrative, time-related trait r_{max} explains variation in MMR and AS (and to a lesser extent, RMR) in addition to that explained by body mass and temperature. Although we did not observe a difference in the intercept of the allometric relationship of metabolic rate for sharks and teleosts, additional variation in metabolic rates across species may be explained by environmental oxygen availability, oxygen uptake capacity across the gills, and activity levels (Bigman et al., 2021, 2023a, 2023b; Rubalcaba et al., 2020), and by further exploration of physiological differences in energy metabolism (Speers-Roesch & Treberg, 2010; Watanabe & Payne, 2023). Our analysis supports the idea of a metabolic pace-setting of life history and r_{max}, which is the first step towards understanding the physiological basis of population dynamics and, by extension, recovery potential. Future work, combined with the evolutionary (interspecific) relationship between metabolic rate and r_{max} examined in this paper may provide insight as to how population dynamics are linked to the morphological, ecological, and environmental features shaping metabolic rates. This work contributes to our understanding of the evolution of a diversity of fish life history strategies across a common fast–slow physiology/life history continuum and may ultimately help

us predict the population-level consequences of overfishing in a changing climate.

AUTHOR CONTRIBUTIONS

SG, JSB, and NKD contributed to the project's conception, design, and analysis. SG and SW collected the data. SG performed all analyses and data visualizations. All authors contributed to the interpretation of the results. SG, JSB, and NKD drafted the manuscript and supplementary information with input from all authors. NKD supervised the project.

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CONFLICT OF INTEREST STATEMENT

We have no competing interests.

DATA AVAILABILITY STATEMENT

All data and code necessary to reproduce the results in this study are archived on Github (https://github.com/sarahgravel/Rmax-MR-ms). We place no restrictions on data or code availability.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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