Body mass, temperature, and depth shape the maximum intrinsic rate of population increase in sharks and rays

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Abstract

An important challenge in ecology is to understand variation in species' maximum intrinsic rate of population increase, r_{max} , not least because r_{max} underpins our understanding of the limits of fishing, recovery potential, and ultimately extinction risk. Across many vertebrates, terrestrial and aquatic, body mass and environmental temperature across important correlates r_{max} across species. In sharks and rays, specifically, r_{max} is known to be lower in larger species, but also in deep-sea ones. We use an information-theoretic approach that accounts for phylogenetic relatedness to evaluate the relative importance of body mass, temperature and depth on r_{max} . We show that both temperature and depth have separate effects on shark and ray r_{max} estimates, such that species living in deeper waters have lower r_{max} . Furthermore, temperature also correlates with changes in the mass scaling coefficient, suggesting that as body size increases, decreases in r_{max} are much steeper for species in warmer waters. These findings suggest that there (as-yet understood) depth-related processes that limit the maximum rate at which populations can grow in deep sea sharks and rays. While the deep ocean is associated with colder temperatures, other factors that are independent of temperature, such as food availability and physiological constraints, may influence the low r_{max} observed in deep sea sharks and rays. Our study lays the foundation for predicting the intrinsic limit of fishing, recovery potential, and extinction risk species based on easily accessible environmental information such as temperature and depth, particularly for data-poor species.

Key-words: Demography, elasmobranch, chimaera, global change, life-history theory, mortality, population growth rate

Introduction

Ecologists often have to inform policy decisions with knowledge and experience rather than data. A classic and ongoing challenge is that of making a decision about whether a species overfished or not. Overexploitation is the leading cause of extinction risk in the ocean and a major cause also on land (Maxwell *et al.* 2016; Reynolds *et al.* 2005). A large body of work shows that maximum size, either length or weight is a simple heuristic that can guide our thinking about extinction risk. Setting aside the desirability or catchability of different sized fishes, broadly speaking, the larger-bodied species have slower life histories and tend to decline faster when fished (Jennings *et al.* 1998; Reynolds *et al.* 2005). Body size data are among the most widely available traits but it is only one dimension of the life histories of indeterminate-growing species (Chichorro *et al.* 2019). The second dimension of life histories tends to be comprised of time-related “speed of life” traits, such as age at maturity, maximum age, and von Bertalanffy growth rates (Juan-Jordá *et al.* 2013). In the few cases where high quality data can be found, it is increasingly clear that speed of life traits are the better correlate of population dynamics and extinction risk (Anderson *et al.* 2011; Juan-Jordá *et al.* 2015).

The maximum intrinsic rate of population increase (of species at small population sizes) r_{max} is the integration of speed of life traits and “is perhaps the most fundamental parameter in population biology” (Myers & Worm 2005). Estimates of r_{max} are commonly used limit reference points as they are equivalent to the fishing mortality that will drive a species to extinction as well as defining the maximum rate of population recovery (Hutchings *et al.* 2012; Dulvy *et al.* 2004; Myers *et al.* 1997). Ever larger databases of life history traits make it easier to calculate r_{max} , providing an opportunity to seek ecological explanations for variation in maximum intrinsic rate of population increase. Indeed, Southwood (1977) viewed habitat quality as the template shaping population growth rates. In the ocean, thermal habitat quality changes profoundly with temperature, such that tropical species have faster life histories and dynamics (Munch & Salinas 2009; Juan-Jordá *et al.* 2013) but attain smaller sizes (Cheung *et al.* 2013; Fisher *et al.* 2010; Jennings *et al.* 2008). From a metabolic perspective alone, at high temperature, fishes are squeezed between low oxygen solubility and high oxygen demand due to temperature-forced metabolic rates (Pörtner *et al.* 2017; Rubalcaba *et al.* 2020; Pauly 2021). Furthermore, within a given thermal habitat, aquatic species exhibit a range of oxygen demands as a result of differing lifestyles, activity patterns and trophic levels, which may have consequences for life histories and population dynamics (Killen *et al.* 2010; 2016; Wong *et al.* 2020). Similar patterns have been observed on land, where allometric variation in mammal production rates (analogous to r_{max}) can also be shaped by differences in lifestyle and trophic level (Sibly & Brown 2007, note that temperature is not an axis of variation in endotherms).

The sharks, rays, and chimaeras (class Chondrichthyes, hereafter referred to as “sharks and rays”) are an ideal taxon for studying the aquatic allometry of demographic rates as they encompass a broad range of sizes and occur across a wide range of temperatures and habitats. The lack of a pelagic larval stage in sharks and rays allows for a more straightforward estimation of population productivity with limited life-

history data than their bony counterparts (Myers & Mertz 1998; Pardo *et al.* 2016). Maximum intrinsic rate or population increase r_{max} among sharks and rays is known to decrease with increasing size (Hutchings *et al.* 2012; Dulvy *et al.* 2014b) and depths (García *et al.* 2008; Simpfendorfer & Kyne 2009). However, previous work has only considered categorical habitat classifications, and there is some evidence that the relationship between r_{max} and body size breaks down in the deep sea as even small deep-water sharks and rays have very low r_{max} (Forrest & Walters 2009; Rigby & Simpfendorfer 2015), suggesting there are stronger constraints on the mass scaling of r_{max} occurring at greater depths than those imposed by body mass and temperature. Thus, depth provides an interesting environmental gradient of energy availability (among other things) to explore interspecific variation in r_{max} .

Here, we examine the separate roles of temperature and depth on the maximum intrinsic rate of population increase and mass scaling relationship among sharks and rays by using estimates of temperature-at-depth derived from species distributions maps (thermal habitat templates) with an information-theoretic approach, while accounting for phylogenetic non-independence.

Methods

Data

To determine the role of temperature, depth, and the scaling of body mass on maximum intrinsic rate of population increase, r_{max} of marine sharks and rays, we gathered three types of data: life-history parameters (maximum weight and r_{max}), species-specific environmental traits (median depth and temperature of occurrence), and phylogenetic trees to account for evolutionary relationships in the model-fitting process. Maximum reported body mass (in grams) was obtained from FishBase (Froese & Pauly 2016) using the *rfishbase* package (Boettiger *et al.* 2012). We used maximum weight instead of weight at maturity as it is more readily available in the literature, and at a first approximation they are proportional to each other. When body mass data were unavailable, maximum length data were converted to body mass using species-specific length-to-weight conversions also sourced from FishBase. Data for r_{max} were obtained from a modified Euler-Lotka model following Pardo *et al.* (2016).

Median depth estimates for each species as reported from Dulvy *et al.* (2014a), and temperature-at-depth were derived from species distributions maps. These maps were obtained from AquaMaps which is an online resource of global species distribution models for over 25,000 aquatic species (Kaschner *et al.* 2015).

The core distributions for each species (i.e. where probability of occurrence ≥ 0.9) were overlaid with the International Pacific Research Center's interpolated dataset of gridded mean annual ocean temperatures across 27 depth levels (0-2000 m below sea level), which is based on measurements from the

Argo Project (see http://apdrc.soest.hawaii.edu/projects/Argo/data/statistics/On_standard_levels/Ensemble_mean/1x1/m00/index.html for data and more information). This temperature interpolation covers most of the world's oceans, but has incomplete coverage of some shallow coastal areas, such as the Indo-Pacific Triangle and the southeast coast of South America.

To calculate a temperature that characterizes the thermal distribution of each species, we selected the depth level from the grid that was closest to the species' median depth, and from that grid extracted all the temperature grid points that overlaid the species' core distribution. From this distribution of temperature values, we calculated the median and set as the temperature value for each species. For example, if a species' median depth was 130 m we used temperatures from the 150 m depth layer to estimate median annual temperature as 130 m is closer to 150 than 100 m. In species that are known to be mesotherms (e.g. family Lamnidae) we added a correction factor of 3.5 °C.

The phylogenetic trees were obtained from Stein *et al.* (Stein *et al.* 2018) and we followed their scientific nomenclature. Their analyses did not provide a single tree but a distribution of possible trees with the same topology but differing branch lengths. We ran our analyses by using 20 different trees sampled from their distribution. The results were almost identical regardless of which tree was used, and therefore we only report our findings when using only a single tree (see Table S1 in the Supplementary materials).

Metabolic scaling expectations

The availability of consistent estimates of environmental temperature derived from species distributions maps allow us to draw from metabolic scaling theory. Savage *et al.* (2004, see equation 8) showed that across multiple taxa, r_{max} is related with body mass and temperature,

$$r_{max} \propto i_0 M^\beta e^{-E/k_B T}, \quad (1)$$

where r_{max} is the maximum intrinsic rate of population increase (in year⁻¹), i_0 is a taxon-specific normalization constant, M is the adult body mass of a species (in grams), β is the scaling exponent, E is the activation energy, k_B is the Boltzmann constant (8.617×10^{-5} eV), and T is temperature (in Kelvin). The equation above can be simplified when transformed to log-space:

$$\log(r_{max}) \propto \log(i_0) + \beta * \log(M) + -E * 1/k_B T, \quad (2)$$

which is equivalent to a simple linear model

$$\log(r_{max}) = \beta_0 + \beta_1 * \log(M) + \beta_2 * 1/k_B T, \quad (3)$$

where the intercept β_0 is the log-transformed normalization constant, the coefficient β_1 is the mass scaling, and β_2 is the negative activation energy $-E$, which is the coefficient of inverse temperature $1/k_B T$. We do not use a taxon-specific normalization constant ($i_0 = \beta_0$) as we are using a phylogenetic covariance matrix instead of a taxonomic nested structure. Equation 3 is what would be expected from metabolic scaling theory, and is one of the multiple hypotheses we compare in this study.

What is the role of temperature and depth in the mass scaling relationship of r_{max} ?

We compared nine different models, each representing a different hypothesis of how r_{max} might vary with body mass, depth, and temperature, using an information-theoretic approach (Burnham & Anderson 2002). We scaled and centered the data for temperature and depth.

To assess whether the estimated median temperature for each species was indeed informative, we also included a model where r_{max} is explained only by variation in body mass. We compared all models using the corrected Akaike Information Criterion (AICc). If including a parameter improved a model's AICc value by less than 2, we considered that parameter to be uninformative (Arnold 2010).

[Table 1 about here.]

To account for non-independence among closely related species, we fitted phylogenetic linear models using the `pgls` function in the `caper` package (Orme *et al.* 2013), running on R version 3.3.2 (R Core Team 2016). The phylogenetic covariance matrix, which is contrasted with the residuals from each model, was adjusted using Pagel's λ . This allows for encompassing a wide range of covariance structures corresponding to different trait phylogenetic signal values under a Brownian mode of trait evolution, ranging from no signal at all (i.e. classic OLS; $\lambda = 0$) to Brownian motion ($\lambda = 1$) (Revell 2010).

We tested for collinearity by estimating variance-inflation factors (VIF) for all coefficients in the models explored using the `car` package (Fox & Weisberg 2011). None of the VIF values estimated were greater than 2 (except when interactions are included, which is expected). However, depth and temperature are positively correlated (Pearson's $r = 0.64$); although this correlation is lower than the threshold of $|r| > 0.7$, where collinearity severely distorts model estimation (Dormann *et al.* 2013), providing further evidence that our models are robust to collinearity.

Results

We collected temperature, body mass, depth, and r_{max} data for 63 chondrichthyan species including 40 sharks, 20 rays, and three chimaeras (Fig. 1).

[Figure 1 about here.]

The model with the greatest support included temperature and depth as well as an interaction term between body mass and temperature (Table 2). This model also explained the greatest amount of variation (adjusted $R^2 = 0.33$).

The model that included the same variables as the top-ranked model as well as an interaction term between body size and depth, received one third the support of the top-ranked model, but had an $\Delta AICc$ value greater than 2 without an increase in adjusted R^2 . Thus, we considered the interaction between body size and depth to be uninformative and the model was not considered further (Arnold 2010).

All three other models that had marginal support ($5 \leq \Delta AICc \leq 7$) also included temperature: one was similar to the top-ranked model, but lacked the effect of depth; one included a main effect of temperature, while the effect of body mass varied with depth; and the other includes all the main effects with no interactions (Table 2).

The effect size of body mass in all models is around -0.3 (see shaded areas in Fig. 2, Table 3), which overlaps to the expectation of $-1/4$ predicted by metabolic scaling theory (Brown *et al.* 2004). Intercepts also consistently overlap zero for all models, albeit with high uncertainty (Table 3). The inclusion of only an additive effect of temperature to the relationship between r_{max} and body mass was uninformative ($\Delta AICc$ 10 $\rightarrow$ 9.8), but inclusion of the interaction between body mass and temperature resulted in an improved model fit ($\Delta AICc = 5.0$; Table 2). In contrast, the addition of additive depth alone or an interaction with depth did not improve the relationship between r_{max} and mass ($\Delta AICc$ 11 $\rightarrow$ 9.2); however, the addition of depth to the model with an interaction between body mass and temperature improved this model's support twelvefold (weight of 0.63 vs. 0.052, Table 2). This effect of depth is consistently negative across the top-ranked models, indicating that r_{max} decreases with increasing depth.

The interaction between body mass and temperature was always positive (Table 3) indicating that the mass-scaling coefficient becomes shallower (i.e. slope increasing from a negative value towards zero) with decreasing temperatures. In the top-ranked model, this change in slope with body mass results in the effect of temperature being positive for species up to ~ 3 kg maximum weight, however for larger species it switches directions and the relationship between temperature on r_{max} becomes increasingly negative with increasing maximum weight (Fig. 3b). Given that this best model did not have any interaction terms including depth, predicted r_{max} values decrease with increasing depth (Fig. 3a). Therefore, this model only resulted in plausible temperature effect sizes, based on the expectation from metabolic scaling theory where this coefficient of the inverse of temperature should be negative ($-E$ in eq. 2), for species less than 3 kg in size. However, this interpretation of the coefficient direction needs to be taken with caution given that including interactions might be more difficult to translate into a mechanistic understanding of biological rates.

There was a strong phylogenetic signal from the residuals of r_{max} in all ten models examined. Estimated

λ ranged between 0.78 and 0.87 with the best model having the lowest λ value (Table 3).

[Table 2 about here.]

[Figure 2 about here.]

[Table 3 about here.]

[Figure 3 about here.]

Discussion

We generally find that maximum intrinsic rate of population increase is lower in larger bodied species. However, we also found two intriguing depth and temperature related effects. First, we found that r_{max} decreases at greater depths across marine sharks and rays. Further, the relationship between mass and r_{max} is temperature-dependent, such that r_{max} decreases with increasing body mass more steeply at higher temperatures. We also found that the scaling of body mass and r_{max} changes across a temperature gradient, which is in line with the observation by Rigby & Simpfendorfer (2015) and suggests the absence of a relationship between size and r_{max} in deep-sea sharks and rays is perhaps due to the low temperatures found in the deep sea rather than depth itself. In other words, it is temperature rather than depth that “flattens” the mass-scaling of r_{max} in sharks and rays, and species that live in colder environments have a shallower mass-scaling relationship with r_{max} than those that live in warmer waters. Overall, the interaction between the effect of body mass and temperature likely drives the non-linear scaling of shark and ray r_{max} . Our findings imply that body size might not be a good indicator of r_{max} among cold-water shark and ray species, which is an important consideration for the conservation and management of these often data-poor species.

There is increasing evidence that the allometries of biological rates can be non-linear, which can stem from multiple separate mechanisms acting concurrently (Kolokotronis *et al.* 2010; Glazier 2005; 2015). Thus, differences in temperature could potentially affect scaling relationships via separate mechanisms (Ohlberger *et al.* 2012; Bruno *et al.* 2015). The differing effects of physiological, energetic, and geometric processes on biological rates across allometries could explain the non-linearity of the relationship observed in this study and are discussed below.

As dissolved oxygen concentrations decrease as water temperature increases (Pauly 2010), the largest bodied species and individuals may become more oxygen limited, which potentially explains why r_{max} decreases more steeply with increasing body size in warmer water species than colder water ones (Rubalcaba *et al.* 2020). One mechanism that might plausibly account for this is the gill-oxygen limitation theory (GOLT, Pauly & Cheung 2018; Pauly 2021). According to this theory, gill surface area imposes a stronger limitation on oxygen uptake as organisms grow larger, which results in less energy allocated to growth

and reproduction under warmer conditions (i.e. waters with less dissolved oxygen). While physiologists dispute the directionality of this mechanism (e.g. Lefevre *et al.* 2018; Seibel & Deutsch 2020) it is increasingly clear that individuals with ablated gills have lower metabolic rate and maximal metabolic rate may be depressed in larger individuals in warmer (Pauly 2010; Rubalcaba *et al.* 2020). Assuming that (gill) oxygen limitation is stronger in larger species than smaller ones, oxygen uptake might not be limiting in smaller species where other factors might be shaping r_{max} . Thus, the positive effect of temperature on r_{max} in smaller species might be a direct result of increased speed of chemical and metabolic reactions as hypothesized by metabolic theory (Brown *et al.* 2004; Savage *et al.* 2004). In larger species, the positive effect of temperature on metabolic reactions could be completely overridden by the oxygen limitation that gills pose as organisms increase in volume (Pauly & Cheung 2018), resulting in a negative relationship between temperature and r_{max} . Nonetheless, some species might be behaviourally evading these temperature (and oxygen) constraints. For example, the Whale Shark (*Rhincodon typus*) is the largest extant fish and lives in warm waters throughout the world's oceans, yet it performs deep dives (>1000 m) into cold waters which are hypothesized to aid in thermoregulation to dissipate excess heat (Thums *et al.* 2012), and our finding leads us to speculate that they perhaps also access waters with higher oxygen concentrations. While the effect of oxygen concentrations across depth on r_{max} was not explored in this manuscript, it might further explain the low r_{max} estimates seen among deep sea species in line with the expectations from the GOLT and other general theories of oxygen limitation (Pörtner *et al.* 2017; Deutsch *et al.* 2020; Rubalcaba *et al.* 2020; Pauly 2021).

The existence of a depth dimension to r_{max} , albeit complex, is worth exploring further. Many potential mechanisms could drive the decrease in r_{max} among chondrichthyans with increasing depth, all of which relate to the amount of energy available for metabolic processes: temperature, light, and consequently primary production decrease below the photic zone (Gage & Tyler 1991; Jahnke 1996); metabolic capacity and requirements decrease with depth as dissolved oxygen and activity levels decrease (Childress *et al.* 1990; Seibel & Drazen 2007); animal biomass, and hence food availability, also decreases with increasing depth (Rex *et al.* 2006); even the unique physiology of sharks and rays can increase the energetic cost of living in the deep, and consequently reduce the energy available for production (Treberg & Speers-Roesch 2016). Comparative studies of metabolic rate in marine organisms suggest that the lower metabolic rate seen in deep-water (>1000 m) species is a result of the “visual-interactions hypothesis” (Childress *et al.* 1990; Seibel & Drazen 2007), rather than lower food availability or other factors. This hypothesis posits that deep-sea species have lower activity levels as they interact with predators and prey on much smaller spatial scales, or less frequently, than shallow water ones, as the distance at which predators and prey interact is reduced as light levels drop, resulting in lower basal metabolic rates and hence lower productivities (Drazen & Seibel 2007), and also shallower mass-scaling of metabolic rate in deeper waters (Rubalcaba *et al.* 2020). A decrease in r_{max} with increasing depth could also arise from the unique physiological challenges on chondrichthyans imposed by living in the deep, that limit their ability to use available energy for production. Treberg & Speers-Roesch (2016) hypothesized two separate physiological constraints limiting energy

availability in deep water chondrichthyans: the energetic cost of lipid accumulation for buoyancy, and nitrogen limitation due to their osmoregulatory strategy. These physiological limitations could be acting in concert with energetic limitations of low food availability to reduce even further the capability of deep-sea chondrichthyans to grow in size and produce offspring. The complex energetic gradients discussed above can potentially affect the productivity and population growth rates of species found at different depth, even after temperature is accounted for, and as such, depth can be thought of as an added axis of variation in the slow-fast life-history continuum (Sibly & Brown 2007).

The strong phylogenetic signal in the residuals of r_{max} suggests that other aspects of biology shape their maximum population growth rate, which are likely evolutionarily conserved traits. This likely stems, in part, from estimates of r_{max} being strongly influenced by reproductive output (Pardo *et al.* 2018), which is strongly conserved among closely related species (Dulvy & Reynolds 1997). This strong phylogenetic signal opens up the door for predictive modelling of r_{max} based on phylogenetic relationships.

While our study is a first attempt at understanding the relationship between r_{max} , size, and the environment, there is a considerable amount of unexplained variation in our models. Considering the caveats when interpreting the findings of this study might enable future studies to improve model fits. First, there is considerable amount of collinearity between depth and temperature (Pearson's $r = 0.64$). This is somewhat unavoidable as warmer waters are almost chiefly found in shallow depths, while deep waters are consistently cold. While the diagnostic tests we performed suggest that our results are robust to this collinearity, it is important to bear this in mind, particularly if our framework is to be adapted in the future for predictive purposes. Second, our study is limited by the choice of hypotheses being examined. While we compared nine different hypotheses using an information theoretic approach, it is possible that other hypotheses not considered in this study are better at explaining the patterns in the data. Including other environmental variables mentioned above, such as dissolved oxygen or net primary production, could result in models that are better supported in the data than the models compared in this study. Concomitantly, we only explored simple interactions from a linear modelling framework; other non-linear frameworks for modelling might be better supported by the data. Third, we used maximum weight as our metric of mass as it is the most readily available trait among data-poor sharks and rays, however it is also among the most variable and our choice of this life-history trait might contribute to the low R^2 of our models. Weight at maturity is a likely better parameter to use, albeit more difficult to estimate, as it is more precise than estimates of maximum weight, and also aligns better with expectations of metabolic scaling (Savage *et al.* 2004) and life-history theories (Charnov *et al.* 2007). Lastly, our method of accounting for mesothermy (i.e. incrementing environmental temperature by a fixed amount for all mesotherms) might not be the most adequate; there are likely large interspecific differences in the degree of mesothermy, and also how the temperature differential varies across a range of environmental temperatures.

Our study explored the relationships between body mass, temperature, and depth with the maximum intrinsic rate of increase of sharks and rays and paves the way for further investigation of the mechanisms be-

hind these relationships. For example, investigating how the mass-scaling relationship in chondrichthyans from solely shallow environments varies with temperature might confirm that the apparent “flattening” of the mass scaling relationship of productivity at depth was indeed due to temperature. Taking into account additional spatial datasets that provide information on nutrient availability in the deep sea, such as sedimentation rates or organic carbon burial rates (Jahnke 1996), could provide a better understanding of the degree to which food availability limits productivity among deep-sea sharks and rays. Similarly, incorporating data on dissolved oxygen content would elucidate whether the observed temperature effects, particularly among medium to large-sized species, are a result of oxygen limitation. Alternatively, exploring in more detail whether the effect of depth on r_{max} levels off after a certain threshold (as it does for basal metabolic rate in pelagic fishes, supporting the visual-interactions hypothesis) or it is continuous would help elucidate the mechanism driving the observed relationship with depth. Identifying the mechanisms behind these observed relationships among body size, temperature, and depth will eventually provide a much clearer understanding of how the productivity, and therefore the vulnerability of species, varies across the world’s oceans.

Acknowledgements

We are grateful to Jennifer Bigman, Philina English, Sarah Gravel, Daniel Greenberg, Peter Kyne, Florent Mazel, Arne Mooers, and Elan Stopnitzky for their insightful comments on the manuscript and help with the figures. We acknowledge AquaMaps for making their data freely available and especially Kristin Kaschner for discussions on distribution model outputs. SAP & NKD were funded by Natural Sciences and Engineering Research Council, and NKD was also funded by the Canada Research Chairs Program.

Data accessibility

Data and analyses are available as a GitHub repository:
<http://www.github.com/sebpardo/shark-rmax-scaling>.

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Table 1: Models of correlates of maximum intrinsic rate of population increase (r_{max}) tested in our analysis and the hypotheses associated with each.

Model	Hypothesis
$\log(r_{max}) \sim \log(M)$	r_{max} only varies with body mass
$\log(r_{max}) \sim \log(M) + depth$	r_{max} varies with body mass and depth
$\log(r_{max}) \sim \log(M) + 1/k_B T$	r_{max} varies with body mass and temperature
$\log(r_{max}) \sim \log(M) + 1/k_B T + depth$	r_{max} varies with body mass, temperature, and depth
$\log(r_{max}) \sim \log(M) + 1/k_B T * depth$	r_{max} varies with body mass, temperature, and depth, and the effect of temperature varies with depth
$\log(r_{max}) \sim \log(M) * depth$	r_{max} varies with body mass and depth, and the effect of mass (i.e. scaling coefficient) varies with depth
$\log(r_{max}) \sim \log(M) * 1/k_B T$	r_{max} varies with body mass and temperature, and the effect of mass (i.e. scaling coefficient) varies with temperature
$\log(r_{max}) \sim \log(M) * depth + 1/k_B T$	r_{max} varies with body mass, temperature, and depth, and the effect of mass (i.e. scaling coefficient) varies with depth
$\log(r_{max}) \sim \log(M) * 1/k_B T + depth$	r_{max} varies with body mass, temperature, and depth, and the effect of mass (i.e. scaling coefficient) varies with temperature
$\log(r_{max}) \sim \log(M) * 1/k_B T + \log(M) * depth$	r_{max} varies with body mass, temperature, and depth, and the effect of mass (i.e. scaling coefficient) varies with temperature as well as depth

Table 2: Comparison of $\log(r_{max})$ models using standard and corrected Akaike Information Criteria (AICc), number of parameters (n), negative log-likelihood (-LL), adjusted R^2 , and Akaike weights. The model with lowest AIC is shown in bold, while the models with $\Delta AICc \leq 2$ are highlighted in grey.

$\log(r_{max}) \sim$	n	-LL	AICc	Adj. R^2	$\Delta AICc$	Weights
$\log(M)$	2	-45.5	95.1	0.17	10	0.004
$\log(M) + depth$	3	-44.8	96.1	0.17	11	0.003
$\log(M) + invtemp$	3	-44.2	94.9	0.19	9.8	0.005
$\log(M) + invtemp + depth$	4	-41.3	91.2	0.24	6.1	0.03
$\log(M) + invtemp * depth$	5	-41.2	93.5	0.23	8.4	0.009
$\log(M) * depth$	4	-42.8	94.3	0.21	9.2	0.006
$\log(M) * invtemp$	4	-40.7	90.1	0.26	5	0.052
$\log(M) * depth + invtemp$	5	-39.7	90.6	0.27	5.5	0.04
$\log(M) * invtemp + depth$	5	-37	85.1	0.33	0	0.63
$\log(M) * invtemp + \log(M) * depth$	6	-36.9	87.2	0.32	2.1	0.221

Table 3: Coefficient estimates (95% CI as estimated from standard errors shown in brackets) for all models of $\log(r_{max})$. The model with the lowest $\Delta AICc$ value is marked in bold and the models with $\Delta AIC < 2$ are highlighted in grey. Pagel's λ is the estimate of branch length transformation on the phylogenetic tree.

$\log(r_{max}) \sim$	Intercept	$\log(M)$	invtemp	depth	$\log(M):invtemp$	$\log(M):depth$	invtemp:depth	Pagel's λ
$\log(M)$	-0.01 (-1.01 - 1.00)	-0.31 (-0.48 - -0.14)	-	-	-	-	-	0.85 (0.59 - 0.96)
$\log(M) + depth$	-0.03 (-1.00 - 0.94)	-0.30 (-0.46 - -0.13)	-	-0.19 (-0.50 - 0.13)	-	-	-	0.81 (0.46 - 0.96)
$\log(M) + invtemp$	0.02 (-0.99 - 1.03)	-0.33 (-0.50 - -0.16)	0.25 (-0.06 - 0.56)	-	-	-	-	0.87 (0.64 - 0.96)
$\log(M) + invtemp + depth$	-0.05 (-0.97 - 0.87)	-0.30 (-0.46 - -0.15)	0.49 (0.13 - 0.86)	-0.47 (-0.84 - -0.11)	-	-	-	0.80 (0.45 - 0.94)
$\log(M) + invtemp * depth$	-0.05 (-0.98 - 0.88)	-0.31 (-0.47 - -0.15)	0.52 (-0.01 - 1.06)	-0.53 (-1.45 - 0.39)	-	-	0.06 (-0.81 - 0.93)	0.80 (0.45 - 0.94)
$\log(M) * depth$	0.10 (-0.85 - 1.04)	-0.31 (-0.48 - -0.15)	-	-1.52 (-2.87 - -0.18)	-	0.28 (0.00 - 0.56)	-	0.79 (0.43 - 0.95)
$\log(M) * invtemp$	0.09 (-0.86 - 1.04)	-0.33 (-0.48 - -0.17)	-1.75 (-3.24 - -0.25)	-	0.40 (0.11 - 0.69)	-	-	0.85 (0.60 - 0.96)
$\log(M) * depth + invtemp$	0.06 (-0.85 - 0.97)	-0.32 (-0.48 - -0.16)	0.45 (0.09 - 0.81)	-1.54 (-2.84 - -0.25)	-	0.23 (-0.04 - 0.51)	-	0.80 (0.45 - 0.94)
$\log(M) * invtemp + depth$	0.07 (-0.79 - 0.93)	-0.31 (-0.46 - -0.16)	-1.55 (-2.98 - -0.12)	-0.48 (-0.82 - -0.14)	0.41 (0.13 - 0.69)	-	-	0.78 (0.47 - 0.93)
$\log(M) * invtemp + \log(M) * depth$	0.04 (-0.83 - 0.91)	-0.31 (-0.46 - -0.15)	-1.97 (-4.02 - 0.08)	0.03 (-1.78 - 1.83)	0.50 (0.08 - 0.92)	-0.11 (-0.50 - 0.28)	-	0.78 (0.47 - 0.93)

Figure 1: Phylogeny, body mass, maximum intrinsic rate of population increase (r_{max}), temperature, and median depth in sharks, rays, and chimaeras. Phylogenetic tree is based on from Stein *et al.* (2018), body mass estimates were sourced from FishBase (Froese & Pauly 2016), r_{max} estimates from from Pardo *et al.* (2016), median depth values from Dulvy *et al.* (2014a), and mean annual temperature values (at median depth) were estimated based on species distribution maps from AquaMaps (Kaschner *et al.* 2015) and global temperature grids from the Argo database. Asterisks (*) denote temperature values corrected for mesothermy. Horizontal dotted lines indicate separate taxonomic orders.

Figure 2: Coefficient plots for the four models of $\log(r_{max})$ with lowest AICc values. Lighter colours indicate models with decreasing support based on $\Delta AICc$. Error bars show the 95% confidence intervals, and effect sizes were considered significant when confidence intervals do not overlap zero. Shaded areas show the expected effect sizes for body mass (-0.33 to -0.25) and temperature (-1.0 to -0.6) based on metabolic scaling theory.

Figure 3: Relationship between maximum weight and maximum intrinsic rate of population increase r_{max} , in log space, for 63 chondrichthyan species. Median depth and temperature for each species are shown by the point size and colour, respectively. Median temperatures are corrected for species which have body temperatures that are higher than their surroundings. Fitted lines show predicted relationships based on the top-ranked model. (a) Predicted allometric changes of r_{max} across median depths (10, 500, 1000 m) but constant median temperature (6 C), and (b) predicted allometric changes of r_{max} for three different median temperatures (6, 10, 20 C) but constant median depth (10 m).