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Fundamental insights into ontogenetic growth from theory and fish

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Abstract

The fundamental features of growth may be universal, because growth trajectories of most animals are very similar, but a unified mechanistic theory of growth remains elusive. Still needed is a synthetic explanation for how and why growth rates vary as body size changes, both within individuals over their ontogeny and between populations and species over their evolution. Here we use Bertalanffy growth equations to characterize growth of ray-finned fishes in terms of two parameters, the growth rate coefficient, *K*, and final body mass, m_∞. We derive two alternative empirically testable hypotheses and test them by analyzing data from FishBase. Across 576 species, which vary in size at maturity by almost nine orders of magnitude, *K* scaled as $m_\infty^{-0.23}$. This supports our first hypothesis that growth rate scales as $m_\infty^{-0.25}$ as predicted by metabolic scaling theory; it implies that species which grow to larger mature sizes grow faster as juveniles. Within fish species, however, *K* scaled as $m_\infty^{-0.35}$. This supports our second hypothesis which predicts that growth rate scales as $m_\infty^{-0.33}$ when all juveniles grow at the same rate. The unexpected disparity between across- and within-species scaling challenges existing theoretical interpretations. We suggest that the similar ontogenetic programs of closely related populations constrain growth to $m_\infty^{-0.33}$ scaling, but as species diverge over evolutionary time they evolve the near-optimal $m_\infty^{-0.25}$ scaling predicted by metabolic scaling theory. Our findings have important practical implications because fish supply essential protein in human diets, and sustainable yields from wild harvests and aquaculture depend on growth rates.

Significance statement

Understanding growth of fish is important, both for regulating harvests of wild populations for sustained yields, and for using artificial selection and genetic engineering to increase productivity of domesticated fish stocks. We developed theory to account for how growth rate varies with body size, within individuals as they grow to maturity, and across species as they evolve. Data on fish growth in FishBase supported our theoretical predictions. We found that growth rates scaled differently in populations of the same species than they scaled across species. We suggest that similar developmental programs of close relatives constrain growth, but as species diverge over evolutionary time they evolve the near-optimal -1/4 power scaling predicted by metabolic scaling theory.

Author contributions: R.M.S, J.B., C.V. and J.H.B. designed research, S.M.L. extracted the data from FishBase, J.B., C.V., R.M.S. and J.H.B. performed research and analyzed data, and R.M.S, J.B., J.M.G., A.K-B., C.V. and J.H.B. wrote the paper.

Growth is a universal attribute of life. All organisms have life cycles that include growth. Growing organisms take up energy and material resources from their environment, transform them within their bodies, and allocate them among maintenance, growth, and reproduction. Over ontogeny, large, multicellular, complex animals increase in mass by many orders of magnitude, from microscopic zygotes to much larger mature adults. In such animals growth necessarily entails integration of three phenomena. First, growth is fueled by metabolism as energy-rich carbon compounds are respired to generate the ATP that powers the assembly of organic molecules and essential elements to synthesize biomass. Second, mass and energy balance are regulated so that uptake exceeds expenditure and a stock of biomass accumulates. Third, the synthetic process is integrated with ontogenetic development so that growth is regulated as body size increases by orders of magnitude and differentiated tissues and organs are produced.

Growth trajectories of most animals are nearly identical when rescaled by body mass at maturity and time to reach mature size (Fig. 1). This suggests that the fundamental features of growth may be universal or nearly so (1-8). Nevertheless, how energy and materials are processed to regulate growth as body size changes over both ontogeny and phylogeny remain poorly understood (9). Since growth is powered by metabolism, scaling of metabolic rate, both within individuals over ontogenetic development and across species over phylogenetic evolution, is relevant. Across species the scaling of mass-specific metabolic rate with adult body mass is generally around -1/4, but there has been debate as to whether the same scaling applies to ontogenetic growth (10-12).

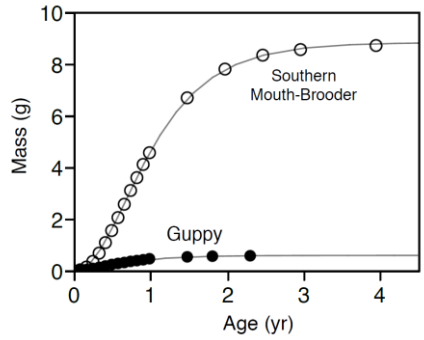

Fig. 1. Individual body mass plotted against age for the Southern mouth-brooder *Pseudocrenilabrus philander* and the guppy *Poecilia reticulata.* The curves represent fitted Bertalanffy growth equations.

Theoretical models and empirical studies of fish growth have the potential to inform how metabolic processes fuel and regulate growth (4, 7, 10, 13). Fish vary in mature body size by nearly 9 orders of magnitude, from less than 5 mg for the dwarf pygmy goby (*Pandaka pygmae*) to more than 2 tonnes for the ocean sunfish (*Mola mola*), and show substantial within-species as well as across-species variation in final body size. Interestingly, however, with the exception of a few freshwater species the vast majority of fish species start life at a nearly constant size, eggs approximately 1 mm in diameter and 1 mg in mass (14, 15). To reach mature size they grow less than 1 order of magnitude for the smallest species, such as the dwarf goby, and about 11 orders of magnitude for the largest fish, such as ocean sunfish and giant tunas (16). Fish occur in an enormous variety of environments, including nearly all marine and fresh waters and a range of temperatures from below freezing (0^o C) in the Antarctic Ocean to above 40^o C in hot springs.

It has long been known that mass-specific growth rates of fish, like other animals, decrease with increasing body size, both within individuals over ontogenetic development and across taxa over phylogenetic evolution (13, 17). Data on fish growth are typically quantified using the Bertalanffy model, which has three parameters: neonate mass m_0, final body mass, m_∞, and a growth rate

coefficient, *K*. We developed two models to account for how *K* might scale with m_∞. Scaling according to the -1/3 power is expected if growth rate after hatching is the same for all fish. This is plausible if the fish are all the same species, but might also hold across species since most start life at similar sizes, about 1 mg in mass. One the other hand metabolic scaling theory predicts -1/4 scaling across species. We tested these predictions using empirical growth data from FishBase and found some support for both models. Within species coefficients scaled close to the -1/3 power, but across species they scaled close to -1/4 . This unexpected disparity challenges existing theory. We suggest that the within-species scaling reflects shared ontogenetic development programmes, which are modified by natural selection over phylogenetic evolution towards the optimum of -1/4 predicted by metabolic scaling theory. Because much of the animal protein in human diets worldwide comes from fish that are either caught in the wild in the oceans or cultured on fish farms, these theoretical and empirical aspects of fish growth should be important in implementing fishery regulations and aquacultural practices to ensure sustainable and economical yields.

Theory

Here we derive two mathematical models producing contrasting predictions about the scaling of growth rate with final body mass. The predictions apply to both within- and across-species scaling, which we expected to be the same. We start from the premise that growth is well described by the Bertalanffy growth equation ((1, 13); examples in Fig. 1). A common form of the Bertalanffy growth equation has three parameters: neonate mass m_0, asymptotic mature mass m_∞, and growth coefficient, *K*. The equation specifies individual juvenile mass, *m* as a function of age, *t*, as:-

$$m = m_\infty[1 - (1 - \left(\frac{m_0}{m_\infty}\right)^{1/3})\, e^{-Kt/3}]^3. \quad (1)$$

Differentiation of equation (1) gives the Bertalanffy growth equation in an alternative form:

$$g = \frac{1}{m}\frac{dm}{dt} = K[\left(\frac{m_\infty}{m}\right)^{1/3} - 1]\,. \quad (2)$$

where *g* is relative growth rate, so the proportionate increase in body mass per unit time when the fish is of mass *m*. Note that according to this formulation, *g* is inherently a mass-specific growth rate, because it is indexed in terms of *m*. Additional consideration of equation (2) gives the two hypotheses investigated in this paper.

1) Hypothesis 1: K scales as $m_\infty^{-1/4}$. Consider first *g* when the fish is at a specified proportion of final body mass – e.g., ½ m_∞. Then Eq. 2 gives $g_{\frac{1}{2}m_\infty} = K\left\{2^{1/3} - 1\right\}$. Viewed in this way $g_{\frac{1}{2}m_\infty}$ is proportional to *K*, so *K* is an index of growth rate (18). Hence *K* is a biological rate, and metabolic theory predicts that mass-specific biological rates generally scale across species negatively with body size and positively with temperature *T* as:

$$K = K_0 {m_\infty}^{-\alpha}\, e^{-E/cT}, \quad (3)$$

Where K_0 is a normalization constant, α is the allometric scaling exponent which usually is approximately 1/4, *T* is environmental temperature in kelvin (= °C + 273.2), *E* is an "activation energy" which is usually approximately 0.65 eV for processes governed by respiration, and *c* is Boltzmann's constant (c = 8.62 x 10^{-5}eVK^{-1}) (12, 19). Taking logarithms we get:

$$\log_e K = -\alpha \log_e m_\infty - E/cT + \log_e K_0 \quad (4)$$

So in a regression of $\log_e K$ on $\log_e m_\infty$ and $1/cT$ the regression coefficients are predicted to be –α or ≈-1/4 and – E or ≈-0.65, respectively.

2) Hypothesis 2: K scales as $m_\infty^{-1/3}$. Our second hypothesis is also developed from Eq. 2. With the exception of a few freshwater species, offspring of nearly all bony fish hatch at very similar size, around a millimeter long, corresponding to a mass of around 0.001 g (14, 15). So, neonate mass, m_0, is nearly invariant, and rapid growth after hatching would seem to confer a large fitness advantage. According to this idea we might expect all juveniles to grow at the same speed, as fast as possible, if they are at the same temperature. It follows that after adjusting for temperature the relative growth rate at hatching when mass = 0.001 g, $g_{0.001}$, should be the same for all fish. Setting m = 0.001 in Eq. 2, and noting that $\left(\frac{m_\infty}{m}\right)^{1/3}$ is then $\gg 1$, gives $g_{0.001} \approx 10\, K\, {m_\infty}^{\frac{1}{3}}$. If $g_{0.001}$ is the same for all fish then $K\, {m_\infty}^{\frac{1}{3}}$ must also be constant, in other words:

$$K \propto {m_\infty}^{-\frac{1}{3}},$$

giving a regression coefficient of – 1/3 in a regression of $\log_e K$ on $\log_e m_\infty$.

So Hypotheses 1 and 2 differ in the value of the coefficient or the slope of the regression line in a plot of $\log_e K$ on $\log_e m_\infty$. Hypothesis 1 predicts that the coefficient is –1/4 , whereas Hypothesis 2 predicts it is – 1/3.

The following analysis aims to evaluate these alternative predictions both among closely related populations and across different species, and to explore their implications. Because the growth data in FishBase are presented in terms of the Bertalanffy coefficient, *K*, we are unable to comment on the consequences of using other, more explicitly mechanistic growth models (e.g., (4, 7, 10)).

Results

We obtained data on K, m_∞ and water temperatures of ray-finned fishes (Class Actinopterygii) from FishBase as described in Methods. Data were available for 3,119 non-captive populations belonging to 576 species, with populations varying in their *K* and m_∞ values, but data on water temperatures were available for only 136 species. To find the value of the within- and across- species regression coefficients in a regression of $\log_e K$ on $\log_e m_\infty$ and $1/cT$, we used a phylogenetic generalized linear mixed model (PGLMM, (20)) separating within-species variation from the overall relationship across species using the within-subject centering approach of (21) with two fixed-effects: average m_∞ per species, $m_{\infty across}$, and within-species deviation from $m_{\infty\ across}$, $m_{\infty within}$. Across-species variations in the effects of $m_{\infty within}$ were included as random effects. To obtain a single indicator of water temperature, T, we calculated the average of the species minimum and maximum temperatures, expressed it in kelvin and included it as an additional species-level fixed-effect parameter.

The phylogenetic regression equation for the model without temperature, illustrated in Fig. 2a, was

$$\log_e K = -0.23\ (\pm \text{SE } 0.01)\ \log_e m_{\infty across} - 0.35\ (\pm \text{SE } 0.01)\ \log_e m_{\infty within} + 0.25\ (\pm \text{SE } 0.65) \quad (5)$$

with phylogenetic heritability (h^2, *Methods*) 0.90 ± SE 0.01, n=576, and this accounted for 17% of the variance (R^2_{adj}, (22)).

The phylogenetic regression equation for the model with temperature, illustrated in Fig. 2b and c, was

$\log_e K$ = - 0.23(+/- SE 0.02) $\log_e m_{\infty across}$ - 0.36(+/- SE 0.02) $\log_e m_{\infty within}$ - 0.31 (+/- SE 0.07) $1/cT$ + 12.75 (± SE 2.77), (6)

with phylogenetic heritability 0.85 +/- SE 0.027, n=136, and this accounted for 27% of the variance (R^2_{adj}). So including temperature did not change the value of the coefficients of m_∞, but it substantially increased the variance accounted for.

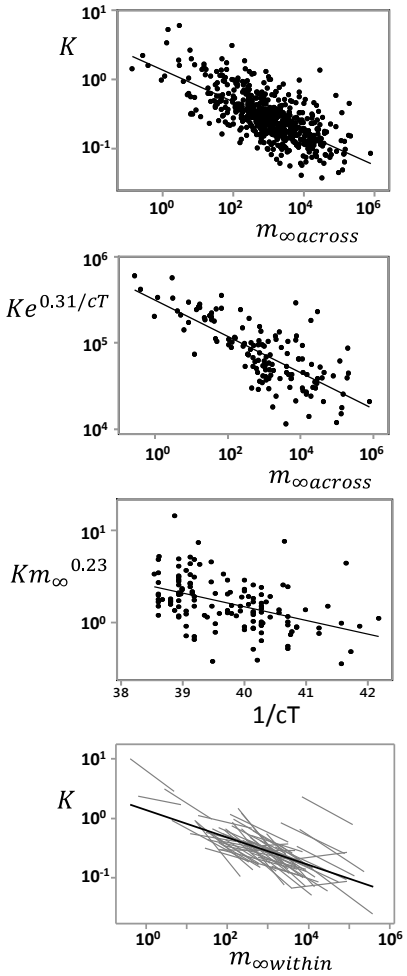

Fig. 2. Effects of final body size, m_∞, and temperature, T, on the Bertalanffy growth coefficient K of ray-finned fishes. (A) K as a function of m_∞ for 576 species without temperature correction, one point per species. The slope of the regression line, illustrating Eqn 5, is – 0.23. (B) Temperature-corrected K ($Ke^{0.31/cT}$) as a function of m_∞ for 136 species where temperature data are available, one point per species. The slope of the regression line, illustrating Eqn 6 is again – 0.23. (C) Mass-corrected K ($Km_\infty{}^{0.23}$) as a function of temperature, plotted as 1/cT, one point per species. The slope of the regression line is -0.31. (D) Within-species variation in K as a function of m_∞ for the 58 species with at least 5 populations and more than a ten-fold variation in m_∞, one regression line per species (grey lines). The black line is the across-species regression from (A) with the slope of -0.23; 71% of the within-species slopes are steeper than this.

The data are illustrated in bivariate plots in Fig. 2. Since the value of the regression coefficient, -0.23, in the across-species regression of $\log_e K$ on $\log_e m_{\infty across}$ is very close to –1/4 and significantly different from – 1/3 for the within-species analysis, we reject Hypothesis 2 in favor of Hypothesis 1. However, the within-species regression coefficient of $\log_e K$ on $\log_e m_{\infty within}$ was – 0.35, much

closer to and not significantly different from – 1/3 but significantly different from - 1/4 (Fig. 2D). Although the main effect of $\log_e m_{\infty within}$ was – 0.35, there was across-species variation in the effect of $m_{\infty within}$, as shown in Fig. 2D (ΔDIC < - 200, *Methods*). The within-species relationship was not significantly affected by any of the lifestyle variables: environment, reproductive guild, reproductive mode, fertilization type, or feeding type, but there was a small effect of trophic level (Methods and SI). A negative relationship between $\log_e K$ and $\log_e m_\infty$ within fish species was shown by D. Pauly (e.g., (13, 17), but his reported coefficient (- 0.67, (17) p. 62) was much less than ours (- 0.35 +/- 0.01) in part because more data are now available.

The finding that the regression coefficient in the across-species regression of $\log_e K$ on $\log_e m_\infty$ is – 0.23 has important implications for the growth of fry. For fry of mass m = 0.001 Eq. 2 gives $g_{0.001} \approx 10\, K\, {m_\infty}^{\frac{1}{3}}$, and since we have shown that $K \propto {m_\infty}^{-0.23}$, it follows that g at size 0.001 g scales as ${m_\infty}^{-0.23}\, {m_\infty}^{0.33}$, i.e.,. as ${m_\infty}^{0.1}$. So $g_{0.001}$ increases with increasing m_∞. To independently assess whether fish species that grow to be larger grow faster as fry we searched for empirical studies that measured initial growth rate directly. Winemiller and Rose (15) provide relevant data for 221 species of North American marine and freshwater fishes, where juvenile growth was measured as: i) "larval growth": the mean increment in total length from hatching to an age of one month; and ii) "young of the year growth" (YOY): the mean increment in total length from hatching to age one year. The data set encompassed substantial variation in final size across species: up to 2 orders of magnitude in m_∞. A phylogenetic correlation between K and m_∞ for the 203 species in these data which are also present in the phylogeny confirms that species with larger maximum adult sizes do indeed grow faster as both larvae (Fig 3A, r = 0.22, Bayes factor = 4.7) and young of the year (Fig 3B, r = 0.62, Bayes factor = 60.1). However, neither larval nor YOY growth rates are correlated with egg size (Fig 3C and 3D, Bayes factors < 2). These results corroborate the analysis of Winemiller and Rose (15) and demonstrate that direct empirical measurements of juvenile growth across different fish species support the prediction of Hypothesis 1.

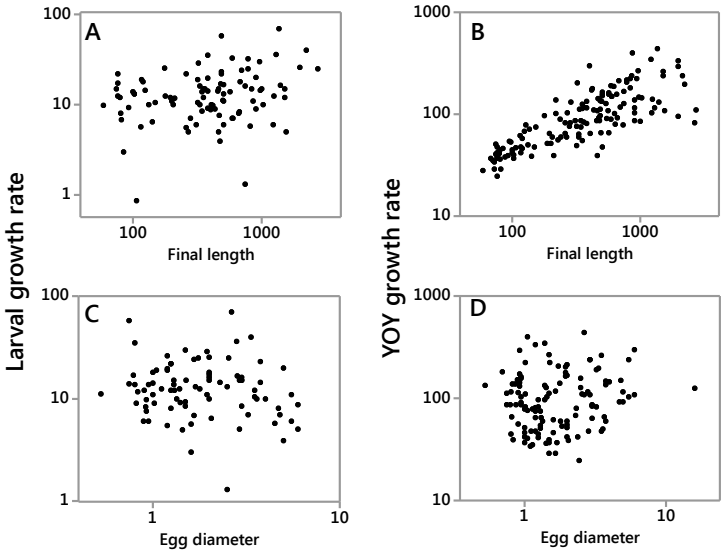

Fig. 3. Fish species that grow to larger final size have higher growth rates as juveniles. (A) larval growth rate, measured as mm/month during the first month (N = 96), and (B) "young of the year" (YOY) growth rate, measured in mm/year, both plotted as a functions of final length on log scales (N = 144). (C and D) growth rates of juveniles are not correlated with egg size, measured as diameter in mm (N = 86 for C and N = 122 for D). Data from (15) kindly provided by K. Winemiller, also available from http://www.infotrieve.com/support.

Discussion

Growth is fueled by metabolism, so growth rates – like rates of metabolism and most other biological processes – are predicted to scale with body mass and temperature according to Eq. 3. The across-species scaling with body mass of growth rate, measured empirically by the slope of the relationship between $\log_e K$ and $\log_e m_\infty$ was -0.23 ± SE 0.01 (Fig. 2A). This is very close to and within the confidence intervals of the value of – 0.25 predicted by metabolic scaling theory (4, 12, 19, 23). It is also close to the value of – 0.21 +/- SE 0.01 (though this was not phylogenetically adjusted) for the slope of mass-specific metabolic rate on $\log_e m_\infty$ across species reported in (24). The temperature dependence of growth rate is given by the slope of the relationship between $\log_e K$ and $1/cT$. Our value of -0.31 (+/- SE 0.06) is similar to the value of – 0.43 obtained by Clarke and Johnston (24) for the temperature dependence of metabolic rate. Both values are somewhat less than the value of 0.65 eV predicted by metabolic scaling theory (19, 25)), but well within the range of values reported in empirical studies of various taxa, including fish (25, 26). Some of the variation in the relationship between $\log_e K$ and $\log_e m_\infty$ may reflect imprecision in the estimation of environmental temperature during ontogeny, as many fish move between water masses and temperatures over ontogeny, and some of it is related to variation across species in gill area (13, 14)). This is because metabolism is fueled by oxygen taken up across the gills, so that gill surface area correlates with metabolic rate. These results support the theoretical and mechanistic linkage of growth rate to metabolic rate. However the finding that the across-species relationship between $\log_e K$ and $\log_e m_\infty$ is – 0.23 has the implication that fish species that grow to larger mature size grow faster as small juveniles. This is supported by the measured growth rates of juveniles (Fig. 3) (15). This may seem puzzling because, as mentioned in developing Hypothesis 2, one might expect hatchlings, regardless of species and adult size, to grow as fast as possible.

Contrary to expectation the within-species relationships between $\log_e K$ and $\log_e m_\infty$ differed from the across-species relationship; the average slope within-species was -0.35, very close to and not significantly different from -1/3. This is surprising in view of the fact that metabolic rate generally appears to scale similarly with body size within individuals over ontogeny as across species within large taxonomic groups (10, 11). Moreover, it shows that it is biologically possible for fish of very different mature sizes to have very similar growth rates in early ontogeny. If everything else were equal, natural selection should seemingly act to maximize growth rate and all fish would grow equally fast when very small. The fact that K scales as $m_\infty^{-\frac{1}{4}}$ across species implies that it is not optimal in the long term for all juveniles to grow as fast as possible; juveniles of species with small final sizes grow more slowly. So what else is not equal?

The phenomenon that young of larger species grow faster than similar-sized individuals of smaller species is actually a very general feature of empirically measured growth in many animal taxa in addition to fish (e.g., (5, 7)). We believe that this phenomenon results from two tradeoffs i) Between growth and maintenance/reproduction such that individuals of smaller species start to produce more mature kinds of cells, tissues, and organs at sizes when individuals of larger species are still allocating mostly to structures and functions devoted to growth (9, 27). A dwarf goby (m_∞ = 5 mg) is already slowing growth and allocating to maintenance and reproduction when it weighs only 2.5 mg, whereas a 2.5 mg tuna (m_∞ = 500,000 kg) is still a tiny larva allocating to juvenile structures and functions so as to grow at near-maximal rate. ii) Between growth and survival, such that larger species obtain high rates of food acquisition and growth at the expense of high rates of juvenile mortality (cf. (9, 28, 29). Fish species of large size, such as tunas, billfish, and ocean sunfish, which start life as tiny hatchlings weighing about 1 mg, must have extremely high rates of energy assimilation to support their very high growth rates. Their larvae feed on planktonic organisms, and their morphology and physiology reflect extreme specialization for capturing, ingesting, and digesting prey, and this results in higher assimilation rates than individuals of smaller mature size (9).

A consequence of this lifestyle is a very high rate of juvenile mortality, presumably due to some combination of predation and starvation, which is balanced by enormous fecundity of the very few individuals that manage to survive to maturity (females lay millions of eggs in one spawning and they spawn many times as they grow from reproductive size to maximum size). By contrast, a tiny goby that also lays eggs weighing about 1mg, can lay only a few small clutches in its lifetime. In order for enough offspring to survive and reproduce, juvenile gobies must minimize mortality due to predation and starvation by allocating to "maintenance" traits.

So if *K* scaling as $m_\infty{}^{-\frac{1}{4}}$ represents the evolutionary optimum, why doesn't Hypothesis 1 and the above theoretical explanation also apply to within-species growth rates? We believe the reason is that most of the within-species variation reflects sub-optimal phenotypic and genetic changes over a few generations (Fig. 4). FishBase does not indicate the cause of the variation in m_∞ within species, but some fish species are well known to exhibit extreme variation in mature size due to stunting in response to low food supply, and to morphological, physiological, and behavioral specializations for different trophic roles or reproductive tactics (e.g., (30-32)). These divergent phenotypes have been shown to be due to some combination of phenotypic plasticity and a few genes of large effect (e.g., (33, 34)). Each fish species has an ontogenetic program that has been honed by natural selection over its phylogenetic history to closely integrate ontogenetic growth and development in adaptation to intrinsic traits, such as body form, life history, and breeding system, and to extrinsic environmental conditions, such as water velocity, oxygen concentration, food supply, population density, and predation regime. We suggest that when fish of similar genetic stock grow to different mature sizes, the common ontogenetic program constrains the growth trajectory so that individuals grow at similar rates when they are small juveniles even though they mature at different sizes. This leads to the testable hypothesis that as populations adapt to different environments over evolutionary time, the ontogenetic program is modified by natural selection so that scaling of *K* changes from $m_\infty{}^{-1/3}$ to $m_\infty{}^{-1/4}$.

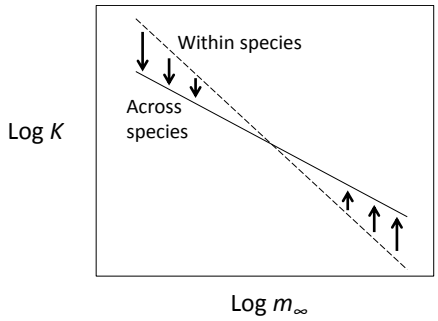

Fig. 4. Schematic depiction of how evolutionary changes occur in scaling of *K* with m_∞. Individuals within closely related populations are constrained to scale with slope – 1/3 (dashed line). Due to tradeoffs between growth and maintenance, natural selection favors faster growth in species that attain large sizes (upward arrows) and slower growth in species that mature at small sizes (downward arrows). Over evolutionary time the ontogenetic program changes until the optimal scaling is attained (solid line with slope – ¼). Note that if the steeper within-species scaling were continued to either extremely small or large sizes, the fish would have unrealistically slow or fast growth rates, respectively (see Fig 2D).

The way this played out in evolution is seen in the high phylogenetic heritabilities of the across-species relationship between $\log_e K$ and $\log_e m_\infty$ (Eqns 5 and 6). It indicates that species which have relatively recently diverged from common ancestors tend to have similar values of *K* and m_∞. Additional support for the ontogenetic program explanation comes from extrapolating the within-species regression lines for individual species in Fig. 2C to the entire range of fish body sizes. It is immediately apparent that some species would grow unrealistically slowly or fast, up to an order of magnitude slower or faster than any extant species of such extreme size (Fig. 4).

Can our results be related to the ontogenetic growth model (OGM) of (4) (see also (7, 10))? We were unable to do this, because the OGM is written in the 1/4 powers of metabolic scaling theory, whereas our analysis used the coefficient *K* obtained by fitting the Bertalanffy growth equation, which is written in terms of 1/3 powers. To illustrate the problem consider the OGM written in its most general form as

$$\frac{1}{m}\frac{dm}{dt} = \frac{B_0}{E_m {m_\infty}^{1-\alpha}}\left(\frac{{m_\infty}^{1-\alpha}}{m^{1-\alpha}} - {m_\infty}^{1-\beta} m^{\beta-1}\right) \quad (7)$$

(rearranging (10) equation 2 and Appendix equations), where α and β are the metabolic scaling exponents for the rate of energy assimilation during growth and the rate of energy expenditure for maintenance, respectively, B_0 is a normalization constant, and E_m is the quantity of metabolic energy required to create a unit of biomass. This and the Bertalanffy model in equation (2) can both hold identically over a range of values of m only if $\alpha = \frac{2}{3}$, $\beta = 1$, and

$$K = \frac{B_0}{E_m {m_\infty}^{1/3}}. \quad (8)$$

This gives $K \propto {m_\infty}^{-1/3}$ if B_0 and E_m are constants. To have the observed interspecific scaling of $K \propto {m_\infty}^{-1/4}$ would require that either B_0 or E_m scale with *m* to a 1/12 power. If instead of the Bertalanffy *K* a growth coefficient from the OGM had been recorded by fish workers, the analyses might – or might not – give different results. This highlights the potential for compiling and analyzing data on important parameters of fish growth in addition to Bertalanffy's *K*, to allow development of alternative models.

Our findings, together with earlier studies of fish growth (e.g., (9, 13-15, 17)) have important practical implications. Fish harvested from both wild populations and aquaculture operations supply a large and increasing fraction of the protein that is essential in the human diet. The growth rates of these fish are directly relevant to the capacity of wild and cultured stocks to provide sustainable commercial food supplies for at least three reasons. First, high growth rates of wild populations should contribute to their capacity to sustain yields under harvest. So it is not surprising that some fish with exceptionally high growth rates such as Pacific salmon (*Onchoryunchus* spp.) and mahi mahi (*Coryphaena hippurus*) support relatively sustainable commercial fisheries. Second, high growth rates should also be important in choosing species for aquaculture and domestication. So it is not surprising that fish used in aquaculture, such as Atlantic salmon (*Salmo salar*), some cichlids (species of *Oreochromis*, *Sarotherodon*, and *Tilapia*), and catfish (*Pangasianodon* spp. and *Ictalurus punctatus*), exhibit high growth rates. Third, some domesticated stocks have additionally been modified to increase growth rates using a combination of artificial selection and genetic modification.

Comparing the growth trajectories and life history traits of wild and farmed fish offers insights into both the patterns and processes of ontogenetic growth and development that have evolved under natural selection in the ancestral populations and the extent to which these patterns and processes can be altered by artificial selection and genetic modification. For example, AquaBounty Technologies have created *AqauAdvantage* salmon from a stock of Atlantic salmon (*Salmo salar)* which was previously subjected to strong artificial selection. *AqauAdvantage* salmon have been genetically modified to produce all-female triploid individuals containing two inserted genes: the opAFP-GHc2 promoter from ocean pout (*Zoarces americanus*) and a growth hormone from the much larger chinook salmon (*Oncorhynchus tshawytscha*) (http://en.wikipedia.org/wiki/AquAdvantage_salmon). In aquaculture, where they are supplied with abundant, high-quality food, caged to exclude predators, and treated with antibiotics to control diseases, some stocks of salmon have growth rates, measured as Bertalanffy *K,* 2-3 times faster than

wild populations. [This is according to our analysis of published data; claims that some transgenic stocks exhibit "growth enhancement" more than 17 times greater than wild populations appear to be based on differences in mature sizes (35)]. The exceptionally high growth rates of domesticated stocks have been achieved by selecting for high rates of energy intake (food assimilation) and for allocation of metabolic energy to growth (rapid biomass production) at the expense of energy expenditure on activity (lower swimming speed), predator avoidance (reduced vigilance and escape behavior) and reproduction (reduced mating behavior and lower egg production) (e.g., (36, 37)). So, greatly accelerated growth has been achieved at the expense of traits for survival and reproduction under natural conditions as discussed above. Like factory-farm turkeys, fryer chickens, and hogs, some farmed fish stocks have been so modified to grow fast to produce food for humans that they have lost many traits required to survive in the wild.

Our theoretical and empirical analysis of fish growth highlights the insights that can come from combining mathematical theory with compilation and analysis of large, high-quality databases. It is apparent that fish exemplify general patterns and processes observed in other animals. For example, higher juvenile growth rates in species that grow to larger adult sizes are also seen in mammals and birds (see, e.g., (3, 11, 18, 38)). It is also apparent that we are still some ways from having a general unified theory of growth. We need more explicitly mechanistic models for how the life history evolves in response to tradeoffs between growth and survival, and to energy allocation tradeoffs between maintenance, growth, and reproduction. Additional studies of fish will continue to have much to contribute, especially if FishBase or other data bases can be expanded to include additional quantitative data on growth beyond the Bertalanffy *K*s used in this study.

Materials and Methods

Values of K and m_∞ were extracted from FishBase on 30/9/2014 together with species-level data where available for water temperature and 6 additional lifestyle variables (environment, reproductive guild, reproductive mode, fertilization type, trophic level, feeding type).

We used the species-level phylogeny of ray-finned fishes (Class Actinopterygii) presented in (39). Species names were matched between the phylogeny and the data using official synonym lists extracted from FishBase. In two cases (*Salmo trutta* and *Sarotherodon galilaeus*), multiple synonyms for a single species were found in the tree. In both cases the data were excluded from the analysis. 576 of the species in our phylogeny are found in the data.

We used the deviance information criterion (DIC) to assess the contribution of individual variables to a PGLMM, where lower DICs are preferred (20). A ΔDIC of < - 3 when comparing models with and without a given character is considered evidence of a significant contribution of that variable (40, 41). We calculated phylogenetic heritability (h^2), identical to Pagel's lambda (42), from the phylogenetic variance of our models, to determine the importance of species' shared ancestry: values close to 1 indicate strong phylogenetic signal. All models were implemented within a Bayesian framework and were run for a total of 1,000,000 iterations, sampling every 1,000 after removing the first 100,000. All chains were run multiple times to ensure convergence.

For the re-analysis of data from Winemiller and Rose (15), we matched 203 of the 221 species in the original data to the fish phylogeny. We report mean phylogenetic correlations (r) in a Bayesian framework using the same model conditions described for the PGLMMs and using all available data (Fig 3). Significance was assessed by comparison to a non-correlational model using Bayes factors estimated using a stepping-stone sampler (43) (1000 stones with 100,000 iterations per stone) as implemented in BayesTraits (44). A Bayes factor of >2 is considered positive support for the correlation, and >10 is considered to give very strong support (45).

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