Regular paper

Testing predictions of length at first maturity of teleostean fishes, given their maximum length

by

Çetin KESKİN & Daniel PAULY* (2)

Abstract. – This contribution presents a test of a hypothesis published in 1984 that teleostean fishes mature and spawn when they reach the threshold value of $L_{max}{}^{D}/L_{m}{}^{D}$ of 1.35 (95% CI: 1.22-1.53). Here, L_m is the average length at first maturity of the fish in a given population, L_{max} is the maximum length reached by the individuals in that population, and D a parameter ranging between 0.3 and 1.2 in fish which relates their body size, via their gill surface area, to their oxygen consumption. The data analysed here, which include 120 L_{max}/L_m pairs in 57 fish species from the published literature on marine and freshwaters in Southeastern Europe and West Asia, lead to a new ratio estimate of 1.44 (95% CI: 1.41-1.48), when all cases are given the same weight and 1.30 (95% CI: 1.17-1.43) when the phylogeny of the 57 species is explicitly accounted for. Both sets of results are within the confidence intervals of the earlier estimate and thus corroborate the above hypothesis.

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Résumé. – Test d'une méthode pour prédire la longueur à la première maturité des poissons à partir de leur longueur maximale.

Cette contribution présente un test de l'hypothèse publiée en 1984 selon laquelle les poissons téléostéens atteignent leur première maturité quand ils atteignent le seuil critique du rapport $L_{max}{}^{D}/L_{m}{}^{D}$ de 1,35 (95% intervalle de confiance 1,22-1,53). Dans ce contexte, L_m est la longueur moyenne à la première maturité (ou puberté) des membres d'une population de poissons, L_{max} est la longueur maximale observée parmi cette population, et D est un paramètre dont la valeur, entre 0,3 and 1,2 relie la taille des poissons, par l'intermédiaire de la superficie de leurs branchies, à leur consommation d'oxygène. Les données analysées, à savoir 120 couples de valeurs de L_{max} et L_m extraites de la littérature scientifique représentant 57 espèces de poissons des eaux douces et de mer du sud-est de l'Europe et du Moyen-Orient, ont permis une nouvelle estimation du rapport sus-cité de 1,44 (95% intervalle de confiance 1,41-1,48), si toutes les populations sont pondérées de la même façon, et 1,30 (95% intervalle de confiance 1,17-1,43) si l'on tient compte de la phylogénie des 57 espèces. Ces résultats sont tous deux compris dans l'intervalle de confiance calculé préalablement, et sont donc compatibles avec l'hypothèse initiale.

Key words
Maturation
Hormonal cascade
Juvenile-to-adult transition
Gill-Oxygen Limitation Theory

INTRODUCTION

Contrary to mammals and especially birds, fish mature and begin reproducing at small sizes relative to the maximum size they can reach. This applies when this maximum size is a length (L_{max}), but it is particularly obvious when the maximum size is expressed as the weight (W_{max}) that fish can ultimately reach if they survive long enough (Pauly, 2021a).

Length at first maturity (L_m) is of considerable interest to fisheries managers because catching too many immature fish leads to recruitment overfishing (Myers, 2001; Froese, 2004). This parameter is also important to aquaculturists, because farmed fish are expected to grow rapidly toward market size and not devote resources to reproduction (Pullin, 1996; Byerly *et al*., 2005; Amarasinghe and Pauly, 2021).

Yet many studies supposedly devoted to the investigation of the dynamics of size at first maturity fail to provide any insight on this process, notably because age at first maturity is often reported (instead of L_m) without anyone having demonstrated how individual fish could know their age such that they could use it as a heuristic (Budaev *et al*., 2019) to influence their maturation schedule. Also, L_m values are frequently reported without the corresponding L_{max} values, although it has been known for decades that the L_m/L_{max} ratio is reasonably stable within different species and groups of species (Beverton and Holt, 1959). This second point is indeed so well established that the ratio of L_m to L_∞, the asymptotic length in the von Bertalanffy equation, which is roughly equivalent to L_{max}, has been called a "Beverton and Holt invariant" (Charnov, 1993).

Froese and Binohlan (2000) studied the relationships between L_m and L_∞ (also including additional predictor variables) in 265 fish species in FishBase (www.fishbase.org), which yielded an average scaling factor of ≈ 0.9. The simplest relationships they derived is:

$$\log(L_m) = 0.898 \times \log(L_\infty) - 0.0782 \quad (1)$$

when L_m and L_∞ are in cm.

A scaling factor of 0.9 implies that the L_m/L_{max} ratio is not "invariant." Here, however, we suggest that L_m and L_{max} are close correlates because it is the same factors that deter-

(1) Faculty of Aquatic Sciences, Istanbul University, Ordu Street No: 8, 34134 Laleli Fatih, Istanbul, Turkey. seahorse@istanbul.edu.tr.
(2) *Sea Around Us*, Institute for the Oceans and Fisheries, University of British Columbia, Vancouver B.C. Canada, V6T 1Z4. d.pauly@oceans.ubc.ca
* Corresponding author

mine the values L_m and L_{max} take, *i.e.*, the metabolic rate of fish and the dimensional tension between gills growing as a 2-dimensonal surface increasingly limiting the O_2 supplied to their 3-dimensional bodies (Pauly, 1984, 2021a, b).

Thus, Pütter (1920), followed by von Bertalanffy (1938), proposed that the growth rate of fish and other water-breathing ectotherms can be conceived as the difference between two processes, *i.e.*,

$$\text{Growth rate} = H \times W^d - k \times W \quad (2)$$

where the rate of growth in terms of weight (W, or more precisely mass) is the difference between a positive term ($H \times W^d$), within which H is the coefficient of 'anabolism,' *i.e.*, the synthesis of the body's proteins, and a negative term ($k \times W$), within which k is the coefficient of 'catabolism,' *i.e.*, the degradation of the same proteins. Important here is that d is < 1; thus, when weight increases, $k \times W$ increases more rapidly than $H \times W^d$, and growth ceases when $H \times W^d = k \times W$.

Note that the exponent d, in Pütter's and von Bertalanffy's formulation was perceived as referring to a surface (S) limiting anabolism, but whose nature was not specified. Because S was assumed to grow proportionally to body length squared ($S \times L^2$), and the weight of bodies usually grow proportionally to body length cubed ($W \times L^3$; Froese, 2006), this limiting surface was assumed to always scale with weight with $d = 2/3$. This assumption is built in the von Bertalanffy Growth Function (VBGF), which was introduced to fisheries by Beverton and Holt (1957), and is now widely used in ichthyology.

Pauly (1981, 2021a) interpreted the first of the processes on the right side of this equation ($H \times W^d$) as the synthesis of the molecules making up the body of water-breathing ectotherms (WBE), the second process ($k \times W$) being the loss of the quaternary structures (= spontaneous denaturation) of these molecules. Such loss of quaternary structure renders these molecules dysfunctional, and they rejoin the amino-acid pool (mainly maintained by digested and assimilated food), which provides both the building back and the 'fuel' for the synthesis of native proteins (Nelson and Cox, 2017).

Energy in the form of ATP is required for synthesis of native proteins; thus, the first term is dependent on the supply of oxygen to the body's cells, which is itself proportional to W^d, while d was conceived as a scaling factor linking an actual surface, *i.e.*, the gill surface area, to body weight (Pauly, 1981, 2021a).

A number of reviews have shown that in most (postlarval) teleosts, d ranges between 0.6 and 0.9 (Muir and Hughes, 1969; De Jager and Dekkers, 1975; Palzenberger and Pohla, 1992; Pauly, 2019). This means that as fish grow, the surface area of their gills per unit body weight inexorably declines to a level at which the oxygen supplied by these gills is just sufficient to support their routine activities (feeding, avoiding predators) without allowing for further growth

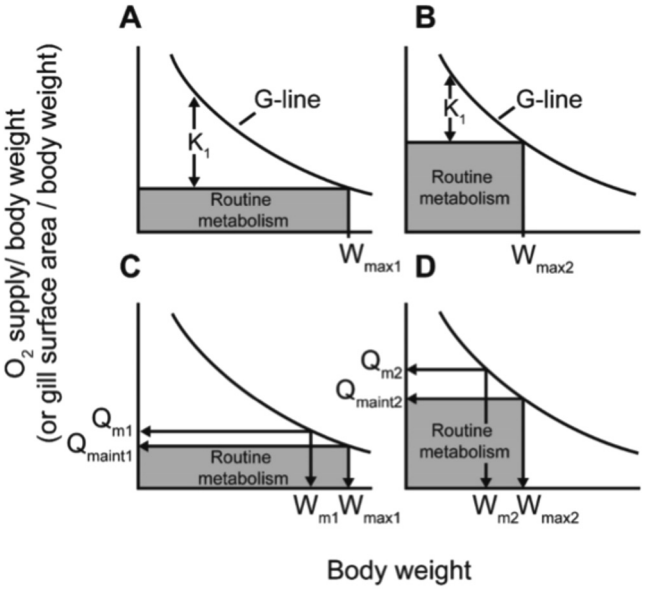


Figure 1. – Schematic representation of how, in fish, a declining relative gill surface area (G-lines in **A**-**D**) and thus oxygen (O_2) supply imposes a limit to body weight (W_{max}) when the oxygen reaches a level just sufficient for maintenance (Q_{maint} in **A**). When a stress factor (*e.g.*, a higher temperature) increases the O_2 demand for maintenance, W_{max} is reached at smaller sizes (**B**). Maturation and spawning must occur at a size $W_m < W_{max}$, implying an O_2 supply $Q_m > Q_{maint}$ (**C**). This contribution suggests that the ratio Q_m/Q_{maint} is similar and constant among fishes, thus enabling them to adjust their value of W_m under stress condition (**D**; see text).

(Fig. 1A). Therefore, when their environment imposes oxygen-demanding stress on them, they must remain smaller (see, *e.g.*, Kolding *et al.*, 2008; Cheung *et al.*, 2013; Pauly and Cheung, 2017; also see Fig. 1B).

Except for semelparous species such as Pacific salmon (Crespi and Teo, 2002), spawning, in teleosts occurs long before growth ceases. Conventionally, maturation and spawning in fish are represented as a hormonal cascade triggered by a response to environmental cues (see, *e.g.*, Hoar, 1970; Bhattacharya, 1999; Podhorec and Kouril, 2009; Pankhurst, 2016). However, this is clearly incomplete because young/small fish in all long-lived species go through several spawning seasons and the many environmental maturation stimuli they provide, but without their maturation being triggered (Pauly, 2021b).

Rather, fish must reach a certain critical size before they perceive the species-specific or population-specific environmental cues that trigger maturation, and which only then release the hormonal cascade leading to maturation and spawning (Fig. 1C). However, this critical size cannot be a species- or population-specific invariant, because this would prevent individuals from responding, via their phenotypic plasticity, to local changes of environmental conditions (Kolding *et al.*, 2008; Schnell and Seebacher, 2008; Svan-

bäck and Schluter, 2012; Wilson *et al*., 2019; Amarasinghe and Pauly, 2021).

Pauly's (1984) hypothesis is that fish initiate spawning in response to the oxygen stress they experience as their oxygen supply (Q_m) relative to their routine oxygen requirement (Q_{maint}), drops to a threshold level (Q_m/Q_{maint}) of about 1.35, with a 95% confidence interval (CI) of 1.22-1.53, estimated using the method of Fieller (1940). A fixed ratio of this sort enables L_m to be automatically adjusted downward when environmental conditions are stressful (Fig. 1D).

This ratio was originally estimated from 56 L_{max} (*i.e*., L_u, for 'ultimate' length in Pauly, 1984) and L_m data pairs in 56 population of 34 marine fish species, *i.e*., making use of the fact that plotting $L_{max}{}^D$ vs $L_m{}^D$, is mathematically equivalent to plotting Q_m vs Q_{maint} (Pauly, 1984) when, from simplicity's sake, D is used instead of $3(1 - d)$, with 3 as the commonly encountered exponent of LWR in fish (Froese, 2006). However, no allowance was then made for the dissimilar number of cases by species, nor was the phylogeny of the 34 species accounted for. This was considered for the first time in Chen *et al*. (2021), who estimated the mean ratio $L_{max}{}^D/L_m{}^D$ of freshwater and marine fishes from Chinese water.

This contribution presents an additional test of Pauly's (1984) hypothesis, which explicitly accounts for the biasing effect of phylogeny in both Pauly's original dataset and in the new data set that we assembled from freshwater and marine fish from southeastern Europe and West Asia, *i.e*., in and around Turkey.

MATERIAL AND METHODS

A dataset was assembled, mainly from peer-review literature, which comprised 120 pairs of mean length at first maturity (L_m) and the corresponding maximum length (L_{max}), meaning the same locality, period and sex (and generally from the same publication). Note that L_m is the length at which 50% of the individual in a given population become mature, which is higher than the length at which some individual first become mature.

The L_{max} values were used to obtain estimates of maximum weight (W_{max}) using a species-specific length-weight relationships (LWRs) given in Table S1 of our Supplementary Materials. Then, as in Pauly (1984), estimates of d were derived (see Supplementary Material, Tab. S1) from:

$$d = 0.674 + 0.0357 \times \log(W_{max}) \quad (3)$$

where W_{max} is expressed in g and which was derived from metabolic and gill area studies covering a wide range of fish sizes (Pauly, 1981). Then we defined

$$D = 3 \cdot (1 - d) \quad (4)$$

with $L_{max}{}^D/L_m{}^D = Q_m/Q_{maint}$ (Pauly, 1984, 2021a).

The mean ratio of interest here, between $L_{max}{}^D$ and $L_m{}^D$ was computed based on two approaches. The first approach consisted of plotting the 120 cases of $L_{max}{}^D$ and $L_m{}^D$ assembled in Table S1 in a regression with zero intercept, which estimated the mean ratio in question as its slope.

The second approach considered that the number of cases in each of the 57 species in Table S1 was very uneven, ranging from 1 to 7 (mean ≈ 2), and that some species were more closely related than others. The biases that these two effects cause were corrected for by averaging within species with more than one case, and by using phylogeny to account for the bias of non-independence as species share parts of their evolutionary history. This was done by using a fish phylogeny from the *Fish Tree of Life* using the *fishtree* package in R (Rabosky *et al*., 2018; Chang *et al*., 2019), which was pruned to match the species in our dataset (Fig. S1).

The tree in Figure S1 describes how our 57 species are related through the length of their branches, which are scaled to time, and express the time elapsed since a species broke off from another species. A covariance matrix is the created from those branch lengths, with each species providing the column and row names, and the branch lengths between the respective species providing the content of the cells (with the diagonals = 0 because they refer to the same species). This matrix was then used as a random effect in the model to adjust the residual errors in a model such that they account for the known shared autocorrelation between species. This obviates the effect of a variable on another variable, which, when compared across species, could simply be due to the fact that species are related, and thus give a false significant result.

RESULTS

The L_m and L_{max} values assembled cover 120 data pairs in 57 species and 31 families of mainly marine fish from Southeastern European and West Asian marine and freshwater bodies. When these 120 data pairs are plotted as a linear regression without intercept, and without accounting for phylogeny, they suggest a slope for (*i.e*., a mean estimate of) $L_{max}{}^D/L_m{}^D$ of 1.44 (95% CI: 1.41-1.48); see Table I and Figure 2A.

When phylogeny is considered, the reduced data set (because not all fish species in Table S1 were included in the available *fishtree*) yielded a mean ratio for $L_{max}{}^D/L_m{}^D$ of 1.30 (95% CI: 1.17-1.43); see Table I and Figure 2B.

Finally, Table II demonstrates not only that the coefficients of variation (= standard deviation/mean) of the ratio L_{max}/L_m of different subsets of the data in Table S1 are much lower than those of L_{max} and L_m separately, but that the $L_{max}{}^D/L_m{}^D$ ratio has the lowest coefficients of variation.

Table I. – Estimates of the $L_{max}{}^{D}/L_{m}{}^{D}$ ratio as the slope of linear regressions with a zero intercept.

Data set	Sample size (n)	Slope of regression	Lower 95% C.I. limit	Upper 95% C.I. limit
All observations	120	1.44	1.41	1.48
All species; spp. with multiple observations reduced to mean L_m and L_{max}.	57	1.45	1.40	1.50
Species on *fishtree* **without** phylogeny accounted for in regression	50	1.43	1.38	1.48
Species on *fishtree* **with** phylogeny accounted for in regression	50	1.30	1.17	1.43
Baseline study (Pauly, 1984), all observations, but **without** phylogeny[a]	56	1.34	1.30	1.39
Baseline study (Pauly, 1984), **with** phylogeny	34	1.32	1.17	1.42

[a] The numbers in this row differ slightly from those in Pauly (1984, 2021b) because the estimates presented here were obtained using regressions of $L_{max}{}^{D}$ vs Lm^{D} (w/ intercept = 0), whereas the mean ratio $L_{max}{}^{D}/L_{m}{}^{D}$ was previously obtained by dividing the sum of the $L_{max}{}^{D}$ values by the sum of the $L_{m}{}^{D}$ values; also, the wider C.I. was based on Fieller (1940).

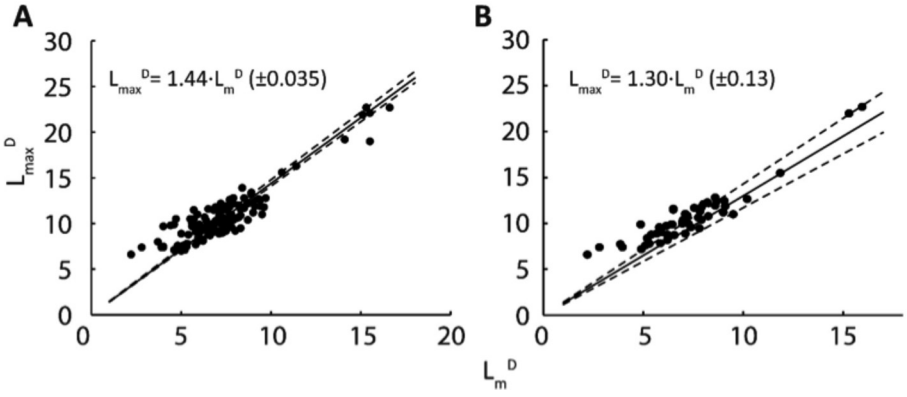


Figure 2. – Plots of $L_{max}{}^{D}$ vs $L_{m}{}^{D}$ in marine and freshwater teleosts. **A**: All 120 cases and 57 species in Table S1, *i.e.*, not accounting for multiple cases in several species, nor for they phylogeny. **B**: Using 50 species, accounting for multiple cases and phylogeny (see also Table I). Note that the apparent mismatch between the data points and the regression line in **B** is a feature of phylogenetic correction and not an error.

Table II. – Coefficients of variation (st. dev./mean) of the variables and derived ratios in Table S1 and subsets thereof.

Dataset	n	L_m	L_{max}	L_{max}/L_m	$L_{max}{}^{D}/L_{m}{}^{D}$
All observation	120	1.10	1.20	0.27	0.19
All grouped by species	57	1.13	1.35	0.27	0.21
All species on phylogenetic tree	105	1.09	1.21	0.27	0.19
All species on phylogenetic tree grouped by species	49	1.13	1.36	0.27	0.21

DISCUSSION

Whether or not phylogeny is accounted for, and the relationship between species from a phylogeny (tree) is used as a random effect in a model to adjust the residual error for known autocorrelation, our results are compatible with the baseline study of Pauly (1984; see Tab. I) and with the results of Amarasinghe and Pauly (2021), Meyer and Schill (2021) and Chen *et al*. (2021).

We also note that the results of Pauly (1984), which were based on data that are now part of the Supplementary Material of Pauly (2021a), while taxonomically diverse, were no suffering from much phylogenetic bias. This is likely to also apply to the results of Meyer and Schill (2021), which were derived from three closely-related salmonid species, and the results of Amarasinghe and Pauly (2021), derived from 7 species of cichlid fishes.

Overall, our study provides more evidence that mean length at first maturity varies with the maximum length that the fish of given species can reach, but that this co-variation is not fully captured by the notion of an 'invariant' ratio. Rather, it is the $L_{max}{}^{D}/L_{m}{}^{D}$ ratio that appears to be invariant, at about 1.35. This gives support to the interpretation provided above of the 'dimensional tension' between 2-D gill surface areas supplying oxygen to growing 3-D bodies providing the threshold that triggers the hormonal cascade leading to maturation and spawning.

Finally, we suggest that the variance around the estimate of the $L_{max}{}^{D}/L_{m}{}^{D}$ ratio of ~ 1.35 is due to its role as the key element of a heuristic (*sensu* Budaev *et al*., 2019) used by individual fish to 'choose' when they should start to respond to the environmental stimuli that are conventionally seen as

triggering maturation and spawning (Pauly, 2021b). Like all heuristics, however, the mechanism proposed by Pauly (1984) is not failsafe, mainly because fish, like human, cannot reliably predict the future. For example, stressful environmental conditions (causing an increase in oxygen consumption, and thus, via the heuristic, leading to a small size at first maturity) could subsequently improve. In such a case, an early maturation would forfeit the benefit of additional pre-maturation growth, which would allow for more eggs to be produced. Conversely, in a habitat with rapidly degrading conditions, the heuristic would lead to puberty being reached too late, leading to subsequent egg production being suboptimal, if achieved at all.

This new hypothesis could be tested, as the variance about the 1.35 ratio should be inversely related to the predictability of the environmental conditions to which the fish are exposed. While such test cannot be done with the limited datasets available today, a larger dataset (*e.g.*, assembled from FishBase; Froese and Pauly, 2021) may be suitable, and we consider this the next step in examining the hypothesis tested here.

CONCLUSION

While it has long been known that, in fish, mean length at first maturity and maximum length are tightly correlated, a hypothesis proposed in 1984 suggested that this close correlation was caused by the same factor – metabolic stress – acting on the juvenile-to-adult transition of fish as well as on the maximum size they can reach. This hypothesis, originally proposed based on data for a range of marine species was so far tested and corroborated with data from freshwater fish, *i.e.*, 3 salmonid species (Meyer and Schill, 2021), 7 cichlid species from 3 continents (Amarasinghe and Pauly, 2021), and fishes from Chinese waters (Chen *et al*., 2021). Here, it was tested with 57 fish species in 120 populations from in southeastern and west Asian fresh and marine waters. The result was a full corroboration, which suggests that not only is there a causal, although non-linear relationship between the mean length at first maturity and the maximum length of fish in a given population, but also that this relationship can be used to predict mean lengths at first maturity from maximum lengths, or vice-versa, and how both lengths will react to stresses, *e.g.*, as caused by ocean and freshwater warming.

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Online supplementary materials

Figure S1. – Phylogenetic tree pruned from the *Fish Tree of Life* in the *fishtree* package in R (Rabosky *et al*., 2018; Chang *et al*., 2019), such as to match the species in Table S1.
Available at https://sfi-cybium.fr/sites/default/files/supplementary-files/Keskin%20FB3%20supp%20mat%20online%20fig%201%20%5Bearly%20view%5D.pdf

Table S1. – Fishes used in the present study (n = 120), ordered alphabetically by family (n = 31), then genus (n = 48) and species (n = 57). Length at first maturity (L_m) and maximum length (L_{max}) of the fishes used to compute L_m^D and L_{max}^D. Ecosystem types (E): 0: Freshwater, 1: Seawater, 2: Brackish water; Sex (females, ♂; male, ♀: Female); *a* and *b*: parameters of length-weight relationship parameters of the formula $W = a \cdot L^b$, as used to estimate W_{max}.
Available at https://sfi-cybium.fr/sites/default/files/supplementary-files/Keskin%20FB3%20supp%20mat%20online%20tab%20S1%20%5Bearly%20view%5D.pdf