The MATURITY and GILLS Table: The Relationship Between the First Maturity and the Respiration of Fishes

In most fish biology textbooks, reproduction is perceived as a costly process wherein 'energy' is transferred from somatic to gonad growth. Hence, somatic growth is said to be slowed or even stopped depending on the extent of the 'energy' transfer. However, it is generally not appreciated that this conceptualization, of which multiple variants exist, is only a hypothesis which, like all scientific statements about the world, is subject to rejection if it is incompatible with well-established facts.

The most important reason for the survival of this conceptualization is that its outward plausibility rests on the representation of growth as proceeding in length, which it does not: 'energy' certainly does not have the dimension of length, or length per time. Once somatic growth is - correctly - viewed in terms of mass or weight per time (Pauly and Liang 2022; Froese and Pauly 2023), this hypothesis is refuted. Except for species whose maximum lengths do not exceed 10 cm (Pauly 2021a), fish tend to reach first maturity at sizes *below* that at which they experience their highest growth rate in weight (*dW/dt*).

Thus, perceiving that 'energy' being transferred from somatic growth to the elaboration of gonads as the *cause* for growth in length declining after first maturity is a case of the '*post hoc, ergo hoc*' fallacy, which considers that an event (1) is the cause of an event (2) simply because event (1) occurred before event (2).

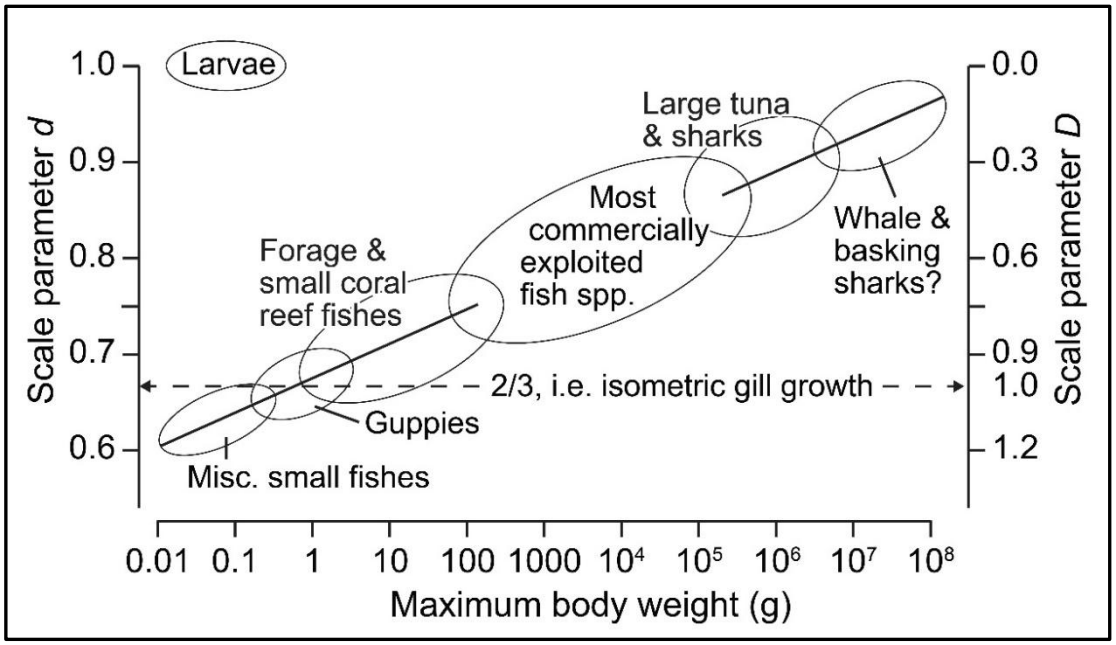

Figure 1. Showing that in fish, the parameters *d* and *D* are related to the maximum weight reached by various taxa (modified from figure 2 in Pauly 1981); the straight line is based on the relations $d = 0.674 + 0.0357 \cdot \log(W_{max})$, with live weights in g based on 27 estimates of *d* from studies of gill surface or respiration, all documented in table 2 of Pauly (1981: Ref. 2015).

An alternative hypothesis originally proposed by Pauly (1984) and which has survived multiple test (notably by Kolding *et al*. 2008 and Meyer and Schill 2021) is that the onset of maturation and spawning is due to the fact that in adult fish, gill growth (which determines oxygen *supply*) scales with body weight (which determines oxygen *demand*) with exponent d <1. Thus, when fish grow, their relative oxygen supply (Q) declines until a 'maturation threshold' is reached, at which point the hormonal cascade is initiated which leads to spawning (Pauly 2021b).

The maturation threshold is defined as Q_m/Q_{maint}, where Q_m is the relative respiration rate at L_m, the length at first maturity and Q_{maint} is the relative respiration rate at L_{max}, i.e., of non-growing individuals (of the same population) that do all what fish do, except growth (hence Q_{maint}, i.e., Q for maintenance). Moreover, as shown algebraically by Pauly (1984), the threshold ratio Q_m/Q_{maint} is numerically equal to L_{max}^D/L_m^D , where $D = b(1-d)$, here called as Gill Growth Pointer (GGP), b is the exponent of a length-weight relationship, with b usually ≈ 3 (Froese 2006), and d ranging from 0.6 to 0.9, and usually estimated from the relationship in Figure 1 (i.e., Equation 26 in Pauly 1981), here called as Gill Growth Index (GGI).

Table 1. Studies establishing the existence and similarity of the numerical value of a spawning threshold (i.e., L_{max}^D/L_m^D) in various groups of bony fishes.

Group of teleosts	L_{max} or L_∞ range (cm)	Number of species	Number of 'cases'	Estimate (± s.e.)[a)]	Reference
Miscellaneous (mainly) marine species[b)]	1.9 -250	34	56	1.36 (± 0.06)	Pauly (1984)
Freshwater salmonids in Idaho, US.	11.0 -48.1	4	51	1.35 (± 0.04)	Meyer and Schill (2021)
Cichlid fish from 3 continents	4.2 - 55	7	41	1.35 – 1.40	Amarasinghe and Pauly (2021)
Chinese freshwater and marine fish	5.3-102	117	241	1.40 (± 0.021)	Chen *et al.* (2021)
Freshwater and marine fish in/around Turkey	2.5 - 219	57	120	1.44 (± 0.035)	Keskin and Pauly (2023)
22 of 25 sturgeon species[c)]	116-323	22	22	1.35 (± 0.03)	Chu and Pauly (2024a)
Indian Ocean pelagics	26.2 - 311	18	18	1.36 (± 0.04)	Gunwardane *et al.* (2024)
Indo-Pacific & Atlantic coral reef fish	1.8 - 176	131	207	1.35 (± 0.02)	Chu and Pauly (2024b)
'All' teleosts	1.8 - 311	390	756	1.37 (± 0.02)	New value; see also Warren and Pauly (2024, figure 2a)

a) As computed by Microsoft Excel for the slope of a linear regression with the intercept set at zero.
b) A table including the raw data used for this study was included in the Supplementary Materials of Pauly (2021a).
c) This excludes the Syr-Darya and Chinese sturgeons, both extinct, and beluga, a manifest outlier.

The mean spawning threshold of 34 species in 56 populations of bony fishes estimated as 1.36 (± 0.06) by Pauly 1984, which was later confirmed by a large number of studies (Table 1).

All of the individual L_{max}, L_m and D estimates used for the studies in Table 1 are now included in FishBase or will be in subsequent releases, along with estimates for other bony fish, and for Chondrichthyes (from Warren 2023), most of which, however, have significantly lower values of L_{max}^{D}/L_m^{D} for reasons explained in Warren and Pauly (2024).

Stored primarily in the MATURITY table, $L_{\max}$ and L_m must always originate from the same study with the same length type, hence $L_{\max}$ is not the maximal length of the species, but of the sample used in the study (field name: $L_{\max}$*Sample* to avoid ambiguities). However, the length type used in MATURITY and MATURITYGILLS may differ, so they both need to be stored independently. Note that the asymptotic length L_{inf} may also be used instead of L_{max}.

List of methods to compute the D-values

- From D = 3(1-d), with d from Equation 26 in Ref. 2015
- From D = b(1-d), with d from Equation 26 in Ref. 2015
- From D = 3(1-d), with d from a study of O2 consumption
- From D = b(1-d), with d from a study of O2 consumption
- From D = 3(1-d), with d from a study of gill surface area
- From D = b(1-d), with d from a study of gill surface area
- From D = 3(1-d), with d assumed to be 2/3
- From D = b(1-d), with d assumed to be 2/3
- From D = 3(1-d), with d set at an assumed value
- D = b(1-d), with d set at an assumed value

For the two last options, the assumed d-value is indicated in the Comments.

Graphs

Currently, graphs are available to display the L_{max}^{D}/L_m^{D} ratios for the following groups:

<u>For Chondrichthyes - Cartilaginous fishes:</u>

All (sharks, skates and rays, chimaeras); Selachii (sharks); Holocephali (chimaeras); Marine Batoidea (skates and rays); Freshwater Batoidea (skates and rays); Euryhaline Batoidea (skates and rays).

<u>For Actinopterygii and Sarcoterygii - Bony fishes *sensu lato*:</u>

All (incl. coelacanths and lungfishes); Acipenseridae (sturgeons and paddlefishes); Cichlidae (cichlids); Coral reef fishes; Fishes from China; Fishes from Türkiye.

The graphs for cartilaginous fishes are separate from those of bony fishes because the mean L_{max}^{D}/L_m^{D} ratios of the former are significantly lower than the latter.

Table and fields

Name of the table: **MATURITYGILLS** (linked to the MATURITY table)

Fields:

GGI: Gill Growth Index = *d*, given in publications or computed from *D* (*d*=(*b*-*D*)/*b*).

GGP: Gill Growth Pointer = *D*, given in publications or computed from *d* (*D*=*b*(1-*d*)).

matGillMethod: see the list above.

L_m: length at first maturity.

L_{max}Sample: the maximum length of individuals sampled for the computation of d.

LengthType: TL, SL, HL, WD, Other (specified in Comments).

isLinf: No/Yes indicates if the LmaxSample used is an asymptotic length.

b: exponent of the length-weight relationship used to compute D, if given.

ReproductiveLoadSample: = L_m / $L_{max}Sample$ (RLS).

MaturationThresholdSample: =$L_{max}Sample^D$ / L_m^D (MTS).

Sex*: mixed, male, female, unknown.

Doubtful: if the results seem doubtful: "Yes" or Null. Note: "No" is not an option as it is difficult to assert the reliability in absence of usable criteria.

C_Code*: foreign identifier in the table COUNTRYREF.

E_Code*: foreign identifier (or key, hence "K", as "I" is difficult to differentiate with lower-case "L" – "l", and the "one" digit - "1") in the table ECOSYSTEMREF. Used when the study covers several countries.

Locality*: locality and time period of the catch of sampled individuals.

matGillMainRef_FK: foreign identifier of the main reference used.

matRef_FK: foreign identifier of the reference of the MATURITY data used by the main reference, if relevant.

matGillDataRef_FK: foreign identifier of the reference of original data used by the main reference, if relevant.

Comments: any other comments.

* These fields are possibly extracted for the MATURITY table.

Web site

On the Internet, you can access this table by clicking on the Maturity/Gills rel. link in the:

- 'Info by Topic' section in the 'Search' page.
- 'More information' section in the 'Species Summary' page.

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Daniel Pauly and Nicolas Bailly

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