

Why do fish reach first maturity when they do?

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1 | INTRODUCTION

Why do fish reach first maturity when they do – the question posed by the title of this contribution – is usually not asked by fish biologists. This could be because there seem to be obvious answers, *i.e.*, they reach first maturity when they become adults or they have evolved that way. Nonetheless, a moment of reflection suffices to realize that such “explanations” are either circular (because reaching first maturity means that a fish becomes an adult) or non-explanatory (because everything that fish can do results from their evolution). The explanation provided here relies on the concepts and parameters in Table 1.

Textbooks usually attempt to answer the question in the title question by describing a process supposedly triggered by environmental “stimuli” or “input” experienced at the onset of the spawning season, passed on to the hypothalamus, and thence to a hormonal cascade (Figure 1). Thus, Bhattacharya (1992) wrote the following as caption to what is now Figure 1a: “Hormonal control of reproduction in fishes: Environmental stimuli like photoperiod, temperature, etc., are received by exteroceptors [*sic*] and reach the brain (hypothalamus). Environmental cues result in secretion of GnRH from the brain which in turn causes the release of pituitary GtH. GtH acts on the testis or ovary and stimulates the production of steroid hormones. An exceptional steroid hormone, 17 α , 20 β -diOHprog, released from the testis and ovary induces the final maturation of germ cells leading to spermiation and ovulation (spawning).” and Pankhurst (2016) provided a similar interpretation for a figure, presented in a simplified form as Figure 1b in this study.

Nonetheless, the question of the title remains unanswered. Many longer-lived fishes also experience the environmental input provided by successive seasons for several years as fully formed juveniles. They have eyes to see the stimuli and hypothalamus and pituitary to process them; yet they do not mature and spawn (Table 2; Figure 2). Note that this does not change if the stimuli for spawning are only experienced at specific places because the question would then become, why do pre-maturing fish fail to move to those unique places?

One of these unique places is the Sargasso Sea (Deelder, 1984), in which the female European eel *Anguilla anguilla* spawns after up to 3 years as a leptocephali (Tesch, 1977), and 9–20 years as yellow and silver eels, with males spending only 6–12 years in the later stages (Bauchot, 1986). This implies that the pre-adults remain for several years nearly ready to undertake the arduous trek to the Sargasso Sea, but lack a trigger to commit themselves to it.

This is similar to the snapper (family: Lutjanidae), grouper (family: Serranidae) and other fish that, at specific times of the year, swim to the specific site of spawning aggregations (Sadovy & Domeier, 2005), often at the edge of the shelf (Heyman & Kobara, 2011). Here again, this is only a specific part of the population (*i.e.*, the fish responding to “aggregation stimuli”) that swims to the aggregation site, whereas others (the pre-adults) may perceive but do not respond to such stimuli.

2 | TENTATIVE ANSWERS TO THE QUESTION

In fish that live several years (*e.g.*, those in Table 2), three distinct time scales can be defined for maturation, spawning and related processes: (a) a longer time scale, during which the size (and thus the age) at which a fish matures for the first time is determined; (b) a medium time scale (months to weeks), during which gonadal maturation takes place, as triggered by environmental stimuli and (c) a short time scale (days to seconds) for those processes that often require the presence of mates, and which occur just before shedding and fertilization of ova (courtship, hydrating of ova, etc.). The “when” in the title of this contribution applies only to the time scale in (a). The elements in (b) and (c) are adequately covered by the processes summarized in Figure 1 and related concepts.

Very few colleagues have perceived the problem posed by the question in the title (Table 3). Iles (1974) saw the problem, but his answer is that the lives of fishes follow a predetermined “growth programme” within which maturation and spawning are performed as a sort of subroutine. Moreover, he failed to formulate any hypothesis that would have helped to identify this “programme” and

TABLE 1 Definitions of the major concepts applying to fishes (excluding live bearing and semelparous species) used in this article^a

Item	Definition
Adult	An individual which has matured and spawned
Asymptotic length, weight or size	The mean length or weight that the individuals of a given species or one of its populations would reach if they were to grow indefinitely (see L_{∞} and W_{∞})
D	A summary parameter, defined as $D = b(1 - d)$, where b is the exponent in an LWR (see d for its definition). Because b is often (approximately) equal to 3 (Froese, 2006), one can also define $D' = 3(1 - d)$; this is not used here
d	In fish, the exponent in the relationship linking gill surface area and body weight, <i>i.e.</i> , $GSA = \alpha \cdot W^d$. Note that d , because it links a surface with a volume, must be < 1 , which is empirically verified
Exteroceptor	A sensory receptor that receives external stimuli
First maturity	The size or age at which a fish elaborates and spawns ova or spermatozoa for the first time
GSA: gill surface area	The surface (<i>e.g.</i> , in cm^2) through which the oxygen in the water surrounding a fish must diffuse to become available to its metabolism. This surface grows according to $GSA = \alpha \cdot W^d$, where α is species-specific variable, W is the body weight and $d < 1$.
Hormonal cascade	The sequence of activation reactions that involve hormones and imply the stepwise amplification of an initial stimulus
Invariant (also "Beverton and Holt invariant")	Here: a ratio whose mean value remains unchanged when estimated from different species and populations with different life-history parameters (particularly L_{max} and L_{∞})
L_m	Length at first maturity, usually taken as the length at which 50% of a cohort reach first maturity, but also applies to a single individual
L_{max}	Usually the maximum length on record for a species or one of its populations
LWR: length-weight relationship	Relationships of the form $W = a \cdot L^b$, where a is species- and population-specific and also oscillates seasonally, whereas b is usually between 2.5 and 3.5, and also oscillates seasonally
L_{∞} , asymptotic length	The mean length that the individuals of a given species or one of its populations would reach if they were to grow indefinitely; except for very large fishes, $L_{\text{max}} \approx L_{\infty}$
Maintenance metabolism	The oxygen consumption of fish that have stopped growing and only maintain their weight
Maturation	The process during which ova or spermatozoa are elaborated within the body of a fish, and leads to ovulation and spermiation
Necessary condition	A necessary condition must be present for an event to occur, but this is not sufficient. For an event to occur, both the sufficient and the necessary condition(s) must be met
Pre-adults	Late juveniles that are ready to mature and spawn but which have not yet done so
Spawning	The release or deposition of ova or spermatozoa, of which some will be fertilized or will fertilize to produce larvae
Stimulus/stimuli	A thing or event that evokes a specific functional reaction in an organ or tissue
Sufficient condition(s)	It is a logical fallacy to assume that an event will occur because sufficient conditions are met. For it to occur, the necessary condition must first be met
T_m	The age at first maturity, usually taken as the age at which 50% of a cohort reach first maturity, but also applies to a single individual
T_{max}	Longevity, usually the maximum age on record for a species or one of its populations
Trigger	Here, as a noun: something causing an action or process to be initiated; as a verb: to initiate, actuate, or set off
Q_m	The oxygen supply (via the GSA) of a fish of size L_m and W_m (<i>i.e.</i> , at first maturity), divided by its weight (<i>e.g.</i> , in $\text{mg} \cdot \text{h}^{-1} \cdot \text{g}^{-1}$)
Q_{maint}	The oxygen supply (via the GSA) of a fish at L_{max} and W_{max} (or L_{∞} and W_{∞}), <i>i.e.</i> , sizes at which it does not grow, but only maintain its size, divided by its weight (<i>e.g.</i> , in $\text{mg} \cdot \text{h}^{-1} \cdot \text{g}^{-1}$)
W_{∞} , asymptotic weight	The mean weight that the individuals of a given species or one of its populations would reach if they were to grow indefinitely. Note that for large fishes, $W_{\text{max}} < W_{\infty}$ (Pauly, 2021)

^aOriginal definitions are based on Pauly (2019, 2021) or modified from FishBase (www.fishbase.org) and other anonymous Internet sources.

implementation mechanism. Moreover, there was apparently no follow-up to this idea. This is possibly because of the dominance of the belief that the ratio of mean length at first maturity (L_m) to asymptotic length (L_{∞}), earlier labelled "reproductive load" by Cushing (1975), is a "Beverton and Holt invariant" or even "invariant" (Charnov, 1993).

The issue here is not only that using the word "invariant" is not explanatory in itself, but that L_m/L_{∞} is not invariant. This was reported

by Froese and Binohlan (2000), who studied the relationships between L_m and L_{∞} (while accounting for other variables or not) in 265 fish species in 88 Families. They obtained an average scaling factor of 0.9, and the most straightforward of their empirical relationships is:

$$\log(L_m) = 0.898 \cdot \log(L_{\infty}) - 0.0782... \quad (1)$$

where L_m and L_{∞} are in centimetres.

FIGURE 1 Standard representation of the process supposed to explain why fish spawn when they do. These processes start with generic environmental “stimuli” or “inputs,” which are passed on to the hypothalamus, and thence to the pituitary, etc. Nonetheless, these representations fail to explain how the fish in question, which may have experienced several “spawning seasons” as pre-adults without responding to environmental stimuli or input for maturation and spawning, suddenly begin to do so. [Panel (a) is modified from Bhattacharya, 1992; panel (b) is simplified from Pankhurst, 2016]

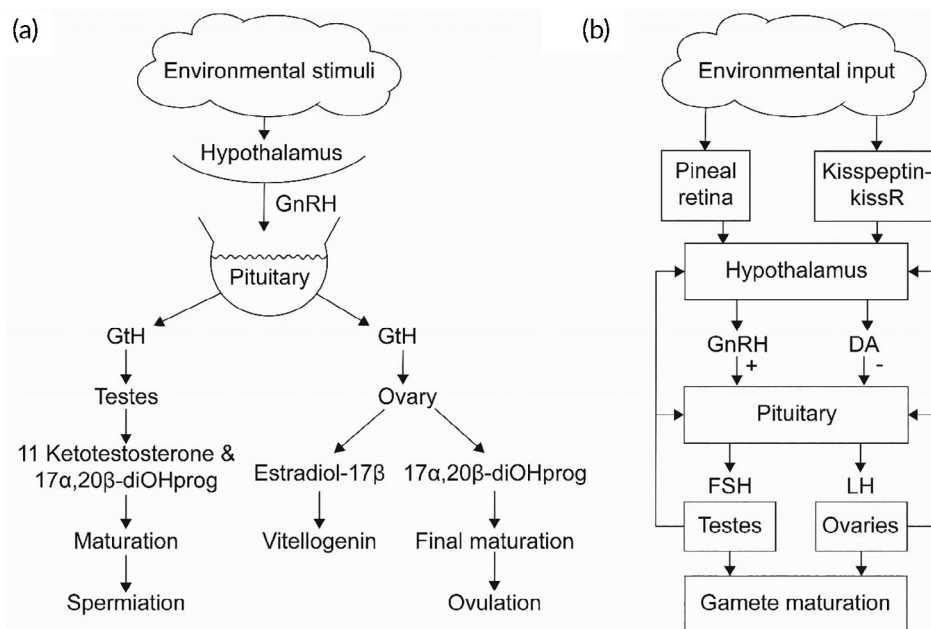


TABLE 2 Age at first maturity (T_m) and longevity (T_{max}) of 10 long-lived fish, i.e., species whose pre-adults experience multiple “spawning seasons” without spawning

Species	Location	T_m (years)	T_{max} (years)	References
Lingcod <i>Ophiodon elongatus</i>	California Current	4	16	Shanks and Eckert (2005)
Alaska pollock <i>Gadus chalcogrammus</i>	Eastern Sea of Okhotsk	4-5	25	Sergeeva (2003)
Pacific cod <i>Gadus macrocephalus</i>	Bering Sea and Aleutian Islands	6	18	Witherell (1996)
Southern sand flathead <i>Platycephalus bassensis</i>	Southern Australia	7-9	21	Brown (1977)
Dusky grouper <i>Epinephelus marginatus</i>	Southern Mediterranean	12	50	Tsikliras and Stergiou (2015)
Lake sturgeon <i>Acipenser fulvescens</i>	Nottaway River	20	154	Magnin (1966), Anderson (1954)
Kaluga <i>Huso dauricus</i>	Amur Estuary	21	80	Koshelev and Ruban (2012), Sytova et al. (2004)
White sturgeon <i>Acipenser transmontanus</i>	Fraser River, B.C.	11-34 ^a	104	Semakula and Larkin (1968) Rien and Beamesderfer (1994)
Giant grenadier <i>Albatrossia pectoralis</i>	North Pacific	23	56	Tuponogov et al. (2008)
Orange roughy <i>Hoplostethus atlanticus</i>	New Zealand	34	93	Doonan (1994), Andrews et al. (2009)

^aThese estimates are confirmed by Doroshov et al. (1997), who also mention that males “reach puberty at a younger age” and that “cultured females reach puberty at a considerably younger age compared to wild fish.”

Equation (1) implies that fish with $L_{\infty} = 10$ cm will become mature at 6.6 cm, whereas fish with $L_{\infty} = 1000$ cm will become mature at 412 cm. Thus, the ratio L_m/L_{∞} is not invariant.

This brings us to the proposed explanations based on life-history theory (Roff, 1984; Parker (1992). This theory shows that the L_m values selected by the fishes of a given population will lead to evolutionarily stable strategies. This begins with the von Bertalanffy Growth Function (VBGF), i.e.,

$$L_t = L_{\infty} \left(1 - e^{-K(t-t_0)} \right) \dots \quad (2)$$

where t is the age (e.g., in years), L_{∞} is the asymptotic length, K is the growth constant of dimension time^{-1} , which indicates the rate at which L_{∞} is approached, and t_0 is the hypothetical age when $L = 0$. When the VBGF applies, the optimal age at maturity (A_m) in an evolutionarily stable population is:

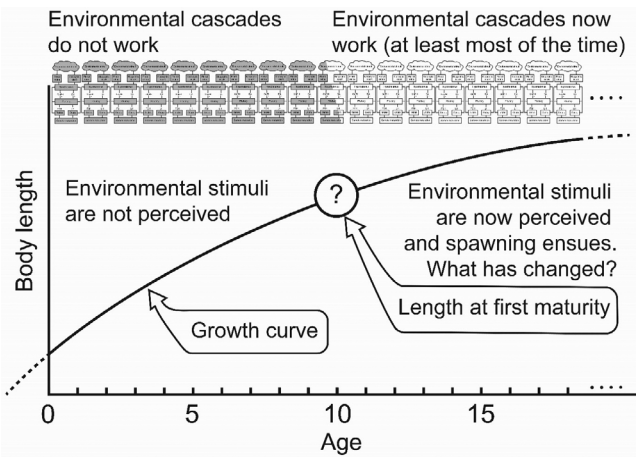


FIGURE 2 Illustration of why the endocrine-only explanation of why fish spawn when they do is incomplete. The pre-adult juveniles of long-lived fish species experience multiple “spawning seasons” where the hormonal cascades shown in Figure 1 should be triggered by environmental stimuli, yet these cascades (here smaller versions of Figure 1b) are not triggered off (grey micro-cascades). Only once a critical size (L_m , W_m) is reached are the environmental stimuli perceived as what they are and responded to (light micro-cascades)

$$A_m = \frac{1}{K} \ln \left(\frac{3K+M}{M} \right) \dots \quad (3)$$

where K is as defined above for the VBGF and M is the pre-maturation, instantaneous mortality rate (Roff, 1984; Parker (1992).

Nonetheless, while Equation (3) may correctly describe the dynamics of growth and reproduction within persistent fish populations, it does not resolve the question in the title, which applies to individual fish. Individual fish know neither their age nor the natural mortality prevailing among the pre-adults of their population and would not be interested if they knew these things.

Here, what is required is explaining how an individual fish “knows” that is the right time for it to mature and spawn, *i.e.*, providing a heuristic that an individual fish can use (Budaev *et al.*, 2019). Thorpe (1990) differs from other authors (Table 3) in understanding that the answer to this question indeed requires a mechanism that pertains to individual fish. His solution is that “in environments providing greater feeding opportunities, fish develop faster and mature earlier. This suggests that it is the physiological performance of the fish during the critical season for initiation of maturation which determines whether it will mature that year. Exactly how the fish monitors its performance is unknown, but the author has suggested elsewhere (Thorpe, 1986) that it is physiologically aware of its growth rate through its rate of accumulation of surplus energy, and through hormone kinetics associated with storage of that energy. If this rate is above a genetically determined threshold, gonadal maturation will be triggered, and reallocation of energy resources to include maturation will be set in train [...] Pauly (1984) put forward essentially the same idea, but focused on the rate of oxygen consumption as the critical indicator of physiological state of the fish.”

3 | A MECHANISM FOR THE JUVENILE-TO-ADULT TRANSITION

Given that the rate of “accumulation of surplus energy,” *i.e.*, the synthesis of new body proteins is directly related to the rate of O_2 acquisition – because O_2 is required for the synthesis of protein, Thorpe’s explanation is compatible with Pauly’s (1984) explanation of why fish reach maturity when they do (see also Imsland, 1999). This explanation was, and still is (Pauly, 2021), that gill surface area (GSA) increases with weight (W) according to

$$GSA = a \cdot W^d \dots \quad (4)$$

with $d < 1$ (De Jager & Dekkers, 1974; Pauly, 2021). This means that as fish grow, their relative gill surface area (GSA/W) declines, and thus, their relative O_2 supply (Q) must decline as well.

The relative O_2 supply at first maturity cannot be as low as the relative O_2 supply at maximum (W_{max}) or asymptotic weight (W_{∞}), both of which may be called Q_{maint} because they correspond to the oxygen supply at a weight that can only be maintained, but not exceeded.

Thus, because the production of gonad material is metabolically costly, Q_m must be higher than Q_{maint} and thus $W_m < W_{max}$ or $W_m < W_{\infty}$ (cf. Figure 3a,c). The question now becomes: given that Q_{maint} differs between the different populations of the same species, *e.g.*, because they are exposed to different temperatures (Figure 3b,d) and between the different individuals of a given population (because some individuals are calm, whereas others are skittish), how does W_m vary when W_{max} varies, or how does Q_m vary when Q_{maint} varies?

Given length–weight relationships (LWR) of the form $W = a \cdot L^b$, one can show that $L_{max}^{b(1-d)}/L_m^{b(1-d)}$ is mathematically equivalent to Q_m/Q_{maint} (Pauly, 1984). Nonetheless, to simplify things, given that in most LWRs, the exponent b equals 3, or near 3 (Froese, 2006), a new parameter is defined, *i.e.*, $D = 3(1 - d)$. The argument below would be identical if $D' = b(1 - d)$ was defined.

As it turns out, L_{max}^D/L_m^D (and hence Q_m/Q_{maint}) appeared to be invariant in 56 populations and 34 fish species ranging from $L_{\infty} = 2$ to 250 cm. The average ratio was initially estimated at 1.36 (Pauly, 1984), and a 95% c.i. was later calculated, using the method of Fieller (1940), to range between 1.22 and 1.53 (Pauly, 2019, 2021).

Here, the same data (see table S1 in the supplementary materials of Pauly, 2021) were reanalysed while considering the bias caused by an unequal number of cases by species and the phylogenetic disparity of the 34 species included in the analysis (Figure 4a). This corrected the estimate of L_{max}^D/L_m^D to 1.32 (c.i. = 1.17–1.42). Nonetheless, the corrected estimate remains statistically indistinguishable from the estimate of 1.35 by Meyer and Schill (2020), who studied 51 populations in three salmonid species (Figure 4b), from 1.30 (1.17–1.43) in 51 species of freshwater and marine fishes in and around Turkey (Figure 4c; C. Keskin & D. Pauly, unpublished data), from 1.41 (1.37–1.44) in 96 species of Chinese freshwater and marine fishes (Figure 4a; Chen *et al.*, in press) and from 1.35 (1.18–1.53) in the females of 41 natural or feral populations of 7 species of Cichlidae, including 4 tilapia species in Amarasinghe and Pauly (2021).

TABLE 3 Ten examples of reasons the authors gave to explain why the fishes they studied matured when they did^a

Quote (from the authors' abstracts or summaries)	Comment ^b
"The influence of genetic factors seems clear. Nonetheless, ecological factors affecting condition or growth rate of the fish seem also to be involved. Interdependence between age of maturation and size was found within families, although no minimum size need be attained before the maturation process starts." (Nævdal, 1983)	The author appears confused by seemingly contradictory literature data. No threshold size or age is mentioned
"Fish usually mature as their somatic growth levels off, where energetic costs of maintenance approach energy intake. After maturation, growth also stagnates because of resource allocation to reproduction." (Jonsson & Jonsson, 1993)	The authors suggest "that the control of maturation is linked to size and growth rate" and "genetically programmed"
"Fishes in exploited stocks mature earlier at large of smaller sizes because of both genetic and plastic responses. The latter occur commonly when reduced competition for food leads to faster growth." (de Roos <i>et al.</i> , 2006)	Only "harvesting size" had a threshold in their simulation, not length at first maturity
"Recent observations suggest fishing pressure is driving the evolution of smaller female maturation size in some fish stocks." (Andersen <i>et al.</i> , 2007)	The authors allow the possibility of a lower limit for L_m but did not say why
"Two-dimensional probabilistic maturation reaction norms (PMRNs) define the probabilities that individuals mature as a function of age and size [...] After removing the contribution of variation in growth and mortality, any remaining changes is not necessarily purely genetic. Environmental factors may exist that affect the propensity to mature at a certain size and age." (Kraak, 2007)	Correlational study; no mention of a threshold being required for maturation to be affected
"The results show that the maturation trends in Northeast Arctic cod could be variously interpreted as showing a strong environmental effect, no genetic effect, or a strong genetic effect." (Marshall & McAdam, 2007)	A "critical size or physiological state" is mentioned but without follow-up
"[P]atterns of genetically determined growth and maturation are influenced by mortality rates and density-dependent processes, and maturation and growth parameters interact to mediate the evolution of one another." (Wang & Höök, 2009)	A "maturation length threshold" is mentioned, but its nature is not specified
"Increased mortality from fishing is expected to favor faster life histories, realized through earlier maturation, increased reproductive investment, and reduced postmaturation growth [...] Molecular genetic methods have so far contributed minimally to understanding such fisheries-induced evolution." (Heino <i>et al.</i> , 2015)	No threshold or lower limit is suggested for the size at first maturity
"Probabilistic maturation reaction norms (PMRNs) were used to investigate the maturation schedules of cod, haddock and whiting in the Firth of Clyde to determine if typical length at maturity have changed significantly since 1986. [...] Trends in temperature and abundance were shown to have only marginal effects upon PMRN positions, so temporal trends in maturation schedules appear to have been due to a combination of plastic responses to other environmental variables and/or fishing." (Hunter <i>et al.</i> , 2015)	No threshold or lower limit is suggested for the much-reduced sizes at first maturity of these three species
"Maturation schedules in fish are considered flexible, energy-allocation strategies (Diekmann & Heino, 2007) and there has been a general assumption that there is a nutrition or condition threshold above which maturity will occur." (Lowerre-Barbieri, 2018) ^c	No threshold or lower limit is suggested for the size at first maturity

^aAs obtained from Google Scholar with the search term "cause of maturation in fishes."

^bThe comments refer to the entire papers, not only their abstract.

^cThis book chapter had no abstract, and thus the quote originates from the section on "Maturity," p. 377.

Overall, Figure 4a–e presents the estimates of the ratio L_{\max}^D/L_m^D which are all compatible with each other, and with the first (1984) estimate of this ratio. Jointly, they strongly support the hypothesis that different species of fish, which experience similar hormonal cascades when they spawn, also use similar respiratory stress thresholds as a trigger for these cascades.

Two variants from the proposed mechanisms may also be mentioned here, which, once reinterpreted, actually support the idea of a close relationship between size-related oxygen stress and maturation triggering.

The first is the "abortive maturation" or "skipped spawning" phenomenon (Hickling, 1930; Iles, 1974; Rideout *et al.*, 2005), occurring mainly in young fish. Pauly (2019) suggested that their relatively small size is enough to induce some respiratory stress, but which is not sufficient for the hormonal cascade in Figure 1 to be completed to

spawning. Skipped spawning also appears to occur in abundant year classes, whose individuals must compete for food, which reduces their growth (Folkvord *et al.*, 2014), which is analogous to the case of juveniles not having grown sufficiently.

The other phenomenon that has the potential to be explained is the intermittent spawning in long-lived fishes such as some sturgeon (family: Acipenseridae), which do not appear to spawn every year, as do most adults fish in temperate waters. Instead, they may spawn at intervals of 4–9 years, as Semakula and Larkin (1968) stated for the white sturgeon (*Acipenser transmontanus*).

In the context of the mechanism for the juvenile-to-adult transition hypothesized by Pauly (1984), it is the increase in the mass of living tissues (generating an oxygen demand which is increasingly difficult for the gills to meet) that indirectly produces the stress leading to maturation and spawning. Thus, when a fish

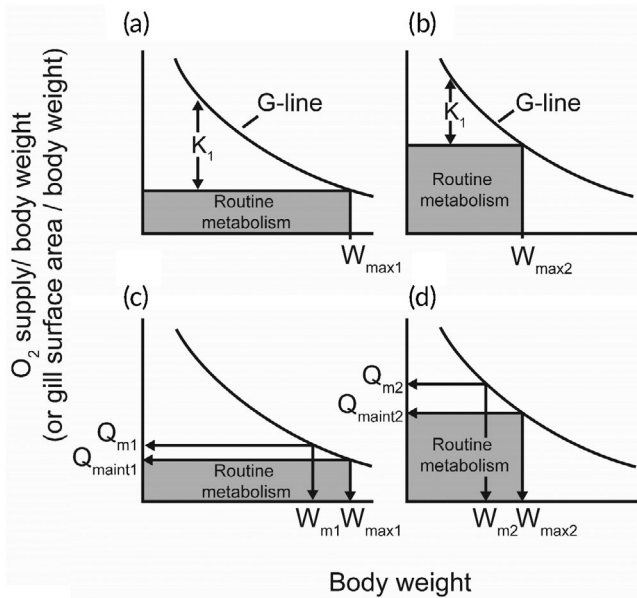


FIGURE 3 Schematic representation of the links, in fish, between respiration, growth and reproduction. In fish, a declining relative gill surface area (G-lines in a–d) and thus oxygen (O_2) supply imposes a limit to body weight (W_{max}) when the oxygen reaches a level just sufficient for maintenance [Q_{maint} in (a)]. When a stress factor (e.g., a higher temperature) increases the O_2 demand for maintenance, the scope for growth (K_1) declines, and 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]

spawns, *i.e.*, loses (gonadal) tissue that previously had to be supplied with oxygen, its relative gill area increases, facilitating its renewed growth until the next spawning season, when the respiratory stress reappears. Nonetheless, in sturgeon (which grow slowly and tend to become very old), several years may pass after a spawning event before their body mass (including incipient gonads) may again cause their relative GSA to drop to the threshold triggering the hormonal cascade in Figure 1.

This hypothesis, if independently corroborated, would further boost the more general hypothesis that it is the tension between the growth of GSA (which limits the supply of oxygen to a fish's body) and the growth of that body (which generates the oxygen demand) which triggers the hormonal cascade leading to gonad maturation and spawning.

4 | DISCUSSION

As Table 3 and Figure 5 suggest, a few authors have sensed that the standard answer to the question in the title is insufficient and that a critical size (or less frequently age) must be reached before fish can respond to the environmental stimuli that supposedly initiate maturation and spawning. Nonetheless, postulating that “size” or “age” influences or contributes to initiating sexual maturation, as illustrated in

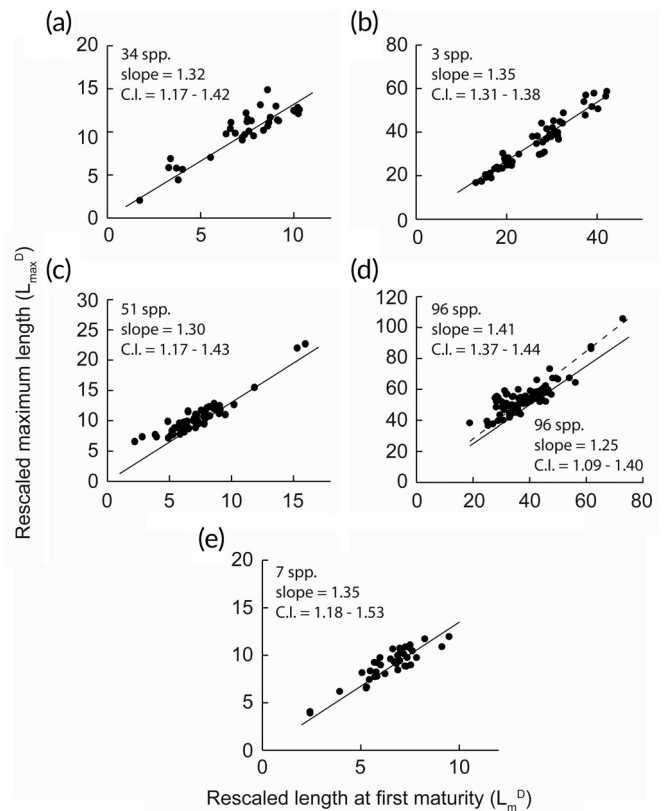


FIGURE 4 This figure shows that the same respiratory threshold triggers reproduction in fish. Estimation of the ratio $Q_m/Q_{maint} \sim 1.35$ in teleost fishes, based on the mathematically equivalent ratio L_{max}^D/L_m^D . (a) Data of Pauly (1984), reduced to the number of unique marine species and accounting for phylogeny; (b) data of Meyer and Schill (2020) on salmonid spp.; (c) C. Keskin and D. Pauly (unpublished data) on freshwater and marine fishes in and around Turkey, including accounting for phylogeny; (d) Chen *et al.* (in press) on freshwater and marine fishes of China, including accounting for phylogeny; note that when phylogeny is considered [as in (d)], the regression lines are shifted to the right and seem not to fit the data; (e) finally pertains to the females of 41 populations in 7 species of cichlids (Amarasinghe & Pauly, 2021)

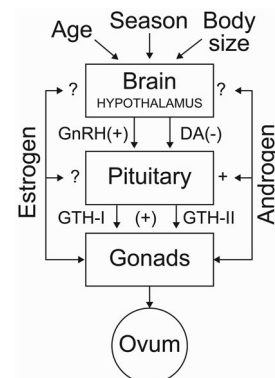


FIGURE 5 Representation of the hormonal cascade in white sturgeon *Acipenser transmontanus* (slightly modified from Doroshov *et al.*, 1997), suggesting that “Age” and “Body Size” somehow impact the onset of maturation, and also implying that “Season” provides the key environmental stimuli

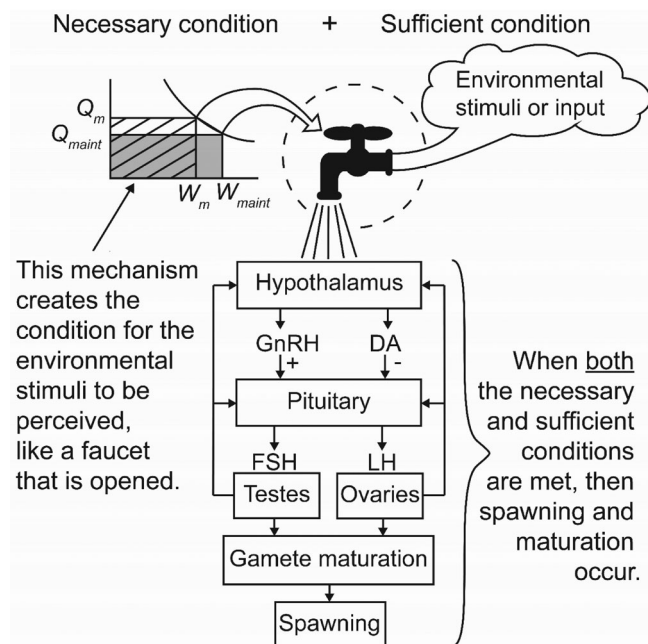


FIGURE 6 Schematic representation of how the *necessary* condition for individual fish to reach maturity may be combined with the *sufficient* condition(s) for their maturation and spawning. A faucet is used here to explain how, before $Q_m \sim 1.35 \cdot Q_{\text{maint}}$ is reached, environmental stimuli for maturation and spawning do not reach the hypothalamus, and thus cannot initiate what they can in larger fish, for which $Q_m < 1.35 \cdot Q_{\text{maint}}$

Figure 5, is not an explanation. A mechanism is still required that links the postulated cause(s) to the initiation of maturation (Figure 6).

The probabilistic maturation reaction norms (PMRNs), which many authors use to present the maturation stages of fish they study as a function of their size and/or age (see Table 3 for examples), only describe the data at hand and do not explain things either.

As outlined in Pauly (2019, 2021), the criterion for an explanation within a scientific (sub-) discipline is that it should “map” the process to be explained onto the consensual knowledge, of a more fundamental discipline. For example, the fact that in over 80% of all fish species the males remain smaller than the females may be explained by the observation that males tend to be more skittish (and/or aggressive) than females, which would imply that they devote more resources (“energy,” *i.e.*, food + oxygen) to moving around and less to somatic growth (Pauly, 2018). There is no need for an infinite regress (*i.e.*, to explain the explanation, etc.) because the proposed explanation relies on the consensual fact, established by physiologists (and aquaculture practitioners), that active fish divert more resources from somatic growth than calm fish. This is also the reason why domesticated fish are less active than their wild counterparts (Vincent, 1960; Pauly, 2019). By this criterion, stating that maturation is “influenced” by age or size is a problem statement, not an explanation.

Some authors who account for the effect of fishing, whether illustrated by a PMRN or not (see Table 3), appear to view fishing-induced changes of length at first maturity as potentially continuous, whereas

others admit to thresholds. Nonetheless, these postulated thresholds are not further examined. Moreover, many contributions devoted to elucidating the dynamics of length at first maturity do so without reference to the further growth of the fish they study, and hence the maximum size they reach (see, *e.g.*, Duponchelle & Panfili, 1998; Meyer *et al.*, 2003). This precludes identifying factors that would simultaneously influence L_m and L_{max} , its strongest correlate (see Figure 3).

The reader will have realized that this contribution has two components, sharply different conceptually and in terms of the evidence they require. The first poses a question that is not part of standard textbooks and other components of the literature on fish reproduction. Yet, it is an eminently legitimate question, and it is strange – and probably bad science – that it is not being asked in the form used here.

The second part of this contribution discusses the few attempts that have been made to answer this question. Of these attempts, it is suggested here that the response provided in Pauly (1984) and elaborated upon in Pauly (2019, 2021), and which has survived repeated tests, is correct.

Put differently, the idea is that in individual fish, once their body growth has led (at W_m) to the decline in relative GSA and reached a critical level of oxygen supply ($Q_m \sim 1.35 \cdot Q_{\text{maint}}$), the *necessary* condition for the fish to respond to environmental stimuli for maturation has been reached. This then leads to the possibility of the *sufficient* conditions needed for the hormonal cascade leading to maturation and spawning to come into effect (Figure 5).

This hypothesis may be wrong, and the colleagues who challenge the triggering mechanisms proposed here may be right. Nonetheless, it must be realized that not agreeing with the explanation provided here leaves the question unanswered: Why do fish reach first maturity when they do?

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