

A reconceptualization of the interactions between spawning and growth in bony fish

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Summary: Among fishery biologists and even ichthyologists, maturation and spawning of fish are viewed as processes that use “energy” that would otherwise be applied to somatic growth, which is supposed to explain why post-maturity growth *in length* tends to decline. This widespread conceptualization may be called the “reproductive drain hypothesis” (RDH). However, when growth is correctly viewed as involving body mass, and is thus expressed *in weight*, post-maturity turns out (in iteroparous bony fish whose maximum length exceeds 10 cm) to accelerate after first maturity, despite its energy cost. This, and other common observations flatly contradict the RDH, and the time has come to withdraw this hypothesis. As a contribution towards this task, we propose an alternative reconceptualization of fish spawning consistent with what is known about fish biology.

Keywords: Von Bertalanffy, reproductive drain, maturation, gill-oxygen limitation theory (GOLT).

Reconceptualización de la interacción entre desove y crecimiento en peces óseos

Resumen: Los biólogos pesqueros e incluso los ictiólogos tienden a ver la maduración y el desove de los peces como procesos que usan “energía” que, de otro modo, sería aplicada al crecimiento somático, lo cual se supone que explica por qué el crecimiento post-maduración, en lo que se refiere a *longitud*, tiende a declinar. Esta popular conceptualización puede ser denominada “Hipótesis del Drenaje Reproductivo” (RDH). Sin embargo, cuando el crecimiento es visto de manera correcta como un proceso que involucra el volumen o masa corporal y, por lo tanto, se expresa *en peso*, la post-maduración (en peces óseos iteróparos cuya longitud máxima supera los 10 cm) se acelera luego de la primera maduración, a pesar de su costo energético. Esta, y otras observaciones comunes, contradicen la RDH y, por lo tanto, ha llegado el momento de jubilar esta hipótesis. Para contribuir con esta tarea, se propone una reconceptualización alternativa del desove en peces, la cual es consistente con el conocimiento existente sobre la biología de los peces.

Palabras clave: Von Bertalanffy, drenaje reproductivo, maduración, Teoría de la Limitación del Oxígeno Branquial (GOLT)

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INTRODUCTION

Fish spawning is a process that fisheries scientists and ichthyologists are familiar with, so much so that for several decades they have failed to re-examine whether their view of this process is compatible with all the specifics we also know about spawning.

Figure 1 illustrates the conventional conceptualization of fish spawning, in which it is perceived as a costly process wherein “energy” is transferred from somatic to gonad growth, thus abruptly impacting on somatic growth (which is strangely and erroneously viewed as a linear process). Thus, depending on the extent of the “energy” transfer, somatic growth is slowed down or even stopped. However, it is generally not appreciated that this conceptualization, of which multiple variants exist (see, e.g., Hubbs 1926, Charnov 2008, Quince et al. 2008), is only a hypothesis which, like all scientific statements about the world, is subject to being rejected if it is incompatible with well-established facts.

The first and perhaps most important reason for the survival of this conceptualization—here called the “reproductive drain hypothesis” (RDH)—is that its outward plausibility rests on the representation of growth as proceeding in length, which it does not, as “energy” certainly does not have the dimension of length. Once somatic growth is—correctly—viewed in terms of mass or weight (Fig. 2), the RDH is refuted. As soon as (iteroparous) fish can reach a maximum weight exceeding a few grams, they tend to reach first maturity at sizes below that at which they experience their highest growth rate.

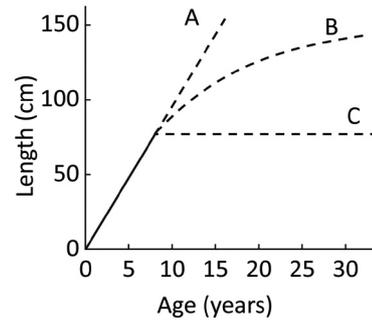


Fig. 1. – Representation of the “reproductive drain hypothesis”, i.e. the notion that reaching the size at first maturity relationship causes previously “linear” growth (line A) to decline due to “energy” previously used for somatic growth being transferred to the elaboration of gonads, with line B implying a small and line C a large transfer of “energy” (modified from Figure 2 in Lester et al. 2004).

Thus, the transition from “energy” transferred from somatic growth to the elaboration of gonads is a case of the post hoc, ergo propter hoc fallacy that considers that an event (1) is the cause of an event (2) simply because event (1) occurred before event (2).

Earlier authors, notably Iles (1974), have also noted that the usual narrative does not make sense. Thus, he wrote, with regard to the age and size at first maturity of fish that “[d]espite the fact that at some time during this stage of the life history large quantities of protein, ultimately derived from the same food sources that sustain body growth, will be newly required for gonad development, there is no indication that the growth pattern is disrupted or disturbed. Indeed, under ‘normal’ con-

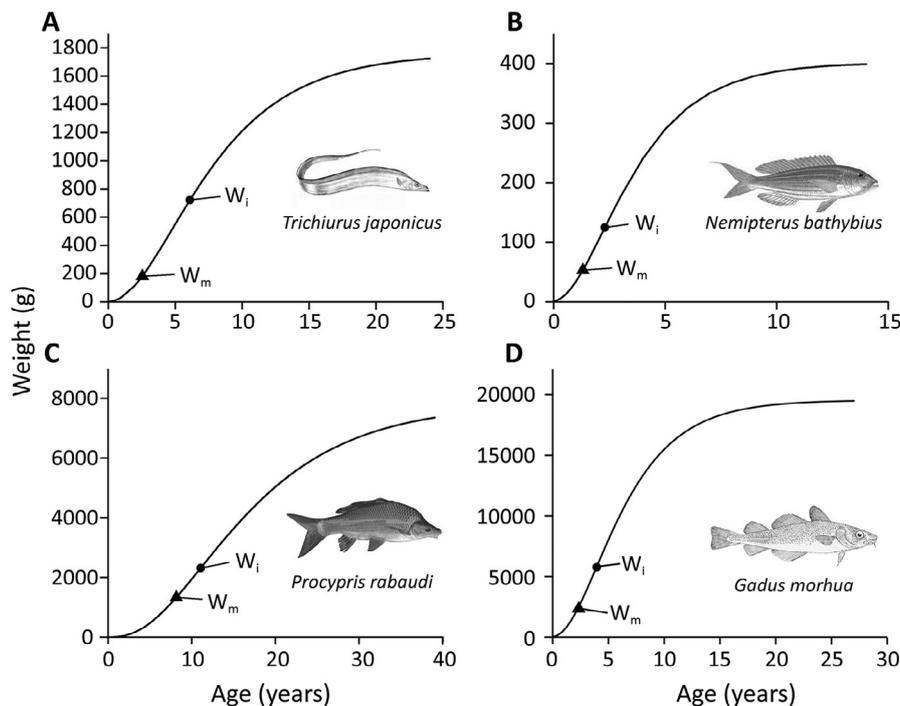


Fig. 2. – Illustrating the fact that, when growth in weight is considered, in fish reaching more than about 10 cm maximum length, the weight at first maturity (W_m) is reached at a size at which growth is accelerating, i.e. well below the weight at which maximum growth rate is attained (at W_i); A, largehead hairtail (*Trichiurus japonicus*), based on data in Shi et al. (2020); B, yellowbelly threadfin bream (*Nemipterus bathybius*), based on data in Li et al. (2009); C, rock carp *Procypris rabaudi*), based on data in Wang et al. (2015); D, Atlantic cod (*Gadus morhua*), based on data in Le Franc (1970).

ditions it appears that it is singularly unaffected by the new physiological and metabolic demands which the fish is called upon to meet. The fact that, for most species of fish, unlike those of mammals and birds, growth continues after the attainment of the adult stage is one of the most characteristic features of the growth of fishes”.

However, the “programme” that he then proposed as an alternative did not explain how fish manage to spawn at the “right” size, i.e. at the size that is a predictable fraction of the maximum size they can reach in a given environment. (Pauly 2019).

In the following, we present a reconceptualization of spawning based on Pauly (2019, 2021a, 2019b) and evidence presented on Chen et al. (2022) and other authors. However, before this can be presented, a brief review of fish growth and related matters is necessary.

MATERIALS AND METHODS

Since Pütter (1920), the growth rate (dW/dt) in fish and other animals is often conceived as a differential equation

$$dW/dt = HW^d - kW \quad (1)$$

where W is the weight (i.e. mass), H is the rate of synthesis of body, $0 < d < 1$ is the exponent of a relationship of the form $S = \alpha \cdot W^d$ which limits protein synthesis, and k is the rate of protein denaturation, or, more precisely, the rate by which denaturation exceeds the refolding of spontaneously unfolding protein.

When $d=2/3$, corresponding to $S=\alpha \cdot L^2$ and $W=a \cdot L^3$, the integration of Equation 1 into a growth curve is the von Bertalanffy Growth Function (VBGF), which for growth in length has the form

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

where L_t is the mean length at age t of the animals in question, L_∞ is their asymptotic size, i.e. the mean size attained after an infinitely long time, K is a growth coefficient (here in year⁻¹; with $k=3K$) and t_0 is a parameter adjusting for the fact that the VBGF usually fails to describe the growth of the earliest (larval) stages of fish (see also Table 1).

For growth in weight, this becomes

$$W_t = W_\infty \cdot (1 - e^{-K \cdot (t - t_0)})^3 \quad (3)$$

Table 1. – Definitions of the parameters (and their units), symbols and acronyms used in this contribution.

Item (unit)	Definition
α	Proportional to...
α	Multiplicative term in relationship linking gill surface and weight, i.e. $S = \alpha \cdot W^d$
a	Multiplicative term of a length-weight relationship, i.e. $W = a \cdot L^b$
A	Threshold value of $L_{\max}^D / L_m^D \sim 1.35$, corresponding to $Q_m / Q_{\text{maint}} \sim 1.35$
b	Exponent of a length-weight relationship, i.e. $W = a \cdot L^b$
d	Exponent in a relationship linking respiratory surface and weight, i.e. $S = \alpha \cdot W^d$
D	$D = b(1-d)$, used to simplify some equations; note also $D' = 3(1-d)$
dW/dt	Growth rate
H	Coefficient of anabolism, i.e. of protein synthesis
k	Coefficient of catabolism; here: of protein denaturation. Note: $k = 3K$
K (year ⁻¹)	In the VBGF, the rate at which asymptotic size is approached
L (cm)	Any measure of length, with L_t the length at age t
L_∞ (cm)	Asymptotic length in the VBGF, as reached after an infinitely long time
L_m (cm)	Mean length at first maturity in a given population
L_m / L_∞	Reproductive load, usually close to L_m / L_{\max}
L_m / L_{\max}	Reproductive load, usually close to L_m / L_∞
L_{\max} (cm)	Maximum length in a given population; generally close to L_∞
LWR	Length-weight relationship, of the form $W = a \cdot L^b$
Q_m	Weight-specific oxygen consumption at first maturity
Q_{maint}	Weight-specific oxygen consumption at maximum or asymptotic weight
RDH	Reproductive drain hypothesis
RL	Reproductive load, i.e. L_m / L_{\max} or L_m / L_∞
S (cm ²)	A surface; here respiratory surface, i.e. gill surface area, as in $S = \alpha \cdot W^d$
t (year)	Absolute age; relative age = $t - t_0$
t_0 (year)	The usually negative “age” at $L = 0$ predicted by the VBGF
W (g)	Weight (or mass); W_t is weight at age; here fresh, or wet weight
W_∞ (g)	Asymptotic weight in the VBGF, as reached after an infinitely long time
W_i (g)	Inflexion point of a growth curve in weight, i.e. weight at which dw/dt is highest
W_m	Mean weight at first maturity; weight corresponding to L_m

where W_∞ is the weight corresponding to L_∞ , all other parameters are defined as above and the exponent ($b=3$) at the right is justified by the fact that it is the most common exponent of the length-weight relationship (LWR) in fish (Froese 2006, Hay et al. 2020, see also FishBase: www.fishbase.org).

Equation (2) has no inflexion point (dL/dt declines linearly with length), but Equation (3) has an inflexion point (W_i , where dW/dt is at a maximum) at $W_i = 0.296 \cdot W_\infty$.

Pauly (2019, 2021a) interpreted Pütter's equation in terms of the oxygen required for synthesis of native protein (the first term on the right side of Equation 1) and to replace denatured proteins (the second term on the right side of Equation 1). In this interpretation, d refers to the respiratory surface area of the gills or similar organs, i.e. 2-D structures whose growth cannot keep up with that of a 3-D body requiring oxygen. Hence, $d < 1$ and generally ranges between 0.55 and 0.95 in fish and other metazoans that breathe water (De Jager and Dekker 1974, Pauly 1981).

When $d \neq 2/3$, the VBGF is "generalized" and becomes

$$L_t = L_\infty \cdot (1 - e^{-K \cdot D(t-t_0)})^{1/D} \tag{4}$$

for length, and

$$W_t = W_\infty \cdot (1 - e^{-K \cdot D(t-t_0)})^{b/D} \tag{5}$$

for weight, where $D = b(1 - d)$ and where b is the exponent of an LWR of the form $W = a \cdot L^b$, with b generally 3, or near 3 (see above).

Equation 4 has an inflection point when $D \neq 1$ at age $t_i = t_0 - (\ln(D)/K \cdot D)$ and length $L_i = L_\infty \cdot (1 - e^{-(\ln(D))^{1/D}})$, while Equation (5) has an inflection point at age $t_i = t_0 - (\ln(D/b)/K \cdot D)$ and weight $W_i = W_\infty \cdot (1 - (D/b))^{b/D}$, which implies

$$W_i / W_\infty = (1 - (D/b))^{b/D} \tag{6}$$

In practice, the difference between the standard VBGF (Equations 2 and 3) and the generalized VBGF can be neglected when fitting a set of age-at-length, tagging-recapture, or length-frequency data with a growth curve, especially in fishes where the growth of gill surface area does not differ much from the $2/3$ value assumed in the standard VBGF (i.e. up to $d \approx 0.85$). This is the case for small fishes, e.g. coral fishes and small pelagic fishes, such as herrings, sardines and anchovies, where $d \approx 0.75$, and medium-sized species, e.g. carp or cod, where $d \approx 0.80$ (De Jager and Dekker 1974; see also Fig. 3). Only with higher value does the fit of the standard VBGF became problematic, e.g. in the case of Atlantic bluefin tuna (*Thunnus thynnus*), where $d = 0.90$ (Muir and Hughes 1969), notably because the estimates of asymptotic length (L_∞) that are generated by fitting the equation to reliable age-at-length data tend to be much larger than the maximum length (L_{max}) in a given population, which is not the case when the special VBGF is used (Pauly 2021a). As the overwhelming majority of applications of the VBGF are to species in which d is relatively close to

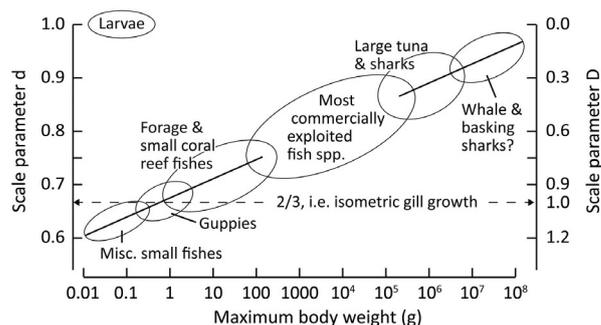


Fig. 3. – Showing that in fish, the parameter d and D are related to the maximum weight reached by various taxa (modified from Figure 2 in Pauly 1981); the straight line is based on the relations $d = 0.674 + 0.0357(\log(W_{max}))$, with live weight in g.

$2/3$ (see FishBase: www.fishbase.org), the fact that the standard VBGF differs slightly from a physiologically correct equation is usually ignored. This is also what was done here.

It is well-established that the mean length at first maturity (L_m) of the individual in a given population of iteroparous fish is a predictable ratio of the asymptotic length (L_∞) or maximum length (L_{max}) and generally ranges from 0.4 to 0.6 in fish that reach larger sizes and from 0.6 to 0.8 in fish that remain small (Beverton and Holt 1959, Pauly 2021a). Thus, this ratio does not deserve the name "Beverton and Holt invariant" that Charnov (2008) gave it. Rather, we use here the term "reproductive load" for the L_m/L_∞ (or the similar L_m/L_{max}) ratio as used by Cushing (1981), which resonates with the RDH mentioned above.

That reproductive loads are not invariant, but vary systematically among fishes of widely different sizes was demonstrated by Froese and Binohlan (2000) who, based on data from 265 fish species from 88 Families and 27 Orders in FishBase (www.fishbase.org), derived the relationships:

$$\log(L_m) = 0.898 \cdot \log(L_\infty) - 0.0782 \tag{7}$$

where L_m and L_∞ are in cm.

This model expresses that fish with $L_\infty \approx 10$ cm will have L_m values of 6 to 7 cm, while fish of $L_\infty \approx 100$ and 1000 cm will have L_m values near 50 and 400 cm, respectively.

In the following, we present corroborations of the gill-oxygen limitation theory (GOLT; Pauly 2019, 2021a) that result from following up on these considerations.

RESULTS

Because their gill surface area, with $d < 1$, which supplies oxygen to their growing bodies, cannot keep up with their weight, and hence with their oxygen demand, relative oxygen supply declines with body weight. This decline of relative oxygen supply has its limit when $HW^d - kW = 0$, i.e. when the oxygen supply meets only the requirements for maintenance (Q_{maint}), with nothing left for further somatic growth. Pauly

(2019) and Pauly and Liang (2022) elaborate on the seasonal trade-off allowing the elaboration and release of reproductive products under these conditions.

It is evident that gonads, which require oxygen for their synthesis, will have to be elaborated when fish are smaller than L_{max} and hence their relative oxygen supply higher, i.e. $Q_m > Q_{maint}$, where Q_m is the relative oxygen supply at first maturity. Also, it can be shown that, given LWR of the form $W = a \cdot L^b$ and gill surface area-body weight relationship of the form $S = \alpha \cdot W^d$, the ratio L_{max}^D / L_m^D is equivalent to the ratio Q_m / Q_{maint} (Pauly 1984).

Numerous studies covering hundreds of species suggest that in growing iteroparous bony fishes maturation and spawning is initiated when a threshold ratio $L_{max}^D / L_m^D \sim 1.35$ is reached, as was first demonstrated for 56 populations of marine fish in 34 species by Pauly (1984) and confirmed for 51 populations in 3 freshwater salmonid species by Meyer and Schill (2021), for 41 populations in 7 species of cichlids by Amarasinghe and Pauly (2021) and for 241 populations in 132 freshwater and marine species by Chen et al. (2022). This established that the threshold ratio $L_{max}^D / L_m^D \sim 1.35$ acts as a heuristic (*sensu* Budaev *et al.* 2019) which individual fish can rely on (Pauly 2021b) and which is compatible with life-history theory (Morbey and Pauly 2022). We shall use the label $A = L_{max}^D / L_m^D \sim 1.35$ because it signifies a beginning (in German *Anfang*—the letters of the English alphabet are exhausted).

Given its definition and LWRs, $A = (W_{max}^{1/b} / W_m^{1/b})^D$ and its inverse A^{-1} is:

$$A^{-1} = (W_m^{1/b} / W_{\infty}^{1/b})^D \tag{8}$$

Thus, $A^{-1} = (W_m / W_{\infty})^{D/b}$ or

$$W_m = W_{\infty} (1/A)^{b/D} \tag{9}$$

By combining equation (6) and (9), we obtain

$$W_i / W_m = (1 - (D/b))^{b/D} / A^{-b/D} \tag{10}$$

When $W_i > W_m$, we also have:

$$(1 - (D/b))^{b/D} > A^{-b/D} \tag{11}$$

which implies $(1 - (D/b)) > A^{-1}$. Now, given the definition of $D = b \cdot (1 - d)$, we have

$$d > A^{-1} \text{ implies } W_i > W_m \tag{12a}$$

$$d \approx A^{-1} \text{ implies } W_i \approx W_m \tag{12b}$$

$$d < A^{-1} \text{ implies } W_i < W_m \tag{12c}$$

Thus, while for $d < 1/1.35$ (i.e. 0.74, generally occurring in small, short-lived and often semelparous fishes; see Fig. 3) spawning occurs after their growth rate (dW/dt) has started to decline, this is not the case in larger iteroparous, longer-lived fish in which $d > 0.75$. This explains why, e.g., the maturity of cod and similarly large species occurs well before these fish have spawned (Fig. 2), thus refuting the RDH.

As, an alternative, we propose a new framework for understanding the concept of a “spawning season”. For

simplicity’s sake, we shall here assume one spawning season per year, occurring in the spring (Pauly and Liang 2022), as the extension of the conceptualization presented would here would require further elaboration to account for autumn spawning in temperate fish (Warlen and Burke 1990) or monsoonal spawning in fishes of the Indo-Pacific (Longhurst and Pauly 1987).

This new framework should explain the processes taking place such that various aspects of fish spawning, which had remained unexplained or been treated as anomalies, can be straightforwardly accounted for, i.e. without ad hoc hypotheses. This requires a second heuristic, the “cusp catastrophe”.

The cusp catastrophe, or “cusp”, is one of the seven topological entities which, as shown by Thom (1975), are sufficient to describe *qualitatively* the transitions among a maximum of four “control factors”, and to distinguish areas where the transitions would be smooth from areas where they would be sudden (thus the term “catastrophe”, the cause of many misunderstanding). With its two control factors, the cusp can easily be used to represent sudden transitions between, e.g., two biologically relevant variables (Woodcock and Davis 1980). Our use of the cusp is illustrated by the example of a growth curve in Figure 4, whose insert represents a cusp and the two control factors that adapt it to maturation and spawning events. Thus, our cusps have body size and time (here one year, given one spring spawning season per year) as control factors.

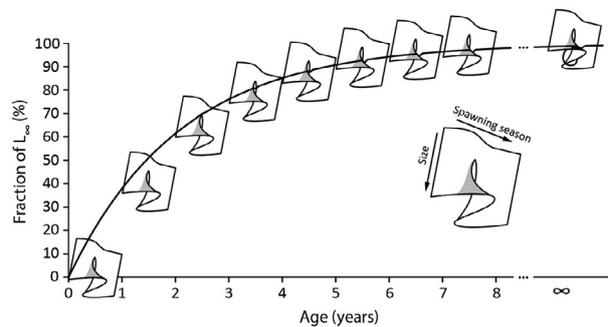


Fig. 4. – A representation of fish growth as a succession of cusps, with the young fish being too small to enter the region (shaded grey) where spawning occurs. This region is approached in pre-adults which may undergo an (abortive) maturation, but fail to spawn. In the year following, however, their size will be higher than that associated with $Q_m / Q_{maint} \sim 1.35$, and maturation and spawning can proceed. In the following years, size increases are associated with a spawning season that starts earlier and ends later, until maximum size is approached, when spawning often occurs repeatedly, and the body weight is reset at a lower value, which allows growth to be re-initiated.

Young fish (age 1 and 2 in Fig. 4) are too small for their A-ratio to have fallen to 1.35, so they entirely avoid the region of the cusp where maturation and spawning occurs. At 3 years, the largest fish of a cohort will mature and spawn, the smallest will not, and the fish of intermediate size may undergo an abortive maturation, i.e. elaborate production of gonads which, however, are resorbed and not shed (Iles 1974; review in Rideout et al. 2005).

This “skipped spawning”, performed “*more often by young and small fish*” and often when food is scarce

(Jørgensen et al. 2006), is therefore neatly explained without requiring elaborate models of trade-offs between reproductive output, growth and survival, which individual fish could not use as heuristic to “decide” whether to spawn or not.

Subsequent growth in year 4 and beyond pushes the fish deeper onto the shaded areas of the cusps in Figure 4, implying that the maturation of larger (older) fish should start earlier than that of smaller fish, and end later in the season, while smaller (younger) fish mature (and spawn) only during the peak of the season. This is confirmed by numerous authors, such as Rijnsdorp (1989) for plaice *Pleuronectes platessa* in the North Sea, and Trippel et al. (1997), who summarized their review by stating that “[t]he importance of female size to recruitment success is reinforced by the observation that large females commonly start spawning earlier in the season [...], continue for longer and produce larger eggs with higher viability than smaller females.”

The cusp often implies that once a phase transition has occurred, the system displays “hysteresis”, wherein the behaviour in question (in this case spawning) loops repeatedly at the highest age in Figure 4, above the ∞ symbol. As it happens, this is precisely the behaviour of large, old fish, which may spawn repeatedly during a spawning season, while small adults usually spawn only once, or even skip spawning. The interpretation of this behaviour is as follows: once a large fish has spawned, i.e., lost some of the tissues that it has to supply with oxygen, it has a higher gill area/body weight than before spawning, and hence it can in principle return to its usual activities, including feeding. This leads to increased body weight, and thus renewed lowering of the gill area/body weight ratio, which can (at least in large individuals) cause rapid re-maturation and repeated spawning (Trippel et al. 1997). This cycle can repeat itself within a spawning season until the temperatures drops and the respiratory stress declines, at which point the reproductive season ends.

DISCUSSION

The case made above was that a heuristic determines the overall readiness of fish to mature and spawn as a function of their metabolic rate (Q) relative to their maintenance metabolism (Q_{maint}). Specifically, in longer-lived iteroparous fish this heuristic readies them to perceive seasonal (i.e. within-year) environmental maturation and spawning stimuli only when the threshold A is reached (see Table 1 and the above equation for the definition and properties of A) and not earlier (Pauly 2021b).

Another heuristic, the cusp, then provides a graphic metaphor for spawning. Indeed, the cusp links three phenomena which to date had not been tied to a common explanatory framework (skipped spawning, size-dependent reproductive seasons and spawning hysteresis). Figure 4 thus represents an integrated view of the life of a long-lived fish as a succession of cusps, each “entered” at another size (corresponding to successive ages), thus implying a different set of responses by the individual fish.

Obviously, maturation and spawning are more complicated than is presented in this account. Notably, these processes involve the release of numerous hormones in response to environmental stimuli (Pankhurst 2016). However, as shown in Pauly (2021b), based on multiple long-lived fish species that fail to respond to such seasonal stimuli during many years (even decades) of pre-adulthood during which they could perceive these stimuli, the “hormonal cascade” leading to maturation and spawning is not self-starting. What is required for such maturation and spawning is an internal state that is related to the size of the fish (Fig. 4), i.e. to their relative oxygen supply.

Finally, the reconceptualization presented here implies that, rather than being, in analogy to humans, the life-threatening and often debilitating event that giving birth is, spawning in fish is a seasonally liberating event, which frees females from a quivering mass of eggs that must be supplied with scarce oxygen and thus enables them to grow again.

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