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Post-spawning growth acceleration in fish as a result of reduced live weight and thus, increased food conversion efficiency

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Abstract The conventional view of spawning in iteroparous bony fish, i.e., the "reproductive drain hypothesis," is based on the observation that somatic growth (in length) slows down noticeably at approximately the time fish attain maturity, and hence the assumption is made that investment in gonadal development slows down growth. However, when this is translated as growth in weight, the weight at first maturity (or puberty) is usually smaller than the weight at which growth rate is highest, i.e., weight growth accelerates after first maturity. We solve this conundrum, with some emphasis on female cod (*Gadus morhua*), by proposing the hypothesis that the substantial loss of body mass experienced by fish as a result of spawning is quickly compensated for by increased somatic growth after the spawning period, notably because of the increase in food conversion efficiency resulting from a sudden loss of body weight, which necessarily leads to a large increase in relative oxygen supply via the gills. This is consistent with the argument developed elsewhere that declining relative oxygen supply by the gills, whose surface area cannot keep up with increasing body weight, is the reason for growth rate declining with weight in adult fish.

Keywords Atlantic cod · Food conversion efficiency · Gill-Oxygen Limitation Theory (GOLT) · Respiration · Somatic growth

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Introduction

A conventional view of the relationship between fish growth and reproduction is that fish grow rapidly until they begin to mature and spawn (see, e.g., Hubbs (1926); Jones (1976); Lagler et al. (1977); Sebens (1987); Day and Talyor (1997); Lester et al. (2004); Charnov (2008); Quince et al. (2008); White et al. (2022)). This view of reproduction being a drain on somatic growth is usually illustrated with growth curves in length, in which, indeed, growth appears to slow down after first maturity is reached, usually past 40–60% of asymptotic length.

However, growth is a process primarily involving weight (or "mass"), and when the mean weight of first maturity (W_m) in most fish populations is plotted onto their growth curve curves in weight, W_m is smaller than W_i, the inflection point of a (von Bertalanffy) growth curve in weight. In other words, in the majority of fish species, growth *accelerates after* first maturity and spawning (Pauly 2021; Pauly and Liang 2022; Froese and Pauly 2023). Exceptions to the observation that $W_m < W_i$ occur, for obvious reasons, in semelparous fishes, and in small fish species with maximum lengths of < 10 cm (see Pauly (2021) or Pauly and Liang (2022) for the likely reason).

The reproductive drain hypothesis is thus refuted: growth in fish is not reduced by reproduction; rather, as succinctly put by Iles (1974) "far from growth depending on maturity, on the contrary, maturity depends on growth."

Here, in support of Iles' dictum, we present evidence that the substantial loss of body mass experienced by females as a result of spawning is compensated for by rapid somatic growth after the spawning period, called "compensatory" or "catch-up growth" by Jobling et al. (1994). We also provide a simple mechanism for what Jobling et al. (1994) calls a "phenomenon [that] is incompletely understood." We point to an alternative hypothesis for the decline of growth with increasing body size and show that fast growth after spawning is one of its predictions.

A revision of the idea that reproduction reduces or stops growth is also needed because the reproductive drain hypothesis continues to be used to inform many current debates about the impact of climate change on fishes and other aquatic animals. The global trend to smaller body sizes at higher temperatures is often explained by a redistribution of energy to earlier reproduction (see, e.g., Wootton et al. (2022); Audzijonyte et al. (2019)). This perspective on the interaction between growth and reproduction at increased temperatures is often based on resource allocation models (Kozłowski et al. 2004) or on the so-called Dynamic Energy Budget (DEB) Theory (Moreira et al. 2022; Lavaud et al. 2021), according to which reproductive investment causes somatic growth to slow down. According to this hypothesis, adult growth continuously competes with reproduction, and the allocation of energy to both processes is a crucial factor in life-histories and one not confounded by other variables (Kooijman 2000).

Another model for which the assumption of reduced growth due to reproductive investment played a major role was developed by Van der Have and De Jong (1996). According to these authors, maximum body size is reduced at higher temperatures because "developmental differentiation" is more temperature-sensitive than growth. Energy is thus thought to be invested in maturation, for example, gonadal development, and less in somatic growth, which would then result in smaller final sizes.

In contrast, we show below that spawning itself, by reducing the body mass which requires to be supplied with oxygen, decreases the mass per unit gill surface area and thus increases food conversion efficiency. This, combined with heavy feeding, quickly compensates for the growth deficit incurred during pre-spawning period, with spawning thus having overall having a minor impact on growth.

Material and methods

A literature search was conducted for reports on the gonadosomatic index (GSI) of fish, i.e., the percent weight of ovaries (or testes) relative to female (or males) body weight in iteroparous gonochoric bony fish, which explicitly covered both the periods before and after spawning events. The literature search, which focused on temperate latitudes, was complemented with original data on relative gonad weights of the 6 main commercial species of fish from the Western Baltic Kiel Bight, Germany, from a monitoring survey conducted in collaboration with commercial fishers in Kiel Bight, Germany (Froese et al. 2020).

The GSI data are complemented with a review of the literature on the immediate post-spawning growth of “spring spawning” fish, i.e., a phenomenon that is typical for the majority of fish species at temperate latitudes. Table 1 defines the parameters and acronyms used in this contribution.

These data are contextualized through interpretation by Pauly (2021) of the growth model of Pütter (1920), i.e., the following:

$$\frac{dW}{dt} = HW^{d} - kW \tag{1}$$

where W is the weight (i.e., mass); H is the rate of synthesis of body proteins; d is the exponent of a relationship of the form $S = \alpha \times W^{\mathrm{d}}$ where S is the surface of the respiratory area which supplies the oxygen required for protein synthesis, and k is the net rate of spontaneous protein denaturation (Pauly and Lam 2023).

Here, the following points are important:

1) The value of the parameter d ranges in fish between 0.6 and 0.9 (De Jager and Dekkers 1974), which implies that as fish grow, the oxygen supply that is provided by their gills gradually declines (irrespective of countermeasures such as the synthesis of novel haemoglobins, increased circulation, reliance on glycolytic enzymes, etc.), which leads to asymptotic growth.
2) Spontaneous protein denaturation, which occurs throughout the body, itself requires no oxygen (Goldberg and St John 1976; Hawkins 1991), but requires that the denaturated proteins be replaced through re-synthesis, which does consume oxygen (Pauly and Lam 2023).
3) Growth ceases when $HW^{\mathrm{d}} = kW$, at which point food conversion efficiency (FCE) = growth increment/food consumed = 0, by definition.

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

Item (unit)	Definition
$\propto$	Proportional to…
a	Multiplicative term in an LWR, relationship, a relationship linking FCE and weight, or linking gill surface and weight, i.e., $S = \alpha \times W^{\mathrm{d}}$
b	Exponent of a length-weight relationship, i.e., $W = a \times L^{\mathrm{b}}$; usually, $b = 3$ or $b \approx 3$
β_1	Exponent of an equation linking FCE with body weight
β_2	Exponent of Eq. 4, also linking FCE with body weight
CF	Condition factor, i.e., $W \times 100/L^3$ (W in g; L = total length, cm)
d	Exponent in a relationship linking respiratory surface and weight, i.e., $S = \alpha \times W^{\mathrm{d},}$
dW/dt	Growth rate, in weight (or mass)
FCE	Food conversion efficiency, i.e., (somatic) growth increment/food ingested (per time period)
GSI	Gonadosomatic Index, i.e., (gonad weight)/(body weight) × 100
H	Coefficient of anabolism, i.e., of protein synthesis
k (year^{-1})	Coefficient of catabolism; here: of protein denaturation; note that $k = 3K$
K (year^{-1})	In the VBGF, the rate at which asymptotic size is approached
L (cm)	Any measure of body length, with L_{t} the length at age t
L_∞ (cm)	Asymptotic length in the VBGF, reached after an infinitely long time
LWR	Length-weight relationship, of the form $W = a \times L^{\mathrm{b}}$
R	Relative respiration rate, i.e., consumption of O_2 divided by body weight
S (cm^2)	A surface; here respiratory surface, i.e., gill surface area, as in $S = \alpha \times W^{\mathrm{d}}$
t (year)	Absolute age; relative age = $t - t_0$
t_0 (year)	The usually negative ’age’ at $L = 0$ predicted by the VBGF
VBGF	Von Bertalanffy growth function; here: Eq. 2
W (g)	Weight (or mass); W_{t} is weight at age t; here: fresh or wet weight
W_∞ (g)	Asymptotic weight in the VBGF, as reached after an infinitely long time

This implies that the growth of fish can generally be described by the von Bertalanffy growth function (VBGF), of the following form:

$$L_t = L_\infty\left(1 - e^{-K(t-t0)}\right) \quad (2)$$

where L_t is the length at age t; L_∞ is the asymptotic length, i.e., the mean length the individuals of a given population would reach if they grew indefinitely (which roughly corresponds to L_{max}, the largest length attained by the oldest fish in a population); K is the rate of dimension time^{-1} (here: year^{-1}; with $k = 3K$) at which L_∞ is approached, and t_0 is the hypothetical age at zero length. The version of the VBGF in (2) assumes $d = 2/3$, which causes slight deviations, ignored here, from a version based on anatomically and physiologically correct values of d (see Pauly 2021). Also, we ignore here seasonal growth oscillations, which can be described by variants of the VBGF (Pauly 2019).

The corresponding model for growth in weight is as follows:

$$W_t = W_\infty\left(1 - e^{-K(t-t0)}\right)^b \quad (3)$$

where W_∞ is the asymptotic weight, usually derived from L_∞ via a length-weight relationship (LWR) of the form $W = a \times L^b$, with b generally having a value of, or near, 3 (Froese 2006), and where $W_\infty \approx W_{max}$, in analogy to $L_\infty \approx L_{max}$.

An important implication of $d < 1$ is that as fish grow, less oxygen is available per unit body weight to turn the ingested food into metabolically useful "energy" (e.g., ATP), which causes large fish to either reduce their relative food intake per unit of time and/or causes them to excrete food-derived compounds "by the gills and kidney as incompletely oxidized nitrogenous compound"—the latter point quoted from Webb (1978), who cites supporting evidence in Forster and Goldstein (1969), Savitz (1969), Olson and Fromm (1971), and Niimi and Beamish (1974).

Pauly (1986) proposed a relationship between food conversion efficiency (FCE = growth increment/food ingested; Gerking 1952, 1971) that is compatible with the VBGF (Silvert and Pauly 1987) and which has the form of the following:

$$\text{FCE} = 1 - \left(W/W_\infty\right)^{\beta_2} \quad (4)$$

where FCE is predicted for a given weight (W) from W_∞ and β_2, the latter being estimated as the slope (with sign changed) of log(1 − FCE) *vs.* log(W), with W_∞ either estimated as the intercept of the regression with the abscissa or entered externally to obtain a compatible estimate of β_2.

Note that either choice implies that FCE at W_∞ or W_{max} must be zero, which is not an assumption but a fact. Thus, fish that have reached their terminal weight or approached their asymptotic weight may live for decades eating much larger rations than they ate when juveniles and still not grow, i.e., they maintain the same seasonally averaged weight. Examples are the orange roughy (*Hoplostethus atlanticus*), which lives without appreciable post-maturity growth for up to 100 years (Fenton et al. 1991); the bluespine unicorn fish (*Naso unicornis*), whose post-maturity growth remains negligible in over 4 decades (Andrews et al. 2016); or other coral reef species such as the parrotfish (Scaridae) "where were clear asymptotic sizes [are] achieved early in life" (Choat et al. 1996; hundreds more could be cited; see FishBase http://www.fishbase.org). This establishes that at W_{max} or near W_∞, their annualized food conversion efficiency (FCE = growth increment/food consumed) must be zero.

Equation 4 provides a better fit than the traditional model (i.e., FCE = $a \times W^{\beta}{}_1$), notably by avoiding prediction of FCE > 1 at very small sizes and values > 0 when $W > W_\infty$, both of which are impossible (Pauly (1986); see also Temming (1994a, 1994b); Temming and Herrmann (2009) for more information on Eq. 4, FCE, and related issues).

The parameters β and W_∞ of Eq. 4 can be estimated via its linearized version, i.e., the following:

$$-\log(1 - \text{FCE}) = \beta_2 \times \log\left(W_\infty\right) - \beta_2 \cdot \log(W) \quad (5)$$

which allow estimating β_2 (with sign changed) of a regression, then W_∞ from the intercept, i.e., β_2·log(W_∞). The β_2-parameter can also be estimated with widely scattered FCE data, as in our case (or even with only one FCE − W data pair) when W_∞ is set externally.

Here, the 17 pairs of FCE estimates for Atlantic cod (*Gadus morhua*) in Table 2 of Edwards et al. (1972) were plotted as −log(1 − FCE) against the corresponding log(W) values, with a regression line forced through an asymptotic weight of 10,000 g being used to estimate

Table 2 Weight of fully mature gonads in percent of the body weight of (mainly) female iteroparous fish from temperate seas and freshwaters, in descending order of the (midrange) percent (GSI) value

Species (sex)	%	Source
Scophthalmus maximus	30+	This study
Platichthys flesus	27–30+	This study
Clupea harengus	25–30	This study; also “20+” in Iles (1974)
Pleuronectes platessa	25–30	This study
Coregonus lavaretus	25–27	Rösch (2000)
Gadus morhua	20–30	Trippel et al. (2014) and this study
Limanda limanda	20–27	This study
Perca fluviatilis	16–28	Le Cren (1951) and Heibo et al. (2005)
Acipenser fulvescens	8–12	McKinley et al. (1998)

the parameter β_2 in Eq. 4. This procedure was performed twice, first with all data points and then without the highest and lowest FCE estimates, which may have been experimental artifacts.

Results

Table 2 shows that the relative weight of the fully mature gonads of temperate fish routinely exceeds 25% of total body weight, which also applies to the 6 species from Kiel Bight (Fig. 1). Spawning thus strongly reduces the weight of fish and their condition factor (CF; see Fig. 2). This pattern is confirmed in both marine species and freshwater fish, even if the latter tend to be lower than the former.

Figure 2 documents visually the loss of weight and the resulting change in body shape (CF = 0.8) following spawning in an (iteroparous) Atlantic salmon (*Salmo salar*) in Newfoundland (see Reddin et al.

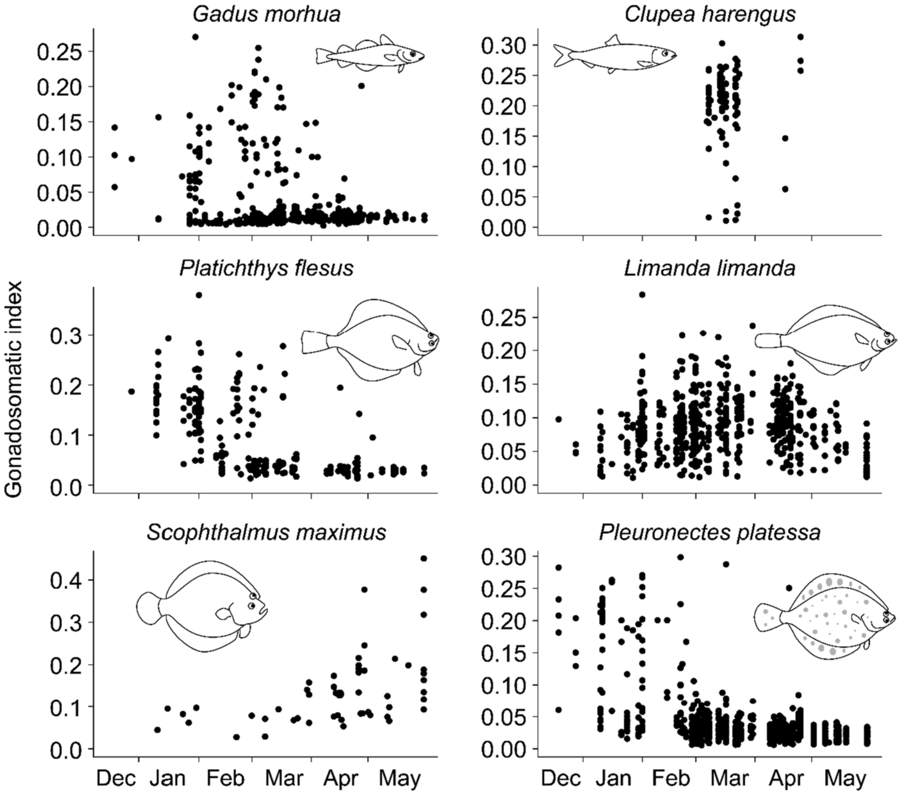

Fig. 1 Gonadosomatic index (ovary weight relative to whole body weight) for females of the main commercial fish species in Kiel Bight in 2020, 2021, and 2022. Note that all species spawn in spring, with flounder (*P. flesus*) and plaice (*P. platessa*) starting in January and turbot (*Scophthalmus maximus*) starting in April/May and that peak ovary weight is near or above 30% of body weight in all 6 species (see Froese et al. (2020) for a description of the project that generated the raw data used to produce this figure)

Fig. 2 Illustrating one aspect of fish spawning that is usually neglected. **a** An Atlantic salmon (*Salmo salar*) immediately after spawning, i.e., a lean 'kelt' of 63.8 cm and weighing 2.06 kg. **b** The same fish 51 days after it spawned, with a length of 66.7 cm and a weight of 2.25 kg. The gill surface area of the kelt (in **a**), which was not reduced by spawning, had a low body mass to supply with oxygen, and hence the kelt's food conversion efficiency was high.

(2011)) and the rapid regain of weight and body shape (CF = 1.0) resulting from less than 2 months of post-spawning feeding with an increased FCE.

Figure 3 illustrates an estimation of the parameter $\beta_2 = 0.089$ in cod, which Table 3 shows as fitting well within earlier estimates of this parameter, in spite of the wide scatter of the Edwards et al. FCE data. Also note that Edwards et al. (1972) also estimated the oxygen consumption (R) in cod, which was related to weight according to $R \propto W^{0.82}$, implying $S \propto W^{0.82}$, where S is gill surface area, and 0.82 is a good estimate of d for cod (see De Jager and Dekkers (1974); Pauly (2021)).

Tables 4 and 5, pertaining to Atlantic cod and to bony fishes in general, respectively, present quotes which stress (1) that fish growth after spawning is very rapid and (2) that this rapid growth is generally attributed to intensive feeding, but not to increased food conversion efficiency, although this is likely to be a major contributing factor to their increasing weight (Fig. 4).

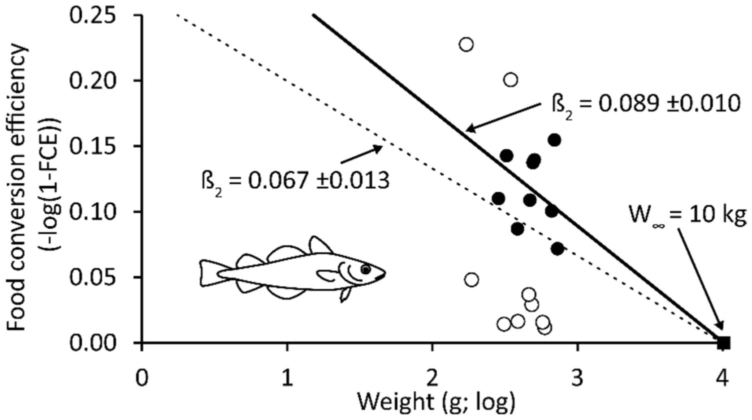

Fig. 3 Food conversion efficiency (FCE = growth increment/food ingested) of Atlantic cod *Gadus morhua* (from Table 2 in Edwards et al. (1972)); fitted with the equation FCE = 1 − $(W/W_\infty)\beta_2$, with $\beta_2 = 0.089 \pm 0.010$ (S.E.) and $W_\infty = 10{,}000$ g (see also Table 3). The open circles, referring to very high and very low FCE values, were considered outliers, if they are included (dotted line), $\beta_2 = 0.066 \pm 0.013$ (S.E.), but this (non-significant) difference has no effect on the logic of argument presented here

Table 3 Estimates of the parameter β_2 relating food conversion efficiency to the weight of fish (see Eq. 4), with the asymptotic weights (W_∞) related to these estimates

Species	β_2	W_∞ (g)	Remarks and source(s)
Holocanthus bermudensis	0.040	800	Pauly (1986), based on Menzel (1958)
Limanda limanda (♀)	0.073	756	Pauly (1986), based on Pandian (1970)
Channa striata	0.077	1290	Pauly (1986), based on Pandian (1967)
Limanda limanda (♂)	0.089	149	Pauly (1986), based on Pandian (1970)
Gadus morhua	0.089	10,000[a]	Figure 2 and Edwards et al. (1972)
Epinephelus guttatus	0.136	1148	Pauly (1986), based on Menzel (1960)

[a]Assuming an asymptotic length of 100 cm and an LWR with $a = 0.01$ and $b = 3$, i.e., likely values for Atlantic cod (Daan 1974; http://www.fishbase.org)

Table 4 Various statement about the occurrence and the putative cause(s) of (i) post-spawning growth acceleration and/or (ii) increase feeding in Atlantic cod (*Gadus morhua*)[a]

Statement	Source
"Ravenous feeding behavior of post-spawning cod […] likely contributed to the lack of an annual somatic cost of reproduction in our study."	Trippel et al. (2014)
"Evidence of post-spawning recovery growth was found in the current study, and high growth rates were maintained throughout the summer months."	Pedersen and Jobling (1989)
"From June to September, the growth rate in female cod was twice the rate of male cod, but in September the weight of the female fish was not significantly different from the male […showing] that the female cod underwent a compensatory growth."	Solberg and Willumsen (2008).
"The data from the surveys do not indicate any large difference in growth between the sexes before maturity, but show slightly higher weights-at-age for females after maturity."	Ajiad et al. (1999)
"During the summer, the […] reproducing fish, having finalized their spawning, showed compensatory growth […which] resulted in similar mean final weights in September."	Korsøen et al. (2013)
"Cod hunt and feed during the [spring] spawning season and lost weight [excluding weight of stomach and gonads] is regained within about two months." [Translated from German]	Froese et al. (2020, p. 14)
"After spawning, compensatory growth occurs in fish, and the peak in growth rates estimated in this study at the beginning of autumn reflects this recovery growth […]."	Mion et al. (2020)
"An abrupt increase in feeding activity, particularly by females, occurred during the last quarter of spawning or shortly after the release of the last egg batch"	Fordham and Trippel (1999)

[a]Figure 2 illustrates why the spawning of cod, by reducing their weight, increases their food conversion efficiency, which would increase their post-spawning growth rate even if their appetite was not elevated (which it is)

Figure 4a, based on combining Eq. 3 with Eq. 4, shows food conversion efficiency (FCE) smoothly declining with age (a result that is independent of the precise estimate of β_2). On the other hand, accounting for the loss of body mass at spawning, i.e., of gametes which consume oxygen supplied via the gills until the moment when spawning occurs generates the more realistic trajectory of Fig. 4b. In this figure, the sudden increase of FCE following spawning is due to body weight decreasing while gill surface area is unaffected by spawning. Combined with the "ravenous" feeding of cod immediately post-spawning (see Table 4), this leads to "phenomenal" post-spawning growth.

Discussion

At the end of their "Reconceptualization of Spawning," Pauly and Liang (2022) suggested that "[f]inally, 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

Table 5 Various statements about the occurrence and the putative cause(s) of (i) post-spawning growth acceleration and/or (ii) increased feeding in temperate iteroparous bony fish

Species	Statement	Source
Acipenser fulvescens	"Since the spawning occurs in June, this [i.e., the markings on bones] would suggest that rapid growth is resumed during that same year, right after spawning, in time to produce a broad annulus for that season"	Roussow (1957)
Clupea harengus	"[…] rapid gonad growth is preceded by rapid somatic growth; the two processes do not run concurrently."	Iles (1964)
Merluccius merluccius	"post-spawning females […] peaks had an accelerated growth, evidencing the recovery after the energy expenditure in spawning."	García-Fernández et al. 2022
Nibea japonica ♀	"They exhibited slow pre-spawning growth, which increased sharply after spawning." [Translated from Chinese]	Mao et al. (2012)
Salmo salar	"The growth of Atlantic salmon during the marine phase can be phenomenal, as evidenced by the consecutive spawning kelts [i.e., post-spawning individuals] in our study that more than doubled in weight in the 44–76 days at sea."	Reddin et al. (2011)
Oncorhynchus mykiss ♀	"[…] growth rate[s] were elevated by 10 weeks after spawning in reproductive (i.e., consecutive spawning) versus non-reproductive (i.e., skip spawning) individuals."	Jenkins et al. (2019)
Oncorhynchus mykiss	"Resumption of growth following breeding subtends the worn edge of the scale[s] of the breeding fish with new scale material and a permanent scar is recorded."	Greeley (1933)
Pleuronectes platessa	"In spring, after spawning and as food intake increases, numerous concentric organic lamellae are deposited […] which jointly form the white, reflecting layers of otoliths." [Translated from German]	Heincke (1908, p. 84-95)
Trachurus mediterraneus	"Our data agree with those of Sirotenko and Istomin (1978) for *Trachurus mediterraneus ponticus*, which increased feeding intensity about 80% after its spawning period"	Jardas et al. (2004)
Exploited fish species in the Azov and Black Seas	"Plentiful accumulation of fat in the postspawning period is not achieved by a reduction of the activity of the fish but, on the contrary, by the maintenance of a high level of activity – vigorous feeding – which may be termed hyperphagia…" [Translated from Russian]	Shul'man (1974, p. 224)
Fish in general	"Following spawning, the energy reserves of fish my be seriously depleted and the fish may be thin and in poor condition. During the post-spawning period the reserves will be replenished, and, provided that food supplies are adequate, rates of weight gain may be very rapid."	Jobling (1994, p. 194-195)

eggs that must be supplied with scarce oxygen, and thus enable them to grow again."

In this study, this idea was turned into a testable hypothesis: the sudden reduction of the live weight (or mass) of fish caused by spawning, which can be as high as 30% and beyond (Table 2), increases their oxygen supply per body weight because their gill surface area is not affected by spawning. This increases their food conversion efficiency (Fig. 4B), for the same reason that increasing weight reduces it, i.e., because the respiratory surface (S) of the gills relates to body weight according to $S \propto W^d$, with $d < 1$, which induces in large individuals an internal hypoxia that reduces growth in a manner analogous to external hypoxia (Chabot and Dutil 1999; Kolding et al. 2008).

Thus, if the fundamental feature of the Gill-Oxygen Limitation Theory (GOLT; Pauly 2021) is correct which holds that the ratio between gill surface area (and hence oxygen supply) and the fish body's demand for oxygen impacts on their growth, then after spawning, fish ought to experience a phase

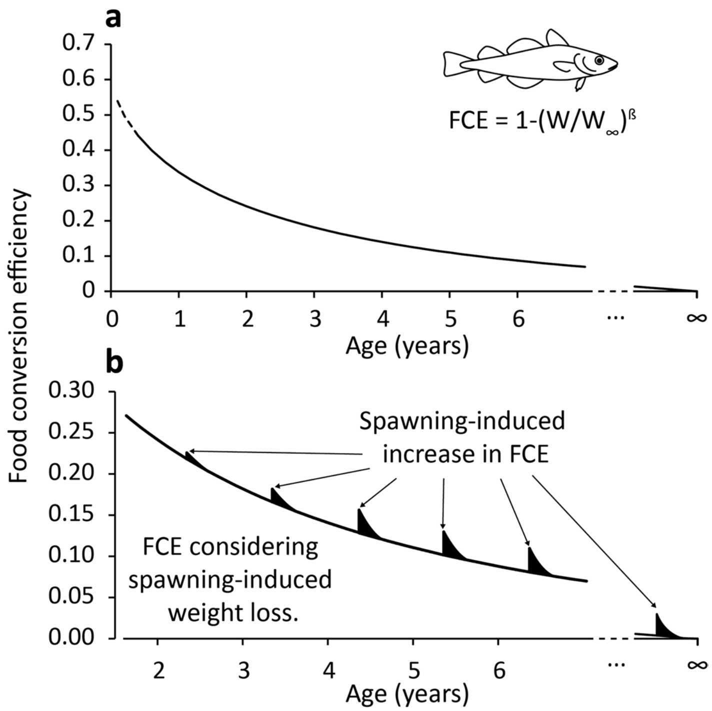

Fig. 4 Plots of food conversion efficiency (FCE = growth increment/food consumed) vs. age for a fish with the parameters $W_\infty = 10{,}000$ g, $K = 0.2$ year^{-1}, $t_0 = -0.1$ year, and $\beta_2 = 0.089$. **a** Without accounting for spawning. **b** Accounting for a spawning-induced loss of 10% of body weight at first spawning (i.e., at 2 years of age), 20% at 3 years, and 30% at 4 years and thereafter, which generates FCE increases of 3% at 2 years, 9.4% at 3, 21% at 4, 28% at 5, and 36% at 6, while the percent increase at $t = \infty$ is not defined. Also, the plot accounts for a 3-month post-spawning weight-recovery period after which FCE is again at the "predicted" level

of accelerated growth. Such an accelerated growth phase is well documented in the literature (Tables 4 and 5), although the cause(s) for this distinct phase is (are) usually not identified. Of course, this phenomenon is often masked/confounded by a number of factors including spawning behavior itself, the rising water temperatures that frequently occur at the time of spring time spawning and/or increased activity of post-spawning fish, including nest guarding.

According to the GOLT, the period of post-spawning accelerated somatic growth is due to more oxygen being devoted to growth because the total weight of fish bodies—which require oxygen for maintenance—is reduced while their gill surface area is not. This necessarily increases the FCE, as shown in Fig. 4b, which then converts increased feeding into a much-increased growth, until the all weight loss is compensated for.

Accelerated growth in fishes and other ectotherms are well-documented, notably by von Bertalanffy (1934, 1951). Endocrinological studies have sometimes described this phenomenon as "compensatory growth" but they often have remained ambiguous about the energetic prerequisites for the increase in somatic mass or only discussed food supply as the decisive factor that enables further growth (e.g., Won and Borski (2013); Caldwell et al. (2013); Jobling et al. (1994)). Ali et al. (2003) highlighted the role of hyperphagia after a period of reduced growth, but without mentioning changes in food conversion efficiency. Converting more food requires an increase an oxygen supply, and this can be realized by the changing relationship between body mass and gill surface area after spawning.

As mentioned above, this contribution does not deal with the seasonal growth of fish, which is largely due to changes in temperatures and its impact on their oxygen supply and demand (Pauly 2019). Thus, Fig. 4 is incomplete, as neither of its panels accounts for the effect on growth of the increase in temperature which usually follows upon spring spawning. However, the point of this contribution is to show that the simple fact of a loss of live weight at spawning is sufficient to explain post-spawning growth acceleration, i.e., to select one from the various hypotheses proposed by Jobling et al. (1994) who wrote that "[the] bulk of the experimental data point to the fact that rates of weight gain increase, and food conversion [efficiency] is improved, in fish recovering from food deprivation. There are undoubtedly several mechanisms involved in producing these responses. These mechanisms may include the development of hyperphagia, changes in energetic expenditure, and improvements in the efficiency of energy utilization."

The first two of these "mechanisms" are mere restatements of the issue at hand; the third happens to correspond to the hypothesis suggested here—with the difference that with Eq. 4 and Fig. 4B, we actually explain how "the efficiency of energy utilization" is improved.

These considerations also imply that *ad hoc* hypotheses to explain why fish feed intensely after, but not before spawning, may be superfluous. One such hypothesis (Trippel et al. 2014) is that "[B]ody size cavity restriction associated with hydrated ovaries may also play a role in limiting ingestion during the gravid state" (Weeks 1996).

However, Michalsen et al. (2008) commented as follows on a study by Hoar et al. (1983): "They suggested that feeding activity could be affected by less space being available in the body cavity for food, or possibly associated with a change in hormone levels during spawning, which might reduce an individual's appetite. As the feeding of male [cod] in our study was suppressed during spawning to an even greater degree than that of females, the thesis of lack of space does not seem convincing."

As for the possible "changes in hormone levels," this was a typical *ad hoc* hypothesis, which would not be informative even if it were tested, because one would not know, after establishing that such changes occurred, that this was the cause for the decline in appetite and not an intermediate step. Rather, it is sufficient to note that pre-spawning gravid females are so challenged by having to supply oxygen to their ovaries that they have little oxygen to direct to the assimilation of ingested food, and thus they stop feeding in the final period before spawning. Then, post-spawning, they can catch up, and as their lower body mass is well supplied with oxygen, their growth for 2–3 months is faster than would be predicted without spawning having taken place.

The argument presented above dealt overwhelmingly with fish species occurring in high latitudes, exposed to strong seasonal fluctuation of temperature and resource availability, resulting in well-defined and relatively short spawning periods. In lower latitudes, where such fluctuations are generally less pronounced, fish spawning tends to occur over longer periods, often related to monsoon winds (Longhurst and Pauly 1987; Navaluna and Pauly 1988). This may be the reason why fishes from lower latitudes, even though they are likely to also rely on FCE-driven mechanism presented above, tend to lower to have lower GSI than fish of higher latitudes, e.g., 4–6% in bluefin tuna (*Thunnus thynnus*) (Heinisch et al. 2008), 3–4% in skipjack (*Katsuwonus pelamis*) (Stéquert et al. 2001), or even 1.3–1.5% in yellowfin (*Thunnus albacares*) (Stéquert et al. 2001).

The recent debate around reproduction and growth in a warming world may have missed the implications of fish growth fluctuating seasonally. For example, Audzijonyte et al. (2019) state that "one key problem with the growth efficiency approaches that rely on a von Bertalanffy function […] is that they ignore the single evolutionary goal of every organism—reproduction." This statement ignores the fact that the asynchrony between seasonal changes in body weight and relative gill surface area generates periods during which food growth efficiency can be very high, which, combined with heavy feeding and a high food conversion efficiency, can quickly compensate for the cost of producing gonad material.

While they do this implicitly, the different versions of von Bertalanffy growth equations, when not modified to include seasonal changes, cannot explicitly account for interactions between growth, feeding, and reproduction. However, seasonalized versions of the VBGF for both length and weight growth exist (review in Pauly 2019); they could be modified to allow transforming the VBGF into model of growth explicitly accounting for reproduction and thus respond to a frequent critique of the standard VBGF.

In summary, it appears the surge in somatic growth rates often seen in fish after spawning is caused by an increase in food conversion efficiency attributable to the weight loss that results from spawning itself.

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Data availability All the data used in this study are presented in its text and figures.

Declarations

Ethics approval No approval of research ethics committees was required as this study analyzed only previously published data.

Conflict of interest The authors declare no competing interests.

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