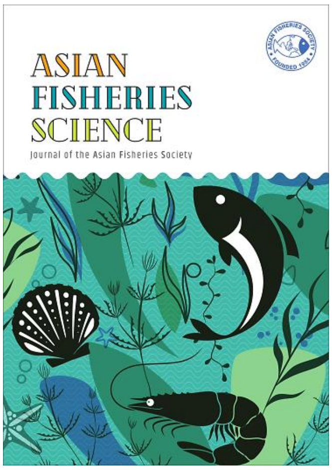

The Relationship Between Size at Maturity and Maximum Size in Cichlid Populations Corroborates the Gill-Oxygen Limitation Theory (GOLT)

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Abstract

Fish generally mature at a smaller fraction of their maximum sizes than birds and mammals. The farmed tilapia (Family Cichlidae) can tolerate adverse conditions that result in stunting and which also cause the fish to spawn at small size. Such spawning at small size (or 'early spawning') is usually perceived as a unique feature of tilapia. The mechanism that explains how stressful environmental conditions tend to reduce the maximum size that fish can reach is very general and should apply to all fish. However, not all fish species are equally hardy, and most fish do not survive in the stunted or dwarf form under stressful environmental conditions. Tilapia, and other cichlids, on the other hand, can handle stressful conditions, if by remaining stunted. The present study shows that tilapia and other cichlids do not spawn 'earlier' than other teleosts. Rather, they are exceptionally tolerant of stressful environmental conditions, but with elevated metabolism. By reducing their growth and the maximum size they can reach 'stunting', they also reduce the sizes at which their maturity is initiated ('early spawning'). This corroborates the gill-oxygen limitation theory (GOLT), which identifies spawning as an event rather than a determinant of fish growth.

Keywords: Cichlidae, freshwater fish, Gill-Oxygen Limitation Theory, *Oreochromis*, stunting

Introduction

Relative to mammal and birds, fish achieve first maturity at a smaller fraction of the maximum size they are capable of reaching, particularly when growth in weight is concerned (Pauly, 2021). Among many of the ichthyologists working on the family Cichlidae, which include tilapia of genus *Oreochromis* as important farmed species, this 'early maturation' has often been interpreted as a taxon-specific phenotypic response to unstable environmental conditions. Numerous explanations have been proposed for this perceived unique feature, involving *r* vs. *K*-selection (Pianka, 1970), or precocial-altricial dichotomy (Noakes and Balon, 1982), which evokes a continuum from 'capital breeding', a situation in which reproduction is performed by stored energy, to 'income breeding', where concurrent energy is used for reproduction (Stephens et al., 2009; McBride et al., 2015).

Iles (1973) attempted to attribute the 'early maturity' phenomenon that many aquaculturists complain about as a unique "resource limitation due to overcrowding". Specifically, he argued that in tilapia populations, maturation at an earlier age and increased relative fecundity enable fish to withstand high mortality rates under adverse environmental conditions. Jointly, these hypotheses presented 'early maturity' as a problem specific to cichlids, particularly to tilapia of the genus *Oreochromis*, e.g., Nile tilapia (*Oreochromis niloticus* (Linnaeus, 1758)), which is very important in tropical and semitropical aquaculture.

Another issue is that these hypotheses were embedded in another, higher-level but largely unexamined hypothesis. Thus, among ichthyologists, the process of transition from immature stage to maturity is generally perceived as a "reproductive drain" in that fish, once they reach sexual maturity, exhibit slower growth because the energy previously available for growth is switched to gonadal development (Charnov, 2008; Quince et al., 2008).

Pauly (1984) showed that the ratio of oxygen supply at maturity (Q_m) to that at the maximum size (Q_{max})*, i.e., the ratio Q_m/Q_{max} is similar in a wide range of fish species. On the other hand, the ratio of mean length at first maturity (L_m) to maximum length (L_{max}) or asymptotic length, (L_∞, which is equivalent) declines with sizes (Froese and Binohlan, 2000; Pauly, 2021), which is incompatible with being what Charnov (2008) called a "Beverton and Holt invariant".

Also, most conventional accounts of the hormonal cascade that leads to maturation and spawning in teleosts are presumed to start with "environmental input" or stimuli that supposedly trigger reproduction (see, e.g., Figure 8.1 in Pankhurst, 2016). Such accounts, however, fail to consider that the juveniles of long-lived species can pass through several spawning seasons without perceiving the environmental input or stimuli that supposedly trigger reproductive activity.

What is missing from such accounts is a factor generating an individual's *internal* readiness to perceive these environmental input or stimuli the same way that adult fish do. This internal readiness, as hypothesised by Pauly (1984) is provided by the ratio of their metabolic rate (Q) relative to their routine metabolism (i.e., Q/Q_{maint}), which declines as the weight of individuals grows faster than the surface area of their gills (see, e.g., De Jager and Dekker, 1975). The triggering value was shown to be $Q_m/Q_{maint} \approx 1.36$ (Pauly, 1984), with 95 % confidence interval (C.I) ranging from 1.22 to 1.53 estimated with the method of Fieller (1940; www.graphpad.com/quickcalcs/ErrorProp1.cfm).

This hypothesis was elaborated upon in Pauly (2019a, b, 2021) and it is now a key element of his gill-oxygen limitation theory (GOLT). Besides supportive evidence presented by various authors, e.g., Thorpe (1990), Thorpe et al. (1998) and Lowe-McConnell (2000), three explicit tests of this aspect of the GOLT have been performed so far:

(1) Kolding et al. (2008) concluded from laboratory experiments that the low oxygen condition reduced the growth and size at first maturity of Nile tilapia as predicted by the GOLT;

(2) Diaz-Pauli et al. (2017) reported similar results for similar experiments with guppies *Poecilia reticulata* Peters, 1859;

(3) Meyer and Schill (2021) showed that in 51 stream-dwelling population of 3 species of salmonids, the ratio L_{max}^D *vs.* L_m^D (equivalent to the ratio Q/Q_{maint}), was 1.35, almost exactly the same as obtained by Pauly (1984).

There are still objections to the GOLT, however, notably by Lefevre et al. (2017a, b); they are dealt with in Pauly and Cheung (2017, 2018), and particularly in Pauly (2021).

Here, the generality of the GOLT is tested by asking whether first maturation in tilapia occurs 'earlier' than in other teleosts, as is commonly stated. This opportunity is also used to assess whether different approaches for estimating the parameter D affect the ratio L_{max}^D / L_m^D in a more than negligible way.

Materials and Methods

The maximum length (L_{max}; total length, in cm), mean length at first maturity (L_m; total length, in cm) and the parameters a and b of length-weight relationship (LWR) of the form $W = a{\cdot}L^b$ for 41 in the females of natural or feral cichlid populations from different geographical regions were obtained from the published literature. In some populations of *Oreochromis mossambicus* (Peters, 1852) and *O. niloticus*, data were available only for both sexes combined. Nevertheless, in *Oreochromis* species, the adult males exhibit territorial behaviour and defend reproductive arenas in the littoral zones of lakes and reservoirs. Hence, catch samples in the fisheries of *Oreochromis* species were assumed to be dominated by females because fishing operations are generally performed in limnetic zones of lakes and reservoirs. Accordingly, the maximum lengths in sexually unassigned catch samples were assumed to be estimates of female L_{max}.

In the present analysis, only estimates of L_{max} were considered that could be linked (preferably in the same contribution) to the estimates of L_m, while the latter had to explicitly refer to the length at which 50 % of the females were found to be mature.

Growth, in fish, is generally assumed to conform to concepts developed by von Bertalanffy (1938, 1949, 1951), who built on earlier work by Pütter (1920). Their key feature is that growth rate (dw/dt) can be seen as the difference between two processes, i.e.,

$$dw/dt = Hw^d - kw \qquad (1)$$

where the two terms on the right are usually called anabolism and catabolism, respectively, and where $d < 1$. That is, an increase of body mass (dw/dt) is the difference between body mass (i.e., protein molecules) that is (are) newly (Hw^d) synthesised and body mass (kw) that becomes degraded (i.e., proteins that are denatured; Pauly 2019b). As mentioned by Pauly (2021), in "water-breathing ectotherms" such as fishes and aquatic invertebrates, the parameter d in Eq. 1 is equivalent to the exponent (dG) of the relationship between respiratory (gill) surface area (G) and body weight (W) of the form $G = aW^{dG}$, which indicates the process of anabolism requiring oxygen through respiratory (gill) surface of fish.

Integrating the differential equation in (1) when d is set equal to 2/3 yields the von Bertalanffy Growth Function (VBGF), which for length has the form:

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*The term Q_{max} is replaced by Q_{maint} further in the text; note that $Q_{max} = Q_{maint}$

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

where L_t is the mean length, e.g., total length (TL), as used here, L_∞ is the asymptotic length, i.e., the mean length they would attain after an infinitely long life, K a growth coefficient (time^{-1}) and t_o is the (usually negative) age they would have at L = 0 if they had always grown as predicted by the VBGF, and which can here be neglected.

Equation (2) assumes that growth stops (at L_∞) when $Hw^d = kw$, which is unavoidable because d, the scaling factor between the surface area of the gills (and hence of oxygen supply to the body) and body weight is < 1, and thus cannot keep up as weight (and hence oxygen demand) increases. When $d \neq 2/3$, but still <1, the integration of equation (1) yields a general form of the VBGF; for length, this is:

$$L_t = L_\infty(1-e^{-KD(t-t_0)})^{1/D} \qquad (3)$$

where $D = b(1-d)$ and b is the exponent of an LWR.

The definition of D allows different approaches for its estimation. Thus, D can be seen as variable because population-specific estimates of b are available (see Table 1); these values can be combined with an estimate of d = 0.8, which appears to be a suitable mean value for cichlids in general (Fernandes and Rantin, 1986; Kisia and Hughes, 1992; van Dam and Pauly, 1995). Alternatively, estimates of d can be obtained by using the equation:

$$d = 0.674+0.0357.\log(W_{max}) \qquad (4)$$

with W_{max} in g is the weight corresponding to L_{max} (Pauly, 1981, 2019a), and which can be used if different values of d can be assumed to apply to different species and populations of cichlids.

Thus, $D1 = b\cdot(1 - 0.8)$ and $D2 = b\cdot(1 - d)$ are defined, and the results are compared with those of Pauly (1984), who used the definition $D3 = 3\cdot(1 - d)$. This is also based on equation (4), but b is assumed constant, i.e., b = 3, which is the average value b takes in the overwhelming majority of fish (Froese, 2006; see also www.fishbase.org).

Results

The best documented cichlid species considered here is the Nile tilapia (*O. niloticus*), an extremely important farmed species (Pullin et al., 1996), represented by 12 native (N) or feral/introduced (F) populations in Brazil (F); Ethiopia (N); Kenya (N); Uganda (N) and Sri Lanka (F). Next were the redbelly tilapia (*Coptodon zillii* (Gervais, 1848)) with 14 populations from Egypt (N); Nigeria (N) and Uganda (N), and Mozambique tilapia, formerly distributed widely for farming (Pullin et al., 1997), with 12 populations in Australia (F), Hong Kong (F) and Sri Lanka (F). Additional species were the redbelly tilapia (*C. zillii*) with 13 introduced population in small Uganda volcanic crater lakes (F), blackchin tilapia (*Sarotherodon melanotheron* Rüppell, 1852), a species occurring in West African mixohaline lagoons (Pauly, 1976, 2002), a populations in Ghana (N), one jewelfish (*Hemichromis bimaculatus* Gill, 1862) population from Algeria (N) and one each of Agassiz's dwarf cichlid (*Apistogramma agassizii* (Steindachner, 1875)) and banded dwarf cichlid (*Apistogramma bitaeniata* Pellegrin, 1936), both native in the Amazon Basin.

Thus, L_m and L_{max} data pairs were identified for the females of 41 natural or feral populations in 7 species of cichlids, ranging in total length from 4.2 cm in *A. agassizii* in Aningal Lake, Amazon Basin, to 55 cm in *O. niloticus* in Lake Victoria, Uganda (Table 1).

Table 2 summarised the data in Table 1 in the form of the mean ratio $L_{max}{}^D/L_m{}^D$ for *O. niloticus*, *O. mossambicus*, *C. zillii* and for all cichlids (see also Fig. 1).

These ratios, whether based on *D1* or *D2* are all close to the ratio of 1.36 estimated by Pauly (1984), who applied *D3* to several marine fishes (Table 2).

Discussion

The results of the present study suggest that cichlids, including species of *Oreochromis* do not spawn as 'smaller sizes' than other species of marine fishes, as can be inferred from their mean $L_{max}{}^D/L_m{}^D$ ratio of 1.35 or 1.40 (depending on *D1* or *D2*, see Table 2), which is essentially the same as obtained by Pauly (1984) for marine teleosts (1.36) and by Meyer and Schill (2021) for freshwater salmonids (1.35).

The impression that cichlids, especially farmed species, possess a unique mechanism to respond to stressful conditions - spawning 'early' – is erroneous, and caused by the hardiness of these species, especially regarding their tolerance of high temperatures and hypoxia (Burggren et al., 2019).

The mechanism that explains how stressful environmental conditions (e.g., elevated temperatures or hypoxia) tend to reduce the maximum size that fish can reach is very general and should apply to all fish (Pauly, 2019a, 2021). However, not all fish species are equally hardy, and rather than surviving in stunted form when environmental conditions are stressful, most fish die. Thus, their stunted or 'dwarf form' do not exist and neither do they spawn at small sizes. Whereas tilapia, and other cichlids, can handle stressful conditions if by remaining stunted. Given the constancy of the $L_{max}{}^D/L_m{}^D$ ratio (~ 1.35), this mean that stunted tilapia and other cichlids can spawn at very small size. It is

Table 1. Maximum length (L_{max}; total length in cm), length of first maturity (L_m; total length in com), multiplicative term (*a*) and exponent (*b*) of length-weight relationship and sampling localities (and references) of the females of 41 cichlid populations. For definition of *D1*, see text.

No.	Species	L_{max}	L_m	*a*	*b*	*D1*	Locality (References)
1	*Oreochromis niloticus* (Linnaeus, 1758)	47	21	0.0295	2.494	0.499	Minneriya, Sri Lanka (Amarasinghe, 1990; Amarasinghe and De Silva, 1992; Amarasinghe et al., 2017)
2	*O. niloticus*	34	22.6	0.0940	2.203	0.441	Victoria, Sri Lanka (Amarasinghe et al., 2017)
3	*O. niloticus*	39	22.5	0.0385	2.837	0.567	Kaudulla, Sri Lanka (Amarasinghe, 1990; Amarasinghe and De Silva, 1992)
4	*O. niloticus*	55	31	0.015	3.140	0.628	Lake Victoria 1998-99 (Njiru et al., 2006; Njiru et al., 2008)
5	*O. niloticus*	49	26	0.019	3.010	0.602	Lake Victoria 2014-15 (Yongo and Outa, 2016; Yongo et al., 2018)
6	*O. niloticus*	40	24.6	0.0256	2.500	0.500	Lake Koka, Ethiopia (Tesfaye et al., 2016)
7	*O. niloticus*	40	28	0.0820	3.011	0.602	Lake Naiwasha 2017, Kenya (Waithaka et al., 2020)
8	*O. niloticus*	40	28	0.0310	2.860	0.572	Lake Naiwasha, Kenya (Waithaka et al., 2020)
9	*O. niloticus*	39	23.4	0.0366	2.884	0.577	Barra Bonita Reservoir, SE Brazil (Novaes and Carvalho, 2012)
10	*O. niloticus*	55	24.5	0.0240	2.960	0.592	Lake Victoria, Uganda (Balirwa, 1994, figures 1 & 2)
11	*O. niloticus*	52	25.3	0.0230	3.010	0.602	Lake Kyoga, Uganda (Balirwa, 1994, figures 1 & 2)
12	*O. niloticus*	36	27.5	0.0190	3.117	0.623	Lake Wamala, Uganda (Bwanika et al., 2007)
13	*Oreochromis mossambicus* (Peters, 1852)	33.5	15.5	0.032	2.792	0.558	Tabbowa, Sri Lanka (Amarasinghe, 1988, 2002)
14	*O. mossambicus*	36	20.5	0.090	2.498	0.500	Pimburettewa, Sri Lanka (De Silva 1985, 1986; Amarasinghe, 1987).
15	*O. mossambicus*	37	17	0.028	2.841	0.568	Parakrama Samudra, Sri Lanka (Amarasinghe, 1988; Amarasinghe et al., 1989); L_{max} ≈ mean of 3 basins.
16	*O. mossambicus*	39	21	0.0577	2.576	0.515	Kaudulla, Sri Lanka (De Silva, 1985, 1986; Amarasinghe, 1990; Amarasinghe and De Silva, 1992)
17	*O. mossambicus*	38	19.5	0.0497	2.863	0.573	Minneriya, Sri Lanka (De Silva, 1985, 1986; Amarasinghe, 1990; Amarasinghe and De Silva, 1992)
18	*O. mossambicus*	32	19	0.031	2.845	0.569	Udawalawe, Sri Lanka (De Silva, 1985, 1986; Athukorala and Amarasinghe, 2010)
19	*O. mossambicus*	28	17	0.061	2.642	0.528	Chandrikawewa, Sri Lanka (De Silva, 1985, 1986; Athukorala and Amarasinghe, 2010)
20	*O. mossambicus*	30.5	19.2	0.0179	2.999	0.600	Victoria, Sri Lanka (Amarasinghe et al., 2017)
21	*O. mossambicus*	18.5	13	0.062	2.574	0.515	Tissa wewa, Sri Lanka (De Silva, 1985, 1986; Pet et al., 1996)

Table 1. Continued.

No.	Species	L_{max}	L_m	*a*	*b*	*D1*	Locality (References)
22	*O. mossambicus*	31	20.2	0.0303	3.056	0.611	Plover Cove Reservoir, Hong Kong (Hodgkiss and Man, 1977)
23	*O. mossambicus*	30	21.8	0.0011	2.390	0.478	North Pine Dam, Brisbane (Arthington and Milton, 1986)
24	*O. mossambicus*	30	21.8	0.0463	2.941	0.588	North Pine Dam, Brisbane (Arthington and Milton, 1986; Blühdorn and Arthington, 1990)
25	*Coptodon zillii* (Gervais, 1848)	16	8.5	0.0207	2.900	0.580	Egypt (Mahomoud et al., 2011)
26	*C. zilli*	19.7	15.5	0.0135	2.800	0.560	Lake Kanyango, Uganda (Efitare, 2007; Efitare et al., 2009)
27	*C. zilli*	23.5	15.9	0.0468	2.800	0.560	Lake Lugembe, Uganda (Efitare, 2007; Efitare et al., 2009)
28	*C. zilli*	24.3	14	0.0219	3.000	0.600	Lake Kifuruka, Uganda (Efitare, 2007; Efitare et al., 2009)
29	*C. zilli*	21.1	14	0.0191	3.000	0.600	Lake Lyantond, Uganda (Efitare, 2007; Efitare et al., 2009)
30	*C. zilli*	23.4	14	0.0158	3.000	0.600	Lake Wandakara, Uganda (Efitare, 2007; Efitare et al., 2009)
31	*C. zilli*	23.3	14	0.0102	3.100	0.620	Lake Mwegenywa, Uganda (Efitare, 2007; Efitare et al., 2009)
32	*C. zilli*	28.7	16.2	0.0166	3.000	0.600	Lake Rukwanzi, Uganda (Efitare, 2007; Efitare et al., 2009)
33	*C. zilli*	23	13.5	0.0105	3.100	0.620	Lake Nyinabulitwa, Uganda (Efitare, 2007; Efitare et al., 2009)
34	*C. zilli*	27	14	0.0468	2.800	0.560	Lake Nyanswiga, Uganda (Efitare, 2007; Efitare et al., 2009)
35	*C. zilli*	17.6	13.7	0.0195	3.000	0.600	Lake Nkuruba, Uganda (Efitare, 2007; Efitare et al., 2009)
36	*C. zilli*	20.4	13	0.0105	3.000	0.600	Lake Kasenda, Uganda (Efitare, 2007; Efitare et al., 2009)
37	*C. zilli*	22.2	13.8	0.0105	3.100	0.620	Lake Ntanda, Uganda (Efitare, 2007; Efitare et al., 2009)
38	*Sarotherodon melanotheron* Rüppell, 1852	22	14.2	0.0540	2.808	0.562	Brimsu Reservoir, Ghana (Mireku et al., 2016)
39	*Hemichromis bimaculatus* Gill, 1862	10.2	5.7	0.0276	2.800	0.560	Algeria (Guezi et al., 2015)
40	*Apistogramma agassizii* (Steindachner, 1875)$^{(a)}$	4.16	2.51	0.0206	3.000	0.600	Aningal Lake, Amazon (de Oliveira and de Queiroz, 2017)
41	*Apistogramma bitaeniata* Pellegrin, 1936$^{(a)}$	4.38	2.53	0.0209	3.000	0.600	Aningal Lake, Amazon (de Oliveira and de Queiroz, 2017)

(a)The total lengths for the two *Apistogramma* species were obtained by multiplying their standard lengths by 1.26; their LWRs were derived using the method of Hay et al. (2020) from length-weight pairs in table 1 of de Oliveira and de Queiroz (2017), due to their LWRs being questionable.

Table 2. L_{max}^D vs L_m^D ratios and their 95 % confidence intervals (C.I.) female fish of the family Cichlidae, based on data in Table 1 and the method of Fieller (1940); see footnote for the methods used to estimate *D*. SD = standard deviation.

No.	Taxon (N)	*D**	Mean L_{max}^D	SD	Mean L_m^D	SD	L_{max}^D/L_m^D	Low C.I.	High C.I.
1	Six cichlid spp. (n = 41)	*D1*	6.90	2.08	5.12	1.43	1.35	1.18	1.53
2		*D2*	9.08	1.79	6.48	1.42	1.40	1.28	1.54
3	*Oreochromis niloticus* (Linnaeus, 1758) (n = 12)	*D1*	8.77	2.16	6.41	1.39	1.37	1.12	1.66
4		*D2*	9.76	1.41	7.06	1.03	1.38	1.22	1.56
5	*Oreochromis mossambicus* (Peters, 1852) (n = 12)	*D1*	6.78	1.20	5.05	0.78	1.34	1.16	1.54
6		*D2*	9.04	1.43	6.52	1.22	1.39	1.20	1.61
7	*Coptodon zillii* (Gervais, 1848) (n = 13)	*D1*	6.32	0.74	4.76	0.46	1.33	1.22	1.45
8		*D2*	9.59	1.04	6.79	0.78	1.41	1.29	1.55
9	Thirty-four spp. (n = 56) of marine fishes in Pauly (1984, 2021)	*D3*	9.81	2.91	7.21	2.30	1.36	1.22	1.53

*$D1 = b\cdot(1\text{-}0.8)$; $D2 = b\cdot(1\text{-}d)$ and $D3 = 3\cdot(1\text{-}d)$, with *d* used in *D2* and *D3* estimated from the equation $d = 0.674+0.0357.\log(W_{max})$, with W_{max} in g is the weight corresponding to L_{max} (see text).

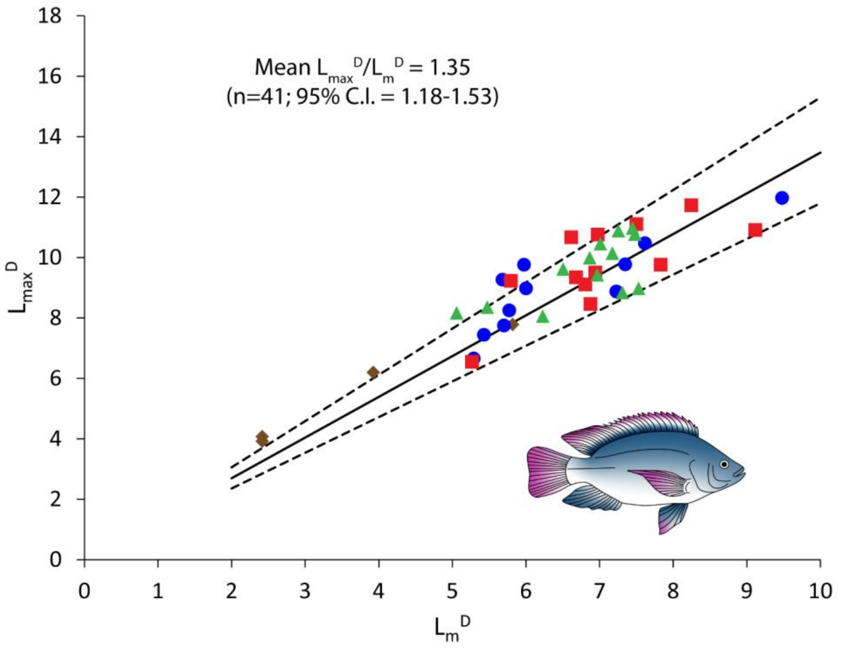

Fig. 1. Relationship between L_{max}^D and L_m^D in the females of 7 species and 41 cichlid populations (solid line). Blue dots = *O. mossambicus* (n = 12); red squares = *O. niloticus* (n = 12); green triangles = *C. zillii* (n = 13) and brown diamonds = 4 other species (n = 4). The dotted lines indicate the 95 %confidence interval.

their hardiness that matters here, not a hypothetical tendency toward early spawning.

However, while it is well established that stressful environmental condition (as e.g., occur in small freshwater reservoirs compared with larger ones) reduce both the maximal size that cichlid fish can reach (Lowe-McConnell, 1982, 2000; Eyeson, 1983; Lorenzen, 2000) and their size at first maturity (De Silva, 1986; Duponchelle and Panfili, 1998; Lorenzen, 2000), the causes of relative constancy of the L_m/L_{max} ratio (or its inverse) was rarely studied in tilapia.

Indeed, many articles purporting to study length at first maturity in tilapia fail to report on the maximum individual sizes reached by the populations in question (see e.g., Duponchelle and Panfili, 1998). Other articles report on *age* at first maturity (t_m), although no theory that appears to exist would explain how (*i*) individual fish would keep track of their age and (*ii*) how a certain age being reached would trigger maturation and spawning.

In contrast, individual fish can monitor their current metabolic rate (Q) relative to their maintenance rate (Q_{maint}) (rather like we human can tell that we are out of breath). As they grow, their metabolic rate declines because their gill surface area does not keep up with their weight. When their relative metabolic rate declines and approaches 1.35, this triggers the hormonal cascade leading to maturation and spawning, with the latter requiring a mate (Pauly, 1984, 2019a, 2021). Thus, metabolic rate determines both size and first maturity and maximum size, the latter of which occurs when $Hw^d = kw$ (see above). This is why L_m and L_{max} must be studied together.

There is supporting experimental evidence for the GOLT from Nile tilapia (Kolding et al., 2008) and guppies (Diaz-Pauli et al., 2017), along with comparative studies based on analytical stream-dwelling salmonid populations (Meyer and Schill, 2021). Its critiques, notably by Lefevre et al. (2017a, b), are refuted in Pauly (2021). The present analysis was based on maximum lengths (L_{max}), mean lengths at first maturity (L_m) and the parameters a and b of length-weight relationship of 41 females of natural or feral cichlid population in Africa, Asia and South America. The results indicate that cichlids, including species of *Oreochromis* do not spawn at 'smaller sizes' than other species of teleosts, as can be inferred from their mean L_{max}^D/L_m^D ratio of 1.35 to 1.40 (see above for definition of D), which is essentially the same as the estimates obtained by Pauly (1984) for marine teleosts (1.36) and by Meyer and Schill (2021) for freshwater salmonids (1.35). Hence, our analysis corroborates the GOLT and explains the hitherto poorly understood phenomenon of 'stunting' or 'dwarfing' in the family Cichlidae.

Conclusion

The conventional view of 'stunting' or 'dwarfing' in tilapias was assumed to occur when the fish are in unstable or stressful environments, and they utilise unique adaptive mechanisms to mature early in their life. Thus, because of the "reproductive drain" caused by the transfer of energy from growth to reproduction, their growth is affected, and they remain small. Pauly (1984, 2019a, b, 2021) presented evidence showing that this view is erroneous, and that it inverts the cause. In fact, when conditions are stressful, growth (including juvenile growth) declines, which induces maturation and spawning. The environment with elevated temperatures, or lower oxygen, or crowding stress fish, which manifest itself in higher oxygen requirements. However, as fish grow, their oxygen supply (Q) declines because the surface area of their gills does not keep up with their increasing weight (Pauly 1984, 2019b, 2021); thus, stress impacts growth. With a fixed Q_m/Q_{maint} ratio (corresponding to L_{max}^D/L_m^D), tilapia, under stressful conditions, can adjust the size at first maturity downward like any other fish, i.e., without any 'cichlid-specific early-spawning' mechanism.

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