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

UPALI S. AMARASINGHE1,*, DANIEL PAULY2
1Department of Zoology and Environmental Management, University of Kelaniya, Kelaniya 11600, Sri Lanka
2Sea Around Us, Institute for the Oceans and Fisheries, The University of British Columbia, Vancouver, British Columbia, Canada

*E-mail: zoousa@kln.ac.lk | Received: 20/12/2020; Accepted: 28/02/2021

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 ($Q_{\text{max}}$), i.e., the ratio $Q_m/Q_{\text{max}}$ 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 ($L_{\text{max}}$) or asymptotic length ($L_a$, which is equivalent) declines with sizes (Froese and Binohlan, 2000; Pauly, 2021), which is incompatible with 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., $Q/Q_{\text{max}}$), 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 $Q_m/Q_{\text{max}} = 1.36$ (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. (1988) 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-Pauly 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 $L_{\text{max}}^2$ vs. $L_m^2$ (equivalent to the ratio $Q/Q_{\text{max}}$, 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 $L_{\text{max}}^2/L_m^2$ in a more than negligible way.

### Materials and Methods

The maximum length ($L_{\text{max}}$; 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 $W = aL^b$ 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 $L_{\text{max}}$.

In the present analysis, only estimates of $L_{\text{max}}$ 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.,

$$\frac{dw}{dt} = Hw^d - kw$$

where the 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 ($d\hat{Q}$) of the relationship between respiratory (gill) surface area ($\hat{G}$) and body weight ($W$) of the form $\hat{G} = aW^{d\hat{Q}}$, 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:

*The term $Q_{\text{max}}$ is replaced by $Q_{\text{max}}^\infty$ further in the text; note that $Q_{\text{max}}^\infty = Q_{\text{max}}$.*
\[ L_z = L_o (1 - e^{-K(t-t_o)}) \]  

(2)

where \( L_z \) is the mean length, e.g., total length (TL), as used here, \( L_o \) 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 \( L_o \)) when \( Hw^2 = kw \), 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 \( d = 2/3 \), but still < 1, the integration of equation (1) yields a general form of the VBGF; for length, this is:

\[ L_z = L_o (1 - e^{-KD(t-t_o)}) \]

(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:

\[ d = 0.674 + 0.0357 \cdot \log(W_{ma}) \]

(4)

with \( W_{ma} \) in g is the weight corresponding to \( L_{ma} \) (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, \( D1 = b(1 - 0.8) \) and \( D2 = b(1 - d) \) are defined, and the results are compared with those of Pauly (1984), who used the definition \( D3 = 3(1 - d) \). 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 (\( C. \ zillii \) (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 (\( S. \ melantheron \) Rüppell, 1852), a species occurring in West African mixohaline lagoons (Pauly, 1976, 2002), a populations in Ghana (N), one jewelfish (\( H. \ bimaculatus \) Gill, 1862) population from Algeria (N) and one each of Agassiz’s dwarf cichlid (\( A. \ agassizii \) (Steindachner, 1875)) and banded dwarf cichlid (\( A. \ bitaeniata \) Pellegrin, 1936), both native in the Amazon Basin.

Thus, \( L_{ma} \) and \( L_{ma} \) 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 I).

Table 2 summarised the data in Table 1 in the form of the mean ratio \( L_{ma}/L_{ma}^0 \) 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 \( O. \ mossambicus \) do not spawn as ‘smaller sizes’ than other species of marine fishes, as can be inferred from their mean \( L_{ma}/L_{ma}^0 \) 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, 2019b, 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 stunted or ‘dwarf form’ do not exist and neither do...
Table 1. Maximum length ($L_{\text{max}}$; total length in cm), length of first maturity ($L_m$; total length in cm), 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 $D_1$, see text.

| No. | Species                     | $L_{\text{max}}$ | $L_m$ | $a$    | $b$    | $D_1$ | Locality (References)                                                                 |
|-----|-----------------------------|------------------|-------|--------|--------|-------|--------------------------------------------------------------------------------------|
| 1   | *Oreochromis niloticus*     | 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  | 3.100  | 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*   | 33.5             | 15.5  | 0.032  | 2.792  | 0.558 | Tabbowa, Sri Lanka (Amarasinghe, 1988, 2002)                                           |
| 14  | *O. mossambicus*            | 38               | 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); $L_{\text{max}} = \text{mean of 3 basins}$ |
| 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)                          |
| No. | Species                        | L_max | L_m  | a    | b     | Df   | 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, 1988)                                 |
| 24  | O. mossambicus                | 30    | 21.8 | 0.0463 | 2.941 | 0.588 | North Pine Dam, Brisbane (Arthington and Milton, 1988; 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 | 0.0488 | 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 Rukwanz, 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     | 22    | 14.2 | 0.0540 | 2.808 | 0.562 | Brimsu Reservoir, Ghana (Mireku et al., 2016)                                           |
| 39  | Hemichromis bimaculatus Gill, | 10.2  | 5.7  | 0.0276 | 2.800 | 0.560 | Algeria (Guezi et al., 2015)                                                           |
| 40  | Apistogramma agassizii         | 4.16  | 2.51 | 0.0206 | 3.000 | 0.600 | Aningal Lake, Amazon (de Oliveira and de Queiroz, 2017)                                 |
| 41  | Apistogramma bitaeniata       | 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. $L_{\text{max}}^D$ 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 $L_{\text{max}}^D$ | SD  | Mean $L_m^D$ | SD  | $L_{\text{max}}^D/L_m^D$ | 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      |

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

Fig. 1. Relationship between $L_{\text{max}}^D$ 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 $L_m/L_{\text{max}}$ 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 ($Q_{\text{m}}$), 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 $Hw^{2} = kw$ (see above). This is why $L_{m}$ and $L_{\text{max}}$ must be studied together.

There is supporting experimental evidence for the GOLT from Nile tilapia (Kolding et al., 2008) and guppies (Díaz-Pauli et al., 2017), along with comparative studies based on analytical stream-dwelling salmonid populations (Meyer and Schill, 2021). Its critiques, notably by Lefevere et al. (2017a, b), are refuted in Pauly (2021). The present analysis was based on maximum lengths ($L_{\text{max}}$), 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 $L_{\text{max}}/L_{m}$ 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 tilapia 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 ($O$) 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 $Q_{m}/Q_{\text{m}}$ ratio (corresponding to $L_{\text{max}}/L_{m}$), 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.

Acknowledgements

We thank Ms. Elaine Chu for her assistance with tabulating our results, and drafting Figure 1.

References

Amarasinghe, U.S. 1987. Status of the fishery of Pimburettewa wewa, a man-made lake in Sri Lanka. Aquaculture and Fisheries Management 18:375–385. https://doi.org/10.1111/j.1365-2109.1987.tb00376.x

Amarasinghe, U.S. 1988. Growth-overfishing: a potential danger in Sri Lankan reservoir fishery. In: Reservoir fishery management and development in Asia (ed. de Silva, S.S.), pp. 105–112. International Development Research Centre, Ottawa, Canada.

Amarasinghe, U.S. 1990. The fishery of two man-made lakes in Sri Lanka, and strategies for management. Ph.D. Thesis. University of Ruhuna, Sri Lanka. 237 pp.

Amarasinghe, U.S. 2002. The fishery and population dynamics of Oreochromis mossambicus and Oreochromis niloticus (Osteichthyes, Cichlidae) in a shallow irrigation reservoir in Sri Lanka. Asian Fisheries Science 15:7–20.

Amarasinghe, U.S., De Silva, S.S. 1992. Population dynamics of Oreochromis mossambicus and O. niloticus (Cichlidae) in two reservoirs of Sri Lanka. Asian Fisheries Science 5:37–61.

Amarasinghe, U.S., De Silva, S.S., Moreau, J. 1989. Spatial changes in growth and mortality and effects on the fishery of Oreochromis mossambicus (Pisces, Cichlidae) in a man-made lake in Sri Lanka. Asian Fisheries Science 2:57–68.

Amarasinghe, U.S., Jayasinghe, R.P.P.K., Moreau, J. 2017. Length-based stock assessment of Oreochromis mossambicus and O. niloticus (Actinopterygii: Perciformes: Cichlidae) in multi-mesh gillnet fisheries in reservoirs of Sri Lanka. Acta Ichthyologica et Piscatoria 47:265–277. https://doi.org/10.3750/AIP.02147

Arthington, A.H., Milton, D.A. 1988. Reproductive biology, growth and age composition of the introduced Oreochromis mossambicus (Cichlidae) in two reservoirs, Brisbane, Australia. Environmental Biology of Fishes 2:35–44. https://doi.org/10.1007/BF00842980

Athenkora, D.A., Amarasinghe, U.S. 2010. Population dynamics of commercially important fish species in two reservoirs of the Walawe river basin, Sri Lanka. Asian Fisheries Science 23:71–90. https://doi.org/10.33977/L afs.2010.23.1.007

Balirwa, J.S. 1994. The biology, ecology, population parameters and the fishery of the Nile tilapia, Oreochromis niloticus (L.). In: The biology, ecology, management and conservation of the fisheries of Lakes Victoria, Kyoga and Nabusga, pp. 26–38. Fisheries Research Institute, Uganda. http://aquaticcommons.org/id/eprint/20289

Blühdorn, D.R., Arthington, A.H. 1990. Somatic characteristics of an Australian population of Oreochromis mossambicus (Pisces: Cichlidae). Environmental Biology of Fishes 29:277–291. https://doi.org/10.1007/BF00001985

Burggren, W.W., Mendez-Sánchez, J.F., Martínez Bautista, G., Peña, E., Martínez García, R., Alvarez Gonzalez, C.A., 2019. Developmental changes in oxygen consumption and hypoxia tolerance in the heat and hypoxia-adapted tabasco line of the Nile tilapia Oreochromis niloticus, with a survey of the metabolic literature for the genus Oreochromis. Journal of Fish Biology 94:732–744. https://doi.org/10.1007/BF00001985
Bwanika, O.N., Murie, D.J., Chapman, L.J. 2007. Comparative age and growth of Nile tilapia (Oreochromis niloticus L.) in lakes Nabugabo and Wamala, Uganda. Hydrobiologia 589:287-301. https://doi.org/10.1007/s10750-007-0746-y

Charnov, E. 2008. Fish growth: Bertalanffy k is proportional to reproductive effort. Environmental Biology of Fishes 83:185-187. https://doi.org/10.1007/s10641-007-9316-5

De Jager, S., Dekkers, W.J. 1975. Relations between gill structure and activity in fish. Netherlands Journal of Zoology 25: 276-308. https://doi.org/10.1186/10292897-85X0120

de Oliveira, J.C., de Queiroz, H.L. 2017. Life history traits of two dwarf cichlids species in the white waters of the Amazonian floodplain. Environmental Biology of Fishes 100:1497-1505. https://doi.org/10.1007/s10641-017-0960-8

De Silva, S.S. 1985. Body condition and nutritional ecology of Oreochromis mossambicus (Pisces, Cichlidae) populations of man-made lakes in Sri Lanka. Journal of Fish Biology 27:621-633. https://doi.org/10.1111/j.1365-2468.1985.tb03207.x

De Silva, S.S. 1986. Reproductive biology of Oreochromis mossambicus populations of man-made lakes in Sri Lanka: a comparative study. Aquaculture and Fisheries Management 17:31-47. https://doi.org/10.1111/j.1365-7183.1986.tb00083.x

Díaz-Paule, B., Kolding, J., Joykantak, G., Heino, M. 2017. Effects of ambient oxygen and size-selective mortality on growth and maturation in guppies. Conservation Physiology 5:cox010. https://doi.org/10.1093/conphys/cox010

Duponchelle, F., Panfil, J. 1998. Variations in age and size at maturity of female Nile tilapia, Oreochromis niloticus, populations from man-made lakes of Côte d’Ivoire. Environmental Biology of Fishes 52:453-465. https://doi.org/10.1023/A:1007463731509

Eftare, J. 2007. Life history variation in tilapia populations within the crater lakes of Western Uganda: the role of size-selective predation. Ph.D. Dissertation, University of Florida, USA, 189 pp.

Eftare, J., Chapman L.J., Murie, D.J. 2009. Fish condition in introduced tilapias of Ugandan crater lakes in relation to deforestation and fishing pressure. Environmental Biology of Fishes 85:63-75. https://doi.org/10.1007/s10641-009-9461-2

Eyeson, K.N. 1983. Stunting and reproduction in pond-reared Sarotherodon melanochrom. Aquaculture 31:257-267. https://doi.org/10.1016/0044-8486(83)90137-4

Fernandes, M.N., Rantin, F.T. 1986. Gill morphometry of cichlid fish, Oreochromis (Sarotherodont) niloticus. Ciencia e Cultura 38:192-198.

Fieller, E.C. 1940. The biological standardisation of insulin. Journal of the Royal Statistical Society (Supplement) 1(1):1-64. https://doi.org/10.2307/2983830

Froese, R. 2006. Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. Journal of Applied Ichthyology 22:241-253. https://doi.org/10.1111/j.1439-0426.2006.00805.x

Froese, R., Binohlan, C. 2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. Journal of Fish Biology 56:758-773. https://doi.org/10.1111/j.1095-8649.2000.tb00870.x

Guezi, R., Kara, H.H. 2015. Age, growth and reproduction of the endangered jewelfish Hemichromis bilocatus (Cichlidae) in the valley of Oued Righ (South-eastern Algeria). International Journal of Ichthyology 39:301-307. https://doi.org/10.26028/CYBIUM/2015-394-008

Hay, A., Xian, W., Bailly, N., Liang, C., Pauly, D. 2020. The why and how of determining length-weight relationships of fish from preserved museum specimens. Journal of Applied Ichthyology 36:373-379. https://doi.org/10.1111/jai.14014

Hodgkiss, I.J., Man, H.S.H. 1977. Age composition, growth and body condition of the introduced Sarotherodon mossambicus (Cichlidae) in Plover Cove Reservoir, Hong Kong. Environmental Biology of Fishes 18:257-266. https://doi.org/10.1007/BF00842980

Iles, T.D. 1973. Dwarfing or stunting in the genus Tilapia (Cichlidae): a possibly unique recruitment mechanism. Rapports et Procès-Verbaux des Réunions du Conseil Permanent International Pour l'Exploration de la Mer 164:247-254.

Kisia, S.M., Hughes, G.M. 1992. Estimation of oxygen-diffusing capacity in the gills of different sizes of tilapia, Oreochromis niloticus. Journal of Zoology 227:405-415. https://doi.org/10.1111/j.1469-7998.1992.tb04503.x

Kolding, J., Haug, L., Stefansson, S. 2008. Effect of ambient oxygen on growth and reproduction in Nile tilapia (Oreochromis niloticus). Canadian Journal of Fisheries and Aquatic Sciences 65:1413-1424. http://dx.doi.org/10.1139/F08-059.

Lefevre, S., McKenzie, D.J., Nilsson, G.E. 2017a. Models projecting the fate of fish populations under climate change need to be based on valid physiological mechanisms. Global Change Biology 23:3448-3458. https://doi.org/10.1111/gcb.13652

Lefevre, S., McKenzie, D.J., Nilsson, G.E. 2017b. In modelling effects of global warming, invalid assumptions lead to unrealistic projections. Global Change Biology 24:553-556. https://doi.org/10.1111/gcb.13978

Lorenzen, K. 2000. Population dynamics and management. In: Tilapias: biology and exploitation. (eds. Beveridge, M.C.M., McAndrew, B.J.), pp. 183-225. Fish and Fisheries Series 25, Kluwer Academic Publishers, Dordrecht, the Netherlands. https://doi.org/10.1007/978-94-011-4008-9_6

Lowe-McConnell R.H. 2000. The role of tilapias in ecosystems. In: Tilapias: Biology and exploitation. (eds. Beveridge, M.C.M., McAndrew, B.J.), pp. 129-162. Fish and Fisheries Series 25, Kluwer Academic Publishers, Dordrecht, the Netherlands. https://doi.org/10.1007/978-94-011-4008-9_5

Lowe-McConnell, R.H. 1982. Tilapias in fish communities. In: The biology and culture of tilapias, (eds. Pullin, R.S.V., Lowe-McConnell, R.H.) pp. 83-115, ICLARM Conference Proceedings 7, Manila, Philippines.

Mahomoud, W., Amin, A., Elboray, K., Ramadan, A., El-Halfawy, M. 2011. Reproductive biology and some observation on the age, growth, and management of Tilapia zilli (Gerv, 1848) from Lake Timsah, Egypt. International Journal of Fisheries and Aquaculture 3:16-26.

McBride, R., Somarakis, S.R., Fitzhugh, G., Albert, A., Yaragina, N., Wenschel, M., Alonso-Fernández, A., Basiline, G. 2015. Energy acquisition and allocation to egg production in relation to fish reproductive strategies, Fish and Fisheries 16:23-57. https://doi.org/10.1111/faf.12043

Meyer, K.A., Schill, D.J. 2021. The Gill-Oxygen Limitation Theory and size at maturity maximum size relationships for salmonid populations occupying flowing waters. Journal of Fish Biology 98:44-49. https://doi.org/10.1111/jfb.14555

Mireku, K.K., Blay, J., Yankson, K. 2016. Reproductive biology of Blackchin tilapia, Sarotherodon melanochrom (Pisces: Cichlidae) from Brimsu Reservoir, Cape Coast, Ghana. International Journal of Fisheries and Aquaculture 8:42-54. https://doi.org/10.5897/JIFA2015.051

Njiru, M., Ojok, J., Getabu, A., Jembe, T., Owili, M., Ngugi, C. 2008. Increasing dominance of Nile tilapia, Oreochromis niloticus (L) in Lake Victoria, Kenya: Consequences for the Nile perch Lates niloticus (L) fishery. Aquatic Ecosystem Health & Management 11:42-49. https://doi.org/10.1080/1463980701878090
Njiru, M., Ojuok, J.E., Okeyo-Owuor, J.B., Muchiri, M., Ntiba, M.J., Cowx, I.G. 2006. Some biological aspects and life history strategies of Nile tilapia Oreochromis niloticus (L.) in Lake Victoria, Kenya. African Journal of Ecology 44:30-37. https://doi.org/10.1111/j.1365-2028.2006.00610.x

Noakes, D.G.L., Balon, E.K. 1982. Life histories of tilapias: an evolutionary perspective. In: The biology and culture of tilapias. (eds. Pullin, R.S.V., Lowe-McConnell, R.H.), pp. 81-82. ICARFM Conference Proceedings 7, International Centre for Living Aquatic Resources Management, Manila, Philippines.

Novaes, J.L.C., Carvalho, E.D. 2012. Reproduction, food dynamics and exploitation level of Oreochromis niloticus (Percoformes: Cichliidae) from artisanal fisheries in Barra Bonita Reservoir, Brazil. Revista de Biologia Tropical (International Journal of Tropical Biology and Conservation) 60:721-734. https://doi.org/10.15517/rbt.v60i2.1387

Pankhurst, N.W. 2016. 8. Reproduction and development. In: Biology of stress in fish, Schreck, C.B., Tort, L., Farrell, A.P., Brauner, C.J. (Eds.), Fish physiology, vol. 35. Elsevier, Amsterdam, pp. 295-331. http://dx.doi.org/10.1016/B978-0-12-802728-8.00008-4

Pauly, D. 1978. The biology, fishery and potential for aquaculture of Tilapia melanotilapia in a small West African lagoon. Aquaculture 7:33-49. https://doi.org/10.1016/0044-8486(78)90030-2

Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung 28:251-282.

Pauly, D. 1984. A mechanism for the juvenile-to-adult transition in fishes. Journal du Conseil / Conseil Permanent International pour l'Exploration de la Mer 41:280-284. https://doi.org/10.1093/icesjms/41.3.280

Pauly, D. 2002. Spatial modelling of trophic interactions and fisheries impacts in coastal ecosystems: a case study of Sakumo Lagoon, Ghana. In: The Gulf of Guinea large marine ecosystem: environmental forcing and sustainable development of marine resources. (eds. McGlade, J., Cury, P., Koranteng, K.A., Hardman-Mountford, N.J.). 289-296 pp. Elsevier Science, Amsterdam.

Pauly, D. 2019a. Gasping fish and panting squids: oxygen, temperature and the growth of water-breathing animals. 2nd Edition. Excellence in ecology 22. International Ecology Institute, Oldendorf/Luhe, Germany. 279 pp.

Pauly, D. 2019b. A précis of gill-oxygen limitation theory (GOLT) with some emphasis on the eastern Mediterranean. Mediterranean Marine Ecology 20:688-702. https://doi.org/10.1080/0934298X.1985.12319

Pauly, D. 2021. The gill-oxygen limitation theory (GOLT) and its critics. Science Advances 7: eabc6050. https://doi.org/10.1126/sciadv.abc6050

Pauly, D., Cheung, W.W.L. 2017. Sound physiological knowledge and principles in modelling shrinking of fishes under climate change. Global Change Biology 24:e15-e26. https://doi.org/10.1111/gcb.13831

Pauly, D., Cheung, W.W.L. 2018. On confusing cause and effect in the oxygen limitation of fish. Global Change Biology 24:e743-e744. https://doi.org/10.1111/gcb.14383

Pet, J.S., Gevers, G.J.M., Van Densen, W.L.T., Vlijbergen, J. 1996. Management options for a more complete utilization of the biological fish production in Sri Lankan reservoirs. Ecology of Freshwater Fish 5:1-14. https://doi.org/10.1111/j.1600-0633.1996.tb00032.x

Pianka, E.R. 1970. On r and K selection. American Naturalist 104:592-597. http://www.jstor.org/stable/2459020

Pullin, R.S.V., Lazard, J., Legendre, M., Amon Kothias, J.B., Pauly D. 1996. Proceedings of the third international conference on tilapia in aquaculture, 11-18 November 1991, Abidjan, Côte d'Ivoire. ICARFM

Conference Proceedings 41, International Centre for Living Aquatic Resources Management, Manila, Philippines. 574 pp.

Pullin, R.S.V., Palomares, M.L.D., Casal, C.V., Day M.M., Pauly, D. 1997. Environmental impacts of tilapias. In: Tilapia aquaculture – Proceedings from the fourth international symposium on Tilapia in aquaculture. (ed. Fitzsimmons, K.), pp. 554-570. Northeast Regional Agricultural Engineering Service Cooperative Extension, Ithaca, New York.

Pütter, A. 1920. Studien zur Theorie der Reizvorgänge. Pflüger’s Archiv für die gesamte Physiologie des Menschen und der Tiere 180:280-290. https://doi.org/10.1007/BF01755092

Quince, C., Abrams, P.A., Shuter, B.J., Lester, N.P. 2008. Biphasic growth in fish I: Theoretical foundations. Journal of Theoretical Biology 254:197-206. https://doi.org/10.1016/j.jtbi.2008.05.029

Stephens, P.A., Boyd, I.L., McNamara, J.M., Houston, A.J. 2008. Capital breeding and income breeding: their meaning, measurement, and worth. Ecology 90:2057-2067. https://doi.org/10.1890/08-1369.1

Testfaye, G., Wolff, M., Taylor, M. 2018. Gear selectivity of fishery target resources in Lake Koka, Ethiopia: evaluation and management implications. Hydrobiologia 765:277-295. https://doi.org/10.1007/s10750-018-2420-0

Thorpe, J.E. 1990. Variation in life-history strategy in salmonids. Polish Archive of Hydrobiology 37:3-12.

Thorpe, J.E., Mangel, M., Metcalfe, N.B., Huntingford, F.A. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, Salmo salar L. Evolutionary Ecology 12:581-599. https://doi.org/10.1023/A:1022351814644

van Dam, A.A., Pauly, D. 1995. Simulation of the effects of oxygen on food consumption and growth of Nile tilapia, Oreochromis niloticus (L.). Aquaculture Research 26:427-440. https://doi.org/10.1111/j.1365-2109.1995.tb00932.x

von Bertalanffy, L. 1938. A quantitative theory of organic growth (Inquiries on growth laws. II). Human Biology 10:181-213. www.istor.org/stable/41447359

von Bertalanffy, L. 1948. Das biologische Weltbild. Europäische Rundschau. In English: Problems of life: an evolution of modern biological and scientific thought. John Wiley and Sons, New York. 216 pp.

von Bertalanffy, L. 1951. Problems of general system theory. Human Biology 23:302-312. www.istor.org/stable/41448003

Waithaka, E., Yonge, E., Outa, N., Mutethya, E. 2020. Population Biology of Nile tilapia (Oreochromis niloticus) in Lake Naivasha, Kenya. Lakes & Reservoirs: Science, Policy and Management for Sustainable Use 25:244-249. https://doi.org/10.1016/j.lre.20139

Yonge, E., Outa, N. 2016. Growth and population parameters of Nile tilapia, Oreochromis niloticus (L.) in the open waters of Lake Victoria, Kenya. Lakes and Reservoirs: Research and Management 21:375-379. https://doi.org/10.1111/lre.12154

Yonge, E., Outa, N., Kito, K., Matsushita, Y. 2018. Studies on the biology of Nile tilapia (Oreochromis niloticus) in Lake Victoria, Kenya: in light of intense fishing pressure. African Journal of Aquatic Science 43:195-198. https://doi.org/10.2989/16086954.2018.1455574