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## Indices of Overall Growth Performance of 100 Tilapia (Cichlidae) Populations\*

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### Abstract

Four indices for comparing the overall growth performance of fishes ( $\omega$ ,  $P$ ,  $\phi$ , and  $\phi'$ ) proposed by various authors are assessed, based on growth parameter estimates in 100 populations of tilapia in fifteen species of the genera *Tilapia*, *Sarotherodon* and *Oreochromis*, from inland waters in Africa and Asia. The best index, i.e., the one whose distribution was most similar to a normal distribution was  $\phi'$  ( $= \log_{10} K + 2 \log_{10} L_{\infty}$ ); the worst index was  $\omega$  ( $K=L_{\infty}$ ). The best growth performance in all populations investigated was in *Oreochromis niloticus* from Lake Kainji, Nigeria, the worst in *O. mossambicus* from Lake Sibaya (South Africa). Some theoretical and practical implications of these findings are discussed.

### Introduction

Growth comparisons of fish based on a single parameter have been found to be misleading (Pauly 1979; Kimura 1980; De Merona 1983; Moreau et al. 1985). Several authors have proposed indices of overall growth performance based on two parameters (Gallucci and Quinn 1979; Pauly 1979; Munro and Pauly 1983; Pauly and Munro 1984). These indices, all take account of the feature that "the growth curves of different fishes cannot be compared directly because the curves themselves are produced by growth rates that are constantly changing with time and size" (Pauly 1979). Hence, these indices all

relate to a given part of a growth curve, selected as representative of overall growth performance.

This contribution compares the growth performance of 100 "populations" of tilapias (males and females are treated here as separate "populations" whenever their growth parameters had been, or could be estimated separately). Altogether fifteen species, belonging to the genera *Tilapia*, *Sarotherodon* and *Oreochromis* (Cichlidae: Teleostei) are covered, most of them from African inland waters. The aims are:

- to review briefly and explore the characteristics of some indices of growth performance that have been proposed in the literature; and

- to identify those tilapia populations which, in nature at least, have the highest growth performance, and hence to help identify African strains of tilapia with aquaculture potential in Asia.

Throughout this paper, the von Bertalanffy Growth Formula (VBGF) is used to express the growth of fish (von Bertalanffy 1957); it has, for growth in length the form

$$L_t = L_{\infty}(1 - \exp(-K(t-t_0))) \quad \dots 1)$$

and for growth in weight

$$W_t = W_{\infty}(1 - \exp(-K(t-t_0)))^3 \quad \dots 2)$$

where  $L_t$  (or  $W_t$ ) are length (or weight) at age  $t$ ,  $L_{\infty}$  (or  $W_{\infty}$ ) the asymptotic size,  $K$  and  $t_0$  are constants with dimensions 1/time and time, respectively. Four indices of growth performance are presented and evaluated here.

*Parameter  $\omega$* . Gallucci and Quinn (1979) pointed out the need for independence between  $L_{\infty}$  and  $K$  to (1) improve the quality of estimates; (2) increase the flexibility of the VBGF; and (3) allow for statistical comparison of growth performance. They proposed an alternative to equation (1), i.e.,

$$L_t = (\omega/K) (1 - \exp(-K(t-t_0))) \quad \dots 3)$$

where

$$\omega = K \cdot L_{\infty} \quad \dots 4)$$

Gallucci and Quinn (1979) suggested that the parameter  $\omega$ , which expresses growth rate ( $dl/dt$ ) at  $t_0$ , is suited for comparison, mainly because its distribution is



more normal than that of  $K$  or  $L_{\infty}$  taken separately. The  $\omega$  index has been used by Kipling (1983), Appeldoorn (1983) and Beukema and Meehan (1985).

**Parameter  $P$ .** Pauly (1979) formulated the following criteria for an index of growth performance of fish: (1) it should relate to growth in weight, so as to allow comparison of species with different shapes; (2) it should consist of a single value and be easy to compute; and (3) it should be biologically interpretable.

The first derivative of equation (2), which expresses the growth rate of fish, has a single maximum  $(dw/dt)_{max}$  whether it is plotted against time or against weight. Therefore, the growth rate at the inflexion point ( $W_i$ ) of equation (2) can be used as standard for comparisons within and between species of different shapes. Note also that the fish of weight  $W_i$  usually represent, in nature, the bulk of their cohort (Philippart 1977). Compare with  $\omega$  which expresses  $dl/dt$  at length  $L = 0$  and hence at a cohort weight of zero.

Growth rate at the inflexion point of equation (2) is given by

$$dw/dt_{max} = (4/9) KW_{\infty} \quad \dots 5$$

Hence one can define

$$P = \log_{10}(K \cdot W_{\infty}) \quad \dots 6$$

whose antilog is directly proportional to  $(dw/dt)_{max}$ . Because of this,  $P$  is the only one of the four growth indices presented here whose value can be computed even when growth parameters are not available. In such cases,  $P$  can be computed from the slope of the steepest part of a weight growth curve.

**Parameter  $\phi$ .** The parameter  $\phi$ , introduced by Munro and Pauly (1983) is based on the growth parameter estimates compiled and analyzed by Pauly (1978, 1979; Table 1). It is defined by

$$\phi = \log_{10}K + (2/3) \log_{10} W_{\infty} \quad \dots 7$$

**Parameter  $\phi'$ .** Pauly (1979), working with a large compilation of growth parameter estimates (Pauly 1978) noted that the relationship between  $K$  and  $L_{\infty}$  is, between different fish stocks of the same species, not one of strict proportionality (as assumed, e.g., by Gallucci and Quinn 1979). Rather, this relationship is, on the average

$$\log_{10}K = \phi' - (2/3)\log_{10}L_{\infty}^3 \quad \dots 8$$

which leads to the definition

$$\phi' = \log_{10}K + 2 \log_{10}L_{\infty} \quad \dots 9$$

Table 1 gives a summary of the data which lead to the mean slope estimate of 2/3 for equation (7). The parameter  $\phi'$  has been used, among others, by Pauly (1980), Munro and Pauly (1983) and Pauly and Munro (1984), who also introduced the new symbol  $\phi'$  to replace "a" used earlier.

The relationship of  $\phi'$  to  $\phi$  is given in Table 2 with the interrelationships and dimensions of all four growth performance indices presented here.

## Materials and Methods

Table 3 presents the growth parameters used to test the four indices of growth performance. They were either taken from the reference cited, or computed, using standard methods, from size-at-age data in the cited literature. When necessary, length-to-weight conversions were performed.

For each index, the arithmetic mean, standard deviation and coefficient of variation, in percentages (C.V. = s.d. x 100/mean), were computed for important species in Table 3 (Table 4) and for the whole data set (Fig. 1).

The properties expected from the "best" index of overall growth performance are:

- it should be normally distributed when applied to a large number of populations belonging to closely-related taxa (such as the tilapias); and
- its variance should decrease as one descends from higher to lower taxonomic levels.

## Results and Discussion

As shown in Fig. 1 the distribution of  $P$ ,  $\phi$  and  $\phi'$  values are essentially normal and rather sharply peaked suggesting that these three indices, especially  $\phi'$  can indeed be used as indices of growth performance. Table 4 gives results for six species. Parameter  $\phi'$  has the lowest C.V. values, followed by  $P$  and  $\phi$ ;  $\omega$  has C.V. values 2-3 times higher than the other three indices.

Thus, our conclusion is that  $\phi'$  has properties which make it useful as an index of overall growth performance in fish, while  $\omega$  performed so badly that it should not be used for such purpose, notwithstanding the suggestion of Gulland (1983) that  $\omega$  "might be useful in distinguishing differences in the early growth rate of different populations."

Note that  $\phi'$  fulfilled both criteria for a "best" index of growth performance, as, besides having a low variance for the combined data set in Table 3, it also had a lower variance when applied to separate species (Table 4).

That  $\phi'$  performed better than the indices based on weight ( $P$ ,  $\phi$ ) is somewhat surprising, but can probably be



explained by the fact that tilapia species have similar shapes, and that in most populations in Table 3,  $W_{\infty}$  was estimated from  $L_{\infty}$  using length-weight relationships not estimated jointly with the specific values of  $L_{\infty}$ , thus adding variance to the  $W_{\infty}$  estimates.

Finally, the fact that  $\phi'$  has a dimension such that fish growth performance is related to surface area (Table 2), agrees with the suggestion of Pauly (1979, 1981, 1984) that respiratory surface area (i.e., gills) and hence oxygen supply are factors limiting fish growth. However, the limiting surfaces for growth (i.e., the gills) need not grow in proportion to length<sup>2</sup> or weight<sup>2/3</sup>. Rather the index  $\phi'$  and  $\phi$  imply length<sup>2</sup> or weight<sup>2/3</sup> only because the von Bertalanffy equation is structured around this assumption (see von Bertalanffy 1957). Thus, one would certainly obtain an equally good index of growth performance based on a power between 2/3 and 1 as occur in most fishes (Pauly 1979, 1981).

Based on the index  $\phi'$  one can infer that *Oreochromis niloticus* and *S. galilaeus* in Lake Kainji, Nigeria, are the best-growing fishes of the lot considered here, while the worst is *O. mossambicus* in Lake Sibaya, South Africa. The irony of this is that it is now very difficult to prevent wild *O. mossambicus* from reducing, through hybridization, the growth performance of introduced strains of *O. niloticus* and *S. galilaeus* (Pullin 1983; Tanaguchi et al. 1985). Clearly, growth comparisons of wild fish stocks, based on a suitable index of overall growth performance should be performed as part of the process leading to the selection of species for transfers and introductions.

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Table 1. Statistics of the 138 empirical regressions used to derive mean slope of  $-2/3$  for plots of  $\log_{10} K$  on  $\log_{10} W_{\infty}$  or  $\log_{10} L_{\infty}^3$ .

Type of summary data	Number of regressions	Regression statistics			95% confidence interval
		Mean slope <sup>b</sup>	s.d. of slopes	s.e. of mean slope	
$\log_{10} K$ on $\log_{10} L_{\infty}^3$	119 <sup>b</sup>	-0.632	0.386	0.035	-0.563 -0.701
$\log_{10} K$ on $\log_{10} W_{\infty}$	19	-0.714	0.279	0.064	-0.580 -0.848
Overall mean (unweighted)	138	-0.673 <sup>c</sup>	-	-	-
Overall mean (weighted by n)	138	-0.643	0.374 <sup>d</sup>	0.032	-0.581 -0.705 <sup>e</sup>

<sup>a</sup>Adapted from Tables X, XI and XIII a to h in Pauly (1979), based on growth parameters compiled in Pauly (1978).  
<sup>b</sup>Including one plot each for the tilapia species *Oreochromis exulatus*, *O. niloticus* and *O. mossambicus* and excluding 7 plots with positive values of b.

<sup>c</sup>The plots of  $\log_{10} K$  on  $\log_{10} W_{\infty}$ , although less numerous, involved growth parameter values previously checked for consistency; their mean value of b = 0.714 may thus be given the same weight as the mean b derived from the plots of  $\log_{10} K$  on  $\log_{10} L_{\infty}^3$ .

$$s.d._{1+2} = \sqrt{[(s.d._1^2(n_1 - 1)) + (s.d._2^2(n_2 - 1))] / (n_1 + n_2 - 2)}$$

<sup>e</sup>Note that 95% confidence interval includes  $-2/3$ , i.e., the value that would be expected given the assumption of  $-2/3$  built in the von Bertalanffy equation (see text).

Table 2. Algebraic relationships between and dimensions of the four growth performance indices  $\omega$ , P,  $\phi$  and  $\phi'$ .

Parameter	$\omega$	P	$\phi$	$\phi'$	
$\omega$	$\omega$	$= 10^P / (a \cdot L_{\infty}^3)$	$= \phi - \log_{10} L_{\infty} - \frac{2}{3} \log_{10} a$	$= 10^{\phi'} / L_{\infty}$	growth rate in length (L/t)
P	$= \log_{10} (\omega \cdot a \cdot L_{\infty}^3)$	P	$= \phi' + \frac{1}{3} \log_{10} W_{\infty}$	$= \phi' + \frac{1}{3} \log_{10} W_{\infty} + \frac{2}{3} \log_{10} a$	growth rate in weight ( $\log_{10} [L^3/t]$ )
$\phi'$	$= \log_{10} (\omega \cdot L_{\infty})$	$= P - \frac{1}{3} \log_{10} W_{\infty} - \frac{2}{3} \log_{10} a$	$= \phi - \frac{2}{3} \log_{10} a$	$= \phi'$	growth rate in units of surface area ( $\log_{10} [L^2/t]$ )
$\phi$	$= \log_{10} (\omega \cdot L_{\infty}) + \frac{2}{3} \log_{10} a$	$= P - \frac{1}{3} \log_{10} W_{\infty}$	$= \phi$	$= \phi' + \frac{2}{3} \log_{10} a$	growth rate in units of surface area ( $\log_{10} [L^2/t]$ )

<sup>a</sup>The parameter "a" refers to a length-weight relationship of the form  $W = a \cdot L^b$  in which, for simplicity's sake, isometry is assumed (i.e., in which the value of b is set equal to 3).