Aquaculture Research, 2005, **36,** 100–109 doi: 10.1111/j.1365-2109.2004.01191.x

Fitting growth with the von Bertalanffy growth function: a comparison of three approaches of multivariate analysis of fish growth in aquaculture experiments

Gertjan De Graaf[1] & Mark Prein[2]

[1]Nefisco foundation, Amsterdam, the Netherlands

[2]WorldFish Center, Penang, Malaysia

Correspondence: G De Graaf, Nefisco Foundation, Lijnbaansgracht 14 C, 1015 GN, Amsterdam, the Netherlands. E-mail: deGraaf@Nefisco.org

Abstract

Three approaches for multivariate analysis of fish growth in aquaculture experiments with Nile tilapia (*Oreochromis niloticus niloticus* L.) based on the von Bertalanffy growth curve are presented and compared. The approaches are: an extended Gulland-and-Holt (GH) plot, a forced extended GH plot and a multilinear regression analysis for the growth parameter K. All three models provide valuable insight into the major environmental factors influencing the daily growth rate and explain 28–46% of the variance of the observed daily growth rate of the used data set. For all three methods, the modelled parameter is significantly related to the net yield of Nile tilapia and can, therefore, be used for the predictive modelling of management scenarios. The extended GH plot loads the influence of environmental parameters upon L_∞, while the forced extended GH plot and Direct fitting of K load the influence on the growth parameter K. The latter is more in the tradition of aquaculture research. But the forced extended GH plot and Direct fitting of K can only be applied if L_∞ of the cultured species is known, as the selected L_∞ influences the variance in the regression variables.

Keywords: aquaculture, extended Gulland-and-Holt plot, extended forced Gulland-and-Holt-plot, multivariate analysis, Nile tilapia, von Bertalanffy growth curve

Introduction

The main process of interest in aquaculture is growth of the cultured species and its related production (Hepher & Pruginin 1980). The simplest procedure is to determine the length of time needed to reach market size (i.e. weight) and to express this growth rate as g day^{-1}. For the analysis of weight changes of fish, various sophisticated models are available (Ricker 1975). But any model must take into account the way in which the growth rate of fish slows down with increasing age and weight (Pitcher & Hart 1982), which is not the case if the growth rate is expressed in g day^{-1}.

In aquaculture feeding experiments, with data available over short periods of growth (δt), the specific growth rate: $\alpha = [\ln W_t - \ln W_0/\delta t]100$, where W_0 is the weight at time $t = 0$,W_t is the weight at time t, is often used as it encompasses this phenomenon comprehensively (Weatherly 1972; Huisman 1974; Hogendoorn, Jansen, Koops, Machiels, van Ewijk, & van Hees 1983).

A second well-known growth model, often used in fisheries, is that of von Bertalanffy, $L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right)$, who based his formulation on physiological considerations (von Bertalanffy 1951; Pauly 1981). In the model, L_t is the length at time t, L_∞ *is* the asymptotic length – the mean length the fish of a given stock would reach if they were to grow indefinitely, K is the growth rate parameter, or the rate at which L_∞ is approached and t_0 the age of the fish at zero length if it had always grown in a manner described by the equation. It assumes that fish grow towards some theoretical maximum length or weight, and the closer the length gets to the maximum, the slower the rate of size change will be (von Bertalanffy 1951; Pitcher & Hart 1982). Recently, the von Bertalanffy growth curve has become more popular in aquaculture research (Pauly, Moreau & Prein 1988; Springborn, Jensen, Chang & Engle 1992; Pauly, Prein & Hopkins 1993).

Pauly and colleagues (1988) used the von Bertalanffy growth curve to compare the overall growth performance of Nile tilapia (*Oreochromis niloticus*) in open water and aquaculture and concluded that aquaculture systems based on Nile tilapia failed to exploit fully the growth potential of this species. Pauly and colleagues (1993) developed a multivariate analysis method of fish growth in aquaculture derived from the von Bertalanffy growth curve. This 'extended Gulland-and-Holt (GH) plot' permitted them to identify and quantify key variables controlling fish growth including environmental and treatment variables to explain variance in growth of fish.

De Graaf (2004) and Springborn and colleagues (1992) used the von Bertalanffy growth curve in the development of a simulation model for the rearing of *Oreochromis niloticus niloticus* (L.).

However, it is often not realized that L_∞ and the growth parameter K in the von Bertalanffy growth curve are correlated: different combinations of K and L_∞ can give almost the same fit to data, except when a wide range of ages is represented. Again, a high value of K combines with a low value of L_∞ and *vice versa* (Sparre & Venema 1992). For fish stock assessment, this characteristic of the von Bertalanffy growth curve is not a constraint, as a good description of growth in the analytical fisheries models is more important than visualizing 'the correct' physiological processes behind growth. In aquaculture, this characteristic (i.e. obtaining two parameters) makes the application of the von Bertalanffy growth curve for the mere comparison of growth cumbersome, in contrast to other methods. The need for a single parameter for comparison of growth for one species raised under different conditions or for different species has been addressed with the introduction of 'Phi-prime': $\varphi' = \text{Log}\,K + 2\,\text{Log}\,L_\infty$, (Pauly & Munro 1984; Gayanilo & Pauly 1997), which includes the values of L_∞ and K.

Prein (1993) applied the standard GH plot and the extended GH plot to a large data set of integrated livestock fish farming experiments of *O. niloticus* in the Philippines. The standard fit provides one value for $L_\infty = 25.4$ cm and one value for $K = 3.62$ year^{-1}. This pair of growth parameters expresses the central tendency in the whole of the combined experiments (Pauly *et al.* 1993). In a multivariate analyses with the extended GH plot the impact of higher nutrient loads, and other environmental parameters on daily growth, are separately treated and provide a fixed value for the growth parameter K and a variable value for L_∞, depending on the values of the different environmental parameters. The method provided valuable insight into the different processes behind the daily growth in the different experiments.

One of the most important factors in aquaculture is oxygen. In most fish, oxygen enters the body through the gill surface and the relation between growth of the gill surface and body growth upon oxygen availability is discussed by van Dam and Pauly (1995): 'Because a surface does not grow as fast as a volume, the maximum oxygen supply per gram of body weight can be expected to decrease as the fish grows, assuming that the efficiency of the uptake does not change with body size. Pauly (1981) translated this concept into a balanced oxygen equation: oxygen available for growth equals oxygen entering the body minus oxygen needed for catabolism and anabolism. As the fish grows bigger, the oxygen supply limits the amount of energy that is available for growth. Eventually, the fish can consume just enough oxygen for its maintenance requirements. Body and gills cease to grow and the fish has attained its maximum size'. Hogendoorn and colleagues (1983) explained the limited growth with bio-energetic principles, as for the African catfish (*Clarias gariepinus* Burchell 1822) the metabolic scope for growth relatively decreases with increasing fish weight. Van Dam and Pauly (1995) simulated the growth of *O. niloticus* with a model that encompassed bio-energetic principles as well as maximum potential oxygen uptake based on the allometric relation between body weight and gill surface area. Their results provided strong support for the oxygen limitation theory. The results further revealed that an increased protein intake could cause a decrease in the maximum size of the Nile tilapia, due to an increased oxygen need for metabolism of the higher protein intake. This phenomenon could explain the wide range of the maximum size of Nile tilapia observed in nature. If it is assumed that in aquaculture experiments the range of dietary protein levels is limited, then the concept also implies that the studied species has a more or less fixed value for L_∞ in the von Bertalanffy growth curve.

The practical use of the existing multivariate method (Pauly *et al.* 1993; Prein 1993) in aquaculture is complicated, as the variance in growth is loaded on L_∞ and not on the growth parameter K, i.e. increased growth is expressed with a constant growth parameter K and a larger maximum length and *vice versa*. This is mathematically correct, but biologically not always correct.

This paper compares the use of the existing multivariate method for the analyses of growth in aquaculture experiments, with alternatives: a 'forced GH plot' (Pauly 1984), an 'extended forced GH plot' or a 'direct fit of K', whereby in the alternative methods L_∞ is fixed and the influence of environmental factors is loaded on the growth parameter K.

Materials and methods

The data set

Results from a 4-year study at the Fresh water Aquaculture Center of the Central Luzon State University (CLSU) near Munoz, Philippines were used as a source for data. The aim of the study was to develop economically viable small-scale integrated livestock-fish culture methods suitable for the Philippines, based entirely on livestock manure inputs. Details of the experimental design and results are given in Cruz and Shehadeh (1980), Hopkins and Cruz (1980, 1982), Hopkins, Cruz, Hopkins and Chong (1981), Hopkins, Pauly, Cruz and van Weerd (1982), Hopkins, Inocencio and Cruz (1983) and PCARRD (1982). Data processing is given by Prein (1993) as he analysed the same data set with a standard extended GH plot and with Path analysis. Only a general overview is given here.

One hundred sixteen growth experiments were conducted from 1979 to 1981 in 24 backyard sized ponds (0.04 or 0.1 ha). Treatments were always duplicated or triplicated. The ponds were stocked in polyculture of 85% Nile tilapia (*O. niloticus*) as the main crop, 14% common carp (*Cyprinus carpio carpio* L.) as a bottom stirrer and 1% predator, either snakehead (*Channa striata* Bloch 1793) or the Thai catfish (*Clarias batrachus* L.). The overall stocking densities were 10 000 or 20 000 fish ha^{-1} and the average size of *O. niloticus* at stocking was usually 2.5 cm.

Nutrient inputs to the ponds were either inorganic fertilizer or fresh manure from pigs, ducks or chickens kept in stalls on the pond dikes. The experimental duration was set to match a period of 90 days that tilapia took to attain a local market size of 60 g. Fish size data were obtained by bi-weekly sampling and at harvest. The average daily manure input was determined on a dry weight basis. Dissolved oxygen was measured early in the morning.

The original data set contains 713 record sets and after deleting records with negative growth, i.e. the records where the mean length of the sampled fish was smaller than the mean length at the previous sampling time, 650 remained. For each growth interval data each record encompassed mean growth rate, stocking density, pond area, mean manure load and mean dissolved oxygen. At random, 325 records were selected for developing the multiple regression models. The remaining 325 records were used to check the different models. A second data set contained the stocking and harvest summaries of the experiments and was used to compare modelled growth with net yields.

Gulland-and-Holt plots

The standard GH plot

The von Bertalanffy growth curve implies that the growth rate ($\mathrm{d}L/\mathrm{d}t$) declines linearly with length. This relation between length and growth rate can be used to estimate the two parameters L_∞ and K. In a standard GH plot, the growth rate $\mathrm{d}L/\mathrm{d}t$ of an experimental interval is plotted over the mean length in that interval (Gulland & Holt 1959). The differential form is

$$\frac{\mathrm{d}L}{\mathrm{d}t} = K(L_\infty - L_{\mathrm{mean}}) \tag{1}$$

or in terms of growth increments per interval (length L_1 and L_2);

$$\frac{L_2 - L_1}{t_2 - t_1} = a + b\left(\frac{L_1 + L_2}{2}\right) \tag{2}$$

Providing the growth parameters
$K = -b$,
$L_\infty = a/-b$.

Standard forced GH plot

In a 'forced GH plot', L_∞ is known and $\mathrm{d}L/\mathrm{d}t$ is plotted against $L_\infty - L_{\mathrm{mean}}$ or in terms of growth increments per interval (length L_1 and L_2);

$$\frac{L_2 - L_1}{t_2 - t_1} = K\left(L_\infty - \frac{L_1 + L_2}{2}\right) \tag{3}$$

whereby K is the slope of the regression through the origin.

In the present study, L_∞ is fixed at 30.8 cm, resulting from the extended GH plot, obtained previously from the data set (Prein 1993).

Extended GH plot

The standard GH plot can be extended into a multiple regression form, permitting environmental and treatment variables to be considered simultaneously in the same analysis (Pauly *et al.* 1993):

$$\frac{dL}{dt} = a + b_1 L_{\text{mean}} + b_2 X_2 + b_n X_n \tag{4}$$

Or in terms of growth increments per interval (length L_1 and L_2);

$$\frac{L_2 - L_1}{t_2 - t_1} = a + b_1\left(\frac{L_1 + L_2}{2}\right) + b_2 X_2 + b_n X_n \tag{5}$$

The growth parameters are estimated from:

$K = -b_1$,

$L_\infty = (a + b_2X_2 + \cdots + b_nX_n)/-b_1$.

whereby $X_2, \ldots, X_n$ are environmental and treatment variables simultaneously recorded during the growth increment. Their influence is loaded on the value of L_∞. As environmental and treatment variables, the square root of stocking density (kg m^{-3}), dissolved oxygen (mg L^{-1}), pond area (m^2) and daily manure load (kg ha^{-1} day^{-1}) are used.

Extended forced GH plot

In the extended forced GH plot, the influence of environmental parameters is loaded on the growth parameter K, while L_∞ is kept constant. The standard forced GH plot can be transformed into a multiple regression form:

$$\frac{dL}{dt} = (\alpha + \beta_1 X_1, \ldots, \beta_n X_n)(L_\infty - L_{\text{mean}}) \tag{6}$$

or

$$\frac{dL}{dt} = \alpha(L_\infty - L_{\text{mean}}) + \beta_1 X_1(L_\infty - L_{\text{mean}}), \ldots, \beta_n X_n(L_\infty - L_{\text{mean}}) \tag{7}$$

By creating the variables: $X_1(L_\infty - L_{\text{mean}})$, $X_2(L_\infty - L_{\text{mean}}), \ldots, X_n(L_\infty - L_{\text{mean}})$ and using them in the multiple regression, K can be calculated as:

$$K = \alpha + \beta_1 X_1, \ldots, \beta_n X_n \tag{8}$$

whereby, again, $X_1, \ldots, X_n$ are environmental and treatment variables simultaneously recorded during the time interval of the fish growth increment.

K approach

An alternative is to determine the growth parameter K for each incremental growth interval, which can be directly calculated from (Sparre & Venema 1992):

$$K = \frac{-1}{t_2 - t_1} \text{Ln}\left[\frac{L_\infty - L_2}{L_\infty - L_1}\right] \tag{9}$$

Subsequently, the impacts of the different environmental and treatment variables on the growth parameter K were evaluated with standard multiple regression:

$$K = \alpha + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_n X_n \tag{10}$$

where, again, $X_1, \ldots, X_n$ are environmental and treatment variables simultaneously recorded during the growth increment.

Results

Standard GH plots

The standard GH plot and the standard forced GH plot over the entire data set are presented in Figs 1 and 2. The results provide $L_\infty = 25.8$ cm, $K = 3.24$ year^{-1} and $\varphi' = 3.34$ for the standard GH plot and $L_\infty = 30.8$, $K = 2.41$ year^{-1} and $\varphi' = 3.36$ for the standard forced GH plot.

Multivariate plots

The results of the extended GH plot, the forced extended GH plot and the multilinear regression for K are presented in Tables 1 and 2.

The results provide a value for $L_\infty = 28.3$ cm, calculated with the mean values of the environmental parameters, $K = 2.73$ year^{-1} and $\varphi' = 3.34$ for the standard extended GH plot, and $L_\infty = 30.8$, $K = 2.23$ year^{-1}, calculated with the mean values of the environmental parameters and $\varphi' = 3.36$ for the forced extended GH plot.

With the exception of manure load in the forced extended GH plot all variables are adding significantly to the regressions (Table 1). The standardized β coefficients indicate that in both extended plots, length,

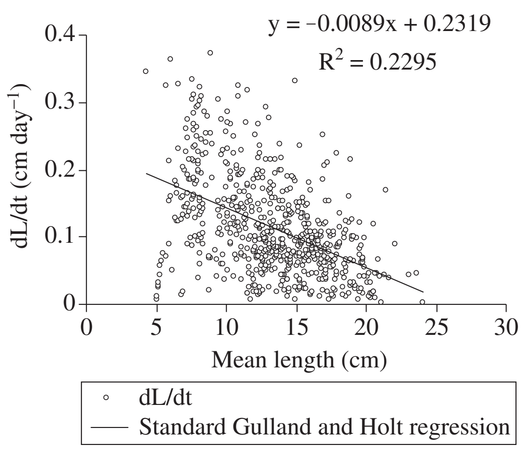

Figure 1 Standard Gulland-and-Holt plot for the overall data set.

stocking density and dissolved oxygen are the major variables in the regression. For the multilinear regression for *K*, the β coefficients indicate that stocking density and dissolved oxygen are the major variables in the model.

The standard extended GH plot explains 46% of the total variation in growth (dL/dt) in the total data set with the environmental and treatment variables, whereby, the majority of the variation is explained by two variables only: length and dissolved oxygen. The multilinear regression for *K* explains 28% of the total variation in growth (*K*) by the environmental and treatment variable, and again a major portion of the variation is explained by two variables only: stocking density and dissolved oxygen. Increasing the value of $L_\infty = 61$ cm, in the multilinear regression for *K*, increases the explained variance for *K* to 38%. For the forced extended GH plot, the variance cannot be explained similarly as the regression is fitted through the origin (Eisenhauer 2003).

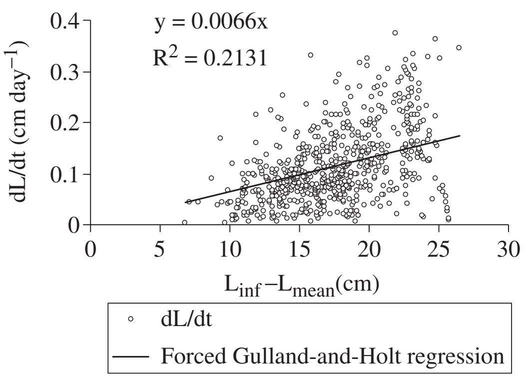

Figure 2 Standard forced Gulland-and-Holt plot for the overall data set.

In Fig. 3, values of dL/dt and K as calculated with three regression models are plotted against observed values and the calculated regression lines; $y = (0.8...)x$, indicate that all three models slightly under estimate the observed values. The Pearson correlation coefficient between observed and simulated values for the standard extended GH plot, the forced extended GH plot, and the direct fit of *K* are significant ($P \leq 0.01$) with values of 0.63, 0.66 and 0.46 respectively.

Modelled growth for individual experiments

The results of the three regression analyses were used to calculate *K* or L_∞ with summarized data of 116 experiments, where net yields are known. The results of the regressions were applied over the mean values of the environmental parameters to calculate the overall value of *K* or L_∞ throughout the experiments. In

Table 1 Results of the standard extended Gulland-and-Holt (GH) plot, the forced extended GH plot and multilinear regression ($n = 325$)

	Standard extended GH			Forced extended GH			Multilinear *K*		
Model parameters	**Coefficient**	**β**	**Significance**	**Coefficient**	**β**	**Significance**	**Coefficient**	**β**	**Significance**
L_{mean} or $L_\infty - L_{mean}$	−0.00748	−0.407	0.000	0.00975	1.315	0.000			
Stocking density	−0.17399	−0.350	0.001	−0.01348	−0.536	0.000	−4.23969	−0.468	0.000
Pond area	0.00004	0.173	0.000	0.00000	0.289	0.000	0.00075	0.171	0.000
Manure	0.00029	0.155	0.006	0.00001	0.104	0.069	0.00604	0.176	0.004
Dissolved oxygen	−0.01330	−0.334	0.000	−0.00091	−0.395	0.000	−0.24499	−0.338	0.000
Constant	0.24615		0.000				3.22287	0.000	0.000

Table 2 Percentage of total explained variation for the different variables for the standard extended Gulland-and-Holt (GH) plot and the multilinear regression for *K*

	Standard extended GH plot		Multilinear *K* regression	
Model parameter	**Sum of squares**	**Explained variation (%)**	**Sum of squares**	**Explained variation (%)**
Length	0.4945	28.0		
Stocking density	0.0375	2.1	53.3338	9.9
Dissolved oxygen	0.2035	11.5	74.9433	14.0
Pond area	0.0683	3.9	19.0359	3.5
Manure load	0.0086	0.5	4.2432	0.8
Total	1.7637	46.1	536.9596	28.2

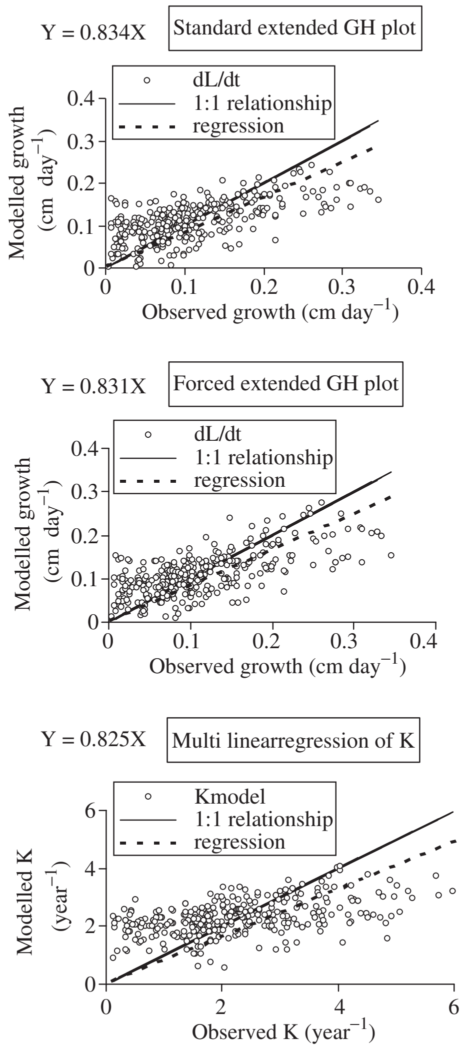

Figure 3 Predicted and observed growth and K of Nile tilapia for the standard extended GH plot, the forced extended GH plot and the multilinear regression of K; the dotted line is the regression and the bisector (solid line) represents perfect agreement between observed and modelled values ($n = 325$).

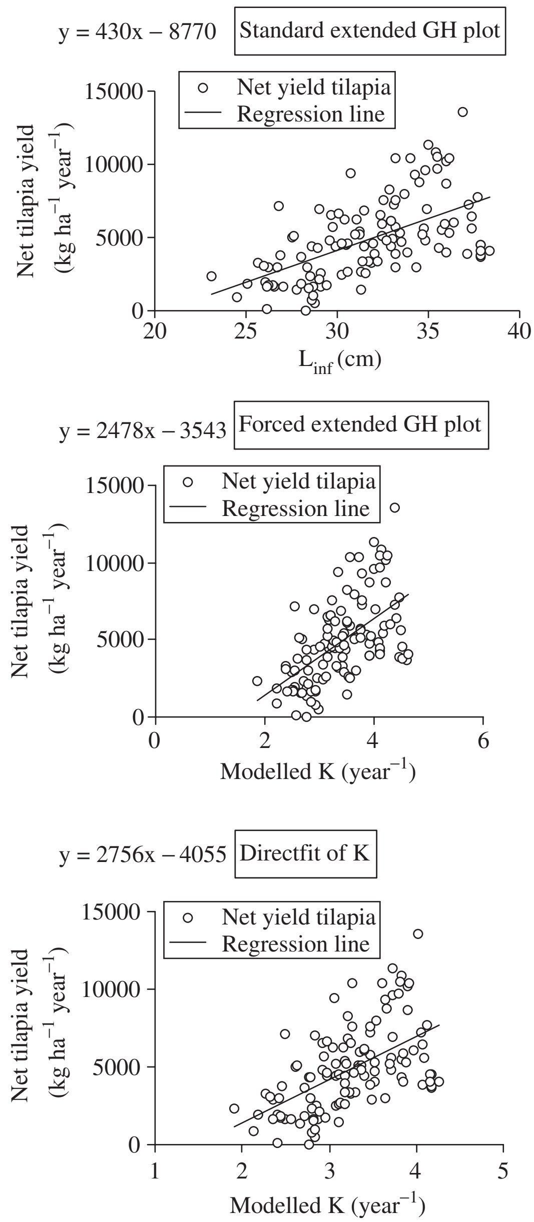

Figure 4 Relation between calculated K, L_∞ and net yield of tilapia.

Fig. 4, the net yield of Nile tilapia is plotted against these calculated growth parameters. All three calculated regressions are significant ($P \leq 0.001$), indicating a close relation between the modelled parameters and net yield for all three methods.

Discussion

Multivariate models

Multivariate models have been extensively used and discussed by Prein, Hulata and Pauly (1993). The analyses with the extended GH plot in the study of Prein (1993) and with the extended GH and the forced extended GH plot in the present study give almost similar results. It identified stocking density, dissolved oxygen, pond area and manure load as significant variables affecting the daily growth of Nile tilapia. The slight difference between the results of the extended GH plot of Prein (1993) and the present study is due to a difference in removing outliers from the original data set. The results between the extended GH plot and the forced extended GH plot should be similar, as the same data set was used and in terms of variance within the data set, the mathematical form of the regression, the extended GH and the forced extended GH plot are identical.

At first glance, the strange negative relationship between dissolved oxygen and growth, indicating that Nile tilapia growth is higher when early morning dissolved oxygen levels are lower, is explained by Prein (1993) by the fact that dissolved oxygen levels are directly controlled by the amount of phytoplankton, an important nutritional component for tilapia, in the pond. With higher phytoplankton abundance the amplitude of the diurnal dissolved oxygen variation increases, characterized by the highest levels of saturation in the early afternoon and the lowest level near zero at dawn. However, this is in contradiction with the results of the simulation model of van Dam, Huisman and Rabbinge (1996), which indicated that growth of tilapia was oxygen-limited, even though mean early-morning dissolved oxygen levels was higher than 4 mg L^{-1}.

The multilinear regression for *K* explains 28–38% of the variance in growth, compared with 46% in the standard extended GH plot. The standard GH plot includes L_{mean}, which means that this model encompasses the basic characteristic of fish growth, a reduction in growth rate as they become larger, reflected by 28% of the variance explained by this variable alone. Excluding this variable, as is the case in the multilinear regression for *K*, makes the method less valuable. Secondly, the way in which *K* is estimated from the data set (Equation 9) results in a reduction of the variance of *K* at higher values of L_∞, due to the logarithm of the fraction that includes L_∞ (Fig. 5). The inverse is occurring in the forced GH plot

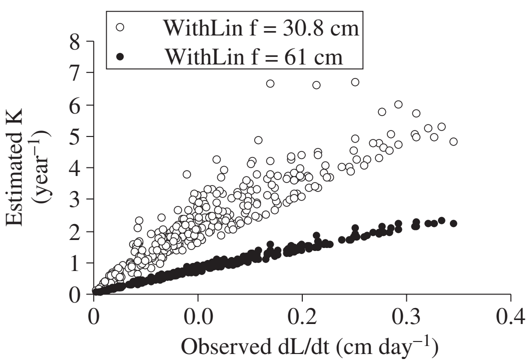

Figure 5 Effect of increasing the value of L_∞ in the estimation of the growth parameter *K*.

Table 3 Comparison of forced extended Gulland-and-Holt plot applied with two values of L_∞: $L_\infty = 30.8$ and $L_\infty = 61$ cm

	$L_\infty = 30.8$ cm		$L_\infty = 61$ cm	
Variable	β coefficient	Variance explained (%)	β coefficient	Variance explained (%)
$L_\infty - L_{\text{mean}}$	1.35	76.0	1.49	72.7
Manure	0.10	0.2	0.11	0.0
Stocking density	− 0.54	6.0	− 0.79	6.0
Area	0.29	0.6	0.26	0.6
Dissolved oxygen	− 0.40	2.6	− 0.35	2.6

(Equation 7). A higher value of L_∞ increases the variance of the environmental variables. However, the overall impact in the regression is less (Table 3), as the variance of the most important variable $L_\infty - L_{\text{mean}}$ does not change. The impact of L_∞ on the variance of the different parameters implies that the forced extended GH plot and the multilinear regression of *K* can only be applied if L_∞ for the raised species is known.

Regarding the regression coefficients (Fig. 3), all three models slightly underestimate the growth rate of Nile tilapia in a similar way. Regression through the origin of observed and simulated data provides standardized results, which facilitates comparison of methods or between different simulated variables. However, removing the constant in regression through the origin also diminishes the model's fit to the data (Eisenhauer 2003), which is clearly visible by distribution of the calculated values around the bisector (Fig. 3) and the Pearson correlation coefficients. In the multilinear regression for *K*, low observed values of *K* are overestimated and high observed values of *K* are underestimated, resulting in a low Pearson correlation coefficient. However, both are counteracting and result in a reasonable regression coefficient if fitted through the origin. Still, the higher Pearson correlation coefficients in the extended GH plots indicate that they are providing more reliable results.

For all three models, a higher L_∞ or *K* results in a higher net yield of Nile tilapia and, therefore, they can be used to predict net yields under different management scenarios. Differences between the three models are mainly related to explanation of the variance in the observed growth and the complexity/

Table 4 Comparison of the three models

Criteria	Standard extended Gulland-and-Holt (GH) plot	Forced extended GH plot	Direct modelling of K
Model variable	L_∞	K	K
Variance in observed growth rate explained	Good	Not applicable	Acceptable
Predictive value	Good	Good	Good
Simplicity	Straightforward	New fitting parameter to be created	Straightforward
Objectivity	L_∞ and K are estimated through the model	L_∞ has to be known	L_∞ has to be known

simplicity of the model. The major characteristics are presented in Table 4.

No strong recommendations can be given as to which model to use in aquaculture experiments as each model has some advantages and disadvantages. From a scientific point of view, the standard extended GH plot gives the best performance as it is completely objective and explains the highest percentage of the variance in the observed data. However, a disadvantage of the standard GH plot is that it loads the variation in growth on L_∞, which is biologically not always correct. A disadvantage of the forced extended GH plot is that due to its characteristic, a regression through the origin, analysis of variance cannot be compared with the analysis of variance applied for the standard extended GH plot or the multiple-linear regression of K, i.e. Tables 2 and 3 cannot be compared (Eisenhauer 2003). However, the β coefficients of the regressions in a forced extended GH plot still identify the major driving forces.

From an aquaculture perspective, the forced extended GH plot and direct fitting of K are preferred as they use a 'growth parameter' to explain or predict differences in net yields. However, this approach implies that L_∞ for the raised species is known, especially as the value of L_∞ influences the variance.

In the present study, a value for L_∞ of 30.8 cm is used, which corresponds to a weight of about 750 g. With a corresponding K of 2.23 year^{-1}, tilapia will reach a weight of about 250 g in about four months, after which the growth rate decreases (Fig. 6).

In terms of the weight at harvest, the selection of L_∞ of 30.8 describes general culture practices well (Melard 1986; de Graaf, Galemoni & Banzoussi 1996). The results of Melard (1986) indicated that the growth rate reduced to almost zero after about 250 days, with tilapia reaching a weight of about 650 g, which more or less conforms to the model with

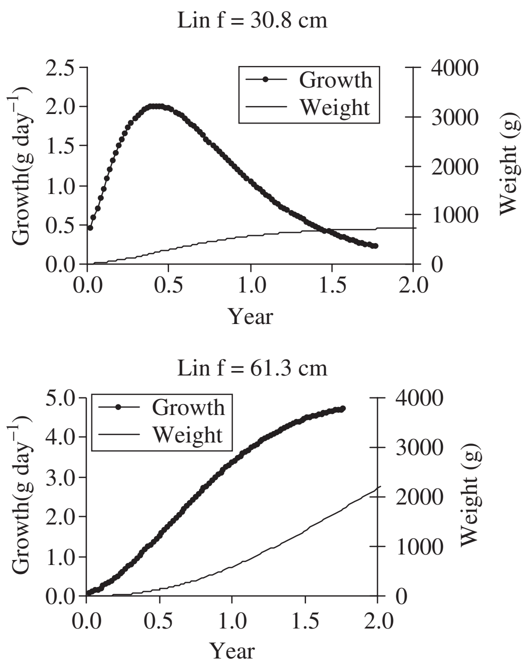

Figure 6 Comparison of weight and daily growth rate with different values of L_∞, with $\varphi' = 3.3$.

$L_\infty = 30.8$ cm. However, in nature L_∞ up to 61.3 cm has been reported (*www.fishbase.org*). With such an L_∞, the size of harvest after 4 to 5 months does not change significantly, but the growth is maintained for a longer period of time and the fish can reach a larger size (Fig. 6). Such a growth pattern is not realistic for aquaculture, and it stresses the need of a well-defined *maximal* L_∞ for aquaculture if the forced extended GH plot or direct fits of K are to be used, especially if the results are used in predictive modelling of aquaculture practices (de Graaf 2004). Considering the fact that farmers will always try to keep the environmental conditions at optimum and will a use limited range of dietary protein levels, variation in L_∞ will be limited and defining a *maximal* L_∞ is possible and should be further studied.

Acknowledgments

We are grateful to the WorldFish Center/ICLARM and Dr Kevin Hopkins for making the data available. The valuable comments on the oxygen limitation theory given by Dr Anne van Dam are highly appreciated. We are also grateful to two anonymous reviewers for constructive comments on the first draft of the manuscript. We thank Tracy Barnett for editing the manuscript. This study was funded by NEFISCO foundation and support by the board is gratefully acknowledged.

References

Cruz E.M. & Shehadeh Z.H. (1980) Preliminary results of integrated pig–fish and duck–fish production tests. In: *Integrated Agriculture-Aquaculture Farming Systems, ICLARM Conference Proceedings*, Vol. 4 (ed. by R.S.V. Pullin & Z.H. Shehadeh), pp. 225–238. ICLARM, Manila, Philippines.

van Dam A.A. & Pauly D. (1995) Simulation of the effect of oxygen on food consumption and growth of Nile tilapia *Oreochromis niloticus* (L.). *Aquaculture Research* **26**, 427–440.

van Dam A.A., Huisman E.A. & Rabbinge R. (1996) Simulation of food and oxygen limitations on the growth of Nile tilapia, *Oreochromis nilotics* L. in fish ponds. *Aquaculture Research* **27**, 463–478.

Eisenhauer J.G. (2003) Regression through the origin. *Teaching Statistics* **25**, 76–80.

de Graaf G.J. (2004) Optimisation of the pond rearing of Nile tilapia (*Oreochromis niloticus niloticus* L.): the impact of stunting processes and recruitment control. PhD Thesis, Wageningen University, Wageningen, the Netherlands.

de Graaf G.J., Galemoni F. & Banzoussi B. (1996) Successful recruitment control of Nile tilapia, *Oreochromis niloticus* by the African catfish, Clarias gariepinus (Burchell 1822) and the African snakehead, *Ophiocephalus obscuris*, I. A biological analyses. *Aquaculture* **146**, 85–100.

Gayanilo F.C. & Pauly D. (1997) FAO-ICLARM stock assessment tools (FISAT), reference manual. *FAO Computerized Information Series (Fisheries)*, No. 8. FAO, Rome, Italy, 262pp.

Gulland J.A. & Holt S.J. (1959) Estimation of growth parameters for data at unequal time intervals. *Journal du Conseil International pour l'Explorations de la Mer* **25**, 47–49.

Hepher B. & Pruginin Y. (1980) Tilapia culture in ponds under controlled conditions. In: *The Biology and Culture of Tilapia. ICLARM Conference Proceedings*, 7, Manila, Phillipines (ed. by R.S.V. Pullin & R.H. Lowe-McConnell), pp. 185–205. ICLARM, Manila, Philippines.

Hogendoorn H., Jansen J.A.J., Koops W.J., Machiels M.A.M., van Ewijk P.H. & van Hees J.P. (1983) Growth and production of the African catfish, *Clarias lazera* (C&V.) II. Effects of body weight, temperature and feeding level in intensive tank culture. *Aquaculture* **34**, 265–285.

Hopkins K.D. & Cruz E.M. (1980) High yields but still questions: three years of animal–fish farming. *ICLARM Newsletter* **3**, 12–13.

Hopkins K.D. & Cruz E.M. (1982) *The ICLARM-CLSU Integrated Animal–Fish Farming Project*: *Final Report*. ICLARM Technical Reports, 5, 96pp. ICLARM, Manila, Philippines.

Hopkins K.D., Cruz E.M., Hopkins M.L. & Chong K.C. (1981) Optimum manure loading rates in tropical freshwater fish ponds receiving untreated piggery wastes. In: *ICLARM, The ICLARM Integrated Animal–Fish Farming Project, Poultry–Fish and Pig–Fish Trials*. ICLARM Technical Report, 5, 29pp. ICLARM, Manila, Philippines.

Hopkins D.K., Pauly D., Cruz E.M. & van Weerd J.M. (1982) An alternative to predator–prey ratios in predicting recruitment. *Meersforschung, Reports Marine Research* **29**, 125–135.

Hopkins K.D., Inocencio P. & Cruz E.M. (1983) Water quality in integrated livestock–fish ponds. *Journal World Mariculture Society* **14**, 495–504.

Huisman E.A. (1974) A study on optimal rearing conditions for carp (*Cyprinus carpio* L.). PhD Thesis, Wageningen University, Wageningen, the Netherlands, 95pp.

Melard Ch. (1986) Les bases biologiques de l'elevage intensif du Tilapia du Nil, recherches sur la biologie d'*Oreochromis* (Tilapia) *niloticus* L. (Pisces Cichlidae) en elevage experimental: reproduction, croissance, bioenergetique. *Cahiers d'Ethologie Applique* **10**, 224pp.

Pauly D. (1981) The relationship between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Meeresforschung* **28**, 251–282.

Pauly D. (1984) Fish population dynamics in tropical waters: a manual for use with programmable calculators. *ICLARM Studies and Reviews* **8**, 33–70.

Pauly D. & Munro J.L. (1984) Once more on the comparison of growth in fish and invertebrates. *ICLARM Fishbyte* **2**, 21.

Pauly D., Moreau J. & Prein M. (1988) A comparison of overall growth performance of tilapia in open waters and in aquaculture. In: *The Second International Symposium on Tilapia in Aquaculture. ICLARM Conference Proceedings*, Vol. 15 (ed. by R.S.V. Pullin, T. Bhukaswan, K. Tonguthai & J.L. Maclean), pp. 469–479. ICLARM, Manila, Philippines.

Pauly D., Prein M. & Hopkins K.D. (1993) Multiple regression analysis of aquaculture experiments based on the "extended Gulland-and-Holt plot": model derivation, data requirements and recommended procedures. In: *Multivariate Methods in Aquaculture Research: Case Studies of Tilapias in Experimental and Commercial Systems, ICLARM Studies and Reviews*, Vol. 20 (ed. by M. Prein, G. Hulata & D. Pauly), pp. 13–23. ICLARM, Manila, Philippines.

PCARRD (1982) Integrated fish–pig farming. In: *Technology,* Vol 4, pp. 1–16. Philippine Council for Agriculture and Resources Research Development, Los Banos, Philippines.

Pitcher T.J. & Hart P.J.B. (1982) *Fisheries Ecology*. Chapman & Hall, London, UK, 408pp.

Prein M. (1993) Multiple research and path analysis of Nile tilapia growth on integrated livestock–fish culture in the Philippines. In: *Multivariate Methods in Aquaculture Research: Case Studies of Tilapias in Experimental and Commercial Systems, ICLARM Studies and Reviews,* Vol. 20 (ed. by M. Prein, G. Hulata & D. Pauly), pp. 50–66. ICLARM, Manila, Philippines.

Prein M., Hulata G. & Pauly D., Editors (1993) Multivariate methods in aquaculture research: case studies of tilapias in experimental and commercial systems. *ICLARM Studies and Reviews* **20,** 221pp.

Ricker W.E. (1975) Computation and interpretation of biological statistics of fish populations. *Bulletin of Fisheries Research Board of Canada* **191**, 382pp.

Sparre P. & Venema S.C. (1992) *Introduction to tropical fish stock assessment, Part 1 – manual.* FAO fisheries technical paper 306-1 rev. 1, FAO, Rome, Italy, 376pp.

Springborn R.R., Jensen A.L., Chang W.Y.B. & Engle C. (1992) Optimum harvest time in aquaculture: an application of economic principles to a Nile tilapia, *Oreochromis niloticus* (L.), growth model. *Aquaculture and Fisheries Management* **23**, 639–647.

von Bertalanffy L. (1951) *Theoretische Biologie, Zweiter Band: Stoffwechsel, Wachstum.* A Francke AG Verlag, Bern, Switzerland, 418pp.

Weatherly A.H. (1972) *Growth and Ecology of Fish Populations*. Academic Press, London, UK, 293pp.