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A Multivariate Model of Tilapia Growth, Applied to Seawater Tilapia Culture in Kuwait[a]

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Abstract

Traditional analyses of aquaculture growth experiments usually consider only the yield at the end of the experiments and ignore the growth data collected during intermediate samplings. A multivariate model based on an expansion of the "Gulland and Holt Plot" used in fisheries biology provides a methodology to extract growth information from the data from intermediate samplings. This model is applied to data from three tilapia yield experiments conducted in seawater in Kuwait. The effects of temperature, sex ratio and fish length on growth rate are quantified.

Introduction

Estimation of growth rates under different culture regimes is an essential part of aquaculture research. Three common expressions of growth rates were used with the following frequencies in Avault (1985).

absolute growth rates (g or g/day)	66 %
instantaneous rates of growth	28 %
von Bertalanffy growth function	6 %

Detailed presentations of these and other growth expressions can be found in Ricker (1979).

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Absolute growth rates are commonly used with analysis of variance (ANOVA) procedures to evaluate treatment effects in aquaculture yield trials. However, absolute rates are subject to severe restrictions. They can only be compared among groups of fish with the same starting size that have been observed for equal periods of time and under identical environmental conditions. Thus, valid generalizations from absolute rates are extremely difficult to make.

Instantaneous growth rates and growth functions such as the von Bertalanffy growth function (VBGF) are not subject to restrictions on initial size or period of time. The forms of growth assumed by these functions closely approximate many observed fish growth series (Ricker 1979).

This paper presents a detailed description of a multivariate method for analyzing fish growth in aquaculture experiments, which was presented in brief by Pauly and Hopkins (1983). The method uses multiple regression equations to evaluate the effects of environmental variables on growth. The parameters of VBGF can be estimated from those equations. Data from seawater tilapia culture experiments in Kuwait were analyzed to illustrate the method, which has also been used with integrated livestock-fish data by Hopkins and Cruz (1982) and Prein (1985). A similar method, without the ability to estimate VBGF coefficients, was used by Jones and Strawn (1985) in analyzing data from a cage culture experiment.

Derivation of the method

This method was first proposed by Pauly and Ingles (1981) for use in analyzing temperature effects on growth in a mark-recapture experiment with coral reef fish. The method was later named the "Extended Gulland and Holt Plot" by Pauly (1984) because the basic assumption was originally presented by Gulland and Holt (1959). The basic assumption is that the growth rate of fish (in length) decreases linearly as the fish grow larger and can be expressed as:

$$dL/dt = a + bL \qquad \text{... 1)}$$

where L is length, t is time, and a and b are empirically determined constants. The differential equation (1) can be replaced by the following difference equation if the time interval is short:

$$\Delta L_t/\Delta t = a + b\overline{L}_t \qquad \text{... 2)}$$

where ΔL_t is the increase in length during period t, t is the duration of period t, and $\overline{L}_t$ is the arithmetic mean of the lengths at the beginning and end of period t.

As weight is of more interest than length to the aquaculturist, an alternative equation (form) using weight is substituted.

$$\frac{\Delta \sqrt[3]{W_t}}{\Delta t} = a + b\ \overline{\sqrt[3]{W_t}} \qquad \text{... 3)}$$

where $\Delta \sqrt[3]{w_t}$ is the change in the cube root of fish weight fish during period Δt and $\overline{\sqrt[3]{W_t}}$ is the arithmetic mean of the cube root of fish weights at the start and end of period t.

Equation (3) suggests that only weight affects growth rate. However, the regression equations can be expanded into multiple regressions of the form:

$$\frac{\Delta \sqrt[3]{w_t}}{\Delta t} = a + b_1\ \overline{\sqrt[3]{w_t}} + b_2 x_{2,t} + \ldots + b_n x_{n,t} \ldots \text{ 4)}$$

where $X_{2,t}$, $X_{3,t}$ ... $X_{n,t}$ are variables conceived as affecting growth rate during period t. These variables can be continuous variables such as temperature, or qualitative variables such as the presence or absence of antibiotic in the feed. Qualitative variables are included by the use of dummy variables (e.g., 1 = presence of antibiotic while 0 = absence of antibiotic). Given measurements of these variables during each time interval t, multiple regression techniques can be used to identify which of the variables have a significant effect on growth (i.e., identify slopes, b, which vary significantly from 0). The values of the slopes quantify the effects.

As the Extended Gulland and Holt Plot is based on multiple regression, it is constrained by the basic assumptions of the regression method being used. The Ordinary Least Squares method has these basic assumptions:

1. Homoscedasticity
2. Nonstochastic independent variables
3. No autocorrelation
4. Number of observations exceeds the number of coefficients to be estimated.
5. No multicollinearity

Homoscedasticity means that the error terms are not correlated with any of the independent variables. For example, the variation in growth must be the same whether the fish weight is 10 g, 100 g or any other number. Nonstochastic independent variables mean that the independent variables are fixed by the experimenter and do not vary randomly. No autocorrelation means that there is no relationship between the error terms in successive periods and implies there is no relationship between the independent variable, X_n, in period i and X_n in period i-1. Multicollinearity refers to correlations between the independent variables. Detailed presentations of these assumptions can be found in statistics texts such as Gujarati (1978) and Kmenta (1986).

In aquaculture experiments, the usual practice is to sample each pond a number of times throughout the experimental period. Clearly, the growth rate in period t is related to the growth rate in period t-1 and the assumption of no autocorrelation is violated. Although the Ordinary Least Squares method would provide unbiased estimates of the coefficients to Equation 4, the F and t statistics would be overestimated, precluding hypothesis testing (e.g., comparison of the effects of different independent variables). Therefore, a Generalized Least Squares procedure should be used. Assuming that only first-order autocorrelation exists, the following transformation will remove the autocorrelation (Gujarati 1978):

$$Y_t - pY_{t-1} = a(1-p) + b_n (X_{n,t} - pX_{n,t-1}) \qquad \dots 5)$$

where $p = 1 - 0.5d$ ... 6)

and d is the Durbin-Watson statistic. The transformation in Equation (5) leads to the loss of the first observation in each set of data. If the number of observations is small, alternative transformations can be used in order to include the first observation(s) (Kmenta 1986; Gujarati 1978).

In addition to the constraints imposed by the regression procedure, there are some other limitations to the Extended Gulland and Holt Plot. The fish samples should be unbiased and the sampling period should be short enough to ensure the validity of Equation (2) but not so short that growth is obscured by variation inherent in random sampling.

The VBGF can be expressed in terms of weight:

$$W_t = W_\infty (1 - e^{-K(t-t_0)})^3 \qquad \dots 7)$$

where W_t is the weight at time t, and W, K and t_0 are constants. W_∞ corresponds to the average maximum weight which could be attained by fish in the population. These VBGF parameters can be estimated from a Gulland and Holt Plot as follows:

$$K = -b_1 \qquad \dots 8)$$

$$W_\infty = (a/K)^3 \qquad \dots 9)$$

$$t_0 = t + \frac{1}{K} \ln \left(\frac{\sqrt[3]{W_\infty} - \sqrt[3]{W_t}}{\sqrt[3]{W_\infty}} \right) \qquad \dots 10)$$

If the Extended Gulland and Holt Plot is used, K and t_0 of the VBGF for weight are again estimated according to equations (8) and (10), respectively, whereas W_∞ for a given set of environmental conditions is estimated as follows:

$$W_\infty = ((a + b_2X_{2t} \dots\dots + bnX_n)/K)^3 \qquad \dots 11)$$

To estimate t_0 using Equation (10), the average weight, W, of fish of a known age, t, is required. If absolute age data are not available, recursive forms of the VBGF can be used (Prein 1985).

AN EXAMPLE

Data Collection

The data for this example were collected during the course of three experiments conducted at the Mariculture and Fisheries Department (MFD), Kuwait Institute for Scientific Research, Salmiya, Kuwait. The growth and mortality rates of the tilapia in seawater were measured during these experiments. Only a summary of the experimental procedures is presented here. Additional details can be found in Hopkins et al. (1986).

The fish used in the experiments were produced in freshwater or brackishwater (3 ppt salinity) and were acclimated to seawater (38-41 ppt) before the experiments started. Loading rates were low (0.1 kg/liter/min) for small fish (<10 g) and were increased to 1 kg/liter/min as the fish grew larger (>50-100 g). The feeding regime approached satiation feeding. Supplemental aeration was provided with diffusers or airlifts.

The fish were anesthetized with a mixture of quinaldine:acetone:ethyl alcohol before handling. The fish were sampled 9-10 times during the experiments in addition to the initial and harvest samples. Bulk weights and counts were made during sampling. All fish were sexed externally at harvest using diluted ink to highlight the genital papillae.

In the first experiment, 1 g *Oreochromis aureus* and *O. spilurus* fingerlings of both sexes were stocked into 5-6 m^3 outdoor raceways in August 1982. The fish were harvested in April 1983 after 246-253 culture days.

In the second experiment, the male fish which were harvested at the end of Experiment 1 were restocked into the raceways in late April 1983, grown for an additional 175 days and harvested in October 1983.

The third experiment started in August 1983. Five groups of 1-2 g fingerlings were stocked into 2-m^3 circular tanks:

O. spilurus	both sexes
O. spilurus	testosterone treated
O. aureus	testosterone treated
O. aureus x *O. spilurus*	both sexes
"Red" tilapia	testosterone treated

The testosterone treated fish had been fed a diet containing 100 mg ethynyl testosterone per 1 kg feed for 6 weeks prior to this experiment in an attempt at sex reversal. The groups containing both sexes had been fed an identical diet without the testosterone. Any dead fish during the first two weeks were removed from the tanks and replaced with fish of similar size. Experiment 3 ended in March 1984 after 226 culture days. Details of fish size, per cent males, numbers and temperatures in the three experiments are summarized in Table 1.

Data Analysis

The first Extended Gulland and Holt Plot hypothesized for these seawater growth experiments was:

$$\frac{\Delta \sqrt[3]{W_t}}{\Delta t} = a + b_1 \overline{\sqrt[3]{W_t}} + b_2 T_t + b_3 M_t + b_4 D_t \quad \ldots 12)$$

where $\Delta \sqrt[3]{W}$ is the change in the cube root of fish weight during period t, Δt is the duration of interval t, $\overline{\sqrt[3]{W_t}}$ is the arithmetic mean of the cube root of fish weight at the start and end of period t, T_t is the average temperature (°C) during period t, M_t is the fraction (in decimals) of males in the fish population during period t, and D_t is the fish density (kg/m^3) during period t. Temperature effects on growth rate can be simply represented using a quadratic parabola (Ricker 1979). However, because the upper temperatures encountered in the experiments did not exceed the optimum temperatures for tilapia growth (Chervinski 1982), only the linear temperature term is used in Equation (12). Fish density refers only to

Table 1. Fish weights, numbers, percentage of males and culture temperatures.

Experiment number	Length (days)	Number of replicates	Number of sampling periods	Temperature range (°C)	Males (%)	Av. weight (g)	Stocking av. density (/m³)	Av. wt. (g)	Harvest av. survival (%)
Oreochromis aureus									
1	253	4	10	19-30	58	1	126	58	55
2	175	2	11	23-28	100	67	50	239	56
3	226	2	11	20-28	85[a]	1	154[b]	33	23
O. spilurus									
1	246	3[c]	10	19-30	39	1	243	59	66
2	175	2	11	23-28	100	106	50	371	83
3	226	2	11	20-28	50	2	102[b]	70	82
3	226	2	11	20-28	75[a]	3	101[b]	80	70
O. aureus (female) x *O. spilurus* (male) hybrid									
3	226	2	11	20-28	70	1	102[b]	67	95
Red tilapia from Taiwan									
3	226	2	11	20-28	80[a]	1	105[b]	132	38

[a] Testosterone-treated fish.

[b] Includes replacement of dead fish within 2 weeks of stocking.

[c] A fourth replicate was lost because of a water supply failure. Data are available for 3 sampling periods before the loss.

a space relationship between fish in these experiments and is not directly related to water quality because the water flows were increased as the fish grew larger.

The *O. spilurus* data from all three experiments were pooled and analyzed as follows:

1. A correlation matrix containing all of the variables was constructed in order to determine the degree of multicollinearity (Table 2). Density, D_t, showed a high degree of correlation with $\sqrt[3]{W_t}$. As the maximum densities (16 kg/m³) attained in the experiments were much lower than densities commonly attained in intensive tilapia culture systems (Balarin and Haller 1982), it can be assumed that density effects were relatively unimportant in these experiments. Therefore, density was eliminated as one of the independent variables. Equation (12) was thereby reduced to

$$\frac{\Delta \sqrt[3]{W_t}}{\Delta t} = a + b_1 \overline{\sqrt[3]{W_t}} + b_2 T_t + b_3 M_t \qquad \text{... 13)}$$

2. An Ordinary Least Squares procedure was performed. As expected, the Durbin-Watson statistic indicated a significant degree of autocorrelation (d = 2.704 with 3 regressors and 99 observations).
3. The transformation in Equation (5) was then applied and the regression performed again. Results of that regression are presented in Table 3. The indication of autocorrelation by the Durbin-Watson statistic was inconclusive.
4. Steps 1 to 3 were then repeated for the *O. aureus* data. The coefficient of the percentage males had the wrong sign and was insignificant (T = -0.064, significance level of T = 0.95). Therefore, percentage of males was dropped from the model

Table 2. Correlation of independent variables within *Oreochromis spilurus* data in experiments 1-3.

Variables	Correlation coefficient (r) $\sqrt[3]{W_t}$	 Temperature	 % Males	 Density
$\sqrt[3]{W_t}$	1.000	0.003	0.600	0.887
Temperature	—	1.000	0.556	−0.151
% Males	—	—	1.000	0.306
Density	—	—	—	1.000

Table 3. Results of regression of *O. spilurus* data which had been transformed to remove first degree autocorrelation.

	Variables $\sqrt[3]{W_t}$	 Temperature		 % Males	 Constant
Coefficients, b	−0.00522	0.002012		0.01857	−0.03417[a]
Standard error of b	−0.00160	0.000389		0.00628	0.01296
Standardized beta	−0.54559	0.44598		0.33947	
T statistic	4.923	5.169		2.956	2.636
Significance level of T	0.0000	0.0000		0.004	0.01
R square			0.479		
Number of cases			87		
F statistic			26.09		
Significance level of F			0.0000		
Durbin-Watson statistic			2.365		

[a] The constant in this regression = a(1 − p) where p = −0.35. Therefore, the a value to be used in estimating VBGF coefficients is −0.02531.

and regression procedure was conducted using the remaining transformed data (Table 4).

5. Correlation matrices were then computed for the red tilapia and the *O. aureus* x *O. spilurus* hybrid data. Unfortunately, for these two groups, the $\sqrt[3]{W_t}$ and temperature data were highly correlated (r = -0.965 for red tilapia and -0.952 for the hybrid). This multicollinearity resulted because these fish were grown only in Experiment 3. Experiment 3 started in August as water temperatures were starting to drop and finished in April when temperatures were starting to rise again. Thus, the fish were growing larger as the temperature dropped. If the experiment had been continued with larger fish growing at higher temperatures, the multicollinearity would have been eliminated. As it is impossible to isolate the effects of size and temperature on growth based on the available data for the red tilapia and the hybrids, the Extended Gulland and Holt Plot could not be used to analyze the data for these fish.
6. The coefficients of the VBGF were then computed for *O. spilurus* and *O. aureus* for several different sets of conditions (Table 5). Example plots of growth curves prepared using these VBGF coefficients are presented in Figs. 1 and 2.

COMPARING THE EXTENDED GULLAND AND HOLT PLOT AND ANOVA

Using the Extended Gulland and Holt Plot to analyze growth through time is much more involved than using ANOVA to determine if there are differences in weight at harvest. Is the extra effort justified? A comparison of the results and conclusions based on an ANOVA of the

Table 4. Results of regression analysis of *Oreochromis aureus* data which had been transformed to remove first degree autocorrelation.

		Variables	
	$\sqrt[3]{W_t}$	Temperature	Constant
Coefficients, b	—0.002596	0.002675	—0.05502[a]
Standard error of b	0.000811	0.000311	0.00989
Standardized beta	—0.2590	0.6972	
T statistic	3.200	8.614	5.563
Significance level of T	0.0020	0.0000	0.0000
R square		0.525	
Number of cases		76	
F statistic		40.3	
Significance level of F		0.0	
Durbin-Watson statistic		2.172	

[a] The constant in this regression = a (1 — p) where p = —0.26565. Therefore, the a value to be used in estimating VBGF coefficients is —0.04347.

Table 5. Estimated coefficients of the VBGF for two tilapia species cultured in seawater.

Species	Temperature (°C)	% Males	K (day^{-1})	W_∞ (g)	t_o[a] (days)
O. spilurus	22	50	0.00522	158	−4.15
	25	50	0.00522	283	3.35
	28	50	0.00522	461	8.43
	22	100	0.00522	371	6.30
	25	100	0.00522	581	10.55
	28	100	0.00522	858	13.70
O. aureus	22	b	0.00260	208	−36.21
	25	b	0.00260	733	−10.29
	28	b	0.00260	1,775	1.79

[a] Arbitrarily assumes that a 1 g fish is 35 days old.

[b] Percentage males had no measurable effect on growth of *O. aureus* in these experiments.

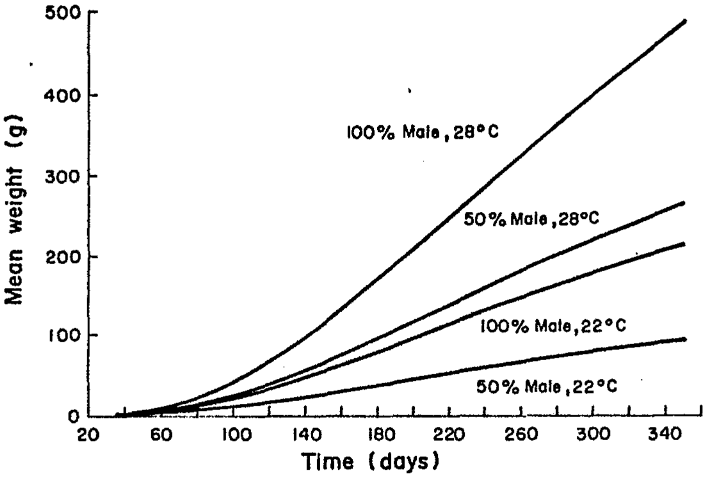

Fig. 1. *O. spilurus* growth curves at different temperatures and percentages of male fish.

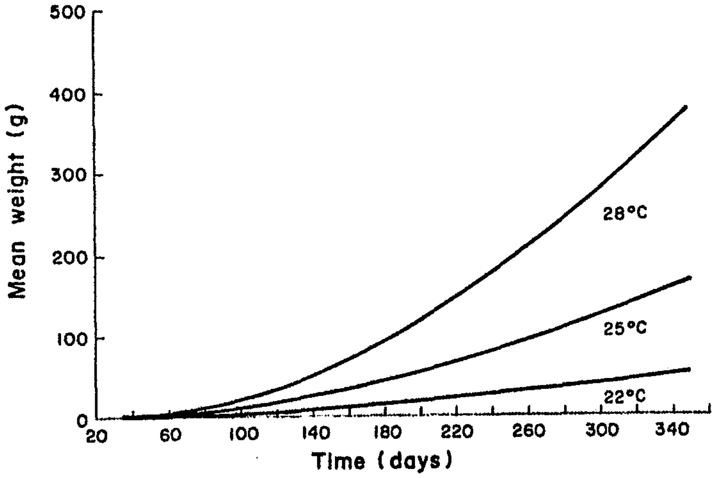

Fig. 2. *O. aureus* growth curves at different temperatures.

seawater tilapia data (Hopkins et al. 1986) and results and conclusions based on the Extended Gulland and Holt Plot shows that the Extended Gulland and Holt Plot can be used to extract additional valuable information from a typical aquaculture data set.

A summary of the results and conclusions based on ANOVA follows:

Experiment 1 (August 1982-April 1983). There was no significant difference in average harvest weight of *O. spilurus* and *O. aureus*. However, the *O. spilurus* males were larger than the *O. aureus* males. Complicating factors were a higher percentage of males for *O. aureus* than for *O. spilurus*, higher densities in the *O. spilurus* tanks than in the *O. aureus* tanks, and the loss of the fourth *O. spilurus* replicate because of a water failure.

Experiment 2 (April-October 1983). There was no significant difference in the instantaneous growth rates of 100%-male groups of *O. spilurus* and *O. aureus*.

Experiment 3 (August 1983-March 1984). The 85%-male groups of *O. aureus* were significantly smaller than the other groups of fish. There were no significant differences between the hybrids, the 50%-male *O. spilurus* and the 75%-male *O. spilurus* groups. The red tilapia were significantly larger than the other four groups of fish.

General Conclusions Based on Experiments 1 to 3. The *O. spilurus* males grow faster than *O. aureus* under winter conditions in Kuwait. Red tilapia grow fastest.

The Extended Gulland and Holt Plots and the VBGFs derived from those plots led to the following conclusions:

1. The most important factor affecting the growth of *O. spilurus* in seawater was fish weight, followed by temperature. Proportion of males had the least effect (based on an examination of the standardized beta coefficients).
2. The most important factor affecting the growth of *O. aureus* in seawater was temperature followed by fish weight. Proportion of males had no measurable effect on *O. aureus* growth. The probable reason for the difference in the effect of proportion of males between the *O. aureus* and *O. spilurus* was that *O. aureus* did not produce viable spawns in seawater while *O. spilurus* did.
3. The effects of fish size, water temperature and proportion of males on growth rate were quantified and the VBGF, a widely accepted mathematical representation of fish growth, was derived for *O. aureus* and *O. spilurus* at various combinations of temperature (19-30°C) and proportion of males (39-100%).
4. Plots of the VBGFs for *O. spilurus* and *O. aureus* indicated that 100% male groups of *O. spilurus* have a higher initial growth rate than *O. aureus*, particularly at lower temperatures. However, the W_∞ for *O. spilurus* are smaller than the W_∞ for *O. aureus*. Thus, the growth of *O. spilurus* will be superior unless a large harvest size (>700 g) is desired and the water temperature is high ($\geq$ 28°C).
5. No conclusions about the hybrid and red tilapia were made using the Extended Gulland and Holt Plot as the data for these two groups of fish showed severe multicollinearity which could not be removed.

As can be seen from the preceding results, using the Extended Gulland and

Holt Plot can yield more information from a typical aquaculture data set than does ANOVA. This additional information quantifying the effects of fish size, proportion of males and environmental factors such as temperature are particularly useful in bioengineering and bioeconomic models. Also, the Extended Gulland and Holt Plot has the following attributes:

- the fish size does not have to be the same in each culture unit (pond, tank, etc);
- the culture periods for each replicate do not have to be the same length;
- the number of degrees of freedom in the statistical analyses is greatly increased because each sampling period is an observation thereby reducing the number of replicated culture units;
- Analysis of residuals can be used to test for linearity of response;
- the derived VBGFs provide a means of linking aquaculture data with growth models used in the general field of fishery biology and population modelling.

The first two attributes are particularly useful in that they allow the comparison of data collected by different researchers for different periods of time with different sizes of fish and to salvage data from replicates which are "lost" due to nonexperimental factors (e.g., water supply failure, fish theft, etc.). All the growth data collected before the "loss" can still be included in the analyses.

The Extended Gulland and Holt Plot does not replace ANOVA. Rather, it is an additional tool for analyzing aquaculture data sets. The Extended Gulland and Holt Plot is particularly suited for screening and quantifying the effects of a large number of variables with a minimum number of culture units. However, if the aquaculture conditions (e.g., initial stocking size, length of culture period, temperature regimes, etc.) are controlled or are relatively constant, ANOVA is probably more efficient statistically than the Extended Gulland and Holt Plot.

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