

## A BIOENERGETICS GROWTH MODEL FOR NILE TILAPIA (*Oreochromis niloticus*) BASED ON LIMITING NUTRIENTS AND FISH STANDING CROP IN FERTILIZED PONDS

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### INTRODUCTION

Aquaculture ponds are complex ecosystems. Computer modeling is a valuable tool for the analysis of complex systems (Cuenco, 1989) and is becoming an important component of research efforts that are directed toward improving our understanding of aquaculture pond ecosystems and developing management practices that optimize resource utilization (Piedrahita, 1988).

Nile tilapia (*Oreochromis niloticus*) is one of the most popular species cultured in many tropical countries (including Thailand). Nile tilapia are commonly grown in semi-intensive culture using fertilization to increase primary production that is used by tilapia for food (Boyd, 1976; Diana et al., 1991). A significant increase in fish yield following the successful addition of fertilizers is generally due to the growth of algae and the subsequent transformation of algae to fish flesh through food webs of ponds (McNabb et al., 1990). Nitrogen, phosphorus, and carbon are three important nutrients required for algal growth. The C:N:P ratio for algae is approximately 40:7:1 by weight (Round, 1973; Vallentyne, 1974; Wetzel, 1983). There is considerable inconsistency in algal yields obtained from ponds receiving the same inputs of nitrogen and/or phosphorus fertilizers (McNabb et al., 1990). A shortage of dissolved inorganic carbon may be one cause of inconsistent yields (McNabb et al., 1988). Therefore, it is essential to identify which of these three nutrients is a limiting factor for primary production when estimating the amount of natural foods available to fish growth.

Various growth models have been developed for Nile tilapia (Liu and Chang, 1992; Nath et al., 1993; Bolte et al., 1995); however, none of them have linked a limiting nutrient with Nile tilapia growth. Liu and Chang (1992) modeled the parameter of

relative feeding level ( $f$ ) using a fertilizer richness parameter to estimate the available food resources parameter in Ivlev's equation (1961). They assumed this fertilizer richness parameter would correspond to the amount of chicken manure added to the ponds. However, manure input rates cannot be easily extended for use in ponds that receive various levels of fertilizer inputs or a mixture of organic and synthetic fertilizers, because an estimate of the fertilizer richness parameter would be required (Bolte et al., 1995). Moreover, Ivlev (1961) assumed that natural food availability was a function of the number of fish instead of fish standing crop as suggested by Hephher (1978). It is more accurate to estimate  $f$  as a function of fish standing crop and potential net primary productivity derived by a limiting nutrient rather than fish number and total fertilizer input.

The purpose of this study was: 1) to develop a bioenergetics growth model for Nile tilapia cultured in fertilized ponds through the synthesis of currently available information on fish physiology and pond dynamics; and 2) to use the model to evaluate the effects of different factors (body size, temperature, dissolved oxygen (DO), unionized ammonia (UIA), and food availability) on Nile tilapia growth in fertilized ponds.

### THE MODELS

#### Model Development

The model was written using a dynamic modeling language called STELLA® II (High Performance Systems, Inc., 1990) and was based on a model developed by Ursin (1967). The model used a time step of one day, and the equations were solved

using a 4th-order Runge-Kutta numerical integration method.

Ursin (1967) indicated that anabolism and catabolism may have different exponents in relation to fish weight (with subsequent effects on fish growth) and expressed the rate of change of fish body weight as the difference between anabolism and catabolism:

$$dW/dt = H W^m - k W^n \quad (1)$$

where

$W$  = fish weight (g),

$t$  = time (day),

$H$  = coefficient of net anabolism ( $g^{1-m} d^{-1}$ ),

$m$  = exponent of body weight for net anabolism,

$k$  = coefficient of fasting catabolism ( $g^{1-n} d^{-1}$ ),

$n$  = exponent of body weight for fasting catabolism.

Because gross catabolism comprises feeding and fasting catabolism (Ursin, 1967), equation 1 can be re-written as:

$$dW/dt = b dR/dt - (a b dR/dt + K W^n) \quad (2)$$

where

$dR/dt$  = daily ration ( $g d^{-1}$ ),

$b$  = efficiency of food assimilation (dimensionless),

$a$  = fraction of the food assimilated that is used for feeding catabolism (dimensionless).

The terms,  $b dR/dt - (a b dR/dt + K W^n)$ , on the right hand of equation 2 represent gross anabolism, feeding catabolism and fasting catabolism, respectively. From an energetic point of view, the parameter  $b$  refers to the proportion of the gross energy or food intake that is available as metabolizable energy (Nath et al., 1993) and is typically not constant but decreases with increasing food availability for most fish, including tilapias (Caulton, 1982). The parameter  $a$  accounts for further losses of metabolizable energy via heat increment and urinary excretion (Nath et al., 1993). Thus, gross

energy available for metabolism is represented by  $b dR/dt$  on the right hand side of equation 2, whereas the second and third terms,  $a b dR/dt$  and  $K W^n$ , represent feeding and maintenance requirements.

Fish growth is influenced not only by intrinsic factors such as fish size but also by a variety of environmental factors (Brett, 1979), including water temperature (Brett et al., 1969; Elliott, 1976), photoperiod (Gross et al., 1965), dissolved oxygen (Stewart et al., 1967; Doudoroff and Shumway, 1970), unionized ammonia concentrations (Colt and Tchobanoglous, 1978) and food availability (Brett, 1971). These factors affect fish growth via their impacts on food consumption (Brett, 1979; Cuenco et al., 1985). Due to the warm climate and shallowness of most tropical fish ponds, temperature and photoperiod are not likely to be limiting for food consumption.

Cuenco et al. (1985) reported that food consumption was not affected when DO was above a critical limit ( $DO_{crit}$ );  $DO_{crit}$  decreased more or less linearly with decreasing DO levels until a minimum level ( $DO_{min}$ ) was reached, below which fish would not feed. The function ( $\delta$ ) describing the effects of DO on food consumption would be expressed as:

$$\delta = 1.0 \quad \text{if } DO > DO_{crit} \quad (3a)$$

$$\delta = (DO - DO_{min}) / (DO_{crit} - DO_{min}) \quad \text{if } DO_{min} \leq DO \leq DO_{crit} \quad (3b)$$

$$\delta = 0.0 \quad \text{if } DO < DO_{min} \quad (3c)$$

Colt and Armstrong (1981) and Cuenco et al. (1985) indicated that food consumption was not affected when UIA was below a critical limit ( $UIA_{crit}$ ) and food was not consumed when UIA reached a maximum level ( $UIA_{max}$ ), between which food consumption decreased with increasing UIA. The function ( $v$ ) describing the effects of UIA on food consumption could be expressed as follows:

$$v = 1.0 \quad \text{if } UIA < UIA_{crit} \quad (4a)$$

$$v = (UIA_{max} - UIA) / (UIA_{max} - UIA_{crit}) \quad \text{if } UIA_{crit} \leq UIA \leq UIA_{max} \quad (4b)$$

$$v = 0.0 \quad \text{if } UIA > UIA_{max} \quad (4c)$$

The quantity of natural food consumed by tilapia, based on modeling rations proposed by Ursin (1967), is expressed as:

$$dR/dt = d \nu h f W^m \quad (5)$$

where

$h$  = coefficient of food consumption ( $\text{g}^{-1} \text{m} \text{d}^{-1}$ ) and

$f$  = relative feeding level ( $0 < f < 1$ , dimensionless).

To link the relative feeding level with potential net primary productivity (PNPP) and standing crop of Nile tilapia, Ivlev's (1961) equation can be modified as following:

$$f = r/R = 1 - \exp(-s P/B) \quad (6)$$

where

$r$  = actual daily ration ( $\text{g d}^{-1}$ ),

$R$  = maximal daily ration ( $\text{g d}^{-1}$ ),

$s$  = coefficient of food proportionality (dimensionless),

$P$  = PNPP ( $\text{g C m}^{-3} \text{d}^{-1}$ ), and

$B$  = standing crop of Nile tilapia ( $\text{g m}^{-3}$ ).

However, Ivlev (1961) initially defined  $P$  as concentration of natural food and  $B$  as the number of fish.

PNPP used to estimate the quantity of natural food in ponds is the minimal PNPP ( $P_c$ ,  $P_n$ , and  $P_p$ ) derived from total dissolved inorganic carbon (DIC), total dissolved inorganic nitrogen (DIN) and total dissolved inorganic phosphorus (DIP), respectively (see equation 7).

$$P = \text{Min}(P_c, P_n, P_p) \quad (7)$$

The following equations for calculating  $P_c$ ,  $P_n$ , and  $P_p$  are based on Lannan (1993):

$$P_c = 12\lambda (A/50) \{[(\text{H}^+)^2/k_1 + \text{H}^+ + k_2]/(\text{H}^+ + 2k_2)\} \quad (8)$$

$$k_1 = (T/15 + 2.6) 10^{-7} \quad (8a)$$

$$k_2 = (T/10 + 2.2) 10^{-11} \quad (8b)$$

where

$P_c$  = PNPP derived from DIC ( $\text{g C m}^{-3} \text{d}^{-1}$ ),

$\lambda$  = efficiency of carbon fixation (dimensionless),

$A$  = alkalinity ( $\text{mg CaCO}_3 \text{l}^{-1}$ ),

$\text{H}^+$  = hydrogen ion concentration ( $\text{moles l}^{-1}$ ),

$k_1$  = the first dissociation constant for carbonate/bicarbonate system,

$k_2$  = the second dissociation constant for carbonate/bicarbonate system,

$T$  = water temperature ( $^{\circ}\text{C}$ ).

The constants of 12 and 50 in equation 10 are gram equivalent weights of C and  $\text{CaCO}_3$ .

In equations 9 and 10, it is assumed that there is no threshold concentration of DIN or DIP below which the respective nutrients are not available for photosynthesis even though observations by Hephher (cited by Boyd, 1979) suggest that such thresholds may exist. However, until definitive information is available, the simplifying assumption that all the DIN and DIP are available seems reasonable (Lannan, 1993).

$$P_n = 40 D_n / 7 \quad (9)$$

$$P_p = 40 D_p \quad (10)$$

where

$P_n$  = PNPP derived from DIN ( $\text{g C m}^{-3} \text{d}^{-1}$ ),

$D_n$  = DIN ( $\text{mg N l}^{-1}$ ),

$P_p$  = PNPP derived from DIP ( $\text{g C m}^{-3} \text{d}^{-1}$ ),

$D_p$  = DIP ( $\text{mg P l}^{-1}$ ).

The constants of 40 and 7 were based on carbon:nitrogen:phosphorus ratios of 40:7:1 by weight (Round, 1973; Vallentyne, 1974; Wetzel, 1983).

Finally, the growth rates ( $dW/dt$ ) of Nile tilapia can be expressed as follows:

$$dW/dt = \{b(1-a) \delta \nu h [1 - \exp(-s P/B)] W^m\} - k W^n \quad (11)$$

Ursin (1967) and Sperber et al. (1977) assumed that the coefficient of catabolism ( $k$ ) increases exponentially with temperature. Nath et al. (1993) modified this exponential form to include the minimum temperature below which the fish species can not survive ( $T_{min}$ ) as follows:

$$k = k_{min} \exp [j (T - T_{min})] \quad (12)$$

where

$k_{min}$  = coefficient of fasting catabolism ( $g^{1-m}d^{-1}$ ) at  $T_{min}$  and

$j$  = constant to describe temperature effects on catabolism ( $1/^\circ C$ ).

### Parameter Estimations

Nath et al. (1993) analyzed oxygen consumption data for fasting Nile tilapia and estimated the mean for  $n$  to be 0.81, but they retained  $n = 1$  in their growth model because insertion of  $n = 0.81$  during their test runs of the model resulted in growth rates for tilapia far in excess of observed rates. This finding was consistent with the results of Liu and Chang (1992); however, in the present model  $n = 0.81$  and  $m = 0.67$  (approximated by Ursin, 1967) were used.

I assumed the efficiency of food assimilation ( $b$ ) to be 0.62 (Nath et al., 1993), which was the mean value of the range of assimilation efficiencies (0.53-0.70) for Nile tilapia reported by Meyer-Burgdorff et al. (1989). The parameter  $b$  was assumed to be constant in this model, although it was found to decrease with increased food intake (Meyer-Burgdorff et al., 1989) and to be influenced by other factors such as temperature (Caulton, 1982). The values of parameters  $a$  and  $h$  were assumed to be 0.53 (Nath et al., 1993) and 0.8 (Bolte et al., 1994) in this model, respectively, for Nile tilapia feeding on natural foods in fertilized ponds.

Based on laboratory experiments with Nile tilapia (Gannam and Phillips, 1993),  $T_{min}$  appears to be about 15°C. Nath et al. (1993) used data on fasting Nile tilapia from Satoh et al. (1984), who estimated  $k_{min}$  and  $j$  to be 0.00133 and 0.0132, respectively. These estimations were also used in this model.

Nile tilapia can tolerate low DO and survive environments where other fish species can not exist (except air breathing species) (Boyd, 1990)

due to its ability to use atmospheric oxygen when DO concentration drops to less than 1 mg l<sup>-1</sup> (Chervinski, 1982). The lowest tolerance limit of DO reported for Nile tilapia ranges from 0.1 to 0.3 mg l<sup>-1</sup> under different environmental conditions (Ahmed and Magid, 1968; Magid and Babiker, 1975). However, DO<sub>crit</sub> and DO<sub>min</sub> have not been well defined. Teichert-Coddington and Green (1993) reported that a practical threshold DO for Nile tilapia was not greater than 10% of saturation. Therefore, DO<sub>crit</sub> and DO<sub>min</sub> used in the present model were 1.0 and 0.3 mg l<sup>-1</sup>, respectively. Abdalla (1989) determined that UIA<sub>max</sub> = 1.40 mg l<sup>-1</sup> and UIA<sub>crit</sub> = 0.06 mg l<sup>-1</sup> for Nile tilapia.

To estimate coefficient of food proportionality ( $s$ ), data from three fertilized ponds (Diana et al., 1994) were used. The experiment was conducted for 162 days at the Ayutthaya Freshwater Fisheries Station located at Bang Sai, Thailand. Using the above equations, the estimated mean value of  $s$  was 17.31 ± 1.25.

### Data Requirement for Model Validation

Almost all values of parameters used in the model were derived from the literature. To test the validity of the model, simulated outputs were compared with independently obtained experimental results that were not used during the process of model development. The following two sets of experimental data were used to validate the present model.

The first experiment (Diana et al., 1996) was conducted for 328 days at the Ayutthaya Freshwater Fisheries Station located at Bang Sai, Thailand. Each pond was fertilized with urea and triple superphosphate (TSP) at rates of 28 kg N and 7 kg P ha<sup>-1</sup> wk<sup>-1</sup>, and stocked at three fish m<sup>-2</sup> with 8- to 10-g, sex-reversed male Nile tilapia on 15 January 1993. Five treatments, which included three ponds per treatment, received first feeding at 50 g, 100 g, 150 g, 200 g, and 250 g. The growth of Nile tilapia was simulated at the following fertilization stages: 29, 71, 141, 169, and 225 days for each of the above treatments. The second experiment (Knud-Hansen et al., 1993) was conducted for 146 days at the Ayutthaya Freshwater Fisheries Station. Five treatments with three replications received 20, 60, 100, 140, and 180 kg chicken manure (dry weight) ha<sup>-1</sup> wk<sup>-1</sup> and were supplemented with urea and TSP to give all treatments N and P inputs of 28 and 7 kg ha<sup>-1</sup> wk<sup>-1</sup>, respectively. Each pond was stocked at 1.6 fish m<sup>-2</sup>

with 13- to 16-g, sex-reversed male Nile tilapia on 12 October 1989. Experimental ponds were not aerated or mixed artificially during the culture period. From the experiments the following initial values and input variables were used:

1. initial mean body weight (g);
2. stocking densities (fish m<sup>-2</sup>);
3. survival rates (%);
4. surface area (m<sup>2</sup>) and volume (m<sup>3</sup>) of ponds;
5. monthly measured DO concentrations at dawn (mg l<sup>-1</sup>);
6. biweekly measured water temperature (°C), pH, NH<sub>3</sub>-N (mg l<sup>-1</sup>), total NO<sub>2</sub>-N and NO<sub>3</sub>-N (mg l<sup>-1</sup>), soluble reactive phosphorus (mg l<sup>-1</sup>), alkalinity (mg CaCO<sub>3</sub> l<sup>-1</sup>) at 0900-1000 hr.

DIN and DIP were estimated based on the total dissolved inorganic nitrogen and phosphorus levels in fertilizers and background levels in water. These estimates assumed that DIP changed linearly between biweekly water quality measurements and assuming that DIN and DIP diminished linearly to measured levels after adding fertilizers and then remained at those levels until the next fertilization. To calculate dissolved inorganic nitrogen and phosphorus, all nitrogen and phosphorus contents in inorganic fertilizers were assumed to be dissolved in inorganic forms. Based on the study by Nath (1992, cited by Nath and Lannan, 1993), percentages of dissolved inorganic nitrogen and phosphorus in chicken manure were assumed to be 60% and 80% of total nitrogen and phosphorus, respectively.

Standing crop of Nile tilapia (*B*) was estimated by the simulated daily mean weight and the number of Nile tilapia surviving. It was assumed that all mortality of Nile tilapia occurred at stocking.

### Sensitivity Analysis

Sensitivity analysis was carried out to evaluate relative magnitudes of the effects of model parameters or variables on Nile tilapia growth by comparing the percentage of changes in growth when varying parameters or variables by 10% about a baseline value (Table 1). For the baseline simulation the following mean values from the above two experiments were used: initial fish size was 13 g; survival rate was 88%; water temperature was 28.5°C; DO was 3 mg l<sup>-1</sup>; alkalinity was 85 mg CaCO<sub>3</sub> l<sup>-1</sup>; NH<sub>3</sub>-N was 0.65 mg l<sup>-1</sup>;

NO<sub>2</sub>+NO<sub>3</sub>-N was 0.55 mg l<sup>-1</sup>; soluble reactive phosphorus was 0.20 mg l<sup>-1</sup>; pH was 8.1; fertilization rate was 28 kg N and 7 kg P ha<sup>-1</sup> wk<sup>-1</sup>. All the above values were held constant for the entire baseline simulation. In order to determine the effects of DO and UIA on growth, the value of DO was set just below its critical limit (0.9 mg l<sup>-1</sup>) and UIA was set just above its critical limit (0.07 mg l<sup>-1</sup>).

### RESULTS

The simulated growth curves fit closely to the observed data in 15 ponds for each experiment (Figures 1 and 2). The model detected the growth variation within each treatment with the same N and P inputs and showed that the variation was caused mainly by the alkalinity differences among ponds. This indicated that carbon was a limiting nutrient. In each treatment growth was greater in ponds with higher alkalinity. Under the model assumptions, primary production was limited by carbon during 55 to 96% of the culture period of the first experiment and 66 to 99% of the culture period of the second experiment. Ponds where primary production was carbon-limited for greater portions of the culture period demonstrated poor growth. When predicted and observed final weights were compared using Spearman's Rank Correlation Coefficient ( $r_s$ ), they were significantly correlated ( $r_s = 0.84$ ,  $df = 28$ ,  $P < 0.05$ ). The predicted and observed mean weights were also fitted by simple linear regression ( $y = -0.17 + 1.02x$ ,  $r^2 = 0.89$ ,  $df = 238$ ,  $P < 0.05$ , Figure 3). Statistical testing of the slope (1.02) and the  $y$ -intercept (-0.17) of the regression line revealed that there was no significant departure from a slope of 1.0 ( $P > 0.05$ ) or from a  $y$ -intercept of 0 ( $P > 0.05$ ), indicating agreement between predicted and observed values.

The parameters listed in decreasing order of sensitivity are as follows:  $m$ ,  $a$ ,  $b$ ,  $h$ ,  $s$ ,  $n$ ,  $k_{min}$ , and  $j$  (Table 1). Parameters related to net energy from feeding activity were more sensitive than parameters related to fasting catabolism. Results of a sensitivity analysis for five key variables (Table 2) showed that tilapia growth was most sensitive to food availability when DO was above its critical limit, but was most sensitive to DO when it was below the critical limit. UIA became the third most sensitive variable for Nile tilapia growth when UIA was limited, although sensitivity (about 0.45 for a 10% change) was low. Also, growth was more sensitive to DO than UIA. Water temperature was the least sensitive variable in the model.

Table 1. Sensitivity analysis of model parameters with no limiting factors (None) or DO or UIA as a limiting factor. Parameters are ranked according to mean absolute magnitudes of the percent change of simulated final mean weight with no limiting factors. Negative values indicate that fish weight decreased with an increase in parameter value.

Parameter	Percent Change of Simulated Final Mean Weight					
	+10% for Parameter			-10% for Parameter		
	<i>None</i>	<i>DO Limiting</i>	<i>UIA Limiting</i>	<i>None</i>	<i>DO Limiting</i>	<i>UIA Limiting</i>
Exponent of body weight for net anabolism ( <i>m</i> )	32.23	31.55	32.20	-22.64	-22.28	-22.62
Fraction of food assimilated that is used for feeding catabolism ( <i>a</i> )	-9.69	-9.77	-9.69	9.46	9.56	9.47
Efficiency of food assimilation ( <i>b</i> )	8.40	8.48	8.41	-8.58	-8.65	-8.58
Coefficient of food consumption ( <i>h</i> )	8.40	8.48	8.41	-8.58	-8.65	-8.58
Coefficient of food proportionality ( <i>s</i> )	6.60	6.47	6.59	-6.84	-6.72	-6.83
Exponent of body weight for fasting catabolism ( <i>n</i> )	-2.20	-2.20	-2.20	1.50	1.51	1.50
Coefficient of fasting catabolism ( $k_{min}$ )	-0.44	-0.46	-0.44	0.45	0.46	0.45
Constant to describe temperature effects on catabolism ( <i>j</i> )	-0.08	-0.08	-0.08	0.08	0.08	0.08

Table 2. Sensitivity analysis of key model variables affecting fish growth when there are no limiting factors (None) or only DO or UIA as a limiting factor. Variables are ranked according to mean absolute magnitudes of the percent changes of simulated final mean weight with no limiting factors. Negative values indicate that fish weight decreased with an increase in parameter value.

Variable	Percent Change of Simulated Final Mean Weight					
	+10% for Variable			-10% for Variable		
	<i>None</i>	<i>DO Limiting</i>	<i>UIA Limiting</i>	<i>None</i>	<i>DO Limiting</i>	<i>UIA Limiting</i>
Food Availability	6.60	6.47	6.59	-6.84	-6.72	-6.83
Initial Tilapia Size	0.56	0.66	0.56	-0.58	-0.69	-0.59
Temperature	-0.24	-0.24	-0.24	0.24	0.24	0.24
DO	0	12.66	0	0	-13.05	0
UIA	0	0	-0.45	0	0	0.45

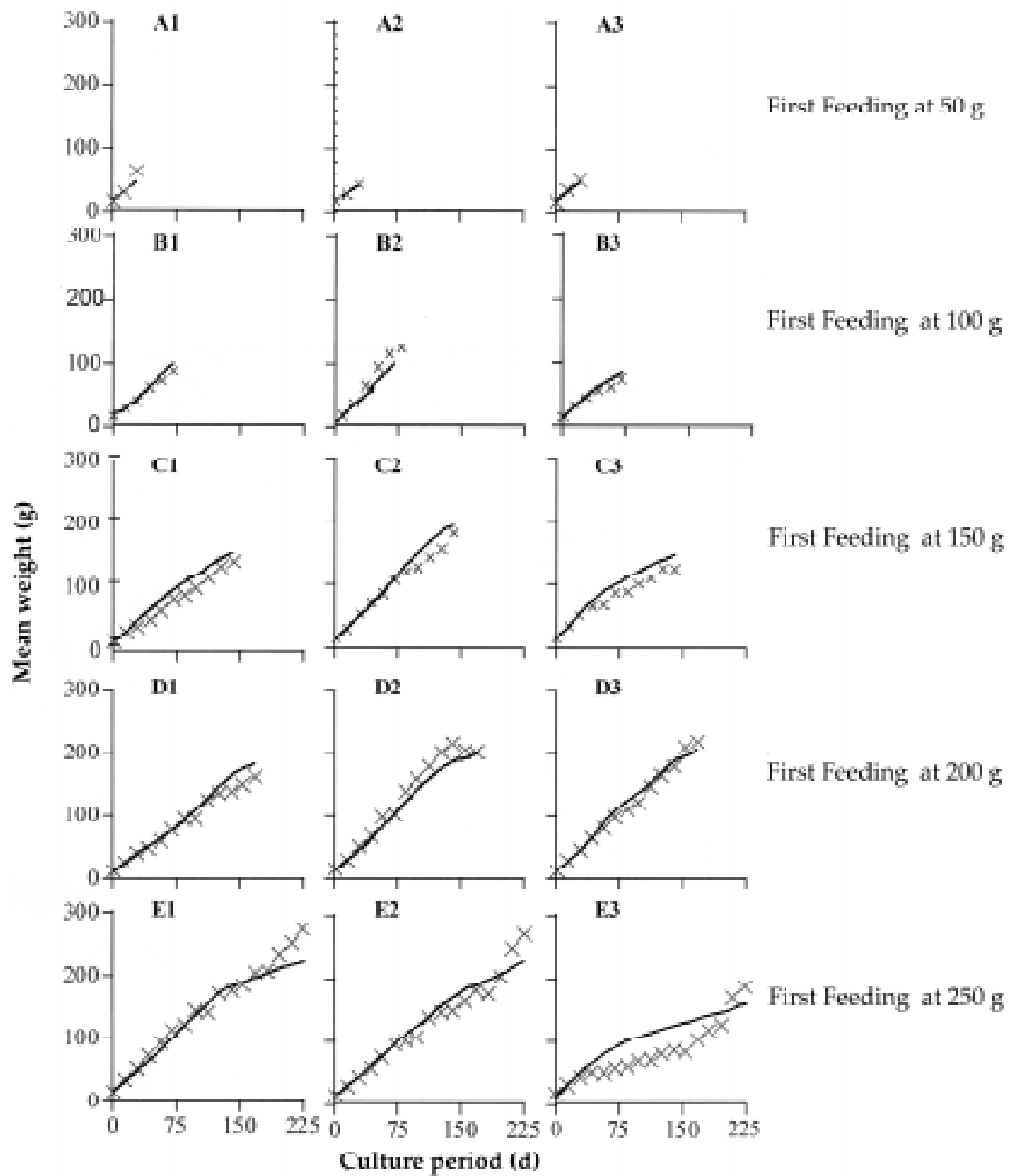


Figure 1. Comparison of Nile tilapia growth predicted by the model (line) with that observed (x) during the fertilization stage of the experiment of Diana et al. (1996). From the top down, each row (A through E) of graphs represents the treatments with first feeding at 50, 100, 200, and 250 g, respectively.

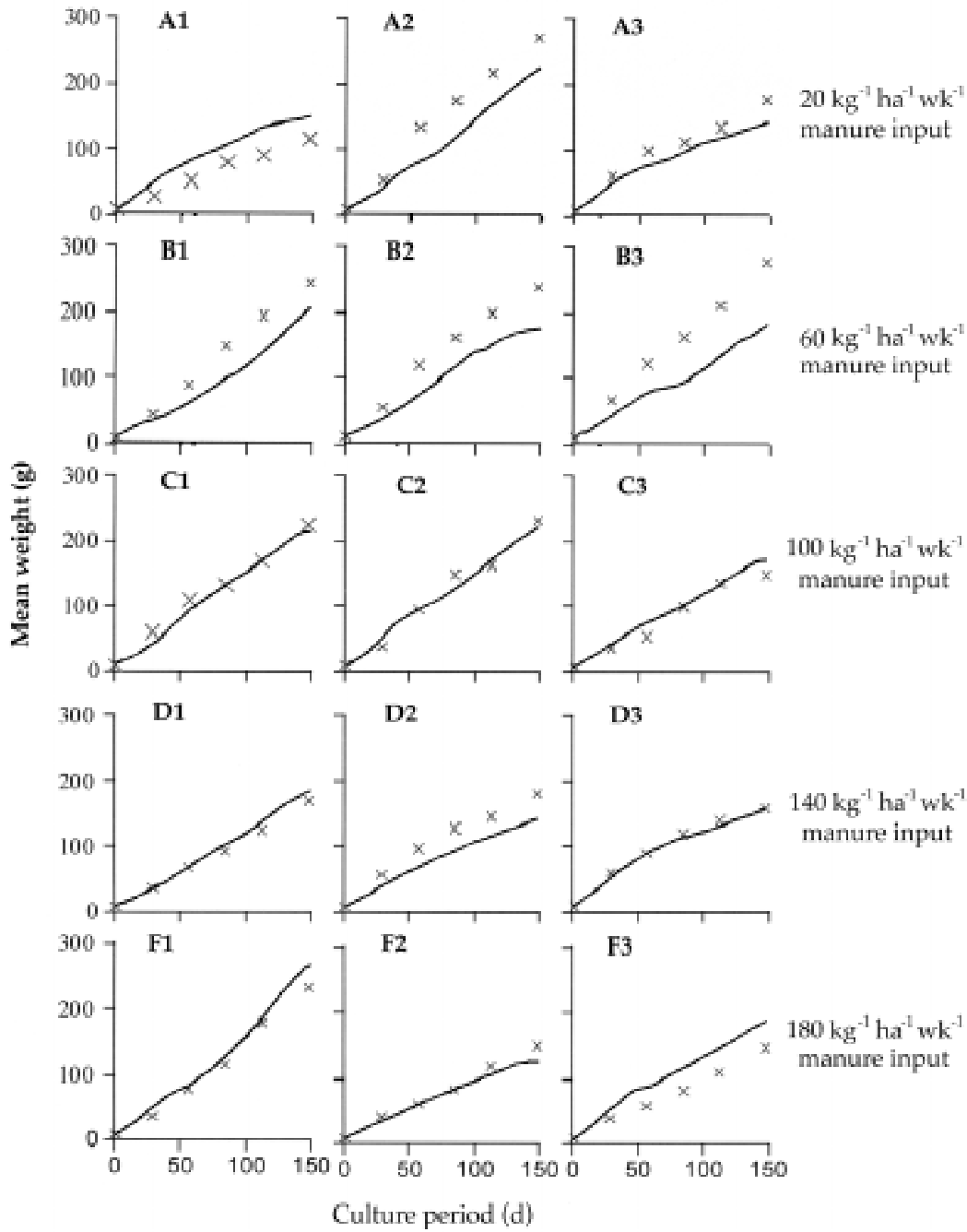


Figure 2. Comparison of Nile tilapia growth predicted by the model (line) with that observed (x) during the experiment of Knud-Hansen et al. (1989). From the top down, each row (A through E) of graphs represents the treatments with chicken manure inputs at 20, 60, 100, 140, and 180 kg ha<sup>-1</sup> wk<sup>-1</sup>, respectively.



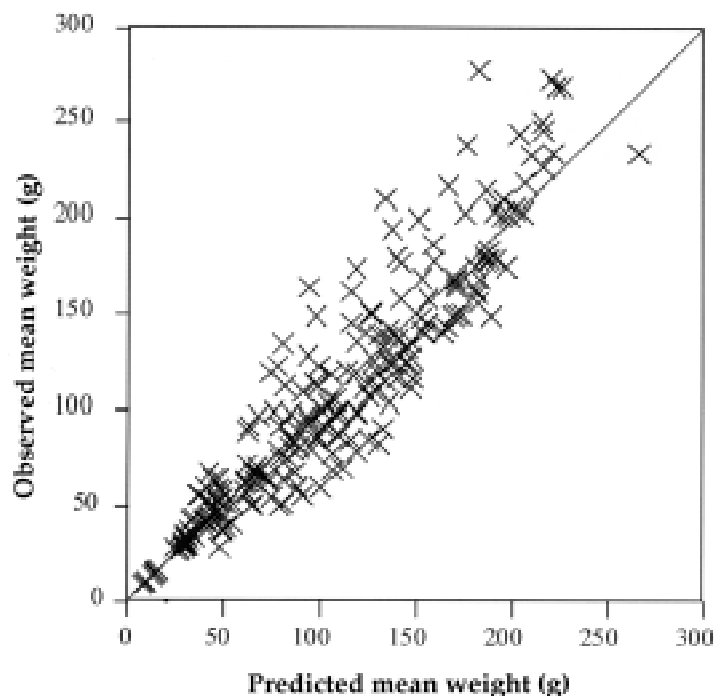


Figure 3. Comparison between predicted and observed mean weight of Nile tilapia in 30 ponds at Ayutthaya, Thailand. The line represents values where observed and predicted values are equal.

## DISCUSSION

A new bioenergetics growth model was validated using Nile tilapia growth data in 30 ponds receiving either only inorganic fertilizers (urea and TSP) or different combinations of chicken manure plus inorganic fertilizers. The strength of this model in comparison with previous models (Liu and Chang, 1992; Nath et al., 1993; Bolte et al., 1995) is that it is able to estimate the relative feeding level parameter which describes food availability to Nile tilapia. In the present model, Ivlev's (1961) relative feeding level based on fish number and food concentrations was modified to be a function of fish standing crop and potential net primary productivity estimated by limiting nutrients. Liu and Chang (1992) estimated relative feeding level (Ivlev, 1961) using a fertilizer richness parameter that corresponded to the amount of chicken manure added to the ponds; however, it was difficult to extend this fertilizer richness parameter for use in ponds receiving other fertilizers (Bolte et al., 1994). Nath et al. (1993) expressed the relative feeding level as a function of fish stocking density; the relationship between relative feeding levels and stocking densities of a red variant of *Oreochromis niloticus* fed to satiation with commercial feed (Zonneveld and Fadholi, 1991) was used for

this estimation. However, Nath et al. (1993) did not consider nutrient inputs and fish standing crop when estimating relative feeding level. On the other hand, Bolte et al. (1994) expressed the relative feeding level as a ratio of fish critical standing crop to actual standing crop in a pond, but several studies have suggested that the critical standing crop either did not exist for tilapia or occurred before the first biweekly or monthly fish sampling (Zonneveld and Fadholi, 1991; Green, 1992; Diana et al., 1994; Diana et al., 1996). Thus, compared with the above previous models, the present model provides a more reasonable basis for estimating relative feeding level and the effects of fertilization practice on natural food availability and, ultimately, on Nile tilapia growth.

Among some 19 elements which are known to be required by primary producers in aquatic food webs (Wetzel, 1983), phosphorus and nitrogen have received the greatest attention relative to the use of fertilizers to promote fish yields (Boyd, 1982). The present model has detected growth variations that are due to dissolved inorganic carbon, which has limited Nile tilapia growth in ponds that have received identical, high inputs of nitrogen and phosphorus. This is consistent with results reported

by McNabb et al. (1988) and Knud-Hansen et al. (1993). McNabb et al. (1988) suggested that dissolved inorganic carbon may be one cause of growth variation in ponds with the same loading rates of phosphorus and/or nitrogen. Furthermore, Knud-Hansen et al. (1993) reported that there was a significant linear correlation between mean alkalinity and mean net primary productivity and, in turn, between mean alkalinity and net yield of Nile tilapia. However, reasons were unclear as to why alkalinity steadily diminished in some ponds (Knud-Hansen et al., 1993). Simulation results of the present model accurately predicted fish growth without considering the role of manure-derived detritus as a food source. This finding supports the conclusions of Schroeder and Buck (1987) and Knud-Hansen et al. (1993), who reported that manure-derived detritus had only a minor influence on tilapia production. In the ponds with low alkalinity, the accumulation of dissolved inorganic nitrogen and phosphorus caused the low utilization efficiency of fertilizers and reduced water quality (concentrations of  $\text{NH}_3$  were high and DO concentrations were low). In order to maximize nutrient efficiency while minimizing production costs and the development of adverse environmental conditions, research should focus on carbon utilization and the balance of nitrogen, phosphorus, and carbon inputs.

The sensitivity analysis for parameters produced results similar to Cuenco et al. (1985); food consumption parameters were more critical than metabolism parameters. Among all parameters,  $m$ , the exponent of body weight for anabolism, was the most sensitive parameter affecting Nile tilapia growth. Liu and Chang (1992) reported that  $n$ , the exponent of body weight for fasting catabolism, was the most sensitive parameter in their model. They used a much greater value of  $k$  than in the present model, which might overemphasize fasting catabolism as a component of total metabolism. Water temperature in the present model was the least sensitive parameter, a result that was consistent with the observations by Yi (1997) that water temperature did not seem to be limiting to Nile tilapia growth in tropical, shallow ponds.

Several model refinements should be implemented once the necessary data is collected. The threshold concentrations of DIN or DIP, below which nitrogen and phosphorus are not available for photosynthesis should be determined. In the present model the efficiency of food assimilation ( $b$ ), the third most

sensitive parameter was assumed to be constant in the absence of experimental data for efficiency of food assimilation at different temperatures for Nile tilapia (Nath et al., 1993). However, other studies have indicated that  $b$  decreases with increased food intake for Nile tilapia (Meyer-Burgdorff et al., 1989) and that other factors such as temperature also influence  $b$  (Caulton, 1982). Additional research should be conducted to further define this parameter. Moreover, the model should be reparameterized to simulate the growth of other fish species cultured in different environments.

### ANTICIPATED BENEFITS

In this model, the growth of Nile tilapia in fertilized ponds has been linked directly to limiting nutrients and fish standing crop which are the bases for the estimation of naturally available foods. The model indicates that growth variations in ponds receiving the same nitrogen and phosphorus inputs were caused by carbon limiting primary production. Model results will improve our understanding of aquaculture pond ecosystems and will be useful for the optimization of fertilizer utilization.

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