A Bioenergetics Growth Model for Nile Tilapia (*Oreochromis niloticus*) in a Cage-Cum-Pond Integrated Culture System

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Introduction

Integrated aquaculture systems have not been adequately studied because of their complexity (Edwards et al., 1988). While aquaculture research has provided a great deal of information on pond dynamics over the past decades, there has been relatively little effort toward integrating that information into a meaningful and consistent description of pond production systems (Cuenco et al., 1985a). Computer modeling is a valuable tool for the analysis of complex systems (Cuenco, 1989) and is becoming an important component of research efforts to improve our understanding of aquaculture pond ecosystems and to develop management practices to optimize resource utilization (Piedrahita, 1988).

Nile tilapia is one of the most popular cultured species in many tropical countries such as Thailand. Various growth models have been developed for this species (Liu and Chang, 1992; Nath et al., 1994; Bolte et al., 1995; Yi, submitted); however, these models are for Nile tilapia cultured primarily in fertilized ponds with or without supplemental feeding. Modeling techniques have yet to be applied to integrated aquaculture such as a cage-cum-pond system, in which large Nile tilapia are fattened in cages and smaller Nile tilapia are nursed in open water to utilize wastes derived from cages (Yi et al., 1996; Yi, 1997).

The purpose of this study was to develop a bioenergetics growth model for Nile tilapia in both cages and open-ponds of the cage-cum-pond integrated culture system. This was accomplished through the synthesis of currently available information in fish physiology and pond dynamics and the subsequent modification of current models to evaluate the effects of body size, temperature, dissolved oxygen (DO), unionized ammonia (UIA), and food availability on the growth of both caged and open-pond Nile tilapia. This model will allow aquaculture managers to evaluate appropriate management strategies and predict outcomes in the cage-cum-pond integrated culture system.

The Models

Model Development

The model was written using a dynamic modeling language called STELLA® II (High Performance Systems, Inc. 1990) 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.

Adding artificial feed to a pond has a fertilizing effect and thus increases the amount of natural foods in the pond (Cuenco et al., 1985b), making both artificial feed and natural foods are available to fish. Thus, based on Ursin's work (1967), growth (dW/dt in g d^{-1}) of both caged and open-pond Nile tilapia in a cage-cum-pond integrated culture system (Yi, et al., 1996; Yi, 1997) can be expressed as follows:

$$dW/dt = [b_a (1 - a_a)\, dR_a/dt] + [b_n (1 - a_n)\, dR_n/dt] - kW^n \quad (1)$$

where

b_a = efficiency of artificial feed assimilation (dimensionless),

a_a = fraction of the assimilated artificial feed used for feeding catabolism (dimensionless),

dR_a/dt = daily ration of artificial feed (g d^{-1}),

b_n = efficiency of natural food assimilation (dimensionless),

a_n = fraction of assimilated natural foods used for feeding catabolism (dimensionless),

dR_n/dt = daily ration of natural foods (g d^{-1}),

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

W = fish body weight (g), and

n = exponent of body weight for fasting catabolism (dimensionless).

Key variables affecting fish growth are fish size, DO, UIA, water temperature, photoperiod, and food availability. The impact of these variables on growth is mediated through their effect on food intake and they are of an interactive nature (Brett, 1979; Cuenco et al., 1985a). Due to warm climate and the shallowness of most tropical fish ponds, temperature and photoperiod are not likely to limit food consumption. Thus, the daily ration of artificial feed and natural foods can be expressed as:

$$dR_a/dt = \delta \upsilon F_a \quad (2a)$$

$$dR_n/dt = \delta \upsilon F_n \quad (2b)$$

where

δ = DO factor (dimensionless),

υ = UIA factor (dimensionless),

F_a = availability of artificial feed (g d^{-1}),

F_n = availability of natural foods (g d^{-1}).

Based on the previous work (Cuenco et al., 1985a), the functions d and u describe the effects of DO and UIA on food intake and are expressed as:

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

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

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

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

$$\upsilon = (UIA_{max} - UIA)/(UIA_{max} - UIA_{crit})$$

$$\text{if } UIA_{crit} \le UIA \le UIA_{max}) \quad (4b)$$

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

where

DO_{min} = a minimum DO level (mg l^{-1}),

DO_{crit} = a critical DO limit (mg l^{-1}),

UIA_{max} = a maximum UIA level (mg l^{-1}),

UIA_{crit} = a critical UIA level (mg l^{-1}).

Food consumption is not affected when DO is above DO_{crit} or when UIA is below UIA_{max}. Decreases in food consumption are more or less linear with decreasing DO or increasing UIA until DO_{min} or UIA_{max} is reached. Fish do not feed when DO is below DO_{min} or UIA is above UIA_{max} (Cuenco et al., 1985a).

Artificial feed is given to fish in many different ways; however, not all feed is available to fish. The actual amount of artificial feed that fish consume depends on many factors, such as physical quality of the feed and application methods. Thus, a parameter for feeding efficiency *(q)* is introduced in the model to describe the amount of given artificial feed that fish are able to consume. In the cage-cum-pond integrated culture system (Yi et al., 1996; Yi, 1997), caged tilapia were given a high quality floating pelleted feed at rates based on sampled body weight; however, a small portion of the feed was probably knocked out of cages due to vigorous swimming activity of caged tilapia (Collins, 1971; Coche, 1979; McGinty, 1991; Yi, 1997). I assumed that the amount of natural foods consumed by caged tilapia is negligible, so the availability of both artificial feed and natural foods for caged tilapia can be expressed as:

$$F_{ac} = q_c f_c W_s \quad (5a)$$

$$F_{nc} = 0 \quad (5b)$$

where

F_{ac} = availability of artificial feed to caged tilapia (g d^{-1}),

q_c = feeding efficiency on artificial feed for caged tilapia,

f_c = feeding rates (BWD),

W_s = sampled body weight of caged tilapia (g),

F_{nc} = availability of natural foods to caged tilapia (g d^{-1}).

Thus, based on equations 2a and 2b, the food quantity consumed by caged tilapia can be described as follows:

$$dR_{ac}/dt = \delta_c \upsilon_c q_c f_c W_s \quad (6a)$$

$$dR_{nc}/dt = 0 \quad (6b)$$

where

dR_{ac}/dt = daily ration of artificial feed for caged tilapia (g d^{-1}),

δ_c = DO factor for caged tilapia,

υ_c = UIA factor for caged tilapia,

dR_{nc}/dt = daily ration of natural foods for caged tilapia (g d^{-1}).

Fish confined in cages use less energy for feeding activity compared to fish at large in ponds. Thus, a parameter (*e*) is introduced to describe the reduction of food energy used by caged fish for feeding catabolism compared with pond fish. Then, equation 1 can be re-written for growth rates of caged tilapia (dW_c/dt) as follows:

$$dW_c/dt = b_a (1 - a_a e) \delta_c \upsilon_c q_c f_c W_s - kW_c^n \quad (7)$$

where

e = coefficient of reduction of food energy used by caged tilapia for feeding catabolism (dimensionless) and

W_c = body weight of caged tilapia (g).

The total waste feed from cages, including that knocked out of cages and that uneaten by caged tilapia due to low DO and/or high UIA, is available to open-pond tilapia. Thus, the daily availability of artificial feed to individual open-pond tilapia is expressed as follows:

$$F_{ap} = f_c W_s (1 - \delta_c \upsilon_c q_c) (N_c/N_p) \quad (8)$$

where

F_{ap} = availability of artificial feed to open-pond tilapia (g d^{-1}),

N_c/N_p = ratio of total number of surviving tilapia in cages to that of surviving tilapia in open pond, which divides total wasted feed from cages evenly to each open-pond tilapia.

The availability of natural foods to open-pond tilapia is based on the modeling rations proposed by Ursin (1967) and expressed as:

$$F_{np} = f_p W_p^m \quad (9)$$

where

F_{np} = availability of natural foods to open-pond tilapia (g d^{-1}),

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

W_p = body weight of open-pond tilapia (g),

m = exponent of body weight for net anabolism.

Yi (submitted) modified Ivlev's (1961) equation for the relative feeding level, and expressed it to be the function of potential net primary productivity (PNPP) and standing crop of Nile tilapia as the following:

$$f_p = 1 - \exp(-s P / B) \quad (10)$$

where

s = coefficient of food proportionality (dimensionless),

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

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

Based on Lannan (1993), Yi (submitted) estimated the parameter, P, using the following:

$$P = \mathrm{Min}(P_c, P_n, P_p) \quad (11)$$

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

$$k_1 = (T/15 + 2.6)\, 10^{-7} \quad (12a)$$

$$k_2 = (T/10 + 2.2)\, 10^{-11} \quad (12b)$$

$$P_n = 40\, D_n/7 \quad (13)$$

$$P_p = 40\, D_p \quad (14)$$

where

P_c = PNPP derived from dissolved inorganic carbon (DIC) (g C m^{-3} d^{-1}),

P_n = PNPP derived from dissolved inorganic nitrogen (DIN) (g C m^{-3} d^{-1}),

P_p = PNPP derived from dissolved inorganic phosphorus (DIP) (g C m^{-3} d^{-1}),

λ = efficiency of carbon fixation (dimensionless),

A = alkalinity (mg $CaCO_3$ l^{-1}),

H^+ = hydrogen ion concentration (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 (°C),

D_n = DIN (mg N l^{-1}), and

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

The constants 12 and 50 in equation 12 are gram equivalent weights of C and $CaCO_3$, respectively, and 40 and 7 in equations 13 and 14 are based on carbon:nitrogen:phosphorus ratios of 40:7:1 by weight (Round, 1973; Vallentyne, 1974; Wetzel, 1983).

Thus, availability of natural foods to individual, open-pond tilapia (F_{np}) is expressed as follows:

$$F_{np} = [1 - \exp(-s P/B)]\, W_p^m \quad (15)$$

Experimental evidence suggests that tilapias under culture conditions prefer artificial feed to natural foods (Schroeder, 1978). Therefore, it is assumed that Nile tilapia will take artificial feed independently of the concentration of natural food resources, and that they will consume natural foods whenever they can not meet their daily food intake requirements from artificial feed (Jamu and Piedrahita, 1996). Thus, the daily ration of artificial feed (dR_{ap}/dt) and natural foods (dR_{np}/dt) for open-pond tilapia can be expressed as follows:

$$dR_{ap}/dt = F_{ap}\, q_p \qquad dR_{np}/dt = h\,[\delta_p\, \upsilon_p\, (F_{ap}+F_{np})-F_{ap}]$$
$$\text{if } F_{ap} < \delta_p\, \upsilon_p\, (F_{ap}+F_{np}) \qquad (16a)$$

$$dR_{ap}/dt = F_{ap}\, q_p \qquad dR_{np}/dt = 0$$
$$\text{if } F_{ap} = \delta_p\, \upsilon_p\, (F_{ap}+F_{np}) \qquad (16b)$$

$$dR_{ap}/dt = \delta_p\, \upsilon_p\, q_p\, (F_{ap}+F_{np}) \qquad dR_{np}/dt = 0$$
$$\text{if } F_{ap} > \delta_p\, \upsilon_p\, (F_{ap}+F_{np}) \qquad (16c)$$

where

q_p = feeding efficiency on artificial feed for open-pond tilapia (dimensionless),

h = coefficient of food consumption (g^{1-m} day^{-1}),

$F_a + F_n$ = total daily food availability to open-pond tilapia, and

$\delta_p\, \upsilon_p\, (F_a + F_n)$ = total daily ration.

Instead of determining the maximum daily ration of open-pond tilapia, growth attainable in one day for open-pond tilapia is set at maximum growth (4.16 g day^{-1}), which was observed for Nile tilapia fed with pelleted feed in chemically fertilized ponds in an experiment reported by Diana et al. (1996). Thus, growth rates (dW_p/dt) of open-pond tilapia can be expressed as follows:

$$dWp/dt = b_a\,(1 - a_a)\, dR_{ap}/dt + b_n\,(1 - a_n)\, dR_{np}/dt - k\, W_p^{\,n} \qquad (17)$$

$$dW_p/dt \leq 4.16 \qquad (17a)$$

Ursin (1967) and Sperber et al. (1977) assumed that the coefficient of catabolism (k) increases exponentially with temperature. Nath et al. (1994) modified this exponential form to include the minimum temperature below which the fish species can not survive (T_{min}) in the following equation:

$$k = k_{min} \exp\,[\, j\,(T - T_{min})] \qquad (18)$$

where

k_{min} = coefficient of fasting catabolism (g^{1-n} day^{-1}) at $T_{min,}$

j = constant to describe temperature effects on catabolism (1/°C).

Parameter Estimation

Nath et al. (1993) analyzed oxygen consumption data of fasting Nile tilapia and estimated the mean for n to be 0.81. Ursin (1967) suggested that the exponent m approximated to 0.67. These two values were used in the present model.

For Nile tilapia feeding on natural foods in fertilized ponds, I assumed the efficiency of natural food assimilation (b_n) and the fraction of assimilated food used for feeding catabolism (a_n) to be 0.62 and 0.53 (Nath et al., 1994), respectively; these values were based on the work reported by Meyer-Burgdorff et al. (1989). The energy cost of feeding activity for fish fed with dry pellet diets was found to be 14.9% of gross energy ingested (Schalles and Wissing, 1976), implying that the parameter a_a for artificial feed is (0.149)/(b_a). By regression analysis of data on metabolic rates of Nile tilapia at swimming speeds from 0 to 60 cm s^{-1} (Farmer and Beamish, 1969), the parameter e was estimated to be 0.327. Assuming that tilapia in cages performed no active swimming activity and that tilapia at large had an average metabolic rate from the range of swimming speeds cited above. Then, parameters, b_a and a_a, were estimated to be 0.946 ± 0.03 and 0.158 ± 0.005, respectively, using growth data from caged tilapia in two randomly selected ponds from 30 experimental ponds of a cage-cum-pond integrated culture system (Yi, et al., 1996; Yi, 1997). For floating pellets, I assumed that all feed provided could be eaten by tilapia at large in ponds, thus, feeding efficiency with artificial feed for open-pond tilapia (q_p) was 1.0. For caged tilapia, I assumed that 5% of the pelleted feed was knocked out of cages, thus, feeding efficiency for caged tilapia (q_c) was 0.95. The values of parameters h and s were assumed to be 0.8 (Bolte et al., 1995) and 17.31 (Yi, submitted), respectively, in this model for Nile tilapia at large in ponds.

Based on laboratory experiments with Nile tilapia (Gannam and Phillips, 1993) T_{min} appears to be about 15°C. Nath et al. (1994) used data on fasting Nile tilapia from Satoh et al. (1984) to estimate k_{min} and j to be 0.00133 and 0.0132, respectively.

Abdalla (1989) investigated the effects of ammonia on Nile tilapia growth and determined that UIA_{max} = 1.40 mg l^{-1} and UIA_{crit} = 0.06 mg l^{-1}. However, DO_{crit} and DO_{min} have not been well defined. Nile tilapia can tolerate low DO and survive in water where only air breathing fish species can exist (Boyd, 1990) because Nile tilapia are able to use atmospheric oxygen when DO concentration drops to less than 1 mg l^{-1} (Chervinski, 1982). The lowest DO concentrations tolerated by Nile tilapia ranged from 0.1 to 0.3 mg l^{-1} under different environmental conditions (Ahmed and Magid, 1968; Magid and Babiker, 1975). Teichert-Coddington and Green (1993) reported that a practical DO threshold for Nile tilapia was not greater than 10% of saturation. Thus, DO_{crit} and DO_{min} for open-pond Nile tilapia used in the present model were 1.0 and 0.3 mg l^{-1}, respectively. Fish contained at high densities in cages are unable to seek out zones of favorable water quality and may be more susceptible to fluctuations in pond water quality, particularly low DO concentrations, than are free-ranging fish (Hargreaves et al., 1991). Therefore, DO_{crit} and DO_{min} for caged Nile tilapia were assumed to be 1.2 and 0.3 mg l^{-1}, respectively.

Data Requirements for Model Validation

Almost all values for parameters used in the present model were derived from the literature. To test the validity of the model, simulated results were compared with independently obtained experimental results which were not used during model development. The data used to validate the present model were collected from three experiments carried out at the Asian Institute of Technology, Thailand from August 1994 to September 1995. These experiments were conducted in 30 earthen ponds (335 m^2 or 395 m^2 in surface area and 330 m^3 in volume) over 90 days to investigate the effects of different stocking densities (30, 40, 50, 60 and 70 fish m^{-3}) of caged Nile tilapia, (one, two and three cages per pond), and the stocking densities of open-pond Nile tilapia (1.4 and 2.0 fish m^{-3}) on growth performance of both caged and open-pond fish (Yi et al., 1996; Yi, 1997). Two of these ponds were randomly selected to estimate parameters b_a and a_a. In the cage-cum-pond integrated culture system, caged tilapia were fed with floating pelleted feed, while growth of open-pond tilapia was dependent solely on the wastes derived from cages. From the experiments, the following initial values and input variables were used:

1. initial mean body weight of both caged and open-pond tilapia (g);
2. stocking densities of caged tilapia and open-pond tilapia (fish m^{-3});
3. survival rates of caged tilapia and open-pond tilapia (%);
4. cage size (m^3) and the number of cages in each pond (cages per pond);
5. surface area (m^2) and volume (m^3) of ponds;
6. contents of moisture, nitrogen, and phosphorus in feed and tilapia;
7. monthly dawn DO concentrations (mg l^{-1});
8. daily water temperature (°C), which was predicted by use of the model described by Nath (1996);
9. biweekly measured pH and alkalinity (mg $CaCO_3$ l^{-1}) between 0900 and 1000 h.

Floating pelleted feed was given daily to caged tilapia at feeding rates (f_c) of 3, 2.5, and 2% body weight during the first, second, and third months, respectively. The daily feed amount ($f_c W_s$) was adjusted based on daily observed mortality and biweekly sampled weight of caged tilapia.

Lin et al. (1988) reported that nitrogen fixation was of considerable magnitude in organically and inorganically fertilized ponds containing Nile tilapia. The mean nitrogen fixation rate in their ponds (0.11 mg N l^{-1} day^{-1}) was used in the present model. Thus, DIN was estimated as the sum of dissolved inorganic nitrogen levels from cage wastes and nitrogen fixation, and DIP was estimated as the dissolved inorganic phosphorus from cage wastes. Nath (1992, cited by Nath and Lannan, 1993) determined that percentages of dissolved inorganic nitrogen and phosphorus in chicken manure were 60 and 80% of total nitrogen and phosphorus, respectively. Without definitive information on the solubility of cage wastes, the same percentages were used in the present model to estimate dissolved inorganic nitrogen and phosphorus levels from cage wastes. The total nitrogen and phosphorus contents in cage wastes were estimated as the difference between quantities of nitrogen and phosphorus contained in given feed and in carcasses of caged tilapia.

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

Parameter	Percentage Change of Simulated Final Mean Weight					
	+10% for Parameter			-10% for Parameter		
	None	*DO Limiting*	*UIA Limiting*	*None*	*DO Limiting*	*UIA Limiting*
CAGED NILE TILAPIA						
b_a = efficiency of assimilation of artificial feed	15.61	11.17	15.52	-13.82	-10.22	-13.75
q_c = feeding efficiency with artificial feed	15.61	11.17	15.52	-13.82	-10.22	-13.75
n = exponent of body weight for fasting metabolism	-2.52	-2.60	-2.52	1.63	1.72	1.63
a_a = fraction of the assimilated artificial feed used for feeding metabolism	-0.80	-0.58	-0.79	0.80	0.58	0.79
e = coefficient of reduction of food energy for feeding catabolism	-0.80	-0.58	-0.79	0.80	0.58	0.79
k_{min} = coefficient of fasting catabolism at T_{min}	-0.44	-0.48	-0.44	0.44	0.48	0.44
j = constant to describe temperature effects on catabolism	-0.09	-0.10	-0.09	0.09	0.10	0.09
m = exponent of body weight for net anabolism	0	0	0	0	0	0
h = coefficient of food consumption	0	0	0	0	0	0
s = coefficient of food proportionality	0	0	0	0	0	0
b_n = efficiency of natural food assimilation	0	0	0	0	0	0
a_n = fraction of assimilated natural foods used for feeding metabolism	0	0	0	0	0	0
q_p = feeding efficiency of open-pond tilapia fed artificial food	0	0	0	0	0	0

The standing crop of open-pond Nile tilapia (B) was estimated from the simulated daily mean weight and the number of open-pond Nile tilapia surviving. It was assumed that all mortality of open-pond Nile tilapia occurred at stocking.

Sensitivity Analysis

Sensitivity analysis was carried out to evaluate the relative magnitude of effects of model parameters or variables on growth of both caged and open-pond tilapia. This was done by comparing the percentage change in growth when varying a parameter or variable by 10% about a baseline value (Tables 1 and 2). For the baseline simulation the following mean values from the above three experiments were used: initial sizes of caged tilapia and open-pond tilapia were 121 g and 28 g, respectively; stocking densities of caged tilapia and open-pond tilapia were 50 fish m^{-3} and 1.7 fish m^{-3}, respectively; survival rates of caged tilapia and open-pond tilapia were 86.2% and 91.5%, respectively; the number of cages per pond was two; feeding rate of caged tilapia was 2.5% BWD; water temperature was

Table 1. Continued.

Parameter		Percentage Change of Simulated Final Mean Weight					
		+10% for Parameter			-10% for Parameter		
		None	*DO Limiting*	*UIA Limiting*	*None*	*DO Limiting*	*UIA Limiting*
OPEN-POND TILAPIA							
q_c	= feeding efficiency with artificial feed	-27.46	-6.22	-26.50	3.49	5.44	22.66
m	= exponent of body weight for net anabolism	18.38	10.52	18.02	-13.68	-7.77	-13.41
a_n	= fraction of assimilated natural foods used for feeding anabolism	-6.37	-3.10	-6.24	6.26	3.06	6.12
b_n	= efficiency of natural food assimilation	5.56	2.71	5.43	-5.64	-2.74	-5.52
h	= coefficient of food consumption	5.56	2.71	5.43	-5.64	-2.74	-5.52
s	= coefficient of food proportionality	4.90	2.71	4.79	-5.04	-2.77	-4.94
b_a	= efficiency of assimilation of artificial feed	2.42	8.47	2.74	-2.29	-7.76	-2.59
q_p	= feeding efficiency with artificial feed of open-pond tilapia	1.39	5.29	1.55	-1.38	-5.27	-1.56
n	= exponent of body weight for fasting catabolism (dimensionless)	-1.55	-2.07	-1.57	1.11	1.43	1.12
k_{min}	= coefficient of fasting catabolism at T_{min}	-0.38	-0.44	-0.38	0.38	0.45	0.37
a_a	= fraction of the assimilated artificial feed used for feeding metabolism	-0.31	-1.13	-0.35	0.31	1.14	0.35
j	= constant to describe temperature effects on catabolism	-0.08	-0.09	-0.08	0.07	0.09	0.07
e	= coefficient of reduction of food energy for feeding catabolism	-0.05	-0.15	-0.06	0.04	0.15	0.05

30.5°C; DO was 1.8 mg l^{-1}; alkalinity was 93 mg $CaCO_3$ l^{-1}; pH was 7.4; and UIA was 0.03 mg l^{-1}. All the above values were held constant for the entire baseline simulation. In order to determine the effects of DO and UIA on Nile tilapia growth, the value of DO was set just below its critical limit (0.9 mg l^{-1}) and UIA was set just above its critical limit (0.07 mg l^{-1}).

Results

The simulated growth curves for both caged and open-pond tilapia fit well to observed data in ten treatments each with three replications (Figure 1). Linear regression showed that there was a statistically significant relationship between predicted and observed mean weights for both caged tilapia ($y = 12.10 + 1.02x$, $r^2 = 0.95$, df = 68, $P < 0.05$, Figure 2) and open-pond tilapia ($y = 7.77 + 0.92x$, $r^2 = 0.83$, df = 68, $P < 0.05$, Figure 2). The slope (1.02) and the y-intercept (12.10) of the regression line for caged tilapia were not significantly different from a slope of 1.0 ($P > 0.05$) and a y-intercept of 0 ($P > 0.05$). The same test for open-pond tilapia showed that there was no significant departure of the slope (0.92) from 1.0 ($P > 0.05$), but there was significant departure of the y-intercept (7.77) from 0 ($P < 0.05$). However, Spearman's rank correlation coefficient (r_s)

Table 2. Sensitivity analysis of key model variables affecting fish growth with no limiting factors (None) or with 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 (None). Negative values indicate that fish weight decreased with an increase in parameter value.

Variable	Percentage Change of Simulated Final Mean Weight					
	+10% for Variable			-10% for Variable		
	None	*DO Limiting*	*UIA Limiting*	*None*	*DO Limiting*	*UIA Limiting*
CAGED NILE TILAPIA						
Artificial Feed Availability	15.61	11.17	15.52	-13.82	-0.22	-13.75
Size of Caged Tilapia	7.61	8.30	7.63	-7.61	-8.29	-7.62
Temperature	-0.18	-0.20	-0.18	0.18	0.19	0.17
DO	0	17.13	0	0	-15.00	0
UIA	0	0	-0.77	0	0	0.77
Natural Food Availability	0	0	0	0	0	0
Size of Open-Pond Tilapia	0	0	0	0	0	0
OPEN-POND TILAPIA						
Artificial Feed Availability	8.68	10.66	8.82	-8.27	-10.06	-8.41
Natural Food Availability	5.56	2.99	5.44	-5.64	-3.02	-5.53
Size of Caged Tilapia	3.35	4.97	3.40	-3.48	-5.01	-3.54
Size of Open-Pond Tilapia	1.87	1.33	1.84	-1.85	-1.32	-1.83
Temperature	-0.15	-0.18	-0.16	0.15	0.18	0.15
DO	0	-3.12	0	0	0.52	0
UIA	0	0	0.97	0	0	-0.98

indicated that predicted and observed final weights of open-pond tilapia were significantly correlated ($r_s = 0.81$, df = 8, $P < 0.05$). When predicted and observed final weights of caged tilapia were compared using Spearman's rank correlation coefficient, they were also significantly correlated ($r_s = 0.80$, df = 8, $P < 0.05$). Therefore, there were agreements between predicted and observed values of both caged and open-pond tilapia.

The model showed that carbon was not a limiting nutrient for primary production in the cage-cum-pond integrated culture. Growth of open-pond tilapia was limited by phosphorus which limited primary production when the total number of tilapia stocked in cages was not greater than 200 fish per pond. With a cage stocking density greater than 200 fish per pond, phosphorus was limiting during the early part of the experiment, but then the limiting nutrient became nitrogen. The percentage of the culture period during which primary production was limited by nitrogen increased from 0 to 84.4% as the total number of tilapia stocked in cages increased (with resultant increases in artificial feed) from 200 to 600 fish per pond. Nitrogen from biological nitrogen fixation accounted for 44.2 to 74.8% of total nitrogen available for primary production and increased with decreases in the total number of tilapia stocked in cages. Under the model assumptions, pelleted feed accounted for only 13.8 to 14.6% of the growth of open-pond tilapia when DO was above DO_{crit} (1.2 mg l^{-1}) for caged tilapia. However, these percentages ranged from 19.0 to 51.0% when DO was less than 1.2 mg l^{-1}, and increased with an increase in the number of days that DO was below this critical level.

Sensitivity analysis for the parameters (Table 1) showed that parameters for caged tilapia affected

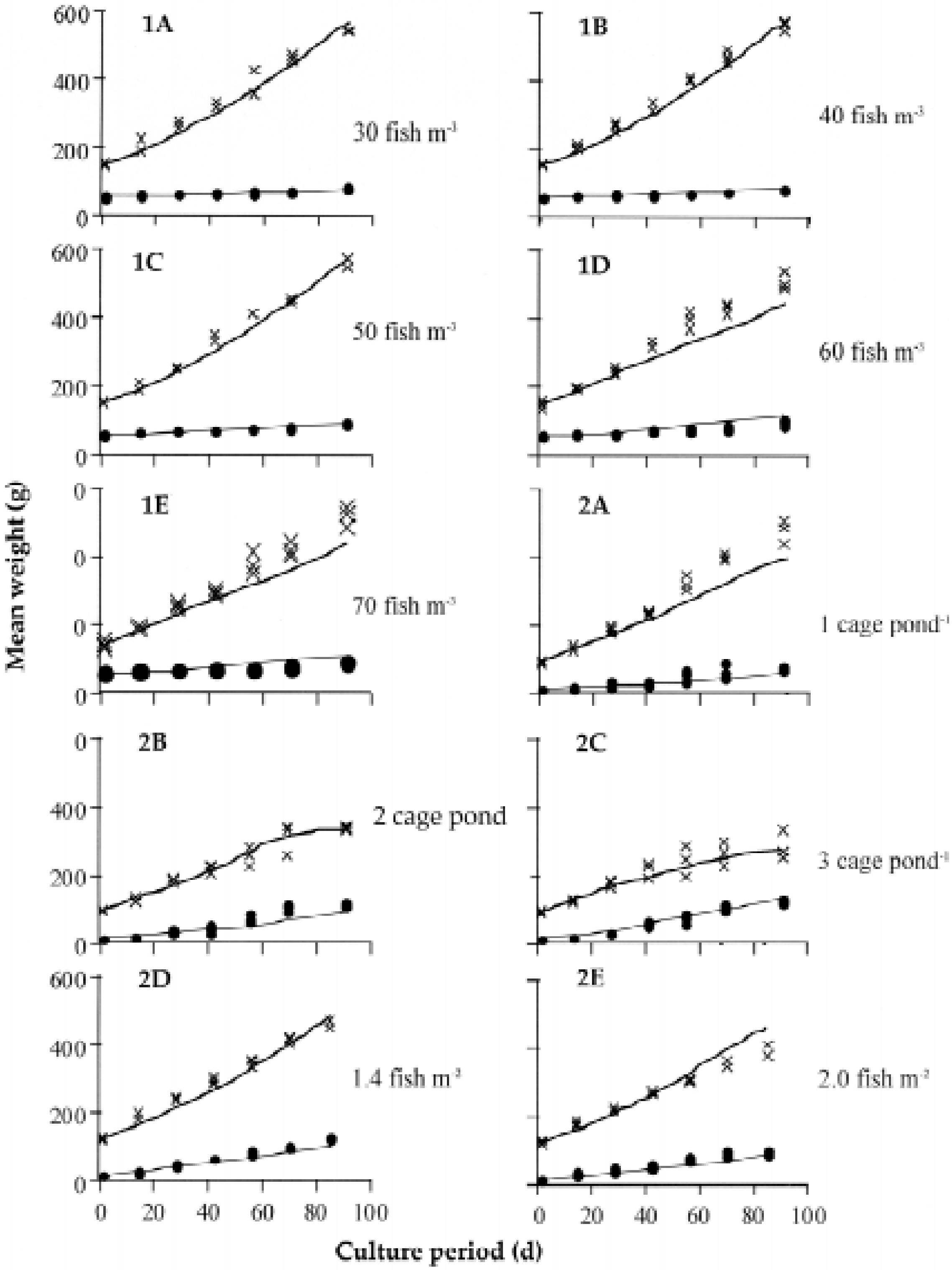

Figure 1. Comparison of model data with the growth of caged (•) and open-pond (x) Nile tilapia (*Oreochromis niloticus*) as recorded by Yi (1997b). Graphs 1A-E represent the treatments for stocking densities of caged tilapia at 30, 40, 50, 60, and 70 fish m^{-3}, respectively. Graphs 2A-C represent the treatments with one, two, or three cages per pond, respectively. Graphs 3A-B represent the treatments for stocking densities of open-pond tilapia at 1.4 and 2.0 fish m^{-2}, respectively.

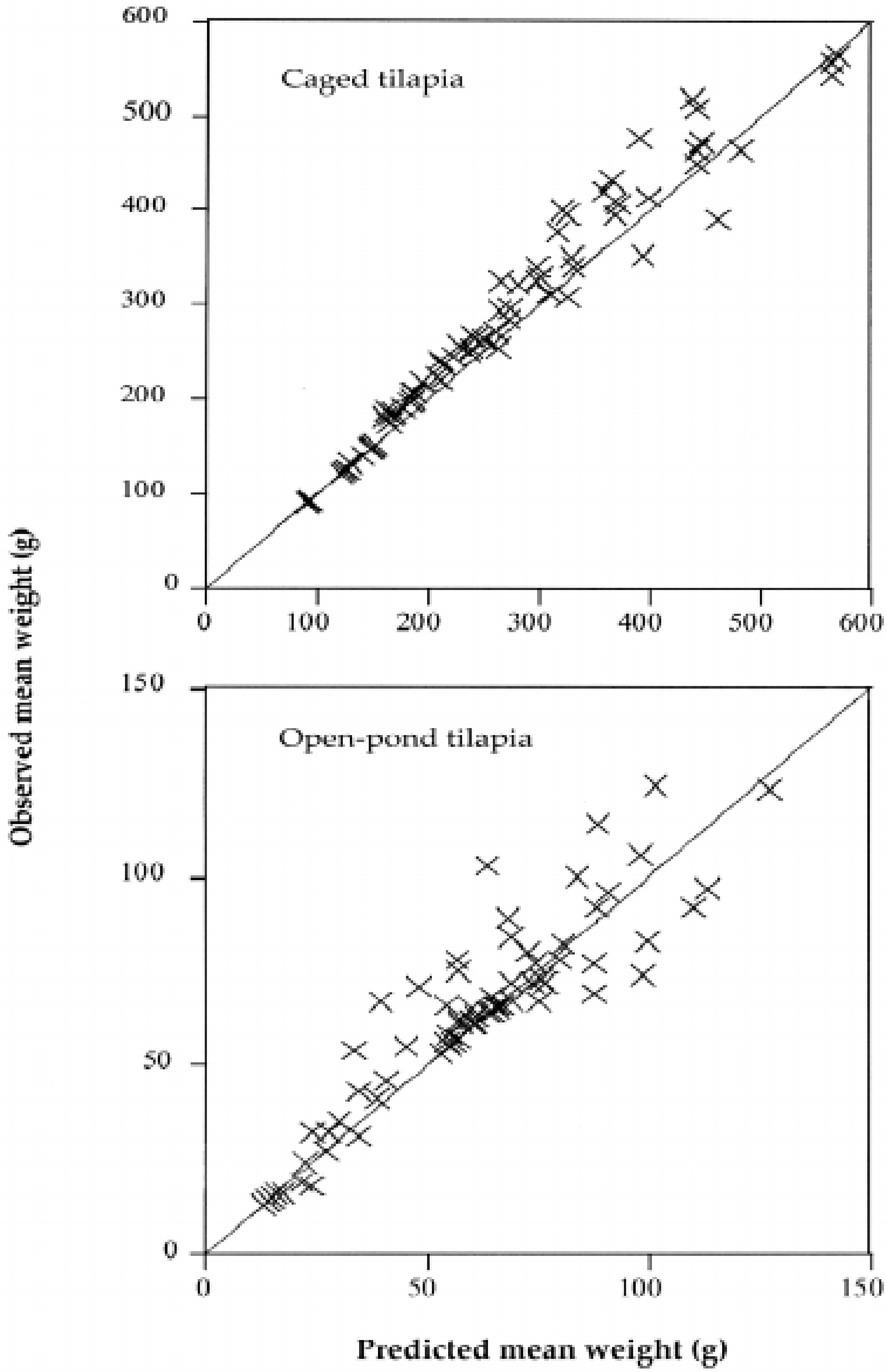

Figure 2. Comparison between predicted and observed mean weights of caged and open-pond tilapia in 28 ponds in the experiments of Yi (1997). The line represents equality (where observed weight equals predicted weight).

growth of open-pond tilapia but not the reverse. The efficiency of artificial feed assimilation (b_a) was the most sensitive parameter influencing growth of caged tilapia. When DO was not a limiting factor for open-pond tilapia (>1.0 mg l^{-1}), the most sensitive parameter affecting growth of open-pond tilapia was the feeding efficiency of caged tilapia (q_c), followed by the exponent of body weight for anabolism (m), which became the most sensitive parameter when DO was limited. The parameters related to net energy from foraging natural foods (a_n, b_n, h, s) were more important for open-pond tilapia than those related to artificial feed (b_a, a_a) when DO was not limited. However, the relative importance of natural foods was reduced and that of artificial feed was increased when DO was limited. Moreover, b_a became the second most sensitive parameter affecting growth of open-pond tilapia when DO was below the critical limit. Compared with DO, UIA has smaller effects on the growth of both caged and open-pond tilapia. Beyond the critical limit (0.06 mg l^{-1}), UIA slightly reduced the importance of artificial feed for caged tilapia and the importance of natural foods for open-pond tilapia, but slightly increased the importance of artificial feed on open-pond tilapia. UIA did not change the order of sensitivity of the parameters to growth of open-pond tilapia whereas DO did influence the ordering of parameters.

Sensitivity analysis for key variables affecting Nile tilapia growth (Table 2) showed that the growth of caged tilapia was most sensitive to artificial feed availability followed by the stocking size of caged tilapia when DO was not limited, but growth was most sensitive to DO when it was limited. UIA was the third most sensitive parameter affecting growth of caged tilapia when UIA was limited, although the sensitivity (about 0.77 for a 10% change) was low. When both DO and UIA were limiting factors, artificial feed became more important and natural foods less important for growth of open-pond tilapia. However, DO (even below the critical limit) was not the variable most affecting the growth of open-pond tilapia; growth of open-pond tilapia was most sensitive to the amount of artificial feed available to caged tilapia.

Lowering water quality (by decreasing DO or raising UIA 10%, respectively) further reduced the growth of caged tilapia and increased the growth of open-pond tilapia. The growth of open-pond tilapia was more sensitive to variables affecting caged tilapia than the variables affecting their own growth. Growth was least sensitive to water temperature for both caged and open-pond tilapia. When DO and UIA did not reach their critical limits, the growth of neither caged nor open-pond tilapia was affected.

Discussion

The present model was validated using growth data reported by Yi et al. (1996) and Yi (1997) of both caged and open-pond Nile tilapia in 28 ponds from a cage-cum-pond integrated culture system. Compared with previous models for Nile tilapia growth (Liu and Chang, 1992; Nath et al., 1994; Bolte et al., 1995; Yi, submitted), this model incorporated a new parameter, feeding efficiency (q, including q_c and q_p), to describe the physical form and application method of artificial feed and natural nitrogen fixation processes. These modifications may make it possible to simulate the growth of Nile tilapia in culture systems with varying availability of natural foods and/or different types of artificial feed.

Fish growth is affected largely by the nutritional quality and quantity of food. The parameters b and a, efficiency of food assimilation and fraction of the assimilated food used for feeding catabolism, reflected the nutritional quality of different foods. For natural foods, average values of b and a are used for all food resources in ponds. Even though it is relatively convenient to use the unique values of b and a for each type of artificial feed given to fish, it is, nonetheless, difficult to determine complex compositions of such food resources under different culture conditions. High quality feed has a large b value and a small a value. However, fish growth is also affected by physical form and application method of feed, which affect the amount of feed fish are able to consume. These are described by the feeding efficiency parameter in the present model. For floating pellets, q was assumed to be 1 based on its physical form when it was given to tilapia at large in ponds; however, q was 0.95 for tilapia confined in cages because it was assumed that 5% of the feed given was knocked out of cages due to vigorous swimming activity of caged tilapia (Collins, 1971; Coche, 1979; McGinty, 1991; Yi, 1997). For other types of artificial feed, q ranges from 0 to 1. Thus, this parameter allows one to simulate how fish growth is affected in different culture systems receiving different artificial feeds. Jamu and Piedrahita (1996) incorporated a parameter, the coefficient of feed quality, in their model to describe the effects of variable feed quality on fish growth; however, this parameter only accounted for how the nutritional quality of feed affected fish growth, which had been described by other parameters *b* and *a*.

A significantly large amount of nitrogen fixation may occur in Nile tilapia ponds fertilized organically or inorganically (Lin et al., 1988). Even though nitrogen fixation rates fluctuated over a wide range (Lin et al., 1988), the mean rate of nitrogen fixation was used in the present model. The simulated results indicated that nitrogen derived from natural biological fixation was an important source of nitrogen input in ponds, a finding consistent with conclusions made by Lin et al. (1988). Yi (submitted) reported that the simulated growth of Nile tilapia in well-fertilized ponds (4 kg N ha^{-1} day^{-1} and 1 kg P ha^{-1} day^{-1}) was limited as a result of carbon limiting primary production during 55 to 99% of the culture period; however, the present model indicated that carbon was not a limiting nutrient to primary production in the cage-cum-pond integrated culture system fertilized by cage wastes at rates of 0.62 to 2.36 kg N ha^{-1} d^{-1} and 0.12 to 0.53 kg P ha^{-1} d^{-1} (Yi, 1997). Growth of open-pond tilapia was limited due to phosphorus and nitrogen limiting primary production during the entire period of the experiments. This implies that carbon limitation might not occur in fed ponds unless fertilizer is also applied or that organic inputs add carbon to the water. These results suggest that the balance of fertilizer inputs should be evaluated carefully in both fertilized and fed ponds to maintain good water quality, maximize nutrient utilization, reduce nutrient discharge, and minimize production costs.

Simulation of open-pond tilapia growth by the present model explained why Yi (1997) found that open-pond tilapia grew faster when water quality declined (low DO and high UIA) than when water quality was maintained at optimal levels (DO above and UIA below their respective critical limits). Food consumption of caged tilapia was reduced when water quality was depleted. This caused slower growth of caged tilapia and, thus, more uneaten artificial feed, which was then available to the open-pond tilapia. The total food consumption of open-pond tilapia was also reduced; however, tilapia consumed high quality artificial feed instead of lower quality natural food, because Nile tilapia prefer artificial feed to natural foods under culture conditions (Schroeder, 1978). Therefore, instead of observing a reduction in the growth of open-pond tilapia in depleted water quality conditions, an increase in growth was observed to some extent. This also explained why the growth of open-pond tilapia was more sensitive to parameters related to the availability of artificial feed than the parameters related to the availability of natural foods, when water quality declined.

Some modifications might be made to the model once the necessary information is available. For example, further definition of water quality parameters, especially DO, is necessary to determine how food consumption and ultimately the growth of Nile tilapia are affected. Growth is much more sensitive to water quality parameters when they become limiting factors. Parameters related to feed intake and net energy from feeding (q_c, q_p, b_a, b_n, a_a, a_n) are also sensitive to the model output but are not well defined, thus, more research is required. The model also should be reparameterized to simulate growth of other fish species cultured in different environments.

Anticipated Benefits

This study led to the development of a model that successfully simulates the growth of caged tilapia feeding on artificial pelleted feed and open-pond tilapia which depend on the wastes of cage cultured tilapia. This study has indicated that the primary production in ponds fertilized by cage wastes is limited by nitrogen and phosphorus. The results will be useful for our understanding and management of integrated aquaculture systems.

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