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A model for food nutrient dynamics of semi-intensive pond fish culture

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Abstract

A dynamic model was developed to explain food nutrient dynamics in a semi-intensive aquaculture pond and to determine food nutrient requirements for supplementary feeds for Nile tilapia. The model links food nutrient production with elementary nutrient dynamics and fish growth by including four sectors: food nutrients, fish growth, elementary nutrients, and dissolved oxygen. The model, developed by using STELLA II software, simulated a field experiment that was designed to determine limiting nutritional factors for fish growth in fertilized ponds. Simulation results show that supplementary feeding compensates for natural food nutrient deficiencies. Results also reveal that protein supplements are necessary for increasing fish yields of fertilized ponds. Comparison of the data from simulation and observation indicates that the simulation values have a close correspondence with observed data, and the model is able to capture essential food nutrient dynamics in semi-intensive aquaculture ponds.

Keywords: Fertilization; Autotrophic food nutrient; Heterotrophic food nutrient; Nutrient dynamics; Supplementary feeding

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Nomenclature

a, b	light extinct coefficient for phytoplankton and heterotrophic component
AFC, HFC, SFC	consumption rate of autotrophic and heterotrophic components, and supplementary feed by fish
AFG	autotrophic food growth due to phytoplankton growth
AFM, AFR	autotrophic food loss rate due to phytoplankton respiration and entering heterotrophic food pool
AF_e, HF_e	autotrophic and heterotrophic food nutrient in term of energy
AF_p, HF_p	autotrophic and heterotrophic food nutrient in term of protein
AWFT	air/water interface film thickness
c, d	regressive parameter describing temperature effect on fasting catabolism
DICO	diffusion coefficient
DOC, DOS	dissolved oxygen concentration, and saturation DO concentration
DO_{crit}	critical DO limit
DO_{df}	oxygen exchange rate between air and water body
d_w	water depth
f(FQ)	food quality limiting function for food assimilation
f(I)	light limiting function for phytoplankton growth
f(N,P)	elementary nutrient limiting function for phytoplankton growth
f(WQ)	water quality limiting function for food consumption
f_1(DO), f_2(DO)	DO limiting function for aerobic processes and fasting catabolism
$f_1(T)$, $f_2(T)$, $f_3(T)$	temperature-dependent functions for phytoplankton growth, fish food consumption and fasting catabolism
FA, FC	fish anabolism and catabolism
FAPP	fish appetite
$FAPP_{max}$	maximum FAPP
FB, FP	total fish biomass and fish number in the pond
FB_i, FP_s	individual fish biomass and total fish number during fish stocking
FB_m	mean fish biomass
FB_s	average fish size at which f_{sm} is normalized at 1
f_a, f_h	autotrophic and heterotrophic food availability
FIXN	N-fixation rate by phytoplankton
f_{sm}, f_{sn}	functions for fish size effect on food consumption and fasting catabolism
FT_N, FT_P	inorganic nitrogen and phosphorus loading from fertilization
FW	fish fecal wastes
h_a, h_h	coefficient of autotrophic and heterotrophic food consumption

h_N, h_P	half-saturation INC and IPC for phytoplankton growth
HFD, HFS	heterotrophic food loss rate due to decomposition and sedimentation
I_0, I_r	light intensity and reference intensity for phytoplankton growth
INC, IPC	total inorganic nitrogen and phosphorus concentration
k_d, k_s	coefficient of heterotrophic food decomposition and sedimentation
k_{DO}, k_{DOf}	coefficient of DO on aerobic biological activity and fasting catabolism
k_{DOT}, k_{NHT}	weighting factor of DO depletion and UIA toxicity to food consumption
k_{fast}, k_{feed}	coefficient of fasting and feeding catabolism
k_{fn}, k_{an}, k_{hn}	N content of fish, phytoplankton, and heterotrophic components
k_{fo}, k_{ho}, k_{ao}, k_{sno}	DO coefficient for fish catabolism, heterotrophic food decomposition, phytoplankton oxygenation and respiration, and bottom organic decay
k_{fp}, k_{ap}, k_{hp}	phosphorus content of fish, phytoplankton, and heterotrophic components
k_{m1}	coefficient of autotrophic food entering heterotrophic food pool
k_{m2}	coefficient of fish mortality
k_{maxa}	maximum assimilation coefficient
k_n	N-fixation coefficient of phytoplankton
k_{nf}	effect of INC on N-fixation
k_{NH}	fraction of UIA to INC
k_{nl}	coefficient of inorganic nitrogen loss to air
k_{p1}, k_{p2}, k_{p3}	P:E ratio of phytoplankton, heterotrophic components, and supplemental feed
k_{PE}	coefficient of PE on food assimilation
k_{pr}	release coefficient of phosphorus in sediment
k_{ps}	coefficient of inorganic phosphorus sedimentation
k_r	coefficient of phytoplankton respiration
k_{se}	supplementary feed energy content
k_{sn}	release coefficient of nitrogen in sediment
k_{T1}, k_{T2}	coefficient of temperature below and above T_{opta} on phytoplankton growth
k_{TI}	coefficient of toxicity index on food consumption
m, n	exponent of individual fish biomass for food consumption and fasting catabolism
PE	ratio of dietary protein to energy
PE_{opt}, PE_{min}	optimal and minimum PE for fish growth

Q_{10}	a term to express the relative increase in the rate of a biological activity with an increase in temperature of 10 °C
Q_{DO}	DO quantity in pond water column
R_{kp3}	required protein content of supplementary feed
RSF	requirement for supplementary feed
s	proportionality coefficient of natural food quantity to fish biomass
SFA	supplemenetary feeding rate
T	water temperature
TFC	total food consumption
TI	toxicity index
TIN, TIP	total dissolved inorganic nitrogen and phosphorus in water column
T_{maxf}, T_{optf}	maximum and optimum temperature for tilapia growth
TNS, TP	total nitrogen and phosphorus quantity in sediment
T_{opta}	optimal temperature for phytoplankton growth
V_{pond}	pond water volume

1. Introduction

Successful management of tropical fish ponds for biologically optimal fish growth requires provision of necessary nutrients in a balanced manner via fertilization and supplementary feeding. Fertilization provides exogenous elementary nutrients (carbon, nitrogen and phosphorus) for enhancing natural food productivity for omnivorous fish like Nile tilapia, while supplementary feeding provides exogenous food nutrients (energy, protein, etc.) compensating for the nutritional deficit of natural food.

Studies of pond fertilization (Swingle, 1968; Boyd, 1990) and supplementary feeding (Ling, 1967; Spataru et al., 1980) have addressed qualitative and quantitative requirements of fertilizers and feeds as well as input–output analyses of nutrients. However, as a pond culture system consists of complex interactions among elementary nutrients, bacteria, primary and secondary producers, an understanding of the qualitative and quantitative food nutrient (energy and protein) dynamics in a fertilized pond is necessary. A pond ecosystem model that elucidates relationships among fertilization, food nutrient production, supplementary feeding, and fish growth can serve as an explanatory tool for understanding complex pond ecosystem behavior and making proper decisions on fertilization and supplementary feeding.

Li et al. (1998) developed a nutrient dynamic model for exploring food nutrient production in a fertilized aquaculture pond. Building on this research, the current study modifies the model to address food nutrient dynamics in a supplementary feeding aquaculture pond. This new model captures the essential dynamic characteristics of elementary nutrient cycling, food nutrient production and fish growth. Based on an analysis and integration of existing information available on

food nutrient production in a cultural pond, the model is formulated as a set of mathematical equations and implemented using STELLA II simulation tool (High Performance Systems and Inc., 1997). The model is applied to simulate a field experiment that was designed to determine nutritional limiting factors for fish growth in semi-intensive cultural ponds. The paper discusses the simulation results and ends with conclusions.

2. Material and methods

2.1. Conceptualization of the model

The proposed model links food nutrient dynamics (energy and protein) to elementary nutrient (C, N, P) cycling and fish growth. The conceptual model, consisting of the process of natural food production, and interactions between natural food supplies and supplementary feeding practices in a semi-intensive culture pond, is described in Fig. 1 using Odum (1983) symbols.

In a pond ecosystem, autotrophic producers convert elementary nutrients (e.g. C, N, P) into food nutrients (energy, protein etc.) where production capacity is determined by the quantity of incident radiation, turbidity, water temperature and elementary nutrients. Limited availability of elementary nutrients in a natural pond can limit primary productivity, which can limit food nutrients for fish. Provision of exogenous elementary nutrients for primary and/or heterotrophic production can enhance fish productivity. Inorganic fertilizers provide exogenous elementary nutrients for autotrophic food nutrient production. Organic fertilizers support

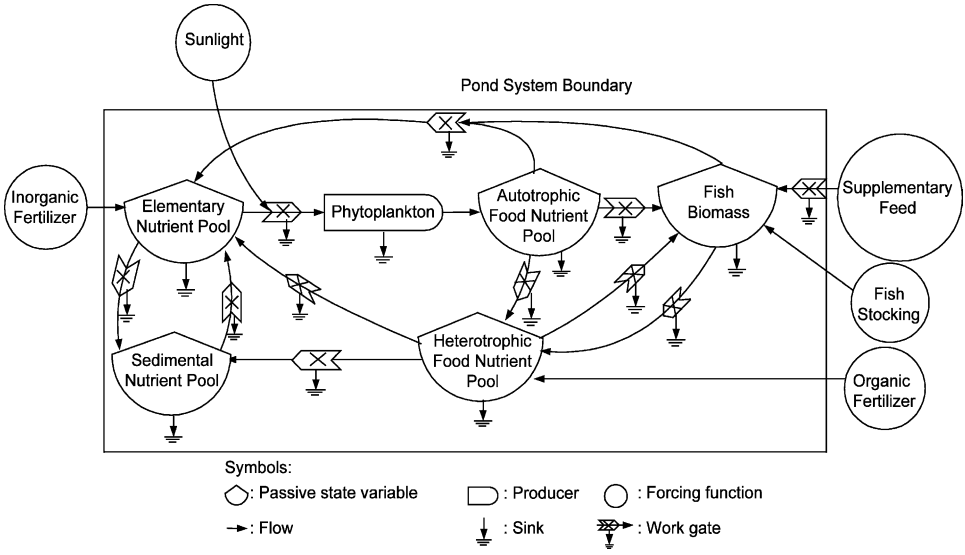

Fig. 1. Conceptual model of nutrient dynamic model in a fertilized pond using Odum (1983) symbols.

heterotrophic production and stimulate autotrophic food production by releasing elementary nutrients through their decomposition. In the presence of unlimited elementary nutrients, primary productivity reaches a maximum value set by the solar energy penetrating the pond water (Schroeder, 1980), at which autotrophic food productivity achieves its maximum value. A fertilized pond contains a critical mass of food nutrients (CMFN) that is the quantity of food nutrients at which critical standing crop is attained (Hepher, 1978). After CMFN is reached, food nutrient deficiencies develop and exogenous supplementing food nutrients should be provided for further fish growth. Energy is a basic food nutrient and energy supplementation is widely applied in pond aquaculture practice. However, maintaining dietary protein to energy ratio (P:E ratio) is considered important as it minimizes protein catabolism.

2.2. Model's assumptions

This study uses male Nile tilapia (*Oreochromis niloticus*, 10–300 g in weight) as the target species. The following assumptions are made: (a) food nutrient sources for Nile tilapia originate from autotrophic and heterotrophic sources in fertilized ponds; (b) inorganic nitrogen and phosphorus are regarded as two limiting elementary nutrients in food nutrient production, and the decomposition of organic matter in semi-intensive culture pond supplies enough carbon dioxide to support good phytoplankton growth (Boyd, 1972); (c) protein content of phytoplankton is assumed to be a constant; (d) P:E ratio is taken as a feed quality index, and high protein content enhances fish growth; (e) there are no lethal abiotic factors in well-managed fish pond; (f) dissolved oxygen (DO) and inorganic nitrogen are taken as important indices of water quality; (g) survival rate of fish is constant; (h) the cultural pond is homogeneous; and (i) water inflow is provided only to replace evaporation and seepage losses and maintain a stable depth (100 cm).

2.3. Model's structure and mathematical representation

As shown in Fig. 1, the model integrates relevant living, nonliving and management components as a functional ecosystem. Four sectors are used in the model development: food nutrients, fish growth, elementary nutrients, and dissolved oxygen. Mathematical representation of the model is formulated as below.

2.3.1. Food nutrient sector

Autotrophic food and heterotrophic food are two sources of natural food for tilapia in an aquaculture pond. Autotrophic food represents living autotrophic components in a pond that can be grazed by tilapia. Photosynthesis by phytoplankton is a unique source of autotrophic food, while losses of autotrophic food include tilapia grazing, phytoplankton respiration and mortality. Based on previous work (Piedrahita, 1984; Wolfe et al., 1986; Li et al., 1998), the following equations are used to describe autotrophic food nutrient (energy and protein) dynamics:

$$dAF_e/dt = AFG - AFC - AFR - AFM \quad (1)$$

$$AFG = \mu_{max} AF_e f(N,P) f(I) f_1(T) \quad (2)$$

$$AFR = AF_e k_r \quad (3)$$

$$AFM = AF_e k_{m1} \quad (4)$$

$$dAF_p/dt = dAF_e/dt k_{p1} \quad (5)$$

where AF_e and AF_p are autotrophic food quantity in terms of energy (kcal pond^{-1}) and protein (g protein pond^{-1}), AFG is autotrophic food growth due to phytoplankton growth (kcal day^{-1} pond^{-1}), AFC and AFR are autotrophic food loss rate (kcal day^{-1} pond^{-1}) due to tilapia grazing and phytoplankton respiration, AFM is a rate of autotrophic food entering heterotrophic food pool (kcal day^{-1} pond^{-1}) due to phytoplankton mortality and harvest by secondary producers, μ_{max} is a maximum growth coefficient for phytoplankton growth (day^{-1}), f(N,P), f(I) and f_1(T) are limiting functions of elementary nutrients, solar radiation and water temperature to phytoplankton growth (dimensionless), k_r is a coefficient of phytoplankton respiration (day^{-1}), k_{m1} is a coefficient of autotrophic food entering heterotrophic food pool due to phytoplankton mortality and harvest by secondary producers (day^{-1}), and k_{p1} is protein content of phytoplankton (g protein kcal^{-1}).

Functions representing elementary nutrient limitation (Zison et al., 1978), light limitation (Wolfe et al., 1986), and phytoplankton growth vs. temperature relationship similar to a Gaussian probability curve (Tamiya et al., 1964) are expressed as:

$$f(N,P) = \min[INC/(INC + h_N), IPC/(IPC + h_P)] \quad (6)$$

$$f(I) = I_0 \exp[-(aAF_e + bHF_e)]/I_r \quad (7)$$

$$f_1(T) = \begin{cases} \exp[-k_{T1}(T - T_{opta})^2] & \text{if } T \leqslant T_{opta} \\ \exp[-k_{T2}(T_{opta} - T)^2] & \text{if } T > T_{opta} \end{cases} \quad (8)$$

where INC is total inorganic nitrogen concentration (mgN l^{-1}), IPC is total inorganic phosphorus concentration (mgP l^{-1}), h_N and h_P are half-saturation INC (mgN l^{-1}) and IPC (mgP l^{-1}), I_0 is the light reaching the surface of the water (10^6 cal m^{-2} day^{-1}), HF_e is the quantity of heterotrophic food nutrient in term of energy (kcal pond^{-1}), a and b are light extinct coefficients for autotrophic and heterotrophic components (pond kcal^{-1}), I_r is reference sunlight intensity for phytoplankton growth (10^6 cal m^{-2} day^{-1}), T is water temperature (°C), T_{opta} is optimal temperature for phytoplankton growth (°C), k_{T1} and k_{T2} are effects of temperature below and above T_{opta} on growth (°C^{-2}).

Heterotrophic food refers to all living and non-living heterotrophic components of particulate organic matters in a pond that can be grazed by tilapia. Sources of heterotrophic food in chemically fertilized ponds include autotrophic food mortality and fish fecal wastes. Heterotrophic food decline is determined by decomposition, sedimentation, grazing by fish and the respiration of living heterotrophic components. Assuming heterotrophic food loss of per unit heterotrophic microorganisms' respiration is equal to that of per unit non-living heterotrophic matter decomposition, mathematical equations for heterotrophic food dynamics can be expressed as

(Li et al., 1998):

$$dHF_e/dt = AFM + FW - HFC - HFS - HFD \quad (9)$$

$$HFS = HF_e k_s \quad (10)$$

$$HFD = HF_e k_d f_1(DO) \quad (11)$$

$$dHF_p/dt = dHF_e/dt k_{p2} \quad (12)$$

where FW is fish fecal wastes (kcal day^{-1} pond^{-1}), HFC, HFD and HFS are heterotrophic food loss rate (kcal day^{-1} pond^{-1}) due to tilapia grazing, decomposition and sedimentation, k_s and k_d are coefficients of heterotrophic food sedimentation and decomposition (day^{-1}), f_1(DO) is the effect of DO on an aerobic process (dimensionless), HF_p is the quantity of heterotrophic food nutrient in term of protein (g protein pond^{-1}), and k_{p2} is protein content of heterotrophic food (g protein kcal^{-1}).

Decomposition of heterotrophic particles is an aerobic process which slows down as DO is lower than 4 mg l^{-1} (Wolfe et al., 1986). Based on Wolfe et al. (1986) and Li et al. (1998), f_1 (DO) can be expressed as:

$$f_1(DO) = \begin{cases} \exp[-k_{DO}(4 - DOC)^2] & \text{if } DO < 4 \\ 1 & \text{if } DO \geqslant 4 \end{cases} \quad (13)$$

where k_{DO} is a coefficient of DO on aerobic biological activity ((mg DO l^{-1})$^{-2}$), and DOC is dissolved oxygen concentration (mg DO l^{-1}).

2.3.2. Fish growth sector

The fish growth sector consists of two state variables: fish biomass and fish population. Fish biomass accumulation depends on fish growth rate which is the difference between anabolism and total catabolism (Ursin, 1967), while fish population is determined by fish stocking and mortality in a male tilapia monoculture pond. Mathematical equations for fish biomass and fish population in a cultural pond can be expressed as (Li et al., 1998):

$$dFB/dt = FP_s FB_i + FA - FC - FP k_{m2} FB_m \quad (14)$$

$$dFP/dt = FP_s - INT(FP k_{m2}) \quad (15)$$

where FB and FP are total fish biomass (kcal pond^{-1}) and fish number (fish - pond^{-1}), FP_s and FB_i are stocking fish number (fish day^{-1} pond^{-1}) and individual fish biomass (kcal fish^{-1}) during fish stocking, FA and FC are anabolism and total fish catabolism (kcal day^{-1} pond^{-1}), k_{m2} is fish mortality coefficient (day^{-1}), FB_m is mean fish biomass (kcal fish^{-1}) which equals to FB divided by FP, and INT is a mathematical function which gives the largest integer less than or equal to expression.

2.3.2.1. Anabolism. Anabolism is dependent on food consumption (Ursin, 1967; Nath and Lannan, 1993) and food quality (Wolfe et al., 1986). It is expressed as (Li et al., 1998):

$$FA = k_{maxa} TFC f(FQ) \quad (16)$$

$$\mathrm{TFC} = \mathrm{AFC} + \mathrm{HFC} + \mathrm{SFC} \tag{17}$$

where k_{maxa} is a maximum assimilation coefficient (dimensionless), TFC is total food consumption (kcal day^{-1} pond^{-1}), f(FQ) represents the effect of food quality on food assimilation (dimensionless), and SFC is supplemental feed consumption (kcal day^{-1} pond^{-1}).

Daily natural food consumption rate is primarily influenced by fish weight, size (Ursin, 1967), temperature, food availability, and water quality (Cuenco et al., 1985; Wolfe et al., 1986). Assuming that fish grazing on each natural food source has a paralleling mechanism, daily grazing rate of fish on each natural food source can be expressed as (Li et al., 1998):

$$\mathrm{AFC} = \mathrm{FB}h_a f_a f_{sm} f_2(T) f(\mathrm{WQ}) \tag{18}$$

$$\mathrm{HFC} = \mathrm{FB}h_h f_h f_{sm} f_2(T) f(\mathrm{WQ}) \tag{19}$$

where h_a and h_h are the coefficients of autotrophic and heterotrophic food consumption (day^{-1}), f_a and f_h are autotrophic and heterotrophic food availability (dimensionless), f_{sm}, f_2(T), and f(WQ) are functions (dimensionless) to describe the effects of fish size, temperature, and water quality on food consumption.

Natural food availability in a fertilized pond depends upon the standing natural food quantity and fish biomass (Hepher, 1978; De Silva, 1993; Li et al., 1998). Ivlev's equation (Ivlev, 1961) for the relative feeding level is modified to represent natural food availability:

$$f_a = 1 - \exp[-s(\mathrm{AF_e}/\mathrm{FB})^{2.2}] \tag{20}$$

$$f_h = 1 - \exp[-s(\mathrm{HF_e}/\mathrm{FB})^{2.2}] \tag{21}$$

where s is a proportionality coefficient of food nutrient quantity to fish biomass (dimensionless).

The effect of fish size on food consumption is used to adjust food consumption per unit of individual fish biomass. It is an exponential equation of average individual fish size (Wolfe et al., 1986):

$$f_{sm} = (\mathrm{FB_m}/\mathrm{FB_s})^{\mathrm{m}} \tag{22}$$

where m is the exponent of individual fish biomass for food consumption, and $\mathrm{FB_s}$ is an average fish size (kcal fish^{-1}) at which f_{sm} is normalized at 1 (Wolfe et al., 1986).

The effect of temperature on fish food consumption is calculated by biological growth vs. temperature function (O'Neill et al., 1972, cited by Nath and Lannan, 1993):

$$f_2(T) = V^x \exp[x(1 - \mathrm{V})] \tag{23a}$$

$$V = (T_{maxf} - T)/(T_{maxf} - T_{optf}) \tag{23b}$$

$$x = [S_1^2(1 + (1 + 40/S_2)^{0.5})^2]/400 \tag{23c}$$

$$S_1 = \ln Q_{10}(T_{maxf} - T_{optf}) \tag{23d}$$

$$S_2 = \ln Q_{10}(T_{maxf} - T_{optf} + 2) \tag{23e}$$

where T_{maxf} and T_{optf} are the maximum and optimum temperature for tilapia, V, x, S_1 and S_2 are auxiliary variables for calculating f_2(T), Q_{10} is a term to express the

relative increase in the rate of a biological activity with an increase in temperature of 10 °C.

Wolfe et al. (1986) used toxicity index to describe the interactive impacts of DO and unionized ammonia (UIA) on food consumption. Based on Wolfe et al. (1986) and Li et al. (1998), $f(\mathrm{WQ})$ can be expressed as:

$$\mathrm{TI} = k_{\mathrm{DOT}}(1 - f_{\mathrm{i}}(\mathrm{DO})) + k_{\mathrm{NHT}}\mathrm{INC}k_{\mathrm{NH}} \tag{24}$$

$$f(\mathrm{WQ}) = \exp(-k_{\mathrm{TI}}\mathrm{TI}^2) \tag{25}$$

where TI is toxicity index (dimensionless), k_{DOT} is a weighting factor for DO depletion toxicity to food consumption (dimensionless), k_{NHT} is a weighting factor for UIA toxicity to food consumption $((\mathrm{mgN\,l^{-1}})^{-1})$, k_{NH} is a fraction of UIA to INC (dimensionless), and k_{TI} is a coefficient of toxicity index on food consumption (dimensionless).

Fish appetite satiation is taken as a limit of supplementary feed consumption (Cuenco et al., 1985; Wolfe et al., 1986) and expressed as:

$$\mathrm{FAPP} = \mathrm{FAPP}_{\max}\mathrm{FB}f_{\mathrm{sm}}f(\mathrm{WQ}) \tag{26}$$

where FAPP is fish appetite (kcal $\mathrm{day^{-1}}$ $\mathrm{pond^{-1}}$) and $\mathrm{FAPP}_{\max}$ is the maximum FAPP ($\mathrm{day^{-1}}$).

Based on fish appetite, natural food consumption, supplementary feed availability, and food assimilation, the requirement for supplementary feed, actual consumption of supplementary feed and fish fecal waste can be calculated by following equations:

$$\mathrm{RSF} = \begin{cases} \mathrm{FAPP} - (\mathrm{AFC} + \mathrm{HFC}) & \text{if } (\mathrm{FAPP} > \mathrm{AFC} + \mathrm{HFC}) \\ 0 & \text{if } (\mathrm{FAPP} \leqslant \mathrm{AFC} + \mathrm{HFC}) \end{cases} \tag{27}$$

$$\mathrm{SFC} = \min(\mathrm{RSF},\ \mathrm{SFA}) \tag{28}$$

$$\mathrm{FW} = \mathrm{SFA} - \mathrm{SFC} + \mathrm{TFC} - \mathrm{FA} \tag{29}$$

where RSF is the requirement for supplementary feed (kcal $\mathrm{day^{-1}}$ $\mathrm{pond^{-1}}$), SFA is supplemenetary feed availability from supplemenrary feeding (kcal $\mathrm{day^{-1}}$ $\mathrm{pond^{-1}}$).

According to Bowen (1982), protein is the dietary component most important in limiting fish growth. Protein levels are taken as a food quality index and expressed as P:E ratio. The effect of P:E ratio on food assimilation can be calculated by:

$$f(\mathrm{FQ}) = \begin{cases} 1.0 & \text{if } \mathrm{PE} \geqslant \mathrm{PE}_{\mathrm{opt}} \\ \exp\{-k_{\mathrm{PE}}[(\mathrm{PEopt} - \mathrm{PE})/(\mathrm{PEopt} - \mathrm{PEmin})]^{0.85}\} & \text{if } \mathrm{PE}_{\min} < \mathrm{PE} \leqslant \mathrm{PE}_{\mathrm{opt}} \\ \exp(-k_{\mathrm{PE}}) & \text{if } \mathrm{PE} < \mathrm{PE}_{\min} \end{cases} \tag{30}$$

where PE is P:E ratio (g protein $\mathrm{kcal^{-1}}$), k_{PE} is a coefficient of PE on food assimilation ((g protein $\mathrm{kcal^{-1}})^{-2}$), $\mathrm{PE}_{\min}$ and $\mathrm{PE}_{\mathrm{opt}}$ are the minimum and optimal P:E ratio (g protein $\mathrm{kcal^{-1}}$) for tilapia growth.

P:E ratio of total consumed food by fish and the requirement of protein content from supplementary feed are calculated by:

$$PE = (AFCk_{p1} + HFCk_{p2} + SFCk_{p3})/TFC \quad (31)$$

$$R_{k_{p3}} = (PE_{opt}TFC - AFCk_{p1} - HFCk_{p2})/SFC \quad (32)$$

where k_{p3} is the P:E ratio of supplementary feed (g protein kcal^{-1}), and R_{kp3} is the required protein content of supplementary feed (g protein kcal^{-1}).

2.3.2.2. Catabolism. Catabolism can be identified into two categories: fasting catabolism and feeding catabolism (Ursin, 1967). Fasting catabolism is influenced by body weight, size (Ursin, 1967; Nath and Lannan, 1993), temperature and DO (Ross and Ross, 1983), whereas feeding catabolism is assumed as a fraction of consumed food (Ursin, 1967; Nath and Lannan, 1993). Hence, total catabolism can be calculated by:

$$FC = TFCk_{feed} + FBk_{fast}f_{sn}f_2(DO)f_3(T) \quad (33)$$

$$f_{sn} = (FB_m/FB_s)^n \quad (34)$$

where k_{fast} and k_{feed} are fasting and feeding catabolism coefficients (day^{-1}), f_{sn}, f_2(DO) and f_3(T) are functions (dimensionless) to describe effects of fish size, DO and temperature on fasting catabolism, and n is an exponent for individual fish fasting catabolism.

Ross and Ross (1983) reported that fish respiration rises linearly as temperature increases, and decreases sharply as DO concentration falls below a critical point. The following functions provide a good fit to observations by Ross and Ross (1983):

$$f_2(DO) = \begin{cases} \exp[-k_{DOf}(DO_{crit} - DOC)^2] & \text{if } DO < DO_{crit} \\ 1 & \text{if } DO \geqslant DO_{crit} \end{cases} \quad (35)$$

$$f_3(T) = c + dT \quad (36)$$

where K_{DOf} is a coefficient of DO on fasting catabolism ((mg DO l^{-1})$^{-2}$), DO_{crit} is the critical DO limit (mg DO l^{-1}) above which fasting catabolism is not affected by DO, c (dimensionless) and d ($^{\circ}$C^{-1}) are regressive parameters to describe the effect of water temperature on fasting catabolism.

2.3.3. Elementary nutrient sector

Inorganic nitrogen and phosphorus are considered as necessary ingredients of nearly all fishpond fertilization (Hepher, 1958; Boyd, 1990). Total dissolved inorganic nitrogen and phosphorus in water, and total nitrogen and phosphorus in sediment are set as four state variables. This simplification is based on following assumptions: (a) the growth rate of phytoplankton is regulated by total dissolved inorganic nitrogen and phosphorus concentrations in water (Wolfe et al., 1986); (b) two constituents of inorganic nitrogen: ammonia and nitrate, are equally likely to be assimilated by the phytoplankton present (Wolfe et al., 1986); and (c) total loss of nitrogen (ammonia diffusion to air and denitrification of nitrite) is assumed to be a fraction of total dissolved inorganic nitrogen amount. Based on previous work (Wolfe et al., 1986; Li et al., 1998), mass balance equations for nitrogen and phosphorus are expressed as:

$$\mathrm{dTIN/d}t = \mathrm{FC}k_{\mathrm{fn}} + \mathrm{AFR}k_{\mathrm{an}} + \mathrm{HFD}k_{\mathrm{hn}} + \mathrm{TNS}k_{\mathrm{sn}} + \mathrm{FT_N} - (\mathrm{AFG}k_{\mathrm{an}} - \mathrm{FIXN}) - \mathrm{TIN}k_{nl} \quad (37)$$

$$\mathrm{dTNS/d}t = \mathrm{HFS}k_{\mathrm{hn}} - \mathrm{TNS}k_{\mathrm{sn}} \quad (38)$$

$$\mathrm{dTIP/d}t = \mathrm{FC}k_{\mathrm{fp}} + \mathrm{AFR}k_{\mathrm{ap}} + \mathrm{HFD}k_{\mathrm{hp}} + \mathrm{TPS}k_{\mathrm{pr}}/d_{\mathrm{w}} + \mathrm{FT_P} - \mathrm{AFGk_{ap}} - \mathrm{TIPk_{ps}}/d_{\mathrm{w}} \quad (39)$$

$$\mathrm{dTPS/d}t = \mathrm{TIP}k_{\mathrm{ps}}/d_{\mathrm{w}} + \mathrm{HFS}k_{\mathrm{hp}} - \mathrm{TPS}k_{\mathrm{pr}}/d_{\mathrm{w}} \quad (40)$$

where TIN and TIP are total dissolved inorganic nitrogen (gN pond^{-1}) and phosphorus (gP pond^{-1}) in water column, TNS and TPS are total nitrogen (gN pond^{-1}) and phosphorus (gP pond^{-1}) in sediment, $\mathrm{FT_N}$ and $\mathrm{FT_P}$ are inorganic nitrogen (gN day^{-1} pond^{-1}) and phosphorus (gP day^{-1} pond^{-1}) from fertilization, FIXN is N-fixation rate by phytoplankton (gN day^{-1} pond^{-1}), k_{fn}, k_{an} and k_{hn} are nitrogen contents of fish tissue, phytoplankton and heterotrophic components (gN kcal^{-1}), k_{sn} is a release coefficient of nitrogen in sediment (day^{-1}), k_{nl} is a coefficient of inorganic nitrogen loss to air (day^{-1}), k_{fp}, k_{ap} and k_{hp} are phosphorus contents of fish tissue, phytoplankton and heterotrophic components (gP kcal^{-1}), k_{pr} is a release coefficient of phosphorus in sediment (cm day^{-1}), k_{ps} is a coefficient of inorganic phosphorus sedimentation to sediment (cm day^{-1}), and d_{w} is water depth (cm).

N-fixation rate is influenced by phytoplankton quantity and inorganic nitrogen concentration (Wirat, 1996). Based on Wirat (1996) and Li et al. (1998), it can be expressed as:

$$\mathrm{FIXN} = k_{\mathrm{n}}\mathrm{AF_e}\exp(-k_{\mathrm{nf}}\mathrm{INC}^2) \quad (41)$$

where k_{n} is N-fixation coefficient of phytoplankton (gN kcal^{-1} day^{-1}), and k_{nf} is an coefficient of INC on N-fixation ((mg l^{-1})$^{-2}$)

2.3.4. Dissolved oxygen sector

In a static water pond, DO is produced by photosynthesis and depleted by various biological activities: plankton and fish respiration, benthic respiration, and the decomposition of detritus (Boyd, 1990). The exchange of DO in water with air is another source of oxygen for adjusting DO concentration (Boyd, 1990). Based on previous work (Wolfe et al., 1986; Boyd, 1990; Li et al., 1998), DO dynamics can be expressed as:

$$\mathrm{d}Q_{\mathrm{DO}}/\mathrm{d}t = \mathrm{AFG}k_{\mathrm{ao}} \pm \mathrm{DO_{df}} - \mathrm{FC}k_{\mathrm{fo}} - \mathrm{AFR}k_{\mathrm{ao}} - \mathrm{HFD}k_{\mathrm{ho}} - \mathrm{TNS}k_{\mathrm{sn}}/k_{\mathrm{hn}}k_{\mathrm{sno}} \quad (42)$$

$$\mathrm{DO_{df}} = [\mathrm{DICO(DOC - DOS)}/(\mathrm{AWFT}d_{\mathrm{w}})V_{\mathrm{pond}}]/1000 \quad (43)$$

where Q_{DO} is DO quantity in pond water column (g DO pond^{-1}), k_{ao} is oxygenation rate per kcal energy synthesis and respiration by phytoplankton (g DO kcal^{-1}), k_{fo} and k_{ho} are DO deletion coefficient of fish catabolism and heterotrophic component decomposition (g DO kcal^{-1}), k_{sno} is a DO deletion coefficient of bottom organic decay (g DO kcal^{-1}) which is represented by TNS release, $\mathrm{DO_{df}}$ is oxygen exchange rate between air and water body

Table 1
Values of parameters used for model simulation

Parameter	Value	Reference
k_{p1}	0.14	Calculated from Cummins and Wuycheck (1971), Boyd (1990)
μ_{max}	1.6	Jorgensen et al. (1986), Li et al. (1998)
k_{m1}	0.6	Jorgensen et al. (1986), Li et al. (1998)
k_r	0.1	Jorgensen et al. (1986), Li et al. (1998)
h_N	0.2	Jorgensen et al. (1986)
h_P	0.02	Jorgensen et al. (1986)
k_s	0.14	Mitsch and Reeder (1991)
k_d	0.12	Anderson (1987)
h_a	0.51	Li et al. (1998)
h_h	0.05	Li et al. (1998)
a	0.000017	Calculated from Li et al. (1998)
b	0.000015	Calculated from Li et al. (1998)
k_{T1}	0.004	Estimated from Tamiya et al. (1964), Li et al. (1998)
k_{T2}	0.008	Estimated from Tamiya et al. (1964), Li et al. (1998)
k_{p2}	0.12	Calculated from Cummins and Wuycheck (1971), Boyd (1990)
k_{maxa}	0.75	Meyer-Burgdorff et al. (1989)
k_{feed}	0.31	Calculated from Nath and Lannan (1993)
k_{fast}	0.005	Nath and Lannan (1993)
n	−0.12	Wolfe et al. (1986)
m	−0.3	Estimated from Wolfe et al. (1986), Li et al. (1998)
FB_s	20	Calculated from Wolfe et al. (1986)
Q_{10}	2.37	Nath and Lannan (1993)
c	0.59	Estimated from Ross and Ross (1983), Li et al., 1998
d	0.027	Estimated from Ross and Ross (1983), Li et al. (1998)
DO_{crit}	1.0	Teichert-Coddington and Green (1993)
PE_{min}	0.025	Bowen (1982)
PE_{opt}	0.09	Bowen (1982)
k_{PE}	0.45	Estimated from Bowen (1982), Li et al. (1998)
k_n	0.01	Estimated from Wirat (1996), Li et al. (1998)
k_{nf}	0.47	Estimated from Wirat (1996), Li et al. (1998)
$FAPP_{max}$	0.17	Calculated from Wolfe et al. (1986)
k_{nl}	0.17	Estimated from Wolfe et al. (1986), Li et al. (1998)
k_{sn}	0.003	Calculated from Voinov and Akhremenkov (1990)
k_{ap}	0.001	Mitsch and Reeder (1991)
k_{pr}	0.06	Estimated from Mitsch and Reeder (1991), Li et al. (1998)
k_{ps}	28	Estimated from Wahby (1974), Li et al. (1998)
DICO	2	Wolfe et al. (1986)
AWFT	0.018	Estimated from Wolfe et al. (1986), Li et al. (1998)
k_{ao}, k_{ho}, k_{fo}, k_{sno}	0.28	Calculated from Hall and Moll (1975)
k_{hp}	0.001	Li et al. (1998)
k_{DOT}	4.0	Wolfe et al. (1986)
k_{NHT}	4.0	Wolfe et al. (1986)
k_{DOf}	2.5	Estimated from Ross and Ross (1983), Li et al. (1998)
k_{fn}	0.017	Calculated from Shrestha (1994)
k_{fp}	0.002	Li et al. (1998)
k_{NH}	0.365	Estimated from Wolfe et al. (1986), Li and Yakupitiyage (2000)
s	21.08	Yi (1998)
k_{DO}	0.14	Estimated from Wolfe et al. (1986), Li et al. (1998)
k_{TI}	0.012	Estimated from Wolfe et al. (1986), Li et al. (1998)

(g DO day^{-1} $pond^{-1}$), DICO is a diffusion coefficient (cm^2 day^{-1}), DOS is DO saturation in water (mg DO l^{-1}), V_{pond} is pond water volume (l $pond^{-1}$), AWFT is air/water interface film thickness (cm), and the value of 1000 is the converting coefficient of unit mg to g.

2.4. Model implementation and calibration

STELLA II (High Performance Systems and Inc., 1997) was used for model development and implementation. This simulation tool provides a user-friendly graphic interface. Under STELLA environment, the modeler can use the basic building blocks to define the objects and the functional relationships. The basic graphical building blocks include stocks, flows, converters and connectors. Stocks are used to represent storage, which can be changed with flows. Flows are defined and regulated by converters. Converters are used to store algebraic relationships, define external input to the model and hold values for constants. Connectors serve to indicate the cause-effect relations among the model elements (stocks, flows and converters). The model is represented by differential and difference equations that can be solved with either Euler's or Runge-Kutta method.

The calibration process of the model includes the determination of model parameters and initial values for all state variables. Parameters are selected from a range of feasible values, then tested in the model, and adjusted until satisfactory agreement between predicted and observed variables is obtained. Calibration of the nutrient dynamic model for fertilized aquaculture ponds was performed by Li et al. (1998). The current study further calibrates the model for supplementary feeding aquaculture ponds.

Based on laboratory experiments with Nile tilapia, T_{optf} and T_{maxf} appear to be about 30 °C (Caulton, 1982) and 41 °C (Denzer, 1967), respectively. Optimal temperature for phytoplankton growth is about 30 °C (Tamiya et al., 1964). Values of other parameters derived or estimated from the literature are shown in Table 1. k_{an} and k_{hn} are calculated by k_{p1} and k_{p2} divided by a N to protein coefficient (6.25 g protein/gN). Other parameters were collected from field experiments.

2.5. Sensitivity analysis and assessment of goodness-of-fit

Both sensitivity analysis and assessment of goodness-of-fit are used to validate the model. Sensitivity analysis, performed by defining a base case and shifting one parameter with a plausible variation while keeping all other parameter values constant, tests the response of the model behavior to variations in selected parameters. Cuenco et al. (1985) suggested varying the parameters by about $\pm$ 10% of baseline value for sensitivity analysis. The responses of mean fish weight, autotrophic and heterotrophic food nutrient concentrations to this variation are used for sensitivity evaluation in this study.

The reproduction of observed records is the most important test for evaluating model performance. The goodness-of-fit of model results can be assessed by graphical and statistical tests. Graphical comparisons examine whether or not the

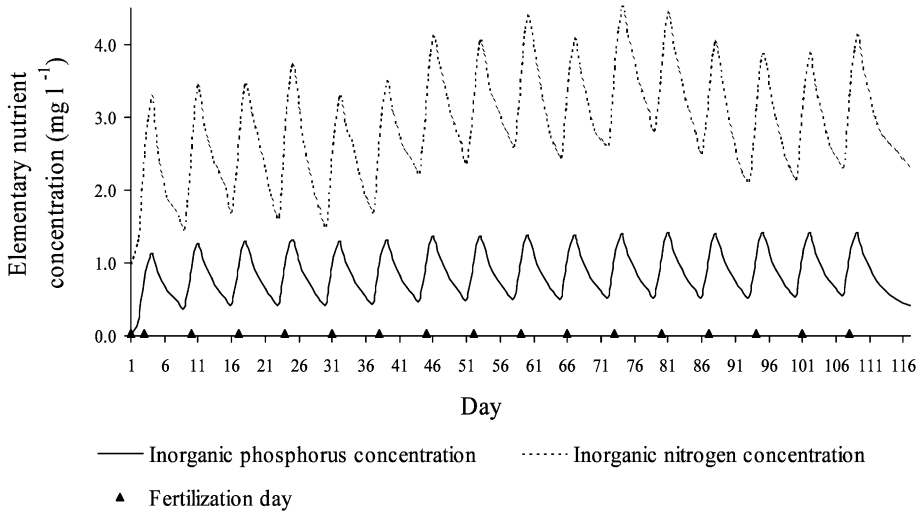

Fig. 2. Simulated elementary nutrient concentration in the ES treatment.

model reproduces dynamic patterns of food nutrients in an aquaculture pond, while statistical tests determine whether or not there exists a significant difference in system behaviors from model simulation and field observation. One sample *t*-tests and Pearson correlation are used to assess the goodness-of-fit between observed and simulated values (Rose and Swartzman, 1988). One sample *t*-tests are used to test for significant differences in average values from observation and simulation, while Pearson correlation between observed and simulated values at a particular sampling point is used to assess the similarity of dynamics and trends over time.

2.6. Experimental description

The experiment used for model simulation was conducted from 28th November 1994 to 24th March 1995 at the Asian Institute of Technology (AIT) research facility to determine limiting nutritional factors in fertilized tilapia ponds with supplementary feeding. Ponds were fertilized once a week using urea and triple super phosphate at a rate of 4 kg N and 2 kgP ha^{-1} day^{-1}. Two supplementary feeding treatments were used: (1) fertilization + energy supplement (ES) and (2) fertilization + energy + protein + vitamin supplement (EPVS). The ES treatment, composed by 98% cassava starch and 2% corn oil, contains 92.6% dry matter, 0.25% ash and 0.61% crude protein. The EPVS treatment, formulated using 4% fishmeal, 50% soybean meal, 39% cassava starch, 2% corn oil, 3% di-calcium phosphate and 2% vitamin premix, contains 90.76% dry matter, 7.78% ash and 24.39% crude protein. On the dry matter basis, food nutrient contents in terms of energy and protein are 3700 kcal kg^{-1} and 0.003 g protein $kcal^{-1}$ in the ES treatment, and 3950 kcal kg^{-1} and 0.062 g protein $kcal^{-1}$ in the EPVS treatment. The feed mix was pelleted using a mincer, then dried and stored in a freezer until use. Experimental treatments were arranged

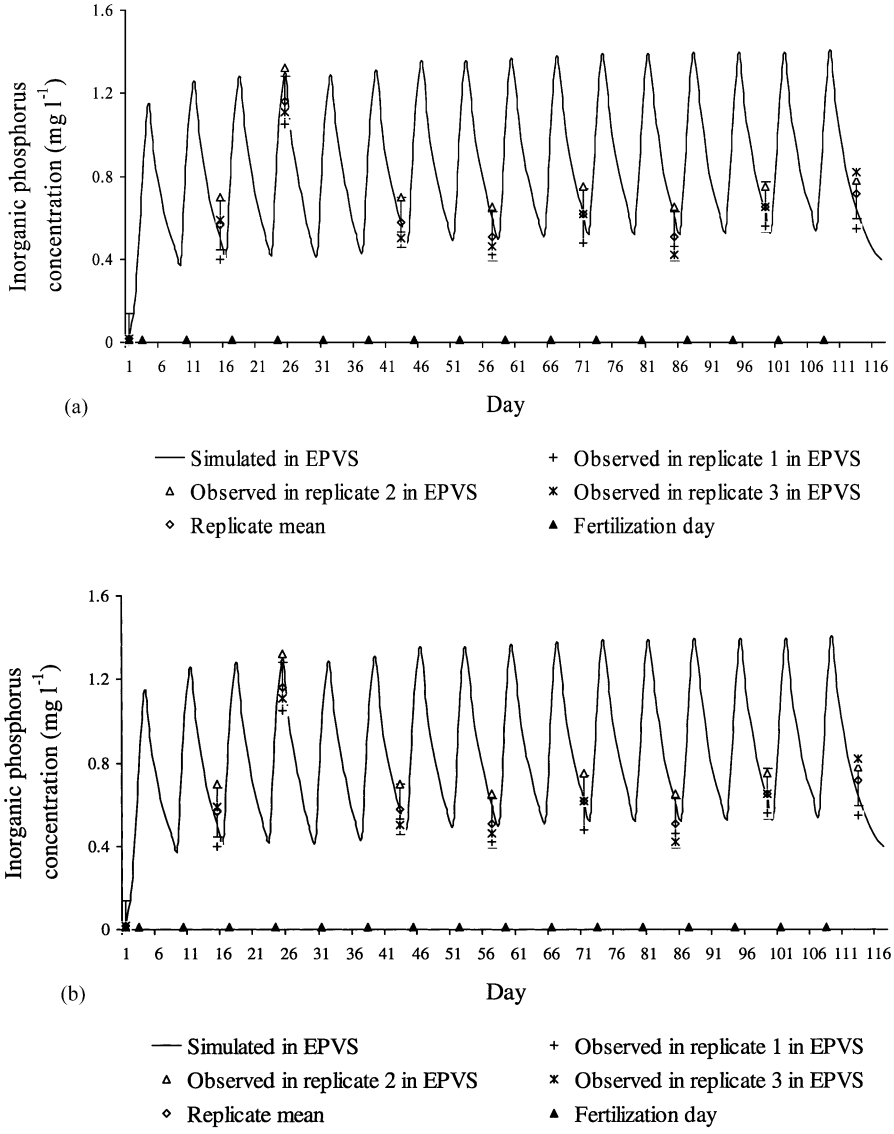

Fig. 3. Simulated and observed inorganic phosphorus concentration in two treatments. (a) Simulated vs. observed values in the ES treatment. (b) Simulated vs. observed values in the EPVS treatment.

in a completely randomized design with three replicates. Nile Tilapias weighing approximate 25 g were stocked in 200 m^2 ponds on 2nd December 1994 at a rate of 4 fish m^{-2}. Fish were fed once a day at a rate of 3% of fish body weight, but maximum feed load was limited to 100 kg dry matter ha^{-1} day^{-1} in order to avoid water quality problems. Fish body weight at the sampling day was used to calculate the feeding rate applicable at the next sampling time. Water quality parameters were

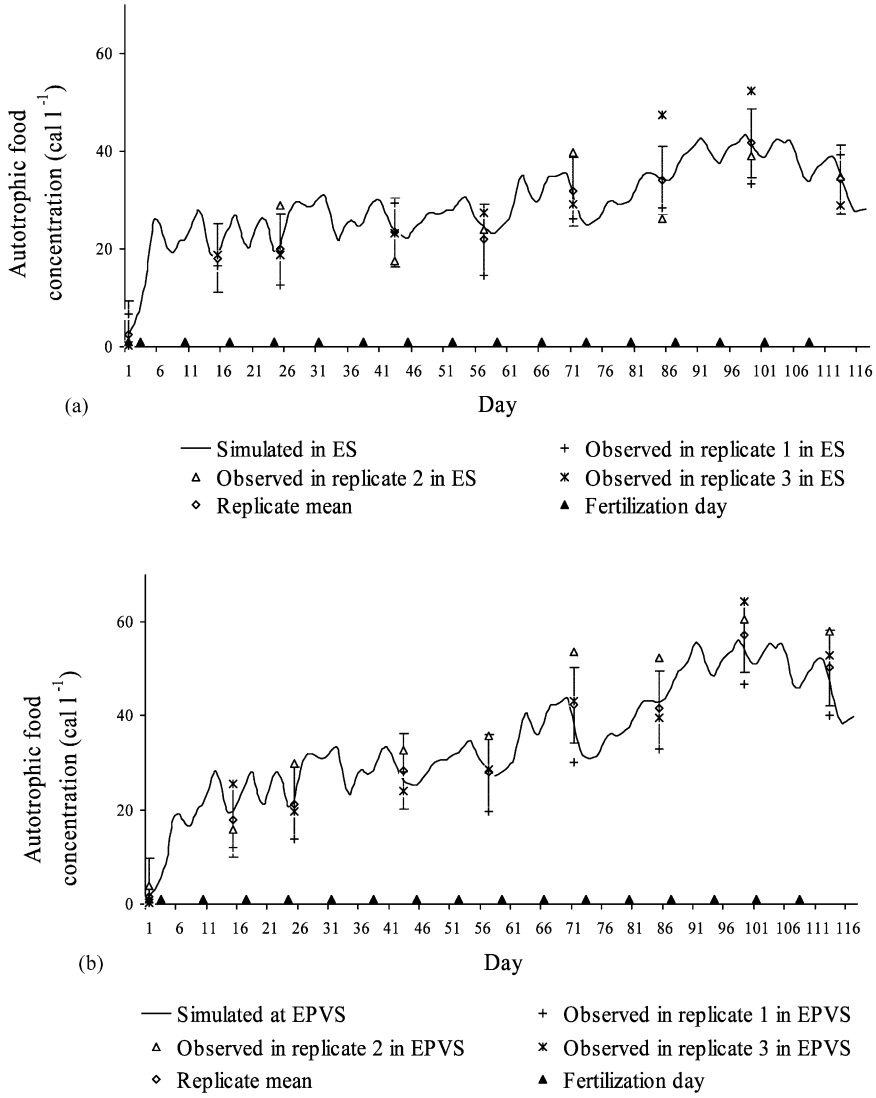

Fig. 4. Simulated and observed autotrophic food concentration in two treatments. (a) Simulated vs. observed values in the ES treatment. (b) Simulated vs. observed values in the EPVS treatment.

measured every 2 weeks and fish were sampled every 2 weeks. Initial values of water quality parameters were measured at 28th November 1994. AF_e was estimated by measured Chlorophyll-a concentrations, while HF_e was estimated by volatile suspended solid minus AF_e. Fish mortality coefficient was 0.002 day^{-1} during experimental period. T and I_0 were recorded by the AIT meteorological station. The average solar radiation during experimental period was 6.547×10^6 cal m^{-2} day^{-1} and was used as a reference solar radiation (I_r). Initial nitrogen and phosphorus in

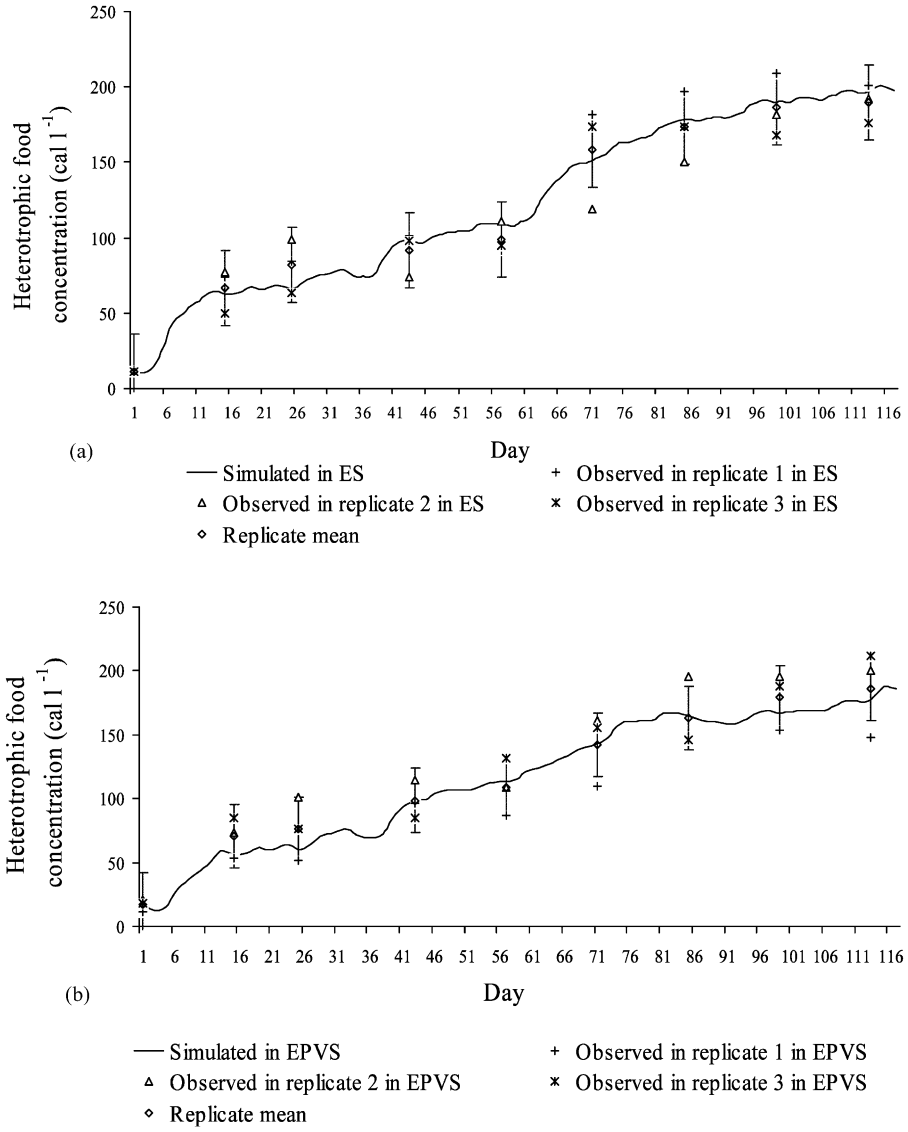

Fig. 5. Simulated and observed heterotrophic food concentration in two treatments. (a) Simulated vs. observed values in the ES treatment. (b) Simulated vs. observed values in the EPVS treatment.

sediment were estimated from Boyd (1990), Shrestha (1994), Li et al. (1998). For the purpose of comparison, simulated values for TIN, TIP, AF_e, HF_e, and Q_{DO} in the ponds were converted into concentrations by dividing pond water volume, while FB into mean fish weight by dividing fish number and a converting coefficient of energy to dry weight of tilapia, then multiplying a wet weight to dry weight ratio.

3. Results of simulation run of the model

The input data set for the model use includes initial values of state variables, meteorological variables (solar radiation and temperature) and management strategies (fish stocking, fertilization and supplementary feeding regimes). Autotrophic food concentration, heterotrophic food concentration, INC, IPC, DOC and mean fish weight are chosen as indicators of food nutrient dynamic behavior.

3.1. Elementary nutrient concentrations

Fig. 2 shows responses of both inorganic nitrogen and phosphorus concentrations to the ES treatment. Results indicate that simulated inorganic nitrogen and phosphorus concentrations are strongly influenced by fertilization regimes. Patterns from model simulation are similar to those reported by Boyd and Musig (1981) i.e. inorganic nitrogen and phosphorus concentrations increase with the addition of inorganic fertilizers, and then decline due to both the assimilation by phytoplankton growth and the loss to the environment. Since inorganic nitrogen and phosphorus were applied weekly, the quick depletion of inorganic nitrogen and phosphorus can only be compensated with a time lag from the next periodical application of fertilizers.

The pattern and numerical change of simulated inorganic nitrogen and phosphorus concentrations are same in the two treatments due to same fertilization regimes. A visual examination of inorganic phosphorus concentration from simulation and observation at sampling points is shown in Fig. 3. Results show that values from model simulation range within observed values in the two treatments and supplementary feed type has no influence on elementary nutrient concentration.

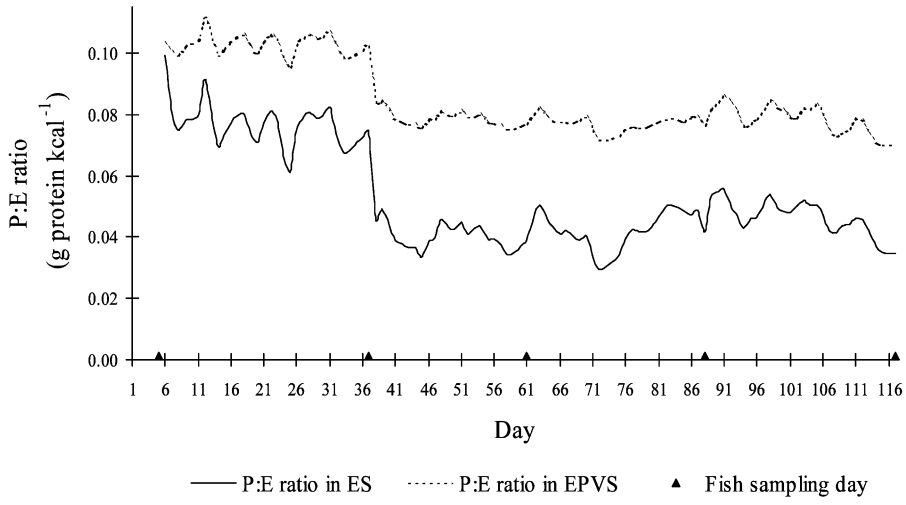

Fig. 6. Simulated P:E ratio in consumed food by fish in two treatments.

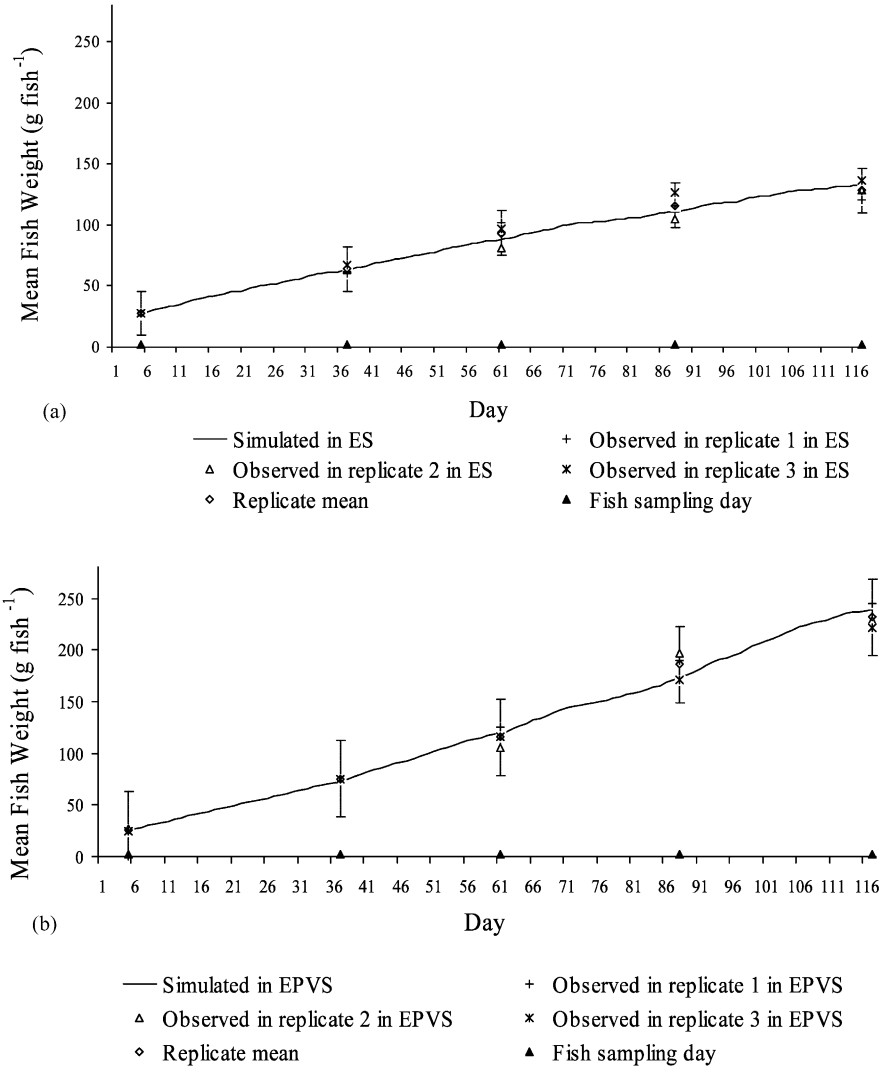

Fig. 7. Simulated and observed mean fish weight in two treatments. (a) Simulated vs. observed values in the ES treatment. (b) Simulated vs. observed values in the EPVS treatment.

3.2. Food nutrient concentrations

Simulated autotrophic food nutrient dynamics in the two treatments is shown in Fig. 4. At the initial stage without fish stocking, although autotrophic food nutrient concentration is low in a natural state, autotrophic food nutrients rapidly increase due to an increase in inorganic nutrient concentrations resulting from chemical fertilization. After fish stocking, fish cropping stunts phytoplankton growth and affects the fluctuation in autotrophic food nutrients in association with the

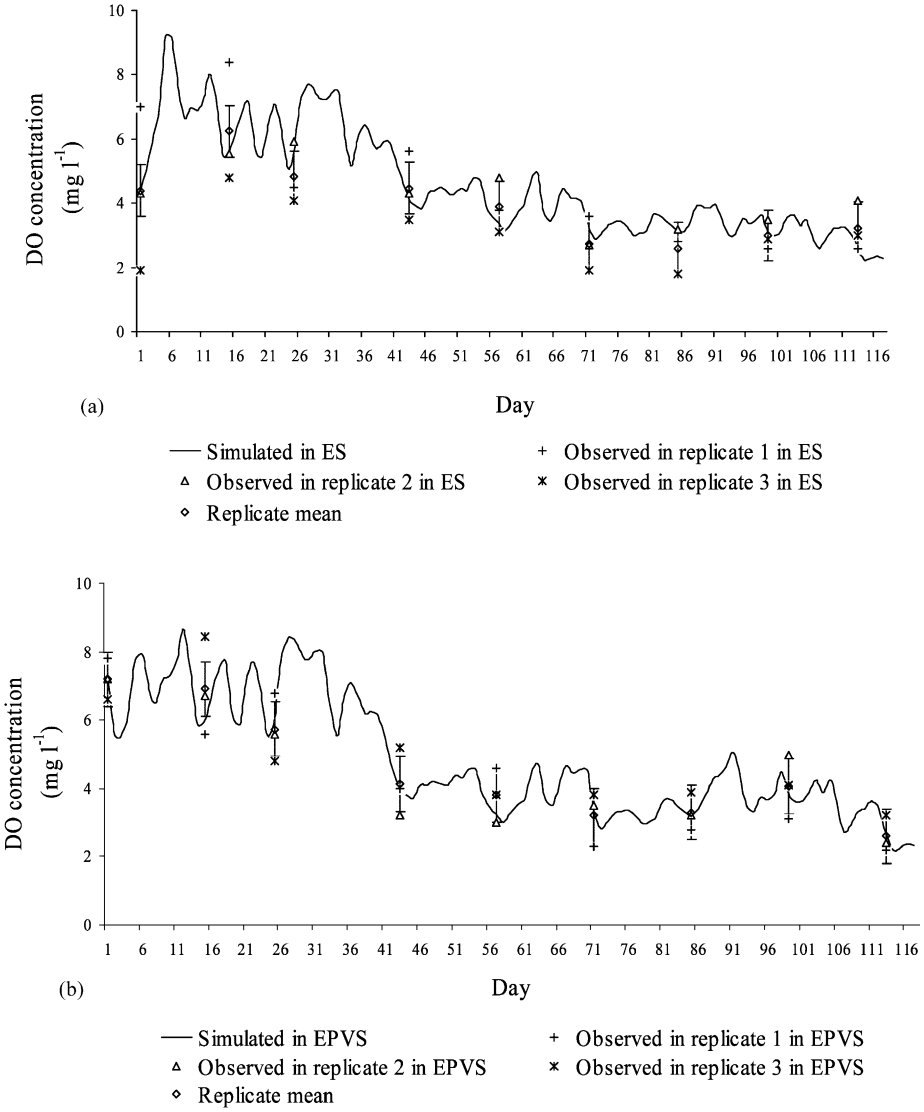

Fig. 8. Simulated and observed DO concentration in two treatments. (a) Simulated vs. observed values in the ES treatment. (b) Simulated vs. observed values in the EPVS treatment.

fertilization regime. Heterotrophic food nutrient concentration rises at the initial stage due to the increases in both autotrophic food quantity and fish fecal waste from supplementary feeding, but it grows toward a plateau due to a fixed supplementary feeding rate between two fish sampling points (Fig. 5). Further increases in supplementary feed after fish sampling resume heterotrophic food nutrient accumulation.

The two supplementary feeding treatments do not change behavioral patterns of autotrophic and heterotrophic food nutrients (Figs. 4 and 5), but they do influence their numerical behavior due to different feed quality. A higher protein content in supplementary feed improves food assimilation. This increases fish biomass and reduces feed waste. More fish biomass lowers autotrophic food availability and consumption, while less feed waste improves light penetration. As a result, the EPVS treatment increases autotrophic food nutrient quantity (Fig. 4b). Average autotrophic food nutrient concentration from simulation in the EPVS treatment is 18.45% higher than that in the ES treatment. The two treatments do not produce a significant difference in heterotrophic food nutrient concentrations before the third fish sampling point (the 88th day) because the sum of heterotrophic food sources from phytoplankton mortality and feed waste is quantitatively comparable in both treatments.

The comparison of simulation data with observed data at sampling points in Fig. 4 and Fig. 5 indicates that predicted autotrophic and heterotrophic food nutrient concentrations are consistent with observed trend and well within the range of observed data from three replicates. However, a large range of observed autotrophic food nutrient concentrations among replicate ponds at a few sampling points indicates that there are some uncertain factors which influence autotrophic and heterotrophic food nutrient dynamics, such as suspended non-organic particulate, water inflow and wind. They should be taken into consideration in future studies.

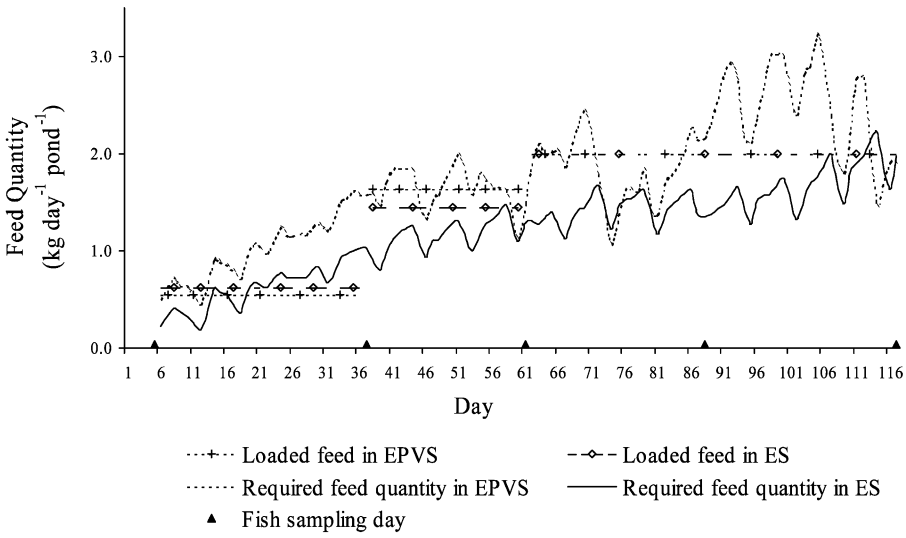

Fig. 9. Comparison of loaded and required feed quantity in two treatments.

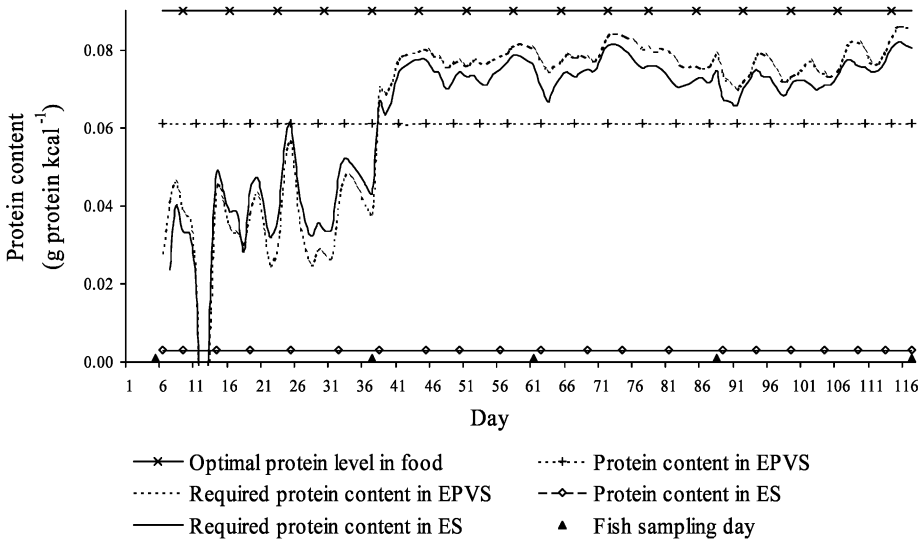

Fig. 10. Comparison of applied and required protein content in two treatments.

3.3. Food quality and fish growth

The quality of food-consumed by fish varies with the combination of natural food consumption and supplementary feed consumption. Simulated P:E ratio of food-consumed by fish in both treatments is shown in Fig. 6. At the beginning stage, although supplementary feed contains low protein in the ES treatment, consumed natural food with high protein content partially compensates protein deficit in supplementary feed at this stage. This results in a relatively high P:E ratio in food-consumed by fish in the ES treatment. Fish growth does not have significant difference between the two treatments in this stage (Fig. 7). After the first fish sampling, the rate of supplementary feed loading increases. Fish consume more supplementary feed, which significantly reduces P:E ratio of food-consumed. P:E ratio of food-consumed by fish is about 0.08 g protein $kcal^{-1}$ in the EPVS treatment and about 0.04 g protein $kcal^{-1}$ in the ES treatment. Protein becomes a limiting nutrient factor for fish growth in the ES treatment. Results show that, although the rate of supplementary feeding is the same, the EPVS treatment produces a higher mean fish weight with 239.49 g $fish^{-1}$ from simulation than that with 132.6 g $fish^{-1}$ from the ES treatment. The comparison of mean fish weight from simulation and observation indicates that simulated results are consistent with data from field observation and match the observed mean fish weight (Fig. 7).

3.4. Dissolved oxygen concentrations

Simulated DO concentration in Fig. 8 indicates that dynamic behavior of DO concentration in the two treatments is identical. At the initial stage, DO concentra-

Table 2
Effect of changing selected parameters on fish weight and food nutrient concentrations

Parameter	Change (%)	Mean fish weight Changed (%)	Autotrophic food concentration Changed (%)	Heterotrophic food concentration Changed (%)
k_{p1}	−10	−6.09	−2.14	3.35
	+10	5.68	2.19	−3.12
μ_{max}	−10	−27.89	−31.57	−5.59
	+10	20.89	27.73	6.18
k_{m1}	−10	13.96	28.83	2.20
	+10	−12.39	−27.56	−2.81
k_r	−10	1.83	3.28	0.63
	+10	−1.83	−3.75	−0.62
a	−10	−9.16	−15.00	−2.87
	+10	8.37	15.64	2.82
k_s	−10	−3.54	−6.74	6.56
	+10	2.63	6.25	−5.94
k_d	−10	−1.22	−3.93	1.28
	+10	1.24	4.43	−1.22
k_{hn}	−10	−2.00	−2.34	−0.66
	+10	1.78	2.30	0.60
k_{la}	−10	−0.80	0.75	2.24
	+10	0.34	−0.88	−2.11
k_{maxa}	−10	−24.92	−15.5	3.06
	+10	26.09	13.63	−3.97
k_{fast}	−10	2.56	0.92	0.76
	+10	−2.49	−1.11	−0.72
k_{feed}	−10	8.08	2.66	−0.78
	+10	−8.43	−3.86	0.59
$FAPP_{max}$	−10	−3.65	−2.09	0.39
	+10	1.38	1.02	−0.86
m	−10	−2.83	−0.67	2.15
	+10	2.22	0.45	−2.31
k_{se}	−10	−0.76	3.78	−8.60
	+10	−4.20	−7.89	8.85
k_{p3}	−10	−9.54	−6.09	1.46
	+10	12.63	8.40	−2.33

tion increases with phytoplankton growth. After fish stocking and supplementary feed adding, DO concentration fluctuates due to a comprehensive effect of oxygenation from photosynthesis and DO depletions from fish respiration and heterotrophic decomposition. Since DO depletions are small in this stage of the comparison with oxygenation, DO concentration stays at a high level. After the first fish sampling at the 37th day, supplementary feeding rate increases, which produces more feed wastes. As a result, more DO is depleted by heterotrophic decomposition, and an obvious decline in DO concentration after the 37th day can be observed. In the late stage, DO concentration appears at a low level because of its considerable depletion from fish respiration and heterotrophic decomposition. DO concentration

Table 3
Results of one sample t-tests and correlation coefficients

Treatments	Variables	P at one tail	Correlation coefficient
ES	Mean fish weight (g fish^{-1})[a]	0.49^{ns}	0.983**
	Autotrophic food concentration (cal l^{-1})	0.44^{ns}	0.997**
	Heterotrophic food concentration (cal l^{-1})	0.45^{ns}	0.991**
	Inorganic phosphorus concentration (mg l^{-1})	0.44^{ns}	0.961**
	Dissolved oxygen (mg l^{-1})	0.43^{ns}	0.882***
EPVS	Mean fish weight (g fish^{-1})[a]	0.47^{ns}	0.996**
	Autotrophic food concentration (cal l^{-1})	0.46^{ns}	0.986**
	Heterotrophic food concentration (cal l^{-1})	0.47^{ns}	0.992**
	Inorganic phosphorus concentration (mg l^{-1})	0.44^{ns}	0.925**
	Dissolved oxygen (mg l^{-1})	0.49^{ns}	0.839***

ns: not significant.
[a] Since fish was sampled every four weeks, interpolated values between two fish sampling points were used for statistical analysis.
** Significant at $P = 0.001$.
*** Significant at $P = 0.01$.

in the EPVS treatment is higher than that in the ES treatment in most time of simulation period. This trend is consistent with observed data even though there is a wide range of observed DO concentrations in the two treatments (Fig. 8).

3.5. Requirement for supplementary feed

The quantity of supplementary feed required by fish is determined by the difference between fish appetite and natural food consumption. Simulated results in Fig. 9 indicate that the quantity of supplementary feed required increases as fish grow, but it fluctuates due to periodical application of chemical fertilizers which produce toxic UIA. Since fish grow faster in the EPVS treatment, more supplementary feed is required in the EPVS treatment.

In practice, the determination of the quantity of supplementary feed to be applied during field experimentation was based on fish sampling data. A fixed feeding rate was applied between two sampling points. Since fish sampling points are limited while the actual requirement for supplementary feed changes with fish appetite and natural food consumption, there exists a significant difference between the field loading rate and the actual requirement for supplementary feed (Fig. 9). Supplementary feed in the ES treatment is overloaded in most simulation time, but feed overloading in the EPVS treatment only appears in a few time periods due to the problem of poor water quality which is caused by low DO and high UIA. Simulated results show that, when only energy supplements are used, a supplementary feeding rate with less than 3% of fish body weight is able to meet fish growth requirement, but when energy supplements with a high protein content are loaded, a higher supplementary feeding rate can be applied.

The required protein content in supplementary feed is calculated on the basis of the assumption that optimal protein content for fish growth is about 0.09 g protein $kcal^{-1}$ (Bowen, 1982). Fig. 10 compares the required protein content with actual content applied in supplementary feed. Before the first fish sampling, protein content with 0.03–0.05 g protein $kcal^{-1}$ in supplementary feed is enough for tilapia growth because protein-rich natural food consumed by fish is able to compensate for the deficiency of protein in supplementary feed. After the first fish sampling, the quantity of loaded supplementary feed increases and fish consume more supplementary feed. Protein deficit in supplementary feed cannot be compensated by natural food. Protein content with 0.07–0.08 g protein $kcal^{-1}$ in supplementary feed is required for optimal fish growth

3.6. Sensitivity analysis and assessment of goodness-of-fit

The EPVS treatment is taken as a base case for sensitivity analysis. Base values of autotrophic food nutrient concentration, heterotrophic food nutrient concentration, INC, IPC, and DOC at initial day were 1.63 cal l^{-1}, 16.86 cal l^{-1}, 1.0 mgN l^{-1}, 0.01 mg P l^{-1}, and 7.2 mg DO l^{-1}, respectively. Base mean fish weight at stocking day with 40.7 kcal $fish^{-1}$ (26.04 g $fish^{-1}$) was used. Mean fish weight, autotrophic and heterotrophic food concentrations on the harvesting day were applied for sensitivity comparison. As shown in Table 2, all selected-parameter variations have small impacts on heterotrophic food nutrient (between −8.60 and 8.85%), but their influence on autotrophic food nutrient and mean fish weight varies. Variations in values of parameters related to phytoplankton growth and fish feeding practice have significant influence on autotrophic food nutrient and mean fish weight. Autotrophic food nutrient and mean fish weight are most sensitive to the variations in μ_{max}, k_{m1}, a and k_{maxa}. The response of autotrophic food nutrient concentration to variations in those four parameters varies from −31.57 to 28.83%, while mean fish weight from −27.89 to 26.09%. The influence of variations in protein content of supplementary feed on mean fish weight is from −9.54 to 12.63%. The results are consistent with the assumptions established by the model. A more detailed sensitivity analysis of the parameters influencing phytoplankton growth and the fish feeding mechanism can help to understand food nutrient dynamics and fish growth in an aquaculture pond.

Graphical comparison in Figs. 3–5, 7 and 8 shows that simulated values are properly staying within the bounds of field measurement. The simulated values are close to the mean values from observations at sampling points. However, a wide range of observed values among three replicates may question whether the model can qualitatively replicate the observed nutrient dynamics and fish growth behavior. More rigorous statistical assessment for goodness-of-fit of model results with observed values at sampling points is made and summarized in Table 3. Statistical comparison is based on observed mean values and simulated data over time. Results indicate that there is not significant difference in mean values from simulation and observation. P at one tail ranges from 0.43 to 0.49. Positive correlation coefficients are very significant (from 0.839 to 0.997). High positive correlation coefficients

reveal that the error is unsystematic and random, and that the model can catch the essential food nutrient dynamics in an aquaculture pond.

In summary, the simulation of the model for an on-station supplementary feeding trial shows that the simulation values stay within the bounds of measurement error, and fit the measured data quite well. The model is able to capture the most important food nutrient dynamics and quantitatively reproduces the nutrient dynamics and fish growth behavior.

4. Discussion and conclusions

Supplies of food nutrients in fish culture ponds are directly dependent upon natural food productivity and supplementary feeding. Decisions regarding fertilization and supplementary feeding are especially important because they are major determinants of both food nutrient sources for fish growth and major causes of water quality problems. In order to explain food nutrient dynamics in fertilized tilapia ponds and to determine requirements for supplementary food nutrients for tilapia growth, modeling provides an effective methodology for organizing and integrating existing information available on food nutrient production in a fertilized pond. The development and simulation run of the nutrient dynamics model have been useful in identifying critical research needs to expand and complement our knowledge of food nutrient dynamics in aquaculture ponds.

Previous models of pond dynamics have incorporated natural food production components (Piedrahita, 1984; Liepmann and Stephanopoulos, 1985; Wolfe et al., 1986; Nath and Lannan, 1993), and the effects of feed quality on fish growth (Cacho et al., 1990; Masser et al., 1991), but have not explicitly represented food nutrient dynamics and requirement by fish in a fertilized fish culture pond. This study focuses on the dynamic process of food nutrient production and shows that interactions between elementary nutrient sector and food nutrient sector, along with fish growth sector, have an effect on food nutrient production in an aquaculture pond. The study demonstrates that the model can be used to identify limiting food nutrients and their requirement for fish growth in a fertilized pond. Simulation runs of the model indicates that supplementary feeding is able to compensate for food nutrient limitations and permit further fish growth, and that a higher protein content in supplementary feed can significantly improve fish growth.

The comparison of results from simulation and observation shows the model behavior has a good correspondence to observed behavior, and the simulation values fit the observed data quite sufficiently. The model is able to capture the trends of elementary nutrient and food nutrient dynamics. The model can be effectively used to design and manage semi-intensive aquaculture ponds for improving food nutrient production and increasing fish yield. Before the simulation run of the model, the state variables must be initialized, and the exogenous factor variables, including climatic parameters and management strategies, must be determined and fed into the model. Other parameters may be changed according to application conditions.

Changing the values of the exogenous variables reflecting management strategies can be used to test the effect of different management decisions on nutrient dynamics.

The food nutrient model focuses on long-run growth and explicitly excludes the diel cycle and stratification as well as other spatial variations. However, although dynamic behavior of food nutrient production and fish growth generated indigenously are endogenous to the model, there are exogenous variables that may significantly influence pond ecosystem behavior. In order to increase the ability of the model to replicate historical data, it is recommended to take diel change, stratification of food nutrient dynamics and more exogenous variables, such as rain, water inflow, and wind into the model in the further study.

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