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Conceptualization and validation of a dynamic model for the simulation of nitrogen transformations and fluxes in fish ponds

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Abstract

Nitrogen is a key element in aquatic environments and an important pond management variable. In aquaculture systems, nitrogen accumulation eventually leads to a deterioration of the system. The interactions between various *N*-species are complex and difficult to integrate. Modelling can improve our ability to evaluate this complex system. This paper integrates existing knowledge about nitrogen transformations in fish ponds into a model that calculates the amount of various *N*-compounds in the water column and in the sediment. The model is also used to gain insight into the relative importance of transformation processes between the various *N*-compounds. The model was divided into three modules: fish, phytoplankton and sediment-water. The fish module is based on physiological and bio-energetic principles. The phytoplankton dynamics module is based on physico-chemical principles of alga growth. The water–sediment module is based on the bacterial transformations and chemical fluxes of *N*-species across the water–sediment interface. Relationships and parameters were taken from the literature, except for a few parameters that were estimated by fitting model predictions to observed data. The model was implemented in Turbo Pascal (7.0) using a fixed time step of 1 h and it was calibrated using a set of data from an earthen fish pond stocked with *Colossoma macropomum*. The validation was performed using data from earthen ponds stocked with *Oreochromis niloticus*. The difference between the calibrated and validated model was related to the fish species. All concentrations of the various *N*-species present were simulated well, except the *N* retained in organic matter in the sediment (average relative error -0.34). Sensitivity analysis revealed that the concentrations of inorganic-*N* compounds, both in the water column and in the sediment, are more affected by changes in specific parameters included in the fish and phytoplankton modules than other forms of nitrogen in the pond. The model works well, except for organic matter accumulation in the sediment. Further research should concentrate on a better understanding of the bottom organic matter dynamics, to make the model a more comprehensive predictive tool.

Keywords: Fish culture; Nitrogen dynamics; Modelling; Fish pond; Simulation

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1. Introduction

Nitrogen is a key element in aquatic environments and aquaculture systems. Nitrogen input, in the form of feeds/fertilizers, is needed to enhance aquatic production of cultivated animals and it is considered an important pond management variable. Nitrogen input in aquaculture systems also increases the potential of pollution to the surrounding environment. Although the basic processes of the nitrogen cycle are known, the ways in which they are linked together is poorly understood and have to be investigated further.

In ponds, nitrogen is present in different forms. Wasted feed, dead plankton and feces are mineralized and the resulting different dissolved nitrogen species can be re-used by autotrophic organisms forming again complex molecules (Diab and Shilo, 1986). Oxygen availability, water temperature, pH, light penetration and bacterial species composition in the system characterize these transformations (Painter, 1970; Otsuki and Hanya, 1972; Stanford et al., 1975; Andersen, 1977).

The metabolic end products of feeds, as well as the microbial decomposition of organic matter in the surrounding water, lead to increased concentrations of free ammonia and nitrite, both toxic to fish even at low concentrations (Meade, 1985).

Control of nitrogen transformation processes in the pond and optimal feed utilization in aquaculture systems are needed. A better understanding of the fluxes and transformations of nitrogen in aquacultural production systems is needed and the development of appropriate simulation models of pond aquaculture is recommended (Lannan et al., 1983). Models of varying degrees of complexity were used for the research of nitrogen compound transformations in aquaculture and mathematical approximations of these processes can be found in the literature. General principles of computer modeling of aquaculture systems have been reviewed by Bolte et al. (1986), Piedrahita (1988) and van Dam (1990).

Numerous studies concentrated on N-transformation in aquaculture and processes of the N-cycle were described mathematically. Paulson (1980) presented different models of ammonia excretion for trout; Lightfoot et al. (1993) presented a steady-state nitrogen model for a wetland rice field ecosystem with and without fish; Piedrahita et al. (1984) and Piedrahita (1991) simulated dissolved inorganic nitrogen concentrations in ponds; and Kochba et al. (1994) developed a model to evaluate the effect of water exchange rate on dissolved inorganic nitrogen concentration in intensively aerated fish ponds. Hargreaves (1997) developed a model for ammonium dynamics in channel catfish ponds. Lorenzen et al. (1997) used a mathematical model to investigate the impact of farming intensity and water management on nitrogen dynamics; Montoya et al. (1999) simulated nitrogen dynamics in intensive shrimp culture systems, focusing mainly on shrimp growth in systems with no primary productivity; Nielsen et al. (1999) simulated nitrogen dynamics in aquacultural farming systems with combined growth and harvest of rice and crayfish; Jamu (1999) also described the dynamics of nitrogen in integrated aquaculture–agriculture systems; and Verdegem et al. (2000) proposed a bio-energetic model of growth and waste production of tilapia in recirculation systems.

This paper integrates existing knowledge about nitrogen transformations in fish ponds into a predictive model for tilapia (*Oreochromis niloticus*) and tambaquí (*Colossoma macropomum*) ponds in the tropics, a model that calculates every hour the quantities present of different N-compounds in the water column and in the sediment of ponds. After calibration and validation, the model can be used (1) to evaluate the sensitivity of the N-cycle to changes in the individual processes; (2) to identify the principal sinks for N in the system; and (3) to identify those processes that need further study.

2. Model description

2.1. General model description

The model contains three modules: the fish module, the phytoplankton module and the sediment-water module. The fish module is based on the model proposed by Machiels and Henken

(1986, 1987) and later adjusted for tilapia by van Dam and Penning de Vries (1995). The model developed by Jiménez-Montealegre et al. (1995) was used as a basis for the phytoplankton module. The sediment-water module was newly developed and concentrates on transformations and fluxes between inorganic and organic *N*-compounds in both the water column and the sediment; within this module other biota normally found in sediments is included and it is considered as organic nitrogen. The principal *N*-compounds, *N*-transformations and *N*-fluxes in the model are conceptualized in Fig. 1. Tables 1 and 2 present the principal variables considered in each module and a description of the variables used and the related equations are presented in Appendix A. A prefix was used in each variable name to distinguish between types of variable (*r*_, refers to rate variables; *s*_, refers to state variables; *a*_, refers to auxiliary variables; and *p*_, refers to parameters).

Table 1
Principal state, rate and auxiliary variables used in the water–sediment module

Water–sediment module		
	Dimensions	Symbol
State variables		
N–N_2 in sediments	mg N l^{-1}	*s*_n2sed
N–N_2 in water	mg N l^{-1}	*s*_n2wat
N–NH_3 in sediments	mg N l^{-1}	*s*_nh3sed
N–NH_3 in water	mg N l^{-1}	*s*_nh3wat
N–NH_4^+ in sediments	mg N l^{-1}	*s*_nh4sed
N–NH_4^+ in water	mg N l^{-1}	*s*_nh4wat
N–NO_3^- in sediments	mg N l^{-1}	*s*_no3sed
N–NO_3^- in water	mg N l^{-1}	*s*_no3wat
Organic nitrogen in sediments	mg N l^{-1}	*s*_ornsed
Rate variables		
Ammonia excretion rate	mg N l^{-1} h^{-1}	*r*_ammnpro
Ammonification rate in sediments	mg N l^{-1} h^{-1}	*r*_ammonifsed
Ammonification rate in water	mg N l^{-1} h^{-1}	*r*_ammonifwat
Denitrification rate in sediments	mg N l^{-1} h^{-1}	*r*_denitrifsed
Egestion rate of protein	mg N l^{-1} h^{-1}	*r*_egspro
N–N_2 flux rate	mg N l^{-1} h^{-1}	*r*_n2flux
N–NH_3 flux rate	mg N l^{-1} h^{-1}	*r*_nh3flux
Refill rate for N–NH_4^+	mg N l^{-1} h^{-1}	*r*_nh4fill
N–NH_4^+ flux rate	mg N l^{-1} h^{-1}	*r*_nh4flux
Nitrification rate in sediments	mg N l^{-1} h^{-1}	*r*_nitrifsed
Nitrification rate in water	mg N l^{-1} h^{-1}	*r*_nitrifwat
Refill rate for N–NO_3^-	mg N l^{-1} h^{-1}	*r*_no3fill
N–NO_3^- flux rate	mg N l^{-1} h^{-1}	*r*_no3flux
Phytoplankton dead rate	mg N l^{-1} h^{-1}	*r*_phytom
Uneaten feed (dry matter)	mg N l^{-1} h^{-1}	*r*_uneadm
Volatilisation rate of N–N_2	mg N l^{-1} h^{-1}	*r*_volatn2
Volatilization rate of N–NH_3	mg N l^{-1} h^{-1}	*r*_volatnh3

The model analyses *N*-transformations and fluxes between compartments in stagnant water ponds. The *N*-inputs considered are the protein in the feed and the dissolved *N*-compounds in the in-flow water. Nitrogen fixation is considered negligible in aquaculture ponds (El Samra and Oláh, 1979; Lin et al., 1988) and was ignored in this model. In the fish module, a distinction is made between wasted (e.g. non-consumed) and consumed feed; the consumed feed is partly transformed into fish biomass and the rest is excreted (as ammonium) or egested (as feces). It is assumed that fish growth is only based on the feed input and not on other sources from the pond biota. Phytoplankton assimilates both nitrate and ammonium ions for growth. In the sediment/water module, the *N*-transformations and *N*-fluxes between the various *N*-compounds in water and sediment are included. Organic matter in the sediment is composed of wasted feed, dead phytoplankton and feces. Decomposition of organic matter in the sediment results in ammonia–ammonium ($N-NH_3 + N-NH_4^+$), that may be transformed into NO_3^- and possibly N_2, both in the water and in the sediment by nitrification–denitrification. Both seepage and biota that could escape from the system (flying insects) are considered irrelevant for the nitrogen balance and the emission of gaseous nitrogen ($N-NH_3$ and $N-N_2$) is assumed to be the only loss of nitrogen from the system.

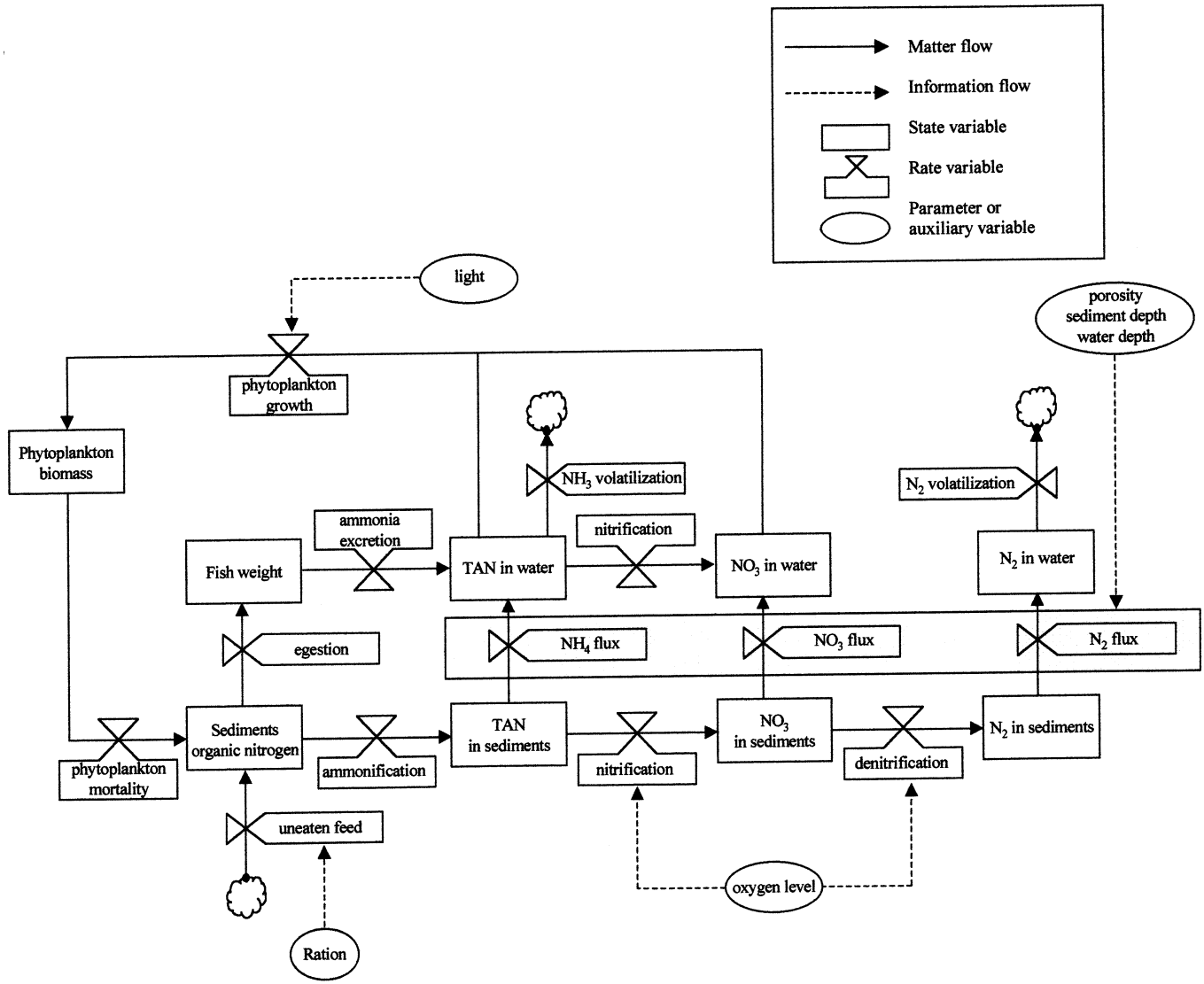

Fig. 1. Conceptual model of nitrogen transformations and fluxes and relations between modules. All state variables have dimensions of mg N l^{-1}

Table 2
Principal state, rate and auxiliary variables used in the phytoplankton and fish modules

	Dimensions	Symbol
Phytoplankton module		
State variables		
Phytoplankton biomass	mg N l^{-1}	*s*_phytobiom
Dead phytoplankton biomass	mg N l^{-1}	*s*_phytodead
Rate variables		
Growth rate	mg N l^{-1} h^{-1}	*r*_phytogrowth
Death rate	mg N l^{-1} h^{-1}	*r*_phytom
Auxiliary variables		
Light limitation factor	0–1	*a*_lighlim
Nutrient limitation factor	0–1	*a*_nutrilim
Radiation per hour	ly h^{-1}	*a*_radhor
Water temperature	°C	*a*_temp
Fish module		
State variables		
Amount of amino acids converted into protein	g amino acids	*s*_aapool1
Amount of amino acids converted into glucose	g amino acids	*s*_aapool2
Total pool of glucose available	g glucose	*s*_glpool
Total pool of body lipid	g lipids	*s*_libiom
Organic matter in sediments	mg N l^{-1}	*s*_ormsed
N–NH_3 in water	mg N l^{-1}	*s*_nh3wat
Individual fish weight (fresh weight)	g	*s*_wf
Rate variables		
Rate of gluconeogenesis	mg amino acids l^{-1} d^{-1}	*r*_aagluc
Amino acid oxidation rate	mg amino acids l^{-1} d^{-1}	*r*_aaox
Nitrogen in ammonia excreted	mg N l^{-1} h^{-1}	*r*_ammnpro
Ammonium excretion rate	g N–NH_4^+ h^{-1}	*r*_ammpro
Rate of digestion of carbohydrates from feed	g carbohydrates h^{-1}	*r*_cardig
Egestion rate of protein as nitrogen, in faeces	mg N l^{-1} h^{-1}	*r*_egspron
Real feeding rate (dry weight)	g feed h^{-1}	*r*_fdrtdm
Lipid digestion rate	g lipid h^{-1}	*r*_lipdig
Lipid oxidation rate	g lipid h^{-1}	*r*_lipox
Lipid synthesis rate from glucose	g lipid h^{-1}	*r*_lipsyn2
Amino acid production rate from digested feed	g amino acids h^{-1}	*r*_prodig
Protein synthesis rate	g protein h^{-1}	*r*_prosyn
Uneaten feed (dry basis)	g feed h^{-1}	*r*_uneadm
Nitrogen in uneaten feed	mg N l^{-1} h^{-1}	*r*_unean
Fish growth rate (fresh basis)	g fish h^{-1}	*r*_wfrate
Auxiliary variables		
Daily feed ration (fresh weight)	g feed	*a*_ration
Proportion of energy supplied by fat	0–1	*a*_aalirat
Fraction of protein in feed	% dry matter	*a*_feedpr

2.2. Fish module

The module (Fig. 2) was developed by Machiels and Henken (1986, 1987) on the basis of physiological and biochemical principles. In the module, fish grow on the basis of the bio-energetics of feed intake and digestion. Digestion of feed protein, carbohydrates and lipids results in amino acids, glucose, fatty acids and glycerol. Amino acids are used for the synthesis of protein or glucose; fatty acids and glucose are used for the synthesis of body lipids. van Dam and Penning de Vries (1995) assumed that the relative oxidation of lipids and protein for energy is determined by the protein feeding level and the protein/energy ratio of the feed. This approach allows the estimation of the ammonia excretion and feces egestion rates of the fish:

$$r\_\text{ammnpro} = \left(\frac{14}{17}\right) \times 0.16 \times \left[\left(\frac{r\_\text{aaox}}{24}\right) + \left(\frac{r\_\text{aagluc}}{24}\right)\right] \quad (1)$$

where (14/17) is the nitrogen to ammonia ratio; 0.16, the percentage of nitrogen in protein; $r_$ammnpro, the ammonium excretion rate (mg N l^{-1} h^{-1}); $r_$aaox, the amino acid oxidation rate (mg amino acids l^{-1} d^{-1}); and $r_$aagluc, the gluconeogenesis rate (mg amino acids l^{-1} d^{-1}).

$$s\_\text{nh3wat}(t) = s\_\text{nh3wat}(t - dt) + (r\_\text{ammnpro} - r\_\text{volatnh3} - r\_\text{nh3flux}) \times dt \quad (2)$$

where $s_$nh3wat is the $N–NH_3$ in water (mg N l^{-1}); $r_$ammnpro, the ammonium excretion rate (mg N l^{-1} h^{-1}); $r_$volatnh3, the NH_3 volatilisation rate (mg N l^{-1} h^{-1}); and $r_$nh3flux, the NH_3 flux rate from/towards the sediments (mg N l^{-1} h^{-1}).

$$r\_\text{egspron} = 0.16 \times r\_\text{egspro} \quad (3)$$

where $r_$egspron is the feces egestion rate (mg N l^{-1} h^{-1}); and $r_$egspro, the protein egestion rate (g protein h^{-1}).

Feed is given hourly and in the present model the uneaten feed was also included (Verdegem et al., 2000):

$$r\_\text{unean} = a\_\text{ration} \times p\_\text{mors} \quad (4)$$

where $r_$unean is the uneaten feed (mg N l^{-1} h^{-1}); $a_$ration, the feed ration (g feed, dry weight); and $p_$mors, the fraction of feed not eaten (0–1).

The excreted ammonia becomes part of the dissolved ammonia in water and both the feces and the uneaten feed adds to the organic nitrogen pool in the sediments (Fig. 1, Eq. (9)). Because in the model of van Dam and Penning de Vries (1995) all variables were expressed in gram fresh weight, variables were converted to mg N l^{-1} to make the fish module compatible with the other modules. The model assumes a 12-h feeding period. For further details, reference is made to Machiels and Henken (1986, 1987) and van Dam and Penning de Vries (1995).

2.3. Phytoplankton module

The module is based on a dynamic simulation model for the blooming of *Oscillatoria agardhii* (Jiménez-Montealegre et al., 1995). The biomass of phytoplankton is assumed to be affected by two different rates: growth and natural mortality (Fig. 3). Light and nutrient availability directly control growth rate and limitations are assumed to be multiplicative:

$$r\_\text{phytogrowth} = p\_\text{maxgrphyto} \times a\_\text{nutrilim} \times a\_\text{lighlim} \times s\_\text{phytobiom} \quad (5)$$

where $r_$phytogrowth is the phytoplankton growth rate (mg N l^{-1} h^{-1}); $p_$maxgrphyto, the rate constant for phytoplankton growth (h^{-1}); $a_$nutrilim, the nutrients limitation factor (0–1); $a_$lighlim, the light limitation factor (0–1); and $s_$phytobiom, the phytoplankton biomass (mg N l^{-1}).

Light limitation is based on the formula proposed by Di Toro et al. (1971), taking into account the equation proposed originally by Steele (1965) which assumes an optimum radiation with a reduction of growth at intensities both above and below the saturation level. Light extinction is based on Beer's law with provision for self-shading due to suspended biomass and photoperiod is used to estimate the actual radiation every hour. Nutrients (ammonium, nitrate and phosphorus) come from refill water, fish excretion and organic matter decomposition (both in the water column and in the sediments); its availability is used to estimate the limitation for growth using the relation of Monod kinetics. It was assumed that the phytoplankton species use ammonium first and, only when this ion is depleted, nitrate secondly (Syrett, 1981; McCarthy, 1981). The phytoplankton natural mortality rate is a function of the water temperature:

$$r\_\text{phytom} = p\_\text{mrphyto} \times \exp(a\_\text{tecorm}) \times s\_\text{phytobiom} \quad (6)$$

where $r_$phytom is the phytoplankton death rate (mg N l^{-1} h^{-1}); $p_$mrphyto, the rate constant for phytoplankton mortality (h^{-1}); and $a_$tecorm, the temperature correction for mortality (h^{-1}).

For further details, reference is made to Jiménez-Montealegre et al. (1995).

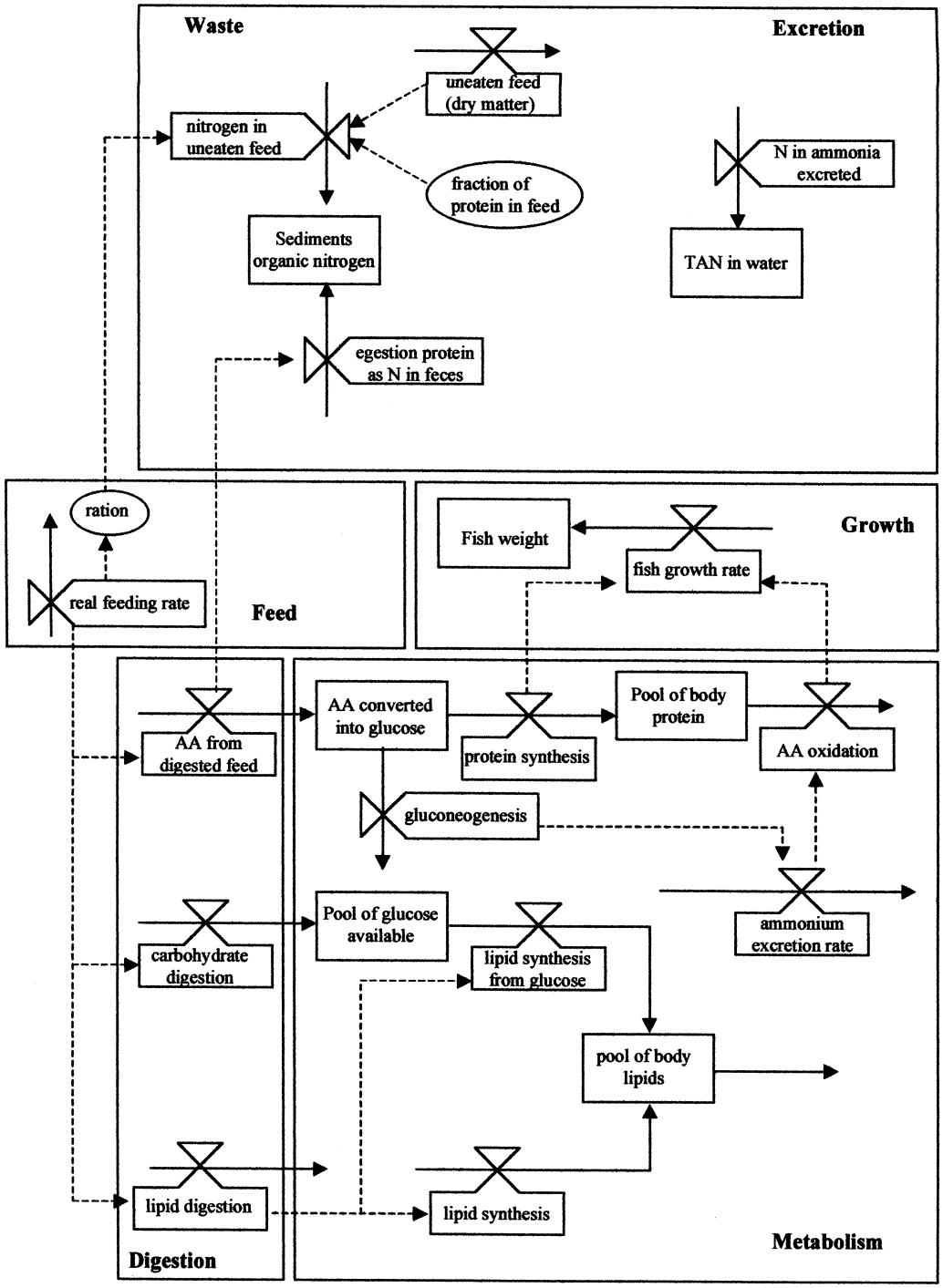

Fig. 2. Fish module relational diagram.

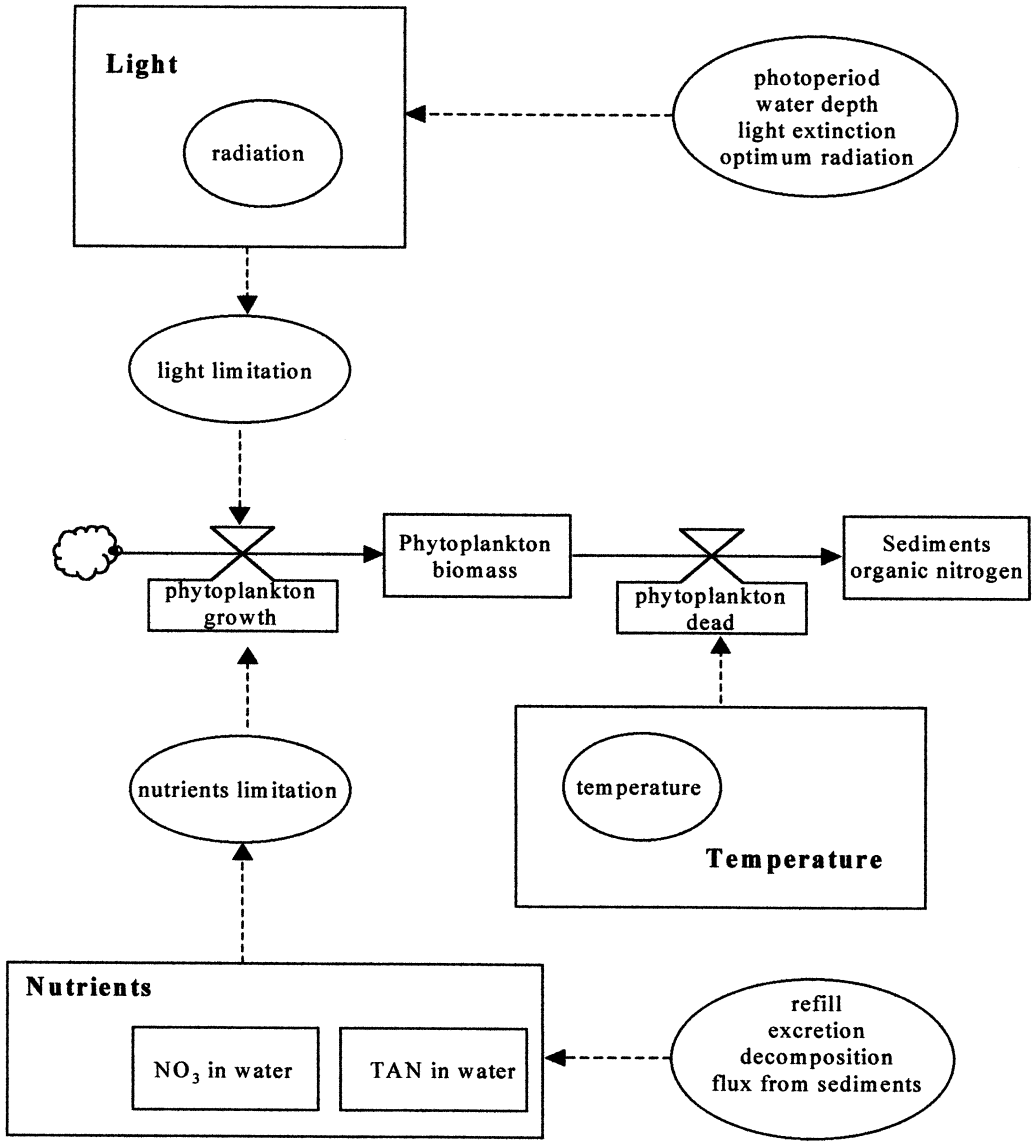

Fig. 3. Phytoplankton module relational diagram.

2.4. Water–sediment module

Water and sediment compartments are highly correlated in ponds and are considered together as a module that holds several state variables (Fig. 4). Water pH and dissolved oxygen were inputs of the model; minimum values for these parameters were considered in the respective equations. Organic matter is made of wasted feed, dead phytoplankton and feces from fish. The amount of wasted feed is difficult to assess in ponds. Frier et al. (1995) proposed a model in which the fraction of feed eaten can be calculated by iteration, knowing the actual fish growth for a given period and the amount of feed offered. Phillips et al. (1985) estimated that 15–30% of the feed in rainbow trout cage culture is wasted; Thorpe et al. (1990) found feed losses of 19% in salmon cage culture; and van

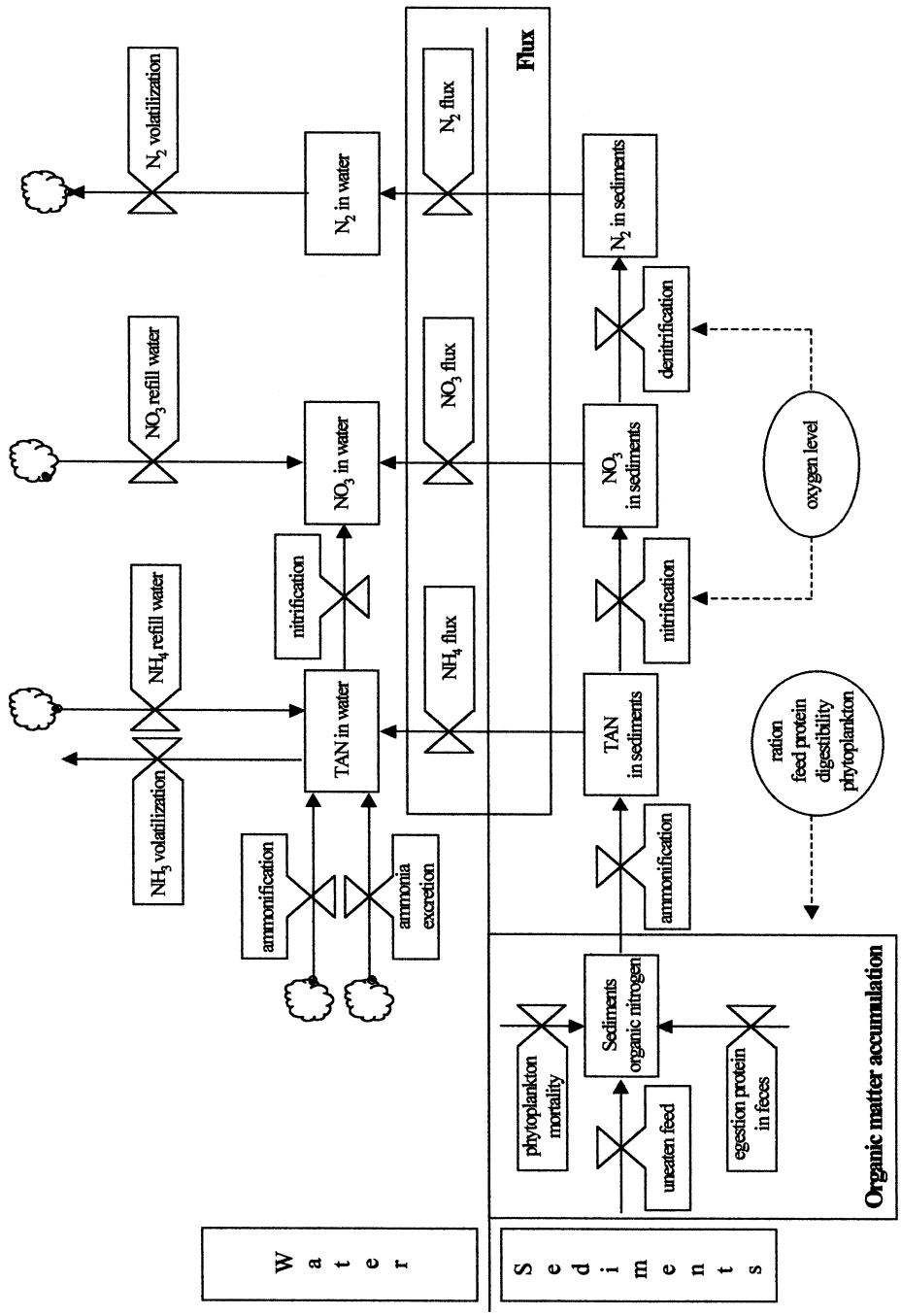

Fig. 4. Water–sediment module relational diagram.

der Meer et al. (1995) found for *C. macropomum*, raised in recirculation units and fed at levels near satiation, feed losses fluctuating between 9 and 20% irrespective of the fish size. In our model, this value was set to 35% considering the system conditions (earthen fish pond, low fish density). Dead phytoplankton first decompose in the water column:

$$r\_\text{ammonifwat} = \text{if } (a\_\text{phwat} > 2) \text{ and } (a\_\text{dowat} > 2) \text{ then } (s\_\text{phytodead} \times p\_\text{ammonifwat}) \text{ else } 0 \quad (7)$$

where $r_$ammonifwat is the ammonification rate in the water column (mg N l^{-1} h^{-1}); $a_$phwat, the water pH; $a_$dowat, the dissolved oxygen in water (mg O_2 l^{-1}); $s_$phytodead, the dead phytoplankton biomass (mg N l^{-1}); and $p_$ammonifwat, the rate constant of ammonification in water (h^{-1}).

The rest of the organic matter (wasted feed, partly decomposed phytoplankton, feces) is assumed to settle and decompose in the sediments:

$$r\_\text{ammonifsed} = \text{if } (a\_\text{phsed} > 2) \text{ and } (a\_\text{dosed} > 2) \text{ then } (s\_\text{ornsed} \times p\_\text{ammonifsed}) \text{ else } 0 \quad (8)$$

where $r_$ammonifsed is the ammonification rate in the sediments (mg N l^{-1} h^{-1}); $a_$phsed, the sediment pH; $a_$dosed, the dissolved oxygen in sediment water (mg O_2 l^{-1}); $s_$ornsed, the organic nitrogen in sediments (mg N l^{-1}); and $p_$ammonifsed is the rate constant for ammonification in sediments (h^{-1}).

$$s\_\text{ornsed}(t) = s\_\text{ornsed}(t - dt) + (r\_\text{unean} + r\_\text{egspron} + r\_\text{phytom} - r\_\text{ammonifsed}) \times dt \quad (9)$$

where $r_$unean is the rate of nitrogen input in uneaten feed (mg N l^{-1} h^{-1}); and $r_$egspron, the egestion rate of protein (as nitrogen) in feces (mg N l^{-1} h^{-1}).

The compound resulting from ammonification/mineralization is total ammonia nitrogen (TAN, $N-NH_3 + N-NH_4^+$). Its concentration is influenced by pH and dissolved oxygen levels (Reddy and Patrick, 1984; Oláh et al., 1987). In the model, the percentage of free ammonia is based on pH and temperature conditions (Delincé, 1992). In the water column, ammonium can be used by phytoplankton for growth (see above), be transformed into nitrate:

$$r\_\text{nitrifwat} = \text{if } (a\_\text{dowat} > 2) \text{ then } (p\_\text{nitrifwat} \times s\_\text{nh4wat}) \text{ else } 0 \quad (10)$$

where $r_$nitrifwat is the nitrification rate in water (mg N l^{-1} h^{-1}); $a_$dowat, the dissolved oxygen in water (mg O_2 l^{-1}); $p_$nitrifwat, the rate constant for nitrification in water (h^{-1}); and $s_$nh4wat, the dissolved $N-NH_4^+$ in the water column (mg N l^{-1}) or be diffused to the sediments based on a concentration gradient:

$$r\_\text{nh4flux} = -p\_\text{porosity} \times p\_\text{nh4dif} \times \left[\frac{\left(\frac{s\_\text{nh4sed} - s\_\text{nh4wat}}{1000} \right)}{p\_\text{seddepth}} \right] \quad (11)$$

where $r_$nh4flux is the flux of $N-NH_4^+$ (mg N l^{-1} h^{-1}); $p_$porosity, the soil porosity (dimensionless); $p_$nh4dif, the diffusion coefficient for $N-NH_4^+$ (m^2 h^{-1}); $s_$nh4sed, the dissolved $N-NH_4^+$ in sediments (mg N l^{-1}); and $p_$seddepth, the sediment depth down to $dNH_4^+/dx = 0$ (m).

The flux of nutrients is based on Fick's first law of diffusion, corrected for porosity and tortuosity of the sediments (Berner, 1980). Due to the higher concentration of nutrients frequently found in the sediments (Boyd et al., 1994) the flux is most likely to occur from the sediments towards the water column and possibly transformed into nitrate and/or nitrogen gas:

$$r\_\text{nitrifsed} = \text{if } (a\_\text{dosed} > 2) \text{ then } (p\_\text{nitrifsed} \times s\_\text{nh4sed}) \text{ else } 0 \quad (12)$$

where $r_$nitrifsed is the nitrification rate in sediments (mg N l^{-1} h^{-1}); $a_$dosed, the dissolved oxygen in sediment water (mg O_2 L^{-1}); $p_$nitrifsed, the rate constant for nitrification in sediments (h^{-1}); and $s_$nh4sed, the dissolved $N-NH_4^+$ in the sediments (mg N l^{-1}).

The latter process is oxygen dependent (Sharma and Ahlert, 1977) and in the model is taken in account. When oxygen is depleted in the sediments, nitrate can be transformed into nitrogen gas via denitrification:

$$r\_\text{denitrifsed} = \text{if } (a\_\text{dosed} > 2) \quad \text{then } 0$$

$$\text{else } (p\_\text{denitrifsed} \times s\_\text{no3sed}) \tag{13}$$

where $r_$denitrifsed is the denitrification rate in sediments (mg N l^{-1} h^{-1}); $a_$dosed, the dissolved oxygen in sediment water (mg O_2 l^{-1}); $p_$denitrifsed, the rate constant for denitrification (h^{-1}); and s_no3sed, the dissolved NO_3^- in the sediments (mg N l^{-1}).

Both ammonia and nitrogen gas (if any) can escape to the air via volatilization depending on its concentration in the water. The rate constants for volatilization consider the diffusion coefficient of the respective gas and the thickness of the water–air interface:

$$r\_\text{volatn2} = p\_\text{volatn2} \times s\_\text{n2wat} \tag{14}$$

where $r_$volatn2 is the $N–N_2$ volatilisation (mg N l^{-1} h^{-1}); $p_$volatn2, is the constant for $N–N_2$ volatilization rate (h^{-1}); and $s_$n2wat, the dissolved $N–N_2$ in the water column (mg N l^{-1}).

$$r\_\text{volatnh3} = p\_\text{volatnh3} \times s\_\text{nh3wat} \tag{15}$$

where $r_$volatnh3 is the NH_3 volatilisation (mg N l^{-1} h^{-1}); $p_$volatnh3, the constant for NH_3 volatilization rate (h^{-1}); and $s_$nh3wat, the dissolved $N–NH_3$ in the water column (mg N l^{-1}).

2.5. Model implementation and parameterization

The model was implemented in Turbo Pascal (7.0) using the Euler's rectangular method for numerical integration. Because processes, such as oxygen consumption and/or production, could have high rates of change, the time coefficient for each state variable was calculated. The highest rate of increase (or decrease) during the simulation was identified and the relative rate for that period calculated. Time coefficients, defined as the inverse of the relative rate of change, varied from 1.96 to 92.31 h. de Wit and Goudriaan (1978) suggest that the time step for rectangular integration should be one tenth of the smallest time coefficient. However, a fixed time step of 1 h was selected because a further reduction of the time step in the model did not improve the simulations substantially.

The program uses the following input data: water temperature, water pH, dissolved oxygen in both water and sediments, the rate of input of ammonium and nitrate via refill water and the amount of feed offered daily. The general output of the model is the nitrogen concentration in water and sediments (as organic-*N*, $N–NH_4^+$ and $N–NO_3^-$) and the nitrogen stored in fish and phytoplankton biomass.

3. Material and methods

3.1. Experimental data collection for calibration

The data for the calibration (Table 3) were collected during an experiment designed for this purpose. A stagnant pond with an area of 65-m^2 and 1.2 m depth was used. The pond was stocked with *C. macropomum* (Cuvier 1818) at a density of 1.1 fish per m^2. Fish were fed a 32% protein commercial feed; weekly average fish weight was used to estimate the amount of feed offered, considering a feeding rate of 2.5% body weight per day and the amount of feed given was used as an input of the model. Dissolved oxygen, water pH and temperature in the middle of the water column were measured at 06:00 and 18:00 h. The dissolved oxygen and the temperature for each hour were estimated using linear interpolation assuming peak values at those hours. To estimate the hourly value of pH, the concentration of H_3O^+ was also interpolated and the pH value obtained.

The pond was sampled weekly for nitrogen contents in phytoplankton, sediments and water. The nitrogen cycle, especially the rates of transformation of dissolved inorganic compounds, is very dynamic and important changes in concentrations occur during the day (Meade, 1985; Mires et al., 1990; Abdalla et al., 1996). Sampling was performed at noon. For the comparison between simulated and observed values, this fact was considered by comparing only values from similar hours of sampling.

Dissolved nitrogen ($N–NO_3^-$ and $N–NH_4^+ + N–NH_3$) in water and sediments was determined using traditional methods (APHA, 1989). Organic nitrogen in water, sediments and phytoplankton

Table 3
Experimental data collected to perform the calibration of the model

Day*	State variable						
	*s*_nh4wat (mg N l^{-1})	*s*_nh4sed (mg N l^{-1})	*s*_no3wat (mg N l^{-1})	*s*_no3sed (mg N l^{-1})	*a*_fishw (g $fish^{-1}$)	*s*_phytobiom (mg N l^{-1})	*s*_ornsed (mg N l^{-1})
Initial	0.081	0.206	0.619	0.105	35.0	0.322	140.29
7	0.032	0.026	0.546	0.167	42.1	0.766	139.10
14	0.102	0.078	0.539	0.200	50.0	0.869	138.72
21	0.190	0.135	0.555	0.259	62.4	0.803	140.23
28	0.239	0.181	0.585	0.416	74.9	0.906	139.75
35	0.290	0.191	0.596	0.563	90.8	0.880	140.50
42	0.334	0.224	0.624	0.689	108.4	0.960	141.13
49	0.419	0.263	0.644	0.849	128.1	0.994	141.24
56	0.439	0.318	0.700	0.963	151.5	1.032	142.34

For symbol explanation see Table 1 and Table 2. *, Samplings were performed at noon on the indicated day.

was determined using the method of AOAC (1980). The nitrogen stored in fish biomass was calculated weekly based on average fish weight and the determination of total nitrogen in fish flesh at harvest was determined using the micro-Kjeldahl method (AOAC, 1980). After each weekly sampling, the volume of water lost via evaporation was replaced with water of known nitrogen (nitrate and ammonium ions) concentration. Soil porosity was also determined following the method described by Corredor and Morell (1985).

3.2. Calibration

The fish module was first calibrated for *Colossoma*. Field and laboratory determinations at the beginning of the experiment were used as initial values (Table 4). Calibration was carried out by adjusting the equation coefficients in order to improve the fit between simulated and observed data. During the process, one selected coefficient value was changed at a time and the model was run for the whole simulation period. When the coefficient was previously reported in the literature, that value was used as the initial value for the simulation; in some cases a range for the coefficient was reported in literature, so the calibration was performed changing the coefficient within that range. Calibrated rate coefficients are indicated in Table 5. The degree of agreement between simulated and observed data over the whole simulation was determined at every time when field data were available, calculating the relative error:

Table 4
Initial conditions used in the simulations

Variable	Symbol	Dimension	Calibration *Colossoma macropomum*	Validation *Oreochromis niloticus*
Fish number	*a*_fishnb	#	70	960
Fraction of protein in feed (wet)	*a*_feedpr	% In dry matter	0.32	0.30
Carbohydrate digestibility coefficient	*p*_digca	%	0.60	0.50
Lipids digestibility coefficient	*p*_digli	%	0.80	0.50
First factor for lipid oxidation rate	*p*_fac1	Dimensionless	6.456	4.300
Second factor for lipid oxidation rate	*p*_fac2	Dimensionless	0.9046	1.2000
Minimum fat % in fresh weight of fish	*p*_lipfin	%	3.5	3.0
Pond area	*p*_pondarea	m^2	65	800
Protein percentage in fish (fresh weight)	*p*_prperc	g protein (100 g fish)$^{-1}$	15.0	17.0
Reference temperature for routine metabolism	*p*_reftemp	°C	25	26
Routine metabolism coefficient	*p*_rmcf	mole ATP g$^{-0.8}$ h^{-1}	1.05e^{-3}	1.21e^{-3}
Total pool of body lipid	*s*_libiom	g lipid	2.800	2.808
NH_3 in sediments	*s*_nh3sed	mg N l−1	0.105	0.002
NH_3 in water	*s*_nh3wat	mg N l−1	0.002	0.005
NH_4^+ in sediments	*s*_nh4sed	mg N l−1	0.206	0.105
NH_4^+ in water	*s*_nh4wat	mg N l−1	0.081	0.240
NO_3^- in water	*s*_no3wat	mg N l−1	0.619	0.114
Organic nitrogen in sediments	*s*_ornsed	mg N l−1	140.29	38.18
Phytoplankton biomass	*s*_phytobiom	mg N l−1	0.322	0.113
Total body protein biomass (dry matter)	*s*_prbiom	g protein	5.95	5.97
Individual fish weight (wet weight)	*s*_wf	g	35.0	35.1

Only parameters changed during calibration and validation runs are included.

Table 5
Coefficient values used in the model after calibration

Variable	Symbol	Units	Value	Initial source
Gram of amino acids needed for 1 mole ATP	*p*_aaatp	g amino acid (mole ATP)$^{-1}$	4.76	(van Dam and Penning de Vries, 1995)
Fraction of digested protein used for gluconeogenesis	*p*_aafdgl	Dimensionless	0.05	(Machiels and Henken, 1986)
Ammonification in sediments rate coefficient	***p*_ammonifsed**	h^{-1}	5.04e^{-6}	(Berner, 1974)
Ammonification in water rate coefficient	***p*_ammonifwat**	h^{-1}	5.04e^{-3}	(Otsuki and Hanya, 1972)
Ratio carbon/nitrogen in phytoplankton	*p*_cnratio	g C (g N)$^{-1}$	6.622	Redfield ratio
Constant for extinction	***p*_constext**	Dimensionless	0.085	After Scavia (1980)
Denitrification rate coefficient in sediments	*p*_denitrifsed	h^{-1}	(0.0318∗exp (0.078∗ (*a*_temp−20))	(Stanford et al., 1975)
Diffusion coefficient for NH_3	***p*_diffcoefnh3**	cm^2 h^{-1}	0.115	(Broeker, 1974)
Carbohydrate digestibility coefficient	*p*_digca	%	0.50	(van Dam and Penning de Vries, 1995)
Lipid digestibility coefficient	*p*_digli	%	0.50	(van Dam and Penning de Vries, 1995)
Protein digestibility coefficient	*v*_digpr	%	0.80	(van Dam and Penning de Vries, 1995)
Light extinction due to water	***p*_exwa**	m^{-1}	0.27	(Scavia, 1980)
First factor for aalirate equation	***p*_fac1**	Dimensionless	4.3	Estimated after van der Meer and van Dam (1998)
Second factor for aalirate equation	***p*_fac2**	Dimensionless	1.2	Estimated after van der Meer and van Dam (1998)
Initial lipid	*p*_iliper	% fw	8.0	(van Dam and Penning de Vries, 1995)
Half saturation constant for nitrogen	***p*_kn**	mg N l^{-1}	0.3	(Chen and Orlob, 1975)
Cost of lipid synthesis	*p*_liatco	mole ATP g^{-1}	0.015	(van Dam and Penning de Vries, 1995)
Gram of lipids needed for 1 mole ATP	*p*_liatp	g lipid (mole ATP)$^{-1}$	1.96	(van Dam and Penning de Vries, 1995)
Minimum fat percentage in fresh weight of fish	*p*_lipfin	%	3.0	(van Dam and Pauly, 1995)
Phytoplankton growth rate coefficient	***p*_maxgrphyto**	h^{-1}	0.104	(Scavia, 1980)
Fraction of feed given to fish but not eaten	***p*_mors**	0–1	0.35	Estimated
Phytoplankton mortality rate coefficient	***p*_mrphyto**	h^{-1}	2.08e-4	(Jørgensen et al., 1978)
Cost of gluconeogenesis	*p*_neoatco	mole ATP g^{-1}	−0.095	(Li and Gregory, 1974)
Diffusion coefficient for NH_3	***p*_nh3dif**	m^2 h^{-1}	1.0	(Brezonik, 1994)
Diffusion coefficient for NH_4^+	***p*_nh4dif**	m^2 h^{-1}	1.7107e-4	(Li and Gregory, 1974)
Nitrification in sediments rate coefficient	***p*_nitrifsed**	h^{-1}	0.010	(Bansal, 1976)
Nitrification in water rate coefficient	***p*_nitrifwat**	h^{-1}	4.17e-4	(Bansal, 1976)
Diffusion coefficient for NO_3^-	***p*_no3dif**	m^2 h^{-1}	6.84e-6	(Li and Gregory, 1974)
Pond area	*p*_pondarea	m^2	70	Own observation
Soil porosity	*p*_porosity	Dimensionless	0.84	Own observation
Cost of protein synthesis	*p*_pratco	mole ATP g^{-1}	0.075	(van Dam and Penning de Vries, 1995)

Table 5 (*Continued*)

Variable	Symbol	Units	Value	Initial source
Protein percentage in fresh weight	*p*_prperc	g prot (100 g fish)$^{-1}$	17.00	(van Dam and Penning de Vries, 1995)
Q_{10} factor metabolism	*p*_q10	Dimensionless	2.0	(Machiels and Henken, 1986)
Saturation light intensity	*p*_radop	ly h^{-1}	1.67	(van Liere et al., 1978)
Reference temperature for routine metabolism	*p*_reftemp	°C	26	(Saint-Paul, 1988)
Routine metabolism coefficient	*p*_rmcf	mole ATP g$^{-0.8}$ h^{-1}	5.04e-5	(van der Meer and van Dam, 1998)
Routine metabolism exponent	*p*_rmex	Dimensionless	0.8	(van der Meer and van Dam, 1998)
Maximum temperature for phytoplankton	*p*_temax	°C	35	(Chen and Orlob, 1975)
Volatilization of NH_3 rate coefficient	***p*_volatnh3**	h^{-1}	3.19e-3	(Wolfe et al., 1986)
Water depth	*p*_waterdepth	m	1.2	Own observation
Water/sediment film thickness	***p*_zfilm**	cm	0.3	(Wolfe et al., 1986)

Calibrated coefficients are in boldface.

$$\mathrm{RE} = \frac{S_{\mathrm{sim}} - S_{\mathrm{obs}}}{\frac{1}{2}(S_{\mathrm{sim}} + S_{\mathrm{obs}})} \tag{16}$$

in which RE is the relative error and S_{sim} and S_{obs} are the simulated and observed values of the state variables at each moment. This way of calculating the RE takes into account the fact that both observed and simulated values are an approximation of the real value. Using a reiterative trial and error procedure, the coefficients were adjusted until the RE was at least equal or lower than 0.25 for any sampling period ; the same procedure was used for each coefficient. Final simulation was performed when all coefficients were set (Table 5) and the average relative error (ARE) for each state variable was used to assess the agreement for the whole experiment (van Dam et al., 1996).

3.3. Sensitivity analysis

In order to evaluate which parameters mainly determine the *N*-transformations and fluxes between compartments in the system, a sensitivity analysis was used. Each time a selected rate coefficient was changed by $\pm 10\%$ of the value that gave the best fit between simulated and observed data maintaining the other coefficients unchanged. The difference between the value of the state variable at each sampling date for the highest rate coefficient ($+10\%$) and the value for the lowest rate coefficient (-10%) expressed as a percentage of the value using the coefficient obtained after calibration was used to quantify the sensitivity of the model to that particular coefficient (Piedrahita, 1986). The result of this analysis is used as a guide to further experiments and study: if the influence of a certain parameter is relatively small, further analyses may be left for some time, but if the influence is large, more work should be invested in a further analysis of the section of the program where this parameter plays a role (de Wit and Goudriaan, 1978).

3.4. Validation

For the validation of the model, independent data sets were used (Table 6). Two stagnant ponds of 800 m^2 and 1.2 m depth were stocked with 35.1 g (± 7.0 S.D.) *O. niloticus*, at a density of 1.2 fish m^{-2}. Fish were grown for 91 days and sampled every 3 weeks, sampling at least 50% of the entire pond population. Fish were fed a 3 mm 30% protein pellet. Average fish weight was used to estimate the amount of feed offered using a feeding rate of 2.5% body weight per day. The daily ration was divided into two equal portions and administrated at 07:00 and 15:00 h; fish were not fed on sampling days. Table 4 compares the initial conditions for the calibration and valida-

Table 6
Experimental data collected to perform the validation of the model

Day*	*s*_nh4wat (mg N l^{-1})	*s*_nh4sed (mg N l^{-1})	*s*_no3wat (mg N l^{-1})	*a*_fishw (g $fish^{-1}$)	*s*_phytobiom (mg N l^{-1})	*s*_ornsed (mg N l^{-1})
Initial	0.240 (0.027)	0.105 (0.011)	0.114 (0.012)	35.1 (7.0)	0.113 (0.028)	38.18 (1.4)
7	0.011 (0.002)	0.077 (0.055)	0.111 (0.037)		0.527 (0.017)	38.76 (2.2)
14	0.087 (0.031)	0.067 (0.041)	0.076 (0.010)		0.752 (0.036)	38.02 (1.3)
21	0.096 (0.041)	0.087 (0.014)	0.095 (0.012)	61.8 (12.8)	0.837 (0.051)	41.14 (3.7)
28	0.192 (0.061)	0.162 (0.014)	0.114 (0.011)		0.854 (0.043)	45.53 (2.3)
35	0.250 (0.020)	0.153 (0.027)	0.162 (0.007)		0.961 (0.032)	58.03 (5.3)
42	0.261 (0.016)	0.174 (0.027)	0.189 (0.024)	102.4 (12.2)	1.085 (0.089)	54.54 (7.8)
49	0.412 (0.095)	0.281 (0.069)	0.168 (0.005)		0.879 (0.181)	64.45 (8.5)
56	0.327 (0.042)	0.211 (0.027)	0.192 (0.007)		0.923 (0.135)	82.23 (3.8)
63	0.427 (0.055)	0.266 (0.081)	0.273 (0.016)	161.3 (19.1)	1.017 (0.067)	83.34 (7.4)
70	0.344 (0.210)	0.388 (0.040)	0.401 (0.064)		1.076 (0.087)	85.54 (9.5)
77	0.624 (0.083)	0.355 (0.149)	0.439 (0.107)		1.204 (0.072)	85.14 (8.0)
84	0.621 (0.212)	0.504 (0.013)	0.406 (0.048)	236.1 (19.8)	1.191 (0.080)	81.52 (12.9)
90	0.791 (0.015)	0.509 (0.068)	0.422 (0.067)		1.125 (0.137)	90.83 (19.8)

For symbol explanation see Table 1 and Table 2. S.D. is indicated between brackets. *, Samplings were performed at noon on the indicated day.

tion runs. Dissolved oxygen, water pH and temperature in the water column were measured twice a day and interpolated to obtain hourly values, as in the calibration experiment. Ponds were sampled weekly, at noon, for nitrogen contents in phytoplankton, sediments and water using the methods described.

4. Results

Most of the coefficients used in the model were taken from the literature; when information was not available, the coefficients were estimated by fitting model predictions to observed data for a time series of data and for all the state variables.

The calibrated model was run for the whole experimental period (56 days in this case) and simulated values were plotted against the observed values (Fig. 5). Ammonium and nitrate concentrations in the water column (*s*_nh4wat and *s*_no3wat) were well simulated with predicted values randomly around the observed values. Simulated values for sediment organic and inorganic nitrogen compounds were higher than observed values most of the time, but average relative errors (AREs) remained equal or <0.11 (Table 7). The agreement between simulated and observed fish weight and phytoplankton biomass was good. Fig. 6 presents the temporal dynamics of the system for two selected variables (organic nitrogen and ammonium in sediments) after calibration and validation.

The combination of all the coefficient values gave at the end relative errors oscillating between 0 and -0.23 (Table 7). The simulation of ammonium in the sediments (*s*_nh4sed) presented the highest positive deviation from observed values on days 7 and 21 ($+0.22$ and $+0.16$, respectively) while the highest negative deviation occurred on days 7 and 12 (-0.23 and -0.12, respectively) for the simulation of nitrate in the sediments (*s*_no3sed). The concentration of ammonium in the sediments also presented the higher average relative error (ARE) for the whole simulation period.

The response of the state variables to a 10% increment and 10% decrement in the value of selected parameters was used as a quantification of model sensitivity (Piedrahita, 1986); sensitivity analysis was used to identify coefficients which have a strong effect over different state variables. Table 8 summarizes the sensitivity to selected parameters and the corresponding state variable(s). The concentration of ammonium in the water column (*s*_nh4wat) was strongly affected

by the percent of protein in the feed and by the routine metabolism exponent; this last coefficient also had an important effect on the concentration of ammonium in the sediments (*s*_nh4sed) and on the fish weight (*s*_fw). Fish weight was also strongly affected by the protein digestibility coefficient.

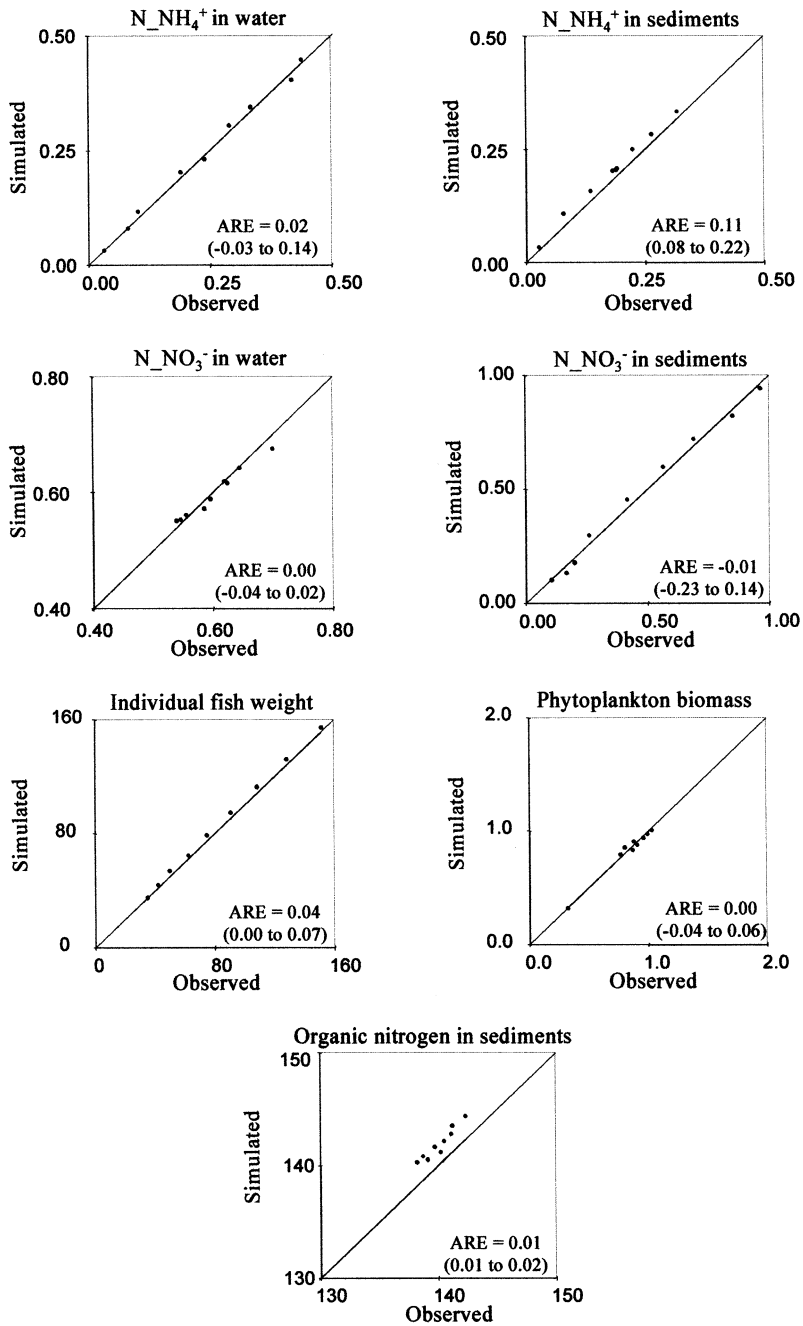

Fig. 5. Calibration results for the model. The bisector represents perfect agreement between simulated and observed values (ARE, average relative error; relative errors range is given within brackets).

Table 7
Relative errors (RE*) of state variables after calibration

Day of simulation	State variable						
	$N–NH_4^+$ (water)	$N–NH_4^+$ (sediments)	$N–NO_3^-$ (water)	$N–NO_3^-$ (sediments)	Fish weight	Phytoplankton	Organic *N* (sediments)
1	0.00	0.08	0.00	−0.03	0.00	0.00	0.02
7	0.00	0.22	0.01	−0.23	0.05	0.03	0.01
14	0.14	0.10	0.02	−0.12	0.07	−0.04	0.02
21	0.07	0.16	0.01	0.14	0.04	0.06	0.01
28	−0.03	0.11	−0.02	0.09	0.05	−0.03	0.01
35	0.05	0.08	−0.01	0.06	0.04	0.03	0.01
42	0.03	0.11	−0.01	0.04	0.04	−0.02	0.01
49	−0.04	0.07	0.00	−0.03	0.03	−0.02	0.02
56	0.02	0.05	−0.04	−0.02	0.02	−0.02	0.01
ARE**	0.02	0.11	0.00	−0.01	0.04	0.00	0.01

*, $RE = (S_{sim} - S_{obs}/(1/2)*(S_{sim} + S_{obs}))$, where S_{sim} is the simulated state value and S_{obs} is the observed state value. **, $ARE = \left(\Sigma RE/n\right)$, where ARE is the average relative error and n is the number of observations.

The validation was performed using two independent data sets from earthen ponds. Fourteen field data points collected weekly in both ponds were used to evaluate the model performance. Most of the coefficients obtained during calibration (Table 5) were maintained unchanged, whereas the only parameters being changed were the initial conditions of the system and the fish species-specific coefficients (see Table 4). Because the fish species was changed, the corresponding coefficients that characterize the species were also changed accordingly and the fish module was first calibrated for this species. Fish density and initial weight were maintained similar. The pond area and the initial conditions, especially the amount of organic nitrogen in the sediments, were also different.

Figs. 6 and 7 present the comparison between the predicted output from the simulation model and the experimental data used during the validation and Table 9 summarizes the relative errors for the principal state variables. For all state variables, there were no significant differences between the two ponds (paired *t*-test, $P > 0.05$), so data sets could be averaged. The organic nitrogen in the sediments (*s*_orgnsed) was poorly simulated, especially after day 28; the average relative error (ARE) was also the highest (-0.34) indicating that predicted values were lower than observed values. Simulated values for ammonium in the sediments (*s*_nh4sed) were, most of the time, lower than observed values and presented a high ARE (-0.19); nitrate concentration in the water column (*s*_no3wat) was better simulated than ammonium (*s*_nh4wat). The fish weight (*s*_fw) and the phytoplankton biomass (*s*_phytobiom) were well simulated by the model, presenting the lowest ARE. In the case of fish, this was expected as we calibrated the fish module first for this species.

5. Discussion

Comprehensive models on nitrogen dynamics in aquacultural systems have been presented (e.g. Nielsen et al., 1999; Montoya et al., 1999) but they are focused on systems under different biological and physical conditions as studied here. A comprehensive simulation model, covering the fish, phytoplankton and the pond physical environment in tropical aquacultural ponds under a semi-intensive production system was developed, calibrated and validated. Most of the initial values of the coefficients used in the model were found in the literature and were set after calibration within reported ranges (Table 5). Data used for calibra-

tion and validation originated from ponds of different area (800 vs. 65 m^2) and length/surface area ratio (0.15 vs. 0.50); this could affect the ecological conditions of the systems, but the model simulates fairly well most of the nitrogen allocation sources in the pond.

5.1. Simulation of inorganic nitrogen species in the water column

Total ammonium nitrogen (TAN) and nitrate in the water column were fairly well simulated. In the model it was considered that TAN originates from mineralization in situ of organic nitrogen, fish excretion or diffusion from the sediments, and that mineralization was influenced by pH and dissolved oxygen (Reddy and Patrick, 1984; Oláh et al., 1987). This approach led to reasonable accurate prediction.

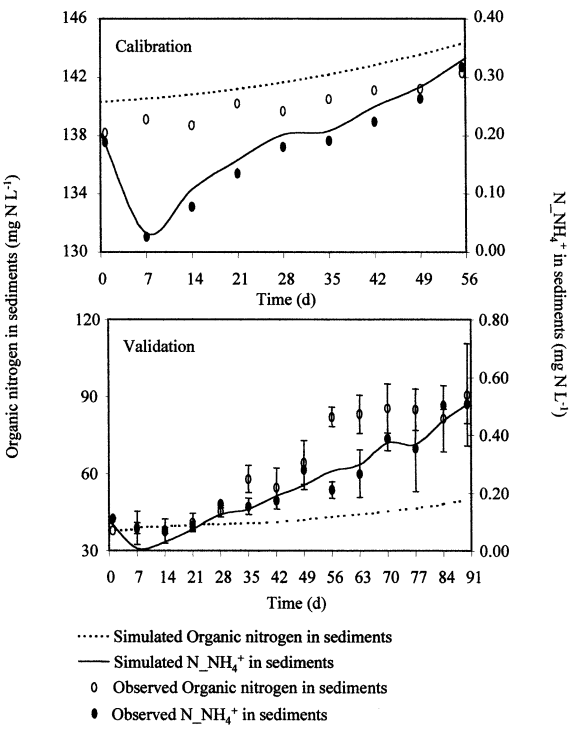

Fig. 6. Temporal dynamics of the model for organic nitrogen and ammonium in the sediments. Upper and lower graphs present the predicted output from the simulation model and experimental data after calibration and validation (mean, $n = 2$), respectively.

The nitrate concentration in the water was also predicted with reasonable accuracy. According to Sharma and Ahlert (1977), nitrification is a function of dissolved oxygen, temperature, pH, substrate concentration, light and number of nitrifying bacteria. Numbers of nitrifying bacteria were not included in the present work, assuming that the pond is at a steady state regarding microbial population. Hargreaves (1997) assumed that the nitrification rate could be described by a first-order reaction. The first order constant is then temperature dependent ($p\_\text{nitrifwat} = 0.002 + 0.0025 * a\_\text{temp}$). In our model, the nitrification coefficient ($p\_\text{nitrifwat}$) was set constant (Table 5) and it was assumed that nitrification did not proceed when dissolved oxygen was lower than 2 ppm (Knowles et al., 1965; Wuhrmann, 1968); the rate of nitrification was determined by substrate concentration when oxygen was above this value (Eq. (10)). Both approaches gave similar results with differences between simulated and observed dissolved nitrate and ammonium concentrations not higher than 15%.

During validations, positive and negative differences between simulated and observed values of $N–NH_4^+$ or $N–NO_3^-$ often opposed each other (Table 9). This is possibly related to variations in the nitrification rate. However, changing the value used for the rate constant of nitrification (4.17e-4 (h^{-1}), Bansal, 1976), the simulations were not improved. Another explanation could be the uptake rate of TAN by the phytoplankton and TAN's concentration considering the phytoplankton 'preference' for ammonium instead of nitrate (McCarthy, 1981): at the higher negative $N–NH_4^+$ difference (day 14), the phytoplankton uptake rate was 39.28 mg N m^{-2} d^{-1}, while at the higher positive difference (day 70), the uptake rate was 20.24 mg N m^{-2} d^{-1}. If the uptake rate of TAN is higher than estimated it causes a negative difference of its concentration.

5.2. Phytoplankton

Phytoplankton biomass increased from an initial concentration of 0.322 to 1.032 mg of nitrogen per litre. When the nitrogen content in the dead phytoplankton was also taken into account,

Table 8
Sensitivity analysis

Coefficient	Module	State variable affected	±10%*
Gram of amino acids needed for 1 mole ATP	Fish	$N–NH_4^+$ in water	18.3
		$N–NH_4^+$ in sediments	16.7
		Fish weight	−15.9
Protein digestibility coefficient	Fish	Fish weight	22.6
Routine metabolism exponent	Fish	$N–NH_4^+$ in water	25.4
		$N–NH_4^+$ in sediments	22.3
		$N–NO_3^-$ in sediments	18.0
		Fish weight	−20.9
Fraction of protein in feed	Fish	$N–NH_4^+$ in water	21.6
		$N–NH_4^+$ in sediments	19.7
		$N–NO_3^-$ in sediments	16.6
Carbon/nitrogen ratio	Phytoplankton	$N–NO_3^-$ in water	15.5
		Phytoplankton	−18.4
Constant for light extinction	Phytoplankton	$N–NO_3^-$ in water	15.5
		Phytoplankton	−18.4

Effect of increasing or decreasing by 10% the indicated coefficient. *, Numbers indicate the difference between the final value of the state variable when the respective coefficient was increased by 10% and the value of the state variable when the coefficient was decreased by 10% as a percentage of the state variable value obtained using the coefficient after calibration. The sign represents under- or over-estimation depending on whether the sign is negative or positive. The table includes only coefficients whose change affected by $>15\%$ the value of any state variable.

the total produced biomass of algae was estimated to be 1.16 mg l^{-1} on day 56. The importance of phytoplankton as a regulator of ammonia concentrations in fish ponds is well known (Tucker et al., 1984; Krom et al., 1989), and uptake of dissolved inorganic nitrogen from the water column is the primary pathway of nitrogen removal (Barica, 1974; Boyd, 1974). The uptake rate of nitrogen by phytoplankton was 264.4 mg N m^{-2} d^{-1} at the beginning of the experiment, decreasing during the growing cycle, partly due to nutrient and light limitations, the last caused by algal self-shading.

To facilitate practical use of the model, phytoplankton biomass was measured as chlorophyll-a concentration which does not permit separation of phytoplankton biomass into species or groups of algae. Still, the proposed model was accurate enough to predict phytoplankton concentrations. During calibrations, phytoplankton was very well simulated with an ARE of 0 and REs $\not> 0.06$. Validation, using different initial conditions for phytoplankton, such as initial biomass and pond area (Table 4), also resulted in good agreement of simulated and observed data.

5.3. Simulation of nitrogen species in the sediments

The concentrations of inorganic nitrogen in the sediments were less well simulated than in the water column. The ammonium concentration in the sediments presented a high ARE after calibration (0.11, Table 7) with always positive REs since model estimations exceed observed values. Several factors could have caused this. Ammonium can be adsorbed by negatively charged soil colloids (Boyd, 1995). Soil pH was assumed to follow a daily fluctuating pattern based on field determinations and, if actual pH values were lower than assumed, then part of the $N–NH_4^+$ would not be accounted for. Since laboratory measurements of TAN included both dissolved and adsorbed nitrogen in sediments, cation exchange capacity (CEC) was not considered. Sediment samples used for the laboratory analysis were taken from the upper 5 cm layer.

According to Diab and Shilo (1986), the concentration of free and bound ammonia is lower in the upper layer, increases with depth up to 15–20 cm and decreases in deeper layers. The profile of $N-NH_4^+$ seems important to consider and a separation of layers could result in a better simulation of nitrogen compounds in the sediments. Finally, if part of the dissolved $N-NH_4^+$ seep through the pond bottom, model overestimations will occur. Although seepage data were not available, the

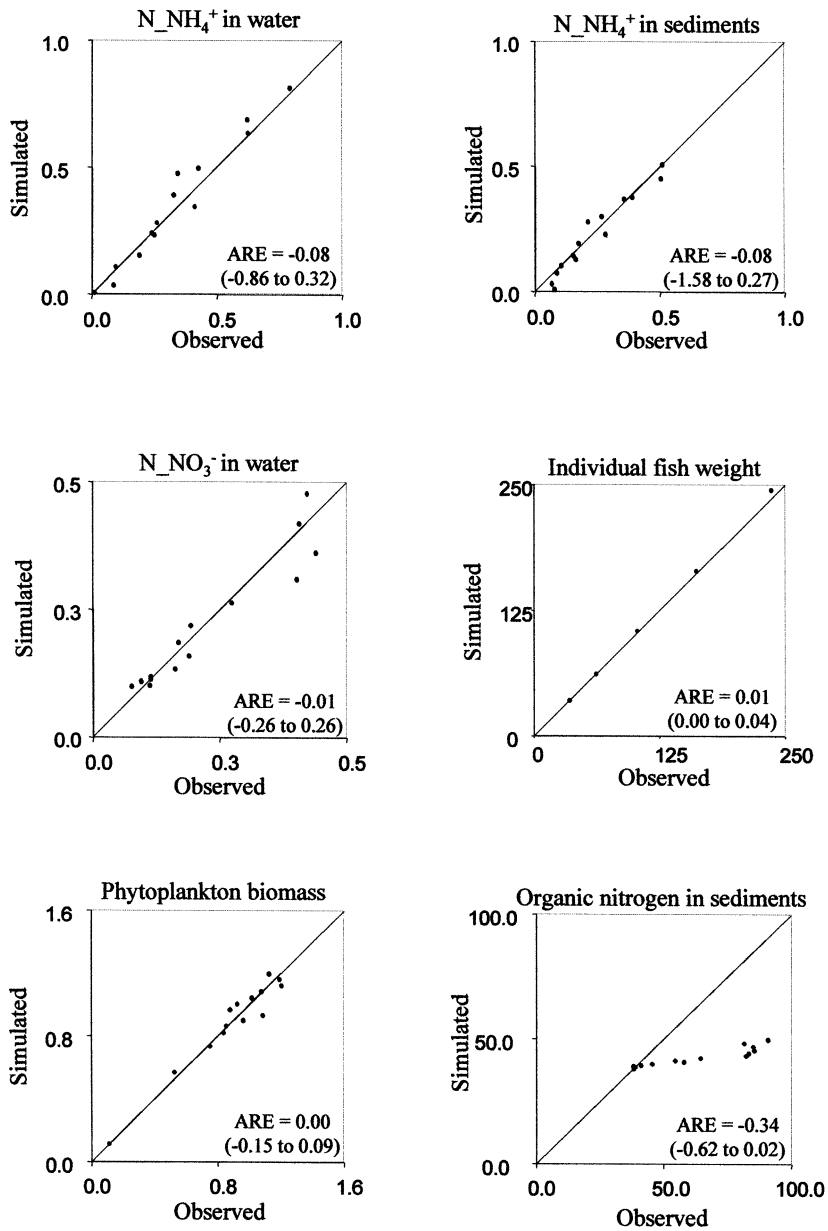

Fig. 7. Predicted output from the simulation model and experimental data (mean, $n = 2$) used during validation. The bisector represents perfect agreement between simulated and observed (ARE, average relative error; relative errors range is given within brackets).

Table 9
Relative errors (RE*) of state variables obtained during validation

Day of simulation	State variable					
	$N–NH_4^+$ (water)	$N–NH_4^+$ (sediments)	$N–NO_3^-$ (water)	Fish weight	Phytoplankton	Organic *N* (sediments)
1	0.00	0.00	0.00	0.00	0.00	0.00
7	−0.76	−1.58	−0.10		0.07	−0.01
14	−0.86	−0.74	0.26		−0.02	0.02
21	0.11	−0.15	0.14	0.00	−0.02	−0.04
28	−0.23	−0.24	0.03		0.01	−0.13
35	−0.07	−0.06	−0.20		−0.07	−0.35
42	0.07	0.10	−0.17	0.02	−0.15	−0.28
49	−0.18	−0.21	0.10		0.09	−0.42
56	0.17	0.27	0.13		0.08	−0.62
63	0.15	0.12	−0.04	0.02	0.02	−0.61
70	0.32	−0.03	−0.26		0.00	−0.61
77	0.02	0.04	−0.20		−0.07	−0.58
84	0.10	−0.11	0.03	0.04	−0.03	−0.51
90	0.03	0.00	0.12		0.06	−0.59
ARE**	−0.08	−0.19	−0.01	0.01	0.00	−0.34

REs are calculated for the average of the two ponds used. *, $RE = (S_{sim} - S_{obs}/(1/2)*(S_{sim} + S_{obs}))$, where S_{sim} is the simulated state value and S_{obs} is the observed state value. **, $ARE = \left(\Sigma RE/n\right)$, where ARE is the average relative error and n is the number of observations.

ponds used were rather old and seepage in earthen ponds is reduced over time (Boyd, 1990). Another possible pathway for $N–NH_4^+$ is the diffusion towards the water column; according to Hargreaves (1998), sediments are a source of ammonium to the water column; within the diffusion rates equations both the concentration gradient between water and sediments and a fixed soil porosity ($p\_porosity = 0.84$) were included. As stated before, $N–NH_4^+$ in the water column was well simulated and, again, any increase of the coefficients of the flux rate equation did not improve the simulations any further. The nitrate concentration in the sediments was fairly well simulated, although it can be noticed that highest positive difference of $N–NH_4^+$ and highest negative difference of $N–NO_3^-$ also occurred on the same day (day 7).

Organic matter accumulated in the observed system. Martin et al. (1998) found that up to 38% of the nitrogen entering the ponds may accumulate in the sediments. The calibrated organic nitrogen in the sediments was well simulated (Fig. 5). However, validation proved that this state variable is not well simulated (Fig. 6). The organic nitrogen in the sediment might partly be incorporated in biota as insect larvae that fly out from the system; reports on insect larval abundance in shallow ponds are highly variable, being in the order of < 0.5 up to > 100 g m^{-2} (e.g. Merla and Müller, 1970; Drake and Arias, 1995; Stagliano et al., 1998). Information on this respect is scarce and should be investigated further.

To keep the model simple, the ammonification rate was modeled as a first-order reaction with respect to organic matter concentration, taking into account a minimum pH and dissolved oxygen to proceed. The dynamics of organic matter decomposition is much more complex. Anaerobic decomposition of organic matter was not considered in the model. However, anaerobic bacteria in sediments can produce ammonium at the same rate (or even higher) as aerobic ones (Jacobsen and Jörgensen, 1975). The anaerobic ammonia production is dependent on the C:N ratio of the organic material, soil texture, pH, temperature

and nutrient availability (Reddy and Patrick, 1984). Further, higher oxygen concentrations affect the microbial transformations of nitrogen or organic carbon degradation (Avnimelech et al., 1992). Therefore, it might be useful to include the sedimentation-resuspension of organic matter in future studies. Avnimelech and Wodka (1988) found that resuspended material accounted for 50% of the total sedimentation flux in a reservoir of 8 m deep and this value is much higher in aquaculture ponds (Avnimelech et al., 1999).

5.4. Simulation of fish growth

Well documented and reported values of parameters from literature were directly used for the growth simulations of tilapia and *Colossoma* (Table 4). Simulation for the size used (35–155 g in calibration runs, 35–270 g in validation runs) resulted in REs $\not> 0.07$. Because of the good agreement between simulated and observed values, any further assessment of these coefficients is not a priority for model improvement.

Feed sources are difficult to assess in fish ponds, particularly in extensive or semi-intensive systems. In manured fish ponds, 50–80% of the fish yield originates from algal-based food webs harvested primarily after the algae had been processed within the detritus of the pond bottom (Schroeder, 1987). Depending on the fish species, phytoplankton could be an important natural food source for fish cultured in extensive culture systems (Yusoff and McNabb, 1997). In our case, it was assumed that fish preferred artificial feed to natural feed and fish take artificial feed independent of the concentration of natural feed sources (Schroeder, 1978; Milstein et al., 1995; Jamu, 1999). The amount of feed not eaten is also difficult to assess (Nijhof, 1994; van der Meer et al., 1995), but the assumption that 35% of the feed offered was not eaten ($p\_mors = 0.35$) proved adequate. The effect of this parameter on the simulation of fish growth is presented in Fig. 8. Sensitivity analysis (see below) demonstrated that changing this value $\pm 10\%$ did not result in large effect on the simulation results. Only when this coefficient was changed by $> 30\%$ (that is increasing or decreasing p_mors to 0.45 or 0.25), the simulation of state variables, such as TAN in water or sediments, were affected.

The fish growth module, in general, had a strong impact on the N budget in water and in sediments. This is logical since feed nitrogen is the largest N-input, and feed utilization and metabolism should have a large influence on the sinks of nitrogen in the system. The fact that the model

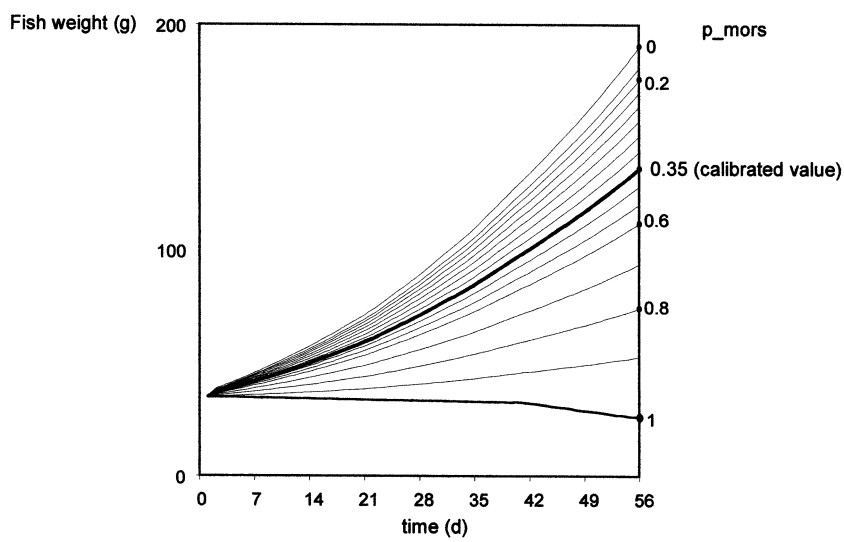

Fig. 8. Effect of feed spill parameter (p_mors) on fish growth.

simulates most *N*-variables well also means that such dynamic modeling of metabolic processes is a good approach.

5.5. Sensitivity analysis

Varying parameters over a certain range and comparing their relative influence on the end result was the aim of the sensitivity analysis. This exercise resulted in the identification of coefficients with important effects on the model simulations. The principal state variables affected by changing the specific coefficients were $N-NH_4^+$ and $N-NO_3^-$ both in water and sediments (Table 8). This is an important result from the point of view of aquaculture system managements, considering that the concentrations of these two forms of nitrogen are frequently difficult to predict. The C:N ratio in phytoplankton presented an important effect on the phytoplankton module. In the model, this parameter was used to convert phytoplankton biomass into organic carbon, so it influences the rate of degradation of organic matter. With a large C:N ratio, the substrate does not supply enough nitrogen to satisfy microbial requirements (Boyd, 1990). Hence, nitrogen will be immobilized rather than mineralized.

6. Conclusions

In summary, the approach followed in this work resulted in a better understanding of the nitrogen dynamics in fish ponds. The model simulates fairly well most of the nitrogen allocation sources in the pond. Specific effects on $N-NH_4^+$ and $N-NO_3^-$ concentrations, both in water and in sediments are related to coefficients of processes included in the fish and phytoplankton modules. As stated before, the simulation of these two state variables were good after calibration and during validation, so changes in their coefficients would not be a priority for model improvement. Simulated organic nitrogen in sediments was most of the time higher than observed values. Special attention should be given to soil organic matter equations; the dynamics of organic matter accumulating in the sediments, especially the processes of deposition/accumulation and decomposition are the most likely causes of error in the model and should be studied. Another important addition that should be incorporated in future versions of the model is the dynamics of the microbial biomass as a source of feed for the cultivated organisms. Research is needed to study how bacteria can incorporate ammonia and how bacterial biomass can be utilized by fish.

This model can be used as a research tool for earthen ponds stocked with tilapia or tambaquí. But application of the model is still limited by its rather high data requirements. Data sets of experiments that include all the necessary measurements along a growing cycle are not available, but badly needed for further improvement of the model. Also, data sets from other pond environments are needed to make the model applicable to a wider range of culture environments. The fish growth compartment can be calibrated for different fish species, but could also be adapted for the simulation of shrimp growth. The model may then also be applied to shrimp culture systems, where water quality deterioration and negative environmental impacts are still widespread problems.

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Appendix A. Variables used in the model during calibration and respective equation involved

Variable	Related equation
p_aaatp	$r\_aaox = a\_aaswtch * r\_atpmet * p\_aaatp$
p_aafdgl	$s\_aapool1(t) = s\_aapool1(t–dt) + ((1–p\_aafdgl) * r\_prodig - r\_prosyn) * dt$ $s\_aapool2(t) = s\_aapool2(t - dt) + (p\_aafdgl * r\_prodig - r\_aagluc) * dt$
$p\_ammonifsed$	$r\_ammonifsed$ = if ($a\_phsed > 2$) and ($a\_dosed > 2$) then ($s\_ornsed * p\_ammonifsed$) else 0
$p\_ammonifwat$	$r\_ammonifwat$ = if ($a\_phwat > 2$) and ($a\_dowat > 2$) then ($s\_phytodead * p\_ammonifwat$) else 0
$p\_cnratio$	$a\_poc = s\_phytobiom * p\_cnratio$
$p\_constext$	$a\_totlext = p\_exwa + p\_constext * a\_poc$
$p\_denitrifsed$	$p\_denitrifsed = (0.0318 * \exp(0.078 * (a\_temp - 20)))/24$
$p\_diffcoefnh3$	$p\_volatnh3 = p\_diffcoefnh3/(p\_waterdepth * 100 * p\_zfilm)$
p_digca	$r\_cardig = r\_fdrtdm * (a\_feedca) * p\_digca * 1.11$
p_digli	$r\_lipdig = r\_fdrtdm * (a\_feedli) * p\_digli * 0.96$
p_digpr	$r\_prodig = r\_fdrtdm * (a\_feedpr) * p\_digpr * 1.18$ $r\_egspro = ((1 - p\_digpr) * a\_feedpr * r\_fdrtdm)$
p_exwa	$a\_totlext = p\_exwa + p\_constext * a\_poc$
p_fac1, p_fac2	$a\_aalirat = \mathrm{MAX}(0, 0.95 - (p\_fac1/100) * a\_prolev - (p\_fac2/100) * (a\_pe * \mathrm{SQRT}(\mathrm{SQRT}(a\_prolev))))$
p_iliper	Initial lipid
p_kn	$a\_nutrilim$ = if ($a\_nleft <= 0$) then 0 else ($nleft/(p\_kn + a\_nleft)) * (a\_nleft)) * (a\_pleft/(p\_kp + a\_pleft))$
p_liatco	$r\_atplip = p\_liatco * r\_lipsyn1$
p_liatp	$r\_lipox = a\_liswtch * r\_atpmet * p\_liatp$
p_lipfin	$a\_aaswtch$ = if $a\_liperc > p\_lipfin$ then $(1 - a\_aalirat)$ else 1 $a\_liswtch$ = if $a\_liperc > p\_lipfin$ then $a\_aalirat$ else 0
$p\_maxgrphyto$	$r\_phytogrowth = p\_maxgrphyto * (a\_nutrilim * a\_lighlim) * s\_phytobiom$
p_mors	$r\_fdrtdm = a\_ration * a\_feeddm * (1 - p\_mors)$ $r\_fdrtfw = a\_ration * (1 - p\_mors)$ $r\_uneadm = a\_ration * a\_feeddm * p\_mors$ $r\_uneafw = a\_ration * p\_mors$
$p\_mrphyto$	$r\_phytom = p\_mrphyto * \exp(a\_tecorm) * s\_phytobiom$
$p\_neoatco$	$r\_atpneo = p\_neoatco * r\_aagluc$
p_nh3dif	$r\_nh3flux = (-p\_porosity * p\_nh3dif * (((s\_nh3sed - s\_nh3wat)/1000)/p\_seddepth)) * (1000/(24 * p\_waterdepth))$
p_nh4dif	$r\_nh4flux = (-p\_porosity * p\_nh4dif * (((s\_nh4sed - s\_nh4wat)/1000)/p\_seddepth)) * (1000/(24 * p\_waterdepth))$
$p\_nitrifsed$	$r\_nitrifsed$ = if $a\_dosed > 4$ then ($p\_nitrifsed * s\_nh4sed$) else 0
$p\_nitrifwat$	$r\_nitrifwat$ = if ($a\_dowat > 2$) then ($p\_nitrifwat * s\_nh4wat$) else 0
p_no3dif	$r\_no3flux = (-p\_porosity * p\_no3dif * (((s\_no3sed - s\_no3wat)/1000)/p\_seddepth)) * (1000/(24 * p\_waterdepth))$
$p\_pondarea$	$a\_pondvol = (p\_pondarea * p\_waterdepth) * 1000$
$p\_porosity$	$r\_n2flux = (-p\_porosity * p\_n2dif * (((s\_n2sed - s\_n2wat)/1000)/p\_seddepth)) * (1000/(24 * p\_waterdepth))$

	$r\_nh3flux = (-p\_porosity*p\_nh3dif*(((s\_nh3sed-s\_nh3wat)/1000)/p\_seddepth))*(1000/(24*p\_waterdepth))$
	$r\_nh4flux = (-p\_porosity*p\_nh4dif*(((s\_nh4sed-s\_nh4wat)/1000)/p\_seddepth))*(1000/(24*p\_waterdepth))$
	$r\_no3flux = (-p\_porosity*p\_no3dif*(((s\_no3sed-s\_no3wat)/1000)/p\_seddepth))*(1000/(24*p\_waterdepth))$
p_pratco	$r\_atppro = p\_pratco*r\_prosyn$
p_prperc	$r\_wfrate = (r\_prosyn-r\_aaox)/(p\_prperc/100)$
	$r\_wfraten = 0.16*r\_wfrate*(p\_prperc/100)*(1000/a\_pondvol)*a\_fishnb$
p_q10	$r\_roumet = p\_q10 \wedge ((a\_temp-p\_reftemp)/10)*p\_rmcf*(s\_wf \wedge p\_rmex)$
p_radop	$a\_lighlim = ((2.178*a\_phoper)/(a\_totlex*p\_waterdepth))*(\exp(-(a\_decisor/p\_radop)*\exp(-a\_totlext*p\_waterdepth))$ $-\exp(-(a\_decisor/p\_radop)*\exp(-a\_totlext*p\_waterdepth))$
$p\_reftemp$	$r\_roumet = p\_q10 \wedge ((a\_temp-p\_reftemp)/10)*p\_rmcf*(s\_wf \wedge p\_rmex)$
p_rmcf	$r\_roumet = p\_q10 \wedge ((a\_temp-p\_reftemp)/10)*p\_rmcf*(s\_wf \wedge p\_rmex)$
p_rmex	$r\_roumet = p\_q10 \wedge ((a\_temp-p\_reftemp)/10)*p\_rmcf*(s\_wf \wedge p\_rmex)$
$p\_seddepth$	$r\_n2flux = (-p\_porosity*p\_n2dif*(((s\_n2sed-s\_n2wat)/1000)/p\_seddepth))*(1000/(24*p\_waterdepth))$
	$r\_nh3flux = (-p\_porosity*p\_nh3dif*(((s\_nh3sed-s\_nh3wat)/1000)/p\_seddepth))*(1000/(24*p\_waterdepth))$
	$r\_nh4flux = (-p\_porosity*p\_nh4dif*(((s\_nh4sed-s\_nh4wat)/1000)/p\_seddepth))*(1000/(24*p\_waterdepth))$
	$r\_no3flux = (-p\_porosity*p\_no3dif*(((s\_no3sed-s\_no3wat)/1000)/p\_seddepth))*(1000/(24*p\_waterdepth))$
p_temax	$a\_tecorm = \text{if } a\_temp > p\_temax \text{ then } (a\_temp-p\_temax) \text{ else } 0$
$p\_volatnh3$	$p\_volatnh3 = p\_diffcoefnh3/(p\_waterdepth*100*p\_zfilm)$
	$r\_volatnh3 = p\_volatnh3*s\_nh3wat$
$p\_waterdepth$	$r\_n2flux = (-p\_porosity*p\_n2dif*(((s\_n2sed-s\_n2wat)/1000)/p\_seddepth))*(1000/(24*p\_waterdepth))$
	$r\_nh3flux = (-p\_porosity*p\_nh3dif*(((s\_nh3sed-s\_nh3wat)/1000)/p\_seddepth))*(1000/(24*p\_waterdepth))$
	$r\_nh4flux = (-p\_porosity*p\_nh4dif*(((s\_nh4sed-s\_nh4wat)/1000)/p\_seddepth))*(1000/(24*p\_waterdepth))$
	$r\_no3flux = (-p\_porosity*p\_no3dif*(((s\_no3sed-s\_no3wat)/1000)/p\_seddepth))*(1000/(24*p\_waterdepth))$
	$a\_lighlim = ((2.178*a\_phoper)/(a\_totlex*p\_waterdepth))*(\exp(-(a\_decisor/p\_radop)*\exp(-a\_totlext*p\_waterdepth)))$ $-\exp(-(a\_decisor/p\_radop)*\exp(-a\_totlext*p\_waterdepth))$
	$a\_pondvol = (p\_pondarea*p\_waterdepth)*1000$
	$p\_volatn2 = p\_diffcoefn2/(p\_waterdepth*100*p\_zfilm)$
	$p\_volatnh3 = p\_diffcoefnh3/(p\_waterdepth*100*p\_zfilm)$
p_zfilm	$p\_volatn2 = p\_diffcoefn2/(p\_waterdepth*100*p\_zfilm)$
	$p\_volatnh3 = p\_diffcoefnh3/(p\_waterdepth*100*p\_zfilm)$

Parameters

*p*_aaatp, g amino acids needed for 1 mole ATP; *p*_aafdgl, fraction of digested protein used for gluconeogenesis; *p*_ammonifsed, instant rate of ammonification in sediments; *p*_ammonifwat, instant rate of ammonification in water; *p*_cnratio, ratio carbon/nitrogen in phytoplankton; *p*_constext, constant for extinction; *p*_denitrifsed, instant rate of denitrification; *p*_diffcoefn2, diffusion coefficient for N2; *p*_diffcoefnh3, diffusion coefficient for NH3; *p*_digca, carbohydrate digestibility coefficient; *p*_digli, lipid digestibility coefficient; *p*_digpr, protein digestibility coefficient; *p*_exwa, light extinction due to water; *p*_fac1, first factor for aalirat equation; *p*_fac2, second factor for aalirat equation; *p*_iliper, initial lipid; *p*_kn, half saturation constant for nitrogen; *p*_kp, half saturation constant for phosphorus; *p*_liatco, cost of lipid synthesis; *p*_liatp, g lipids needed for 1 mole ATP; *p*_lipfin, minimum fat percentage in fresh weight of fish; *p*_maxgrphyto, instant rate of phytoplankton growth; *p*_mors, fraction of feed given to fish but not eaten; *p*_mrphyto, instant rate of phytoplankton mortality; *p*_neoatco, cost of neoglucogenesis; *p*_nitrifsed, instant rate of nitrification in sediments; *p*_nitrifwat, instant rate of nitrification in water; *p*_n2dif, diffusion coefficient for N2; *p*_nh3dif, diffusion coefficient for NH_3; *p*_nh4dif, diffusion coefficient for NH_4; *p*_no3dif, diffusion coefficient for NO3; *p*_pondarea, pond area; *p*_porosity, soil porosity; *p*_pratco, cost of protein synthesis; *p*_prperc, protein percentage in fresh weight; *p*_q10, Q10 factor metabolism; *p*_radop, saturation light intensity; *p*_reftemp, ref. temp. routine metabolism; *p*_rmcf, routine metabolism coefficient; *p*_rmex, routine metabolism exponent; *p*_seddepth, sediment depth; *p*_temax, maximum temperature for phytoplankton; *p*_volatnh3, instant rate of volatilization of NH_3; *p*_volatn2, instant rate of volatilization of N_2; *p*_waterdepth, water depth; *p*_zfilm, water/sediment film thickness.

State variables

*s*_aapool1, amount of AA converted into protein; *s*_aapool2, amount of AA converted into glucose (gluconeogenesis); *s*_n2sed, N2 in sediments; *s*_n2wat N2 in water; *s*_nh3sed, NH_3 in sediments; *s*_nh3wat, NH_3 in water; *s*_nh4sed, NH_4^+ in sediments; *s*_nh4wat, NH_4^+ in water; *s*_no3sed, NO3 in sediments; *s*_no3wat, NO3 in water; *s*_ornsed, amount of organic nitrogen matter in sediments; *s*_phytodead, organic N (as dead phytoplankton) in water; *s*_phytobiom, phytoplankton biomass; *s*_wf, individual fish weight (wet weight).

Auxiliary variables

*a*_aalitrat, proportion of energy supplied by fat; *a*_aaswtch, switch, becomes 1 when fat percentage of fish falls below *p*_lipfin, thus switching energy to 100% protein oxidation; *a*_decisor; *a*_dosed, dissolved oxygen in sediment; *a*_dowat, dissolved oxygen in water; *a*_feedca, fraction of carbohydrate in feed (wet); *a*_feeddm, fraction of dry matter in feed; *a*_feedli, fraction of lipid in feed (wet); *a*_feedpr, fraction of protein in feed (wet); *a*_fishnb, number of fish present initially; *a*_lighlim, light limitation factor; *a*_liperc, fat percentage of the fish; *a*_liswtch, switch, becomes 0 when fat percentage of fish falls below *p*_lipfin, thus switching off lipid oxidation; *a*_nleft, N that remains in water; *a*_nutrilim, nutrients limitation; *a*_pe, feed protein/gross energy ratio; *a*_phoper, photoperiod; *a*_phsed, sediments pH; *a*_phwat, water pH; *a*_pleft, *P* that remains in water; *a*_poc, organic carbon in phytoplankton; *a*_pondvol, pond volume; *a*_prolev, actual protein feeding level; *a*_ration, daily feed ration; *a*_tecorm, temperature correction for mortality; *a*_temp, water temperature; *a*_totlext, total light extinction.

Rates

*r*_aagluc, rate of gluconeogenesis; *r*_aaox, amino acid oxidation rate; *r*_ammonifsed, ammonification in sediments; *r*_ammonifwat, ammonification in water; *r*_atplip, rate of energy use for lipid synthesis from lipid; *r*_atpmet, rate of energy use for total metabolism; *r*_atpneo, rate of energy use for gluconeogenesis; *r*_atppro, rate of energy use for protein synthesis; *r*_cardig, rate of digestion of carbohydrates from feed; *r*_egspro, egestion rate protein; *r*_fdrtdm, real feeding rate; *r*_fdrtfw, feed consumption rate; *r*_lipdig, lipid digestion rate; *r*_lipox, lipid oxidation rate; *r*_lipsyn1, lipid synthesis rate from digested lipids; *r*_n2flux, flux of N2; *r*_nh3flux, flux of NH_3; *r*_nh4flux, flux of NH_4^+; *r*_nitrifsed, nitrification in sediments; *r*_nitrifwat, nitrification in water; *r*_no3flux, flux of NO3; *r*_phytogrowth, phytoplankton growth;

*r*_phytom, phytoplantation death; *r*_prodig, amino acid production rate from digested feed; *r*_prosyn, protein synthesis rate; *r*_roument, routine metabolic rate; *r*_uneadm, uneaten feed (dw); *r*_uneafw, uneaten feed (fw); *r*_volatnh3, ammonia volatilization; *r*_wfrate, fish growth rate; *r*_wfraten, fish growth rate in terms of nitrogen.

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