

Modeling the effect of nitrogen input from feed on the nitrogen dynamics in an enclosed intensive culture pond of black tiger shrimp (*Penaeus monodon*)

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Abstract—In the present study, a mathematical model was developed to evaluate the effect of nitrogen (N) input from feed on the N dynamics under different feeding scenarios in a well aerated and enclosed culture pond of black tiger shrimp (*Penaeus monodon*). Three feeding levels were examined: underfeeding, optimum feeding and overfeeding. The model was formulated using field data gathered from an earthen pond (0.69 ha) which was stocked with shrimp post larvae at a density of 340,000 individuals ha⁻¹ and grown for 151 d. The model suggested that the underfeeding rate (329 kg N ha⁻¹ cycle⁻¹) observed from the study pond, which was being underfed, resulted in the ingestion of the natural productivity in the pond. With the underfeeding practice, phytoplankton assimilated ammonia and nitrate+nitrite at the rates of 412 and 52 kg N ha⁻¹ cycle⁻¹, respectively, while nitrification rate in the water column was 45 kg N ha⁻¹ cycle⁻¹. The coupled processes of nitrification and denitrification in sediment were nearly equal at rates averaging 207 and 206 kg N ha⁻¹ cycle⁻¹, respectively. Optimum feeding indicated that the larger N input accelerated the accumulation of N in shrimp and phytoplankton as well as the accumulation of N in the water column and sediment. The coupled processes of nitrification and denitrification were accelerated to the rates of 298 and 292 kg N ha⁻¹ cycle⁻¹. The overfeeding practice indicated that the extra N did not accelerate the process of N assimilation by phytoplankton due to light limitation, but accelerated the N processes in the sediment resulting in the active removal of N from the enclosed shrimp culture pond through the denitrification process (343 kg N ha⁻¹ cycle⁻¹). Thus, the mathematical model developed by the present study proved to be an effective tool in understanding N dynamics and gives informative data for farm management in the enclosed culture pond of black tiger shrimp.

Key words: modelling, nitrogen dynamics, closed system, *Penaeus monodon*

Introduction

Marine shrimp culture has proven to be one of the fastest-growing food producing sectors in Thailand. Shrimp farmers tend to increase production simply by stocking at high density and increasing consumption of artificial feed (Williams et al. 1996, Arnold et al. 2006). To ensure growth of shrimp in an intensive culture, shrimp farmers prefer to provide excess feed. However, this often results in overfeeding and potentially increases N and organic matter loads in effluent discharge which results in environmental deterioration of both ponds and coastal waters (Burford and Lorenzen 2004, Islam et al. 2004). On the other hand, underfeeding practice at high stocking densities can lead to lesser amount of N input and shrimp may depend more on the natural foods

especially at the beginning of rearing (Reymond and Lagardère, 1990) and subsequent low survival due to starvation and cannibalism (Abdussamad and Thampy 1994).

Enrichment of N in shrimp ponds can lead to changes in the microbial community structure and accompanying processes (Tookwinas and Songsangjinda 1999, Songsangjinda et al. 2006). Many previous studies reported that N plays a key role in the dynamics of material cycling in both water and sediment of shrimp ponds as well as other aquaculture systems (Hargreaves 1998, Burford et al. 2003a, Thakur and Lin 2003) due to its dual roles as nutrient and toxicant (Burford and Lorenzen 2004). N input from feed can be transformed in different forms, such as dissolved organic N (DON) and ammonia in metabolic wastes and leaching from artificial feed and particulate organic N (PON) in dead plankton and feces (Burford and Williams 2001). Nitrogen

mineralization produces different forms of dissolved nitrogenous compound, which are utilized by autotrophic organisms (Diab and Shilo 1986), and contributes to the dynamics of N in pond water and bottom sediments. The control of N transformation processes and optimum feed utilization in shrimp culture are necessary to maintain good environmental conditions for shrimp growth. However, it is inherently difficult to quantitatively understand the complexity of N cycling in shrimp pond ecosystems using general explanations of good pond management practices.

Mathematical modeling can be a promising tool to evaluate this complexity in aquaculture systems. Burford and Lorenzen (2004) studied N dynamics in open-managed intensive shrimp ponds and evaluated re-mineralization processes in the sediment. The results quantified the rates of sediment re-mineralization processes that released inorganic N (ammonia) into the water column for recycling. In their study, however, the variation of N input from feed that might be varied due to different feeding practices (Chanratchakool 1994) was not taken into account.

In the present paper, we improved the mathematical model representing N dynamics in an enclosed intensive culture pond of black tiger shrimp (*Penaeus monodon*) in order to evaluate the effect of N input from feed on the N processes occurring in the pond under three different feeding scenarios. We also run the model to evaluate the dynamics interactions between phytoplankton and bacterial processes and N exchange at the water-sediment interface, which may significantly affect the N dynamics in the water column. This understanding could explore the complex response of N dynamics in a shrimp pond ecosystem to different levels of N input from feed, which is beneficial to the shrimp pond management.

Materials and Methods

Observations and chemical analysis

Data were collected from a closed intensive culture pond of black tiger shrimp (*Penaeus monodon*) (pond area 0.69 ha) located in Songkhla, Thailand. Shrimp post larvae of 16 d after hatching (PL16) were stocked at 340,000 PL ha⁻¹. The cultivation was maintained for 151 d until the harvest of shrimp of about 946 kg (1,371 kg ha⁻¹). About 3,790 kg of artificial feed (40% protein) was fed using dispersal technique throughout the production cycle. During the first 35 d, feeding (2–4 meal d⁻¹) of artificial feed was increased according to feeding table. Thereafter until the harvest the amount of feed (5 meal d⁻¹) was controlled based on observation of remaining feed on the tray (6 trays ha⁻¹). No fertilizer was used during the production cycle. At harvest, shrimp mortality was calculated at about 72% and high food conversion ratio (FCR) was about 4.01.

Field observation was carried out from May 2004 to November 2004. Water temperature in the pond varied between 26.0–30.5°C during the daytime over the production cycle. Salinity averaged at about 29±5.2 (Songsangjinda et al. 2006). The depth of water was managed at about 1.4 m within the optimum depth for water circulation (Chanratchakool 1994). Strong aeration was obtained using 8 sets of 2 hp paddle wheels as it is necessary to maintain oxic condition of the surface sediment. Water was not exchanged since dissolved oxygen (DO) concentration remained above >4 mg l⁻¹ throughout the production cycle (Chin and Ong 1994).

Water and sediment samples were collected biweekly from 4 locations in pond on the same day and various forms of N compounds (total dissolved N (TDN), PON, total ammonia (TAN), nitrate (NO₃⁻) and nitrite (NO₂⁻)) were analyzed. TAN was determined using the method described by Sasaki and Sawada (1980). The Cu–Cd reduction method was applied for NO₃⁻ determination (American Public Health Association: APHA 1985). NO₂⁻ was determined according to Bendschneider and Robinson (1952). In the present study, NO₃⁻+NO₂⁻ was referred to as NOX. TDN was analyzed according to the method of Hansen and Koroleff (1999). PON in the water samples was collected on a pre-combusted glass-fiber filter (Whatman GF/F) and the concentration determined using a CHN analyzer (LECO: model CHN900). Dissolved inorganic phosphate (DIP) was analyzed using the ascorbic acid method (APHA, 1985). Chlorophyll *a* (Chl *a*) samples were prepared by filtering the pond water with a membrane filter (Sartorius, φ=0.45 μm). The amount of Chl *a* in the sample after extraction with 90% acetone was determined spectrophotometrically and calculated using the equation of SCOR/ UNESCO (Strickland and Parsons 1972).

Sediment samples were collected immediately after the water sampling. The texture of sediment was silty-clay. Interstitial water was extracted from 20 g wet sediment with 30-ml 2N KCl overnight in refrigerator and then centrifuged at 3000 rpm for 5 min. The supernatant was removed and adjusted to the volume 200 ml using de-ionized water and filtered through GF/C before nutrient analysis (Chuan and Sugahara 1984). TAN, NO₂⁻, NO₃⁻, and TDN were analyzed by the methods described above. PON content in the sediment was analyzed using the high temperature combustion technique with a CHN analyzer (LECO 900). Sediment nitrogen concentration was converted from mg kg⁻¹ to mg l⁻¹ based on sediment density and the amount of interstitial water.

Structure of the model

The model developed in the present study consisted of 5 state variables (TAN_w, NOX_w, DON_w, PHY_w, SH_w) in the water column and 4 state variables (TAN_s, NOX_s, DON_s, PON_s) in the sediment in addition to gaseous N with all associated physical, chemical and biological processes (Fig. 1).

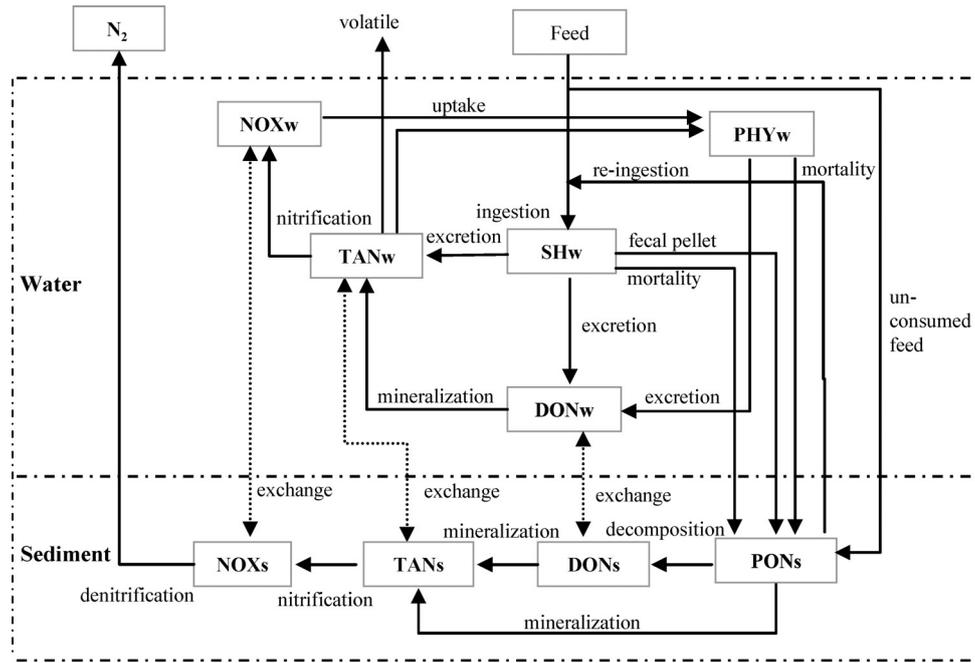


Fig. 1. Conceptual framework of N dynamics in shrimp pond.

Table 1. Symbols, definitions and units of state variables.

Symbols	Definitions	Units
PHYw	Phytoplankton N in the water column	mg l ⁻¹
SHw	Shrimp biomass in the water column	mg l ⁻¹
PONs	Particulate organic N in the sediment	mg l ⁻¹
DONw, DONs	Dissolved organic N in the water and sediment	mg l ⁻¹
TANw, TANs	Total ammonium N in the water and sediment	mg l ⁻¹
NOXw, NOXs	Nitrate and nitrite in the water and sediment	mg l ⁻¹

The symbols and units of these stated variables are defined in Table 1. Descriptions of the terms used in the present model are listed in Table 2. A summary of model equations and parameter values used in the present model are shown in Tables 3 and 4, respectively.

Estimation of N stocks and processes

The state variables for N stocks in shrimp, phytoplankton and the compartments in water column were set after Burford and Lorenzen (2004). The PON and N compartments in sediment were elaborated from the conceptual role in re-mineralization of sediment in shrimp pond reported by Burford and Lorenzen (2004) to cover all the processes of decomposition, mineralization, nitrification and denitrification generally occurring in shrimp ponds (Burford et al. 2002, Songsangjinda et al. 2004, Casillas-Hernández et al. 2006). The mass-balance equations of these nine state variables were given as follows:

$$\frac{dSHw}{dt} = N_{\text{ingested}} - TANw_{SHexc} - DONw_{SHexc} - N_{\text{fecal}} - N_{\text{mortal}}$$

$$\frac{dPHYw}{dt} = PHYw_{\text{growth}} - PHYw_{\text{mortal}} - PHYw_{\text{exc}}$$

$$\frac{dDONw}{dt} = DONw_{PHYexc} + DONw_{SHexc} - DONw_{\text{min}} \pm DONw_{\text{dif}}$$

$$\frac{dTANw}{dt} = TANw_{SHexc} + DONw_{\text{min}} - PHYw_{\text{growth}} \times \left(\frac{TANw}{TANw + NOXw} \right) - TANw_{\text{nitri}} - TANw_{\text{volat}} \pm TANw_{\text{dif}}$$

$$\frac{dNOXw}{dt} = TANw_{\text{nitri}} - PHYw_{\text{growth}} \times \left(\frac{NOXw}{NOXw + TANw} \right) \pm NOXw_{\text{dif}}$$

$$\frac{dPONs}{dt} = N_{\text{unconsum}} + N_{PHYmortal} + N_{\text{mortal}} + N_{\text{fecal}} - N_{\text{reingested}} - PONs_{\text{decomp}} - PONs_{\text{min}}$$

$$\frac{dDONs}{dt} = PONs_{\text{decomp}} - DONs_{\text{min}} \pm DONw_{\text{dif}}$$

$$\frac{dTANs}{dt} = PONs_{\text{min}} + DONs_{\text{min}} - TANs_{\text{nitri}} \pm TANw_{\text{dif}}$$

$$\frac{dNOXs}{dt} = TANs_{\text{nitri}} - NOXs_{\text{denitri}} \pm NOXw_{\text{dif}}$$

Table 2. Description of the terms used in the present model.

Symbols	Definitions	Units
A_t	Total dissolved N waste	$\text{mg l}^{-1} \text{ day}^{-1}$
N_t	Number of shrimp	ind. l^{-1}
W_t	Shrimp mean weight	g
$N_{\text{feedinput}}$	Nitrogen input to shrimp pond	$\text{mg l}^{-1} \text{ day}^{-1}$
$\text{feed}_{\text{input}}$	Daily feeding	$\text{mg l}^{-1} \text{ day}^{-1}$
N_{ingested}	Nitrogen ingestion by shrimp	$\text{mg l}^{-1} \text{ day}^{-1}$
N_{SH}	Nitrogen remaining rate in shrimp body per day	$\text{mg l}^{-1} \text{ day}^{-1}$
N_{feces}	Nitrogen excrete by shrimp as a form of fecal pellet	$\text{mg l}^{-1} \text{ day}^{-1}$
ΔW_t	Weight increase in shrimp body per day	$\text{g l}^{-1} \text{ day}^{-1}$
$N_{\text{reingested}}$	Re-ingestion of PONs on sediment surface	$\text{mg l}^{-1} \text{ day}^{-1}$
N_{unconsum}	Unconsumed feed on the sediment surface	$\text{mg l}^{-1} \text{ day}^{-1}$
N_{mortal}	Shrimp mortality	$\text{mg l}^{-1} \text{ day}^{-1}$
$\text{PHYW}_{\text{growth}}$	Phytoplankton growth	$\text{mg l}^{-1} \text{ day}^{-1}$
$\text{PHYW}_{\text{mortal}}$	Phytoplankton mortality	$\text{mg l}^{-1} \text{ day}^{-1}$
PHYW_{exc}	Phytoplankton excretion	$\text{mg l}^{-1} \text{ day}^{-1}$
Llight	Light limitation for phytoplankton	—
k	Extinction coefficient due to phytoplankton and other sources	—
$L_{\text{N,P}}$	Nutrient limitation for phytoplankton	—
T	Water temperature	$^{\circ}\text{C}$
DONw_{min}	Mineralization of DONw to TANw	$\text{mg l}^{-1} \text{ day}^{-1}$
$\text{TANw}_{\text{nitr}}$	Nitrification in water	$\text{mg l}^{-1} \text{ day}^{-1}$
$\text{TANw}_{\text{volat}}$	Volatilization of TAN in water	$\text{mg l}^{-1} \text{ day}^{-1}$
$\text{PONs}_{\text{decom}}$	Decomposition of PONs to DONs	$\text{mg l}^{-1} \text{ day}^{-1}$
PONs_{min}	Mineralization of PONs to TANs	$\text{mg l}^{-1} \text{ day}^{-1}$
DONs_{min}	Mineralization of DONs to TANs	$\text{mg l}^{-1} \text{ day}^{-1}$
$\text{TANs}_{\text{nitr}}$	Nitrification in sediment	$\text{mg l}^{-1} \text{ day}^{-1}$
$\text{NOXs}_{\text{denitri}}$	Denitrification in sediment	$\text{mg l}^{-1} \text{ day}^{-1}$
C_{dif}	Diffusion of DON, TAN and NOX at sediment-water interface	$\text{mg m}^{-2} \text{ day}^{-1}$
Z_{ox}	Oxic layer depth of sediment	m
$R_{\text{o,s}}$	Total oxygen consumption rate in sediment	mg O m^{-3}
DO	Dissolved oxygen concentration in overlying water	mg l^{-1}

N processed by shrimp

Shrimp was the first organism to ingest and assimilate N input from feed then excreted as metabolic waste. According to Burford and Lorenzen (2004), shrimp metabolic wastes consisted mainly of ammonia (90%) and dissolved organic N (10%). The shrimp mean weight (W_t) was given by a von Bertalanffy growth function (Gulland 1983). The number of shrimp (N_t) was given by an exponential mortality model (Burford and Lorenzen 2004).

N input to shrimp pond ($N_{\text{feedinput}}$) by formulated feed was calculated from daily feeding, dry weight—wet weight ratio and percentage of N in dried artificial feed. Feeding tray observation was used to estimate the feeding activity of

Table 3. A summary of model equations.

$\text{DONw}_{\text{SHexc}}$	$= 0.1 \times A_t$
$\text{TANw}_{\text{SHexc}}$	$= 0.9 \times A_t$
A_t	$= a \times N_t \times W_t^b$
N_t	$= N_0 \times \exp(-c \times t)$
W_t	$= (W_{\infty}^{1/3} - (W_{\infty}^{1/3} - W_0^{1/3}) \times \exp(-g \times t))^{-3}$
$N_{\text{feedinput}}$	$= \text{feed}_{\text{input}} \times \text{feed}_{\text{dw}} \times n_{\text{feed}}$
N_{ingested}	$= N_{\text{SH}} + A_t + N_{\text{feces}(t)}$
N_{SH}	$= \Delta W_t \times n_{\text{SH}}$
N_{feces}	$= f \times N_{\text{ingested}}(t - \Delta t)$
$N_{\text{reingested}}$	$= N_{\text{ingested}} - N_{\text{feedinput}}$
N_{unconsum}	$= N_{\text{feedinput}} - N_{\text{ingested}}$
N_{mortal}	$= (N_t - N_{t+1}) \times W_t \times n_{\text{SH}}$
$\text{PHYW}_{\text{growth}}$	$= g_{\text{max}} \times \exp(k_T \times T) \times L_{\text{N,P}} \times L_{\text{light}} \times \text{PHYw}$
L_{light}	$= (e/k) \times \exp(-I_0/I_{\text{sat}}) \times \exp(-k \times z) - \exp(-I_0/I_{\text{sat}})$
k	$= k_{\text{Chl a}} \times \text{Chl a} + k_{\text{other}}$
$L_{\text{N,P}}$	$= \min(\text{TAN} + \text{NOX}) / (\text{TAN} + \text{NOX} + k_{\text{N}}), \text{DIP} / (\text{DIP} + k_{\text{P}})$
$\text{PHYW}_{\text{mortal}}$	$= k_{\text{PHYmortal}} \times \exp(k_T \times T) \times \text{PHYw}$
PHYW_{exc}	$= k_{\text{PHYexc}} \times \text{PHYW}_{\text{growth}}$
DONw_{min}	$= k_{\text{wmin}} \times \exp(k_T \times T) \times \text{DO} / (\text{DO} + k_{\text{O}_{\text{wmin}}}) \times \text{DONw}$
$\text{TANw}_{\text{nitr}}$	$= k_{\text{wnitr}} \times \exp(k_T \times T) \times \text{DO} / (\text{DO} + k_{\text{O}_{\text{wnitr}}}) \times \text{TANw}$
$\text{TANw}_{\text{volat}}$	$= k_{\text{wvolat}} \times \text{TANw}$
$\text{PONs}_{\text{decom}}$	$= k_{\text{sdecom}} \times \exp(k_T \times T) \times \text{DO} / (\text{DO} + k_{\text{O}_{\text{sdecom}}}) \times \text{PONs}$
PONs_{min}	$= k_{\text{smin1}} \times \exp(k_T \times T) \times \text{DO} / (\text{DO} + k_{\text{O}_{\text{smin1}}}) \times \text{PONs}$
DONs_{min}	$= k_{\text{smin2}} \times \exp(k_T \times T) \times \text{DO} / (\text{DO} + k_{\text{O}_{\text{smin2}}}) \times \text{DONs}$
$\text{TANs}_{\text{nitr}}$	$= k_{\text{snitr}} \times \exp(k_T \times T) \times \text{DO} / (\text{DO} + k_{\text{O}_{\text{snitr}}}) \times \text{TANs}$
$\text{NOXs}_{\text{denitri}}$	$= k_{\text{sdenitri}} \times \exp(k_T \times T) \times \text{DO} / (\text{DO} + k_{\text{O}_{\text{sdenitri}}}) \times \text{NOXs}$
C_{dif}	$= 2\phi D'(C_s - C_w) / z_{\text{ox}}$
z_{ox}	$= \text{SQRT}(2D'_{\text{DO}} \text{DO} / R_{\text{o,s}})$
$R_{\text{o,s}}$	$= \alpha_{\text{o/n}} \times k_{\text{sdecom}} \times \text{PONs}$

shrimp and to prevent overfeeding. Underfeeding, however, could occur when improper feeding management was practiced due to low visibility. Therefore, in the present study, an indirect method was adopted to calculate ingested N (N_{ingested}) based on daily N mass balance in shrimp body that depended on N retention in shrimp body, the total N waste and fecal pellet N.

In our model, the N input from feed was compared to the N ingested. The N input from feed less than N ingested indicated underfeeding and re-ingestion of PONs on sediment surface. On the other hand, the N input from feed larger than N ingested indicated overfeeding and sinking of the unconsumed feed to accumulate as PONs on the sediment surface.

N processed by phytoplankton

Phytoplankton growth rate depends on light intensity, nutrients availability and water temperature (Steele 1962, Eppley 1972, Burford and Lorenzen 2004). The light limitation coefficient was given by the integral of Steele's (1962) light inhibition model over the water column, with light conditions defined by Lambert-Beer law according to Burford and Lorenzen (2004). Phytoplankton mortality ($\text{PHYW}_{\text{mortal}}$) was defined as an exponential function of water temperature. N excretion by phytoplankton (PHYW_{exc}) was defined as a func-

Table 4. Parameter values used in the present model.

Symbols	Definitions	Units	Values	Sources
a	N waste produced by one shrimp	mg g ⁻¹ day ⁻¹	4.0	1
b	Allometric scaling factor of metabolism	—	0.75	2
N ₀	Shrimp stocking density	ind. l ⁻¹	0.024	Meas
c	Shrimp mortality	day ⁻¹	0.009	Meas
W _∞	Shrimp maximum weight	g	15.6	Meas
W ₀	Shrimp stocking weight	g	0.009	Meas
g	Shrimp growth rate	day ⁻¹	7.5×10 ⁻³	1
feed _{dw}	Dry weight - wet weight ratio	—	0.92	Meas
n _{feed}	Percentage of N in dried formulated feed	%	0.065	Meas
n _{SH}	N content in shrimp	mg g ⁻¹	20.5	Meas
f	N content in shrimp fecal pellet	—	0.18	Cal
g _{max}	Maximum specific growth rate of phytoplankton	day ⁻¹	0.98	Cal
k _p	Half saturation constant for uptake of inorganic phosphorus	mgP l ⁻¹	0.03	3
k _n	Half saturation constant for uptake of inorganic nitrogen	mgN l ⁻¹	0.06	Cal
k _T	Temperature coefficient	°C ⁻¹	0.0693	4
I ₀ /I _{sat}	Ratio surface/saturation light intensity	—	2.4	1
k _{PHYexc}	Ratio of extra-cellular excretion to photosynthesis	day ⁻¹	0.135	5
k _{PHYmortal}	Mortality of phytoplankton at 0°C	day ⁻¹	0.02	Cal
k _{CHL}	Extinction coefficient due to chlorophyll a	m ⁻¹ mg ⁻¹	18.7	Meas
k _{other}	Extinction coefficient due to non-chlorophyll a	m ⁻¹ mg ⁻¹	2.5	6
z	Water depth	m	1.4	Meas
k _{wmin}	Mineralization coefficient in water at 0°C	day ⁻¹	0.01	5 (wr)
kO _{wmin}	Half saturation constant of oxygen for mineralization	mg l ⁻¹	0.001	Cal
k _{wvolat}	Volatilization rate of TAN	day ⁻¹	0.05	1
k _{wnitri}	Nitrification coefficient in water at 0°C	day ⁻¹	0.01	5 (wr)
kO _{wnitri}	Half saturation constant of oxygen for nitrification	mg l ⁻¹	2.0	7
k _{sdecom}	Decomposition coefficient in sediment at 0°C	day ⁻¹	0.01	7
kO _{sdecomp}	Half saturation constant of oxygen for PONs decomposition	mg l ⁻¹	0.5	7
k _{smin1}	Mineralization coefficient from PONs to TANs at 0°C	day ⁻¹	0.01	7
kO _{smin1}	Half saturation constant of oxygen for PONs mineralization	mg l ⁻¹	0.5	7
k _{smin2}	Mineralization coefficient from DONs to TANs at 0°C	day ⁻¹	0.05	7
kO _{smin2}	Half saturation constant of oxygen for DONs mineralization	mg l ⁻¹	0.5	7
k _{snitri}	Nitrification coefficient in sediment at 0°C	day ⁻¹	0.8	Cal
kO _{snitri}	Half saturation constant of oxygen for nitrification	mg l ⁻¹	2.0	7
k _{sdenitri}	Denitrification coefficient in water at 0°C	day ⁻¹	2.0	8
kO _{sdenitri}	Half saturation constant of oxygen for denitrification	mg l ⁻¹	4.0	7
D' _{DON}	Diffusion coefficient of DON	m ² day ⁻¹	1.5×10 ⁻⁵	Cal
D' _{TAN}	Diffusion coefficient of TAN	m ² day ⁻¹	2.0×10 ⁻⁵	8
D' _{NOX}	Diffusion coefficient of NOX	m ² day ⁻¹	2.0×10 ⁻⁵	8
D' _{DO}	Diffusion coefficient of DO	m ² day ⁻¹	2.0×10 ⁻⁵	9
α _{o/n}	Oxygen to nitrogen ratio of organic matter	gO/gN	19.71	—
φ	Porosity of sediment pond	—	0.4	Meas

Sources: 1. Burford and Lorenzen (2004), 2. Burford and Williams (2001), 3. Eppley et al. (1969), 4. Eppley (1972), 5. Kawamiya et al. (1995), 6. Burford (1997), 7. Chapelle et al. (2000), 8. Li and Gregory (1974), 9. Wang et al. (2003), wr; within range, Meas; data measured for the present study and Cal; Calibration.

tion depending on phytoplankton growth (Kawamiya et al. 1995).

N content in phytoplankton (PHYw) was estimated from the ratio of PON/Chl *a* which had been subtracted from the non-phytoplankton PON. The daily ratio of N content in phytoplankton was calculated using the interpolation technique of the biweekly-measured data.

Although N fixation was possible to occur in aquaculture pond with presence of cyanobacteria (Hargreaves,

1998), it was not considered in the model due to the conditions of high DO and availability of TAN+NOX in shrimp pond throughout the production cycle according to the suggestion in Smith (1990) and Fay (1992).

N processed by bacteria in water column

Major processes of N cycle due to bacteria in the water column of shrimp pond were considered mineralization of DONw by heterotroph and nitrification of TANw by chemo-

autotrophs (nitrifying bacteria). Denitrification in the water column was ignored because of the oxic condition of water column ($\text{DO} > 4.0 \text{ mg l}^{-1}$) throughout the culture period. The equations were constructed to be dependent on temperature and DO in the water column according to Chapelle et al. (2000).

N processed in sediment

In the present study, the active sediment layer, which plays major roles in the N dynamics in the pond, was assumed to be 2 cm thick according to Songsangjinda et al. (2006) which included a thin layer of oxic sediment on the top and a deeper layer of anoxic sediment. The decomposition of PONs was defined as a process to produce DONs. PONs and DONs were also mineralized to produce TANs and then, transformed to NOXs by nitrification which may occur in the oxic surface sediment. All forms of dissolved N accumulate in the sediment interstitial water. All functions used to calculate the sediment decomposition, mineralization, nitrification and denitrification were assumed to be dependent on temperature and DO in the water column according to Chapelle et al. (2000).

Sediment decomposition and nitrification occur in the oxic sediment layer and consume oxygen supplied from the water column. Although the aeration management was carried out to maintain sediment in oxic condition throughout the culture period, anoxic condition was able to occur in the deeper sediment layer after dissolved oxygen was rapidly consumed in a few millimeters zone of the oxic layer and denitrification could occur in the deeper sediment layer. It was reported that denitrification can contribute to the removal of N by up to 30% of total N budget in the pond in case of open-managed intensive shrimp pond (Funge-Smith and Briggs 1998), and about 25% and 65% removal of N input from feed specifically for the open and closed cycle shrimp ponds in Thailand (Songsangjinda et al. 2004).

N flux across sediment-water interface

The sediment-water interface was an active zone where N compounds exchange between the sediment and the water column. Dead phytoplankton, fecal pellets and unconsumed feed were sources of N accumulation and burial in the sediment. Exchange of N in dissolved forms depended on the relative concentration gradients between the water column and the sediment interstitial water and was considered to follow Fick's first law of diffusion (Berner 1980).

N volatilization

N volatilization in aquaculture pond was attributed to the diffusion of unionized ammonium to the atmosphere. Ammonia volatilization was enhanced by increase of ammonia concentration, pH, temperature, evaporation rate and wind speed (Hargreaves 1998). In this study, we calculated

the ammonia volatilization by using the equation reported in Burford and Lorenzen (2004).

Simulation of the model

The dynamic model was developed using the software STELLA[®] Research version 8 © High Performance Systems Inc. (2003), and ran with a time step of 0.02 d. The calculations were carried out by Euler's method.

Scenario analysis

Based on field observation, farmers tend to manage feeding in different ways, i.e. underfeeding, optimum feeding and overfeeding depending on their skill. In this study, three scenarios were analyzed in order to evaluate how the N dynamics in the enclosed shrimp pond responded to different levels of N input from feed. The first was a field observation scenario that was explained previously. The amount of N input from feed of this scenario was about $329 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$. From the preliminary test, this amount of N input was evaluated to be underfeeding practice.

The second scenario aimed to analyze the N dynamics under the assumption that shrimps were efficiently fed (optimum feeding) throughout the production cycle which could harvest shrimps at the body weight of 20 g and survival rate of 75%. These values represent the average values of those in successful intensive shrimp culture in Thailand (Songsangjinda, unpublished data). In this assumption, the daily N requirement was determined using the equation of N_{ingested} explained earlier. The amount of N input from feed of the second scenario was predicted at about $978 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$.

The third scenario was aimed to analyze N dynamics under the assumption of overfeeding by 20% of the second scenario ($1,174 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$). This scenario demonstrated improper feed management that led to overfeeding and increasing of food conversion ratio (FCR) and production cost (Thongrak et al. 1997). In addition, more nutrients and organic matter loaded into shrimp pond could generate greater impact on nutrient dynamics in the shrimp culture systems (Montoya et al. 2000, McIntosh et al. 2001, Burford et al. 2003a).

Results

Water and sediment qualities

Over 151 d of production cycle, the concentration of daytime DO varied between $6.1\text{--}6.9 \text{ mg l}^{-1}$ while pH varied in the range of $7.0\text{--}8.3$. The concentrations of N in water column showed negligible differences between the beginning and end of the production cycle except the concentration of chlorophyll *a* and TAN which showed gradual increase through to the end of production cycle from 32 to $266 \mu\text{g l}^{-1}$

and from 0.01 to 0.70 mg l⁻¹, respectively. There was only negligible accumulation of PON, TAN and NOX in the sediment evaluated from their values at the beginning and the end of production cycle because of the reduction of N concentration in sediment at harvest (Table 5).

The results from model simulation for shrimp weight, N concentrations in PHYw, TANw, NOXw, TANs and NOXs

are shown in Fig. 2. The concentration of N in PHYw gradually increased throughout the production cycle, which indicated growth of phytoplankton over the production period. The concentrations of TANw and NOXw showed marked variations over the production cycle when compared to those in the sediment. The predicted values of PHYw showed less agreement between predicted and measured values during

Table 5. Summary of water and sediment qualities in the enclosed shrimp pond.

Sources	Parameters	Begin	End	Range	Average±SD
Water	pH	8.2	7.7	7.0–8.3	7.8±0.3
	DO at day time (mg l ⁻¹)	9.4	9.0	6.1–9.4	7.3±1.1
	TAN (mg l ⁻¹)	0.01	0.70	0.00–1.52	0.32±0.45
	NOX (mg l ⁻¹)	0.18	0.06	0.01–0.26	0.10±0.08
	DIP (mg l ⁻¹)	0.01	0.02	0.01–0.05	0.02±0.01
	Chlorophyll a (µg l ⁻¹)	32	266	15–266	99±78
Sediment	PON (mg kg ⁻¹ dry sediment)	785	650	300–803	577±153
	TAN (mg kg ⁻¹ dry sediment)	15.9	7.1	2.7–115.8	17.7±31.1
	NOX (mg kg ⁻¹ dry sediment)	4.7	5.0	0.4–18.8	4.7±4.5

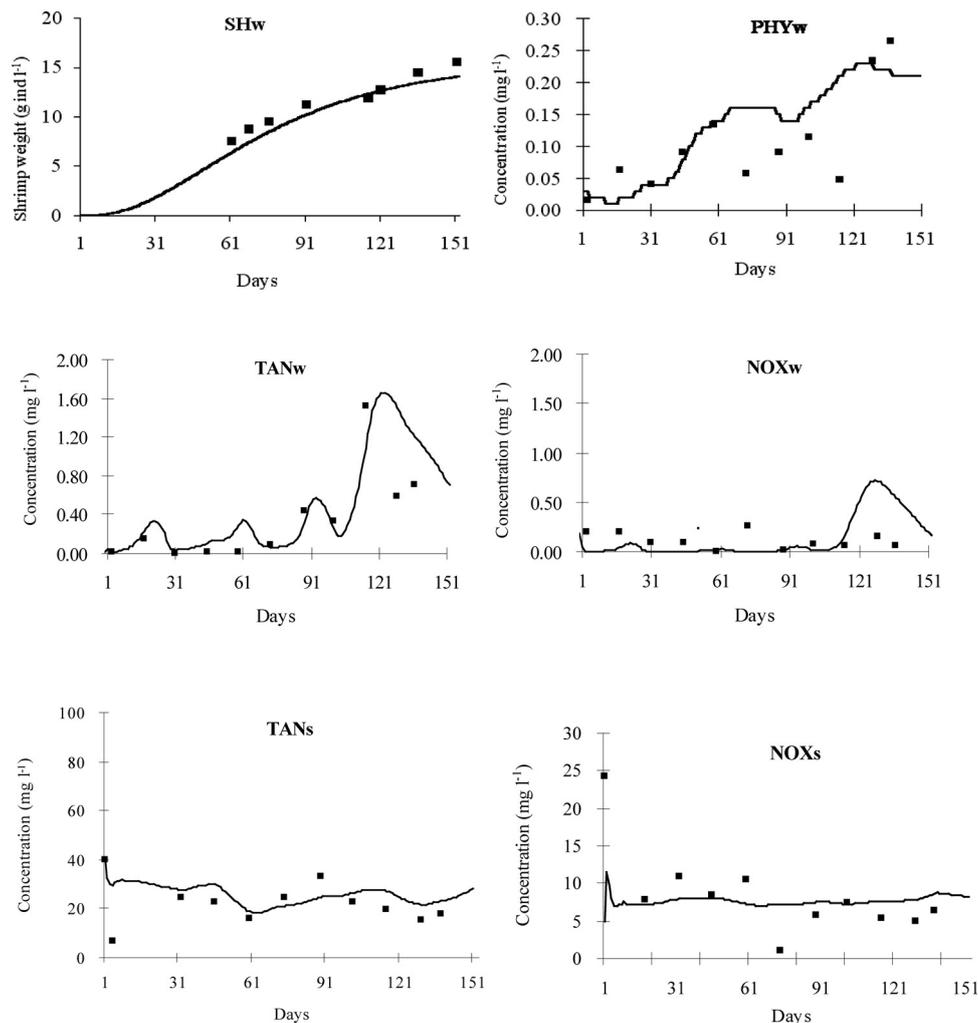


Fig. 2. Predicted (—) and observed (■) shrimp weight, N in phytoplankton (PHYw) and state variables of N in water (w) and sediment (s) over a 151 days of production cycle in an enclosed shrimp culture pond.

month 3 and 4, TANw and TANs showed reasonable agreement with the measured values. (Fig. 2).

N dynamics in the shrimp culture pond

The predicted value of N ingested by shrimp was higher than the value of N input from feed except only in the first three weeks, which indicated that the practice was mostly underfeeding (Fig. 3). The N input from feed drastically fluctuated from the 50th day to the end of production cycle, which indicated less efficiency of feed management. The N ingested by shrimp reached the peak after 70–80 d with the rate $0.3 \text{ mg N l}^{-1} \text{ d}^{-1}$ and decreased to the level of $0.2 \text{ mg N l}^{-1} \text{ d}^{-1}$ at the end of the grow out.

The N dynamics over 151 d of production cycle in water column and sediment of the enclosed shrimp pond were illustrated in Fig. 4. Results showed that shrimp were the biggest producer of TANw ($363 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$) in the water column of shrimp pond while N accumulation in shrimp was

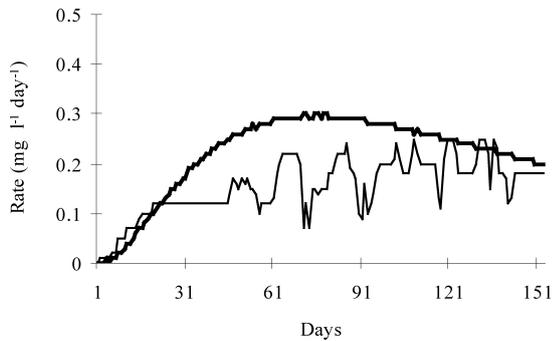


Fig. 3. Predicted values of N processed by shrimp; (a) input with feed (—) and N ingestion by shrimp (---) over 151 days of production in the shrimp culture.

about $27 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$. On the other hand, phytoplankton was a main contributor of PONs to the sediment ($382 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$). Mineralization of DONw by bacteria that input to TANw was relatively smaller ($123 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$) when compared to shrimp excretion. NOXw was a minor source of N for phytoplankton growth ($52 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$) comparing to the ammonia assimilation ($412 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$). Nitrification in the water column ($45 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$) was also minor assimilation process when compared to the roles of phytoplankton in ammonia and NOX assimilations.

Sediment demonstrated a role of N source in shrimp pond. PONs was decomposed to DONs ($134 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$). The TAN mineralization from DONs and PONs was about 75 and $134 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$, respectively. Denitrification was a major process ($206 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$) in the sediment and tightly coupled with nitrification ($207 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$). The efflux of DON ($42 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$) was the largest portion of dissolved N fluxes compared to those of TAN ($16 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$) and NOX ($5 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$).

Scenario analysis

A comparison of N accumulation and rates of N processed under 3 feed input scenarios was carried out and the result is shown in Table 6. The first scenario (field observation) demonstrated underfeeding ($329 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$), due to the re-ingestion of PONs that was about $148 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$. However, a negligible amount of uneaten feed was found at the early period of the production cycle when fixed rate of feeding was practiced. This scenario showed less accumulation of N in all state variables of the

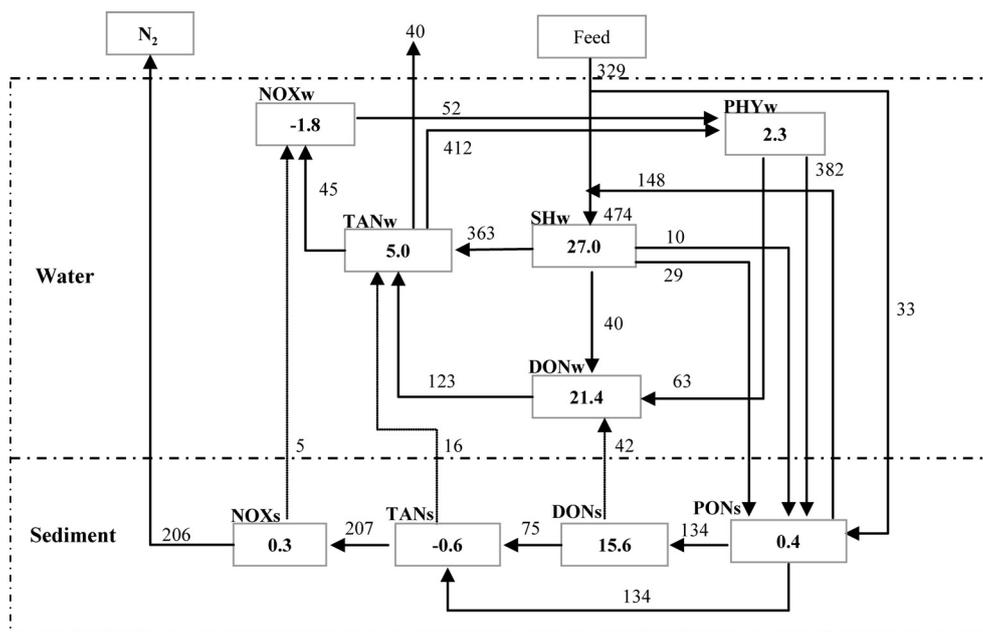


Fig. 4. N dynamics and budget ($\text{kg N ha}^{-1} \text{ cycle}^{-1}$) in the water column and sediment of the enclosed shrimp culture pond.

Table 6. Comparison of N accumulation in state variables and rates of N processes in three scenarios of N input from feed into the enclosed black tiger shrimp culture pond over 151 days of production cycle.

State variable/ N processes	Scenario 1 (under- feeding)	Scenario 2 (optimum feeding)	Scenario 3 (overfeeding)
N accumulation in state variables (kg N ha⁻¹)			
SHw	27.0	104.0	104.0
PHYw	2.3	2.7	2.7
DONw	21.4	42.4	44.9
TANw	5.0	72.5	74.8
NOXw	-1.8	96.8	101.7
PONs	0.4	108.9	206.8
DONs	15.6	69.6	103.4
TANs	-0.6	2.7	5.6
NOXs	0.3	0.4	0.7
Rates of N processes by/in (kg N ha⁻¹ cycle⁻¹)			
Shrimp			
Feed input	329	978	1174
Ingestion	474	978	978
Re-ingestion	148	0	0
Unconsumed feed	33	0	196
Excretion to DON	40	88	88
Excretion to TAN	363	794	794
Fecal pellet	10	15	15
Mortality	29	17	17
Phytoplankton			
TAN consumption	412	529	529
NOX consumption	52	121	123
Extra-cellular excretion	63	88	88
Mortality	382	530	532
Water column			
Mineralization	123	186	191
Volatilization	40	195	201
Nitrification	45	213	219
Sediment			
Decomposition to DONs	134	226	279
Decomposition to TANs	134	226	279
Mineralization	75	103	116
Nitrification	207	298	351
Denitrification	206	292	343
Fluxes			
DON flux	42	53	59
TAN flux	16	29	39
NOX flux	5	5	6

water column and sediment. The N dynamics in water column processed by shrimp (10–474 kg N ha⁻¹ cycle⁻¹) and phytoplankton (52–412 kg N ha⁻¹ cycle⁻¹) were greater than the dynamics processed by bacteria in the water column (45–123 kg N ha⁻¹ cycle⁻¹). The N dynamics at sediment-water interface indicated that the sediment was a source of dissolved N (5–42 kg N ha⁻¹ cycle⁻¹) in the water column.

In the second scenario the N input from feed increased to 978 kg N ha⁻¹ cycle⁻¹. This scenario resulted in zero amounts of N in the processes of re-ingestion and uneaten

feed except the fecal pellet that was about 15 kg N ha⁻¹ cycle⁻¹. This scenario increased the N accumulation in both water column and sediment indicated by the higher values in most stage variables than those of the first scenario (42.4–108.9 kg N ha⁻¹ cycle⁻¹) except PHYw, TANs and NOXs (0.4–2.7 kg N ha⁻¹ cycle⁻¹). The N dynamics by shrimp (0–978 kg N ha⁻¹ cycle⁻¹) increased directly by the effect of N input from feed. Although the N dynamics by phytoplankton increased to 88–530 kg N ha⁻¹ cycle⁻¹, phytoplankton mortality was a major process to sink PONs into the sediment. The N dynamics by bacteria in the water column and sediment were in ranges of 186–213 and 103–298 kg N ha⁻¹ cycle⁻¹. The amount of N removed as N₂ increased to about 292 kg N ha⁻¹ cycle⁻¹, which was also higher than that of the underfeeding.

In the third scenario, the increase of N input from feed by 20% of the amount of optimum feeding did not show a significant accumulation in the water column. However, sediment was the area that was affected by overfeeding especially the accumulation of PONs and DONs (206.8 and 103.4 kg N ha⁻¹ cycle⁻¹). Shrimp processes did not respond to the overfeeding due to the amount of extra feed (196 kg N ha⁻¹ cycle⁻¹) that was directly added into the sediment. N dynamics by phytoplankton was almost the same with that of the second scenario. The same phenomenon occurred in the N dynamics by bacteria in the water column, but not for the N dynamics by bacteria in the sediment that significantly increased to the amount of 116–351 kg N ha⁻¹ cycle⁻¹. Nitrification and denitrification showed the highest response (351 and 343 kg N ha⁻¹ cycle⁻¹) of bacterial process in the sediment of the overfeeding scenario among the three scenarios.

Discussion

Model improvement

The model constructed in the present study improved the model presented by Burford and Lorenzen (2004) which considered only 5 state variables of the N dynamics in open shrimp culture system. Our model defined 9 state variables which included 5 variables in water column (including shrimp process) and 4 variables in sediment which elaborate all main processes of N dynamics that often occur in intensive shrimp- and other aquaculture ponds (Hargreaves 1998, Burford et al. 2002, Avnimelech and Ritvo 2003).

The predicted values of SHw well agreed with the measured values of shrimp weight. Result from our trial using a von Bertalanffy growth parameters ($W_0=0.005$ and $W_\infty=75.6$ g) suggested by Burford and Lorenzen (2004) to predict shrimp weight in the enclosed shrimp pond showed that shrimp weight was overestimated. This probably suggests that the value of W_∞ obtained from Burford and Lorenzen (2004) was not appropriate to be applied for the enclosed

shrimp culture pond. In the present study, the weight of PL (W_0) was about 8.9×10^{-3} g and the weight of harvested shrimp (W_∞) was 15.6 g after 151 d of production cycle. This harvested shrimp weight indicated poor growth compared to the average of about 16.8–17.2 g after 56 d of production in the experimental tank with the water exchange system (Smith et al. 2002). When we used the values of W_0 and W_∞ of the present study in the von Bertalanffy function, the predicted values of shrimp weight was improved from the previous trial and showed good fit with the measured values from the pond. This significant agreement suggests that the growth parameters (W_∞) in the enclosed pond were probably smaller than that of the open shrimp culture system.

The predicted values of PHYw, TANw and TANs reasonably agreed with the measured values. However, the model could not predict correctly the PHYw during the period of 70–110 d and during the end of production cycle when the value of PHYw drastically decreased. Songsangjinda et al. (2006) suggested that the high values of Chl *a* during a crush of *Oscillatoria* observed in their study may be attributable to nano-sized phytoplankton (2–20 μ m length), which could not be completely collected with the 20 μ m phytoplankton net used in their study, as well as in this study. The presence of this nano-sized phytoplankton in shrimp pond was also reported by Burford et al. (2003b) and Alonso-Rodríguez and Póez-Osuna (2003). Since the present model did not take phytoplankton succession into account, the predicted values could disagree with the measured values especially during the period of community change. This also affected the poor prediction on the stock of state variables in the water column and sediment (NOXw and NOXs). However, the complicated relationships of these biological processes which occurred in the shrimp pond may be a limitation for constructing complete mathematical model in shrimp ponds due to still insufficient understanding, equations and quantitative data related to these processes. Therefore the results from this study could probably be acceptable at the present time to explain the complexity of N dynamics in enclosed shrimp ponds.

N dynamics

Thakur and Lin (2003) reported that feed is the major source (76–92%) of N input into the closed systems of intensive shrimp culture. Feeding is an important management in commercial shrimp farms that can have significant effects on the water quality, growth, health and survival of the cultured shrimp (Smith et al. 2002). The results of the present study indicate that N input from feed was insufficient for the daily requirement judging from N metabolisms of shrimp (Fig. 3). This underfeeding was probably a major factor, which led to the low production ($1,371 \text{ kg ha}^{-1}$) and high FCR (4.01) at the end of production cycle. Thus, N input from feed of the underfeeding practice could not really reflect the total

amount of N ingested by shrimp of the present study. Our results suggest that the growth of shrimp in the enclosed pond is partly dependent on the ingestion of organic detritus at the bottom of the pond. Similar result was observed in the flow through earthen ponds where the natural productivity in the pond could provide supplemental nutrition to enhance growth of shrimp (Otoshi et al. 2003). However, the natural productivity in the enclosed shrimp pond of the present study was probably limited especially as a result of long term underfeeding that might force shrimp to ingest more of the organic detritus accumulated on the bottom of the pond and resulted in a consequent decrease in shrimp biomass and N ingestion after about 80 d of culture as shown in Fig. 3. The limiting of organic detritus and the underfeeding practice after 81 d might contribute to a lesser amount of PON in the surface sediment in the pond. In addition, oxic conditions in the surface sediment maintained by paddle wheel aerators could be another factor that reduced the amount of PON by enhancing microbial processes to transform PON into various forms of N.

In decapod crustaceans, the final metabolites are mainly ammonia and the rest are dissolved organic N compounds such as urea, amino acids and other organic compounds (Regnault 1987). In the present study, ammonia excretion from shrimp was a major source of TANw ($363 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$) before supplied to the plankton assimilation and nitrification processes (Fig. 4). The other forms of N wastes produced by shrimp such as DON ($40 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$) and fecal pellet ($10 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$), were minor. However, DON from the shrimp fecal pellet was reported to be less bio-available and tends to accumulate in shrimp pond (Burford and Williams 2001). This is probably attributed to the higher accumulation of DON than TAN+NOX in the water column (Fig. 4). These indicate the great effect of shrimp which is the main processor of N input from feed and contribute to the other organisms involved in N dynamics in water column of shrimp ponds.

DONs was produced by the autolysis of settled phytoplankton cells or the hydrolysis of other particulate organic N (Hargreaves 1998) in the surface sediment and release into water column. In addition, DONw was also mineralized by proteolytic and heterotrophic bacteria to form dissolved inorganic nitrogen (Hargreaves 1998). However, this amount of N mineralization by bacteria was less than the amount of ammonia assimilations by phytoplankton. The predicted values showed that ammonia assimilation by phytoplankton was about 7.9 times of NOX assimilation (Fig. 4). This probably suggests that phytoplankton plays an important role in ammonia assimilation in water column of shrimp ponds.

Jiménez-Montealegre et al. (2002) described that the uptake rate of nitrogen by phytoplankton decreased during the growing cycle of fish, partly due to nutrient and light limitations caused by algal self-shading. The large fluctuation of

TAN was also demonstrated in closed *P. monodon* culture systems, which was generally attributed to variation in assimilation by phytoplankton and nitrifying bacteria (Burford and Glibert 1999, Thakur and Lin 2003, Burford et al. 2003b). These suggest that the N dynamics affect more on nutrient limitation that obviously affect phytoplankton growth, succession and mortality.

The rapid assimilation of TAN by phytoplankton was usual when competing with nitrifying bacteria in the water column, and the magnitude was about 9.2 times higher in phytoplankton uptake in the present study. This is probably attributed to the active role of phytoplankton in water column on N assimilation compared to the role of nitrifying bacteria in nitrification process (Fig. 4). It appeared that the nitrification process was substantially slow while phytoplankton was primarily responsible for the process of TAN assimilation in the enclosed shrimp culture pond. Unlike nitrification, the rate of mineralization of DON gradually increased towards the end of production cycle. This indicates that heterotrophic bacteria in the water column play a more vital role in the N dynamics in the enclosed shrimp culture pond with the underfeeding practice. The nitrification rate is restricted by the availability of surface area of substrate, dissolved oxygen, and possibly by light inhibition (Hargreaves 1998).

In aquaculture pond, alkaline pH and higher temperatures favor the form of TAN to be unionized ammonia, which is a gaseous form (Hargreaves 1998). The volatilization of TAN may be an important mechanism for ammonia removal during the late afternoon in poorly buffered (total alkalinity $<20 \text{ mg l}^{-1}$ as CaCO_3) ponds, when pH of water may rise in response to the depletion of CO_2 in water column by photosynthetic assimilation of phytoplankton (Hariyadi et al. 1994). The model used in the present study predicted that the amount of TAN volatilization was about $40 \text{ kg N ha}^{-1} \text{ cycle}^{-1}$. The strong aeration was probably one of the factors that accelerated TAN removal through this mechanism through the diffusion into the atmosphere.

Nighttime dissolved oxygen in the studied pond was maintained to be above 4.0 mg l^{-1} in order to provide oxic condition in the entire ecosystem throughout the production cycle. Nitrifying bacteria require oxygen to derive energy from reduced N. The half-saturation concentration for oxygen was higher for *Nitrobacter* than for *Nitrosomonas* at 30°C suggesting that nitrite oxidation is more sensitive to low oxygen (Hargreaves, 1998). The lowest value of dissolved oxygen in the early morning measured in the present study was much higher than the half saturation value used in the model and resulted in complete nitrification and no denitrification occurring in the water column. The strong aeration might have provided sufficient oxygen to the sediment layer. Penetration of oxygen into sediment was a key factor regulating DON mineralization and nitrification processes in sediments (Rysgaard et al. 1994, Hargreaves 1998).

Within the sediment, the active DONs mineralization and nitrification processes might have constantly occurred resulting in a decrease of organic N in the sediment at the beginning. The TANs and NOXs stocks were quite stable compared to a large input from phytoplankton mortality. This indicated that transformation of N by bacterial communities in the sediment layer was likely active and balanced between the input and processes of N at the surface sediment of a shrimp culture pond.

Oxygen supplied from the overlying water is the energetically preferred terminal electron acceptor for the oxidation of organic matter in the sediment. However, when oxygen concentration becomes limiting (about 0.1 to 0.2 mg l^{-1} or ORP value $< -220 \text{ mV}$) heterotrophic facultative anaerobes switch the terminal electron acceptor from DO to nitrate and produce N_2 by denitrification (Hargreaves 1998). The almost equal amounts of nitrification and denitrification rates shown in Fig. 4 was a good evidence and revealed that almost all nitrate produced by nitrification in sediment was completely removed to N_2 gas via denitrification. This probably indicated that a coupling processes between nitrification and denitrification in the enclosed shrimp pond was relatively tight. Hargreaves (1998) reported the denitrification process in aquaculture ponds varied in a wide range of $25\text{--}50 \text{ mg N m}^{-2} \text{ day}^{-1}$ and closely coupled with strong nitrification. However, the magnitude of N removal by denitrification might decrease and when sediment nitrification was limited by the depth of oxygen penetration into the sediment, nitrate supply to the denitrification process would decrease. Compared to the result of the present study, the coupling process of N in sediment of the enclosed shrimp pond was predicted to remove about 60% of N input from feed and increased with the increase in amount of N input from feed. This is probably attributed to the strong aeration practice daily that could provide oxic condition to the bottom of the pond throughout the production cycle. This practice also resolved the limitation of oxygen penetration into the sediment which enhanced the coupling processes of nitrification/denitrification. The denitrification was estimated to be about 30% of N input from feed in the open-managed intensive shrimp pond (Funge-Smith and Briggs 1998). The study done by Songsangjinda et al. (2004) also estimated denitrification rates of about 25% of N input from feed in the open system shrimp culture pond but increased to about 65% in the closed cycle shrimp pond. Thus, the tight coupling processes of nitrification and denitrification in sediments were probably a common and effective pathway to remove N from shrimp pond.

Conclusion

Mathematical modeling is widely used to predict the re-

sults of complex processes in many fields. In the present study, the results revealed that with the underfeeding practice, shrimp were forced to ingest more of the PON in the sediment of the enclosed pond. Phytoplankton actively processed N in water column while the process of nitrifying bacteria was minor in water column. A tight coupling process of nitrification and denitrification was attributed to the major processes of N dynamics in the sediment and favored the conversion of N towards N_2 which was consequently the main N removal process from the shrimp pond.

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