



Modeling nitrogen dynamics in intensive shrimp ponds: the role of sediment remineralization

M.A. Burford^{a,*}, K. Lorenzen^b

^aCentre for Riverine Landscapes, Griffith University, Nathan, Queensland 4111, Australia

^bEnvironmental Science & Technology, Imperial College London, Prince Consort Road, London SW7 2BP, UK

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Abstract

A mathematical model is used to investigate the role of sedimentation and remineralization in the sediment on nitrogen (N) dynamics in intensive shrimp culture ponds. The model describes the key processes involved in N cycling that underpin the dynamics of total ammoniacal N (TAN), nitrate/nitrite (NOX) and chlorophyll *a* (CHL) concentrations and the sediment N pool. These parameters may, in high concentrations, impact negatively on the shrimp or the adjacent aquatic environment when water is discharged from ponds. The model was calibrated for an Australian commercial shrimp (*Penaeus monodon*) pond. Most N enters the pond system as TAN from shrimp excretion of dietary N and decomposition of wasted feed, and is subsequently taken up by phytoplankton, which, on senescence, is sedimented and remineralized. Sediment remineralization is the dominant source of TAN in the water column for all but the beginning of the production cycle. The remineralization rate of sedimented N was estimated at 6% day⁻¹. Nonetheless, sediment acts as a net sink of N throughout the production cycle. The effect of management strategies, including increased stocking densities, water exchange and sludge (=sedimented material) removal, on water quality was examined. Model outputs show that using current shrimp farming techniques, with water exchange rates of 7% day⁻¹, an increase in stocking densities above 60 animals m⁻² would result in unacceptably high TAN concentrations. Both sludge removal and water exchange provide effective ways of reducing TAN and NOX concentrations and may allow substantially higher stocking densities. However, sludge removal may be the more acceptable option, given the need to meet strict regulatory requirements for discharge loads in some countries and the desire to reduce water intake to improve biosecurity.

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* Corresponding author. Tel.: +61-7-3875-6723; fax: +61-7-3875-7615.

E-mail address: m.burford@griffith.edu.au (M.A. Burford).

1. Introduction

The mid 1980s to early 1990s was a period of rapid growth in the production of cultured shrimp, particularly in south east Asia and Central America. However, the shrimp aquaculture industry is facing unprecedented criticism for unsustainable practices (Naylor et al., 1998, 2000). This has included the discharge of pond waters high in nutrients and phytoplankton with the potential to cause eutrophication of coastal waterways, destruction of mangrove and wetland habitats and depletion of world fish stocks to make shrimp feed. The continuation of unsustainable practices has the potential to significantly hamper farm production of shrimp. The future of the industry relies on the development of more sustainable practices.

Historically, reducing the eutrophication resulting from shrimp farming and optimizing pond water quality have been achieved largely using a trial and error approach where new designs and management approaches are evaluated based on on-farm observations. This approach has resulted in gains for the industry; however, there is increasing recognition of the need to understand the natural processes in pond systems to reduce discharge loads and improve water quality (Tacon, 1996; Burford et al., 2001; Jory et al., 2001). Mathematical modeling is a powerful tool to aid the understanding of system dynamics, test hypotheses and synthesize empirical studies (Hilborn and Mangel, 1997; Lorenzen et al., 1997).

Nitrogen (N) plays a key role in the dynamics of aquaculture systems due to its dual role, in various forms, as a nutrient and toxicant. N dynamics in intensive aquaculture ponds have been studied using mathematical modeling by, for example, Hargreaves (1997), Lorenzen et al. (1997) and Lefebvre et al. (2001). Lorenzen et al. (1997) showed that uptake by phytoplankton and subsequent sedimentation are key processes in N dynamics in shrimp ponds operating at low water exchange rates, but ignored remineralization of sedimented N (Meijer and Avnimelech, 1999; Burford and Longmore, 2001). Others (Hargreaves, 1997; Jiménez-Montealegre et al., 2002) have modeled total ammoniacal N (TAN) remineralization as a constant or temperature-dependent sediment flux without considering the dynamics of the sludge N pool explicitly.

Experimental studies indicate that feed inputs during the production cycle account for the bulk of N inputs to many shrimp ponds (Briggs and Funge-Smith, 1994; Jackson et al., 2003). Much of the N input not incorporated into shrimp tissue enters the water column as TAN is taken up by phytoplankton and settles on the sediment as particulate organic N. This creates a pile of anoxic sludge with a high organic loading. Alternatively, N input is deposited directly as uneaten feed or faeces (Burford and Williams, 2001). Part of the sludge N is remineralized to enter the water column again as TAN. Such recycled N may account for the bulk of TAN input into the water column late in the production cycle (Burford and Longmore, 2001).

The present study aims to elucidate the dynamics of N sedimentation and remineralization in the course of a production cycle and to evaluate the potential of sludge removal as an alternative way of reducing toxic N components within the pond and in the wider environment. A mathematical model of N dynamics (Lorenzen et al., 1997) is extended to incorporate a sludge N pool and the associated fluxes. Parameters of the N dynamics model are estimated by fitting the model to observed water quality data for an Australian shrimp pond. The model is used to analyze the role of sedimentation and remineralization

in N dynamics throughout the production cycle and to predict the effects of various management practices, including sludge removal and different rates of water exchange on pond water quality.

2. Materials and methods

2.1. Conceptual model

A previous conceptual model of N dynamics in shrimp ponds (Lorenzen et al., 1997) was extended to incorporate a sludge N pool and the remineralization process (Fig. 1). For the purposes of the model, N input was assumed to be exclusively formulated feed since previous studies have shown that only a small proportion of the N input was in the form of water and stock (5–10%) (Briggs and Funge-Smith, 1994; Jackson et al., 2003). In the model, waste N is generated from shrimp feeding on formulated feed. The N can enter the water column as TAN from shrimp excretion or remineralization of wasted feed and as dissolved organic N (DON).

TAN may be transformed via a number of pathways: assimilated by phytoplankton (CHL), volatilized as gaseous ammonia, converted to nitrite/nitrate (NOX) via nitrification processes or discharged during water exchanges. Nitrate may in turn be assimilated by phytoplankton or discharged during water exchanges. A previous study by Burford and Longmore (2001) measured denitrification directly and showed that the sediment and particularly the sludge was highly anoxic, and nitrate concentrations were low, thereby preventing denitrification. Therefore, denitrification was excluded from the conceptual

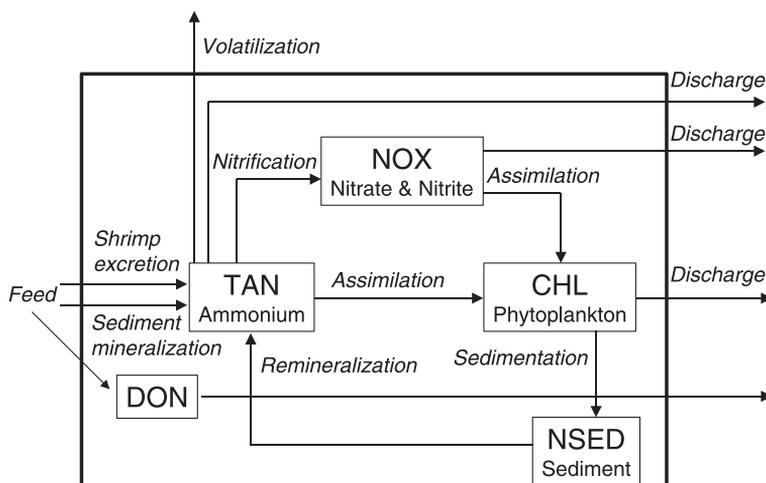


Fig. 1. Conceptual model of N input, transformation and removal in intensive shrimp ponds. Arrows represent pathways and boxes indicate the key N components represented as state variables in the model: TAN = total ammonia N; NOX = nitrate plus nitrite; CHL = chlorophyll *a* as a measure of phytoplankton, and hence particulate N biomass; DON = dissolved organic N; and NSED = N buried in the sludge.

model. The phytoplankton biomass, expressed as CHL, is either discharged during water exchanges or deposited on the pond floor. The resulting detritus may be remineralized by bacteria to form TAN or buried in the sludge (NSED).

Dissolved organic N (DON) is produced in significant quantities in shrimp ponds as a result of the addition of shrimp feed (Burford and Williams, 2001). However, much of it is refractory and not readily utilized by the natural biota (Burford, 2000), and therefore is shown as an isolated pool in the model.

2.2. Mathematical model

The mathematical model of Lorenzen et al. (1997) was modified based on the conceptual model to incorporate a NSED pool, the sludge N remineralization process and a DON pool (Fig. 1). The resulting model had five state variables representing the main N components: TAN, NOX, DON, NSED and particulate N in the form of phytoplankton, expressed as units of CHL.

The N dynamics model is given by the following set of coupled differential equations for the five state variables:

$$\frac{dC_{\text{TAN}}}{dt} = qA_t + rM_{\text{NSED}} - (n + v + f)C_{\text{TAN}} - gcC_{\text{CHL}} \left(\frac{C_{\text{TAN}}}{C_{\text{TAN}} + C_{\text{NOX}}} \right) \quad (1)$$

$$\frac{dC_{\text{NOX}}}{dt} = nC_{\text{TAN}} - fC_{\text{NOX}} - gcC_{\text{CHL}} \left(\frac{C_{\text{NOX}}}{C_{\text{NOX}} + C_{\text{TAN}}} \right) \quad (2)$$

$$\frac{dC_{\text{CHL}}}{dt} = gC_{\text{CHL}} - (f + s)C_{\text{CHL}} \quad (3)$$

$$\frac{dM_{\text{NSED}}}{dt} = scC_{\text{CHL}} - rM_{\text{NSED}} \quad (4)$$

$$\frac{dC_{\text{DON}}}{dt} = (1 - q)A_t - fC_{\text{DON}} \quad (5)$$

where C_{TAN} = TAN concentration (mg l^{-1}); t = time (day); q = proportion of N waste entering the water as TAN (with the remainder entering the water as DON); A_t = total N waste input per unit time ($\text{mg g}^{-1} \text{day}^{-1}$); r = remineralization rate of TAN in the sludge (day^{-1}); M_{NSED} = mass of N (mg) in the sludge l^{-1} of pond water; n = nitrification rate (day^{-1}); v = volatilization rate of ammonia (day^{-1}); f = water exchange rate (day^{-1}); g = phytoplankton growth rate (day^{-1}); c = N/CHL ratio of phytoplankton; C_{NOX} = NOX concentration (mg l^{-1}); C_{CHL} = CHL concentration; s = sedimentation rate of phytoplankton (day^{-1}); C_{DON} = DON concentration (mg l^{-1}).

Note that the mass of N in the sludge M_{NSED} is given l^{-1} of water to maintain direct comparability with the concentrations expressed as $mg\ l^{-1}$. Eqs. (4) and (5) are new additions to the equations of Lorenzen et al. (1997), and Eq. (1) has been modified to incorporate TAN flux from remineralization of NSED. The sub-models for N waste input and phytoplankton growth (Eqs. (6)–(12)) are identical to those used in Lorenzen et al. (1997) with the exception that no P limitation term is considered in the phytoplankton growth equation (Eq. (9)).

The total N waste input A_t was assumed to be proportional to the metabolism of the shrimp population:

$$A_t = aN_tW_t^b \quad (6)$$

where a is the N waste produced by one shrimp at unit weight ($mg\ g^{-1}\ day^{-1}$) and b is the allometric scaling factor of metabolism. The number N_t of shrimp is given by an exponential mortality model:

$$N_t = N_0e^{-Mt} \quad (7)$$

with N_0 as the stocking density (l^{-1}) and M the natural mortality rate (day^{-1}) of shrimp. Shrimp mean weight W_t is given by a von Bertalanffy growth function (Gulland, 1983):

$$W_t = (W_\infty^{1/3} - (W_\infty^{1/3} - W_0^{1/3})e^{-Kt})^3 \quad (8)$$

where W_∞ (g) and K (day^{-1}) are the von Bertalanffy growth parameters and W_0 (g) is the weight at stocking.

The growth rate g of phytoplankton is defined as:

$$g = g_{\max}L_{\text{light}}L_N \quad (9)$$

where g_{\max} (day^{-1}) is the maximum growth rate in the absence of limitation, and L_{light} and L_N are the light and TAN plus nitrate limitation coefficients, respectively. It was assumed that phosphate was not limiting to growth. The light limitation coefficient is given by the integral of Steele's (1962) light inhibition model over the water column, with light conditions defined by the Lambert–Beer law:

$$L_{\text{light}} = \frac{e}{k} \left(\exp\left(-\frac{I_0}{I_{\text{sat}}}\exp(-kz)\right) - \exp\left(-\frac{I_0}{I_{\text{sat}}}\right) \right) \quad (10)$$

where I_0/I_{sat} is the ratio of the surface light intensity to the saturating light intensity, k is the extinction coefficient (m^{-1}) and z is the pond depth (m). The extinction coefficient is the sum of extinction due to CHL and extinction due to other sources:

$$k = k_{\text{Chl}}C_{\text{Chl}} + k_{\text{other}} \quad (11)$$

where k_{chl} is the extinction per unit CHL concentration ($\text{m}^{-1} \text{mg}^{-1}$) and k_{other} is the extinction due to other sources. Nitrogen limitation is defined by the Michaelis–Menten model:

$$L_{\text{N}} = \frac{C_{\text{TAN}} + C_{\text{NO}}}{(C_{\text{TAN}} + C_{\text{NO}}) + K_{\text{SN}}} \quad (12)$$

where K_{SN} (mg l^{-1}) is the half-saturation constant for nitrogen.

Phytoplankton were assumed to assimilate both TAN and NOX in proportion to their relative concentrations in the water column. Nitrification, volatilization, sedimentation, remineralization and discharge of N were described as first-order rate processes (Lorenzen et al., 1997). The model was implemented in Microsoft Visual Basic.

2.3. Data used for model calibration

The model was calibrated using data from a commercial shrimp pond in southeast Queensland, Australia ($27^{\circ}45'S$, $153^{\circ}20'E$). The earthen pond (1 ha) was stocked with *Penaeus monodon* postlarvae at a density of 40 animals m^{-2} and maintained for 160 days before harvesting to give a biomass of 5.5 ton ha^{-1} . Average water temperatures over the season in this pond were 25.0 ± 2.1 °C at 0600 h and 26.8 ± 2.1 °C at 1500 h. Commercial feed was added throughout the growout cycle with the amount added being adjusted using feeding trays. The FCR was 1.9. The water was aerated with paddlewheels. The pond had periodic water exchanges after the first 65 days. This involved lowering the pond depth by approximately 20% then refilling with inlet water from the adjacent estuary. Water exchange volumes were recorded. Previous sampling of the inlet water at this farm, and Australian shrimp farms on similar river systems, has shown that the nitrogen loads from this source are low (Burford, 1997; Jackson et al., 2003).

The shrimp numbers and weight were estimated weekly after the first 4 weeks (when shrimp were sufficiently large to catch) using cast netting and weighing of approximately 100 shrimp. The total N added to the pond and incorporated into shrimp tissue was determined from the total feed input, shrimp yield and proximate analysis of feed and shrimp. The proportion of N present as dissolved organic N was also accounted for and assumed to be refractory for the purposes of the model.

TAN was measured in the commercial ponds every 4 h from day 75 by automated sampling (Aqualab, Greenspan Technology) and passing the sample by a gas diffusion electrode (Orion). Values were ground truthed against spot measurements of TAN using colorimetric techniques (American Public Health Association, 1995). Water samples for CHL and NOX were taken weekly from day 75 at one site in the pond. Previous sampling had determined that the shrimp ponds with mechanical aeration are horizontally well mixed so sampling at one site was representative of the pond (Burford, 1997). TAN, CHL and NOX data for earlier in the production cycle were taken from regular monitoring in five ponds at the same farm in previous years.

For CHL analyses, water samples were filtered through GF/F glass fibre filters. The filters were frozen until analyzed by sonicating filters in ice-cold acetone (Jeffrey and Welshmeyer, 1997). For NOX analyses, water samples were filtered through 0.45 μm membrane filters then frozen. NOX was analyzed using the spongy cadmium method (Jones, 1984).

Nutrient sampling and quantification of the sludge pile were conducted at the end of the growth season in the shrimp pond (Burford and Longmore, 2001). The area and depth contour of the sedimented particulate matter, i.e. inner sludge zone, in each pond was measured by walking calibrated transects across each pond and measuring the depth of the sludge each 2 m. In addition, sediment cores (50 mm deep, 24 mm diameter) were taken from nine sites in the inner sludge region. In the laboratory, the cores from all sites in each region were pooled and mixed thoroughly. A subsample was taken for total Kjeldahl N analysis. Samples were freeze-dried, sieved, digested and total Kjeldahl N was analyzed using an autoanalyzer (Technicon, 1977).

2.4. Model calibration

The model was calibrated as follows: all parameters that could be estimated directly, such as shrimp growth, mortality rates and N waste input were determined from the relevant data, while most N dynamics parameters (flux rates) were estimated by fitting the model to observed water quality dynamics.

Parameter values estimated independently were determined. VBGF parameters were estimated from data on stocking and weekly shrimp weights (Table 1). The mortality rate was estimated from numbers stocked and harvested. The total N waste (TAN and DON) input rate was determined so that cumulative inputs over the production cycle equaled the

Table 1
Model parameter values

Parameter	Values	Reference
<i>Management/environment parameters</i>		
Shrimp growth rate VBGF K (day^{-1})	0.0075	Burford (unpublished data)
Shrimp maximum weight VBGF W_{∞} (g)	75.6	Burford (unpublished data)
Shrimp stocking weight VBGF W_0 (g)	0.005	Burford (unpublished data)
Shrimp mortality M (day^{-1})	0.0055	Burford (unpublished data)
Waste N input A ($\text{mg g}^{-1} \text{day}^{-1}$)	4.0	Estimated from N budget
Proportion of N entering as TAN q	0.9	Burford (unpublished data)
Allometric scaling of TAN excretion b	0.75	Burford and Williams (2001)
Pond depth z (m)	1.5	
Extinction coefficient Non-Chl a k_{other} (m^{-1})	2.5	Burford (1997)
Extinction coefficient Chl a k_{chl} ($\text{m}^{-1} \text{mg}^{-1}$)	14	Burford (1997)
Water exchange f (day^{-1})		
Day 1–65	0	
Day 65 onwards	0.05	Burford (unpublished data)
<i>N dynamics parameters (estimated)</i>		
Phytoplankton growth rate g (day^{-1})	1.45	
Ratio surface/saturating light intensity I_0/I_{sat}	2.4	
N/CHL ratio of algae c	13	
N half-saturation K_{SN} (mg l^{-1})	0.008	
Sedimentation rate s (day^{-1})	0.8	
Nitrification rate n (day^{-1})	0.15	
Volatilization rate v (day^{-1})	0.05	
Sludge remineralization rate r (day^{-1})	0.06	

total feed N input minus the N incorporated into shrimp tissue. The proportions of total N waste entering the water as TAN and DON, respectively, were based on the N budgets measured by Burford and Williams (2001). Extinction coefficients from CHL and non-chlorophyll solids were based on light intensity profiles from ponds at this farm (Burford, 1997).

N dynamics parameters were estimated by fitting the model to observations of TAN, NOX and CHL over the course of a production cycle. The model was fitted using the method of maximum likelihood with a normal error model (Hilborn and Mangel, 1997). The method involved fitting the model to time series of TAN, NOX and CHL simultaneously, as the total likelihood of the data given that the parameter estimates equaled the product of the likelihood of individual data series. In order to test whether accounting for sediment remineralization significantly improved the fit of the model, confidence limits for r were derived from a likelihood profile.

2.5. Management scenarios

The model was used to evaluate the outcomes of two management scenarios, both simulated according to the waste N input rate observed at the end of the production cycle. The first scenario modeled variation in water exchanges ($0-100\% \text{ d}^{-1}$) and stocking density ($0-160 \text{ m}^{-2}$) without sludge removal. The second scenario modeled variation in sludge removal ($0-100\% \text{ d}^{-1}$) and stocking density ($0-160 \text{ m}^{-2}$) without water exchange.

3. Results

3.1. Model calibration

The model provided fitted well to the observed TAN, NOX and CHL concentrations throughout the production cycle (Fig. 2). The model predicted a low TAN concentration ($<0.1 \text{ mg l}^{-1}$) for the first 100 days of the season. Thereafter, input exceeded phytoplankton uptake capacity and TAN increased rapidly to reach 1.6 mg l^{-1} by the end of the growout season. CHL concentrations increased steadily over much of the growout season but leveled off after about 100 days reaching a plateau at 0.12 mg l^{-1} as self-shading limited production. Observed and predicted NOX concentrations remained low until TAN increased significantly in the latter part of the growing season and increased rapidly after day 120.

The sedimentation rate was estimated as 0.8 day^{-1} while the remineralization rate of sludge N was estimated as 0.06 day^{-1} (i.e. 6% of the sludge N pool is remineralized day^{-1}) (Table 1). A 95% confidence interval for r was estimated as $[0.04, 0.7] \text{ day}^{-1}$, i.e. r is significantly different from 0 and therefore, accounting for sediment remineralization improves the fit of the model significantly.

3.2. Role of sedimentation and remineralization

Sedimentation and remineralization play a major role in N dynamics over the production cycle (Fig. 3). The highest concentration of N is in the sludge pool, which increases steeply

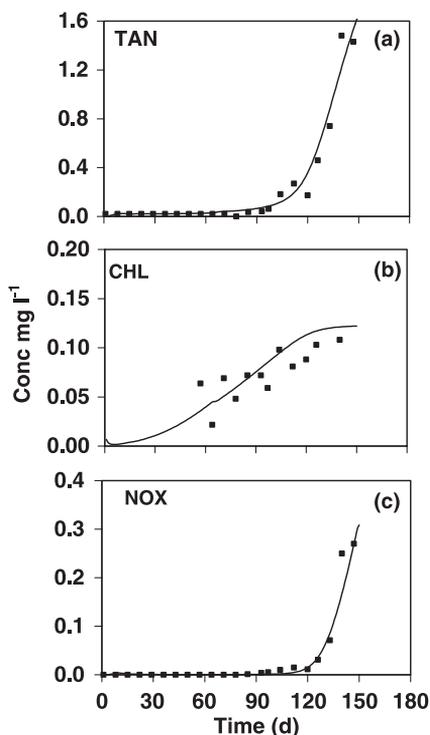


Fig. 2. Predicted (solid lines) and measured (solid squares) concentrations of (a) total ammonia N (mg l^{-1}); (b) CHL ($\mu\text{g l}^{-1}$); and (c) NOX (mg l^{-1}) in a shrimp pond over a production cycle.

over much of the cycle but plateaus towards the end of the production cycle (Fig. 3a). This equates to $2.5 \times 10^8 \text{ mg N pond}^{-1}$. In comparison, $3.2 \times 10^8 \text{ mg N pond}^{-1}$ was measured as the total amount of N in the sludge in this pond at the end of the season. The total phytoplankton N (N Chl) and TAN have much lower concentrations. This is the net result of the continued input of new TAN originating from feed, the sedimentation of phytoplankton N and remineralization of sludge N. The TAN flux from sludge remineralization exceeds the flux of new TAN originating from feed inputs throughout the later stages of the cycle (Fig. 3b). Sedimentation exceeds remineralization of N throughout the cycle, leading to the rapid buildup of sludge N. However, both fluxes converge towards an equilibrium in the last part of the cycle. The limitation of phytoplankton production due to self-shading limits the N sedimentation flux even if new TAN inputs continue to rise. The stabilization of the sedimentation rate eventually gives rise to an equilibrium where sedimentation and remineralization fluxes are equal and the sludge N pool is constant.

3.3. N concentrations and fate in relation to farming intensity and water exchange

Predictions of the impact of farming intensity and water exchange on TAN and CHL concentrations and the fate of N waste at the end of the production cycle were generated

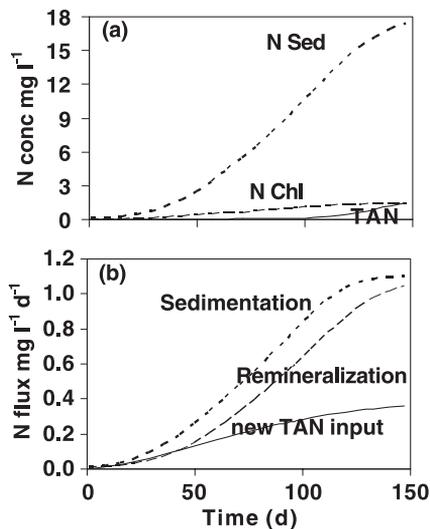


Fig. 3. Predicted dynamic of (a) major N pools (mg l^{-1}) and (b) N flux ($\text{mg l}^{-1} \text{day}^{-1}$) over the period of the production cycle. The sediment N pool is expressed as a mass l^{-1} of water and shown on the same scale as the concentrations of the other N components.

to assess whether the inclusion of sludge remineralization in the model affected the patterns predicted by Lorenzen et al. (1997) and Lorenzen (1999). The effect of a range of stocking densities and water exchange rates on TAN and CHL concentrations at the end of the production cycle was determined. TAN levels increased with decreasing water exchange rates and increasing stocking densities (Fig. 4a). Increasing stocking densities increased CHL concentrations up to a stocking density of 20 animals m^{-2} . However, above these densities, there was no further increase in CHL (Fig. 4b). Increasing water exchange rates decreased CHL, and above exchange rates of 30% day^{-1} , CHL was virtually absent.

The percentage of N waste in the dissolved, particulate and sludge pools, and volatilized changed substantially with water exchange rates and stocking densities (Fig. 4c–f). The proportion of N discharged in the dissolved form increased with water exchange rate but increasing stocking density had little effect above 40 animals m^{-2} (Fig. 4c). The proportion discharged as particulate N was highest at water exchange rates of 20% day^{-1} and decreased at higher and lower water exchange rates (Fig. 4d). The proportion of N waste in the sludge decreased with increasing water exchange rates and stocking densities (Fig. 4e). The proportion volatilized increased with stocking density and decreased with increasing water exchange rates (Fig. 4f).

3.4. The effect of sludge removal

Removal of only 10–20% of sludge per day reduced remineralization and hence TAN concentrations to 20–30% of values without sludge removal (Fig. 5a). NOX

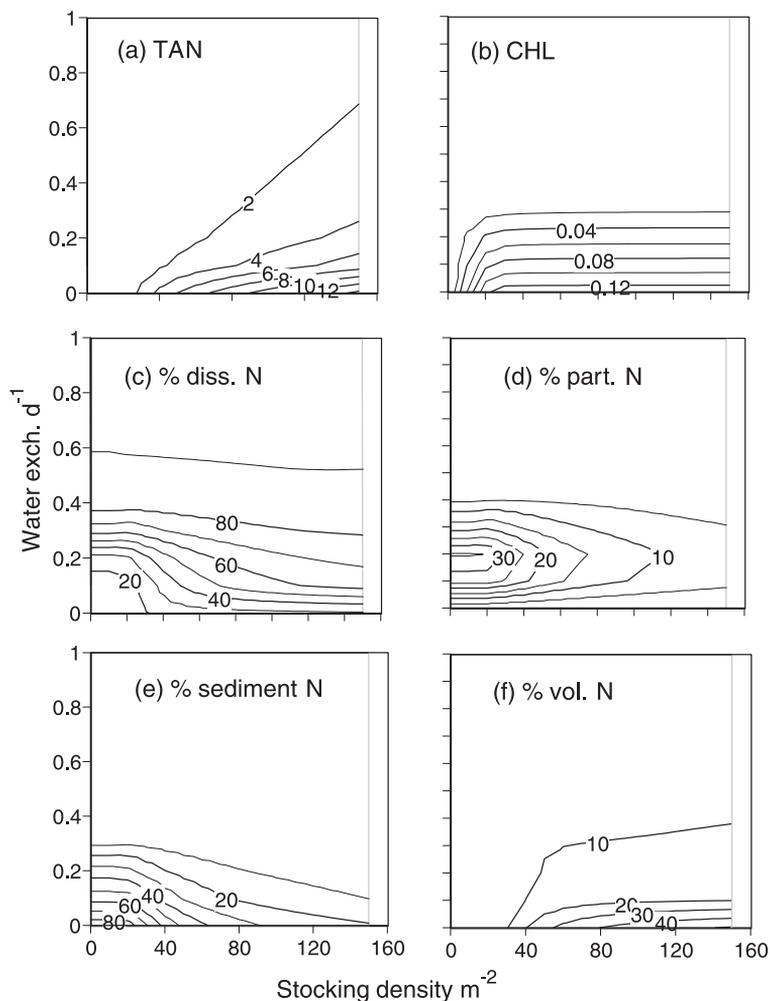


Fig. 4. Predicted concentrations of (a) TAN (mg l^{-1}); (b) CHL ($\mu\text{g l}^{-1}$); and fate of N waste (%) in the (c) dissolved = diss; (d) particulate = part; (e) sludge; and (f) volatilized = vol fractions in a shrimp pond at the end of the production cycle as a function of water exchange rates and shrimp stocking densities, with no sludge removal.

concentrations were relatively low ($<1 \text{ mg l}^{-1}$) at low stocking densities ($<50 \text{ m}^{-2}$) so sludge removal had a less dramatic effect (Fig. 5b). However, at higher stocking densities, removal of 10–20% of sludge substantially reduced NOX concentrations. DON concentrations increased with increasing stocking densities but were not affected at all by the sludge removal rate. CHL increased with increasing stocking densities up to a plateau defined by self-shading, but the increase was steepest at low sludge removal rates and far more gradual at high sludge removal rates (Fig. 5d). Overall,

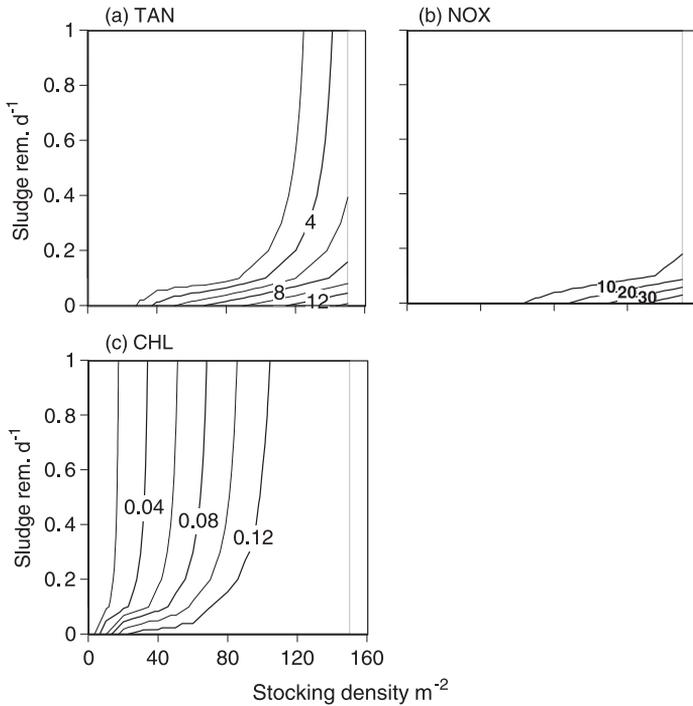


Fig. 5. Predicted concentrations of (a) TAN (mg l⁻¹); (b) NOX (mg l⁻¹); and (c) CHL (μg l⁻¹) in a shrimp pond at the end of the production cycle as a function of sludge removal rates and shrimp stocking densities, with no water exchange.

low sludge removal rates of 10–20% day⁻¹ are sufficient to exert a strong effect on TAN, NOX and CHL concentrations, while higher rates of removal have little further effect.

4. Discussion

4.1. The model

The incorporation of sludge remineralization in the N dynamics model of Lorenzen et al. (1997) permitted the analysis of the dynamic interactions of N input, sedimentation and remineralization in the course of a production cycle. Although empirical studies have demonstrated the importance of remineralization processes in determining TAN concentrations (Sornin et al., 1990; Krom, 1991; Jiménez-Montealegre, 2001; Burford and Longmore, 2001), previous models have either ignored remineralization or modeled the process as a constant or temperature-dependent flux without consideration of the dynamics of N accumulation in the sludge. The present study clearly indicates that the dynamics of

the sediment N pool is a major driver of water quality change in the course of the production cycle and should be considered explicitly.

The model provided an excellent fit to time series of TAN, CHL and NOX concentrations in an Australian commercial shrimp farm. Concentrations were also comparable with the range of concentrations measured in other shrimp pond studies (Briggs and Funge-Smith, 1994; Tookwinas and Songsangjinda, 1999; Jackson et al., 2003). Additionally, extrapolating NSED on a whole pond basis compared favorably with measured NSED values for this pond. However, it must be acknowledged that it is difficult to accurately measure the amount of sludge in earthen ponds. Another study of NSED in Australian shrimp ponds only found values 20% of that in our study (Jackson et al., 2003).

There have been few studies of nitrogen dynamics in shrimp ponds to compare with the parameter values estimated in the model. Estimated maximum phytoplankton growth rates and N: chlorophyll ratios were very similar to values determined experimentally in shrimp ponds (Burford and Pearson, 1998; Burford et al., 2002; Jackson et al., 2003). Nitrification rates have generally not been studied in intensive earthen shrimp ponds with water exchange, but nitrate and nitrite concentrations generally remain low throughout the growth season (Briggs and Funge-Smith, 1994; Tookwinas and Songsangjinda, 1999; Jackson et al., 2003). Additionally, a study of bacterial populations in shrimp ponds using an rDNA molecular technique found no evidence of nitrifiers (Baiano, 2002). It has been hypothesized that the rates of water exchange are such that relatively slow growing nitrifiers cannot become established since in ponds with no water exchange, nitrification rates were significant (Bratvold and Browdy, 1998). Therefore, the relatively low rates of nitrification estimated in our study are not likely to be underestimates.

A study of TAN diffusion due to sludge remineralization in shrimp ponds late in the growth season found lower rates (0.39×10^7 mg N pond⁻¹ day⁻¹, Burford and Longmore, 2001) than those estimated using the model (1.53×10^7 mg N pond⁻¹ d⁻¹). This discrepancy may reflect difficulties in measuring TAN diffusion directly as well as the simplistic model assumption of a constant rate of remineralization applied to the whole sediment N pool. It seems likely that the uppermost layer of sludge accounts for a large share of remineralization while deeper layers become progressively isolated from the water column. The upper layer may be disturbed when benthic chambers are deployed, most likely resulting in an underestimate of flux. On the other hand, the assumption of a constant rate of N remineralization throughout the cycle is likely to underestimate flux early in the cycle, but overestimate flux later on when an increasing proportion of N is locked in the deeper layers. This emphasizes again that consideration of sediment N dynamics is very important to water quality management, and that further research on measuring and modeling the different components of this pool is highly desirable.

It is difficult to compare rates of N dynamics in shrimp pond with other aquaculture pond systems due to differences in stocking, feed wastage, water exchange rates and other management practices that ultimately affect the rates of nitrogen cycling. However, estimated ammonia volatilization rates of 5% of TAN concentrations in our study were comparable with the 4% for channel catfish ponds (Gross et al., 1999).

4.2. Implications of N remineralization

Remineralization of N at the sludge–water interface plays a major role in the dynamics of N over the production cycle and dominates TAN inputs over much of the production cycle, a prediction consistent with empirical studies (Burford and Longmore, 2001). Incorporation of N remineralization in the model had little effect on the basic relationships between farming intensity, water management and the concentrations and fate of N components derived in earlier studies where the process has been ignored (Lorenzen, 1999; Lorenzen et al., 1997). This may seem surprising, given the large contribution of remineralized TAN to total TAN production in the pond. However, while TAN remineralization implies that N cycles through the plankton-sludge system at a high rate, the resulting concentrations and fate are determined by the net fluxes between compartments. When fitting a model to data that does not allow for remineralization, the estimated sedimentation rate more closely reflects the net N sedimentation rate, and the overall predicted N dynamics may be very similar to those predicted by a model that allows for recycling and uses gross flux rates.

The model predicts that N sedimentation and remineralization fluxes converge towards equilibrium as the former is limited by phytoplankton production (which in turn is limited by self-shading) while the latter increases as N accumulates in the sludge. This equilibrium defines a carrying capacity of the pond for cumulative N removal over the course of the culture cycle. In the present case, this carrying capacity is estimated as about 18 mg l^{-1} or 27 g m^{-2} . Once the carrying capacity is reached, sediment N needs to be removed or otherwise made unavailable for remineralization if sedimentation is to remain a net N removal process. In this study the equilibrium is approached towards the end of the cycle, and it is at this point that TAN and NOX levels increase significantly. This definition of carrying capacity is different from that given in Lorenzen et al. (1997), based only on current phytoplankton uptake capacity while neglecting the role of sludge N dynamics. Neither of these definitions are likely to be entirely correct. Remineralization of sludge N is clearly important to water quality dynamics, and this inevitably means that current N uptake capacity is partly determined by the history of sludge N accumulation. On the other hand, it is unlikely that the entire sludge N pool will remain subject to remineralization, as an increasing proportion is likely to be locked in the deeper layers of sludge. To resolve this problem, it will be necessary to measure and model the different sludge N components explicitly.

The model developed in this study has shown that there is little benefit, in terms of TAN concentrations, in water exchange rates greater than $10\% \text{ day}^{-1}$ when stocking densities are low ($<40 \text{ animals m}^{-2}$). At high stocking densities ($>100 \text{ animals m}^{-2}$), water exchanges of less than $20\% \text{ day}^{-1}$ would maintain TAN concentrations $<4 \text{ mg l}^{-1}$ and should not compromise shrimp growth (Allan et al., 1990). Higher water exchange rates ($>30\%$) gave little benefit in terms of reducing TAN since CHL was effectively diluted at a rate faster than the potential phytoplankton growth rate. Phytoplankton plays a key role in controlling TAN in shrimp ponds (Burford and Glibert, 1999).

In more recent years, water exchange rates in some countries have decreased as a biosecurity measure to prevent the spread of disease and as environmental regulations for nutrient and suspended solids discharges have become more stringent (Funge-Smith and

Briggs, 1998). In South East Asia, water exchange rates have decreased from 17.5% in 1998 to present values of 7% (McIntosh and Avnimelech, 2001). Coupled with constraints on farmers regarding water exchange, shrimp farmers are under pressure to become increasingly competitive. One method for achieving this is to increase yields by increasing stocking densities. The modeling approach has shown that in order to maintain TAN at levels that will not compromise shrimp growth, i.e. below 4 mg l^{-1} , stocking densities cannot be increased above $60 \text{ animals m}^{-2}$ at current water exchange rates of 7%.

Increasing stocking densities beyond $60 \text{ animals m}^{-2}$ requires new methods of managing TAN levels. One avenue is to remove the buildup of sludge from ponds. By accounting for N remineralization explicitly, the model developed here has been used to analyze this management option. Previous studies have shown that substantial amounts of TAN are released from the sludge in shrimp ponds as a result of remineralization of organic detritus (Burford and Longmore, 2001). The modeling approach has now shown that removal of 10–20% of sludge day^{-1} throughout the production cycle is sufficient to maintain TAN levels below critical thresholds even when stocking densities are as high as 140 m^{-2} with zero water exchange. At this rate of removal, there is also sufficient TAN for optimal algal growth. The key to effective removal of N from the sludge pool is to maximize sedimentation, coupled with effective mechanisms for periodically removing sludge from ponds (Hopkins et al., 1994). Methods such as the use of central drains and siphons have proven partially successful but often labour intensive at commercial farms (Browdy et al., 2001). There is a need for more effective mechanisms for sludge removal and concentration for on-land disposal.

The model provides a tool for examining effects of management strategies on a whole-of-season basis. Therefore, it does not reflect the rapid short-term oscillations of parameters such as CHL and TAN and should be viewed in this context. Additionally, the model does not include rates of grazing on phytoplankton. A previous study have shown that many zooplankton species are only present in numbers sufficient to substantially impact phytoplankton biomass in the first few weeks of the production cycle (Coman et al., 2003; Preston et al., 2003). It has been hypothesized that predation by shrimp is the cause for the reduction in zooplankton numbers.

The present model provides insights into the role of sludge remineralization, but still has some limitations that may be resolved through further combined experimental and modeling studies. In particular, the representation of remineralization as a constant rate process acting on the total sludge N pool is simplistic. Sedimentation of phytoplankton results in layers of loose organic matter that may become partly incorporated into the inorganic sludge matrix. The sludge N pool thus consists of several compartments with their own dynamics and differential availability to remineralization. Additionally, the rate of diffusion of TAN into the water column will vary depending on the density and other characteristics of the sludge. A more detailed analysis of the sedimentation and remineralization process may lead to refinements of the model.

In conclusion, accounting for the role of sludge remineralization in the dynamics of N in shrimp ponds makes little difference to the evaluation of management strategies that do not involve manipulation of the sludge N pool. However, it indicates that sludge removal provides an alternative mechanism to water exchange to improve water quality and minimize environmental effects. Although sludge removal would require additional

infrastructure and hence cost, our model indicates that much higher stocking densities should be achieved, potentially offsetting this cost and ultimately improving profitability.

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