Review

Nitrogen biogeochemistry of aquaculture ponds [1]

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Abstract

Nitrogen (N) biogeochemistry of aquaculture ponds is dominated by biological transformations of N added to ponds in the form of inorganic or organic fertilizers and formulated feeds. Nitrogen application in excess of pond assimilatory capacity can lead to the deterioration of water quality through the accumulation of nitrogenous compounds (e.g., ammonia and nitrite) with toxicity to fish or shrimp. Principal sources of ammonia include fish excretion and sediment flux derived from the mineralization of organic matter and molecular diffusion from reduced sediment, although cyanobacterial nitrogen fixation and atmospheric deposition are occasionally important. Principal sinks for ammonia include phytoplankton uptake and nitrification. The magnitude of losses by ammonia volatilization and ammonium fixation to cation exchange sites is minor, but unknown. Interactions between pond sediment and water are important regulators of N biogeochemistry. Sediment represents a source of ammonia and a sink for nitrite and nitrate. The large volume of reduced sediment suggests that the potential for N removal by denitrification is high, although the magnitude of N removal by this mechanism is low because nitrification and denitrification are tightly coupled in aquatic sediments and sediment nitrification is limited by the depth of sediment oxygen penetration. Nitrogen biogeochemistry of aquaculture ponds is affected by feeds and feeding practices, water exchange and circulation, aeration, pond depth and other management procedures. Opportunities for management of N biogeochemistry are limited and goals are based largely on the intensity of fish production. © 1998 Published by Elsevier Science B.V. All rights reserved.

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1. Importance of nitrogen in pond culture systems

The efficiency of fish nitrogen (N) assimilation has important implications for water quality and profitability of pond aquaculture. Results from a variety of culture systems indicate that, on average, about 25% (range: 11 to 36%) of N added as feed or other nutrient input is recovered by the target organism (Table 1). Protein sources such as fish meal and soybean meal are the most expensive components of formulated feeds and improvement in the efficiency of N assimilation and utilization will thus improve the economics of fish production.

The inherent efficiency of nutrient utilization by fish implies that N loading of aquaculture ponds may be limited by the capacity to assimilate nitrogenous excretion, which may have a deleterious impact on water quality and fish growth. Following dissolved oxygen, the accumulation of dissolved inorganic nitrogen (DIN) is the factor most likely to limit feeding rate in aquaculture ponds (Knud-Hansen et al., 1991b).

Ammonia [2] is excreted as the end product of protein catabolism, and may be toxic if allowed to accumulate. Ammonia toxicity is manifest by hyperactivity, convulsions, loss of equilibrium, lethargy and coma. However, ammonia toxicity in aquaculture ponds is most likely expressed as the sublethal reduction of fish growth or suppression of immunocompetence, rather than as acute toxicity leading to mortality. Colt and Tchobanoglous (1978) demonstrated linear reduction of channel catfish growth over the range 0.05 to 1.0 mg l^{-1} NH_3–N and a calculated 50% reduction of growth at about 0.5 mg l^{-1} NH_3–N. The mechanisms of ammonia toxicity have not been firmly established. However, a combination of plasma sodium depletion (Colt and Tchobanoglous, 1978; Tomasso et al., 1980), biochemical effects of Krebs cycle suppression by depletion of α-ketoglutarate (Sousa and Meade, 1977; Smart, 1978) resulting in reduced ammonia excretion, and other factors (Meade, 1985) are implicated. The toxicity of un-ionized ammonia is a function of pH, temperature, alkalinity and total ammonia concentration measured at the gill surface (Szumski et al., 1982). Ammonia is more toxic to fish at elevated pH and temperature, which shifts the ionization equilibrium toward the toxic, unionized gaseous form. The risk of elevated pH and unionized ammonia is greater in poorly buffered (low alkalinity) ponds in the late afternoon.

The contribution of ammonia excretion to N flow in aquaculture ponds is substantial. If 25% of input N is retained by fish, then 75% of input N is excreted. Nitrogen excretion can be partitioned into dissolved (62%) and particulate (13%) fractions (Folke and Kautsky, 1989). For example, at a feeding rate of 100 kg ha^{-1} d^{-1} (32% protein feed), ammonia excretion would be 317 mg N m^{-2} d^{-1}. Alternately, using a feed-based estimate of ammonia excretion of 30 g N kg^{-1} feed (Colt and Orwicz, 1991), then 300 mg N m^{-2} d^{-1} are excreted.

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[2] Ammonia exists as a component of a pH- and temperature-dependent equilibrium in natural waters. Across the range of pH most commonly encountered in natural waters (6.5 to 9.0), the equilibrium favors the aqueous, ionized form (NH_4^+), or 'ammonium'. Elevated pH (> 9.3) favors the gaseous, unionized form (NH_3), or 'ammonia'. The convention adopted here will be to use the term 'ammonia' to refer to unionized ammonia plus ionized ammonium ($NH_3 + NH_4^+$) expressed as nitrogen by mass unless otherwise explicitly indicated.

Table 1
Estimates of the range (%) of nitrogen recovered by fish and released to the environment in various aquaculture production systems

Fish species	Production system[a]	Recovered Fish	Released			Refs.
			Total	Dissolved	Solid	
polyculture	P	11–16	84–89			Schroeder et al., 1990
Anguilla japonica	P	14–25	75–86			Chiba, 1986
Oreochromis niloticus	P	18–21	79–82			Green and Boyd, 1995
Oreochromis spp.	P	25–29	75–81			Avnimelech and Lacher, 1979
Morone saxatilis	P	22	78			Daniels and Boyd, 1989
Ictalurus punctatus	P	27	73			Boyd, 1985
Sparus aurata	P	36	64			Krom et al., 1985
S. aurata	P	26	74			Neori and Krom, 1991
S. aurata	T	27		66	7	Neori and Krom, 1991
S. aurata	T	30		60	10	Porter et al., 1987
Oncorhynchus mykiss	C	21		49	30	Phillips and Beveridge, 1986
O. mykiss	C	25		60	15	Pillay, 1992
O. mykiss	C	25–29	71–75			Penczak et al., 1982
Salmo salar	C	25		62	13	Folke and Kautsky, 1989
Salmo salar	C	25		65	10	Gowen and Bradbury, 1987
Clarias macrocephalus	C	24	76			Lin et al., 1993
I. punctatus	R	14	86			Worsham, 1975
O. mykiss	R	19		74	7	Foy and Rosell, 1991a,b

[a] Production system codes: P = earthen pond, T = tank, C = cage, R = raceway.

Fish also excrete fecal solid wastes that settle to the sediment along with senescent phytoplankton and other particulate organic matter. By the mass balance approach (13% N as particulate solids), then 67 mg N m^{-2} d^{-1} are excreted as fecal solids at a feeding rate of 100 kg ha^{-1} d^{-1}. Alternately, fecal solids can account for up to 50% by weight of dry weight feed applied to the pond (Colt and Orwicz, 1991). Feces from catfish fed a 32% protein feed are 13.1% protein (Brown et al., 1989). By this analysis, fecal solids contribute 104 mg N m^{-2} d^{-1}. A large fraction of this organic matter is rapidly hydrolyzed and mineralized, representing an additional source of ammonia.

Nitrite is another potentially-toxic nitrogenous compound that may accumulate in fish culture ponds. Nitrite is released as an intermediate product during nitrification and denitrification. The toxicity of nitrite is expressed through the competitive binding of nitrite to hemoglobin forming methemoglobin, which does not have the capacity to carry oxygen.

Nitrogen may limit the primary productivity of ponds in which fish yields are dependent upon the development of autotrophic food webs. Thus, organic and inorganic fertilization programs may be directed toward increasing the availability of N for phytoplankton (Noriega-Curtis, 1979; Green et al., 1989; Schroeder et al., 1990; Knud-Hansen et al., 1991a,b).

Nitrogen discharged in fish pond effluents may degrade the quality of receiving waters. Given the inherent nutrient utilization efficiency described above, large quantities of nutrients may be released to the environment. Compared to concentrations in

influent water, Ziemann et al. (1992) measured an increase of total N and ammonia and a decrease of nitrate in the effluent from freshwater fish and prawn ponds and marine fish and shrimp ponds. Similarly, Tucker and Lloyd (1985a) measured higher concentrations of total N and ammonia and lower concentrations of nitrate in channel catfish ponds as compared to nearby receiving streams. Most of the N discharged from fish ponds is associated with algal and detrital biomass.

In general, the discharge of N to the environment from ponds is comparatively lower than that from raceways and cages. Schwartz and Boyd (1994) measured the quantities of nutrients discharged during the draining and harvest of three channel catfish ponds and calculated that 18.6 g N kg^{-1} fish were released to the environment. The discharge of N from shrimp ponds is variable and depends upon water exchange rate. Estimates of the quantity of N discharged from shrimp ponds range from 17 to 58 g N kg^{-1} shrimp (Smith, 1995) to 102 ± 25 g N kg^{-1} shrimp (Briggs and Funge-Smith, 1994). In contrast, from 37 to 180 g N kg^{-1} rainbow trout were discharged from raceways (Alabaster, 1982) and from 95 to 102 g N kg^{-1} rainbow trout were discharged from cages (Hall et al., 1992).

2. Processes related to nitrogen flux in aquaculture ponds

2.1. Feeding and fertilization

Application of formulated feeds constitutes the main ($> 90\%$) input of N to semi-intensive fish ponds. For example, at a feeding rate of 100 kg ha^{-1} d^{-1} (10 g m^{-2} d^{-1}) of 32% protein feed, more than 500 mg N m^{-2} d^{-1} are added to ponds. Organic and inorganic fertilizers may also supply significant quantities of N to fish ponds. In systems managed for autotrophic productivity, a net fish yield of 30 to 40 kg ha^{-1} d^{-1} (3 to 4 g m^{-2} d^{-1}) is possible at a loading of 700 to 800 mg N m^{-2} d^{-1} from a combination of organic and inorganic sources (Schroeder et al., 1990; Knud-Hansen et al., 1991b). Experience suggests that this represents the upper limit to N loading of fish ponds without degradation of water quality. Smaller amounts of N may be added from water supplied to replace losses due to evaporation and seepage, or from atmospheric deposition, particularly during the dry season in the tropics.

2.2. Nitrogen fixation

Nitrogen may be added to fish ponds by the reduction of atmospheric dinitrogen by heterocystous cyanobacteria. Nitrogen fixation ranged from 6 to 23 mg N m^{-2} d^{-1} during the dry season and 21 to 57 mg N m^{-2} d^{-1} during the rainy season in tropical fish ponds (Lin et al., 1988). Nitrogen fixation averaged 24 mg N m^{-2} d^{-1} in a tropical freshwater fish pond and accounted for 10% of estimated N input (Acosta-Nassar et al., 1994). El Samra and Oláh (1979) measured an average nitrogen fixation rate of 4 mg N m^{-2} d^{-1} in a temperate aquaculture pond. The quantity of N added to aquaculture

ponds by fixation depends largely upon species composition of the phytoplankton community (significant proportion of heterocystous cyanobacteria) and ammonia concentration. The extent of inhibition of N fixation is inversely related to ammonia concentration (Lin et al., 1988). Nitrogen fixation is a minor, but occasionally important contributor to the N budget of aquaculture ponds receiving formulated feeds.

2.3. Phytoplankton uptake of inorganic nitrogen

Phytoplankton uptake of DIN from the water column of aquaculture ponds is the primary pathway of nitrogen removal. Semi-intensive aquaculture ponds often develop dense phytoplankton populations (chlorophyll $a > 250$ μg l^{-1}, Secchi disk visibility < 20 cm) in response to a high rate of nutrient input. Phytoplankton blooms in most fed aquaculture ponds are likely light-limited (Laws and Malecha, 1981; Smith and Piedrahita, 1988), suggesting nutrients are available at concentrations exceeding those limiting uptake or are supplied in excess of cellular requirements.

Nitrogen uptake by phytoplankton can be estimated by several methods, all yielding results of similar magnitude. Phytoplankton carbon fixation in temperate fish ponds varies from 1 to 3 g C m^{-2} d^{-1} over an annual cycle (Boyd, 1990). In tropical ponds, carbon fixation by phytoplankton can approach 5 to 10 g C m^{-2} d^{-1} (Krom et al., 1989; Schroeder et al., 1991). Assuming phytoplankton uptake of nutrients is approximately proportional to the Redfield ratio (C:N:P = 106:16:1), N uptake ranges from about 150 to 450 mg N m^{-2} d^{-1} in temperate ponds, and from 750 to 1500 mg N m^{-2} d^{-1} in tropical ponds (Table 2). Sustained (1 to 3 month) phytoplankton production of 15 to

Table 2
Estimated magnitude of and primary factors affecting the important nitrogen processes in aquaculture ponds

Process	Rate (mg m^{-2} d^{-1})	Primary factors affecting rate
Excretion		
(gills)	0–300	feeding rate, dietary protein
(fecal)	70–100	feeding rate
Nitrogen fixation	0–50	ammonia concentration, heterocystous cyanobacteria
Phytoplankton uptake		
(temperate)	0–450	phytoplankton density
(tropical)	750–1500	temperature
Ammonia volatilization	0–50	pH, temperature, wind speed
Ammonium adsorption	?	soil mineralogy
Sediment–water ammonia flux	25–150	temperature, overlying water DO
Nitrification		
(summer)	25	temperature
(sping/fall)	150	ammonia concentration
Coupled nitrification–denitrification	25–50	temperature, sediment O$_2$ penetration
Organic matter accumulation (burial)	variable	organic matter C:N

25 g dry matter m^{-2} d^{-1} in algal mass cultures has been demonstrated, and higher production (30 to 40 g m^{-2} d^{-1}) was possible over shorter periods (Goldman, 1979). Assuming the N content of phytoplankton with no nutrient deficiency is 5 to 10% of dry matter (Jørgensen et al., 1991), maximum N assimilation under light-limited conditions typical of eutrophic aquaculture ponds is equivalent to about 750 to 2000 mg N m^{-2} d^{-1}, although higher uptake rates are possible in algal mass cultures grown under optimum conditions (Goldman, 1979).

A third approach toward assessment of the magnitude of phytoplanktonic N uptake can be derived from maximum uptake rates (V_{max}) determined for natural populations of *Microcystis aeruginosa* and *Oscillatoria agardhii*, common cyanobacteria in hypereutrophic aquaculture ponds. Assuming a chlorophyll *a* concentration of 250 µg l^{-1}, a chlorophyll *a* composition of 1.5% of phytoplankton dry weight and V_{max} ranging from 1.5 to 4.0 µg N mg dry weight^{-1} h^{-1} (Kappers, 1980), then nitrogen uptake rates range from 600 to 1600 mg N m^{-2} d^{-1}. Clearly, phytoplankton uptake is a powerful mechanism for conversion of potentially-toxic inorganic N to relatively-stable organic N.

Ammonia is the preferred N substrate for phytoplankton, and only after it has been depleted (< 0.03 mg N l^{-1}) will significant quantities of nitrate be assimilated (Syrett, 1981; McCarthy, 1981). Nitrate assimilation and incorporation is an energetically less-favorable pathway of N nutrition for phytoplankton, as enzymatic-reduction to ammonia within the phytoplankton cell is necessary before incorporation into cellular amino acids.

Dissolved inorganic nitrogen uptake generally follows Michaelis–Menten enzyme–substrate kinetics in which uptake rate is a hyperbolic function of concentration. Half-saturation concentrations (K_s) for the assimilation of DIN by marine phytoplankton range from 0.01 to 0.10 mg N l^{-1} (Eppley et al., 1969), although internal concentrations required to saturate internal enzyme systems may be 1 to 2 orders of magnitude greater (Syrett, 1981) suggesting that nutrients are concentrated within the phytoplankton cell. Given the generally elevated DIN concentrations in semi-intensive aquaculture ponds (0.5 to 3 mg l^{-1}), it is not likely that substrate concentrations limit phytoplankton growth.

In aquaculture ponds, the regulation of DIN concentration is mediated primarily by phytoplankton (Tucker et al., 1984; Krom et al., 1989). In these studies, short-term variation in ammonia concentration was inversely related to phytoplankton density. During phytoplankton die-offs, ammonia concentration increased dramatically. As phytoplankton density increased, ammonia concentration declined. In addition, seasonal changes in phytoplankton density affect DIN concentrations in aquaculture ponds (Tucker and van der Ploeg, 1993). Dissolved inorganic nitrogen concentrations in commercial catfish ponds were greatest in winter when phytoplankton density was lowest, despite seasonally minimal feeding rates and temperature.

Dissolved inorganic nitrogen concentrations may be affected by phytoplankton species composition. In Israeli brackishwater fish ponds, chlorophytes and chrysophytes dominated phytoplankton blooms in winter and spring, whereas cyanobacteria were dominant in summer (van Rijn et al., 1986). The presence of cyanobacteria was coincident with low (< 0.01 mg N l^{-1}) concentrations of DIN. A similar successional

pattern was observed in commercial catfish ponds (Tucker and van der Ploeg, 1993), although cyanobacteria were dominant throughout the year.

2.4. Ammonia volatilization

The equilibrium between gaseous, unionized ammonia (NH_3) and aqueous, ionized ammonium (NH_4^+), which has a pK_a of 9.24 at 25°C, is strongly affected by pH and much less strongly affected by temperature. Alkaline pH and higher temperature favors the unionized, gaseous form. As a crude approximation, at pH 9.3, about 50% of ammonia is unionized; at pH 8.3, about 10% is unionized; and, at pH 7.3, about 1% is unionized. Volatilization is thus enhanced at elevated pH due to equilibrium relationships and the resultant increase in the partial pressure of ammonia gas. Ammonia volatilization is not important at pH < 7.5. Volatilization may be important as a mechanism of ammonia removal during the late afternoon in poorly-buffered (total alkalinity < 20 mg l^{-1} as $CaCO_3$) ponds, when pH may exceed 9 in response to the depletion of CO_2 from solution by phytoplankton (Hariyadi et al., 1994). Murphy and Brownlee (1981) calculated ammonia volatilization rates in a hypereutrophic lake dominated by *Aphanizomenon flos-aquae* during the late afternoon (pH > 9) of a windy day that were an order of magnitude greater than the rate of phytoplankton uptake of ammonia. Schroeder (1987) estimated ammonia volatilization of 50 mg N m^{-2} d^{-1} from manure-loaded polyculture ponds at pH 8 and 0.5 mg N l^{-1} as ammonia. Volatilization was estimated to account for the loss of 30% of N added to an intensive shrimp pond and 8% of N added to a semi-intensive shrimp pond (Lorenzen et al., 1997). However, ammonia volatilization was inconsequential as a mechanism of nitrogen removal in a model of a temperate wastewater stabilization pond (Ferrara and Avci, 1982). During summer, when environmental conditions favor volatilization, ammonia concentrations were seasonally minimal. In general, ammonia volatilization is enhanced by increased ammonia concentration, pH, temperature, evaporation rate and wind speed.

2.5. Processes associated with organic matter

2.5.1. Sedimentation and resuspension

Aquaculture ponds are generally shallow, characterized in part by minimal organic matter decomposition within truncated water columns. Organic inputs, senescent phytoplankton, fish fecal solids and uneaten feed settle from the water column to the sediment. In ponds fertilized by manures or agricultural by-products, direct consumption by fish is minimal and most of the input settles to the sediment. In addition, as much as 50% of the algal standing crop (about 10 g algal dry weight m^{-2} d^{-1}) may settle to the sediment surface each day (Schroeder et al., 1991). A simulation model that partitioned the fate of N added to semi-intensive shrimp ponds predicted that 48 to 66% would settle to the pond bottom in the form of phytoplankton (Lorenzen et al., 1997). Sediment traps in freshwater fish ponds collected 200 to 500 g dry matter m^{-2} d^{-1}, most derived from previously-deposited material resuspended by the foraging activity of fish (Schroeder et al., 1991). The settling rate of organic matter in intensive shrimp ponds

can exceed 800 g dry matter m^{-2} d^{-1} (Wyban and Sweeney, 1989). The resuspension of pond sediments has rendered accurate estimation of organic deposition difficult. Greater mineralization of the easily-decomposed fraction of settled organic matter (e.g., phytoplankton) may occur in the water column during resuspension than in the sediment (Overnell et al., 1995).

2.5.2. Regeneration (mineralization) and diffusion

Settled particulate organic matter develops into a dynamic, flocculent layer at the sediment–water interface (Visscher and Duerr, 1991; Hopkins et al., 1994). Schroeder (1987) demonstrated maximum heterotrophic activity in the flocculent sediment layer extending 2 cm above the firm sediment surface by measuring the rate of weight loss of cotton cloth. In shrimp ponds enriched by bagasse-based pellets, microbial biomass and density increased with the depth of the flocculent layer (Visscher and Duerr, 1991). Microbial density of all functional groups was maximum in the turbid layer above the sediment of an experimental fish tank when compared to densities in the water column and sediment (Ram et al., 1981).

The extent of decomposition of organic matter in the water column of shallow aquaculture ponds is minimal compared to that occurring at the sediment–water interface. Mineralization of organic matter and the consequent regeneration of nutrients at the sediment–water interface of aquaculture ponds is important as a source of ammonia to the water column and a sink for dissolved oxygen. A simulation model describing ammonia dynamics in commercial catfish ponds estimated that 25 to 33% of the ammonia supplied to the water column was derived from the sediment (Hargreaves, 1997).

The rate of decomposition of organic matter deposited at the sediment–water interface is likely very rapid. The quality of recently-deposited organic matter is high (low C:N ratio) and the half-life of organic N deposited to sediments is likely on the order of 1 to 2 weeks (Nixon and Pilson, 1983). In addition, sediment ammonia flux increased rapidly (within days) in response to a pulsed input of plankton-derived particulate organic matter and returned to background rates only after 1 to 2 months (Kelly and Nixon, 1984; Jensen et al., 1990). In San Francisco Bay sediments, the rate of sediment ammonia production is directly related to sediment C and N content (Caffrey, 1995). Thus, a substantial fraction of the organic N settling to the sediment is rapidly mineralized and returned to the water column as ammonia.

Dissolved organic nitrogen (DON) is produced by the autolysis of settled phytoplankton cells or the hydrolysis of other particulate organic N. DON is further mineralized by proteolytic, heterotrophic bacteria to dissolved inorganic substances (e.g., ammonia produced by deamination of DON). Jana and Roy (1985) measured seasonal variation in the abundance of mineralizing bacteria in fish pond sediment over three years. Abundance of protein mineralizing bacteria (10^4 to 10^5 cells g^{-1}) and ammonifying bacteria (10^5 to 10^6 cells g^{-1}) were maximum during winter (November to January) and minimum during March and September. Bacterial density was directly related to management intensity, although site-specific differences were also apparent.

Despite the relatively high efficiency of organic matter decomposition mediated by aerobic heterotrophic bacteria and the deposition and rapid mineralization of high

quality organic matter at the sediment surface, most decomposition in sediments takes place in the anaerobic layer where the quality of the accumulated organic matter is low (high C:N ratio), and therefore, relatively recalcitrant to decomposition (e.g., fulvic and humic acids). Foree et al. (1971) found that a large quantity of nitrogen in phytoplankton cells was not mineralized after one half to one year of aerobic (50%) or anaerobic (60%) decomposition. Anaerobic decomposition is characterized by (1) incomplete oxidation of organic matter, (2) reduced microbial cell yield per unit substrate, and (3) reduced assimilatory requirement for N by anaerobic microbes (Reddy and Patrick, 1984). Thus, in general, relatively more N is released from organic matter decomposition under anaerobic conditions.

Ammonia accumulates in the reduced sediment layer because the biochemical pathway of ammonia transformation requires oxygen. Concentrations of sediment pore-water or interstitial ammonia may be an order of magnitude greater than those of the water column. Schroeder (1987) measured porewater ammonia concentrations of 10 mg N l^{-1} at 1 to 4 cm sediment depth one month after filling a fish pond and 100 mg N l^{-1} in a manure pile in the same pond. Porewater ammonia concentration increased with pond age and water temperature (Masuda and Boyd, 1994). Porewater ammonia concentration of a 40-year old fish pond was over 20 mg N l^{-1}. Elevated porewater ammonia concentrations are mostly of concern with respect to the growth and survival of cultivated species with benthic feeding or burrowing habits, particularly crustaceans.

The profile of porewater ammonia in sediment is typified by a low concentration at the sediment–water interface that increases rapidly with depth. In response to a concentration gradient, ammonia diffuses from the reduced sediment layer to the oxidized surface where it is subject to oxidation to nitrate or further diffusion to overlying water. The depth of maximum porewater ammonia concentration is a function of organic matter concentration and the rate of diffusion to the sediment–water interface.

Ammonia flux from the sediment can be enhanced by the burrowing activities of macrofauna (bioturbation). Macrofauna can increase the effective surface area of sediment by 125% (Hylleberg and Henriksen, 1980). Benthic invertebrates increased the flux of ammonia from marine sediment by 50%, primarily by the irrigation of burrows that may extend from 8 to 12 cm into the sediment (Henriksen et al., 1980; Blackburn and Henriksen, 1983). The concept of bioturbation has been extended to benthivorous fish, although the functional effects of burrow irrigation by benthos and foraging behavior by benthivorous fish are different. Blackburn et al. (1988) attributed 30% of the solute flux from the sediment of a marine fish pond to disturbance by fish. In fish (tilapia and mrigal) exclosure experiments, Riise and Roos (1997) measured greater sediment oxygen uptake, ammonia flux, and denitrification associated with oligochaete burrowing activities inside exclosures. Grazing by benthivorous fish on benthic inverte-brates limits the loss of N through denitrification and promotes benthic–pelagic coupling and the internal recycling of N through sediment resuspension (Breukelaar et al., 1994; Cline et al., 1994; Riise and Roos, 1997).

To summarize, sediments are a source of ammonia to the water column of aquacul-ture ponds (Table 3). Most of this ammonia is derived from the regeneration of N from the mineralization of relatively high-quality, recently-settled organic matter at the sediment–water interface. A smaller and variable source of ammonia is derived from

Table 3
Estimates of ammonia flux (mg N m^{-2} d^{-1}) from freshwater, estuarine and marine sediments

Ammonia flux	Refs.	Comments
Freshwater		
0.3–3.1	Acosta-Nassar et al., 1994	new tropical fish pond
2.5–3.6	Reddy et al., 1990	Lake Okeechobee, FL
4.2	Schroeder, 1987	manured polyculture pond—diffusive flux + benthic regeneration
5–15	Fillos and Swanson, 1975	eutrophic lake and river ediments
< 10 (aerobic)	Rysgaard et al., 1994	freshwater lake sediment
75 (anaerobic)		
11.4	Avnimelech, 1984	intensive fish pond—mineralization kinetics model
23	Hesslien, 1977	ELA Lake 227, Canada
19.6–43.2,	Erickson and Auer, in press	freshwater reservoir sediment;
31.2 (mean)	anaerobic release rate; 8°C	
29–44	Freedman and Canale, 1977	White Lake, MI
65	Cerco, 1989	20°C
78	Wickman and Auer, in press	Onodaga Lake, NY
25 (winter)	Hargreaves, 1997	simulation model, catfish ponds
150 (summer)		
11–159	Smith and Fisher, 1986	Lake Calado, Brazil
85 (mean)		
36–168	Höhener and Gächter, 1994	Lake Sempach, Switzerland
42–140	Jellison et al., 1993	Mono Lake, CA
185	Riise and Roos, 1997	polyculture fish pond, Thailand
Estuarine		
0–252	Kemp and Boynton, 1984	Patuxent River estuary
10–231	Klump and Martens, 1981	Cape Lookout Bight, NC
-10–207	Reay et al., 1995	Chesapeake Bay
43 (annual mean)		
70	Callender and Hammond, 1982	Potomac River estuary
77	Vidal and Morguí, 1995	Alfacs Bay, Spain
175	Phoel et al., 1981	York River estuary, VA
119–271,	Smith and Fisher, 1986	Choptank River
197 (mean)		
29–882	Sumi and Koike, 1990	Japanese estuary
Marine		
8.8–11.7	Blackburn et al., 1988	marine fish pond
10.5 (mean)		
11 (mean)	Hargrave et al., 1993	Atlantic salmon cage culture site
22 (maximum)		
50–148	Blackburn and Henriksen, 1983	Danish marine sediments
0–144	Caffrey, 1995	North San Francisco Bay
6–172		South San Francisco Bay
182	Blackburn, 1979	Limfjorden, Denmark
370	Klump and Martens, 1989	Cape Lookout Bight, NC
70–672	Mackin and Swider, 1989	Flax Pond

mineralization of organic matter in the reduced sediment layer. Ammonia diffuses into the water column in response to a concentration gradient extending from the reduced sediment layer to the sediment–water interface, a process that may be enhanced by macrofauna or sediment resuspension.

2.5.3. Organic matter accumulation

Most of the nitrogen in aquaculture pond sediments is associated with organic matter, the accumulation rate of which is variable and largely dependent upon input quality. The settling of organic matter and the accumulation of that fraction of organic matter resistant to decomposition in the sediment was the primary mechanism of nitrogen removal in a model of a wastewater stabilization pond (Ferrara and Avci, 1982). Small increases in sediment organic matter (0.23% year^{-1}) and N (0.02% year^{-1}) were measured in ponds after eight years of channel catfish culture (Tucker, 1985). Similarly, Munsiri et al. (1996) measured only small differences in soil N concentrations in young (2 to 3.5 years) or old (8.4 to 11.5 years) shrimp ponds, and most N accumulated in the upper 2.5 cm of sediment. Using nutrient budget estimates of Schroeder (1987) and assuming accumulation in the 0 to 5 cm layer only, N accumulated in sediment by about 0.07% after a 4-month culture period. Organic N of a tropical fish pond sediment increased by about 0.06% after four months, accounting for 65% of input N (Acosta-Nassar et al., 1994). Small increases in total N of shrimp pond sediment were measured after six months, although spatial variability was more pronounced than temporal variability (Smith, 1996). Organic carbon in the upper 5-cm sediment layer of tropical fish ponds enriched by chicken manure increased by about 0.1% month^{-1} (Ayub et al., 1993). Similarly, 70% of input N accumulated in the sediments of tropical fish ponds enriched by chicken manure (Green and Boyd, 1995). Chiba (1986) recovered 8 to 13% of input N as sediment organic N in an intensive eel pond with continuous water circulation. Hopkins et al. (1994) recovered 15 to 22% of N input to semi-intensive shrimp ponds as bottom organic deposits (sludge) in which sediment was periodically suspended by aeration or allowed to settle in place. Approximately 31% of input N was calculated to accumulate in a tropical shrimp sediment after 2 to 3 production cycles (Briggs and Funge-Smith, 1994). Despite the addition of large quantities of organic matter to aquaculture ponds, average N concentration of soils from 358 freshwater and 346 brackishwater fish ponds were 0.28% and 0.30%, respectively (Boyd et al., 1994a).

2.6. Ammonium adsorption

Ammonium (NH_4^+) may weakly adsorb to negatively-charged cation exchange sites on the surface of clay minerals or organic matter in the sediment. Adsorbed (exchangeable) ammonium is important as a source of ammonia to the overlying water and as a sink for ammonia produced from DON mineralization. Acosta-Nassar et al. (1994) estimated that about 2% of the N added to a freshwater fish pond was stored in the adsorbed pool, although undoubtedly greater amounts of adsorbed ammonium were derived from the mineralization of soil autochthonous or previously-deposited sediment organic matter.

Adsorbed NH_4^+ and porewater ammonia are in equilibrium, so profiles of adsorbed NH_4^+ and porewater ammonia are similar. The ratio of adsorbed NH_4^+ to porewater ammonia (partition coefficient) is variable, but generally much greater than 1. Differences in the partition coefficient are related to the cation exchange capacity of soil, adsorbed and porewater ammonia concentrations, season (temperature) and sediment depth.

The concentration of adsorbed ammonium is affected by sediment drying and re-wetting. The exchangeable ammonium pool declined rapidly to very low levels after 6 weeks of drying a fish pond sediment (Diab and Shilo, 1986). Following refilling, the adsorbed ammonium pool increased within 10 days to levels equivalent to about 50% of that before draining and continued to increase during the cropping cycle (Shilo and Rimon, 1982; Diab and Shilo, 1986). Presumably, nitrification was responsible for reduction in exchangeable ammonium concentration, although evidence that adsorbed ammonium can be utilized by nitrifying bacteria is equivocal. The loose adsorption of exchangeable ammonium to sediment and the association of nitrifying bacteria with particles are evidence in support of the importance of this process (Seitzinger, 1990).

The dynamic nature of the adsorbed ammonium pool is further illustrated by measurement of the complete and rapid desorption of ammonium from a sandy sediment after two hours following suspension by wind-driven water turbulence (Simon, 1989). Similarly, Reddy et al. (1996) measured a release rate of ammonia of 67 to 85 mg N m^{-2} min^{-1} from resuspended sediment collected from Lake Apopka, Florida with most of the release occurring within 15 min. Ammonium supplied to the water column by desorption from sediment solids was estimated to exceed that supplied by diffusive flux. Suspension of aquaculture pond sediments by aeration or wind-driven water turbulence may increase, at least temporarily, the concentration of ammonia in the water column.

2.7. Nitrification

Nitrification is the sequential, two-step oxidation of ammonia to nitrate. The process is mediated by predominately two bacterial genera. The oxidation of ammonia is mediated by *Nitrosomonas* and the oxidation of nitrite is mediated by *Nitrobacter*. The organisms are chemoautotrophic, gram-negative, motile rods with long generation times (20 to 40 h). The reactions proceed as follows:

$$NH_4^+ + 1\,1/2\,O_2 \rightarrow NO_2^- + 2H^+ + H_2O$$

and

$$NO_2^- + 1/2\,O_2 \rightarrow NO_3^-$$
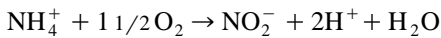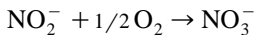
Thus, two moles of oxygen are required for each mole of NH_4^+ oxidized.

These organisms derive energy from the oxidation of NH_4^+ and NO_2^-. The free energy yield (ΔG) from the oxidation of NH_4^+ is about -65 kcal $mole^{-1}$, and that from the oxidation of NO_2^- is about -18 kcal $mole^{-1}$ (Focht and Verstraete, 1977). Thus, over three times as much NO_2^- must be oxidized to support an equivalent microbial growth to that derived from the oxidation of NH_4^+.

Nitrification rates of estuarine sediments range from 15 to 25 mg N m^{-2} d^{-1} (Henriksen and Kemp, 1988) and are probably representative of those of aquaculture pond sediments, although no direct measurements have been made (Table 4). Assuming 5 to 10% of sediment oxygen demand is utilized for nitrification (Henriksen and Kemp, 1988) then about 25 to 50 mg N m^{-2} d^{-1} is oxidized, equivalent to 5 to 10% of daily N input. Thus, the magnitude of nitrification is a relatively small in relation to the rate of other N transformations during the production cycle. Nitrification rates are elevated only during periods between cropping cycles when pond soils are aerated as they dry.

Nitrification is affected by dissolved oxygen concentration, temperature, substrate concentration, pH, numbers of nitrifying bacteria, and availability of surfaces. Many of these factors are interrelated and their effect on nitrification is complex.

Nitrifying bacteria require oxygen to derive energy from reduced N. The half-saturation concentration (K_m) for oxygen ranges from 0.3 to 0.9 mg l^{-1} and is directly related to temperature (Painter, 1970). The K_m for oxygen is higher for *Nitrobacter* than for *Nitrosomonas* at 30°C suggesting that nitrite oxidation is more sensitive to low oxygen

Table 4
Nitrification rate (mg N m^{-2} d^{-1}) estimates in the sediments of marine and freshwater systems

Nitrification rate	Refs.	Location/Comments
0	Blackburn et al., 1988	tropical marine fish pond
0.4–0.9 (mean = 0.5)	Acosta-Nassar et al., 1994	tropical freshwater fish pond
1–35	Riise and Roos, 1997	polyculture fish pond, Thailand
0–42	Henriksen, 1980	Danish coast
4–18	Henriksen et al., 1981	Danish coast
3–48	Billen, 1978	Belgian coast (North Sea)
11	Blackburn and Henriksen, 1983	Danish coast
11	Lindau et al., 1988b	rice soil
13	DeLaune and Lindau, 1989	Lac des Allemands, LA
15		Little Lake, LA
	Henriksen et al., 1980	Danish coast
16		without fauna
28–35		with fauna
7–37 (mean = 20)	Hansen et al., 1981	Danish coast
7–45 (mean = 20)	MacFarlane and Herbert, 1984	Scottish estuary
8–34 (mean = 22)	Nishio et al., 1983	Japanese coast
24	Boynton et al., 1980	Patuxent River estuary
26–30	Jenkins and Kemp, 1984	Patuxent River estuary
30	DeLaune and Smith, 1987	Lake Verret, LA
7–45 (mean = 39)	Seitzinger et al., 1984	Narragansett Bay
27–67 (mean = 45)	Koike and Hattori, 1978	Japanese coast
59–76	Jensen et al., 1994	freshwater lake sediment
	Chaterpaul et al., 1980	freshwater stream sediment
29		without fauna
69		with fauna
63	Vanderborght et al., 1977	Belgian coast (North Sea)
67	Rysgaard et al., 1994	freshwater lake sediment
60–152	DeLaune et al., 1991	Calcasieu River, LA

concentrations at warm temperature. With all other conditions sufficient, nitrification rate is constant at dissolved oxygen concentrations above 2 mg l^{-1}. The K_m for oxygen of nitrifying bacteria is several orders of magnitude greater than that of heterotrophic aerobic bacteria, suggesting that heterotrophic bacteria may be competitively more successful than nitrifying bacteria at low oxygen concentration.

Oxygen penetration into sediment is a key factor regulating nitrification (Reddy and Patrick, 1984; Rysgaard et al., 1994). The depth of oxygen penetration into aquatic sediments is typically on the order of 1 to 5 mm and is inversely related to temperature (Revsbech et al., 1980). Although nitrification increases with temperature, the volume of sediment involved in nitrification is restricted by the depth of oxygen penetration, which exerts control on overall nitrification rate. Nitrification potential was demonstrated in reduced sediment (6 to 8 cm depth) indicating the ability of nitrifying bacteria to survive in anaerobic environments, although actual nitrification was restricted to the sediment surface (Hansen et al., 1981; Henriksen et al., 1981). Nitrification activity of dormant, nitrifying bacteria in anoxic sediment layers will increase rapidly (within hours) in response to exposure to oxygen in overlying water (Jensen et al., 1993). Nitrification potential was minimum during the summer, coincident with minimum sediment oxygen penetration. The depth of oxygen penetration, and consequently nitrification rate, is also inversely related to the sedimentation of organic matter, which is maximum in warmer months.

The optimum temperature range for growth of pure cultures of nitrifying bacteria (25 to 35°C) is fairly narrow, although the scope for growth (3 to 45°C) is much wider (Focht and Verstraete, 1977). The Q_{10} of nitrification ranges from 1.7 to 3.3 between 20 and 30°C (Fenchel and Blackburn, 1979). Evidence of differential sensitivity of the two principal nitrifying genera to temperature is equivocal, but tends to implicate the greater sensitivity of nitrite oxidizers to low temperature, particularly at pH values outside the optimum range (Focht and Verstraete, 1977). However, climatic and other environmental variables exert strong selection pressures on populations of nitrifying bacteria, suggesting that adaptation to local conditions is also likely. Thus, information derived from laboratory studies of pure cultures should be viewed with qualification.

Nitrification rate is also affected by substrate concentration. In aquaculture pond sediments, ammonia is supplied (1) by the mineralization of organic N at the sediment–water interface, (2) diffusion of ammonia from the reduced sediment layer to the sediment–water interface, and (3) the bulk water. Half-saturation concentrations (K_m) for substrate increase with temperature (20 to 32°C) and range from 1 to 10 mg N l^{-1} for ammonia oxidation, and from 5 to 9 mg N l^{-1} for nitrite oxidation (Painter, 1970). Ammonia concentrations in commercial catfish ponds are usually < 3 mg N l^{-1} (Tucker and van der Ploeg, 1993), and the highest concentrations occur during the winter when phytoplankton biomass is minimal. Nitrite concentrations in channel catfish ponds are usually < 0.2 mg N l^{-1} with seasonal maxima in the spring and fall. Such low concentrations in the bulk water impose substrate limitation on nitrification in aquaculture ponds, suggesting that the kinetics of nitrification are first-order with respect to substrate concentration. However, nutrient regeneration at the sediment–water interface and ammonia diffusion from reduced sediment may be sufficient to surmount substrate limitation.

Nitrifying bacteria require slightly alkaline pH (7 to 8.5) for optimal growth. At pH > 8.5, *Nitrobacter* may be inhibited more than *Nitrosomonas*, resulting in an accumulation of nitrite (Fenchel and Blackburn, 1979). Increased nitrification at alkaline pH suggests that NH_3 may be the substrate for nitrification. Also, unionized ammonia can inhibit nitrite oxidation at 0.1 to 1.0 mg NH_3–N l^{-1} (Belser, 1979). However, these concentrations are rarely observed in fish ponds as they are also toxic to fish. Finally, pH is important because two hydrogen ions are released for each mole of ammonia oxidized. Natural waters usually contain sufficient alkalinity to buffer an increase in hydrogen ion concentration from nitrification.

Nitrifiers are lithotrophic, requiring organic or mineral surfaces for attachment. Nitrifier density in the soil at the sediment surface (10^6 to 10^9 cm^{-3}) is about three orders of magnitude greater than that in the water column (10^3 to 10^4 ml^{-1}). The abundance of ammonia oxidizers (10^4 to 10^5 cells g^{-1}) in sediment is greater than that of nitrite oxidizers (10^3 cells g^{-1}) (Ram et al., 1981; Ram et al., 1982). The sediment surface is the locus for mineralization of particulate organic matter settling from the water column. In addition, ammonium may be concentrated on sediment mineral particles (clays) as part of the cation exchange complex. Competition for surfaces between heterotrophic and nitrifying bacteria may contribute to limitation of population density of the latter group.

Nitrification at the sediment–water interface is more important than nitrification in the water column in stratified or periodically-mixed fish ponds. Nitrification in the water column is restricted by the availability of surfaces and possibly by light inhibition. Nitrification may increase temporarily following phytoplankton die-offs in response to elevated ammonia concentration. Water column nitrification is an important mechanism of ammonia transformation in high-intensity pond systems in which particles suspended by mechanical aeration are sites of active mineralization and nitrification.

In flooded soils, nitrification and denitrification are closely coupled. A two-layer model has been developed to describe the interdependence of these two processes (Reddy and Patrick, 1984). By the two-layer model, ammonia diffuses from the reduced sediment layer along a concentration gradient to the surface, where it is oxidized by nitrifying bacteria. Nitrate diffuses in response to a concentration gradient to the reduced sediment layer where it is denitrified to dinitrogen gas that evolves to the atmosphere through gas ebullition. Thus, although oxygen inhibits denitrification, the reaction indirectly requires oxygen for the production of nitrate.

A complementary theory has been developed to explain the seemingly contradictory coexistence of oxic and anoxic processes within an oxic environment. Jørgensen (1977) found that detrital particles of 100 μm to several mm may have anoxic centers. Paerl (1984) estimated that detrital aggregates, biofilms, microbial mats and planktonic symbioses ranging from 100 μm to several mm in thickness can have reduced microzones (Paerl, 1984; Paerl and Pinckney, 1996). Jenkins and Kemp (1984) argued that calculation of the effective nitrate diffusion distance (≈ 80 μm) suggests that denitrification must be tightly coupled with nitrification and occur in reduced microzones within the oxidized layer of the sediment surface. The quantity of reduced microsites depends on (1) oxygen consumption rate, (2) oxygen diffusion rate, and (3) particle geometry (Focht and Verstraete, 1977).

The pattern of nitrification following the establishment of conditions favorable for process development is characterized by the rapid oxidation of ammonia, an accumulation of nitrite coincident with a decline in ammonia, and after a lag period, a decline in NO_2^-. This characteristic pattern explains, in part, the bimodal distribution of annual nitrite concentration maxima measured in warm temperate commercial catfish ponds (Tucker and van der Ploeg, 1993). Interpretation of factor analysis of the data of Tucker and van der Ploeg (1993) suggested that sediment oxygenation was an important regulator of nitrification in these ponds (Hargreaves and Tucker, 1996).

During the summer, nitrification in aquaculture pond sediments is most likely limited by the depth of oxygen penetration (typically 1 to 5 mm). In estuarine sediments, the summer depression of nitrification rate has been attributed to limited oxygen diffusion into sediments (Hansen et al., 1981; Jenkins and Kemp, 1984). During the summer, the rate of input of organic matter to aquaculture pond sediment is maximum due to maximum feeding rates and standing crops of phytoplankton, and are coincident with maximum seasonal temperatures. The decomposition of recently deposited organic matter by large and active populations of aerobic, heterotrophic bacteria limit the diffusion of oxygen into sediment. Although operation of aerators may prevent near-sediment dissolved oxygen from declining to concentrations < 2 mg l^{-1}, it is likely that a laminar benthic boundary layer (≈ 100 μm) depleted of dissolved oxygen develops at the sediment–water interface in the summer. Stirring of sediments during pond aeration may increase the depth of oxygen diffusion (Revsbech et al., 1980). In the water column, nitrification is low because ammonia is present at substrate-limiting concentrations due to rapid uptake by large and actively-growing phytoplankton populations.

As temperature declines during the fall, dissolved oxygen concentration of the water column increases due to reduced feeding rate and pond respiration and increased oxygen solubility. Sediment oxygen demand declines as metabolic activity of bacteria is depressed by cooler temperatures and reduced inputs of organic matter from the water column. Consequently, the depth of oxygen penetration into the sediment surface increases, thereby increasing the volume of sediment that is involved in nitrification. In the water column, nitrification is stimulated by increases in ammonia resulting from reduced uptake by phytoplankton.

Nitrification rate is reduced during the winter due to seasonally minimal temperatures. In the spring, as temperature increases, organic N accumulated is rapidly mineralized to ammonia and the rate of nitrification is once again stimulated, producing another sharp increase in water column nitrite concentration. As temperature increases further, water column dissolved oxygen declines, sediment oxygen penetration and nitrification are reduced.

In summary, the interaction between temperature and the depth of sediment oxygen penetration exerts control over nitrification in fish pond sediments. The interaction between temperature and substrate concentration exerts control over nitrification in the water column. During summer in catfish ponds sediment nitrification is controlled (limited) by oxygen penetration into the sediment and low substrate concentrations in the water column, despite seasonally maximum temperatures. During the fall, control of nitrification shifts from oxygen penetration (sediment) or substrate concentration (water column) to temperature. During the winter, low temperature limits nitrification. During

the spring, control of nitrification shifts from temperature to sediment oxygen penetration.

2.8. Nitrate reduction

Nitrate may follow several biochemical pathways following production by nitrification. Plants and microbes may reduce nitrate to ammonia for incorporation into cellular amino acids (assimilatory nitrate reduction). Nitrate may function as a terminal electron acceptor during the oxidation of organic matter and thereby supply energy for microbial growth. Nitrate respiration results in the reduction of nitrate to dinitrogen (denitrification) or ammonia (dissimilatory nitrate reduction to ammonia).

$$NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$$
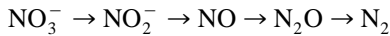
Oxygen is the energetically preferred terminal electron acceptor for the oxidation of organic matter. However, when oxygen concentration becomes limiting (~ 0.1 to 0.2 mg l^{-1} or $E_h < 220$ mV), heterotrophic facultative anaerobes shift to nitrate as the terminal electron acceptor. The energetic yield from the oxidation of organic carbon (e.g., glucose) by nitrate ($\Delta G = -649$ kcal mole^{-1}) is only slightly less than that by oxygen ($\Delta G = -686$ kcal mole^{-1}).

Unlike the limited species diversity of bacteria mediating nitrification, at least 14 genera of bacteria can reduce nitrate, and *Pseudomonas*, *Bacillus* and *Alcaligines* are the most prominent numerically (Focht and Verstraete, 1977). Also, the growth, activity and population density of denitrifying bacteria exceed that of nitrifying bacteria. Most denitrifying bacteria are considered facultative anaerobes. Although denitrification is inhibited by oxygen, the reaction occurs primarily near the sediment surface, possibly in reduced (suboxic) microzones in the oxidized sediment surface layer.

The rate of denitrification depends on temperature, concentrations of nitrate, organic carbon, and oxygen, and the population density of denitrifying bacteria (Table 5). Denitrification rates increase with substrate concentration. Denitrification rates in estuaries correspond with seasonal (spring) peaks in nitrate loading (Andersen et al., 1984). However, denitrification rates in most natural aquatic systems are first order with respect to nitrate concentration, and can be considered substrate limited. In aquaculture ponds, nitrate is typically < 0.5 mg N l^{-1} (Ziemann et al., 1992; Tucker and van der Ploeg, 1993), a concentration likely below reported half-saturation constants (K_m) for denitrification. Nitrate concentrations in temperate aquaculture ponds are maximum during winter, when phytoplankton blooms are minimal.

Kinetic constants vary with available carbon (reductant). Reported K_m values range from 0.1 to 170 mg N l^{-1}, and increase in direct relation to carbon (Focht and Verstraete, 1977). In a multiple (stepwise) regression model, dissolved organic carbon concentration was the most important predictor of denitrifying bacteria abundance in tropical fish ponds (Jana and Patel, 1985). The large quantity and low C:N ratio of settled organic matter in aquaculture ponds suggests that carbon limitation of denitrification is not likely.

Aquatic sediments consist of a very thin oxidized layer overlying a much thicker anoxic layer. Therefore, the potential for denitrification in fish ponds is very high.

Table 5
Denitrification rate (mg N m^{-2} d^{-1}) estimates in the sediments of marine and freshwater systems

Denitrification rate	Refs.	Location/Comments
1.4–3.6	Messer and Brezonik, 1983	Lake Okeechobee acetylene blockage
3.6–7.1		mass balance
0.1–7.4	Acosta-Nassar et al., 1994	tropical freshwater fish pond
2.3	Oren and Blackburn, 1979	Kysing Fjord, Denmark (~ 0.15 mg l^{-1} NO$_3^-$–N)
2.7–10.9	Kaspar, 1982	intertidal mud flat
3.6–7.2	Chan and Knowles, 1979	eutrophic ponds
5	Tirén, 1977	oligotrophic Swedish lake
3.4–13	Nishio et al., 1983	Japanese coast
3.6–18	Sweerts and de Beer, 1989	eutrophic lake (Vechten)
3.8	Smith and DeLaune, 1983	freshwater/estuarine eutrophic lake sediments
0–29	Billen, 1978	Belgian coast
4–55	Cerco, 1989	Potomac River (10–30°C, 8 mg l^{-1} DO, 0.21–0.63 mg l^{-1} NO$_3^-$–N)
4–71	Andersen et al., 1984	Danish estuary; seasonal variation
10–40	Henriksen et al., 1980	Danish coast
14	Sørensen, 1978	Danish coast
14–20	Chan and Campbell, 1980	eutrophic Canadian lake
18–35	Nielsen, 1992	eutrophic stream bed
17–34	Seitzinger et al., 1984	Narragansett Bay
< 25	Rysgaard et al., 1994	freshwater sediment
25–40	Tirén, 1977	3 eutrophic Swedish lakes
26–30	Jenkins and Kemp, 1984	Patuxent River estuary (spring)
29	Vanderborght et al., 1977	Belgian coast
1.5–57	Lindau et al., 1990	urea-treated rice plot
47–81	Roos and Eriksen, 1995	semi-intensive polyculture pond
	Blackburn et al., 1988	marine fish ponds
14–25		acetylene blockage
71–119		nitrite + nitrate reduction
56–69	Krom, unpublished (cited in Blackburn et al., 1988)	marine fish ponds
52	D'Angelo and D'Angelo, 1993	Lake Okeechobee
57	Riise and Roos, 1997	polyculture fish ponds, Thailand
58	Andersen, 1977	Byrup Langsø (lab cores)
110		Byrup Langsø (mass balance)
34		Kvind Sø (lab cores)
85		Kvind Sø (mass balance)
100–500		enriched lake sediment
45	DeLaune and Smith, 1987	Lake Verret, LA—nitrate reduction
34–52	DeLaune et al., 1991	Calcasieu River, LA
95–160	van Kessel, 1977	enriched ditch sediment
100–200	Nishio et al., 1982	polluted estuary, Japan
101–296	Seitzinger and Nixon, 1985	enriched marine mesocosm
367	Lindau et al., 1988a	enriched bottomland hard-wood forest swamp plot
33–342	Lindau et al., 1990	KNO$_3$-treated rice plots
420–490	Binnerup et al., 1992	enriched, bioturbated marine sediment

Although denitrification is an anaerobic process, it is largely dependent on oxygen concentration for the production of nitrate through nitrification. Factors that stimulate nitrification (e.g., warm temperature, abundant oxygen) will also stimulate denitrification. In aquatic sediments in which the nitrate concentration in the overlying water is low, the denitrification rate will be limited by the nitrification rate, which in turn is regulated by the depth of sediment oxygen penetration (Rysgaard et al., 1994; Jensen et al., 1994). The presence of an oxidized sediment layer also increases the diffusion distance of nitrate from the overlying water to anoxic sediment thereby reducing the rate of denitrification of nitrate derived from the overlying water.

A wide range of Q_{10} values have been reported, possibly reflecting the broad generic diversity of denitrifying bacteria. Most Q_{10} values range from 1.4 to 3.4 between 15 and 35°C (Focht and Verstraete, 1977). Denitrifier activity is sharply curtailed below 15°C. Q_{10} values are affected by the concentration of oxidant (nitrate) and reductant (organic carbon) as well as oxygen concentration. At 34°C denitrification rate was much less affected by oxygen concentration than at 19°C (Focht and Verstraete, 1977). The abundance of denitriyifying bacteria in tropical fish pond sediment was maximum during summer (10^4 cells g^{-1}) and minimum during winter (10^3 cells g^{-1}) (Jana and Patel, 1985). Comparable abundance and seasonal patterns were observed in the water column. In Israeli fish pond sediment, the abundance of denitrifying bacteria increased with intensity of management and ranged from 10^4 to 10^6 cells g^{-1} (Ram et al., 1982).

3. Management practices affecting nitrogen biogeochemistry

3.1. Feeds and feeding practices

Feeds and feeding practices have a dramatic impact on ammonia concentration in fish pond water. Ammonia was strongly correlated with daily feeding rate in channel catfish ponds over the range 0 to 224 kg ha^{-1} d^{-1} (Tucker et al., 1979; Cole and Boyd, 1986). Ammonia increased in response to dietary protein concentration and total protein fed over the range 24% to 40% (Li and Lovell, 1992). However, un-ionized ammonia (NH_3) concentration was not affected by dietary protein concentration. Temporary withdrawal of feed (9 days) did not reduce ammonia in channel catfish ponds (Tidwell et al., 1994). Ammonia concentration was not different in channel catfish ponds in which fish were fed once daily to satiation at 0830 h, 1600 h, 2000 h, or with demand feeders (Robinson et al., 1995).

3.2. Water exchange

Various water management practices have been evaluated to reduce ammonia concentration in fish ponds. Water exchange rates of 0, 1, 2 or 4 pond volumes over three months (July to September) were insufficient to affect water quality in channel catfish ponds (McGee and Boyd, 1983). A simulation model of semi-intensive shrimp ponds predicted that ammonia concentrations would be minimum with no water exchange,

increase to a maximum at water exchange rates of 0.2 to 0.4 d^{-1}, and decrease at water exchange rates exceeding 0.4 d^{-1} (Lorenzen et al., 1997). A water exchange rate of 0.025 d^{-1} was sufficient to reduce ($P < 0.05$) ammonia concentration in intensive (44 m^{-2}) shrimp ponds compared to ponds with no water exchange (Hopkins et al., 1993). Ammonia concentration in ponds with a water exchange rate of 0.25 d^{-1} was not different from that of inlet water.

In high-biomass (> 10 kg m^{-2}), intensive fish ponds (500 m^3), a hydraulic retention time > 24 h in rearing units was necessary for nitrification to proceed to completion (Diab et al., 1992). Greater water exchange rates led to washout of nitrifying bacteria.

3.3. Water circulation and aeration

Semi-intensive pond systems for the culture of channel catfish and penaeid shrimp employ paddlewheel aeration to maintain dissolved oxygen concentration. The effects of aeration and circulation on DIN concentrations are a complex function of feeding rate, sediment suspension, duration of aeration and phytoplankton density. Ammonia concentration was only slightly lower ($P > 0.05$) and nitrite concentration slightly higher ($P > 0.05$) in channel catfish ponds (50 kg feed ha^{-1} d^{-1}) aerated for 6 h during the night as compared to ponds aerated on an emergency basis only (Lai-Fa and Boyd, 1988). Ammonia concentration increased slightly and nitrite concentration increased substantially in channel catfish ponds (up to 90 kg feed ha^{-1} d^{-1}) aerated nightly compared to those of unaerated control ponds (Hollerman and Boyd, 1980). Similarly, concentrations of ammonia, nitrite and nitrate were directly related to duration of aeration (emergency, nightly, continuous) in channel catfish ponds (Thomforde and Boyd, 1991). The suspension of sediment particles by aeration may have promoted rapid desorption of exchangeable ammonium and stimulated nitrification in the water column. Continuous paddlewheel aeration reduced ammonia concentrations slightly in brackish-water shrimp ponds, but concentrations were not different from unaerated ponds (Sanares et al., 1986). Un-ionized ammonia concentrations were not affected by continuous paddlewheel aeration in freshwater ponds stocked with tilapia at 3000 kg ha^{-1} (Ver and Chiu, 1986).

In Taiwan, Israel and Hawaii, intensive pond systems have been developed in which water is circulated continuously by paddlewheel aeration, and water and settled organic matter are periodically or continuously removed from a center drain (Avnimelech et al., 1986; Wyban and Sweeney, 1989; Fast and Boyd, 1992). Phytoplankton uptake is insufficient to assimilate the large quantity of ammonia generated as a consequence of high feeding rate and stocking density. In such high-intensity ponds, nitrification in the water column is the most important mechanism of ammonia transformation. Despite nitrate accumulation in the water of such circulated systems, the sediment was assumed to be the site of substantial denitrification. Total N may exceed 30 mg N l^{-1} (mostly present as nitrate) (Avnimelech et al., 1986). Treatment of effluent discharged from intensive circulated water systems must address solid (phytoplankton) and dissolved (nutrient) components (Lorenzen et al., 1997).

High-intensity pond systems have been integrated with larger, extensive reservoirs. Hydraulic detention time in the intensive component is sufficient to allow water-column

nitrification to proceed to completion. Effluent is directed to the reservoir, where solids are deposited and denitrification takes place before recirculation to the high-intensity ponds.

3.4. Pond depth

In shrimp ponds, ammonia concentration was not significantly affected by pond depth, although nitrite and nitrate were inversely related to pond depth (Carpenter et al., 1986). Presumably, reducing water depth in a pond with a high phytoplankton density will reduce light limitation of phytoplankton growth and thereby enhance nutrient uptake (Piedrahita, 1991).

3.5. Organic carbon addition

Avnimelech et al. (1989) demonstrated a practical technique to recycle excess N into fish. Dissolved inorganic nitrogen limitation can be established in intensive, circulated fish ponds by adding a carbon-rich substrate (e.g., cellulose, sorghum meal) that promotes the formation of microbial biomass. The resulting heterotrophic production (single-cell protein) may be utilized as a food source by carp and tilapia (Schroeder, 1978; Beveridge et al., 1989; Rahmatullah and Beveridge, 1993).

3.6. Microbial augmentation

Microbial augmentation refers to the supplementation of pond waters or soils with concentrated bacterial suspensions with the goal of reducing soil organic matter, improving dissolved oxygen concentration and removal of ammonia. In studies conducted in shrimp and channel catfish ponds, differences in shrimp or fish production and ammonia, nitrite and nitrate concentrations in ponds supplemented with bacteria was not significantly different from that of untreated control ponds (Boyd et al., 1984; Tucker and Lloyd, 1985b; Chiayvareesajja and Boyd, 1993; Queiroz and Boyd, 1998).

3.7. Ion exchange

Ion exchange is a well-known and effective means of removing ammonium from water in recirculating fish culture systems (Spotte, 1979). Naturally-occurring ion exchange materials, such as the zeolite clinoptilolite, have been added to shrimp ponds at 200 kg ha^{-1} month^{-1} (Chien, 1992) to 380 kg ha^{-1} month^{-1} (Briggs and Funge-Smith, 1996). The efficacy of ion exchange is affected by the ionic strength of water, by occlusion of exchange sites by dissolved organic carbon, and by the particle size of the exchange resin (Spotte, 1979). In general, the removal of ammonium from water is reduced as salinity increases. Briggs and Funge-Smith (1996) demonstrated no removal of ammonium at salinities ranging from 0 to 30 ppt and concluded that the application of ion exchange materials to shrimp ponds was not effective.

3.8. Sediment management

Most sediment management techniques are undertaken while the pond is drained between cropping cycles. Drying is probably the most important, practical, and cost-effective sediment management technique. Drying promotes oxidation of accumulated organic matter (Ayub et al., 1993) and nitrification of mineralized N (Diab and Shilo, 1986), although the optimum soil moisture content for organic matter decomposition is about 20% (Boyd, 1992). Shrimp pond soils in Ecuador are dried for an average of 10 days after harvest (Peterson and Daniels, 1992). Pond soils may be tilled to hasten the decomposition process, although five weeks of drying are required before heavy equipment can enter the pond. Organic matter may be physically removed from intensive shrimp ponds manually, by suction dredges or earthmoving equipment, or flushed out by hydraulic jets (Clifford, 1992), although these practices have potentially negative environmental impacts associated with the discharge of organically-enriched effluent, and further, the efficacy of these practices is questionable. The effect of two sediment management practices on soil chemical properties from two shrimp farms was evaluated in Australia (Smith, 1996). One one farm sediments were removed following the cropping cycle and on the other sediments were redistributed following drying. No difference in total N was detected in soils from the two farms. Given the similar chemical composition of new shrimp pond soils to piles of excavated sediment, particularly with respect to organic matter concentration, the practice of sediment removal from shrimp ponds appears unjustified (Boyd et al., 1994b).

Ponds may be limed after draining and drying to raise soil pH to levels promoting decomposition, particularly in brackishwater ponds constructed on acid-sulfate soil and in areas with low alkalinity water supplies. Ponds are typically limed at 1000 to 3000 kg ha^{-1} depending on soil pH (Boyd, 1992). Fertilization of brackishwater shrimp pond soils by 50 to 200 kg urea ha^{-1} reduced sediment organic matter (Peterson and Daniels, 1992) although urea application did not reduce organic carbon in manured freshwater fish ponds (Ayub et al., 1993).

Sediment management techniques during the cropping cycle while the pond is full have not been fully evaluated. Brackishwater shrimp ponds may be dredged during the cropping cycle to remove accumulated organic matter or a chain may be dragged across the pond bottom periodically (Costa-Pierce and Pullin, 1989; Fast and Boyd, 1992; Beveridge et al., 1994).

3.9. Sediment management implications

Management approaches toward sediments can be divided into two types based upon the desired goal. In ponds receiving nutrients supplied in excess of assimilatory capacity, or where autotrophic food webs are not important for increased fish yields, but are only important for water quality management, the promotion of conditions that maximize the potential of the pond to remove excess N is desirable. Dentrification is the process with the greatest potential to remove N although the preliminary transformation of reduced (ammonia) to oxidized (nitrate) N is required. Management techniques that improve oxic

conditions at the sediment–water interface will promote rapid mineralization and coupled nitrification–denitrification. Likewise, techniques that promote water-column nitrification will increase substrate in the bulk water to concentrations that will stimulate sediment denitrification.

For ponds in which fish yields are based on primary productivity, promotion of nutrient recycling within the pond will maximize nutrient availability for phytoplankton. Anaerobic sediment conditions will allow the diffusion of ammonia mineralized under reduced conditions or regenerated at the sediment–water interface to diffuse into the water column where it will be available for phytoplankton. However, this goal is incompatible with the management requirement of maintaining adequate dissolved oxygen for fish production.

4. Research needs

Much of the research on nitrogen cycling in shallow aquatic ecosystems has been conducted in estuarine or lacustrine environments. Much of this information is directly applicable and relevant to describing rates and controlling factors of various N transformation processes in aquaculture ponds. However few controlled studies of N cycling, specifically directed toward the unique circumstances prevalent in earthen aquaculture ponds, have been carried out and there are several important gaps in information that remain to be filled. The design and conduct of experiments should be formulated with a view toward the development of practical management procedures that enhance fish growth and production.

Of primary concern is a more complete understanding of factors regulating the concentrations of the two nitrogenous compounds with potential toxicity to cultured organisms—ammonia and nitrite. Concentration reductions can be achieved by a decrease in the production rate or an increase in the removal rates of each of these compounds. Although phytoplankton management is an elusive goal of aquaculturists and currently beyond the scope of management control in pond culture, research efforts directed toward regulation of phytoplankton biomass, activity and community composition has profound implications for the maintenance of water quality conditions favorable for fish production. Generally, conditions that promote rapid rates of primary production tend to result in low ammonia concentration. In addition, the interacting roles of the factors that regulate nitrification (temperature, oxygen and substrate concentration) in the water and the sediment of aquaculture ponds require elucidation.

Of secondary interest, processes related to the interaction between the sediment and the water column of aquaculture ponds are poorly understood. The role of the sediment as a source of ammonia to the overlying water and practical management techniques to limit the rate of sediment diffusion are necessary. At this time, the effect of depositional events, such as the sudden, rapid collapse of an algal population, on sediment and water chemistry can only be inferred from studies in the marine environment. Similarly, the role and importance of sediment resuspension and bioturbation in shallow lakes and estuarine environments is fairly well understood and appreciated; yet, comparable

information and appreciation is lacking in the aquaculture pond context. As stated previously, practical sediment management will depend on the goals of the culturist: the incorporation of benthivorous fish would favor internal N recycling under conditions of relative N scarcity, while enhancement of bioturbation by the benthos would favor removal processes under conditions of N excess relative to assimilative capacity. The development of imaginative experimental approaches are required to evaluate practical techniques to achieve these goals.

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