JOURNAL OF THE
WORLD AQUACULTURE SOCIETY

Vol. 30, No. 1
March, 1999

The Potential Use of Mangrove Forests as Nitrogen Sinks of Shrimp Aquaculture Pond Effluents: The Role of Denitrification

VICTOR H. RIVERA-MONROY

Department of Biology, University of Southwestern Louisiana, POB 42451, Lafayette, Louisiana 70504 USA

LUIS A. TORRES AND NIXON BAHAMON

Instituto de Investigaciones Marinas y Costeras (INVEMAR), A.A. 1016. Santa Marta, Colombia

FEDERICO NEWMARK

Corporacion Centro de Investigacion de la Acuicultura de Colombia (CENIACUA), Calle del Curato No. 38-49, San Diego, Cartagena, Colombia

ROBERT R. TWILLEY

Department of Biology, University of Southwestern Louisiana, POB 42451, Lafayette, Louisiana 70504 USA

Abstract

A generalized nitrogen budget was constructed to evaluate the potential role of mangrove sediments as a sink for dissolved inorganic nitrogen (DIN) in shrimp pond effluents. DIN concentrations were measured in pond effluents from three semi-intensive shrimp ponds along the Caribbean coast of Colombia between 1994–1995. Mean NH_4^+ concentrations in the discharge water for all farms were significantly higher (67 ± 12 μg/L) than in the adjacent estuaries (33 ± 8 μg/L). Average NH_4^+ concentrations in the pond discharge over all growout cycles were similar, representing an approximate doubling in relation to estuarine water concentrations. In contrast, NO_2^- + NO_3^- concentrations were similar in both pond effluent and estuarine waters. Dissolved inorganic nitrogen loading of the ponds was similar. The estimated reduction of DIN in pond effluents by preliminary diversion of outflow to mangrove wetlands rather than directly to estuarine waters would be ≥ 190 mg N/m² per d. Based on this nitrogen loss and depending upon the enrichment rate, between 0.04 to 0.12 ha of mangrove forest is required to completely remove the DIN load from effluents produced by a 1-ha pond.

The exchange of coastal waters in shrimp aquaculture ponds is important to assure optimal survival and high yields of shrimp. Although recent studies show that water exchange is not necessary to maintain yields (Hopkins et al. 1993, 1995a, 1995b; Martinez-Cordova et al. 1995, 1996), water exchange is still a common management practice in semi-intensive shrimp pond operations. There are possible deleterious effects of effluent from shrimp ponds on the water quality of the coastal zone (Ziemann et al. 1992; Twilley et al. 1993; Dierberg and Kiattisimkul 1996; Bardach 1997). Water is usually discharged into estuaries at rates dependent on the amount of water pumped into the ponds (usually expressed as a percentage of pond volume). The cumulative impact of pond effluent on the environmental quality of estuaries is proportional to the discharge volume and nutrient concentration (Twilley 1989; Csavas 1994). A reduction in environmental quality of the estuary can have a negative feedback effect on shrimp pond operations (Smith 1996). "Self-pollution" is defined as the pumping of water into aquaculture ponds, previously discharged to the estuary, which contains increased concentrations of nutrients and contaminants, and lower concentrations of dissolved oxygen (Csavas 1994; Jory 1995a). This recycling can have negative effects on overall shrimp yield by promoting infectious diseases, noxious algae blooms, introducing toxic substances and increasing sediment loads (Ziemann et al. 1992). Self-pollution is the result of a combination of factors such as poor engineering design of aquaculture ponds, poor management practices (e.g., excess feed application and fertilization), and the effect of high water residence times of adjacent estuaries where pond effluents are discharged. After the complete or partial collapse of poorly regulated shrimp industries in Taiwan (Liao 1992), Thailand (Stanley 1993; Briggs and Funge-Smith 1994), China (Wang et al. 1995), and Ecuador (Olsen 1995), the shrimp industry has been made more aware of the necessity of sustainable and rational industry development through the maintainance of higher standards of environmental quality (Ziemann et al. 1992; Csavas 1994; Briggs and Funge-Smith 1994; Thia-Eng 1997).

Several methods have been proposed to ameliorate the impact of shrimp pond effluents on the water quality of adjacent estuaries including, improved pond designs (Dierberg and Kiattisimkul 1996; Sandifer and Hopkins 1996), construction of wastewater oxidation-sedimentation ponds, reduction of water exchange rates (Hopkins et al. 1993; Martinez-Cordova et al. 1995), reduction of nitrogen and phosphorous input from feed (Jory 1995b), removal of pond sludge (Boyd et al. 1994; Sandifer and Hopkins 1996) and a combination of semiclosed farming systems with settling ponds and biological treatment ponds using polycultures (Sandifer and Hopkins 1996; Dierberg and Kiattisimkul 1996). Another proposed method is to use mangrove wetlands as filters of pond discharge prior to the release of effluents to estuarine waters (Twilley et al. 1993; Robertson and Phillips 1995). The use of wetlands for processing water pollution from wastewater has been effective in reducing organic matter, suspended sediments, and nutrients in semitropical and temperate regions (Kadlec and Knight 1996). The use of mangrove wetlands in tropical regions to treat effluents from shrimp farming is not generally practiced as treatment has not been required of shrimp producers. Moreover, many shrimp aquaculture ponds have been constructed in or adjacent to mangrove wetlands causing the functional loss of these wetlands in the coastal zone (Twilley et al. 1993; Csavas 1994; Robertson and Phillips 1995).

Mangrove forests function as sinks of inorganic nitrogen (N) (Corredor and Morell 1994; Rivera-Monroy et al. 1995a; Alongi 1996; Rivera-Monroy and Twilley 1996) and phosphorus (P) (Alongi 1996). Forested wetlands also contribute dissolved and particulate organic carbon and nitrogen to coastal waters (Twilley 1985, 1988; Rivera-Monroy et al. 1995a). The net transport of nitrogen in mangroves depends on the exchange rate of inorganic and organic nutrients with coastal waters. As mangrove forests can be N or P limited (Feller 1995; Twilley 1995), high inorganic N demand by decomposing leaf litter and plant uptake may regulate efficient N recycling on the forest floor that could serve as mechanisms for nutrient retention (Twilley 1988; Alongi and Sasekumar 1992).

Estimates of N loading from shrimp ponds into coastal waters are limited (Ziemann et al. 1992), making it difficult to assess the potential use of mangrove wetlands to ameliorate nutrient inputs from pond effluents. Results from studies evaluating the effect of secondary sewage effluent on mangrove wetlands indicate that these wetlands have a large nutrient assimilative and dissimilative capacity. Mangrove wetlands effectively treated low concentrations of organic and inorganic N in wastewater discharged over one year without any apparent negative impact on plant growth (Wong et al. 1995). Also, Corredor and Morell (1994) showed that sediments in a fringe mangrove forest were capable of removing, via denitrification, 10 to 15 times the NO_3^- added in the effluent from a sewage treatment plant. Therefore, denitrification in mangrove soils can potentially improve the environmental quality of shrimp pond effluents.

Integrated pond-mangrove farming systems can ameliorate the impacts of pond effluent on the water quality of coastal waters. Ranges of wetland : shrimp pond ratios vary from 2 to 22 depending on the capacity for nitrogen removal by mangrove sediments relative to the anticipated loading rate (Robertson and Phillips 1995). While Robertson and Phillips (1995) pointed out that the loss of porewater NH_4^+ and NO_3^- from mangrove sediments depends on, among other factors, the degree of sediment denitrification, the proposed ratio was based on the conservative assumption that plant uptake was the only sink of excess DIN in mangrove sediments. Other processes such as sedimentation, denitrification, and sediment-water exchange were not included, and therefore underestimated the potential loss of N from pond effluents. The relative contribution of denitrification to the loss of excess N from pond effluents within mangrove wetlands is the focus of our analysis.

In this paper we evaluate the potential role of mangrove wetlands as sinks of inorganic nitrogen concentrations in shrimp pond effluents via denitrification. This evaluation is based on the water quality and management of three semi-intensive shrimp ponds along the Caribbean coast of Colombia. Monthly measurements in each pond of inorganic N concentrations between 1994–1995 were compared to nitrogen removal rates measured in riverine, basin and fringe mangrove wetlands. We estimated the amount of N that can be removed from these pond effluents prior to discharge to estuarine waters. A general nitrogen budget was calculated for each pond based on nitrogen transformations and several state variables to assess the amount of total N that was discharged to adjacent coastal waters. Finally, these N loadings were compared to published values in other geographical regions.

Materials and Methods

The three semi-intensive ponds were stocked primarily with *Penaeus vannamei* and were representative of three commercial farms (Fig. 1). Ponds in each farm are located along estuaries characterized by salinity regimes regulated by their proximity to river discharge. The farms are located between longitudes 75° and 76° west, and latitudes 9° and 11° north (Fig. 1) and were constructed in agricultural land (Agrosoledad and Aquacultivos) or salinas (Acuipesca) (Newmark et al. 1993). During the study period three shrimp crops were harvested (Table 1).

In general, the climate along the Caribbean coast of Colombia is dry (arid) with an annual water deficit of 1,031 mm/yr due to evapotranspiration (1,431 mm/yr) exceeding precipitation (400 mm/yr). Dry and wet seasons are well defined with a dry season from December to April, a short rainy season from May to June, a short dry season from July to August and a longer rainy season from September to November. The temperature regime is isomegathermic with annual means between 27–28 C and daily fluctuations of 8–9 C. Tides are semidiurnal, with a range of 50 cm (Newmark et al. 1993).

Dissolved inorganic nitrogen concentrations (DIN), temperature, and salinity were measured monthly inside each pond, in pond effluents, and in adjacent estuarine waters from June 1994 to September 1995. Water samples (500 mL) were filtered (Whatman GF/C) and stored on ice for chemical analysis within 1–2 d of collection. Portions of each water sample were analyzed for NH_4^+ concentrations by the phenolhypochlorite method (Solórzano 1969) and for NO_3^- + NO_2^- by cadmium reduction and autoanalysis of NO_2^- (Grasshoff et al. 1983). Salinity and temperature were measured at the time of sample col-

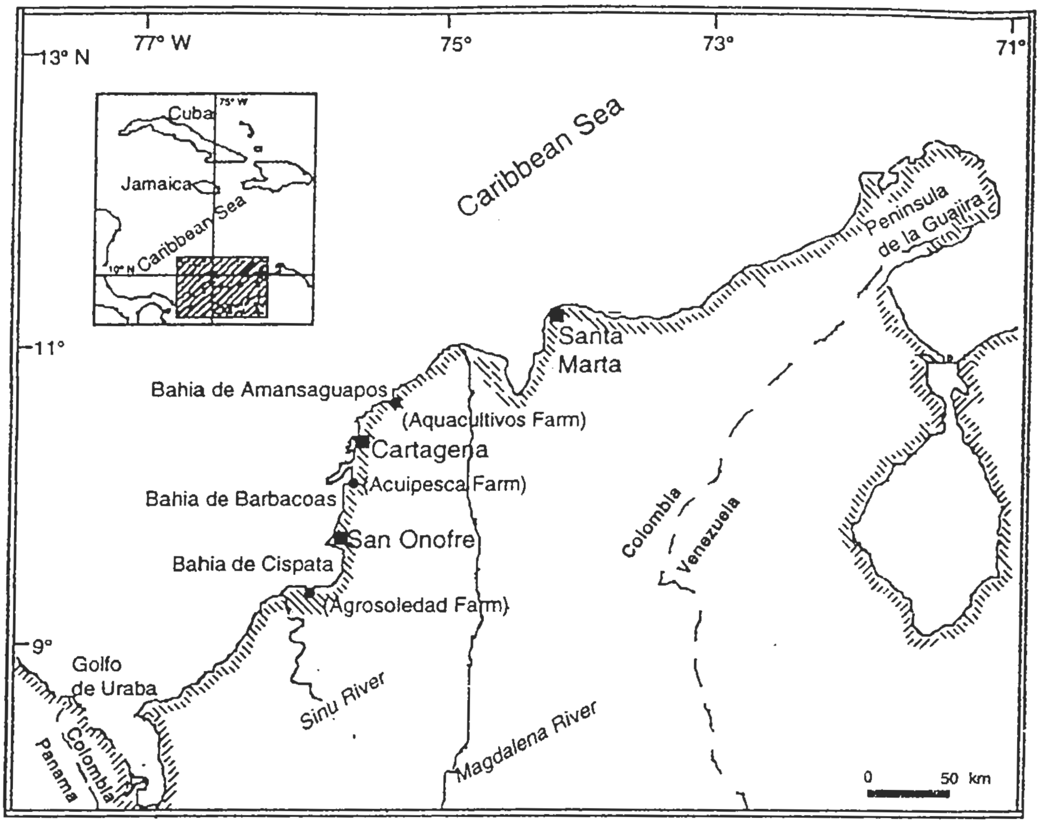

FIGURE 1. *Location of shrimp farms along the Caribbean coast of Colombia.*

lection with a portable salinometer (Salyn-it®).

Information about pond management (Table 1) was collected to estimate N budgets for each pond. Dissolved inorganic nitrogen fluxes into and out of the ponds were estimated using water exchange rates (Table 1) and mean concentration of NH_4^+ and NO_3^- + NO_2^- in the estuary and pond effluents during the three growout cycles (Table 2). Nitrogen budgets for each pond included feed, inflow water, fertilizer, chicken manure, and shrimp stock as N inputs and were compared to shrimp harvest, pond discharge water, and "remainder" as N outputs (Table 3). The last term represents the remaining N in particulate and dissolved organic form that could accumulate in the sediment or be exported to the estuary. Effluent particulate and dissolved organic nitrogen concentrations and sediment N accumulation were not measured during the study. Nitrogen export associated with pond discharge includes only DIN, and therefore underestimates the amount of total N exported into adjacent coastal waters. Because total nitrogen has not been measured in semi-intensive shrimp ponds in the Caribbean coast of Colombia, it is difficult to evalaute the magnitude of such underestimation. The N budget for each pond was then compared to other budgets describing semi-intensive shrimp pond operations in Southeast Asia and Latin America (Clifford 1994; Robertson and Phillips 1995).

A general N budget (Table 4) was estimated for a mangrove forest receiving pond effluents using DIN concentrations measured in Colombia as well as published nitrogen fluxes representing different nitrogen transformations in mangrove forests (Table 5). Loading rates of shrimp pond effluent into the mangrove forest were estimated for each pond using water exchange rates, pond volume (Table 1), and mean DIN concentrations (Table 2). These DIN loading rates were ranked as low (0.11 kg/ha per d) and high (0.22 kg/ha per d). Tidal input of DIN

TABLE 1. *Management variables in semi-intensive shrimp pond operations in different geographic regions. Values of variables for ponds in Colombia are means of four measurements.*

	Acuipesca (Colombia)	Agrosoledad (Colombia)	Aquacultivos (Colombia)	Aquacam C.A (Venezuela)	Tra Vinh Province (Vietnam)	Chantaburi Province (Thailand)[c]
Stocking density (PL/m)[a]	13	24	17	19	4[b]	52
Average weight (g/PL)	0.01	0.01	0.01	0.01	0.5	0.5
Culture period (d)	100	119	112	110	182	122
Growout cycle (yr)[d]	3.1	3.1	3.3	3.3	2.0	2.9
Pond area (ha)	9.0	10.4	5.6	10.1	1.0	0.4
Depth of pond (m)	1.3	1.3	1.3	1.2	1.0	nr[e]
Yield of shrimp (kg/ha per yr)	3,026	6,358	5,755	7,840	1,000	13,790
Water exchange (d)	0.07	0.10	0.07	0.03	0.10	nr
Feed conversion ratio (FC)	1.0	1.4	1.3	0.8	10.0	1.9
N content of shrimp (%FW)[f]	2.7	2.7	2.7	2.9	2.9	2.9
N content of feed (%FW)	4.0	5.8	4.8	5.6	5.0	7.1
Feed moisture (%)	12.0	12.0	12.0	12.0	nr	nr
Fertilizer	Yes	Yes	Yes	Yes	No	Yes
Chicken manure N (%FW)	1.2	1.2	1.2	1.2	nr	nr
Urea N (%FW)	46.0	46.0	46.0	46.0	nr	nr
Feed input (kg/ha per yr)	3,038	9,149	7,651	5,949	10,000	26,420
Fertilizer (kg/ha per yr)					No	Yes
Chicken manure[g]	4,393	2,468	5,168	330	nr	nr
Urea	25	60	34	198	nr	nr
Feed + fertilizer (kg/ha per yr)	7,456	11,676	12,853	6,445	10,000	26,420

[a] Cultivated species: Colombia and Venzuela-*Penaeus vannamei* (this study, Clifford 1994), Vietnam-*Penaeus merguiensis* and *P. monodon* (Robertson and Phillips 1995), Thailand-*Penaeus monodon* (Robertson and Phillips 1995).

[b] Juveniles.

[c] Intensive operation.

[d] Includes down time.

[e] Not reported.

[f] 2.7%, Boyd and Teichert-Coddington (1995); 2.9%, Robertson and Phillips (1995).

[g] Tee seed cake was applied instead of chicken manure.

TABLE 2. *Mean values (±SE) of physicochemical variables measured in adjacent estuarine waters and pond effluents in three semi-intensive shrimp farms in Colombia during three growout cycles.*

Variable	Growout cycle	Estuary: Acuipesca[a]	Estuary: Agrosoledad[b]	Estuary: Aquacultivos[a]	Estuary: Overall mean
Salinity (ppt)	1	24.0 (0.7)	12.0 (2.9)	40.2 (1.2)	22.9 (1.8)
	2	21.2 (3.3)	14.4 (4.9)	17.7 (5.4)	
	3	28.7 (3.5)	17.7 (3.7)	34.7 (4.0)	
Temperature (C)	1	32.6 (0.6)	30.2 (0.6)	31.0 (1.0)	30.6 (0.2)
	2	31.6 (0.7)	29.8 (0.2)	28.9 (0.3)	
	3	31.0 (0.6)	30.4 (0.7)	29.7 (0.5)	
NH_4^+ (µg/L)	1	15.0 (4.5)	28.4 (14.6)	11.5 (4.0)	33.5 (8.0)
	2	15.5 (8.8)	42.3 (27.6)	14.4 (13.4)	
	3	37.9 (20.0)	14.4 (11.6)	36.6 (27.4)	
$NO_2^- - NO_3^-$ (µg/L)	1	19.7 (17.1)	14.6 (14.8)	11.8 (6.3)	30.4 (6.7)
	2	26.5 (12.7)	42.3 (27.6)	45.2 (14.0)	
	3	64.0 (32.5)	14.4 (11.6)	57.7 (37.1)	

[a] Period: cycle 1, July–September 1994; cycle 2, October–January 1995; cycle 3, February–June 1995.

[b] Period: cycle 1, July–September 1994; cycle 2, November 1994–March 1995; cycle 3, April–August 1995.

to the mangrove forest was estimated using mean concentrations measured in the adjacent estuaries and assuming a daily diurnal tide of 0.3 m (Newmark et al. 1993). A mean tidal loading rate was estimated by using the average concentration of DIN in coastal waters at each farm (Table 2) (0.10 $[NH_4^+]$ + 0.07 $[NO_2^- + NO_3^-]$ = 0.17 kg/ha per d). The rate of nitrogen fixation (0.10 kg/ha per d) is based on estimates from different substrates (sediment, prop roots, and fresh and aged leaf litter) of mangrove forests in southern Florida (Kimball and Teas 1975; Zuberer and Silver 1975, 1978; Pelegri et al. 1997). A one-way ANOVA was performed to evaluate the overall difference in DIN concentrations between pond effluents and adjacent coastal waters.

Results and Discussion

Overall mean DIN concentrations in pond effluents from the farms from Colombia were similar to reported values from other tropical regions. Mean effluent concentrations of 35 µg/L for $NO_2^- + NO_3^-$ and 59 µg/L for NH_4^+ were reported for marine shrimp earthen ponds in Hawaii (Zieman et al. 1992). Whereas the mean NH_4^+ concentration in the effluent from all Colombian ponds (67 µg/L ± 12) was significantly higher (one-way ANOVA, df = 74, MSE = 4,119.3, P = 0.025) than that of the adjacent estuaries (33 µg/L ± 8). In contrast, $NO_2^- + NO_3^-$ concentrations of pond effluent and estuarine waters were similar (Table 2) among the three farms. $NO_2^- + NO_3^-$ concentrations were similar to mean values of managed shrimp ponds in Thailand (34 µg/L), but lower than the average NH_4^+ concentration (109 µg/L) in these Thai ponds (Chaiyakam et al. 1992). Generally, mean NH_4^+ concentrations in pond effluents of shrimp ponds under intensive operation in Thailand range from 210 to 900 µg/L (Briggs and Funge-Smith 1994).

The recovery of N associated with harvest of shrimp is <50% (range: 30–41%) of the N input to the Colombian ponds (Table 3). A lower food conversion ratio of shrimp harvested in Venezuela (Clifford 1994) resulted in a higher N recovery (48% of input). The low N recovery associated with shrimp yield in Vietnam (5%) and Thailand (20%) reflects poor feed conversion. About 78% of the N in the shrimp feed is wasted due to poor feed conversion rates and loss of nutrients through leaching (Csavas 1994). These results compare to N recoveries estimated for intensive shrimp

TABLE 2. *Extended.*

Pond effluent			
Acuipesca	Agrosoledad	Aquacultivos	Overall mean
27.2 (0.6)	13.0 (3.1)	42.0 (1.2)	25.0 (1.9)
22.2 (4.1)	14.0 (4.7)	20.2 (3.6)	
36.0 (1.5)	20.2 (3.7)	36.5 (3.7)	
32.8 (0.9)	36.8 (0.9)	31.0 (0.8)	30.6 (0.3)
31.5 (0.7)	29.8 (0.3)	28.6 (1.0)	
31.4 (0.8)	31.2 (0.5)	28.6 (0.6)	
36.0 (8.1)	33.6 (7.8)	24.8 (6.9)	67.2 (12.3)
96.7 (52.1)	153.9 (59.9)	92.5 (40.5)	
53.8 (21.7)	36.5 (20.4)	64.3 (32.1)	
24.8 (6.4)	13.0 (3.5)	12.3 (3.4)	34.3 (8.3)
20.3 (9.8)	43.3 (13.7)	123.5 (14.0)	
30.0 (21.4)	17.5 (9.2)	28.0 (13.9)	

TABLE 3. *Nitrogen budgets (kg/ha per yr) for semi-intensive shrimp ponds in different geographic regions.*

	Acuipesca (Colombia)	Agrosole-dad (Colombia)	Aquaculti-vos (Colombia)	Aquacam C.A (Venezuela)[a]	Tra Vinh Province (Vietnam)	Chantaburi Province (Thailand)
Inputs						
Feed	106.93	466.96	323.18	291.60	500.00	1,868.00
Inflow water	24.80	40.56	44.35	48.91	64.00	43.00
Fertilizer	11.55	27.38	15.79	91.08	0.00	62.00
Chicken manure	52.71	29.61	62.01	3.96	0.00	1.00
Shrimp stock	0.12	0.22	0.16	0.19	1.18	1.00
Total input	196.11	564.73	445.39	437.30	565.18	1,975.00
Outputs						
Shrimp harvest	81.70	171.66	155.38	211.68	29.40	405.00
Pond discharge water (DIN)[b]	34.10	73.78	59.14	90.52	128.00	199.00
Remainder[c]	80.31	319.29	230.87	117.86	407.78	1,371.00
Total output	196.11	564.73	445.39	437.3	565.18	1,975.00

[a] Venezuela, Clifford (1994); Vietnam and Thailand, Robertson and Phillips (1995).
[b] DIN = Dissolved Inorganic Nitrogen ($[NO_2 + NO_3] + [NH_4]$).
[c] Remainder = Total input − (shrimp harvest + discharge water).

ponds in Thailand where only 24% of the nitrogen added as feed and fertilizer was incorporated into the shrimp harvested (Briggs and Funge-Smith 1994). Similarly, Phillips et al. (1993) estimated that 63–78% of nitrogen fed to shrimp in an intensive pond culture was lost to the environment, either within the pond or discharged to the adjacent coastal waters.

Total annual N pond input in Colombia was 565 kg/ha per yr in Agrosoledad, 445 kg/ha per yr in Aquacultivos, and 196 kg/ha per yr in Acuipesca (Table 3). N inputs in Agrosoledad and Aquacultivos are similar to values observed in Venezuela (438 kg/ha per yr) (Clifford 1994) and Vietnam (565 kg/ha per yr) (Robertson and Phillips 1995) but were lower than for Thailand (1975 kg/ha per yr) (Robertson and Phillips 1995). The amount of DIN in effluent was 17%, 13%, and 13% of total N input in Acuipesca, Agrosoledad, and Aquacultivos, respectively. This proportion is lower than in Venezuela (20%) and Vietnam (23%).

TABLE 4. *Generalized N budget (kg/ha per d) for a mangrove forest receiving effluents from shrimp aquaculture ponds. Total numbers represent the potential N treatment capacity after accounting for N gains and losses at low and high effluent loading rates. The negative sign indicates net N losses (i.e., N losses are greater than gains (TN = Total Nitrogen; DIN = NH_4^+ + $[NO_2^- + NO_3^-]$).*

Processes	N form	Low	High
Gains			
Pond effluent loading	NH_4^+	0.08	0.15
	$NO_2^- + NO_3^-$	0.03	0.07
Tidal loading	NH_4^+	0.10	0.10
	$NO_2^- + NO_3^-$	0.07	0.07
Nitrogen fixation	N_2	0.01	0.01
Losses			
Denitrification	N_2	1.49	1.49
N accumulation in soil	TN	0.19	0.19
Plant uptake	DIN	0.56	0.56
Total		−1.95	−1.85

TABLE 5. *Nitrogen fluxes (kg/ha per d) used for the calculation of daily fluxes shown in Fig. 2.*

Location	Mangrove type	Dominant species	Denitrification: Potential direct	Denitrification: coupled	Sediment-water exchange: $NO_2 + NO_3$	Sediment-water exchange: NH_4^+	N accumulation	N required for primary production	N fixation	References
Mexico	Riverine	*Rhizophora mangle*	0.74	0.1	—	—	0.16	—	—	Lynch et al. 1989; Rivera-Monroy and Twilley 1996
Mexico	Fringe	*Rhizophora mangle*	0.03	—	0.002	0.014	0.13	—	—	Lynch et al. 1989; Rivera-Monroy et al. 1995a; Rivera-Monroy et al. 1995b; Rivera-Monroy and Twilley 1996
Florida	Fringe/Basin	*Rhizophora mangle/Avicennia germinans*	—	—	0.03	0.05	0.16	0.53[c]	0.01	Lynch et al. 1989; Rivera-Monroy and Twilley 1996; Rivera-Monroy and Twilley unpublished results; Kimball and Teas 1975; Zuberer and Silver 1975; 1978; Pelegri et al. 1997
Puerto Rico	Fringe	*Rhizophora mangle*	2.39[a]	—	—	—	—	—	—	Corredor and Morell 1994
Puerto Rico	Basin	*Avicennia germinans*	2.41[b]	—	—	—	—	—	—	
Ecuador	Riverine	*Rhizophora harrisonii*, *R. mangle*	—	—	—	—	0.31	—	—	Twilley et al. in review
Australia	Fringe/Basin	*Rhizophora stylosa*, *R. lamarcki*, *R. apiculata*	—	—	0.006	0.015	—	0.60[d]	—	Alongi 1996; Robertson and Phillips 1995
	Mean		1.39	—	0.012	0.026	0.19	0.56	—	

[a] Average flux along a 122 m transect.
[b] Average flux from low, middle, and intertidal zones.
[c] Based on litterfall (Pelegri et al. 1997).
[d] Based on litterfall, wood accumulation, and root production (Robertson and Phillips 1995).

The lowest export of DIN relative to annual N input was observed in Thailand. The "remainder" category ranged from 40% to 54% of the total N input to ponds in Colombia, 30% in Venezuela, 72% in Vietnam, and 69% in Thailand. The remainder category includes particulate and dissolved organic nitrogen that was exported to the estuary or deposited in pond sediments.

Nitrogen budgets of a mangrove forest receiving high (0.22 kg/ha per d) and low (0.11 kg/ha per d) loading rates of pond effluents indicate that forested wetlands are an efficient sink of DIN from pond effluent (Table 4). The availability of NO_3^- under anoxic conditions controls direct denitrification rates. Direct denitrification depends on NO_3^- that diffuses into sediments, while coupled nitrification-denitrification is supported by NO_3^- produced by nitrification (oxidation of NH_4^+ to NO_3^-) in the surface layers of the sediment (Jenkins and Kemp 1984; Henriksen and Kemp 1988). N loss through denitrification (direct + coupled) can represent a sink of >60% of DIN loaded to a forest from pond effluent and tidal inundation (Table 4). Moreover, denitrification rates are >7 times higher than effluent loading rates indicating that denitrification could account for the potential loss of all DIN entering the forest as pond discharge. Although denitrifying bacterial biomass in mangrove sediments is unknown, substantial sediment bacterial productivity and biomass have been measured (Alongi 1988). Denitrifying bacteria are more abundant in wetland soils used to treat wastewater discharge (i.e., treatment wetlands), than in natural wetlands (Kadlec and Knight 1996). Determinations of actual and potential denitrification rates in mangrove sediments receiving effluent from a wastewater treatment plant showed that microbial communities are capable of adapting to high effluent concentrations (Corredor and Morell 1994). In that study, denitrification increased 10 fold after adding up to 33 times the NO_3^- concentration found in sediment pore waters. Adaptation of denitrifiers to elevated N concentration has also been observed in NO_3^- polluted estuaries (King and Nedwell 1987).

Mass balance of N for a mangrove forest at low and high effluent loading rates resulted in a N treatment capacity of 1.95 and 1.85 kg/ha per d, respectively (Table 4). These estimates are similar and represent the potential for removal of DIN by a mangrove forest after accounting for all nitrogen losses. The N treatment capacity of fringe, basin, and riverine mangrove forests was evaluated using both high and low effluent mass loading rates and mean rates of N accumulation, plant uptake, nitrogen fixation, and direct and coupled denitrification reported for each type of mangrove forest (Table 5). Estimated N budgets for different types of mangroves at low and high mass loading rates also showed high N treatment capacities (Table 6) ranging from 1.13 to 2.80 kg/ha per d, with the highest capacity estimated for fringe mangroves. The lowest capacity was estimated for riverine mangroves at high loading rates (Table 4), due to lower reported potential denitrification rates (Table 5).

TABLE 6. *Estimated nitrogen treatment capacity for different mangrove forest ecological types after accounting for gains and losses of DIN ($[NO_2^- + NO_3^-] + [NH_4^+]$, see Table 4) at low and high effluent mass loading rates (kg/ha per d). Rates are based on mean DIN concentrations from three semi-intensive shrimp ponds in Colombia.*

DIN effluent loading rates		Forest type		
		Fringe	Basin	Riverine
Low	(0.11)	2.80	2.69	1.22
High	(0.22)	2.69	2.58	1.13

N loss by denitrification in mangroves can be compared to wetlands specifically designed for nutrient treatment, which can remove from 60 to 95% of the loaded DIN. Denitrification in a *Phragmites*-gravel subsurface flow treatment wetland unit accounted for 75 to 90% of nitrogen loss (Stengel et al. 1987). A natural isotope study in unvegetated microcosms in treatment wetland showed that between 60–70% of the $^{15}N\text{-}NO_3^-$ added was lost by denitrification (Cooke 1994). Similarly, Bartlett et al. (1979) reported loss of approximately 94% of the added N in microcosms of unvegetated sediments that simulated treatment wetlands. These proportions are similar to our estimate of 62% of DIN loss, which could increase depending on the NO_3^- loading rate and the type of mangrove wetland receiving the effluent.

Rates of denitrification are regulated by C:N ratios in sediments along with DIN concentrations. The high C:N ratios of mangrove sediments (C:N > 25) (Alongi 1996; Rivera-Monroy and Twilley 1996) suggest that denitrification is not limited by carbon. Denitrification occurs if nitrogen enrichment is sufficient to overcome competition for substrate by other non-denitrifying bacteria and plants. In a laboratory study, NO_3^- enrichments of 1.6 kg N/ha to sediments with different C:N ratios (22 vs 27) suggest that NO_3^- enrichment is important in controlling denitrification rates (Rivera-Monroy et al. 1995b; Rivera-Monroy and Twilley 1996). In contrast to direct denitrification, N loss due to coupled nitrification-denitrification from mangrove soils does not occur until high NH_4^+ enrichments are applied (3.6 kg N/ha). The direct relationship between increased NH_4^+ concentration and coupled nitrification-denitrification rate indicates that this process contributes to the reduction of DIN loaded to mangrove forests.

The amount of organic matter accumulation among different types of mangroves varies less than the sedimentation of mineral sediments. Nitrogen accumulation varies in relation to rates of organic matter accumulation, and in mangrove wetlands ranges from 0.17 to 0.31 kg/ha per d. Accretion rates in mangroves subject to high nitrogen loadings from wastewater are lacking, but we chose the mean value of that range (Table 5) to calculate the N accumulation in our N mass balance estimates (Table 4).

Plant uptake could also account for all the DIN (pond effluent + tidal) entering a mangrove forest. N uptake by mangrove trees sequester significant amounts of N by incorporation into plant tissue (Clough et al. 1983). Robertson and Phillips (1995) estimated that the N requirement to support total net forest production in *Rhizophora*-dominated forests was 0.56 kg/ha per d. We used this rate of N uptake in our mass balance calculations (Table 4).

Field studies of the long term effect of wastewater discharge on mangrove primary productivity and N preferences by mangrove species are scarce. One study evaluating the effect of sewage addition on the nutrient status of mangrove soils and plants (dominant species: *Aegiceras corniculatum, Kandeli candel* and *Avicennia marina*) in China showed that effluents (mean total N mass loading rate equal to 11 kg N/ha per d) had no effect on soil nitrogen concentrations (total N, NH_4^+, and NO_3^-) (Wong et al. 1995). Plant nutrient content indicated that mangrove soils and plants were capable of treating nutrient excess without apparent negative impact on plant growth suggesting that all N was immobilized in the sediment. In contrast to the study in China, intense direct fertilization of mangrove forests with N resulted in higher N content in leaves and high plant grow rates (Onuf et al. 1977), and an increase in the rate of new leaf production (Boto and Wellington 1983). These studies demonstrate that plant uptake and sediment immobilization were the mechanisms responsible for the removal of N inputs.

Based on estimates of N required to sustain primary production in an "average," humid tropical *Rhizophora* forest, Robertson and Phillips (1995) proposed that 2 to 3 ha of forest are required to filter N in the effluent from a 1-ha, semi-intensive shrimp pond. This proposed wetland : pond ratio assumed that all N exported from the pond (i.e., pond discharge water + remainder, Table 2) was available for plant uptake (0.6 kg N/ha per d, Table 5), and that plant uptake was the only sink for N effluent. Based on these assumptions, we estimated a wetland : pond ratio of 0.5, 1.8, 1.3, and 1.2 for Acuipesca, Agrosoledad, Aquacultivos, and Aquacam, respectively. Lower wetland : pond ratios calculated for the ponds evaluated in this study are due to lower N output and higher shrimp harvest compared to ponds in Thailand (Table 2). Robertson and Phillips (1995) recognized that their estimates of N removal from effluent by mangrove forests were conservative because denitrification was not included. If denitrification is included (1.49 kg/ha per d), the wetland : pond ratios would decrease to 0.1 and 0.5 in Colombia, and 0.3 in Venezuela. However, our analysis assumes that all N is available for plant uptake. A more realistic estimate would consider only pond discharge water since it contains NO_3^- and NH_4^+, which are the main nitrogen forms available for plant uptake and denitrification. Therefore, corrected ratios would be 0.04, 0.10, 0.08, and 0.12 for Acuipesca, Agrosoledad, Aquacultivos, and Aquacam, respectively (average = 0.10). This significant reduction of the forest to pond area ratio emphasizes the importance of denitrification.

Further experiments at different combinations of sediment C:N ratio and enrichment rate are needed to generate a response surface (Montgomery 1991) to evaluate the effect of these variables on denitrification rates. In addition, confidence in our mass balance estimates is restricted by the limited number of denitrification studies in different types of mangrove wetlands. NH_4^+ enrichment studies of basin and fringe mangrove forest are needed to evaluate if there is a significant stimulation of coupled nitrification-denitrification which will allow a more complete evaluation of N loss after adding pond effluents. These studies could help to determine the NH_4^+ enrichment rates that cause shift from N immobilization to denitrification.

Because of the lack of information in some treatment combinations and the confounding effect of mangrove types, our mass balance calculations of N loss (Table 4) and wetland:pond area ratio for the farms in Colombia should be considered as preliminary estimates. Although the reduction of this ratio is substantial (by >500%) in comparison to Robertson and Phillips's (1995) estimates, the average 0.1:1.0 ratio is an optimal upper limit for DIN. Further information is needed to evaluate the effect of high concentrations of DON and PN in pond effluents on N cycling in mangrove forests (Clough et al. 1983; Boto 1992; Tam and Wong 1993; Wong et al. 1995). Long term effects of pond effluent on mangrove N cycling are linked to the potential increase of coupled nitrification-denitrification as a result of the increase of NH_4^+ through mineralization of DON and PN. Unfortunately, since few studies of mineralization and nitrification rates in mangrove sediments have been conducted (Rivera-Monroy and Twilley 1996), it is not possible to evaluate their potential contribution in the transformation of PN and DON to inorganic nitrogen from both *in situ* production (e.g., litter decomposition) and pond effluents. Although the lack of data on organic N concentrations in this study limits our recommendations, establishment of quantitative relationships between N enrichment and denitrification rates initiates evaluation of a conceptual framework to evaluate the impacts of pond effluents on N cycling in mangrove forests. This framework can provide information for the design of specific experiments to address particular processes, such as the importance of denitrification in treatment of PN and DON.

Before mangroves are used for nutrient treatment of pond effluents, engineering designs and costs should be evaluated. Engineering and economic aspects must be balanced to provide optimum delivery of pond effluent for a specific environmental setting, mangrove ecological type, and management practices. Effluent dispersion should be designed as a continuous sheet flow to allow homogenous interaction between the sediment and effluent, while avoiding erosion and significant changes in the microtopography of the forest floor. We recommend pilot studies and a modelling approach to evaluate biological variables, operating costs of the system, and engineering performance (Losordo and Westerman 1994; Sandifer and Hopkins 1996; Leung and El-Gayar 1997). Consideration of the nutrient treatment capacities of mangrove wetlands in the design of integrated shrimp-wetland farming systems will allow a better evaluation of the potential effects of long term nutrient enrichment. Our estimates of the magnitude of N removal from pond effluents by denitrification emphasizes the functional importance of mangrove wetlands and the need to integrate these ecosystems into shrimp aquaculture management programs.

Acknowledgments

Partial support for this work was provided by INVEMAR and CENIACUA through a cooperative agreement with the University of Southwestern Louisiana. COLCIENCIAS provided financial support through the research project "Desarrollo y optimization del cultivo de camarones marinos (*Penaeus vannamei, P. stylirostris,* y *P. schmitti*)" directed by Federico Newmark (Code No. 2105-09-030-93). We thank Dominique Gautier and three anonymous reviewers for their criticisms, which greatly improved the first version of this manuscript. We also thank Capt. Francisco Arias (INVEMAR) and Dr. Segio Martinez (CENIACUA) for logistics and facilities during the preparation of this manuscript.

Literature Cited

Alongi, D. M. 1988. Bacterial productivity and microbial biomass in tropical mangrove sediments. Microbial Ecology 15:59–79.

Alongi, D. M. 1996. The dynamics of benthic nutrient pools and fluxes in tropical mangrove forests. Journal of Marine Research 54:123–148.

Alongi, D. M., and A. Sasekumar. 1992. Benthic communities. Pages 137–172 *in* A. I. Robertson, and D. M. Alongi, editors. Tropical mangrove ecosystems. 41. Coastal and Estuarine Studies. American Geophysical Union, Washington, D.C., USA.

Bardach, J. E. 1997. Aquaculture, pollution, and biodiversity. Sustainable aquaculture. Pages 87–100 *in* J. E. Bardach, editor. John Wiley and Sons, New York, USA.

Bartlett, M. S., L. C. Brown, N. B. Hanes, and N. H. Nickersen. 1979. Denitrification in freshwater wetland soil. Journal of Environmental Quality 8: 460–464.

Boto, K. B. 1992. Nutrients and mangroves. Pages 129–145 *in* D. W. Connell, and D. H. Hawker, editors. Pollution in tropical aquatic systems. CRC press, Inc., Boca Raton, Florida, USA.

Boto, K. G., and J. T. Wellington. 1983. Phosphorous and nitrogen nutritional status of a northern Australian mangrove forest. Estuaries 7:61–69.

Boyd, C. E., and D. Teichert-Coddington. 1995. Dry matter, ash, and elemental composition of pond-cultured *Penaeus vannamei* and *P. stylirostris.* Journal of the World Aquaculture Society 1:88–92.

Boyd, C. E., P. Munsiri, and B. F. Hajek. 1994. Composition of sediment from intensive shrimp ponds in Thailand. World Aquaculture 25:53–55.

Briggs, M. R. P., and S. J. Funge-Smith. 1994. A nutrient budget of some intensive marine shrimp ponds in Thailand. Aquaculture and Fisheries Management 25:789–811.

Chaiyakam, K. P., P. Songsangjinda, and D. Tunvilai. 1992. Water quality and production of two management systems of tiger shrimp culture in Songkhla Province. National Institute of Coastal Aquaculture, Department of Fisheries, Songkhla, Thailand.

Clifford, C. H. 1994. Semi-intensive sensation. World Aquaculture 25:6–104.

Clough, B. F., K. G. Boto, and P. M. Attiwill. 1983. Mangroves and sewage: a re-evaluation. Pages 151–161 *in* H. J. Teas, editor. Tasks for vegetation science. 8, Tasks for Vegetation Science. W. Junk, The Hague, Netherlands.

Cooke, J. G. 1994. Nutrient transformations in a natural wetland receiving sewage effluent and the implications for waste treatment. Water Science Technology 29:209–217.

Corredor, J. E., and M. J. Morell. 1994. Nitrate depuration of secondary sewage effluents in mangrove sediments. Estuaries 17:295–300.

Csavas, I. 1994. Important factors in the success of shrimp farming. World Aquaculture 25:34–56.

Dierberg, F. E., and W. Kiattisimkul. 1996. Issues, impacts, and implications of shrimp aquaculture in Thailand. Environmental Management 20:649–666.

Feller, I. C. 1995. Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). Ecological Monographs 52: 477–505.

Grasshoff, K., M. Erhardt, and K. Kremling. 1983. Methods of seawater analysis. Verlag Chemie, New York, USA.

Henriksen, K., and W. M. Kemp. 1988. Nitrification in estuarine and coastal marine sediments. Pages 207–249 *in* T. H. Blackburn, and J. Sorenson, editors. Nitrogen cycling in coastal marine environments. John Wiley and Sons Ltd, New York, USA.

Hopkins, J. S., R. D. Hamilton, P. A. Sandifer, C. L. Browdy, and A. D. Stokes. 1993. Effect of water exchange rate on production, water quality, effluent characteristics and nitrogen budgets of intensive shrimp ponds. Journal of the World Aquaculture Society 24:303–320.

Hopkins, J. S., P. A. Sandifer, and C. L. Browdy. 1994. Sludge management in intensive pond culture of shrimp: Effect of management regime on water quality sludge characteristics, nitrogen extinction, and shrimp production. Aquacultural Engineering 13:11–30.

Hopkins J. S., P. A. Sandifer, and C. L. Browdy. 1995a. A review of water management regimes which abate the environment impacts of shrimp farming. Pages 157–166 *in* C. L. Browdy, and J. S. Hopkins, editors. Swimming through troubled water. World Aquaculture Society, Baton Rouge, Louisiana, USA.

Hopkins J. S., P. A. Sandifer, and C. L. Browdy. 1995b. Effect of two protein levels and feed rate combinations on water quality and production of intensive shrimp ponds operated without water exchange. Journal of the World Aquaculture Society 26:93–97.

Jenkins, M. C., and W. M. Kemp. 1984. The coupling of nitrification and dentrification in two estuarine sediments. Limnology and Oceanography 29:609–619.

Jory, D. E. 1995a. Global situation and current megatrends in marine shrimp farming. Aquaculture Magazine July/August 74–83.

Jory, D. E. 1995b. Management of natural productivity in marine shrimp: semi-intensive ponds. Aquaculture Magazine November/December 90–100.

Kadlec, R. H., and R. L. Knight. 1996. Treatment wetlands. CRC Press, Lewis Publishers, Boca Raton, Florida, USA.

Kimball, M. C., and H. J. Teas. 1975. Nitrogen fixation in mangrove areas of southern Florida. Pages 651–660 *in* G. E. Walsh, S. C. Sneadaker, and H. J. Teas, editors. Proceedings of the international symposium on biology and management of mangroves. University of Florida, Gainsville, Florida, USA.

King, D., and D. B. Nedwell. 1987. The adaptation of nitrate reducing bacterial communities in estuarine sediments in response to overlying nitrate load. FEMS (Federal European Microbiology Society) Microbiology and Ecology 45:15–28.

Leung, P., and O. El-Gayar. 1997. The role of modelling in the managing and planning of sustainable aquaculture. Pages 149–176 *in* J. E. Bardach, editor. Sustainable aquaculture. John Wiley and Sons, New York, USA.

Liao, I. C. 1992. Marine prawn culture industry of Taiwan. Pages 653–675 *in* W. Fast, and L. J. Lester, editors. Marine shrimp culture: principles and cultures. Elsevier, Amsterdam.

Losordo, T. M., and P. W. Westerman. 1994. An analysis of biological, economic, and engineering factors affecting the cost of fish production in recirculating aquaculture systems. Journal of the World Aquaculture Society 25:193–203.

Lynch, J. C., J. R. Meriwether, B. A. McKee, F. Vera-Herrera, and R. R. Twilley. 1989. Recent accretion in mangrove ecosystems based on ^{137}Cs and ^{210}Pb. Estuaries 12:284–299.

Martinez-Cordova, L. R., H. C. Villareal, and M. A. Porchas. 1995. Culture of white shrimp *Penaeus vannamei* in reduced water exchange ponds in Sonora, Mexico. World Aquaculture 26:47–48.

Martinez-Cordova L. R., H. C. Villareal, and M. A Porchas. 1996. Culture of shrimp *Penaeus vannamei* without food in a discharge lagoon of a shrimp farm. World Aquaculture 27:68–69.

Montgomery, D. C. 1991. Design and analysis of experiments. John Wiley & Sons, New York, USA.

Newmark, F., I. Moreno, A. Vallejo, and L. A. Torres. 1993. Influencia de la productividad primaria y secundaria en la produccion de camarones marinos cultivados (*Penaeus vannamei, P. stylirostris,* y *P. schmitti*) en el litoral Caribe Colombiano, INVEMAR, Informe tecnico.

Olsen, B. S. 1995. Struggling with an emergy analysis: Shrimp mariculture in Ecuador. Pages 207–215 *in* C. A. S. Hall, editor. Maximum power. University Press of Colorado, Niwot, Colorado, USA.

Onuf, C. P., J. M. Teal, and I. Valiela. 1977. Interaction of nutrients, plant growth and herbivory in a mangrove ecosystem. Ecology 58:514–526.

Pelegri, S. P., V. H. Rivera-Monroy, and R. R. Twilley. 1997. A comparison of nitrogen fixation (acetylene reduction) among three species of mangrove litter, sediments and pneumatophores in south Florida, USA. Hydrobiologia 356:73–79.

Phillips, M. J., C. Kwei Lin, and M. C. M. Beveridge. 1993. Shrimp culture and the environment: Lessons from the world's most rapidly expanding warmwater aquaculture sector. Pages 171–197 *in* R. S. V. Pullin, H. Rosenthal and J. L. Maclean, editors. Environment and aquaculture in developing countries. ICLARM Conference Proceedings 31. International Center for Living Aquatic Resources Management, Manila, The Phillipines.

Rivera-Monroy, V. H., and R. R. Twilley. 1996. The relative role of denitrification and immobilization on the fate of inorganic nitrogen in mangrove sediments. Limnology and Oceanography 41:284–296.

Rivera-Monroy, V. H., J. W. Day, R. R. Twilley, F. Vera-Herrera, and C. Coronado-Molina. 1995a. Flux of nitrogen and sediment in a fringe mangrove forest in Terminos Lagoon, Mexico. Estuarine Coastal and Shelf Science 40:139–160.

Rivera-Monroy, V. H., R. R. Twilley, R. G. Boustany, J. W. Day, F. Vera-Herrera, and M. C. Ramirez. 1995b. Direct denitrification in mangrove sediments in Terminos Lagoon, Mexico. Marine Ecology Progress Series 126:97–109.

Robertson, A. I., and M. J. Phillips. 1995. Mangroves as filters of shrimp pond effluent: predictions and biogeochemical research needs. Hydrobiologia 295:311–321.

Sandifer, P. A., and J.S. Hopkins. 1996. Conceptual design of a sustainable pond-based shrimp culture system. Aquaculture Enginering 15:41–52.

Smith, P. T. 1996. Physical and chemical characteristics of sediments from prawn farms and mangrove habitats on the Clarence River, Australia. Aquaculture 146:47–83.

Solórzano, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnology and Oceanography 14:799–801.

Stanley, B. 1993. Thailand shrimp farming brings wealth, problems. Aquaculture News 6:28–32.

Stengel, E., W. Carduck, and C. Jebsen. 1987. Evidence for denitrification in artificial wetlands. Pages 543–550 *in* K. R. Reddy, and W. H. Smith, editors. Aquatic plants for water treatment and resource recovery. Magnolia Publishing, Orlando, Florida, USA.

Tam, N. F., and Y. S. Wong. 1993. Retention of nutrients and heavy metals in mangrove sediment receiving wastewater of different strength. Environmental Technology 14:719–729.

Thia-Eng, C. 1997. Sustainable aquaculture and integrated coastal management. Pages 177–200 *in* J. E. Bardach, editor. Sustainable aquaculture. John Wiley and Sons, New York, USA.

Twilley, R. R. 1985. The exchange of organic carbon in basin mangrove forests in a southwest Florida estuary. Estuarine Coastal and Shelf Science 20: 543–557.

Twilley, R. R. 1988. Coupling of mangroves to the productivity of estuarine and coastal waters. Pages 155–180 *in* B. O. Jansson, editor. Coastal-offshore ecosystems: interactions. 22, Lectures Notes on Coastal and Estuarine Studies. Springer-Verlag, Berlin, Germany.

Twilley, R. R. 1989. Impacts of shrimp mariculture practices on the ecology of coastal ecosystems in Ecuador. Pages 91–120 *in* S. Olsen, and L. Arriaga, editors. Establishing a sustainable shrimp mariculture industry in Ecuador. The University of Rhode Island, Narragansett, Rhode Island, USA.

Twilley, R. R. 1995. Properties of mangrove ecosystems and their relation to the energy signature of coastal environments. Pages 43–62 *in* C. A. S. Hall, editor. Maximum power. University Press of Colorado, Colorado, USA.

Twilley, R. R., A. Bodero, and D. Robadue. 1993. Mangrove ecosystem biodiversity and conservation in Ecuador. Pages 105–127 *in* C. S. Potter, J. I. Cohen, and D. Janczewski, editors. Perspectives on biodiversity: case studies of genetic resource conservation and development. AAAS Press, Washington, D.C. USA.

Wang, Q., C. Yang, and Y. Yu. 1995. The shrimp farming industry in China: past development, present status, and perspectives on the future. Pages 1–12 *in* C. L. Browdy, and J. S. Hopkins, editors. Swimming through troubled water. Proceedings of the special session on shrimp farming aquaculture '95, World Aquaculture Society. Baton Rouge, Louisiana, USA.

Wong, Y. S., C. Y. Lan, G. Z. Chen, S. H. Li, X. R. Chen, Z. P. Liu, and N. F. Y. Tam. 1995. Effect of wastewater discharge on nutrient contamination of mangrove soils and plants. Hydrobiologia 295: 243–254.

Ziemann, D. A., W. A. Walsh, E. G. Saphore, and K. Fulton-Bennet. 1992. A survey of water quality characteristics of effluent from Hawaiian aquaculture facilities. Journal of the World Aquaculture Society 23:180–191.

Zuberer, D. A., and W. S. Silver. 1975. Mangrove-associated nitrogen fixation. Pages 643–653 *in* G. E. Walsh, S. C. Sneadaker, and H. J. Teas, editors. Proceedings of the international symposium on biology and management of mangroves. University of Florida, Gainesville, Florida, USA.

Zuberer, D. A., and W. S. Silver. 1978. Biological dinitrogen fixation (acetylene reduction) associated with Florida mangroves. Applied and Environmental Microbiology 35:567–575.