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Evaluation of nitrogen cycling and fish production in seasonal ponds ('Fingerponds') in Lake Victoria wetlands, East Africa using a dynamic simulation model

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Abstract

A dynamic model was developed to simulate nitrogen (N) flows and fish production in seasonal wetland fish ponds (Fingerponds) based on organic manuring and natural food production. The model incorporates pond water depth, food availability, fish stocking densities, fish and fingerling weights at stocking, reproduction rate, manure type and application rates. The ponds were fertilized fortnightly with 1042 kg ha^{-1} chicken manure. The model captured the dynamics of hydrology, nutrients and fish and demonstrated that similar fundamental processes underlie fish production in these systems. The model predicted annual fish yields of up to 2800 kg ha^{-1}. Simulated fish production, chlorophyll *a* and dissolved inorganic N concentrations were comparable with field measurements. Using the model, N budgets and estimates of all N flows were made. Most of the N input into the ponds (60–70%) accumulated in the bottom detritus of the pond and only 8–10% was converted into fish biomass, of which about half consisted of small fish. Fish production in Fingerponds was limited by turbidity induced light limitation and by nutrient limitation. Reduction of variability of fish production should come from reduced turbidity and sufficient nutrient input to minimize light limitation and maximize fish growth.

Keywords: ecosystem services, Fingerponds, integrated production systems, Lake Victoria, papyrus wetland, sustainable use, water quality

Introduction

Fingerponds are earthen ponds dug at the seasonally inundated landward edge of lacustrine or riverine tropical wetlands and stocked naturally with fish following flood recession. They are integrated agriculture–aquaculture systems, unique in their dependence on natural flood events for initial water supply and fish stocking. The fish that are trapped in the ponds can be farmed and cropped and provide protein for resource-poor communities, particularly in the dry season. This has been demonstrated in experimental Fingerponds in the Rufigi floodplain, Tanzania and in the wetlands surrounding Lake Victoria in Uganda and Kenya (e.g., Denny, Kipkemboi, Kaggwa & Lamtane 2006; Kipkemboi, Van Dam, Ikiara & Denny 2007; Kaggwa, Van Dam, Balirwa, Kansiime & Denny 2009).

Animal manure application can enhance net phytoplankton productivity in Fingerponds to average levels of up to 2.9 g C m^{-2} day^{-1} (Kaggwa 2006). This is within the normal range in organically fertilized ponds (e.g., 2.4–4.4 g C m^{-2} day^{-1} in ponds in Honduras and Panama; Green, Phelps & Alvarenga 1989; Teichert-Coddington, Green & Phelps 1992). The natural productivity in these systems is supported by an autotrophic pathway in which solar energy is used by primary producers (mainly phytoplankton) for the photosynthetic fixation of carbon, nitrogen (N) and phosphorus. The resulting algal biomass is utilized by fish, either directly or indirectly via the heterotrophic pathway (Schroeder 1978; Schroeder, Wohlfarth, Alkon, Helevy & Krueger 1990). The pathways are linked through fluxes of inorganic and organic nutrients (Delincé 1992).

Nitrogen plays a vital role in fish culture due to its dual role as a nutrient and a toxicant. While it is deliberately added to pond systems to enhance primary productivity, some of its dissolved components (notably unionized ammonia and nitrite) must be kept below toxic levels to prevent fish mortality. The greater part (64–89%) of all N added to fish ponds accumulates in the sediment or is lost through volatilization or discharge (Hargreaves 1998). The challenge in pond management is therefore to maintain good water quality while maximizing the retention of N in harvestable products and minimizing N discharge into the environment (Jiménez-Montealegre 2001). This is particularly important for aquaculture around Lake Victoria, which suffers from eutrophication with low oxygen concentrations and deteriorating water quality as a result (Scheren, Zanting & Lemmens 2000; Kayombo & Jørgensen 2005).

Directly after flood recession, water levels in Fingerponds are regulated by contiguous lake and/or river water levels and then by surface runoff, rainfall, evaporation and seepage. As the culture period progresses and the dry season approaches, water levels begin to fall and the ponds may dry out completely (Kipkemboi, Van Dam, Mathooko & Denny 2007). Fish growth is governed by external factors (such as climate, pond inputs and water level) and internal pond factors (water quality, primary productivity and fish reproduction). Most of these factors were investigated experimentally in field experiments with Fingerponds (Kaggwa, Kansiime, Denny & Van Dam 2005; Kaggwa, Kasule, van Dam & Kansiime 2006; Kipkemboi, van Dam & Denny 2006; Kipkemboi, Van Dam, Ikiara *et al.* 2007; Kipkemboi, Van Dam, Mathooko *et al.* 2007; Kaggwa *et al.* 2009). Formulation of management strategies for these systems requires a proper understanding of the interactions between internal and external factors. Regulation of fertilizer application regimes is an essential part of the management strategy. Food supply to the fish should be optimized while avoiding deterioration of pond water quality and subsequent negative impacts on the environment.

To increase the understanding of this complex system and provide a consistent description of the Fingerpond production system using the accumulated research results, a dynamic model was constructed that took into consideration the major factors determining fish growth in a Fingerpond. The overall objective of the model was an integral evaluation of the processes determining fish production. Specific objectives were: (a) to relate fish yields to the natural food production and management of Fingerponds; (b) to compute N budgets and flows for two different types of Fingerponds; and (c) to make recommendations for further research and pond management. The model was calibrated using data from four experimental Fingerpond sites on the shores of Lake Victoria in Uganda and Kenya.

Material and methods

Data collection

Field experiments with Fingerponds were conducted from May 2003 to April 2004. Four Fingerponds of 24 × 8 m were dug in each of the four sites located in the flood zone of Lake Victoria wetlands; Gaba (N 0°14′59.9″, E 32°28′14.4″) and Walukuba (N 0°25′58.2″, E 33°14′59.8″), Uganda; and Kusa (S 0°3′55.9″, E 34°53′21.3″ and Nyangera (S 0°3′55.9″, E 340 4′52.2″), Kenya. Water quality data, including temperature (°C), dissolved oxygen (DO), total suspended solids, ammonium nitrogen, nitrate nitrogen (NO_3-N), chlorophyll *a* (Chl *a*) and secchi depth visibility were collected monthly between 10:00 and 14:00 hours over a full production cycle (Kaggwa 2006; Kipkemboi 2006; Kaggwa *et al.* 2009) following standard methods (APHA 1995).

Total numbers and weights of adult fish (various species, but dominated by the tilapias *Oreochromis niloticus, Oreochromis variabilis and Oreochromis leucostictus*) and their fingerlings were determined at stocking and at harvest. The total N added to the ponds was determined from the chicken manure input and from calculations of N fixed by Cyanobacteria. Additional data on tilapia growth and N cycling were adopted from the literature (Delincé 1992; Hargreaves 1998; Jiménez-Montealegre 2001; Jamu & Piedrahita 2002; Jiménez-montealegre, Verdegem, Van Dam & Verreth 2002; van Dam & Verdegem 2005; van Dam, Dardona, Kelderman & Kansiime 2007).

Pond sediment samples were collected at the beginning and the end of the culture period and analysed for total N. Daily measurements of photosynthetically active radiation (PAR) were taken in Kirinya wetland, Jinja (2 km from the Walukuba location) using a SKYE 4 channel radiometer with light sensors (Skye Instruments 21, Llandrindod Wells, UK) and at the pond site in Kusa, Kenya using a WEATHER HAWK silicon pyranometer sensor (Campbell Scientific, 815 West 1800 North Logan, UT, USA). Light extinction coefficients (k_t) were estimated from secchi depth (Poole & Atkins 1929).

System description

Fingerponds are constructed with the pond bottom below the groundwater table and depend entirely on seasonal lake and river flood events for initial filling. Once the flood recedes, water levels are regulated by seepage, precipitation, evaporation and runoff. Distinctive differences in water levels were noted between the sites. The ponds in Uganda (referred to as the 'lake-dependent ponds' or simply 'lake ponds') were located in the lake floodplain and had relatively stable water levels, whereas the sites in Kenya ('river floodplain ponds' or 'river ponds') were also affected by river hydrology. In Kusa, the ponds dried out completely and showed the most distinctive drop in water level. Daily variations in PAR also differed among the sites with notably higher values occurring in Kirinya (Fig. 1).

Water quality in the two locations was also distinctively different (Table 1). In general, dissolved inorganic nitrogen (DIN) concentrations were lower in the Ugandan lake ponds than in the Kenyan river ponds (Fig. 2). However, DIN concentrations increased over the grow-out period, particularly in Nyangera. Chlorophyll *a* concentrations did not show much variation with time except in Walukuba where a rise was noted in the last 2 months of the culture period. Suspended solids were relatively high (above 50 mg L^{-1}), especially in Nyangera. In general, secchi depth visibility in all the ponds was low, although in Kusa it exceeded 25 cm.

Conceptual model and assumptions

Because of its vital role in fishponds (see 'Introduction'), N was chosen as the model currency and all variables were expressed in grams of N. In the model, three layers were distinguished: the pond sediment consisting of soil with interstitial pore water; the detritus layer in which all dead organic material in the pond accumulate and are mineralized by microbes and other heterotrophs; and the water column which harbours fish, phytoplankton and dissolved and suspended materials. Phytoplankton and detritus were regarded as the main food sources for fish. Pond hydrology determined the length of the culture period (Fig. 3).

Based on their observed dominance in the ponds, in the model all fish were assumed to be tilapia (*Oreochromis* spp.). Macrophytes did not occur in the ponds and did not play an important role as food for the fish. Periphyton productivity in the ponds (Kaggwa *et al.* 2006) as well as zooplankton production and biomass (Pokorny̌, Přikryl, Faina, Kansiime, Kaggwa, Kipkemboi, Kitaka, Denny, Bailey, Lamtane & Mgaya 2005) were low. Macrophytes, periphyton and zooplankton were therefore not included in the model. Oxygen concentrations in the pond were above 2 mg L^{-1} in the early morning and never dropped below 4 mg L^{-1} during the day (Kaggwa 2006), and therefore were assumed to be within acceptable ranges for growth and survival of tilapia and not part of the model. Furthermore, it was assumed that no lethal abiotic factors existed in the ponds and that the decomposition of organic matter supplied enough carbon dioxide to support phytoplankton growth (Boyd 1972). The pond was assumed to be homogeneously mixed. As the average water temperature was similar in three of the four sites and the variation was small (maximum coefficient of variation was 7.7%, see Table 1), we decided not to include temperature as a driving variable in the model.

The protein content of the phytoplankton as well as fish mortality were assumed to be constant. Denitrification was considered negligible because there was hardly any nitrate in the ponds (Kaggwa 2006).

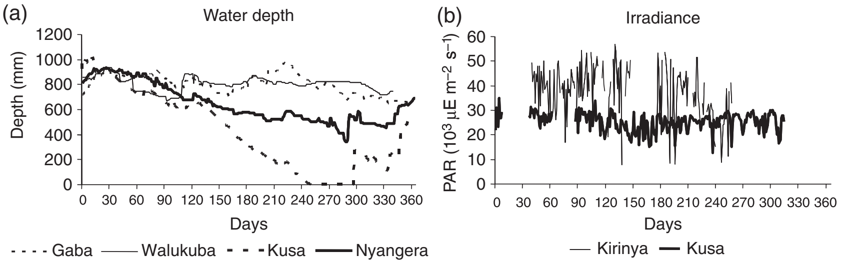

Figure 1 Daily observed pond water depth (mm) in the four Fingerpond locations (a) and photosynthetic active radiation (µE m^{-2} s^{-1}) for Kirinya near Walukuba, Uganda and Kusa wetlands, Kenya (b), May 2003–April 2004.

Table 1 Observed water and fish variables for manured Fingerponds in Gaba and Walukuba (Uganda) and Kusa and Nyangera (Kenya)

	Gaba	Walukuba	Kusa	Nyangera
Water quality				
pH	7.7–8.7	8.6–9.3	7.5–8.2	8.5–8.9
EC (μS cm^{-1})	414 (6.2)	1423 (7.4)	5867 (14.6)	6633 (23.4)
Temperature (°C)	24.3 (3.5)	26.0 (6.9)	26.4 (5.2)	26.9 (7.7)
DO (mg L^{-1})	4.4 (34.3)	6.3 (31.6)	7.3 (29.5)	10.5 (29.1)
TSS (mg L^{-1})	129.8 (44.4)	139.3 (25.1)	94.2 (29.3)	258.3 (32.6)
DIN (mg L^{-1})	0.45 (180.7)	0.34 (42.5)	0.92 (46.3)	1.16 (54.0)
N:P ratio	6.3 (33.6)	3.2 (27.6)	17.6 (157.6)	6.0 (66.1)
Chl *a* (μg L^{-1})	65.6 (60.4)	163.0 (96.7)	58.4 (68.2)	91.7 (51.0)
Secchi depth (cm)	17.5 (7.4)	19.2 (21.2)	32.8 (13.6)	13.8 (11.8)
Extinction coefficient k_t (m^{-1})	8.3 (14.2)	6.3 (18.2)	4.3 (14.2)	10.7 (11.1)
Fish				
Functional period (day)	310	219	228	189
No. of fingerlings initial census	151 (76.6)	18 (147.2)	613 (14.4)	1850 (13.4)
No. of fingerlings final harvest	1218 (99.0)	1155 (42.3)	126 (87.4)	4459 (16.5)
Individual fingerling weight initial census (g)	3.4 (56.8)	3.8 (71.1)	1.7 (55.6)	0.5 (–)
Individual fingerling weight final harvest (g)	1.3 (21.8)	1.8 (18.3)	14.2 (31.4)	3.2 (33.6)
Individual fish weight initial census (g)	21.3 (128.8)	41.8 (121.9)	87.8 (66.0)	30.3 (49.1)
Individual fish weight final harvest (g)	55.5 (1.5)	46.8 (10.0)	85.0 (18.5)	120.1 (61.1)
No. of fish initial census	113 (45.4)	138 (113.4)	46 (89.9)	150
No. of fish final harvest	2095 (72.4)	1096	94 (27.6)	198 (39.9)

All values are means of monthly measurements during the functional period (coefficient of variation in brackets) in two (Gaba) or three (other locations) ponds, except for pH values which are minimum to maximum ranges.

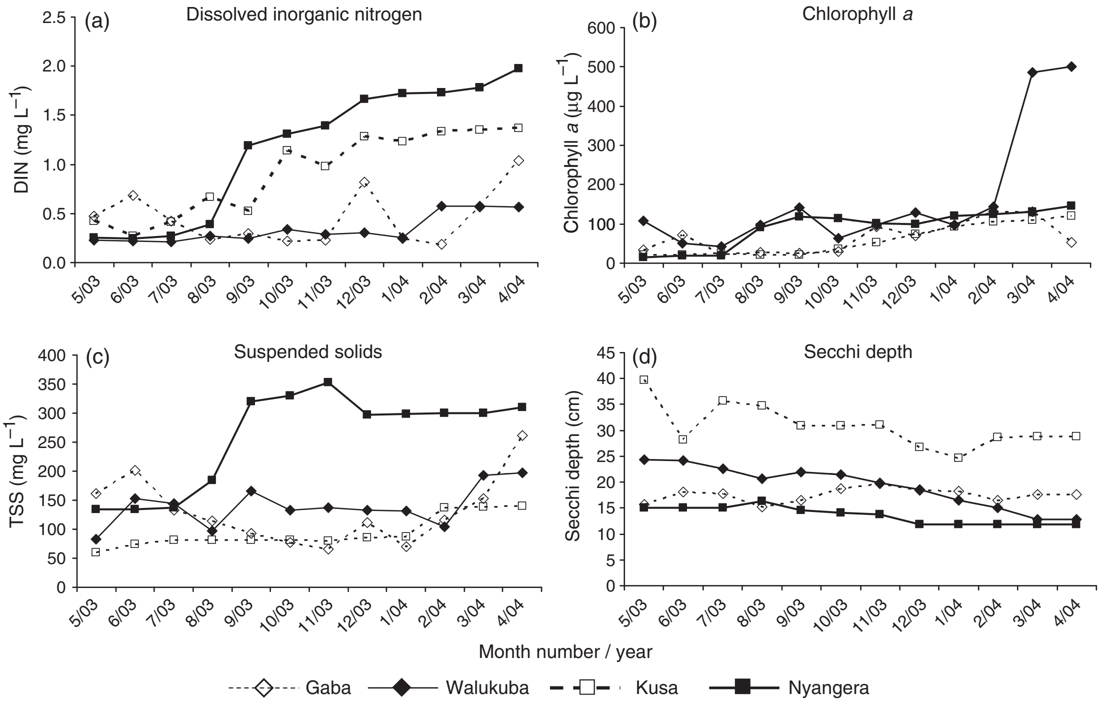

Figure 2 Observed water quality trends in the four Fingerpond locations, May 2003–April 2004.

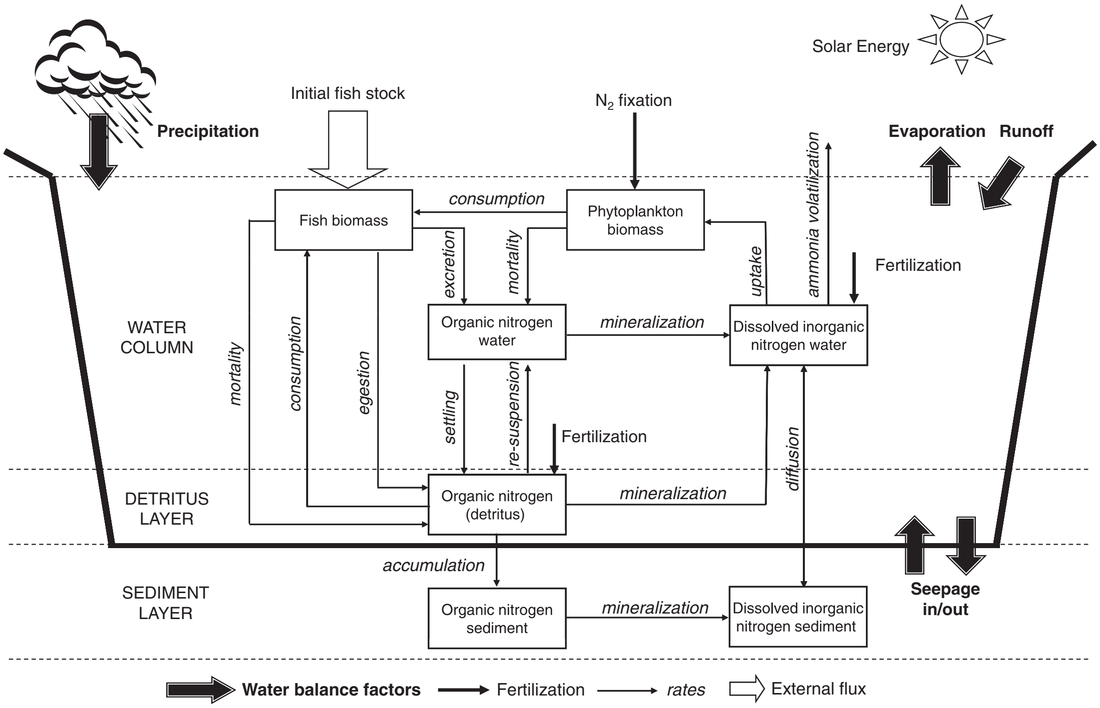

Figure 3 Conceptual model showing main nitrogen and water stocks and flows within a Fingerpond. Divisions between atmosphere, water, detritus and sediment layers are represented by dotted lines. Also indicated are water balance factors (shaded block arrows), fish stocking (open block arrow), fertilization (bold arrows) and nitrogen conversion processes (thin arrows). Denitrification was not included in the model. In the simulation model, fish were separated into adults and fingerlings.

Nitrogen fixation has been considered negligible in other studies (El Samara & Oláh 1979; Lin, Tansakul & Apihapath 1988) but in this study N:P ratios were low (< 7). Coupled with high densities of Cyanobacteria (including those with heterocysts like *Anabaena circinalis*), these conditions favoured N fixation and a rate equation for N fixation was added to the model, contributing to the phytoplankton biomass. All N was assumed to be in organic (ON) or in dissolved inorganic form (DIN, the sum of ammonia and NO_3-N; nitrite was below detectable limits). The model was made up of three modules: hydrology, phytoplankton–water–detritus–sediment and fish (Fig. 4).

Hydrology module

The hydrology module was based on the water balance model for Fingerponds in Kenya by Kipkemboi, Van Dam and Denny (2007) (Fig. 4a). Water levels were measured daily using a staff gauge installed at the midpoint of one length side of each pond. Evaporation was estimated from the Class 'A' pan evaporation using a pan coefficient of 0.81 (Boyd 1985) after correction for rainfall on rainy days. Rainfall was determined daily at 09:00 hours using a rain gauge stationed 5 m away from the second pond at each location. Groundwater levels were measured from five piezometers (wells) set along a transect at the second pond of each location (see Kaggwa 2006; Kipkemboi 2006 for details). Tables with daily evaporation, precipitation and groundwater measurements for a given site were included in the model as driving variables. Runoff was calculated from the precipitation and the maximum infiltration rate ($\mathrm{mm\,day^{-1}}$) using the curve number method and curve number 90 (U.S. Soil Conservation Service 1972) as in Kipkemboi, Van Dam, Mathooko *et al.* (2007). Seepage was calculated from measured groundwater levels using an empirical linear relationship between ground water level and seepage.

Phytoplankton–water–detritus–sediment module

This module included six state variables: phytoplankton biomass (N_{phyto}), dissolved inorganic nitrogen in

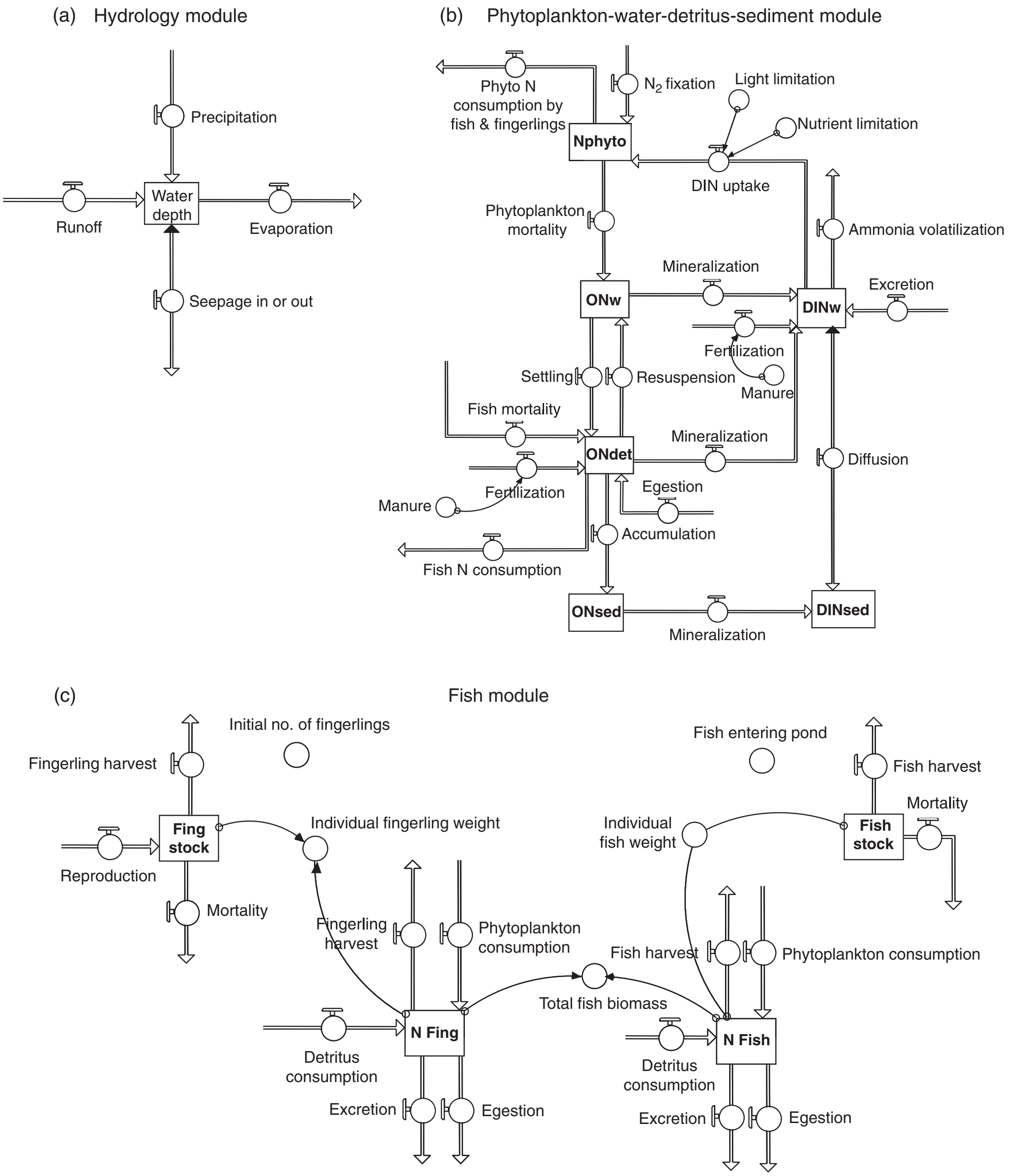

Figure 4 Relational diagrams for sub-modules. (a) Hydrology. Changes in water depth were calculated from the difference between precipitation, runoff and seepage into the pond, and evaporation and seepage out of the ponds; (b) Phytoplankton–water–detritus–sediment; and (c) Fish module. All state variables were expressed in g N, either as dissolved inorganic nitrogen (DIN) or organic nitrogen (ON) or nitrogen (N) contained in N_{phyto} (phytoplankton), N_{fing} (fingerlings), N_{fish} (adult fish). Other suffixes: sed (sediment), det (detritus), w (water). Diagrams modified from STELLA, version 8 (High Performance Systems).

the water column (DIN_w), organic nitrogen in the water column (ON_w), organic nitrogen in detritus (ON_{det}), organic nitrogen in the sediment and dissolved inorganic nitrogen in the sediment (DIN_{sed}) (Fig. 4b).

Phytoplankton growth rate can be modelled using the logistic equation

$$\frac{dN_{phyto}}{dt} = r_{phyto} \times N_{phyto}\left(1 - \frac{N_{phyto}}{N_{phyto,max}}\right) \qquad (1)$$

or

$$\frac{\mathrm{dN_{phyto}}}{\mathrm{d}t} = r_{\mathrm{phyto}} \times \mathrm{N_{phyto}} - K_{\mathrm{mor,phyto}} \times \mathrm{N_{phyto}^2} \quad (2)$$

in which $\mathrm{N_{phyto}}$ is the phytoplankton biomass (in g N), r_{phyto} is the maximum N uptake rate and $K_{\mathrm{mor,\,phyto}}$ is the mortality coefficient (equivalent to $r_{\mathrm{phyto}}/\mathrm{N_{phyto,\,max}}$). The first term of Eq. (2) represents N uptake, and the second term represents mortality. Light and N limitation were added to Eq. (2) by applying a Michaelis–Menten equation:

$$\frac{\mathrm{dN_{phyto}}}{\mathrm{d}t} = r_{\mathrm{phyto}} \times \mathrm{N_{phyto}} \times \left(\frac{I_{\mathrm{Z}}}{I_{\mathrm{Z}} + K_{light}}\right) \times \left(\frac{\mathrm{C_{DIN_w}}}{\mathrm{C_{DIN_w}} + K_{\mathrm{DIN}}}\right) - K_{\mathrm{Mor,phyto}} \times \mathrm{N_{phyto}^2} \quad (3)$$

in which I_z is the light intensity (irradiance) at pond depth z ($\mu\mathrm{E\,m^{-2}\,s^{-1}}$), K_{light} is the half saturation constant for light ($\mu\mathrm{E\,m^{-2}\,s^{-1}}$), $\mathrm{C_{DIN_w}}$ is the concentration of DIN in the water (in $\mathrm{g\,m^{-3}}$) and K_{DIN} is the half saturation constant for DIN uptake ($\mathrm{g\,m^{-3}}$). In 'Results', $[1 - I_{\mathrm{Z}}/(I_{\mathrm{Z}}+K_{\mathrm{light}})]$ and $[1 - \mathrm{C_{DIN_w}}/(\mathrm{C_{DIN_w}} + K_{\mathrm{DIN}})]$ are referred to as the light and nutrient limitation factor respectively. In the model, light intensity was computed based on the Beer–Lambert law from measured light intensity at the sites.

Dissolved inorganic nitrogen in the water column was produced by mineralization of ON in the water and detritus, diffusion from the sediment and from fertilization. Fertilization was computed from the manure application rate and the N content of the manure, assuming that a proportion of the manure contributed to $\mathrm{DIN_w}$ and the rest to $\mathrm{ON_{det}}$. Dissolved inorganic nitrogen in the water column disappeared through uptake by phytoplankton [Eq. (3)], ammonia volatilization and diffusion to the sediment. Dissolved inorganic nitrogen (ammonia) volatilization was modelled as a first-order process:

$$\mathrm{DIN_{volatilization}} = k_{\mathrm{volat}} \times \mathrm{C_{DIN_w}} \quad (4)$$

in which k_{volat} is the first-order rate constant for volatilization of ammonia N. Diffusion was modelled according to Fick's second law (Jamu & Piedrahita 2002; Jiménez-Montealegre *et al.* 2002):

$$\mathrm{DIN_{diffusion}} = K_{\mathrm{diff}} \times P \times \left(\frac{\mathrm{C_{DIN_w}} - \mathrm{C_{DIN_{sed}}}}{D}\right) \times A \quad (5)$$

in which K_{diff} is the diffusion coefficient for DIN (in $\mathrm{m^2\,day^{-1}}$), P is the porosity of the soil (dimensionless), $\mathrm{C_{DIN_w}}$ and $\mathrm{C_{DIN_{sed}}}$ are the concentrations of DIN in the water column and pore water, respectively, D is the sediment depth (m) and A is the pond surface area ($\mathrm{m^2}$).

Changes in $\mathrm{ON_w}$ were calculated as the difference between phytoplankton mortality (contributing dead algal matter to the $\mathrm{ON_w}$), re-suspension of $\mathrm{ON_{det}}$, settling of $\mathrm{ON_w}$ to the detritus layer and mineralization of $\mathrm{ON_w}$ to $\mathrm{DIN_w}$. All these rates were modelled as first-order equations.

Changes in $\mathrm{ON_{det}}$ were computed as the difference between settling, fish mortality, fertilization and egestion by fish (all contributing to production of $\mathrm{ON_{det}}$), and re-suspension, consumption by fish, accumulation of ON in the sediment and mineralization to $\mathrm{DIN_w}$ (all contributing to disappearance of $\mathrm{ON_{det}}$). For a description of fish mortality, egestion and consumption, see 'Fish module'. Mineralization and accumulation were described as first-order processes.

Organic nitrogen in the sediment was modelled as the balance of accumulation from $\mathrm{ON_{det}}$ and mineralization to DIN in the sediment pore water ($\mathrm{DIN_{sed}}$), both as first-order processes. Dissolved inorganic nitrogen in the pore water ($\mathrm{DIN_{sed}}$) was assumed to diffuse to and from the water column. Loss of DIN from the pore water through seepage was calculated from the seepage rate in the hydrology module and the concentration of $\mathrm{DIN_{sed}}$.

Fish module

In the fish module, a distinction was made between fish entering the pond with the flood, and fingerlings originating from fish reproducing within the ponds after the start of the culture period (Fig. 4c). The fish module consisted of four state variables: fish biomass ($\mathrm{N_{fish}}$, in g N), fingerling biomass ($\mathrm{N_{fing}}$, in g N), number of fish ($\mathrm{Stk_{fish}}$) and number of fingerlings ($\mathrm{Stk_{fing}}$).

It was assumed that after an initial stocking of the fish by the flood, the number of fish decreased through fish loss and mortality according to a first-order equation. From the total number of fish, the number of mature fish was calculated by assuming that the individual fish weight in the population was normally distributed with an average weight (W_{fish}) and a standard deviation ($\mathrm{SD_{fish}}$). If the weight at first maturity was $W_{\mathrm{fish,\,mat}}$, then the normal deviate Z was calculated as

$$\mathrm{Z} = \frac{\mathrm{abs}(W_{\mathrm{fish,mat}} - W_{\mathrm{fish}})}{\mathrm{SD_{fish}}} \quad (6)$$

From Z, the area under the normal curve can be derived (Snedecor & Cochran 1980) and the proportion of immature fish ($\mathrm{Prop}_{\mathrm{NotMat}}$) was calculated as

$$\mathrm{Prop}_{\mathrm{NotMat}} = \mathrm{IF}\left(W_{\mathrm{fish}} < W_{\mathrm{fish,mat}}\right)\mathrm{THEN}\ (\mathrm{Anc} + 0.5)\mathrm{ELSE}(0.5\mathrm{Anc}) \tag{7}$$

in which Anc is the area under the normal curve. The number of immature fish was then calculated by multiplying $\mathrm{Prop}_{\mathrm{NotMat}}$ with the total number of fish.

Changes in fish biomass ($\mathrm{N}_{\mathrm{fish}}$) were modelled as the difference between consumption of phytoplankton and detritus and egestion, excretion and mortality (van Dam & Verdegem 2005). Feed intake by an individual fish was expressed with a logistic equation:

$$\text{Feed intake} = r_{\mathrm{fish}} \times W_{\mathrm{fish}} \times \left(1 - \frac{W_{\mathrm{fish}}}{W_{\mathrm{fish,max}}}\right) \tag{8}$$

in which r_{fish} is the dry matter feed intake of the fish (day^{-1}), W_{fish} is the average individual fresh weight of the fish (g) and $W_{\mathrm{fish,\,max}}$ is the maximum individual weight of the fish in the population (g). The model computes W_{fish} by dividing total fish biomass by the number of fish. Total consumption of the fish stock (in $\mathrm{g\,N\,day}^{-1}$) was expressed as

$$\mathrm{N}_{\mathrm{consfish}} = r_{\mathrm{fish}} \times W_{\mathrm{fish}} \times \left(1 - \frac{W_{\mathrm{fish}}}{W_{\mathrm{fish,max}}}\right) \times \mathrm{Stk}_{\mathrm{fish}} \times \mathrm{C}_{\mathrm{feedN}} \tag{9}$$

in which $\mathrm{C}_{\mathrm{feedN}}$ is the N content of the feed (% dry matter).

In the model, the total consumption by fish was divided among the phytoplankton and the detritus. It was assumed that tilapia prefer phytoplankton and switch to detritus when the concentration of phytoplankton drops. This was achieved by relating the proportion of phytoplankton in the diet to the concentration of Chl *a* applying a Michaelis–Menten equation:

$$\mathrm{Prop}_{\mathrm{Phyto,Diet}} = \mathrm{Prop}_{\mathrm{Phyto,Diet,max}} \times \frac{C_{\mathrm{chl}\,a}}{C_{\mathrm{chl}\,a} + K_{\mathrm{chl}\,a,\mathrm{fish}}} \tag{10}$$

in which $C_{\mathrm{chl}\,a}$ is the concentration of Chl *a* and $K_{\mathrm{chl}\,a,\,\mathrm{fish}}$ is the half saturation constant for phytoplankton uptake by fish. The proportion of detritus in the diet was then calculated as

$$\mathrm{Prop}_{\mathrm{DetrDiet}} = 1 - \mathrm{Prop}_{\mathrm{PhytoDiet}} \tag{11}$$

Egestion and excretion were computed from the consumption rate assuming that the N assimilation percentage (digestibility) was constant and that a fixed percentage of the assimilated N was excreted:

$$\mathrm{N}_{\mathrm{egestion}} = \mathrm{N}_{\mathrm{consfish}} \times (1 - DC) \tag{12}$$

$$\mathrm{N}_{\mathrm{excretion}} = \mathrm{N}_{\mathrm{consfish}} \times DC \times \mathrm{Excr} \tag{13}$$

in which *DC* is the N digestibility coefficient and Excr is the proportion of digested N that is excreted.

The number of fingerlings ($\mathrm{Stk}_{\mathrm{fing}}$) was computed from the difference between the reproduction rate and the fingerling mortality rate. Reproduction rate was formulated as

$$\text{Reprod rate} = \frac{\mathrm{Stk}_{\mathrm{fish,mat}} \times \mathrm{Fec} \times \mathrm{SexRat}}{\mathrm{SpawnInt}} \tag{14}$$

in which Fec is the fecundity (no. of surviving fry per female per spawn), SexRat is the sex ratio of the fish (expressed as the number of females divided by the total number of fish) and SpawnInt is the spawning interval (day).

Fingerling growth rate, egestion and excretion were modelled as for fish. However, fingerling individual weight was assumed to be constant. This meant that any change in fingerling biomass was a result of changes in the numbers of fingerlings.

Model implementation and parameterization

The model was implemented in STELLA 8.0 for Windows (High Performance Systems, Hanover, NH, USA) with rectangular integration and a time step of 1/32 day. Parameter values (Table 2) were derived from field observations and measurements (pond hydrology, light extinction coefficient, DIN, Chl *a* concentrations and fish growth and yield), by calibration of the model or from literature the on similar models (mainly Jamu 1998; Jiménez-Montealegre 2001; Jiménez-Montealegre *et al.* 2002; van Dam & Verdegem 2005).

The model was initialized using data from the experiments (Table 3). Manure input rate was $20\,\mathrm{kg}\ 2\ \mathrm{weeks}^{-1}\mathrm{pond}^{-1}$, manure N content 2.3% in dry matter, initial fish density $1\,\mathrm{m}^{-2}$, sex ratio 1:1, and no harvesting was performed during the culture period. Two versions of the model were used: one for a lake floodplain pond (culture period 300 days) and another for a river floodplain pond (decreasing water level and culture period 200 days). Monthly mean water quality values of the ponds in each location were used for model calibration. The relationship between groundwater level and seepage was calibrated to the actual water levels in Gaba (lake-dependent pond) and Kusa (river-dependent pond). The uptake/consumption rates of phytoplankton and the food consumption rates of fish were then adjusted to give levels of DIN, Chl *a* and fish biomass that resembled the observations in the experimental ponds as much as possible.

Table 2 Parameters used in the model

Component	Parameter	Name	Unit	Value	Remarks
Phytoplankton	Maximum phytoplankton DIN uptake rate	r_{phyto}	day^{-1}	2	C
	Half saturation constant DIN limitation	K_{DIN}	g m^{-3}	0.7	Chen and Orlob (1975)
	Half saturation constant light limitation	$K_{\text{light lim}}$	dL	200	C
	Extinction coefficient non algal	$K_{\text{non-algal}}$	dL	5*, 3†	C
	Mortality rate constant	$K_{\text{mort phyto}}$	g N day^{-1}	0.005	Jamu (1998), Jiménez-Montealegre (2001)
	Nitrogen fixation coefficient	K_{Nfix}	g N day^{-1}	0.0009	C
	Phytoplankton Chlorophyll *a* content	$\text{Phyto}_{\text{Chl } a}$	$\text{g Chl } a\ (\text{g dm})^{-1}$	0.01	F
	Phytoplankton N content	Phyto_{N}	g N (g dm)^{-1}	0.08	van Dam and Verdegem (2005)
Detritus	First-order mineralization rate constant ON_{w}	$\text{K min ON}_{\text{w}}$	day^{-1}	0.01	C
	First-order mineralization rate constant ON_{det}	$\text{K min ON}_{\text{det}}$	day^{-1}	0.003	C
	First-order mineralization rate constant ON_{sed}	$\text{K min ON}_{\text{sed}}$	day^{-1}	0.001	C
	First-order settling rate constant	K_{sett}	g N day^{-1}	0.005	C
	First-order resuspension rate constant	K_{resus}	g N day^{-1}	0.0025	C
	First-order sediment accumulation coefficient	K_{accum}	g N day^{-1}	0.00525	C
	Detritus density	$\text{Initial}_{\text{det density}}$	g N m^{3}	0.3	F
	Detritus N content	$\text{ON}_{\text{det ini}}$	g N	0.04	van Dam and Verdegem (2005)
DIN	Diffusion coefficient for DIN	K_{diff}	$\text{m}^{2}\text{ day}^{-1}$	0.002	Jamu (1998), Jiménez-Montealegre (2001)
	First-order ammonia volatilization coefficient	K_{volat}	g N day^{-1}	0.038	C
	Critical dissolved inorganic nitrogen in water	$\text{DIN}_{\text{w crit}}$	g m^{-3}	0.1	Delincé (1992)
Fish	Fish weight at first maturity	W_{mat}	g	50	de Graaf (2004)
	Standard deviation fish weight	Sigma_{W}	dL	15	F
	Weight at infinity	W_{inf}	g	500	C
	Fecundity	Fe	dL	25	C
	Spawn interval	Spawn_{nt}	d	30	C
	Sex ratio	Sex_{at}	dL	0.5	F
	Fish dry matter total feeding level	$\text{FL}_{\text{dm fish}}$	dL	0.009	C
	Half saturation constant Chl *a* in diet	$\text{K}_{\text{Chl } a \text{ fish diet}}$	dL	50	C
	Maximum proportion phytoplankton in diet	$\text{Max}_{\text{prop phyto fish diet}}$	dL	0.75	C
	Digestiblity coefficient	DC	dL	0.5	Gangadhar *et al.* (2004)
	Nitrogen excretion rate as proportion of digested nitrogen	$\text{N}_{\text{excretion}}$	dL	0.3	Oh *et al.* (2001)
	Mortality rate constant	$\text{K}_{\text{mort fish}}$	g N day^{-1}	0.0006	F
Fingerlings	Fingerling dry matter total feeding level	$\text{FL}_{\text{dm fing}}$	dL	0.048	C
	Half saturation constant Chl *a* in diet	$\text{K}_{\text{Chl } a \text{ fish diet}}$	dL	0.5	C
	Maximum proportion phytoplankton in diet	$\text{Max}_{\text{prop phyto fing diet}}$		0.5	C
	Mortality rate constant	$\text{K}_{\text{fing mort}}$	g N day^{-1}	0.015	C
Light	Irradiance standard deviation	Irrad_{SD}	dL	280	F
Hydrology	Maximum filtration rate	Max_{FR}	mm day^{-1}	28.2*, 25.1†	C
	Critical depth	$\text{Crit}_{\text{depth}}$	mm	300	F
Soil	Soil porosity	P	dL	0.8	Jiménez-Montealegre (2001)
	Sediment depth	D	m	0.15	Jiménez-Montealegre (2001)

Unless indicated values were based on estimates from own observations.

*Lake-dependent ponds and

†River-dependent ponds.

**Value computed from ranges given.

C, calibration; F, estimated from field measurements; dL, dimensionless; DIN, dissolved inorganic nitrogen.

Table 3 Initial conditions of simulations (dL denotes dimensionless)

Variable	Name	Unit	Value
Organic nitrogen in water dry matter density	$ON_{w\ dm\ density}$	$g\,N\,dm\,m^{-3}$	0.5
Detritus density	$Det_{density}$	$g\,N\,dm\,m^{-3}$	0.3
Dissolved inorganic nitrogen in water	C_{DINw}	$g\,N\,m^{-3}$	0.471
Individual fingerling stocking weight	$Fing_W$	g	1
Individual stocking fish weight	$Fish_W$	g	30
Number of fingerling stocking pond	Fing no.	dL	200
Organic nitrogen in water	ON_{sed}	$g\,N\,m^{-3}$	3
Phytoplankton chlorophyll *a*	$Initial_{phyto\ Chl\ a}$	$\mu g\,L^{-1}$	34.4
Pond water depth	$Initial_{pondw\ depth}$	mm	720

Results

Hydrology

The lake floodplain pond did not dry up while the water levels in the river floodplain pond began to drop after 20 days, reaching the critical pond water depth (0.3 m) by the end of the culture period of 200 days. The lake pond had higher and more constant precipitation and lower evaporation than the river pond leading to a more constant water level. However, seepage rates were higher in the lake pond. For both pond types, a linear relationship between groundwater level and seepage was used, with low groundwater levels leading to seepage out of, and high groundwater levels to seepage into the pond. With this relation, the models were able to mimic the average water levels in the two pond types (Fig. 5).

Phytoplankton, water, detritus and sediment

In the model for the lake-dependent pond, simulated Chl *a* in the water column increased to about 75 g m^{-3} at the end of the culture period. This was lower than the Chl *a* observed in the ponds (about 120 g m^{-3}; Fig. 6a). The river pond model showed increasing Chl *a* levels (Fig. 6b) to about 145 g m^{-3} at the end of the culture period (higher than measurements of about 95 g m^{-3}). Simulated DIN_w in the lake pond increased to about 1.3 g m^{-3} on day 230, after which it declined to 0.9 g m^{-3}. A fluctuating level of 0.2–0.7 g m^{-3} was measured (Fig. 6c). Dissolved inorganic nitrogen in the water column concentrations in the lake pond model steadily increased between 0.25 and 0.60 g m^{-3} while measurements fluctuated between 0.28 and 0.78 (Fig. 6d).

In the model of the lake-dependent pond, the light limitation factor increased from about 0.4–0.6, suggesting a slight increase in light limitation. Nutrient limitation decreased in this pond, as shown by the decrease in nutrient limitation factor from about 0.9 to a value of 0.4 (Fig. 7a). In the river pond, light limitation was less severe than in the lake pond with values of the limitation factor between 0.2 and 0.1. Nutrient limitation in the river pond was strong in the beginning (0.94) but decreased towards the end of the culture period (0.72; see Fig. 7b). In both models, an increase in ON_w (to about 16 and 25 g N m^{-3} in the lake and river pond respectively) and detritus (to 34 and 25 g N m^{-2}, respectively, at the end of the period) was simulated (Fig. 7c and d).

Fish

The simulated number of fish reduced steadily in both pond types due to mortality (Fig. 8a and b). In both models, all fish were mature after about 170 days. The simulated number of fingerlings increased to 4392 and 3818 per 192 m^2 pond at the end of the culture period in the lake pond and river pond model respectively. Individual weight at the end of the culture period of the stocked fish was 181 g (lake-dependent pond) and 100 g (river-dependent pond). Total simulated fish yields were 2625 and 1492 kg ha^{-1} respectively. In the lake pond, this yield consisted of roughly equal biomasses of fish and fingerlings (about 25 000 g each). In the river pond, there was more adult fish (some 17 000 g) than fingerlings (11 600 g).

The proportion of phytoplankton in the diet of the adult fish and fingerlings increased from about 0.25 and 0.17 in the beginning, to about 0.46 and 0.30 at the end of the culture period in the lake pond model (Fig. 8c). In the river pond, the proportion of phytoplankton in the diet increased during the culture period from 0.22 to 0.56 for the adult fish and from 0.15 to 0.37 for the fingerlings (Fig. 8d). The total uptake of N by fingerlings at the end of the culture period was about double that of the adult fish in the lake pond. In the river pond, fingerlings consumed 2.3 times the amount of N that the adult fish consumed.

Nitrogen budgets and flows

Total N input was 10 727 and 7087 g for the lake-dependent and river-dependent pond respectively

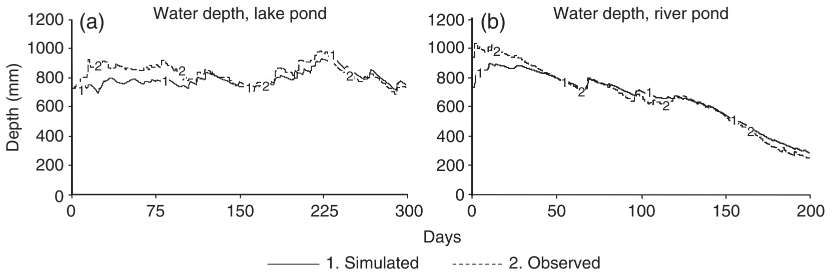

Figure 5 Simulated and observed pond water depth over the period of May 2003–April 2004 for lake-dependent (a) and river-dependent (b) Fingerponds.

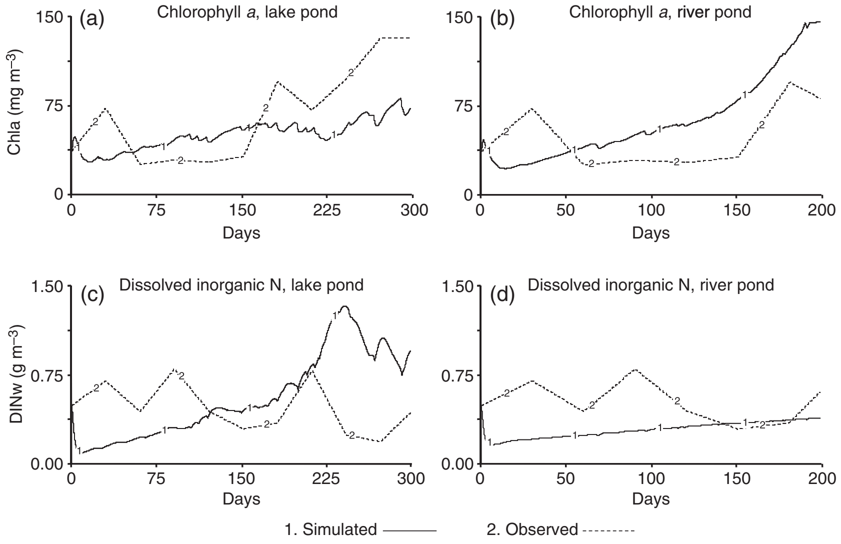

Figure 6 Simulated and observed Chlorophyll *a* (Chl *a*, in mg m^{-3}) and dissolved inorganic nitrogen (DIN, in g m^{-3}) in the water column.

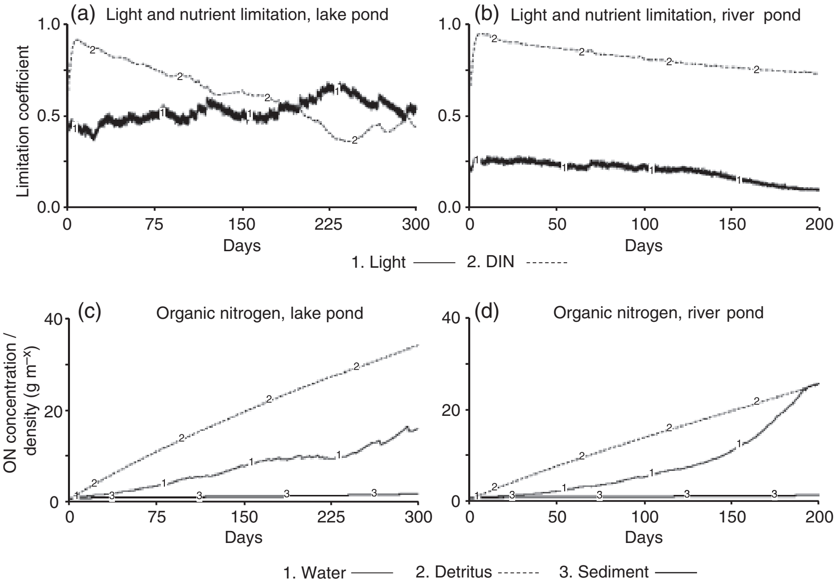

Figure 7 Simulated light and dissolved inorganic nitrogen (DIN) limitation and results for organic nitrogen (ON) in water (g m^{-3}), detritus and sediment (g m^{-2}).

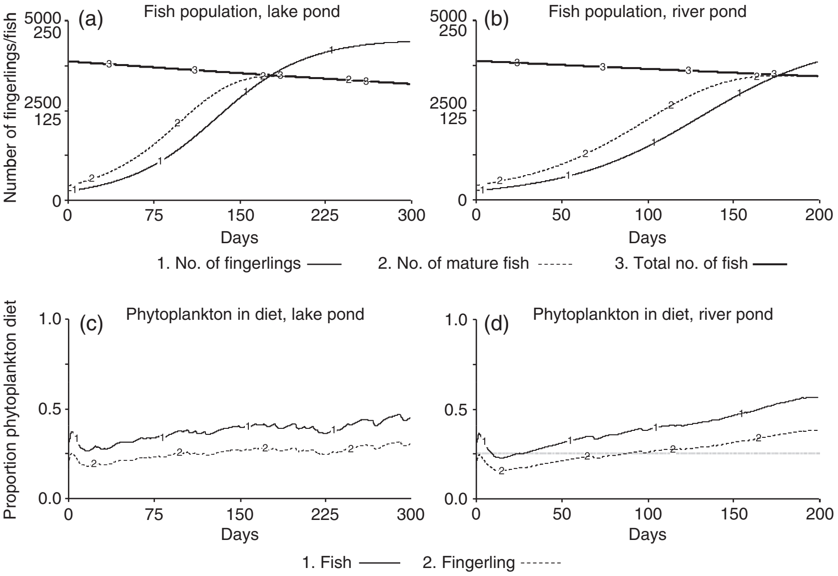

Figure 8 Simulated fingerling and fish numbers (a, b) and proportion of phytoplankton in fish and fingerling diets (c, d) in lake-dependent and river-dependent Fingerpond.

(Table 4). The majority of this input came from the manure, of which 95% was assumed to contribute directly to the ON in the detritus. Nitrogen fixation provided 8.1 and 7.3% (lake and river pond) of the N input, resulting in a flow of 15.1 and 13.4 mg N m^{-2} day^{-1} in both ponds (Table 5). This is within the range of 6–57 mg N m^{-2} day^{-1} for N fixation reported in the literature (Schroeder 1987; Lin *et al.* 1988; Acosta-Nassar, Morell & Corredor 1994).

The major part of N input accumulated in detrital ON at the pond bottom (60.2% and 68.3% for the lake and river pond respectively) and in the water column (just over 20% in both pond types). The slightly lower accumulation in the lake pond was related to the higher simulated DIN concentration in this pond, which led to higher volatilization loss. Volatilization rates reported in the literature range from 0.5 to about 50 mg N m^{-2} day^{-1} (Schroeder 1987; Abdallah, Mcnabb & Batterson 1996; Gross, Boyd & Wood 2000) and the rates calculated by the model fall within this range (9.64 and 3.12 mg N m^{-2} day^{-1}; Table 5). Because of the higher seepage in the lake pond, DIN loss through seepage was higher here (1.5% of N input versus 0.3% in the river pond).

Total N assimilation by phytoplankton (DIN uptake plus N fixation) in the models was 133 and 105 mg N m^{-2} day^{-1} in the lake-dependent and river-dependent ponds, respectively, which was below the range reported for temperate fishponds (150–450 mg N m^{-2} day^{-1}) and much lower than rates reported for productive tropical ponds (750–1500 mg N m^{-2} day^{-1}; Hargreaves 1998). Of the total N input, 10.5% and 8.2% ended up in fish biomass in the lake and river model, respectively, of which slightly more than half was in fingerling biomass.

Table 4 Nitrogen balance for the lake-dependent and river-dependent ponds over the whole culture period as calculated by the model (for more explanation, see text)

	Lake pond (300 days)		River pond (200 days)	
Variable	g N	% of total input	g N	% of total input
Total ON fertilization	9364	87.3	6243	88.1
Total DIN fertilization	493	4.6	329	4.6
Total N fixation	869	8.1	516	7.3
Total N import	10 727		7087	
Ammonia volatilization	555	5.2	120	1.7
DIN seepage	88	0.8	11	0.2
Total N export	643		131	
Phytoplankton	43	0.4	29	0.4
Fish	514	4.8	287	4.1
Fingerlings	613	5.7	290	4.1
DIN$_{w}$	80	0.7	− 44	− 0.6
DIN$_{sed}$	7	0.1	− 2	0.0
ON$_{w}$	2196	20.5	1464	20.7
ON$_{det}$	6459	60.2	4843	68.3
ON$_{sed}$	171	1.6	89	1.3
Total N storage	10 084		6956	

ON, organic nitrogen; DIN, dissolved inorganic nitrogen; N, nitrogen; DIN$_{w}$, dissolved inorganic nitrogen in the water column; DIN$_{sed}$, dissolved inorganic nitrogen in the sediment; ON$_{w}$, organic nitrogen in the water column; ON$_{det}$, organic nitrogen in detritus; ON$_{sed}$, organic nitrogen in the sediment.

Table 5 Average nitrogen flows (in mg N m^{-2} day^{-1}) for a lake-dependent and river-dependent pond as calculated by the model for a culture period of 300 and 200 days respectively

Process	Lake pond (GB)	River pond (KS)
DIN uptake by phytoplankton	117.9	91.9
Consumption		
Of phytoplankton by fish	15.6	13.7
Of phytoplankton by fingerlings	22.9	17.7
Of detritus by fish	13.0	10.0
Of detritus by fingerlings	32.8	20.8
Egestion		
By fish	14.3	11.9
By fingerling	27.8	19.2
Excretion		
By fish	4.3	3.6
By fingerlings	8.4	5.8
Mortality		
Of fish	1.1	0.8
Of fingerlings	8.9	5.9
Of phytoplankton	93.8	73.1
Diffusion		
Into sediment	1.0	<0.01
Into water column	0.1	0.3
Mineralization		
In water	53.5	35.9
From detritus	55.2	39.8
From sediment	0.7	0.6
Resuspension	46.0	33.2
Settling	48.1	32.3
Accumulation	3.7	2.9
Ammonia volatilization	9.6	3.1
DIN seepage	1.5	0.3
Nitrogen fixation	15.1	13.4
N input from fertilizer		
ON into detritus	162.6	162.6
DIN into water	8.6	8.6

ON, organic nitrogen; DIN, dissolved inorganic nitrogen.

Discussion

The model was developed with data from two sets of ponds in Uganda and Kenya and captures the factors that determine the productivity of Fingerponds in one quantitative framework. There are several uncertainties about parameter values and the model was not validated with independent data. For now, this limits the interpretation and use of the model for practical purposes like pond management or detailed water quality prediction. However, calibration of the model to the observed water levels (Fig. 5), Chl *a* and DIN concentrations (Fig. 6) and fish yields ensured that the simulations were realistic representations of the pond system. In this way, the model contributes to an improved understanding of these complex systems and helps to identify options for improved management.

The model was based on the assumption that only *Oreochromis* species stocked Fingerponds. Initial censuses showed that several other fish species were present, such as haplochromines, clariids and *Protopterus aethiopicus*, but these generally represented $<10\%$ of the number stocked (Pokornŷ *et al.* 2005; Kaggwa *et al.* 2009). While *Oreochromis* juveniles are omnivorous, feeding on algae, zooplankton and insect larvae (Tudorancea, Fernando & Paggi 1988), adults feed on phytoplankton, detritus or periphyton (Jauncey & Ross 1982; Getachew 1987). Stomach content analysis of adult fish showed that detritus constituted the bulk of the fish diet (Kaggwa *et al.* 2009) and similar diets for tilapias in natural ecosystems were reported (e.g., Tadesse 1999). Tilapias are opportunistic and versatile in their choice of food and shift to other food resources when certain foods are scarce. The modelled diet of phytoplankton and detritus was therefore realistic. Detritus is a mix of low-quality organic matter (including dead phytoplankton) and more nutritious heterotrophic microorganisms and macroinvertebrates. In the model, detritus was assumed to have a lower N content than phytoplankton and therefore resulted in slower fish growth.

The fingerlings exerted a high feeding pressure. In the model, higher proportions of phytoplankton in the fingerling diet [i.e., by increasing $Prop_{Phyto,\,Diet,\,max}$ in Eq. (10)] resulted in phytoplankton concentrations that were too low or even zero, especially towards the end of the culture period. The model suggests that as the culture period progressed, consumption by fingerlings was at least double that of the adult fish. This stresses the need to manage the fingerling density, which is a challenge because initial stocking densities in Fingerponds depend on natural flood events. Stock management was attempted through manual sexing and removal of fingerlings using traditional fishing methods, e.g. use of baskets and netting (Brummett 2002). Piscivorous fish, e.g. Clarias sp. can also be used as a means of reducing fingerlings (de Graaf, Galemoni & Banzoussi 1996). However, curbing recruitment in these systems proved very difficult (Kaggwa 2006; Kipkemboi 2006).

Light limitation was one of the main hindrances for higher primary production. Fingerponds are turbid, and one of the main differences between the lake-dependent and river-dependent ponds was the higher turbidity in the lake pond model. This was based on observations in Gaba, where high non-algal turbidity was observed (Kaggwa *et al.* 2009). The difference cannot be attributed conclusively to the difference in pond type but is probably caused by site-specific factors (e.g., soil type) and was incorporated in the model through the non-algal turbidity coefficient (Table 2). As a result, light limitation was stronger in the lake ponds. The model does not account for increased resuspension as a result of wind action. This may be an important cause of turbidity in Fingerponds, especially as water levels are reduced in the course of the culture period.

Fish and fingerling biomass accounted for 8–10% of the total N input. This is in the same range as that found in other manured fish ponds (Edwards 1993; Acosta-Nassar *et al.* 1994; Hargreaves 1998; Gross *et al.* 2000; Azim 2001). About half of this N was in fingerling biomass, again stressing the importance of fish reproduction in the functioning of the ponds. The ON input of up to 244 $\mathrm{mg\,N\,m^{-2}\,day^{-1}}$ from manure in the Fingerponds was lower than the normal range for semi-intensive fish ponds of 700–800 $\mathrm{mg\,N\,m^{-2}\,day^{-1}}$ (Schroeder *et al.* 1990; Knud-Hansen, McNabb & Batterson 1991). For Fingerponds, pond water levels determine the quantity of manure that can be added to these closed systems. While manuring had a positive effect on fish production in Fingerponds (Kaggwa *et al.* 2009), simulations with increasing manure applications suggested that applications over 30 kg per fortnight per pond did not further increase Chl *a* concentrations and did not have much effect on fish biomass. The model predicted maximum fish yields of 1500–2800 $\mathrm{kg\,ha^{-1}}$ for a 200–300-day culture period. This is close to the highest yield of 2670 $\mathrm{kg\,ha^{-1}}$ obtained in 310 days in Ugandan Fingerponds (Kaggwa *et al.* 2009) and similar to yields of 800–2000 $\mathrm{kg\,ha^{-1}\,year^{-1}}$ from comparable waste-fed polyculture systems (albeit with controlled stocking) elsewhere in Africa (e.g., Brummett & Noble 1995; Ofori, Asamoah & Prein 1996).

Nutrient limitation in the ponds is apparent, and with low N:P ratios particularly N is limiting. Towards the end of the culture period, DIN limitation decreased, partly as a result of the concentration of nutrients in low water levels. The quantity of N added to aquaculture ponds by fixation depends largely upon species composition of the phytoplankton community, presence of heterocystous cyanobacteria and ammonia concentration. We were not able to quantify the proportion of heterocystous cyanobacteria in the pond. With high ammonia concentrations, N_2 fixation is minimal (Lin *et al.* 1988). In view of the low N:P ratios and the presence of Cyanobacteria, N fixation may be more important than the model suggests. It is not clear if the assumption that denitrification losses from Fingerponds are negligible is reasonable. On average, DO concentrations in the ponds were not favourable for denitrification. This might change with cycles of natural flooding and subsequent drying out of ponds (i.e., of reduced and oxidized conditions) and the accumulation of organic matter. Dissolved inorganic nitrogen limitation can be lowered with higher N input but this effect is limited by the turbidity-induced light limitation. Mitigation of turbidity should be a priority for improving phytoplankton productivity in Fingerponds. This can be achieved by constructing ponds in sites with suitable soil and in such a way that water levels can be maintained as long as possible. This will also increase the success of periphyton substrates in Fingerponds (Kaggwa *et al.* 2006). Moreover, it will help to increase fish growth and prevent excessive reproduction. De Graaf *et al.* (1996) found that early breeding of Nile tilapia (*O. niloticus*) in ponds and stunting of somatic growth could be controlled by increasing the feed supply.

As in many other fishponds (Hargreaves 1998), most of the N input into Fingerponds ends up at the pond bottom. Organic N accumulation in detritus and sediment accounted for 60–70% of the total N in the pond systems. The accumulation of N at the pond bottom offers potential for the use of pond detritus and sediments as crop fertilizers in integrated production systems (Muendo, Stoorvogel, Verdegem, Gamal & Verreth 2007). In Fingerpond systems, these sediments were used effectively to fertilize the vegetable gardens on the pond banks (Kipkemboi, Van Dam, Ikiara *et al.* 2007) and contributed to the integration of the ponds with the agricultural component of the system. Aquaculture is frequently held responsible for considerable nutrient discharges into the environment (e.g., Edwards 1993). Fingerponds in their current form are an exception because of the relatively low external nutrient input and the natural hydrological regime. Nitrogen losses from Fingerponds through leaching were low because water level decrease was more due to evaporation than to seepage. When manure from local livestock is collected and used as a pond input, Fingerponds do not lead to additional nutrient inputs into the wetlands. Rather, the ponds serve to concentrate nutrients in the detritus and sediment, from where they can be utilized to enhance crop production. In this sense, Fingerpond systems could be used to increase the efficiency of nutrient and land use, increase food production intensity and contribute to a reduction of the widespread conversion of papyrus wetlands in East Africa for extensive crop production (Owino & Ryan 2007). A preliminary analysis showed that the environmental impact of Fingerponds is limited (Kipkemboi, Van Dam & Denny 2007). However, more large-scale introduction of Fingerponds should be accompanied with a thorough impact analysis and take a precautionary approach. Provided that the model is developed further and improved, it can be used as a supporting tool for the implementation and management of Fingerponds on a wider scale.

Fingerponds contribute to sustainable management of wetlands because they enhance fish production (and therefore contribute to the livelihoods of wetland communities) without negatively affecting the ecological and hydrological functioning of the wetlands through nutrient discharge or drainage. The downside of this is that fish production is variable (and therefore more risky for the fish farmer) because there is little control over fish stock and water supply. Further implementation and development of this technology can be supported by research into improved pond engineering to maintain sufficient water levels with naturally harvested water as long as possible. Also, the use of locally produced fish foods to increase somatic growth of fish and reduce reproduction should be explored.

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References

Abdallah A.A.F., McNabb C.D. & Batterson T.R. (1996) Ammonia dynamics in fertilized fish ponds stocked with Nile Tilapia. *The Progressive Fish-Culturist* **58**, 117–123.

Acosta-Nassar M.V., Morell J.M. & Corredor J.E. (1994) The nitrogen budget of a tropical semi-intensive freshwater fish culture pond. *Journal of the World Aquaculture Society* **25**, 261–270.

APHA (1995) *Standard Methods for Examination of Water and Wastewater*, 19th edn. American Public Health Association, Washington, DC, USA.

Azim M.E. (2001) *The potential of periphyton-based aquaculture production systems*. PhD thesis, Fish Culture and Fisheries Group, Wageningen Institute of Animal Sciences, Wageningen University, the Netherlands, 219pp.

Boyd C.E. (1972) Sources of CO_2 for nuisance blooms of algae. *Weed Science* **20**, 492–297.

Boyd C.E. (1985) Pond evaporation. *Transactions of the American Fisheries Society* **114**, 299–303.

Brummett R.E. (2002) Comparison of African tilapia partial harvesting systems. *Aquaculture* **214**, 103–114.

Brummett R.E. & Noble R. (1995) *Aquaculture for African smallholders. ICLARM Technical Report*, Vol. 46. ICLARM, Manila, Philippines, 69pp.

Chen C.W. & Orlob G.T. (1975) Ecologic simulation for aquatic environments. In: *Systems Analysis and Simulation in Ecology*, Vol. III (ed. by B.C. Patten), pp. 475–587. Academic Press, New York, NY, USA.

de Graaf G.J. (2004) Optimisation of the pond rearing of Nile Tilapia (*Oreochromis niloticus* L). The impact of stunting processes and recruitment control. *PhD thesis*. Wageningen University, Wageningen, the Netherlands, 167pp.

de Graaf G.J., Galemoni F. & Banzoussi B. (1996) Recruitment control of Nile tilapia, *Oreochromis niloticus*, by the African catfish, *Clarias gariepinus* (Burchell 1822), and the African snakehead, *Ophiocephalus obscuris*. I. A biological analysis. *Aquaculture* **146**, 85–100.

Delincé G. (1992) *The Ecology of the Fish Pond Ecosystem with Special Reference to Africa*. Kluwer Academic Publishers, Dordrecht, the Netherlands, 230pp.

Denny P., Kipkemboi J., Kaggwa R.C. & Lamtane H. (2006) The potential of fingerpond systems to increase food production from wetlands in Africa. *International Journal of Ecology and Environmental Sciences* **32**, 41–47.

Edwards P. (1993) Environmental issues in integrated agriculture-aquaculture and wastewater fed fish culture systems. In: *Environment and Aquaculture in Developing Countries. ICLARM Conference Proceedings* (ed. by R.S.V. Pullin, H. Rosenthal & J.H.L. Maclean), pp. 139–170. ICLARM, Manila, Philippines and GTZ, GmbH, Germany.

El Samara M.J. & Oláh J. (1979) Significance of nitrogen fixation in fish ponds. *Aquaculture* **18**, 367–372.

Gangadhar B., Keshavanath P., Ramesh T.J. & Priyadarshini M. (2004) Digestibility of bamboo grown periphyton by carps and tilapia. *Journal of Applied Aquaculture* **15**, 151–162.

Getachew T. (1987) A study on an herbivorous fish, *Orechromis niloticus* L., diet and its quality in two Ethiopian Rift Valley lakes, Awassa and Zwai. *Journal of Fish Biology* **30**, 439–449.

Green B.W., Phelps R.P. & Alvarenga H.R. (1989) The effect of manures and chemical fertilizers on the production of *Oreochromis niloticus* in earthen ponds. *Aquaculture* **76**, 37–42.

Gross A., Boyd C.E. & Wood C.W. (2000) Nitrogen transformations and balance in channel catfish ponds. *Aquacultural Engineering* **24**, 1–14.

Hargreaves J.A. (1998) Nitrogen biochemistry of aquaculture ponds. *Aquaculture* **166**, 181–212.

Jamu D.M. (1998) *Modelling organic matter and nitrogen dynamics in integrated aquaculture/agriculture systems: effects of cycling pathways on nitrogen retention and system productivity.* PhD thesis, University of California, Davis, USA.

Jamu D.M. & Piedrahita R.H. (2002) An organic matter and nitrogen dynamics model for the ecological analysis of integrated aquaculture/agriculture systems: I. model development and calibration. *Environmental Modelling and Software* **17**, 571–582.

Jauncey K. & Ross B. (1982) *A Guide to Tilapia Feeds and Feeding*. University of Sterling, Scotland, UK, 111pp.

Jiménez-Montealegre R., Verdegem M.C.J., van Dam A.A. & Verreth J.A.J. (2002) Conceptualization and validation of a dynamic model for the simulation of nitrogen transformations and fluxes in fish ponds. *Ecological Modelling* **147**, 123–152.

Jiménez-Montealegre R.A. (2001) *Nitrogen transformations and fluxes in fish ponds: a modeling approach.* PhD thesis, Wageningen University, the Netherlands, 185pp.

Kaggwa R.C. (2006) *Fingerponds: managing nutrients and primary productivity for enhanced fish production in Lake Victoria's wetlands, Uganda.* PhD thesis, UNESCO-IHE Institute for Water Education, the Netherlands, 202pp.

Kaggwa R.C., Kansiime F., Denny P. & van Dam A.A. (2005) A preliminary assessment of the aquaculture potential of two wetlands located in the northern shores of Lake Victoria, Uganda. In: *Natural and Constructed Wetlands: Nutrients, Metals and Management* (ed. by J. Vymazal), pp. 350–368. Backhuys Publishers, Leiden, the Netherlands.

Kaggwa R.C., Kasule D., van Dam A.A. & Kansiime F. (2006) An initial assessment of the use of wetland plants as substrates for periphyton production in seasonal wetland fishponds in Uganda. *International Journal of Ecology and Environmental Sciences* **32**, 63–74.

Kaggwa R.C., van Dam A.A., Balirwa J.S., Kansiime F. & Denny P. (2009) Increasing fish production from wetlands at Lake Victoria, Uganda using organically manured seasonal wetland fish ponds. *Wetland Ecology and Management* **17**, 257–277.

Kayombo S. & Jørgensen S.E. (2005) Lake Victoria - experience and lessons learned brief. In *Managing Lakes and their Basins for Sustainable use: a Report for Lake Basin Managers and Stakeholders*. International Lake Environment Committee Foundation, Kusatsu, Japan. Available at http://www.ilec.or.jp/eg/lbmi/pdf/27_Lake_Victoria_27February2006.pdf (accessed 4 May 2009).

Kipkemboi J. (2006) *Fingerponds: Seasonal integrated aquaculture in East African Fresh water wetlands. Exploring their potential for wetland wise-use strategies*. PhD thesis, UNESCO-IHE Institute for Water Education, the Netherlands, 168pp.

Kipkemboi J., van Dam A.A. & Denny P. (2006) Biophysical suitability of smallholder integrated aquaculture-agriculture systems (Fingerponds) in East Africa's Lake Victoria freshwater wetlands. *International Journal of Ecology and Environmental Sciences* **32**, 75–83.

Kipkemboi J., van Dam A.A. & Denny P. (2007) Smallholder integrated aquaculture (Fingerponds) in the wetlands of Lake Victoria, Kenya: assessing the environmental impacts with the aid of Bayesian networks. *African Journal of Aquatic Science* **32**, 219–234.

Kipkemboi J., van Dam A.A., Ikiara M.M. & Denny P. (2007) Integration of smallholder wetland aquaculture-agriculture systems (Fingerponds) into riparian farming systems at the shores of Lake Victoria, Kenya: socio-economics and livelihoods. *The Geographical Journal* **173**, 257–272.

Kipkemboi J., van Dam A.A., Mathooko J.M. & Denny P. (2007) Hydrology and the functioning of seasonal wetland aquaculture–agriculture systems (Fingerponds) at the shores of Lake Victoria, Kenya. *Aquacultural Engineering* **37**, 202–214.

Knud-Hansen C.F., McNabb C.D. & Batterson T.R. (1991) Application of limnology for efficient nutrient utilization in tropical pond aquaculture. *Verhandlungen des Internationalen Verein für Limnologie* **24**, 2541–2543.

Lin C.K., Tansakul V. & Apihapath C. (1988) Biological nitrogen fixation as a source of nitrogen input in fish ponds. In: *The Second International Symposium on Tilapia in Aquaculture. ICLARM Conference Proceedings*, Vol. 15 (ed. by R.S.V. Pullin, T. Bhukaswan, K. Tonguthai & J.L. Maclean), pp. 53–58.

Muendo P.N., Stoorvogel J.J., Verdegem M.C.J., Gamal E.N. & Verreth J.A.J. (2007) The role of fish ponds in farms' nutrient balances. In: *Fishponds in Farming Systems* (ed. by A.J. van der Zijpp, J.A.J. Verreth, L.Q. Tri, M.E.F. van Mensvoort, R.H. Bosma & M.C.M. Beveridge), pp. 125–133. Wageningen Academic Publishers, Wageningen, the Netherlands.

Ofori J.K., Asamoah A. & Prein M. (1996) Experiments for integrated agriculture aquaculture system design. In: *Research for the Future Development of Aquaculture in Ghana, ICLARM Conference Proceedings*, Vol. 42 (ed. by M. Prein, J.K. Ofori & C. Lightfoot), pp. 37–41. BMZ/GTZ, Bonn & Eschborn, Germany.

Oh S.Y., Jo J.Y., Park J., Noh K. & Kim I.B. (2001) *Effects of Body Weight, Ration Size and Dietary Protein Level on Ammonia Excretion and Faecal Production by Nile tilapia, Oreochromis niloticus. 6th Asian Fisheries Forum, Book of Abstracts.* Asian Fisheries Society, Manila, Philippines, 117pp.

Owino A.O. & Ryan P.G. (2007) Recent papyrus swamp habitat loss and conservation implications in western Kenya. *Wetland Ecology and Management* **15**, 1–12.

Pokornỳ J., Přikryl I., Faina R., Kansiime F., Kaggwa R.C., Kipkemboi J., Kitaka N., Denny P., Bailey R., Lamtane H.A. & Mgaya Y.D. (2005) Will fish pond management principles from the temperate zone work in tropical Fingerponds. In: *Natural and Constructed Wetlands: Nutrients, Metals and Management* (ed. by J. Vymazal), pp. 382–399. Backhuys Publishers, Leiden, the Netherlands.

Poole H.H. & Atkins W.R.G. (1929) Photo-electric measurements of submarine illumination throughout the year. *Journal of the Marine Biological Association of the UK* **16**, 297–324.

Scheren P.A.G.M., Zanting H.A. & Lemmens A.M.C. (2000) Estimation of water pollution sources in Lake Victoria, East Africa: application and elaboration of the rapid assessment methodology. *Journal of Environmental Management* **58**, 235–248.

Schroeder G.L. (1978) Autotrophic and heterotrophic production of microorganisms in intensely manured fish ponds, and related fish yields. *Aquaculture* **14**, 303–325.

Schroeder G.L. (1987) Carbon and nitrogen budgets in manured fish ponds on Israel's coastal plain. *Aquaculture* **62**, 259–279.

Schroeder G.L., Wohlfarth G., Alkon A., Helevy A. & Krueger H. (1990) The dominance of algal-based food webs in fish ponds receiving chemical fertilizers plus organic manures. *Aquaculture* **86**, 219–229.

Snedecor G.W. & Cochran W.G. (1980) *Statistical Methods*, 7th edn. The Iowa State University Press, Ames, IA, USA, 507 pp.

Tadesse Z. (1999) The nutritional status and digestability of *Oreochromis niloticus* L. diet in Lake Langeno, Ethiopia. *Hydrobiologia* **416**, 97–106.

Teichert-Coddington D.R., Green B.W. & Phelps R.P. (1992) Influence of site and season on water quality and tilapia production in Panama and Honduras. *Aquaculture* **105**, 297–314.

Tudorancea C.R., Fernando C.H. & Paggi J.C. (1988) Food and feeding ecology of *Oreochromis niloticus* (Linnaeus 1758) juveniles in Lake Awassa (Ethiopia). *Archiv für Hydrobiologie Supplement* **79**, 267–289.

U.S. Soil Conservation Service (1972) Hydrology. In: *SCS National Engineering Handbook, Section 4*. USSCS, U.S Government Printing Office, Washington, DC, USA, 400pp.

van Dam A.A. & Verdegem M.C.J. (2005) Utilization of periphyton for fish production in ponds: a systems ecology perspective. In: *Periphyton: Ecology, Exploitation and Management* (ed. by M.E. Azim, M.C.J. Verdegem, A.A. van Dam & M.C.M. Beveridge), pp. 91–111. CABI Publishing, Oxon, UK.

van Dam A.A., Dardona A., Kelderman P. & Kansiime F. (2007) A simulation model for nitrogen retention in a papyrus wetland near Lake Victoria, Uganda (East Africa). *Wetland Ecology and Management* **15**, 469–480.