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High stocking densities reduce *Oreochromis niloticus* yield: model building to aid the optimisation of production

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Abstract − Small-scale fish farming in tropical Africa is mainly based on pond culture of Nile tilapia *Oreochromis niloticus* with supplementary organic fertilisation. Until recently, the 'high' stocking densities practised (2 fish·m^{-2}) led to stunted populations and very low yields. Since 1996, rural fish farming developed significantly in Côte d'Ivoire. Only a dramatic decrease in stocking densities allowed fish farmers to produce marketable-sized tilapia with reasonable yield in extensive culture. Density control is achieved through tilapia monosex male culture and stocking the predator *Hemichromis fasciatus*. Further development of low-input tilapia farming requires improvement of production results. A growth model based on maximal growth and ingestion, maintenance needs and efficiency of food for growth was developed to explain and help optimise production results. The model was validated with farm and experimental data and demonstrated that, for a given rearing period (from 30–50 g fingerling, to market-size), yield increased with density, but then decreased beyond an optimal density. When market-weight target is set, the same variation of yield according to stocking density is observed. Densities of 2 to 3 fish·m^{-2} markedly reduce tilapia yield in extensive culture. Moreover, increasing market weight from 150 to 450 g·fish^{-1} will only induce a limited decrease in maximal yield (around 20 %) if the density is lowered and the rearing period lengthened. This decrease is more than compensated by the higher price of large tilapia. Using rearing cycle data, the model can predict the results of alternate combinations of stocking density and duration of rearing period under the same pond management. Thus, production results can be optimised given the objectives and constraints of each fish farmer. This model is a valuable tool to develop extensive tilapia farming in tropical areas, and raises questions for researchers. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

growth model / stocking density / tropical pond management / yield-density interactions / monosex male tilapia / *Oreochromis niloticus* / Africa

Résumé − Les fortes densités d'empoissonnement réduisent le rendement du tilapia *Oreochromis niloticus* : un modèle pour optimiser la production. La pisciculture artisanale en Afrique tropicale est basée sur l'élevage du tilapia *Oreochromis niloticus* en étangs fertilisés. Avec les « fortes » densités d'empoissonnement habituellement conseillées (2 poissons·m^{-2}) les poissons produits étaient de petite taille et les rendements très faibles. Depuis 1996, la pisciculture rurale extensive s'est développée en Côte d'Ivoire ; seule une réduction drastique des densités d'empoissonnement a permis aux pisciculteurs d'obtenir des tilapias de taille marchande avec des rendements raisonnables. L'élevage de tilapia monosexe mâle associé à un poisson carnassier, *Hemichromis fasciatus*, permet ce contrôle de la densité. Pour optimiser les résultats, un modèle de croissance a été développé à partir d'équations sur la croissance et l'ingestion maximales, les besoins de maintenance et l'efficacité de l'alimentation. Le modèle, validé par des données obtenues dans des stations de recherche expérimentale et dans une pisciculture, a démontré que, pour une durée d'élevage donnée (de juvéniles de 30–50 g aux poissons de taille marchande), le rendement augmente d'abord avec la densité d'empoissonnement, puis diminue au-delà d'une densité optimale. Quand la taille marchande est fixée, les mêmes variations du rendement en fonction de la densité sont observées. Des densités de 2 à 3 poissons·m^{-2} réduisent significativement le rendement du tilapia en élevage extensif. En outre, augmenter la taille marchande de 150 à 450 g induira une baisse de rendement limitée (environ 20 %) si la densité d'empoissonnement est diminuée et la durée d'élevage allongée. Cette baisse est plus que compensée par le meilleur prix de vente des gros tilapias. Partant des données d'un cycle de grossissement, le modèle peut prédire les conséquences sur la production de modifications de densité et de durée d'élevage. Ainsi, les résultats de production peuvent être optimisés selon les objectifs et les contraintes de chaque pisciculteur. Ce modèle constitue un outil pour développer la pisciculture extensive du tilapia en zone tropicale. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

modèle de croissance / densité d'empoissonnement / pisciculture tropicale / interactions rendement-densité / Tilapia monosexe mâle / *Oreochromis niloticus* / Afrique

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1. INTRODUCTION

African small-scale fish farming is mainly based on Nile tilapia *Oreochromis niloticus* (L.) rearing in earthen ponds with daily organic fertilisation and no addition of pelleted feed. For many years, most fish farming development services (see for example Gopalakrishnan and Coche, 1994) have recommended 'high' stocking densities (2 to 3 fish·m^{-2}). Under the extensive culture conditions practicable in Africa, this led to the production of 'stunted' fish unsuited to the market requirements, and very low yields. This situation was partly responsible for the poor development of this farming activity in some areas. Since 1996, fish farming developed significantly in rural areas of Côte d'Ivoire. Only a dramatic decrease in stocking densities allowed fish farmers to produce marketable-sized fish with reasonable yields. Rural fish farmers have constraints of market requirement, cash flow, water resources and limited access to organic fertilisers. The optimisation of their production is highly dependent upon careful choice of stocking densities, and further development of extensive tilapia farming requires a better understanding of the yield-density relationship.

The yield increase brought about by stocking at lower densities (0.1 to 1 tilapia·m^{-2}) is in accordance with other studies considering different fish densities with a constant food resource. Almost all these studies report the same observation: high densities decrease net yields of numerous organisms, including fish (Lorenzen, 1996), crustaceans (Wyban et al., 1987), molluscs (Mgaya and Mercer, 1995; Fréchette et al., 1996) and mammals (Béranger and Micol, 1981). For the Nile tilapia, Diana et al. (1991) observed a non-significant decrease of yield at the highest density, as did Liu and Chang (1992). In contrast, in most of the studies dealing with tilapia yield-density relationships, tilapia are fed either ad libitum or with rations proportional to biomass (that increase with increasing stocking density), leading to a positive correlation between tilapia stocking density and yield (e.g. Edwards et al., 1981; Delincé, 1992).

Côte d'Ivoire, as other equatorial countries, has small annual thermal and photoperiodic variations. This allows continuous fish production, as long as there is enough water to fill the ponds. Field results suggested that higher final carrying capacities with bigger fish could be obtained by reducing tilapia stocking densities. This is in accordance with the hypothesis of decreasing relative maintenance needs with increasing body weight (Hepher, 1988). According to the formulae of maintenance rations given by Mélard (1986), the carrying capacity in 400-g fish is 39 % higher than that formed by fish of 200 g (see below, equation (3)).

Using this carrying capacity approach, this study aimed to conceive a model to compare rearing cycles (from fingerlings to market-sized tilapia) with various stocking densities and rearing period lengths, and thereby provide a tool to predict on-farm production results under equatorial conditions. The growth model was built from the equations given by Mélard (1986), based on the food ration ingested by tilapias. Its validity was established by three sets of rearing cycle results obtained in earthen ponds in Côte d'Ivoire, allowing the calculation of the main parameter, pond ration. Simulations were then run, predicting the production results obtained with various stocking densities and rearing period durations under the same pond management conditions.

2. MATERIALS AND METHODS

2.1. Model building

The model was based on individual daily growth rate, which depends on the individual daily ration offered to the tilapia. The part of the individual ration directed to maintenance or to growth depends on the weight of the fish and the size of the ration. The calculation of each part was based on the equations given by Mélard (1986), concerning (1) tilapia growth rate, (2) maximal ration and (3) maintenance ration, according to the body weight. The fourth criterion used was the net conversion efficiency.

According to Mélard (1986), temperature and body weight are the main features determining *O. niloticus* growth. The theoretical daily weight gain (DWG) for tilapia without limiting factors follows the equation:

$$DWG_{max} = A \times T^{B} \times W^{C \times T^{D}} \quad (1)$$

in which DWG_{max} is in g·fish^{-1}·d^{-1}, T is the temperature in degrees Celsius and W is the body weight in grams. Constants A, B, C, D are determined by numerical estimation, to obtain the equation:

$$DWG_{max} = 17 \times 10^{-9} \times T^{4.785} \times W^{3.397 \times T^{-0.579}} \quad (1a)$$

For the model, we used the equation for T = 30 °C (which is a common water temperature in Côte d'Ivoire); this equation fits the best growth rates observed during a competition organised for fish farmers in Côte d'Ivoire (Oswald et al., 1997). At T = 30 °C, the maximum daily weight gain calculated from equation (1a) is:

$$DWG_{max} = 0.199 \times W^{0.474} \quad (1b)$$

According to Mélard (1986), the maximum ration (R_{mx}) tilapia can absorb each day is described by the equation:

$$R_{mx} = 0.192 \times W^{0.685} \quad (2)$$

in which R_{mx} is measured in grams of standard food·d^{-1} and W is the body weight in grams.

Under identical conditions, the daily maintenance ration (R_{mt}), corresponding to zero growth, is described by the equation:

$$R_{mt} = 0.035 \times W^{0.564} \quad (3)$$

We assumed that equations (2) and (3), obtained at 26 °C, are valid at 30 °C. Indeed, although differences can be substantial for small sizes, Mélard (1986) reports that as *O. niloticus* grows, its metabolism becomes more and more independent on temperature. For large sizes, the temperature-induced differences become negligible.

The fourth element of the model is the net conversion efficiency (NE), as defined by Brown (1957). NE is the efficiency of the part of the ration directed to growth, once the maintenance needs are satisfied. NE is calculated as the ratio of fish weight gain to the difference between the ingested ration and the maintenance ration (scope for growth). Some authors (Mélard, 1986; Hepher, 1988) believe that this net efficiency rises when the ration is reduced (situation of nutritional competition). However, observations made in Côte d'Ivoire (Glasser et al., in press), contradict this hypothesis. It seems that in fertilised ponds, the tilapia diet lacks proteins, which can decrease assimilation efficiency (Bowen et al., 1995). This could explain the sharp decrease in tilapia growth sometimes observed in low productivity culture environments. The NE was therefore assumed, in a first approximation, to be independent of the ration level, i.e. equal to the NE at maximum feeding level.

$$NE = DWG_{max} / (R_{mx} - R_{mt}) \quad (4)$$

Daily weight gain is calculated each day. As long as the individual ration R_{ind} available in the pond is greater than R_{mx}, the DWG is maximum (equation (1b)). As soon as R_{ind} becomes limiting (inferior to R_{mx}), the maintenance needs are satisfied by part of the ration, and the rest is converted into weight gain according to the fish NE, calculated from equation (4):

if $R_{ind} \geq R_{mx}$ then, $DWG = DWG_{max}$

if $R_{ind} < R_{mx}$ then, $DWG = (R_{ind} - R_{mt}) \times NE = DWG_{max} \times (R_{ind} - R_{mt}) / (R_{mx} - R_{mt})$

If we know R_{ind} and the initial mean weight, then growth for a given rearing period can be calculated. All the fish present in the pond share the total food available in the pond, i.e. pond ration (R_{pond}). The individual ration (R_{ind}) is thus inversely proportional to fish density ($R_{ind} = R_{pond}$/density). The main parameter of the model is therefore pond ration R_{pond}. Because of the applied objective of the model, simplified hypotheses to estimate R_{pond} were chosen. Their adequacy is assessed by the model's goodness of fit to production data (see below). Two hypotheses about this ration were made. First, we assumed that tilapia density remained constant for the rearing period: this implies low mortality rates and absence of fry proliferation. The latter condition is achieved by monosex male tilapia culture, stocking of a predator fish (e.g. *Hemichromis fasciatus* (Peters) in Côte d'Ivoire) and pond draining between two rearing cycles. Second, we assumed that the total quantity of food for tilapias in the pond was roughly constant for the whole rearing cycle, whatever the fish size. This can be justified by the fact that in tropical areas temperature and light intensity are almost constant throughout the year, and because fish farmers do not modify the daily amount of pond fertiliser applied during the rearing period. This assumption was also based on the diversity of tilapia food resources (Bowen, 1982). Despite the variation in quantity and quality of the various food resources in the pond, the fish were thought to be opportunist enough to ensure a constant quality of food ingested by adjusting their dietary composition.

Behavioural effects and other variation factors (such as social interactions) related to density were assumed to be negligible compared to the density-related sharing of the pond trophic resources. Monosex male culture prevents tilapias from important reproductive investment, so the effects of density on reproduction were also neglected.

If we know R_{pond}, the stocking density and the fish weight, then daily weight gain and net yield can be calculated until the end of the rearing period. Conversely, given the production results of a rearing cycle (initial and final mean weights, stocking density and rearing period), it is possible to make a numerical estimation of the theoretical pond ration (R_{pond}). Based on the pond ration obtained from a previous cycle, the model allows prediction of yield and final mean weight under the same pond management scheme but utilising alternate fish densities and rearing periods.

2.2. Validation process

The validity of the model was assessed with data collected in Côte d'Ivoire from research stations and a fish farm. Sets of data corresponding to our hypotheses were chosen: rearing cycles with different stocking densities but the same pond management scheme: same fish farm, same amount of fertilisers, fish densities remaining constant over time (low mortality, no fry proliferation, use of *Hemichromis fasciatus* as a predator). Only net yields were considered, as they take into account initial mean weight, and are thus more significant from a biological point of view.

For a given set of data, pond rations were calculated for each cycle (using initial mean weight, final mean weight, rearing period and tilapia density) and compared. If the calculated pond rations were homogenous and independent of fish density and duration of the rearing period, the model was assumed valid. This means that the model described the observed differences in growth (and yield) as the result of density differences in a constant-ration pond.

Table I. Characteristics of the three data sets used to validate the growth model.

Location	Gagnoa station	Bouaké station*	Fish farm at Daloa
Densities compared (tilapia·m^{-2})	0.1, 0.2, 0.4	0.4, 0.7, 1.0	1.2, 1.5, 1.7, 1.9
Fertilisation (kg DM**·ha^{-1}·d^{-1})	0	250	375
Rearing period (d)	96	186	101 to 207

* From Dabbadie (1996), with author's permission. ** DM: dry matter of rice bran.

This validation process was applied to three sets of data (see *table I*).

– The first set was obtained from the experimental station at Gagnoa. Three stocking densities of hand-sexed male *O. niloticus* were compared, each replicated twice, in 250 to 400-m^2 ponds (mean depth: 1 m) equipped with acadja (artificial reef: 10 bamboo sticks·m^{-2} planted in the pond bottom), without fertilisation. Initial mean weight was 84 g.

– The second set of data was obtained by Dabbadie (1996) in a research station located in Bouaké. Tilapia at three densities was cultured during 186 d, starting with *O. niloticus* males weighing 100 g. The 400-m^2 ponds (mean depth: 1 m) were fertilised with 1 kg rice bran·pond^{-1}·d^{-1}, on a dry matter base.

– Thirdly, four rearing cycles were selected from a fish farm situated in Daloa, in accordance with the model's hypotheses (constant density during cycle, no fry proliferation), with stocking densities from 1.2 to 1.9 tilapia·m^{-2}. Initial mean weights were between 19 and 37 g (*table IV*).

2.3. Simulation conditions

Rearing cycles with varying densities and rearing periods were simulated assuming an initial mean weight of 30 g and a theoretical pond ration of 1 g·m^{-2}·d^{-1}. This ration corresponds to low productivity environments like the unfertilised ponds of the Gagnoa station experiment, which in turn reflect pond management in rural areas.

3. RESULTS

3.1. Validation of the model

Table II presents the results of the Gagnoa station experiment. Poor performance of the predator *Hemichromis fasciatus* was responsible for the appearance of some tilapia fry during the rearing period (in most cases it was less than 10 % of the biomass). The density increase above 0.2 fish·m^{-2} did not induce any yield increase, but resulted in a large decrease in

Table II. Production results of the Gagnoa station experiment comparing three densities of hand-sexed male *O. niloticus*, with two replicates, in a low-productivity environment (acadja without fertilisation), for a rearing period of 96 d.

	Pond No.					
	1	4	2	5	3	6
Stocking density (tilapia·m^{-2})	0.1		0.2		0.4	
Male yield (t·ha^{-1}·y^{-1})	0.4	0.8	1.1	1.1	1.1	0.8
Total yield* (t·ha^{-1}·y^{-1})	0.5	0.9	1.1	1.1	1.3	0.8
Male DWG** (g·fish^{-1}·d^{-1})	1.04	2.12	1.49	1.64	0.78	0.59
Mean total yield ± SE (t·ha^{-1}·y^{-1})	0.7 ± 0.3		1.1 ± 0.0		1.0 ± 0.3	
Mean DWG ± SE (g·fish^{-1}·d^{-1})	1.58 ± 0.76		1.57 ± 0.11		0.68 ± 0.13	
Model-calculated pond ration (g·m^{-2}·d^{-1})	0.31	0.71	0.87	0.98	0.95	0.74

* Total yield: *O. niloticus* male and fry. ** DWG: daily weight gain.

Table III. Production results and model-calculated pond rations from a trial on *O. niloticus* densities carried out in Bouaké by Dabbadie (1996)*, for a rearing period of 186 d (initial mean weight: 100 g·fish^{-1}).

Stocking density (tilapia·m^{-2})	0.4	0.7	1.0
Final individual mean weight (g·fish^{-1})	512	373	293
Calculated pond ration (g·m^{-2}·d^{-1})	3.11	3.35	3.43

* with author's permission.

Table IV. Production results and model-calculated ration from four *O. niloticus* rearing cycles from a fish farm in Daloa with identical food and fertiliser inputs.

Cycle No.	1	2	3	4
Stocking density (tilapia·m^{-2})	1.2	1.5	1.7	1.9
Initial mean weight (g·$fish^{-1}$)	32	34	19	37
Final mean weight (g·$fish^{-1}$)	134	131	133	137
Rearing period (d)	101	128	207	181
Net yield (t·ha^{-1}·y^{-1})	3.1	2.9	2.5	3.5
Calculated pond ration (g·m^{-2}·d^{-1})	3.11	2.97	2.65	3.12

tilapia weight gain. The absence of fertiliser in pond No. 1 during the previous cycle (in contrast to the other ponds) could explain the lower yield. However, it corresponds to yields obtained by fish farmers in unfertilised ponds. With the exception of pond No. 1, the model-calculated pond rations were homogenous, which means that the model explained variations in mean weight (and therefore in yield) as the result of density variations under a constant pond ration. The mean daily pond ration was equal to 0.93 g·m^{-2}·d^{-1} with a coefficient of variation of 14 %. For Dabbadie's experiment (results in *table III*), the theoretical pond rations also exhibited good homogeneity (mean: 3.30 g·m^{-2}·d^{-1}, coefficient of variation: 5 %). In the Daloa fish farm results, calculated pond rations were also homogenous (mean: 2.96 g·m^{-2}·d^{-1}; coefficient of variation: 7 %) and independent of density (results in *table IV*).

In these three cases, the model could explain net yield variations as the result of density variations under a constant food ration. The model and its hypotheses describe quite accurately the field data, thus it can be considered valid.

The model was also tested on growth curves carefully monitored during a fish farmer competition (Oswald et al., 1997). The theoretical rations obtained from the results of the best rearing cycles were between 4.4 and 9.6 g·m^{-2}·d^{-1}. Between the simulated growth curves and those actually observed, the gap was less than 10%, which can easily be explained by sampling error alone.

3.2. Simulation results

The effects of varying stocking densities on net yield were simulated by successively imposing two conditions: the duration of the rearing period (set at 100 or 300 d), and the fish market-size target (set at 150 or 450 g). These two conditions correspond to the main constraints on fish farmers' choices.

For a given rearing period (*figure 1*), net yield increased with density, and then decreased beyond an optimal density that maximises the yield. This optimal density slightly decreased when rearing period lengthened. The maximum yield, obtained at densities of 0.4 to 0.5 fish·m^{-2}, was almost three-fold higher than the yield obtained at 3 fish·m^{-2}, and more than 50 % higher than that obtained when stocking density is 2 fish·m^{-2}. Moreover, it was impossible to obtain market-sized fish at 2 fish·m^{-2}, even after a 300-d rearing period.

For a given market-size target (*figure 2*), net yield increased with density, and then decreased when density was above the optimal level. The optimal density rapidly decreased as the fish size target increased. For the pond ration chosen here, the optimal density was equal to 0.4 fish·m^{-2} for 150-g fish and 0.2 fish·m^{-2} for 450-g fish. When density increased, the required rearing period to obtain market-sized tilapia dramatically rose. Above a certain density level, it was impossible to reach the weight objective, whatever the duration of the rearing period. When the fish target size increased, the maximum yield slightly decreased: the maximum yield for 450-g fish is only 21 % lower than that for 150-g fish (lengthening the rearing period by 159 d). Even for the larger weight target (450 g), the yield was more than twice that of any yield obtained at 3 fish·m^{-2}.

Comparative simulations were also run for daily pond rations varying from 0.5 g·m^{-2}·d^{-1} (poor culture environment corresponding to the most extensive farms without fertilisation) to 5 g·m^{-2}·d^{-1} (corresponding to high fertilisation levels). The variations of yields was similar, although the values of the maximum yields and optimal densities differed according to pond

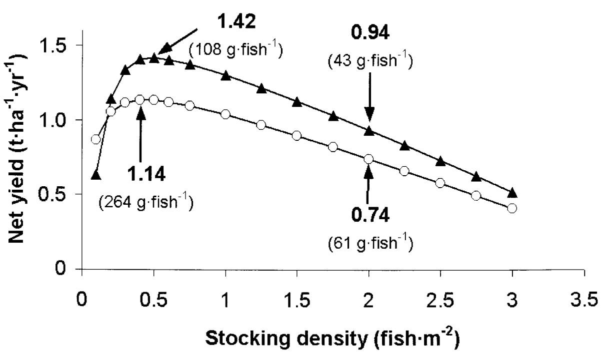

Figure 1. Simulated net yields at different stocking densities, for different rearing periods: 100 d (▲) or 300 d (○). The calculated values are compared for optimal density and 2 fish·m^{-2} (values in bold correspond to net yields, numbers in brackets indicate the final mean weight reached).

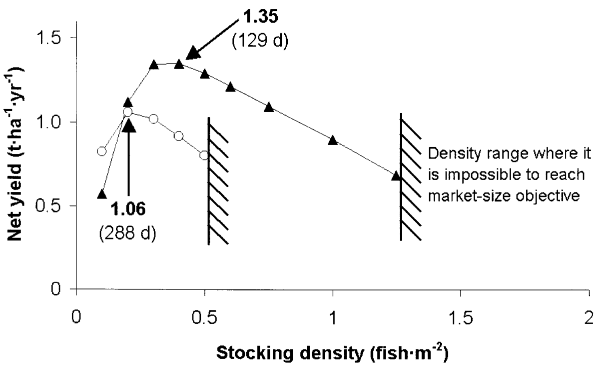

Figure 2. Simulated net yields obtained at different densities for different fish mean weight objectives: 150 g (▲) or 450 g (○). The maximal net yields are indicated in bold; the numbers in brackets correspond to the rearing periods.

rations. In extensive culture environments, the decrease in yield beyond the optimal density was much quicker than in highly fertilised environments.

3.3. Applications of the model to field results: a prediction tool

From the production results of one or more rearing cycles, it was possible to estimate the theoretical pond ration (cf. section 3.1). Knowing this pond ration, growth and yield can be simulated for the same culture environment, but with varying densities and/or rearing periods.

Simulation from the station experiment results (R_{pond} = 0.93 g·m^{-2}·d^{-1}) confirmed that it was not possible to improve the tilapia yield of a low productivity environment using higher stocking densities. A density of 2 fish·m^{-2} would dramatically reduce the yield in such an environment.

From Dabbadie's experiment, the model predicted that with a 300-g·fish^{-1} final weight objective and a 100-g·fish^{-1} initial weight, a maximal yield equal to 3.9 t·ha^{-1}·y^{-1} would be obtained at a density of 0.6 fish·m^{-2}.

The Daloa fish farmer tested various densities and rearing periods. His precarious financial situation led him to seek the best compromise between density and duration of rearing period. Cash-flow constraints forced him to shorten his rearing cycles, and thus he produced small fish. His results were not satisfactory, neither for yield increase nor for final weight (*table IV*). The model simulations (*table V*) indicated a better solution. By decreasing the stocking density (from 1.7 to 0.8 fish·m^{-2}), the fish farmer could obtain a 40 % higher yield with a shorter rearing period and a higher final mean weight, which would represent an improvement both in cash flow and revenue. By choosing longer rearing periods and lower densities, the farmer would produce fish with a much higher market value (final individual weight close to 300 g) and obtain higher yields, which would increase his income.

4. DISCUSSION

This model describes the interactions between yield and stocking density observed in tilapia farming in Côte d'Ivoire. From the results of a rearing cycle, leading to the estimation of the pond ration parameter, it is possible to predict the consequences of alternate rearing periods or stocking densities, assuming the same pond management strategy (fertilisation) is applied. It allows the optimisation of fish farmers' production results, given their targets (e.g. market-size) and/or constraints (e.g. duration of the rearing period, availability of fingerlings). The model was deliberately simplified to ease field application, and only requires data on weight, density and duration of rearing period. Validation was achieved with three independent sets of data obtained in Côte d'Ivoire, because of the lack of other published data fitting the model hypotheses: constant tilapia density throughout the rearing period, no fry proliferation, same management (fertilisation or food) for all the densities compared. Despite the small number of replicates, the validation on three sets of data obtained in ponds of various productivity levels, as well as growth curves, ensures the robustness of the model.

The model results highlight the fact that comparing yields obtained at different stocking densities is valid only if the duration of the rearing period is taken into account. This is confirmed by the data of Knud-Hansen and Lin (1996) who, for 2.5 months, observed a positive correlation between density and yield, and then a dramatic decrease of yield for the highest densities. Yield decrease at high density can be explained by the situation of food competition, leading to slower growth and higher relative maintenance needs. The possible impact of increased social interactions was not integrated in the model. For a given pond ration, which can be interpreted as the food availability for tilapia, each market-size target has an optimal fish

Table V. Optimum yields predicted by the model for different market-weight targets of the fish farmer in Daloa (cf. production results in *table IV*), from 30-g fingerlings.

Final mean weight target (g·fish^{-1})	150	250	300	450
Maximum yield (t·ha^{-1}·y^{-1})	4.0	3.6	3.5	3.2
Rearing period (d)	108	178	228	292
Optimal stocking density (fish·m^{-2})	1.0	0.8	0.8	0.6

density that maximises the net yield. The higher the market-weight target, the lower the appropriate optimal density. In the same way, for each rearing period duration, it is possible to determine an optimal tilapia density that maximises its yield. Similarly, the longer the rearing period, the lower the appropriate optimal density. Conversely, for each stocking density, it is possible to find a rearing period that maximises the yield.

Seeking to produce bigger tilapia (from 150 to 450 $g \cdot fish^{-1}$) will only induce a limited decrease in yield (around 20 %), provided that a lower stocking density and a longer rearing period are carefully chosen. This decrease is more than compensated by the higher price of the product. Whatever the pond ration, to obtain a good yield of 450-g tilapia (i.e. close to the maximum yield), it is necessary to ensure a 1.5-$g \cdot fish^{-1} \cdot d^{-1}$ daily growth during the first months, 1.3 $g \cdot fish^{-1} \cdot d^{-1}$ for 300-g fish, and 1 $g \cdot fish^{-1} \cdot d^{-1}$ for 150-g fish.

The model underlines the difficulty of predicting the results of low-productivity environments, due to a higher variability: a small error in density can lead to a dramatic drop in yield (see for example the negative yield obtained at 2 $tilapia \cdot m^{-2}$ by Ofori et al., 1996). Therefore, it is often necessary to complement this approach by monitoring fish growth. Working on a growth objective depending on the market-size target is a reliable method for these extensive ponds.

Despite the model's suitability to field data, some aspects would deserve further development: in some cases we observed underestimation of maximal growth rate. Some parameters could lead to false results for large fish sizes (> 500 g), because they do not reflect possible changes in food requirements of large tilapia (for example a lesser demand in protein, see Bowen, 1982).

Application of this model could greatly improve the technical and economical results of small-scale tilapia fish farming in tropical Africa. The model generated solutions to two main issues for tilapia fish farming development in the future: the adequacy of commercialised fish to consumer wishes and the possibility of producing marketable fish in rural areas with very low levels of fertilisation (or even without fertilisation). The main requirement is the control of fish density, through pond draining between two rearing cycles and the use of an efficient predator species like *Hemichromis fasciatus*.

5. CONCLUSION

This model can explain the very large variations in tilapia size observed under similar pond management conditions, and predicts the results of stocking density or rearing period variations, in order to optimise tilapia production. It can be applied to extensive tilapia fish farming under tropical conditions. The model reveals a method, accessible to numerous fish farmers, to transform 'stunted' tilapia populations into marketable products through the control of density and rearing period duration, which could sustain extensive fish farming development. With parameter adjustments, the same approach could be used in other climatic areas.

The authors wish to emphasise the usefulness of such investigations which, performed under sufficiently rigorous conditions, produce a lot of practical information. This kind of information is crucial for the further development of fish farming in situations of low input availability, where only optimised production is profitable for many low-revenue farmers from Africa and other tropical areas. A more agronomic approach of fish yield in pond modelling (similar to the studies of cattle stocking rates that exceed pasture capacity – see for example Béranger and Micol, 1981) could be very fruitful. Developing such models may be an excellent prelude to the study of interactions between fertilisation level and pond productivity, thus allowing a synthetic approach complementary to that commonly used.

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