Simulation of optimal harvesting strategies for small-scale mixed-sex tilapia (*Oreochromis shiranus* Boulenger 1896) ponds using a bio-economic model

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**Abstract**

A cohort-based bio-economic biomass growth and economic model, validated with data from experiments conducted in Malawi, was used to identify an optimal harvesting strategy for mixed-sex tilapia ponds. Three harvesting scenarios (baseline, economic optimum time +10 days and economic optimum time) were used. In each harvesting scenario four options were explored: (i) no further harvest, harvest every (ii) 60 days, (iii) 90 days and (iv) 120 days after initial harvest. The lowest simulated yield (48.7 kg ha⁻¹ year⁻¹) was obtained when no partial harvesting was carried out and fish were harvested after 365 days. Maximum yield (441.6 kg ha⁻¹ year⁻¹) was obtained when partial harvests were carried out every 90 days starting with a first harvest of fish weighing 60 g or more at day 90. Maximum financial returns (US$2561 ha⁻¹ year⁻¹) were obtained when partial harvests were carried out every 120 days starting with the first harvest at day 90 and removing all fish ≥ 60 g. The model simulations indicate that mixed-sex tilapia culture may be profitable for tilapia farmers in Africa where markets accept small (60–150 g)-sized fish. The study further shows that a cohort-based population growth model can be reliably incorporated in tilapia production models to simulate fish yields in mixed-sex tilapia production systems. However, incorporation of intergenerational competition effects could improve the model’s utility as a decision support tool for managing mixed-sex tilapia production.

**Keywords:** *Oreochromis shiranus*, tilapia, mixed sex, bio-economic model, partial harvesting

**Introduction**

Mixed-sex culture of tilapia in ponds is the most prevalent production system for small-scale farmers in sub-Saharan Africa (Jamu & Ayinla 2003). This system is valued for its ability to produce seed for restocking and to produce fish for the market using available resources (de Graaf, Dekker, Huisman & Verreth 2005). The major drawback of mixed-sex pond culture is the high level of uncontrolled reproduction in grow-out ponds, leading to stunted somatic growth and high competition for food and other resources (e.g. dissolved oxygen) between stocked fish and juveniles (Msiska & Cantrell 1985; Pauly, Moreau & Prein 1988; Rackocy & McGinty 1989; Maluwa 1990). Competition for resources reduces overall fish yields and the market size of harvested fish.

Tilapia recruits are generally considered as a fish farming nuisance (Yong-Sulem, Thanchou, Nguefack & Brummett 2006). Hence, a number of studies have focused on developing methods for reducing reproduction and removal of recruits through photoperiod manipulation, use of predator species such as African catfish (*Clarias gariepinus* Burchell 1822) or African snakehead (*Parachanna obscura* Günther 1861) (Fisher & Grant 1994; Kwei Lin, Yi & Diana 2001; Biswas, Morita, Yoshikazi, Maita & Takeuchi 2005; Yong-Sulem et al. 2006). One major strategy to reduce competition for pond resources without the use of predator species revolves around controlling recruitment through partial harvesting to keep the pond near, but below, the carrying capacity for a greater portion of the grow-out period (Allen,
Botsford, Schuur & Johnson 1984). Partial harvesting has the advantage of reducing the standing stock, stunting of fish during the latter parts of the culture period, increasing fish growth rates and yield and spreading out the overall harvest over a long period, thereby ensuring farmers of a regular income (Brummett & Noble 1995).

Partial harvesting of tilapia invariably results in harvesting of small-sized (60–1500 g) fish. Because of diverse consumer preferences for fish market size in different sub-Saharan African countries, a market for small fish exists and their production may not necessarily affect the financial performance of small-scale fish farms (Brummett 1995; Brummett, Gockowski, Bakwovi & Etaba 2004; de Graaf et al. 2005). Therefore, farmers can increase overall fish yield and income by harvesting small fish several times during the year without affecting farm profitability.

Studies conducted using different tilapia species have shown that partial harvesting can increase overall gross yields (Knud-Hansen & Kwei Lin 1996; Brummett 2000) and financial returns (Kaunda 1992). Brummett (2002) proposed a partial harvesting regime that involves growing fish undisturbed for 122 days and thereafter partially harvesting the ponds weekly. Kaunda (1992) carried out a simple bio-economic analysis and found that optimum financial returns for small-scale mixed-sex tilapia ponds were obtained when half of the recruits were removed every 2 months. These results do not show exactly what optimal yields and financial returns would be obtained at the end of the production period. There is still a need, therefore, to determine the optimum number of partial harvests and harvest size that can give higher yields and financial returns to small-scale fish farmers. Because of the complexity of the decision-making process for optimizing yields and financial returns, use of simulation models could codify and simplify the determination of optimal harvesting strategies for mixed-sex tilapia ponds.

Models developed over the last 30 years to simulate fish yield and profit maximization for pond aquaculture have typically used bio-energetic approaches (Jorgensen 1976; van Dam & Pauly 1995; Jamu & Piedrahita 2002a, b), linear programming, multi-period linear programming, optimal control theory, dynamic programming and marginal analysis (Allen et al. 1984). For example, Talpaz and Tsar (1982) used optimal control theory to maximize profit by manipulating harvest, stock density and water flow as decision variables. Budget simulation analysis has also been used to study economies of size in shrimp production (Adams, Griffin, Nichols & Bricks 1980).

Various individual-based tilapia models have recently been produced as decision-support tools for tilapia culture and management (Jamu & Piedrahita 2002a; de Graaf et al. 2005). These models do not incorporate financial and/or economic models. However, small- and medium-scale aquaculture farms in Africa are evolving from subsistence to commercial enterprises and private investments in aquaculture are increasing (Jamu & Ayinla 2003). Therefore, the inclusion of financial sub-models in the existing aquaculture models could increase the utility of models for forecasting biological production and simulating management options that optimize production and financial returns and hence lead to a practical decision-support tool for mixed-sex tilapia farming. Furthermore, the models could be used to provide simulations for the development of financial and business models for potential aquaculture entrepreneurs and finance institutions. Such information may open opportunities for financial support from microfinance and other financial institutions to support the further growth of small-scale commercial aquaculture in sub-Saharan Africa.

The objective of this study therefore was to develop a mixed-sex tilapia model and use it to identify a financially optimal harvesting strategy for mixed-sex tilapia ponds. Thus, this paper addresses the question of identifying how often and what sizes of fish a farmer should harvest in order to obtain higher accumulated yield and financial returns. In order to achieve this, a mechanistic cohort-based model for biomass growth of mixed-sex Oreochromis shiranus was developed using an existing generic bioenergetic fish growth simulation model (Jamu & Piedrahita 2002a). Oreochromis shiranus is one of the indigenous mossambicoid tilapia species used in small-scale integrated aquaculture in Malawi.

Materials and methods

General

The mixed-sex culture system imposes a complex decision-making process for fish farmers on how they can maximize yield and financial returns through partial harvesting. The decision making is further complicated because of the inadequacies of information on what yields and financial returns to expect at the end of the production period. What is unknown is
how often and at what sizes a farmer should harvest in order to obtain higher accumulated yield and higher financial returns at the end of the production period. The problem in deciding how to maximize yield and financial returns is complicated because the stock is undergoing a growth process, and the decision to determine the number and size of harvests is executed over time. The solution of the problem requires modelling the fish biomass growth process of mixed-sex culture (biological sub-model) and harvest frequencies to guide the fish farmer on what yields and financial returns to expect for a given culture period. The former is achieved through the incorporation of a financial sub-model.

The biological model is presented at three levels: individual fish growth, population growth and biomass growth for each cohort. Cacho (1997) identifies the factors that primarily determine individual fish growth: temperature, water quality, food intake, diet quality, body weight and composition. The financial model relates pond inputs, current biomass and market prices to farm-gate profits.

The effect of harvesting strategies on the total fish population was considered through various stock manipulation procedures. The decisions that were made at this level related to harvesting dates, fish size by weight and harvest frequencies. The interaction between the biological and financial components of the model is through the harvesting function. In order to meet the objective set in the financial model of maximizing net returns, partial harvests strategies that evened out net cash flow through out the production period were established. Three harvesting periods, namely at 60, 90 and 120 day interval, were compared. The goal was to identify an interval giving the highest discounted net returns.

We use the integrated aquaculture–agriculture system model developed by Jamu and Piedrahita (2002a) to simulate fish growth. The model simulates fish growth using a bioenergetics approach. Bioenergetic modelling of fish involves the use of energy balances to determine biomass growth. The biomass growth (somatic and reproductive) is represented as a positive balance in energy after subtracting energy losses due to metabolic, faecal and intermediate waste products from energy gained from food (Jobling 1994; Lucas 1996). As fish growth can also be affected by feed quality, feed intake rate and preference by fish for certain feed resources and the genetics of the fish being grown, the model incorporates the effects of feed quality, feed preference, water quality and genetic coefficients on fish growth. Details on how these are incorporated in the model are described in Jamu and Piedrahita (2002a). In the present study, Jamu and Piedrahita’s model was modified to include spawning, recruitment and harvesting.

The expanded model was calibrated and verified using literature parameter values and data from fish production experiments carried out at the Malawi National Aquaculture Center (Chikafumbwa, Costa-Pierce, Jamu, Kadongola & Balarin 1993; Brummett & Noble 1995). The model was then tested with an independent data set from fish production experiments (Maluwa & Costa-Pierce 1993; Brummett 2000). Details of modifications and additions made to the Jamu and Piedrahita (2002a) model are presented below.

### Individual fish growth

The fish bioenergetics model Jamu and Piedrahita (2002a) is given as

$$\frac{dW}{dt} = \left(1 - a\right) \left( R \sum_{i=1}^{I} b_i q_i \right) - j_{\min} \exp(s(T - T_{\min})) W^n$$

$$R = h f T_\delta W^m$$

where $a$ is the fraction of food assimilated that is used for anabolism (dimensionless); $q_i$ is the coefficient describing effect of $i$th feed quality on fish growth (dimensionless); $b_i$ is the digestibility for the $i$th feed resource (dimensionless); $R$ is the feed intake rate (g day$^{-1}$); $j_{\min}$ is the coefficient of fasting catabolism at $T_{\min}$ (g$^j$ day$^{-1}$); $h$ is the coefficient of food consumption (g$^f$ day$^{-1}$); $f$ is the relative feeding level (dimensionless); $T_\delta$ is the fish temperature parameter (0–1) (dimensionless); $\delta$ is the function describing the effects of the dissolved oxygen on feed intake (0–1) (dimensionless); $W$ is the weight of a fish (g); $t$ is the time (day); $m$ is the exponent of body mass for anabolism (dimensionless); $s$ is the constant (C$^{-1}$); $T$ is the water temperature (°C); $T_{\min}$ is the minimum temperature below which the species will not feed (°C); $n$ is the exponent of body mass for catabolism (dimensionless) and $g$ is the fish genetic coefficient (dimensionless). Details of the coefficients are explained in Jamu and Piedrahita (2002a).

To model individual fish growth for each cohort, the following differential equation was added to Jamu
and Piedrahita’s (2002a) model:

\[
\frac{dW_k(t)}{dt} = \left( (1-a) \left( R \sum_{i=1}^{s} b_{ih} \right) - \beta \exp(s(T-T_{\text{min}})) \right) W_k(t) \]

\( W_k(t_k) = W_0 \) \( (t \geq t_k) \) \hspace{1cm} (2)

where \( W_k(t) \) is the individual fish weight (g) of the \( k \)th cohort at time \( t \); \( W_k(t_k) = W_0 \) is the initial individual fish weight of the \( k \)th cohort that was recruited at time \( t = t_k \); the other variables and constants in Eq. (2) are as defined in Eq. (1).

To apply Eq. (2), the following assumptions on reproduction were made: the sex ratio was 1:1 (Vicentini & Araújo 2003); females become sexually mature at 20 g and at this weight they have their first spawn; the subsequent spawns of a given cohort occur every 21 days; and the individual fish weight of each spawned cohort is 0.001 g. The assumptions are based on the results of the reproductive behaviour studies of \( O. \ shiranus \) (Maluwa 1990).

**Fish population**

The total number of fish in a pond is dependent on three factors: initial number stocked, mortality and reproduction. In mixed-sex tilapia ponds reproduction results in development of different (age and size) cohorts. To model fish population for each cohort, a size-structured reproduction model based on the number of females and factors affecting fingerling growth and survival was used. To determine when a new cohort population should be introduced, it was assumed that fish weight at first spawning was 20 g and fish were spawned every 21 days. The population size of each recruited cohort was modelled using the following differential equation (Ricker 1975; Springborn, Chang & Engle 1992):

\[
\frac{dN_k(t)}{dt} = -\sigma N_k(t \geq t_k), \quad N_k(t_k) = \eta \varpi \rho P \]

\( N_k(t_k) \) depended on the number of stocked fish at time \( t = t_k \), \( \eta \) is the proportion of females and the number of fingerlings each female produced per spawn. As \( O. \ shiranus \) is a complete spawner, a birth-purse model is assumed in which individuals give birth to all their offspring on the day of spawning. This assumption is consistent with results of Lazard and Legendre (1996) who showed that in tilapias eggs are laid and fertilized in batches and the fry are released at each spawning. The removal of recruits was modelled by modifying Eq. (3) for each cohort to include a harvest function, \( h(t) \). Equation (3) then becomes

\[
\frac{dN_k}{dt} = -\sigma N_k - h_k(t \geq t_k), \quad N_k(t_k) = \eta \varpi \rho P \]

\( h(t) \) is the value of \( N_k(t_k) \) depended on the number of fish in the parent cohort, the proportion of females and the number of fingerlings each female produced per spawn. As \( O. \ shiranus \) is a complete spawner, a birth-purse model is assumed in which individuals give birth to all their offspring on the day of spawning. This assumption is consistent with results of Lazard and Legendre (1996) who showed that in tilapias eggs are laid and fertilized in batches and the fry are released at each spawning. The removal of recruits was modelled by modifying Eq. (3) for each cohort to include a harvest function, \( h(t) \). Equation (3) then becomes

\[
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The financial sub-model consisted of a financial performance function that relates pond inputs, current biomass and market prices to profits. The net returns at each partial harvest of a given stock manipulation procedure was modelled using the following equation (Cacho 1997):

\[
\pi_n(t) = R_n(t) - C_n(t) \]

where \( \pi_n(t) \) is profit in US$ ha\(^{-1}\) for the \( n \)th partial harvest for a given manipulation procedure, \( R_n(t) \) and \( C_n(t) \) are revenue and production costs at time \( t \) of the \( n \)th partial harvest of a given manipulation procedure. Revenue is in US$ kg\(^{-1}\) and is expressed as a function of biomass harvested at any
time $h(t)$ and constant fish cost. Production cost $C_n(t)$ is a function of the cost of harvesting services and cost of feed.

Revenue and production costs were modelled using the following equations:

$$R_n(t) = P h(t)$$

(7)

$$C_n(t) = c_1 f(t) + c_2$$

(8)

where $P$ is the constant fish cost (US$ kg^{-1} \times h(t)$) is the biomass harvested at time $t$ (kg); $c_1$ is the feed cost per kg (US$ kg^{-1}$); $f(t)$ is the amount of feed supplied to the pond at time $t$ (kg day$^{-1}$); $c_2$ is cost occurring at time of harvest, which consist of the cost of hiring seine net and the labour cost of harvesting (US$).

Fish production cost at time $t = 0$, which gave the start up cost, was given by

$$C_0(0) = c_0 N_1(0)$$

(9)

where $c_0$ is the fingerling cost (US$ fingerling$$^{-1}$) and $N_1(0)$ is the initial number of fingerlings stocked.

To find the stocked manipulation procedure that gave optimum net returns, net returns realized at each partial harvest were discounted. Discounting was carried out because a sum to be received or spent in the future is worth less now due to the time value of money. This method eliminates the currency value differences resulting from time (Shafto 1991). The discounting factor, $100$, was calculated as (Cacho 1997)

$$\beta = \frac{1}{1+r} \times 100$$

(10)

where $r$ is the discount rate. For each stock manipulation procedure, the discounted net returns realized at each partial harvest were summed to give net present value (NPV). $\Pi$. Net present value of an investment is defined as the difference between the present value of its revenues and the present value of its costs (Leung, Hochman, Rowland & Wyban 1990). Net present value is used to compare the profitability of two or more alternative investments. Net present value, $\Pi$, was modelled using the equation

$$\Pi = \sum_{n=0}^{l-1} [R_n(t) - C_n(t)] \beta^l + [R_l(t) - C_l(t)] \beta^l,$$

(11)

where $\Pi$ is the nth partial harvest of a given stock manipulation procedure; $n = l$ is the final harvest and $t$ is the time (days). The functions $R_n(t)$, $C_n(t)$ and $\beta$ are as defined in Eqs. (6) and (10).

To apply Eqs. (6) to (11), the following assumptions were incorporated in the model: fingerling cost of US$0.01 fingerling$$^{-1}$; the price of fish of US$0.89 kg$$^{-1}$, which is assumed to be constant and independent of fish size; feed cost of US$0.02 kg^{-1}$ and total weigh for supplemental food (maize bran) per day was 3% of mean fish body weight (Chikafumbwa et al. 1993) multiplied by the fish population; cost of harvest labour at US$111 ha^{-1} harvest^{-1}$, the current minimum rural wage rate; discount rate of 50%.

Simulations conditions and parameterization

Production experiments for $O. shiranus$ conducted at the National Aquaculture Center, Malawi provided data on mixed-sex culture, size structure of the fish population and on survival rates was obtained from experiments conducted by Chikafumbwa et al. (1993) and Brummett and Noble (1995). The data set contains yield parameters on stocking [mean stocking weight (20.9 ± 2.7)] and stocking density (2 fish m$^{-2}$) and harvest [mean final weight (37.4 g)]; % survival (86.6%); and % contribution of recruits to final yield (68%). These data were used to parameterize the spawning, recruitment and harvesting sub-models. It was not necessary to calibrate the fish growth model because the model has been validated for a wide range of environmental conditions (Bolte, Nath & Ernst 1994; Jama & Piedrahita 2002a). The mortality rate of recruits, $\sigma$, was calculated from the percentage of fish survival. The number of fingerlings produced, $\sigma$, by each female spawn was estimated from the extrapolated net yield (kg ha$^{-1}$ year$^{-1}$) and the proportion of females of the parent population. Estimates of the values of these parameters are $\sigma = 0.001$, $\omega = 0.7$ and $\eta = 0.500$. Estimates of the harvesting function values were determined by the mean fish weight (g) at each partial harvest. The values of parameters are: $\xi = 1$ and $\zeta = 1$. The value, $\omega$, number of females per spawn was calibrated from the initial estimate of $\omega = 0.7$ by successive adjustments until the model output values were within range (± 1 standard deviation) of the observed values and the model output followed the pattern of observed values. Values of the parameters and constants used in the model are presented in Table 1.

The model output was graphically compared with observed data from tilapia trials at the Malawi National Aquaculture Center. The data set encompasses mixed-sex tilapia experiments designed to investigate improved pond-management systems such as fish stocking rates, pond inputs and integrated farming technologies (Brummett & Noble 1995). The standard deviation statistic was used to evaluate model fit to observed data. Thus, when simulated
fish weight values were within one standard deviation and the model output followed the observed pattern for fish weights, then the model was said to be reliable for simulating individual fish weight and reproduction.

Determination of biological and economical optimal harvesting strategies

After the model was verified, it was applied to a hypothetical smallholder fish farm with a 200 m² pond (modal pond size for Malawi small-scale fish farmers) to determine the stock manipulations and harvesting strategy that would give higher financial returns. The modelling study consisted of simulations of three different stock manipulation and harvesting scenarios, which were based on: (i) recommended time (120 days) to start partial harvesting (Brummett 2002) and (ii) 10 days more than the optimum time to partial harvest and (iii) optimum time to partial harvest (after \( t_e \) days, where \( t_e \) is the economic optimum time), which is estimated from the model. The later simulations were performed to compare the consequences of partial harvesting a few days after the optimum time and at a recommended time. To determine the stock manipulations and harvesting strategy that would give highest net returns, indices on NPV and net yields were used. These indices were calculated as net yield or NPV at a given harvest frequency divided by net yield or NPV for no partial harvest regime and expressed as a percentage. These formed net yield and NPV indices that have been used to compare different stock manipulation and harvesting strategies in this study. The indices represent increases in net yield or NPV for each harvest strategy over the baseline condition (no partial harvest). The simulations were on the following three scenarios on stock manipulation and harvesting strategies:

Scenario I: Harvesting fish \( \geq 60 \) g starting at 120 days (recommended time) thereafter: (1) no partial harvest, (2) every 60 days, (3) every 90 days and (4) every 120 days.

Scenario II: Harvesting fish \( \geq 60 \) g starting at day \( t_e +10 \) thereafter: (1) no partial harvest, (2) every 60 days, (3) every 90 days and (4) every 120 days.

Scenario III: Harvesting fish \( \geq 60 \) g starting at day \( t_e \) (economic optimum time) thereafter: (1) no partial harvest, (2) every 60 days, (3) every 90 days and (4) every 120 days.

Fish production system for all scenarios was as follows: mixed-sex \( O. \) shiranus (initial weight = 50 g) were stocked in 200 m² pond at a stocking density of 2 fish m⁻². Maize bran was applied to the pond as supplementary feed at 3% mean fish body weight per day. Maize bran was used because it is the basic supplemental feed that most fish farmers use for tilapia production in Malawi (Mutambo & Langston 1996). The model was run for a period of 365 days and simulation results from 200 m² ponds were converted to per hectare basis.

Results

Model verification

The model simulations generally followed the fish growth trends but tended to overestimate individual fish growth from day 25 to day 60 (Figs 1 and 2). Simulated individual fish weights in the last 10 days of production (Figs 1 and 2) and final fish biomass (Table 2) were within observed values.

Determination of biological and economical optimal harvesting strategies

Farmers typically aim to maximize harvests and financial returns. The biological basis for harvesting when fish biomass growth rate is at maximum is that it provides higher overall yields in an unfinished stock (Pauly 1984). This happens when \( B_{max}/2 \), where \( B_{max} \) is the maximum biomass. The economic
optimum time to harvest fish occurs when profit of fish biomass sold at the market is at a maximum value (Springborn et al. 1992). This point occurs where marginal revenue is equal to marginal cost, that is, when the rate of change in revenue is equal to zero. These two criteria were used to identify the optimum time to harvest in this study. Figure 3 shows simulated fish biomass and revenue obtained if all the fish biomass in the pond was sold at farm gate. Based on the above criteria, the optimum harvest time was estimated from the model to be 90 days for either maximizing yield or maximizing profit (Fig. 3).

Results of net yield, NPV and indices for net yield and NPV are presented in Tables 3 and 4. All simulations of the three scenarios gave positive net yield and present values (Table 4). In all scenarios, net yields and NPVs from the other harvesting strategies were higher than the harvesting strategy where there was no recruit removal between stocking and end of fish production period.

Results presented in Table 3 further show that a fish farmer who practices Scenario II would obtain a higher net yield of 4062 kg ha$^{-1}$year$^{-1}$ (Table 3) and net financial returns of US$1063 ha$^{-1}$year$^{-1}$ (Table 4) than a fish farmer practicing Scenario I. In the latter case, a lower net yield of 1521 kg ha$^{-1}$year$^{-1}$ (Table 3) and a financial return of US$967 ha$^{-1}$year$^{-1}$ (Table 3) are obtained. For Scenarios I and II, there was no change in NPV or net yield from switching from a harvesting strategy of every 60 days to every 90 days and every 120 days.

For Scenario III, the results indicate that the highest simulated yield of 4416 kg ha$^{-1}$year$^{-1}$ can be obtained by practicing the harvesting strategy of every 60 days (Table 3) and the highest financial returns of US$2561 ha$^{-1}$year$^{-1}$ can be obtained by practicing a harvesting strategy of every 120 days (Table 3). The corresponding net fish yield index for the highest financial returns was 297 while that for NPV was 379 (Table 4).

**Discussion**

In two simulations (Figs 1 and 2), simulated weight was higher than observed weight during the first half of the culture period. This might have been because of the underlying assumptions that were incorporated from the model to be 90 days for either maximizing yield or maximizing profit (Fig. 3).
in the model. In particular, the cohort-based individual fish growth model incorporates an assumption of a spawning frequency of 21 days and the cohort-based population model incorporates a birth-pulse assumption in which individuals give birth to all offspring on the day of spawning. These assumptions may have caused an overestimation of dissolved oxygen as all offspring might not have been born and therefore there was no competition for oxygen between stocked fish and offspring. This meant that there was no oxygen limitation mechanism on fish growth rate, resulting in higher simulated fish yields. Brummett (2000) noted that larger fish have higher absolute metabolic rates than small fish and are expected to experience oxygen stress more frequently than small fish. The other reason may have been the fact that a dietary shift from omnivory to macrophytophagy occurs in this fish species at 10–11 cm during the juvenile to adult transition (Caulton 1982), which was not included in the model. Thus, the behavioural and physiological changes occurring as the fish mature may restrict their ability to capture and digest foods other than plants (Bowen 1987). The model could therefore be improved by incorporating a function or parameter that captures the dietary shift from omnivory into macrophytophagy into the feed preference factor. In Fig. 3, sampling error, i.e. a sample with larger proportion of recruits, might have reduced the overall mean weight of fish in the ponds. Simulated fish biomass values were lower than observed in O. shiranus fish biomass in ponds. The failure of the model to replicate the observed fish biomass could have been because of the assumption on a spawning frequency of 21 days that may have contributed to having fewer fingerling recruits at the time of harvest. An alternative cause may be the absence of modelling reproduction-related processes. Reproduction affects growth through a loss of biomass during spawning and through energy expenditure. Thus the loss of biomass from spawned eggs could have contributed to the observed discrepancy. The assumptions that fish population in the pond is only affected by mortality rate, low-dissolved oxygen levels, acute ionized ammonia toxicity may also have contributed to discrepancies. There are other factors that affect fish population such as predation and poor handling during sampling. Predation and poor handling during sampling were not included in the model. de Graaf et al. (2005) incorporated mortality due to predation as a function of predator density and the standard length of the prey (Nile tilapia). In this case, predators such as monitor lizards, birds and otters are exogenous to the system and their interaction with stocked fish is difficult to model. Therefore, it is not recommended to explicitly model predation mortality in the production system modelled here. The problem of modelling predation exogenous to the

Table 3 Simulated net yield (kg ha⁻¹·year⁻¹) and net present value (NPV) (US$) of Oreochromis shiranus for different harvesting strategies in Scenarios I, II and III

<table>
<thead>
<tr>
<th>Harvest strategy</th>
<th>Scenario</th>
<th>Net yield</th>
<th>NPV</th>
<th>Net yield</th>
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<td>487</td>
<td>675</td>
<td>1521</td>
<td>967</td>
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<td>60 days</td>
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<td></td>
<td>III</td>
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Table 4 Indices for net yield and net present value (NPV) of Oreochromis shiranus for different harvesting strategies in Scenarios I, II and III

<table>
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<tr>
<th>Harvest strategy</th>
<th>Scenario</th>
<th>Net yield</th>
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<td>143</td>
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system could be a source of discrepancy that users of the model should be aware of. Poor handling on the other hand is a management problem and could be reflected by a multiplier whose values could range from 0 (very poor management) to 1 (very good management). This multiplier could then be incorporated in the population equation (Eq. (3)). The simulated fish biomass value at time of harvest for the treatment that involved *O. shiranus* in ponds receiving a daily input of maize bran was within one standard deviation to the observed value. In this treatment, the model generally replicated the pattern of fish biomass growth.

In this modelling study, the optimum time to harvest was similar on either maximizing yield or economic returns. This may be because daily feed cost was minimal and therefore the rate of change of fish biomass was close to the rate of change of net revenue.

All harvesting strategies for all given scenarios had positive NPVs, indicating profitable situations, and this can be explained by the fact that for harvest Scenario III, the first harvest is carried out at neither the optimum economic time nor the biological optimum time. For Scenarios I and II, no change in NPV or net yield arises from switching from a harvest strategy of every 60 days to every 90 days and every 120 days. This may be because of the assumptions made regarding reproduction, specifically on subsequent spawns occurring every 21 days. At the time of first harvest, most cohorts may have attained the harvest weight of 60 g. This could imply that by the first harvest the fish in the harvestable value of > 60 g may have included three or more cohorts, consequently leaving a large proportion of juveniles in the pond that took longer to reach the harvestable weight. In fact, in the subsequent periodic harvesting times, the fish farmers will be unable to harvest at all as the fish would not have reached the harvestable weight of 60 g. Thus, if the fish farmer was to harvest during those subsequent periodic harvesting times, the net yields and financial returns would be the same as the results indicated. It should be noted that partial harvesting relies on complementary and/or synergistic food partitioning among age groups (Brummett & Mattson 1996). This aspect was not included in this model. It is suggested that consideration of a full range of several scenarios and also varying the value of the fish weight at harvest could increase the utility of the model in determining optimal harvest strategies for mixed-sex tilapia culture.

Using these three scenarios as a base, the simulation results indicate that a harvesting strategy of every 120 days, starting at day 90 (Scenario III), can give greatest financial returns. Delaying partial harvest to start at 100 or 120 days is economically unattractive because these harvesting strategies in general give both low overall yields and NPVs by comparison. These results agree with the expected biological basis for harvesting when fish growth rate is at maximum (Pauly 1984).

Profitability of aquaculture operations can be affected by feed costs and fish prices. Feed is the single largest expenditure in semi-intensive and intensive systems (Mbahinzireki, Dabrowski, Lee, El-Saidy & Wisner 2001) and can constitute 40–50% of total production costs. Dey (2000) showed that profitability was sensitive to the variation of size of tilapia and the relative prices of different species. In this simulation study, sensitivity analysis of profitability levels in response to changes in input costs and fish prices was not performed because such analysis are site specific and depend on production and marketing conditions (cost of inputs, prices) prevailing in a specific location and therefore not relevant for this study. However, the model can be used as a business or production planning tool to identify profitable harvesting strategies and examine the impacts of varying input and output prices on the profitability of the production system in different locations. This information could be contained in production and technical manuals that can be used by farmers and extension workers.

The study shows that a cohort-based population growth model can be reliably incorporated in tilapia production models to simulate production of different mixed-sex tilapia production systems. However, incorporation of intergenerational competition effects could improve the model’s utility as a decision support tool for managing mixed-sex tilapia production. The study further suggests that partial harvesting has the potential of increasing yields and economic returns for small-scale fish farmers and that mixed-sex tilapia culture may be profitable for tilapia farmers in Africa where markets accept small (60–100 g)-sized fish and climatic conditions and water resources allow for more than 2 harvests year−1. Repeating this practice year in year may result in selection for early maturity and ultimately reductions in individual fish sizes and production. Therefore, to ensure that the farming remains profitable and sustainable in the long term, proper husbandry practices such as broodstock exchange and periodic complete harvests should be undertaken.
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