OPTIMISATION OF THE POND REARING OF NILE TILAPIA (*OREOCHROMIS NILOTICUS NILOTICUS* L.)

The impact of stunting processes and recruitment control

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Abstract

Stunting is often considered as a major bottleneck for the pond rearing of Nile tilapia (*Oreochromis niloticus niloticus* L.) and was a major topic in this study. Neonteny: the earlier breeding of tilapia in ponds takes place, but is not a bottleneck as with appropriate feeding levels the somatic growth is maintained. The study indicated that aggravation of the living conditions is not a major cause of the observed earlier breeding. Real stunting takes place at low feeding levels but can be avoided by higher feeding levels or by elimination of recruitment through polyculture with either the African catfish (*Clarias gariepinus* Burchell) and the African snakehead murrel (*Parachanna obscura* Günther). Recruitment of Nile tilapia is completely controlled at stocking densities of 8300 large catfish ha^{-1} or 725 large snakehead ha^{-1}. The difference in predation efficiency between the two species is related to their feeding strategies: omnivorous *vs* piscivorous. Mass production of fingerlings of the African catfish was carried out in ponds protected against frogs by aluminium roof plates. The results showed that the developed system is labour orientated, technical reliable and economic feasibly when the fingerlings can be sold for US$ 0.07 a piece. An Individual Based Simulation model for the pond rearing of the Nile tilapia for mixed or mono sex culture, and for poly culture with the African Catfish or African Snakehead is presented. The model visualized major underlying ecological processes in tilapia farming and indicated that growth and its relation to feed quality, recruitment and prey-predator relations are major topics in tilapia farming modelling. The model can serve as a predictive and decision-making support tool after some slight adaptations discussed.

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VOORWOORD

In 1986 vertrok ik naar Congo Brazzaville, mijn eerste lange standplaats, na enkele jaren gewerkt te hebben met graskarpers in Egypte, zalmforel in Nederland, zeebaars in Griekenland en garnalen in Vietnam. De Wereld Voedsel en Landbouw Organisatie van de Verenigde Naties (FAO) had mij aangenomen voor een project om de kweek van de Nijl tilapia te stimuleren op het platteland van Congo Brazzaville. In dit project moest ik mijn Congolese collegae assisteren bij de bedrijfsvoering van 5 viskwekerijen. Voor mijn vertrek verzamelde ik zoveel mogelijk literatuur over de teelt van Nijl tilapia. Tijdens het lezen, bleek al gauw dat "stunting" en/of de overmatige productie van jong broed, een van de belangrijkste problemen voor de teelt van Nijl tilapia was. Ingelezen en wel vertrok ik en ging aan de slag. Na wat eerste financiële problemen op de kwekerijen ging na 1.5 jaar de productie lekker lopen en behaalden we opbrengsten van 5-6 ton per hectare. Na anderhalf jaar vis voeren en mensen opleiden begon langzamerhand mijn interesse te verschuiven naar het willen begrijpen van fundamentele processen in de teelt van Nijl tilapia. Zeker omdat wij het zoveel genoemde "stunting" niet echt tegen kwamen. We hadden wel veel jongbroed maar bedrijfstechnisch was dit niet echt een probleem. Met het motto "meten is weten" zijn we op alle visteelt stations intensiever en meer regelmatig vissen gaan meten. Om de productie van de stations verder te verhogen, begonnen we de Nijl tilapia te kweken samen met lokaal beschikbare roofvissen (de Afrikaanse meerval en de Afrikaanse slangkopvis). Uitvoering van onderzoek was niet gepland in het project, en had ook geen prioriteit. Er was dan ook geen duidelijk onderzoeksprogramma en een budget. Alle "experimenten" kwamen voort uit een meer of minder voortgaande lijn in de bedrijfsvoering om de productie te verbeteren, aangevuld met wat "hobbyisme" van mijzelf, want vissen voeren gaat op een zeker moment ook vervelen.

Na vijf jaar kwam ik een ervaring rijker terug in Nederland en wist ik redelijk hoe ik Nijl tilapia in vijvers moest kweken en besloot ik om mijn ervaringen te gaan opschrijven. Nadat ik in 1992 mijn eerste epistel geschreven had vroeg ik Prof. dr. E.A. Huisman of hij er kritisch naar wilde kijken en er met een rode pen door heen te gaan. "Geen probleem", zei hij . Bij het tweede stuk vroeg hij mij hoeveel ik er nog wilde schrijven. Ik antwoordde "vier of vijf", en kreeg een tweede vraag: "Waarom ga je er niet op promoveren ?". Ja en waarom eigenlijk niet, misschien had ik toen "nee" moeten zeggen, want het duurde allemaal wat langer dan verwacht. De eerste drie meer biologische publicaties gingen redelijk vlot, ook gezien het feit dat ik het schrijven als een soort hobby naast mijn full-time werk als consultant deed. In het opkomende PC tijdperk gonsde het aan de leerstoel visteelt en visserij van de simulatie modellen en ook ik vond dat een Tilapia simulatie model een van de laatste onderdelen moest worden van mijn werk. Met dit model wilde ik mijn theorieën over "stunting" testen. Zo gezegd zo gedaan, en in 1997 bouwde ik samen met wat computer whizzkids en wat eigen geld een simulatie model.. Helaas het model kon mijn theorieën niet bewijzen en het geld was op. Mijn werk richtte zich op dat moment meer op de visserij en het was belangrijker daarover te publiceren. Gedurende enkele jaren sluimerde het simulatie model wat op de achtergrond en bleef Prof. dr. E.A. Huisman vragen hoe het met de voortgang ging. Ik was er nog steeds van overtuigd dat het simulatie model goed gebruikt zou kunnen worden als een trainings-module voor beginnende kwekers of studenten in de tropen, maar dan moest het wel aangevuld worden met economische en financiële modules. Verzoeken tot financiering hiervoor werd helaas overal afgewezen. In 2001 besloot Nefisco om met eigen financiering, in samenwerking met Pieter Dekker van Xi-advies, een opzet te maken voor een meer praktische versie van het model. De resultaten werden enthousiast ontvangen en in 2003 besloot GTZ (Duitse Ontwikkelings Samenwerking) om de ontwikkeling van de "economische optimalisatie module" van het simulatie model te financieren. Met als gevolg dat in Januari 2004 "TFST", Tilapia Farming Simulation Tool het levenslicht zag.

Door deze ontwikkelingen kwam er in 2003 ook weer vaart in de 'afgesproken promotie'. De wetenschappelijke basis voor "TFST" werd opgeschreven en in Januari 2004 kon ik Prof. dr. E.A. Huisman vertellen dat ik eindelijk klaar was.

In de hoop dat dit enige helderheid verschaft in de achtergronden en de lijn van dit proefschrift, wens ik U veel leesplezier, voor zover het lezen van proefschriften leesplezier kan verschaffen ☺.

Gertjan de Graaf

CHAPTER 1: GENERAL INTRODUCTION

AQUACULTURE DEVELOPMENTS AND THEIR IMPORTANCE FOR LOW-INCOME-FOOD-DEFICIT COUNTRIES (LIFDCS)

With a total reported production volume of 130 million tonnes (t) in 2000, fisheries and aquaculture are important for global food security, providing about 16% of the total animal protein supplies. However, the production statistics are strongly dominated by China and the reliability was questioned recently (FAO, 2002, Watson and Pauly, 2001). Therefore, the general practice is to discuss the production of China, separately from the rest of the world.

The world fish production (China excluded) totalled 92 million ton in 2002, of which 77% was obtained from marine fisheries, 7% from inland fisheries and 16% from aquaculture (Figure 1)

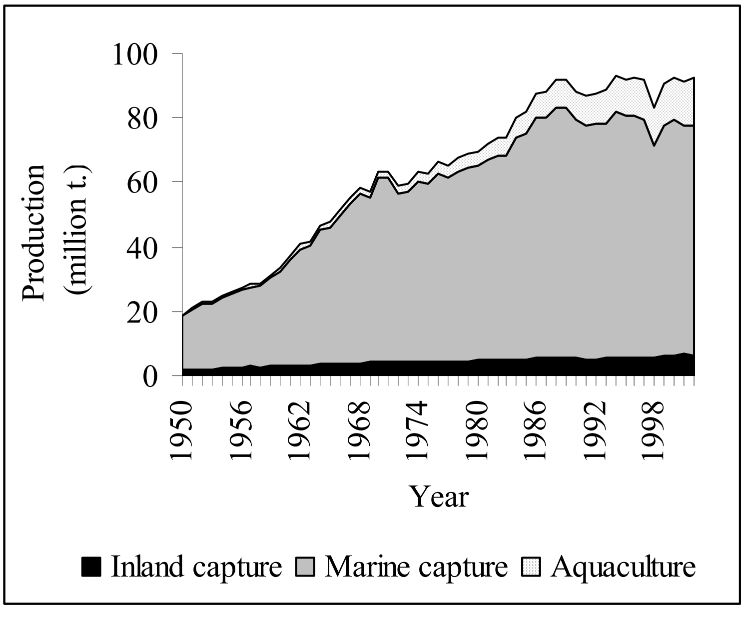

Figure 1: Historic world fish production (China excluded, FAO, 2003).

The contribution of inland and marine capture fisheries to the overall production stabilised in the period from 1980 to 2002. The contribution of aquaculture to the global supply of fish, crustaceans and molluscs increased from 3.5% of the total production in 1970 to 16.5% in 2002, giving an average compounded rate of 6.5% year^{-1}, compared with only 2.8% of farmed meat production systems (Delgado *et al*., 2003, FAO, 2003). Outside China, the world's population has been increasing more quickly than the total food fish supply from production, resulting in a decreased global per capita fish supply from 14.6 kg in 1987 to 13.1 kg in 2002 (FAO, 2002). Stabilising or increasing the per capita food availability can, therefore, only be obtained from aquaculture production, both from traditional rural aquaculture and intensive commercial aquaculture of high-value species (Delgado *et al*., 2003).

The bulk of the aquaculture production (70%) is raised in developing countries and low-income, food-deficit countries (LIFDCs). Aquaculture in LIFDCs has been growing steadily with about 8% year^{-1} since 1970, while aquaculture growth in industrial countries has been growing at an average rate of only 4% year^{-1} (Figure 2). Further, about 60% of the raised fish and crustaceans consist of omnivorous/herbivorous or filter feeding species, feeding at the bottom of the ecological chain, while only 29% of the production consists of the high value, carnivorous species, feeding at the top of the ecological chain (Figure 3). The remaining 11% consist of shrimps and prawns.

The importance of the omnivorous, herbivorous or filter feeders for aquaculture in LIFDCs is clear. In the LIFDCs, most of the fish are raised in ponds and 4.4 million tonnes year^{-1} or 55% of the total annual cultured fresh- or brackish water fish production (7.9 million tonnes year^{-1}) consists of 8-10 species only (Figure 4). With 12.1% of this total cultured production, Common carp (*Cyprinus carpio carpio* L) is the most important species, followed by Tilapia spp. with 9.3% and Silver carp *(Hypophthalmichthys mollitrix* Valenciennes 1844) with 8.4%. More details on the development of tilapia farming are presented in the next paragraph.

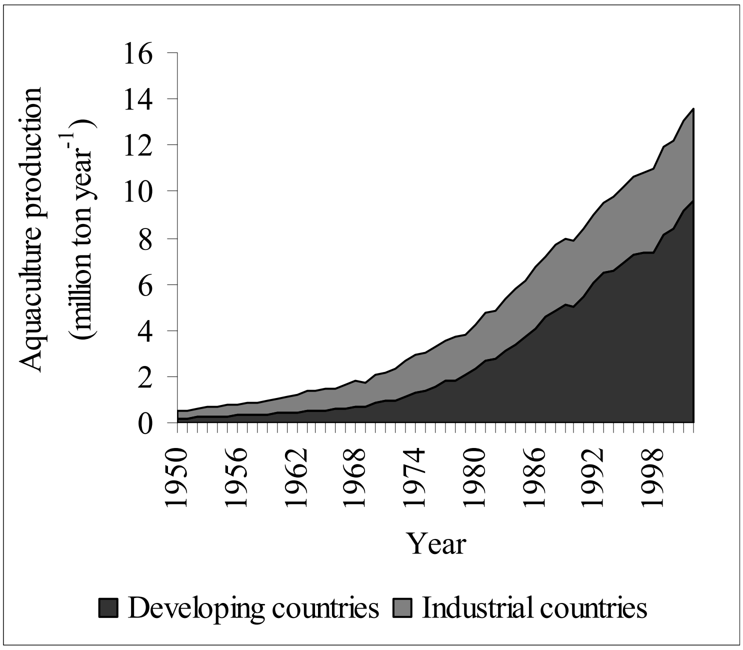

Figure 2: Aquaculture production in developing and industrial countries since 1950 (FAO, 2003).

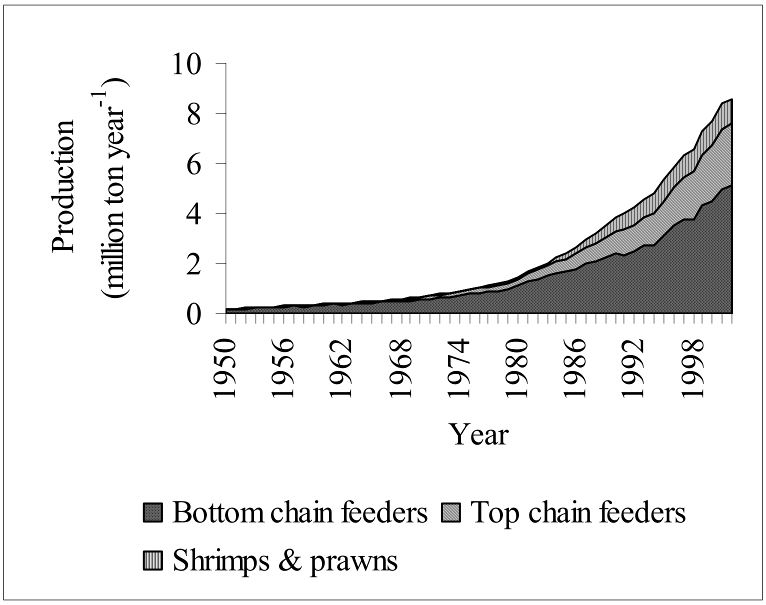

*Figure 3**:** Aquaculture production of omnivorous/herbivorous/filter-feeders, carnivorous fish and shrimp/prawns since 1950 (FAO, 2003).*

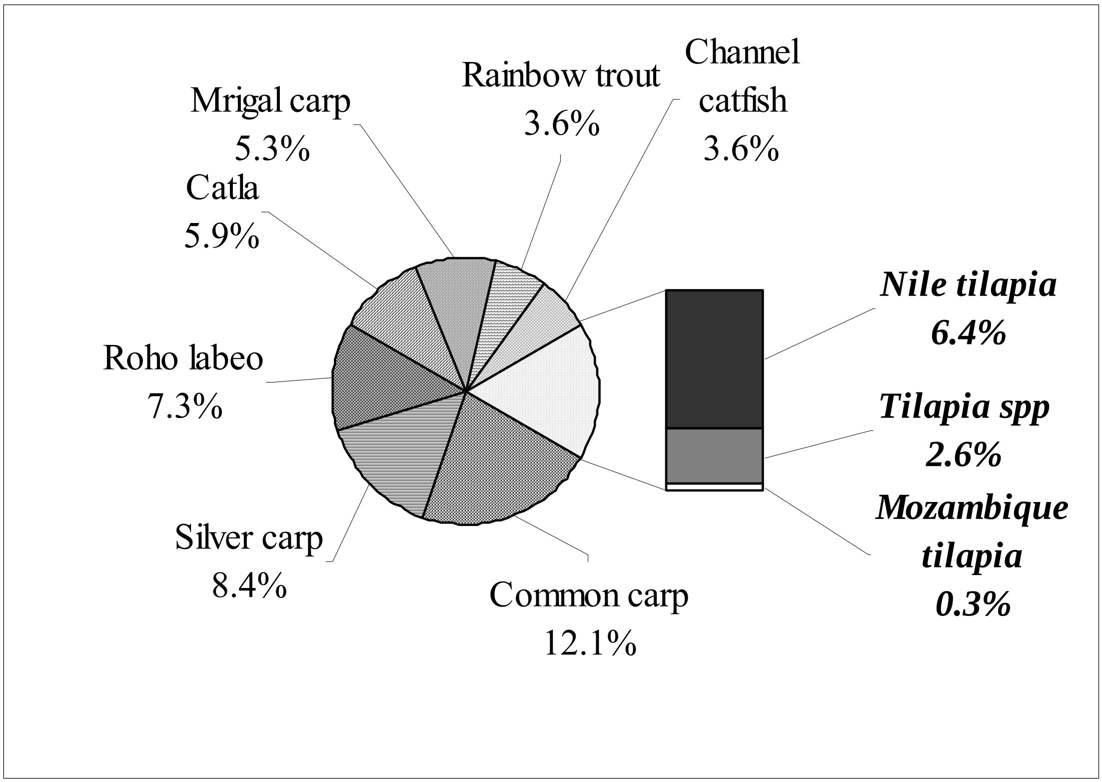

*Figure 4**:** Top-ranking species cultured in fresh or brackish water in 2002. Percentage indicates proportion of total annual aquaculture production in fresh or brackish water (FAO, 2003). Species; Nile tilapia (Oreochromis niloticus niloticus L), Mozambique tilapia (Oreochromis mossambicus Peters 1852), Common carp (Cyprinus carpio carpio L), Silver carp (Hypophthalmichthys mollitrix Valenciennes 1844), Roho labeo (Labeo rohita Hamilton 1822), Catla (Catla catla Hamilton 1922), Mrigal (Cirrhinus cirrhosus Bloch 1795), Rainbow trout (Oncorhynchus mykiss Walbaum 1792), Channel catfish (Ictalurus punctatus Rafinesque1818).*

TILAPIA FARMING

Tilapias, originally from Africa, have been reared for centuries. During the last 50 years, interest in their aquaculture potential has led to a nearly worldwide production and distribution. Because of its contribution to world food production through aquaculture operations, tilapias generated much enthusiasm in many developing countries after World War II. In the 1960s and 1970s, tilapia culture was geared towards the production of food for local consumption and for the diversification of rural activities related to agriculture and animal husbandry. Soon after its first expansion, tilapia culture made no further progress and has, in many cases, even declined, resulting in the abandonment of fish farms by discouraged farmers. This failure has been attributed to the harvesting of too many small stunted tilapia from over-populated ponds because of the use of poor husbandry techniques; the dependency on subsidized extension services and fingerling distribution centers; misjudgement of the motivation of the rural fish farmers by policy makers, and the creation of the myth that the rural farmer will willingly take up fish farming for food security or as a source of protein for their family; failure to apply adequate resources, which may be naturally limiting such as water and feed (Huisman, 1986, de Graaf and Janssen, 1996; Alceste an Jory, 2002).

It is often stated that the major biological problems in pond rearing of mixed-sexed Nile tilapia (*Oreochromis niloticus niloticus* L) is its excessive recruitment. At harvest, 28% to 70% of the total biomass consists of low-value fingerlings (Bardach *et al*. 1972; Ruwet *et al*., 1976; McGinty, 1985; Huisman, 1986; Lovshin *et al*., 1990). Under natural conditions, Nile tilapia starts to reproduce at a size of 20 cm to 30 cm (Lowe-McConnell, 1958 and Gwahaba, 1973). However, cultured Nile tilapia reproduces at a much smaller size of 8 cm to 13 cm or 20 g to 40 g. (Siraj *et al*., 1983; Melard, 1986; Galman *et al*., 1986 and de Silva and Radampola, 1990). The stunting of Nile tilapia can lead to a reduction of somatic growth. For reproduction of Nile tilapia, this would mean that spawners were “relatively old and small.” However, the smaller size at first maturation could also be caused by earlier breeding, and this would mean that spawners are “young and small.” From a production point of view, the two concepts are different as a reduction of somatic growth certainly reduces the final production, while earlier breeding does not automatically lead to a reduced level of production.

The majority of tilapia is still farmed traditionally in earthen ponds in rural areas. For individual farmers, extension officers or staff members of fisheries departments, the stunting of tilapia is still considered to be a problem, often because of negative experiences in the past. However, the poor husbandry techniques applied, such as low feeding rates and long rearing periods, are often not considered. For other species, poor husbandry techniques result in reduced or zero growth, but the impacts are less severe. If a farmer, who rears common carp, is short of money to buy feed for his fish, this will result in the carp not growing anymore, and may be even losing some weight. However, the carp will continue to grow once the financial position of the farmer improves and he starts feeding his fish again, so that he is still able to harvest fish of a commercial size. For tilapia farming, the picture is different, as even in periods without feeding they continue to reproduce. This worsens the availability of feed, and once the farmer starts feeding again there will be more “fish mouths” to be fed.

Monosex culture of males has been used in order to overcome this problem. The all-male fingerlings required are obtained through manual sexing (Shell, 1968), through hybridisation (Pruginin, 1967; Lovshin *et al.*, 1990), or through hormone-induced sex reversal (Eckstein and Spira, 1965; Guerrero, 1975; Shelton *et al.*, 1978). Major constraints for the successful use of monosex culture in rural areas are the relatively large size (35 g) of fingerlings needed for successful manual sexing, the difficulty to maintain pure strains of parent stock for hybridisation, and the availability or production of "sex-reversal" feed.

Another alternative to control the recruitment is the introduction of a predator fish. The following species were used with varying success in combination with Nile tilapia: *Micropterus salmoides* (McGinty, 1985), *Lates niloticus* (Lazard, 1980; Bedawi, 1985; El Gamal, 1992), *Ophiocephalus striatus* (Hopkins *et al.*, 1982), *Hemichromis fasciatus* (Lazard, 1980), *Cichla ocellaris* (McGinty, 1983; Verani *et al.*, 1983), and *Clarias gariepinus* (Lazard 1980; Janssen, 1985). The efficiency of a predator is determined by its capacity to prey upon the larval Nile tilapia. Piscivorous species like *Ophiocephalus striatus* require lower stocking densities to eliminate all fingerlings than the more omnivorous *Clarias gariepinus* (Hopkins *et al.*, 1982; Janssen, 1985).

The methods applied in tilapia farming are diverse; it can be a mixed culture, poly-culture with predators or mono-sex, and all male culture. Next to the use of proper husbandry techniques, the success of the rearing method applied depends on local consumer preferences, economics, availability, and costs of inputs. For example, in Congo-Brazzaville, mixed culture is financially feasible as the market accepts all sizes of tilapia. Poly-culture with snakeheads applied to reduce the number of fingerlings at harvest, does not improve the financial performance because the resulting improved tilapia growth did not compensate for the reduction in gross product value generated by the sale of the fingerlings. However, in Ivory Coast, a mono-sex, all-male culture is a prerequisite as the market demands tilapia with a weight of 250 g or higher (de Graaf, unpublished data).

- Since 1970, the farmed tilapia production in Asia (excluding China) increased on the average 11.5% year^{-1} and reached 0.48 million tons in 2002. In Africa, the production remained more or less stable until 1997 and increased rapidly since then to an annual production of about 0.19 million tonnes in 2002 (Figure 5). The production in North America and South America is relatively low (45,000 and 75,000 tonnes year^{-1}), but the production is growing at an impressive average annual rate of 57% and 37%, respectively.

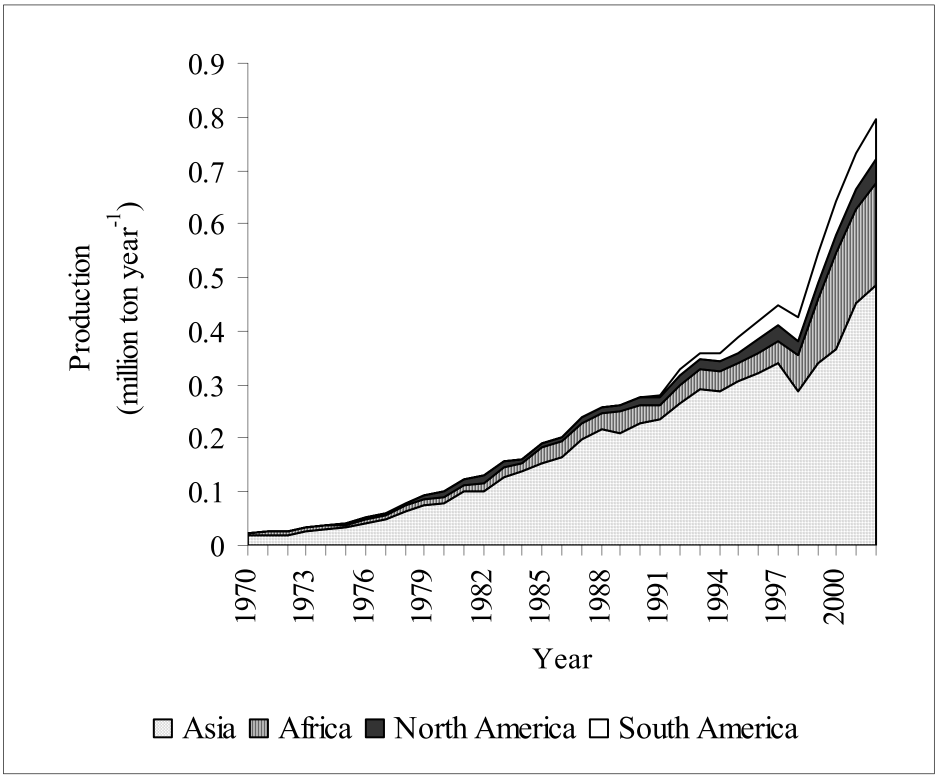

Figure 5: Annual production of farmed tilapia obtained in Asia, Africa, South America and North America (FAO, 2002).

The top producing countries, if based upon per capita annual production of tilapia, are the Philippines, Thailand, Nicaragua and Jamaica (Figure 6).

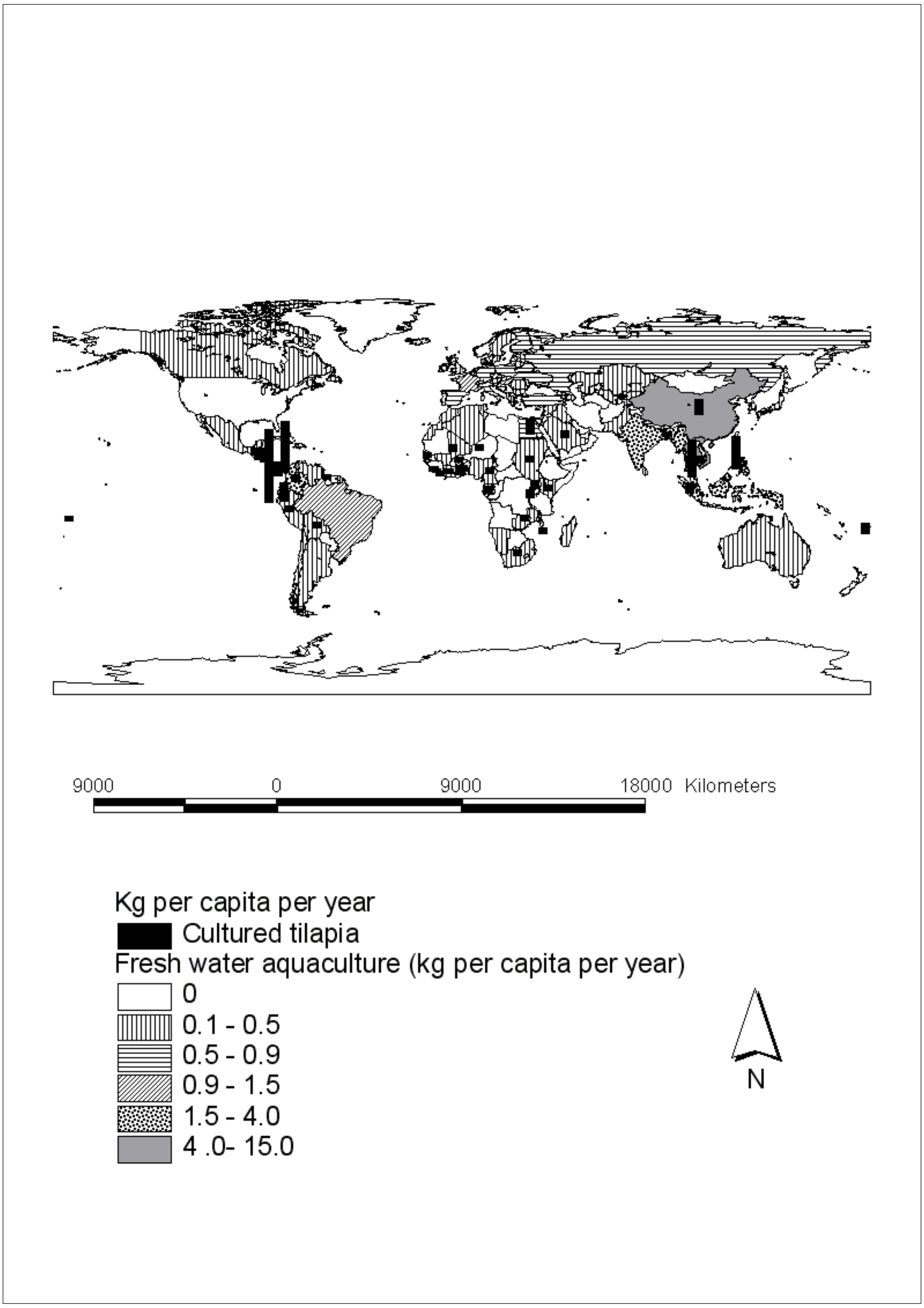

Figure 6: Worldwide distribution of total freshwater aquaculture production and cultured tilapia (kg capita^{-1} year^{-1}).

Much of this boom is attributable to an expanded area and, to a much lesser extent, to improved husbandry techniques (Delgado *et al.*, 2003). However, fresh water will become an increasingly scarce resource over the next 20 years (Rosegrant *et al.*, 2002), making further expansion of the area for freshwater aquaculture difficult. Consequently, further expansion of farmed production has to be obtained through improved husbandry techniques increasing the yield ha^{-1}. There is considerable scope for this expansion, as 65% of the worldwide farmed tilapia is produced without the use of modern compound feeds (Naylor *et al*., 2000). Even without advocating the use of compound feeds, the obtained production levels of 2 to 3 t ha^{-1} $year^{-1}$, as obtained, for example, in Bangladesh (de Graaf and Latif, 2002), are far below the production levels of, for example, 4 t to 6 t ha^{-1} $year^{-1}$, obtained with relatively simple all male tilapia farming systems in ponds, where agricultural by-products were used as feed (Lazard, 1986). This intensification will be facilitated by economic processes. Low–yield systems tend to be more common when skilled labour and land is ample available (Kusumanstanto *et al*., 1998; Delgado *et al*., 2003). As demand for aquaculture products grows and investment levels rise, the value of cultivated area rises relative to labour and purchased inputs, provoking substitution of the latter for the former (Delgado *et al*., 2003). As a consequence high-value aquaculture will intensify. However, the rate of intensification will depend on reliable cost-effective husbandry techniques, availability of inputs, effective market chains, and extension of the husbandry techniques towards the individual farmers.

OVERVIEW OF THE CHAPTERS

The major objective of the present study was to optimise husbandry techniques of the pond rearing of Nile tilapia in relation to its excessive reproduction. The study can be divided in three main topics:

1. The reproduction of pond reared Nile tilapia
2. The impact of recruitment on growth of Nile tilapia and the consequences for management
3. Development of a simulation model for the pond rearing of Nile tilapia

The thesis is divided in seven chapters.

Chapter 1 provides information on the present status of aquaculture and its importance for the world food supply. Further it provides an overview of the developments and problems encountered with the rearing of Nile tilapia and set the frame for the present study.

Chapter 2 describes the reproductive biology of pond reared Nile tilapia. Length at first maturation and gonadal and oocytes development is studied in order to give an answer on the question of whether the so-called stunting of Nile tilapia is caused by "early breeding" or by "reduction of somatic growth". From a management point of view the two are fundamentally different, as "early breeding" does not have to lead to lower yields, while "reduction of somatic growth" always lead to lower yields. In the latter case the stocked tilapia are growing slowly and are relatively old when they reproduce.

Chapter 3 addresses the question if excessive recruitment automatically leads to stunting of somatic growth of Nile tilapia. It describes the results of poly-culture of Nile tilapia with African catfish or African snakehead murrel as carried out in Congo Brazzaville. The efficiency of recruitment control by the two predators is analysed. Further the impact of the predator, its size at stocking, and its stocking density is analysed with respect to key husbandry parameters for Nile tilapia. In the analysis special attention is given to the impact of recruitment on the growth of the original stocked Nile tilapia.

Chapter 4 describes a method for the mass production of fingerlings of African catfish in earthen ponds. This method is developed, as fingerlings were needed for the experiments described in Chapter 3.

Chapter 5 describes an individual based simulation model using a population dynamics approach. The model was developed to test the hypothesis that stocking ponds with fingerlings of 25-35 gram, propagated in Africa, will lead to a change in sex ratio, of the stocked fingerlings, if low feeding levels are used. The latter is explained in Figure 7.
Figure 7-A, presents the distribution of fingerlings, original stocked females and original stocked males at harvest of properly fed ponds. The average weight at harvest is 25, 110, 220 gram for respectively fingerlings, stocked females and stocked males (de Graaf, unpublished data). In this case, selecting fish of 25-35 g, for stocking of the next pond, will result in stocking with "real fingerlings".

In Figure 7-B, the distribution at harvest is presented for a pond not fed properly, where stunting of somatic growth occurred. In this case the average weight at harvest is 20, 60, 135 g, for respectively fingerlings, stocked females and stocked males. Selecting fish of 25-35 g will result here in using "real fingerlings" and "old but small females" for stocking the next pond. The overall consequence is that more females are stocked, leading to even higher recruitment and a further reduction in growth.

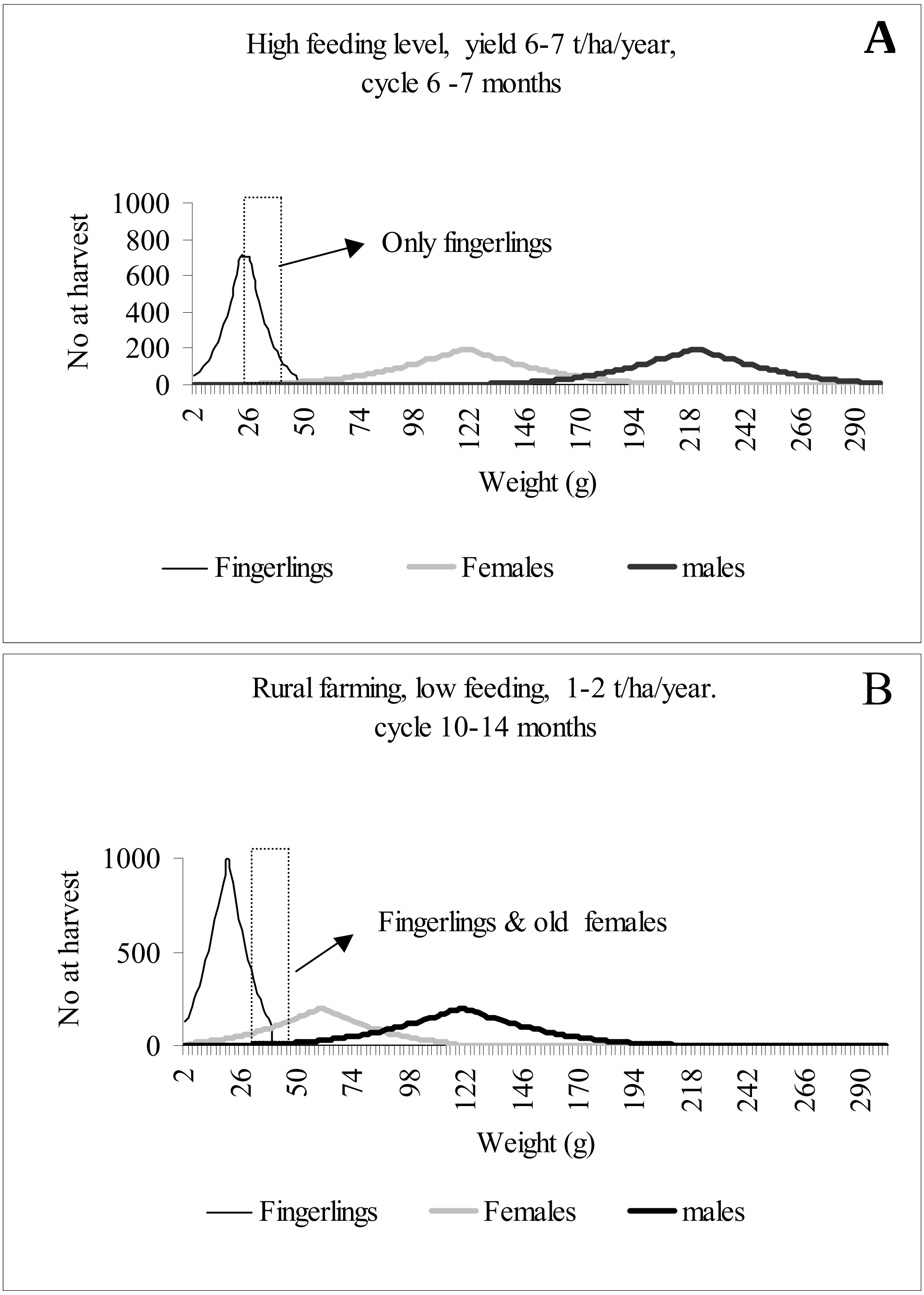

Figure 7: Distribution at harvest of fingerlings, stocked females and stocked males of Nile tilapia from ponds properly fed (A) and from ponds with limited feeding (B).

Due to the hypothesis, for the simulation model a population dynamics approach was needed, as the major topics are growth and recruitment. Individual based modelling was deliberately chosen as it allows inclusion of stochastic behaviour. To extend its use, prey-predator relationships were added to the initial model. The model was calibrated with data from Congo Brazzaville and validated with three in depended datasets. The results of validation will indicate the reliability of the model of international use.

Chapter 6 describes the use of the von Bertalanffy growth function in aquaculture experiments. The von Bertalanffy growth curve is one of the basic elements in the model described in chapter 5 and is gaining popularity in aquaculture experiments. However, the von Bertalanffy growth function has different characteristics if compared with traditionally used growth functions. The characteristics are discussed and three multivariate models for the von Bertalanffy growth function are developed and tested with a dataset of tilapia farming from the Philippines. One of the multivariate models was used in the validation of the model described in Chapter 5.

Chapter 7 presents a discussion on the overall results. Stunting is placed in an evolutionary context, is discussed in relation to husbandry techniques. Further developments of pond rearing of Nile tilapia and eventual use of the simulation model are discussed

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CHAPTER 2: THE REPRODUCTIVE BIOLOGY OF POND REARED NILE TILAPIA (*OREOCHROMIS NILOTICUS NILOTICUS* L.)

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ABSTRACT

The reproductive performance of female Nile tilapia, *Oreochromis niloticus niloticus* L., reared in ponds under tropical conditions was studied. The experiments used stock matured to the age of 2-4 month and a size of 30-50 g. Oocyte development proved a better indicator for the determination of the size at first maturation than the development of the gonado somatic index. The Nile tilapia became "stunted" in the sense that early breeding took place, but the somatic growth of the stock still continued. This result indicates that earlier breeding of Nile tilapia is not a real bottleneck for the expansion of this production sector. No relation was found between the condition factor and the size at first maturation or the relative fecundity. This led to the conclusion that aggravation of the living conditions is not a major cause of earlier breeding of pond reared *O. niloticus*.

Key words: fecundity; stunting; *Oreochromis niloticus niloticus* L; reproduction; oocyte development; pond rearing.

INTRODUCTION

Nile tilapia, *Oreochromis niloticus niloticus* L. is an important species in aquaculture because of its fast growth and its resistance against harsh conditions. Fingerlings of *O. niloticus* are easy to produce and reproductive potential is influenced by the environment (Lowe-McConnell, 1982), the year class (Siraj *et al.*, 1983; Rana and Macintosh, 1988), the protein level of the feed (Wee and Tuan, 1988; de Silva and Radampola, 1990) or by strain differences (Hulata *et al.*, 1988; Lester *et al.*, 1988 and Smitherman *et al.*, 1988).

However, excessive recruitment and subsequent stunting of *O. niloticus* in grow-out ponds is often seen as a major problem in tilapia farming (Bardach *et al.*, 1972; Ruwet *et al.*, 1976; Guerrero, 1982; McGinty, 1985 and Lovshin *et al.*, 1990). The massive numbers of fingerlings, born during the rearing period, use the feed intended for the stocked adults. Consequently the growth rate of adult tilapia decreases and fewer marketable-sized fish can be harvested (de Graaf *et al.*, 1996). Under natural conditions *O. Niloticus* starts to reproduce at a size of 20-30 cm (Lowe-McConnell, 1958 and Gwahaba, 1973). However, cultured *O. Niloticus* reproduces at a much smaller size of 8-13 cm or 20-40 g. (Siraj *et al.*, 1983; Melard, 1986; Galman *et al.*, 1986 and de Silva and Radampola, 1990).

The stunting of *O. niloticus* can lead to a reduction of somatic growth. For reproduction of *O. niloticus* this would mean that spawners were “relatively old and small”. However, the smaller size at first maturation could also be caused by earlier breeding and this would mean that spawners are “young and small”. From a production point of view the two concepts are different as a reduction of somatic growth certainly reduces the final production, while earlier breeding does not lead automatically to a reduced level of production.

The objective of the present study was to determine the reproductive performance of female *O. niloticus* reared in ponds under tropical conditions and relate this to stunting processes.

MATERIALS AND METHODS

EXPERIMENTAL PROCEDURES

The present study was carried out between 1989-1990 at the National Fish Culture Station, Djoumouna, Republic of Congo. *Oreochromis niloticus* was reared in grow-out ponds (0.2-1.2 ha) with a stocking density of 2.0-2.2 m^{-2}. The fingerlings used for stocking were obtained from nursery ponds (0.01-0.05 ha) and were about 2-3 months old. The fish were fed six days per week with wheat bran at a daily ration of 6%-11% of the total biomass, adjusted monthly to take into account the changing size of *O. niloticus* (Table 1).

*Table 1**:** The feeding level as used for* O. niloticus *at the fish culture station of Djoumouna (Republic of Congo).*

Average weight of fish (g)	Feeding level (% of total biomass day^{-1})
0-25	11
25-50	10
50-100	9
100-150	7
150-200	6

The Nile tilapia used in the present study was a cross between a stock of un-traceable origin, present in the Congo from the mid 50s and a "Red-Benin" stock imported from Ivory Coast in the early 80s.

Female *O. niloticus* were sampled when the ponds were stocked, during the grow-out period and at harvest. The weight of the sampled specimens varied between 10 and 150 g. Body weight, total length and the weight of the ovary were determined for all sampled specimens (n=532). A part of the ovary was taken from 154 females, and this was weighed and preserved in 10% formaldehyde, after which the length of 75-100 oocytes (oocytes are pear-shaped) was measured and classified as “white” or ‘yellow” according to their colour. The total number of oocytes larger than 1.2 mm, was counted in 104 preserved samples.

Production parameters of 4 sampled grow-out ponds were determined. At harvest, the total weight of *O. niloticus* was determined and 300-1000 specimens were sampled at random, weighed individually, and classified as male, female or fingerling.

ANALYSES OF DATA

The Gonado Somatic Index (GSI, %) was calculated as:

$$GSI = \left(\frac{Weight\ ovary}{total\ body\ weight} \right) 100$$

The condition factor (K, g.cm^{-3}) was calculates as:

$$K = \left(\frac{body\ weight}{body\ length^3} \right) 100$$

A histological examination of ovaries of *O. niloticus* obtained from ponds in Kenya and Bangladesh indicated that “yellow oocytes” are mainly oocytes in yolk globule stage (de Graaf, unpublished data). Therefore, in the present paper the “white” and “yellow” oocytes were classified as peri-nucleolus/yolk-vesicle and yolk globule oocytes, respectively

The means of all GSI-values, K-values and oocyte lengths are presented with the standard error of the mean (± SEM). A one-way analysis of variance (ANOVA) was used in comparing the mean length of the peri-nucleolus/yolk vesicle and yolk globule oocytes at different weight classes of females, whereby the data were grouped in weight classes of 0-10 g., 10.1-15 g., 15.1-20 g., and so on.

In order to study the relation between the condition factor and the fecundity of females, all data were grouped in the following length classes; 9.1-10, 10.1-11, 11.1-12 and 12.1-13 cm; significance of correlation was tested in and between these classes.

All curves were fitted with the computer program MsExcel and significance of correlation was tested with a Spearman rank correlation test (Sokal and Rohlf, 1981).

RESULTS

SIZE AT FIRST MATURATION

The sexual maturation of the female Nile tilapia becomes visible through development of the oocytes of young females obtained from nursery ponds. (Figure 1). Only peri-nucleolus/yolk vesicle oocytes with an average length of 0.57±0.17 mm were found in the ovaries of females weighing 0-10 g. In the 10-15 g. weight class, yolk globule oocytes with an average length of 1.84±0.07 mm appeared. The yolk globule oocytes increased significantly ($P \leq 0.01$) to a length of 2.31±0.16 mm in 25-30 g. weight class, while the length of the peri-nucleolus/yolk vesicle oocytes did not change significantly. In females larger than 30 g. the average length of the yolk globule oocytes was 1.83±0.06 mm and no significant differences were found among the higher weight classes indicating a size at first maturation of 30 g.

The smallest mature female found, had a weight of 12.7 g, a length of 8.7 cm and a GSI of 5.3%. The relation between the average GSI and the body weight of female Nile tilapia is presented in (Figure 2) and can be described with the following equation:

$$GSI = \frac{1}{0.32 + \frac{63.3}{body\ weight^2}} \qquad (R=0.\ 68,\ P \leq 0.01)$$

This relation indicated a size at first maturation of approximately 40 g if the GSI (2.9%) is used as a major indicator for reproduction of *O. niloticus*.

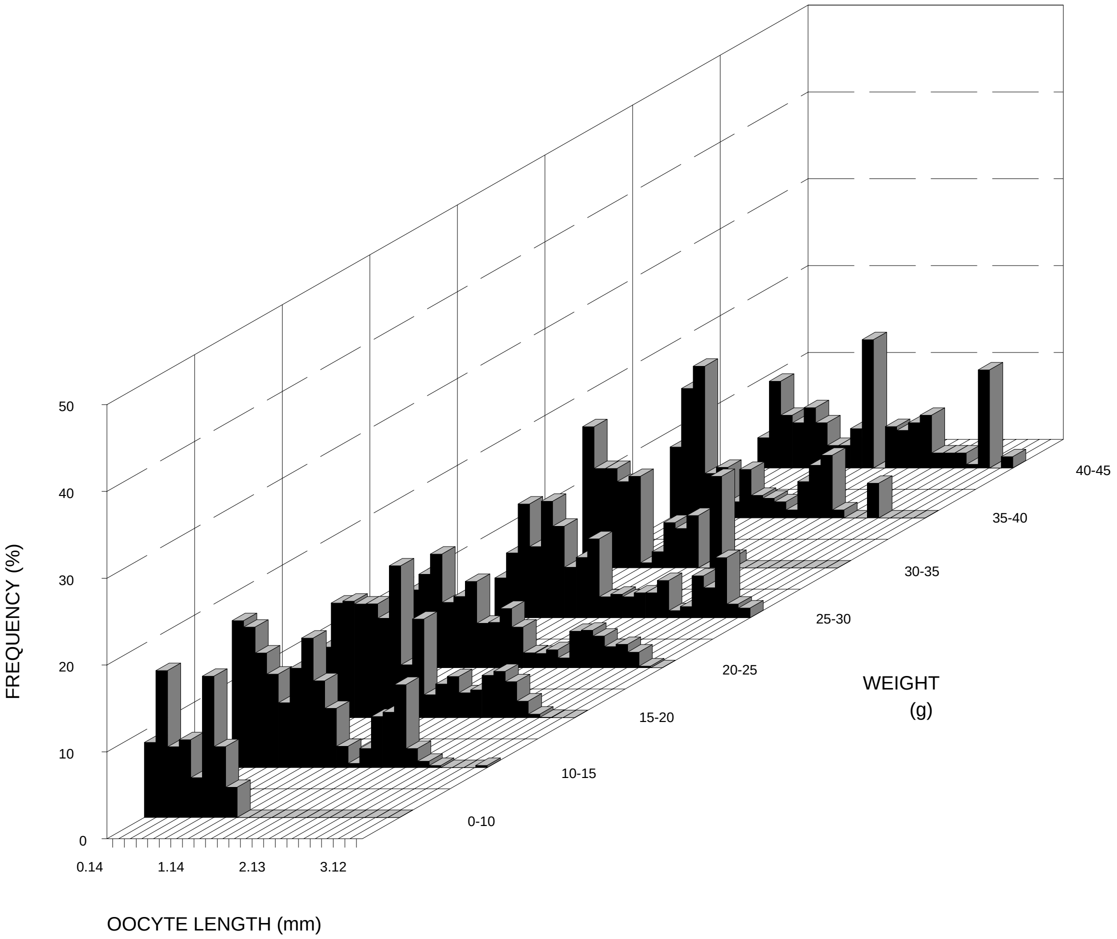

Figure 1: The frequency distribution of oocytes in different weight classes of young, pond reared, O. niloticus.

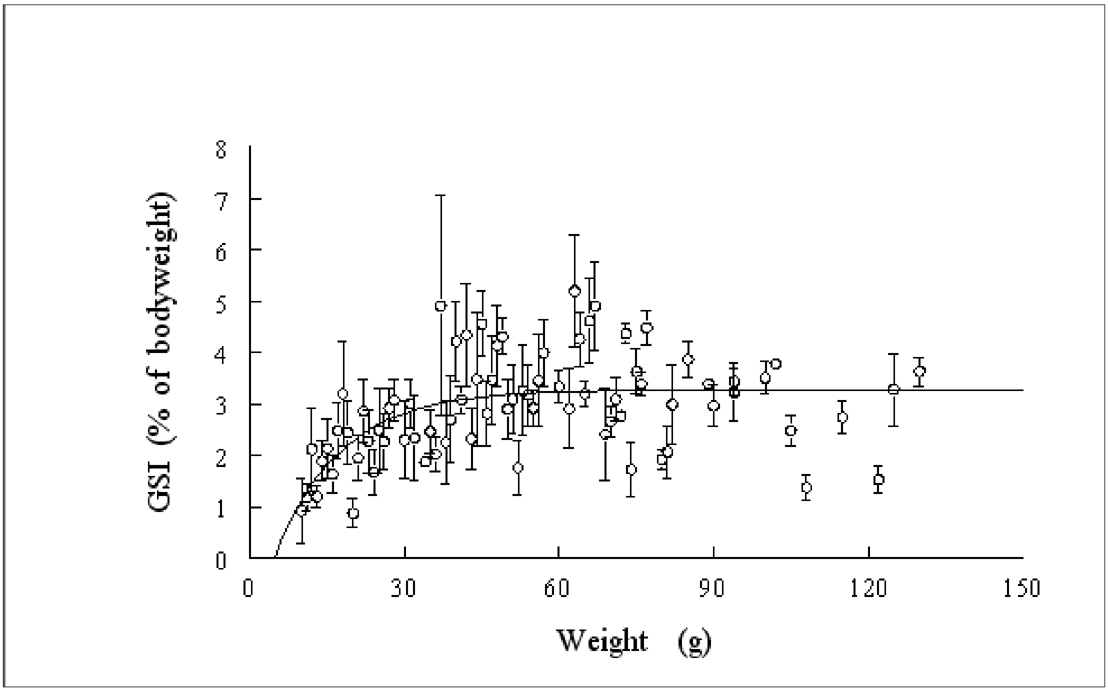

Figure 2: The relation between the weight (g) of pond reared female O. niloticus *and their Gonado Somatic Index (% of body weight).*

OOCYTES DEVELOPMENT

The relation between the GSI and the frequency of occurrence of the different sizes of the oocytes is presented in Table 2. Figure 3 presents the relation between the GSI and the length of peri-nucleolus/yolk vesicle and yolk globule oocytes. At a low GSI (0-1%), the ovary contained mainly peri-nucleolus/yolk vesicle oocytes with an average length of 0.56±0.02 mm, and the average length of the peri-nucleolus/yolk vesicle oocytes remained unaffected with increasing GSI values (Figure 3). Yolk globule oocytes appeared at a GSI of 1-2 % and their size and their frequency of occurrence increased throughout the further development of the ovary (Figure 3, Table 2). The two types of oocytes were clearly separated because of their difference in: colour, size and frequency of occurrence. Figure 3 further indicates a maximum length of 1.2 mm for the peri-nucleolus/yolk vesicle oocytes and a length range from 1.4 to 2.7 mm for the yolk globule oocytes. No significant relationship was found between the size of the female and the length of the yolk globule oocytes.

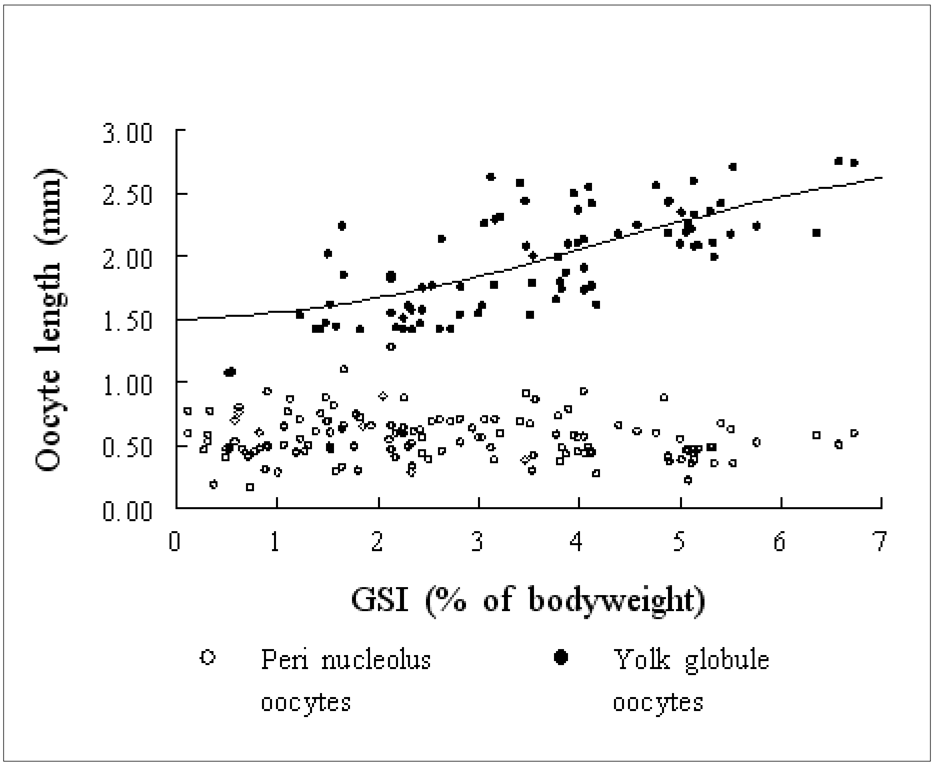

Figure 3: The relation between the Gonado Somatic Index and the length of peri-nucleolus and yolk globule oocytes of pond reared O. niloticus.

Table 2: Percentage of occurrence (± SEM) of peri-nucleolus/yolk vesicle and yolk globule oocytes in relation to the gonado somatic index (GSI, % of body weight) of the ovary.

GSI class (%)	Peri-nucleolus/yolk vesicle oocytes (length ≤1.2 mm)	Yolk globule oocytes (length > 1.2 mm)	No. of fish analysed
0 – 1	98.8±0.23	1.21±0.23	27
1 – 2	85.3±4.11	14.7±4.11	32
2 – 3	76.9±4.57	23.1±4.57	29
3 – 4	52.8±3.18	47.2±3.20	25
4 – 5	47.0±4.61	53.0±4.61	17
5 – 6	40.4±4.70	59.6±4.70	21
6 – 7	15.5±12.61	84.5±12.61	3

FECUNDITY AND CONDITION FACTOR

Absolute fecundity was determined as the number of yolk globule oocytes in the ovaries of females with a GSI larger than 3%. This in order to count only the most advanced stages of yolk globule oocytes which were expected to ovulate during the next spawning period. This relation between the length of the females and the absolute fecundity is presented in Figure 4.

The absolute fecundity varied between 50 and 220 oocytes per fish and increased with increasing fish length. This relation can be described with the curve:

$$F = 1.060L^{1.91} \qquad (\mathrm{R}=0.56,\ P \leq 0.01).$$

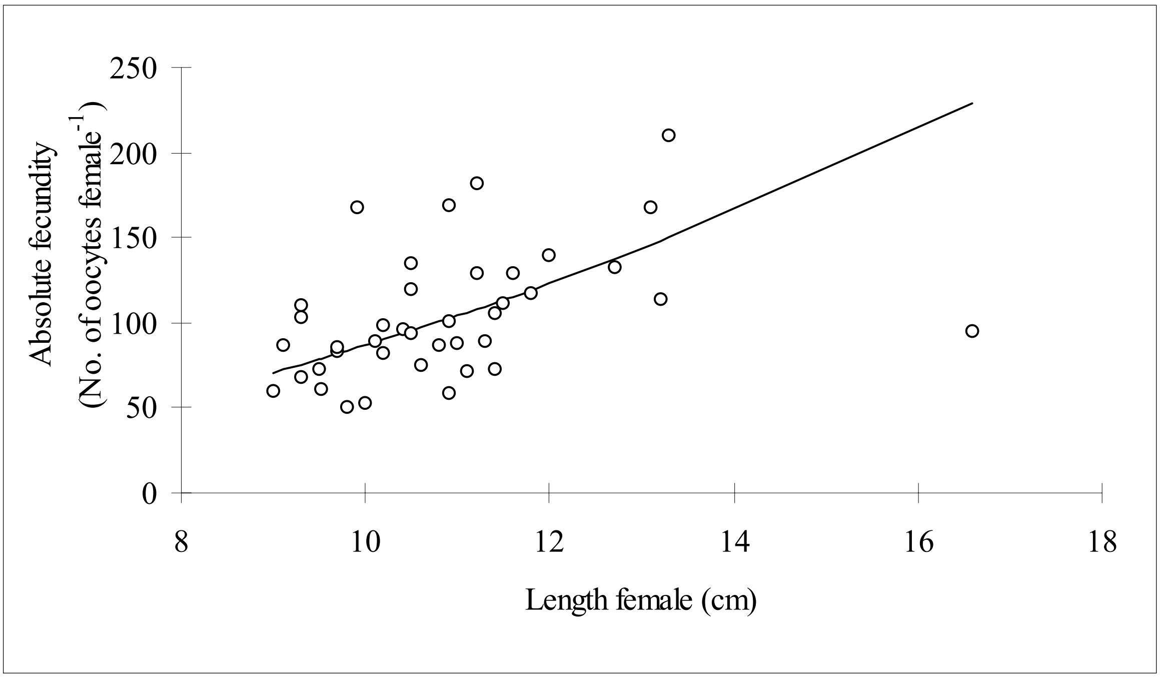

Figure 4: The relation between the length (cm) of pond reared O. niloticus *and the absolute fecundity (no. of yolk globule oocytes per female). The value at a length of 16 cm was not used for the calculation of the regression line.*

The relative fecundity (number of yolk globule oocytes per gram female) is presented in Figure 5 and this figure decreased from six oocytes per gram at a length of 9 cm to two oocytes per gram at a length of 16 cm. The relation can be described with the curve:

$$F = 37.8L^{-0.92} \qquad (R=0.31, P \leq 0.08)$$

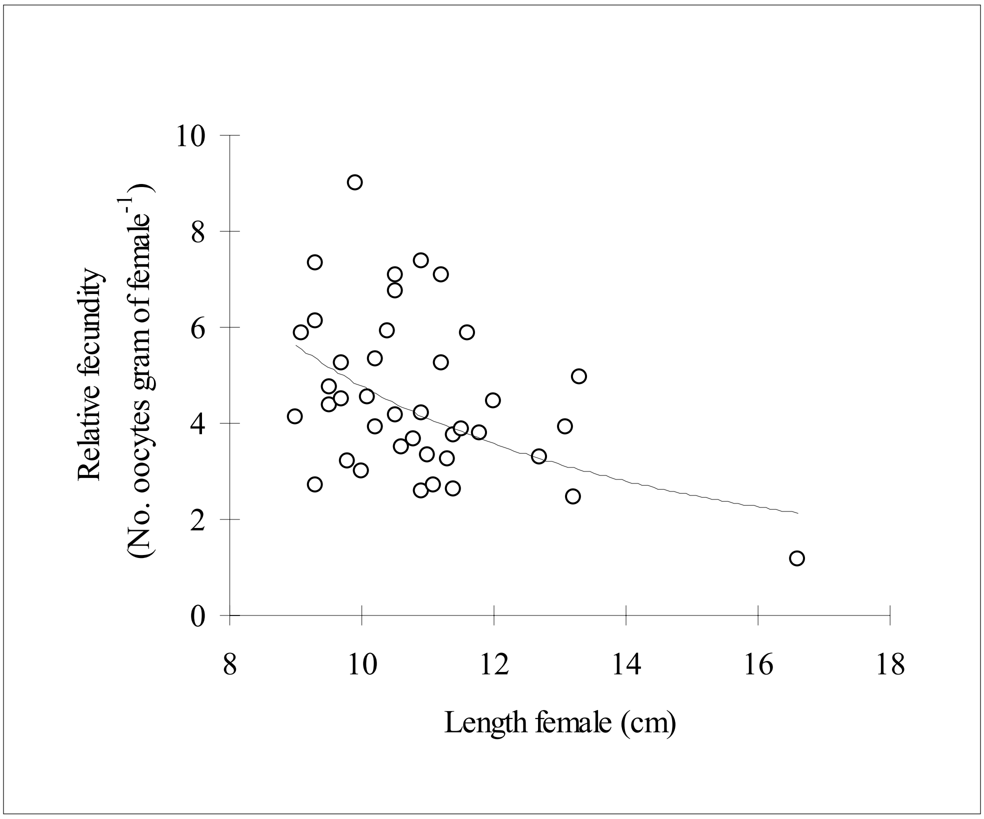

Figure 5: The relation between the length (cm) of pond reared O.niloticus *and the relative fecundity (no. of yolk globule oocytes per gram of female). The value at a length of 16 cm was not used for the calculation of the regression line.*

The condition factor of female Nile tilapia varied between 1.40% and 3.14% with an average ± SEM of 1.87±0.032. No significant relation existed ($P \geq 0.05$) between the condition factor and the absolute or relative fecundity in the different length classes.

PRODUCTION PARAMETERS AND GROWTH RATES

The mean production parameters and growth rates of *O. niloticus* as obtained from the sampled grow-out ponds (n=4) are presented in Table 3.

Table 3: Mean production data (± SEM) for O. niloticus *in grow-out ponds (n=4).*

Production parameter	Mean ± SEM
Average stocking weight (g)	20.3±5.5
Rearing period (days)	219±7.8
Standing stock at harvest (kg ha^{-1})	4814±647
Net yield (kg ha^{-1} day^{-1})	20±2.4
Average weight of male tilapia at harvest (g)	192±7
Average weight of female tilapia at harvest (g)	69±4
Average weight of tilapia fingerlings at harvest (g)	14.6±1.5
Growth rate male tilapia (g day^{-1})	0.78±0.03
Growth rate female tilapia (g day^{-1})	0.22±0.02

DISCUSSION AND CONCLUSIONS

OOCYTE DEVELOPMENT

O. niloticus is a “plurimodal spawner”: several groups of oocytes in different stages of vitellogenesis are found in females and each group slightly larger than the previous group (Hyder, 1970; Babiker and Ibrahim, 1979 and Peters, 1983). The most advanced yolk globule oocytes ovulate at spawning, after which the GSI drops to 1-1.5%, and 14% of the remaining oocytes are in a yolk vesicle or yolk globule stage (de Graaf, unpublished data on *O niloticus* from Kenya and Bangladesh). These remaining, smaller yolk globule oocytes will continue to develop and ovulate in the next spawning period. This phenomenon explains the relative short time of 30-40 days, in between different spawnings (Ruwet *et al.*, 1976) as well as the more or less continuous seed production in hapa-systems after daily removal of eggs and fry (Hughes and Behrends, 1983 and Verdegem and McGinty, 1987).

SIZE AT FIRST MATURATION

In young *O. niloticus* the yolk globule oocytes reached a maximum average length of 2.31±0.16 mm at a body weight of 25-30 g, whereas the average length slightly decreased to 1.83±0.06 mm, in the weight range of 30-45 g. The most likely cause for this is that a number of sampled females spawned just prior to sampling. Consequently, the remaining, less advanced yolk globule oocytes reduced the mean length of all measured yolk globule oocytes.

A maximum mean GSI of 3% is reached at a body weight of 40-50 gram. This size at first spawning is larger than the size at first spawning as indicated by oocyte development. However determination of the exact size at first maturation by using the GSI is difficult as *O. niloticus* does not have a distinct spawning period; this species reproduces once the fish are mature and once spawning criteria (e.g. temperature, mating) are met. Consequently, all the different stages of oocyte development and related GSI levels are found in females larger than the size at first maturation, resulting in an average GSI of 3%.

A first time maturation size of 30-50 gram is not exceptional for reared Nile tilapia. Similar sizes at first maturation have been reported by Siraj *et al.*, (1983); Melard (1986); Galman *et al.*, (1988); Lester *et al.*, (1988) and de Silva and Radampola (1990). However, the size at first maturation of the Nile tilapia used however, is small compared to a size of 20-30 cm (150-250 g) at which these fish reproduce under natural conditions (Lowe-McConnell, 1958 and Gwahaba, 1973). Therefore, it seems that the tilapia used in the experiment became "stunted" in the form of early breeding. However, this stunting did not lead to a reduction of somatic growth since a mean growth rate of 0.78 g day^{-1} for males and a mean net yield of 7400 kg ha^{-1} year^{-1}, as obtained from the sampled grow-out ponds (Table 3) is comparable with growth rates of 0.6-1.2 g day^{-1} and net yields of 5600-11000 kg ha^{-1} year^{-1}, as obtained in monosex male tilapia in cages or all-male tilapia hybrid culture in ponds using commercial pellets or chicken feed (Coche, 1977; Lovshin *et al.*, 1990; Philippart *et al.,* 1979 and Melard, 1986). The growth rate of the *O. niloticus* stock used in the present study could be further increased by removing the fingerlings through the use of a predator such as *Clarias gariepinus* (Burchell) or *Ophiocephalus obscures* (Gunther 1861), while the fish still continued to reproduce at an early age as was found by de Graaf *et al.*, (1996). The present results indicate that stunting in the form of earlier breeding is not a major bottleneck for the expansion of the Nile tilapia production sector.

According to Lowe-McConnell (1982), factors such as a low condition factor, lower water depths, a smaller habitat or a high fishing intensity could lead to earlier breeding. In the present study, the pond reared *O. niloticu*s had a relatively high condition and still started to reproduce at an early age and small size. This could indicate that aggravation of the living conditions is not a major cause of earlier breeding of pond reared *O. niloticus*

FECUNDITY

The general definition of Bagenal (1968) "fecundity is the number of ripe oocytes in the female prior to the next spawning" was used in the present study. In *Tilapia spp*. and *Oreochromis spp*. the number of spawned eggs depends on the weight of the ovary or the GSI, the size of the eggs, the size or age of mature females and the degree of parental care (Welcomme, 1967; Hyder, 1970; Siddiqui, 1977; Babiker and Ibrahim, 1979; and Siraj *et al*., 1983).

A maximum GSI of 7% was found in the present study. This is comparable with the maximum GSI of 6 -7% found by Macintosh *et al*., (1988) and Melard (1986) but is rather different from the maximum GSI levels of 3.6%, 4.8% and 3.9% reported by Babiker and Ibrahim (1979), Behrends and Smitherman (1983) and Srisakultiew and Wee (1988), respectively.

The length of the oocytes, which are ready to be ovulated, varies from 2 to 2.6 mm (Figure 5). Similar egg sizes of 1.8-2.45 mm were reported by Babiker and Ibrahim, (1979); Siraj *et al.* (1983) and Smitherman *et al.* (1988). However, Lowe-McConnell (1955) reported a maximum length of ≈ 4 mm: the difference could be that the latter is a "real" maximum size, which is rarely found, while the other values represent the average size of ripe oocytes.

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CHAPTER 3: RECRUITMENT CONTROL OF NILE TILAPIA, *OREOCHROMIS NILOTICUS NILOTICUS* (L.), BY THE AFRICAN CATFISH, *CLARIAS GARIEPINUS* (BURCHELL 1822) AND, THE AFRICAN SNAKEHEAD, *PARACHANNA OBSCURA* (GÜNTHER 1861)

A BIOLOGICAL ANALYSIS

GERTJAN DE GRAAF, FELIX GALEMONI AND BERNARD BANZOUSSI

ABSTRACT

The recruitment of *Oreochromis niloticus niloticus* (stocked at 20,000-22,000 ha^{-1}) was completely controlled by large *Clarias gariepinus* (6.8-130 g) and large *Parachanna obscura* (75-206 g) at stocking densities of 8,300 catfish ha^{-1} or 725 snakehead ha^{-1}. The difference in predation efficiency between the two species is related to their feeding strategies: omnivorous *vs* piscivorous. The elimination of the Nile tilapia fingerlings caused the growth rate of male and female Nile tilapia to increase significantly ($P \leq 0.05$) with both predator types. However the net yield decreased in the case of predation by snakehead ($P \leq 0.05$) but did not change in the case of predation by catfish. Analysis of the results indicated that food shortage is a limiting factor. This limitation can be removed by increasing the feed supply directly with additional feed or indirectly by the elimination of the Nile tilapia fingerlings. The results led to the conclusion that stunting of somatic growth in Nile tilapia is mainly related to the husbandry techniques applied.

Small catfish (weight ≤3.65 g) and small snakehead (weight ≤2 g) were not capable of controlling recruitment completely; at harvest 3.7 % and 8.9 % of tilapia fingerlings (of total harvested biomass) persisted for, respectively, catfish and snakehead at the highest stocking densities. Incomplete recruitment control by small, stocked predators is mainly related to the later onset of piscivorous feeding and the low survival rates (24-34%).

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Key words: *Clarias gariepinus Parachanna obscura*, *Oreochromis niloticus niloticus*, polyculture, recruitment control.

INTRODUCTION

One of the major problems in pond rearing of mixed-sexed *Oreochromis niloticus niloticus* (syn. *Tilapia nilotica*) is its excessive recruitment. At harvest 28-70% of the total biomass consists of low-value fingerlings (Bardach *et al.*; 1972, Ruwet *et al.*, 1976; McGinty, 1985; Lovshin *et al.*, 1990). Monosex culture of males has been used in order to overcome this problem. The all-male fingerlings required are obtained through manual sexing (Shell, 1968), through hybridisation (Pruginin, 1967; Lovshin *et al.*, 1990), or through hormone-induced sex reversal (Eckstein and Spira, 1965; Guerrero, 1975; Shelton *et al.*, 1978). Major constraints for the successful use of monosex culture in rural areas are the relatively large size (35 g) of fingerlings needed for successful manual sexing, the difficulty to maintain pure strains of parent stock for hybridisation, and the availability or production of "sex-reversal" feed.

Recruitment can be controlled by the introduction of a predator fish. The following species were used with varying success in combination with *Oreochromis niloticus*: *Micropterus salmoides* (McGinty, 1985), *Lates niloticus* (Lazard, 1980; Bedawi, 1985; El Gamal, 1992), *Ophiocephalus striatus* (Hopkins *et al.*, 1982), *Hemichromis fasciatus* (Lazard, 1980), *Cichla ocellaris* (McGinty, 1983; Verani *et al.*, 1983) and *Clarias gariepinus* (Lazard 1980; Janssen, 1985). The efficiency of a predator is determined by its capacity to prey upon the larval Nile tilapia. Piscivorous species like *Ophiocephalus striatus* require lower stocking densities to eliminate all fingerlings than the more omnivorous *Clarias gariepinus* (Hopkins *et al.*, 1982; Janssen, 1985). The results of these more or less artificial prey-predator systems have been analysed mathematically by Hopkins *et al.* (1982). McGinty (1983) and Verani *et al.* (1983).
The present study investigated the efficiency of *Parachanna obscura* and *Clarias gariepinus* in controlling the recruitment of *Oreochromis niloticus* in large-scale, polyculture in the Republic of Congo (Brazzaville). This paper covers the biological aspects of the results, the economic aspects will be presented in a second paper

MATERIALS AND METHODS

EXPERIMENTAL PROCEDURES

All experiments were carried out between 1986-1990 at the National Fish Culture Station, Djoumouna, (Brazzaville, lat. 4°15'S; long. 15°15'E), Republic of Congo. Grow-out ponds with an average water depth of 1 m and surface areas between 0.04 and 1.2 ha were stocked with fingerlings of *O. niloticus* (15-30 g) in combination with either *C. gariepinus* (1.5-130 g) or *P. obscura* (0.5-206 g). The stocking rate of *O. niloticus* remained more or less fixed at 20,000-22,000 ha^{-1} while predator stocking rates varied between 0-20,000 ha^{-1} for *C. gariepinus* and 0-4,000 ha^{-1} for *P. obscura*.

The fingerlings of *O. niloticus* were a hybrid between a stock of untraceable origin, present in the Congo from the early 50s, and a "Red-Benin" stock imported from Ivory Coast in the early 80s. The fingerlings of *C. gariepinus* were produced through artificial reproduction and nursed in protected ponds as described by De Graaf *et al*. (1995). Fingerlings of *P. obscura* were purchased at the Brazzaville fish market.

The fish were fed 6 days $week^{-1}$ with wheat bran at a daily rate of 4%-11% of the total biomass of *O. niloticus* or of the combined total biomass of *O. niloticus* and *C. gariepinus* in the case of polyculture. All ponds were sampled monthly with a cast net and individual weight of males, females and fingerlings of *O. niloticus* were measured to determine the growth rates and adjust the feeding levels for the following month. In the case of the tilapia-clarias polyculture, it was necessary to assume that the weight of clarias was equal to the weight of the stocked Nile tilapia as the catfish were rarely caught during the monthly sampling. The biomass of *P. obscura* was not taken into consideration for the calculation and adjustment of feeding level as this species is piscivorous (Adebesi, 1981).

All experiments were carried out over a period of four years, during which the overall performance of the fish culture station improved. During the first 2 years of the experiments, the feeding levels ("low level") were lower than those used during the last two years of the experiments ("high level") due to budgetary restriction (Table 1).

The sex ratio of *O. niloticus* at stocking was determined by dissection and observation of the gonads of 100-200 fingerlings per pond from each of 46 ponds. From all ponds at harvest, the total weight of *O. niloticus* and the predator was determined and 300-1,000 specimens were sampled at random (sample size depended on pond size), weighed individually and classified as male, female, fingerling or predator.

Table 1: Low and high feeding levels as used at the fish culture station of Djoumouna, 1986-1990.

Average weight fish (g)	Daily feeding rate (% of total biomass)	
	Low ('86-'88)	High ('88-'90)
0-25	6	11
25-50	6	10
50-100	5	9
100-150	4	7
150-200	4	6

DATA ANALYSIS

All experiments were carried out at a production station under rehabilitation and not at an established research station, and consequently several practical problems were encountered during the experiments. Therefore, the results from ponds, which were influenced by calamities with a "natural" or "human" origin, such as broken dikes, contamination with wild fish (especially *Hemichromis fasciatus*), and unauthorized harvesting of fish, were excluded from the data set.

The results of all experiments were divided into eight groups, taking into account the feeding level, "low" *vs* "high"; predator type, "without predator", "*C gariepinus*" or "*P. obscura*" as predator; and the size of the predator at the time of stocking, "small" *vs* "large fish". The division between the size classes of the predators was as follows:

Small predator:	*C. gariepinus* ≤ 3.6 g
	P. obscura ≤ 2 g
Large predator:	*C. gariepinus* 6.8-130 g
	P. obscura 75-206 g

The percentage of fingerlings at harvest is always calculated as percentage of the total harvested biomass. The number of predators stocked per female *O. niloticus* was calculated only for those experiments where the sex ratio of the *O.niloticus* fingerlings was determined prior to stocking.

Statistical analyses of the data was executed with the computer program Statistical Package for Social Science (SPSS); the probability levels and correlation coefficients are given in absolute values as calculated by this program, unless the parameters were grouped. The means of all individual values are presented with the standard error of the mean (SEM).

Differences in net yield, rearing period, standing stock and the average weight of Nile tilapia at harvest were tested with a separate-variance Student's T-test or a pooled-variance Student's T-test with a F-probability level of 0.05

The influence of predator density, the percentage of stocked *O. niloticus* females, and the stocking weight of *O. niloticus* on the percentage of tilapia fingerlings at harvest was evaluated by multiple linear regression analysis according to the model:

$$y_i = b_0 + b_1x_1 + b_2x_2 + b_3x_3 + e_i$$

in which

y_i	percentage of fingerlings at harvest
b_0	intercept
x_1	stocked predator density (no.ha^{-1})
x_2	percentage of stocked female Nile tilapia (%)
x_3	stocking weight of Nile tilapia (g)
b_1 to b_3	regression coefficients
e_i	error term

The regression was performed stepwise, disregarding the independent F-values of each variable. The partial correlation coefficient and F-value for change were calculated for each independent variable after it was entered in the model. All curves were fitted with the computer program Slidewrite 5; the significance of correlation was tested with a Spearman rank correlation test (Sokal and Rohlf, 1981).

RESULTS

Over the entire research period, 92 experiments were carried out corresponding with an overall production area of 23 ha and a total yield of 79 ton of *O. niloticus*, 3.4 ton of *C. gariepinus*, 0.8 ton of *P. obscura*. The mean production data of all experiments are presented in (Table 2-Table 4).

Table 2: Mean production data (±SEM.) for rearing of O. niloticus without predators at low and high feeding level.

Production parameters	Low feeding level	High feeding level[a]
Average stocking weight *O. niloticus* (g)	19.9±1.5	20.3±5.5
Rearing period (days)	219±10	219±7.8
Standing stock at harvest (kg ha^{-1})	3380±297	4814±647*
Net yield (kg ha^{-1} day^{-1})	14±1.5	20±2.4*
Average weight male tilapia at harvest (g)	142±9	192±7*
Average weight female tilapia at harvest (g)	60±5	69±4
Average weight tilapia fingerlings at harvest (g)	16.5±2.2	14.6±1.5
Growth rate male tilapia (g day^{-1})	0.57±0.05	0.78±0.03**
Growth rate female tilapia (g day^{-1})	0.19±0.09	0.22±0.02

[a] Compared with low feeding level (* $P \leq 0.05$, ** $P \leq 0.005$)

EFFECTS OF FEEDING LEVELS ON PRODUCTION PARAMETERS

In experiments without a predator under a high feeding level, the standing stock at harvest increased by 42%, the net yield increased by 47%, the growth rate of male tilapia increased by 36% and the final weight of male tilapia increased by 35% (Table 2), in comparison with results from the experiments without a predator under a low feeding level.

EFFECTS OF PREDATORS ON PRODUCTION PARAMETERS

Comparison of the mean production values from polyculture with a predator (irrespective of the predator density) with the mean production values of rearing experiments without a predator for a low feeding level are presented in Table 3. Polyculture with *C. gariepinus* resulted in a significantly faster growth rate of male tilapia, a higher final weight of male and female tilapia, compared with rearing tilapia alone ($P \leq 0.05$). Furthermore the standing stock at harvest and the net yield of *C. gariepinus* and *O. niloticus* was not significantly different from the standing stock at harvest and net yield of tilapia raised without a predator. Polyculture with *P. obscura* resulted in a higher final weight of male and female tilapia ($P \leq 0.05$) if compared with rearing tilapia alone. Furthermore, at harvest a lower net yield of *P. obscura* and *O. niloticus* was observed ($P \leq 0.05$) compared with the net yield of tilapia raised without a predator.

Table 3: Mean production data (±SEM) for rearing of O. niloticus *in combination with predators at a low feeding level.*

Production parameters	No Predator	*C. gariepinus*[a] 6.8 g≤weight≤130 g	*P. obscura*[a] 75 g≤weight≤206 g
Average stocking weight *O. niloticus* (g)	19.9±1.5	23.8±4.9	23±8.2
Rearing period (days)	219±10	213±13	242±24
Standing stock at harvest (kg ha^{-1})	3380±297	3891±421	2735±408
Net yield (kg ha^{-1} day^{-1})	14±1.5	16±2.6	10±1.5*
Average weight male tilapia at harvest (g)	142±9	193±31*	182±23*
Average weight female tilapia at harvest (g)	60±5	80±11*	90±19*
Average weight tilapia fingerlings at harvest (g)	16.5±2.2	37.5±11.8	19.1±7.5
Growth rate male tilapia (g day^{-1})	0.57±0.05	0.81±0.14*	0.67±0.13
Growth rate female Tilapia (g day^{-1})	0.19±0.02	0.27±0.07	0.28±0.1
Average weight predator at harvest (g)	_._	208±45	654±124
Survival rate predator (%)	_._	62.1±8.4	75.9±13.6

[a] Compared with no predator (* $P \leq 0.05$)

Comparison of the mean production values from polyculture with a large predator with the mean production values of rearing experiments without a predator for a high feeding level are presented in Table 4. Polyculture with *C. gariepinus* resulted in a significantly faster growth rate of male and female tilapia, a higher final weight of male, female and fingerlings of tilapia, if compared with rearing tilapia alone ($P \leq 0.05$). Furthermore, the standing stock at harvest and the net yield of *C. gariepinus* and *O. niloticus* was not significantly different from the standing stock at harvest and net yield of tilapia raised without a predator. Polyculture with *P. obscura* resulted in a higher final weight of female tilapia ($P \leq 0.05$) compared with rearing tilapia alone. Furthermore, at harvest a lower standing stock of *P. obscura* and *O. niloticus* was observed ($P \le 0.05$) compared with the standing stock of tilapia raised without a predator.

Table 4: Mean production data (±SEM.) for rearing of O. niloticus *in combination with large predators at high feeding level.*

Production parameters	No predator	*C. gariepinus*[a] 6.8 g≤weight≤130 g	*P. obscura*[a] 75 g≤weight≤206
Average stocking weight *O. niloticus* (g)	20.3±5.5	22.8±3.7	27.7±2.6
Rearing period (days)	219±7.8	176±16*	180±10*
Standing stock at harvest (kg ha^{-1})	4814±647	4953±629	3416±232*
Net yield (kg ha^{-1} day^{-1})	20±2.4	22±2.3	16±1.4
Average weight male tilapia at harvest (g)	192±7	225±8**	192±6
Average weight female tilapia at harvest (g)	69±4	92±9*	85±5*
Average weight tilapia fingerlings at harvest (g)	14.6±1.5	34.1±6.6*	26.9±7.3
Growth rate male tilapia (g day^{-1})	0.78±0.03	1.19±0.14*	0.93±0.06
Growth rate female tilapia (g day^{-1})	0.22±0.02	0.43±0.08*	0.33±0.3*
Average weight predator at harvest (g)	_	201±19	491±73
Survival rate predator (%)	_	70.5±9.7	60.3±7.1

[a] Compared with no predator, (* $P \le 0.05$, ** $P \le 0.01$).

Table 5: Multiple linear regression of experiments with different types of predators. Three independent variables, stocking density of predator, percentage of stocked female O. niloticus *and the stocking weight of* O. niloticus*, are related to the dependent variable: the percentage of fingerlings at harvest. In the last row of the table the linear regression between the percentage of fingerlings at harvest and the predator density at harvest is presented. Partial R is the part correlation coefficient (the correlation between Y and* X_i *when the linear effects of the other independent variables have been removed from* X_i*, F-change is the F-value for change calculated for each independent variable after it was entered in the model, df the degrees of freedom, R is the correlation coefficient and F is the F value. (** $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$*)*

Independent variables	Experimental groups			
	"Small" *C. gariepinus*	"Large" *C. gariepinus*	"Small" *P. obscura*	"Large" *P. obscura*
Predator density stocked (no. ha^{-1})				
Partial R	-0.715^{***}	-0.517^{**}	-0.108	-0.748^{***}
F-change	33.9^{***}	10.09^{**}	0.277	39.4^{***}
Df	27	28	22	34
Percentage of ♀♀ *O. niloticus* stocked				
Partial R	0.041	-0.023	0.088	-0.083
F-change	0.116	0.021	0.151	0.217
Df	27	28	22	34
Stocking weight *O. niloticus* (g)				
Partial R	-0.008	-0.198	0.130	-0.149
F-change	0.004	1.482	0.328	0.710
Df	27	28	22	34
Predator density at harvest (no. ha^{-1})				
R	-0.660^{***}	-0.364^{**}	-0.421^{*}	-0.650^{***}
F	20.09^{***}	15.4^{**}	4.538^{*}	24.2^{***}
Df	27	28	22	34

EFFECTS OF PREDATOR SIZE AND PREDATOR DENSITY ON THE RECRUITMENT OF NILE TILAPIA

Multiple linear regression analyses indicate that experiments with small catfish, large catfish and large snakehead, the variation in percentage of total harvested biomass of *O. niloticus* fingerlings was related to the density of the predator both at stocking and at harvest (Table 5). Stocking weight of *O niloticus* and the percentage of stocked females of *O. niloticus* did not contribute significantly to the correlation coefficient (Table 5).

In the experiments with small snakeheads, the percentage of total harvested biomass made up by *O. niloticus* fingerlings was at least 8.9% and was not significantly related to the stocking density of the predator; however, it was significantly related to the number of predators harvested per ha (Table 5). Note that the survival rate of the small predators was 33.5 ± 6.8 and 24.5 ± 10.2 for, respectively, small catfish and small snakehead.

The effect of predator density on the recruitment of Nile tilapia becomes clearer when the feeding level is not taken into consideration (Figure 1). The results of small snakehead were not significant and were excluded from this analysis.

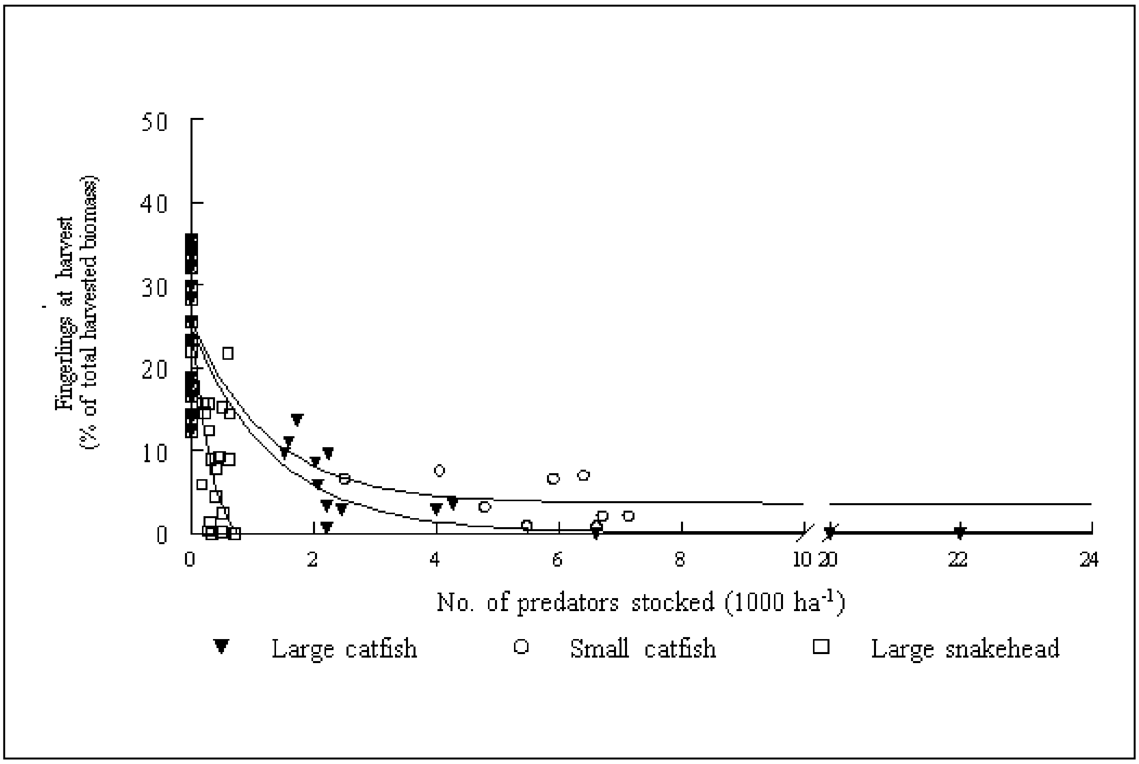

Figure 1: Percentage of the total harvest consisting of tilapia fingerlings in relation to the density of small and large C. gariepinus *and large* P. obscura, *irrespective of feeding level.*

The regression lines are described with the following equations:

Polyculture with small *C. gariepinus*

% of fingerlings = $3.636 + 21.89 * e^{(\text{-no. of catfish stocked}/1255)}$ (R=0.84, $P \leq 0.01$)

Polyculture with large *C. gariepinus*

% of fingerlings = $0.095 + 24.65 * e^{(\text{-no. of catfish stocked}/1357)}$ (R=0.84, $P \leq 0.01$)

Polyculture with large *P. obscura*

% of fingerlings = $-2.99 + 27.89 * e^{(\text{-no. of stocked snakeheads}/331)}$ (R= 0.83, $P \leq 0.01$)

The regression lines indicate that large catfish and large snakeheads were able to control the recruitment of Nile tilapia completely; less than 0.15 % of the total harvested biomass were fingerlings at a stocking density of 8,300 catfish ha^{-1} and 725 snakeheads ha^{-1}. Small catfish were not able to completely control the recruitment of Nile tilapia; 3.7% of the total harvested weight consisted of tilapia fingerlings at a stocking density of 7,300 catfish ha^{-1}.

EFFECTS OF PREDATOR DENSITY ON THE NET ANNUAL YIELD AND THE DIFFERENT CATEGORIES OF FISH

The relationship between predator stocking density and the net annual yield and the division of the net annual yield among tilapia fingerlings, male tilapia, female tilapia and predator are presented in Figure 2 and Figure 3.

In polyculture with large catfish, a high stocking density of catfish increased the net production significantly at the low feeding level, but this phenomenon did not occur at high feeding levels.

In polyculture with large snakeheads, at both feeding levels, the net annual yield decreased significantly at high snakehead stocking densities.

EFFECTS OF THE PRESENCE OF NILE TILAPIA FINGERLINGS ON THE GROWTH RATE OF ADULT NILE TILAPIA

The daily growth rate of male and female Nile tilapia in experiments with a high feeding level and a predator were not always significantly different from male and female daily growth rates without a predator. Predator stocking density, the type of predator, the size of the predator, and the resulting quantity of fingerlings at harvest obscure the results.

The relation between the daily growth rate (g day^{-1}) of male and female O. niloticus and the percentage of fingerlings at harvest (in percentage of the total harvested biomass) for the two different feeding levels is presented in Figure 4. The growth rate of male and female *O. niloticus* decreases as the percentage of fingerlings increases. The relation can be described by the following regression lines:

Male *O. niloticus*, high feeding level

$(\text{Growth rate})^{0.5} = 1.064 - 0.008*(\%\text{ of fingerlings at harvest})$ (R=0.62, *P*≤0.01)

Male *O. niloticus*, low feeding level

$(\text{Growth rate})^{0.5} = 0.865 - 0.005*(\%\text{ of fingerlings at harvest})$ (R=0.41, *P*≤0.05)

Female *O. niloticus*, high feeding level

$(\text{Growth rate})^{0.5} = 0.591 - 0.004*(\%\text{ of fingerlings at harvest})$ (R=0.38, P≤0.05)

Female *O. niloticus*, low feeding level

$(\text{Growth rate})^{0.5} = 0.583 - 0.006*(\%\text{ of fingerlings at harvest})$ (R=0.62, P≤0.01)

DISCUSSION AND CONCLUSIONS

RECRUITMENT CONTROL

Large catfish and large snakeheads were able to control the recruitment of Nile tilapia completely; less than 0.15% of the total harvested biomass consisted of fingerlings at a stocking density of 8300 catfish ha^{-1} (ratio predator : parent-prey=1:2.7) or at 725 snakehead ha^{-1} (ratio predator:parent-prey = 1:30). Similar predation efficiencies in the successful control of the recruitment of *O. niloticus* were reported for other piscivorous species ; *Lates niloticus*, ratio 1:37 (Lazard, 1980), *Channa striata*, ratio 1:32, (Hopkins *et al.*, 1982) and *Hemichromis fasciatus*, ratio 1:17 (Lazard,1980). The difference in efficiency between the two species is probably caused by their feeding habits and mode of predation. *C. gariepinus* is an omnivore (Munro, 1967, de Kimpe and Micha, 1974) and feeds on the supplied wheat bran, which reduces its motivation to search for Nile tilapia fry, while *P. obscura* is strictly piscivorous (Adebisi, 1981).

Successful recruitment control in a mixed culture of *O. niloticus* at a predator:parent-prey ratio of 1:5 or a stocking density of 2,500 predators ha^{-1} was reported for *C. gariepinus* by Lazard (1980). Middendorp (1996a, b), however, found that *C. gariepinus* was unable to control the recruitment of *O. niloticus* in an all-male culture with 0.9% females: predator:parent-female tilapia ratio of 1:0.1, or a stocking density of 400-1,500 predators ha^{-1}. In a mixed culture, recruitment was controlled effectively at a predator : parent-prey ratio of 1:8 or a density of 2,000 predators ha^{-1}.

"Small" catfish and "small" snakeheads were unable to control the recruitment of Nile tilapia completely; a fingerling percentage of 3.7 and 8.9 of the total biomass harvested persisted for, respectively, catfish and snakehead. Similar results for *C. gariepinus* were found by Janssen (1985) and for *Channa striata* by Hopkins *et al*. (1982). The difference in efficiency of predation between small or large fish is probably related to survival rate and the onset of piscivory. The low survival rates in our experiments with small predators caused the real existing predator density to drop below 8,300 ha^{-1} and 725 ha^{-1} for, respectively, catfish and snakehead. Recruitment of Nile tilapia was only controlled in those experiments where the survival rate of especially small snakeheads was high, which explains the correlation between the percentage of fingerlings at harvest and the snakehead density at harvest. Janssen (1985) found that even at high stocking densities small *C. gariepinus* (20,000 ha^{-1}) still fail to control the recruitment of *O. niloticus* completely, which indicates that other factors are also of importance.

The question is whether small predators are unable to predate on the Nile tilapia larvae or whether they have a different food preference, not shifting to a more piscivorous feeding habit until later. The size of the Nile tilapia larvae/fry is not a limiting factor for catfish. Hecht and Appelbaum (1988) found that *C. gariepinus* in a similar size range as in this study can predate on fish with a length of 30 mm. Munro (1967) reports that the stomach of small *C. gariepinus* (0.02-4 g) obtained from natural waters contained mainly Chironomid larvae, Cladocera, Copepoda and Ostracoda. This, combined with the results that *C. gariepinus* larger than 7 g, completely control Nile tilapia recruitment, could indicate that small *C. gariepinus* have a specific food preference for zooplankton and probably shift to a more piscivorous behaviour once they reach a weight of 7-8 g. Such ontogenetic shifts from planktivorous to piscivorous feeding at an early age, have been reported for other fish species: *Stizostedion lucioperca* (van Densen, 1985); *Micropterus salmoides* (Keast and Eadie, 1985) and *Stizostedion vitreum* (Cuff, 1980).

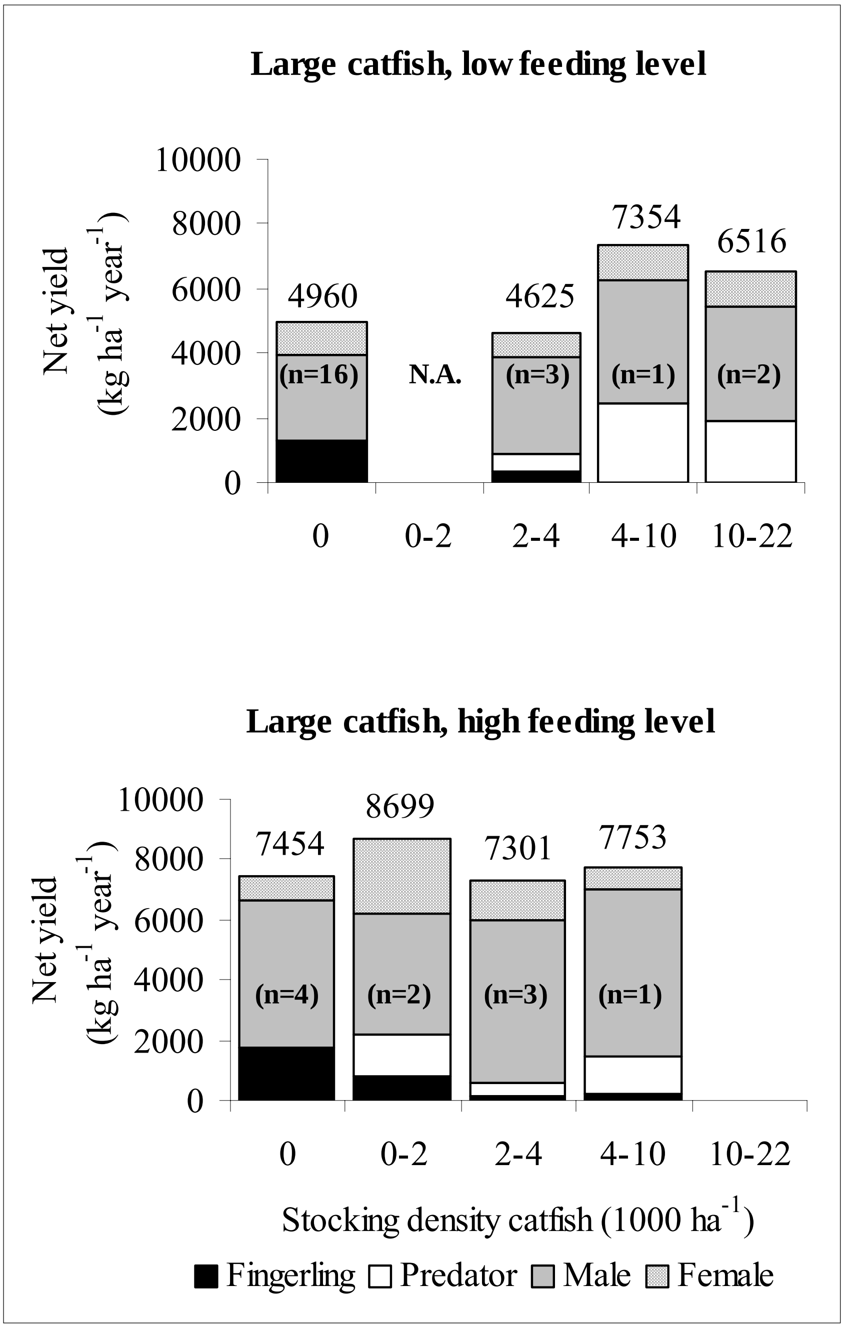

Figure 2: Relationship between stocking density of large C. gariepinus *and the net annual yield of fingerling, male and female* O. niloticus *and a predator for polyculture with O. niloticus under low or high feeding regime. The total annual yield (kg ha^{-1} year^{-1}) is presented over each graph.*

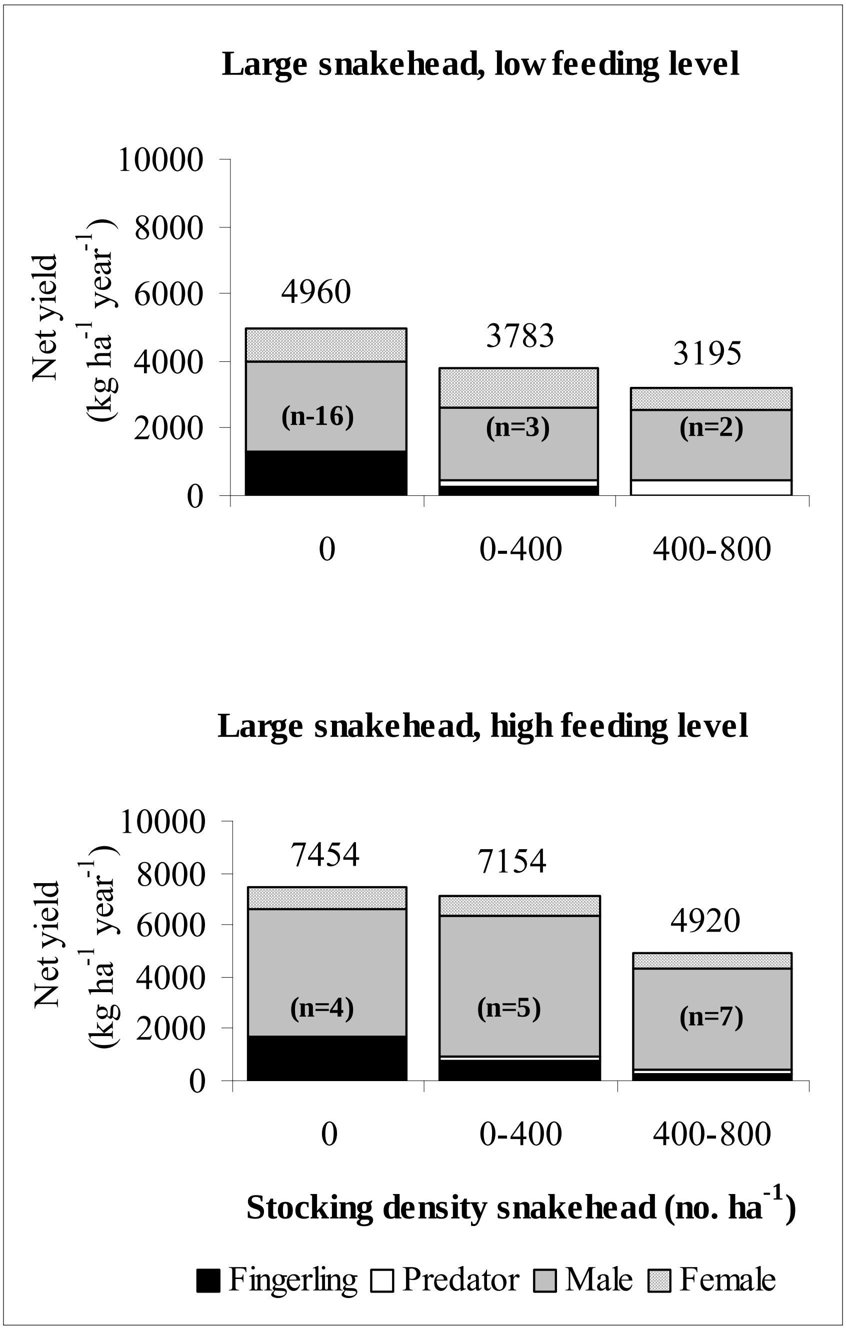

Figure 3: Relationship between stocking density of large P. obscura *and the net annual yield of fingerling, male and female* O. niloticus *and the predator for polyculture with O. niloticus under low or high feeding regime. The total annual yield (kg ha*$^{-1}$ *year*$^{-1}$*) is presented over each graph.*

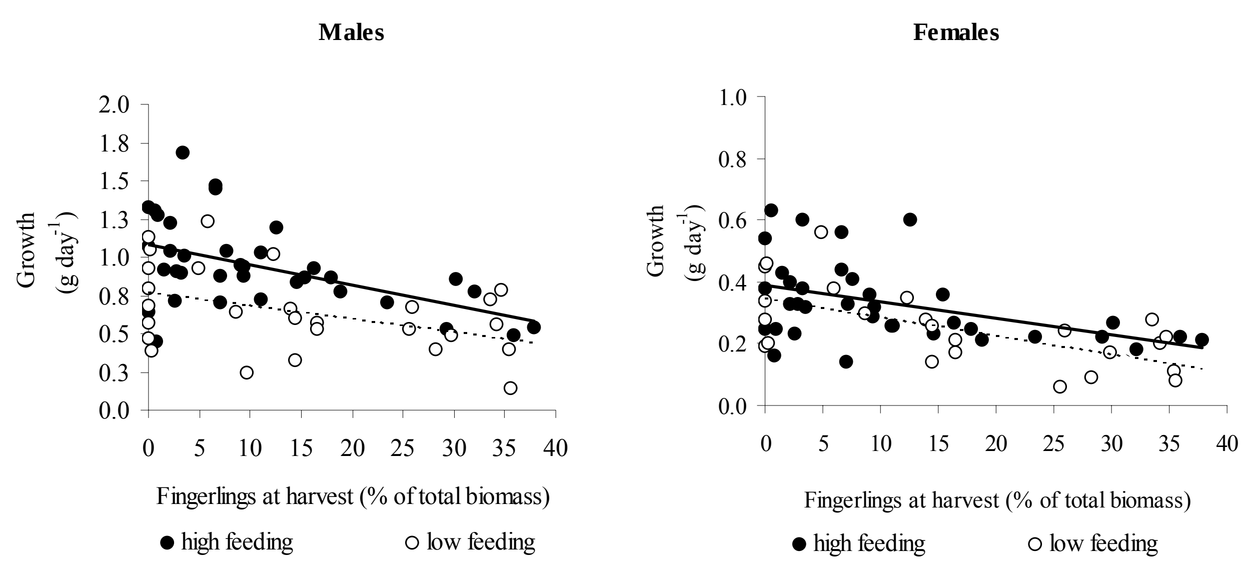

Figure 4: Relationship between the daily growth rate (g day^{-1}) of male and female O. niloticus and the percentage of the total harvested biomass consisting of tilapia fingerlings as obtained with a high feeding level (solid line) and a low feeding level (dashed line).

YIELD AND GROWTH

Recruitment control by a piscivorous predator such as *P. obscura* reduced the net yield, while in experiments with the omnivorous *C. gariepinus* the net yield increased at the low feeding level or remained stable at the high feeding level. A reduction of the yield has been observed before in similar experiments for other piscivorous species such as *Lates niloticus* (Ofori, 1988); *Megalops cyprinoides* (Fortes, 1980); *Micropterus salmoides* (McGinty, 1985) and *Cichla ocellaris* (McGinty, 1983). Lazard (1980) reports that yields with *C. gariepinus* as a predator are higher than yields in experiments with *Lates niloticus* or *Hemichromis fasciatus*. With piscivorous species the fingerling biomass is converted into a lower predator biomass. The lost fingerling biomass could not be fully compensated by the observed higher growth rates of male and female Nile tilapia. In our experiments, *C. gariepinus* fed on the Nile tilapia fry and on the extra wheat bran, as the catfish density was also taken into consideration for the determination of the daily feeding rate. Consequently the lost fingerling biomass is replaced by an equal or higher biomass of *C. gariepinus*.

Ofori (1988) found that the loss in biomass is economically compensated by the higher price of the larger Nile tilapia. The situation in the Republic of Congo is somewhat different and the economic consequences of the different predator systems will be presented in a separate article.

The presence of approximately 25 % (on weight basis) of fingerlings in a mixed culture of *O. niloticus* interferes within the production process through feed competition between the originally stocked tilapia and their offspring. Consequently the growth of adult Nile tilapia is restricted. This interference is rather strong because the metabolism of small fish is higher than the metabolism of large fish (Winberg, 1956) and consequently 1 kg of fingerlings consume more feed than 1 kg of adult fish. This food shortage can be eliminated by directly increasing the feeding level (low *vs* high feeding level), or by indirectly increasing the feeding level by removing the fingerlings through the introduction of a predator. Both actions result in an increased growth rate of the adult Nile tilapia. In this respect it is interesting to note the "stunting" process of Tilapia, which has been often mentioned as a limiting factor in Tilapia rearing (Ruwet *et al.*, 1976; Guerrero, 1980; Mires, 1980; Hepher and Pruginin, 1980; McGinty, 1983) and discussed extensively by Noakes and Balon (1982) and by Fryer and Iles (1972). Noakes and Balon (1982) conclude that the phenomenon is not one of "stunting of somatic growth", but one of an "earlier breeding of the fish". The present study confirms this theory; Nile tilapias were stunted because they started to reproduce at an age of 3 months at a weight of 30 g (de Graaf, unpublished results, 1989). Limited growth was observed, but from an aquacultural point of view this is not a serious problem as it can be compensated by increasing the feed supply for the stocked specimen. Even in a mixed culture without predator, the observed growth rates of male Nile tilapia to the sizes harvested were comparable with the growth rates obtained in monosex male culture with commercial pellets or chicken feed pellets as feed (Coche, 1977; Philippart *et al.*, 1979; Melard, 1986). Therefore, it could be concluded that stunting of the growth in pond rearing of Nile tilapia is more a matter of husbandry technique and the carrying capacity of the rearing system than related to the species itself.

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CHAPTER 4: THE ARTIFICIAL REPRODUCTION AND FINGERLING PRODUCTION OF THE AFRICAN CATFISH *CLARIAS GARIEPINUS* (BURCHELL 1822) IN PROTECTED AND UNPROTECTED PONDS

G.J. de GRAAF, F. GALEMONI AND B. BANZOUSSI

ABSTRACT

In order to obtain an appropriate and reliable method for the mass-production of C*larias gariepinus* (Burchell 1822) fingerlings, experiments on artificial reproduction and pond rearing were carried out in the Republic of Congo in 1987-1991. Reproduction could be induced throughout the year using common carp pituitaries (3 mg kg^{-1} female). The average relative fecundity of females varies between 1.3 % ± 0.3 (SEM) and 14.3 % ± 1.3 (SEM). The average hatching percentage of the obtained eggs varies between 28.4 % ± 4.5 (SEM) and 59.1 % ± 3.7 (SEM) respectively in the dry and rainy season. The fluctuation of the relative fecundity as well as the fluctuation of the hatching percentage follows the seasonal fluctuation in rainfall and temperature. The use of a net cage made of mosquito netting (1 m^3, 0.5 mm mesh size) and the roots of water hyacinth (*Eichornia crassipes*) as an egg incubator proved to be reliable. In ponds not protected against frogs an average of 5.0 ± 2.9 (SEM) fingerlings m^{-2} per 40 days cycle were obtained, where as in ponds completely surrounded by a wall of aluminium roof plates (0.8 m high) the average production was 32.3 ± 3.3 (SEM) fingerlings m^{-2} per 40 days cycle, when they are stocked with approximately 100 larvae m^{-2}. Increasing the larval stocking density or extending the rearing period did not improve the final production. The main causes of low production in unprotected ponds are competition for food resources due to the presence of phytophagous frog larvae and cannibalism among the fingerlings of *Clarias gariepinus*. An analysis showed that the studied system is labour orientated, technical reliable and economic feasibly when the fingerlings can be sold for US$ 0.07 a piece.

Keywords: artificial reproduction, *Clarias gariepinus*, fingerlings, pond nursing.

Aquaculture Research, 1995, 26: 233-242

INTRODUCTION

Since the 1970s the African catfish, *Clarias gariepinus* (Burchell 1822), has been considered to be a fish of great promise for fish farming in Africa. Its growth rate is high, it is very resistant and appreciated in a wide number of African countries. The development of a reliable method for the production of *C. gariepinus* fingerlings is one of the priorities of aquaculture research in Africa (Anonymous, 1987a). Hormone-induced reproduction of the African catfish using deoxycorticosterone acetate (DOCA, 50 mg kg^{-1} female), human chorionic gonadotropin (HCG, 2500 I.U. kg^{-1} female) and common carp pituitaries (3 mg kg^{-1} female) has been carried out successfully (El Bollock, 1976; Hogendoorn *et al.,* 1975 and 1980a; Micha, 1976; Kelleher et al., 1976).

The main problem of fingerling production in ponds is the survival rate, which is unreliable and varies between 0 and 60 fingerlings m^2 $cycle^{-1}$ (Hogendoorn *et al*., 1976; Kelleher *et al*., 1976; Micha 1976; Hogendoorn, 1979). It has been suggested that the lack of appropriate feed and the presence of predators are likely causes of mortality.

Hogendoorn (1980) and Hogendoorn *et al*. (1981) successfully developed an intensive production system for fingerlings of the African catfish based on the use of *Artemia salina* nauplii and commercial trout starter as a feed. The existence of a technically feasible method and a manual in which the techniques are described (Viveen *et al*., 1985) does not, however guarantee a successful implementation, as the impact of local socio-economic and technical conditions are often under-estimated (Anonymous, 1987b). The introduction of intensive rearing methods in the Central African Republic and in Ivory Coast encountered technical and economic problems (Janssen, 1985a, b, c; de Graaf, 1989).

In this study an effort was made to combine technically feasible methods with the socio-economic conditions of the Republic of Congo in order to obtain an appropriate and reliable method for the mass production of *Clarias gariepinus* fingerlings.

MATERIALS AND METHODS

Throughout all the experiments brood fish with a weight between 200 and 700 were used. They were kept in a pond at an average density of 1.5 fish m^{-2} and were fed six days a week with wheat bran at a ration of 5% of their total biomass and with trash fish irregularly.

ARTIFICIAL REPRODUCTION

Induced ovulation was stimulated in the females with an intra-muscular injection of acetone dried common carp pituitary material suspended in a 0.9 % NaCl solution. The collection of ovulated eggs and their fertilization was carried out using the dry-method described by Hogendoorn *et al*. (1980) and Woynarowich *et al*. (1980). Records were kept of the weight of individual females and the total weight of eggs produced. Utilising the natural adhesiveness of the catfish eggs, approximately 300 g of fertilised eggs were attached to the roots of water hyacinth (*Eichhornia crassipes*) and placed in a cage made of mosquito netting (1 m^3, mesh size 0.5 mm), floating in a concrete basin with running water (5-10 l min^{-1}) obtained by gravity from the river Djoumouna. The water temperature varied between 22 ^{0}C (dry season) and 28 ^{0}C (rainy season). Ten hours after hatching the water hyacinth was removed from the cage. Three days after hatching when the yolk sac had been absorbed, the larvae were harvested and counted. Hatching rate of the eggs was determined in two ways: one sample of 80-100 eggs was counted and attached to the water hyacinth roots and placed in a bucket containing 2 l of water, while another sample of 80-100 eggs was counted and placed in petri disk containing 15 ml of water. In each samples the total number of hatched larvae was determined 8 -10 hours after the onset of hatching.

THE POND REARING OF FRY

Three days after hatching, the larvae of *C. gariepinus* were stocked in earthen ponds (100-150 m^2, 0.8 m water depth) at densities varying between 7 and 200 larvae m^{-2}. Two types of ponds were used: protected ponds, completely surrounded by a wall, 0.8 m high, made of aluminium roof plates, and unprotected ponds. All ponds were filled with water and fertilized with chicken dung (50 kg per 100 m^2) 1 week before stocking. From the day of stocking, the fish were fed 6 days a week with wheat bran at a rate of 1 kg 100 m^2 day^{-1}. At harvest the ponds were completely drained and the total number of fingerlings and their average weight was determined. Throughout all experiments frog larvae present in the ponds were captured and their stomach content was analysed.

ANALYSES OF DATA

The specific growth rate of the fingerlings was calculated with the formula:

$$W_t = W_o \left(1 + \frac{a}{100} \right)^t$$

W_t the weight of the fingerlings at harvest,

W_0 the weight of the 3 days old stocked larvae.

a the specific growth rate expressed in % of body weight per day

t the nursing period, in days

The initial weight of the 3 days old larvae was not determined. It is assumed that the genetic variability is limited, and the weight of 2.3 mg (Hogendoorn, 1980) was used for all calculations.

Statistical analyses of the data were executed by using the computer programme SPSS (Statistical Package Social Science). The means of individual values are given with the standard error of the mean (SEM). The seasonal fluctuation of the relative fecundity and hatching percentage was clearly evident and required no further analyses. The influence of the different incubation techniques on the hatching rates was examined on the basis of paired observation per female, using the Wilcoxon Matched-pairs signed-rank Test (Sokal and Rohlf, 1981).

In order to facilitate analyses, the results obtained from nursing in ponds were grouped. The following classification was used:

protection; yes or no

low density: stocking density ≤ 50 larvae m^{-2}

medium density: 51 larvae m^{-2} ≤ stocking density ≤100 larvae m^{-2}

high density: 101 larvae m^{-2} ≤ stocking density ≤ 200 larvae m^{-2}

short duration: nursing period ≤ 50 days

long duration: nursing period ≥ 51 days

A separate-variance Student's t-test or a pooled-variance Student's t-test (depending on the equality of the variances), with a F-probability level 0.05, was used in comparing the fingerling production, survival rate, biomass, weight at harvest and specific growth rate.

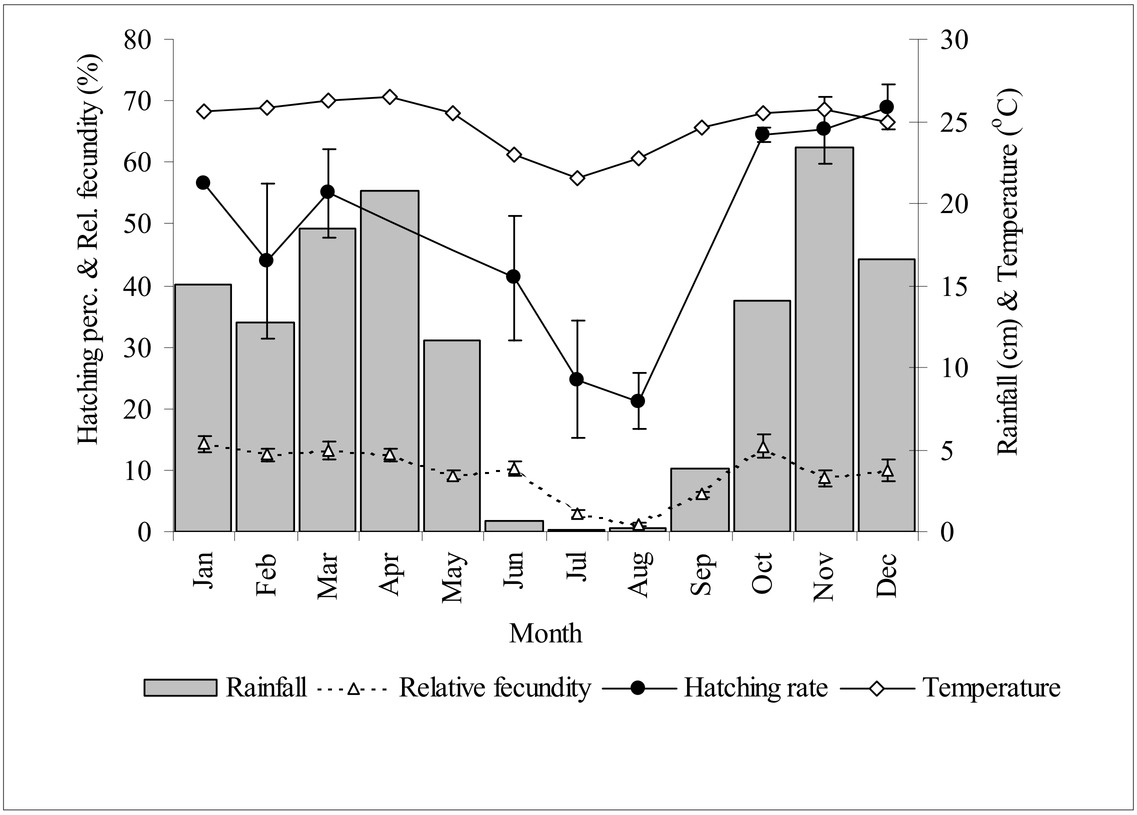

Figure 1: The relative fecundity (% of total body weight), hatching percentage (% of total eggs) of Clarias gariepinus, average monthly rainfall* (cm) and average air-temperature* (^{0}C) measured in Brazzaville, bars indicate SEM. * Source: Deceuninck (1988).

RESULTS

ARTIFICIAL REPRODUCTION AND LARVAL PRODUCTION

It proved possible to reproduce *C. gariepinus* artificially throughout the year in the Republic of Congo. Figure 1 shows the relative fecundity, $F = \left(\frac{weight\ eggs}{weight\ female} \right) 100$, obtained from 155 females, the hatching percentage obtained from 70 females, the average monthly rainfall and the average monthly air temperature registered in Brazzaville. The last two data sets are from Deceuninck (1988). The relative fecundity varies between 1.3 % ± 0.3 (SEM) in August and 14.3 % ± 1.3 (SEM) in January and follows the seasonal fluctuations in air temperature and rainfall.

Figure 1indicates that the quality of the eggs obtained changes during the season and the pattern follows the seasonal fluctuation in rainfall and air temperature. Average hatching percentage of 59.1 % ± 3.7 (SEM.) and 28.4 % ± 4.5 (SEM) were obtained during the rainy season (October-May, n=42) and during the dry season (June-September, n=28), respectively. No significant differences (P=0.53, n=30 incubations) were found in using either water hyacinth or a Petri disk as egg incubator The hatching percentage were 37.1 % ± 4.6 (SEM) and 34.1 % ± 4.2 (SEM) respectively.

FINGERLING PRODUCTION IN PONDS

The overall results obtained in 45 rearing experiments are given in Table 1 and Table 2. The results, after a preliminary grouping of the data, are presented in Table 3. Within the protected ponds, the fingerling production, the survival rate and the final biomass was significantly higher than in unprotected ponds. However, the mean weight of the fingerlings and their specific growth rate was significantly lower in the protected ponds. Increasing the rearing period in protected ponds results in a significant decrease of the fingerling production and specific growth rate and significantly increases the final biomass and mean weight at harvest. Increasing the stocking density from 'low' to 'medium' has its effect of increases the number of fingerlings at harvest and growth rate, but decreases the final biomass harvested. A further increase in stocking density, from 'medium' to 'high' reduces the survival rate significantly.

Table 1: The overall results of the fingerling production of C. gariepinus *in unprotected ponds.*

No. of larvae stocked (m^{-2})	No. of fingerlings harvested ($m^{-2)}$	Weight of fingerlings (g)	Duration (days)	Survival (%)	Growth rate (% day^{-1})	Class[a]
8	0.02	155.0	71	0.3	16.9	L&L
10	2.60	54.0	115	24.8	9.1	L&L
10	0.00	-	60	0.0	-	L&L
29	8.40	2.8	36	28.7	21.8	L&S
30	1.90	4.1	38	6.3	21.7	L&S
32	1.20	12.8	34	3.6	28.8	L&S
34	0.00	-	37	0.0	-	L&S
39	0.00	-	60	0.0	-	L&S
53	0.00	-	45	0.0	-	M&S
68	0.00	-	45	0.0	-	M&S
68	1.30	5.5	37	1.9	23.4	M&S
71	0.60	8.2	37	0.9	24.7	M&S
71	0.70	22.4	45	1.0	22.6	M&S
75	2.10	15.5	39	2.8	25.3	M&S
87	0.90	2.9	37	1.1	21.2	M&S
100	27.10	2.9	45	27.2	17.1	M&S
100	26.50	1.4	45	26.5	15.3	M&S
100	0.00	-	45	0.0	-	M&S
100	1.20	16.9	44	1.2	22.4	M&S
100	0.00	-	37	0.0	-	M&S
200	1.70	69.5	104	0.9	10.4	H&L

[a] Classification: density (L, low; M, medium; H, high) and duration (L, long; S, short) , e.g. L&L denotes low density, long duration.

Table 2: The overall results of the fingerling production of C. gariepinus *in protected ponds.*

No. of larvae stocked (m^{-2})	No. of fingerlings harvested (m^{-2})	Weight of fingerlings (g)	Duration (days)	Survival (%)	Growth rate (% day^{-1})	Class[a]
19	11.4	8.5	107	60.3	7.9	L&L
34	22.8	2.8	39	60.3	19.9	L&L
44	17.4	11.9	129	39.9	6.8	L&L
68	22.8	0.9	39	33.7	16.6	M&S
68	35.9	2.8	44	53	17.4	M&S
68	11.1	4.1	38	16.3	21.8	M&S
68	47.5	0.6	36	69.5	16.5	M&S
69	17.6	2.6	36	25.6	21.5	M&S
69	30.1	2.7	36	43.7	21.7	M&S
69	26.2	3.7	38	38.0	21.4	M&S
69	16.4	2.3	44	23.6	17.0	M&S
70	43.7	3.9	37	62.8	22.2	M&S
72	14.8	3.1	39	20.5	20.2	M&S
75	23.8	0.6	43	33.3	13.8	M&S
75	37.0	3.2	37	49.2	21.6	M&S
81	61.9	0.7	40	75.9	15.3	M&S
100	44.2	1.9	46	44.2	15.7	M&S
100	38.9	1.6	40	38.9	17.7	M&S
100	38.9	2.4	45	38.9	16.7	M&S
100	39.1	1.1	35	39.1	19.2	M&S
100	21.5	5.2	59	21.5	13.9	M&L
116	13.0	3.4	72	11.2	10.6	H&L
138	22.0	1.5	36	15.9	19.7	H&S
146	22.9	3.7	48	15.7	17.4	H&S

[a] Classification: density and duration, coded as in Table 1.

Table 4 presents the results, after grouping the data in such a way that the presence of a protecting wall is the only variable within one class. Within the classes (low & short, low &

long; medium & short) the results indicates that in protected ponds the fingerling production, survival rate and biomass at harvest are higher and the weight of the fingerlings and their growth rate is lower in comparison to the unprotected ponds. These results proved to be significant in the medium and short class only.

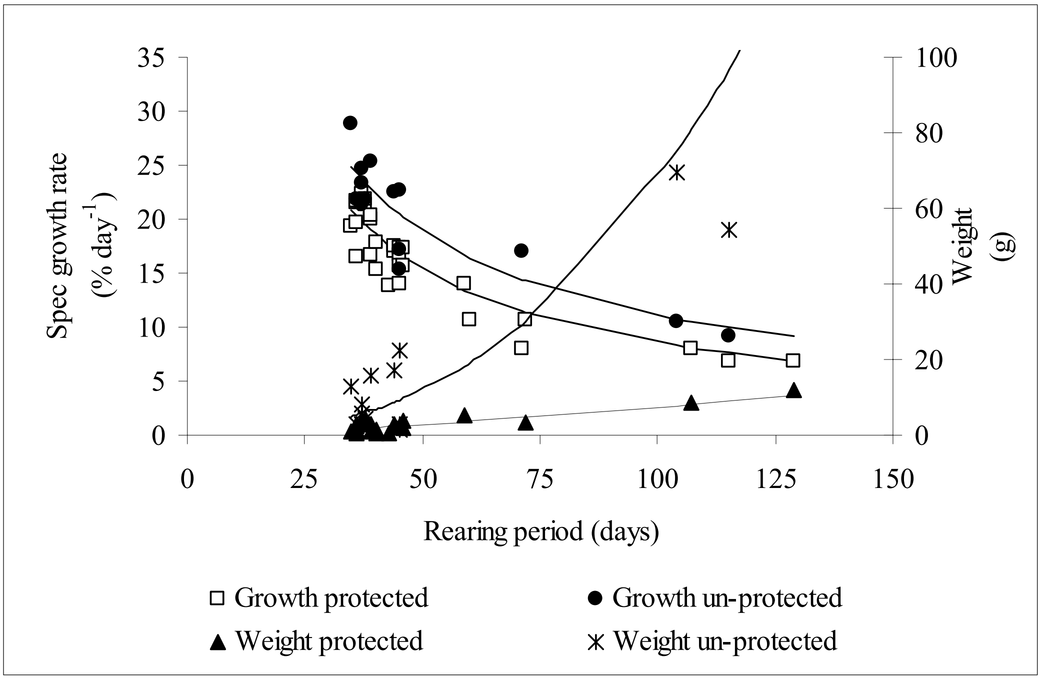

Figure 2: Mean weight at harvest (g) and specific growth rate (% of body weight day^{-1}) of Clarias gariepinus after the start of exogenous feeding in protected and un-protected ponds.

The specific growth rate and mean weight of the fingerlings obtained in the unprotected ponds was slightly higher (P=0.041 and P=0.028) than in the protected ponds. This distinction becomes more visible when these two parameters are related to the duration of rearing (Figure 2). In both cases the specific growth rate decreases and the mean weight of the fingerlings increases over time. The regression lines can be described as follows:

Specific growth rate, unprotected:

$\mathrm{Ln}(y) = 5.95 - 0.77 * \mathrm{Ln}(x)$, $R^2 = 0.84, P \leq 0.001$

Specific growth rate, protected:

$\mathrm{Ln}(y) = 6.06 - 0.85 * \mathrm{Ln}(x)$, $R^2 = 0.88, P \leq 0.001$

Mean weight at harvest, unprotected:

$\mathrm{Ln}(y) = 2.50 * \mathrm{Ln}(x) - 7.29$, $R^2 = 0.50, P \leq 0.01$

Mean weight at harvest, protected:

$\mathrm{Ln}(y) = 1.42 * \mathrm{Ln}(x) - 4.54$, $R^2 = 0.39, P \leq 0.01$

There is a significant correlation ($R^2 = 0.61$, $P \leq 0.01$) between the average weight of the fingerlings at harvest and the number of fingerlings produced per m^2 pond area (Figure 3).

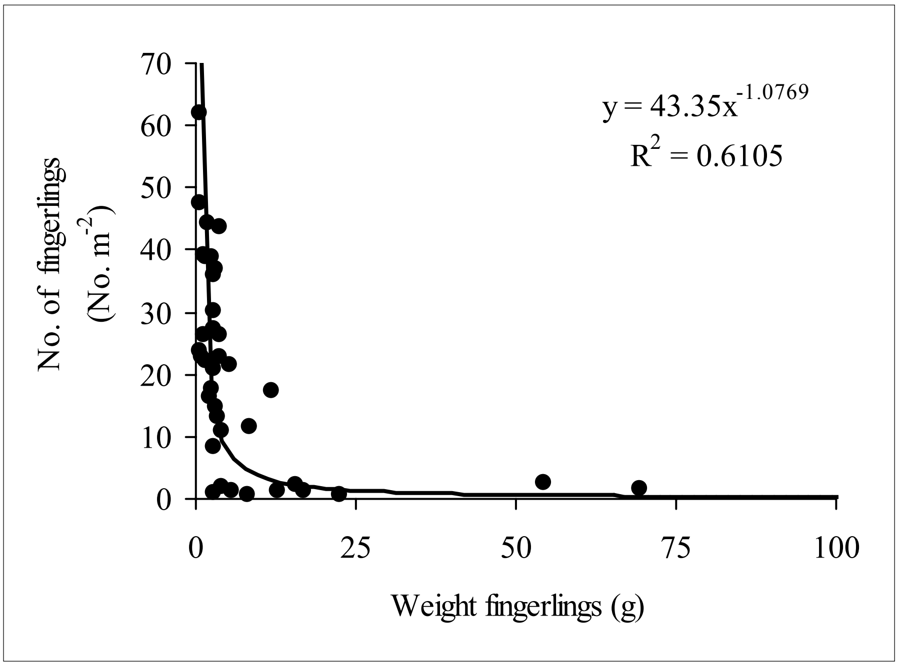

Figure 3: Relation between weight at harvest (g) and the number of Clarias gariepinus *fingerlings harvested from protected and un-protected ponds (no.* m^{-2} *cycle*$^{-1}$*).*

In unprotected ponds 5-8 kg of frog larvae per 100 m^2 was always present. Three species were found; *Rana occipitalis* (Gunther 1858), *Ptychadena pumilio* (Boulenger 1920) and *Xenopus tropicalis* (Gray 1864). The contents of 126 stomachs showed only material of plant origin.

Table 3: Fingerling production, survival rate, mean weight at harvest, total biomass harvested and growth rate of C. gariepinus obtained from protected or unprotected nursery ponds, stocked at low, medium or high larval densities wit a short or long rearing period. Values are means ± SEM. Data are compared among one class difference only.

Class	Fingerlings (no. m^{-2})	Survival (%)	Weight at harvest (g)	Biomass (kg ha^{-1})	Growth (% day^{-1})	n
Protected	28.3±2.7***	38.7±3.7***	3.1±0.5	735±95**	17.7±0.9	24
Not protected	3.6±1.7	6.0±2.7	26.74±11.2*	359±117	20.1±1.5*	2
Protected & short	30.7±2.9**	39.9±3.9	2.3±0.3	652±85	18.7±0.5***	20
Protected & long	15.8±2.3	33.2±10.7	7.2±1.8*	1149±339*	9.8±1.6	4
Protected &low	16.5±2.7	53.5±6.7	7.7±2.6	1203±448*	11.6±4.1	3
Protected & medium	31.7±3.7*	40.4±3.9	2.4±0.3	689±96	18.4±0.7**	18
Protected & medium	31.7±3.7	40.4±3.9***	2.4±0.3	689±96	18.4±0.7	18
Protected & high	19.3±3.2	14.3±1.5	2.8±0.6	540±157	15.9±2.7	3

*, $P \leq 0.05$, **, $P \leq 0.01$, ***, $P \leq 0.001$

*Table 4**:** Fingerling production, survival rate, mean weight at harvest, total biomass harvested and growth rate of C.gariepinus obtained from protected or unprotected nursery ponds, stocked at low, medium or high larval densities with a short or long rearing period. Values are means ± SEM. Within each class the protected and not protected ponds were compared.*

Class	Fingerlings (no. m^{-2})	Survival (%)	Weight at harvest (g)	Biomass (kg ha^{-1})	Growth (% day^{-1})	n
Low & short and not protected	2.8±1.8	9.6±6.4	6.5±3.1	153±46	22.3±2.2	4
Low & short and protected	20.7	60.2	2.7	571	18.3	1
Low & long and not protected	0.6±0.6	6.3±6.2	104.8±50.2	712±681	12.3±3.7	4
Low & long and protected	14.3±3.0**	50.1±10.2**	10.2±1.7	1519±550	6.9±0.5	2
Medium & short and not protected	5.0±2.9	5.2±2.9	9.4±2.7*	247±88	19.9±1.2**	12
Medium & short and protected	32.3±3.3***	41.5±4.0***	2.3±0.3	664±98**	16.9±0.6	17
Medium & long and not protected	n.a	n.a	n.a	n.a	n.a	0
Medium & long and protected	21.5	21.5	5.2	1118	12.9	1
High & short and not protected	n.a	n.a	n.a	n.a	n.a	0
High & short and protected	22.4±0.4	15.8±0.1	2.6±1.1	589±259	16.9±1.3	2
High & long and not protected	1.6	0.8	3.4	1160	9.8	1
High & long and protected	13	11.2	69.5	442	9.8	1

*, P ≤ 0.05, **, P ≤ 0.01, ***, P ≤ 0.001

DISCUSSION

The fact that *C. gariepinus* can be reproduced artificially throughout the year under tropical conditions corresponds with the results obtained by Kelleher *et al.* (1976), Micha (1976) and Janssen (1985a) in the Central African Republic. The reduction of the relative fecundity of females kept in outdoor ponds during the dry season, when water temperature decreases, was also found by Janssen (1985a) in the Central African Republic and by Me Amoin (unpublished results) in Ivory Coast and by Richter *et al*. (1987) in Israel. The relative fecundity is less than 5% in July and August, when water temperature falls below 25 ^{0}C. Similar results were obtained by Richter *et al*. (1987) in Israel. The relative fecundity was less than 5 % when the water temperature falls below 25 ^{o}C. Similar results were obtained by Richter *et al*. (1987) in Israel where the relative fecundity was less than 5% during 6-7 months, when the water temperature was below 25 ^{o}C. These results indicate that maturation processes with *C. gariepinus*, kept in outdoor ponds, are influenced by annual changes in water temperature and that the absolute water temperature is a major factor. The seasonal fluctuation of relative fecundity could be a problem for the year round production of fingerlings. It can however be lessened by keeping the broodstock indoors, under more or less controlled conditions. In this respect, it is interesting to compare the results of some experiments in which the husbandry of the broodstock differed as follows: constant water temperature of 25 ^{o}C and large fluctuation in light periodicity (Hogendoorn *et al*., 1980 and Richter *et al*.,1987), small variation in light periodicity and seasonal fluctuating water temperature of 22-29 ^{o}C (Janssen, 1985a). Keeping the brood stock indoors at 25 ^{0}C increases the relative fecundity and a high percentage of normal larvae can be obtained but the relative fecundity still follows the variation in photoperiodicity during the 18 month the experiments were carried out (Richter *et al*., 1987). A complete break down of the natural annual reproduction cycle was obtained by Janssen (1985 a) in the Central African Republic after the broodstock was kept over one year indoors at high but still fluctuating temperatures. It indicates that also light periodicity is of importance within the natural reproduction processes of *C. gariepinus* and probably takes care of the "fine-tuning" of the processes as it is in the long run overruled by high water temperatures. The method of keeping the broodstock indoors was used in Central Africa and Ivory Coast and encountered some serious problems. "Crack head" disease, low growth rates of the broodstock and high mortalities of larvae produced by this broodstock because of an oedemic disease were observed (Janssen, 1985a and de Graaf, 1989). "Crack head" disease has been reported earlier in the intensive rearing of catfish in Thailand and the lack of appropriate feed is the most likely cause (Anonymous, 1981). This is supported by the fact that "crack head" disease rarely occurs at the indoor hatcheries in the Netherlands where high quality feed is used. During this study the decrease in egg production during the dry season was compensated for by the use of larger numbers of females per reproduction trial.

The use of water hyacinth as a support for eggs is comparable with the "kakabans" used for the incubation of common carp (*Cyprinus carpio* L*)* eggs (Huet, 1972). The yearly average hatching percentage (35%) is low due to the influence of the dry season. Hatching percentage during the rainy season (59.1%) can be compared with results of earlier field studies (Micha, 1976; Hogendoorn, 1979 and Janssen 1985a).

The production in unprotected ponds is highly variable, as observed by others (Hogendoorn *et al.*, 1976; Kelleher *et al.*, 1976; Micha, 1976 and Hogendoorn, 1979). The production in protected ponds is about 8 times higher than that of unprotected ponds and proved to be reliable. The fact that increasing the stocking density above 100 larvae m^{-2} and extending the rearing period to 50 days or more does not improve the final production of fingerlings, indicates the limits of the system. Stocking protected ponds with approximately 100 larvae m^{-2} and harvesting them after 35-40 days is considered to be optimal.

Three factors are probably influencing fingerling production in ponds;

- The presence of amphibian predators like adult frogs. Nugent (cited by Kelleher *et al.*, 1976) estimated the mortality due to this kind of predation at 10%; this study however cannot confirm that estimate due to the fact that it has not been measured.
- A competition for food resources. Phytoplankton levels, in the unprotected ponds, are reduced in by the presence of phytophagous frog larvae, consequently leading to a reduction in availability of zooplankton, needed by the catfish larvae. This effect is critical during the first days of exogenous feeding of the larvae and determines the limits of the nursery system, which is dependent on natural food production. Production levels upto 800 fingerlings m^{-2} are reported by Hecht *et al.* (1988); the nursing ponds, however are stocked with 10 day old larvae which passed the critical moment before which live food or a real "baby" diet (Verreth *et al.*, 1991) is essential for survival and production.
- Sibling cannibalism has been observed earlier among fry of *C. gariepinus* in hatcheries (Janssen, 1985c) and has been studied in detail by Hecht and Appelbaum (1988). Within aquarium experiments two types of cannibalism can be distinguished; type 1 or tail first cannibalism, where predator and prey size are almost equal, occurring in a weight range of 0.006 g - 0.9 g, and type 2 or head first cannibalism, where predator size exceeds prey size, occurring in a weight range of 0.9 g - 4.6 g. Once the weight of the fish exceeds 4.6 g, cannibalism ceased to exist in these aquarium experiments because the mouth width of the largest fish in the sibling population is smaller than the head width of the smallest fish. In ponds two groups of fingerlings can be distinguished 40 days after stocking: a small group (0- 3%) with an average weight of 8-12 g, and a large group (about 97%) of fingerlings weighing 0.5 - 3 g. It is most likely that type 2 cannibalism continues to be of importance due to its

higher size variation as compared with the experiments of Hecht and Appelbaum. (1987). This phenomenon explains why after a long rearing period the number of fry harvested is low and their average weight is high (Figure)

A final average weight of 2.3 ± 0.3 g and a specific growth rate of 16.9 ± 0.6 % day^{-1} obtained in protected ponds with a 'short' rearing cycle is comparable with results obtained by Hogendoorn (1980) and Hecht and Appelbaum (1987) under controlled hatchery conditions, where the fish were fed up to satiation with commercial dry feed and nauplii of *Artemia salina*. The difference in growth between the protected and nun-protected ponds indicates that maximum growth is not yet attained in protected ponds and that the maximum carrying capacity of the used system has been reached. The limiting factor is most likely the lack of animal protein due to the limited availability of zooplankton.

The production cost of US$ 0.07 (16.4 FCFA) for a fingerling from the studied system (based on the 1989 price index for Republic of Congo) is less than the 29 FCFA, calculated for a hatchery in the Central African Republic, where nauplii of *Artemia salina* and dry feeds were used (Janssen, 1985a). A comparison of the costs of the two systems is presented in Table 5 and indicates that pond rearing is labour intensive, while hatchery rearing is capital and technology intensive. This, as well as the production price, must be taken into consideration when production units are being planned.

Table 5: Division of costs as percentage of the total production costs of two Clarias gariepinus *fingerling productions systems in Africa: Pond rearing (this study) and hatchery rearing using nauplii of* Artemia salina *and composed feeds (Janssen, 1985b).*

	Costs of pond rearing (% of total costs)	Costs of hatchery rearing (% of total costs)
Manpower	68.0	16.2
Depreciation of investments	6.1	56.2
Operating costs	25.9	27.6

In conclusion, the artificial reproduction and mass rearing of *C. gariepinus* throughout the year is technically possible under tropical conditions by using 'low cost' adapted methods and this study does not support the conclusion of Richter *et al*. (1987) that broodfish should preferably be raised in a hatchery in order to ensure a continuous production of viable eggs.

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An instruction video on the rearing method described in this paper has been produced by the project "Development of rural fish farming in Congo", FAO/UNDP/RPC/88/007, and can be obtained from Nefisco foundation, *www.Nefisco.org*, info@Nefisco.org.

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CHAPTER 5: SIMULATION OF NILE TILAPIA (*OREOCHROMIS NILOTICUS NILOTICUS* L.) CULTURE IN PONDS, THROUGH INDIVIDUAL BASED MODELLING, USING A POPULATION DYNAMIC APPROACH

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ABSTRACT

A simulation model for the rearing of the Nile tilapia (*Oreochromis niloticus niloticus* L) for mixed or mono sex culture, and for poly culture with the African Catfish (*Clarias gariepinus* Burchell 1822) or African Snakehead (*Parachanna obscura* Günther 1861) is presented. The model is based on population dynamics and follows an Individual Based approach. The model consists of a tilapia submodel representing population dynamics, growth and recruitment and a predator submodel representing the predation process and population dynamics and growth of the used predator. The model was calibrated with data obtained in Congo Brazzaville and validated with data from the Philippines, Thailand and Ivory Coast. The model visualized major underlying ecological processes in tilapia farming and indicated that growth and its relation to feed quality, recruitment and prey-predator relations are major topics in tilapia farming modelling. The model can serve as a predictive and decision-making support tool after some slight adaptations discussed.

Key words: *Clarias gariepinus*, Individual based tilapia farming simulation model, *Oreochromis niloticus niloticus* L., *Parachanna obscura*,

INTRODUCTION

Tilapias, originally from Africa, have been reared for centuries. During the last 50 years, interest in their aquaculture potential has led to a nearly worldwide production and distribution. Because of its contribution to world food production through aquaculture operations, tilapia generated much enthusiasm in many developing countries after the Second World War. In the 1960s and 1970s, tilapia culture focused on the production of food for local consumption and on the diversification of rural activities related to agriculture and animal husbandry. Soon after its first expansion, tilapia culture made no further progress and has in many cases even declined, resulting in the abandonment of fish farms by discouraged farmers. This failure has been attributed to the harvesting of too many small, stunted tilapia from overpopulated ponds due to poor husbandry techniques; the dependency on subsidized extension services and fingerling distribution centres; misjudgement of the motivation of the rural fish farmers by policymakers; and the creation of the myth that the rural farmer will willingly take up fish farming for food security or as a source of protein for their family; failure to apply adequate resources, such as water and feed, which may be naturally limiting (de Graaf and Janssen, 1996; Alceste and Jory, 2002). However, during the past 20 years, commercially viable techniques have been developed:

- Mono-sex culture of males whereby the all-male fingerlings are obtained through manual sexing (Shell, 1968), through hybridisation (Pruginin, 1967; Lovshin *et al.*, 1990) or through hormone induced sex-reversal (Eckstein and Spira, 1965; Guerrero, 1975; Shelton *et al.*, 1978)
- Recruitment control by the introduction of predator fish (Lazard, 1980; Hopkins *et al.*, 1982; Verani *et a*l., 1983; McGinty, 1985; de Graaf *et al.*, 1996)
- The introduction of genetically improved strains of tilapia (Pullin *et al.*, 1991)

The methods applied in Nile tilapia (*Oreochromis niloticus niloticus* L) farming are diverse; they include mixed culture, poly-culture with predators or mono-sex (all male) culture. The success of the methods applied depends on local consumer preferences, economics, availability, and costs of inputs. For example in Congo Brazzaville, mixed culture is financially feasible and poly culture with snakeheads, applied to reduce the number of fingerlings at harvest, does not improve the financial performance, as the resulted improved growth did not compensate for the reduction in gross product value generated by the sale of the fingerlings. However, in Ivory Coast, mono-sex, all male culture is a prerequisite, as the market demands tilapia with a weight of 250 g or higher (de Graaf, unpublished data). Deciding which method is optimal under certain conditions can be complex, and decision support models based on simulation models of tilapia farming could facilitate this process.

Over the last decades a number of computer simulation models for finfish farming have been developed (Cuenco *et al*., 1985; Machiels and Henken, 1986; Ross and Mckinsey, 1989; van Dam and Penning de Vries, 1995; van Dam and Pauly, 1995; van de Meer and van Dam, 1999). However, most of the models are based on physiological and bio-energetic principles, and are therefore not suitable to simulate the predator-prey processes that take place in poly culture of Nile tilapia with a predator. For the latter, simulation models based on fisheries population dynamics (Sparre and Venema, 1992) as applied by Fisher and Grant (1994) are more suitable.

Individual Based Models (IBMs) have become popular for modelling fish populations as they apply the principle that properties of ecological systems can be derived by considering the properties of individuals constituting them. (Grimm, 1999). Individual based population models simulate the behaviour of each member of a biological population as an individual. These models differ from traditional state-variable models in which population size is described as an aggregated variable. The advantages of individual based models include the following:(1) A variety of types of differences among individuals in the population can be accommodated (2) complex decision making by individual processes can be simulated and (3) local interactions in space and the effects of stochastic temporal and spatial variability are easily handled (DeAngelis *et al*., 1999).

This paper presents an individual based tilapia farming model based on principles of fisheries population dynamics.

MATERIAL AND METHODS

MODEL STRUCTURE

The general structure of the model is shown in Figure 1 and all symbols used there are listed in Table 1. The model is written in Matlab, version 6.5 (The MathWorks, Inc, *www.mathworks.com*)

Table 1: List of abbreviations used in Figure 1.

Name	Description
CV-Kf	Coefficient of variation in growth parameter K of female tilapia
CV-Km	Coefficient of variation in growth parameter K of male tilapia
CV-Kp	Coefficient of variation in growth parameter K of the predator
CV-Lf	Coefficient of variation in the length distribution of female tilapia
CV-Lm	Coefficient of variation in the length distribution of male tilapia
CV-Lp	Coefficient of variation in the length distribution of the predator
Deaths	Natural death leaving the system
K	von Bertalanffy growth constant (day^{-1})
L(t) female	Length of female tilapia (cm)
L(t) male	Length of male tilapia (cm)
L(t) predator	Length of predator (cm)
L(t) recruits	Length of recruit tilapia (cm)
$L\infty$	von Bertalanffy maximum length (cm)
LW predator	Length weight relation predator
LW Tilapia	Length weight relation tilapia
M	Natural mortality rate (day^{-1})
N(t) female	No of female tilapia
N(t) male	No of male tilapia
N(t) predator	No of predators
P	Mortality of tilapia caused by predator (day^{-1})
Pred dens	Predator density (no m^{-2})
Pred type	Predator species
R	Recruitment (No female-1 day-1)
W(t) females	Weight female tilapia (g)
W(t) males	Weight male tilapia (g)
W(t) predator	Weight predator (g)

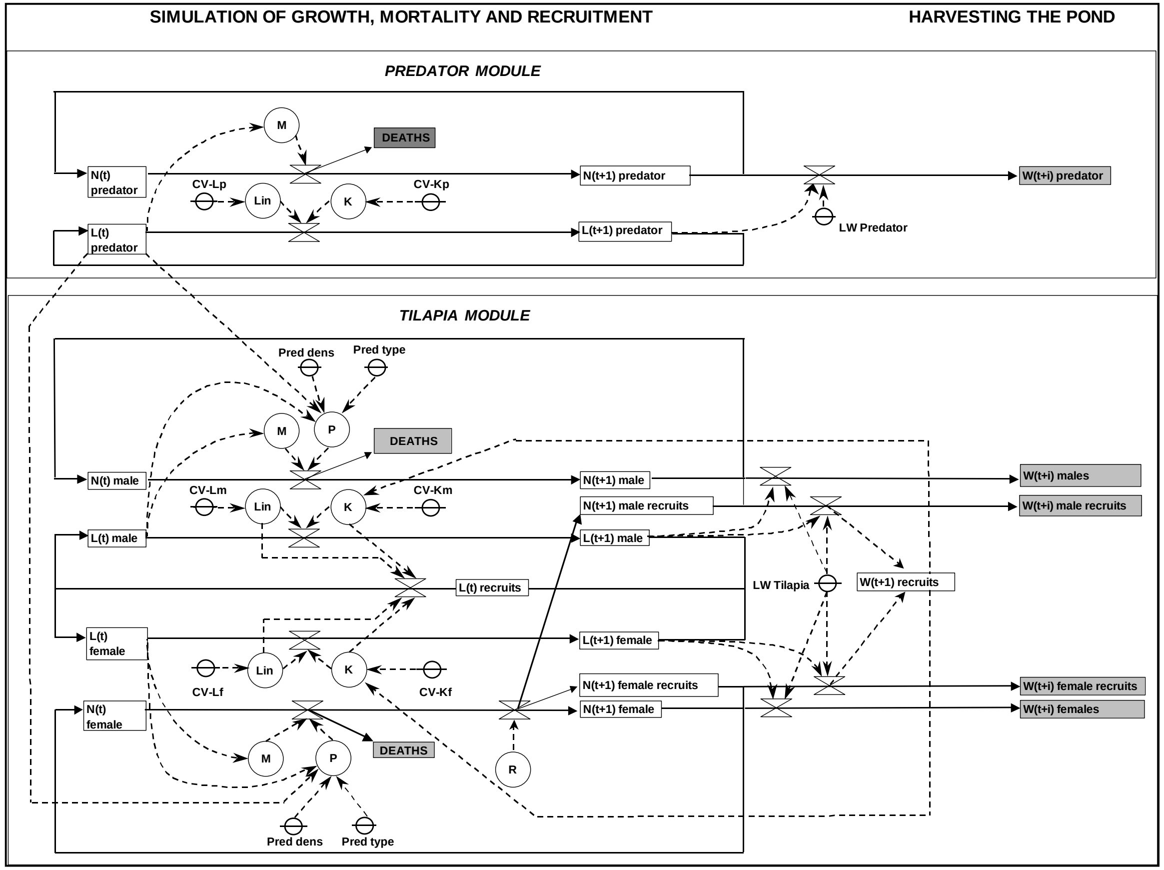

Figure 1: Relational diagram of the individual based tilapia farming model according to Forrester's conventions (de Wit and Goudriaan, 1978). Stated variables are presented by rectangles, rates of change by valves, auxiliary variables by circles, and parameters by circles with cross bars. The flow of material is represented by solid arrows and the flow of information by dotted arrows. Abbreviations are explained in Table 1.

The overall simulation model consists of two modules:

1. A module for the simulation of tilapia (males, females and recruits)
2. A module for the simulation of a stocked predator

The simulation model is based on the principles of length based fish stock assessment (Sparre and Venema, 1992), whereby, for each module, growth is simulated according to the von Bertalanffy growth function (Somers, 1988) and the evolution of the number of fish is simulated with an exponential decay model of the form:

$$N_t = N_0 e^{-z\Delta\Delta} \tag{1}$$

Where N_0 is the initial number of individuals at time t=0 and N_t is the remaining number at time *t.* Z is the instantaneous mortality rate, which in case of tilapia consists of natural mortality (M_{til}) and mortality by a predator (P_{til}) if present. In case of the predator, it consists of natural mortality of the predator only (M_{pred}).

The model starts with an initial number of male and female tilapia and predators. During initialisation, each individual fish is at randomly given a length and the growth parameters K and L_∞ are assigned. Normal distribution around the mean initial value is achieved with the coefficient of variation for the different parameters through:

$$V = V_{mean}\left(1 + randn.CV\right) \tag{2}$$

Where:

V = Generated value for each individual

Vmean = Mean initial value

Randn = Random generation of numbers in which arrays are normal distributed with a mean 0 and variance 1

CV = Provided coefficient of variation

With this process the stochasticity of the model is controlled for the key parameters: Length at stocking, L_∞ and K, for male and female tilapia, their recruits and the predator.

The model calculates with steps of 1 day ($\Delta t = 1$ day). Every day the model calculates the length increment for each individual fish according to the von Bertalanffy growth function:

$$\frac{dL}{dt} = K.\left(L_\infty - L_t\right) \qquad (3)$$

Growth of the parent stock is negatively related to the proportion of fingerlings (de Graaf *et al*, 1996) and incorporated into the model with:

$$K = K_{init} . e^{-aP_{fingerlings}} \qquad (4)$$

Where:

K_{init} = the initial value of the growth parameter assigned to each individual fish

a = constant

$P_{fingerlings}$ = proportion of fingerlings in the system, on a weight basis

With the exponential decay model the *daily probability of dying* (P_d) for each individual fish is expressed as:

$$P_d = 1 - e^{-(M+P)} \qquad (5)$$

Whereby M is the natural mortality and P is the mortality caused by the predator. The natural mortality of tilapia and the predator is a function of the length of the fish. The mortality of tilapia caused by the predator is a function of the length of the tilapia and the length of the predator. A fish will die in the model if a random number from a uniform distribution between 0 and 1, generated for the fish, is less then P_d.

When the female tilapia reaches their length at first maturity, they generate a number of recruits every day. Growth parameters are assigned to the newborn recruits and they follow the same simulation cycle as the parent stock.

After each step of one day, the weight of individuals is calculated with length-weight relationship and this is further used to calculated total biomass for the different groups: original stocked male tilapia, original stocked female tilapia, recruited male tilapia, recruited female tilapia and predator. The total weight of stocked tilapia and recruited tilapia is used to calculate the proportion of the fingerlings present in the system, used for the adjustment of daily growth rates.

PARAMETER ESTIMATES

THE DATA SET FOR CALIBRATING

Parameters used to calibrate the model are based on data collected between 1986 and 1990 at the National Fish Culture Station, Djoumouna in the Republic of Congo. The data were used previously to analyse the recruitment control of Nile Tilapia by the African catfish (*Clarias gariepinus,* Burchell, 1822) and African snakehead (*Parachanna obscura* Günther, 1861) (de Graaf *et al*., 1996). The data were collected from grow-out ponds with an average water depth of 1 m and surface areas between 0.04 and 1.2 ha, stocked with fingerlings of *O. niloticus* (15-30 g) in combination with either *C. gariepinus* (1.5-130 g) or *P. obscura* (0.5-205 g). The stocking rate of *O. niloticus* remained more or less fixed at 20,000-22,000 ha^{-1}, while predator stocking rates varied between 0-20,000 ha^{-1} for *C. gariepinus* and 0-4,000 ha^{-1} for *P. obscura.* The fish were fed 6 days week^{-1} with wheat bran at a daily rate of 4%-11% of the total biomass of *O.niloticus* or the combined total biomass of *O. niloticus* and *C. gariepinus*. In case of poly culture with *P. obscura* the feeding rate was adjusted according to the biomass of *O. niloticus* only as *P. obscura* is considered to be strictly carnivorous. All experiments were carried out over a period of four years, during which the overall performance of the station improved. During the first two years of the experiments, the feeding levels (‘low level’) were lower than those used during the last years of the experiments (‘high level’) due to budgetary restrictions (Table 2). From all ponds at harvest, the total weight of *O. niloticus* and the predator were determined and 300-1000 specimens were sampled at random, weighed individually, and classified as male, female, fingerling or predator.

Table 2: Low and high feeding levels used at the fish culture station of Djoumouna, 1986-1990.

Average weight fish (g)	Daily feeding rate (% of total biomass)	
	Low ('86-'88)	High ('88-'90)
0-25	6	11
25-50	6	10
50-100	5	9
100-150	4	7
150-200	4	6

GROWTH

Monthly length frequency data for male and female tilapia were available from 44 experiments. The data were entered and further analysed with the software package for length based fish stock assessment FISAT (Gayanilo and Pauly, 1997). As the growth parameters K and L_∞ are interrelated, i.e. different values of the parameters may produce similar growth curves (Sparre and Venema, 1992), estimation of the parameters was carried out in two steps.

First, the length frequencies were smoothed with an average of three, after which L_∞ was estimated with a Powel-Wetherall plot (Wetherall *et al.*, 1987). This resulted in a maximum L_∞ of 32.5 cm for male tilapia, and 23 cm for female tilapia. In a second step, the growth parameter K was estimated over the smoothed frequency distributions, with the automatic search routine of ELEFAN in FISAT, whereby L_∞ was kept constant at 32.5 cm and 23 cm for males and females respectively and K was varied with steps of 0.1 year^{-1}.

Previous analysis of the overall data (de Graaf *et al.*, 1996) indicated that growth depends on the feeding level and the proportion of fingerlings in the ponds at harvest. Analysis of the estimated K values for these aspects indicates a similar pattern. Growth of the males is significantly related to the feeding level and reducing the feeding level from high to low, diminish the growth parameter K with 23%, while for female tilapia there is no significant difference (Table 3).

Table 3: Mean values (±SEM) of growth parameter K for Nile tilapia at high and low feeding level.

	High feeding		Low feeding		
	K (year^{-1})	n	K (year^{-1})	n	p
Male tilapia	1.321±0.076	33	1.025±0.116	12	0.048
Female tilapia	1.087±0.077	31	1.120±0.122	10	0.835

For both male and female tilapia, the growth rate diminishes if the proportion of fingerlings at harvest increases Figure 2. For a low feeding level, this relationship could not be constructed due to insufficient length frequency data.

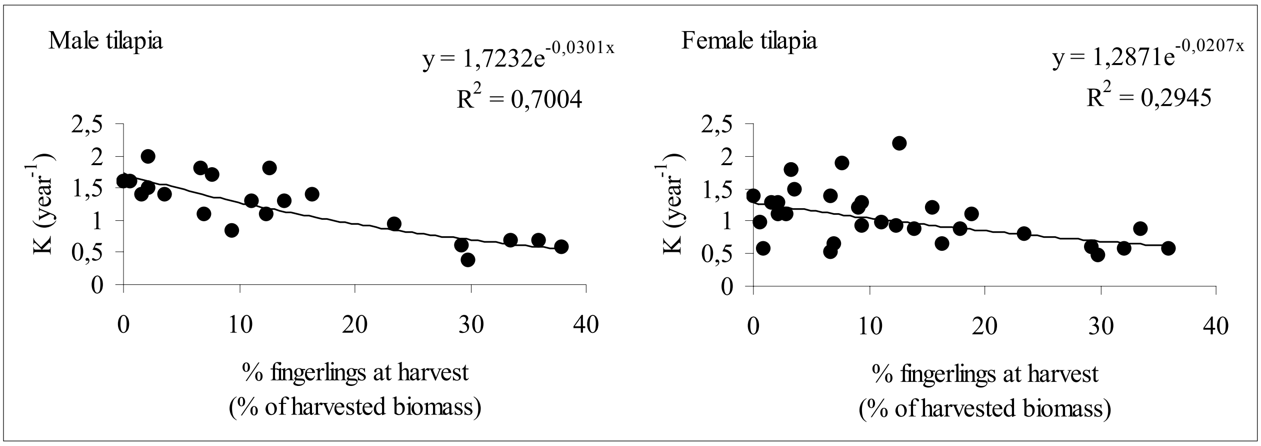

Figure 2: The relation between the proportion of fingerlings at harvest and growth parameter K for male and female tilapia at high feeding level.

Figure 2, gives a maximum mean growth rate of 1.73 and 1.28 year^{-1} for respectively male and female tilapia. This growth rate will diminish either by a lower feeding level or by the biomass of the fingerlings coming into the system. For the model, it is assumed that estimated values for the reduction for feeding level, and reduction due to the presence of fingerlings, as estimated at high feeding levels, are also valid for low feeding levels. The values of the growth parameters for Nile tilapia used in the model are presented in Table 4.

Table 4: Growth parameters for Nile tilapia as used in the model.

	L_∞ male (cm)	L_∞ female (cm)	Kmax male ($year^{-1}$)	Kmax female ($year^{-1}$)
Low feeding level	32.5	23	1.38	1.02
High feeding level	32.5	23	1.73	1.28

In the model the reduction in growth due to the presence of fingerlings is calculated as:

$$K_{n+1} = K_n e^{-0.04\%fingerlings_n} \qquad (6)$$

Where:

K_{n+1} = used growth rate

K_n = growth rate on the previous day

% fingerlings = fingerlings on the previous day in % of total tilapia biomass

Preliminary runs of the model indicated that the different growth rate of male and female tilapia caused extreme dichotomy in the distribution of female and male fingerlings at harvest, with the 80-90% of the fingerling biomass consisted of males. Some dichotomy occurs in fingerling distribution (de Graaf, unpublished data) but not in this extent. Therefore in the model the growth parameters of fingerlings between 0.8 and 10 cm is set at the average L∞=27,5 and K =1.5 and K =1,2 for respectively high and low feeding level. Once the fingerlings reach a length of 10 cm, they are assigned new growth parameters according to their sex and feeding level

Growth parameters for *P. obscura* were estimated from the dataset with the modified Appeldoorn method (Gayanilo and Pauly, 1997) using the length at stocking and the length at harvest. For *C. gariepinus* growth could not be estimated with the data set and the parameters were extracted from *www.fishbase.org*.

C. gariepinus is omnivorous and feeding levels in the experiments were adjusted to its biomass, therefore it is assumed that its’ growth rate diminish also with 23% at low feeding rates, which is not the case for *.P. obscura* as it is piscivorous. The growth parameter for *C. gariepinus* and *O, obscura* as used in the model are presented in Table 5.

Table 5: Growth parameter of African catfish and African snakehead as used in the mode.l

	L_∞ catfish (cm)	K catfish (year^{-1})	L_∞ snakehead (cm)	K snakehead (year^{-1})
Low feeding level	120	0.31	87	0.65
High feeding level	120	0.40	87	0.65

LENGTH-WEIGHT RELATIONSHIP

An allometric function is used to describe the relation between body length L (cm) and body weight W (g) of Nile tilapia, catfish and snakehead. For tilapia: $W = 0.0152*L^{3.077}$, for catfish: $W = 0.00731*L^{2.99}$ and for snakehead: $W = 0.0059*L^{3.008}$ are used

MORTALITY

Within the system, there are two types of mortality:

1. The natural mortality of tilapia and the stocked predator
2. The mortality of tilapia fingerlings caused by the stocked predator

Natural mortality can be described with an allometric relationship with the body weight in fish (Peterson and Wroblewski 1984; McGurk 1986; Lorenzen 1996) of the form:

$$M_w = M_u W^{-b} \tag{7}$$

Where M_w is natural mortality at weight W, M_u is mortality at unit weight and b is the allometric exponent. Lorenzen (1996, 2001) indicated that mortality of fish in natural ecosystems is governed by a consistent allometric relationship with parameters b = -0.3 and M_u =3 year^{-1}. However, for stocking experiments and aquaculture, b = -0.3 proved to be adequate but M_u was found highly variable and could not be fixed at 3 year^{-1}. Converting this relationship into a length based one gives the form:

$$M_w = M_u a^{-0.3} L^{-0.3b} \tag{8}$$

Where a and b are the components of the length-weight relationships, resulting in the following relationships for natural mortality of tilapia, catfish and snakehead:

$M_{tilapia} = 3.51*M_u*L^{-0.931}$

$M_{catfish} = 4.37*M_u*L^{-0.897}$

$M_{snakehead} = 4.66*M_u*L^{-0.926}$

In the rearing experiment, tilapia had a survival rate of 70-80% and in the model, M_u=1 was used. Catfish and snakehead had a survival rate of 50-60% and M_u=4.5 was used.

In the model, the catfish and snakehead only prey on tilapia in the range of 0.8-10 cm, as catfish and snakehead can consume a tilapia up to about 10% of its own body weight (de Graaf, unpublished data). In their early life, catfish are mainly planktivorous and shift to a more piscivorous behaviour most likely occurs once they reach a weigh of 7-8 g (Munro, 1967, de Graaf *et al*, 1996). Therefore, in the model the mortality of tilapia is related to the density (no ha^{-1}) of all clarias and snakehead larger than 8 cm and the length of the tilapia, with larger tilapia having a lower risk of predation. The overall relation between mortality due to predation (P), the predator density (D) and the length of Tilapia (L) in the model has the form:

$$P_{by\ clarias} = \frac{280 D_{clarias>8\,cm} L_{til}^{-1.5}}{365} \tag{9}$$

$$P_{by\ snakehead} = \frac{1600 D_{snakehead>8\,cm} L_{til}^{-1.5}}{365} \tag{10}$$

LENGTH AT FIRST MATURITY AND RECRUITMENT

The tilapias in the experiments were stunted, in the sense that they reproduced at an early age, having a weight of 30-50 g (de Graaf *et al.*, 1999). Therefore, in the model the length at first maturity was set at 12.5 cm. Although it is known that absolute fecundity of tilapia increases with the length of the female tilapia (Melard, 1986; de Graaf *et al.*, 1999), this aspect is not incorporated in the model, as at the same time larval production reduces with increasing length of the female tilapia (Melard, 1987). Therefore recruitment in the model is constant and set at 0.3 recruits mature-female^{-1} day^{-1}: the average fingerling production per female as presented by Melard (1987), assuming a mortality of 60% between larvae and fingerling.

CALIBRATION AND VALIDATION

The model was calibrated with the results of 62 rearing experiments carried out in Congo Brazzaville during 1986-1990 (de Graaf *et al.*, 1996). As input for the model the following data were used: pond size, number of rearing days, length of the stocked fingerlings, proportion of male fingerlings at stocking, number and length of the stocked predator and feeding level ('low' or 'high'). For each experimental data set, the model was run 10 times with the coefficient of variation set at 20%. Calibration was done by adjusting the values of key parameters for: mortality, recruitment, growth reduction due to lower feeding level and due to the biomass of fingerlings, until the best agreement between observed and simulated data was reached. Agreement between simulated (Y) and observed (X) values was quantified using linear regression through the origin, Pearson's correlation coefficient and the deviation (D) of Y from X expressed as $D=100(Y-X)/X$ (in %)

VALIDATION

The model was validated with three different data sets:

Data from 24 experiments carried out by the Center for Tropical Forestry in Ivory Coast in 1979 and 1980 (CTFT, 1979, 1980; Lazard, 1980). This data set mainly encompasses rearing experiments with all-male hand-sexed Nile tilapia, whereby recruitment due to sexing errors was completely controlled by the stocked predator *Hemichromis fasciatus*. In the validation, a high density of large catfish was used to simulate complete control of recruitment, but the simulated data of the predator were not used in the further analysis.

Data from 104 experiments with poly culture of Nile tilapia with the snakehead murrel (*Channa striata* Bloch, 1793) carried out in 1978/79 out by ICLARM/CLSU in the Philippines (Hopkins and Cruz, 1982; Prein *et al.*, 1993). Preliminary analysis of the data indicated that the growth rates of tilapia observed in these experiments ($L\infty=25.4$ and $K=3.62$ year^{-1}) were much higher then observed in Africa. Further, a large range of feeding levels was used, strongly influencing the growth rates of the stocked Nile tilapia (Prein *et al.*, 1993). Both factors resulted in a large underestimation of major parameters by the model. Therefore, for each experiment the overall growth parameter K was estimated with an "extended forced

Gulland Holt plot" (de Graaf and Prein, Chapter 5) with L_∞=30.8 cm as input. The obtained values of K and L_∞=30.8 were used as input. Further the standard model settings of African snakehead were used to simulate the impact of the snakehead murrel (*C. striata*).

Data from 18 experiments with poly culture of Nile tilapia with the snakehead murrel (*C. Striata*) carried in 2000 out by the Asian Institute of Technology in Thailand (Lin *et al*., 2001).

SENSITIVITY ANALYSIS AND STOCHASTIC BEHAVIOR

A sensitivity analysis was carried out to investigate the impact of four model input parameters: growth parameter K, stocking length of the tilapia fingerlings, length at first maturity of tilapia and the recruitment of tilapia, on model outputs. The model was simulated for a 200-day rearing period, whereby each parameter was increased in steps of 10%, and the model results (length male tilapia at harvest, length female tilapia at harvest, net yield tilapia, net yield male tilapia, net yield female tilapia, % male tilapia at harvest, % female tilapia at harvest, % tilapia fingerlings at harvest) were stored. Sensitivity coefficients were defined by linear regression between the rate of change of the parameter and the rate of change of the model output.

To study the stochastic behaviour, the model was simulated for a 200-day rearing period whereby the coefficient of variation of the growth parameter K of all tilapia was increased in steps of 10% and the model results were stored.

RESULTS

CALIBRATION

The simulated and observed values for tilapia net yield, predator net yield, the percentage of tilapia fingerlings, male tilapia and female tilapia at harvest are presented in Figure 3. The overall quantitative data for the different components are presented in Table 6. The regression coefficients indicate that the model underestimates the total net yield of tilapia and the percentage of females at harvest, and overestimates the total net yield of the predator and the percentage of fingerlings at harvest. High deviation of simulated values from the observed values takes place for the percentage of fingerlings and the percentage of females at harvest. The very high values are mainly due to some low observed values.

*Table 6: Overall results of the calibration with data from Congo Brazzaville (** P<0.01).*

Parameter	Regression coefficient	Pearson's correlation coefficient	D (%)	D_{max} (%)	D_{min} (%)
Total net yield tilapia	0.86	0.486^{**}	-2	164	-53
Total net yield predator	1.23	0.826^{**}	6	206	-92
% tilapia fingerlings at harvest	1.14	0.825^{**}	-106	92	-2140
% male tilapia at harvest	0.96	0.700^{**}	2	43	-42
% female tilapia at harvest	0.87	0.535^{**}	-34	60	-877

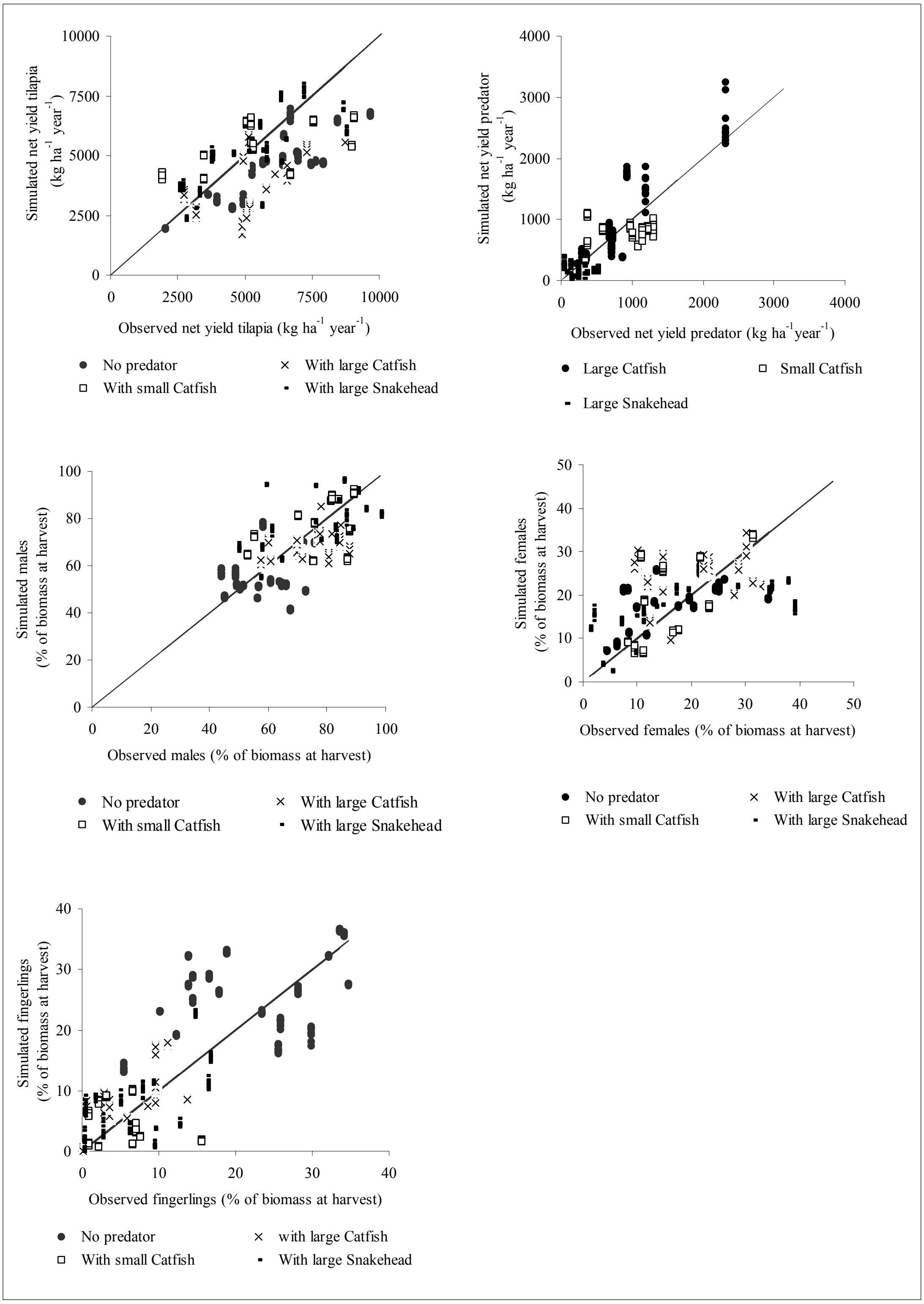

Figure 3: Observed and simulated data for the calibration with the data set of Congo Brazzaville. The bisector represents perfect agreement between simulated and observed values.

VALIDATION

DATA FROM IVORY COAST: ALL-MALE NILE TILAPIA

The simulated and observed values for tilapia net yield, the length of male tilapia at harvest and the percentage male and female tilapia at harvest are presented in Figure 4. The overall quantitative data for the different components are presented in Table 7. The results indicate that net yields and the length of males at harvest are underestimated by the model for this data set, especially for short rearing periods.

*Table 7: Overall results of the validation with data from Ivory Coast (** P<0.01).*

Para meter	Regression coefficient	Pearson's correlation coefficient	D (%)	D_{max} (%)	D_{min} (%)
Net yield tilapia	0.75	0.409^{**}	-12	57	-48
Length male tilapia at harvest	0.97	0.043	-2	15	-15
% male tilapia at harvest	0.99	0.956^{**}	0	1	-1
% female tilapia at harvest	0.95	0.942^{**}	-8	85	-61

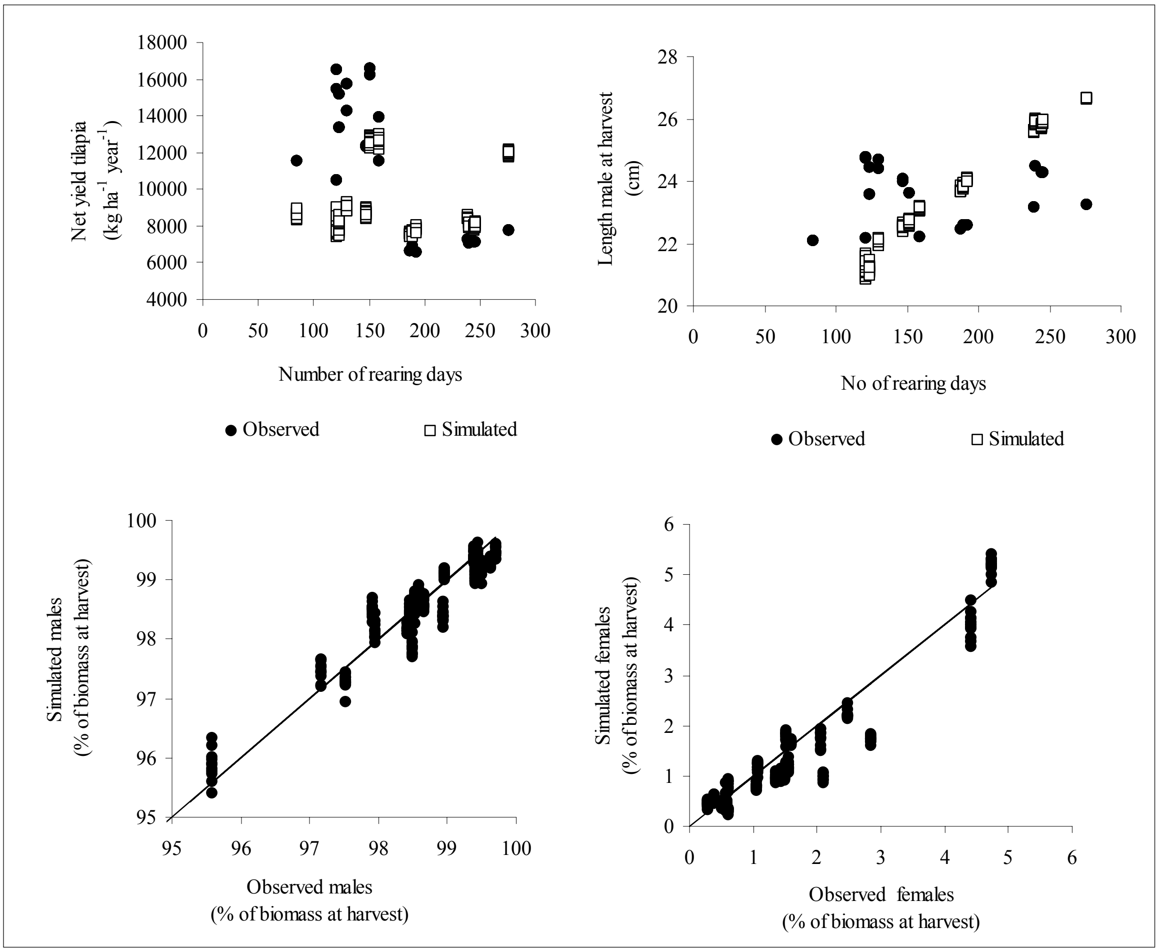

Figure 4: Observed and simulated data for validation with the data set of Ivory Coast. The bisector represents perfect agreement between simulated and observed values.

DATA FROM THE PHILIPPINES: NILE TILAPIA WITH SNAKEHEAD MURREL

The simulated and observed values for tilapia net yields, the length of tilapia at harvest and the percentage of fingerlings at harvest are presented in figure 5. The overall quantitative data for the different components are presented in Table 8. The results indicate that for this data set, the model underestimates the percentage of fingerlings at harvest and consequently the net yields are also underestimated. The very high values of D_{max} found are mainly observed at low values of the parameter. In the dataset, in ponds without a predator, about 65% of the biomass at harvest consists of fingerlings, while the model provides 22%. This excessive recruitment could be the result of a more pronounced stunting i.e. earlier reproduction of tilapia. Changing the length at first maturity in the model from 12.5 to 6 cm gives some improvement as the model provides 36% of fingerlings at harvest. However, this is still far below the observed data (Figure 6).

*Table 8: Overall results of the validation with data from the Philippines (** P<0.01).*

Parameter	Regression coefficient	Pearson's correlation coefficient	D (%)	D_{max} (%)	D_{min} (%)
Net yield tilapia	0.74	0.466^{**}	34	2574	-78
Length tilapia at harvest	0.97	0.722^{**}	0	38	-36
% tilapia fingerlings at harvest	0.29	0.795^{**}	240	5160	-99

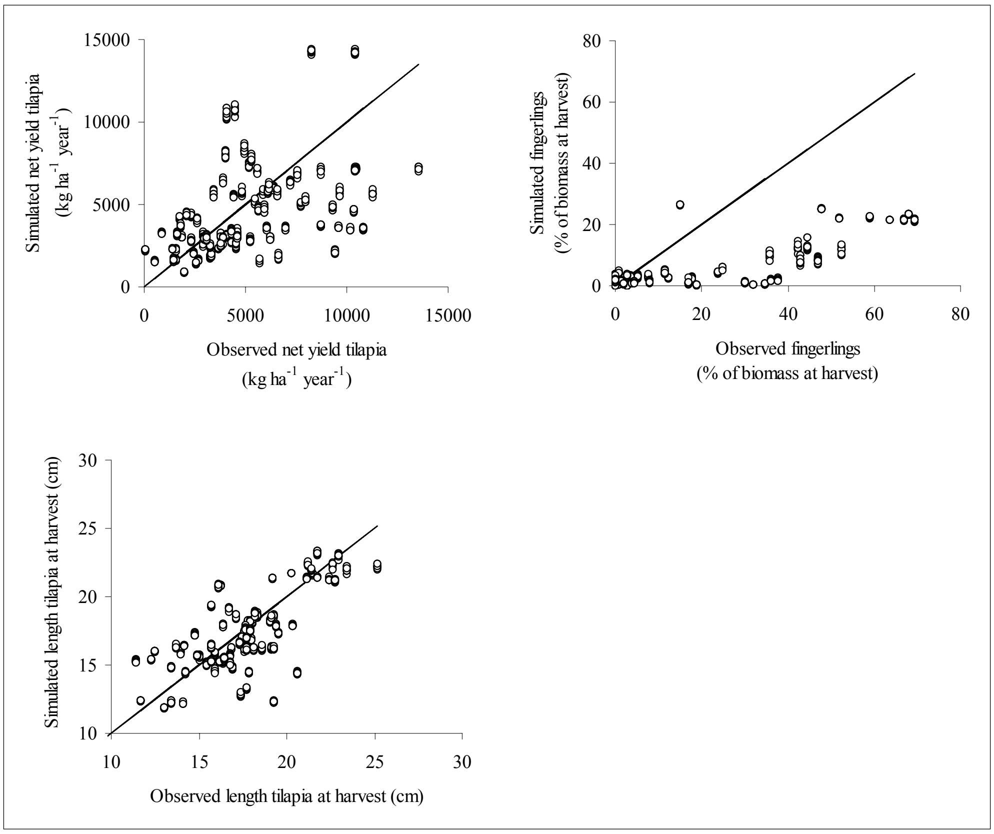

Figure 5: Observed and simulated data for the validation with the data set of the Philippines. The bisector represents perfect agreement between simulated and observed values.

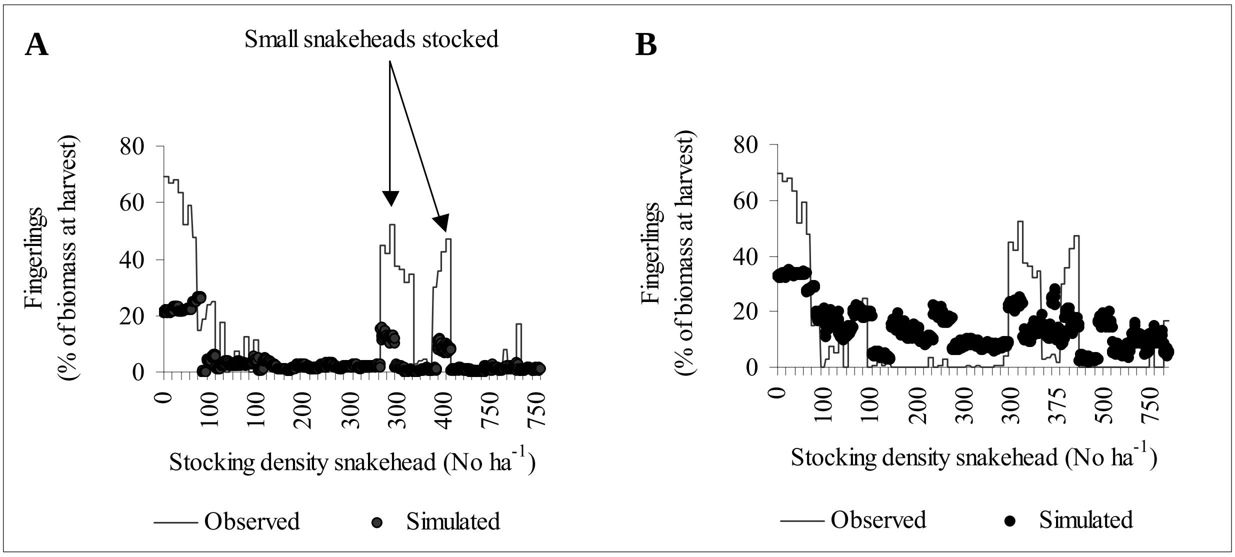

Figure 6: The percentage of fingerlings at harvest modelled with a length at first recruitment of 12.5 (A) and 6 cm (B).

DATA FROM THAILAND: NILE TILAPIA WITH SNAKEHEAD MURREL

The overall quantitative data for the different components are presented in Table 9. The results indicate that for this data set, the model underestimates the net yields and overestimates the % of fingerlings at harvest (Figure 7).

*Table 9: Overall results of the validation with data from Thailand (** P<0.01).*

Para meter	Regression coefficient	Pearson's correlation coefficient	D (%)	D_{max} (%)	D_{min} (%)
Net yield tilapia	0.82	0.220^{**}	-16	87	-70
Length tilapia at harvest	0.96	0.099	-4	20	-16
% tilapia fingerlings at harvest	1.16	0.827^{**}	37	82	-13

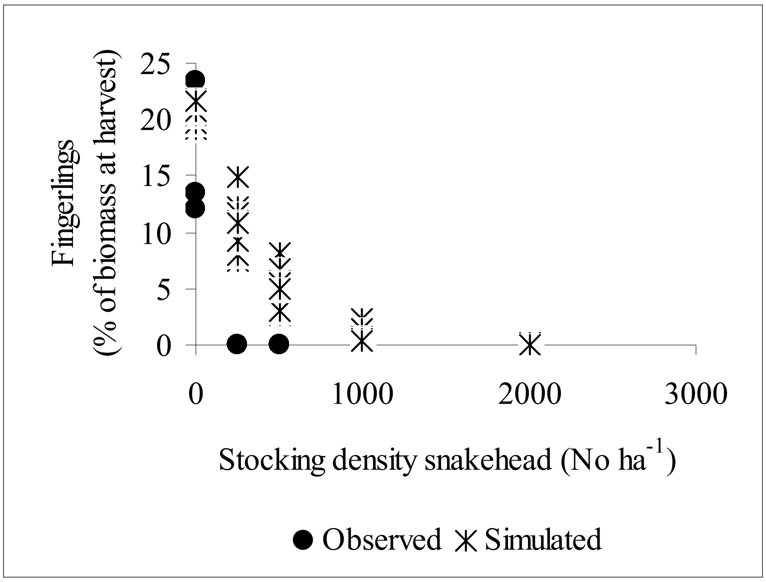

Figure 7: Observed and simulated fingerlings at harvest with different stocking rates of snakeheads.

In the experiments, fingerlings of tilapia with a length of about 7 cm are stocked in combination with snakeheads with a length of about 24 cm. In the model settings, all fingerlings less then 10 cm are predated by snakeheads larger then 10 cm. With this setting, in the model, the initially stocked tilapia is immediately preyed upon by the stocked snakehead. Consequently, the simulated net yield reduces with the increasing stocking density of snakehead. This was not observed in the experiments (Figure 8) and explains the underestimation of net yields by the model.

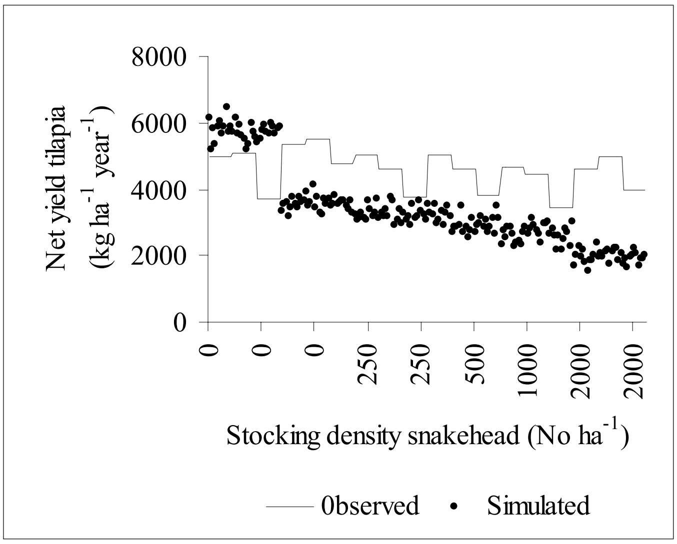

Figure 8: Relation between stocking density and observed and simulated net yield of tilapia.

SENSITIVITY OF THE MODEL

Sensitivity analysis (Table 10) indicates that changing the value of the growth parameter K has major impacts on the model results for the biomass at harvest of stocked males and fingerlings. Increasing the stocking length mainly impacts the biomass at harvest of stocked females and fingerlings and increasing the length at first maturity mainly reduces the fingerling productions. Further, the results indicate that the model is rather un-sensitive for changes in the recruitment rate of female tilapia.

Table 10: Changes in output of the model (in %) after increasing the input value of: K, Stocking length, length at first maturity and recruitment of tilapia with 10%.

	K	Stocking length	Length at first maturity	Recruitment
Length male harvest	2,6	2,5	3,6	-0,7
Length female harvest	1,7	4,1	2,3	-0,6
Total biomass at harvest	14,3	14,5	3,3	-0,2
Male biomass at harvest	10,1	9,4	10,5	-1,1
Female biomass at harvest	5,4	19,3	6,7	1,2
Fingerling biomass at harvest	34,3	23,6	-19,3	3,5
% male at harvest	-2,1	-2,7	7,1	-1,3
% female at harvest	-4,4	2,6	11,4	-1,2
% fingerlings at harvest	9,9	4,8	-22,3	4,5

STOCHASTIC BEHAVIOUR

The stochastic behaviour of the model is illustrated with some examples in Figure 9. Increasing the CV for the growth parameter K of tilapia results in a significant increase in the standard deviation of: the length of stocked tilapia at harvest, the length of newly recruited tilapia at harvest and in the net yields of the newly recruited tilapia at harvest. The standard deviation for total net yield or the net yields of stocked Tilapia did not change. Increasing the CV of K results further in a decrease in the length at harvest of the stocked tilapia, in total net yield and net yield of stocked tilapia, and in an increase in the net yields of the newly recruited tilapia.

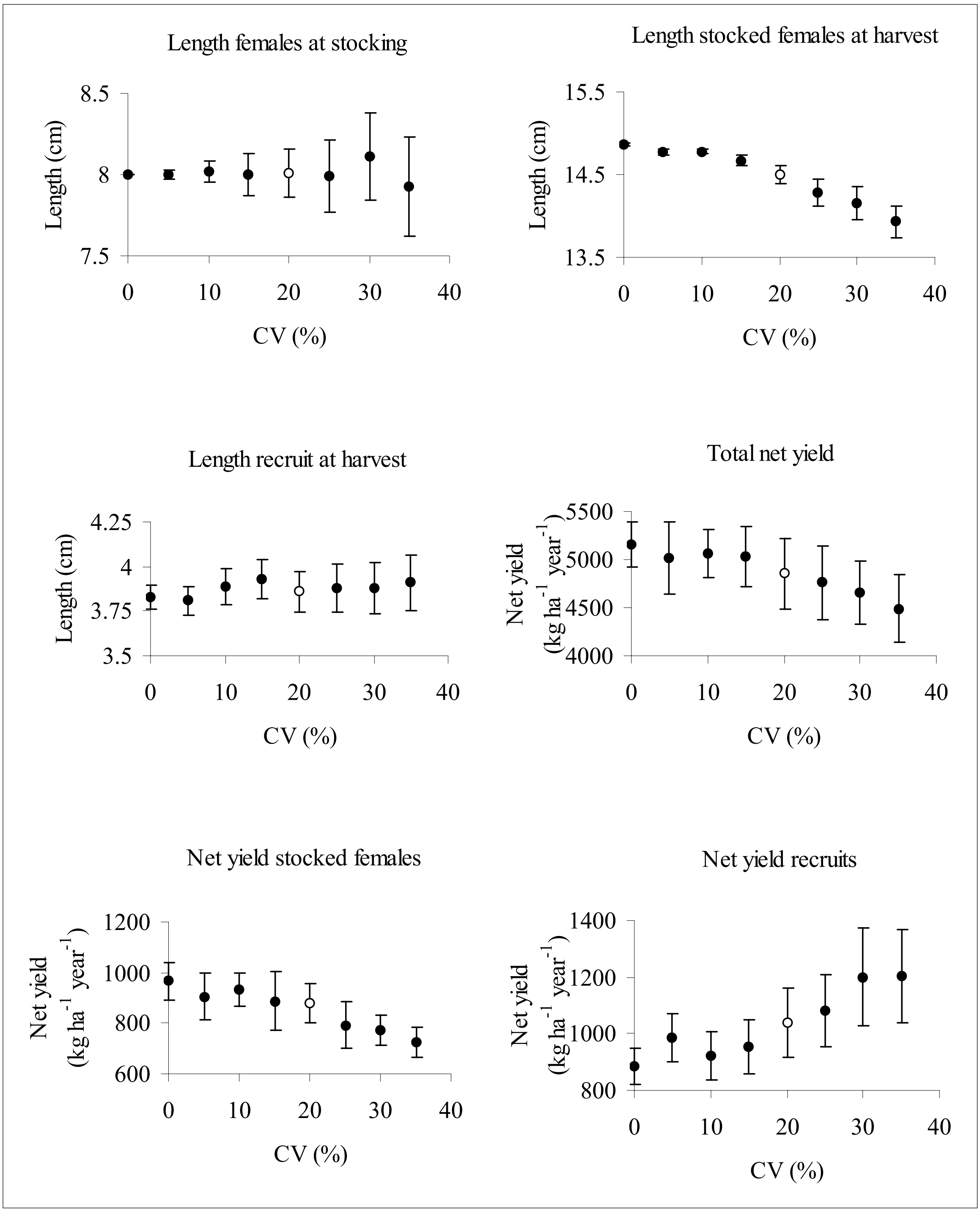

Figure 9: The stochastic behaviour of the model, after increasing the CV of the growth parameter K (open dot indicate standard model settings).

DISCUSSION

SENSITIVITY AND STOCHASTICITY

Although it is difficult to characterize sensitivity in complex models in an absolute sense (van Nes *et al.*, 2002), relative ranking of the different parameters can give insight into which parameters are the most important driving forces in the model and consequently in the real system. The sensitivity analysis indicated that relatively small changes in the growth rate have an important impact on the final harvested biomass. This stresses the importance of improving the growth rate of tilapia through improving the quality of the feed, genetic selection for fast-growing tilapia, proper pond maintenance, etc. Stocking larger fingerlings also generates a disproportionately higher biomass at harvest. Therefore, the ratio between the price per kilo of fingerlings of a certain size and the farm-gate price per kilo of harvested fish determines if stocking larger fingerlings is economically attractive.

The major reasons why individual based modelling forms the basis of the present model is that it eliminates the problem of dispersion in size distribution as the fish grows older, as encountered in traditional state variable models (Buijse *et al.*, 1992) and it handles, therefore, stochastic variability more easily. The stochastic characteristics of the model become clear in the increased standard deviation for the individual model outputs after increasing the CV of the growth parameter K (Figure 9). The fact that the standard deviation of the total net yield does not change is caused by the structure and feedback mechanisms in the model: an increase in the biomass of newly recruited females automatically reduces the growth rate of the stocked parents, resulting in a lower net yield of the stocked parents and leading to an overall softening of the variability in total net yields.

CALIBRATION AND VALIDATION

The model provides good results in the calibration with the data set from Congo Brazzaville. However, this should be the case as the individual parameters of the model were obtained from this data set. Running the model for three independent datasets indicated three major points of attention:

1. For the data set of Ivory Coast, growth is underestimated,

2. For the data set of the Philippines, there is a large difference in the recruitment of tilapia,
3. For the data set of Thailand, there is a difference in predation efficiency and in the prey-predator relation itself.

GROWTH

Growth in the model is described with the von Bertalanffy growth curve and is a function of both $L\infty$ and growth parameter K. Comparison of growth performance in general is done with Phi-prime= $\text{Log}(K)+2\text{Log}(L_{\infty})$ (Gayanilo and Pauly, 1997). Pauly *et al.* (1987) compared the growth performance of *O. niloticus* from 64 rearing experiments collected Worldwide and found an average $\Phi=3.21\pm0.03$ (sem). This is comparable with $\Phi=3.27\pm0.01$ (sem) for the data set of the Philippines, but with an $\Phi=2.91\pm0.5$ the growth in Congo Brazzaville, used for calibration, is slightly lower. For the Philippines, the growth parameters were known and the model was adjusted accordingly and gives acceptable results.

Growth, which is one of the most sensitive input parameters of the model, is mainly determined by the quantity and quality of the feed provided (Santiago *et al.*, 1987; Wee and Tuan, 1987). Therefore, in absence of known growth parameters, as was the case in the validation with data from Ivory Coast and Thailand, the model only gives acceptable results if the feeding regime is more or less the same as in Congo Brazzaville. This results in a kind of lottery, which went well for the data set from Thailand but not for the data set of Ivory Coast. This is not a practical approach, and a first step in improving the model should be to relate growth performance to feeding level and feed quality. For the latter the percentage of dry matter protein, the feeding efficiency (Yang Yi, 1999) or the content of essential amino acids could be used.

RECRUITMENT

The excessive recruitment and subsequent stunting of *O. niloticus* in grow out ponds is often seen as a major bottleneck in tilapia farming (Bardach *et al.*, 1972; Ruwet *et al.*, 1976; McGinty, 1985; Lovshin et *al.*, 1990). In the experiments of Congo Brazzaville, used for the calibration of the model, the tilapia became “stunted” in the sense that early breeding took place, but the somatic growth of the stock still continued (de Graaf *et al.*, 1999). In Congo

Brazzaville, tilapia were stocked with a length of about 10 cm and they started breeding at a length of about 12 cm. Without a predator about 20-30% of the biomass at harvest consisted of fingerlings (de Graaf *et al.*, 1996). In the experiments of the Philippines, tilapia were stocked with a length of about 6 cm and without a predator about 70% of the biomass at harvest consisted of fingerlings (Figure 6), twice as observed in Congo Brazzaville. It could be reasoned that in the Philippines the tilapia reproduces even at a smaller length. Reducing the length of first maturity to 6 cm in the model, results in a higher percentage of fingerlings at harvest (38%), still significantly lower then the observed values (Figure 6).

From a biological point of view, reducing the length of first maturity to 6 cm is questionable as such early breeding has not been reported. Environmental factors can have a major influence on egg and fry survival of tilapia (Hopkins *et al.*, 1982), and the difference between the fingerling production between the experiments in the Philippines and Congo Brazzaville are more likely caused by differences in natural mortality of the newly recruited tilapias.

At present the recruitment is constant, but the model could be further improved by quantifying the recruitment to the size of the female tilapia. This will not be easy as two phenomena are interfering with each other. It is known that the absolute fecundity (no oocytes per female) increases with increasing size of the female tilapia (Melard, 1986; de Graaf *et al.*, 1999), so it is expected that larger females produce more larvae. For an individual spawning this is correct, but if looked at in terms of the larval production per unit of time the relation is inverse: larger females produce less larvae per day (Melard, 1986). The latter is caused by three factors:

- The relative fecundity (no.of oocytes per gram of female) reduces with increasing length of the female (Babiker and Ibrahim, 1979; Melard, 1986; de Graaf *et al.*, 1999)
- The spawning frequency reduces if tilapia are becoming older and larger (Lowe McConnell, 1955; Mires, 1982; Guerrero and Garcia, 1983; Melard, 1986)
- Large male tilapia reproduces less often with large and more aggressive female tilapia (Melard and Philippart, 1981)

The relation between daily larval production and the length (L) of the female spawner as found by Melard (1986) can be described with:

$$Daily\ recruits = -0.0007L^4 + 0.0475L^3 - 1.1007L^2 + 10.9553L - 36.9885$$

A preliminary run of the model (the model is not completely calibrated again for this situation) using this relation instead of constant recruitment indicates the relatively large influence of the length at first maturation and the stocking length of the fingerlings on the percentage of biomass at harvest and the final net yields (Figure 10). The highest percentage of fingerlings will be found if the stocked fingerlings are reproducing from the first day e.g. “Stocking length = Length at first maturity”. Fewer fingerlings will be obtained if the stocked fingerlings are smaller than the length at first maturity, as during the first part of the rearing cycle they do not yet reproduce, but stocking small fingerlings also results in substantially lower net yields. Stocking fingerlings that are larger than the length at first maturity also results in fewer fingerlings at harvest as the larger the female the less fingerlings are produced daily. The results of this preliminary simulation indicates the importance of the length at first maturation and it could be that next to selected breeding programmes for fast growing tilapia such as GIFT (Pullin *et al.,* 1991), tilapia farming could also substantially benefit from selective breeding programmes for late-maturing females.

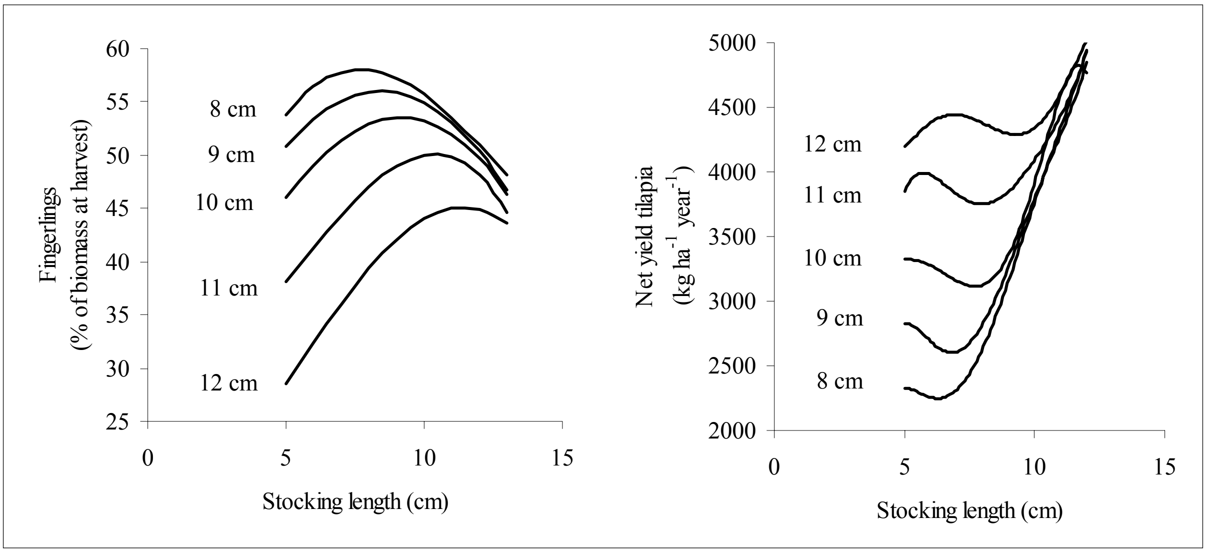

Figure 10: The effect of length at first maturity and stocking length on the percentage of fingerlings at harvest and the net tilapia yields.

PREY-PREDATOR RELATIONS

The results of the validation with data on the polyculture of tilapia with the murrel snakehead indicated that the maximum length of a tilapia of 10 cm, a snakehead can predate, is too large. From the field observations in Thailand, it becomes clear that a snakehead with a length of 24 cm cannot predate a tilapia of 7 cm. Further, the efficiency of predation as observed in Thailand is higher if compared to the results of the model (Figure 7) This could be related to the species, as the model is calibrated for *P. obscura* while in the experiments *C. striatus* was used. However, it is more likely related to the much larger size of the predator used in Thailand, as mortality by the predator, in the model, is not yet continuously related to the length of the predator.

This prey-predator relationship should be further studied and incorporated in the model through either Holling or Lotka Volterra type equations (Lotka, 1925; Volterra, 1926; Holling, 1959;).

THE MODEL

Van Dam (1990, 1995) reviewed the development of models for the pond rearing of fish and distinguished two approaches: "Descriptive-empirical" or "Explanatory-theoretical" models.

Empirical models describe data without explaining the mechanisms causing the relationship between data. Relations between predator density and the efficiency to control Tilapia recruitment in ponds (Lazard, 1980; Hopkins *et al.*, 1982; de Graaf *et al.*, 1999) are typical examples of such empirical models.

Theoretical models are based on the knowledge of biological processes underlying the production system. Theoretical models are often more complex to build, but they have the advantage of providing insight into basic processes in the system. The most theoretical models are based on balanced equations for the different flow rates in the system. The latter can be energy, mass, nitrogen, respiration, in case of bio-energetic models (Machiels and Henken, 1986; Ross and Mckinsey, 1989; van Dam and Penning de Vries, 1995; van Dam and Pauly, 1995; van de Meer and van Dam, 1999) or numbers, growth, mortality or value, in case of tilapia farming models based on population dynamics (Springborn *et al.*, 1992, Fischer and Grant, 1999).

The present model is a theoretical model based on population dynamics. Using population dynamics instead of mass balance, as a basis for the model was a deliberate choice as the mathematics of fisheries population dynamics (Sparre and Venema, 1992) allows us to incorporate prey-predator relations and an Individual Based Modelling approach.

The individual based approach resulted in a good stochasticity of the model, whereby the absence of stochasticity in net yields is a result of interacting biological processes.

Calibration of the model indicated that finding optimal settings is finding a compromise between the results of the different parameters. This as the model is large, with many parameters and most of them interacting. For example natural mortality impacts the stocked as well as the newly recruited tilapia. In the present calibration the most optimal mortality was selected to get the fingerlings right; this mortality rate is slightly too high for the stocked tilapia and consequently the net yields are underestimated.

Modelling of recruitment, prey-predator relations and the relation between growth and feed quality are still too simplistic. However, in general, it can be concluded that the results of the model are useful for the simulation of different tilapia farming systems; mixed sex, mono sex or poly culture with African catfish or snakeheads and can serve as a predictive and decision-making support tool after inclusions of the discussed topics. Including economic or financial parameters for the inputs (fingerlings, feed, labour, investments) and outputs (farm-gate prices) would lead to a practical tilapia farming decision model.

ACKNOWLEDGEMENTS

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CHAPTER 6: FITTING GROWTH WITH THE VON BERTALANFFY GROWTH FUNCTION. A COMPARISON OF THREE APPROACHES OF MULTIVARIATE ANALYSIS OF FISH GROWTH IN AQUACULTURE EXPERIMENTS

GERTJAN DE GRAAF AND MARK PREIN

ABSTRACT

Three approaches for multivariate analysis of fish growth in aquaculture experiments with Nile tilapia (*Oreochromis niloticus niloticus* L.) based on the von Bertalanffy growth curve, are presented and compared. The approaches are: an extended Gulland-and-Holt plot, a forced extended Gulland-and-Holt plot and a multi- linear regression analysis for the growth parameter K. All three models provide valuable insight into the major environmental factors influencing daily growth rate and explain 28% to 46% of the variance of the observed daily growth rate. For all three methods, the modelled parameter is significantly related with the net yield of Nile tilapia and can, therefore, be used for the predictive modelling of management scenarios. The extended Gulland-and-Holt plot loads the influence of environmental parameters upon L_∞, while the forced extended Gulland-and-Holt plot and Direct fitting of K loads the influence on the growth parameter K. The latter is more in the tradition of aquaculture research. But the forced extended Gulland-and-Holt plot and Direct fitting of K can only be applied if L_∞ of the cultured species is known, this as the selected L_∞ influences the variance in the regression variables.

Keywords: Aquaculture, extended Gulland-and-Holt plot, extended forced Gulland-and-Holt-plot, multivariate analysis, Nile tilapia, von Bertalanffy growth curve.

INTRODUCTION

The main process of interest in aquaculture is growth of the cultured species and its related production (Hepher and Pruginin, 1981). The simplest procedure is to determine the length of time needed to reach market size (i.e. weight) and to express this growth rate as gram day^{-1}. For the analysis of weight changes of fish, various sophisticated models are available (Ricker, 1975). But any model must take into account the way in which the growth rate of fish slows down with increasing age and weight (Pitcher and Hart, 1982), which is not the case if the growth rate is expressed in gram day^{-1}.

In aquaculture feeding experiments, with data available over short periods of growth, the specific growth rate: $\alpha = \frac{lnW_t - lnW_0}{\delta t}.100$ is often used as it encompasses this phenomenon comprehensively (Weatherly, 1972; Huisman, 1974 and Hogendoorn *et al.*, 1983).

A second well-known growth model, often used in fisheries, is that of von Bertalanffy, $L_t = L_\infty.\left(1 - e^{-K(t-t_0)}\right)$, who based his formulation on physiological considerations (von Bertalanffy 1951; Pauly, 1981). It assumes that fish grow towards some theoretical maximum length or weight, and the closer the length gets to the maximum, the slower the rate of size change will be (von Bertalanffy, 1951; Pitcher and Hart, 1982). Recently, the von Bertalanffy growth curve is getting more popular in aquaculture research.

Pauly *et al.* (1988) used the von Bertalanffy growth curve to compare the overall growth performance of Nile tilapia (*Oreochromis niloticus*) in open water and aquaculture and concluded that aquaculture systems based on Nile tilapia failed to fully exploit the growth potential of this species. Pauly *et al.* (1993) developed a multivariate analysis method of fish growth in aquaculture derived from the von Bertalanffy growth curve. This “extended Gulland-and-Holt plot” permitted them to identify and quantify key variables controlling fish growth including environmental and treatment variables to explain variance in growth of fish.

De Graaf *et al.* (Chapter 4) and Springborn *et al.* (1992) used the von Bertalanffy growth curve in the development of a simulation model for the rearing of *Oreochromis niloticus niloticus (L)*.

However, it is often not realized that L_∞ and the growth parameter K in the von Bertalanffy growth curve are correlated: different combinations of K and L_∞ can give almost the same fit to data, except when a wide range of ages is represented. Again, a high value of K combines with a low value of L_∞ and vice versa (Sparre and Venema, 1992). For fish stock assessment, this characteristic of the von Bertalanffy growth curve is not a constraint, as a good description of growth in the analytical fisheries models is more important than visualizing "the correct" physiological process behind growth. In aquaculture, this characteristic (i.e. obtaining two parameters) makes the application of the von Bertalanffy growth curve for the mere comparison of growth cumbersome, in contrast with other methods. The need for a single parameter for comparison of growth for one species raised under different conditions or for different species, has been addressed with the introduction of "Phi-prime": $\varphi' = \text{LogK} + 2\text{LogL}_\infty$, (Pauly and Munro, 1984; Gayanilo and Pauly, 1997), which includes the values of L_∞ and K.

Prein (1993) applied the standard Gulland-and-Holt-plot and the extended Gulland-and-Holt plot to a large data set of integrated livestock fish farming experiments of *O. niloticus* in the Philippines. The standard fit provides one value for $L_\infty = 25.4$ cm and one value for $K = 3.62$ year^{-1}. This pair of growth parameters expresses the central tendency in the whole of the combined experiments (Pauly *et al*, 1993). In the extended Gulland-and-Holt plot the impact of higher nutrient loads, and other environmental parameters on daily growth, are separately treated and provide a fixed value for the growth parameter K and a variable value for L_∞, depending on the values of the different environmental parameters. The method provided valuable insight into the different processes behind the daily growth in the different experiments. The practical use of the plot in aquaculture is more complicated, as the variance in growth is loaded on L_∞ and not on the growth parameter K, i.e. increased growth is expressed with a constant growth parameter K and a larger maximum length and vice versa. This is mathematically correct, but difficult to explain to a general audience.

One of the most important factors in aquaculture is oxygen. In most fish, oxygen enters the body through the gill surface and the relation between growth of the gill surface and body growth upon oxygen availability is discussed by van Dam and Pauly (1995): 'Because a surface does not grow as fast as a volume, the maximum oxygen supply per gram of body weight can be expected to decrease as the fish grows, assuming that the efficiency of the uptake does not change with body size. Pauly (1981) translated this concept into a balanced oxygen equation: oxygen available for growth equals oxygen entering the body minus oxygen needed for catabolism and anabolism. As the fish grows bigger, the oxygen supply limits the amount of energy that is available for growth. Eventually, the fish can consume just enough oxygen for its maintenance requirements. Body and gills cease to grow and the fish has attained its maximum size'. Hogendoorn, *et al*. (1983) explained the limited growth with bio-energetic principles, as for the African catfish (*Clarias gariepinus* Burchell, 1822) the metabolic scope for growth relatively decreases with increasing fish weight. Van Dam and Pauly (1995) simulated the growth of *O.niloticus* with a model that encompassed bio energetic principles as well as maximum potential oxygen uptake based on the allometric relation between body weight and gill surface area. Their results provided strong support for the oxygen limitation theory. The results further revealed that an increased protein intake could cause a decrease in the maximum size of the Nile tilapia, due to an increased oxygen need for metabolism of the higher protein intake. This phenomenon could explain the wide range of the maximum size of Nile tilapia observed in nature.

If it is assumed that in aquaculture experiments the range of dietary protein levels is limited, then the concept also implies that the studied species has a more or less fixed value for L_∞ in the von Bertalanffy growth curve.

Fixing L_∞ in the analysis of growth in aquaculture experiments through a "forced Gulland-and-Holt plot" (Pauly, 1984), through an "extended forced Gulland-and-Holt plot", or through a direct fit of K, whereby the influence of environmental factors are loaded on the growth parameter K could be more practical and is discussed and compared in the present paper.

MATERIALS AND METHODS

THE DATA SET

Results from a four-year study at the Fresh water Aquaculture Center of the Central Luzon State University (CLSU) near Munoz, Philippines were used as a source for data. The aim of the study was to develop economically viable small-scale integrated livestock-fish culture methods suitable for the Philippines, based entirely on livestock manure inputs. Details of the experimental design and results are given in Hopkins and Cruz (1980,1982), Cruz and

Shehadeh (1980), Hopkins *et al.* (1981, 1982, 1983) and PCARRD (1982). Data handling is given by Prein (1993) as he analysed the same data set with a standard extended Gulland-and-Holt-plot and with Path analysis. Only a general overview is given here.

One hundred sixteen growth experiments in 18 experimental groups were conducted from 1979 to 1981 in 24 back yard sized ponds (0.04 or 0.1 ha). Treatments were always duplicated or triplicated. The ponds were stocked in polyculture of 85% Nile tilapia (*O. niloticus*) as the main crop, 14% common carp (*Cyprinus carpio carpio* L) as a bottom stirrer and 1% predator, either snakehead (*Channa striata* Bloch 1793) or the Thai catfish (*Clarias batrachus* L). The overall stocking densities were 10,000 or 20,000 fish ha^{-1} and the average size of *O. niloticus* at stocking was usually 2.5 cm.

Nutrient inputs to the ponds were either inorganic fertilizer or fresh manure from pigs, ducks or chickens kept in stalls on the pond dikes. The experimental duration was set to match a period of 90 days that tilapia took to attain a local market size of 60 g.

Fish size data were obtained by bi-weekly sampling and at harvest. Average daily manure input was determined on a dry weight basis. Dissolved oxygen was measured in the early morning.

The original data set contains 713 record sets and after deleting records with negative growth, 650 remained. At random, 325 records were selected for developing the multiple regression models. The remaining 325 records were used to check the different models. A second data set contained the stocking and harvest summaries of the experiments and was used to compare modelled growth with net yields.

GULLAND-AND-HOLT PLOTS

THE STANDARD GULLAND-AND-HOLT PLOT

The von Bertalanffy growth curve implies that the growth rate (dL/dt) declines linearly with length. This relation between length and growth rate can be used to estimate the two parameters L_∞ and K. In a standard Gulland-and-Holt plot (GH plot), the growth rate dL/dt of an experimental interval is plotted over the mean length in that interval (Gulland and Holt, 1959). The differential form is:

$$\frac{dL}{dt} = K(L_{\infty} - L_{mean}) \tag{1}$$

Or in terms of growth increments per interval (length L_1 and L_2);

$$\frac{L_2 - L_1}{t_2 - t_1} = a + b\left(\frac{L_1 + L_2}{2}\right) \tag{2}$$

Providing the growth parameters

K=-b

L_{∞}=a/-b

STANDARD FORCED GULLAND-AND-HOLT PLOT

In a "forced GH plot", L_{∞} is known and dL/dt is plotted against L_{∞}-L_{mean} or in terms of growth increments per interval (length L_1 and L_2);

$$\frac{L_2 - L_1}{t_2 - t_1} = K\left(L_{\infty} - \frac{L_1 + L_2}{2}\right) \tag{3}$$

Whereby K is the slope of the regression through the origin.

In the present study, L_{∞} is fixed at 30.8 cm, resulting from the extended GH plot, obtained previously from the dataset (Prein, 1993).

EXTENDED GULLAND-AND-HOLT PLOT

The standard GH plot can be extended into a multiple regression form, permitting environmental and treatment variables to be considered simultaneously in the same analysis (Pauly *et al.*, 1993):

$$\frac{dL}{dt} = a + b_1 L_{mean} + b_2 X_2 + b_n X_n \tag{4}$$

Or in terms of growth increments per interval (length L_1 and L_2);

$$\frac{L_2 - L_1}{t_2 - t_1} = a + b_1\left(\frac{L_1 + L_2}{2}\right) + b_2 X_2 + b_n X_n \tag{5}$$

The growth parameters are estimated from:

$K = -b_1$

$L_\infty = (a + b_2X_2 + \ldots + b_nX_n)/-b_1$

Whereby $X_2 \ldots X_n$ are environmental and treatment variables simultaneously recorded during the growth increment. Their influence is loaded on the value of L_∞. As environmental and treatment variables the square root of stocking density (kg m^{-3}), dissolved oxygen (mg l^{-1}), pond area (m^2) and daily manure load (kg ha^{-1} day^{-1}) are used.

EXTENDED FORCED GULLAND-AND-HOLT PLOT

In the extended forced GH plot, the influence of environmental parameters is loaded on the growth parameter K, while L_∞ is kept constant. The standard forced GH plot can be transformed into a multiple regression form:

$$\frac{dL}{dt} = (\alpha + \beta_1 X_1 \ldots \beta_n X_n)(L_\infty - L_{mean}) \tag{6}$$

or

$$\frac{dL}{dt} = \alpha(L_\infty - L_{mean}) + \beta_1 X_1 (L_\infty - L_{mean}) \ldots \beta_n X_n (L_\infty - L_{mean}) \tag{7}$$

By creating the variables: $X_1(L_\infty - L_{mean})$, $X_2(L_\infty - L_{mean}) \ldots X_n(L_\infty - L_{mean})$ and using them in the multiple regression, K can be calculated as:

$$K = \alpha + \beta_1 X_1 \ldots \beta_n X_n \tag{8}$$

Whereby, again, $X_1 \ldots X_n$ are environmental and treatment variables simultaneously recorded during the time interval of the fish growth increment.

K APPROACH

An alternative is to determine the growth parameter K for each incremental growth interval, which can be directly calculated with (Sparre and Venema, 1992):

$$K = \frac{-1}{t_2 - t_1} Ln\left[\frac{L_\infty - L_2}{L_\infty - L_1}\right] \tag{9}$$

Subsequently, the impact of the different environmental and treatment variables on the growth parameter K were evaluated with standard multiple regression:

$$K = \alpha + \beta_1 X_1 + \beta_2 X_2 + .\beta_n X_n \tag{10}$$

Where, again, $X_1 \ldots . X_n$ are environmental and treatment variables simultaneously recorded during the growth increment.

RESULTS

STANDARD GULLAND-AND-HOLT PLOTS

The standard GH plot and the standard forced GH plot over the entire dataset are presented in Figure 1 and Figure 2. The results provide L_∞=25.8 cm, K=3.24 year^{-1}, and φ'=3.34 for the standard GH plot and L_∞=30.8, K=2.41 year^{-1} and φ'= 3.36 for the standard forced GH plot.

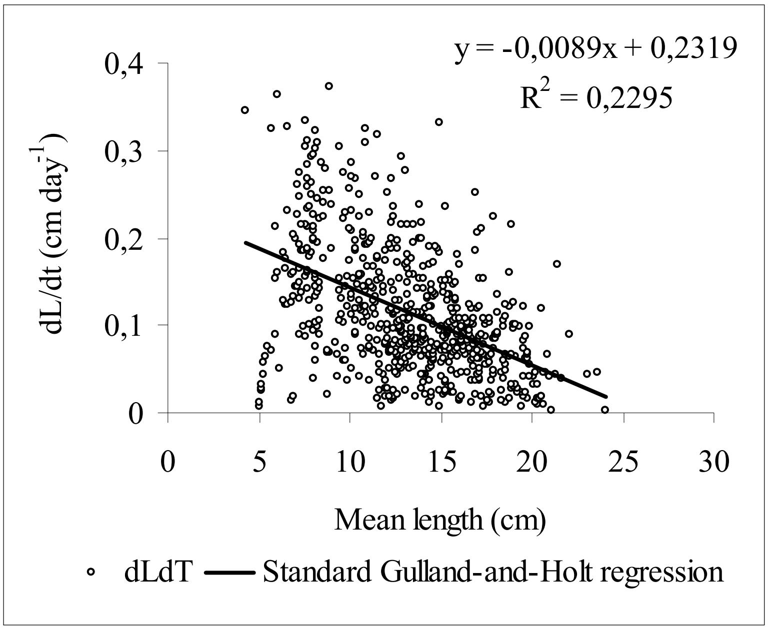

Figure 1: Standard Gulland-and-Holt plot for the overall dataset.

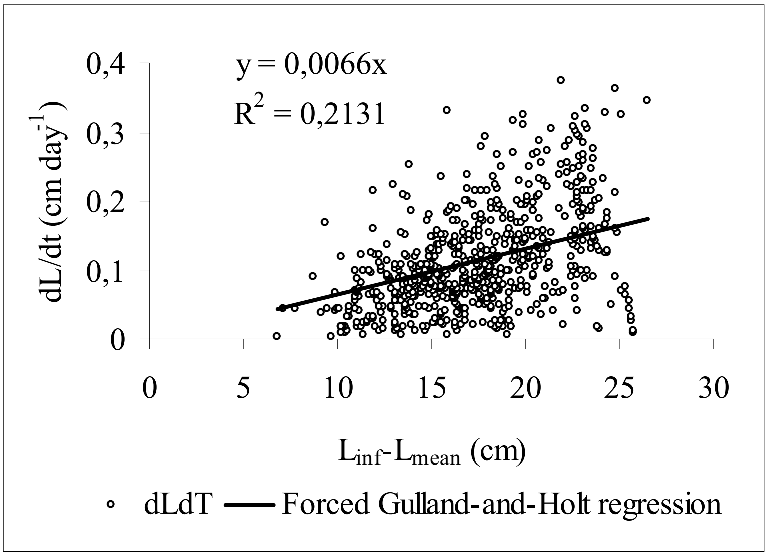

Figure 2: Standard forced Gulland-and-Holt plot for the overall dataset.

MULTI VARIATE PLOTS

The results of the extended GH plot, the forced extended GH plot, and the multi- linear regression for K are presented in Table 1 and Table 2.

The results provide a value for L_∞ =28.3 cm, calculated with the mean values of the environmental parameters, K=2.73 year^{-1}, and φ'=3.34 for the standard extended GH plot, and L_∞ =30.8, K=2.23 year^{-1}, calculated with the mean values of the environmental parameters, and φ'= 3.36 for the forced extended GH plot.

The standardised Beta coefficients indicate that in both extended plots, length, stocking density and dissolved oxygen are the major variables explaining variation in length growth rate. For the multi-linear regression for K, stocking density, and dissolved oxygen are the major driving forces in the model.

The standard extended GH plot explains 46% of the total variation in growth (dL/dt) in the total data set with the environmental and treatment variables (n=325). The multi-linear regression for K explains 28% of the total variation in growth (K) by the environmental and treatment variables. Increasing the value of L_∞ =61 cm, in the multi-linear regression for K, increases the explained variance for K to 38%. For the forced extended GH plot, the variance cannot be explained similarly as the regression is fitted through the origin (Eisenhauer, 2003).

Table 1: Results of the standard extended GH plot, the forced extended GH plot and multi-linear regression (n=325, P<0.05).

Model parameters	Standard extended GH		Forced extended GH		Multi-linear K	
	Coefficient	Beta	Coefficient	Beta	Coefficient	Beta
L_{mean} or L_{∞}-L_{mean}	-0.00748	-0.407	0.009746	1.315		
Stocking density	-0.17399	-0.350	-0.013478	-0.536	-4.23969	-0.468
Pond area	0.00004	0.173	0.000003	0.289	0.00075	0.171
Manure	0.00029	0.155	0.000011	0.104	0.00604	0.176
Dissolved oxygen	-0.01330	-0.334	-0.000912	-0.395	-0.24499	-0.338
Constant	0.24615				3.22287	

Table 2: The percentage of total explained variation for the different variables for the standard extended GH plot and the multi-linear regression for K.

Model parameter	Standard extended GH plot		Multi- linear K regression	
	Sum of squares	Explained variation	Sum of squares	Explained variation
Length	0.4945	28.0%		
Stocking density	0.0375	2.1%	53.3338	9.9%
Dissolved oxygen	0.2035	11.5%	74.9433	14.0%
Pond area	0.0683	3.9%	19.0359	3.5%
Manure load	0.0086	0.5%	4.2432	0.8%
TOTAL	1.7637	46.1%	536.9596	28.2%

In Figure 3, values of dL/dt and K as calculated with three regression models are plotted against observed values and the results indicate that all three models slightly under estimate the observed values. The Pearsons correlation coefficient between observed and simulated values for the standard extended GH plot, the forced extended GH plot, and the direct fit of K are respectively 0.63, 0.66, and 0.46.

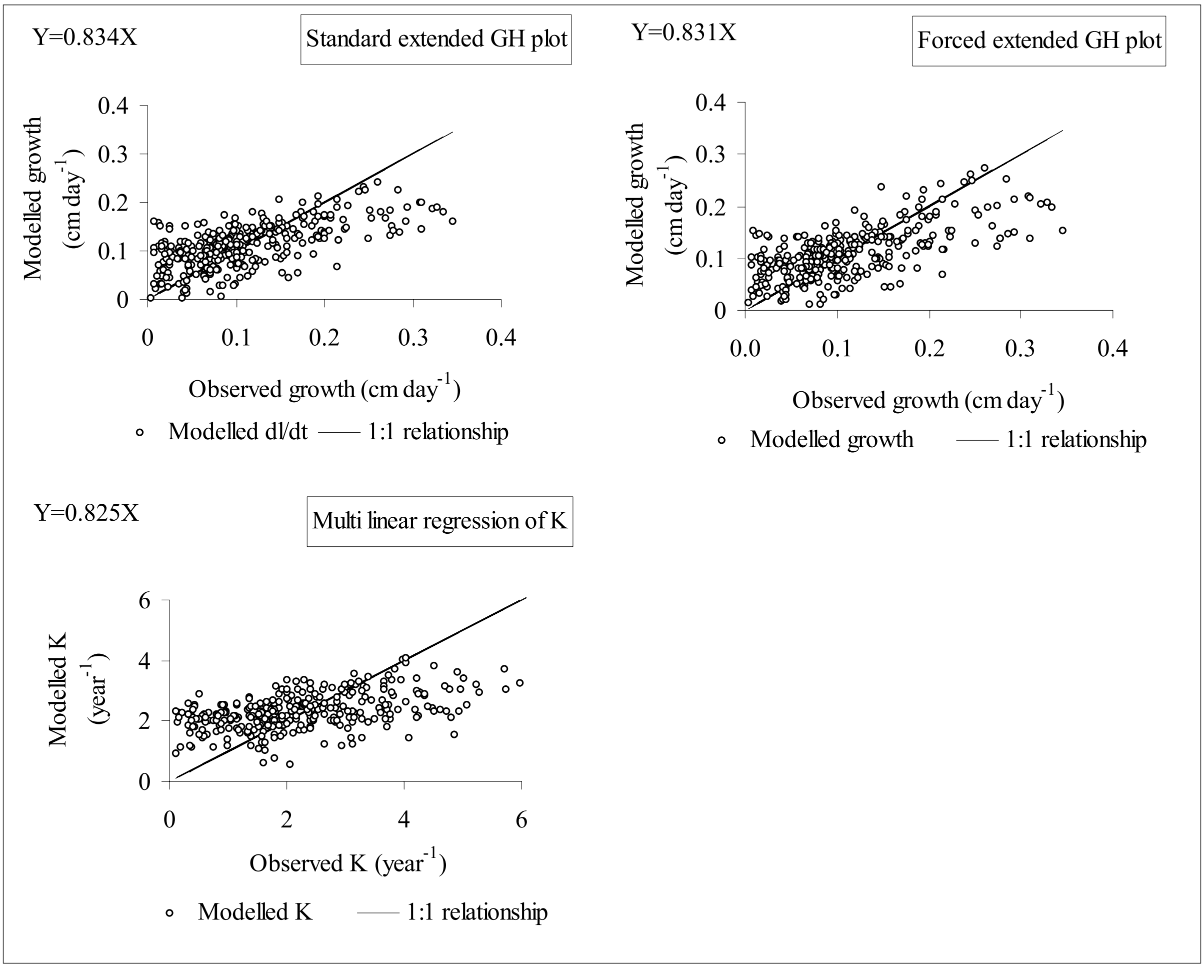

Figure 3: Predicted and observed growth and K of Nile tilapia for the standard extended GH plot, the forced extended GH plot and the multi-linear regression of K, the bisector represents perfect agreement between observed and modelled values (n=325).

MODELLED GROWTH FOR INDIVIDUAL EXPERIMENTS

The results of the three regression analyses were used to calculate K or L_∞ with summarized data of 116 experiments, where net yields are known. The results of the regressions were applied over the mean values of the environmental parameters to calculate the overall value of K or L_∞ throughout the experiments. In Figure 4 the net yield of Nile tilapia is plotted against these calculated growth parameters, indicating a close relation between the modelled parameters and net yield for all three methods.

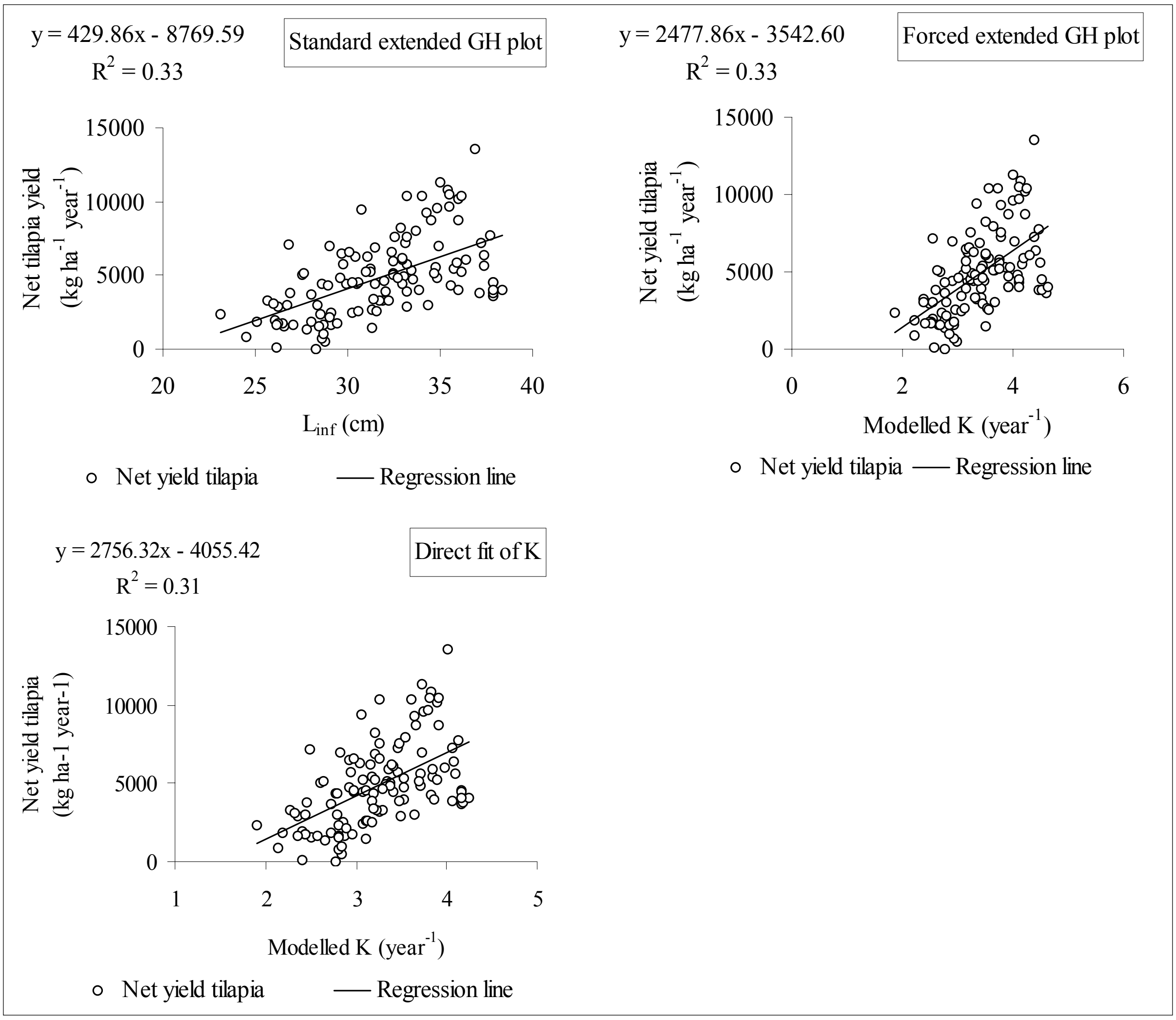

Figure 4: The relation between calculated K, L_∞, and net yield of tilapia.

DISCUSSION

MULTIVARIATE MODELS

Multivariate models have been extensively used and discussed by Prein *et al.* (1993). The analyses with the extended GH plot in the study of Prein (1993) and with the extended GH and the forced extended GH plot in the present study give almost similar results. It identified stocking density, dissolved oxygen, pond area and manure load as significant variables affecting the daily growth of Nile tilapia. The slight difference between the results of the extended GH plot of Prein (1983) and the present study is due to a difference in removing outliers from the original dataset. The results between the extended GH plot and the forced extended GH plot should be similar, as the same data set was used and in terms of variance within the dataset, the mathematical form of the regression, the extended GH and the forced extended GH plot are identical.

At first sight, the strange negative relationship between dissolved oxygen and growth, indicating that Nile tilapia growth is higher when early morning dissolved oxygen levels are lower is explained by Prein (1993) by the fact that dissolved oxygen levels are directly controlled by the amount of phytoplankton, an important nutritional component for tilapia, in the pond. With higher phytoplankton abundance the amplitude of the diurnal dissolved oxygen variation increases, characterized by the highest levels of saturation in the early afternoon and the lowest level near zero at dawn. However, this is in contradiction with the results of the simulation model of van Dam *et al*. (1996), which indicated that growth of tilapia was oxygen-limited, even though mean early-morning dissolved oxygen levels was higher than 4 mg l^{-1}.

The multi-linear regression for K explains 28% to 38% of the variance in growth, compared to 46% in the standard extended GH plot. The standard GH plot, includes L_{mean}, which means that this model encompasses the basic characteristic of fish growth, a reduction in growth rate as they become larger, reflected by 28% of the variance explained by this variable alone. Excluding this variable, as is the case in the multi-linear regression for K, makes the method less valuable. Secondly, the way in which K is estimated from the data set (equation 9) results in a reduction of the variance of K at higher values of L_∞, due to the logarithm of the fraction which includes L_∞ (Figure 5). The inverse is happening in the forced GH plot (equation 7). A higher value of L_∞ increases the variance of the environmental variables. However, the overall impact in the regression is less (Table 3), this as the variance of the most important variable L_∞ -L_{mean} does not change. The impact of L_∞ on the variance of the different parameters, implies that the forced extended GH plot and the multi-linear regression of K can be only applied if L_∞ for the raised species is known.

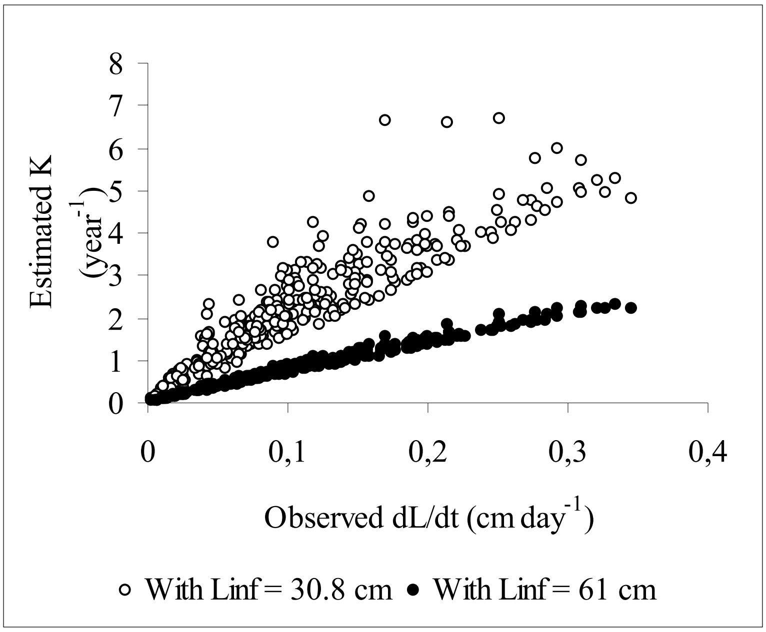

Figure 5: The effect of increasing the value of L_∞ in the estimation of the growth parameter K.

Table 3: Comparison of forced extended GH plot applied with two values of L_∞, L_∞ = 30.8 cm and L_∞ =61 cm.

Variable	L_∞ = 30.8 cm		L_∞ = 61 cm	
	Beta Coefficient	Variance Explained	Beta Coefficient	Variance Explained
L_∞-L_{mean}	1.35	76.0%	1.49	72.7%
Manure	0.10	0.2%	0.11	0.0%
Stocking density	-0.54	6.0%	-0.79	6.0%
Area	0.29	0.6%	0.26	0.6%
DO	-0.40	2.6%	-0.35	2.6%

Regarding the regression coefficients (Figure 3), all three models slightly underestimate the growth rate of Nile tilapia in a similar way. Regression through the origin of observed and simulated data provides standardized results, which facilitates comparison of methods or between different simulated variables. However, removing the constant in regression through the origin also diminishes the model's fit to the data (Eisenhauer, 2003), which is clearly visible by distribution of the calculated values around the bisector (Figure 3) and the Pearson correlation coefficients. In the multi-linear regression for K, low observed values of K are over-estimated and high-observed values of K are under-estimated, resulting in a low Pearson correlation coefficient. However, both are counteracting and result in a reasonable regression coefficient if fitted through the origin. Still, the higher Pearson correlation coefficients in the extended GH plots indicate that they are providing more reliable results.

For all three models a higher L_∞ or K results in a higher net yield of Nile tilapia and, therefore, they can be used to predict net yields under different management scenarios. Differences between the three models are mainly related to explanation of the variance in the observed growth and the complexity/simplicity of the model. The major characteristics are presented in Table 4.

Table 4: Comparison of the three models

Criteria	Standard extended GH plot	Forced extended GH plot	Direct modelling of K
Model variable	L_∞	K	K
Variance in observed growth rate explained	Good	Not applicable	Acceptable
Predictive value	Good	Good	Good
Simplicity	Straight forward	New fitting parameter to be created	Straight forward
Objectivity	L_∞ and K are estimated through the model	L_∞ has to be known	L_∞ has to be known

From a scientific point of view, the standard extended GH plot gives the best performance as it is completely objective, explains a high percentage of the variance in the observed data, and it predicts well. A disadvantage of the forced extended GH plot is that due to its characteristic, a regression through the origin, analysis of variance cannot be compared with the analysis of variance applied for the standard extended GH plot or the multiple-linear regression of K (Eisenhauer, 2003). However the beta coefficients of the regressions, still identifies the major driving forces.

From an aquaculture perspective the forced extended GH plot and direct fitting of K are preferred as they use a "growth parameter" to explain or predict differences in net yields. However, this approach implies that L_∞ for the raised species is known

In the present study, a value for L_∞ of 30.8 cm is used, which corresponds to a weight of about 750 g. With a corresponding K of 2.23 year^{-1}, tilapia will reach a weight of about 250 g in about four months, after which the growth rate decreases (Figure 6).

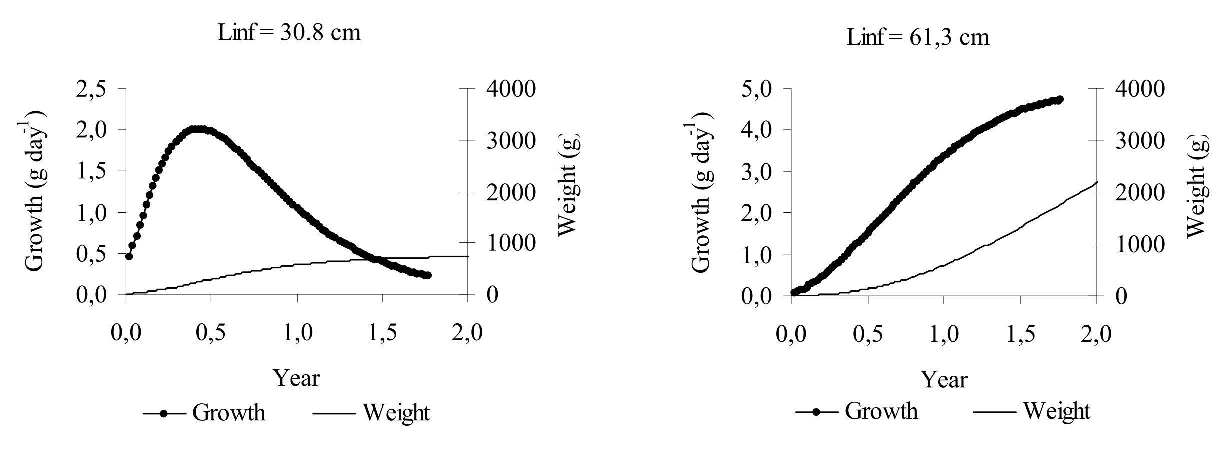

Figure 6: Comparison of weight and daily growth rate with different values of L_∞, with $\Phi'=3.3$.

In terms of the weight at harvest, the selection of L_∞ of 30.8 describes general culture practices well (Melard, 1986; de Graaf *et al.*, 1996). Results of Melard (1986) indicated that the growth rate reduced to almost zero after about 250 days, with tilapia reaching a weight of about 650 g, which more or less conforms to the model with L_∞ = 30.8 cm. However, in nature L_∞ up to 61.3 cm has been reported (*www.fishbase.org*). With such a L_∞, the size of harvest after 4 to 5 months does not change significantly, but the growth is maintained for a longer period of time and the fish can reach a larger size (Figure 6). Such a growth pattern is not realistic for aquaculture, and it stresses the need of a well defined *maximal* L_∞ for aquaculture if the forced-extended GH plot or direct fits of K are to be used, especially if the results are used in predictive modelling of aquaculture practices (de Graaf *et al*., Chapter 4)

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CHAPTER 7: GENERAL DISCUSSION

INTRODUCTION

The objective of the present study was to obtain a better understanding of how stunting processes of the Nile tilapia influence the pond rearing of this species. In Chapter 2 we analysed the reproduction of pond reared Nile tilapia with special emphasis on the age or length at first maturity. In Chapter 3, we analysed different pond rearing systems and the impact of controlling recruitment. In Chapter 4 we analysed a simple pond nursing system for the African catfish, which provides the fingerlings needed tilapia farming experimented in Chapter 3. In Chapter 5 we present an individual based simulation model for the pond rearing of Nile tilapia based on the results of Chapter 2 and 3. The model is based on population dynamic principles as this allows the incorporation of prey-predator relationships, in case tilapia is reared together with a predator to control recruitment. In Chapter 6 we discuss the use of the von Bertalanffy growth curve in aquaculture experiments.

STUNTING OF NILE TILAPIA

THE EVOLUTIONARY FRAME OF STUNTING PROCESSES ACCORDING TO NOAKES AND BALON (1982)

A general concept applied to early life histories of fish is the so-called “r and K-strategy”.

- “r-strategists” are species with a short growth interval, early maturation, high fecundity, reduced parental care and short life span. They are often found in habitats such as flood plains and shallow lakes, where rapid colonisation is favourable, with extreme natural and fisheries mortality, or with highly variable environmental conditions (Noakes and Balon, 1982; Welcomme, 2001; de Graaf, 2003 (a, b); de Graaf and Marttin, 2003).
- “K-strategists” are species with a prolonged growth interval, late maturation, reduced fecundity, increased parental care and an extended life span. They are found in habitats with more or less stable environmental conditions and low natural and fisheries mortality.

Noakes and Balon (1982) developed an evolutionary model for the reproduction strategies of tilapias, alongside the “r and K strategy”. Their model provides a good theoretical concept of stunting processes of tilapias and is summarized below.

Noakes and Balon (1982) placed reproduction strategies in an evolutionary perspective through evolutionary sequences, or back and forth alteration from “altricial” to “precocial” forms. They used the terms altricial (generalist) and precocial (specialist) in the general ecological sense:

- Altricial recruits are those that are relatively small and incompletely developed, and have a prolonged larval/embryonic period and early maturation and resemble “r-strategists”.
- Precocial recruits are relatively more developed, at a particular time in ontogeny, and have a truncated larval period and delayed maturation and resemble “K strategists”.

Cichlids, including tilapias, are in general classified in two reproductive guilds: “guarders”, which direct custodial care towards the embryo outside the body, and “bearers” which take up the fertilized eggs into the buccal cavity. In their evolutionary model, guarders are generally more altricial (r-strategy) and bearers are more precocial (K-strategy). Bearers are more specialised, which is illustrated by relevant life history data for guarding and bearing tilapias (Table 1).

Table 1: Comparison of tilapine species in natural populations (from Noakes and Balon, 1982).

Characteristic	Guarders (altricial)	Bearers (precocial)
Fecundity	Up to 7 000 eggs	Up to 1 000
Egg diameter (mm)	1-1.5	Up to 5
Yolk (% lipid)	Less then 25	Up to 45
Yolk colour	Clear pale yellow	Opaque orange
Size at onset of feeding (mm)	5-6	9-10
Age at first reproduction (years)	0.5-2.0	1-4
Total length at first reproduction	Up to 20	Up to 40
Courtship	Prolonged, monogamous	Brief, polygamous
Juvenile mortality	Relatively higher	Relatively lower
Longevity (years)	Up to 7	Up to 9

Noakes and Balon assume that bearers were derived from ancestral riverine guarding species. If conditions did not permit guarding (e.g., unsuitable substrate for a nest, with danger of exposure, etc.) and hence bearing was favoured, mouth brooding would most likely be the end result of an extended evolutionary progression. Bearing and its attendant adaptations are an advanced, precocial life style, seemingly ill suited for a fluvial species invading recently inundated areas. However, the key point of their model is the nature of the described development. In a real sense tilapias have the best of two worlds and two life styles. Through heterogeneous shifts in development in ontogeny they can quickly adapt towards a more altricial mode to take advantage of new habitats (e.g. seasonal flooded lakes, new impoundments), or revert to a more precocial mode under other circumstances (e.g., more stable, long term conditions in large lakes, high competitive diversity of fish taxa) while remaining in the same reproductive guild. In other words tilapias retain the ability to successfully invade newly created marginal aquatic habitats through altricial responses. Stocking these fish in ponds or other aquaculture facilities closely replicates invading a newly created river floodplain or shallow lake. The response of the fish is identical in both situations. There is a shift towards a more altricial life style, with an earlier onset of reproductive maturity as well as production of more numerous, and smaller eggs.

Following their model, Noakes and Balon (1982) suggest that the use of more altricial tilapias or guarders in aquaculture may have considerable potential and that feeding the fish in aquaculture is not advised. Both recommendations have practical implications; as guarders in principle reproduce at a lesser length (Table 1) and the consequences for aquaculture would be equal to the use of a bearer that shifts to an earlier length at first maturation. Feeding of fish is inherent to the objective of aquaculture: to produce marketable sized tilapia in a relatively short time span, and reducing the feeding level to avoid earlier maturation is in contradiction with this objective and will not be economically feasible.

A major aspect of the discussion is the semantic use of the word “stunting” as it is often used in the sense that somatic growth is reduced or halted and that earlier breeding takes place. This semantic use is inappropriate, confusing and unfortunately too often found in publications on the rearing of Nile tilapia. Stunting encompassed two different interrelated processes: growth and reproduction. The size at first maturation of the Nile tilapia in our experiments is small compared to a size of 20-30 cm (150-250 g) at which these fish reproduce under natural conditions (Lowe-McConnell, 1958 and Gwahaba, 1973). Therefore, the tilapia used in the experiment became "stunted" in the sense of early breeding. However, this stunting did not lead to a reduction of somatic growth since a mean growth rate of 0.78 g day^{-1} for males and a mean net yield of 7400 kg ha^{-1} year^{-1}, as obtained from the sampled grow-out ponds is comparable with growth rates of 0.6-1.2 g day^{-1} and net yields of 5600-11 000 kg ha^{-1} year^{-1}, as obtained in monosex male tilapia in cages or all-male tilapia hybrid culture in ponds using commercial pellets or chicken feed (Coche, 1977; Lovshin *et al.*, 1990; Philippart *et al.,* 1979 and Melard, 1986). Therefore the two processes should be separated and defined by the different terms: “Neonteny”, is the ability to breed successfully while still in the juvenile stage of development (Fryer and Iles, 1972) and “stunting”, is the reduction of somatic growth.

NEONTENY

Our study indicates that a major topic in tilapia farming is neonteny. Noakes and Balon (1982) provide a good frame for the evolutionary processes. However, they also correctly stated that the signals, which stimulate this shift into earlier reproduction, are not really known. According to Fryer and Iles (1972) and Lowe-McConnell (1982), factors such as a low condition factor, lower water depths, smaller habitat or high fishing intensity could lead to earlier breeding. In the present study, the pond reared Nile tilapia had a relatively high condition factor and still started to reproduce at an early age and small size. This could indicate that aggravation of the living conditions is not a major cause of earlier breeding of pond reared Nile tilapia. Good knowledge of the signals that lead to a shift towards earlier maturation is however of utmost importance, especially as simulation indicates the benefits of using late maturing species in the grow-out of Nile tilapia (Chapter 5). Unfortunately, research on this aspect of tilapia farming has never been a priority.

STUNTING OF SOMATIC GROWTH

Our study indicates that high growth can be obtained even if neonteny is occurring and Nile tilapia are reproducing at an early age. Reduction of growth can take place but this is mainly related to feeding level. The presence of approximately 25 % (on weight basis) of fingerlings in a mixed culture of Nile tilapia interferes within the production process through feed competition between the originally stocked tilapia and their offspring. Consequently the growth of adult Nile tilapia is restricted. This interference is rather strong because the metabolism of small fish is relatively higher than the metabolism of large fish (Winberg, 1956) and consequently 1 kg of fingerlings consume more feed than 1 kg of adult fish. This issue can be addressed by directly increasing the feeding level or by indirectly increasing the feeding level by removing the fingerlings through the introduction of a predator. Both actions result in an increased growth rate of the adult Nile tilapia.

From our study it can be concluded that early breeding of Nile tilapia is not a bottleneck for the development of Nile tilapia farming. The excessive recruitment in pond rearing of mixed-sexed Nile tilapia, often mentioned as the major biological problem (Bardach *et al.*, 1972; Ruwet *et al.*, 1976; McGinty, 1985; Lovshin *et al.*, 1990) will only lead to reduction of somatic growth if the ponds are not properly fed. Therefore, in general it can be concluded that stunting of Nile tilapia is a management problem and not a biological problem.

POLY CULTURE OF NILE TILAPIA WITH PREDATORS

Large catfish and large snakehead were able to control the recruitment of Nile tilapia completely; less than 0.15% of the total harvested biomass consisted of fingerlings at a stocking density of respectively 8300 catfish ha^{-1} or 725 snakehead ha^{-1}. During the past thirty years, similar experiments were carried out for different predators: *Lates niloticus* (Lazard, 1980; Bedawi, 1985; El Gamal, 1992), *Channa striata*, (Hopkins *et al*., 1982), *Hemichromis fasciatus*, (Lazard, 1980). *Micropterus salmoides* (McGinty, 1985), *Cichla ocellaris* (McGinty, 1983; Verani *et al*., 1983) and in general it can be concluded that recruitment of Nile tilapia can be easily controlled through poly-culture with a predator. Differences in the efficiency of recruitment control are determined by feeding habits and mode of predation (Chapter 3). From a biological point of view these systems are reasonably well mastered. However, a major point of attention, which is often ignored, is the economics of the systems.

Recruitment control by a piscivorous predator often leads to a reduction in net yields (Fortes, 1980; Lazard 1980; McGinty, 1983, 1985; Ofori, 1988 and Chapter 3). With piscivorous species the fingerling biomass is converted into a smaller predator biomass. The lost fingerling biomass cannot be fully compensated by the higher growth rates of male and female Nile tilapia. Ofori (1988) found that the loss in biomass is economically compensated by the higher price of the larger Nile tilapia. The situation in the Republic of Congo Brazzaville was different, as fingerlings could be sold for consumption on the local market. The farmgate price of snakehead was only about four times higher than the farmgate price of fingerlings. With a conversion of 6 kg of fingerlings into 1 kg of snakehead, polyculture with snakehead results in a financial loss (Figure 1). These findings stress the importance of including local economics in tilapia farming studies and development plans, as it is the major factor for the success or failure of such schemes.

Figure 1: Relation between the Gross Product Value of harvested fingerlings and the stocking densities of snakeheads.

THE NURSING OF AFRICAN CATFISH FINGERLINGS

A reliable source of African catfish fingerlings is a prerequisite for the development of poly culture of the Nile tilapia with this predator or for monoculture of the African catfish and development of a reliable method for the production of African catfish fingerlings was regarded a priority of aquaculture research in Africa (Anonymous, 1987a).

Hogendoorn (1980) and Hogendoorn and Vismans (1980) successfully developed an intensive production system for fingerlings of the African catfish based on the use of *Artemia salina* nauplii and commercial trout starter as a feed. The existence of a technically feasible method and a manual in which the techniques are described (Viveen *et al*., 1985) does not, however guarantee a successful implementation, as the impact of local socio-economic and technical conditions are often under-estimated (Anonymous, 1987b). The introduction of intensive rearing methods in the Central African Republic and in the Ivory Coast encountered technical and economic problems (Janssen, 1985a, b, c; de Graaf, 1989).

Our study indicates that the artificial reproduction and mass rearing of African catfish throughout the year is technically possible under tropical conditions by using “low-cost” adapted methods. Provision of a high phyto and zooplankton bloom in the early nursing phase, and harvesting the ponds before cannibalism becomes serious, is essential. The distribution of the production costs of the developed method is more coherent with the socio-economic conditions in rural Africa where labour is in surplus, if compared with the distribution of the costs for a more western style hatchery. However, recent developments in Bangladesh have shown that mass production of catfish fingerlings in “low-tech” hatcheries based on feeding with Tubifex tubifex (Muller) or larval shrimp feed, (i.e., nauplii of *Artemia salina* are not used) is technically feasible and highly profitable (de Graaf, unpublished data; Middendorp, 1998).

SIMULATION OF TILAPIA FARMING

The original objective of the model was to test the hypothesis that using fingerlings of 25-35 gram, selected from ponds where neonteny and severe stunting has taken place, aggravates the process as more and more female fish are stocked. The model could not prove the hypothesis. Surprisingly, simulation of repeated stocking of fingerlings with a weight of 25-35 g, resulted in a lower percentage of stocked females and not in the expected higher percentage of females (Figure 2). The major reason for this unexpected result is the growth difference between male and female tilapia: male tilapia are growing faster than female tilapia and this phenomenum is incorporated in the preliminary version of the model. This means that also the recruited male tilapia are growing faster than the recruited female tilapia and as a result most of the fingerlings of 25-35 g are male (Figure 3). Some dichotomy occurs in fingerling distribution (de Graaf, unpublished data) but not in this extent. A general problem is that the von Bertalanffy growth function used in the model is not very suitable for the growth of juvenile fish (Sparre & Venema, 1998) and in the final model the growth parameters of fingerlings between 0.8 and 10 cm are given equal values for male and female Nile tilapia. With this setting simulation of repeated stocking of fingerlings with a weight of 25-35 g, results in about 50 percent of stocked females (Figure 4)

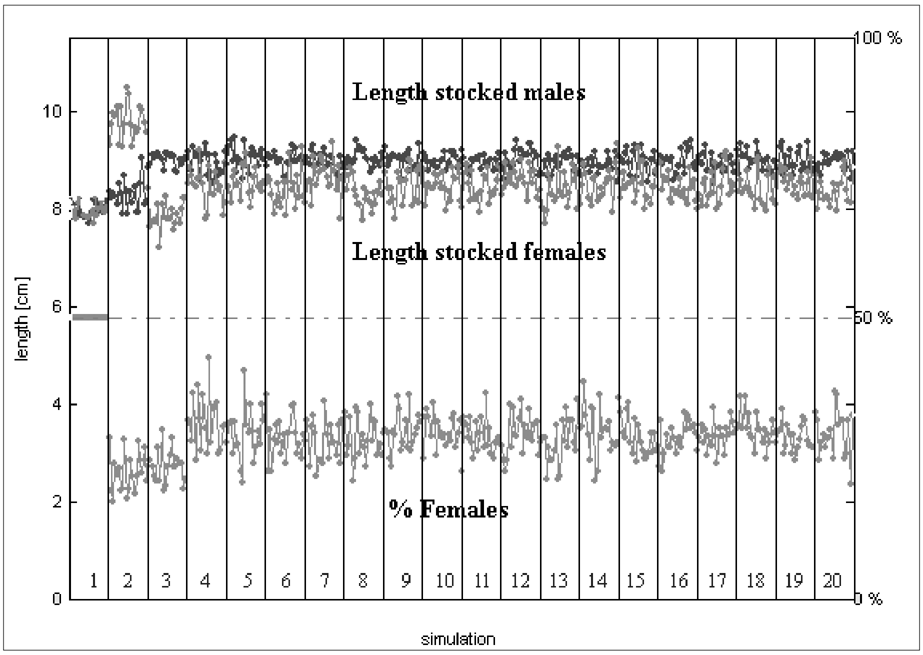

Figure 2: Simulation results of repeated stocking with fingerling weighing 25-35 g as obtained with the first version of the model.

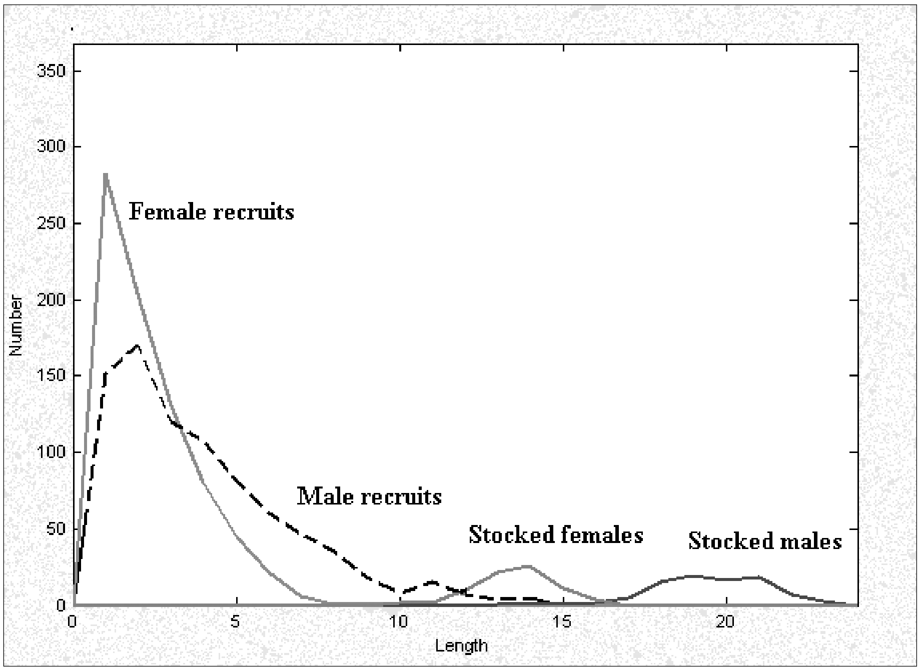

Figure 3: Distribution of recruited male and females and stocked male and female Nile tilapia as simulated with a first version of the model.

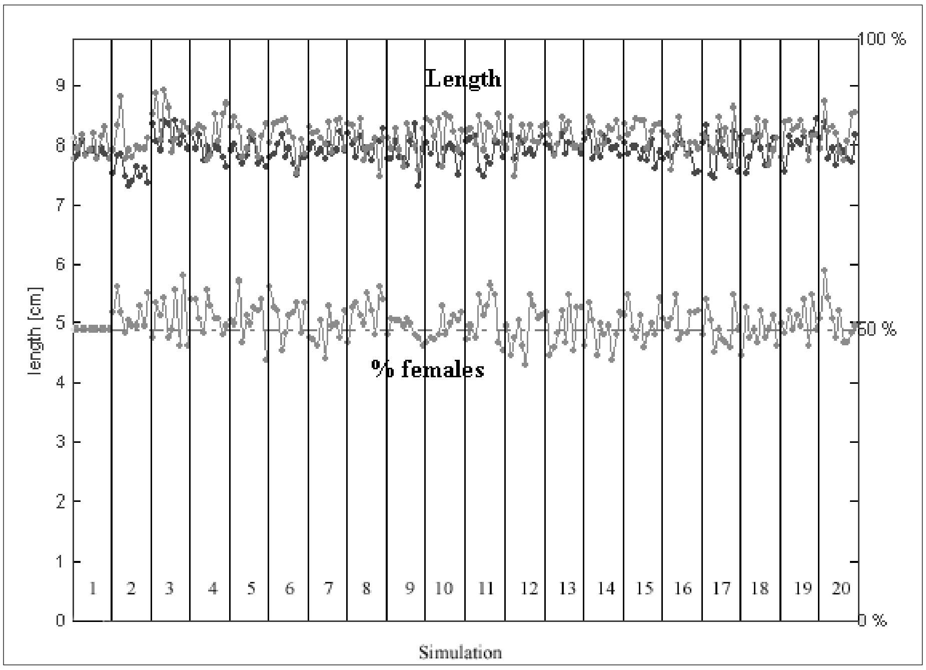

Figure 4: Results of repeated stocking with fingerling weighing 25-35 g as simulated with the final version of the model.

From the onset, a major objective was to develop a Tilapia Farming Support Tool that can assist farmers in choosing the appropriate tilapia farming system and husbandry techniques, based on sound biological and economic criteria. The starting point for the development of the model was that the over-riding motivation for farmers to embark on tilapia farming is profit including additional income (Marzan *et al*., 1995; Sevilleja, 2000). Within this concept, tilapia farming is an “agro-economic activity” and not a “subsistence activity” aimed at the provision of additional fish for home consumption, as assumed for tilapia farming development schemes, implemented in the 1970-80s. This is important, as this concept has guided the way the model was set up. This type of commercial aquaculture aims at yields of 3-6 t ha^{-1} year^{-1}, which can only be obtained with external feeding. Within this concept, the development of phytoplankton, periphyton and zooplankton, the oxygen consumption of fish and the available oxygen in the pond, are less important, as the whole process and the final production is driven by the quantity and quality of the feed supplied. Therefore, the model was based on population dynamics and not on traditional modelling based on nutrient flows or bio-energetic processes (Cuenco *et al*., 1985; Machiels and Henken, 1986; Ross and Mckinney, 1989; van Dam and Penning de Vries, 1995; van Dam and Pauly, 1995; van de Meer and van Dam, 1999). In the model, everything what happens inside the fish, related to growth, oxygen uptake, is a "black box" and the quantity and quality of feed supplied is related to a standard maximum growth rate. This allowed clearer emphasis on major population dynamic processes such as recruitment, mortality and prey-predator processes. Modelling of recruitment, prey-predator relations and the relation between growth and feed quality are still too simplistic. However, in general, it is concluded that the results of the model are useful for the simulation of different tilapia farming systems; mixed sex, mono sex or poly culture with African catfish or snakehead and can serve as a predictive and decision-making support tool after inclusions of the discussed topics. Including economic or financial parameters for the inputs (fingerlings, feed, labour, investments) and outputs (farm-gate prices) would result in a practical tilapia farming decision model.

Dey *et al*., (2000) investigated the technical efficiency of tilapia grow-out operations in the Philippines and provides a basic concept for development:

"Increases in yields can result from the development and adoption of new technologies and improvement in the economic efficiency of farming operations. The economic efficiency consists of two components:

1. Technical efficiency, which reflects the ability of a farm to obtain maximum output from a given set of inputs and available technology
2. Allocative efficiency, which reflects its ability to use the inputs in optimal proportions, given their respective prices (Farrell, 1957; Coelli 1995)

It has been shown that efforts designed to improve efficiency as a means of increasing agricultural output are more cost-effective than introducing new technology if farmers are not making efficient use of existing technology (Belbase and Grabowski, 1985; Shapiro 1983)"

Next to China, the Philippines are the second producer of farmed tilapia in the world. After a spectacular increase in production in the early 70s, the production stabilised in the 1990s at about 80 000 t year^{-1}, but continued to increase further since 1999 (Figure 5).

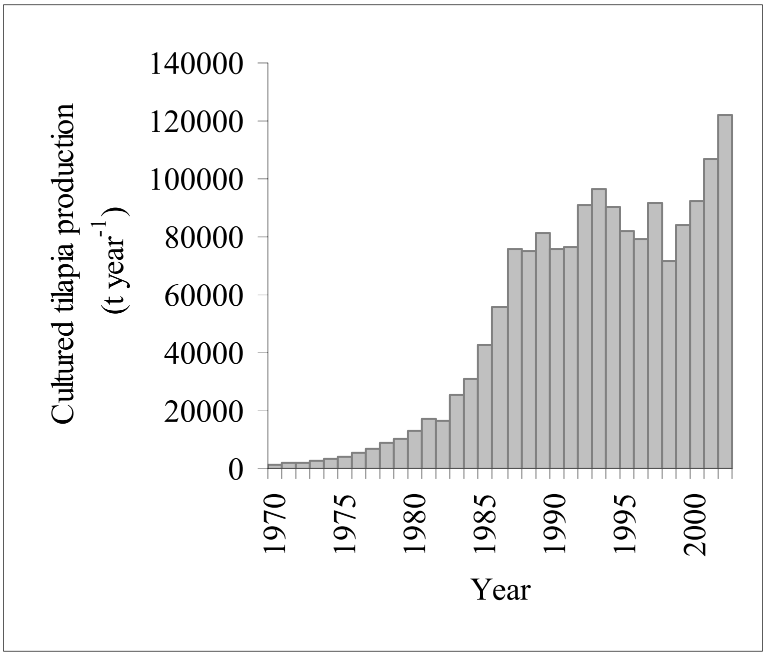

Figure 5: Farmed tilapia production in the Philippines since 1970 (FAO, 2003)

The study of Dey *et al*. (2000) indicated a mean level of technical efficiency of 83% and they concluded that improvement of yields can be mainly achieved through the development and adoption of a new technology, e.g., genetically improved tilapia strains with a better performance in terms of growth and survival. Tilapia farming in the Philippines is well developed, illustrated by the fact that they are the second highest ranking producer in Asia. Technical efficiency here is exceedingly high. However, it can be safely assumed that technical efficiencies in the majority of the developing countries are not that high and that yields can be increased considerably by improving and optimising rearing methods. Accordingly, a practical Tilapia Farming Support Tool based on simulation of various husbandry scenarios could play a useful role.

THE VON BERTALANFFY GROWTH CURVE AND AQUACULTURE EXPERIMENTS

The von Bertalanffy growth curve is one of the basic inputs of numerous fisheries stock assessment models (Sparre and Venema, 1992) and is used to describe growth in the simulation model presented in Chapter 5. It is gaining popularity in aquaculture research, especially due to its potential in serving as an instrument for multi-variate analysis, and thus facilitating evaluation of the impact of multiple variables on growth (Prein *et al.*, 1993, Chapter 6). However, it is often not realized that L_∞ and the growth parameter K in the von Bertalanffy growth curve are correlated: different combinations of K and L_∞ can give almost the same fit to data, except when a wide range of ages is represented. Again, a high value of K combines with a low value of L_∞ and vice versa (Sparre and Venema, 1992). In aquaculture, this characteristic (i.e. obtaining two parameters) makes the application of the von Bertalanffy growth curve for the mere comparison of growth cumbersome.

The analysis presented in Chapter 6 indicates that fixating L_∞ in the analysis of growth in aquaculture experiments through a "forced Gulland-and-Holt plot" (Pauly, 1984), or through an "extended forced Gulland-and-Holt plot" is an alternative. However, these methods can only be applied provided such a "maximal L∞" for the different species can realistically be determined..

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SUMMARY-SAMENVATTING

OPTIMIZATION OF THE POND REARING OF NILE TILAPIA (*OREOCHROMIS NILOTICUS NILOTICUS* L.)

The impact of stunting processes and recruitment control

INTRODUCTION

With a total reported 130 million tonnes (t) in 2000, fisheries and aquaculture are important for global food security, providing about 16% of the total animal protein supplies. Outside China, the world's population has been increasing more quickly than the total food fish supply, resulting in a decreased global per capita fish supply from 14.6 kg in 1987 to 13.1 kg in 2002. Stabilising or increasing the per capita food availability can, therefore, only be obtained from aquaculture production, both from traditional rural aquaculture and intensive commercial aquaculture of high-value species. The bulk of the aquaculture production (70%) is raised in developing countries and low-income, food-deficit countries (LIFDCs). Further, about 60% of the raised fish and crustaceans consist of omnivorous/herbivorous or filter feeding species, feeding at the bottom of the food chain, while only 29% of the production consists of the high value, carnivorous species, feeding at the top of the food chain. With an annual production of 790 000 t, or 9.3% of the total world cultured production in fresh or brackish water, tilapia ranks second in the list of most important cultured species.

Since 1970, the farmed tilapia production in Asia (excluding China) increased on the average with 11.5% year^{-1} and reached 0.48 million tons in 2002. In Africa, the production remained more or less stable until 1997 and increased rapidly since then to an annual production of about 0.2 million tonnes in 2002. Much of this boom is attributable to an expanded area and, to a much lesser extent, to improved husbandry techniques. Fresh water will become an increasingly scarce resource over the next 20 years, making further expansion of the area under freshwater aquaculture difficult. Consequently, further expansion of farmed production has to be obtained through improved husbandry techniques increasing the yield per hectare.

It is often stated that the major biological problems in pond rearing of mixed-sexed Nile tilapia is its excessive recruitment. Under natural conditions, Nile tilapia starts to reproduce at a size of 20 cm to 30 cm. However, cultured Nile tilapia reproduces at a much smaller size of 8 cm to 13 cm. This stunting of Nile tilapia can lead to a reduction of somatic growth. For reproduction of Nile tilapia, this would mean that spawners were "relatively old and small." However, the smaller size at first maturation could also be caused by earlier breeding, and this would mean that spawners are "young and small." From a production point of view, the two concepts are different as a reduction of somatic growth certainly reduces the final production, while earlier breeding does not automatically lead to a reduced level of production.

THE THESIS

This thesis, studied the pond rearing of the Nile tilapia with special emphasis on stunting processes and recruitment control. After a general introduction, results on the reproductive performance of female Nile tilapia, reared in ponds under tropical conditions is presented in Chapter 2. The experiments used stock matured at the age of 2-4 month and a size of 30-50 g. Oocyte development proved a better indicator for the determination of the size at first maturation than the development of the gonado somatic index. The Nile tilapia became "stunted" in the sense that early breeding took place, but the somatic growth of the stock still continued. This result indicates that earlier breeding of Nile tilapia is not a real bottleneck for the expansion of this production sector. No relation was found between the condition factor and the size at first maturation or the relative fecundity. This led to the conclusion that aggravation of the living conditions is not a major cause of earlier breeding of pond reared Nile tilapia.

In Chapter 3, the results of recruitment control of Nile tilapia through poly culture with a predator is presented. The recruitment of Nile tilapia (stocked at 20,000-22,000 ha^{-1}) was completely controlled by large African catfis (6.8-130 g) and large snakehead (75-206 g) at stocking densities of respectively 8,300 catfish ha^{-1} or 725 snakehead ha^{-1}. The difference in predation efficiency between the two species is related to their feeding strategies: omnivorous versus piscivorous. The elimination of the Nile tilapia fingerlings caused the growth rate of male and female Nile tilapia to increase significantly ($P \leq 0.05$) with both predator types. However the net yield decreased in the case of predation by snakehead ($P \leq 0.05$) but did not change in the case of predation by catfish. Analysis of the results indicated that food shortage is a limiting factor. This limitation can be removed by increasing the feed supply directly with additional feed or indirectly by the elimination of the Nile tilapia fingerlings. The results led to the conclusion that stunting of somatic growth in Nile tilapia is mainly related to the husbandry techniques applied. Small catfish (weight ≤3.65 g) and small snakehead (weight ≤2 g) were not capable of controlling recruitment completely; at harvest 3.7 % and 8.9 % of tilapia fingerlings (of total harvested biomass) persisted for, respectively, catfish and snakehead at the highest stocking densities. Incomplete recruitment control by small, stocked predators is mainly related to the later onset of piscivorous feeding and the low survival rates (24-34%).

In Chapter 4, a low cost method for the mass production of fingerlings of the African catfish is discussed. Reproduction could be induced throughout the year using common carp pituitaries (3 mg kg^{-1} female). The average relative fecundity of females varies between 1.3 % ± 0.3 (SEM) and 14.3 % ± 1.3 (SEM). The average hatching percentage of the obtained eggs varies between 28.4 % ± 4.5 (SEM) and 59.1 % ± 3.7 (SEM) respectively in the dry and rainy season. The fluctuation of the relative fecundity as well as the fluctuation of the hatching percentage follows the seasonal fluctuation in rainfall and temperature. The use of a net cage made of mosquito netting (1 m^3, 0.5 mm mesh size) and the roots of water hyacinth (*Eichornia crassipes*) as an egg incubator proved to be reliable. In ponds not protected against frogs an average of 5.0 ± 2.9 (SEM) fingerlings m^{-2} per 40 days cycle were obtained, where as in ponds completely surrounded by a wall of aluminium roof plates (0.8 m high) the average production was 32.3 ± 3.3 (SEM) fingerlings m^{-2} per 40 days cycle, when they are stocked with approximately 100 larvae m^{-2}. Increasing the larval stocking density or extending the rearing period did not improve the final production. The main causes of low production in unprotected ponds are competition for food resources due to the presence of phytophagous frog larvae and cannibalism among the fingerlings of African catfish. An analysis showed that the studied system is labour oriented, technical reliable and economic feasibly when the fingerlings can be sold for US$ 0.07 a piece.

A simulation model for the rearing of the Nile tilapia for mixed or mono sex culture, and for poly culture with the African catfish or African snakehead is presented in Chapter 5. The model is based on population dynamics and follows an “Individual Based” approach. The model consists of a tilapia submodel representing population dynamics, growth and recruitment and a predator submodel representing the predation process and population dynamics and growth of the used predator. The model was calibrated with data obtained in Congo Brazzaville and validated with data from the Philippines, Thailand and Ivory Coast. The model visualized some underlying ecological processes in tilapia farming and indicated that growth and its relation to feed quality, recruitment and prey-predator relations are major topics in tilapia farming modelling. The model can serve as a predictive and decision-making support tool after some slight adaptations as discussed.

In Chapter 5, three approaches for multivariate analysis of fish growth in aquaculture experiments with Nile tilapia based on the von Bertalanffy growth curve, are presented and compared. The approaches are: an extended Gulland-and-Holt plot, a forced extended Gulland-and-Holt plot and a multi- linear regression analysis for the growth parameter K. All three models provide valuable insight into the major environmental factors influencing daily growth rate and explain 28% to 46% of the variance of the observed daily growth rate. For all three methods, the modelled parameter is significantly related with the net yield of Nile tilapia and can, therefore, be used for the predictive modelling of management scenarios. The extended Gulland-and-Holt plot loads the influence of environmental parameters upon L_∞, while the forced extended Gulland-and-Holt plot and direct fitting of K loads the influence on the growth parameter K. The latter is more in the tradition of aquaculture research. But the forced extended Gulland-and-Holt plot and direct fitting of K can only be applied if L_∞ of the cultured species is known, this as the selected L_∞ influences the variance in the regression variables.

In a general discussion, the results overall results are discussed and placed in the context of stunting, recruitment control and the development of tilapia farming. The main conclusion is that the semantic use of the word “stunting” is often not appropriate as two different processes take place in the rearing of Nile tilapia: “Neonteny”, the ability to breed successfully while still in the juvenile interval of development and “Real Stunting”, the reduction of somatic growth. Why neonteny takes place is still not understood, but the study indicates that this phenomenon is not a bottleneck for tilapia farming as long as they are properly fed. Real stunting or reduction of somatic growth is related to low feeding levels and can be avoided by proper husbandry techniques such as high feeding levels or by the reduction of the number of fingerlings through poly-culture with a predator. Economics of Tilapia farming can be divers and are the major driving forces behind the worldwide development of tilapia farming. With some adaptations, the presented Tilapia farming simulation model could be used as a tool to support further developments of this important sector.

OPTIMALISATIE VAN DE VIJVERTEELT VAN NIJL TILAPIA (OREOCHROMIS NILOTICS NILOTICUS L.)

De invloed van stunting en de controle van rekrutering

INLEIDING

Met een jaarlijkse productie in het jaar 2000 van 130 miljoen ton, ongeveer 16% van de totale dierlijke eiwitproductie zijn de visserij en de visteelt belangrijk voor de wereld voedselvoorziening. Als China buiten beschouwing wordt gelaten dan zien we dat de wereld bevolking sneller groeit dan de de vis produktie. Met als gevolg dat de beschikbaarheid aan vis daalde van 14.6 kg per persoon in 1987 tot 13.1 kg per persoon in 2002. Stabilisatie of of een verdere stijging van de bijdrage van vis aan de wereld voedsel voorziening kan daarom alleen komen uit de visteelt. Dit kan komen uit traditionele visteelt in vijvers, maar ook uit intensieve visteelt van soorten met een hoge commerciële waarde. Het grootste deel van de geteelde vis (70%) wordt geproduceerd in ontwikkelingslanden en de zogenaamde lage-inkomen landen waar in het algemeen gebrek aan voedsel is (Low Income Food Deficient Countries, LIFDCs).

Ongeveer 60% van de gekweekte vis en de schaaldieren bestaat uit soorten die alles-eters (omnivoor) of planten-eters (herbivoor) zijn, soorten die zich laag in de voedsel keten voeden. Slechts 29% van de gekweekte vis bestaat uit soorten met een hoge commerciële waarde, welke, veelal afhankelijk zijn van dierlijke eiwitten (carnivoren) en zich dus voeden in de top van de voedsel keten. De resterende 11% bestaat uit garnalen. Tilapia, behoort tot de eerste groep en met een jaarlijkse productie van 790.000 ton, 9.3% van de totale hoeveelheid vis die op de wereld in zoet en brak water wordt geproduceerd, staat deze vis als tweede op de ranglijst van de belangrijkste soorten gekweekte vis.

Sinds 1970, steeg de productie van gekweekte tilapia in Azië met gemiddeld 11,5% per jaar en tot 0,48 miljoen ton in 2002 (China uitgezonderd). In Afrika, bleef de productie min of meer stabiel tot 1997, waarna het snel steeg snel tot een jaarlijkse productie van ongeveer 0,2 miljoen ton in 2002. Veel van deze stijging is toe te schrijven aan een uitbreiding van het totale oppervlakte gebruikt voor visteelt (meer vijvers), en in mindere mate, aan verbeterde kweek technieken, met hogere opbrengsten per hectare. In de komende decennia zal zoet water steeds schaarser worden, en verdere uitbreiding van het aantal vijvers wordt hierdoor beperkt. Derhalve zal een verdere stijging van de hoeveelheid wereldwijd gekweekte zoetwater vis voornamelijk moeten komen door een hogere opbrangst per hectare dankzij verbetering van de teelt technieken.

Er wordt vaak vermeld dat overmatige rekrutering, of de overmatige productie van jongbroed, een van de belangrijkste biologische problemen in vijverteelt van Nijl tilapia is. Onder natuurlijke omstandigheden begint een Nijl tilapia zich bij een lengte van 20 tot 30 cm voort te planten. In een vijver begint Nijl tilapia zich echter al voort te planten bij een lengte van 8-13 cm. Dit zogenaamde “stunten” van de Nijl tilapia kan leiden tot een vermindering van de groei. Voor reproductie van de Nijl tilapia, betekend dit dat deze paaiende vissen." vrij oud en klein” zijn. Het kan echter ook het geval zijn dat deze voortplantende vissen “vroeg rijp” zijn, en dit zou betekenen dat deze paaiende vissen “jong en klein” zijn. Productie en visteelt technisch, zijn de twee concepten totaal verschillend. Een vermindering van de groei, dus “vrij oud en klein” betekent dat ook het rendement verminderd, terwijl “vroegrijp” niet automatisch tot een vermindering van het rendement hoeft te leiden..

HET PROEFSCHRIFT

Voor dit proefschrift werd de optimalisatie van de vijver teelt van Nijl tilapia bestudeerd, waarbij speciale aandacht werd gegeven aan de invloed van stunting en de controle van de rekrutering. Na een algemene inleiding worden in Hoofdstuk 2 de resultaten van voortplantingsbiologie van gekweekte Nijl tilapia gepresenteerd. In de studie worden vissen gevolgd die op een leeftijd van 2-4 maanden, met een gewicht van 30-50 g, geslachtsrijp worden. Het volgen van de ontwikkeling van de oocyten is een betere methode voor het vaststellen van de geslachtsrijpheid dan het volgen van de Gonado Somatische Index. De Nijl tilapia beginnen te “stunten”, in de betekenis dat zij zich op een vroege leeftijd beginnen voort te planten, terwijl de groei gewoon door gaat. Dit wijst erop dat een vroege geslachtsrijpheid geen beperking hoeft te zijn voor een verdere uitbreiding van de teelt van Nijl tilapia. Er wordt geen relatie gevonden tussen de conditie factor en de lengte waarbij Nijl tilapia zich voor het eerst voortplant en de relatieve vruchtbaarheid. Dit leidt tot de conclusie dat de verslechtering van de levensomstandigheden geen belangrijke oorzaak is van de vroege geslachtsrijpheid van de in vijvers gekweekte Nijl tilapia..

In Hoofdstuk 3 worden de resultaten van de controle van de rekrutering van Nijl tilapia, doormiddel van poly-cultuur met een roofvis (Afrikaanse meerval en Afrikaanse slangkopvis) behandeld. De rekrutering van Nijl tilapia (bezetting 20.000-22.000 ha^{-1}) wordt volledig gecontroleerd door grote Afrikaanse meerval (6.8-130 g) en grote Afrikaanse slangkopvis (75-206 g) bij een bezetting van 8.300 meervallen ha^{-1} of 725 slangkopvissen ha^{-1}. Het verschil in de effectiviteit van de predatie tussen de twee soorten wordt bepaald door hun voedsel strategie: omnivoor (meerval) versus carnivoor (slangkopvis). Het verminderen van het jongbroed van Nijl tilapia heeft tot gevolg dat de groei van de uitgezette oude Nijl tilapia beduidend toeneemt ($P \leq 0.05$). De netto opbrengst vermindert echter als slankopvis gebruikt wordt ($P \leq 0.05$) en blijft gelijk als meervallen werden gebruikt. De analyse van de resultaten wijst erop dat het voedseltekort de beperkende factor voor de groei is. Deze beperking kan worden opgeheven door het voederniveau direct te verhogen, of door het verwijderen van het jongbroed van Nijl tilapia door middel van roofvissen, waarbij het voeder niveau op een indirecte wijze wordt verhoogd.. De conclusie is dat vermindering van de groei bij Nijl tilapia voornamelijk wordt veroorzaakt door de gebruikte bedrijfsvoering.. Kleine meerval (gewicht≤3.65 g) en kleine slangkopvis (gewicht≤2 g) kunnen de rekrutering van Nijl tilapia niet volledig controleren. Bij de hoogste bezettingsgraad van kleine meerval en kleine slangkopvis bestaat de tilapia oogst nog steeds voor 3,7% (voor meerval) en 8,9% (voor slangkopvis) uit jongbroed van Nijl tilapia. Deze onvolledige controle van de rekrutering door kleine roofvissen wordt voornamelijk bepaald doordat deze pas later prooivis gaan eten en door hun lage overlevingspercentage (24-34%).

In Hoofdstuk 4 wordt een goedkope en simpele methode voor de massa productie van jongbroed van de Afrikaanse meerval behandeld.. De vissen kunnen het hele jaar worden voortgeplant m.b.v. karper hypofyse (3 mg kg^{-1} vis). De gemiddelde relatieve vruchtbaarheid van wijfjes varieert tussen 1,3% ± 0,3 (SEM) en 14,3% ± 1,3 (SEM). Het gemiddelde uitkomst percentage van de eieren varieert tussen 28,4% ±4,5 (SEM) in het droge seizoen en 59,1% ± 3,7 (SEM) in het regen seizoen. De variatie in de relatieve vruchtbaarheid en het uitkomst percentage van de eieren volgt de seizoensgebonden schommeling in regenval en temperatuur. Het gebruik van een kooi van muskietengaas (1 m^3, 0,5 mm maaswijdte) voor het houden van de larven en het gebruik van de wortels van de waterhyacint (Eichornia crassipes) als ei-incubator blijkt een betrouwbare methode te zijn. In onbeschermde vijvers wordt gemiddeld 5,0 ± 2,9 (SEM) jongbroed m^2 per cyclus van 40 dagen verkregen. In vijvers die tegen kikkers worden beschermd, door een muur van aluminium golfplaten (hoogte 0,8 m) is de gemiddelde productie 32,3 ± 3,3 (SEM) jonge vissen m^2 per cyclus van 40 dagen, in beide gevallen met een bezetting van 100 larven 100 m^2. Verhoging van de bezettingsgraad of een verlenging van de cyclus verhoogt de productie niet. De belangrijkste oorzaken van lage productie in onbeschermde vijvers zijn toe te schrijven aan de voedselconcurrentie door de aanwezigheid van algen-etende kikkerlarven en kannibalisme onder de jonge Afrikaanse meervallen. De studie toont aan dat de methode technisch en economisch betrouwbaar is wanneer het jongbroed voor 0.07 US$ per stuk verkocht konden worden.

In Hoofdstuk 5 wordt een simulatiemodel voor een gemengde of mono-sex cultuur van Nijl tilapia in combinatie met de Afrikaanse meerval of de Afrikaanse slangkopvis behandeld. Het model is gebaseerd op populatie dynamica en is “Individual Based”, d.w.z. het volgt iedere vis afzonderlijk gedurende de gehele simulatie. Het model bestaat uit een tilapia submodel dat de populatie dynamica, groei en rekrutering van tilapia berekent en een roofvis submodel dat de predatie en populatie dynamica van de roofvissen berekent. Het model wordt gekalibreerd met gegevens uit Congo Brazzaville en gevalideerd met gegevens uit de Filippijnen, Thailand en Ivoorkust. Het model visualiseert sommige fundamentele ecologische processen in de teelt en geeft aan dat de relatie tussen groei en voeder kwaliteit, rekrutering en de prooi-predatoor relaties belangrijk zijn in de kweek van Nijl tilapia. Met enkele aanpassingen kan het model gebruikt worden ter ondersteuning van de besluitvorming in de bedrijfsvoering van tilapia kwekerijen.

In Hoofdstuk 6 worden drie methodes vergeleken voor multi-variantie analyse voor de groei van Nijl tilapia in visteelt-experimenten. Groei is gebaseerd op de von Bertalanffy groei functie en wordt benaderd door een “uitgebreide Gulland-en-Holt functie”, een “gedwongen uitgebreide Gulland-en-Holt functie” en een “directe multi-lineaire regressie analyse voor de groeiparameter K”. Alle drie modellen geven waardevol inzicht in de belangrijkste milieufactoren die de groei beïnvloeden en verklaren 28% tot 46% van de waargenomen variatie in de groei. Voor alle drie methodes is de netto opbrengst van de Nijl tilapia duidelijk gerelateerd aan de gemodelleerde groei parameter. De methodes kunnen daarom gebruikt worden ter voorspelling van de opbrengsten van Nijl tilapia, onder verschillende bedrijfsvoeringen. Bij “de uitgebreide Gulland-en-Holt functie” varieert de maximale lengte van de vis onder invloed van de milieuparameters, terwijl bij de “gedwongen uitgebreide Gulland-en-Holt functie”en de “directe multi-lineaire regressie van K” de groeiparameter K varieert onder invloed van de milieuparameters. Dit laatste is meer in overeenstemming met de traditioneel gebruikte methoden in visteeltonderzoek. De “gedwongen uitgebreide Gulland-en-Holt functie” en de “directe multi-lineaire regressie van K” kunnen slechts worden toegepast als de maximale lengte van de gebruikte soorten bekend is omdat de gekozen maximale lengte van de vis de regressie variabelen beïnvloedt.

In de algemene discussie worden de resultaten van alle hoofdstukken besproken en geplaatst in de context van stunting, rekrutering, de controle van de rekrutering, en verdere ontwikkeling van de tilapia teelt. De belangrijkste conclusie is dat het gebruik van het woord “stunting” vaak niet correct is aangezien er twee verschillende processen plaatsvinden tijdens de kweek van Nijl tilapia: "neonteny", de vissen kunnen zich reeds voortplanten op een zeer jeugdige leeftijd, en "echte stunting", een vermindering van de groei. Waarom neonteny op treedt is nog niet bekend, maar de studie toont aan dat dit fenomeen geen knelpunt is voor de teelt van Nijl tilapia zolang zij correct gevoerd worden. Het “echte stunten”, de vermindering van de groei, wordt veroorzaakt door te weinig voer. Dit kan worden opgeheven door een juiste bedrijfsvoering met hogere voedergiften, of door de vermindering van het aantal jongbroed van de Nijl tilapia d.m.v. een poly-cultuur met een predator. De economie is de belangrijkste drijvende kracht achter de wereldwijde ontwikkeling van de tilapia teelt. Met enige aanpassingen kan het tilapia simulatie model als hulpmiddel worden gebruikt om verdere ontwikkelingen van deze belangrijke sector te ondersteunen.

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CURRICULUM VITAE

Gertjan de Graaf was born on 27 January 1954 in Franeker, the Netherlands. In 1972, he graduated from "Het Groen van Prinsteren Lyceum (secondary school) in Vlaardingen, the Netherlands, and studied subsequently Biology at Wageningen Agriculture University. He obtained his M.Sc degree in Biology in 1980. After his graduation he worked in aquaculture development projects in Egypt and Vietnam and set up one of the first marine rainbow trout farms in the Netherland and a gilthead bream farm in Greece. In 1986 he joined the Food and Agriculture Organisation of the United Nations and assisted the management of fish culture centers of the Government of Congo Brazzaville. During this assignment from 1986-1990, most of the data for this thesis were collected. Since 1990, he operates as an independed consultant in aquaculture and fisheries and was founder of NEFISCO, a non profit foundation for the development of tropical aquaculture and fisheries. Since 1990 he assisted a large number of development projects on aquaculture and fisheries in: Bangladesh, Vietnam, Cambodia, Kenya, Ivory Coast, Burkina Faso, Senegal, Ukraine and Rumania. In his spare time he wrote down his experiences in these projects in a number of scientific papers and over the last 10 years he (co-)authored more than 20 papers in peer reviewed journals of which three are part of the present thesis. He published a book on inland fisheries management in Bangladesh, and two training manuals on the rearing of the African Catfish and on the use of Geographical Information Systems in inland fisheries management for the Food and Agriculture Organisation of the United Nations.

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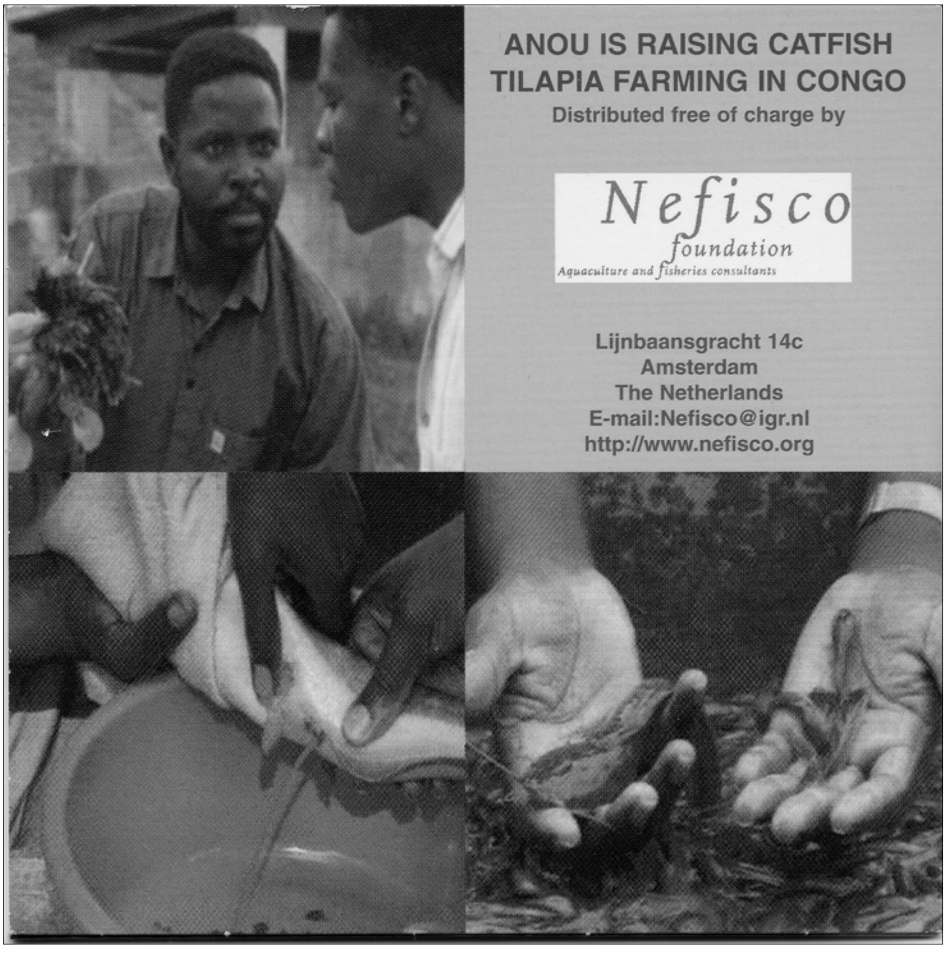

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