

# THE TILAPIINI TRIBE: ENVIRONMENTAL, AND SOCIAL ASPECTS OF REPRODUCTION AND GROWTH

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## Summary

Tilapias have become one of the three most important groups of commercial fish species. With over 70 species, the group of tilapia exhibits a large variety of adaptation responses to match the vast array of existing ecological habitats (either under natural conditions or following introductions). These important adaptive potentialities of tilapia could be related to their various reproductive/growth strategies. Some traits of these interactions between reproductive cycle and growth present a great plasticity and can be modulated by many environmental and/or social factors. The main characteristics of tilapia reproduction and growth and the effects of environmental factors on these traits are reviewed. Tilapias have been classified according to three main different genera, mainly on the basis of their parental behavior.

The present review will briefly report the main characteristics of reproduction, which can be sensitive to environmental and/or social factors, and the influence of such external factors on the reproductive capacity. In tilapia, genetic factors and temperature levels, and genotype–temperature interactions, determine sex: high temperatures can increase the proportion of males in some progenies. Age at first maturity can vary to a great extent, depending on the rearing conditions and strains. Most tilapia species need a minimal temperature of 20–22°C in order to breed. Under tropical conditions, a continuous reproduction is generally described within a tilapia population; however, seasonal variations in the intensity of reproductive activity related to seasonal changes. In the wild, the two major environmental factors for tilapia spawning are certainly temperature and rainfalls or flooding. However, many other environmental and/or social factors can also influence some reproductive characteristics of tilapia and then their reproductive efficiency: stocking density, sex-ratios, food quality and quantity, water quality (salinity, pH, and oxygen), stress, pollutants.... but also some other factors, such as the nycthemeral periodicity, the environmental complexity (breeding sites), the parental care or the social interactions.

Growth characteristics of tilapias are also reviewed: external morphology of male and female were very similar, except for the relative size of the head and relative heights measured along the vertebral axis which were respectively lower in female than in male. There is a relative growth in height associated with a relative development of dorsal muscle but also of visceral area. The growth of the caudal part of tilapia was either isometric or lower than body length. Allometry coefficient for body heights and head traits was higher in male than in female. The opposite was found for allometry coefficient for body length. Thus differential growth between male and female is associated with differential development of different part of fish. Whole body growth results in tilapia as in other fish species of growth of different tissues and mainly of skeletal muscle tissues. Post natal growth of fish muscle is very original as both increase in the number of fiber (hyperplasia) and increase in the size of fiber (hypertrophy) contribute to increase in muscle mass. The hyperplastic process seems to be predominant in juvenile growth. Furthermore, an increase in the rate of growth is associated in most of the cases studied rather with an increase in recruitment of new fibers than with an increase in the size of fibers. Tilapia present some particularities since analysis of this process in this species showed that there were no anatomical separations between peripheral muscle fiber and deep fiber. Analysis of fiber size distribution in white muscle show a relative high frequency of small diameter fiber. This demonstrates indirectly that hyperplastic process contribute to white muscle growth as it is in most of the fish species studied especially in juvenile. Furthermore, this study demonstrated that there were no great differences in the size of white muscle fibers between male and female. However the percentage of small diameter fibers was higher in male than in female and consequently the distribution of fibers size was significantly different between male and female. Such a difference suggested that hyperplastic growth of white muscle was stimulated in male as compared to female. Various factors can influence growth: strain effects, food availability, efficiency of food utilization, and social interactions. Some of the major determinants of the sexual dimorphism growth are reported.

## **1. Introduction**

Some tilapias species have most of the desirable traits of an "ideal candidate" for aquaculture: well suited to domestication, fast growth, mainly "herbivorous" in the broad sense but also flexible and opportunistic in their feeding habits (ability to convert efficiently organic wastes into high quality protein), continuous reproduction throughout the year, high tolerance to a wide range of culture conditions, high disease resistance, important domestic, and natural genetic resources. Due to these favorable traits, various tilapia species native to Africa have been widely transferred throughout the world since 1939 (they were available in over 105 countries in 1979), especially in many Asian and South American countries where they have colonized a wide range of habitats. Therefore, tilapias have become one of the three most important groups of commercial fish species (annual production of 801.000 metric tons in 1996: the most important producers of tilapia are China, the Philippines, Thailand, and Indonesia. Moreover, this group continues to expand faster than the average global expansion in food fish culture both in developing countries (Egypt), in some European countries (Belgium), and in the USA (total US consumption of tilapia: 53.000 metric tons).

With over 70 species, the group of tilapia exhibits a large variety of adaptation responses to match the vast array of existing ecological habitats (either under natural conditions or following introductions): freshwater, lagoon, brackish/marine or even hyper-salty waters, rivers with rapids, alkaline or acid waters, volcanic lakes, open or closed estuaries, geothermal hot waters, and deep or marshy lakes.

These important adaptive potentialities of tilapia could be related to their various reproductive/growth strategies. Some traits of these interactions between reproductive cycle and growth present a great plasticity and can be modulated by many environmental and/or social factors. The main characteristics of tilapia reproduction and growth and the effects of environmental factors

on these traits will be reviewed. Among all the 70 species of tilapias, *O. niloticus* and *O. aureus* contribute to more than 90% of the annual production of the group; hybrids of *Oreochromis* including red tilapia have also been extensively used. Therefore, the present review will mainly focus on these two major species.

## 2. Taxonomy and Parental Behavior

In the order of the Perciforms, more than 1200 species mostly originating from Africa or South/Central America belong to the family of the *Cichlidae*. Among this family, all the 70 Tilapiine species exhibit a high degree of parental care; therefore they have been classified according to three main different genera, mainly on the basis of their parental behavior (see Table 1), but also based on differences in feeding habits and biogeography:

- *Tilapia*: Substrate spawners guarding the eggs into the nest
- *Sarotherodon*: Paternal or bi-parental mouth brooders
- *Oreochromis*: Maternal mouth brooders

Parental behaviour	Species
<i>Tilapia</i> : Substrate spawners	<i>Tilapia zillii</i> <i>T. rendalli</i> <i>T. sparrmanii</i>
<i>Sarotherodon</i> : Paternal or bi-parental mouth brooders	<i>Sarotherodon melanotheron</i> <i>S. galilaeus</i>
<i>Oreochromis</i> : Maternal mouth brooders	<i>Oreochromis niloticus</i> <i>O. aureus</i> <i>O. mossambicus</i> <i>O. spilurus</i> <i>O. hornorum</i> <i>O. macrochir</i>

Table 1. Main tilapia species of the three genera and their parental behaviors.

Over the last decade, identification and characterization of genetic markers that may be used for fisheries/aquaculture purposes (management and/or improvement of strains) or evolution studies (the evolutionary relationships between these three genera is still under debate) have increased dramatically.

## 3. Biology and Physiology of Reproduction in Tilapias

In tilapia, the reproductive efficiency is the result of several biological characteristics:

- A precocious sexual maturity
- A continuous and asynchronous breeding all year round under suitable conditions
- The nest establishment by males and an aggressive territory's protection by both parents
- A sequential oviposition of successive egg batches (about thirty to fifty eggs) immediately followed by the fertilization of each group of ova
- A parental care provided to the eggs immediately after their fertilization in mouth brooding species, this behavior is associated with a migration of the breeding fish to a planted and thus protected area

On the whole, these biological characteristics may rapidly lead towards an excessive recruitment of fry, overcrowding and dwarfism in a confined environment, and in a situation of competition for food. Therefore, a better knowledge of the environmental factors, which are able to affect the reproductive capacity could be of practical use and should improve the profitability of their culture. The present review will briefly report the main characteristics of reproduction, which can be sensitive to environmental and/or social factors, and the influence of such external factors on the reproductive capacity.

### 3.1 Sex Determination and Gonadal Sex Differentiation

The most effective solution to face the problem of uncontrolled reproduction, overcrowding, and dwarfism in tilapia species is the use of monosex populations; as there is an important sexual dimorphism of growth in favor of males in tilapia, male monosex populations are required. Therefore, the mechanisms of sex determination and gonadal sex differentiation in tilapia have attracted considerable interest in this group of species.

#### 3.1.1 Genetic Sex Determination

In tilapias, as in most teleost species, sex chromosomes are not sufficiently divergent to be recognized by microscopic analysis of chromosome preparations; however, indirect approaches (inter-specific and intraspecific mating and backcrosses, progeny testing of hormonally sex-reversed fry, and chromosome set manipulation) demonstrated that sex determination seems to be predominantly determined by a pair of sex chromosomes. This suggests the existence of a major sex-determining gene in the heterogametic sex.

Within the group of tilapias, the heterogametic sex can be the male or the female depending upon the species. As a matter of fact, ZZ/ZW and XX/XY species can be found together within the same genus (Table 2), i.e. females have the homogametic genotype XX and males are heterogametic XY in *O. niloticus* (as in mammals), and conversely, males have the homogametic genotype ZZ and females are heterogametic ZW in *O. aureus* (as in birds).

<b>Determination Female homogamety XX/XY</b>	<b>Male homogamety ZZ/ZW</b>
<i>O. niloticus</i>	<i>O. aureus</i>
<i>O. mossambicus</i>	<i>O. macrochir</i>
	<i>O. hornorum</i>

Table 2. The two monofactorial models of genetic sex determination in tilapia.

However, conversely to some other fish species (i.e. the rainbow trout), the control by a pair of sex chromosomes should be less strict in tilapia, because sex ratios frequently deviate from the predictions of the heterogametic models.

#### 3.1.2 Gonadal Sex Differentiation

As endocrine and environmental aspects of gonadal sex differentiation in fish have been recently reviewed, we will mainly mention the major principles.

In fish, as in all the vertebrates, sex differentiation refers to the development of testes or ovaries from the undifferentiated gonads; the chronology of this process is highly variable from one species to the next, but also within a given species (rearing or natural conditions will influence the growth rate and thus the gonadal ontogenesis). Therefore, the time scale adopted for the kinetics of gonadal development has to be expressed in terms of the age of larvae in days multiplied by degrees post-fertilization (PF) instead of only in days PF (as it appeared in most published studies). Moreover, there is a lack of definitive criteria for the detection of the very first signs of gonadal sex differentiation. Until now, the precocious differentiation of female germ cells (meiotic activity, shortly after active germ cells proliferation) contrasts with the late appearance of similar features in future spermatocytes in most fish species, including tilapia. In *O. niloticus*, these very first signs can be detected after 750° days (28 days post-fertilization at 27°C). However, in tilapia, hormonal sex-inversion treatment to be optimally effective have to begin before 370–400° days (14–15 days post-fertilization at 27°C), otherwise the gonads will be irreversibly involved in a differentiation process according to the genotype. This sensitive period and data concerning steroidogenic potentialities of the gonads during this period strongly suggest that the process of gonadal sex differentiation can be initiated around this period of gonial proliferation.

### **3.1.3 Endocrine Factors**

As in reptiles and birds, steroids seem to play a key role in the process of gonadal sex differentiation in fish. More specifically, estrogens seem to be produced specifically before and during the ovarian differentiation; moreover, inhibition of estrogens production increases the proportion of males.

Conversely, active androgens (11-oxygenated androgens in fish) seem to be specifically produced during the testicular differentiation, and such compounds have a strong masculinizing potency.

Therefore steroids (at least estrogens, in females) are probably key physiological steps in the regulation of the gonadal sex differentiation.

### **3.1.4 Environmental Factors: Temperature Influence**

Generally, sex ratios of tilapia species fit imperfectly with monofactorial models of genetic sex determination based on a strict pair of sex chromosomes. In tilapias, as in most teleosts, sex differentiation can be influenced by some specific exogenous factors: whereas salinity has no significant effect on sex ratio, temperature seems to be the most important environmental determinant of sex in tilapias as in various other fish species.

Low temperatures do not affect the proportion of males in *O. niloticus*, *O. aureus* and in the red tilapia from the Red Florida strain; conversely, in the same species, a functional testicular differentiation can be induced by high temperatures (>32–34°C): high temperatures (34–35°C) can increase the proportion of males, for treatments covering the sensitive period (starting not later than 13 days PF, 351° days, and lasting 10 days or more) at least in some progenies. All-male populations have been produced in the most sensitive progenies of both *Oreochromis* species, whereas in some other progenies, high temperatures in *O. niloticus* do not affect the proportion of males. Therefore, in tilapia, genetic factors and temperature levels, and genotype/temperature interactions determine sex.

### **3.1.5 Genotype/Temperature Interactions**

In *O. niloticus*, sensitivity of a progeny to temperature treatment strongly depends upon the breeding pairs: a given female can successively produce highly sensitive (up to 100% male

population at 35°C) and non sensitive (absence of any significant deviation of sex ratio at high temperature) progenies when mated with two different male breeders (and *vice versa*); conversely, successive progenies produced by a same pair of breeders will present a similar sensitivity to high temperature treatments. In *O. aureus*, all male or almost monosex male populations are obtained in high temperature-treated groups.

### 3.2 Spawning and Reproductive Behavior

The biology of reproduction of many tilapia species in natural waters and under culture conditions is well documented; conversely, the influence of specific environmental factors has received less attention. Therefore, the present review will only briefly mention the major characteristics of tilapia reproduction but rather focus on recent data concerning environmental influences

Age at first maturity can vary to a great extent, depending on the rearing conditions and strains (see Table 3). Generally tilapia species reproduce at a smaller size under cultured conditions compared to natural conditions: sexual maturation is delayed in stable habitats such as large lakes and dams, and conversely precocious maturation are reported in unstable environments (smaller water bodies: shallow lagoons, flood plains, and ponds). As an example, in *O. niloticus*, the size at first maturation is reported to be 30–50 g. in cultured conditions *versus* 150–250 g. under natural conditions.

Locality/strain	Maturation size (mm)	
L. Turkana	390	
L. George (1960)	280	
L. George (1960)	245	
L. George (1972)	200	
Egypt	200	
L. Edward	170	
L. Albert, lagoon	100	
		Maturation Age (months)
Average in the wild		24
Tanks	105	3
Aquarium	90	3–4
Lagoons, ponds	60	
Average in culture conditions	100–170	4–6

Table 3. Size/Age of *O. niloticus* at sexual maturity under various conditions.

#### 3.2.1 Annual Cycle of Reproductive Activity in *Oreochromis spp.* under Natural Conditions

Most tilapia species need a minimal temperature of 20–22°C in order to breed. Under tropical conditions, where such temperatures are not a limiting factor, a continuous reproduction is generally

described within a tilapia population; however, seasonal variations in the intensity of reproductive activity related to seasonal changes (rainy season) have been reported. In the wild, when temperatures reach 19–20°C, males belonging to *Oreochromis* species, move into shallow water, delimit and protect aggressively a territory where they establish a nest. Mature females move into these spawning areas and visit one or several nests after a brief courtship. Successive egg batches (about thirty to fifty eggs or more) are laid through a sequential oviposition either in the same nest or in neighboring nests (successive polygyny and/or polyandry in *Oreochromis* species versus monogamy in *Sarotherodon* species); the male and eggs collected into the female mouth immediately fertilize each group of ova in the nest. The female before their fertilization can collect some of these batches; as the female at the male urino-genital papilla can directly collect sperm, a possible fertilization of these ova into the mouth of the females is still under debate. Following the fertilization and collect of the last egg batch, females retreat for fry brooding first into sheltered water and second into shallow terrace waters or flooded eulittoral grassland when the fry reached 9–10 mm. After release by the incubating female, fry form large shoals and occupy shallow water during the day, and deeper water at night.

Conversely, under specific conditions (sub-tropical and temperate regions) where temperatures and/or photoperiod present more important variations, well-defined breeding season(s) are reported for most tilapia species. Peaks of reproductive activity are associated with increasing photoperiods and warmest temperatures; conversely, low spawning rates are described during the decrease in temperature and photoperiod, emphasizing the importance of external factors on these tropical species.

### 3.2.2 Egg Size

Egg size is species specific, and within each species, it is unclear as to whether maternal characteristics such as age, size and weight are the major factors influencing egg size. But egg size is also related to the parental care: the evolution of parental behavior has led to an increase in egg size and to a parallel decrease in number of eggs per progeny. The mean egg wet weight is respectively 0.51 mg (mini/maxi: 0.42/0.59 mg) in *T. zillii*, 7.3 mg (mini/maxi: 5/9.5 mg) in *O. niloticus* and 19.4 mg (mini/maxi: 12.5/25 mg) in *S. melanotheron*, (author unpublished data); the mean egg size (ellipsoid or ovoid in shape) is respectively 1.65–2.6 (minor axis) × 2.0–3.15 mm (major axis) in *O. niloticus*, and 1.53–1.56 × 1.1–1.12 mm in *T. zillii*. Egg size can also be influenced by some external factors such as feeding conditions.

## 3.3 Influence of External and Social Factors on the Reproductive Efficiency

In the wild, the two major environmental factors for tilapia spawning are certainly temperature and rainfalls or flooding. However, many other environmental and/or social factors can also influence some reproductive characteristics of tilapia and then their reproductive efficiency: stocking density, sex ratios, food quality and quantity, water quality (salinity, pH, and oxygen), stress, and pollutants. At last, some other factors, such as the nycthemeral periodicity, the environmental complexity (breeding sites), the parental care or the social interactions, are still weakly documented.

### 3.3.1 Influence of Water Temperature, Seasonal Photoperiodicity, and Light Intensity

Under tropical or sub-tropical climates, seasonal differences concern mainly temperature regime and rainfalls; conversely, the photoperiod regime remains relatively constant during all the year. However, in limpid water, the lunar cycle can also influence the reproductive activity in *O. niloticus*:

in Lake Victoria, highest proportions of mature females are rather related to full moon than to new moon; moreover, a lunar periodicity of reproductive activity has been reported for *T. mariae* in the Ethiop River. In both studies, the moonlight could have enhanced the effectiveness of parental behavior. Similarly, the influence of sunlight has been already reported in wild populations. As tilapias have been transferred in many countries they can face various photoperiod regimes including seasonal photoperiods; for example, tilapias are produced in warm water from a nuclear power plant in some EC countries, such as Belgium, under a seasonal photoperiod (see Figure 1).

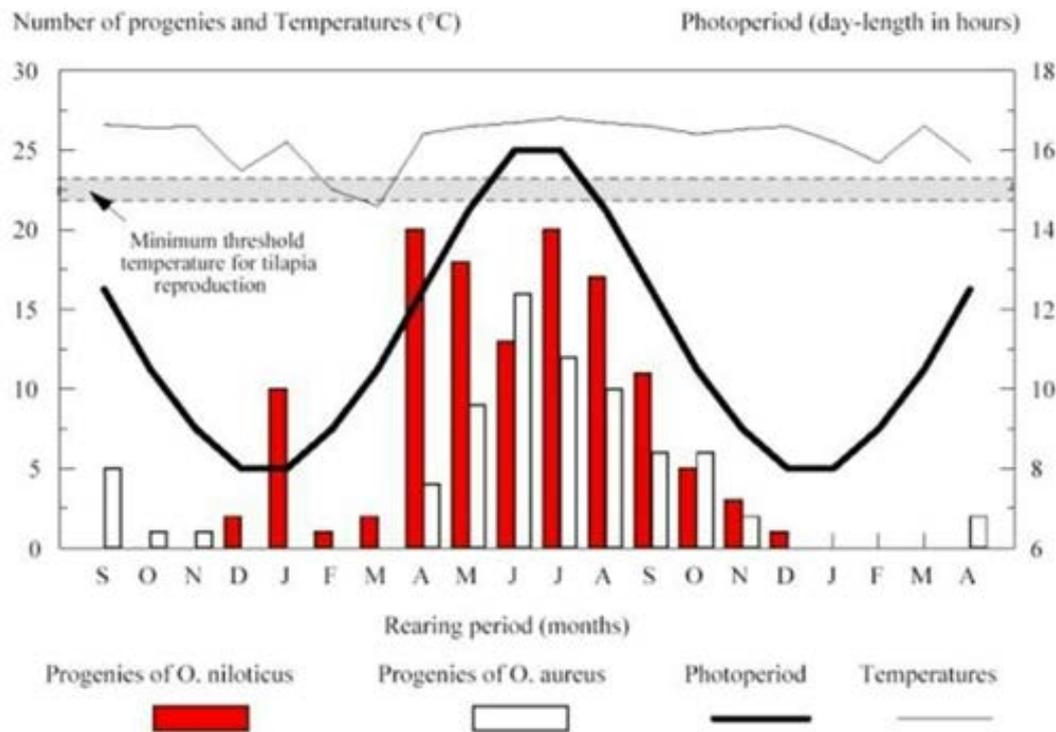


Figure 1 (redrawn from Baroiller et al., 1997). Evolution of the spawning activity of the two major tilapia species, *Oreochromis niloticus* and *O. aureus*, under natural seasonal temperate photoperiod. Breeders were maintained at a sex ratio of 10 females/3 males in a 4m<sup>2</sup>/1.6m<sup>3</sup> tank supplied with water from a nuclear power plant. Fry were collected every week from the mouth brooding females during respectively 13 (December–December) and 20 months (September–September) for *O. niloticus* and *O. aureus*.

Under favorable water temperatures (>22–24°C), the profiles of spawning activities are clearly related to those of photoperiod regimes for both tilapia species: spawning activity is stimulated by long (>12L) and increasing photoperiods (a peak of activity is associated with the highest values in temperature and photoperiod), and conversely, inhibited by short and decreasing length-day. However, even under favorable temperatures, a resting period is observed for *O. aureus*, under short photoperiods (8L: 16D), whereas a few progenies are still obtained from *O. niloticus* breeders. Moreover, during this period of weak spawning activity, *O. niloticus* breeders are still sensitive to temperature variations: increasing temperatures stimulate the reproduction rates (January) whereas decreasing temperatures inhibit the production of progenies (February–March).

In a similar way, the seed production in *O. spilurus*, is more than two times higher under a 14L: 10D regime than under 13L: 13D photoperiod: this could be related to a higher mean spawning rate (suggesting a possible influence on female-female interactions) at a light duration of 14h/day, but also a slight increase in fecundity.

Thus, photoperiod and temperature can strongly influence the reproduction of tilapia through synergic effects.

### 3.3.2 Influence of Nycthemeral Periodicity

In many species, spawning occurs during a specific period of the day: under favorable conditions, diurnal changes in the male and/or female spawning behavior suggest a nycthemeral periodicity for reproduction. In the wild (*Oreochromis karomo*) just as well under laboratory conditions (*O. mossambicus*, *O. aureus*, *O. niloticus*) evidences of a diurnal reproductive cyclicality are scarce in tilapia.

In aquarium conditions, at constant favorable photoperiod (12L: 12D) and temperature (27°C) regimes, *O. niloticus* breeders spawned almost exclusively (almost 99% of the reproductions) during the afternoon of the light period, ranging from 1 to 7.30 P.M (see Figure 2). More than 84% of the reproductive activity (82 spawnings have been considered) is observed during a narrow window (2–5 P.M.), and peaked out around 3 P.M. (35%). Only one reproduction (1%) was observed in the morning.

Figure 2 (from Baroiller *et al.*, 1997). Nycthemeral periodicity of spawning activity in *Oreochromis niloticus*. One male and 3-4 females were maintained in each 260–300 l-aquarium at 27°C. Mature breeders were selected based on their breeding condition, i.e. the protuberance of the genital papilla for females, the coloration pattern for males. This experiment was conducted during one year. The breeding time was determined to the nearest quarter of an hour.

In *O. aureus*, a similar periodicity is reported under 14L: 10D photoperiod regime (light on at 8 A.M.): almost 98% of the reproductions also occurred during the afternoon of the light period, ranging from 1 to 7 P.M. A phase shifting of the light cycle resulted in a corresponding shift in the period of spawning. Therefore such periodicity is clearly related to light.

In a very close species, *O. mossambicus*, the expression of specific male-reproductive behavioral sequences (aggressiveness and territoriality) reached a climax during a very similar portion of the day (middle of the afternoon) in large laboratory tanks. As a very similar pattern of nycthemeral periodicity is still reported in all-male populations, the presence of females is not a limiting factor. A diurnal rhythm of endocrine secretions could be one of the physiological bases for such cyclicality.

### 3.3.3 Influence of Salinity

*O. mossambicus* and *S. melanotheron* could breed in seawater, and even at higher salinities (*O. mossambicus*: 49 ‰, *T. zillii*: 43‰). However, in most tilapia species tolerant to salinity, reproduction activity and fecundity are considerably reduced in medium to high salinity (>20‰) or even suppressed (sea water). In *O. spilurus*, fecundity in brackish water (3–4‰) is twice higher than in seawater (38–41‰). Some few reproductions are reported to occur in *O. aureus* and *O. niloticus* at respective maximum salinities of 19 and 32 ‰. In this latter species, most of the female breeders are gravid in 30–35‰ saline waters, but very few or even no spawning occurs; however, the precise effect of salinity inducing such inhibition remains unknown. This could be at least partially related to an extremely poor hatching success of eggs produced in sea water, or to a low fertilization rate; however, other factors such as an inhibition of some male or/and female reproductive behavior sequences cannot be excluded.

### 3.3.4 Environmental Complexity

In the wild, breeding sites are generally considered as limiting factors for tilapia reproduction; moreover, cannibalism by fingerlings or even by older recruits and/or breeders have been described in tilapias under both natural and culture conditions. Therefore, modifications of environmental complexity should improve both spawning rates and seed survival. The addition of artificial shelters (for each of them, three breeze-blocks were disposed perpendicularly) in a raceway (RW1) indeed induced a consistent enhancement of seed production in *O. niloticus* (see Figure 3).

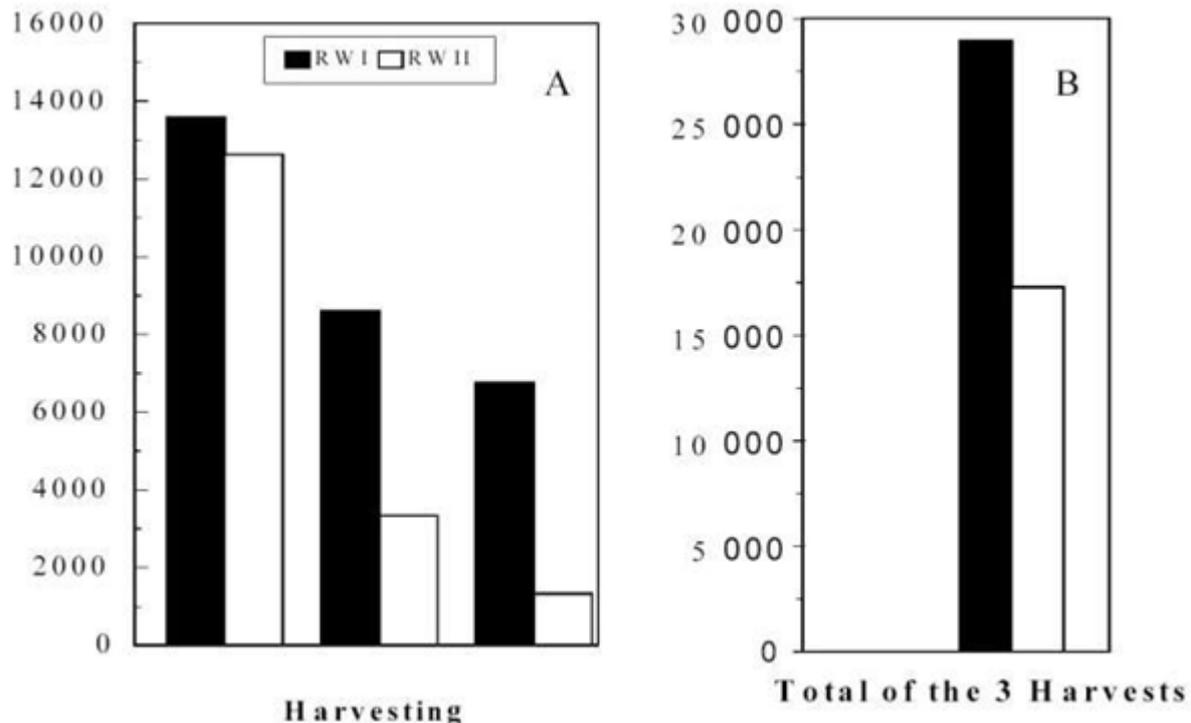


Figure 3 (from Baroiller *et al.*, 1997). Influence of environmental complexity (presence of artificial shelters in a race-way) on fry production in *O. niloticus*: 15 male and 45 female breeders was maintained in two 12 m<sup>2</sup> race-way, in presence (RW1) or absence (RW2) of five artificial shelters (three breeze-blocks were disposed perpendicularly to form an artificial shelter). Every 14 days, eggs and fry were collected from the mouth of each female and counted; the same breeders were replaced in the same raceway after each harvest. A total of three successive harvests were made during the experiment.

Very similar fry productions are obtained in both raceways at the first harvest: 13600 seeds (21.6 seed/female/day) in the presence of 5 artificial shelters versus 12615 seeds (20 seed/female/day) in the control RW2 raceway. Since the second harvest, seed outputs declined either drastically (89.4%) in the control (12615® 3341® 1333), or more slightly (50.4%) in the presence of shelters (13600® 8606® 6750). At final harvest, the mean fry productions in RW1 and RW2 were respectively 10.7 and 2.1 seed/female/day. Cumulated seed outputs resulting from 3 successive harvests in RW1 is 1.7 times higher than in RW2: the total seed production was 28956 in RW1 (15.3 seed/female/day) and 17289 in RW2 (9.1 seed/female/day).

Dominant females could be mainly involved in the first yield fry production. Due to the 14 days interval between successive harvests, the second seed production (at least) should mainly result from the subordinated females. Thus, artificial shelters could have allowed the spawnings of subordinated females by stimulating and masking them from the non-incubating dominating females. Therefore, both reproductive spawning rates and fry survival could be enhanced by this modification of environmental complexity: the presence of artificial shelters could probably

stimulate the nesting behavior and then an enhancement of the reproductive activity of dominant breeders, but also allow the access to reproduction for subordinated males and females and at last could decrease the cannibalism of the young progenies by older recruits/breeders, or/and predation.

Therefore, environmental complexity could be of major importance on reproductive efficiency in tilapia.

### 3.3.5 Influence of Parental Behavior: Interactions between Breeding Cycles and Parental Care

The major influence of social and behavioral factors on reproduction has been already reviewed in tilapia. Parental care is provided since the fertilization time and lasts until the total resorption of the yolk vesicle in *Sarotherodon* sp. or more in *Oreochromis* sp. In *Oreochromis niloticus*, as well as in all the other *Oreochromis* species, three successive behavioral sequences have to be associated with the reproductive cycle (see Table 4): the incubation of eggs and larvae, the guarding period and the definitive fry release.

<b>Strict incubation</b>	<b>Guarding</b>	<b>Definitive release</b>
Eggs are collected just after fertilization (PF) and incubated until $\frac{3}{4}$ of the yolk vesicle resorption. Hatching occurred around 3–4 days PF	First release of the fry, becoming increasingly independent of the female during the day, but taking refuge into the mouth in times of danger and every night)	Females definitively reject the attempts of the fry to enter her mouth. Cannibalism can often occur by the mother.
10–16 days PF	16–23 days PF	20–25 days PF

Table 4. Behavioral sequences associated with breeding cycle in *O. niloticus*, and its duration (min–max in days post-fertilization). (From Tacon et al., 1996)

However, some incubating females can naturally (unfertilized eggs, or/and cannibalism) or experimentally (suppression) loose their eggs. Ovarian development and especially vitellogenesis and the inter-spawning period can be delayed by a typical maternal mouth brooding behavior or conversely, stimulated by eggs/fry suppression. The twelve-days difference between typical cycles (associated with a complete mouth brooding behavior) and those of non-incubating females approximately has to be related to the twelve-days period of strict incubation, which has been artificially or naturally suppressed in the latter group (see Table 5).

<b>Females</b>	<b>Incubating</b>	<b>Non-incubating</b>
Mean inter-spawning period:	26.7	14.6
Min–max	25–33	12–18

Table 5. Inter-spawning period in *O. niloticus* incubating/non-incubating females (from Tacon et al., 1996)

By modulating the duration of their mouth brooding behavior, females can thus influence the duration of their inter-spawning periods. In the extreme, female breeders in *T. mariae* could eat a seed when the eggs' number became too low, in order to prepare a more numerous progeny; this is associated with a shorter inter-spawning period.

Such interactions between maternal behavior and ovarian cycle in tilapia are already used to favor a spawning synchrony in tilapia.

### 3.3.6 Influence of Social Interactions

The major influence of various social and behavioral factors on reproduction has been already reported in tilapias. However, very few studies have analyzed the relative involvement of individual breeders in the fry production within a spawning group, or a population.

In *O. niloticus*, *O. aureus* and the red tilapia, the reproductive activity of individually tagged male and female breeders has been investigated during long-term periods (8–12 months) in tanks or raceways.

*Oreochromis niloticus* (15 males/45 females) and red tilapia (18 males/54 females) breeders were maintained in 12 m<sup>2</sup> raceways under a natural photoperiod (about 12 h. light: 12 h. dark = 12L: 12D) and ambient temperatures (24-29°C) with circulating fresh water. The fish were fed twice daily with tilapia food at a 1% rate of their body weight. At 10 (red tilapia) or 14 days (*O. niloticus*) intervals, eggs and fry were removed from the mouth of each breeder and counted; the same breeders were replaced in the same raceway after each harvest. A total of three (*Oreochromis niloticus*), or thirty- (red tilapia) harvests were made during the experiment.

In the red tilapia (see Figure 4) and *O. niloticus* (see Figure 5), the reproductive activity of individually tagged male and female breeders has been investigated during long term periods (8–11 months) respectively in tanks or race-ways. 47 and 371 progenies have been respectively recorded for *O. niloticus* (0.6 progenies/female/month) and the red tilapia (0.7 progenies/female/month). This corresponded to a yield fry production of 13.6 and 6.6 fry/female/day (48.6 and 22 fry/kg of female/day) respectively for the red tilapia and *O. niloticus*.

The red tilapia was reared under natural photoperiod and temperatures. In this species, three major patterns of spawning activity could be determined: during the three first months (phase 1, Figure 4), yield fry production gradually increased to reach a peak associated with a synchronization of female reproduction (60% of the females). In a second phase (phase 2, Figure 4), spawning activities consists of successive high (40–50% of the females) and low (20% of the females) yield fry production. During the third phase (phase 3, Figure 4), a very constant basal activity concerned only 10% of the females. This basal activity was associated with favorable temperatures (>24°C) and day length (>11L: 13D) at least during 50 days (harvests 22 to 26).

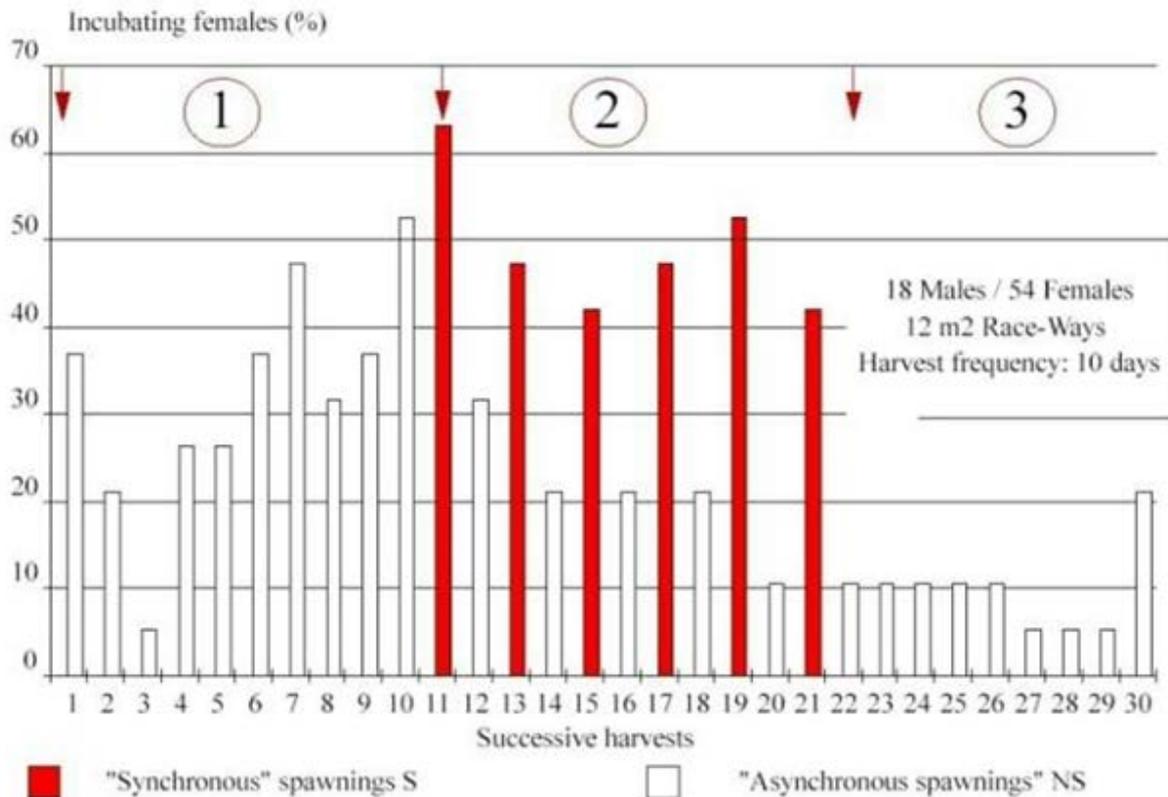


Figure 4 (from Baroiller *et al.*, 1997). Evolution of the proportion of red tilapia (Red Florida strain) incubating females during successive harvests. Breeders (18 males/54 females) were maintained in 12m2 raceways under natural temperature and photoperiod

Besides, *O. niloticus* reared under constant temperature and photoperiod, presented 2 phases (see Figure 5): in the first one (7 first harvests), successive increases (10 to 50%) in the proportion of incubating females alternated with successive absence of reproduction. As for the red tilapia, the second phase (harvests 8 to 25) consisted of successive spawning peaks involving 2–3 females separated by a basal reproductive activity of only one female. Individual number of spawning ranged between 1 and 8 for *O. niloticus* (8 months) and 0–14 for the red tilapia (10 months).

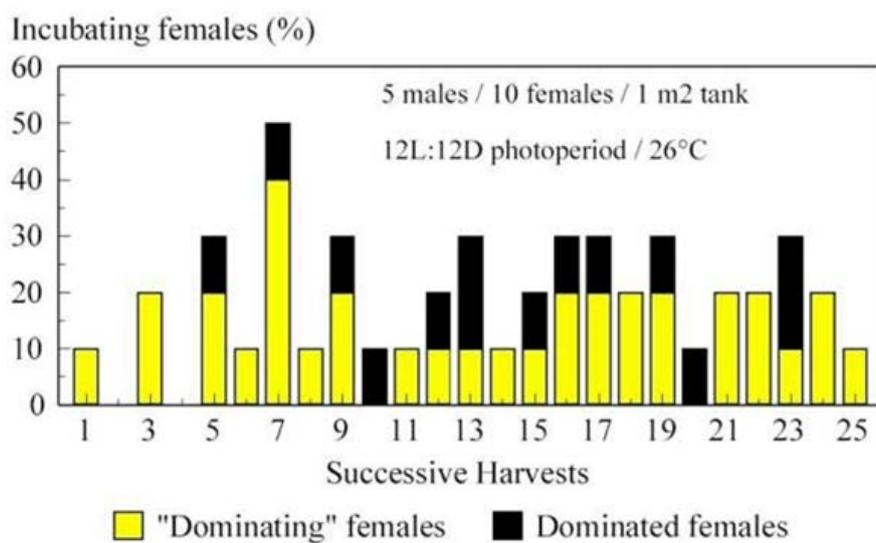


Figure 5. (From Baroiller *et al.*, 1997). Evolution of the proportion of *O. niloticus* incubating females during successive harvests. Breeders were maintained in a thermo-regulated recirculating water (26°C) under a constant 12L: 12D photoperiod.

Due to this huge variability in the individual spawning potential in both species, yield fry production was mainly dependent upon some breeders. In *Oreochromis niloticus*, 3 females produced half of all the progenies, whereas 3/4 of the spawnings concerned the 5 most active females (see Figure 6).

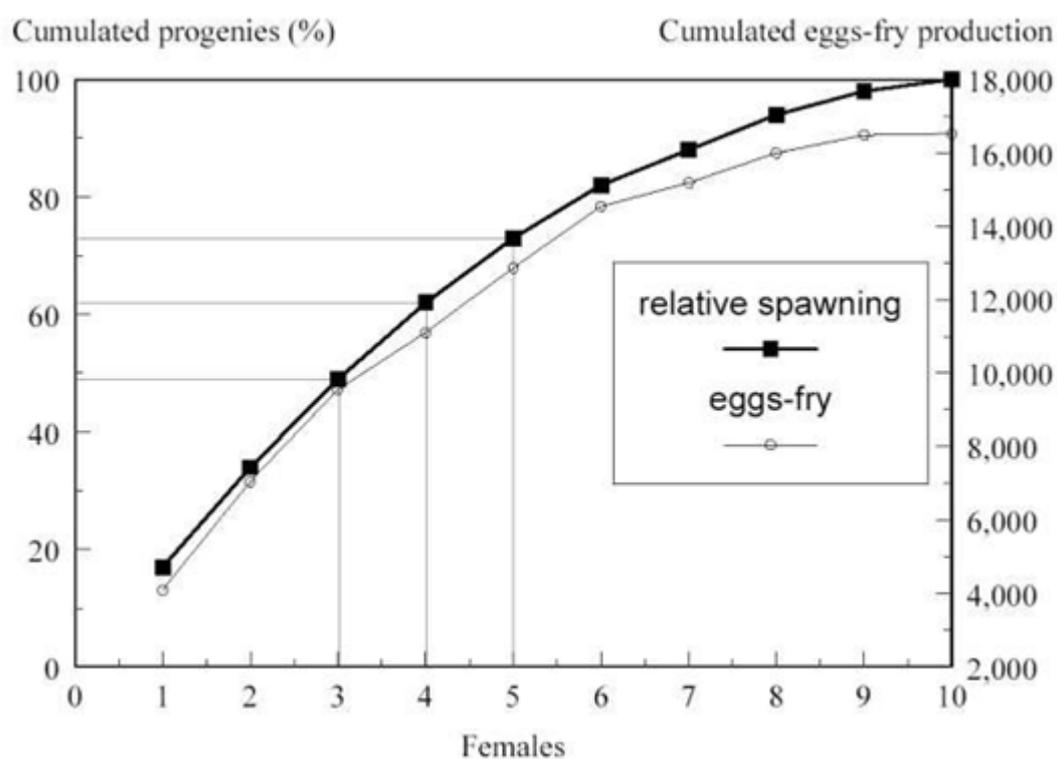


Figure 6. (From Baroiller *et al.*, 1997). Individual involvement of the *O. niloticus* females in the spawning activity.

Moreover, within these active breeders, the average number of eggs-fry produced per spawning was higher (370 seed/progeny) than that of the 5 other females (237 seed/progeny). This was not related to the respective mean body weight of these breeders (295 g. for the active females versus 304 g. for the other).

Very similar results were observed with the red tilapia: during the most productive phase (phase 2, Figure 4), 7 females (out of 19 tagged females) produced 36 progenies (out of 56). Here again, the number of eggs-fry produced by these active females (860) was higher than that of the other females (622). Similar data (not shown) were recorded with *O. aureus*.

45 and 36 seeds have been respectively recorded for *O. niloticus* (8 months; 5.6 seeds/month) and *O. aureus* (12 months; 3 seeds/month). Individual number of spawning ranged between 1 and 8 for *O. niloticus* and 0–12 for *O. aureus*

All the females have spawned in *O. niloticus* whereas only 70% of the females bred for *O. aureus*. When seed were removed from incubating females at a 10 day interval, few males and females were involved in the overall fry production; apparently, the other females only took part into spawning activity during the inter spawning period of the most active breeders.

Individual potential of females in a spawning group is mainly characterized by the huge variability of their reproductive characteristics.

All the females have spawned at least one time in *O. niloticus*; a similar situation is observed for the red-tilapia as only one female did not produce any progeny. Under different rearing conditions (constant/natural temperatures and photoperiod), 8 to 14 successive spawnings have been respectively obtained from some *O. niloticus* (8-months study) and red tilapia (10-months study) females.

Huge variability was observed within the females of a same spawning group in both spawning frequency (inter-spawning period) and fertility. Even if all the females have spawned in the group, most of the progenies and the fry were produced by only few of them.

In *O. niloticus* spawning groups, a hierarchy is established with some dominant females spawning more than the others. In these two studies, although an optimal temperature was maintained throughout the experiment, individual females have never spawned more than six or seven times in a year, with very heterogeneous inter-spawning periods. Populations of tilapias breeders could contain dominant females characterized by their relatively higher spawning activity. Frequent and complete harvests of seed from the mouth of the incubating females reduced the inter-spawning period, due to the relationship between maternal behavior and reproductive cycle. The establishment of hierarchies in stable breeder group, which inhibits reproduction, has been also described for *O. mossambicus*; harvesting stress could be able to disrupt this hierarchy. However, in *O. niloticus*, or in the red tilapia seed production was mainly dependent upon the dominant females even after 25 to 30 successive harvests. Thus removal of seed improves output mainly by stimulating vitellogenesis more than by allowing subordinated fish to breed.

### **3.3.7 Influence of Nutrition**

In *O. mossambicus*, the number of eggs produced per spawning is reduced by a restricted food supply; conversely, the spawning frequency increased under similar feeding conditions. In *O. niloticus*, fish fed high protein levels (32 and 40%) reached puberty earlier with oocytes growing and maturing faster than individuals fed lower levels (25%). Females fed 20 and 35% protein diets produced higher number of eggs per spawning than those fed 10%; relative fecundity and egg size did not differ between the two feeding regimes.

The feeding level influences fish size at first maturity: mean proportion of mature individuals decreases with decreasing food supply.

## **4. Growth Characteristics of Tilapias**

### **4.1 Analyses of Somatic Growth Components**

#### **4.1.1 Growth Allometry of Different Body Trait**

External morphology analysis in tilapia has been oriented to the sex age. It revealed a dimorphism in urino-genital papilla (2 slits in female and one in male), pelvic fins (reaching or passing the anus in male and not in female), anal, and dorsal fins (rounded in female and pointed in male), and mouth. Recently a study has realized a more systematic analysis of the external conformation of male and female, and has searched parameters, which better discriminated the two sexes in connection with growth difference linked to the sex.

External landmarks (fin basis, head profile) were measured on numeric image of fish and morphology was studied either by analysis of whole set of landmarks coordinate according to

Bookstein and Rohlf analysis or by analysis of morphology traits calculated as distances between landmarks or area enclosed by landmarks. The results of the first analysis showed that external morphology was relatively homogeneous within a group of fish once size effect has been corrected (see Figure 7) and the main variability was observed for ventral profile. External morphology of male and female were also very similar, except for the relative size of the head and relative heights measured along the vertebral axis, which were respectively lower in female than in male.

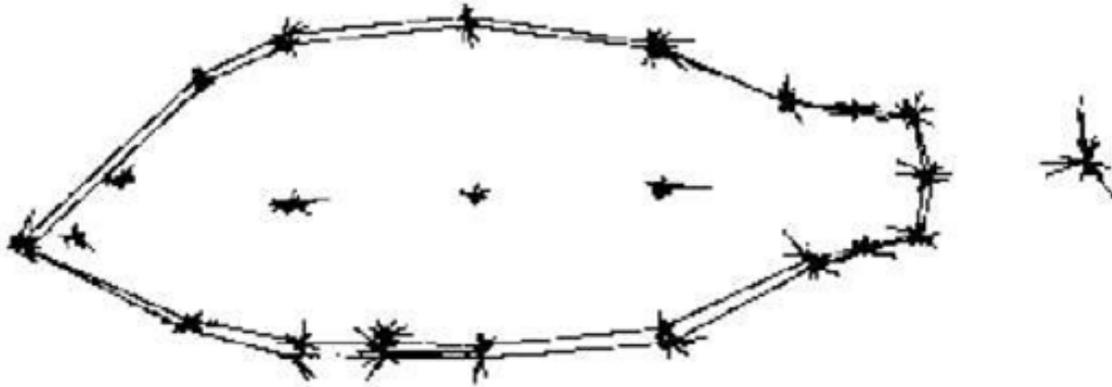


Figure 7. (From Fauconneau *et al.*, 1997). Morphology of tilapia (*Oreochromis niloticus*) analyzed from a set of landmarks measured of fish. The line inside represents females and line outside males. The morphology differences between individuals at one point are drawn as a vector line.

Allometry relationship between morphometric traits and standard length of fish are given in Table 6. There was a relative growth in height associated with a relative development of dorsal muscle but also of visceral area at the stages studied (40–60g). The growth of the caudal part of tilapia was either isometric or lower than body length. Allometry coefficient for body heights and head traits was higher in male than in female. The opposite was found for allometry coefficient for body length. Thus differential growth between male and female is associated with differential development of different part of fish.

Standardized morphometric traits calculated with specific male and female allometry coefficient did not show any difference in head traits (see Table 6) except for head height, which was higher in male than in female. Otherwise, founded a difference in mouth traits particularly concerning the mouth length. The length of the posterior part of fish (starting from first dorsal fin radius) was different between male and female and also the height of caudal peduncle, which was higher in male than in female however such difference was not significant ( $P > 0.05$ ). It has been observed in another study that the length and the width of the caudal peduncle were different between male and female, and this could be related to difference in activity, and locomotion of male and female. Finally the standardized height of male was higher than those of female especially in the anterior part of the fish between the head and the middle of dorsal fin. These differences resulted more of a higher height in male of the ventral part of the fish (viscera) than of the dorsal (muscle) part.

ALLOMETRY COEFFICIENT						STANDARDIZED TRAITS		
		Total	Male	Female	Sign.	Male	Female	Sign.
<b>WEIGHT (g)</b>	Body weight	3.10	3.61	2.39	*	51.1	46.3	*
<b>AREA (cm<sup>2</sup>)</b>	Head	2.08	2.45	1.86	**	5.5	5.3	
	Muscle	2.06	2.27	2.00	*	19.4	19.3	**
	Viscera	2.49	2.33	2.21		11.3	10.4	
<b>HEIGHT (cm)</b>	Head	1.10	1.12	0.99	*	3.3	3.2	*
	Maximum height	1.21	1.28	1.02	**	4.4	4.3	**
	Caudal peduncle	0.94	1.00	0.91		1.9	1.8	
<b>LENGTH (cm)</b>	Head	1.02	1.32	0.90	**	3.4	3.4	
	Anterior length	1.00	0.54	1.20	**	2.4	2.3	*
	Posterior length	0.82	0.73	0.89	*	5.7	5.6	

Table 6. Allometry coefficient with body standard length of different morphometric traits and standardized morphometrics traits at a mean length of 13.5 cm in male and female tilapia *Oreochromis niloticus* (Bouaké strain) (From Fauconneau *et al.*, 1997). Sign.: ANOVA analysis for allometry coefficient and Student t-test for standardized traits: \*: P < 0.05, \*\*: P < 0.01

#### 4.1.2 Characteristics of Muscle Growth

Whole body growth results in tilapia as in other fish species of growth of different tissues and mainly of skeletal muscle tissues. Growth of muscle has been characterized in most of farmed fish species but never in tilapia except for few studies on red muscle ultra-structure.

Post natal growth of fish muscle is very original as both increase in the number of fiber (hyperplasia) and increase in the size of fiber (hypertrophy) contribute to increase in muscle mass. The hyperplastic process seems to be predominant in juvenile growth. Furthermore, an increase in the rate of growth is associated in most of the cases studied rather with an increase in recruitment of new fibers than with an increase in the size of fibers. Tilapia present some particularities since analysis of this process in this species showed that there were no anatomical separations between peripheral muscle fiber and deep fiber. Such a characteristic has never been described in a teleost fish except in flat fish. It could be related to the locomotion of tilapia. The specificity of peripheral fibers (red muscle) and deep fibers (white muscle) has thus to be confirmed by analysis of metabolic and contractile characteristics of fibers by histochemical and histoimmunological methods. Ultra-structural analysis of these fibers and analysis of contractile protein have however demonstrated that these fibers correspond to slow oxidative and fast-twitch glycolytic fibers respectively. However, as in the others fish species, it was observed differences in mean size of fibers between superficial fibers and deep fibers and this were in concordance with such a classification.

Analysis of fiber size distribution in white muscle show a relative high frequency of small diameter fiber. This demonstrate indirectly that hyperplastic process contribute to white muscle growth as it is in most of the fish species studied especially in juvenile. Furthermore, these studies demonstrated that there were no great differences in the size of white muscle fibers between male and female. However the percentage of small diameter fibers was higher in male than in female and

consequently the distribution of fibers size was significantly different between male and female. Such a difference suggested that hyperplastic growth of white muscle was stimulated in male as compared to female.

## 4.2 Factors Influencing Growth

It is well known that all tilapia species did not grow at the same rate. However, the majority of growth comparisons has been based on observations from the wild populations and is often restricted to measurement of maximum size rather than the growth rate. Analyzing specific growth rate of six tilapia species (*Oreochromis niloticus*, *O. aureus*, *O. mossambicus*, *O. macrochir*, *O. spilurus* and *Sarotherodon galilaeus*), the best rate was observed in *Oreochromis niloticus* and the lowest in *O. aureus*. If it is well documented that *O. niloticus* has the best growth, the result concerning *O. aureus* is surprising as many others studies show that its performance is usually comparable to those of *O. niloticus* under a range of conditions. *O. niloticus* and *O. aureus* grew more rapidly than *O. mossambicus* and *O. macrochir*. Comparing the growth performances of *Oreochromis niloticus* and *Sarotherodon melanotheron* (starting with equivalent initial age and size, 9 g), *O. niloticus* achieved the best growth (mean body weight after 74 rearing days of 75 g and 52 g for males and females respectively) and *S. melanotheron* the lowest (24 g and 25 g for males and females respectively).

Otherwise, a strain effect was also demonstrated in many tilapia species. These differences were not only environmental factors effects since under the same rearing conditions they remained. Thus, comparing the growth performances of 8 strains of *Oreochromis niloticus* (Egypt, Ghana, Senegal, Kenya, Israel, Singapore, Thailand, and Taiwan) found high significant differences among them. In *Sarotherodon melanotheron*, comparing growth performances of 3 strains (from Senegal, Ebrié lagoon in Ivory Coast, and Lower Kouilou in Congo) Populations from Senegal were characterized by higher growth than the other two populations.

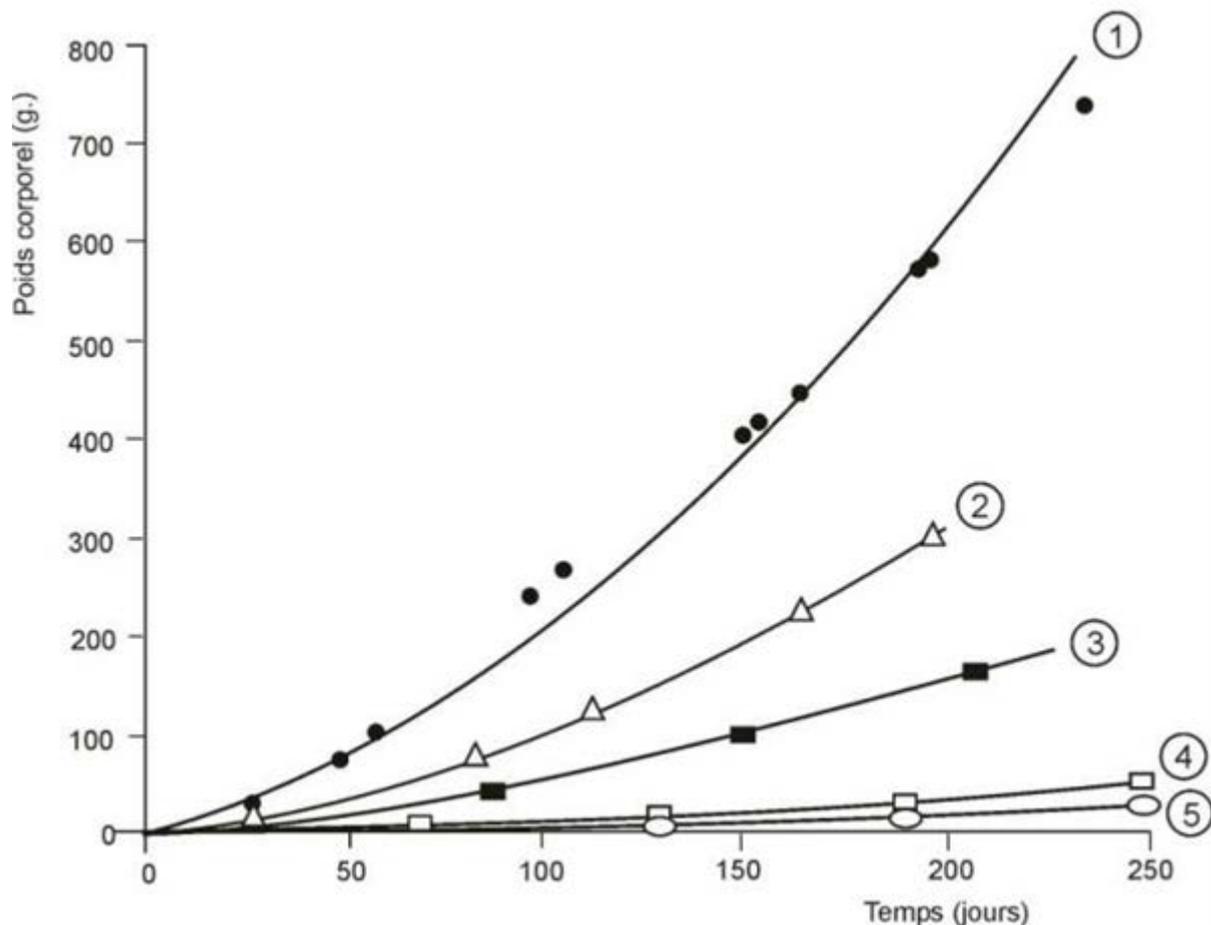
The nature of factors implied in the growth in general and the differential growth linked to the sex particularly can vary according to feeding conditions (quality and quantity) and territory competition or social hierarchy.

### 4.2.1 Food Availability

In natural habitat, the growth of fish is influenced by such behavioral interaction and environmental factors as temperature, food availability, salinity, and pH, etc Then, it is not uncommon to find natural tilapia population with widely varying growth pattern. This is generally due to differences in food availability, which result from overcrowding. In experimental ponds and small natural bodies water, stunting is very readily observed. In lake Tchad, an average weight of 18 g. is observed in the natural population (few amount of food) at 7 month of age while at the same age, an average weight of 650 g. were obtained in pond with a weak density and an abundant artificial and natural feed (see Figure 8). Stunting of tilapia in natural environments is an adaptation to high mortality rates associated with extreme environmental conditions. The effects of environment and sex on the growth of 8 *Oreochromis niloticus* strains in 11 environmental conditions (extremely poor to normal and representative farming conditions) accounted for 73% at 22% of the growth variation respectively.

Efficiency of food utilization is high in farmed fish as a result of optimum supply of food corresponding in quality, quantity and timing to metabolic requirements. Such optimums have been reached thanks to nutritional studies, and also by testing various feeding schedules and studying feeding behavior. Indeed, feeding schedules and especially number of meals and times of feeding per day have a significant positive effect on growth of *Oreochromis niloticus*. Otherwise, the effect

of increasing feeding rates have been tested in different experimental facilities and show that high feeding rate (above ad libitum) resulted in reduce growth individual variation. In *O. niloticus* feeding activity was almost exclusively diurnal and peak activity were observed at dawn and at twilight, probably related either to a disappearance of social hierarchy (morning) or to a compensatory feeding activity after daily social interactions (evening). In this experiment, food intake pattern was similar whatever the sex ratio (monosex male or female, mixed sex) and voluntary feed intake seemed to be lower in the monosex male group than in other groups. Furthermore, monosex males groups present the lowest food conversion ratio. This difference could be probably explained by anabolic effect of androgens, which is well documented in tilapia. Figure 8. Growth of *Oreochromis niloticus* in different environmental conditions (in M elard, 1986). 1:



Natural conditions in Soudan; 2: Natural conditions in Lake Tchad; 3: 1m<sup>3</sup> floating cage, high density; 4: 4m<sup>3</sup> floating cage, high density; 5: 150m<sup>2</sup> pond, low density.

#### 4.2.2 Social Interactions

Rearing conditions, particularly sex ratio of the population could affect the growth performances of each sex, probably through social interactions. In *Oreochromis niloticus*, the growth of males decrease more or less strongly according to breeding conditions (monosex or mixed sex), but it remains always superior to that of females. In monosex population, the difference between the two sexes remained important. In *Sarotherodon melanotheron*, it was observed an important increase in growth rate of males when they were held in monosex population (0.49g.d<sup>-1</sup>) as compared to rearing in mixed population (0.32g.d<sup>-1</sup>), but the growth of females remained stable (0.41g.d<sup>-1</sup>). When they were held in mixed population, contrarily to *Oreochromis niloticus*, the growth of females is superior to that of males. In *Tilapia guineensis*, the growth of both males and females is not affected by the type of breeding (mixed or monosex), males presenting always the best growth rate (0.41g.d<sup>-1</sup> for males and 0.27g.d<sup>-1</sup> for females). A recent study show that modifying the sex-ratio in rearing

population could modify the intensity of social interaction and enhanced growth rate of males and females.

Social interactions between individual and sexual interaction between the two sexes could modulate individual growth potential and especially differential growth between male and female. Mixing male and female of the same cohort or fish from different cohorts resulted in lowering of growth performances. These results demonstrated the contribution of individual interaction related to social and feeding behavior on the expression of growth potential in tilapia.

Taking into account the influences of food availability in connection with social interactions and metabolic requirement, several cases can be proposed to explain the different growth pattern observed:

- When fish are in a situation of food restriction, available energy, brought by the food, is used in priority to cover needs of maintenance, at the expense of reproduction. This situation is characterized by null growth rate, observed when fish are starved or feed to 1% of their body weight, and by exacerbation of food competitions. Animals maintained in these conditions, express badly whole their genetic growth potential. These individuals were characterized generally by a very particular physiological status. An increase of plasma levels of the growth hormone (GH) linked to a diminution of binding sites receptivity is observed. Low thyroxine (T4) and triiodothyronine (T3) levels are also found. Plasma levels of sexual steroids are relatively weak, and sometimes no difference were observed between the two sexes
- When brought energy increased and allowed to cover needs of maintenance, the weak surplus would be assigned in priority to the reproduction. The food competition remained strong in this situation. Nevertheless, a resumption of the growth, although weak, is observed. Animals (mean body weight of 60g) feed at 2% of their body weight could be in this situation. This resumption of the growth is characterized by very weak of GH levels and very important increase of T3 levels particularly in males. A significant increase of plasma rate of sexual steroids is observed, what reinforces the hypothesis of an important orientation of the energy surplus toward to reproduction more than to growth
- When the food is brought in excess (over 3% of bodyweight), the surplus of energy is assigned to the growth and to the reproduction. High growth is obtained. This situation is characterized by very weak food competitions; nevertheless other types of social interactions are observed, territorial and/or hierarchical behavior. A strong expression of genetic potential of fish placed in these conditions is observed. The differential growth linked to the sex appears far more late that in the two precedent cases, and its expression is very strongly linked to sexual hormones. Animals placed in these conditions would adopt a strategy of late sexual maturation. A strong difference of growth between males and females in these groups are observed

### **4.3 Sexual Dimorphism Growth**

Differential growth between male and female is well known in tilapias. In several tilapia species, growth of male is systematically higher than that of female. However, in some others and in particular conditions, growth of female could be better than that of male. Age or size at which divergence of growth performances between the two sexes occurs has not been unequivocally established. Comparing seven strains of *Oreochromis niloticus* (Egypt, Israel, Ghana, Senegal, Taiwan, Thailand, and Singapore strains), growth curves of males and females are similar, males invariably growing faster than females, but age or size at which male and female growth diverged are different. In their conditions, the sexual dimorphism appears in all their strains between 10 and 20 g. In an investigating project on physiological determinism of sexual growth dimorphism with

"Bouaké" strain, the sex related differential growth appears at 25 g. Another results obtained in floating cages in Niger River revealed that there is no significant difference in growth performances between males and females until 150 g. These differences in the onset of divergences in growth performances could be related to environmental factor.

Although many works have described this sex related differential growth, there are few data on mechanisms involved. The lower growth of female may be due to the fact that they are mouth brooders and did not feed during this period. But, it has been emphasized that this difference in growth is not directly related to reproduction and would be expressed at early stages. It occurs after the onset of gonad ontogenesis and before sexual maturity. Thus, it is the consequence neither of the vitellogenesis nor of the mouth incubation of eggs and fry by females.

As demonstrated previously, this different sex related growth is not due to a greater food intake of males as suggested by previous studies. Besides significant differences in food conversion were found between males and females and this could more explained, but partially, the sexual growth dimorphism. This difference is associated with significant differences in steroid and thyroid hormones plasma levels, which are known for their anabolic effects on growth. The involvement of these anabolic hormones in the apparition and maintenance of different growths between males and females has been analyzed experimentally by modifying directly or indirectly the hormone environment (feeding ration, gonadectomy, hormone supplements or deficiencies. A decrease of males' growth is observed when they are treated with estradiol-17 $\beta$  (an estrogen) while inhibition of this hormone synthesis shows an increased in females growth. On the other hand increase 11-ketotestosterone (an androgen) levels in gonadectomised females (by adrenosterone implant) does not stimulate their growth. The anabolic effect of androgens would be therefore minor, except if there are specific binding sites in males. However, no positive effect is observed in males as compared to gonadectomised individuals. These results suggest a negative regulation of the growth of females by the estradiol-17 $\beta$ . This could reveal another mechanism of differential growth determinism. It could be imagined a diminution of the growth of females linked to an increase of plasma levels of estradiol-17 $\beta$  after sexualisation and at the moment of the sexual maturation onset.

## Glossary

<b>Allometry</b>		:Animal growth mode in which certain organs grow more fast (or more slowly) than the whole body.
<b>Androgens</b>		:Male gonadal sex hormones.
<b>(11-oxygenated) Androgens</b>		:Androgens specifically found in fish.
<b>Asynchronous breeding</b>		:Each female has its own sexual cycle.
<b>Dwarfism</b>		:Under some rearing conditions, individuals of a population will mature and reproduce precociously, and due to overpopulation and competition for food, they will stop growing.
<b>Endocrine</b>		:Production of hormones secreted directly into blood.
<b>Estrogens</b>		:Female gonadal sex hormones.
<b>Fecundity</b>		:Number of mature oocytes in the gonads per body weight unit.
<b>First maturity</b>		:Age, body length or body weight at which individuals become sexually mature.
<b>Food conversion ratio</b>		:This ratio designates the relationship between weight gain and food intake; lower is this ratio, better it is.
<b>Germ cells</b>		:These cells only will differentiate into the gametes (spermatozoa and eggs).
<b>Gonadal Differentiation</b>	<b>Sex</b>	:Development of testes or ovaries from undifferentiated gonads.
<b>Gonadectomised</b>		:Fish in which gonads were removed after a surgical operation.
<b>Gonial cells</b>		:These germ cells will proliferate by mitosis before undergoing meiosis and differentiation.
<b>Guarding period</b>		:During this period, fry can leave the mouth of their incubating parent.
<b>Herbivorous</b>		:Species eating only vegetables.
<b>Heterogametic</b>		:A heterogametic breeder will provide two types of gametes (i.e. a man will provide both X and Y spermatozoa).
<b>Histochemical and histoimmunological methods</b>	<b>and</b>	:Histological techniques to characterize enzymatic systems, proteins using specific precursors or antibodies.
<b>Homogametic</b>		:A homogametic breeder will provide only one type of gametes (i.e. a woman will only provide X oocytes).
<b>Hormonally sex-reversed fry</b>		:In lower vertebrates, exogenous sex hormones can functionally direct the sex differentiation towards testes (androgens) or ovary (estrogens). It is therefore possible to produce individual with a phenotype, which is not in accordance with its sexual genotype (i.e. an XX male).
<b>Isometry</b>		:Organs grow proportionately to the whole body.
<b>Landmarks</b>		:Outstandingly points like beginning of the dorsal fin or the end of caudal fin.
<b>Masculinizing potency</b>		:The capacity of a molecule (i.e. androgens) to masculinize a fry independently of its genotype.
<b>Monogamy</b>		:Reproduction involving only one male and one female.
<b>Monosex populations</b>		:Populations only composed of males (all-male population) or of females (all-female population).
<b>Mouth brooding species</b>		:Species in which fry are protected into the mouth of their male or/and female parent.
<b>Nycthemeral</b>		:A 24-hour cycle.
<b>Oocytes</b>		:These female germ cells will produce ova following meiosis steps.
<b>Oviposition</b>		:Oocytes are first ovulated into the ovarian cavity and then laid in the nest or in the water.

<b>Photoperiod</b>	:Duration and pattern of light/dark periods in 24 hours.
<b>Polyandry</b>	:A same female will reproduce with several males.
<b>Polygyny</b>	:A same male will reproduce with several females.
<b>Recruitment of new fibers</b>	:Synthesis of new fibers.
<b>Red muscle</b>	:Peripheral muscle, which forms a triangular strip in the lateral, line zone.
<b>Red tilapia</b>	:Some tilapias strains have been developed from some rare mutations of their pigmentation exhibiting a red coloration.
<b>Resorption of the yolk vesicle</b>	:In fish, embryos will develop on their own yolk reserves, and therefore first feeding will begin when yolk reserves have been used up. :During this specific period, it is possible to direct the gonadal sex differentiation towards testes or ovary by hormonal or environmental treatment.
<b>Sensitive period</b>	:The mechanisms that direct sex differentiation.
<b>Sex Determination</b>	:Secondary sexual characteristics (coloration, growth, and morphology of fins).
<b>Sexual dimorphism</b>	:Red muscle + white muscle.
<b>Skeletal muscle</b>	:These male germ cells will produce spermatozoa following meiosis steps.
<b>Spermatocytes</b>	:The capacities of some specific cells to synthesize steroids.
<b>Steroidogenic potentialities</b>	:The two main thyroid hormones.
<b>Thyroxine (T4) and triiodothyronine (T3)</b>	:In fish, as in other vertebrates, gonads are first undifferentiated whatever the genetic sex of the individual is.
<b>Undifferentiated gonads</b>	:During this stage of oogenesis, a specific glyco-protein is produced by the liver, and incorporated by the oocytes to provide the future yolk reserves for the embryo development.
<b>Vitellogenesis</b>	:Deep fibers, which constituted about 95% of fish total muscle.
<b>White muscle</b>	

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