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 hyperplasic 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 hyperplasic 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 hyperplasic 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**
Tilapia: Substrate spawners	*Tilapia zillii* *T. rendalli* *T. sparrmanii*
Sarotherodon: Paternal or bi-paternal mouth brooders	*Sarotherodon melanotheron* *S. galilaeus*
Oreochromis: Maternal mouth brooders	*Oreochromis niloticus* *O. aureus* *O. mossambicus* *O. spilurus* *O. hornorum* *O. macrochir*

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).

Determination Female homogamety XX/XY	**Male homogamety ZZ/ZW**
O. niloticus	*O. aureus*
O. mossambicus	*O. macrochir*
	O. hornorum

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.

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Biographical Sketches

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Aboubacar Toguyeni graduated from Rennes University and Ecole Nationale Supérieure Agronomique de Rennes (France) with his D.Sc. and Ph.D. Biology and Agronomy. He is presently Professor in the Institut du Développement Rural-Université Polytechnique de Bobo-Dioulasso (IDR-UPB) in Burkina Faso. His research topics mainly focused on the reproduction and growth interactions in fish, particularly in tilapia. He has developed much collaboration with different lab (France, Wales, Belgium, Portugal, Philippines, Niger, Ivory Coast,) and development projects.