

Influence of Environmental and Social Factors on the Reproductive Efficiency in Three Tilapia Species, *Oreochromis niloticus*, *O. aureus*, and the Red Tilapia (Red Florida Strain)

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Abstract

Due to their important adaptive potentialities, tilapia have colonised a wide range of habitats which could be related to their various reproductive strategies. Some traits of the reproductive cycle present a great plasticity and can be modulated by many environmental and/or social factors. We investigated some of them under controlled conditions in three tilapia species, *Oreochromis niloticus*, *O. aureus* and the red tilapia (Red Florida strain). At a constant temperature, a clear influence of a seasonal photoperiod is demonstrated on the reproductive activity of *O. aureus*. Under a typical tropical 12L:12D photoperiod, most reproductions occurred in the mid-afternoon (3 p.m.). Environmental complexity strongly stimulated the production; both reproductive activity and fry survival seemed to be stimulated by the presence of artificial shelters.

The reproductive cycle of *Oreochromis niloticus* is characterised by the variability of its periodicity: vitellogenesis can be delayed or stimulated by the maternal behaviour as demonstrated by eggs/fry suppression or exchange experiments. In *Oreochromis 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 race-ways. 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. The individual characteristics of the clutches produced by these two types of females have been compared. The importance of social factors in the reproductive efficiency of tilapia species is discussed.

Introduction

Under favourable conditions, tilapias have a continuous but fluctuating reproductive activity throughout the year (Baroiller and Jalabert, 1989). Synchronisation of the female reproduction may allow adequate supply of fry for intensive rearing, but also the production of eggs/fry of a defined calibre; this is a requisite condition for producing male monosex populations, chromosome manipulations or hybridisation. At last, this contribute to homogenise the growth of cultured populations. Moreover, inhibition of spawning is required to avoid overpopulation and dwarfism in mixed populations (Baroiller and Jalabert, 1989). A better knowledge of the environmental factors which are able to affect the reproductive capacity of tilapias could be put to practical use. The major environmental factors for tilapia breeding in the wild are certainly temperature (Hyder, 1970) and rainfalls and/or flooding (Lowe Mc Connell, 1959); most of tilapia species need a minimal temperature of 22-24°C for reproduction (Terkatin-Shimony *et al.*, 1980; Philippart and Ruwet, 1982). Many other environmental and/or social factors can also play a modulatory role on periodicity of reproduction, such as stocking density, sex-ratios, food quality and quantity, water quality (salinity, pH, oxygen,...), stress, pollutants...(Lam, 1983; Mélard, 1986). However some other factors are still weakly documented.

Many studies have analysed the effects of photoperiodicity on the reproductive activity of temperate fish species (review of Lam, 1983). In tropical or sub-tropical conditions, seasonal differences are mainly related to temperature and rainfalls whereas photoperiod remains almost constant all the year. However, in a few cichlid fishes living in clear waters, reproductive activity can be also modulated by the lunar cycle: in *Oreochromis niloticus*, the proportion of females at an advanced stage of gonadal maturity is greater in Lake Victoria during full moon than during new moon (Okorie, 1973), and in *Tilapia mariae*, a lunar periodicity of the breeding activity is observed in the Ethiop River in Nigeria (Schwank, 1987). In both cases, the important variable could be the moonlight itself, by enhancing the effectiveness of parental care (Moyer, 1975; Schwank, 1987). Such a sensitivity to the light intensity has been already reported in wild populations through the influence of sunlight (Lowe Mc Connell, 1959). As tilapias have been introduced in many countries they can artificially face various light intensities or photoperiod regimes and even seasonal photoperiods in some EC countries; for example, tilapias are successfully reared in warm water from heated effluents such as nuclear power-plant or other industrial processes (Balarin and Haller, 1982; Mélard *et al.*, 1989).

Many species spawn at a specific time of the day (Lam, 1983): at a favourable temperature and photoperiod, evidence for diurnal changes in the male and/or female behaviour suggested a nycthemeral cyclicity for reproduction. Even if the field observations of Lowe-Mc Connell (1956) suggested a diurnal cyclicity in *Oreochromis karomo*, the only two experimental evidences of a spawning periodicity in tilapia have been provided for males in *Oreochromis mossambicus* (Munro and Singh, 1987) and for females in *Oreochromis aureus* (Marshall and Bielic, 1996).

It is generally assumed, from studies in the wild, that breeding sites are limiting factors for tilapia (Kolding, 1993); moreover, in fry production under culture condition, precocious cannibalism by the older recruits seems to be involved in the decreasing yields observed during successive harvests (Baroiller and Jalabert, 1989). Artificial modifications of the environmental complexity could provide both nest sites and/or shelter for the young progenies.

The major role of various social and behavioural factors in reproduction has been demonstrated in tilapia (Aronson, 1951; Marshall, 1972; Silvermann, 1978a,b; Baroiller and Jalabert, 1989 for review). Some of these studies have focused on behaviour/reproduction interactions in tilapia (Peters, 1963; Smith and Haley, 1988; Little *et al.*, 1993; Tacon *et al.*, 1996; Gautier *et al.*, 1996). But very few studies have analysed the relative individual potential of females in a spawning group (Mires, 1982).

A better knowledge of these interactions could improve spawning synchrony or inhibition of reproduction; thus, the influence of seasonal photoperiodicity, maternal behaviour, environmental complexity, or female-female interactions on some reproductive characteristics has been investigated under controlled conditions in *Oreochromis niloticus*, *O. aureus* and/or the red tilapia (Red Florida strain).

Material and methods

Basic cycle and influence of maternal behaviour

Oreochromis niloticus ("Bouaké" strain) breeders weighing between 50 and 150 g were maintained in aquarium at a sex-ratio of 1:3 (male:female), under ambient temperatures (24-29°C) and photoperiod (12L:12D). Ten incubating females were isolated and allowed to perform their maternal behaviour; ten other incubating females were deprived of their eggs on the day following their spawning. In the first group, the duration of the incubation (first release of the fry) and the guarding phase (definitive fry release) and at last, the occurrence of a cannibalism behaviour were recorded; in both groups (incubating and non-incubating females), females based on their breeding condition, i.e. the development of the genital papilla were returned to a male breeder for a second spawning and inter-spawning interval was determined.

Influence of nycthemeral periodicity

Oreochromis niloticus ("Bouaké" strain) females reared under constant temperature (26°C) and photoperiod (12L:12D) were chose based on their breeding condition, i.e. the development of the genital papilla; matings were done in 260-300 l. aquarium (one male / 3-4 females). Females were allowed to perform a normal 10 days incubation. This experiment was conducted during one year. The time of breeding was recorded to the nearest quarter of an hour.

Influence of seasonal photoperiodicity

Two species, *O. niloticus* (Israel strain) and *O. aureus* (Manzala strain, Egypt), were used in this experiment. Breeders (3 males and 10 females) were maintained in 4m²/1.6 m³ tanks supplied with thermoregulated water (25-27°C) from a power plant (Mélard *et al.*, 1989). This experiment was respectively conducted during twelve and twenty months for *O. niloticus* and *O. aureus*. Each individual was tagged with passive integrated tags (Indextel Rhone-Mérieux). At 7-days intervals, eggs and/or fry (seed) were removed from the mouth of each breeder and counted; the relative fecundity (number of eggs/kg/spawning) was determined according to the individual weight at the time of control. The same breeders were replaced in the same tank after each harvest.

Relative involvement of individuals in a spawning groups

O. niloticus breeders (five males and ten females) were maintained in 1 m² tanks under a constant photoperiod (12 h. light: 12 h. dark = 12L:12D) with recirculating fresh water thermoregulated at 26±1°C; the red tilapia breeders (18 males / 54 females) were maintained in 12 m² race-way under natural temperature and photoperiod with running water. The fish were fed twice daily with tilapia food at a 1% rate of their body weight. All the breeders for *O. niloticus* and 19 out of 54 females were individually tagged. Preliminary experiments demonstrated that these 19 females constitute a representative sample of the all female population. This experiment was respectively conducted during eight and 10 months for *O. niloticus* and the red tilapia. Successive harvests were performed at a 10-days frequency. A total of twenty-four (*O. niloticus*) or thirty (red tilapia) harvests were made during the experiment.

Environmental complexity

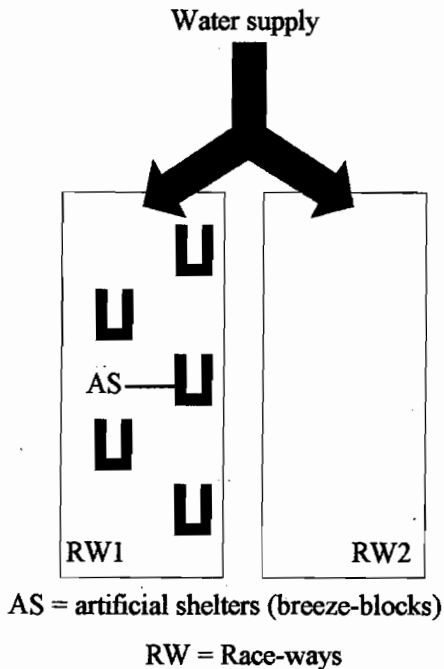


Figure 1: Disposition of the artificial shelters in the race-way

Oreochromis niloticus (15 males, average weight 288 g / 45 females, average weight 186 g) and red tilapia (18 males, average weight 294 g / 54 females 162 g) breeders were maintained in 12 m² race-ways 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 race-ways for further reproductions. A total of three (*Oreochromis niloticus*) or thirty (red tilapia) harvests were made during the experiment.

For *Oreochromis niloticus* experiments, five artificial shelters were made by disposing perpendicularly three breeze-blocks; in the control race-way, there was no shelter (figure 1).

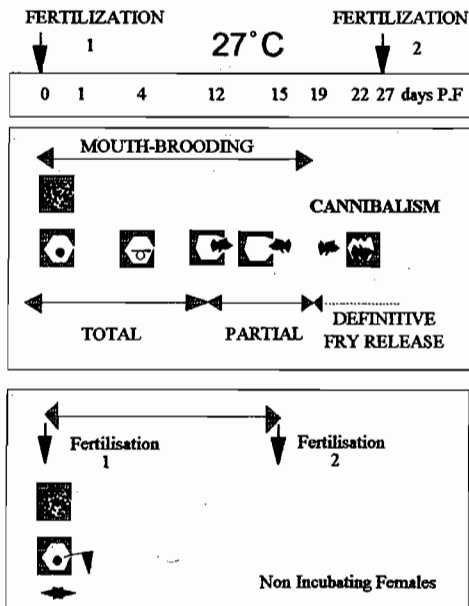
For the red tilapia strain, a random sample of 19 out of 54 females was individually tagged with PIT tags implanted into the dorsal musculature.

Male and female breeders were maintained in 1 m² tanks under a constant (12 h. light: 12 h. dark = 12L:12D) with recirculating fresh water thermoregulated at 27°C.

For *O. niloticus*, the developmental stage of the fry was determined following a simplified classification (1=eggs, 2=eyed, 3=hatched larvae, 4=swimming fry, 5=vesicle-resorbed fry).

Results

Basic cycle and influence of maternal behaviour



Twelve days after a strict (or total) incubation period, a guarding sequence of 7 days was performed by the females before the definitive fry release (fig. 2). In aquarium, cannibalism can already occurs approximately 3 days later.

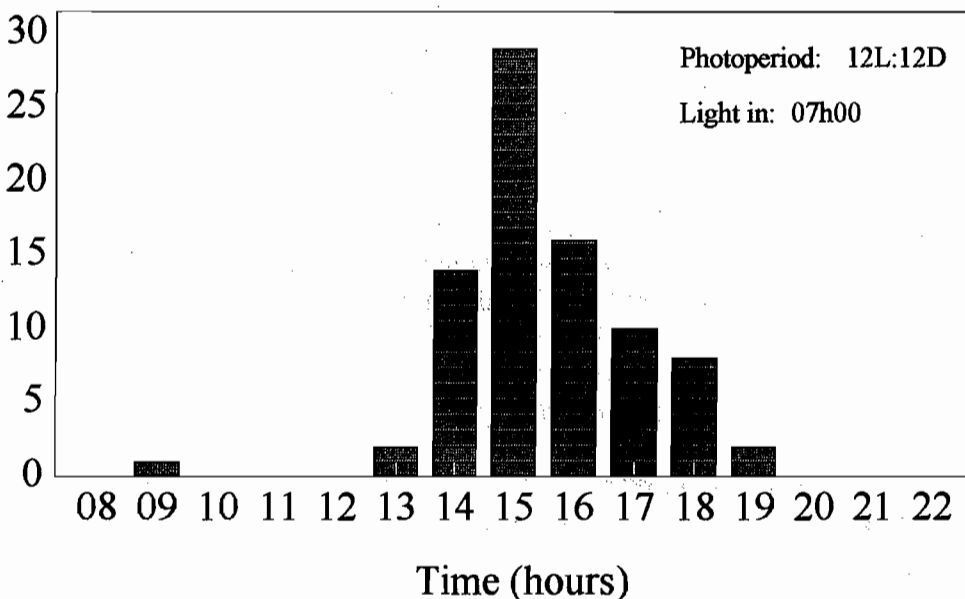
Females from this incubating group exhibited a 27- days interspawning interval compared to 15 days in non-incubating females.

This inter-spawning period is characterised by the variability of its duration depending on the females, but also on the successive cycles of a defined female. This variability is related to those of the respective durations of the strict incubation (10-16 days) and the guarding (16-23 days after fertilisation) sequences.

Figure 2: relationship between the behavioural sequences and the reproductive cycle in *O. niloticus* (drawn from the data of Tacon *et al.*, 1996).

Influence of nycthemeral periodicity

A total of 82 spawnings has been recorded (fig. 3). When maintained on 12L:12D in aquarium at 27°C, *O. niloticus* breeders reproduced almost exclusively (almost 99% of the reproductions) during the afternoon of the light period, ranging from 1 to 7.30 P.M.. 84.2 % of the spawning activity occurred between 2 and 5 P.M., with a peak around 3 P.M. (35 % of



the reproductions). Only one reproduction out of 82 (1 %) occurred in the morning.

Figure 3: Nychthemeral rhythm of spawning activity in *Oreochromis niloticus*. Breeders were chosen based on their breeding condition, i.e. the development of the genital papilla for females, and the colouration pattern for males; matings were done in 260-300 l. aquarium (one male / 3-4 females). This experiment was conducted during one year. The time of breeding was recorded to the nearest quarter of an hour.

Influence of seasonal photoperiodicity

A minimum range of 22-24°C is needed for tilapia reproduction. With the exception of a two-months-period (mid-January-March), water temperature was always above this critical threshold during the twenty months experiment (fig. 4). The two tilapia species present different profiles in their spawning activity. In *Oreochromis niloticus*, reproductions take place all the year, without any resting period. The period of intense spawning activity (April-August) correspond to the highest temperatures and photoperiod. Autumn and winter are characterised by the weak reproductive activities of *O. niloticus* breeders. First spawnings in *O. aureus*, occurred in spring (end of March) with increasing photoperiod (12L:12D) and temperatures. Spawning activity reached a peak when temperature and photoperiod were at their highest values and began to decline just after. From the end of November when photoperiod was minimal (8L:16D) to the end of the winter, no reproduction could be recorded. After this 3 months resting period spawning activity resumed again in April with increasing temperatures and photoperiod.

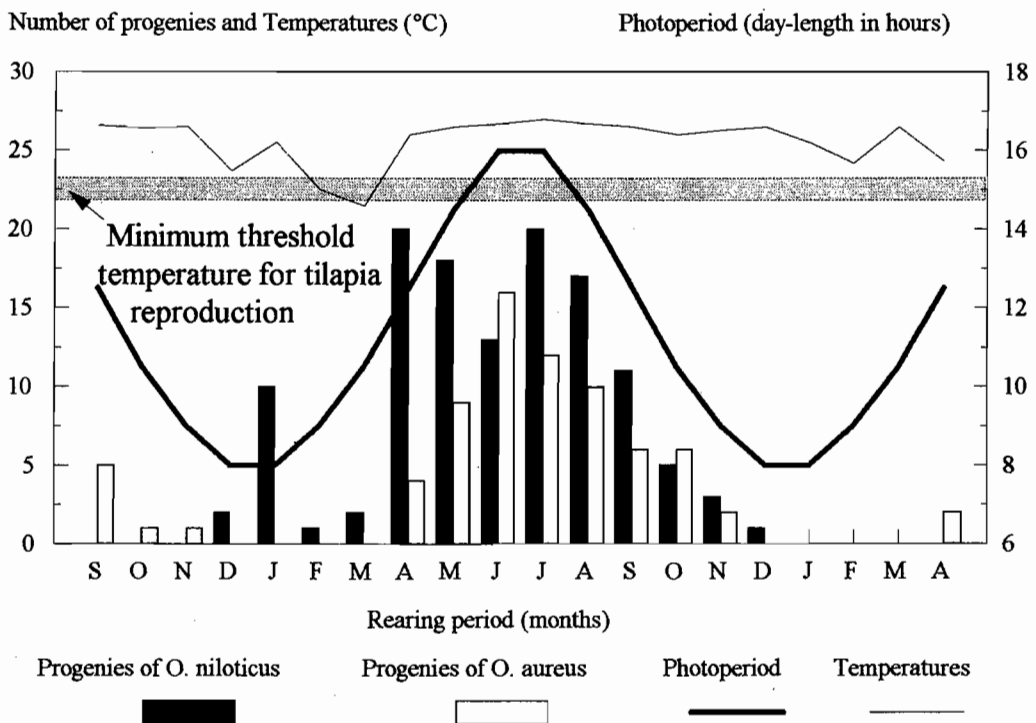


Figure 4: Evolution of the spawning activity of *Oreochromis niloticus* and *O. aureus* under a natural seasonal photoperiod. Breeders (10 females/3 males) were maintained in a 4m²/1.6m³ tank supplied with water from a nuclear power plant. Fry were collected from the mouth of

the females every week. The experiment was respectively conducted 13 (December-december) and 20 months (September-september) for *O. niloticus* and *O. aureus*

Influence of environmental complexity

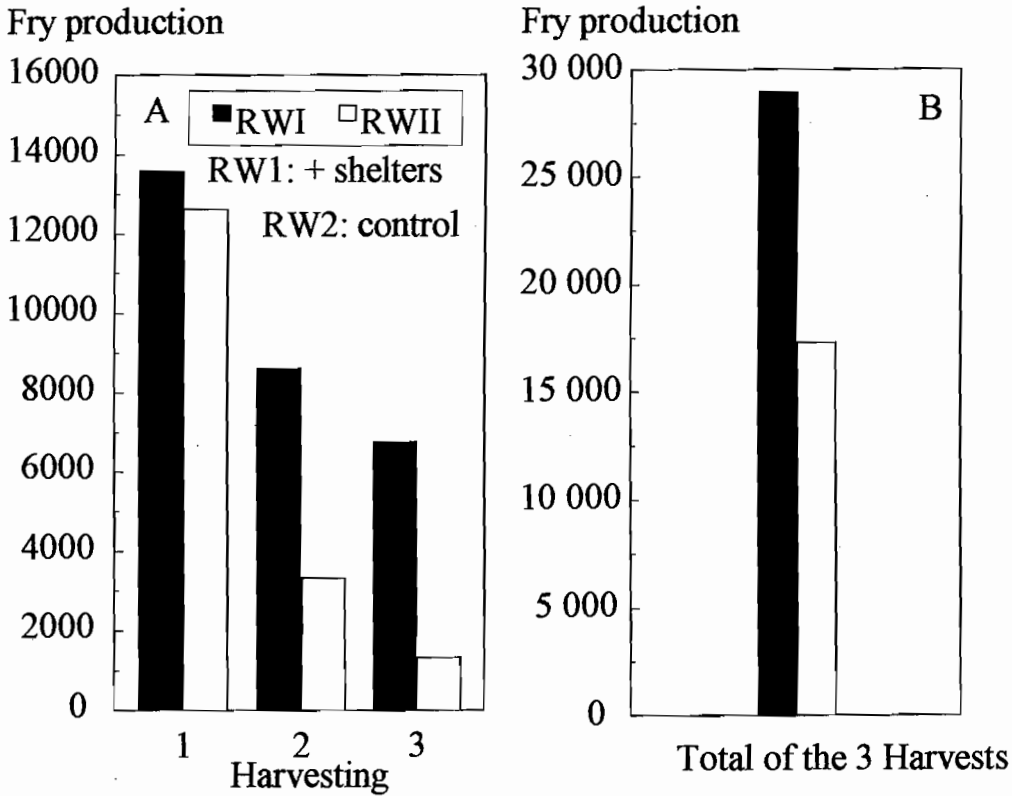


Figure 5: Evolution of *O. niloticus* fry production after successive (A) or cumulated (B) harvests in 12m² race-ways. Breeders (15 males/45 females) were maintained in two race-4 ways (RW1 and RW2). Five artificial shelters were disposed in RW1, whereas RW2 was devoid of such structures. At 14-days intervals, eggs and fry were collected from the mouth of the female breeders and counted.

Fry production was very similar in both race-ways at the first harvest with a slight advantage to RW1 (presence of 5 artificial shelters): 13600 seed against 12615 in RW2 (fig. 5). This correspond to an average of 21.6 seed/female/day for RW1 and 20 seed/female/day in RW2. Since the second harvest, fry outputs decrease, drastically (89.4%) in the control (12615→3341→1333), and more slightly (50.4%) in that having shelters (13600→8606→6750). At the last harvest, the mean fry yield was 10.7 seed/female/day in RW1 and only 2.1 seed/female/day in RW2. The total production of RW1 resulting from 3 harvests is 1.7 time higher than in RW2 (28956/17289); taking into account the 42 days of culture, this represents an average fry yield of 15.3 seed/female/day in RW1 and 9.1 seed/female/day in RW2.

Relative reproductive activity of individually tagged male and female breeders

In the red tilapia (fig. 6) and *O. niloticus* (fig. 7), 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, fig. 6), 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, fig. 6), 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, fig. 6), a very constant basal activity concerned only 10% of the females. This basal activity was associated with favourable temperatures ($>24^{\circ}\text{C}$) and daylength ($>11\text{L}:13\text{D}$) at least during 50 days (harvests 22 to 26).

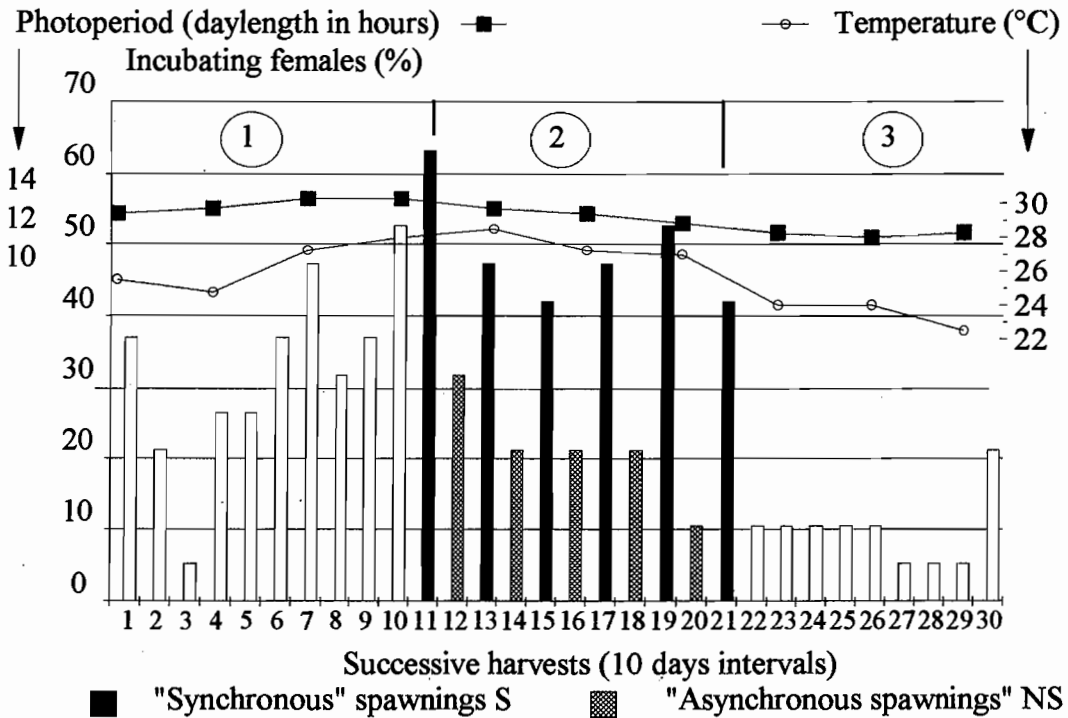


Figure 6: Evolution of the proportion of red tilapia incubating females during successive harvests. Breeders (18 males/54 females) were maintained in 12m² race-ways under natural temperature and photoperiod.

Besides, *O. niloticus* reared under constant temperature and photoperiod, presented 2 phases (fig. 7): 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).

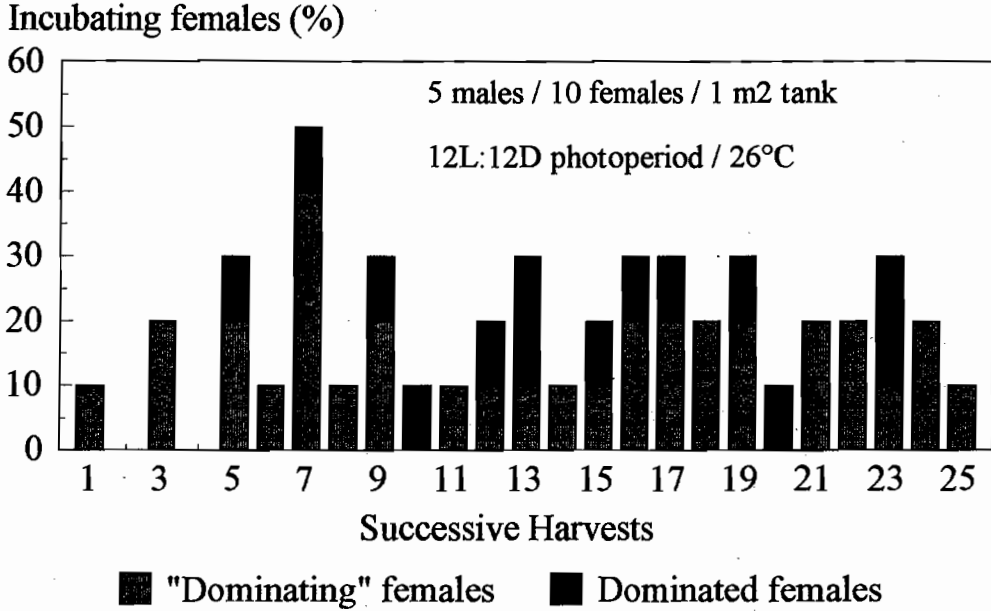


Figure 7: Evolution of the proportion of *O. niloticus* incubating females during successive harvests. Breeders were maintained in a thermoregulated recirculating water (26°C) under a constant 12L:12D photoperiod.

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 (fig. 8).

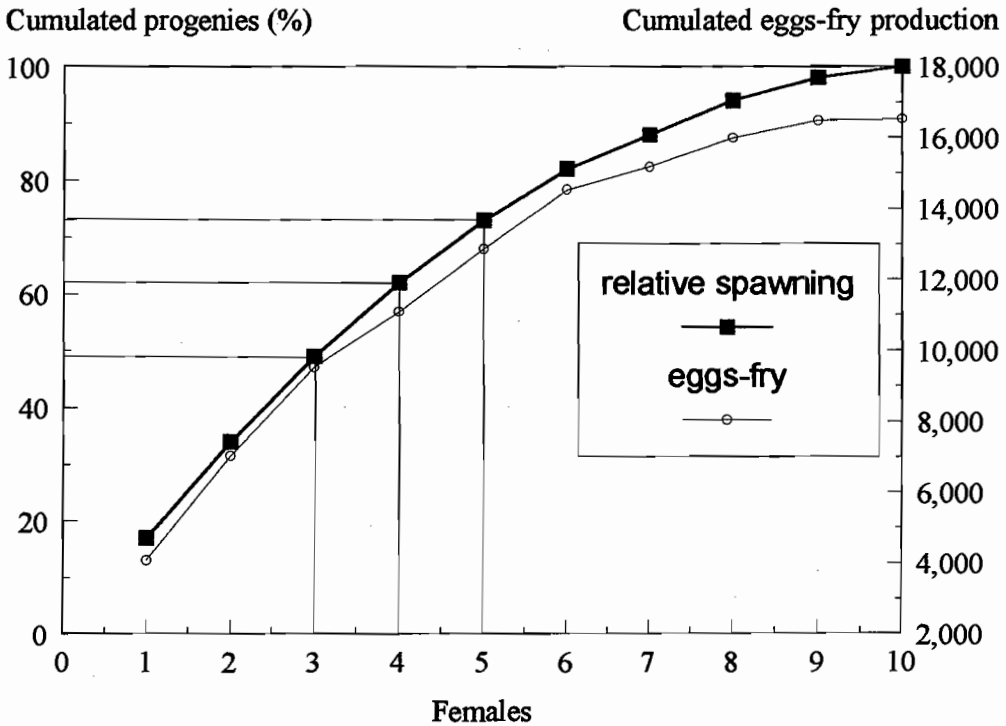


Figure 8: Individual involvement of the *O. niloticus* females in the spawning activity. Moreover, within these active breeders, the average number of eggs-fry produced per spawning was higher (370 seed/progeny) than that of the 5 other females (237 seed/progeny). This was not related to the respective 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, fig. 6), 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*.

Discussion

Oreochromis niloticus reproductive cycle, as all the *Oreochromis* species, is characterised by three successive behavioural sequences: the incubation of eggs and larvae, the guarding period and the definitive fry release (Keenleyside, 1991). Ovarian development is slower during the guarding phase (Tacon *et al.*, 1996); vitellogenesis and the inter-spawning period can be delayed by the maternal behaviour or stimulated by eggs/fry suppression (Peters, 1963; Smith et Haley, 1988; Little *et al.*, 1993; Tacon *et al.*, 1996); this was confirmed by exchange experiments of eggs by foreign broods of various ages (Gautier *et al.*, 1996). The twelve-days difference between typical cycles with maternal behaviour and those of non-incubating females corresponds approximately to the period of total incubation which has been artificially suppressed in the latter group.

By modulating her parental care, females can thus reduce or delay the interspawning period. An extreme example is provided by *T. mariae*: when the eggs' number of a seed became too low, this tilapia species could eat it to prepare a more numerous progeny (Schwank, 1986). In this case, the inter-spawning period will be also reduced. These relationships between the expression of maternal behaviour and ovarian development in tilapia are already used to improve spawning synchrony in tilapia (Little *et al.*, 1993; Little *et al.*, 1996). Identification of the physiological relay involved in this inhibitory effect of maternal behaviour on ovarian development should improve the control of reproduction (synchronization and/or inhibition) in tilapia.

In both *O. niloticus* and *O. aureus*, photoperiods strongly influence the spawning activity: reproduction is stimulated by long photoperiods (>12L) and inhibited by short length-day. However, even if temperature is favourable, spawning activity is totally inhibited in *O. aureus* under short photoperiod (8L:16D), whereas a few progenies are still produced by *O. niloticus* breeders. During these period of weak reproductive activity, *O. niloticus* is still very sensitive to temperature variations: increasing temperatures stimulate the spawning activity (January) whereas decreasing temperatures inhibit the production of progenies (February-March). Thus photoperiod and temperature strongly influence the reproduction at least in these two tilapia species through synergic effects. In *O. mossambicus* photoperiods did not affect spawning at 25°C, which can even occur in continuous darkness or continuous light (review of Lam, 1983): Under seasonal conditions, photoperiod can thus be a major factor for tilapia reproduction.

Munro and Singh, (1987) presented evidence that males of *Oreochromis mossambicus* are mainly territorial during the afternoon: the peak of this reproduction-related behaviour took

place between 1 and 5 P.M. This male cyclicity would not appear to be dependent on the presence of females. This study suggested that females may ovulate at a particular time of day, as it has been previously demonstrated in the goldfish (Stacey *et al.*, 1979) and as it is suggested by the field observations of Lowe-Mc Connell (1956) for another species of tilapia (*O. karomo*).

Our results on a daily periodicity of the reproductive behaviour confirm those observed in the blue tilapia, *O. aureus* (Marshall and Bielic, 1996). In both species, spawning activities is mainly restricted to the afternoon when light on occurred in the morning (7 A.M. in our study; 8 A.M. in their study). In both species, almost if not all the first reproductions may occur 7 h. after after the light on. However, in *O. niloticus* some rare female may spawn early in the morning; this is never observed in *O. aureus*. This could be an alternative for subordinate individuals: such a similar strategy was hypothesized to explain some feeding activities during the dark period in *O. niloticus*, as in these species, feeding is essentially a diurnal activity (Toguyeni *et al.*, 1997).

In both *O. niloticus* and *O. aureus*, ovipositions took place within a 7-9 hour range with a spawning nycthemeral peak around 9-11 hour after the light on. This periodicity seems to be linked to the light on as demonstrated by a corresponding shift in the period of spawning activity consecutively to phase-shifting the light cycle in *O. aureus* by 7 hours (Marshall and Bielic, 1996).

Individual potential of females in a spawning group is mainly characterised 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 (Rothbard, 1979; Mires, 1982). 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 (Mires, 1982). Populations of tilapias breeders could contain dominant females characterised by their relatively higher spawning activity (Mires, 1982). Frequent and complete harvests of seed from the mouth of the incubating females reduced the interspawning period, due to the relationship between maternal behaviour and reproductive cycle (Peters, 1983; Little *et al.*, 1993; Tacon *et al.*, 1996). 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 (Turner, 1986). However, in our study, on *O. niloticus*, or red tilapia seed production was mainly dependent upon the dominant females even after 25 to 30 successive harvests. Thus we assume that removal of seed improve output mainly by stimulating vitellogenesis more than by allowing subordinate fish to breed.

As far as we know, there are no reports on experimental evidence of the influence of environmental complexity on reproduction and/or cannibalism of fry by the older recruits. Two complementary hypothesis could explain the increase of the mean fry yield following the introduction of artificial shelters in the race-way: a stimulation of the nesting behaviour and then the reproduction rate of the breeders, or the partial or total inhibition of cannibalism of fry by the older recruits. In some african fish farms, indeed, the first fry harvesting in ponds was carried out only after 1.5-2 months, when the yield fry production was maximum. However, as some older recruits escaped from this first harvesting, they became very efficient predators for younger fry. The simultaneous increase in the mean weight of the harvested fry and the progressive yield decrease strongly suggested a major role of cannibalism (Baroiller and Jalabert, 1989).

However, in the present experiment on the influence of environmental complexity on reproduction, *O. niloticus*, fry will be able to leave the mouth of their mother 12 days after fertilization (Tacon et al., 1996; the present paper). As we used a two weeks inter-harvest period, fry resulting from precocious spawnings (those having done in the two first days following the new rearing period after a harvest) have only two days in average during which they will be a potential prey for older recruits. Thus we assume that the artificial shelters should have stimulated or synchronised the reproductive activity more than decreasing the cannibalism. From our studies on the relative individual potential of females in a spawning group, we hypothesized that dominant females could be mainly involved in the first yield fry production. Taking into account to the 14 days interval between successive harvests, we assume that the second seed production (at least) should mainly result from the subordinate females. Thus, artificial shelters could have allowed the spawnings of subordinate females by stimulating and masking them from the non-incubating dominating females.

Note: This article includes original results published by Tacon *et al.*, (1996) *Aquaculture*, 146: 261-275.

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