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Rapid phenotypic changes of reproductive traits in response to experimental modifications of spatial structure in Nile tilapia, *Oreochromis niloticus*

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Abstract − The reproductive characteristics of *Oreochromis niloticus*, a multiple spawner, have been compared between populations submitted experimentally to three types of spatial structure. Fish from a same original stock were divided and reared for 2 months in: 1) concrete tanks with a bare bottom, 2) concrete tanks with a sandy bottom, or 3) concrete tanks equipped with an artificial reef. The females were then killed and their gonads examined for sexual stage and fecundity determination. Fecundity was inversely correlated to the spatial complexity of the environment whereas oocyte size tented to increase together with spatial complexity. Females placed in tanks with artificial reefs presented a lower fecundity and reproductive investment and bigger oocytes than those maintained in the bare bottom tanks. Fish reared in tanks with a sandy bottom had intermediate reproductive traits. The response of females to changes in the spatial structure of their environment was observed after only one or two reproductive cycles, providing the first experimental evidence of such rapid phenotypic adaptation to environmental complexity. The results also indicate that the perception of living space, arising from the availability of refuges and spawning sites, is more likely to influence the reproduction of tilapias than substrate quality. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

tilapia / reproduction / phenotypic plasticity / spatial organisation / adaptability / Ivory Coast

Résumé − **Adaptation phénotypique rapide des caractéristiques de reproduction des tilapias, *Oreochromis niloticus*, en réponse à des modifications expérimentales de l'environnement.** Les caractéristiques de reproduction ont été comparées chez des femelles *Oreochromis niloticus* soumises expérimentalement à trois types d'organisation spatiale. Des poissons issus d'un même stock ont été placés pendant 2 mois dans des bacs en béton équipés soit d'un récif artificiel, soit d'un fond recouvert de sable, soit d'un fond nu. Les femelles ont ensuite été sacrifiées pour déterminer leur stade de maturation sexuelle et leur fécondité. La fécondité des femelles est inversement corrélée à la complexité de leur environnement alors que le poids ovocytaire tend à augmenter avec la complexité spatiale. Les femelles placées dans les bacs équipés d'un récif artificiel ont une fécondité et un effort de reproduction plus faible et de plus gros ovocytes que celles placées dans les bacs non aménagés. Les femelles placées dans les bacs avec un fond en sable présentent des caractéristiques intermédiaires. La réponse des femelles au changement de la structure spatiale de leur environnement a été observée après seulement un à deux cycles de vitellogenèse. Ces résultats constituent la première démonstration expérimentale d'une adaptation phénotypique aussi rapide à une modification de l'environnement. Ils suggèrent également que la structuration de l'espace, au travers de la multiplication des refuges et probablement des sites de nidification, exerce une plus grande influence sur la reproduction des tilapias que la qualité du substrat. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

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1. INTRODUCTION

The availability of spawning sites is a crucial and sometimes limiting factor in the development of cichlid populations, particularly of tilapias (McKaye, 1977; Pullin and Lowe-McConnell, 1982). In areas where spawning grounds are restricted, the territorial behaviour of tilapias may prevent weaker and/or

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subordinated individuals from reproducing (Kohda, 1995). On the other hand, substrate quality may also influence reproductive behaviour and parental care (Bruton and Gophen, 1992), and the energetic balance between reproductive and feeding activity has been shown to affect the reproductive cycle (Keenleyside, 1991). Food availability may then directly influence the choice of spawning sites (Ward and Samarakoon, 1981), and predation pressure on brooders, eggs or fry may also be determinant (Keenleyside, 1991; Kolding, 1993). In Ivory Coast, where the present work was carried out, most of the hydroelectric and agropastoral reservoirs are characterised by the abundance of immersed stumps and dead trees. These structures provide refuges for brooders and fry, but also constitute a substrate for epiphytic plankton development on which tilapias can feed (Dempster et al., 1993, 1995; Shrestha and Knud-Hansen, 1994). They might also increase the number of spawning sites. While investigating the reproductive strategies of *Oreochromis niloticus* (Linnaeus, 1758) in the Ivoirian reservoirs (Duponchelle and Panfili, 1998; Duponchelle et al., 1998, 1999, 2000), questions about the potential effects of these natural structures on the reproductive traits of the Nile tilapia arose. Immersed stumps and dead trees may be considered as ‘natural acadjas’. Acadjas are dense masses of woody branches installed in shallow water, traditionally used in lagoon fisheries in Benin (Welcomme, 1972). Acadjas technique (masses of woody branches installed on the bottom, or bamboo stems vertically fixed in the ground) is also used to increase fish production in extensive aquaculture (Legendre et al., 1989; Hem and Avit, 1994; Hem et al., 1995). Legendre and Ecoutin (1996) observed variations in the reproductive traits of *Sarotherodon melanotheron* reared in different lagoon enclosures: fish reared in bare enclosures produced consistently more and smaller oocytes than those reared in enclosures with acadjas. However, these results did not distinguish between the specific trophic or protective effects of these structures.

In the present study, the specific effects of spatial organisation on reproductive traits of *Oreochromis niloticus* females are experimentally investigated.

2. MATERIAL AND METHODS

This study was carried out in concrete tanks at the Idessa (*Institut des Savanes*) aquaculture station in Bouaké, Ivory Coast, between September and November 1996. The *Oreochromis niloticus* used for this experiment were ‘Bouaké strain’ brooders.

2.1. Experiment

Three types of environment structure and substratum were tested during this investigation: tanks with a bare bottom, tanks with a sandy bottom (10 cm thickness), or tanks equipped with an artificial reef. Each treatment was replicated once, thus six identical concrete tanks (12 m^2) were used. Artificial reefs, each comprising 100 hollow bricks positioned in order to create many tunnels and refuges, were strictly identical in both replicates. A constant water level (1 m) was maintained in each tank during the entire experiment. Water quality was maintained in the tanks by a constant external water flux. Environmental variables were controlled once a week. Throughout the experiment, water temperature varied between 24.6 and 25.1°C at 9h00, and between 25.5 and 28.1°C at 16h00, oxygen between 2.08 and 5.97 mg·L^{-1} at 9h00, and between 4.85 and 7.78 mg·L^{-1} at 16h00, and pH between 6.72 and 7.35.

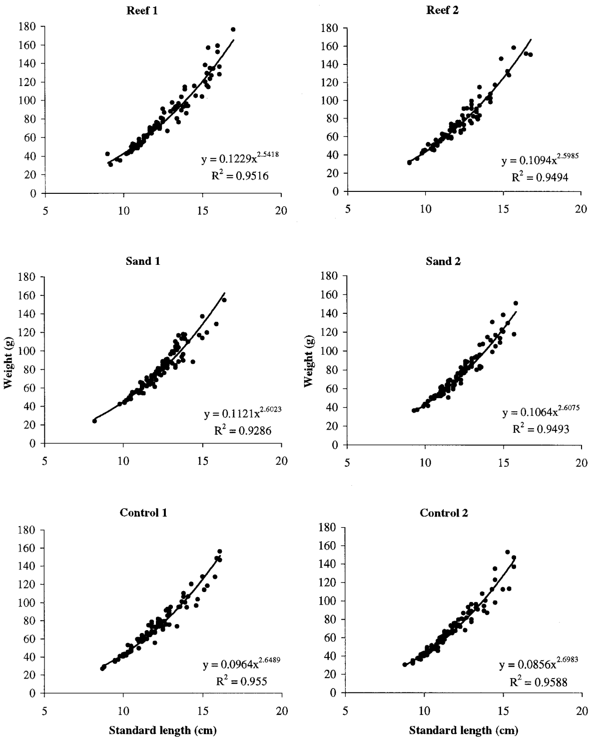

Figure 1. Length–weight relationships of *Oreochromis niloticus* females in each tank at the end of the experiment.

One hundred fifty *Oreochromis niloticus* females and fifty males (weighing between 50 and 150 g) were reared in each tank. Length–weight relationships of females in each tank are given in *figure 1*. All the fish were obtained from two successive batches of fry from the same brooders. Particular attention was given to experimental design in order to get similar and comparable size distribution of fish in the different groups. They were fed twice a day with a 30% crude protein powdered feed, distributed six days a week at a daily rate of 3% of fish biomass.

2.2. Reproductive characteristics

After 2 months of experiment, all fish were caught and females were dissected to analyse their reproductive characteristics.

The sexual maturity scale used was that of Legendre and Ecoutin (1989). Stage 1 comprises immature females, stage 2, females beginning maturation, and stage 3, maturing females. Stage 4 is characteristic of females that are going to reproduce, stage 5 of ovulated females, and stage 6 of post-spawning females.

Standard length was measured to the nearest 1 mm, and body weight to the nearest 1 g. The gonads were checked macroscopically for maturity stage and then weighed to the nearest 0.1 g for the gonado–somatic index (*GSI*) calculation (gonad weight / total body weight × 100). Gonads in advanced vitellogenesis (stages 4 and 5) were fixed in 5% formalin for later estimation of fecundity and oocyte size.

Fecundity is considered here as the number of oocytes to be released at the next spawn (absolute fecundity or potential fecundity; see Coward and Bromage, 2000 for review). It is estimated, from gonads in the final maturation stage (stage 4), by the number of oocytes belonging to the largest diameter modal group. This oocyte group is clearly separated from the rest of the oocytes to the naked eye and corresponds approximately to oocytes that are going to be laid. For each individual, fecundity was calculated from a portion of the gonad representing at least 50% of the total ovaries weight, and then extrapolated to the total weight of the ovary.

Oocyte weight measurements were all carried out on samples preserved in 5% formalin for 3 weeks. The individual average oocyte weight was determined by weighing 50 oocytes from those taken for fecundity estimates. In order to compare mean oocyte weight between treatments, measurements need to be made on oocytes at a similar vitellogenic stage, i.e. on oocytes whose growth has been completed. The *GSI* threshold above which the oocyte weight and diameter no longer increase significantly for female *Oreochromis niloticus*, was determined. This threshold is reached at a *GSI* ≥ 4% for females whose body weight is < 150 g, and at *GSI* ≥ 3% for females whose body weight is ≥ 150 g (Duponchelle 1997).

The spawn weight (absolute fecundity × mean oocyte weight) is used as an index of the reproductive investment per female and per spawn. It is calculated only for the females whose *GSI* is above the threshold previously defined (i.e. for the females used in oocyte weight measurements).

2.3. Statistical analysis

Absolute fecundity, in tilapias as in many other fishes, is positively correlated to size and to body weight (Albaret, 1982; Duarte and Alcaraz, 1989; Winemiller and Rose, 1992; Legendre and Ecoutin, 1989, 1996). The spawn weight is also positively correlated to the body weight in tilapias (Legendre and Ecoutin, 1996; Duponchelle, 1997). Therefore, the estimation of differences between populations was made by comparing regression lines between fecundity, or spawn weight, and body weight. The slopes and intercepts of regressions were compared by an analysis of covariance (Scherrer, 1984) followed by a 2 by 2 comparison method. As the type I error increases when more than two populations are compared pairwise (Scherrer, 1984) a probability α' was calculated so that the overall α ($\alpha = 0.05$ in our case) was maintained over the $k(k-1)/2$ comparisons:

$$\alpha = 1 - (1 - \alpha')^{0.5[k(k-1)]},$$
$$\text{then: } \alpha' = 1 - (1 - \alpha)^{2/[k(k-1)]}$$

The comparisons of mean oocyte weights were carried out using a one-way ANOVA and the multiple comparison procedure of Newman–Keuls (Scherrer, 1984).

3. RESULTS

The relative distribution of sexual maturity stages among tanks and treatments is summarised in *table I*. Stage 6-3 corresponds to a post-spawning gonad almost filled with the new batch of oocytes in more advanced vitellogenesis and looks like a stage 3 gonad with remaining empty areas and some atretic follicles. The presence of stage 6-3 indicated that after spawning, females were directly entering a new vitellogenesis cycle. A high percentage of stage 4r (4 'resorbed', which corresponds to a stage 4 in which at least 20% of the oocytes that were ready to be released became atretic) was observed in each tank in very similar proportions. The proportion of sexually active females

Table I. Relative proportions of female *Oreochromis niloticus* sexual maturity stages in each experimental tank.

Tanks	Stages 1, 2, 3	Stages 4, 5, 6	Stage 6-3	Stage 4r	Total sexually active
Reef 1	26	39	13	22	61
Reef 2	32.6 (29.3)	29.2 (34.1)	3.4 (8.2)	34.6 (28.4)	63.5
Sand 1	35.7	27.6	7.1	29.6	57.2
Sand 2	38.1 (36.9)	31.9 (29.8)	5.2 (6.2)	24.7 (27.1)	56.6
Control 1	40	29	7	24	53
Control 2	46.1 (43.1)	28.5 (28.8)	2.9 (4.9)	22.5 (23.2)	51

Values are percentages, and means for treatment indicated in parentheses. Total sexually active sums up the females in stages 4, 4r, 5, 6.

(ready to spawn or just spent females: stages 4, 4r, 5 and 6) was high in every tank: 51 to 63.5% (*table I*). However, this proportion increased from the control tanks to the tanks with an artificial reef. As there was no significant difference of sexually active females among replicates of a same treatment (χ_i^2 test, $P > 0.05$), replicates were pooled for inter-treatment comparison. The proportion of sexually active females differed significantly between reef tanks and control tanks only (χ_i^2 test, $P = 0.001$).

Covariance analysis revealed that fecundity of females varied significantly between tanks ($F_{5,107} = 3.721$, $P = 0.0038$). However, as no difference was found between replicates ($F_{1,37} = 0.452$, $P > 0.05$ for reef tanks, $F_{1,34} = 5.253$, $P > 0.05$ for sand tanks, $F_{1,31} = 0.969$, $P > 0.05$ for bare tanks), data from replicate tanks were pooled for between-treatment comparisons. Significant differences of fecundity were found between treatments ($F_{2,100} = 8.392$, $P = 0.0004$).

The fecundity–weight regressions of females for each treatment are shown in *figure 2* and the corresponding statistical relationships in *table II*. The fecundity of a female weighing 100 g, which corresponded to the middle of the weight range of females used, and the mean oocyte weight are shown for each population in *figure 3*. After 2 months spent in these rearing conditions, females from the artificial reef tanks had a lower fecundity and bigger oocytes than females from control tanks, whereas females from the sandy bottom tanks presented intermediate characteristics. An inverse relationship was observed between oocyte weight and fecundity of females between treatments ($r^2 = 0.992$, $P = 0.055$). Nevertheless, the observed differences in oocyte weight between treatments were not statistically significant ($F_{2,59} = 0.680$, $P = 0.511$). Differences of fecundity between females from the sandy bottom tanks and the control tanks were not significant, nor were those between females from reef tanks and sandy bottom tanks. By contrast, fecundity of females in the reef tanks was significantly lower ($F_{1,73} = 20.137$, $P < 0.0001$) than that observed in the control tanks, this difference being expressed by intercept variation.

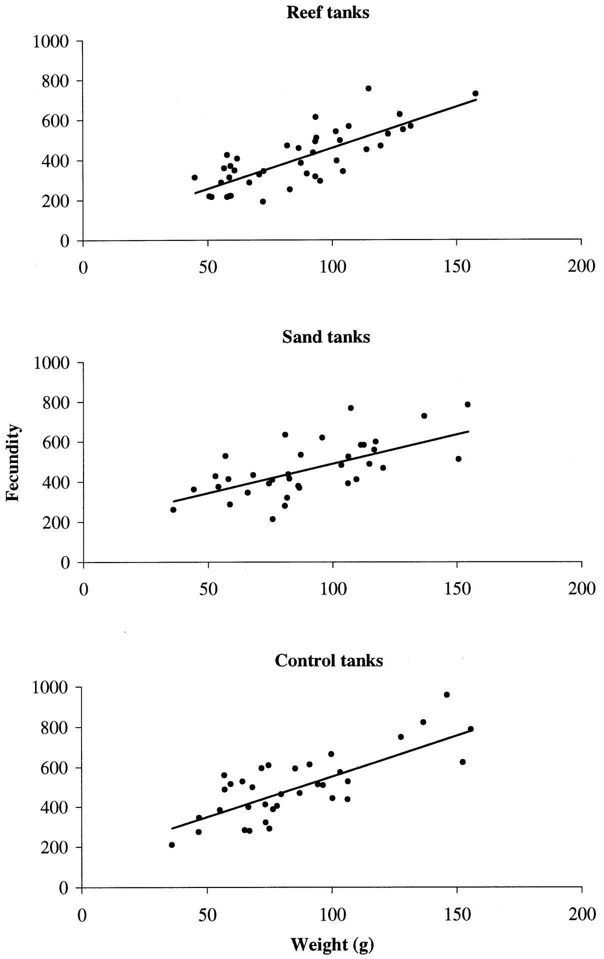

Figure 2. Fecundity–weight relationships of *Oreochromis niloticus* females for each treatment. Statistical relationships are given in *table II*.

The reproductive investment per female, characterised by the spawn weight (*figure 4, table II*), also differed significantly between the treatments ($F_{2,58} = 3.912$, $P = 0.026$). No significant difference was found between the females of the reef tanks and the females of the sand tanks, nor between the females of the sand tanks and the females of the control tanks. However, the reproductive investment per female was

Table II. Statistical relationships between fecundity or spawn weight and body weight for *Oreochromis niloticus* females in each treatment.

Treatment	N	Regression	r^2	P
Reef	41	$F = 54.2 + 4.06\ W$	0.608	< 0.001
	25	$SpW = -1.425 + 0.051\ W$	0.851	< 0.001
Sand	35	$F = 198.9 + 2.92\ W$	0.415	< 0.001
	18	$SpW = -0.762 + 0.045\ W$	0.761	< 0.001
Control	35	$F = 147.4 + 4.07\ W$	0.559	< 0.001
	18	$SpW = -0.655 + 0.048\ W$	0.872	< 0.001

F: fecundity; *SpW*: spawn weight; *W*: body weight; *N*: number of females used (note that *N* is the same for spawn weight and oocyte weight estimations); r^2: regression coefficient; *P*: significance level.

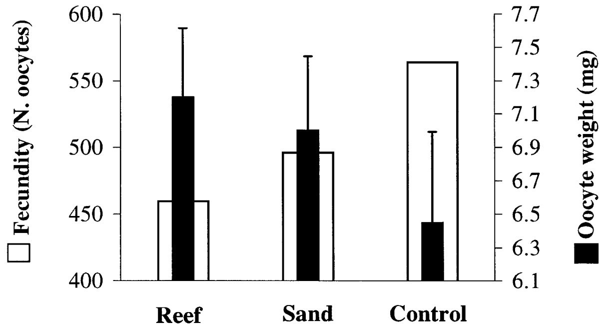

Figure 3. Fecundity of *Oreochromis niloticus* females and mean oocyte weight (± SE) depending on rearing environment. For clarity purposes, values were equated for 100 g standard females (calculated from statistical relationships given in *table II*).

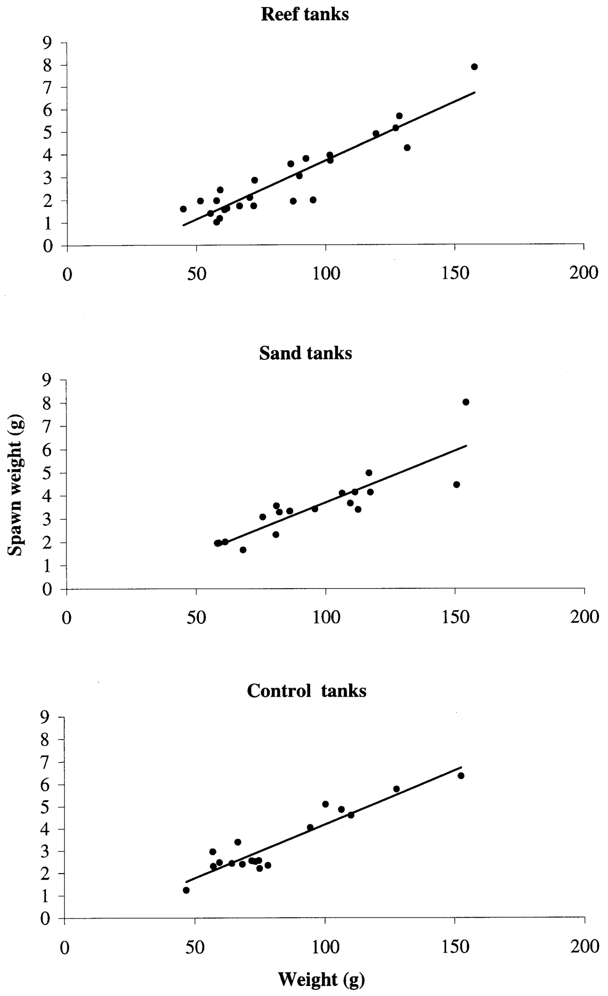

Figure 4. Spawn weight–body weight relationships of *Oreochromis niloticus* females for each treatment. Statistical relationships are given in *table II*.

significantly lower in the reef tanks than in the control tanks (*$F_{1,41}$ = 8.082, P = 0.007*).

4. DISCUSSION

The results indicated that the structure of living space influences the reproductive characteristics of tilapias and suggested it is more important than substrate quality. As the physico–chemical factors, fish mean size, food ration and distribution were similar between tanks during the whole experiment, the differences most probably reflect the influence of spatial organisation. An inverse relationship was found between the number and the weight of oocytes produced by the females, although the observed differences in oocyte weight were not significant among treatments. Egg size is often less variable than other reproductive traits (Stearns, 1992). Possibly, observed differences would have been even more pronounced with a longer experiment duration. It is indeed likely that the duration of the experiment was too short to obtain the full range of fish's phenotypic response to different environmental structures. Owing to this short duration, the maturation state of the fish groups placed in tanks at the beginning of the experiment might have been important. Fish of certain groups could have been in more advanced maturation than others. If small sized tilapia females tend to have a higher relative fecundity than larger individuals (Gohar et al., 1972; Siraj et al., 1983), they also tend to have a lower absolute and relative fecundity for their first reproductive cycle (Baroiller, personal communication). A difference between the number of females in a first reproductive cycle and the number of females that had already reproduced between the treatments might partially account for why oocyte sizes were not statistically different. A high proportion of ripe gonads in advance resorption was observed in each tank. High rates of atresia in fish are frequently related to insufficient or varying food supply or quality (Scott, 1962; Hislop et al., 1978; Robb 1982; reviewed by Wootton, 1979), suboptimal temperature and environmental conditions (Phillipart and Ruwet, 1982; Wohlfarth and Hulata, 1983), or to the end of the breeding season (Barbieri et al., 1994; Hunter and Macewicz, 1985; Hunter et al., 1986). However, these hypotheses are unlikely in this study, as food was supplied regularly and in sufficient amount, temperature and other physico–chemical conditions were adequate and reproduction occurs all year long at the Bouaké station. More probably, the number of males used (1 for 3 females) might have been insufficient in the special conditions of this experiment. Indeed, in every tank, 51 to 63.5% of the females were ready to spawn or just spent at the same time. When several females exhibit synchronous spawning, males may fail to reproduce with all of them. This phenomenon was observed in *Sarotherodon melanotheron* when the sex ratio was experimentally displaced in favour of females (Legendre and Trebaol, 1996). Males *Oreochromis* are able to spawn several times within the same day (Lowe-McConnell, 1959; Peters, 1971) but the capacity to fertilise successive clutches of eggs declines during the day (Rana, cited by Little et al., 1996). Moreover, females tend to mate preferably with unspawned males with ripe gonads (Silverman, 1978a, b). In the absence of a sufficient number of males, females do not experience the necessary conditions to spawn, and ripe oocytes are subsequently resorbed (Peters, 1963; Jobling, 1995). The similar proportions of resorption observed in each tank reinforce this hypothesis.

Changes of fecundity in response to modification of spatial structure appeared to occur faster than changes in oocyte size. After only 2 months of experimental rearing conditions, females placed in tanks equipped with artificial reefs had a significantly lower fecundity than females in the control tanks, whereas females from sandy bottom tanks had an intermediate fecundity. These results are consistent with those obtained on *Sarotherodon melanotheron* reared in bared or acadja enclosures in Ébrié Lagoon (Legendre and Ecoutin, 1996). However, the differences of reproductive characteristics observed for *Sarotherodon melanotheron* in these different rearing conditions were achieved for a constant spawn weight (Legendre and Ecoutin, 1996), whereas the spawn weight differed significantly between females reared in the reef tanks and in the control tanks in this study. Variations of reproductive investment per female were also reported between *Oreochromis niloticus* populations from man-made lakes of Ivory Coast (Duponchelle, 1997).

Spatial organisation is thus likely to rapidly modify the reproductive characteristics of tilapias, particularly fecundity. Different hypothesis may explain the observed decrease in absolute fecundity in the reef tanks. One might hypothesise that more food is lost in crevices in tanks with reefs, resulting in less food available for fish, hence in a decreased fecundity. However, this seems very unlikely as most of the food is consumed instantly before it reaches the bottom, all the fish being close to the surface at feeding time. Another potential explanation is that the presence of reefs (through augmentation of either shelters or breeding sites) would enhance the breeding rate of females (as attested by the higher proportion of sexually active females), which would eventually lead to a decreased absolute fecundity for the spawning females. This last hypothesis finds support in a relatively similar experiment. An experiment of egg and fry production, where *O. niloticus* were similarly placed in bare race-ways and race-ways equipped with artificial shelters (hollow bricks positioned in U), provided useful complementary results (Baroiller et al. 1997). The eggs and fry produced in these two situations were compared during three successive 14 days periods. It was found that more progenies were produced in presence of artificial shelters than in their absence. We observed that the presence of artificial shelters decreased absolute fecundity and tended to increase egg size whereas Baroiller et al. (1997) observed a consistent enhancement of fry production with shelters.

An increased fry production associated with a smaller absolute fecundity in the presence of artificial shelters can be achieved complementarily through different processes: 1) in *O. niloticus* spawning groups, a hierarchy is rapidly established and dominant females spawn more frequently than others (Rothbard, 1979). It is very probable that the presence of shelters and the multiplication of breeding sites may improve the access to reproduction for subordinate females. 2) Stimulation of spawning frequency for both dominant and subordinate females. 3) The fry production might have been also enhanced by an improved survival of fry born from bigger eggs. It is indeed well documented that the size of eggs enhances fry survival, allowing them to fit resource availability, to escape the size class targeted by predators and to feed upon larger particles (Bagenal, 1969, 1978; Marsh, 1986; Sargent et al., 1987; Wootton, 1990, 1994).

Another striking result is the rapidity at which changes in reproductive characteristics occurred. The plasticity of reproductive and growth traits is well known and documented in tilapias (Lowe-McConnell, 1958, 1982; Trewavas, 1983; Baroiller and Jalabert, 1989; Legendre and Ecoutin, 1989, 1996; James and Bruton, 1992; Duponchelle and Panfili, 1998; Duponchelle et al., 1998, 1999, 2000). Nevertheless, as far as we know, it is the first experimental evidence of such rapid phenotypic changes in response to environmental variation: modifications of reproductive traits were observed after only 2 months. Assuming that the mean interval between two successive spawns is about 4 weeks in culture conditions for *O. niloticus* (Fishelson, 1966; Tacon et al., 1996), our results show that one or two vitellogenesis cycles are sufficient to observe significant variations in reproductive characteristics, in fecundity particularly.

These results demonstrate that the spatial organisation of their living space, probably through the multiplication of refuges and breeding sites, influences the reproductive characteristics of tilapias. They also show that the phenotypic response of tilapias to a modification of their environment can be effective within one or two reproductive cycles only. This should find immediate applications in tilapia aquaculture and deserves further investigations.

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