OREOCHROMIS NILOTICUS (CICHLIDAE) IN LAKE AYAME, COTE D'IVOIRE: LIFE HISTORY TRAITS OF A STRONGLY DIMINISHED POPULATION

by

Fabrice DUPONCHELLE (1) & Marc LEGENDRE (1, 2)

ABSTRACT. - *Oreochromis niloticus* has become rare in Lake Ayame, presumably because of the competition with another species of tilapia, *Sarotherodon melanotheron*. Its breeding season, size and age at first sexual maturity, fecundity and egg size were studied between October 1994 and October 1996. The breeding season occurred during the period from January to September, with a peak between April-May and July. The fish matured in their first year at 10 months old, at a size range between 11.6 cm and 13.5 cm SL. They produced few (416 and 343 eggs for a 100 g female in 1995 and 1996, respectively) but large eggs (7.7-7.9 mg as a mean). Life history traits of *O. niloticus* in Lake Ayame are compared to those obtained for other populations in Côte d'Ivoire, and discussed in relation to the interspecific competition with *S. melanotheron*.

RÉSUMÉ. - *Oreochromis niloticus* (Cichlidae) dans le lac d'Ayame, Côte d'Ivoire: caractéristiques de reproduction d'une population fortement diminuée.

Oreochromis niloticus est devenu rare dans le lac d'Ayame, probablement en raison de la compétition qui l'oppose à une autre espèce de tilapia, *Sarotherodon melanotheron*. La saison de reproduction, la taille et l'âge de première maturation sexuelle, la fécondité et la taille des ovocytes ont été étudiés chez *O. niloticus* entre octobre 1994 et octobre 1996. La saison de reproduction avait lieu entre janvier et septembre avec un pic d'activité entre avril-mai et juin. La maturité était atteinte dans la première année à 10 mois, à une longueur standard variant entre 11,6 et 13,5 cm. Les femelles produisaient peu d'ovocytes (416 et 343 ovocytes pour 100 g de poids du corps, respectivement en 1995 et 1996) mais de grosse taille (7,7-7,9 mg en moyenne). Ces caractéristiques de reproduction sont comparées à celles d'autres populations de Côte d'Ivoire et discutées à la lumière de la compétition interspécifique avec *S. melanotheron*.

Key words. - Cichlidae - *Oreochromis niloticus* - Tilapia - Africa - Côte d'Ivoire - Man-made lake.

Ayame was the first hydroelectric dam built in Côte d'Ivoire. Established on the river Bia, in the south-east of the country, the reservoir was filled in 1959. The inundated area, covering approximately 14,000 ha (Lessent, 1971), was an undulating zone covered by a dense rain forest, most of which was not removed before the reservoir's filling. The lake waters therefore are characterised by a typical dark colour resulting from an intense vegetal decomposition. In Côte d'Ivoire, the only water courses where *Oreochromis niloticus* (Linnaeus, 1758) could originally be found were the tributaries of the Niger and

---

(1) IRD/GAMET, 361 rue J.R. Breton, BP. 5095, 34000 Montpellier, FRANCE. [fabrice.duponchelle@mpl.ird.fr]
(2) ORSTOM, Instalasi Penelitian Perikanan Air Tawar, Jl. Ragunan, Pasar Minggu, P.O. Box 7220/Jkspm, Jakarta 12540, INDONESIA.

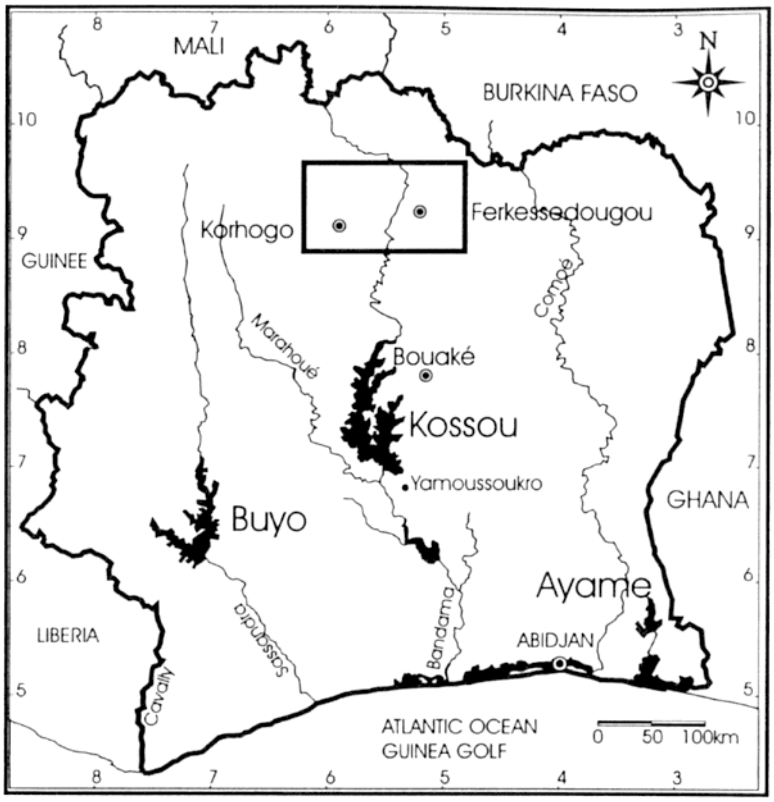

Fig. 1. Hydrographic map of Côte d'Ivoire (Africa), with the large hydroelectric lakes. The shaded rectangular zone in the north side of the country corresponds to the area where the agro-pastoral reservoirs are located.

Volta drainage in the North of the country (Daget and Iltis, 1965; Teugels and Thys van den Audenaerde, 1992). To compensate for the lack of phytoplanctonic fish species in the lake, *O. niloticus* fingerlings raised from brooders caught in the Volta river, were introduced into Lake Ayame in 1962 (Lessent, 1971). A few years after its introduction, *O. niloticus* represented over 50% of fish catches in the lake (Lessent, 1971), and though its relative production decreased after 1973 due to utilisation of smallest mesh size by fishermen and new gears (cast-nets and traps) providing better catches of *Heterotis niloticus* and *Chrysichthys walkeri* (Doudet, 1979), it remained an important species in the catches. However, the species now appears to be in strong decline, since the apparition in 1984 (Gourène *et al.*, 1999) of another tilapia species, *Sarotherodon melanotheron* (Rüppell, 1852), originating from the Ivorian lagoon. *S. melanotheron* is a brackish water species, naturally occurring in lagoons, estuaries and lower river courses from Senegal to Congo (Trewavas, 1983; Teugels and Thys van den Audenaerde, 1992). The origin of this latter species in Lake Ayame remains controversial and two hypothesis are opposed: *S. melanotheron* would have been either introduced accidentally by aquaculture trials, or a population of this species would have been isolated by the dam's closure and would have developed progressively to become dominant since 1984 (Gourène *et al.*, 1999). However, it seems that the hypothesis of isolation be more plausible (G. Teugels, pers. com., Sept. 1998). *S. melanotheron*, which now constitutes the major part of the catches (Vanga *et al.*, in press), seems to have displaced *O. niloticus* to the north of the lake, the only place where its catches are still significant.

In a comparison of *O. niloticus* life history traits in the agro-pastoral reservoirs of the northern Côte d'Ivoire and in the main hydro-electric reservoirs of the country (Fig. 1) (Duponchelle, 1997), the special case of the Lake Ayame population is particularly interesting. Apart from recent man-made lakes in San Pedro region in which *S. melanotheron* might have been isolated as well, Lake Ayame is the only lake in Côte d'Ivoire where *O. niloticus* is not dominant and where it is in competition with *S. melanotheron* (Gourène *et al.*, 1999). Moreover, all the *O. niloticus* introductions in Côte d'Ivoire, except those of Lake Ayame, were carried out using a domestic stock (Bouaké strain) reared at the IDESSA (Institut des Savannes) Aquaculture Station in Bouaké, produced by crossing stocks from the Nile basin and the Volta basin (Rognon, 1993; Lazard and Rognon, 1997). Therefore, all the *O. niloticus* introduced in Côte d'Ivoire have a common geographic origin, except those of Lake Ayame, which descend from fishes of the Volta basin (Lazard, 1990). This paper focuses on the life history characteristics of *O. niloticus* in the particular conditions of Lake Ayame and compare them with other Ivorian populations.

MATERIAL AND METHODS

A total of 1345 *Oreochromis niloticus* females were collected between October 1994 and October 1996. During the first year, samples were collected in October, November, December 1994 and in June 1995. During the second year, samples were collected monthly from December 1995 to October 1996. A minimum of 100 females was analysed each sampling month. Nearly all the fish were obtained from the region of Yahou in the northern part of the lake, well above Ebikro. In October 1994, owing to the quasi absence of *O. niloticus* at the Ayame station close to the dam, a week was spent on the lake visiting the fishermen camps to get some specimens. We were told that this species was now very rarely found in the south of the lake and to go further north in the region of Yahou, where we did find enough specimens for our study.

For each fish, total and standard lengths (TL and SL) were measured to the nearest mm, and body weight to the nearest gram. 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 were fixed in 5% formalin for subsequent estimation of fecundity and oocyte size. The maturity scale used was that of Legendre and Écoutin (1989). Stage 1 comprises immature females, stage 2, females beginning maturation and stage 3, maturing females. Stage 4 is characteristic of females which are going to reproduce, stage 5 of ripe females and stage 6 of post-spawning females.

Seasonal evolution of sexual activity was determined from the monthly proportions (in %) of the different stages of sexual maturation. In order to eliminate the small immature females which would give a biased weight to the immature stages (1 and 2) and to define more precisely the reproductive season, only females of a size which was superior or equal to the size at first sexual maturity were taken into account for this analysis.

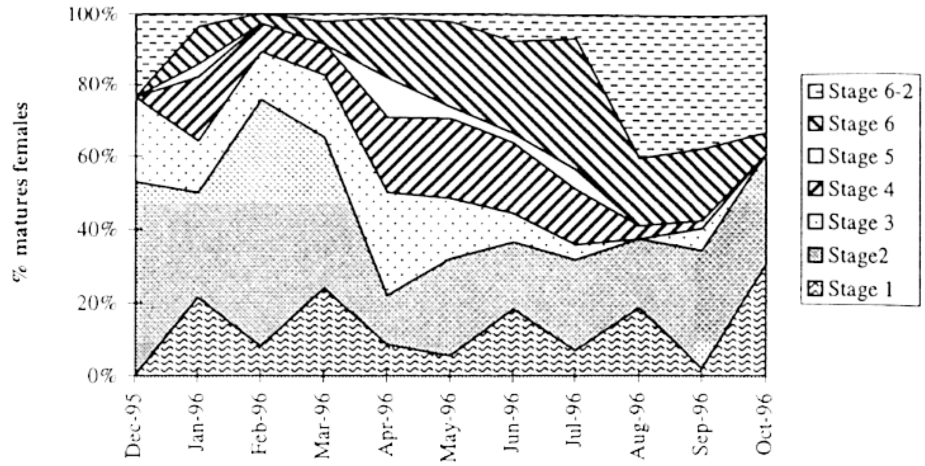

Fig. 2. Seasonal evolution of sexual maturity stages (monthly cumulated percentages) of *Oreochromis niloticus* females in Lake Ayame between December 1995 and October 1996.

Size at first sexual maturity was determined by fitting the fraction of mature females to a logistic function by non-linear regression according to the procedure described in Duponchelle and Panfili (1998): the average size at first maturation (L_{50}) is defined as the standard length at which 50% of the females are at an advanced stage of the first sexual cycle during the reproductive season. In practice, this is the size at which 50% of the females have reached stage 3 of the maturity scale. To avoid classifying resting females as immature, samples for size and age at maturity were collected during the peak of breeding season (June to August), when resting females are rare. Age at maturity was determined from otolith readings according to the procedure described in Duponchelle and Panfili (1998).

Fecundity and oocyte weight were determined as described in Duponchelle *et al.* (1998). In order to compare mean oocyte weight between successive years, the measurements need to be made on oocytes in a similar vitellogenic stage, then on oocytes whose growth is completed. The GSI threshold above which the oocyte weight and diameter no longer increase significantly for female *O. niloticus*, was determined. This threshold is reached at a GSI $\geq$ 4 for females whose body weight is less than 150 g and at GSI $\geq$ 3 for females whose body weight is superior or equal to 150 g (Duponchelle, 1997).

For the estimations of mean oocyte weight (and diameter), only females whose GSI satisfied the defined threshold were taken into account. This explains why the number of females considered for this estimation is less than the one corresponding to fecundity estimates.

Statistical analysis

Logistic models of size at maturity were compared for successive years using the maximum likelihood method (Tomassone *et al.*, 1993) as described in Duponchelle and Panfili (1998). As fecundity is positively correlated to size and to body weight in tilapias (Albaret, 1982; Legendre and Écoutin, 1989, 1996; Duponchelle *et al.*, 2000), estimation of fecundity differences between the two years were made by comparing regression lines between fecundity and female body weight. The regressions were compared by an analysis of covariance (Scherrer, 1984). Interannual comparisons of mean oocyte weight were performed by t-test (Scherrer, 1984).

Environmental data

Data on temperature and rainfall were provided by the Belgo-Ivorian cooperation program: "Évolution de la biodiversité des poissons après la construction d'un barrage: cas de la rivière Bia en Côte d'Ivoire" (Evolution of fish biodiversity after a dam construction: case of the Bia river in Côte d'Ivoire). Day-length monthly means were calculated from sunset and sunrise hours obtained at the web site of the "Bureau des Longitudes" (http://www.bdl.fr/).

RESULTS

Breeding season

Relative proportions of stages 4, 5 and 6 show that for *O. niloticus*, most of the breeding activity was spread over a period from January to September, with a peak between April-May and July. This was confirmed by the high proportion of resting females (stage 6-2) between July and December (Fig. 2). A surprisingly high proportion of immature females was found all year long even during the period of intense reproductive activity.

No particular relation was observed between the percentage of reproductively active females (stages 4-5-6) and the water temperature (Fig. 3A). However, the increased number of active females in March corresponded with an increase in water temperature. The relatively high percentage of active females in January is probably overestimated due to the low number of females (25) above the size at maturity (see below) in the January sample, and the real value is probably between the December and February values. The seasonal progression of the percentage of females 4-5-6 appeared well related to the annual rainfall cycle. The peak of sexual activity was observed during the peak of the wet season (Fig. 3B). Concurrently, a good relation was also observed with the photoperiod cycle, estimated by the day-length. The peak of breeding activity was observed during the summer solstice and the resting period corresponded with the winter solstice (Fig. 3C). Rainfall and day-length have parallel annual cycles as shown in figures 3B and C.

Age and size at maturity

Size at first sexual maturity of *O. niloticus* females for 1995 and 1996 is presented in table 1. Size at maturity increased by almost 2 cm between the two successive years, from 11.6 to 13.5 cm. The statistical comparison of the logistic curves (Fig. 4) revealed that this difference was significant (Table 1). In 1996, female *O. niloticus* in Lake Ayame

Table 1. - Size at first sexual maturity (L_{50} ± sd) of *Oreochromis niloticus* females in Lake Ayame in 1995 and 1996. N: total number of females used; n: number of females in the size range of 1 cm above and 1 cm below the L_{50}. The L_{50} comparison between 1995 and 1996 is indicated by the maximum likelihood test (SML) compared to $\chi^2 = 5.99$ (df = 2, $\alpha = 5\%$). *: significant difference ($p < 0.05$).

1995			1996			S_{ML}	1995 vs 1996
N	n	L_{50} (cm)	N	n	L_{50} (cm)		
200	118	11.6 ± 0.13	306	237	13.5 ± 0.72	-8.6	*

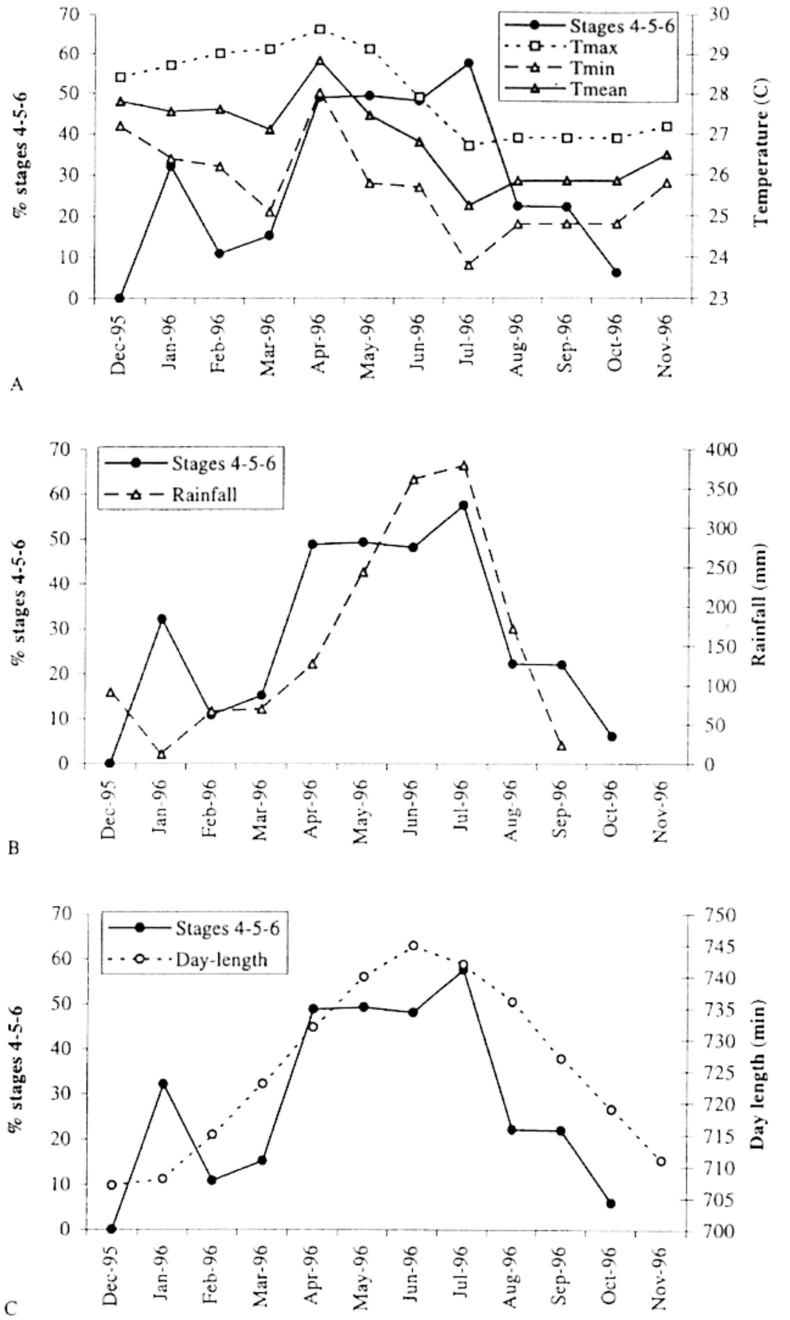

Fig. 3. Monthly proportions of sexual maturity stages 4-5-6 (which characterise the spawning season) of *Oreochromis niloticus* females. **A**: In relation to temperature (minimum, maximum and average) in Lake Ayame. **B**: In relation to rainfall in Lake Ayame. **C**: In relation to day-length in Lake Ayame.

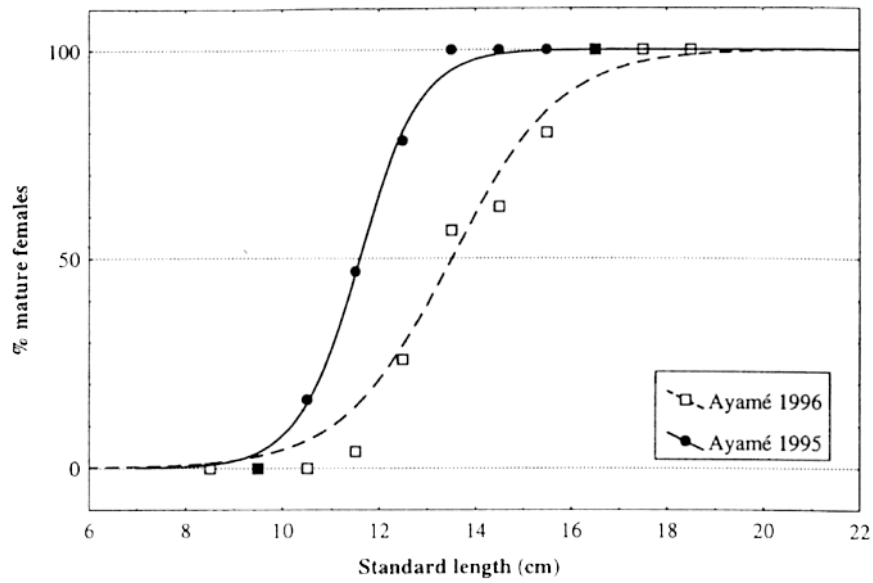

Fig. 4. Percentage of mature *Oreochromis niloticus* females by 10 mm standard length intervals, fitted to a logistic function in 1995 and 1996 for Lake Ayame.

matured in their first year, at 10 months, with a monthly growth rate of 1.4 cm (Table II).

Fecundity, oocyte size and spawn weight

Absolute fecundity of *O. niloticus* in Lake Ayame varied from 160 oocytes for a female of 46.2 g to 625 for a female of 156.5 g in 1995, and from 178 oocytes for a fish of 77.8 g to 717 for a fish of 208.6 g in 1996. The statistical relationships for both years are given in table III. The comparison of regression lines between fecundity and body weight revealed a highly significant intercept difference between the two years

Table II. Age at first sexual maturity (A_{50} ± sd) and mean monthly growth rate (L_{50}/A_{50}) of *Oreochromis niloticus* females in Lake Ayame in 1996.

N	A_{50} (days)	A_{50} (months)	L_{50}/A_{50} (cm/month)
14	302 ± 42	9.9	1.4

Table III. Statistical relationships between fecundity (F) and body weight (W) of *Oreochromis niloticus* females in 1995 and 1996 in Lake Ayame. Number of females used (N), correlation coefficient (r), probability (p), and comparison of regression line between the two years by covariance analysis. *: significant intercept difference ($F_{1, 111}$ = 17.07, $p < 0.001$).

Year	N	Relationships	r	p	1995 vs 1996
1995	38	F = 164.4 + 2.52 W	0.605	< 0.0001	***
1996	76	F = 92.6 + 2.50 W	0.720	< 0.0001	

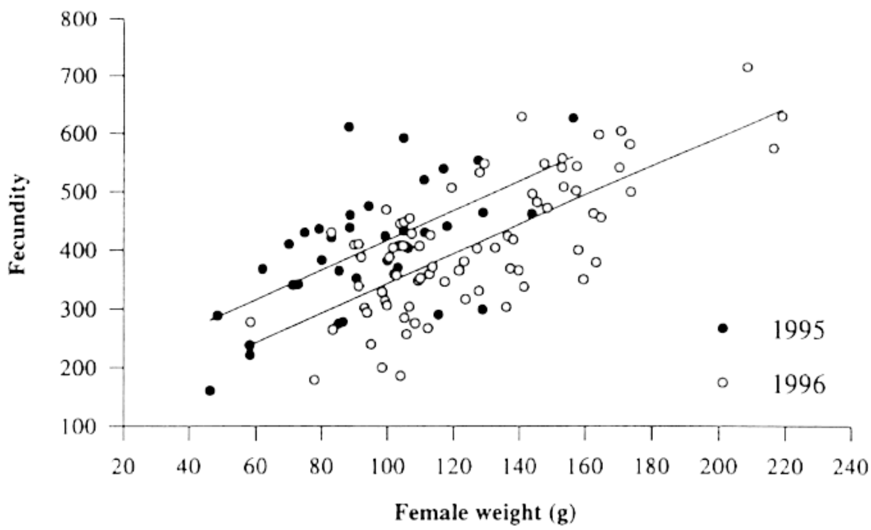

Fig. 3. — Regression lines between fecundity and body weight of *Oreochromis niloticus* females in Lake Ayame in 1995 and 1996.

(Table III). The fecundity was significantly lower in 1996 than in 1995 (Fig. 3). In return, the oocyte weight was higher in 1996 than in 1995, although this difference was not significant (Table IV).

DISCUSSION

Influence of latitude on *O. niloticus* breeding season appears throughout the literature (for reviews see Lowe-McConnell, 1958; Trewavas, 1983). In Israel, the northern limit of the species, reproduction occurs in April and May. It stretches progressively from March to September between 15°N and 10°N, and is no longer limited to a single season below 10°N. Despite the low latitude of Lake Ayame, 5° N, the breeding season of *O. niloticus* is restricted to a defined period, from January to September. The same breeding season is observed in 1996 for this species in the agro-pastoral man-made lakes of the northern Côte d'Ivoire situated at 10°N, while it occurs all year long in the hydroelectric Lake Kossou in the centre of the country (Duponchelle *et al.*, 1999). In Lake Ayame, the peak of breeding activity (between April-May and July) is shorter than in the agro-pastoral reservoirs (March to September) or in Lake Kossou (March to October). Whatever

Table IV. — Mean (± standard deviation) oocyte weight of *Oreochromis niloticus* females for 1995 and 1996 in Lake Ayame. N: number of females used, comparison between the two years. ns: non significant difference ($p > 0.05$).

1995		1996		1995 vs 1996
N	Mean oocyte weight (mg)	N	Mean oocyte weight (mg)	
3	7.7 ± 0.44	24	7.9 ± 0.9	ns

the period of the year, the proportion of sexually active females was much lower in Lake Ayame than in the agro-pastoral reservoirs or in Lake Kossou. During the peak of breeding activity, only 55% of stages 4-5-6 were found in Lake Ayame, while 85% and 80% were observed in Kossou and in agro-pastoral reservoirs, respectively.

If the beginning of the *O. niloticus* breeding season or the peak of sexual activity appears to be linked to increasing temperatures for latitudes greater than 20° (El Zarka *et al.*, 1970; review by Trewavas, 1983), it seems correlated to the rainy season and rise in water level in the lower latitudes (Lowe-McConnell, 1982; Trewavas, 1983; Stewart, 1988; Legendre and Jalabert, 1988; Mukankomeje, 1992). This corresponds to observations made in Lake Ayame, where a good relationship was observed between the breeding season and the rainfall cycle. However, though the rainfall patterns in the north and the south of the country are different, this relationship between breeding season and rainfall cycle was not observed in Lake Kossou and in the agro-pastoral reservoirs (Duponchelle *et al.*, 1999). In March, the relation between the increase of temperature and the number of active females suggested that the temperature might influence the onset of maturation. A close correlation ($r = 0.763$, $p < 0.05$) was found between the breeding season and the day-length cycle in Lake Ayame, as in all the reservoirs studied in the country. A multiple linear regression between stages 4-5-6 and the environmental variables (day length, temperature, rainfall) revealed that day length was the only factor contributing significantly to the model, which explained between 66 and 85% of the variation. It was concluded that the seasonality of *O. niloticus* breeding activity was mainly determined by the annual cycle of photoperiod in Côte d'Ivoire (Duponchelle *et al.*, 1999).

O. niloticus size at first sexual maturity was higher in Lake Ayame than in the small agro-pastoral reservoirs (6 to 620 ha), but smaller than in the large Lake Kossou (80,000 ha) (Duponchelle and Panfili, 1998). This confirms the positive correlation between size at maturity and the size of the water body frequently observed for tilapia species (Lowe-McConnell, 1958, 1982; De Silva, 1986; Legendre and Écoutin, 1989, 1996; Duponchelle and Panfili, 1998). Among the eight populations studied in Côte d'Ivoire, *O. niloticus* from Lake Ayame presented the oldest age at first sexual maturity and this was mainly due to their slower growth rate (1.4 cm/month) compared to the other populations (1.7 to 2.2 cm/month) (Duponchelle and Panfili, 1998). Size at maturity reveals to be a very plastic trait as a difference of 2 cm was observed between the two consecutive years. The same increase in L_{50} was observed in almost all the other populations studied during the same period.

An inverse tendency was found for fecundity. A decrease of fecundity was observed between the two years, together with an increased egg size. These changes also appeared in most of the other populations (Duponchelle *et al.*, 2000). Nevertheless, the population of Lake Ayame was distinguished from all other populations by its significantly lower fecundity and its larger eggs, in 1995 as well as in 1996. It is interesting to note that *S. melanotheron* also presented a lower fecundity and larger oocytes in Lake Ayame (Kone and Teugels, 1999) than in its natural environment (Legendre and Écoutin, 1989, 1996). Although they apparently present the same reproductive strategy in Lake Ayame, *O. niloticus* population is decreasing while *S. melanotheron* population increases.

One might hypothesise that the decline of *O. niloticus* in Lake Ayame was due to abiotic environmental constraints such as pollution or overexploitation, and that *S. melanotheron* would have taken advantage of vacant niches. However, neither pollution nor overexploitation has ever been thoroughly studied in Lake Ayame. The intensive use of insecticides by the lakeshore plantations might constitute a real pollution. However, the smallest agro-pastoral reservoir (Korokara termitière, 6 ha) studied in the north (Duponchelle, 1997) is surrounded by intensive onion cultures directly on the reservoir's banks (Fromageot, 1996). The use of insecticide is so massive that it is the only agro-pastoral reservoir studied without bilharzia (P. Cecchi, pers. com., Jan. 2000), and *O. niloticus* is the dominant species. Insecticide pollution can not be responsible for *O. niloticus* decrease in Lake Ayame. Despite the decreasing production of *O. niloticus* due utilisation of smaller mesh size by fishermen (Doudet, 1979) and an observed decreased mean size (Service des Eaux et Forêts, pers. com., Oct. 1994), a degree of overexploitation leading to such a diminished population is particularly unlikely in Lake Ayame given the exceptional abundance of stumps and dead trees preventing effective fishing in most areas and the well known resilience of this species. Among all the *O. niloticus* populations studied in Côte d'Ivoire, the population from Lake Ayame was the most distinct from the others, in term of its reproductive characteristics. It has a relatively shorter and less intense breeding season compared to the other populations, a delayed maturity associated with a low fecundity and large eggs. According to life history theory, this association of reproductive traits is characteristic of a population living in a stable environment (Lowe-McConnell, 1982; Noakes and Balon, 1982), with high interspecific competition and a high juvenile mortality (Schaffer 1974a, 1974b; Michod, 1979; Law, 1979; Reznick, 1982, 1989; Reznick and Endler, 1982; Reznick and Bryga, 1987; Reznick *et al.*, 1990). This might correspond quite well with the situation of *O. niloticus* in Lake Ayame. While it represented a significant portion of fish catches in the whole lake since its introduction in 1962 (Lessent, 1971), *O. niloticus* has now become rare and has been displaced to the north of the lake, in the region of Yahou, by another tilapia species, *S. melanotheron*. It is not known whether *O. niloticus* and *S. melanotheron* have the same trophic and/or breeding requirements in the particular conditions of Lake Ayame. However, these two species, which usually do not share the same habitat (brackish water versus freshwater), have very similar juvenile and adult trophic habits (Trewavas, 1983 for review). Moreover, like *O. niloticus*, *S. melanotheron* reproduces almost all year long in Lake Ayame (Koné and Teugels, 1999) and their peaks of breeding activity largely overlap. Thus, a high juvenile mortality resulting from an intense competition between the two species could have led to the decreased numbers and the observed association of reproductive traits for *O. niloticus*. The different geographic origin of *O. niloticus* from Lake Ayame could also partly explain why its reproductive characteristics are different from those of the other populations studied, though it does not help explaining its spectacular decline. Rearing fish from lakes Kossou and Ayame in a common environment for several months and comparing their reproductive traits, as it was done on the fish of Kossou and of one of the agro-pastoral reservoirs (Duponchelle *et al.*, 1998), would help answering this question.

Acknowledgements. We wish to acknowledge Jacques Panfili and Sami Hassani for otolith preparation and interpretation, and Jean-Baptiste Assamoa for laboratory assistance. We would also thank Jesus Nunez Rodriguez, Philippe Cecchi and Jacques Lemoalle for the useful discussions we shared. This study was supported by ORSTOM Department of Inland Waters, and Department of Earth, Ocean and Atmosphere.

REFERENCES

ALBARET J.J. 1982. Reproduction et fécondité des poissons d'eau douce de Côte d'Ivoire. *Rev. Hydrobiol. trop.*, 15(4): 347-371.

DAGET J. & A. ILTIS, 1965. Poissons de Côte d'Ivoire (d'eaux douces et saumâtres). *Mem. IFAN*, 74, 385 p.

DE SILVA S.S., 1986. Reproductive biology of *Oreochromis mossambicus* populations of man-made lakes in Sri Lanka: A comparative study. *Aquacult. Fish. Manag.*, 17: 31-38.

DUPONCHELLE F., 1997. Reproduction du tilapia (Pisces, Cichlidae) *Oreochromis niloticus* (Linnaeus, 1758) dans les retenues artificielles de Côte d'Ivoire: analyse comparative des modalités de reproduction et approche expérimentale de leur déterminisme. Thèse de Doctorat, 167 p. Univ. de Bretagne Occidentale.

DUPONCHELLE F. & J. PANFILI, 1998. Variations in age and size at maturity of female Nile tilapia, *Oreochromis niloticus*, populations from man-made lakes of Côte d'Ivoire. *Env. Biol. Fish.*, 52: 453-465.

DUPONCHELLE F., POUYAUD L. & M. LEGENDRE, 1998. Evidence of environmental effects on reproductive characteristics in Nile tilapia (*Oreochromis niloticus*) populations from man-made lakes of Côte d'Ivoire. *Aquat. Living Resour.*, 11(3): 137-144.

DUPONCHELLE F., CECCHI P., CORBIN D., NUNEZ J. & M. LEGENDRE, 1999. Spawning season variations of female Nile tilapia, *Oreochromis niloticus*, from man-made lakes of Côte d'Ivoire. *Env. Biol. Fish.*, 56: 377-389.

DUPONCHELLE F., CECCHI P., CORBIN D., NUNEZ J. & M. LEGENDRE, 2000. Variations in fecundity and eggs size of female Nile tilapia, *Oreochromis niloticus*, from man-made lakes of Côte d'Ivoire. *Env. Biol. Fish.*, 57: 155-170.

DOUDET T., 1979. La pêche artisanale dans la retenue artificielle d'Ayame (Côte d'Ivoire). *Notes Doc. Pêche Piscicult.*, C.T.F.T., Nouvelle série, 19: 1-26.

EL ZARKA S., SHAHEEN A.H. & A.A. EL ALEEM, 1970. Reproduction of *Tilapia nilotica* L. *Bull. Inst. Ocean. Fish. Cairo*, 1: 193-204.

FROMAGEOT A., 1996. Étude des petits paramètres maraîchers dans un village du nord de la Côte d'Ivoire: Korokara, 195 p. Univ. Paris 10.

GOURÈNE G., TEUGELS G.G., HUGUENY B. & D.F.E. THYS VAN DEN AUDENAERDE, 1999. Évaluation de la diversité ichtyologique d'un bassin ouest-africain après la construction d'un barrage. *Cybium*, 23(2): 147-160.

KONE T. & G.G. TEUGELS, 1999. Données sur la reproduction d'un tilapia estuarien (*Sarotherodon melanotheron*) isolé dans un lac de barrage ouest africain. *Aquat. Living Resour.*, 12(4): 1-5.

LAW R., 1979. Optimal life histories under age-specific predation. *Am. Nat.*, 114: 399-417.

LAZARD J., 1990. Transferts de poissons et développement de la production piscicole. *Rev. Hydrobiol. trop.*, 23: 251-265.

LAZARD J. & X. ROGNON, 1997. Genetic diversity of tilapia and aquaculture development in Côte d'Ivoire and Niger. *Bamidgeh*, 49: 90-98.

LEGENDRE M. & J.M. ÉCOUTIN, 1989. Suitability of brackish water tilapia species from the Ivory Coast for lagoon aquaculture. I - Reproduction. *Aquat. Living Resour.*, 2: 71-79.

LEGENDRE M. & J.M. ÉCOUTIN, 1996. Aspects of the reproductive strategy of *Sarotherodon melanotheron*: comparison between a natural population (Ebrie lagoon, Côte d'Ivoire) and different cultured populations. *In:* 3rd Int. Symp. on Tilapia in Aquaculture, Abidjan, Côte d'Ivoire (Pullin R.S.V., Lazard J., Legendre M., Amon Kothias J.-B. & D. Pauly, eds), pp. 326-338. ICLARM Conf. Proc. 41. Manille (Philippines): ICLARM.

LEGENDRE M. & B. JALABERT, 1988. Physiologie de la reproduction. *In:* Biologie et Écologie des Poissons d'Eau douce africains (Lévêque C., Bruton M.N. & G.W. Ssentongo, eds), pp. 153-187. Paris: ORSTOM.

LESSENT P., 1971. Aménagement piscicole de retenues artificielles de Côte d'Ivoire. *Notes Doc. Pêche Piscicult.*, C.T.F.T., Nouvelle série, 2: 45-56.

LOWE-MCCONNELL R.H., 1958. Observations on the biology of *Tilapia nilotica* Linné in East African waters. *Rev. Zool. Bot. Afr.*, 57: 129-170.

LOWE-MCCONNELL R.H., 1982. Tilapias in fish communities. *In:* The Biology and Culture of Tilapias (Pullin R.S.V. & R.H. Lowe-McConnell, eds), pp. 83-113. ICLARM Conf. Proc. 7. Manille (Philippines): ICLARM.

MICHOD R.E., 1979. Evolution of life histories in response to age mortality factors. *Am. Nat.*, 113: 531-550.

MUKANKOMEJE R., 1992. Production algale et consommation par le tilapia, *Oreochromis niloticus* L., au Lac Muhazi (Rwanda). Thèse de Doctorat, 254 p. Faculté des Sciences de Namur.

NOAKES D.L.G. & E.K. BALON, 1982. Life histories of tilapias: an evolutionary perspective.. *In:* The Biology and Culture of tilapias (Pullin R.S.V. & R.H. Lowe-McConnell, eds), pp. 61-82. ICLARM Conf. Proc. 7. Manille (Philippines): ICLARM.

REZNICK D.A., 1982. The impact of predation on life history evolution in Trinidadian guppies: Genetics of observed life history patterns. *Evolution*, 36: 1236-1250.

REZNICK D.A., 1989. Life history evolution in guppies: 2-repeatability of field observations and the effects of season on life histories. *Evolution*, 43(6): 1285-1297.

REZNICK D.A. & H. BRYGA, 1987. Life history evolution in guppies: 1-phenotypic and genotypic changes in an introduction experiment. *Evolution*, 41: 1370-1385.

REZNICK D.A. & J.A. ENDLER, 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution*, 36: 160-177.

REZNICK D.A., BRIGA H. & J.A. ENDLER, 1990. Experimentally induced life history evolution in a natural population. *Nature*, 346: 357-359.

ROGNON X., 1993. Diversité génétique et relations phylogénétiques chez les tilapias (Pisces: Cichlidae): comparaison des données du polymorphisme enzymatique et mitochondrial. Thèse de Doctorat, 175 p. Univ. de Paris 11.

SCHAFFER W.M., 1974a. Selection for optimal life histories: The effects of age structure. *Ecology*, 55: 291-303.

SCHAFFER W.M., 1974b. Optimal reproductive effort in fluctuating environments. *Am. Nat.*, 108: 783-790.

SCHERRER B., 1984. Biostatistique. 850 p. Boucherville: Gaëtan Morin.

SIRAJ S.S., SMITHERMAN R.O., CASTILLO-GALLUSER S. & R.A. DUNHAM, 1983. Reproductive traits for three year classes of *Tilapia nilotica* and maternal effects on their progeny. *In:* Proc. Int. Symp. on Tilapia in Aquaculture (Fishelson L. & Y. Yaron, eds), pp. 210-218. Israël: Tel Aviv Univ.

STEWART K.M., 1988. Change in condition and maturation of the *Oreochromis niloticus* population of Ferguson's Gulf, Lake Turkana, Kenya. *J. Fish Biol.*, 33: 181-188.

TEUGELS G.G. & F.E. THYS VAN DEN AUDENAERDE, 1992. Cichlidae. *In:* Faune des Poissons d'Eaux douces et saumâtres de l'Afrique de l'Ouest, Tome 2 (Lévêque C., Paugy D. & G.G. Teugels, eds), pp. 714-779. Paris: ORSTOM.

TOMASSONE R., DERVIN C. & J.-P. MASSON, 1993. Biométrie: Modélisation de Phénomènes biologiques. 553 p. Paris: Masson.

TREWAVAS E., 1983. Tilapiine Fishes of the Genus *Sarotherodon*, *Oreochromis* and *Danakilia*. 583 p. London: British Museum (Natural History).

VANGA A.F., GOURÈNE G. & G.G. TEUGELS, in press. Contribution de l'étude socio-économique de la pêche continentale au lac de barrage hydroélectrique d'Ayame (Côte d'Ivoire). *Tropicultura*.

Reçu le 14.10.1999.
Accepté pour publication le 16.02.2000.