Environmental Biology of Fishes **56:** 375–387, 1999.

Spawning season variations of female Nile tilapia, *Oreochromis niloticus*, from man-made lakes of Côte d'Ivoire

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Received 29 April 1998 Accepted 22 December 1998

Key words: seasonality, inter-annual variations, fish, cichlid

Synopsis

The spawning season of *Oreochromis niloticus* females was studied over two annual cycles in 6 small agropastoral and 2 large hydroelectric reservoirs of Côte d'Ivoire (Ayamé and Kossou), situated between 5 and 10°N of latitude. Reproduction occurred during a marked season in the agropastoral reservoirs and in Lake Ayamé, whereas it was continuous in Lake Kossou. Spawning season differed between reservoirs and among years within the same reservoir. Seasonal changes in temperature, rainfall, day length, chlorophyll a concentration and water level often corresponded with changes in the annual spawning cycle. However, annual periodicity of *O. niloticus* reproduction was more likely influenced by the ephemerides cycle.

Introduction

Fish constitute the main animal protein source in Africa. However, halieutic potential is under utilised in most of Africa's 20 000 man-made lakes (Vallet[1]). In West Africa, drought during the 1970's and increasing demographic pressure have prompted the construction of many of these structures (Cecchi [2]).

Naturally infrequent in Ivorian waters (Daget & Iltis 1965, Rognon 1993), *Oreochromis niloticus* L. (Pisces, Cichlidae) was introduced in the hydrographic system in 1962 (Lessent 1971) and has colonised all Côte d'Ivoire waterways (Teugels et al. 1988). *O. niloticus* is highly prized in aquaculture, and has met great success in the natural and man-made environments from ecological and economical points of view. This has lead the Côte d'Ivoire authorities to continue its introduction in the small agropastoral reservoirs (Lazard & Rognon 1997) in the North of the country where it could represent an important supplementary source of protein.

The spawning season of *O. niloticus* is influenced by latitude (reviews by Lowe-McConnell 1958, Jalabert & Zohar 1982, Trewavas 1983, Legendre & Jalabert 1988). In Israel, the northern limit for this species in natural conditions, *O. niloticus* spawns during April and May, whereas the spawning season is protracted progressively from March to September between 15°N and 10°N, and is no longer limited to a single season below 10°N.

[1] Vallet, M.F. 1993. Intensification de la gestion des plans d'eau en Afrique francophone. Doc. Techn. CPCA 22, FAO, Rome. 58 pp.
[2] Cecchi, P. 1998. De la construction d'un objet pluridisciplinaire: les 'Petits-Barrages' du nord de la Côte d'Ivoire. Natures-Sciences-Sociétés 6: 673–683.

However, contrasting with the literature, preliminary observations carried out on the reproduction of *O. niloticus* in small agropastoral reservoirs of the Northern part of Côte d'Ivoire (5–10°N of latitude) suggested the existence of a restricted spawning season. A comparative study of the reproductive traits of *O. niloticus* was initiated in eight man-made lakes of Côte d'Ivoire during two consecutive annual cycles in order to obtain accurate data on its reproductive cycle in these waterbodies. In the present study, inter-population differences and inter-annual changes of female *O. niloticus* spawning season in these reservoirs are presented, and discussed with regards to influence of environmental parameters. A new light is shed on the role of photoperiod, often neglected in tropical environments, which may have interesting applications for spawning synchrony, that remains one of the main issues in aquaculture of tilapia.

Materials and methods

We collected data from *Oreochromis niloticus* populations in six small agropastoral reservoirs (Korokara-Serpent, Korokara-Termitière, Lokpoho, Sambakaha, Solomougou and Tiné) (6–620 ha) of the northern Côte d'Ivoire and two large hydroelectric lakes, Kossou (80 000 ha) and Ayamé (14 000 ha) (Figure 1). Study areas were described by Duponchelle & Panfili (1998). Fish were bought to local fishermen. The three main gears used to catch *O. niloticus* were baited traps, castnets and gillnets. In the agropastoral reservoirs, where usually one or two fishermen operated, we have tried to provide gears to fishermen whenever one of the three was missing. To reduce the potential sampling bias related to gear selectivity, we made sure that, each month, an approximately equivalent number of females was taken from each of the three gears. In the hydroelectric reservoirs, the large number of fishermen allowed us to use the same process without providing gears. Between August 1994 and August 1995, *O. niloticus* females were collected in the six agropastoral reservoirs. Three of these six reservoirs (Korokara-Serpent, Sambakaha, Tiné) were studied during a second year between August 1995 and October 1996, to assess inter annual variations within the same population. The reservoirs chosen were those in which reproductive characteristics of *O. niloticus* females differed more markedly. The hydroelectric reservoirs were sampled during the flood season in 1994, and during the low-water season in 1995. Lake Kossou was sampled monthly from June 1995 to October 1996, and Lake Ayamé was sampled from December 1995 to October 1996. Thus, seasonal progression of sexual activity was studied only for the small reservoirs between August 1994 and August 1995, larger lakes were not sampled sufficiently. Spawning season was studied for the three selected agropastoral reservoirs (Korokara-Serpent, Sambakaha, Tiné) and the two hydroelectric lakes between August 1995 and October 1996.

We attempted to collect one hundred females per site each month with a size distribution as broad as possible. On each fish total and standard lengths (TL, SL) were measured to the nearest 1 mm, and body weight to the nearest 1 g. The gonads were checked macroscopically for maturity stages. The maturity scale used was that of Legendre & Ecoutin (1989). Stage 1 is distinctive of immature females, stage 2 of females beginning maturation and stage 3 of 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. Stage 6-2 is distinctive of resting females. Gonads containing a high proportion of retained oocytes in atresia were classified as stage 5-6. However, owing to their extremely low occurrence during the study, they were considered as negligible and are not presented.

Seasonal progression of sexual activity was determined from the monthly proportions (in %) of the different stages of sexual maturation. Only females which size was greater than or equal to the size at first sexual maturity were used in analysis, 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 spawning season. Size at first sexual maturity was determined according to the procedure described in Duponchelle & Panfili (1998).

Environmental data

Monthly means of rainfall and air temperature were obtained from IDESSA (Institut Des Savannes) stations of Ferkessedougou and Bouaké. Mean air temperature corresponded to monthly average of minimal and maximal recorded temperatures.

Water temperature, water concentration in chlorophyll a and water level were monitored in Sambakaha. Limnological characteristics, including chlorophyll a measurements, were recorded every 5 to 6 weeks. The values used in analysis correspond to global

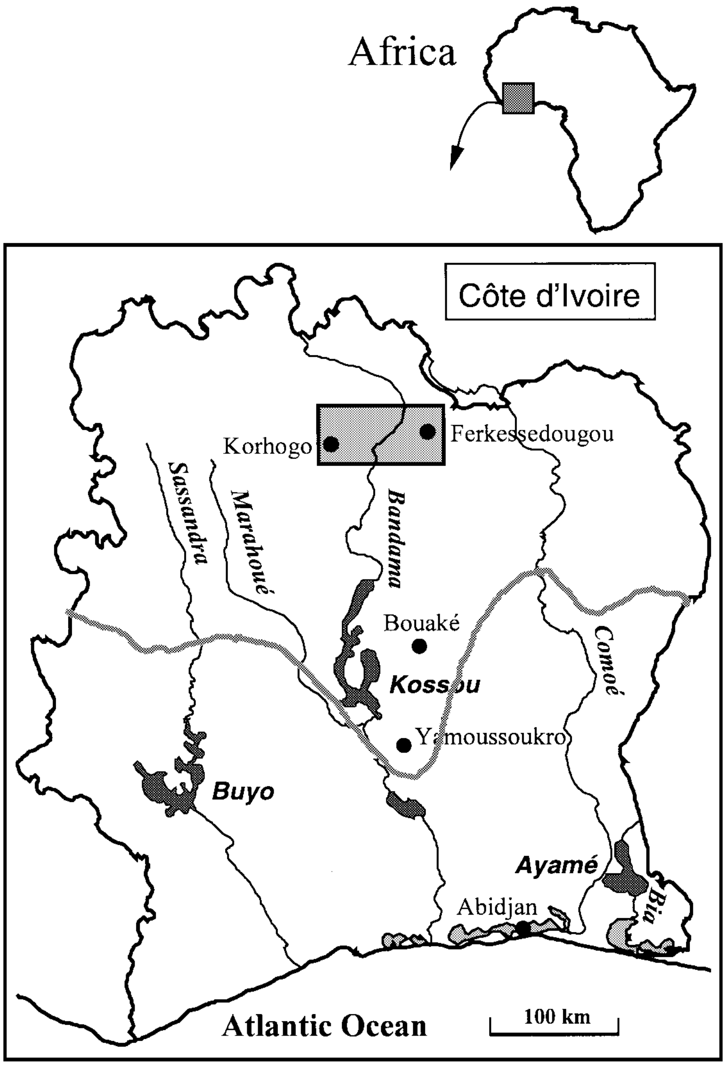

Figure 1. Hydrographic map of Côte d'Ivoire (Africa). The thick black line corresponds to the limit between the rain forest area (south) and the savanna area (north). The six agropastoral reservoirs are located in the shaded rectangular zone in the north side of the country.

means, that include all data collected at each sampling time: 3 stations (downstream, upstream and intermediary position), 2 or 3 samples according to depth at each of these stations, and 2 consecutive collecting days (during the afternoon, and early in the morning of the next day) to insure diurnal periodicity. Chlorophyll a concentrations were determined by the fluorometric method on phytoplankton retained on Whatman GF/F filters and methanol extraction (Yentsch & Menzel 1963). Water temperatures were measured ($\pm 0.5\,^{\circ}$C) between 6:00–7:00 h and 17:00–18:00 h each day and reported as monthly means. Air temperature was monitored in place of water temperature for the hydroelectric reservoirs. Monthly day-length means were calculated for the following towns (Figure 1): Ferkessedougou, Bouaké and Aboisso (just near the hydroelectric lake of Ayamé), from sunset and sunrise hours obtained at the web site of the Bureau des Longitudes (http://www.bdl.fr/).

Statistical analysis

Influence of the different environmental factors on the percentage of reproductively active females was analysed by a multiple linear regression (Scherrer 1984), using the Jandell Scientific Statistical Package. Basic assumptions of the model (normality, homoscedasticity and absence of multicollinearity between independent variables) were satisfied.

Results

A total of 8277 *Oreochromis niloticus* females, weighing between 5 and 975 g, were analysed between August 1994 and October 1996 (Ayamé 1345, Kossou 1889, and 5043 in the agropastoral reservoirs).

Periodicity of spawning season

The seasonal progression of *O. niloticus* sexual activity was not determined for each agropastoral reservoir because of discontinuity of data in some of them (Table 1). However, the annual cycle of maturity stages was very similar in all these reservoirs, which are located in the same geographic area, in a perimeter of about 80 km (Figure 1). Hence, data collected in these waterbodies were pooled for a global estimation of the reproductive period (Figure 2). The reservoir of Sambakaha (Figure 3a), which was the most intensively sampled (Table 1), was chosen as illustrative model for the agropastoral reservoirs.

Relative proportions of stages 4, 5 and 6 show that, in the agropastoral reservoirs, most of the reproductive activity was spread over a period from January to September, with a peak between April–May and August. This was confirmed by the high proportion of resting females (stage 6-2) between July and December 1995, and as soon as beginning of July 1996 (Figure 2). Nevertheless, visual observation of young at each field sampling and the presence, however limited, of maturity stages 4, 5, and 6 outside of this period suggested the existence of residual reproductive activity outside the regular season, at least during year 1994. Ripe females (stages 4 and 5) were not found between October and December 1995, and only a few post- spawning females (stage 6) were collected.

The most striking difference between 1995 and 1996 concerned the peak of sexual activity during the breeding period. Sexual activity reached a maximum between May and August in 1995, whereas this maximum was reached between April and August in 1996. Percentage of stage 4-5-6 females was about 50% in April 1995, whereas it reached about 70% in April 1996. In 1995, such a high percentage of mature fish was not observed before June. The peak of sexual activity was observed sooner and lasted longer in 1996 than in 1995. However, the beginning and the end of the

Table 1. Sampling frequency in each reservoir. Korokara-S, Korokara-T, Lokpoho, Sambakaha, Solomougou, and Tiné are the agropastoral reservoirs. Ayamé and Kossou are the hydroelectric reservoirs.

	1994					1995							
	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.
Ayamé			X	X	X						X		
Korokara-S						X		X	X	X	X	X	X
Korokara-T	X			X		X		X	X	X	X	X	X
Kossou			X	X							X	X	X
Lokpoho	X	X						X	X	X	X	X	X
Sambakaha	X		X	X				X	X	X	X	X	X
Solomougou	X	X	X	X				X	X	X	X	X	X
Tiné		X	X	X				X	X	X	X	X	X

	1995				1996									
	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.
Ayamé				X	X	X	X	X	X	X	X	X	X	X
Korokara-S							X	X	X		X	X	X	
Kossou	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Sambakaha	X	X	X	X	X	X	X	X	X	X	X	X	X	
Tiné			X	X	X	X			X		X	X	X	

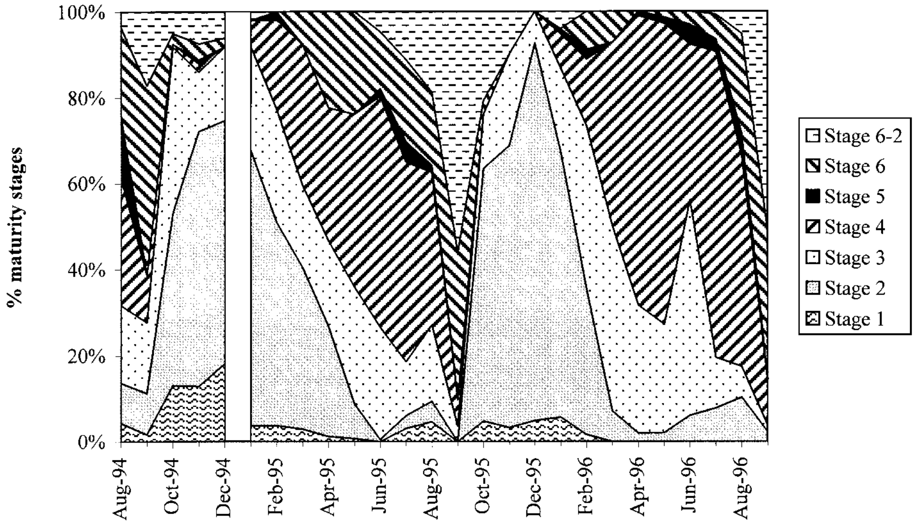

Figure 2. Seasonal progression of sexual maturity stages (monthly cumulated percentages) of *Oreochromis niloticus* females in the agropastoral reservoirs between August 1994 and September 1996.

whole breeding season were quite similar for the two years.

In hydroelectric Lake Kossou (Figure 3b), breeding period appeared not restricted to a definite season. Stages 4-5-6 were observed all year round, although in weak proportions from October to January. The period of increasing sexual activity also lasted longer in Kossou than in agropastoral reservoirs. As a matter of fact in October 1996, percentage of stages 4-5-6 was still around 70% in Lake Kossou, while it did not exceeded 45% in the agropastoral reservoirs.

Inter-annual variations of spawning season within a same reservoir could be clearly illustrated taking Lake Kossou as an example (Figure 3b). In 1995, sexual activity was yet considerably lowered in October, with only 15% of stages 4-5-6, whereas the percentage of reproducing fish remained as high as 70% in October 1996. Intensity of sexual activity during the breeding period was also greater in 1996 than in 1995, as about 80% of stages 4-5-6 were observed in June 1996 against 60% only in June 1995.

In hydroelectric Lake Ayamé (Figure 3c), reproduction appeared to be limited to the period from January to September, with a maximum between April and July. However, during all observed periods, proportions of stages 4-5-6 were always smaller than those found in Kossou or in agropastoral reservoirs. During the peak of sexual activity, only 55% of stages 4-5-6 were found in Lake Ayamé, whereas 85% and 80% were observed in Kossou and in agropastoral reservoirs, respectively. Unlike in the others reservoirs, important proportions of immature females (stages 1 and 2) were also found all year long in Lake Ayamé, even during the peak of sexual activity.

Altogether, the results indicated that 1996 was a more favourable year for reproduction than 1995, both in agropastoral reservoirs of the northern Côte d'Ivoire and in hydroelectric Lake Kossou in the centre of the country. This was illustrated by an earlier and longer peak of sexual activity in agropastoral reservoirs, but a similar global season of reproduction. For the Kossou population, intensity and global duration of spawning season were greater in 1996.

Relation to the environmental parameters

In Lake Kossou, reproduction started during the period of warmer temperatures and seemed to increase with decreasing temperature (Figure 4a). However, as illustrated on Figure 4c, water temperature decreases slower than air temperature. It could then be considered that most of the reproduction period occurred during the warmer temperatures, even though apparently part of breeding period lasted after temperature decrease. The breeding cycle corresponded relatively well with intensity of rainfalls (Figure 4b).

In agropastoral reservoirs, illustrated by Sambakaha, reproduction started just after the coldest temperatures, when temperature started to rise. The main reproductive activity occurred during warmer temperatures

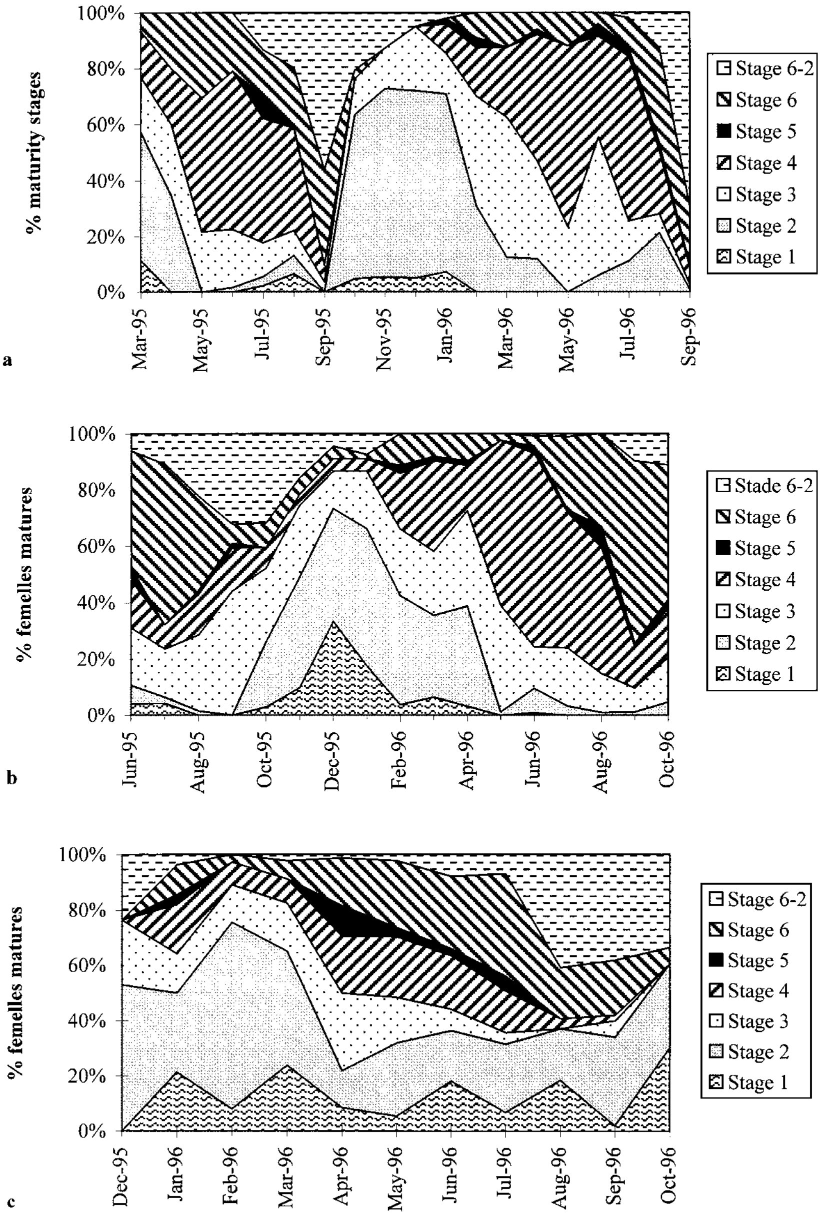

Figure 3. Seasonal progression of sexual maturity stages (monthly cumulated percentages) of *Oreochromis niloticus* females in the reservoirs of Sambakaha (a), Kossou (b) and Ayamé (c).

(Figure 4c). Breeding started during the dry season, increased with first rains and stopped with increasing rainfall (Figure 4d). In other respects, breeding cycle was correlated with the cycle of chlorophyll a concentration ($r = 0.756$, $p = 0.007$), but with a slight temporal shift (Figure 5a). In 1995 as in 1996, increase of chlorophyll a concentration occurred one month before the initiation of breeding activity. The peak of sexual activity corresponded with the peak of chlorophyll a concentration. Reproduction was maximal during dry season and during flooding, and minimal during the high water level in agropastoral reservoirs (Figure 5b).

Although the cycle of these diverse environmental variables corresponded quite well with the annual

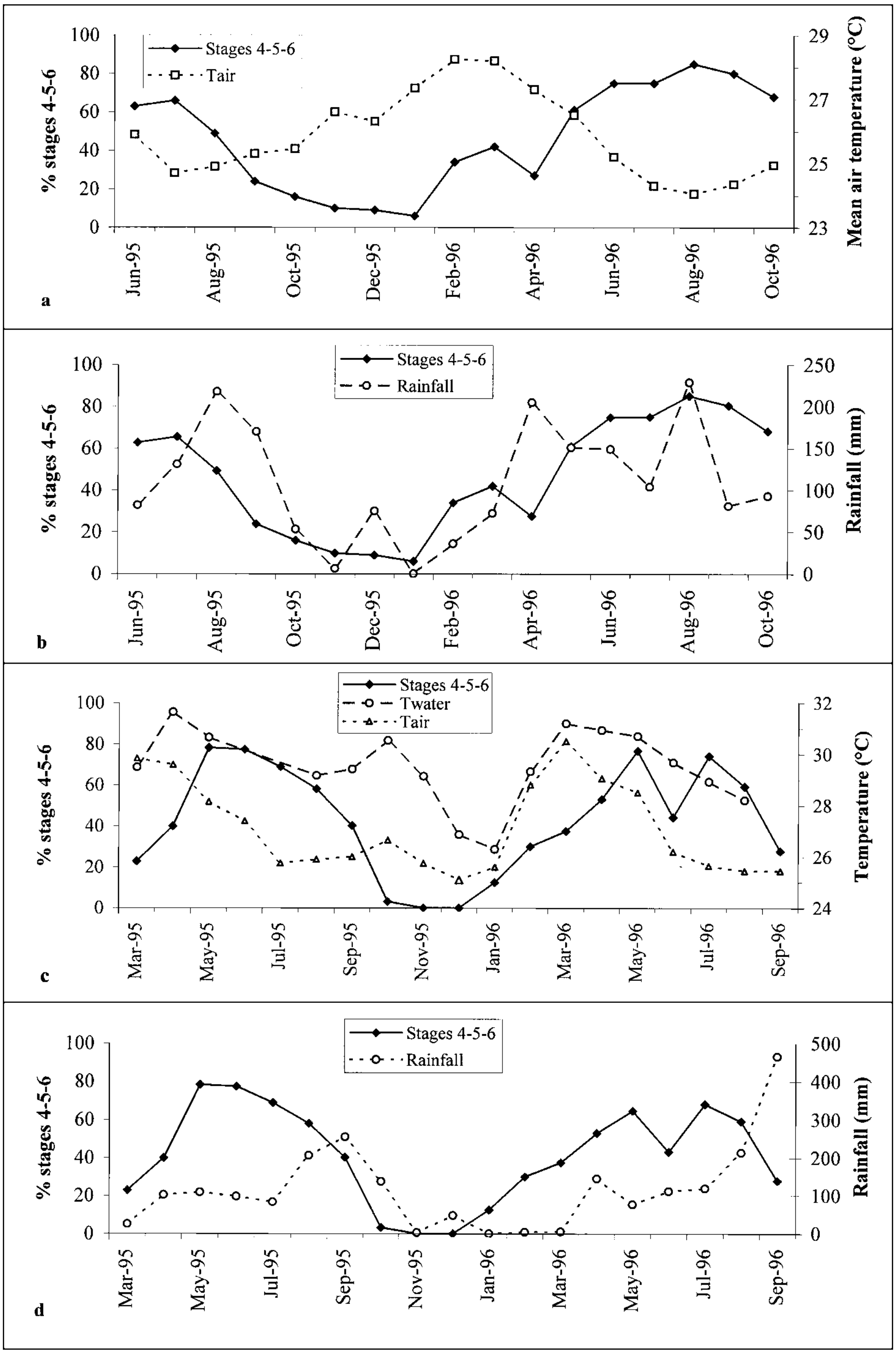

Figure 4. Monthly proportions of sexual maturity stages 4-5-6 (which characterise the spawning season) of *Oreochromis niloticus* females, in relation with temperature and rainfall in the reservoirs of Kossou (respectively a and b) and Sambakaha (respectively c and d).

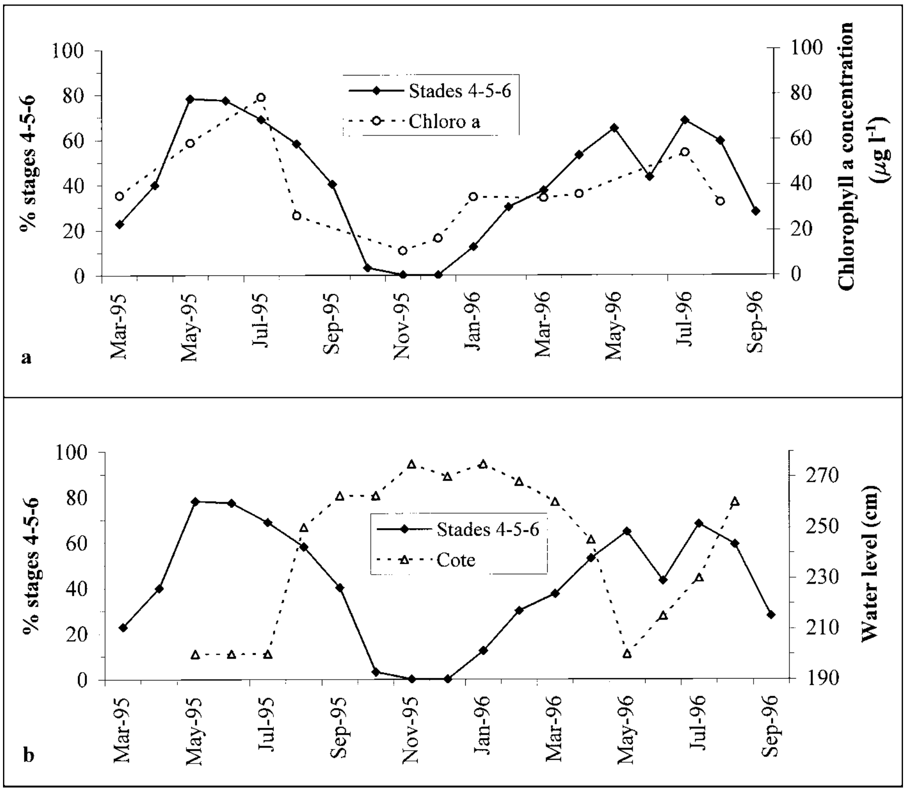

Figure 5. Monthly proportions of sexual maturity stages 4-5-6 (which characterise the spawning season) of *Oreochromis niloticus* females, in relation with chlorophyll a concentration (a) and water level (b) in the reservoir of Sambakaha.

breeding cycle of *Oreochromis niloticus*, none could explain precisely the observed cycle periodicity. The only constant phenomenon, apparent in all reservoirs, was that the maximum of reproduction always occurred in June, during summer solstice, and the minimum in December, during winter solstice. A correlation between breeding cycle and day length was then hypothesised. The annual cycle of day length was calculated for each latitude: 5°15 N for Ayamé, 7°42 N for Kossou and 9°30 N for the agropastoral reservoirs. In each studied reservoir, breeding cycle was correlated (agropastoral reservoirs: $r = 0.914$, $p < 0.0001$; Sambakaha: $r = 0.910$, $p < 0.0001$; Kossou: $r = 0.750$, $p = 0.0005$; Ayamé: $r = 0.763$, $p = 0.006$) with annual cycle of day length (Figures 6a, b, c, d). This correlation was observed also for successive years within one reservoir. Multiple linear regression analysis were performed between the percentage of stages 4-5-6 and environmental variables (day length, temperature, rainfall) for the populations of Kossou and Sambakaha, in order to verify that day length was the most important factor explaining the periodicity of breeding cycle. For the populations of Sambakaha (Table 2) and Kossou (Table 3), no multicollinearity was found between independent variables. Day length was the only environmental factor contributing significantly to the model, which explained 85 and 66% of the variation of the dependant variable, for Sambakaha and Kossou, respectively.

Discussion

In tilapias, the beginning of breeding season or the peak of sexual activity appears to be linked with increasing temperatures at latitudes greater than 20° (El Zarka et al. 1970, reviews by Jalabert & Zohar 1982, Trewavas 1983), and seemed to correspond with rainy season and rise in water level at lower latitudes (Lowe-McConnell 1958, 1959, 1982, Trewavas 1983, Legendre & Jalabert 1988, Stewart 1988, Mukankomeje 1992). In central Niger Delta, spawning season of *O. niloticus* is not

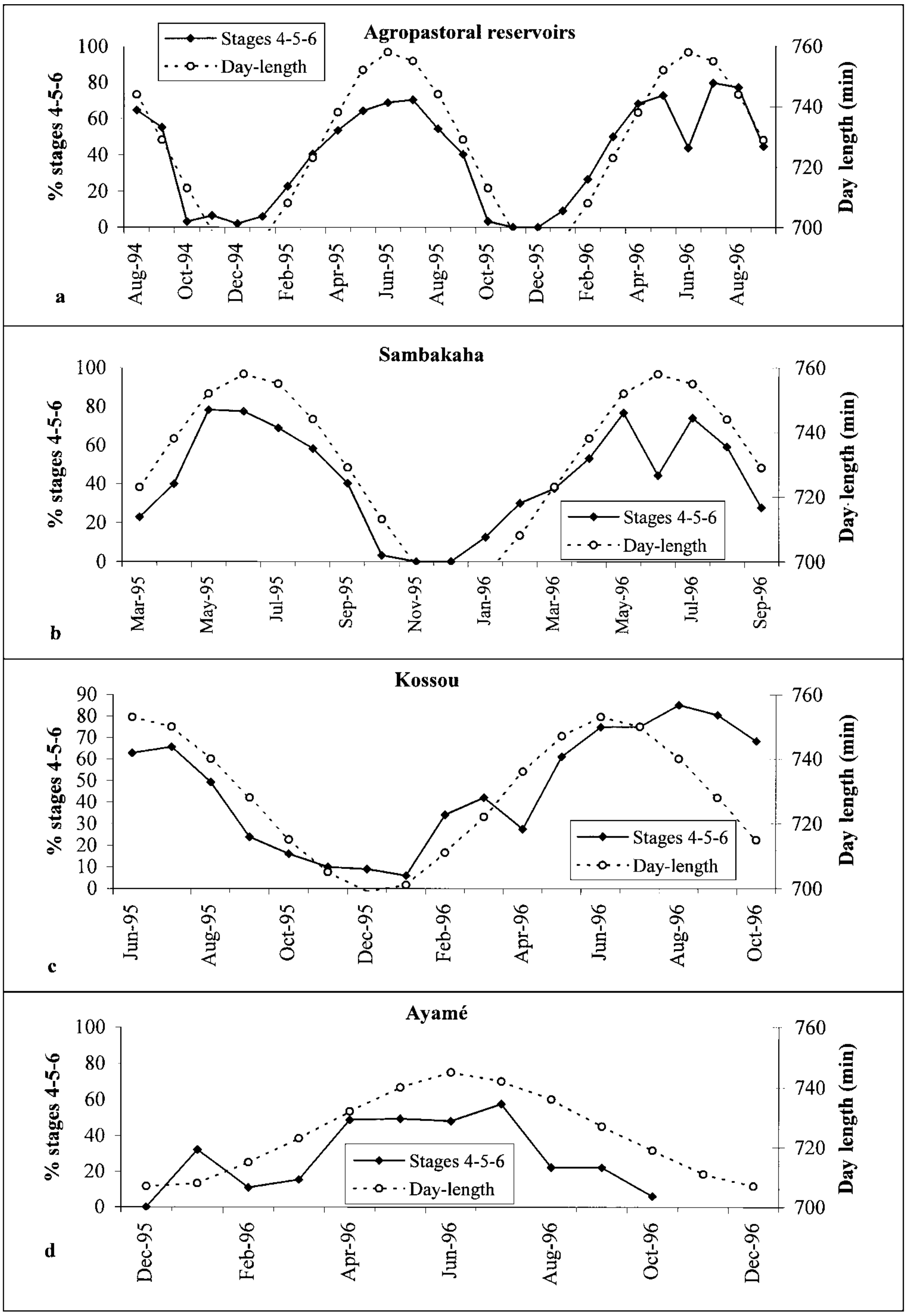

Figure 6. Monthly proportions of sexual maturity stages 4-5-6 (which characterise the spawning season) of *Oreochromis niloticus* females, in relation with day length, for the agropastoral reservoirs altogether (a), and in the reservoirs of Sambakaha (b), Kossou (c) and Ayamé (d).

Table 2. Results of the multiple linear regression model between the percentage of stages 4-5-6 (dependent variable) and day-length, water temperature and rainfall (independent variables) in Sambakaha Reservoir. Number of observations (n), F-statistic (F), coefficient of determination (r^2), variance inflation factor (VIF). VIF is a measure of multicollinearity (a value < 4 indicate no multicollinearity with the other independent variables).

ANOVA	Degree of freedom	Sum of square	Mean square	n	F	Significance level	r^2
Regression	3	10633.8	3544.6	18	25.7	$p < 0.0001$	0.846
Residuals	14	1931.9	138.0				
Total	17	12565.8	739.2				

Model	Coefficient	Standard error	t	Significance level	VIF
Constant	−781.541	105.006	−7.443	$p < 0.0001$	
Day-length	1.205	0.166	7.256	$p < 0.0001$	1.73
T. water	−1.840	2.350	−0.783	$p = 0.447$	1.33
Rainfall	−0.029	0.043	−0.668	$p = 0.515$	1.35

Table 3. Results of the multiple linear regression model between the percentage of stages 4-5-6 (dependent variable) and day-length, water temperature and rainfall (independent variables) in Lake Kossou. Number of observations (n), F-statistic (F), coefficient of determination (r^2), variance inflation factor (VIF). VIF is a measure of multicollinearity (a value < 4 indicate no multicollinearity with the other independent variables).

ANOVA	Degree of freedom	Sum of square	Mean square	n	F	Significance level	r^2
Regression	3	7919.7	2639.9	17	8.55	$p = 0.002$	0.664
Residuals	13	4012.5	308.7				
Total	16	11932.2	745.8				

Model	Coefficient	Standard error	t	Significance level	VIF
Constant	−447.635	273.00	−1.640	$p = 0.125$	
Day-length	0.952	0.319	2.985	$p = 0.010$	1.87
T. air	−7.533	3.318	−1.973	$p = 0.070$	1.35
Rainfall	−0.050	0.084	−0.593	$p = 0.564$	1.81

limited to the flooding period (July–October), part of the population also spawns during low water season (February–June) (Benech[3], Benech & Dansoko 1994). In small reservoirs in Burkina Faso, *O. niloticus* reproduces from end of April to August, with a peak between June and August. In these waterbodies, temperature rather than hydrology is hypothesised to regulate the reproduction (Baijot et al.[4]). In Lake Awasa, Ethiopia, *O. niloticus* breeds all year long, with a major peak of sexual activity from January to Marsh, and a minor

[3] Benech, V. 1990. Contribution á la connaissance de la reproduction de quelques espèces d'intérêt halieutique dans le delta central du Niger. ORSTOM-IER, études halieutiques du Delta Central du Niger. Actes de l'atelier de Bamako, 20–23 novembre 1990. 16 pp.

[4] Baijot, E., J. Moreau & S. Bouda. 1994. Aspects hydrobiologiques et piscicoles des retenues d'eau en zone soudano-sahélienne. Centre Technique de Coopération Agricole et Rurale (CTA), Commission des Communautés Européennes (CCE), Bruxelles. 250 pp.

one in July and August. The increased phytoplanktonic concentrations during the rainfalls at these two periods were associated to the intensification of sexual activity (Demeke[5]). In the present study, carried out in man-made lakes of Côte d'Ivoire situated between 5 and 10°N, breeding activity of *O. niloticus* extended from January to September, with an intensification between April–May and August. Among the reservoirs studied, only the population from Lake Kossou seemed to reproduce all year long, despite a pronounced decrease (less than 10% of sexually active females) from November to January. The periodicity of the annual breeding cycle seems mainly determined by the day length cycle (see below). However, in 1995 as in 1996, the increase of chlorophyll a concentration (index of trophic availability) occurred one month before the initiation of reproductive activity, and could also act in the starting up of gonad maturation. Variation in resource availability may initiate reproduction of tropical species with multiple spawning patterns (Kramer 1978, Lowe McConnell 1979).

Water temperature can regulate tilapias reproductive cycles (Hyder 1970, Marshall 1979, Baijot et al. 1994, Cornish & Smit 1995, Chmilevskiy 1995, 1996). In agropastoral reservoirs of Côte d'Ivoire, *O. niloticus* reproduced during periods of warmer temperatures, whereas in Lake Kossou, reproduction continued after the temperature decreased. The observed lack of sexual activity in November and December in agropastoral reservoirs corresponds to a period during which a relatively cold dry wind, Harmattan, blows north of Côte d'Ivoire. This wind may decrease the water temperature below 22°C, under which *O. niloticus* stops to reproduce (Wohlfarth & Hulata 1983, Parrel et al.[6]). However, during the same period, breeding activity decreased or stopped in lakes Kossou and Ayamé, where the influence of Harmattan is far weaker and often unnoticeable. Influence of rainfall on tilapia reproduction is also well documented, although its role is often difficult to isolate from that of flooding (Lowe-McConnell 1958, 1959, 1982, Trewavas 1983, Legendre & Jalabert 1988, Stewart 1988). In Côte d'Ivoire, rainfall incidence on reproduction was not the same in all the reservoirs. While rainfall cycle corresponded relatively well with reproduction in Lake Kossou (centre of the country), reproduction started during the dry season, increased with the first rains and stopped with increasing rains in agropastoral reservoirs of the northern country. Thus, periodicity of breeding cycle could be explained neither by temperature nor by rainfall alone, whose annual cycle is generally shifted from reproduction cycle.

The regulation of photoperiod on fish reproduction is well established in temperate regions, whereas it is often neglected in tropical and sub-equatorial regions because of its relative constancy. The role of photoperiod has been mentioned only for the development of gonads and reproductive activity in *Tilapia macrocephala* (Aronson 1951), the starting up of gonads maturation in *O. mossambicus* (Hyder 1970, Cornish & Smit 1995) and the timing of spawning in *O. aureus* (Marshall & Bielic 1996). Recently, a close relation was observed between day-length and breeding activity for *O. niloticus* and *O. aureus* breeders reared in tanks supplied with water from a nuclear power plant in Belgium (Baroiller et al. 1997, Desprez & Mélard 1998). These studies show that the spawning season of tropical fish species subject to permanent warm waters appears closely related to the natural photoperiod of the temperate rearing area. Moreover, even when temperature was favourable, spawning activity was totally inhibited for *O. aureus* and strongly reduced for *O. niloticus* under short photoperiod. The same phenomenon was observed in Sambakaha Reservoir, as illustrated by Figure 4c: the peak of temperature recorded in October 1995 did not induce recovery of reproductive activity. In the man-made lakes of Côte d'Ivoire, it appears that periodicity of *O. niloticus* breeding cycle is strongly correlated to the annual day-length cycle whichever the observed reservoir. This correlation was reproducible from one year to another within one reservoir. A correlation between breeding cycle and concentration in chlorophyll a was also found in Sambakaha reservoir. However, the fact that in controlled conditions with regular and optimised food supply breeding activity stopped when day-length decreased (Baroiller et al. 1997, Desprez & Mélard 1998), suggests that resource availability is not the determining factor in explaining breeding seasonality in tilapias.

Agreement of our results, registered in natural conditions, with those obtained by Baroiller et al. (1997) and Desprez & Mélard (1998) in controlled situations leads to the following hypothesis. Breeding seasonality

[5] Demeke, A. 1995. Communication of the XXVI Congress of International Association of Theoretical and Applied Limnology, 22–29, July, Sao Paulo.

[6] Parrel, P., I. Ali & J. Lazard. 1990. Le développement de l'aquaculture au Niger: un exemple d'élevage de tilapia en zone sahélienne. *In*: Méthodes Artisanales d'Aquaculture du Tilapia en Afrique, CTFT, Département du CIRAD. 82 pp.

of tilapias would be controlled at two different levels: a high level, regulated by an astronomic constant (photoperiod), that determines the periodicity of the annual breeding cycle; and a lower level, controlled by the conjunction of environmental variables (temperature, rainfall, resource availability . . .), that modulates the inter-annual variations in breeding intensity and duration.

Influence of day length on the reproductive periodicity of *O. mossambicus* can also be observed in Cornish & Smit (1995), although it appears less clearly than in the present study. This may be due to the use of gonado-somatic index (GSI) to characterise the spawning season, instead of sexual maturity stages. At the end of spawning season, stages 6 (post spawning) which correspond to low GSI (around 1%), are predominant and constitute a large part of maturity stages in %. This explains why the GSI curve decreases faster than stages 4-5-6 curve. Using maturity stages, correlation between spawning season and day length would probably be far better. GSI, which is a well adapted tool to assess spawning season for fishes with only one spawning event in the year, appears less adapted for multiple spawning fishes because a same low GSI value (for example between 0.5 to 1.5%) can characterise totally different stages of gonad maturation (a gonad in beginning maturation as well as a post spawning gonad, in our example). Thus, sexual maturity stages constitute a far more precise tool than GSI to determine spawning season in fishes which reproduce several times during an annual cycle.

Stimuli involved in the intensification of sexual activity are not really well known. As previously seen in literature, it is often related to rainfall or flooding. In Ivoirian agropastoral reservoirs, flooding occurs only at the end of the reproduction peak. Our results suggest that intensification of reproduction would be induced by flooding preconditions, such as the first rains, which occur in each reservoir at the beginning of reproduction intensification. In other respects, the maximum of reproduction always occurs during the maximum day length and intensification of reproductive activity may be regulated by the conjunction of these two factors. Our results indicated that photoperiod should be considered more closely in explaining tilapias breeding seasonality. Experiments under controlled conditions could allow assessing more precisely the often neglected role of photoperiod in control of tilapias reproduction.

Acknowledgements

We wish to acknowledge Serge Thomas and Jean-Baptiste Assamoa for their help in collecting and monitoring environmental data on agropastoral reservoirs. We also thank IDESSA for providing data concerning air temperature and rainfalls. We specially acknowledge Jacques Lemoalle for the useful discussions we shared and for his valuable suggestions. This study was supported by ORSTOM Department of Inland Waters.

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