

Variations in fecundity and egg size of female Nile tilapia, *Oreochromis niloticus*, from man-made lakes of Côte d'Ivoire

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Synopsis

Fecundity and oocyte size of *Oreochromis niloticus* females were studied over a period of two annual cycles in six small agropastoral and three large hydroelectric reservoirs of Côte d'Ivoire. Important differences in fecundity and oocyte size were observed among populations and within the same population between successive years. An inverse correlation was found between size and number of oocytes produced by females. This inverse relationship occurred for a constant spawn weight during the first year of study, but not during the second year. Monthly mean residuals of regressions between fecundity and female body weight have shown a seasonal variation in fecundity. The peak of fecundity corresponded with the maximum resource availability and the flooding eminence, which may have a great impact on parents and offspring fitness.

Introduction

Cichlids, and especially tilapias, are fish with high biotic potentials. Ecological and economical success is due mostly to their exceptional adaptive capabilities (Wootton 1984). Depending on environmental characteristics, tilapias may direct the allocation of their resources to reproduction rather than growth (Fryer & Iles 1972, Lowe-McConnell 1982). Therefore, in natural waterbodies, one tilapia species can show large variations in its reproductive characteristics (Lowe-McConnell 1982). In culture situations, tilapias tend to produce more but smaller oocytes than under natural conditions (Fryer & Iles 1972, Legendre & Ecoutin 1989). Intensification in culture conditions also leads to a smaller size at first maturity, smaller oocyte diameter and more oocytes per spawning (Legendre & Ecoutin 1996).

Oreochromis niloticus L. (Pisces, Cichlidae) is one of the main tilapia species used in aquaculture throughout the world. It has been introduced widely in Côte d'Ivoire, where it was initially rare (Daget & Iltis 1965). Since then, it has colonised all Ivorian waterways (Teugels et al. 1988). *O. niloticus* is now one of the most important freshwater fishes of Côte d'Ivoire, from both economical and ecological point of view.

Life histories of tilapias have been described and discussed in several publications (Fryer & Iles 1972, Lowe-McConnell 1982, Noakes & Balon 1982, Stewart 1988, Ribbink 1990, Keenleyside 1991, Kolding 1993). However, comparative studies of the same species subjected to different environments are scarce and concern only a few cases: *Oreochromis mossambicus* (De Silva 1986, James & Bruton 1992), *Tilapia guineensis* and *Sarotherodon melanotheron* (Legendre & Ecoutin 1989, 1996).

Although *Oreochromis niloticus* is the most often introduced tilapia species in the world, it has never been subjected to such comparative study since the work of Lowe-McConnell (1958) in East African Great Lakes. Lowe-McConnell's study focused mainly on growth, breeding season and size at maturity, and was based on data collected irregularly along the annual cycle. Recently, a comparative analysis of reproductive characteristics of *O. niloticus* females was carried out in nine man-made lakes of Côte d'Ivoire, over a period of two annual cycles, between August 1994 and October 1996. Age and size at first sexual maturity (Duponchelle & Panfili 1998), spawning season (Duponchelle et al. 1999), fecundity and oocyte size were compared and analysed in relation with environmental parameters. The present paper focuses specifically on seasonal and inter-annual variations of fecundity and oocyte size among *O. niloticus* populations from man-made lakes of Côte d'Ivoire.

Material and methods

This study was carried out in three large hydroelectric lakes located in different areas of Ivorian territory, and six small agropastoral reservoirs in northern Côte d'Ivoire, between Korhogo and Ferkessedougou (Figure 1). These reservoirs were chosen for the diversity of environmental conditions and sizes (6–80 000 ha) that they represented. The waterbodies can be classified into three main groups: (1) Small pastoral reservoirs: Korokara-Serpent (15 ha), Korokara-Termièrre (6 ha) and Sambakaha (25 ha). (2) Small agricultural reservoirs: Lokpoho (620 ha), Solomougou (500 ha) and Tiné (45 ha). (3) Large hydroelectric reservoirs: Ayamé (14 000 ha), Buyo (60 000 ha) and Kossou (80 000 ha).

Between August 1994 and August 1995, fecundity, mean weight and diameter of oocytes in advanced vitellogenesis, and spawn weight of *Oreochromis niloticus* females were compared in the nine reservoirs. To assess inter-annual variations for a same population, five of the nine reservoirs (Korokara-Serpent, Sambakaha, Tiné, Ayamé, Kossou) were studied during a second year, between August 1995 and October 1996. These were chosen according to the diversity of environmental conditions and to the reproductive traits differences observed during the first year among populations.

For this study, we attempted to collect hundred females per site each month, with a size distribution

as broad as possible. In the agropastoral reservoirs, females were captured, then placed in drums containing formalin and dissected at the end of each month. Before being placed in the formalin, flanks of fishes were incised to facilitate preservation of gonads. For the hydroelectric reservoirs, the greater number of commercial fishers generally allowed the collection of about 100 females in a single day; therefore fish were always dissected fresh. In order to ensure the homogeneity of data taken from the two types of sampling, a comparison between body weight of fresh fishes and body weight of the same fishes, after being fixed three weeks in formalin, was undertaken using 100 females. No significant difference was found between fresh weight and fixed weight by a Mann-Whitney test ($p = 0.449$).

On each fish, total and standard lengths (TL, SL) were measured to the nearest 1 mm, and body weight to the nearest 1 g. Gonads were checked macroscopically for maturity stage and those in advanced vitellogenesis (stage 4) were removed and placed in 5% formalin. Gonads were then weighed to the nearest 0.1 g for the gonado-somatic index (GSI) calculation (gonad weight \times 100/total body weight). In order to ensure homogeneity of data on GSI and oocyte measurements, gonads collected on fresh fishes were always weighed after being fixed for a minimum of two weeks in 5% formalin.

The maturity scale used was that of Legendre & Ecoutin (1989). Briefly, 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 that are going to reproduce, stage 5 of ripe females and stage 6 of post-spawning females.

Fecundity is defined here as the number of oocytes to be released at the next spawn, and correspond to the absolute fecundity. 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 released. For each individual, fecundity was calculated from a sample representing at least 50% of ovary weight, then reported to the total weight of the ovary.

Oocyte weight and diameter measurements during the first year of study and oocyte weight during the second year were all carried out on samples preserved in 5% formalin. The average oocyte weight per female, was determined by weighing 50 oocytes (Peters 1963)

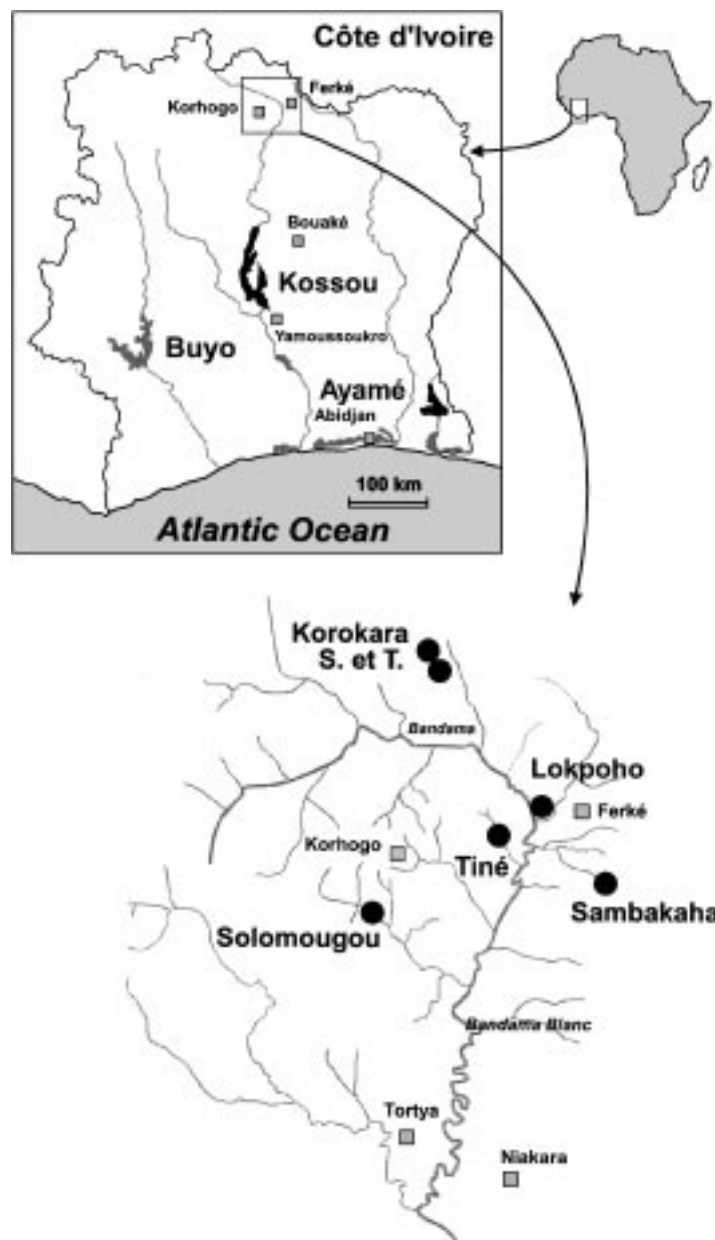


Figure 1. Hydrographic map of Côte d'Ivoire, with large hydroelectric reservoirs and detail of the agropastoral reservoirs region.

belonging to those considered for fecundity estimates. The average oocyte diameter was determined by the geometric mean of the larger and smaller diameters of each oocyte on a sample of 30 oocytes per female (Siraj et al. 1983).

In order to compare mean oocyte weight and diameter of various populations, the measurements need to be

made on oocytes in a similar vitellogenic stage, then on oocytes whose growth is completed. The GSI threshold was determined above which the oocyte weight and diameter do no longer evolve significantly for female *Oreochromis niloticus*: 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 greater than or equal to 150 g (Duponchelle 1997). The spawn weight (mean oocyte weight \times fecundity), representing the amount of gonadal material produced by a female during a reproductive cycle was used as an index of the reproductive effort.

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

Environmental data

Rainfall and air temperature data were monthly means, 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 and chlorophyll a concentration were measured every 5 to 6 weeks in some of the agropastoral reservoirs studied here. For convenience, only one of them, Sambakaha, will be presented as an illustrative example. Chlorophyll a concentrations were determined by the fluorometric method on phytoplankton retained on Whatman GF/F filters and after methanol extraction (Yentsch & Menzel 1963). Water temperature was measured ($\pm 0.5^\circ\text{C}$) between 6:00–7:00 h and 17:00–18:00 h and are presented as monthly means. For the hydroelectric lakes, air temperature is used instead of water temperature.

Monthly day-length means were calculated for the following towns (Figure 1): Ferkessedougou, Bouaké and Aboisso (just near the hydroelectric lake Ayamé), from sunset and sunrise hours, obtained at the web site of the Bureau des Longitudes (<http://www.bdl.fr/>).

Statistical comparisons

Fecundity and spawn weight are, in tilapias as in many other fishes, positively correlated to size and to body weight (Albaret 1982, Duarte & Alcaraz 1989, Legendre & Ecoutin 1989, 1996, Winemiller & Rose 1992). Therefore, estimation of differences between populations was made by comparing regression lines between fecundity and female body weight. The regressions were compared by an analysis of covariance (Scherrer 1984) followed by a 2×2 comparison method. First, slopes were compared, and populations whose slopes were not significantly different were then

compared for intercepts. 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. The new α' was calculated by the following formula:

$$\alpha' = 1 - (1 - \alpha)^{2/(k(k-1))}.$$

Inter-annual comparisons of fecundity in the same population were considered as independent analysis and were performed by covariance analysis.

As absolute fecundity and relative fecundity (fecundity per kg of female) are positively correlated to fish body weight in tilapias (Legendre 1992), the residuals of regressions between fecundity and body weight were used to search for seasonal variations of fecundity. This method allows us to eliminate the effect of weight and to present fecundity as a monthly mean for each population, provided a large number of monthly observations are made. For this reason, only the results concerning the populations of Kossou and Sambakaha (an hydroelectric and an agropastoral reservoirs), for which enough data are available, are described.

Comparisons of mean oocyte weights and diameters were carried out using a one-way ANOVA followed by the multiple comparison test of Duncan (Scherrer 1984). Inter-annual comparisons of mean oocyte weights in a same population were also considered as independent analysis and were performed by t-test when application conditions were satisfied and by Mann-Whitney rank sum test when they were not satisfied.

Results

Between August 1994 and October 1996, 8556 *Oreochromis niloticus* females (Ayamé 1345, Buyo 279, Korokara-Serpent 989, Korokara-Termitière 469, Kossou 1889, Lokpoho 496, Sambakaha 1700, Solomougou 519 and Tiné 870) were analysed.

Fecundity

Fecundity of *O. niloticus* varied from 149 to 2797, for fish weighing between 36 and 975 g in 1995, and from 178 to 1898, for fish weighing between 78 and 501 g in 1996 (Table 1). Fecundity increases linearly with female body weight ($r = 0.820$, $p < 0.001$ in 1995;

Table 1. Statistical relationships between fecundity (F) and body weight (W) of *Oreochromis niloticus* females in 1995 and 1996 in the reservoirs. Number of females used (N), correlation coefficient (r) and probability (p).

Reservoirs	Year	N	Relationships	r	p
Kossou	1995	87	$F = 277.7 + 2.91 W$	0.839	< 0.0001
	1996	246	$F = 335.2 + 2.04 W$	0.834	< 0.0001
Buyo	1995	99	$F = 197.1 + 3.64 W$	0.681	< 0.0001
Ayamé	1995	38	$F = 164.4 + 2.52 W$	0.605	< 0.0001
	1996	76	$F = 92.6 + 2.50 W$	0.720	< 0.0001
Lokpoho	1995	153	$F = 368.6 + 2.01 W$	0.667	< 0.0001
Solomougou	1995	122	$F = 260.5 + 3.14 W$	0.800	< 0.0001
Tiné	1995	47	$F = 337.2 + 2.59 W$	0.882	< 0.0001
	1996	135	$F = 476.9 + 2.20 W$	0.806	< 0.0001
Sambakaha	1995	212	$F = 103.3 + 3.61 W$	0.861	< 0.0001
	1996	160	$F = 98.3 + 3.16 W$	0.834	< 0.0001
Korokara-S	1995	197	$F = 317.8 + 2.69 W$	0.765	< 0.0001
	1996	243	$F = 264.2 + 2.86 W$	0.735	< 0.0001
Korokara-T	1995	124	$F = 152.5 + 3.78 W$	0.548	< 0.0001

$r = 0.770$, $p < 0.001$ in 1996) (Figures 2, 3). Comparison between the corresponding regression models revealed marked differences in fecundity among populations in 1995 ($F_{8,1061} = 2.563$, $p < 0.01$) and in 1996 ($F_{4,850} = 7.903$, $p < 0.001$) (Table 2).

The fecundity for a female of 100 g and 200 g, estimated using the statistical relationships (Table 1) and the mean oocyte weight are shown for each population in Figures 4a and 4b for 1995, and in Figures 5a and 5b for 1996. We decided to show the calculated fecundity for a fish of 100 g and 200 g because of the weak overlapping size range of certain populations in the regressions between fecundity and body weight (Figures 2, 3). As an example, for the populations of Ayamé and Korokara-T, regressions were calculated for females weighing between 30 and 180 g. For these populations, fecundity estimates of a 200 g fish are thus extrapolations realised from the regression line prolongation. Conversely, for the populations of Kossou and Lokpoho, a fish of 100 g is just mature, and corresponds to the first values used for the regression calculation.

Beyond the possibility of direct comparison among populations, (Figures 4, 5) this presentation highlights the inverse relationship existing between oocyte size and number at spawning ($r = 0.670$, $p = 0.048$ for a 100 g fish, and $r = 0.547$, $p = 0.127$ for a 200 g fish in 1995; $r = 0.657$, $p = 0.229$ for a 100 g fish, $r = 0.843$, $p = 0.073$ for a 200 g fish in 1996). Generally, populations with low fecundities have the largest oocytes (Ayamé, Lokpoho, Sambakaha in 1995, and Ayamé,

Kossou, Sambakaha in 1996). Conversely, populations with high fecundities present the smallest eggs (Buyo, Kossou, Tiné in 1995, and Korokara-S, Tiné in 1996). However, intermediate situations were observed in 1995 where high fecundities (Korokara-Serpent, Solomougou, Korokara-Termitière) were associated with relatively large oocytes. Except for the populations of Korokara-S and Tiné, fecundity was lower in 1996 than in 1995. Thus, fecundity may vary from one year to another within the same population; the observed differences being significant (Table 2). Only females from Korokara-S and Tiné presented similar fecundities for the two years.

Oocyte weight and diameter

No relation was found between oocyte weight and female body weight. The range of oocyte weight varied between 4.5 and 7.7 mg in 1995 and between 5.8 and 7.9 mg in 1996 (Table 3). ANOVA revealed significant differences of oocyte weight between populations in 1995 ($F_{187} = 5.92$, $p < 0.0001$) and in 1996 ($F_{245} = 41.6$, $p < 0.0001$). Multiple comparison tests showed that most of the differences that appeared graphically (Figures 4, 5) were significant (Table 4). The population of Ayamé, where fecundity differed from most other populations, also differed from others according to egg weight criteria. The population of Kossou, characterised by one of the highest fecundities, presented also the lowest weight and diameter of eggs

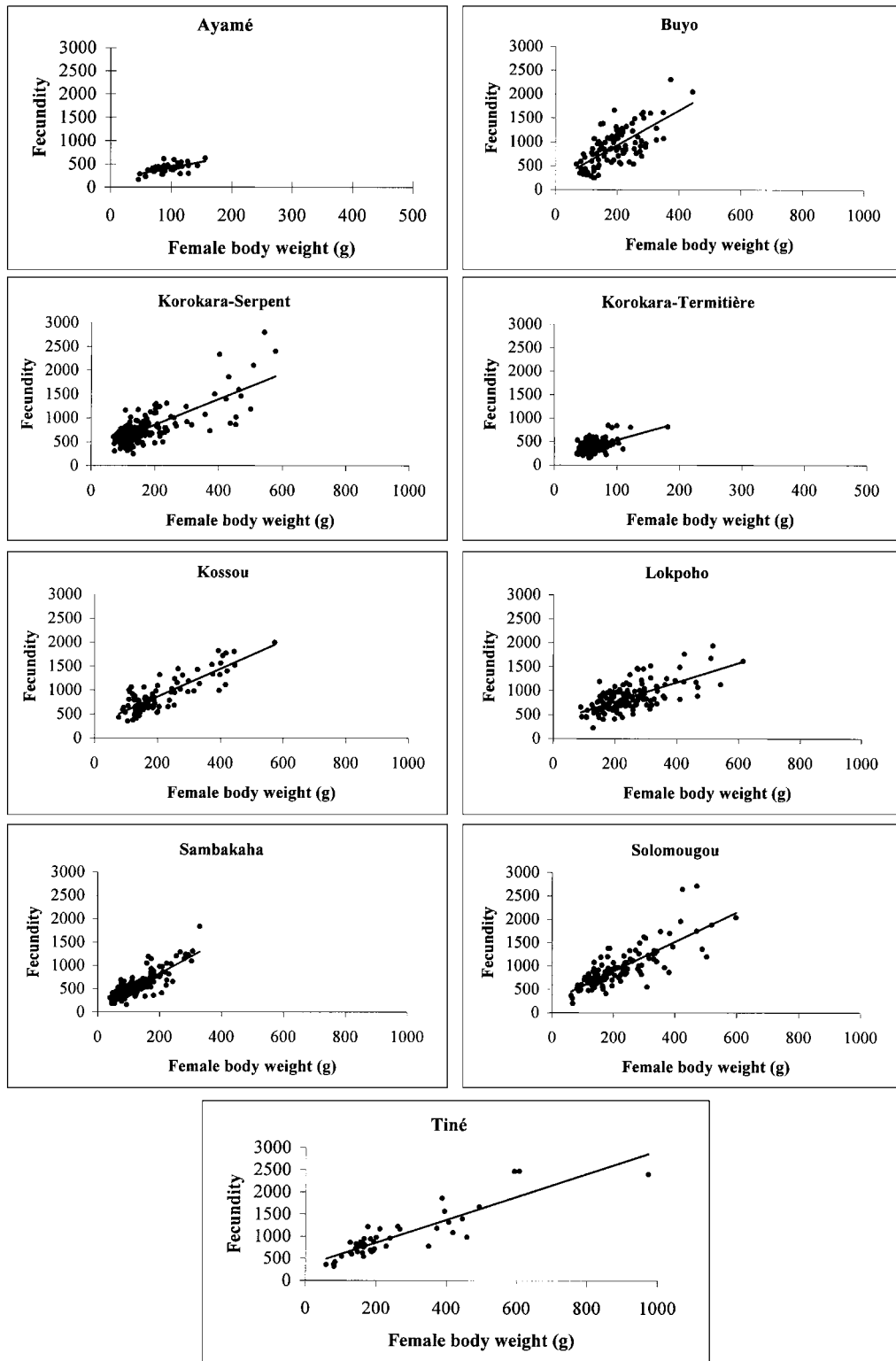


Figure 2. Regression lines between fecundity and body weight of *Oreochromis niloticus* females in each reservoir in 1995.

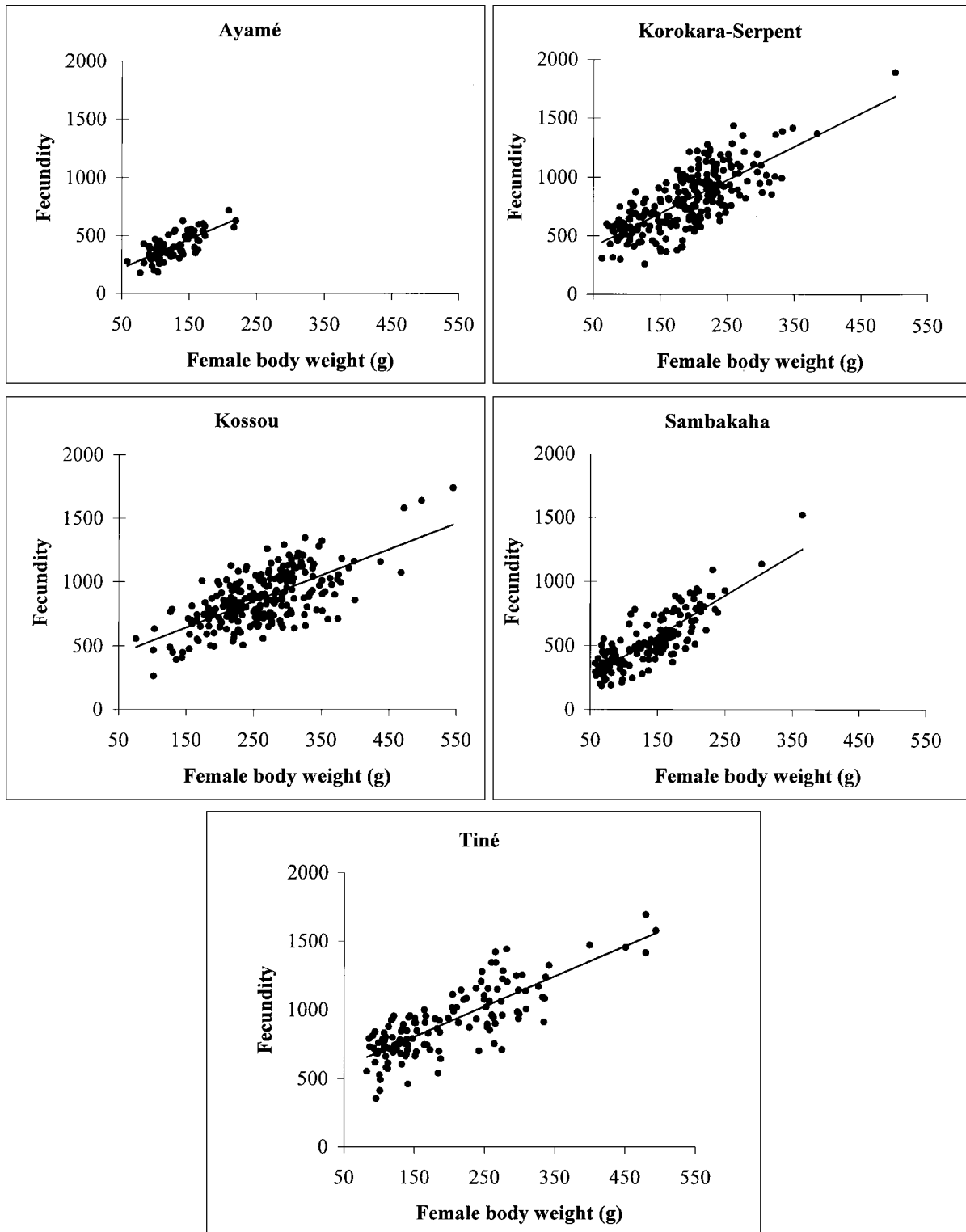


Figure 3. Regression lines between fecundity and body weight of *Oreochromis niloticus* females in each reservoir in 1996.

Table 2. Comparisons of regression lines between fecundity and body weight of *Oreochromis niloticus* females between the reservoirs, above the diagonal: in 1995, below the diagonal: in 1996 (italics). The diagonal (bold) presents the inter annual comparisons (1995 vs. 1996) in the reservoirs sampled for both years.

Reservoirs	Kossou	Buyo	Ayamé	Lokpoho	Solomougou	Tiné	Sambakaha	Korokara-S	Korokara-T
Kossou	#	ns	*	#	ns	ns	#	ns	ns
Buyo			ns	#	ns	ns	*	ns	ns
Ayamé	*		*	*	*	*	ns	*	*
Lokpoho					#	ns	#	*	ns
Solomougou						ns	*	ns	ns
Tiné	*		*			ns	ns	ns	ns
Sambakaha	#		*			#	#	#	*
Korokara-S	*		*			#	*	ns	*
Korokara-T									

ns = non significant.

#= significant slope differences ($p < 0.05$).

* = significant intercept differences ($p < 0.05$).

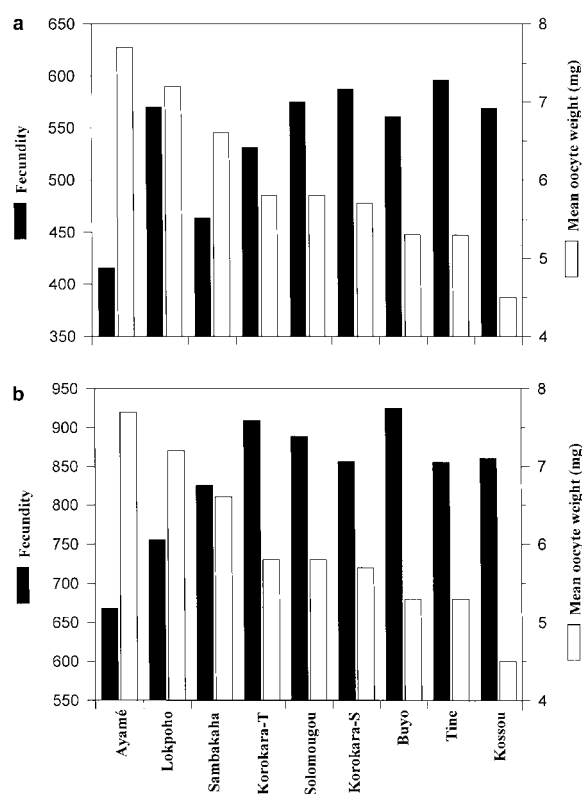


Figure 4. Fecundity of *Oreochromis niloticus* female of 100 g (a) and 200 g (b) (calculated from statistical relationships given in Table 1) and mean oocyte weight for each population in 1995.

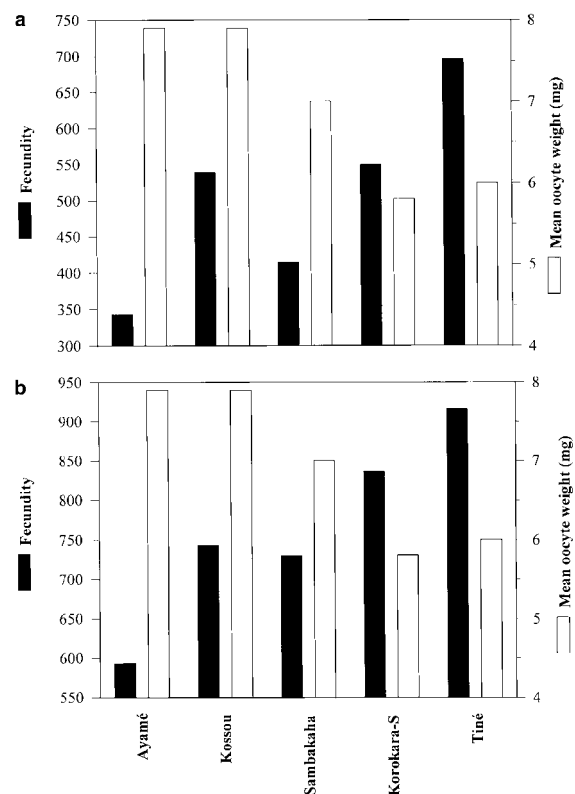


Figure 5. Fecundity of *Oreochromis niloticus* female of 100 g (a) and 200 g (b) (calculated from statistical relationships given in Table 1) and mean oocyte weight for each population in 1996.

Table 3. Mean (\pm standard deviation) oocyte weight and diameter of *Oreochromis niloticus* females for 1995 and oocytes weight for 1996. N = number of females used. Fecundity of a 100 g (F_{100}) and 200 g female (F_{200}) in 1995 and 1996.

Reservoirs	1995					1996			
	F_{100}	F_{200}	N	Mean oocyte weight (mg)	Mean oocyte diameter (mm)	F_{100}	F_{200}	N	Mean oocyte weight (mg)
Kossou	569	860	6	4.5 \pm 0.92	2.1 \pm 0.17	539	743	43	7.9 \pm 1.1
Buyo	561	925	5	5.3 \pm 0.77	2.2 \pm 0.15				
Ayamé	416	668	3	7.7 \pm 0.44	2.5 \pm 0.15	343	593	24	7.9 \pm 0.9
Lokpoho	570	771	22	7.2 \pm 2.16	2.5 \pm 0.26				
Solomougou	575	889	36	5.8 \pm 1.09	2.3 \pm 0.16				
Tiné	596	855	9	5.3 \pm 0.91	2.3 \pm 0.14	697	916	62	6.0 \pm 1.0
Sambakaha	464	825	41	6.6 \pm 1.38	2.4 \pm 0.18	414	730	47	7.0 \pm 1.3
Korokara-S	587	856	28	5.7 \pm 1.00	2.3 \pm 0.15	550	836	70	5.8 \pm 0.9
Korokara-T	531	909	38	5.8 \pm 1.06	2.3 \pm 0.15				

Table 4. Inter population comparisons of *Oreochromis niloticus* females mean oocyte weight, above the diagonal: in 1995, below the diagonal: in 1996 (italics). The diagonal (bold) presents the inter-annual comparisons in the reservoirs sampled for both years.

Reservoirs	Kossou	Buyo	Ayamé	Lokpoho	Solomougou	Tiné	Sambakaha	Korokara-S	Korokara-T
Kossou	*	ns	*	*	ns	ns	*	ns	ns
Buyo			*	*	ns	ns	*	ns	ns
Ayamé	<i>ns</i>		ns	ns	*	*	ns	*	*
Lokpoho					*	*	ns	*	*
Solomougou						ns	ns	ns	ns
Tiné	*		*			ns	ns	ns	ns
Sambakaha	*		*			*	ns	ns	ns
Korokara-S	*		*			<i>ns</i>	*	ns	ns
Korokara-T									

ns = non significant.

* = significant differences ($p < 0.05$).

in 1995, and differed significantly from the populations of Ayamé, Lokpoho and Sambakaha on this criteria.

In 1996, females of all the reservoirs produced larger oocytes than in 1995 (Table 3), even though most of these differences were not significant (Table 4). The most striking case was observed with Kossou females: oocyte weight doubled between these two years; moreover, only females of Kossou showed significant difference between 1995 and 1996 based on this criteria.

Spawn weight

Spawn weight corresponds to the amount of gonadal material produced by a female during a reproductive cycle and can be considered an instant index of

reproductive effort. No significant difference was found between the populations while comparing the regression lines between spawn weight and body weight in 1995 ($F_{8,170} = 1.026$, $p > 0.05$), but differences were found in 1996 ($F_{4,233} = 6.25$, $p < 0.001$). Inter-population comparisons revealed that these differences were fewer than for fecundity and oocyte size (Table 5). However, inter-annual differences of spawn weight also appeared in a same population.

Relation between fecundity and environmental factors

A seasonal variability of fecundity was observed for *O. niloticus* females in the Sambakaha and Kossou

Table 5. Comparisons of regression lines between spawn weight and body weight of *Oreochromis niloticus* females between the reservoirs, in 1996. The diagonal (bold) presents the inter-annual (1995 vs. 1996) comparisons.

Reservoirs	Kossou	Ayamé	Tiné	Sambakaha	Korokara-S
Kossou	ns	ns	#	*	ns
Ayamé		ns	*	ns	ns
Tiné			#	#	ns
Sambakaha				*	ns
Korokara-S					#

ns = non significant.

= significant slope differences ($p < 0.05$).

* = significant intercept differences ($p < 0.05$).

reservoirs. In Sambakaha, maximum fecundity occurs during the first rainfalls, and decreases when rainfalls increase (Figure 6a). Maximum fecundity is observed about one month after the highest temperatures, in 1995 and in 1996 (Figure 6b), and fecundity variation is closely related to the day-length cycle (Figure 6c). Fecundity is at maximum when the chlorophyll a concentration is highest, hence when resource availability is at its maximum, just before flooding (Figure 6d). In the Kossou Reservoir, the same tendency is observed concerning rainfalls (Figure 7a), temperature (Figure 7b) and day-length (Figure 7c) in 1996. In 1995, no correlation could be observed between fecundity residuals profile, rainfalls and day-length; fecundity seemed to correspond better with temperature variations.

Discussion

In this study, comparisons between *O. niloticus* populations have shown important differences in fecundity and egg size. The inverse relationship observed between mature oocyte size and number is in agreement with previous results reported in tilapias (Peters 1963, De Silva 1986, Legendre & Ecoutin 1989, 1996) and other fishes (Mann & Mills 1979, Albaret 1982, Stearns 1983, Duarte & Alcaraz 1989, Elgar 1990). By contrast, Smitherman et al. (1988) did not find any correlation between these reproductive traits on the three *O. niloticus* strains that they studied in Côte d'Ivoire, Ghana and Egypt. This inverse relationship appears at the inter-population level in our study, but is less evident at the intra-population level. Contrasting with the clear inverse relationship between size and number of eggs produced by females of a same population

in *Tilapia guineensis* and *Sarotherodon melanotheron* (Legendre & Ecoutin 1996), *O. niloticus* females of a same population can display both high fecundity and large eggs.

Fecundity and egg size are highly variable traits, which can differ among populations but also within one population between consecutive years. According to the energetic cost of gamete production, food is probably one of the most important environmental factors involved in regulation of fecundity (Wootton & Evans 1976, Wootton 1979). Food quality and particularly the effect of dietary proteins on reproduction have been studied in tilapias with conflicting results. Santiago et al. (1985) and Chang et al. (1988) observed an increased young production for breeders fed with higher protein level, in *O. niloticus* and red hybrid (*O. niloticus* × *O. mossambicus*) respectively. Conversely, Wee & Tuan (1988) reported a negative effect of higher protein level on spawning frequency and fecundity of *O. niloticus*.

In other fish species, a decrease in fecundity is generally observed with a reduction of feeding levels (Bagenal 1969, Wootton 1973, Billard & De Fremont 1980, Springate et al. 1985). However, as fecundity is generally linearly related to fish body weight, effect of feeding on fecundity may be difficult to discriminate from the effect resulting of weight gain (Wootton 1982). A decrease in fecundity was observed at the lowest feeding levels in *Cichlasoma nigrofasciatum* (Townshend & Wootton 1984) and *O. mossambicus*, although spawning frequency and total number of eggs produced increased in the latter species (Mironova 1977).

In most of the reservoirs studied, *O. niloticus* females produced fewer and bigger oocytes in 1996 than in

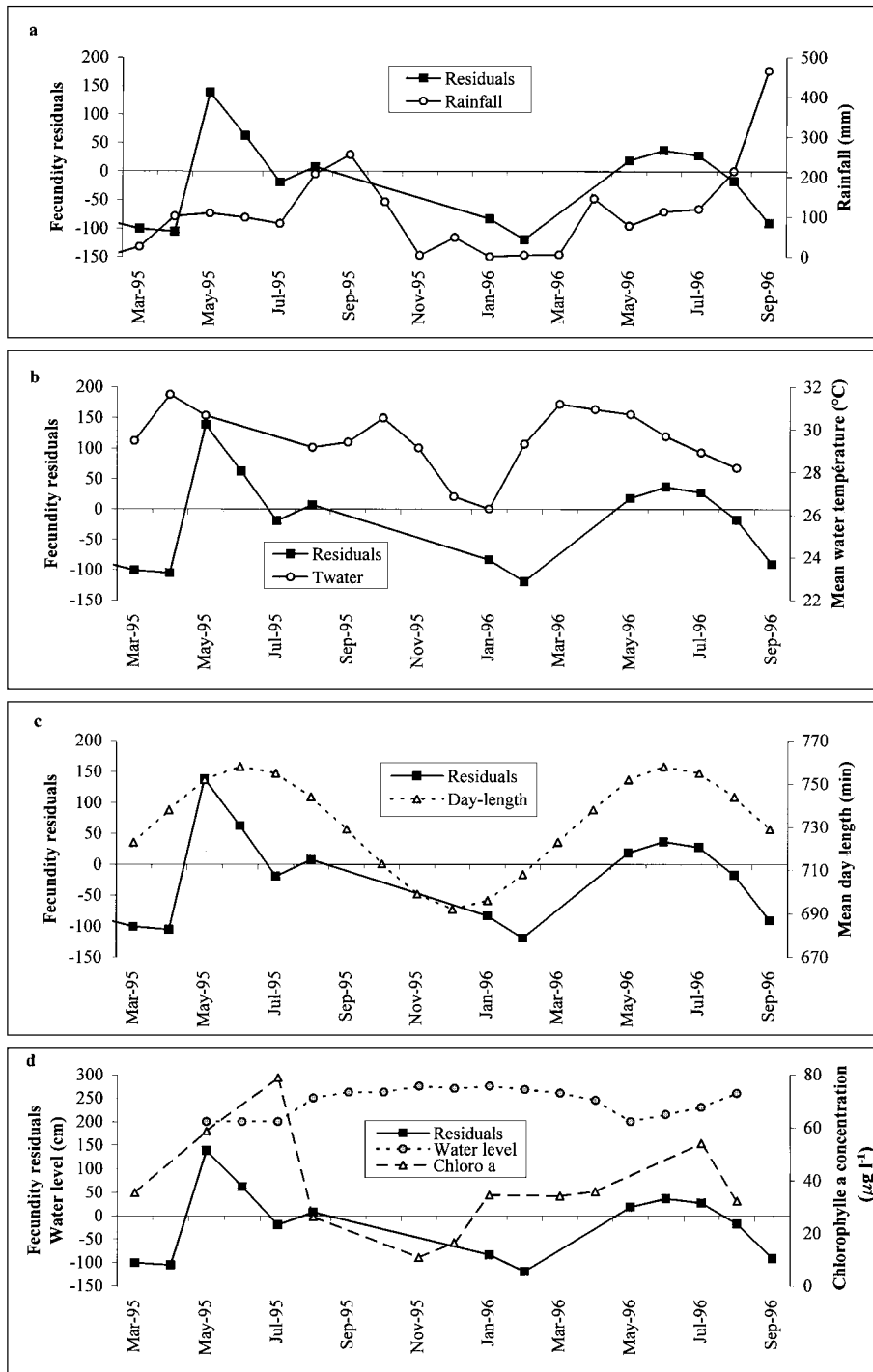


Figure 6. Relation between seasonal cycle of fecundity residuals of *Oreochromis niloticus* females and rainfall (a), temperature (b), day-length (c), chlorophyll a concentration and water level (d), in the reservoir of Sambakaha.

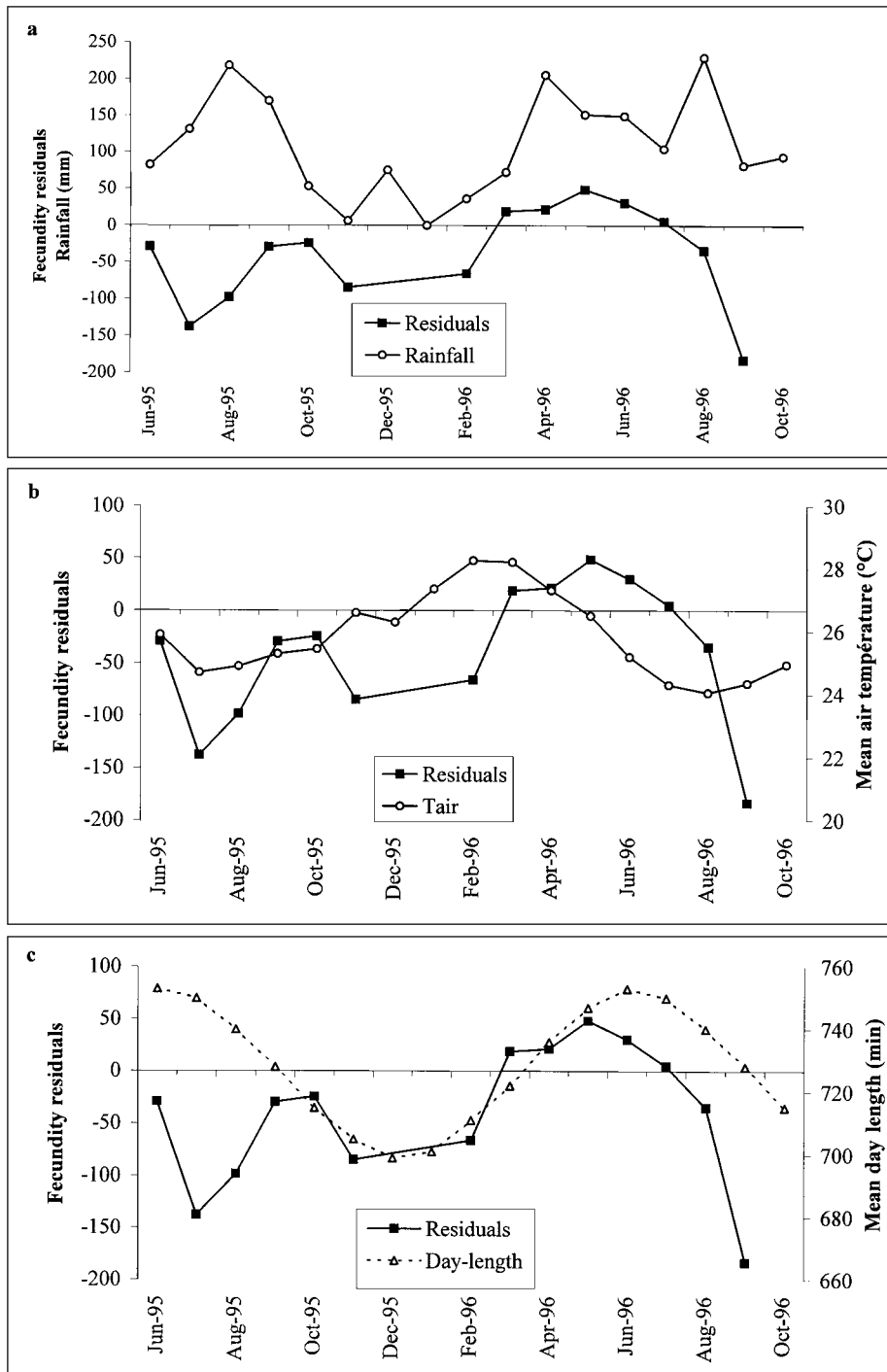


Figure 7. Relation between the seasonal cycle of fecundity residuals of *Oreochromis niloticus* females and rainfall (a), temperature (b), and day-length (c), in the reservoir of Kossou.

1995. A reduction in resource availability may account for this fecundity decrease in 1996, as chlorophyll a concentrations were lower than in 1995 (Figure 6d). Fecundity was reported to decrease after successive spawns in cichlids (Townshend & Wooton 1984). The earlier and longer peak of sexual activity observed during the breeding season of 1996 (Duponchelle et al. 1999) may explain the decrease in fecundity and the increased egg size observed during the same year. According to life history theory, a decrease in fecundity together with an increase in egg size should occur when juvenile mortality increases (Murphy 1968, Gadgil & Bossert 1970, Schaffer 1974a, b, Wilbur et al. 1974, Law 1979, Michod 1979). Theory also predicts, in this case, an increased size at maturity, which was observed in 1996 for all the populations (Duponchelle & Panfili 1998). In other respects, low fecundity, large eggs and higher size at maturity, are characteristic of populations facing stable environment, marked by a high interspecific competition (Pianka 1970, Lowe-McConnell 1982, Noakes & Balon 1982), where the populations are subjected to high juvenile mortality (Reznick 1982, Reznick & Endler 1982, Reznick & Briga 1987, Reznick et al. 1990). Thus, increased predation on juvenile and/or unfavourable trophic conditions for juveniles may have occurred during the 1996 spawning season. However, hypothesis of unfavourable trophic conditions for juveniles in 1996 may contrast with the observations realised about breeding season, which was more favourable in 1996 than in 1995 (Duponchelle et al. 1999).

Spawn weight appeared to be the less variable trait between populations. The inverse relationship between egg size and number occurred for a constant spawn weight in 1995. The amount of gonadal material produced by the females during a reproductive cycle was thus constant from one population to another in 1995, but not in 1996. By contrast, in *O. mossambicus* (Peters 1963), *Tilapia guineensis* and *Sarotherodon melanotheron* (Legendre & Ecoutin 1996), variations in egg size and number occurred with a constant spawn weight.

The use of regression residuals between fecundity and female body weight showed seasonal variations of fecundity during the course of a spawning season in the reservoir studied. Fecundity was at maximum during the first rains, when day-length was also at maximum, and shifted by approximately one month with maximum temperatures. We also observed that fecundity was highest when resource availability, assessed by the chlorophyll a concentration, was highest, just before

the flooding period. Evolutionary consequences of correlation between maximum immediate reproductive effort, maximum resource availability, and flooding imminence, may be important for parents and offspring fitness. Increased resource availability at this period would lower energetic cost for food search and would allow to better support energetic cost of gamete production. In other respects, during flooding, water penetrates the shore vegetation, opening secluded areas of feeding and refuge for juveniles, which optimise their survival and growth (Ward & Samarakoon 1981). Also, the rising waters on the banks and the presence of vegetation offer protection to the brooders and increases the number of spawning sites, which is a crucial and sometimes limiting factor in the development of tilapia populations (McKaye 1977, Pullin & Lowe-McConnell 1982). It is at this period that *O. niloticus* colonises the plants on the banks of small reservoirs, making its capture very difficult.

Phenotypic differences in life-history traits observed among populations can result either from genetic variation and/or from the effect of environmental variation on a plastic phenotype. The question could be asked for the observed variations of reproductive characteristics among populations in this study. All the introductions of *O. niloticus* in Côte d'Ivoire, except those of Lake Ayamé, were with a domestic strain (Bouaké strain) reared at the IDESSA aquaculture station in Bouaké, produced by crossing stocks from the Nile and the Volta basins (Rognon 1993, Lazard & Rognon 1997). As a consequence, all the *O. niloticus* introduced in Côte d'Ivoire have a common genetic origin, except those of Ayamé Reservoir that originated only from fishes of the Volta basin (Lazard 1990). However, according to Reznick's results with guppies, *Poecilia reticulata*, experiencing size selective predation, 30 to 60 generations are required to induce genetic differences in life-history traits (Reznick et al. 1990). Thus, allowing an equivalent number of generations, and according to age at first sexual maturity of *O. niloticus* populations in the studied reservoirs (Duponchelle & Panfili 1998), 15 to 40 years would be necessary to evolve genetic differences in reproductive traits. *O. niloticus* was first introduced in Kossou in 1971 (Bearez¹) and in the small reservoirs around 1980. Some populations have then been separated for a time (about 25 years) which may be sufficient to allow genetic differentiation.

¹ Bearez, P. 1988. Fonctionnement de la pêche sur le lac de Kossou. Rapport d'étude, ENGREF, Montpellier. 26 pp.

The high variability of reproductive traits observed within one population between consecutive years in this study suggests a strong environmental component in the differences observed among populations. Moreover, when sharing a common environment (pond or aquariums) for five months, reproductive traits of fish from the Kossou and Sambakaha reservoirs, which were among the most different, were no longer different (Duponchelle et al. 1998). Therefore, according to these results and to their common genetic origin (the Bouaké strain), the variations of reproductive traits observed among populations (except Ayamé) in this study may be considered as the result of phenotypic plasticity of this species in response to the different environmental conditions of the reservoirs.

High variability of age and size at maturity (Duponchelle & Panfili 1998), spawning season (Duponchelle et al. 1999), fecundity and egg size, both among populations and within one population between successive years, strongly emphasises the difficulty to correctly describe the reproductive characteristics of a species on the basis of a single annual cycle.

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