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Evidence of environmental effects on reproductive characteristics of Nile tilapia (*Oreochromis niloticus*) populations from man-made lakes of Ivory Coast

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Abstract – Large differences in reproductive traits were observed between populations of *Oreochromis niloticus* sampled in 9 man-made lakes of Ivory Coast. In order to assess whether these variations in reproductive characteristics resulted from short term adaptation or from a longer evolutionary process, living specimens were caught in the two most differentiated populations in term of life history traits, and placed in a common environment in culture conditions. Genetic analysis of fish from these two populations were performed using four microsatellite markers and revealed that both descended originally from the same strain (Bouaké station) which was constituted from broodfish initially caught in the Nile and Volta basins. Fish from the two populations were subjected to a common environment (pond and aquariums) for five months. Then, their reproductive characteristics were analysed and no significant differences were found in fecundity, egg size and spawning frequency. These results indicate that reproductive differences between the two populations, originally observed in the two reservoirs, mostly reflect the phenotypic plasticity of the species in facing different environmental conditions. © Ifremer/Elsevier, Paris

Reproduction / fecundity/ genetics/ DNA microsatellite markers / tilapia / Africa

Résumé – Évidence de l'effet environnemental sur les caractéristiques de reproduction des populations de tilapia du Nil (*Oreochromis niloticus*) dans les petits barrages de Côte-d'Ivoire. La comparaison des caractéristiques de reproduction des femelles *Oreochromis niloticus* dans neuf petits barrages de Côte-d'Ivoire a révélé d'importantes différences entre les populations. Ces différences pouvaient être dues à une adaptation rapide des poissons à leur environnement ou à un processus évolutif plus long. Afin de le vérifier, des poissons de deux des populations présentant les paramètres de reproduction les plus différents ont été capturés vivants et placés dans un environnement commun en situation d'élevage. L'analyse génétique des poissons des deux populations, réalisée en utilisant quatre marqueurs microsatellites, a révélé qu'ils étaient issus d'une même souche (« souche Bouaké »), constituée à partir de géniteurs provenant des bassins du Nil et de la Volta. Après avoir partagé un environnement commun (étang ou aquarium) pendant 5 mois, la fécondité, le poids ovocytaire moyen et la fréquence de ponte des femelles des deux populations, qui étaient significativement différents dans leurs milieux respectifs, ne différaient plus. Ces résultats indiquent que les différences de reproduction observées en milieu naturel entre les deux populations sont principalement le fait de la plasticité phénotypique de l'espèce face à des conditions environnementales différentes. © Ifremer/Elsevier, Paris

Reproduction / fécondité / génétique / marqueurs microsatellites d'ADN / tilapia / Afrique

1. INTRODUCTION

Oreochromis niloticus were rare in waters of Ivory Coast, with a distribution limited to the tributaries of the Niger and Volta drainages in the Northern part of the country [7, 26]. However, they have been introduced in many waterbodies and have now colonized all the country water courses [35]. Most of the specimens of *O. niloticus* inhabiting the freshwaters of Ivory Coast are supposed to descend originally from strains reared at the Aquaculture station of the 'Institut Des Savanes' (Idessa) in Bouaké. A first strain obtained from brooders caught in the Volta was introduced in

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the hydroelectric lake Ayamé in 1962 to remedy the shortage of indigenous phytoplanktonic species [17], and a second strain produced by crossing stocks from the Nile basin (Edward Lake) and the Volta basin [14, 26] was introduced in lake Kossou in 1971 [3] and in several agro-pastoral reservoirs around 1984. However, in the northern part of the country, the status of populations inhabiting agro-pastoral reservoirs remains unclear due to the proximity of the Niger and Volta tributaries and the possibility of multiple stocking or colonizing events with fish from various origins.

Study on 6 agro-pastoral and 3 hydroelectric reservoirs of Ivory Coast revealed important differences in reproductive traits of *O. niloticus* populations. These differences were expressed by variations in age and size at first sexual maturity [10], fecundity and oocyte size [9]. 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. Relative contribution of these two components is expected to vary with the type of environmental uncertainty. For short-term environmental variability (one individual's lifetime) phenotypic plasticity should account for most of the phenotypic variation while for long-term environmental variability (several generations), genetic variation is expected to contribute more to phenotypic variation [12]. Similarly, plastic phenotypes which respond rapidly to short-term variations could be selectively advantageous in environments where selective pressures are variable in direction and amplitude [6, 13, 37]. It is essential that the relative importance of these components are separated in order to interpret correctly the adaptive significance of the phenotypic variation [5].

After a one year study of the reproductive traits of *Oreochromis niloticus* females in nine reservoirs of Ivory Coast, populations from two of these reservoirs, Kossou (hydroelectric lake) and Sambakaha (pastoral reservoir), between which reproductive traits were among the most different, were chosen for further investigation. The origin of these two populations was checked using four microsatellite markers (VNTR: Variable Number of Tandem Repeats). In order to assess whether the phenotypic differences observed in the natural environment were due to genetic or environmental variation, *O. niloticus* brooders from the Kossou and Sambakaha reservoirs were caught and placed in the same environment for five months, in a pond or aquariums, and then examined to analyse their fecundity, egg size and spawning frequency.

2. MATERIAL AND METHODS

2.1. Origin of *Oreochromis niloticus* populations from Kossou and Sambakaha reservoirs

The genetic variability of Kossou and Sambakaha populations was characterized at 4 microsatellite loci, SMEL1, SMEL2, SMEL3 and SMEL4 (Pouyaud et al., unpubl.) by genotyping 300 individuals from each reservoir. Specimens of *O. niloticus* from the Bouaké strain, Lake Edward at Mweya, Lake Volta at Akosumbo, Niger River at Sélingué, Bamako, Mopti and Niamey, and Nile River at Chobra were also characterized at the same loci in order to define possible genetic contributions of these fish stocks to the populations of Kossou and Sambakaha. The genetic markers were isolated from a partial genomic bank of *Sarotherodon melanotheron* DNA. Codominant Mendelian inheritance of the observed polymorphism was confirmed by family studies and no mutations were detected (Pouyaud et al., unpubl.). Chelex 100 (5 %) was used for DNA extractions from alcohol preserved tissues (roughly 1 mg) following a standard protocol [39] with proteinase K in 500 µL. One µL of the supernatant was used per reaction. The Polymerase Chain Reactions (PCR) were performed in 10 µL of a mix containing 0.2 units of Taq DNA polymerase (Promega), 1.5 mM $MgCl_2$, 100 µM of each dNTP, 1X reaction buffer and 10 pmol of each primer. One of the two primers was covalently linked to fluoresceine at its 5' end. The PCR program used was: 35 s at 95 °C, 60 s at annealing temperature, 29 cycles of the following steps: 60 s at 72 °C, 35 s at 91 °C and 35 s at annealing temperature. This cycling was followed by a 60 s elongation step at 72 °C. Annealing temperature was 53 °C for SMEL1, SMEL2, SMEL3 and 50 °C for SMEL4. Amplification products were resolved with an automatic sequencer (Pharmacia) by electrophoresis on 6 % polyacrylamide denaturing gels.

2.2. Analysis of reproductive characteristics in a same environment

Oreochromis niloticus from populations of the two reservoirs (Kossou and Sambakaha), known for their different size at first maturity, fecundity and oocyte size, were caught using gillnets, cast-nets and baited traps, and brought alive to the Idessa (Institut Des Savanes) aquaculture station in Bouaké, Ivory Coast. Two experiments were conducted using these fish, one in a pond and the other in aquariums.

2.2.1. Experiment in pond

About 150 females and 50 males of each populations were tagged in order to identify their origin. Three rays of the dorsal fin were close-cropped for the population of Sambakaha. The same operation was repeated every two months because of fin regeneration. Trials to tag the fish using alcyan blue (500 mg in 5 mL distilled water) were not successful due to the rapid disappearance of the blue spots made on the opercula or ventral face of the fish using a dermojet. Fish from both populations were then placed on the same day in the same pond (400 m^2) at a stocking density of 0.75 fish per m^2. They were fed at 3 % body weight per day, six days a week, with a 30 % crude protein powdered feed.

After five months in the communal pond, all the fish were caught and females analysed for their reproductive traits. Each fish was measured for standard length to the nearest mm and body weight to the nearest g. The gonads were checked macroscopically for maturity stage and then weighed to the nearest 0.1 g for the gonado-somatic index (GSI) calculation (gonad weight × 100 / total body weight). Gonads with oocytes in advanced vitellogenesis were fixed in 5 % formalin for later estimation of fecundity and oocyte size.

The sexual maturity scale used was that of Legendre and Ecoutin [15]. 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.

Fecundity was considered here as the number of oocytes to be released at the next spawn (absolute fecundity). It is estimated by the number of oocytes belonging to the largest diameter modal group, in gonads at the final maturation stage (stage 4). This oocyte group is clearly separated from the rest of the oocytes and visible to the naked eye; it corresponds approximately to oocytes which are going to be ovulated [20]. 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.

The individual average oocyte weight was determined by weighing 50 oocytes belonging to the largest diameter modal group. In order to compare mean oocyte weight of females from both populations, the measurements needed to be made on oocytes at an equivalent vitellogenic state, i.e., oocytes whose growth has been completed. The GSI threshold above which the oocyte weight and diameter no longer evolve significantly was determined for *Oreochromis niloticus* females. This threshold was reached at a GSI ≥ 4 for females whose body weight was < 150 g and at GSI ≥ 3 for females whose body weight was ≥ 150 g [9].

2.2.2. Experiment in aquariums

Five pairs of males and females from each populations were individually placed in 400 L aquariums and followed for 5 months. Each aquarium was equipped with an external filter and provided with a constant air supply. Aquariums were not thermoregulated and temperature oscillated between 23.3 and 24.7 °C at 9.00 AM and between 24.7 and 26.2 °C at 4.00 PM. Physico-chemical conditions were very similar from one aquarium to the next during the experiment. Oxygen concentration varied between 4.18 and 8.50 $mg \cdot L^{-1}$, pH varied between 6.76 and 7.61. Fish were fed at 2 % body weight per day, six days a week, with a 30 % crude protein pelleted feed.

Reproductive traits, such as breeding frequency and parental investment in eggs and fry care, which are very difficult to observe in natural environment became accessible in these experimental conditions. During this experiment, the spawning frequency, duration of egg incubation and fry care, real absolute fecundity and mean egg weight were recorded. Females were weighed after each spawn and feeding rate adjusted consequently.

The spawning frequency was determined by the time interval, in days, between two successive spawns. Duration of egg oral incubation was estimated by the time lapse between spawning and the first release of fry. Duration of fry care corresponded to the time lapse between the observation of first release of fry and complete ending of oral incubation.

Real absolute fecundity was determined by counting eggs on photos after removing them from the mouth of incubating females. Removing eggs from an incubating female's mouth leads to an acceleration of the following reproductive cycle [34] and skews spawning frequency observation. A female tilapia may retake its eggs if they are returned to the aquarium within a few minutes. In practice, when a new incubating female was identified, it was forced to spit out the eggs according to the method of Gauthier et al. [11], weighed and replaced in its aquarium. Eggs were then rapidly spread in a plate filled with water, photographed and carefully replaced in the female's nest. This manipulation never exceeded 10 min. Mean egg weight was estimated after photography by weighing a sample of 50 eggs.

Females were observed each morning to identify those which were going to reproduce (according to behaviour and genital papilla criteria) or those which had spawned during the night. In order to ensure homogeneity of sampling, eggs were always collected within a period not exceeding 12 h after spawning.

2.3. Statistical analysis

Allelic frequencies were calculated for each locus using the BIOSYS 1 software package [33]. Genetic relationships among analysed populations were characterized by Nei's [19] genetic distance calculated using the Genedist program (PHYLIP software package; Felsenstein, v. 3.5).

In tilapias as in many other fishes, the fecundity is positively correlated to size and to body weight [1, 8, 15, 16, 40]. Therefore, the estimation of differences between populations for fish reared in pond was made by comparing regression lines between fecundity and body weight. The slopes and intercepts of regressions were compared by an analysis of covariance [29]. The comparisons of mean oocyte weights were carried out using a Student's *t*-test [29].

For fish reared in aquariums, the range of female body weight was too narrow in both populations to adjust regression line between fecundity and female body weight. Thus comparisons were made on the basis of relative fecundity (absolute fecundity/body weight × 1 000). Even though a negative correlation between relative fecundity and weight is frequently

observed in tilapias, such a relation was not found in the weight range of females used in this experiment (110 to 280 g). Comparisons of relative fecundity and egg weight among the two populations were carried out using a Student's *t*-test.

3. RESULTS

3.1. Origin of *O. niloticus* populations of Kossou and Sambakaha reservoirs

Table I gives the collection of alleles and their respective allelic frequency for each analysed population. Each wild population was characterized by private alleles, such as alleles (126) and (129) at locus 1 and allele (136) at locus 2 in Edward Lake, allele (093) at locus 3 and allele (074) at locus 4 in Volta Lake, alleles (090), (102) and (108) at locus 4 in Chobra. However, an exception was observed in the wild populations from the Niger River which were monomorphic at all investigated loci. Imprinting of both Nile and Volta origins was confirmed in the Bouaké strain by the presence of allele (126) at locus 1 and allele (093) at locus 3. The occurrence of allele (108) at locus 1 and allele (093) at locus 3 in populations of both Sambakaha and Kossou reservoirs indicated that these populations shared a common origin and descended from the Bouaké strain. Although allele (108) was not found in the Bouaké strain in its actual state, its presence in fish from both reservoirs indicated a Nilotic influence that could have been brought only through this aquaculture strain. By contrast, the possibility of an exclusive origin from wild populations of the Niger basin was not confirmed because fish samples from Sélingué, Bamako, Mopti and Niamey were monomorphic for the alleles of highest frequency observed at each locus in the Sambakaha and Kossou populations as well as in the Bouaké strain.

Nei's genetic distances between each population are given in *table II*. No genetic differentiation was found between the populations of Sambakaha and Kossou reservoirs on the basis of the four loci studied. Moreover, these two populations presented very low genetic variation when compared to the Bouaké strain from which

Table I. Allelic frequencies observed at each microsatellite locus in the various populations of *Oreochromis niloticus* studied. Values between brackets correspond to amplified allele size in base pair. N: number of fish sampled.

	Locus 1		Locus 2		Locus 3		Locus 4	
Bouaké strain	(108)	0.000	(132)	1.000	(087)	0.000	(072)	1.000
	(123)	0.980	(134)	0.000	(091)	0.950	(074)	0.000
N = 50	(126)	0.020	(136)	0.000	(093)	0.050	(090)	0.000
	(129)	0.000					(102)	0.000
							(108)	0.000
Sambakaha	(108)	0.080	(132)	1.000	(087)	0.000	(072)	1.000
	(123)	0.920	(134)	0.000	(091)	0.990	(074)	0.000
N = 300	(126)	0.000	(136)	0.000	(093)	0.010	(090)	0.000
	(129)	0.000					(102)	0.000
							(108)	0.000
Kossou	(108)	0.070	(132)	1.000	(087)	0.000	(072)	1.000
	(123)	0.930	(134)	0.000	(091)	0.992	(074)	0.000
N = 300	(126)	0.000	(136)	0.000	(093)	0.008	(090)	0.000
	(129)	0.000					(102)	0.000
							(108)	0.000
Edward Lake (Nile)	(108)	0.000	(132)	0.000	(087)	0.850	(072)	1.000
	(123)	0.650	(134)	0.950	(091)	0.150	(074)	0.000
N = 20	(126)	0.100	(136)	0.050	(093)	0.000	(090)	0.000
	(129)	0.250					(102)	0.000
							(108)	0.000
Volta Lake	(108)	0.000	(132)	1.000	(087)	0.000	(072)	0.500
	(123)	1.000	(134)	0.000	(091)	0.850	(074)	0.500
N = 10	(126)	0.000	(136)	0.000	(093)	0.150	(090)	0.000
	(129)	0.000					(102)	0.000
							(108)	0.000
Chobra (Nile)	(108)	0.150	(132)	0.750	(087)	0.550	(072)	0.800
	(123)	0.850	(134)	0.250	(091)	0.450	(074)	0.000
N = 20	(126)	0.000	(136)	0.000	(093)	0.000	(090)	0.050
	(129)	0.000					(102)	0.100
							(108)	0.050
Niger River (Sélingué, Bamako,	(108)	0.000	(132)	1.000	(087)	0.000	(072)	1.000
Mopti & Niamey)	(123)	1.000	(134)	0.000	(091)	1.000	(074)	0.000
	(126)	0.000	(136)	0.000	(093)	0.000	(090)	0.000
N = 60	(129)	0.000					(102)	0.000
							(108)	0.000

Table II. Nei's genetic distance between each pair of analysed populations; BS: Bouaké strain, S: Sambakaha, K: Kossou, E: Edward Lake, V: Volta Lake, C: Chobra, NR: Niger River.

	NR	C	V	E	K	S	BS
BS	0.0006	0.1068	0.0722	0.6715	0.0015	0.0018	0.0000
S	0.0014	0.1101	0.0777	0.6871	0.0000	0.0000	
K	0.0011	0.1100	0.0770	0.6860	0.0000		
E	0.6783	0.2832	0.9166	0.0000			
V	0.0727	0.1845	0.0000				
C	0.1099	0.0000					
NR	0.0000						

they were descended (d = 0.0015 ± 0.001). Genetic distances also indicated a stronger influence of the Volta rather than the Nile population in the Bouaké strain (d = 0.0722 ± 0.002 between Bouaké and Volta Lake, d = 0.6715 ± 0.003 between Bouaké and Edward Lake and d = 0.1068 ± 0.002 between Bouaké and Chobra).

3.2. Reproductive characteristics in pond

Comparison of regression lines between fecundity and female body weight of the Sambakaha (F = 164.6 + 3.3 W, r = 0.705, $P < 0.001$) and Kossou (F = 153.8 + 3.4 W, r = 0.871, $P < 0.0001$) populations showed no significant difference after five months of rearing in a communal pond environment ($F_{1,112} = 0.124$, $P > 0.05$). In addition, no significant difference was found between the mean oocyte weight of females originating from Sambakaha or Kossou reservoirs ($t = -0.869$, 60 df, $P > 0.05$).

In order to facilitate comparisons between the number and size of eggs produced by females of Kossou and Sambakaha populations in their reservoirs of origin and in the communal pond, the fecundity of fish of 100 and 200 g body weight, calculated using the statistical relationships, and the mean oocyte weight are given for each population in *table III*. Fecundity values of Kossou and Sambakaha populations in pond were intermediate to those observed for the two populations in their 'natural' environment while oocyte weight values in pond were higher than those observed in the two reservoirs.

3.3. Reproductive characteristics in aquariums

Results are summarized in *table IV*. No significant difference in relative fecundity ($t = 1.160$, 32 df, $P > 0.05$) nor in oocyte weight ($t = -1.410$, 32 df, $P > 0.05$) was found between females of populations from Sambakaha and Kossou reservoirs reared in aquariums.

Low success of egg retaking, respectively 16 % and 35 % for the females of Kossou and Sambakaha, led to low sample sizes which impeded statistical comparison of egg incubation and fry care duration. Nevertheless, in fish for which measurement was possible, duration of egg incubation and fry care were very similar for both populations. Mean incubation period varied between 9 and 12 days for the Kossou females and between 10 and 12 days for those of Sambakaha. Duration of fry care varied between 7 and 8 days for the females of Kossou and between 5 and 10 days for those of Sambakaha. However, spawning frequency appeared highly variable both between the different females and from one spawn to another in individual females. It varied between 15 and 99 days for the females of Kossou and between 22 and 98 days for those of Sambakaha. Shorter spawning intervals were recorded when females ate their eggs just after retaking.

4. DISCUSSION

Analysis carried out using microsatellite markers proved that populations of Sambakaha and Kossou reservoirs shared a common genetic origin and descended

Table III. Reproductive characteristics of *Oreochromis niloticus* females in their respective reservoirs of origin and after 5 months of rearing in communal pond: number of fish observed (N), absolute fecundity of a fish of 100 g (Fec100) and 200 g body weight (Fec200) calculated from the statistical relationships and mean oocyte weight ± standard deviation (n: number of corresponding fish).

Populations	N	Fec100	Fec200	Oocyte weight (mg)
Natural reservoirs				
Kossou	87	569	860	4.5 ± 0.9 (n = 6)
Sambakaha	212	464	825	6.6 ± 1.4 (n = 41)
Culture ponds				
Kossou	49	498	842	7.5 ± 1.6 (n = 28)
Sambakaha	67	492	819	7.8 ± 1.3 (n = 34)

Table IV. Mean values (± standard deviation) of *Oreochromis niloticus* females reproductive traits in aquariums. N1 : number of fish considered for fecundity, egg weight and spawning interval estimations. N2 : number of fish considered for estimations of duration of incubation and fry care.

Populations	N1	Range of female body weight (g)	Absolute Fecundity	Relative Fecundity (egg·kg^{-1})	Mean egg weight (mg)	Spawning interval (d)	N2	Duration of incubation (d)	duration of fry care (d)
Kossou	17	140-270	1 104 ± 234	5 672 ± 1619	7.2 ± 1.2	30.6 ± 20.8	3	10.7 ± 1.5	7.7 ± 0.6
Sambakaha	17	110-160	641 ± 172	5 065 ± 1415	7.8 ± 1.0	44.8 ± 22.4	6	11.0 ± 0.6	7.0 ± 1.8

from the Bouaké strain. The genetic contribution of brooders from both Volta basin (1957) and Nile basin (1968) to the constitution of the Bouaké strain [26, 38] was also confirmed in this study. However, as already pointed out by Rognon [26], the Volta influence was predominant. In the present analysis, the fact that the Edward Lake influence was less marked in the Bouaké strain than the Chobra influence may indicate that the population sampled in Edward Lake was not representative of brooders caught in the same area, approximately 30 years ago, when the strain was constituted.

Relative contribution of genetic variability and phenotypic adaptedness in observed life-history variations among fish populations in natural environments has been analysed in several studies [4, 21–23, 25, 31, 32]. However, most of these were conducted on the F1 or F2 generations of brooders initially caught in the wild. They have all demonstrated that even though it is possible to show that variability of some reproductive traits has a genetic basis, estimation of the relative contribution of genetic and phenotypic variation in observed differences is far more complicated. The present study differs from the others in that it was conducted directly on fish caught in their natural environments and then placed in identical environmental conditions and rearing structures.

The latter approach allowed us to show that *O. niloticus* females from Kossou and Sambakaha reservoirs, which were significantly different in terms of absolute fecundity and oocyte size in their 'natural' environments, no longer differed when sharing the same environment, pond or aquarium, for a 5-month period. The fecundity of females in pond was intermediate to that observed in females of the same populations in their natural environments while oocytes produced were bigger in pond. This was in agreement with the observations of Duponchelle [9] who found that the inverse relationship between egg size and number in *Oreochromis niloticus* is weaker than that observed in other tilapia species, such as *Sarotherodon melanotheron* and *Tilapia guineensis* [15, 16]. Results of the experiment in aquariums emphasized the important individual variability of reproductive characteristics in females *O. niloticus*, particularly concerning spawning interval which can vary in a ratio of 1 to 4 from one spawn to another for a given female. No apparent reason was found to explain this variability, not even egg consumption. Low success of egg retaking, 16 % and 35 % for the females of Sambakaha and Kossou respectively, corresponds to the values (25 %) reported by Tacon [34].

Experiments of reciprocal fish transfer between natural environments, such as those realized by Mann et al. [18] on two populations of *Cottus gobio*, or by Reznick and Bryga [24] on two populations of *Poecilia reticulata*, could reinforce the present results. Nevertheless, the experiments conducted in pond and aquariums clearly indicate that the reproductive differences observed initially between the populations of Kossou and Sambakaha in their natural environments mostly reflected the phenotypic plasticity of this species enabling them to face the different environmental conditions of these reservoirs.

Oreochromis niloticus is a fish known to have one of the most widespread geographic distribution in Africa. This species was able to colonize many kinds of environments, such as hot alkaline springs in Ethiopian highlands, several crater lakes in East Africa, deep lakes of the Rift Valley and various rivers and waterbodies all across Africa. In the course of evolution, this situation has resulted in important morphological [36] and genetic differentiation [1, 27, 28, 30] that led to the recognition of the existence of several subspecies. As a consequence, the range of phenotypic plasticity observed in this study on *O. niloticus* populations descending from the Bouaké strain may be only representative for the two subspecies that were used to constitute this strain, i.e., *Oreochromis niloticus* present in the Volta River but also in all other river basins of West Africa and the Lower Nile and *O. niloticus eduardianus* present in the Edward, Georges and Tanganyika lakes. It would be interesting to carry out complementary investigations on the reproductive characteristics of the other subspecies present on the Ethiopian highlands and lakes of the Rift Valley. As these populations show strong genetic differentiation [1], they may also display noticeable differences in their reproductive traits and adaptative responses to environmental variations.

For aquaculture, the present results underline the importance of environmental conditions on fecundity and egg size of *O. niloticus* and suggest that manipulation of rearing conditions could be used for a greater control on fry production. Further studies are still necessary for a better understanding of the nature and role of environmental factors implicated in the regulation of vitellogenesis and reproductive activity of this species.

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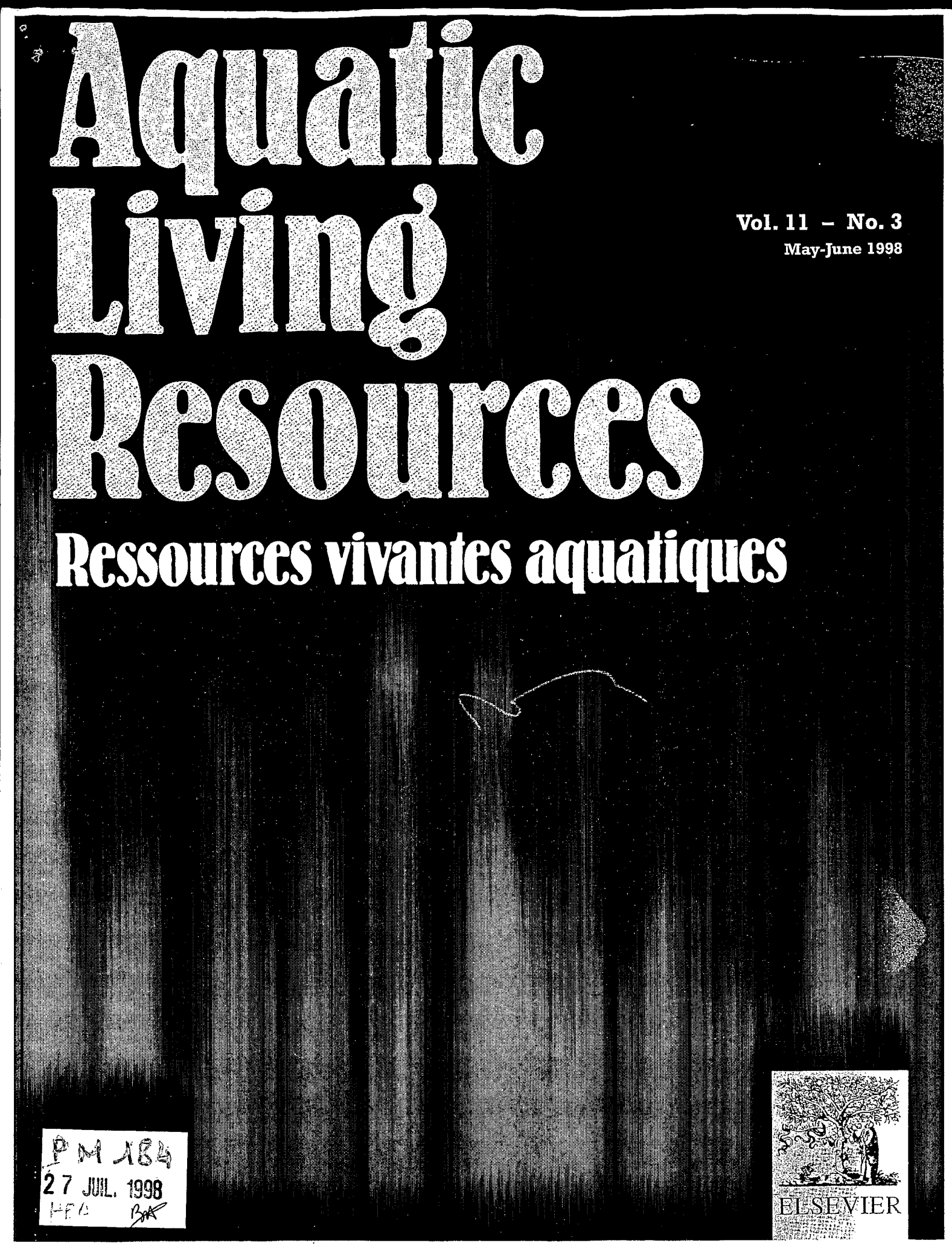

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