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# Influence of salinity on the life-history traits of the West African black-chinned tilapia (*Sarotherodon melanotheron*): Comparison between the Gambia and Saloum estuaries

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**Abstract –** The West-African neighbouring Gambia and Saloum estuaries function in different ways, the first being normal (saltier waters in the lower river, salinity range 0-38) and the second being inverse (saltier waters in the upper river, salinity range 36-90). The common cichlid species *Sarotherodon melanotheron* was collected in both systems over 16 months (June 2001 to September 2002) at five locations. We quantified reproductive traits from macroscopic examination of the gonads, oocyte counts and measurements, and growth from interpretation and measurements of an otolith sub-sample. There was a clear seasonal cycle of reproduction in the estuaries with a peak at the beginning of the wet season (May-July). Size at maturation was smaller in the more saline environment, the Saloum, for both females (170 mm in Gambia and 131 mm in Saloum) and males (162 and 113 mm respectively). The relative fecundity was lower and the oocyte size was bigger in the freshwater location of the Gambia river. Growth, estimated by counting the annual opaque zones on whole otoliths, was reduced in the hypersaline environment of the Saloum ($L_\infty$ = 198 mm, $K$ = 0.26). Differences are less obvious between the growth in the Gambia ($L_\infty$ = 238 mm, $K$ = 0.21) and that in the Saloum with a salinity of less than 60 ($L_\infty$ = 244 mm, $K$ = 0.22). All these observations suggest that *S. melanotheron* is able to withstand saltier environments by limiting its growth, reducing the size-at-maturity, and changing its fecundity, but the most profound changes are only visible in hypersaline conditions.

**Key words:** Hypersalinity / Reproduction / Age estimation / Growth / Environmental stress / Cichlidae

**Résumé – Influence de la salinité sur la croissance et la reproduction du tilapia estuarien ouest-africain *Sarotherodon melanotheron* : comparaison entre les estuaires de la Gambie et du Saloum.** Les deux estuaires ouest-africains de la Gambie et du Saloum présentent un mode de fonctionnement différent : le premier a un gradient de salinité normal, les zones les plus salées étant situées en aval (salinité de 0 à 38), tandis que le second possède un gradient inverse, avec une salinité plus élevée en amont (salinité de 36 à 90). L'espèce commune *Sarotherodon melanotheron* (Cichlidae) a été échantillonnée dans les deux systèmes pendant 16 mois (de juin 2001 à septembre 2002) au niveau de cinq stations. Les paramètres de la reproduction ont été quantifiés à partir de l'examen macroscopique des gonades, et du comptage et des mesures des ovocytes. La croissance a été calculée à partir de l'interprétation d'un sous-échantillon d'otolithes. Un cycle saisonnier de reproduction est mis en évidence dans les deux estuaires avec un pic au début de la saison des pluies (mai-juillet). Les tailles de première maturité sont plus petites dans l'environnement le plus salé, le Saloum, à la fois pour les femelles (170 mm en Gambie et 131 mm au Saloum) et pour les mâles (162 et 113 mm respectivement). La fécondité relative est plus faible mais les ovocytes plus gros, dans la station la moins salée de Gambie. La croissance, estimée par comptage des zones opaques annuelles des otolithes entiers, est réduite dans la zone hyperhaline du Saloum ($L_\infty$ = 198 mm, $K$ = 0,26). Les différences de croissance sont moins marquées en Gambie ($L_\infty$ = 238 mm, $K$ = 0,21) et dans le Saloum de salinité inférieure à 60 ($L_\infty$ = 244 mm, $K$ = 0,22). Toutes ces observations suggèrent que *S. melanotheron* est capable de supporter des environnements plus salés en limitant sa croissance, en réduisant sa taille de première maturité sexuelle et en changeant sa fécondité. Les changements les plus marqués ne sont cependant visibles que dans les conditions hyperhalines.

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## 1 Introduction

Climate change has been particularly evident in West Africa in the last 30 years. Increased drought has led to a significant decrease in freshwater flow, also leading to an increase of the salinity level of the waters in connection with the sea (i.e. waters with salinities much higher than that of the sea). This is the case for the inverse estuary of the Sine Saloum in Senegal where salinity can exceed 130 upstream during the dry season. This type of perturbation undoubtedly has consequences on fish populations and can modify their structure (Blaber 1997; Lévêque and Paugy 1999; Whitfield and Elliott 2002). In West-African estuaries, subjected both to seasonal variations and long-term climate effects, environmental changes have direct effects on life-history traits of fish populations, and particularly on reproductive traits (Albaret 1999). Observed divergence in life-history traits may have two origins that can interact: genetic and/or phenotypic plasticity changes (Stearns 1992), but it is often difficult to determine which one has a preponderant effect.

Tilapiine fishes (Cichlidae family), endemic to Africa, are widely distributed in tropical areas and have colonised a wide range of inland waters as natural or introduced species. The production of tilapia in African inland waters reached about 466 000 tonnes in 2000 (Vannuccini 2003). Among them, the genus *Sarotherodon* includes species that account for a large part of catches in estuaries and lagoons. These species are particularly adapted to brackish-water conditions, where they are subjected to regular or random changes in environmental conditions that can lead to physiological adaptations. The black-chinned tilapia, *Sarotherodon melanotheron*, characteristic of estuarine and lagoon ecosystems in West-Africa, exhibits high tolerance to low levels of dissolved oxygen (Dussart 1963; Philippart and Ruwet 1982), high tolerance to turbidity, good resistance to pollution and to a high range of temperatures (from 17 to more than 32 °C, Welcomme 1972), and euryhalinity up to 90 in the Casamance estuary (Albaret 1987) and even 130 in the Senegalese Saloum estuary (Albaret, personal communication). It has an omnivorous diet (Fagade 1971) and can change its diet in function of the environment (Kone and Teugels 2003). *Sarotherodon melanotheron* has an unusual reproductive behaviour, with mouth brooding by the male, which can be performed several times a year, for example in Togo (Laë et al. 1984) and in numerous other lagoons of the Gulf of Guinea (Fagade 1974; Legendre and Ecoutin 1989). The life-history traits of this species seem to vary greatly with environmental conditions. For example changes in reproductive traits have been observed in introduced populations of black-chinned tilapia in various mangrove ecosystems (Faunce 2000) or when breeding in sea or fresh water (Gilles, IRD, Montpellier, France, pers. comm.). Variation in size at first maturity is common in tilapias (Faunce 2000), but it is not known whether these variations result from dwarfism (fish old for their size) or neoteny (early maturation with normal size for the age) (Eyeson 1983). This reflects, in fact, limited data on growth of tilapias in their natural environment although large variations have been suggested (Ekau and Blay 2000). No study has attempted to validate and use age estimations from seasonal marks recorded in calcified structures. Although earlier studies have focused on validating age estimation using otolith microstructures (Ekau and Blay 2000; Panfili and Tomás 2001), they only recorded growth during the first year of life and also demonstrated large variations.

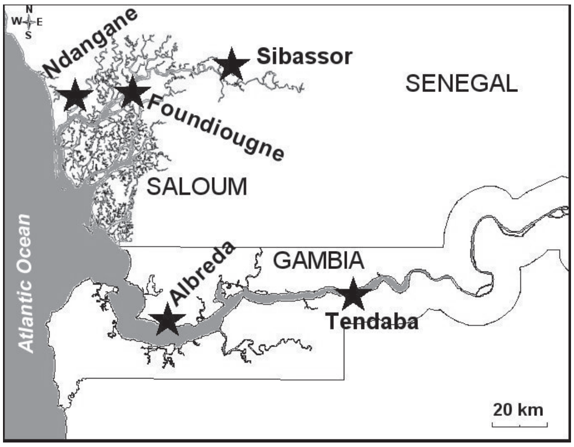

**Fig. 1.** Map of the sampling locations for black-chinned tilapia (*Sarotherodon melanotheron*) in the Gambia and Saloum estuaries.

An understanding of salinity effects on life-history traits of *Sarotherodon melanotheron heudelotii* is essential to predict responses of fish populations to rapid environmental change. Our study focused on life-history variation between two contrasting neighbouring estuaries in West Africa, the inverse hyperhaline estuary of the Saloum in Senegal and the estuary of the Gambia, which has a normal salinity gradient. These contrasted gradients are assumed to have direct or indirect effects on the environment, representing the main environmental constraint. This study aims at understanding the capacity of different populations of black-chinned tilapia to settle and adapt in these contrasting biotopes. Reproductive and growth parameters were quantified over a 1.5 year period.

## 2 Materials and methods

### 2.1 Sampling design

Samples were collected monthly between June 2001 and September 2002 at three locations in the Saloum estuary and at two locations in the Gambia estuary (Fig. 1). These locations were selected to represent salinity gradients, Sibassor in the Saloum being the most saline station and Tendaba in the Gambia the least. Each month, the salinity was measured in situ with a refractometer. Fish sampling was carried out by local fishermen using castnets with small mesh sizes to capture the maximum size range of *S. melanotheron*. Our objective was to collect at least 5 individuals for each 10 mm fork length class. Each sample was stored in 95% ethanol until processing. In the laboratory, all fish were measured (fork length, *FL*, in mm), weighed (total mass, *W*, in g), sexed, the stage of gonad maturity was recorded (see below), and their otoliths (*sagittae*) were extracted and stored dry in referenced microtube vials. The range of sizes was well distributed for most locations, the largest individual and the largest mean were encountered in Tendaba (Table 1). Samples were only missing or less representative in June 2001 and in August 2002 in Albreda.

**Table 1.** Characteristics of the total sample of *Sarotherodon melanotheron* individuals. GA, Gambia estuary. *FL*, fork length in mm; SD, standard deviation.

| Stations | *n* | Min-Max *FL* (mm) | Mean (SD) *FL* (mm) | Salinity range |
|---|---|---|---|---|
| Tendaba (GA) | 1129 | 45–220 | 112 (32) | 0–30 |
| Albreda (GA) | 919 | 59–198 | 99 (23) | 17–38 |
| Ndangane | 1361 | 37–194 | 110 (27) | 36–58 |
| Foundiougne | 1290 | 41–200 | 109 (29) | 38–57 |
| Sibassor | 1267 | 26–183 | 101 (29) | 47–90 |

## 2.2 Condition data

The condition factor (*Kc*) was calculated using the standard formula:

$$Kc = \frac{W}{FL^3} \times 10^5$$

where *W* is the total mass (g) and *FL* is the fork length (mm). Mean values of *Kc* were compared using a one-way ANOVA (with Scheffe's test for group homogeneity) and were also monitored over the year.

## 2.3 Reproductive data

Sexual maturity was determined according to Legendre and Ecoutin (1989). For females, stage 1 corresponds to immatures, stage 2 to a beginning of maturation, stage 3 to maturing females, stage 4 to females that are about to reproduce, stage 5 to ovulating females, and stage 6 to post-spawning females. For males, stage 1 corresponds to immatures, stages 2 and 3 to developing testicles, stage 4 to mature individuals, and stage 5 to spermiant gonads. For females, the gonads were removed when possible and weighed ($W_G$ in g). The gonado-somatic index (*GSI*) was calculated for each female using the formula:

$$GSI = \frac{100 \quad W_G}{W}.$$

Changes in the percentage of individuals with a stage equal to or greater than 3 (i.e. almost mature or mature) and the changes in the mean of *GSI* were monitored monthly in order to evaluate the seasonality of reproduction.

Average size at first maturity ($L_{50}$) was defined as the fork length at which 50% of the females are at an advanced stage of the first sexual cycle (at least stage 3 of the maturity scale) during the previously determined reproductive season (to avoid classifying resting females as immature). The $L_{50}$ was estimated by fitting the fraction of mature females per 20 mm FL intervals to a logistic function by a non-linear regression (quasi-Newton method, Statistica® software):

$$MF = \frac{100}{1 + e^{-a(L - L_{50})}}$$

where *MF* is the percentage of mature females per size class (20 mm), *L* is the central value of each size class, *a* and $L_{50}$ are constants of the model.

Gonads of mature females (stages 4 and 5) were stored in 95% ethanol. Before measuring the gonad developmental stage (e.g. number and size of oocytes), they were immersed in a saline (salinity 35) solution for 72 h, and then manually shaken before being immersed in a Gilson solution (100 ml ethanol, 9 ml glacial acetic acid, 20 ml of 60% nitric acid, 20 g mercury(II) chloride and 875 ml distilled water). Absolute fecundity was considered to be the number of oocytes which would be released at the next spawning. This was estimated by manual counting of the number of oocytes belonging to the largest modal size group ($n = 69$ females). The relative fecundity, which is used to compare different populations, is the ratio of absolute fecundity and mass in kg. The diameter and the volume of 20 oocytes per individual in an advanced stage of maturity (4 or 5) were measured by image processing for 11 females. For each individual, 50 oocytes were measured using the Image J freeware software following different steps: grey-level image acquisition from a Sony tri-CCD camera linked to a binocular microscope, contrast enhancement and thresholding to obtain a binary image, noise filtering and extraction of measurements after calibration (area, perimeter, maximum and minimum diameter). Mean values were compared using a one-way ANOVA (Statistica® software).

## 2.4 Age and growth data

A sub-sample of otoliths was examined to estimate the individual age and to calculate growth. For each month and for each location, a sample of two otoliths per 10 mm size class (*FL*) was collected. After the examination of several otoliths from different locations, a standard interpretation protocol was chosen as follows: an image of the whole right otolith was taken with TNPC software (Visilog, Noesis, France), under a binocular microscope with reflected light against a dark background. An image data bank was constructed; each otolith was then read by one reader from the core area to the edge and then back to the centre again; opaque zones were counted and measured on the radius of the posterior face. The interpretation of the presence or absence of an opaque zone was done taking into account its presence on all the otolith faces. The formation in the otolith edge of a zone was interpreted as translucent, opaque or undetermined; the last opaque zone was not counted if it was on the otolith margin, and thus in formation. The process of validation of the opaque zone deposition in time was done by calculating the percentage of opaque edges throughout the year. If the cycle of the formation corresponded to one opaque zone per year, it was interpreted as an *annulus*. The individual age in months was then calculated taking into account the mean date of birth in the population (given by the reproductive study), the date of capture and the number of opaque zones. The von Bertalanffy growth function (VBGF) was calculated using a non-linear estimation (quasi-Newton method, Statistica® software):

$$L = L_\infty \left(1 - \exp\left(-K\left(t - t_0\right)\right)\right)$$

where *L* is the mean length of an individual at time *t*, $L_\infty$, *K* and $t_0$ the parameters of the model.

The growth parameters of the VBGF were compared using the likelihood ratio test (Tomassone et al. 1993) and applying

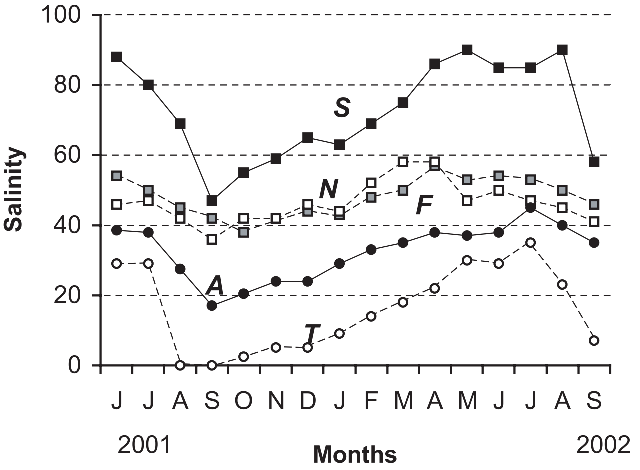

**Fig. 2.** Monthly variation of the salinity in the different sampling stations: rounded and squared symbols represent Gambia and Saloum estuaries respectively. A, Albreda (Gambia); F, Foundiougne (Saloum); N, Ndangane (Saloum); S, Sibassor (Saloum); T, Tendaba (Gambia).

the weighted sum of squares of Kimura (1980). For $k$ populations, the likelihood ratio test was $S_{\mathrm{LR}}$ compared with $\chi^2$ using 3 degrees of freedom (3 parameters):

$$S_{\mathrm{LR}} = \sum_{i=1}^{k} n_i \left[\ln\left(s_c^2\right) - \ln\left(s_k^2\right)\right]$$

where $n_i$ is the number of individuals of the $k^{\mathrm{th}}$ population, $S_c^2$ is the residual variance of the pooled model (for all populations), and $S_k^2$ is the residual variance of the models of the $k$ populations. The same likelihood ratio test was used to compare the growth models two-by-two.

## 3 Results

### 3.1 Salinity parameters

Salinity showed strong seasonal variation in both estuaries, falling at the beginning of the rainy season (June-July) each year and reaching a minimum in September (Fig. 2). The rainy season ended in October-November. The highest salinity occurred at the end of the dry season (April-May). Salinities in the Gambian locations were always lower than those of the Saloum estuary throughout the year (Fig. 2). The salt concentration in the Gambia (Albreda and Tendaba) reached its highest value, close to that of sea water, at the end of the dry season but was null at Tendaba after the rains in August. The functioning of the Gambian estuary is similar to many estuaries, with a lower salinity value upstream. The salt concentration in the Saloum (Ndangane, Foundiougne, and Sibassor) was always much higher than that of sea water, reaching a minimum at Ndangane (located closest to the sea) of about 40 psu. Although the Ndangane and Foundiougne stations are rather far apart (about 30 km), the salinities in these areas were similar, that of Ndangane becoming lower during the rainy season. The upstream Sibassor station had an extremely high salinity level, reaching 50 in September each year and about 90 in May (Fig. 2). It is thus an example of an area with extreme environmental constraints. The functioning of the Saloum is clearly inverse, the upper-river site being the most saline at all times of year. In 2002, the rainy season started later and the salinity level did not decrease before July-August.

**Table 2.** Condition factor *Kc* (mean ± standard error) of *Sarotherodon melanotheron* at the scale of estuaries and each location. *n*, number of individuals. The same letter given after the means of a column (estuaries or locations) signifies that the values do not differ significantly between groups ($p > 0.05$).

| | *Kc* | *SE* | *n* | Salinity | |
|---|---|---|---|---|---|
| | | | | Monthly average | Range |
| GAMBIA (GA) | $1.90^{a}$ | 0.06 | 1988 | 22 | 0–38 |
| SALOUM | $1.82^{b}$ | 0.17 | 3854 | 55 | 36–90 |
| Tendaba (GA) | $1.96^{c}$ | 0.04 | 1098 | 14 | 0–30 |
| Ndangane | $1.94^{c}$ | 0.04 | 1361 | 47 | 36–58 |
| Albreda (GA) | $1.84^{cd}$ | 0.05 | 890 | 30 | 17–38 |
| Foundiougne | $1.84^{cd}$ | 0.04 | 1260 | 47 | 38–57 |
| Sibassor | $1.67^{d}$ | 0.04 | 1233 | 70 | 47–90 |

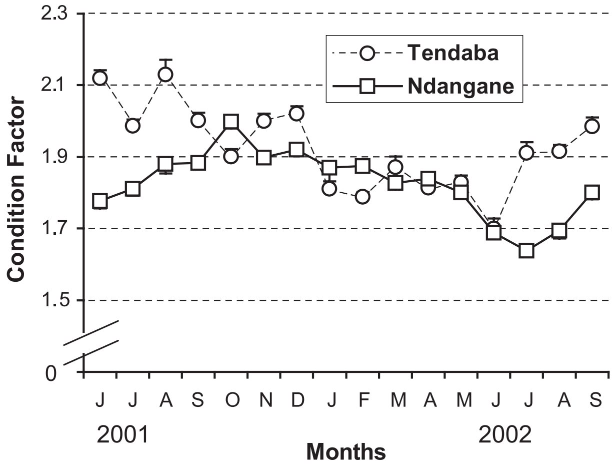

**Fig. 3.** Monthly variation of the condition factors of *Sarotherodon melanotheron* in Tendaba (Gambia) and in Ndangane (Saloum) during the period June 2001 – September 2002.

### 3.2 Condition factor

The average condition factor (June 2001–September 2002) differed significantly between estuaries (Table 2, ANOVA, $p < 0.05$): the condition of *Sarotherodon melanotheron* in Saloum being lower than that in Gambia. Condition factor also differed significantly among sampling locations (Table 2, $p < 0.05$), with a lower value for the hyperhaline area of Sibassor, but without a hierarchical classification in relationship with the altitude in the estuary. There was a variation in condition factor during the observation period, which seems in relationship with the seasonal salinity of the environment (Fig. 3) but without statistical correlation: the condition was lowest in July, at the beginning of the rains and highest in October at the end

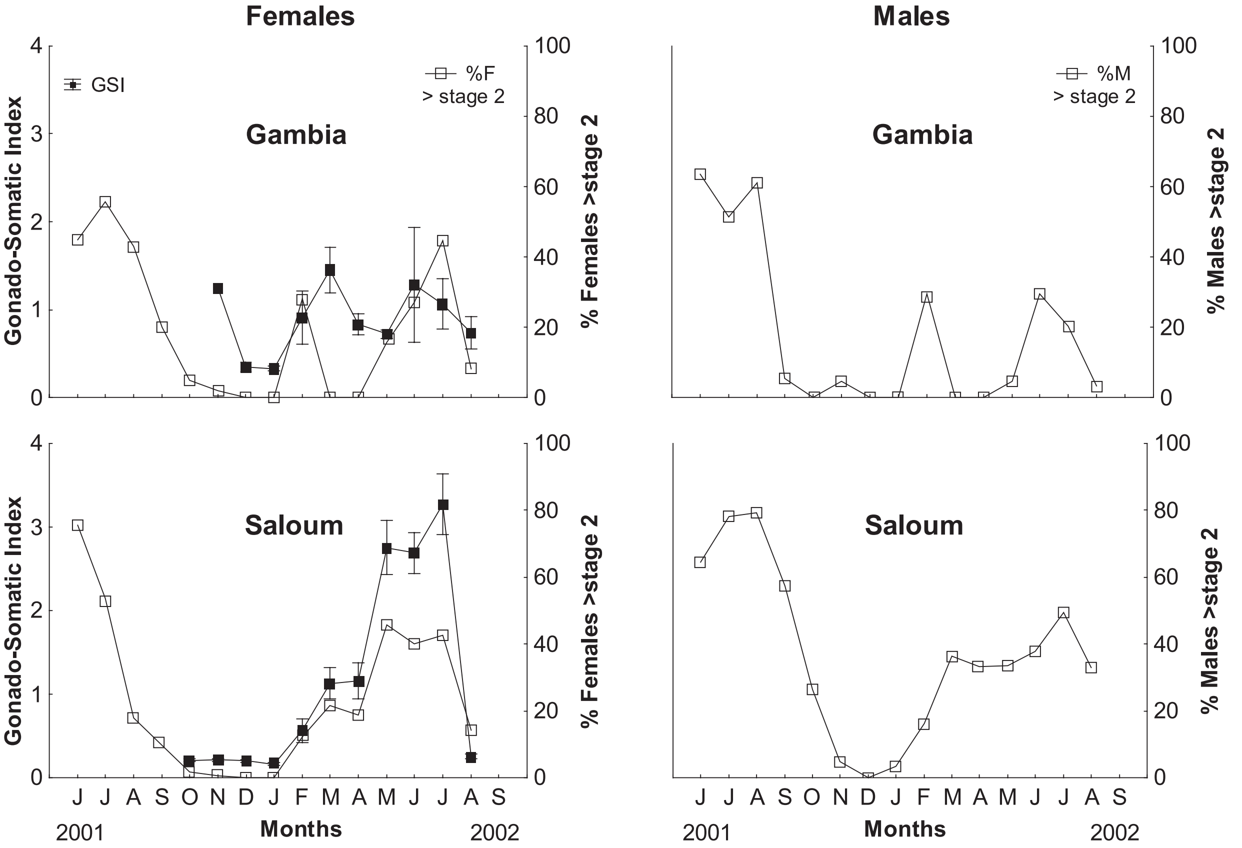

**Fig. 4.** Monthly evolution of the gonado-somatic index (mean GSI ± standard deviation) and the percentage of different sexual stages of *Sarotherodon melanotheron* in the Saloum and Gambian estuaries.

of the rainy season. Although the condition seems to be cyclic between the two years, with an increase after June for the same location, there were notable differences between sites (Fig. 3, Ndangane vs. Tendaba).

### 3.3 Reproduction

In these environments, two periods of intensive reproductive activity were observed during our study (Fig. 4). These periods matched the beginning of the rainy season in 2001 and in 2002, but with varying intensity (Fig. 4). The cycle was more apparent in Saloum where reproduction (indicated by the percentage of mature individuals above stage 2) started before the rainy season, in about February, and reached a peak at the beginning of the rains (in June-July). Similarly in Gambia, the percentage of mature females was highest in July each year and reached a minimum at the end of the year in November-December (at the end of the rainy season), with a slight shift between the females and the males (Fig. 4). For both females and males in Gambia there was a start of the reproductive activity in February 2002, followed by a halt in March-April. The changes in the gonado-somatic index (*GSI*) of the females exhibited the same pattern but for the Gambian females it did not follow exactly the percentage of mature fish, and its variability was higher than in the Saloum (Fig. 4). In conclusion the reproductive season for *S. melanotheron* in the Saloum lasted from March to August, and in the Gambia from May to September. For the next analysis (i.e. growth calculation), 1 June was assumed to be the date of birth of the individuals in the populations.

For both females and males the sizes at first maturity ($L_{50}$) were higher in the Gambia than in Saloum (170 and 131 mm for females, and 162 and 113 mm for males respectively, Fig. 5 and Table 3). This parameter also varied greatly among study sites and between sexes. For the females, the highest value of $L_{50}$ was encountered at Tendaba (184 mm), whereas the lowest was found at Foundiougne (126 mm), and for males the highest was at Albreda (171 mm) and the lowest also in Foundiougne (111 mm) (Table 3). The $L_{50}$ for the females and the males in Sibassor (143 and 114 mm respectively) were above or close to the values of the other locations in the Saloum. Whatever the sex, the sizes at first maturity were similar at Ndangane and Foundiougne (Table 3). The most unexpected value was that of the females at Sibassor, which was high compared to the other values in the Saloum.

The relative fecundity of females also varied among sites (Fig. 6, one-way ANOVA, $F_{(4,64)} = 2.61$, $p = 0.043$). Females in the least saline location of Tendaba had the lowest relative fecundity (3545 ± 543 oocytes kg$^{-1}$). The highest fecundity was encountered at Albreda (6305±814 oocytes kg$^{-1}$). In the Saloum, Sibassor had a lower and more variable fecundity (4582 ± 728 oocytes kg$^{-1}$). Oocyte sizes (area) also differed among locations (one-way ANOVA, $F_{(4,215)} = 33.41$,

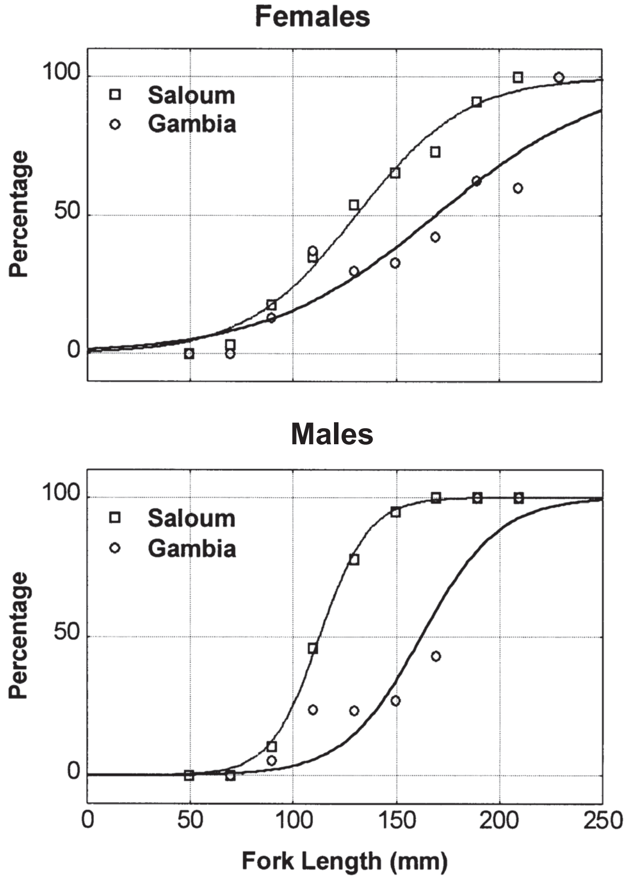

**Fig. 5.** Logistic function estimated from the percentage of mature individuals per size class for female and male *Sarotherodon melanotheron* in the Saloum and Gambia *n* estuaries, during the 2001-2002 seasons of reproduction.

$p < 0.0001$). There was an inverse tendency between oocyte sizes and fecundities in the different locations (Fig. 6). The biggest oocytes were found in Tendaba (7.7 ± 0.2 $mm^2$) and the smallest in Albreda (5.0 ± 0.2 $mm^2$). No clear relationship was found between the relative fecundity, the oocyte size and the salinity.

### 3.4 Age and growth

The age of *Sarotherodon melanotheron* in the Gambia and Saloum estuaries was estimated using the interpretation of opaque zones on the whole otoliths viewed on a dark background and under reflected light. This interpretation was facilitated with the use of an image database of the otoliths, allowing the results to be re-examined at anytime. The alternation of translucent and opaque zones on the whole otolith was clear enough to count them. The otolith core was opaque, surrounded by an opaque zone of variable width. Some otoliths were difficult or impossible to interpret and were excluded from the calculation of the age.

The monthly changes in the percentage of opaque edges on the otoliths validated the deposit of one opaque zone per year (Fig. 7): the formation of the opaque zone started at the

**Table 3.** Sizes at maturity, $L_{50}$ (mm) (estimated ± standard error) for the females and males of *Sarotherodon melanotheron* in the Saloum and Gambian estuaries and stations, during the reproductive period June 2001-September 2002. *n*, number of individuals; $d^2$, coefficient of determination (percentage of variance explained).

| | $L_{50}$ (mm) | *SE* (mm) | $d^2$ (%) | *n* |
|---|---|---|---|---|
| | Females | | | |
| GAMBIA (GA) | 170 | 8 | 87.9 | 488 |
| SALOUM | 131 | 3 | 98.2 | 1073 |
| | | | | |
| Tendaba (GA) | 184 | 7 | 89.4 | 294 |
| Albreda (GA) | 137 | 12 | 73.8 | 194 |
| Ndangane | 128 | 4 | 95.3 | 393 |
| Foundiougne | 126 | 2 | 99.2 | 348 |
| Sibassor | 143 | 11 | 80.8 | 332 |
| | Males | | | |
| GAMBIA | 162 | 7 | 89.2 | 522 |
| SALOUM | 113 | 1 | 99.8 | 988 |
| | | | | |
| Tendaba (GA) | 162 | 6 | 92.2 | 328 |
| Albreda (GA) | 171 | 6 | 68.6 | 194 |
| Ndangane | 115 | 1 | 99.6 | 307 |
| Foundiougne | 111 | 0 | 99.9 | 368 |
| Sibassor | 114 | 2 | 99.0 | 313 |

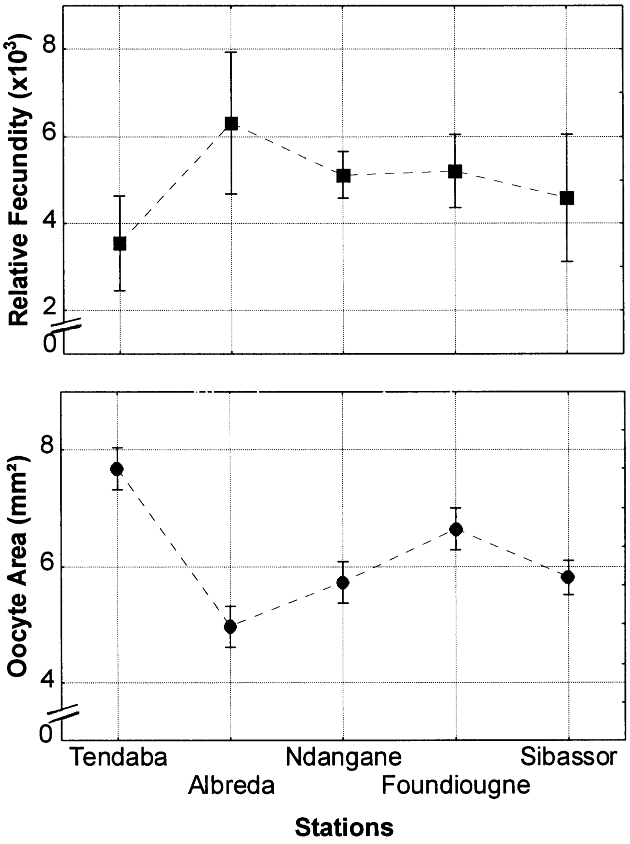

**Fig. 6.** Means and 95% confident intervals of the relative fecundity and the oocyte size (area) of *Sarotherodon melanotheron* in the two different ecosystems (Gambia and Saloum).

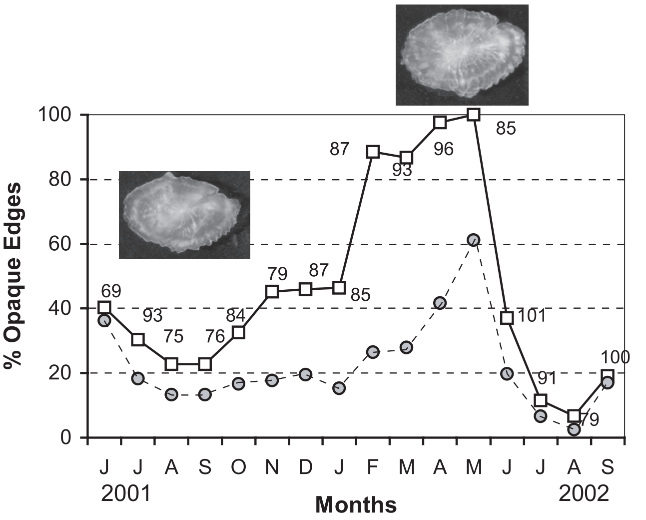

**Fig. 7.** Variation over time (June 2001 to September 2002) of the percentage of opaque edges on the margin of *Sarotherodon melanotheron* otoliths. Samples are pooled from all the stations in the Saloum and Gambia. Numbers on the plot correspond to the number of individuals monthly analysed. Percentages are calculated for the whole sample of otoliths with undetermined edges (●, opaque, translucent and undetermined) and without undetermined edges (□, opaque and translucent only).

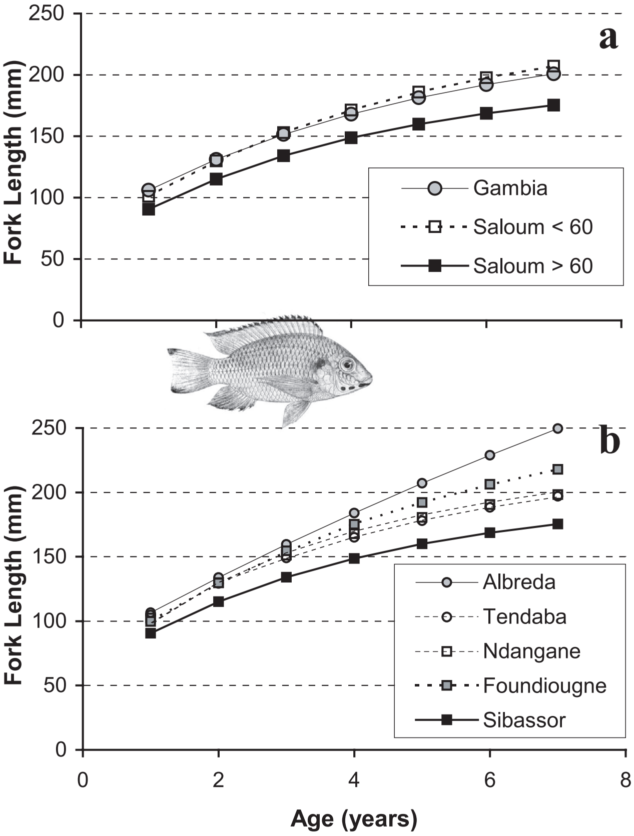

**Fig. 8.** Von Bertalanffy growth functions calculated for *Sarotherodon melanotheron* depending on the level of salinity (a) and on the sampling station (b). Drawing of *S. melanotheron* from Lévêque et al. (1990).

beginning of the year, after the rainy season, and ended just before the rains, in May. The translucent zone appeared at the beginning of the rainy season and grew during this season. The validation was similar including the otoliths with a non interpretable edge (i.e. with a percentage of opaque plus translucent zones that sometimes did not reach 100%, Fig. 7). The opaque zone formation coincided with a period of environmental stress for the fish, and was considered as an *annulus*, whereas the translucent zone corresponded to more favourable conditions. Otoliths were easier to interpret during the rainy season (August-October), and less at other periods (e.g. February). This can be explained by the formation of an opaque zone around the otolith during the dry period that could prevent a clear observation of the internal structures. Otoliths also seemed more difficult to interpret in the Gambia than in the Saloum. The appearance of the *annulus* corresponded with the date of birth chosen for the population (1 June). The individual age could then be calculated in months using the number of opaque zones (*annuli*), the date of birth and the date of capture.

VBGF showed a growth reduction in Sibassor, the location of highest salinity, i.e. above 60 (Fig. 8, Table 4), this being significantly different from all other locations ($S_{\mathrm{LR}}$ = 1142.7, $p < 0.0001$). Growth differed significantly between the pooled Saloum data, salinity <60, and the pooled Gambia data ($S_{\mathrm{LR}}$ = 547.1, $p < 0.0001$), with a higher growth in the Gambia. Comparing the growth models among locations, the highest growth occurred at Albreda and the slowest at Sibassor. The high estimate of the asymptotic length in Albreda (Table 4) was probably due to the small number of large individuals in the sample. But the comparison of the growth during the first 5 years between the locations still showed a better growth at Albreda and a lower growth at Sibassor. Growth rates did not differ between Tendaba and Ndangane. All these observations suggest that the growth is highest in an environment with an intermediate level of salinity whereas growth is inhibited in higher or lower salinities.

## 4 Discussion

The life history trait differences observed among locations in Saloum and Gambia may result from environmentally induced variation (developmental plasticity), genetic variation, or their interaction (Stearns 1992). All black-chinned tilapia populations from Senegal and Gambia have been assigned to the sub-species *Sarotherodon melanotheron heudelotii* (Gourène et al. 1993; Pouyaud 1994; Falk et al. 2003). However, populations within this geographic area present an extensive genetic structuration. Thus, allozymic (Gourène et al. 1993; Pouyaud 1994) and microsatellite loci (Pouyaud et al. 1999) indicate low or even no gene flow, even at micro-geographical scales (i.e. the Saloum-Gambian estuary). Gourene et al. (1993) assumed that this population structure could be the result of the poor dispersion ability of this species, but Pouyaud et al. (1999) also noticed that this genetic structure had no geographical basis and varied with time. This interesting result has been assumed to be the consequence of kin aggregation, inbreeding and shoaling behaviour, facilitated by

**Table 4.** Parameters of the von Bertalanffy growth functions calculated for the *Sarotherodon melanotheron* in the Saloum and Gambian estuaries in 2001-2002. *n*, number of individuals; *SE*, standard error; $d^2$, coefficient of determination (percentage of explained variance).

| | *n* | $L_\infty$ (mm) | *SE* (mm) | *K* | *SE* | $t_0$ (year) | $d^2$ (%) | *L* range (mm) | Age range (year) |
|---|---|---|---|---|---|---|---|---|---|
| GAMBIA (GA) | 302 | 238 | 19 | 0.21 | 0.04 | −1.80 | 80.6 | 45−220 | 0−7 |
| SALOUM < 60 psu | 466 | 244 | 17 | 0.22 | 0.03 | −1.37 | 80.7 | 41−200 | 0−7 |
| SALOUM > 60 psu | 181 | 198 | 14 | 0.26 | 0.04 | −1.37 | 85.3 | 26−177 | 0−8 |
| Tendaba (GA) | 185 | 232 | 22 | 0.21 | 0.04 | −1.80 | 81.5 | 45−220 | 0−7 |
| Albreda (GA) | 117 | 609 | - | 0.06 | 0.07 | −2.45 | 81.1 | 59−198 | 0−4 |
| Ndangane | 222 | 225 | 19 | 0.25 | 0.05 | −1.39 | 79.3 | 53−194 | 0−7 |
| Foundiougne | 244 | 273 | 33 | 0.19 | 0.04 | −1.39 | 82.1 | 41−200 | 0−7 |
| Sibassor | 181 | 198 | 14 | 0.26 | 0.04 | −1.37 | 85.3 | 26−177 | 0−8 |

the mouth-brooding reproductive behaviour observed in this species. Lastly, the population structure in this species is difficult to determine and is probably more related to the kin relationship among shoals rather to any geographical considerations. However, we have assumed that our sampling strategy, favouring multiple samplings at the same location each month for one year and a half, allows us to estimate history traits of the populations rather than of the family. Moreover the contrasted salinity gradients are assumed to be the main environmental constraint, directly or indirectly acting on fish communities, available food and ecological niches.

In the Saloum and Gambia, black-chinned tilapia exhibited an annual cycle of reproduction, with a more intense activity during the rainy season and reduced activity at the beginning of the dry season. The cycle was more apparent in Saloum than in Gambia, but may reflect a stronger sampling effort in the Saloum. This cycle contrasts with the observation of continuous reproduction in more equatorial areas such as lagoons in Togo (Laë et al. 1984), Ivory-Coast (Legendre and Ecoutin 1989) and Nigeria (Fagade 1974), and lakes in Ivory Coast (Kone and Teugels 1999), but is similar to the marked cycle described under a more sub-tropical climate (Faunce 2000). Nevertheless, reproduction can occur in the Saloum and Gambia even outside the main reproductive period, since small individuals were found in the catches throughout the year. The age estimation of these individuals, using the daily otolith increments, could be used to back-calculate the date of birth and verify this assumption.

If the seasonality of reproduction does not seem to be affected by the salinity inversion in the Saloum, we demonstrate that environmental pressures, mainly via the salinity, lead to changes in both reproductive and growth life-history traits. These changes are also linked to individual condition. The main modification in the reproductive traits concerns the change in the size at maturity, with a reduction of this size with increasing salinity. This is demonstrated in relationship to the sampling locations, even if the sizes at maturity for both females and males in the most upstream location of Sibassor were not significantly different from the other locations in the Saloum (Table 3). This could be linked to the fact that Sibassor is close to a peanut factory, which could influence the behaviour and the growth of the fish in this area (see below). The sizes at maturity estimated for males were smaller than those for females, at all study locations. Several authors (Kone and Teugels 1999; Faunce 2000) have reached the same conclusion but Legendre and Ecoutin (1989) showed similar values for both sexes in lagoons. The calculated sizes at maturity in the Gambia were not very different from those calculated in other environments: 176 mm (fork length) for females in lagoons of Ivory Coast (Legendre and Ecoutin 1989), 135 mm (standard length) for females and 129 mm (SL) for males in freshwater (Kone and Teugels 1999), 180 mm (SL) for females and 163 for males in Florida (Faunce 2000). The reduction of this size, that was observed here in the more saline Saloum, has also been observed when the fish are bred in aquaculture (Legendre and Ecoutin 1989). This trait modification seems to be linked with a more stressful environment. Observations of a reduction of the size at maturity have been reported for other tilapia species, particularly in the freshwater species *Oreochromis niloticus* (Duponchelle and Panfili 1998; Duponchelle et al. 1998; Duponchelle and Legendre 2001). Rapid phenotypic changes in reproduction traits in response to environmental changes for tilapias have been suggested rather than genetic differences (Duponchelle et al. 1998; Duponchelle and Legendre 2001). Nevertheless the direct effect of salinity in experimental conditions has not been tested yet on black-chinned tilapia. Further studies may be required to fully understand the effect of salinity on life history characters of black-chinned tilapia, and to understand the origin of these differences (environmentally induced phenotypic variation and/or genetic variation).

The fecundity of black-chinned tilapia seemed to be more affected by low salinity: in the less saline environment, the relative fecundity was lower with larger oocytes. Kone and Teugels (1999) have made the same observations in a freshwater lake in the Ivory Coast. In one experimental study on the changes of reproduction characteristics of *S. melanotheron* in fresh and sea water (Gilles, IRD, Montpellier, pers. comm.), some researchers have observed a significantly lower size and weight of eggs in sea water. These authors thought that this adaptation could be related to two effects: in sea water to compensate for energy expenditure on osmoregulation, but also to the fact that a smaller egg size in sea water could decrease the exchanges with the external surface reducing energy expenditure to maintain osmolarity. In our study, intermediate or high salinities (35−90) did not show any significant relationship with fecundity or oocyte size. Further analysis using rank correlations with more individuals from natural environments are necessary to highlight a possible relationship.

The annual climatic cycle in the Sene-Gambian area, with one long dry season (November to June) and one rainy season (July to October), greatly influences the growth of fish in both the Saloum and Gambian ecosystems. Otolith analysis revealed the formation of an opaque zone each year coinciding with the dry season, and a translucent zone corresponding to a growth during more favourable conditions in the rainy season. Our results are the first demonstration of seasonal growth for this species. The growth of the black-chinned tilapia was very variable for any given population or between populations. A higher growth rate was found in the Gambian populations, reflecting the better condition of fish in this ecosystem compared to the Saloum. The lowest growth and condition factor were recorded in the upstream and more saline Sibassor site. The black-chinned tilapia is able to alter its diet if environmental conditions change (Kone and Teugels 2003). The presence of a peanut factory close to the Sibassor site (see above), that could have had a nutritional influence on populations by providing an additional food source from waste products from that factory, did not seem to favourably influence growth. In this area, the direct and indirect environmental pressure from salinity was the most important constraint on growth. In a comparable study of the bonga shad species, *Ethmalosa fimbriata*, in the same environment (Panfili et al., in press), the growth was better in the Saloum with a higher condition factor than in the Gambia. The relationships between growth and condition in these peculiar environments seem to be positively correlated. There is little published information on the growth of *S. melanotheron* in its natural environment, and even in aquaculture (Pauly et al. 1988). The growth rates observed in Saloum, and especially in the Gambia, are much higher than those reported by Pauly et al. (1988) in the Ivory Coast. In our study, the observed differences in growth were mainly visible above a salinity of 60, suggesting that environmental constraints are effective in hyperhaline conditions. In these extreme conditions, energy allocation to osmoregulation processes is probably high and at the expense of the growth. In intermediate conditions (i.e. less than 60), the regulation of the energy allocation maintains comparable growth whatever the salinity. In terms of growth rates, freshwaters are probably not optimal for this brackish-water species, as is shown by the comparison of Tendaba and Albreda, the optimal conditions being intermediate salinities (close to those of the seawater). This interpretation is in accordance with the results of Iwama et al. (1997) who have observed a lower oxygen consumption in sea water than in freshwater or in hyperhaline sea water for a tilapia species (*Oreochromis mossambicus*).

In conclusion, the seasonal climate in the area of the Sene-Gambian estuaries influences the life-history traits of the black-chinned tilapia, in terms of reproduction and growth. We observed a reduction of growth rates (above 60) and a reduction of the size at maturity with increasing salinity. The observed reduction of the size at maturity therefore seems to be due to a reduction of the growth but also to an earlier maturity. The relative fecundity and oocyte size were more variable between locations. The adaptation to variations in salinity could involve osmoregulation processes and energy expenditure and allocation to biological traits.

In the fish communities of estuaries and lagoons, the black-chinned tilapia is probably the species most capable of withstanding extremely high salinities, above 120 (Lévêque 1999). This can probably be correlated with the observed life-history trait variations. This species presents a potential for aquaculture in brackish-waters (Eyeson 1983; Pullin et al. 1988; Legendre and Ecoutin 1989; Legendre et al. 1989; Pullin et al. 1996) but in intensive culture, the species has shown poor potential and has been disappointing (Legendre et al. 1989), probably because the environmental conditions were sub-optimal. These authors therefore recommended extensive rearing. In the interest of aquaculture, all parameters should therefore be chosen carefully to obtain best growth. Complementary experiments in mesocosms should be conducted with a population of the same genetic origin to directly test the effects of variations in salinity on the life-history traits (reproduction and growth).

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