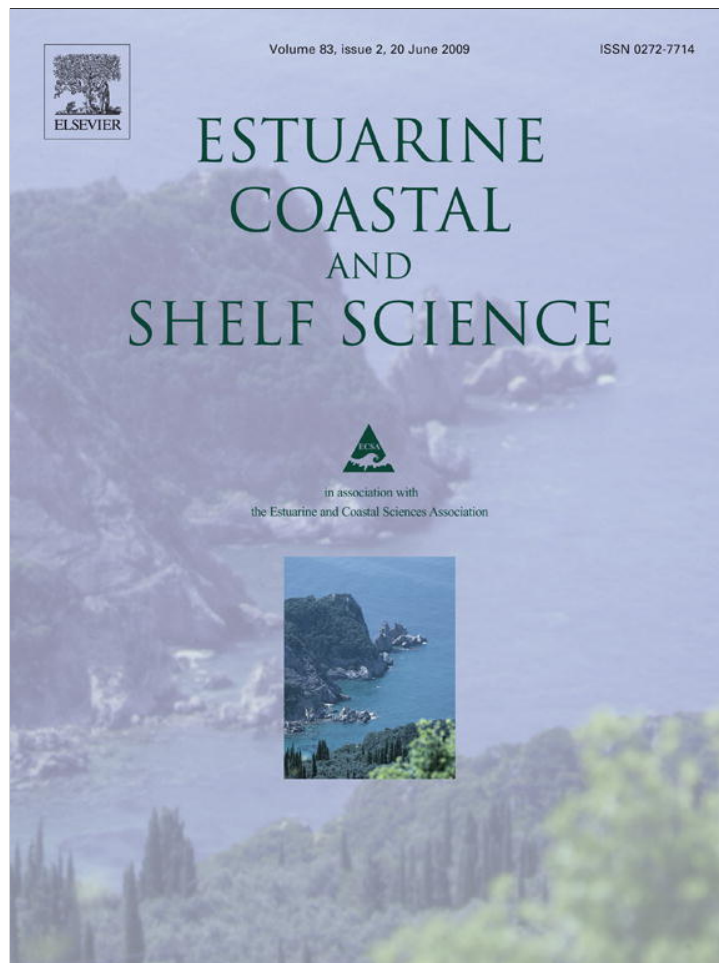


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## Effects of the environment on fish juvenile growth in West African stressful estuaries

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### ABSTRACT

The knowledge of juvenile fish growth in extreme environmental conditions is a key to the understanding of adaptive responses and to the relevant management of natural populations. The juvenile growth of an extreme euryhaline tilapia species, *Sarotherodon melanotheron* (Cichlidae), was examined across a salinity gradient (20–118) in several West African estuarine ecosystems. Juveniles were collected during the reproduction period of two consecutive years (2003 and 2004) in six locations in the Saloum (Senegal) and Gambia estuaries. Age and growth were estimated using daily otolith microincrements. For each individual, otolith growth rates showed three different stages (slow, fast, decreasing): around  $4 \pm 0.5 \mu\text{m d}^{-1}$  during the first five days,  $9 \pm 0.5 \mu\text{m d}^{-1}$  during the next 15 days and  $4 \pm 0.50 \mu\text{m d}^{-1}$  at 60 days. Growth modelling and model comparisons were objectively made within an information theory framework using the multi-model inference from five growth models (linear, power, Gompertz, von Bertalanffy, and logistic). The combination of both the model adjustment inspection and the information theory model selection procedure allowed identification of the final set of models, including the less parameterised ones. The estimated growth rates were variable across spatial scales but not across temporal scales (except for one location), following exactly the salinity gradient with growth decrease towards the hypersaline conditions. The salinity gradient was closely related to all measured variables (condition factor, mean age, multi-model absolute growth rate) demonstrating the strong effect of hypersaline environmental conditions—induced by climate changes—on fish populations at an early stage.

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### 1. Introduction

Drastic variations in fish population sizes can result from subtle changes in individual growth during early life stages (Houde, 1987; Campana, 1996). Juvenile growth histories have life-long and even trans-generational effects on various characteristics of adult populations ranging from parental reproductive schedules to key life-history trade-offs (Taborsky, 2006). Assuming that mortality decreases and fecundity generally increases with body size, the faster the growth rates of juveniles, the more the global fitness of future adult populations will be enhanced (Shepherd and Cushing, 1980; Anderson, 1988; Suthers, 1998). This scenario has been generalised across animal taxa (Taborsky, 2006) and has been demonstrated for several fish species (Campana, 1996; Oozeki et al., 2003). The knowledge of juvenile growth is thus a key to the understanding of fish biology and to the relevant management of natural populations.

Within the plurality of environments occupied by fish, estuarine ecosystems make the highest contribution to global food production across the globe and to the total economic value of ecosystem services (Costanza et al., 1997). Although estuaries are essential to the present and future sustainability of human activities, they represent fluctuating environments where climatic and anthropomorphic effects are extremely pronounced. Estuarine ecosystems are also essential for many fish species inhabiting or using them as nursery habitats. Climate is already recognised as one of the strongest influences on juvenile fish growth during their residency in estuarine or coastal waters (Ormerod, 2003); we can thus expect climate variations to be responsible for most of the future changes in fish assemblages and populations.

Within this context, stressful estuarine ecosystems (i.e. with highly fluctuating environmental conditions, such as temperature, salinity, hypersaline waters, across different temporal and spatial scales) provide a unique opportunity to investigate the effect of environmental disturbances on juvenile fish growth and consequently to provide information on their potential impact on future populations. In such ecosystems, constraints are induced mainly by

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physicochemical variables such as salinity, temperature, dissolved oxygen, turbidity and biological variables such as food availability or predation, impacting both survival and recruitment (Limburg et al., 1999; Whitfield and Elliott, 2002; Whitfield, 2005). During the last decades, West African estuarine ecosystems have been particularly impacted by climate change (Pagès and Citeau, 1990). These areas with scarce rains and high evaporation rates are very sensitive to the increase in salinity levels, such as occurring in South Africa (Harrison, 2004). For example, the functioning of the Saloum delta and Casamance estuary in Senegal experienced a dramatic modification due to the strong reduction of freshwater inputs resulting from a drought phenomenon. Indeed, the Saloum delta is presently hypersaline and characterised by an inverse salinity gradient (range 36–140), the salinity in the upper river being higher than the one of the coastal waters (Pagès and Citeau, 1990). This stressful environment has pressured the fish species to develop adaptive responses both at the assemblage and population levels (Panfili et al., 2006).

The best biological model to measure the impact of salinity in hypersaline environments is certainly the tilapia species, *Sarotherodon melanotheron* (Rüppell), a euryhaline cichlid endemic from estuarine ecosystems in West Africa, and exploited by small-scale fisheries in this area. Its main characteristic is an extreme euryhalinity, ranging from 0 to 134 (Whitfield, 1999; Panfili et al., 2006). The adaptive responses of populations submitted to hypersaline stressful conditions could be highlighted by the study of the juvenile growth of *S. melanotheron*, for example in the Saloum delta. The individual growth rates can be calculated using otolith (ear stone) daily microincrements (Campana and Neilson, 1985). Paperno et al. (1997) showed that microincrement width is positively related to the condition factor and fish growth rates.

Given the intrinsic variability expressed by individual sizes, a mathematical expression of the mean population growth is necessary (Katsanevakis, 2006). This is generally achieved relying common *a priori* chosen models such as the Gompertz (Takagi et al., 2006; Narimatsu et al., 2007) or von Bertalanffy equations (Katsanevakis and Maravelias, 2008). However, the choice of such growth models can be made objectively within the “model selection” framework. This information theory framework, based on the likelihood theory, is a modern approach now widely used across biological fields of research (Johnson and Omland, 2004; Hobbs and Hurlbourn, 2006) and recognised as an emerging tool for the study of fish growth (Shono, 2000; Imai et al., 2002; Fey and Linkowski, 2006; Katsanevakis and Maravelias, 2008). Furthermore, this framework allows making robust inferences based on all the models for which the data support evidence. This is achieved using model averaging, taking thus into account the potential uncertainty as to which model is the best in describing the growth of the studied fish.

In the present study, the growth of juvenile tilapias *Sarotherodon melanotheron* was investigated across a salinity gradient in a hypersaline environment in West Africa (Saloum estuary in Senegal vs. Gambian estuary in Gambia). Five growth models were compared within the “model selection” framework, and a multi-model growth curve resulting from information theory criteria comparisons and expert analysis of biological representativeness was then used to compare population growths across the salinity gradient. The aim of the study was to test the assumption that hypersaline conditions have a direct impact on juvenile fish growth.

## 2. Materials and methods

### 2.1. Sampling design

Fish were sampled every two weeks during the recruitment period in June and July of 2003 and 2004, in five locations of the

Saloum estuary (Missirah, Ndangane, Foundiougne, Sibassor and Koïlal) and one location of the Gambia estuary (Tendaba) (Fig. 1). These locations were chosen to best represent the salinity gradient, from brackish water (Tendaba, Gambia) to the highest salinity water (Koïlal, Saloum, Senegal). Fish were captured with the help of local fishermen using a beach seine net with a 5 mm mesh size. In the field, the captured fish were first anaesthetised and killed with a lethal dose of phenoxyethanol and were then preserved in 95% ethanol until dissection. Temperature and salinity (measured with a refractometer) were recorded in a single measurement for every sampling at the location of fish capture (i.e. close to the estuary shore). In the laboratory, ten individuals were randomly chosen per each 10 mm size-class from 10 to 60 mm (fork length  $L$ ), for each location and sample date. These individuals were also weighed (total weight,  $W$ , g), macroscopically sexed (female, male, undifferentiated), and their otoliths (*sagittae*) were extracted, rinsed with distilled water, dried and preserved in referenced microtube vials. Among the ten individuals per size-class, one right otolith was randomly sub-sampled for preparation, age estimation and growth rate calculation.

### 2.2. Otolith preparation and examination

In order to observe both the otolith core and microincrements until the edge, the otoliths were prepared using the validated method described by Panfili and Tomás (2001) which includes four main stages: (1) whole otolith embedding in polyester resin (Sody 33, ESCIL, France), (2) after hardening, otolith transverse sectioning including the core with a low speed diamond saw (Isomet, BUEHLER®), (3) section mounting on microscope slides using thermofusible resin (Crystalbond® 509), and (4) grinding and polishing both faces with 1200 grit sandpaper and successive aqueous aluminium powder (3  $\mu\text{m}$ , 1  $\mu\text{m}$  and 0.33  $\mu\text{m}$ ) on polishing cloths. The final thin otolith sections were observed with a light microscope (Olympus BX 41) under transmitted light coupled with coloured video camera (Sony 3CCD). Magnification was between  $\times 400$  and  $\times 1000$ . A calibrated image of each otolith transverse section was recorded and microincrements were measured using the TNPC software (Visilog®, Noesis SA, France). Otolith increments in this species, i.e. the alternative L- (elevated) zones and D- (depressed) zones (sensu Kalish et al., 1995), were validated daily by Panfili and Tomás (2001). D-zones were manually counted on the images: two counts were done by one reader at two different times, first from the core until the ventral edge and inversely. If no significant difference was calculated using a paired  $t$ -test for each location and the whole sample, the mean of counts was used to estimate the age. Microincrement widths were measured between two consecutive D-zones during the first two months of life (60 first microincrements).

### 2.3. Data analysis

The potential differences in environmental and fish conditions between the locations were investigated using 2-way ANOVA. For each analysis normality and homoscedasticity were checked prior the use of ANOVA.

The condition factor ( $K_c$ ) was calculated on the whole fish sample using the following formula:

$$K_c = \frac{W}{L^3} \times 10^5$$

where  $W$  is the total mass (g) and  $L$  the fork length (mm).

The growth of *Sarotherodon melanotheron* was analysed based on length-at-age data (age  $t$  in days was estimated from otolith examination). As the growth was only studied across a short time range, a panel of five models ranging from a simple linear equation



Fig. 1. Map of the sampling locations (circles) in the Saloum and the Gambia estuaries.

to three parameters non-linear equations was compared (linear, power, Gompertz, von Bertalanffy and logistic, Table 1). Models were fitted using the Nelder–Mead algorithm with residual sum of squares (*RSS*) as a criterion. Under the assumptions of residual normality and homoscedasticity (previously verified), *RSS* was directly linked to the likelihood (Burnham and Anderson, 2002). This relationship allowed comparing model performances based on their likelihoods. The biological representativeness and the fit of the five models were investigated in order to select a set of relevant models on which the final inference was based. The confrontation of the models was performed within the so-called “model selection” framework based on the likelihood theory (Burnham and Anderson, 2002; Kadane and Lazar, 2004). This discrimination methodology relies on the evaluation of the strength of evidence in the data for each model and is more relevant within this context than classical tools such as the adjusted coefficient of determination ( $R^2$ ) for which strong theoretical bases are missing.

Table 1

Description of the growth models used in the study. The formula gives the fork length (*L*) function of the age (*t*) and several parameters: *a* and *b*, constants;  $L_0$ , size of fish at age zero; *G*, instantaneous growth rate;  $L_\infty$ , asymptotic length; *K*, growth coefficient,  $t_0$ , predicted age at which *L* is zero.

Name	Formula	Parameters			Asymptotic
		<i>P1</i>	<i>P2</i>	<i>P3</i>	
Linear	$L = a + bt$	<i>a</i>	<i>b</i>	–	No
Power	$L = at^b$	<i>a</i>	<i>b</i>	–	No
Gompertz	$L = L_\infty \exp(-\exp(-G(t - t_0)))$	$L_\infty$	<i>G</i>	$t_0$	Yes
von Bertalanffy	$L = L_\infty (1 - \exp(-K(t - t_0)))$	$L_\infty$	<i>K</i>	$t_0$	Yes
Logistic	$L = L_\infty / [1 + \exp(-at + b)]$	$L_\infty$	<i>a</i>	<i>b</i>	Yes

Furthermore, even if  $R^2$  could assess model fit (i.e. percentage of explained variance), it is generally not consistent for model selection within the non-linear regression context (Ratkowsky, 1983). The criterion used to compare growth models in the present study was the corrected Akaike’s information criterion (*AICc*) defined by Hurvich and Tsai (1989). This criterion is derived from the seminal Akaike’s information criterion (*AIC*) proposed by Akaike (1973) and accounts for small sample sizes (i.e. when the ratio of sample size *n* over the number of estimated parameters *p* is lower than 40), as is the case of this study (Burnham and Anderson, 2002). *AICc* is given by the following equations:

$$AICc = -2\log(L(\hat{\theta}/y)) + 2p\left(\frac{n}{n-p-1}\right)$$

where  $L(\hat{\theta}/y)$  is the likelihood of the data giving the parameter vector, *p* is the number of fitted parameters in the model (plus one for the estimated variance) and *n* the sample size. Equivalently for *RSS*, the formula can be written (Johnson and Omland, 2004):

$$AICc = n\log\left(\frac{RSS}{n}\right) + 2p\left(\frac{n}{n-p-1}\right)$$

The lower the *AICc*, the better the model is considered to reflect the data. Because *AICc* is a relative measure, absolute values are not relevant to compare models and the selection is based on Akaike Weights, *w* (Burnham and Anderson, 2002). For a fitted model *i*, *w<sub>i</sub>* is given by:

$$w_i = \frac{e^{(-1/2\Delta_i)}}{\sum_{r=1}^N e^{(-1/2\Delta_r)}}$$

where  $N$  is the number of models and  $\Delta_i$  is defined as  $\Delta_i = AICc_i - AICc_{\min}$  with  $AICc_{\min}$  the  $AICc$  value for the best model. Akaike's weights are interpreted in terms of probabilities for a given model of being the best of a defined sets of alternative models to reflect the data (Burnham and Anderson, 2002; Johnson and Omland, 2004). When the data supports more than a single model (i.e. all  $w_i$  are lower than 0.9), robust growth curves can be inferred by averaging inferences inside the confident set of models with respect to their  $w_i$ . In the present study, the selection procedure was a two-step process: (1) all five models were fitted to the datasets, equations that failed respecting the regression hypotheses (normality and homoscedasticity of the residuals) or failed to produce relevant parameters estimates (e.g.  $L_{\infty}$ ) were discarded from the analysis; (2) in a second step, Akaike differences were examined to select only the models with a high probability of relevance for growth modelling. Once irrelevant models were discarded, robust growth curves were constructed by model averaging across the final model set.

A general comparison of modelled growth curves between stations and years was performed using an analysis of the residual sum of squares, ARSS (Chen et al., 1992). The growth rate in length, averaged across the derivatives of the final growth models with respect to time (Campana and Jones, 1992) was then investigated across the age range to illustrate and further analyse the possible differences in growth previously detected by ARSS.

### 3. Results

#### 3.1. Environment and fish condition

All sampling campaigns were carried out at the beginning of the rainy season (June–July) but salinity in the Saloum was always higher than that of the sea (35), except for the Missirah location where the minimum recorded salinity was 32 (Fig. 2). Salinities in the Gambia estuary were always lower than those of downstream

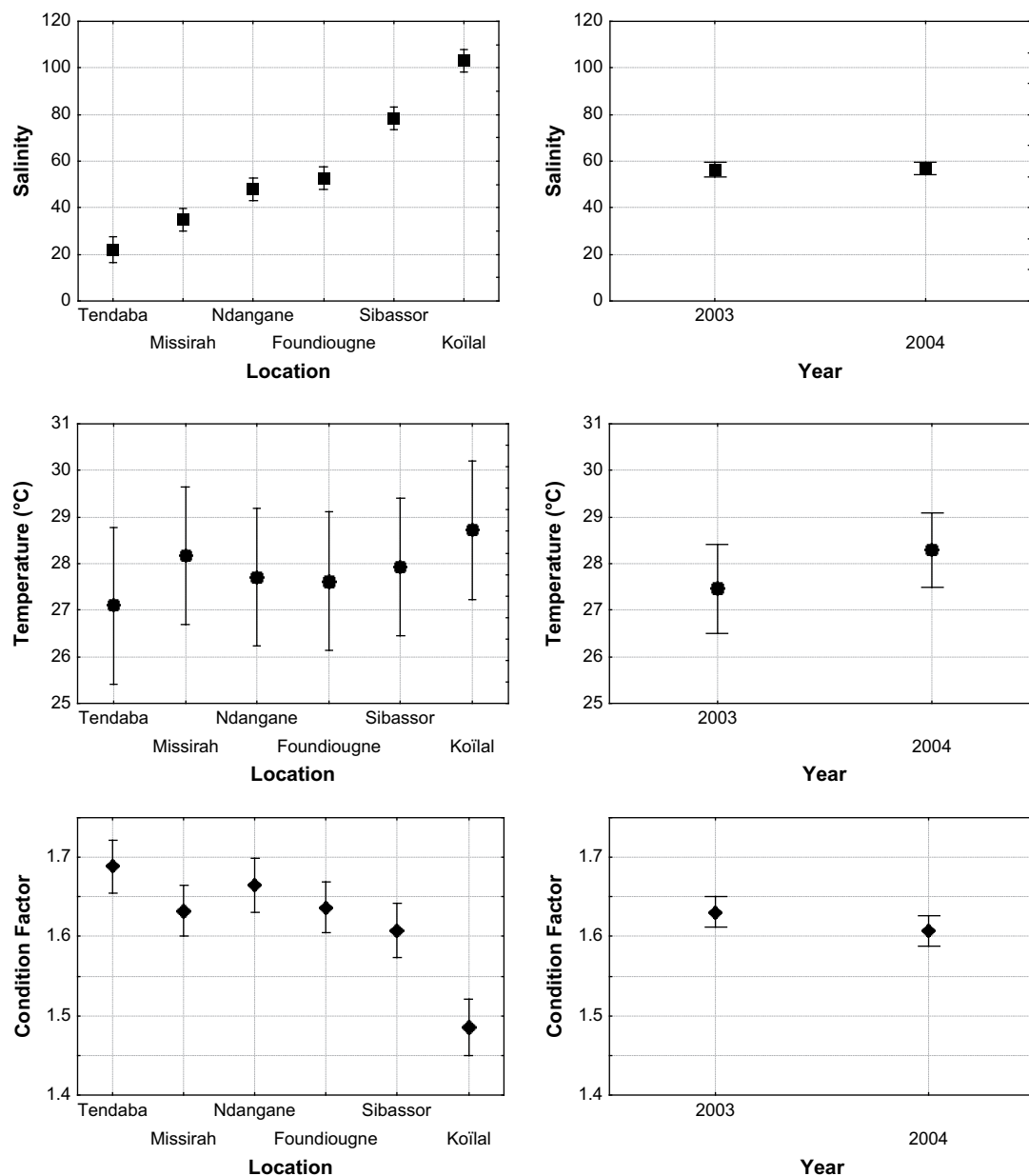


Fig. 2. Salinity, temperature and condition factor variations (means  $\pm$  95% confidence intervals) in the different sampling locations and for the two consecutive years. For temperature and salinity,  $n = 31$  at each location. For condition factor,  $n = 370$  at Tendaba,  $n = 380$  at Missirah,  $n = 343$  at Ndangane,  $n = 375$  at Foundiougne,  $n = 334$  at Sibassor and  $n = 316$  at Koïlal.

**Table 2**

Age estimations from otolith sub-sample of *Sarotherodon melanotheron* including fork length ( $L$ , range and mean  $\pm$  SD), number of microincrements corresponding to the age in days (range and mean  $\pm$  SD) and salinity variations in 2003 and 2004 in the different locations in Gambia and Saloum estuaries.  $n$ , number of individuals.

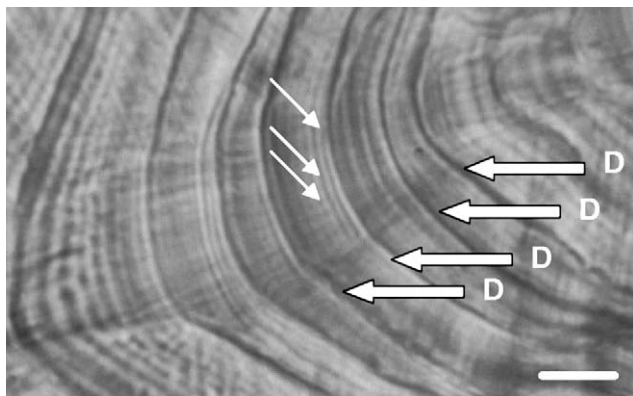
Location	2003			2004			Salinity range
	$n$	Min–Max $L$ (mm)	Min–Max Age (days)	$n$	Min–Max $L$ (mm)	Min–Max Age (days)	
Tendaba	15	20–57 (39.3 $\pm$ 12.8)	43–120 (74 $\pm$ 27)	20	18–57 (40.8 $\pm$ 13.4)	31–130 (88 $\pm$ 31)	20–27
Missirah	15	16–56 (38.3 $\pm$ 13.8)	39–132 (82 $\pm$ 28)	20	19–57 (38.3 $\pm$ 13.2)	44–154 (95 $\pm$ 36)	30–40
Ndangane	15	17–59 (37.0 $\pm$ 13.8)	34–148 (92 $\pm$ 39)	20	23–59 (41.4 $\pm$ 11.4)	63–180 (116 $\pm$ 38)	48–50
Foundiougne	15	18–52 (34.8 $\pm$ 11.5)	48–170 (94 $\pm$ 30)	20	15–55 (39.3 $\pm$ 13.0)	29–179 (99 $\pm$ 44)	49–55
Sibassor	15	20–57 (39.3 $\pm$ 12.8)	32–143 (89 $\pm$ 39)	20	19–59 (40.2 $\pm$ 13.4)	44–234 (124 $\pm$ 62)	70–94
Koïlal	15	18–58 (37.1 $\pm$ 14.5)	35–200 (135 $\pm$ 50)	20	20–57 (43.2 $\pm$ 11.8)	43–219 (140 $\pm$ 53)	90–118

Saloum. The Saloum estuary showed a clear inverse functioning with higher salinities upstream at the Koïlal location, and a salinity gradient was recorded between the locations (Fig. 2). Two-way ANOVA showed significant salinity differences between locations ( $F_{5,29} = 146.7$ ,  $p < 0.05$ ) but not between consecutive years ( $F_{1,29} = 0.444$ ,  $p > 0.05$ ) and no interaction was recorded between the two factors ( $F_{5,29} = 0.544$ ,  $p > 0.05$ ). On the other hand, mean temperatures were identical (Fig. 2) both for the locations ( $F_{5,29} = 0.517$ ,  $p > 0.05$ ) and the years ( $F_{1,29} = 1.887$ ,  $p > 0.05$ ), with no interaction between factors ( $F_{5,29} = 1.302$ ,  $p > 0.05$ ).

Means of condition factors were not significantly different between 2003 and 2004 for each location (Fig. 2 and 2-way ANOVA,  $F_{1,2106} = 2.925$ ,  $p = 0.087$ ). In the Saloum estuary, the condition factor of juveniles differed significantly between the locations in relation to the salinity level (Fig. 2), the highest values being recorded at Tendaba and Ndangane (2-way ANOVA,  $F_{5,2106} = 16.194$ ,  $p = 0.00$ ). Condition factors were not significantly different between the Tendaba location in Gambia and the downstream Saloum locations. Condition factors in Koïlal, being the lowest, differed from all other locations (Fig. 2).

### 3.2. Otolith microincrements and growth rates

The age estimations from otolith readings of juveniles *Sarotherodon melanotheron* are summarised in Table 2. The mean of the two individual otolith readings was used to estimate the age because no difference was observed between them (paired  $t$ -test,  $t = 0.136$ ,  $df = 478$ ,  $p = 0.891$ ). Primary increments corresponding to daily microincrements were classically composed of one L-zone and one D-zone deposited around a core. All microincrements were clearly interpretable from the core until the otolith edge for individuals under 20 days and after this age, the microincrements near the edge were thinner and more difficult to interpret. The difficulty



**Fig. 3.** Part of otolith section in light microscopy viewed under transmitted light of a juvenile *Sarotherodon melanotheron* captured in the hypersaline area in the Saloum estuary (salinity  $> 60$ ). Numerous checks (D) are alternating with primary increments (D-zone interpreted for age estimation indicated by thin arrows). Scale bar = 5  $\mu$ m.

when interpreting microincrements was more pronounced in the highest salinity locations (Fig. 3): in Sibassor and Koïlal, otoliths presented numerous checks (i.e. deeper discontinuities in the otolith structure) close to the edge alternating with regular primary increments for ages equal or superior to 150 days.

The range of otolith growth rates, expressed by the mean of microincrement widths, showed high variability with age for all individuals in all locations with a common growth pattern (Fig. 4): mean increment width between increments 1 and 5 (1st and 5th day) was  $3.91 \mu\text{m d}^{-1} \pm 0.82$  in 2003 and  $4.20 \mu\text{m d}^{-1} \pm 0.86$  in 2004, thereafter increasing steadily to  $8.42 \pm 0.90 \mu\text{m d}^{-1}$  in 2003 and  $9.50 \pm 1.25 \mu\text{m d}^{-1}$  in 2004 at increment number around 15. After a maximum at increment 15, the mean increment width decreased to  $4.25 \pm 0.41 \mu\text{m d}^{-1}$  at the 61st day in 2003 and  $4.21 \pm 0.77 \mu\text{m d}^{-1}$  in 2004 (Fig. 4). The means of these four growth stages did not differ between the two consecutive years ( $t$ -tests): for phase I,  $t = -1.321$  ( $df = 58$ ,  $p = 0.191$ ); for phase II,  $t = -0.9625$  ( $df = 124$ ,  $p = 0.351$ ); for phase III,  $t = -0.624$  ( $df = 551$ ,  $p = 0.532$ ); and for all phases,  $t = 1.32$  ( $df = 670$ ,  $p = 0.191$ ).

### 3.3. Growth modelling

The individual sizes of sampled juveniles varied between 16 and 58 mm in 2003 and 15 and 59 mm in 2004 (Table 2). The estimated ages varied between 31 and 200 days in 2003 and 28 and 234 days in 2004 (Table 2): an increase in the mean ages was observed across the salinity gradient for both years. The regression results for *Sarotherodon melanotheron* growth models are presented in Table 3. The mean  $R^2$  value was 0.865 assuming a reasonable adjustment by the models. The Gompertz and logistic equations could not fit the data for the Tendaba location in 2004 and for the Koïlal location in 2003 (i.e. model adjustments induced non-normality and non-homoscedasticity of the residuals). Furthermore, according to the different criteria (smallest RSS, highest  $R^2$  and highest  $w_i$ ), the support for these models in the dataset was generally low (Table 3). These sigmoid equations, more relevant to growth modelling for wider age ranges, were thus discarded from the final set of models. Von Bertalanffy models failed in predicting reliable asymptotic lengths ( $L_\infty$ , i.e.  $P1$ , Table 3). The support for this model in the data was low in a majority of cases (Table 3): the von Bertalanffy model was thus also discarded from the final set of models. The linear and power models were generally equally favoured across the datasets and provided the lowest Akaike differences in the majority of cases (Table 3): they were thus selected as the final set of models for growth modelling and comparisons.

The juvenile growths calculated with multi-model averaging were not different between years at each location, except for Sibassor (Table 4, Fig. 5). Multi-model averaged growth curves were significantly different in the extreme location of Tendaba from all other locations, both in 2003 and 2004 (Table 5). On the other hand, multi-model absolute growth rates decreased between locations following the salinity gradient in both 2003 and 2004 (Fig. 6). For

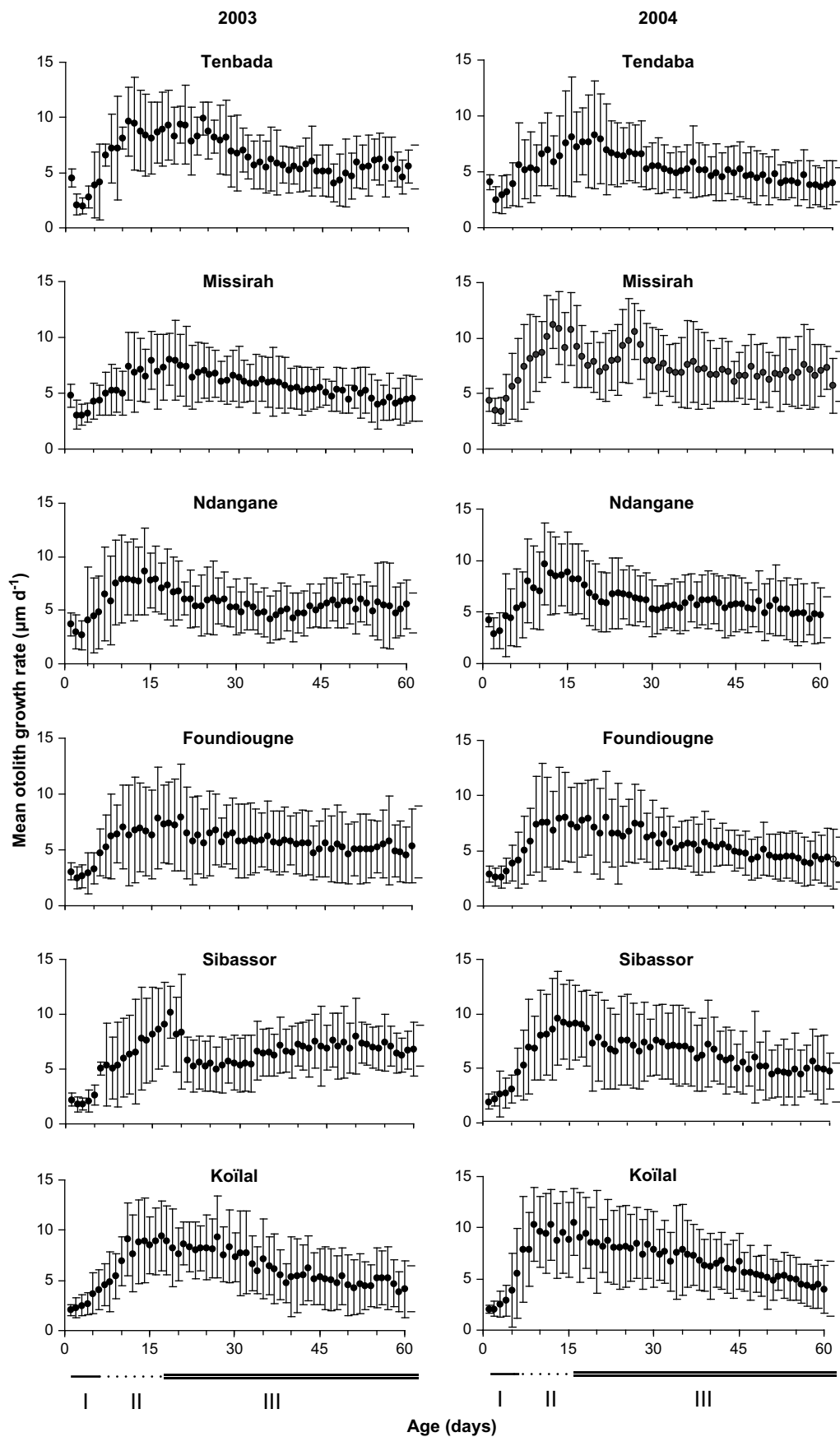


Fig. 4. Variations of daily otolith growth rates (mean  $\pm$  SD) in juvenile *Sarotherodon melanotheron* in June–July 2003 and 2004 at the different locations. Three phases of otolith accretion (I, II and III) are indicated below after being visually determined.

**Table 3**

Fitting results for growth models and parameter estimates: residual sum of squares (RSS), coefficient of determination ( $R^2$ ) and Akaike weights  $w$ . The best values for the chosen criterion, the highest Akaike weights  $w$ , are in bold. Details for parameters ( $P1$ ,  $P2$ ,  $P3$ ) are listed in Table 1.

Model (per location)	2003						2004					
	$P1$	$P2$	$P3$	RSS	$R^2$	$w$	$P1$	$P2$	$P3$	RSS	$R^2$	$w$
<b>Tendaba</b>												
Linear	-1.17	0.52		282.60	0.93	0.06	4.82	0.41	0.00	405.18	0.91	<b>0.38</b>
Power	0.50	1.00		284.81	0.93	0.06	0.89	0.86	0.00	395.10	0.91	<b>0.48</b>
Gompertz	62.20	0.03	49.34	177.21	0.97	<b>0.31</b>						
von Bertalanffy	71.29	0.02	26.90	186.38	0.96	0.21	104.89	0.01	6.69	381.04	0.92	0.14
Logistic	58.86	0.05	3.00	173.25	0.97	<b>0.36</b>						
<b>Missirah</b>												
Linear	-0.43	0.47		304.24	0.92	<b>0.35</b>	8.27	0.31	0.00	843.60	0.78	<b>0.21</b>
Power	0.47	1.00		304.51	0.92	<b>0.35</b>	1.24	0.76	0.00	805.23	0.79	<b>0.33</b>
Gompertz	79.28	0.02	63.05	279.62	0.93	0.10	59.09	0.02	49.98	739.06	0.82	0.16
von Bertalanffy	151.81	0.00	10.20	294.88	0.92	0.07	66.85	0.01	16.17	743.75	0.82	0.15
Logistic	67.31	0.03	2.33	266.97	0.93	0.14	55.95	0.03	2.06	740.03	0.82	0.16
<b>Ndangane</b>												
Linear	6.93	0.33		498.71	0.85	<b>0.40</b>	10.36	0.27	0.00	483.81	0.84	0.02
Power	1.08	0.79		503.31	0.85	<b>0.38</b>	1.29	0.73	0.00	442.47	0.86	0.04
Gompertz	81.61	0.01	70.30	484.14	0.86	0.07	58.40	0.02	61.29	312.07	0.92	<b>0.29</b>
von Bertalanffy	100.70	0.01	0.00	508.08	0.86	0.05	62.38	0.01	32.87	329.83	0.91	0.17
Logistic	65.56	0.02	1.75	471.44	0.87	0.09	56.44	0.03	2.47	297.09	0.92	<b>0.48</b>
<b>Foundiougne</b>												
Linear	5.50	0.31		573.76	0.74	0.13	12.90	0.27	0.00	579.33	0.85	0.09
Power	0.86	0.82		548.54	0.75	0.18	2.16	0.64	0.00	509.81	0.87	<b>0.31</b>
Gompertz	56.11	0.03	59.60	416.80	0.83	<b>0.21</b>	58.13	0.02	42.69	452.68	0.90	<b>0.21</b>
von Bertalanffy	62.87	0.01	28.29	452.44	0.81	0.11	65.04	0.01	6.61	457.46	0.89	0.19
Logistic	53.56	0.04	2.73	388.04	0.84	<b>0.36</b>	55.56	0.03	1.70	455.66	0.89	0.20
<b>Sibassor</b>												
Linear	11.37	0.31		205.74	0.94	<b>0.27</b>	15.66	0.20	0.00	575.10	0.86	0.04
Power	1.97	0.67		190.76	0.95	<b>0.47</b>	2.41	0.59	0.00	492.15	0.89	0.17
Gompertz	68.24	0.02	45.72	183.12	0.96	0.09	58.07	0.02	50.51	401.50	0.92	<b>0.27</b>
von Bertalanffy	75.19	0.01	0.00	192.03	0.95	0.07	62.04	0.01	13.52	410.12	0.91	0.22
Logistic	61.36	0.02	1.50	181.15	0.96	0.10	56.20	0.03	1.77	397.16	0.92	<b>0.30</b>
<b>Koïlal</b>												
Linear	12.48	0.18		1019.68	0.59	<b>0.50</b>	15.36	0.20	0.00	606.95	0.81	<b>0.29</b>
Power	1.96	0.60		1031.94	0.59	<b>0.46</b>	2.31	0.60	0.00	584.81	0.82	<b>0.42</b>
Gompertz							67.82	0.01	56.13	575.62	0.83	0.10
von Bertalanffy	59.03	0.01	0.00	1087.09	0.57	0.05	68.81	0.01	0.00	591.00	0.82	0.08
Logistic							62.03	0.02	1.29	571.45	0.83	0.11

each location, there was the general tendency to the decrease of the growth rates with age. The hypersaline location of Koïlal presented the lowest multi-model absolute growth rates whereas that of Tendaba presented the highest (Fig. 6). All modelled data suggested that juvenile growth of *Sarotherodon melanothron* was negatively correlated with the level of ambient salinity. It was confirmed by the linear regression between the multi-model absolute growth rate (at a defined common age) and salinity (Fig. 7). The same tendency was observed for the condition factor (Fig. 7).

**4. Discussion**

The salinities encountered in these ecosystems showed extremely high variations, from 20 up to 118, and, in order to simplify the following interpretations, we chose to classify the waters into three different categories (Panfili et al., 2004b): mesohaline (0–35), metahaline (35–60) and hyperhaline (60–120).

**4.1. Otolith microincrement characteristics**

The daily deposit of otolith microincrements has been validated for the tilapia *Sarotherodon melanothron* by Ekau and Blay (2000)

and Panfili and Tomás (2001). In the present study, microincrements were clearly interpretable in the least saline locations (Tendaba, Missirah, Ndangane, and Foundiougne) but were less clear and surrounded by numerous discontinuities in the hypersaline locations of Sibassor and Koïlal. These checks are interpreted as structures induced by different external stresses (Campana and Neilson, 1985). They can also have a physiological origin, for example during ontogenetic transitions (Nishimura, 1993) or during reproduction (Massou et al., 2004). Nevertheless, checks were generally located after 150 days of life, thus long after the larval stage for this species and no mature individuals were ever captured during the sampling period. Otolith checks in *S. melanothron* can then be interpreted as consequences of stress for individuals living in hypersaline environments which undoubtedly operated at individual levels, without knowing the exact cause of this stress.

**Table 4**

ARSS test for the pair comparisons of multi averaged growth models between years 2003 and 2004. \*, significant differences ( $p < 0.05$ ).

Location	Tendaba	Missirah	Ndangane	Foundiougne	Sibassor	Koïlal
F value	1.680	2.875	0.907	1.046	5.646	1.457
p value	0.193	0.053	0.450	0.387	0.004*	0.247



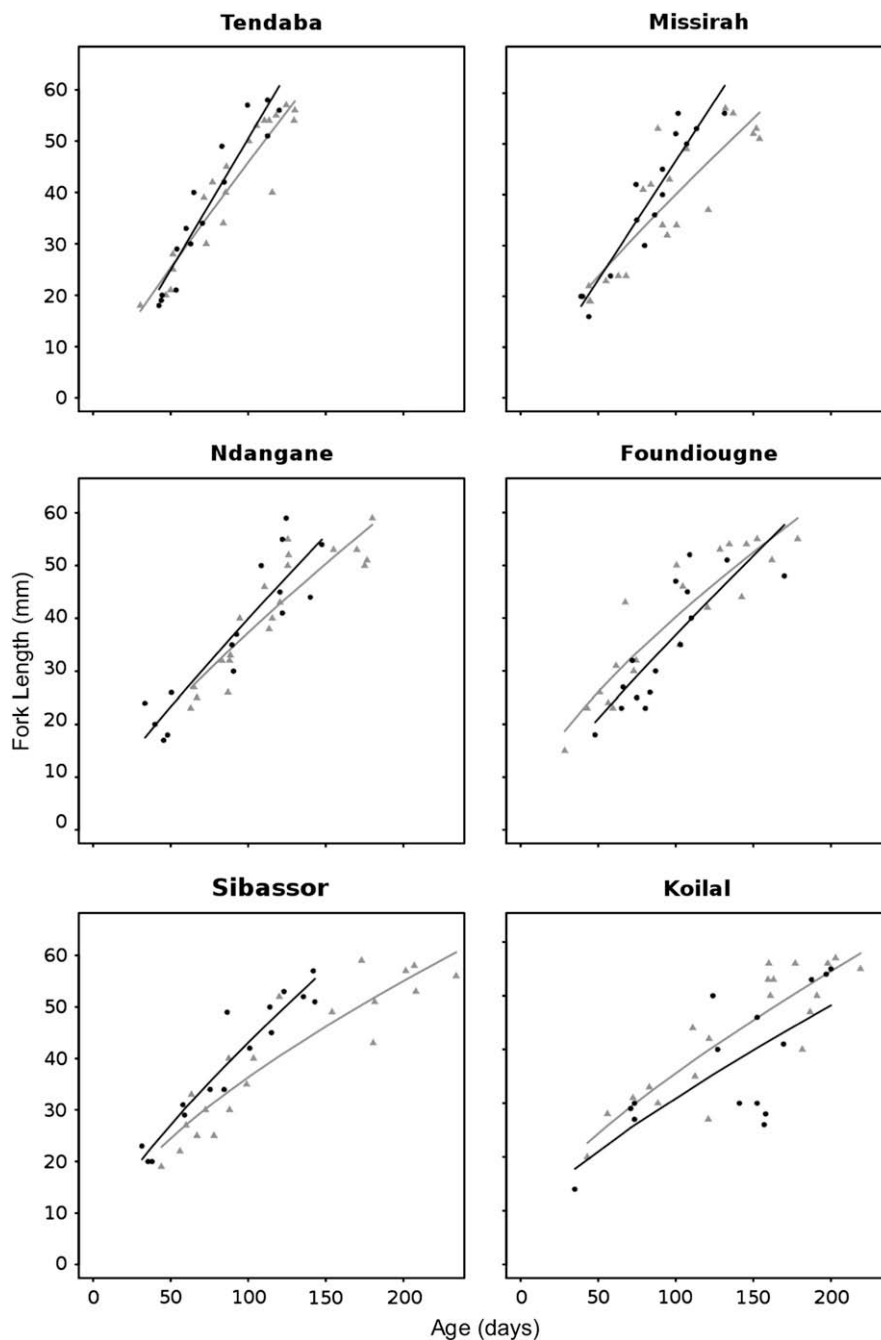


Fig. 5. Growth of juvenile *Sarotherodon melanotheron* in each location in 2003 (black circles, continuous curve) and 2004 (grey triangles, discontinuous curve) using a model averaging.

For all the individuals of the present study, otolith growth patterns during the first months of life can be divided into three different stages: the first one with low growth rates, the second with very fast growth rates and the third with a smooth decrease of growth rates with time. These stages can be related to the early development of tilapias during their young life including the yolk-stage, the larval and then the juvenile stages. Similar otolith growth patterns have been described in Clupeids (Thorrold and Williams, 1989; Ohshimo et al., 1997) and the hake *Merluccius merluccius* for which each growth stage corresponded to a change in feeding behaviour (Alvarez and Cotano, 2005). Variations in the widths of microincrements with a pronounced peak after about 10 days were described for other species such as *Engraulis japonicus* (Takasuka

et al., 2003). The general increase of increment width during the second stage suggested a rapid growth after the first feeding with a common pattern for the species but not different from one location to another.

#### 4.2. Growth modelling

Growth parameter estimates were not reliable for the von Bertalanffy growth model and the adjustments failed to satisfy the regression hypotheses for the Gompertz and logistic models for two datasets. The problem of unrealistic estimates has already been underlined where only part of the size and/or age ranges of a species is available (Welsford and Lyle, 2005). The small range of

**Table 5**

ARSS test for the pair comparisons of multi averaged growth models between locations in 2003 (upper right) and in 2004 (bottom left) showing the *F* and *p* (in italic) values. \*, significant differences ( $p < 0.05$ ).

2004	2003					
	Tendaba	Missirah	Ndangane	Foundiougne	Sibassor	Koïlal
Tendaba		0.98	5.58	8.67	5.68	11.21
Missirah	3.00		2.85	5.47	2.93	9.45
Ndangane	9.12	0.76		0.42	0.87	4.27
Foundiougne	3.71	0.19	0.75		2.96	1.94
Sibassor	12.97	2.38	0.98	2.09		7.08
Koïlal	12.97	2.85	1.71	2.64	-0.03	
	<i>0.000*</i>	<i>0.044*</i>	<i>0.005*</i>	<i>0.000*</i>	<i>0.004*</i>	<i>0.000*</i>
	<i>0.000*</i>	<i>0.044*</i>	<i>0.059</i>	<i>0.005*</i>	<i>0.054</i>	<i>0.000*</i>
	<i>0.000*</i>	<i>0.526</i>		<i>0.740</i>	<i>0.472</i>	<i>0.015*</i>
	<i>0.021*</i>	<i>0.905</i>	<i>0.530</i>		<i>0.052</i>	<i>0.151</i>
	<i>0.000*</i>	<i>0.087</i>	<i>0.413</i>	<i>0.120</i>		<i>0.001*</i>
	<i>0.000*</i>	<i>0.052</i>	<i>0.183</i>	<i>0.065</i>	<i>1.000</i>	

sizes and ages in the present study could also explain the failure of sigmoid growth models in fitting datasets. Although the logistic model was selected for four datasets (Tendaba 2003, Ndangane 2004, Foundiougne 2003 and Sibassor 2004) this result was not consistent across the years: a two-parameter model was favoured in all other cases. For these datasets, the plateau estimated by the logistic model for advanced ages reflected more a high variability of ages at high lengths rather than maximum theoretical lengths (Fig. 5). The selection of the sigmoid equation for these locations could thus be considered as an artefact.

These results exemplify the need for a careful examination of the models' predictions in the selection process of a set of models. Although an expert evaluation of the models' fit and adjustment is necessary for the final model set specification, it is not sufficient. Indeed, what allowed us to identify the final set of models was the combination of a model adjustment inspection with an information theory model selection procedure. The two simplest equations were the best compromise to model and compare the growth of *Sarotherodon melanotheron* during the early life stages along the salinity gradient. This final decision was consistent with the visual inspection of the raw data (Fig. 5) that exhibited linear to convex growth patterns and thus demonstrated the accuracy of the information theoretical framework for growth model selection. However, there remained substantial uncertainty as to which of these models was the best for growth modelling in the present study (Table 3, Fig. 5). This potential pitfall was overcome by the construction of robust inferences through multi-model inference

taking into account the uncertainty about model selection. It has been recently highlighted that multi-model inference based on information theory is a more robust alternative to study fish growth (Katsanevakis, 2006; Katsanevakis and Maravelias, 2008).

#### 4.3. Growth rate variations

Differences in individual growth variations during the fish juvenile stage living in estuarine habitats are influenced by abiotic and biotic factors (Peterson-Curtis, 1997) such as temperature, salinity and food availability. In this study, temperature influence could be discarded because no differences were detected both between locations and years during the sampling period. Nevertheless, it was virtually impossible to determine the exact temperature regime experienced by each individual fish and the temperature measurements in the present study were only undertaken punctually during the sampling period. In tilapias, inter-population growth variability is common (Admassu and Ahlgren, 2000) and variations are extreme during the first year (Fryer and Iles, 1972). In this study, the growth of *Sarotherodon melanotheron* was variable across the spatial scales but less across the temporal scales (except for one location). All locations could be considered as separate populations, as demonstrated by the extensive genetic differentiation in this geographical area evidenced by microsatellite markers (Pouyaud et al., 1999). This sedentary lifestyle has also been highlighted using otolith micro-chemical markers (Diouf et al., 2006). This behaviour could be a consequence of the reproduction style involving mouth brooding.

In this study, a lower growth rate was recorded in the hypersaline area of the Saloum estuary, at the Koïlal location, both in 2003 and 2004. Moreover, differences in growth rates followed the salinity gradient during two consecutive years, a decrease in growth being linked to an increase in environmental salinity. This was consistent with the lower fish condition compared to other less saline locations. Such differences along the estuarine locations may result from environmental conditions, genetic history or their interaction (Stearns, 1992). If genetic differentiation cannot be discarded in this case (see above), Lowe-McConnell (1982) also stated that environmental pressures are often stronger than genetic ones in the case of tilapias growing in separate areas. In this study, the extreme salinity gradient was considered as the main environmental constraint, acting both directly and indirectly on fish populations through the modification of environmental conditions (e.g. food availability, even though not measured). Salinity is a parameter well-known for having a direct influence on fish

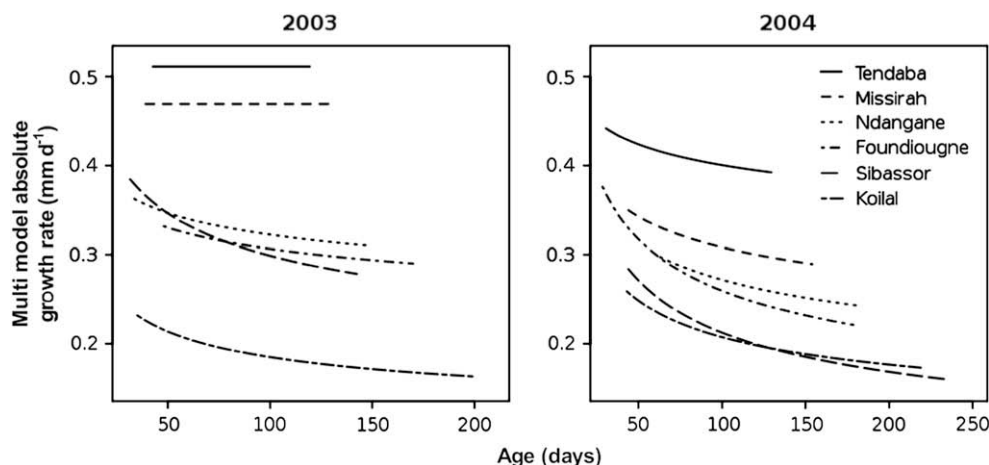


Fig. 6. Multi-model absolute growth rates over the age ranges of juvenile *Sarotherodon melanotheron* for all locations in 2003 and 2004.

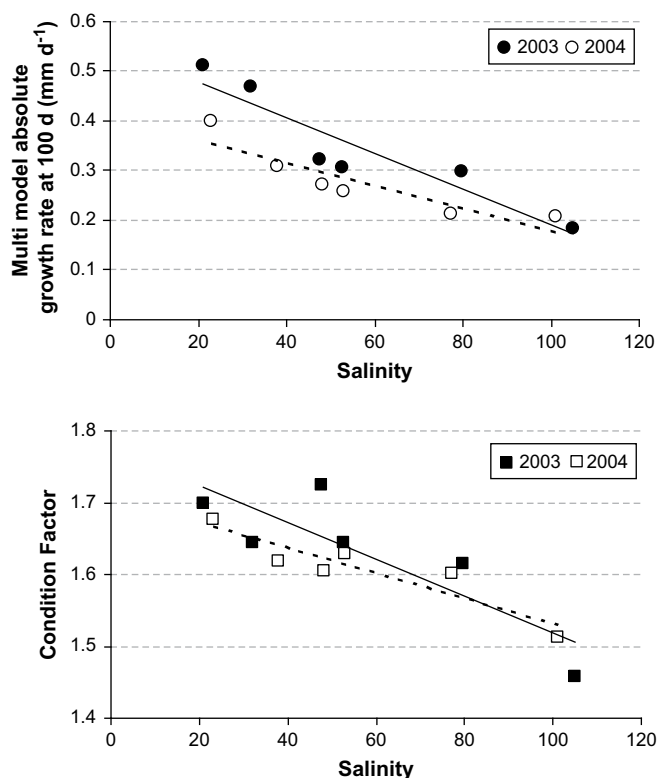


Fig. 7. Relationship between salinity and multi-model absolute growth rates at age 100 days and condition factors of juvenile *Sarotherodon melanotheron* in 2003 and 2004. Salinities were averaged for each location during the sampling period of each year. Multi-model absolute growth rates were calculated for each location (i.e. salinity) at 100 day-old (which was a common data in all age ranges). Condition factors were averaged for each location (i.e. salinity). Linear regressions are presented: ●—:  $Y = -0.0036X + 0.5515$  ( $R^2 = 0.862$ ,  $p < 0.05$ ); ○—:  $Y = -0.0023X + 0.4063$  ( $R^2 = 0.809$ ,  $p < 0.05$ ); ■—:  $Y = -0.0026X + 1.7757$  ( $R^2 = 0.7227$ ,  $p < 0.05$ ); □—:  $Y = -0.0018X + 1.7068$  ( $R^2 = 0.8406$ ,  $p < 0.05$ ).

growth (Boeuf and Payan, 2001). Within this context, the results obtained were in total concordance with those obtained on adults of the same species in the same area by Panfili et al. (2004a). These authors have described a decrease in the growth rates in *Sarotherodon melanotheron* together with salinity increase (>60). For other species, Langford and Targett (1994) showed that Weakfish juveniles presented spatial variations in growth rates and condition along an estuary with different salinity regimes. Variations in quality of habitat, density and food availability can dramatically influence the growth rates at a small scale (Gibson, 1994). Prey availability and their usage have not been quantified in this study but the condition factor, reduced with the salinity increase, can also be a proxy of food availability and consuming. The correspondence between the reduction of growth rate and condition factor tended to reinforce the hypotheses on an indirect effect of hypersaline conditions. As *S. melanotheron* is one of the rare species encountered in the hypersaline Saloum (Panfili et al., 2006), also capable of change in feeding regime depending on the environmental conditions (Kone and Teugels, 2003), its adaptation to this extreme environment has a direct influence on its potential growth through food availability. In such a situation, the feeding behaviour of the species is probably the key to understand the growth decrease in constrained habitats.

Otolith growth rates were not different between two consecutive years at each location, except in one case (Sibassor in Saloum). This observation reinforces those demonstrating that the effect of location (i.e. most of the time population) is stronger than that of

time (i.e. season or years) (Sogard et al., 2001). Studies of more than two consecutive years could reinforce the hypothesis on the relative weight of space against time on growth variation during the first life history stages.

## 5. Conclusion

In conclusion, information theory criteria together with multi-model inference can be recommended to construct a more robust inference for growth comparisons. The Akaike weight selection method tended to elect a less parameterised model, which also reinforced the comparisons within the multi-model framework. This method is not limited to compare juvenile growth but could also be used to compare adult life-history strategies, as recently illustrated (Katsanevakis and Maravelias, 2008). For *Sarotherodon melanotheron*, the spatial variability in juvenile growth, linked with the salinity gradient along hypersaline estuarine conditions, has more influence than time variability and should directly impact adult populations. The identification of the mechanisms inducing the juvenile survival and growth rates contributes to a better understanding of recruitment in adult populations (Campana, 1996). Physiological experiences, together with feeding testing, should be conducted on this species to verify the possible assumption that the energy allocation shifted to osmoregulation instead of body growth for adaptation. The final aim will be to anticipate adaptive mechanisms induced by global change and the onset of new hypersaline environments.

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