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Influence of salinity on life history traits of the bonga shad *Ethmalosa fimbriata* (Pisces, Clupeidae): comparison between the Gambia and Saloum estuaries

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ABSTRACT: The common West African bonga shad represents a large part of the fish biomass in 2 neighbouring estuaries that function in different ways. The Gambia estuary has a normal salinity gradient, while the Saloum has an inverse gradient. Bonga shad *Ethmalosa fimbriata* were collected in both ecosystems during a 16 mo period (June 2001 to September 2002) at 5 locations, to investigate the role of salinity on life history traits. The main traits were studied at a spatio-temporal scale: reproduction from macroscopic examination of the gonads, oocyte counting and measuring, and growth from interpretation and measurements of a sub-sample of otoliths. Analysis of genetic differentiation at 3 intronic and 1 anonymous nuclear gene loci was also carried out to investigate differences between estuaries and among locations. The results did not show any allelic frequency heterogeneity between populations, indicating that populations of both estuaries represent 1 single panmictic unit, and that selection is not significantly acting on these loci. Hence, the response of the different traits to environmental variation may primarily represent phenotypic plasticity. The seasonal cycle of reproduction was clearer in the Saloum, occurring during a long period (January to August). The calculated size at maturity was reduced for both sexes in the upper Saloum, where the salinity was highest. The relative fecundity and the oocyte size were larger in the Saloum. On the otoliths, translucent zones, formed each year at the end of the rains (September to October), were used to estimate the age in months. Growth rates were reduced in the hypersaline environment of the Saloum, whereas growth differences were smaller between the Gambia and the pooled Saloum data, with a salinity < 60 psu. Growth was faster in the lower parts of the Saloum, related to better conditions for fish. The results illustrate that an environment with high salinity (> 60 psu) affects the growth, reduces the size-at-maturity and increases the fecundity of *E. fimbriata*.

KEY WORDS: West Africa · Life histories · Genetic structure · Reproduction · Growth · Environmental stress

INTRODUCTION

Global climatic changes have particularly affected West Africa during the last 30 yr. In the Sahel, these perturbations mainly resulted in a drought period that led to a significant decrease in freshwater flow, and to an increase of the evaporation rate, which has affected many West African estuarine ecosystems. This is especially the case for the inverse estuary of the Sine Saloum in Senegal (Pagès & Citeau 1990). Perturba-

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tions such as climatic changes have consequences on the fish populations and community structure (Blaber 1997, Lévêque & Paugy 1999, Whitfield & Elliott 2002). In West African estuaries, subjected both to seasonal modification and long-term climate effect, environmental changes have a direct effect on the life history strategies of fish populations and, particularly, on reproductive traits (Albaret 1999). Changes in life history traits can affect reproduction, but also growth, habitat occupation and foraging behaviour. Observed modifications in life history traits may have 2 origins that can interact: genetic and/or phenotypic plasticity changes (Stearns 1992), but it is often difficult to determine which one has the preponderant effect.

Among the Clupeidae, the bonga shad *Ethmalosa fimbriata* is common in all brackish environments along the West African coast, from Mauritania to Angola, and it is one of the most important fish targets of the inland small-scale fisheries in countries such as Nigeria, Cameroon and the Ivory Coast (Charles-Dominique 1982, Moses et al. 2002). The total landing in West African waters reached 160 659 t in 2000 (source of data: FAO), of which 12 255 t was taken in the Sine Saloum (Senegal) in 2000 (Deme et al. 2001). This euryhaline species is encountered in salinities from 5 to 90 psu (Charles-Dominique & Albaret 2003). Its reproduction occurs mainly in lagoons and estuaries, where fish complete their life cycle, but, according to some authors (see Charles-Dominique 1982), spawning is also possible at sea, in a few cases, for large adults. Reproduction may be possible throughout the year, but this assumption is poorly documented. *Ethmalosa fimbriata* tolerates a wide range of salinities from the oligohaline waters of coastal rivers to the hypersaline waters of the Saloum and Casamance estuaries in Senegal (Charles-Dominique & Albaret 2003). Movements of this species are known to be partially induced by salinity conditions in the estuaries, since the distribution range within an estuary fluctuates with seasons (for normal estuaries, when the rainy season begins, upstream salinity decreases, and individuals migrate downstream; Charles-Dominique 1982). A migration of adults from the sea towards the estuary for spawning is also suggested by the seasonal pattern of abundance of mature adults observed in some estuaries such as those of the Saloum and the Senegal (Charles-Dominique & Albaret 2003). Such reproductive migrations are similar to migrations observed in the sub-family of Alosinae. However, no information about a real homing behaviour migration is available for *E. fimbriata*.

Previous studies have documented changes in the life history features of *Ethmalosa fimbriata* with environmental conditions (Charles-Dominique 1982, Charles-Dominique & Albaret 2003). For instance, the average size at first maturity appeared to be very variable among the populations as it ranged between 81 and 84 mm, for males and females, respectively, in Bietry lagoon, Ivory Coast (Albaret & Charles-Dominique 1982), and 185 mm for females in the Gambia River (Scheffers 1976). Populations living in open estuaries with a marked marine phase are larger at maturity, whereas populations living in lagoons with limited movement toward the sea are smaller (Charles-Dominique 1982). Variation of such life history traits is considered to be an adaptive answer to stressful conditions when the variation is observed between subpopulations of the same estuarine system. Thus, Albaret & Charles-Dominique (1982) and Guyonnet et al. (2003) suggested that the very low size at maturity in Bietry Bay (much lower than in the rest of Ebrié lagoon) was due to high pollution levels in this part of the lagoon. This observation could be explained by either an early maturation, with a normal size for age, that could have counterbalanced the mortality of older adults and/or a dwarfism phenomenon (fish old for their size) that could have resulted from an energy allocation to detoxification processes, rather than to growth or reproduction. These hypotheses need further investigation. However, no growth study has been carried out to demonstrate a decrease in age at maturity in highly perturbed environments, and there is still a possibility of natural dwarfism, as is supposed to occur in Nokoue Lake in Benin (Charles-Dominique 1982), where low size at first maturity may also be due to a different kind of perturbation (e.g. over-fishing; Laë 1997). The impact of salinity on the growth and physiology of fish has been studied mainly in experimental environments (Boeuf & Payan 2001), but it undoubtedly plays a role in the growth processes linked with energy costs.

In this context, trying to understand the effect of water salinity on the life history traits of one of the most common species in African estuarine ecosystems is essential for a better understanding of the adaptive responses of fish populations to major changes in their environment. We have chosen to study the impact of salinity in 2 contrasting estuaries in West Africa: the inverse hyperhaline estuary of the Saloum in Senegal, where the highest salinity values are recorded (>130 psu) in the upper reaches, and the estuary of the Gambia River which has a normal salinity gradient, and where the highest salinity values (35 to 45 psu) are located in the lower estuary. Populations of *Ethmalosa fimbriata* were sampled for >1 yr in order to study reproductive and growth characteristics. We complemented life history data with the analysis of genetic differentiation at 3 intronic (non-coding sequence of a gene) and 1 anonymous nuclear loci (genome sequence), searching for possible relationships between

life history trait variation and genetic differentiation and verifying that our samples belong to only 1 taxonomic unit. The aim of this study was to understand the capacity for the populations to settle in and adapt to contrasted biotopes.

MATERIALS AND METHODS

Sampling design. Samples were collected monthly between June 2001 and September 2002 at 3 locations in the Saloum estuary and at 2 locations in the Gambia estuary (Fig. 1). The choice of these locations considered the salinity gradients, Sibassor being the most saline station and Tendaba the least. Each month, the salinity was measured *in situ* with a refractometer, and fish sampling was carried out in the commercial landings of the small-scale fishery and directly from local fishermen. The main fishing gear used were purse seines and sometimes 'kili' (a small trawl pulled by hand by 2 people) and/or the traps (stownets), in order to obtain the largest size range of the target species, *Ethmalosa fimbriata*. A stratified sampling design was adopted for fish size. At least 5 individuals per 20 mm fork length class were collected. Each sample was stored in 95% ethanol. In the laboratory, all fish were measured (fork length, FL, in mm; Table 1), weighed (total weight, *P* in g), the sex and gonad maturity stage were determined, and the otoliths (sagittae) were extracted and stored dry in referenced microtube vials.

Genetic data. A sub-sample of *Ethmalosa fimbriata* was used in order to determine the genetic structure of this species in the Gambia and Saloum estuaries. Details on sampling, sampling areas, sampling dates, salinity conditions and fishing gear are presented in Table 2. We investigated genetic differentiation among samples by studying polymorphism at 3 intronic loci (i.e. non-coding regions of gene) and 1 anonymous nuclear gene locus. Total genomic DNA was extracted from fins using the phenol/chloroform protocol (Sambrook et al. 1989). Samples were analysed for genetic variation at 4 nuclear loci including the 4th intron of the *aldolase* B, the 2nd intron of 2 glyceraldhyde-3-phosphate deshydrogenases (*GAPDH slow* and *fast*) and a novel anonymous nuclear-DNA locus (*Myoglo2*). The

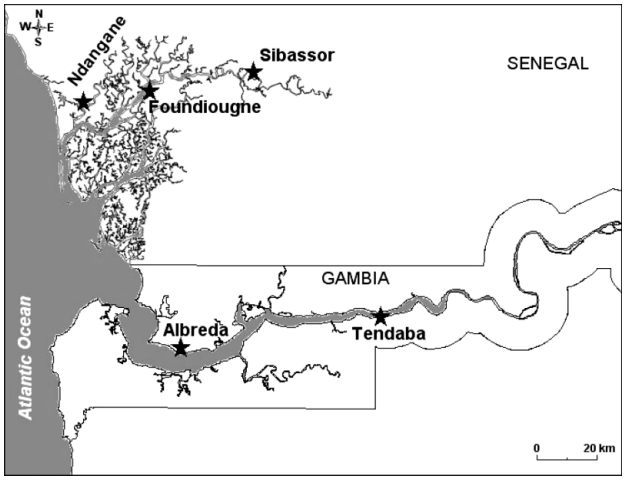

Fig. 1. Map of the sampling stations in the Gambia and Saloum estuaries

aldolase B and *GAPDH* introns were PCR-amplified using, respectively, the primers *Aldo 5F*/*Aldo 3.1R* and *Gpd 2F*/*Gpd 3R* of Hassan et al. (2002). The *Myoglo2* locus was selected on the basis of apparent Mendelian variation on polyacrylamide gels. This locus was amplified using a set of primers designed for the amplification of the 2nd intron of the myoglobin gene. Specific primers *Myo2EFI F* (5′-ACT ATG TTA GAG ATG CAT AC-3′) and *Myo2EFI R* (5′-TTA AAG ATG CCA TCA ACG TCC-3′) were designed by one of us (J.-D.D.) from the alignment of sequences of allelic PCR (polymerase chain reaction) products excised from the gels and separately re-amplified. A BLAST alignment (Altschul et

Table 1. *Ethmalosa fimbriata.* Length measures of the samples by station

Population	Fork length (mm)				
	n	Min.	Max.	Mean	SD
Tendaba	838	35	295	129.6	30.7
Albreda	567	42	286	116.6	43.5
Ndangane	282	57	280	161.8	72.9
Foundiougne	426	41	258	150.8	78.6
Sibassor	565	43	243	112.0	41.2

Table 2. *Ethmalosa fimbriata.* Characteristics of individuals sampled for the genetic analysis. (Fo and F12: temporal replicates)

Population	River system	Code	Date, 2001	Salinity (psu)	Fishing gear	Sample size
Sibassor	Saloum	S10	21 Nov	59	Purse seine	50
Foundiougne	Saloum	Fo	01 Jul	50	Purse seine	50
Foundiougne	Saloum	F12	21 Nov	42	Shrimp net	50
Albreda	Gambia	A6	20 Nov	24	Shrimp net	50
Tendaba	Gambia	CP35-39	10 Jun	10–16	Purse seine	40

al. 1997) of our sequences in GenBank did not provide a match with any known DNA sequences. Hence, although defined from 1 intron of the myoglobin gene in fish, the *Myoglo2* locus cannot be considered as one of the intronic genetic markers related to the myoglobin gene in *E. fimbriata*.

Individual PCR amplifications of size alleles at the *Aldolase B*, *Myoglo2*, *GAPDH slow* and *fast* loci were performed in 10 to 20 µl of reaction mixture containing 0.25 U *Taq* polymerase (Promega) in its buffer, 0.4 µM of each primer (1 primer per set for *GAPDH* and *Aldolase B* were labelled at the 5′ extremity with either fluorochrome TAMRA [Eurogentec]), 1.5 mM $MgCl_2$ (Promega), or 74 µM each of dNTP and 1 µl DNA template. Amplification conditions were 35 cycles consisting of denaturation at 94°C for 30 s, annealing at 52°C (*Aldolase B*, *GAPDH slow* and *fast*) or 53°C (*Myoglo2*) for 30 s and extension at 72°C for 30 s. Amplification products were used undiluted and mixed with formamide loading dye, and denaturated at 94°C for 5 min. A total of 3 to 10 µl (*Myoglo2*) of denaturated PCR products were loaded into 6% denaturing polyacrylamide gel and run using 1 × TBE buffer. Except for the *Myoglo2* locus, locus polymorphisms were screened at 585 nm (TAMRA) and visualised using a Hitachi FMBIO II scanner and appropriate software (Hitachi Instruments). For the *Myoglo2* locus, gels were ethidium bromide stained and scored. Reference samples of known genotype were used to standardise scoring at each locus.

Expected heterozygosities (*He*) were estimated from raw genotype data using the GENETIX software (Belkhir et al. 2000). Deviations from Hardy-Weinberg expectations within samples and allele-frequency differences among populations were estimated using Weir & Cockerham's (1984) $\hat{f}$ and $\hat{\theta}$ estimators of f and θ, respectively. f and θ are Weir & Cockerham's (1984) equivalents of Wright's (1951) fixation indices, F_{is} and F_{st}, respectively. Tests of the null hypothesis of no significant departure from Hardy-Weinberg expectations ($f = 0$) and panmixia ($\theta = 0$, i.e. no genetic differentiation between samples) were performed by random permutations of alleles and individuals from the original matrix of genotypes, respectively. Critical significance levels for multiple testing were corrected following the sequential Bonferroni procedure (Rice 1989). Linkage disequilibrium between pairs of nuclear loci (i.e. non-random associations of particular genotypes) were tested with the GENEPOP software using exact tests (Raymond & Rousset 1995).

Distinct genetic parameters should respond to selection, such as gene diversity (Nei 1987), the total number of alleles at each locus, and allele frequencies in populations. Investigating variations of such parameters should consider variations between locations and estuaries. Unbiased observed gene diversity was computed according to Nei (1987) using the program CONTRIB developed by Petit et al. (1998), available at http://www.pierroton.inra.fr/genetics/labo/Software/Contrib/. This program was also used to compute the relative contribution (CT%) of each population to the overall observed gene diversity. Estimates of CT% were used to identify populations contributing less or more than average to overall gene diversity. Finally, this program was used to compute standardised allelic richness for each population (Petit et al. 1998). As sample size varies between locations, allelic richness may vary greatly from one sample to another (i.e. small samples generally have a lower number of alleles than larger samples). Direct and simple comparison of allelic richness is not straightforward. Hence, allelic richness was standardised to that of the smallest sample over populations and over loci using a 'rarefaction method' (details in Petit et al. 1998). Leberg (2002) proved that this method provides an unbiased estimate of allelic richness for a given sample size, allowing sample comparisons. Comparisons of observed gene diversity and standardised allelic richness were carried out using 1-way ANOVA between locations and using Fisher's *t*-tests when comparing estuaries (Saloum vs Gambia) or salinity conditions (high salinity locations vs low salinity locations) (Sokal & Rohlf 1995).

Condition data. The condition factor (K) was calculated using standard methods from individual length and weight data, following the formula:

$$K = \frac{P}{FL^3} \times 10^5 \quad (1)$$

where P is the total weight (in g) and FL is the fork length (in mm). Data were checked for normality and homogeneity of variances. Significant differences were then revealed by 1-way ANOVA followed by Tukey's multiple means comparison test.

Reproduction data. In the laboratory, sexual maturity stage was determined macroscopically. For females, Stage 1 corresponds to immature individuals, Stage 2 to sexual rest or to the very beginning of sexual activity, Stage 3 to maturing females with very small oocytes, Stage 4 to mature females that are about to reproduce, Stage 5 to ovulating females and Stage 6 to post-spawning females (Fontana 1969, Albaret & Gerlotto 1976). For males, Stage 1 and Stage 2 correspond to immature and sexually inactive individuals, Stage 3 to developing testicles, Stage 4 to mature individuals and Stage 5 to spermiant gonads (Fontana 1969, Albaret & Gerlotto 1976). If the gonad could not be classified into one of the previous stages, the individual was labelled as undifferentiated. When possible, gonads were removed and weighed (P_G, in g) in

both sexes. The gonado-somatic index (GSI) was calculated for each individual following the formula:

$$GSI = \frac{100 \times P_G}{P} \quad (2)$$

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

The average size at first maturity (L_{50}) was defined as the FL at which 50% of the individuals of either sex were at an advanced stage of the first sexual cycle (at least Stage 3 of the maturity scale) during the reproductive season determined previously (to avoid classifying resting females or males as immature). Following Duponchelle & Panfili (1998), the L_{50} was estimated by fitting the fraction of mature females or males per 20 mm FL interval to a logistic function by a non-linear regression (quasi-Newton method, Statistica Statsoft® software):

$$\%MF = \frac{100}{1 + e^{[-a \times (L - L_{50})]}} \quad (3)$$

where %MF is the percentage of mature females by size class (20 mm), L is the central value of each size class, a and L_{50} are constants of the model. The values were compared between ecosystems and/or locations.

Gonads of mature females (Stages 4 and 5) were preserved in 95% ethanol. Before measuring gonad activity (e.g. number and size of oocytes), gonads were immersed in a saline (35 psu NaCl) solution for 72 h, then they were manually shaken before being immersed in Gilson solution (100 ml ethanol, 9 ml acetic acid glacial, 20 ml 60% nitric acid, 20 g mercury[II] chloride and 875 ml distilled water) for 72 h. The absolute fecundity was computed as the number of oocytes released at next spawning. For this, a subsample of the middle part of the gonad was weighed, and oocytes belonging to the largest modal size group were manually counted. The absolute fecundity of the sub-sample was then calculated for the total gonad weight. The relative fecundity, which provides a comparison between different populations, is the ratio between the absolute fecundity and the individual weight (in kg). The diameter and the volume of oocytes were measured by image processing in females at an advanced stage of maturity (4 or 5). For each individual, 100 oocytes were measured using the Image J software (freeware) 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, circumference, maximum and minimum diameter). Data were checked for normality and homogeneity of variances, and mean values were compared using a 1-way ANOVA (Statistica Statsoft software).

Age and growth data. Otoliths were extracted from a sub-sample in order to estimate the individual age and to calculate the growth. For each month and for each location, a stratified sample of 3 otoliths per 20 mm size class (FL) was collected. After 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 the TNPC software (Visilog), under a binocular microscope and reflected light against a dark background. An image data bank was constructed; each otolith was then read by 1 reader from the core area to the edge on the rostrum and on the posterior face, and back again to the centre; translucent zones were counted and measured on the radius of the rostrum and posterior face. Interpretation of the presence or absence of a translucent zone was done taking into account its presence on all the otolith faces; the last translucent zone was not counted if it was on the otolith margin and thus in formation. Non-interpretable otoliths were discarded from the analysis. The process of validation of the translucent zone deposition in time was done by measuring the distance between the last translucent zone and the margin; the monthly changes in the relative marginal distance, the ratio between the distance of the last translucent zone from the edge and the distance separating the 2 last zones were monitored for 1 yr. If the formation cycle corresponded to 1 translucent zone yr^{-1}, 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 reproduction study), the date of capture and the number of translucent zones. The von Bertalanffy growth function (VBGF) was calculated using a non-linear estimation (quasi-Newton method, Statistica Statsoft software):

$$L = L_\infty \times \left\{1 - \exp[-K \times (t - t_0)]\right\} \quad (4)$$

where L is the mean FL of an individual at time t and L_∞, K and t_0 are parameters of the model.

The growth parameters of the VBGF were compared using the likelihood ratio test (Tomassone et al. 1993) and applying the weighted sum of squares (Kimura 1980). For k populations, the likelihood ratio test is S_{LR} compared with χ^2 with 3 df (3 parameters):

$$S_{LR} = \sum_{i=1}^{k} m_i \times \left[\ln(s_c^2) - \ln(s_k^2)\right] \quad (5)$$

where m_i is the number of individuals of the k^{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 by pairs.

RESULTS

Data and size distributions

The total number of *Ethmalosa fimbriata* sampled was 1405, in Gambia and 1273 in Saloum (Table 1). The maximum size of the fish was always <300 mm. Fig. 2 illustrates the size distributions of each monthly sample at each location. The commercial landings of *E. fimbriata* are seasonal (from January to June). For this reason gaps are present in the samples over the year. The low salinity during the rainy season also reduced the catch of the individuals during some periods (e.g. August to November, and/or at Tendaba). Finally, for some locations and at particular time of the year, some of the medium size classes between 100 and 180 mm FL were missing (e.g. Foundiougne in January 2002, Ndangane; Fig. 2).

Salinity parameters

There were strong monthly variations in salinity in both estuaries (Fig. 3). Each year, the salt concentra-

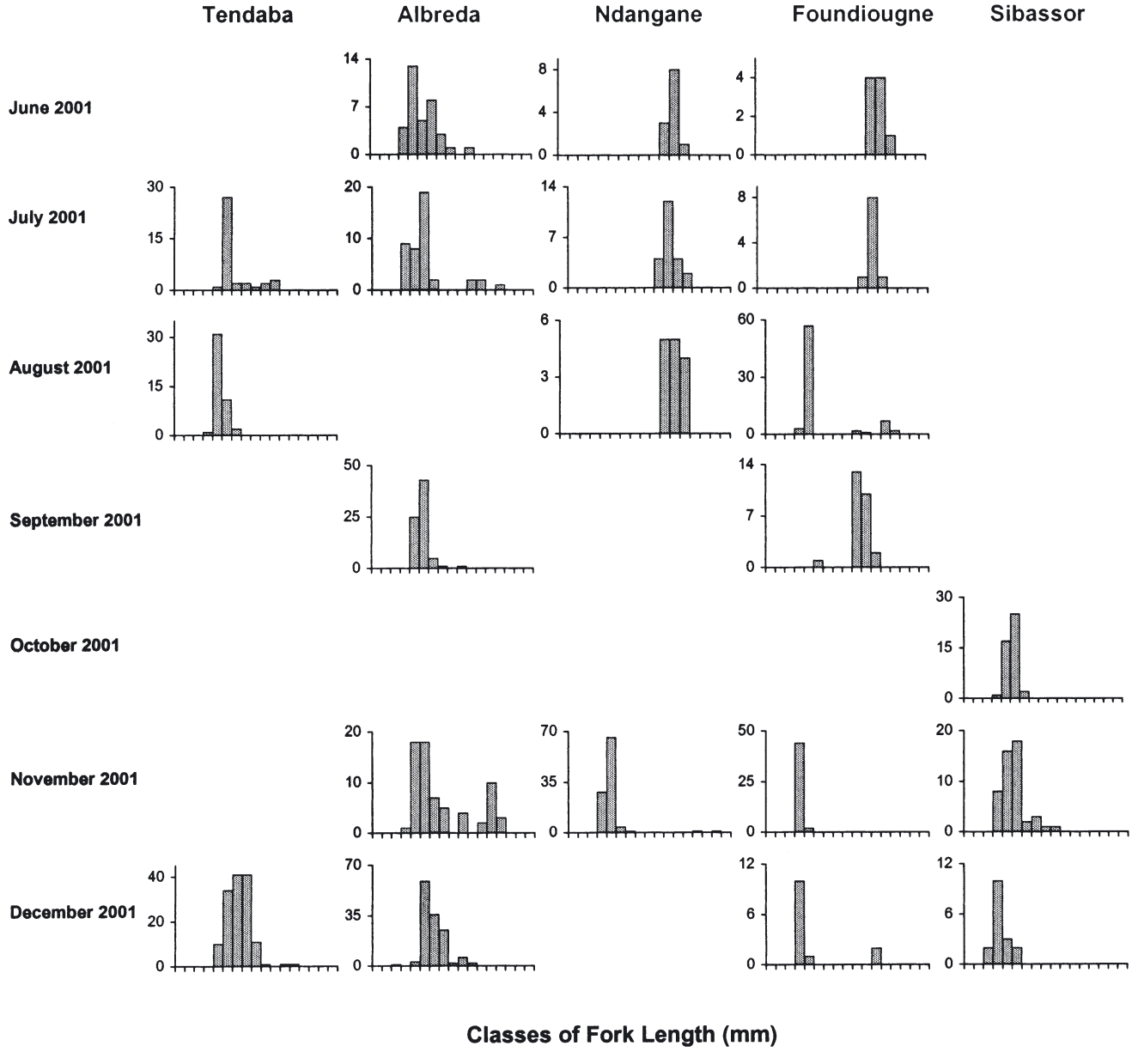

Fig. 2. *Ethmalosa fimbriata.* Size distributions of the monthly samplings at the different stations

tion in the waters fell at the beginning of the rainy season (June to July) and reached a minimum in September. The rainy season ended in October to November. The highest salinity occurred at the end of the dry season (April to May), possibly later in the Saloum (June or even July) because the rainy season was late in

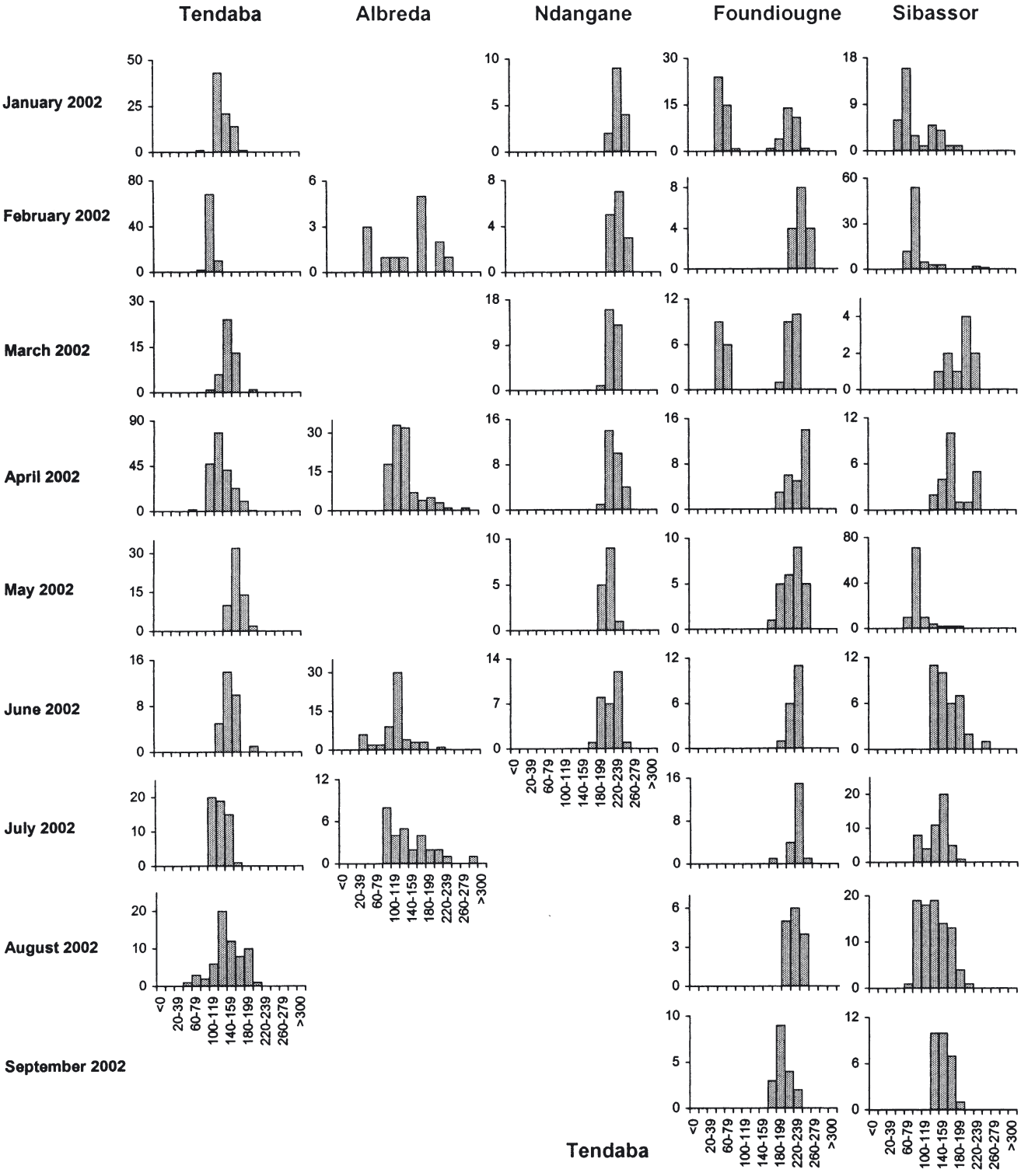

Fig. 2 (continued)

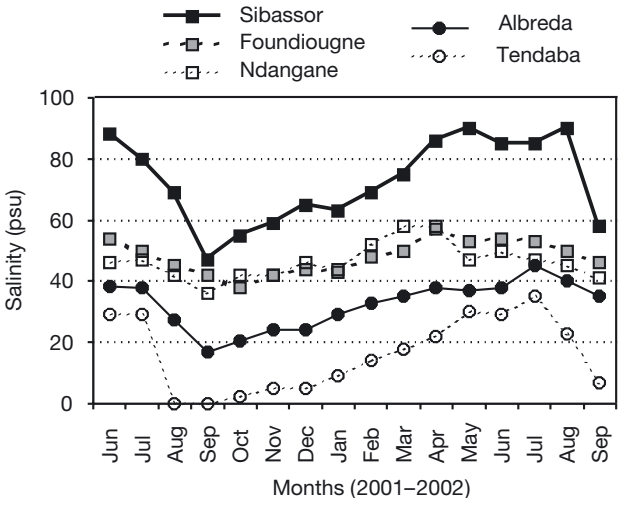

Fig. 3. Monthly evolution of the salinity at the different sampling stations: round and square symbols represent Gambia and Saloum, respectively

2002. Throughout the year, the salinities in the Gambian locations were always lower than those of the Saloum estuary (Fig. 3). The salinity level in the Gambia (Albreda and Tendaba) reached a maximum value close to that of the seawater (40 psu) at the end of the dry season. It was 0 psu, at Tendaba, after the rains in August. The results show a classical 'normal' functioning of the Gambia estuary, with lower salinity values upstream. The salt concentration in the Saloum (Ndangane, Foundiougne and Sibassor) was always higher than that of seawater, reaching a minimum in Ndangane (located near the ocean) of about 40 psu. Although the Ndangane and Foundiougne stations are far apart (around 30 km), the salinities in these areas were similar. The upstream station of Sibassor had an extremely high salinity level, reaching a brief minimum of about 50 psu in September each year and a peak of about 90 psu in May (Fig. 3), providing an example of an inverse estuary situation with extreme environmental constraints. The highest salinities occurred in the upper reaches of the estuary throughout the year. In 2002, the rainy season was shifted with a later start and the salinity level did not decrease before August. The reduction of the salinity and/or the appearance of freshwater conditions (in the Gambia estuary) at one period of the year explains the absence of samples in some locations (Fig. 2). This was particularly evident for the Tendaba station which was entirely freshwater during the rainy season.

Population genetic analysis

A total of 240 *Ethmalosa fimbriata* from the Gambia and Saloum estuaries were screened for intronic or anonymous nuclear sequence length variation (Table 2). A total of 18 alleles were observed at the *Aldolase B* (H = 0.89 to 0.87), 15 alleles at the *GAPDH fast* (H = 0.89 to 0.83) and 5 alleles at the *Myoglo2* and *GAPDH slow* loci (H = 0.72 to 0.59 and H = 0.49 to 0.12, respectively) (Table 3). With the exceptions of the *GAPDH slow* locus in both populations and the *Myoglo2* locus in the Sibassor population, no heterozygote deficit was observed. Recurrent deviation from Hardy-Weinberg equilibrium at the *GAPDH slow* locus could be evidence for null alleles due to mutations in the primer sequences, despite the sequences being located in exons of the gene. Hence,

Table 3. *Ethmalosa fimbriata.* Estimates of population genetic parameters at nuclear loci (N: sample size; *n*: number of alleles; *Hê*: expected heterozygosity; $\hat{f}$: estimate of Weir & Cockerham's (1984) equivalent of fixation index). **Bold** values are still significant after the Bonferroni correction (Sokal & Rohlf 1995). Multiple-locus parameters were estimated on all loci except *GAPDH slow*. $^{\star}p < 0.025$, $^{\star\star}p < 0.01$, $^{\star\star\star}p < 0.001$

	S10 Sibassor	Fo Foundiougne	F12 Foundiougne	A6 Albreda	CP35-39 Tendaba
GAPDH fast					
n	11	11	9	12	11
Hê	0.869	0.845	0.847	0.888	0.828
$\hat{f}$	−0.045	−0.072	0.109	0.057	−0.054
N	43	42	45	37	39
GAPDH slow					
n	4	4	4	4	5
Hê	0.245	0.324	0.294	0.121	0.526
$\hat{f}$	0.367*	0.317*	**0.686*****	**0.383*****	**0.753*****
N	45	27	43	40	15
Aldolase B					
n	14	12	13	14	13
Hê	0.887	0.870	0.888	0.871	0.875
$\hat{f}$	−0.034	−0.072	0.044	−0.050	0.034
N	36	44	40	35	39
Myoglo2					
n	5	5	5	5	3
Hê	0.721	0.634	0.647	0.637	0.564
$\hat{f}$	0.182*	−0.078	−0.169	0.098	0.050
N	44	41	49	33	28
Multi-locus					
n	8.5	8	7.75	8.75	8
Hê	0.681	0.668	0.669	0.629	0.698
$\hat{f}$	0.056	−0.026	0.084*	0.046	0.150*

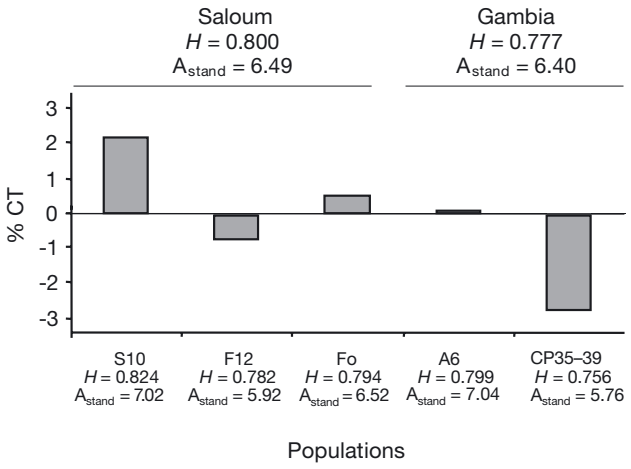

Fig. 4. *Ethmalosa fimbriata.* Contribution to the total genetic diversity (CT%) of each sample. (*H*: mean observed heterozygosity; A_{stand}: standardised allelic richness estimated according to the method of Petit et al. (1998); A6: Albreda; CP35-39: Tendaba; F12: Foundiougne; Fo: Foundiougne; S10: Sibassor)

the *GAPDH slow* locus was discarded from further analyses.

No linkage disequilibrium was detected over the complete data set. Average gene diversities and standardised allelic richness for each population and each estuary are given in Fig. 4. Average gene diversities computed over the 3 loci did not show significant differences between populations (1-way ANOVA, $F_{(4,10)} = 0.011$, $p > 0.05$), between estuaries (Saloum vs Gambia; $t = 0.044$, $p > 0.05$, 3 df), or between populations pooled by salinity characteristics (Sibassor vs others; $t = 0.106$, $p > 0.05$, 3 df). As for gene diversity, the results for standardised allelic richness (using the smallest observed sample size n = 28; Table 3) did not show any significant results either. However, despite no significant difference in gene diversity or allelic richness, it was shown that the Sibassor population contributed relatively more to gene diversity than other populations (CT% = +2.11%), especially, more than the Tendaba population (CT% = –2.78%; Fig. 4). No significant difference in allele frequencies as measured by F_{st} were detected among pairwise population comparisons, including a comparison between temporal replicates at Foundiougne (Table 4). When all populations from the Saloum estuary were grouped and compared to all Gambian populations, no genetic structure was observed ($F_{st} = -0.0013$). Last, the Sibassor population did not appear to be different from any of the other populations ($F_{st} = 0.0018$, $p > 0.05$). Hence, using these loci, the results demonstrated that the hypothesis of panmixia cannot be ruled out and that *Ethmalosa fimbriata* certainly behaves as a single population covering all the sampling area.

Table 4. *Ethmalosa fimbriata.* Multi-locus pair theta (θ) measured from *GAPDH fast*, *Aldolase B* and *Myoglo2* data. *GAPDH slow* was discarded from this analysis because of its high level of *F*îs. No significant differences were observed (tested by permutation) (A6: Albreda; CP35-39: Tendaba; F12: Foundiougne; Fo: Foundiougne; S10: Sibassor)

θ	S10	Fo	F12	A6	CP39-35
S10	–	–0.0016	0.0046	0.0003	0.0051
Fo		–	0.0064	–0.0003	–0.0042
F12			–	0.0002	0.0034
A6				–	0.0037
CP35-39					–

Condition factor

There were significant differences in condition factors calculated for the whole sample for the whole period (June 2001 to September 2002) between each estuary (ANOVA, $F_{(1,2511)} = 11.48$, $p < 0.05$; Table 5), the condition of *Ethmalosa fimbriata* in the Saloum being higher than that in Gambia. Moreover the condition was significantly different between sampling locations ($p < 0.05$; Table 5), without a hierarchical classification in relation to the distance from the sea in the estuary and with a higher value for the Ndangane area. The condition was also significantly different between months for both estuaries (ANOVA, $p < 0.05$), but a clear yearly cycle was only observed in the Gambia estuary, with the lowest *K*-value being encountered in June 2002 ($K = 0.76 \pm 0.12$) and the highest in December 2001 ($K = 1.36 \pm 0.07$), indicating a better condition at the end of the rainy season.

Table 5. *Ethmalosa fimbriata.* Condition factors (mean $K \pm$ SE) at the scale of estuaries and each station (n: number of individuals). The same letter given after the means among estuaries or stations signifies that the values do not differ significantly between groups ($p > 0.05$)

	K	SE	n
Estuary			
Gambia	1.268[a]	0.243	1278
Saloum	1.386[b]	0.247	1235
Station			
Ndangane	1.574[c]	0.523	274
Foundiougne	1.352[d]	0.435	397
Sibassor	1.318[d]	0.365	564
Albreda	1.270[d]	0.409	448
Tendaba	1.268[d]	0.301	830

Reproduction

As revealed by the monthly changes in the GSI and the percentage of mature individuals, the reproductive activity followed an annual cycle that ended at the end of the year (October to December), for both females and males in the Saloum (Fig. 5). The changes in the GSI for the females strictly followed the change in percentage of mature individuals in Saloum. Such a cycle was less clear in the Gambia (Fig. 5), probably because of the difficulty of obtaining large individuals in this estuary (Fig. 2). Nevertheless the reproductive activity was less intensive at the end of the year, whereas some individuals were mature or had a high GSI in other periods. The maximum GSI values were much higher in the Saloum than in the Gambia. In conclusion, the duration of the reproductive season of *Ethmalosa fimbriata* in both estuaries covered a long period of the year (from January to September). The complete cessation of reproduction was probably very short, and did not exceed 2 or 3 mo during the time frame of this study. For the next analysis (i.e. growth calculation), April 1 was assumed to be the date of birth of the fish in the populations.

The computation of the size at first maturity (L_{50}) was carried out with fish caught during the reproductive period in both environments (January to September) during 2002. For both females and males, the L_{50} was higher in the Gambia than in the Saloum (Fig. 6, Table 6). The type of estuarine ecosystem had a strong

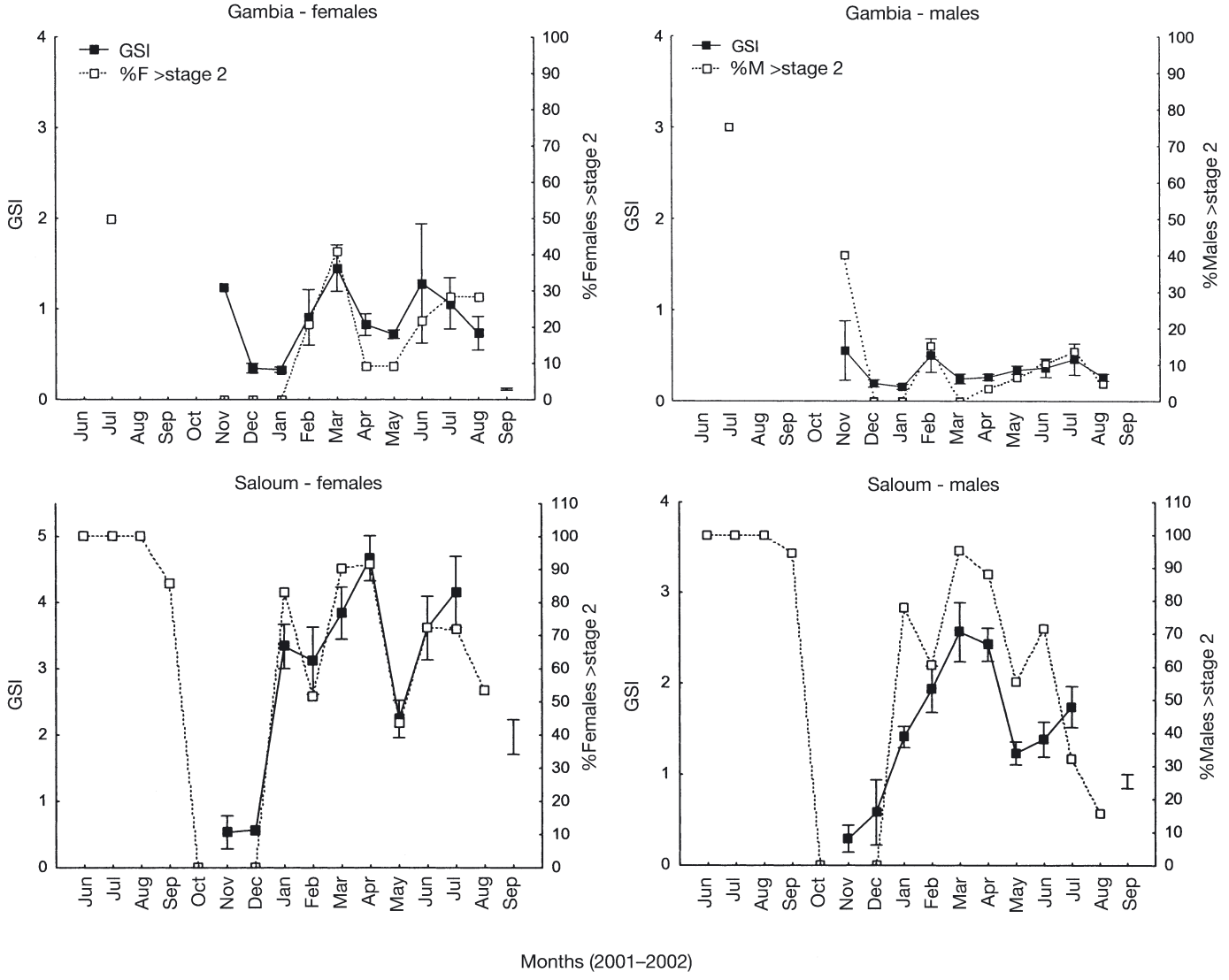

Fig. 5. *Ethmalosa fimbriata.* Monthly evolution of the gonado-somatic index (mean GSI ± SD) and percentage of different sexual stages, in the Gambia (upper panels) and Saloum (lower panels) estuaries

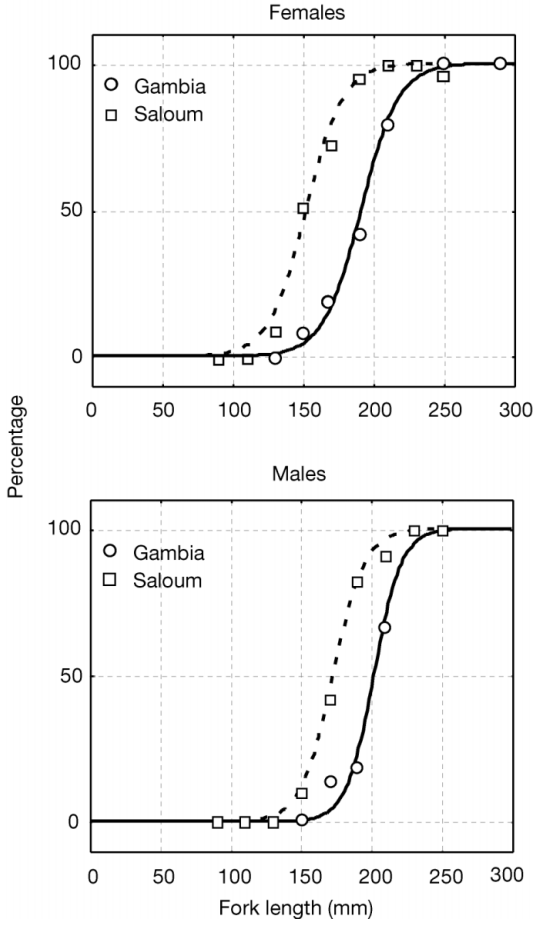

Fig. 6. *Ethmalosa fimbriata.* Logistic function computed from the percentage of mature individuals per size class for females (upper panel) and males (lower panel) in the Gambia and Saloum estuaries during the season of reproduction in 2002

effect on this parameter. For both females and males, the highest value of L_{50} was encountered at Tendaba, whereas the lowest was found at Sibassor (Table 6). The calculation was impossible for the Ndangane and Foundiougne stations because of a lack of a fit to the model.

There were significant differences in relative fecundity of the females between the different locations, with a higher fecundity in the Saloum (1-way ANOVA, $F_{(1,32)} = 5.54$, $p < 0.05$; Fig. 7). Significant differences between the oocyte sizes (area) of the females between the Gambia and the Saloum were also recorded, with a greater size in the Saloum (1-way ANOVA, $F_{(1,1377)} = 7.50$, $p < 0.05$; Fig. 7). This observed difference could not be assigned to a difference between maturation stages because the oocyte areas were identical between Stages 4 & 5 (1-way ANOVA, $F_{(1,1377)} = 0.00275$, $p > 0.05$). Finally, the oocytes were larger and more numerous in the Saloum, showing more effective reproduction in this estuary.

Age and growth

Ethmalosa fimbriata age in the Gambia and Saloum estuaries was estimated using the interpretation of thin translucent zones on the whole otoliths viewed on a dark background and under reflected light. The alternation of translucent and opaque zones on the whole otolith was sufficiently clear to count them. The zones on the rostrum axis were clearer than on the posterior axis, or any other area of the otolith. The core was translucent, well defined and clearly visible even in the largest fish, surrounded by a first opaque zone which could be composed of thinner opaque and translucent bands. Some otoliths were difficult or impossible to interpret due to their opacity or the difficulty of interpreting the edge (translucent vs opaque). These otoliths were discarded from further analysis.

The monthly variation in the relative marginal distance on the otoliths validated that 1 translucent zone was produced per year (Fig. 8). This zone appeared during the second part or at the end of the rainy season (October), with a possible shift between the 2 consecutive years (width lower in September 2002), probably linked with the delay of the rainy season. The otolith growth during the following months, which corresponded to opaque zone formation, could be associated with more favourable conditions. The translucent zone formation was therefore considered to be an annulus. Theoretically, if birth occurred in April or in

Table 6. *Ethmalosa fimbriata.* Sizes at maturity (estimated L_{50} ± SE) for females and males in Saloum and Gambian estuaries and at individual stations during the reproduction period in 2002 (n: number of individuals; d^2: coefficient of determination [percentage of explained variance])

	L_{50}	SE	d^2 (%)	n
Estuary		Females		
Gambia	192	1.4	99.5	254
Saloum	153	1.9	99.0	299
Station				
Tendaba	204	3.4	96.1	191
Albreda	169	–	100.0	63
Sibassor	153	1.9	99.1	167
Estuary		Males		
Gambia	202	1.9	98.3	243
Saloum	173	0.9	99.8	324
Station				
Tendaba	194	–	99.2	177
Albreda	190	11.0	78.5	66
Sibassor	185	1.4	99.4	147

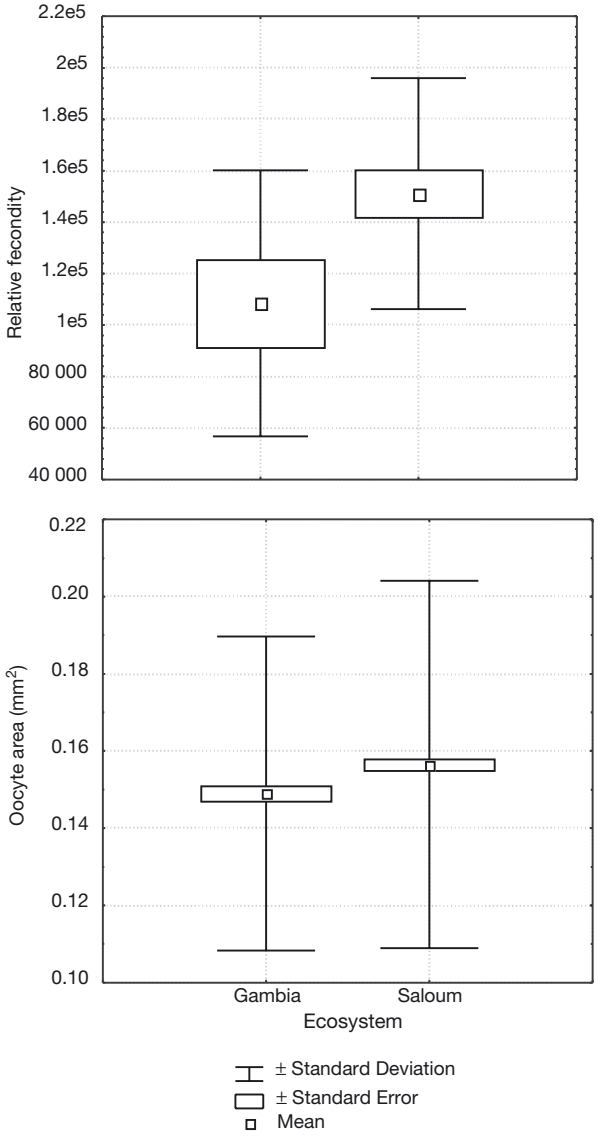

Fig. 7. *Ethmalosa fimbriata.* Relative fecundity (upper panel) and size of oocytes (area, lower panel) in the 2 different ecosystems (Gambia and Saloum)

the following months, the opaque zone surrounding the otolith core could have been crossed by thin translucent bands that do not correspond to a single year's growth; these formations were frequently observed inside the otoliths. The individual age could then be calculated in years or months using the number of translucent zones (annuli), the date of birth and the date of capture. When the first annulus was observed in the population, the fish were already 6 mo old, with 1 April as the theoretical birth date of the population.

The calculated VBGF demonstrated a clear reduction of growth in the areas with highest salinity, i.e. >60 psu (Fig. 9, Table 7), that differed from all other locations (S_{LR} = 443.8, p = 0.000). The growth rate was higher in the Saloum at <60 psu than in the Gambia (S_{LR} = 264.1, p = 0.000). When comparing growth models between stations, the highest growth rate occurred at Foundiougne, whereas the slowest occurred at Sibassor. The growth rates were identical in the lower part of the Saloum and in the Gambia (Fig. 9, Table 7). Hence, the growth rate appeared to be higher in an environment with a high salinity (above that of seawater), and the highest or lowest salinities were not optimal for growth.

DISCUSSION

An understanding of the factors explaining life history trait variation in fish populations inhabiting contrasting habitats may allow us to forecast how these populations could respond to changes in their environment. Such understanding may influence management of fisheries of locally important species such as *Ethmalosa fimbriata*. Observed divergence in life history traits may have 2 origins that can, at least partially, interact: (1) genetic change and (2) phenotypic plasticity (e.g. Stearns 1992, Falconer & Mackay 1996). However, it is known that disentangling the respective role of each process is difficult (e.g. Howard et al. 2001, Hendry 2002) and requires reciprocal transplant experiments that could be difficult with fish (e.g. Conover & Schultz 1995).

Nevertheless, in this study, genetic parameters such as genetic diversity or allelic richness did not differ

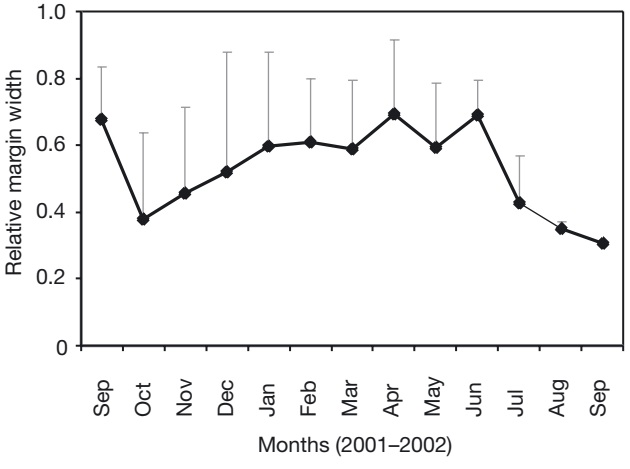

Fig. 8. *Ethmalosa fimbriata.* Evolution over time (September 2001 to September 2002) of the mean and SD of the relative marginal distance (distance between the last translucent zone and the edge divided by the distance separating the 2 last translucent zones) on otoliths

between populations or estuaries, and did not differ between locations with contrasting salinity levels. Empirical observations have previously demonstrated that these variables might respond to both natural or human-driven changes in environmental conditions (e.g. Scribner et al. 1992, Heithaus & Laushman 1997). Furthermore, no allele-frequency heterogeneity was detected in this study. Bonga shad *Ethmalosa fimbriata* from the Saloum and the Gambia estuaries apparently share the same gene pool, indicating that only 1 panmictic population inhabits the area. This result contrasts with those previously obtained with species of the sub-family Alosinae such as the American shad *Alosa sapidissima*, which shows a homing behaviour that preserves significant genetic differentiation between estuaries (Brown et al. 2000). Using allozymic loci, Smith & Tolliver (1987) also reported genetic differentiation in the blueback herring *Alosa aestivalis* from neighbouring localities. *E. fimbriata* exchanges migrants between nearby estuaries (Gambia and Saloum) and, from a genetic point of view, migrants may interbreed successfully. A simple admixture of differentiated populations (without breeding contact) should lead to significant deficits in heterozygotes ('Wahlund effect') and linkage disequilibrium between loci, which were not observed in our data. Hence, our results suggest a lack of homing behaviour (more generally, a lack of 'biased reproductive behaviour') in *E. fimbriata*; furthermore, it appears impossible to define any putative sub-populations that may possess genotypes and patterns of genetic differentiation related to peculiar environmental conditions. The growth and reproductive differences observed for *E. fimbriata* may be considered to be an adaptive answer to environmental conditions and, mainly, to high-salinity pressure. Similar results have already been obtained for the American shad (Bentzen et al. 1989), in which differences in reproductive traits were not associated with any specific mitochondrial clade. Our results indicate that a selection process does not seem to acting at the level of the genome for these particular loci (i.e. they do not represent QTLs, 'quantitative trait loci', that may support the genetic basis of ecophenotypic differentiation). The markers used here were most probably neutral, and may have failed to elicit any selective influence. However, introns are located between gene coding sequences, and, for 2 reasons, appear to be

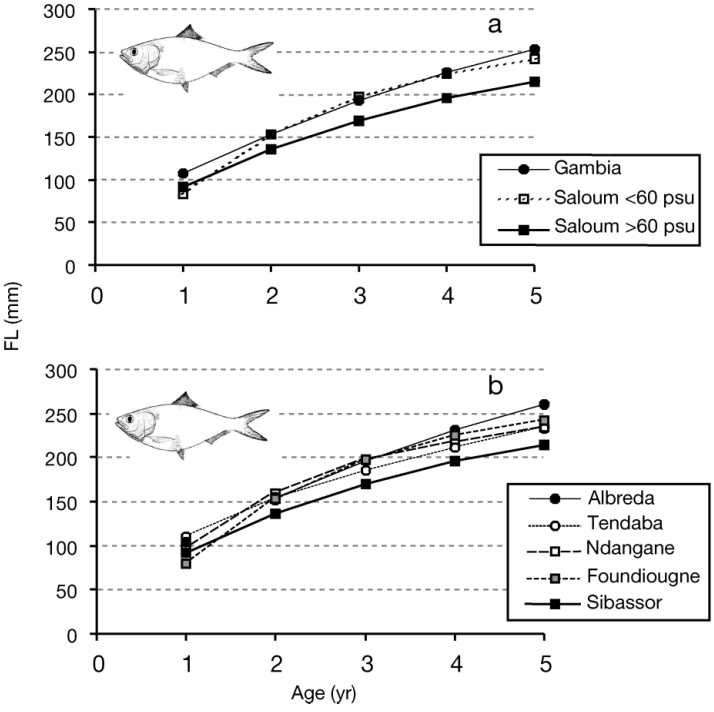

Fig. 9. *Ethmalosa fimbriata.* Von Bertalanffy growth function calculated as a function of the level of salinity (a) and as a function of sampling station (b). *E. fimbriata* image from Lamboeuf (FAO in Froese & Pauly 2003)

Table 7. *Ethmalosa fimbriata.* Parameters of the von Bertalanffy growth functions calculated for the Gambia and Saloum estuaries from 2001 to 2002. d^2: coefficient of determination (percentage of explained variance)

	n	L_∞	SE	K	SE	t_0	d^2 (%)	FL range	Age range
Estuary									
Gambia	188	407	119	0.17	0.08	−0.84	67.3	50–286	0–6
Saloum < 60 psu	134	270	21	0.46	0.09	0.20	87.3	41–256	0–5
Saloum > 60 psu	131	276	47	0.28	0.09	−0.46	76.7	35–226	0–4
Station									
Tendaba	104	313	130	0.23	0.17	−0.87	59.3	54–221	0–4
Albreda	84	400	122	0.19	0.09	−0.62	53.4	50–286	0–6
Ndangane	53	257	29	0.49	0.16	0.01	87.0	41–256	0–5
Foundiougne	81	266	24	0.50	0.12	0.29	87.6	43–255	0–4
Sibassor	131	276	47	0.28	0.09	−0.46	76.7	35–226	0–4

good candidates for observing the fingerprint of selection at the genome level. First, the theory of 'genetic hitchhiking' states that neutral loci linked to selected loci could be governed more by selection than the genetic drift that is traditionally the main evolutionary force acting on neutral loci (e.g. Barton 2000, Gillespie 2000). As introns are embedded within potentially selected exons, they could be used to detect selection acting at loci of interest. Second, Hare & Palumbi (2003) recently showed that, in mammals, introns consist of sequences that are more conserved than expected. Introns could, therefore, play a role in gene regulation and be selected. Hence, despite the remaining lack of evidence for fish, introns may be more accurate loci for investigating selection at the genomic level and for establishing relationships with life history and/or environmental data than e.g. microsatellite loci (Jarne & Lagoda 1996). However, this does not imply that there are no selective processes occurring within sub-populations living in the hypersaline parts of the Saloum estuary. Lack of genetic differentiation at the screened loci is not absolute proof that genetic changes due to natural selection do not occur, or that phenotypic plasticity alone explains life history variation. It is now well established that ecophenotypic changes driven by natural selection are often more easily detectable using life history or morphological traits than with suites of molecular markers that are subject to genetic drift in numerous organisms (see Hendry 2002, review in McKay & Latta 2002), including fish (e.g. Koskinen et al. 2002).

In the Saloum/Gambian ecosystem complex, we observed a high degree of genetic homogeneity, but differences in life history traits were recorded between the sampling locations. These differences are probably a phenotypic response to local conditions. The salinities encountered in these ecosystems showed extremely high variations, from 0 up to 90 psu, and, in order to simplify the following interpretations, we have chosen to classify the waters into 3 different categories: mesohaline (0 to 35 psu), metahaline (35 to 60 psu) and hyperhaline (60 to 90 psu) (Albaret et al. 2004).

Ethmalosa fimbriata reacts to salinity conditions at reproductive, condition and growth levels. The reproductive adaptation concerns fine life history traits such as the length at first maturity (reduction at high salinities), fecundity (lower at a low salinity) and oocyte size (higher at high salinity). The impact of the environment on a reduction of the size at maturity has already been observed in temperate areas, for example, for brown trout subjected to different degrees of lake acidification (Hesthagen & Jonsson 2002) or for American plaice populations subjected to different temperatures (Morgan & Colbourne 1999). In tropical areas, changes in size at maturity have been mentioned several times, but mainly for inland species. The common tilapia species (Cichlidae), widely exploited and bred in West African inland waters, have shown a clear adaptation (i.e. reduction) of their size at maturity as a function of their environment (Legendre & Ecoutin 1989, Duponchelle & Panfili 1998, Duponchelle et al. 1998, Panfili et al. 2004). *E. fimbriata* also responds to pollution (Albaret & Charles-Dominique 1982, Charles-Dominique & Albaret 2003, Guyonnet et al. 2003) and to overfishing (Laë 1997) with a reduction of the size at maturity. More generally, the reduction of the length at maturity for different species can also reflect an adaptive response to intensive exploitation (Smith 1994). As there is no evidence for overfishing or pollution in the Gambia and Saloum estuaries (Laë et al. 2004), we have demonstrated here for the first time a response of reproductive traits to salinity. Nevertheless, the length-at-maturity values observed in females in the Gambia and Saloum, 191 and 153 mm, respectively, are much higher than those observed in Ivory Coast lagoons, where they range from 145 to 84 mm (Guyonnet et al. 2003). The environmental pressures in this latter ecosystem seem to affect this trait more strongly. It is not possible to conclude that there has been a phenotypic response in this trait, as the populations of the Gulf of Guinea could genetically diverge from those of the Sene/Gambian complex, because the distribution appears to be fragmented along the African coasts (Charles-Dominique & Albaret 2003). Until now nothing was known about the real significance of the observed reduction, i.e. whether it resulted from early maturation, with a normal size at age, and/or from a dwarfism phenomenon (fish old for their size). The present study revealed a clearly slower, rate of growth for this species in hyperhaline zones (>60 psu), but not at intermediate salinities (around 50 psu). Moreover, growth was similar between locations during the first years of life (Fig. 9). It is therefore impossible to conclude at present that early maturation occurs in bonga shad. Further study using fine-scale evaluation of growth, for example using daily primary otolith increments, is still needed to estimate precisely the age at maturity.

Both relative fecundity and oocyte size are higher for *Ethmalosa fimbriata* in the Saloum than in areas with lower salinities. The values of relative fecundity in the Gambia and Saloum (110 and 150 oocytes g^{-1}, respectively) are closer to those observed in Ghana by Blay & Eyeson (1982) than to the much higher values (up to 300 oocytes g^{-1}) in the Ivory Coast (Albaret & Gerlotto 1976). On the other hand, the oocyte sizes in both Saloum and Gambian estuaries were similar to those of Ivory Coast (Albaret & Gerlotto 1976). The observed differences could reflect geographical divergences,

with isolated populations living in different environments (estuaries vs lagoons); alternatively, evolution of these life history traits could have occurred during the last 20 yr, with the impact of environmental (e.g. Saloum) and/or human influences, to which all West African aquatic ecosystems have been subjected to differing degrees. It is not possible to choose between these explanations, even though the Gambia estuary could be considered a reference ecosystem with normal functioning. Nevertheless, both fecundity and oocyte size are currently higher in the Saloum, indicating that a moderate salinity constraint (<60 psu) is favourable for *E. fimbriata* reproduction. This observation is in contrast with that made in a similar study conducted in the same environments on a tilapia species, *Sarotherodon melanotheron* (Panfili et al. 2004), but the reaction norm of tilapia, which is a mouth brooder, is probably biologically different from that of pelagic clupeid species.

Finally, phenotypic changes in the reproductive traits of *Ethmalosa fimbriata* can be related to the rapid reaction to environmental conditions, as has been demonstrated by Duponchelle & Legendre . (2001) for a tilapia species, *Oreochromis niloticus*. The most surprising result is the increase in oocyte size with the increase in salinity. Nevertheless, even though differences in the sizes between Saloum and Gambia are significant, the values are relatively close (Fig. 7). This increase currently seems unfavourable, because the size of the egg area in contact with the water would require osmoregulation and egg buoyancy would change (Depêche & Billard 1994). Further study on egg physiology and development (effect of salinity) is necessary to support hypotheses on the role of egg size.

Salinity also undoubtedly has an effect on the growth of fish (Calow & Forbes 1998, Boeuf & Payan 2001). In their review, Boeuf & Payan (2001) emphasised the greater growth potential at intermediate salinities. Our results show the same tendency, if we consider that, among species that can live in salinities up to 90 psu (measured here), 'intermediate salinities' are probably those between 35 and 55 psu, i.e. within the metahaline area. On the other hand, these salinities are already extremely high compared with those encountered by most species living in estuaries functioning normally (Blaber 1997, Whitfield & Elliott 2002). Growth was therefore better in the metahaline Saloum and poorer in the Gambia with its mesohaline waters and lower in hyperhaline Saloum (>60 psu). Nevertheless, the largest decrease in growth rate was observed under hyperhaline conditions. This last result seems surprising for this pelagic clupeid, which is capable of reacting to high salinity by migrating towards a more favourable environment. A similar growth decrease under hyperhaline conditions has been found in the common tilapia species *Sarotherodon melanotheron*, living in the same environments (Panfili et al. 2004). Furthermore, the water quality of the Gambia River could also explain the lower growth rate, because it is much more turbid than the Saloum (Albaret et al. 2004). In fact, excessively high water turbidity has been shown to negatively affect growth rate and many other life history traits (e.g. feeding efficiency) (Whitfield 1998, Whitfield & Elliott 2002). In addition to salinity, the turbidity undoubtedly has an effect on the growth of bonga shad. This observation can also be related to the condition factor values determined in our study, which were lower in the Gambia and were indirectly linked with growth rates (a lower condition factor indicates suboptimal feeding, which leads to a lower growth rate). In their review of bonga shad biology, Charles-Dominique & Albaret (2003) have given estimates on the growth of West African shad based on published records from the 1970s and 1980s. Unfortunately these data are scarce and difficult to use for comparison, even though they show 2 levels of growth, 1 of them having values close to those of the present study. Nevertheless, the growth in the Saloum and Gambian ecosystems is currently lower than in other areas of the Gulf of Guinea 20 yr ago. For Nigeria, King (1997, source of data: http://www.fishbase.org) has estimated growth parameters (L_∞ = 336 mm and K = 0.36) comparable to those of the Saloum and Gambia estuaries. In our study, growth was also similar in all locations during first 2 yr, and it mainly decreased in hyperhaline environments thereafter. This observation may indicate that the migratory behaviour of this species may not be as strong in the face of environmental constraints. After a few months, energy allocation to growth processes, therefore, appears to be more restricted in higher salinity environments, suggesting that osmoregulation is an important energy demand, at the expense of growth. In intermediate conditions (i.e. <60 psu), the regulation of energy allocation maintains similar growth rates whatever the salinity. In terms of growth rates, freshwater is probably not optimal for this brackish-water species. Iwama et al. (1997) observed lower oxygen consumption in seawater than in freshwater or hyperhaline seawater for a tilapia species, and this could be in accordance with the results on *E. fimbriata*.

In conclusion, the panmictic population of *Ethmalosa fimbriata* in the Saloum/Gambia complex of ecosystems adapts its life history traits to different levels of reproduction and growth as a function of salinity. The metahaline Saloum area (<60 psu) presents the best conditions in terms of condition factor, reproduction and growth. Other environmental factors, either natural (e.g. turbidity) or human (e.g. intensive fishing),

could also interact with salinity, but this latter factor seems to have a preponderant effect on the life history traits of this species.

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LITERATURE CITED

Albaret JJ (1999) Les peuplements des estuaires et des lagunes. In: Lévêque C, Paugy D (eds) Les poissons des eaux continentales africaines. Editions de l'IRD, Paris, France, p 326–349

Albaret JJ, Charles-Dominique E (1982) Observation d'une taille à la première maturation sexuelle exceptionnellement faible chez *Ethmalosa fimbriata* Bowdich dans une baie polluée de la lagune Ebrié (Côte d'Ivoire). Doc Sci Cent Rech Océanogr Abidjan XIII (2):23–31

Albaret JJ, Gerlotto F (1976) Biologie de l'ethmalose (*Ethmalosa fimbriata* Bowdich) en Côte d'Ivoire. I. Description de la reproduction et des premiers stades larvaires. Doc Sci Cent Rech Océanogr Abidjan VII (1): 113–133

Albaret JJ, Simier M, Darboe FS, Ecoutin JM, Raffray J, Tito de Morais L (2004) Fish diversity and distribution in the Gambia Estuary, West Africa, in relation to environmental variables. Aquat Living Resour 17:35–46

Altschul SF, Madden TL, Schäffer AA, Zhang J, Zhang Z, Miller W, Lipman DJ (1997) Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. Nucleic Acids Res 25:3389–3402

Barton NH (2000) Genetic hitchhiking. Philos Trans R Soc Lond 355:1553–1562

Belkhir K, Borsa P, Raufaste N, Chikhi L, Bonhomme F (2000) GENETIX version 4.02, logiciel sous WINDOWSTM pour la génétique des populations. Laboratoire Génome et Populations, Univ. Montpellier 2, Montpellier, France

Bentzen P, Brown GC, Leggett WC (1989) Mitochondrial DNA polymorphism, population structure, and life history variation in American shad (*Alosa sapidissima*). Can J Fish Aquat Sci 46:1446–1454

Blaber SJM (1997) Fish and fisheries of tropical estuaries. Chapman & Hall, London

Blay J, Eyeson KN (1982) Observations of the reproductive biology of the shad, *Ethmalosa fimbriata* (Bowdich), in the coastal waters of Cape Coast, Ghana. J Fish Biol 21: 485–496

Boeuf G, Payan P (2001) How should salinity influence fish growth? Comp Biochem Physiol C 130:411–423

Brown BL, Gunter TP, Waters JM, Epifanio JM (2000) Evaluating genetic diversity associated with propagation-assisted restoration of American shad. Conserv Biol 14: 294–303

Calow P, Forbes VE (1998) How do physiological responses to stress translate into ecological and evolutionary processes. Comp Biochem Physiol A 120:11–16

Charles-Dominique E (1982) Exposé synoptique des données biologiques sur l'ethmalose (*Ethmalosa fimbriata* S. Bowdich, 1825). Rev Hydrobiol Trop 15:373–397

Charles-Dominique E, Albaret JJ (2003) African shads, with emphasis on the West African shad *Ethmalosa fimbriata*. Am Fish Soc Symp 35:27–48

Conover DO, Schultz ET (1995) Phenotypic similarity and the evolutionary significance of countergradient variation. Trends Ecol Evol 10:248–252

Deme M, Diadhiou HD, Thiam D (2001) Effort de pêche, captures spécifiques et valeurs économiques des débarquements de la pêche continentale dans le fleuve Sénégal et au Sine Saloum. UICN, ISRA, Dakar

Depêche J, Billard R (1994) Embryology in fish: a review. Société Française d'Ichthyologie, Museum National d'Histoire Naturelle, Paris

Duponchelle F, Legendre M (2001) Rapid phenotypic changes of reproductive traits in response to experimental modifications of spatial structure in Nile tilapia, *Oreochromis niloticus*. Aquat Living Resour 14:145–152

Duponchelle F, Panfili J (1998) Variations in age and size at maturity of female Nile tilapia, *Oreochromis niloticus*, populations from man-made lakes of Cote d'Ivoire. Environ Biol Fishes 52:453–465

Duponchelle F, Pouyaud L, Legendre M (1998) Evidence of environmental effects on reproductive characteristics of Nile tilapia (*Oreochromis niloticus*) populations from man-made lakes of Ivory Coast. Aquat Living Resour 11: 137–144

Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics. Addison Wesley Longman, Harlow

Fontana A (1969) Etude de la maturité sexuelle des sardinelles *Sardinella eba* (Val.) et *Sardinella aurita* C. et V. de la région de Pointe-Noire. Cah Ser Océanogr 7: 101–114

Froese R, Pauly D (2003) FishBase. Available at www.fishbase.org

Gillespie JH (2000) The neutral theory in an infinite population. Gene 261:11–18

Guyonnet B, Aliaume C, Albaret JJ, Casellas C, Zerbi A, Lasserre G, Do Chi T (2003) Biology of *Ethmalosa fimbriata* (Bowdich) and fish diversity in the Ebrie Lagoon (Ivory Coast), a multipolluted environment. ICES J Mar Sci 60: 259–267

Hare MP, Palumbi SR (2003) High intron sequence conservation across three mammalian orders suggests functional constraints. Mol Biol Evol 20:969–978

Hassan M, Lemaire C, Fauvelot C, Bonhomme F (2002) Seventeen new exon-primed intron-crossing polymerase chain reaction amplifiable introns in fish. Mol Ecol Notes 2:334–340

Heithaus MR, Laushman RH (1997) Genetic variation and conservation of stream fishes: influence of ecology, life history, and water quality. Can J Fish Aquat Sci 54: 1822–1836

Hendry AP (2002) Q_{ST} > = <> < F_{ST}? Trends Ecol Evol 17:502

Hesthagen T, Jonsson B (2002) Life history characteristics of brown trout in lakes at different stages of acidification. J Fish Biol 60:415–426

Howard DJ, Marshall JL, Braswell WE, Coyne JA (2001) Examining evidence of reproductive isolation in sockeye salmon. Science 291:1853

Iwama GK, Takemura A, Takano K (1997) Oxygen consumption rates of tilapia in fresh water, sea water and hypersaline sea water. J Fish Biol 51:886–894

Jarne P, Lagoda PJL (1996) Microsatellite, from molecules to populations and back. Trends Ecol Evol 11:424–429

Kimura DK (1980) Likelihood methods for the Von Bertalanffy growth curve. Fish Bull 77:765–776
King RP (1997) Growth performance of Nigerian fish stocks. Naga ICLARM 20:31–35
Koskinen MT, Haugen TO, Primmer CR (2002) Contemporary fisherian life-history evolution in small salmonid populations. Nature 419:826–830
Laë R (1997) Does overfishing lead to a decrease in catches and yields? An example of two West African coastal lagoons. Fish Manag Ecol 4:149–164
Laë R, Ecoutin JM, Mendy A, Raffray J, Weigel JY, Sadio O, Djobe O (2004) Effects of a targeted shrimp (*Penaeus notialis*) exploitation on fish catches in the Gambia Estuary. Aquat Living Resour 17:75–85
Leberg P (2002) Estimating allelic richness: effects of sample size and bottlenecks. Mol Ecol 11:2445–2449
Legendre M, Ecoutin JM (1989) Suitability of brackish water tilapia species from the Ivory Coast for lagoon aquaculture. I. Reproduction. Aquat Living Resour 2:71–79
Lévêque C, Paugy D (1999) Les poissons des eaux continentales africaines. Editions de l'IRD, Paris
McKay JK, Latta RG (2002) Adaptive population divergence: markers, QTL, and traits. Trends Ecol Evol 17:285–291
Morgan MJ, Colbourne EB (1999) Variation in maturity-at-age and size in three populations of American plaice. ICES J Mar Sci 56:673–688
Moses BS, Udoidiong OM, Okon AO (2002) A statistical survey of the artisanal fisheries of south-eastern Nigeria and the influence of hydroclimatic factors on catch and resource productivity. Fish Res (Amst) 57:267–278
Nei M (1987) Molecular evolutionary genetics. Columbia University Press, New York
Pagès J, Citeau J (1990) Rainfall and salinity of a sahelian estuary between 1927 and 1987. J Hydrol (Amst) 113: 325–341
Panfili J, Mbow A, Durand JD, Diop K, Diouf K, Thior D, Ndiaye P, Laë R (2004) Influence of salinity on the life-history traits of the West African black-chinned tilapia (*Sarotherodon melanotheron*): comparison between the Gambia and Saloum estuaries. Aquat Living Resour 17:65–74
Petit RJ, El Mousadik A, Pons O (1998) Identifying populations for conservation on the basis of genetic markers. Conserv Biol 12:844–855
Raymond M, Rousset F (1995) Genepop (v. 1.2): population genetics software for exact tests and ecumenicism. J Hered 86:248–249
Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223–225
Sambrook J, Fritsch EF, Maniatis T (1989) Molecular cloning: a laboratory manual, 2nd edn. Cold Spring Harbor Laboratory, New York
Scheffers WJ (1976) The fishery resources of Gambia. Project technical paper no. 1. Project GAM/72/006, FAO, Rome
Scribner KT, Wooten MC, Smith MH, Kenendy PK, Rhodes OEJ (1992) Variation in life history and genetic traits of Hawaiian mosquitofish populations. J Evol Biol 5:267–288
Smith MH, Tolliver D (1987) Blueback herring and the stock concept (abstract). In: Kumpf HE, Vaught RN, Grimes CB, Johnson AG, Nakamura EL (eds) Proceedings of the stock identification workshop (Panama City Beach, Florida, 1985). US Marine and Fisheries Service, Panama City Beach, FL, p 181
Smith PJ (1994) Genetic diversity of marine fisheries resources: possible impacts of fishing. FAO Fish Tech Pap, 344
Sokal RR, Rohlf FJ (1995) Biometry, 2nd edn. Freeman, New York
Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
Tomassone R, Dervin C, Masson JP (1993) Biométrie: modélisation de phénomènes biologiques. Masson, Paris, France
Weir BS, Cockerham CC (1984) Estimating *F*-statistics for the analysis of population structure. Evolution 38:1358–1370
Whitfield AK (1998) Biology and ecology of fishes in southern African estuaries. Ichthyological monographs, no. 2. J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa
Whitfield AK, Elliott M (2002) Fishes as indicators of environmental and ecological changes within estuaries: a review of progress and some suggestions for the future. J Fish Biol 61:229–250
Wright S (1951) The genetical structure of populations. Ann Eugen 15:323–354

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