

## Age and growth of *Anguilla anguilla* in the Camargue lagoons

P. MELIÀ\*†, D. BEVACQUA\*, A. J. CRIVELLI‡, G. A. DE LEO§,  
J. PANFILI¶ AND M. GATTO\*

\*Dipartimento di Elettronica e Informazione, Politecnico di Milano, via Ponzio 34/5, I-20133 Milano, Italy, ‡Station Biologique de la Tour du Valat, Le Sambuc, F-13200 Arles, France, §Dipartimento di Scienze Ambientali, Università degli Studi di Parma, Parco Area delle Scienze 33A, I-43100 Parma, Italy and ¶IRD, BP 1386, Dakar, Sénégal

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Age and total length ( $L_T$ ) data from a 11 year monitoring of the *Anguilla anguilla* eel population of the Camargue lagoons (Rhône delta, southern France) were collected for glass, yellow and silver eels. Three distinct models were calibrated to describe the growth process of undifferentiated eels, females and males, respectively. Uncertainty of parameter estimates was evaluated by bootstrapping. Females were characterized by larger asymptotic body size ( $L_T$ ) than males ( $580 \pm 50$  v.  $388 \pm 13$  mm) and faster growth, whilst the Brody growth coefficient was larger for males than for females (means  $\pm$  s.d.  $3.00 \cdot 10^{-3} \pm 1.68 \cdot 10^{-3}$  v.  $1.73 \cdot 10^{-3} \pm 0.50 \cdot 10^{-3}$ ). Sexual differentiation was estimated to begin at  $204 \pm 38$  mm mean  $\pm$  s.d., i.e. at the end of the second year in the lagoons, well before the  $L_T$  at which macroscopic differentiation became possible (c. 300 mm). Males probably leave the lagoon or die (due to either natural or fishing mortality) within the first 3 years, whilst females can remain up to 5 years. Sexual differentiation and maturation have a major role in shaping the  $L_T$  structure of the population. The  $L_T$  and mass ( $M$ ) data were fitted by allometric curves ( $M = aL_T^b$ ). The calibration of distinct curves for data from different years indicated that the allometric coefficient  $a$  was subject to wider interannual fluctuations than the allometric exponent  $b$ . A negative correlation linked the average  $L_T$  and the allometric exponent ( $r = -0.58$ ,  $P < 0.01$ ).

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Key words: age and size-structured demography; *Anguilla anguilla*; body growth; eel.

### INTRODUCTION

The European eel *Anguilla anguilla* (L.) has long been an important economic resource for fishermen in many Atlantic and Mediterranean coastal areas. The European eel stock, however, has been declining since the early 1970s, with official catches diminishing from >20 000 t in 1968 to c. 7000 t at the end of the 1990s (FIGIS, 2004). Although true catches in the 1990s may be almost twice larger than official data, due to illegal and unreported catches (Moriarty &

†Author to whom correspondence should be addressed. Tel.: +39 02 2399 3680; fax: +39 02 2399 3412; email: melia@elet.polimi.it

Dekker, 1997), there is general agreement that *A. anguilla* are now seriously threatened (Moriarty & Dekker, 1997; EIFAC/ICES, 2003). Therefore, the development of sustainable exploitation strategies and active conservation policies is fundamental for the maintenance of the European eel and other *Anguilla* stocks all over the world (Dekker *et al.*, 2003).

Despite the concern of the scientific community about the fate of European eels, the present knowledge of the stock status is chiefly based on indirect measurements (as total harvests or catches per unit effort). Detailed and time-extensive demographic data are indeed lacking since the mid 1980s, when Vøllestad & Jonsson (1988) published the results of their 13 year monitoring in the Imsa River (south-west Norway). Recent studies have mostly been limited to short-term surveys. This might be due to reduced funding for long-term investigation because the European eel is losing its commercial interest after being heavily exploited.

For this reason, the extensive dataset presented and analysed here is of particular importance. It has been collected during a long-term survey in the Rhône delta lagoons (Camargue, southern France), where the total length ( $L_T$ ) structure of the local population was monitored during 11 years, from 1993 to 2003. A statistical analysis was performed on the data to single out the main features of the population and determine the factors that influence its structure. The dataset was then used to calibrate a growth model that is specifically suited for anguillid populations.

Although a number of studies have been carried out to describe body growth of the European eel since the late 1970s (Rossi & Colombo, 1976*a, b*; Moriarty, 1983; Vøllestad, 1985; Fernández-Delgado *et al.*, 1989; De Leo & Gatto, 1995; Poole & Reynolds, 1996; Svedäng, 1999; Aprahamian, 2000), most of them have been limited to the recording of growth rates. Only few recent studies have led to the formulation or calibration of a growth model. De Leo & Gatto (1995), for instance, calibrated a von Bertalanffy growth model, with parameters differentiated by sex, on data from the intensively exploited European eel population of the Comacchio lagoons (north-east Italy). Poole & Reynolds (1996) calibrated an analogous model on data from an unexploited system at Burrishole (western Ireland). No model, however, has ever accounted for a realistic description of European eel growth before sexual differentiation.

The main features of the European eel's biological cycle are currently rather well-known, at least for its continental phase, but there is still a need for realistic and well tuned demographic models based on large datasets from long-term studies and derived by means of rigorous calibration procedures. Devising reliable growth models is the basis for the development of sound population models. These, in turn, can provide an effective framework for a better understanding of the consequences of different management policies on the long-term demography of the European eel. In the present study, three distinct growth curves were calibrated for undifferentiated, male and female European eels, under the hypothesis that the fish follow the same growth path before sexual differentiation. Non-parametric statistics (bootstrapping) were used to derive probability distributions for parameter estimates and assess their uncertainty.

## MATERIALS AND METHODS

European eels were collected at two sites in the brackish waters of the Rhône delta (Camargue, southern France; Fig. 1): Capelière, in the Vaccarès Lagoon (6400 ha) and Malagroty, in the Impériaux Lagoon (4600 ha). The lagoons are connected to the Mediterranean Sea at Grau de la Fourcade, near Saintes Maries de La Mer, by sluice gates which regulate the water flow to and from the lagoons.

From March 1993 to November 1996, 1808 European eels were caught at Capelière. The fishing device was the capêchade, an eel pot with a 6 mm mesh-size and a 40 m guiding net, called paradière. The  $L_T$  of the fish was measured, and, occasionally, their mass ( $M$ ). From January 1997 to November 2003, 18 300 European eels were caught at Capelière and Malagroty with the same fishing devices. Their  $L_T$ ,  $M$ , sex and stage of sexual maturation (yellow or silver eel) were determined. Fish <300 mm were classified as undifferentiated, whilst longer fish were sexed by gonad inspection. The stage of sexual maturation was determined according to Pankhurst's (1982) ocular index. Otoliths from a sub-sample of 352 individuals caught between October 1997 and September 1998 were used for ageing. For each individual, the whole right and left otoliths were read immersed into rosemary essential oil (in order to enhance the visualization of the growth marks) under a binocular microscope with reflected light against a dark background. Otolith examination was helped by digital image acquisition and the construction of an image data bank. Both otoliths were then read twice by one reader from the core area to the edge and then back to the centre again: opaque zones were read as annual increments. Age estimation was done according to the validated method described in Panfili & Ximénès (1994). Two hundred and ninety one individuals were successfully aged, the otoliths of the others remaining non-interpretable.

Between 1993 and 2003, glass eels were also sampled at different sites in the Vaccarès and Impériaux lagoons with a fry net (with a 0.5 mm mesh-size and a 20 m leading net) and close to Fourcade sluice gates (with a hand-net). A total of 1327 individuals were caught and their  $L_T$  and  $M$  were measured.

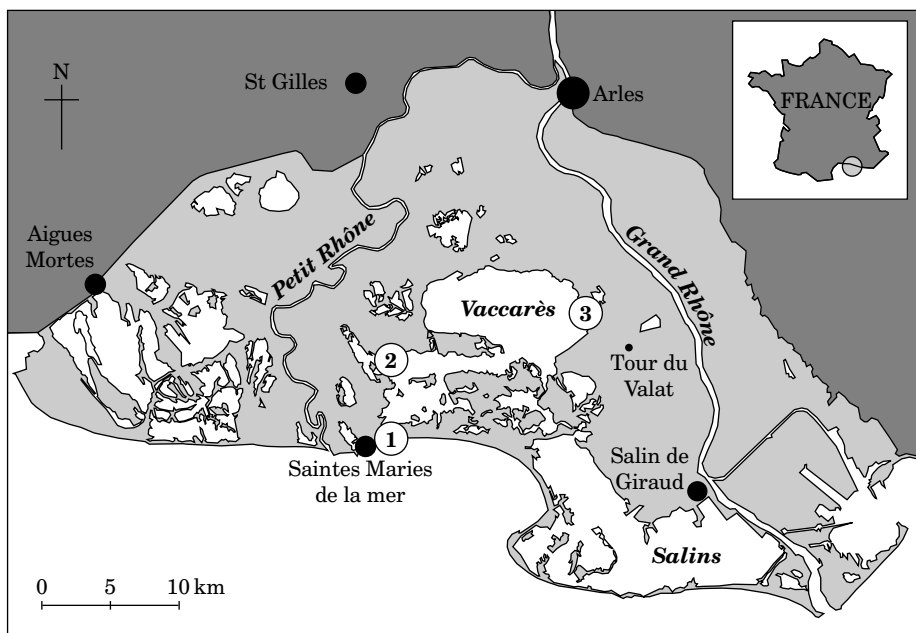


FIG. 1. The Camargue lagoons (1, the position of Fourcade sluice gates; 2, the sampling station at Impériaux; 3, the sampling station at Vaccarès).

## RESULTS

## LENGTH AND AGE STRUCTURE OF THE POPULATION

The basic  $L_T$  statistics of the 1327 glass eels sampled between 1993 and 2003 are given in Table I. The average  $L_T$  varied between 60 and 65 mm. The basic statistics of  $L_T$  data for the 20 108 adult European eels (yellow and silver) caught between 1993 and 2003 at Capelière and Impériaux are given in Table II. The average  $L_T$  of adult fish varied between *c.* 200 and 400 mm. The  $L_T$  structure of the adult population is shown in Fig. 2(a).

To analyse the population structure in more detail, data were divided into groups according to sex and sexual maturation stage. As data collected between 1993 and 1996, however, include only  $L_T$  (not sex and maturation stage), only the 1997–2003 dataset has been considered in the following. The basic  $L_T$  statistics for the different categories considered are given in Table III. Length distributions by sex and maturation categories are shown in Fig. 2(b), (c). Some key features of the  $L_T$  structure are immediately apparent from the histograms: males were rarely >400 mm, whereas female  $L_T$  had a much wider range [Fig. 2(b)]. By maturation stage, the  $L_T$  of yellow eels was rarely >300 mm, whilst the  $L_T$  distribution of silver eels was bimodal, with a lower mode at *c.* 350 mm and a higher mode *c.* 600 mm, corresponding to mature males and females, respectively [Fig. 2(c)]. The age distribution of the sub-set of 291 European eels aged between 1997 and 1998 is shown in Fig. 3(a). The age structure was bimodal, with peaks at one and three annuli. Most European eels underwent sexual maturation after 2 or 3 years of residence in the lagoon [Fig. 3(b)]. Females could remain in the lagoon up to 5 years, whereas no males stayed longer than 3 years. A classification by sexual maturation stage (*i.e.* yellow *v.* silver eels) was not possible because the aged sample comprised only three silver eels.

## TOTAL LENGTH AND MASS

Total length and  $M$  are usually linked by an allometric relationship:  $M = aL_T^b$ , where  $a$  is the intercept and  $b$  the slope coefficient. A  $L_T$  and  $M$  curve was

TABLE I. Basic statistics of total length data (by year) for the 1993–2003 glass eel sample

Year	Number of eels	Mean $\pm$ s.d. (mm)	Minimum (mm)	Maximum (mm)
1993	16	65 $\pm$ 5	58	77
1994	238	62 $\pm$ 4	52	74
1995	34	65 $\pm$ 6	54	91
1996	13	61 $\pm$ 3	57	66
1997	47	60 $\pm$ 4	52	68
1998	258	60 $\pm$ 3	52	69
1999	74	62 $\pm$ 4	54	70
2000	381	61 $\pm$ 3	52	72
2001	8	61 $\pm$ 2	58	63
2002	145	63 $\pm$ 4	53	72
2003	113	63 $\pm$ 3	56	71

TABLE II. Basic statistics of total length data (by year) from the 1993–2003 sample of adult European eels

Year	Number of eels	Mean $\pm$ s.d. (mm)	Minimum (mm)	Maximum (mm)
1993	576	392 $\pm$ 108	102	748
1994	665	294 $\pm$ 182	57	762
1995	282	383 $\pm$ 157	76	784
1996	285	342 $\pm$ 117	138	733
1997	4243	220 $\pm$ 82	68	661
1998	7842	190 $\pm$ 71	60	688
1999	1774	219 $\pm$ 84	73	735
2000	1736	233 $\pm$ 106	64	717
2001	1009	254 $\pm$ 88	80	722
2002	1105	291 $\pm$ 91	75	700
2003	591	287 $\pm$ 99	62	664

calibrated on the entire 1997–2003 dataset and separately on the data of each maturation and sex category. The uncertainty of the parameter estimates was assessed by bootstrapping (Efron, 1979) the original data (1000 iterations for each dataset). Results are given in Table IV. Parameter estimates are significantly different between maturation stages and among sex categories (*t*-test,  $P < 0.01$  for all pair-wise comparisons). Silver eels had the lowest value of *a* and *b*. This was indeed obvious, as they were slimmer because of metamorphosis (gonad development, reduction of the gut and cessation of feeding). The estimates of *a* and *b* for undifferentiated eels were practically identical to those of yellow eels. This is not unexpected, as the majority of yellow eels were undifferentiated. The allometric exponent *b* of females was greater than that of males, whilst *a* was higher for males.

To find out possible interannual variation in allometric parameters, *a* and *b* were estimated for each year from 1993 to 2003 (data from 1993 to 1996 were not used in the preceding analysis due to the lack of data about sex and maturation) (Fig. 4). The coefficient *a* was affected by a considerably higher degree of variability than the allometric exponent *b* [between-year coefficients of variation (CV) were 39 and 2%, respectively]. The two parameters were linked by a conspicuous negative correlation [ $r = -0.95$ ,  $P \ll 0.01$ , see Fig. 4(*a*)]. Also, the allometric exponent correlated negatively with the average  $L_T$  of European eels in the same year [ $r = -0.58$ ,  $P \ll 0.01$ , see Fig. 4(*b*)], which in turn was positively correlated with coefficient *a* ( $r = 0.40$ ,  $P < 0.01$ ).

## GROWTH MODEL

The classical von Bertalanffy (1957) model was used as a basis to describe European eel growth. In its differential form, it links body length to age by means of the following equation:  $dL/dx = k(L_\infty - L)$ , where  $L_\infty$  is the asymptotic mean  $L_T$  and *k* is the Brody growth constant. Due to the strong sexual differentiation of European eels, calibrating a single growth curve would not provide a realistic description of growth. For this reason, previous growth

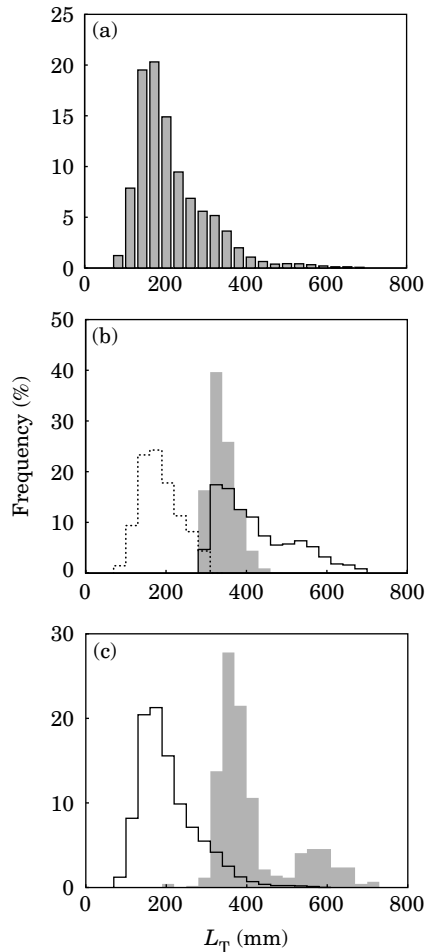


FIG. 2. Total length distribution (30 mm classes) of 18 300 European eels caught between 1997 and 2003 at Vaccarès and Impériaux: (a) entire sample, (b) divided by sex (⋯, undifferentiated; ■, males and □, females) and (c) divided by maturation stage (□, yellow and ■, silver eels). The frequency is relative to total numbers in each class.

models have used different growth curves for females and males (De Leo & Gatto, 1995; Poole & Reynolds, 1996). Since European eels remain sexually undifferentiated for *c.* 2 to 3 years and sex is not genetically determined, a third growth curve was introduced to describe the growth of undifferentiated European eels. All fish were assumed to share the same growth curve until age  $x^*$ , at which sexual differentiation takes place, and then to follow two distinct growth paths according to the sex they have assumed. The equations were as follows:

$$L(x) = L_0 + (L^* - L_0)(1 - e^{-k_U x})(1 - e^{-k_U x^*})^{-1} \text{ for } x \leq x^* \text{ (undifferentiated)} \quad (1)$$

$$L(x) = L_{\infty F} - (L_{\infty F} - L^*)e^{[-k_F(x - x^*)]} \text{ for } x > x^* \text{ (females)} \quad (2)$$

TABLE III. Basic statistics of total length data for the 1997–2003 adult European eel sample

Group	Number of eels	Mean $\pm$ s.d. (mm)	Minimum (mm)	Maximum (mm)
Undifferentiated	15 317	186 $\pm$ 48	60	299
Males	1585	342 $\pm$ 31	300	476
Females	941	423 $\pm$ 95	300	722
Yellow	17 421	208 $\pm$ 77	60	714
Silver	418	416 $\pm$ 96	300	722
Total*	18 300	217 $\pm$ 87	60	735

\* The sex and maturation categories do not add up to 18 300 because sex and maturation stage could not be determined for some fish.

$$L(x) = L_{\infty M} - (L_{\infty M} - L^*)e^{-k_M(x-x^*)} \text{ for } x > x^* \text{ (males)} \quad (3)$$

where  $L_0$  is the  $L_T$  at age zero (which is conventionally set to the age at which glass eels become pigmented and metamorphose to elvers),  $L^* = L(x^*)$  is the  $L_T$  at age  $x^*$ ,  $k_U$ ,  $k_F$ , and  $k_M$  are the Brody growth constants for undifferentiated, female and male European eels, and  $L_{\infty F}$  and  $L_{\infty M}$  are the asymptotic mean  $L_T$  of females and males, respectively. Equation 1 is still a von Bertalanffy curve, albeit written in a slightly unusual form. In fact, this provides the  $L_T$  at sexual

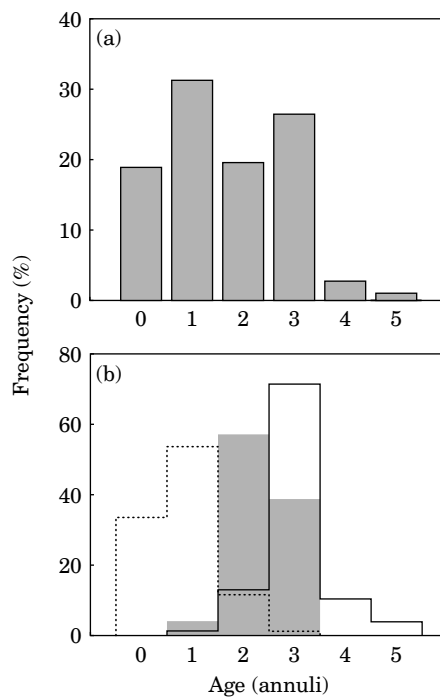


FIG. 3. Age distribution of 291 European eels sampled between 1997 and 1998 at Vaccarès and Impériaux: (a) entire sample and (b) by sex (⋯, undifferentiated; ■, males; □, females). The frequency is relative to total numbers in each class.

TABLE IV. Results of the total length and mass allometric relationships (mean  $\pm$  s.d.) calculated from the 1997–2003 data

Group	Number of eels	$a$	$b$	$\sigma^2_{\text{expl}}$
Undifferentiated	15 311	$2.24 \cdot 10^{-7} \pm 0.06 \cdot 10^{-7}$	$3.37 \pm 0.01$	96
Males	1585	$8.14 \cdot 10^{-7} \pm 2.12 \cdot 10^{-7}$	$3.15 \pm 0.04$	79
Females	940	$5.25 \cdot 10^{-7} \pm 0.72 \cdot 10^{-7}$	$3.22 \pm 0.02$	96
Yellow	17 414	$2.29 \cdot 10^{-7} \pm 0.05 \cdot 10^{-7}$	$3.36 \pm 0.00$	98
Silver	418	$8.43 \cdot 10^{-7} \pm 1.64 \cdot 10^{-7}$	$3.15 \pm 0.03$	95
Total*	18 293	$2.36 \cdot 10^{-7} \pm 0.04 \cdot 10^{-7}$	$3.36 \pm 0.003$	98

$a$  and  $b$ , regression coefficients;  $\sigma^2_{\text{expl}}$ , the per cent of explained variance.

\* Numbers are slightly lower than those reported in Table II because a few eels were not weighed.

differentiation instead of the asymptotic mean  $L_T$  for undifferentiated fish, as this latter parameter would lack any biological meaning (the growth process begins to slow down only when European eels are already differentiated).

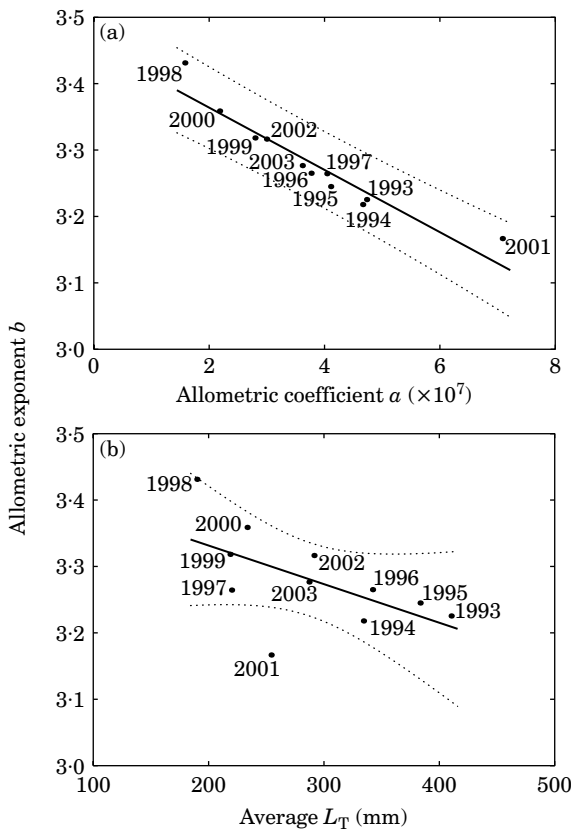


FIG. 4. Interannual variation of the total length and mass relationship between 1993 and 2003. (a) Comparison of the allometric coefficients and (b) comparison of the allometric exponent and mean total length. —, linear regression; . . . . , 95% CI.

Equation 1 can be derived straightforwardly from the equivalent, yet more usual form  $L(x) = L_{\infty U} - (L_{\infty U} - L_0)e^{-k_U x}$ .

The growth model was calibrated with the data from the 291 European eels caught between 1997 and 1998, for which  $L_T$ , age and sex data were available. As data were collected in different years (1997 and 1998) and at different stations (Vaccarès and Impériaux), a three-way ANOVA was performed with respect to fishing station, catch year and sex to verify the homogeneity of the dataset. Results showed that neither spatial location (ANOVA,  $P = 0.12$ ) nor catch year ( $P = 0.21$ ) significantly affected the mean  $L_T$  in 1997–1998, whilst sex had a strong, statistically significant effect ( $P < 0.001$ ).

To perform a rigorous calibration of the growth curves, the number of annuli in the otolith (which is indeed the only age indicator available) must be transformed to a 'true' age (in days). The precise assignment of age to a fish requires the assumption that all European eels recruited in a given year entered the lagoon simultaneously at a given (average) date. As glass eel recruitment in the Camargue usually peaks between March and April, this date was set at 1 April. Then age was calculated as the difference between the day of capture and the day of recruitment plus a number of years equalling the number of annuli counted *via* otolith inspection. The number of annuli in the otolith corresponded to the number of years a European eel had spent in the lagoon.

Equations (1), (2) and (3) have eight unknown parameters ( $L_0$ ,  $x^*$ ,  $L^*$ ,  $k_U$ ,  $k_F$ ,  $k_M$ ,  $L_{\infty F}$  and  $L_{\infty M}$ ), to be estimated from the data. Since the three curves must intersect in a unique point, corresponding to age and  $L_T$  at which sexual differentiation occurs, the calibration of the three curves must be carried out concurrently. The simultaneous estimation of the eight parameters, however, is computationally difficult. Hence, the calibration procedure was split in three sequential steps. First,  $L_0$  was estimated as the average  $L_T$  of glass eels caught between 1997 and 1998. Then,  $L_{\infty F}$  and  $L_{\infty M}$  were estimated by fitting two distinct von Bertalanffy growth curves (for females and males, respectively) to adult European eel data, and discarding the corresponding values of  $k_F$  and  $k_M$ . In fact, asymptotic mean  $L_T$  estimates depend mostly upon  $L_T$  data at older ages, and are likely to be less influenced than Brody coefficients by the values assumed by the other parameters. The optimal values of  $L_{\infty F}$  and  $L_{\infty M}$  were found by minimizing the mean squared error between the logarithms (under the hypothesis of multiplicative error) of observed and predicted age and  $L_T$  data of females and males, respectively. Finally, having fixed the values of  $L_0$ ,  $L_{\infty F}$  and  $L_{\infty M}$ , equations 1, 2 and 3 were fitted on age- $L_T$  data of undifferentiated, female and male European eels (again by minimizing the mean squared error between the logarithms of observed and predicted data) to estimate the remaining five parameters ( $x^*$ ,  $L^*$ ,  $k_U$ ,  $k_F$  and  $k_M$ ).

Age and  $L_T$  at sexual differentiation were estimated from the data; however, European eels  $< 300$  mm had not been sexed due to the impossibility of macroscopically distinguishing males from females. Therefore, to use age and  $L_T$  data of those individuals between  $L^*$  and 300 mm (*i.e.* for which sexual differentiation was supposed to have occurred but could not be detected), the model calibration was performed in the following way: first, the  $L_T$  a European eel would have been if it was a female and if it was a male was estimated on the basis of current parameter values; then, the corresponding prediction errors were

calculated; finally, each error was multiplied by the fraction of individuals of the corresponding sex at differentiation and the overall error was derived as the sum of the two.

The sex ratio at differentiation could not be simply calculated from the overall catch. The corresponding estimate would indeed be biased in favour of females, which mature later and consequently spend a longer time in fresh water compared to males (pers. obs.). As males stay in the Camargue lagoons no longer than 3 years, an unbiased estimate of the sex ratio could be obtained by considering only those European eels that were already sexually differentiated but were <3 years old. The sub-sample of 291 European eels aged between 1997 and 1998, however, contained only 41 individuals satisfying these constraints, too small a number to obtain a significant estimate. Hence, 90% CI for  $L_T$  were calculated from the sub-set of sexually differentiated European eels <3 years (306–530 mm for females and 305–388 mm for males, respectively). Then, all fish with a  $L_T$  within the previously calculated CI were selected from the whole set of 12 085 European eels caught between 1997 and 1998, resulting in 301 females and 467 males. The resulting estimate of the sex ratio at differentiation was skewed in favour of males, *c.* 1 : 1.55. Thus, the corresponding weights used to calculate the prediction error for sexually differentiated eels <300 mm were 0.39 and 0.61 for females and males, respectively.

The uncertainty associated with parameter estimates was assessed by bootstrapping (Efron, 1979; De Leo & Gatto, 1995). During the extraction of the sub-set of European eels to be aged, fish were divided into 25 mm  $L_T$  classes, and an approximately constant number of fish per class (independent of the relative abundance of that class) was aged. Therefore, the bootstrap procedure was stratified (Efron & Tibshirani, 1986) in  $L_T$  classes to follow the original sampling scheme. Original data were resampled 1000 times, generating an empirical probability distribution for each parameter. The basic statistics for the model parameters are given in Table V and Fig. 5 shows the original dataset and the fitted curves. The median values of the parameters' distributions were used instead of the means, as they are much less influenced by extreme values. The correlation matrix of the eight parameters (Table VI) shows some significant correlations

TABLE V. Basic statistics of growth curve parameters (see equations 1, 2 and 3), as obtained by bootstrapping the 1997–1998 dataset

Parameter	Mean $\pm$ s.d.	Median	Percentiles	
			5	95
$L_0$ (mm)	60.0 $\pm$ 0.2	60.0	59.7	60.3
$x^*$ (day)	609 $\pm$ 126	653	317	690
$L^*$ (mm)	204 $\pm$ 38	215	115	240
$k_U$ (day <sup>-1</sup> )	7.18 $10^{-2} \pm 45.5 10^{-2}$	0.10 $10^{-2}$	0.01 $10^{-2}$	19.9 $10^{-2}$
$L_{\infty F}$ (mm)	580 $\pm$ 50	573	511	668
$k_F$ (day <sup>-1</sup> )	1.73 $10^{-3} \pm 0.50 10^{-3}$	1.66 $10^{-3}$	1.11 $10^{-3}$	2.66 $10^{-3}$
$L_{\infty M}$ (mm)	388 $\pm$ 13	386	370	410
$k_M$ (day <sup>-1</sup> )	3.00 $10^{-3} \pm 1.68 10^{-3}$	3.05 $10^{-3}$	1.66 $10^{-3}$	4.65 $10^{-3}$

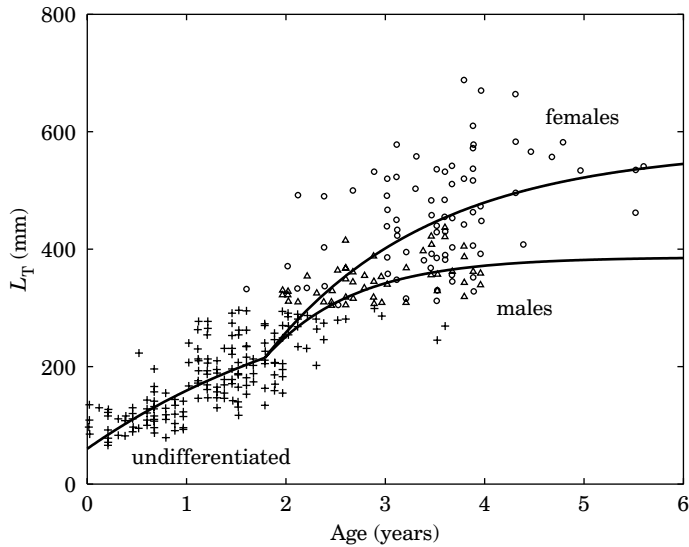


FIG. 5. Median growth curves of undifferentiated (+), female (o) and male ( $\Delta$ ) European eels.

between parameter estimates. In particular, there was a negative correlation between the Brody coefficients and  $L_T$  at differentiation and  $L_\infty$  for sexually undifferentiated and differentiated European eels, respectively [Fig. 6(a)]. Age  $x^*$  and length  $L^*$  at sexual differentiation were also clearly correlated although positively [Fig. 6(b)].

## DISCUSSION

European eels reach the Camargue lagoons as glass eels, with an average  $L_T$  of *c.* 60–65 mm, and then become elvers at *c.* 65–75 mm. They undergo sexual differentiation after *c.* 2 years, and become sexually mature after 2 to 3 years of residence in the lagoons. Sexual differentiation and maturation have a major role in shaping the length structure of the population. Males are likely to leave the

TABLE VI. Correlation matrix of the eight parameter estimates (see equations 1, 2 and 3)

	$L_0$	$x^*$	$L^*$	$k_U$	$L_{\infty F}$	$k_F$	$L_{\infty M}$	$k_M$
$L_0$								
$x^*$	0.045							
$L^*$	0.046	0.973**						
$k_U$	0.136	-0.356**	-0.364**					
$L_{\infty F}$	-0.072	0.138	0.125	-0.087				
$k_F$	0.058	0.295**	0.284**	-0.065	-0.726**			
$L_{\infty M}$	0.087	-0.008	0.008	0.080	-0.128	0.047		
$k_M$	-0.007	0.563**	0.467**	-0.186	0.278**	0.064	-0.554**	

\*\* $, P < 0.01$ .

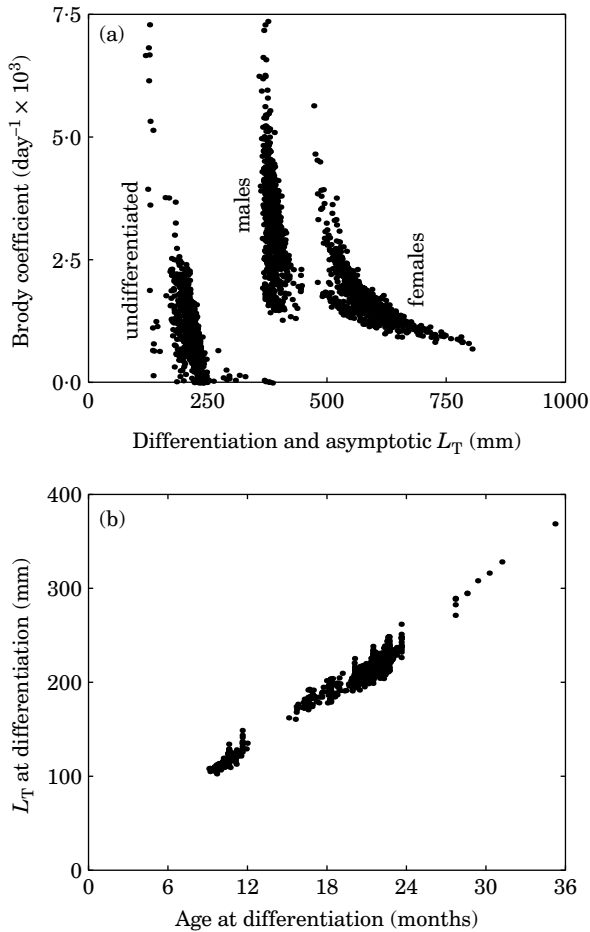


FIG. 6. Bootstrap distribution (●, bootstrap replicate) of body growth parameters from the 1997–1998 dataset. (a) Total length at differentiation and asymptotic total lengths (for sexually undifferentiated and differentiated European eels, respectively) and the Brody coefficient and (b) age and total length at sexual differentiation.

lagoons or die (due to either natural or fishing mortality) within the first 3 years, whilst females can remain up to 5 years. These are rather short times compared to those observed by De Leo & Gatto (1995) at Comacchio (up to 8 years for males and 15 years for females), and much shorter than those recorded by Poole & Reynolds (1996) at Burrishole (up to 33 and 57 years for males and females respectively). In addition to geographical variation, a major cause of this large difference is probably due to the different management of these populations: whilst yellow eels are intensively fished in the Camargue, only migrating silver eels are caught at Comacchio and Burrishole.

Total length and mass data were very well fitted by allometric curves. The calibration of distinct curves for data from different years indicates that the allometric coefficient  $a$  is subject to wider interannual fluctuations than the allometric exponent  $b$ . A negative correlation linked the average  $L_T$  and  $b$ .

This is possibly due to differences in the composition of the catch: samples with higher average  $L_T$  probably comprised a higher fraction of sexually mature European eels, which were characterized by lower values of  $b$ .

The  $L_T$  structures at Vaccarès and Impériaux were not significantly different during 1997–1998, thus allowing the aggregation of age and  $L_T$  data over space and time to calibrate the growth model. Had the  $L_T$  structures at the two study sites remained similar also over the whole study period, and had there been significant interannual variations of  $L_T$ ? A three-way ANOVA was performed on the 1997–2003 dataset (no data were recorded at Impériaux before 1997). Results confirmed that sex was the factor with the strongest influence ( $P < 0.001$ ) but revealed that both fishing station ( $P < 0.001$ ) and catch year ( $P < 0.001$ ) had a significant effect on  $L_T$ .

The model proposed here provides a realistic description of the growth process of the European eel, which is characterized by strong sexual differentiation and delayed sex determination. The introduction of a growth curve for undifferentiated eels overcomes a major drawback of earlier growth models (De Leo & Gatto, 1995; Poole & Reynolds, 1996) in which the growth paths of males and females were differentiated from the early developmental stages. As in many other fish species (Parker, 1992) females grow faster than males (as can be noted by comparing the slopes of the growth curves in Fig. 5) and become larger, as their asymptotic body size was *c.* 50% higher than that of males (Table V; Poole & Reynolds, 1996). Data suggest that growth is more variable in females than in males (compare the dispersion of the observed data around the median growth curves). The higher variability in female growth is reflected in the uncertainty of parameter estimates, and in particular the asymptotic body size (coefficient of variation 9 and 3% for females and males, respectively). The parameter affected by the highest uncertainty was  $k_U$ , the Brody coefficient of undifferentiated fish. In fact, a von Bertalanffy curve was used to describe their growth mainly for the sake of consistency with the curves for differentiated fish. A linear approximation, however, would have performed equally well, because from the data there was no evidence of a slowing down of the growth process before sexes differentiate. Sexual differentiation occurs at *c.* 21 months [Fig. 6(b)]. Total length at differentiation was between 210 and 220 mm, which is less than the  $L_T$  at which macroscopic differentiation became possible (300 mm). Colombo & Grandi (1996), however, revealed that European eels <200 mm are also undifferentiated histologically, whilst the formation of the early Syrski organ (a small testis initially containing both male and female germ cells) begins between 200 and 220 mm.

The model proposed here can be used as a powerful tool to describe the growth process of anguillids and (combined with information about recruitment, mortality and migration rates), to provide a robust basis for the development of reliable demographic models of eel populations. It can be applied to other eel populations, provided that sufficient length, age and sex data are available. As the number of parameters to be estimated is rather high, the number could be reduced by fixing some of them *a priori*. This should be done with extreme caution, however, because of the high plasticity of anguillid body growth (De Leo & Gatto, 1995). Eel growth is indeed controlled by ecological factors, such as food availability and water temperature (Panfili *et al.*, 1994), and might also

be influenced by demographic factors such as population size (Moriarty, 1973). Aprahamian (2000), however, found no significant relationships between growth rate and European eel density or biomass at 15 sites in England. Length at sexual differentiation  $L^*$  probably varies less than other parameters, but age at sexual differentiation  $x^*$  could vary from one population to another due to different environmental conditions. It is indeed likely that the actual trigger for sexual maturation is associated with a critical body size rather than a given age. Asymptotic length can vary as well from site to site. De Leo & Gatto (1995) obtained higher values for both  $L_{\infty F}$  ( $762 \pm 14$  mm) and  $L_{\infty M}$  ( $418 \pm 23$  mm) of the Comacchio eel population. Poole & Reynolds (1996) reported even higher ranges for  $L_{\infty F}$  (varying between 1433 and 1507 mm) and  $L_{\infty M}$  (659–700 mm) at Burrishole. Estimates of the Brody growth constant are even more variable: De Leo & Gatto (1995) report  $k_F = 0.23 \pm 0.01 \text{ year}^{-1}$  ( $6.30 \cdot 10^{-4} \pm 0.27 \cdot 10^{-4} \text{ day}^{-1}$ ) and  $k_M = 0.35 \pm 0.056 \text{ year}^{-1}$  ( $9.59 \cdot 10^{-4} \pm 1.53 \cdot 10^{-4} \text{ day}^{-1}$ ), whilst Poole & Reynolds estimated  $k_F = 0.013 \text{ year}^{-1}$  ( $3.56 \cdot 10^{-5} \text{ day}^{-1}$ ) and  $k_M = 0.031\text{--}0.036 \text{ year}^{-1}$  ( $8.49 \cdot 10^{-5}\text{--}9.86 \cdot 10^{-5} \text{ day}^{-1}$ ). A direct comparison of these values, however, is not possible, as previous models did not contemplate a distinct growth curve for undifferentiated European eels. Length at recruitment  $L_0$  can also vary, depending upon the time glass eels need to reach their habitat. Vøllestad & Jonsson (1988) reported an average  $L_T$  of glass eels of  $75 \pm 8$  mm, and Poole & Reynolds (1996) found a similar figure (72 mm).

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