

A simplified method to estimate body growth parameters of the European eel *Anguilla anguilla*

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Providing an accurate description of body growth patterns is crucial to build realistic demographic models, as body size is a primary determinant of most vital rates (Brown *et al.*, 2004). This is particularly challenging in freshwater anguillids, like the European eel *Anguilla anguilla* (L. 1758), which are characterized by large variation of body size among individuals and across spatial scales (Vøllestad, 1992; Panfili *et al.*, 1994; De Leo & Gatto, 1995; Melià *et al.*, 2006a, b). Furthermore, sex differentiation is delayed in *A. anguilla* as most individuals go through a transitory intersexual stage where gonads contain both male and female structures (Colombo *et al.*, 1984; Colombo & Grandi, 1996; Devlin & Nagahama, 2002; Geffroy *et al.*, 2013). Females grow much larger than males, the latter never growing beyond 45 cm (Durif *et al.*, 2005). A common practice to account for sex dimorphism in anguillid body growth is to derive separate von Bertalanffy growth curves for females and males (De Leo & Gatto, 1995; Poole & Reynolds, 1996; Lin & Tzeng, 2010). This approach, however, is not adapted to species with delayed sex differentiation and makes it difficult to use age–length data from juvenile anguillids appropriately. Data from such individuals cannot be used to calibrate either of the two curves, male or female. Many *A. anguilla* below 20 cm in total length (L_T) are still sexually undifferentiated (Colombo & Grandi, 1996; Geffroy *et al.*, 2013), and even if sex differentiation has already taken place, it is still undetectable macroscopically. Histological sex determination, which is

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required for eels measuring between 20 and 30 cm, is expensive and time consuming. For this reason, separate estimates of body growth parameters for females and males may be biased owing to incomplete covering of the whole length–age range. Melià *et al.* (2006a, b) proposed a modified von Bertalanffy growth model that explicitly considers a unique body growth curve during the sexually undifferentiated phase, with a subsequent splitting into two curves, one for males and the other for females.

The original formulation of Melià *et al.*'s (2006a) model is the following:

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

$$L_T(x) = L_{\infty F} - (L_{\infty F} - L^*) e^{-k_F(x-x^*)} \quad \text{for } x > x^* \quad (\text{females}) \quad (1b)$$

$$L_T(x) = L_{\infty M} - (L_{\infty M} - L^*) e^{-k_M(x-x^*)} \quad \text{for } x > x^* \quad (\text{males}), \quad (1c)$$

where L_0 is L_T at age 0 (conventionally, the age at metamorphosis from glass eel to sexually undifferentiated yellow eel); x^* and L^* are age and L_T at sex differentiation; k_U , k_F and k_M are the Brody growth constants for undifferentiated, female and male *A. anguilla*; and $L_{\infty F}$ and $L_{\infty M}$ are the asymptotic mean L_T of females and males, respectively. Equation 1a, which is written in a form that points out L_T at sexual differentiation instead of the asymptotic mean L_T (the latter parameter lacks a biological meaning in the case of undifferentiated *A. anguilla*), can also be written in a classical von Bertalanffy form as $L_T(x) = L_{\infty U} - (L_{\infty U} - L_0) e^{-k_U x}$.

Although Melià *et al.*'s (2006a) model can be calibrated on the basis of age–length data by means of standard non-linear fitting techniques, it is not included in commercial software packages for fishery statistics and, possibly for this reason, it has never been used to derive body growth curves from stocks other than those to which it was originally applied by the authors (Melià *et al.*, 2006b). Also, a reliable estimation of the parameters of this model requires that the whole age–length range of the considered stock is well represented in the sample. Morphometric and age data, however, are less frequently recorded for juvenile *A. anguilla* than for silver eels, making the calibration of the model difficult or even impossible.

The aim of this work was to derive simple relationships to estimate the parameters of Melià *et al.*'s (2006a) model (L_0 , x^* , L^* , k_U , k_F , k_M , $L_{\infty F}$ and $L_{\infty M}$) that could be applied to data-poor cases where site-specific age–length data are available only for silver eels. The following simplifying hypotheses were made: (1) that both the age and body size ranges can be linearly rescaled to fit body growth patterns from different sites and (2) that scaling coefficients can be simply derived on the basis of L_T and age of silver eels. To rescale the body size range, it was assumed that L^* and L_{∞} are proportional to the average L_T of silver eels λ . To rescale the age range, it was assumed that x^* is proportional to the average age of silver eels ξ and that the Brody coefficients k are proportional to $(x^*)^{-1}$ for undifferentiated *A. anguilla* and ξ^{-1} for sexually differentiated *A. anguilla*. The latter hypothesis appears reasonable provided that body growth does not deviate too much from linearity.

To test the robustness of these assumptions and derive estimates of proportionality coefficients, data from six *A. anguilla* stocks were used. Three datasets were previously used by Melià *et al.* (2006b) to compare body growth of *A. anguilla* in three

TABLE I. Body growth parameters [median values obtained by the calibration procedure described in Melià *et al.* (2006a)] of six *Anguilla anguilla* stocks.

Parameter	Vaccarès	Fumemorte	Comacchio	Loire	Burrishoole	Irish rivers*
L_0 (cm)†	7.00	7.00	7.00	7.00	7.00	7.00
x^* (year)	1.79	2.16	1.02	1.57	5.74	4.38
L^* (cm)‡	21.50	21.50	21.50	21.50	21.50	21.50
k_U (year ⁻¹)	0.15	1.21	4.67	0.42	0.023	0.024
$L_{\infty F}$ (cm)	56.96	52.35	54.84	81.55	59.88	66.36
k_F (year ⁻¹)	0.65	0.35	0.44	0.13	0.07	0.16
$L_{\infty M}$ (cm)	38.78	39.50	43.00	38.98	36.70	38.14
k_M (year ⁻¹)	1.15	0.64	0.80	0.82	0.23	0.30
λ_F (cm)	55.40	58.61	54.25	73.13	54.16	60.09
λ_M (cm)	38.27	37.77	42.55	39.19	36.96	37.03
ξ_F (year)	4.08	5.75	8.29	14.93	29.61	17.00
ξ_M (year)	2.96	3.17	6.49	7.23	19.6	13.72
$\bar{\xi}$ (year)§	3.52	4.46	7.39	11.08	24.605	15.36

*River Shannon, River Corrib, River Garavogue and River Moy.

† L_0 was set *a priori* to 7.0 cm for all stocks (according to Daverat *et al.*, 2012).

‡ L^* was set *a priori* to 21.5 cm (according to Colombo & Grandi, 1996; Melià *et al.*, 2006b).

§ $\bar{\xi}$ is the average value of ξ (age of silver eels) for females and males.

Mediterranean sites (two in the Camargue lagoons, in southern France, and one in the Comacchio lagoons, in north-east Italy). Age estimation of French samples was performed by reading whole otoliths (Melià *et al.*, 2006a; Panfili *et al.*, 2012), whereas otoliths of Italian samples were read after grinding (Carrieri *et al.*, 1992). Three other datasets were selected from Atlantic sites to ensure a wider coverage of the distribution range of the species. The first (656 individuals, including 40 undifferentiated *A. anguilla*, 492 females and 124 males) was collected in the Loire River (France) between 1994 and 2002 [data partly published in Durif *et al.* (2005)]. Otoliths were ground (after embedding in synthetic resin), etched using 10% EDTA for 15 min and stained with 5% toluidine blue. The second (691 individuals, 47 undifferentiated *A. anguilla*, 418 females and 226 males) was collected in the Burrishoole catchment (north-west Ireland) between 1986 and 2005 [data partly published in Poole & Reynolds (1996)]. Age was determined *via* cutting and burning (Graynoth, 1999), a refinement of the traditional burn and crack method (Moriarty, 1973). The last one (66 individuals, 13 undifferentiated *A. anguilla*, 32 females and 21 males) was collected in different sites of four Irish rivers in 2003 [River Shannon, River Corrib, River Garavogue and River Moy; data taken from Arai *et al.* (2006)]. Otolith reading was performed after etching with 1% HCl for 60 s and staining with 1% toluidine blue (Arai *et al.*, 2006).

Melià *et al.*'s (2006a) model was calibrated on all datasets, and the resulting estimates of body growth parameters (Table I) were used to analyse the relationship linking those parameters and L_T and age of silver eels. Results are summarized in Fig. 1. The link between L_{∞} and λ and between k and ξ^{-1} (for which estimates are distinct for females and males) was tested *via* ANCOVA and, where no differences between sexes were detected, *via* linear regression. Parameter x^* , which is common to both sexes (it

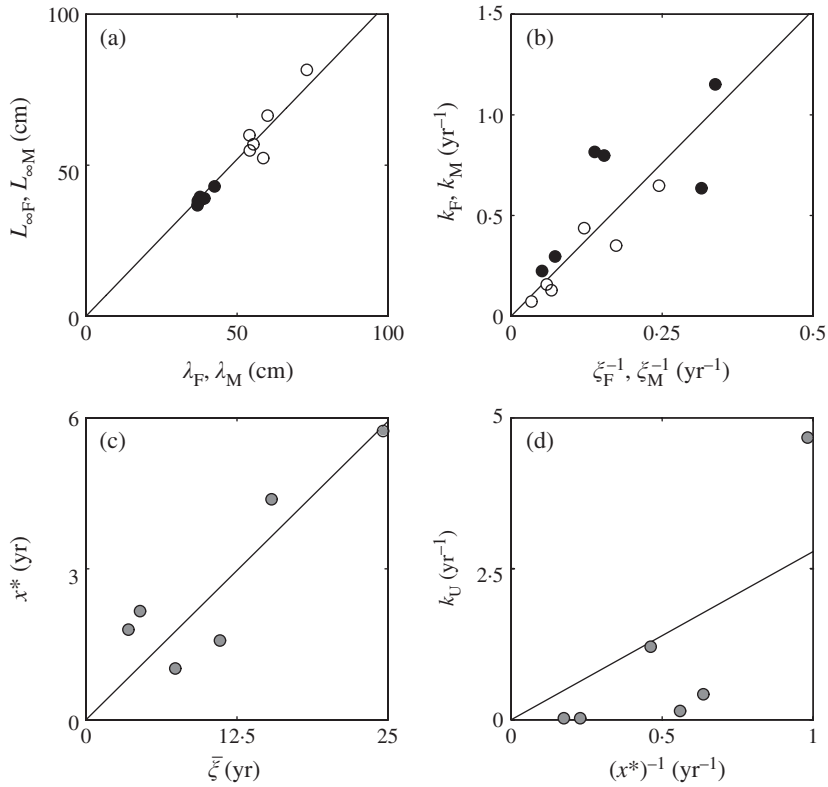


FIG. 1. Regressions linking body growth parameters of *Anguilla anguilla* from different Mediterranean and Atlantic locations. (a) Asymptotic L_T v. body length of silver eels (○, females and ●, males; $y = 1.04x$), (b) Brody coefficient v. inverse of silver eel age (○, females and ●, males; $y = 3.04x$), (c) age at sexual differentiation (●, average between sexes) v. silver eel age ($y = 0.24x$) and (d) Brody coefficient v. inverse of age at sexual differentiation (●, undifferentiated eels; $y = 2.79x$).

defines, together with L^* , the point at which the three parts of the modified von Bertalanffy curve join together), was contrasted with the average value of ξ for females and males, whereas parameter k for undifferentiated *A. anguilla* was contrasted with the reciprocal of age at sex differentiation, $(x^*)^{-1}$. ANCOVA of L_{∞} with sex as a factor and λ as a covariate revealed no significant differences in slope ($F_{1,8} = 0.23$, $P > 0.05$) and intercept ($F_{1,9} = 0.73$, $P > 0.05$) between females and males; the linear regression of L_{∞} against λ held a non-significant intercept ($t = -1.17$, $P > 0.05$) but a significant slope equal to 1.04 ($t = 50.07$, $P < 0.001$). ANCOVA of k with sex as a factor and ξ^{-1} as a covariate revealed no significant differences in slope ($F_{1,8} = 0.11$, $P > 0.05$) and intercept ($F_{1,9} = 3.78$, $P > 0.05$) between females and males; the linear regression between k and ξ^{-1} had a non-significant intercept ($t = 0.85$, $P > 0.05$) but a significant slope equal to 3.04 ($t = 9.27$, $P < 0.001$). In the linear regressions between x^* and ξ and between k_U and $(x^*)^{-1}$, intercepts were always non-significant ($t = 0.68$, $P > 0.05$ and $t = -1.50$, $P > 0.05$, respectively), where the slopes were significant and equal to 0.24 ($t = 8.26$, $P < 0.001$) for x^* against ξ , and 2.79 ($t = 3.07$, $P < 0.05$) for k_U against $(x^*)^{-1}$.

TABLE II. Pearson’s correlation between observed age–length data and predictions obtained with Melià *et al.*’s (2006a) model (1) with parameters calibrated on the relevant dataset and (2) with parameters derived from equation 2. All correlations were highly significant ($P < 0.001$)

Model	Vaccarès	Fumemorte	Comacchio	Loire	Burrishoole	Irish rivers
Calibrated	0.80	0.79	0.91	0.80	0.75	0.83
Simplified	0.78	0.79	0.96	0.80	0.73	0.82

In synthesis, the following proportionality relationships between λ and ξ and the parameters of Melià *et al.*’s (2006a) model are proposed:

$$\begin{aligned}
 x^* &= 0.24\bar{\xi} \\
 L_{\infty F} &= 1.04\lambda_F \\
 L_{\infty M} &= 1.04\lambda_M \\
 k_U &= 2.79(x^*)^{-1} \\
 k_F &= 3.04\xi_F^{-1} \\
 k_M &= 3.04\xi_M^{-1},
 \end{aligned} \tag{2}$$

where subscripts U, F and M indicate sex (undifferentiated, female and male *A. anguilla*), while $\bar{\xi}$ is the average value of ξ for females and males. The relationship linking parameters k_U and x^* is subject to the largest uncertainty [Fig. 1(d)]. In principle, this might be caused by a violation of the assumption of proportionality between k_U and $(x^*)^{-1}$; however, the growth of undifferentiated *A. anguilla* is usually very close to linear (while it is not for sexually differentiated *A. anguilla*, for which, in contrast, the relationship provides a quite good fit). Therefore, the cause of the poor fit is most likely the large variation in the estimates of these two parameters (Melià *et al.*, 2006b). The different methods used to estimate age in different samples represent another possible source of uncertainty (ICES, 2009), although for this exercise it is not thought to be a problem. The relatively small number of datasets used in the analysis (owing to the scarcity of samples covering sufficiently wide ranges of L_T and age) is another factor that may reduce the robustness of the results. Despite the simplifications introduced by the proposed relationships and the limits of the analysis, Table II shows that the fitting performances (Pearson’s correlation between observed data and model predictions) of the model with parameters rigorously calibrated on the full age–length dataset and those of the corresponding model with parameters derived from L_T and age of silver eels only (*via* equation 2) are almost equivalent.

Environmental variables such as temperature and salinity can explain a large part of observed body growth variation over large geographic scales (Daverat *et al.*, 2012). The generalization of Melià *et al.*’s (2006a) model presented here is not intended to provide insight into the relationships linking body growth parameters of *A. anguilla* and environmental variables. The effect of environmental variables may be mediated by reaction norms that may have differential consequences on body size and biological

times, violating the assumption that the link between age and L_T does not significantly change across sites and developmental stages. Anthropogenic factors, such as fishing, may also affect body growth patterns by exerting different selective pressures in different environments (Bevacqua *et al.*, 2012). All these points are crucial to a deeper understanding of anguillid biology and worth further investigation, but are outside the scope of this work. Instead, the purpose of this method is to provide a rapid and easy-to-use way to apply Melià *et al.*'s (2006a) model when data do not cover a sufficiently wide age–length range to derive reliable curves for the two sexes. It allows a preliminary estimation of model parameters on occasions in which there is little time and resources to perform a complete calibration of the model. The availability of a body growth model, even if not subject to a rigorous calibration procedure, is critical for a realistic description of other size-dependent life-history traits, such as sexual maturation (Bevacqua *et al.*, 2006) or natural and fishing mortality (Bevacqua *et al.*, 2009, 2011). Such a model constitutes a preliminary, yet fundamental step for the development of demographic models, which in turn are urgently required to test and design effective plans for the conservation management of *A. anguilla*.

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