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One century of eel growth: changes and implications

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Abstract – A cooperative effort gathered a large European length-at-age data set (N = 45,759, Lat. 36S–61N Long. 10W–27E) for *Anguilla anguilla*, covering one century. To assess the effect of global warming during the last century and habitat effects on growth, a model was fitted on the data representing the conditions met at the distribution area scale. Two GLMs were designed to predict eel log(GR): one model was fitted to the whole data and the other was fitted to the female data subset. A model selection procedure was applied to select the best predictors among sex, age class, five temperature parameters and six habitat parameters (depth, salinity and four variables related to the position in the catchment). The yearly sum of temperatures above 13 °C (TempSUP13), the relative distance within the catchment, sex, age class, salinity class and depth class were finally selected. The best model predicted eel log(GR) with a 64.46% accuracy for the whole data and 66.91% for the female eel data. Growth rate (GR) was greater in habitats close to the sea and in deep habitats. TempSUP13 variable had one of the greatest predictive powers in the model, showing that global warming had affected eel growth during the last century.

Key words: European eel; growth; otolith; habitat; temperature

Introduction

The European eel (*Anguilla anguilla* (L.)) has a large distribution area during its growth phase throughout Europe and the Mediterranean coast of Africa (Schmidt 1909; Dekker 2003a,b). Since the early 20th century (Gemzøe 1908), eel growth patterns are investigated, based on age estimation derived from seasonal marks on otolith and scales. The deposition of annual rings in eel otoliths was validated (Mounaix 1991; Meunier 1994; Poole & Reynolds 1996a), ensuring that the use of otoliths for age estimation is reliable. While the validity of the different methods of eel ageing was debated with passion, recent work showed that the two main otolith preparation methods in use were consistent with each other (ICES 2009). Despite some reviews of variability of eel growth (Berg 1990; Fontenelle 1991), to our knowledge, no global model of eel growth was published at the scale of the distribution area. The investigation of eel age and length at maturation (silver) for both sexes revealed that length at silvering was less variable than age (Vøllestad 1992; Jessop 2010). These results also showed that growth was highly variable across the area of distribution and correlated with latitude.

Growth is a key parameter in population dynamics. Along with other processes, growth has implications on the lifetime mortality of fish by modulating the time

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taken to reach maturity. Growth also conditions the reproductive success by affecting size at reproduction and fecundity (Rose et al. 2001). Animal species with distribution areas encompassing a wide range of latitudes, such as mammals and birds (Meiri & Dayan 2003) and fish (Campana et al. 1996; Frisk & Miller 2006), exhibit geographical variations in their growth traits. These latitudinal variations in growth of fish can be attributed to temperature, which has a major influence on variations in fish growth (Brett 1979), and to other factors related to environment (e.g., hydrology and food availability) or to the individual fish traits (sex and genetics).

The effect of temperature on eel growth is well known in aquaculture (Dosoretz & Degani 1987; Holmgren 1996; Ciccotti & Fontenelle 2001), where eels are reared at an optimal temperature of 23–25 °C. It was also demonstrated that eel growth in culture ceased under a temperature of 12 °C (Sadler 1979). It is likely that global warming has also affected eels' habitats over the last century. Temperature has already increased by 2 °C in a century, and projections of climate in Europe predict an increase of 1.4–5.8 °C of the temperatures within 50 years (IPCC 2001). Contradictory to many cold water fish species, eel growth rates (GRs) would benefit from this temperature increase (Reist et al. 2006).

Other habitat parameters, together with temperature, may potentially affect growth dynamics of eels. Salinity was found to have a positive effect on eel growth (Boeuf & Payan 2001; Edeline & Elie 2004). In Mediterranean sites, it was shown that growth is faster in brackish sites than in freshwater sites in the vicinity (Panfili et al. 1994). Field observations showed that low pH oligotrophic habitats contain slower growing eels (Moriarty 1979; Poole et al. 1992; Poole & Reynolds 1998) than more trophic habitats in the same region (Moriarty 1983). Likewise, GRs and body condition near the estuary are often higher than in the upper reaches of a river catchment (Daverat et al. 2006; Lasne et al. 2008). In a previous study (Lamaison et al. 2006), the variability of eel growth was investigated along the single Garonne catchment gradient based on the analysis of 850 individual length-at-age data. The resulting model identified salinity, depth, distance to the sea and presence of tide as significant habitat parameters affecting eel growth.

In addition, there has been a dramatic decline in recruitment of European eel, *A. anguilla* (L.), across most of Europe since the early 1980s (Dekker 2003a,b; ICES 2006). The causes of this decline are probably multiple and complex and may include a combination of oceanic factors (Castonguay et al. 1994; Friedland et al. 2007) and continental factors such as fishing, obstructions to migration and turbines, pollution, diseases and parasites (ICES 2005). The reduction in eel recruitment may have directly affected the density of local populations and thus indirectly (through competition) the growth dynamics and sex ratios of eels.

The objective of the present analysis was to identify the influence of temperature and habitat characteristics on the variability of eel growth at the scale of its distribution range, throughout the last century, and discuss the results in relation to climate change and eel management.

Material and methods

Selection of the data

Data were collated from literature and unpublished sources containing individual yellow European eel terminal length (mm) at age (year) data from 1900 to 2006, estimated from otoliths readings with a precision of 10 mm for length and 1 year for the age. The heterogeneous nature of the data, collected from different collection methods and strategies and different age readers, was a potential source of bias. Nevertheless, we made the hypothesis that these sources of bias would be small enough to detect a significant length–age relationship. A strict selection of the data was made to overcome other sources of bias. Data derived from the reading of scales were not included because of the unreliability of the method (Ehrenbaum & Marukawa 1913). Annual deposition of rings in otoliths was validated for eels (Meunier 1994; Mounaix & Fontenelle 1994; Poole & Reynolds 1996b). Three methods of eel age estimation have been recognised to be accurate and precise, so that we have chosen data using these three corresponding methods: burning and cracking, etching and dying, and *in toto* reading of whole otoliths (Panfili et al. 2002); however, *in toto* has limited use for eels under 5 years of age (ICES 2009). *In toto* clearing of whole otoliths underestimates the age of eels older than 5 years. In the present work, only individual lengths at age estimated from in toto under 5 years of age were retained, and the otolith preparation method was recorded but not included in the analysis as a parameter (Panfili et al. 2002). An age of 0 years was attributed to glass eels, so that only the continental age was considered here, and this age corresponds to an initial length (L_i) of 70 mm. Data originated from restocking programs or aquaculture experiments were not included in the present study, and growth data determined from silver eels were not included either, because at this stage growth has ceased and the habitat that the silver eels would have originated from was not always known. The data were classified by sex (female, male or undifferentiated). The 61 different sources of data, extensively reported in the Appendix S1, were mainly literature articles (1913–2006), some unpublished data from the authors and data gathered by the joint EIFAC/ICES Working Group on eels (WGEEL) in 1990 (Willem Dekker, pers. comm.). The data set was split into two subsets: two-thirds of the data were randomly assigned to a training data set while the rest (one third) of the data were assigned to a validation data set.

Parameters explored

The choice of variables to be included in the various growth models was influenced by previous work performed on eel growth (Aprahamian 2000; Melià et al. 2006) and eel ecology (Daverat & Tomas 2006; Imbert et al. 2008). Parameters were recorded to describe the data or to calculate variables to be included in the models. In addition to the length at age, the sex, physical habitat characteristics and year of sampling were recorded.

Physical habitat characteristics

Habitat was described with the geographical position (latitude and longitude), temperature, salinity (units or class variable), depth (units or class variable), the distance to the sea along the river course and the total river length. Wikipedia (http://fr.wikipedia.org/, 2006) provided the missing river lengths, and Google earth (http://earth.google.fr/index.html) provided the missing longitude and latitude. Because of poor precision of the values, salinity (brackish or freshwater) and water depth (≤ 1 or >1 m) were set as class variables with two levels and were further tested as variables in the growth models. The position of the eel habitat along the river course was recorded. Four positional variables were tested in the models, the distance to the sea, the distance to the source of the river, the total river length and a fourth variable named ‘Relative distance’. ‘Relative distance’ was calculated by dividing the distance to the sea of the site by the total river length. ‘Relative distance’ was more likely to explain the gradient of habitats along a catchment and to allow comparison between sites of different catchment dimensions than the distance to sea alone (Imbert et al. 2008).

Global warming effect, latitude and period of time

Air temperature was used as a proxy for water temperature effect on eel growth (Erickson & Stefan 2000). To correctly assess the effect of temperature and warming that had occurred during the period covered by the samples (1900–2006), we used the age of each fish and its corresponding date and location of capture to reconstruct individual lifespan monthly temperature series extracted from CRU TS 2.1 data set (Mitchell & Jones 2005). CRU TS 2.1 data set (Mitchell & Jones 2005) comprises 1224 monthly grids of observed air temperature (from local weather stations), for the period 1901–2002, and covers the global land surface at 0.5 degree resolution. For eels killed after 2002, mean monthly air temperatures series from local weather stations were used. Consequently, five temperature variables were tested in the growth model. The first variable was the mean temperature, and the four other temperature variables tested, named ‘TempSUP10’, ‘TempSUP11’, ‘TempSUP12’ and ‘TempSUP13’, similarly to growing degree days, were calculated as the yearly average of sum of temperatures above respectively, 10, 11, 12 and 13 °C experienced by each individual fish.

An age class effect (intervals of 1 year) was introduced in the model as a parameter to account for population demography and for individual growth trajectories. Individual GR will tend to decrease as the eel is getting older. In addition, fast growing eels have a higher probability of maturing earlier in age than slow growing eels and then migrate from their habitat earlier (Vøllestad 1992), thereby implying that the older eels were the slower growers.(Vøllestad 1992). The consequence of fast growing eels leaving the population is the decrease in the population mean GR at the older ages.

Altogether, 13 variables were tested in the candidate growth models: distance to the sea; distance to the source; distance to the sea + distance to the source; relative distance; class of salinity; class of depth; mean temperature; growing degree day (above 10 °C); growing degree day (above 11 °C); growing degree day (above 12 °C); growing degree day (above 13 °C); age class; and sex class.

Model design and selection

For this growth model, the selected response variable was normalised GR, i.e., the logarithm of GR of an individual eel defined by:

$$\log(\mathrm{GR}) = \log((L - L_\mathrm{i})/\mathrm{age})$$

with L as the length of the fish (mm), L_i as the initial length at continental arrival (age 0) and age as the continental age of the eel in years.

Previous works had already shown the appropriate use of linear models to compare populations GRs (Allen 1976). Two GLMs were used to assess statistical association between the log(GR) sex, age, habitat and temperature with a Gaussian distribution of error and identity link. One GLM was applied to the whole data set encompassing all the sex classes (global model) and another GLM was applied to the female eels (female model). An informative theoretical approach (Burnham & Anderson 2002) was used to assess which hypotheses, formulated as individual models with habitat and temperature predictor variables, best explained the eel GR. Sets of 720 and 360 candidate GLMs were formulated and estimated respectively for the global data set and for the female data subset. Predictor variables could include sex (De Leo & Gatto 1995) or a temperature variable (among 'mean. Temp.', 'TempSUP10', 'TempSUP11', 'TempSUP12' or 'TempSUP13'), or a river position variable (among 'Relative distance', 'distance to sea', 'distance to source', or 'distance to sea + distance to source'), or depth, or salinity, or the age class effect. The GLMs were fitted using the glm function in the R language/environment (R Development Core Team 2007). The models were ranked using ΔAIC. Finally, the accuracies of the predictions were assessed with validation data previously excluded from the model fitting.

Results

Description of the data

A total data set of 45,759 individual fish length-at-age data were collected from 146 locations (Fig. 1). The amount of data per range of latitude (Fig. 2) showed that the 50–55°N was most represented in the data and the 35–40°N less well represented. There was less data available for the 1940–1960 period of time (only two sites, with solely male eels) and the larger amount of data for the 1980–2000 period of time (Fig. 3). Most eels were <15 years old (Fig. 4). The length distribution showed a mode around 350 mm for male eels, and a mode around 500 mm for female eels (Fig. 5). Overall, female eels outnumbered males and undifferentiated eels in the data (Figs 4 and 5).

Growth model

Both the model fitted to the whole data and the model fitted to the female data subset selected the same variables, with the exception of the sex class in the female model. Among the 720 candidate GLMs fitted on the whole data, only one single model was selected, as the second ranked model had a ΔAIC of 13.5 which is well above the value of 2, defined as a threshold value under which models are considered equivalent. The selected model explained 64.46% (adjusted R^2) of the variance of the log(GR), had a null deviance of 3941.7 on 8646 degrees of freedom, a residual deviance of 1401.0 on 8602 degrees of freedom and an AIC of 7738.8. Among the 360 candidate models fitted on the female eel data, only one single model was selected, as the second ranked model had a ΔAIC of 20. The selected female model explained 66.91% (adjusted R^2) of the variance of the log(GR), had a null deviance of 1531.08 on 5410 degrees of freedom, a residual deviance of 506.48 on 5368 degrees of freedom and an AIC of 2096.5. The female model and the global models selected the same variables, that is, TempSUP13, salinity class, depth class, relative distance and age class (Tables 1 and 2).

Equation

The growth equation can be obtained using the coefficients in Table 1 and 2, using the value of continuous parameters (TempSUP13, Ratiodistsea) and setting the class variables to a value of 1 if present or 0 if absent. As an example, the equation of the prediction of a female eel GR (female model), in age 5 year class is presented:

$$\begin{aligned}\log(\mathrm{GR}) = {} & 4.2299082(\pm 0.0272711) \\ & + 0.0075774(\pm 0.0002364)\,\mathrm{TempSUP13} \\ & - 0.2506349(\pm 0.0153639)\,\mathrm{Ratiodistsea} \\ & + 0.0280343(\pm 0.0086946)\,\mathrm{Marine} \\ & + 0.0623457(\pm 0.0096879)\,\mathrm{Depthsup1m} \\ & - 0.3139456(\pm 0.0257519)\,\mathrm{Ageclass5}\end{aligned}$$

Effects

An inverse link function (exponential) was used to plot the effect of each parameter on the GR.

Age class effect

A significant decrease in GR with age was observed for the global model (Fig. 6a) and for the female growth model (Fig. 7a).

Sex effect

The results from the total eel growth model, for both sexes, showed a sexual dimorphism of growth with female eels exhibiting faster growth (Fig. 6b) than male eels. Undifferentiated eels had the lowest GR.

Temperature effect

Among the five temperature parameters ('mean Temperature', 'TempSUP10', 'TempSUP11', 'TempSUP12' or 'TempSUP13') tested in the model, TempSUP13 was selected. Eel GR was positively correlated with temperature with the best correlation with the annual average of sum of temperature above 13 °C (Figs 6c and 7b).

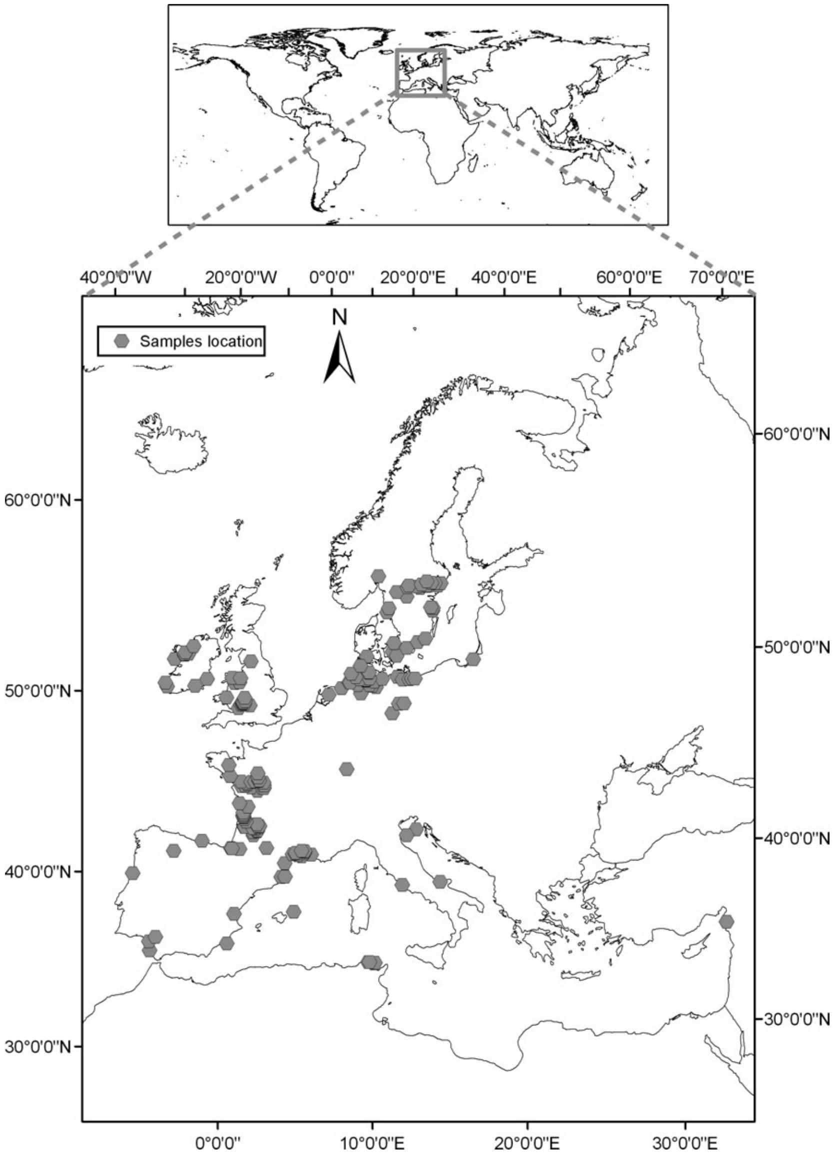

Fig. 1. Map showing the location of collection of the different data sets.

Habitat effects

Salinity class, relative distance from the sea and depth class, in that order of importance, were selected in the best model, showing the influence of habitat parameters on eel growth. To understand the effects of habitat, parameter values were combined and plotted to represent realistic scenarios of habitats. We characterised habitat according to the relative distance from the sea, its salinity and depth and created two classes, presented in Figs 6d and 7c for an 'estuary' type habitat and a 'river' type habitat. Both effects were presented for a 5 years old female eel, and a mean value of the temperature parameter 'Temp-SUP13'. For the 'river' type habitat, the relative distance parameter was set to one, and depth class less than one metre and freshwater salinity class were chosen. For the 'estuary' type habitat, relative distance parameter was set to zero; the above one metre depth class and the marine salinity class were chosen. GR of 'estuary' type habitats was higher than GR of 'river' type habitats (Figs 6d and 7c).

Validation, model performance

Performance of the global model and the female model was explored graphically [Fig. 8, global model, (a,b), female model, (c,d)]. The plot of observed values versus predicted values for both models (Fig. 8a,c) showed a good fit, except for a very little part of the data. The mean error between the validation data and the model prediction was 1.06 mm year^{-1} for the global model and 1.00 mm year^{-1} for the female model.

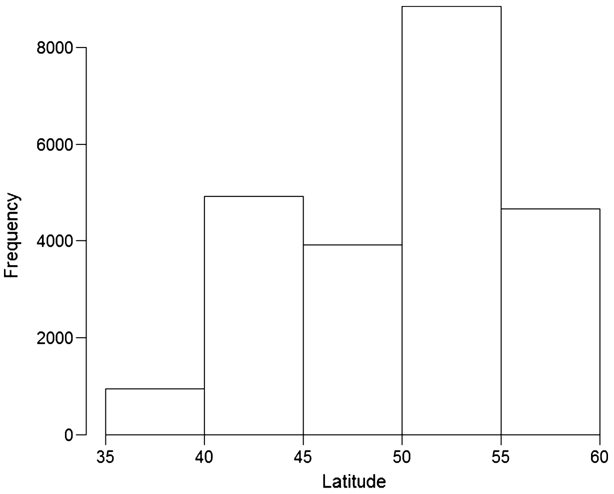

Fig. 2. Number of eels in the data, following latitude.

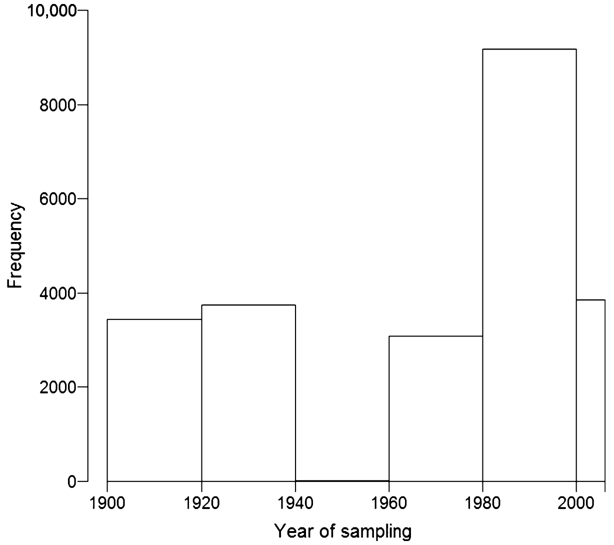

Fig. 3. Number of eels in the data, following period of collection.

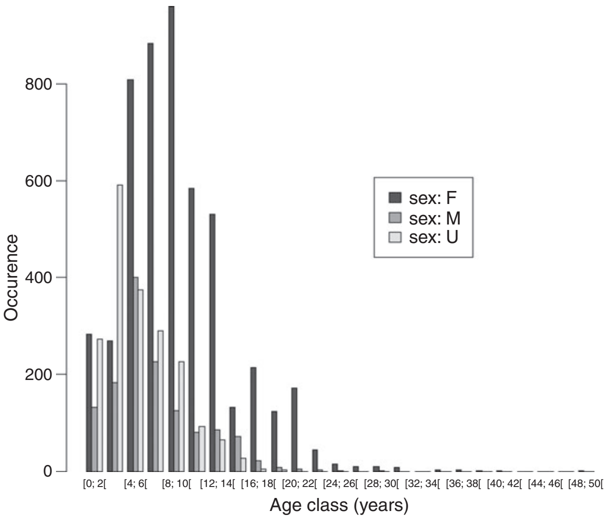

Fig. 4. Age class frequency of the data set.

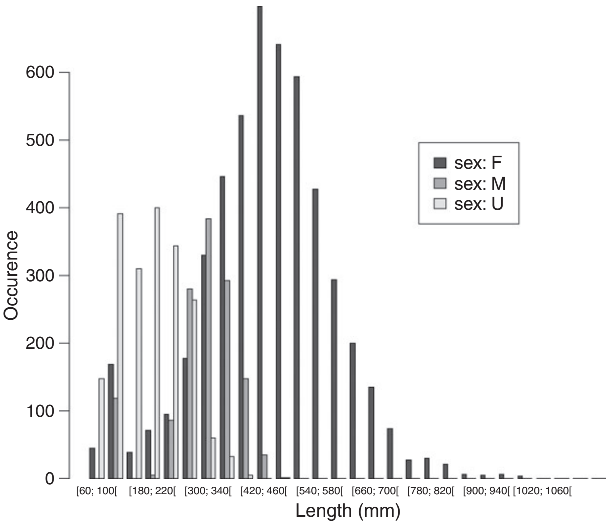

Fig. 5. Length class frequency of the data set.

Discussion

Although mathematical models have already been used to describe European eel growth at the local scale (Moriarty 1983; De Leo & Gatto 1995; Poole & Reynolds 1996c), no global model exists to predict eel (*A. anguilla*) GR across its geographical range. The procedure of model selection in this paper allowed the selection of relevant predictors of eel growth such as the sex, relative distance to sea, salinity and depth classes, cumulative temperature and age. The moderate performance (64.46% and 66.91% accuracy) of the present models may be a counterpart of its simplicity. The mean error was relatively low (around 1 mm year^{-1}) but the visual examination of Fig. 8 showed that for a very small proportion of the data, GR was not predicted with accuracy. There was no general pattern in the data predicted with the lowest accuracy, except most of the overestimated data came from some small French streams and that most of underestimated data came from Swedish lake.

The selection of the age predictor in both the global model and the female models was in accordance with the general form of a fish population growth curve where GR decreases as the fish is getting older. For eel, emigration of maturing individuals may reinforce the decrease in GR with age in a population-based model. We hypothesised that fast growing individuals mature and silver at a younger age and then migrate. Hence, fast growing individuals are removed from the data as the age of the population is increasing, increasing the apparent drop in GR. Previous work on eel suggested that female silvering was size, rather

Table 1. Coefficient values and associated probability of the global model.

Parameter	Estimate	SD	*t* Value	Pr (>|*t*|)
(Intercept)	4.5215606	0.0204268	221.355	<2e−16***
TempSUP13	0.0056942	0.0002045	27.839	<2e−16***
class_sexM	−0.1660791	0.0093514	−17.760	<2e−16***
class_sexU	−0.5569070	0.0108334	−51.407	<2e−16***
class_depthsup1m	0.0409277	0.0083541	4.899	9.80e−07***
class_selMarine	0.0508390	0.0085054	5.977	2.36e−09***
ratiodistsea	−0.2641504	0.0132095	−19.997	<2e−16***
classage2	−0.1909239	0.0197908	−9.647	<2e−16***
classage3	−0.2638326	0.0190231	−13.869	<2e−16***
classage4	−0.4604791	0.0190947	−24.116	<2e−16***
classage5	−0.5524782	0.0193547	−28.545	<2e−16***
classage6	−0.5906220	0.0222305	−26.568	<2e−16***
classage7	−0.6618712	0.0231005	−28.652	<2e−16***
classage8	−0.7791524	0.0230198	−33.847	<2e−16***
classage9	−0.8373239	0.0246096	−34.024	<2e−16***
classage10	−0.8313118	0.0258090	−32.210	<2e−16***
classage11	−0.8968473	0.0269994	−33.217	<2e−16***
classage12	−0.9369006	0.0290948	−32.202	<2e−16***
classage13	−1.0367159	0.0265979	−38.977	<2e−16***
classage14	−1.0981445	0.0380935	−28.828	<2e−16***
classage15	−1.1272327	0.0419524	−26.869	<2e−16***
classage16	−1.1301553	0.0563437	−20.058	<2e−16***
classage17	−1.1252112	0.0330917	−34.003	<2e−16***
classage18	−1.2355196	0.0549628	−22.479	<2e−16***
classage19	−1.2649469	0.0427012	−29.623	<2e−16***
classage20	−1.2780214	0.0408263	−31.304	<2e−16***
classage21	−1.3304789	0.0495814	−26.834	<2e−16***
classage22	−1.3547388	0.0901473	−15.028	<2e−16***
classage23	−1.4452010	0.0814660	−17.740	<2e−16***
classage24	−1.3774239	0.1291498	−10.665	<2e−16***
classage25	−1.3779581	0.1231976	−11.185	<2e−16***
classage26	−1.5759406	0.2027946	−7.771	8.68e−15***
classage27	−1.4389961	0.2027703	−7.097	1.38e−12***
classage28	−1.6000603	0.2339733	−6.839	8.54e−12***
classage29	−1.6860092	0.1440810	−11.702	<2e−16***
classage30	−1.6578861	0.1538718	−10.774	<2e−16***
classage31	−1.6268903	0.2339219	−6.955	3.79e−12***
classage33	−1.5926837	0.4040785	−3.942	8.16e−05***
classage34	−1.9514619	0.2860603	−6.822	9.59e−12***
classage35	−1.7345608	0.4040651	−4.293	1.78e−05***
classage37	−1.8055060	0.2338535	−7.721	1.29e−14***
classage38	−1.5063511	0.4042422	−3.726	0.000196***
classage41	−1.6770956	0.4040813	−4.150	3.35e−05***
classage48	−2.3660631	0.4040810	−5.855	4.93e−09***
classage49	−1.8938006	0.4040810	−4.687	2.82e−06***

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1.

than age, dependent and therefore fast growers would silver at a younger age than slower growers (Vøllestad 1992; Jessop 2010). The sexual dimorphism, with females growing faster than males, shown by our model was in accordance with previous observations (Vøllestad 1992; De Leo & Gatto 1996; Poole & Reynolds 1996b; Melià et al. 2006). The lower GR of undifferentiated eels was consistent with the hypothesis of a length dependant sexual differentiation (Colombo & Grandidr 1996) for *A. anguilla*, where fast growers differentiate first and thus ‘disappear’ from the undifferentiated group. However, another study on silver eels of stocked origin (Holmgren et al. 1997) showed contradictory results determined by comparing males and females of different age classes using mean length-at-age estimates.

The temperature predictor, an annual average of sum the temperature above 13 °C (TempSUP13), selected in the best models had a great relative importance. The positive relation found between TempSUP13 and GR was in accordance with the common observation of higher GR s in the south Europe as in Italy (Rossi & Colombo 1976), than in the north of Europe (Sinha & Jones 1967) and the correlation of GR with latitude (Vøllestad 1992). Under the most probable scenarios of climate change, eel GR would globally increase, especially in the northern part of its distribution area. This hypothesis

Table 2. Coefficient values and associated probability of the female model.

Parameters	Estimate	SE	*t* Value	Pr (>|*t*|)	Level of significance
(Intercept)	4.2299082	0.0272711	155.106	2e−16	***
TempSUP13	0.0075774	0.0002364	32.047	2e−16	***
class_selMarine	0.0280343	0.0086946	3.224	0.00127	**
class_depthsup1m	0.0623457	0.0096879	6.435	1.34e−10	***
ratiodistsea	−0.2506349	0.0153639	−16.313	2e−16	***
classage2	0.0085457	0.0295453	0.289	0.77241	
classage3	−0.2138235	0.0266080	−8.036	1.13e−15	***
classage4	−0.2466496	0.0259448	−9.507	2e−16	***
classage5	−0.3139456	0.0257519	−12.191	2e−16	***
classage6	−0.3107241	0.0276007	−11.258	2e−16	***
classage7	−0.3601976	0.0289277	−12.452	2e−16	***
classage8	−0.4850743	0.0285836	−16.970	2e−16	***
classage9	−0.5257343	0.0292474	−17.975	2e−16	***
classage10	−0.5395996	0.0302816	−17.819	2e−16	***
classage11	−0.6070969	0.0311862	−19.467	2e−16	***
classage12	−0.5936834	0.0325769	−18.224	2e−16	***
classage13	−0.7401664	0.0310316	−23.852	2e−16	***
classage14	−0.7178715	0.0403341	−17.798	2e−16	***
classage15	−0.7407471	0.0430650	−17.201	2e−16	***
classage16	−0.8059230	0.0508538	−15.848	2e−16	***
classage17	−0.8735977	0.0336537	−25.958	2e−16	***
classage18	−0.9630330	0.0505927	−19.035	2e−16	***
classage19	−0.9821666	0.0406026	−24.190	2e−16	***
classage20	−0.9999416	0.0381115	−26.237	2e−16	***
classage21	−1.0115581	0.0436399	−23.180	2e−16	***
classage22	−1.0138082	0.0668854	−15.157	2e−16	***
classage23	−1.1791134	0.0704537	−16.736	2e−16	***
classage24	−1.1466849	0.1005254	−11.407	2e−16	***
classage25	−1.1704645	0.1280855	−9.138	2e−16	***
classage26	−1.3892404	0.1559372	−8.909	2e−16	***
classage27	−1.0317021	0.1558789	−6.619	3.98e−11	***
classage28	−1.2708234	0.1559834	−8.147	4.59e−16	***
classage29	−1.2233153	0.1399988	−8.738	2e−16	***
classage30	−1.2788197	0.1559847	−8.198	3.02e−16	***
classage31	−1.4133144	0.3085951	−4.580	4.76e−06	***
classage33	−1.3087406	0.3083540	−4.244	2.23e−05	***
classage34	−1.5455685	0.1794023	−8.615	2e−16	***
classage35	−1.3842153	0.3083549	−4.489	7.30e−06	***
classage37	−1.5295552	0.1793785	−8.527	2e−16	***
classage38	−1.6049475	0.2190295	−7.328	2.69e−13	***
classage41	−1.4178056	0.3083967	−4.597	4.38e−06	***
classage48	−2.1069092	0.3083961	−6.832	9.31e−12	***
classage49	−1.6346526	0.3083960	−5.300	1.20e−07	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

was also supported by previous work on eel distribution and abundance models predicting a northward expansion of eel abundance (Lassalle & Rochard 2009). Whether the temperature increase in the southern part of the present distribution will provide less favourable conditions for eel growth is questionable. We hypothesised that the favourability of southern part would remain equivalent to present, as the temperature increase will be lower in lower latitudes than in higher latitudes. Besides, distribution models did not predict a future change in eel abundance in the southern part of the distribution (Lassalle & Rochard 2009). However, considering the continuous decline of eel natural recruitment level, especially in the northern regions, the scenario of higher abundance and higher GR of eels in the northern regions (Scandinavia, Baltic sea…) is improbable. Fish with large distribution areas were found to display a gradient of growth related to their thermal optimum along a latitudinal gradient (Frisk & Miller 2006; Lassalle et al. 2008), although the relation between thermal optimum and growth is not always straight forward and can be altered by genetic adaptation or habitat variation (Imsland & Jonassen 2001). However, the present study did not support the hypothesis that eels colonising higher latitudes become acclimated to lower temperatures.

The present study showed that habitat parameters (relative distance to sea, salinity and depth) had a strong influence on eel growth. To our knowledge, it is the first model of eel growth accounting for habitat variables independently of latitude and temperature.

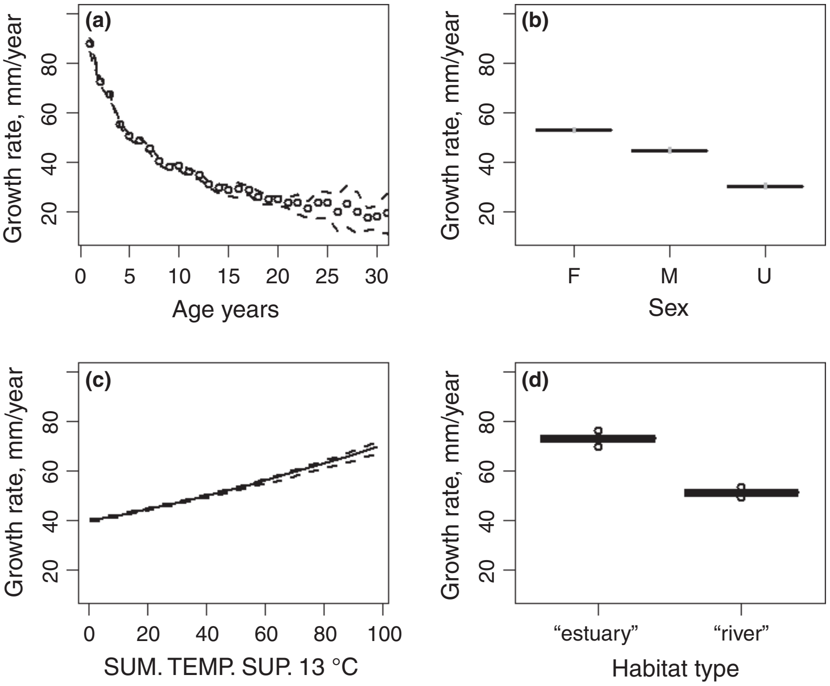

Fig. 6. Effects of the different parameters of the growth model fitted on the whole data (global model). An inverse link function (exponential) was used to plot the effect of each parameter on the growth rate.

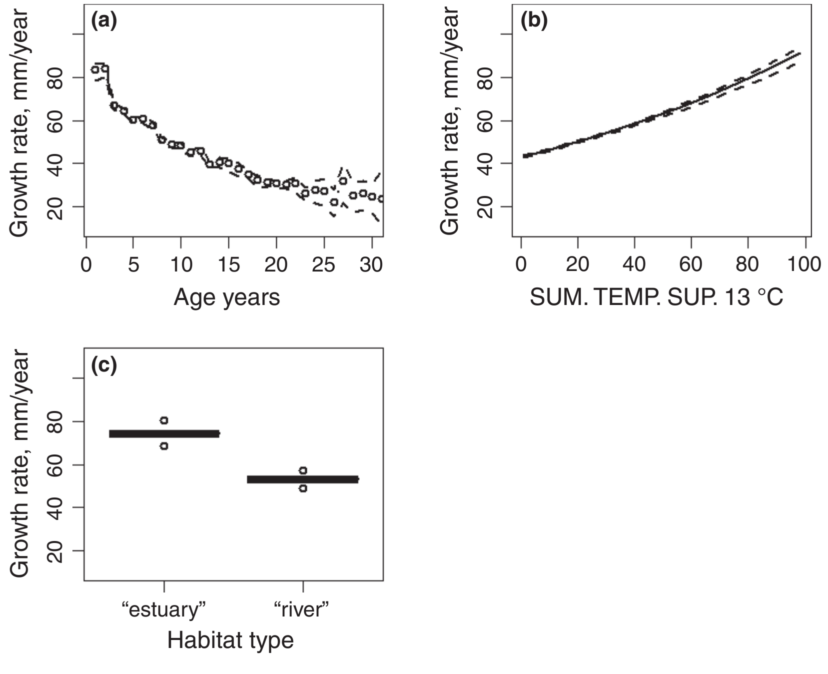

Fig. 7. Effects of the parameters of the growth model fitted on the female data subset (female model). An inverse link function (exponential) was used to plot the effect of each parameter on the growth rate.

The results showed that eel growth in the upper reaches of a catchment was slower than closer to the sea. The GR of other benthic fish species differed following the habitat types they colonised (Tupper & Boutilier 1995; Le Pape et al. 2003); in some cases, these differences could be attributed to the local productivity of habitats (Basilone et al. 2004). The results also suggested a positive effect of depth on growth. Reviews of eel GRs stated that GRs were higher in brackish or freshwater marshes close to the

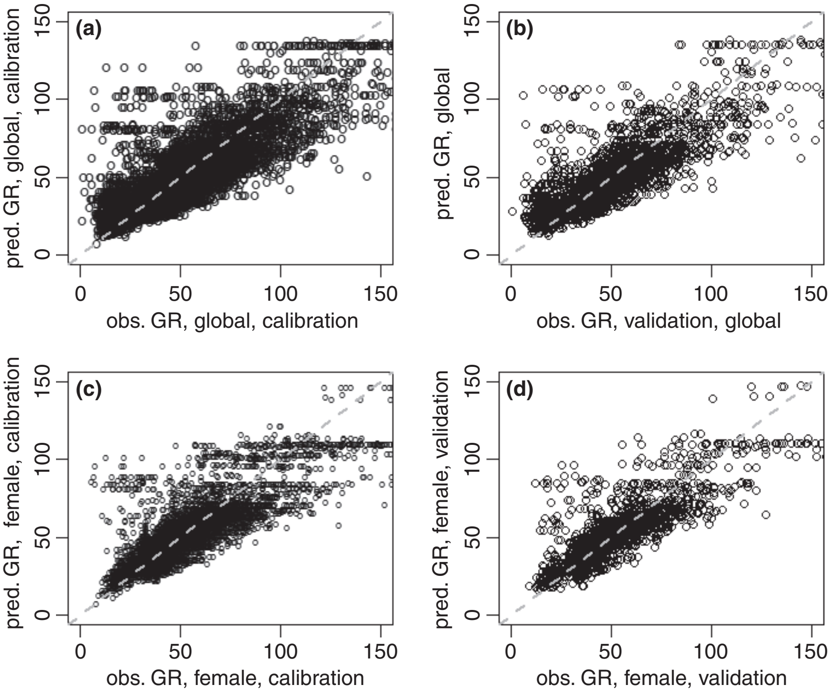

Fig. 8. Performance of the global model (a and b) and the female model (c and d); plot of observed versus predicted values for the calibration data sets (a and c) and plot of observed versus predicted values for the validation data sets (b and d).

sea (Fontenelle 1991) than GRs in the rivers (Fernandez-Delgado et al. 1989; Lobon-Cervia et al. 1995) but they failed in separating the effects of latitude and habitat. Previous work that focused on a single catchment at a time, as in the Gironde Garonne Dordogne catchment (Daverat & Tomas 2006) and in the Vilaine catchment (Mounaix & Fontenelle 1994), also concluded that growth was faster in the estuary rather than upstream in the catchment.

The decline in recruitment of eel and the management of eel stock has become a major concern and priority of the European Union. The EU brought in a Regulation (Council Regulation 1100/2007), along with the inclusion of eel in the EU Data Collection Regulation, requiring that eel management plans were established by Member States for River Basins. Eel Management Plans have stimulated increased attention and extensive efforts across Europe to assess eel production against management target. Given the paucity of information on locally specific eel production, scientists and managers rely on model-based comparisons between habitats across the range of eel, as do those tasked with national and international comparisons. A robust understanding of the variation of key life history processes such as growth, natural mortality and maturation is fundamental to support these regional extrapolations. As such, the present model may be useful in extrapolating from catchments where good growth data exist to areas where there are little or no data, despite an accuracy of only 64.46% for the whole data and 66.91% for the female eel data. The parameters required by the model – temperature location, salinity class, depth class, distance to sea and total river length – can be easily found for any specific ecosystem. Similar frameworks have been established for salmon using stock-recruitment and smolt production estimates correlated with latitude and wetted catchment area (Crozier & Booth 2003). Along with some basic parameters such as length, may this tool would provide the basis for a similar analysis for eel, thereby contributing significantly to the eel management and conservation processes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Litterature source of length-at-age data.