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# BIOLOGY LETTERS

## Future growth potential can affect female size at maturation of a long-lived semelparous fish

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1 **Future growth potential can affect female size at maturation of a**  
2 **long-lived semelparous fish**

3  
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13  
14 **Summary**

15 The relationship between female size at maturity and individual growth trajectories of a  
16 long-lived semelparous species of fish was investigated using the European eel. A  
17 Bayesian model was applied to 338 individual growth trajectories of maturing  
18 migration-stage females from France, Ireland, Netherlands and Hungary. This clearly  
19 showed that when prospects for further growth were low, the onset of silvering process  
20 would be triggered for the eels to leave growth habitats and migrate to the spawning  
21 area. Therefore, female eels tended to attain larger body size when growth prospect was  
22 high enough to risk spending extra time in their growth habitats.

23  
24  
25 **Keywords:** *Anguilla anguilla*; European eel; otolith; growth; probability of maturation

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28

## 29 **1. Introduction**

30 For most animals, the set of factors determining the timing of reproduction are  
31 important for their fitness. Long-lived species are thought to respond to environmental  
32 constraints by adjusting their effort for reproduction [1]. Once an individual is able to  
33 mature, thereafter the processes can be controlled by long-term predictive cues such as  
34 photoperiod, food supply and temperature. Factors such the frequency of reproduction  
35 referred to as iteroparity and semelparity may influence the body size at maturation [2].  
36 Age and size at maturation are key life-history traits that affect growth rate, survival and  
37 fecundity [3-4].

38 The relation between size and the probability of maturing has been intensively  
39 studied using the probabilistic maturation reaction norm (PMRN) [5] with respect to  
40 phenotypic changes related to evolutionary responses. The PMRN could be affected  
41 by the individual growth histories, but how growth affects size and age at maturation is  
42 not fully understood yet [6].

43 The European eel *Anguilla anguilla* is a long-lived semelparous fish species that  
44 undertakes exceptionally long catadromous transoceanic migrations both at the larval  
45 stage while dispersing to their juvenile growth habitats in rivers, lakes, and lagoons in  
46 Europe and again as “silver eels” that mature as they migrate to the spawning area in the  
47 Sargasso Sea. Silver eels migrate downstream predominantly during high river-flow  
48 periods and new-moon phases [7], and androgen hormones appear to be important to  
49 facilitate the initiation of the migrations as the silvering process begins [8]. Large  
50 variations in the size and age at silvering of European eels [9] indicate though, that a  
51 range of factors affect the timing of the start of the silvering process that differ among  
52 individuals or geographic locations. Although it's possible to evaluate the proximate  
53 environmental or endocrine conditions when maturation and the silver eel spawning  
54 migrations begin, what triggers the activation of this process itself is not yet known.

55 The 6,000 km or longer migration of European eels requires that enough energy is  
56 stored in their bodies to be able to complete the long journey, so there must be a  
57 threshold size before eels would start to mature and become silver eels. Maturation of  
58 females is thought to be responsible for a size-maximizing strategy [10], because  
59 fecundity is entirely determined by body size. Enlargement of the body is  
60 advantageous for females, whereas the growth phase over a decade or more can  
61 increase the risk of mortality. This tradeoff between size at maturity and growth rate

62 suggests that females should start the process of silvering when growth is slowing down  
63 and no better growth prospects are expected.

64 We investigated the link between maturation probabilities and the body size of  
65 European eels. We tested the hypothesis that the probability to become a maturing  
66 silver eel was linked to growth patterns of eels, with poor growth prospects leading to a  
67 higher probability of silvering being triggered at smaller sizes.

68

## 69 **2. Materials and methods**

70 Data about body size and age of silver-phase female European eels ( $n = 338$ ) were  
71 used from Europe (Ireland, France, Netherlands and Hungary) for the years 2000–2007  
72 to overview these traits widely from a population. Data were extracted from  
73 EU-FP5th EELREP database (Loire, Ste. Eulalie, Grevelingen, Balaton, Certes, Nive  
74 and Rhine river systems) and additional data from the Burrishoole and Corrib rivers  
75 were obtained (R. Poole unpublished).

76 Individual growth trajectories were acquired using the data of otoliths (calcium  
77 carbonate structures of the inner ear of fishes). Back-calculation analysis was  
78 undertaken using a relationship between body size and otolith radius. Measurements  
79 were made of the radius (mm) of the  $i$ th annuli ( $R_i$ ), which is the distance from the  
80 otolith mark at recruitment to the continental habitats to the  $i$ th annuli, and of the radius  
81 (mm) of the otolith at capture ( $R$ ), which is the distance from the mark at recruitment to  
82 the otolith edge. The  $L_T$  of the fish at age  $i$  yrs ( $L_i$ , mm) was estimated using the  
83 following formula:  $L_i = L_r + (L - L_r) R_i R^{-1}$ , where  $L_r$  is the mean  $L_T$  of glass eels when  
84 they recruit to coasts [11], and  $L$  is the  $L_T$  at capture (mm). Annual body increment  
85 ( $G_i$ : mm/year) was calculated as  $G_i = L_i - L_{i-1}$ .

86 The average growth rate of a particular period (differential of individual size-age  
87 relationship) and growth acceleration/deceleration (second-order differential of  
88 individual size-age relationship) were selected as explanatory variables. Logistic  
89 regression models describing the probability of silvering were set up where we tested if  
90 body size and growth histories over the year preceding silvering were a significant  
91 proximate cue(s) for silvering. The basic form for these logistic models was  $\text{logit}(p) =$   
92  $\text{log}_e[p(1-p)^{-1}] = c_0 + c_1 L_{t,i} + c_2 L'_{t,i} + c_3 L''_{t,i} + \text{Inds}$ , where  $p$  is the probability of  
93 silvering (early maturation),  $c_0$  is a constant,  $c_1$  is the coefficient for the size effect ( $L_{t,i}$ )  
94 at various age  $t$  of individual  $i$ ,  $c_2$  is the coefficient for the individual growth ( $L'_{t,i}$ ) from

95 age  $t-4$  to age  $t$  of individual  $i$ ,  $c_3$  is the coefficient for the acceleration/deceleration of  
96 growth ( $L''_{t,i}$ ) between age  $t-4 \sim t$  and age  $t-5 \sim t-1$  of individual  $i$ , and  $Inds$  is the  
97 random-effect of individuals.

98 Silvering probability was fitted to a sigmoid curve using the Bernoulli distribution.  
99 We deployed constant prior as the priors and hyperpriors and used Markov chain Monte  
100 Carlo to draw samples from the distributions of interest. Three chains were initiated at  
101 the maximum likelihood estimates and were run for 5000 iterations as a burn in, after  
102 which every fifth iteration was recorded to remove autocorrelation, until 1000 samples  
103 had been obtained. To assess the significance of the parameters, the estimated  
104 probability distributions of parameters were confirmed to not include zero within the  
105 range of the distribution. Convergence of the parameters estimated was confirmed by  
106 the iteration figures and that R-hat was close to 1. The random effect was assessed by  
107 the deviance information criterion (DIC) for the significance in the model. The  
108 programs R (R2Winbugs package) and WinBugs were used for the Bayesian analysis.

109

### 110 **3. Results**

111 Silver eel females from Ireland, France, Netherlands and Hungary had a wide range  
112 of total lengths at silvering that was from 436 to 982 mm, except for one smaller eel that  
113 was 377 mm ( $n = 338$ , figure 1b). The size distribution showed that for the onset of  
114 silvering maturation for eels to occur, there must first be an enlargement of the body  
115 beyond a certain minimum size, which appears to be about 430 mm, with only one  
116 outlier. The ages and growth rates of silver eel females ranged widely from 4 to 44  
117 yrs-old and from 12.1 to 148.2 mm yr<sup>-1</sup>, respectively. Annual body increment ( $G_i$ ) of  
118 females was relatively stable but with a large variance until age 10, and then it  
119 decreased until 20 yrs-old when it stabilized again (figure 1a).

120 Size ( $L_{t,i}$ ), average growth ( $L'_{t,i}$ ) and the acceleration/deceleration of growth ( $L''_{t,i}$ )  
121 had a significant effect on the probability of silvering for females in the model. The  
122 significant improvement of the random-effect model fit was confirmed by the lower  
123 DIC (1554) of the model than that of a model having only fixed effects (1619).  
124 Convergence of parameters was confirmed visually and the R-hats ranged from 1.02 to  
125 1.15 (table 1). Estimated distributions of parameters  $L_{t,i}$ , positively, and  $L'_{t,i}$  and  $L''_{t,i}$   
126 negatively affected the silvering probability of eels (figure 2) and the distributions of  
127 parameters did not include zero within the ranges (table 1), indicating that lower growth

128 in recent years and/or a large growth deceleration leads to a higher probability of  
129 silvering.

130

#### 131 **4. Discussion**

132 This study demonstrated that when the prospect for further growth in their present  
133 habitats was low, eels tended to start the silvering maturation process and leave those  
134 growth habitats to start their spawning migrations. This indicates that constant high  
135 growth leads to a larger size at silvering, whereas poor or decreasing growth results in  
136 eels silvering earlier at smaller sizes. Such a strategy would be adaptive if mortality  
137 during the growth phase is low enough to take the risk to spend more time in the growth  
138 stage as a long-lived semelparous fish.

139 Our model is in agreement with the dynamics of endocrine factors during silvering.  
140 In silver eels, growth-related physiological traits are reduced whereas  
141 maturation-related physiological traits are enhanced [12-13]. From an  
142 endocrinological point of view, the silvering corresponds to a conversion of the somatic  
143 growth mode into a maturation mode. A deceleration of growth may be a cause or a  
144 consequence of this conversion.

145 Our results suggested that the silvering size was linked with deceleration of growth  
146 in addition to growth rates. In fact, our model is likely to apply well to the case of the  
147 north and south distribution areas of eels, such as old larger eels in Ireland and small  
148 younger eels in Italian lagoons [14]. Steady growth of larger and older female silver  
149 eels in Ireland [15] suggested that the prospect of further stable moderate growth within  
150 present habitats could result in the postponement of the onset of silvering. In addition,  
151 larger eels might have relatively small risks for staying in northern-latitude  
152 low-productivity habitats because they are one of the top predators in their aquatic  
153 ecosystems. In the high-productivity ecosystems adjacent to the Mediterranean Sea,  
154 eels would face higher mortality compared to that in the North. If the mortality or  
155 variability of mortality were relatively high in a region, a trade-off between somatic  
156 growth and the risk of dying before reproduction would lead to a female tactic shifting  
157 to maturing at the earliest possible opportunity [9]. Traits related to the reproductive  
158 migration could be affected by large-scale environmental changes among long-lived  
159 migratory species like sea birds and salmon [e.g. 16-17]. For a large panmictic  
160 population of eels, silvering being triggered by a reduction of growth is likely an

161 evolutionary adaptation that allows eels to maximize the benefits of inhabiting a wide  
162 range of habitats with various levels of growth potential.

163

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166

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- 214

215 **Figure captions**

216 **Figure 1.** (a) The estimated mean body increment (growth in 1 year) and standard  
217 deviation (bars) and (b) size and age at silvering maturation of individual female  
218 European eels.

219

220 **Figure 2.** Probability curves of silvering maturation as a function of body size (total  
221 length) in the Bayesian model for (a) recent 5-yrs growth ( $L'_{t,i}$ ) and (b) the deceleration  
222 of growth ( $L''_{t,i}$ ) with several values of growth or trends.

223

224 **Table 1.** Parameter estimates with 95% confidence intervals from the best probability  
225 of silvering maturation model for female European eels with random effect of  
226 individuals.

parameter	estimate $\pm$ SD	95% CI	R hat
body size ( $L$ )	0.016 $\pm$ 0.003	0.011 ~ 0.021	1.15
recent 5-yrs growth ( $L'$ )	-0.015 $\pm$ 0.003	-0.021 ~ -0.009	1.13
inclination of growth ( $L''$ )	-0.032 $\pm$ 0.005	-0.041 ~ -0.023	1.02

227

228 **Short title:** Growth prospect affect size to mature

229

230 **Competing interests**

231 We have no competing interests.

232

233 **Authors' contributions**

234 K.Y., F.D., K.T., P.E. and R.P. conceived the idea. K.Y. and F.D. designed the study and  
235 conducted data analyses. K.Y., F.D., N.F., R.S., M.J.M. drafted the manuscript. All  
236 authors contributed to revise it and gave final approval for publication.

237

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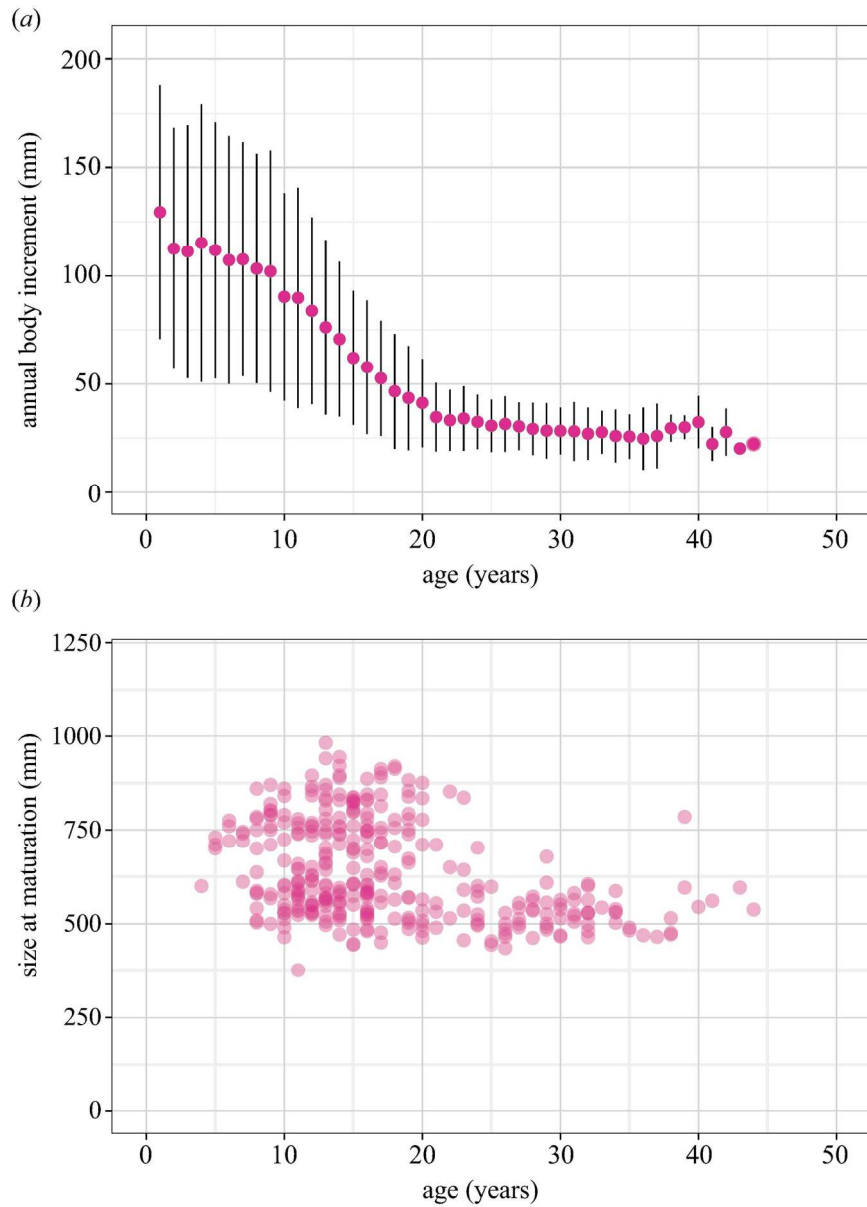


Figure 1. (a) The estimated mean body increment (growth in 1 year) and standard deviation (bars) and (b) size and age at silvering maturation of individual female European eels.

figure 1

156x219mm (300 x 300 DPI)

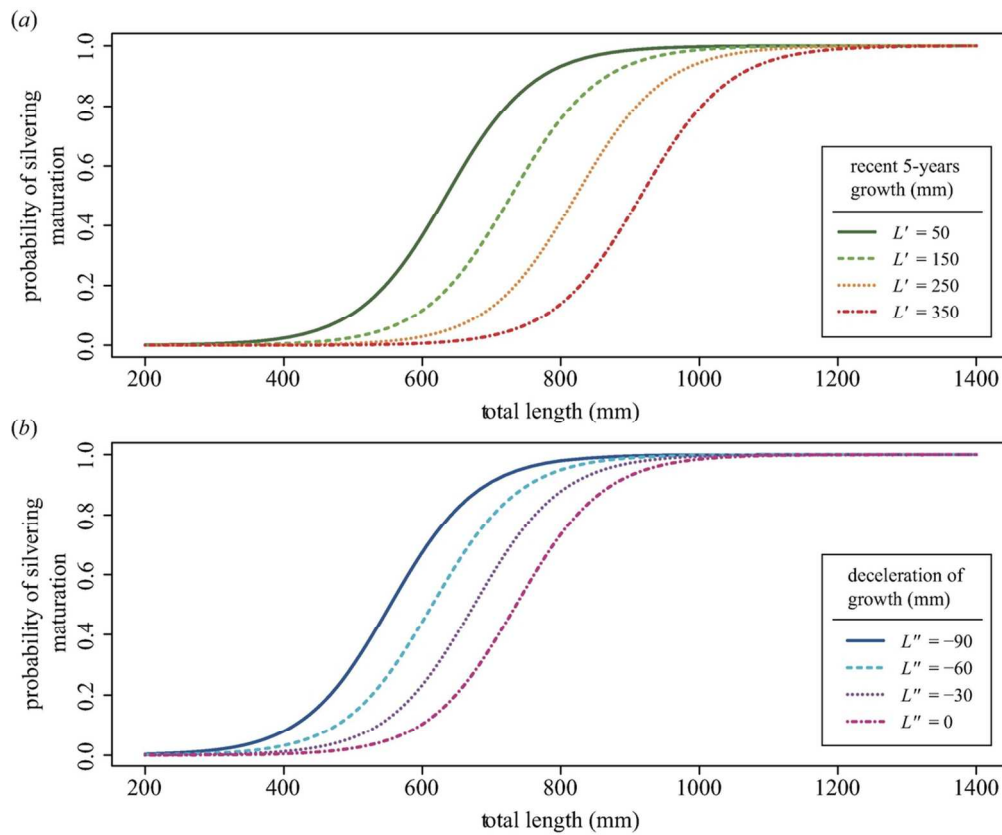


Figure 2. Probability curves of silvering maturation as a function of body size (total length) in the Bayesian model for (a) recent 5-yrs growth ( $L't, i$ ) and (b) the deceleration of growth ( $L''t, i$ ) with several values of growth or trends.

figure 2  
100x83mm (300 x 300 DPI)