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

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

Kazuki Yokouchi[1,2]*, Françoise Daverat[1], Nobuto Fukuda[2], Ryusuke Sudo[3], Michael J. Miller[4], Katsumi Tsukamoto[4], Pierre Elie[1], Russell Poole[5]

[1]*Unit EPBX, IRSTEA, 50 Avenue de Verdun, F-33612 Cestas Cedex, France*
[2]*National Research Institute of Fisheries Science, FRA, Yokosuka, 238-0316, Japan*
[3]*National Research Institute of Aquaculture, FRA, Minami-ise, 516-0193, Japan*
[4]*College of Bioresource Sciences, Nihon University, Fujisawa, 252-0880, Japan*
[5]*Marine Institute, Furnace, Newport, Co. Mayo., Ireland*
**kazuki.yokouchi@affrc.gp.jp*

Summary

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

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

1. Introduction

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

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

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

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

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

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

2. Materials and methods

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

Individual growth trajectories were acquired using the data of otoliths (calcium carbonate structures of the inner ear of fishes). Back-calculation analysis was undertaken using a relationship between body size and otolith radius. Measurements were made of the radius (mm) of the *i*th annuli (R_i), which is the distance from the otolith mark at recruitment to the continental habitats to the *i*th annuli, and of the radius (mm) of the otolith at capture (R), which is the distance from the mark at recruitment to the otolith edge. The L_T of the fish at age i yrs (L_i, mm) was estimated using the 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 they recruit to coasts [11], and L is the L_T at capture (mm). Annual body increment (G_i : mm/year) was calculated as $G_i = L_i - L_{i-1}$.

The average growth rate of a particular period (differential of individual size-age relationship) and growth acceleration/deceleration (second-order differential of individual size-age relationship) were selected as explanatory variables. Logistic regression models describing the probability of silvering were set up where we tested if body size and growth histories over the year preceding silvering were a significant proximate cue(s) for silvering. The basic form for these logistic models was ligit(p) = $\log_e[p\,(1 - p)^{-1}] = c_0 + c_1\, L_{t,\,i} + c_2\, L'_{t,\,i} + c_3\, L''_{t,\,i} + Inds$, where p is the probability of silvering (early maturation), c_0 is a constant, c_1 is the coefficient for the size effect ($L_{t,\,i}$) at various age t of individual i, c_2 is the coefficient for the individual growth ($L'_{t,\,i}$) from age t-4 to age t of individual i, c_3 is the coefficient for the acceleration/deceleration of growth ($L''_{t,\,i}$) between age t-4 ~ t *and* age t-5 ~ t-1 of individual i, and *Inds* is the random-effect of individuals.

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

3. Results

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

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

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

4. Discussion

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

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

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

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Figure captions

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 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.

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

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

Short title: Growth prospect affect size to mature

Competing interests

We have no competing interests.

Authors' contributions

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

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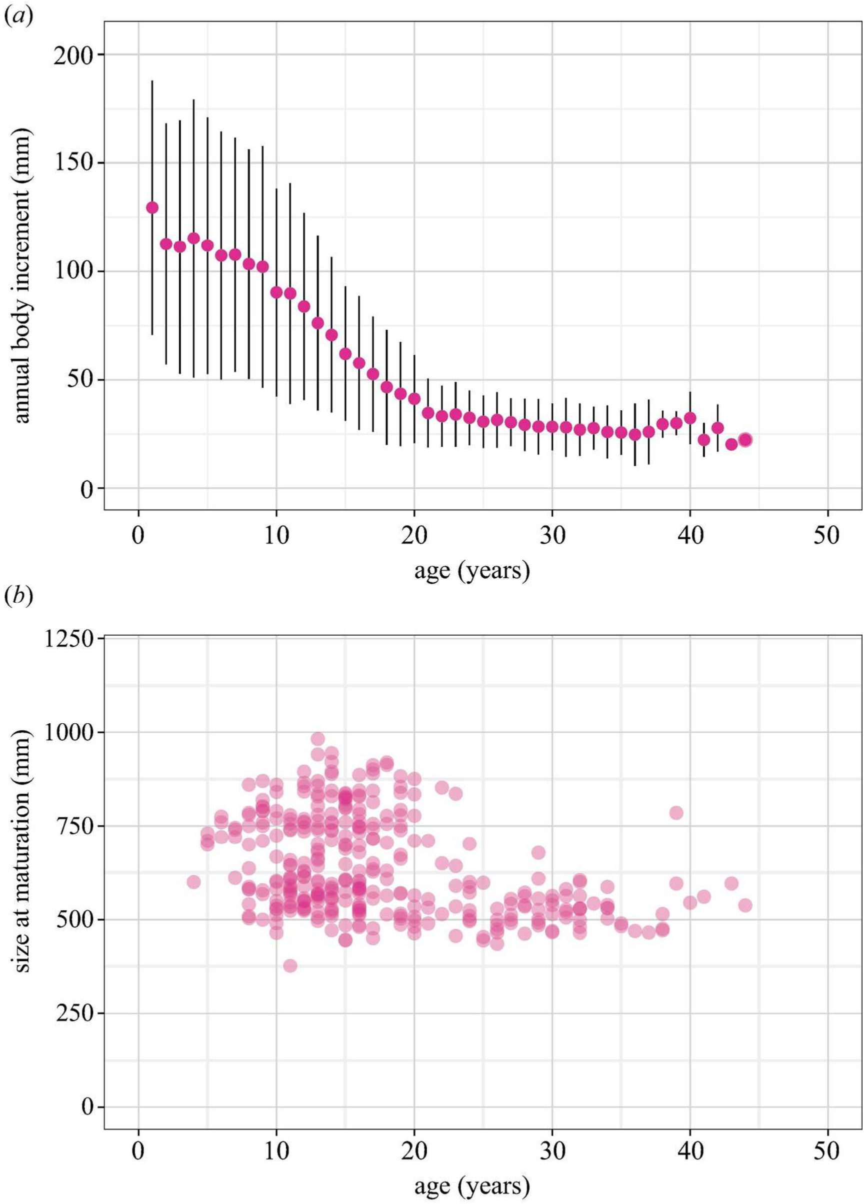

Figure 1. (a) The estimated mean body increment (growth in 1 year) and standard deviation (bars) and (b) size and age at silvering maturation of individual female European eels.
figure 1
156x219mm (300 x 300 DPI)

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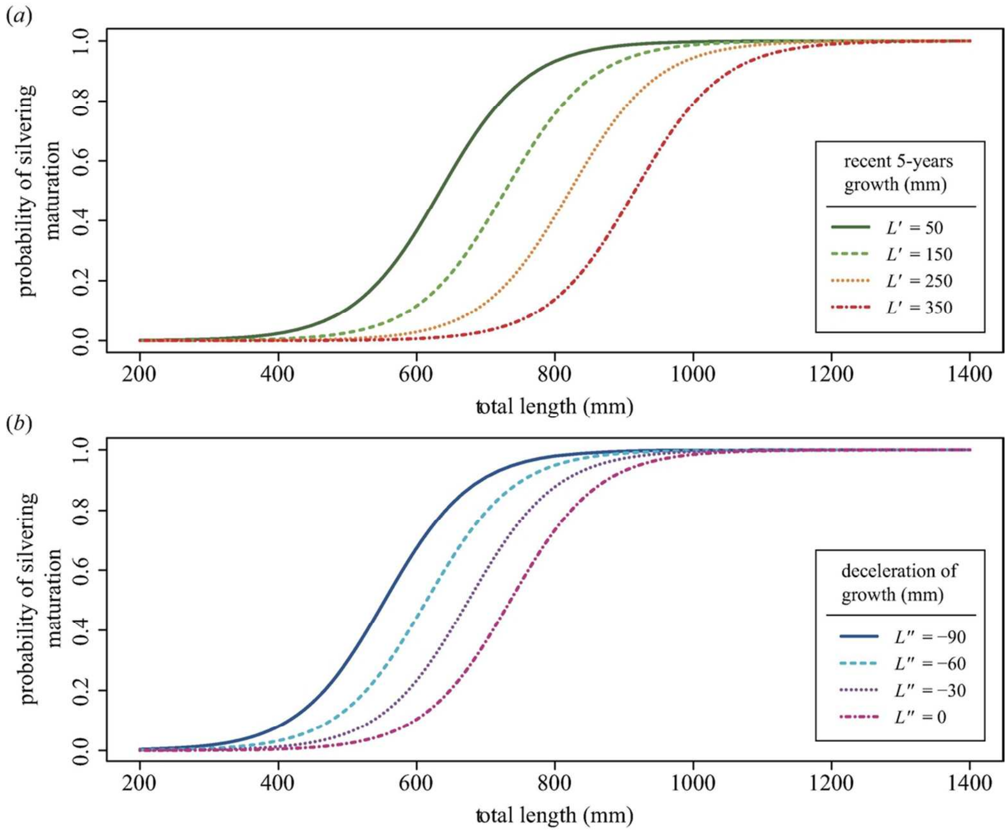

Figure 2. Probability curves of silvering maturation as a function of body size (total length) in the Bayesian model for (a) recent 5-yrs growth (L't, i) and (b) the deceleration of growth (L''t, i) with several values of growth or trends.
figure 2
100x83mm (300 x 300 DPI)