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Growth during the first summer at sea modulates sex-specific maturation schedule in Atlantic salmon

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Abstract: Recent decline in abundance of Atlantic salmon (*Salmo salar*) and concomitant changes in life history may result from a decline in the growth conditions during marine migration. Available literature suggests the existence of a sex-specific reaction norm linking maturation with environmental growth conditions at sea. However, the extent to which this mechanism explains variations in age at maturity remains unclear. Using a historical collection of scales (1987–2017) from the Sélune River, France, we showed that marine growth declined over the first summer and remained stable during the subsequent periods at sea among returning salmon. Results support the hypothesis of a sex-specific probabilistic reaction norm, with individual probability to return after 1 year at sea increasing when growth increases. Females may require higher growth than males to attain their maturation threshold. This mechanism is a good candidate to explain temporal variability in sea-age at return at both the individual and population level in the Sélune population and in many other southern European populations.

Résumé : Les baisses récentes de l'abondance des saumons atlantiques (*Salmo salar*), ainsi que des changements concomitants du cycle biologique pourraient découler d'une détérioration des conditions de croissance durant la migration en mer. La documentation disponible semble indiquer l'existence d'une norme de réaction dépendant du sexe qui relie la maturation aux conditions ambiantes durant la croissance en mer. La mesure dans laquelle ce mécanisme pourrait expliquer les variations de l'âge à la maturité demeure toutefois incertaine. En utilisant une collection historique (1987–2017) d'écailles provenant de la rivière Sélune (France), nous démontrons que la croissance en mer diminuait durant le premier été, pour ensuite demeurer stable durant les périodes subséquentes en mer chez les saumons de retour à la rivière. Les résultats appuient l'hypothèse d'une norme de réaction probabiliste dépendant du sexe, la probabilité individuelle de retour après 1 an en mer augmentant de concert avec la croissance. Les femelles pourraient nécessiter une croissance plus forte que les mâles pour atteindre leur seuil de maturation. Ce mécanisme est un bon candidat pour expliquer la variabilité temporelle de l'âge en mer au moment du retour tant à l'échelle de l'individu que de la population dans la population de la rivière Sélune et de nombreuses autres populations d'Europe méridionale. [Traduit par la Rédaction]

Introduction

Climate change has induced widespread changes in the physical characteristics of the marine environment over recent decades, including increased sea-surface temperature (SST) and ocean acidification (Hoegh-Guldberg and Bruno 2010; IPCC 2019). A growing body of evidence suggests that these changes are associated with a reduction in the productivity of several marine ecosystems. In the Northern Hemisphere, reduced marine productivity has resulted in modifications in population abundance and community composition from phytoplankton to the highest trophic levels (e.g., including seabirds and predatory fish; Sandvik et al. 2005; Barbraud and Weimerskirch 2006; Hoegh-Guldberg and Bruno 2010; Mills et al. 2013; Capuzzo et al. 2018). Reduced marine productivity is thought to affect organisms by decreasing food availability (in quality and quantity; Carscadden et al. 2001; Mills et al. 2013) and distribution (the food is more patchily distributed; Friedland et al. 2018). These factors may directly impact migration timing, size, age at maturation, and survival, with consequent long-term modification to the life-history strategies of many predator fish (Kuparinen et al. 2009; Jonsson and Jonsson 2011; Fenkes et al. 2016; Vargas-Chacoff et al. 2018). Developing a better understanding of the ecological drivers responsible for changes in population life history is necessary to guide management actions towards conservation and sustainable exploitation of marine resources.

Anadromous salmon species (*Salmo salar* and *Onchrorhyncus* spp.) utilize the marine environment to maximize their somatic growth. Marine growth is particularly critical for females, whose body size at spawning relates to the number and mass of eggs they produce (Hansen and Quinn 1998; Hanson et al. 2020). Changes in growth conditions at sea and their attendant effects on female fecundity could therefore have important implications for salmon population dynamics, as highlighted by the disproportional contributions of BOFFFF (big old fat fertile female fish) to recruitment in several species (Hixon et al. 2014). Atlantic salmon (*Salmo salar*, hereinafter salmon) is an emblematic species of the North Atlantic Ocean. Like many other anadromous species, populations have declined dramatically in abundance since the 1970s (Limburg and Waldman 2009). Despite substantial local and international management

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efforts, including fishery closures, salmon abundance remains at oftentimes historical low levels, notably in the Northeast Atlantic (Chaput 2012; Olmos et al. 2019). Evidence suggests that these widespread and dramatic declines are due largely to a reduction in marine survival during the first months (summer–autumn) at sea after smolt migration (Beaugrand and Reid 2012; Friedland et al. 2009; Olmos et al. 2019, 2020). Concomitant with population declines, the size of adult salmon returning to their natal river has decreased (Aprahamian et al. 2008; Todd et al. 2012; Bal et al. 2017). Together, these trends support the hypothesis that growth conditions at sea have and continue to deteriorate (Friedland and Reddin 2000; Juanes et al. 2004; Friedland et al. 2005; McCarthy et al. 2008; Jonsson and Jonsson 2011; Bal et al. 2017).

The life cycle of anadromous salmon is characterized by a high diversity of life histories (Mills 1989; Aas et al. 2010; Erkinaro et al. 2019). In South European populations, the life cycle is typically 2 to 4 years long; most of the juveniles spend one or two winters in fresh water before migrating to sea as smolts. Salmon spend between one (1SW) or two (2SW) winters at sea before returning to their natal rivers as mature individuals to spawn (Hansen and Quinn 1998). Changes in the duration of the marine phase, which translate into changes in the age structure of returning individuals, have been previously documented (Jonsson et al. 2016; Chaparro-Pedraza and Roos 2019; Olmos et al. 2019). Part of the variations in the duration of the marine phase is genetically determined (Barson et al. 2015). However, there have been marked differences in the timing and the amplitude of these changes across the distributional range of salmonid populations (Jonsson and Jonsson 2011; Otero et al. 2012; Jonsson et al. 2016; Olmos et al. 2019), suggesting that the underlying mechanism(s) are more complex and likely involve other factors, potentially including declining growth opportunity at sea.

In salmonids, seaward migration is followed by a surge in body growth, while their return migration to natal stream generally takes place following the physiological "decision" to mature. Individuals that return at older ages are generally larger, have higher fecundity, and have potentially greater reproductive success (Fleming 1998). Maturation schedule and marine growth are therefore closely related (Ishida et al. 1993). However, the trade-off for delaying maturation is an increase in the probability of mortality prior to reproduction (Stearns 1977). The timing of the maturation decision is therefore a key fitness component driven by selection forces (genetic component) and the environment (plastic component) (Dieckmann and Heino 2007). The probabilistic maturation reaction norm (PMRN) is a commonly used concept describing an individual's probability of maturing at a given age as a genetically set function of size or growth rate (Stearns and Koella 1986; Silverstein et al. 1997; Hutchings and Jones 1998). It postulates that the capacity to mature is conditioned by the acquisition of sufficient energy, or by reaching a certain physiological threshold (defined by the genotype), to meet the metabolic and physiological costs of reproduction (Thorpe 2007). Thus, for a given threshold, fast-growing individuals are more likely to mature early, while slower-growing individuals are likely to delay maturation decision for a year. Available knowledge supports the hypothesis that maturation decision occurs in the autumn at sea, a year prior spawning, and depends on the environmental condition and the energy reserves accumulated during the summer and early autumn (Rowe and Thorpe 1990; Silverstein et al. 1998; Campbell et al. 2003). Hence, the body length reached at the end of the first summer at sea, which results from the cumulated growth during the freshwater phase and the first summer at sea, would be critical in determining whether individuals will mature after 1 year or later. Because most of the realised growth occurs during the first summer at sea, the expectation is that growth during this period is a key determinant of the maturation schedule.

Moreover, this trade-off is likely to be different for males and females assuming they incur different metabolic and physiological costs of reproduction. Hence, sex-specific maturation reaction norms are expected. In salmonids, the relationship between body size and fecundity is generally greater in females than in males (Fleming 1996, 1998). Thus, females may achieve a greater fitness advantage by delaying their return to reach a larger body size at the time of maturation than males, thereby resulting in a higher maturation threshold in females compared with males. Empirical evidence for such sex-specific maturation trade-offs have been documented for wild salmon populations in which the average age of returning females is higher than that of males (Hutchings and Jones 1998). However, to date, no sex-specific PMRN in relation to growth at sea has been established.

Recent changes in growth conditions at sea offer an opportunity to test the hypothesis that marine growth modulates an individual salmon's maturation decision and therefore its age as a returning adult and, ultimately, the age and sex structure of the returning population. In this study, our specific objectives were (*i*) to test for the existence of changes in growth over the last 30 years, with a special focus on the first summer at sea that is thought to be critical for life-history choices and (*ii*) to investigate empirical evidence for a sex-specific relationship between individual growth experienced until the end of the first summer at sea and age of individual returning adults (i.e., a maturation reaction norm). As salmon growth at sea and maturation decision are not directly observable, we relied on the data collected over the last 30 years on individuals returning to the Sélune River, France, to track individual life history trajectories throughout their marine sojourn. This data consists of individual scale samples that provide indirect observations of individual growth experiences (Ombredane and Baglinière 1992). Growth increments observed on the scales of returning individuals were considered as a proxy of body length at different life stages (Francis 1990; Heidarsson et al. 2006; Thomas et al. 2019). If fast-growing individuals have a higher probability to mature after the first summer at sea, we expect 1SW returning individuals to show higher cumulated growth to the end of the first summer than 2SW individuals. The deterioration in quantity or quality of prey available for salmon at sea might have reduced growth and constrained an increasing proportion of individuals to delay maturation (Friedland and Reddin 2000; Juanes et al. 2004; Friedland et al. 2005; McCarthy et al. 2008; Jonsson and Jonsson 2011). The expectation under the hypothesis of a sex-specific reaction norm is that females would be more affected by those changes than males, the same growth reduction leading to a stronger reduction in the probability of maturation for females than for males.

Materials and methods

Study population and data collection

This study uses data from a self-sustaining population of wild Atlantic salmon reproducing in the Sélune and Sée rivers. These two rivers share a common estuary in the Bay of Mont-Saint-Michel (Normandy, France, 48°38′N, 3°37′W; Fig. 1) and drain a 1038 km^2 basin dominated by agriculture and livestock production. Further details about this study site can be found in Baglinière et al. (1990, 2005), Bal et al. (2014, 2017), and Forget et al. (2018). On average through time, this population is dominated by 1SW individuals (86%), and females represent the majority of 2SW returning adults (80%). There is no commercial fishery associated with coastal waters, but recreational angling in these rivers accounts for an average of 180 1SW and 70 2SW declared landings per year. Since 1987, a national mandatory salmon catch reporting system has recorded detailed information on returning adults in fresh water. For every salmon caught, total length (mm), mass (g), and a sample of scales for age determination (following Shearer 1992) are returned to the National Centre for the Interpretation of Salmonid Catches (https://www6.rennes.inrae.fr/u3e_eng/ABOUT-US/Organisation/The-migratory-fish-hub/CNICS) and stored as part

Fig. 1. Sélune–Sée estuary location (Normandy, France, 48°38′N, 3°37′W). Figure produced in QGIS version 3.14.16. [Colour online.]
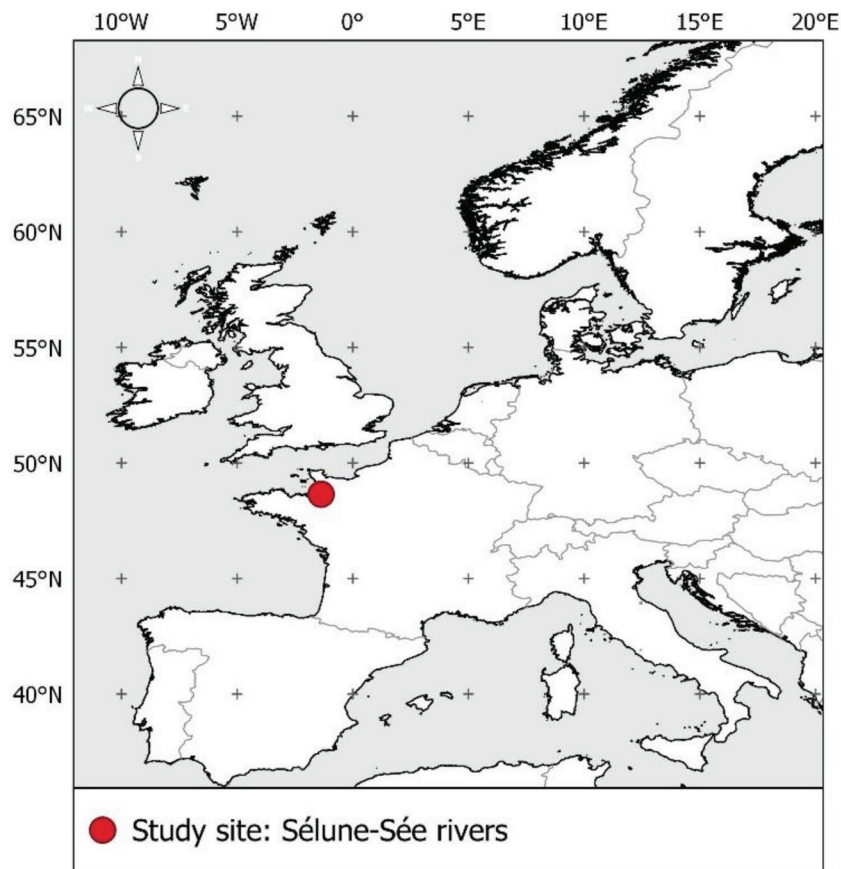
of the COLISA collection (collection of ichthyologic samples; Marchand et al. 2019). As angling effort tends to be biased towards 2SW individuals, the age composition of returning salmons cannot be inferred from these data (CNICS, unpublished data).

The growth pattern in scales of returning salmon is an indirect tracer of their individual growth history. From the 8704 individual scale samples recorded over the period 1987–2017 for the Sélune–Sée population, a subsample of scales from 30 individuals per year and per sea-age was selected for the analysis of individual life history (total sample size for 1SW = 921 and 2SW = 927). Multiple spawners and three sea winter individuals represented a very low proportion of the individuals in this population (≤1% of the catches) and thus were excluded from the analysis. Most fish were caught in spring and summer soon after their entry into fresh water. Individuals captured after a possible prolonged period in fresh water were removed from the selection because of the high chance that their scales would have been corroded. Subsampling was done independently of the sex of individuals, which was not known prior to the analysis. Detailed sample sizes are presented in Table A1. Scales were used for growth analysis and sex determination.

Growth analysis and sex determination

The analysis of growth patterns from scales was performed by a single aging specialist. For each individual, one scale was scanned using a stereomicroscope (Discovery V8, Zeiss) and an optic camera (Infinity 3, Lumenera). Each circuli was semi-automatically detected on a transect line along the longest axis of the scale (ICES 1984) using Image Pro Premier software 9.2 (Media Cybernetics). Nondetected circuli were added manually. The distance (mm) between the center of the scale and each circuli was recorded. Measures of realised growth of the scale were used in subsequent analyses, as scale

growth has been found to be proportional to body growth and can be considered as a proxy of fish body length at different life stages (Dahl 1910; Lee 1920; Francis 1990; Heidarsson et al. 2006; Thomas et al. 2019), justifying our choice to use the absolute value of growth increments measured on the scales as direct proxy of body length increments. Based on marked changes in the intercirculi spacing, key features in the growth patterns were identified and interpreted as the transition from river to sea and the beginning and the end of each winter season (Baglinière et al. 1985; Ombredane and Baglinière 1992; Thomas et al. 2019). The position of the edge of the scale was recorded. Seven different periods of growth (hereinafter growth periods) were defined from the scale: (1) river (Riv), from the center to the river-to-sea transition; (2) first summer (Sum1), from the river-to-sea transition to the beginning of the first winter; (3) first winter (Win1), from the beginning to the end of the first winter; (4) plus growth (Plus), from the end of first winter to the edge of the scale in 1SW; (5) second summer (Sum2), from the end of the first winter to the beginning of the second winter in 2SW; (6) second winter (Win2), from the beginning to the end of the second winter in 2SW; and (7) the cumulated growth (Riv+Sum1), from the center to the beginning of the first winter. This cumulated growth (Riv+Sum1) is a proxy of salmon body length at the end of first summer at sea. Note that we considered plus growth in 2SW individuals to be negligible. The straight-line-distance growth increment across each period (mm) was used as a proxy of the realized growth over the corresponding period.

A preliminary analysis on a subsample of 100 individuals was carried out to explore the sensitivity of the growth measurement to the number of scales considered per individual. Results showed that intra-individual variability in growth measurement (between different scales of the same individual) was much smaller than

interindividual variability (between individuals; Fig. A1). This result suggests that sampling one scale per individual is appropriate to investigate interindividual differences in growth trajectories. The genetic sex of each fish was assessed using a molecular q-PCR sex marker multiplexing protocol (A.-L. Besnard, personal communication).

Statistical analysis

Temporal changes in individual body length of returning adult and growth at sea

Temporal variation in growth during all growth periods (e.g., Sum1, etc.) for each fish was analyzed using general additive models (GAMs; Wood 2017). GAMs are flexible and efficient tools to analyze nonlinear temporal signals and have been used widely to analyze trends in fish life history (Véron et al. 2020), including salmonids (Otero et al. 2014; Bal et al. 2017; Oke et al. 2020). Statistical analyses were run in R (version 3.5.1) using the gam() function in R package mgcv (version 1.8-31; Wood 2017). Let us denote $Riv_{t,age,sex,i}$, $Sum1_{t,age,sex,i}$, $Win1_{t,age,sex,i}$, $Plus_{t,sex,i}$, $Sum2_{t,sex,i}$, $Win2_{t,sex,i}$, and $(Riv+Sum1)_{t,age,sex,i}$ the growth increments measured over the different periods for each individual i of a given sea-age (1 or 2 years) and sex (male or female), with t denoting the year of smolt migration. Considering the year of smolt migration (rather than the year of return) allows for aligning individuals of different ages to the same influence of growth conditions at sea. Temporal trends in individual growth during these seven growth periods were assessed independently. We considered additive and interaction effects of sea-age and sex on the intercept. In addition, we tested effects of sea-age and sex on the smoothed temporal trends, fitting different trends by sea-age or sex when appropriate. The most complex models considered for each growth period are as follows:

$$(1) \qquad Riv_{t,age,sex,i} = \alpha + a_{age} + b_{sex} + c_{age,sex} + s_{age,sex}(t) + \varepsilon_{t,age,sex,i}$$

$$(2) \qquad Sum1_{t,age,sex,i} = \alpha + a_{age} + b_{sex} + c_{age,sex} + s_{age,sex}(t) + \varepsilon_{t,age,sex,i}$$

$$(3) \qquad Win1_{t,age,sex,i} = \alpha + a_{age} + b_{sex} + c_{age,sex} + s_{age,sex}(t) + \varepsilon_{t,age,sex,i}$$

$$(4) \qquad Plus_{t,sex,i} = \alpha + b_{sex} + s_{sex}(t) + \varepsilon_{t,sex,i}$$

$$(5) \qquad Sum2_{t,sex,i} = \alpha + b_{sex} + s_{sex}(t) + \varepsilon_{t,sex,i}$$

$$(6) \qquad Win2_{t,sex,i} = \alpha + b_{sex} + s_{sex}(t) + \varepsilon_{t,sex,i}$$

$$(7) \qquad (Riv + Sum1)_{t,age,sex,i} = \alpha + a_{age} + b_{sex} + c_{age,sex} + s_{age,sex}(t) + \varepsilon_{t,age,sex,i}$$

where α stands for a general intercept, a_{age} is the additive effect of sea-age, b_{sex} is the additive effect of sex, $c_{age,sex}$ is the additive effect due to any interaction between age and sex, and $s_{age,sex}(t)$ and $s_{sex}(t)$ are nonparametric smoothing functions (regression splines) describing the effect of smolt year t for different combinations of sea-age and sex, respectively. $\varepsilon_{t,age,sex,i}$ are independent and identically distributed normal errors. Here, sea-age (a_{age}) and sex (b_{sex}) test for systematic average difference in growth trajectories between 1SW and 2SW individuals and males and females, respectively. The effect of sex (b_{sex}) tests for potential intrinsic difference in growth between males and females, which may be attributed to sex-specific energy allocations (Fleming 1996, 1998). Different smooth temporal trend between age and sex, or both, would be interpreted as different temporal patterns

in the response to environmental condition at sea. Different terms in the most complex models (eqs. 1–7) were selected using a stepwise model comparison approach based on the second-order Akaike information criterion (AIC$_c$, i.e., AIC for small samples; Hurvich and Tsai 1989; Burnham and Anderson 2002). This approach includes selection from among smoothed functions specific to each combination of sea-age and sex ($s_{age,sex}(t)$), to each sea-age ($s_{age}(t)$), to each sex $s_{sex}(t)$, or common to all individual ($s(t)$). The degree of smoothness of each regression spline was determined using the generalized cross-validation score (Craven and Wahba 1978) that minimizes the prediction error while optimizing the number of knots in the regression spline, as implemented by default in the gam() function of R package mgcv (version 1.8-31; Wood 2017). We calculated percent change in growth increments over the study period from the fitted smooth temporal trends.

Probabilistic maturaton reaction norm (PMRN)

Given that the physiological decision to mature in Atlantic salmon is commonly believed to be made in the late summer–autumn (Rowe and Thorpe 1990; Friedland and Haas 1996; Mangel and Satterthwaite 2008), we tested the effect of the cumulated growth (Riv+Sum1) as a proxy of body length at the end of summer on the maturation decision. By contrast, Win1, Plus, Sum2, and Win2 might be considered as growth trajectories dependent upon the maturation decision and are not selected as explanatory variables of maturation decision. As individuals are nonobservable at the time of the maturation decision, we modelled the probability to return as 1SW (hereinafter denoted Pmat.1SW) as a proxy for the probability to mature after one summer spent at sea. We modelled Pmat.1SW as a linear function of (Riv+Sum1) on the logit scale in a general linear model (GLM; McCullagh and Nelder 1989) assuming binomial errors. As constraints on the maturation decision might be different in males and females, we also tested for a sex-specific response to growth. The most complex model considered was

$$(8) \qquad logit(Pmat.1SW_{i,sex}) = \alpha + b_{sex} + \beta_{sex} \times (Riv + Sum1)_{i,sex}$$

where $Pmat.1SW_{i,sex}$ is the probability to return after 1 year spent at sea of individual i of a given sex, α is a general intercept, b_{sex} is the additive effect of sex, and β_{sex} is a coefficient describing the change in the (logit) probability to mature for a unit change of $(Riv+Sum1)_{i,sex}$ for the given sex. Starting with the most complex model (eq. 8), nested models were compared using AIC$_c$ in a stepwise approach. To quantify the sex difference in the probabilistic reaction norm, we can derive the cumulated growth needed to reach 50% probability to return as 1SW fish from the intercept and slope of this model, which is given by $G50_{sex} = -(\alpha + b_{sex})/\beta_{sex}$.

Results

Sex and temporal patterns in growth

Among 1SW fish (854 fish), 390 (46%) in our study population were genetically identified as females and 464 (54%) as males. Among 2SW fish (869 fish), 769 (88%) were identified as females and 100 (12%) as males. Genetic sex determination was not successful for 83 individuals that were therefore excluded from further analysis.

Temporal trends show different patterns among the river growth and the five marine growth periods (Fig. 2, Figs. 3A–3F). As expected, growth was higher during summer periods, and especially during the first summer at sea, when it was also the most variable among years (Fig. 2).

The best model for growth in river (Riv) included specific intercepts for sea-age and sex and a common temporal trend for all individual (Fig. 3A; Table 1A). The additive effects of sea-age and sex and the common temporal effect accounted for only a small amount of deviance explained, particularly for the additive

Fig. 2. Mean growth increments during each growth period over the time series: river (Riv); first summer (Sum1); first winter (Win1); plus growth (Plus); second summer (Sum2); and second winter (Win2) at sea calculated for one-sea- and two-sea-winter (1SW and 2SW).
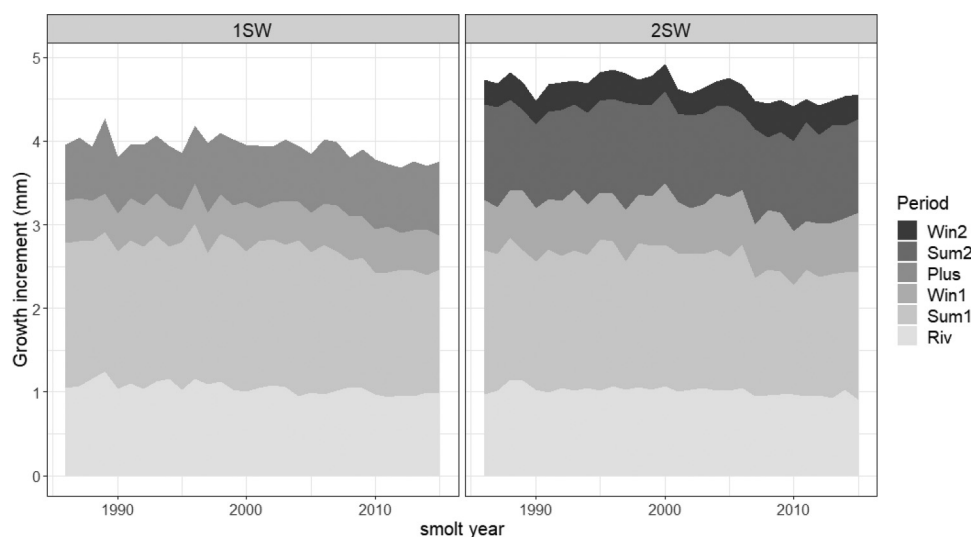

Fig. 3. Smoothed temporal trends in growth during seven growth periods: river (A), first summer (B), first winter (C), plus growth (D), second summer (E), and second winter (F) at sea and the cumulated growth (Riv+Sum1) (G) for one-sea- and two-sea-winter (1SW and 2SW) males and females (M–F) where measurements were available. Shaded bands represent 95% confidence intervals, and dots represent individual data.
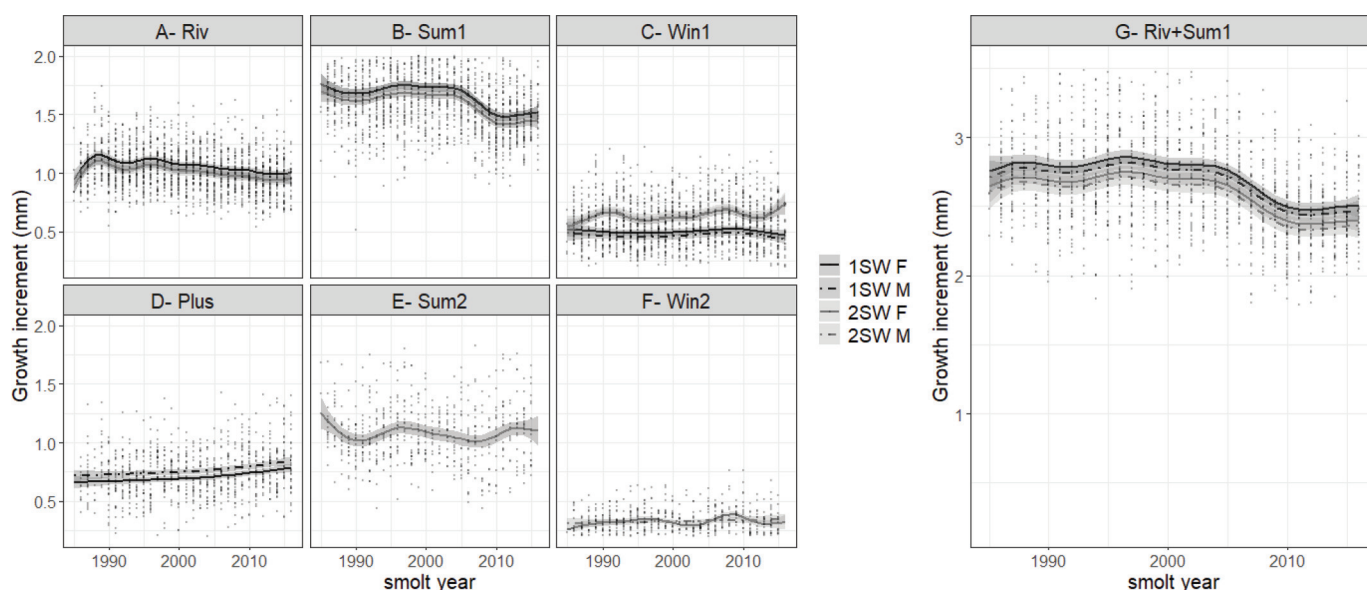
effects of sea-age and sex (1% compared with 8% for the temporal effect), suggesting that their effects were only weak. However, temporal variations of growth during the freshwater phase was very low compared with the marine phases (see below). Over the study period, river growth increment declined only slightly by 0.036 mm (−3.6%) on average, as calculated from the fitted smooth temporal trend.

The model that best explained variations in growth during Sum1 included an additive effect of age and a smoothed temporal trend common to all sex and age combinations (Fig. 3B; Table 1B). Results highlight that for a given cohort of smolts, fish returning as 1SW always had higher growth over the first summer at sea than their 2SW counterparts. Growth during Sum1 declined simultaneously among all age and sex classes. Particularly clear is a drop in Sum1 growth since the early 2000s, the lowest growth

being recorded for the 2011 smolt cohort (Fig. 3B). In this recent period, growth during Sum1 was on average 0.28 mm (−16%) shorter than it was at the beginning of the study period.

Interestingly, most of the variability in the cumulated growth during (Riv+Sum1) was attributable to variability in growth during the first summer at sea (Sum1). The cumulated growth during (Riv+Sum1) displayed a temporal pattern similar to Sum1 growth, with a clear drop from the beginning of the 2000s (Fig. 3G). The model that best explained variations in growth during (Riv+Sum1) included an interaction between age and sex and a smoothed temporal trend common to all sex and age combinations (Fig. 3G; Table 1G). The lowest growth was recorded for the 2011 smolt cohort, with a growth increment on average 0.31 mm (−11%) shorter than it was at the beginning of the study period.

Table 1. AIC_c and percentage of deviance explained (%Dev) for GAM models describing growth during the river phase (A), first summer (B), first winter (C), plus growth (D), second summer (E), second winter (F) at sea, and the cumulated growth (Riv+Sum1) (G) testing the effects of smolt year (t), sea-age (a_{age}), and sex (b_{sex}) and any interaction between sea-age and sex ($c_{age,sex}$).

Effect	Model	AIC_c	ΔAIC_c	edf	%Dev
A. Riv					
No trend	α	−990	115	2	0
	$\alpha + b_{sex}$	−990	115	3	<1
	$\alpha + a_{age}$	−993	112	3	<1
	$\alpha + a_{age} + b_{sex}$	−1000	105	4	1
	$\alpha + a_{age} + b_{sex} + c_{age,sex}$	−1001	104	5	1
Common trend	$\boldsymbol{\alpha + a_{age} + b_{sex} + c_{age,sex} + s(t)}$	**−1105**	**0**	**14**	**8**
Age-specific trends	$\alpha + a_{age} + b_{sex} + c_{age,sex} + s_{age}(t)$	−1095	10	16	7
Sex-specific trends	$\alpha + a_{age} + b_{sex} + c_{age,sex} + s_{sex}(t)$	−1096	9	10	9
Age- and sex-specific trends	$\alpha + a_{age} + b_{sex} + c_{age,sex} + s_{age,sex}(t)$	−1094	11	13	7
B. Sum1					
No trend	α	413	219	2	0
	$\alpha + b_{sex}$	415	221	3	<1
	$\alpha + a_{age}$	405	211	3	<1
	$\alpha + a_{age} + b_{sex}$	406	212	4	1
	$\alpha + a_{age} + b_{sex} + c_{age,sex}$	406	212	5	1
Common trend	$\boldsymbol{\alpha + a_{age} + s(t)}$	**194**	**0**	**10**	**14**
Age-specific trends	$\alpha + a_{age} + s_{age}(t)$	200	6	15	14
Sex-specific trends	$\alpha + a_{age} + s_{sex}(t)$	201	7	16	15
Age- and sex-specific trends	$\alpha + a_{age} + s_{age,sex}(t)$	208	14	24	15
C. Win1					
No trend	α	−735	282	2	0
	$\alpha + b_{sex}$	−800	217	3	4
	$\alpha + a_{age}$	−992	25	3	15
	$\alpha + a_{age} + b_{sex}$	−992	25	4	16
	$\alpha + a_{age} + b_{sex} + c_{age,sex}$	−995	22	5	16
Common trend	$\alpha + a_{age} + b_{sex} + c_{age,sex} + s(t)$	−1007	10	11	17
Age-specific trends	$\boldsymbol{\alpha + a_{age} + b_{sex} + c_{age,sex} + s_{age}(t)}$	**−1017**	**0**	**16**	**18**
Sex-specific trends	$\alpha + a_{age} + b_{sex} + c_{age,sex} + s_{sex}(t)$	−1008	9	14	18
Age- and sex-specific trends	$\alpha + a_{age} + b_{sex} + c_{age,sex} + s_{age,sex}(t)$	−1011	6	19	18
D. Plus					
No trend	α	−285	38	2	0
	$\alpha + b_{sex}$	−298	25	3	2
Common trend	$\boldsymbol{\alpha + b_{sex} + s(t)}$	**−323**	**0**	**5**	**5**
Sex-specific trends	$\alpha + b_{sex} + s_{sex}(t)$	−320	3	6	5
E. Sum2					
No trend	α	77	12	2	0
	$\alpha + b_{sex}$	79	14	3	<1
Common trend	$\boldsymbol{\alpha + s(t)}$	**65**	**0**	**9**	**4**
Sex-specific trends	$\alpha + s_{sex}(t)$	71	6	10	4
F. Win2					
No trend	α	−898	18	2	0
	$\alpha + b_{sex}$	−897	19	3	<1
Common trend	$\alpha + s(t)$	−910	6	9	5
Sex-specific trends	$\boldsymbol{\alpha + s_{sex}(t)}$	**−916**	**0**	**11**	**6**
G. Riv+Sum1					
No trend	α	1006	308	2	0
	$\alpha + b_{sex}$	1007	309	3	<1
	$\alpha + a_{age}$	994	296	3	<1
	$\alpha + a_{age} + b_{sex}$	990	292	4	1
	$\alpha + a_{age} + b_{sex} + c_{age,sex}$	992	294	5	1
Common trend	$\boldsymbol{\alpha + a_{age} + b_{sex} + s(t)}$	**698**	**0**	**12**	**8**
Age-specific trends	$\alpha + a_{age} + b_{sex} + s_{age}(t)$	706	8	16	7
Sex-specific trends	$\alpha + a_{age} + b_{sex} + s_{sex}(t)$	707	9	17	9
Age- and sex-specific trends	$\alpha + a_{age} + b_{sex} + s_{age,sex}(t)$	717	19	21	7

Note: $s_{age,sex}(t)$, $s_{age}(t)$, $s_{sex}(t)$, or $s(t)$ represent the smoothed temporal trend specific or not to each combination of sea-age and sex. ΔAIC_c is relative to the best model ($\Delta AIC_c = 0$) indicated in bold. "edf" indicates estimated degrees of freedom.

Growth during Win1 was substantially lower than during Sum1 (Fig. 3C). The best model for Win1 included a temporal trend specific to each age class and intercepts specific to each combination of sea-age and sex (Table 1C). Female 1SW individuals had on average higher growth during Win1 than 1SW males, but the deviance explained by the sex effect was low (4%). The temporal smooth displayed no discernable trend through time; on average for all sea-age and sex combinations, growth increment changed by +0.047 mm (+7.8%) from the beginning to the end of the study period.

Over the last two decades, Plus growth in 1SW returning adults increased by 0.13 mm (+18%), as calculated from the fitted smooth temporal trend (Fig. 3D). Males had on average higher Plus growth than females (Table 1D). Growth during Sum2 and Win2 showed temporal variability among 2SW individuals (Tables 1E, 1F), but there was no discernable trend through time (Figs. 3E and 3F). On average, Sum2 changed by −0.069 mm (−5.9%) and Win2 by +0.03 mm (+10.3%) from the beginning to the end of the study period. The best model for Win2 included a temporal trend specific to each sex, but this sex effect only explains very low proportion of the deviance (1%; Table 1E).

A sex-specific probabilistic reaction norm

We found a significant positive effect of the cumulated growth during (Riv+Sum1) on the probability to return as 1SW, together with a strong effect of sex (Fig. 4). The best model explained 16% of the deviance, most of which was explained by the sex effect (Table 2). No interaction for (Riv+Sum1) × β_{sex} was detected, suggesting that the shape of the probabilistic reaction norm is the same for males and females. However, females need to achieve a larger body size than males to have the same probability to return after 1SW (Fig. 4). This is illustrated by the estimation of the cumulated growth measured on scales needed to reach 50% probability to return as 1SW fish, estimated at 1.16 mm for males and 3.74 mm for females. Within the range of observed cumulated (Riv+Sum1) growth values on scales, the probability to mature as 1SW ranges from 8% to 51% for females and from 46% to 90% for males.

We also tested for the influence of Sum1 and Riv separately on the probability to return as 1SW. Significant effects were found for both, but interestingly the contribution of Sum1 in explaining age of returning salmon was 2.5 times higher (as measured by percentage of deviance explained). The influence of Sum1 was significant and influenced the probability to return as 1SW with the same model form as for the cumulated growth (Riv+Sum1), but the percentage of deviance explained by Sum1 was lower than for (Riv+Sum1). Taken together, these results support the hypothesis that growth during the first summer at sea has an overwhelming influence on the maturation decision.

Discussion

Our results provide new insights into a mechanism driving an individual's sex-dependent maturation decision and show that this decision could be responsible for temporal changes in population age structure among returning anadromous fish. The strength of our study is in the detailed analysis of a large sample of scales collected over 30 years on a single river, combined with molecular sex determination. This allowed us to characterize marine growth during several seasons and thereby test hitherto untested hypotheses about how growth variations relate to life-history choices for males and females separately. Specifically, we demonstrated that postsmolt growth during the first summer at sea is an important determinant of the maturation decision in a southern European salmon population and may affect interannual variation in population age structure. This provides valuable information to better predict salmon population dynamics and develop appropriate management measures to mitigate the

Fig. 4. Estimated probabilistic maturation reaction norm showing the individual probability to return after 1SW (Pmat.1SW) as a function of the cumulated growth during river and first summer at sea (Riv+Sum1) for males and females. G50 M and G50 F represent the respective cumulated growth needed to reach 50% probability to mature as 1SW fish estimated for males and females. Individual observations are represented for reference.
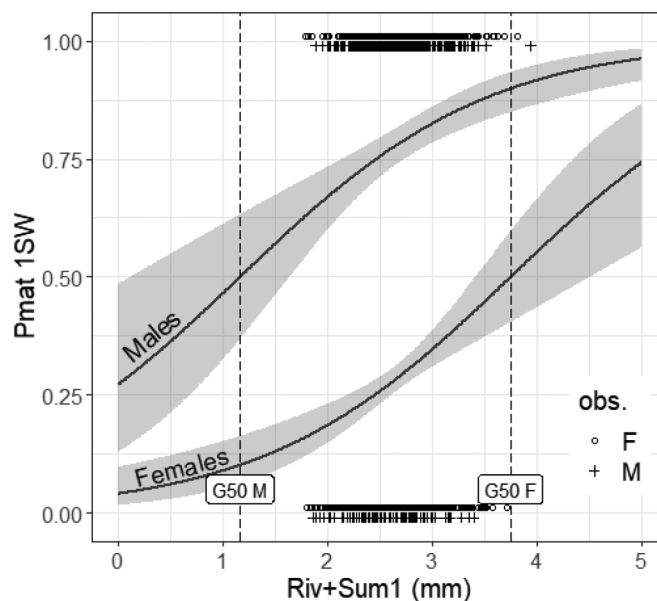

Table 2. AIC$_c$ and percentage of deviance explained (%Dev) for logistic regressions for the individual probability to return as 1SW (Pmat.1SW) testing the effects of the cumulated growth ($\beta_{sex} \times$ (RivSum1)$_i$), sex (b_{sex}), and any difference in slope between males and females (β_{sex}).

Effects	AIC$_c$	ΔAIC$_c$	edf	%Dev
α	2058	328	1	0
$\alpha + \beta \times$ (Riv+Sum1)$_i$	2044	21	2	1
$\alpha + b_{sex}$	1751	314	2	15
$\alpha + b_{sex} + \beta \times$ (Riv+Sum1)$_i$	**1730**	**0**	**3**	**16**
$\alpha + b_{sex} + \beta_{sex} \times$ (Riv+Sum1)$_{i,sex}$	1732	2	4	16

Note: ΔAIC$_c$ is relative to the best model (ΔAIC$_c$ = 0) indicated in bold. "edf" indicates estimated degrees of freedom.

effect of climate change, especially among southern European populations.

Changing growth conditions during the first summer at sea impacts phenotypic traits

Growth increments measured on scales are proxy of body length increments (Francis 1990; Heidarsson et al. 2006; Thomas et al. 2019), and change in body length increments due to change in growth conditions may impact phenotypic traits of salmon returning to their natal river to spawn. Our results demonstrated that salmon experience a decreased growth at the beginning of their marine sojourn (i.e., during their first summer at sea). Interestingly, first summer growth was also the most variable period of growth and showed the strongest decline over the last three decades.

Previous studies reported that mean total length of salmon returning to the Sélune–Sée rivers decreased over recent decades, and this pattern was even more pronounced in 1SW salmon (Bal et al. 2017). Because growth during the later part of the marine migration (i.e., first winter and second year at sea) showed little change during the period of this study, the critical

postsmolt growth phase during the first summer at sea (Friedland and Haas 1996; Friedland 1998) likely explains the widespread decline in body length of returning salmon previously reported (Jonsson et al. 2016; Bal et al. 2017; Todd et al. 2020).

Changes in first summer growth increment is likely to be attributed to a response to changes in marine environmental conditions encountered by salmon during the first summer at sea. In the present case study, a change in smolt migration phenology that would reduce the duration of the growth period over the first summer is unlikely, as no trend in smolt run timing was detected at the nearby fish trap (analysis not shown). Our results are consistent with similar patterns found in other populations and further support a response to large-scale environmental forcing during the marine phase. A recent study showed a decrease in the occurrence of continuous fast growth patterns in the early 2000s among 1SW salmon returning to Scotland, in correlation with SST anomalies in the Norwegian Sea during the early months at sea (Todd et al. 2020). Rapid increase in SST in the Norwegian sea, an area were postsmolts from our study population potentially feed during the first summer at sea (Dadswell et al. 2010; Jonsson et al. 2016; Olmos et al. 2020), has been reported. Jonsson et al. (2016) reported that the decline in salmon body length is unlikely to be explained by the direct effect of global increase in SST affecting metabolic costs, but rather by indirect mechanism(s). Our results provide further evidence to support the findings by Jonsson et al. (2016), who attributed a decrease in size of returning individuals to a decrease in postsmolt growth or growth during the first summer at sea. In the North Atlantic Ocean, increase in SST was correlated with marked changes in food webs, ecosystem functioning (Beaugrand and Reid 2012; Frainer et al. 2017), and a reduction in the abundance and energetic quality of available salmon prey (Mills et al. 2013; Renkawitz et al. 2015).

Interestingly, the common temporal trend in first summer growth among sea-age and sex supports the idea that all individuals were exposed to similar environmental conditions during this early phase of the marine migration, even if some of them underwent longer migrations and returned as 2SW individuals. Although salmon marine migration journey remains largely speculative, our results add to the limited empirical evidence suggesting that 1SW and 2SW European salmon use a common feeding ground until the end of first autumn or early winter, potentially located in the Norwegian Sea (Dadswell et al. 2010; Jacobsen et al. 2001; Haugland et al. 2006). In addition, our study supports the hypothesis that individuals might visit different areas and (or) feed on different prey during their first and second years at sea (Dadswell et al. 2010; Renkawitz et al. 2015).

Sex-specific differences in PMRN

Our results support the hypothesis that maturation decision is modulated by individual cumulated growth (considered as a proxy of body size) during the river phase and the first summer at sea in both males and females, with small body size increasing the probability to postpone maturation. This negative correlation between individual marine growth and the age of returning salmon is consistent with previous empirical studies (Friedland and Haas 1996; Friedland et al. 1997; Silverstein et al. 1997; Campbell et al. 2003) and theoretical work (Mangel and Satterthwaite 2008). The theory of proximate mechanisms developed by Mangel and Satterthwaite (2008) and Thorpe et al. (1998) postulated that maturation decision occurs in November, based on the body lipid content. Following this decision, the maturation process should be completed by the following autumn. However, if the state of maturing fish deteriorates during the winter following the maturation decision, the maturation process could still be interrupted during the following spring (Silverstein et al. 1997; Shearer and Swanson 2000; Campbell et al. 2003; Mangel and Satterthwaite 2008). First summer at sea displayed the highest and most variable growth, and further analyses showed its higher contribution in explaining age of returning salmon. Thus, postsmolt marine growth can be considered an important predictor of future maturation decision. This illustrates that growth during some key (and short) life-history periods can influence age at maturity (Siegel et al. 2018).

Our results also suggest that maturation decision impacts subsequent growth trajectories. In the Sélune–Sée population, 1SW fish exhibited on average lower growth than 2SW individuals during their first winter at sea. These results are consistent with the idea that maturation decision will change the balance of energy allocation, with more energy devoted to gametogenesis and less energy to somatic growth. As the maturation process is costly (Thorpe 2007; Fenkes et al. 2016), 1SW individuals might slow down their somatic development to initiate the maturation process, mobilizing their reserves for gonadic growth (Hunt et al. 1982; Todd et al. 2008). In addition to those physiological changes, the fact that temporal trends in growth were no longer common between 1SW and 2SW individuals during the first winter at sea might also support the idea of a spatial separation of maturing and nonmaturing fish soon after the maturation decision.

Our results provide strong evidence for the existence of a reaction norm that differs between males and females, with females requiring a larger size to achieve a maturation probability comparable to that of males. This result is consistent with a study by Siegel et al. (2018) on Alaskan Chinook salmon (*Oncorhynchus tshawytscha*). Using a long-term dataset of individual phenotypes, including systematic molecular sex determination, they were able to demonstrate that males had a higher probability to mature after one winter at sea than females. Our results are consistent with the idea that females' fitness is more strongly related to body length than are males (Fleming 1996), suggesting that natural selection for larger body length is stronger for females than for males. A sex-specific maturation reaction norm driven by body length can explain the widely reported difference in age at maturation between males and females.

Perspectives

Our study paves the way for a comprehensive framework to explain temporal variability in salmon life history and of temporal variability in the age and sex composition of returns in particular. Further research is needed to complete the description of the underlying mechanisms. Long-term changes in age at maturity is multifactorial, but temporal variations in growth over the first summer at sea might be a key factor to explain the change in age of salmon returning to southern European rivers. A decline in postsmolt growth may constrain more fish to stay additional year(s) at sea before maturing, thus leading to the observed increase in the proportion of 2SW among returns in the recent years. Other studies have reported decreasing trends in the proportion of early maturing individuals among European salmon populations over the last decade. The timing and amplitude of these changes varied widely among populations, suggesting that key environmental drivers of salmon maturation decision might be due to factors acting at both large and local scales (Jonsson et al. 2016; Otero et al. 2012; Olmos et al. 2019).

Change in the environment might also affect the relative contribution of selective forces driving maturation decision (Reznick et al. 1990), which might be expected to manifest in changes to the probabilistic reaction norm over time (Via and Lande 1985; Kirkpatrick and Heckman 1989). Further analyses should investigate potential modification in the shape of the maturation reaction norm over time. The expectation would be an evolution towards earlier age at maturation for the same body size. If confirmed, a gradual change in the shape of the reaction norm could be considered as a mechanism by which salmon may buffer the negative impact of climate change on their population dynamics, by slowing down the dramatic pace of change in age at maturity

and population structure induced by slower growth at sea. Siegel et al. (2018) already reported a long-term decline in growth thresholds for maturation in Chinook salmon, with no clear link to change in growth condition. Recent progress in molecular genetics have shown that maturation age has a strong genetic support in salmon, with different allele of the *VGLL3* gene controlling a major part of the phenotype (Barson et al. 2015). Combining phenotypic and genotypic approaches could give new insights into sex-specific maturation strategies (Czorlich et al. 2018). In particular, quantifying the variation in *VHLL3* gene allele frequency in the population might explain an important part of the variance in age at maturation (Barson et al. 2015).

Scales are an invaluable resource from which to learn about individual life-history strategies and their implications for population dynamics and evolutionary trade-offs. However, one notable limitation to scale analysis is the reliance on a nonrandom subsample of the population that survived to until returning to fresh water, rather than a sample of the entire population at the time of the maturation decision. This is a fundamental issue in our analysis that may bias inferences on temporal changes in growth but also on the PMRN. Ultimately, it hampers our ability to predict the variation in phenotypic traits of returning adults that results from intricate combination of (at least) two unobserved and size-dependent processes: mortality and maturation. When relying on data from survivor fish, size- or growth-selective mortality may bias inferences on the temporal variations of growth at sea. Fishing mortality at sea should be low, especially since a moratorium was imposed in the 1990s on offshore fisheries in their primary fishing grounds (Chaput 2012). Our understanding of natural mortality is incomplete, but acknowledging that mortality is size-dependent such that higher growth would convey a survival advantage (Gregory et al. 2018, 2019), then drawing inferences from survivors might be biased toward over-representation of the "best-growing individuals". Specifically, if individuals with lower growth are under-represented, then the decline in growth observed over the study period might be underestimated. Also, because natural mortality is supposed to be the highest during the first months at sea, the worst underestimation of growth decline probably concerns the first summer at sea period. Biased inferences on growth at sea, and in particular on growth during the first summer at sea, may in turn have dramatic consequences on the estimation of the probabilistic reaction norm. If lower growth is actually associated with a lower probability to mature as 1SW, the positive effect of growth during the first summer at sea on the maturation probability is likely higher than the one inferred from our data.

Ultimately, future exciting research avenues would consist in improving data collection and building predictive models that overcome the confounding factors of maturation and survival. More accurate estimates of growth and survival could be derived from direct sampling of salmon caught and tagged at sea. But tracking salmon at sea is difficult, and current methods are expensive and limited to larger individuals that can bear the monitoring devices without impacting their natural behaviour (Lennox et al. 2017). Additionally, samples of salmon caught at sea from scientific surveys and commercial fisheries bycatch may provide complementary data to that of the current investigation. Finally, modelling approaches may be employed to examine the intricate relationships among the factors of growth, maturation, and size-dependent mortality on PMRN as well.

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Appendix A

Fig. A1 and Table A1 appear below.

Fig. A1. Intra-individual and interindividual variability in the size of the scale for a sample of four scales per individual for 100 individuals from Scorff River, France; boxplots indicate the size of the scale for each individual.
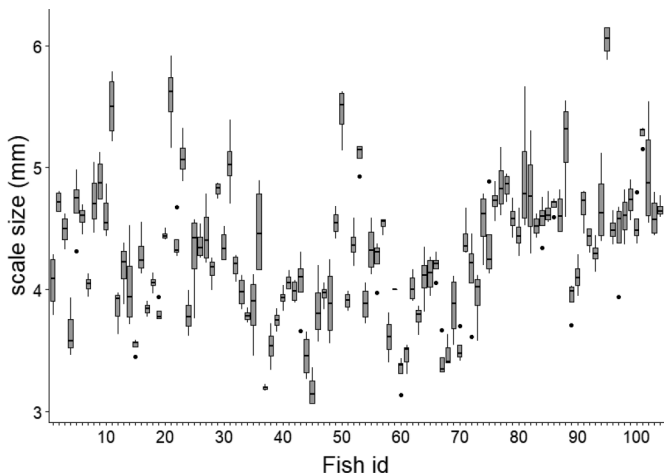

Table A1. Sample size for each smolt year for one-sea-winter (1SW) and two-sea-winter (2SW), males (M) and females (F) and unsuccessfully determined sex (N).

Smolt year	1SW				2SW			
	Total	F	M	N	Total	F	M	N
1986	25	8	4	13	30	5	0	25
1987	28	3	21	4	30	26	3	1
1988	8	1	7	0	30	21	3	6
1989	22	6	11	5	31	24	2	5
1990	30	9	20	1	30	24	4	2
1991	30	18	11	1	30	26	2	2
1992	30	13	14	3	30	22	7	1
1993	30	12	17	1	30	26	3	1
1994	30	19	11	0	32	30	2	0
1995	30	12	17	1	30	26	3	1
1996	30	16	14	0	30	27	3	0
1997	30	6	22	2	30	27	3	0
1998	30	12	18	0	30	27	2	1
1999	30	15	15	0	30	27	3	0
2000	30	11	17	2	31	28	3	0
2001	29	10	19	0	30	29	1	0
2002	25	14	11	0	30	28	1	1
2003	30	17	13	0	30	27	3	0
2004	30	15	15	0	30	30	0	0
2005	30	18	12	0	30	29	1	0
2006	30	14	16	0	30	23	6	1
2007	30	12	18	0	30	26	4	0
2008	30	17	13	0	26	22	4	0
2009	30	18	12	0	23	16	7	0
2010	30	10	20	0	30	25	5	0
2011	30	14	16	0	30	26	4	0
2012	30	17	13	0	30	27	3	0
2013	30	8	22	0	30	24	6	0
2014	30	16	14	0	30	27	3	0
2015	30	14	16	0	30	21	6	3
2016	30	15	15	0	26	23	3	0