


REGULAR ARTICLE

A multi-population approach supports common patterns in marine growth and maturation decision in Atlantic salmon (*Salmo salar* L.) from southern Europe

Cécile Tréhin^{1,2,3}  | Etienne Rivot^{1,3} | Valentin Santanbien¹ | Rémi Patin^{1,4} | Stephen D. Gregory^{5,6,7} | Ludivine Lamireau² | Frédéric Marchand² | William R. C. Beaumont⁵ | Luke J. Scott⁵ | Robert Hillman⁸ | Anne-Laure Besnard¹ | Pierre-Yves Boisson¹ | Lisa Meslier¹ | Andrew R. King⁹ | Jamie R. Stevens⁹ | Marie Nevoux^{1,3}

¹DECOD (Ecosystem Dynamics and Sustainability), INRAE, Institut Agro, IFREMER, Rennes, France

²U3E, Experimental Unit of Aquatic Ecology and Ecotoxicology, INRAE, OFB, Rennes, France

³MIAME- Management of Diadromous Fish in their Environment, OFB, INRAE, Institut Agro, UNIV PAU & PAYS ADOUR/E2S UPPA, Rennes, France

⁴Univ. of Grenoble Alpes, CNRS, Univ. Savoie Mont Blanc, LECA, Grenoble, France

⁵Salmon and Trout Research Centre, Game and Wildlife Conservation Trust, River Laboratory, Wareham, UK

⁶Centre for Environment, Fisheries and Aquaculture Science (Cefas), Weymouth, UK

⁷Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Poole, UK

⁸Environment Agency, Sir John Moore House, Bodmin, UK

⁹Department of Biosciences, Faculty of Health and Life Sciences, Hatherly Laboratories, Exeter, UK

Correspondence

Cécile Tréhin, U3E, Experimental Unit of Aquatic Ecology and Ecotoxicology, INRAE, OFB, 65 rue de St Brieuc, 35042 Rennes, France.
Email: cecile.trehin@inrae.fr

Funding information

European Regional Development Fund through the Interreg Channel VA Programme

Abstract

This study provides a regional picture of long-term changes in Atlantic salmon growth at the southern edge of their distribution, using a multi-population approach spanning 49 years and five populations. We provide empirical evidence of salmon life history being influenced by a combination of common signals in the marine environment and population-specific signals. We identified an abrupt decline in growth from 1976 and a more recent decline after 2005. As these declines have also been recorded in northern European populations, our study significantly expands a pattern of declining marine growth to include southern European populations, thereby revealing a large-scale synchrony in marine growth patterns for almost five decades. Growth increments during their sea sojourn were characterized by distinct temporal dynamics. At a coarse temporal resolution, growth during the first winter at sea seemed to gradually improve over the study period. However, the analysis of finer seasonal growth patterns revealed ecological bottlenecks of salmon life histories at sea in time and space. Our study reinforces existing evidence of an impact of early marine growth on maturation decision, with small-sized individuals at the end of the first summer at sea being more likely to delay maturation. However, each population was characterized by a specific probabilistic maturation reaction norm, and a local component of growth at sea in which some populations have better growth in some years might further amplify differences in maturation rate. Differences between populations were smaller than those between sexes, suggesting that the sex-specific growth threshold for maturation is a well-conserved evolutionary phenomenon in salmon. Finally, our results illustrate that although most of the gain in length occurs during the first summer at sea, the temporal variability in body length at return is buffered against the decrease in post-smolt growth conditions. The intricate combination of growth over successive seasons, and its interplay with the maturation decision, could be regulating body length by maintaining diversity in early growth trajectories, life histories, and the composition of salmon populations.

KEYWORDS

life-history traits, long-term monitoring, post-smolt growth, probabilistic maturation reaction norm, retrospective growth analysis, scale archive

1 | INTRODUCTION

Global climate change is impacting populations worldwide, with effects on their distribution, abundance, demographic rates, and life-history traits (LHT) (Parmesan & Yohe, 2003; Root et al., 2003). Any changes in LHT are likely to impact population dynamics and the resilience of populations to anthropogenic or environmental pressures (Pelletier et al., 2011; Sæther & Bakke, 2000; Stearns, 1992). Atlantic salmon (*Salmo salar*, hereafter referred to as salmon) is a migratory fish facing the cumulative effects of anthropogenic pressures, including climate change, throughout its complex life cycle, which occurs in both freshwater and the marine environment (Gillson et al., 2022; Jonsson & Jonsson, 2009; Thorstad et al., 2021). The abundance of salmon populations has suffered a global decline since the 1970s with no sign of recovery despite the closures of the main commercial fisheries at salmon marine feeding grounds off the Faroe Islands and West Greenland in the 1990s, and the closure of net fisheries in coastal areas throughout their range since then (Chaput, 2012; Olmos et al., 2019). Evidence suggests that these widespread declines are—in part—a result of a reduced salmon marine survival during their first months (summer–autumn) at sea after smolt migration (Beaugrand & Reid, 2012; Friedland et al., 2009; Olmos et al., 2020). Major changes in the age structure of adults that return to freshwater for spawning, which essentially results from changes in the duration of the marine phase before sexual maturation, have also been widely observed (Chaparro-Pedraza & de Roos, 2019; Jonsson et al., 2016; Olmos et al., 2019; Otero et al., 2012). Concomitantly with their decline in abundance, the body size of returning adults also decreased markedly for many different populations (Bacon et al., 2009; Bal et al., 2017; Jonsson et al., 2016; Todd et al., 2012).

Reduction in the abundances, body size, and early marine survival has been observed across most salmon populations in the North Atlantic, despite them spawning in geographically and temporally separated freshwater habitats (Chaput, 2012; Olmos et al., 2020). Global ecosystem changes in the North Atlantic Ocean are now recognized as a major threat to the salmon population (ICES, 2017, 2021). Evidence suggests that ocean warming may have an indirect impact on salmon food resources and a direct impact on metabolic rates, both potentially negatively impacting marine growth rate and other growth-mediated LHT (Friedland et al., 2017; Mills et al., 2013; Renkawitz et al., 2015; Todd et al., 2008; Utne et al., 2021).

The complexity of salmon life histories, together with their long-range migration behavior, necessitates a multidimensional approach to understand the factors affecting their growth at sea and consequences for LHT. It requires combining a multiple-year and a within-year approach, to separate out different growth phases within the marine phase, together with a multi-population approach, to separate

out pan-population “common signals” shared by distant populations from the variability due to “population-specific signals.”

Retrospective growth analysis, that is, the analysis of growth patterns of returning salmon from their scales (or more rarely, otoliths and vertebrae), has a great potential for such a multidimensional approach, providing valuable clues about salmon growth at sea during the whole duration of the marine sojourn, when salmon are not directly observable. Historical scale collections are available for many populations spread over their geographical range and provide the material required to investigate changes in growth for multiple populations. Available literature suggests that any change in marine growth, both during the early marine phase and during later phases, may have significant consequences on population abundance, age and size structure, and the sex ratio of adults returning to spawn after their marine sojourn, and thus their number of offspring. Investigation of post-smolt growth from historical scale collections of returning adults has received particular attention. Indeed, growth during the first months at sea has been shown to be positively correlated to marine survival and smolt return rates (Friedland et al., 2000, 2009). The size obtained by the end of the first summer at sea has also been correlated to the age at maturation, with small body size increasing the probability to postpone maturation, and females requiring a larger size to achieve a maturation probability comparable to that of males (Hutchings & Jones, 1998; Mobley et al., 2021; Tréhin et al., 2021). Growth patterns for later periods of the marine sojourn have been much less investigated, although their influence on salmon survival and other life histories may also be critical. For instance, Barajas et al. (2021) recently demonstrated that diminished growth during late marine stages was associated with low return rates in the Penobscot River salmon population (Maine, USA).

Many studies have reported temporal variation in the early post-smolt growth among multiple populations through the North East Atlantic (NEA). Growth during the first months at sea (or post-smolt growth) was maximal in the 1960s and declined sharply in the 1970s (Friedland et al., 2009). In more recent years, several studies provided convergent evidence of a marked decline in marine growth around 2005, probably in response to an environmental anomaly, as observed for multiple populations in the NEA (Harvey et al., 2022; Todd et al., 2021; Tréhin et al., 2021; Vollset et al., 2022).

Despite the growing evidence for pan-population common signals in growth patterns, they are also subject to a large variability due to population-specific signals. Indeed, location-specific factors, such as local adaptation (Hutchings, 2011), carry-over effects of local conditions in the freshwater phase (Gregory et al., 2017; Metcalfe & Thorpe, 1990), differences in migration timing (Jonsson et al., 2017) and migration routes, parasites or predation during the marine phase (Friedland et al., 2009; Tirronen et al., 2022; Vollset et al., 2022), are all likely to create variable responses between populations.

When comparing groups of salmon populations along a latitudinal gradient spanning the Norwegian coast, Vollset et al. (2022) showed that variability in post-smolt growth increased toward the south, and the 2005 decline in marine growth was also more pronounced in the south of Norway than at mid and northern latitudes. This stronger signal in southern populations echoes the decline in salmon abundance (by sea age) that was more severe in southern Europe (Chaput, 2012; Jonsson & Jonsson, 2009; Olmos et al., 2019). Populations of salmon at the edge of the species' distribution are the most vulnerable to changes in freshwater conditions (Jonsson & Jonsson, 2009; Nicola et al., 2018), and warming of the marine environment may have an even more detrimental impact on the persistence of these populations (Nicola et al., 2018; Piou & Prévost, 2013). Tracking the spatial extent of such an ecological phenomenon throughout the Atlantic basin would help better understand the response of salmon to global changes.

In this study, we investigated long-term changes in the marine growth in a group of five geographically close salmon populations of the English Channel, southern Europe. We applied retrospective growth analysis to scales of 6528 returning adults collected over the period 1969–2017 to provide a detailed description of the long-term and seasonal temporal variability in salmon marine growth over a long time series spanning their entire marine phase. The multi-population approach allows us to separate out the variability in growth due to common signals in all populations from the variability due to signals that is specific to each population. Assuming that our study populations migrate to the Norwegian sea foraging area (Dadswell et al., 2010; Gilbey, Utne, Wennevik, Beck, Kausrud, Hindar, de Leaniz, et al., 2021; MacKenzie et al., 2012; Mork et al., 2012), we expected to detect temporal features in the common signal that are similar to those reported in other NEA populations. We also predicted a rapid decrease in the influence of the population-specific signals upon sea entry, as fast growth in the shared marine environment would override any carry-over effect of the freshwater environment on marine growth. Finally, we correlated growth to maturation decision and discussed the consequences of long-term trends in marine growth on maturation schedule and population structure.

2 | MATERIALS AND METHODS

2.1 | Study sites and data collection

In this study, we used biometric data and scale samples collected over 49 years (1969–2018) from wild salmon in five rivers of the English Channel: Tamar, Frome, Bresle, Sélune, and Scorff (Figure 1). At all sites (except the Frome), trapping devices are operated every year to sample returning adults as part of a dedicated scientific monitoring programme. Additionally, data from salmon scales caught by anglers are reported and included in the study (all sites). All individuals are measured (fork length or total length), weighed, and scales collected from a standard zone for age determination (following Shearer, 1992). We converted all measures of total length for

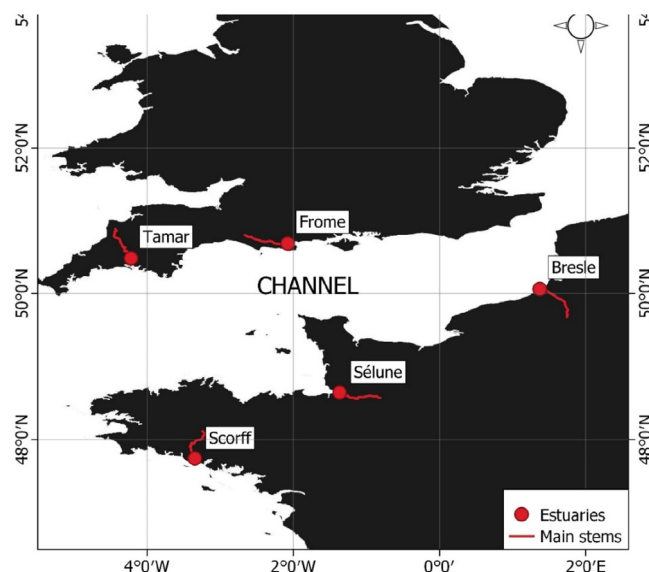


FIGURE 1 Location of the five study populations of Atlantic salmon (*Salmo salar*): Scorff (47°42' N, 3°22' W), Sélune (48°39' N, 1°29' W), Bresle (50°03' N, 1°22' E), Frome (50°41' N, 1°59' W), Tamar (50°21' N, 4°10' W). Figure produced with QGIS version 3.14.

adults caught by anglers on Rivers Scorff and Sélune into fork length using the linear relationship: $\text{length} = -5.69 + 0.95 \times \text{total length}$, as estimated from a dataset of double measurements made on a subset of adults caught at the trap from these two populations (Nevoux, personal communication). Most salmon return as mature maiden adults after one winter at sea (1SW), or more rarely after two winters at sea (2SW). Salmon returning after three winters at sea or after a previous spawning are uncommon, representing less than 1% of the records, and were not included in our analysis. More details about main river characteristics, salmon sampling, and sample size are provided in Table 1.

2.2 | Retrospective growth analysis

To analyse spatio-temporal variability in salmon growth, we selected a subsample of scales from 30 returning adults per year, per sea-age class, and per population when available. Scales from adults caught late in the season were excluded, as they become eroded when salmon mature, which may result in an underestimation of late marine growth (Shearer, 1992). The total sample size was 6528 adults sampled over periods spanning from 22 to 47 years, depending on the population (Table S1). A single operator analysed all the scales from the five populations according to a standard protocol. One scale per fish was digitalized and the image scaled using a stereomicroscope (Zeiss Discovery V8) and an optic camera (Lumenera Infinity 3). All circuli were semi-automatically detected and labeled on a transect line along the longest axis of the scale (following ICES, 1984) using the computer software Media Cybernetics Image Pro Premier 9.2. The transition from river to sea and the first and second winter

TABLE 1 Characteristics of the study sites, study populations of Atlantic salmon (*Salmo salar*), and sample size used in this study (see also Table S1 for more details about sample size).

Population	Scorff	Sélune	Bresle	Frome	Tamar
Region, country	Brittany, France (47° 42' N, 3° 22' W)	Normandy, France (48° 39' N, 1° 29' W)	Normandy, France (50° 03' N, 1° 22' E)	Dorset, England (50° 41' N, 1° 59' W)	Devon, England (50° 21' N 4° 10' W)
Coordinates (estuary)					
Catchment area	480 km ²	1038 km ²	748 km ²	454 km ²	920 km ²
Stage	Smolt	Smolt	Smolt	Smolt	Smolt
Period	1995–2018	1985–2018	1988, 1993, 1994, 2005–2018	2006–2018	2002–2017
Sampling method	Trapping	Trapping	Trapping	Trapping	Trapping
	Anglers (< 1995)	Anglers	Anglers	Anglers	Anglers
	Trapping (> 1995)				
Number of scales analysed for growth	723	958	313	388	448
Number of scales analysed for sex	666	833	202	379	399
Proportion of females in sample	53.1%	15W: 49.5% 25W: 83.9%	15W: 46.7% 25W: 88.2%	15W: 69.1% 25W: 93.3%	15W: 49.0% 25W: 83.0%
References	(Azam et al., 2020; Bal et al., 2017; Marchand et al., 2018; Perrier et al., 2011)			(Lauridsen, 2020)	(Hendry et al., 2007; Hillman, 2020)

annulus were defined based on marked changes in the inter-circuli spacing (Baglinière et al., 2022; Shearer, 1992).

Many studies on marine growth only investigated the early marine post-smolt phase, spanning the first summer, autumn, and winter of the salmon marine sojourn until the beginning of the first winter at sea, which is considered as the most critical stage at sea and when most of the marine growth takes place (Friedland et al., 2009; Harvey et al., 2022; Todd et al., 2021; Vollset et al., 2022). Salmon growth may show contrasting patterns and trends between summer and winter periods, which may reveal seasonal changes in food availability, spatial distribution, and physiology and maturation status (Tréhin et al., 2021). In addition, growth after the first winter at sea may provide insightful clues about ongoing environmental changes, as reported for North American populations (Barajas et al., 2021). To investigate this seasonal variability, growth patterns were analysed at a seasonal scale across multiple seasons. Freshwater growth (Riv) was defined as the distance between the center of the scale and the end of the freshwater zone on the scale. Marine growth was split into five distinct periods: the first summer (Sum1) was measured as the distance between the end of the freshwater zone and the end of the first summer at sea; the first winter (Win1) was measured as the width of the first marine winter annulus; then, the second summer (Sum2) was measured as the distance between the end of the first winter annulus and the end of the second summer at sea; the second winter (Win2) was measured as the width of the second marine winter annulus. Note that Sum2 and Win2 are available only for fish that return as 2SW. In addition, we recorded the plus growth (Plus), measured in 1SW as the distance between the end of the first marine winter annulus and the edge of the scale. As 2SW salmon return to the river early in the season, we do not observe any plus growth following the second winter at sea. In salmonids, scale growth is positively correlated to growth in body length (Dahl, 1910; Francis, 1990), which was confirmed in our dataset (Figure S1). We therefore interpret the width (in millimeters) of each growth period as a proxy of body length increment during that given period.

2.3 | Molecular sexing

To compare growth trajectories and maturation patterns between males and females, we assessed the genetic sex of each individual using DNA extracted from scales. Samples from English populations were analysed using a duplex PCR using primers that amplify a short section of the male-specific *sdY* (sexually dimorphic on the Y-chromosome) gene and primers for the fatty acid-binding protein 6b (*fabp6b*) gene (amplification positive controls) as described in King and Stevens (2020) and King et al. (2022). For the River Tamar, results for 6 years (2007–2009 and 2015–2017) were taken from King et al. (2022). Samples from French populations were analysed with a q-PCR sex marker multiplexing protocol (Besnard et al. 2023). No DNA could be extracted from the scales of adults caught on the River Frome, which were historically cleaned with a caustic solution for better visualization.

2.4 | Partitioning common and population-specific temporal variability in growth

To quantify the amount of variability in growth, we modeled the temporal variability in (i) the body length of returning adults (Lad) and (ii) the width of scale bands corresponding to the five different periods of growth from the same returning adults. To quantify the spatio-temporal variability in growth from body length and scales, we used linear mixed effects models that included temporal random effects to partition out the temporal variability that is common to all populations from that which is population-specific and even population \times sea-age specific. Temporal variation was analysed by using smolt migration year as temporal random effects to align temporal variability in marine growth across sea-age classes. As fixed effects, we tested the effect of population and sea-age (when appropriate, i.e., for the variables Lad, Sum1, and Win1; whereas Plus, Sum2, and Win2 concern 2SW fish only). We did not account for smolt age in the models because it was highly biased toward 1-year-old individuals in all our populations, and it was not controlled for in our subsample of scales. The parametric formulas of the beyond optimal model (sensus Zuur et al., 2009), that is, the model that includes all potential effects, for each of the growth response variables considered were as follows:

1. $Lad_i = A + B_{pop} + C_{age} + D_{age:pop} + \alpha_t + \beta_{t|pop} + \gamma_{t|pop:age} + \varepsilon_i$
2. $Riv_i = A + B_{pop} + C_{age} + D_{age:pop} + \alpha_t + \beta_{t|pop} + \gamma_{t|pop:age} + \varepsilon_i$
3. $Sum1_i = A + B_{pop} + C_{age} + D_{age:pop} + \alpha_t + \beta_{t|pop} + \gamma_{t|pop:age} + \varepsilon_i$
4. $Win1_i = A + B_{pop} + C_{age} + D_{age:pop} + \alpha_t + \beta_{t|pop} + \gamma_{t|pop:age} + \varepsilon_i$
5. $Plus_i = A + B_{pop} + \alpha_t + \beta_{t|pop} + \varepsilon_i$
6. $Sum2_i = A + B_{pop} + \alpha_t + \beta_{t|pop} + \varepsilon_i$
7. $Win2_i = A + B_{pop} + \alpha_t + \beta_{t|pop} + \varepsilon_i$

where i stands for an individual from smolt migration year t , pop stands for the population of origin, and age the sea-age at return. Fixed and random effects are noted as capital Latin letters and Greek letters, respectively. A stands for a general fixed intercept representing the average growth. Estimates of A depend upon identifiability constraints set to estimate fixed effects. In this study, A is estimated as the average growth for the combination of the first (alphabetical or numerical) category of all fixed effects; B_{pop} is a fixed effect of population of origin representing average differences in growth resulting from factors specific to each

population, for example, phenotypic, environmental, and/or genetic background; C_{age} is the fixed effect of sea-age representing difference in growth resulting from physiological and/or behavior response to the timing of the maturation decision; and $D_{age:pop}$ is the fixed effect due to any interaction between population and age. Given that sex difference in marine growth is assumed to be negligible when sea-age is taken into account (Tréhin et al., 2021), we did not account for fixed effect of sex in the models. Random temporal effects were included to test for the strength of common and specific signals in temporal variation in growth. α_t denotes temporal variations due to a common signal in all populations and sea-ages. Nested random effects of population within year $\beta_{t|pop}$ were introduced to test for temporal variations due to signals specific to each population. An additional nested effect of sea-age $\gamma_{t|pop:age}$ was introduced to test for temporal variations in growth that would be specific to maturation strategy within each population. All random effects were independent, normally distributed, and centered on zero. ε_{ij} is an independent and identically normally distributed residual error term. All growth variables were z-standardized so that their variability could be compared directly between populations and periods. Models were fitted to the entire time series from 1969 to 2017.

2.5 | Estimating the probabilistic maturation reaction norm

We built population-specific probabilistic maturation reaction norms (PMRNs) to model the link between growth and maturation decision (Dieckmann & Heino, 2007). Following the methodology developed by Tréhin et al. (2021), we used binomial mixed effect models to investigate how change in the size reached at the end of the first summer at sea, measured as the cumulated growth increments during the freshwater phase until the end of the first summer at sea (RivSum1), influences the probability of maturing as a 1SW. As fish are not directly observable at the time they actually mature at sea, but are only observed when they return, the PMRN models the probability to mature as 1SW conditioned by the fact that the fish survived until it returned (Heino et al., 2002). The parametric formulation of the beyond optimal model was as follows:

$$8. \text{logit}(\text{Pmat.1SW}_i) = A + B_{pop} + C_{sex} + D \times \text{RivSum1}_i + \alpha_t + \beta_{t|pop}$$

where i stands for an individual that migrated as smolt in year t , of a certain sex and from a population pop . To test for an effect of cumulative growth increments on the probability of maturing, RivSum1 was introduced as a single fixed coefficient, constant across sexes and populations (D , the slope of the logistic curve). To test for possible differences in the PMRN between populations and sexes, effects of the population of origin B_{pop} and sex C_{sex} were included as additive fixed effects. We also introduced temporal random effects α_t and $\beta_{t|pop}$ to test for temporal variability due to common signals and signals specific to each population, respectively. As the sex could not be assessed for adult salmon from the River Frome, individuals from this population were excluded from this analysis. We computed estimates of G50, that is the value of the cumulated growth increments that returns a 0.5 maturation probability, such as:

$$9. \widehat{G50}_{pop} = -(\widehat{A} + \widehat{B}_{pop} + \widehat{C}_{sex}) / \widehat{D}$$

where \widehat{A} , \widehat{B}_{pop} , \widehat{C}_{sex} , and \widehat{D} are maximum likelihood estimates of fixed parameters. Therefore, we used the best-fitted models to predict Pmat.1SW using the average growth observed during 1983–2004 (a period of high growth) and 2005–2017 (a period of low growth). Predictions were realized using fixed effects only, with all random effects being fixed to zero.

2.6 | Implementation

All model parameters were estimated in R (R-4.0.0; R Development Core Team, 2018) using the lmer() and glmer() functions in the package lme4 (version 1.1-23; Bates et al., 2014). The top-down strategy was used to select the fixed and random effects (Zuur et al., 2009). Starting with the beyond optimal model incorporating all possible fixed effects, we selected the optimal structure of the random component using the second-order AICc (Burnham & Anderson, 2002; Liang et al., 2008) with restricted maximum likelihood (REML) estimators. Then, accounting for the selected random effects structure, we selected the optimal structure of fixed effects using AICc with ML estimators. Finally, the significance of random effects was tested based on the selected fixed effects structure to confirm the structure of the random temporal variations. We checked normality for all random terms and quantified the variance explained by the fixed effects (marginal R^2) and the variance explained by both fixed and random effects (conditional R^2) for the final model (Nakagawa & Schielzeth, 2013). Detailed statistical results are provided in the Supplementary Material.

3 | RESULTS

3.1 | Partitioning out the temporal variability in individual growth

As expected, the length of adults was longer among 2SW than among 1SW salmon, but it also differed between populations, with evidence of both common and specific signals in temporal variations in adult lengths (Figure 2; Table 2). The length of returning adults started to decline at the beginning of the 2000s (Figure 2), suggesting major changes in marine growth conditions. This decline in body size was more pronounced in 1SW than in 2SW salmon. The temporal variability in adult body length was best described by the random effect term representing a common signal, which had the greatest variance (standard deviation [sd] = 0.02; Tables 2 and S4). Additionally, the random effect terms representing signals specific to each population and each sea-age were selected, but captured less temporal variance than the random effect term representing a common signal (Table 2; Table S2). The final optimal model explained 78% of the total variance, and the model with fixed effects only explained 75% of the variance. This suggests that the fixed effects of sea-age, population, and their

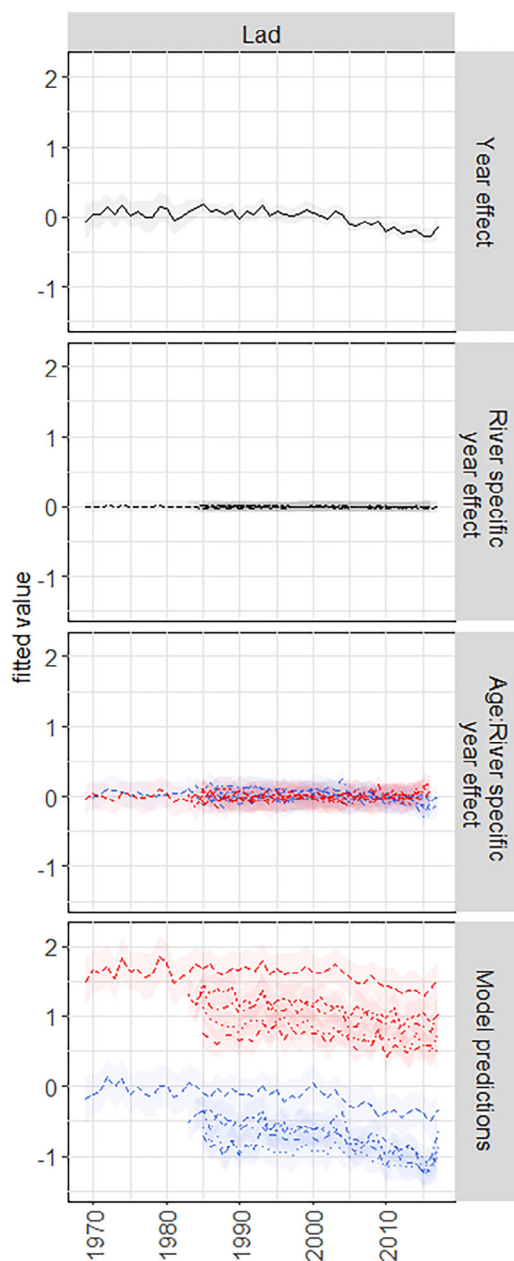


FIGURE 2 Partitioning out the temporal variability in adult body length (Lad) in Atlantic salmon (*Salmo salar*). Upper panel: estimates of the year random effects (smolt year) representing a common signal in temporal variability of all populations and all sea-age classes. Before 1983, common signal is built only from the data available on the Frome population; upper intermediate panel: estimates of the year random effects representing signals in temporal variability specific to each population; lower intermediate panel: estimates of the year random effects specific to each sea-age class in each population; lower panel: model predictions summing all fixed and random effects. Populations: Sélune (dotted line), Bresle (dashed line), Frome (long-dashed line), Scorff (dash-spaced line), and Tamar (dot-dashed line). Sea-age classes: 1SW (blue) and 2SW (red); common trends are in solid black line, and 95% confidence intervals are indicated by the shaded areas.

interactions explained most of the variance, with only 3% of the total variance being captured by the random effect terms. The length of adults from the Frome River was noticeably longer than the average

adult length, being on average 5.4 cm larger for 1SW and 6.1 cm larger for 2SW.

Growth increments revealed contrasting patterns of temporal variations throughout different periods of the life in freshwater and the marine environment (Table 2; Figure 3; Figure S2). Results revealed strong fixed and population-specific signals in scale growth during the river phase (Riv), together with a common signal in temporal interannual variability with no noticeable trend. The final optimal model explained 33% of the total variance, of which 26% was captured by the fixed effects of population and sea age (Table 2; Table S3).

Growth during the first summer at sea (Sum1) was the most variable growth period, as shown by the high value of the sum of temporal random effect terms variances. The marginal R^2 (7%) was much lower than the conditional R^2 (25%), thus indicating that the temporal random effect terms representing common and specific signals captured most of the variability, the influence of fixed effects being less pronounced. The scales of salmon from different populations revealed different growth patterns during the first summer at sea (Table 2; estimates of population effects in Table S4), with the growth bands being narrower in the Bresle than in any other population. Furthermore, growth during the first summer at sea was higher in salmon returning after 1SW than in those returning after 2SW (Figure S2; estimates of sea-age effects in Table S4). The temporal variability in Sum1 was characterized by two periods of sharp decline: one in 1975 that was supported by historical scale records available on the Frome, and one in 2005–2010 (Figure 3). This variability was best described by the random effect term representing a common signal to all populations and sea-ages, which captured more variability ($sd = 0.15$) than the random effect term representing specific signals specific to each population ($sd = 0.02$) (Table 2; Table S4). This indicates a strong temporal synchronicity across populations and sea-ages. The pan-population common signal in the temporal variability in Sum1 captured a long-term decline in early marine growth. In contrast, the population-specific signals in temporal variability in Sum1 did not show any long-term trends.

The partitioning of the temporal variance between fixed and random effect terms was more balanced for growth during the first winter at sea (Win1) (conditional $R^2 = 26\%$, marginal $R^2 = 14\%$; see Table 2). Growth patterns were different between sea-age classes (Table 2), growth bands being on average narrower in salmon returning after 1SW. Differences between sea-ages were higher than those between populations (Figure 3; Table S5). The temporal variability in Win1 was best explained by both random effect terms representing common and specific signals. The random effect term representing a pan-population common signal in growth patterns captured more variability and showed a gradual linear increase over time, whereas the random effect term representing population-specific signals remained flat over the time series (Figure 3). Some of the temporal variability was also specific to each sea-age class, suggesting different growth trajectories among individuals with different maturation schedules.

We selected identical model structures for Plus, Sum2, and Win2 growth variables, with generally a limited amount of variance captured

TABLE 2 Modeling the temporal variability in Atlantic salmon (*Salmo salar*) growth in five populations of southern Europe.

Response variable	Model selected	Conditional R ²	Marginal R ²	Standard deviation of random effects			
				α_t	$\beta_{t pop}$	$\gamma_{t pop age}$	ε_i
Fish body length							
Lad	A + B _{pop} + C _{age} + D _{pop,age} + α_t + $\beta_{t pop}$ + $\gamma_{t pop age}$ + ε_i	78%	75%	0.02	0.002	0.01	0.21
Scale growth increment							
Riv	A + B _{pop} + C _{age} + D _{pop,age} + α_t + $\beta_{t pop}$ + $\gamma_{t pop age}$ + ε_i	33%	26%	0.02	0.04	0.01	0.67
Sum1	A + B _{pop} + C _{age} + α_t + $\beta_{t pop}$ + ε_i	25%	7%	0.15	0.02	-	0.78
Win1	A + B _{pop} + C _{age} + D _{pop,age} + α_t + $\beta_{t pop}$ + $\gamma_{t pop age}$ + ε_i	26%	14%	0.04	0.02	0.06	0.76
Plus	A + B _{pop} + α_t + $\beta_{t pop}$ + ε_i	11%	1%	0.05	0.05	-	0.89
Sum2	A + B _{pop} + α_t + $\beta_{t pop}$ + ε_i	11%	3%	0.05	0.04	-	0.89
Win2	A + B _{pop} + α_t + $\beta_{t pop}$ + ε_i	17%	7%	0.06	0.04	-	0.84

Note: For each response variable, the structure of the best model is presented, as well as the percentage of variance explained by both fixed and random effects (conditional R^2) and by fixed effect only (marginal R^2) for the selected model, and the variance associated to the different random effect terms: that representing a pan-population common signal in temporal variability (α_t), that representing the population-specific signal in temporal variability ($\beta_{t|pop}$), the sea-age specific random effects ($\gamma_{t|pop|age}$), and the residual variance ($\varepsilon_{t,pop,i}$). The response variables are body length of adult (Lad); width of the growth increment on scales for five periods of growth: freshwater phase (Riv), first summer at sea (Sum1), first winter at sea (Win1), plus growth (Plus), second summer at sea (Sum2), second winter at sea (Win2); and the individual probability to return after 1SW (Pmat.1SW).

by the models (conditional $R^2 < 20\%$; Table 2; Tables S6–S8). During each of these periods, growth was best explained by a fixed population-specific effect, and random effect terms representing common and specific signals in their temporal variability (Table 2). The common signal in Plus and Win2 phases showed a slight increasing trend over the study period (Figure 3).

3.2 | Sex- and population-specific maturation reaction norms

The probability of maturing was best explained by a positive effect of the growth variable RivSum1, a sex effect, and a population effect (Table 3). The probability Pmat.1SW was higher in males than in females for any given size in all populations (Figure 4), as also illustrated by the G50 metric (Table 4). The reaction norms for the Bresle population differed markedly from those of the other populations, with males and females maturing on average at a smaller size than their counterparts from other populations (Table 3; Figure 4). As a consequence, the decline in early marine growth after 2005 was predicted to decrease Pmat.1SW. The amplitude of this change depended on the amount of the decline in growth, as well as on the shape of the reaction norm. For instance, the change in Pmat.1SW was small in Tamar and Bresle male salmon because of a small reduction in average marine growth in the former, and a rather flat reaction norm for the range of growth values considered in the latter (Figure 4). Interannual variations in the reaction norm were substantial (including a common temporal signal decreased the AICc by 115 points, Table S9), but temporal variations were mostly explained by population-specific signals without clear temporal trends (Figure S3).

4 | DISCUSSION

Our multi-population approach, spanning 49 years and five populations, provides a regional picture of long-term change in the marine growth of Atlantic salmon during the marine phase of their life cycle and at the southern edge of their distribution. Given that freshwater growth, as measured on the scales of returning salmon, remained stable over the study period, we provide empirical evidence that the observed decline in the length of returning adults may be attributable to a decline in growth potential at sea. Overall, our results indicate a pan-population common signal in marine growth, which—somewhat alarmingly—is a decline in marine growth across all populations and is consistent with the decline in the adult body length at return. Assuming that growth and length attained positively correlate to survival (Chaput et al., 2019; Gregory et al., 2019), the decline in marine growth is consistent with the large-scale and long-term decline in salmon return rate (Friedland, 1993; Friedland et al., 2000; Friedland et al., 2009; Vollset et al., 2022).

The analysis of growth at the seasonal level provides a more temporally resolved understanding needed for the identification of specific ecological bottlenecks in salmon life histories at sea in time and space. Analyses that average temporal variability over longer time frames will have overlooked those specific events. Results presented here showed that the growth was maximal during the first summer at sea. The first summer at sea is also when the growth showed the highest temporal variability, with marked declines over the study period. This result is consistent with the available literature highlighting the high sensitivity and important role of the early post-smolt period to environmental variations (Friedland, 1998; Friedland et al., 2000; Peyronnet et al., 2007). This result contrasts with the growth observed over the later

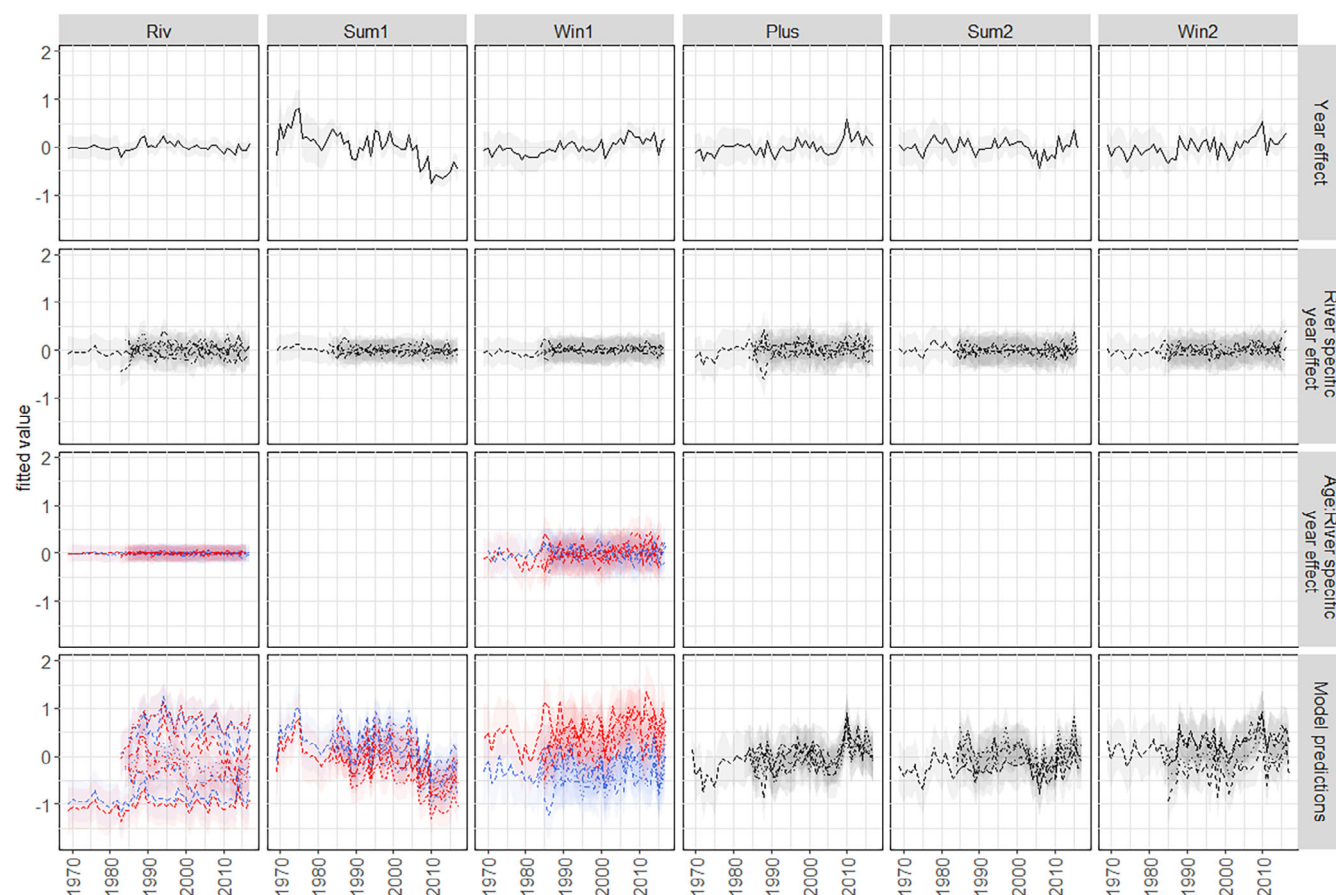


FIGURE 3 Partitioning out the temporal variability of the width of the growth increment on scales of Atlantic salmon (*Salmo salar*) for five periods of growth: river (Riv), first summer at sea (Sum1), first winter at sea (Win1), plus growth (Plus), second summer at sea (Sum2), and second winter at sea (Win2). Upper panel: estimates of the year random effects (smolt year) representing a common signal in temporal variability of all populations and all sea-age classes. Before 1983, common signal is built only from the data available on the Frome population; upper intermediate panel: estimates of the year random effects representing signals in temporal variability specific to each population; lower intermediate panel: estimates of the year random effects specific to each sea-age class in each population. Lower panel: model predictions summing all fixed and random effects. Populations: Sélune (dotted line), Bresle (dashed line), Frome (long-dashed line), Scorff (dash-spaced line), and Tamar (dot-dashed line); Sea-age classes: 1SW (blue) and 2SW (red); common trends are in solid black line, and 95% confidence intervals are indicated by the shaded areas.

TABLE 3 Modeling the probability to mature after 1SW in returning Atlantic salmon (*Salmo salar*) (Pmat.1SW) as a function of cumulated growth during river and first summer at sea (RivSum1), sex, and population.

Response variable	Model selected	Conditional R^2	Marginal R^2	α_t	$\beta_{t pop}$
Pmat.1SW	$A + B_{pop} + C_{sex} + D \times (RivSum1)_{t,sex,pop,i} + \alpha_t + \beta_{t pop}$	38%	26%	0.13	0.52

Note: The structure of the best model is presented, as well as the percentage of variance explained by both fixed and random effects (conditional R^2) and by fixed effects only (marginal R^2) for the selected model, and the variance associated to the different random effect terms representing a pan-population common signal (α_t), population-specific signals ($\beta_{t|pop}$) on temporal variability in Pmat.1SW.

seasons at sea that did not exhibit decreasing trends over the time series. Indeed, growth during the first winter at sea seemed to improve gradually over the study period. Further temporally resolved monthly or weekly growth patterns could potentially offer a better temporal and spatial resolution and understanding of specific ecological bottlenecks in salmon growth at sea. However, the lack of a consensus on the timing of circuli deposition on scales (Carlson et al., 2021; Peyronnet et al., 2007; Thomas et al., 2019;

Todd et al., 2014) would require strong assumptions and potentially higher uncertainty.

For all periods of growth during the marine phase, the fixed population effect was selected in the models, thus indicating that the growth of two individuals from the same population was more similar than the growth of two individuals from different populations. Interestingly, we found no evidence that this population-specific component of individual growth weakened over the duration of the marine

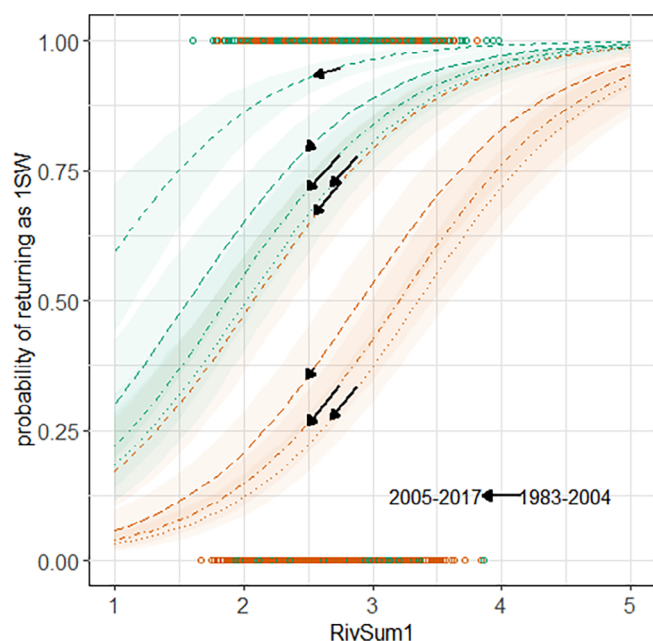


FIGURE 4 Probabilistic maturation reaction norm showing the individual probability to mature after 1SW in returning Atlantic salmon (*Salmo salar*) (Pmat.1SW) as a function of cumulated growth during river and first summer at sea (RivSum1), sex, and population. Populations: Sélune (dotted line), Bresle (dashed line), Scorff (dash-spaced line), and Tamar (dot-dashed line); sex: female (brown) and male (green); 95% confidence intervals are indicated by the shaded areas. Random effect of year is not represented; see Figure S2 for further details on random effects. Arrows illustrate the change in Pmat.1SW as predicted from the model from the average post-smolt growth observed during 1983–2004 (a period of high growth) and 2005–2017 (a period of low post-smolt growth). Predictions were realized using fixed effects only, with all random effects being fixed to zeros.

sojourn. Rather, the amount of deviance explained by the models decreased from one season at sea to the next, suggesting that the variability between individual growth trajectories increases with progression through the seasons. Similarly, some heterogeneity in marine growth between neighboring populations was also reported across the North Atlantic Ocean (Friedland et al., 2009; Vollset et al., 2022) and the Baltic Sea (Jacobson et al., 2021). This heterogeneity between populations questions whether the information from intensive surveys on a few index rivers should be used to inform management actions on other rivers where no information is available. Indeed, the ubiquity of these population-specific signals could confound pan-population common signals, which may lead to management actions with no or unwanted effects on specific populations.

TABLE 4 Sex- and population-specific G50 for Atlantic salmon (*Salmo salar*) calculated as the mean cumulated growth RivSum1 for a probability Pmat.1SW = 0.5. G50 estimates are computed from maximum likelihood estimates of the fixed coefficients of the selected model: $G50_{sex, pop} = -(A + B_{pop} + C_{sex})/D$.

	Bresle	Scorff	Sélune	Tamar
G50 Female (mm)	2.07	3.36	3.20	2.91
G50 Male (mm)	0.73	2.02	1.87	1.57

Our multi-population approach has proven successful in identifying ecological patterns of regional and global significance. It provides a regional, pan-population common signal of post-smolt growth variability that is separate from population-specific signals. Despite some differences among populations, we provide empirical evidence of salmon life history being influenced by common signals in the marine environment. The migration of salmon from different populations to common oceanic foraging grounds may synchronize the temporal variability in growth across geographically distant populations (Chaput, 2012; Olmos et al., 2020). For the first summer growth, the amount of temporal variability explained by the random effect term representing a common signal among all five populations was three times larger than that explained by the random term representing population-specific signals. Specifically, we identified an abrupt decline in growth in 1976 (based on the Frome samples), as well as a more recent decline after 2005 that both appeared similar in amplitude (−0.29 mm between 1975 and 1981, and −0.28 mm between 2004 and 2010). The former decline has been also recorded in Ireland and Scotland (Friedland et al., 2009; Peyronnet et al., 2007), whereas the latter decline has been detected in populations from Scotland and from all over southern and western Norway (Harvey et al., 2022; Todd et al., 2021; Vollset et al., 2022).

With this study, we significantly expand a pattern of declining marine growth among northern European salmon populations to include southern European populations, thereby revealing a large-scale synchrony in marine growth patterns for almost five decades. Evidence of a common signal in the first summer growth across large groups of populations from southern Europe is consistent with the existence of a common summer feeding ground in the Norwegian Sea (Bradbury et al., 2021; Dadswell et al., 2010; Gilbey, Utne, Wennevik, Beck, Kausrud, Hindar, de Leaniz, et al., 2021). Vollset et al. (2022), and other authors have attributed the 2005 decline to the low amount of Arctic water entering the North Atlantic Ocean at that time, associated with high sea surface temperature, low phytoplankton abundance, low abundance, and low energetic content of salmon prey species in the NEA region. Interestingly, the sharp decline in post-smolt growth observed in 2005 was not detected in the growth of salmon populations from northern Norway (Vollset et al., 2022). In Europe, southern populations are the most distant from the feeding grounds (Dadswell et al., 2010; Gilbey, Utne, Wennevik, Beck, Kausrud, Hindar, de Leaniz, Garcia de Leaniz, et al., 2021; Jacobsen et al., 2012). Therefore, they may incur the highest travel cost, the highest environmental variability, and be at greater risk of ecological mismatch between migration phenology and resource availability. Environmental variability may be exacerbated in populations farther

away from a shared feeding ground at sea and may explain the greater severity in the decline of salmon abundance in the southern areas of the species' range (Chaput, 2012; Jonsson & Jonsson, 2009).

In the literature, we could not find empirical evidence of an ecosystem change at the scale of the North Atlantic basin. Indeed, the sharp decline in early post-smolt growth (first summer) reported in southern European populations, feeding in the Norwegian sea, was not detected in salmon populations from northern Norway (Vollset et al., 2022) or North America (Barajas et al., 2021; Hogan & Friedland, 2010; Tillotson et al., 2021), at a time when these post-smolts are expected to be already up at the feeding grounds in the Arctic waters of the White Sea and Barents Sea, and to the Labrador Sea, respectively. The locations of feeding grounds remain imprecisely defined over space and time, as it proves extremely difficult to directly track and catch smolts at sea (especially for small populations). Inferring ecosystem anomalies, such as the events of the late 1970s and 2005, from calcified animal structures, including salmon scales, may help to better understand the migration behaviors, including spatio-temporal aggregations, of salmon populations at sea.

Temporal variations in growth during later phases at sea after the first summer were more variable among populations and less easily interpretable. From our results, growth during the first winter at sea seemed to gradually improve over the study period. Although the temperature has been generally negatively related to body length (Todd et al., 2008, 2021; but see Harvey et al., 2022), a warming climate may actually provide better feeding opportunities for salmon over the harsh winter months at northern latitudes, especially when compared with the likely higher temperatures prevailing at southern latitudes.

Our results show that the temporal variability in body length at return is buffered with regard to the variability observed in early post-smolt growth. In our study populations, the body length of returning adult salmon became smaller over the years, as observed in many other populations across Scotland (Bacon et al., 2009; Todd et al., 2008), Ireland (Quinn et al., 2006), Norway (Jonsson et al., 2016), and France (Bal et al., 2017). However, none of those studies, including the present one, can detect a sharp decline in body length after 1975 and 2005, similar to the trends reported in the first summer growth at sea. Although most of the gain in length occurs during the first summer at sea (Tréhin et al., 2021), adult body length is a result of growth over successive and contrasting seasons. A mechanism of compensatory growth at the individual level (Barajas et al., 2021), or the improvement in growth conditions in the winter season (this study), may compensate for an initial slow growth and attenuate the overall decline in body length after the marine sojourn. Finally, the intricate relationship between growth trajectories and the maturation decision may also explain the loss of correlation between early marine growth and body size at return. Indeed, the timing of the maturation decision depends on growth itself (Tréhin et al., 2021, this study). Individuals of small size at the end of the first summer at sea were more likely to delay maturation, which offers the opportunity of another year of growth, if the individual survives. As such, the maturation decision can be considered as a key demographic transition

regulating body length by shuffling early growth trajectories, life histories, and the age- and sex-specific structure of salmon populations.

Our study reinforces evidence of sex-specific PMRNs driven by early marine growth. Each population was characterized by a specific reaction norm, but differences between populations were smaller than those between sexes. This suggests that a sex-specific growth threshold is a well-conserved evolutionary phenomenon in salmon, which is likely regulated by common selective forces (Debes et al., 2014; Hutchings, 2004; Siegel et al., 2018). This could explain some of the widely reported differences in age at maturity between male and female salmon (McPhee et al., 2016; Siegel et al., 2018; Tréhin et al., 2021). Our results suggest that for a given amount of growth, even small differences between reaction norms can lead to significant differences in the maturation decision, as observed in the Bresle, Scorff, Sélune, and Tamar populations, and may explain differences in age structure of returning adults among those populations. Specifically, variations in growth over the study period lead to higher variability in the proportion of 1SW among females, whereas male reaction norms reached a plateau for this range of growth. Differences among populations may be further amplified by the specific signal in their growth at sea, with some population having better growth in some years. Adaptive selection forces could potentially modify the shape of the reaction norm, acting as a buffering mechanism against the detrimental effect on fitness of lower growth at sea (Griff et al., 2003; Siegel et al., 2018). However, although we detected some temporal variability in maturation probability, we did not detect any trend in the reaction norm over time.

Salmon population dynamics at the North Atlantic basin scale supported basin-wide synchrony in their survival and maturation (Olmos et al., 2019). For their second year at sea, 2SW salmon from southern Europe are reported to be feeding off the west coast of Greenland, together with salmon from North America (Dadswell et al., 2010; Gilbey, Utne, Wennevik, Beck, Kausrud, Hindar, de Leaniz, Garcia de Leaniz, et al., 2021; Jacobsen et al., 2012; Reddin & Friedland, 1999). Thus, ongoing environmental change in Greenland waters is expected to influence feeding conditions for salmon from Europe and North America. This advocates extension of our study to the North Atlantic basin scale. However, examination of the available empirical evidence failed to pinpoint the expected similarities in growth trajectories between European and North American populations (Barajas et al., 2021; Hogan & Friedland, 2010). This result is consistent with Tirronen et al. (2022) who suggested a non-stationarity and recent divergence in the ecological response of European and North American salmon populations. One exciting research avenue would be to extend our analysis to a larger set of populations across the North Atlantic basin to embrace more contrasting environments and a wider range of life histories. This would allow to better partition out a pan-population common signal from population-specific local signals in the timing and the amplitude of population response across the species' range (Olmos et al., 2019). To go further in that direction, we recommend that greater attention is paid to the harmonization of metrics used to describe growth from scales (e.g., Peyronnet et al., 2007) to allow robust multi-population comparison across large spatial scales.

AUTHOR CONTRIBUTIONS

William R. C. Beaumont, Stephen D. Gregory, Robert Hillman, Frédéric Marchand, and Luke J. Scott provided the biological data and prepared the scale samples. Ludivine Lamireau and Frédéric Marchand conducted growth measurements. Anne-Laure Besnard, Pierre-Yves Boisson, Andrew R. King, Lisa Meslier, and Jamie R. Stevens conducted the molecular sexing. Cécile Tréhin, Etienne Rivot, Valentin Santanbien, Rémi Patin, and Marie Nevoux conducted the statistical analysis. Cécile Tréhin, Etienne Rivot, and Marie Nevoux conceived the initial idea and wrote the main paper in collaboration with the other coauthors. All authors discussed results and implications, providing significant inputs to the manuscript at all stages.

ACKNOWLEDGMENTS

We are grateful to all the people involved in collecting the data used in this study, including present and past members of INRAE 1036 U3E, INRAE DECOD, OFB, GWTC, Environment Agency, and University of Exeter. We are grateful to the National Center for the Interpretation of Salmonid Catches for running the national catch declaration scheme on Atlantic salmon in France, with the technical and financial support of INRA 1036 U3E. The study was partly funded by the European Regional Development Fund through the Interreg Channel VA Programme (project: SAMARCH), which funded the salary of Cécile Tréhin, Ludivine Lamireau, Lisa Meslier, Pierre-Yves Boisson, Valentin Santanbien, Rémi Patin, Andrew R. King, and Stephen D. Gregory and provided financial support for data collection and analysis.

ORCID

Cécile Tréhin  <https://orcid.org/0000-0002-8625-3513>

REFERENCES

- Azam, D., Basilico, L., Beaulaton, L., Marchand, F., & Prévost, E. (2020). *Trois décennies d'observations et de recherche sur les poissons migrateurs* (60 p). Office français de la biodiversité, Collection Comprendre pour agir.
- Bacon, P. J., Palmer, S. C. F., MacLean, J. C., Smith, G. W., Whyte, B. D. M., Gurney, W. S. C., & Youngson, A. F. (2009). Empirical analyses of the length, weight, and condition of adult Atlantic salmon on return to the Scottish coast between 1963 and 2006. *ICES Journal of Marine Science: Journal du Conseil*, 66, 844–859.
- Baglinière, J.-L., Jeannot, N., Nevoux, M., Lamireau, L., Lange, F., Josset, Q., & Marchand, F. (2022). Guide pour l'interprétation des écailles et l'estimation de l'âge chez le saumon atlantique (*Salmo salar*) dans les populations françaises. *Guides et Protocoles*, 164. https://oai-gem.ofb.fr/exl-php/document-affiche/ofb_recherche_oai/OUVRE_DOC/49795?vue=ofb_recherche_oai&action=OUVRE_DOC&cid=49795&fic=doc00073107.pdf (Accessed 5 December 2022)
- Bal, G., Montorio, L., Rivot, E., Prévost, E., Baglinière, J.-L., & Nevoux, M. (2017). Evidence for long-term change in length, mass and migration phenology of anadromous spawners in French Atlantic salmon *Salmo salar*: Changing *S. salar* size and phenology. *Journal of Fish Biology*, 90, 2375–2393.
- Barajas, M. M. F., Sheehan, M. T. F., Haas-Castro, M. R., Ellingson, M. B., & Mills, D. K. (2021). Retrospective analysis of marine growth and relationships to return rates of Penobscot River Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Science*, 79, 863–874.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*.
- Beaugrand, G., & Reid, P. C. (2012). Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. *ICES Journal of Marine Science*, 69, 1549–1562.
- Besnard, A.-L., Meslier, L., Jousseau, T., Nevoux, M., Marchand, F., & Laune, S. (2023). Fast, safe and high-throughput Real-Time PCR protocol for molecular sex identification in *Salmo salar*, applicable to historic scale collections. *bioRxiv*. <https://doi.org/10.1101/2023.09.05.556299>
- Bradbury, I. R., Lehnert, S. J., Messmer, A., Duffy, S. J., Verspoor, E., Kess, T., Gilbey, J., Wennevik, V., Robertson, M., Chaput, G., Sheehan, T., Bentzen, P., Dempson, J. B., & Reddin, D. (2021). Range-wide genetic assignment confirms long-distance oceanic migration in Atlantic salmon over half a century. *ICES Journal of Marine Science*, 2021, 1434–1443. <https://doi.org/10.1093/icesjms/fsaa152>
- Burnham, K. P., & Anderson, D. R. (2002). A practical information-theoretic approach. In *Model selection and multimodel inference* (2nd ed., pp. 70–71). Springer-Verlag.
- Carlson, L. G., Sheehan, T. F., Tillotson, M. D., & Mills, K. E. (2021). Date of marine annulus formation in Atlantic salmon (*Salmo salar*) and implications for retrospective growth analyses using scales. *Journal of Fish Biology*, 99, 796–806.
- Chaparro-Pedraza, P. C., & de Roos, A. M. (2019). Environmental change effects on life-history traits and population dynamics of anadromous fishes. *The Journal of Animal Ecology*, 88, 1178–1190.
- Chaput, G. (2012). Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science*, 69, 1538–1548.
- Chaput, G., Carr, J., Daniels, J., Tinker, S., Jonsen, I., & Whoriskey, F. (2019). Atlantic salmon (*Salmo salar*) smolt and early post-smolt migration and survival inferred from multi-year and multi-stock acoustic telemetry studies in the Gulf of St. Lawrence, Northwest Atlantic. *ICES Journal of Marine Science*, 76, 1107–1121.
- Dadswell, M., Spares, A., Reader, J., & Stokesbury, M. (2010). The North Atlantic subpolar gyre and the marine migration of Atlantic salmon *Salmo salar*: The 'merry-go-round' hypothesis. *Journal of Fish Biology*, 77, 435–467.
- Dahl, K. (1910). *The age and growth of salmon and trout in Norway as shown by their scales*. Salmon and Trout Assoc <https://www.biodiversitylibrary.org/bibliography/27730>.
- Debes, P. V., Fraser, D. J., Yates, M., & Hutchings, J. A. (2014). The between-population genetic architecture of growth, maturation, and plasticity in Atlantic Salmon. *Genetics*, 196, 1277–1291.
- Dieckmann, U., & Heino, M. (2007). Probabilistic maturation reaction norms: Their history, strengths, and limitations. *Marine Ecology Progress Series*, 335, 253–269.
- Francis, R. I. C. C. (1990). Back-calculation of fish length: A critical review. *Journal of Fish Biology*, 36, 883–902.
- Friedland, K. (1993). Marine survival of north American and European Atlantic salmon: Effects of growth and environment. *ICES Journal of Marine Science*, 50, 481–492.
- Friedland, K., Hansen, L. P., Dunkley, D. A., & McLean, J. E. (2000). Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES Journal of Marine Science*, 57, 419–429.
- Friedland, K. D. (1998). Ocean climate influences on critical Atlantic salmon (*Salmo salar*) life history events. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 119–130.
- Friedland, K. D., Dannewitz, J., Romakkaniemi, A., Palm, S., Pulkkinen, H., Pakarinen, T., & Oeberst, R. (2017). Post-smolt survival of Baltic salmon in context to changing environmental conditions and predators. *ICES Journal of Marine Science*, 74, 1344–1355.

- Friedland, K. D., MacLean, J. C., Hansen, L. P., Peyronnet, A. J., Karlsson, L., Reddin, D. G., Maoiléidigh, N. Ó., et al. (2009). The recruitment of Atlantic salmon in Europe. *ICES Journal of Marine Science: Journal du Conseil*, 66, 289–304.
- Gilbey, J., Utne, K. R., Wennevik, V., Beck, A. C., Kausrud, K., Hindar, K., de Leaniz, C. G., Garcia de Leaniz, C., Cherbonnel, C., Coughlan, J., Cross, T. F., Dillane, E., Ensing, D., García-Vázquez, E., Hole, L. R., Holm, M., Holst, J. C., Jacobsen, J. A., Jensen, A. J., ... Verspoor, E. (2021). The early marine distribution of Atlantic salmon in the North-East Atlantic: A genetically informed stock-specific synthesis. *Fish and Fisheries*, 22, 1274–1306.
- Gilbey, J., Utne, K. R., Wennevik, V., Beck, A. C., Kausrud, K., Hindar, K., de Leaniz, C. G., et al. (2021). The early marine distribution of Atlantic salmon in the North-East Atlantic: A genetically informed stock-specific synthesis. *Fish and Fisheries*, 22, 1274–1306.
- Gillson, J. P., Bašić, T., Davison, P. I., Riley, W. D., Talks, L., Walker, A. M., & Russell, I. C. (2022). A review of marine stressors impacting Atlantic salmon *Salmo salar*, with an assessment of the major threats to English stocks. *Reviews in Fish Biology and Fisheries*, 32, 879–919.
- Gregory, S. D., Ibbotson, A. T., Riley, W. D., Nevoux, M., Lauridsen, R. B., Russell, I. C., Britton, J. R., Gillingham, P. K., Simmons, O. M., & Rivot, E. (2019). Atlantic salmon return rate increases with smolt length. *ICES Journal of Marine Science*, 76, 1702–1712.
- Gregory, S. D., Nevoux, M., Riley, W. D., Beaumont, W. R. C., Jeannot, N., Lauridsen, R. B., Marchand, F., Scott, L. J., & Roussel, J. M. (2017). Patterns on a parr: Drivers of long-term salmon parr length in U.K. and French rivers depend on geographical scale. *Freshwater Biology*, 62, 1117–1129.
- Grift, R., Rijnsdorp, A., Barot, S., Heino, M., & Dieckmann, U. (2003). Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Marine Ecology Progress Series*, 257, 247–257.
- Harvey, A., Skaala, Ø., Borgstrøm, R., Fjeldheim, P. T., Christine Andersen, K., Rong Utne, K., Askeland Johnsen, I., Fiske, P., Winterthun, S., Knutar, S., Sægrov, H., Urdal, K., & Alan Glover, K. (2022). Time series covering up to four decades reveals major changes and drivers of marine growth and proportion of repeat spawners in an Atlantic salmon population. *Ecology and Evolution*, 12, e8780.
- Heino, M., Dieckmann, U., & GODØ, O. R. (2002). Measuring probabilistic reaction norms for age and size at maturation. *Evolution*, 56, 669–678.
- Hendry, K., Sambrook, H., & Waterfall, R. (2007). Assessment of salmon stocks and the use of management targets; a case study of the river Tamar, England. *Fisheries Management and Ecology*, 14, 7–19.
- Hillman, R. (2020). Tamar Salmon and sea trout Index River monitoring report, 2020. *Environment Agency*, 11.
- Hogan, F., & Friedland, K. D. (2010). Retrospective growth analysis of Atlantic salmon *Salmo salar* and implications for abundance trends. *Journal of Fish Biology*, 76, 2502–2520.
- Hutchings, J. A. (2004). Norms of reaction and phenotypic plasticity in salmonid life histories. In A. P. Hendry & S. C. Stearns (Eds.), *Evolution illuminated: Salmon and their relatives* (pp. 154–174). Oxford University Press.
- Hutchings, J. A. (2011). Old wine in new bottles: Reaction norms in salmonid fishes. *Heredity*, 106, 421–437.
- Hutchings, J. A., & Jones, M. E. B. (1998). Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 22–47.
- ICES. (1984). Report of the Atlantic salmon scale reading workshop. Aberdeen, Scotland, 23–28 April 1984. Copenhagen.
- ICES. (2017). Report of the Workshop on Potential Impacts of Climate Change on Atlantic Salmon Stock Dynamics (WKCCISAL). report. https://ices-library.figshare.com/articles/report/Report_of_the_Workshop_on_Potential_Impacts_of_Climate_Change_on_Atlantic_Salmon_Stock_Dynamics_WKCCISAL_/19290416/1.
- ICES. (2021). Working Group on North Atlantic Salmon (WGNAS) report. https://ices-library.figshare.com/articles/report/Working_Group_on_North_Atlantic_Salmon_and_WGNAS_2021_Addendum/18621548/4.
- Jacobsen, J. A., Hansen, L. P., Bakkestuen, V., Halvorsen, R., Reddin, D. G., White, J., Maoiléidigh, Ó., et al. (2012). Distribution by origin and sea age of Atlantic salmon (*Salmo salar*) in the sea around the Faroe Islands based on analysis of historical tag recoveries. *ICES Journal of Marine Science*, 69, 1598–1608.
- Jacobson, P., Whitlock, R., Huss, M., Leonardsson, K., Östergren, J., & Gårdmark, A. (2021). Growth variation of Atlantic salmon *Salmo salar* at sea affects their population-specific reproductive potential. *Marine Ecology Progress Series*, 671, 165–174.
- Jonsson, B., Jonsson, M., & Jonsson, N. (2017). Influences of migration phenology on survival are size-dependent in juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Zoology*, 95, 581–587.
- Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, 75, 2381–2447.
- Jonsson, B., Jonsson, N., & Albretsen, J. (2016). Environmental change influences the life history of salmon *Salmo salar* in the North Atlantic Ocean. *Journal of Fish Biology*, 88, 618–637.
- King, R. A., & Stevens, J. R. (2020). An improved genetic sex test for Atlantic salmon (*Salmo salar* L.). *Conservation Genetics Resources*, 12, 191–193.
- King, R. A., Toms, S., & Stevens, J. R. (2022). Evaluating the importance of accurate sex ratios on egg deposition targets and conservation limit compliance for Atlantic salmon (*Salmo salar* L.) in the River Tamar, south-west England. *Fisheries Management and Ecology*, 30(2), 161–170. Portico. <https://doi.org/10.1111/fme.12609>
- Lauridsen, R. B. (2020). Fisheries research review 2020. *Game and Wildlife Conservation Trust*, 28. <https://www.gwct.org.uk/media/1234772/Fisheries-Report-2020.pdf>.
- Liang, H., Wu, H., & Zou, G. (2008). A note on conditional AIC for linear mixed-effects models. *Biometrika*, 95, 773–778.
- MacKenzie, K. M., Trueman, C. N., Palmer, M. R., Moore, A., Ibbotson, A. T., Beaumont, W. R. C., & Davidson, I. C. (2012). Stable isotopes reveal age-dependent trophic level and spatial segregation during adult marine feeding in populations of salmon. *ICES Journal of Marine Science*, 69, 1637–1645.
- Marchand, F., Aymes, J.-C., Gueraud, F., Guillard, J., Goulon, C., Hamelet, V., Lange, F., et al. (2018). Colisa, the collection of ichthyological samples. *Portail Data INRAE*, V1. <https://doi.org/10.15454/D30DJM>.
- McPhee, M., Leon, J., Wilson, L., Siegel, J., & Agler, B. (2016). Changing growth and maturity in Western Alaskan Chinook Salmon, *Oncorhynchus tshawytscha*, brood years 1975–2005. *North Pacific Anadromous Fish Commission Bulletin*, 6, 307–327.
- Metcalfe, N. B., & Thorpe, J. E. (1990). Determinants of geographical variation in the age of seaward-migrating Salmon, *Salmo salar*. *Journal of Animal Ecology*, 59, 135–145.
- Mills, K. E., Pershing, A. J., Sheehan, T. F., & Mountain, D. (2013). Climate and ecosystem linkages explain widespread declines in north American Atlantic salmon populations. *Global Change Biology*, 19, 3046–3061.
- Mobley, K. B., Aykanat, T., Czorlich, Y., House, A., Kurko, J., Miettinen, A., Moustakas-Verho, J., Salgado, A., Sinclair-Waters, M., Verta, J. P., & Primmer, C. R. (2021). Maturation in Atlantic salmon (*Salmo salar*, Salmonidae): A synthesis of ecological, genetic, and molecular processes. *Reviews in Fish Biology and Fisheries*, 31, 523–571.
- Mork, K. A., Gilbey, J., Hansen, L. P., Jensen, A. J., Jacobsen, J. A., Holm, M., Holst, J. C., Ó Maoiléidigh, N., Vikebø, F., McGinnity, P., Melle, W., Thomas, K., Verspoor, E., & Wennevik, V. (2012). Modelling the migration of post-smolt Atlantic salmon (*Salmo salar*)

- in the Northeast Atlantic. *ICES Journal of Marine Science*, 69, 1616–1624.
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142.
- Nicola, G. G., Elvira, B., Jonsson, B., Ayllón, D., & Almodóvar, A. (2018). Local and global climatic drivers of Atlantic salmon decline in southern Europe. *Fisheries Research*, 198, 78–85.
- Olmos, M., Massiot-Granier, F., Prévost, E., Chaput, G., Bradbury, I. R., Nevoux, M., & Rivot, E. (2019). Evidence for spatial coherence in time trends of marine life history traits of Atlantic salmon in the North Atlantic. *Fish and Fisheries*, 20, 322–342.
- Olmos, M., Payne, M. R., Nevoux, M., Prévost, E., Chaput, G., Du Pontavice, H., Guitton, J., et al. (2020). Spatial synchrony in the response of a long range migratory species (*Salmo salar*) to climate change in the North Atlantic Ocean. *Global Change Biology*, 26, 1319–1337.
- Otero, J., Jensen, A. J., L'Abée-Lund, J. H., Stenseth, N. C., Størvik, G. O., & Vøllestad, L. A. (2012). Contemporary Ocean warming and freshwater conditions are related to later sea age at maturity in Atlantic salmon spawning in Norwegian rivers. *Ecology and Evolution*, 2, 2192–2203.
- Parnesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.
- Pelletier, F., Moyes, K., Clutton-Brock, T. H., & Coulson, T. (2011). Decomposing variation in population growth into contributions from environment and phenotypes in an age-structured population. *Proceedings of the Royal Society B: Biological Sciences*, 279, 394–401.
- Perrier, C., Guyomard, R., Bagliniere, J.-L., & Evanno, G. (2011). Determinants of hierarchical genetic structure in Atlantic salmon populations: Environmental factors vs. anthropogenic influences. *Molecular Ecology*, 20, 4231–4245.
- Peyronnet, A., Friedland, K. D., Maoileidigh, N. Ó., Manning, M., & Poole, W. R. (2007). Links between patterns of marine growth and survival of Atlantic salmon *Salmo salar*, L. *Journal of Fish Biology*, 71, 684–700.
- Piou, C., & Prévost, E. (2013). Contrasting effects of climate change in continental vs. oceanic environments on population persistence and micro-evolution of Atlantic salmon. *Global Change Biology*, 19, 711–723.
- Quinn, T. P., McGinnity, P., & Cross, T. F. (2006). Long-term declines in body size and shifts in run timing of Atlantic salmon in Ireland. *Journal of Fish Biology*, 68, 1713–1730.
- R Development Core Team. (2018). R: A language and environment for statistical computing (7094). <https://www.r-project.org/> (Accessed 9 December 2021).
- Reddin, D. G., & Friedland, K. D. (1999). A history of identification to continent of origin of Atlantic salmon (*Salmo salar* L.) at West Greenland, 1969–1997. *Fisheries Research*, 43, 221–235.
- Renkawitz, M. D., Sheehan, T. F., Dixon, H. J., & Nygaard, R. (2015). Changing trophic structure and energy dynamics in the Northwest Atlantic: Implications for Atlantic salmon feeding at West Greenland. *Marine Ecology Progress Series*, 538, 197–211.
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, 421, 57–60.
- Sæther, B.-E., & Bakke, Ø. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, 81, 642–653.
- Shearer, M. W. M. (1992). Atlantic salmon scale reading guidelines (No. 188). International Council for the Exploration of the Sea.
- Siegel, J., Adkison, M., & McPhee, M. (2018). Changing maturation reaction norms and the effects of growth history in Alaskan Chinook salmon. *Marine Ecology Progress Series*, 595, 187–202.
- Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press.
- Thomas, K., Hansen, T., Brophy, D., Maoileidigh, Ó., & Fjellidal, P. G. (2019). Experimental investigation of the effects of temperature and feeding regime on scale growth in Atlantic salmon *Salmo salar* post-smolts. *Journal of Fish Biology*, 94, 896–908.
- Thorstad, E. B., Bliss, D., Breau, C., Damon-Randall, K., Sundt-Hansen, L. E., Hatfield, E. M. C., Horsburgh, G., Hansen, H., Maoileidigh, N. Ó., Sheehan, T., & Sutton, S. G. (2021). Atlantic salmon in a rapidly changing environment—Facing the challenges of reduced marine survival and climate change. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31, 2654–2665.
- Tillotson, M. D., Sheehan, T. F., Ellingson, B., Haas-Castro, R. E., Olmos, M., & Mills, K. E. (2021). Non-stationary effects of growth on the survival of north American Atlantic salmon (*Salmo salar*). *ICES Journal of Marine Science*, 2021, 2967–2982. <https://doi.org/10.1093/icesjms/fsab174>
- Tirronen, M., Hutchings, J. A., Pardo, S. A., & Kuparinen, A. (2022). Atlantic salmon survival at sea: Temporal changes that lack regional synchrony. *Canadian Journal of Fisheries and Aquatic Sciences*, 79, 1697–1711.
- Todd, C. D., Friedland, K. D., MacLean, J. C., Whyte, B. D., Russell, I. C., Lonergan, M. E., & Morrissey, M. B. (2012). Phenological and phenotypic changes in Atlantic salmon populations in response to a changing climate. *ICES Journal of Marine Science*, 69, 1686–1698.
- Todd, C. D., Hanson, N. N., Boehme, L., Revie, C. W., & Marques, A. R. (2021). Variation in post-smolt growth pattern of wild one sea-winter salmon (*Salmo salar* L.) and its linkage to surface warming in the eastern North Atlantic Ocean. *Journal of Fish Biology*, 98, 6–16.
- Todd, C. D., Hughes, S. L., Marshall, C. T., MacLEAN, J. C., Lonergan, M. E., & Biuw, E. M. (2008). Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. *Global Change Biology*, 14, 958–970.
- Todd, C. D., Whyte, B. D. M., MacLean, J. C., Revie, C. W., Lonergan, M. E., & Hanson, N. N. (2014). A simple method of dating marine growth circuli on scales of wild one sea-winter and two sea-winter Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 71, 645–655.
- Tréhin, C., Rivot, E., Lamireau, L., Meslier, L., Besnard, A.-L., Gregory, S. D., & Nevoux, M. (2021). Growth during the first summer at sea modulates sex-specific maturation schedule in Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 78, 659–669.
- Utne, K. R., Pauli, B. D., Haugland, M., Jacobsen, J. A., Maoileidigh, N., Melle, W., Broms, C. T., Nøttestad, L., Holm, M., Thomas, K., & Wennevik, V. (2021). Poor feeding opportunities and reduced condition factor for salmon post-smolts in the Northeast Atlantic Ocean. *ICES Journal of Marine Science*, 78, 2844–2857.
- Vollset, K. W., Urdal, K., Utne, K., Thorstad, E. B., Sægvog, H., Raunsgard, A., Skagseth, Ø., Lennox, R. J., Østborg, G. M., Ugedal, O., Jensen, A. J., Bolstad, G. H., & Fiske, P. (2022). Ecological regime shift in the Northeast Atlantic Ocean revealed from the unprecedented reduction in marine growth of Atlantic salmon. *Science Advances*, 8, eabk2542.
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Tréhin, C., Rivot, E., Santanbien, V., Patin, R., Gregory, S. D., Lamireau, L., Marchand, F., Beaumont, W. R. C., Scott, L. J., Hillman, R., Besnard, A.-L., Boisson, P.-Y., Meslier, L., King, A. R., Stevens, J. R., & Nevoux, M. (2023). A multi-population approach supports common patterns in marine growth and maturation decision in Atlantic salmon (*Salmo salar* L.) from southern Europe. *Journal of Fish Biology*, 1–14. <https://doi.org/10.1111/jfb.15567>