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

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Abstract :

This study provides a regional picture of long-term change in Atlantic salmon growth at the southern edge of their distribution, using a multi-population approach spanning 49 years and 5 populations. We provide empirical evidence of salmon life history being influenced by a combination of common signals in the marine environment, as well as 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 5 decades. Growth increments during their sea sojourn were characterised 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, 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 individuals of small size at the end of the first summer at sea being more likely to delay maturation. However, each population was characterised 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 the differences between sexes, suggesting that 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. This article is protected by copyright. All rights reserved.

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

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Introduction

Global climate change is impacting populations worldwide, with effects on their distribution, abundance, demographic rates, and life history traits (LHT) (Parmesan and 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 (Stearns, 1992; Sæther and Bakke, 2000; Pelletier *et al.*, 2011). 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 (Jonsson and Jonsson, 2009; Thorstad *et al.*, 2021; Gillson *et al.*, 2022). 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 following smolt migration (Friedland *et al.*, 2009; Beaugrand and Reid, 2012; 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 (Otero *et al.*, 2012; Jonsson *et al.*, 2016; Chaparro-Pedraza and de Roos, 2019; Olmos *et al.*, 2019). Concomitantly with their decline in abundance, the body size of returning adults also decreased markedly for many different populations (Bacon *et al.*, 2009; Todd *et al.*, 2012; Jonsson *et al.*, 2016; Bal *et al.*, 2017).

Reduction in the abundances, body size, and early marine survival have 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 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 (Todd *et al.*, 2008; Mills *et al.*, 2013; Renkawitz *et al.*, 2015; Friedland *et al.*, 2017; Utne *et al.*, 2021).

The complexity of salmon life histories, together with their long-range migration behaviour, necessitates a multi-dimensional 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 analyses, i.e., the analysis of growth patterns of returning salmon from their scales (or more rarely, otoliths and vertebrae) has a great potential for such a multi-dimensional 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, but also 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-smolts 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 and 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 (USA, Maine).

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 (Todd *et al.*, 2021; Tréhin *et al.*, 2021; Harvey *et al.*, 2022; 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 (Metcalfe and Thorpe, 1990; Gregory *et al.*, 2017), 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 towards 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 (Jonsson and Jonsson, 2009; Chaput, 2012; Olmos *et al.*, 2019). Populations of salmon at the edge of the species' distribution are the most vulnerable to changes in freshwater conditions (Jonsson and 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 (Piou and Prévost, 2013; Nicola *et al.*, 2018). 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 change in the marine growth in a group of five geographically closed 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 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.*, 2010a; MacKenzie *et al.*, 2012; Mork *et al.*, 2012; Gilbey *et al.*, 2021a), we expected to detect temporal features in the common signal that are similar to those reported in other North East Atlantic 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.

Material & Methods

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 program. 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 adults caught by anglers on river Scorff and Sélune into fork length using the linear relationship: *length = -5.69 + 0.95 × 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, *pers. comm.*). 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 is provided in Table 1.

2. Retrospective growth analysis

To analyse spatio-temporal variability in salmon growth, we selected a sub-sample 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 labelled 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 annulus were defined based on marked changes in the inter-circuli spacing (Shearer, 1992; Baglinière *et al.*, 2022).

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; Todd *et al.*, 2021; Harvey *et al.*, 2022; Vollset *et al.*, 2022). Salmon growth may show contrasted patterns and trends between summer and winter periods, which may reveal seasonal change in food availability, spatial distribution and changes in physiology and maturation status (Tréhin *et al.*, 2021). In addition, growth after the first winter at sea may also 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 centre 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 only available for fish that return as 2SW. In addition, we also 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 mm) of each growth period as a proxy of body length increment during that given period.

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 Polymerase Chain Reaction (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 & Stevens (2020) and King *et al.* (in press). For the river Tamar, results for six years (2007-2009 and 2015-2017) were taken from King *et al*. (in press). Samples from French populations were analysed with a q-PCR sex marker multiplexing protocol (A.-L. Besnard, *pers. comm.*). No DNA could be extracted from the scales of adults caught on the river Frome, which where historically cleaned with a caustic solution for better visualization.

4. Partitioning common and population-specific temporal variability in growth

To quantify the amount of variability in growth, we modelled 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 include temporal random effects to partition out the temporal variability that is common to all populations from that which is population-specific, and even population × 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; while Plus, Sum2 and Win2 concern 2SW fish only). We did not account for smolt age in the models because it was highly biased towards one-year-old individuals in all our populations, and was not controlled for in our subsample of scales. The parametric formulation of the beyond optimal model (sensus Zuur *et al.*, 2009), i.e. the model that includes all potential effects, for each of the growth response variable considered were:

(1) $\mathrm{Lad}_i = A + B_{pop} + C_{age} + D_{age:pop} + \alpha_t + \beta_{t|pop} + \gamma_{t|pop:age} + \varepsilon_i$

(2) $\mathrm{Riv}_i = A + B_{pop} + C_{age} + D_{age:pop} + \alpha_t + \beta_{t|pop} + \gamma_{t|pop:age} + \varepsilon_i$

(3) $\mathrm{Sum1}_i = A + B_{pop} + C_{age} + D_{age:pop} + \alpha_t + \beta_{t|pop} + \gamma_{t|pop:age} + \varepsilon_i$

(4) $\mathrm{Win1}_i = A + B_{pop} + C_{age} + D_{age:pop} + \alpha_t + \beta_{t|pop} + \gamma_{t|pop:age} + \varepsilon_i$

(5) $\mathrm{Plus}_i = A + B_{pop} + \alpha_t + \beta_{t|pop} + \varepsilon_i$

(6) $\mathrm{Sum2}_i = A + B_{pop} + \alpha_t + \beta_{t|pop} + \varepsilon_i$

(7) $\mathrm{Win2}_i = A + B_{pop} + \alpha_t + \beta_{t|pop} + \varepsilon_i$

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 the present work, *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, e.g. phenotypic, environmental and/or genetic background; C_{age} is the fixed effect of sea-age representing difference in growth resulting from physiological and/ or behaviour 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 centred on zero. ε_i 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.

5. Estimating the probabilistic maturation reaction norm

We built population-specific probabilistic maturation reaction norms (PMRN) to model the link between growth and maturation decision (Dieckmann and 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:

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

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 difference 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 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:

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

where $\hat{A}$, $\hat{B}_{pop}$, $\hat{C}_{sex}$ and $\hat{D}$ are maximum likelihood estimates of fixed parameters. Hence 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, all random effects being fixed to zero.

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 Akaike's information criterion AICc (Burnham and 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 and Schielzeth, 2013). Detailed statistical results are provided in the Supplementary Material.

Results

1. Partitioning out the temporal variability of individual growth

As expected, the length of adults was longer among 2SW than 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 2000's (Figure 2), suggesting major change 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; Table 2, Table S4). Additionally, the random effect terms representing signals specific to each population and each sea-age were also 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 interactions explained most of the variance, with only 3% of the total variance being captured by the random effect terms. Length of adults from the Frome were 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 inter-annual 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 the long-term decline in early marine growth. In contrast, the population-specific specific signals in temporal variability in Sum1 did not show any long-term trends.

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 differences 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 representing a pan-population common signal in growth patterns captured more variability and showed a gradual linear increase over time, while 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 by the models (conditional $R^2 < 20\%$; Table 2; Tables S6, S7, 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).

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). Inter-annual 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).

Discussion

Our multi-population approach, spanning 49 years and 5 populations, provides a regional picture of long-term change in 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 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 et al. 1993; 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 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 growth was maximal during the first summer at sea. The first summer at sea is also when 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 growth observed over the later 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 (Peyronnet *et al.*, 2007; Todd *et al.*, 2014; Thomas *et al.*, 2019; Carlson *et al.*, 2021) 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 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 neighbouring 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, that may lead to management actions with no or unwanted effects on specific populations.

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 5 populations was three times larger than the amount of variability 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 (Peyronnet *et al.*, 2007; Friedland *et al.*, 2009), while the latter decline has been detected in populations from Scotland and from all over Southern and Western Norway (Todd *et al.*, 2021; Harvey *et al.*, 2022; 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 5 decades. Evidence of a common signal in 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 (Dadswell et al., 2010; Bradbury *et al.*, 2021; Gilbey *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 North-East Atlantic 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.*, 2010b; Jacobsen *et al.*, 2012; Gilbey *et al.*, 2021b). 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 (Jonsson and Jonsson, 2009; Chaput, 2012).

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 (Hogan and Friedland, 2010; Barajas *et al.*, 2021; 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 behaviours, including spatio-temporal aggregations, of salmon populations at sea.

Temporal variations of 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 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 regards 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 (Todd *et al.*, 2008; Bacon *et al.*, 2009), 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 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 contrasted seasons. A mechanism of compensatory growth at the individual level (Barajas *et al.*, 2021), or the improvement of 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. Lastly, 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 a sex-specific probabilistic maturation reaction norms driven by early marine growth. Each population was characterised by a specific reaction norm, but differences between populations were smaller than differences 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 (Hutchings, 2004; Debes *et al.*, 2014; 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 of growth over the study period lead to higher variability in the proportion of 1SW among females, while 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 (Grift *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 (Reddin and Friedland, 1999; Dadswell *et al.*, 2010b; Jacobsen *et al.*, 2012; Gilbey *et al.*, 2021b). 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 (Hogan and Friedland, 2010; Barajas *et al.*, 2021). 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.

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Contributions

WRCB, SDG, RH, FM and LJS provided the biological data and prepared the scale samples; LL and FM conducted growth measurements; A-LB, P-YB, RAK, LM and JRS conducted the molecular sexing; CT, ER, VS, RP and MN conducted the statistical analysis; CT, ER, and MN conceived the initial idea and wrote the main paper in collaboration with the other co-authors. All authors discussed results and implications, providing significant inputs to the manuscript at all stages.

Supporting information

Table S1: Number of scales of Atlantic salmon (*Salmo salar*) analysed for growth and sex per population, smolt year, and sea age.

Table S2: Modelling the temporal variability in the adult length (Lad) of Atlantic salmon (Salmo salar) as a function of random and fixed effects.

Table S3: Modelling the temporal variability in the river growth (Riv) of Atlantic salmon (*Salmo salar*) as a function of random and fixed effects.

Table S4: Modelling the temporal variability in the first summer growth (Sum1) of Atlantic salmon (*Salmo salar*) as a function of random and fixed effects.

Table S5: Modelling the temporal variability in the first winter growth (Win1) of Atlantic salmon (*Salmo salar*) as a function of random and fixed effects.

Table S6: Modelling the temporal variability in the plus growth (Plus) of Atlantic salmon (*Salmo salar*) as a function of random and fixed effects.

Table S7: Modelling the temporal variability in the second summer growth (Sum2) of Atlantic salmon (*Salmo salar*) as a function of random and fixed effects.

Table S8: Modelling the temporal variability in the second winter growth (Win2) of Atlantic salmon (*Salmo salar*) as a function of random and fixed effects.

Table S1: Modelling the probability to mature after 1SW (Pmat.1SW) in returning adult Atlantic salmon (*Salmo salar*) as a function of random and fixed effects.

Figure S1: Relationship between individual body length (Lf) and scale size in adult (R^2 = 48%) Atlantic salmon (*Salmo salar*).

Figure S2: Temporal variability in the mean growth increments measured on scales of Atlantic salmon (*Salmo salar*) for the different growth periods in each population and sea-age classes.

Figure S3: Partitioning out the temporal variability in the probability to mature after 1SW in returning Atlantic salmon (*Salmo salar*) (Pmat.1SW).

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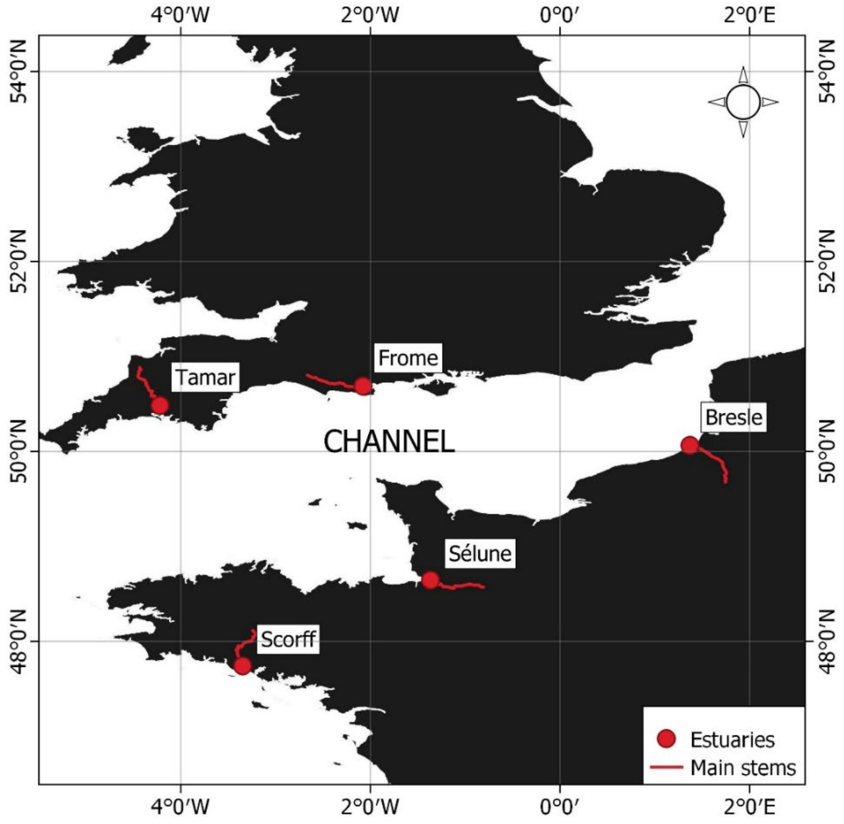
4°0′W
2°0′W
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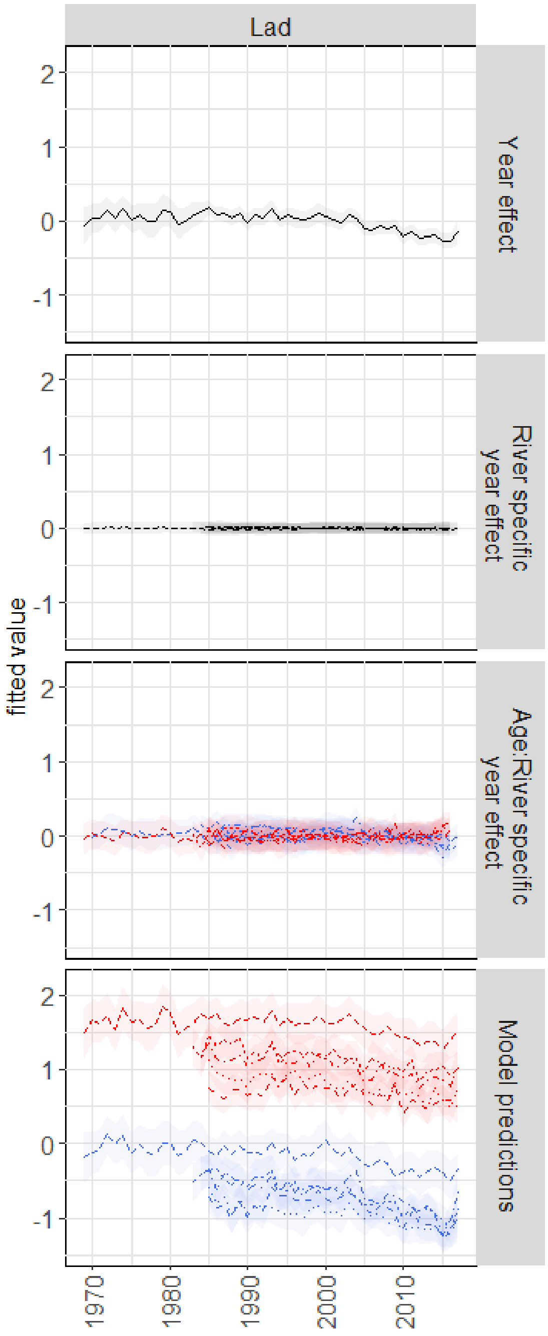
54°0′N
52°0′N
50°0′N
48°0′N
Tamar
Frome
Bresle
CHANNEL
Sélune
Scorff
Estuaries
Main stems

Figure 1


Lad
Year effect
River specific year effect
Age:River specific year effect
Model predictions
fitted value
2
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1970
1980
1990
2000
2010

Figure 2

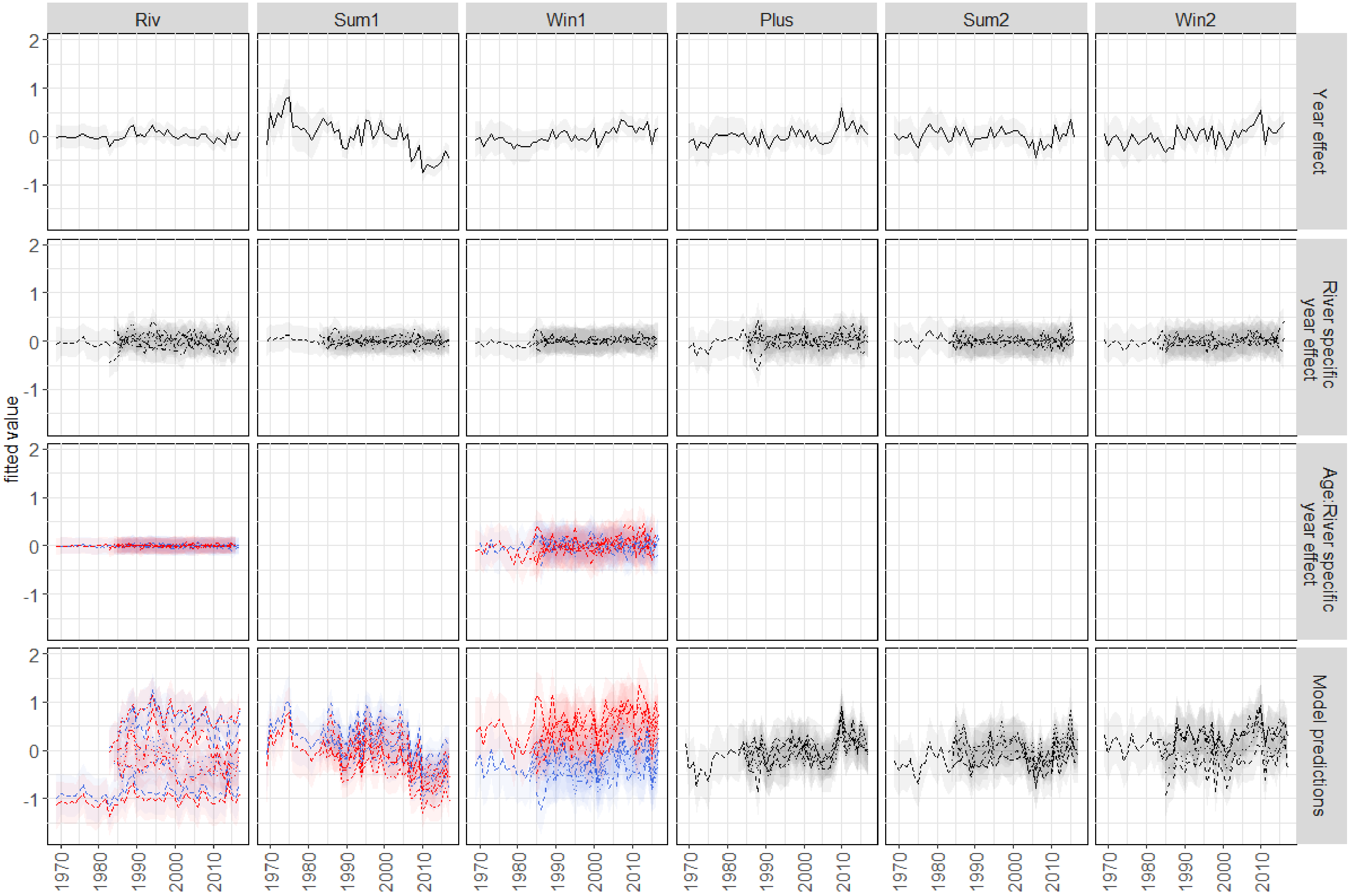
Riv
Sum1
Win1
Plus
Sum2
Win2
Year effect
River specific year effect
Age:River specific year effect
Model predictions
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Figure 3

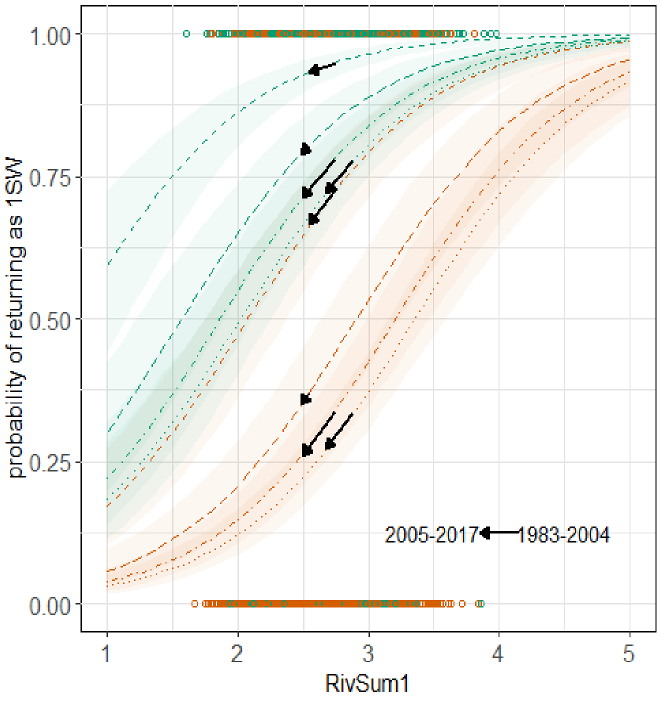
1.00
0.75
0.50
0.25
0.00
probability of returning as 1SW
1
2
3
4
5
RivSum1
2005-2017
1983-2004

Figure 4

Figure captions

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.

Figure 2: Partitioning out the temporal variability of 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

Figure 3: Partitioning out the temporal variability of the width of the growth increment on scales of Atlantic salmon (*Salmo salar*) for 5 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.

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, all random effects being fixed to zeros.

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 Coordinates (estuary)	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)	
Catchment area	480 km^2		1038 km^2		748 km^2		454 km^2		920 km^2	
Stage	Smolt	Adult	Smolt	Adult	Smolt	Adult	Smolt	Adult	Smolt	Adult
Period	1995-2018	1987-2018	1985-2018	1987-2018	1988, 1993, 1994, 2005-2018	1985-2018	2006-2018	1971-2018	2002-2017	1986-1989, 2003-2017
Sampling method	Trapping	Anglers (<1995) Trapping (>1995)	Trapping	Anglers	Trapping	Trapping	Trapping	Anglers	Trapping	Trapping
Number of scales analysed for growth	723	1842	958	1806	313	1141	388	737	448	1002
Number of scales analysed for sex	666	1520	833	1723	202	641	379	0	399	821
Proportion of females in sample	53.1%	1SW: 49.5% 2SW: 83.9%	65.0%	1SW: 46.7% 2SW: 88.2%	75.4%	1SW: 69.1% 2SW: 93.3%	51.4%	NA	60.8%	1SW: 49.0% 2SW: 83.0%
References	(Perrier *et al.*, 2011; Bal *et al.*, 2017; Marchand *et al.*, 2018; Azam *et al.*, 2020)						(Lauridsen, 2020)		(Hendry *et al.*, 2007; Hillman, 2020)	

Table 2: Modelling the temporal variability in Atlantic salmon (*Salmo salar*) growth in 5 populations of southern Europe. 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 R²) and by fixed effect only (Marginal R²) 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 ($\beta_{t|pop:age}$), 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 5 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).

Response variable	Model selected	Conditional R²	Marginal R²	Standard deviation of random effects			
				α_t	$\beta_{t\|pop}$	$\gamma_{t\|pop\|age}$	ε_i
Fish body length							
Lad	$A + B_{pop} + C_{age} + D_{pop,age} + \alpha_t + \beta_{t\|pop} + \gamma_{t\|pop\|age} + \varepsilon_i$	78%	75%	0.02	0.002	0.01	0.21
Scale growth increment							
Riv	$A + B_{pop} + C_{age} + D_{pop,age} + \alpha_t + \beta_{t\|pop} + \gamma_{t\|pop\|age} + \varepsilon_i$	33%	26%	0.02	0.04	0.01	0.67
Sum1	$A + B_{pop} + C_{age} + \alpha_t + \beta_{t\|pop} + \varepsilon_i$	25%	7%	0.15	0.02	-	0.78
Win1	$A + B_{pop} + C_{age} + D_{pop,age} + \alpha_t + \beta_{t\|pop} + \gamma_{t\|pop\|age} + \varepsilon_i$	26%	14%	0.04	0.02	0.06	0.76
Plus	$A + B_{pop} + \alpha_t + \beta_{t\|pop} + \varepsilon_i$	11%	1%	0.05	0.05	-	0.89
Sum2	$A + B_{pop} + \alpha_t + \beta_{t\|pop} + \varepsilon_i$	11%	3%	0.05	0.04	-	0.89
Win2	$A + B_{pop} + \alpha_t + \beta_{t\|pop} + \varepsilon_i$	17%	7%	0.06	0.04	-	0.84

Table 3: Modelling 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. The structure of the best model is presented, as well as the percentage of variance explained by both fixed and random effects (Conditional R²) and by fixed effects only (Marginal R²) 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.

Response variable	Model selected	Conditional R²	Marginal R²	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