





## Original Article

# Non-stationary effects of growth on the survival of North American Atlantic salmon (*Salmo salar*)

Michael D. Tillotson <sup>1,\*</sup>, Timothy F. Sheehan<sup>2</sup>, Brandon Ellingson<sup>2</sup>, Ruth E. Haas-Castro<sup>2</sup>, Maxime Olmos <sup>3</sup>, and Katherine E. Mills<sup>1</sup>

<sup>1</sup>Gulf of Maine Research Institute, Portland, Maine, USA

<sup>2</sup>National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Woods Hole, Massachusetts, USA

<sup>3</sup>University of Washington School of Aquatic and Fishery Sciences, Seattle, Washington, USA

\*Corresponding author: tel: (206) 605-8416; e-mail: [mtillotson@gmri.org](mailto:mtillotson@gmri.org)

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The productivity of Atlantic salmon (*Salmo salar*) has declined markedly since the 1980s, in part because of changing ocean conditions, but mechanisms driving this decline remain unclear. Previous research has suggested differential recruitment dynamics between the continental stock groups, with post-smolt growth influencing the survival of populations in Europe, but not North America. We used a large, representative archive of North American, multi sea-winter salmon scales to reconstruct long-term changes in growth between 1968 and 2018. We then modeled relationships between annual growth indices, estimates of maturation rates, and post-smolt survival, while allowing for the possibility of non-stationary dynamics. We found that marine growth of MSW salmon has changed over the past 50 years, generally increasing despite declining survival. However, we found strong evidence of a non-stationary influence of post-smolt growth on survival. Prior to a period of rapid change in the ocean environment during the late 1980s, post-smolt growth was positively related with survival, similar to the pattern observed in European populations. These findings suggest that the mechanisms determining marine survival of North American and European salmon populations may have diverged around 1990. More generally, our results highlight the importance of considering non-stationary dynamics when evaluating linkages between the environment, growth, and survival of Atlantic salmon.

**Keywords:** growth, marine survival, non-stationary, salmon, scale analysis

## Introduction

Atlantic salmon (*Salmo salar*) have for centuries been an iconic fish of the North Atlantic, historically supporting valuable commercial fisheries and to this day representing the pinnacle of angling for many recreational fishermen (Parrish *et al.*, 1998). Despite its almost legendary status, this anadromous species has experienced a series of dramatic declines in abundance throughout much of its range, with many populations now extirpated and others persisting in dangerously depleted states (Aas *et al.*, 2011). At the North Atlantic scale, historical declines can largely be explained by overexploitation and modifications of freshwater habitats (Saunders *et al.*, 2006; Chaput, 2012). However, the most recent decline from rela-

tively high abundance during the 1970s to extremely low abundance and productivity, which has persisted since the 1990s, occurred despite vast reductions in fisheries mortality and widespread efforts to conserve and restore freshwater habitats (Olmos *et al.*, 2019; ICES, 2020).

Because of the broad spatial scale over which low productivity has been observed since the 1990s (Olmos *et al.*, 2019), and the relative stability of freshwater production in populations where it has been assessed (e.g. Jonsson and Jonsson, 2004; Todd *et al.*, 2012), it is generally agreed that a shift towards unfavourable conditions at sea is primarily responsible for reduced lifetime survival of Atlantic salmon (ICES, 2020; Olmos *et al.*, 2020). Moreover, the timing of rapidly declining survival during the 1980s and 1990s

coincided with a series of complex changes in the North Atlantic climate and ecosystem that impacted salmon's physical habitats, prey, and predators (Beaugrand *et al.*, 2003; National Research Council, 2004; Mills *et al.*, 2013). This apparent regime shift began during the late 1980s and manifest as a series of cascading changes in abiotic and biotic characteristics (MERCINA Working Group, 2001; Beaugrand, 2009; Hátún *et al.*, 2009; Mills *et al.*, 2013), ultimately impacting some of the world's most valuable and iconic fisheries, including Atlantic cod (Beaugrand *et al.*, 2003) and American lobster (Fogarty and Gendron, 2004) in addition to Atlantic salmon (Mills *et al.*, 2013).

Potential links between ecosystem changes and Atlantic salmon marine survival have been examined at scales from single rivers to the Atlantic basin in aggregate, and significant relationships have been found with myriad environmental and ecological indices including various metrics of sea surface temperature, large-scale climate patterns including the North Atlantic Oscillation and Atlantic Multidecadal Oscillation and abundance or quality of various prey (e.g. copepods, *Calanus finmarchicus*; capelin, *Mallotus villosus*) (Beaugrand, 2009; Beaugrand and Reid 2003; Friedland *et al.*, 2009a; Todd *et al.*, 2012; Mills *et al.*, 2013; Friedland *et al.*, 2014; Renkawitz *et al.*, 2015; Olmos *et al.*, 2020). Predation of Atlantic salmon by a range of species including fish (Friedland *et al.*, 2012; Daniels *et al.*, 2018; Strøm *et al.*, 2019), seabirds (Montevecchi *et al.*, 2002), and marine mammals (Amiro, 1998; Strøm *et al.*, 2019) has also been observed or inferred to impact salmon ocean productivity, and populations of many predators have increased substantially since the 1970s (Zanden and Rago, 1999; National Research Council, 2004). However, the collective results of these many efforts have failed to provide a mechanistic understanding of persistently low salmon marine productivity, limiting the specificity of management responses apart from broad reductions in harvest (ICES, 2020). Where likely mechanisms of reduced marine survival have been identified, they seem insufficient to explain the basin-wide pattern of decline, being generally driven by local processes (Friedland *et al.*, 2009a, 2009b, 2012). Conversely, where significant environment-productivity correlations have been identified at sufficiently broad spatial scales, the mechanisms are uncertain (Friedland *et al.*, 2014; Olmos *et al.*, 2020), though Mills *et al.*, (2013) presented a plausible bottom-up hypothesis for poor Atlantic salmon survival based on observed declines in the quality of important prey resources.

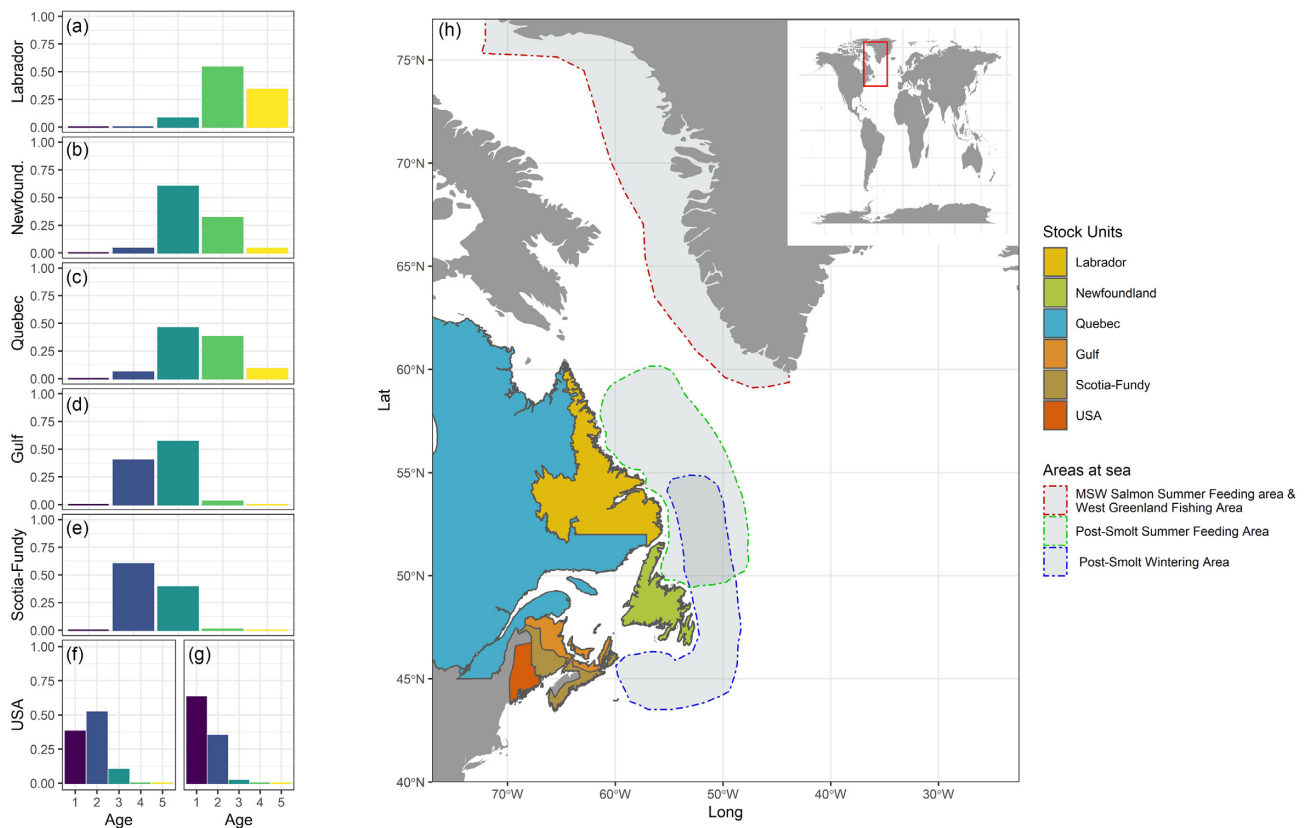
This continued uncertainty arises in part from the practical challenge of observing salmon at sea, but also from the complexity and flexibility of their life history, which makes it difficult to isolate mortality from other demographic processes such as maturation. Atlantic salmon typically spend 1–7 years rearing in their natal rivers before migrating to sea as “smolts”, with substantial variation in age and size at ocean entry occurring between populations and across years (Chaput *et al.*, 2006). The post-smolt phase begins after ocean entry and continues until growth slows during the first winter at sea, and this period appears to play a disproportionate role in determining both lifetime survival and age-at-maturity (Hansen and Quinn, 1998; Hutchings and Jones, 1998). Rapid growth during this period is thought to confer a higher chance of survival, and also increase the likelihood of maturing after only one winter at sea (Hansen and Quinn, 1998). Fish in the early maturing group that survive to reproduce are referred to as one sea winter (1SW) spawners, while those that delay maturation during the first

winter and return to freshwater after two or more years are called multi sea winter (MSW) spawners. The maturation “decision” also has important implications for subsequent marine movements, with most North American and Southern European MSW salmon undertaking extended migrations, which include a period of feeding in the coastal waters off West Greenland (Figure 1) during the second summer and fall at sea (Aas *et al.*, 2011). In contrast, 1SW individuals are assumed to not migrate to Greenland since they are rarely encountered in the fishery that takes place there (Sheehan *et al.*, 2019). Because of these features of the salmon life history, the processes of maturation, migration, and survival are fundamentally linked to growth (Thorpe *et al.*, 1998; Mangel and Satterthwaite, 2008).

Given this central role, it is not surprising that growth has received substantial attention among salmon researchers investigating the causes of depressed at-sea survival. Many large archives of salmon scales exist and have been utilized to examine long-term patterns in growth (e.g. Friedland *et al.*, 2009a, 2009b). These studies are possible because Atlantic salmon have leptoid scales, which grow approximately in proportion to length and display concentric rings (i.e. circuli) that indicate distinct periods of fast and slow growth (Fukuwaka and Kaeriyama, 1997; Panfili *et al.*, 2002). These scale features allow for reconstruction of seasonal or annual growth histories, which can be compared with annual indices of abundance or survival. This approach has in prior cases revealed potential survival bottlenecks by identifying significant growth–survival correlations during the post-smolt phase (e.g. Peyronnet *et al.*, 2007; Friedland *et al.*, 2009b) and supported the hypothesis that growth plays a central role in mediating the influence of environmental change on salmon survival (Friedland *et al.*, 2005).

However, this apparent influence of post-smolt growth on subsequent survival has only been detected in European salmon populations (Peyronnet *et al.*, 2007; Friedland *et al.*, 2009a), while similar studies of North American populations have found no significant growth–survival relationships (Friedland *et al.*, 2009b; Hogan and Friedland, 2010; Izzo and Zydlewski, 2017). Contrary to these discrepancies, recent studies report basin-scale trends in post-smolt survival and consistent responses to changes in the ocean environment by salmon from both continents (Olmos *et al.*, 2020). These findings suggest a common mechanism linking environmental change and salmon productivity, and so there is a need to better understand whether the inconsistency in growth–survival relationships truly reflects differential processes between continents or if limitations in the data or analyses of prior studies can explain the disagreement.

To address this issue, we analyzed a unique scale growth dataset while taking advantage of recent advances in the estimation of post-smolt survival (Olmos *et al.*, 2019) and an emerging understanding that environmental influences on salmon productivity can be non-stationary (i.e. the influence of covariates may vary in direction or intensity through time; Litzow *et al.*, 2018, 2019). The biological data and scale archive from the West Greenland fishery sampling program represent one of the most comprehensive and representative sources of information on Atlantic salmon at sea (Sheehan *et al.*, 2019). MSW spawners from the entire North American (i.e. Maine, USA to Ungava Bay in Northern Quebec, Canada) and Southern European distribution are present and observed in the fishery roughly in proportion to their abundance (Bradbury *et al.*, 2016; Jeffery *et al.*, 2018). Individuals are captured during their second summer at sea, and their scales therefore provide a record of the



**Figure 1.** (a)–(g) Smolt age distributions by stock unit as reported by ICES (2020). Changes in hatchery rearing techniques impacted USA age distributions so before (f) and after (g) 1990 are shown separately. (h) Study area showing North American Atlantic salmon stock units and presumed seasonal marine distributions.

complete post-smolt growth period while also representing both fish that are destined to survive as well as those that will not survive to return to their home rivers as adults. The analysis of these scales should therefore be somewhat less impacted by “survivor bias” that is pervasive in retrospective growth analyses (i.e. growth patterns of salmon that survive, and are therefore observable, may not be representative of the non-survivors) than samples collected from adult salmon. The sampling program provides nearly continuous temporal coverage from the late 1960s through present. Therefore, these scales provide several decades of data before and after the North Atlantic environmental shifts of the late 1980s, allowing for consideration of differential growth–survival relationships between regimes.

By combining these comprehensive growth data with the outputs of an Atlantic salmon life cycle model that explicitly separates the confounded processes of post-smolt survival and maturation (Olmos *et al.*, 2019, 2020), we rigorously tested the hypothesis that, as in European populations, marine survival is positively related to growth in North American Atlantic salmon. We achieve this objective by addressing three primary questions: (i) How have freshwater, post-smolt, and subsequent marine growth changed over time and in relation to the late 1980s regime shift? (ii) Across the complete time series, is growth during any of these periods significantly related to rates of post-smolt survival or the proportion of a cohort maturing as 1SW? (iii) Are the relationships between growth, sur-

vival, and maturity consistent between high- and low-productivity regimes?

## Methods

### Data acquisition and processing

#### Field sampling

Scales were obtained from an archive of samples collected during long-term monitoring of the West Greenland salmon fishery (Sheehan *et al.*, 2019). Like most long-term sampling, some variation in the field methods occurred over the history of the West Greenland sampling program as a result of changes in the fishery and refinement of methods (Magurran *et al.*, 2010; Sheehan *et al.*, 2019). While these changes may result in increased variability, we do not believe they are likely to introduce biases relevant to our hypotheses, and so apart from the correction for date of capture (described below), we have used the raw data. Samples were available for years 1968–2018, except for 1972–1973 (scales could not be located), 1977, and 1993–1994 (no sampling occurred). Biological data including length, weight, smolt age, and continent-of-origin were paired with all scale samples, and for a subset of samples, individuals were assigned a region-of-origin (ROO) using genetic methods (Bradbury *et al.*, 2016). Although the genetic methods have a resolution of at least 13 North American ROO, to allow for comparison with survival and maturity rates, the genetic assign-

ments were grouped geographically to match the six North American stock units (Labrador, Newfoundland, Quebec, Gulf, Scotia-Fundy, and US; Figure 1) reported on annually by the International Council for the Exploration of the Sea (ICES) (ICES, 2020).

#### Scale selection and reading

Scales were selected from a subset of the archive that included only North American origin salmon that had spent one winter at sea (i.e. destined to mature as 2SW or older). We then randomly selected samples with a target sample size of 75 scales per year, which was achieved for all years except 1976 ( $n = 52$ ), 1998 ( $n = 57$ ), and the aforementioned missing years. Scales were impressed on acetate slides and were examined on a compound microscope at 20x magnification. Scale images were captured by an Olympus DP73 microscope camera at high resolution ( $4800 \times 3600$  pixels) with CellSens Entry and calibrated at 1.9  $\mu\text{m}$  per pixel. One representative scale from each fish was measured along a singular transect stretching from the focus of the scale to the edge, aligned on the longest axis using Image Pro Plus 7 (Media Cybernetics, [www.mediacy.com](http://www.mediacy.com)). Scale circuli were identified using standardized protocols, intercirculus spacings were measured and distances from the focus to various scale features were calculated (ICES 2011). Identified scale features included the first marine circulus (FMC), which is deposited shortly after ocean entry, the first summer maximum (FSM), which delineates summer and winter growth periods, and the first marine annulus (M1), which is formed at the end of the first winter at sea.

#### Data processing, summarization, and visualization

Scale measurements were partitioned into four segments corresponding to different marine life history phases. The four growth segments were from the focus to the FMC, which reflects freshwater growth, from the FMC to the FSM, which represents first summer growth, from the FSM to M1 for first winter growth, and from M1 to the scale's edge, which for our samples describes the incomplete second year of growth, hereafter referred to as plus growth (Figure 2). From these four segments, we calculated several cumulative growth increments, including the post-smolt increment (first summer + first winter), marine increment (first summer + first winter + plus growth), and scale radius (freshwater + marine). For each segment, the primary variable of interest was the growth increment (i.e. the sum of intercirculus spacings), but we also calculated average intercirculus spacing (i.e. increment/# of circuli), which reflects the average growth rate achieved during a given period and should be less sensitive to differences in the amount of time spent in each phase. The fishery at West Greenland generally occurs between August and October. Because fish are growing rapidly during this period, sample date is highly likely to influence the plus growth variables. As such, year-to-year changes in the sample distribution could potentially influence apparent temporal trends in plus growth. This potential source of bias was addressed in the temporal trend analyses by including sample week as a covariate in models of plus growth. For the calculation of descriptive statistics and all other analyses, we adjusted the plus growth increment by regressing it against sample week, and then adding the mean to the model residuals.

Long-term trends and interannual variability in average and extreme growth, survival, and maturity (explained below) were first visually evaluated by plotting annual quantiles including 0.05, 0.5 (i.e. median), and 0.95 for all variables. To better quantify the magnitude of temporal variation, we then averaged each variable by

decade and by productivity regime. These regimes were built upon Chaput *et al.*'s (2005) identification of the non-stationarity in productivity of Atlantic salmon that Mills *et al.*, (2013) refined to identify a series of sequential shifts in climate indices, regional environmental variables, and salmon productivity metrics during the late 1980s. Following from these results, we used 1990 as the delimiting year between high (pre-1990) and low-productivity regimes. We compared growth and demographic variables between decades using analysis of variance (ANOVA) and Tukey honest significant differences tests, and between regimes using Welch's T-tests with a two-sided alternative hypothesis. For ease of comparison, we then converted raw differences to % change from the first decade or productivity regime.

#### Marine survival and maturity estimates

The production of 1SW and MSW Atlantic salmon depends fundamentally on demographic rates of mortality and maturation. ICES compiles data on Atlantic salmon catch and abundance for catch advice of mixed-stock salmon fisheries at sea (ICES, 2020) and these data were recently used as the basis of a Bayesian life-cycle model (Olmos *et al.*, 2019, 2020) that forecasted abundance for North American and European stock units and provided estimates of post-smolt survival and 1SW maturation proportion (see Supplementary Materials for model details). Estimation of these two demographic parameters was a central focus of the life-history model and the outputs were subjected to extensive sensitivity analyses (Olmos *et al.*, 2019). Moreover, the model predictions provide a parsimonious explanation of the broadly observed pattern of coincident declines in marine survival and increases in the relative prevalence of 1SW spawners (ICES, 2020). Although primarily interested in survival, the influence of age-at-maturity could not be ignored because maturation determines the proportion of the stock complex that migrates to Greenland and can be directly influenced by growth in early life stages (Thorpe *et al.*, 1998; Tréhin *et al.*, 2021). As such, in similar fashion to the effect of survivor bias, there is the potential for a "maturity bias" where systematic growth differences exist between potential MSW and 1SW spawners. If the strength of this bias changes through time, it could drive patterns of growth in our MSW sample. It was infeasible to construct a comparable dataset of 1SW spawners in order to directly measure any such differences, and so we instead considered this maturity variable in our correlational analyses while accepting that the observable relationships integrate both the direct effect of growth on maturity, and the potential impact of any maturity bias.

For comparisons of growth, survival, and maturity, we used the life-cycle model outputs for the North American stock units, including posterior 5th, 50th, and 95th quantile estimates of post-smolt survival and proportion maturing at 1SW. The model was configured as reported in Olmos *et al.* (2019), which assumes a density-independent egg-to-smolt survival relationship with a common homogeneous freshwater survival rate among stock units. The post-smolt survival and the proportion of fish maturing as 1SW are modelled as multivariate random walks in the logit scale, which simulates spatial covariation associated with environmental stochasticity. Survival after the post-smolt period is assumed to be constant. Compared with Olmos *et al.* (2019), the model was extended to cover smolt years 1971–2015 (45 years total) and include all 25 stock units (in North America, Southern and Northern Europe) across the Atlantic salmon distribution range in the North Atlantic (ICES, 2020).

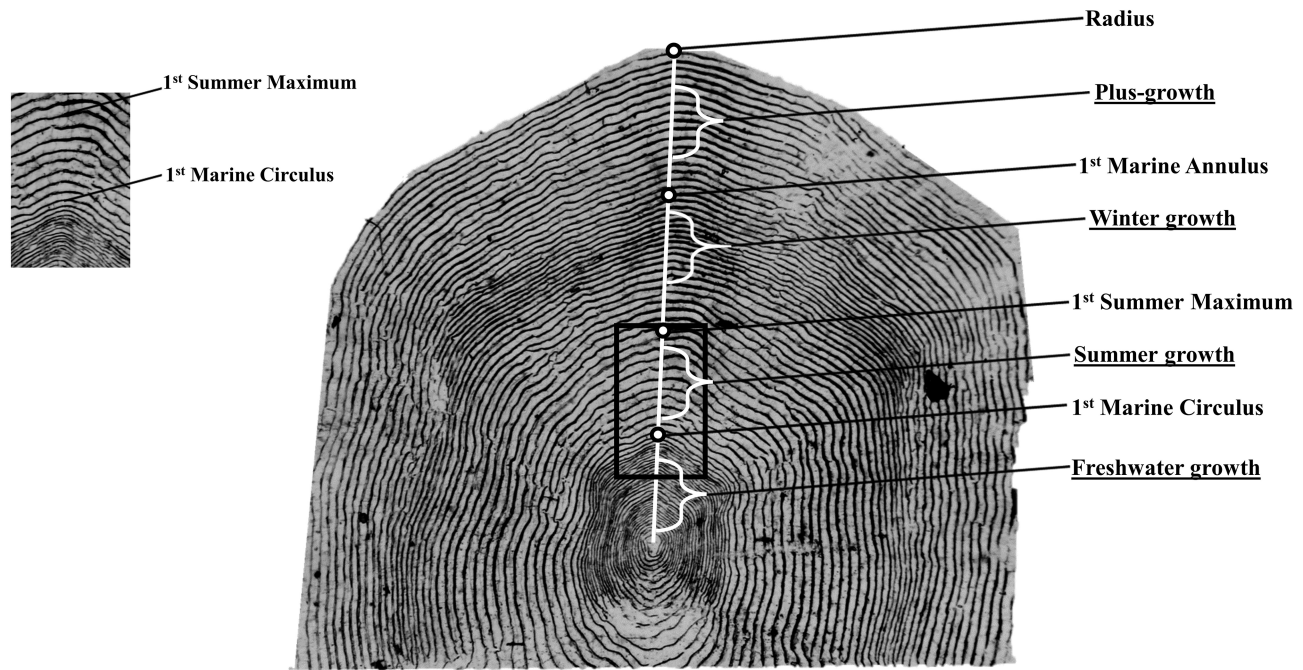


Figure 2. Representative image of scale with growth markers and increments identified.

Table 1. Summary of temporal trend GAM models.

Response	Predictor	Type	Coefficients/estimated degrees of freedom and p-values					R <sup>2</sup> adjusted
			Age-1	Age-2	Age-3	Age-4	Age-5	
<b>Freshwater</b>								
Growth increment	Intercept	Parametric	1.03	0.82***	0.82***	0.97*	1.12*	0.19
	Year	Smoothed	1.39***	4.05***	0.9***	0.00*	0.00	
Mean spacing	Intercept	Parametric	0.027	0.025***	0.024***	0.024***	0.024***	0.07
	Year	Smoothed	0.00	2.56***	1.62***	0.412	0.00	
<b>First marine summer</b>								
Growth increment	Intercept	Parametric	0.83	0.79	0.75*	0.69***	0.65***	0.12
	Year	Smoothed			4.81***			
Mean spacing	Freshwater	Smoothed			1.75***			0.12
	Intercept	Parametric	0.06	0.067***	0.068***	0.069***	0.069***	
	Year	Smoothed			6.13***			0.26
	Freshwater	Smoothed			2.01***			
<b>First marine winter</b>								
Growth increment	Intercept	Parametric	0.90	1.00**	0.92	0.79**	0.73***	0.40
	Year	Smoothed	3.63***	4.94***	5.19***	3.71***	2.73***	
Mean spacing	1st summer	Smoothed	0.96***	1.00***	1.70***	1.00***	0.922***	0.26
	Intercept	Parametric	0.054	0.056***	0.056***	0.055***	0.055***	
	Year	Smoothed			6.36***			0.26
	1st summer	Smoothed			1.00***			
<b>Plus growth</b>								
Growth increment	Intercept	Parametric	1.08	1.01***	1.02***	1.02**	1.00**	0.30
	Year	Smoothed			7.78***			
Mean spacing	Post-smolt	Smoothed	1.00	1.00***	1.00***	1.00***	1.00*	0.33
	Intercept	Parametric	0.060	0.059	0.059	0.059	0.059	
	Year	Smoothed			2.54***			0.33
	Post-smolt	Smoothed			7.00**			
	Sample week	Smoothed			1.40***			0.33
	Sample week	Smoothed			1.40***			

For parametric terms, values are regression coefficients, while for smoothed terms, estimated degrees of freedom are given. The significance of smolt-age-specific intercepts is measured relative to the reference category of age-1 smolts. \*\*\*:  $p < 0.001$ , \*\*:  $p < 0.01$ , \*:  $p < 0.05$ .

## Statistical analysis and modeling approach

### Long-term trends in growth

To describe long-term trends in growth increments and average spacings while accounting for potentially confounding intrinsic factors, we fit a generalized additive model (GAM; Zuur *et al.*, 2009) for each variable and scale segment (eight models total; Table 1). Models were developed *a priori* based on known characteristics of Atlantic salmon growth, and model selection through comparison of Akaike's information criterion corrected for small samples sizes (AICc) was used to determine if, for each parameter, an interaction with smolt age should be included (Hurvich and Tsai, 1989). The salmon in our sample originates from Maine to Northern Quebec and thus vary in many important ways that may influence freshwater and marine growth, including smolt age, genetics, migration route, migration distance, and thermal experience. Accounting for this variability is important, but ROO assignments were only available for around one-third of the samples and were biased heavily towards recent years. Inclusion of region of origin in the models would therefore be problematic. As such, we included smolt age as a proxy since it generally follows a latitudinal gradient with younger smolt ages in the southern regions and older in the north (Figure 1; Chaput *et al.*, 2006). This variable should therefore capture some of the important differences in timing of ocean entry and in freshwater and nearshore environments that could substantially influence growth between populations. Substantial overlap in smolt age does occur between regions, and so we interpret the influence of smolt age cautiously. In the models, smolt age was treated as a factor, and when preferred in the model selection process, individual smooths were estimated for each factor level.

Our goal was to describe seasonal trends, with the assumption that changes in growth during a specific period result from environmental and trophic conditions experienced during that period. However, there is the possibility that growth prior to the season of interest may have carryover effects, which complicates the interpretation of period-specific trends. Salmon growth during a given season can be influenced by the prior growth history of an individual through genetic influences on growth rate (Solberg *et al.*, 2013) or compensatory processes (Nicieza and Braña, 1993; Ali *et al.*, 2003). To address this issue, we included a prior growth increment or average spacing as an independent variable in models when possible. No prior growth information was available for freshwater growth, so models for this scale segment included only year of capture and smolt age as predictors. For the first summer scale segment, independent variables included freshwater increment or average spacing as appropriate, in addition to year of capture and smolt age. First winter models included the corresponding first summer growth variables, while models for the plus growth included a first-year variable (i.e. sum of first winter and summer), year of capture, smolt age, and week of capture to account for potential sampling date bias discussed above. As noted previously, interactions with smolt age were included when preferred in the model selection process. Models were fit using the "gam" function in the R package "mgcv" (Wood, 2003). For all models, the gamma argument—a penalization on complex smooths—was set to 3 to achieve reasonably simple smooths, and the select argument—which allows individual model terms to be automatically removed from the model—was set to "TRUE" while all other arguments were set to their defaults.

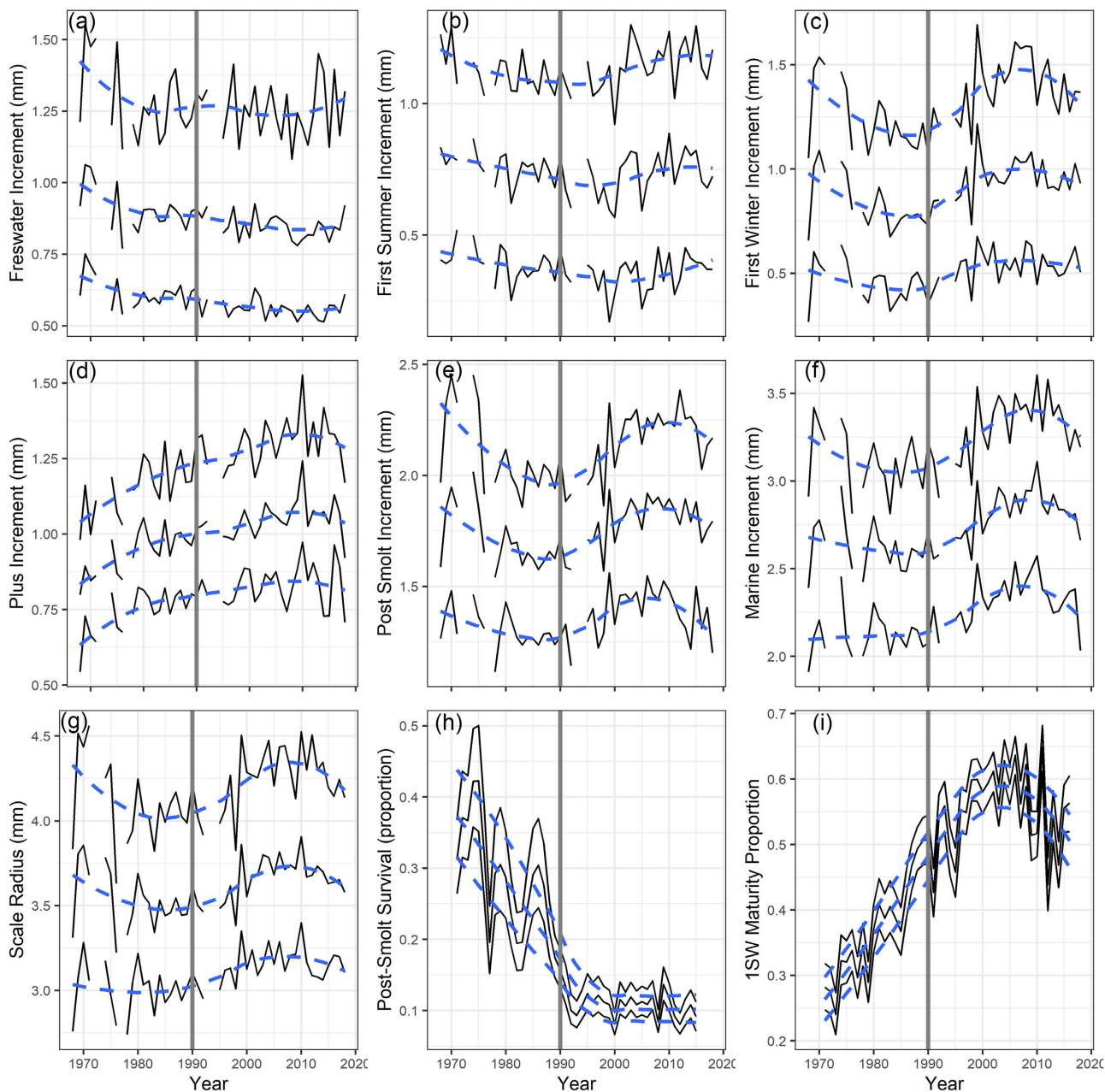
### Influence of growth on post-smolt survival and 1SW maturation proportion

We modeled the relationships between post-smolt survival or 1SW maturation proportion and each growth increment, including the cumulative increments (post-smolt, marine, and scale radius). Although plus growth will not have a direct, mechanistic influence on maturity or post-smolt survival since it occurs after both are determined, the reverse relationship seems probable, with demographic variables impacting the growth characteristics of the fish that are ultimately observable in the Greenland sample. Indeed, because this is a correlational analysis, all the modeled relationships are potentially capturing these indirect impacts of demographics on apparent growth in addition to the direct impacts of growth on survival and maturity. Because of this inherent ambiguity, we determined it was appropriate to include plus growth in this portion of our analysis. Preliminary investigation indicated that models including average spacing produced results very similar to the increment models. So, to avoid redundancy, we focused only on increments for our analyses. Increments from individual scales were averaged by year, while annual estimates of post-smolt survival and 1SW maturation proportion were calculated as regionally weighted means. For weighting, we assumed that the regional composition reflected in the ROO estimates and was representative of the population and constant over time: Quebec accounted for more than one-third of samples, Labrador and the Gulf of Saint Lawrence each around a quarter, and Newfoundland, Scotia-Fundy, and the US each contributed less than 5%. These proportions and their stability through time were consistent with the results of previous studies (e.g. Bradbury *et al.*, 2016). In total, paired demographic and growth data were available for 40 years after accounting for the shorter demographics time series (1971–2015) and missing years of growth data (1972, 1973, 1977, 1993, and 1994). Examination of the partial autocorrelation functions for survival and maturity time series indicated extremely high correlation at 1-year time-lags ( $r = 0.88$  and  $r = 0.71$ , respectively), indicating that these data may not be suitable for standard linear modeling or correlation analyses. To address this challenge, we again used GAMs to model growth–survival and growth–maturity relationships, and also considered models that allowed for separate smooths for each productivity regime. We then evaluated the presence of residual autocorrelation at a 1-year lag using R's partial autocorrelation function ("pacf"). Models were compared using AICc and we hypothesized that preference for a simple additive model would more strongly suggest a mechanistic link between variables, while preference for a regime-based model would suggest more complex, and potentially non-stationary dynamics (Litzow *et al.*, 2018).

## Results

### Summary of growth, survival, and maturity patterns

Visual inspection of average and extreme growth increments between 1968 and 2018 indicated variable trends between the seasonal increments. Freshwater growth appears to have declined modestly in a mostly linear fashion (Figure 3a), while both the first summer and winter at sea showed an initial decline and subsequent increase (Figure 3b and c) and plus growth increased throughout the time series (Figure 3d). Overall, the general trends do not seem to vary between quantiles. With some minor variation, the trends in post-smolt increment (Figure 3e), marine increment (Figure 3f),



**Figure 3.** Seasonal (a)–(d) and cumulative (e)–(g) growth increments, post-smolt survival (h), and 1SW maturity rate (i) through time for North American Atlantic salmon, 1968–2018. Growth variables reflect patterns observed in Greenland fisheries samples, while demographic variables are derived from the entire North American stock complex. Bold vertical line at 1990 reflects approximate timing of regime shift in the North Atlantic ecosystem. Black lines show 5th, 50th, and 95th quantiles and dashed blue lines are LOESS smooths intended to highlight long-term, non-linear trends for each quantile.

and scale radius (Figure 3g) all show similar patterns of an initial decline and subsequent increase as seen in the first summer and winter increments. Post-smolt survival declined over the time series with a notable, abrupt drop around 1990 and relative stability thereafter (Figure 3h). Meanwhile, the proportion of a cohort maturing as 1SW increased through the early 2000s, followed by stabilization and a modest decline (Figure 3i).

Comparisons between decades and productivity regimes indicated that the visually apparent patterns reflected generally significant differences at the  $p < 0.01$  level based on ANOVAs and T-tests

(Table 2). All variables had significant differences between decades with between two and five statistically distinct groups. In percentage terms, the largest changes by far occurred in the survival and maturity variables, with changes greater than  $\pm 70\%$  relative to the 1968–1977 period. For the growth variables, freshwater and first summer growth showed maximum declines of 8–12% while plus growth increased  $\sim 20\%$  over the time series and first winter growth saw an initial decline of 20% followed by a recovery to 1968–1977 levels. The cumulative effect of changes in seasonal growth at sea resulted in a  $\sim 10\%$  net flux in marine growth with an initial decline

**Table 2.** Decadal and productivity regime means and relative changes in Atlantic salmon growth, post-smolt survival, and 1SW maturation rate from 1968–2018.

Decade	Seasonal and cumulative scale increments (mm)						Proportion of cohort		
	Fresh.	1st sum.	1st wint.	Plus	Post-smolt	Marine	Radius	Post-smolt survival	1SW maturity
1968–1977	0.90 <sup>(0.0)a</sup>	0.81 <sup>(0.0)a</sup>	0.98 <sup>(0.0)a</sup>	0.90 <sup>(0.0)a</sup>	1.87 <sup>(0.0)a</sup>	2.74 <sup>(0.0)a</sup>	3.68 <sup>(0.0)a</sup>	0.37 <sup>(0.0)a</sup>	0.33 <sup>(0.0)a</sup>
1978–1987	0.89 <sup>(-0.9)a</sup>	0.74 <sup>(-8.3)b</sup>	0.78 <sup>(-20.5)b</sup>	0.98 <sup>(8.5)b</sup>	1.64 <sup>(-12.7)b</sup>	2.60 <sup>(-5.2)b</sup>	3.51 <sup>(-4.6)b</sup>	0.26 <sup>(-29.2)b</sup>	0.39 <sup>(19.9)b</sup>
1988–1997	0.88 <sup>(-1.9)a</sup>	0.70 <sup>(-12.9)b</sup>	0.83 <sup>(-14.7)c</sup>	1.10 <sup>(11.1)b</sup>	1.65 <sup>(-12.1)b</sup>	2.63 <sup>(-4.1)b</sup>	3.53 <sup>(-3.9)b</sup>	0.14 <sup>(-61.3)c</sup>	0.50 <sup>(54.9)c</sup>
1998–2007	0.87 <sup>(-3.5)a</sup>	0.72 <sup>(-10.2)b</sup>	0.97 <sup>(-0.4)a</sup>	1.07 <sup>(17.6)c</sup>	1.82 <sup>(-2.8)a</sup>	2.86 <sup>(4.4)c</sup>	3.75 <sup>(2.1)a</sup>	0.11 <sup>(-70.2)d</sup>	0.60 <sup>(84.3)d</sup>
After 2007	0.82 <sup>(-8.8)b</sup>	0.78 <sup>(-2.7)a</sup>	0.96 <sup>(-1.5)a</sup>	1.10 <sup>(20.8)d</sup>	1.82 <sup>(-2.7)a</sup>	2.89 <sup>(5.6)c</sup>	3.74 <sup>(1.6)a</sup>	0.10 <sup>(-72.8)e</sup>	0.53 <sup>(64.3)e</sup>
<b>Regime</b>	<b>Fresh.</b>	<b>1st sum.</b>	<b>1st wint.</b>	<b>Plus</b>	<b>Post-smolt</b>	<b>Marine</b>	<b>Radius</b>	<b>Post-smolt survival</b>	<b>1SW maturity</b>
1968–1989	0.89 <sup>(0.0)x</sup>	0.75 <sup>(0.0)x</sup>	0.82 <sup>(0.0)x</sup>	0.97 <sup>(0.0)x</sup>	1.70 <sup>(0.0)x</sup>	2.63 <sup>(0.0)x</sup>	3.55 <sup>(0.0)x</sup>	0.27 <sup>(0.0)x</sup>	0.39 <sup>(0.0)x</sup>
1990–2018	0.85 <sup>(-4.2)y</sup>	0.74 <sup>(-2.3)x</sup>	0.95 <sup>(16.2)y</sup>	1.07 <sup>(10.1)y</sup>	1.79 <sup>(5.7)y</sup>	2.83 <sup>(7.4)y</sup>	3.71 <sup>(4.4)y</sup>	0.11 <sup>(-60.1)y</sup>	0.56 <sup>(41.3)y</sup>

Superscript values indicate % change relative to 1968–1977 for decadal changes and relative to 1968–1990 for productivity regime changes. Superscript letters indicate significant ( $p < 0.01$ ) differences between decadal or productivity regime mean values based on ANOVA and Tukey honest significant differences tests.

of ~5%, followed by a recovery and ultimately an increase of ~5%. Scale radius followed a similar pattern, but with a smaller increase in recent decades resulting from declining freshwater growth. All variables except first summer growth varied significantly between productivity regimes, with freshwater growth and post-smolt survival lower and 1SW maturity proportion and all other growth variables higher after 1989.

### Long-term trends and the influence of prior growth

The results of the GAM analyses were consistent with patterns of change in the raw growth increments, but also identified substantial variation between smolt ages and highlight the importance of accounting for previous growth when analyzing scale increments. Model comparisons preferred smolt-age-specific smoothing functions for both freshwater variables and first winter growth increment models, and shared smoothing for the effect of year in all other cases (Table 1 and Figure 4). For the freshwater scale segment, growth increment was positively associated with smolt age, as would be expected with longer periods of freshwater residence (Figures 4a and 5a). The freshwater growth increment declined in age-2 and age-3 smolts, but remained stable among the older ages. Age-1 smolts showed a markedly different pattern, with rapid increases in growth increment through the early 1990s followed by a plateau. Meanwhile, average freshwater spacing remained constant apart from age-2 smolts, for which it declined slightly (Figure 4b). Age-1 smolts had notably higher average circulus spacing while in freshwater than all other ages. The sample of age-1 smolts is both small ( $n = 66$ ), contributing to higher uncertainty, and the growth patterns are likely influenced by hatchery rearing because naturally produced age-1 smolts are uncommon in North American populations (Chaput, 2006), so results for this group should be interpreted cautiously.

First summer growth varied inversely with smolt age (Figures 4c and 5b), consistent with expectations given the substantially longer marine growing season experienced by southern stocks (typical smolt ages 1–3), which may enter marine waters several months earlier than the northernmost populations (typical smolt ages 3–5; Otero *et al.*, 2014). The temporal trend in first summer growth increment was shared among smolt ages and, consistent with the decadal comparison, shows declining growth until a nadir around 1995, followed by a partial recovery. Average first summer spacing fluctuated through time, but remained stable prior to 1990, and

trended upward thereafter (Figure 4d). The first winter growth increment showed both the most extreme changes and greatest differences between smolt ages (Figure 4e). A period of declining growth occurred from the beginning of the time series until the mid-1980s, but was much more extreme among younger smolts, with the decline nearly absent in the age-4 and age-5 groups. After a period of relative stability, first winter growth increments increased substantially among all ages during the 1990s and early 2000s. The temporal trend in first winter average spacing was much less variable and shared by all smolt ages, increasing until the 1980s and relatively stable thereafter (Figure 4f).

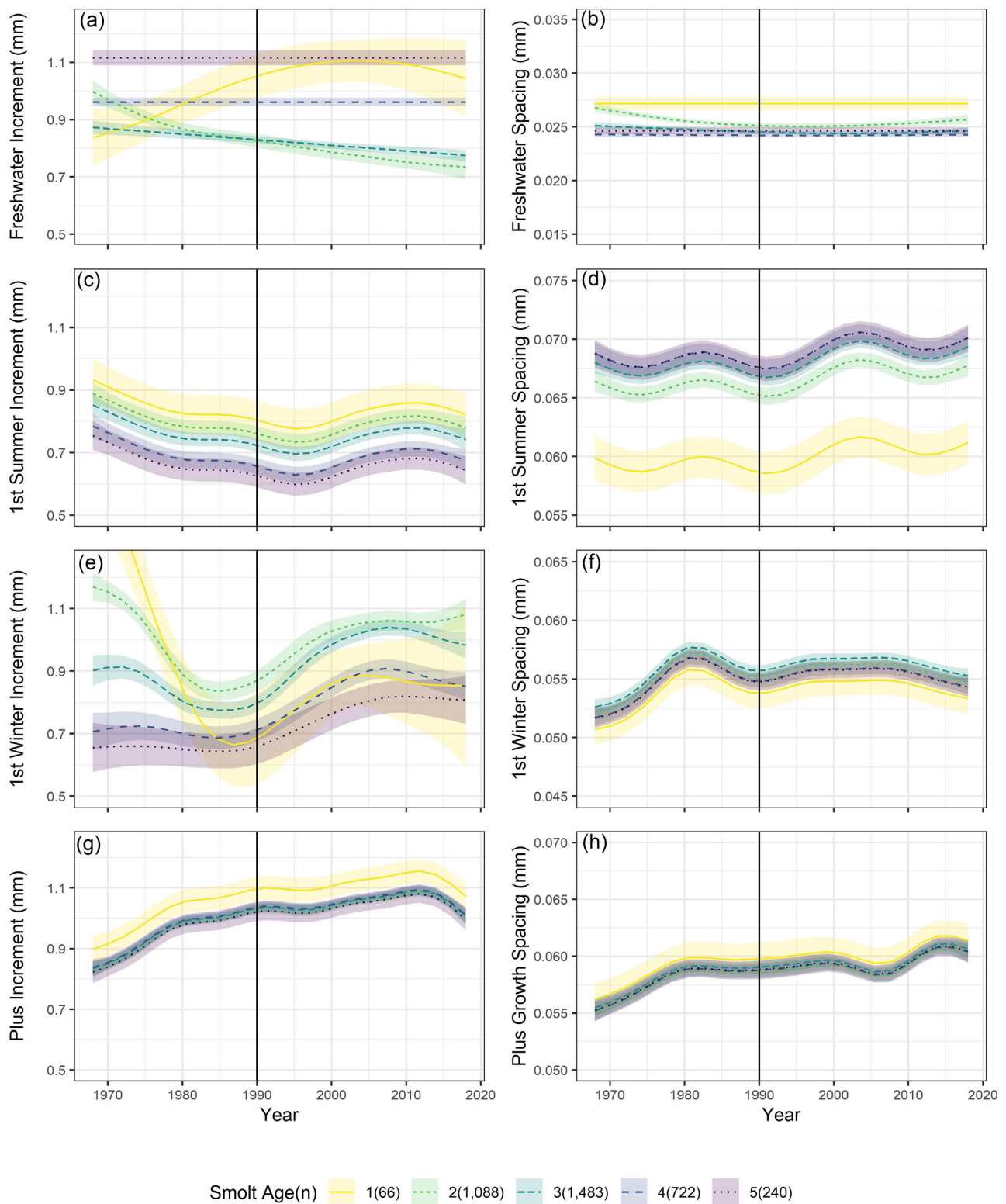
Temporal patterns in the plus growth variables were relatively simple, with shared trends and almost no variability in average values between smolt-ages (Figure 4g and h). Plus growth increments and average spacing both increased almost continuously over the time series, with relatively rapid change occurring during the 1970s. Growth increment does show some indication of declining after the early 2010s, but this is driven almost entirely by 2018, the final year of the time series (Figure 3d), and so the persistence of this change is highly uncertain. As anticipated, week of capture was significant in both plus growth models (Table 1), with a strong linear and positive influence on growth increment and average spacing.

In all cases, the relationships between subsequent growth periods were significant, essentially linear, and varied little between smolt ages, but the direction of these relationships differed in interesting ways (Figure 5). For growth increments, there was a negative influence of freshwater growth on first summer growth, and first summer growth on first winter growth (Figure 5a and b), but a positive influence of total first year growth on the plus growth segment (Figure 5c). Meanwhile, for average spacing, the relationships between periods were all positive (Figure 6a–c).

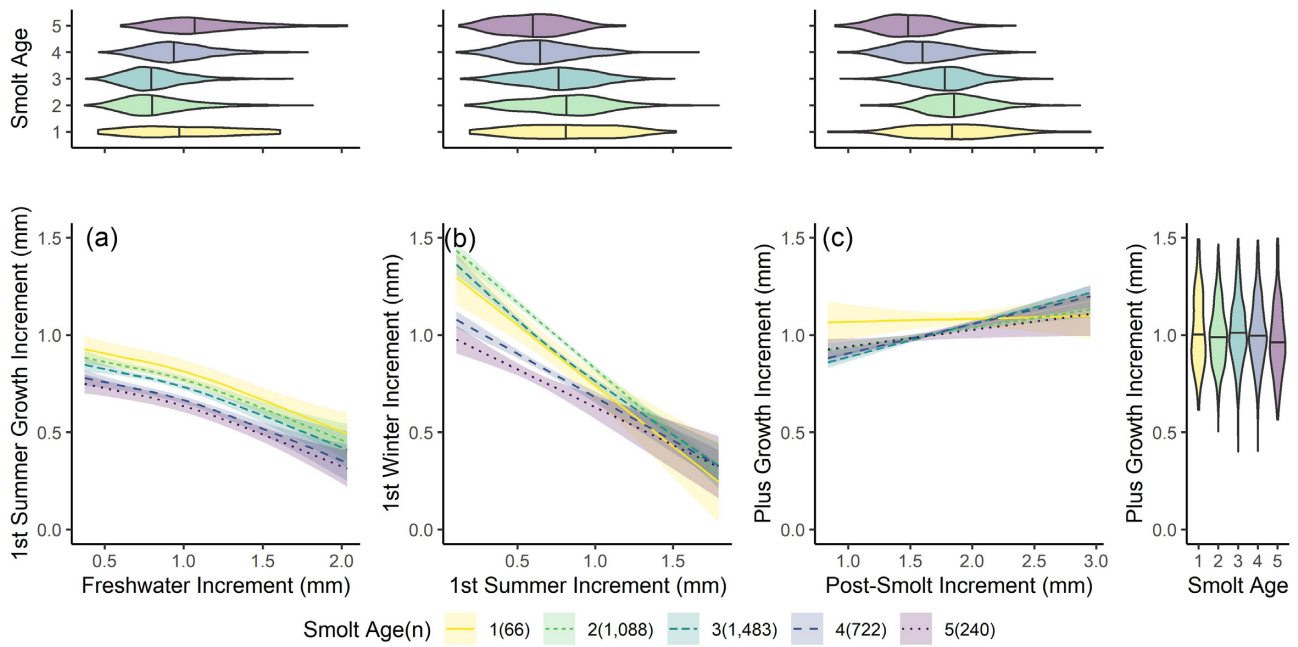
### Relationships between growth, survival, and 1SW maturation proportion

Of the seven simple GAMs relating post-smolt survival to a single growth increment, four identified a significant and generally negative influence of growth, while freshwater increment was weakly, but positively related with survival (Table 3 and Figure 7a–f). Despite several highly significant growth–survival relationships, these simple models had generally poor explanatory power with adjusted  $R^2$  values ranging from 0.02 for the first summer growth incre-

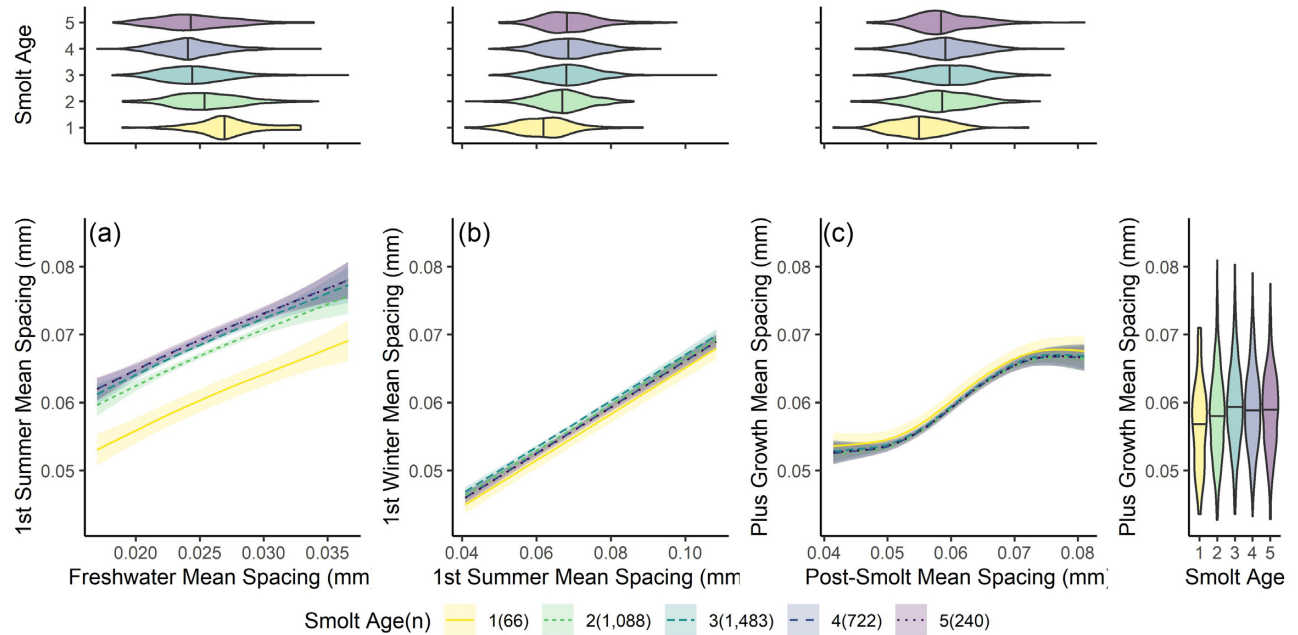




**Figure 4.** Age-specific temporal trends in growth increments [(a), (c), (e) and (g)] and average intercirculus spacing [(b), (d), (f), and (h)] identified using multivariate GAM analyses. Lines show partial dependence (i.e. effect when all other independent variables are held at their mean) of seasonal growth increments and mean intercirculus spacings on sample year and shaded areas show 95% confidence intervals. Vertical line at 1990 reflects approximate timing of regime shift in the North Atlantic ecosystem.



**Figure 5.** GAM results with lines showing partial dependence (i.e. effect when all other independent variables are held at their mean) of seasonal marine growth increments on subsequent growth increments, and shaded areas showing 95% confidence intervals. Marginal violin plots show age-specific distributions of each growth increment.



**Figure 6.** GAM results with lines showing partial dependence (i.e. effect when all other independent variables are held at their mean) of mean intercirculus spacing on subsequent growth increments, and shaded areas showing 95% confidence intervals. Marginal violin plots show age-specific distributions of each growth increment.

ment to 0.39 for the plus growth increment and residual autocorrelation at a 1-year lag was highly significant ( $r = 0.70-0.88$ ; all  $p < 0.001$ ) in all but one case (plus growth increment,  $r = 0.46$ ;  $0.01 < p < 0.05$ ). Models relating growth to post-smolt survival that included an interaction with productivity regime were strongly favoured in all comparisons (all  $\Delta AICc > 10$ ), had much greater explanatory power ( $R^2 = 0.81-0.88$ ) and substantially lower resid-

ual autocorrelation (Table 3). In five of these seven models (Figure 7a, b, d, e, and f), there was a significant influence of the growth variable during the pre-1990 regime, but none of the relationships were significant after 1990. Notably, all growth increments except freshwater and plus growth were *positively* related to post-smolt survival prior to 1990, the opposite of the pattern seen in the simple GAMs.

**Table 3.** Comparison and validation results for simple and productivity regime-based GAMs relating growth increments to post-smolt survival and maturity.

Independent variable	Dependent variables	R <sup>2</sup> Adjusted	AICc	Residual AR (1)	Approximate sign	
					1971–1989	1990–2015
logit(Post-Smolt Survival) ~	Freshwater Increment*Regime	0.84	10	0.27	0	0
	Freshwater Increment	0.11	74	0.79***	+	*
	First Summer Increment*Regime	0.85	6	0.22	+	**
	First Summer Increment	0.02	79	0.87***	0	0
	First Winter Increment*Regime	0.88	-1	0.30	+	***
	First Winter Increment	0.12	74	0.77***	-	*
	Plus Growth Increment*Regime	0.81	16	0.34*	0	0
	Plus Growth Increment	0.39	59	0.46*	-	***
	Post-Smolt Increment*Regime	0.88	-1	0.23	+	***
	Post-Smolt Increment	0.07	77	0.83***	0	0
	Marine Increment*Regime	0.85	7	0.33*	+	**
	Marine Increment	0.19	71	0.70**	-	*
	Scale Radius*Regime	0.86	3	0.27	+	**
	Scale Radius	0.10	75	0.74***	-	*
logit(1SW Maturity Rate) ~	Freshwater Increment*Regime	0.59	18	0.28	0	0
	Freshwater Increment	0.05	49	0.65**	-	*
	First Summer Increment*Regime	0.64	13	0.18	0	0
	First Summer Increment	0.05	49	0.66	0	0
	First Winter Increment*Regime	0.66	11	0.11	-	*
	First Winter Increment	0.16	45	0.56**	+	**
	Plus Growth Increment*Regime	0.61	18	0.26	0	0
	Plus Growth Increment	0.32	36	0.33	+	***
	Post-Smolt Increment*Regime	0.61	10	0.13	-	*
	Post-Smolt Increment	0.05	49	0.66**	0	0
	Marine Increment*Regime	0.61	16	0.18	0	0
	Marine Increment	0.19	43	0.59**	+	***
	Scale Radius*Regime	0.63	15	0.16	0	0
	Scale Radius	0.12	46	0.54**	+	*

All smooths were relatively simple and “approximate sign” indicates if the growth variable had a generally positive (+), negative(-), or non-significant (0;  $p \geq 0.05$ ) influence on the response. \*\*\*:  $p < 0.001$ , \*\*:  $p < 0.01$ , \*:  $p < 0.05$ .

Significant influences of growth were also identified in five of seven simple models relating growth and 1SW maturity proportion (Table 3), with freshwater increment negatively related with 1SW maturity while first winter, plus growth, marine growth, and scale radius had significant positive influence (Figure 7g–i). Again, the models including an interaction with productivity regime performed much better than the simple models in all metrics considered including AICc, explanatory power (simple models:  $R^2 = 0.05–0.32$ , regime models  $R^2 = 0.59–0.66$ ) and residual auto-correlation, which was not significant for any of the regime models (Table 3). Prior to 1990, both first winter and post-smolt increments show weak, negative relationships with 1SW maturity proportion, but no growth variables showed a significant influence on maturity during both productivity regimes.

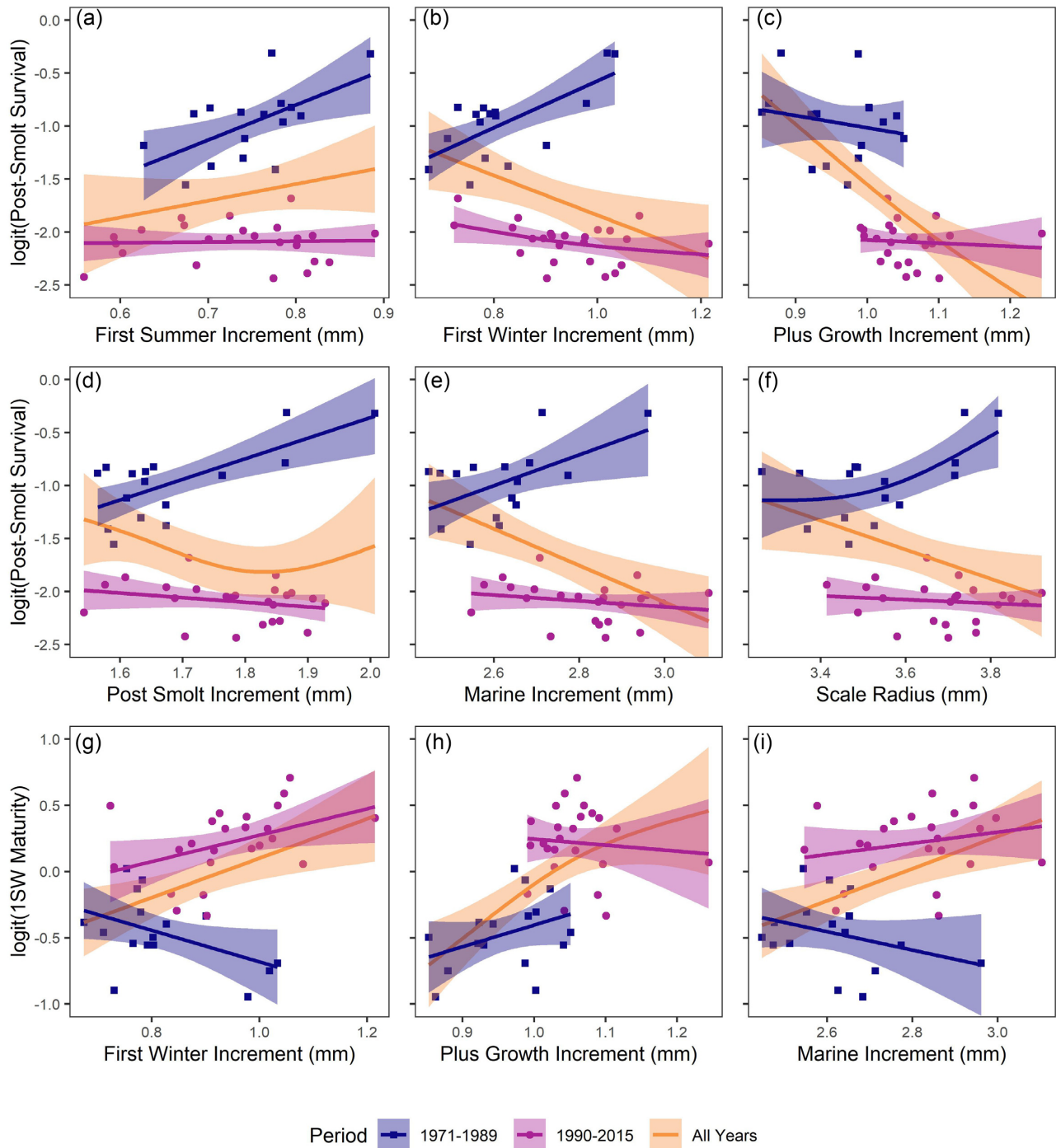
## Discussion

### Long-term growth trends

We used a large and representative scale archive to explore patterns in North American Atlantic MSW salmon growth over five decades and identified significant, long-term growth trends during freshwater and marine residence. The freshwater growth increment declined over the time series, but GAM analysis indicated this change occurred only in age-2 and age-3 smolts [these age groups represent ~70% of individuals sampled in Greenland over

the time series (Sheehan *et al.*, 2019)]. Impacts of climate change on freshwater habitats have influenced the migration timing of Atlantic salmon smolts from across the species’ range (Otero *et al.*, 2014), and the same processes may also influence growth. It is not clear why this pattern would vary by smolt age, but it could plausibly reflect differential impacts of climate change across the species range, assuming that smolt age is serving as an effective proxy for latitude. Regardless of the mechanism driving the declining trend in freshwater increment, smaller size at ocean entry might be expected to result in higher mortality during the difficult freshwater-marine transition. However, the results of previous studies considering size-selective mortality of Atlantic salmon smolts have been mixed (Kallio-Nyberg *et al.*, 2004; Friedland *et al.*, 2006, 2009b; Jutila *et al.*, 2006). As such, the potential consequences of declining smolt size for population productivity and dynamics are uncertain, but the ~20% reduction in freshwater increment among age-2 smolts is nevertheless notable and these results suggest the need for comparative studies of freshwater growth trends across a latitudinal gradient.

Marine growth increment considered in aggregate changed non-linearly but increased modestly over the entire time series, with substantial variation apparent when partitioned by year, season, and smolt age. Growth trends that differ by season or year are not uncommon or unexpected given Atlantic salmon’s distant migrations and use of distinct ocean habitats (Aas *et al.*, 2011). However, the



**Figure 7.** Fits of simple and productivity regime GAM models with at least one highly significant ( $p < 0.01$ ) growth–survival (a)–(f) or growth–maturity (g)–(i) relationship.

greater complexity in first winter growth patterns relative to first summer is surprising since the salmon are most separated in space (because of geographic variation in the point of ocean entry) and time (because of differences in the timing of seaward migration between populations) during the early summer and are thought to generally converge by their first autumn at sea (Friedland and Reddin, 2000; Aas *et al.*, 2011). This pattern may result in part from how “summer” and “winter” are typically defined in scale analysis. A generally accepted approach invokes the summer maximum

as the dividing point between summer and winter growth periods (ICES, 2011). This distinction results a counterintuitive situation where the winter growth increment is often larger than the summer increment. The winter increment as analyzed here therefore captures a much longer period than the summer increment, which may simply provide more opportunity for growth differences within and between years to be manifest. Moreover, the actual date on which summer maximum occurs could vary based on the latitude at which a population enters the ocean, and this could influence the diver-

gence in trends between smolt ages that appear in the first winter growth increment. A probable hypothesis for the relative stability of first summer growth is that strong, size-selective processes operate during the first months at sea, serving to homogenize growth patterns among the fish that survive this period. However, with our data, it is not possible to separate the influence of environmental conditions and size-selective processes on observable growth patterns.

Comparison of long-term growth trends between studies is complicated by varying delineations of growth periods and definitions of growth variables, but the post-smolt period has been the most commonly analyzed and defined fairly consistently. Friedland *et al.* (2009b) provide one of the most comprehensive analyses of post-smolt growth in European populations, with long growth time series for multiple stocks (1960–2000) and a shorter time series of European origin scales from the Greenland fishery (1977–2000). Their results suggest that peak post-smolt growth occurred during the 1970s and declined substantially thereafter. A similar 1970s peak was identified by Friedland *et al.* (2009b) in post-smolt growth of MSW salmon from the Miramichi River, Canada. This peak was not apparent in analyses of scales from five rivers in Maine (Hogan and Friedland, 2010; Izzo and Zydlewski, 2017). The divergent results from Maine suggest that the pattern may not be universal, but these populations currently constitute a very small proportion of the North American stock complex and have been increasingly supported by artificial propagation (Izzo and Zydlewski, 2017). Thus, in combination with the results from European and Canadian populations, our results strengthen the perspective that Atlantic salmon from both sides of the Atlantic experienced a period of particularly high post-smolt growth from the late-1960s through the early-1970s, and that this period had ended by 1980.

The coherence between post-smolt growth in North American and European salmon populations does not appear to have persisted in recent decades. Friedland *et al.* (2009b) reported temporal trends in post-smolt increment for 1SW and MSW salmon from the Miramichi River between the late 1960s and late 1990s that are qualitatively similar to our findings of declining post-smolt growth through the 1970s with a low point in the 1980s and subsequent increase through the early 2000s (Figure 3e). Hogan and Friedland (2010) similarly reported an increase in the post-smolt increment from the mid-1980s through ~2000 in a set of Maine rivers. In contrast, Friedland *et al.* (2009a) observed mostly stable post-smolt growth of MSW salmon across multiple European populations during a similar timeframe. A provocative hypothesis can be developed from these collective results: the relative importance of regional and basin-scale drivers of Atlantic salmon growth vary over time, and so synchrony at the scale of the North Atlantic may be a transient phenomenon. This hypothesis could be addressed using a meta-analytical approach through updating and integration of previously published North American and European growth records.

### Relationships between sequential growth periods

The principal objectives of many recent analyses of Atlantic salmon growth have been to identify time periods that most strongly correlate with probable extrinsic drivers of growth (i.e. temperature and food availability; Izzo and Zydlewski, 2017), or, as in this study, to evaluate the impact of growth during specific periods on marine survival (Peyronnet *et al.*, 2007; Friedland *et al.*, 2009a, 2009b), in both cases using correlational analyses. An assumption of this

approach is that changes in growth during a specific period were driven primarily or exclusively by external conditions during that same period. This assumption may be violated if there is a strong relationship between growth in adjacent life history phases because trends in later growth periods may then reflect carryover effects of environmental changes experienced earlier in life.

In our analyses, prior growth was a significant predictor of all marine growth increments and average spacings (Table 1). The relationship between the freshwater and first summer increments was significant and negative, a pattern not regularly observed in previous studies of single populations (Friedland *et al.*, 2006, 2009a; McCarthy *et al.*, 2008; Hogan and Friedland, 2010). This observation suggests that larger smolts tended to grow less during their first summer at sea. Similarly, the first summer and first winter increments were negatively related, but post-smolt and plus growth increments were positively related. In contrast, average spacing was positively and significantly related through all phases of the life history, suggesting that smolts that grew faster in freshwater continue growing faster during their first year in the ocean and beyond. The discrepancies between increments and average spacings appear counterintuitive, but Izzo and Zydlewski (2017) reported a similar pattern of negatively correlated growth increments, but consistent, positive correlations among mean spacings in sequential growth periods for salmon from several rivers in Maine. It seems likely that these differences result from multiple, potentially counteracting mechanisms that govern the relationships between sequential growth increments. On one hand, innate growth potential should result in consistently positive relationships between increments, while on the other, compensatory, and size-selective processes may dampen or overwhelm this presumably genetic mechanism. The geographic scope of an analysis and associated level of genetic diversity may therefore influence which mechanism dominates. Thus, although we believe it is important to account for prior growth when analyzing temporal trends in seasonal or annual scale increments, we take average circulus spacing to be the more reliable metric for evaluating mechanistic relationships between sequential growth periods.

In summary, it is clear that seasonal or annual growth recorded on salmon scales is not determined only by conditions experienced during that period, but also by the prior growth of an individual. The practical implications of this finding for scale analysis will vary depending on the questions being addressed. When evaluating long-term trends in seasonal or annual scale growth, an approach like that reported here seems prudent (i.e. including a metric of previous growth in multivariate models). The same approach is suitable when examining the relationships between growth and temporally specific environmental conditions, as demonstrated by Izzo and Zydlewski (2017). For comparisons of growth and survival, this influence of prior growth may complicate efforts to identify specific growth periods that are particularly important, but should not reduce the ability to detect an overall relationship between these variables, which was our goal in this study.

### Associations between growth, survival, and maturation

Atlantic salmon marine survival has remained low for the past three decades, and multiple lines of evidence indicate that changes in the North Atlantic ecosystem are impacting salmon productivity indirectly through bottom-up trophic processes (Beaugrand *et al.*, 2003; Friedland *et al.*, 2009a; Mills *et al.*, 2013; Renkawitz *et al.*, 2015; Olmos *et al.*, 2020). Bottom-up control of salmon survival implies re-

duced availability of high-quality prey, and we therefore anticipated a positive relationship between marine growth—either in aggregate or seasonally separated—and survival. Contrary to these expectations, when the entire time series was considered together, the significant relationships between marine growth and survival identified within the GAMs were consistently negative (Table 3), implying that growth has a negative association with survival.

This is a surprising and provocative result, but by allowing for the possibility of non-stationary relationships between growth and survival, it is clear that these are most likely spurious relationships driven by the rapid shift between periods of high and low survival around 1990. Indeed, the strongest relationship—a negative influence of plus growth—loses all statistical significance when productivity regime is included in the model, and regime alone explains more of the variability in survival (Table 3). Meanwhile, post-smolt growth and its seasonal components (i.e. first summer and winter) show the hypothesized, positive relationship with survival prior to 1990 when productivity regime is included. Thus, contrary to prior reports (e.g. Friedland *et al.*, 2009a; Hogan and Friedland, 2010), it appears that growth may indeed influence the survival of North American Atlantic salmon, or at least did prior to 1990. Why growth and survival might have become decoupled after 1990 is uncertain, but this pattern further supports the notion that a common mechanism could have controlled recruitment in European and North American populations when productivity was relatively high, but independent processes have become more important during the low productivity regime.

Combined with other recent studies documenting non-stationary impacts of environmental conditions on salmon productivity (Litzow *et al.*, 2018, 2019), these results highlight a need to re-evaluate the prevailing hypotheses regarding the relative importance of growth in European and North American Atlantic salmon recruitment dynamics (Friedland *et al.*, 2009a; Hogan and Friedland, 2010). Marine survival for many Atlantic salmon populations seems to have changed in a non-linear fashion around 1990 (Olmos *et al.*, 2019), and, as shown by our models relating growth and survival, this step change can drive spurious correlations and obscure true relationships if stationary processes are assumed. Given this, it would be valuable to update and reanalyze growth data from European populations to allow for comparison between productivity regimes. Ultimately, an integrated analysis that incorporates populations from both continents and allows for non-stationary growth–survival relationships should be pursued to fully resolve the role of growth in Atlantic salmon marine survival.

As with survival, there is evidence of non-stationary dynamics in the relationship between growth and maturity. Visually, there appears less separation between regimes, and results for the complete time series showed the expected pattern of higher growth associated with more fish maturing as 1SW. However, the productivity regime models were strongly preferred in the model comparison (Table 3), and this positive relationship was not preserved within either regime for any growth variable. Interpreting these findings is made difficult by the fact that our sample includes only fish that will become MSW spawners, which vary as a proportion of the total stock complex, likely in part as a function of post-smolt growth (Hutchings and Jones, 1998). The prevailing theory for many salmonids, including Atlantic salmon, is that maturation schedule is determined by a population-specific norm of reaction, such that individuals have a genetically determined growth (or growth rate) threshold, which if exceeded during the first year at sea will initiate the maturation process (Hutchings, 2011). Following from this under-

standing, if post-smolt growth conditions are particularly good, a larger proportion of the populations should mature after one year, and therefore not migrate to Greenland. At the same time, year-to-year variation in the growth–maturation threshold—because of adaptive evolution of this trait within populations, shifting demographics such as sex ratios, or changes in the relative abundance of populations with different thresholds—would also influence the proportion of the population observable at Greenland. Given our data (and indeed most scale growth data), it is impossible to separate the influence of these two potential mechanisms. This issue obviously has the most direct bearing on interpretation of the growth–maturity relationship, but may also have implications for any retrospective analysis of scale growth. Indeed, the challenge of disentangling changes in growth from temporal variation in selective processes that serve to filter which individuals are ultimately available for sampling (i.e. survivor and maturity biases) is a pervasive problem in the field of scale analysis. However, the degree to which such variability impacts the utility of scale archives for investigating relationships between environmental change, growth, and survival has not been rigorously addressed. Understanding the sensitivity of reconstructed growth to variation in size-selective mortality and maturation is an important area of future research that will ultimately determine how retrospective growth analyses are interpreted and applied toward management and conservation efforts.

## Conclusion

The scale archive from West Greenland fishery sampling provided a unique opportunity to examine long-term trends in growth for the entire North American Atlantic salmon stock complex. Collectively these results complement previous studies that have examined scale growth trends in single populations or smaller stock groupings, and help to clarify the generalizability of previously observed patterns. We described temporal trends in growth, finding a modest decrease in freshwater growth among some smolt ages and a larger, consistent increase in growth during the second year at sea across the entire time series. Post-smolt growth was relatively high during 1960s and 1970s, lower during the 1980s and increasing thereafter. The post-smolt growth trend was similar to several previous studies of North American populations (Friedland *et al.*, 2009b; Hogan and Friedland, 2010), and prior to the 1990s, also similar to growth trends observed in European populations (Friedland *et al.*, 2009a). Collectively, these results show that marine growth of North American Atlantic salmon has been higher during the past 20 years than during the period of relatively high marine survival prior to 1990. However, comparison of stationary and non-stationary models indicated that these concurrent trends do not reflect a true negative growth–survival relationship. Instead, prior to 1990, post-smolt growth was positively and significantly correlated with survival, and thereafter survival declined, apparently independent of growth. It therefore appears that growth played a similar role in determining survival of European and North American salmon populations prior to large-scale changes in the ocean environment around 1990. These results raise several critical questions: (i) Why have growth and survival become uncoupled for North American populations? (ii) Was marine survival of North American and European salmon populations regulated by similar mechanisms prior to 1990? (iii) What environmental or demographic changes might explain the apparent divergence in the importance of growth between the continents during recent decades? To address these questions,

we encourage integrated analysis of growth and survival for populations from both continents that explicitly considers the possibility of non-stationary relationships.

## Supplementary Data

Supplementary material is available at the ICESJMS online version of the manuscript.

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## Data availability statement

All data used in the analyses reported herein will be shared upon reasonable request to the corresponding author or project supervisors (kmills@gmri.org or tim.sheehan@noaa.gov).

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