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Evidence for spatial coherence in time trends of marine life history traits of Atlantic salmon in the North Atlantic

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Abstract

A hierarchical Bayesian life cycle model is presented that considers spatial covariation of marine life history traits of Atlantic salmon (*Salmo salar*) populations in the North Atlantic. The model is based on a collective analysis of the dynamics of 13 stock units (SUs) from two continental stock groups (CSGs) in North America and Southern Europe in a single hierarchical model over the period 1971–2014. The model sets up a new assessment framework for Atlantic salmon stocks. It also provides a framework to investigate the drivers of changes in Atlantic salmon population dynamics including disentangling the effects of fisheries from those of environmental factors in a hierarchy of spatial scales. It is used to test the hypothesis of a strong spatial synchrony in marine life history dynamics of Atlantic salmon populations. The trends in two key parameters associated with the early marine phase of the life cycle are estimated: (i) the marine survival during the first summer–autumn spent at sea and (ii) the proportion of fish maturing after the first winter at sea. The results provide evidence of a decline in the marine survival together with an increase in the proportion of fish that mature after the first winter at sea, common to all SUs. Our results show an increased coherence in the covariations of trends in these two marine life history traits related to geographic proximity of SUs which support the hypothesis of a coherent response of geographically proximate Atlantic salmon populations that likely share similar migration routes.

KEYWORDS

hierarchical Bayesian model, marine survival, maturation probability, spatial covariation, spatial synchrony, stage-based life cycle model

1 | INTRODUCTION

Marine and freshwater ecosystems are impacted by multiple stressors such as overharvesting (Christensen et al., 2003), habitat degradation (Halpern et al., 2008) and climate change (Hoegh-Guldberg & Bruno, 2010). Evidence and data are accumulating, showing that demographic and ecological mechanisms controlling the productivity of fish populations operate at different life stages and at a hierarchy of spatial and temporal scales (Petitgas et al., 2013). The development of life cycle models that incorporate a comprehensive representation of the spatial and temporal heterogeneity of those mechanisms is needed to assess the effects of multiple stressors on fish populations (Rochette, Le Pape, Vigneau, & Rivot, 2013; Stelzenmüller, Schulze, Fock, & Berkenhagen, 2011). Such a consideration is a prerequisite in the provision of reliable scientific advice and in the identification of the most appropriate fisheries and ecosystem management policies (Clark, 2001; Griffith, Fulton, Gorton, & Richardson, 2012; Kuparinen, Mäntyniemi, Hutchings, & Kuikka, 2012).

Collective analysis of the dynamics of multiple populations that in certain periods share common environments offers a powerful approach for improving our understanding of the demographic and ecological mechanisms shaping the response of populations to multiple stressors (Walter et al., 2017). By simultaneously considering multiple populations, large-scale ecological processes can be more readily partitioned from local effects, random demographic noise and sampling errors (Myers, Mertz, & Bridson, 1997; Soberon & Nakamura, 2009). Specifically, it provides a framework for partitioning the effects of factors impacting each population differentially from those that are susceptible to impact groups of populations simultaneously (Lahoz-Monfort et al., 2013; Parmesan & Yohe, 2003; Ranta, 1997).

The worldwide decline of many diadromous migratory fish populations over the last century has received considerable attention (Limburg & Waldman, 2009). The life cycle of diadromous fish is variously shaped by the spatial segregation of populations in freshwater habitats as well as the spatial and temporal overlap of populations during the marine phase. This makes them sensitive to multiple environmental and anthropogenic stressors acting at a hierarchy of spatial and temporal scales, with factors operating at sea most likely to synchronize the dynamics of large groups of populations. For example, the widespread decline in European Eel (*Anguilla anguilla*, Anguillidae) recruitment from Mauritania to Norway has been correlated to environmental conditions on the spawning ground of eels in the Sargasso Sea (Bonhommeau et al., 2008). Several species of Pacific salmon (*Oncorhynchus* spp.) have also shown a strong regional synchrony of declines in recruitment in the last decades, suggesting a response to factors operating at large spatial scales (Malick, Cox, Mueter, Dorner, & Peterman, 2017; Mueter, Peterman, & Pyper, 2002). Changes in marine conditions, specifically the timing of the spring phytoplankton bloom and variations in sea surface temperatures, have been proposed as the most likely synchronizing factors for these Pacific salmon species (Peterman, Dorner, & Rosenfeld, 2012).

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Atlantic salmon (*Salmo salar*, Salmonidae) populations have also undergone a widespread North Atlantic decline in abundance over the last four decades (Chaput, 2012; ICES, 2017a; Jonsson & Jonsson, 2004). It is an obligate freshwater spawner with a strong homing behaviour to natal rivers such that the species is structured into hundreds of local populations in eastern North America, Europe and Russia. During the marine phase of the life cycle, many populations migrate to common feeding grounds in the North Atlantic, located off the coast of West Greenland (WG), in the Labrador Sea

and in the Norwegian Sea, where they may be under the common influence of environmental marine conditions and sea fisheries.

Stock assessment models for Atlantic salmon have been developed based on data aggregated at the scale of regional or national stock units (SU) over the North Atlantic area within three continental stock groups (CSGs): eastern North America (NA), Southern European (SE) and Northern European (NE) (Crozier et al., 2004; Potter et al., 2004). The objective of these models was to reconstruct long-term series (starting in the early 1970s) of abundance at sea before any marine fisheries (pre-fishery abundance, PFA, measured at the January 1 of the first winter spent at sea) and to forecast the returns of adult salmon to their natal rivers (homewaters). These models have been incorporated in a risk analysis framework to assess the consequences of mixed-stock marine fisheries on the returns (Chaput, Legault, Reddin, Caron, & Amiro, 2005; ICES, 2015a) and to assess compliance of realized spawning escapement to conservation limits (biological references point below which the stock should not pass) at the SU and CSG scales. Although the main marine commercial fisheries were closed or were severely reduced since the early 1990s, these PFA reconstruction models estimated that the abundances of Atlantic salmon at sea declined farther for almost all SUs in the North Atlantic. In parallel, surveys of salmon populations on several rivers across the species range indicate a general decline in the return rates of migrating juveniles to adults. There was no evidence of a generalized decline in the freshwater survival or juvenile production (Crozier, Potter, Prévost, Schön, & Maoiléidigh, 2003) suggesting that declines in marine survival rates, acting at a broad spatial scale at sea, were responsible for the estimated declines in PFA (Chaput, 2012).

Beyond their use for stock assessment, outputs of PFA models have also been used for ecological studies attempting to unravel the signals of changes in marine ecosystems. Friedland, Shank, Todd, McGinnity, and Nye (2014) provided one of the first comparative analyses of trends in abundance at sea (estimated at the PFA stage) in the NA and SE CSG. The authors found negative correlations between the Atlantic Multidecadal Oscillation and PFA abundances in both CSG. Specifically, the declines of PFA observed in the early 1990s in both CSGs appear synchronous with a change from a cooler to a warmer phase of sea surface temperatures (SST) in the early 1990s. Additional analyses of the relationships of finer spatio-temporal scale variations in SST and recruitment indices (based on catches for NA stocks and on tag returns for SE stocks) revealed slightly different responses between the CSGs. Warm temperatures in early spring negatively affected the recruitment index in NA, whereas recruitment in SE was negatively correlated with warmer SST in late summer.

Other analyses run independently for SUs in SE (Beaugrand & Reid, 2012) and NA (Mills, Pershing, Sheehan, & Mountain, 2013) used proxies of marine survival derived from PFA models to suggest a bottom-up trophic-based mechanism for the declining trends in marine survival. The proposed mechanism is that warmer water temperatures would negatively impact the productivity of the North Atlantic pelagic food web, thereby altering feeding and growth opportunities for Atlantic salmon during the marine phase. In addition, PFA model results showed that trends differed between life histories: the abundance of

fish maturing after two winters spent at sea (2SW fish) declined more sharply than the abundance of fish maturing after one winter spent at sea (1SW fish) (ICES, 2017a). But the mechanisms that would account for this differential decline for the two sea-age classes are still not clear (Jonsson & Jonsson, 2004; Jonsson, Jonsson, & Albretsen, 2016).

Pre-fishery abundance models suffer from major weaknesses that hinder their relevance for analysing the demographic and ecological processes underlying the decline of European and American Atlantic salmon populations. To date, the PFA models used for formulating catch advice at ICES (2015a,b) rely on a coarsely constructed stock-recruitment dynamic, defined as the productivity parameter between the eggs (measure of the spawning stock) and abundance at the PFA stage (recruitment). Statistical inferences on the time series of productivity parameters are susceptible to time-series bias because the dynamic link between PFA and subsequent egg depositions is not represented (Massiot-Granier et al., 2014; Su & Peterman, 2012). The lack of flexibility in the modelling framework also restricts the integration of the large amount of available data and knowledge of demographic and population dynamics. As such, hypotheses on drivers and mechanisms of changes cannot be easily tested (Massiot-Granier et al., 2014).

More importantly, different and independent PFA models were developed for the three CSGs. Some core demographic hypotheses are not harmonized among these models. Specifically, the two European models explicitly consider 1SW and 2SW fish in the population dynamics, while the current model for NA, which was developed for catch advice purposes at West Greenland, only considers the dynamics of 2SW fish (Chaput et al., 2005). The NA model implicitly assumes that 2SW spawners only produce 2SW fish in future cohorts, and excludes contributions of 1SW and multisea-winter spawners. Temporal variations of marine survival proxies for NA SUs analysed by Mills et al. (2013) consider only the 2SW component and are therefore not comparable to the SE PFA models analysed by Beaugrand and Reid (2012). These structural differences in models preclude the simultaneous analysis of the population dynamics among the SUs in the North Atlantic. This approach also ignores any covariance structure in the dynamics of the SUs even though the SUs may share common environments at sea and be jointly exploited in sea fisheries.

Our main contribution to advancing opportunities for understanding population dynamics is the development of a methodological framework for the combined analysis of Atlantic salmon population dynamics across a large number of SUs in SE and NA. The model sets up new foundation for Atlantic salmon stock assessment in the North Atlantic and provides a structural basis for analysing the mechanisms that shape population responses to variations in marine ecosystems. We extend the framework developed by Massiot-Granier et al. (2014) for one SU to include the dynamics of all SUs in NA and SE within a single unified hierarchical Bayesian life cycle approach with populations following a similar life history process (Buckland, Newman, Fernández, Thomas, & Harwood, 2007; Buckland, Newman, Thomas, & Koesters, 2004; Clark, 2004; Parent & Rivot, 2013; Rivot, Prévost, Parent, & Baglinière, 2004). The new framework allows for modelling

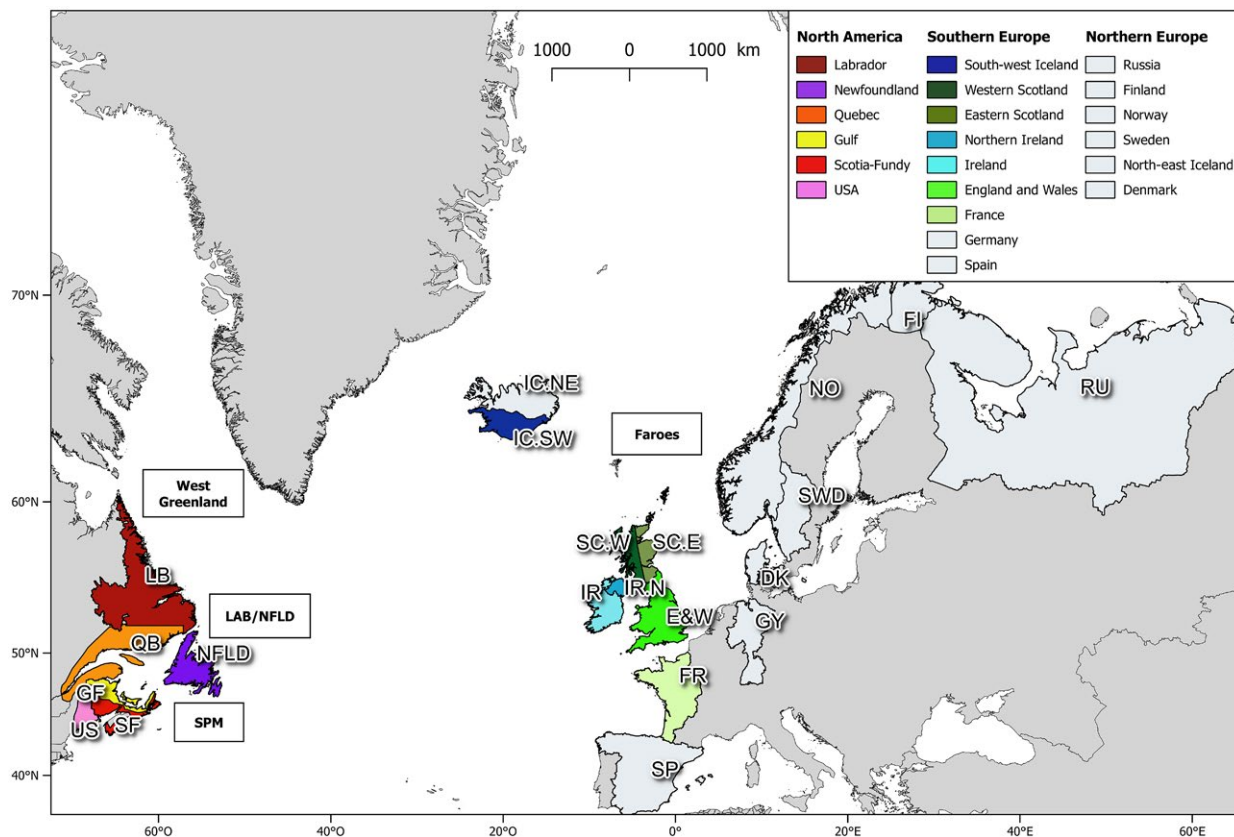


FIGURE 1 Stock units (SUs) defined as groups of spawning rivers for Atlantic salmon with the same migration routes as per ICES (2015b). SUs of North America: NFLD, Newfoundland; GF, Gulf; SF, Scotia-Fundy; US, USA; QB, Quebec; LB, Labrador. SUs in Southern Europe: IR, Ireland; E&W, UK (England and Wales); FR, France; SC.E, UK (eastern Scotland); SC.W, UK (western Scotland); IR.N, UK (Northern Ireland); IC.SW, south-west Iceland. SUs in grey are not included in our model: GY, Germany; SP, Spain; and SUs of Northern Europe: RU, Russia; FI, Finland; NO, Norway; SWD, Sweden; IC.NE, north-east Iceland; DK, Denmark. Boxes indicate the main fisheries at sea operating on mixed stocks: Faroes, West Greenland, Labrador and Newfoundland (LAB/NFLD), and Saint Pierre and Miquelon (SPM)

covariations among all SUs and for partitioning the effects of fisheries from the effects of environmental factors at a hierarchy of spatial scales, including at the level of the North Atlantic, of each CSG, and for each SU within a CSG. We used this new framework to test the hypothesis of a common response of populations across the North Atlantic. Because fish from NA and SE both feed in the North Atlantic Ocean, temporal variations in marine survival and in the proportion of fish maturing as 1SW would be expected to exhibit common trends among SUs in the North Atlantic. Following the theory of geographic covariance (Bjørnstad, Ims, & Lambin, 1999; Walter et al., 2017), we expect the covariance to be greater among SUs within the same CSG than among SUs across CSG because the marine migration routes are likely to be more similar for fish from the same CSG (NA or SE).

2 | MATERIALS AND METHODS

2.1 | Model design

The model is formulated in a Bayesian hierarchical state-space framework (Buckland et al., 2004; Clark, 2004; Cressie, Calder,

Clark, Hoef, & Wikle, 2009; Parent & Rivot, 2013; Rivot et al., 2004) that incorporates stochasticity in population dynamics as well as observation errors. To keep the presentation concise, all model equations and data sources are detailed in Supporting Information S1.

2.1.1 | Spatial structure

Thirteen SUs, as defined in ICES (2017a), are considered in the model, 6 SUs from the NA CSG (indexed by $r = 1, \dots, 6$: 1 = Newfoundland, 2 = Gulf, 3 = Scotia-Fundy, 4 = USA, 5 = Quebec and 6 = Labrador) and 7 SUs from the SE CSG (indexed by $r = 7, \dots, 13$: 7 = Ireland, 8 = UK (England and Wales), 9 = France, 10 = UK (Scotland east), 11 = UK (Scotland west), 12 = UK (Northern Ireland) and 13 = south-west Iceland) (Figure 1). A SU is defined on the basis of freshwater areas. All salmon populations within a SU are assumed to undertake a similar migration route at sea (Dadswell, Spares, Reader, & Stokesbury, 2010; Potter et al., 2004; Rago, Reddin, Porter, Meerburg, Friedland, & Potter, 1993). Germany and Spain (SE CSG), and SUs from the Northern Europe CSG are not considered at this stage because of an incomplete time series of data.

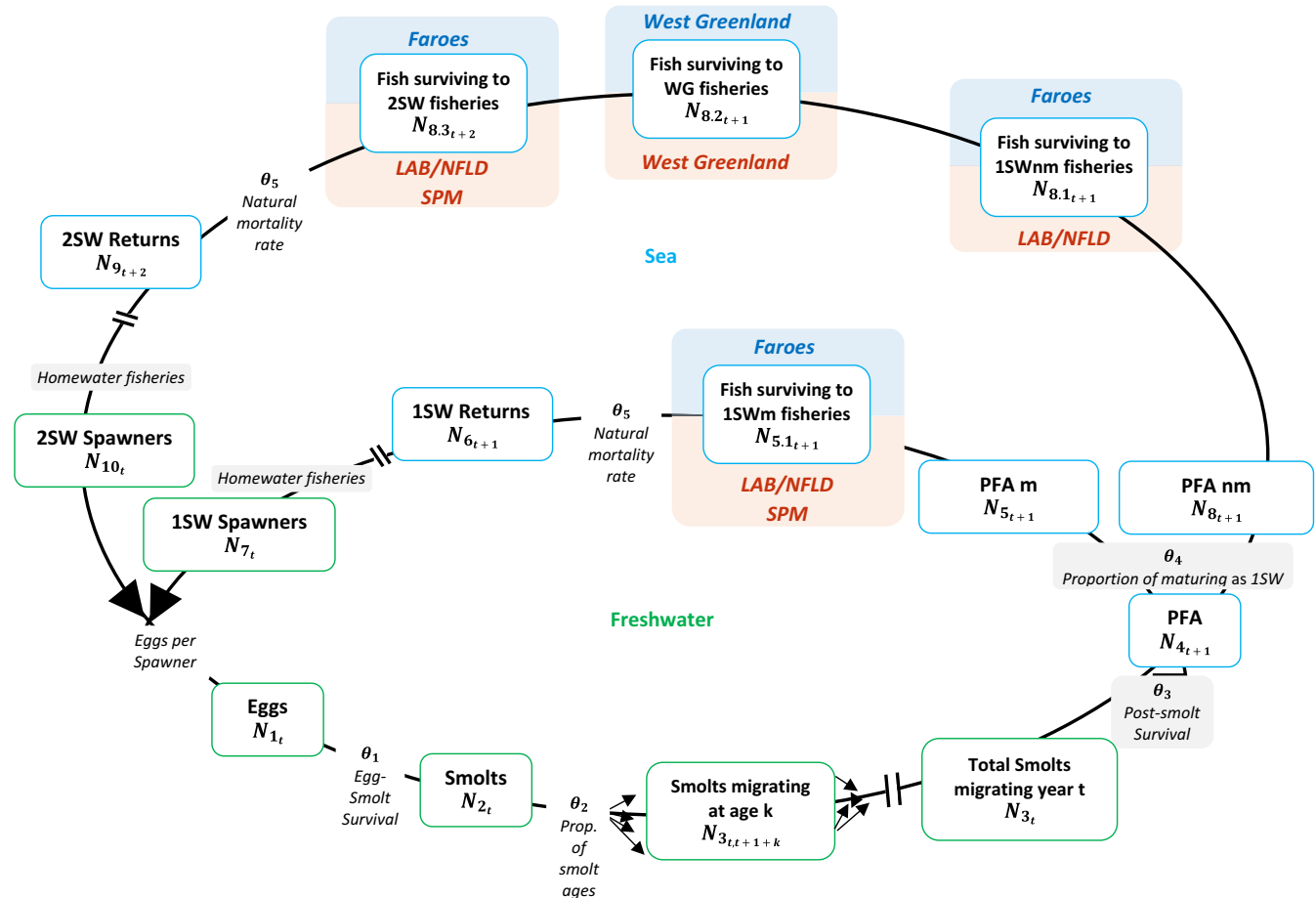


FIGURE 2 Structure of the age- and stage-based life cycle model. $N_{1,t,r}$ is the total number of eggs calculated from $N_{7,t,r}$ and $N_{10,t,r}$. $N_{3,t,r}$ is the total number of smolts migrating in year t , as the sum of all smolts of age $a = 1, \dots, 6$ that migrate at year t . Red and blue boxes represent the migration routes with the associated sequential fisheries at sea that are specific for SUs from NA and SE, respectively. Double bars indicate where cut in the time indices has been introduced to make notations easier. Light-shaded stages (eggs per spawner, proportion of smolt ages and natural mortality) are transitions with parameters fixed or assigned with very informative prior distributions. Shaded (dark, blue or red) stages (exploitation rates, post-smolt survival and proportion of fish maturing as 1SW) are parameters estimated from time series of data

2.1.2 | Variability of life histories

The population dynamic of each SU is represented by a homogeneous age- and stage-structured life cycle model, applied to all SUs (Figure 2). The model structure incorporates variations in the age of out-migrating juveniles from freshwater (i.e., smolt ages) and the sea age of returning adults among SUs. Smolts migrate to sea after 1–6 years in freshwater (depending on SU). Following the approach used by ICES for catch advice purposes (ICES, 2015a), only two sea-age classes are considered in the model: maiden salmon that return to homewaters to spawn after 1 year at sea, referred to as one-sea-winter (1SW) salmon, or grilse, and maiden salmon that return after two winters at sea (2SW). This is a simplification of the larger diversity of life history traits as some maiden fish may spend more than two winters at sea before returning to spawn, and some salmon return as repeat spawners. Maiden spawners older than 2SW are relatively rare in North America and Southern Europe, and the six smolt-age by two sea-age combinations represent the essence of life history variation.

The model tracks the abundance of fish ($N_{s,t,r}$) for each SU (r) by year (t) and life stage (s), sequentially from eggs (N_1) to 1SW (N_7) or 2SW (N_{10}) spawners for the period 1971–2014, year of return to rivers (Figure 2). Spawners are fish that contribute to reproduction and that therefore survived all sources of natural and fishing mortality. The transition rates between stages (s) for each SU (r) in year t are denoted $\theta_{s,t,r}$.

2.1.3 | Hypotheses to separate the sources of variability

As recognized by the data constraints already expressed in the existing PFA models used by ICES (ICES, 2015a) and discussed by Massiot-Granier et al. (2014), the quality and information provided by the data are limited, which restricts the number of population dynamic parameters that can actually be estimated. The framework is primarily designed to estimate the abundance at various life stages along the life cycle, the exploitation rates of all fisheries and the two parameters that implicitly assume that most of the temporal variability

TABLE 1 Summary of model configurations

Models configurations	Freshwater phase		Marine phase	
	Egg-to-smolt survival		Smolt-to-PFA survival	Proportion maturing as 1SW Fisheries
F1	Density-independent Homogeneous among SU	CV temporal variability = 5%		
F2		CV temporal variability = 20%–80%		
F3	Density-dependent Variable among SU	CV temporal variability = 20%–80%		
M1			Non-diagonal (plain) variance–covariance matrix	
M2			Two blocks variance–covariance matrix with a priori no covariation between any pairs of SU from two different continental stock groups	
M3			Diagonal variance–covariance matrix with a priori no covariance	
E1				SU-specific information data to allocate catches
E2				No data to allocate catches in distant marine fisheries

Note. Shaded grey cells indicate the baseline configuration. See Supporting Information S1 for details of parameterization.

occurs during the first months of the marine phase: the post-smolt marine survival rates (from out-migrating smolts to the PFA stage as of January 1 of the first winter at sea) and the proportions of fish maturing as 1SW, for each SU. To separate the variability in the natural and fishing mortality during the freshwater and marine phase and in the proportion of fish that mature as 1SW, we use the framework described in ICES (2015a) and Massiot-Granier et al. (2014).

Freshwater phase

The number of eggs spawned in each SU by year is derived from the annual number of returning 1SW and 2SW spawners and the SU-specific sex ratio and fecundity values; these are considered fixed and constant over time (Table S1.1).

In the absence of information on the total smolt production at the scale of SUs, the parameters of the freshwater phase (eggs to out-migrating smolt production) are fixed. Three modelling hypotheses (F_1 , F_2 and F_3) of egg-to-smolt survival were compared (Table 1; Table S1.2). The baseline configuration (F_1) considers a density-independent egg-to-smolt survival relationship with a common homogeneous survival rate among SUs, constant over time and modelled with very low interannual stochastic variability (Table 1; Table S1.2). As fecundity and freshwater survival are fixed a priori, there is no temporal variation in the freshwater phase of the life cycle. This implicitly assumes that any changes in the stock productivity over time are the result of variations in dynamics in the marine phase, which may inflate the importance of variation in the post-smolt survival. We assessed the robustness of inferences on post-smolt survival rates and the proportions maturing as 1SW to alternate hypotheses. In model configuration

F_2 , we explore the consequences of higher interannual stochasticity in the egg-to-smolt survival rates (Table 1; Table S1.2). This increased interannual variability in the freshwater phase may change the inferences of the marine-phase parameters. In model configuration F_3 , we assess the consequences of incorporating a density-dependent egg-to-smolt survival relationship (Chaput et al., 1998; Gibson, 1993; Kennedy & Crozier, 1993) on inferences of the marine-phase dynamics (Table 1, Table S1.2). As the number of eggs spawned varies in the time series, the incorporation of a density-dependent egg-to-smolt survival relationship results in variations in the egg-to-smolt survival rates over time which can vary the number of smolts going to sea and subsequently modify the inferences of post-smolt survival rates.

The total number of smolts produced by a cohort is attributed to river-age classes using SU-specific smolt-age proportions which are considered fixed and constant over time (Table S1.1).

Marine phase

Smolts of different ages migrating seaward in any year (t) are pooled together once at sea. Returns rates from smolts to 1SW and 2SW adults result from the combination of natural mortality, fishing mortality and a maturation schedule. The PFA stage is defined as abundance of post-smolts at January 1 of the first winter at sea, and prior to any fisheries. Survival from smolts to the PFA stage may vary among years and SUs. Fish at the PFA stage can then mature (and return as 1SW adults) or delay maturation until the following winter (and return as 2SW adults). The proportion of fish maturing as 1SW may vary with year and SUs.

Natural mortality rates after the PFA stage are fixed, assumed constant in time, homogeneous among all SUs and identical for

maturing and non-maturing fish (Table S1.1). Under this assumption, the proportion of the PFA abundance that matures is confounded with the mortality difference between 1SW and 2SW salmon. Fishing mortality is modelled as a temporal sequence of fisheries operating on mixtures of SUs along the migration routes, as well as on each SU in homewaters. Fisheries exploitation rates may vary by year and SU and are assigned weakly informative priors (Table S1.3).

2.1.4 | Covariation among SUs

The model explicitly incorporates two components of covariation in the population dynamics among the 13 SUs. The first component of covariation is in the life history processes at sea, and this is considered using variance–covariance matrices (Figure 3). The post-smolt survival (denoted $\theta_{3_{t,r}}$) and the proportion of fish maturing as 1SW (denoted $\theta_{4_{t,r}}$) are modelled as multivariate random walks in the logit scale which simulates spatial covariation associated with environmental stochasticity. Random variations are drawn from multivariate normal distributions with variance–covariance matrices Σ_{θ_3} and Σ_{θ_4}

(Minto, Mills, Flemming, Britten, Worm, & Rose, 2014; Ripa & Lundberg, 2000):

$$\left(\text{logit} \left(\theta_{3_{t+1,r}} \right) \right)_{r=1:13} \sim \text{MVNormal} \left(\left(\text{logit} \left(\theta_{3_{t,r}} \right) \right)_{r=1:13}, \Sigma_{\theta_3} \right) \quad (1)$$

$$\left(\text{logit} \left(\theta_{4_{t+1,r}} \right) \right)_{r=1:13} \sim \text{MVNormal} \left(\left(\text{logit} \left(\theta_{4_{t,r}} \right) \right)_{r=1:13}, \Sigma_{\theta_4} \right) \quad (2)$$

Because of the geographic proximity of the freshwater habitats and early migration routes at sea among SUs of the same CSG, the covariances among SUs in the time trends of post-smolt survival and proportion of fish maturing as 1SW are expected to be greater within a CSG than between CSGs. To test this hypothesis, three alternative structures of the variance–covariance matrices were examined (Table 1; Table S1.3). In the reference model M_1 , no a priori hypotheses about the covariation structure of 13×13 variance–covariance matrices Σ_{θ_3} and Σ_{θ_4} are made. In M_2 , Σ_{θ_3} and Σ_{θ_4} are defined by continental blocks, considering a priori no covariation (i.e.,

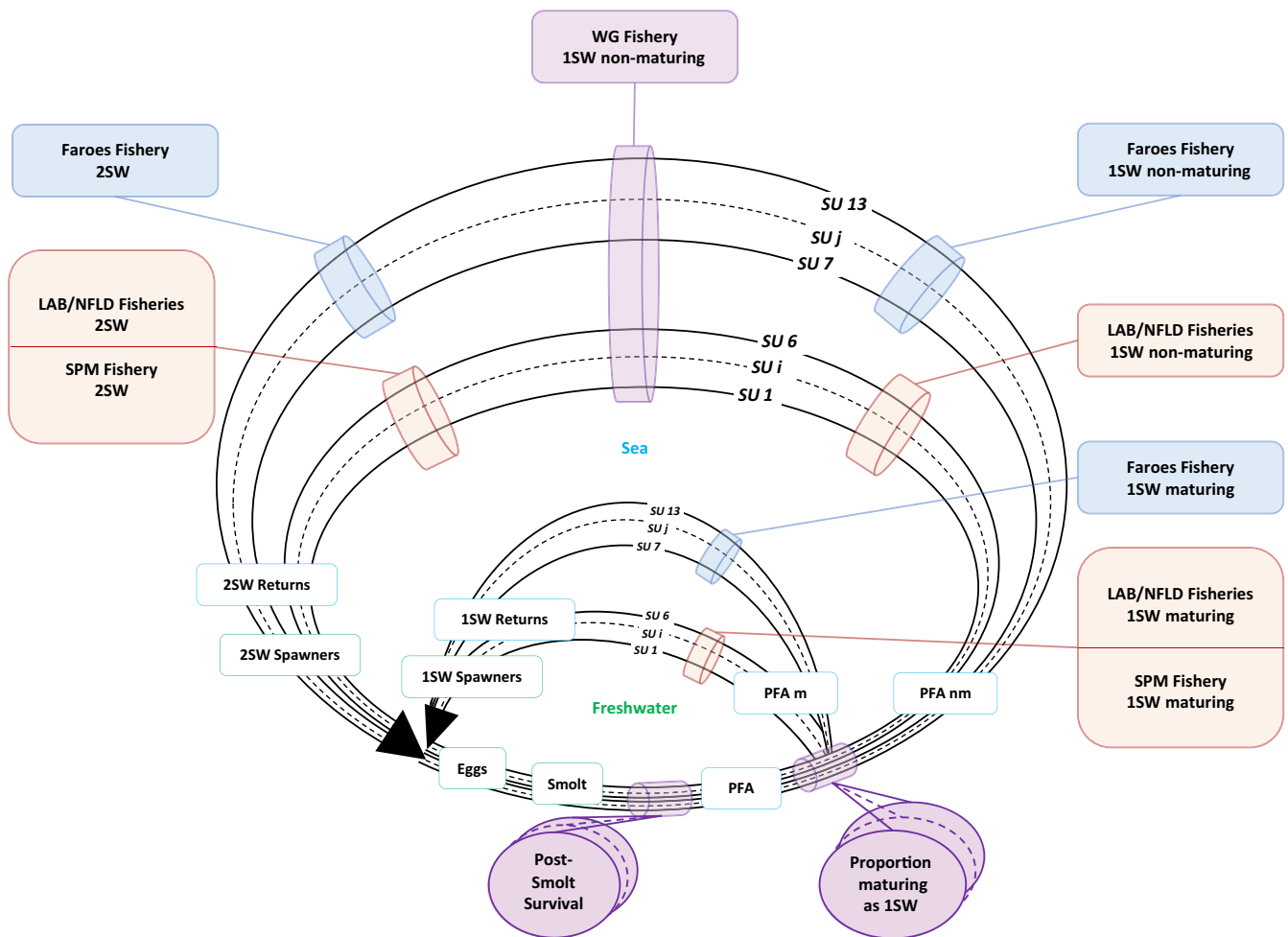


FIGURE 3 Covariation structure among the 13 stock units in the full model. Sources of covariation are twofold: (i) covariations in the time series of post-smolt survival and proportion maturing as 1SW (depending on the model structure M_1 , M_2 and M_3 ; see Table 1); (ii) covariations through fisheries operating on mixtures of SUs at sea. Red boxes refer to NA SUs ($i = 1, \dots, 6$), blue boxes refer to SE SUs ($j = 1, \dots, 7$), and purple boxes refer to both NA and SE SUs

independence) between SUs of different CSGs. In M_3 , a diagonal variance–covariance matrix is assumed, imposing a priori independence between SUs. In all model variations, the variance–covariance matrices (Σ_{θ_3} and Σ_{θ_4}) are assigned weakly informative priors (Table S1.3).

The second source of covariation among SUs is the harvest dynamics of the sequential marine fisheries that operate on mixtures of SUs, with the portfolio of SUs available for each fishery dependent on marine migration route hypotheses.

2.2 | Time series of data and likelihood

The model incorporates observation errors for the time series of returns and catches (time series 1971–2014; subscript $t=1, \dots, 44$). The full likelihood function for the general state-space model is then based on the combination of all observation equations for the returns, homewater catches and catches at sea, for 1SW and 2SW separately. Building an integrated model (Maunder & Punt, 2013; Rivot et al., 2004; Schaub & Abadi, 2011) that explicitly integrates complicated observation models would dramatically increase the complexity of the full model. Therefore, a sequential approach (Michielsens et al., 2008; Staton, Catalano, & Fleischman, 2017) is used that consists of (i) processing observation models separately to reconstruct probability distributions that synthesize observation uncertainty around the time series of catches and returns for the 13 SUs and (ii) using those distributions as likelihood approximations in the population dynamics state-space model. Probability distributions for returns and catches are derived from a variety of raw data and observation models, specific to each SU (except for the mixed-stock fisheries at sea) as originally developed by ICES to provide input for PFA models (see ICES, 2015b and Supporting Information S1 for further details). These consist of the following: (i) time series (1971–2014) of estimates (approximated as log-normal distributions) of the number of maturing anadromous Atlantic salmon that return to homewaters for each of the 13 SUs by 1SW and 2SW maiden sea-age classes; (ii) time series of estimates (approximated as log-normal distributions) of homewater catches for each SU by sea-age class; and (iii) time series of estimates (approximated as log-normal distributions) of catches for the mixed-stock fisheries at sea operating sequentially on combinations of SUs, and using additional data on the SU origin of the catches.

2.2.1 | Abundance of returns

Independent log-normal distributions were used to approximate the likelihood of the returns, described by means and coefficients of variation (CV) specific to the SU, year and sea-age class (Supporting Information S1, Figure S1.1).

2.2.2 | Homewater fisheries

The homewater fishery pools all fisheries capturing returning fish in coastal, estuarine and freshwater areas. Independent log-normal

distributions were used to approximate the likelihood of the homewater catches, with means specific to each SU, year and sea-age class (Supporting Information S1, Figure S1.2). Because homewater catches are generally provided with small observation errors, we used log-normal distributions with relative errors arbitrarily fixed to a CV = 0.05 around the point estimates.

2.2.3 | Distant marine fisheries

Catches of the distant marine fisheries are derived from the declared catches reported in ICES (2015a). Fish originating from NA and SE have different migration routes at sea to reach the common feeding grounds in West Greenland after the 1st winter at sea. Most of the sea fisheries considered operate on a mixture of stocks from one CSG, except for the West Greenland (WG) fishery which harvests non-maturing salmon from a mixture of stocks from NA and SE (Figures 2 and 3; Supporting Information S1, Tables S1.4 and S1.5).

For each fishery considered, the likelihood equations of the catches of fish from a SU consist of log-normal distribution of observation errors of the total catches by sea-age class, summed over all SUs exploited by the fishery, which is combined with Dirichlet likelihood terms for the proportion of catches allocated to each SU (Supporting Information S1, Figures S1.3–S1.6 and Table S1.6). Observation errors on the total catches and on the proportions are considered independent across fisheries, years and SU.

Fisheries operating on a mixture of North American SUs

North America fish maturing in the first year at sea (1SWm) may be exploited on their return migrations to rivers in the marine fisheries of Newfoundland and Labrador (NFLD/LAB) and at Saint Pierre et Miquelon (SPM) (Figure 3; Supporting Information S1, Table S1.4). Salmon that do not mature during the first year at sea (1SWnm) may be caught in the LAB/NFLD marine fisheries and at WG as 1SWnm, and as 2SW salmon on their migration to homewaters in the LAB/NFLD and SPM fisheries.

Catches of 1SWnm at WG may originate from any of the 13 SUs from NA and SE (Tables S1.4 and S1.5). A compilation of individual assignment data based on discriminant analyses of scale characteristics and genetic analyses was used to allocate the catches in the WG fishery to the 13 SUs (Bradbury et al., 2016; ICES, 2017a,b) (Supporting Information S1, Figure S1.6).

LAB/NFLD and SPM fisheries exploit a mixture of SUs from only NA. Data and expert opinion are used to partition catches of 1SWm, 1SWnm and 2SW in the LAB/NFLD fishery originating from Labrador ($r = 6$) from those originating from the other NA SUs (ICES, 2017a,b). The SPM fishery is assumed to not catch any fish from Labrador (Supporting Information S1, Figures S1.3 and S1.4), and the exploitation rate of Labrador salmon was fixed to zero in this fishery. Other than these assumptions and in the absence of data to differentially allocate catches to each of the six SUs in NA, catches were assigned assuming that exploitation rates were homogeneous among the six SUs (ICES, 2017a,b).

Fisheries operating on mixtures of South European SUs

1SWm fish from SE are susceptible to be harvested in the Faroes (FA) fishery before they return to homewaters (Supporting Information S1, Table S1.5). Fish that mature as 2SW may be first harvested at FA as 1SWnm in the first winter at sea, before migrating to the WG feeding grounds where they are susceptible to be harvested together with fish from NA. Those that survive the WG fishery are susceptible to be harvested at FA as 2SW fish before migrating back to their homewaters.

Total catches of 1SWm, 1SWnm and 2SW at FA are allocated to each of the seven SUs in SE using limited genetic assignment data which are set as fixed and constant over time (ICES, 2017a; Supporting Information S1, Table S1.6).

Sensitivity to changes in the hypotheses for mixed fisheries catch allocations

The hypotheses made in our model to allocate marine fishery catches to each SU differ from those used by ICES. Catches attributed to the NA CSG are allocated to each SU in NA by considering a homogeneous and time-varying harvest rate among SUs (ICES, 2015a). Catches attributed to the SE CSG are allocated to each SU by using fixed and constant proportions of total catches (ICES, 2015a). We examine the consequences of using stock assignment data based on genetics to assign the origin of the catches to SUs, which allows harvest rates to vary by SU. Inferences based on those data (model E₁, Table 1) are used to test the hypothesis that the SUs may not be harvested homogeneously in the mixed-stock fisheries, that is, the proportion of a SU in the catch may not reflect the proportion of the SU in the North Atlantic. A simpler homogeneous harvest rate model, without any data to allocate catches in the distant marine fisheries (E₂, Table 1), was also examined, and inferences of post-smolt survivals, proportions of fish maturing as 1SW and exploitation rates are compared to those obtained with the full model E₁ which incorporates SU-specific information on origin of catches in the mixed-stock marine fisheries.

2.3 | MCMC simulations, convergence and posterior checking

Bayesian posterior distributions were approximated using Monte Carlo Markov chain (MCMC) methods in JAGS (<http://mcmc-jags.sourceforge.net>; release 3.4.0) through the Rjags (www.Rproject.org) package (JAGS code is available on GitHub: <https://github.com/MaxOlmos/SALMOGLOB-Life-Cycle-Model>). Two independent MCMCs with dispersed initialization values were used. The level of autocorrelation of MCMCs is very high (still significant at lag 30), and as a result, the first 10⁶ iterations were used as a burn-in period. To reduce the autocorrelation in the MCMC sample used for final inferences, one out of 30 iterations post burn-in was kept and this sample of 30,000 iterations per chain was used to characterize the posterior distribution. Convergence was assessed using the Gelman–Rubin statistic (Brooks & Gelman, 1998) as implemented in the R Coda package (`gelman.diag()`) (Supporting Information S6).

Model fit to each data source was assessed by verifying that the credibility envelope of the posterior predictive distribution of each variable contained the observation (Supporting Information S4). In addition, Bayesian *p*-values calculated from χ^2 discrepancy tests (Gelman, Carlin, Stern, & Rubin, 2014) were calculated to check the ability of the model to replicate a posteriori data similar to those observed. Because the main sources of pseudo-observations used to fit the models consist in the time series of returns, Bayesian *p*-values of returns are reported in Supporting Information S5.

2.4 | Comparison of hypotheses for the covariation between SUs

To test which hypothesis about the extent of geographic covariation is best supported by the data, the three different forms for the variance–covariance matrices (Table 1) were compared using W-AIC criteria. The W-AIC is adapted to compare hierarchical models of any structure fitted to the same data sets (Gelman et al., 2014; Hooten & Hobbs, 2015; Watanabe, 2013). It can be considered as a generalization of the deviance information criterion (Gelman et al., 2014; Vehtari, Gelman, & Gabry, 2017) but has the advantage of being directly related to the posterior predictive ability of the model. A difference in DIC >5 is considered to provide strong support in favour of the model with the lowest W-AIC.

The extent of spatial synchrony for post-smolt survival and of the proportion of fish maturing as 1SW were quantified using the cross-correlation matrix between the time series of $\text{logit}(\theta_{3_{it}})$ (respectively $\text{logit}(\theta_{4_{it}})$), directly calculated from the variance–covariance matrix Σ_{θ_3} (resp. Σ_{θ_4}) as $\rho = \sqrt{\text{diag}(\Sigma)^{-1} \times \Sigma \times \text{diag}(\Sigma)^{-1}}$. We compared the average cross-correlations among SUs of the same CSG and among SUs of different CSGs.

2.5 | Using the model to evaluate catch options at sea

ICES provides advice to a regional fisheries management organization (NASCO) for management of the Faroes and West Greenland mixed-stock salmon fisheries. The risk framework developed by ICES summarizes the probability that the returns to homewaters are less than the defined management objectives for different levels of catches (ICES, 2015a). To demonstrate the potential of our model to be used in this management context, we conduct a risk analysis for different level of catches at West Greenland. Consistent with the ICES framework, we provide forecasts for 5 years starting after the last year of our assessment model (2013–2017). We calculate the probability of each SU achieving its management objectives individually or of simultaneous attainment of objectives for the SUs within a CSG. Details are provided in Supporting Information S3.

3 | RESULTS

3.1 | Model evaluation

Model comparisons support the hypothesis of a strong coherence among the 13 SUs in the time series of post-smolt marine survivals

and the proportions of fish maturing as 1SW. Model M_3 with no covariance among SUs (diagonal variance-covariance matrix Σ_{θ_2} and Σ_{θ_4}) has the highest W-AIC criteria value (W-AIC $M_3 = 2,203$) and is not supported by the data relative to the other models. There is also evidence of covariation between SUs across CSG. Model M_1 with unconstrained variance-covariance matrices has a smaller W-AIC value (W-AIC $M_1 = 2,071$) than model M_2 (W-AIC $M_2 = 2,081$) which assumed independence between SUs of different CSG. The model configuration M_1 combined with freshwater hypothesis F_1 is retained for all further analyses.

Posterior predictive checks do not indicate any strong inconsistencies between the model M_1 a posteriori and the data. Posterior predictive distributions show that the model fits well to all observations (Supporting Information S4). Bayesian p -values calculated for 1SW and 2SW returns are all relatively close to 0.5 for almost all combinations of SUs and years, showing that the model a posteriori is able to replicate the abundances of returns to homewaters used to fit the model (Supporting Information S5). There is, however, evidence of poor fit for some particular combinations of SUs and years, for example, France (1SW returns, years 1993 and 1994), England & Wales (2SW returns, years 1981, 1990 and 2013) and Northern Ireland (2SW returns, years 2012, 2013 and 2014).

3.2 | A widespread decline of abundances

Posterior estimates of returns (total 1SW + 2SW; Figure 4a) show consistent declining trends from the early 1970s to the 2010s. Returns at the end of the time series were estimated to be ~20% of the abundances at the beginning of the 1970s, with exception of the Labrador and Newfoundland SUs in NA where returns increased post-1990s. The proportion of 1SW salmon in returns is highly variable among SUs (Figure 4b), with the 1SW age class dominant in some SUs (e.g., Newfoundland and Ireland) whereas 2SW salmon were more abundant in other SUs (e.g., United States and Quebec). The proportions of 1SW in returns show a consistent increasing trend from the early 1970s to the early 1980s, followed by a plateau or slight decline depending on SU.

Trends in spawner and return abundances may differ due to variations in homewater fishery exploitation rates (Figure 4c,d). Egg depositions follow the same general temporal trends as spawners (Figure 4e). The proportion of eggs spawned by 1SW is highly variable among SUs (Figure 4f). It is particularly high in Newfoundland (97% of eggs from 1SW) and Ireland (75% of eggs from 1SW), and low in United States (<1% of eggs from 1SW) and Quebec (<10% of eggs from 1SW).

There is a widespread decline of PFAs for all SUs in NA and SE (Figure 4g) with exception of the south-west Iceland and Newfoundland SUs where PFA increased slightly after the 1990s. The total PFA abundance (sum over the 13 SUs) declined by a factor 3 from about 6 million in the mid 1970s to 2 million fish in the early 2010s. Time series of total PFA in each CSG show very similar continuous declines, by a factor 3, between the 1970s and the 2010s (Figure 4h).

3.3 | A strong spatial coherence in temporal variations of post-smolt marine survival and proportion of fish maturing as 1SW

3.3.1 | Post-smolt marine survival

Overall, time series of post-smolt survivals show a consistent decline, with a strong drop in the 1990s, followed by a slight increase in the early 2000s before declining again until 2013 (Figure 5a). The average survivals over the 13 SUs show a decline by a factor 3 in the natural scale between the early 1970s and the 2010s (not shown). This pattern is consistent with the decline in the abundance at the PFA stage. Average survivals calculated over the 6 SUs of NA and 7 SUs of SE exhibit similar trends. All SUs show time trends in survival that are consistent with the average, except for Northern Ireland, Ireland and Labrador that show larger variations with a marked increase in the 1990s, and the United States with a stronger decline than the average in the 1990s.

The pairwise correlation matrix confirms the strong spatial coherence of the time trends among SUs and supports the hypothesis that the covariance would be stronger within CSG (within NA or within SE) than between CSG. The vast majority of pairwise correlations are positive (Figure 5b), with an average correlation over all SUs of 0.18 (Figure 5c). Average correlations calculated between SUs within the same CSG (within NA = 0.35; within SE = 0.18) are higher than between SUs from two different CSGs (average = 0.12) (Figure 5c). The low average correlation within SE is mostly driven by a few pairwise low correlations between Ireland and eastern and western Scotland, between Northern Ireland and England and Wales, and between south-west Iceland and most of the other SUs. The strongest correlations are found between pairs of geographically proximate SUs in NA, in particular between United States and Scotia-Fundy (0.67), between Scotia-Fundy and Gulf (0.64), and between Scotia-Fundy and Quebec (0.46). The strongest correlations between European SUs are for France and Northern Ireland, (0.32), eastern Scotland and England & Wales (0.36), and eastern and western Scotland (0.31).

3.3.2 | Proportion of fish maturing as 1SW

The proportions of fish maturing as 1SW differ among SUs (Figure 6a). Average estimates are about 0.1 (~ -4 in the logit scale) for SUs with returns largely dominated by 2SW fish (e.g., United States). By contrast, some SUs have returns dominated by 1SW fish (e.g., Labrador, Newfoundland, Ireland) and average proportions of fish maturing as 1SW are close to 0.9 (~ +4 in the logit scale).

Time trends in the proportion of 1SW maturing also show a strong coherence among SUs. These are in accordance with the expectation of higher correlations between SUs of the same CSG. Overall, there is an increasing trend from the 1970s to the 1990s that corresponds to declines in the proportions of 2SW fish in the returns followed by a levelling off or even a decline from the 2000s (Figure 6a). All time trends are consistent with the average trend, except for France which shows a consistent decline during the entire period.

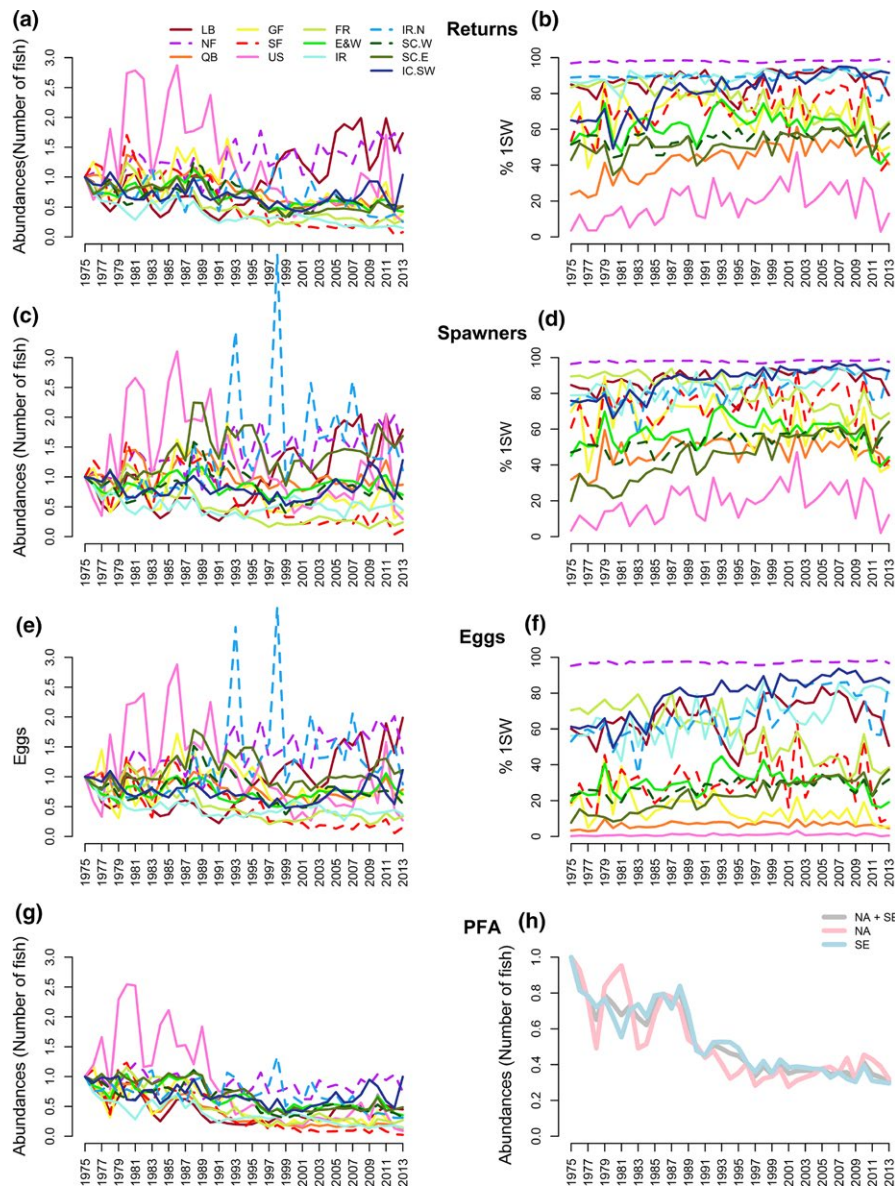


FIGURE 4 Time series of estimated abundances at various stages in the life cycle. Panels represent: (a) total returns to homewater (1SW + 2SW); (b) proportion of 1SW in returns; (c) total spawners (1SW + 2SW); (d) proportion of 1SW in spawners; (e) total egg deposition by spawners; (f) proportion of eggs spawned by 1SW; (g) total PFA; and (h) standardized PFA over all SUs, and by continental stock groups. Trend lines are medians of marginal posterior distributions. Abundances are standardized to the first year values

As observed for the post-smolt survival, most of the pairwise correlations are positive across the 13 SUs (Figure 6b), with an average correlation of 0.2 (Figure 6c). Some rare negative correlations occur between SUs of the same CSG (e.g., -0.28 between south-west Iceland and Northern Ireland; -0.14 between France and Ireland). Average correlations between SUs within the same CSG (within NA = 0.44; within SE = 0.18) are higher than those between SUs from two different CSGs (average = 0.12) (Figure 6c). The low average correlation within SE is mostly driven by a few pairwise low correlations between France and the other SUs, between Northern Ireland and England and Wales and Ireland, and between south-west Iceland and most of the other SUs, except England and Wales and Ireland. The strongest correlations are estimated for geographically proximate SUs in NA, in particular between United States, Scotia-Fundy, Gulf

and Quebec SUs (correlations of 0.48–0.75). The strongest correlations between SUs in SE are for eastern and western Scotland (0.60), Scotland and Ireland, Scotland (east and west) and England & Wales, and Ireland and England & Wales (correlations from 0.17 to 0.60).

3.4 | Sensitivity analysis

3.4.1 | Effect of increasing the interannual variability in the egg-to-smolt survival (F_2)

Increasing the coefficient of variation of the interannual variability in the egg-to-smolt survival results in greater temporal variation in egg-to-smolt survival estimates (Figure S2.1). Because part of the interannual variability is captured by the egg-to-smolt survival, temporal

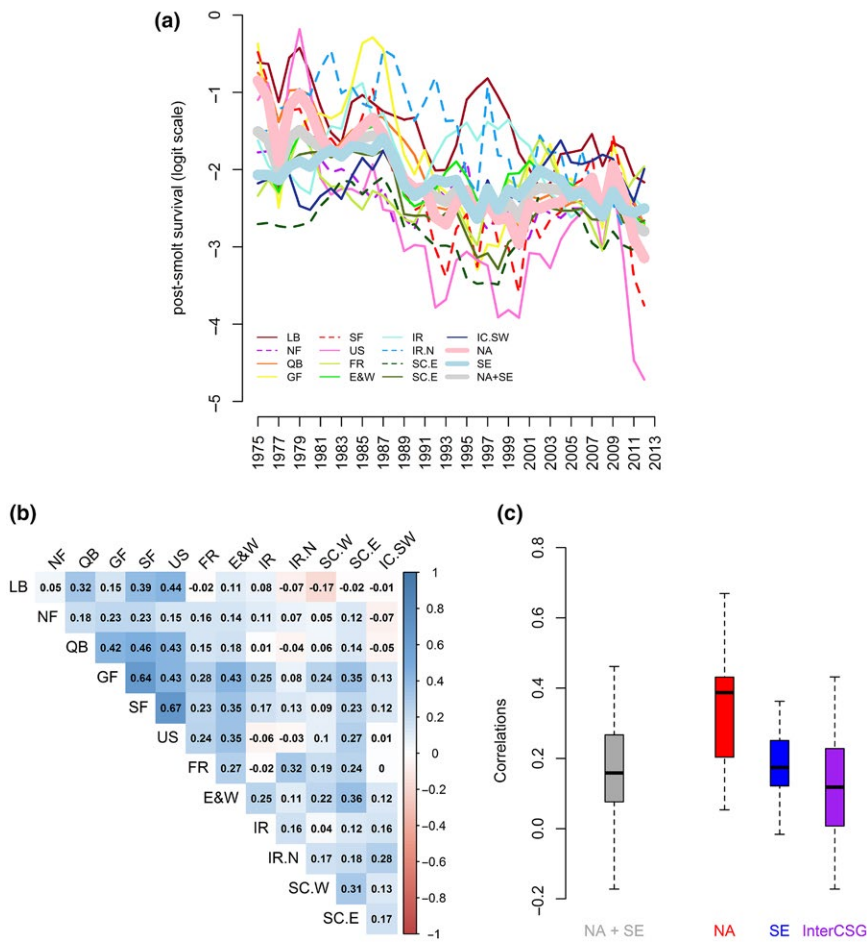


FIGURE 5 Time trends and synchrony in post-smolt survival rates. (a) Time series of post-smolt survivals estimated for the 13 SUs (medians of marginal posterior distributions). Thick lines are the average calculated over all 13 SUs (grey), the 6 SUs of NA (pink) and the 7 SUs of SE (blue). (b) Pairwise correlation matrix calculated between all pairs of SUs in NA and SE. (c) Box plots are average pairwise correlations calculated between all SUs (NA + SE), between SUs within the same continental stock group (NA or SE), and between SUs that belong to two different continental stock groups (InterCSGs)

variations of the estimated post-smolt survival rates are smoothed by comparison with the baseline configuration F_1 (Figure S2.2). However, the overall time trends in post-smolt survival time series are robust to an increase in the egg-to-smolt interannual variance. Spatial covariances among the time series of post-smolt marine survivals are fairly robust to an increase in the egg-to-smolt interannual variance in the range $CV_{01} = 0.05-0.4$ (Figure S2.3a). Further increasing the variance ($CV_{01} = 0.6-0.8$), however, diminishes the spatial covariation of the time series (Figure S2.3a). In particular, the covariations become very low among SUs of the SE CSG. Covariations within the NA CSG are less affected. Trends and spatial covariance in the time series of proportions of 1SW maturing are robust to an increase in the interannual variability in the egg-to-smolt survival (Figure S2.3b).

3.4.2 | Effect of considering density-dependent egg-to-smolt survival (F_3)

The combination of the density-dependent assumption and the egg depositions produces egg-to-smolt survivals on average much higher than the model with density-independent survival which was fixed to 0.07% (Figure S2.1). As explained by Massiot-Granier et al. (2014), higher egg-to-smolt survivals are logically balanced by lower estimates of post-smolt survivals (Figure S2.2). But because the egg deposition varies over the time series, introducing

density dependence in freshwater results in temporal variations in the egg-to-smolt survivals (Figure S2.1). However, inferences on the time trends and spatial covariance of post-smolt survivals are robust to the assumption of density dependence of egg-to-smolt survivals and the effect remains marginal compared to the effect of increasing the interannual variation in the egg-to-smolt survival rates (Figure S2.3a). Trends and spatial covariance in the time series of proportion of 1SW maturing are also fairly robust to the assumption of density dependence in the egg-to-smolt survival (Figure S2.3b).

3.4.3 | Sensitivity to the hypothesis of catch allocation in mixed-stock fisheries (E_2)

Estimated exploitation rates of the fisheries operating at sea on a mixture of SU are sensitive to the hypothesis of catch allocation between the different SUs. Overall, the data used to allocate catches do not support the hypothesis of a homogeneous exploitation rate among the 13 SUs. As illustrated for the WG fishery which operates on a mixture of the 13 SUs from both CSGs (Figure 7), considering the fishery exploitation rate to be homogeneous among SUs leads to an estimate of exploitation rate of about 30% at the beginning of the time series and that drastically declines in the early 1990s following quota reductions (Figure 7). Using the data to differentially allocate catches among SUs leads to highly contrasted exploitation

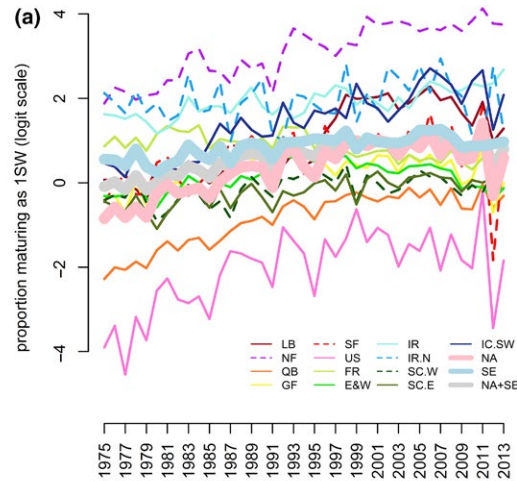
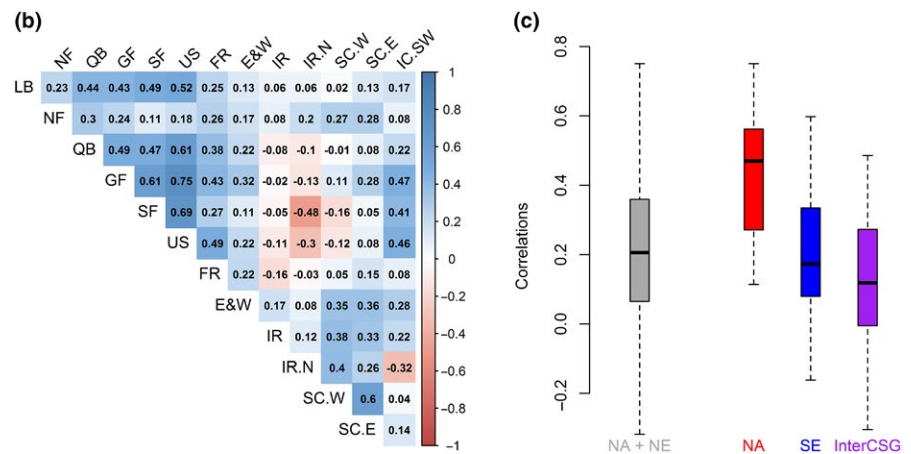


FIGURE 6 Time trends and synchrony in the proportion of fish maturing as 1SW. (a) Time series of the proportion of fish maturing (logit scale) as 1SW estimated for the 13 SUs (medians of marginal posterior distributions). Thick lines are the average calculated over all 13 SUs (grey), the 6 SUs of NA (pink) and the 7 SUs of SE (blue). (b) Pairwise correlation matrix calculated between all pairs of SUs in NA and SE. (c) Box plots are average pairwise correlations calculated between all SUs (NA + SE), between SUs within the same continental stock group (NA or SE), and between SUs that belong to two different continental stock groups (InterCSGs)



rates among SUs. Interestingly, however, inferences on the time series of the marine survival and proportion of 1SW maturing were not sensitive to the hypothesis for allocating catches among SUs. As well, under the hypothesis of a homogeneous exploitation rate, the covariance between SUs does not increase.

3.5 | Evaluating catch options for mixed-stock marine fisheries

In accordance with ICES results (ICES, 2015a), all scenarios of catches at WG (including zero catches) provide a null probability of simultaneously achieving the management objectives for all SUs (Figure S3.1). However, the general assessment hides substantial heterogeneity among SUs. The probabilities of achieving management objectives are higher for the SUs in Southern Europe. Northern Ireland, France, Southwest Scotland and England and Wales have the highest probabilities of achieving their management objectives (probabilities between 0.5 and 1 for the no fishery scenario). In contrast, SUs from NA such as United States, Scotia-Fundy, Gulf and Quebec (and Ireland from SE) have very low probabilities (between 0 and 0.4 for the no fishery scenario) of achieving their management objectives. Differing catch options at West Greenland have minimal differences on the probability of achieving management objectives,

except for Labrador, Newfoundland, Quebec and Gulf SUs that have the highest exploitation rate at WG.

4 | DISCUSSION

4.1 | A new modelling framework for population dynamics and stock assessment in the North Atlantic

We developed an integrated hierarchical Bayesian life cycle model to simultaneously estimate the abundance of post-smolts at sea, post-smolt survival rates and proportions maturing as 1SW, for 13 SUs in SE and NA. The model is an age- and stage-based life cycle model that considers 1SW and 2SW life history strategies and harmonizes the life history dynamics among SUs in NA and SE. It provides a framework to quantify the spatial coherence in the temporal variations of the post-smolt survivals and the proportions of 1SW salmon in a hierarchy of spatial scales across the North Atlantic. It also represents a major improvement to the assessment and forecast models of Atlantic salmon currently used by ICES.

The stock assessment and forecasting approach currently used by ICES considers the NA and SE continental stock groups separately, and these models have different demographic structures (Chaput, 2012; ICES, 2015a). The life cycle model presented in this paper

provides a singular harmonized framework to simultaneously assess two sea-age classes of Atlantic salmon for thirteen SUs in NA and SE. All the model properties are integrated into the forecast process: (i) all sources of uncertainty in the model (interannual stochasticity) and the parameters (joint posterior distribution) are readily integrated in the forecasts; (ii) temporal variations in post-smolt survivals and in the proportions of fish maturing as 1SW incorporate the covariation among SUs in both the inference and forecasting phases; and (iii) a single model is used to forecast the population dynamics of all SUs simultaneously, which is of particular interest when assessing catch options for mixed-stock fisheries operating on a mixture of stocks from both NA and SE. We illustrate the usefulness of our model as a tool to provide catch options for the WG salmon fishery but it can also be used to provide catch options for other fisheries, or to assess conservation measures for the different sea-age classes or the SUs separately.

The integrated life cycle framework is expandable and provides an opportunity to assimilate additional sources of information. Specifically, we demonstrate the usefulness of adding a likelihood function to assimilate data to allocate catches at West Greenland among the 13 SUs as currently defined, which is more realistic than the hypothesis of a homogeneous harvest rate among SUs (ICES, 2015a). Highly heterogeneous estimates of exploitation rates among SUs are thus revealed, showing that some SUs in NA (Labrador, Quebec and Newfoundland) are exploited at higher rates than other SUs at West Greenland. The life cycle model that integrates genetic information on the composition of mixed-stock catches is an important tool to better inform management measures (Cunningham et al., 2017). Interestingly, inferences on other parameters in the model (post-smolt marine survival and proportion of fish maturing as 1SW) were fairly robust to the hypotheses on exploitation rates at WG.

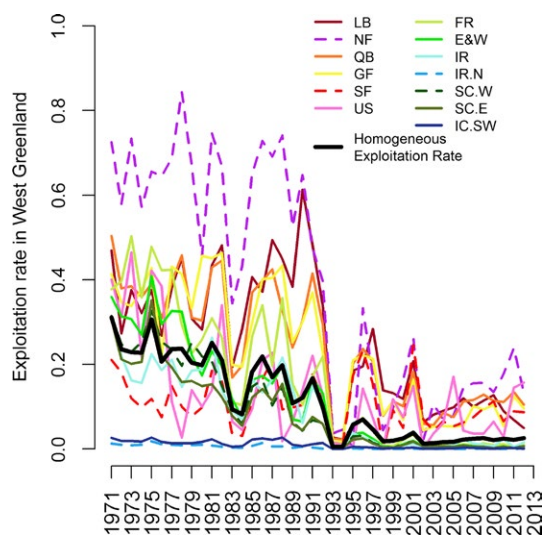


FIGURE 7 Time trends of points estimates (medians of marginal posterior distributions) of exploitation rates in the West Greenland fishery (1SW non-maturing fish) operating on a mixture of SUs from both NA and SE. Colours lines: estimates obtained with data to allocate catches among the different SUs (E_1). Thick black line: estimates obtained under the hypothesis of a homogeneous harvest rate among all SUs (E_2)

The reasons for the lack of sensitivity to this assumption are two-fold. First, the overall trends of exploitation rates, marked by a shift in the early 1990s following major management measures, remain unchanged in the two hypotheses. Second, exploitation at WG concerns only the non-maturing component which is not the major component of the abundance at the PFA stage; thus, it has less influence on the parameters that control stock productivity up to the PFA stage. We also demonstrate the possibility of improving the biological realism of the freshwater phase by considering temporal variation and density dependence in the egg-to-smolt survival rates. Although smolt production data are not available at the scale of SUs yet, our model demonstrates the usefulness of developing new likelihood functions or informative priors to better separate the spatial and temporal variations in survival between the freshwater and the marine phases.

The model is structured in a hierarchical Bayesian state-space framework that integrates both process and observation errors. Observation errors on returns and catches are integrated through a sequential approach, similar to the one developed in stock assessment models for Atlantic salmon in the Baltic (Michielsens et al., 2008) and Chinook salmon in Alaska (Staton et al., 2017). Probability distributions on returns and catches at sea were derived separately from the life cycle model and then used to approximate likelihoods (Michielsens et al., 2008). This contrasts with Massiot-Granier et al. (2014) who developed a fully integrated observation model for returns. The choice of using a sequential or an integrated approach represents a trade-off between model realism and computational efficiency (Maunder & Punt, 2013; Staton et al., 2017). A fully integrated model would provide a more transparent view of how the data are incorporated in the entire process being modelled. It would also allow for the option of incorporating covariation in observation errors of 1SW and 2SW annual returns. However, the currently used observation models are highly heterogeneous among SUs (ICES, 2015b) and developing a fully integrated model capturing all these specificities would come at a high cost of increased model complexity, and increased computational burden for Bayesian statistical inference.

Time series of marine survivals and proportions of fish maturing as 1SW are modelled as latent random walks (RW) with covariation among SUs. The RW is a simple and flexible structure for modelling trends and shifts over time. Previous studies have used RW assumptions with covariation to model coherence in temporal variations among populations (Minto et al., 2014; Peterman, Pyper, & Grout, 2000). No a priori hypothesis on the sign of covariation among SUs is made in our approach, and inferences on covariation and correlation among SUs are derived directly from the posterior distribution of the model parameters. Other approaches have been used to assess coherence and covariation among several time trends including using Pearson correlations (Holt & Peterman, 2004; Peterman et al., 2012), principal component analysis (Beaugrand & Reid, 2012; Peterman et al., 2012) or dynamic factor analysis (Baudron, Needle, Rijnsdorp, & Tara Marshall, 2014; Malick et al., 2017; Mills et al., 2013). All of the above are post hoc analyses where covariation is not implicitly included in the model, but computed a posteriori from point estimates, thus excluding parameter uncertainty.

4.2 | Unravelling the geographic covariation in key demographic parameters

The model constitutes an important tool for future improvement of our understanding of the mechanisms driving the response of Atlantic salmon populations to variations in biological and environmental factors in a hierarchy of spatial scales. Formulating the dynamics of all SUs in a single hierarchical model provides the framework for modelling covariations among different populations that may share part of their migration routes at sea and may be exploited by the same marine fisheries. The model provides a structure for identifying the spatial scales of the temporal variations in marine survivals and in the sea-age composition of returns for SUs distributed across a broad gradient of longitude and latitude in the North Atlantic.

Consistent with expectations, our results show an increased coherence in temporal variation of marine survivals and proportions of fish maturing as 1SW with geographic proximity. We found strong support for a coherence in the temporal variation of post-smolt marine survivals among the 13 SUs of NA and SE, represented by a collective decline in the marine survival over the 1971–2014 time series. Similarly, the proportions of fish maturing as 1SW increased for almost all SUs from the 1970s to the 1990s and then reached a plateau or started to decrease thereafter. There is also stronger covariation in dynamics among SUs within the same CSG than among SUs of different CSGs. Within the same CSG, correlations between time series of both post-smolt survivals and proportions of fish maturing as 1SW are higher for geographically proximate SUs, most likely explained by the similarity in post-smolt habitat and migration routes at sea.

In the absence of smolt production data at the scale of SUs, the parameters of the freshwater-phase dynamic were assumed and fixed. However, inferences on trends and spatial covariances of post-smolt survivals and proportions maturing as 1SW were found to be robust to changes in freshwater dynamic modelling hypotheses, specifically to the introduction of interannual stochasticity and density dependence. When considering a realistic level of interannual stochasticity in the freshwater survival ($CV = 40\%$; median value found in the literature), a significant part of the interannual variability in post-smolt survivals is explained by variations in the freshwater phase but the overall trends and spatial covariance in post-smolt survivals and proportions maturing as 1SW remain unchanged. The effect of a density-dependent assumption is marginal relative to interannual stochasticity in egg-to-smolt survival.

Synchronous variations among distant populations may result from dispersal among populations or from the synchronizing influence of spatially correlated fluctuations in drivers of population dynamics such as through environmental forcing (Moran effect) or via trophic interactions (Liebhold, Koenig, & Bjørnstad, 2004; Walter et al., 2017). Dispersion is unlikely to influence the observed pattern of synchrony in Atlantic salmon at the spatial scale of the North Atlantic. Atlantic salmon return to their natal river with high fidelity, and massive straying over hundreds of kilometres is unlikely (Aas,

Einum, Klemetsen, & Skurdal, 2010). The absence of smolt production data at the scale of SUs makes it difficult to disentangle the role of variability in the freshwater phase (egg-to-smolt survivals) from that during the early marine phase (post-smolt survival) in defining abundance of Atlantic salmon. However, synchronous variation in egg-to-smolt survivals is less likely at the North Atlantic scale than would be expected during the marine phase. Data from the few but geographically dispersed monitored rivers (Crozier et al., 2004; Prevost, 2003) do not provide any compelling evidence of large-scale declines and synchronous variations in freshwater productivity (Griffith et al., 2012). Moreover, because of the variability in the duration (smolt ages) of the freshwater phase among SUs, it is less likely that factors acting on the freshwater phase could synchronize yearly post-smolt abundances across distant populations with contrasting smolt-age structures. The hypothesis of a response to the influence of factors affecting Atlantic salmon during the early marine post-smolt phase is best supported by the literature (Friedland, 2003; Friedland, Reddin, McMenemy, & Drinkwater, 2003; Todd et al., 2012).

The coherent temporal decline in post-smolt survivals among the 13 SUs in NA and SE is consistent with previous analyses suggesting a response of Atlantic salmon populations in the North Atlantic Ocean to large-scale changes in the marine environment (Beaugrand & Reid, 2012; Friedland et al., 2014; Mills et al., 2013). Direct effects on metabolic costs associated with the global increase in SST in the North Atlantic are unlikely to explain the observed changes (Jonsson et al., 2016). Previous studies suggest an indirect effect of an increase in SST through ecosystem mechanisms. It has been suggested that bottom-up control on food resources during the early marine phase of post-smolt migration may have negatively affected both growth and survival (Beaugrand & Reid, 2012; Friedland, Moore, & Hogan, 2009; Jensen et al., 2012). A major trophic shift in the North Atlantic Ocean has been documented in the early 1990s with reported changes at different trophic levels from zooplankton communities to seabird populations (Beaugrand, Edwards, Brander, Luczak, & Ibanez, 2008; Durant, Anker-Nilssen, & Stenseth, 2003). Reductions in the abundances and the energetic quality of prey may have altered Atlantic salmon growth at sea (Mills et al., 2013; Otero et al., 2012; Renkawitz, Sheehan, Dixon, & Nygaard, 2015) and consequently survival through size-dependent mortality (Friedland & Reddin, 2000; Gislason, Daan, Rice, & Pope, 2010; Peyronnet, Friedland, Maoiléidigh, Manning, & Poole, 2007).

The higher synchrony of life history dynamics at the post-smolt stage among SUs within the same CSG relative to different CSG is in accordance with differences in early marine-phase migration routes of these salmon populations. It is also consistent with interpretations by Friedland et al. (2014) that the mechanisms driving Atlantic salmon abundance differ between NA and SE. Growth variations during the summer months of the post-smolt year have been hypothesized as being critical for the survival of SE SUs (Friedland et al., 2008, 2014; McCarthy, Friedland, & Hansen, 2008; Peyronnet et al., 2007). In particular, Jensen et al. (2012) and Haugland, Holst, Holm, and Hansen (2006) reported positive correlations between

marine growth in the Norwegian Sea and the condition factor of returning fish, with years of high or low growth rates associated with good or poor, respectively, condition factors of returning fish. By contrast variations in predation pressure in early spring have been hypothesized to be the main driver of early post-smolt survival in NA (Friedland et al., 2014). Indeed, predator abundances increase along with spring temperatures leading to higher post-smolts mortality in migration corridors.

Despite the overall spatial coherence observed within the same CSG, an important part of the variance is not explained by global trends at the scale of CSG and the variability among SUs within the same CSG remains high. Results show a higher coherence for geographically proximate SUs within the same CSG. This supports the hypothesis of a response to more local environmental or trophic factors affecting Atlantic salmon during the earlier marine phase of the life cycle, when post-smolts from geographically proximate SUs are more likely to experience similar marine environmental conditions. The spatial coherence in time trends is stronger among SUs in North America than in Southern Europe. Higher spatial coherence in NA may result from more similar migration routes among SUs in NA than in SE. Stronger correlations are especially obtained between United States, Scotia-Fundy, Gulf and Quebec SUs that all have longer migration routes through the Gulf of Maine and Scotian Shelf or the Gulf of St. Lawrence to the feeding areas in the Labrador Sea and at West Greenland. Temporal variations in dynamics of those SUs differ from Newfoundland and Labrador which are characterized by different sea-age structure of the returning adults (dominated by 1SW fish) and different migration routes at sea with freshwater habitats much closer to or directly leading to the feeding areas in the Labrador Sea and West Greenland. Weaker correlations observed in SE may be explained by the diversity of marine environments and associated growth conditions encountered during the post-smolt migration leading to the feeding areas in the Norwegian Sea. For instance, post-smolt diet reported by Haugland et al. (2006) show high spatial and temporal variability of prey composition, dominated by blue whiting (*Micromesistius poutassou*, Gadidae) in the slope current in the west of the United Kingdom, followed by sandeel (*Ammodytes* spp.) and herring (*Clupea harengus*, Clupeidae) in the North Sea and the Norwegian Sea. The authors also suggest that post-smolt growth conditions could be limited by competition with herring in the Norwegian Sea. Although difficult to assess, one cannot exclude artefacts resulting from differences in the quality of the data. In particular, stronger correlations observed among SUs in NA could partly be a consequence of more homogeneous methods and models to estimate the returns. In particular, the observation models are more homogeneous among the five Canadian regions (5 of 6 SUs in NA) than among the seven SUs in Europe that are managed as independent jurisdictions (except eastern and western Scotland) (ICES, 2015b). Finally, spatial and temporal heterogeneity of hatchery stocking could explain part of the variability across SUs. However, to our best knowledge, no collated data exist at the scale of SU that could be used to provide a quantitative assessment of the effect of stocking although hatchery stocking is considered to be

small relative to natural production. An exception, however, is the case of the United States stock unit in NA that is dominated by the Penobscot River stock (Maine) which includes stocking of juvenile and hatchery-reared adult spawners. For the United States, the adult hatchery releases are included in the estimated number of spawners in the model and returns include fish originating from natural spawning and hatchery releases.

The patterns of geographic covariation observed for Atlantic salmon are similar to the ones found for Pacific salmon (*Oncorhynchus* spp.). Several studies report positive correlations between geographically proximate populations, but weaker correlations at increasing geographic distances, suggesting that shared environmental conditions impact Pacific salmon stocks at a regional scale (Bradford, Taylor, & Allan, 1997; Malick, Adkison, & Wertheimer, 2009; Malick & Cox, 2016; Peterman et al., 2012; Sharma, Vélez-Espino, Wertheimer, Mantua, & Francis, 2013). However, part of the variation in abundance and population dynamics is not explained at these regional scales, indicative of the influence of some combination of local ocean conditions or stock-specific responses to similar environmental conditions.

Our study also provides the first simultaneous analysis of changes in both marine survival and proportion of fish maturing as 1SW in Atlantic salmon at the scale of the North Atlantic. The proportions of fish maturing as 1SW differ widely between SUs, with some SUs dominated by 1SW and others characterized by a more balanced composition of sea ages at return. Proportions of fish maturing as 1SW increased for almost all SUs from the 1970s to the 1990s, and levelled off or decreased for some SUs since the 2000s. The strong spatial synchrony in temporal trends suggests a response to broad spatial-scale environmental forcing (Blanchet & Dubut, 2012; Friedland & Haas, 1996; Summers, 1995). Age at first maturity is known to be environmentally plastic and mediated by growth in fish and in salmonids in particular (Mangel & Satterthwaite, 2008; Marshall, Kjesbu, Yaragina, Solemdal, & Ulltang, 1998; Thorpe, Mangel, Metcalfe, & Huntingford, 1998).

The non-monotonic relationship between the post-smolt survival and the proportion of fish maturing as 1SW, as observed in our results, may be explained by a plastic adaptive response to changes in environmental conditions. Maximizing fitness results from a trade-off between reproduction and survival (Stearns, 1992). When growth conditions at sea deteriorate, the increased risk of mortality during an extra year at sea may exceed the reproductive benefits associated with extra feeding opportunities, thus fostering an earlier age at maturation (Jonsson et al., 2016). The increase in the proportion of early maturing fish associated with a decline in survival observed during the first part of the time series would be consistent with a response in degradation of growth conditions at sea. But in the recent period, environmental conditions might have been so degraded that survival still declines when physiological thresholds triggering maturation could not be reached in the first year thus precluding maturation as 1SW (Alm, 1959; Wilbur & Rudolf, 2006).

4.3 | Limits and directions for future research

Our modelling exercise collates the data and expertise available for Atlantic salmon from SUs in both NA and SE CSGs. The life-cycle modelling framework makes it possible to unravel the effects and consequences of large-scale ecosystem changes which are susceptible to impact large groups of populations. An important limitation of the approach described is that it is based on fishery-dependent data with a low resolution in demographic processes (abundances, ages at sea migration, sea ages at return and fecundity) and that must be compensated by strong demographic hypotheses. However, the described framework helps to prioritize further research directions and data collection.

To improve our understanding of the response of Atlantic salmon populations to ecosystem changes, future research should investigate the influence of environmental covariates on the trends in marine survival and proportion of 1SW maturing fish. Following approaches already used (Grosbois et al., 2008; Lahoz-Monfort, Morgan, Harris, Wanless, & Freeman, 2011; Lahoz-Monfort et al., 2013), a hierarchical model could be developed that would allow partitioning the year-to-year variation into common (synchronous) and SU-specific (asynchronous) terms and to correlate those terms with proxies of growth conditions calculated in space and time domains at sea defined in accordance with the migration routes (Mills et al., 2013).

Extending the approach to Northern Europe (NE) SUs would also allow for further increasing the gradient of environmental variation and would contribute to an even better understanding of the response of Atlantic salmon populations to large-scale ecosystem changes. ICES (2015a) provides a short time series (1995–2014) of Northern Europe CSG productivities and probabilities of 1SW maturing. The NE CSG shows a general decline in productivity although not as pronounced as for the NA and SE CSGs, and a constant trend in the proportion of 1SW maturing, suggesting a likely synchrony among the three CSGs, over the North Atlantic. At this time, data for NE SUs were not available, but incorporating these data into the model would allow for extending the modelling framework to virtually all SUs in the North Atlantic.

Another exciting prospect would be to further increase the biological realism of the model. Compensatory density-dependent egg-to-smolt survival was parameterized using defined spawner conservation limits for the SUs. Egg depositions and smolt production are monitored on a limited number of rivers across the Atlantic salmon distribution range in the North Atlantic (Chaput et al., 1998; ICES, 2013; Prevost, 2003). Some new indicators of juvenile production are even available at the scale of SU (Malcolm et al., 2019). Complementing the model with those data would provide valuable information on density-dependent egg-to-smolt survival rates and smolt-age compositions. This would ultimately allow an exploration of environmental factors affecting marine survival, separate from the freshwater effects. The representation of life histories could also be improved. In particular, fish that spend more than two winters at sea or repeat spawners are not considered. Those fish with a high spawning potential can

represent a non-negligible proportion of spawners in some SUs and should be integrated in future development of the model, contingent upon reliable data being available. Extending the model to Northern European CSG would specifically require adding older sea ages into the model, because of the older average sea age of maturation in the Northern Europe populations than in the current life cycle model.

Further analyses to test whether there might be support for specifying different variance-covariance matrices for post-smolt survival and proportion of fish that mature as 1SW maturation would allow for exploring the possibility that those life history traits are driven by different ecological processes. But inferences on the proportion of fish maturing as 1SW strongly depend upon our modelling hypotheses in the marine phase and should therefore be interpreted with caution. As already analysed by Massiot-Granier et al. (2014), estimated trends in the proportion of fish maturing as 1SW result from trends in the proportion of 1SW to 2SW in returns (observed) which are analysed under the hypothesis of a constant natural mortality after the PFA stage. Because 1SW and 2SW have different migration routes, an interesting perspective to this work would be to explore the possibility of environmentally driven variations in marine survival specific to the sea ages. Another research avenue would be to explore the intricate relationships between marine survival and maturation schedule. Survival and maturation are two key components of fitness (Mangel & Satterthwaite, 2008; Marshall et al., 1998; Thorpe et al., 1998). They cannot be considered independent, the trade-off reflecting the cost of reproduction. Another challenging perspective is therefore to explore how to transfer concepts of probabilistic reaction norms (Buoro, Prévost, & Gimenez, 2010; Morita, Morita, Fukuwaka, & Matsuda, 2005; Olsen et al., 2005) into our multi-population model to explore the hypothesis of a plastic response of populations to changes in environmental conditions susceptible to jointly impact post-smolt survival and proportion of fish maturing as 1SW.

Finally, our model assumes no heritability in phenotypic traits such as sea age at maturity. However, a recent study suggests a relatively strong heritability for age at maturity in Atlantic salmon and a genetic architecture inducing strong dependencies on sex (Barson et al., 2015). Some of the trends in the relative proportions of 1SW to 2SW in returns could therefore reflect an evolutionary response induced by the historic selective exploitation of older and bigger fish (Thorpe, 2007) or by environmental changes with a greater impact on 2SW fish because of different migration routes at sea.

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