

Benchmarking the north atlantic salmon stock assessment: a new life cycle model to evaluate salmon mixed stock status and fisheries management scenarios across the north atlantic basin

Maxime Olmos, Remi Lemaire-Patin, Pierre-yves Hernvann, James Ounsley, Maud Queroue, Geir Bolstad, Peder Fiske, Gérald Chaput, Etienne Prévost, Marie Nevoux, et al.

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BENCHMARKING THE NORTH ATLANTIC SALMON STOCK ASSESSMENT: A NEW LIFE CYCLE MODEL TO EVALUATE SALMON MIXED STOCK STATUS AND FISHERIES MANAGEMENT SCENARIOS ACROSS THE NORTH ATLANTIC BASIN

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Important note

 This WP is based the version of the Life Cycle model developed in 2021. The structure of the LCM is based on the one described in Olmos et al. (2019). The catch allocation rule is different between the LCM and the PFA models. In particular, in the PFA models, the catch allocation rule at West Greenland allocates catches among SU within the same complex in proportion to the pre fishery abundance. In e LCM, catches at WG are allocated using proportions based on genetic data.

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1 INTRODUCTION

Atlantic salmon (*Salmo salar*) (hereafter A. salmon) figures prominently in emblematic migratory species of the Atlantic Ocean and is characterized by a highly evolved homing ability that is the root of its structure into individual river populations. After spending their first years in rivers of the eastern North America and the western Europe, juvenile A. salmon migrate to common feeding grounds in the North Atlantic, especially aggregating off West Greenland, in the Labrador Sea, and the Faroes Islands and Norwegian Sea (Aas et al., 2010; D. Mills, 1989), where they grow over multiple winters before heading back to their home waters once mature. A. salmon are susceptible to be harvested at several stages in their life cycle. While some fisheries affect individual salmon populations in coastal areas before entering their natal river or in freshwater (final stages of spawning migration), mixed stock fisheries harvest populations originating from various continental habitats in high seas foraging areas, in West Greenland or in the vicinity of the Faroe Islands (Chaput, 2012; ICES, 2017). These areas are also where salmon populations are exposed to common marine environmental conditions (Beaugrand & Reid, 2003, 2012; Friedland et al., 2014; K. E. Mills et al., 2013).

The regulation of mixed stock high seas fishery was of sufficient concern that an international body (the North Atlantic Salmon Conservation Organization (NASCO; http://www.nasco.int/)) was formed in 1982 and a treaty subsequently signed by participating countries to manage the marine fisheries impacting different stock of A. salmon (Windsor and Hutchinson, 1994). The annual stock status reports developed by the Working Group North Atlantic Salmon of the International Council for the Exploration of the sea (ICES/CIEM WGNAS) and the subsequent scientific advices provided to the NASCO have formed the basis for the negotiations and

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subsequent management of these fisheries. West Greenland and Faroe high sea fisheries are managed following a fixed escapement strategy aiming to achieve the spawner (or egg) requirements for the contributing stocks on both sides of the Atlantic Ocean (Chaput, 2012; W. Crozier et al., 2003; W. W. Crozier et al., 2004; Potter et al., 2004). Until 2020, ICES has advised this management by recommending maximum catch levels based on a forecast of A. salmon abundance prior to the high seas fisheries exploitation (Pre Fishery Abundance, PFA). The socalled PFA models used for stock assessment of 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 (CSG), i.e. eastern North America (NA), Southern European (SE) and Northern European (NE) (Chaput, 2012; W. W. Crozier et al., 2004; Potter et al., 2004). Each of these three independent models reconstructs long-term series of abundance at sea before marine fisheries for a given CSG and forecasts the returns of adults in their natal rivers of the matching SUs (homewaters). PFA models have been incorporated in a risk analysis framework to assess the consequences of mixed stock marine fisheries at West Greenland and Faroes on the returns (Friedland et al., 2005; ICES, 2015) and assess compliance of realized spawning escapement to conservation limits (biological references point below which the stock should not pass) at both the SU and CSG scales.

However, PFA models suffer from three weaknesses (here after [W]) that hinder their relevance for analysing the demographic processes driving the population's dynamics of European and American A. salmon populations. [W1] PFA models rely on a constructed stock-recruitment dynamic. Since they do not explicitly represent the population dynamics as a life cycle, there is no dynamic link between PFA and subsequent egg deposition. Thus, the productivity required by the models to forecast the returns, which is roughly inferred from reconstructions, may be susceptible

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to time series bias. In addition, the lack of flexibility in the modeling framework restricts the hypotheses that can be explored on drivers and mechanisms of changes in A. salmon demographics and population dynamics. [W2] The PFA modeling framework actually works as a combination of two models. A first model, the run reconstruction model relies on estimates of the abundance of fish returning to spawn and biological parameters (sex ratio, fecundity and mean proportion of smolts ages) to estimate the potential number of spawners or eggs (measure of the Stock) for each year of the time series. The same model is used to estimate the abundance of fish at the PFA stages (measure of the Recruitment), through a back-calculation procedure (similar to a Virtual Population Analysis) using data on catches at sea and hypothesis on natural mortality rates at sea. Hence, the measure of the stock and the recruitment are derived from the same data, whilst they are considered independent in the rest of the process. A second part of the modelling framework consists of estimating the productivity parameters between the Stock and the Recruitment for all years of the historical time series, and uses time series hypothesis (random walk) to forecast the evolution of the productivity parameter during three years after the last year of the assessment. This forecast of the productivity parameters serves as a basis to forecast the PFA and the number of fish that returns to homewater based on catches scenarios at sea. [W3] The three PFA models are independent and some of their core demographic hypotheses are not harmonized. The fact that SE and NE models consider the dynamics of both one-sea-winter and two-sea-winter fish while the NA model only considers that of the latter precludes the simultaneous analysis of the population dynamics among all SU in the North Atlantic (Chaput et al., 2005). Therefore, these structural differences rule out 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.

This paper aims to bring a major contribution to improve the scientific basis for A. salmon stock assessment. We then address weaknesses [W1]-[W3] from PFA models by developing a Bayesian life cycle modelling framework for the combined analysis of A. salmon population dynamics across a large number of SU in the North Atlantic Ocean. To this goal we extend the framework developed by Olmos *et al.*, (2019) for North American and Southern European CSG to include the dynamics of all SU of the three CSG representing the all Atlantic salmon distribution (Northern Europe, Southern Europe and North America) within a single harmonized and unified hierarchical Bayesian life cycle approach with populations following a similar life history process. The final goal of this paper is to provide a benchmark for the assessment and forecast models currently used by ICES for Atlantic salmon stock assessment in the North Atlantic.

To this end, using the same dataset, we compare previous PFA assessment models from ICES (ICES, 2018) with our Bayesian life cycle model to illustrate how our new approach improve the scientific basis for Atlantic salmon stock assessment. We illustrated how the life cycle model outperformed PFA models by investigating how harmonizing life histories and considering covariation in demographic parameters may (i) provide new insight about the life history parameters driving the dynamic of all North Atlantic salmon population; (ii) impact hindcast analysis, (iii) forecast analysis and (iv) risk analysis.

2 MATERIAL AND METHODS

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- In this section we focus on two main aspects of our modelling exercise. First, we present the outlines of the Bayesian life cycle modelling framework for the combined analysis of A. salmon population dynamics across a large number of SU in the North Atlantic. Then, we present the general framework used to compare PFA and LCM models.
 - 2.1 Outlines of the hierarchical Bayesian life cycle model
- The life cycle model is formulated in a Bayesian hierarchical state-space framework (Buckland et al., 2004; Cressie et al. 2009; Parent & Rivot, 2012; Rivot et al., 2004) that incorporates stochasticity in population dynamics as well as observation errors. We extended the framework developed by Olmos et al. (2019) (all SU from North America and Southern Europe) to include the dynamics of all SU of the three CSG (North America, Southern Europe and Northern Europe).

 To keep the presentation concise, below we resume the important characteristics of the model and all model equations and data sources are detailed in Supp.Mat.I.
- 178 2.1.1 Spatial structure integrating all SUs within the North Atlantic basin
- The model considers the dynamics of 25 SU (subscript r = 1, ..., N with N=25) (Fig. 1):
- 6 SU from NA CSG, indexed by r = 1, ..., 6: 1 = Newfoundland, 2 = Gulf, 3 = Scotia-Fundy,
- 181 4 = USA, 5 = Quebec and 6 = Labrador;
- 8 SU from the SE CSG, indexed by r = 7, ..., 14: 7 = France, 8 = UK England and Wales, 9
- 183 = Ireland, 10 = UK Northern Ireland FO, 11 = UK Northern Ireland FB, 12 = UK Scotland
- East, 13 = UK Scotland West, 14 = Iceland South-West;

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- 11 SU from NE CSG, indexed by r= 15, ..., 25: 15 = Iceland North-East, 16 = Sweden, 17 =
 Norway South-East, 18 = Norway South-West, 19 = Norway Middle, 20 = Norway North, 21
 = Finland, 22 = Russia Kola Barents, 23 = Russia Kola White Sea, 24 = Russia Arkhangelsk
 Karelia and 25 = Russia River Pechora.
- SU are defined on the basis of freshwater areas. All salmon within a SU are assumed to have the same demographic parameters and to undertake a similar migration route at sea.
- 191 2.1.2 A harmonized life cycle model accounting for variability of life history traits

The model is built in discrete time on a yearly basis (subscript t=1,...,n with n=47 in this present application based on data from 1971 to 2017). The population dynamic of each of the 25 SU is represented by an age- and stage-structured life cycle model (Fig. 2). The model 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 to 6 years in freshwater (depending on SU). Following the approach used by ICES for catch advice purposes (ICES 2022), only two sea-age classes are considered in the model: maiden salmon that return to homewaters to spawn after one 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. However, 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 considered (starting in 1971, year of return to rivers) (Fig. 2; Supp.Mat.I). Spawners are fish that contribute to reproduction and that survived all sources of natural and fishing mortality. All transition rates between stages s for each SU (r) in year t are denoted $\theta_{s_{t,r}}$.

210 2.1.3 Covariation among the 25 Sus

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The model explicitly incorporates two components of temporal covariation among all SUs (Fig. 2). First, the post-smolt survival (called productivity in PFA models, - so in this manuscript post-smolt survival and productivity defined the same variable- denoted $\theta_{3_{tr}}$) and the proportion of fish maturing as 1SW (denoted $\theta_{4_{tr}}$) are modelled as multivariate random walks in the logit scale which captures spatial covariation associated with environmental stochasticity. Random variations are drawn from multivariate Normal distributions in the logit scale with variance-covariance matrices \sum_{8_3} and \sum_{8_4} (Ripa and Lundberg, 2000; Minto et al., 2014):

218 (1)
$$(logit(\theta_{3_{t+l,r}})) \sim MVNormal((logit(\theta_{3_{t,r}}))) \sim \sum_{s=1:N} \sum_{s=1:N$$

219 (2)
$$(logit(\theta_{4_{t+l,r}})) \sim MVNormal((logit(\theta_{4_{t,r}})) \sim \sum_{r=1:N} \sum_{4})$$

- with N = the number of SU in the model (here N=25).
- The pairwise correlation matrix ρ can be calculated from the variance-covariance matrix:

222 (3)
$$\rho = j \overline{diag(\Sigma)}^{-1} \times \Sigma \times j \overline{diag(\Sigma)}^{-1}$$

The second source of covariation among SU is the harvest dynamics of the sequential marine fisheries that operate on mixtures of SUs, with the portfolio of SU available for each fishery dependent on marine migration route hypotheses (Fig. 2 and Fig. Supp.Ma.I).

2.2 Toward a new stock assessment model for the WGNAS

- In this section we present how the hierarchical life cycle model may improve the assessment of north Atlantic salmon by (i) highlighting the main differences between the currently used stock assessment (PFA models) and the hierarchical life cycle model (Fig.3, Table.1, Supp.Mat.II), (ii) presenting the data we used and (iii) defining the risk analysis framework we used to compare both approaches.
- 232 2.2.1 Limits of PFA models and improvement through the life cycle model
- We highlight the limits of the PFA models and how the life cycle model may address and solve
- those limits in Table 1. Details about the currently used PFA models can be found in Supp. Mat.
- 235 II and in previous studies (Rago et al., 1993; Crozier et al., 2004; Chaput et al., 2005; ICES, 2018)
- 236 2.2.2 Likelihood function and data

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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 for, 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

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244 and catches are derived from a variety of raw data and observation models, specific to each SU 245 (except for the mixed-stock fisheries at sea) as originally developed by ICES to provide input for 246 PFA models (see ICES, 2015b and Supporting Information S1 for further details). 247 For both PFA and life cycle models these consist of the following in time series (1971–2017) of 248 estimates (approximated as log-normal distributions) of the number of maturing anadromous 249 Atlantic salmon that return to homewaters for each of the 13 SUs by 1SW and 2SW maiden sea-250 age classes (Supp.Mat.I, Figure.1). 251 Because the life cycle is expandable and provides an opportunity to assimilate new sources of 252 information to improve the ecological and biological realism of the model, other times series are 253 implemented in the likelihood component of the model such as (ii) time series of estimates 254 (approximated as log-normal distributions) of homewater catches for each SU by sea-age class; 255 and (iii) time series of estimates (approximated as log-normal distributions) of catches for the 256 mixed-stock fisheries at sea operating sequentially on combinations of SUs, and using additional 257 data on the SU origin of the catches. More details about how the data are implemented in the PFA 258 and life cycle model can be found in (Supp.Mat.II. Table SII.1). 259 Forecasting and risk analysis framework 2.2.3 260 For both PFA and life cycle models we used probabilistic forecasts from the models to evaluate 261 the probability that egg deposition fall below management objectives for different catch options in 262 the Western Greenland and the Faroes fisheries.

The forecasted abundance of eggs deposition after all marine distant fisheries (but before

homewater fisheries) is then compared to the management objectives defined below. The same

models are used for fitting the historical time series and forecasting. In the case of the life cycle

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model, an exception are the transitions that involve a fishing mortality, modelled by directly retrieving catches to the abundance (this is because scenarios are defined by fixing catches and not harvest rates). For the life cycle model, the post-smolt marine survival and the proportion maturing are forecasted following the multivariate random walks defined at equations (1)-(2). For the NA PFA, only the post-smolt marine survival is forecasted following the multivariate random walks (the model tracking only 2SW). For the NE PFA model the post-smolt marine survival and the proportion maturing are forecasted following random walks with no covariance structure among SUs. Because of the random walk hypothesis, the forecasted marine survival and proportion maturing during the forecasting period will remain at the same average level than the last year of the fitted time series, but with an uncertainty that increases with time due to error propagation through the random walk. Parameters uncertainty is integrated using Monte Carlo simulation, by simulating multiple population trajectories with parameters randomly drawn in the posterior MCMC sample. 2.2.3.1 Management objectives- Conservations Limits (CLs) In managing Atlantic salmon fisheries, NASCO (1998) has adopted a fixed escapement strategy (Potter, 2001), in recognition of the importance of the spawning stock to subsequent recruitment. Management objectives are based on Conservation Limits (CLs) as defined by ICES and NASCO. CLs are defined as the quantity of eggs that should be deposited by spawners to produce a desired production of smolts (Table 2). Following the principles adopted by NASCO (1998) CLs for North Atlantic salmon have been defined by ICES WGNAS as limit reference points, in the sense that having abundance of eggs spawned falls below these limits should be avoided with high probability.

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Management objectives in SE and NE are to reach or exceed CLs for both 1SW and 2SW fish. However, in NA management objectives currently defined by ICES consider the 2SW fish component of the returns only. However, in this paper, CLs for North America have been defined as the total required egg deposition for both sea age classes (1SW+2SW) for all SU including North America. CLs used by ICES are only available at a more aggregated spatial scale than SU defined in our life cycle model (Table 2). Specifically, one CL is available for Scotland (sum of Eastern Scotland and Western Scotland in life cycle model), one CL for Norway (sum of 4 SU in life cycle model, South-East Norway, South-West Norway, Middle Norway and North Norway) and one CL for Russia (sum of 4 SU in life cycle model, Russia Kola Barents Russia Kola White Sea, Russia Arkhangelsk Karelia and Russia River Pechora). To be compared to the CLs defined by ICES, eggs deposition in the life cycle model were then summed to match with the spatial scale considered for CLs. Finally, abundances defined at different life stages, demographic parameters and fisheries exploitation rates posterior estimated from the life cycle model were also aggregated over the PFA spatial scale (representing 17 SU or aggregation of SU) to be compared to PFA posterior estimates.

- 303 2.2.3.2 Risk analysis framework for the Western Greenland and the Faroes fishery
- 304 SUs from NA, SE and NE are all potentially harvested by the West Greenland fishery (although
- 305 the proportion of fish originating from Northern Europe is very low in West Greenland catches).
- 306 A risk framework for the provision of catch advice for the West Greenland fishery has been applied
- since 2003 by NASCO and ICES (ICES, 2013).
- 308 Only fish from SE and NE are potentially harvested at the Faroes fisheries. There is currently no
- agreed framework for the provision of catch advice for the Faroes fishery adopted by NASCO.
- However, NASCO has asked ICES, for a number of years, to provide catch options or alternative

311 management advice with an assessment of risks relative to the objective of exceeding stock 312 conservation limits for salmon in the European area (NE and SE complexes). 313 As an important contribution, our new life cycle model provides a unique framework for evaluating 314 catch options for the Faroes and West Greenland separately or simultaneously and for all SU 315 separately or simultaneously. 316 For the purpose of demonstration, in this paper 36 scenarios that consider both Faroes and West-317 Greenland catches were then built by crossing 6 combinations of catches from 0 to 2500 tons (0, 318 500, 1000, 1500, 2000, 2500) for both the Western Greenland and Faroes fisheries. For each 319 scenario, catches options were converted to number of fish really caught using mean weight of fish 320 following ICES (2015a). Population dynamics was simulated with homewater catches and 321 proportions to allocate catches at West Greenland and Faroes fisheries to the different SU fixed to 322 the average of the last five years of the time series of data (2013-2017), and 0 catches for other distant fisheries. 323 324 For the West Greenland fishery, the catch of 1SW salmon of North American and European origins 325 is further discounted by the fixed sharing fraction (Fna) historically used in the negotiations of the 326 West Greenland fishery, that is a 40%:60% West Greenland:(North America & Europe) split. For instance, in a scenario with a 100t quotas, a total of 250t are actually caught, 150t are reserved for 327 328 the Western Greenland fishery and 100t are reserved for the North American and European 329 commercial fishery (note that the scientific advice given by ICES since several years is a quotas 330 of 0t). 331 For each scenario, we provide forecasts during three years (in this application, 2018-2020) starting 332 after the last year of our assessment model (2017). Monte Carlo simulations are run to integrate 333 over both process' errors and parameters' uncertainty. Parameters uncertainty is integrated by

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randomly sampling the parameters in the joint Bayesian posterior distribution probability around
parameters, which captures the covariance structure among the parameters. For a given set of
parameters, the population dynamics is simulated including process error (i.e., inter-annual
variability).

The probability of each SU (or aggregation of SU as defined in Table 2) achieving its CL
individually and the probability of this being achieved by all management units simultaneously

individually and the probability of this being achieved by all management units simultaneously within a same CSG (i.e. in the same given year) are calculated from Monte Carlo trials. This allows managers to evaluate both individual and simultaneous achievement of management objectives in making their management decisions.

- 2.2.3.3 Expected differences in forecast and risk analysis between life cycle and PFA models
 We expect that most of the differences we might observe between PFA and life cycle model will
 rely on two main reasons:
 - The demographic structure between PFA and life cycle models can be different. PFA
 models rely on different life history hypothesis depending on CSG: NE and SE PFA models
 consider both 1SW and 2SW life histories while NA PFA model considers only 2SW life
 history
 - 2. The way the PFA and life cycle models handle differently the uncertainty can lead to major differences, and have an impact on hindcast, forecast and risk analysis.
 - o In the life cycle model all latent variables are correlated through the life cycle structure whereas in the PFA model, all latent variables are not linked (similar to a stock recruitment dynamic). This will change how the uncertainty is propagated between the different parameters and latent variables.

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356	0	In the PFA models, the stock abundances (lagged eggs for NEAC and lagged	
357		spawners for NAC) is defined in the model through a prior distribution which is not	
358		updated within the model and so the uncertainty is not propagated through the other	
359		latent variables and parameters. Here again, this will create a big difference in term	
360		of how the uncertainty is quantified and propagated between the life cycle and PFA	
361		models	
362	0	Finally, in PFA models, the only likelihood function is defined for the distribution	
363		of returns whereas in the life cycle models the likelihood function include the	
364		distribution of returns, the distributions of both freshwater and fisheries catches and	
365		the proportion to allocate the catches to each stock units.	
366	0	To sum up, we argue that those differences in how PFA and life cycle models	
367		account for uncertainty will generate strong differences in the approximation of	
368		Bayesian posterior distributions.	
369	2.2.4 MCM	IC simulations and model checking	
370	The life cycle	model and the PFA models have different statistical structures. So the number of	
371	iterations to n	nake the model converged and to generate Bayesian posterior distributions are	
372	different.		
373	73 Life cycle model		
374	Bayesian post	terior distributions were approximated using Monte Carlo Markov Chain (MCMC)	

methods using Nimble (https://r-nimble.org) (de Valpine et al., 2017). The Nimble code for our

model is available on GitHub: https://github.com/MaxOlmos/SALMOGLOB-Life-Cycle-

Model/blob/master/model_nimble_compPFA.r. Two independent MCMC chains with dispersed

initialization values were used. The level of autocorrelation of MCMC chains is very high (still significant at lag 30). The first 200 000 iterations were used as a burn-in period. For each chain, to reduce the autocorrelation in the MCMC sample used for final inferences, one out of 400 iterations post burn-in was kept and the resulting sample of 4000 iterations per chain was used to characterize the posterior distribution (total iteration is 3 200 000). Convergence was assessed using the Gelman-Rubin statistic (Brooks & Gelman, 1998) as implemented in the R Coda package (gelman.diag()). Following the methodology developed in Olmos et al. (2019), the model fit to each data source was assessed by checking that the 90% credibility envelope of the posterior predictive distribution of each variable contained the observation. In addition, Bayesian p-values calculated from chisquare discrepancy tests (Gelman et al., 2014a) were calculated to check the ability of the model to replicate a posteriori data similar to those observed. As in Olmos et al. (2019, 2020), posterior predictive distributions show that the model fits well to all observations, and posterior predictive checks do not indicate strong inconsistencies between the model a posteriori and the data. Those results are not developed further in this paper (see Olmos et al. (2019) for more details)

NAC PFA model

Two independent MCMC chains with dispersed initialization values were used. The first 10 000 iterations were used as a burn-in period. For each chain to reduce the autocorrelation in the MCMC sample used for final inferences, one out of 100 iterations post burn-in was kept and the resulting sample of 50000 iterations per chain was used to characterize the posterior distribution (total iteration is 80 000)

NEAC PFA model

Two independent MCMC chains with dispersed initialization values were used. The first 3000 iterations were used as a burn-in period. For each chain to reduce the autocorrelation in the MCMC sample used for final inferences, one out of 100 iterations post burn-in was kept and the resulting sample of 7 000 iterations per chain was used to characterize the posterior distribution (total iteration is 20 000).

3 RESULTS

- In this section we first present the new results provided by the life cycle model for Atlantic salmon across the North Atlantic basin. Then we present the results of the comparison between the PFA
- and LCM models.
- 410 3.1 A harmonized life cycle to estimate temporal variations and spatial coherence of
- demographic parameters across the North Atlantic basin
- 412 3.1.1 A widespread decline of abundances in all CSG
- The model estimates time series of all key life stages in the model for all SU or for any aggregation
- of SU at the scale of SU or countries (Supp.Mat.III. Fig. SIII.1). Time series of total PFA in each
- 415 CSG show very similar continuous declines by a factor 3, between the 1970s and the 2010s (Fig.4)
- with a stronger decline for the NA CSG. The decline in PFA is marked by a strong decrease in
- abundances in the 1990s.
- 418 3.1.2 Post-smolt survival rate
- The time-series of post-smolt survival for the 25 SU show a common decreasing trend over years
- 420 (Fig.5a -d). The trends averaged over all SU of the same CSG exhibit slightly different tendencies
- over the years. The post-smolt survival in NA exhibit a strong decline by a factor 3 in the period
- 422 1985-1995. This decline is also observable in SE with a sharp decline by a factor 1.8 in 1987. The
- sharp decline in the late 80's-early 90's is less visible in NE. Trend in NE shows a continuous and
- smoothed decline over the period.

The majority of pairwise correlations are positive, with a median correlation among all SU of 0.084

± 0.139 (correlations are calculated in the logit scale; Fig.5e and Fig.5f). In general, correlations

are stronger between geographically close SU. The results show strong correlations for SU within

NA (0.333), followed by SE (0.138) and NE (0.083). Correlations between the NE SU are stronger

for the block of SU going from Sweden (East) to Russia-KB (West).

3.1.3 Proportion of fish maturing as 1SW

Time trends in the proportion of fish that mature as 1SW also show a strong coherence among SU. These are in accordance with the expectation of higher correlations between SU 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 (Fig.6a -d). All time trends are consistent with the average trend, except for France which shows a consistent decline during the entire period. Consistently with the low proportion of 1SW observed in the returns, the two most eastern SU, Russia-AK and Russia-RP, and US differ from the others SU with a very low probability of maturing. As observed for the post-smolt survival, most of the pairwise correlations are positive across the 24 SU, with an average correlation of 0.1 (correlations are calculated in the logit scale; Fig.6e and Fig.6f). In general, the correlations are stronger for geographically close SU. The results show strong correlations for SU within NA (0.409), followed by SE (0.149) and NE (0.087).

443	3.2 Comparisons between the new life cycle and currently used PFA models to asse	ess and
444	forecast salmon population dynamic and to evaluate catch options for mixed	l stock
445	marine fisheries	
446	Most of the differences we might observe in the following sections between PFA and life	e cycle
447	models will rely on two main reasons defined previously in section 2.2.2.3: the difference	ence in
448	demographic structures between PFA and life cycle model and how the uncertainty is con-	sidered
449	and propagated in the model by the PFA and the life cycle frameworks.	
450	Overall, the life cycle model generates more accurate posterior estimates of abundance	dances,
451	demographic parameters and fishery exploitation rates for both hindcast and forecast analys	is (Fig.
452	7, Fig.8 and Supp.Mat.III. Fig.SIII.2-18.). In the following sections we analyzed results pe	er CSG
453	for hindcast and forecast analysis and finally we explored how both PFA and life	models
454	performed to evaluate catch options for mixed stock marine fisheries.	
455	3.2.1 Hindcast and Forecast analysis	
456	In this section we provide a comparison of the key variables and parameters constituting bo	th PFA
457	models and life cycle models: Productivity (1SW and/or 2SW), Proportion of fish matu	ring as
458	1SW, Eggs deposition, Pre-Fishery Abundance (1SW and/or 2SW), Returns (1SW and/or 2SW)	2SW).

3.2.1.1 Europe : NE and SE

460 Hindcast

Because most of the results are consistent between all stock units within SE and NE CSGs, we propose in this section to present the results for only one SU, Scotland. We provided results for other stock units in Supp.Mat.III.

Posterior estimates of abundances (Eggs deposition, PFA, Returns) and demographic parameters (Productivity and proportion of fish maturing as 1SW) are consistent between the life cycle and PFA models over the time-serie from 1978 to 2020 (Fig.7 and Supp. Mat.III). For both PFA and LCM models trends in Returns (1SW and 2SW), PFA (1SW and 2 SW) and eggs deposition (total 1SW + 2SW) show a general temporal decreasing trend; trend in productivity shows a decline while proportion in fish maturing as 1SW show an increasing trend over the time-series.

For SE and NE stock units, results highlight few differences in posterior distributions for PFA and LCM models. Those differences mainly concern times series of PFA non maturing and Productivity for FR and EW stock units. For FR and EW stock units, differences in posterior distributions for PFA and LCM result in how the predictions might fit the data in the life cycle

Forecast

Overall, for both PFA and LCM models, forecasted years (2018-2019-2020) show a common pattern. LCM showed more accurate predictions. Uncertainties in forecast from PFA models can be really big. As a consequence, when considering the forecast for the egg deposition, even if PFA and life cycle predict similar median, they show different Bayesian posterior distributions due to

model, as already highlighted in Olmos et al. (2019) (see Supp. Mat in Olmos et al. 2019).

how the models account and propagate differently the uncertainty. Such a difference might have an impact on the risk analysis (see section 3.2.2).

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Hindcast In this section we presented the results for only two SUs, GF and NF, which illustrate the main differences between posterior estimates from PFA and life cycle models for NA SUs. We provided results for other stock units in Supp.Mat.III. Posterior estimates of abundances (Eggs deposition, PFA, Returns) and demographic parameters (Productivity) are not fully consistent between the life cycle and PFA models over the time-serie from 1971 to 2020 (Fig.8, Supp. Mat. III). The reason is because PFA models for NA CSG considers only fish non-maturing after the first winter at sea. Then, for stock units having returns largely dominated by 2SW (US, Scotia-Fundy, Quebec, Gulf), posterior estimates of abundances (Fig. 8.e, Fig. 8.f and Fig. 8.h, Supp. Mat. III) and productivity show a similar trends and values for both PFA and life cycle models (see purple 2SW productivity from the LCM and blue PFA productivity Fig. 8.g). However, for SUs having returns largely dominated by 1SW (Labrador and Newfoundland), consistency between PFA and life cycle models will depend on how parameters and variables are accounting for only non-maturing fish or for both maturing and non maturing fish. Variables and parameters specific to non-maturing fish as, 2SW Returns (Fig. 8.g) and PFA of fish non maturing the first year at sea (Fig.8.h) show consistent temporal pattern and value between PFA and life cycle model. However, in the life cycle model eggs deposition is defined as

the sum of eggs from both 1SW and 2SW fish while PFA model only track 2SW fish. Posterior

estimates of eggs deposition from the life cycle model were estimated to be 5 times larger than estimates from PFA models.

- 503 Forecast
- Overall, for both PFA and LCM models, forecasted years (2018-2019-2020) show differences.
- 505 LCM showed more accurate predictions. Uncertainties in forecast from PFA models can be really
- 506 big.
- 507 Note: In this version (13.10.2023) of the manuscript we are facing some issues with how the PFA 508 model forecast the egg deposition. Indeed, PFA models built by the WGNAS are defined to forecast 509 Pre-fishery abundances only. But to be able to compare PFA and life cycle models we had to model 510 transitions between PFA stages and eggs stages for the PFA models. For the hindcast it worked 511 well but for the forecast years 2019-2020 present higher values than hindcasted years, which does 512 not make sense for now. We are still investigating the reason and hope to provide a response for 513 the benchmark. However, we argue that it does not impact our demonstration showing that the life 514 cycle model is an operational to assess salmon population across the North Atltantic basin
- 515 3.2.2 Risk analysis: Evaluating catch options for mixed stock marine fisheries
- 516 3.2.2.1 Eggs deposition compared to CLs
- Results show how uncertainty in the forecasts increases with forecasting horizon. This is mostly
 the consequence of uncertainty propagation through time in forecasts of the post-smolts survival
 and proportion maturing modelled as multivariate random walks. Results show that the life cycle
 model generates more accurate posterior estimates than PFA (Fig. 7 and 8).

3.2.2.2 The West Greenland mixed stock fishery

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The probability that the eggs deposition achieves the CLs under any fishing scenarios is directly quantified through Monte Carlo draws. The probabilities of achieving management objectives are higher for the stocks in Northern and Southern Europe (Fig. 9). Stocks from Northern Europe have the highest probabilities of achieving their management objectives. In Southern Europe, Northern Ireland, Southwest Iceland, Scotland and England and Wales and Northern Ireland have the highest probabilities of achieving their management objectives. In contrast, Ireland and France from SE, and stocks from NA such as US, Scotia-Fundy and Gulf have very low probabilities of achieving their management objectives. As expected, different catch options at West Greenland have minimal influence on the probability of achieving management objectives for stocks that represent only a very low proportion of the catches at West Greenland, such as all stocks of NE (that represent less than 5% of the total fish harvested in West Greenland) and most of the stocks of SE. Because they present the highest exploitation rate at WG, stocks from NA such as Labrador, Quebec, and Gulf have their probability of achieving management objectives decreasing when catch options increase. When assessed at the scale of stock complexes (i.e. by comparing the total egg deposition at the scale of stock complex to the total CL at the scale of stock complex), probabilities to achieve conservation limits are the highest for Northern Europe, the lowest for southern Europe, and intermediate for North America (Fig 9). The North American stock complex logically revealed the most sensitive to catches scenarios at WG (Fig. 9) When comparing PFA and LCM models, results are pretty consistent. Differences exists for SU from NA CSG like NF that considers only fish non-maturing after the first winter at sea Fig. 9). In NE and SE CSG, differences exist for NO and RU stocks between PFA and LCM (Fig. 9). Those

differences can be explained by the fact that in the life cycle models the risk analysis is carried out for all stock units constituting NO (NO.MI, NO.NO, NO.SE,; NO.SW) and RU (RU.AK, RU.KB; RU.KW, RU.RP) by summing a posteriori the abundances of eggs deposition whereas in PFA models, the risk analysis is conducted from aggregated data, where the calculated productivity is the aggregated productivity of a given stock unit. Differences in uncertainties generated by each model can also explain some observed differences in Fig.9. For example, for IR SU (Fig. 9 and Supp.Mat.III Fig.SIII.8), the probability to reach the conservation limit is higher is higher with the PFA model than with the life cycle model. But both PFA and life cycle model predict the same abundance in term of median (Supp.Mat.III Fig.SIII.8). The only difference is that for the life cycle model the posterior distribution is narrower (uncertainty is lower) and so only a small part of the posterior distribution overlaps the conservation limits (meaning that for the life cycle model fewer Monte Carlo draws are above the conservation limits), which generates a lower probability of reaching the conservation limit.

3.2.2.3 The Faroes mixed stock fisheries

As expected, SU from North America are insensitive to catch options at Faroes as fish from North America are not supposed to be caught there (Fig. 10). Catch options at Faroes influence the probability of achieving management objectives for European SU only (Fig. 10). Southwest Iceland, Northeast Iceland, England and Wales, Northern Ireland, Norway and Russia have the highest probabilities of achieving their management objectives (Fig. 10). By contrast France, Scotland and Sweden have low probabilities of achieving their management objectives. Logically, Sweden and Norway that represent the highest proportion of catches at Faroes are the most sensitive to the catch options at Faroes.

When assessed at the scale of stock complexes (i.e. by comparing the total egg deposition at the scale of stock complex to the total CL at the scale of stock complex), probabilities to achieve conservation limits are the highest for Northern Europe and the lowest for southern Europe (Fig 10). The Northern European stock complex logically revealed the most sensitive to catches scenarios at Faroes. (Fig. 10).

Results between PFA and LCM are consistent. The mains differences occurs again for Norway and Russia stock units which have the specificity to have their productivity calculated from aggregated stock units whereas in the life cycle model productivity and eggs depositions are estimated for each stock unit constituting Norway and Russia and then aggregated to be compared to PFA outputs. And the main differences can also be explained by how the uncertainty is quantified by the PFA and life cycle model.

577 3.2.2.4 Evaluating catch options for both Faroes and West Greenland Fisheries

The new life cycle model allows for the first time to evaluate simultaneously catch options in Faroes and West Greenland (Fig. 11). As already shown with the independent assessment of Faroes and West Greenland fisheries, Southwest Iceland have the highest probabilities of achieving their management objectives and Ireland the lowest.

Interestingly, eggs deposition in France England&Wales and in Norway are more sensitive to catch options in the Faroes fisheries than in the West Greenland fishery. Indeed, those three stock units (or aggregated stock units) represent 50% of the catches in the 1SW maturing Faroes fishery, and a few amounts of fish harvested in the West Greenland fishery.

4 CONCLUSION

The new life cycle model provides a singular harmonized framework to simultaneously assess two sea-classes of Atlantic salmon for all SU in North America and Europe. This represent a paradigm shift from the stock assessment and forecasting approach currently used by ICES considers the North American and European (Southern and Northern) continental stock groups separately and these models have different demographic structures. It also allows for modelling covariations among all SU 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.

Moving from PFA models to life cycle model to assess, forecast and carry out risk analysis for Atlantic salmon stock unit across the all North Atlantic basin will change the workflow of the WGNAS (Fig.12).

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Table 1 :Weaknesses of the currently used stock assessment (PFA models) and proposed improvements through the hierarchical life cycle model.

Forecasts of the returns are based on forecasts of	model
 Forecasts of the returns are based on forecasts of productivity between a spawning potential and abundance at the PFA stage (measure of the recruitment) But the dynamic link between PFA and subsequent egg depositions is not represented; so statistical inferences on productivity is susceptible to time series bias Lack of flexibility in the statistical modelling framework restricts the integration of the large amount of available data and knowledge 	 A life cycle to represent all stages and life histories. This integrated life cycle framework is expandable Assimilates new sources of information to improve the ecological and biological realism of the model
A combination of three models i. The same model is used to estimate the abundance of fish at the PFA stages (recruitment) and to estimate the potential number of spawners or eggs (stock) ii. A model to forecast the evolution of the productivity parameter iii. The forecast model serves as a basis to forecast the PFA and the number of fish that return to homewater based on catches scenarios at sea	 The same model is used for both the inferences hindcasting and forecasting phases All the model properties and sources of uncertainties are readily integrated into the forecast process.
 The two European models explicitly consider 1SW and 2SW fish in the population dynamics, The model for NA only considers the dynamics of 2SW implicitly assumes that 2SW spawners only produce 2SW fish in future cohorts, and excludes contributions of 1SW Temporal variations of productivities are therefore not comparable to the PFA models built for the European CSG considering both 1SW and 2SW productivity. Cannot evaluate the commonality in temporal trends between all SU in the North Atlantic. Ignores any covariance structure in the dynamics of the SU that may share common environments at sea that are exploited in sea fisheries Precludes evaluation of the consequences of scenarios on multiple stock complexes simultaneously 	 A single unified life cycle approach with all populations following a similar life history process A framework to enhance the ecosystem approach. This framework analyzes the mechanisms that shape population responses to variations in marine ecosystems by modelling covariations among all SU by partitioning the effects of fisheries from the effects of environmental factors at a hierarchy of spatial scales Evaluate catch options for the Faroes and West Greenland separately or simultaneously and for all SU
	 But the dynamic link between PFA and subsequent egg depositions is not represented; so statistical inferences on productivity is susceptible to time series bias Lack of flexibility in the statistical modelling framework restricts the integration of the large amount of available data and knowledge A combination of three models i. The same model is used to estimate the abundance of fish at the PFA stages (recruitment) and to estimate the potential number of spawners or eggs (stock) ii. A model to forecast the evolution of the productivity parameter iii. The forecast model serves as a basis to forecast the PFA and the number of fish that return to homewater based on catches scenarios at sea The two European models explicitly consider 1SW and 2SW fish in the population dynamics, The model for NA only considers the dynamics of 2SW i. implicitly assumes that 2SW spawners only produce 2SW fish in future cohorts, and excludes contributions of 1SW ii. Temporal variations of productivities are therefore not comparable to the PFA models built for the European CSG considering both 1SW and 2SW productivity. Cannot evaluate the commonality in temporal trends between all SU in the North Atlantic. Ignores any covariance structure in the dynamics of the SU i. that may share common environments at sea ii. that are exploited in sea fisheries Precludes evaluation of the consequences of scenarios on

 $Table\ 2: Management\ objectives\ relevant\ to\ the\ development\ of\ catch\ options\ for\ the\ stocks\ units\ in\ NA,\ SE\ and\ NE.$

North America				
Stock Units	CLs	References		
Labrador	243660000	O'Connel et a	1. 1997	
Newfoundland	267780000	Reddin et al. 2009		
Quebec	50380000	Atlantic salmon management plan 2016, Ministère des Forêts, de la Faune et des Parcs (2016).		
Gulf	248680000	Cameron et al. 2009, Breau et al. 2009, Chaput et al. 2010, Cairns et al. 2015		
Scotia Fundy	224140000	Gibson et al. 2014, Bowlby et al. 2013, Jones et al. 2014		
US	435369000	Baum, E.T. 1995		
Southern Europe				
Stock Units		CLs	References	
Iceland (south+west) Scotland Northern Ireland		64273104		
		1609542000		
		56281942		
Ireland		710711690	ICES, 2015a	
England&Wales		211419850		
France		55165500		
Northern Europe				
Stock Units		CLs	References	
Iceland (north+	east)	23889096		
Sweden 13997100 Norway 444064980 ICES, 20				
		444064980	ICES, 2015a	
Finland		104278220		

Russia

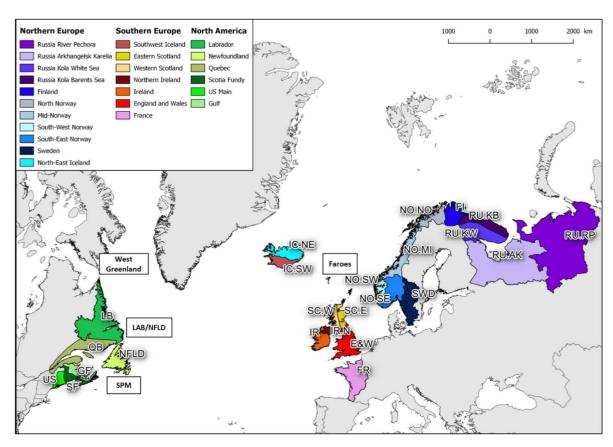


Figure 2: Spatial repartition of the 25 stock units considered in North Atlantic. Stock units of North America: NFDL=Newfoundland, GF=Gulf, SF=Scotia-Fundy, US=USA, QB=Quebec and LB=Labrador; Stock units in Southern Europe: IR=Ireland, E&W=England&Wales, FR=France, E.SC=Eastern Scotland, W.SC=Western Scotland, N.IR=Northern Ireland, IC.SW=South-West Iceland; Stocks units in Northern Europe: FI=Finland, IC.NE=North-East Iceland, NO.MI=Middle Norway, NO.NO=North Norway, NO.SE=South-East Norway, NO.SW=South-West Norway, RU.AK=Russia Arkhangelsk Karelia, RU.KB=Russia Kola Barents Sea, RU.KW=Russia Kola White Sea, RU.RP=River Pechora, SWD=Sweden. UPDATE NI SUs

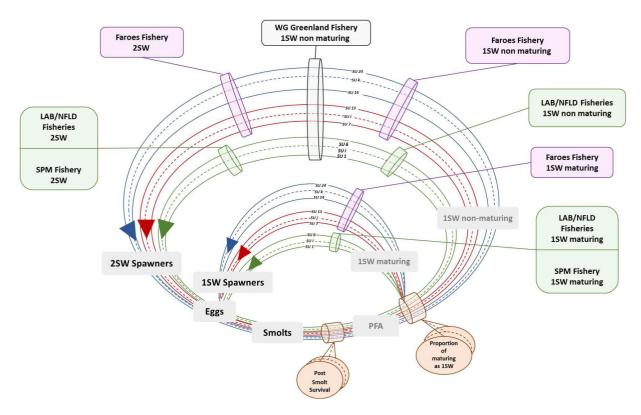


Figure 3: Structure of the age- and stage-based life cycle model for the 25 SU. Grey boxes: different stages during the marine (grey) and freshwater (black) phases. Green circles belong to NA SU, Red circles belong to SE SU and blue circles belong to NE SU. Cylinder: sources of covariations among the 24 SU. Orange cylinders: key parameters (post-smolt survival and maturing probability). Purple cylinders: fisheries operating on mixture of SE and NE SU. Green cylinders: fisheries operating on mixture of NA, SE and NE SU.

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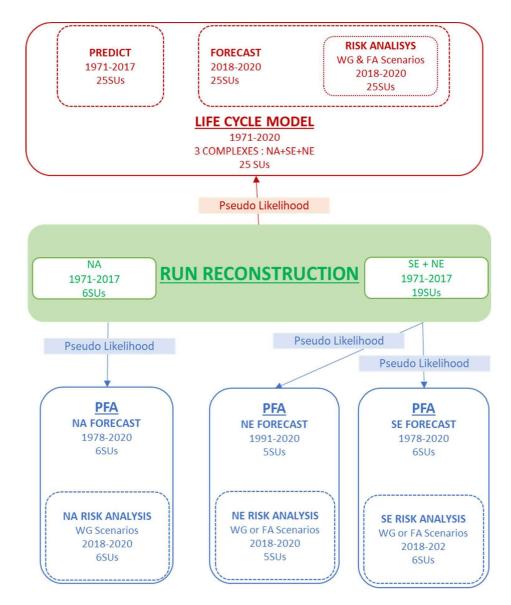


Figure 4: Outline of the modelling flows for PFA (blue) and life cycle (red) models. Run reconstruction (in green) are processing observation models that reconstruct probability distributions synthesizing observation uncertainty around the time series of catches and returns for the 25 SUs. Outputs from the Run Reconstruction models are used as pseudo observation for both the PFA models and the life cycle model. PFA models are defined for each complex whereas life cycle model is a unique framework integrating all complexes with the same statistical model.

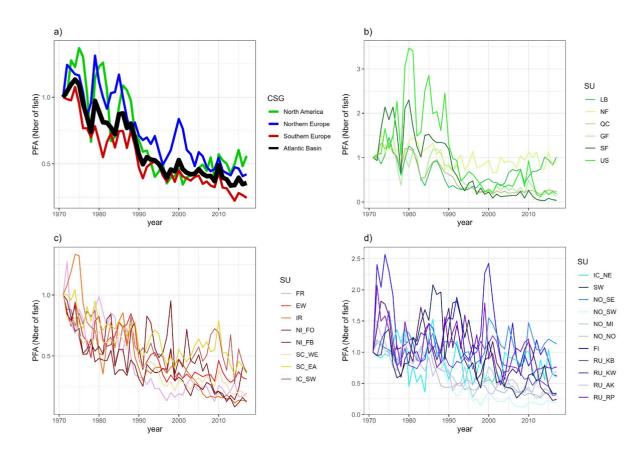


Figure 5 Time series of estimated abundances at the PFA stage (maturing + non maturing PFA) for all SU for the three continental stock groups: (a) summed by CSG and all CSG (Atlantic basin), (b) North America, (c) Southern Europe; (d) Northern Europe. Thick lines: median of the marginal posterior distributions. PFA are standardized to the first year values.

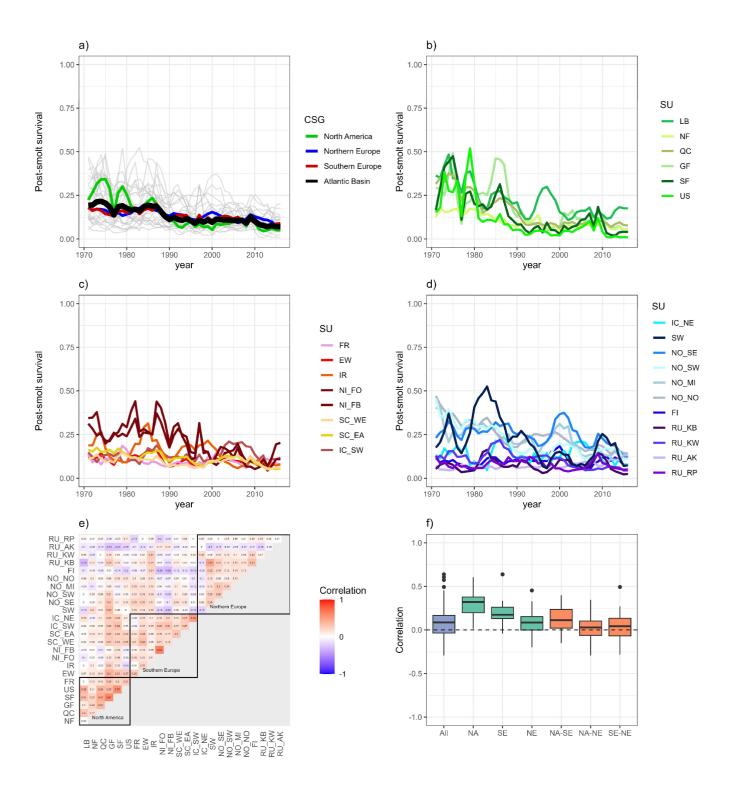


Figure 6: Post-smolt survival: (a) Time series of smolt-PFA survival (also called productivity) (median of the marginal posterior distributions plotted in the natural scale) for the 25 SU (thin grey lines), averaged over the three continental stock groups (thick color lines) and averaged across all CSG (Atlantic basin, thick black line). (b) –(c) –(d) Time series of post-smolt survival (median of the marginal posterior distributions plotted in the natural scale) for the 25 SU grouped by continental stock groups (North American, Southern Europe and Northern Europe respectively). (e) Pairwise correlations calculated between all SUs (median of the posterior distribution from the variance-covariance matrix in the logit scale). (f) Pairwise correlations (calculated in the logit scale) averaged over all SUs, over SU within the same CSG (NA, SE, NE) and over pairs of SU that belong to two different CSG (NA-SE, NA-NE and SE-NE).

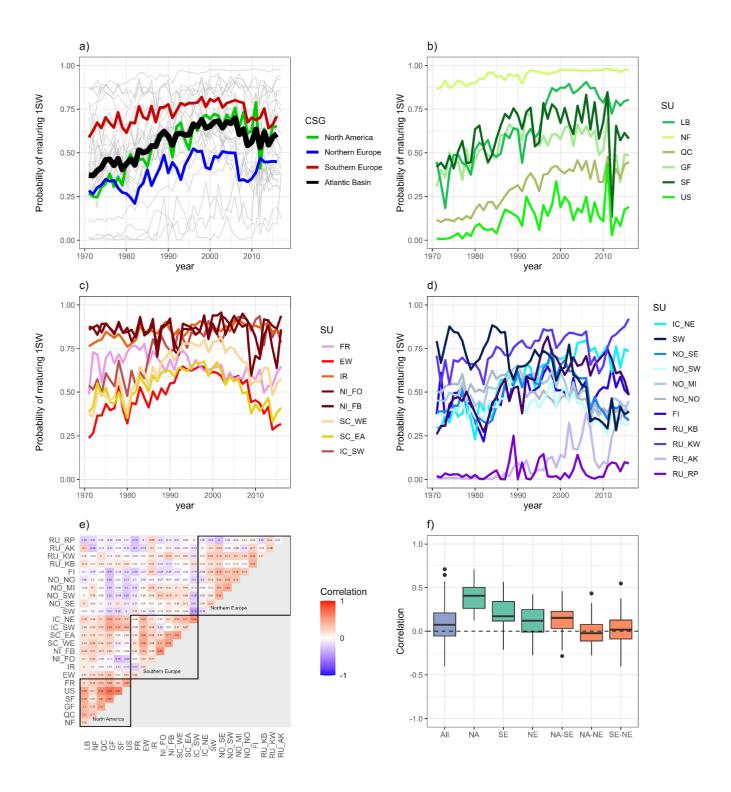


Figure 7: Proportion of maturing as 1SW: (a) Time series of proportion of maturing as 1SW (median of the marginal posterior distributions plotted in the natural scale) for the 25 SU (thin grey lines), averaged over the three continental stock groups (thick color lines) and averaged across all CSG (Atlantic basin, thick black line). (b) –(c) –(d) Time series of proportion of maturing as 1SW (median of the marginal posterior distributions plotted in the natural scale) for the 25 SU grouped by continental stock groups (North American, Southern Europe and Northern Europe respectively). (e) Pairwise correlations calculated between all SUs (median of the posterior distribution from the variance-covariance matrix in the logit scale). (f) Pairwise correlations (calculated in the logit scale) averaged over all SUs, over SU within the same CSG (NA, SE, NE) and over pairs of SU that belong to two different CSG (NA-SE, NA-NE and SE-NE).

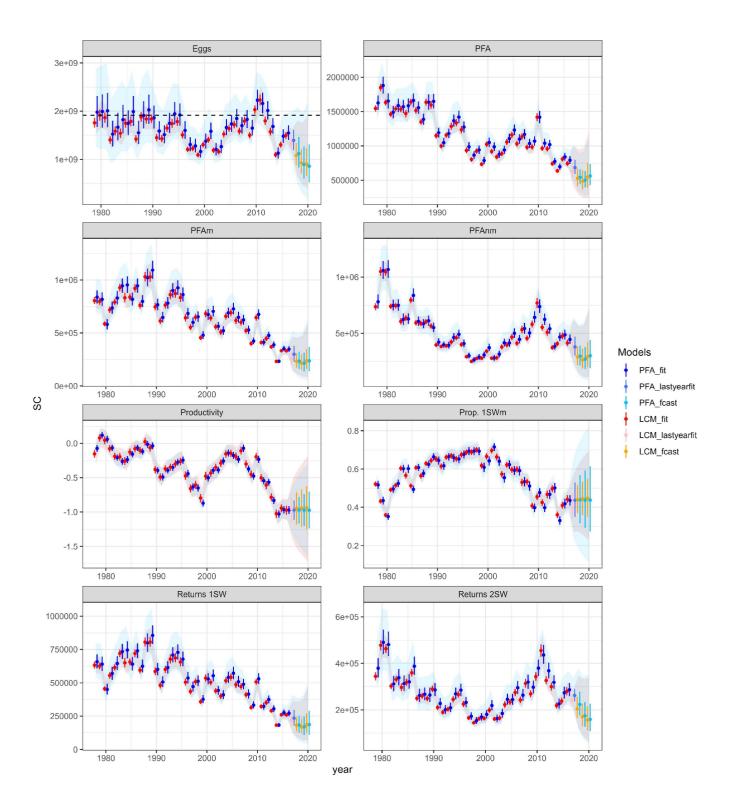


Figure 8: Probability distributions of the number of egg potentially spawned, PFA (total PFA.m + PFA.nm), PFA.maturing (PFA.m, PFA.non maturing (PFAn), Productivity, Proportion of fish maturing as 1SW, Returns 1SW, and Returns (2SW) for Scotland. Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red: Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland and Faroes)

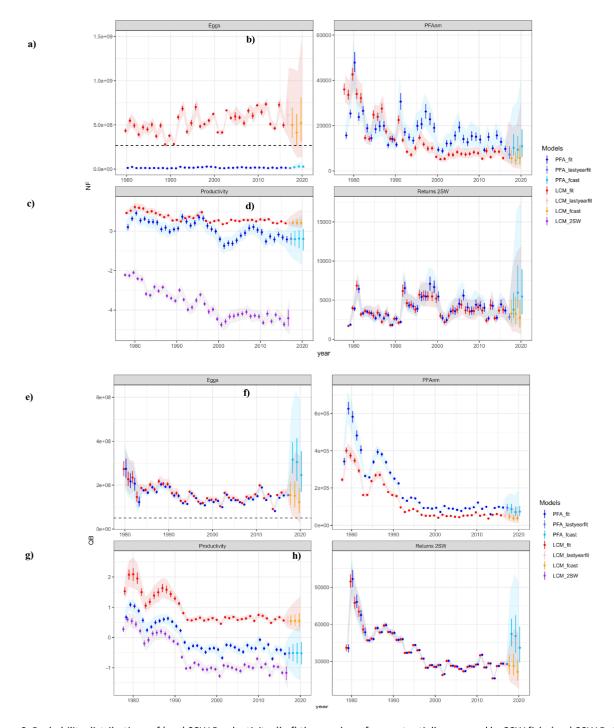


Figure 9: Probability distributions of (a, e) 2SW Productivity, (b, f) the number of egg potentially spawned by 2SW fish, (c, g) 2SW Returns, and (d, h) PFA.nm for Quebec (a - f) and Newfoundland (e-h). Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red: Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland)

Figure 10: Probability to reach Conservation Limits obtained under different catches options at West Greenland. Catches options: 0, 500, 1000, 1500, 2000 and 2500 tons (3 years projections). (LB, NF, QB, GF, SF, US) North America; (EW, IR, N.IR, SC, IC.SW) Southern Europe; (IC.NE, SW, NO, FI, RU) Northern Europe. Panels (NA, SE, NE) give probabilities to simultaneously achieving the management objectives for all SU of North America (NA), Southern Europe (SE) and Northern Europe (NE). Models: circle=Life cycle model (LCM), triangle= PFA

Figure 11: Probability to reach Conservation Limits obtained under different catches options at Faroes. Catches options: 0, 500, 1000, 1500, 2000 and 2500 tons (3 years projections). (EW, IR, N.IR, SC, IC.SW) Southern Europe; (IC.NE, SW, NO, FI, RU) Northern Europe. Panels (NA, SE, NE) give probabilities to simultaneously achieving the management objectives for all SU of North America (NA), Southern Europe (SE) and Northern Europe(NE). Models: circle=Life cycle model (LCM), triangle=PFA. Stock Units of North America are not impacted by Faroes fisheries and are not represented.

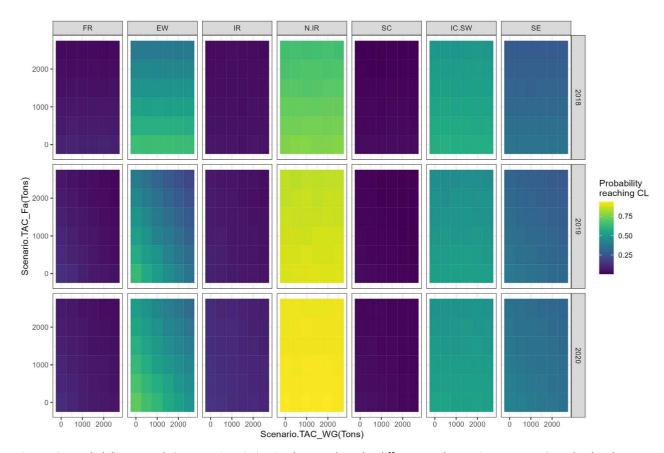


Figure 12a: Probability to reach Conservation Limits simultaneously under different catches options at West Greenland and Faroes: 0, 500, 1000, 1500, 2000 and 2500 tons (3 years projections) for SU of the Southern European complex potentially impacted by both mixed stock fisheries.

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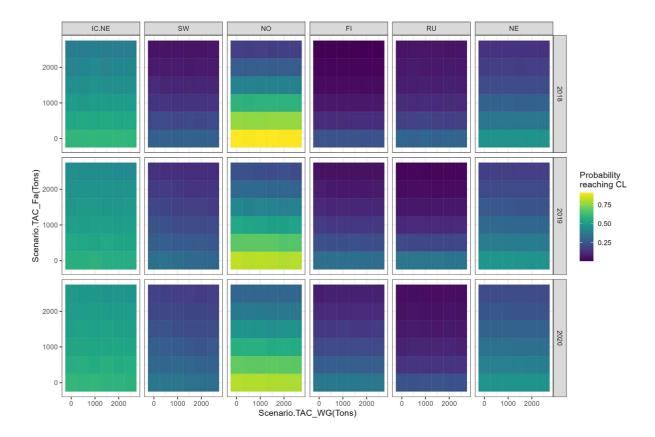


Figure 11b: Probability to reach Conservation Limits simultaneously under different catches options at West Greenland and Faroes: 0, 500, 1000, 1500, 2000 and 2500 tons (3 years projections) for SU of the Northern European complex potentially impacted by both mixed stock fisheries.

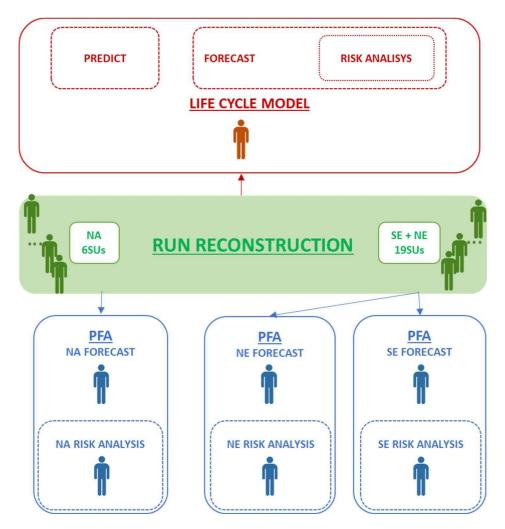


Figure 13: Conceptual representation about how the new life cycle model impacts the workflow of the WGNAS in term of human resource and interactions.

6 SUPP.MAT.1. - Detailed process and observation equations of the Bayesian life cycle model

1.1 Population dynamics

1.1.1 Simplified life history

The age- and stage-structured life cycle model has a similar structure for each SU. It includes variation in the age of juveniles out-migrating from freshwater (i.e. smolts) and the sea-age of returning adults. Smolts migrate seaward after 1 to 6 years spent in freshwater (depending on SU). Two sea-age classes are considered in the model: Maiden salmon that return and reproduce after one year at sea, referred to as one-sea-winter (1SW) salmon or grilse, and maiden salmon that return after two winters spent at sea (2SW). This is a simplification of the variety of life history as some maiden fish may spent more than two winters at sea before returning to spawn, or some may be repeat spawners. However, those fish are rare and the 6 smolt-ages × 2 sea-ages combinations capture the essence of life history variations.

1.1.2 Eggs deposition

The total number of eggs potentially spawned in year t for SU r is calculated from the number of 1SW ($N_{7_{t,r}}$) and 2SW ($N_{10_{t,r}}$) spawners escaping the homewater fisheries and the average number of eggs potentially spawned per 1SW and 2SW salmon, denoted $eggs_{1,t,r}$ and $eggs_{2,t,r}$ (Table 2):

(A1.1)
$$N_{1_{tr}} = N_{7_{tr}} \times eggs_{1,t,r} + N_{10_{tr}} \times eggs_{2,t,r}$$

1.1.3 Egg-to-smolt transition

The egg-to-smolt transition consists of two steps: the survival from egg-to-smolt per cohort, and the distribution of the surviving smolts according to their age at downstream migration.

1.1.3.1 Egg-to-smolt survival

Because no smolt production data is available at the scale of SU, it is difficult to separate the variability of the egg-to-smolt survival from that of the post-smolt survival, and parameters of the egg-to-smolt transitions have to be fixed. The egg-to-smolt survival is density independent, with average survival rate θ_1 arbitrarily fixed to 0.007 (Hutchings & Jones, 1998; Massiot-Granier et al. 2014) for all years and all SU (Table 2). Environmental stochasticity is modelled by logNormal random noise with variance $\sigma_{8_1}{}^2$ fixed to an arbitrarily value corresponding to $CV_{8_1}{}^2 = log(CV_{8_1}{}^2 + 1)$ which is a median values for the inter-annual variability found in

the literature (Prevost et al., 2003; Pulkkinen et al., 2013). The total number of smolts produced in the cohort c (corresponding to egg deposition of year c), denoted $N_{2_{cr}}$ is then modelled as:

This model configuration only allows for random stochasticity in the egg-to-smolt survival and does not account for any compensation neither (but see Olmos et al. 2019 for a sensitivity analysis to inclusion of density dependence). This implicitly assumes that any trends in the stock productivity over time are a response to changes in the marine phase, what may inflate the importance of trends in the post-smolt survival.

1.1.3.2 Distribution according to smolt ages

The probabilities of a smolt in the cohort c migrating at age a = 1, ..., 6 at year t = c + a + 1, denoted $\theta_{2_{c,a,r'}}$ are fixed to their averaged proportions $psm_{1:6,r}$ specific to each SU (Table 2).

Given $\theta_{2_{c,a,r'}}$, the number of smolts from the cohort c that migrate at age a year t = c + a + 1 is modelled as:

(A1.4)
$$N^1_{2_{\text{c.a.t}=c+a+l.r}} = \theta_{2_{\text{c.a.r}}} \times c_{\text{c.r.}}$$

Last, the number of smolts migrating in the spring of year *t* is the sum of all smolts of different ages (and therefore of different cohorts) migrating in year *t*:

(A1.5)
$$N_{3_{\text{t,r}}} = \sum_{a=1}^{a=6} N_{2_{\text{c=t-a-l,a,t,r}}}^{1}$$

Note:

In a previous model version, smolt ages distribution ($\theta_{2_{c,a,r}}$) was estimated. Proportion of smolt ages were set a tight Dirichlet prior distribution. However, this transition revealed serious bottleneck for computational time needed to reach convergence. A simpler solution using fixed proportions is then adopted to keep reasonable model execution time.

1.1.4 Marine phase

The marine phase is modelled as a sequence of three blocks of transitions: survival from smolts to the PFA stage, the maturation of fish at the PFA stage, and the fishing and natural mortality between PFA and returns.

1.1.4.1 Post-smolt survival and proportion of fish maturing as 1SW

Time series of post-smolt survivals ($\theta_{3_{t,r}}$) and the proportion of fish maturing as 1SW ($\theta_{4_{t,r}}$) are modelled as multivariate random walks in the logit scale. Random variations are drawn from multivariate Normal distributions with variance-covariance matrix Σ_{8_3} and Σ_{8_4} that define the covariations among the SU (Minto et al., 2014; Ripa and Lundberg, 2000):

$$(A1.6) \begin{tabular}{ll} First year (for $r=1$: N): $logit(\theta_{3_{t=l,r}}) \sim Normal(0,1)$\\ Then $(logit(\theta_{3_{t+l,r}}))$_{r=1:N}$ $\sim MVNormal ((logit(\theta_{3_{t,r}}))$_{r=1:N}$, \sum_{3})\\ First year (for $r=1$: N): $logit(\theta_{4_{t=l,r}}) \sim Normal(0,1)$\\ Then $(logit(\theta_{4_{t+l,r}}))$_{r=1:N}$ $\sim MVNormal ((logit(\theta_{4_{t,r}}))$_{r=1:N}$, \sum_{4})\\ \hline \end{tabular}$$

Then, given the number of smolts migrating in year t ($N_{3_{t,r}}$) and the post-smolt survival ($\theta_{3_{t,r}}$), the number of posts-smolts that survive to the PFA stage ($N_{4_{t+l,r}}$) in January of year t+1 is modelled as:

(A1.8)
$$N_{4_{t+1}r} = \theta_{3_{t}r} \times N_{3_{t}r}$$

Given the number of fish at the PFA stage ($N_{4_{t+l,r}}$) and the maturation rate ($\theta_{4_{t+l,r}}$), mature ($N_{8_{t+l,r}}$) and non mature fish ($N_{8_{t+l,r}}$) at the PFA stage are modelled as:

(A1.9)
$$N_{S_{t+l,r}} = \theta_{4_{t+l,r}} \times N_{4_{t+l,r}}$$

(A1.10) $N_{8_{t+l,r}} = (1 - \theta_{4_{t+l,r}}) \times N_{4_{t+l,r}}$

Note: For this 2018 version, those transitions were modelled as stochastic, using lognormal distribution with standard deviation fixed to a very low value. In the current version (2023). Those transitions are now modelled as deterministic to keep reasonable model execution time.

1.1.4.2 Sequential marine fisheries and natural mortality

After the PFA stage, both maturing and non-maturing fish are subject to natural mortality and sequential fisheries mortalities operating on mixed stocks (Tables 4 & 5). The following modelling structure applies for each of those transitions. For any marine fishery f, operating in year t on a number of fish $N_{\rm f_{t,r}}$ originated from the stock unit r with an exploitation rate $h_{\rm f_{t,r}}$, the catches $C_{\rm f_{t,r}}$ (unknown states) and the number of fish that escape the fishery $N_{\rm fesc}$, are modelled as:

(A1.11)
$$C_{f_{t,r}} = h_{f_{t,r}} \times N_{f_{t,r}}$$

(A1.12) $N_{f.esc_{t,r}} = (1 - h_{f_{t,r}}) \times N_{f_{t,r}}$

Exploitation rates $h_{f_{t,r}}$ are modelled as variable over time but their variability across SU is modelled differently depending on the data available to allocate catches to each SU and on expert knowledge about migration routes. Exploitation rates of the West Greenland fishery (WG; operating on a mixture of SU from North America and Europe) and of the Faroes fishery (FA; operating on SU from Europe only) were all supposed to vary across years and SU (Tables 5 & 6).

For the fisheries specific to the SU from NA (Table 5), because no proportion data are available to allocate catches among SU, catches were allocated to each SU by considering a single h homogeneous for all SU. There is however an exception to this general rule (Prévost et al., 2009): for the Labrador/Newfoundland (LAB/NFDL and Saint-Pierre et Miquelon (SPM) fisheries on 1SWm and 2SW fish, a separate h is estimated for Labrador SU, and a single h is considered for the five other North American SU, corresponding to catch allocation proportional to abundance.

All fisheries at sea are separated by periods of time where only natural mortality occurs (ICES, 2018; Potter, 2016; Prévost et al., 2009). Fish that escape the fishery f at year t hence suffer natural mortality rate $\theta_{\S,f} = e^{-M \times \Delta t,f}$ where the monthly mortality rate M is fixed, constant across years and SU's ($M = 0.03 \cdot month^{-1}$; Table 2) and the duration $\Delta_{t,f}$ (in months) are assumed known and constant across years but with some variations among SU to account for variability in migration routes (Tables 4 & 5):

(A1.13)
$$N_{f+1_{tr}} = (1 - \theta_{S_{tf}}) \times N_{f.esc_{tr}}$$

1.1.4.3 From returns to spawners (homewater catches)

Fish that escape all marine mortality and return as 1SW fish $(N_{6_{tr}})$ or 2SW fish $(N_{9_{tr}})$, are subject to homewater fisheries that operate locally on each SU. Homewater fisheries are modelled with exploitation rates h_{HWf_{tr}} that are assumed to vary with years and SU and for the two sea-age classes separately (Tables 5 & 5). Homewater fishery harvest rates are estimated. After homewater fishery, a proportion of fish may potentially delay spawning to the next year. The proportion of delayed spawners are supposed known but varies with SU, years and sea-age classes and are denoted $p_{\text{delSp}_{t,r}}$ (specific for 1SW and 2SW). Fish that do not delay spawning are potentially subject to an additional fishery with harvest rate denoted $h_{\text{sup}_{t,r}}$ (specific for 1SW and 2SW). Fish that delay spawning to the next year may then be subject to a specific fishery with (estimated) harvest rates $h_{\text{delSp}_{\text{tr}}}$ (specific to 1SW and 2SW). An additional survival rate ($\theta_{6_{\text{tr}}}$ or $\theta_{9_{t,t'}}$ for 1SW and 2SW, respectively) is then finally applied on all remaining fish before spawning. In practice, the proportion of delayed spawners is non-zero only for Russian stock units. The supplementary harvest rate $h_{\text{sup}_{\text{tr}}}$ (and associated catches) are non null only for Scotland East and West. But these transitions are modelled uniformly for all stock units with zero proportion of delayed spawners in the data and zero additional catches for almost all SU. Last, the number of 2SW spawners in the US stock unit is also supplemented by stocking. The transition is also modelled uniformly for all SU but the number of fish stocked $n_{Stock.2SW_{tr}}$ is null for all SU except USA. Finally, the number of fish that escape the homewater fishery and potentially spawn as 1SW $(N_{7_{tr}})$ and 2SW $(N_{10_{tr}})$ are modelled as:

(A1.14)
$$N_{7_{t,r}} = ((1 - h_{\text{HWf.1S}_{t,r}}) \times (1 - p_{\text{delSp.1SW}_{t,r}}) \times (1 - h_{\text{sup.1S}_{t,r}}) \times N_{6_{t,r}} + (1 - h_{\text{HWf.1SW}_{t-l,r}}) \times p_{\text{delSp.1SW}_{t-l,r}} \times (1 - h_{\text{delSp.1SW}_{t,r}}) \times N_{6_{t-l,r}}) \times \theta_{6_{t,r}}$$
(A1.15)
$$N_{10_{t,r}} = ((1 - h_{\text{HWf.2SW}_{t,r}}) \times (1 - p_{\text{delSp.2SW}_{t,r}}) \times N_{9_{t,r}} + (1 - h_{\text{HWf.2SW}_{t-l,r}}) \times p_{\text{delSp.2SW}_{t-l,r}} \times (1 - h_{\text{delSp.2SW}_{t,r}}) \times N_{9_{t,r}} + n_{\text{Stock.2SW}_{t,r}} \times p_{\text{delSp.2SW}_{t-l,r}} \times (1 - h_{\text{delSp.2SW}_{t,r}}) \times N_{9_{t,r}} + n_{\text{Stock.2SW}_{t,r}}$$

1.2 Observation equations

The model incorporates observation errors for all time series of returns and catches. A sequential approach (Michielsens et al., 2008; Staton et al., 2017) is used that consists of two steps:

- In a first step, observation models are processed separately to reconstruct probability distributions that synthetize observation uncertainty around catches and returns for each year and each of the 25 SU. Probability distributions for returns and catches are derived from a variety of raw data and observation models, specific to each SU and each year and originally developed by ICES to provide input for PFA models for NA (Rago et al., 1993) and SE (Potter et al., 2004b) stock units.
- In a second step, those distributions are used to approximate likelihoods in the population dynamics state-space model.

1.2.1 Returns

Returns are estimated for each year, each SU and for the two sea-age classes separately. Raw data used to estimate return essentially consist in homewater catches available at the scale of rivers or regional fishery jurisdictions, scaled by harvest and declaration rates and then aggregated at the scale of larger stock units. Uncertainties then essentially arise from a numerical (Monte Carlo) integration of uncertainties about harvest and declaration rates. Other fishery independent information like counting fences or mark and recapture data can also be used. Detailed description of the raw data and models used in each SU is provided in the WGNAS Stock Annex for Atlantic salmon (Crozier et al., 2003; ICES, 2002, 2015b; Potter et al., 2004b; Rago et al., 1993).

1.2.1.1 The case of Northern NEAC SU

ICES provides a shorter time series of data for Northern NEAC SU because some data are missing for Norway for the first time of the time series before 1982. The Norwegian data for the period 1971-1982 were completed using the following hypotheses (*Com pers*. Geir Bolstad and Peder Fiske, NINA):

- Homewater catches Catch data for Norway (homewater catches, 1SW and 2SW separately) for the period 1971-1982 were extracted from the ICES WGNAS report of year 2002 (table 3.3.3.1f. Allocations of catches among the four regions of Norway was done using averages proportions calculated from the first five years for which data are available 1983-1987.
- Returns The probability distribution of returns (1SW and 2SW, separately) was estimated by
 dividing the catches by guesstimates of exploitation rates and unreported catches for the
 period 1982-1971. Harvest rates and unreported catches were extrapolated backwards in time
 from year 1983. Uncertainty about those rates was bumped by 20% to account for the
 additional uncertainty due to extrapolation.

• Note that all MSW were considered as 2SW as for all other European SU.

The resulting probability distributions of returns are shown in Fig. 1. Numerical integration of uncertainty support the hypothesis that the returns are logNormaly distributed, allowing to approximate the likelihood for the returns as follows. For any year t and SU r, the expected mean of the distribution derived from the observations models for 1SW (respectively, 2SW) returns in log scale, denoted $\mathbb{E}_{\log(R_{\text{ISW}_{\text{t,r}}})}$ (resp. $\mathbb{E}_{\log(R_{\text{2SW}_{\text{t,r}}})}$), is considered as an observed realization of a Normal distribution of non-observed returns (in log-scale) $N_{6_{\text{t,r}}}$ (resp. $N_{9_{\text{t,r}}}$), with known variance σ^2 (resp. σ^2) set to the value derived from the observation errors models. These observation errors are considered independent across years, SU and sea-age classes.

$$\begin{split} &(\text{A1.16}) \qquad & \mathbb{E}_{\log(R_{1\text{S}} \text{ t,r})} \sim Normal(\log(N_{6_{\text{tr}}}), \sigma_{1\text{SW}_{\text{t,r}}}^2) \\ &(\text{A1.17}) \qquad & \mathbb{E}_{\log(R_{2\text{SW}_{\text{t,r}}})} \sim Normal(\log(N_{9_{\text{t,r}}}), \sigma_{2\text{SW}_{\text{t,r}}}^2) \end{aligned}$$

1.2.2 Homewater catches

The homewater fisheries take adult fish that are mainly returning to the natal rivers to spawn. Point estimates of total catches reported by ICES (ICES 2018) pool all homewater fisheries capturing returning fish in coastal areas, estuaries and freshwater, for each SU, each year and each sea-age class separately. They are here denoted $\mathbb{E}_{log(C_{HW,ISW_{t,r}})}$ and $\mathbb{E}_{log(C_{HW,2SW_{t,r}})}$ for 1SW and 2SW fish, respectively. The likelihood term for homewater catches is built from logNormal observation errors with known observation error. Available knowledge support that homewater catches are known with only few errors. Relative error is then arbitrarily fixed to CV=0.05 for both sea-ages, for all years and all SU (but note this value can be changed to acknowledge for greater observation errors). Observation errors are considered independent across years, SU and sea-age classes. The likelihood terms associated with homewater catches are:

$$(A1.18) \\ \mathbb{E}_{\log(C_{\text{HW.ISW}_{\text{t,r}}})} \sim Normal(\log(h_{\text{HWf.1SW}_{\text{t,r}}} \times (1 - p_{\text{delSp.1SW}_{\text{t,r}}}) \times N_{6_{\text{t,r}}}), \sigma_{\text{HW.1SW}}^2)$$

$$(A1.19) \\ \mathbb{E}_{\log(C_{\text{HW.2SW}_{\text{t,r}}})} \sim Normal(\log(h_{\text{HWf.2SW}_{\text{t,r}}} \times (1 - p_{\text{delSp.2SW}_{\text{t,r}}}) \times N_{9_{\text{t,r}}}), \sigma_{\text{HW.2SW}}^2)$$
with $\sigma_{\text{HW.1SW}}^2 = \sigma_{\text{HW.2SW}}^2$ the variance corresponding to CV=0.05.

Observation model for the delayed catches are modelled using the same hypothesis and the same CV of observation errors.

1.2.3 Catches at sea for sequential distant marine fisheries operating on mixed stocks

For any marine fishery *f* operating on a mixture of SU, likelihood equations consist in logNormal observation errors on the total catches summed over all SU (still based on the same likelihood

approximation method), eventually supplemented by Dirichlet likelihood terms to adjust the proportion of catches allocated to each SU when proportion data are available (Table 7 and Fig. 2 - 6). Observation errors on the total catches and on the proportions are considered independent across fisheries, years and SU.

Observation models based on ICES (2018) data are built independently from the state-space model to estimate logNormal probability distributions of total catches at sea for each fishery f and each year t, with expected mean and variance (in log-scale) denoted $\mathbb{E}_{\log(C_{-})}$ and σ^2_f , respectively. Variances σ^2_f are derived by integrating uncertainty in the catch declaration rates, the proportions of fish of wild origin in the catches, and sampled biological characteristics of the catches including average weight of a fish used to convert catches in weights to number of fish, and scale samples used to separate the two sea-age classes in the catches. An exception is for the WG fishery for which observation errors are considered to be low (ICES 2005b) and fixed to CV = 0.1.

By denoting $C_{f_t} = \sum C_{f_{t,r}}$ the total catches from the state process summed over all SU, the likelihood term for the total catch is modelled as:

(A1.20)
$$\mathbb{E}_{\log(C_{f_t})} \sim Normal(log(C_f), \sigma^2_{f_t})$$

Proportion of catches allocated to each SU are available for the West Greenland fishery (European and North American continental stock groupings) and for the Faroes fishery (1SWm and 1SWnm, and 2SW, for the European continental stock groupings only).

Proportions used to allocate West Greenland catches to each of the 25 SU in North America and Europe (Fig. 5) are derived from a compilation of individual assignment data from scale reading and genetic analyses. Proportions of the total catches at WG are first attributed to European and North American based on scales (1971-1999) and genetics samples (2000-2017) (ICES 2017a; ICES 2017b). Then, proportions attributed to each SU within the European stock group are fixed through time as compiled from ICES (2017b). Within the North American continental stock group, proportions are based on Bradbury et al. (2016a,2016b) that provide estimates of the proportion of fish originated from North American SU for 13 years based on genetic samples. The average value of the 13 years are used for the years without available data.

Proportions used to allocate Faroes catches to European SU are derived from a compilation of assignment data from scale reading (to separate fish from Southern and Northern Europe origin) and genetics data to allocate to each SU (ICES, 2018). Data are not informative enough to account for annual variability and those proportions are considered constant over the time series (Table 7, Fig. 2-4).

When available, observed proportion of each SU in the total catches, denoted $p_{f_{t,r}}^{obs}$ enters into a Dirichlet likelihood modelled as:

(A1.21)
$$(p_{f_{t,r=1}}^{obs}, ..., p_{f_{t,r=2}}^{obs}) \sim Dirichlet (\eta_{sample} \times (p_{f_{t,r=1}}, ..., p_{f_{t,r=2}}))$$

where $p_{f_{tr}} = \frac{c_{f_{tr}}}{c_{f_t}}$ is the proportion of fish from SU r in the total catches calculated from the state process.

When no proportions data are available, only the logNormal likelihood on total catches is used. The hypothesis of a homogeneous exploitation rate among SU replaces the Dirichlet likelihood. As a direct consequence, the proportions of any SU in the catches are set in pro-rata to the abundance among the SU just before the fishery.

Table 1. Summary of the main life stages and transitions of the life cycle model.

Stages	Transitions	Param	Observation equations		
N1: Eggs	$N7_{t} \rightarrow N1_{t}$	Sex-ratio and fecundity	Fixed	No	
	$N10_{t} \rightarrow N1_{t}$				
N2: Total number of Smolt	$N1_{\rm t} \rightarrow N2_{\rm t}$	Freshwater survival (θ_1)	Fixed	No	
		- Average value	Fixed = 0.007		
		- Lognormal noise	Fixed CV = 0,4		
N3: Number of smolts in each age	N3 _{t+1+1}	Proportion of smolt age (P _{smolt})	Fixed	No	
class (6 age classes)	$N2_t \rightarrow N3_{t+1+a}$				
	$N3_{t+1+6}$				
N3tot : Total number of smolts migration year t	$N3_{ m tot}_{ m t}$	T	T	No	
N4 : PFA (Pre Fishery Abundance)	$N3_{\text{tot}_{t}} \rightarrow N4_{t+1}$	Post-smolt survival (θ₃)	Estimated (Multivariate random walk with covariation among SU)	No	
N5 : PFA maturing	$N4_{\rm t} \rightarrow N5_{\rm t}$	Proportion maturing PFA (θ_4)	Estimated (Multivariate	No	
N8 : PFA non maturing	$N4_{\rm t} \rightarrow N8_{\rm t}$		random walk with covariation among SU)		

N5.1 1SW maturing (1 SWm) Faroes fishery	$N5_{\rm t} \rightarrow N5.1_{\rm t}$	Natural mortality (<i>M</i>) Harvest rates	Fixed Estimated (non informative prior)	Catches Faroes 1SWm observed with LogNorma errors and known variance		
N8.1 : 1SW non maturing (1 <i>SWnm</i>) Faroes fishery	$N8_{\rm t} \rightarrow N8.1_{\rm t}$	Natural mortality (<i>M</i>) Harvest rates	Fixed Estimated (non informative prior)	Catches Faroes 1SWnm observed with LogNorma errors and known variance		
N8.2 : 2 <i>SW</i> Faroes fisheries	$N8.1_{\rm t} \rightarrow N8.2_{\rm t+1}$	Natural mortality (<i>M</i>) Harvest rates	Fixed Estimated (non informative prior)	Returns 1SW and 2SW observed with LogNormal errors and known variance		
N6 : Returns $1SW$ N9 : Returns $2SW$	$N5.1_{t} \rightarrow N6_{t}$ $N8.2_{t} \rightarrow N9_{t}$	Natural mortality (<i>M</i>)	Fixed Fixed			
N7 : Spawners 1 <i>SW</i> N10 : Spawners 2 <i>SW</i>	$N6_{t} \rightarrow N7_{t}$ $N9_{t} \rightarrow N10_{t}$	Harvest rates	Estimated (non informative prior)			

		NAC							S.NEAC								
		LB	NF	QB	GF	SF	US	FR	E&W	IR	NI.FO	NI.FB	SC.W	SC.E	IC.SW		
Egg to smolts survival		($\theta_{1_{t,r}} \sim Lc$	gnormal	y distribı	ited with	average	value E	1 = 0.0	07 and	inter-annu	al variabili	ty <i>CV</i> 1 =	0.4			
	$psm_{1,r}$	0	0	0	0	0	0.377	0.917	0.23	0.05	0.38	0.38	0.2	0.05	0		
	$psm_{2,r}$	0	0.041	0.058	0.398	0.6	0.52	0.083	0.75	0.75	0.59	0.59	0.5	0.45	0.05		
Duonaution of smalt ages	$psm_{3,r}$	0.077	0.598	0.464	0.573	0.394	0.103	0	0.02	0.2	0.03	0.03	0.3	0.45	0.73		
Proportion of smolt ages	$psm_{4,r}$	0.542	0.324	0.378	0.029	0.006	0	0	0	0	0	0	0	0.05	0.21		
	$psm_{5,r}$	0.341	0.038	0.089	0	0	0	0	0	0	0	0	0	0	0		
	$psm_{6,r}$	0.04	0	0.01	0	0	0	0	0	0	0	0	0	0	0		
Natural mortality rate (per month) after the PFA stage (for 1SW and 2SW fish)								M :	= 0.03 · 1	month-	1						
Migration duration between stages								S	ee Table	5 and 6							
Number of eggs per fish	$eggs_{1,r}$	1500	3000	468	547	917	200	1552	1350	2040	1972	1972	2000(*)	2000(*)	2501		
(*)	$eggs_{2,r}$	5500	4000	6402	5956	6107	5500	5520	4550	5950	4069	4069	6000(*)	6000(*)	6149		

Table 2. (continuing)

							N.NE	AC				
		IC.NE	SW	NO.SE	NO.SW	NO.MI	NO.NO	FI	RU.KB	RU.KW	RU.AK	RU.RP
Egg to smolts survival		$\theta_{1_{r,t}} \sim \text{Log}$	normaly	distribute	ed with ave	rage value	$\mathbb{E}_{1} = 0.0$	007 and	interannua	al variabilit	y <i>CV</i> 1 = 0).4
	psm _{1,r}	0	0.07	0	0	0	0	0	0	0	0	0
	$psm_{2,r}$	0.09	0.65	0.379	0.379	0.057	0.003	0	0.05	0.1	0.05	0
Duran autian of amale and	$psm_{3,r}$	0.37	0.25	0.524	0.524	0.608	0.263	0.26	0.4	0.6	0.55	0.6
Proportion of smolt ages	$psm_{4,r}$	0.49	0.03	0.094	0.094	0.316	0.583	0.59	0.4	0.3	0.4	0.4
	$psm_{5,r}$	0.05	0	0.004	0.004	0.019	0.138	0.14	0.1	0	0	0
	$psm_{6,r}$	0	0	0	0	0	0.012	0.01	0.05	0	0	0
Natural mortality rate (per after the PFA stage (for 18 2SW fish)						1	M = 0.03 ·	month ⁻	1			
Migration duration betwee	en stages						See Table	5 and 6				
Number of eggs per fish	$eggs_{1,r}$	1974	1500	887	887	1050	450	600	350	2700	450	450
(*)	$eggs_{2,r}$	7350	4200	4944	4944	5128	6673	10010	10000	4200	9600	10500

Table 3. Parameters of the marine phase drawn in non-informative prior and for which update from the data is expected. Note that harvest rates for the West Greenland and Faroes fishery are parameterized on the logit scale and written as the sum of a grand mean and yearly, region-specific and residual effects. Such a parameterization revealed needed to avoid miss fit of the proportions used to allocate the total catches to the different SU.

Note: Two different matrices for the post-smolt survival (Σ_{θ_2}) and for the proportion of fish maturing as 1SW (Σ_{θ_2})

 $\sum_{8^{-1}} \sim Wishart(\Omega, \delta)$ with scale matrix Ω set as the N×N identity matrix and δ the degree of freedom set to N

Exploitation rate of West Greenland and Faroes mixed stock fisheries (for any year t and stock unit r)

$$\begin{split} logit(h_{\mathrm{f_{t,r}}}) \sim logit_h_mu_{\mathrm{f}} + logit_h_time_{\mathrm{f,t}} + logit_h_su_{\mathrm{f,r}} + logit_h_res_{\mathrm{f,t,r}} \\ logit_h_mu_{\mathrm{f}} \sim N(-5,\!4) \\ logit_h_time_{\mathrm{f,t}} \sim N(0,\!4) \\ logit_h_su_{\mathrm{f,r}} \sim N(0,\!4) \\ logit_h_res_{\mathrm{f,t,r}} \sim N(0,\!4) \end{split}$$

Exploitation rate of other fisheries f (NA marine fisheries and homewater fisheries) (for any year t and stock unit r)

 $h_{f_{tr}} \sim Beta(1,2)$

Table 5. Summary of the duration among stages and the sequential fisheries (operating on mixed stocks at sea and homewater fisheries) for stock units in the North American continental stock grouping (Source: ICES 2018; Prévost et al., 2009).

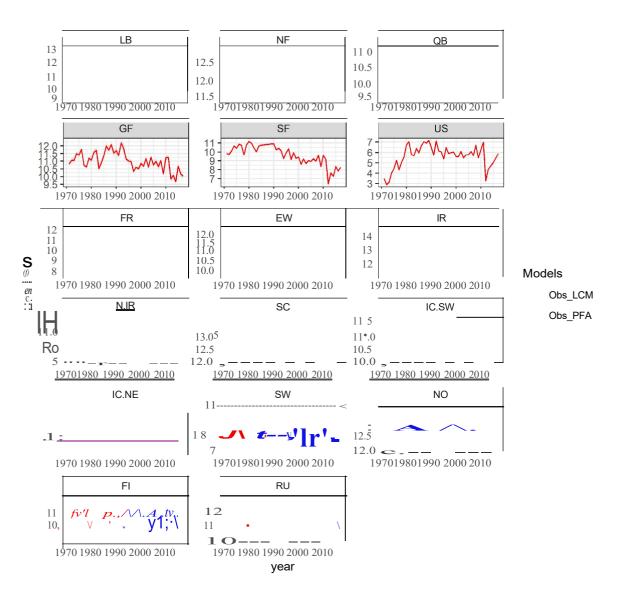
North American continental stock grouping										
Stages/Fisheries	Migration duration	Exploitation rate								
PFA maturing										
\downarrow	7 months									
1SWm NFDL/LB/SPM Fisheries		Variable among years (NFDL zone 3-7) Homogeneous among SU (NFDL zone 8-14, LAB, SPM) Specific estimate for SU = Labrador + homogeneous among all other SU								
↓ D · LCW	1 month	for SU = Labrador + nomogeneous among all other SU								
Returns 1SW	0	W. H. GH								
1SW homewater Fishery ↓ Spawners 1SW	0	Variable among SU								
PFA non maturing										
\downarrow	7 months									
1SWnm NFDL/LB Fisheries		Variable among years Homogeneous among SU								
\downarrow	2 months	Ç Ç								
1SWnm West Greenland Fishery		Variable among years and SU + data to allocate catches among SU. Allocation in two steps 1) prop. to allocate fish from North America / Europe; 2) prop. to allocate North American fish among SU in NA								
\downarrow	8 months									
2SWm NFDL/LB/SPM Fisheries		Variable among years (NFDL zone 3-7): Homogeneous among SU (NFDL zone 8-14, LAB, SPM): Specific estimate for SU = Labrador + homogeneous among all other SU								
\downarrow	1 month	101 50 Labrador - nomogeneous among an other 50								
Returns 2SW ↓	0									
2SW homewater Fishery	0	Variable among years and SU								
Spawners 2SW										

Table 6. Summary of the duration among stages and the sequential fisheries (operating on mixed stocks at sea and homewater fisheries) for stock units in the Southern and Northern European continental stock groupings (Source: ICES 2018; Potter, 2016).

Southern and Northern Europe continental stock groupings											
Stages/Fisheries	Migration duration	Exploitation rate									
PFA maturing											
↓	0.5 months										
1SWm Faroes Fishery		Variable among years and SU									
•		+ data to allocate catches among SU									
\downarrow	7.5 months										
Returns 1SW		Variable among years and SU + data to allocate catches among SU									
\	0	data to anocate catches among 50									
1SW homewater Fishery		Variable among years and SU									
↓	0										
Spawners 1SW											
PFA non maturing											
\	0.5 months										
1SWnm Faroes Fishery		Variable among years and SU									
15 William Larges Tishery	0.5	+ data to allocate catches among SU									
V	8.5 months	Variable among years and SII									
		Variable among years and SU + data to allocate catches among SU. Allocation									
1SWnm West Greenland		two steps: 1) prop. to allocate fish from Europe									
Fishery		North America; 2) prop.to allocate European fis									
ı		among SU in Europe									
↓	5 months	Variable among years and SU									
2SWm Faroes Fishery		+ data to allocate catches among SU									
\downarrow	3.5 months										
Returns 2SW											
\	0	**									
2SW homewater Fishery	0	Variable among years and SU									
Spawners 2SW	0										

Table 7. Proportions to allocate the total catches among different SU from Southern and Northern Europe in the Faroes fishery. Proportions sum to 1 for each fishery and are considered constant over time (Source: ICES 2018). Fish originated from North America are not harvested in the Faroes fishery.

S.NEAC						N.NEAC													
	FR	E&W	IR	NI.FO	NI.FB	SC.W	SC.E	IC.SW	IC.NE	SW	NO.SE	NO.SW	NO.MI	NO.NO	FI	RU.KB	RU.KW	RU.AK	RU.RP
1SW maturing	0.021	0.083	0.328	0.053	0.013	0.103	0.268	0.014	0.006	0.001	0.015	0.003	0.026	0.018	0.010	0.008	0.028	0.001	0.001
1SW non maturing	0.007	0.054	0.027	0.004	0.001	0.064	0.129	0.005	0.006	0.011	0.097	0.033	0.185	0.136	0.05	0.022	0.055	0.024	0.083
2SW	0.007	0.054	0.027	0.004	0.001	0.064	0.129	0.005	0.006	0.011	0.097	0.033	0.185	0.136	0.05	0.022	0.055	0.024	0.083





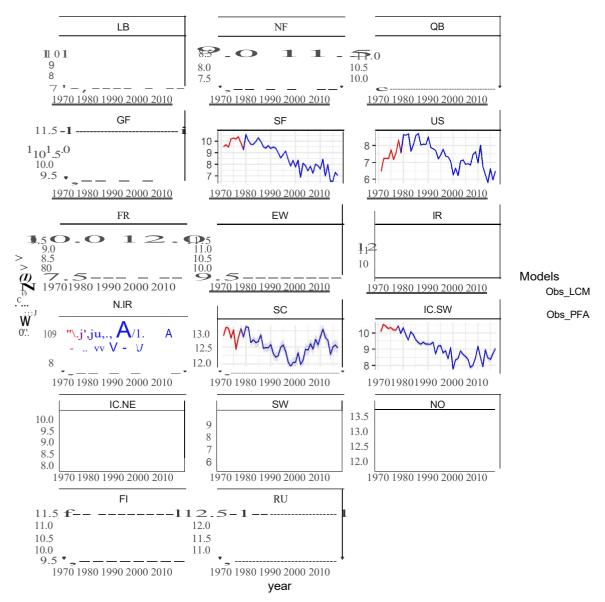


Figure 14: Probability distributions (median, quantiles 5% and 95%) of the number of fish returning as 1SW and 2SW for SU of North America, Southern Europe and Northern Europe for PFA (blu) and LCM (red) (Source: ICES 2018).

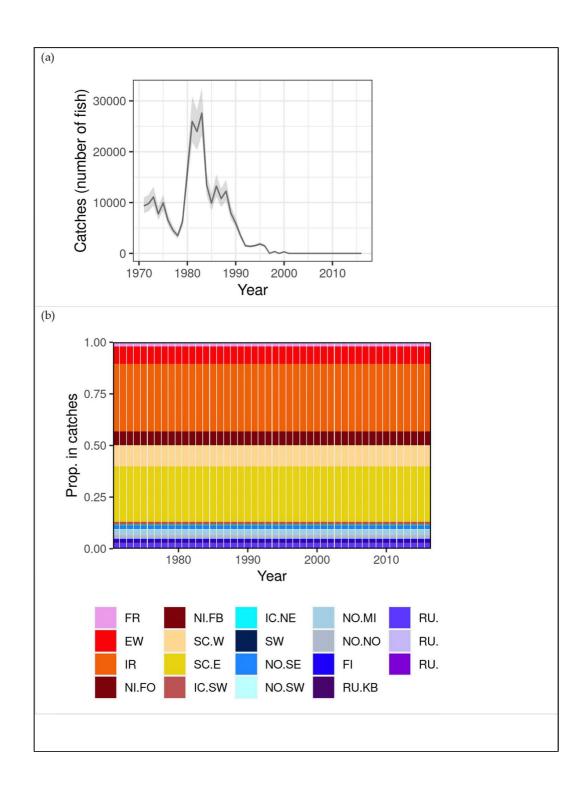


Figure 2 : (a) Time series of total catches of the 1SW maturing stage in the Faroes fishery (Source: ICES 2015b); (b) proportions of the catches attributed to South European and North European stock units (Source: ICES 2015b). (Proportions attributed to SU from NA are 0).

Figure 3: (a) Time series of total catches of the 1SW maturing stage in the Faroes fishery (Source: ICES 2015b); (b) proportions of the catches attributed to South European and North European stock units (Source: ICES 2015b). (Proportion attributed to SU from NA are 0).

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Figure 4: (a) Time series of total catches of the 2SW maturing stage in the Faroes fishery (Source: ICES 2015b); (b) proportions of the catches attributed to South European and North European stock units (Source: ICES 2015b). (Proportion attributed to SU from NA are 0).

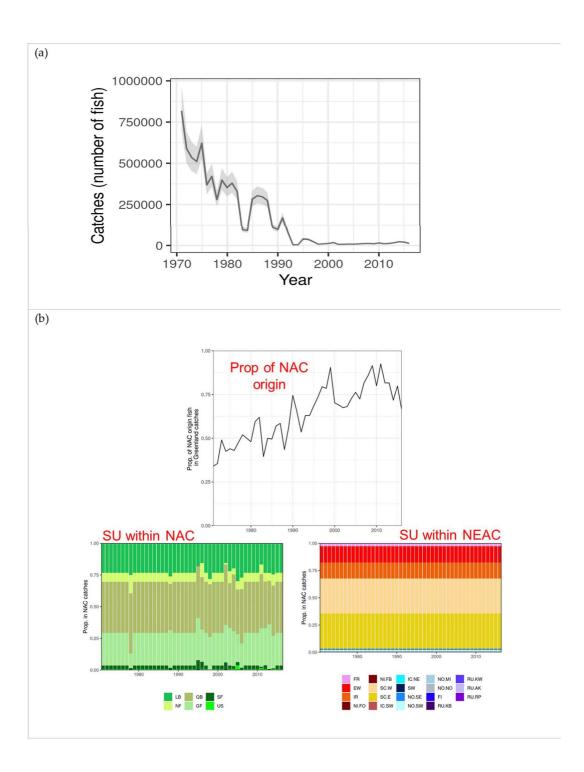


Figure 5: (a) Time series of total catches of 1SW non-maturing in the West Greenland fishery (Source: ICES 2018); (b) Proportions of the catches attributed to North American / European stock complex (top), attributed to North American stock units within North American stock complex (bottom left) and attributed to European stock units within European stock complex (bottom right). Genetics data (Bradbury et al (2016)) provide estimates of the proportion of fish originated from the 7 SU of North America (Olmos et al 2019). Total catches and proportions were updated from Olmos et al. (2019) to account for fish of NE SU.

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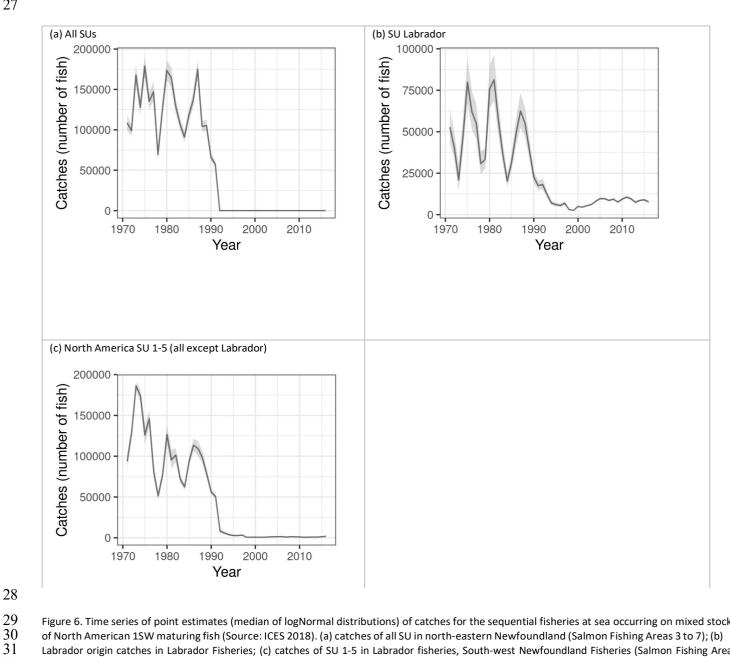


Figure 6. Time series of point estimates (median of logNormal distributions) of catches for the sequential fisheries at sea occurring on mixed stocks of North American 1SW maturing fish (Source: ICES 2018). (a) catches of all SU in north-eastern Newfoundland (Salmon Fishing Areas 3 to 7); (b) Labrador origin catches in Labrador Fisheries; (c) catches of SU 1-5 in Labrador fisheries, South-west Newfoundland Fisheries (Salmon Fishing Areas 8 to 14A) and in the Saint Pierre and Miguelon fisheries.

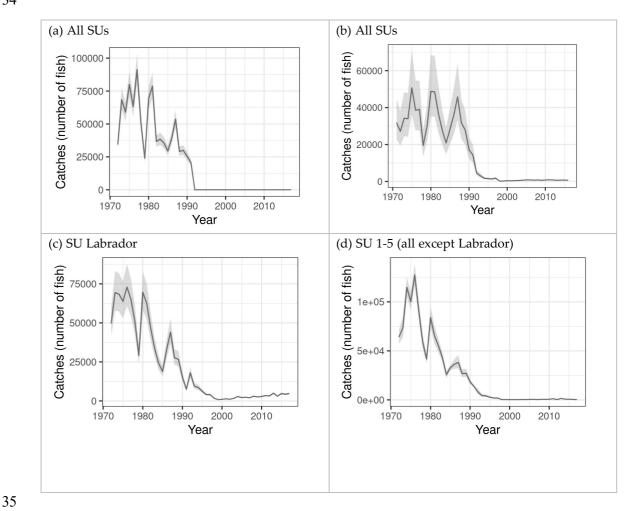


Figure 7. (Continuing). Time series of distribution (median and quantiles 5% and 95% of logNormal distributions) of catches for the sequential fisheries at sea occurring on mixed stock fisheries, on North American 1SW non-maturing fish (Source: ICES 2018). (a) 1SW catches for all SUs in north and eastern Newfoundland (Salmon Fishing Areas 3 to 7); (b) 2SW catches for all SUs in north and eastern Newfoundland (Salmon Fishing Areas 3 to 7); (c) 2SW Labrador (SU 6) origin catches in the Labrador fisheries; (d) 2SW catches of SU 1-5, in Labrador fisheries, south and west Newfoundland Fisheries (Salmon Fishing Areas 8 to 14A) and in the Saint Pierre and Miguelon fisheries.

7 SUPP.MAT.II: Comparison between the PFA and life cycle modelling framework

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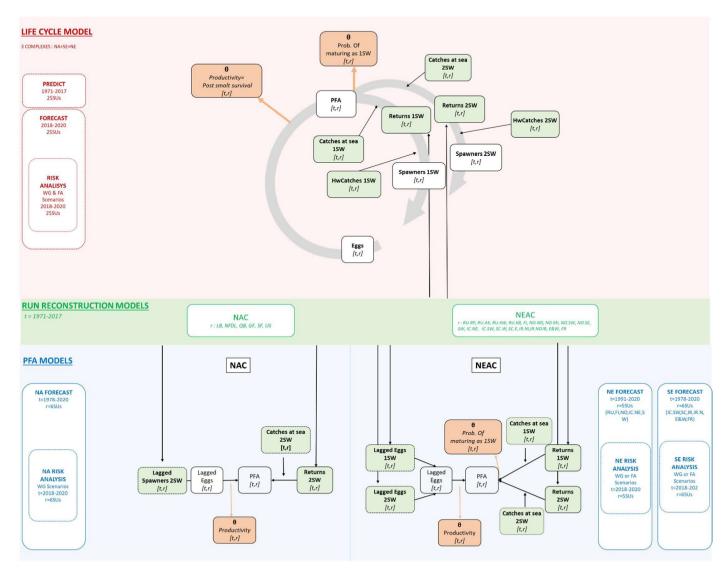


Figure SII.15: Structure of the stage-based life cycle model (red) and the PFA models (green). Run reconstructions models (green) are observation models generating input data for both PFA and life cycle models

Table SII.2: Comparison of the model resolution, the likelihood, the hypothesis of the parameters to estimate, and the information priors used in PFA and life cycle model

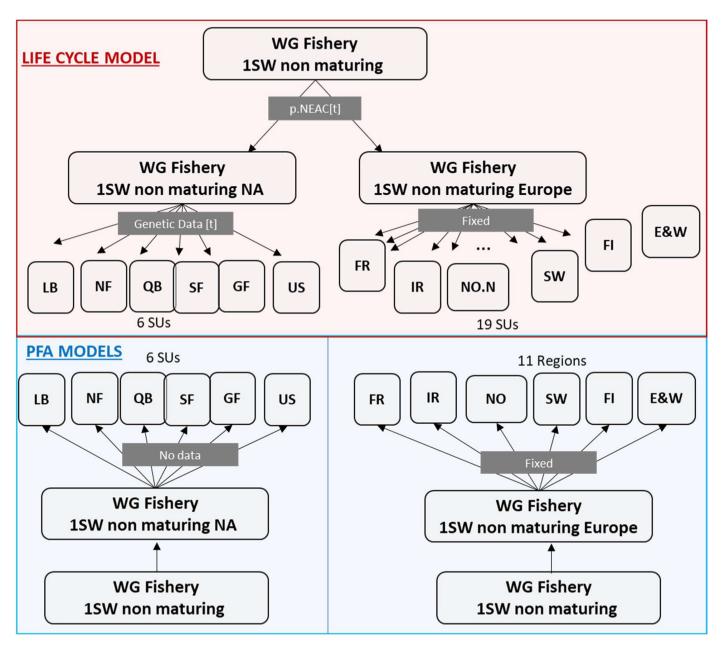
			PFA NA FORECAST	PFA Europe FORECAST		LIFE CYCLE
				Southern Europe	Northern Europe	LIFE CICLE
5	Temporal resolution [t]		1978-2017	1978-2017	1991-2017	1971-2017
Model Resolution	Spatial resolution [r]		6 SUs	6 Regions: Fr, E&W, SC, IR, IC.SW, N.IR	5 Regions: IC.NE, SW, NO,RU,FI	25 SUs
ž	Life History at sea [a]		1SW	1SW & 2SW	1SW & 2SW	1SW & 2SW
	Abundances of Returns [t,r,a]		LogNormal Distibution	LogNormal Distribution	LogNormal Distribution	LogNormal Distribution
	HomeWater Catches (and delayed Spawners) [t,r,a]		-	-	-	LogNormal Distribution
		Catches in the Faroes fisheries (1SWm, 1SWnm, 2SW) [t,a]	-	No Likelihood Prior Distributions	No Likelihood Prior Distributions	LogNormal Distribution
		Prop. of catches attributed to SUs in the Faroes fisheries (1SWm, 1SWnm, 2SW) [t,r,a]	-	Fixed	Fixed	Dirichlet Distribution
 B		Catches in the LAB/NFLD/SPM fisheries (1SWm, 1SWnm, 2SW) [t,a]	No Likelihood Prior Distributions	-	÷	LogNormal Distribution
Likelihood	Catches at sea	Prop. of catches attributed to SUs in the LAB/NFLD/SPM fisheries (1SWm, 1SWnm, 2SW)	Homogeneous exploitation rates (no data, except LB) based on proportion of regional abundance	-	-	Homogeneous exploitation rates (no data)
		Catches in the West Greenland fisheries [t,a]	No Likelihood Prior Distributions	No Likelihood Prior Distributions	No Likelihood Prior Distributions	Dirichlet Distribution
		Prop. of catches attributed to SUs in the 1SWm West Greenland fisheries [t,r,a]	Homogeneous exploitation rates (no data) based on proportion of regional abundance	Fixed and stationnary	Fixed and stationnary	SU-specific genetic information data to allocate catches accross year Dirichlet Distribution

Table SII.3 (continued): Comparison of the model resolution, the likelihood, the hypothesis of the parameters to estimate, and the information priors used in PFA and life cycle model

		PFA NA FORECAST	PFA Europe FORECAST		LIFE CYCLE
			Southern Europe	Northern Europe	LIFE CYCLE
Estimated parameters	Productivity[t,r]	Multivariate random walks in the log scale, with covariations among all stock units	Random walks in the log scale. No covariance structure among SUs	Random walks in the log scale. No covariance structure among Sus	Multivariate random walks in the log scale. Random variations are drawn from multivariate normal distributions with variance-covariance
	Proportion of fish maturing as 1SW [t,r]	-	Random walks in the logit scale No covariance structure among SUs	Random walks in the logit scale. No covariance structure among Sus	Multivariate random walks in the log scale. Random variations are drawn from multivariate normal distributions with variance-covariance
	Fisheries exploitation rates[t,r,a]	derived	derived	derived	Estimated with a prior distribution
	Pre-Fishery abundance[t,r]	Random effect	derived	derived	derived
Variables and Parameters fixed or drawn in tight informative priors	Number of eggs per fish	Fixed	Fixed	Fixed	Fixed
and Parameters fixed or tight informative priors	Proportion of smolt ages	-	-	-	Informative prior
aramete	Natural mortality rate (per month) after the PFA stage (for 1SW and 2SW fish)	Fixed	Fixed	Fixed	Informative prior
s and Patight in	Migration duration between stages	Fixed	Fixed	Fixed	Fixed
Variable	Lagged Eggs/Spawners	Normal distribution	Normal distribution	Normal distribution	Information from Lagged Eggs/Spawners is accounted by the likelihood of homewater catches

Table SII.4: Comparison between the hypothesis used to forecast and carry out the risk analysis using PFA and life cycle models

	PFA NA FORECAST	PFA Europe FORECAST		LIFE CYCLE
		Southern Europe	Northern Europe	LIFE CICLE
Risk Analysis	Probability of meeting region specific 2SW eggs deposition CLs	Probability of meeting region specific 1SW and 2SW eggs deposition CLs	Probability of meeting region specific 1SW and 2SW eggs deposition CLs	Probability of meeting region specific 1SW and 2SW eggs deposition CLs
Forecasted years	2018-2020	2018-2020	2018-2020	2018-2020
Fishing Scenarios in Faroes Fisheries	-	TAC = 0, 500, 1000, 1500, 2000, 2500	TAC = 0, 500, 1000, 1500, 2000, 2500	TAC = 0, 500, 1000, 1500, 2000, 2500
Fishing Scenarios in Faroes Fisheries	TAC = 0, 500, 1000, 1500, 2000, 2500	TAC = 0, 500, 1000, 1500, 2000, 2500	TAC = 0, 500, 1000, 1500, 2000, 2500	TAC = 0, 500, 1000, 1500, 2000, 2500
Fisheries Catches at sea and proportion to allocate catches to Sus for years 2018-2020	Fixed to the average of the last five years of the time series of data (2013-2017)	Fixed to the average of the last five years of the time series of data (2013-2017	Fixed to the average of the last five years of the time series of data (2013-2017	Fixed to the average of the last five years of the time series of data (2013-2017
Homewater catches	-	-	-	Fixed to the average of the last five years of the time series of data (2013-2017



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8 Supp.Mat.III: RESULTS

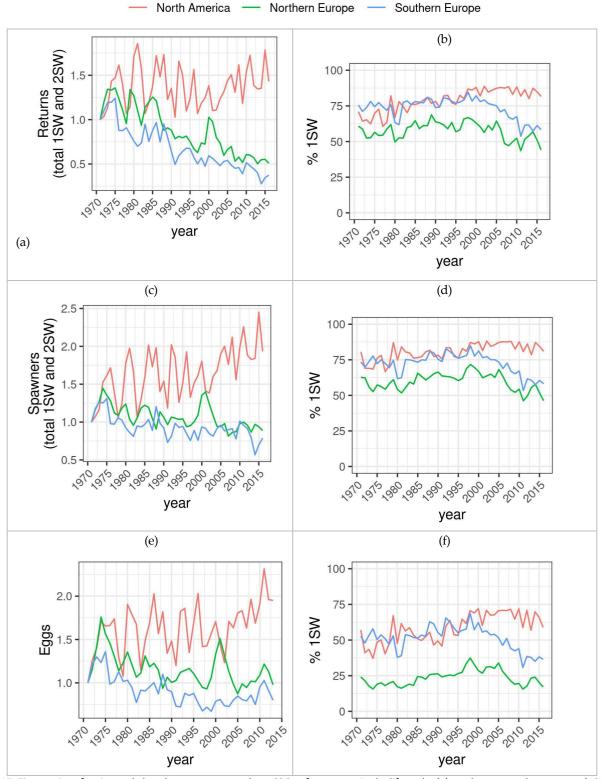


Figure SIII.17: Time series of estimated abundances aggregated per CSG at four stages in the life cycle. (a) total returns to homewater (1SW + 2SW); (b) proportion of 1SW in returns; (c) total spawners (1SW + 2SW); (d) proportion of 1SW in spawners; (e) total egg deposition by spawners; (f) proportion of eggs spawned by 1SW. Trend lines are medians of marginal posterior distributions. Abundances are standardized to the first year values.

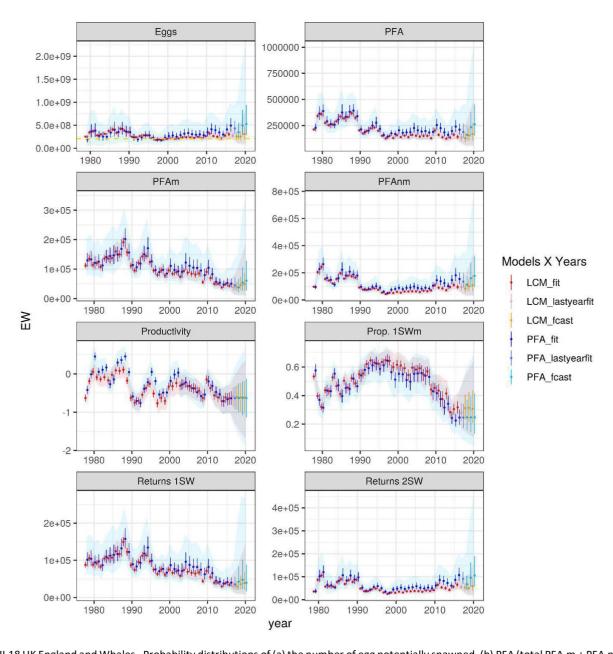


Figure SIII.18 UK England and Whales - Probability distributions of (a) the number of egg potentially spawned, (b) PFA (total PFA.m + PFA.nm), (c) PFA.m, (d) PFA.nm, (e) Productivity, () Proportion of fish maturing as 1SW, (g) Returns 1SW, and Returns (2SW). Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red: Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland and Faroes)

Figure SIII.19 Finland - Probability distributions of (a) the number of egg potentially spawned, (b) PFA (total PFA.m + PFA.nm), (c) PFA.m, (d) PFA.nm, (e) Productivity, () Proportion of fish maturing as 1SW, (g) Returns 1SW, and Returns (2SW). Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red: Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland and Faroes)

Figure SIII.20 France - Probability distributions of (a) the number of egg potentially spawned, (b) PFA (total PFA.m + PFA.nm), (c) PFA.m, (d) PFA.nm, (e) Productivity, () Proportion of fish maturing as 1SW, (g) Returns 1SW, and Returns (2SW). Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red: Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland and Faroes)

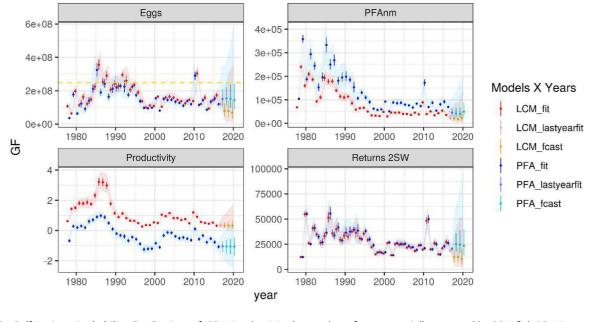


Figure SIII.21 Gulf Region - Probability distributions of 2SW Productivitythe number of egg potentially spawned by 2SW fish 2SW Returns, and PFA.nm. Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red: Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland)

Eggs

PFA

Figure SIII.22 Iceland North-east - Probability distributions of (a) the number of egg potentially spawned, (b) PFA (total PFA.m + PFA.nm), (c) PFA.m, (d) PFA.nm, (e) Productivity, () Proportion of fish maturing as 1SW, (g) Returns 1SW, and Returns (2SW). Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red: Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland and Faroes)

Figure SIII.23 Iceland South West - Probability distributions of (a) the number of egg potentially spawned, (b) PFA (total PFA.m + PFA.nm), (c) PFA.m, (d) PFA.nm, (e) Productivity, () Proportion of fish maturing as 1SW, (g) Returns 1SW, and Returns (2SW). Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red: Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland and Faroes)

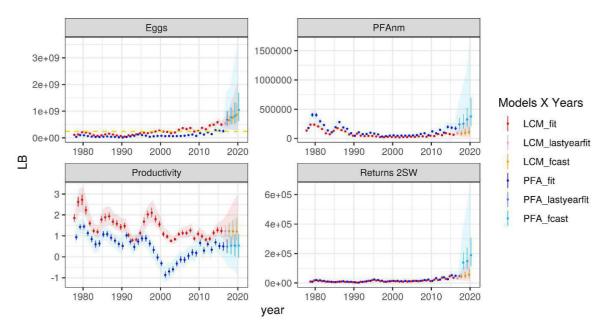


Figure SIII.25 Labrador - Probability distributions of (a) the number of egg potentially spawned by 2SW fish 2SW Returns, (b) and PFA.nm (c) productivity of 2SW fish, (d) Returns 2SW. Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red : Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland)

Figure SIII.26 UK Northern Ireland - Probability distributions of (a) the number of egg potentially spawned, (b) PFA (total PFA.m + PFA.nm), (c) PFA.m, (d) PFA.nm, (e) Productivity, () Proportion of fish maturing as 1SW, (g) Returns 1SW, and Returns (2SW). Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red: Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland and Faroes)

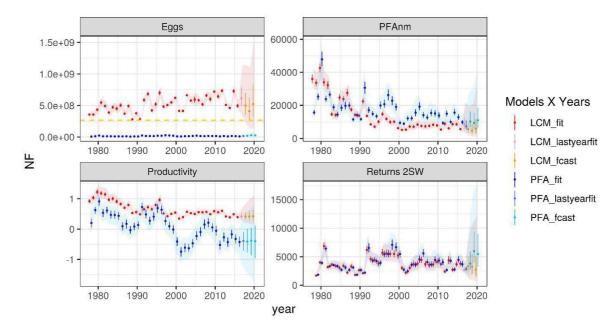


Figure SIII.27 Newfoundland - Probability distributions of (a) the number of egg potentially spawned by 2SW fish 2SW Returns, (b) and PFA.nm (c) productivity of 2SW fish, (d) Returns 2SW. Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red : Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland)

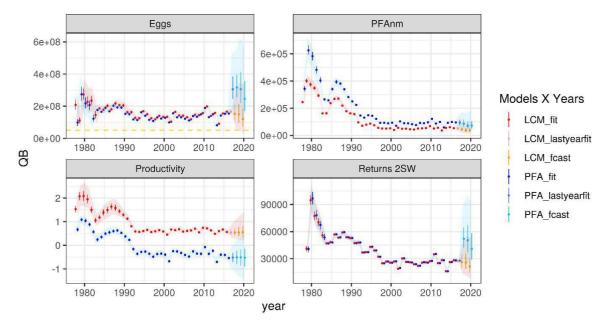


Figure SIII.29 Quebec - Probability distributions of (a) the number of egg potentially spawned by 2SW fish 2SW Returns, (b) and PFA.nm (c) productivity of 2SW fish, (d) Returns 2SW. Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red : Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland)

Figure SIII.30 Russia - Probability distributions of (a) the number of egg potentially spawned, (b) PFA (total PFA.m + PFA.nm), (c) PFA.m, (d) PFA.m, (e) Productivity, () Proportion of fish maturing as 1SW, (g) Returns 1SW, and Returns (2SW). Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red: Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland and Faroes)

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Figure SIII.31 Scotland - Probability distributions of (a) the number of egg potentially spawned, (b) PFA (total PFA.m + PFA.nm), (c) PFA.m, (d) PFA.nm, (e) Productivity, () Proportion of fish maturing as 1SW, (g) Returns 1SW, and Returns (2SW). Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red: Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland and Faroes)

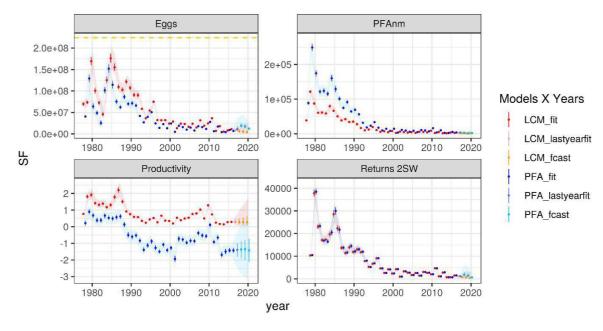


Figure SIII.32 Scotia-Fundy - Probability distributions of 2SW Productivitythe number of egg potentially spawned by 2SW fish 2SW Returns, and PFA.nm. Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red: Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland)

Figure SIII.33 Sweden - Probability distributions of (a) the number of egg potentially spawned, (b) PFA (total PFA.m + PFA.nm), (c) PFA.m, (d) PFA.nm, (e) Productivity, () Proportion of fish maturing as 1SW, (g) Returns 1SW, and Returns (2SW). Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red: Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland and Faroes)

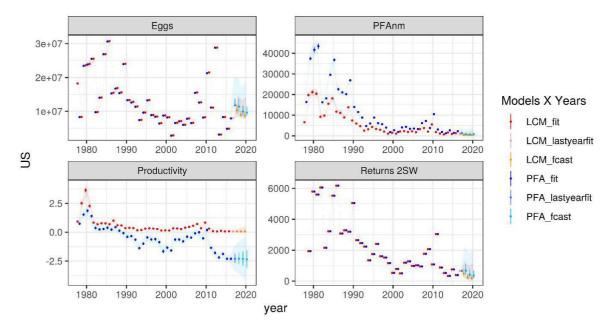


Figure SIII.34: USA - Probability distributions of 2SW Productivitythe number of egg potentially spawned by 2SW fish 2SW Returns, and PFA.nm. Thick point is the median and line represent the 95% posterior credibility interval. Blue: PFA model; Red: Life cycle model (LCM); Dark color: historical time series; Light colors: Forecasted years (under the scenario of no catches at West Greenland)