



Original Article

Embedding stock assessment within an integrated hierarchical Bayesian life cycle modelling framework: an application to Atlantic salmon in the Northeast Atlantic

Félix Massiot-Granier^{1,2,3*}, Etienne Prévost^{2,3}, Gérald Chaput⁴, Ted Potter⁵, Gordon Smith⁶, Jonathan White⁷, Samu Mäntyniemi⁸, and Etienne Rivot¹

¹Agrocampus Ouest, UMR 0985 ESE Ecologie et Santé des Ecosystèmes, Rennes, France

²INRA, UMR 1224 ECOBIOP Aquapôle, 64310 Saint Pée-sur-Nivelle, France

³Université de Pau & Pays de l'Adour, UMR 1224 ECOBIOP, UFR Sciences et Techniques Côte Basque, 64600 Anglet, France

⁴Fisheries & Oceans Canada, Moncton, NB E1C 9B6, Canada

⁵Centre for Environment, Fisheries and Aquaculture Science Lowestoft Laboratory, Suffolk, United Kingdom

⁶Marine Scotland Science, Inchbraoch House, South Quay, Ferryden, Montrose, Angus DD10 9SL, UK

⁷Inst Marine, Fisheries Sci Serv, Oranmore, Galway, Ireland

⁸Fisheries and Environmental Management Group (FEM), Department of Environmental Sciences, University of Helsinki, Helsinki, Finland

*Corresponding author: tel: +33 2 23 48 54 56; fax: +33 2 23 48 55 35, e-mail: fmassiot@agrocampus-ouest.fr

Massiot-Granier, F., Prévost, E., Chaput, G., Potter, T., Smith, G., White, J., Mäntyniemi, S., and Rivot, E. Embedding stock assessment within an integrated hierarchical Bayesian life cycle modelling framework: an application to Atlantic salmon in the Northeast Atlantic. – ICES Journal of Marine Science, 71: 1653–1670.

Received 6 June 2013; accepted 19 December 2013; advance access publication 13 February 2014.

We developed a hierarchical Bayesian integrated life cycle model for Atlantic salmon that improves on the stock assessment approach currently used by ICES and provides some interesting insights about the population dynamics of a stock assemblage. The model is applied to the salmon stocks in eastern Scotland. It assimilates a 40-year (1971–2010) time-series of data compiled by ICES, including the catches in the distant water fisheries at Faroes and West Greenland and estimates of returning fish abundance. Our model offers major improvements in terms of statistical methodology for A. salmon stock assessment. Uncertainty about inferences is readily quantified in the form of Bayesian posterior distributions for parameters and abundance at all life stages, and the model could be adapted to provide projections based on the uncertainty derived from the estimation phase. The approach offers flexibility to improve the ecological realism of the model. It allows the introduction of density dependence in the egg-to-smolt transition, which is not considered in the current ICES assessment method. The results show that this modifies the inferences on the temporal dynamics of the post-smolt marine survival. In particular, the overall decrease in the marine survival between 1971 and 2010 and the sharp decline around 1988–1990 are dampened when density dependence is considered. The return rates of smolts as two-sea-winter (2SW) fish has declined in a higher proportion than return rates as one-sea-winter (1SW) fish. Our results indicate that this can be explained either by an increase in the proportion maturing as 1SW fish or by an increase in the mortality rate at sea of 2SW fish, but the data used in our analyses do not allow the likelihood of these two hypotheses to be gauged.

Keywords: Atlantic salmon, complex of populations, hierarchical Bayesian model, integrated life cycle, mixed stock fishery, North Atlantic, pre-fishery abundance, stock assessment.

Introduction

Atlantic salmon (*Salmo salar* L.) is an anadromous fish with a life cycle that includes spawning in freshwater, up to 6 years of in-river juvenile rearing, followed by a migration to sea to feeding grounds, and

typically 1–4 years of feeding before maturation and return to fresh-water for spawning (Aas *et al.*, 2011). Atlantic salmon populations are assessed and managed at several scales, from river-specific stock units (Chaput *et al.*, 1999; Prévost and Chaput, 2001; Ó Maoiléidigh

et al., 2004), to national or broader regional population complexes that combine populations supposed to share common demographic trends (Potter *et al.*, 2004; Michielsens *et al.*, 2008; Chaput, 2012).

Atlantic salmon that reproduce in rivers of eastern North America and Northeast Atlantic countries of Europe undertake wide-ranging migrations to common feeding grounds in the North Atlantic, where they are exposed to common marine environmental conditions (Friedland *et al.*, 2013; Mills *et al.*, 2013). When present at the West Greenland feeding grounds and in the vicinity of the Faroe Islands, they may be harvested in mixed stock fisheries, referred to as the distant water fisheries (Chaput, 2012; ICES, 2012). To manage those fisheries, advice is provided by the International Council for the Exploration of the Sea (ICES) (ICES, 2013), based on a forecast of A. salmon abundance prior to the high seas fisheries exploitation (the Pre Fishery Abundance, i.e. post-smolt abundance on 1 January of the first winter at sea prior to any fisheries, hereafter denoted PFA). A fixed escapement strategy has been adopted with the objective of achieving the spawner requirements for the contributing stocks on both sides of the Atlantic Ocean (Crozier *et al.*, 2003; Chaput, 2012).

Presently, ICES has developed models for population assessment at the scale of three multinational stock complexes: the Northwest stock complex (NW) aggregating stocks of Northeast America, and the southern and northern Northeast stock complexes (S.NE and N.NE, respectively), aggregating stocks of Western Europe, Iceland and Russia (Chaput, 2012; ICES, 2013). For each of the three stock complexes assessment, models similar to classical cohort analysis have been developed. The baseline sources of information are the homewater catches, which are scaled by harvest and declaration rates to estimate annual returns to homewaters. Starting from the return estimates, the abundance of the cohort is then reconstructed up to the PFA stage using data for high seas catches and a fixed natural mortality rate (Rago *et al.*, 1993; Potter *et al.*, 2004; Chaput, 2012). Abundance at PFA stage is disaggregated into maturing and non-maturing components, associated with the two most important sea-age classes of returns, fish that return after one (1SW) and two winters (2SW) spent at sea, respectively. Stock productivity and its evolution over time is assessed by the ratio between the PFA of each year (the recruitment variable) and the spawning stock size (spawners and eggs for NW and NE stock complexes, respectively). The latter is directly derived from the estimated returns minus the homewater catches. For each of the three stock complexes, various statistical models [including phase shift or autocorrelated random walk; (Crozier *et al.*, 2003; Chaput *et al.*, 2005; Chaput, 2012)] have been developed to evaluate the variability of the stock productivity over time (beginning in 1971) and to forecast abundance up to three years forward. These models are incorporated in a risk analysis framework to assess the consequences of mixed stock marine fisheries on the returns at a stock complex scale (Chaput *et al.*, 2005; ICES, 2013).

In addition to their use for providing catch advices, results of these assessment models have been used to analyse how abundance and productivity have changed over time, and to characterize associations with ecosystem conditions throughout the North Atlantic Ocean (Beaugrand and Reid, 2012; Friedland *et al.*, 2013; Mills *et al.*, 2013). Both the abundance of A. salmon and the stock productivity have been declining throughout the species range. Decline in stock productivity has been attributed to a decline in marine survival (Aas *et al.*, 2011), and recent analyses suggest a response of survival to changes in marine thermal conditions and in the lower trophic levels of the marine ecosystem of A. salmon (Beaugrand and Reid, 2012; Friedland *et al.*, 2013; Mills *et al.*, 2013).

Assessment models also show that the abundance of the 2SW component of returns has declined more than the 1SW component, for both the NW and the S.NE stock complexes (ICES, 2013), but the mechanisms that would produce this differential decline for the two sea-age classes have not been analysed.

The models developed to date assimilate extensive datasets and provide some fundamental concepts for quantitative assessment of A. salmon stocks at the scale of the Atlantic Ocean. However, they also suffer from methodological weaknesses and lack of flexibility that should be addressed in order to improve the A. salmon population assessments.

First, the statistical methodology could be improved. The models used by ICES do not explicitly represent the dynamic link between PFA and subsequent spawning potential, and as a result are susceptible to time-series bias (Walters, 1985; Caputti, 1988; Su and Peterman, 2012), which may in turn result in biased estimates of stock productivity.

Second, the modelling approach lacks flexibility, which precludes the assimilation of the large amount of ecological knowledge and available data on A. salmon population dynamics. The complex life cycle of A. salmon is only coarsely represented. Strong hypotheses on the demographic processes are implicitly made, and the method does not allow estimating the extent to which results depend upon these hypotheses to be assessed. In particular, the transition between the spawning potential and the post-smolt stage (PFA) uses a single productivity parameter that integrates the demographic processes of the freshwater phase (egg-to-smolt) and the first months of the post-smolt marine phase. The model implicitly assumes that any changes in the stock productivity over time are a response to changes in the marine phase, without taking into account any effect of compensation in the freshwater phase. Available knowledge and data about the density-dependent egg-to-juvenile survival (Jonsson *et al.*, 1998; Elliott, 2001) cannot be used because the freshwater phase is not separated out. Also, the maturing and non-maturing components of the PFA are directly estimated from the returns of 1SW and 2SW fish, respectively, assuming a constant natural mortality rate at sea between PFA and returns. The implicit hypothesis is that changes in the relative proportion of the two sea-age classes in the returns result from changes in the proportion of maturing PFA and not in the mortality rate at sea, although both hypotheses are still discussed in the literature (Chaput, 2012).

To address these deficiencies, we embedded the stock assessment model developed by ICES within an integrated hierarchical Bayesian life cycle approach. Hierarchical Bayesian Models (HBMs) are an effective approach for incorporating complex demographic processes within statistical models assimilating multiple sources of noisy and incomplete data (Thomas *et al.*, 2005; Buckland *et al.*, 2007; Parent and Rivot, 2012). HBMs have been applied to age- and stage-structured fish population dynamic models (Rivot *et al.*, 2004; Ruiz *et al.*, 2009; Swain *et al.*, 2009) and fish stock assessment (Millar and Meyer, 2000; Lewy and Nielsen, 2003; Fleischman *et al.*, 2013; Rochette *et al.*, 2013). They provide a fair appraisal of the uncertainty in estimates and predictions (McAllister *et al.*, 1999; Harwood and Stokes, 2003) and have the potential to improve the biological realism of fish stock assessment models (Kuparinen *et al.*, 2012). HBMs have already been applied to the A. salmon life cycle at the scale of single-river stocks (Rivot *et al.*, 2004) and are currently used for stock assessment at the scale of the Baltic Sea (Michielsens *et al.*, 2008).

The focus of this paper is on the improvements to the methodology and not to the data; the model therefore uses the same

dataset as the assessment model currently used by ICES (ICES, 2013). As an illustrative case, the model is applied to a subset of the ICES data, accounting for the salmon stocks in the eastern Scotland stock complex, the largest regional component of the S.NE stock complex assessed by ICES. We demonstrate how the flexibility of the approach has the potential to improve the population assessment. The Bayesian framework offers a consistent probabilistic rationale for estimating trends in abundance and demographics together with the associated uncertainty. As HBMs work by separating out the population dynamics (process equations) from the data assimilation (observation equations and informative priors), the different hypotheses on the population dynamics are explicit and can be assessed without changing the data assimilation scheme. We rely on this flexibility to assess the extent to which estimated trends in the abundance, and key transition rates, are sensitive to changes in some demographic hypotheses, and how this may lead to reconsidering the interpretations of demographic response to environmental forcing.

Material and methods

Outlines of the modelling approach

The hierarchical (state–space) formulation of the model accommodates both the stochasticity in the population dynamics and observation errors. The population dynamics include both demographic (between individual variability) and environmental (between-year variability of transition rates) stochasticity (Engen *et al.*, 1998).

The population dynamic (non-observed) is represented by an age- and stage-structured life cycle model, including different life histories and both natural and fishing mortalities (Figure 1). Abundance at different life stages s and years t is denoted $N_{s,t}$. Note the numeric subscripts used for the life stages s (1–14) are qualitative values to track the life stages sequentially from the egg stage ($s = 1$) to the spawning adult stages ($s = 8$ or 14, depending on sea age of spawners) (Figure 1). The number of eggs potentially spawned each year, t , denoted $N_{1,t}$, are derived from the estimates of returning females that survive the homewater fisheries. The egg-to-smolt transition is modelled without representing intermediate parr stages. $N_{2,t}$ denotes the total number of smolts produced from reproduction in year t . Smolts of age i that migrate seaward after 1 to I years spent in freshwater ($I = 4$ for eastern Scotland) are denoted $N_{3,i,t+I+1}$. Once at sea, smolt ages are pooled together, and $N_{3,t}$ denotes the total number of smolts migrating in the spring of year t . Return rates from smolts to spawners of different sea ages result from the combination of natural mortality, maturation and fishing mortality. The number of post-smolts that survive to the PFA stage (i.e. the number of post-smolts at 1 January of their first winter at sea, just prior to the Faroes fishery) is denoted $N_{4,t+1}$. Only fish that mature after one or two winters at sea are represented. Fish maturing after one sea winter (1SW) are denoted from $N_{5,t+1}$ to $N_{8,t+1}$ and fish maturing after the second sea winter at sea (2SW) are denoted from $N_{9,t+1}$ to $N_{14,t+2}$. Fishing mortality is represented as a sequence of fisheries along their migration route, including the fisheries at Faroes and West Greenland and those in homewaters. Mature 1SW fish that escape the Faroes fishery ($N_{6,t+1}$) survive their migration back to homewaters ($N_{7,t+1}$) and finally escape the homewater fishery ($N_{8,t+1}$) to spawn as 1SW fish. Non-mature 1SW fish that successively escape the Faroes fishery ($N_{10,t+1}$), the Greenland fishery ($N_{11,t+1}$), the Faroes fishery again as 2SW ($N_{12,t+2}$), survive through their migration back to homewaters ($N_{13,t+2}$) and finally escape the 2SW homewater fishery ($N_{14,t+2}$) to spawn in their natal rivers as 2SW fish.

The Bayesian framework is used to assimilate information from the data and informative prior distributions to estimate the number of fish in each age and life stage ($N_{s,t}$) and time-series of key transition rates: the smolt-to-PFA survival rate, the proportion of fish maturing after the first winter at sea, and the fishing mortalities during the Faroes and Greenland fisheries. The main data sources are the time-series (40 years; 1971–2010) of homewater catches for the two sea-age classes and the catches at sea (Faroes and Greenland fisheries), all derived from the ICES compilation. Observation errors are only considered for homewater catches. The latter are related to returns by observation equations that account for uncertainty in the capture process and in the catch reporting rates. No observation errors are considered for the distant water fisheries.

Informative prior distributions or fixed values are assigned to several parameters of the demographic or observation processes. In particular, an informative prior is used for the harvest rates of the homewater fisheries (ICES, 2013). This is a critical component in the model for estimating the abundance of returns. Also, because no direct observations are available for the smolt production at the scale of population complexes, and to avoid problems with model identifiability, parameters for egg-to-smolt survival are fixed from the literature, an informative prior is used for the average proportion of smolts in each age class, and environmental stochasticity in the egg-to-smolt transition is modelled with a very low variance.

Without changing the system described in Figure 1 or the data assimilation scheme, the modelling framework is used to explore how alternative demographic hypotheses can affect the inferences (Table 1). First, we compare the influence of assuming density-independent (H_1 ; the hypothesis tacitly followed by the ICES Group) and density-dependent (H_2) egg-to-smolt survival. As the number of eggs spawned varies in the time-series, introducing a density-dependent egg-to-smolt survival results in variations in the egg-to-smolt survival over time. This leads to different estimates of smolt numbers than when considering a constant egg-to-smolt survival, and may in turn modify inferences made on smolt-to-PFA survival rates. Second, we explore the consequences of considering two alternative hypotheses to explain the decrease in the proportion of fish returning as 2SW: (i) an increase in the proportion of post-smolts maturing after their first winter at sea (H_3) (the hypothesis currently followed by the ICES Group), or (ii) a constant proportion maturing but a decrease in the marine survival of non-maturing fish after the 1SW Faroes fishery (H_4).

In the next section, we first detail the equations for the population dynamics (Figure 1) from eggs (stage N_1) to 1SW and 2SW spawners that escape all fisheries (N_9 and N_{14} , respectively). The observation equations that form the likelihood are then provided, followed by justification of prior distributions assigned to parameters (Tables 2 and 3).

Population dynamics

A general structure for demographic stochasticity

Demographic stochasticity is modelled by means of Dirichlet–Multinomial (DM) distributions that can be interpreted as overdispersed multinomial distributions, where overdispersion captures some dependence among individuals (Mäntyniemi *et al.*, 2012) (Appendix 1). If N individuals face a random demographic transition with k outcomes with associated probability $\theta = (\theta_1, \dots, \theta_k)$, then the number of individuals in each outcome (N_1, \dots, N_k) is distributed as a DM distribution with an additional parameter $\eta > 0$ controlling the degree of overdispersion:

$$(N_1, \dots, N_k) \sim DM(N, \theta, \eta) \quad (1)$$

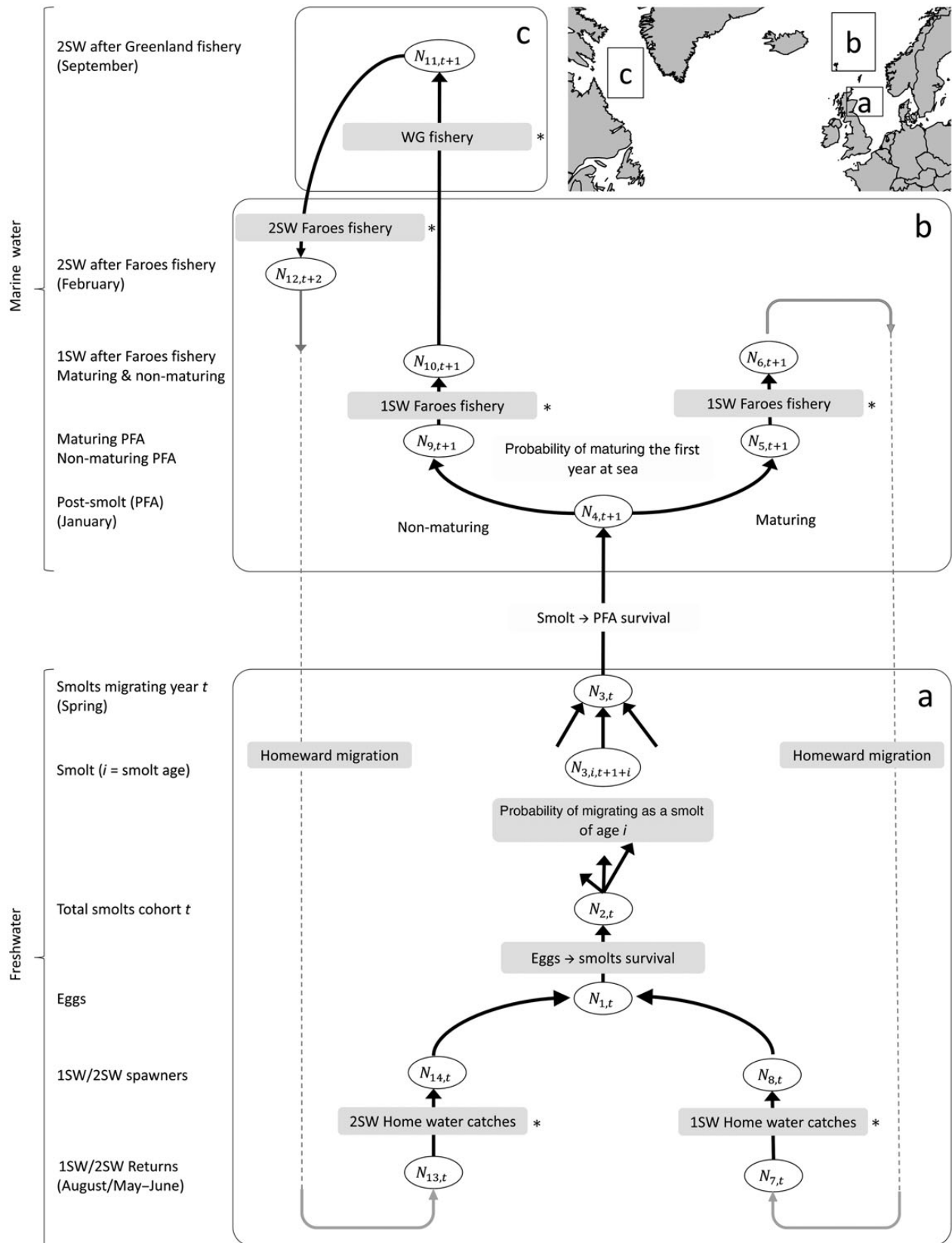


Figure 1. Structure and variables of the life cycle model. Light-shaded stages are transitions with non-informative priors, freely estimated. Dark-shaded transitions have fixed parameters or very informative prior distribution. Asterisks indicate transitions that assimilate data. Letters “a”, “b” and “c” correspond to eastern Scotland, Faroe Islands and West Greenland, respectively.

Table 1. Alternative hypotheses tested for the population dynamics.

Fresh water phase		
Egg-to-smolt survival		
H₁	Density independent. Fixed parameters	
H₂	Density dependent (Beverton&Holt). Fixed parameters	
Marine phase		
	Proportion PFA maturing	Natural mortality rate after PFA stage
H₃	Variable among years Estimated (weakly informative prior)	Equal for 1SW and 2SW fish Constant in time Very tight informative prior
H₄	Constant in time Very tight informative prior	Differ between 1SW and 2SW fish (after 1SW Faroe fishery) 1SW : Constant in time Very tight informative prior 2SW : Variable among years Estimated (weakly informative prior)

The model run with hypotheses H₁ (freshwater phase) and H₃ (marine phase) corresponds to the hypotheses in the assessment model currently used by ICES.

For instance, Appendix 1 shows how a transition involving natural and fishing mortality can be written as a DM with $k = 3$ outcomes for fish that survive, fish that die from natural mortality, and fish that die from fishing (catches). The beta-binomial is a special case of DM for $k = 2$ (e.g. fish that survive or die from natural mortality only), but to avoid multiple notations, the DM notation is kept throughout the paper, even for $k = 2$. The greater η is, the less overdispersed the DM is. When $\eta \rightarrow \infty$, the DM tends toward a multinomial distribution. No data were available to estimate η , and to avoid confusion with environmental stochasticity, η was then fixed to 10^4 so that our results are obtained with a variance of demographic transitions in practice no different from multinomial distributions (or binomial for $k = 2$).

Eggs deposition

For each year t , the number of 1SW and 2SW spawners that escape the homewater fisheries, denoted $N_{8,t}$ and $N_{14,t}$, respectively, are used to compute the total number of eggs potentially spawned, denoted $N_{1,t}$:

$$N_{1,t} = N_{8,t} \times pf_{1SW} \times fec_{1SW} + N_{14,t} \times pf_{2SW} \times fec_{2SW}, \quad (2)$$

where pf_{1SW} and pf_{2SW} are the proportions of females and fec_{1SW} and fec_{2SW} the average fecundities of 1SW and 2SW female salmon, respectively. These are considered known and constant over the time-series (Table 2).

Egg-to-smolt transition

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

Two alternative modelling hypotheses (Table 1) are tested for the egg-to-smolt survival. The first (H₁) considers a density-independent egg-to-smolt survival denoted μ_{θ_2} (Eq. 3). The second (H₂) considers the survival to be density dependent according to a Beverton–Holt relationship with parameters $(\alpha_{\theta_2}, \beta_{\theta_2})$ (Eq. 4). In both hypotheses,

environmental stochasticity is modelled by Lognormal random noise with variance $\sigma_{\theta_2}^2$.

H₁: No density dependence:

$$\log(N_{2,t}) \sim N(\log(\mu_{\theta_2} \times N_{1,t}) - \frac{\sigma_{\theta_2}^2}{2}, \sigma_{\theta_2}^2) \quad (3)$$

H₂: Density dependence:

$$\log(N_{2,t}) \sim N(\log\left(\frac{\alpha_{\theta_2} \cdot N_{1,t}}{1 + \beta_{\theta_2} \cdot N_{1,t}}\right) - \frac{\sigma_{\theta_2}^2}{2}, \sigma_{\theta_2}^2) \quad (4)$$

In the absence of observations relevant to the smolt abundance, fixed values are assigned to μ_{θ_2} , α_{θ_2} , β_{θ_2} and $\sigma_{\theta_2}^2$ to avoid problems with model identifiability (Table 2). In model configuration H₁, the average egg-to-smolt survival μ_{θ_2} is set at 0.7%, according to Hutchings and Jones (1998). When considering density-dependent survival (H₂), two sets of parameter values characterizing different intensities of density dependence are considered. The variability of the egg-to-smolt survival cannot be separated from that of the smolt-to-PFA survival. The variance $\sigma_{\theta_2}^2$ is fixed so that the CV of the between-year variability of the egg-to-smolt survival is arbitrarily set to 5%, so most of the between-year variability in the survival from egg-to-PFA is captured by the smolt-to-PFA survival.

The distribution of the total number of smolts $N_{2,t}$ in $I = 4$ smolt age classes is modelled as a DM distribution, with the probability of a smolt in the cohort t to migrating at age $i + 1$ denoted $\theta_{3,i,t}$ (with $\sum_{i=1}^4 (\theta_{3,i,t}) = 1$) and overdispersion parameter η .

$$(N_{3,1,t+2}, \dots, N_{3,4,t+5}) \sim DM(N_{2,t}, (\theta_{3,1,t}, \dots, \theta_{3,4,t}), \eta) \quad (5)$$

The $\theta_{3,1:4,t}$ are drawn *a priori* in a tight informative Dirichlet prior (Table 2) that allows very little between-year variability in the smolt age proportions.

Henceforth, the river-age of smolts is no longer tracked. $N_{3,t}$ denotes the total number of smolts migrating in the spring of year t .

Marine phase (before homewater fishery)

The marine phase, from smolts (stage $N_{3,t}$) to 1SW and 2SW returning adults that escape the marine fishery but before the homewater fishery ($N_{7,t+1}$ and $N_{13,t+2}$, respectively), is modelled as a sequence of three sea phases: the survival from smolts to the PFA stage, the maturation of fish at the PFA stage, and the natural and fishing mortalities during the PFA to return phase.

Below, we first give the general modelling structure for the sequence of these three phases. Equations (4)–(11) are first written in a general form with parameters that all vary with time. Such a general model, however, is overparameterized, as available data allow the estimation of two rates for each year of smolt migration: the return rate from total smolts ($N_{3,t}$) to 1SW ($N_{7,t+1}$) and 2SW fish ($N_{13,t+2}$), respectively. To avoid problems of model identifiability, some additional hypotheses must be applied by considering some parameters as known and/or constant in time and/or equal for 1SW and 2SW fish. Equations for those additional constraints corresponding to two contrasted demographic hypotheses, H₃ and H₄, (Table 1) are presented in a second step.

Smolt-to-PFA survival and proportion maturing

The survival from smolt ($N_{3,t}$) to PFA stage ($N_{4,t+1}$) and the maturation of fish at PFA stage are modelled sequentially as DM distributions with probability parameters $\theta_{4,t}$ and $\theta_{5,t}$, respectively:

Table 2. Summary of the parameters associated with the freshwater phase.

	Parameters	Definition	Value/Prior
Common parameters	fec_{1SW}, fec_{2SW}	Fecundity (egg number) of 1SW and 2SW females	5000, 10 000
	pf_{1SW}, pf_{2SW}	Proportion of females in 1SW and 2SW	0.40, 0.60
	$(\theta_{3,1,t}, \dots, \theta_{3,4,t})$	Probability of becoming smolt of age $i = 1, \dots, 4$	$\sim Dirich(\eta_s \times (p_1, p_2, p_3, p_4))$ with $(p_1, p_2, p_3, p_4) = (0.05, 0.45, 0.45, 0.05)$ and $\eta_s = 100$
Specific to H ₁	μ_{θ_2} σ_{θ_2}	Constant average egg-to-smolt survival rate Standard deviation	0.7% $\sigma_{\theta_2} = \sqrt{\log(CV_{\theta_2}^2 + 1)}$ with $CV_{\theta_2} = 5\%$
Specific to H ₂	α_{θ_2}	Maximum survival rate	2.2% or 9%
	β_{θ_2}	Intensity of density dependence	$2.1 \cdot 10^{-9}$ or $1.2 \cdot 10^{-8}$
	σ_{θ_2}	Standard deviation	$\sigma_{\theta_2} = \sqrt{\log(CV_{\theta_2}^2 + 1)}$ with $CV_{\theta_2} = 5\%$

Parameters specific to alternative model structure H₁ and H₂ are indicated. Parameters are fixed or drawn in very tight informative distributions (shaded).

$$(N_{4,t+1}, D_{4,t+1}) \sim DM(N_{3,t}, (\theta_{4,t}, 1 - \theta_{4,t}), \eta) \quad (6)$$

$$(N_{5,t+1}, N_{9,t+1}) \sim DM(N_{4,t+1}, (\theta_{5,t+1}, 1 - \theta_{5,t+1}), \eta), \quad (7)$$

where $D_{4,t+1}$ are the smolts that died before PFA stage (not tracked) and $N_{5,t+1}$ and $N_{9,t+1}$ are the maturing and non-maturing components of the PFA, respectively. Models for the between-year variability of $\theta_{4,t}$ and $\theta_{5,t}$ are presented in the section detailing H₃ and H₄.

Sequential marine fisheries

After the PFA stage, salmon are exposed to sequential fisheries and simultaneously experience natural mortality. As detailed in Eq. A1.4 (Appendix 1), these transitions are modelled using DM distributions with rates depending upon fishing mortalities (F), natural mortalities (M) and durations (Δt), all specific to each age class and fishery. Fixed durations specific to each transition are those reported from ICES (2013) (Table 3).

During the 1SW Faroes fishery, maturing ($N_{5,t+1}$ to $N_{7,t+1}$) and non-maturing fish ($N_{9,t+1}$ to $N_{10,t+1}$) are assumed to have the same natural mortality rate $M_{1,t+1}$ because they face the same environmental conditions. After the 1SW Faroes fishery, the migration routes of maturing and non-maturing fish differ, and the two groups of fish are assigned different mortality rates, denoted $M_{2,t+1}$ from stages $N_{10,t+1}$ to $N_{12,t+2}$ (Greenland fishery) and $M_{2,t+2}$ from $N_{12,t+2}$ to $N_{13,t+2}$ (2SW Faroes fishery).

Fish maturing in their first year at sea ($N_{5,t+1}$) are assumed to pass through the Faroes fishery before making their way back to homewaters. Fish escaping the Faroes fishery ($N_{6,t+1}$), that die from natural mortality ($D_{6,t+1}$; not tracked) or are caught ($C_{6,t+1}$; observed), are jointly modelled through a DM distribution with rates $(\theta_{6,1:3,t+1})$ derived from parameters $M_{1,t+1}, F_{6,t+1}$ and duration Δt_{5-6} :

$$(N_{6,t+1}, D_{6,t+1}, C_{6,t+1}) \sim DM(N_{5,t+1}, (\theta_{6,1,t+1}, \theta_{6,2,t+1}, \theta_{6,3,t+1}), \eta) \quad (8)$$

Fish that escape the Faroes fishery and then migrate back to their homewaters have a survival probability of $\theta_{7,t+1}$, derived from the natural mortality rate $M_{1,t+1}$ and the duration Δt_{6-7} :

$$(N_{7,t+1}, D_{7,t+1}) \sim DM(N_{6,t+1}, (\theta_{7,t+1}, 1 - \theta_{7,t+1}), \eta) \quad (9)$$

Fish that mature in their second year at sea ($N_{9,t+1}$) will face successively the Faroes fishery as non-maturing 1SW fish ($N_{9,t+1}$ to $N_{10,t+1}$), the West Greenland fishery ($N_{10,t+1}$ to $N_{11,t+1}$) and then the Faroes fishery for a second time at the 2SW stage ($N_{11,t+1}$ to $N_{12,t+2}$). Escapement, natural mortality and catches for the three fisheries ($C_{10,t+1}, C_{11,t+1}$ and $C_{12,t+2}$, respectively, observed) are modelled sequentially with DM distributions, with rates denoted as $\theta_{10,1:3,t+1}, \theta_{11,1:3,t+1}$ and $\theta_{12,1:3,t+2}$, respectively. These rates are derived from natural mortality, fishing mortality and stage durations ($M_{1,t+1}, F_{10,t+1}, \Delta t_{9-10}$), ($M_{2,t+1}, F_{11,t+1}, \Delta t_{10-11}$) and ($M_{2,t+2}, F_{12,t+2}, \Delta t_{11-12}$), respectively.

$$(N_{10,t+1}, D_{10,t+1}, C_{10,t+1}) \sim DM(N_{9,t+1}, (\theta_{10,1,t+1}, \theta_{10,2,t+1}, \theta_{10,3,t+1}), \eta) \quad (10)$$

$$(N_{11,t+1}, D_{11,t+1}, C_{11,t+1}) \sim DM(N_{10,t+1}, (\theta_{11,1,t+1}, \theta_{11,2,t+1}, \theta_{11,3,t+1}), \eta) \quad (11)$$

$$(N_{12,t+2}, D_{12,t+2}, C_{12,t+2}) \sim DM(N_{11,t+1}, (\theta_{12,1,t+2}, \theta_{12,2,t+2}, \theta_{12,3,t+2}), \eta) \quad (12)$$

Those that survive ($N_{12,t+2}$) migrate back to their homewaters with a probability of surviving of $\theta_{3,t+2}$ defined by the natural mortality rate $M_{2,t+2}$ and duration Δt_{12-13} :

$$(N_{13,t+2}, D_{13,t+2}) \sim DM(N_{12,t+2}, (\theta_{13,t+2}, 1 - \theta_{13,t+2}), \eta) \quad (13)$$

H₃: Variable proportion maturing and constant natural mortality rate after PFA stage

As in most stock assessment models, the natural and fishing mortalities cannot be separated without additional hypotheses. The proportion maturing is also confounded with the mortality differential between 1SW and 2SW fish (Chaput, 2012). Based on the

Table 3. Summary of parameters associated with the marine water phase.

	Parameters	Definition	Value/Prior
Common parameters	$\theta_{4,t}$	Smolt-to-PFA survival rate	$\text{logit}(\theta_{4,t}) \sim \text{AR}_1$
	μ_{θ_4}	Stationary mean	$\sim N(0, 1)$
	ρ_{θ_4}	Correlation	$\sim \text{Unif}(-1, 1)$
	σ_{θ_4}	Standard deviation	$\sim \text{Unif}(0, 1)$
	$F_{f,t}$	Fishing mortality of the fishery <i>f</i>	$\log(F_{f,t}) \sim N(-3, 1)$
	$\Delta t_{5-6 \text{ \& } 9-10}$	Time from 1 January to Faroes fishery	0.5 month
	Δt_{6-7}	Time from end of Faroes fishery to returns as 1SW	7.5 months
	Δt_{10-11}	Time from end of Faroes fishery to Greenland fishery (2SW)	8.5 months
Specific to H ₃	$\theta_{5,t}$	Probability of post-smolt maturing the first year at sea	$\text{logit}(\theta_{5,t}) \sim \text{AR}_1$
	μ_{θ_5}	Stationary mean	$\sim N(0, 1)$
	ρ_{θ_5}	Correlation	$\sim \text{Unif}(-1, 1)$
	σ_{θ_5}	Standard deviation	$\sim \text{Unif}(0, 1)$
	$M_{1,t} = M_1$	Natural mortality rate (per month) for 1SW maturing fish	$\log(M_1) \sim N(\log(0.03), 10^{-4})$
	$M_{2,t} = M_1$	Natural mortality rate (per month) for non-maturing fish after Faroes 1SW fishery	
	$\theta_{5,t} = \theta_5$	Probability of post-smolt maturing the first year at sea	$\text{logit}(\theta_5) \sim N(\text{logit}(0.34), 10^{-4})$
	$M_{1,t} = M_1$	Natural mortality rate (per month) for 1SW maturing fish	$\log(M_1) \sim N(\log(0.03), 10^{-4})$
	$M_{2,t}$	Natural mortality rate (per month) for non-maturing fish after Faroes 1SW fishery up to returns	$M_{2,t} = \lambda_t \times M_1$
	λ_t	Natural mortality ratio	$\log(\lambda_t) \sim \text{AR}_1$
Specific to H ₄	μ_λ	Stationary mean	$\sim N(1, 0.1)$
	ρ_λ	Correlation	$\sim \text{Unif}(-1, 1)$
	σ_{λ}	Standard deviation	$\sim \text{Unif}(0, 2)$

Parameters specific to alternative model structures H₃ and H₄ are indicated. Parameters fixed or drawn in very tight informative prior distributions are shaded.

modelling structure presented above, supplementary hypotheses are made to define two models associated with two contrasting ecological hypotheses, to explain the time variability of return rates by sea-age class.

The first hypothesis (H₃; Tables 1 and 3) corresponds with the approach taken in the stock assessment model used by ICES (ICES, 2013). Both the smolt-to-PFA survival ($\theta_{4,t}$) and the proportion maturing ($\theta_{5,t}$) are estimated and allowed to vary in time. Natural mortality rates after the PFA stage are assumed constant and identical for maturing and non-maturing fish ($M_{1,t} = M_{2,t} = M_1$ for all year *t*), with M_1 drawn in a very tight informative prior distribution. Under these premises, the temporal variability of the return rates for both 1SW and 2SW fish combined is captured by changes in the smolt-to-PFA survival, and the variability of the ratio of return rates of 2SW relative to 1SW fish is captured by changes in the proportion maturing. To eventually capture the effect of smoothed environmental fluctuations, both series of smolt-to-PFA survival ($\theta_{4,t}$) and the proportion maturing ($\theta_{5,t}$) are *a priori* modelled with a first order autoregressive process in the logit scale, with, respectively, stationary means of μ_{θ_4} and μ_{θ_5} , and stationary variances of $\sigma_{\theta_4}^2/(1 - \rho_{\theta_4})$ and $\sigma_{\theta_5}^2/(1 - \rho_{\theta_5})$, as defined in Appendix 2.

$$\text{logit}(\theta_{4,t}) \sim \text{AR}_1(\mu_{\theta_4}, \rho_{\theta_4}, \sigma_{\theta_4}^2) \tag{14}$$

$$\text{logit}(\theta_{5,t}) \sim \text{AR}_1(\mu_{\theta_5}, \rho_{\theta_5}, \sigma_{\theta_5}^2) \tag{15}$$

H₄: Constant proportion maturing and variable mortality of 2SW fish after the 1SW Faroes fishery

The alternative hypothesis (H₄; Tables 1 and 3) assumes that changes in the ratio of return rates of 2SW relative to 1SW fish result from

variations in the natural mortality rate of 2SW fish after the 1SW Faroes fishery, rather than from changes in the proportion maturing. The proportion maturing is assumed constant ($\theta_{5,t} = \theta_5$ for all years *t*), as is the natural mortality rate of 1SW fish ($M_{1,t} = M_1$), but between-year variability of the natural mortality rates of 2SW relative to 1SW fish is accounted for through an autoregressive process on the log-ratio of mortality rates:

$$\begin{cases} M_{2,t} = \lambda_t \times M_1 \\ \log(\lambda_t) \sim \text{AR}_1(\mu_\lambda, \rho_\lambda, \sigma_{\lambda}^2) \end{cases} \tag{16}$$

To facilitate the comparison of inferences between model configurations H₃ and H₄, the proportion maturing θ_5 in H₄ is drawn from a tight informative prior corresponding to the posterior of $\theta_{5,t=1}$ obtained with the model configuration H₃.

Homewater (coastal and freshwater) fishery

As a final step to the life cycle (and independently from hypotheses H₃ and H₄), returning adults ($N_{7,t}, N_{13,t}$) are fished in their homewaters before entering freshwater to spawn ($N_{8,t}, N_{14,t}$). The homewater fishery is a rather punctual process, and so DM distributions are used to model escapement and catches directly from harvest rates (denoted $h_{1SW,t}$ and $h_{2SW,t}$ for 1SW and 2SW fish, respectively), assuming that no natural mortality occurs:

$$\begin{cases} (N_{8,t}, C_{8,t}) \sim \text{DM}(N_{7,t}, (h_{1SW,t}, 1 - h_{1SW,t}), \eta) \\ (N_{14,t}, C_{14,t}) \sim \text{DM}(N_{13,t}, (h_{2SW,t}, 1 - h_{2SW,t}), \eta) \end{cases} \tag{17}$$

where $C_{8,t}$ and $C_{14,t}$ are the number of fish caught by homewater fisheries derived from declared catches (see below). As a critical component of estimating the abundance of returns, informative priors are assigned to the harvest rates $h_{1SW,t}$ and $h_{2SW,t}$ (see below).

Data and observation equations

The model uses several time-series (1971–2010) of catches. Those of the distant water ($C_{6,t}$, $C_{10,t}$, $C_{11,t}$ and $C_{12,t}$) are directly derived from declared catches reported by ICES (ICES, 2013) (Appendix 3). No observation error is considered, i.e. formally, the DM distribution of Eqs. (9)–(13) and (17) define demographic stochasticity and not observational errors.

Time-series of declared homewater catches are available for 1SW and 2SW fish (ICES, 2013), and denoted $c_{1SW,t}^{dec}$ and $c_{2SW,t}^{dec}$, respectively. A binomial observation model is used to capture observation errors arising from uncertainty in the declaration of homewater catches, with informative priors for declaration rates $r_{1SW,t}$ and $r_{2SW,t}$ (Appendix 4).

$$\begin{cases} c_{1SW,t}^{dec} \sim \text{Bin}(C_{8,t}, r_{1SW,t}) \\ c_{2SW,t}^{dec} \sim \text{Bin}(C_{14,t}, r_{2SW,t}) \end{cases} \quad (18)$$

Hence, the likelihood function used to assimilate the time-series of data within the Bayesian model results from the product of Eq. (18) and DM equations (8) and (10)–(12) for the mixed stock catches.

Priors

The proportions of smolts in each age class [the $\theta_{3,1:4,t}$ in Eq. (5)] for all cohorts at time t are drawn *a priori* in independent informative Dirichlet prior distributions, with parameters $\eta_s \times (p_1, p_2, p_3, p_4)$ with $\sum_{i=1}^4 p_i = 1$ and $\eta_s = 100$ (Table 2). Empirical proportions of smolt age classes (p_1, p_2, p_3, p_4) are set according to ICES (2013) and considered fixed among cohorts. The degree of the Dirichlet distribution is arbitrarily fixed to $\eta_s = 100$, and corresponds to the precision in the estimates of the proportions that would have been learned from multinomial samples of size $\eta_s = 100$.

The natural mortality rate for 1SW fish after the PFA stage, M_1 (considered constant, and equal to the natural mortality rate of 2SW in H_3), is drawn *a priori* in a very tight Lognormal prior that corresponds to a mortality rate of 3% per month, similar to the 30% cumulated mortality per year (ICES, 2002). The sensitivity of the inferences to the prior on M_1 is assessed by comparing three runs of the model with the median of a Lognormal informative prior distribution set to 0.03 (baseline configuration), 0.01 and 0.05.

Yearly and independent informative priors based on expertise are set on the harvest rates ($h_{1SW,t}, h_{2SW,t}$) and declaration rates ($r_{1SW,t}, r_{2SW,t}$) of the homewater fisheries (Appendix 4). Those informative priors are critical to estimate abundance of returns in the two sea-age classes. The declaration rate is assumed equal for 1SW and 2SW fish, and its expected mean increases from 0.75 to 0.90 in the time-series (Appendix 4). The harvest rates decrease over the time-series from 0.80 to 0.10 for 1SW fish and from 0.50 to 0.10 for 2SW fish (Appendix 4). We assess the sensitivity of the inferences to the priors for homewater harvest rates by considering three different priors: (i) the baseline informative priors discussed above; (ii) informative priors with a linear decline of the mean between the first and last year of the time-series; (iii) informative priors with a constant expected mean equal to the mean of the first five years of the time-series.

Other parameters of the demographic process (Table 3) are given weakly informative priors as defined by Gelman (2009), i.e. they are loose enough to be updated by the data while being strong enough to exclude biologically unrealistic values.

Computational details

All computations are performed within the R platform (R Development Core Team, 2012). Bayesian posterior distributions are approximated via Monte Carlo Markov Chain (MCMC) methods through the open-source JAGS software (<http://mcmc-jags.sourceforge.net>; JAGS code provided in the *Supplementary data* (last accessed 6 June 2013)). Three independent MCMC chains with different initialization points are used. After an adapting phase of 50 000 iterations, inferences are derived from a sample of 2 000 000 iterations. One out of 100 iterations is kept to reduce the MCMC sampling autocorrelation.

To check convergence of MCMC sampling, the Gelman–Rubin test is applied to all posterior sampling (R ratio < 1.05 for all variables) as implemented in the Coda package of R (Brooks and Gelman, 1998).

The consistency between the model and the data was checked using Bayesian posterior checking procedures (Gelman et al., 2004) designed to check the ability of the model *a posteriori* to replicate homewater catches similar to those observed (detailed in Appendix 5).

Results

We first describe the results obtained with a density-independent egg-to-smolt survival (H_1) and a probability of maturing at the PFA stage that is allowed to vary over time (H_3). This combination corresponds to the hypotheses currently followed in the ICES stock assessment model. We then examine the extent to which the inferences on the time-series of abundance and key transition rates are sensitive to changes of hypotheses in both the freshwater and the marine phase. We successively examine the effects of (i) considering a density-dependent egg-to-smolt survival (H_2), and (ii) a natural mortality rate for 2SW fish that varies in time but with a constant probability of maturing at the PFA stage (H_4). Last, we report the results of the sensitivity analysis to the prior on the harvest rate of homewater catches and on the natural mortality rate M_1 .

Results in model configuration (H_1, H_3)

Posterior checking reveals no inconsistency between the model *a posteriori* and the data. The p -values are 0.487 and 0.452 for 1SW and 2SW catches, respectively, thus showing that the model is able to replicate homewater catches very similar to the observed declared catches for both sea-age classes. Posterior checks obtained under all other configurations (H_2 and H_4) reveal no inconsistency between replicated and observed catches and are not detailed hereafter.

Estimates of the homewater returns of 1SW (N_7) and 2SW fish (N_{13}) (Figure 2) (determined primarily from the homewater catches adjusted by the informative priors for harvest and declaration rates) decreased globally over the past 40 years. The number of 1SW returning salmon in 2010 was less than half that in 1971, and returns of 2SW salmon declined from 1971 to 1996 before dropping to one-fifth of its level at the beginning of the time-series. Owing to reductions in the exploitation rate (Figure A4.1), the number of 1SW spawners (N_8) increased significantly in the 1990s and subsequently fluctuated around 125 000 salmon. The estimated abundance of 2SW spawners (N_{14}) fluctuated between 1971 and 1991, before dropping to a relatively stable low level of about 100 000 fish after 1991.

The estimated egg deposition (N_1), which accounts for fecundity and female proportion among the returning fish, fluctuated widely

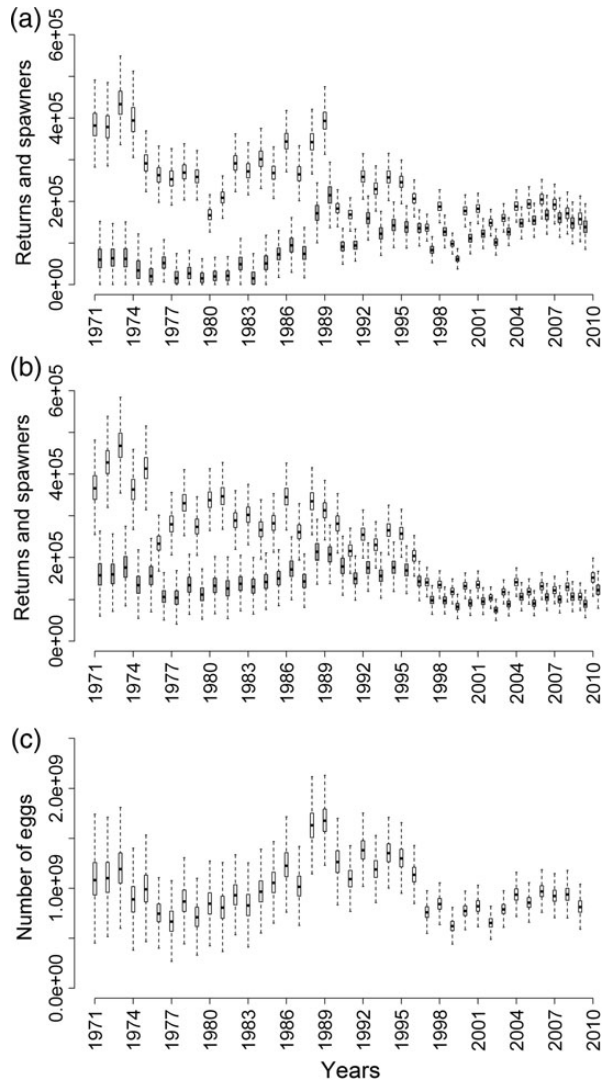


Figure 2. Time-series of marginal posterior distributions of adult returns (white boxplot) and spawners that escaped the homewater fishery (grey boxplot) as 1SW (a) and 2SW (b), and of the resulting egg deposition (c). The upper and lower limits of each box represent the first and third quartiles of posterior distributions; the horizontal bar in the middle of the boxes represents the median values.

throughout the series, reaching a maximum in 1989, but did not show any clear trends (Figure 2c).

The number of post-smolts at the end of the year, and before all fisheries (PFA, N_4) exhibited an overall decrease (Figure 3a), consistent with the observed trends in returning fish abundance. The abundance at the PFA stage reported by ICES (ICES, 2013) for the entire Scotland area (Figure 3a) between 1971 and 2010, corrected by the proportion of fish from west Scotland, is very close to the abundance estimated by our model, and the evolution over time is fully consistent with our estimates.

Estimated smolt-to-PFA survival ($\theta_{4,t}$) demonstrates a sharp decrease since the early 1990s (Figure 3b). The proportion of 1SW fish maturing after the PFA stage ($\theta_{5,t}$) fluctuates with an overall increase over the time-series (Figure 3b). The PFA of maturing 1SW fish (N_5) has decreased continuously since 1971 to <50% of the 1970s abundance in the most recent years (not shown), while non-maturing

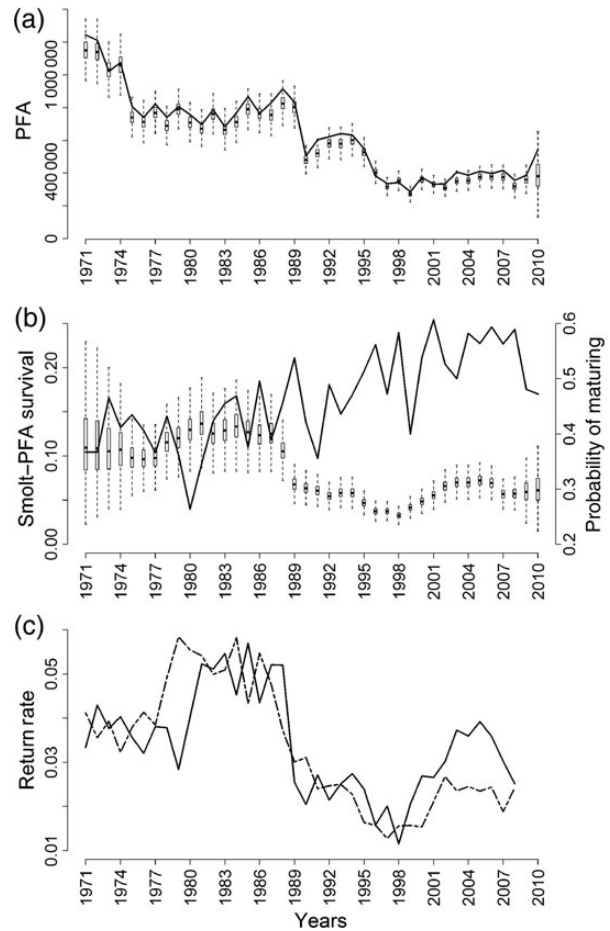


Figure 3. Time-series of marginal posterior distributions of (a) the Pre-fishery Abundance estimate derived from the model we developed for eastern Scotland (boxplot) and the Pre-fishery Abundance estimate for the whole of Scotland by the ICES model (corrected by proportions of fish from West Scotland); (b) the marine survival during the first months at sea (smolt-to-PFA) (boxplot) and the posterior medians of the probability of maturing the first year at sea (solid line); and (c) return rates of smolts as 1SW (solid line) and MSW fish (dashed line). The upper and lower limits of each box represent the first and third quartiles of posterior distributions; the horizontal bar in the middle of boxes represents the median value.

PFA (N_9) declined until the mid-1990s before stabilizing at a very low level (not shown). The joint distribution of $(\theta_{4,t}, \theta_{5,t})$ for each year t does not exhibit any particular pattern of correlation, thus indicating that the two parameters are not confounded, given the information assimilated in the model (not shown).

Estimates of fishing mortality after the PFA stage (not shown) show that the Faroes fishery exploited a small fraction of the 1SW fish (0.5% exploitation rate on average). The cumulative impact of the three high seas fisheries on the non-maturing component is much higher (25% cumulative exploitation rate on average), with highest exploitation (18%) occurring in the Greenland fishery.

The return rates from smolt to 1SW or 2SW adult before homewater exploitation (Figure 3c), which combine life history choices (probability of maturing) and mortality (M and F) during the marine phase, are very comparable between 1SW and 2SW fish until the 1990s, after which the 1SW return rate is higher. Both time-series fluctuate between 1% and 6% and follow the same general

time-trend as the smolt-to-PFA survival rate, with a sharp decline in the late 1980s.

Effect of considering density-dependent egg-to-smolt survival (H_2)

Because the egg deposition fluctuates during the time-series (Figure 2c), introducing a density-dependent (Beverton–Holt type) egg-to-smolt survival (H_2 ; Figure 4a) leads to a fluctuating egg-to-smolt survival, while it is constant in the baseline hypothesis (Figure 4b). Because the egg-to-smolt survival is higher for low egg deposition and lower for high egg deposition, considering a density-dependent egg-to-smolt survival dampens the variation of egg abundance over the time-series. This in turn affects the estimates of abundance and transition rates of older life stages: the fluctuations of smolt abundance is smoothed, which, ultimately, dampens the decline in the estimates of the smolt-to-PFA survival (Figure 4c). Increasing the density dependence in the egg-to-smolt survival tends to smooth the sharp decline in the smolt-to-PFA survival rate in the late 1980s.

Changes in egg-to-smolt survival are balanced by changes in the smolt-to-PFA survival, but do not affect any other model component after the PFA stages.

Effect of considering a constant probability of maturing at PFA stage (H_4)

The consequences of changing from the baseline hypothesis H_3 to H_4 (a constant probability of maturing at the PFA stage but a variable mortality rate of 2SW fish) are explored under the constant egg-to-smolt survival hypothesis (H_1). Estimates of abundance and transition rates from eggs to PFA are not sensitive to changing from H_3 to H_4 . Under H_3 , the estimates of the probability of maturing at PFA stage increase to fit the decreasing proportion of 2SW fish in the total returns (Figure 5a). The alternative model configuration H_4 provides another hypothesis consistent with the decline in the proportion of 2SW fish in returns. The proportion maturing is assumed constant ($\sim 34\%$) but the mortality rates of non-maturing fish after the 1SW Faroes fishery increase notably from 1991 (Figure 5b). The annual variations in the natural mortality rate of 2SW fish under H_4 show a pattern of variation very similar to that of the proportion maturing under H_3 .

Sensitivity analysis to changes in the informative priors

Posterior estimates of all model components are highly sensitive to changes in the informative priors on the harvest rates for the home-water fishery (Figure 6). Given the catches in the homewater fishery (Appendix 4), changing the prior on the harvest rates directly affects the estimates of returns, which in turn affect all life stage and transition rates in the model. The higher the prior expected mean of the harvest rates, the lower the estimates of returns (not shown) and the lower the estimates of the PFA abundance (Figure 6a). This has important consequences for the estimates of the smolt-to-PFA survival rate. At the limit, considering the harvest rate has been constant in the time-series dampens the variations in the time-series of estimated smolt-to-PFA survival rates (Figure 6b). In particular, the drop in survival rate around 1988–1990 is no longer obvious. The increasing trend in the probability of maturing after the first year at sea is also much weaker (Figure 6b).

As expected, M_1 is a scaling factor that balances the smolt-to-PFA survival rate. The lower the expected mean of the prior on M_1 , the lower the posterior estimates of the smolt-to-PFA survival (Figure 7b). Changing the prior on M_1 also affects the probability

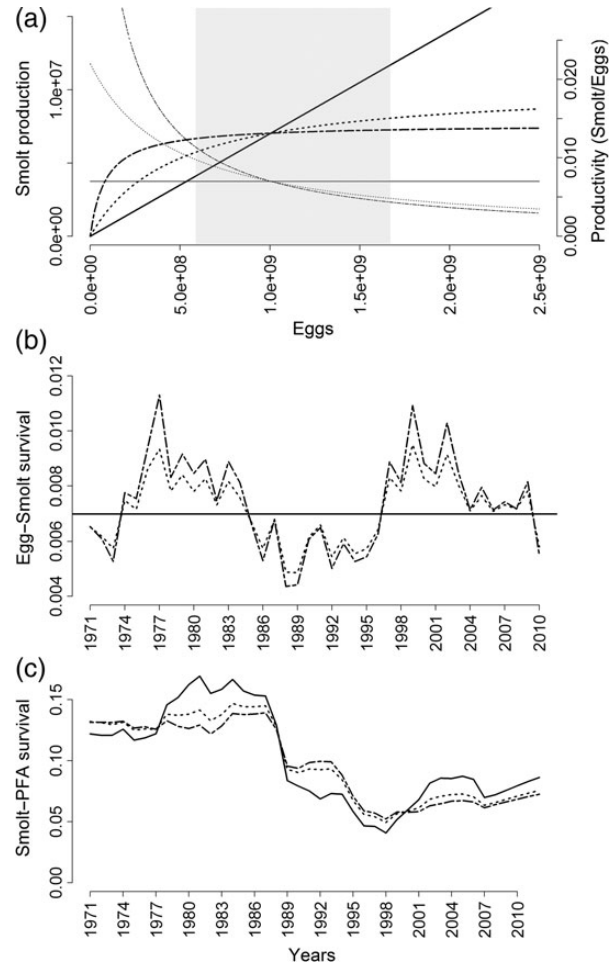


Figure 4. Analysis of sensitivity to changes in the egg-to-smolt survival function (H_1 and H_2). (a) Different egg-to-smolt survival functions tested (bold) and associated smolts/eggs ratios (thin). Solid line: average egg-to-smolt survival fixed to 0.7% (H_1); dotted and dashed–dotted lines: BH density-dependent function (H_2) with different intensity of density dependence with α equal to 2.2 and 9.0%, respectively, and β equal to 2.1×10^{-9} and 1.2×10^{-8} , respectively (Table 2). The shaded area represents the range of egg abundances estimated between 1971 and 2010. Time-series of posterior median estimates of (b) egg-to-smolt survival rate, and (c) smolt-to-PFA survival rate; line codes correspond to egg-to-smolt survival in (a).

of maturing as 1SW. A higher M_1 slightly decreases the differential of cumulated natural mortality between 1SW and 2SW fish, which leads to higher estimates of the proportion maturing (Figure 7c).

Discussion

We developed an integrated life cycle model that improves on the stock assessment approach currently used by ICES and provides new insights about the *A. salmon* population dynamics of a stock assemblage. Eastern Scotland is the largest component of the southern stock complex within the Northeast Atlantic (ICES, 2013) and, thus, is an ideal candidate to illustrate the value of applying our novel modelling approach.

Improving the statistical methodology

As a major improvement, the model is built in a Bayesian state–space framework. The population dynamics, considered as non-observed

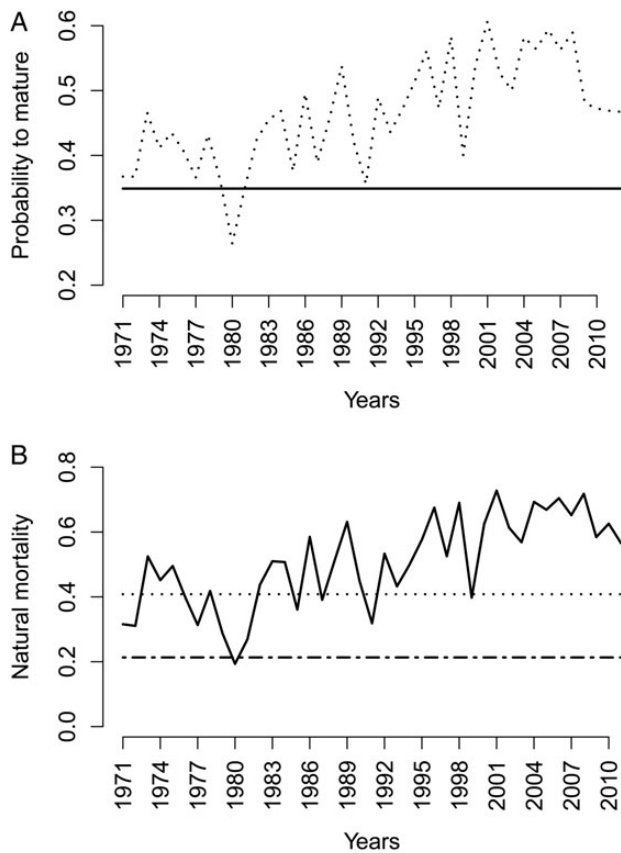


Figure 5. Sensitivity of the model configuration for the PFA-to-return phase (H_3 , H_4) under the configuration H_1 for the freshwater phase. (a) Time-series of posterior median estimates of the probability of maturing the first year at sea (dotted line: H_3 ; bold line: H_4), and (b) the integrated natural mortality faced by 1SW fish (dashed–dotted line) and the integrated natural mortality faced by 2SW fish under H_3 (dotted line) and H_4 (bold line).

processes, are explicitly modelled as a life cycle. Observation equations allow the available data to be assimilated and prior knowledge of all parameters and abundances at each life stage to be updated.

Our novel approach improves the estimates of stock productivity. The current assessment model (Chaput, 2012) relies on a stock–recruitment concept that considers a statistical relationship between spawning potential (lagged eggs) and recruitment (PFA). A critical weakness of the approach is that it does not consider the dependence between the PFA and the subsequent spawning potential, which can result in a time-series bias (Walters, 1985; Caputti, 1988; Su and Peterman, 2012) in productivity estimates. By contrast, our life cycle approach explicitly considers the correlation between the abundance in the different life stages in the time-series.

Uncertainty is readily quantified through the posterior distribution of all parameters and abundance at any life stage. The life cycle is developed in an estimation framework that could be adapted to provide stock projections based on the uncertainty derived in the estimation phase (Dorazio and Johnson, 2003) and could thus be more powerful and useful in the context of decision and risk analysis.

Owing to the Bayesian framework, the various sources of information, data and informative priors, are assimilated in a transparent way. This makes it easier to assess the influence of the informative

priors for the inferences. Our results stress that inferences critically depend upon the informative priors on the harvest rate associated with homewater fisheries. When combined with these priors, the time-series of catches for both sea ages provides the primary quantitative information to scale the abundance of returns. Changing the time trends in the priors for harvest rates drastically affects the estimates of abundance at all life stages and the smolt return rates. The natural mortality rate at sea after the PFA stage (M_1) is also a key prior affecting all quantities estimated by the model. This is a scaling parameter for the abundance: a higher mean of the prior on M_1 increases estimated PFA abundance but does not affect trends in time-series of estimated parameters. Management advice regarding high sea fisheries, however, depends upon a prior hypothesis on this parameter, as increasing M_1 would diminish the impact of high sea catches on the returns.

Improving the ecological realism of the assessment model

Embedding the model within a hierarchical integrated approach explicitly separates out the equations for the population dynamics and the observations. This offers flexibility to improve the ecological realism of the model as different hypotheses regarding the population dynamics can be assessed without changing the data assimilation scheme. With the aim of facilitating the comparison with the current ICES approach, we first ran the model with the same information (data and demographic hypotheses) as implicitly or explicitly applied in the current ICES stock assessment approach with: (H_1) no density dependence in the freshwater phase; and (H_3) between-year variations in the smolt-to-PFA survival and probability of maturing as 1SW fish, though with the natural mortality rate after the PFA stage constant in time and equal for 1SW and 2SW fish. We show how the flexibility of the approach offers the possibility of challenging alternative demographic hypotheses, and we stress how changing the demographic hypothesis can affect inferences and interpretations of the trends.

A critical improvement in the ecological realism of the life cycle model is the separation of the freshwater and the marine phases. This allows the introduction of density dependence in the freshwater phase (H_2). There is ample evidence from river-specific studies that egg deposition is an important variable conditioning juvenile abundance and that recruitment in freshwater is most appropriately modelled as a density-dependent function (Gibson, 1993; Kennedy and Crozier, 1993; Chaput *et al.*, 1998; Jonsson *et al.*, 1998; Elliott, 2001). Considering egg-to-smolt survival as density dependent introduced non-linearity into the dynamics and notably modified the temporal dynamics of marine survival. Fluctuations in the numbers of eggs spawned over time induced fluctuations in the egg-to-smolt survival rate that dampened the variations of egg abundance. This in turn affected the inferences made on the time-series of smolt-to-PFA survival by comparison with those obtained with a constant egg-to-smolt survival. Interestingly, our results stress that the sharp decline in smolt-to-PFA survival around 1988–1990 appears robust to the modelling hypothesis for the freshwater dynamics, although it is dampened when density dependence is considered, meaning that part of the between-year variability of natural mortality could be attributed to density dependence in the stock–recruitment process.

The approach also offers the possibility of exploring alternative hypotheses for the marine phase between smolt and return as adult fish.

The smolts return rates are modelled based on three key processes: the smolt-to-PFA survival (the first months at sea after smolt

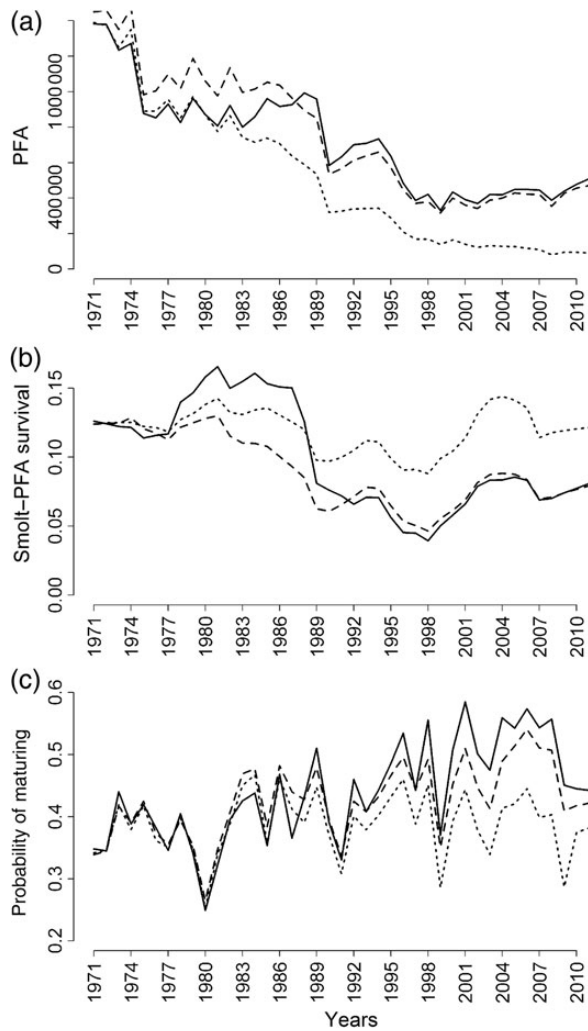


Figure 6. Sensitivity analysis to changes in the informative prior on the harvest rate of homewater fisheries. Time-series of posterior median estimates of (a) abundance of PFA stage, (b) the smolt-to-PFA survival rate, and (c) the probability of maturing. Three scenarios are explored; the baseline scenario with priors used by ICES (see Appendix 4) (bold line), a linear decline of the harvest rate between the first and the last year of the time-series (dashed line), and a constant harvest rate equal to the mean of the five first years (dotted line).

migration), the maturation at PFA stage, and the PFA-to-return transition (for mature or non-mature fish). Combined with hypotheses for the egg-to-smolt transition, the data assimilated in the current approach allow the estimation of the return rates from smolt to 1SW and 2SW adults. The return rates exhibited an overall decreasing trend over the time-series of between 1.5% and 5.0%, with a sharp decline around the years 1988–1990. However, the magnitude of the fluctuations in time may be overestimated: although not represented in our model, environmental variability also occurs during the freshwater phase. The range of the estimated smolt-to-adult return rates were consistent with those obtained from returns of tagged smolts on index rivers. For the Southern NE stock complex, return rates of 1SW fish ranged between 3 and 12% and for 2SW fish between 1 and 3%, and the available time-series, covering a broad spatial scale, exhibited a decreasing trend over the 1980–2010 period (ICES, 2010). The decline in the return rates is consistent

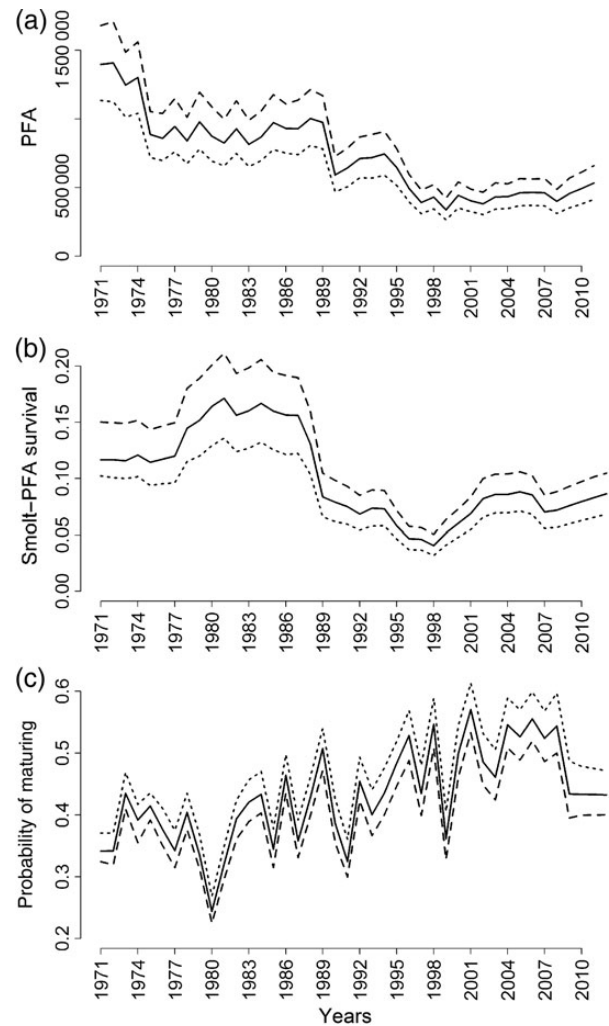


Figure 7. Sensitivity analysis to changes in the informative prior on the natural mortality. Time-series of posterior median estimates of (a) abundance of PFA stage, (b) the smolt-to-PFA survival rate and (c) the probability of maturing the first year at sea. Three scenarios are explored: the baseline (bold line) with the expected mean of the prior distribution on M_1 equal to 0.03; and two others with the expected mean equal to 0.01 (dotted line) and 0.05 (dashed line).

with a large body of literature that lends support to the hypothesis that mortality has increased in the marine phase, associated with recent changes in the Northeast Atlantic ecosystem. Potential drivers include changes in the availability of prey affecting growth and survival (Friedland *et al.*, 2000; Beamish and Mahnken, 2001; Peyronnet *et al.*, 2007, 2008). This would be connected with large scale modification in the distribution and phenology of plankton species in the Northeast Atlantic as a bottom-up response associated with ocean warming (Beaugrand and Reid, 2003; Richardson and Schoeman, 2004; Todd *et al.*, 2012). The sharp decline in return rates identified around 1988–1990 in all the model structures examined, corresponds to the shift in plankton communities in the eastern Atlantic ocean described by Beaugrand and Reid (2003).

To avoid problems with model identification, additional hypotheses were made on the natural mortality rate after the PFA stage; this made it possible to estimate the relative roles of the

smolt-to-PFA and the PFA-to-return phases in the mortality at sea, and to gauge the importance of high seas mixed stock fishing mortalities.

Because the natural mortality at sea after the PFA stage for 1SW fish (M_1) is roughly fixed in all model configurations (drawn in very tight informative prior), most of the between-year variability is captured in the smolt-to-PFA survival, which varies between 3 and 15% with an overall decline over the time-series. The sharp decline in return rates manifests itself as a similar decline in the smolt-to-PFA survival during the 1988–1990 period. However, the range of values (3–15%) critically depends on the hypothetical value of M_1 .

Our results also suggest that there has been a greater decline in the return rate of 2SW fish compared with 1SW fish, at least in the last two decades. This pattern has already been described in Scotland (Youngson *et al.*, 2002; Heddell-Cowie, 2005) and Wales (Aprahamian *et al.*, 2008). In the model configuration that reproduces the hypothesis currently made by ICES, the decreasing smolt-to-PFA mortality rate, common to both life history groups, is offset by an increasing probability of maturing, which brings back relatively more smolts as 1SW versus 2SW fish. But as highlighted by Chaput (2012), without considering additional data, there is confusion between the proportion maturing as 1SW fish and the differential survival between fish maturing as 1SW fish and 2SW fish. To investigate this, we ran a model with the alternative assumption of a constant proportion maturing as 1SW, offset by an increasing trend for the natural mortality rate of 2SW fish after the 1SW Faroes fishery.

Evaluating the support for these alternative (and not mutually exclusive) hypotheses is not possible with the data used in the current exercise. This is a critical issue, however, that future research should address. The alternative hypotheses may have important implications for the management of high seas fisheries. Indeed, considering a higher mortality rate for 2SW fish after the PFA stage would reduce the expected impact of catch regulations for the distant water fisheries aimed at preserving future 2SW fish. Alternative hypotheses also correspond to different ecological mechanisms. An increase in the natural mortality of 2SW fish relative to 1SW fish could be a response to environmental changes that would only affect 2SW fish during their migration to and from West Greenland, without affecting 1SW fish that return after their sojourn around the Faroe Islands. We did not find any evidence in the literature of such a change specific to the migration route. An increase in the proportion of maturing fish could also be interpreted as an adaptive response to changes in the environment (Summers, 1995; Friedland and Haas, 1996; Blanchet and Dubut, 2012). Age at first maturity is known to be environmentally plastic and mediated by growth in fish, and salmonids make no exception to this widespread process (Marshall *et al.*, 1998; Thorpe *et al.*, 1998; Mangel and Sattertwate, 2008). An alternative explanation is that the increase in the proportion maturing as 1SW fish could be an evolutionary response, induced by the historic selective exploitation of older and bigger fish (Thorpe, 2007).

Directions for future improvements

The approach presented provides a framework for structuring further research and data collection. Only a few sources of data besides time-series of homewater and high sea catches are assimilated in the model. Inferences are based on a number of informative priors and a suite of modelling hypotheses, of which the adequacy

can hardly be appraised quantitatively. Embedding the assessment approach within an integrated hierarchical Bayesian modelling framework offers multiple possibilities of extending the model by incorporating additional sources of data. This may result in a reduced dependency of the inferences on strong modelling assumptions and informative priors. This can provide improvement in the ecological realism of the assessment model, and can help learning more about the drivers of salmon abundance in the Atlantic Ocean.

One of the most exciting prospects is taking fuller advantage of the data available on the dynamics of the freshwater phase of *A. salmon*. Time-series of egg-to-smolt data available from a set of monitored rivers (Prévost *et al.*, 2003; ICES, 2013) could be incorporated into the model, to provide information on density-dependent egg-to-smolt survival rates and on smolt age compositions, and could also help evaluate the hypothesis of non-stationarity in the parameters of the freshwater phase during the time-series. As shown in our results, because inferences regarding trends in the marine phase depend upon the freshwater phase parameters, assimilating more data about the egg-to-smolt transition would critically improve the approach. Smolt tagging and recapture data available for several monitored rivers (Miller *et al.*, 2012; Sheehan *et al.*, 2012; ICES, 2013) could also be incorporated into the model to improve the estimates of return rates.

The model presented here also lays the foundation for integrated life cycle modelling at the broader ocean scale. A future research direction would be to consider a hierarchical model to jointly analyse the dynamics of all the regions comprising the S.NE stock complex as defined by ICES (France, Ireland, UK England & Wales, UK Scotland, UK Northern Ireland and South West Iceland). A multi-region model would be a useful tool for assessing the effect of management measures on the distant-water mixed-stock fisheries. Following an approach similar to the one developed by Mills *et al.* (2013) for the North American stock complex, a multi-regional model would also enhance our capacity to detect common trends and to assess the relative effects of environmental factors influencing populations at various spatial scales, such as marine conditions on oceanic foraging areas for mixed stocks or more local environmental factors influencing specific stock components during the first month of life at sea (Friedland *et al.*, 2000; Sharma *et al.*, 2013).

Supplementary data

Supplementary data are available at *ICES Journal of Marine Science* online.

Acknowledgements

This study was made possible by the work of the numerous people who collect and compile the data used by the ICES Working Group on North Atlantic Salmon. We thank Atso Romakkaniemi and Henni Pulkkinen for profitable discussions about harmonizing the Baltic and the Northern Atlantic salmon stock assessment models. The comments of three anonymous reviewers and of the Associate Editor greatly improved the manuscript.

Funding

The research leading to these results has received funding from the European Union's Seventh Framework Programme (FP7/2007–2013) under grant agreement No. 244706/ECOKNOWS project. However, the paper does not necessarily reflect EC views and in no way anticipates the Commission's future policy in the area.

References

- Aas, O., Einum, S., Klemetsen, A., and Skurdal, J. 2011. Atlantic Salmon Ecology. Wiley-Blackwell, Oxford, UK.
- Aprahamian, M. W., Davidson, I. C., and Cove, R. J. 2008. Life history changes in Atlantic salmon from the River Dee, Wales. *Hydrobiologia*, 602: 61–78.
- Baranov, F. I. 1918. On the question of the biological basis of fisheries. Proceedings of the Institute for Scientific Ichthyological Investigations, 1: 81–128. *In Russian*. (Translation by W. E. Ricker, and N. Artin, Indiana University, 1945. 15 pp.)
- Baranov, F. I. 1925. On the question of the dynamics of the fishing industry. *In Russian*. (Translation by W. E. Ricker, and N. Artin, Indiana University, 1945. 15 pp.)
- Beamish, R. J., and Mahnken, C. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography*, 49: 423–437.
- Beaugrand, G., and Reid, P. C. 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology*, 9: 801–817.
- Beaugrand, G., and Reid, P. C. 2012. Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. *ICES Journal of Marine Science*, 69: 1549–1562.
- Blanchet, S., and Dubut, V. 2012. 'Back to the future': how archaeological remains can describe salmon adaptation to climate change. *Molecular Ecology*, 21: 2311–2314.
- Brooks, S. P., and Gelman, A. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, 7: 434–455.
- Buckland, S. T., Newmann, K. B., Fernández, C., Thomas, L., and Harwood, J. 2007. Embedding population dynamics models in inference. *Statistical Science*, 22: 44–58.
- Caputti, N. 1988. Factors affecting the time-series bias in stock recruitment relationships and the interaction between time-series and measurement errors bias. *Canadian Journal of Fisheries and Aquatic Sciences*, 45: 178–184.
- Chaput, G. 2012. Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science*, 69: 1538–1548.
- Chaput, G., Allard, J., Caron, F., Dempson, J. B., Mullins, C. C., and O'Connell, M. F. 1998. River-specific target spawning requirements for Atlantic salmon (*Salmo salar*) based on a generalized smolt production model. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 246–261.
- Chaput, G., Legault, C. M., Reddin, D. G., Caron, F., and Amiro, P. G. 2005. Provision of catch advice taking account of non-stationarity in productivity of Atlantic salmon (*Salmo salar* L.) in the Northwest Atlantic. *ICES Journal of Marine Science*, 62: 131–143.
- Chaput, G., Moore, D., Hayward, J., Shaesgreen, J., and Bubee, B. 1999. Stock status of Atlantic salmon (*Salmo salar*) in the Miramichi river, 1998. Canadian Stock Assessment Research Document, 99/49. Department of Fisheries and Ocean, Ottawa.
- Crozier, W. W., Potter, E. C. E., Prévost, E., Schön, P.-J., and Maoiléidigh, O. 2003. SALMODEL – a coordinated approach towards the development of a scientific basis for management of wild Atlantic salmon in the North-east Atlantic. Report of Concerted Action (SALMODEL).
- Dorazio, R. M., and Johnson, F. A. 2003. Bayesian inference and decision theory – a framework for decision making in natural resource management. *Ecological Applications*, 13: 556–563.
- Elliott, J. 2001. The relative role of density in the stock–recruitment relationship of salmonids. *In Stock, Recruitment, and Reference Point. Assessment and Management of Atlantic Salmon*, pp. 25–55. Ed. by E. Prévost, and G. Chaput. INRA editions, Paris.
- Engen, S., Bakke, O., and Islam, A. 1998. Demographic and environmental stochasticity – concepts and definitions. *Biometrics*, 54: 840–846.
- Fleischman, S. J., Catalano, M. J., Clark, R. A., and Bernard, D. R. 2013. An age-structured state–space stock–recruit model for Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences*, 70: 401–414.
- Friedland, K. D., and Haas, R. E. 1996. Marine post-smolt growth and age at maturity of Atlantic salmon. *Journal of Fish Biology*, 48: 1–15.
- Friedland, K. D., Hansen, L. P., Dunkley, D. A., and MacLean, J. C. 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES Journal of Marine Science*, 57: 419–429.
- Friedland, K. D., Shank, B. V., Todd, C. D., McGinnity, P., and Nye, J. A. 2013. Differential response of continental stock complexes of Atlantic salmon (*Salmo salar*) to the Atlantic Multidecadal Oscillation. *Journal of Marine Systems*, in press. doi:10.1016/j.jmarsys.2013.03.003.
- Gelman, A. 2009. Bayes, Jeffreys, prior distributions and the philosophy of statistics. *Statistical Science*, 24: 176–178.
- Gelman, A., Carlin, J. B., Stern, H., and Rubin, D. B. 2004. Bayesian Data Analysis, 2nd edn. Texts in Statistical Science. Chapman & Hall. 668 pp.
- Gibson, R. 1993. The Atlantic salmon in freshwater: spawning, rearing and production. *Reviews in Fish Biology and Fisheries*, 3: 39–73.
- Harwood, J., and Stokes, K. 2003. Coping with uncertainty in ecological advice: lessons from fisheries. *Trends in Ecology & Evolution*, 18: 617–622.
- Heddell-Cowie, M. 2005. Importance of the River Teviot to Atlantic salmon, *Salmo salar*, rod catches in the River Tweed, Scotland. *Fisheries Management and Ecology*, 12: 137–142.
- Hutchings, J. A., and Jones, M. E. B. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 22–47.
- ICES. 2002. Report of the Working Group on North Atlantic Salmon (WGNAS), 2002. ICES Document CM 2002/ACFM: 14.
- ICES. 2010. Report of the Working Group on North Atlantic Salmon (WGNAS), 2010. ICES Document CM 2010/ACOM: 09.
- ICES. 2012. Report of the Working Group on North Atlantic Salmon (WGNAS), 2012. ICES Document CM 2012/ACOM: 09.
- ICES. 2013. Report of the Working Group on North Atlantic Salmon (WGNAS), 2013. ICES Document CM 2013/ACOM: 09.
- Jonsson, N., Jonsson, B., and Hansen, L. P. 1998. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. *Journal of Animal Ecology*, 67: 751–762.
- Kennedy, G. J. A., and Crozier, W. W. 1993. Juvenile Atlantic salmon (*Salmo salar*) production and prediction. *In Production of Juvenile Atlantic Salmon, Salmo salar*, in Natural Waters. Ed. by R. J. Gibson, and R. E. Cutting. Canadian Special Publication of Fisheries and Aquatic Sciences, 118: 179–187.
- Kuparinen, A., Alho, J. S., Olin, M., and Lehtonen, H. 2012. Estimation of northern pike population sizes via mark–recapture monitoring. *Fisheries Management and Ecology*, 19: 323–332.
- Lewy, P., and Nielsen, A. 2003. Modelling stochastic fish stock dynamics using Markov chain Monte Carlo. *ICES Journal of Marine Science*, 60: 743–752.
- Mangel, M., and Sattertwate, W. H. 2008. Combining proximate and ultimate approaches to understand life history variation in salmonids with application to fisheries, conservation, and aquaculture. *Bulletin of Marine Science*, 83: 107–130.
- Mäntyniemi, S., Romakkaniemi, A., Dannewitz, J., Palm, S., Pakarinen, T., Pulkkinen, H., Gårdmark, A., et al. 2012. Both predation and feeding opportunities may explain changes in survival of Baltic salmon post-smolts. *ICES Journal of Marine Science*, 69: 1574–1579.
- Marshall, E. A., Quinn, T. P., Roff, D. A., Hutchings, J. A., Metcalfe, N. B., Bakke, T. A., Saunders, R. L., et al. 1998. A framework for understanding Atlantic salmon (*Salmo salar*) life history. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(Suppl. 1): 48–58.
- McAllister, M. K., Starr, P. J., Restrepo, V. R., and Kirkwood, G. P. 1999. Formulating quantitative methods to evaluate fishery-management

- systems: what fishery processes should be modelled and what trade-offs should be made? *ICES Journal of Marine Science*, 56: 900–916.
- Michielsens, C. G. J., McAllister, M. K., Kuikka, S., Mäntyniemi, S., Romakkaniemi, A., Pakarinen, T., Karlsson, L., *et al.* 2008. Combining multiple Bayesian data analyses in a sequential framework for quantitative fisheries stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences*, 65: 962–974.
- Millar, R. B., and Meyer, R. 2000. Bayesian state–space modelling of age-structured data: fitting a model is just the beginning. *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 43–50.
- Miller, A. S., Sheehan, T. F., Renkawitz, M. D., Meister, A. L., and Miller, T. J. 2012. Revisiting the marine migration of US Atlantic salmon using historical Carlin tag data. *ICES Journal of Marine Science*, 69: 1609–1615.
- Mills, K. E., Pershing, A. J., Sheehan, T. F., and Mountain, D. 2013. Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. *Global Change Biology*, 19: 3046–3061.
- Ó Maoiléidigh, N., McGinnity, P., Prévost, E., Potter, E. C. E., Gargan, P., Crozier, W. W., Mills, P., *et al.* 2004. Application of pre-fishery abundance modelling and Bayesian hierarchical stock and recruitment analysis to the provision of precautionary catch advice for Irish salmon (*Salmo salar* L.) fisheries. *ICES Journal of Marine Science*, 61: 1370–1378.
- Parent, E., and Rivot, E. 2012. Introduction to Hierarchical Bayesian Modeling for Ecological Data. Applied Environmental Statistics. Chapman & Hall/CRC. 427 pp.
- Peyronnet, A., Friedland, K. D., Maoileidigh, N. ó, Manning, M., and Poole, W. R. 2007. Links between patterns of marine growth and survival of Atlantic salmon *Salmo salar*, L. *Journal of Fish Biology*, 71: 684–700.
- Peyronnet, A., Friedland, K. D., and Ó Maoileidigh, N. 2008. Different ocean and climate factors control the marine survival of wild and hatchery Atlantic salmon *Salmo salar* in the north-east Atlantic Ocean. *Journal of Fish Biology*, 73: 945–962.
- Potter, E. C. E., Crozier, W. W., Schön, P.-J., Nicholson, M. D., Maxwell, D. L., Prévost, E., Erkinaro, J., *et al.* 2004. Estimating and forecasting pre-fishery abundance of Atlantic salmon (*Salmo salar* L.) in the Northeast Atlantic for the management of mixed-stock fisheries. *ICES Journal of Marine Science*, 61: 1359–1369.
- Prévost, E., and Chaput, G. (Eds) 2001. Stock, Recruitment and Reference Points Assessment and Management of Atlantic Salmon. INRA Editions, Paris. 223 pp.
- Prévost, E., Parent, E., Crozier, W., Davidson, I., Dumas, J., Gudbergsson, G., Hindar, K., *et al.* 2003. Setting biological reference points for Atlantic salmon stocks: transfer of information from data-rich to sparse-data situations by Bayesian hierarchical modelling. *ICES Journal of Marine Science*, 60: 1177–1193.
- Rago, P. J., Meerburg, D. J., Reddin, D. G., Chaput, G., Marshall, T. L., Dempson, B., and Caron, F. 1993. A continental run reconstruction model for the non-maturing component of North American Atlantic salmon: analysis of fisheries in Greenland and Newfoundland–Labrador, 1974–1991. *ICES Document CM 1993/M: 26*. 33 pp.
- Richardson, A. J., and Schoeman, D. S. 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. *Science*, 305: 1609–1612.
- Rivot, E., Prévost, E., Parent, E., and Baglinière, J. L. 2004. A Bayesian state–space modelling framework for fitting a salmon stage-structured population dynamic model to multiple time series of field data. *Ecological Modelling*, 179: 463–485.
- Rochette, S., Le Pape, O., Vigneau, J., and Rivot, E. 2013. A hierarchical Bayesian model for embedding larval drift and habitat models in integrated life cycles for exploited fish. *Ecological Applications*, 23: 1659–1676.
- Ruiz, J., González-Quirós, R., Prieto, L., and Navarro, G. 2009. A Bayesian model for anchovy (*Engraulis encrasicolus*): the combined forcing of man and environment. *Fisheries Oceanography*, 18: 62–76.
- Sharma, R., Vélez-Espino, L. A., Wertheimer, A. C., Mantua, N., and Francis, R. C. 2013. Relating spatial and temporal scales of climate and ocean variability to survival of Pacific Northwest Chinook salmon (*Oncorhynchus tshawytscha*). *Fisheries Oceanography*, 22: 14–31.
- Sheehan, T. F., Reddin, D. G., Chaput, G., and Renkawitz, M. D. 2012. SALSEA North America: a pelagic ecosystem survey targeting Atlantic salmon in the Northwest Atlantic. *ICES Journal of Marine Science*, 69: 1580–1588.
- Su, Z., and Peterman, R. M. 2012. Performance of a Bayesian state-space model of semelparous species for stock-recruitment data subject to measurement error. *Ecological Modelling*, 224: 76–89.
- Summers, D. W. 1995. Long-term changes in the sea-age at maturity and seasonal time of return of salmon, *Salmo salar* L., to Scottish Rivers. *Fisheries Management and Ecology*, 2: 147–156.
- Swain, D. P., Jonsen, I. D., Simon, J. E., and Myers, R. A. 2009. Assessing threats to species at risk using stage-structured state–space models: mortality trends in skate populations. *Ecological Applications*, 19: 1347–1364.
- Thomas, L., Buckland, S. T., Newman, K. B., and Harwood, J. 2005. A unified framework for modelling wildlife population dynamics. *Australian and New Zealand Journal of Statistics*, 47: 19–34.
- Thorpe, J. E. 2007. Maturation responses of salmonids to changing developmental opportunities. *Marine Ecology Progress Series*, 335: 285–288.
- Thorpe, J. E., Mangel, M., Metcalfe, M., and Huntingford, F. A. 1998. Modelling the proximate basis of salmonids life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology*, 12: 581–599.
- Todd, C. D., Friedland, K. D., MacLean, J. C., Whyte, B. D., Russell, I. C., Lonergan, M. E., and Morrissey, M. B. 2012. Phenological and phenotypic changes in Atlantic salmon populations in response to a changing climate. *ICES Journal of Marine Science*, 69: 1686–1698.
- Walters, C. J. 1985. Bias in the estimation of functional relationships from time-series data. *Canadian Journal of Fisheries and Aquatic Sciences*, 42: 147–149.
- Youngson, A. F., MacLean, J. C., and Fryer, R. J. 2002. Rod catch trends for early-running MSW salmon in Scottish rivers (1952–1997): divergence among stock components. *ICES Journal of Marine Science*, 59: 836–849.

Appendix 1: Dirichlet–multinomial distribution

Demographic transitions are modelled using Dirichlet–multinomial (DM) distributions that capture demographic stochasticity. The DM distribution can be interpreted as an overdispersed Multinomial distribution.

If N individuals face any demographic transition with k possible outcomes ($i = 1, \dots, k$) with associated probability $\mu_{1:k} = (\mu_1, \dots, \mu_k)$ with $\sum_{i=1}^k \mu_i = 1$, then, given the hypothesis that all individuals are mutually independent and with the same probabilities $\mu_{1:k}$, the numbers of individuals in each outcome (N_1, \dots, N_k) are distributed as a Multinomial distribution, with the variance–covariance structure in Eq. (A1.1). If $k = 2$, then the Multinomial in Eq. (A1.1) is replaced with a binomial.

$$(N_1, \dots, N_k) \sim M(N, \mu_{1:k})$$

$$\begin{cases} E(N_i) = N \mu_i \\ V(N_i) = N \mu_i(1 - \mu_i) \\ cov(N_i, N_j) = -N \mu_i \mu_j \end{cases} \quad (\text{A1.1})$$

A DM distribution is the distribution of (N_1, \dots, N_k) that results from the convolution of the Multinomial in Eq. (A1.1) with a

Dirichlet distribution for (μ_1, \dots, μ_k) (if $k = 2$, the Dirichlet is a beta and the DM is a beta-binomial distribution). The more dispersed the Dirichlet distribution, the more dispersed the DM. Parameters of the Dirichlet distribution for (μ_1, \dots, μ_k) are denoted $(\alpha_1, \dots, \alpha_k)$. A useful way to parameterize a Dirichlet distribution consists of introducing $\eta = \sum_{i=1}^k \alpha_i$, the degree of the Dirichlet distribution, as shown in Eq. (A1.2). η controls the dispersion of the distribution. The larger η , the less dispersed the distribution is.

$$(\mu_1, \dots, \mu_k) \sim (\alpha_1, \dots, \alpha_k)$$

with $\alpha_i = \eta \theta_i$, $\sum_{i=1}^k \theta_i = 1$ and $\eta = \sum_{i=1}^k \alpha_i$

$$\begin{cases} E(\mu_i) = \theta_i \\ V(\mu_i) = \theta_i(1 - \theta_i) \frac{1}{\eta + 1} \\ cov(\mu_i, \mu_j) = -\theta_i \theta_j \frac{1}{\eta + 1} \end{cases}$$

Then, if $\mu_{1:k} = (\mu_1, \dots, \mu_k)$ are distributed as a Dirichlet in Eq. (A1.2), and if (N_1, \dots, N_k) given $\mu_{1:k}$ are distributed as a Multinomial in Eq. (A1.1), then the marginal distribution of (N_1, \dots, N_k) is DM with parameters $\theta_{1:k} = (\theta_1, \dots, \theta_k)$ and η (Eq. (A1.3)).

$$(N_1, \dots, N_k) \sim DM(N, (\theta_1, \dots, \theta_k), \eta)$$

$$\begin{cases} E(N_i) = N_i \theta_i \\ V(N_i) = N \theta_i (1 - \theta_i) \frac{N + \eta}{\eta + 1} \\ cov(N_i, N_j) = -N \theta_i \theta_j \frac{N + \eta}{\eta + 1} \end{cases} \quad (A1.3)$$

The overdispersion factor of the DM distribution (by reference with the variance–covariance of a Multinomial distribution) is $(N + \eta)/(1 + \eta)$. The higher η , the lower the variance of the DM. At the limit when $\eta \rightarrow \infty$, this overdispersion factor \rightarrow and the DM distribution converges to a Multinomial distribution.

Let us now show how a DM distribution can be applied to a demographic transition, where natural and fishing mortality occurs simultaneously. Let us define a number of fish N_t entering a fishery where fish die from natural mortality M , and fishing mortality F , both occurring simultaneously during a duration Δt . Then, the surviving fish $N_{t+\Delta t}$, the fish that die from natural mortality $D_{t+\Delta t}$, and catches $C_{t+\Delta t}$ can be modelled through a DM distribution:

$$(N_{t+\Delta t}, D_{t+\Delta t}, C_{t+\Delta t}) \sim DM(N_t, (\theta_1, \theta_2, \theta_3), \eta) \quad (A1.4)$$

with

$$\begin{cases} \theta_1 = e^{-(F+M)\Delta t} \\ \theta_2 = \frac{M}{F+M} (1 - e^{-(F+M)\Delta t}) \\ \theta_3 = \frac{F}{F+M} (1 - e^{-(F+M)\Delta t}) \end{cases}$$

θ_1, θ_2 and θ_3 represent the probability that a fish will survive, die naturally or be caught, respectively, defined by a Baranov equation (Baranov, 1918, 1925).

If only natural mortality occurs (no fishing), Eq. (A1.4) then collapses to:

$$(N_{t+\Delta t}, D_{t+\Delta t}) \sim DM(N_t, (\theta_1, \theta_2), \eta) \quad (A1.5)$$

$$\text{with } \begin{cases} \theta_1 = e^{-M\Delta t} \\ \theta_2 = (1 - e^{-M\Delta t}) \end{cases}$$

which is also a beta-binomial distribution for the survival, with θ_1 (respectively, $\theta_2 = 1 - \theta_1$) the probability of surviving (of dying, respectively). The transition can be alternatively parameterized directly with $(\theta_1, 1 - \theta_1)$ instead of $(M, \Delta t)$.

Appendix 2: First order autoregressive process

Time-series of several parameters are modelled *a priori* as a first-order autoregressive process to capture smoothed fluctuations in environmental variability. Let us define δ_t a parameter defined for any t on the time-series $t = 1, \dots, n$. The prior distribution on δ_t can be defined by the recursive equation (A2.1):

$$\text{for } t = 1, \dots, n - 1, \delta_{t+1} = \mu_\delta + \rho_\delta (\delta_t - \mu_\delta) + i\delta_t, \quad (A2.1)$$

with the innovations defined as independent random term $i\delta_t \sim N(0, \sigma_{i\delta}^2)$, and ρ_δ the coefficient of correlation with $|\rho_\delta| < 1$. Equation (A2.1) defines a first order autoregressive process (AR_1) with a Normal asymptotic distribution with expected mean μ_δ and variance $\sigma_\delta^2 = \sigma_{i\delta}^2 / (1 - \rho_\delta)$. To initialize the recursive equation (A2.1), the first term can be drawn *a priori* in the stationary distribution:

$$\delta_{t=1} \sim N(\mu_\delta, \sigma_\delta^2) \quad (A2.2)$$

Equations (A2.1) and (A2.2) define the prior distribution for the time-series $\delta_{t=1:n}$ that follows an AR_1 parameterized by the asymptotic expected mean μ_δ , the coefficient of correlation ρ_δ , and the variance of innovations $\sigma_{i\delta}^2$:

$$\delta_t \sim AR_1(\mu_\delta, \rho_\delta, \sigma_{i\delta}^2) \quad (A2.3)$$

If the parameter of interest is constrained between 0 and 1 (i.e. a maturation probability or a survival probability), then the AR_1 can be parameterized in the logit-scale. In the case of a parameter constrained to be >0 , the AR_1 can be parameterized in the log scale.

Appendix 3: Faroes and Greenland distant water fishery

Time-series of catches of Faroes and West Greenland fisheries ($C_{6,t}$, $C_{10,t}$, $C_{11,t}$ and $C_{12,t}$) are directly derived from ICES (2010) and no observation errors are considered (Table A3.1). The number of fish caught and declared in the Faroes, which are available by sea ages ($C_{F1,t}^{dec}$ and $C_{F2,t}^{dec}$), are corrected to account for the proportion of discarded catches, the proportion of wild fish in catches, the proportion of mature fish (for ISW) and the proportion of these catches attributed to eastern Scotland. Catches declared in the western Greenland fishery ($C_{WG2,t}^{dec}$) are corrected to account for the proportion of catches from European stocks and the proportion from eastern Scotland (Figure A3.1). No correction for the declaration rate is needed as estimates of reported catches have already been added to the declared catches (for years 1993–2007).

Table A3.1. Data used to compute the number of fish caught in the mixed stock fisheries at Faroes and West Greenland.

Parameters	Definitions	Values
$C_{F1,t}^{dec}$	Declared 1SW catches in Faroes fishery	Time-series
$C_{F2,t}^{dec}$	Declared 2SW catches in Faroes fishery	Time-series
$C_{WG2,t}^{dec}$	Declared catches in West Greenland fishery	Time-series
	Proportion of fish from Scotland in 1SW maturing fish Faroes catches	0.20
	Proportion of fish from Scotland in 1SW non-maturing fish Faroes catches	0.192
	Proportion of maturing fish in 1SW Faroes catches	0.78
	Proportion of unreported catch rate in Faroes fishery	0.10
	Proportion of wild fish in Faroes fishery	Time-series
	Proportion of fish from NE in West Greenland catches	Time-series
	Proportion of fish from Scotland within catches of Northern European fish	0.645

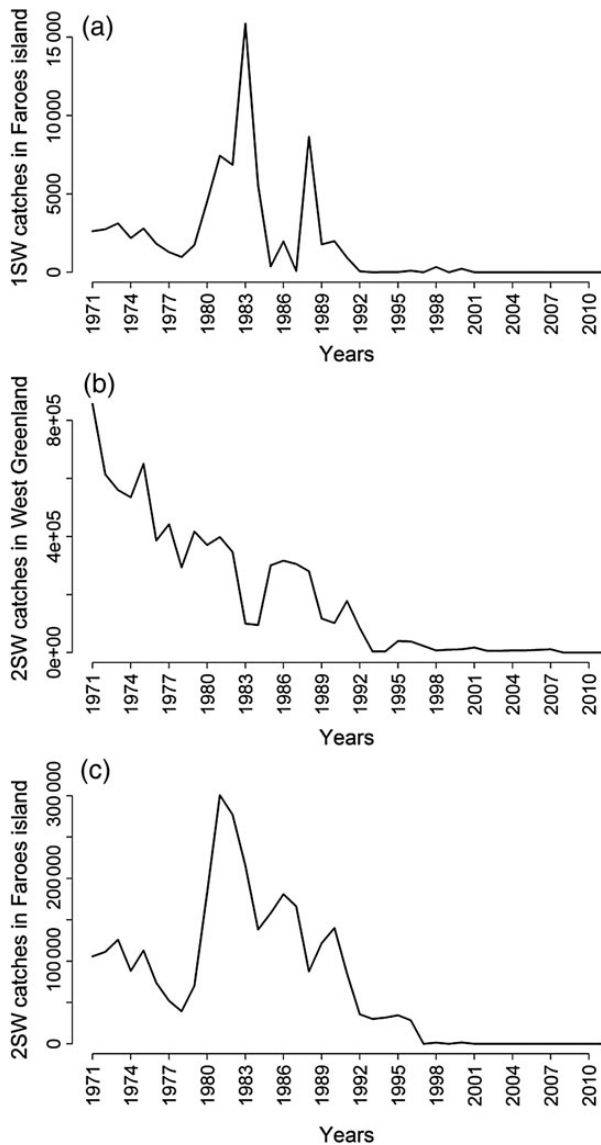


Figure A3.1 Time-series of total catches of (a) 1SW salmon in the Faroes ($C_{F1,t}^{dec}$), (b) non-maturing fish in West Greenland ($C_{WG2,t}^{dec}$), and (c) 2SW fish in the Faroe ($C_{F2,t}^{dec}$).

Appendix 4: Homewater catches

Time-series of declared homewater catches ($C_{1SW,t}^{dec}$ and $C_{2SW,t}^{dec}$) are directly derived from ICES (2010) (Figure A4.1a). Informative priors based on expertise are set for the harvest and the declaration rates of homewater fisheries. The informative prior on declaration

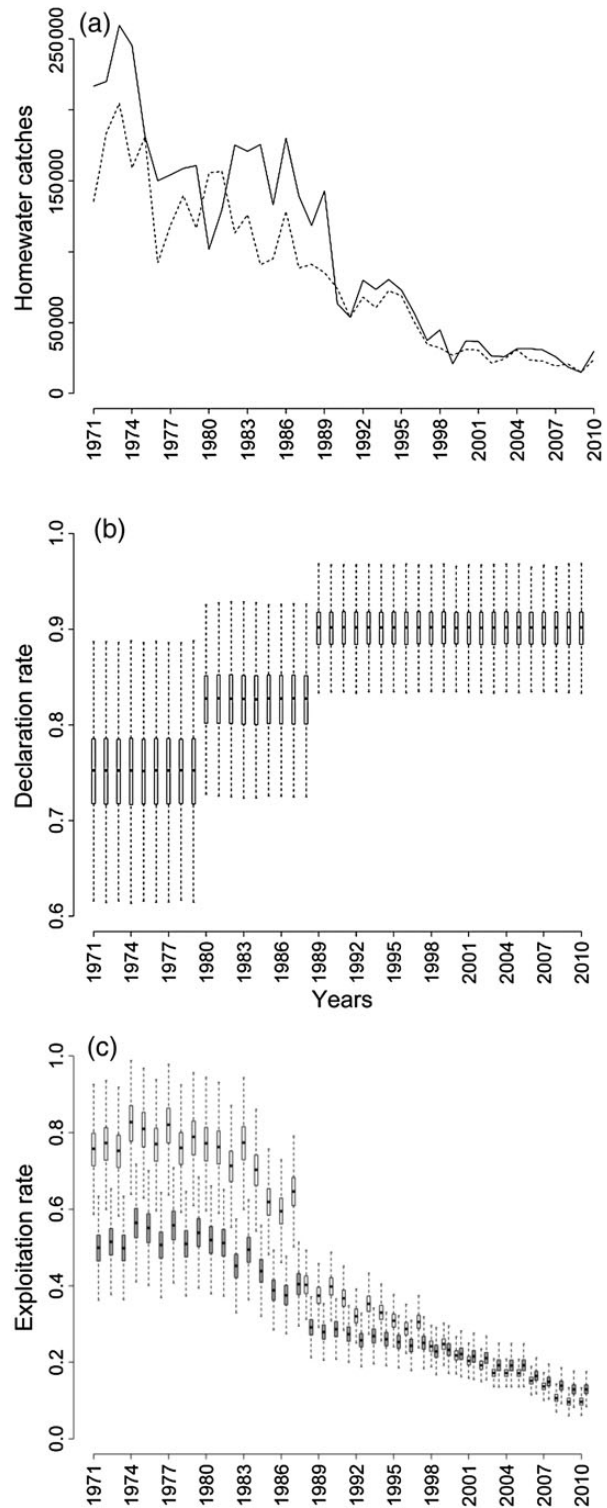


Figure A4.1 Time-series of (a) declared homewater catches of 1SW and 2SW (plain line and dotted line, respectively) and associated (b) exploitation rate (same for both sea ages), and (c) declaration rate for 1SW (white and grey boxplots, respectively).

rates (Figure A4.1b) are based on best judgement estimates made by local river/fisheries managers in some eastern areas of the country (ICES, 2002). Unreported catches are argued to be greater in the west of Scotland than in the east owing to less surveillance of the reporting of salmon catches and to the smaller size and greater number of rivers in the west. Informative priors on exploitation rates (Figure A4.1c) are best estimates derived using reported effort and estimate of standard fishing effort units based on net fishery surveys (ICES, 2002).

Appendix 5: Posterior checking

The consistency between the model and the data is checked using Bayesian posterior checking procedures (Gelman et al., 2004). For each series of homewater catches, the chi-square statistic is computed as a summary measure of the discrepancy over the whole

time-series (Eq. (A5.1)).

$$\chi^2(C_{s,t}^{dec}, (h_{s,t}, r_{s,t})) = \sum_{t=1}^n \frac{(C_{s,t}^{dec} - E(C_{s,t}^{dec} | h_{s,t}, r_{s,t}))^2}{\text{Var}(C_{s,t}^{dec} | h_{s,t}, r_{s,t})}, \quad (\text{A5.1})$$

where n is the number of observations in the homewater catch series and s the sea-age class. For each set of parameters drawn in their joint posterior distribution, the realized discrepancy χ_{obs}^2 computed with the observed values of declared catches $C_{s,t}^{dec}$ is compared with the predicted discrepancy χ_{pred}^2 computed with the posterior predictive replicates of $C_{s,t}^{dec}$. If the data and the model are consistent, observed data should be similar to replicated data simulated *a posteriori* by the model. The Bayesian p -value is the probability that $\chi_{pred}^2 > \chi_{obs}^2$ estimated from a sample of $(h_{s,t}, r_{s,t})$ values drawn in their joint posterior distribution. Very high (> 0.95) or very low (< 0.05) p -values provide serious warning about the possible inconsistencies between the data and the model *a posteriori* (Gelman et al., 2004).

Handling editor: Shijie Zhou