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Deliverable abstract

This deliverable describes the work carried out to harmonize the modelling approaches of the stock assessment of Atlantic salmon. The deliverable consists of three parts each of which is a potentially publishable manuscript: (1) Suggested general methodological approach and an evaluation of the current North Atlantic and Baltic methodologies against this approach; (2) Initial modification of the General Population Dynamics Model (GPDM) for modelling of a single salmon stock; and (3) Introduction and demonstration of a new Bayesian state-space model tailored to the assessment of Atlantic salmon stocks in the North Atlantic. The two last manuscripts come of the first one and thus are appendices of the first manuscript.

Abstract

North Atlantic (NA) stock assessments address the marine phase, estimating returns to home waters, with Pre-Fishery Abundance (PFA) estimated through raising of national (or regional) annual catches by exploitation rates and attributing unreported catch and natural mortality ranges in Monte Carlo simulations. Baltic stocks in contrast, are estimated through integrated Bayesian life cycle state-space models including riverine and sea phases (Michielsens *et al.*, 2008). There is presently no interaction between the two methodologies.

We detail the two approaches specifying similarities in biology, as a prerequisite to their harmonization for parallel inference and risk analysis, independent of scales, available data and management objectives.

Through aggregations of scale and availability, assimilations of data differ. For the Baltic much is performed within the forecasting framework, and while aggregations in the NA case are disparate, finer scale details are available. In the Baltic a scale of "river" is used as the geographical unit, while in the NA, 3 geo-regions are treated independently, each operating at arbitrary regional scales.

To harmonize NA and Baltic approaches, a multi-scale integrated life cycle model in a Hierarchical Bayesian Modelling (HBM) framework is proposed for the NA to capture inherent complexities from mixing of life cycle age and stage cohorts, which is currently not addressed. A stage-structured life cycle approach is proposed, incorporating freshwater and marine phase variability of life histories (survival and life history choices) and auto-regenerated cohort dynamics. This represents a large change in both the modelling and statistical inference framework.

Key structural hypotheses and common informative prior distributions for modelling demographic processes, for both NA and Baltic models are developed. Together with the Bayesian methodology these form the core of the harmonization process.

To harmonize modelling of the demographic process the following items are necessary:

- State-space representation of all life stages including those not directly observed to explicitly separate out modeling of the demographic and observation processes, so as the harmonization of the models for the core ecological process can be thought independently from the data availability.
- Age/stage-based demographic models to integrate biological and ecological knowledge of population dynamics, characterized by seaward migrations of smolts and spawning migration of adults back to freshwater, accommodating intra- and inter-population variability in life history traits.
- Probabilistic demographic transitions and between-years variability of certain parameters to capture both environmental and demographic stochasticity.
- Variable egg to juvenile density-dependent average survival, of classical survival functions.
- Common approach to forecast yearly variations of marine post-smolts survival.

Using common informative prior information to exchange information between Baltic and NA in:

- Time series on egg deposition and recruitment (smolts) for all rivers to describe freshwater stock-recruit dynamics.
- Common informative priors on natural mortality rate after the first year at sea.

A Multi-scale approach incorporating dynamics of stock complexes for:

- Hierarchical structures on parameters to accommodate spatial levels and capture associated level variability.
- Prerequisite to manage multiple instances of mixed and single stock exploitation.
  Introduces flexibility for data assimilation.

A Bayesian framework to assess population dynamics of Atlantic salmon (*Salmo salar* L.) for management purposes - from a generic approach to applications

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Introduction

International assessments of Atlantic salmon (*Salmo salar* L.) stocks are presently undertaken by several means and at several scales. North Atlantic (NA) stock assessments address the marine phase, estimating returns to home waters. For the west Atlantic and east Atlantic population assemblages (hereafter denoted as stock complexes), estimates of Pre-Fishery Abundance (PFA) are made through raising of national (or regional) annual catches by exploitation rates and attributing unreported catch and natural mortality ranges in Monte Carlo simulations. Baltic stocks in contrast, are estimated through an integrated Bayesian life cycle state-space model including the riverine and sea phases (Michielsens *et al*., 2008). There is presently no interaction between the two assessment methodologies.

While the populations are of the same species, there is believed to be limited interaction between them, with Baltic salmon remaining largely within the confines of the Baltic Sea. Similarly there is believed to be limited interaction between populations of the East and West Atlantic, other than multi-sea winter European salmon sharing Greenland feeding grounds with North American salmon (Figure 1). But even with limited interactions and differences in migration ranges, the observed patterns in catches, marine survivals and estimated population sizes show generally similar trends; reductions since the mid 1980s/early 1990s (ICES, 2012a; ICES, 2012b), and this in light of comparable reductions in fishing effort – marine and freshwater – across all areas.

With mounting interest in linking geographically separated systems that have similar processes (Ranta *et al.*, 1997; Post and Forchhammer, 2002; Liebhold *et al.*, 2004 ; Grosbois *et al.*, 2008 ; 2009) and an abiding interest in salmon stock assessments, there is credible interest in bringing assessment methodologies of the three Atlantic salmon population assemblages into alignment. In order to facilitate transfer of knowledge among data sets, variables and parameters, firstly the assessments need to be developed into similar structures.

Here, we detail the Baltic salmon assessment model and propose a new NA salmon assessment model in a Hierarchical Bayesian Modelling framework, and describe their constructs as a necessary step to lay the foundation for harmonizing the modelling approach. This will provide a way to specify similarities in the biology of the species and to harmonize methodological approaches for inferences and risk analysis, independently from the specificities in scales, available data, and management objectives.

Hierarchical Bayesian Models (HBMs; Clark, 2005; Clark, 2007; Cressie *et al.*, 2009) have revealed a valuable approach for integrated life cycle modelling. They have proved successful for embedding complex demographic models within statistical models for various sources of data, and provide inferences together with a fair appraisal of the uncertainty around estimates or predictions (Thomas et al., 2005; Buckland et al., 2007; Parent and Rivot, 2012). HBMs have been applied for age-structured (Millar and Meyer, 2000; Lewy and Nielsen, 2003; Juntunen *et al.*, 2012), stage-structured (Rivot *et al.,* 2004; Ruiz *et al.,* 2009; Swain *et al.,* 2009) fish population dynamics, and have the potential to greatly improve the biological realism in modelling approaches for fisheries stock assessment (Kuparinen *et al.,* 2012).

In the HBM framework (Figure 2), the existing biological and ecological knowledge becomes first integrated into a population dynamic model in the form of a set of one or alternative model structures (deterministic or stochastic equations) and prior distributions on parameters. This body of prior knowledge forms the prior about the population dynamic, and will then be updated after assimilating the available data (Thomas *et al.,* 2005; Buckland *et al.,* 2007; Parent and Rivot, 2012).

An important point here is that the prior structure about the population dynamics should not depend upon the data available, but rather on the available understanding about the causal dependencies of the system described. Because HM's work by explicitly separating out the demographic model from the data assimilation, they provide a flexible and ideal framework for harmonizing the modelling approach, but by maintaining the constitutive specificities in terms of spatial scales and associated level of details in data assimilation process, that characterize the NA and the Baltic models. Beyond these specificities, setting the assessment within the HBM framework has the potential to motivate harmonizing the structure and parameterization of the population dynamic model, which crystallizes the core of knowledge and hypotheses about the demographic processes, and for which many features are common between A. salmon in the NA and in the Baltic. Whenever possible, this means (1) harmonizing the structural forms of the equations used for key demographic transitions and; (2) harmonizing the informative priors on parameters (or harmonizing the methodology used to derive such informative priors).

Setting both assessments in the Bayesian setting will also harmonize the methodology used for quantifying uncertainty about parameters and state variables (through Bayesian posterior distribution) but also about forecasting (through Bayesian posterior predictive distributions) which is critical for harmonizing the way uncertainty is conveyed to risk and decision analysis.

Biology and life history of Atlantic salmon

Many books and articles have been written about Atlantic salmon, exploring various aspects about the species biology, role in ecosystem, conservation, exploitation, and so on. Here, we give a concise description about facts which are essential for understanding the topics covered later in this paper. Atlantic salmon is native to the temperate and subarctic Atlantic Ocean and its adjacent northern sub-basins and catchments. The life histories comprise both anadromous and landlocked forms. We limit our focus on anadromous forms spawning in riverine habitats because they are by far the most common and productive for fisheries.

In brief, the life cycle of anadromous Atlantic salmon populations includes autumn spawning and spring-time hatching of eggs, typically 1-5 years of juvenile rearing in river, an intense migration of juveniles to sea, further migration at sea to the feeding grounds, and typically 1-4 years of feeding before maturation and an intense and precise homing back to the natal river. Atlantic salmon is iteroparous and has been observed to spawn up to six times (Fleming, 1996), thus the life cycle may include several migrations between spawning river and feeding grounds (Figure 3).

Salmon females select their breeding territories from suitable habitats in a river. High fish densities result in competition of the territories and as a result some females may select suboptimal spawning sites or superimposition of spawning nests may occur, killing a fraction of the previously laid eggs. Immediately after the emergence from spawning nests, salmon juveniles establish territories and compete with each other for space and food in river. This period from spawning of eggs to establishing juvenile territories is the first survival bottleneck and the only one ruled by density-dependent processes in salmon's life. After fry stage but before migration juveniles grow slowly and they are called parr. Juveniles migrating to sea are called smolts; they are physiologically prepared for sea life and have changed the behavior from territorial to shoaling animals. During the sea migration to the main feeding grounds salmon are called post-smolts. This period lasts from 6 months to 1 year, during which salmon become piscivorous and the second survival bottleneck takes place. Older non-mature individuals are also referred to as post-smolts or alternatively migratory adults or pre-adults. These individuals grow fast and reach large enough size to recruit to fisheries. Salmon on the main feeding grounds are pelagic predators and eat mainly small prey fish like capelin, sand eel, sprat and small herring (e.g. Lear, 1972; Hansson *et al.,* 2001; Haugland *et al.,* 2006). Fluctuations in abundance of suitable prey fish affects survival of salmon at the onset of feeding (Chaput and Benoit, 2012; Mäntyniemi *et al.,* 2012). Post-spawning mortality comprises the third survival bottleneck in salmon's life; typically less than 10% of the breeding population returning to breed again (Fleming, 1996). Migration back to rivers to spawn is relatively fast and maturing adults become increasingly homeward oriented (e.g. Thorstad *et al.,* 2011). The amount of repeat spawning varies from almost non-existent up to tens of percent between regions and even between populations of the same region (Niemelä *et al.,* 2006). Post-spawn salmon are called kelts before they have again reached their feeding grounds at sea and reconditioned. A repeat spawner can either spawn the next year after the first spawning ('consecutive repeat spawner') or after a longer stay at sea ('alternative repeat spawner'). The majority of repeat spawners are highly fecund large females.

Male and female Atlantic salmon exhibit different life history traits to achieve reproductive success. Both sexes invest the same amount of energy during reproduction, but females invest in egg production whilst males invest in mate competition (Fleming and Einum, 2011). These differences give rise to sex specific age of maturation, behavior and post-spawning mortality. A proportion of male parr mature and do not undergo sea migration, investing in an alternative mate competition and reproduction tactic called 'sneaking'. As a result females comprise the majority of migratory individuals.

Because of the precise homing, spawning rivers sustain genetically distinct populations of Atlantic salmon. Conditions prevailing in the specific natal river and the migration route are also likely to induce adaptation with differentiation in the quantitative traits between the populations (e.g. García de Leániz *et al.,* 2007). Moreover, survival at various life stages may differ remarkably between populations, because river specific conditions (habitat quantity and quality, primary production, water quality, annual flow regime, fish fauna) largely dictate reproduction dynamics of each population. This entails variation in the productivity and resilience to exploitation between populations.

Based on the above, salmon life cycles can be divided into stages characterized by different environments, survival levels, survival factors (both density-dependent and density-independent), behavior, growth and availability to different fisheries and predation. The biological parameters at each stage and in the transition between stages, often differ between populations and between male and female salmon.

Fisheries and current assessment methodologies of salmon

Baltic salmon

Atlantic salmon in the Baltic Sea are harvested by an offshore fishery on the feeding grounds, and by coastal, river mouth and river fisheries during the spawning migration (Christensen and Larsson, 1979; Christensen *et al.*, 1994) (Figure 1). Whilst the offshore fishery is assumed to harvest different salmon populations uniformly, fisheries intercepting spawning migrations harvest different populations by different intensity. Apart from wild salmon, the Baltic Sea supports large numbers of hatchery-reared salmon, which are annually stocked as smolts in the mouths of the rivers regulated by hydropower plants.

Management objectives for Baltic salmon are set against the estimated river specific capacities to produce juvenile salmon, i.e. Potential Smolt Production Capacities (PSPC's). Assessment is designated to provide annual catch (TAC) advice for commercial fishing at sea, taking into account also other removals of fish by human. Since 2002, a Bayesian approach to statistical inference has been used for the assessment (ICES, 2002). An overview of the entire assessment model with the different sub-models, data or information used within the sub-models and their outputs, can be found in Figure 4, and Tables 2 and 3. Population dynamics of each wild river stock are traced separately, but in the sea salmon from all rivers are assumed to face the same natural mortality. Furthermore, fishing mortalities are assumed to be partially the same among river stocks, depending on how similar their migration routes are.

Within the Baltic Sea, no stock-recruit data as such are available. A Bayesian network model (Uusitalo *et al.*, 2005) has been used to obtain the prior distribution for the PSPC of different Baltic salmon rivers. The model is based on expert opinions or judgments of the characteristics of the river environments and the corresponding salmon stocks. Furthermore, a hierarchical analysis of Atlantic salmon stock-recruit data has been undertaken in order to estimate the likely form of the stock-recruit function (Michielsens and McAllister, 2004). Yearly smolt production estimates are required to assess the smolt production in relationship to the PSPC. A mark-recapture model (Mäntyniemi and Romakkaniemi, 2002) is used to obtain yearly smolt production estimates for the rivers with smolt trapping data. For most rivers, however, only electrofishing data are available. Results of the rivers with both electrofishing and smolt trapping data are used within a hierarchical linear regression analysis to estimate the smolt abundance in the rivers with only electrofishing data (ICES, 2004, Annex 2).

A full life history model was developed to assimilate the above information with the rest of the available information about Baltic salmon (Michielsens *et al.*, 2008). The model requires estimation of life history and fisheries related parameters. Tagging data contains much information about these parameters and they are analysed using a mark-recapture model (Michielsens *et al.*, 2006), which is inbuilt in the life history model. The other main sources of data used in the model are catches, effort, spawner counts and catch samples (age distributions, proportions of wild and reared salmon). As a result, fisheries parameters, mortality, maturation rates, stock specific stock-recruit parameters (including PSPC's) and estimates of abundance become updated. The results of the assessment model are used to calculate the probabilities that a management objective is reached or will be reached under different assumptions about future exploitation and states of nature.

North Atlantic

Atlantic salmon from eastern North America and the northeast Atlantic countries of Europe undertake feeding migrations to the NA and have the potential to be harvested in fisheries at West Greenland and the Faroes (Figure 1). These mixed stock high seas fisheries were of sufficient concern that an international body (the North Atlantic Salmon Conservation Organization - NASCO) was formed in 1982 to manage the marine fisheries on Atlantic salmon based on a fixed escapement management strategy. Management advice is based on a forecast of salmon abundance prior to the fisheries, with the objective of achieving the spawner requirements (biomass limits) for the contributing stocks on both side of the Atlantic ocean.

More than 2000 salmon producing rivers have been identified in the NA (Crozier *et al.*, 2003), out of which less than 25% are assessed (Crozier, 2003; ICES, 2001). Hence, models have been developed considering units of stocks at a national or regional scale (Tables 1, 2).

Catch advice is provided for both the Faroes fishery and the West Greenland fishery using two models for stock assessment and forecasting: i) for the non-maturing 1 sea-winter (1SW) salmon of the North West (NW) stock complex (Table 1) (Rago *et al.*, 1993; Chaput *et al.*, 2005) and; ii) for maturing, 1SW salmon (which have spent one winter at sea before returning to their river of origin) and non-maturing, multi sea-winter (MSW) salmon (which spend more than one year at sea and extend their migration to the north-western Atlantic). This includes salmon from the South East and North East (SE and NE) stock complexes, where only the non-maturing MSW salmon are available to the West Greenland fishery (Potter *et al.*, 1998) (Figure 1).

Both models are based on generally similar data and similar approaches, including a variable to define the spawning potential (lagged spawners or lagged eggs, see below) and a recruitment variable termed the PFA (Pre-Fishery Abundance) which is the abundance of post-smolts considered on the 1st of January of the first winter at sea, just before the first high sea fishery, with a function relating the spawning component to the PFA recruitment. The forecast and risk analysis models consist of several steps:

1. Estimation of the PFA just prior to the fishery at Greenland and Faroes (PFA);
2. Estimation of the spawning stock, which would have contributed to the PFA;
3. Development of a model to forecast abundance of PFA in the year of interest;
4. Development of the catch advice in a risk analysis framework.

The estimation of abundance prior to the fishery (PFA) is done using the run-reconstruction models developed by Rago *et al.* (1993) for the NW complex and by Potter *et al.* (1998) for the SE and NE complex (recently reviewed by Chaput (2012)). PFA at year t is estimated from the catch in numbers in each country/region (Figure 5). Catches are raised to take account of i) estimates of non-reported catches, ii) estimates of exploitation rates, and iii) natural mortality in the time intervals between the instants at which PFA and the fisheries are considered (the annual mortality rate being considered known).

The spawning stock contributing to the PFA of the year of interest is calculated by “lagging” forward in time the number of spawners (lagged spawners, LS) for the NW complex or eggs (lagged eggs, LE) for the NE complex, based on the smolt age distributions in each country/region. The lag consists of the smolt age plus two years, one year for the delay between egg deposition and 0+ juveniles and a further year for the first year at sea). The smolt age proportions are assumed to be constant for each country/ region for the entire time series.

For both the NW, and SE and NE complexes, a series of models incorporating a time series of productivity relating LS (or LE) to PFA have been considered by the ICES Working Group (Chaput *et al.*, 2005; Prévost *et al.,* 2005; Chaput and Prévost, 2006). The spawning stages and the subsequent returns are considered respectively as the independent and response variable in a regression-like approach to estimate a productivity parameter over the time series (Chaput, 2012). These assess for constant or non stationary variation in the parameter, through autocorrelated random walk to capture smoothed variability of the productivity in time, or in phase shift models to capture abrupt changes between two levels of productivity.

Recently the PFA models have been set within a Bayesian framework (Prévost *et al.,* 2009; Rivot *et al.,* 2009) to develop forecast and management models. These allow for the incorporation of uncertainty in the observations and in the processes, to provide a structure for multi-year catch advice in a risk analysis framework consistent with the precautionary approach (Punt and Hilborn, 1997).

Rejoinder – Similarities and differences between the assessments

Assessments both in the NA and Baltic regions are designed to answer the expected management related questions. Because the management questions differ, owing to different objectives, performance measures, management tools, regions and fisheries, the methods (assessments) also differ, in order to best answer them. There are, however, shortcomings in this approach of building assessments expressly to answer only initially posed questions: there is a risk that management questions may change over time and assessment tools dedicated to answer a certain set of questions may not be flexible enough to meet the needs of changed management. Moreover, assessments designed this way are typically poorly comparable with one another, even when the underlying biology is similar. Therefore, there is a need to move beyond the current models towards a more flexible approach.

A fundamental difference exists in the scales used for assessments in the Baltic and the NA regions. Because of the relatively small number of A. salmon rivers in the Baltic (≈ 30 rivers), the scale used in the Baltic is close to ideal, as A. salmon can be assessed and managed based on river-specific stock units (Table 2). Models in the NA are developed at a much more aggregated scale. Indeed, more than 2000 salmon producing rivers have been identified in the NA (Crozier *et al.,* 2003), out of which less than 25% are assessed (Crozier, 2003; ICES, 2001). Hence, units of stocks considered are at a broader national or regional scale (Tables 1 and 2). Beyond these fundamental differences, in both cases, there is a need to build a multi-scale modelling approach to capture the true complexity introduced by the various levels of mixing that occurs through the life cycle.

As a direct consequence of operating at different scales, the data assimilation processes have profound differences between the Baltic and the NA regions. For salmon in the Baltic Sea, the assessment is embedded into a Bayesian life cycle modelling framework (Michielsens *et al.,* 2008) which allows for the assimilation of different sources of data at the scale of rivers (Table 2), such as survey of returns or parr densities that cover virtually all Baltic stocks. By contrast, the PFA models (Chaput, 2012) currently used for stock assessment in the NA are far from a life cycle, and the only compatible and inclusive data sets in the NA models are catch statistics aggregated at a national or regional scale, which form the core of the assessment data in the regions (Table 2). Many other data sources are available however (*e.g.* different types of surveys undertaken in many index rivers) and the quality of the assessment procedure would certainly gain through better use all the available data.

A common methodological ground for a harmonized assessment framework

Integrated life cycle models in a Hierarchical Bayesian Modelling (HBM) framework is proposed as a template for harmonizing the modelling approaches for A. salmon stock assessment in the NA and in the Baltic, while maintaining some specificities.

Owing to the approaches presently taken, the NA approach requires more development than the Baltic for the two to be aligned as comparable stage-structured life cycles. Embedding the assessment models for the NA into a fully integrated stage-structured life cycle model, including variability of life histories (*e.g.*, survival and life history choices) during the freshwater and marine phases, and the cohort dynamics represented as an auto-regenerated process represents a large change of both the modelling and the statistical inference framework.

Below we develop some key structural hypotheses and some common informative prior distributions that are used in modelling demographic processes for both the NA and the Baltic models, and that form the core of the harmonization process, together with Bayesian methodology used for statistical inferences. The work reported in appendices A and B is built on this foundation: Appendix A examines how the proposed ideas could be implemented for a single salmon stock, whilst the foundations of the integrated life cycle model which is currently under development for the NA case are detailed in the Appendix B.

The model already developed for the Baltic case is detailed in Michielsens *et al.* (2008) and associated publications Within the ECOKNOWS project the Baltic model has been developed further as described in the report of the Inter-Benchmark Protocol on Baltic Salmon (ICES, 2012c): more observation models have been built up, the flexibility of the model on data assimilation has been increased, and reparameterization of certain parts of the model has been studied to enable similar use of prior information both in the Baltic and in the NA assessments.

Age and stage based life cycle to harmonize modelling of the demographic process

For both the NA and the Baltic, age and stage-based demographic models (Figure 3) is the template to integrate the body of biological and ecological knowledge about A. salmon population dynamics. The primary common features for the demographic models are given below (Table 3).

- The life cycle is characterized by migrations of smolts from rivers to sea and spawning migration of adults back to freshwater. Key life stages and transitions are identified (Figure 3), but the model should be flexible enough to accommodate the intra- and inter-populations variability in life history traits, such as the time spent as juveniles in freshwater before the seaward migration (smolt age; highly variable between regions) and the time spent as post-smolts at sea before maturing and spawning migration back to home waters (sea age, proportion of repeat spawners).

- A state-space representation is needed as all life stages are not directly observed. In particular, the different life stages at sea are not directly observed, but must be explicitly modelled to represent the influence of both natural and fishing mortality at sea. Hypotheses are made on the migration routes at sea and the impact of fishing mortality is modeled through sequential fishery along the migration routes, including off shore fisheries, coastal fishery and estuarine and freshwater fishery.

- The model includes probabilistic demographic transitions and between-years variability of some parameters to capture both environmental and demographic stochasticity.

- The eggs to juveniles survival rate is considered variable but with a density-dependent average survival. Classical density-dependent survival functions such as Beverton-Holt or Ricker forms are planned to be used in both NA and Baltic models.

- The first months of life at sea, i.e. the transition between smolts and post-smolts measured after the first winter at sea, are considered as the most critical period of the marine phase of the life cycle were most of the natural mortality occurs. The project seeks to develop common methodological approaches to forecast the yearly variations of the marine post-smolts survival rates.

Using informative prior information to exchange information between Baltic and NA

The use of common informative prior probability distributions for some key parameters, derived according to methodologies developed in the project would enable the exchange of information between NA and Baltic cases.

- Especially the time series on egg deposition and recruitment (smolts) collected from the rivers across the distribution area of salmon may contain much information about the general patterns and factors affecting the freshwater stock-recruit dynamics of salmon. The project compiles all the available stock-recruit data and carries out a meta-analysis, the outcome of which could then be used as a prior information about the freshwater productivity of salmon.

- Common (or very similar) informative priors on the natural mortality rate (M) after the first year at sea should also be used.

A multi-scale approach to model the dynamic of stock complexes

A. salmon are characterized by high homing abilities and hence each river represents a potentially discrete population. Hierarchical structures on parameters are used to represent different levels of the spatial structure (e.g., local, regional, global) and to capture the variability associated to each level of the hierarchy (Figure 6).

- Such a multi-scale approach allows for quantifying the relative influence of different factors structuring stock productivity, such as the local quality of reproduction zones in freshwater, the quality of regional coastal marine environment used by post-smolts, and the marine environment that is likely to impact productivity at a larger scale.
- The multi-scale approach is a also a prerequisite for managing exploitation, as it allows for quantifying the effect of sequential fisheries along the migration routes, such as estuarine or freshwater fisheries that impact local populations, coastal fisheries that concern populations at a national or regional level, and off shore fisheries harvesting fish from multinational mixed stocks.
- Lastly, it also provides the flexibility to the data assimilation process. In the HBM framework, data assimilation requires defining a set of probabilistic equations to represent the sampling observation process that has generated the data conditionally upon the state variables (and that defines the likelihood). Observations are typically of different nature (abundance, age or stage structure etc.), concern various life stages and different levels of spatial aggregation, and the multi-scale modelling approach often facilitates matching between model and observations. For instance, offshore catches concern aggregated populations, whereas monitoring smolt or spawner abundance in freshwater during migrations, or mark-recapture data may concern only a single population in a large complex of stocks.

Tables

Table 1. Units of stocks considered in the three A. salmon stock complexes in the North Atlantic (ICES, 2010). No aggregated data are available for Spain.

North West (NW)	Southern North East (S. NE)	Northern North East (N. NE)
Newfoundland	Iceland (East and South)	Iceland (West and North)
Labrador	UK (Scotland)	Norway
Québec	UK (N. Ireland)	Sweden
Gulf of St Laurence	Ireland	Finland
Scotia-Fundy	UK (England and Wales)	Russia
U.S.A (Maine)	France	
	Spain (no data)	

Table 2. Similarities (grey cells) and differences (white cells) in the data assimilation process in the NA and Baltic models. Most of the differences are related to the differences in the spatial scales.

<table>
<tr><th></th><th>North Atlantic</th><th>Baltic</th></tr>
<tr><td>Units of stock in the complex of stocks</td><td>National or regional units
- North West complex: 6 units
- S. North East complex: 7 units
- N. North East complex: 5 units</td><td>Rivers
30 rivers, out of which 15 are fully embedded
Aggregated in 6 units during the marine phase</td></tr>
<tr><td>Time series considered
(year of cohort birth)</td><td>1972-2011 for NW and SE stock complex
1990-2011 for the NE stock complex</td><td>1987-2011</td></tr>
<tr><td>Juveniles</td><td>-</td><td>Survey (electrofishing)
Juvenile mortality (M74)</td></tr>
<tr><td>Smolt production</td><td>Total wetted area accessible to salmon (specific to each stock unit)
Average smolt ages (specific to each spatial unit)</td><td>Habitat inventories
Informative priors (based on expert judgment) on river productivity and carrying capacity
Smolts survey for some rivers and some years</td></tr>
<tr><td rowspan="2">Marine phase</td><td colspan="2">Off shore catches on mixed stocks
Proportion of catches from different stock units
Coastal catches
Proportion of wild fish in catches</td></tr>
<tr><td></td><td>Fishing effort on mixed stock fisheries
Tag recapture data</td></tr>
<tr><td>Returns</td><td>National estuarine and freshwater catches)
Informative prior on declaration rates and harvest rates (from expertise)</td><td>River specific survey of returning spawners</td></tr>
</table>

Table 3. Key structural hypotheses used for modelling demographic processes for both the North Atlantic and the Baltic models. White and grey cells are specific and common hypotheses respectively.

	North Atlantic	**Baltic**
Units of stock in the complex of stocks	National or regional - North West complex: 6 units - S. North East complex: 7 units - N. North East complex: 5 units	Rivers 30 rivers, out of which 15 are fully embedded Aggregated in 6 units during the marine phase
Reared / wild fish	No reared fish represented in the dynamics Catches of wild fish at sea considered as a proportion of total catches	Reared and wild fish represented in the dynamics Specific parameters for both categories
Spawners → Eggs	Number of eggs estimated from the number of spawners per sea ages, proportion of females and fecundity of females in each sea age	
Sex	No sex-specific parameters	
Heritability of life history	No heritability of age at smoltification and sea age	
Eggs → Juveniles	Density dependence + Environmental stochasticity Informative priors on the parameters for the average survival derived from the eggs-to-smolts meta-analysis	
	Prior specific to each spatial units	Prior common to all rivers
Smolt ages	Specific to each spatial units	
	Up to age 4+ smolts	Up to 3+ smolts
Smolts → Post-smolts	Survival during the first months at sea allowed to vary in time Specific to each spatial unit Considered as the main driver of change in stock productivity	
M: Natural mortality at sea after the first winter at sea	Informative prior on M Common to all spatial units (except during Baltic coastal migration) Common to all sea ages (Assumed constant over the time series)	
	M ~ 0.36·year^{-1} (a prob. distribution)	M ~ 0.15·year^{-1} (a prob. distribution)
Maturation of post-smolts and sea ages	Only 2 sea ages explicitly represented No repeat spawners Probability to mature as 1SW allowed to vary in time	Up to 5SW fish No repeat spawners Probability to mature as *n*SW fish - sea age specific - not allowed to vary in time
Sequential fishery	Mixed stock fishery at sea Coastal fishery Estuarine and freshwater fishery (specific to each spatial unit)	

Figures

Figure 1. Migration routes of Atlantic salmon in the North Atlantic and Baltic Sea.

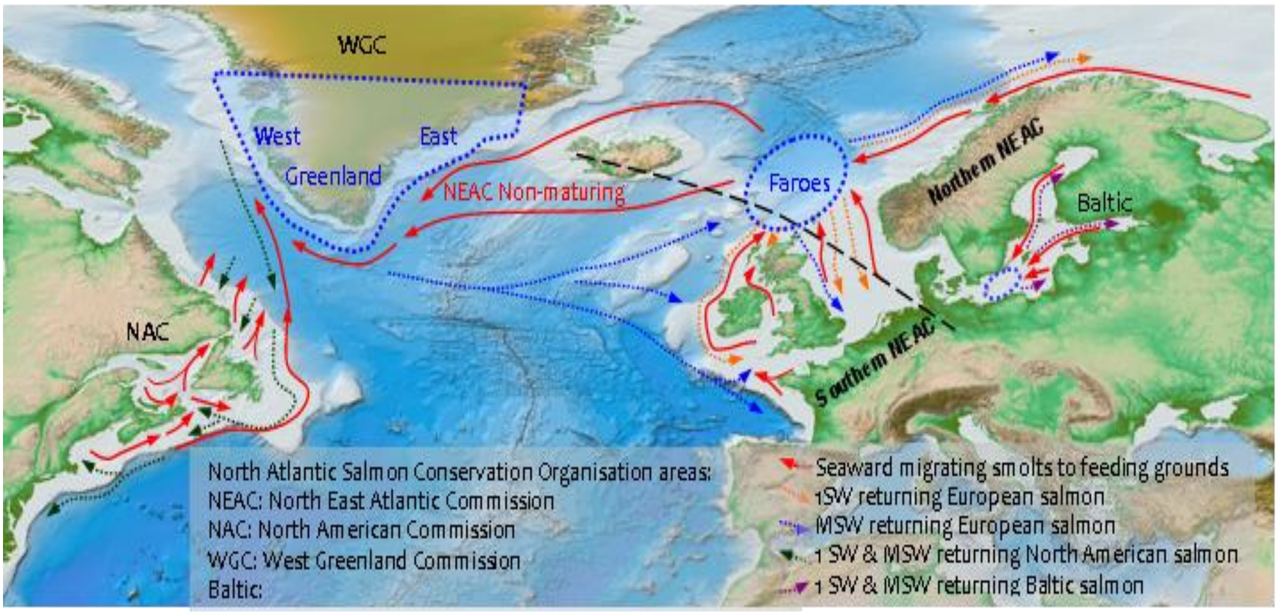


Figure 2. The Bayes rule as a statistical learning mechanism. The prior knowledge is introduced (1) as a prior structure for the demographic transitions; (2) as prior distributions on all parameters and unknown quantities (such as the time series of abundance in the context of stock assessment). The prior knowledge is updated by all available data. Forecasts are derived in the same consistent statistical framework that estimation (posterior predictive distributions) and the consequences of alternative management scenarios can be compared in a probabilistic rationale.

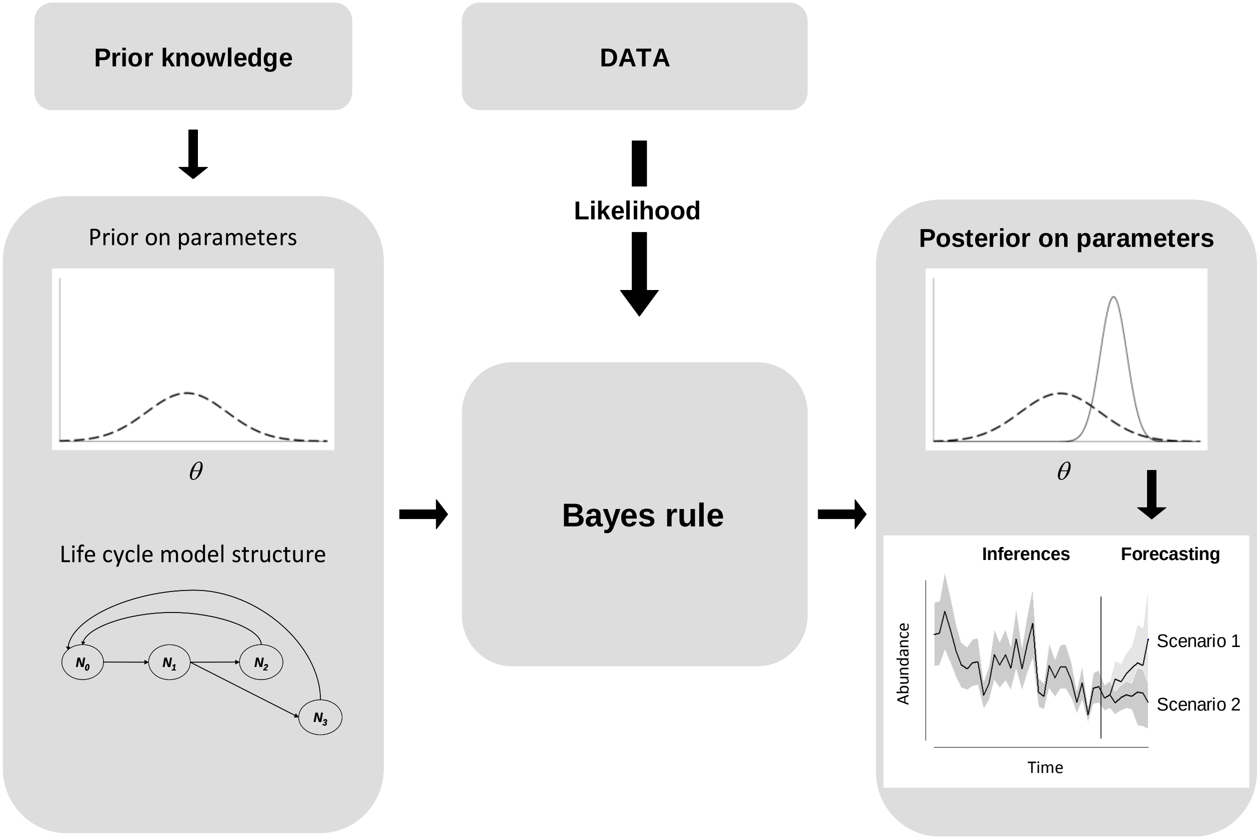


Figure 3. Stage-based Atlantic salmon life cycle model. Each transition (or loop) represents a 1-year step.

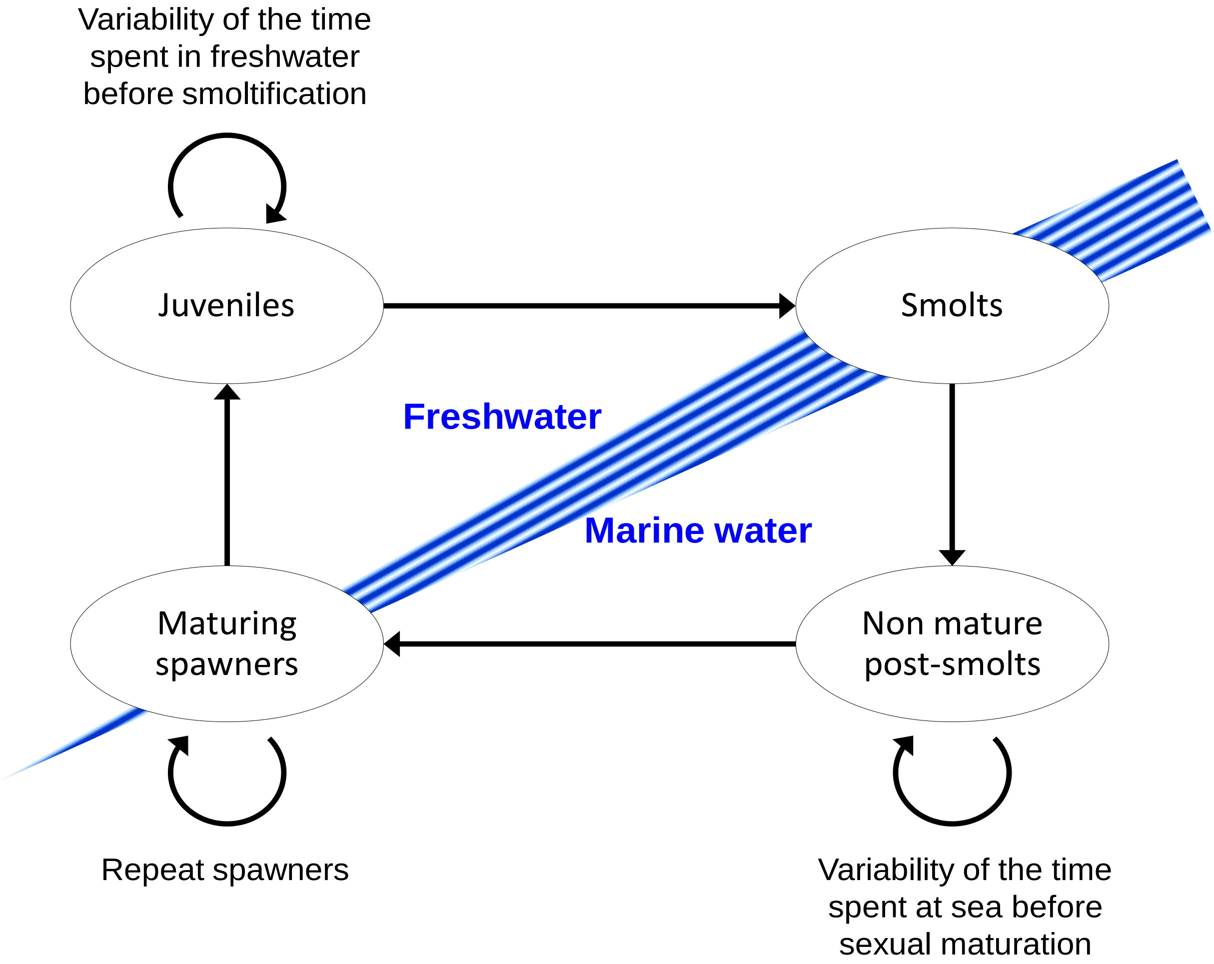


Figure 4. Overview of the entire Baltic assessment model with the different sub-models, data or information used within the sub-models and their outputs (ICES 2012).

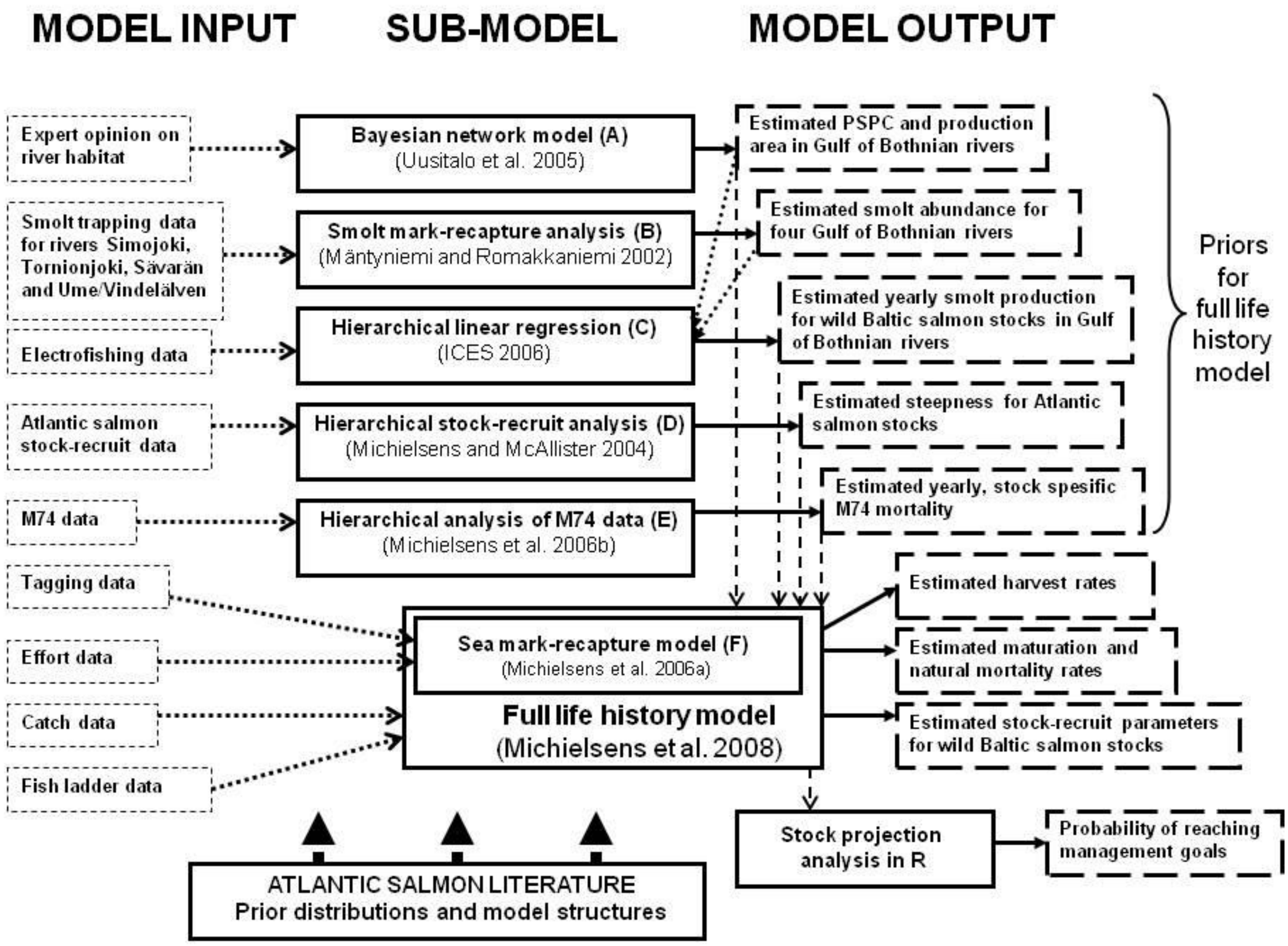


Figure 5. The run reconstruction approach as a basis for the Pre-Fishery Abundance approach.

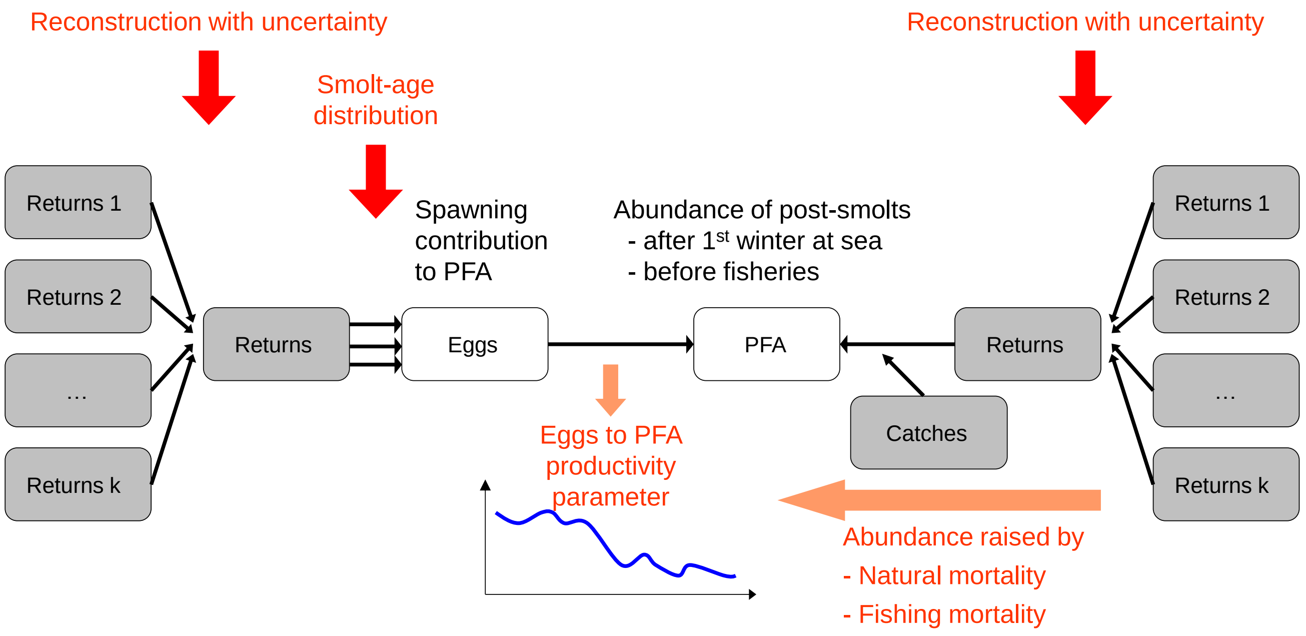
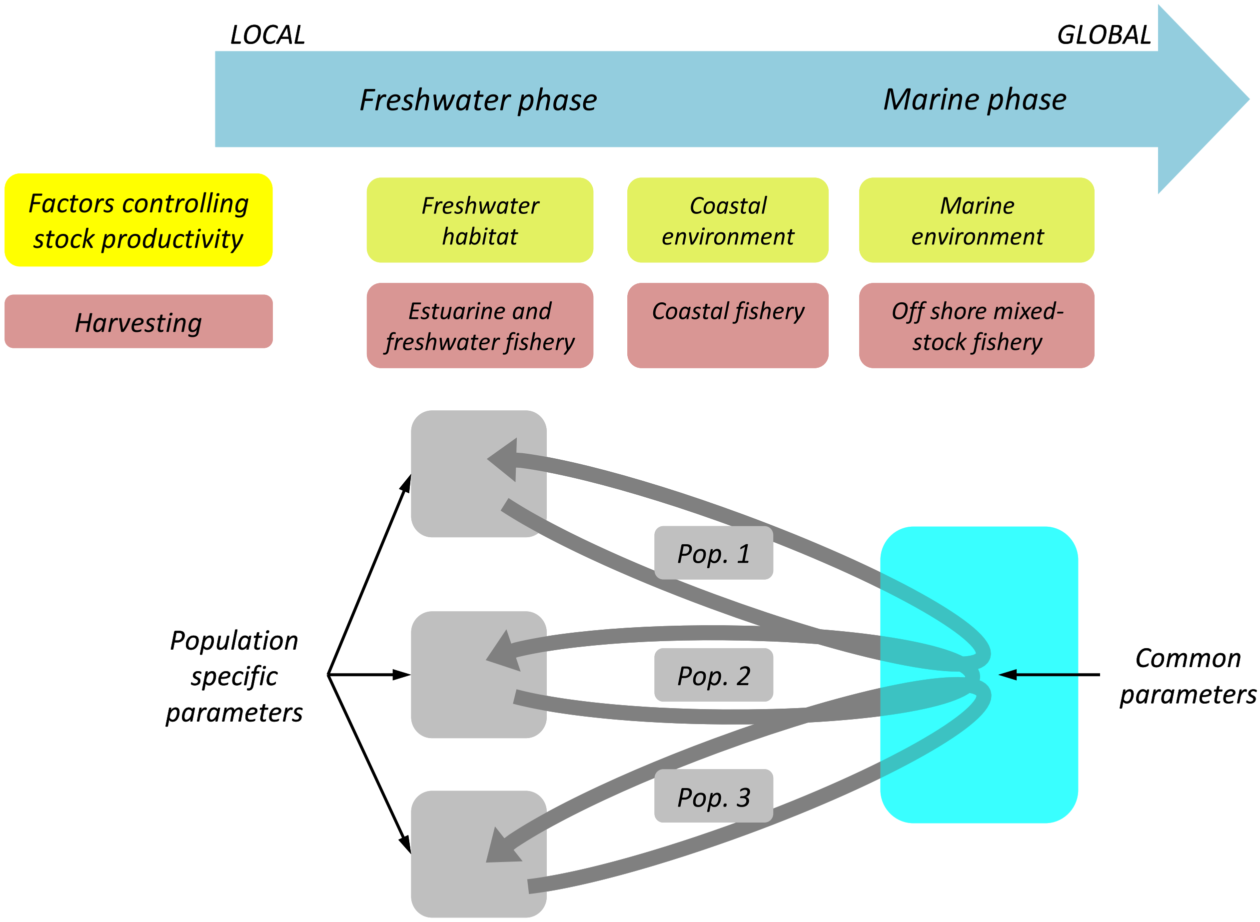


Figure 6. The multi-scale modeling approach used to capture the complexity induced by the various levels of mixing through the life cycle, and to represent the influence of several factors acting on populations, from very local factors acting at the scale of reproduction zones, to those at the global scale, acting when populations are mixed together on off shore feeding grounds. Hierarchical structures on parameters (random effects) are used to represent the different levels of the spatial structure (*e.g.*, local, regional, global) and to capture the variability associated to each level of the hierarchy.



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Appendix A

Modelling the life cycle of a single Atlantic salmon river stock

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Introduction

Many attempts have been to model population dynamics of a salmon stock or population (e.g. Bartholow, 1996; Dumas and Prouzet, 2003; Rivot *et al.,* 2004). 'A stock' is defined here as a river stock (salmon individuals originating from the same spawning river), which may consist of just one population or several sub-populations but with similar dynamics. Almost all the attempts include details about freshwater life of salmon, but few if any include details from the marine life. This can be partly explained by the fact that population/river stock specific models are needed mainly for stock specific management occurring in freshwater, i.e. freshwater life is in focus. However, stock specific management should gain from a coherent, detailed representation of the whole life cycle of a salmon stock; freshwater and marine parts of the life cycle are interrelated and therefore they should not be managed separately from each other.

There has also been a major hindrance to include details about marine life of salmon in these studies. Traditional methods have been unable to utilize diffuse and incomplete data sources typical to the marine phase of salmon. Hierarchical Bayesian state-space models offer a way to overcome this problem (see previous chapter), but so far they have hardly been applied for the marine phase (but see Michielsens *et al.*, 2006; Michielsens *et al.*, 2008; Appendix B),

One solution to model the whole life cycle of a salmon stock is presented here: the General Population Dynamics Model (GPDM; Mäntyniemi, 2012) is modified to make it a suitable platform for the purpose. The same modelling principles which are suggested earlier for the assessment of several stocks and stock complexes are followed, but this approach focuses on building up a platform for inclusion of details and high resolution for the likely parameters of interest. For instance, a separate tracking of males and females within a stock would allow for a more detailed assessment of the stock dynamics, because the effects of sex specific roles and life history strategies on the population dynamics.

The platform we present here is incomplete, because it does not contain all the features common to sea-run salmon populations. Separate tracking of sexes is missing and the reproduction dynamics is not included, either (we feed the model with fixed recruitment). However, the generic and flexible nature of the modelling platform makes it relatively easy for further developments.

The existing ample knowledge base about salmon and its biology gives a good opportunity to set informative priors to various parameters of interest. Here we demonstrate one possible way to utilise the existing information: we adjust priors for natural mortality and maturation so that the outcome in terms of the sea age structure coincides with the knowledge we have about the natural sea age structure of Baltic salmon (e.g. Alm, 1934; Järvi, 1938).

Schematic presentation of the life cycle model

Various presentations exist about salmon's life cycle and the parameters and factors affecting population dynamics of salmon. Here, the presentation aims to collate information which would be useful for a detailed modelling, but it is presented only on a generalized level to avoid entanglement in the often case specific details.

For sea-run Atlantic salmon populations, the life cycle can be divided spatially to riverine, coastal and open sea stages. Individuals of a population occur in and migrate between these areas depending on the individual life history choice, sex and survival, but within certain limits and tendencies as described in the chapter 'Biology and life history of Atlantic salmon'. The spatial division serves as a partial segregation of the life stages of salmon. Moreover, it identifies the different environments salmon is facing during its life, enabling specification of internal and external factors (competition, food, predators, temperature etc.) which affect salmon's life history parameters, especially natural survival. Also fisheries are typically specified following this spatial division.

More than one life stage exists in each of the spatial stages. For instance, post-smolts, kelts, first time matured and repeat spawners all migrate through the coastal migration routes. Therefore, the division to life stages is the primary key to specify the life cycle model and the spatial specification completes the model structure.

Figure A.1 summarizes the above description. Ideally, the life cycle of both sexes and transitions between stages is specified in detail by a state-space presentation. Natural factors and fisheries affecting life history parameters are linked following the established hypotheses. Observations are then assimilated with the model using the HBM framework as described earlier in this paper.

First step of the model development: Example with fixed recruitment and prior distributions for maturation and survival parameters

Next, we illustrate the first step of age and stage based GPDM model with fixed recruitment (1000 smolts per year) and specify prior distributions for the age and/or stage specific maturation and survival parameters. For simplicity, we assume no fishing to take place and as indicated earlier and we also leave at this point the stock-recruitment loop out from the model. This allows us to simplify spatial dimensions of the life cycle (Figure A.1) and concentrate only on the main life stages on feeding and spawning migrations. The main aim is to demonstrate how the prior distributions will impact the size of the population on the feeding and spawning grounds over time and to check that our prior assumptions make sense and provide believable growth of the stock when combined together. Thus, this example offers us a starting point before continuing the work with more complex model versions.

As described in the previous chapter, many biological parameters of salmon depend on the stage of the life cycle the individual belongs to at the specific point of time. Because of this, we separate the life history into the following four stages:

1. Immature salmon at feeding migration

2. Maiden spawning

3. Mature salmon at feeding migration

4. Repeat spawning

Table A.1 illustrates the possible transitions between different stages. The probability to mature and move from stage 1 on stage 2 (p) is assumed to depend on the age (a). Prior distributions for the proportion of maturing salmon at each age are given in Table A.2. From stage 2, all salmon will move to stage 3, returning back to the feeding migration, and after a year, back to the river for repeat spawning. After repeat spawning all salmon will again move back to stage 3. In other words, the mature salmon will keep altering between stages 3 and 4 until they are moved out from the population by the natural mortality. In the model, we have six ages of salmon, age 1 being post-smolts and age 6 being 5 sea winter salmon and older. This means that older salmon than 4SW cannot be distinguished as a cohort, but those keep belonging to the oldest age group until they die.

Following from biology of salmon with existing life history types, all age – stage combinations do not exist and therefore they are ruled out. For example, all post-smolts (age 1) remain at the feeding migration (transition probability into stage 2 is 0) and all 5 sea winter old salmon (age 6) become mature (transition probability into stage 2 is 1), because that is the oldest observed age of first maturation for Atlantic salmon. Furthermore, salmon belonging to ages 1 and 2 cannot yet be on stages 3 or 4 whereas all salmon of age 6 belong either of those two stages.

Survival from annual natural mortality is defined for salmon in different stages based on Table A.3. The post-smolt survival is separated from the survival of other stage 1 salmon, and it is allowed to vary from year to year. For repeat spawning salmon (stage 4) the post-spawning survival is assumed to be the same regardless of the number of earlier (repeat) spawning times.

The model code package for this example is uploaded in the wiki pages of the ECOKNOWS project and is available from the corresponding author upon request. R version 2.15.2 (R Core Team, 2012) and JAGS 3.3.0 (Plummer, 2003) have been used in the modelling.

Results

Based on this model run, we can investigate how the abundances and the age distributions in different life history stages behave over the time series. With the fixed recruitment of 1000 smolts per year we run the model over 25 time steps to give enough time for the stock to reach the stable level of abundance. This stable level has a median around 650 fish with 95% probability interval being roughly [60, 3000]. Figure A.1 illustrates the time series of the stage specific abundances. Immature salmon on the feeding ground (stage 1) are clearly the most abundant, and outnumber salmon which are feeding for the second or more time between the spawnings (stage 3). However, there are some changes for a relatively high abundance of stage 3 salmon, which is apparently a result of such simulation rounds in which survival at stages 2 to 4 are high. This would also lead to high abundance of repeat spawners (stage 4; Figure A.2) because of high survival to the second, third, fourth etc. spawning.

The time series of the age distribution of the maiden spawners (stage 2 salmon) is illustrated in Figure A.2. For simulation technical reasons it is not possible to give zero abundance for any age – stage combination, and thus, the relative proportions for age 1 salmon differ from zero although in principle this age – stage combination should be empty. However, the absolute abundance salmon of age 1 at stage 2 is close to zero throughout the time series. In a stabilized situation, 2- and 3-sea winter spawners (ages 3 and 4) make up the majority of maiden spawners, each accounting for about 40% of them (Figure A.2). Grilse (age 2) and 4-sea winter (age 5) spawners are also similarly abundant and 5-sea winter maiden spawners (age 6) are rare. This age distribution of spawners closely resembles the age distribution reported by Alm (1934) and Järvi (1938) for various Baltic salmon stocks from the period of relatively low fishing intensity. However, the oldest ages of maiden spawners are slightly more abundant in our simulations. Moreover, the abundance of repeat spawners in relation to the abundance of maiden spawners is substantially higher than reported in the past studies.

Discussion and future applications

The greatest advantage of the GPDM framework is its flexibility. Usually population models are designed for a specific fish stock and extending or generalizing the model for the purposes of other stocks or species is very difficult. The core built in GPDM is designed in such a way that it is general for any kind of population, those being fish, birds, mammals etc. The GPDM has already been successfully implemented for herring and European anchovy, and as a multispecies model for some Mediterranean fish species.

Other current alternatives to assess single salmon stocks within a Bayesian framework is to apply the current Baltic assessment model just for one stock (Romakkaniemi, 2008), or to modify the new assessment method designed for the stock complexes of the North Atlantic (Appendix B).

The previous demonstration indicates that the platform modified from the GPDM is a promising step taken towards a generic and flexible tool for salmon stock assessment. Further development of the model would include the following steps:

- Modelling fisheries. For instance, recruitment could denote to the number of tagged and released salmon smolts, and tag recaptures of these individuals from different fisheries can be used to estimate the fisheries specific mortality rates. As a result, data updated estimates can be gained for natural mortalities and stage transition (maturation) probabilities, and those estimates could later be used as informative prior distributions in a model version for the total population.

- Total population model of a river stock could include the prior distributions from tagged population of that river as well as observation models, for example, for different fisheries and smolt/spawner counts or age distributions of the catch sample data. This model would require inclusion of the stock-recruitment function in order to cover the full life cycle. For example, results from Pulkkinen and Mäntyniemi (2013) could be used to provide prior distributions for the stock-recruit relationship.

- A more complex model of the total population could separate sexes, thus giving the opportunity that the maturation, survival and other key parameters may estimate independently for male and female salmon. This would allow inclusion of more complex biological realism into the model and enables modelling of different life history strategies, such as early maturation of male parr and sex specific post-spawning survival which leads to an increasing dominance of females from smolts to repeat spawners.

- The previous steps encompass adding more life stages to the model; inclusion of external factors which affect salmon's life history parameters (Figure A.1) would at the latest require spatial specification of the life cycle. This step would potentially improve the predictive abilities of the model.

Among different stocks of Atlantic salmon many prior assumptions can be made similarly which makes it easier to edit the model for the purposes of other stocks. Here we demonstrated one promising way to set informative priors: although little prior knowledge exists about the likely values of any single survival and maturation parameter of salmon's life, the priors for the parameters can bet adjusted by looking at the suitability of the joint outcome of the priors to the commonly observed demographic features of the populations. We used the historic age distribution of the spawners in the Baltic rivers as the reference against which the priors were adjusted. The resulting age distribution included slightly larger proportion of old spawners, especially repeat spawners, than the historic observations. This is partly due to the fact that we ignored that salmon has a limited lifespan and natural survival must eventually increase as salmon age. However, there are also good reasons why in this method of adjusting priors it is wise not to restrict the joint outcome of the priors too tightly. Similar joint outcome can be attained by quite different combinations of single parameter values, thus there is a risk of choosing 'a wrong combination of values' and by that limiting/centering the range of the values outside the true values.

Many observation models are readily available for data specific for salmon (see, e.g., Michielsens *et al.*, 2008; ICES, 2012; Appendix B). The observation models can be applied for any stocks with similar data, which will again increase scientific learning and remove the need to use repeatedly much effort to tackle the same modelling tasks. This is one reason why data assimilation is expected to be rather straightforward in the model approach presented here.

Many problems in the modelling of the life history of the Baltic salmon stocks have been overcome within the past ten years. The modelling approach tailored for the North Atlantic stock complexes (Appendix B) complements the Bayesian toolbox suitable for the simultaneous assessment of many salmon stocks. The GPDM offers a suitable platform to continue the model development from a point of view of a single stock, hopefully in the future providing us a practical tool for assessing many different stocks independently from each other. This would help us to understand better both the status of stocks from which we have a lot of information, as well as of those from which data is sparse.

Tables

Table A.1. Transition probabilities between different stages. All transitions that have not been presented here have a zero probability.

Transition between stages		
From	To	Probability
1	1	1-p[a]
1	2	p[a]
2	2	0
2	3	1
3	3	0
3	4	1
4	4	0
4	3	1

Table A.2. Proportion maturing per age.

Parameter	Age	Probability/prior distribution	mean	95% PI
p[1]	post-smolts	0		
p[2]	1SW	Beta(1.9,17.1)	0.1	(0.01, 0.27)
p[3]	2SW	Beta(11.6,17.4)	0.4	(0.23, 0.58)
p[4]	3SW	Beta(28.2,18.8)	0.6	(0.46, 0.73)
p[5]	4SW	Beta(35.3,6.2)	0.85	(0.73, 0.94)
p[6]	5SW	1		

Table A.3. Prior distributions (means and 95% probability intervals) for stage specific survival parameters.

	mean	95% PI
Post smolts (stage 1)	0.17	(0.03, 0.40)
Other stage 1 salmon	0.85	(0.75, 0.93)
Spawners (stage 2)	0.35	(0.12, 0.61)
Spawners (stage 4)	0.58	(0.31, 0.79)
Mature salmon, feeding (stage 3)	0.89	(0.81, 0.94)

Figures

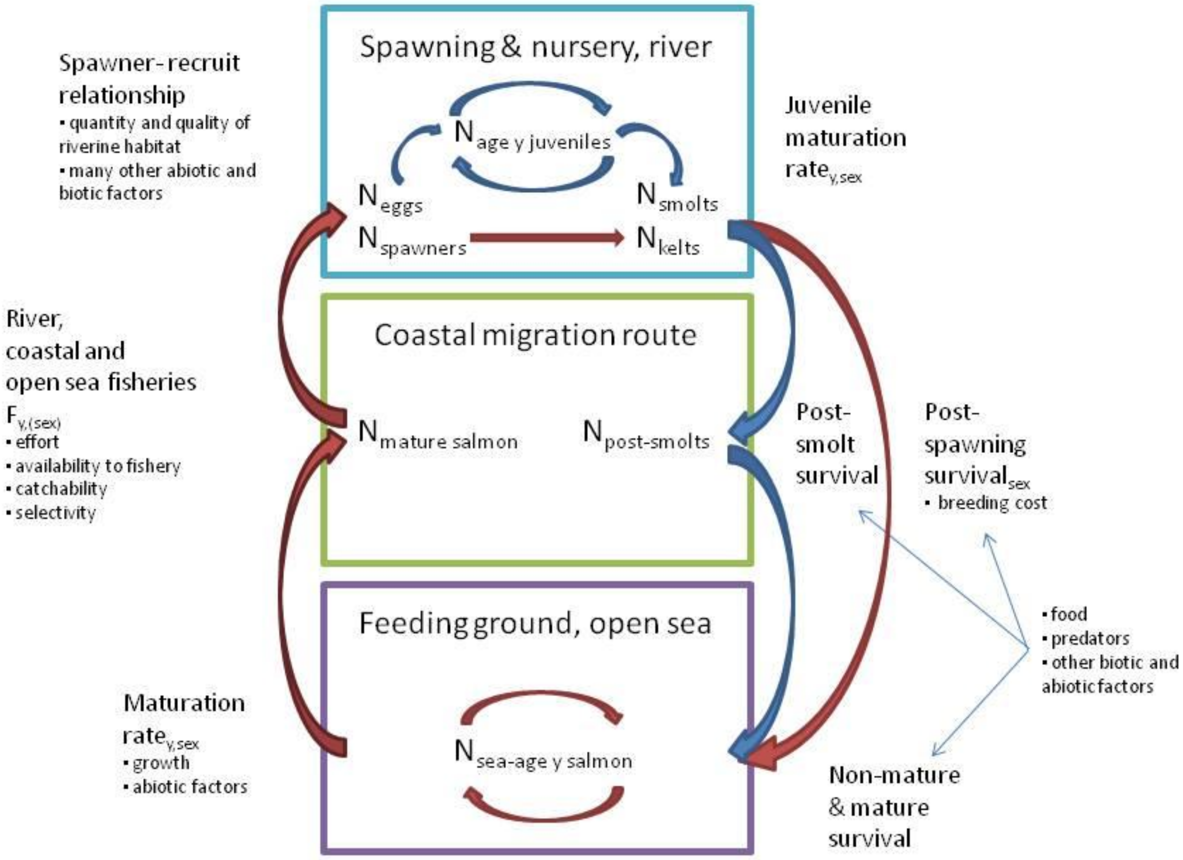

Figure A.1. Schematic presentation of the life cycle of salmon.

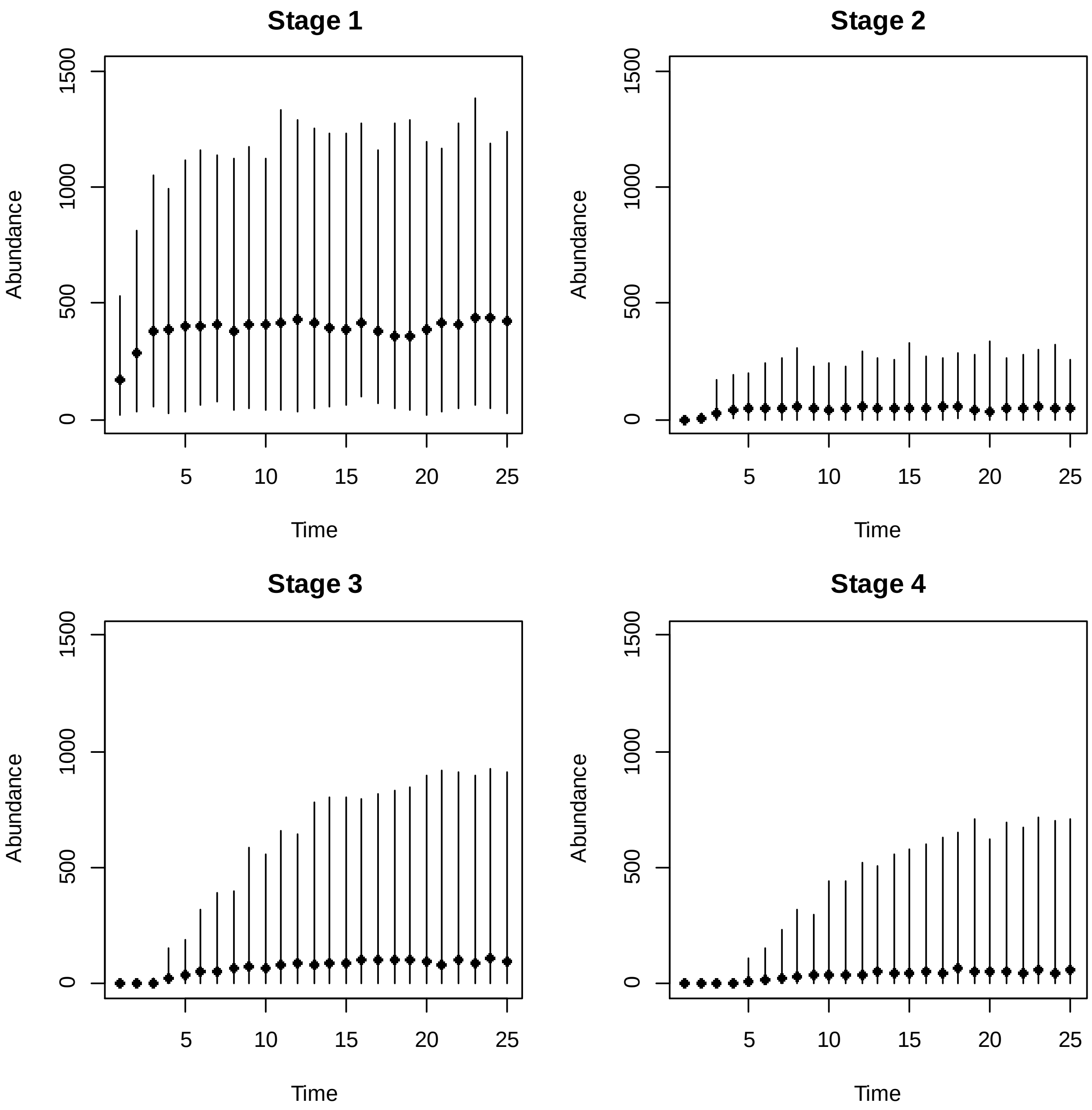

Figure A.2. Stage specific abundances over the time series. Graph illustrates medians and 95% probability intervals of the posterior estimates.

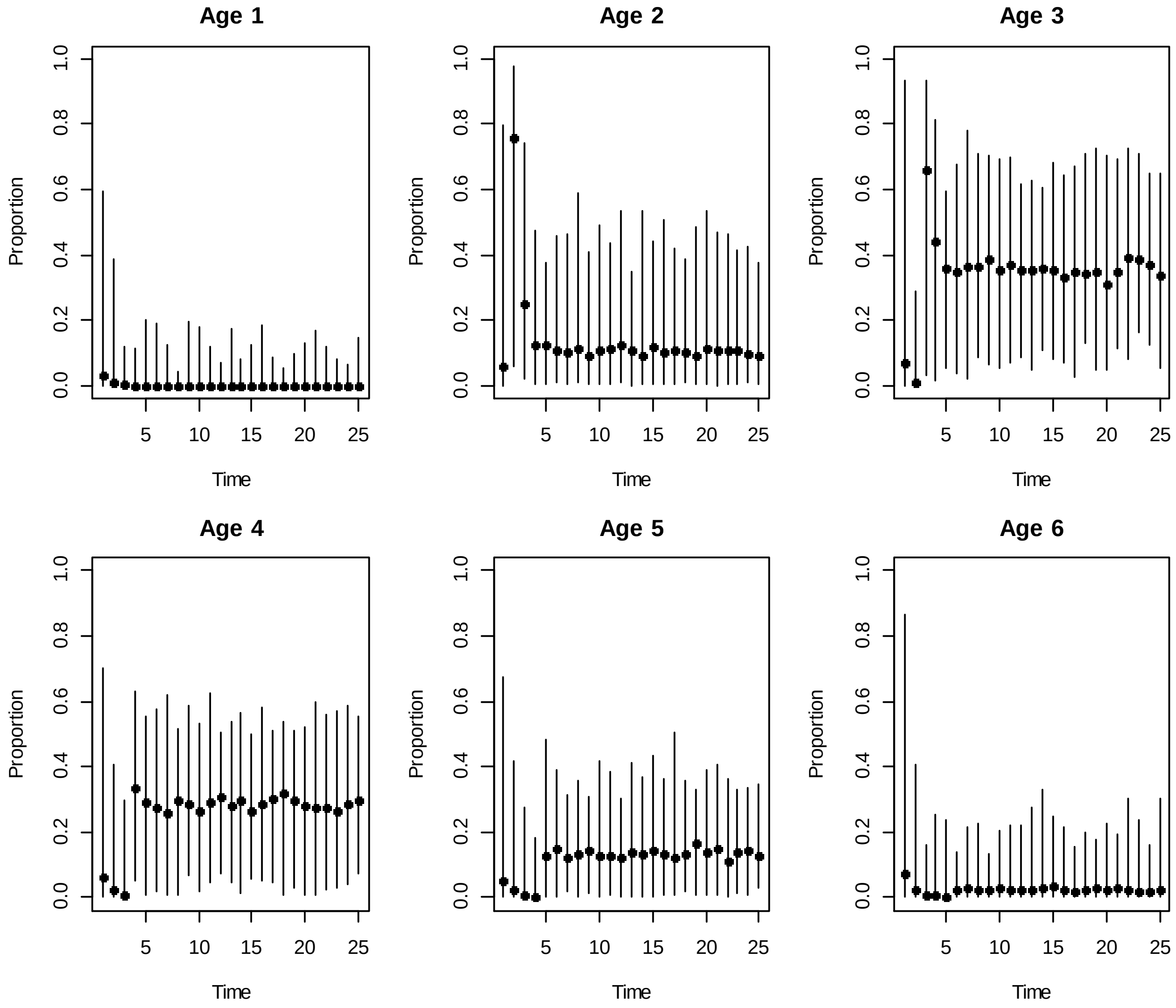

Figure A.3. Age distribution of maiden spawners (stage 2). Graph illustrates medians and 95% probability intervals of the posterior estimates. Age 1 salmon are post-smolts, age 2 are grilse, age 3 are 3-sea winter salmon and so on.

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Appendix B

Embedding A. salmon stock assessment in the North Atlantic within a Hierarchical Bayesian Modeling framework: an application to East Scotland

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Introduction

Atlantic salmon (*Salmo salar* L.) from eastern North America and the northeast Atlantic countries of Europe undertake common feeding migrations to the North Atlantic and have the potential to be havested by the West Greenland and the Faroes fisheries (Chaput, 2012; *ICES*, 2011). These mixed stock marine fisheries were of sufficient concern that an international body (the North Atlantic Salmon Conservation Organization - NASCO) was formed in 1982 to manage them. A fixed escapement strategy has been adopted with the objective of achieving the spawner requirements for the contributing stocks in both sides of the Atlantic Ocean. Management advice on harvesting is provided by ICES based on Pre Fishery Abundance (PFA) models that forecast post-smolts abundance prior to the marine fisheries (recently reviewed by Chaput *et al.* 2012).

Although the river-specific stock unit remains the biologically ideal scale to assess and manage A. salmon stocks, PFA models have been developed at an aggregated spatial scale. Indeed, more than 2000 salmon producing rivers have been identified in the North Atlantic (Crozier *et al.*, 2003), out of which only less than 25% are assessed (Crozier *et al.*, 2003; *ICES*, 2001). In practice, this hampers the use of meta-population models explicitly working as a combination of single rivers. Hence, models have been developed considering complexes of stocks at national or broader regional scales. Forecasts are currently derived based on three models that work independently for three multinational stock complexes: the North West stock complex (NW) and the southern and northern North East stock complexes (S.NE and N.NE, respectively) (Table B.1).

As they are based on similar data, the three models for the three stock complexes rely on similar stock-recruitment approaches (Chaput, 2012). They relate a spawning potential variable (lagged eggs or lagged spawners for the NW and NE stock complex, respectively) contributing to a recruitment of year t. The recruitment variable is the abundance of post-smolts in January of the first year at sea, before any marine fisheries (PFA). A suite of models have been developed by the ICES Working Group (Chaput and Prévost, 2006; Chaput *et al.*, 2005; Prevost *et al.*, 2005). Constant or time-varying spawning potential to PFA ratio (also called productivity parameter) were considered. Auto-correlated random walk to capture smoothed variability of the productivity in time, or phase shift models to capture abrupt changes between two levels of productivity have been used. These models produce PFA forecasts that are incorporated in a risk analysis framework to assess the consequences of mixed stock fisheries on the returns at the scale of stock complexes (Chaput *et al.*, 2005).

The time series of past PFA is obtained by a backward approach reconstructing abundance through time from data (1971-Today) compiled by ICES WGNAS for each national/regional component of stock complexes (Table B.1). The spawning potential of each country/region is derived from estimates of escapement, deduced from estimates of returns to home water. Returns are estimated from home water catches, raised to account for harvest and declaration rates associated to home water fisheries. Harvest and declaration rates are derived from expertise and are the main sources of uncertainty in the model. The spawning stock contributing to the PFA of each year is calculated by “lagging” forward in time the number of spawners (lagged spawners) or eggs (lagged eggs), based on the smolt age distributions in each country/region. The PFA is estimated at the scale of stock complex with the run reconstruction models developed by Rago *et al.* (1993) for the NW complex and by Potter *et al.* (1998) for the S.NE and N.NE complex. The total returns to home water (obtained by summing the returns at the scale of each country) are raised to take into account of high seas catches, including estimates of non-reported catches, and natural mortality at sea in the intervals between the instants at which PFA and the mixed stock fishery are considered.

Certain weaknesses are inherent in the PFA modeling approach. The PFA modelling structure is relatively locked, a form of accounting mechanism, which hampers the use of all available ecological knowledge about A. salmon demography and population dynamic, and does not allow for the assimilation of all sources of data.

First, the demography of A. salmon is roughly represented. It does not explicitly consider the generation renewal in the population dynamics and the freshwater phase is poorly represented. The transition between the spawning potential and the post-smolt stage (PFA) uses a single productivity parameter that aggregates demographic processes of different nature during the freshwater phase (from eggs to smolts) and the first month of the post-smolt marine phase. Available knowledge and data about the density-dependent eggs-juvenile survival cannot be used because the freshwater phase is not represented.

Second, the statistical procedure used to assimilate the various sources of information and to account for their associated uncertainties lacks transparency and flexibility. The procedure for estimating spawning potential and PFA are run separately from the stock-recruitment PFA model in itself. Demography and observation are not integrated in a single integrated model.

The broad scale modelling described in this paper addresses these deficiencies, with the aim of improving catch advice for mixed stock fisheries while providing a framework for a better understanding of Atlantic salmon population dynamics in the Atlantic Ocean. To address these challenges, the current PFA assessment approach is embedded within an integrated hierarchical Bayesian life cycle model. Hierarchical Bayesian Models (HBMs) have proved successful for embedding complex demographic processes within statistical models assimilating multiple sources of data (often noisy and incomplete) (Buckland *et al.*, 2007; Parent and Rivot, 2012; Thomas *et al.*, 2005). HBMs have been applied to age-structured, stage-structured (Rivot *et al.*, 2004; Ruiz *et al.*, 2009; Swain *et al.*, 2009) fish population dynamics and fish stock assessment (Lewy and Nielsen, 2003; Millar and Meyer, 2000). They improve the biological realism in modelling fisheries stock assessments, providing a fairer appraisal of the uncertainty around associated estimates or predictions (Kuparinen *et al.*, 2012).

An integrated life cycle model was developed. Iit explicitly separates out the freshwater from marine phases in the recruitment process. It accounts for different life histories, together with their associated patterns of migrations and the sequence of distant and homewater fisheries. A more transparent Bayesian statistical procedure allows to assimilate different sources of information, in the form of data series and by means of informative priors.

The paper lays the foundation of the model, which is then applied to the Eastern Scotland salmon stock complex, the largest regional component of the S.NE stock complex. This illustrative case study uses the same sources of information as those used by ICES WGNAS in its current PFA approach. The flexibility of the approach is illustrated by testing alternative hypotheses about data or ecological assumptions.

Materials and method

Outlines of the modelling approach

The state-space formulation of the model accommodates both the stochasticity of the demographic processes and random observation errors. Demographic processes are expressed through probabilistic equations involving hidden variables that are linked to data through probabilistic observation equations. Both demography and observations are governed by parameters, among which several are assigned informative prior distributions. The demographics are represented by an age and stage-structured life cycle model including different life histories and natural and fishing mortalities. The freshwater and marine phases were explicitly separated out (Fig. B.1). The freshwater part of the model computes the number of eggs potentially spawned by returning females escaping homewater fisheries, and the egg-to-smolt transition. Both density-independent and density-dependent eggs to smolts survival were tested. Smolts migrate seaward after 1 to 4 years spent in freshwater. Their survival at sea up to PFA stage is assumed variable according to year and the proportion of fish that mature as 1SW fish were considered variable among years. All fish were assumed to mature as 2SW fish at the latest. During the period spent at sea, salmon populations are exploited by a sequence of mixed-stock marine fisheries along their migration routes, while suffering simultaneously natural mortality. 1SW fish are caught by the Faroes fishery. 2SW maturing fish are exploited at the Faroes as 1SW, then by the West Greenland fishery and at the Faroes again. Fish that escape mixed stock marine fisheries are caught by homewater fisheries.

The model includes several sources of variability and uncertainty in the demographic process and in observations.

Demographic stochasticity was modelled by means of Dirichlet-Multinomial (DM) distributions that can be interpreted as overdispersed multinomial distributions. For instance, if X individuals face a random demographic transition with k possible outcomes with associated probability $\theta = (\theta_1, \dots, \theta_k)$, then the number of individuals in states i=1,..,k, $(X_1, \dots, X_k)$ is distributed as a DM distribution:

(1) $$(X_1, \dots, X_k) \sim DM(X, \theta, \eta)$$

where $\eta$is a parameter controlling the degree of overdispersion. The lower η is, the more overdispersed the DM is. At the limit, when $\eta \rightarrow \infty$, the DM converges to a multinomial distribution. If k=2, the DM is a Beta-binomial (Mäntyniemi, 2012).

Environmental stochasticity was accounted for through between-year variability of transition rates including eggs-to-smolts and smolts-to-PFA survival rates, the probability to mature as 1SW fish, and all fishing mortality rates. The between year variability of vital rates was either modeled independently with a logNormal distribution or in an autoregressive process.

The model was fitted to a 40 years time series of data from 1971 to 2011. Observation errors were considered at two stages in the model. Sampling errors were considered for the smolts-age proportions and the home water catches. The latter were related to returns by observation equations which accounted for uncertainty in the capture process and in the catch declaration. No observation errors were considered for mixed stock fisheries at sea.

Bayesian inferences rely on the general theory of state-space models (Buckland *et al.*, 2007; Parent and Rivot, 2012). The joint distribution of all the model quantities, i.e. parameters and states variables, is decomposed into the joint prior on all parameters, the prior on hidden state variables given the parameters, and the sampling distribution of the observations given the state variables and the parameters. We first detail the demographic equations that provide the joint prior for the state variables given the parameters and then the stochastic observation equations that form the likelihood are provided. The prior distributions on parameters are then justified, together with details about the available data.

Equations for the demographic process

Freshwater phase

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

(2) $$N_t^1 = N_t^8 \times pf^1 \times fec^1 + N_t^{14} \times pf^2 \times fec^2$$

where pf^1 and pf^2 are the proportions of females and fec^1 and fec^2 are the average fecundities of 1SW and 2SW, respectively, considered known and constant over time during the time series (Table B.2).

The egg-to-smolt transition consists of two steps: first, the survival from egg to smolt per cohort, second, the distribution of the surviving smolt according to age. In a baseline configuration, the egg-to-smolt survival was modelled as a linear stock recruitment function with a fixed average survival rate, $\mu_{\gamma^1} = 0.7\%$ and a CV = 5% (Table B.1). A Beverton-Holt density dependent survival approach was also tested (see hereafter).

(3) $$\log(N_t^2) \sim N\left(\log\left(N_t^1 \times \mu_{\gamma^1}\right) - \frac{\sigma_{\gamma^1}^2}{2}, \sigma_{\gamma^1}^2\right)$$

The distribution of the total number of smolts N_t^2 per smolt age was modelled as a DM distribution. In Eastern Scotland, smolts from a same cohort can migrate to the marine water after 2 to 5 years spent in freshwater. The probability for a smolt in N_t^2 to migrate at age *i+1* is denoted as $\theta_t^{1,i}$, with $\sum_i \theta_t^{1,i} = 1$.

(4) $$(N_{t+2}^{3,1}, N_{t+3}^{3,2}, N_{t+4}^{3,3}, N_{t+5}^{3,4}) \sim DM(N_t^2, (\theta_t^{1,1}, \theta_t^{1,2}, \theta_t^{1,3}, \theta_t^{1,4}), \eta)$$

Henceforth, the river-age of smolts is no longer tracked, N_t^3 denotes the total number of smolts migrating in spring of year *t*.

Marine phase

During the first months at sea, smolts (N_t^3) undergo two processes considered sequentially: the survival from smolt to PFA stage and the decision to mature in the first year at sea, with probability parameters γ_t^2 and θ_t^2 , respectively.

It was assumed that all smolts migrating the same year have equal vital rates, regardless of their age. Post-smolts at the PFA stage follow a DM distribution:

(5) $$(N_{t+1}^4, D_{t+1}^4) \sim DM(N_t^3, (\gamma_t^2, 1-\gamma_t^2), \eta)$$

where D_{t+1}^4 are the smolts that died before PFA stage.

The maturation process is also modelled as a DM:

(6) $$(N_t^5, N_t^9) \sim DM(N_t^4, (\theta_t^2, 1-\theta_t^2), \eta)$$

where N_t^5 and N_t^9 are the maturing and non-maturing component of the PFA respectively.

Environmental stochasticity was captured by between year variability in survival and maturation parameter. Both parameters, were modelled by an autoregressive process in the logit scale with stationary means μ_{γ^2} and μ_{θ^2}, respectively, and stationary variance $\frac{\sigma_\varepsilon^2}{1-\rho_{\gamma^2}}$ and $\frac{\sigma_\omega^2}{1-\rho_{\theta^2}}$, respectively. For both time series, the first step was drawn in the stationary distribution of the time series.

(7) $$\begin{cases} \gamma_{t=1}^2 \sim N(\mu_{\gamma^2}, \frac{\sigma_\gamma^2}{1-\rho_{\gamma^2}}) \\ logit(\gamma_{t+1}^2) = \mu_{\gamma^2} + \rho_{\gamma^2}(logit(\gamma_t^2) - \mu_{\gamma^2}) + \varepsilon_t \\ \varepsilon_t \sim N(0, \sigma_\gamma^2) \end{cases}$$

(8) $$\begin{cases} \theta_{t=1}^2 \sim N(\mu_{\omega^2}, \frac{\sigma_\theta^2}{1-\rho_{\theta^2}}) \\ logit(\theta_{t+1}^2) = \mu_{\theta^2} + \rho_{\theta^2}\left(logit(\gamma_\theta^2) - \mu_{\theta^2}\right) + \omega_t \\ \omega_t \sim N(0, \sigma_\theta^2) \end{cases}$$

During the marine phase, adult salmon experience natural mortality and sequential fisheries. Salmon maturing in their first year at sea go through the Faroes fisheries, while non-maturing fish face successively the Faroes, West Greenland and Faroes fisheries again on their way back from West Greenland. Fishing and natural mortality are assumed to occur simultaneously during a specific duration considered known for each fishery (Table B.2). All these transitions are modeled similarly using DM distributions with time-and-fishery specific fishing mortality and with a constant natural mortality rate *M*. For a number of fish N_t^f entering the fishery *f* with fishing mortality F_t^f and specific duration Δt_f, the escapement E_t^f, catches C_t^f and fish that died from natural mortality D_t^f are modeled through a DM distribution:

(9) $$(E_t^f, C_t^f, D_t^f) \sim DM(N_t^f, \left(\xi_1^f, \xi_2^f, \xi_3^f\right), \eta)$$

with ξ_1^f, ξ_2^f and ξ_3^f the probability of a fish to survive, be caught or die naturally respectively, defined from a Baranov equation:

$$(10)\qquad \begin{cases} \xi_1^f = e^{-(F_t^f+M)\Delta t_f} \\ \xi_2^f = \frac{F_t^f}{F_t^f+M}(1-e^{-(F_t^f+M)\Delta t_f}) \\ \xi_3^f = \frac{M}{F_t^f+M}(1-e^{-(F_t^f+M)\Delta t_f}) \end{cases}$$

For all fisheries, independent logNormal priors were set on the F_t^f to capture the year-to-year variability (Table B.1).

In Figure B.1, N_t^6 denotes escapement from the 1SW maturing fishery at Faroes N_t^{10}, N_t^{11} and N_t^{12} are the escapement from the fisheries of non-maturing fish at Faroes (1SW), West Greenland and Faroes (2SW). The number of fish caught by each fishery f is provided by the data (*ICES*, 2001) (Table B.2, Table B1.1).

Surviving adults after the marine fisheries denoted by N_t^6 and N_{t+1}^{12} for 1SW and 2SW fish respectively, migrate back to their home waters, with natural mortality *M* during Δt_2 and Δt_5 months respectively.

$$(11)\qquad \begin{cases} (N_t^7, D_t^7) \sim DM(N_t^6, (e^{-M\times\Delta t_2}, 1-e^{-M\times\Delta t_2}), \eta) \\ (N_t^{13}, D_t^{13}) \sim DM(N_t^{12}, (e^{-M\times\Delta t_3}, 1-e^{-M\times\Delta t_3}), \eta) \end{cases}$$

Returning adults will finally be fished in their home waters before breeding in freshwater. Because informative priors were set on the harvest rates denoted *h* (and not on *F*), home water catches were not modelled following the Baranov equation. DM distributions were used to model escapement and catches but assuming that no natural mortality occurs:

$$(12)\qquad \begin{cases} (N_t^8, C_t^8) \sim DM(N_t^7, (h_t^1, 1-h_t^1), \eta) \\ (N_t^{14}, C_t^{14}) \sim DM(N_t^{13}, (h_t^2, 1-h_t^2), \eta) \end{cases}$$

where N_t^8 and N_t^{14} are the number of 1SW and 2SW fish that spawn in year *t*, and C_t^8 and C_t^{14} are the number of fish caught by the homewater fishery.

Assimilation of data and other sources of information

Several sources of data and knowledge are assimilated in the life cycle model, through informative priors, fixed values for some parameters and observation models for the time series of data (40 years; 1970 - Today). In the baseline configuration of the model, we use the same quality and quantity of information used in the ICES WGNAS PFA modeling approach.

Time series of data and observation models

The model assimilates several time series of catches. Those of the mixed stock fisheries ($CF1^m$, $CF1^{nm}$, $CF2$ and $CG2$) were directly derived from ICES (Table B1.1; Appendix B1), and no observation errors were considered (formally, the DM distribution of eq. 9 defines demographic stochasticity and not observation errors). Time series of declared home-water catches are available by sea-age classes (Fig. B.2).

Observation models were built to capture observation errors due to uncertainty on the declaration of homewater catches and uncertainty in the proportion of different river-ages of smolts per cohort.

A Binomial observation model was used with informative priors for reported declaration rates of homewater catches $R_{1,t}$ and $R_{2,t}$.

$$(13) \qquad \begin{cases} C_t^{1SW,dec} \sim Bin(C_t^8, R_{1,t}) \\ C_t^{2SW,dec} \sim Bin(C_t^{14}, R_{2,t}) \end{cases}$$

Following ICES, average proportions of smolt age classes were considered known (and fixed among years) (Table B.2) but a multinomial sampling observation error was used to mimic the fact that these average proportions are derived from a limited sample of size N_S. N_S was arbitrarily set to 100, but other values could be tested, the lower the value, the greater the observation errors:

$$(14) \qquad \begin{cases} N_s^{1:4} = N_s \times p^{1:4} \\ N_S^{1:4} \sim Multinomial(N_s, p^{1:4}) \end{cases}$$

with $p^{1:4}$ the empirical proportions of smolt ages per cohort.

Hence, the whole likelihood function used to assimilate time series of data within Bayesian model results from the product of eqs. (13), (14) and all DM equations for the mixed stock catches.

Fixed parameters

Fixed values were set for almost all parameters of the freshwater phase (Table B.2). Average proportions of females and fecundities of both sea age classes were used to calculate the number of eggs spawned given escapement N_t^8 and N_t^{14}. The average survival from eggs to smolt was set to 0.7% according to Hutchings and Jones (1998). In the absence of any smolt data, the variability of the egg to smolt survival cannot be separated from the smolt to PFA survival. The CV of the between year variability was arbitrarily set to 5% so most of the between year variability in the survival from egg to PFA stage is captured in the smolt-to-PFA survival. Average proportions of smolt age (1 to 4) were set according to ICES WGNAS.

Informative priors

Informative priors were set on several parameters. Natural mortality from PFA stage to homewaters returns (M) was considered to be constant over years and drawn a-priori in a very informative log-normal prior that corresponds to a mortality of 3% per month (equivalent to about 30% of cumulated mortality per year) and a CV=16% (*ICES*, 2002).

Informative priors based on expertise were set on the harvest and the declaration rate of home-water fisheries. The prior on declaration rates are based on best judgment 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 Scotland than in the east, owing to lower surveillance over the reporting of salmon catches and the smaller size and the greater number of rivers in western Scotland. Exploitation rates are guess-estimates derived using reported effort and estimate of standard fishing effort units based on the net fishery survey (*ICES*, 2002).

Sensitivity analysis

In order to provide a better understanding of the model and the uncertainty in the outputs, we assessed the sensitivity of the main outputs (e.g. smolts to PFA survival, maturing proportions, abundances, …) to key parameters and ecological hypotheses. (i) The mean of the informative prior on the parameter M was expected to strongly influence the PFA estimates hence the smolt-to-PFA survival rate. The informative prior on harvest rate provides key information for the model to estimate the number of returning fish based on homewater catches. (ii) Ecological hypotheses, as sensitivity to egg-to-smolt survival or the between year variability structure, are suspected to have a major influence on the inferences about the smolt to PFA survival rate.

The sensitivity of the results to the prior on M was assessed by running the model with a logNormal informative prior distribution with the median set to 0.03 (baseline configuration), 0.01 and 0.05 respectively. Three scenarios of harvest rate for homewater catches have been tested: (i) Informative priors directly derived from ICES (*ICES*, 2002); (ii) A constant harvest rate equal to the mean of the first five years of the time series; (iii) A scenario of linear decline between the first and the last values of the time series. Sensitivity to hypotheses made on the eggs-to-smolt survival was assessed by testing different values of the average survival (0.05, 0.07 (baseline), and 0.09) and also by exploring the influence of a density-dependent survival. Berverton-Holt survival functions were tested with three different sets of parameters that characterize different levels of density dependence in the eggs-to-smolts survival rate (Fig. B.3).

Posterior checking

The consistency between the model and the data was checked using Bayesian posterior checking procedures (Gelman, 2004). For each series of homewater catches the following discrepancy measure was computed as a summary measure of the discrepancy over the whole time series:

$$\chi^2\left(C_t^{i,dec},\left(h_t^i,R_t^i\right)\right)=\sum_{t=1}^{n}\frac{(C_t^{i,dec}-E(C_t^{i,dec}|h_t^i,R_t^i))^2}{Var(C_t^{i,dec}|h_t^i,R_t^i)} \tag{15}$$

where *n* is the number of observations in the homewater catches series and *i* the sea-age of fish. $E(C_t^{i,dec}|h_t^i,R_t^i)$ and $Var(C_t^{i,dec}|h_t^i,R_t^i)$ are the expected mean and variance of homewater catches given parameters $\left(h_t^i,R_t^i\right)$. For each set of parameters drawn in their joint posterior distribution, the realized discrepancy $\chi^{2,obs}$ computed with the observed values of declared catches $C_t^{i,dec}$ were compared to the predicted discrepancy $\chi^{2,pred}$ computed with the posterior predictive replicates of $C_t^{i,dec}$. If the data and the model are consistent, observed data should look similar to replicated data simulated a-posteriori by the model. $\chi^{2,pred}$ should then not be too different to $\chi^{2,obs}$. The Bayesian *p*-value is the probability that $P(\chi^{2,pred} > \chi^{2,obs}$ estimated a-posteriori from a sample of $\left(h_t^i,R_t^i\right)$ values drawn in their posterior distribution. A p-value close to 0.5 indicates consistency between the model and the data, whereas very high (> 0.95) or very low (< 0.05) p-values provide serious warning (Gelman et al., 2004).

Computational details

All computations were performed within the R platform (R Development Core Team, 2012). Bayesian posterior distributions were approximated *via* Monte Carlo Markov Chain methods through the open-source JAGS software (http://mcmc-jags.sourceforge.net). Three independent MCMC chains with different initialization points were used. After an adapting phase of 50000 iterations, inferences were derived from a sample of 2000000 iterations. One out of 100 iterations was kept to reduce the MCMC sampling autocorrelation. All the modeling results have undergone the Gelman-Rubin test (Brooks and Gelman, 1998) as implemented in the Coda package of R to asses convergence of MCMC chains.

The model code package for this example is uploaded in the wiki pages of the ECOKNOWS project and is available from the corresponding author upon request.

Results

Model consistency

Posterior checking realized under the baseline model configuration reveals no inconsistency between the model a-posteriori and the data. p-values were about 0.5 for both 1SW and 2SW catches (Fig. B.4), thus showing that the model is able to replicate very similar catches to observed declared catches for both sea-age classes.

Demography

The estimates of the homewater returns of 1SW (N7) and 2SW (N13) fish (Fig. B.5) result mainly from combination of the information brought by the time series of informative priors on harvest and declaration rates, and of homewater catches. This allows the number of 1SW returning salmons in 2010 to be less than half of that in 1971. Returns of 2SW salmon declined continuously from 1971 to 1996, and then dropped to one-fifth of its level at the beginning of the time series.

As the harvest rates associated with homewater fisheries are high in the first half of the study period, the number of fish that escape the homewater fishery is much lower than returns, with a global declining trend (Fig. B.5). Owing to a drop in the homewater catches (Fig. B.2), the number of 1SW spawners (N8) has significantly increased in the nineties to fluctuate at about 125,000 salmon. Abundance of 2SW spawners (N14) have fluctuated between 1971 and 1991, before dropping to a relatively stable low level of about 100,000 fish.

PFA estimates, post-smolts considered at January 1st of their first winter at sea just prior to the Faroes fishery, both in its maturing (N5) and non-maturing (N9) components (Fig. B.6) exhibited an overall decrease during the 40 years time series. Maturing PFA (N5) has decreased continuously since 1971, to less than 50% of the abundance of the seventies in the last years. Non-maturing PFA (N9) declined until the mid nineties before stabilizing to a very low level.

The proportions of fish which are harvested in each fishery (Fig. B.7), are easier to interpret than F values. The Faroes fishery has a low impact on non-maturing 1SW fish. The cumulative impact of the 3 fisheries experienced by the non-maturing component is much higher, with most of the exploitation occurring in the western Greenland fishery (Fig. B.7). Exploitation rates at the Faroes fishery have always been very low, even after exploitation stopped in 2001.

Parameters for key demographic transitions such as the marine survival during the first months at sea γ_t^2 (smolts → PFA) and the probability to mature in the first year θ_t^2 are estimated for each year (Fig. B.8), the time series being modelled a-priori as a first order autoregressive process. The smolt to PFA marine survival γ_t^2 is characterized by a high between year variability between 4 and 13%, and a sharp decrease since the early nineties. The probability to mature the first year at sea also fluctuates highly but with an overall increase from about 0.35 to 0.55 during the time series.

The joint distributions (γ_t^2, θ_t^2) for each year t do not exhibit any particular pattern of correlation, thus indicating that the two parameters are not confounded given the information assimilated by the model. The time series of both parameters exhibit uncorrelated patterns of variations.

The return rate from smolts to 1SW or 2SW adults before homewater exploitation (Fig. B.9) is an indicator that combines life history choices and mortality (M and F) during the marine phase, and could be compared to some available tag-recapture data. It fluctuates between 3 and 12% and follows the same patterns as the smolts to PFA survival rate.

Sensitivity analysis

Sensitivity to prior on M

Interestingly, the prior on M is updated by the data, the posterior being systematically pushed to lower values than the prior.

As anticipated, the expected mean of the prior on M is a scaling factor for the smolts to PFA survival rate. The lower the expected mean of the prior on the natural mortality after the post-smolts stage, the higher the posterior estimates of the mortality during the smolts → post-smolts transition (Fig. B.10).

Changing the prior on M also impacts the probability to mature as 1SW. A higher M increases the differential of cumulated natural mortality between 1SW and 2SW fish, what leads to lower estimates of the probability to mature as 1SW.

Sensitivity to prior on harvest rate for homewater fishery

Posterior estimates of all compartments of the model are highly sensitive to changes in the informative priors on the harvest rate (Fig. B.11c). For the PFA, the higher the prior expected mean of the harvest rates, the lower the estimates of the abundance. The time series of the smolts to PFA survival rate is highly sensitive to the choice of the prior on *h*. A constant harvest rate tends to dampen the variations in the time series of estimate survival rates. In particular, the drop in survival rate around 1988-1990 is no longer obvious. The increasing trend in the probability to mature the first year at sea is also weaker.

Sensitivity to changes in eggs → smolts survival functions

As suspected, posterior estimates of all compartments of the model are also sensitive to changes in the eggs → smolts survival function (Fig. B.12). Introducing a density-dependent (Beverton-Holt type) survival leads to a higher survival for low egg deposition and to lower survival for high egg deposition. Because the egg deposition fluctuates during the time series (Fig. B.12), the eggs → smolts survival also fluctuates when a density-dependent form is used, while being constant in the baseline hypothesis. The Beverton-and-Holt survival form induces a dampening of the variation of the time series of smolt abundance (Fig. B.12b). It therefore impacts the marine phase by diminishing the overall values of the productivity and their range of variation (Fig. B.12c). The sharp decline in marine survival in 1988-1989 seems robust to changes in the structural form of the eggs → smolts survival function.

Discussion

A substantive contribution to life cycle modeling on a broad ocean scale

The present approach offers a substantial contribution toward integrated life cycle modelling of A. salmon on a broad ocean scale.

It offers substantial improvements to the “accountancy” stock-recruitment approach that forms the basis of the PFA stock assessment model (Chaput, 2012). The integrated life cycle model constitutes a progressive, life cycle stock-recruit dependent procedure, where the population dynamics is first modelled through probabilistic stage-based demographic model, with abundance at stages and associated parameters that are updated by the available data. In the HBM framework, modelling, inferences on any hidden variables or parameters of biological significance and management interest, and forecasts can be derived in a single consistent probabilistic framework (Buckland *et al.*, 2007; Parent and Rivot, 2012; Thomas *et al.*, 2005).

This represents a real methodological improvement to the PFA model that considers a statistical relationship between a spawning potential (lagged eggs) and a recruitment variable (PFA) both derived from the same data sources (returns) by a mixture of forward (lagged eggs) and backward (run reconstruction) approach.

In our approach, the hypotheses on the demographic processes are clearly stated, and the various sources of information, including informative priors and data, are assimilated in a more transparent way, thus making easier to assess the consequences of any changes in the data and model structure. The hypotheses about the biology and ecology of A. salmon are incorporated in the hidden demographic process, instead of being collapsed in the processing of the different inputs needed to run the PFA modelling approach. The life cycle model explicitly separates out the freshwater and the marine phases, and incorporates the variability of life histories (river and sea ages). This allows the effect of both phases in the recruitment process to be separated and to introduce the possibility of density dependence in the freshwater phase. The model also considered the variability of smolts ages in the dynamics instead of having this step collapsed in the calculus of lagged eggs.

Insights to A. salmon population dynamics at the scale of Eastern Scotland

The application to A. salmon in eastern Scotland was an ideal candidate to illustrate the interest to move toward an integrated life cycle model. Beyond the methodological improvements, the model provided some interesting insights about the evolution of A. salmon population dynamics at the scale of stock assemblages in eastern Scotland. Inferences however, should be interpreted with caution, as they are reliant on a number of informative priors and a suite of modelling hypotheses. Below we point out relevant key points inferred from the demographic processes and associated with the trends.

First, it is worth recognizing that inferences critically depend upon the informative priors on the harvest and declaration rates associated with coastal and home water fisheries. When combined with those priors, the time series of catches for both sea ages provided key quantitative information to scale the abundance of returns, from which the eggs deposition is directly deduced. As suspected, changing the time trends in the informative priors on harvest rates drastically impacts the estimates of returns, eggs deposition, and the whole dynamics. It is worth noting however, that estimates of returns and survival rates always exhibited a sharp decline around 1988-1990, even when harvest rates are considered to vary with a very different time trend than that in the baseline configuration.

Second, if annual returns can be inferred from coastal and homewater catches, inferences about all other time series of abundance and demographic rates at any stages between eggs and subsequent returns critically depend upon a set of modelling assumptions, as only few other sources of data except high sea catches are introduced in the model.

The eggs-to-smolts survival was considered constant or with density-dependence. In the baseline configuration, a constant eggs-to-smolt survival rate of 0.7% (derived from literature) was used. Between year variations of the smolts-to-PFA survival and of the probability to mature as 1SW fish were allowed, but M was considered constant over the time series. When interpreted under those hypotheses, the data provided information to estimate time series of return rates from smolts to 1SW and 2SW. First, return rates exhibited an overall decreasing trend over the time series, with a sharp decline around years 1988-1990. Second, the decrease in return rates as 2SW is higher than as 1SW fish.

The model also provided estimates of the survival during the first months at sea after smolt migration. Estimates varied between 15 and 3% with an overall decline over the time series. These values are hardly interpretable however, as inferences critically depend upon hypotheses on M. With constant M and rather low harvest rates of high seas fishery, the sharp decline in return rates logically resulted in a sharp decline in the smolt-to-PFA survival rate in the same period 1988-1990. Under the constant M hypothesis, the higher decrease of return rates as 2SW relative to 1SW logically lead to an overall increase in the probability to mature as 1SW.

We assessed the sensitivity of the estimates to changes in the informative priors on some key parameters. As suspected, the eggs-to-smolts survival rate (if considered constant) and M are scale factors for all quantities in the model, and changes in these parameters did not affect trends in time series of estimated parameters. As discussed by Chaput (2012) however, the nature of advices for managing high sea fisheries will critically depend upon M. Indeed, considering higher (or lower) values of M increases or decreases) the PFA abundance and decreases (or increases) the influence of high sea catches on the returns (respectively).

Considering eggs-to-smolts survival as density-dependent introduced non linearity in the dynamics and drastically modified the inferences made on the smolt-to-PFA survival. Indeed, the fluctuations of the amount of eggs spawned over the time series induced fluctuations in the eggs-to-smolt survival rate, which in turn lead to a different time series of smolts-to-PFA survival than estimated with a constant eggs-to-smolts survival. Interestingly, the sharp decline in survival around 1988-1990 is still robust to changes in this modelling hypothesis.

Results critically depend upon many hypotheses, several of which cannot be tested owing the available data. The results can still, however, be discussed with regards to the literature.

There is ample evidence from river-specific studies that egg deposition is an important conditioning variable of juveniles abundance expressed as a density-dependent response during the freshwater stages (Gibson, 1993; Kennedy and Crozier, 1993; Chaput *et al.*, 1999; Jonsson *et al.*, 1998; Elliott, 2001; Grant and Imre, 2005; Imre *et al.*, 2010), although the average parameters are often difficult to estimate and residual random variations often dominate the signal (Gurney *et al.*, 2010; Michielsens and McAllister, 2004; Rivot *et al.*, 2001). As introducing a non-linear transition deeply modifies the dynamics, considering the possibility of a density-dependence should be recommended as the default choice.

Based on a 0.7% average eggs-to-smolts survival rate, the estimates of return rates was consistent with available data from index rivers for which the return rates have been monitored by mark-recapture. Indeed, for the Southern NE stock complex, return rates of 1SW (2SW) fish range between 3% and 12% (1% and 3% respectively), and the available time series exhibited globally decreasing trends over the period 1980-2010 (*ICES*, 2011).

A large amount of literature also lends support to the hypothesis that mortality has increased in the marine phase, in connection with recent changes in the North east Atlantic ecosystem. The drivers could be a change on the availability of prey that would affect growth and survival (Beamish and Mahnken, 2001; Friedland *et al.*, 2000, 2003; Hogan and Friedland 2010; Peyronnet *et al.*, 2007, 2008), connected with large scale changes in the distribution and phenology of plankton species in the eastern North Atlantic as a bottom-up response of recent ocean warming (Beaugrand and Reid, 2003; Richardson and Schoeman, 2004; Todd *et al.*, 2012). The sharp decline of survival, that is identified around 1988-1990 for all the model structures tested, matches with the shift in plankton communities in the eastern Atlantic Ocean identified by Beaugrand and Reid (2003).

The higher decrease in return rates of 2SW relatively to 1SW salmon has also been widely described in the literature in Scotland (Heddell-Cowie, 2005; Youngson *et al.*, 2002) and Wales (Aprahamian *et al.*, 2008). This trend could be explained either by an increase in the proportion maturing (Hyp. 1) or an increase in the natural mortality rate of 2SW fish relative to the mortality of 1SW (Hyp. 2), or both. Those hypotheses cannot be introduced simultaneously and Hyp. 1 was the only one tested. Indeed, as highlighted by Chaput (2012), the confusion between the proportion maturing as 1SW and the survival after the first winter at sea means that the proportion of fish maturing as 1SW can be estimated if it is assumed that M is constant, and inversely, trends in M can be estimated if one assumes the proportion maturing is constant.

The increase in the proportion maturing as 1SW, that corresponds to a decrease in the age at maturity, could be interpreted as a sign for an evolution induced by historic intensive exploitation of older and bigger fish that would have favoured an earlier maturity (Thorpe, 2007). However, the level of exploitation of A. salmon has been rapidly diminishing over the past 20 years and the observed patterns remain largely unexplained and are probably due to forcing environment factors (Blanchet and Dubut, 2012; Friedland and Haas, 1996).

Foundations for a multi-region model

The approach lays the foundation for integrated life cycle modelling at the broad ocean scale and provides a framework for structuring further research and data collection.

The most direct and exciting perspective might constitute building a hierarchical model to jointly analyse the dynamics for all regions composing the southern North East stock complex (France, UK England & Wales, UK N. Ireland, Ireland, Scotland East & West, and South West Iceland). The model could easily be adapted and applied to those regions for which similar data are already compiled by ICES WGNAS. Hence the present approach is a first step to build a multi-region model, that would be appropriate to evaluate multiple factors (fisheries and environment) affecting A. salmon populations at different life stages and at various spatial and temporal scales.

First, such a model would have the potential to provide tools for assessing the effect of management measures on mixed stock high seas fisheries.

Second, a multi-regional model would also enhance the valorisation of the available data and knowledge about the biology and ecology of A. salmon. For instance, the variability of region specific demographic parameters such as the one characterizing the freshwater phase of the life cycle could be introduced. This would also allow the relative effect of environmental factors influencing populations at various spatial scales to be assessed, 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.

Tables

Table B.1. Parameters and associated prior distributions.

Parameters	Definition	Prior distribution
γ_t^1	Eggs-to-smolts survival rate with $\mu_\gamma = 0.007$ and $\sigma_\gamma^2 = 0.05$	$log(\gamma_t^1) \sim N(\mu_\gamma, \sigma_\gamma^2)$
γ_t^2	Productivity in the first months at sea	$AR1\left(\rho_{logit(\gamma^2)}, \sigma_{logit(\gamma^2)}\right)$
μ_{γ^2}	Stationary mean of the *AR1* process	$\sim N(0,1)$
$\sigma_{logit(\gamma^2)}$	Standard deviation of the *AR1* process	$\sim Unif(0,1)$
$\rho_{logit(\gamma^2)}$	Correlation in the *AR1*	$\sim Unif(-1,1)$
M	Monthly natural marine mortality up to returns	$log(M) \sim N(-5,40)$
$\theta_t^{1,i}$	Probability to become smolt of age *i*	$\sim Dirich(2,2,2,2)$
θ_t^2	Probability of post smolt to mature the first year at sea	$AR1\left(\rho_{logit(\theta^2)}, \sigma_{logit(\theta^2)}\right)$
θ_t^2	Stationary mean of the *AR1* process	$\sim N(0,1)$
$\sigma_{logit(\theta^2)}$	Standard deviation of the *AR1* process	$\sim Unif(0,1)$
$\rho_{logit(\theta^2)}$	Correlation in the *AR1*	$\sim Unif(-1,1)$
F_t^1	Fishing mortality, mature 1SW, Faroes fishery	$log(F_t^1) \sim N(-3,1)$
F_t^2	Fishing mortality, non-mature 1SW, Faroes fishery	$log(F_t^2) \sim N(-3,1)$
F_t^3	Fishing mortality, 2SW, West Greenlad fishery	$log(F_t^3) \sim N(-3,1)$
F_t^4	Fishing mortality, 2SW, Faroes fishery	$log(F_t^4) \sim N(-3,1)$
h_t^i	Exploitation rate for i sea winter fish	-
R_t^i	Catch reporting rates (declaration rates) of homewater catches for i sea winter fish	-

Table B.2. Summary of data and fixed parameters.

Data	Definition	Value
$p^{i:4}$	Proportion of smolt of age i per cohort (observations)	{0.05,0.45,0.45,0.05}
fec^1, fec^2	Fecundity of 1SW and 2SW females	{5000,10000}
$pf^{1,}\ pf^2$	Proportion of females in 1SW and 2SW	{0.40,0.60}
Δt_1	Time up to Faroes fishery	0.5 month
Δt_2	Time up to 1SW Returns	7.5 months
Δt_3	Time up to west Greenland fishery for 2SW	8.5 months
Δt_4	Time up to Faroes fishery for 2SW	5 months
Δt_5	Time up to returns as 2SW	3.5 months
$CF1_t^m$	Catches of mature 1SW in Faroes fishery	-
$CF1_t^{nm}$	Catches of non-mature 1SW in Faroes fishery	-
$CG2_t$	Catches of 2SW in West Greenland fishery	-
$CF2_t$	Catches of 2SW in Faroes fishery	-

Figures

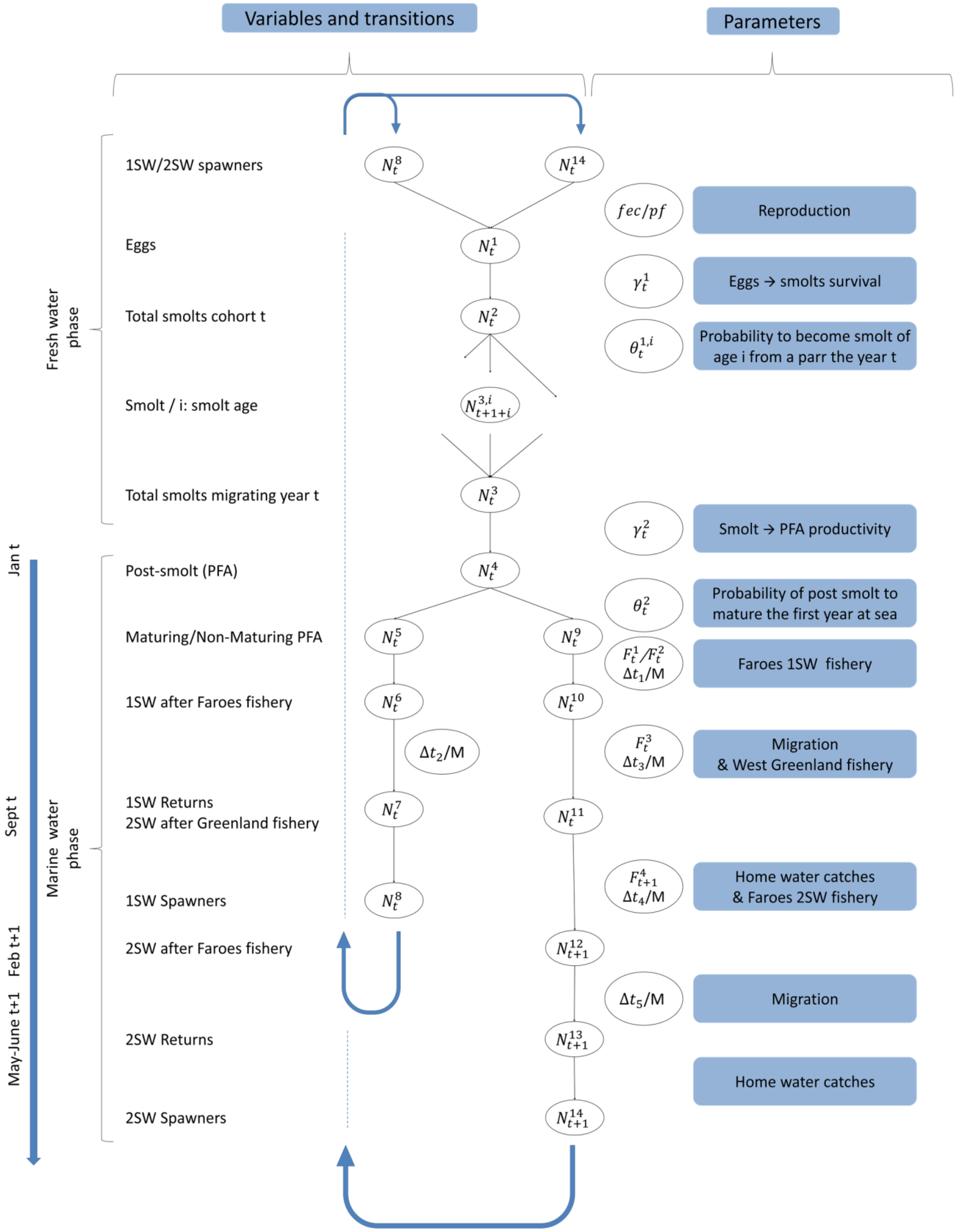

Figure B.1. Structure and variables of the life cycle model.

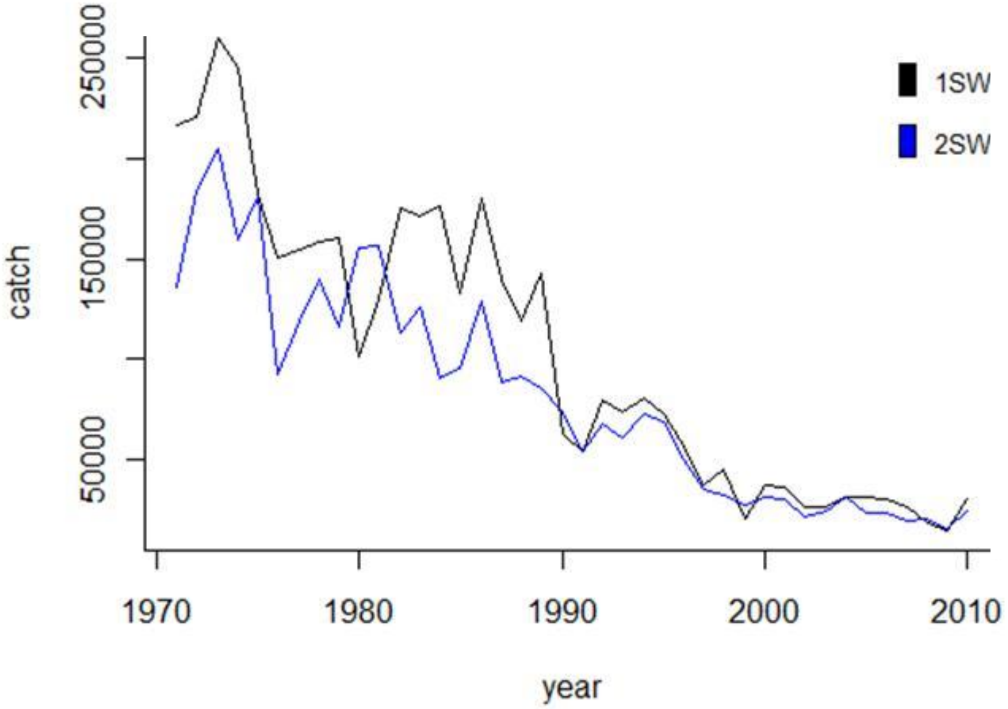

Figure B.2. Home water catches (in numbers) in Eastern Scotland

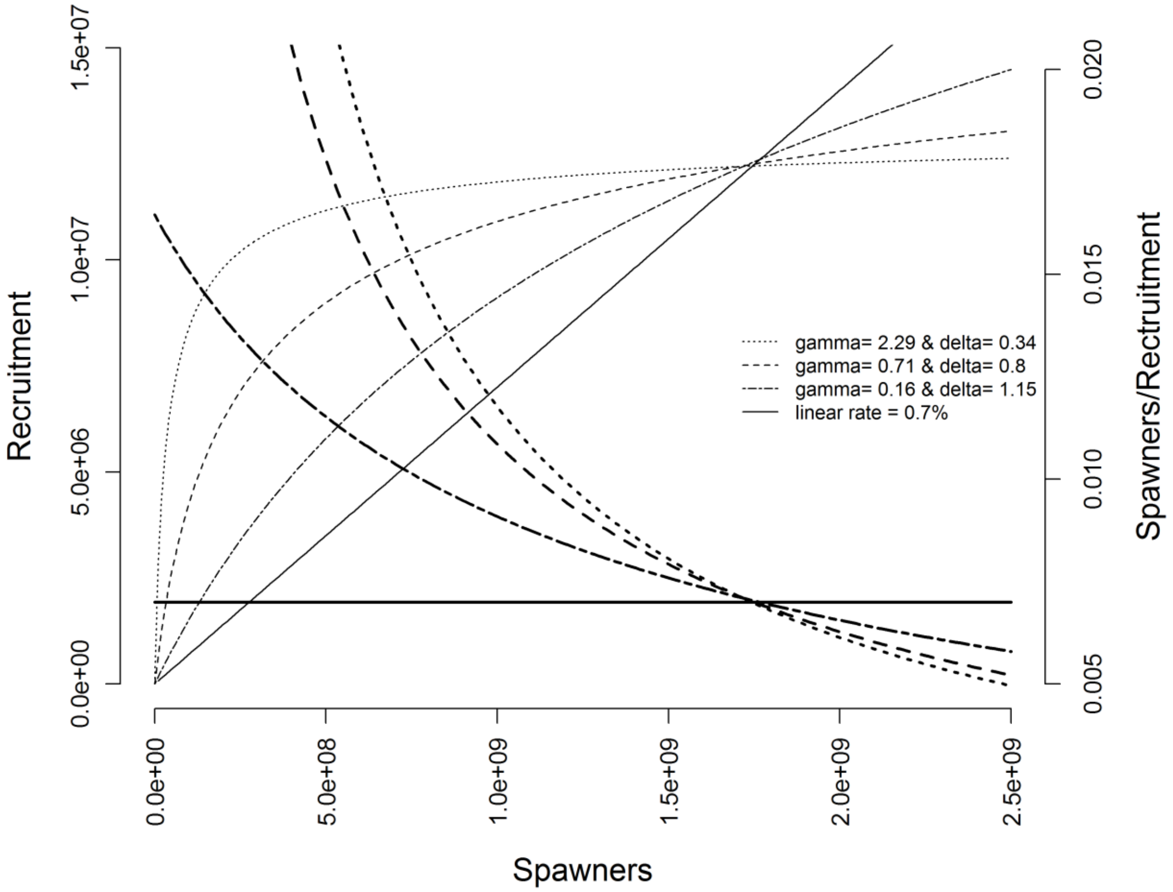

Figure B.3. Eggs → smolts survival functions tested (thin) and associated spawners/recruitment ratio (bold). Status-quo (solid) is a linear function with a slope equal to 0.7% and the small dotted line represents a high slope BH function. The two other lines are in between scenarios.

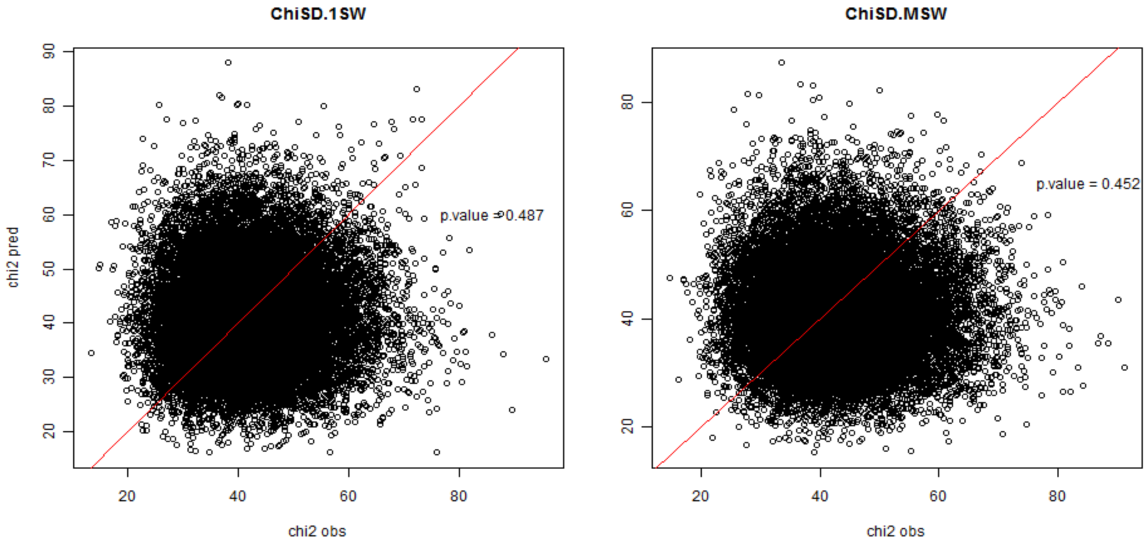

Figure B.4. Discrepancy plot obtained under the baseline model configuration for 1SW (left) and 2SW fish (right). Chi2 obs are realized discrepancies computed with declared (observed) homewater catches, and chi2 pred are predicted discrepancies obtained with posterior predictive replicates of the declared catches. The corresponding p-values are 0.487 and 0.452 respectively.

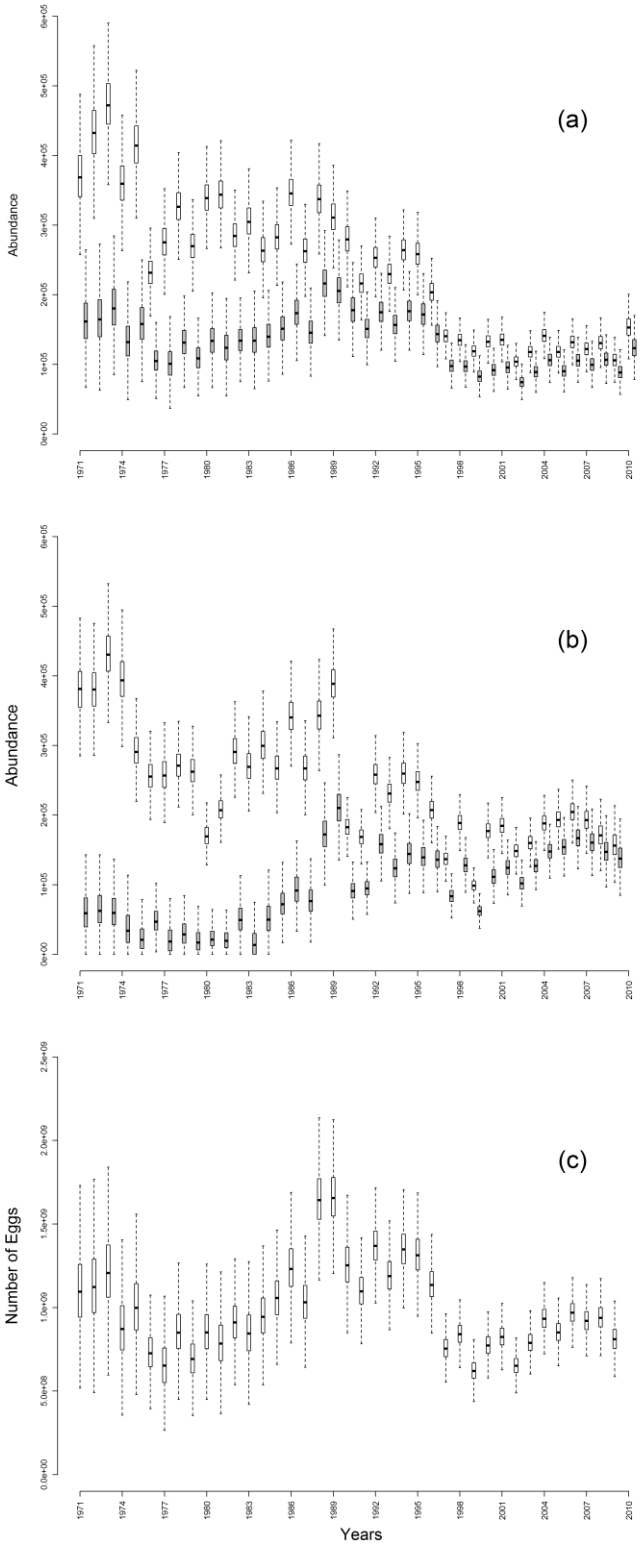

Figure B.5. Marginal posterior distributions of returns (white boxplot) as 1SW (a) and 2SW (b), spawners (grey boxplot) that escape the home water fishery as 1SW and 2SW ((a) and (b), respectively) and total eggs deposition (c).

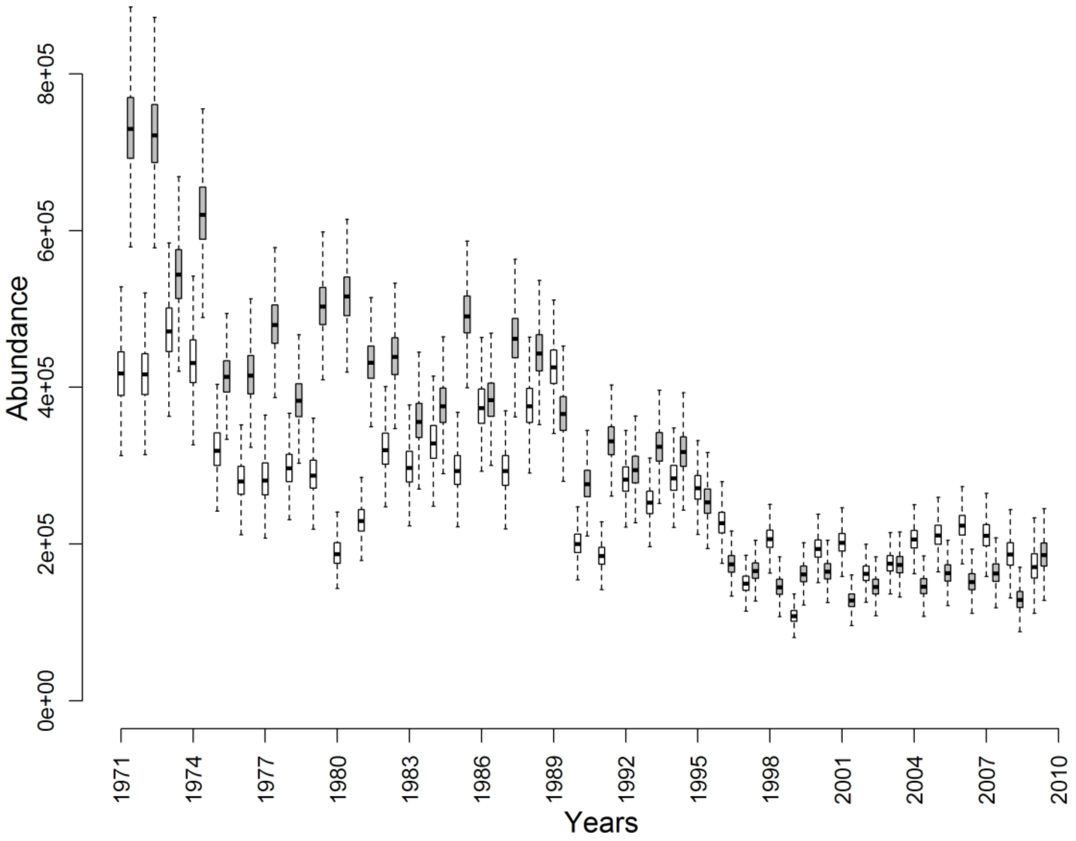

Figure B.6. Marginal posterior distributions of abundance of post-smolts considered at January the 1st of the first winter at sea just prior to the Faroes fishery (PFA), in its maturing (white boxplot) and non-maturing (grey boxplot) component.

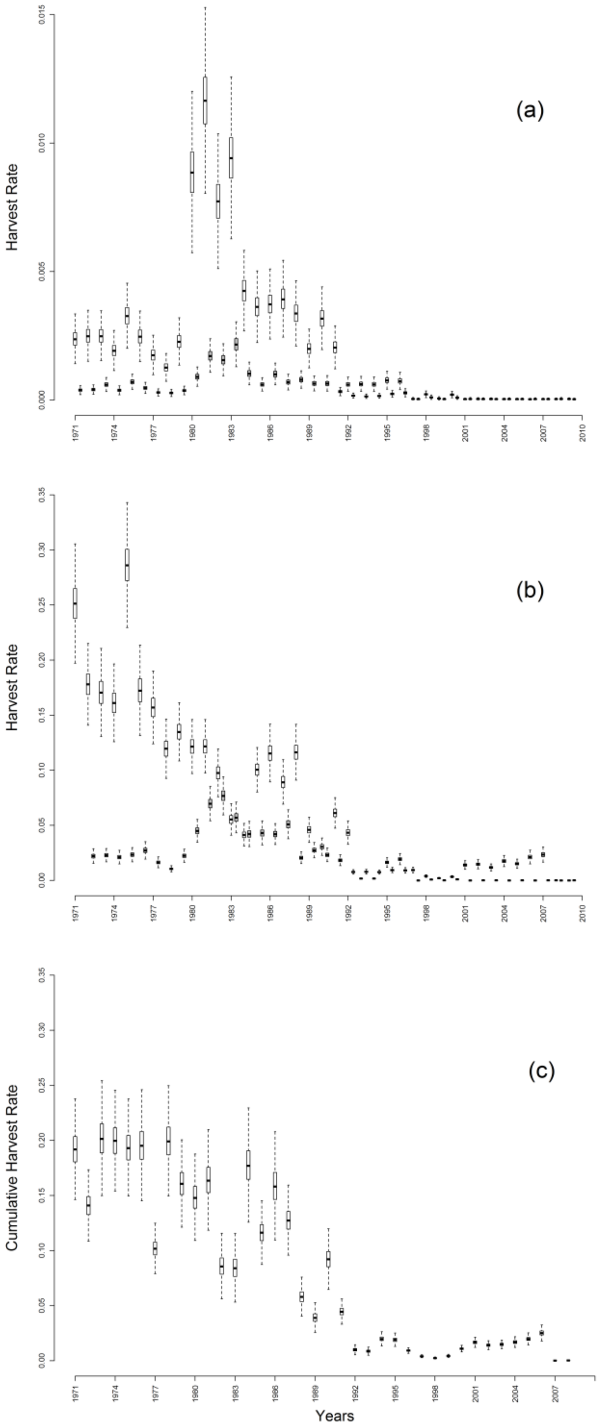

Figure B.7. Marginal posterior distributions of harvest rates estimated for the three sequential fisheries. (a) Faroes for mature (white boxplot) and non-mature (grey boxplot) 1SW fish; (b) western Greenland (white boxplot) and Faroes as 2SW fish (grey boxplot). The cumulative harvest rate for the non-maturing component of the PFA is given in pannel (c). Note that the harvest rates can be >0 even if the declared catches are 0, because of the declaration rate and the DM stochastic model for catches.

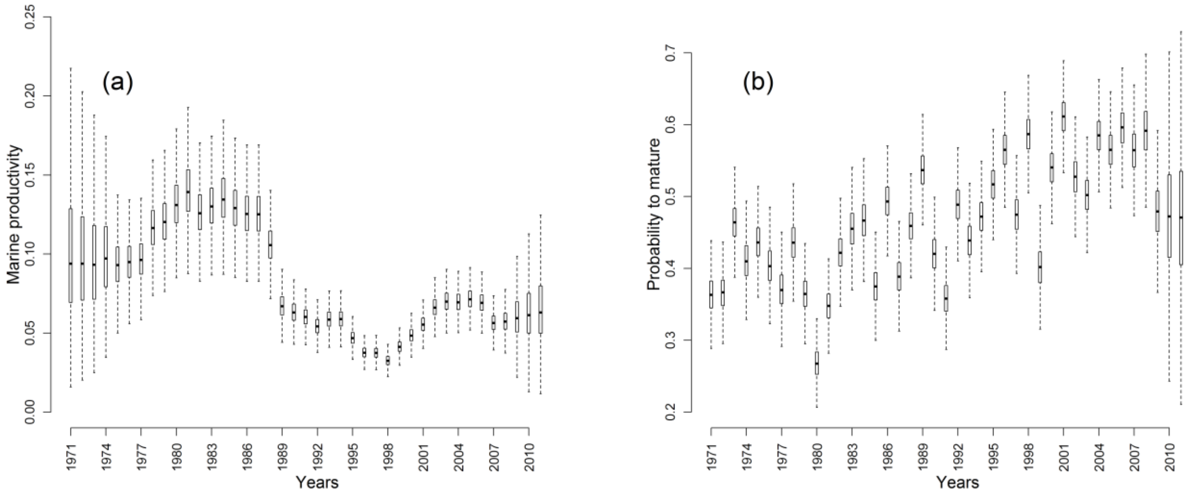

Figure B.8. Marginal posterior distributions of (a) the marine survival during the first months at sea γ_t^2 (smolts → PFA) and (b) the probability to mature the first year at sea.

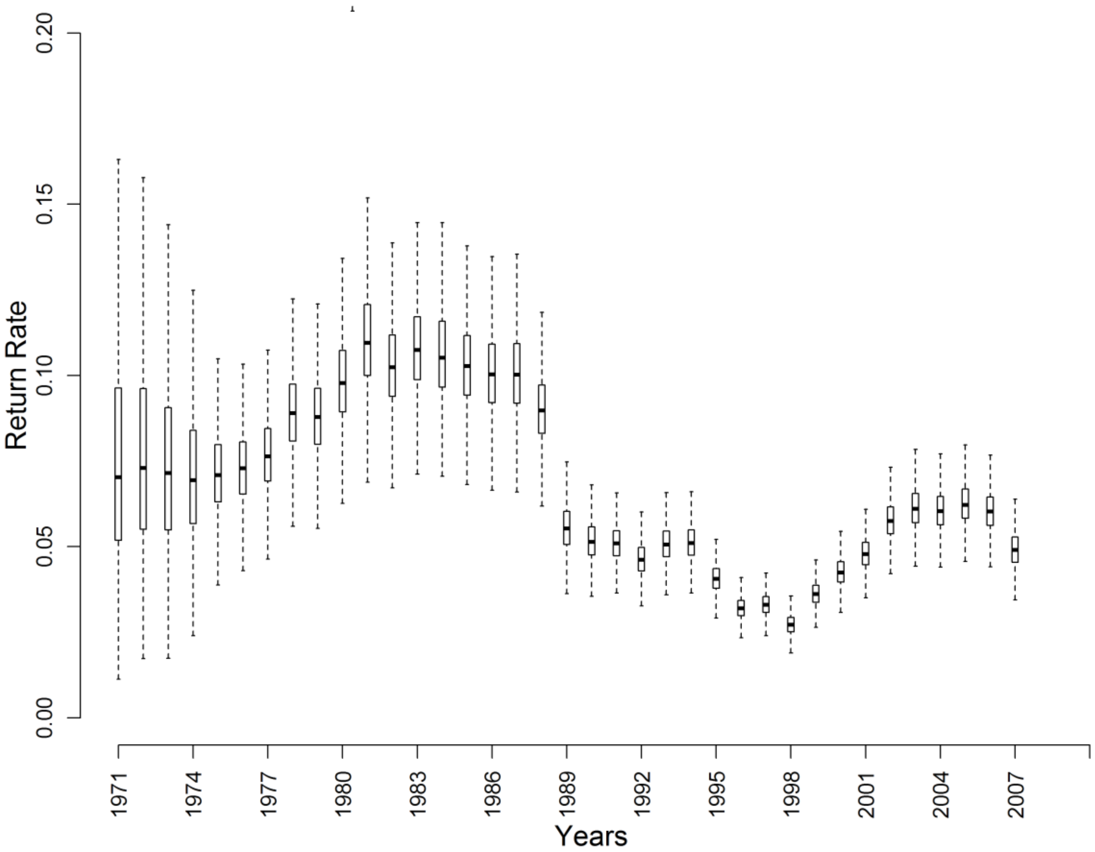

Figure B.9. Marginal posterior distributions of the return rate from smolts to returns as 1SW or 2SW before homewater catches, computed by year of smolts migration.

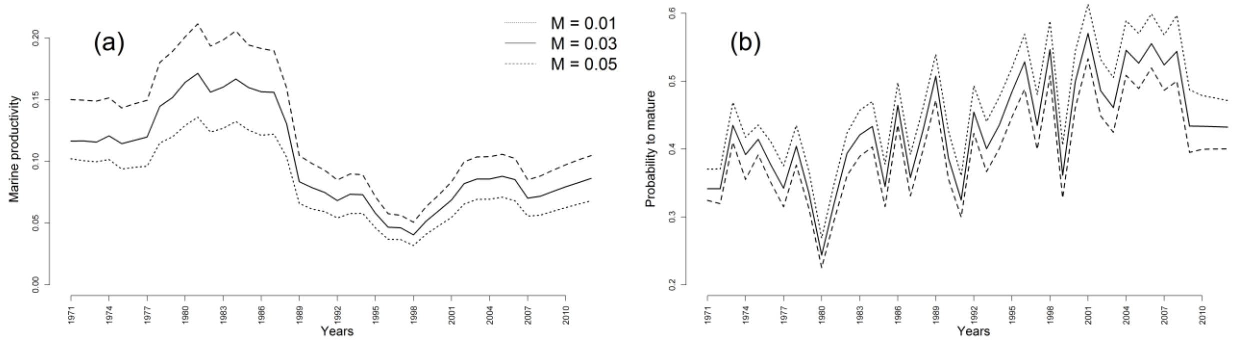

Figure B.10. Sensitivity analysis of (a) the smolts → PFA survival rate, (b) the probability to mature the first year at sea to changes in the informative prior on the natural mortality rate M.

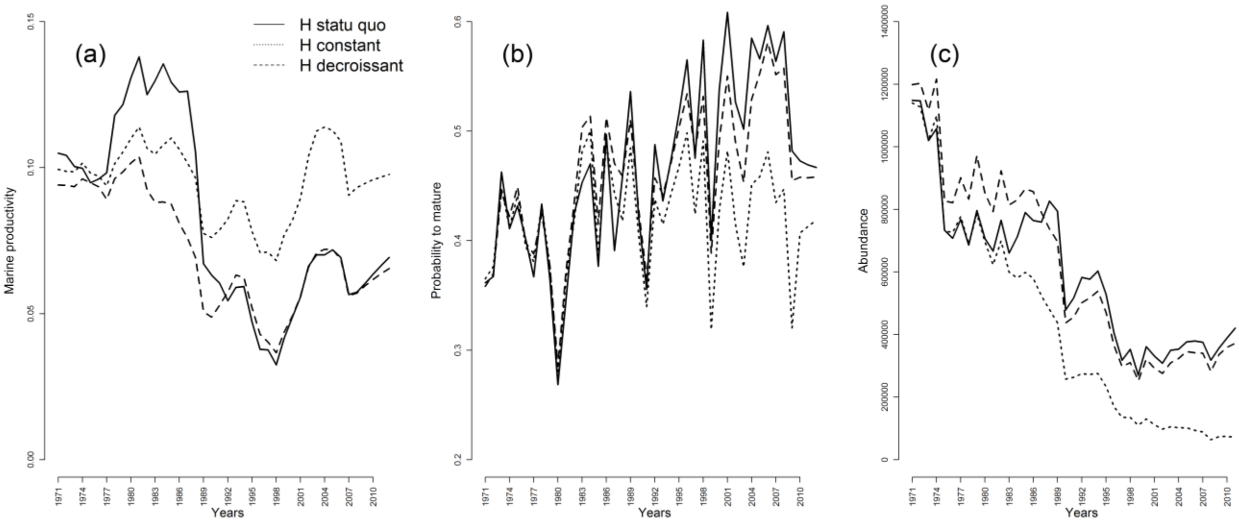

Figure B.11. Sensitivity analysis of (a) the smolts → PFA survival rate, (b) the probability to mature the first year at sea, and (c) the pre-fishery abundance to changes in the informative prior on the harvest rate for homewater fishery.

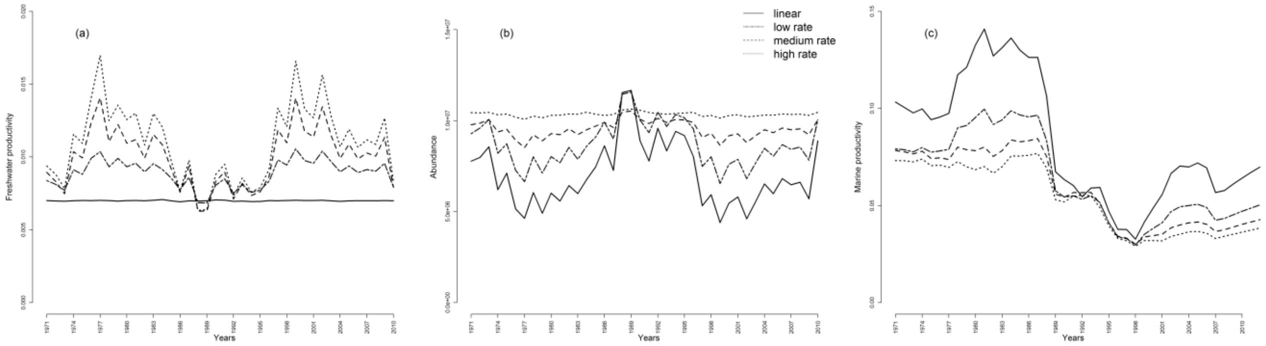

Figure B.12. Sensitivity analysis of (a) the eggs → smolts survival rate, (b) the abundance of smolts per year of cohort birth and (c) smolts → PFA survival rate to changes in the eggs → smolts survival function. In the baseline configuration, the eggs → smolts survival is constant fixed at 0.7%. Three alternative density-dependent survivals (Beverton-Holt form) with a gradient of intensity in the density dependence were tested.

Appendix B1

Time series of catches of the mixed stock fisheries ($CF1^{m}$, $CF1^{nm}$, $CF2$ and $CG2$) were directly derived from ICES and no observation errors were considered (Table B1.1). The number of fish caught the Faroes, which are available by sea ages (1SW and 2SW), were corrected to account for the proportion of unreported catches, of wild fish in catches, mature fish (for 1SW) and the proportion of those catches attributed to Eastern Scotland. Catches in the western Greenland mixed stock fishery were corrected to account for the proportion of catches from European stocks and the proportion from Eastern Scotland. No correction for the declaration rate was needed as estimates of reported catches are already added to declared catches (for years 1993-2007).

Table B1.1. Data used to compute the number of fish caugth in the mixed stock fisheries at Faroes and West Greenland.

Rep_t^i	Reported catches for i sea winter fish	-
$CF1^{dec}$	Declared 1SW catches in Faroes fishery	-
$CF2^{dec}$	Declared 2SW catches in Faroes fishery	-
$CG2^{dec}$	Declared catches in West Greenland fishery	-
$p^{m,country}$	Proportion of maturing fish per country	$p^{m,Scotland} = 0.20$
$p^{nm,country}$	Proportion of non-maturing fish per country	$p^{nm,Scotland} = 0.192$
$p.m.F1_t$	Proportion of maturing fish in faroes fishery	$Unif(0.73,0.83)$
$Unrep.CF1_t$	Unreported rate in faroes fishery	$Unif(0.05,0.15)$
$p.wF_t$	Proportion of wild fish in faroes fishery	$[0.54,1]$
$p.NEAC.G_t$	Proportion of NEAC fishes in catches	
$WG.prop.NEAC^{country}$	Proportion of fishes per country	$WG.prop.NEAC^{scotland} =$

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