

**AGROCAMPUS
OUEST**

CFR Angers

CFR Rennes



Année universitaire : 2014-2015

Spécialité :

Halieutique

Spécialisation (et option éventuelle) :

Ressources et Ecosystèmes Aquatiques

Mémoire de Fin d'Études

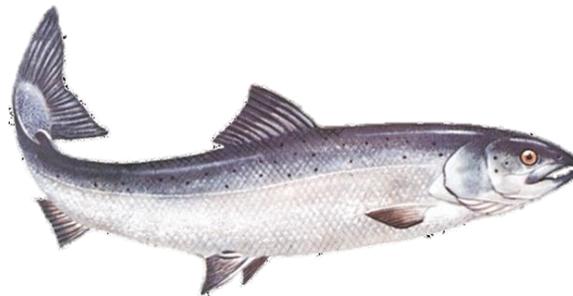
d'Ingénieur de l'Institut Supérieur des Sciences agronomiques, agroalimentaires, horticoles et du paysage

de Master de l'Institut Supérieur des Sciences agronomiques, agroalimentaires, horticoles et du paysage

d'un autre établissement (étudiant arrivé en M2)

Decline in the abundance of Atlantic salmon population in the North Atlantic: Rethinking stock assessment models and exploring ecological mechanisms

Par : Maxime OLMOS



Soutenu à Rennes le 9-09-15

Devant le jury composé de :

Président : Didier GASCUEL, Agrocampus Ouest

Maître de stage : Etienne RIVOT, Agrocampus Ouest

Enseignant référent : Didier GASCUEL, Agrocampus Ouest

Evaluateur extérieur : Verena TRENKEL, Ifremer Nantes

Les analyses et les conclusions de ce travail d'étudiant n'engagent que la responsabilité de son auteur et non celle d'AGROCAMPUS OUEST

Fiche de confidentialité et de diffusion du mémoire

Confidentialité :

Non Oui si oui : 1 an 5 ans 10 ans

Pendant toute la durée de confidentialité, aucune diffusion du mémoire n'est possible⁽¹⁾.
A la fin de la période de confidentialité, sa diffusion est soumise aux règles ci-dessous
(droits d'auteur et autorisation de diffusion par l'enseignant).

Date et signature du maître de stage⁽²⁾ :

Droits d'auteur :

L'auteur⁽³⁾ autorise la diffusion de son travail

Oui Non

Si oui, il autorise

la diffusion papier du mémoire uniquement(4)

la diffusion papier du mémoire et la diffusion électronique du résumé

la diffusion papier et électronique du mémoire (joindre dans ce cas la fiche
de conformité du mémoire numérique et le contrat de diffusion)

Date et signature de l'auteur :

Autorisation de diffusion par le responsable de spécialisation ou son représentant :

L'enseignant juge le mémoire de qualité suffisante pour être diffusé

Oui Non

Si non, seul le titre du mémoire apparaîtra dans les bases de données.

Si oui, il autorise

la diffusion papier du mémoire uniquement(4)

la diffusion papier du mémoire et la diffusion électronique du résumé

la diffusion papier et électronique du mémoire

Date et signature de l'enseignant :

(1) L'administration, les enseignants et les différents services de documentation d'AGROCAMPUS OUEST s'engagent à respecter cette confidentialité.

(2) Signature et cachet de l'organisme

(3).Auteur = étudiant qui réalise son mémoire de fin d'études

(4) La référence bibliographique (= Nom de l'auteur, titre du mémoire, année de soutenance, diplôme, spécialité et spécialisation/Option)) sera signalée dans les bases de données documentaires sans le résumé

REMERCIEMENTS

Tout d'abord, je tiens à exprimer toute ma gratitude et ma reconnaissance envers Etienne Rivot, mon encadrant de stage. Merci pour tout, Etienne : pour ta confiance, ta grande patience, tes conseils toujours avisés et ton accompagnement tout au long de ce stage. J'ai beaucoup apprécié nos échanges et j'ai énormément appris à tes côtés. Ça a été un plaisir de partager ces 6 mois tant sur le plan scientifique qu'humain. Je tiens également à te dire MERCI de me donner l'opportunité de continuer cette aventure avec toi (et les saumons !).

Merci également aux personnes qui ont co-encadré ce stage. Merci à Gérald Chaput pour les données mises à ma disposition et les conseils toujours avisés. Ta connaissance experte du complexe Nord-Américain a été indispensable à la réalisation de ce stage. Merci à Félix Massiot-Granier d'avoir pris du temps pour moi et de m'avoir transmis ses travaux précédents. Et merci à Etienne Prévost, pour ses remarques pertinentes et son avis d'expert sur les résultats obtenus.

Je souhaite remercier maintenant du fond du cœur toute l'équipe Halieutique de l'UMR ESE : Catherine, Sophie, Olivier, Hervé, Didier, Elodie, Jérôme, Marie et Etienne pour m'avoir accueilli et si bien intégré à l'équipe et au « monde de l'Halieutique ». Travailler dans de telles conditions a été très agréable et motivant.

Merci, maintenant aux copains stagiaires, thésard, post-doc du labo, notamment Emilie, Charline, Adri, Martin, Axel « notre zaza à tous », Chidas, Mathieu, Guillaume, Brice et Clément pour leur bonne humeur et les très bons moments partagés. Merci particulièrement à Fabien, je suis très heureux d'avoir partagé ce stage avec toi, et te remercie pour tous tes conseils et ta générosité.

Merci aux copains de Rennes, SAIA, prepa et d'enfance pour leur soutien et leur amitié durant ce stage.

Enfin je tenais à remercier ma famille et en particulier mes parents pour leur soutien perpétuel ; également merci à Marie de me supporter.

RESUME ETENDU EN FRANÇAIS :

Déclin de l'abondance des populations de saumon dans l'atlantique nord : vers une reconsidération des modèles d'évaluation de stocks afin d'explorer les mécanismes écologiques en lien avec ce déclin.

Contexte

Le saumon Atlantique (*Salmo salar*), migrateur amphihaline emblématique a été historiquement très exploité à tel point qu'il est aujourd'hui inscrit sur la liste rouge des espèces menacées de l'IUCN. Il a subi, et subit encore à l'heure actuelle de nombreuses pressions impactant les individus à différentes phases du cycle de vie. Lors de la phase eau douce (phase de reproduction), le saumon Atlantique est soumis à des facteurs susceptibles d'affecter différemment des populations séparées, tels que des modifications de l'habitat ou différentes pressions de pêche en eau douce. Alors que lors de la phase marine (phase commune de migration vers les zones de grossissement), agissent des facteurs susceptibles d'avoir une influence commune sur des populations séparées, tels que des modifications de l'environnement marin ou l'impact des pêcheries sur les stocks partagés.

On observe alors un déclin généralisé des populations de Saumon Atlantique au cours des 40 dernières années et à l'échelle de l'ensemble de son aire de répartition (Amérique du Nord, Europe du Nord et Europe du Sud). Ce déclin s'accompagne également d'une raréfaction des poissons passant plusieurs années en mer. Malgré la mise en place de moratoires de pêche drastiques à partir des années 1990, aucune remontée d'abondance n'est observable à l'échelle de l'ensemble de l'aire de répartition. La littérature semble attribuer ce déclin à la phase marine et plus particulièrement aux premiers mois en mer, qui apparaît comme une phase critique pour la survie des post-smolts. Toutes ces études ont été réalisées à une échelle locale, celle des complexes Nord-Américain, Sud Européen ou Nord Européen, mais aucune approche comparative n'a été réalisée à l'échelle de toute l'aire de répartition.

Objectif

Il devient alors intéressant de se demander si le déclin généralisé des populations ne pourrait pas être une réponse à l'influence de facteurs de pressions agissant à une échelle globale. Cette étude propose alors par une approche de modèle de cycle de vie d'estimer les deux traits de vie caractéristiques des premiers mois de la phase marine : le taux de survie et la probabilité de maturation en mer déclenchant le retour en rivière. Puis, on propose ici, d'identifier les synchronies dans les variations des traits de vie à l'échelle de l'Atlantique (populations européennes et nord-américaines). Enfin cette étude a également pour objectif, d'identifier un(des) facteur(s) de l'environnement à l'origine d'un tel déclin.

Matériels et Méthodes

❖ Construction du modèle

Une approche de modélisation hiérarchique Bayésienne de la dynamique de la population de saumon a été développée, à large échelle spatiale et temporelle. Une telle approche permet de séparer les processus démographiques des processus d'observation. Nous disposons d'une base de données unique compilée par un groupe d'experts internationaux, à large échelle spatiale (6 régions nord-américaines : Terre-Neuve, golfe, Nouvelle Ecosse, Québec, USA, Labrador) et temporelle (1970-2013).

Pour chaque année et chacune des régions, sont disponibles :

- le nombre de saumons retournant en rivière par classe d'âge (1 Hiver de Mer ou 2 Hiver de Mer)
- les captures dans les eaux territoriales par classe d'âge
- les captures en mer sur stocks mélangés
- les données lors de la phase en eau douce : fécondité et âge de smoltification

La mise à jour du modèle de cycle de vie par les données, à l'échelle des 6 régions, permet alors d'estimer, par inférence bayésienne :

- les deux paramètres démographiques clés : survie et probabilité de devenir mature
- les abondances à tous les stades de vie
-

❖ Analyse de données

A l'échelle Nord-Américaine, la synchronie dans les variations des paramètres démographiques est étudiée par Analyse des Composantes Principales (ACP), permettant d'extraire alors une tendance commune à l'échelle Nord-Américaine.

De même, une ACP, regroupant les régions Nord-Américaine et Sud Européenne est réalisée afin d'extraire une tendance commune à l'échelle de l'Atlantique Nord.

Enfin, une approche exploratoire de l'impact de l'environnement sur les traits démographiques a été menée, en étudiant les corrélations entre les signaux communs extraits précédemment à l'échelle de l'atlantique nord et des proxys de variables environnementales.

Résultats

Les résultats mettent en évidence une réponse synchrone des populations des 6 régions américaines allant dans le sens d'une diminution du taux de survie et une augmentation de la probabilité de maturer dès les premiers mois passés en mer.

Plus généralement, les résultats révèlent un déclin de la survie marine et une augmentation de la probabilité de maturer, communs à toutes les régions d'Amérique du Nord et d'Europe du Sud. Les séries temporelles de taux de survie sont corrélées négativement avec un proxy de la température moyenne de la surface de l'océan dans l'Atlantique Nord, l'Oscillation Atlantique Multi-décennale (AMO).

Le modèle construit permet également de proposer des prédictions des abondances à cours termes sous différents scénarios de gestion

Conclusion

Cette étude à l'échelle de l'Atlantique Nord suggère fortement une réponse commune des populations de saumon à des changements globaux, impactant ces populations durant la phase marine, où le réchauffement des océans auraient un impact négatif sur les populations via des mécanismes bottom-up. L'implication de tels mécanismes amène à considérer alors la croissance comme étant au centre des mécanismes démographiques. Considérer la croissance à travers des normes de réaction permettrait donc de faire un lien entre la survie et la probabilité de maturer dès la première année en mer.

CONTENT

1	INTRODUCTION.....	1
1.1	General context.....	1
1.2	Atlantic salmon life cycle	3
1.3	Stock status and stock assessment.....	4
1.4	Insights from large scale approach.....	4
1.5	Towards an integrated life cycle model for A. salmon in the North Atlantic.....	5
2	MATERIAL AND METHODS	6
2.1	Outlines of the model	6
2.2	Data	10
2.2.1	Pre-processing of the time series of Returns and Spawners	10
2.2.2	Fisheries data.....	11
2.2.3	Others biological data.....	14
2.3	Population dynamics	14
2.3.1	Stochastic demographic transitions	14
2.3.2	Fresh water phase	14
2.3.3	Marine phase	15
2.4	Observation equations (likelihood)	18
2.4.1	Catches at sea for sequential mixed stock fisheries	18
2.4.2	Returns	18
2.5	Bayesian fit using MCMC sampling.....	18
2.6	Posterior analysis of the time series of estimated parameters.....	19
2.7	Prediction and spawning requirement for NA.....	19
3	RESULTS.....	21
3.1	Abundances and harvest rates of fisheries at sea	21
3.1.1	Abundances	21
3.1.2	Harvest rates of fisheries at sea	22
3.2	Key life history parameters of the marine phase: Smolt-to-PFA survival and maturing probability.....	23
3.2.1	Smolt-to PFA survival rates.....	23
3.2.2	Probability of maturing after the first year at sea.....	24
3.3	Synchrony between population dynamics in NA and S-Europe	26
3.3.1	Post-smolt survival	26

3.3.2	Probability to mature after the first winter at sea.....	27
3.4	Correlation between post-smolts survival and maturing probability and the Atlantic Multidecadal Oscillation Index.....	28
3.4.1	Post-smolts survival	29
3.4.1	Maturing probability	29
3.5	Forecasts of the returns under management scenarios of catches at sea	30
4	Discussion.....	31
4.1	A large scale modeling approach to unravel the fingerprints of large scale ecosystem changes	31
4.2	Limits of the modelling approach.....	32
4.2.1	A simplified demographic structure.....	32
4.2.2	Sensitivity of the results to some data sources and level of aggregation	34
4.3	A response to a trophic cascade as a possible ecological mechanism	35
4.3.1	A response to bottom-up forcing during the marine phase	35
4.3.2	A trophic cascade.....	36
4.3.3	Growth variations as a pivotal demographic mechanism?	36
4.3.4	Perspectives	36
5	BIBLIOGRAPHY.....	38
6	Appendix	42

LIST OF APPENDIX

Appendix I: Data processing on Returns and Spawners.....	42
Appendix II: Data on Marine fisheries (mixed stocks)	46
Appendix III: Posterior checking.....	47
Appendix IV: Time-series of residual.....	48
Appendix V: Estimated spawners and management objectives in the 6 geographic areas of North America	49
Appendix VI: JAGS code.....	50

LIST OF ILLUSTRATIONS

Figures

Figure 1: Atlantic salmon geographical range and organisation of the different commission of the NASCO: NAC (North American Commission, N-NEAC (North Northeast Atlantic Commission), S-NEAC (South Northeast Atlantic Commission) (source: Aas et al 2011).....	1
Figure 2: Estimated abundance (number of fish, median, and 95% percentile range) of Atlantic salmon by age (1SW and 2SW fish) at maturity.....	2
Figure 3: Atlantic salmon life cycle and the influence of multiple factors on different life stages and different associated spatial scale (Source: Rivot 2013).	3
Figure 4: Map of the 6 stock units (or regions) considered in NA. The 6 regions of NA are represented with their respective Salmon Fishing Areas (SFAs, numbered from 1 to 23) and Québec Management Zones (Qs).	6
Figure 5: Empirical probability distribution of the time series of returns of 1SW and 2SW for Quebec (obtained from n=100 000 Monte Carlo simulations).	11
Figure 6: Point estimates of homewater catches for all regions in NA.....	12
Figure 7: Times series of catches for the sequential fisheries at sea occurring on mixed stocks.....	13
Figure 8: Marginal posterior distributions of the returns of 1SW (a) and 2SW (b) salmon in 6 regions of NA. Shaded area is the posterior uncertainty for each region (first and third quartiles).	21
Figure 9: Marginal posterior distribution of (a) pre-fisheries abundance (number of fish) and (b) standardized pre-fisheries abundance for the 6 regions of North America. Year 1975 is used as standardization. Shaded area is the posterior uncertainty (first and third quartiles).	22
Figure 10: Marginal posterior distributions of harvests rates for the sequential fisheries at sea occurring on mixed stocks	23
Figure 11: Time series of post-smolt marine survival rates for the 6 regions in NA.	24
Figure 12: Time series of probability of maturing after the first year at sea for the 6 regions in NA).....	25
Figure 13: Analysis of the synchrony in the post-smolts survival among the 6 regions in NA and the 8 regions in S-Europe.....	26
Figure 14: Analysis of the synchrony in the proportion maturing among the 6 regions in NA and the 8 regions in S-Europe.....	28

Figure 15: Standardized time series of the global trends (extracted from the PCA at the scale of the North Atlantic Ocean) in (a) the post-smolts survival, and (b) the maturing probability, versus the Atlantic Multidecadal. Plain lines are series smoothed via a multinomial non parametric smoothing (R *loess* function, with a smoothing parameter=0.3).29

Figure 16: Probability of reaching management objective, under different management scenarios of catches at sea30

Tables

Table 1: Summary of the variables of the life cycle model (See Figure 5) 9

Table 2: Summary of the different fisheries data. Uperscript “*obs*” is used here because the catches data will be distinguished from the state variable in the model to include observation errors on catches.....11

Table 3: summary of the parameters (all fixed) of the fresh water phase14

Table 4: Summary of the sequential fisheries and corresponding harvest rates17

Table 5: Parameters associated with the marine water phase. Parameters fixed or drawn in very tight informative prior distribution are shaded.....17

Table 6: 2SW conservation limit and management objective for each region of NAC.....20

Table 7: Pearson’s product-moment correlation between survival (Atlantic, NAC, S-NEAC and) AMO. Atlantic refers to NAC and S-NEAC complexes. Values in parenthesis indicate the p-values of the significance test. * indicates an autocorrelation significate with p-v value <0.05.....29

Table 8: Pearson’s product-moment correlations between probabilities of mature during the first year at sea (Atlantic, NAC, S-NEAC) and AMO. Atlantic refers to NAC and S-NEAC complexes. Values in parenthesis indicate the p-values of the significance test. * indicates an autocorrelation significate with p-value <0.05.30

Table 9: Pearson’s product-moment correlation between survival (Atlantic, NAC, S-NEAC and) AMO. Atlantic refers to N-America and S-Europe. Values in parenthesis indicate the p-values of the significance test. * indicates an autocorrelation significate with p-value <0.05. 34

1 INTRODUCTION

1.1 General context

Atlantic salmon (*Salmo salar*) is one of the most emblematic diadromous fish (Mills, 1989; Shearer, 1992). Its distribution area includes the whole North Atlantic, from the west of Connecticut (USA) to the Ungava Bay (Canada), and from the North of Spain to Norway (Shearer, 1992). There are four important assemblages of populations based on genetic criteria (King et al., 2001; ICES, 2013): North American (USA and Canada), South European, North European and Baltic (ICES, 2014) (Figure 1).

Like the majority of other diadromous fish, Atlantic salmon have undergone a major decline over the past century and over their entire distribution area (Limburg and Waldman, 2009) (Figure 2).

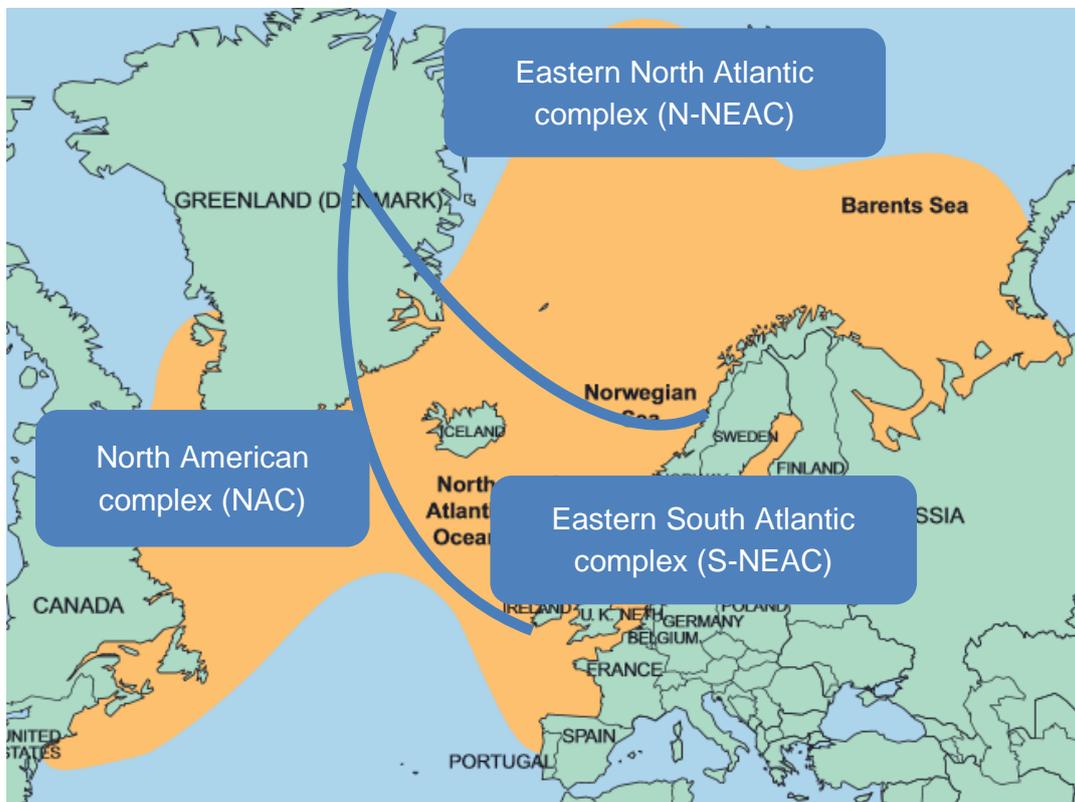


Figure 1: Atlantic salmon geographical range and organisation of the different commission of the NASCO: NAC (North American Commission, N-NEAC (North Northeast Atlantic Commission), S-NEAC (South Northeast Atlantic Commission) (source: Aas et al 2011)

This widespread decline of populations suggests a response of factors acting at a global scale. Such an observation leads to think at large scale to understand what kind of factors drive this common decline, and especially, what is the influence of fishing and global environmental factors on this response.

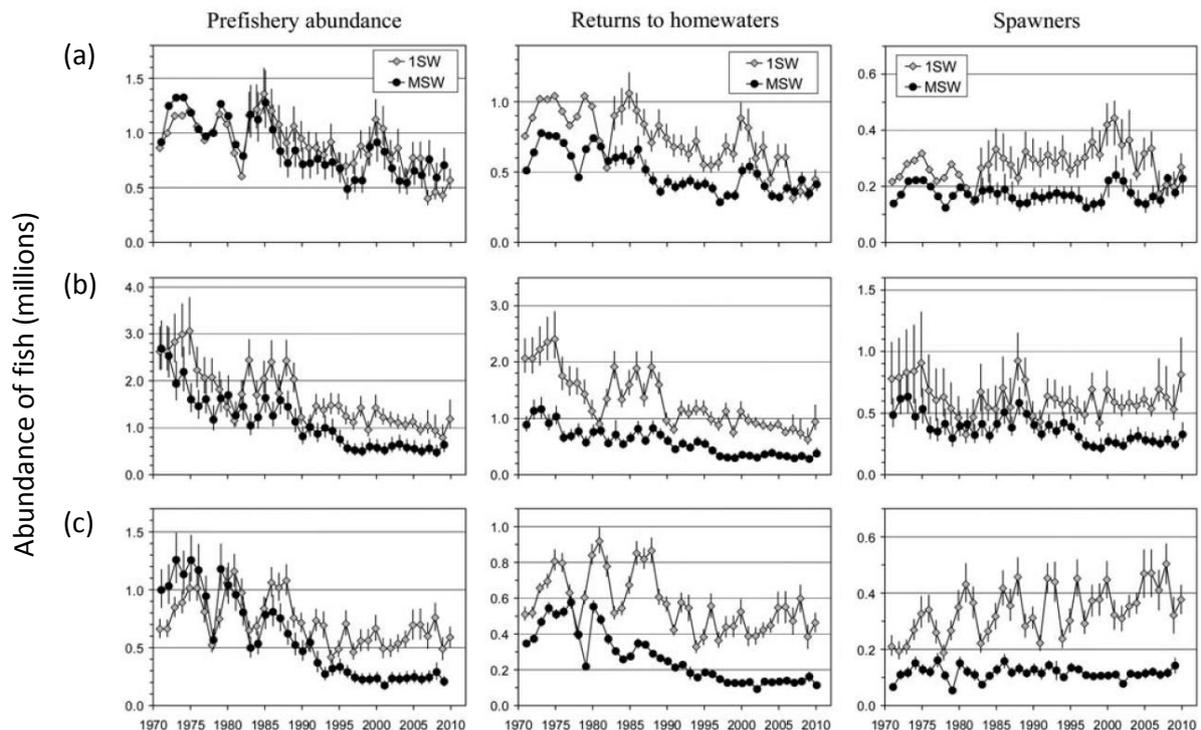


Figure 2: Estimated abundance (number of fish, median, and 95% percentile range) of Atlantic salmon by age (1SW and 2SW fish) at maturity. (left) abundance of post-smolts at sea before any fishery (1st january of the first winter at sea, Pre Fishery Abundance) ; (middle) returning to the coast after exploitation at sea ; (right) as potential spawners after the homewater fisheries. Abundance are given for the three complex of stocks as defined by the North Atlantic Salmon Conservation Organisation (NASCO) : (a) Northern North East Atlantic ; (b) Southern North East Atlantic ; (c) North America (adapted from Chaput et al. 2012). Atlantic salmon has been historically harvested by intense commercial fisheries, mostly operating on the large marine feeding areas. Following the sharp decline of abundance observed in Europe and North America in the 1970's and 1980's, most of the commercial fisheries have been drastically reduced or closed in the early 1990's (Chaput et al. 2012).

The present work is an extension of the thesis of [Massiot-Granier F. \(2014\)](#) that was part of the Atlantic salmon case study to the EU-FP7-ECOKNOWS research project (<http://www.ecoknows.eu>). Our study has two main goals:

1. The first objective stands in the framework of the work for stock assessment of the Working Group on North Atlantic Salmon (WGNAS, ICES). The objective is to improve the methodology of stock assessment models built at the scale of all stock complexes. The project aims at embedding stock assessment within an integrated hierarchical life cycle modeling approach to integrate all sources of information and to quantify uncertainty.
2. The second objective is to rely on this large scale approach to quantify the temporal variations of the key demographic parameters controlling the productivity of the marine phase. Working on large population aggregates would enhance the possibility to unravel fingerprints of large scale ecosystemic changes susceptible to impact populations that spawn in distant rivers but that share common environmental conditions during the marine phase of the life cycle.

1.2 Atlantic salmon life cycle

Atlantic salmon have a complex life cycle shaped by migration between fresh and salt water. Spawning takes place in fresh water from the end of autumn to winter. Eggs hatch under gravel and alevins emerge during the following spring. Juveniles, called parrs, grow in fresh water during one or several years before becoming smolts and reaching the sea (Shearer, 1992, As et al., 2010). After one or several years of long migrations at sea until Greenland or Faroes Islands, (Dadswell et al., 2010), adults return to the river of birth to spawn (homing).

Because of the characteristics of their life cycle, A. salmon are sensible to numerous factors of stress, possibly impacting fish at different life stages and different spatial scales (Figure 3). For life stages when populations are spatially isolated (freshwater phase), populations can be impacted by local factors of stress susceptible to vary within a small spatial range (e.g. degradation of aquatic habitat) impacting directly spawning areas and growth for the juveniles (Gibson, 1993; Jonsson et al., 1998). During the long oceanic migrations, numerous populations can be impacted synchronously to factors acting at global scale (e.g. large scale oceanic environmental conditions).

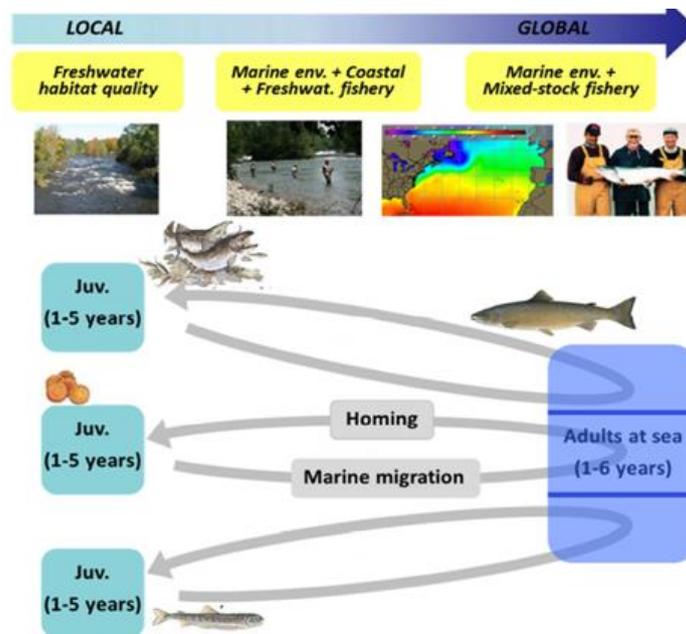


Figure 3: Atlantic salmon life cycle and the influence of multiple factors on different life stages and different associated spatial scale (Source: Rivot 2013).

The widespread decrease of abundance observed over 40 years (Figure 2) strongly suggests that environmental factors could affect salmon survival at sea on a large scale of space and time. The degradation of environmental conditions (e.g. temperature, trophic conditions) during marine migrations and in the spawning grounds would appear to be the main hypothesis to explain decline generalized of abundances (Chaput, 2012; Beaugrand and Reid, 2012; Mills et al., 2013).

Although demographic and ecological mechanisms are still not clear, the literature suggest that the consistent decline of populations is a response of population to large scale environmental forcing affecting the early marine life of post-smolts (Friedland, 1998; Condrón et al., 2005; Beaugrand and Reid, 2012; Friedland et al., 2014). Friedland et al. (2014) and

Mills et al. (2013) suggest a direct or indirect influence of the contemporary Ocean warming leading ecosystemic changes.

1.3 Stock status and stock assessment

A. salmon populations are assessed and managed at different scales. Freshwater habitats and fisheries occurring in homewaters (e.g. coastal, estuarine or freshwater fisheries) are managed by national agencies. When present in the marine feeding grounds (e.g. West Greenland feeding grounds), A. salmon may be harvested in mixed stock fisheries (Chaput, 2012; ICES, 2014). The NASCO (North Atlantic Salmon Conservation Organisation) is an international organization in charge of the management of those fisheries at sea. NASCO receive scientific advice from the Working group on North Atlantic Salmon of the International Council for the Exploration of the Sea (ICES WGNAS). Advice is provided based on a forecast of A. salmon abundance prior to any exploitation at sea (the Pre Fishery Abundance, i.e. post-smolt abundance on 1 January of the first winter at sea prior to any fisheries, hereafter denoted PFA). A fixed escapement strategy has been adopted with the objective of achieving the spawner requirements for the contributing stocks on both sides of the Atlantic Ocean (Chaput, 2012).

ICES has developed models for population assessment at the scale of three multinational stock complexes: the Northwest stock complex (NW) aggregating stocks of Northeast America, and the southern and northern Northeast stock complexes (S.NE and N.NE, respectively), aggregating stocks of Western Europe, Iceland and Russia (Chaput, 2012; ICES, 2013). For each of the three stock complexes, assessment models similar to classical cohort analysis have been developed: data are homewaters catches which are scaled by harvest and declaration rates to estimates annual returns to freshwaters by region. Then with these returns it is possible to reconstruct abundance up to the PFA stage (Rago et al., 1993; Potter et al., 2004; Chaput, 2012).

1.4 Insights from large scale approach

Data series compiled by ICES WGNAS and some of the outputs of the models have already been used to improve the understanding of the mechanisms that underline the decline of A. salmon. Indeed, population models developed by ICES use a considerable amount of data that aggregate information on population abundance at the scale of the whole Atlantic Ocean. The data aggregation at such a large spatial scale offers the unique opportunity to unravel fingerprints of large scale environmental changes on population, and then to improve our understanding on the ecological and demographic mechanisms that underline change in population abundance and demographic structure.

The shift in abundance and in marine productivity of A. salmon in 1990s has been analysed by Beaugrand and Reid (2003; 2012) who correlated synchronous shifts in A. salmon abundance of the Southern European stock complex with shifts in the temperature and in the structure of zooplankton communities observed in the 90's in the northern Atlantic Ocean.

Based on the results of the ICES WGNAS, Mills (2013) demonstrates synchrony in marine productivity among groups of populations reproducing in distant regions in North America (NA in the following). Friedland et al. (2014) and Mills et al. (2013) suggest a direct or indirect

influence of the contemporary Ocean warming, through a *bottom-up* control of salmon population driven by changes in zooplankton community in response to variations in climate and physical marine conditions.

1.5 Towards an integrated life cycle model for *A. salmon* in the North Atlantic

However, as reviewed by [Massiot-Granier et al. \(2014\)](#), modelling approaches developed by ICES suffer from several caveats. None of those analyses are based on a stage-based life cycle model. This impairs to unravel if trends in abundance observed at the scale of the North Atlantic reflect trends in some key life history traits. Also, because the data are available at a very wide spatial scale, building an integrated life cycle model would also allow us to explore the spatial scale of those changes.

The present study is part of a broader research project that aims at building an integrated life cycle model for *A. salmon* population dynamics at the scale of the North Atlantic ocean.

[Massiot-Granier \(2014\)](#) previously developed an effective approach for incorporating complex demographic process within statistical models at the scale of Eastern North Atlantic Ocean. The model allows interpreting the variation of abundance through the analysis of the variation of the two marine demographic parameters. It captures the dynamics of eight groups of populations associated to eight European countries/regions and estimates key population dynamic parameters for each region. The results show that post-smolts survival rate and probability of maturing after the first year at sea are synchronous by regions, reinforcing the hypothesis of a common demographic response of distant populations to large scale ecosystemic changes.

The objectives of the present work are precisely to extend the framework to the complex of stocks reproducing in NA to enhance the spatial scale of the analysis and contribute to the understanding of the demographic and ecological factors that control *A. salmon* population dynamics.

To that end, we present a broad-scale life cycle approach, among six large groups of population in NA, conceived to (i) represent the variation of marine demographic parameters in this area, (ii) quantify the level of synchrony in the variation of these key demographic transition rates at North American scale and over Atlantic area by comparing European demographic parameters estimated by [Massiot-Granier et al. \(2014\)](#) and North American demographic parameters, (iii) explore the influence of environmental factors on these parameters at large spatial scale (iv) and propose prediction of returns of salmon to each regions under different management plan.

2 MATERIAL AND METHODS

2.1 Outlines of the model

Following the methodology developed in Massiot-Granier et al. (2014), the model is built in a hierarchical (state-space) framework (Buckland et al., 2004; Rivot et al., 2004; Parent and Rivot, 2012) that accommodates both the stochasticity in the population dynamics and observation errors.

The population dynamics includes environmental stochasticity in the form of between-year variability of some key transition rate, such as the marine survival of post-smolts during their first year at sea and the probability to mature after the first year at sea.

The model is spatially structured and considers the populations dynamics for different regions in NA. Following ICES (ICES 2014), Atlantic salmon populations in NA are aggregated in 6 stock units (**Figure 4**): Newfoundland, Gulf Regions, Scotia-Fundy, USA, Quebec and Labrador. This aggregation is based on genetic data and won't be discussed in this study. For each of the 6 regions, data are available for 44 years, from 1970 to 2013. In the following, subscripts $t = 1, \dots, 44$ stand for years (1970-2013), and $r = 1, \dots, 6$ stand for the 6 regions (1-Newfoundland, 2-Gulf, 3-Scotia-Fundy, 4-USA, 5-Quebec and 6-Labrador).

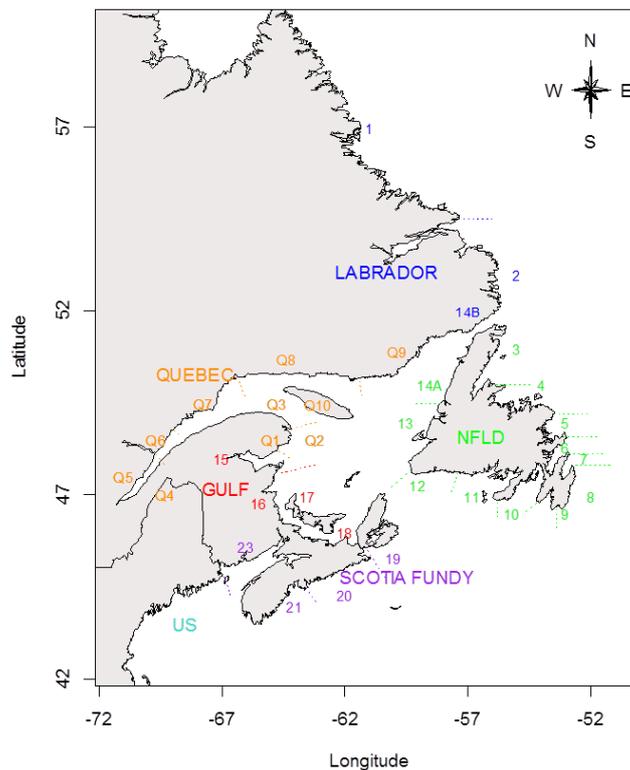


Figure 4: Map of the 6 stock units (or regions) considered in NA. The 6 regions of NA are represented with their respective Salmon Fishing Areas (SFAs, numbered from 1 to 23) and Québec Management Zones (Qs).

The population dynamic (non-observed) is represented by an age- and stage-structured life cycle model, including different life histories and both natural and fishing mortalities (**Figure 5; Table1**). The model tracks the abundance of fish (in number) at different life stages s , years t and region r , and this abundance is denoted $N_{s,t,r}$. The subscripts used for

the life stages s (1–10) can be used to track the life stages sequentially from the eggs ($s = 1$) to the spawning adults ($s = 7$ or 10 , depending on sea age of spawners).

The number of eggs spawned, denoted $N_{1,t,r}$ are directly calculated from the returning fish that survive the homewater fisheries (N_7 and N_{10}). The egg-to-smolt transition is modelled without representing intermediate parr stages. $N_{2,t,r}$ denotes the total number of smolts produced from reproduction in year t . After hatching, juveniles migrate as smolts after 1 to 6 years spent in freshwater (with proportions of smolt-age classes specific to each of the 6 regions, regions further North typically having older smolt ages). Then, up to 6 age-classes of smolts are considered in the model. Smolts of age k that migrate seaward after 1 to 6 years spent in freshwater are denoted $N_{2,k,t+k+1,r}$. Once at sea, smolt ages are pooled together, and $N_{3,t,r}$ denotes the total number of smolts migrating in the spring of year t . Return rates from smolts to spawners of different sea ages result from the combination of natural mortality, maturation and fishing mortality. The number of post-smolts that survive to the PFA stage (i.e. the number of post-smolts at 1 January of their first winter at sea, just prior to the marine fisheries) is denoted $N_{4,t+1,r}$. Only fish that mature after one or two winters at sea are represented. Fish maturing after one sea winter (1SW) are denoted from $N_{5,t+1,r}$ to $N_{7,t+1,r}$ and fish maturing after the second sea winter at sea (2SW) are denoted from $N_{8,t+1,r}$ to $N_{10,t+2,r}$. Fishing mortality is represented as a sequence of fisheries along the migration routes, including the marine fisheries operating on mixed stocks (fish from all regions r mixed together) and the homewaters fisheries operating on fish returning to breed in the regions they are originated from. Mature 1SW fish that escape the Newfoundland and Labrador fisheries ($N_{5,1,t+1,r}$) and then the Saint Pierre et Miquelon fishery ($N_{5,2,t+1,r}$) survive their migration back to homewaters ($N_{6,t+1,r}$) and finally escape the homewater fishery ($N_{7,t+1,r}$) to spawn as 1SW fish. Non-mature 1SW fish that successively escape the Newfoundland and Labrador fisheries ($N_{8,1,t+1,r}$), the West Greenland fishery ($N_{8,2,t+1,r}$), the Newfoundland and Labrador fisheries again as 2SW ($N_{8,3,t+2,r}$), and finally the Saint Pierre et Miquelon fishery ($N_{8,4,t+2,r}$) survive through their migration back to homewaters ($N_{9,t+2,r}$) and finally escape the 2SW homewater fishery ($N_{10,t+2,r}$) to spawn in their natal rivers as 2SW fish.

Following the same methodology that the one developed in Massiot-Granier et al (2014), the Bayesian framework is used to assimilate information from the data and informative prior distributions to estimate the number of fish in each age and life stage ($N_{s,t,r}$) and time-series of key transition rates: the survival rate of smolts during the month at sea (smolt-to-PFA survival rate) and the proportion of fish maturing after the first winter at sea.

Informative prior distributions or fixed values are assigned to several parameters of the demographic or observation processes. In particular, an informative prior is used for the natural mortality at sea after the PFA stage (denoted M), considered constant in time and homogeneous among the 6 regions. Also, because no direct observations are available for the smolt production at the scale of the 6 regions, parameters for egg-to-smolt survival are fixed from the literature (homogeneous among the 6 regions), informative priors are used for the average proportions of smolts in each age class (specific for each regions), and environmental stochasticity in the egg-to-smolt transition is modelled with a very low variance.

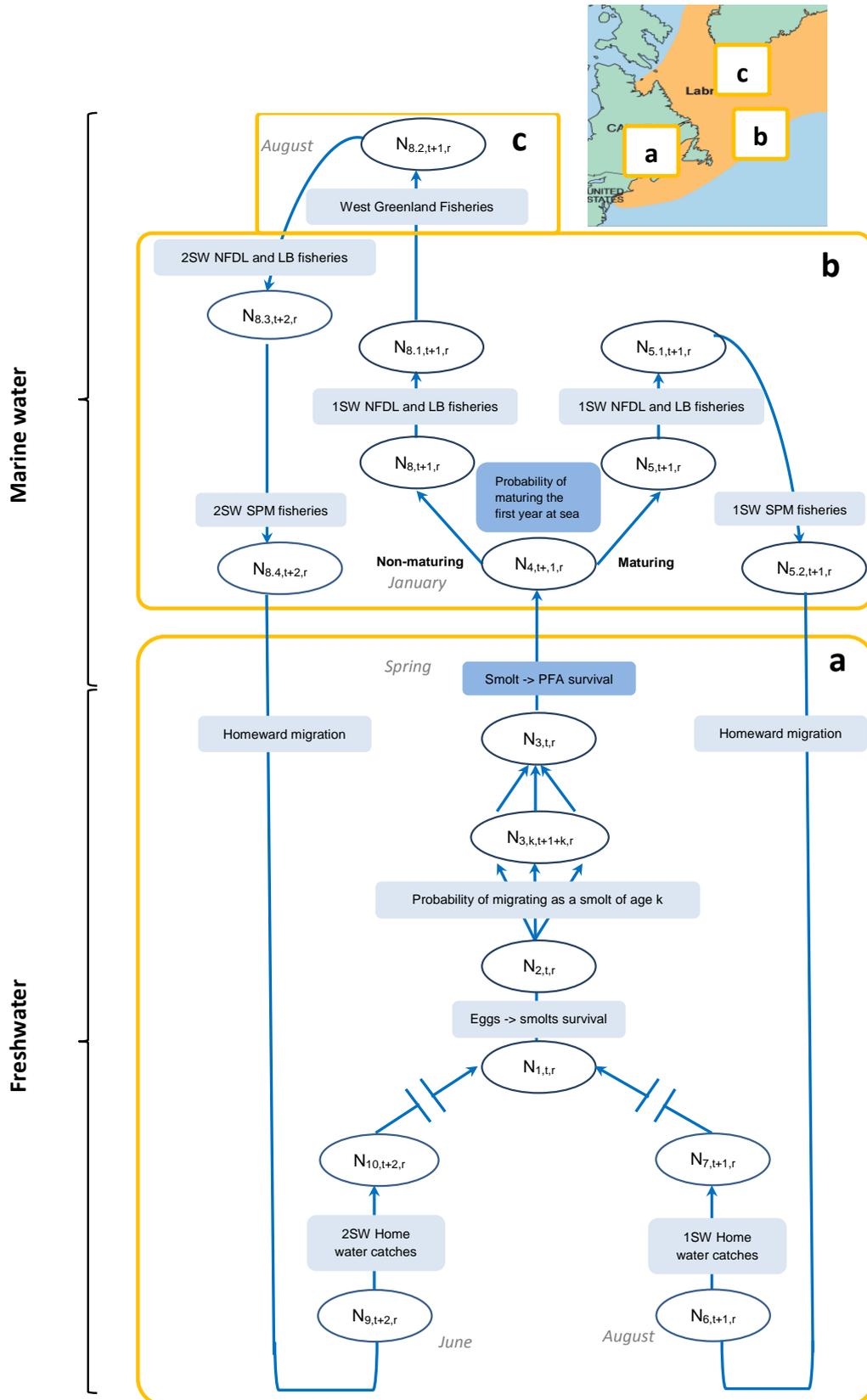


Figure 5: Structure and variables of the life cycle model. Blue dark-shaded stages correspond to transitions with parameters estimated from the data without prior information. Blue light-shaded have fixed parameters or very informative prior distribution. Boxes with letters “a”, “b” and “c” correspond to the migration routes: “a” stands for the freshwater phase (including Homewaters fisheries) ; “b” for NFDL/LB and Saint Pierre and Miquelon fisheries ; and “c” for West Greenland fisheries. The life cycle is reproduced for each of the 6 regions $r=1,\dots,6$. (Adapted from Massiot-Granier et al. 2014)

Table 1: Summary of the variables of the life cycle model (See Figure 5)

Habitat	Factors impacting return rate	Latent variables	Definition		
Fresh Water	Natural mortality	$N_{1,t,r}$	Number of eggs potentially spawned each year		
		$N_{2,c,r}$	Number of smolts produced from reproduction in year c (c stands for the cohort year). There is no intermediate parr stages to represent the egg to smolt transition		
		$N_{2,k,c+k+1,r}$ ($N_{2,c,r} = \sum_{k=1}^6 N_{2,k,c+k+1,r}$)	Number of smolts from the cohort c migrating at sea after k year in freshwater, with k=1:6 in North America		
		$N_{3,t,r}$ ($N_{3,t,r} = \sum_{c=t-7}^{t-2} N_{2,k,c+k+1,r}$)	Number of smolts migrating in the spring of year t		
		$N_{4,t,r}$	Number of post-smolts in the 1 st of January year t (PFA stage)		
Marine water	Maturation	<i>Maturing 1SW</i>		<i>Non-maturing 2SW</i>	
		$N_{5,t+1,r}$	Number of mature fish at the PFA stage	$N_{8,t+1,r}$	Number of non-mature fish at the PFA stage
	Fishing mortality	$N_{5.1,t+1,r}$	Number of 1SW mature fish escaping to NFDL and Lb fisheries	$N_{8.1,t+1,r}$	Number of 1SW non-mature fish escaping to NFDL and Lb fisheries
		$N_{5.2,t+1,r}$	Number of 1SW mature fish escaping to SPM fisheries	$N_{8.2,t+2,r}$	Number of 1SW non-mature fish escaping to West Greenland fisheries
				$N_{8.3,t+2,r}$	Number of 2SW mature fish escaping to NFDL and Lb fisheries
	$N_{8.4,t+2,r}$	Number of 2SW mature fish escaping to SPM fisheries			
Natural mortality	$N_{6,t+1,r}$	Number of 1SW mature fish surviving their migration back to homewaters ("Returns")	$N_{9,t+2,r}$	Number of 2SW mature fish surviving their migration back to homewaters ("Returns")	
Fresh Water	Fishing mortality	$N_{7,t+1,r}$	Number of 1SW escaping the homewater fishery	$N_{10,t+2,r}$	Number of 2SW escaping the homewater fishery

In the next section, we first detail the available data used in the model. Then, we detail the equation for the population dynamics (**Figure 5**) from eggs (stage N_1) to 1SW and 2SW spawners that escape all fisheries (N_7 and N_{10} , respectively; **Figure 5**). Parameters with fixed values or informative priors are then given (**Tables 2 and 5**). Last, we provide the observation equations that form the likelihood of the model.

2.2 Data

The main data sources used to build the model are all derived from the ICES compilation (**ICES 2014**). Data mainly consist in (i) the time-series (44 years; 1971–2013) of estimates of the number of salmon that returns to homewater for spawning after their marine sojourn in each of the 6 regions and for the two main sea-age classes, 1SW and 2SW fish ; (ii) time series of homewater catches available for all regions and both sea age classes ; (iii) time series of catches at sea for the three main fisheries at sea : Newfoundland/Labrador, West Greenland and St Pierre et Miquelon fisheries. Additional hypotheses allow allocating catches of the marine fisheries to any of the 6 regions. Those time series of data are supplemented by additional biological information (fecundity, smolt-ages ...) and by some informative priors on some parameters.

2.2.1 Pre-processing of the time series of Returns and Spawners

Below we explain the pre-processing of the data needed to obtain the time series at the scale of the 6 regions used in the model.

Each region is subdivided in smaller management units called SFAs (Salmon Fishing Areas) that serve as a basis for the monitoring salmon populations and for managing the homewater fisheries (a total of 34 fishing area (SFAs + Qs) in NA; **Figure 4**). Available data fundamentally consist in time series of estimates of the number of returning salmon (returns before the homewater fisheries), and of spawners that escape the homewater fisheries, both available in each different SFAs.

Those data are available for two different size classes of fish, small and large ones. In this study, small fish were considered as 1SW fish, and large ones as 2SW.

Estimates of returns and spawners for any SFA are provided with uncertainty, in the form of Uniform distributions between minimum and maximum bounds, specific for each SFA, year and sea-age class. Monte Carlo simulations ($n=100\ 000$) were run to integrate those uncertainties and to estimate probability distributions of the number of Returns and Spawners at the scale of each of the 6 regions (for each year and sea-age class). **Figure 6** provides an example of the empirical probability distribution of the Returns of 1SW and 2SW fish in Quebec. Empirical distributions for all regions are shown in **Appendix I, Figure A1.1 and Figure A1.2**.

Last, logNormal distributions were fitted on the empirical probability distributions of the Returns obtained by Monte Carlo simulations (**See Appendix I, Figure A1.3**). Parameters of these logNormal distributions are used in the pseudo-likelihood method (2.4.2 Returns).

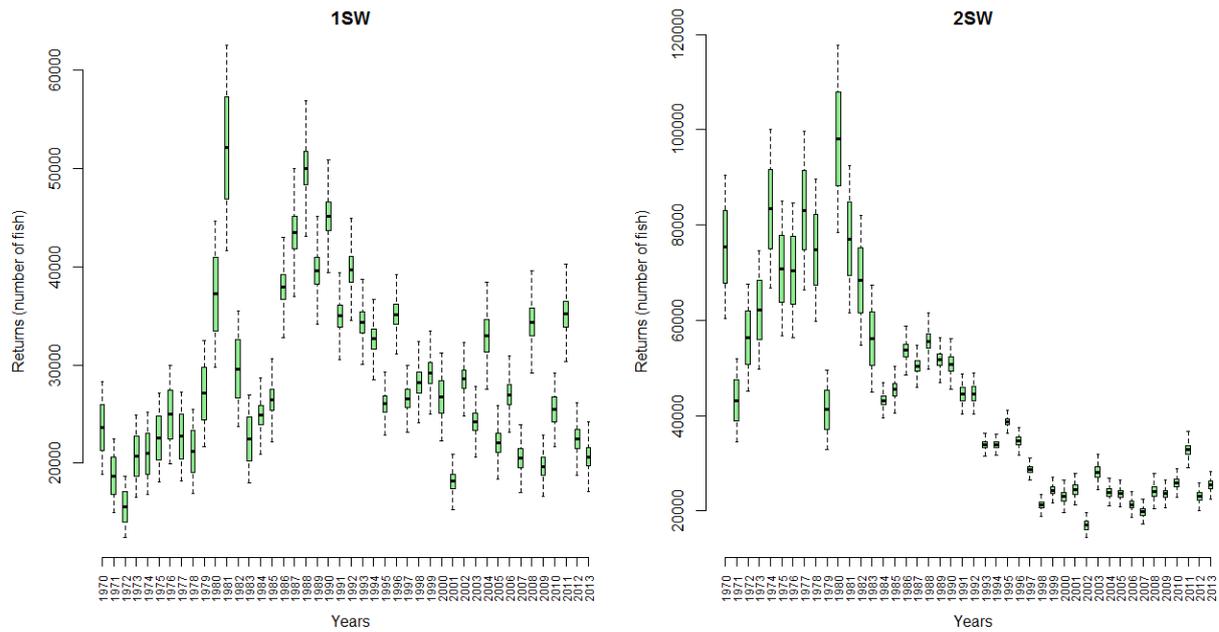


Figure 5: Empirical probability distribution of the time series of returns of 1SW and 2SW for Quebec (obtained from $n=100\,000$ Monte Carlo simulations).

2.2.2 Fisheries data

Atlantic salmon populations are exploited by two kinds of fisheries: Fisheries at sea that operate on mixed stocks during marine migrations, and homewater fisheries, that capture returning fish in estuaries or in freshwater after their marine sojourn. Marine fisheries at sea are operated by Commercial fisheries and residents fishing for food in Newfoundland and Labrador. Homewater fisheries are mostly operated by Aboriginal peoples and by recreational fishers.

Table 2 below provides a synthetic view of the time series of fisheries data considered in the model. The synthetic life cycle model at **Figure 5** visualizes the marine fisheries along the marine migration routes. More details are provided below and in the **Appendix II**.

Table 2: Summary of the different fisheries data. Upperscript “obs” is used here because the catches data will be distinguished from the state variable in the model to include observation errors on catches.

Catches data		Definitions
Homewater fisheries		
1SW	$C_{1SW,t,r}^{obs}$	
2SW	$C_{2SW,t,r}^{obs}$	
Marine fisheries on mixed stocks		
1SW	$C_{5.1,t}^{obs}$	Number of 1SW mature salmons caught in NFD and LB fisheries
mature	$C_{5.2,t}^{obs}$	Number of 1SW mature salmons caught in SPM
1SW non mature and 2SW	$C_{8.1,t}^{obs}$	Number of 1SW non-mature salmons caught in NFD and LB fisheries
	$C_{8.2,t}^{obs}$	Number of 1SW non-mature salmons caught in West Greenland fisheries
	$C_{8.3,Lab,t}^{obs}$	Number of 2SW mature salmons caught in NFD and LB fisheries being Labrador origin fish
	$C_{8.3,Other,t}^{obs}$	Number of 2SW mature salmons caught in NFD and LB fisheries not being Labrador origin fish
	$C_{8.4,t}^{obs}$	Number of 2SW mature salmons caught in SPM

Homewater fisheries

For any regions, point estimates of catches from the Homewater fisheries (in number, for each year and sea-age class) were obtained as the difference between point estimates (posterior medians) of the Returns and Spawners (**Figure 6**). Consequently, no uncertainty is considered in Homewater catches.

Homewater catches of 2SW fish drastically decrease at the end of the 1980s (**Figure 6**). This drop of catches is mainly due to management/conservation measures encouraging the practice of catch and release in rod fisheries targeting large fish (2SW) in some areas of Canada and USA.

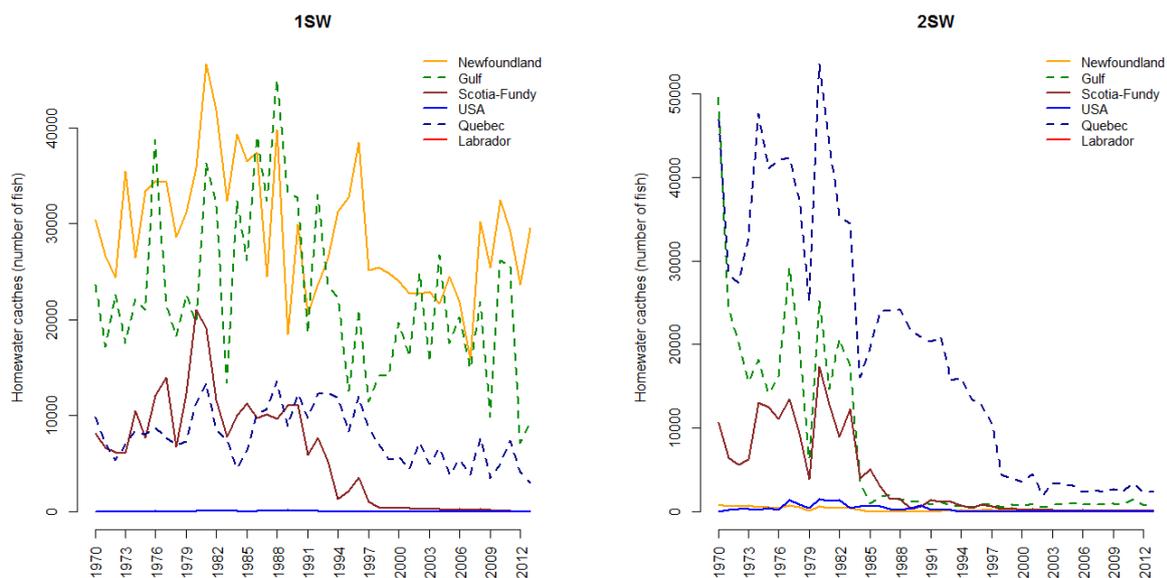


Figure 6: Point estimates of homewater catches for all regions in NA.

Fisheries at sea operating on mixed stocks

Time series of the number of fish caught in the different sequential marine fisheries include uncertainty (except for St Pierre et Miquelon), quantified from expert knowledge and data analysis (see **Appendix II**).

Catches in marine fisheries operate on mixed stocks originated from all regions of NA. Unfortunately, no compiled data are still available that would allow allocating catches to each of the 6 regions considered in the model (some genetic data exist but are still not available for use). Thus in the model, marine fisheries were allocated to any of the 6 regions by considering an homogeneous harvest rate (the catches are allocated proportionally to the relative abundance in the stock mixture). An exception is for Labrador and Newfoundland fisheries on 2SW for which information was available to separate out the catches of fish originated from Labrador from those originated from the 5 other regions considered in the model (**Figure 7**).

- ✓ Labrador and Newfoundland commercial and aboriginal mixed-stock fishery

Labrador (LB) and Newfoundland (NFDL) fisheries first operate on 1SW (mature and non-mature) during their first year at sea, and then on 2SW fish during the second year at sea when fish are coming back from West Greenland foraging areas.

The decline of catches in Labrador and Newfoundland observed since 1980 (**Figure 7**) is mainly due to the reduction in commercial fisheries effort after the closure of important fisheries: the insular Newfoundland fishery in 1992, the Labrador commercial fishery in 1998, the Quebec commercial fishery in 2000. In 2013, all commercial fisheries of Atlantic salmon Labrador and Newfoundland have remained closed.

For 2SW fish, available data allow us to consider separately the catches of fish originated from Labrador from those originated from the 5 other regions considered in the model.

✓ West Greenland Fishery

Catches at West Greenland (WG) consist in non-maturing 1SW fish destined to return to homewater as 2SW or multi sea winter salmons. After numerous regulatory measures taken by NASCO in the 1990s, catches decreased in WG fisheries, reflecting declining abundance of the contributing salmon stocks.

✓ Saint Pierre and Miquelon fisheries

Saint Pierre and Miquelon fisheries include recreational and professional fisheries on both 1SW and 2SW fish. Fish caught at SPM are originated from all North American regions. Catches are quite low relative to other marine fisheries. Data do not present uncertainty (**Figure 7**).

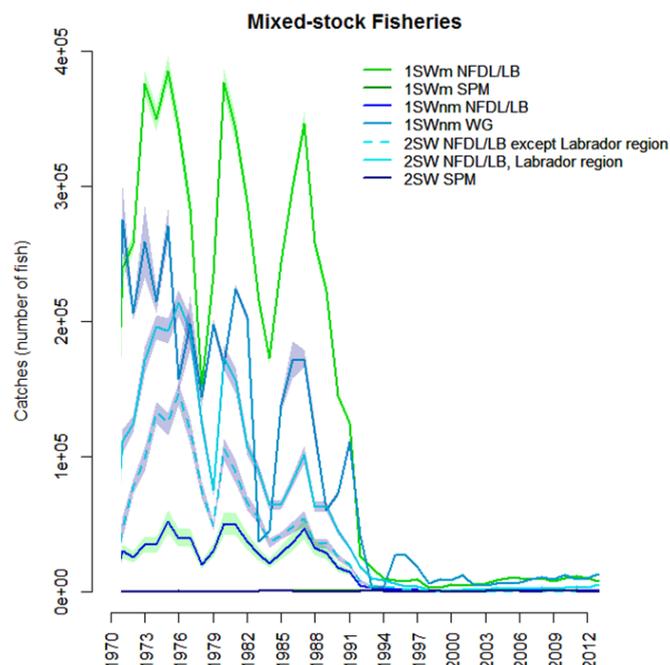


Figure 7: Times series of catches for the sequential fisheries at sea occurring on mixed stocks: Newfoundland/Labrador fisheries and St Pierre et Miquelon on 1SW mature fish (1SWm NFFDL/LB and 1SWm SPM, respectively) ; NFDL/LB and West Greenland on 1SW non mature fish (1SWnm NFFDL/LB and 1SWnm WG, respectively), then NFDL/LB and SPM on 2SW fish (2SW NFFDL/LB and 2SW SPM, respectively). The NFDL/LB fishery on 2SW fish has different harvest rates for fish originating from LB and fish originating from the 5 other regions (Newfoundland, Gulf, Scotia-Fundy, USA, and Quebec). All times series, except Saint Pierre and Miquelon fisheries are represented with uncertainty (shaded area)

2.2.3 Others biological data

The average number of eggs per fish, and the proportion of the different smolts ages are considered known and constant in time (**Table 3**).

Table 3: summary of the parameters (all fixed) of the fresh water phase

Parameter	Regions						
	Newfoundland	Gulf	Scotia Fundy	USA	Quebec	Labrador	
Average number of eggs per 1 SW fish	3000	550	910	200	470	1500	
Average number of eggs per 2 SW fish	4000	6000	6100	550	6400	5500	
Proportion of smolts ages (age 1 to 6)	$psm_{1,r}$	0	0	0	0.4	0	0
	$psm_{2,r}$	0.04	0.4	0.6	0.5	0.06	0
	$psm_{3,r}$	0.6	0.6	0.4	0.1	0.5	0.08
	$psm_{4,r}$	0.3	0.03	0.006	0	0.4	0.5
	$psm_{5,r}$	0.04	0	0	0	0.09	0.3
	$psm_{6,r}$	0	0	0	0	0.01	0.04

2.3 Population dynamics

2.3.1 Stochastic demographic transitions

To simplify the model and speed up the MCMC sampling process, all demographic transitions are modelled using lognormal process noise, with a variance σ^2 arbitrarily fixed to a very low value corresponding to a coefficient of variation $CV=0.01$. Then, for any transition between stage z and $z+1$, with a transition rate denoted θ for genericity (e.g., a survival rate or a harvest rate), the logarithm of the number of fish surviving from the last life stage is noted:

$$(1) \quad \log(N_{z+1}) \sim \text{Normal}(\log(\theta \times N_z) - \frac{1}{2}\sigma^2, \sigma^2)$$

2.3.2 Fresh water phase

Eggs deposition

The total number of eggs potentially spawned is calculated, for each year t and each region r , from the number of 1SW ($N_{7,t,r}$) and 2SW ($N_{10,t,r}$) spawners escaping the homewaters fisheries:

$$(2) \quad N_{1,t,r} = N_{7,t,r} \times \text{eggs}_{1SW} + N_{10,t,r} \times \text{eggs}_{2SW}$$

where eggs_{1SW} and eggs_{2SW} are average number of eggs per 1SW and 2SW salmon. These are considered known and constant over the time-series for each region (**Table 3**).

Egg-to-smolt transition

The egg-to-smolt survival transition is considered density-independent:

$$(3) \quad \text{Log}(N_{2,t,r}) \sim \text{Normal}(\log(\theta_1 \times N_{1,t,r}) - \frac{\sigma^2}{2}, \sigma^2)$$

with egg-to-smolts survival rate θ_1 and variance σ^2 considered known.

The probability of a smolt in the cohort c to migrating at age k in the regions r , denoted $\theta_{2,c,k,r}$ (with $\sum_{k=1}^6 \theta_{2,c,k,r} = 1$) are randomly drawn in tight informative Dirichlet priors with fixed parameters $psm_{1,r}$ specific to each region (see **Table 3**) and a dispersion parameter = 100:

$$(4) \quad \theta_{2,c,k,r} \sim \text{Dirichlet}(100 \times psm_{1,r}, \dots, 100 \times psm_{6,r})$$

Then, given the probabilities $\theta_{2,c,k,r}$, the number of smolts from the cohort c migrating year $c+k+1$ is logNormal:

$$(5) \quad \log(N_{2,c,c+k+1,r}) \sim \text{Normal}(\log(\theta_{2,c,k,r} \times N_{2,c,c+k+1,r} - \frac{1}{2}\sigma^2, \sigma^2)$$

Last, the number of smolts migrating in the spring of year t is the sum of all smolts of different age classes migrating year t :

$$(6) \quad N_{3,t,r} = \sum_{c=t-7}^{t-2} N_{2,c,c+k+1,r}$$

2.3.3 Marine phase

Marine phase is modelled as a sequence of three phases: survival rate from smolts to the PFA stage, the maturation of fish at the PFA stage, and the fishing and natural mortality between PFA and returns stages.

Smolt-to-PFA survival and proportion maturing salmon

To capture the effect of smoothed environmental fluctuations, both smolt-to-PFA survival ($\theta_{3,t,r}$) and the probability of maturing the first year ($\theta_{4,t,r}$) are a priori modelled with a simple random walk in the logit scale, with region specific variances $\sigma_{\theta_{3,r}}^2$ and $\sigma_{\theta_{4,r}}^2$ (both estimated):

$$(7) \quad \text{logit}(\theta_{3,t+1,r}) \sim \text{Normal}(\text{logit}(\theta_{3,t,r}), \sigma_{\theta_{3,r}}^2)$$

$$(8) \quad \text{logit}(\theta_{4,t+1,r}) \sim \text{Normal}(\text{logit}(\theta_{4,t,r}), \sigma_{\theta_{4,r}}^2)$$

Then, given the number of smolts migrating year t ($N_{3,t,r}$) and the smolt-to-PFA survival ($\theta_{3,t,r}$), the number of post-smolts that survive at the PFA stage ($N_{3,t+1,r}$) are modelled as logNormal :

$$(9) \quad \log(N_{4,t+1,r}) \sim \text{Normal}(\log(\theta_{3,t,r} \times N_{3,t,r}) - \frac{\sigma^2}{2}, \sigma^2)$$

Given the number of fish at the PFA stage ($N_{4,t+1,r}$) and the maturation rate ($\theta_{4,t+1,r}$), mature ($N_{5,t+1,r}$) and non mature fish ($N_{8,t+1,r}$) at the PFA stage are then modelled as logNormal:

$$(10) \quad \log(N_{5,t+1,r}) \sim \text{Normal}(\log(\theta_{4,t+1,r} \times N_{4,t+1,r}) - \frac{1}{2}\sigma^2, \sigma^2)$$

$$(11) \quad \log(N_{8,t+1,r}) \sim \text{Normal}(\log((1 - \theta_{4,t+1,r}) \times N_{4,t+1,r}) - \frac{1}{2}\sigma^2, \sigma^2)$$

Sequential marine fisheries

All marine fisheries are modelled as punctual events with harvest rates that are all estimated from the catch data. For any fishery f , operating year t with a harvest rate $h_{f,t}$ on a number of fish originated from the region r denoted $N_{f,t,r}$, fish that escape the fishery are logNormally distributed :

$$(12) \quad \log(N_{f,t,r,esc}) \sim \text{Normal}(\log(h_{f,t} \times N_{f,t,r}) - \frac{1}{2}\sigma^2, \sigma^2)$$

and the number of fish caught $C_{f,r}$ are simply

$$(13) \quad C_{f,r} = h_f \times N_{f,r}$$

For most of the fishery (except the 2SW LB and NFDL fishery), no data are available to allocate the catches to the different regions. Hence, for all marine fishery operating on a mixture of stocks (except the 2SW LB and NFDL fishery), harvest rates were assumed to be homogeneous among regions (but variable in time). Regarding the 2SW LB and NFDL fishery, two different harvest rates were considered: one specific for fish originating from the Labrador, and a second one for fish originating from all other regions. Last, harvest rate in the St Pierre et Miquelon fishery for 2SW fish originating from Labrador is fixed to 0, because SPM is not on the migration routes of those fish.

The different harvest rates for all sequential fisheries at sea for mature fish (from $N_{5,t+1,r}$ to $N_{5.2,t+1,r}$) and non mature fish (from $N_{8,t+1,r}$ to $N_{8.4,t+1,r}$) are summed up in **Table 4** (all corresponding equations are similar to the generic one given below).

Table 4: Summary of the sequential fisheries and corresponding harvest rates

	Harvest rates	Definition
Mature	$h_{5,1,t}$	NFD and LB fisheries on 1SW mature fish
	$h_{5,2,t}$	SPM fishery on 1SW mature fish
Non Mature	$h_{8,1,t}$	NFD and LB fisheries on 1SW non mature fish
	$h_{8,2,t}$	1SW West Greenland fisheries on 1SW non mature fish
	$h_{8,3,lab,t}$	NFL and LB fisheries on 2SW fish originating from LB
	$h_{8,3,other,t}$	NFD and LB fisheries on 2SW fish not originating from LB
	$h_{8,4,t}$	SPM fishery on 2SW fish
	$h_{8,4,Lab,t} = 0$	SPM fishery on 2SW fish originating from Labrador

Natural mortality after sequential fishery

1SW fish that escape the Newfoundland, Labrador and Saint-Pierre Miquelon fisheries and then migrate back to their homewaters have a survival rate θ_5 derived from natural mortality rate M and the duration Δt_1 :

$$(14) \quad \log(N_{6,t+1,r}) \sim \text{Normal}(\log(\theta_5 \times N_{5,2,t+1,r}) - \frac{1}{2}\sigma^2, \sigma^2)$$

$$(15) \quad \theta_5 = \exp(-M \times \Delta t_1)$$

2SW salmon that survive to all marine fisheries ($N_{8,4,t+2,r}$) migrate back to their homewaters with a survival probability θ_6 :

$$(16) \quad \log(N_{9,t+2,r}) \sim \text{Normal}(\log(\theta_6 \times N_{8,4,t+2,r}) - \frac{1}{2}\sigma^2, \sigma^2)$$

$$(17) \quad \theta_6 = \exp(-M \times \Delta t_2)$$

M and Δt_1 and Δt_2 have fixed values derived from the literature (**Table 5**).

Table 5: Parameters associated with the marine water phase. Parameters fixed or drawn in very tight informative prior distribution are shaded.

Parameters	Definitions	Value/prior
$\theta_{3,t,r}$	Smolt-to-PFA survival rate	A specific time series for each region, defined as a random walk (see eq. (7))
σ_{θ_2}	Standard deviation	$\sim U(0,1)$
h_f	Exploitation rates for all marine fisheries (see Table 4)	$\sim \text{Beta}(1,1)$
$\theta_{4,t,r}$	Probability of post smolt maturing the first year at sea	A specific time series for each region, defined as a random walk (see eq. (8))
σ_{θ_4}	Standard deviation	$\sim U(0,1)$
M	Natural mortality rate (per month)	0.03
Δt_1	Time from end Labrador and Newfoundland fishery to returns	1 month
Δt_2	Time from West Greenland fishery to end of 2SW Saint-Pierre and Miquelon fishery	10 months

Homewater catches

Last, the number of spawners (from $N_{7,t+1,r}$ to $N_{10,t+2,r}$) are simply obtained by the difference between the returning fish and the point estimates of homewater catches (no uncertainty included in homewater catches).

2.4 Observation equations (likelihood)

The likelihood function of the general state-space model is built from the combination of observation equations for the catches at sea for all sequential mixed stock fisheries, and for the returns (1SW and 2SW fish).

2.4.1 Catches at sea for sequential mixed stock fisheries

Observed catches as listed in **Tables 2**, correspond to total catches on the mixture of the 6 regions (except the LB/NFDL 2SW fishery for fish originating from Labrador). Catches at sea for sequential mixed stock fisheries as defined for each region by the generic equations (13) are non-observed variables in the model, directly derived from the abundance and the harvest rate associated to each regions r (both non observed). Catches are first summed over all regions (except the LB/NFDL 2SW fishery for fish originating from Labrador that is considered independently). Then, logNormal observation errors are considered between the total non-observed catches and the observed catches. The relative error for observation errors on catches at sea is arbitrarily fixed to CV=10% for all fisheries.

2.4.2 Returns

Information on Returns (for any year, regions and sea-age classes 1SW and 2SW) is introduced using the pseudo-likelihood method (Michielsens et al., 2008) based on the logNormal distributions fitted on the Monte Carlo runs (see **Appendix I, Figure A1.3**): for any year, regions and sea-age classes 1SW and 2SW, the mean of the empirical logNormal distribution of returns is considered as a pseudo-observation, considered as a realization of a logNormal distribution around the non-observed returns and with a σ parameter extracted from the empirical logNormal distribution.

2.5 Bayesian fit using MCMC sampling

All computations are performed within the R platform (R Development Core Team, 2012). Bayesian posterior distributions are approximated via Monte Carlo Markov Chain (MCMC) methods through the open-source JAGS software (<http://mcmc-jags.sourceforge.net>). The JAGS code is provided in **Appendix VI**. Three independent MCMC chains with different initialization points are used. After an adapting phase of 50 000 iterations, inferences are derived from a sample of 180 000 iterations. One out of 30 iterations is kept to reduce the MCMC sampling autocorrelation. To check convergence of MCMC sampling, the Gelman–Rubin test is applied to all posterior sampling (R ratio, 1.05 for all variables) as implemented in the Coda package of R (Brooks and Gelman, 1998) (see an example in **Appendix III**).

2.6 Posterior analysis of the time series of estimated parameters

Patterns of synchrony among regions in the two key life history traits: post-smolts survival at sea (θ_3) and proportion maturing after the first year at sea (θ_4) were analyzed by Principal Component Analyses (PCA) and cross correlations.

The synchrony in the time trends among the regions was analyzed starting from 1975. Indeed, time series of the post-smolt survival rate and the probability of maturing after the first winter at sea for years 1970-1975 strongly depend upon the prior distribution on the number of fish at different stages that was fixed for the first 6 years of the time series. Because the juvenile spent 2 (smolt 1) to 7 (smolt 6) years in freshwater before migrating as smolts, eggs that contribute to the PFA of years 1970-1975 are from returns that are not updated by the data.

Time series of the posterior medians of θ_3 (resp. θ_4) were first scaled, and a PCA on scaled variables (using the 6 regions as “variables” and years as “individuals”) was run. The two first principal components were interpreted as time series of modal signal among the 6 regions (Beaugrand and Reid, 2012; Mills et al., 2013).

For comparison, a PCA was also realized on the time series of post-smolts survival and proportion maturing after the first year at sea estimated by Massiot-Granier (2014) for complex of populations aggregated at the scale of 8 regions/countries in the southern Eastern Atlantic Ocean.

Then, a PCA was realized by pooling the 6 regions for NA and the 8 regions for Southern Europe to extract global trends at the scale of the North Atlantic Ocean.

Last, a preliminary exploration of the relationships between life history traits and proxy of environmental conditions in the North Atlantic Ocean was run by analyzing the correlation between the modal signal in the life history traits extracted from the PCA and the Atlantic Multidecadal Oscillation (AMO ; extracted from <http://www.esrl.noaa.gov/psd/data/timeseries/AM>). AMO is defined as the de-trended annual Sea Surface Temperature (SST) anomalies over the North Atlantic region from 0°-70°N and 75°W -7.5°W, and is considered having a strong influence on climate variability (Enfield et al., 2001). AMO fluctuates between cold and hot period: 1960-1990 was characterized as cold period and since 1995, AMO has been positive so North Atlantic is a warm period. The value averaged over the entire year was considered.

2.7 Prediction and spawning requirement for NA

Once fitted to the data, the population dynamic model was used to forecast the returns in each of the 6 different regions under different scenarios of catches at sea. Data on returns are available up to year 2012, and the model was used to forecast during 5 years (from 2013 to 2017). These 5 years short-term forecast is typically used by the ICES Working Group to provide advices to NASCO to help management of mixed stocks fisheries at sea (ICES 2014).

Monte Carlo runs were used to integrate out all sources of uncertainty in the population dynamic model, including uncertainty about parameters in the form of the joint posterior distributions of all parameters. For any scenario of catches at sea, the model hence provides the posterior predictive probability of the returns for all forecasted years that can be compared to Conservation Limits (CLs) as defined by the ICES WGNAS and the NASCO. The probability that the returns fall above the CLs is used as synthetic criteria to assess the performance of each scenario.

CLs defined by ICES and NASCO are the number of spawners that will achieve long-term average maximum sustainable yield (see O'Connell et al., 1997). In NA, objectives are to attain the 2SW CLs in Labrador, Newfoundland, Quebec and Gulf. For Scotia-Fundy and USA abundances are very low, so the management plan is to achieve a 25% increase in regional returns relative to the average returns in 1992-1996 (Table 6).

Three alternative scenarios were simulated:

- 1) Statu quo: catches used in the prediction are the estimated as the mean of the last 3 years catches (from 2010 to 2012)
- 2) Zero catch: catch used in the prediction are considered null
- 3) Quotas of 1500 tons in West Greenland: during negotiations to set regulatory measures to limit Greenland harvest to sustainable levels, Association of Fishers and Hunters asked a minimum quota of 1500 tons (see report of the Institute of Fisheries Management, <http://www.ifm.org.uk/news/ifm-report-nasco-meeting-canada>)

Table 6: 2SW conservation limit and management objective for each region of NAC

Country and Commission area	Stock area	2SW Conservation limit	Management objective
	Newfoundland	4 022	4 022
	Gulf	30 430	30 430
	Scotia-Fundy	24 705	10 976
	USA	29 199	2 548
	Quebec	29 446	29 446
	Labrador	34 746	34 746
North American Commission		152 548	

3 RESULTS

3.1 Abundances and harvest rates of fisheries at sea

3.1.1 Abundances

The model estimates the posterior distributions for the time series of abundance of salmon in any life stage in the model and any regions.

Returns of the two sea ages classes are directly updated by the pseudo-likelihood equations (see section 2.4.2), and posterior uncertainty is then rather low (**Figure 8**). Residuals, as defined as the difference between the state variable and the posterior medians of the empirical distribution defined from the data show a good fit to the data (**Appendix IV**).

Returns exhibit different time trends between regions and sea-age classes. Newfoundland, Gulf region and Labrador have the largest returns of 1SW fish. Fish returning to USA, Quebec and Gulf region are mostly 2SW fish. Abundance of fish in USA is particularly low relative to the other 5 regions. Time trends of the returns are also very different between the two sea age classes. Difference between 1SW and 2SW fish are particularly marked for Newfoundland and Labrador, with returns of 1SW fish that tend to increase starting from the beginning of the 2000's, when returns of 2SW decrease over the time series.

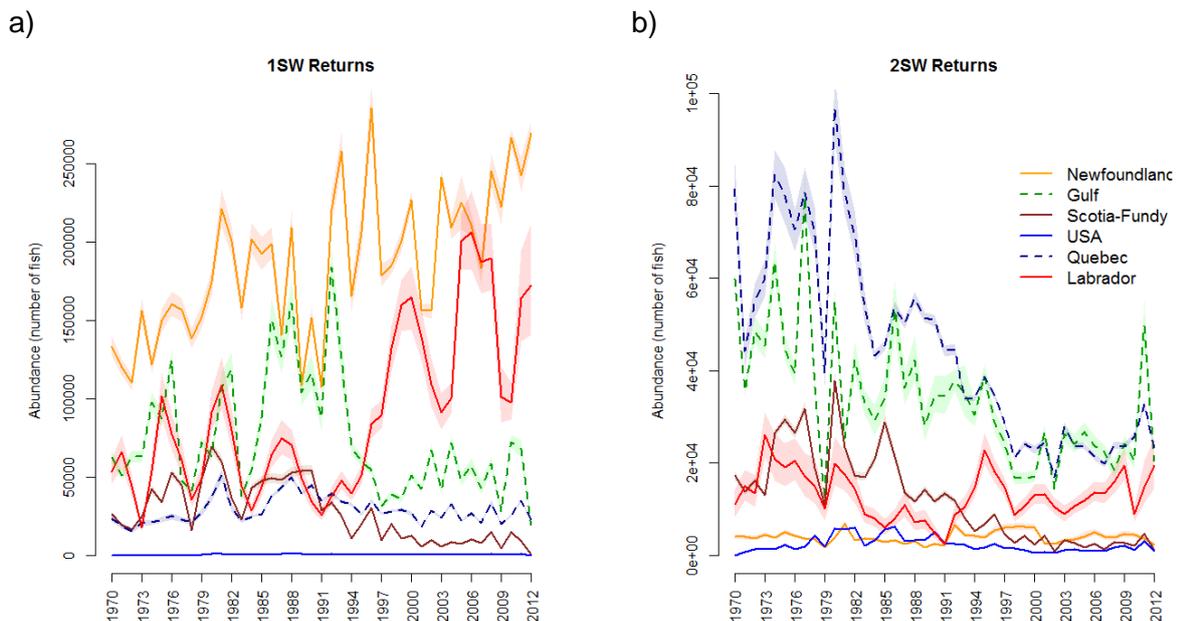


Figure 8: Marginal posterior distributions of the returns of 1SW (a) and 2SW (b) salmon in 6 regions of NA. Shaded area is the posterior uncertainty for each region (first and third quartiles).

Posterior estimates of the abundance of post-smolts at sea (PFA stage, a variable not directly accessible to observation) are keys for stock assessment (**Figure 9**). Time trends of the PFA (before fishery at sea) are different that time trends of returns (after fishery at sea), because the exploitation rate at sea varied considerably over time, mostly after the sharp reduction of exploitation in the early 1990's. PFA abundance generally decreases by a factor of about 6 from 1970 to 2012 (**Figure 9a**).

The PFA differs considerably between the 6 regions. Indeed, 4 regions (Labrador, Newfoundland, Gulf and Quebec) represent 90% of the total abundance. However the relative PFA (**Figure 9b**) shows similar patterns of decline since the 1990's.

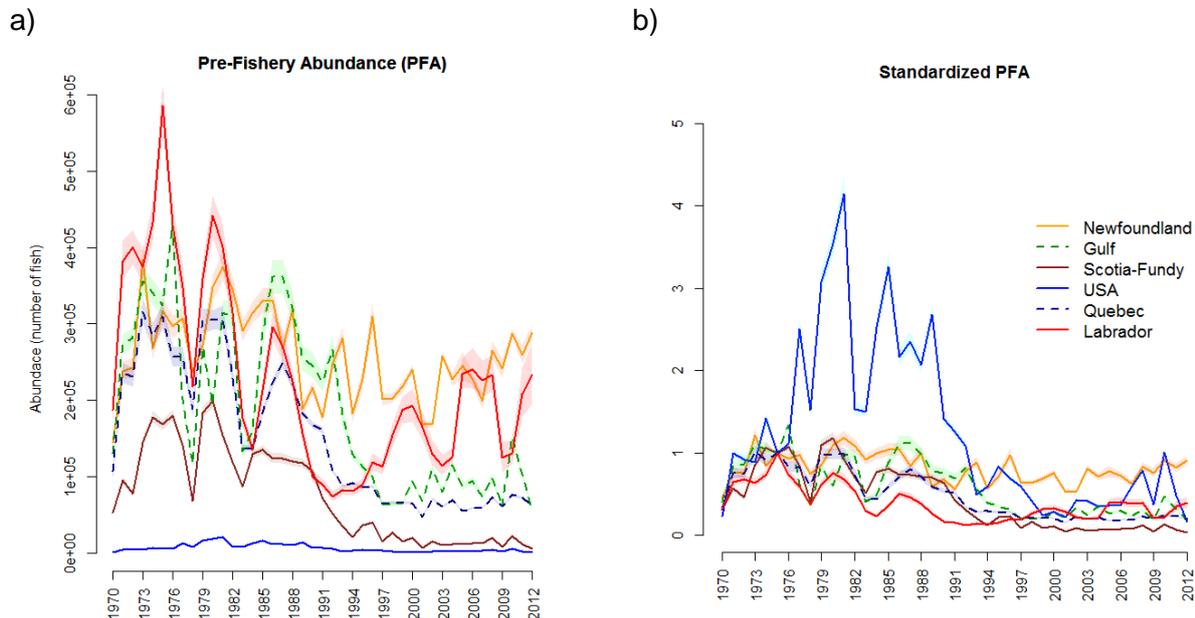


Figure 9: Marginal posterior distribution of (a) pre-fisheries abundance (number of fish) and (b) standardized pre-fisheries abundance for the 6 regions of North America. Year 1975 is used as standardization. Shaded area is the posterior uncertainty (first and third quartiles).

3.1.2 Harvest rates of fisheries at sea

Estimates of harvest rates of fisheries at sea operating on mixed stocks (**Figure 10**) show that A.salmon have been mainly exploited by the West Greenland and Newfoundland/Labrador fisheries, the fisheries at Saint Pierre and Miquelon having a very low impact on abundance.

Overall, results highlight that all harvest sharply declined in the early 1990's (**Figure 10**), following NASCO management measures that imposed drastic reductions of almost all fisheries at sea to mitigate the decline of salmon abundance.

1SW maturing fish (that will return as 1SW fish) are mainly caught in Newfoundland/Labrador fisheries, with harvest rate of 0.5 until the 1990's, just before the important closure of fisheries.

Non maturing fish (that will return as 2SW fish) are first caught in the Newfoundland/Labrador fisheries during the beginning of the second summer at sea, just before moving to the coast of West Greenland, with harvest rate of about 10% before the early 1990's. The most intense fishery of non-maturing fish (in term of number of fish caught) then occurred in the West Greenland fishery, with exploitation rates that reached 40% before the 90's. This fishery target 1 SW salmon migrating during their second summer at sea (the fishing season being between the 1 August and 31 October). The exploitation rate in West Greenland is considered homogeneous among all regions of North America. Then, 2SW fish that escape

the WG fisheries are caught on their way back in the LB/NFDL fisheries. Salmons originating from Labrador are intensively harvested, with harvest rates that have reached 85%, when fish originating from other regions were less intensively exploited (about 35%).

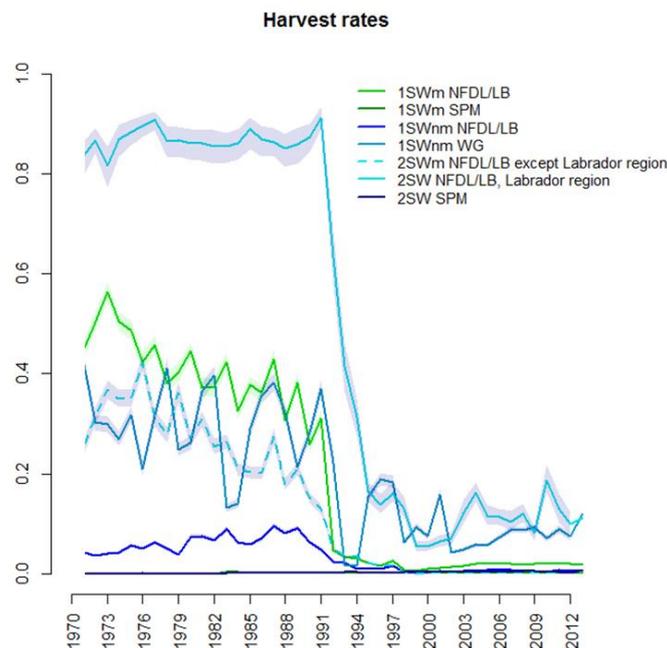


Figure 10: Marginal posterior distributions of harvest rates for the sequential fisheries at sea occurring on mixed stocks: Newfoundland/Labrador fisheries and St Pierre et Miquelon on 1SW mature fish (1SWm NFFDL/LB and 1SWm SPM, respectively) ; NFDL/LB and West Greenland on 1SW non mature fish (1SWnm NFFDL/LB and 1SWnm WG, respectively), then NFDL/LB and SPM on 2SW fish (2SW NFFDL/LB and 2SW SPM, respectively). The NFDL/LB fishery on 2SW fish has different harvest rates for fish originating from LB and fish originating from the 5 other regions (Newfoundland, Gulf, Scotia-Fundy, USA, and Quebec).

3.2 Key life history parameters of the marine phase: Smolt-to-PFA survival and maturing probability

3.2.1 Smolt-to PFA survival rates

Time series of smolt-to-PFA survival rate exhibit a strong declining signal by a factor 6 (from about 0.3 to 0.05) consistent among the 6 regions (**Figure 11a**). Time trends for the Labrador looks different, with a peak in the post-smolt marine survival between 1995 and 1998 that is not observed for the 5 other regions.

The Principal Component analysis on standardized time series shows that the time series are strongly correlated between regions (pairwise correlation ranging from 69% to 94%; not shown). All regions are positively correlated to the first principal component of the PCA (**Figure 11b**) that is interpreted as a common trend shared by all regions, explaining more than 70% of the time signal in the 6 regions. This common trend suggests a main change in post-smolt abundance during the period before the 1990's and after, where the survival has been divided by 3. The second principal component (15.7% of the total variability) synthetizes some differences among the regions observed on a shorter time scale (such as the peak in survival in 1979 observed for USA and Labrador, and in 1986-87 for Gulf and Scotia-Fundy).

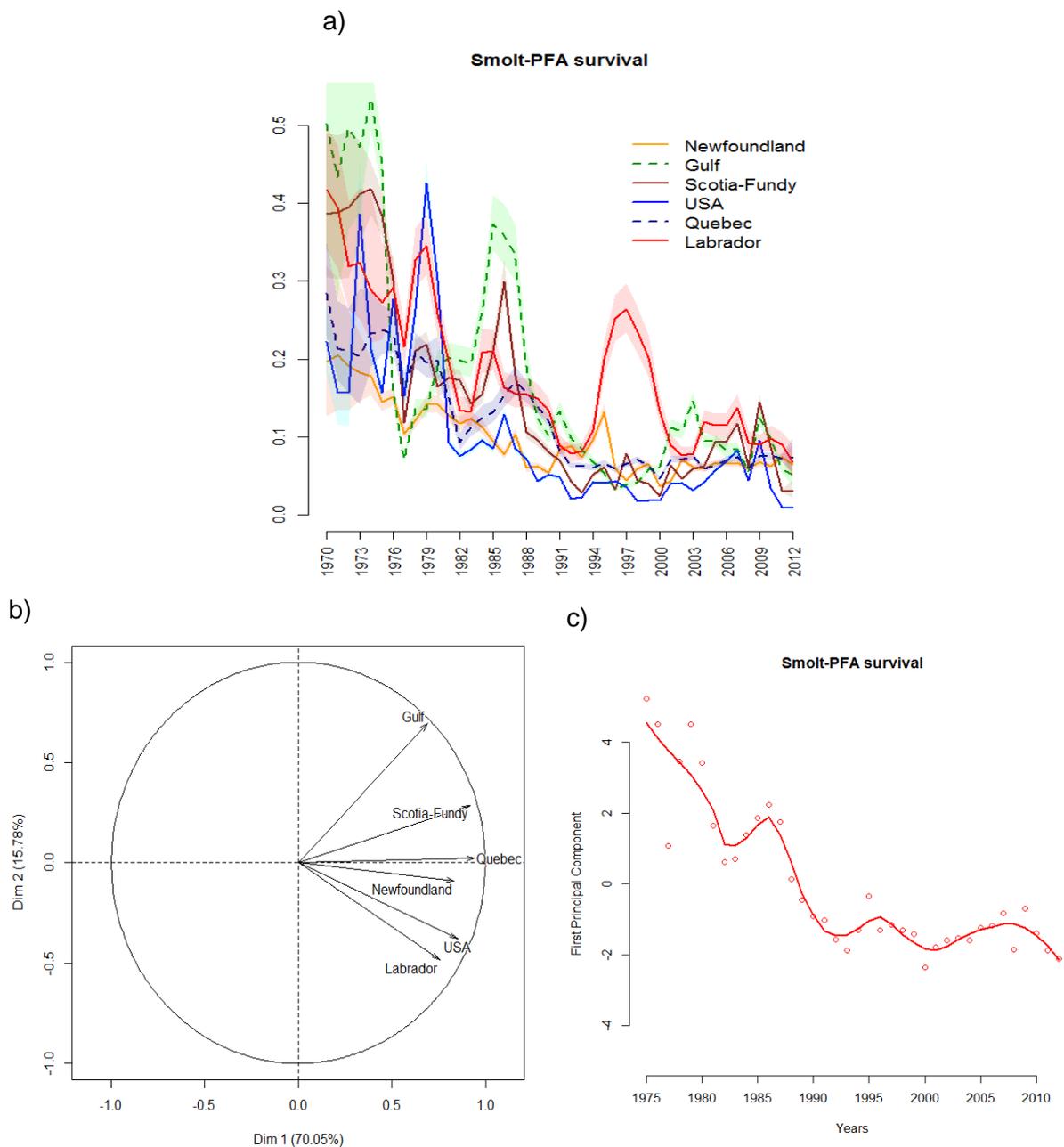


Figure 11: Time series of post-smolt marine survival rates for the 6 regions in NA. (a) Marginal posterior distribution of the post-smolt marine survival (shaded area: 50% posterior credibility interval ; (b) and (c) Synchrony among the different regions of NA investigated by PCA on standardized time series: (b) first and second normalized eigenvectors representing the correlation between the first two principal components of a PCA performed on the table 38 years (from 1975 to 2012) X 6 regions of NA ; (c) Long term consistent trend, plain line (c) is serie smoothed via a multinomial non parametric smoothing (R *loess* function, with a smoothing parameter=0.3).

3.2.2 Probability of maturing after the first year at sea

Results reveal strong differences among regions in the probability of maturing after the first year at sea. Some stocks have a very high maturing probability (e.g. Newfoundland, with returns essentially consisting in 1SW fish, whereas other regions have stock dominated by late maturing fish (e.g. USA or Quebec) (**Figure 12**). Beyond those differences of average levels among regions, time series exhibit a consistent increasing trend of the maturing

probability. The First principal component of the PCA on standardized variables explains more than 57% of the total variability (**Figure 12b** and **Figure 12c**).

Variability among regions in the second principal component (**Figure 12b**) can be interpreted in term of differences in the time signal observed at the end of the time series, in relation with the latitude: the maturing probability tends to decrease at the end of the time series for southern regions (Scotia Fundy, Gulf, Scotia-Fundy and USA), whereas it tends to be more stable for regions further north (Labrador, Newfoundland and Quebec).

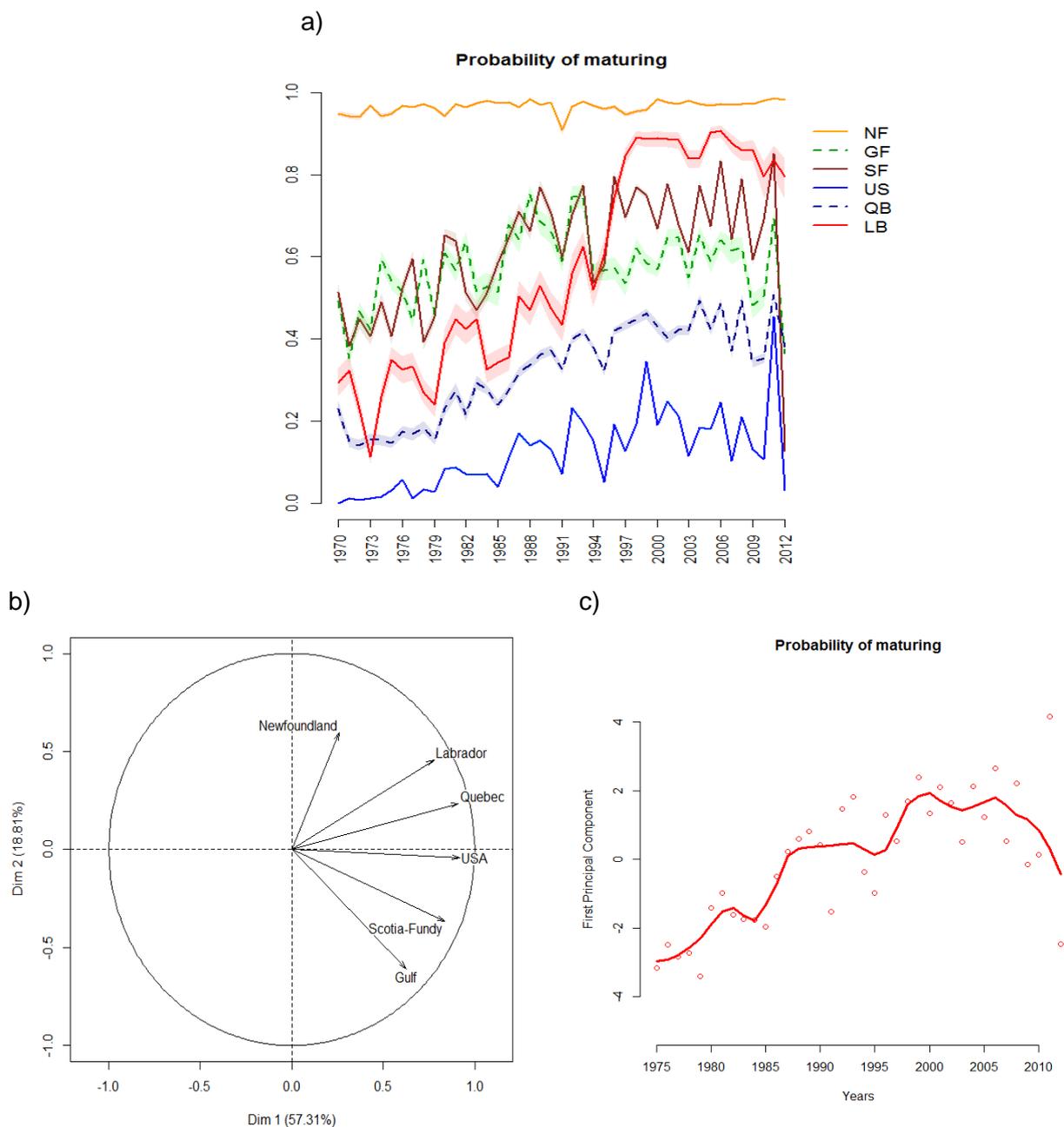


Figure 12: Time series of probability of maturing after the first year at sea for the 6 regions in NA. (a) Marginal posterior distribution of the probability of maturing (shaded area: 50% posterior credibility interval ; (b) and (c) Synchrony among the different regions of NA investigated by PCA on standardized time series: (b) first and second normalized eigenvectors representing the correlation between the first two principal components of a PCA performed on the table 38 years (from 1975 to 2012) X 6 regions of NA; (c) Long term consistent trend, plain line (c) is serie smoothed via a multinomial non parametric smoothing (R loess function, with a smoothing parameter=0.3).

3.3 Synchrony between population dynamics in NA and S-Europe

3.3.1 Post-smolt survival

To further analyze the synchrony in the time series of post-smolt survival between population of NA and S-Europe, a PCA is run by pooling the time series of posterior estimates for the 6 regions in NA (**Figure 13c**) derived from this work) with the time series for the 8 regions in S-Europe (**Figure 13b**) directly extracted from the results of [Massiot-Granier \(2014\)](#).

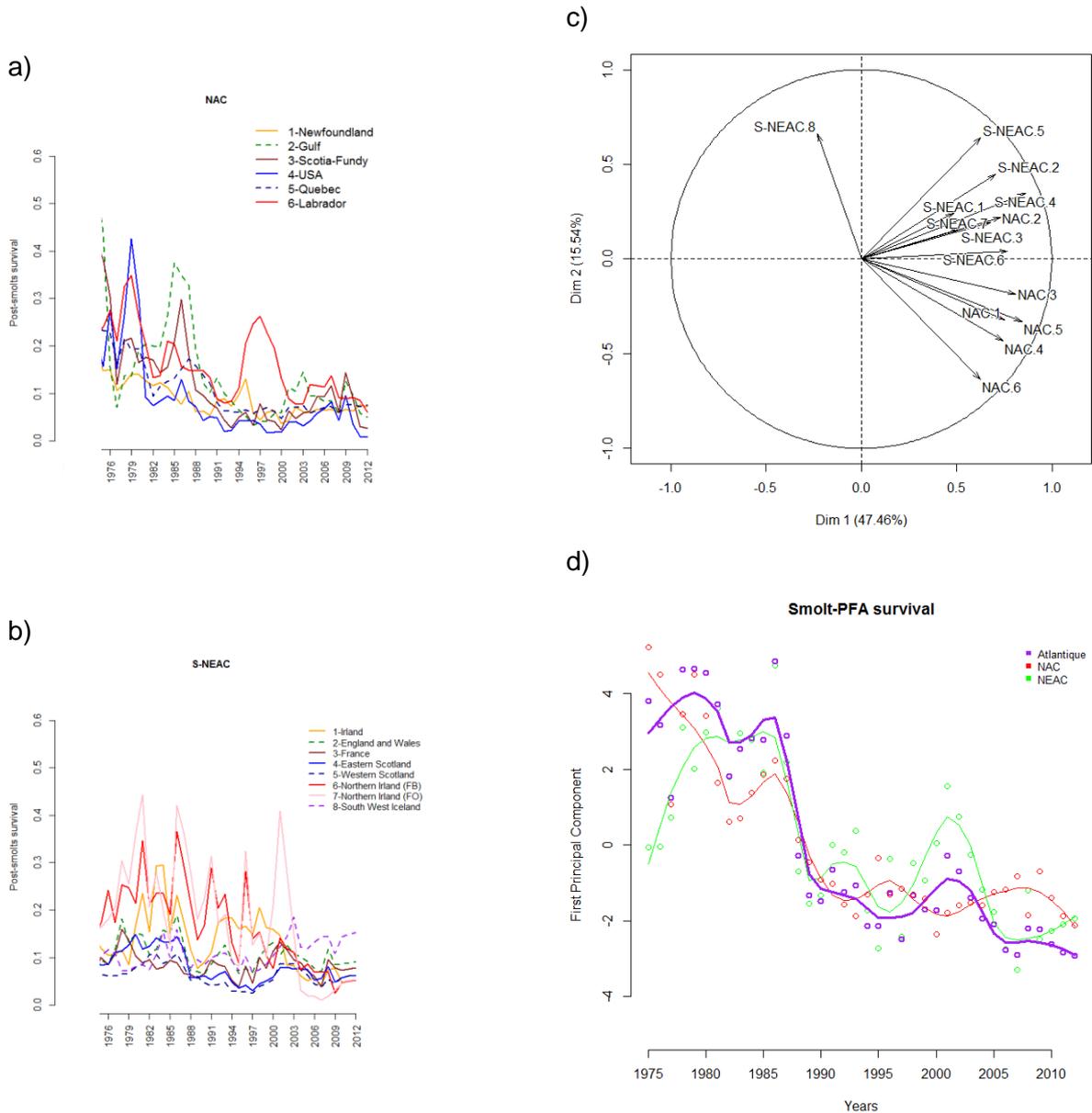


Figure 13: Analysis of the synchrony in the post-smolts survival among the 6 regions in NA and the 8 regions in S-Europe. (a) and (b) marginal posterior distribution of the time series of post-smolts survival for NA (a ; this present study) and S-Europe (extracted from [Massiot-Granier 2014](#)). (c) Dispersion diagram of the first two normalized eigenvectors of the PCA realized on the 6+8 = 14 time series. Item (1 to 6 for NAC and 1 to 8 for NEAC) used in (a) and (b) define the same regions in (c). (d) Long term consistent trend (1975 to 2012) for NA only (red), S-Europe only (green) and all regions considered together (purple); Plain lines (d) are series smoothed via a multinomial non parametric smoothing (R *loess* function, with a smoothing parameter=0.3).

Time series of post-smolts survival for all regions in A and S-Europe are all positively correlated to the first principal component, except South West Iceland (S-Europe) that appeared as negatively correlated because of its increasing trend at the end of the time series that is not observed elsewhere.

The second principal component reveals a negative correlation between NA and S-Europe, survivals of each complex being split on both sides of the secondary axis (**Figure 13c**). This separation has its origin in the years 2000's where survival decreases in NA and increases in S-Europe.

When plotted together, global decreasing trends in the post-smolts survival in NA (extracted from the PCA on the 6 regions in NA only) and S-Europe (extracted from the PCA on the 8 regions in Europe only), appear strongly consistent on the long term (**Figure 13d**). However, differences in the time signal appear on the short term, suggesting slightly different responses of populations between S-Europe and N-AA.

3.3.2 Probability to mature after the first winter at sea

Time series of maturing proportions for NA (this study) and S-Europe ([Massiot-Granier 2014](#)), overall show an upward trend and then stabilization at the end of the time-series (**Figure 14a and Figure 14b**). The PCA realized on all regions reveals a common increasing trend that explains 53% of the total variability (**Figure 14c**).

A notable exception is France (in S-Europe), that is negatively correlated to the first principal component (**Figure 14c**). When looking at the time series in **Figure 14b**, France exhibits a different trend than the other regions, with a rather stable proportion maturing (and not an increase as for all other regions) followed by a marked decrease starting in the 1990's).

The average time trend in the time series shows a first period up to 1995, marked by a consistent increase in the proportion maturing for NA and S-Europe, followed by a second period marked by a clear decrease in the proportion maturing in NA, the inversion of the signal being weaker in S-Europe.

Although less clear than for the survival rate, the second axis of the PCA captures part of the difference between NA and S-Europe, with most of the regions in NA being positively correlated with the second axis, when most of the regions in S-Europe are negatively correlated (**Figure 14c**).

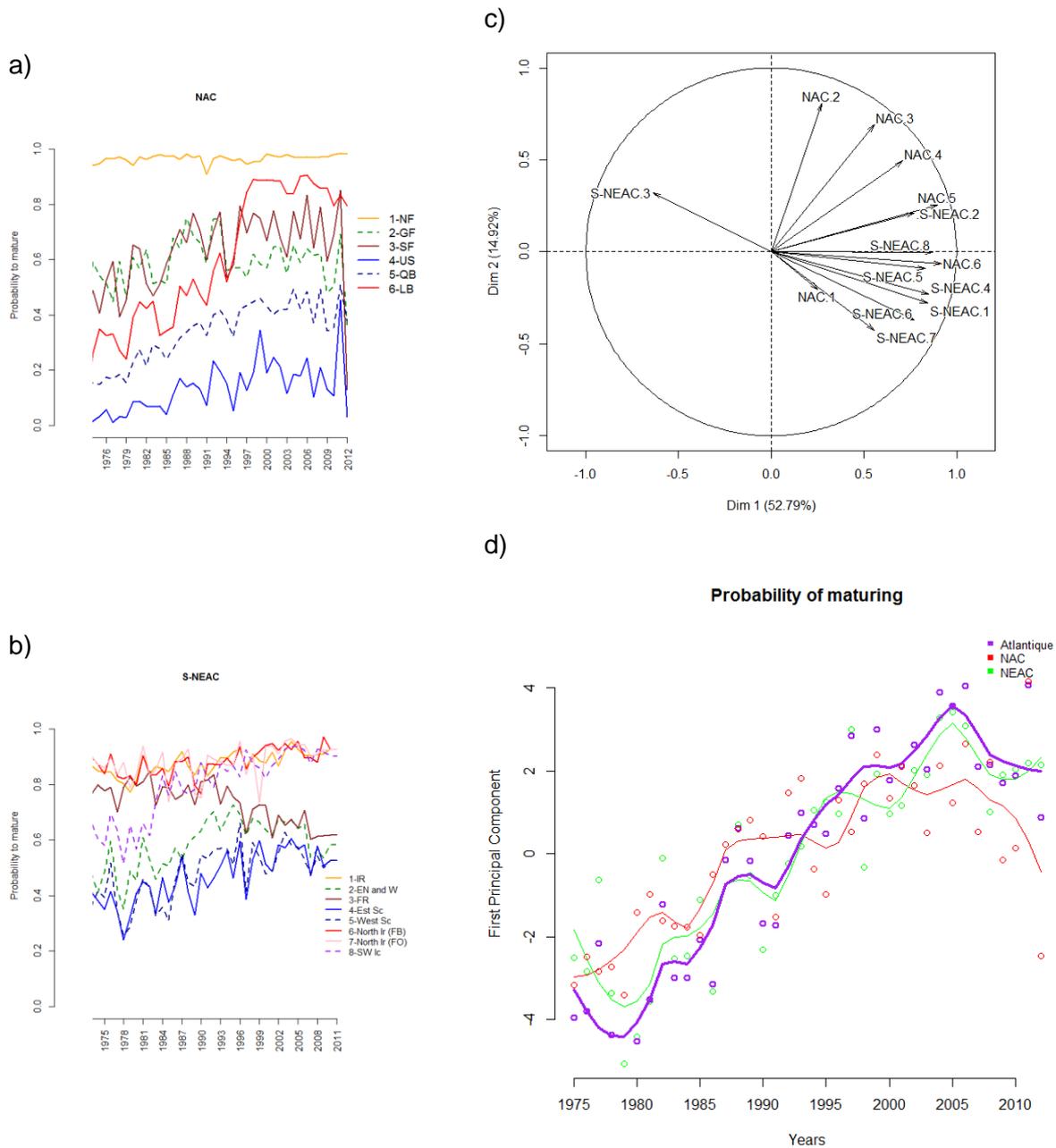


Figure 14: Analysis of the synchrony in the proportion maturing among the 6 regions in NA and the 8 regions in S-Europe. (a) and (b): marginal posterior distribution of the time series of proportion maturing for NA (a ; this present study) and S-Europe (extracted from Massiot-Granier 2014). (c) Dispersion diagram of the first two normalized eigenvectors from the PCA realized on the 6+8 = 14 time series. Item (1 to 6 for NA and 1 to 8 for S-Europe) used in (a) and (b) define the same regions in (c). (d) Long term consistent trend (1975 to 2012) for NA only (red), S-Europe only (green) and all regions considered together (purple) ; Plain lines (d) are series smoothed via a multinomial non parametric smoothing (R *loess* function, with a smoothing parameter=0.3).

3.4 Correlation between post-smolts survival and maturing probability and the Atlantic Multidecadal Oscillation Index

Overall, results reveal synchrony between the variations of key demographic parameters (post-smolts survival and maturing probability) and the AMO, with a critical period in the early 90's in over the North Atlantic.

3.4.1 Post-smolts survival

Correlation between post-smolt survival and AMO reveals negative correlation at two temporal scales.

First, global trends at the scale of the entire time series (1975-2012) are clearly negatively correlated (**Figure 15a and Table 7**), the general increase in the Sea Surface temperature in the North Atlantic Ocean being negatively correlated with the general decrease of the post-smolt survival rate. The sharp decline of the post-smolts survival in the late 80's is not found in the AMO time series.

Beyond the global trends, time series of AMO and post-smolt survival also exhibit variations at a smaller time scale (5-10 years) that appear negatively correlated, this negative correlation being clearer since the 90's. However, correlations tested on the de-trended time series (First difference; **Table 7**) are not significant.

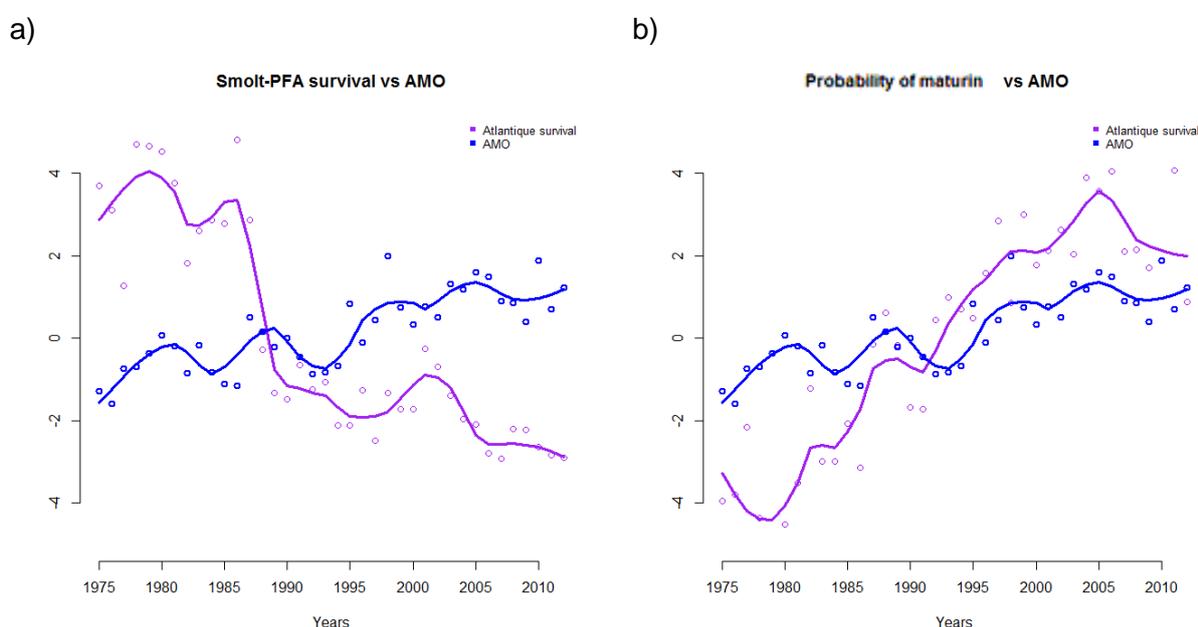


Figure 15: Standardized time series of the global trends (extracted from the PCA at the scale of the North Atlantic Ocean) in (a) the post-smolts survival, and (b) the maturing probability, versus the Atlantic Multidecadal. Plain lines are series smoothed via a multinomial non parametric smoothing (R *loess* function, with a smoothing parameter=0.3).

Table 7: Pearson's product-moment correlation between survival (Atlantic, NAC, S-NEAC and) AMO. Atlantic refers to NAC and S-NEAC complexes. Values in parenthesis indicate the p-values of the significance test. * indicates an autocorrelation significant with p-v value <0.05.

	Atlantic	NAC	S-NEAC
AMO	-0.75* (5.3e-08)	-0.75* (5.3e-08)	-0.60* (6.3e-05)
		<i>First difference</i>	
	-0.03 (0.87)	0.10 (0.54)	-0.11 (0.51)

3.4.2 Maturing probability

The global trend of the probability to mature during the first year spent at sea over the whole time series (1975-2012) is positively correlated with the AMO (**Figure 15b; Table 8**). Interestingly, the maturing probability tend to stabilize (or even to decrease for the S-Europe ;

see **Figure 14d**) in the late 1990's, , what corresponds with the beginning of the warm phase of AMO and the strong Regulatory Measure on the allowable catches for the West Greenland Salmon fishery.

Variations on a smaller time scale (5-10 years) in the maturing probability and AMO also appear as positively correlated (**Figure 15b**), but statistical tests on de-trended time series are not significant (**Table 8**, First difference).

Table 8: Pearson's product-moment correlations between probabilities of mature during the first year at sea (Atlantic, NAC, S-NEAC) and AMO. Atlantic refers to NAC and S-NEAC complexes. Values in parenthesis indicate the p-values of the significance test. * indicates an autocorrelation significant with p-value <0.05.

	Atlantic	NAC	S-NEAC
AMO	0.85* (2.5e-11)	0.80* (1.3e-9)	0.82* (3.4e-10)
	0.27 (0.11)	<i>First difference</i> 0.33* (0.04)	0.11 (0.55)

3.5 Forecasts of the returns under management scenarios of catches at sea

Forecasts of the returns of 1SW and 2SW fish in the 6 regions of NA, show that uncertainty in the returns increases with forecasting time (See **Figure A.5.1, Appendix V**). This is mostly the consequence of the increasing uncertainty in forecasts of the post-smolts survival and proportion maturing, both based on random walk models.

For all scenarios, probability to reach the management objectives (for 2SW only ; **Figure 16**) are highly variables among the 6 regions of NA, with Scotia Fundy and USA having very low probability of reaching CLs, and Newfoundland and Labrador having the highest probability of reaching management objectives. Interestingly however, because of the low status of stocks in NA, probability of reaching management objectives are never higher than 0.6, even under the 0-catch scenario.

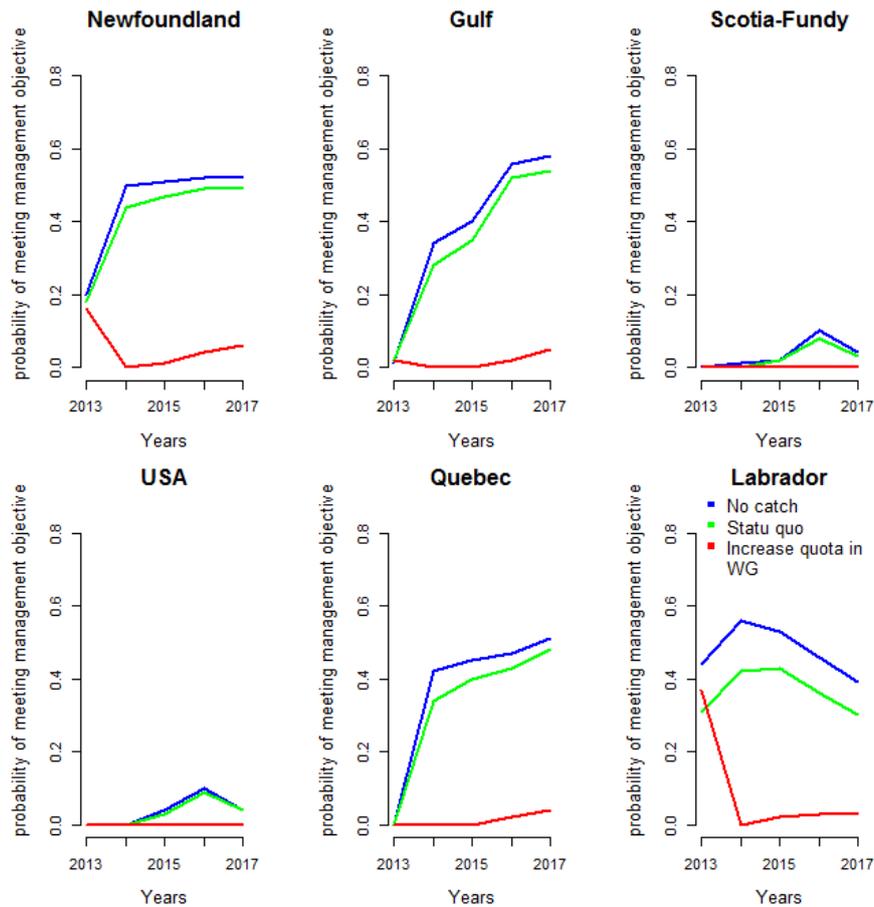


Figure 16: Probability of reaching management objective, under different management scenarios of catches at sea: zero harvest, statu quo and increase quota in West Greenland to 1500 tonnes. Forecasts are done for 5 years, based on the population dynamics model and accounting for posterior uncertainty on all parameters

The 0-catch scenario logically provides the highest probability to reach the conservation limits. Because catches are very low since the late 90's, forecast under the statu quo scenario are not drastically different than under the 0-catch scenario. Allowing a 1500 tons quotas of catches in the West Greenland fishery would seriously impact stock status and produce very low returns in all regions.

4 Discussion

4.1 A large scale modeling approach to unravel the fingerprints of large scale ecosystem changes

The multi-regional hierarchical Bayesian life cycle model brought a substantial contribution to the understanding of the ecological and demographic mechanisms that control population dynamics of *A. salmon*.

The approach developed in this work is built on the model proposed by [Massiot-Graniet et al. \(2014\)](#), who developed a multi-regional modelling approach of the population dynamics for 8 population aggregates in Southern Europe. We provide an extension to the modelling approach to the N. America, and then analyze the common patterns in the time series of key life history traits between N. America and Europe

The decline of abundance in Atlantic received considerable attention in recent years (Mills et al., 2013; Friedland et al., 2014). However, most of those studies analyze trends in abundance, without integrating the data within a stage-based life cycle approach.

The Bayesian integrated life cycle modeling approach allows us to assimilate various sources of information, data and priors (informative or not) compiled by the ICES working group and aggregated at the scale of large stock units. The model explicitly integrates variability of life history in the freshwater (different ages of smoltification) and marine phases (different age at maturity) of the life cycle. In addition, state space model are very adapted in quantifying the uncertainties around estimations and projections generated by the model.

Our results highlight and quantify the spatial coherence in the time trends of post-smolt survival and maturing proportion among 6 stock units in N. America. This strongly suggests a common response of populations to large scale environmental changes impacting salmon population during the marine phase. This hypothesis was further explored by testing the correlation with the Atlantic Multidecadal Oscillation considered as a proxy of environmental conditions in the North Atlantic Ocean.

4.2 Limits of the modelling approach

Before further developing the ecological significance of our results, below we discuss some limits of the modelling approach.

To keep the model as simple as possible, and to keep the MCMC simulation time as fast as possible (about 5 hours for the model presented in this work), simplifying hypotheses have been made. Then, in a first section, we discuss some options to relax some of those hypotheses.

In a second section, we also discuss some limits regarding the quality of some data series and some differences in the size/numbers of stock units between N. America and S-Europe.

4.2.1 A simplified demographic structure

Sensitivity analysis to some fixed parameters

A sensitivity of the results to the natural mortality rate M should be carried out. Indeed Massiot-Granier et al. (2014), show that modification of the value of the natural mortality rate can change the abundance of salmon. Indeed, changing the prior on the natural mortality impacts both natural survival and probability to mature as 1SW. In the approach developed in Massiot-Granier et al. (2014), and in our study, natural mortality at sea during the marine phase is fixed with a very tight prior, so most of the year to year variability is caught by the smolt-to-PFA survival. An interesting perspective would be to define the natural mortality not in a very informative prior common for 1SW maturing fish and 1SW non maturing fish but differently. Indeed, we suggest that natural mortality could be different between North America and Greenland, because salmon are not exposed to the same environment and have different physiological development (2SW are biggest than 1SW).

A hierarchical model to separate out different scales

To assess the impacts of environmental factors on salmon populations at different spatial scales, it would be interesting to explicitly integrate parameters into a hierarchical structure to capture variations on different spatial scales. In its present structure, the model does not include any correlation structure among the time series of key life history parameters. Following [Lahoz-Monfort et al. \(2011, 2013\)](#) or [Massiot-Granier \(2014\)](#), it would be interesting to define each demographic parameter as the sum of a synchronous and asynchronous component, respectively modelled as a random term common to all regions and as a region specific term.

Improving the model for natural and fishing mortality

Results presented in this study are conditioned by strong hypotheses on the exploitation rate on mixed stock fisheries at sea. Catches by regions are not available, so we considered that exploitation rates are homogeneous among regions ((excepted for Labrador). However, there is more and more evidence that mixed stock fisheries do not capture fish originating from Newfoundland, Gulf, Scotia-Fundy, USA and Quebec origins salmon in a proportion equal to their relative abundance at sea. An interesting perspective would be to use available genetic data from survey to improve the realism of the mixed stock fisheries at sea. For instance, an international sampling program to the fishery at West Greenland ([ICES WGNAS, 2014](#)) provides data on the origin of catches at West Greenland that could advantageously be used.

Improving the ecological realism of demographic transitions

Demographic transitions are modelled using lognormal distribution and fishing mortality by an exploitation rate estimated from the catch and the corresponding regional abundances at the time of the fisheries ([Prévost et al., 2012](#)). Fishing and natural mortality are modelled sequentially. Alternative models could be built to that natural and fishing mortality occur simultaneously ([Massiot-Granier et al., 2012](#)).

Only two sea-age classes were considered in the model, 1SW and 2SW. However, returns include fish that spent 3 or more winter at sea before returning, and also multi-spawners (fish that survive after the reproduction) ([O'Connel et al., 1997](#)). Complexifying the portfolio of possible life history would improve the realism of the demographics.

Although evidences exist for density-dependent regulation mechanisms of the survival during the freshwater phase ([Chaput et al., 1998](#); [Elliott, 2001](#)), our approach does not consid

er density-dependence during the egg-to-smolt transition. Data from a set of monitored rivers are available, such as time-series of egg-to-smolt data on 21 index rivers across Atlantic salmon range (12 rivers for North America and nine for Europe were compiled ([Bret, 2012](#); [ICES, 2013](#))). It would be interesting to incorporate this meta-analysis into the model to provide information on density-dependent egg-to-smolt survival rate.

4.2.2 Sensitivity of the results to some data sources and level of aggregation

Data aggregation at the scale of stock units

Information used in the model is compiled by ICES WGNAS (ICES, 2014) and structured at the scale of large stock units through the form of fisheries data and expert knowledge including uncertainty. This spatial structure is not questioned in the model. However large stock units are not necessarily the most meaningful aggregation scale. Indeed because of the homing behavior, working at the watershed or river scale (like in the Baltic as developed in Michielsen et al. 2008) would be more ecologically meaningful and appealing in theory. However, this is not feasible in practice since data are available for only less than 20% of the 2000 A. salmon rivers in NA and Europe.

The quality of the data for the Labrador can be questioned

Overall, variations in the time series of the post-smolts survival are highly synchronous among the six stock units in NA. However, some of the stock units stand out from the pack. In particular, the time series of survival for Labrador shows a different trend, with a peak in 1997 that cannot be found in other stock units. This peak is consistent with a strong increase in the number of 1SW returns in 1997. However, such a sharp variation of returns seems ecologically unlikely, what questions the quality of the data. Further discussions with experts (G. Chaput, DFO Moncton, Canada, com. pers.) confirm that the sharp increase of the returns in 1997 in the Labrador data series should be questioned.

Therefore, a sensitivity analysis was performed to assess the influence of the Labrador on the results. Our results show that the time series of the survival for Labrador is highly correlated (correlation = 0.76) with the first principal component extracted from the PCA, hence suggesting a strong influence of the Labrador time series on the results. The PCA was performed without the Labrador time series. Correlations between the common trends extracted from the PCA and the AMO are significantly impacted by those changes. In particular, correlations tested on the de-trended time-series of Atlantic and AMO has doubled and those between NAC and AMO becomes negative (Table 8).

Table 9: Pearson's product-moment correlation between survival (Atlantic, NAC, S-NEAC and) AMO. Atlantic refers to N-America and S-Europe. Values in parenthesis indicate the p-values of the significance test. * indicates an autocorrelation significant with p-value <0.05.

	Atlantic	N-America	S-Europe
AMO	-0.74* (1.18e-07)	-0.76* (3.5e-08)	-0.60* (6.3e-05)
		<i>First difference</i>	
	-0.13 (0.45)	-0.1 (0.56)	-0.11 (0.51)

Difference in the size/number of stock units between N. America and Europe

Long term component of survival and probability of maturing were defined by analyzing the Principal Components of 6 stock units in NA and 8 in Europe. Because the number of stock units is greater for Europe, this may bias the results by giving more weight to Europe when extracting the common trends. It would be possible to merge the region of North Ireland (FB) with the region of North Ireland (FO) and West Scotland with East Scotland to get 6 regions in S-Europe. However, such an approach is not fully satisfying as post smolt survival of

Northern Ireland (FB) and Northern Ireland (FO) are quite different, especially since the end of the 1990's.

4.3 A response to a trophic cascade as a possible ecological mechanism

4.3.1 A response to bottom-up forcing during the marine phase

Our analysis provides evidence for a decrease of the post-smolts survival rate and an increase of the probability of maturing common to all stock units in N-America and S-Europe.

In agreement with previous study ([Beaugrand and Reid, 2012](#); [Friedland et al., 2014](#)), trends in the time series are attributed to factors acting during the first months of the marine phase.

Our results are consistent with previous work by [Friedland et al. \(2014\)](#) showing a strong coherence in the patterns of post-smolts recruitment among the North American, Southern European and Northern European stock units controlled by bottom-up climate forcing. Variation in thermal conditions seems to be an important factor in the decline of marine survival. AMO, proxy of the SST is negatively correlated with Atlantic marine survival showing that all Atlantic complexes (NAC and S-NEAC) are being negatively impacted by warming ocean condition.

Beyond the general trends shared by all stock units in N. America and S. Europe, our results point some differences between the two sides of the Atlantic ocean. Trends in the post-smolts survival look slightly different between N. America and S-Europe. The probability to mature after one winter spent at sea, also exhibits some differences. In particular, after a general increase, the maturing probability tends to decrease in S-Europe. Such trend can also be observed for some stock units in the south of N. America (e.g. Gulf regions for instance), whereas no decrease is observed for northern region of N. America (Labrador and Newfoundland).

Those results are consistent suggest that different ecological mechanisms can be involved, and are consistent with studies suggesting that climate conditions impact North American and European survival at different time of the year; North American stock seems to be affected during spring time, early in the salmon migration at sea ([Friedland et al., 2003, 2014](#)) while European stock looks to be affected by climate variation occurring during the first summer at sea ([Friedland et al., 2014](#)).

Factors impacting salmon during freshwater phase, such as large scale climate changes for instance, would also be susceptible to impact several distant populations synchronously. However, some non-published data on the smolts production on a set of more than 20 rivers in Europe and North America ([Bret, 2012](#)) suggest no synchrony in the smolts production among distant rivers and those do not support the hypothesis of a response to large scale variations of factors controlling the freshwater phase. Other studies on pacific sockeye salmon ([Griffiths et al., 2014](#)) also show highly contrasted response of different populations to climate change depending on their local lake habitat.

4.3.2 A trophic cascade

Results point out a shift of the post-smolt marine survival in the early 1990's. However, no symmetric shift could be found in the AMO time series, what suggests that other factors (potentially also climate driven) could explain the shift in the post-smolts survival. Previous works suggest a possible response of a bottom-up control that would impact post-smolts survival through a trophic cascade. [Beaugrand and Reid \(2003, 2012\)](#), showed a correlation between salmon abundance and the structure of zooplankton community in the Northern Atlantic Ocean, related to a shift in the sea surface temperature in the North Atlantic Ocean. Those results are reinforced by [Mills et al. \(2013\)](#) who also interpret the decline of salmon population in North America in the 90's through a bottom-up mechanism driven by poor trophic conditions for A. salmon in the North Atlantic ecosystem. Their results also suggest a trophic cascade induced by a modification of climate factors impacting change in phytoplankton and zooplankton availability. [Mills'](#) results show that such changes are correlated with capelin length. Their smaller size might induce a low nutritional value as prey for salmon ([Davoren and Montevicchi, 2003](#)).

4.3.3 Growth variations as a pivotal demographic mechanism?

Previous analyses suggest that early marine survival of post-smolts could be related to growth conditions at sea, with higher growth conditions favorable to a better survival ([Friedland et al., 2009](#); [Jensen et al., 2012](#)). Available data also suggest that different ecological mechanisms could be involved in North America and Southern Europe. Post-smolts survival of Southern European salmons appear to depend strongly on post-smolts growth during summer and early winter, in relation to temperature at sea ([Peyronnet et al., 2007](#); [Friedland et al., 2014](#)). Regarding North American stock units, post-smolts survival would rather be controlled by post-smolt growth during spring time, mainly driven by variation in predation on post-smolts in the following weeks after their migration to the sea ([Friedland et al., 2014](#)).

4.3.4 Perspectives

Combining with the work by [Massiot-Granier \(2014\)](#), our present work set the basis for analyzing the response of A. salmon populations to large scale ecosystemic changes.

A joint analysis of the population dynamics of A. salmon populations in N. America and Europe has the potential to enhance the capacity to unravel fingerprints of global changes. Such a large scale approach allows for increasing the gradient of environmental variations.

Although the models developed for N. America (this study) and S-Europe (based on [Massiot-Granier, 2014](#)) are comparable, what allows us to compare the time series of the post-smolts survival and maturing probability, some differences still exist and further model development are needed to harmonize the two model structures.

But beyond those technical developments, the most exiting perspectives are to improve our understanding of the ecological and demographic mechanisms that underline those changes.

To reinforce the hypothesis of a response of populations to a trophic cascade, correlations between the time series of different life history traits and a set of environmental variable

available (e.g., abundance and structure of macro-zooplankton communities, small pelagic fishes) should be tested at different spatial scales matching with the salmon migration routes.

An interesting approach would then be to explore how variations in growth of fish could explain variations of other life history traits, like post-smolts survival and probability to mature. Probabilistic reaction norms (Morita et al., 2005; Buoro et al., 2010; Olsen et al., 2011) could be used to model how survival and probability to mature could be related to growth of fish. They would allow exploring the hypothesis of a plastic response of populations (Crozier and Hutchings, 2014) to changes in environmental conditions susceptible to have a direct impact on growth and then on survival and proportion maturing. Several studies on A. salmon already established a link between probability of early maturation and growth, suggesting that change in maturing proportion could be an adaptive response to changes in the environment (Summers, 1995; Friedland et al., 1996; Blanchet and Dubut, 2012). Relationships between growth conditions at sea, survival and maturation at sea have also been shown for pacific salmon. For instance Beamish et al. (2004) suggest that during the first year at sea, survival is related to growth, meaning bigger fish are more able to survive during periods of energy deficit.

Our results also raise the issue of possible evolutionary changes in A. salmon populations. Indeed, fisheries have historically targeted the bigger fish with the oldest age at maturation. For instance, the West Greenland fishery operating on mixed stocks has historically targeted non mature fish originating from both N. America and Europe. Homewater fisheries also preferentially target fish that return after several winters spent at sea. In addition, it has been shown salmon parents contribute to age at maturity experimentally (Porter et al., 1986) and from long term stock characteristics (Ritter et al., 1986). Hence, as observed for other fish species like cod (Olsen et al., 2003) the general decrease of the mean age at maturity observed in both N. America and Europe could also be a sign of rapid evolutionary changes toward preferential selection of early maturing fish (Saura et al., 2010). Including a possibility for heredity in growth or age at maturation in the model would consist in an exciting perspective for this work.

5 BIBLIOGRAPHY

- Aas, Ø., and Wiley InterScience (Online service) (2011). Atlantic salmon ecology (Ames, Iowa: Blackwell Pub.).
- Beamish, R.J., Mahnken, C., and Neville, C.M. (2004). Evidence That Reduced Early Marine Growth is Associated with Lower Marine Survival of Coho Salmon. *Transactions of the American Fisheries Society* 133, 26–33.
- Beaugrand, G., and Reid, P.C. (2003). Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology* 9, 801–817.
- Beaugrand, G., and Reid, P.C. (2012). Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. *ICES J. Mar. Sci.* 69, 1549–1562.
- Blanchet, S., and Dubut, V. (2012). “Back to the future”: How archaeological remains can describe salmon adaptation to climate change. *Molecular Ecology* 21, 2311–2314.
- Bret, V., Massiot-Granier, F., Rivot, E., Prévost, E., Smith, G., White, J., and Chaput, G. 2012. Contribution to the modelling of Atlantic salmon (*Salmo salar*) population dynamics at the scale of stock complexe: A bayesian meta-analysis of freshwater survival. 87 pp
- Brooks, S.P., and Gelman, A. (1998). General Methods for Monitoring Convergence of Iterative Simulations. *Journal of Computational and Graphical Statistics* 7, 434–455.
- Buckland, S.T., Newman, K.B., Thomas, L., and Koesters, N.B. (2004). State-space models for the dynamics of wild animal populations. *Ecological Modelling* 171, 157–175.
- Buoro, M., Prévost, E., and Gimenez, O. (2010). Investigating evolutionary trade-offs in wild populations of atlantic salmon (*Salmo salar*): incorporating detection probabilities and individual heterogeneity: estimating trade-offs with mark-recapture data. *evolution* 64, 2629–2642.
- Chaput, G. (2012). Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science* 69, 1538–1548.
- Chaput, G., Legault, C., Reddin, D., Caron, F., and Amiro, P. (2005). Provision of catch advice taking account of non-stationarity in productivity of Atlantic salmon (L.) in the Northwest Atlantic. *ICES Journal of Marine Science* 62, 131–143.
- Condrón, A., DeConto, R., Bradley, R.S., and Juanes, F. (2005). Multidecadal North Atlantic climate variability and its effect on North American salmon abundance. *Geophysical Research Letters* 32.
- Crozier, L.G., and Hutchings, J.A. (2014). Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications* 7, 68–87.
- Dadswell, M.J., Spares, A.D., Reader, J.M., and Stokesbury, M.J.W. (2010). The North Atlantic subpolar gyre and the marine migration of Atlantic salmon *Salmo salar*: the “Merry-Go-Round” hypothesis. *Journal of Fish Biology* no – no.

- Davoren, G., and Montevecchi, W. (2003). Signals from seabirds indicate changing biology of capelin stocks. *Marine Ecology Progress Series* 258, 253–261.
- Elliott, J.M. (2001). The relative role of density in the stock-recruitment relationship of salmonids. *Stock, Recruitment and Reference Points: Assessment and Management of Atlantic Salmon* 25–66.
- Enfield, D.B., Mestas-Nunez, A.M., Trimble, P.J., and others (2001). The Atlantic multidecadal oscillation and its relation to rainfall and river flows in the continental U. S. *Geophysical Research Letters* 28, 2077–2080.
- Friedland, K. (2003). Ocean thermal conditions in the post-smolt nursery of North American Atlantic salmon. *ICES Journal of Marine Science* 60, 343–355.
- Friedland, K.D., and Haas, R.E. (1996). Marine post-smolt growth and age at maturity of Atlantic salmon. *Journal of Fish Biology* 48, 1–15.
- Friedland, K.D., MacLean, J.C., Hansen, L.P., Peyronnet, A.J., Karlsson, L., Reddin, D.G., O Maoileidigh, N., and McCarthy, J.L. (2008). The recruitment of Atlantic salmon in Europe. *ICES Journal of Marine Science* 66, 289–304.
- Friedland, K.D., Shank, B.V., Todd, C.D., McGinnity, P., and Nye, J.A. (2014). Differential response of continental stock complexes of Atlantic salmon (*Salmo salar*) to the Atlantic Multidecadal Oscillation. *Journal of Marine Systems* 133, 77–87.
- Gibson, R.J. (1993). The Atlantic salmon in fresh water: spawning, rearing and production. *Rev Fish Biol Fisheries* 3, 39–73.
- Griffiths, J.R., Schindler, D.E., Ruggerone, G.T., and Bumgarner, J.D. (2014). Climate variation is filtered differently among lakes to influence growth of juvenile sockeye salmon in an Alaskan watershed. *Oikos* 123, 687–698.
- ICES. 2013. Report of the Working Group on North Atlantic Salmon (WGNAS) , 3– 12 April 2013 , Copenhagen, Denmark . ICES CM 2013/ACOM:09. 380 pp.
- ICES. 2014. Report of the Working Group on North Atlantic Salmon (WGNAS) , 19-28 March 2014, Copenhagen, Denmark . ICES CM 2014/ACOM:09. 433 pp.
- Jensen, A.J., O Maoileidigh, N., Thomas, K., Einarsson, S.M., Haugland, M., Erkinaro, J., Fiske, P., Friedland, K.D., Gudmundsdottir, A.K., Haantie, J., et al. (2012). Age and fine-scale marine growth of Atlantic salmon post-smolts in the Northeast Atlantic. *ICES Journal of Marine Science* 69, 1668–1677.
- Jonsson, N., Jonsson, B., and Hansen, L.P. (1998). The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* 67, 751–762.
- King, T.L., Kalinowski, S.T., Schill, W.B., Spidle, A.P., and Lubinski, B.A. (2001). Population structure of Atlantic salmon (*Salmo salar* L.): a range-wide perspective from microsatellite DNA variation. *Molecular Ecology* 10, 807–821.
- Lahoz-Monfort, J.J., Morgan, B.J.T., Harris, M.P., Daunt, F., Wanless, S., and Freeman, S.N. (2013). Breeding together: modeling synchrony in productivity in a seabird community. *Ecology* 94, 3–10.

- Limburg, K.E., and Waldman, J.R. (2009). Dramatic Declines in North Atlantic Diadromous Fishes. *BioScience* 59, 955–965.
- Massiot-Granier, F., Prévost, E., Chaput, G., Potter, T., Smith, G., White, J., Mäntyniemi, S., and Rivot, E. (2014). Embedding stock assessment within an integrated hierarchical Bayesian life cycle modelling framework: an application to Atlantic salmon in the Northeast Atlantic. *ICES Journal of Marine Science: Journal Du Conseil* fst240.
- Massiot-Granier, F. (2014). Dynamique des populations de saumon Atlantique (*Salmo salar*) à l'échelle de son aire de répartition. Séparer les différentes échelles dans les facteurs de forçage par une approche de modélisation hiérarchique bayésienne. 196 pp.
- Michielsens, C.G.J., McAllister, M.K., Kuikka, S., Mäntyniemi, S., Romakkaniemi, A., Pakarinen, T., Karlsson, L., and Uusitalo, L. (2008). Combining multiple Bayesian data analyses in a sequential framework for quantitative fisheries stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences* 65, 962–974.
- Mills, D.H. (1989). *Ecology and management of Atlantic salmon* (London; New York: Chapman and Hall). 351 pp.
- Mills, K.E., Pershing, A.J., Sheehan, T.F., and Mountain, D. (2013). Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. *Global Change Biology* 19, 3046–3061.
- Morita, K., Morita, S.H., Fukuwaka, M., and Matsuda, H. (2005). Rule of age and size at maturity of chum salmon (*Oncorhynchus keta*): implications of recent trends among *Oncorhynchus* spp. *Canadian Journal of Fisheries and Aquatic Sciences* 62, 2752–2759.
- O'Connell, M.F. (1997). Estimates of conservation spawner requirements for Atlantic salmon (*Salmo salar* L.) for Canada (Department of Fisheries and Oceans).
- Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B., and Dieckmann, U. (2004). Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428, 932–935.
- Olsen, E.M., Lilly, G.R., Heino, M., Morgan, M.J., Brattey, J., and Dieckmann, U. (2005). Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 62, 811–823.
- Parent, E., and Rivot, E. (2013). *Introduction to hierarchical Bayesian modeling for ecological data* (Boca Raton: CRC Press).
- Peyronnet, A., Friedland, K.D., Maoileidigh, N. ó, Manning, M., and Poole, W.R. (2007). Links between patterns of marine growth and survival of Atlantic salmon *Salmo salar*, L. *Journal of Fish Biology* 71, 684–700.
- Porter, T.R., Healey, M.C., O'Connell, M.F., Baum, E.T., Bielak, A.T., and Côté, Y. (1986). Implications of varying the sea age at maturity of Atlantic salmon (*Salmo salar*) on yield to the fisheries. *Canadian Special Publication in Fisheries and Aquatic Sciences* 89, 110–117.
- Potter, E., Crozier, W., Schon, P., Nicholson, M., Maxwell, D., Prevost, E., Erkinaro, J., Gudbergsson, G., Karlsson, L., and Hansen, L. (2004). Estimating and forecasting pre-fishery abundance of Atlantic salmon (*L.*) in the Northeast Atlantic for the management of mixed-stock fisheries. *ICES Journal of Marine Science* 61, 1359–1369.

Prévost, E., Chaput, G., Dionne, M., Reddin, D., Atlantic salmon Pre-Fishery Abundance (PFA) and Catch Advice Model 1978-2011 (West Greenland fishery years). Working paper

Rago, P.J., Reddin, D.G., Porter, T.R., Meerburg, D.J., Friedland, K.D., and Potter, E.C.E. (1993). A continental run reconstruction model for the non-maturing component of North American Atlantic salmon: analysis of fisheries in Greenland and Newfoundland-Labrador, 1974-1991. ICES, Copenhagen (Denmark). 1993.

Ritter, J.A., Farmer, G.J., Misra, R.K., Goff, T.R., Bailey, J.K., and Baum, E.T. (1986). Parental influences and smolt size and sex ratio effects on sea age at first maturity of Atlantic salmon (*Salmo salar*). Salmonid Age at Maturity. Can. Spec. Publ. Fish. Aquat. Sci 89, 30–38.

Rivot, E., Prévost, E., Parent, E., and Baglinière, J.L. (2004). A Bayesian state-space modelling framework for fitting a salmon stage-structured population dynamic model to multiple time series of field data. Ecological Modelling 179, 463–485.

Saura, M., Morán, P., Brotherstone, S., Caballero, A., Alvarez, J., and Villanueva, B. (2010). Predictions of response to selection caused by angling in a wild population of Atlantic salmon (*Salmo salar*). Freshwater Biology 55, 923–930.

Shearer, W.M. (1992). The Atlantic Salmon: Natural History, Exploitation and Future Management (Farnham, Surrey: Fishing News Books).

Summers, D.W. (1995). Long-term changes in the sea-age at maturity and seasonal time of return of salmon, *Salmo salar* L., to Scottish rivers. Fisheries Management and Ecology 2, 147–156.

SITOGRAFIE

<http://www.esrl.noaa.gov/psd/data/timeseries/AM>, consulté le 2 juin 2015

<http://www.ifm.org.uk/news/ifm-report-nasco-meeting-canada>, consulté le 30 juillet 2015

6 Appendix

Appendix I: Data processing on Returns and Spawners

Each region is subdivided in smaller management units (management of the homewater fishery) called SFAs (Salmon Fishing Areas). Available data fundamentally consist in time series of estimates of the number of salmon that returns to homewater for spawning after their marine sojourn, and of spawners that escape the homewater fishery, both available in each different SFAs.

Those data are available for two different size classes of fish, small and large ones. In this study, small fish were considered as 1SW fish, and large as 2SW.

Estimates of returns and spawners are provided with uncertainty, in the form of a Uniform distribution between a minimum and maximum bound, specific for each SFA, year and sea-age class.

Range of uncertainty for returns and spawners (minimum and maximum) for each zone (i.e. per river or watershed) were derived from the best available expert knowledge and analyses including variety of sampling methods such as counts of salmon at monitoring facilities, population estimates from mark/recapture studies, and applying angling and commercial catch statistics, angling exploitation rates, and measurement of freshwater habitat (Chaput et al., 2005; ICES, WGNAS 2013).

Monte Carlo simulations were run to integrate those uncertainties and to estimate probability distributions of the Returns and Spawners at the scale of each of the 6 regions (for each year and sea-age class). $n=100\ 000$ independent random draws in Uniform distributions for all SFAs were then summed to integrate uncertainty at the scale of each of the 6 regions. Empirical distribution of the number of fish at the scale of the regions, are no more Uniform but tend to a Normal or a logNormal form (Figure A1.1).

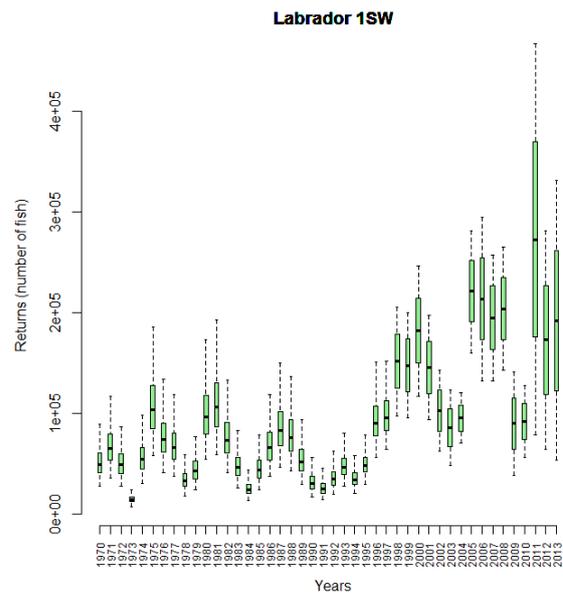
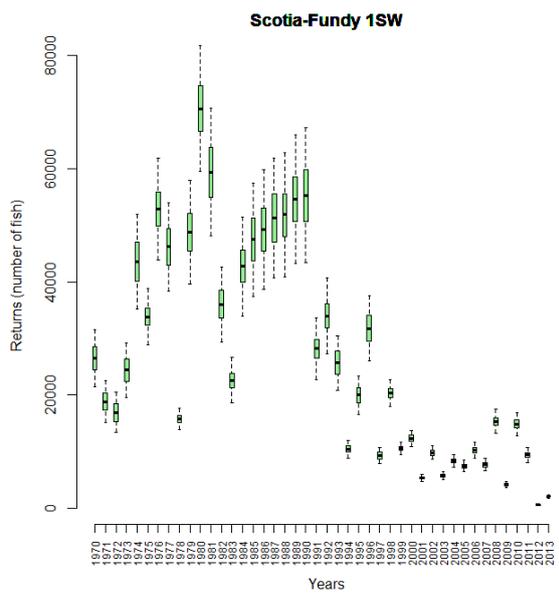
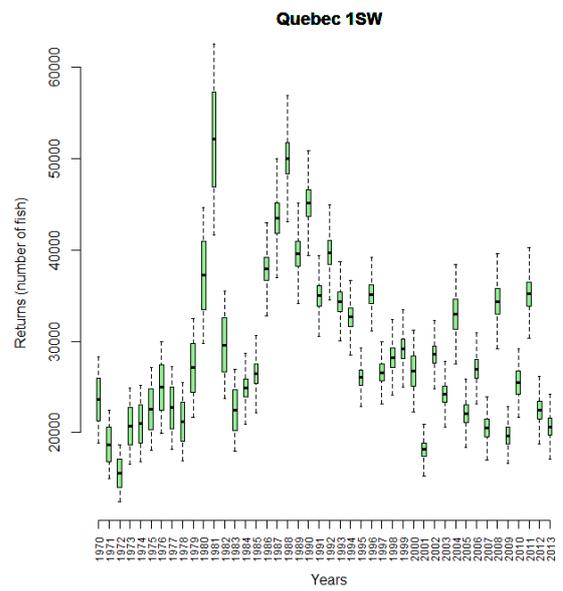
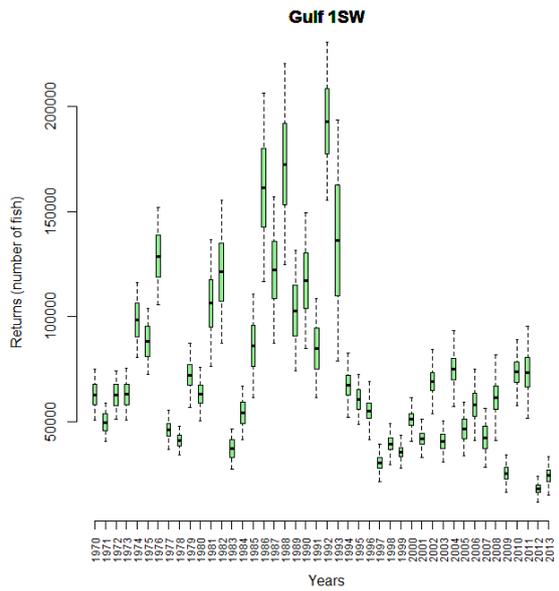
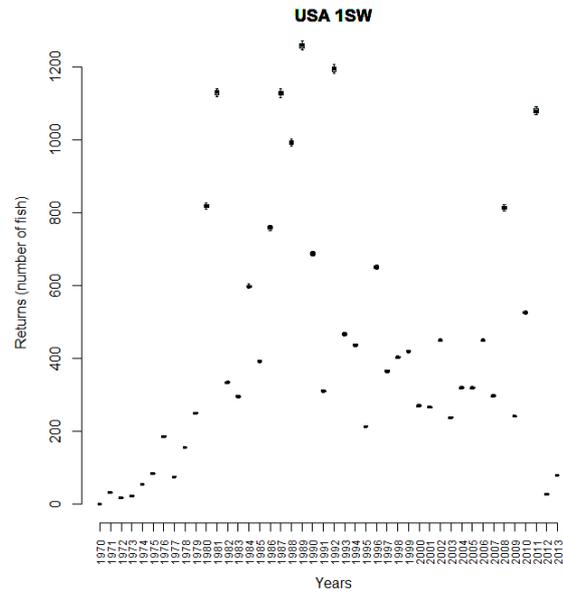
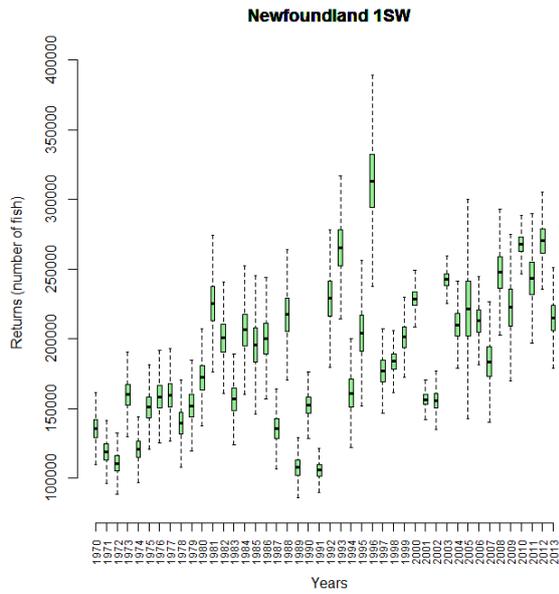


Figure A 1.1: Empirical probability distribution of returns of 1SW to North America (obtained from n=100 000 Monte Carlo Simulation)

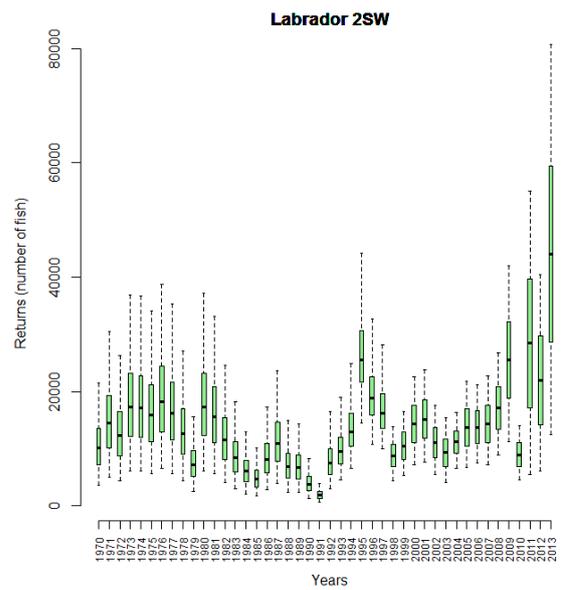
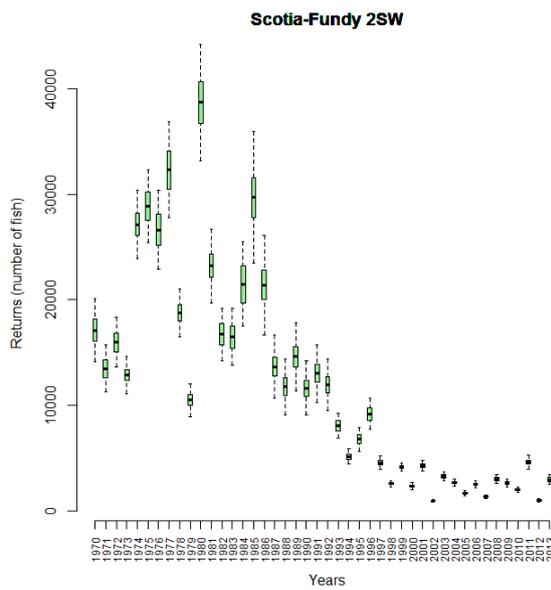
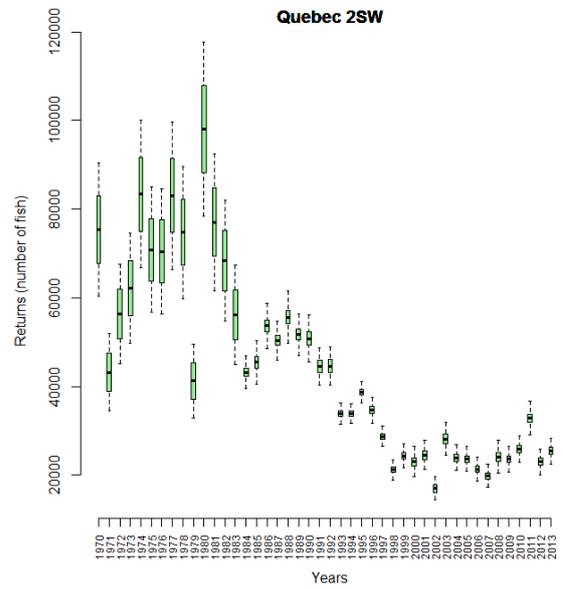
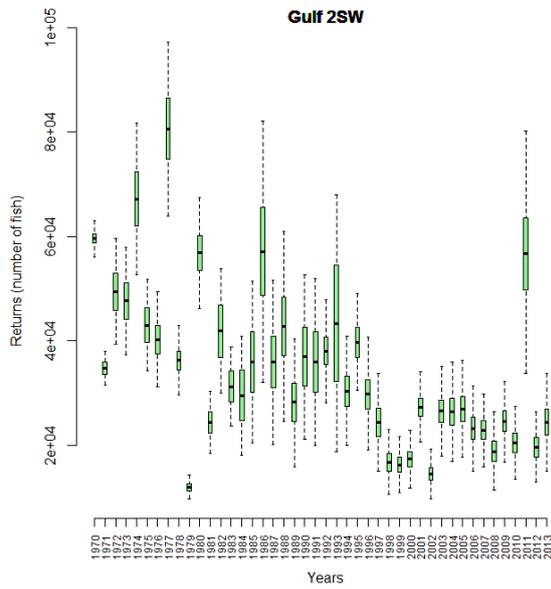
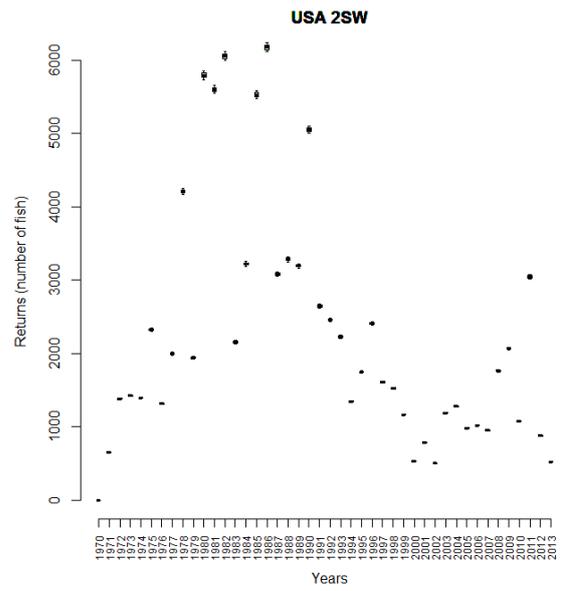
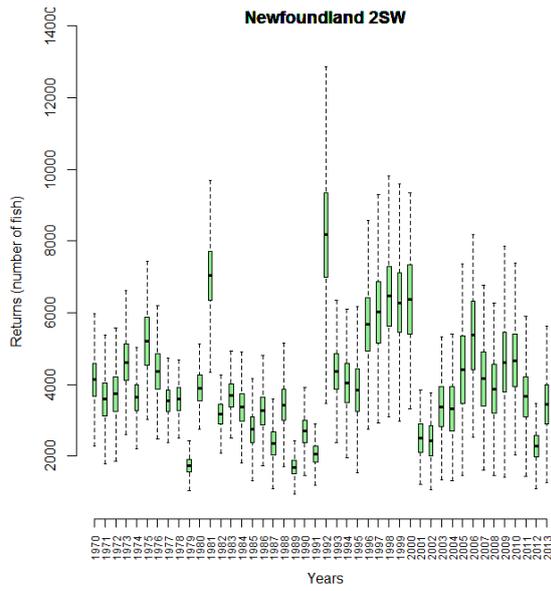


Figure A 1.2: Empirical probability distribution of returns of 1SW to North America (obtained from n=100 000 Monte Carlo Simulation)

LogNormal distributions were fitted on the empirical probability distributions of the Returns obtained by Monte Carlo simulations. LogNormal distributions were preferred to Normal distribution because they generally provide a better fit to the empirical distributions, and because they are adapted to model positive quantities (numbers of fish).

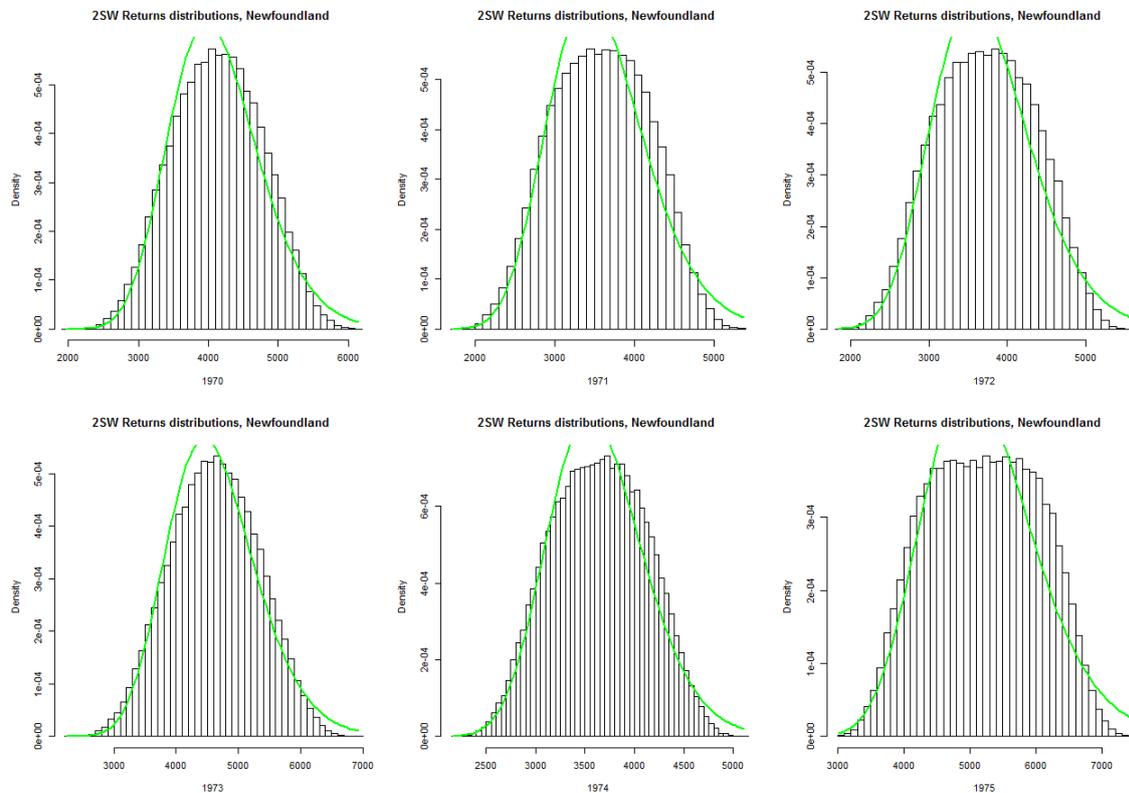


Figure A 1.3: Empirical distributions of the returns to North America (here only the returns of Newfoundland are represented) (derived from n=100 000 Mont carlo simulations) from the year 1970 to 1975. The green line represents the logNormal fit on these distributions

Returns include fish caught by homewater commercial fisheries, except in the case of Newfoundland and Labrador regions to avoid double counting fish, because homewater of those two regions shelter fisheries at sea. Thus, in Labrador and Newfoundland, Returns do not include Aboriginal Peoples', resident food, and commercial catches, only recreational.

Point estimates of Homewater catches (for each year and sea-age class) were obtained as the difference between point estimates (posterior medians) of the Returns and Spawners.

Appendix II: Data on Marine fisheries (mixed stocks)

❖ Labrador and Newfoundland commercial and aboriginal mixed-stock fishery

Labrador and Newfoundland fisheries first operate on 1SW (mature and non mature) during their first year at sea, and then on 2SW fish during the second year at sea when fish are coming back from West Greenland foraging areas.

The decline of catches in Labrador and Newfoundland observed since 1980 is mainly due to the reduction in commercial fisheries effort, with closure important fisheries: the insular Newfoundland fishery in 1992, the Labrador commercial fishery in 1998, the Quebec commercial fishery in 2000. As of 2013, all commercial fisheries of Atlantic salmon Labrador and Newfoundland have remained closed.

Time series of the number of fish caught in the LB and NFDL fisheries include uncertainty, based on expert knowledge and data analysis.

Most of the uncertainty comes from the parameters used to convert the catches in weight in numbers of fish in the different demographic classes considered in the model: 1SW non-maturing, 1SW mature and 2SW fish. Probability distributions on the parameters were derived from catch statistics (ICES, WGNAS, 2013).

For 2SW fish, available information and expert knowledge can be used to consider separately the catches of fish originated from Labrador from those originated from the 5 other regions considered in the model. Indeed, based on expert opinion, the exploitation rate of Labrador differs from the exploitation rate of the five others regions. The commercial and FSC (aboriginal) fisheries were assumed to exploit a higher proportion of Labrador origin 2SW salmon than would be the case for other fisheries.

❖ West Greenland fishery

The fishery catches salmons from America, but from Europe as well. Only the proportion of fish coming from North America is considered in our model. The proportion of North American salmon in the catch has increased strongly since the early 1990s (in the recent years, salmon originated from North America represent 80-90% of the fish caught).

After numerous regulatory measures taken by NASCO in the 1990s, catches decreased in West Greenland fisheries, reflecting declining abundance of the contributing salmon stocks.

Uncertainty in the catches has different source: An extra number of fish (with uncertainty) is added to the statistics to account for unreported catches; Catch statistics are in weight, and then converted in abundance of fish thanks to a sampled mean weight. Finally, a proportion is used to consider only fish coming from North America (the remaining being fish from European coasts), and only the non-maturing 1SW component is considered (Rago et al 1993b).

❖ Saint Pierre and Miquelon fisheries

Saint Pierre and Miquelon fisheries include recreational and professional fisheries on both 1SW and 2SW fish. Fish caught at SPM are originated from all North American regions. Data do not present uncertainty.

Appendix III: Posterior checking

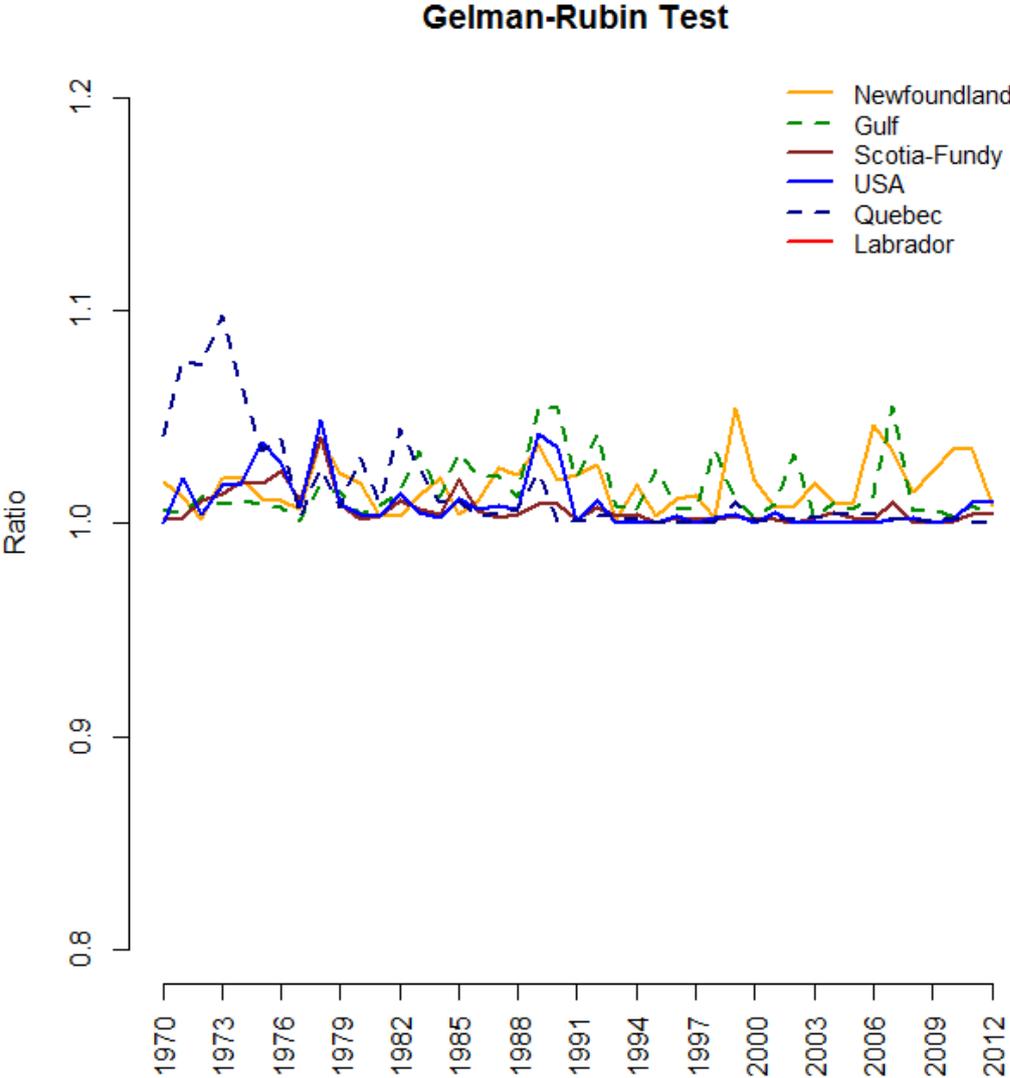
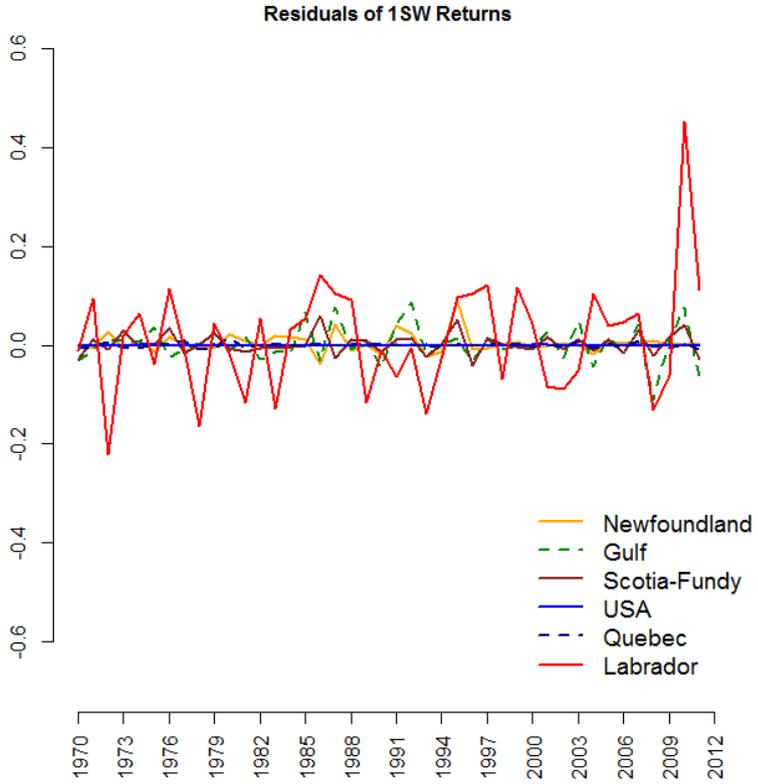


Figure A 3.1: Bayesian posterior checking (Gelman-Rubin Test). Here, the test is realized on the probability of maturing. If the data and the model are consistent, observed data should be similar to replicated data simulated a posteriori by the model, with a value of the ratio near to 1.

Appendix IV: Time-series of residual

a)



b)

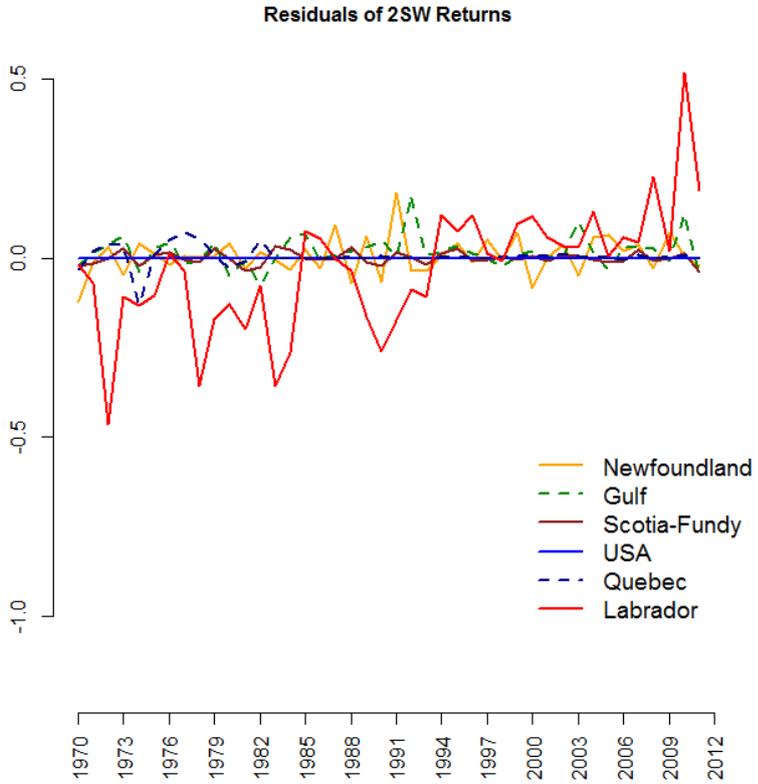


Figure A 4.1: Time-series of residuals of 1SW (a) and 2SW (b) returns

Appendix V: Estimated spawners and management objectives in the 6 geographic areas of North America

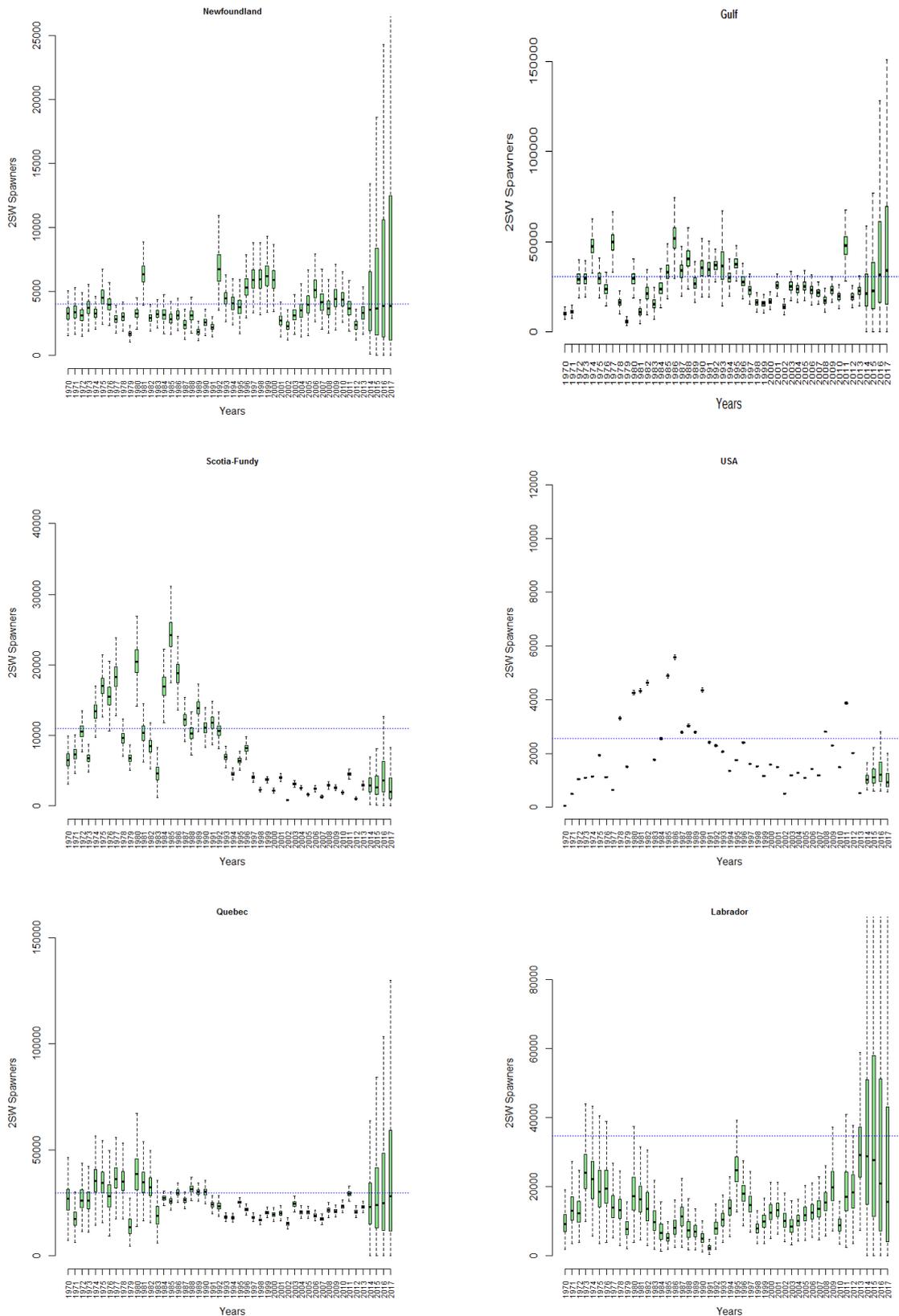


Figure A 5.1: Comparison of the 2SW management objectives (blue dashed line) to the probability distribution of spawners of 2SW in 6 geographic areas of North America. From 2013 to 2017 abundances of spawner are forecasted

Appendix VI: JAGS code

DATA BLOCK

```
data
{
for (r in 1:6)
{
    for (t in 1:n)
    {
        R1sw.m[t,r] <- exp(log.R1sw.m[t,r] + 0.5/log.R1sw.tau[t,r])
        R2sw.m[t,r] <- exp(log.R2sw.m[t,r] + 0.5/log.R2sw.tau[t,r])
    }
}

for (r in 1:6)
{
    for (t in 1:10)
    {
        N1.m[t,r] <- (R1sw.m[t,r]-Cobs.1SW[t,r])*eggs[1,r] + (R2sw.m[t,r]-Cobs.2SW[t,r])*eggs[2,r]
    }

min.log.N1[r] <- log(mean(N1.m[1:10,r])/1000)
max.log.N1[r] <- log(mean(N1.m[1:10,r])*1000)

}

} # end data block
```

MODEL

```
model
{

# Fixed parameters
# -----
# -----
# Number of fish added when necessary to avoid log(0) in logNormal
eps <- 1

# General dummy noise
CV <- 0.01

# Fictive Sample size that controls the amount of information
# in the informative Dirichlet distribution for the repartition of smolts-ages
N.Sample <- 100

# Survival eggs --> Total smolts
s1 <- 0.007
CV.s1 <- 0.05
sigma2.s1 <- log(CV.s1*CV.s1+1)
tau.s1 <- 1/sigma2.s1

# Noise for the proportion of smolts per smolt-ages
CV.psm <- CV
sigma2.psm <- log(CV.psm*CV.psm+1)
tau.psm <- 1/sigma2.psm

M1 <- 0.03
```

```

s3 <- exp(-M1)
s5 <- exp(-11*M1)

# Noise for marine survival transitions
CV.s <- CV
sigma2.s <- log(CV.s*CV.s+1)
tau.s <- 1/sigma2.s

CV.m <- CV
sigma2.m <- log(CV.m*CV.m + 1)
tau.m <- 1/sigma2.m

# prior on Smolts --> PFA survival
mu.s2 <- 0
rho.s2 <- 1
sigma.s2 ~ dunif(0,1)
tau.s2 <- 1/pow(sigma.s2,2)

# prior on probability of maturing the first year at sea
mu.p.ma <- 0
rho.p.ma <- 1
sigma.p.ma ~ dunif(0,1)
tau.p.ma <- 1/pow(sigma.p.ma,2)

# Observation errors on catches for mixed fisheries (mature fish)
CV.C1 <- 0.1
sigma2.C1 <- log(CV.C1 * CV.C1 + 1)
tau.C1 <- 1/sigma2.C1

# Observation errors on catches for mixed fisheries (non mature fish)
V.C2 <- 0.1
sigma2.C2 <- log(CV.C2 * CV.C2 + 1)
tau.C2 <- 1/sigma2.C2

# Prior on the time series of Smolts --> PFA survival
# -----
# -----
for (r in 1:6)
{
  logit.s2[1,r] ~ dnorm(0,1)

  for (t in 1:(n-1))
  {
    logit.s2.m[t+1,r] <- mu.s2 + (logit.s2[t,r]-mu.s2)*rho.s2
    logit.s2[t+1,r] ~ dnorm(logit.s2.m[t+1,r],tau.s2)
  }

  for (t in 1:n)
  {
    logit(s2[t,r]) <- logit.s2[t,r]
  }
}

# Prior on Maturation ----> Probability of maturing the first year

```

```

# -----
# -----

for (r in 1:6)
{
  logit.p.ma[1,r] ~ dnorm(0,1)

  for (t in 1:(n-1))
  {
    logit.p.ma.m[t+1,r] <- mu.p.ma + (logit.p.ma[t,r]-mu.p.ma)*rho.p.ma
    logit.p.ma[t+1,r] ~ dnorm(logit.p.ma.m[t+1,r],tau.p.ma)
  }

  for (t in 1:n)
  {
    logit(p.ma[t,r]) <- logit.p.ma[t,r]
  }
}

```

```

# Population dynamic
# -----
# -----

```

Fresh water phase

```

# Number of spawners = Returns - Homewater catches
# -----

```

```

for ( r in 1:6)
{
  for (t in 1:n)
  {
    N7[t,r] <- max(N6[t,r] - Cobs.1SW[t,r],1)
    N10[t,r] <- max(N9[t,r] - Cobs.2SW[t,r] + (r==4)*Stocking.USA.2sw[t], 1)
  }
}

```

```

# N1 : Number of eggs
# -----

```

```

for (t in 1:n)
{
  N1[t,r] <- N7[t,r]*eggs[1,r] + N10[t,r]*eggs[2,r]
}

```

```

# N2 : Eggs --> total Smolts per cohorts (survival known and fixed to s1)
# -----

```

```

log.N2.m[t,r] <- log(N1[t,r]*s1 + eps) - 0.5/tau.s1
N2[t,r] ~ dlnorm(log.N2.m[t,r],tau.s1)
}

```

```

# N2.c : Smolts distribution by age class : 6 age classes
# -----

```

```

# Dirichlet Informative prior
# Information equivalent to the one gained with a sample size = N.Sample
for ( r in 1:6)
{

```

```

for(k in 1:nSm[r])
{
mu.psm[k,r] <- psm[k,r]*N.Sample
}

for (t in 1:n)
{
psm.stoch[t,1:nSm[r],r] ~ ddirich(mu.psm[1:nSm[r],r])
}

for (t in 1:n)
{
for (k in 1:nSm[r])
{
log.Sm.m[t+1+k,k,r] <- log(psm.stoch[t,k,r]*N2[t,r] + eps) - 0.5/tau.psm
N2.c[t+1+k,k,r] ~ dlnorm(log.Sm.m[t+1+k,k,r],tau.psm)
}
}

```

Marine phase

```

# N3 : Number of smolts migration
# -----
for (t in 1:n)
{
N3.tot[t,r] <- sum(N2.c[t,,r])
}
}

# N4 : Smolt --> PFA (N4) survival (productivity parameter s2[t])
# -----
# s2[t] estimated (prior distribution)
for (r in 1:6)
{
for (t in 1:(n-1))
{
log.N4.m[t+1,r] <- log(s2[t,r]*N3.tot[t,r] + eps) - 0.5/tau.s
N4[t+1,r] ~ dlnorm(log.N4.m[t+1,r],tau.s)
}
}

## Maturation
# N5 : PFA maturing during the first year at sea
# p.ma[t,r] = probability of maturing the first year at sea
# -----
for (r in 1:6)
{
for (t in 1:n)
{
log.N5.m[t,r] <- log(N4[t,r] * p.ma[t,r] + eps) - 0.5/tau.m
N5[t,r] ~ dlnorm(log.N5.m[t,r], tau.m)

log.N8.m[t,r] <- log(N4[t,r] * (1-p.ma[t,r]) + eps) - 0.5/tau.m
N8[t,r] ~ dlnorm(log.N8.m[t,r], tau.m)
}
}

# Homogeneous across the 6 regions

```

```

# Priors: exploitation rate
for (t in 1:n)
  {
    # LB/NFDL on 1SW mature
    h5.1[t] ~ dbeta(1,1)
    # Saint Pierre et Miquelon on 1SW
    h5.2[t] ~ dbeta(1,1)
  }
# Sequential catches at sea
for (r in 1:6)
{
  for (t in 1:n)
  {
    # LB/NFDL on 1SW mature
    C1.m[t,r] <- h5.1[t]*N5[t,r]
    # Saint Pierre and Miquelon on 1SW
    C1.spm[t,r] <- h5.2[t] * (1-h5.1[t])*N5[t,r]
  }
}

# N6: Survivors after sequential catches
for (r in 1:6)
{
  for (t in 1:n)
  {
    log.N6.m[t,r] <- log(s3*(1-h5.2[t])*(1-h5.1[t]) * N5[t,r] + eps) - 0.5/tau.s
    N6[t,r] ~ dlnorm(log.N6.m[t,r],tau.s )
  }
}

# Total catches mature fish (sum accross regions)
for (t in 1:n)
{
  C1.m.tot[t] <- sum(C1.m[t,1:6])
  C1.spm.tot[t] <- sum(C1.spm[t,1:6])
}

# N8 : PFA non maturing during the first year at sea
# (1-p.ma[t,r]) = probability if non maturing the first year at sea
#-----

# Priors: exploitation rate
for (t in 1:n)
{
# Homogeneous accross the 6 regions
LB/NFDL on 1SW non-mature
h8.1[t] ~ dbeta(1,1)

# West Greenlabd on 1SW non-mature
h8.2[t] ~ dbeta(1,1)
}

# Homogeneous accross the 5 regions except Labrador (r=6)
# LB/NFDL on 2SW
for (t in 1:n)
{

```

```

h8.3.other[t] ~ dbeta(1,1)
h8.3.lab[t] ~ dbeta(1,1)

for(r in 1:5)
{
h8.3[t,r] <- h8.3.other[t]
}
h8.3[t,6] <- h8.3.lab[t]
}

# Saint Pierre and Miquelon Fisheries on 2SW
for (t in 1:n)
{
h8.4[t] ~ dbeta(1,1)

for(r in 1:5)
{
h8.4[t,r] <- h8.4[t]
}
h8.4[t,6] <- 0
}

Sequential fisheries at sea
for (t in 1:n)
{
for (r in 1:6)
{
# LBandNF on 1SW non mature
C1.nm[t,r] <- h8.1[t] * N8[t,r]
# West Greenland on 1SW non mature
C.WG1[t,r] <- h.8.2[t] * (1-h8.1[t])*N8[t,r]
}
}

for (r in 1:6)
{
for (t in 1: (n-1))
{
# LBandNF on 2SW
C2.m[t+1,r] <- h8.3[t+1,r] * (1-h8.2[t])*(1-h8.1[t]) * N8[t,r]
# Saint Pierre and Miquelon on 2SW
C2.spm[t+1,r] <- h8.4[t+1,r]*(1-h8.3[t+1,r]) * (1-h8.2[t])*(1-h8.1[t]) * N8[t,r]
}
}

# Total catches (sum accross regions)
for (t in 1:n)
{
C1.nm.tot[t] <- sum(C1.nm[t,1:6])
C.WG1.tot[t] <- sum(C.WG1[t,1:6])
}
for (t in 1:(n-1))
{
C2.tot[t+1] <- sum(C2.m[t+1,1:5])
C2.lab[t+1] <- C2.m[t+1,6]
C2.spm.tot[t+1] <- sum(C2.spm[t+1,1:6])
}
}

```

```

for (r in 1:6)
{
    C2.m[1,r] <- 10
    C2.spm[1,r] <- 1
}

C2.tot[1] <- sum(C2.m[1,1:5])
C2.lab[1] <- C2.m[1,6]
C2.spm.tot[1] <- sum(C2.spm[1,1:6])

# N9: Survivors after sequential catches
#-----
for (r in 1:6)
{
    for (t in 1:(n-1))
    {
        N9.m[t+1,r] <- s5*(1-h2.2.spm[t+1,r])*(1-h2.2[t+1,r])*(1-h.WG[t])*(1-h1.nm[t]) * N8[t,r]
        log.N9.m[t+1,r] <- log(N9.m[t+1,r] + eps) - 0.5/tau.s
        N9[t+1,r] ~ dlnorm(log.N9.m[t+1,r],tau.s )
    }
}

# Observation equations on Returns (pseudo-likelihood)
# -----
# -----

for (r in 1:6)
{
    for (t in 1:(n-1))
    {
        # Returns 1SW
        log.N6[t,r] <- log(N6[t,r])
        R1sw.m[t,r] ~ dlnorm(log.N6[t,r],log.R1sw.tau[t,r])
        res.1[t,r] <- (R1sw.m[t,r] - N6[t,r])/(R1sw.m[t,r] + 0.1)
    }

    # Returns 2SW
    for (t in 1:n)
    {
        log.N9[t,r] <- log(N9[t,r])
        R2sw.m[t,r] ~ dlnorm(log.N9[t,r],log.R2sw.tau[t,r])
        res.2[t,r] <- (R2sw.m[t,r] - N9[t,r])/(R2sw.m[t,r] + 0.1)
    }
}

# Catches at sea
# -----
# -----

# Mature fish
for (t in 1:n)
{
    log.C1.m.tot[t] <- log(C1.m.tot[t] + eps) - 0.5/tau.C1
    Cobs.5.1[t] ~ dlnorm(log.C1.m.tot[t], tau.C1)
    res.h1.m[t] <- (Cobs.5.1[t] - C1.m.tot[t])/(Cobs.5.1[t] + 0.1)
}

```

```

log.C1.spm.tot[t] <- log(C1.spm.tot[t] + eps) - 0.5/tau.C1
Cobs.5.2[t] ~ dlnorm(log.C1.spm.tot[t], tau.C1)
res.h1.spm[t] <- (Cobs.5.2[t] - C1.spm.tot[t])/(Cobs.5.2[t] + 0.1)
}

# Non mature fish
for (t in 1:n)
{
  log.C1.nm.tot[t] <- log(C1.nm.tot[t] + eps) - 0.5/tau.C2
  Cobs.8.1[t] ~ dlnorm(log.C1.nm.tot[t], tau.C2)
  res.h1.nm[t] <- (Cobs.8.1[t] - C1.nm.tot[t])/(Cobs.8.1[t] + 0.1)

  log.C.WG1.tot[t] <- log(C.WG1.tot[t] + eps) - 0.5/tau.C2
  Cobs.8.2[t] ~ dlnorm(log.C.WG1.tot[t], tau.C2)
  res.h.WG[t] <- (Cobs.8.2[t] - C.WG1.tot[t])/(Cobs.8.2[t] + 0.1)
}

for (t in 2:n)
{
  log.C2.tot[t] <- log(C2.tot[t] + eps) - 0.5/tau.C2
  Cobs.8.3.other[t] ~ dlnorm(log.C2.tot[t], tau.C2)
  res.h2[t] <- (Cobs.8.3.other[t] - C2.tot[t])/(Cobs.8.3.other[t] + 0.1)

  log.C2.lab[t] <- log(C2.lab[t] + eps) - 0.5/tau.C2
  Cobs.8.3.lab[t] ~ dlnorm(log.C2.lab[t], tau.C2)
  res.h2.lab[t] <- (Cobs.8.3.lab[t] - C2.lab[t])/(Cobs.8.3.lab[t] + 0.1)

  log.C2.spm.tot[t] <- log(C2.spm.tot[t] + eps) - 0.5/tau.C2
  Cobs.8.4[t] ~ dlnorm(log.C2.spm.tot[t], tau.C2)
  res.h2.spm[t] <- (Cobs.8.4[t] - C2.lab[t])/(Cobs.8.4[t] + 0.1)
}

# Initialisation of the loop on t
# -----
# -----
# Initialisation of the number of smolts not generated by the model
# Initialisation for all smolts that are not generated by the dynamics
# Starting from credible values of number of eggs Eggs
# drawn in Uniform distribution in the log scale
# -----
for (r in 1:6)
{
  for(i in 1:(nSm[1]+1))
  {

# Realistic prior for the number of eggs (specific to each region)
# Bounds of uniform in log-scale are calculated in the data block

log.N1.pr[i,r] ~ dunif(min.log.N1[r],max.log.N1[r])
N1.pr[i,r] <- exp(log.N1.pr[i,r])

# Then Number of juveniles and of smolts is produced with the same model

log.N2.m.pr[i,r] <- log(N1.pr[i,r]*s1) - 0.5/tau.s1
N2.pr[i,r] ~ dlnorm(log.N2.m.pr[i,r],tau.s1)

```

```

# A very informative Dirichlet distribution for the proportion of smolts age
# Equivalent to the information provided by a sample of size N.sample[r]

    for(k in 1:nSm[r])
    {
    mu.psm.pr[i,k,r] <- psm[k,r]*N.Sample
    }

    psm.stoch.pr[i,1:nSm[r],r] ~ ddirich(mu.psm.pr[i,1:nSm[r],r])

    for (k in 1:nSm[r])
    {
    log.Sm.m.pr[i+k+1,k,r] <- log(psm.stoch.pr[i,k,r]*N2.pr[i,r] + eps)-0.5/tau.psm
    N2.c.pr[i+k+1,k,r] ~ dlnorm(log.Sm.m.pr[i+k+1,k,r],tau.psm)
    }
}

# Décalage d'indice pour réaffecter les inits aux variables d'état du modèle

    for (k in 1:nSm[r])
    {
    N2.c[1,k,r] <- N2.c.pr[1+(nSm[r]+1),k,r]
    }

    for (k in 1:nSm[r])
    {
        for (kk in k:nSm[r])
        {
        N2.c[k+1,kk,r] <- N2.c.pr[k+1+(nSm[r]+1),kk,r]
        }
    }
}

# end initialisation number of smolts not generated by the model
# -----
# Other variables

for (r in 1:6)
{
min.log.N4[r] <- 7
max.log.N4[r] <- 17
log.N4.pr[1,r] ~ dunif(min.log.N4[r], max.log.N4[r])
N4[1,r] <- exp(log.N4.pr[1,r])

min.log.N9[r] <- 4
max.log.N9[r] <- 15
log.N9.pr[1,r] ~ dunif(min.log.N9[r], max.log.N9[r])
N9[1,r] <- exp(log.N9.pr[1,r])
}

} # end model

```

	Diplôme : Ingénieur Agronome Spécialité : Halieutique Spécialisation / option : Ressources et Ecosystèmes Aquatiques Enseignant référent : Didier Gascuel
Auteur(s) : Maxime Olmos Date de naissance* : 14/05/1990	Organisme d'accueil : Agrocampus Ouest Adresse : 65, rue de St-Brieuc, 35000 Rennes
Nb pages : 58 Annexe(s) : 18 pages	Maître de stage : Etienne Rivot
Année de soutenance : 2015	
Titre français : Déclin de l'abondance des populations de saumons dans l'Atlantique Nord : vers une reconsidération des modèles d'évaluation de stock afin d'explorer les mécanismes écologiques en lien avec ce déclin.	
Titre anglais : Decline in the abundance of Atlantic salmon population in the North Atlantic: Rethinking stock assessment models and exploring ecological mechanisms	
Résumé : Le saumon Atlantique a subi un important déclin au cours du dernier siècle et sur l'ensemble de son aire de répartition. Ce déclin généralisé a été particulièrement étudié durant ces dernières années mais aucun travail n'a analysé cette chute d'abondance à travers un modèle intégré de cycle de vie. Ce travail repose sur une approche de modélisation hiérarchique Bayésienne de dynamique de la population de saumon développée par F. Massiot-Granier (2014) à l'échelle 8 régions du complexe Sud Européen. Nous proposons dans cette étude une extension de cette approche au complexe Nord-Américain. L'analyse conjointe des deux complexes fournit une vision globale de la dynamique de la population de saumon dans l'Atlantique Nord permettant de comprendre les mécanismes démographiques et écologiques contrôlant cette dynamique. L'analyse de tendances communes dans les séries temporelles des traits de vie (survie durant les premiers mois en mer et probabilité de maturer dès la première année passée en mer) suivant les 14 régions étudiées (6 en Amérique du Nord et 8 en Europe du Sud), est utilisée pour quantifier la cohérence spatiale des tendances temporelles de ces traits de vie des populations de saumon d'Atlantique Nord. Les résultats mettent en évidence un déclin de la survie marine et une augmentation de la probabilité de maturer, communs à toutes les régions d'Amérique du Nord et d'Europe du Sud. Les séries temporelles de taux de survie sont corrélées négativement avec l'OAM, un proxy de la température moyenne de la surface de l'océan dans l'Atlantique Nord. Cette étude à l'échelle de l'Atlantique Nord suggère fortement une réponse commune des populations de saumon à des changements globaux, impactant ces populations durant la phase marine, où le réchauffement des océans auraient un impact négatif sur les populations via des mécanismes bottom-up.	
Abstract: Atlantic salmon, have undergone a major decline over the past century and over their entire distribution area. This widespread decline received considerable attention in recent years but most of those studies analyze trends in abundance, without integrating data in a stage-based life cycle model. The present work is built on the Bayesian hierarchical modelling approach of the population dynamics for 8 stock units in Southern Europe developed in the thesis of F. Massiot-Granier (2014). We provide an extension to the modelling approach to the 6 stock units considered in North America. Taken together, results provide a big picture of A. salmon population dynamics in the North Atlantic that improves the understanding of the ecological and demographic mechanisms controlling population dynamics. Analyses of the common patterns in the time series of key life series traits (survival during the first months at sea and probability of maturing the first year at sea) among the 14 stock units in North America (6) and S-Europe (8) are used to quantify the spatial coherence in the time trends of those two key life history traits among populations in the North Atlantic. Results provide evidence for a decline in the marine survival and for an increase in the maturing probability, common to all stock units in N-America and S-Europe. Time series of marine survival are negatively correlated with the AMO, a proxy of average SST in the North Atlantic. Taken together, results strongly suggest a common response of population to large scale environmental changes impacting salmon population during the marine phase, with warming oceanic conditions having a negative impact on populations through a bottom-up mechanism.	
Mots-clés : Saumon Atlantique, multi-population, large échelle, modèle hiérarchique Bayésien, modèle de cycle de vie intégré, changement climatique	
Key Words: Atlantic salmon, multi-population, large scale, hierarchical Bayesian model, integrated cycle, climate change	

