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**Contribution to the modeling of Atlantic salmon (*Salmo salar*) population  
dynamics at the scale of stock complexes:**

**Meta-analysis of freshwater survival**

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## Abstract

A meta-analysis of the Atlantic salmon freshwater survival was carried out, in order to improve the modeling of the population at the scale of stock complexes. Time series of eggs-to-smolts data on 21 index rivers across the A. Salmon repartition area, together with several covariates associated with the index rivers, were compiled for this study. The meta-analysis was carried out through a Bayesian hierarchical model. The classical Beverton & Holt model was revisited through the explicit parameterization in terms of density dependent and density independent mortality rates. A partially exchangeable hierarchical model was built to incorporate covariates (such as the longitude and the latitude) to capture part of the between rivers variability. This approach offers an efficient framework to predict the parameters of the density-dependent survival (and the associated uncertainty) for any new river for which the associated covariates latitude, longitude, wetted area and mean age of smolts are known. Outcomes of this study were used as prior information about the freshwater productivity in a full age-structured life-cycle model built for East Scotland. This provides an estimate of the time series of A. Salmon marine survival rate for this stock complex.

## Résumé

Une méta-analyse de la survie en eau douce du saumon Atlantique a été développée pour améliorer la modélisation de la population à l'échelle de complexes de stocks. Des séries temporelles de données œufs-smolts provenant de 21 rivières-ateliers de l'aire de répartition du saumon Atlantique, associées à plusieurs covariables caractérisant les cours d'eau, ont été rassemblées pour mener cette étude. La méta-analyse a été développée à travers un modèle hiérarchique Bayésien. Le modèle de Beverton & Holt classique a été revisité par une reparamétrisation en termes de taux de mortalité densité-dépendant et densité-indépendants. Un modèle hiérarchique partiellement échangeable a été construit pour intégrer des covariables (comme la longitude et la latitude) pour capturer une part de la variabilité inter-rivière. Cette approche offre un cadre efficace pour prédire les paramètres de la survie densité-dépendante (et l'incertitude associée) pour n'importe quelle nouvelle rivière pour laquelle sont connues la latitude, la longitude, la surface et l'âge moyen des smolts. Les sorties de cette études ont été utilisées en tant qu'information a priori de la productivité en eau douce dans un modèle de cycle de vie structuré en âge pour l'Écosse-Est. Cela fournit une estimation de la série temporelle du taux de survie en mer du saumon Atlantique pour ce complexe de stock.

## Résumé étendu en français

La plupart des évaluations de stock de population de poissons mise en œuvre impliquent souvent des hypothèses fortes et des approximations qui ne sont pas compatibles avec les connaissances biologiques disponibles pour les espèces. De plus, l'incertitude autour des estimations ne sont pas prises en compte explicitement. Pour améliorer les évaluations, le projet européen FP7-Ecoknows a été créé. Son objectif est d'améliorer l'incorporation des processus biologiques connus dans les modèles d'évaluation.

L'un des stocks étudiés dans le cadre du projet Ecoknows est le Saumon Atlantique. Son évaluation se réalise à large échelle et porte sur la totalité du cycle de vie. Les approches développées actuellement (notamment l'approche PFA (Potter et al. 1998)) se concentrent essentiellement sur les processus en mer à l'échelle de grand complexe de stock (ensemble des populations issues d'Europe ou ensemble des populations issues d'Amérique du Nord) et ne s'intéressent pas aux spécificités de la phase en eau douce (de l'éclosion des œufs à la dévalaison des smolts qui retournent en mer), en particulier le phénomène de densité-dépendance. Pourtant, chaque rivière dans laquelle se développe les jeunes individus répond à des conditions environnementales différentes (Prévost et al. 2003), se traduisant par des dynamiques de survies variables au sein d'un même complexe de stock (Chaput et al., 1998; Metcalfe & Thorpe, 1990; Gibson & Myers, 1988).

Ce stage avait donc pour objectif de modéliser explicitement la survie de l'œuf au smolt en prenant compte de la densité-dépendance. Des informations régionales ont été intégrées pour affiner la perception du processus. Le modèle reste toutefois utilisable à plus large échelle (décision de gestion et prédiction).

Un jeu de données regroupant les séries issues de 21 rivières-ateliers européennes et américaines a été rassemblé grâce aux réseaux du CIEM (Conseil International pour l'Exploration de la Mer) et Ecoknows. Les informations nécessaires à l'étude étaient :

- Une estimation du niveau d'abondance d'œufs déposés chaque année
- Une estimation du nombre de smolt dévalant et de leur décomposition en âge (pour pouvoir retrouver l'année de ponte)
- Les informations concernant la rivière (localisation, surface, ...)

Un modèle de survie de la phase eau douce a été mis en place. Il décompose la mortalité en une part mortalité indépendante et un élément densité-dépendant en adaptant une démarche de Quinn & Deriso (1999). Ces deux taux de mortalité sont supposés constants sur la totalité de la phase en rivière. Il permet d'estimer l'abondance de smolts correspondant à une dépose d'œufs donnée, en connaissant simplement la localisation de la rivière (latitude et complexe de stock (Europe ou Amérique)), sa surface et l'âge moyen des smolts du cours d'eau (approximation de la durée de la phase eau douce).

Ce modèle a été intégré dans une approche Bayésienne hiérarchique (similaire aux modèles développés dans Michielsens & McAllister, 2004 ou Prévost et al., 2001). Le cadre Bayésien consiste en une approche probabiliste de la relation de survie. L'incertitude autour de l'estimation est alors intégrée explicitement. L'approche hiérarchique correspond à intégrer à l'étude un lien entre rivières. On ne considère ni les rivières comme indépendantes, ni totalement comparables en regroupant toutes les données au même niveau. On va plutôt supposer que certaines caractéristiques des rivières sont comparables et peuvent être tirés dans des lois de probabilité communes (existence de mécanismes commun à toute l'espèce, quelque soit la rivière), tout en autorisant la variabilité inter-rivière (spécificités régionales).

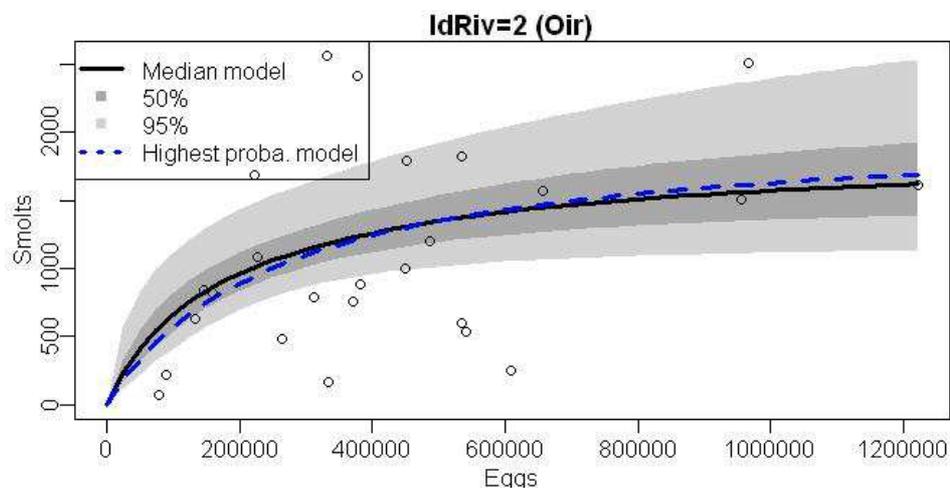
Cette approche permet d'intégrer explicitement l'incertitude à l'étude et rend possible la prédiction des paramètres à une nouvelle rivière où aucune données n'est disponible à travers l'approche hiérarchique (Prévost et al., 2003). Il suffit de connaître les covariables qui conditionnent l'estimation des paramètres dans le modèle.

Le modèle établi prend compte :

- D'une relation entre le taux de mortalité densité-dépendant et la latitude et la longitude
- D'une autocorrélation temporelle de rang un dans les résidus

La convergence du modèle, la sensibilité des résultats aux conditions initiales et l'échangeabilité des rivières ont été vérifiés.

Le modèle permet, pour chaque rivière, de déterminer une relation de survie de l'œuf au smolt (Figure 1) :



*Figure 1: Exemple de fonction de survie en eau douce estimée par le modèle pour la rivière Oir (France). Sur les données disponibles (rond) sont représentés les modèles médian (ligne noire pleine) et le modèle le plus probable (pointillés bleus) et les limites dans lesquelles se trouve le modèle avec une probabilité de 50% (zone gris foncée) et 95% (zone gris clair).*

Pour évaluer l'impact des résultats, la relation de survie de l'œufs aux smolts a été intégré dans un modèle de cycle de vie complet, développé par Félix Massiot-Granier. L'impact de l'intégration de la densité-dépendance est considérable, conduisant le modèle à estimer une survie du smolt au saumon avant exploitation 10 fois plus importante. L'intégration des connaissances biologiques modifie radicalement la vision de la dynamique de population offerte par le modèle de cycle de vie.

L'approche présentée permet une amélioration notable de la modélisation de la survie en eau douce par rapport aux modèles n'intégrant pas de densité-dépendance utilisés habituellement. Utilisant un nombre restreint de covariables, elle prend en compte des spécificités régionales tout en restant compatible avec une étude à large échelle : une prédiction des paramètres du modèle est possible pour toute autre rivière et l'extrapolation à une région est possible.

Toutefois, il faut noter que l'incertitude autour des données n'a pas été pris en compte et que des régions ne sont pas étudié à travers ce travail. De plus, l'hypothèse de constance des taux de mortalité sur l'ensemble de la phase eau douce est très forte et l'intégration de taux de mortalité fonction du temps doit être testée.

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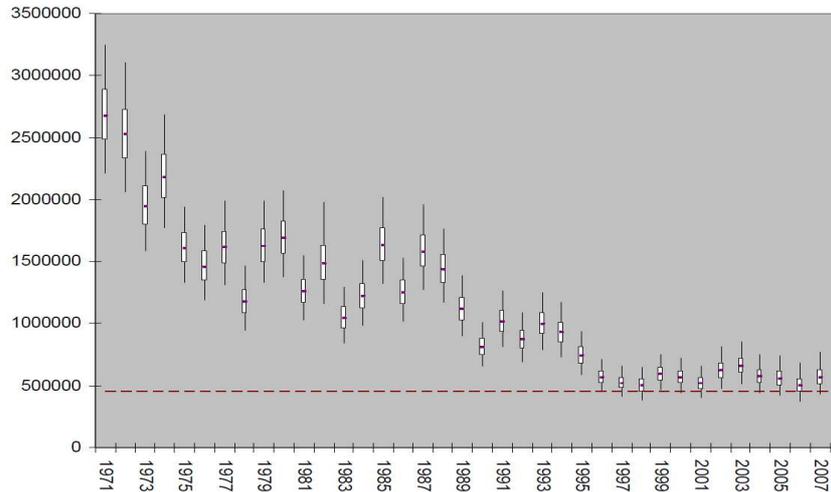
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## 1. Introduction

Over the past two decades, the abundance of wild Atlantic salmon (*Salmo salar* L.) has declined in the North Atlantic (ICES 2010; **Figure 1**). Declines have occurred in both the Northwest and Northeast sides of the Atlantic Ocean, and have been more severe in the southern portions of the species range.



*Fig. 1: Southern Northeast salmon stock abundance of non-maturing individuals after 1 year at sea (Pre-Fishery Abundance) estimated by the ICES WG NAS from 1971 to 2008 (source: ICES 2010).*

Anadromous A. Salmon occupies two distinct habitats during its lifetime: freshwater and marine (**Figure 2**). Reproduction occurs in freshwater. Eggs hatch under the gravels and juveniles (parr) develop in the rivers and migrate to the sea as smolts. The mean age at smoltification is mostly dependent upon the growth opportunity in the river then is largely climate driven (Gibson and Myers, 1988; Metcalfe and Thorpe, 1990; Hutching and Jones, 1998; Bal et al. 2011). For instance, salmon can smoltify after only one year in France, whereas they have to spend at least three years in the river before joining the sea in some Canadian rivers. As a general rule, fish spent one or two years at sea before migrating back to their home water for spawning (Hutchings and Jones, 1998). Although semelparity is the general rule, some populations have non negligible proportion of repeat spawners.

A. Salmon from eastern North America and the northeast Atlantic countries of Europe undertakes feeding migrations to the North Atlantic and has the potential to be harvested in the fisheries at West Greenland and around the Faroes islands (**Figure 3**). These mixed stock high seas fisheries were of sufficient concern that the ICES WGNAS (International Council for the Exploration of the Sea - Working Group on North Atlantic Salmon) (ICES 2010) has proposed modelling tools (the Pre Fishery Abundance – PFA - modelling approach (Rago et al. 1993; Potter et al. 1998; Chaput et al. 2005)) for:

- Providing stock assessment and evaluating the change in stock productivity at the scale of stock complexes in the North Atlantic;
- Providing catch advice in such marine mixed stock fisheries. Management advice, in a currency of harvest tonnage, is predicated on a forecast of salmon abundance prior to the fisheries (= the PFA) and the management of the harvests with the objective of achieving the spawner requirements (biomass limits) for the contributing stocks in both sides of the Atlantic Ocean.

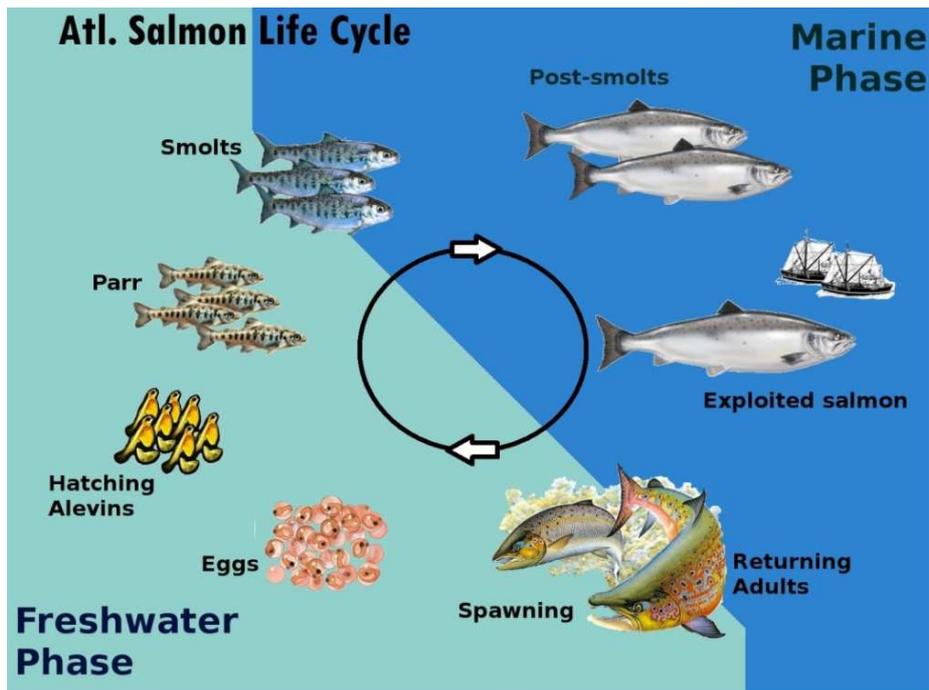


Fig. 2: Atlantic salmon life-cycle

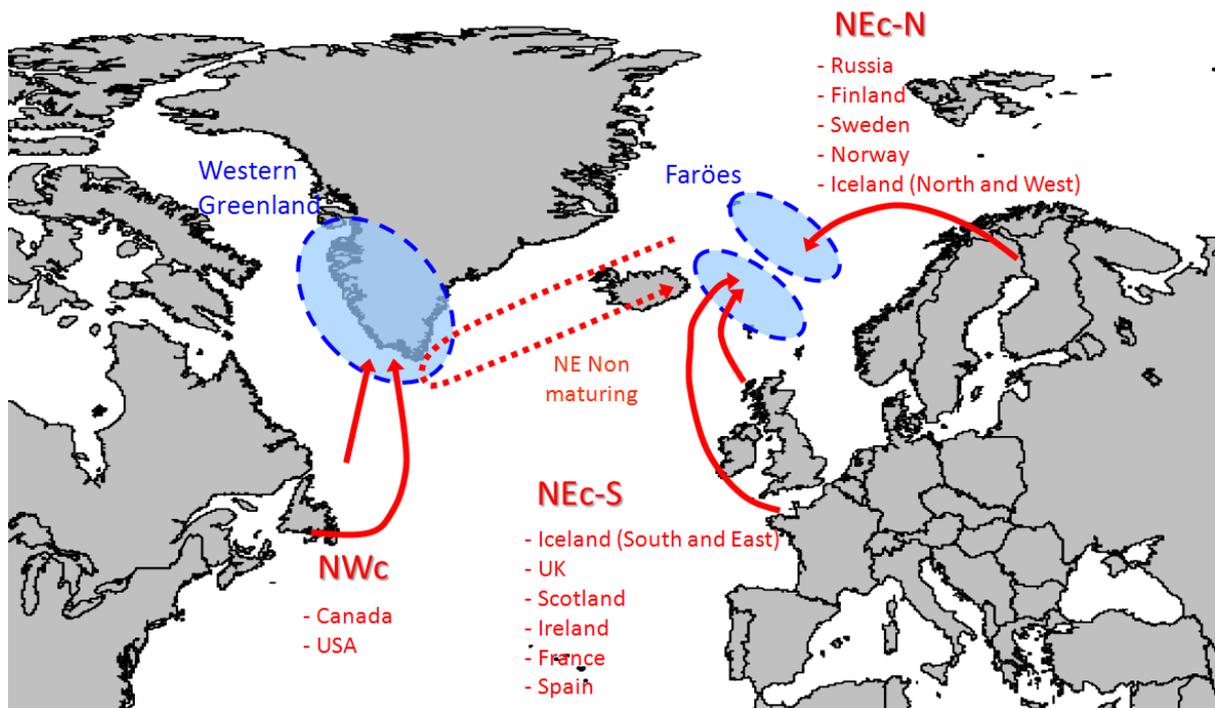


Fig. 3: Stock complexes and migration patterns. Blue areas are fishing zones where adult A. Salmon are exploited. The Northwest complex's (NWc) individuals go to Western Greenland and both Northern Northeast complex (NEc-N) and Southern Northeast complex (NEc-S) salmon are migrating around the Farøes.

The research described in this report has been carried out in the framework of the A. Salmon case study of the FP7-ECOKNOWS (<http://www.ecoknows.eu/>) research project. The current PFA modelling approach has several drawbacks, and the project falls into the context of improving the modelling tools to provide a better understanding of the A. Salmon population dynamics in the Atlantic Ocean. The purpose of the ECOKNOWS project is to improve the model in four directions:

(1) Building a stage-structured life cycle approach

The assessment model will be embedded into a full stage-structured life cycle model. Following cohorts through river parr and smolt classes, sea ages and returns, will offer a more specific framework for following strength of age classes through rather than bulking them together just as it is done in the current PFA modelling approach.

(2) Separating out the freshwater and marine phase

The model structure in its current form hampers the use of the ecological knowledge and data available on the freshwater phase of A. Salmon life cycle. In particular, both the marine and the freshwater phases of the life cycle are collapsed into one single productivity parameter. The approach does not allow a determination of whether the change in productivity has occurred in freshwater, in the first year at sea or both. Although a large amount of information lends support to the hypothesis that mortality has increased in the marine phase (Friedland et al. 2000; 2003; Peyronnet et al. 2007; 2008; Hogan and Friedland 2010), the freshwater juvenile phase is a critical stage in the life cycle. There is ample evidence from river-specific studies that spawning stock is an important conditioning variable of recruitment abundance expressed as a density-dependent response during the freshwater stages (Kennedy and Crozier 1993; Chaput et al. 1998; Grant & Imre, 2005; Imre et al., 2005; Ward et al., 2009).

(3) Accounting for regional specificities within large stock complexes

The model will be designed at the scale of three large stock complexes adopted by ICES WGNAS (Southern North East, Northern North East, and North West), each composed by several countries or regions (for instance, the Southern NE complex will consist in 6 components with their specific dynamics: France, UK-E&W, UK-N, Irl, Scot, Icl) (ICES 2010) (see **Figure 3**), and will assimilate 40 years of data (1970-2010). The objective is to explore long term trends and climate influence on key population parameters shared by several population components, such as marine survival, together with time and spatial variability of region-specific life history traits such as the ones characterizing the freshwater phase of the life cycle.

(4) Embedding the approach in a Bayesian state space modelling approach

The model will be built in a Bayesian state space modelling approach so as to assimilate various sources of information and to account for several sources of uncertainty and variability in the modelling, inference and forecasting (Rivot et al. 2004; Thomas et al. 2005; Buckland et al. 2007; Cressie et al. 2009; Rivot and Parent, 2012).

In this context, the objective of this Master Thesis was to improve the modeling of the density dependent mortality process that occurs during the freshwater phase, between eggs and smolts. To raise this challenge, the available Stock (egg deposition) and Recruitment (smolts production) time series collected from the index rivers in both side of the A. Ocean have been compiled. A meta-analysis was carried out, the outcome of which could be used as informative prior information about the freshwater productivity to improve life cycle models.

The meta-analysis has been carried out through a Bayesian hierarchical model (BHM) (Rivot and Prévost 2002; Parent and Rivot 2012). BHMs have already been proved useful for meta-analysis of stock-recruitment data (Liermann and Hilborn 1997; Chen and Holtby 2002; Crozier et al. 2003; Prévost et al. 2003; Michielsens et McAllister 2004; Forrest et al. 2010). The BHM improves inferences by borrowing strength from data rich to data poor rivers (Myers 2001; Prévost et al. 2003), and to extrapolate the results where no SR data are available (Prévost et al. 2003; Michielsens and McAllister 2004). Posterior predictive distributions of the SR parameters drawn from the meta-analysis of Michielsens and McAllister (2004) are already used in stock assessment models in the Baltic (Michielsens et al. 2008), and the predictions conditioned by the latitude based on the methodology developed by Prévost et al. (2003) are currently used in national stock assessments such as in Ireland (Ó'Maoiléidigh et al. 2004).

In this work, we developed a Bayesian hierarchical model to carry out a meta-analysis of eggs-smolts relationships for A. Salmon at the scale of the three stock complexes mentioned above. The originality of the approach outlined in this paper is threefold:

- (1) – An extensive data set was compiled. Data from 20 index rivers with eggs-smolts data in both east and west coasts of the Atlantic Ocean were collected and analyzed.
- (2) – The focus is on the modeling of the eggs-smolts survival rate; eggs-eggs stock-recruitment data series available for many other salmon rivers were then excluded.
- (3) – It is based on an original parameterization in term of survival rates, which makes explicit the use of covariates such as mean age of smolts and riverine surface area in both modeling and predictions.

The report is organized as follow. In the second section, the data set is presented and the model is detailed. Then, the main results are described before discussing some limits of the approach and further implications of this work. Lots of complementary information could be found in the Appendix.

## 2. Material and methods

### 2.1/ Data

Eggs to smolts data series from 21 rivers across the distribution area (12 from NWc, 7 from NEc-S and 2 from NEc-N) were gathered and combined in the modeling approach (**Table 1**; **Figure 4**; **Appendix 1**). It is worth noting that no previous studies have combined such extensive data set on eggs-to-smolts dynamics for A. Salmon.

This analysis is data demanding but many index rivers in which Atl. salmon population survey is conducted are excluded from this analysis because population survey does not include monitoring of the smolts production. For instance, the Nivelles River (France, see Brun et al., 2011) was not used here because only 0+ juveniles (parr) are monitored through electrofishing, and no information is available for smolt abundance within this river. In Ireland, eggs-to-eggs stock-recruits models have been built for many rivers but for which only adults are monitored (Ó'Maoláidigh et al., 2004).

Data for 21 rivers have been provided by scientists responsible for data collection, or extracted from publications (see **Appendix 1** for details (contact, literature sources ...)). Data from the river Imsa were extracted from a figure published in Jonsson et al, 1998. Data about the abundance of each available cohort from eggs to migrating smolts were prepared as follows:

- Total eggs deposition for each cohort was given from estimates of the number of returning spawners (most often using counting fences or fishways), combined with estimates of proportion of sea ages classes, proportion of females and fecundity for each sea age class. These data are highly river specific and may also depend upon the cohort for each river.
- The total smolt production associated with each cohort (also from counting fence or fishways), together with the age-structure of the smolts, were estimated. The age structure of smolts run is also highly river and cohorts specific. For instance in France, smolts migrating year  $y$  are associated with the cohort corresponding to eggs spawned year  $y-2$  (for 1-years old smolts) or  $y-3$  (for 2-years old smolts).
- Associated covariates for each river (See **Table 1**): localization (see **Figure 4**), river surface, lacustrine part in the wetted area accessible to salmon, etc., all drawn from associated publication or grey literature.

Uncertainty in estimation of the number of eggs spawned and of the number of smolts associated with each cohort was ignored.

When the smolts number is missing for some migrating years, this can preclude reliable estimation of the number of smolts associated with several cohorts (for instance in France, smolts migrating year  $y$  could be related to cohorts associated with eggs spawned at year  $y-2$  and  $y-3$ ). Then, only the longest complete part of the data sets was used. This was the case for the Vesturdalsa, the North Esk and the St-Jean Rivers.

The Naggaragus data series has been excluded from the analysis because the numbers of 0+ stocked exceeded the number of eggs spawned by natural reproduction in many years of the time series, and no sufficient additional information about the survival of 0+ stocked was provided (see details in the **Appendix 1**).

*Table 1: General characteristics of the 21 index rivers used in the project*

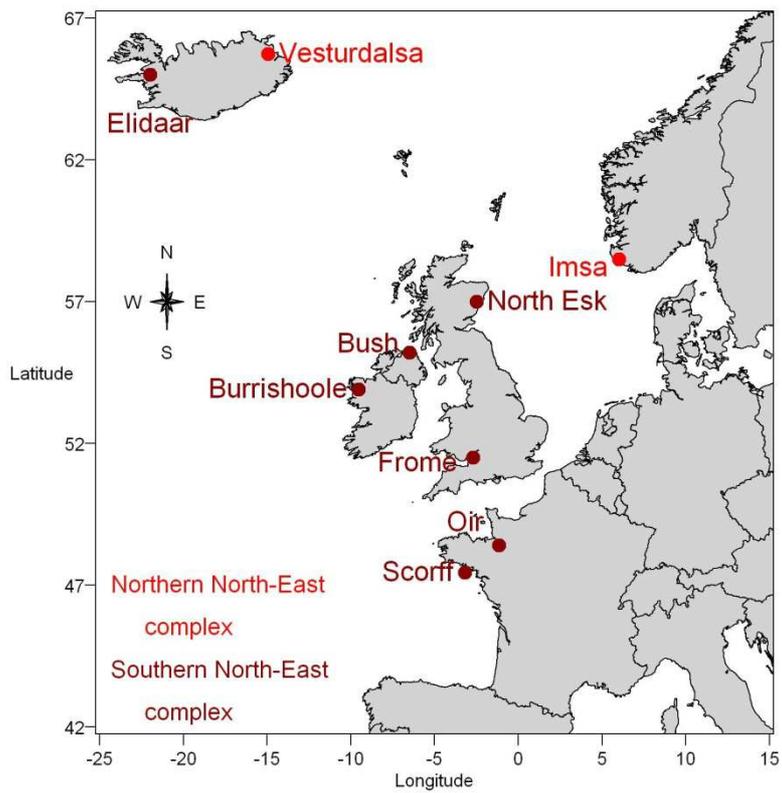
<b>IdRiv</b>	<b>River</b>	<b>Stock Cplx</b>	<b>Country/Region</b>	<b>Lat (°N)</b>	<b>Long (°E)</b>	<b>AWA* (fluvial) (.10<sup>4</sup> m<sup>2</sup>)</b>	<b>AWA* (lac.) (.10<sup>4</sup> m<sup>2</sup>)</b>	<b>Mean Smolt Age</b>	<b>Nb Obs</b>	<b>Obs Period</b>
1	Scorff <sup>+</sup>	NEc S	Fr (Brittany)	47.5	-3.2	70	0	1.20	17	1995 - 2008
2	Oir <sup>+</sup>	NEc S	Fr (Normandy)	48.5	-1.2	5	0	1.14	27	1985 - 2009
3	Vesturdalsa <sup>+</sup>	NEc N	Icl (North East)	65.7	-15	20	0	3.57	16	1985, 1986, 1990 – 2003
4	Elidaar <sup>+</sup>	NEc S	Icl (South West)	65	-22	50	0	2.65	21	1985 – 2004
5	North Esk <sup>+</sup>	NEc S	Scot (East)	57	-2.5	260	8	2.14	15	1987 – 1998, 2003 – 2005
6	Burrishoole <sup>+</sup>	NEc S	Irl (West)	53.9	-10	12.5	441	1.87	28	1979 - 2006
7	Frome <sup>+</sup>	NEc S	UK	51.5	-2.7	61	0	1.02	8	2002 – 2009
8	Bush <sup>+</sup>	NEc S	UK	55.2	-10	85	0	1.73	27	1973 – 2007
9	Trinité <sup>+</sup>	NWc	Ca (Québec)	49.4	-67	211	0	2.99	27	1980 – 2006
10	St-Jean <sup>+</sup>	NWc	Ca (Québec)	48.8	-64	308	0	3.40	22	1985 – 1991, 1994 – 2006
11	NE Brook Trepassey <sup>+</sup>	NWc	Ca (Newfoundland)	46.8	-53.4	6	0	3.61	22	1984 – 2005
12	Western Arm Brook <sup>+</sup>	NWc	Ca (Newfoundland)	51.2	-56.8	29	2017	3.75	35	1971 – 2005
13	Campbellton <sup>+</sup>	NWc	Ca (Newfoundland)	49.3	-54.9	57	4037	3.45	12	1993 – 2004
14	Conne <sup>+</sup>	NWc	Ca (Newfoundland)	47.9	-55.7	132	3187	4.28	20	1986 – 2005
15	Rocky <sup>+</sup>	NWc	Ca (Newfoundland)	47.2	-53.6	108	2191	2.21	21	1987 – 2007
16	Pollet <sup>*</sup>	NWc	Ca (Newfoundland)	46	-10	36	0	2.12	8	1953 – 1960
17	Nashwaak <sup>+</sup>	NWc	Ca (NewBrunswick)	45	-66.6	512	0	2.24	12	1995 – 2006
18	Imsa <sup>*</sup>	NEc N	Norway	58.5	-10	1	1536	1.94	15	1976 – 1990
19	Little Codroy <sup>*</sup>	NWc	Ca (Newfoundland)	47.8	-10	39	0	2.64	7	1954 – 1960
20	Big Salmon <sup>*</sup>	NWc	Ca (Sc-Fundy)	45.4	-65.4	46.5	0	2.60	4	1964 – 1967
Unused	Narraguagus <sup>+</sup>	NWc	USA (Maine)	44.5	-67.9	295	0	2.12	14	1994 – 2007

AWA\*: Accessible wetted area for Atlantic salmon.

<sup>+</sup> data provided by scientists responsible for data collection

<sup>\*</sup> data extracted from publications

River Imsa: extracted from a figure in Jonsson et al., 1998.



b.

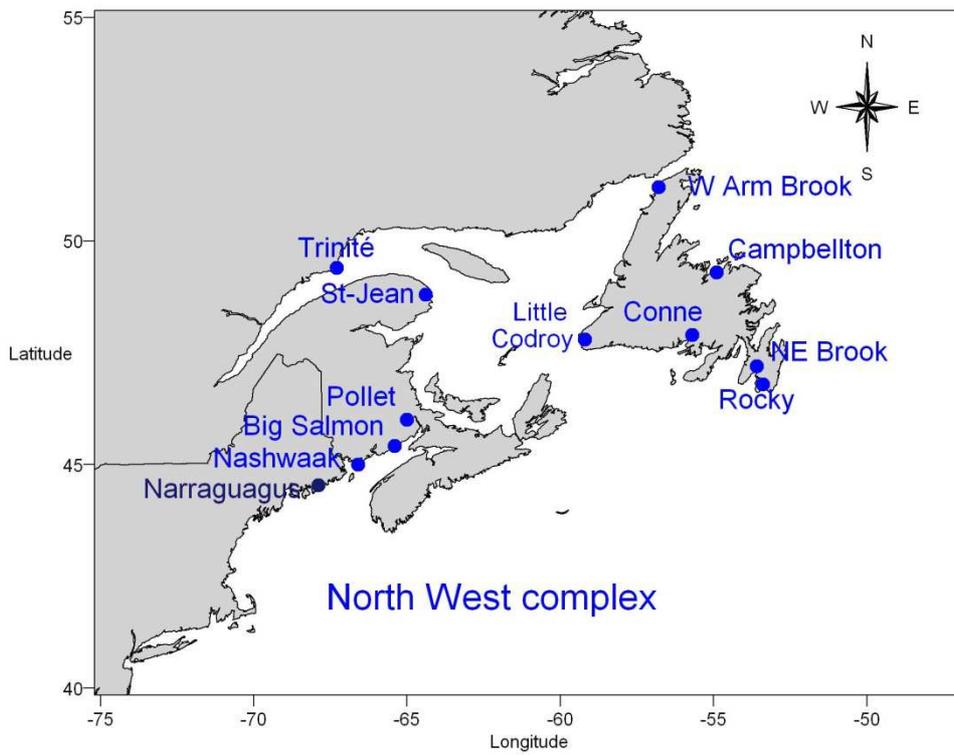
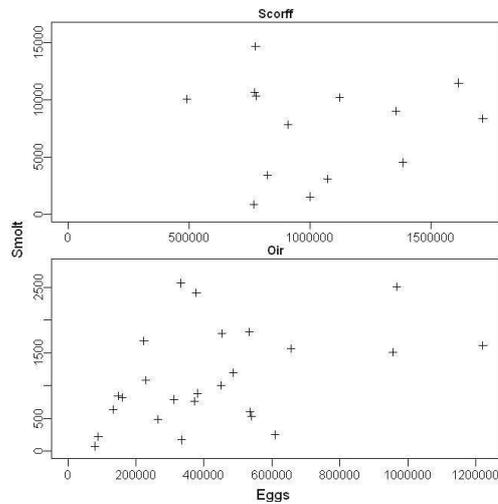


Fig. 4: Localization of the 21 rivers used in this study

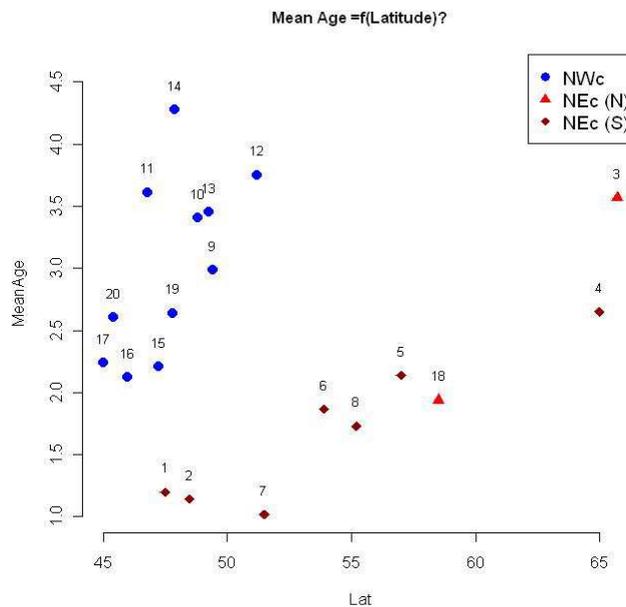
To make the data explicit, **Figure 5** presents the eggs to smolt data series for the Oir and Scorff Rivers in France. Similar data are available for all rivers (see **Appendix 1**).



**Fig. 5:** Eggs-to-smolts data series available for the two French rivers (Scorff and Oir Rivers) both eggs and smolts are in number, without any transformation.

Covariates such as the riverine wetted area or the geographical coordinate (longitude and latitude) will be key candidate factors to explain the between river variability in the eggs-to-smolts dynamics.

The increasing trend in the smolt age with latitude already described by Metcalfe & Thorpe (1990) also clearly appears on our data set (see **Figure 6**). For the same latitude, the mean age of smolts is much greater in the Western side of the A. Ocean than in the eastern side.



**Fig. 6:** Mean age of smolts of the 20 rivers used for the study as a function of the latitude of the stream.

## 2.2/ Hierarchical model for eggs-to-smolts survival

### 2.2.1 Outlines of the model

The data series for the 20 rivers (exclusion of the Naggaragus River) were jointly analyzed through a hierarchical Bayesian model. We give below the main outlines of the methodology:

- The classical Beverton & Holt (BH) density dependent survival model (or stock-recruitment model) describing the relationship between the number of eggs spawned by anadromous females and the number of smolts in the associated cohorts was used. But this model was revisited through an explicit parameterization in term of density dependent and density-independent mortality rate
- Parameters were river-specific, considered constant through time, but between-cohort stochasticity in the eggs to smolts survival rates was considered and modeled through log-normal process errors accounting for autocorrelation in the environmental noise
- A hierarchical Bayesian model was built to jointly analyze the 20 rivers. The hierarchical structure allows for between-rivers variability of the survival parameters and captures the influence of some key covariates (like latitude or complex East or West) in this variability), to improve modeling and prediction.

### 2.2.2 Eggs-to-smolts density dependent survival model

In this section, we describe the parameterization of the classical BH and Ricker models in term of density dependent and independent mortality rates. Further details about the demonstration are given in the **Appendix 2**. All equations and parameters below are river-specific, but indice  $r$  for the river was omitted in this section to simplify the presentation.

Let us assume  $N_t$  the number of individuals in a cohort at each instant  $t$  in the freshwater phase between eggs (measured at  $t=0$ ) and smolts ( $t= \Delta t$ ). Let us denote  $N_0$  the number of eggs ( $N_0=N_{t=0}$ ) and  $N_{\Delta t}$  the subsequent number of smolts ( $N_{\Delta t}=N_{t=\Delta t}$ ) with  $\Delta t$  the mean age of smolts. Let us define  $N_t^* = N_t/A$  the density at each instant  $t$ , where  $A$  is a measure of the riverine wetted area (see **Table 1**). We assume that no migration occurs. Then, only mortality impacts the abundance.

Let us now define the instantaneous per capita mortality rate (PCMR):

$$(1) \quad \frac{1}{N_t} \cdot \frac{dN_t}{dt}$$

and consider 3 alternative hypotheses to model the PCMR:

H0: The PCMR is density independent and denoted  $\delta_t$ :

$$(2) \quad \frac{1}{N_t} \cdot \frac{dN_t}{dt} = -\delta_t$$

H1: The PCMR depends upon the initial population density  $N_0^* = N_0/A$  with a density dependent mortality rate  $\gamma_t$ :

$$(3) \quad \frac{1}{N_t} \cdot \frac{dN_t}{dt} = -\delta_t - \gamma_t \cdot N_0^*$$

H2: The PCMR depends upon the population density at each instant  $t$  with a dependent mortality rate  $\gamma_t$ :

$$(4) \quad \frac{1}{N_t} \cdot \frac{dN_t}{dt} = -\delta_t - \gamma_t \cdot N_t^*$$

If the **mortality rate  $\delta_t$  and  $\gamma_t$  are considered constant through time,  $\delta_t = \delta$  and  $\gamma_t = \gamma$** , equations (2), (3) and (4) can easily be integrated over the whole duration of the freshwater phase (between  $t=0$  and  $t=\Delta t$ ) (Quinn & Deriso, 1999):

H0: Eq. (2) integrates to the classical constant mortality rate equation

$$(5) \quad N_{\Delta t} = N_0 \cdot e^{-\delta \cdot \Delta t}$$

H1: Eq. (3) integrates to a Ricker-type equation with slope at the origin  $\alpha$  and maximum recruitment  $\beta$  (see details in **Appendix A2.1**):

$$(6) \quad N_{\Delta t} = \alpha \cdot N_0 \cdot e^{-\frac{\alpha}{\beta \cdot e^1} \cdot N_0}$$

with

$$(7) \quad \begin{cases} \alpha = e^{-\delta \cdot \Delta t} \\ \beta = \frac{e^{-\delta \cdot \Delta t}}{\frac{\gamma \cdot \Delta t \cdot e^1}{A}} \end{cases}$$

or directly in terms of  **$\delta$  and  $\gamma$** :

$$(8) \quad N_{\Delta t} = N_0 \cdot e^{-\delta \cdot \Delta t - \frac{\gamma}{A} \cdot \Delta t \cdot N_0}$$

H2: Equation (4) integrates to the BH function (Beverton & Holt, 1957) with slope at the origin  $\alpha$  and maximum asymptotic recruitment (or carrying capacity)  $\beta$  (see details in **Appendix A2.2**):

$$(9) \quad N_{\Delta t} = \frac{\alpha \cdot N_0}{1 + \alpha \cdot \beta \cdot N_0}$$

with

$$(10) \quad \begin{cases} \alpha = e^{-\delta \cdot \Delta t} \\ \beta = \frac{1}{\frac{\gamma}{\delta \cdot A} (e^{\delta \cdot \Delta t} - 1)} \end{cases}$$

or directly in terms of  **$\delta$  and  $\gamma$** :

$$(11) \quad N_{\Delta t} = \frac{N_0}{e^{\delta \cdot \Delta t} + \frac{\gamma}{\delta \cdot A} \cdot (e^{\delta \cdot \Delta t} - 1) \cdot N_0}$$

Equations (8) and (11) are alternative parameterizations of the classical Ricker and BH stock-recruitment relationships with number of smolts  $N_{\Delta t}$  as a measure of recruit (hereafter denoted  $Sm$ ) and number of eggs  $N_0$  as a measure of stock (hereafter denoted  $Eg$ ). The main interests of such alternative parameterization are:

- It offers an explicit interpretation of classical Ricker and BH relationship in terms of density dependent survival process during the freshwater phase. In both Ricker and BH formulations, the slope at the origin only depends upon  $\delta$  and  $\Delta t$  whereas the carrying capacity depends upon  $\delta$ ,  $\gamma$ ,  $\Delta t$  and  $A$ .
- The parameters  $\delta$  and  $\gamma$  are comparable between rivers and between models (Ricker and BH) with no need of preliminary standardization of eggs and smolt number.
- The model explicitly introduces two main covariates, the mean age of smolts ( $\Delta t$ ) and the available production area ( $A$ ), which are highly different between rivers.

In the following, the model developments and results were derived using the BH formulation (Eq. 11) only. Indeed, both ecological and empirical analysis favors the BH relationship in modeling freshwater survival. The hypothesis underlying the BH model looks more consistent with density-dependence that occurs continuously during the freshwater phase because of competition for food and space. Moreover, Michielsens and McAllister (2004) have shown that the BH model better explain the data than the Ricker one.

### 2.2.3 Environmental stochasticity (within river variability)

For each river, between cohorts variability of the eggs-to-smolts survival rate about the average BH relationship was introduced via identically distributed logNormal errors.

$$(12) \quad Sm_t = f(Eg_t, \gamma, \delta, \Delta t, A) \cdot e^{\varepsilon_t}$$

with river specific parameters  $\delta$ ,  $\gamma$  and associated covariates  $\Delta t$  and  $A$  and  $f()$  the survival relationship defined in eq. (11).

Lag-1 autocorrelation in the time series of residuals was explicitly modeled. Indeed, first results based on a model with a priori independent logNormal errors showed a significant lag-1 auto-correlation on the distribution of residuals for most of the 20 rivers (see **Appendix 4.1**). A lag-1 autoregressive model with correlation coefficient  $\rho$  (river specific) was used to model the serial auto-correlation:

$$(12) \quad \begin{cases} \varepsilon_t = \rho \cdot \varepsilon_{t-1} + \omega_t \\ \omega_t \sim N(0, \sigma_r^2) \end{cases}$$

For each river, the initialization of the time series was made by drawing the first residual  $\varepsilon_{t=1}$  in a Normal prior distribution with the variance equal to the variance of the stationary process:

$$(13) \quad \begin{cases} \varepsilon_{t=1} \sim N(0, \sigma^*) \\ \sigma^* = \frac{\sigma^2}{1-\rho^2} \end{cases}$$

### 2.2.4 Hierarchical model

A preliminary model considering all rivers independently was run in a first approach. But because data are poorly informative for many rivers, resulting estimates of many parameters (not shown) were highly uncertain and this model was not considered further.

Rather, the data series of the 20 rivers were jointly analyzed through a hierarchical model with the latitude (continuous) and longitude (considered as a categorical covariate with two modality for the North West and North East complexes) considered as covariates to explain part of the between rivers variability.

The hierarchical structure was built for three parameters ( $\delta_r, \gamma_r, \sigma_r$ ). These parameters were assumed to be different between rivers, but drawn from common probability distributions controlled by some parameters (unknown) common to all rivers. Two levels of randomness are then distinguished: within-river variability (through the environmental stochasticity with autocorrelation in eq. (12)) and between rivers variability through the logNormal hierarchical structure. The between river variability of the parameters  $\delta_r, \gamma_r$  and  $\sigma_r$  was modeled via logNormal distributions with unknown mean and variance.

In a preliminary version of the model (not detailed), the sets of these 3 parameters were modeled as exchangeable between rivers. Regarding for these parameters, the rivers were considered a priori as a set of comparable units: Apart from the data, no insight into the phenomena causing variations in the survival relationship among rivers is available, and the difference among the data sets should not have predictable effects on the results of the analysis (Gelman et al. 1995). The exchangeability hypothesis translates into independent and identical prior distribution (iid) of the parameters:

$$(15) \quad \log(\delta_r) \sim N(E_\delta, \sigma_\delta^2)$$

$$(16) \quad \log(\gamma_r) \sim N(E_\gamma, \sigma_\gamma^2)$$

$$(17) \quad \log(\sigma_r) \sim N(E_\sigma, \sigma_\sigma^2)$$

with  $E_\delta, E_\gamma, E_\sigma$  and  $\sigma_\delta^2, \sigma_\gamma^2, \sigma_\sigma^2$  the expected mean and variance (in log scale) for  $\delta$ 's,  $\gamma$ 's and  $\sigma$ 's respectively.

Based on this preliminary version (results not shown), it was shown that a great part of the between rivers variability in the density independent mortality rate  $\delta_r$ 's could be explained by two covariates:

- The longitude, considered as a categorical variable with two modalities for the east and west coast of the North Atlantic Ocean;

- The latitude considered as a continuous variable.

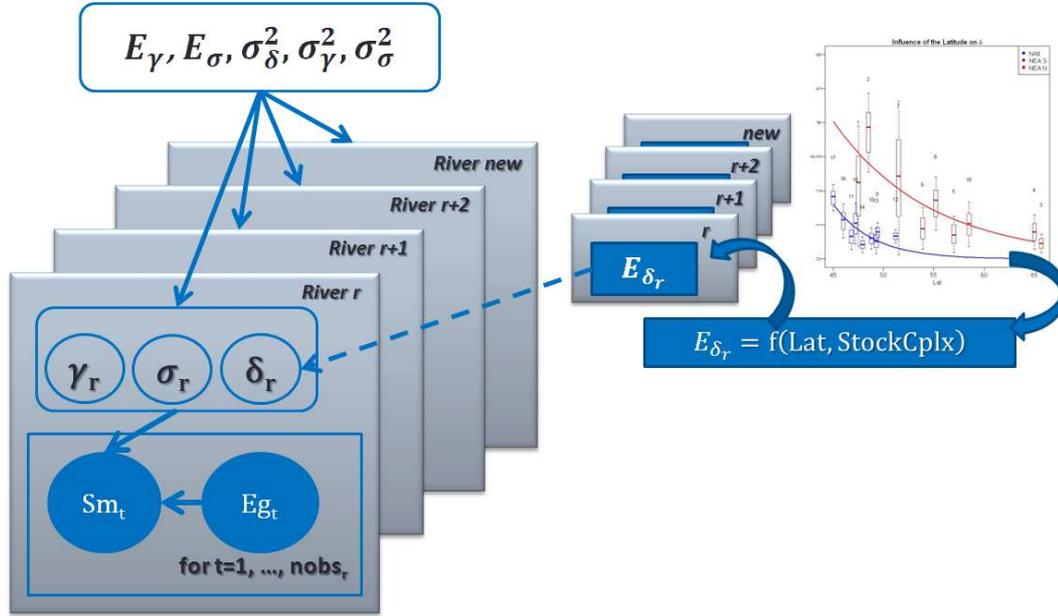
Hence, following Prévost et al. (2003) (but see also Rivot et al. 2008), a partially exchangeable model conditioned by those two covariates was built for the  $\delta_r$ 's, by considering the expected value of  $\log(\delta_r)$  for any river  $r$  depends linearly upon the latitude:

$$(15) \quad \begin{cases} E(\delta_r) = e^{\lambda_1 \cdot (Lat - \overline{Lat}_1) + \kappa_1} & \text{for } NWc \\ E(\delta_r) = e^{\lambda_2 \cdot (Lat - \overline{Lat}_2) + \kappa_2} & \text{for } NEc \end{cases}$$

with  $\lambda$  and  $\kappa$  the parameters depending upon the categorical covariate longitude ( $\lambda_1, \kappa_1$  and  $\lambda_2, \kappa_2$  for Northwest and Northeast complexes respectively) and  $\overline{Lat}$  the mean latitude of the corresponding complex; As only two rivers from Northern North-East Complex were available and that no significant difference was observed in first results, a unique relation with latitude was considered for the Northern and Southern NEc.

The lag-1 autocorrelation coefficient  $\rho_r$ 's (river specific) were modeled independently (see unsuccessful trials about a hierarchical model on the  $\rho_r$ 's in **Appendix 4.2**).

The structure of the model is summarized in the Directed Acyclic graph presented at **Figure 7**.



**Fig. 7:** Representation of the conditioning structure of the final Bayesian hierarchical structure of the model in a Directed Acyclic Graph. Nodes (empty forms) are random variables. The plain arrows represent stochastic link, i.e. the distribution of a child node depends on its parents. Dashed arrows represent deterministic links, i.e. the expected value of  $\delta$  is function of the latitude and the stock complex for each river.  $Sm_i$  and  $Eg_i$  are the series of abundance of smolts and eggs for the monitored river  $r$ . The 'new' index refers to any sparse-data river belonging to the assemblage from which the data-rich rivers are a representative sample.

Rather uninformative priors were set on all hyperparameters and the sensitivity to the choice of the prior distribution was checked by running the model with more dispersed prior distributions on the parameters (see **Table 2**).

**Table 2:** Prior used on the parameters at the top of the hierarchical structure used for both the baseline model and the prior sensitivity study.

Model parameter	Prior Distribution (baseline model)	Prior Distribution (prior sensitivity analyzes)
$\lambda_1, \lambda_2$	Normal(0, $\sigma=0.2$ )	Normal(0, $\sigma=0.6$ )
$\kappa_1, \kappa_2$	Normal(1, $\sigma=0.5$ )	Normal(1, $\sigma=1.5$ )
$\sigma(\delta)$	Unif(0,3)	Unif(0,6)
$E(\gamma)$	LogNormal(1, $\sigma=2.2$ )	LogNormal(1, $\sigma=6.6$ )
$\sigma(\gamma)$	Unif(0,3)	Unif(0,6)
$E(\sigma)$	LogNorm(-1.4, $\sigma=1$ )	LogNorm(-1.4, $\sigma=3$ )
$\sigma(\sigma)$	Unif(0,3)	Unif(0,6)
$\rho_r$	Unif(-1,1)	Unif(-1,1)

### 2.2.5 Test for exchangeability

To check for exchangeability, a leave-one-out validation test was carried out. The hierarchical analysis was run 20 different times, with 20 data sets obtained by excluding one river each time. The posterior probability distributions of the parameters from each trial were compared to assess the exchangeability of the rivers. If the different rivers are exchangeable in terms of the parameters, the exclusion of one data set should not substantially alter the posterior predictive distribution of the parameters at the top of the hierarchical structure.

### 2.2.6 Bayesian computation

Posterior distributions were estimated via Monte Carlo Markov Chain algorithms using an hybrid Gibbs sampler (Gelman et al. 2005). The software JAGS (Just Another Gibbs Sampler) was used through the R software and the package *rjags* (created by Martyn Plummer; information at <http://mcmc-jags.sourceforge.net>). The complete JAGS model is presented in **Appendix 5**. Three independent mcmc chains were run. A burn-in period of 7000 iterations was chosen and one draw every ten of 20000 additional iterations were stocked for estimating the posterior. Convergence of the mcmc algorithm was checked for all parameters through a Gelman-Rubin diagnosis with 3 chains (Gelman & Rubin, 1992).

## 2.3/ Combining the fitted BH eggs-to-smolts survival with a stage-structured life cycle model

To assess the consequences of our results on the population dynamics of A. Salmon, the predicted Beverton & Holt density-dependent survival relationship from eggs to smolts was incorporated into a stage-structured life cycle approach built to model the population dynamics at the scale of the eastern Scotland (this was done in close collaboration with Félix Massiot-Granier).

The structure of the stage-structured life cycle used is similar to the one described in Rivot et al. 2004 or Parent and Rivot, 2012 and is not detailed here.

The life cycle model was primarily designed to estimate the time series of the post-smolt marine survival during the first year at sea, as this is a highly sensible phase in the A. Salmon life cycle. In order to assess the impact of our findings on the estimates of this marine survival, the life cycle model was fitted on a 40-years time series of data by contrasting two alternative hypotheses for the eggs-to-smolts survival:

- A density independent survival rate of 0.9%
- BH density dependent survival function based on our findings and additional covariates that characterize the East Scotland. The prediction of the survival relationships at the scale of this region was based on the posterior predictive distribution of the parameters derived from the hierarchical model (detailed in section 2) and conditioned by the following covariates:
  - o Total riverine area for all salmons rivers in East Scotland : 128 459 138m<sup>2</sup>

Data were provided by Gordon Smith. The total surface was calculated by summing the riverine area of all A. Salmon rivers in the region.

- o The latitude was taken as the mean latitude between Scotland's extreme latitudes : 56.5 °N
- o Mean duration of the freshwater stage : 3.6 years

The North Esk River (the only available index river in this region) was chosen as the indicator of mean smolt age in East Scotland.

### 3. Results

#### 3.1/ Estimation of posterior distributions via mcmc sampling

The convergence of the mcmc chains has been checked for all parameters using the Gelman-Rubin diagnostic. The values of the GR diagnostic do not exceed 1.1 for all parameters.

#### 3.2/ Sensitivity to priors and check for exchangeability

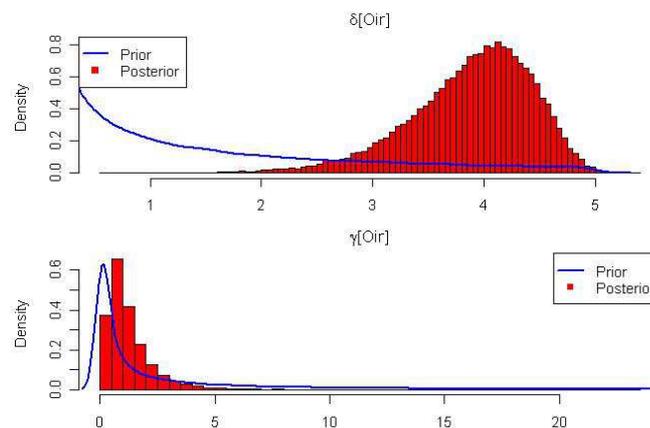
Results do not reveal sensitive to change in the prior distributions for all parameters (not shown).

Results of the test for exchangeability of the different rivers (in the hierarchical structure conditioned by the covariates) are presented in **Appendix 3.1**. Results indicate that the posterior distributions of the key parameters obtained in the 20 trials of the leave-one-out experiment are very similar. Hence, none of the data sets substantially alter the outcome of the hierarchical analysis, showing that the requirement of exchangeability between rivers has been met.

#### 3.3/ Shape of river-specific eggs-to-smolts survival model: example of the Oir River (Fr)

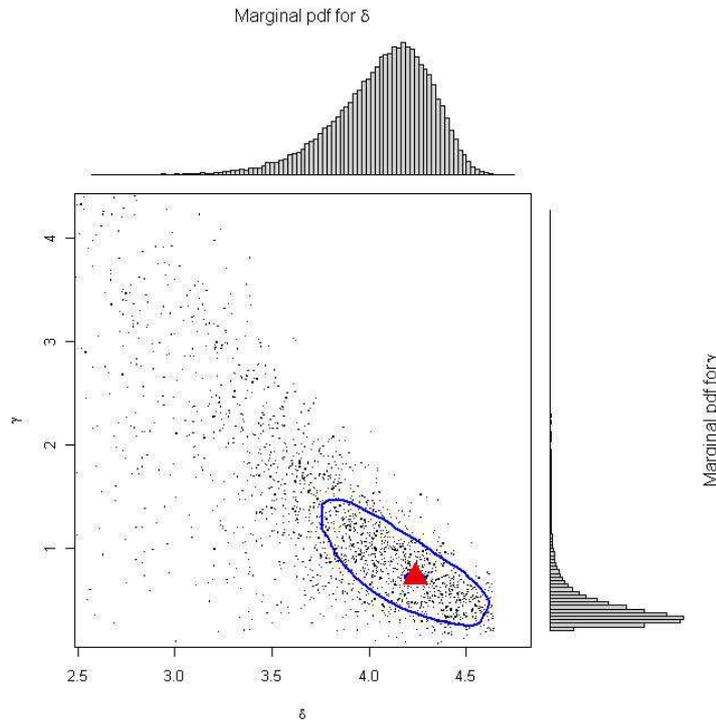
In this section, results obtained for one particular river, the Oir River (France), are detailed. Results obtained for all rivers are given in the **Appendix 1**.

Marginal posterior distributions for all parameters are estimated. Considerable updating of the prior distribution occurs for the parameter  $\delta$  and a weaker updating is observed for  $\gamma$  (**Figure 8**). The posterior distribution of  $\gamma$  has its mode around 0.8, thus giving a high degree of credibility to the existence of density dependent mortality.



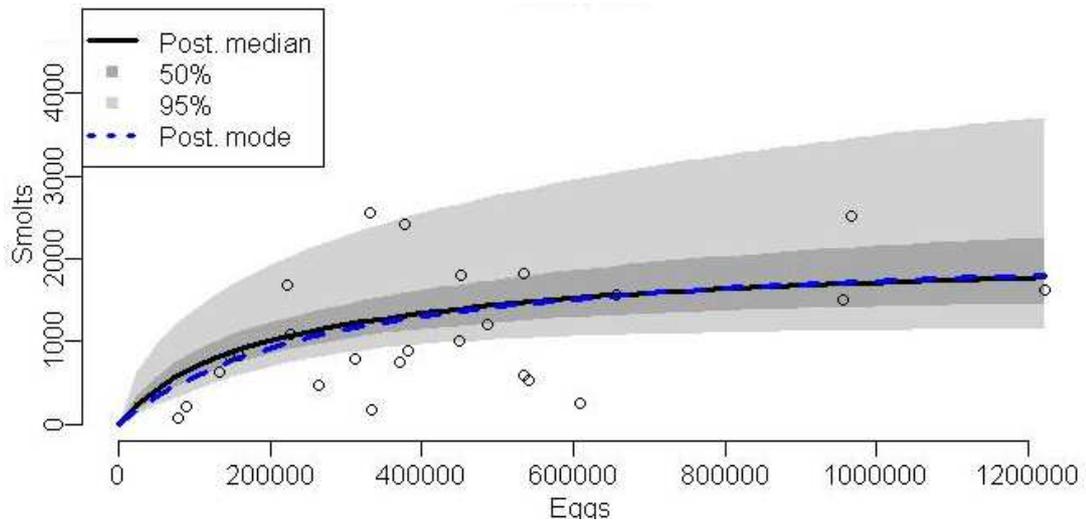
**Fig. 8:** Marginal posterior distribution for parameters  $\delta$  and  $\gamma$  for the Oir River (France).

Parameters  $(\delta, \gamma)$  exhibit a high negative correlation (**Figure 9**). As a consequence, the marginal posterior distributions do not contain all the necessary information to predict the shape of the BH survival function. Indeed, a similar shape for the BH survival function can be obtained either with a high slope at the origin (a low density-independent mortality rate  $\delta$ ) but a low maximum asymptotic level of surviving smolts (a high density-dependent mortality rate  $\gamma$ ), or inversely with a low slope at the origin (a high density-independent mortality rate  $\delta$ ) but a high maximum asymptotic level of surviving smolts (a low density-dependent mortality rate  $\gamma$ ).



**Fig. 9:** Joint posterior distribution of  $(\delta, \gamma)$  for the Oir River (France). A negative correlation between the two parameters is observed. Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

**Figure 10** shows the resulting Beverton & Holt survival function obtained for the Oir river, together with the uncertainty envelop arising from the estimation about the parameters  $(\delta, \gamma)$ . Results indicate that the mean survival is far from density independence. For this river, the residual unexplained variability (environmental stochasticity) is high, with parameter  $\sigma$  estimated at 0.75 (posterior median) what correspond to a logNormal distribution with a CV of 0.85.



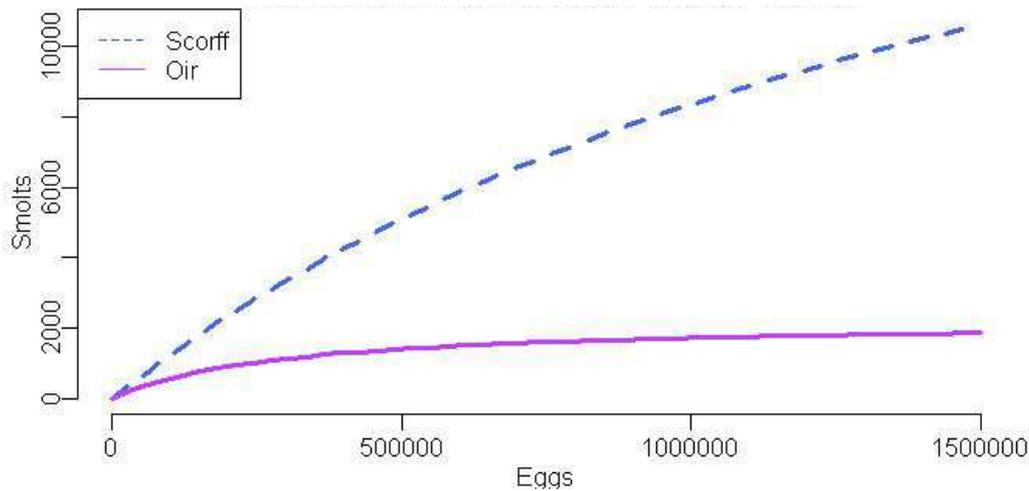
**Fig. 10:** Mean Beverton & Holt survival function estimated for the Oir River. BH functions were drawn with the posterior median (dashed line) and the joint posterior mode (solid line) of parameters  $(\delta, \gamma)$ . The uncertainty envelop (dark grey zone: 50%; light grey zone: 95%) corresponds to uncertainty about the parameters  $(\delta, \gamma)$ . (No logNormal residual variability represented)

### 3.4/ General patterns and variability among the 20 rivers

In this section we outline the main features of the estimates obtained for the 20 rivers included in the hierarchical model.

The joint posterior distributions of the parameters  $(\delta, \gamma)$  for each river are given in the **Appendix 1** and correlation coefficients are given in **Appendix 3.2**. The negative correlation between the two parameters, already detailed for the Oir River, can be generalized for all rivers.

The resulting fitted BH survival function obtained for all rivers are given in the **Appendix 1**. As the model uses river-specific mean smolt age and riverine area, the estimated eggs-to-smolts survival relations are highly different, even for geographically close rivers with similar latitude and longitude and it is therefore not possible to draw all relationships on the same graph. Below we only illustrate results obtained for the two French rivers (**Figure 11**). In this case, the estimated parameters  $\delta$  and  $\gamma$  and the mean age of smolts are similar for both rivers. Most of the difference is due to the riverine area difference ( $70.10^4\text{m}^2$  for the Scorff,  $5.10^4\text{m}^2$  for the Oir River).



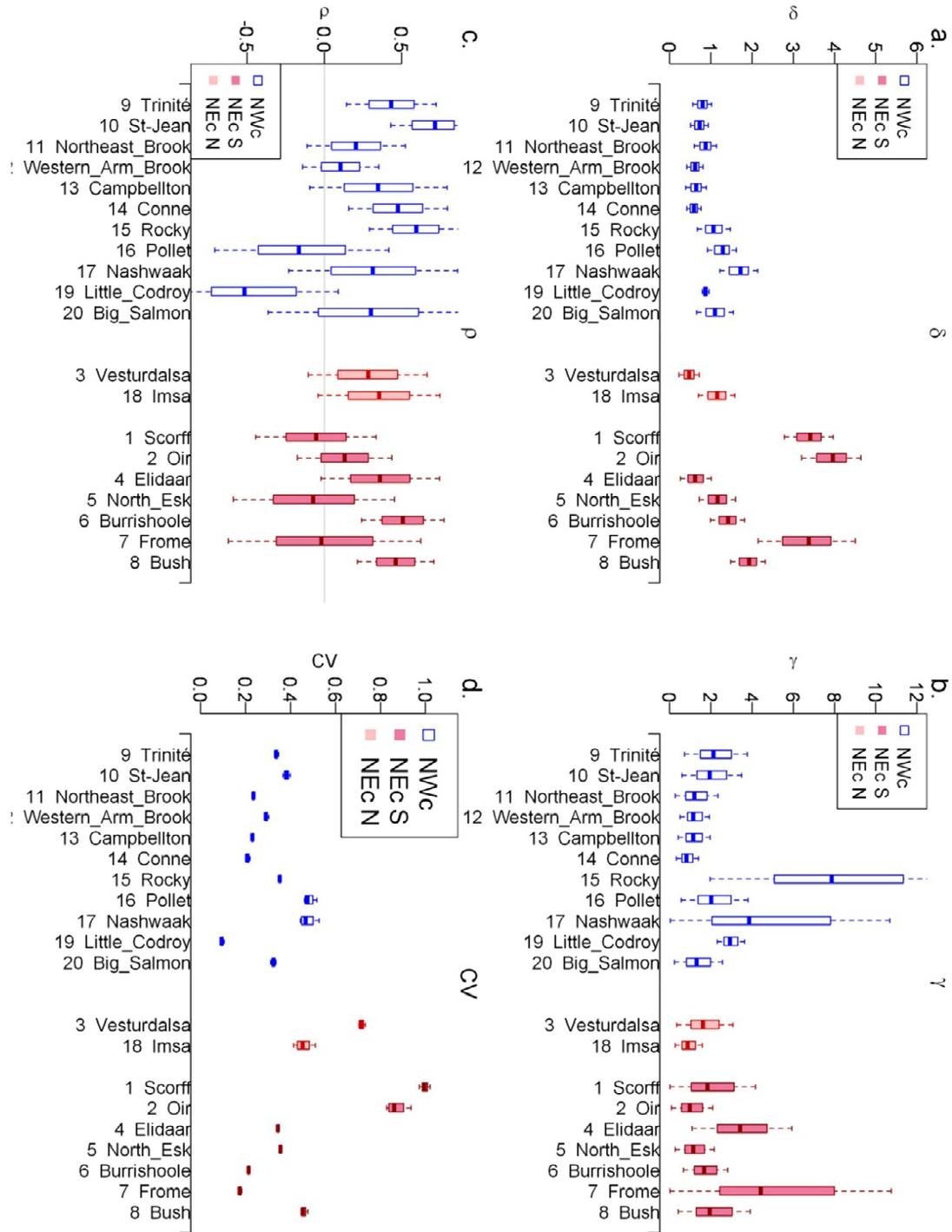
**Fig. 11:** Beverton&Holt survival function obtained for the Scorff R. and the Oir R. The mean BH survival functions are plotted with posterior medians of the parameters ( $\delta$ ,  $\gamma$ ).

The **Figure 12** provides a representation of the marginal distributions of the parameters ( $\delta$ ,  $\gamma$ ,  $\sigma$  (through CV),  $\rho$ ) that facilitates the comparison between rivers. Results exhibit a high between rivers variability in the estimation of all parameters. In particular, the between rivers variability in ( $\delta$ ,  $\gamma$ ) is high (**Figure 12a, 12b**). This will be discussed in relation with the covariates in the next section.

The posterior probability distributions are markedly more informative than the prior probability distributions but still reflect high uncertainty (some example are given in **Appendix 3.3**). Uncertainty about the estimation of the parameters can still be high for some rivers (e.g., Frome River for both  $\delta$  and  $\gamma$  parameters, Nashwaak and Rocky Rivers for the  $\gamma$  parameter distribution), in relation with the number of available observations.

Results are consistent with the hypothesis of a predictable temporal auto-correlation in the unexplained environmental errors. Indeed, estimates of the coefficients  $\rho$  (**Figure 12c**) are positive for almost all rivers, indicating a positive auto-correlation in the residual variability (a good (better than expected) survival year  $y$  has a greater probability to be followed by a good survival year  $y+1$  than by a low survival).

The unexplained environmental variability (as measured by the variance of the logNormal process error) remains high. Marginal distributions of the  $\sigma_r$ 's show high value, corresponding to a coefficient of variation between 0.1 and 1.0 depending on the river (**Figure 12d**). French rivers exhibit the higher inter-annual variability (CV around 1.0 for the Scorff River and around 0.8 for the Oir River). Results have been explored to look for potential relationships between the  $\sigma_r$ 's (or CV's) and some covariates such as the latitude or the mean age of smolts, but no clear pattern could be found (not shown).

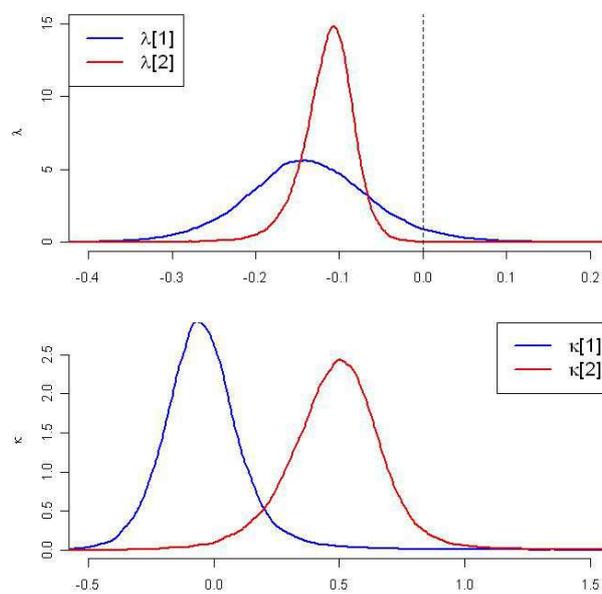


**Fig. 12:** Marginal posterior probability distributions of model parameters  $\delta$  (panel a.),  $\gamma$  (panel b.),  $\rho$  (panel c.) and CV (panel d.). CV is given by the relation  $CV = \sqrt{e^{\sigma^2} - 1}$ . Each box displays the 25th, 50th and 75th percentiles and a representation of the dispersal. Rivers are separated by stock complex.

### 3.5/ Hierarchical structure and effect of covariates

The posterior distributions of the parameters at the top of the hierarchical structure (see parameters in the [Table 2](#)) are given in the [Appendix 3.3](#). Marginal posterior distributions exhibit considerable updating by comparison with priors and no significant correlation between parameters was detected ([Appendix 3.4](#)).

The covariates latitude (continuous) and longitude (categorical) explain a great part of the between rivers variability in the parameters  $\delta$  ([Figure 12.a](#)). Estimates of parameters  $\lambda_1$  and  $\lambda_2$  are clearly negative for both sides of the Atlantic ([Figure 13](#)). This outlines the important negative effect of the latitude on  $\delta$  (thus a positive effect of the latitude on the survival rates). The effect of the covariates latitude also depends upon the longitude. Indeed, parameters  $\lambda$  and  $\kappa$  are different between east and west sides of the Atlantic Ocean ([Figure 13](#)).



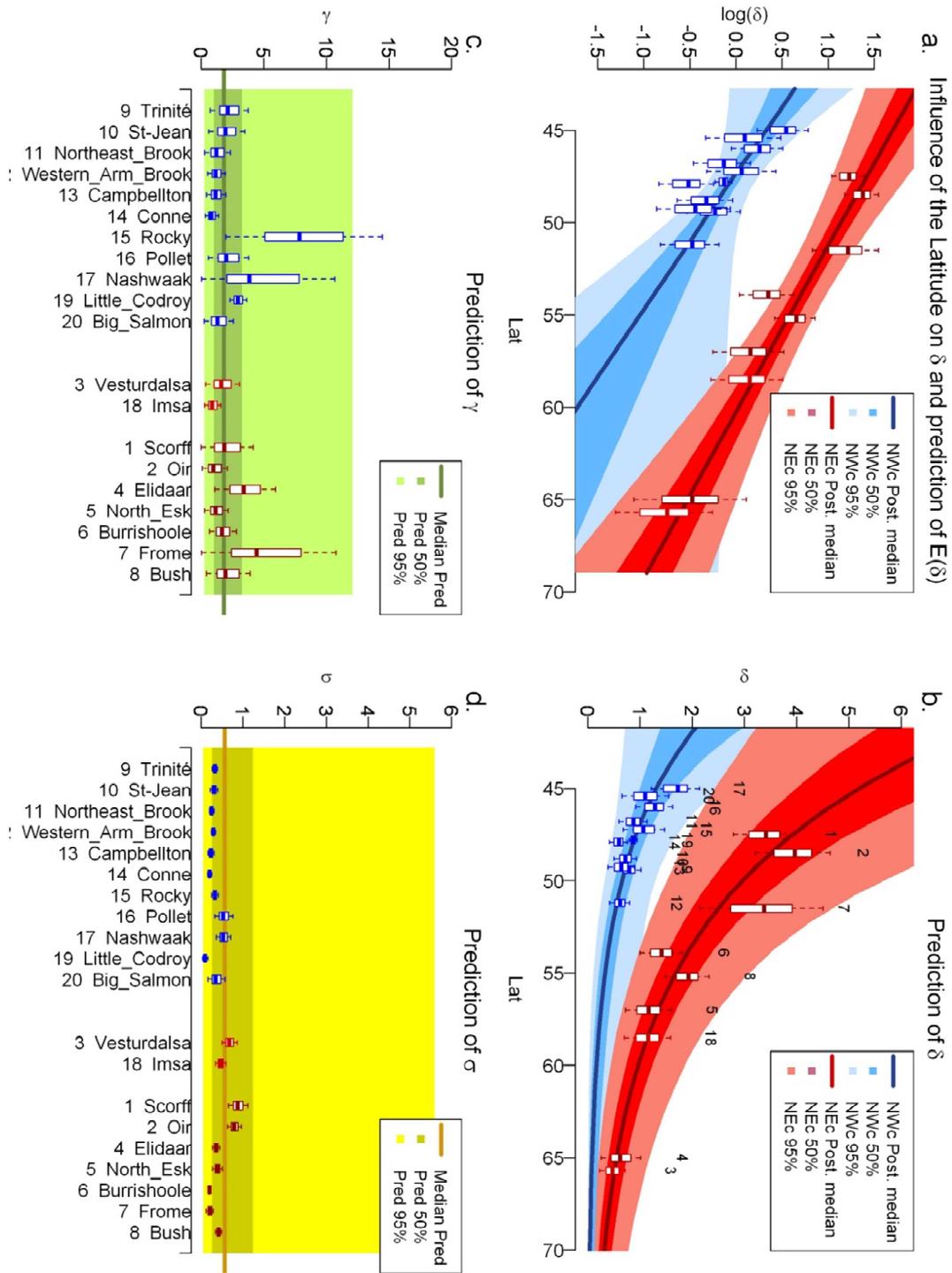
*Fig. 13: Marginal posterior probability distributions for model hyperparameters  $\lambda$  and  $\kappa$  for both the NEc (1) and the NWc (2)*

Relationships between other parameters and covariates have been explored but no other clear relationships could be found.

As an additional result, the posterior distribution of the slope at the origin  $\alpha$  was also computed (see [Appendix 3.5](#)).  $\alpha$  can be directly interpreted as the maximum eggs-to-smolts survival rate (in absence of density-dependence) and has then a directly interpretable ecological meaning. Results highlight that  $\alpha$  ranges between 1.1% (Oir River) to 19.3% (Elidaar River).

### 3.6/ Prediction

As shown by the [Figure 13](#), the expected means of the parameters  $\delta$ 's are closely linked to the longitude (America (NWc) or Europe (NEc)) and the latitude. [Figure 14a](#) provides a representation of the linear relationship between expected mean of the  $\delta$  (in log-scale) and the latitude.

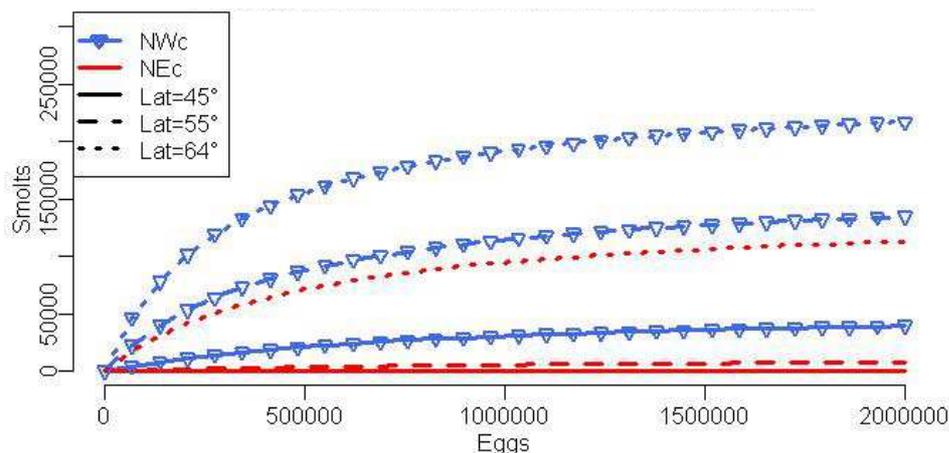


**Fig. 14:** Main predictive outputs from the model. Panel (a): Posterior predictive distributions of  $\log(E(\delta))$  as a function of the latitude and longitude. Uncertainty incorporates uncertainty about parameters only; Panel (b): Posterior predictive distributions of  $\delta$  as a function of the latitude and longitude. Uncertainty incorporates both uncertainty about parameters and logNormal variability. Panel (c) and (d): Posterior predictive distributions of  $\gamma$  and  $\sigma$ . In all panels, the solid lines correspond to posterior median, the light colored (respect dark colored) zone to 50% (respectively 95%) probability. Boxplots are marginal posterior distributions obtained for each river.

The posterior predictive distributions (Prevost et al. 2003; Gelman et al. 2005; Rivot et al. 2008; Rivot and Parent 2012) of the parameter  $\delta$  for any given river, conditionally upon covariates latitude and longitude, can be derived from the hierarchical structure (Figure 14b). The use of those covariates to estimate the expected value of  $\delta$  provides a significant gain in the precision of the posterior predictive inference by comparison with a fully exchangeable model on the  $\delta$ 's (not shown).

As illustrated in Figure 14c and F14d, the posterior predictive of  $\gamma$  and  $\sigma$ , drawn from the fully exchangeable models on these two parameters (e.g. hierarchical models that do not depend upon any covariate) is more uncertain.

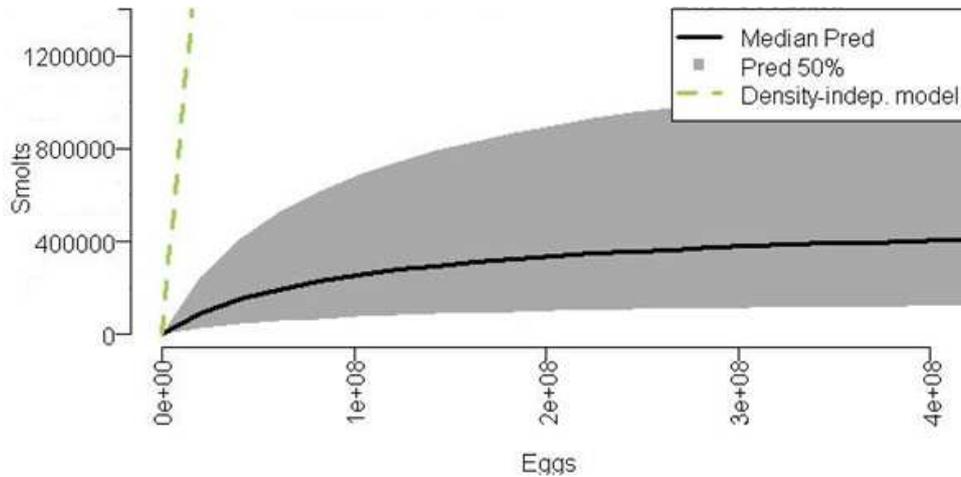
Posterior predictive of the two parameters ( $\delta$ ,  $\gamma$ ) are used to predict the density-dependent BH survival relationship for any river, knowing its stock complex, latitude, wetted riverine area and the mean freshwater phase duration of its associated smolt population. As an illustration, Figure 15 presents six predicted eggs-to-smolts BH survival models generated for three latitudes (45°N, 55°N and 64°N) and for both stock complex (NWc and NEc). A constant riverine area ( $1.10^6\text{m}^2$ ) and mean age of smolts (2 years) were used. When the latitude increases, the density-independent mortality rate  $\delta$  decreases, and the slope at the origin (thus the density-independent survival) increases. The scale of the relationship with latitude differs according to the stock complex.



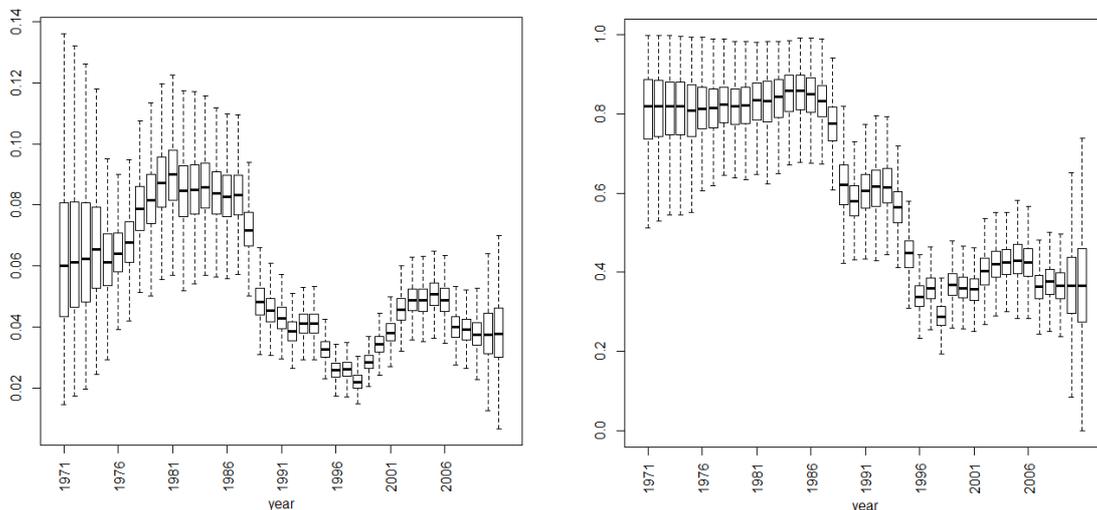
**Fig. 15:** Predicted eggs-to-smolts. Beverton & Holt survival functions obtained for different latitude for the two sides of the Atlantic Ocean. The curves have been drawn with posterior medians of the posterior predictive parameters obtained with variable latitude for a riverine area of  $1.10^6\text{m}^2$  and mean age of smolts of 2 years.

### 3.7/ Combining the fitted BH eggs-to-smolts survival with a stage-structured life cycle model

The resulting mean survival function for East Scotland is presented in **Figure 16**. It is worth noting that the slope at the origin of the BH function (maximal survival rate) is 1.1%, then very close to the 0.9% used as density independent survival rate.



**Fig. 16:** Survival function estimated for East Scotland. Black solid line: survival relationships obtained with posterior medians of the parameters  $\delta$  ( $E(\log(\delta))=0.36$ ;  $\sigma(\delta)=0.62$ ) and  $\gamma$  ( $E(\log(\gamma))=0.34$ ;  $\sigma(\gamma)=0.84$ ) ; Grey area: probability intervals at 50% probability. Green dashed line: The density-independent model used previously in the life-cycle model (survival=0.9%).



**Fig. 17:** Estimated marine survival by a life-cycle approach when taking freshwater survival as linear ( $\delta=0.9\%$ , left panel) or using the developed model to integrate density-dependent mortality (right panel).

**Figure 17** represents the time series of the posterior distribution for the marine survival during the first year at sea, estimated for the Scotland East stock complex, for the two alternative hypotheses about the freshwater survival. Even if the global shape of the

temporal signal is conserved whatever freshwater survival model is used, the integration of density-dependent mortality highly impacts the estimation of the marine dynamics.

- The marine survival is clearly lower when a density independent survival rate is used (approximately a factor 10 between the two alternative hypotheses).
- The shape of the temporal signal is slightly different, with clearer evidence of a shift in the early 90's obtained when using a density-dependent BH function.

## 4. Discussion

### 4.1/ Interest of the approach and findings

The present approach offers a substantial contribution to the modelling of A. Salmon population dynamics at the scale of stock complexes.

An original data base has been compiled. Time series of eggs-to-smolts data (based on abundance survey of smolts and spawners with age structure, sex-ratio of spawners and fecundity) on 21 index rivers across the A. Salmon repartition area, together with several covariates associated with the index rivers, were compiled for this analysis. The present approach relies on a much more extensive data base than other meta-analysis of A. Salmon SR already published (Chaput et al. 1998; Prévost et al. 2001; 2003; Michielsens and McAllister, 2004).

This work relies on an original parameterization of the density dependent survival process. The classical Beverton & Holt model is revisited through the explicit parameterization in terms of density dependent and density independent mortality rates. The duration of the freshwater phase is explicitly used as a covariate. And the parameters could be compared between different forms of survival functions, e.g. Beverton & Holt and Ricker.

As already illustrated in several papers, the Hierarchical Bayesian Modeling framework has been proved successful for extracting average patterns of density dependence from several noisy and data poor stock-recruitment time series (Lierman and Hilborn 1997; Myers et al. 2001; Forrest 2010). Following Prévost et al. (2003) or Michielsens and McAllister (2004), we applied the framework to A. Salmon stock-recruitment analysis to combine data from several index river. A partially exchangeable hierarchical model was built to incorporate covariates (such as the longitude and the latitude) to capture part of the between rivers variability. Our approach hence offers an efficient framework to predict the parameters of the density-dependent survival (and the associated uncertainty) for any new river for which the associated covariates latitude, longitude, wetted area and mean age of smolts are known.

The approach provides estimates for the density independent mortality rate  $\delta$  and the density dependent mortality rate  $\gamma$  for each of the 20 rivers. The parameter  $\delta$  in itself is hardly interpretable, but it is closely linked to the slope at the origin of the survival function, interpreted as the maximum survival rate. We found values between 1.1% (Oir River) and 19.5% (Elidaar River), which were consistent with previous studies (e.g. Prévost et al. 1996 on the Oir River found 2.1%).

Estimates of the density dependent mortality rate  $\gamma$  are always positive, thus indicating that data support the hypothesis of density dependence in the eggs-to-smolts survival.

Results highlight a huge between rivers variability of these parameters ( $\delta$ ,  $\gamma$ ). While we could not find any useful covariate to explain the variability in the  $\gamma$ 's, the latitude (continuous) and the longitude (categorical with two modalities, East and West side of the Atlantic Ocean) explain a great part of the between variability in the  $\delta$ 's. The latitude and longitude can be considered as an approximation of many environmental conditions that control Atlantic salmon productivity. Temperature differences, linked to food availability and day length variations in function of the latitude have been evoked to explain differences in productivity (Metcalf and Thorpe, 1990; Prevost et al. 2003). But latitude can also be considered as a proxy for level of anthropic pressure. At given latitude,  $\delta$  is higher in the North East than in the North West complex. Again, temperature impact on salmon physiology can explain this difference, as the North Atlantic Drift produces a much warmer climate on the eastern coast of the Atlantic than on the west (Metcalf and Thorpe, 1990).

Survival process showed a high between years variability (residuals coefficient of variation can be over 0.5 and reaches 1.0 for the Oir River), a classical pattern in SR analysis (Hilborn et Walters 1992; Hinrichsen, 2001).

A positive temporal auto-correlation signal has been detected for almost all rivers, and modeled via a first order stationary autoregressive process. This prevents from bias in parameters estimation that could result from ignoring autocorrelation (Armstrong and Shelton, 1988). The positive autocorrelation could well result from a response to smoothed environmental variations (e.g. climate), or from competition between overlapping cohorts. Research of correlation with environmental signals was beyond the scope of this study, and no relation between  $\rho$  and the mean age of smolts could be found.

The combination of the eggs-to-smolts density dependent survival function estimated for East Scotland with the age-structured life cycle model provides significant and promising results. The time series of estimates of marine survival rates resulting from the life cycle approach is greatly impacted by the integration of our density-dependent eggs-to-smolts survival function, by comparison with using constant survival rate. The estimations of the marine survival obtained with the density dependent function become closer to the regional estimation given by Hutchings et Jones (1998) (mean smolt-to-returning adults survival at 6% for Ireland and Great Britain,) or Jutilla et al. (2005) (10% of tagged smolts were recaptured as post-smolts for the 19 years of study). The evidence for a drastic decline of the marine survival rate at the beginning of the 90's becomes also clearer.

## 4.2/ Limits of the approach and axes for future improvement

The approach has several limits, both in the data and the modeling approaches, and it provides a framework for structuring further research and data collection.

Results presented here were conditioned by the quality of the data. As in any meta-analysis, compiling several series of data from many different partners requires careful discussions with data providers. Close contact with the partners has already been established to ensure homogeneity in the data set, but further careful discussion will certainly be needed to clarify the specificities of some time series and the limit of the data sets.

For instance, stocking of juveniles from aquaculture (mostly at the 0+ stage) could be far from negligible in certain rivers (e.g. Bush, Narraguagus), what could bias the estimation of

the eggs-to-smolt survival rate because an unknown proportion of smolts can originate from stocked juveniles. The Narraguagus River has been excluded from this analysis because the number of 0+ stocked was comparable to the number of natural eggs deposition for many years in the time series.

Also, this study does not integrate the measurement errors in eggs and smolts number. As pointed out by several authors (Rivot et al. 2001; Kehler et al. 2002; Schute and Kronlund, 2002; Su and Peterman 2012), measurement errors in SR data can induce strong bias in parameters estimates. Including measurement errors is theoretically possible, but was not easily feasible in practice as methods used to estimate the eggs deposition and smolts production are different for each river.

As pointed out by Prévost et al. (2001) and Prévost et al. (2003), available data from index rivers may not be necessarily representative for the average eggs-to-smolts dynamics at the regional scale. Some regions are also not represented (or underrepresented) in the data base although they represent significant habitat for A. Salmon (e.g. Russia, Spain or USA). Hence, care must be taken when using the results to predict the survival in these regions.

How much representative is what we can learn from the data is an important question. But how representative each data set is with regards to the whole data base we have compiled is also questionable. Checking for exchangeability is one method to assess how much each river in the data base is representative of a general pattern. The test of exchangeability that was carried out showed no significant difference in the estimates when any river is removed from the data base. The slight differences observed can be imputed to the Nashwaak River, but this river has the lowest Latitude of NWc, which explains that it has a great influence on the model.

Finally, only a reduced number of covariates was used to explain the between rivers variability. The lacustrine area accessible to salmon was not introduced in the model, although previous studies have shown an impact of this covariate on the carrying capacity of the system (O'Connell & Dempson, 1995, Chaput et al., 1998). However, based on our data set, we could not find any clear pattern of influence of this parameter. Further developments in this direction would be needed to explore the potential influence of this covariate.

Many other climate or habitat covariates could play an important role in the analysis. Water temperature (Mather et al., 2008), pH, macrophyte cover or substrate (Haury et al., 1995) have been shown to influence young freshwater stages survival and repartition. Using more covariates could improve the accuracy of the model. However, the covariates must be easily available for other systems where prediction is needed. A trade-off must be done between model accuracy and covariates availability.

The demonstration could be strengthened by improving some statistical analyses.

First, the fit quality of the model and its capacity to predict reliable recruitment were not tested. Posterior checking analyses must be carried out in the near future to assess the consistency between the fitted model and the data (Gelman et al. 1996 ; Waller et al. 2003 ; Yuan and Johnson 2011).

Results have shown that the variance of the environmental stochasticity seems to decrease when the egg deposition increases (see **Annex A4.2**). Such a pattern of heteroscedasticity has been explored and discussed by Minto (2008) as an indice of density dependence (the lower the variance, the higher the concentration effect due to density

dependence) Explicitly modeling this relationship between the variance and the egg deposition would certainly improve the model.

Although the parameterization of the survival process in terms of density independent and density dependent mortality rates can be generalized for several classical parametric forms (such as Beverton & Holt, Ricker, as shown in the **Appendix 2**), only the Beverton & Holt has been tested. Our results should be contrasted with alternative hypotheses of density dependent process.

Parameters ( $\delta$ ,  $\gamma$ ) revealed a posterior negative correlation for almost all rivers. However, our hierarchical construction does not allow to learn about this correlation. It also not allows to incorporate the correlation in forecasting so as to tighten uncertainty about the predicted density-dependent relationships for new rivers of regions (Pulkkinen et al., 2011).

More fundamentally, several hypotheses that were made about the ecological process are particularly questionable.

The first and probably the strongest assumption is that density dependent and independent mortality rates  $\delta$  and  $\gamma$  are considered constant during the whole freshwater phase from eggs to migrating smolts. However, the mortality during the first months of the freshwater phase (from eggs to fry emergence) is likely to be much higher than the mortality of older parrs (Elliot 2001; Jonsson et al. 2008; Gurney et al. 2010). Because the between rivers variability of the mean age at smoltification (MAS) is very high (from 1.0 year for the Frome River to 4.3 years for the Conne river), considering that the annual mortality rates are constant during the whole freshwater phase, whatever the river, consists in a very strong and questionable hypothesis.

Considering a constant  $\delta$  certainly accentuates the degree of negative correlation between  $\delta$  and the latitude. Indeed, the maximum mortality ( $\alpha$  = slope at the origin) is built as  $\alpha = e^{-\delta.MAS}$ . And the latitude is positively correlated with the MAS. Then, even a constant  $\alpha$  across rivers would have induced a negative correlation between  $\delta$  and the latitude, to balance the positive correlation between MAS and latitude. However, as shown in **Appendix 3.5**, a positive correlation still exists between  $\alpha$  and the latitude, thus showing that the latitude still has a positive effect on the survival (hence a negative on the mortality rate).

Several avenues could be explored to account for a change in the mortality rate over time. The integration of the density dependent per-capita mortality rate (as detailed in the **Appendix 2**) is not so direct when the parameters  $\delta$  and  $\gamma$  are function of time. A promising avenue would consist in searching for parametric relations for the change of  $\delta$  and  $\gamma$  with time, that still allow for explicit mathematical integration. A first approach would consist in considering the whole freshwater phase as a suite of phases with constant mortality rates (but different between phases). Another avenue would be to use general results based on the Ricatti differential equations (Reid, 1972), for which analytical integration still exist for a wide family of continuous parametric function for  $\delta = f(t)$  and  $\gamma = g(t)$ .

The effect of cohort overlapping is not accounted for in our modeling approach. Only the intra-cohort density dependence is considered, whereas juvenile from cohort born at year  $y$  interact with juveniles from many other cohorts, especially in rivers with a high MAS. Moreover, inter-specific interactions, such as competition with brown trout (Heggenes et al. 1999) are not represented. But accounting for such inter-specific interactions in such a large-scale analysis is not feasible in practice as abundance survey for several species are rarely accessible.

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# Appendix

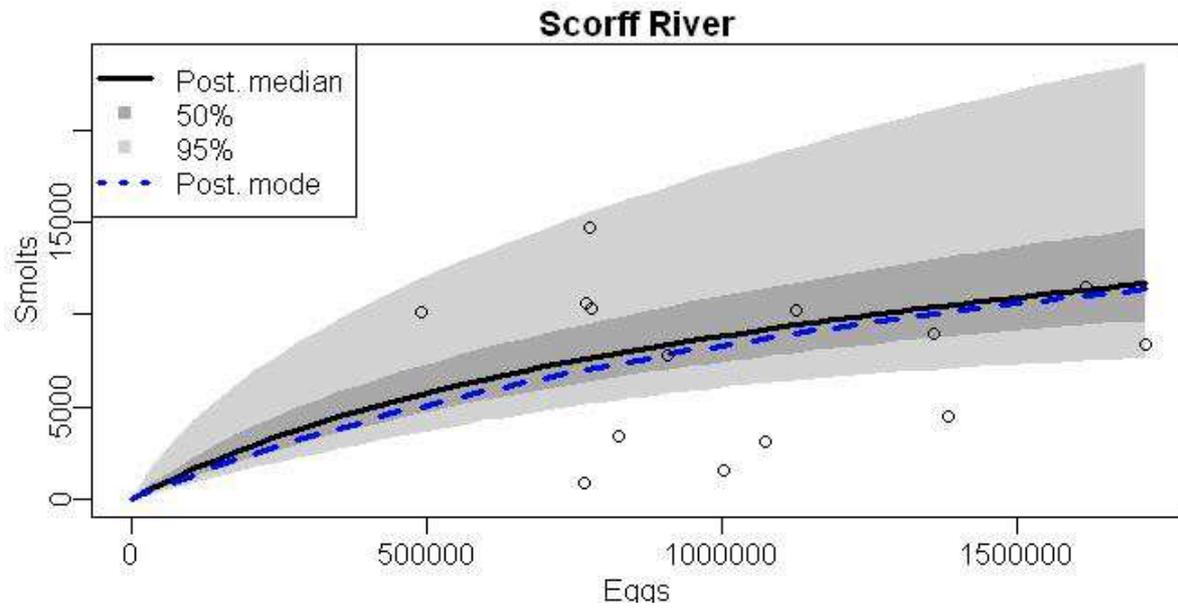
## Appendix 1: Eggs to smolts time series and covariates for the 21 index rivers

*Table A1.1: Regional distribution of all rivers. The presented areas are management units used by ICS WG NAS (ICES 2010).*

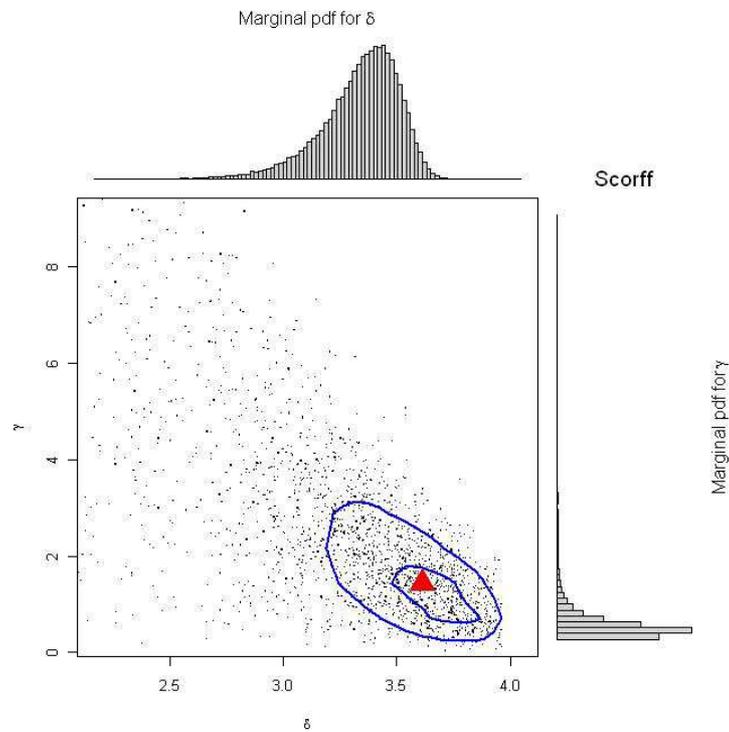
North West complex	Southern North East c.	Northern North East c.
<b><u>Newfoundland</u></b>	<b><u>France</u></b>	<b><u>Iceland (West and North)</u></b>
Northeast Brook Western Arm Brook Campbellton Conne Rocky Little Codroy	Scorff Oir	Vesturdalsa
<b><u>Québec</u></b>	<b><u>Ireland</u></b>	<b><u>Norway</u></b>
Trinité St-Jean	Burrishoole	<i>Imsa</i>
<b><u>Gulf</u></b>	<b><u>UK (N.Ireland)</u></b>	<b><u>Finland</u></b>
	Bush	
<b><u>Labrador</u></b>	<b><u>Spain</u></b>	<b><u>Russia</u></b>
<b><u>Scotia-Fundy</u></b>	<b><u>UK (England and Wales)</u></b>	<b><u>Sweden</u></b>
Nashwaak Pollet Big Salmon	Frome	
<b><u>U.S.A</u></b>	<b><u>UK (Scotland)</u></b>	
Narraguagus (not used)	North Esk	
	<b><u>Iceland (East and South)</u></b>	
	Elidaar	

River	Scorff (Southern NEc, France, Brittany)
Contact	Anne-Laure Caudal (FDPPMA Morbihan), Étienne Prévost (INRA, France)
<u>River Informations</u>	
Latitude	47.5°
Longitude	-3.2°
Riverine Wetted A.	69.71 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	0
Mean Age of Smolts	1.20
ObsPeriod	1995 – 2008 (n <sub>obs</sub> =17)
<u>Monitoring</u>	<p><b>Egg</b> abundance is estimated through the returning adults count and the fecundity estimation. Returning adults are separated in one-sea-winter (1SW) and multiple-sea-winter (MSW) and the proportion of females in each sea-age class is estimated each year. The salmon abundance is estimated through a mark-recapture method similar to the one used for smolts: they are captured, measured and marked at the Moulin des Princes station and their age is evaluated. Then, other operation of abundance estimation are made in Scorff stream, main tributaries and spawning areas with investigation of marks. Female fecundity is estimated through mean estimation on the Massif Armoricaïn (Prévost et Porcher, 1996), which are:</p> <ul style="list-style-type: none"> <li>○ 45% of 1SW salmon are female which are spawning 4058 eggs each;</li> <li>○ 80% of MSW salmon are female, spawning 7227 eggs each.</li> </ul> <p><b>Smolt</b> production is estimated by mark-recapture operation as described in Prévost, 1999. On one site (Moulin du Leslé), trapped smolts going at sea are counted, marked and measured. On a other study site downstream, captured smolts are counted and are examined to look for marks existence. Scales are taken on some fishes (of all size and during all downstream migration) to evaluate their age. The smolt production estimation is conducted with the same method since 2002 (Caudal et Prévost, 2003b). Migrating smolts are supposed independent of the capture operations at the first station and the capture probability is assumed equal for all fishes (without age, size, or migration date bias). This method provides a reliable punctual estimation of migrating flow, but the accuracy of the estimate is suspected to be overestimated.</p>
<u>Bibliography</u>	<p><u>Data origin:</u> Caudal A-L, Prévost E, 2011. <i>État du stock de saumon atlantique du Scorff (Bretagne sud, France) en 2010 : Production de smolts, retour d'adultes, échappement, taux d'exploitation et de survie. Fédération du Morbihan Pour la Pêche et la Protection du Milieu Aquatique, INRA (UMR EQHC). 26p.</i></p> <p>Caudal A.-L. and Prévost E., 2003b. <i>État du stock de saumon atlantique (Salmosalar) du Scorff (Bretagne sud, France) en 2002 : production de smolts, retours d'adultes, échappement, taux d'exploitation et de survie. Fédération du Morbihan pour la pêche et la protection des milieux aquatiques, INRA, 13 p.</i></p> <p>Claude A., 1996 <i>Deux éléments du recrutement du saumon atlantique dans le massif Armoricaïn.</i>,. Master 2 report (ENSAR-INRA), 44 p. (available at the library of AgrocampusOuest, used for the Scorff surface)</p> <p>Prévost E., 1999. <i>État du stock de saumon atlantique (Salmo salar) du Scorff (Bretagne sud, France) en 1998 : production de smolts, retours d'adultes, échappement, taux d'exploitation et de survie. CIEM, Groupe de travail sur le saumon de l'Atlantique nord, Doc. trav. 99/20, 16p.</i></p> <p>Prévost E. and J.-P. Porcher, 1996. <i>Méthodologie d'élaboration de totaux autorisés de captures (TAC) pour le Saumon atlantique (SalmosalarL.) dans le Massif Armoricaïn. Propositions et recommandations scientifiques.</i> GRISAM, Évaluation et gestion des stocks de poissons migrateurs, Doc. sci. tech. 1, 18 p.</p>

Egg-to-smolt relationship estimated by the model

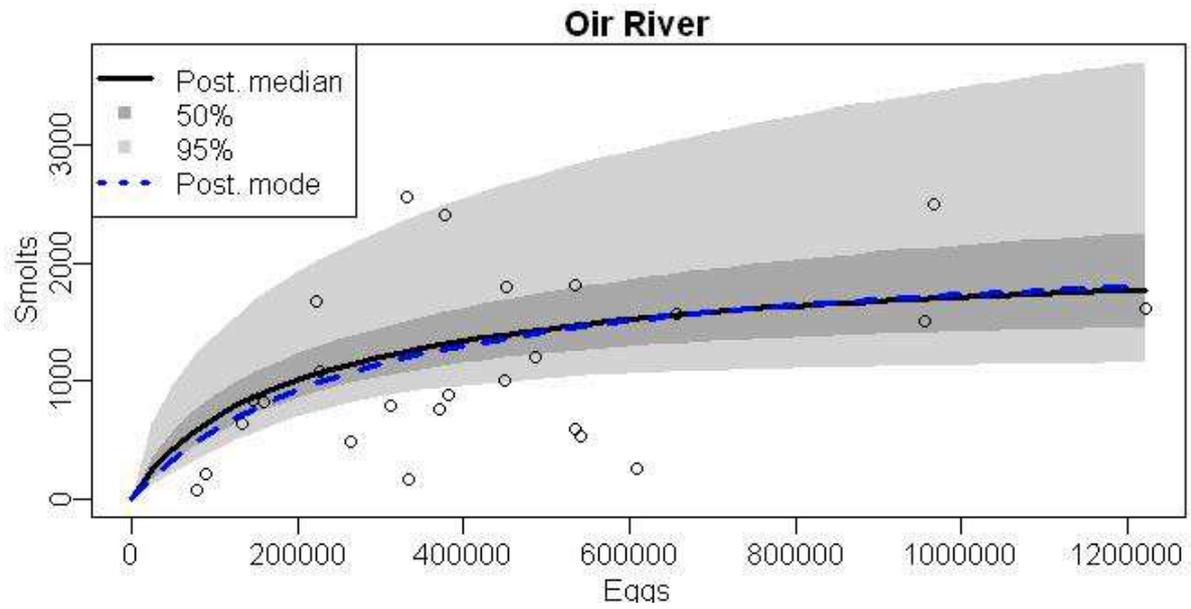


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

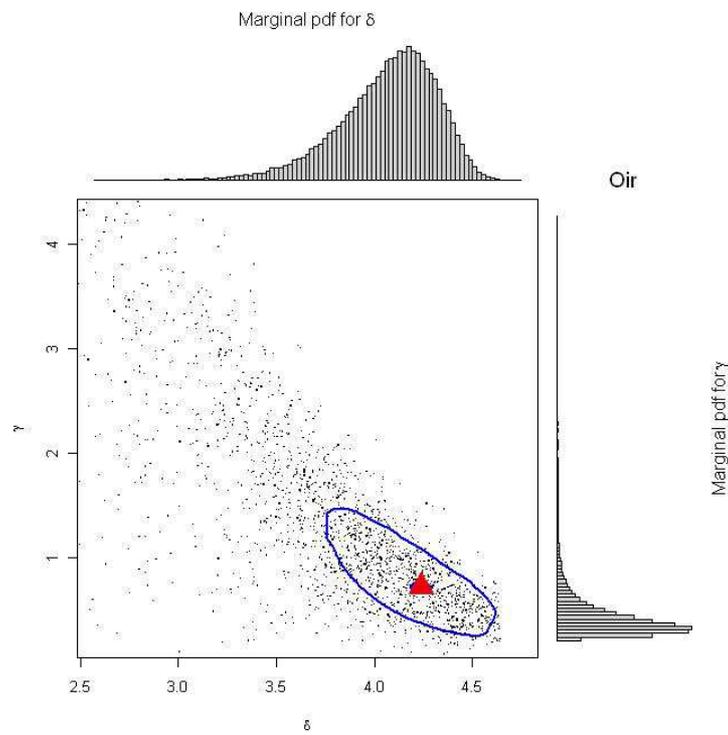


River	Oir River (Southern NEc, France, Normandy)
Contact	Frederic Marchand (INRA, France), Jean-Luc Baglinière (INRA, France)
<u>River Informations</u>	
Latitude	48.5°
Longitude	-1.17°
Riverine Wetted A.	4.8 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	0
Mean Age of Smolts	1.14
ObsPeriod	1985 – 2009 (n <sub>obs</sub> =27)
<u>Monitoring</u>	<p>Spawning adults are estimated by mark-recapture techniques. Full description of the method is provided by Rivot and Prévost (2002). Adult numbers are converted into <b>eggs</b> as described by Prévost et al. (1996) (as for Scorff River).</p> <p><b>Smolt</b> output is estimated yearly by mark-recapture techniques. Full description of the method is provided by Rivot and Prévost (2002). Scale samples are collected each year. Annual smolt production is allocated to spawning year classes based on the estimated age composition of the run.</p>
<u>Bibliography</u>	<p>Claude A., 1996. <i>Deux éléments du recrutement du saumon atlantique dans le massif Armoricaïn</i>. Master 2 report (ENSAR-INRA), 44 p. (available at the library of AgrocampusOuest, used for the Oir surface)</p> <p>Crozier W.W., Potter E.C.E., Prévost E., Schön P-J. and Ó Maoiléidigh N., 2003. A coordinated approach towards the development of a scientific basis for management of wild Atlantic salmon in the North-East Atlantic (SALMODEL). Queen's University of Belfast, Belfast. Chapter 4:71-104.</p> <p>Prévost E. and J.-P. Porcher, 1996. <i>Méthodologie d'élaboration de totaux autorisés de captures (TAC) pour le Saumon atlantique (SalmosalarL.) dans le Massif Armoricaïn. Propositions et recommandations scientifiques</i>. GRISAM, Évaluation et gestion des stocks de poissons migrateurs, Doc. sci. tech. 1, 18 p.</p> <p>Rivot E. and Prévost E., 2002. Hierarchical Bayesian analysis of capture-mark-recapture data. <i>Canadian Journal of Fisheries and Aquatic Sciences</i> 59:1768-1784.</p>

Egg-to-smolt relationship estimated by the model

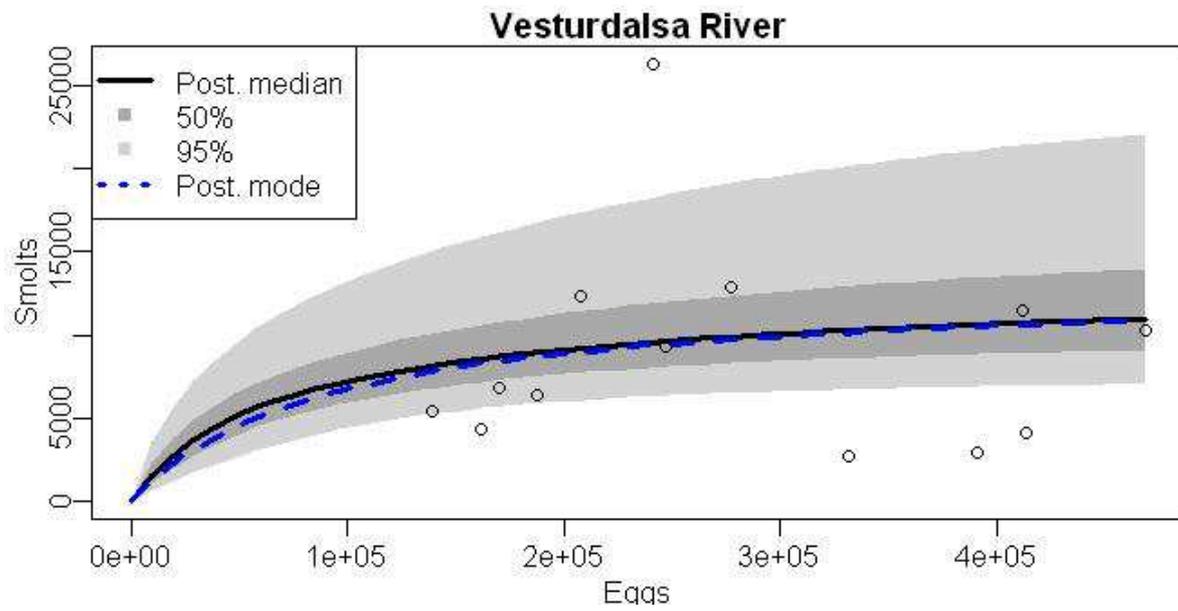


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

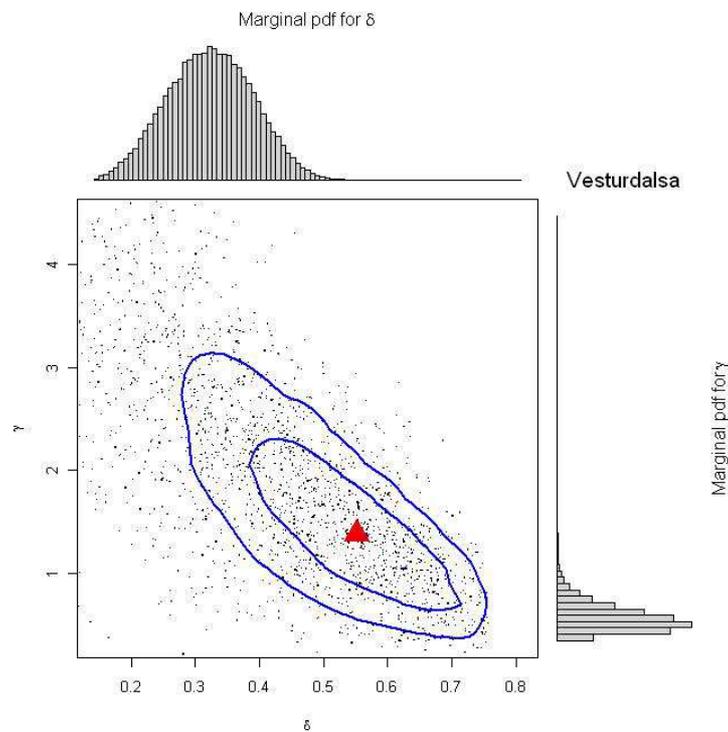


River	Vesturdalsa River (Northern NEc, Iceland)
Contact	Gudni Gudbergsson (Veidimal, Iceland)
<u>River Informations</u>	
Latitude	65.7°
Longitude	-14.96°
Riverine Wetted A.	19.9711 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	0
Mean Age of Smolts	3.57
ObsPeriod	1985, 1986, 1990 – 2003 (n <sub>obs</sub> =16) → 1990 – 2003 (n <sub>obs</sub> =14)
<u>Monitoring</u>	<p>A fish counter has been operated since 1996. Exploitation rate is know in that period and the average is used for back calculation from the rod catch of returns for the whole period. Otherwise the method is the same as used in R. Elidaar. <b>Eggs</b> are estimated by an estimation of 5808 eggs/1SW female and 11776 eggs/2SW females (two-sea-winter).</p> <p><b>Smolt</b> abundance is evaluated by the studies conducted at the fish counter. Smolt ages are estimated by scale sampling.</p>
<u>Bibliography</u>	Crozier W.W., Potter E.C.E., Prévost E., Schön P-J. and Ó Maoiléidigh N., 2003. A coordinated approach towards the development of a scientific basis for management of wild Atlantic salmon in the North-East Atlantic (SALMODEL). Queen's University of Belfast, Belfast. Chapter 4:71-104.

Egg-to-smolt relationship estimated by the model

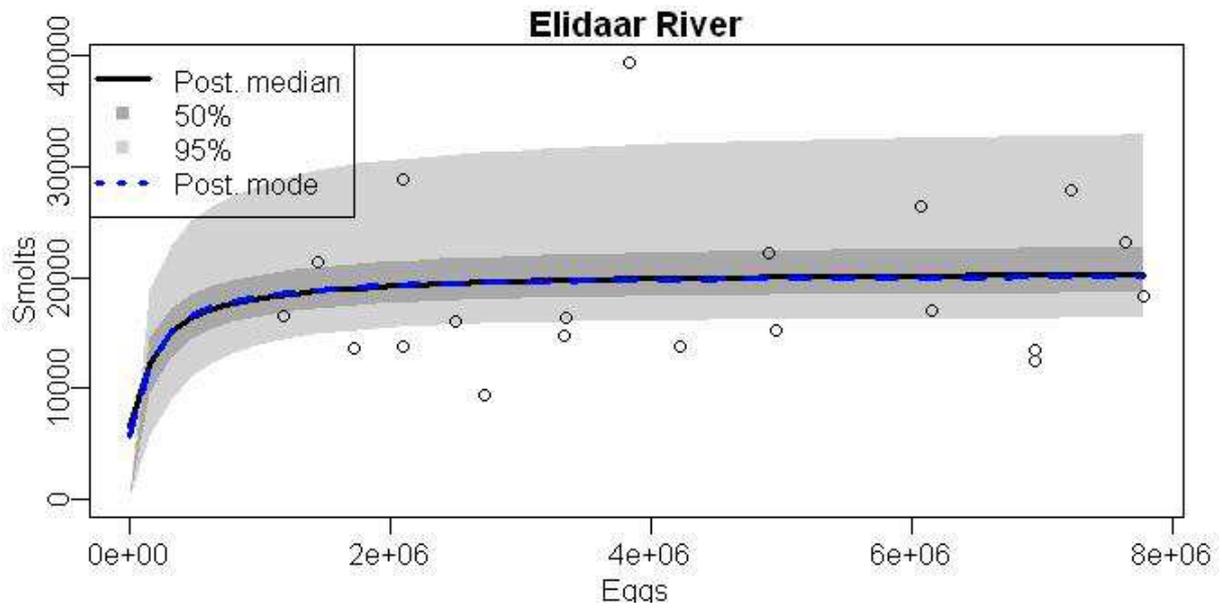


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

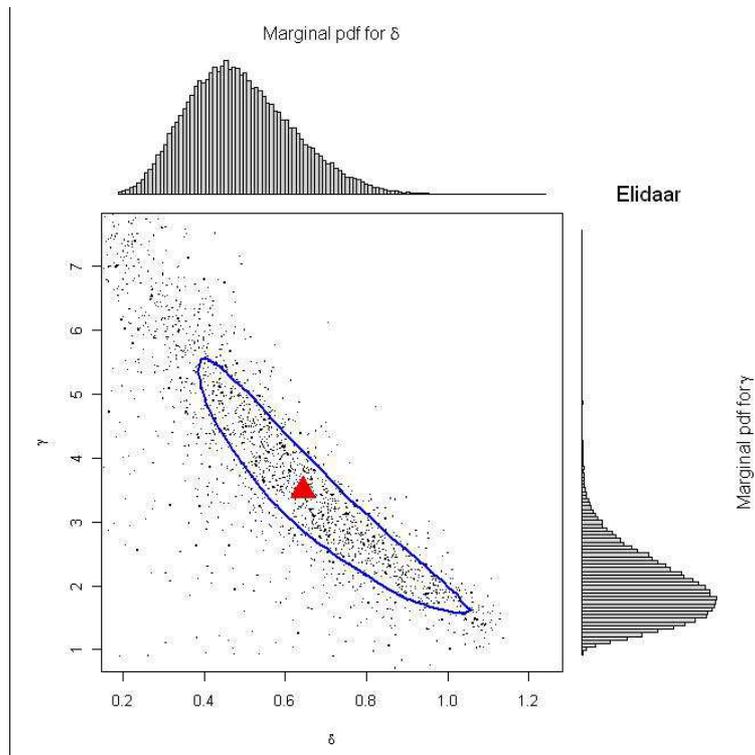


River	Elidaar River (Southern NEc, Iceland)
Contact	Gudni Gudbergsson (Veidimal, Iceland)
<u>River Informations</u>	
Latitude	65°
Longitude	-22°
Riverine Wetted A.	49.59 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	0
Mean Age of Smolts	2.65
ObsPeriod	1985 – 2004 (n <sub>obs</sub> =21)
<u>Monitoring</u>	There is a fish counter in R. Elidaar and a good recording of the catch as in most other rivers in Iceland. The number of 1SW and 2SW in the run is estimated to be the same as in the rod catch and 1SW is dominating. The number of male and female in the spawning stock is estimated proportional to what it is in the rod catch. As the fish in R. Eliddar are smaller than in R. Vesturdalsa the average number of <b>eggs</b> /1SW is 5725 and 10265 for 2SW (based on a study on several salmon stocks) <b>Smolts:</b> same as for R. Vesturdalsa
<u>Bibliography</u>	Crozier W.W., Potter E.C.E., Prévost E., Schön P-J. and Ó Maoiléidigh N., 2003. A coordinated approach towards the development of a scientific basis for management of wild Atlantic salmon in the North-East Atlantic (SALMODEL). Queen's University of Belfast, Belfast. Chapter 4:71-104.

Egg-to-smolt relationship estimated by the model

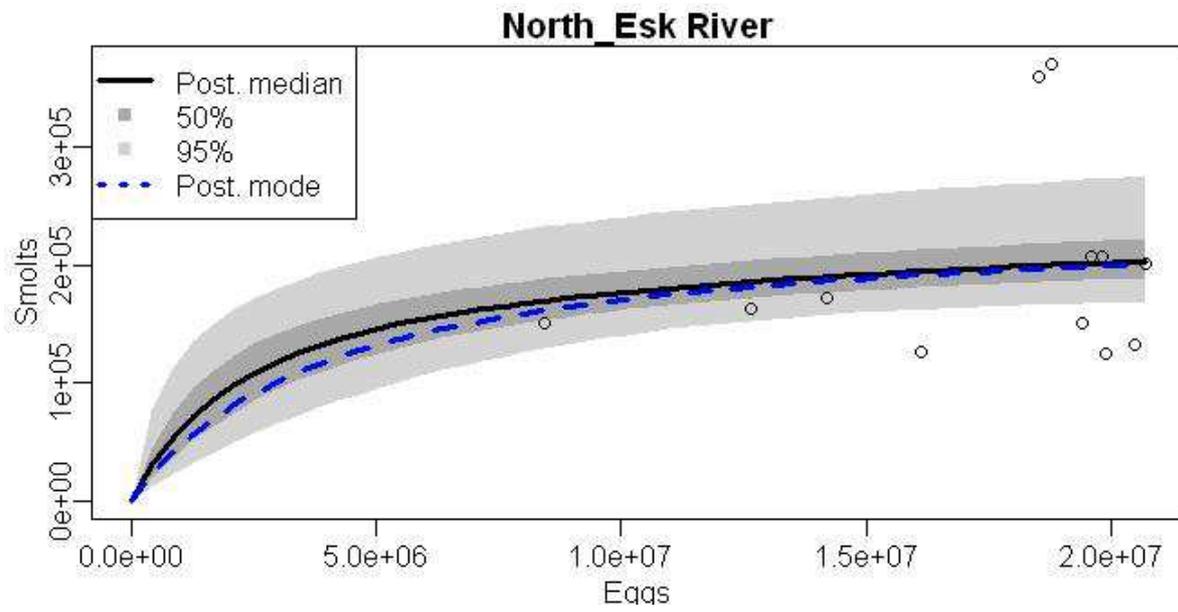


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

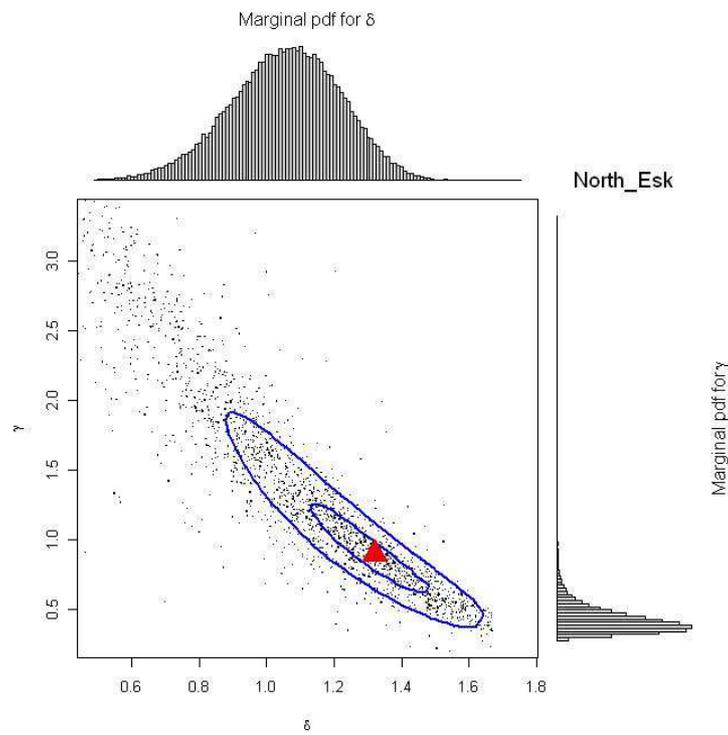


River	North Esk River (Southern NEc, UK, Scotland)
Contact	Gordon Smith (Scottish Government, UK)
<u>River Informations</u>	
Latitude	57°
Longitude	-2.7°
Riverine Wetted A.	260.1924 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	7.724 10 <sup>4</sup> m <sup>2</sup>
Mean Age of Smolts	2.14
ObsPeriod	1987 – 1998, 2003 – 2005 (n <sub>obs</sub> =15) → 1987 – 1998 (n <sub>obs</sub> =12)
<u>Monitoring</u>	<p>Data are produced from counts and reported catches of net and rod fisheries.</p> <ul style="list-style-type: none"> <li>• Spawners are estimated from rivers counts corrected by the rod catch killed (retained and estimate of release mortality). <b>Eggs</b> are then calculated by: <ul style="list-style-type: none"> <li>- an estimate sea age split using sample data,</li> <li>- an estimate of the female proportion from sample data,</li> <li>- an estimate annual median length by month using sample data</li> <li>- an estimate eggs per female using median lengths</li> </ul> </li> <li>• <b>Smolts</b> estimates are the one reported to ICES document: <p>“Estimates of smolt production for the North Esk have been derived using a stratified mark, release and recapture model (Bjorkstedt, 2005) using data collected at a trap sited on a lade that runs parallel to the main river over a distance of approximately 4 km, for the period 1979 to 2011. Of these data, six were considered unreliable. Five of these occurred in years when high flows resulted in too few recaptures to provide an informative estimate (1983, 1986, 1988, 2004 and 2010). In both 2003 and 2011, consistently high flows over much of the latter part of the smolt run resulted in a partial estimate of the smolt production of the river. The data for these years were therefore removed from the time series before it was used, in conjunction with estimates of returning adults, to estimate survival rates. “ (pers. com.)</p> </li> </ul>
<u>Bibliography</u>	Bjorksted, E. P. 2005. DARR 2.0: Updated software for estimating abundance from stratified mark-recapture data. NOAA-TM-NMFS-SWFSC-368

Egg-to-smolt relationship estimated by the model

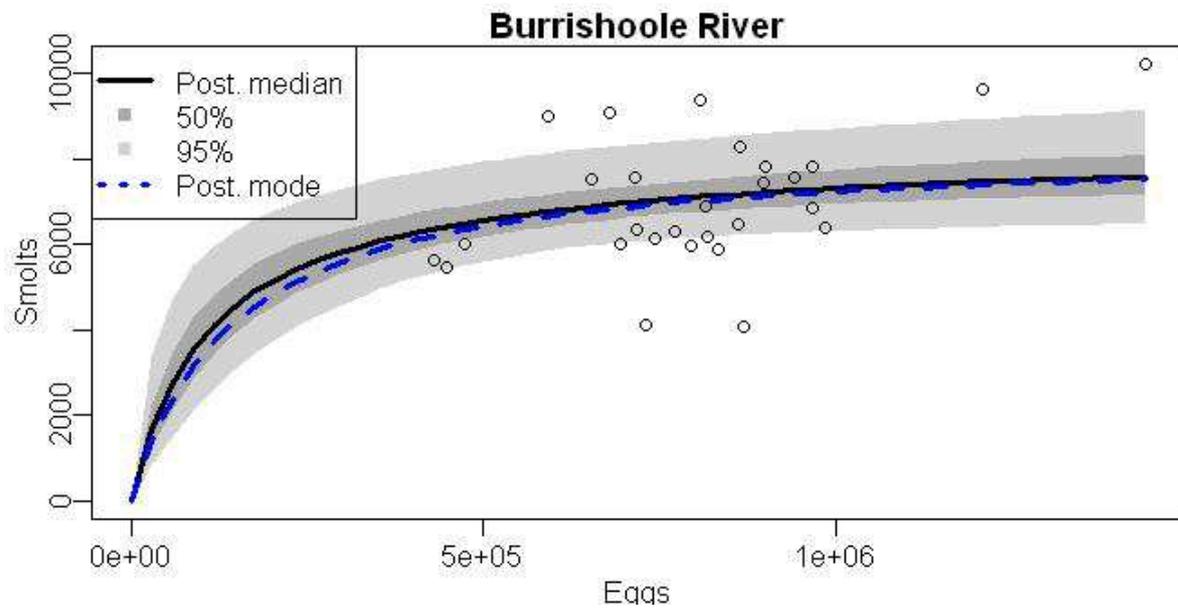


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

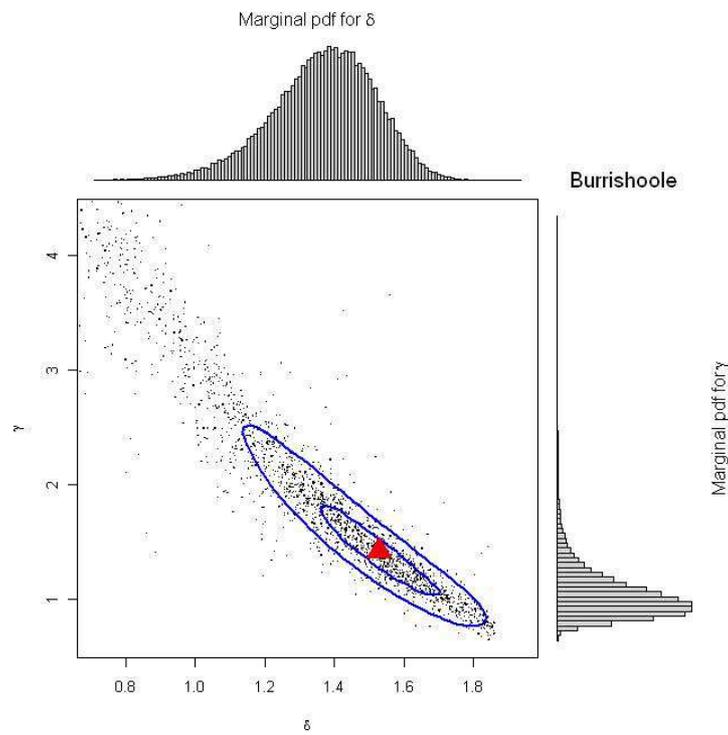


River	Burrishoole River (Southern NEc, Ireland)
Contact	Jonathan White (Marine Institute, Ireland)
<u>River Informations</u>	
Latitude	53.9°
Longitude	-9.55°
Riverine Wetted A.	12.5474 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	440.5631 10 <sup>4</sup> m <sup>2</sup>
Mean Age of Smolts	1.87
ObsPeriod	1979 – 2006 (n <sub>obs</sub> =28)
<u>Monitoring</u>	<p>Hatchery reared salmon are existing in the R. Burrishoole, but they are tagged and the data used in this study was only the one of natural populations.</p> <ol style="list-style-type: none"> <li>Total adult trapping facilities are located directly at the head of tide. Adult counts are corrected for angling losses upstream of the trap to derive spawning escapement. Adult spawner are converted into <b>eggs</b> by applying a constant through time female proportion and fecundity: <ul style="list-style-type: none"> <li>60% of 1SW salmon are female, spawning 2769,56 eggs each.</li> <li>85% of MSW salmon are females, spawning 6184,33 eggs each.</li> </ul> </li> <li><b>Smolts</b> age was only studied in 1981, 1982,1983, 2006 and 2008 and the age class proportions are highly different, as if a shift in smolt distribution in-between: <ul style="list-style-type: none"> <li>Old surveys shows fewer 1+ smolt (≈ 3%) and more 2+ (≈92%) and 3+ (≈5%) (Piggins and Mills, 1985)</li> <li>The Marine Institute of Ireland conducted surveys in 2006 and 2008 that showed more 1+ (≈ 14%) salmon and fewer 2+ (≈ 85%) and 3+ (≈ 1%).</li> </ul> </li> </ol> <p>This changing trend in smolt age distribution was modeled with a linear interpolation from the older state to the latest</p>
<u>Bibliography</u>	<p>Crozier W.W., Potter E.C.E., Prévost E., Schön P-J. and Ó Maoiléidigh N., 2003. A coordinated approach towards the development of a scientific basis for management of wild Atlantic salmon in the North-East Atlantic (SALMODEL). Queen's University of Belfast, Belfast. Chapter 4:71-104.</p> <p>Piggins, D.G. and Mills, C.P.R., 1985. Comparative aspects of the biology of naturally produced and hatchery reared Atlantic salmon smolts. Aquaculture 45, 321- 333.</p>

Egg-to-smolt relationship estimated by the model

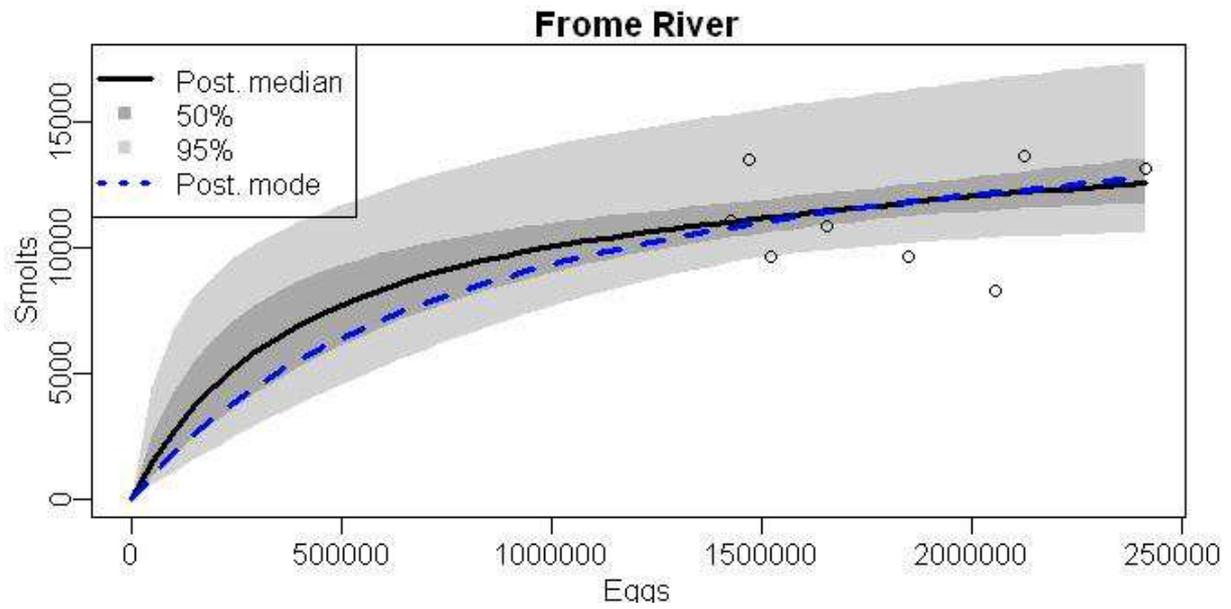


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

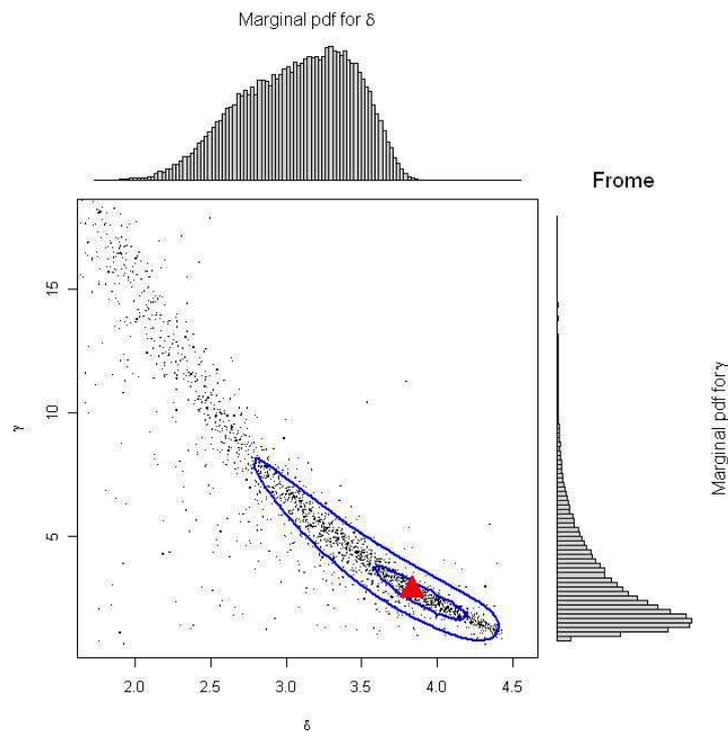


River	Frome River (Southern NEc, UK (England and Wales))
Contact	Anton Ibbotson (Game and Wildlife Conservation Trust, East Stoke, UK)
<u>River Informations</u>	
Latitude	51.5°
Longitude	-2.7°
Riverine Wetted A.	61 10 <sup>4</sup> m <sup>2</sup> (calculated by a raw calculation (average width (10m) x estimated length (61km)))
Lac. Wetted A.	0
Mean Age of Smolts	1.02
ObsPeriod	2002 – 2009 (n <sub>obs</sub> =8)
<u>Monitoring</u>	<p><b>Eggs</b> abundance is estimated by the mean of female proportion and size-fecundity relationship estimated from 1950 to 2002 for the Frome R. Returning adults and female proportion was given for each year.</p> <p><b>Smolts</b> year-class is taken as constant for the Frome R. (95% of 1+ smolt and 5% of 2+ smolts) and the estimation of smolt was given from counting from 2002 to 2011 with a missing year (2005). As this missing data would have make impossible the use of 2 cohorts, the mean value of smolt abundance was taken to fill the only missing year</p>
<u>Bibliography</u>	

Egg-to-smolt relationship estimated by the model

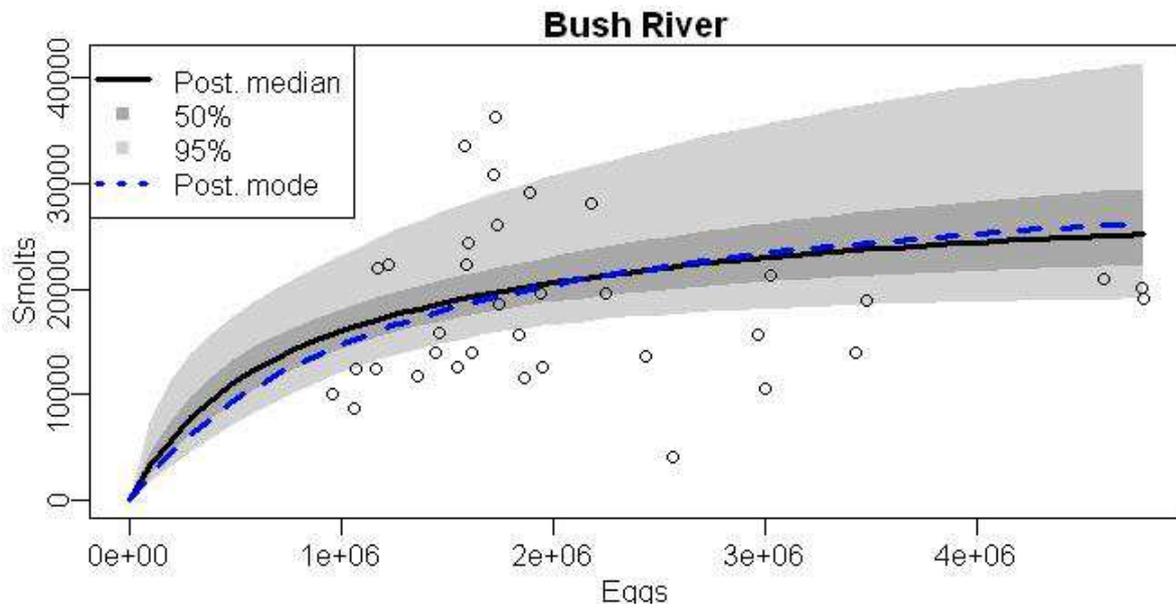


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

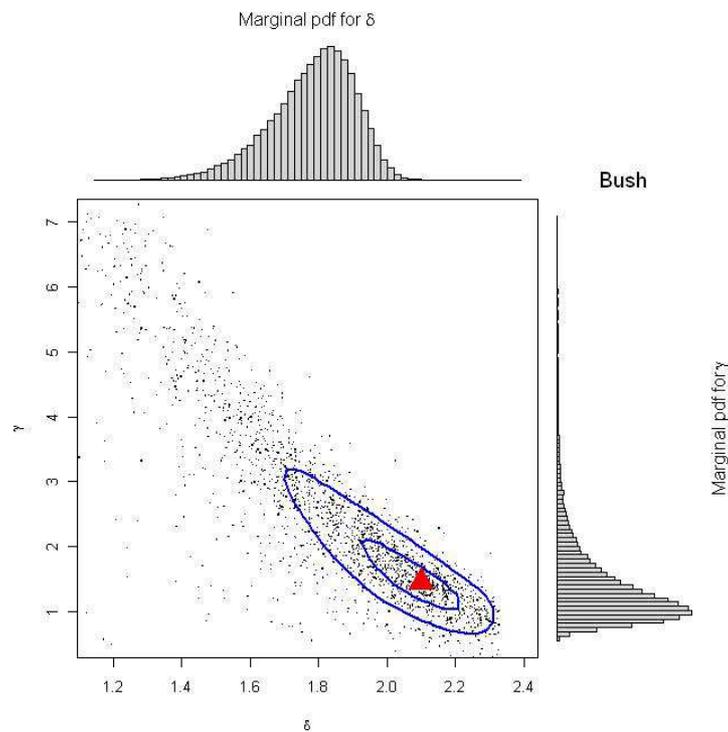


River	Bush River (Southern NEc, UK (Northern Ireland))
Contact	Richard Kennedy/ Dennis Ensing (Agri Food and Biosciences Institute, UK)
<u>River Informations</u>	
Latitude	55.2°
Longitude	-10°
Riverine Wetted A.	84.55 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	0
Mean Age of Smolts	2.99
ObsPeriod	1973 – 2007 (n <sub>obs</sub> =27)
<u>Monitoring</u>	<p>The adults estimates are derived from total trapping of adults 3km from the head of tide. No spawning occurs below the trap. Counts are highly reliable. Adult counts are corrected for angling and other losses upstream of the trap between trapping and spawning time, and a proportion of 0.6 female and 3400 <b>eggs</b> per hen applied to obtain eggs deposited. As the Bush R. is dominated by 1SW fish (90-95%), no returning adult break by time at sea was conducted.</p> <p><b>Smolts</b> are estimated by counting and the age distribution is determined</p> <p>In some years there was some <b>stocking</b> carried out and stocked unfed fry are released (without tagging) in the stream. They are then counted as smolt just as natural individuals. This occurs in 16 years over 35 of the data series. However, field studies have shown that stocked fry have a survival rate to smolt of around 1%, which is very similar to the wild ova to smolt survival (≈1%). The number of stocking fry corresponds to 20% of the natural egg deposition (38% at highest) and the cohort is never driven by this kind of individuals. Preliminary studies have not shown significant differences in survival according to stocking level. Then, equivalence between wild ova and stocked unfed fry was assumed and the number of stocked unfed fry was added to the estimated natural egg deposition.</p>
<u>Bibliography</u>	Crozier W.W., Potter E.C.E., Prévost E., Schön P-J. and Ó Maoiléidigh N., 2003. A coordinated approach towards the development of a scientific basis for management of wild Atlantic salmon in the North-East Atlantic (SALMODEL). Queen's University of Belfast, Belfast. Chapter 4:71-104.

Egg-to-smolt relationship estimated by the model

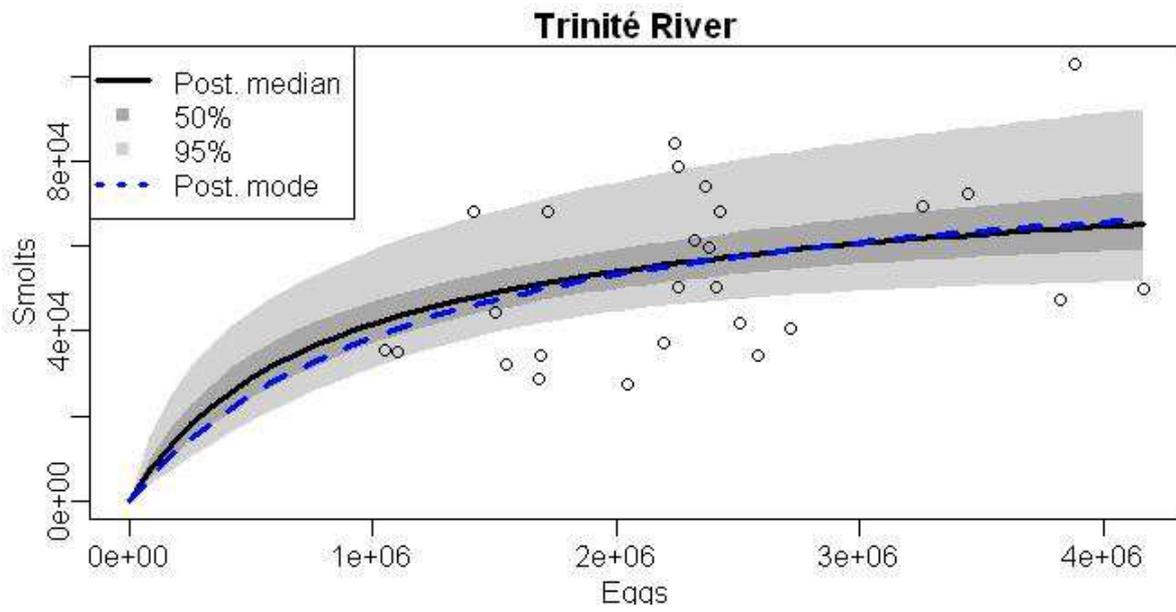


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

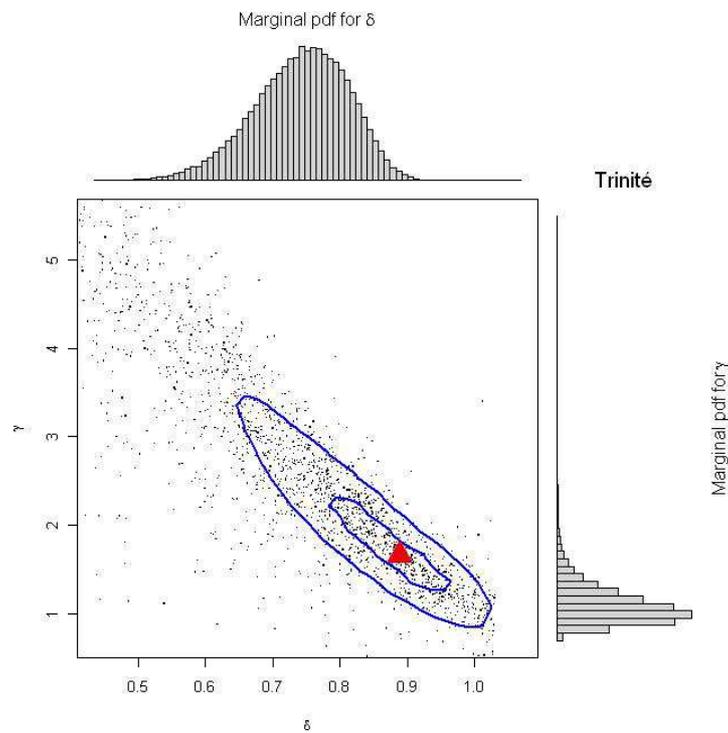


River	Trinité River (NWc, Canada, Québec)
Contact	Mélanie Dionne (Ministère des Ressources Naturelles et de la Faune, Canada, Québec), Valérie Cauchon (MRNF, Canada, Québec)
<u>River Informations</u>	
Latitude	49.4°
Longitude	-67.3°
Riverine Wetted A.	211.19 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	0
Mean Age of Smolts	2.99
ObsPeriod	1980 – 2006 (n <sub>obs</sub> =27)
<u>Monitoring</u>	<b>Eggs</b> are estimated by counted adults in a counting fence Estimation of <b>smolt</b> abundance relies on a mark-recapture method
<u>Bibliography</u>	D. FOURNIER et V. CAUCHON. 2009. Travaux de recherche sur le saumon des rivières Saint-Jean et de la Trinité en 2008, ministère des Ressources naturelles et de la Faune, Direction de l'expertise sur la faune et ses habitats, Service de la faune aquatique, 77 p.

Egg-to-smolt relationship estimated by the model

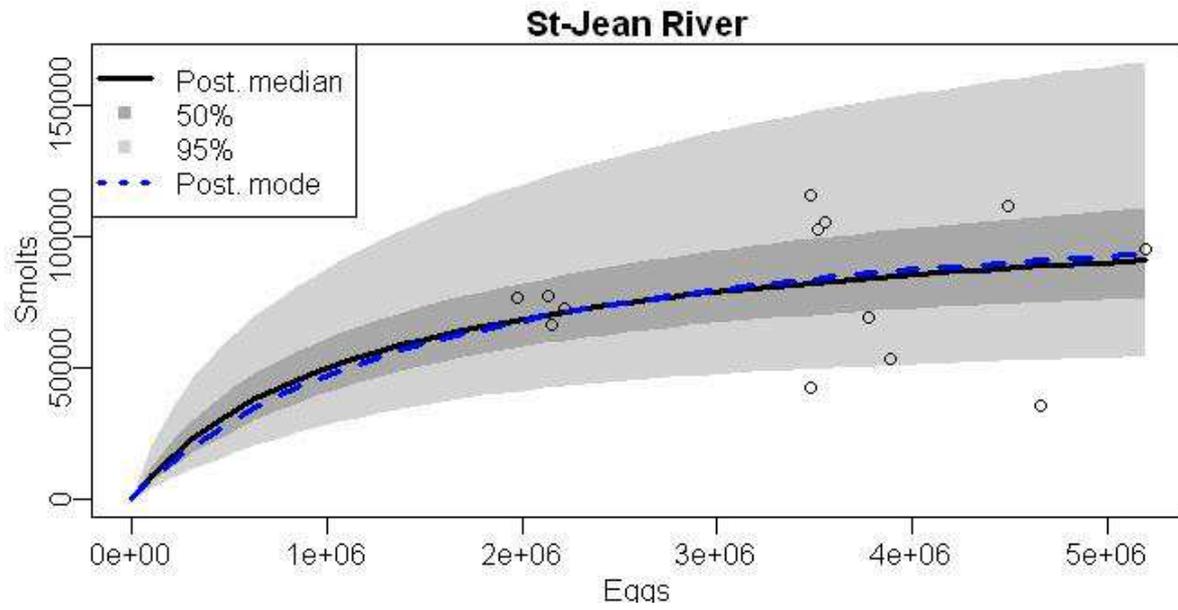


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

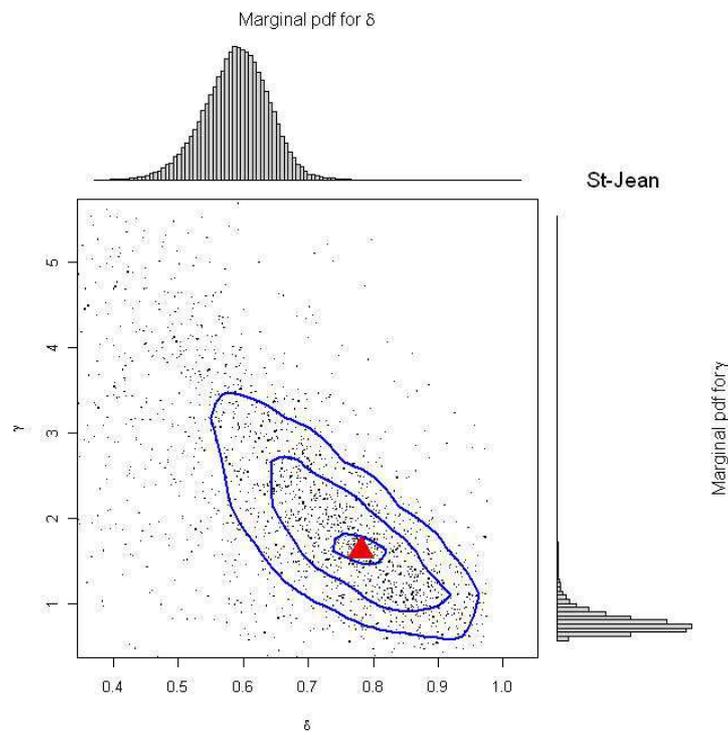


River	St-Jean River (NWc, Canda, Québec)
Contact	Mélanie Dionne (Ministère des Ressources Naturelles et de la Faune, Canada, Québec), Valérie Cauchon (MRNF, Canada, Québec)
<u>River Informations</u>	
Latitude	48.8°
Longitude	-64.4°
Riverine Wetted A.	308.13 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	0
Mean Age of Smolts	3.4
ObsPeriod	1985 – 1991 & 1994 – 2006 (n <sub>obs</sub> =22) → 1994 – 2006 (n <sub>obs</sub> =13)
<u>Monitoring</u>	<b>Eggs</b> are estimated by counted adults in the river by several operations (fishing, apnea observations...) Estimation of <b>smolt</b> abundance relies on a mark-recapture method
<u>Bibliography</u>	D. FOURNIER et V. CAUCHON. 2009. Travaux de recherche sur le saumon des rivières Saint-Jean et de la Trinité en 2008, ministère des Ressources naturelles et de la Faune, Direction de l'expertise sur la faune et ses habitats, Service de la faune aquatique, 77 p.

Egg-to-smolt relationship estimated by the model

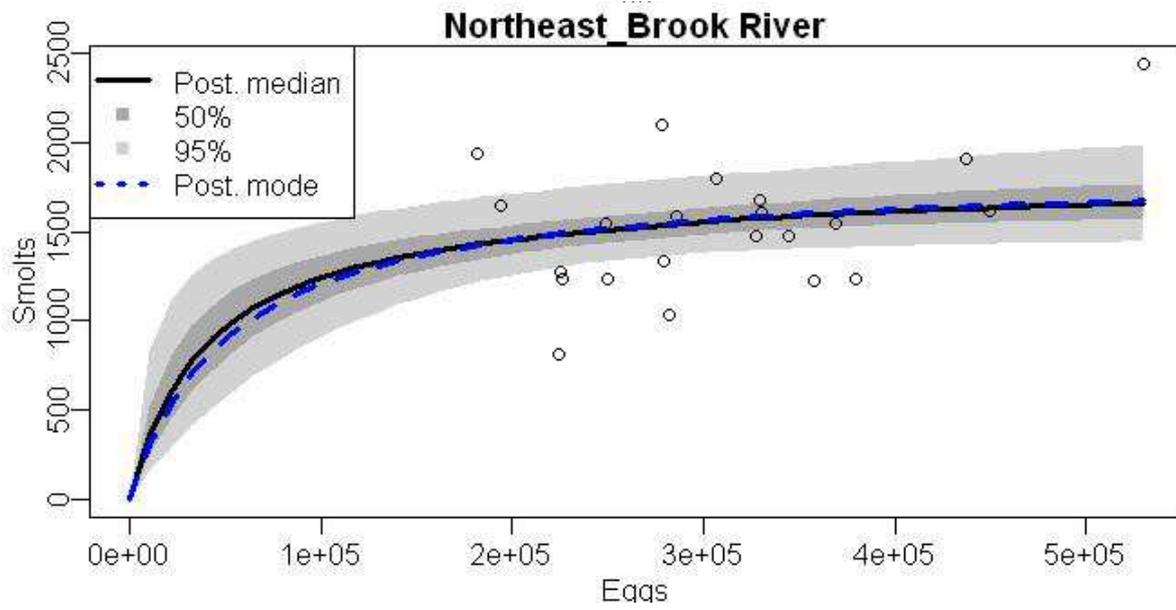


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

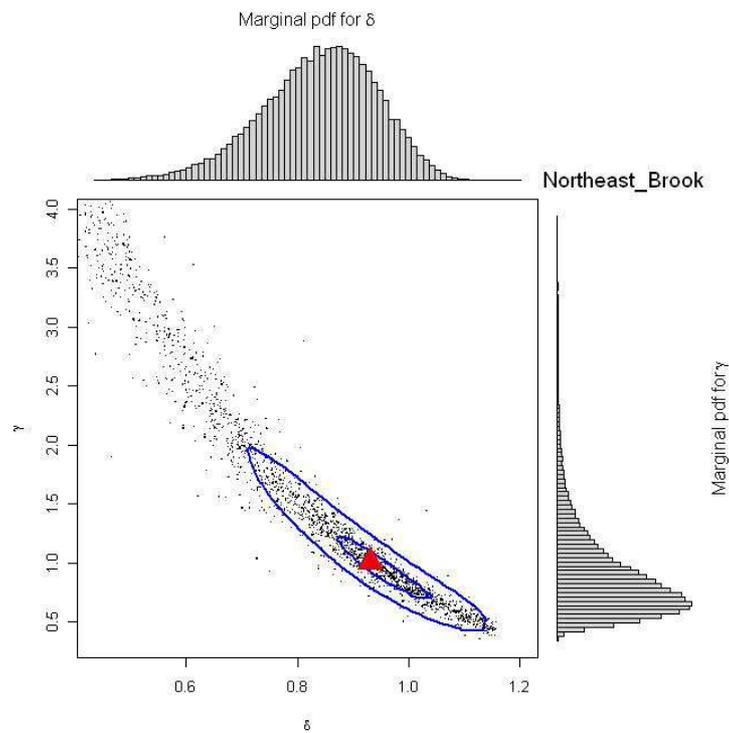


<b>River</b>	<b>Northeast Brook River (NWc, Canada, Newfoundland, Trepassey)</b>
<b>Contact</b>	<b>Martha J. Robertson (Fisheries and Oceans Canada, Canada)</b>
<u>River Informations</u>	
Latitude	46.8°
Longitude	-53.4°
Riverine Wetted A.	5.56 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	0
Mean Age of Smolts	3.61
ObsPeriod	1984 – 2005 (n <sub>obs</sub> =22)
<u>Monitoring</u>	Mark-recapture studies or counting fences allow returning adults (and then egg abundance) and downstream migrating smolts estimations every year for most of studied Newfoundland rivers
<u>Bibliography</u>	O'Connell M.F., Dempson J.B., 1995. Target spawning requirements for Atlantic salmon, <i>Salmosalar</i> L., in Newfoundland rivers. Fisheries Management and Ecology, <b>2</b> . 161 – 170.

Egg-to-smolt relationship estimated by the model

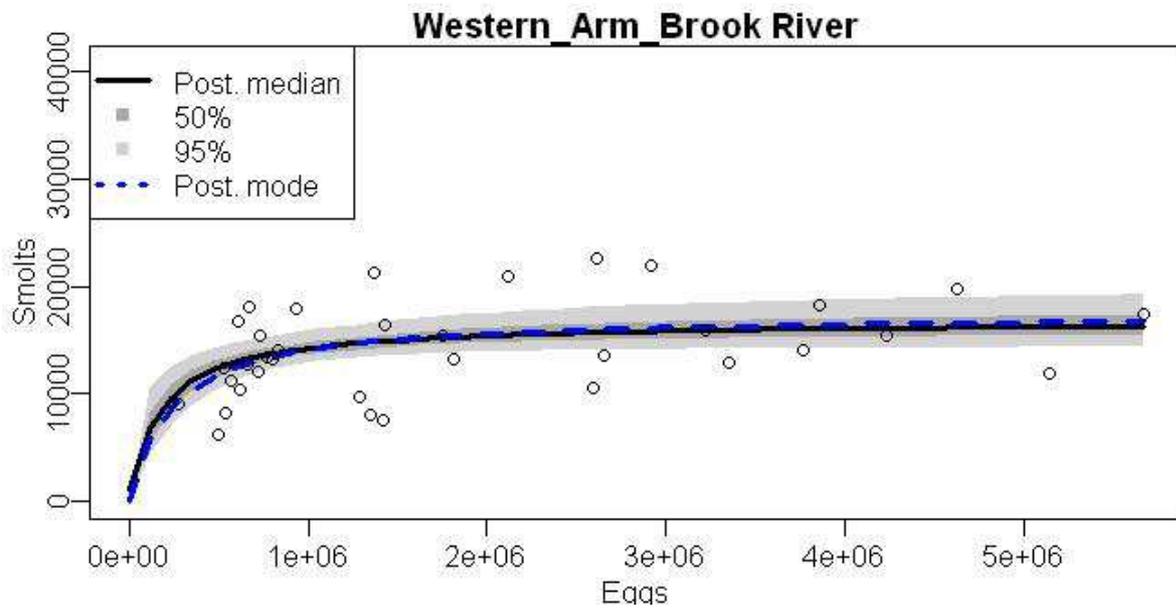


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

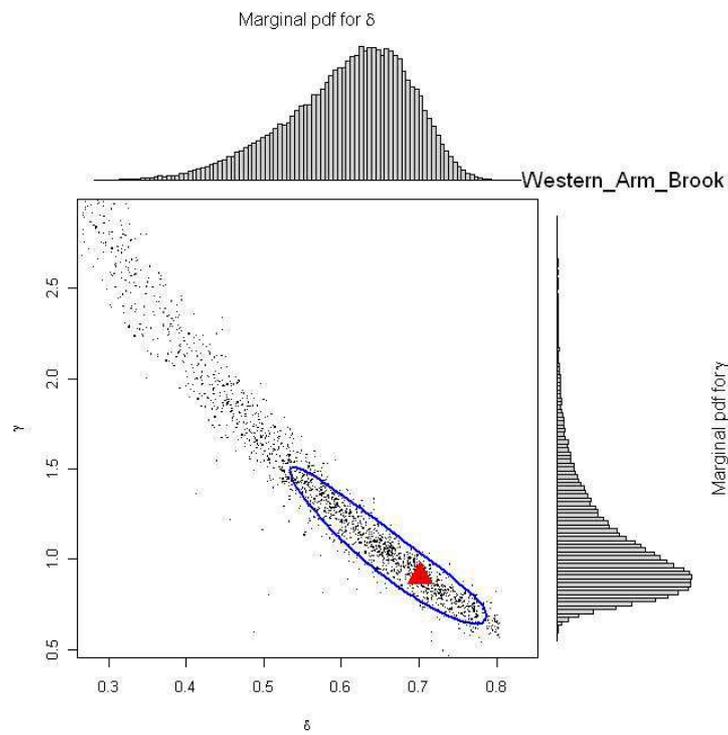


<b>River</b>	<b>Western Arm Brook River (NWc, Canada, Newfoundland)</b>
<b>Contact</b>	<b>Martha J. Robertson (Fisheries and Oceans Canada, Canada)</b>
<u>River Informations</u>	
Latitude	51.2°
Longitude	-56.93°
Riverine Wetted A.	29 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	2017 10 <sup>4</sup> m <sup>2</sup>
Mean Age of Smolts	3.75
ObsPeriod	1971 – 2005 (n <sub>obs</sub> =35)
<u>Monitoring</u>	Mark-recapture studies or counting fences allow returning adults (and then egg abundance) and downstream migrating smolts estimations every year for most of studied Newfoundland rivers
<u>Bibliography</u>	O'Connell M.F., Dempson J.B., 1995. Target spawning requirements for Atlantic salmon, <i>Salmosalar</i> L., in Newfoundland rivers. Fisheries Management and Ecology, <b>2</b> . 161 – 170.

Egg-to-smolt relationship estimated by the model

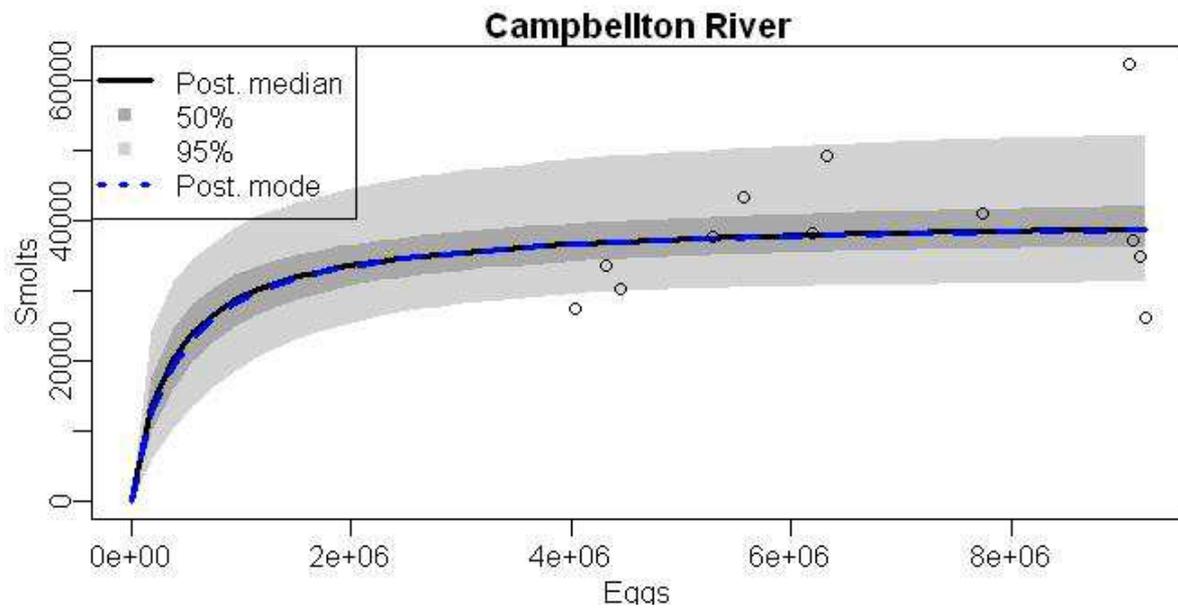


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

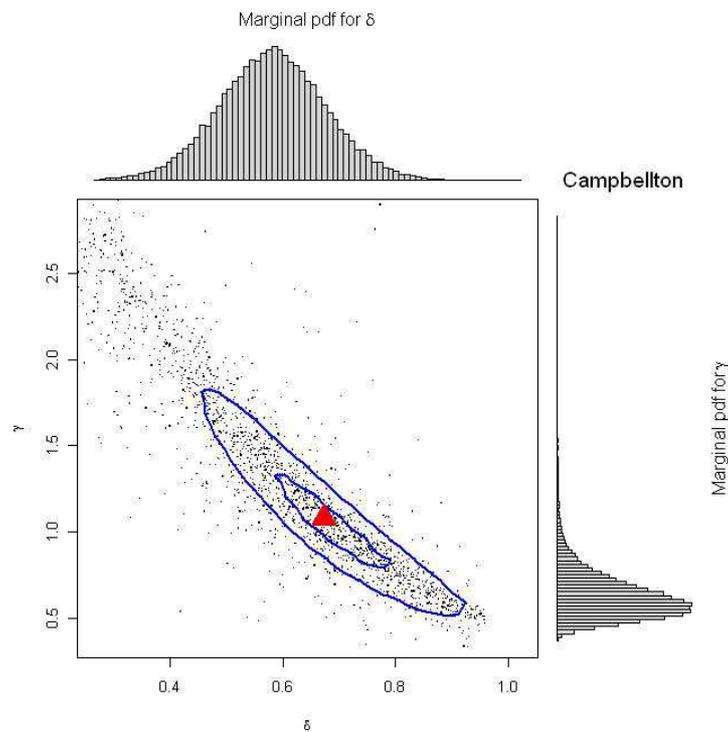


<b>River</b>	<b>Campbellton River (NWc, Canada, Newfoundland)</b>
<b>Contact</b>	<b>Martha J. Robertson (Fisheries and Oceans Canada, Canada)</b>
<u>River Informations</u>	
Latitude	49.27°
Longitude	-54.93°
Riverine Wetted A.	59.6 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	4037 10 <sup>4</sup> m <sup>2</sup>
Mean Age of Smolts	3.54
ObsPeriod	1993 – 2004 (n <sub>obs</sub> =12)
<u>Monitoring</u>	Counting fence installed 345m upstream from the river mouth was used since 1993 to evaluate smolt runs. Adult fence was situated approximately 212 m from the mouth and egg abundance was estimated through a size-dependent fecundity (small or large individuals) of counted females.  Detailed methodology is described in the 2000 report of Downton P.R., REddin D.G. and Johnson R.W.
<u>Bibliography</u>	Downton P.R., REddin D.G. and Johnson R.W., 2001. Status of Atlantic salmon ( <i>SalmosalarL.</i> ) in Campbellton River, Notre Dame Bay (SFA 4), Newfoundland in 2000. Research Document 2001/31. Canadian Science Advisory Secretariat.Fisheries and Oceans Canada.

Egg-to-smolt relationship estimated by the model

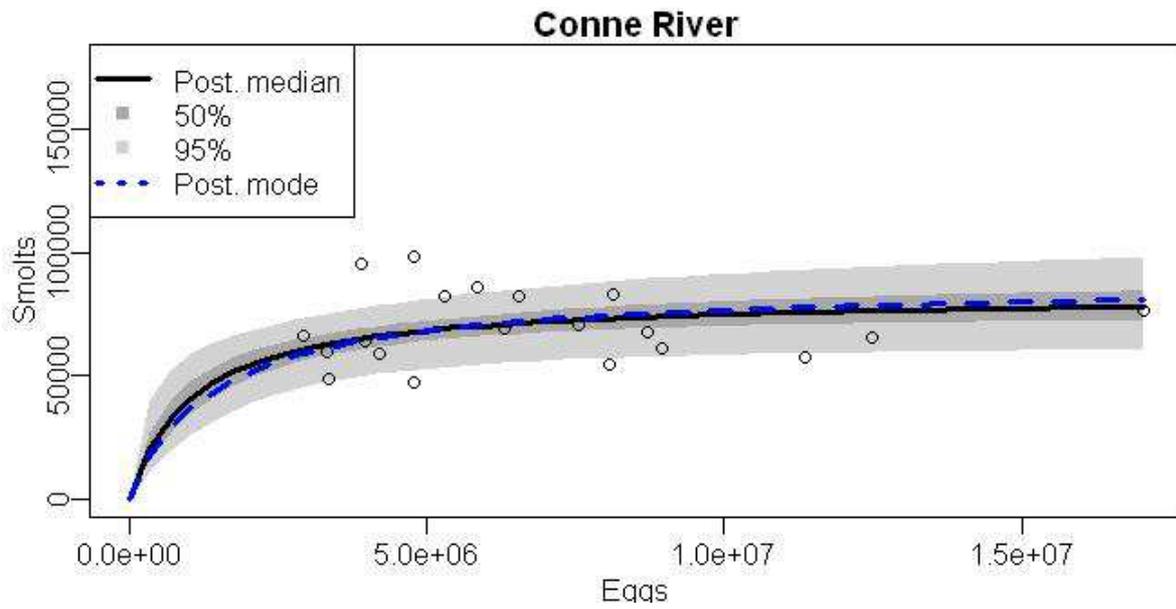


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

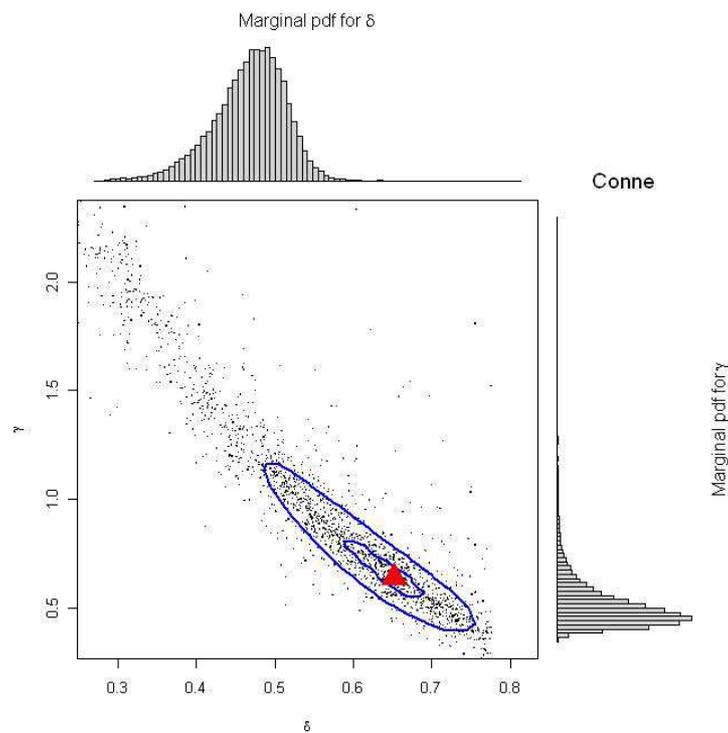


<b>River</b>	<b>Conne River (NWc, Canada, Newfoundland)</b>
<b>Contact</b>	<b>Martha J. Robertson (Fisheries and Oceans Canada, Canada)</b>
<u>River Informations</u>	
Latitude	47.9°
Longitude	-55.7°
Riverine Wetted A.	131.8 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	3187 10 <sup>4</sup> m <sup>2</sup>
Mean Age of Smolts	4.28
ObsPeriod	1986 – 2005 (n <sub>obs</sub> =20)
<u>Monitoring</u>	Mark-recapture studies and counting fences allow returning adults (and then egg abundance) and downstream migrating smolts estimations every year.
<u>Bibliography</u>	<p>O'Connell M.F., Dempson J.B., 1995. Target spawning requirements for Atlantic salmon, <i>Salmosalar</i> L., in Newfoundland rivers. Fisheries Management and Ecology, <b>2</b>. 161 – 170.</p> <p>Dempson, J. et al., 1999. Evaluation of an alternative strategy to enhance salmon populations: Cage rearing wild smolts from Conne River, Newfoundland. <i>ICES Journal of Marine Science</i>, 56(4), p.422-432.</p>

Egg-to-smolt relationship estimated by the model

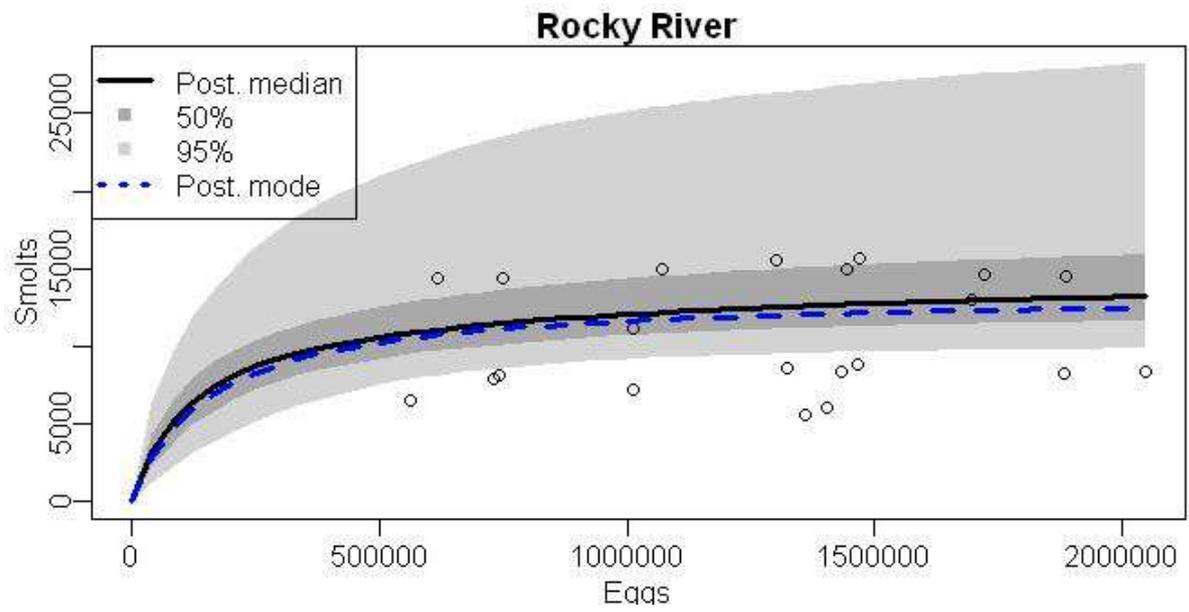


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

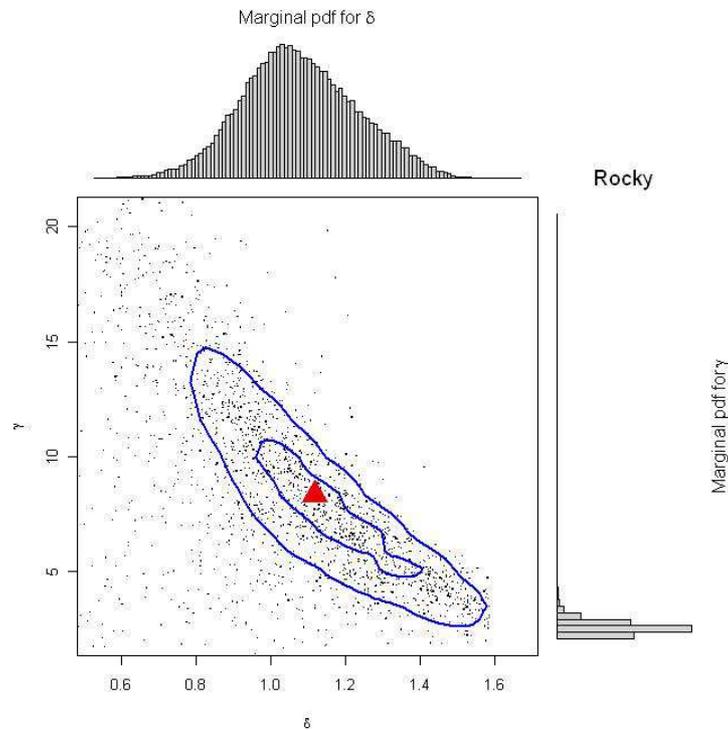


<b>River</b>	<b>Rocky River (NWc, Canada, Newfoundland)</b>
<b>Contact</b>	<b>Martha J. Robertson (Fisheries and Oceans Canada, Canada)</b>
<u>River Informations</u>	
Latitude	47.22°
Longitude	-53.57°
Riverine Wetted A.	108.23 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	2191 10 <sup>4</sup> m <sup>2</sup>
Mean Age of Smolts	2.21
ObsPeriod	1987 – 2007 (n <sub>obs</sub> =21)
<u>Monitoring</u>	Mark-recapture studies or counting fences allow returning adults (and then egg abundance) and downstream migrating smolts estimations every year for most of studied Newfoundland rivers.
<u>Bibliography</u>	O'Connell M.F., Dempson J.B., 1995. Target spawning requirements for Atlantic salmon, <i>Salmosalar</i> L., in Newfoundland rivers. Fisheries Management and Ecology, <b>2</b> . 161 – 170.

Egg-to-smolt relationship estimated by the model

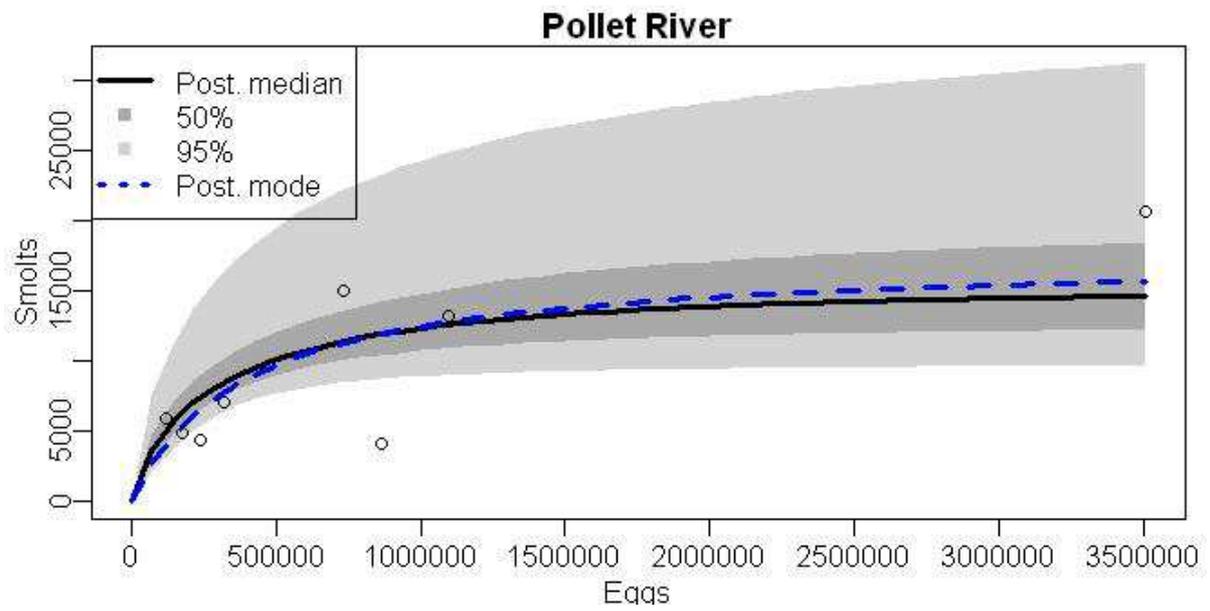


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

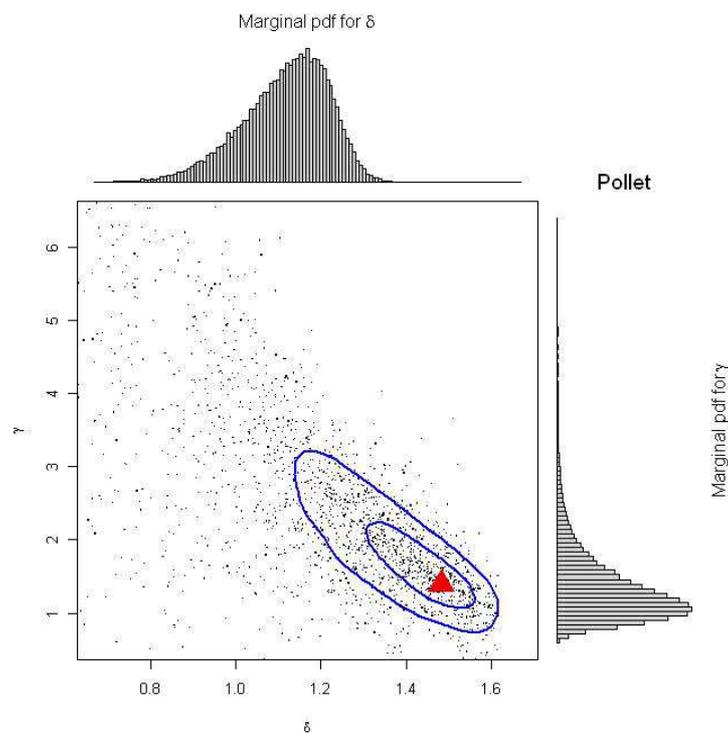


<b>River</b>	<b>Pollet River (NWc, Canada Newfoundland)</b>
<b>Contact</b>	<b>Gérald Chaput (Fisheries and Oceans Canada, Canada)</b>
<u>River Informations</u>	
Latitude	46°
Longitude	-10°
Riverine Wetted A.	36.37 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	0
Mean Age of Smolts	2.12
ObsPeriod	1953 – 1960 (n <sub>obs</sub> =8)
<u>Monitoring</u>	All the adult salmon were enumerated at counting fences or fishways and the estimates of the number of eggs spawned were determined from the biological characteristics of the adults, including proportion of females by size group, fecundity, and average weight or length.
<u>Bibliography</u>	<p><u>Data origin:</u>  Elson, P.F. 1975. Atlantic salmon rivers smolt production and optimal spawning: an overview of natural production. Int. Atl. Salmon Found. Spec. Publ. Ser. 6: 96–119.</p> <p>Chaput, G. et al., 1998. River-specific target spawning requirements for Atlantic salmon (<i>Salmosalar</i>) based on a generalized smolt production model. Canadian Journal of Fisheries and Aquatic Sciences, 55(1), p.246-261.</p>

Egg-to-smolt relationship estimated by the model

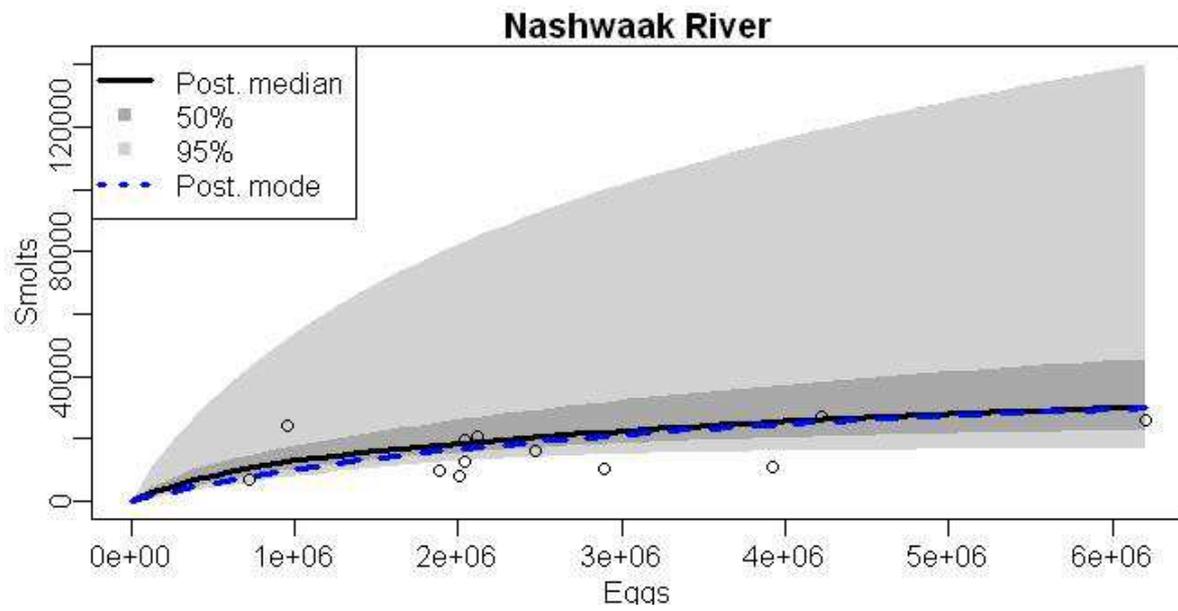


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

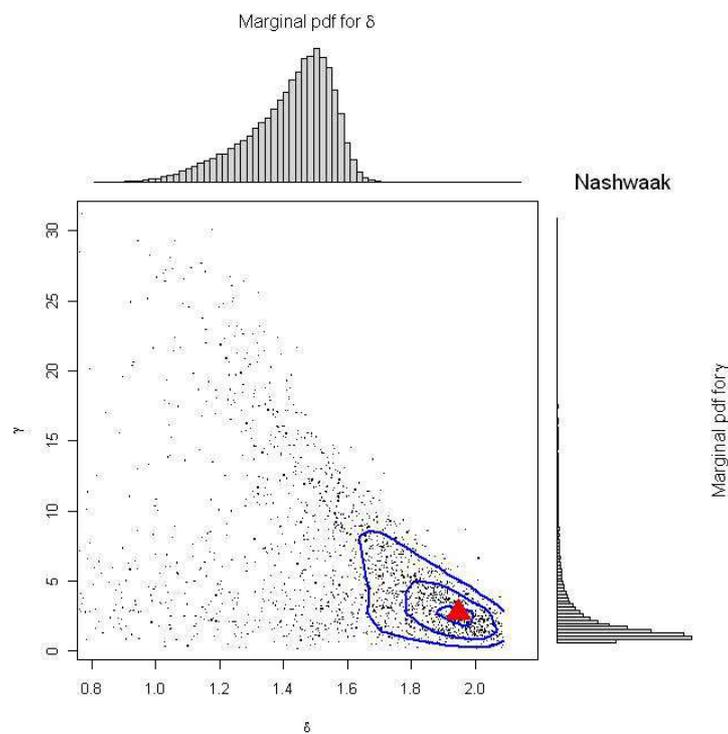


<b>River</b>	<b>Nashwaak River (NWc, Canada, Newfoundland)</b>
<b>Contact</b>	<b>Ross Jones (Fisheries and Oceans Canada, Canada)</b>
<u>River Informations</u>	
Latitude	45°
Longitude	-66.6°
Riverine Wetted A.	512.28 10 <sup>4</sup> m <sup>2</sup> (As only about 90% of the rivers area is assessed by counting methods, the model is using only corresponding surface (90% of the total 7 711 000m <sup>2</sup> of wetted habitat area accessible to salmon).
Lac. Wetted A.	0
Mean Age of Smolts	2.24
ObsPeriod	1995 – 2006 (n <sub>obs</sub> =12)
<u>Monitoring</u>	Returning adults abundance is evaluated in counting fence and smolt one with rotary screw traps.
<u>Bibliography</u>	

Egg-to-smolt relationship estimated by the model

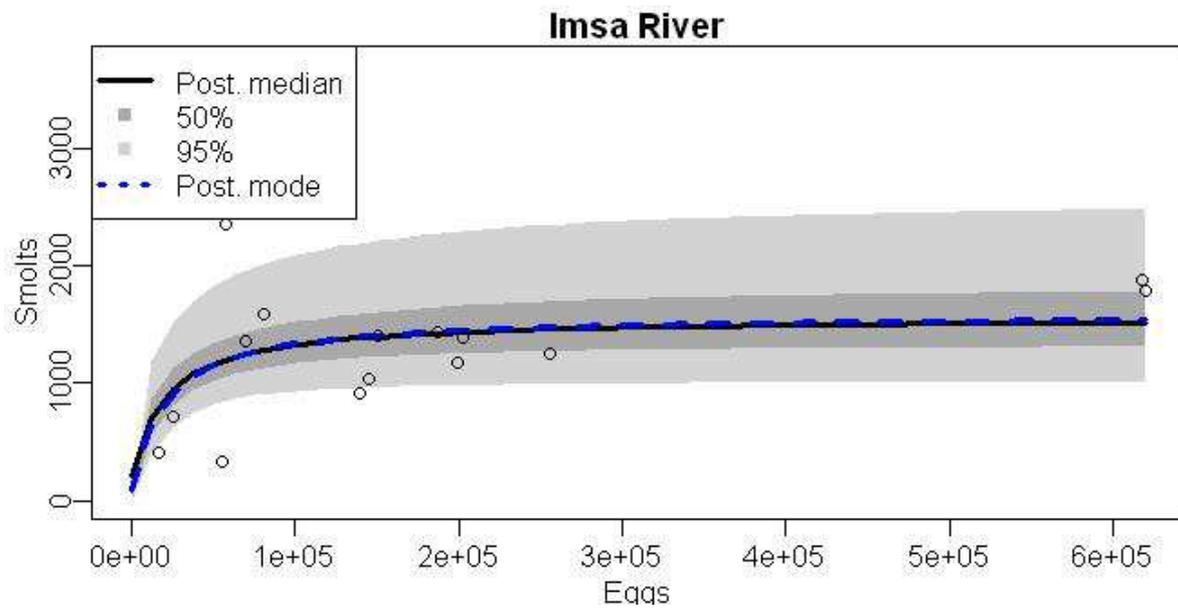


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

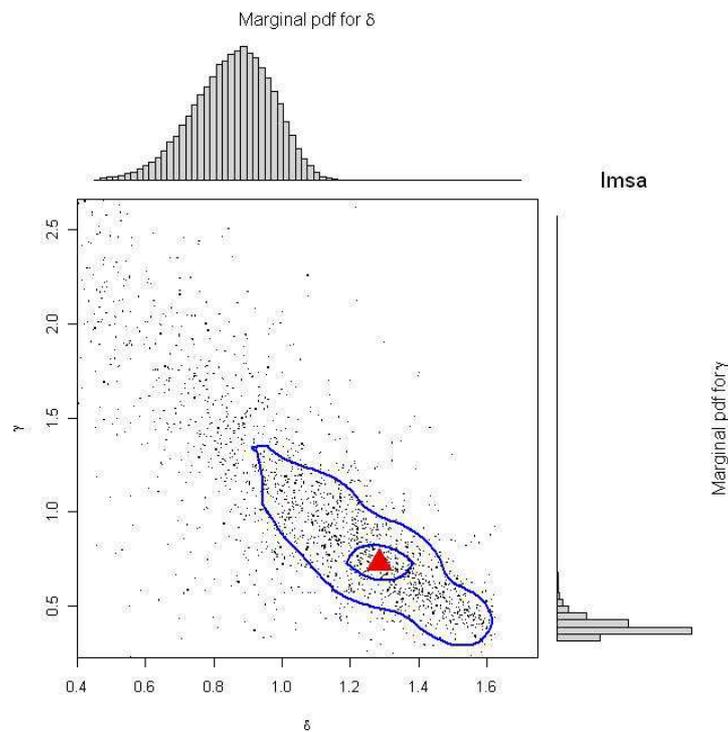


River	Imsa River (NEc, Norway)
<b>Contact</b>	NA
<u>River Informations</u>	
Latitude	58.5°
Longitude	-10°
Riverine Wetted A.	1 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	1536 10 <sup>4</sup> m <sup>2</sup>
Mean Age of Smolts	1.94
ObsPeriod	1976 – 1990 (n <sub>obs</sub> =15)
<u>Monitoring</u>	The method is presented in Jonsson et al. (1998).
<u>Bibliography</u>	<u>Data origin (graph extraction):</u> Jonsson, N., Jonsson, B. & Hansen, L.P., 1998. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon <i>Salmo salar</i> . <i>Journal of Animal Ecology</i> , 67(5), p.751-762.

Egg-to-smolt relationship estimated by the model

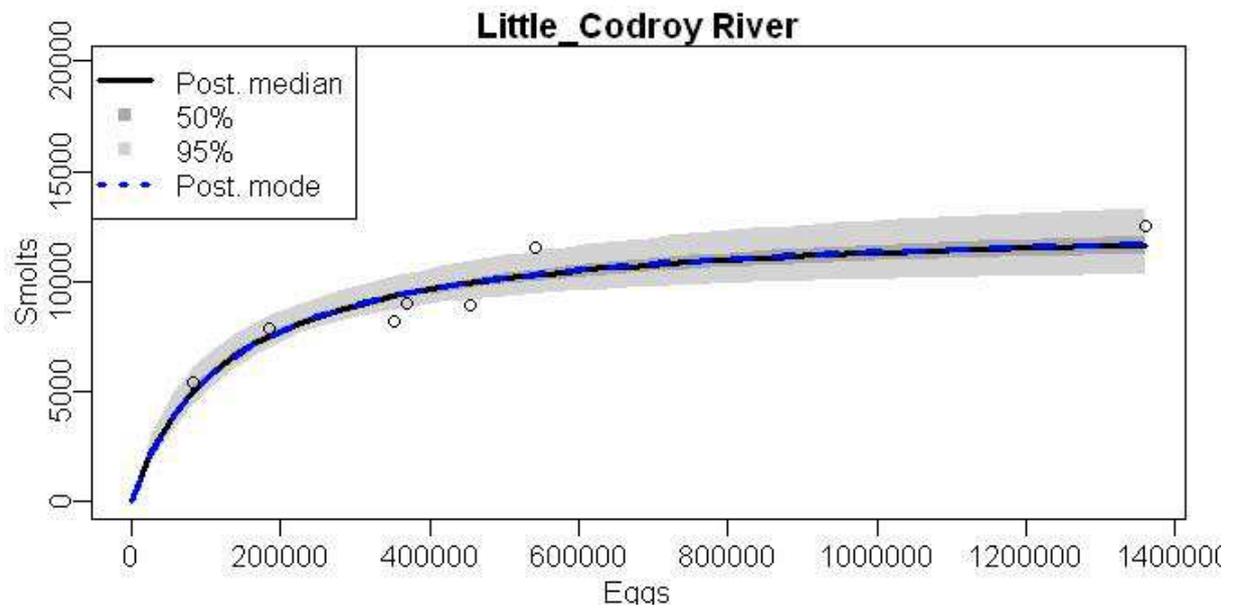


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

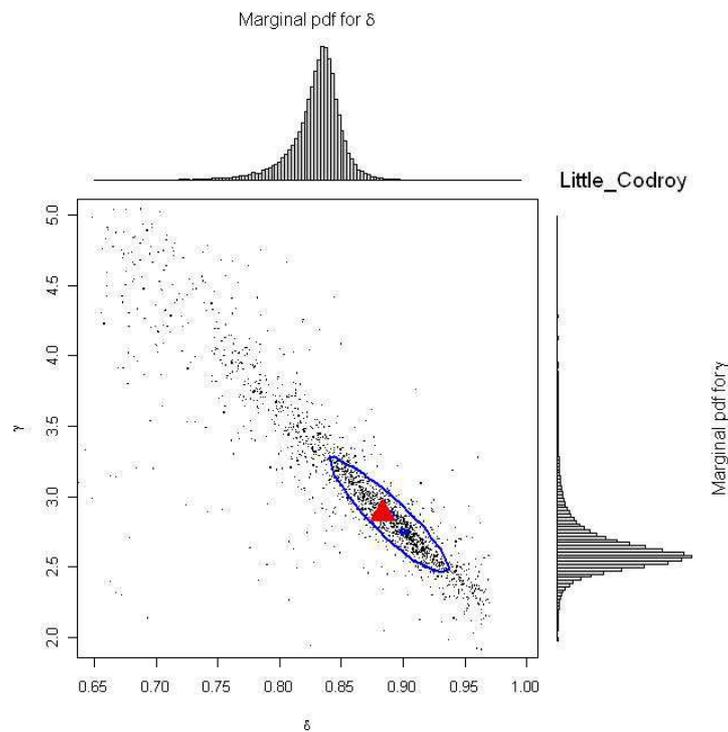


River	Little Codroy River (NWc, Canada, Newfoundland)
Contact	Gérald Chaput (Fisheries and Oceans Canada, Canada)
<u>River Informations</u>	
Latitude	47.8°
Longitude	-10°
Riverine Wetted A.	38.9 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	0
Mean Age of Smolts	2.64
ObsPeriod	1954 – 1960 (n <sub>obs</sub> =7)
<u>Monitoring</u>	The adults return and smolt migration levels are evaluated at counting fence installed just above head of tide The age distribution was supposed constant.
<u>Bibliography</u>	<p><u>Data origin:</u> Michielsens, C.G. &amp; McAllister, M.K., 2004. A Bayesian hierarchical analysis of stock-recruit data: quantifying structural and parameter uncertainties. Canadian Journal of Fisheries and Aquatic Sciences, 61(6), p.1032-1047.</p> <p><u>Originally from:</u> Murray A.R., 1968. Smolt survival and adult utilization of Little codroy River, Newfoundland, Atlantic Salmon. J. Fish. Res. Bd. Canada, <b>25</b>(10):2165-2218.</p> <p>O'Connell M.F., Dempson J.B., 1995. Target spawning requirements for Atlantic salmon, <i>Salmosalar</i> L., in Newfoundland rivers. Fisheries Management and Ecology, <b>2</b>. 161 – 170.</p>

Egg-to-smolt relationship estimated by the model

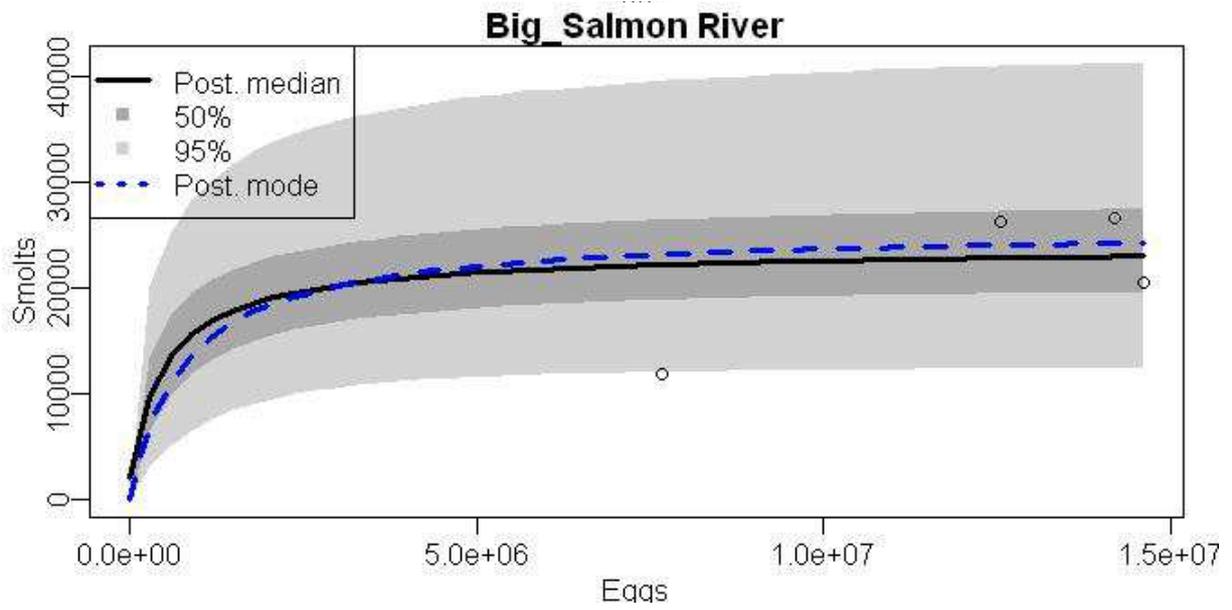


Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.

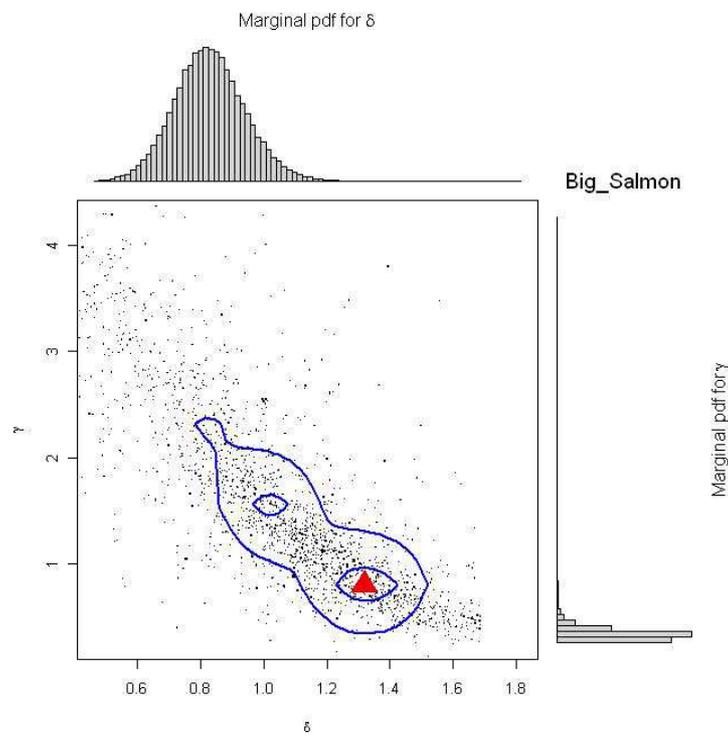


River	Big Salmon River (NWc, Canada, Scotia-Fundy)
Contact	NA
<u>River Informations</u>	
Latitude	45.42°
Longitude	-65.4°
Riverine Wetted A.	46.5 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	0
Mean Age of Smolts	2.60
ObsPeriod	1964 – 1967 (n <sub>obs</sub> =4)
<u>Monitoring</u>	All the adult salmon were enumerated at counting fences or fishways and the estimates of the number of eggs spawned were determined from the biological characteristics of the adults, including proportion of females by size group, fecundity, and average weight or length.
<u>Bibliography</u>	<p><u>Data origin:</u>            Jessop, B.M. 1986. Atlantic salmon (<i>Salmosalar</i>) of the Big Salmon River, New Brunswick. Can. Tech. Rep. Fish.Aquat. Sci. No.1415.</p> <p>Chaput, G. et al., 1998. River-specific target spawning requirements for Atlantic salmon (<i>Salmosalar</i>) based on a generalized smolt production model. Canadian Journal of Fisheries and Aquatic Sciences, 55(1), p.246-261.</p>

Egg-to-smolt relationship estimated by the model



Joint posterior distribution of  $(\delta, \gamma)$ . Blue lines: isoprobability contours; Red triangle: joint posterior mode of the distribution.



<b>River</b>	<b>Narraguagus River (NWc, USA, Maine)</b>
<b>Contact</b>	<b>Timothy Sheehan (NOAA Fisheries Service, Atlantic Salmon Research and Conservation Task)</b>
<u>River Informations</u>	
Latitude	44.54°
Longitude	-67.87°
Riverine Wetted A.	295 10 <sup>4</sup> m <sup>2</sup>
Lac. Wetted A.	0
Mean Age of Smolts	2.12
ObsPeriod	1994 – 2007 (n <sub>obs</sub> =14)
<u>Monitoring</u>	<p>This data series was not used in the model presented because the stocking was determined too strong to allow comparison with all other rivers, where the eggs-to-smolts survival is seen on natural populations.</p> <p>Stocking occurs here every year and unfed fry level represents 9.4 times the natural egg deposit on average and goes over 20 times this natural deposit for 3 years (max 38.3). As there is not any tag or characteristics that could help distinguish natural smolt from the other, the observed eggs-to-smolts survival is mainly the one from stocked individuals.</p>
<u>Bibliography</u>	

## Appendix 2: Detailed implementation of the survival function

### A 2.1: Ricker model (from Quinn & Deriso, 1999)

The per capita mortality rate can be seen as depending upon the initial population density with density dependent mortality rate  $\gamma_t$  and a density independent mortality effect  $\delta_t$ :

$$(1) \quad \frac{1}{N_t} \cdot \frac{dN_t}{dt} = -\delta_t - \gamma_t \cdot N_0^* = -\delta_t - \frac{\gamma_t}{A} \cdot N_0$$

$$\Leftrightarrow \frac{dN_t}{N_t} = -\left(\delta_t + \frac{\gamma_t}{A} \cdot N_0\right) \cdot dt$$

By assuming  $\delta_t$  and  $\gamma_t$  constant between  $t=0$  and  $t=\Delta t$ , we can integrate from state  $t=0$  to state  $t=\Delta t$ :

$$\int_{N=N_0}^{N=N_{\Delta t}} \frac{dN_t}{N_t} = - \int_{t=0}^{t=\Delta t} \left(\delta + \frac{\gamma}{A} \cdot N_0\right) \cdot dt$$

$$\Leftrightarrow \ln(N_{\Delta t}) - \ln(N_0) = -\left(\delta + \frac{\gamma}{A} \cdot N_0\right) \cdot \Delta t$$

$$\Leftrightarrow N_{\Delta t} = N_0 \cdot e^{-\delta \cdot \Delta t - \frac{\gamma}{A} \cdot N_0 \cdot \Delta t}$$

We can easily obtain the classical form of Ricker SR function with the slope at the origin  $\alpha$  and maximum recruitment  $\beta$ :

$$(3) \quad N_{\Delta t} = \alpha \cdot N_0 \cdot e^{-\frac{\alpha}{\beta \cdot e^1} \cdot N_0}$$

with

$$\begin{cases} \alpha = e^{-\delta \cdot \Delta t} \\ \beta = \frac{e^{-\delta \cdot \Delta t}}{\frac{\gamma}{A} \cdot \Delta t \cdot e^1} \end{cases}$$

### A 2.2: Beverton & Holt model (from Quinn & Deriso, 1999)

The per capita mortality rate can be seen as depending upon the population density at each instant  $t$   $N_t^* = N_t/A$  with a density dependent mortality effect  $\gamma_t$  and a density independent mortality effect  $\delta_t$ :

$$(1) \quad \frac{1}{N_t} \cdot \frac{dN_t}{dt} = -\delta_t - \gamma_t \cdot N_t^* = -\delta_t - \frac{\gamma_t}{A} \cdot N_t$$

Simple algebra on eq. (1) leads to:

$$\Leftrightarrow dN_t = -\delta_t \cdot \left[ N_t + \frac{\gamma_t}{A \cdot \delta_t} \cdot N_t^2 \right] \cdot dt$$

$$\Leftrightarrow \frac{dN_t}{N_t + \frac{\gamma_t}{A \cdot \delta_t} \cdot N_t^2} = -\delta_t \cdot dt$$

$$(2) \quad \Leftrightarrow \frac{dN_t}{N_t} - \frac{dN_t}{\frac{\delta_t \cdot A}{\gamma_t} + N_t} = -\delta_t \cdot dt$$

(By the method of partial fractions)

By assuming  $\delta_t$  and  $\gamma_t$  constant between  $t=0$  and  $t=\Delta t$ , we can integrate (2) from state  $t=0$  to state  $t=\Delta t$ .

$$\int_{N=N_0}^{N=N_{\Delta t}} \frac{dN_t}{N_t} - \int_{N=N_0}^{N=N_{\Delta t}} \frac{dN_t}{\frac{\delta \cdot A}{\gamma} + N_t} = - \int_{t=0}^{t=\Delta t} \delta \cdot dt$$

$$\Leftrightarrow \ln(N_{\Delta t}) - \ln(N_0) - \left[ \ln \left| \frac{\delta \cdot A}{\gamma} + N_{\Delta t} \right| - \ln \left| \frac{\delta \cdot A}{\gamma} + N_0 \right| \right] = -\delta \cdot \Delta t$$

$$\Leftrightarrow \ln(N_{\Delta t}) - \ln(N_0) - \left[ \ln \left( \frac{\delta \cdot A}{\gamma} + N_{\Delta t} \right) - \ln \left( \frac{\delta \cdot A}{\gamma} + N_0 \right) \right] = -\delta \cdot \Delta t \quad \left( \text{as } \frac{\delta \cdot A}{\gamma} > 0 \right)$$

$$\Leftrightarrow \frac{N_{\Delta t}}{\frac{\delta \cdot A}{\gamma} + N_{\Delta t}} = \frac{N_0}{\frac{\delta \cdot A}{\gamma} + N_0} \cdot e^{-\delta \cdot \Delta t}$$

$$\Leftrightarrow \frac{1}{N_{\Delta t}} = \frac{\gamma}{\delta \cdot A} \left[ \frac{\frac{\delta \cdot A}{\gamma} + N_0 \cdot (1 - e^{-\delta \cdot \Delta t})}{N_0 \cdot e^{-\delta \cdot \Delta t}} \right]$$

$$\Leftrightarrow N_{\Delta t} = \frac{N_0}{e^{\delta \cdot \Delta t} + \frac{\gamma}{\delta \cdot A} \cdot (e^{\delta \cdot \Delta t} - 1) \cdot N_0}$$

This relation corresponds to the BH stock recruitment with slope at the origin  $\alpha$  and maximum asymptotic recruitment (or carrying capacity of the rivier)  $\beta$ .

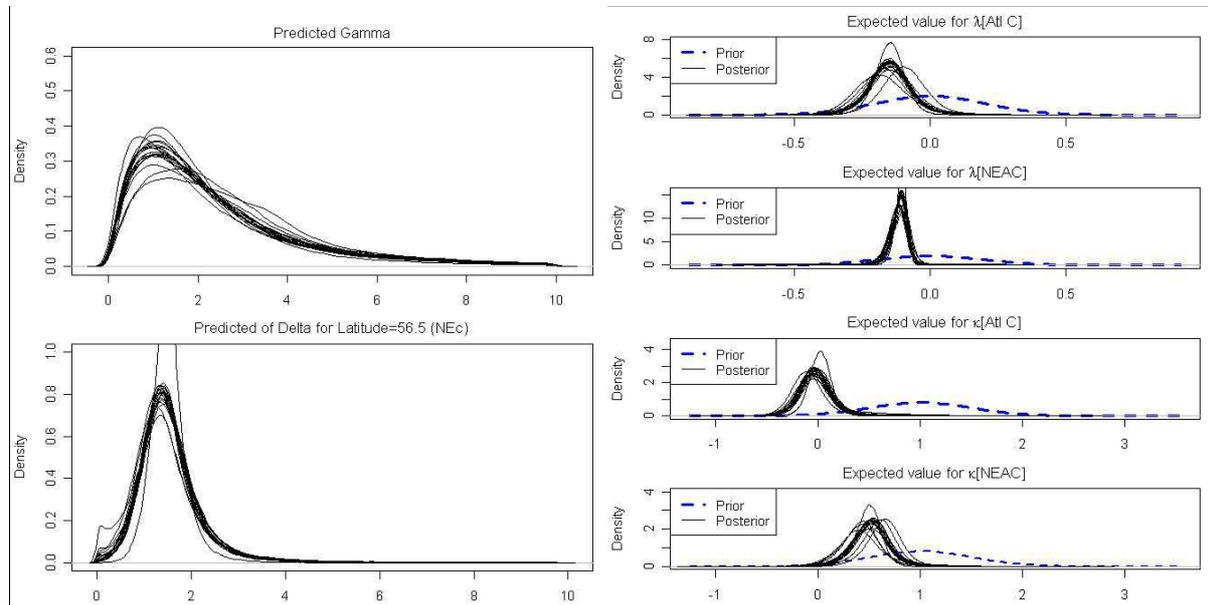
$$(3) \quad N_{\Delta t} = \frac{\alpha \cdot N_0}{1 + \alpha \cdot \beta \cdot N_0}$$

With

$$\left\{ \begin{array}{l} \alpha = e^{-\delta \cdot \Delta t} \\ \beta = \frac{1}{\frac{\gamma}{\delta \cdot A} \cdot (e^{\delta \cdot \Delta t} - 1)} \end{array} \right.$$

## Appendix 3: Detailed results

### A 3.1: Test for exchangeability



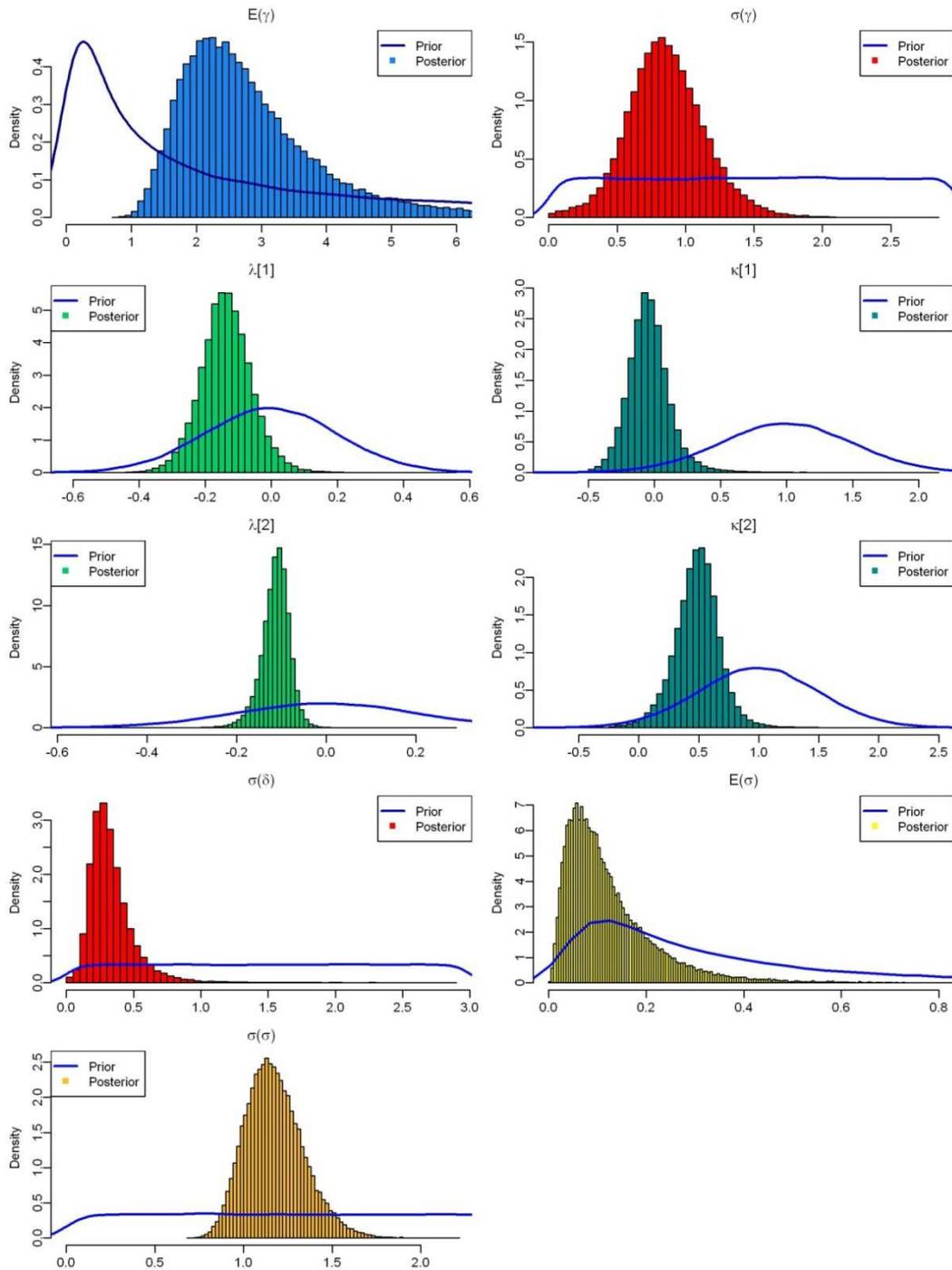
**Fig. A3.1:** Marginal posterior predictive probability distribution of the hyper-parameters  $\lambda$  and  $k$  and resulting posterior predictive for  $\delta$  and  $\gamma$  computed with latitude=56.5°N and longitude=NEc (categorical) corresponding to East Scotland. Black lines are posterior pdf for the 20 models, excluding one river's data series from the analysis at a time.

### A 3.2: Correlation coefficient calculated from the pairwise mcmc samples of $(\delta, \gamma)$ for each river.

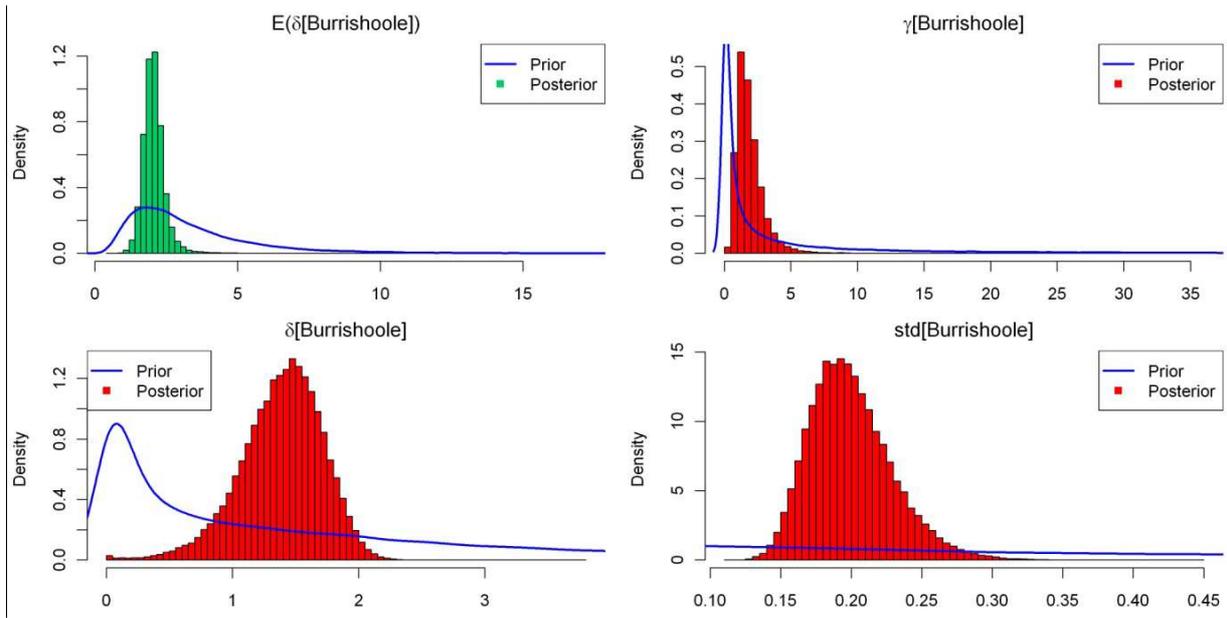
River	Correlation	River	Correlation
1 Scorff	<b>-0,69</b>	11 NE Brook	<b>-0,94</b>
2 Oir	<b>-0,78</b>	12 W Arm Brook	<b>-0,97</b>
3 Vesturdalsa	<b>-0,70</b>	13 Campbellton	<b>-0,87</b>
4 Elidaar	<b>-0,85</b>	14 Conne	<b>-0,84</b>
5 North Esk	<b>-0,89</b>	15 Rocky	<b>-0,70</b>
6 Burrishoole	<b>-0,92</b>	16 Pollet	<b>-0,73</b>
7 Frome	<b>-0,90</b>	17 Nashwaak	<b>-0,57</b>
8 Bush	<b>-0,88</b>	18 Imsa	<b>-0,75</b>
9 Trinité	<b>-0,87</b>	19 Little Codroy	<b>-0,88</b>
10 St-Jean	<b>-0,61</b>	20 Big Salmon	<b>-0,67</b>

### A 3.3: Prior & Posteriors probability density function

Hereafter are presented the priors and posteriors pdf for all the hyper-parameters (Figure A3.3.1) and some examples are given for the parameters estimated for all rivers (Figure A3.3.2).

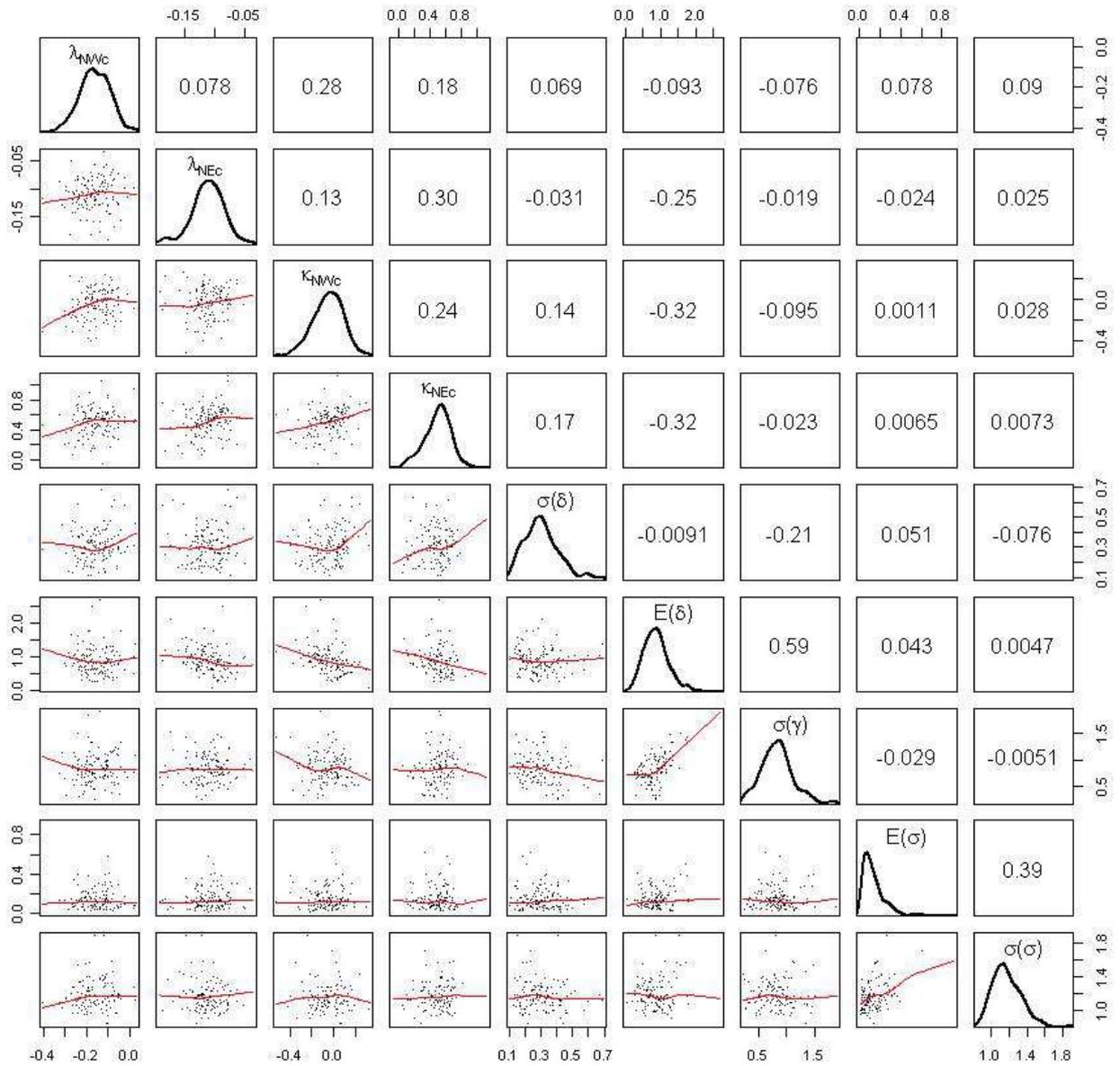


**Fig. A3.3.1:** Priors (blue line) and posteriors (colored histograms) pdf for all hyper-parameters. Priors have been chosen as uninformative as possible.



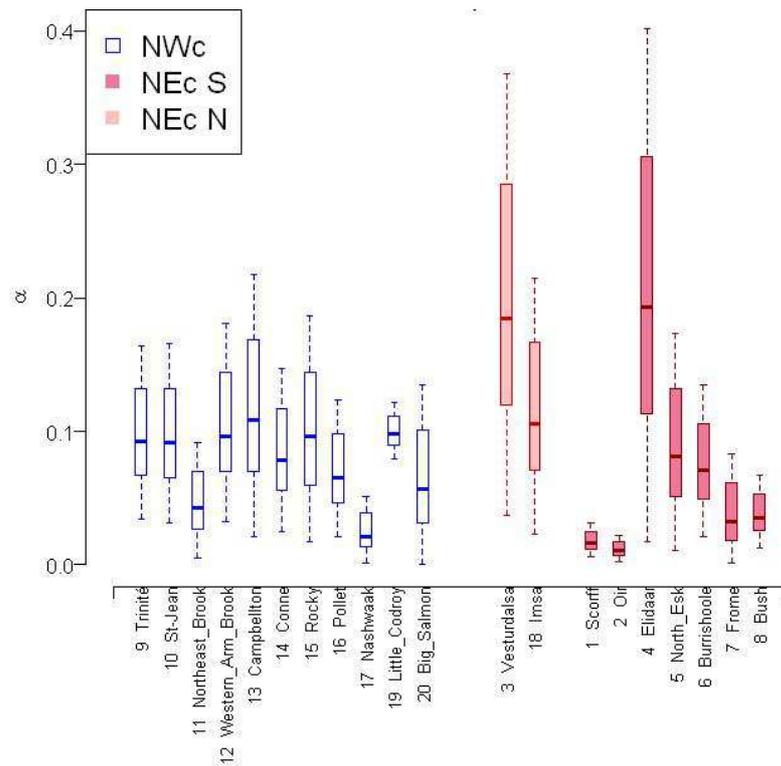
**Fig. A3.3.2:** Examples of parameters prior (blue line) and posterior (colored histograms) probability distribution function (Burrishoole River, Ireland):  $E(\delta)$ ,  $\delta$ ,  $\gamma$  and  $\sigma$ .

### A 3.4: Pairwise correlations of all hyper-parameters

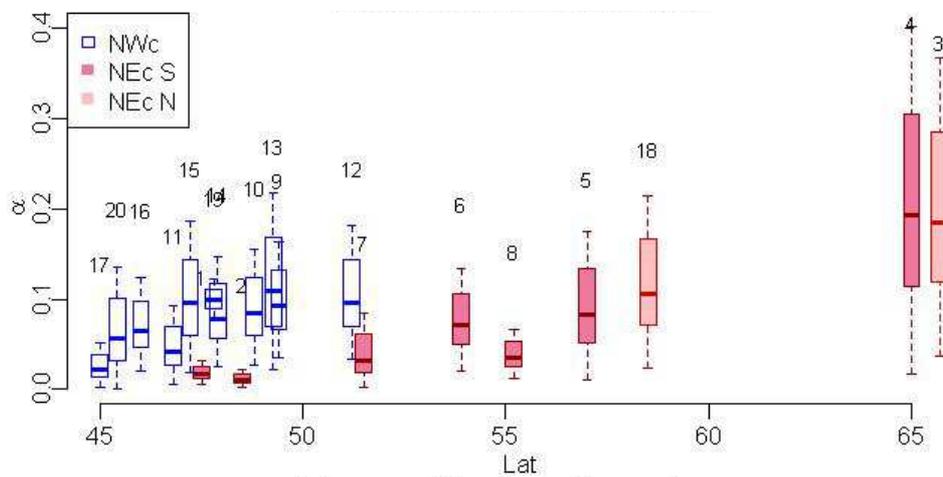


**Fig. A3.4:** Pairwise correlations of all model hyperparameters. The marginal posterior pdf are presented in the diagonal while lower panels show pairwise mcmc plots and the upper panel gives the linear autocorrelation coefficient.

### A 3.5: Posterior pdf of the slope at the origin for the 20 rivers



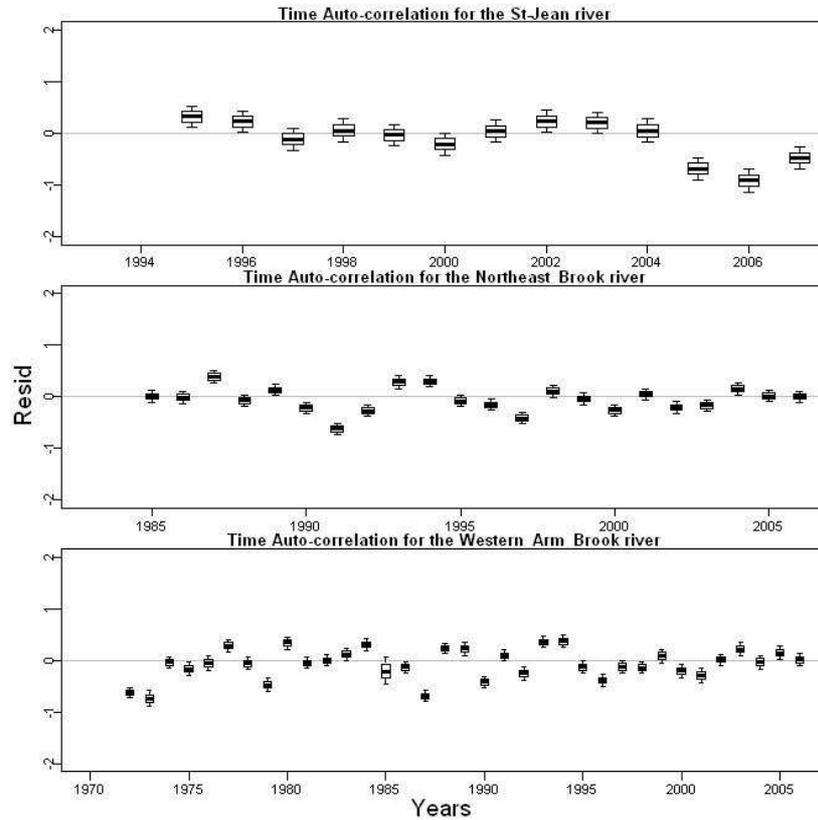
**Fig. A3.5.1:** Posterior probability distribution for the BH model parameter  $\alpha$  (slope at the origin simply obtained from  $\delta$  and  $\Delta t$  via  $\alpha = e^{-\delta \cdot \Delta t}$ ). Each box displays the 25th, 50th and 75th percentiles and a representation of the dispersal. Rivers are separated by stock complex.



**Fig. A3.5.2:** Posterior probability distribution for the BH model parameter  $\alpha$  (slope at the origin simply obtained from  $\delta$  and  $\Delta t$  via  $\alpha = e^{-\delta \cdot \Delta t}$ ) plotted as a function of the latitude. Each box displays the 25th, 50th and 75th percentiles and a representation of the dispersal. Rivers are separated by stock complex.

## Appendix 4: Modeling the environmental stochasticity (within river between-years variability)

### A 4.1: Observation of a pattern of temporal auto-correlation on the residuals



**Fig. A4.1:** Example of time series of residuals ( $\epsilon$ 's) (for three rivers chosen among the 20) illustrating the time-series autocorrelation in the residuals. Residuals were obtained from a preliminary model based on independent logNormal errors  $\epsilon_t$  (eq. (12)).

### A 4.2: Prior Distribution on the correlation coefficient $\rho_r$ 's.

The model presented in the main text (eq. (12)) account for temporal auto-correlation with parameter  $\rho$  considered independent between rivers. A hierarchical structure on  $\rho$  has been investigated, using a translated and dilated prior distribution for  $\rho$  as shown in **Table A4.2**.

**Table A4.2:** Addition to the main parameters and quantities of interest of the model for modeling hierarchical temporal autocorrelation. The prior distributions are indicated only for the free parameters.

Model parameter	Description	Prior Distribution
$\mu_\rho$		Norm(0, $\sigma=2$ )
$\sigma_\rho$		Unif(0,1)
$\rho_r$	For $r=1, \dots, 20$ (rivers) $\text{logit}(X_r) \sim N(\mu_\rho, \sigma_\rho)$ $\rho_r = 2 \cdot (X_r - 0.5)$	

But such a hierarchical structure on  $\rho$  has not been used further. Indeed, such a model showed surprising results (Figure A4.2) with strong shrinkage effect resulting in all estimates of  $\rho$  near 0.4 with no between rivers variability in the  $\rho$ 's.

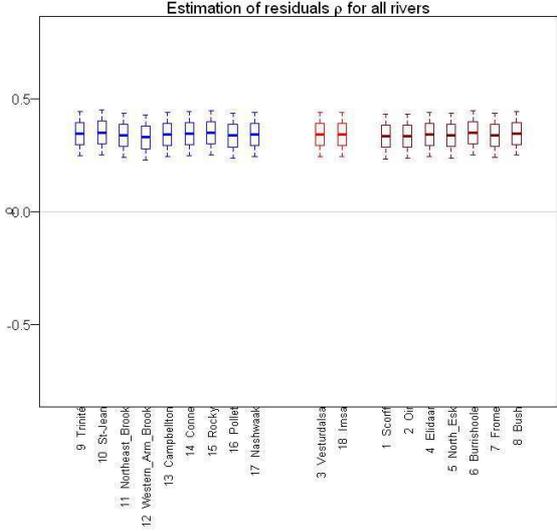
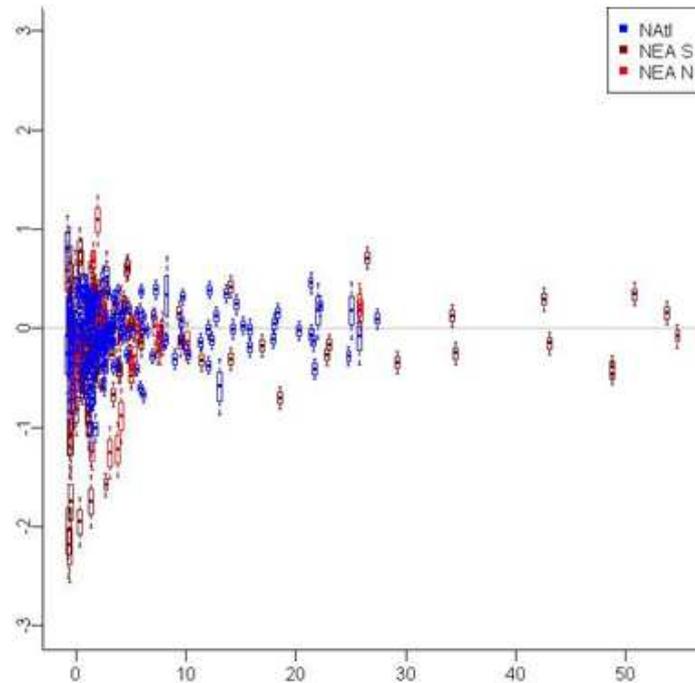


Fig. A4.2: Estimation of  $\rho$  for all rivers by hierarchical structure in the model.

### A 4.3: Heteroscedasticity

For each river, the logNormal environmental variability was based on the hypothesis that  $\sigma_r^2$  is constant for all values of eggs deposition (homoscedasticity). However, a careful look at the residuals points out a pattern of heteroscedasticity.

For each observation, the model residuals were plotted versus the number of eggs for the corresponding spawning year. This number of eggs was standardized for each river relatively to the egg deposition generating half of the maximal smolt abundance ( $\beta/2$ ), in order to scale each observation according to the survival function (highly increasing part (reduced egg abundance) or density-dependent driven part at high egg level). (Figure A4.3):



*Fig. A4.3: Heteroscedasticity pattern in residual distribution of the model: residuals versus standardized eggs deposition*

Residuals are more dispersed for a reduced eggs deposition. This pattern has been studied by Minto et al. (2008) and its incorporation could improve the model accuracy and predictive ability. Also, this pattern is mainly linked to three rivers (Oir, Scorff and Frome Rivers), which represents the three rivers where the mean smolt ages is the lowest.

## Appendix 5: JAGS model

In this appendix is presented the complete model that has been used for the presented model. It has been compiled in R with the rjags package.

```
data {
for (i in 1: obs.nb) {
logSm[i]<-log(Sm[i])
logEg[i]<-log(Eg[i])
}
}

model{
# Define Prior
lambda_p ~ dnorm(0,25)
kappa_p ~ dnorm(1,4)
lambda[1] ~ dnorm(0,25)
kappa[1] ~ dnorm(1,4)
lambda[2] ~ dnorm(0,25)
kappa[2] ~ dnorm(1,4)

stdDelta_p ~ dunif(0,3)
stdDelta ~ dunif(0,3)
tau_Delta<-1/(stdDelta*stdDelta)
tau_Delta_p<-1/(stdDelta_p*stdDelta_p)

g<-1
std_g <-2.2
tau_g<-1/((std_g*g)^2)
E_lgamma ~ dnorm(g,tau_g)
E_lgamma_p ~ dnorm(g,tau_g)
stdGamma ~ dunif(0,3)
stdGamma_p ~ dunif(0,3)
tau_Gamma<-1/(stdGamma*stdGamma)
tau_Gamma_p<-1/(stdGamma_p*stdGamma_p)

# hierarchical structure for tau
E_std_p~dlnorm(-1.4,1)
std_std_p~dunif(0,3)
tau_std_p<-1/(std_std_p*std_std_p)
E_std~dlnorm(-1.4,1)
std_std~dunif(0,3)
tau_std<-1/(std_std*std_std)

std_p ~ dlnorm(E_std_p-(0.5/tau_std_p),tau_std_p)
tau_p <- 1/(std_p*std_p)

ACrho_p ~ dunif(-1,1)          # Rho parameter for temporal auto-correlation

for (r in 1:riv.nb){
# Prior
E_ldelta_p[r] <- lambda_p*LatC[r]+kappa_p
E_ldelta[r] <- lambda[SCplx[r]]*LatC[r]+kappa[SCplx[r]]

ldelta_p[r] ~ dnorm(E_ldelta_p[r]-0.5/tau_Delta_p,tau_Delta_p)
delta_p[r]<-exp(ldelta_p[r])
lgamma_p[r] ~ dnorm(E_lgamma_p-0.5/tau_Gamma_p,tau_Gamma_p)
gamma_p[r]<-exp(lgamma_p[r])
}
```

```

ldelta[r] ~ dnorm(E_ldelta[r]-0.5/tau_Delta,tau_Delta)
lgamma[r] ~ dnorm(E_lgamma-0.5/tau_Gamma,tau_Gamma)

delta[r]<-exp(ldelta[r])
gamma[r]<-exp(lgamma[r])

ACrho[r] ~ dunif(-1,1)

#Observation in initial slope (alpha) scale and beta scale
alpha_p[r]<-exp(-delta_p[r]*MA[r])
beta_p[r]<-1/((gamma_p[r]/(delta_p[r]*AWA[r]))*(exp(delta_p[r]*MA[r])-1))

alpha[r]<-exp(-delta[r]*MA[r])
beta[r]<-1/((gamma[r]/(delta[r]*AWA[r]))*(exp(delta[r]*MA[r])-1))

# tau for residuals (w)
std[r] ~ dlnorm(E_std-(0.5/tau_std),tau_std)
tau[r] <- 1/(std[r]*std[r])

LCor[r] <-0.5/tau[r]          #Laurent's correction

#Init for Residual Time series
  Vsta[r] <- (std[r]*std[r])/(1-(ACrho[r]*ACrho[r])) # stationary var
  eps0[r] ~ dnorm(0,1/Vsta[r])
}

# Initialization for the first observation
logSmEst[1]<-logEg[1]-
log(exp(delta[IdRiv[1]]*MA[IdRiv[1]])+((gamma[1]/AWA[1])/delta[IdRiv[1]]*(exp(delta[IdRiv[1]]*MA[IdRiv[1]])-1)*Eg[1]))
eps[1]<-eps0[1]
logSmEstAC[1]<-logSmEst[1]+eps[1]+0
logSm[1] ~ dnorm(logSmEstAC[1]-LCor[IdRiv[1]], tau[IdRiv[1]]) # - Laurent's
Correction
resid[1]<-logSm[1]-logSmEst[1]          # model total error epsilon
wres[1]<-logSm[1]-logSmEstAC[1]        # innovations w

  for (i in 2:obs.nb){
logSmEst[i]<-logEg[i]-
log(exp(delta[IdRiv[i]]*MA[IdRiv[i]])+((gamma[IdRiv[i]]/AWA[IdRiv[i]])/delta[IdRiv[i]]*(exp(delta[IdRiv[i]]*MA[IdRiv[i]])-1)*Eg[i]))

eps[i]<-(1-equals(i,StartId[IdRiv[i]]))*ACrho[IdRiv[i]]*resid[i-1]+(equals(i,StartId[IdRiv[i]]))*eps0[IdRiv[i]]
logSmEstAC[i]<-logSmEst[i]+eps[i]

logSm[i] ~ dnorm(logSmEstAC[i]-LCor[IdRiv[i]], tau[IdRiv[i]]) # - Laurent's
Correction

resid[i]<-logSm[i]-logSmEst[i]          # model total error epsilon
wres[i]<-logSm[i]-logSmEstAC[i]        # innovations w
  }

for (r in 1:riv.nb){
  variance[r]<-(sd(resid[StartId[r]:EndId[r]]))^2
  CV[r]<-sqrt(exp(variance[r])-1)
  wvariance[r]<-(sd(wres[StartId[r]:EndId[r]]))^2
  wCV[r]<-sqrt(exp(wvariance[r])-1)
}

```

```

# Temporal AutoCor on epsilon?
meanRes[r]<-mean(resid[StartId[r]:EndId[r]])
Rho[r]<-sum((resid[StartId[r]:(EndId[r]-1)]-
meanRes[r])*(resid[(StartId[r]+1):EndId[r]]-
meanRes[r]))/sum((resid[StartId[r]:(EndId[r]-1)]-
meanRes[r])*(resid[StartId[r]:(EndId[r]-1)]-meanRes[r]))

# Temporal AutoCor of innovation w?
wmeanRes[r]<-mean(wres[StartId[r]:EndId[r]])
wRho[r]<-equals(1,AC[r])*sum((wres[StartId[r]:(EndId[r]-1)]-
wmeanRes[r])*(wres[(StartId[r]+1):EndId[r]]-
wmeanRes[r]))/sum((wres[StartId[r]:(EndId[r]-1)]-
wmeanRes[r])*(wres[StartId[r]:(EndId[r]-1)]-wmeanRes[r]))
}

## Prediction
for (t in 1:30){          # Discretisation of the studied latitude interval
  E_ldelPred_Atl[t] <- lambda[1]*LatCPredAtl[t]+kappa[1]
  E_ldelPred_NEA[t] <- lambda[2]*LatCPredNEA[t]+kappa[2]
  ldelCPred_Atl[t]~ dnorm(E_ldelPred_Atl[t]-0.5/tau_Delta,tau_Delta)
  #delPred_Atl[t]<-exp(ldelPred_Atl[t])
  ldelCPred_NEA[t]~ dnorm(E_ldelPred_NEA[t]-0.5/tau_Delta,tau_Delta)
  #delPred_NEA[t]<-exp(ldelPred_NEA[t])
}

#Prediction for East Scotland
E_ldelPred_ES <- lambda[2]*LatCPredES+kappa[2]
ldelPredES ~ dnorm(E_ldelPred_ES-0.5/tau_Delta,tau_Delta)
delPredES<-exp(ldelPredES)

lgamPred ~ dnorm(E_lgamma-0.5/tau_Gamma,tau_Gamma)
gamPred<-exp(lgamPred)

stdPred ~ dlnorm(E_std-(0.5/tau_std),tau_std)
}

```





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**Titre français :**

Contribution à la modélisation de la dynamique de population du Saumon Atlantique (*Salmo salar*) à l'échelle de complexe de stock : Meta-analyse de la survie en eau douce

**Titre anglais :**

Contribution to the modeling of Atlantic salmon (*Salmo salar*) population dynamics at the scale of stock complexes: Meta-analysis of freshwater survival

**Résumé :**

Une méta-analyse de la survie en eau douce du saumon Atlantique a été développée pour améliorer la modélisation de la population à l'échelle de complexes de stocks. Des séries temporelles de données œufs-smolts provenant de 21 rivières-ateliers de l'aire de répartition du saumon Atlantique, associées à plusieurs covariables caractérisant les cours d'eau, ont été rassemblées pour mener cette étude. La méta-analyse a été développée à travers un modèle hiérarchique Bayésien. Le modèle de Beverton & Holt classique a été revisité par une reparamétrisation en termes de taux de mortalité densité-dépendant et densité-indépendants. Un modèle hiérarchique partiellement échangeable a été construit pour intégrer des covariables (comme la longitude et la latitude) pour capturer une part de la variabilité inter-rivière. Cette approche offre un cadre efficace pour prédire les paramètres de la survie densité-dépendante (et l'incertitude associée) pour n'importe quelle nouvelle rivière pour laquelle sont connues la latitude, la longitude, la surface et l'âge moyen des smolts. Les sorties de cette études ont été utilisées en tant qu'information a priori de la productivité en eau douce dans un modèle de cycle de vie structuré en âge pour l'Écosse-Est. Cela fournit une estimation de la série temporelle du taux de survie en mer du saumon Atlantique pour ce complexe de stock.

**Abstract :**

A meta-analysis of the Atlantic salmon freshwater survival was carried out, in order to improve the modeling of the population at the scale of stock complexes. Time series of eggs-to-smolts data on 21 index rivers across the A. Salmon repartition area, together with several covariates associated with the index rivers, were compiled for this study. The meta-analysis was carried out through a Bayesian hierarchical model. The classical Beverton & Holt model was revisited through the explicit parameterization in terms of density dependent and density independent mortality rates. A partially exchangeable hierarchical model was built to incorporate covariates (such as the longitude and the latitude) to capture part of the between rivers variability. This approach offers an efficient framework to predict the parameters of the density-dependent survival (and the associated uncertainty) for any new river for which the associated covariates latitude, longitude, wetted area and mean age of smolts are known. Outcomes of this study were used as prior information about the freshwater productivity in a full age-structured life-cycle model built for East Scotland. This provides an estimate of the time series of A. Salmon marine survival rate for this stock complex.

**Mots-clés :** saumon Atlantique, méta-analyse, modèle hiérarchique Bayésien, smolts, stock-recrutement

**Key Words:** Atlantic salmon, meta-analysis, Bayesian hierarchical model, smolts, stock-recruits