AGROCAMPUS OUEST

☐ **CFR Angers** ☑ **CFR Rennes**

Année universitaire : 2016-2017

Spécialité :Sciences Halieutiques et Aquacoles

Spécialisation (et option éventuelle) :

Ressources et Ecosystèmes Aquatiques

Mémoire de Fin d'Études

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

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

☐ d'un autre établissement (étudiant arrivé en M2)

Defining new conservation limits for Atlantic salmon (*Salmo salar*) populations of Brittany

Clément LEBOT

Soutenu à Rennes le 14 septembre

Devant le jury composé de :

Président : Etienne Rivot (Enseignant-chercheur)

Maître de stage : Etienne Prévost (Enseignant-chercheur)

Enseignant référent : Etienne Rivot (Enseignant-chercheur)

Autres membres du jury (Nom, Qualité):

Guy Fontenelle (Enseignant-chercheur)

Marie Nevoux (Chargée de recherché)

Maxime Olmos (Doctorant)

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Contexte :

Depuis très longtemps, le saumon est présent et exploité dans les cours d'eau des façades Est et Ouest Atlantique. La France étant au Sud de son aire de répartition, les menaces pesant sur ses populations sont donc considérées comme plus importantes que dans le reste de son aire de répartition.

Le caractère anadrome de cette espèce implique une gestion imbriquée à deux échelles spatiales. Une première gestion à l'échelle des rivières qui définit l'échelle spatiale de chaque stock. La gestion à l'échelle des rivières est laissée à la charge de chaque état. Comme les individus de tous les stocks effectuent une migration commune vers les zones de nourriceries autour des Îles Féroé et au Sud du Groenland, une seconde gestion à l'échelle internationale est nécessaire. Elle est coordonnée par la NASCO qui définit les grands principes de gestion de l'espèce.

Depuis 1998, la NASCO a adopté l'approche de précaution pour gérer les populations de Saumon atlantique. Au lieu de deux points de références classiquement définis pour cette approche, à savoir une limite de conservation et une cible de gestion, à ce jour seul une limite a été définie : S_{opt} soit la quantité de reproducteurs qui maximise les captures à long-terme. Ainsi, la stratégie de gestion aujourd'hui préconisée par la NASCO est une stratégie à échappement fixe (échappement correspond à S_{opt}) par la fixation de TAC.

En France, la gestion des populations de saumon est confiée aux comités de gestion des poissons migrateurs qui sont définis à l'échelle régionale. Elle organise la gestion en élaborant des plans de gestion des poissons migrateurs s'opérant tous les 5 ans. Néanmoins, ces plans de gestions doivent être en accord avec les recommandations définies par la NASCO. Pour s'en assurer, la NASCO exige de chaque pays un plan de mise en œuvre des grands principes établis.

Objectifs :

Dans le contexte du renouvellement de son plan de gestion des poissons migrateurs et du plan de mise en œuvre NASCO dans un futur proche, le comité de gestion Bretagne a fait savoir sa volonté de modifier la stratégie de gestion qu'elle appliquait jusqu'alors. L'objectif premier est de recentrer l'objectif des limites de conservation sur la conservation en elle-même plus que sur l'exploitation tout en intégrant certaines recommandations de la NASCO laissé de côté jusqu'à présent.

Matériels et Méthodes

La définition d'un nouveau cadre de référence pour définir les limites de conservation a été mise en place. Celui-ci est basé sur la définition de la conservation adoptée par le Canada, à savoir éviter les faibles recrutements. Deux types de références ont été utilisés pour définir ce que l'on considère comme un faible recrutement : les références théoriques issues du concept de capacité d'accueil (R_{MAX}) et les références historiques issues du recrutement moyen (R_{OBS}). Le premier est défini grâce à la relation de stock-recrutement moyenne alors que le dernier utilise les données de stock-recrutement. En utilisant les différentes sources d'incertitudes autour de la relation moyenne de stock-recrutement, on a défini les limites de conservation comme le niveau de stock qui présente un risque faible de faible recrutement.

La définition de nouvelles limites de conservation concerne 18 rivières qui diffèrent les unes des autres par la taille de leur système productif ou aire d'équivalent radier-rapide. Parmi ces 18 rivières, le Scorff est une rivière atelier utilisée par le CIEM pour produire des estimations de différents stades de développement. La connaissance particulière de la dynamique de cette population nous a poussés à traiter cette rivière comme une référence.

Nous avons tiré profit des données d'indices d'abondances spécifiques à chaque rivière pour estimer des recrutements par année et rivière. Par la suite, la médiane des estimations a été utilisée comme une donnée. Pour les stocks, les médianes d'estimation de retours d'adultes sur le Scorff ont été utilisées comme des données ; pour les autres rivières, on a utilisé les captures.

Le processus d'observation reliant le stock aux captures a été rajouté à la modélisation des relations de stock-recrutement pour intégrer l'incertitude autour de ce processus. Les relations de stock recrutement ont été modélisées en moyenne par une relation de Beverton-Holt à deux paramètres en admettant une erreur log-normal autour de cette moyenne. Les paramètres standards α et R_{MAX} de la relation de Beverton-Holt moyenne sont fixés pour le Scorff et appliqués aux autres rivières avec un facteur multiplicatif défini pour chaque rivière r (γ_r).

Le modèle développé s'intègre dans la cadre de la modélisation bayésienne hiérarchique. La hiérarchisation des paramètres nous permet de créer un lien entre les rivières en tirant les paramètres de chaque rivière dans une loi de probabilité commune. Ainsi, nous pouvons transférer l'information acquise sur le Scorff aux autres cours d'eau. Le bayésien permet lui de décrire de façon complète et explicite l'incertitude utile pour définir le risque tout en nous permettant d'intégrer de la connaissance a priori sur les relations de stock-recrutement moyenne (α et R_{MAX}).

Résultats et Discussion

Les résultats montrent un ajustement des distributions a priori sur les paramètres de Beverton-Holt. Les facteurs multiplicatifs semblent augmenter selon un gradient Est-Ouest ce qui insinue que les rivières à l'ouest de la Bretagne sont plus productives. Les relations de stock-recrutement ajustées ont permis d'évaluer les différentes limites de conservation proposées. Selon la limite de conservation, les variations entre rivières peuvent être assez importantes. Enfin, l'incertitude autour des relations de stock-recrutement est très importante. Elle est causée par l'erreur d'observation du stock, l'erreur du processus de recrutement et l'erreur d'estimation des paramètres de Beverton-Holt.

A la fin de cette étude, une discussion sur la modélisation utilisée apporte des pistes d'amélioration pour limiter le biais des limites de conservation et notamment l'introduction de co-variables pouvant expliquer les variations de captures. Enfin, nous discutons de l'application du cadre théorique développé dans cette étude à différente stratégie de gestion :

- La stratégie à échappement fixe
- L'approche de précaution dans sa totalité

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List of abbreviations:

BCI: Bayesian confidence interval

CL: Conservation limit

CL_1: Stock level associated a risk of 15% to produce less 25% R_{MAX}

CL_2: Stock level associated a risk of 25% to produce less 50% R_{MAX}

CL_3: Stock level associated a risk of 40% to produce less 75% R_{MAX}

CL_4: Stock level associated a risk of 15% to produce less 25% R_{OBS}

CL_5: Stock level associated a risk of 25% to produce less 50% R_{OBS}

CL_6: Stock level associated a risk of 40% to produce less 75% R_{OBS}

ddp: Density-dependence

didp: Density-independence

FET: Fixed escapement target

MT: Management target

PA: precautionary approach

R_{MAX}: Carrying capacity or Maximum average recruitment

R_{OBS}: Mean observed recruitment

SR: Stock-recruitment

S_{opt}: Stock level maximizing the long-term catches

RRE: Riffle-rapid equivalent

CNICS: Centre national d'interprétation des captures de salmonidés

NASCO: The north Atlantic salmon conservation organization

FAO: Food and agriculture organization

ICES: International council for the exploration of the sea.

Introduction

Present and exploited in European and North-American rivers, Atlantic salmon (*Salmo salar*) is an emblematic species which conservation has been a matter of concern for long. Since 1996, the International Union for Conservation of Nature (IUCN) has assessed its extinction risk *as* lower risk / least concern (IUCN, 1996). Nevertheless, biologists and NGOs agree that its conservation is threatened in many areas within its native range (Parrish et al., 1998; WWF, 2001). The threat appears even more significant in countries at the southern edge of its distribution range as France (Verspoor, 2007).

To address A. salmon's conservation issues, its exploitation has been regulated for a long time. However, this regulation is made difficult by the complexity of the life cycle of this species. As an anadromous fish, A. salmon reproduces in freshwater where juveniles grow before undertaking long-distance migrations in the North Atlantic Ocean, up to Sub-Artic feeding areas (**Figure 1.1.**). In these areas, all populations gather together and after one to three years at sea, they return to their home rivers to reproduce (Webb et al., 2007). Each river flowing into the ocean is therefore usually considered as the spatial unit associated to a salmon population, as well as the relevant spatial scale for the management of salmon stocks. At sea, salmon populations are exposed to mixed stock fisheries, so their managements required an international co-operation. In 1984, an inter-governmental organization was created: the North Atlantic Salmon Conservation Organization (NASCO). Through consultation and co-operation, NASCO assists all countries in the conservation, restoration, enhancement and rational management of salmon stocks (NASCO, 1983).

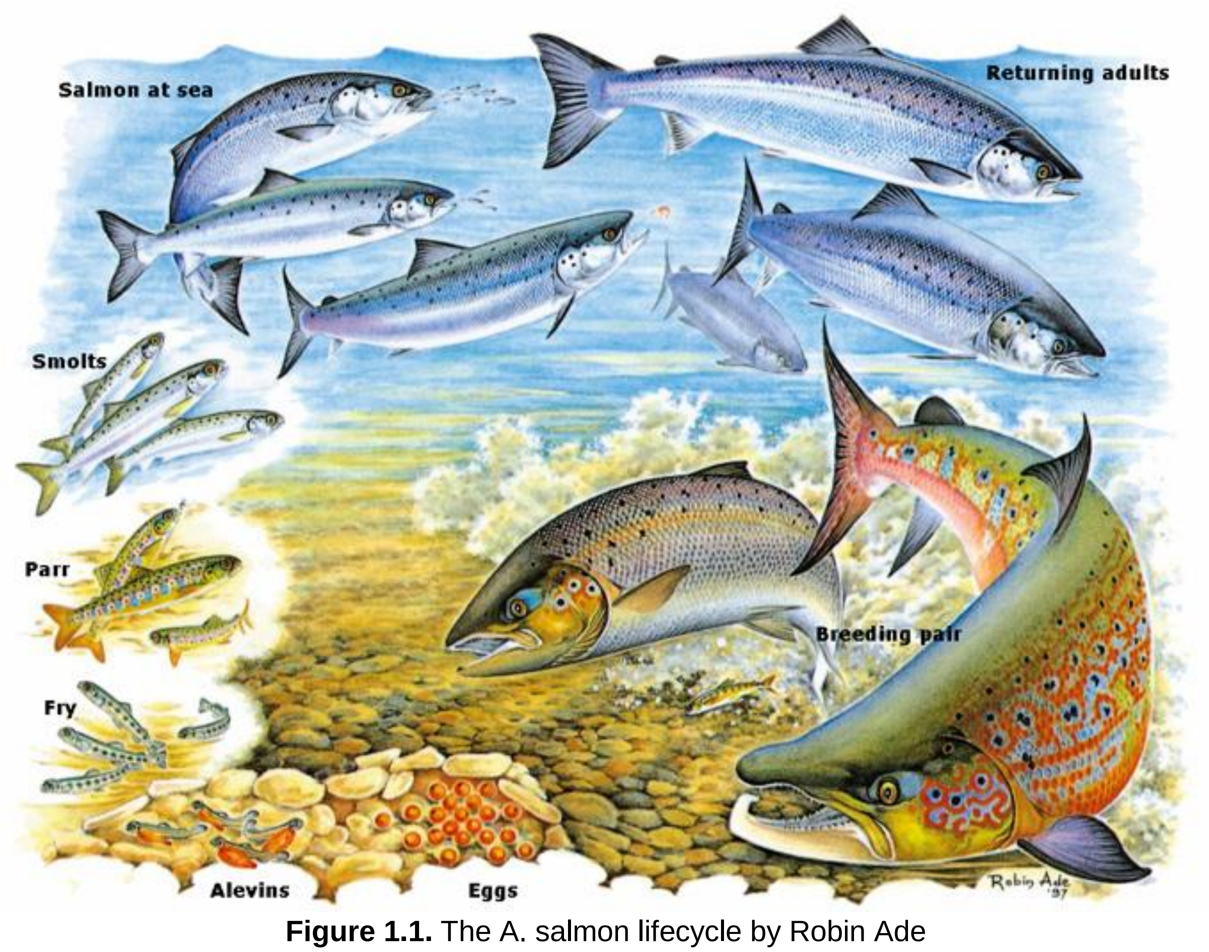

Figure 1.1. The A. salmon lifecycle by Robin Ade

Following the FAO Code of Conduct for Responsible Fisheries (FAO, 1995) and the United Nations Agreement on the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks (United Nations, 1995), NASCO and its contracting parties adopted a Precautionary Approach (PA) (NASCO, 1998). It is a cautious management approach aiming at achieving conservation given the uncertainty of scientific knowledge. It requires the development of Reference Points (RP) to determine the conservation status of each population. NASCO recommends two RP: Conservation Limits (CL) and Management Targets (MT) for each salmon stock. They define three conservation status: "critical" when spawning stock are below CL, "cautious" between CL and MT and "healthy" above MT (NASCO, 1998). To define these spawning stock reference levels, we must question mechanisms driving population renewal (conservation) such as reproductive capacity and juvenile survival. They are summarized in the Stock-Recruitment (SR) relationship between the abundance of spawning stock (Stock) and the number of fish produced in the next generation and available to fisheries (Recruitment). Hence, a CL must be set at a stock level producing enough recruitment to reach population conservation. To be cautious and account for uncertainty, a management target must be significantly higher than the CL.

Presently, only CLs have been defined and used for A. salmon management (ICES, 1995). There is a wide range of options for defining the spawning stock that allows conservation (Potter, 2001). Following the International Council for the Exploration of the Sea (ICES) and United Nations advice (ICES, 1995; United Nations, 1995), NASCO recommends CLs to be set at "the spawning stock level that produces maximum sustainable yield" S_{opt}, commonly known as B_{MSY} for other marine species (NASCO, 1998). To regulate exploitation and maintain stock above S_{opt}, NASCO recommends the establishment of a Total Allowable Catch (TAC) corresponding to the number of recruits left in the population after preserving S_{opt}.

The management of A. salmon is operated at a national scale but must follow NASCO recommendations. Each country must provide a six-year implementation plan summarizing their management strategy. In France, the French Environmental Code entrusts the management of A. salmon to eight Regional Committees (Comité de gestion des poissons migrateurs, COGEPOMI), one of which is for Brittany. They gather various stakeholders: fishers, managers (from Governmental bodies), scientific advisors and NGOs. They define five-year management plans (PLAGEPOMI) in accordance with the French implementation plan presented to NASCO.

Brittany, holds the majority of the French A. salmon populations; i.e. about thirty. A new management strategy has been established in 1996 (Prévost and Porcher, 1996) with no major change since then. It is based on a fishing period and a Total Allowable Catch (TAC). As recommended by NASCO, the TAC is derived from the CL S_{opt} and defined for each river. Once the TAC is reached, local authorities close fisheries. Note that this system essentially applies to the recreational fishery operating in freshwater (rod and line) and has little control on the estuarine and marine catches. Brittany has been a pioneer in applying this new management strategy. Later on, this was applied and adapted to other regions in France. In the context of the revision of both the new 2018-2022 management plan in Brittany and the new French implementation plan in 2019, the COGEPOMI of Brittany identified the need for a profound revision of its current management strategy.

Several authors agree with the need to rethink about the current NASCO operational definition of conservation and how setting S_{opt} as CL helps to achieve it (Chaput et al., 2013; Holt et al., 2009; Potter, 2001). By choosing S_{opt} as conservation's reference point, management of A; salmon aims at preserving at least stock level maximizing long-term catches. Exploitation becomes central in this definition while conservation itself appears as almost subsidiary. Below S_{opt}, besides potential conservation issues, the main concern of managers was the decrease in exploitation potential. Hence, current CL definition holds an ambiguity between exploitation optimization and conservation status. Moreover, the determination of S_{opt} requires the construction of an equilibrium yield curve which is derive from a classical stage-to stage SR relationship. Unobserved recruitment available to fisheries is estimated by making strong hypothesis on marine survival (i.e. natural survival and fishing mortality) (Chaput et al, 2013). Marine catches affecting a single stock are usually poorly known, because of both partial reporting and mixed stock fisheries. As a result, recruitment estimates may therefore be biased as well as CL definitions.

In addition, many recommendations made by the *NASCO Guidelines for the Management of Salmon Fisheries* (NASCO, 2009), are barely integrated into the current French CLs. As recommended by NASCO (2009): "river specific CLs should be established based on data derived from each river". But to estimate CLs, the modeling of SR relationship currently used assumes that stock and recruitment per unit of productive area is homogeneous among rivers. A unique SR relationship, drawn from the SR data and productive area of the Scorff, is readily extrapolated to the other rivers knowing their productive areas. This assumption is questionable given the variability of exposition to anthropogenic pressures and environmental conditions among rivers. NASCO (2009) encourages also that: "the management measures introduced should take into account the uncertainties in the data used » wether due to recruitment variability intra-population or to random measurement errors in the SR data (estimates). To do so, NASCO recommends to set a second reference point MT, significantly higher than CL. Given no particular approach has been recommended by neither NASCO nor ICES, no country has implemented MTs so far and uncertainty remains essentially ignored by most management strategies.

The ultimate objective of this Master's project is to propose a new definition and practical implementation of CLs for rivers of Brittany, integrating river specific data and associated uncertainty while shifting management objective toward conservation rather than exploitation. Although focusing on Brittany Rivers, the new CLs are developed with the aim of being generalized at a broader scale, i.e. France or Europe. This work has been inspired by the recent review of Canadian PA for A. salmon management, which defines conservation as simply avoiding low recruitment (Chaput, 2015; Chaput et al., 2013; DFO, 2009).This study has been developed within the framework of the RENOSAUM project carried out in collaboration by the "Agence Française pour la Biodiversité" (AFB), the "Université de Pau et des Pays de l'Adour" (UPPA) and the "Institut National de la Recherche Agronomique" (INRA). Several CL options are proposed considering different interpretations and concrete translations of the term "low recruitment". Uncertainty is accounted for by working on the probability of avoiding "low recruitment". SR relationship are specifically adjusted for each river by taking advantage of the river specific data available i.e. catches and juveniles (young of the year) abundances indices. To avoid assumptions on marine survival, we consider recruitment at a freshwater stage (young of the year). Both stock and recruitment are standardized by corresponding productive areas. Joint SR modeling of all rivers is carried out through a Bayesian hierarchical model (BHM) proved useful for SR meta-analysis by borrowing strength between data rich and data poor rivers (Chaput, 2015; Liermann and Hilborn, 1997; Michielsens and McAllister, 2004; Myers, 2001; Prévost et al., 2003). SR modeling is undertaken by setting the Scorff as a reference because the long term and comprehensive survey operated on this river provides the longest and most precise time series of stock and recruitment data for Brittany.

Materials & Methods

I. Stock-recruitment relationship: a theoretical framework to incorporate uncertainty into CL definition

A. What is a Stock-recruitment relationship?

As described by Walters and Korman (2001), the SR relationship must be taken “not as a curve, but rather as a family of probability distributions, with means and variances that are dependent on spawning biomass (i.e. stock). According to this definition, a curve connecting the means or modes of such distributions is called a SR curve.” Two types of factors drive the SR relationship:

- **The density-dependent (ddp) factors:** They are generated by windows and bottlenecks occurring mostly during the freshwater part of the A. salmon life cycle, i.e. the reproduction (Beard and Carline, 1991) and the early stages (Gibson, 1993). Negative effect of density is often referring to intraspecific competition (resources, reproduction etc), predation or parasites exposure (Elliot, 2001). Their incidence grows as the spawning stock level increases. Conversely, a positive effect of density (Allee effect) may occur at low stock levels (Elliot, 2001). Benefit of density arise from increasing probability to find mates and improve escapement to predation in condition of saturation of predators. Quite often, evidence of positive density dependence remains elusive by the sole analysis of SR data (Myers et al., 1995; Liermann and Hilborn, 1997). Only negative effects of the density-dependent factors are considered in our study.

- **The density-independent (didp) factors**: They refer to environmental variables defining A. salmon habitat (depth, flow, substrate or food availability). They affect A. salmon populations mostly during extreme events like winter floods or summer droughts (Elliot, 2001).

Many formulations of SR curve and associated uncertainty exist and illustrate various ecological views of the effects of ddp and didp factors on SR survival. Here, the Beverton-Holt function is used for the SR curve as increasing evidence argue in favour of its relevance for A. salmon ((Michielsens and McAllister, 2004; Pulkkinen et al., 2013). The variability surrounding SR curve is assumed to be log-normally distributed (Peterman, 1981; Shelton, 1992; Crittenden, 1994; Bradford, 1995; Walters and Korman, 2001; Prévost et al., 2003).

SR relationship are used to derive CLs based on our definition of conservation i.e. avoiding “low recruitment”. We take advantage of the SR curve and data to propose different definitions of what could be considered as “low recruitment”. Uncertainty is thereafter considered to define stock levels that allow to avoid low recruitment with various probability levels.

B. Using a SR curve and data to define "low recruitment"

For every river, we propose to define « low recruitment » by using two types of references:

- **Theoretical references:** They rely on the SR curve and are derived from the carrying capacity (R_{MAX}). It is defined as the maximum of the average recruitment abundance that can be supported by a given environment (Elliot, 2001). In good environmental conditions, recruitment can be higher than R_{MAX} in some years, but on average over long term, it would never exceed it. For the conservation of a population, it cannot be done any better than to preserve spawning stock size that would produce R_{MAX}. In the framework of a Beverton-Holt function, such a stock size does not exist (it would be infinite). In addition, whatever the spawning stock size, maximizing average recruitment is a goal that can be achieved at best with a 50% probability. Therefore, choosing R_{MAX} as a reference level for defining low recruitment appears as overly ambitious. Nevertheless, R_{MAX} remains a useful theoretical benchmark for recruitment. So, we propose to define "low recruitment" as a percentage of R_{MAX}: and illustrate the approach by choosing 25, 50 and 75% (see **figure 2.1.** for examples).

- **Historical references:** They are based on past observed SR data. Assuming a good conservation status for a given river, a low recruitment could be defined relative to the mean of the observed recruitment (R_{OBS}). The approach is illustrated by using three definitions of "low recruitment": 25% R_{OBS}, 50% R_{OBS} and 75% R_{OBS} (**Figure 2.1.**).

C. Integrating the uncertainty associated to SR relationship into the definitions of CLs

For a given SR model, two main sources of uncertainty affect the SR relationship *i.e.* the uncertainty of SR observations or observation error and the uncertainty of the recruitment process. The former is due to the fact that both the stock and recruitment are not directly observed and exactly known, but rather estimated from indirect or partial observation data. The latter refers to the random variations of recruitment for any given spawning stock level. As only a couple of SR observations are available, the estimates of the parameters of the SR model (i.e. governing the SR curve and the variance of the lognormal process error) is also uncertain and produces the last source of uncertainty.

Observation error, process error, and estimation error of SR model parameters are considered for the definition of CL. For any given spawning stock, we consider the probability that a low recruitment could be produced by integrating over the above three sources of uncertainty. For instance, for a given S value, we calculate the probability that the corresponding recruitment could fall below 50% R_{MAX}, by integrating over the recruitment process error, the estimation error of the SR model parameters, the latter being itself derived by taking into account that SR series are also affected by some estimation error. By doing so we calculate the risk of low recruitment integrated over the main sources of uncertainty of the SR relationship.

Such calculation allows to derive plots of risk of low recruitment as a function of the stock level, low recruitment being defined beforehand. On such a plot, one can identify spawning stock levels that have an acceptable risk of low recruitment. Following Chaput et al. (2013), we define CLs on this basis. We illustrate the approach by considering several CL options corresponding to varying risk levels associated to different definitions of low recruitment. By assuming higher acceptable risk for more stringent definitions of low recruitment, we retained the following options: risk of 15% to produce 25% of R_{MAX} (CL_1) and R_{OBS} (CL_4), risk of 25% to produce 50% of R_{MAX} (CL_2) and R_{OBS} (CL_5) and Risk of 40% to produce 75% of R_{MAX} (CL_3) and R_{OBS} (CL_6) see **figure 2.2.** for example).

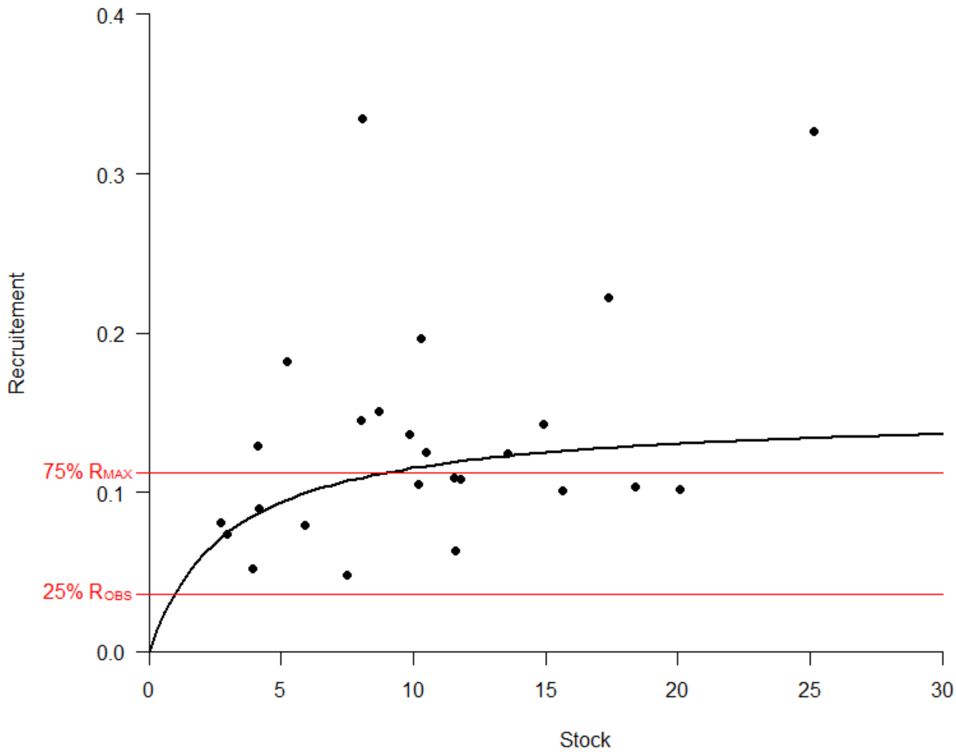

Figure 2.1. Examples of low recruitment references considered: 25% R_{OBS} and 75% R_{MAX}.

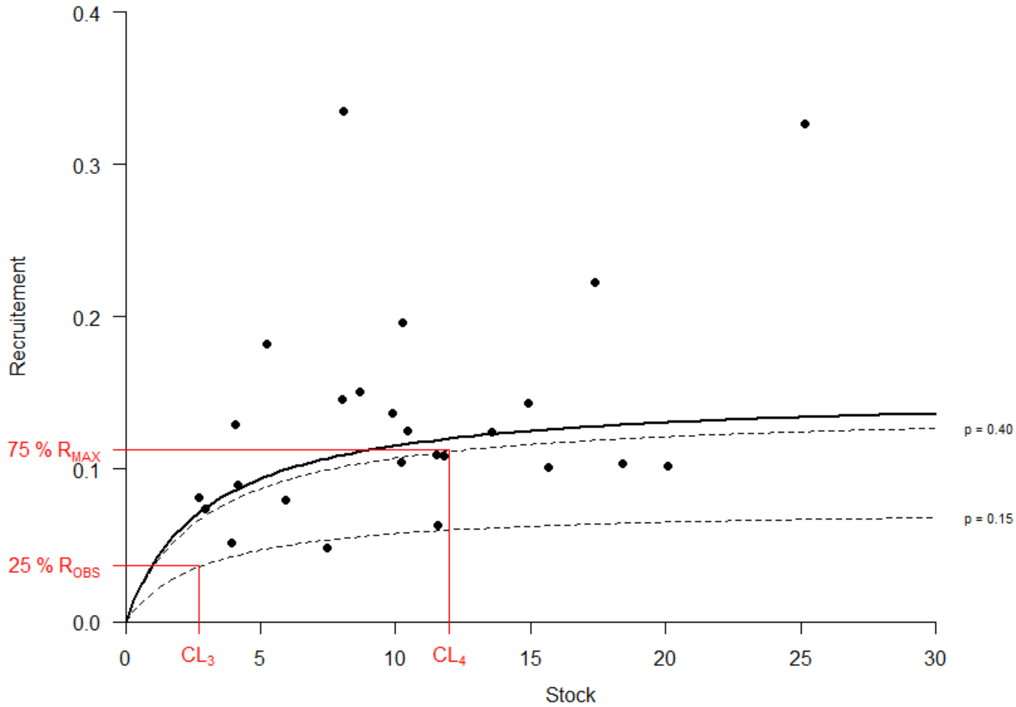

Figure 2.2. Examples of CL considered: CL_3 and CL_4. The solid line is the SR curve, which corresponds to the evolution of the median recruitment. For any given stock level , the risk the expected recruitment falls below the SR curve is 50%. The dotted lines are analogous to the SR curve but for other risk levels, i.e. 15 % and 40%. The intersection of these curves with a pre-determined recruitment level, i.e. 75% and 25% of Rmax, allow to derive the corresponding CLs, CL3 and CL4

II. Rivers and populations of interest and available data

A. Studied populations

Among the thirty rivers of Brittany in which A. salmon populations are managed, only the main eighteen are considered. They are distributed along of the coast of Brittany from the south-eastern (Blavet) to the north-eastern (Couesnon) (**Figure 2.3.**). Rivers sharing a common estuary or with a high spatial proximity - namely the Ellé and the Isole, the Aven and the Ster Goz; the Odet, the Jet and the Steïr, the Aulne and the Douffine and the Mignonne, the Camfrout and the Faou - are pooled together and considered as a single river.

Each river is characterized by its water surface area favorable to juvenile production or productive area, expressed in m^2 of riffles-rapids equivalent (RRE) (Bagliniere and Arribe-Moutounet, 1985; Bagliniere and Champigneulle, 1982; Prévost and Porcher, 1996) and accessible to A. salmon. Since 1994, it is computed thanks to riverine habitat cartography. These cartographic data are regularly updated and provide time-series of productive areas up to 2015 (**Appendix 2.1.**). Across rivers and years, productive areas vary by a factor of 1 to 20. The Yar and Goyen offer the smaller productive areas (about 50 000 m^2 of riffles-rapids area) whereas the Ellé-Isole and Blavet have 350 000 and 650 000 m^2 RRE available for juvenile production.

The Scorff is a reference river for Brittany. Its A. salmon population has been studied and monitored extensively and for a long time. It belongs to the set of index rivers used by ICES to assess the status of the species annually over its entire distribution range (ICES, 2014). It is also used by the COGEPOMI of Brittany as its reference for setting CLs and TACs for the other rivers. Its main stem is 75 km long and its drainage basin is 480 km^2 (Baglinière and Champigneulle, 1986). It flows into the Atlantic Ocean at Lorient and offers a productive area to juvenile of about 200 000 m^2. It is of intermediate size in the set of the rivers of Brittany considered herein. Its A. salmon adult returns and juvenile production have been continuously surveyed since the 90's. Given its unique status, the Scorff is used as a reference further in our analyses.

B. Recruitment data

Scorff

Juvenile abundance indices (AI) are collected in the Scorff since 1993 (24 years up to 2016) (**Appendix 2.1.**). By electro-fishing shallow running water at the beginning of autumn, the sampling protocol targets the 0+ parr or Young-of-the-Year (YoY). About fifty electro-fishing sites are sampled every year according to an accurate protocol (Prévost and Baglinière, 1995; Prévost and Nihouarn, 1999). A significant sampling effort of about 2.5 stations per 10 000 m^2 of RRE is undertaken in this river.

Other rivers of Brittany

In the other rivers, IA are also collected. Time-series vary between rivers from 5 years (2012-2016) for the Mignonne-Camfrout-Faou River to 23 years (1994-2016) for the Odet-Jet-Steïr. Sampling efforts are lower than the Scorff, at an average of 1.2 stations per 10 000 m^2 of RRE.

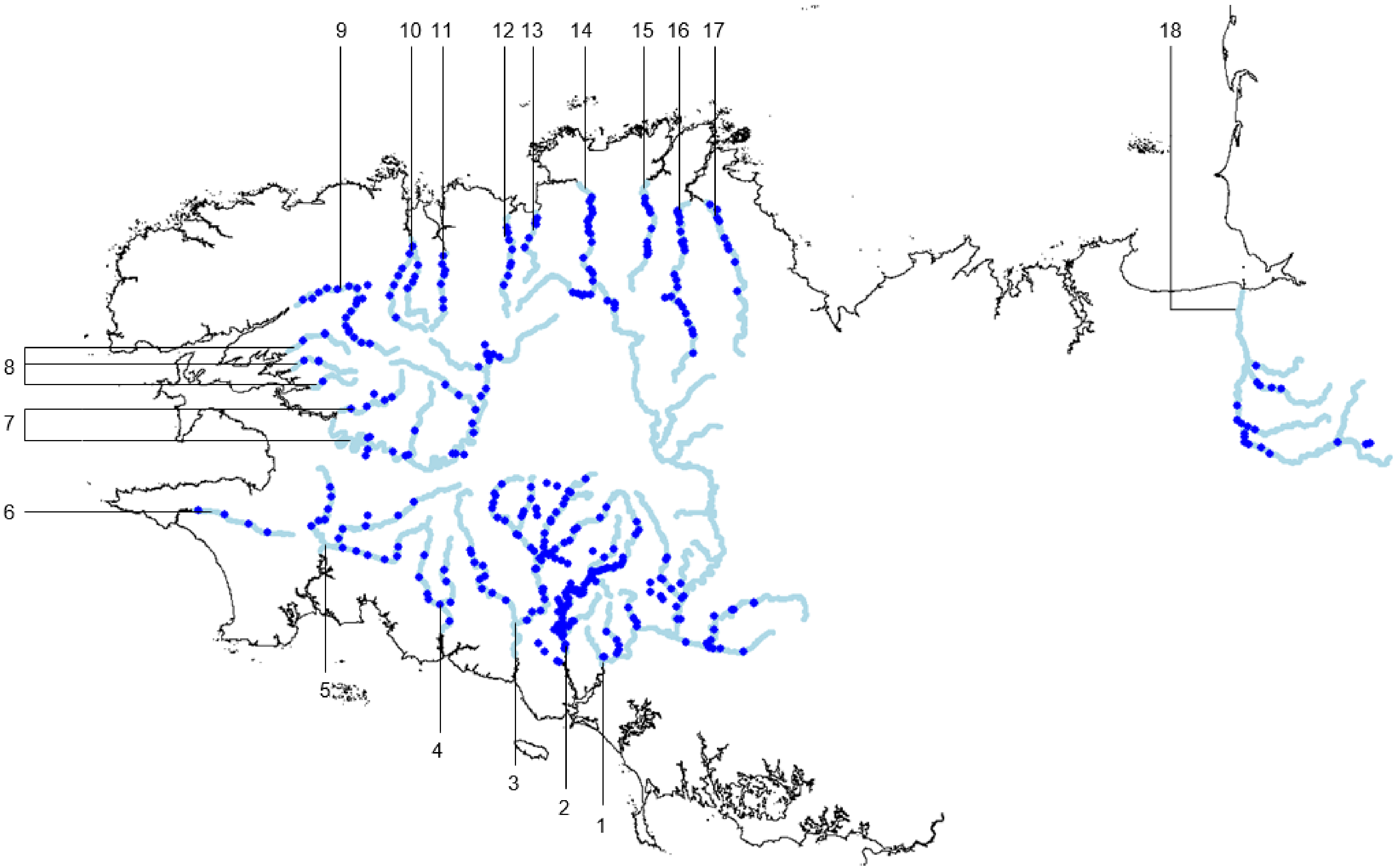

Figure 2.3. Rivers of Brittany considered in this study. Rivers are figured in light blue and sampling stations in darker blue. A number of 1 to 18 is allocated to each river according to a south-eastern to north-eastern gradient. 1: Blavet 2: Scorff 3: Ellé-Isole 4: Aven-Ster Goz 5: Odet-Jet-Steïr 6: Goyen 7: Aulne-Douffine 8: Mignonne-Camfrout-Faou 9: Elorn 10: Penzé 11: Queffleuth 12: Douron 13: Yar 14: Léguer 15: Jaudy 16: Leff 17: Trieux 18: Couesnon

From data to river scale estimates of recruitment

To derive recruitment estimates at the river scale, homogenous across rivers, IA data were processed by a slightly modified version of the statistical model designed by Servanty and Prévost (2016). This model is used to estimate YoY population size and densities (per m² RRE) in the Scorff. It could not be readily generalized to all rivers of Brittany as it uses river flow as a co-variable in a way that is hard to standardize across rivers. A simplified model, but with a hierarchical setting (**Appendix 2.2.**), was built to jointly treat IA data of all rivers, including the Scorff.

Time-series of recruitment

In further analyses, point estimates (i.e. posterior medians) of YoY density at the river scale are used as recruitment data. No measurement errors are integrated. The time-series of recruitment are presented in the **Appendix 2.3.** Between rivers, recruitment varies within a wide range of variation *i.e.* from 0.005 YoY per m^2 of RRE for the Aulne-Douffine in 1998 to 87 for the Queffleuth in 2011. Within rivers, variations of recruitment can be as wide as between rivers (see Queffleuth). Compared to the other rivers, the Aulne-Douffine has the lowest average recruitments, about 0.10 YoY per m^2 of RRE. Time-series trends are observed for 5 rivers, i.e. an increase of YoY densities for the Scorff, the Elorn, the Penzé and the Couesnon and a decrease for the Yar.

C. Adult returns and spawning stock data.

Scorff

Since 1994 and the installation of a trapping device at the head of tide, the “Moulin des Princes” station (Pont-Scorff), adults returns are assessed by capture-mark-recapture (Servanty and Prévost, 2016). A few scales are removed from each fish sampled for ageing. This allows to produce yearly estimates of one sea winter (1SW) and multi-sea winter (MSW) returns separately. Servanty and Prévost (2016) designed a statistical model for estimating annually adult by sea age category. Combined with the catch figures by sea age category obtained from the “Centre National d’Interprétation des Captures de Salmonidés” (CNICS), the spawning escapement is also estimated. The resulting time series of point estimates (posterior medians) of adult returns and spawning escapement are further used as data in this study. Given the difference of reproductive capacity between 1SW and MSW, spawner abundances are combined to derive a number of (potentially) spawned eggs. It is computed by summing the number of eggs spawned by each sea age category obtained by multiplying spawner numbers with their corresponding average proportion of females sex ratio and fecundity per female (**Appendix 2.4.**) Finally, numbers of eggs are expressed in density per m² of RRE using the known productive areas.

Other rivers of Brittany

For the other rivers, only catches from the CNICS are available to estimate adult returns and spawning escapement. A specific model described in the sequel (Materiel & methods III.B) has been designed to this end. Note that this model is also used to estimate adult returns of the Scorff generating the recruitment of 1993 and 1994, using the catches of 1992 and 1993 from the CNICS database.
In the Aulne-Douffine and the Elorn, video-counting devices have been installed at the lower end of each river. In the Elorn, adult returns are available since 2007 and used as observed data like for the Scorff. For the Aulne-Doufine, adult returns are available since 1999 and used as censored data because fish can by-pass the video-counting device.

III. Modeling SR relationship for rivers of Brittany to set CL.

A. Outlines of the model

1. Exploitation sub-model

Apart from the Scorff, there is no stock data available. Only catches provide information about the spawning adult abundance of each river. Thus, before modeling SR relationships, we modeled the observation process linking the stock to the catches (C) using an exploitation sub-model (**Appendix 2.5.**). Its simplified Directed Acyclic Graph (DAG) is presented **figure 2.4.**. In this sub-model, the link is modeled thanks to the adult returns (N) and their corresponding exploitation rates (F). We integrate the Scorff into the modeling to take full advantage of its available data on both the stock and the catches. Unlike the recruitment, this model allows to integrate the error associated to the indirect observation of the stock into the SR modeling (SR sub-model).

2. SR sub-model

Scorff

The SR sub-model is spatially structured and considers the Scorff separately from the other rivers (**Figure 2.4.**). Recruitment and stock data are used to model its specific SR relationship. The SR curve (median recruitment) is modeled using a Beverton-Holt function as several publications argue its relevance for A. salmon (Michielsens and McAllister, 2004; Pulkkinen et al., 2013). Two parameters are considered for the SR curve: maximum survival (α) and carrying capacity (R_{MAX}). Like many authors, we assume the error of the recruitment process to be log-normally distributed (Chaput, 2015; Michielsens and McAllister, 2004; Prévost et al., 2003; Pulkkinen et al., 2013; Walters and Korman, 2001).

Other rivers

For the other rivers, the same formulation of the SR curve and process error are used. To make other rivers benefit from the knowledge acquired from the Scorff, we express each SR curve relative to the SR curve of the Scorff. That is, we use the same parameters (i.e. α and R_{MAX}) and weighted them with a multiplicative factor (δr) specific to each river. Finally, we define the variability of the recruitment process at a river scale (σ_r).

3. BHM framework

Both sub-models use a hierarchical structure to transfer to any given river to the knowledge gained from all the others (Liermann and Hilborn 1997; Myers 2001; Prévost et al. 2003; Michielsens et McAllister 2004; Chaput, 2015). In particular, hierarchical modelling is applied to the exploitation rates, the multiplicative factors and all the variance parameters (Gelman, 2006).

We take advantage of the Bayesian framework to set a full probabilistic model and provide an accurate description of the uncertainty. In addition, it allows us to integrate prior knowledge on the parameters of the SR curve which can be difficult to estimate using SR data only (Walters and Korman, 2001)

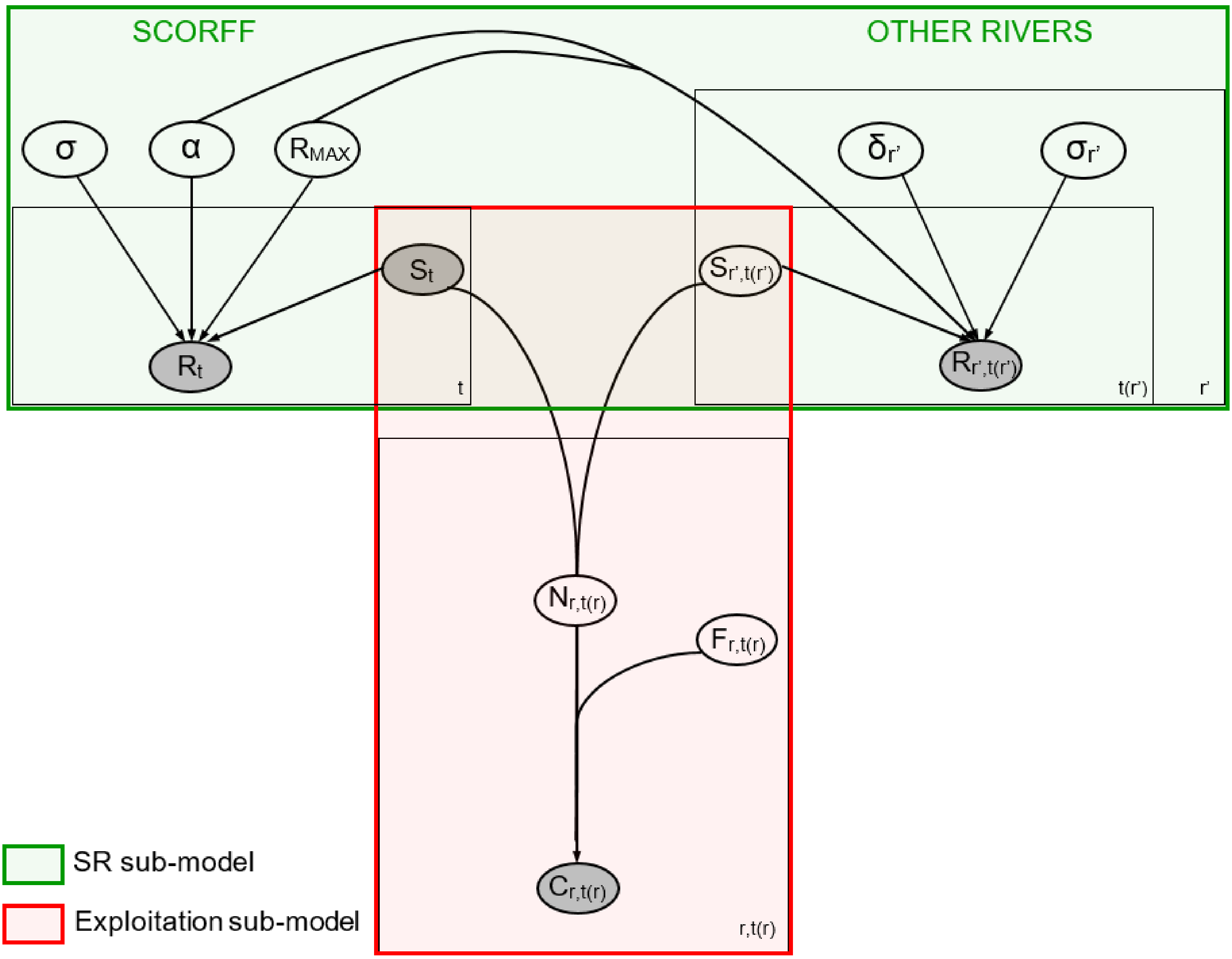

Figure 2.4. Simplified Directed Acyclic Graph of the model used. The exploitation sub-model is figured in red whereas the SR sub-model is figured in green. Each variable and co-variable is represented with respectively an ellipse and a rectangle. When data are available, the form is shaded in grey. r is the number of river Brittany. It is included between 1 and 18. r' is similar than r but exclude the number of the Scorff. t(r) and t(r') illustrate the different time series available for each river.

B. Exploitation sub-model

We model the observation process of the stock by means of a hierarchical model based on a theoretical variable: the density of adult returns (Dreturn). It represents the abundance of returning adults standardized by, i.e. relative to, the river size. We assume it follows a log-normal distribution with a mean ($\mu_{Dreturn}$) for each river *r* and year *t* and a single standard deviation ($\sigma_{Dreturn}$) common to all rivers (1).

$$\log(Dreturn_{r,t}) \sim Normal(\mu_{Dreturn_{r,t}}, \sigma_{Dreturn}) \quad (1)$$

Multiplicative year (ψ_t) and river (ρ_r) effects are combined to set the mean adult return (2).

$$\mu_{Dreturn_{r,t}} = \psi_t \times \rho_r \quad (2)$$

Year and river effects are hierarchically modeled according to log-normal distributions.

$$\log(\psi_t) \sim Normal(\mu_\psi,, \sigma_\psi) \quad (3)$$

$$\log(\rho_r) \sim Normal(0, \sigma_\rho) \quad (4)$$

μ_ψ represents the mean density of adult returns over years and rivers (log scale). σ_ψ and σ_ρ are the standard deviations of the year effect and the river effect respectively.

To separate the two sea ages, we hierarchically modeled the proportion of 1SW (p1SW). It is assumed to be drawn from a beta distribution (5) reparametrized using its mean (μ_{p1SW}) and a sample size (n_{p1SW}) (6).

$$p1SW_{r,t} \sim Beta(a,b) \quad (5)$$

$$a = \mu_{p1SW} \times n_{p1SW} \text{ and } b = n_{p1SW} - a \quad (6)$$

Densities of each sea age are computed using the 1SW proportion (7).

$$D1SW_{r,t} = Dreturn_{r,t} \times p1SW_{r,t} \text{ and } DMSW_{r,t+1} = Dreturn_{r,t} \times (1-p1SW_{r,t}) \quad (7)$$

Numbers of adult returns (N1SW and NMSW) are assumed to be Poisson distributed according to a parameter defined for each sea age (λ1SW and λMSW), river *r* and year *t* (8). These parameters are computed by multiplying sea age specific densities by productive areas that supported the production of the returning aduts in year t (9). Considering YoY mainly smoltify in their second year of life (Dumas and Prouzet, 2003), we use productive area of year t-2 (RRE_{t-2}) for 1SW and t-3 (RRE_{t-3}) for MSW.

$$N1SW_{r,t} \sim Poisson(\lambda 1SW_{r,t}) \text{ and } N1SW_{r,t} \sim Poisson(\lambda MSW_{r,t}) \quad (8)$$

$$\lambda 1SW_{r,t} = D1SW_{r,t} \times SRRE_{t-2} \text{ and } \lambda MSW_{r,t} = DMSW_{r,t} \times SRRE_{t-3} \quad (9)$$

Finally, both sea age catches (C1SW and CMSW) are modeled thanks to binomial laws with respectively N1SW and NMSW draws and FSW and FMSW capture probabilities (i.e. exploitation rates) (10). For each sea age, we assume exploitation rates to be normally distributed on the logit scale with one mean per river ($\mu_{F1SW\,r}$ or $\mu_{FMSW\,r}$) and a unique standard deviation (σ_{F1SW} and σ_{FMSW}) (11). Given exploitation rates are difficult to estimate, we used a hierarchical structure to model mean exploitation rates. Logit-Normal distributions are used with M_{F1SW} and M_{FMSW} and standard deviations $\sigma_{\mu_{F1SW}}$ and $\sigma_{\mu_{FMSW}}$ (12).

$$C1SW_{r,t} \sim Binomial(N1SW_{r,t}, F1SW_{r,t}) \text{ and } CMSW_{r,t} \sim Binomial(NMSW_{r,t}, FMSW_{r,t}) \quad (10)$$

$$\mathrm{logit}(F1SW_{r,t}) \sim Normal(\mu_{F1SW_r}, \sigma_{F1SW}) \text{ and } \mathrm{logit}(FMSW_{r,t}) \sim Normal(\mu_{FMSW_r}, \sigma_{FMSW}) \quad (11)$$

$$\mathrm{logit}(\mu_{F1SW_r}) \sim Normal(M_{F1SW}, \sigma_{\mu_{F1SW}}) \text{ and } \mathrm{logit}(\mu_{FMSW_r}) \sim Normal(M_{FMSY}, \sigma_{\mu_{FMSW}}) \quad (12)$$

Note that 1SW exploitation rates are set to zero for three rivers of the Morbihan (Blavet, Scorff and Ellé-Isole) in 2003 because of exceptional fisheries closure.

Finally, stock (egg density) is derived from the returns using the sea age specific catches, females sex-ratio and fecundity as well as productive areas (13).

$$S_{r,t} = (N1SW_{r,t}\text{-}C1SW_{r,t}) \times \text{females sex-ratio}_{1SW} \times \text{fecundity}_{1SW} + (NMSW_{r,t}\text{-}CMSW_{r,t}) \times \text{females sex-ratio}_{MSW} \times \text{fecundity}_{MSW}) / SRR_{r,t} \quad (13)$$

C. SR sub-model

Scorff

To model the SR curve, we use a Beverton-Holt function (14). It is defined according to two parameters: the maximal survival (α) and the carrying capacity (R_{MAX}). The former is the slope at the origin and quantifies the reproductive performance at low stock (Walters, 2001). The latter was defined in the Materiel & Methods section II.B.. A log-normal stochastic error is assigned to the recruitment process (15).

$$\mu_{R_t} = \frac{S_t}{\frac{1}{\alpha} + \frac{S_t}{R_{max}}} \quad (14)$$

$$R_t \sim \text{Log-Normal}\left(\log\left(\mu_{R_t}\right), \sigma_R\right) \quad (15)$$

Other rivers

The modeling of the SR process assumed for the other rivers is the same as for the Scorff. The SR curve parameters of the the other rivers are that of the Scorff up to a river specific multiplicative factor (δ_r) (16). The process error variability σ_{R_r} is defined for each river (16).

$$\mu_{R_{r,t}} = \left(\frac{S_{r,t}}{\frac{1}{\alpha} + \frac{S_{r,t}}{R_{max}}}\right) \times \delta_r = \frac{S_{r,t}}{\frac{1}{\alpha_r} + \frac{S_{r,t}}{R_{max_r}}} \text{ where } \alpha_r = \alpha \times \delta_r \text{ and } R_{max_r} = R_{max} \times \delta_r \quad (16)$$

$$R_{r,t} \sim \text{Log-Normal}\left(\log\left(\mu_{R_{r,t}}\right), \sigma_{R_r}\right) \quad (17)$$

The multiplicative factors are hierarchically modeled relative to the Scorff (multiplicative factor of 1). We assume a full exchangeability between rivers i.e. each multiplicative factors is drawn independently from the same log-normal distribution with mean μ_δ, and standard deviation σ_δ' (log scale).

$$\delta_r \sim \text{Normal}(\mu_\delta, \sigma_\delta') \quad (18)$$

All the variance parameters (log and logit scales) are hierarchically modeled to facilitate further inferences (Gelman, 2006). The hierarchical structure is set on the precisions (τ_i). We used a reparametrized gamma distribution with a mean parameter (μ_τ) and an inverse scale (rate) instead of a shape and a scale parameter (19).

$$\tau_i \sim \text{Gamma (shape, scale), shape} = \mu_\tau \times \text{rate and scale} = 1/\text{rate} \quad (19)$$

$$\text{where } i \in [\![1:30]\!] \text{ and } I = 30$$

D. Bayesian framework

Prior distributions

All the prior distributions on the hyper-parameters and parameters are presented at **table 2.1.**. We set non-informative and independent priors for all hyper-parameters so that no prior distribution constrain the marginal posterior distributions.

The only exception to this general rule concern the parameters of SR curve for the Scorff. Earlier analysis with non-informative priors yielded nonsensical estimates, with much too high posterior probability associated with unrealistically high values of α or R_{MAX}. It was thus decided to bring some prior information to these variables by setting weakly informative priors. A beta distribution is set to α. The sample size driving the precision of the beta distribution is set to 2, to ensure the prior remains weakly informative and leave ample room for posterior updating by the data. To avoid setting to high prior probability on unrealistically high values, the maximal survival rate observed in the Scorff (4 % in 2003) is used to set By doing so, it is implicitly assumed that given the length of the series of SR observations (24 years), the maximum survival observed is (weakly) indicative of the expected survival at low stock size. Tha same rationale is used to assign a prior distribution to $R_{MAX.}$ An exponential distribution is used with mean corresponding to the maximum recruitment observed in the Scorff (i.e. 0.19 YoY per m^2 of RRE observed in 2003).

Parameter	Definition	Prior distribution
Exploitation sub-model		
μ_{ψ}^{*}	Equation (4)	Uniform(-10,10)
μ_{p1SW}^{*}	Equation (6)	Beta(1,1)
n_{p1SW}^{*}	Equation (6)	Uniform(-10,10) on the log scale
M_{F1SW}^{*}	Equation (12)	Normal(0,100)
M_{FMSW}^{*}	Equation (12)	Normal(0,100)
SR sub-model		
α	Equation (14)	Beta(0.08,1.92)
R_{MAX}	Equation (14)	Exponential(0.19)
μ_{δ}^{*}	Equation (17)	Uniform(-10,10) on the log scale
μ_{τ}^{*}	Equation (19)	Gamma(0.1,10)
rate*	Equation (19)	Gamma(0.1,10)

*Hyper-parameters of the model

Table 2.1. Prior distributions of the parameters and hyper-parameters of the model

Inferences

Posterior inferences and further analysis have been carried out using R and JAGS (version 4.2.0, rjags" package). The joint posterior distribution of all the unknown quantities of the model is approximated by MCMC sampling, using three chains with contrasted initial values. A posterior sample of size 15000 is obtained with a "thinning" of 10 50000 iterations per chain). The convergence of the chains is checked using the Gelman-Rubin index (Rubin and Gelman, 1992) and Geweke stationary test (Geweke, 1992). Whatever the unknown quantity, posterior statistics are derived from their marginal posterior samples (median, standard deviation and Bayesian Confidence Interval (BCI) at 95% to analyze variables). The posterior median is used as a point estimate in the sequel.

Results

I. Diagnostics

Convergence

We diagnose convergence of this model as upper limits of Gelman-Rubin index are lower than 1.1 and Geweke stationary test is passed for all parameters.

Prior distribution updates

Sampling in the joint posterior distribution of all the parameters updates prior distributions (**Table 3.1.**). Compared to the prior distributions, marginal posterior distributions are shrunk and means are modified. Note that the mean of the prior distributions of n_{p1SW} and μ_{δ} is quite high. Indeed, uniform distributions (-10, 10) set on the log scale of the variables lead to an important density of probability for low values offset by a long tail distribution. This long tail have an important effects on estimator like the mean but no effect on other like the median (equal to 1).

Parameter	Prior		Marginal posterior				
Exploitation sub-model	**mean**	**sd**	**mean**	**sd**	**2.5%**	**50%**	**97.5%**
μ_{ψ}	0_{1100}	5.77_{3300}	$-5.60_{0.004}$	$0.22_{0.0001}$	$-6.06_{0.002}$	$-5.60_{0.004}$	$-5.16_{0.006}$
μ_{p1SW}	0.50	0.29	0.81	0.01	0.78	0.81	0.83
n_{p1SW}	1100	3300	34.07	6.33	23.43	33.51	47.99
M_{F1SW}	$0_{0.5}$	$100_{0.5}$	$-3.24_{0.04}$	$0.25_{0.01}$	$-3.75_{0.02}$	$-3.24_{0.04}$	$-2.76_{0.06}$
M_{FMSW}	$0_{0.5}$	$100_{0.5}$	$-1.80_{0.14}$	$0.23_{0.03}$	$-2.25_{0.1}$	$-1.80_{0.14}$	$-1.34_{0.21}$
SR sub-model							
α	0.04	0.11	0.03	0.01	0.02	0.03	0.07
R_{MAX}	0.19	0.19	0.20	0.07	0.11	0.19	0.39
μ_{δ}	1100	3300	1.49	0.31	0.97	1.46	2.20
μ_{τ}	0.01	2.87	4.50	0.73	3.36	4.40	6.22
rate	0.01	2.90	0.85	0.51	0.27	0.74	2.11

Table 3.1. Comparison between prior and marginal posterior distributions of parameter modeled. Mean and standard deviation of the two distributions are presented. 95% BIC and median of the marginal posterior distributions are added. For variables express on another scale than natural, each estimator is index with its natural scale value.

Residual analysis

To assess the fit of the model, we analyzed the standardized residuals of recruitment (**Appendix 3.1.**). For most of the rivers, they are normally distributed i.e. included between -1.96 and 1.96 and homogeneous between years and stock levels. Nevertheless, temporal trends appear for the Scorff and the Elorn. Residual are sensitive to the stock level in three rivers: the Penzé, the Yar and the Couesnon (**Appendix 3.2.**).

II. Exploitation sub-model

A. Exploitation rates

As shown in the **table 3.1.**, the 1SW mean exploitation rates across rivers (M_{FSW}) is 0.04% (median). As presented in the **figure 3.1**, for this sea age, the median exploitation rate of the Scorff is slightly higher than the other rivers (0.06%) and its estimation is sparsely variable (standard deviation of 0.008 on the natural scale). For the other rivers, the median exploitation rates vary from a factor 1 to 10. The lower median value is estimated to 0.01 for the Yar whereas the higher is estimated to 0.10 for the Goyen. The latter have the most variable estimate with a standard deviation of 0.04.

For the MSW, the mean exploitation rate across rivers (M_{FMSW}) is estimated to 0.14%. It is about three times higher than estimate for 1SW. For the Scorff, the mean exploitation rate is relatively smaller than mean across rivers (0.12) and its estimate is sparsely variable (0.01). For the other rivers, the mean estimates are less variable than 1SW and vary from a factor of 1 to 2.5. The lower mean is estimated for the Jaudy (0.08) and the higher for the Elorn (0.2). Estimates of MSW mean exploitation rates are generally more variable than 1SW estimates.

Finally for most of the rivers, no temporal trend on annual exploitation rates is highlighted (**Appendix .3.3.** and **Appendix 3.4.**). Note than 1SW exploitation rates seem to decrease in the Aulne-Douffine. In the Elorn, a significantly higher exploitation rate is estimated for the year 2007.

B. Adult returns

The mean density of adult returns (μ_{ψ}) is estimated to 0.004.m^{-2} of RRE (**table 3.1.**) Median year effects vary with an amplitude of ± 0.002.m^{2} of RRE around mean estimate density (**figure 3.2.**). Maximum medians are estimated for years 1995, 2004 and 2010 whereas minima are estimated in 1997 and 2009.

Random effects of rivers are shown **figure 3.2.**. The median vary between rivers from a factor 1 to 4. Thus, for a particular river of Brittany, median density of adult returns is included between half and twice mean adult density. The median effect of the Scorff is estimated to be a quarter lower than the other rivers ($\rho_2 = 0.75$). For the other rivers, two trends are observed. In the south of the Brest bay (until the Aulne-Douffine), median river effects increase along an east-west gradient. Further north, river effects are more variable with low values for rivers with productive areas smaller than 100 000m^{2}(Mignonne-Camfrout-Faou, Queffleuth, Yar and Leff).

Mean proportion of 1SW (μ_{p1SW}) is estimated to 81% (**table 3.1**). For the Scorff, the proportion of 1SW in the adult returns is decreasing since the end of the 90's. For the other rivers, the variability of the estimates is too high to detect temporal trend.

As 1SW proportion, the high variabilities of 1SW and MSW estimates hide all possible temporal trend (**Appendix 6.5.** and **Appendix 6.6.**). However, we note a slight increase over time for the Ellé-Isole, the Aven-Ster Goz and the Couesnon. The absence of adult return trends spreads to stock estimates (**Appendix 6.7.**).

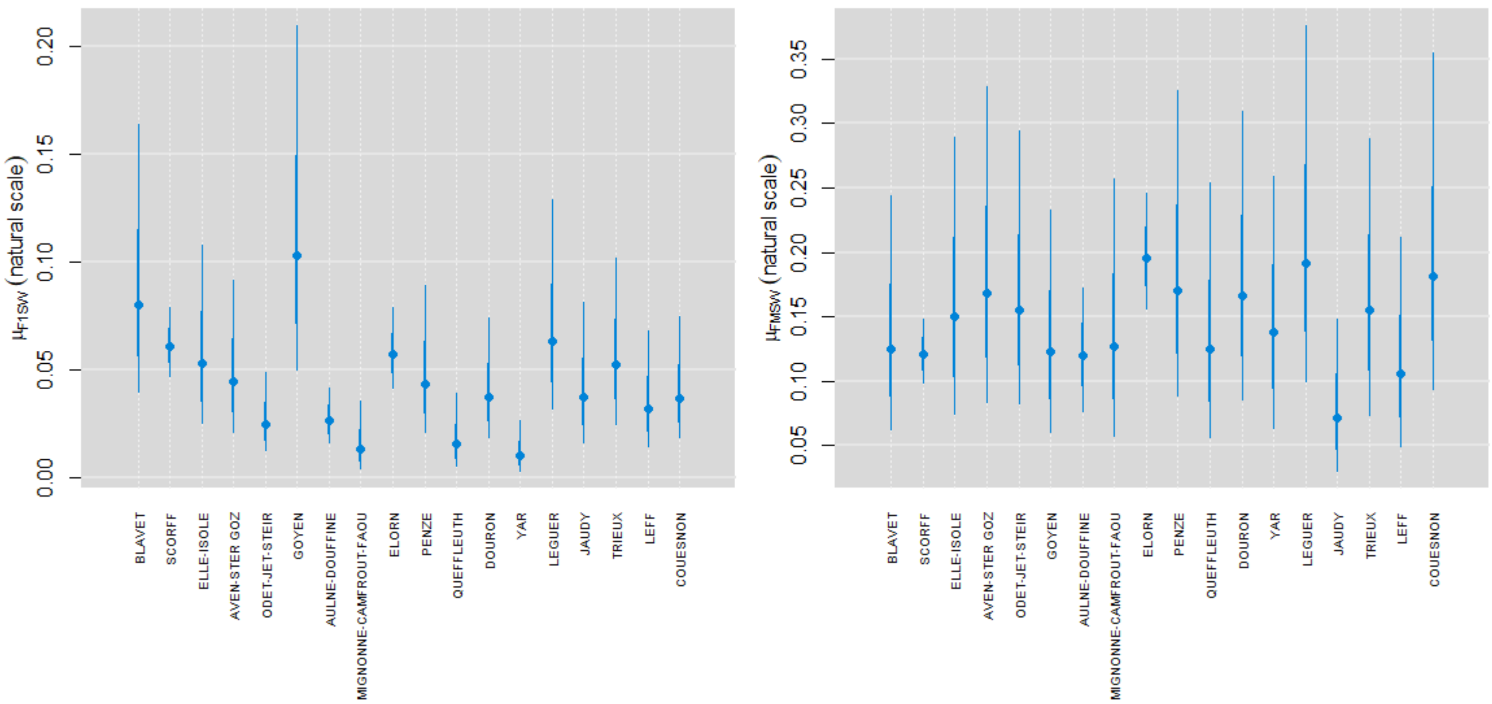

Figure 3.1. Mean exploitation rate per river for both 1SW (left figure) and MSW (right figure)

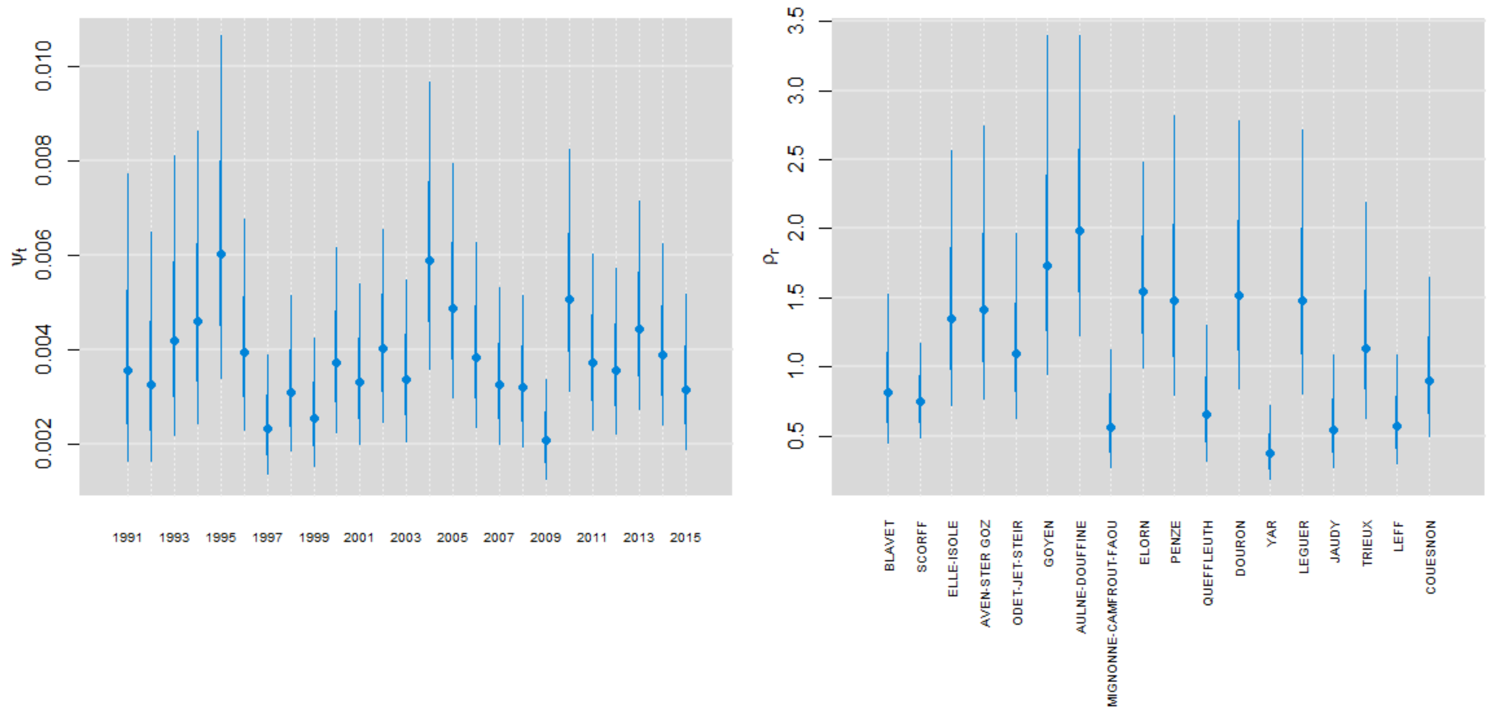

Figure 3.2. Multiplicative effects of years (left) and rivers (right)

III. SR sub-model

A. Estimates of the SR curve parameters of the Scorff and illustration of its SR relationship

Joint posterior distribution of SR curve parameters

The marginal distribution (prior and posterior) as well as the joint posterior distribution of the SR curve parameters are presented **figure 3.3.** The median of the marginal distribution of is 0.03% for α and 0.19 YoY.m2 of RRE for R_{MAX} (**table 3.1.**). The uncertainty of the estimates is important for both parameters as 95% BIC bounds differ from a factor of 4 (95% BIC of α [0.02, 0.07] and R_{MAX} [0.11, 0.39]). Their joint posterior distribution has a « banana » shape and highlight a strong negative relationship between them. It is observed when information provided by the SR data of the Scorff is insufficient to estimate SR curve parameters independently (Walters and Korman, 2001; Bret, 2012). For the Scorff, very low stock level is not observed and as a consequence likelihoods of low and high value of α are equivalent. To fit with the data, low values of α are offset with high values of R_{MAX} and conversely. The weakly informative priors set on both α and R_{MAX} prevent from extreme estimates of these variables.

SR relationship of the Scorff

In the **Figure 3.3**, the SR relationship of the Scorff is presented. It highlights the high uncertainty surrounding the SR curve caused by the observation errors related to the stock, the errors of the recruitment process and the errors of the estimation of SR curve parameters. These three sources of uncertainty result in an overall standard deviation of 0.58 (median on the log scale) surrounding the SR curve.

B. Transferring SR relationship from the Scorff to the other rivers

Multiplicative factors

As presented in the **table 3.1.**, the mean multiplicative effect is estimated to 1.46 (median). The density-dependence is stronger in the Scorff than in the other rivers as its value is lower than the median multiplicative effects of most of the others rivers (**Figure 3.4**). Only two rivers have lower estimates multiplicative factors: the Aulne-Douffine and the Couesnon. The former have the lowest multiplicative factor equal to 0.3 corresponding to a density-dependence five times higher than average. Except the Aulne-Douffine, the medians of multiplicative factors increase along an east-west gradient and lead to a decrease of density-dependence. This result can be interpreted by a difference of geomorphology of the rivers along this gradient.

Uncertainty of recruitment process

Besides multiplicative factors estimates, **Figure 3.4** presents also the estimates of standard deviation (log scale) of all the rivers of Brittany. The standard deviation estimates vary among rivers, which validate the choice of modelling a river specific variance parameter. Noted that the Queffleuth has the most uncertain recruitment process. This result was expected given the high variability of recruitment produced with similar stock levels (See Materials and Methods section II.B.).

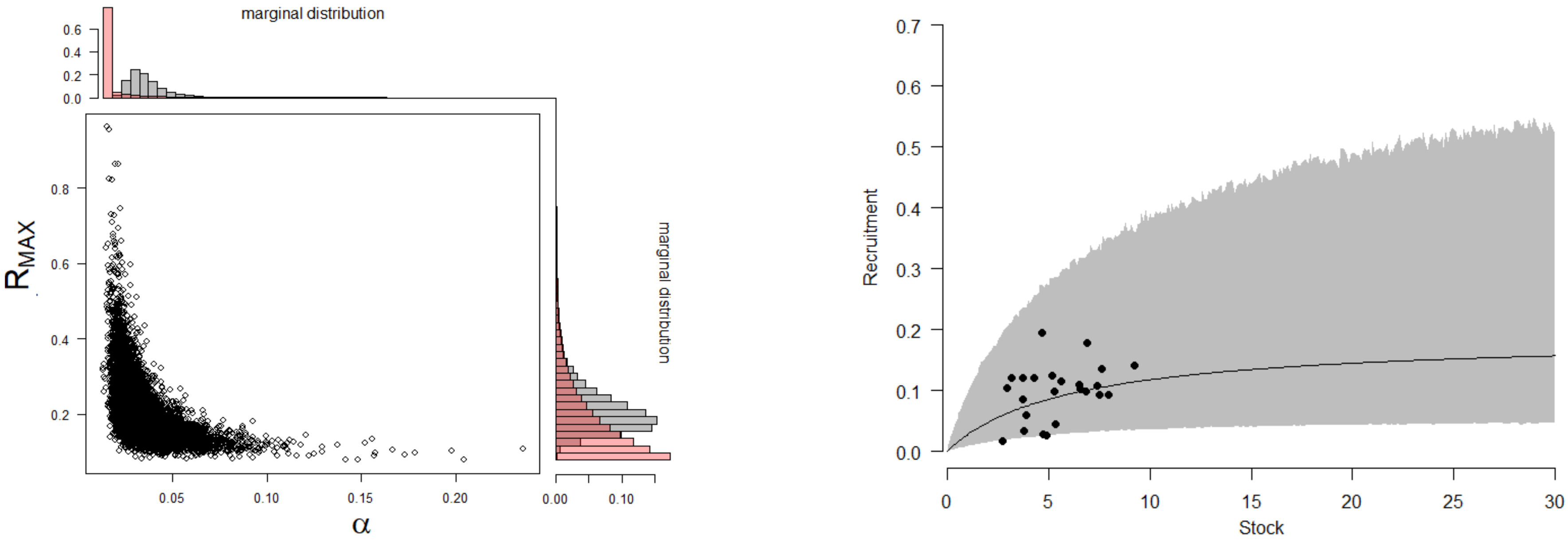

Figure 3.3. Joint posterior distribution of the SR curve parameters of the Scorff (left) and predictions of its SR relationship (right). In the former, prior (red) and posterior (grey) marginal distributions are presented in the marge of the figure. In the latter, shaded area represents the 95% BIC associated to each prediction of recruitment.

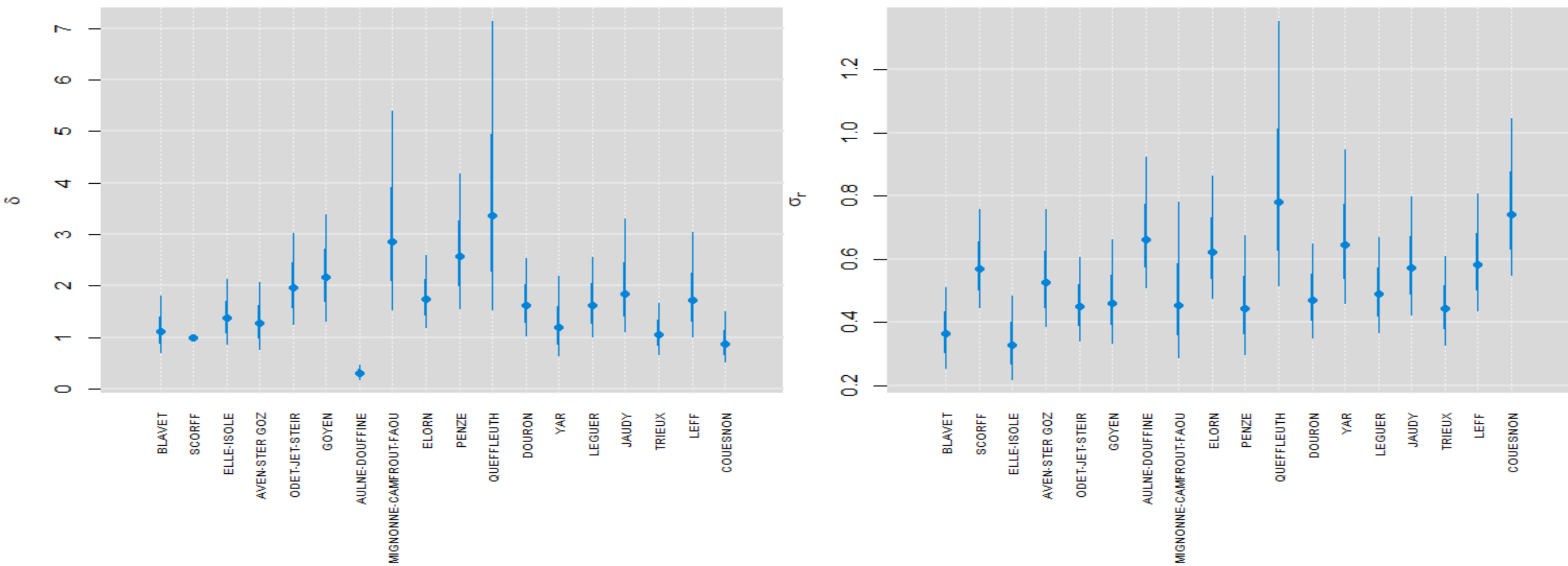

Figure 3.4 Multiplicative factors (left) and standard deviation (right) of every rivers.

IV. How the CLs match with the risk diagrams and the interval of the stock level

Scorff

To set the CLs of the Scorff, we take advantage of risk diagrams (**Figure 3.5.**). For each stock level, it predicts the risk that the recruitment produced will be inferior to the references. Predictions is undertaken each 0.1 stock level between 0 to 30 eggs.m^{-2} of RRE. Thanks to this diagram we could therefore set the propositions of CLs (see paragraph Materials and Methods I.C). The risk diagrams translate the high uncertainty of the SR relationship into the risk associated to recruitment production. Risk curves are drawn for each "low recruitment" references. For all of them, minimum risks obtained for 30 eggs.m^{-2} of RRE are higher than 0. Lower minimum risks associated to historical references are: 0.001, 0.03 and 0.11 for 25, 50 and 75% R_{OBS} respectively. Theoretical references have higher minimum risks equal to 0.02, 0.2 and 0.44 for 25, 50 and 75% R_{MAX} respectively. Thus, for too ambitious definition of "low recruitment" as 75% R_{MAX} the associated risk of 40% is not reached in the interval of predictions.

For theoretical and historical references, higher the percentage considered is, higher the CLs are even if risks decrease. The theoretical CLs, CL_1 and CL_2 respectively associated to 25%R_{MAX} and 50%R_{MAX} are reached under 30eggs.m^{-2} of RRE. CL_1 is set to 6.1 eggs.m^{-2} of RRE and is included in the interval of observed stock whereas CL_2 is set to 19.4 eggs.m^{-2} of RRE and is two times superior to the maximum observed stock level. Compared to R_{MAX} related CLs, CLs using R_{OBS} are lower and less variables. They are all lower than the maximum observed stock levels. Their values vary from 1.9 for CL_4 to 5 eggs.m^{-2} of RRE for CL_6, CL_5 being set to 3.8. Note that CL_4 is lower than the minimum observed recruitment.

The other rivers

The observations established for the Scorff are generalized to the other rivers. That is, CL_3 are higher than maxima of prediction intervals and must not be considered (**Appendix 3.8.** and **Appendix 3.9.**). CL_4 and CL_2 are no included in the interval of observed stock whereas CL_1, CL_5 and CL_6 lay within the interval for most of the rivers.

Nevertheless, for some rivers, these three limits slide out from the stock interval. In the Queffleuth, the limits are relatively higher than in the other rivers (**Figure 3.6.**) and fall above the maximum of the median stock observed. It is mainly due to the high variability of the SR relationship (**Figure 3.4.**) which increase the CL values as recruitment process being more uncertain and the low and narrow stock interval. For this river, CL_4 belongs to the interval of the median stock. The inverse phenomenon is observed for CL_1 and CL_5 in the Goyen and the Ellé-Isole *i.e.* CL_1 and CL_5 fall below their stock interval. For the Goyen, these two CLs are comparable to the other rivers but the relative high stocks in this river make these CLs fall below the interval. For the Ellé-isole, it is rather due to the low standard deviation of its SR relationship that decreases the uncertainty of the recruitment process and the CL values. Despite its wide stock interval, CL_1 and CL_5 are too low to belong to it (**Appendix 3.9.**).

Within theoretical and historical references, the range of variability of the CLs becomes wider when the percentage and the risk increased. Excepted from the Queffleuth, CL_1 is relatively constant with a value of about 5 eggs.m^{-2} of RRE for each river whereas CL_5 and CL_6 varies from 3 to 10 and from 4 to 13 eggs.m^{-2} of RRE respectively. CL_4 and CL_2 are less and more variable respectively.

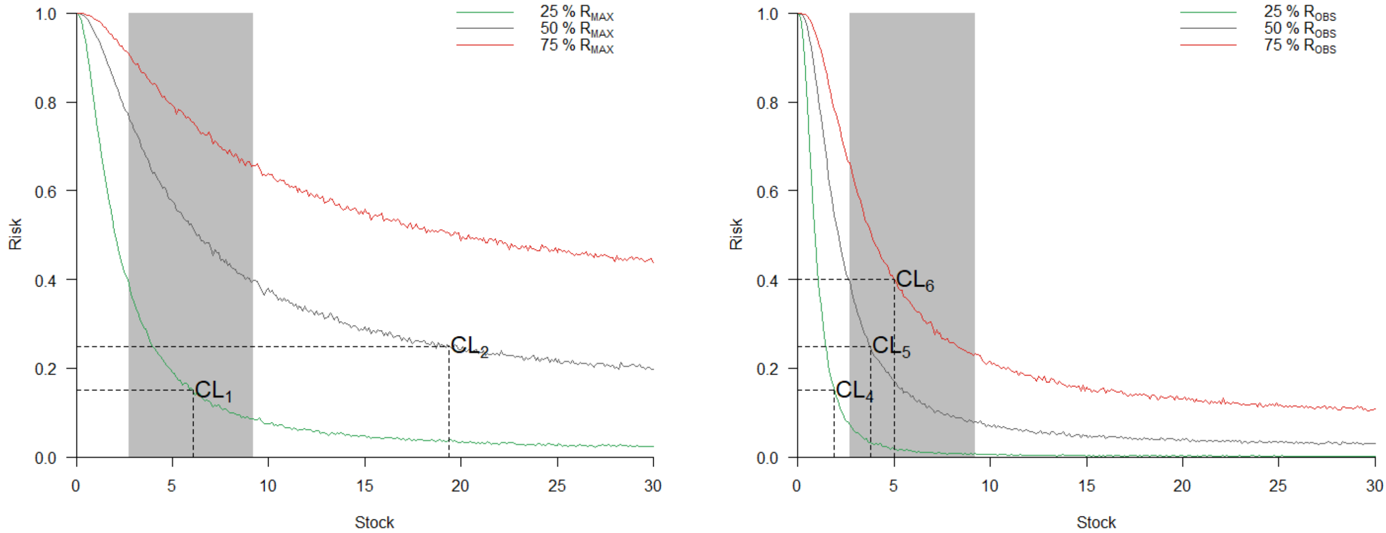

Figure 3.5. Risk diagrams of the two references of low recruitment considered (left: theoretical, right: historical). Each curve represents one percentage of the reference considered. 25% are represented in green, 50% in grey and 75% in red. CLs included in the prediction interval are represented.

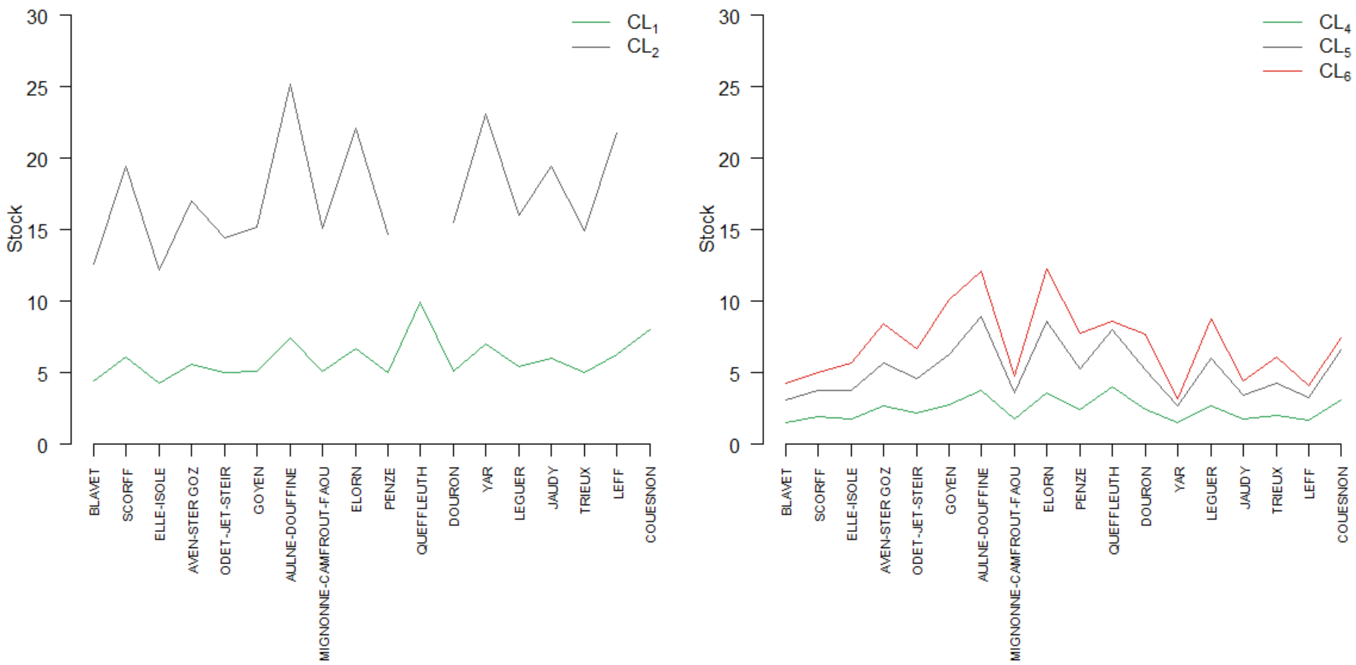

Figure 3.6. Inter-river variability of the CLs. The left graphic shows CLs related to theoretical references and the right graphic the CLs related to historical references.

Discussion

The BHM developed in this study provides estimates of the stock for each river and each year by taking advantage of the catches and the few adult returns data available. Thanks to these estimates and a previous modeling of the recruitment, we are able to predict river specific SR relationships. The propositions of CL made in the Materials & Methods have been set by deriving risk diagrams from the SR relationships. The risk diagrams emphasized the uncertainty of the current knowledge of the ddp dynamics which make CL_3 impossible to reach in the predict interval chosen. The CLs vary between the rivers and the range of variation is specific to each CL.

Nevertheless, some simplistic hypothesis assumed in the modeling may impact the estimates of CLs. So in the subsequent section, we will focus on the possible bias introduced in the CL definitions and offer possible improvement. Both sub-model will be analyzed separately. Afterward, the discussion will emphasize the need of a dialogue between managers and scientists to assess if the new approach considered match with their expectations. If not, we could, however, take advantage of the framework used in this study to set the new fixed escapement target (FET). Finally, the relevance of theoretical and historical reference used to define the CLs or the FET will be assess as well as the CL and the FET themselves.

I. Exploitation sub-model: better account for catch variability to minimize bias

As presented in the results, the estimates of the adult returns and corresponding stocks are highly uncertain. This is the consequence of the limited number of data available to model the stock from the catches. To reduce the possible bias and the uncertainty of the stock estimates, we might reconsider the modeling by introducing co-variables that better account for catches variability.

A. Fishing effort as a co-variable affecting the exploitation rates

One main co-variable that accounts for catches variability and connects it to the stock is the fishing effort. It affects the exploitation rates (Laurec and Le Guen, 1981). By assuming a full exchangeability of the exploitation rates between the rivers, we do not account for possible variability of the fishing effort between the rivers. This hypothesis appears as too permissive and could exacerbate the bias and uncertainty of the estimates of exploitation rates. Therefore, we suggest to introduce a hypothesis of exchangeability conditionally to the fishing effort. Practically, it is equivalent to add a relation between the mean exploitation rates and the fishing effort.

In the rivers of France, A. salmon fishers must report their catches but they have no obligation to inform about their fishing effort. Fishing effort data are therefore difficult to obtain as they require additional sampling. In France, only one study (Salanié et al., 2004) sets up such sampling and quantify an accurate fishing effort *i.e.* the number of visits per river. Nevertheless, the data used originate from a one- year survey and as it does not integrate temporal variability, we suggest to use other sources of information to describe the effort.

Instead of the number of visits per river, we could take advantage of the open angling periods as an effort data. This proxy of the fishing effort is defined at the beginning of each year and for each river. For a given river, the variation of the open angling period is mainly due to the reach of the TAC. Indeed, once the TAC is reached, the exploitation stops and the open angling period is shortened. This proxy could be an interesting variable to discriminate temporal and spatial distribution of the fishing effort if TAC are frequently reached. Note that the effect of this proxy of the fishing effort could be estimated as seven shorten fishing period have occurred in the rivers and years where adult returns data are available (CNICS).

Several modeling of the relation between the open angling period and the exploitation rates could be undertaken. As TAC set on the 1SW is hardly reached and the open angling periods remain poorly variable between the years. This proxy might not enlighten the effort applied on this sea age and may not be modeled. For the MSW, quantitative and qualitative effects could be draw given the data of open angling period used. Quantitative effect will be derived from continuous data such as the total number of fishing days or the number of fishing days lost by the reach of the TAC. We could also construct a qualitative binary effect indicating whether or not the TAC is reached. Each effect should be tested to assess their relevance.

Other proxy of the fishing effort could be related to the mean exploitation rates: the number of fishing licenses. They are necessary to fish A. salmon and each region of Brittany (that is the “Morbihan”, the “Finistère”, the “Côtes d’Armor” and the “Ille-et-Vilaine”) have its own. By using this proxy, we could account for variability of exploitation rates at a broader scale.

B. River flow as a co-variable of the exploitation rates

In the literature, some authors show evidences of the impact of the environment on the catches (Gee, 1980; Mills et al., 1986; L’abée-Lund and Aspås, 1999). One of the co-variable often related to the catches is the river flow. Since the 30’s, evidences of a positive relationship have been demonstrated between the catches and the river flows (Huntsman, 1939; Alabaster, 1970; Potts and Malloch, 1991). To account for the catches variability, as the fishing effort, river flow could be set to the mean exploitation rate. As for the co-variable of effort, many river flow effects could be considered. To better account for temporal variability of the exploitation rates, we may define the river flow effect at an annual scale. Finally, as river flows is related to the rainfall which act at a broad spatial scale, we might considered an effect of the river flows at a regional scale or at the Brittany scale. To estimate these effects, mean daily flow or maximum difference of daily flows within each year could be used as data. In doing so, only quantitative effect will be considered.

II. Feedback on the SR sub-model

A. Defining recruitment as data of YoY densities

1. Impact on the description of the density-dependence

By defining the recruitment as the density of YoY, the model used assumes ddp survival to occur only during the first year of the A. salmon development. Nevertheless, literature shown case of ddp survival in older development stages (Elliott, 2001). In this study, the full description of the ddp survival is therefore questionable.

No major issue comes from the consideration of a freshwater recruitment as ddp survival mainly occurs during this stage (Elliott, 2001). Nevertheless, an older freshwater development stage could have been used to measure the recruitment instead of the YoY: the smolt. It is the last stage before migrating to the sea and could be a good candidate as it offers a full description of the freshwater survival.

To assess if ddp survival occurs between the YoY and the smolt, we take advantage of the estimates of smolt abundance in the Scorff to draw the relation between the YoY-to-smolt survival and the density of YoY (**figure 4.1.**). As no clear survival trend is observed, we could assume no ddp survival between these two stages. Thus, we may assume the SR model used to provide a full description of the ddp survival.

2. Considering no observation error of the recruitment

In this study, we take advantage of the main sources of errors to describe the uncertainty of the SR relationship. Nevertheless, no observation error of the recruitment is considered in this study. To ensure that the recruitment data induced no bias in the description of the uncertainty, we could therefore add its modeling to the model actually used.

B. Feedback on the SR relationship parameters

1. Setting weakly informative priors on the SR curve parameters

In an ideal situation, uninformative priors should have been set on the SR curve parameters of the Scorff to let the model fit with the data. Nevertheless, in previous modeling of the SR relationship, we produce unreliable estimates of these parameters by using such priors. The marginal posterior distribution of the maximal survival rate had a median of 25% and 95% BIC was included between 0.002 and 0.9. This distribution provides an excessively wide range of possible value to intend defining the new CL with.

The variability of the estimates are due to the lack of information for low stock levels which gives similar likelihood for low and high value of maximal survival rate. Given the strong variability of recruitment relatively higher to the stock, to fit with the data, low values of α are offset by high values of R_{MAX} and respectively. As a consequence, variability of maximal survival rate spread to R_{MAX} and estimates of both SR curve parameters become unreliable.

Therefore, to provide biological relevance to the estimates of these parameters, we decided to integrate information into their prior distributions. In other words, we want to give low credits to the extreme value of each SR curve parameter. Unable to formulate a genuine prior distributions carefully, we set weakly informative priors to these variables (O'Hagan, 2006). It is described by Gelman (2006) as a prior distribution "that convey some generally useful information but clearly less than we actually have for the particular problem under study".. Thus, to remain close from purposes of objectivity, weakly informative priors must provide enough information to delete "ridiculous" estimates and wide enough to let the possibility to be updated by the data.

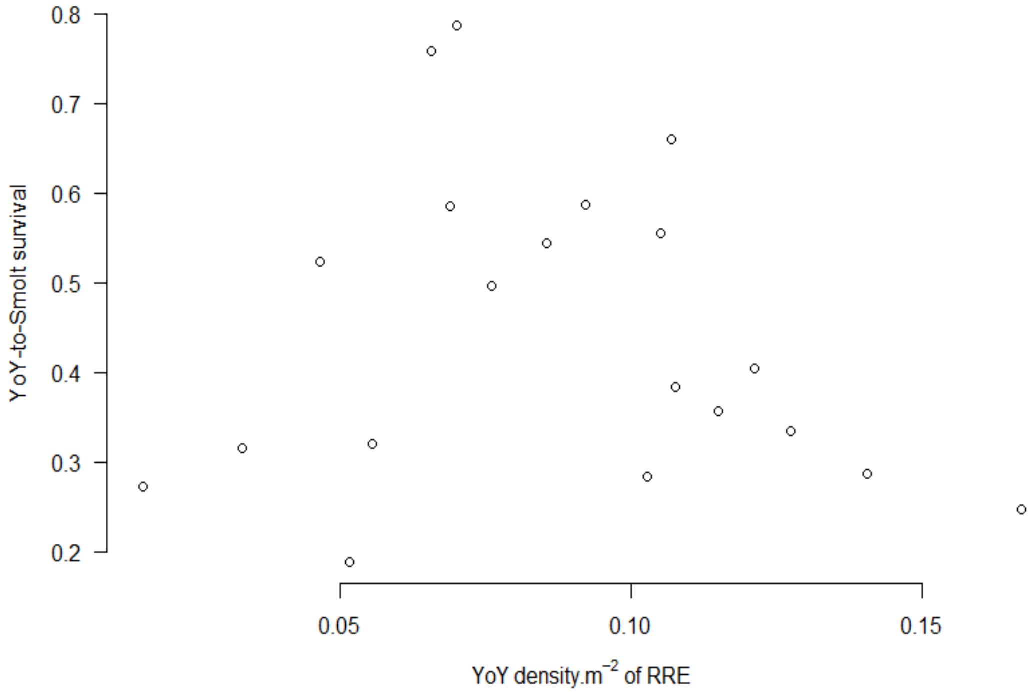

Figure 4.1. Relationship between the density of YoY and the YoY-to-Smolt Survival.

To fit with this definition, we ensure dispersion of the prior distributions of SR curve parameters by setting wide distributions i.e. a reparametrized beta distribution with a low sample size of 2 (95% BCI $\in [10^{-20}, \ 0.41]$) for the maximal survival rate and an exponential distribution with a standard deviation of 0.19 for R_{MAX} (95% BCI $\in$ [0.005, 0.7]). The main issue of these weakly informative priors is the way we introduce information. Instead of using the SR data only to fit the model, we used them to provide prior information for both parameters. We assume the maximum survival rate observed (0.04%) to be a good proxy of the mean of α and the mean of R_{MAX} to the maximum recruitment observed (0.19 YoY.m^{-2} of RRE).

Nevertheless, the impact of the double use of the data remains limited. Indeed, in previous modeling, we undertake a sensitive analysis on the two prior means to assess their impact on the marginal posterior distributions. Mean were multiply by 0.5, 2 and 4 and we assess the impact on posterior marginal distribution by graphical analysis. The modes were unchanged, only the tail of the distributions were shortened. Therefore, the double use of the data seems to have low impact on the estimates apart from the expected impact: discredit the extreme values. Nevertheless, a new sensitive analysis should be undertaken on the model used in this study to confirm this result.

2. The multiplicative factor

To transfer the information collected from the ddp survival of the Scorff to the other rivers, we model a multiplicative factor applied on both α and R_{MAX}. By using such modeling, we assume that these parameters co-vary. In the principle, we can imagine that rivers providing better growth conditions for the A. salmon will provide better survival at any stock level including low stock level (α) and high stock level (R_{MAX}).

Nevertheless, by allocating the same multiplicative factor for these two parameters, we assume a strict relationship between them. This hypothesis is may be too restrictive but it is difficult to assess its relevance as SR data are noisy and stock interval limited. Therefore, the estimates of multiplicative factor specific to each parameter might be difficult.

Finally, if we demonstrate that the weakly informative priors set on these parameters have a significant impact on the inferences, the modeling used will spread this impact to all the other rivers.

3. Depensatory effect

In the context of declined of many stock, in the 90's, some fishery scientists highlighted the need to better understand population dynamics when stock levels are low (Myers et al, 1995; Liermann and Hilborn, 1997). Considering the classic compensation model used in this study, at low stock levels, negative ddp effects are deleted and survival rates increase. Probability of recovery is therefore expected to be high for low stock levels.

An alternative dynamic i.e. depensation, could be considered and leads to low survival rate for low stock levels. Considering this dynamic, the process of recovery will occur within a longer period of time compare to the classic compensation model. As a consequence, the same definition of CLs will be achieve for lower stock levels in the compensation model than the depensation model. To be more cautious, we may reconsider the actual compensation model by adding a depensatory parameter.

Nevertheless, as low stock level is observed neither in the Scorff nor in the Elorn, depensation parameters should be difficult to estimate. Besides estimation issues, only a few evidences shown depensation dynamics of salmonid populations. Liermann and Hilborn (1997) prediction of salmonid depensation parameter have a mean of 1 *i.e.* no depensation occurs in average. By comparing 4 taxa (clupeiforms, gadiforms, pleuronectiforms and salmonids), they demonstrated that salmonid species present the lower probability to undergo depensation. Evidences of depensation have been demonstrated for only two salmonid species: the Coho salmon (*Oncorhynchus kisutch*) and the Pink salmon (*Oncorhynchus gorbuscha*(Myers et al., 1995; Barrowman et al., 2003). Thus, we may not under-estimates CL by using the actual compensation model.

4. Modeling recruitment variance

By using a log-normal distribution to model the error of the recruitment process, we assume an increase of the recruitment error with the stock. It is graphically translated by a wider uncertainty envelop as the stock increase. The impact of such modeling on the CLs is significant. Indeed, increasing of the recruitment production expected by higher stock levels is offset by the increasing of the risk (higher error). By considering no positive relationship between the error and the stock, CLs would be reached for lower stock levels.

It is therefore important to assess if the actual modeling of the error of the recruitment process is relevant. Unlike the widespread belief of the log-normal error of the recruitment process, several authors have demonstrated a negative relationship between the variability of the recruitment and the abundance of the stock (Myers, 2001; Minto et al., 2008). By analyzing the variation of the residuals according to the stock abundances, we find the same results (**Appendix 3.2.**). To decrease the variability of high stock levels, we suggest to model the effect of the stock abundances on the error of the recruitment process by using a regression model.

C. Addressing the issue of residual autocorrelations

The results (section I.C) emphasize a positive temporal autocorrelation of recruitment's residuals for two rivers: the Scorff and the Elorn. In other words, for these rivers, the egg-to-YoY survival has increased over the time. Two categories of factors could have influenced the survival increase: ddp or didp factors. Nevertheless, problem arises when choosing the relevant variable that could described the residual trends. In principle, one could think that temporal changes of recruitment could be explain by an accurate description of each process involve in the SR recruitment and identify each factor impacted them. But in practice, there is too much “noise”, *i.e.* too much ddp and didp factors having both positive and negative effect on recruitment, to provide a credible description of the recruitment variability (Walters and Korman, 2001).

By analyzing the temporal trends of the residuals, a simple solution to this complex issue could be found. As shown in the **appendix 3.1.**, instead of a linear positive autocorrelation of the residuals, we could analyzed the residuals as originated from two different stationary situations. The first corresponding to the older part of the time series where stocks produced less recruits than overall average and the recent part where stocks produced higher recruits. A simple binary effect would be model on the mean recruitment and prediction of CLs would be made by using the recent SR relationship.

Finally, the issue of the positive trend of residuals according to the stocks may be address by assuming a depensatory effect. That is, assuming a translation of the SR curve allowing to fit with the low stock level by shifting the maximal slope to higher stock (depensation effect). By doing so, the weights of this low stock level on the fit will be relax and the model will better fit with the higher stock level by estimating a new R_{MAX}.

D. The particular case of the Aulne-Douffine River

The analysis of the multiplicative factor estimates highlights one outlier: The Aulne-Douffine. The median of its estimates is 3 to 11 times lower than the other rivers. As it seems to present a very different population dynamic from the others populations, the hypothesis of exchangeability of the Aulne-Douffine with the other rivers becomes questionable. We might model it separately from the other rivers.

The specific dynamic of the Aulne-Douffine could be explained by two main factors. First, in the Aulne-Douffine there is a high number of locks which constitute a lot of barrier for the upstream migration which limit the access to reproductive area upstream. Therefore, the recruitment estimates for the stations upstream are lower than the recruitment estimates downstream and will tend to reduce the overall recruitment estimated for the river.

Besides decrease of the recruitment along a downstream-upstream gradient, the estimates of the stock could have been increased artificially. Indeed, in the Aulne-Douffine, a rebuilding program of the stock was decided by the local authority. It results in the introduction of a consequent quantity of juveniles that might increase the stock level.

III. Establishing a dialogue with the managers to assess the relevance of the new CLs

A. Being clear with the difference between CL and MT to choose between a fixed escapement strategy and the full PA

Definitions of CL and MT

The initial PA recommended by the United Nations (1995) defines two categories of reference points: a limit and a target. The limit is defined as a boundary which must not be crossed. It distinguishes the undesirable from the other stock levels (United Nations, 1995).On the other hand, the target is a stock level to aim at. The uncertainty of the biological and environmental process affecting the A. salmon dynamic makes it impossible to hit the target every year. But, the objective of the managers is to maintain observed stock levels close to this target (Potter, 2001). Due to their relative roles in conservation and management, they are named as “conservation limits” and “management target” (United Nations, 1995).

An actual ambiguous definition of CL resulting in a fixed escapement strategy

The ICES recommendation to use S_{opt} as the CL creates an ambiguity between the principles of CL and MT (ICES, 1995). S_{opt} is defined as the stock producing the maximum gain, thus offering the best opportunity to maximize the harvest while maintaining the population viability. Mixing both conservation and exploitation aims, S_{opt} has a clear management relevance and ICES recommends that stock should be managed in order to be maintain at or close to S_{opt}. Such statement accords with the definition of a MT. On the other hand, ICES considered S_{opt} as a CL because stock levels below S_{opt} are considered undesirable as both the expected recruitment and the gain decreases. Following ICES, NASCO adopted S_{opt} as a CL and define it as “the adequate level of stock” (NASCO, 2009).

This confusion between limit and a target persists until today. In terms of management strategy, the implicit aim is to achieve a Fixed Escapement Target (FET) equal to S_{opt}. Given the position of the stock relatively to the FET, two conservation status are defined: “below conservation” and “above conservation”. In France, TACs were developed to ensure the stock would stay in the “above conservation” zone. Hence, the actual management approach refers to a fixed escapement strategy but with the restriction that it is only acceptable to miss above the target.

Choosing between the fixed escapement strategy and the PA

We need a dialogue between scientists, managers and stakeholders to clarify the management approach that should be implemented. At least a choice should be made between:

- The fixed escapement strategy as used until now,
- The PA as defined by the United Nations (1995).

The main interest of the actual strategy lies on its simplicity. It is already well accpeted by managers and stakeholders. The reference used (i.e. FET) reflects a clear and shared management objective: maximizing potential catch while not compromising population viability. It is easier to define than conservation which appears often more subjective or fuzzy.

The second option might be more difficult to appropriate by managers and stakeholders. Applying the PA requires to distinguish the CL from the MT. Scientists can help to clarify the issue. They should insist on the need to define CL under biological basis rather than management purpose (Chaput, 1997). Once a CL and a MT are be identified, three conservation status are defined *i.e.* critical, cautious and healthy. The additional cautious status allows to accounting for the uncertainty arising from various sources, i.e. imperfect scientific knowledge, population dynamics stochasticity. A more flexible management framework will therefore be developed as measures should be adapted to the three conservation status. Adopting such strategy would also align the management of A. salmon with most of the other exploited fish species in Europe.

B. Relevance of the new CLs given the strategy chosen

The risk framework developed for the new CLs can also be used to define FET

The framework developed to define CL in this study was chosen to fit with the PA. In accordance with the CL definition used for most of the European stocks, *i.e.* B_{lim} (ICES, 2017), it is the stock level below which reproductive capacity is reduced. Therefore, we define CL as the stock level corresponding to a low risk of low recruitment. In the context of a fixed escapement strategy, this framework could be adapted to provide the definition of a FET *i.e.* the stock level producing adequate recruitment with moderate risk.

Relevance of theoretical vs historical reference recruitment levels

Once a management strategy is chosen, the discussion with managers and stakeholders should also address the definition of what is considered to be a low or an adequate recruitment. We identify two type of references that could be used: theoretical and historical references. For both type, we consider one candidate (R_{MAX} and R_{OBS}) as examples. But other candidates could be proposed by the managers and stakeholders.

The theoretical reference is based on a concept of population dynamics, namely the carrying capacity. For each river, such references account for its specific ddp dynamic. As a consequence, they provide homogenous definitions of low and adequate recruitment between the rivers. But, this concept is requires some scientific background and may appear too abstract to be understood at once by managers or stakeholders. To improve their appropriation of these reference, scientists must undertake a particular pedagogical effort to render this carrying capacity concept more explicit and accessible.

Conversely, as they refer to observed data, historical references are more explicit and concrete for managers and stakeholders. Their appropriation becomes easier. Nevertheless, the definitions of low and adequate recruitment depend on the prior assessment of the conservation status of the population considered. Indeed, if the historical data refer to a healthy status of conservation (or a status above conservation), CL (or FET) must be lower than (or equal to) R_{OBS}. For more precarious conservation status, CL (or FET) must stand close to (or above) R_{OBS}. The origin of the prior assessment of the conservation status is key. In most instances, it would come from expert judgement, based on not-fully explicit data and some non-formalized underlying model. Therefore, there is a great risk that the CL and FET definitions using historical references might be grounded on heterogeneous foundations, especially if the experts change according to the population at stake. In addition, the lack of explication hampers and obscures the necessary debate around the definition of the conservation status. Thus, despite the appeal of their apparently more concrete meaning, it could be more appropriated to use theoretical rather than historical references, owing to their advantages in terms of clarity and consistency.

Once the type of reference to use id decided, the choice of the percentage of R_{MAX} or R_{OBS} and the level of risk (i.e. probability of low recruitment) associated should be left to the managers and stakeholders too. They will depend on the management strategy but the percentage and risk level used to define a CL should be lower than to define a FET.

Comparing the relevance of the CL or FET thanks to the stock interval.

To assess the relevance of each CL or FET, we suggest to take advantage of the stock interval. As we presented in the section I of the discussion, for most of the rivers the actual description of the stock might be biased by the modeling of the observation process. In addition, the use of the median stock interval might minimize the dispersion of the real stock interval. But the prospects of improvement presented should increase the confidence associated to the stock interval.

With a better representativeness, we should be able to assess the relevance of the CL or FET using this interval. First, it requires to define, in accordance with the managers, the conservation status of each river. The assessment of the relevance of CL will depend on these status considered for each management strategy. If the PA is chosen and the conservation status is defined as:

- Critical, CL should stand close to the upper bound of the stock interval
- Cautious, CL should belong to the stock interval and stand close to its lower bound
- Healthy, CL should stand below the lower bound of the stock interval

Finally, if a fixed escapement is chosen and the conservation status is defined as:

- Below conservation, FET should stand at or above the upper bound of the stock interval
- Above conservation: FET should stand below or at the lower bound of the stock interval

The assessment of the relevance of the CL or the FET will provide a simple framework for manager to see if their expectations fit with the actual knowledge on the population dynamics.

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Annexes

River	Productive area (m^2 of RRE)				Recruitment time-series	Station		
					Initial year	Number*	Sampling effort (number per	
	1993-2004	2005-2011	2012-2015	2016-2018			1993-2004	2005-2011
BLAVET	350763	386247	342946	393985	1997	27	0,77	0,70
SCORFF	200811	200811	200811	229027	1993	53	2,64	2,64
ELLE-ISOLE	341980	658784	658784	669028	2001	41	1,20	0,62
AVEN-STER GOZ	74860	142686	142686	142686	2003	10	1,34	0,70
ODET-JET-STEIR	248976	246236	246236	249049	1994	18	0,72	0,73
GOYEN	48890	53603	53603	53603	2002	4	0,82	0,75
AULNE-DOUFFINE		252659	252659	252659	1997	30		1,19
MIGNONNE-CAMFROUT-FAOU			67855	67855	2012	7		
ELORN	113858	137542	137542	164699	1998	19	1,67	1,38
PENZE		97931	114289	106735	2007	11		1,12
QUEFFLEUTH		40357	68512	68512	2010	7		1,73
DOURON	45180	95451	95451	95451	1998	8	1,77	0,84
YAR	28114	28114	37104	37104	2001	6	2,13	2,13
LEGUER	192438	171893	197283	197283	1997	24	1,25	1,40
JAUDY	103304	47561	47561	47561	1999	10	0,97	2,10
TRIEUX	155904	215992	213733	213733	1997	21	1,35	0,97
LEFF	50500	72305	72305	72305	1997	9	1,78	1,24
COUESNON	97452	101012	110794	110794	1998	24	2,46	2,38
Average	146645	173481	170009	176226		18	1,49	1,33
Average without the SCORFF	142478	171773	168197	173120		16	1,40	1,25

*Total number of stations sampled during the time serie available

Appendix 2.1. Characteristics of each river i.e. temporal trends of productive area, initial year of recruitment time-series (all rivers have been sampled until 2016), number of stations and sampling efforts over the years.

Appendix 2.2. Modeling the observation process of the recruitment

As described paragraph I.B, recruitment data are collected for 18 rivers of Brittany with the same sampling protocol. But estimations are only available for the Scorff thanks to the ORE DiaPFC model (Servanty and Prévost, 2016). Based on this model, we will consider two modeling parts:

- An intercalibration part to model relationship between density and AI
- The modeling of density which derives density from AI sampling and intercalibration relationship.

It will aim to model YoY density for every rivers and provide recruitment estimates.

1. Intercalibaration modeling to connect AI with estimate population's densities derived from successive removal experiences

The intercalibration model used in our study is the same developed by Servanty and Prévost (2016). We will described the main modeling processes but further information is available in their article.

Data

As it is defined, AI is an abundance index or Catches Per Unit Effort (CPUE) where effort's unit is defined as five minutes of electro fishing. It reflects the population density within a multiplicative factor. Hence, to estimate density from AI, we must evaluate the proportional relation between them. To do so, 52 stations have been sampled over 10 rivers of Brittany and Normandy between 1992 and 1997. For each station, besides AI, two successive removals have been done to estimate abundances. Besides, productive areas have been collected to derive density from them. Finally, station's wide have been collected as it affects the proportional relation between AI and estimate density (Prévost and Nihouarn, 1999).

Model

Density of every stations *i* (D_i) are hierarchically modeled thanks to a Gamma distribution with a unique mean (μ_D) and an inverse scale parameter (r_D) (1) . Uninformative priors have been set for these parameters (2).

$$D_i \sim \text{Gamma}(s_D, r_D) \quad (1)$$

$$\mu_D \sim \text{Gamma}(1,0.01),\ r_D \sim \text{Gamma}(0.01,0.01) \text{ and } s_D = \mu_D * r_D \quad (2)$$

Total abundances for each station *i* ($N_{tot\ i}$) before successive removals is modeled according to a poisson law's with mean and variance parameter ($\lambda_{D\ i}$) computes by multiplying density and productive area of each station (3).

$$N_{tot\ i} \sim \text{Poisson}(\lambda_{D_i}) \text{ with } \lambda_{D_i} = D_i * SRR_i \quad (3)$$

Finally, successive catches $C_{1\ i}$ and $C_{2\ i}$ are modeled thanks to binomial distributions with respectively $N_{tot\ i}$ and $N_{1\ i}$ the number of YoY before each catch and $P_{1\ i}$ and $P_{2\ i}$ the associated catch probabilities (4 and 5).

$$C_{1_i} \sim \text{Binomial}(N_{tot_i}, P_{1_i}) \quad (4)$$

$$C_{2_i} \sim \text{Binomial}(N_{1_i}, P_{2_i}) \quad (5)$$

To model the effect of wide (W) on the proportional factor (K_{IA}) between AI and density, we use a log-linear relation with an intercept a and a slope b (6 and 7).

$$\log(K_{IA_i}) = a + b * \log(W_i) \quad (6)$$

$$\text{with } a,b \sim \text{Uniform}(-10,10) \quad (7)$$

The proportional relation is set on the mean number of YoY potentially catch by AI sampling (8).

$$\mu_{\lambda_{IA_i}} = K_{IA_i} * D_i \quad (8)$$

Finally, the likelihood is modeled by a Gamma-Poisson distribution *i.e.* the number of fish caught by AI in each station *i* is distributed according to poisson's law with parameter $\lambda_{IA\,i}$. itself distributed according to gamma's law with mean $\mu_{\lambda_{IA_i}}$ and scale parameter r_{IA} (9 and 10).

$$AI_i \sim \text{Poisson}(\lambda_{IA_i}) \quad (9)$$

$$\text{with } \lambda_{IA_i} \sim \text{Gamma}(s_{IA_i}, r_{IA}),\ r_{IA} \sim \text{Gamma}(k,r) \text{ and } s_{IA_i} = \mu_{\lambda_{IA_i}} * r_{IA} \quad (10)$$

2. Modeling density thanks to AI and the proportional factor

Data

This part of the model used data from the 18 exploited rivers where AI are sampled. The sampling year vary among river from 5 years (2012-2016) for the Mignonne-Camfrout-Faou river to 24 years (1993-2016) for the Scorff. For each river, several stations are sampled and for each stations, besides AI, wide and related productive area are collected.

Model

The model to estimate density from AI for each station *j* sampled the year *t* is almost the same described previously for the intercalibration model. Two main modifications were made. Firstly, to estimate $K_{IA\,t\,j}$, we use the OpenBUGS's cut function on parameter a and b to avoid likelihood information from this part of the model to influenced previous estimations of a and b. Only likelihood information from the intercalibration part of the model will influence estimates of a and b. Secondly, a hierarchical modeling of the density have been done. The density of each station *j* sampled the year *t* is distributed according to a log-normal distribution with a mean for each river *r* and year *t* ($\log(\mu_{D\,r,t})$) and a unique standard deviation σ_D:

$$D_{j,t} \sim \text{Log-Normal}(\log(\mu_{D_{r,t}}), \sigma_D)$$

Additive effects of river *r* and year *t* have been added to the log mean density with a normal error per river and year ($\varepsilon_{r,t}$) of standard deviation σ_D' to allow interactions between these effects:

$$\log(\mu_{D_{r,t}}) = year_t + river_r + \varepsilon_{r,t}$$

$$\varepsilon_{r,t} \sim \text{Normal}(0, \sigma_D')$$

Year and river effects have been hierarchically modeled thanks to normal distributions. River effects are considered as random effects *i.e.* with mean equal to zero and standard deviation σ_R. Year effects are drawn in a normal law with a mean μ_Y representing the log mean density over year and river and standard deviation σ_Y.

$$river_r \sim \text{Normal}(0, \sigma_R)$$

$$year_t \sim \text{Normal}(\mu_Y, \sigma_Y') \text{ where } \mu_Y \sim \text{Uniform}(-10,10)$$

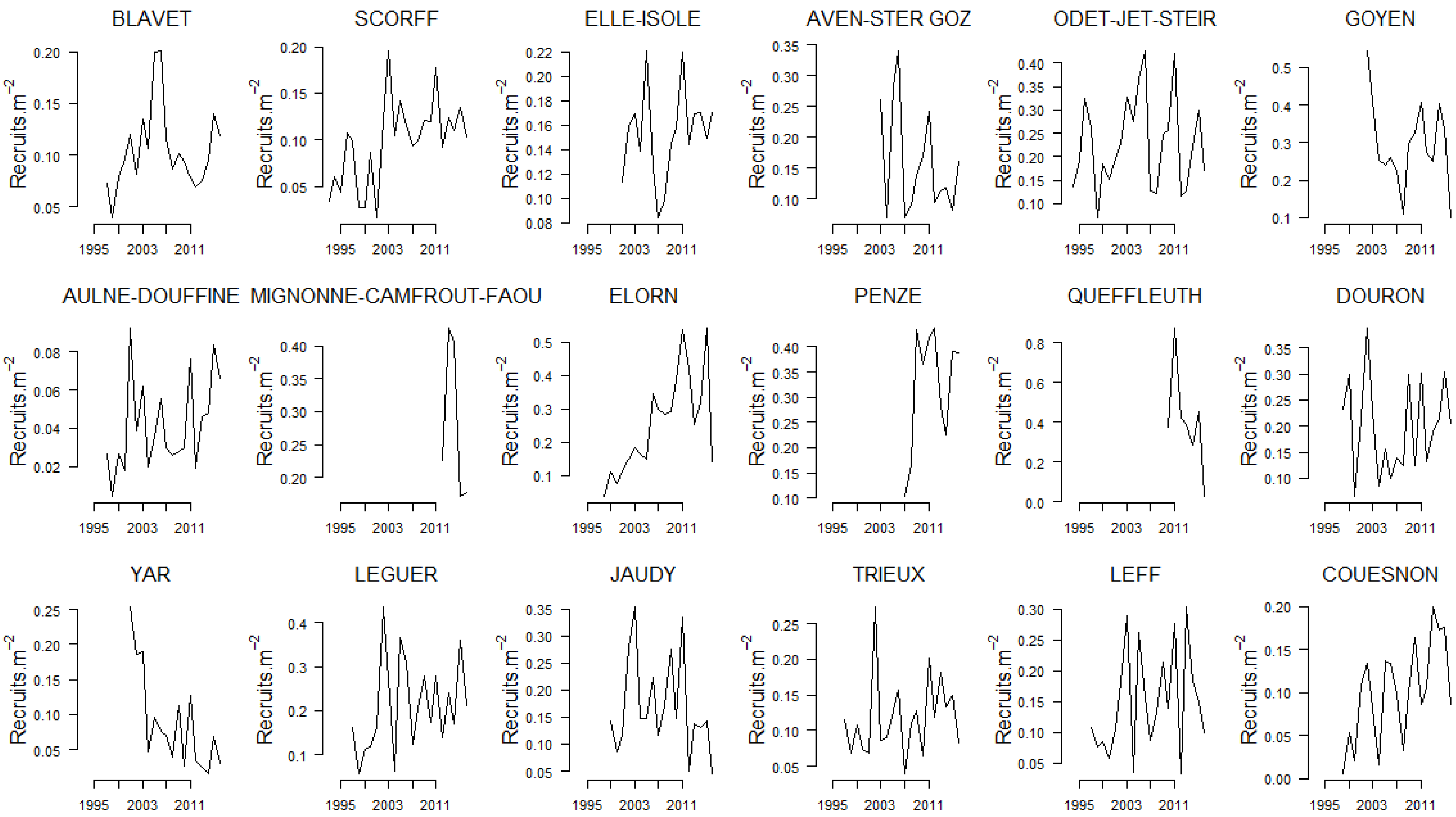
Every standard deviation have been modeled the same way with a non-restrictive uniform distribution between 0 and 20.

Finally, for each year t and river r, recruitment (R) is modeled as the average of the density observed for every j stations of the river r sampled the year t. This average is weighted by the productive area related of each station *j* (Germis, 2013):

$$R_{r,t} = \frac{\sum_{j \in r} D_{j,t} * SRR_{j,t}}{\sum_{j \in r} SRR_{j,t}}$$

Bayesian inferences

Model was coded in R and run with OpenBUGS (version 3.2.3) using “R2OpenBUGS” package. Bayesian inference was undertake thanks to the Gibbs sampling algorithm implemented in OpenBUGS. Three chains of initial values was run with a burnin phase of 10 000 iterations before monitoring variables. 100 000 iterations with a thinning of 20 was sampled for the monitored variables to derived posterior distribution (n=3*5000). The convergence of the chains have been verified using the Gelman-Rubin index (Rubin and Gelman, 1992) and Geweke stationary test (Geweke, 1992).



Appendix 2.3. Median recruitment time-series of every rivers of Brittany

Sea age	Females sex-ratio	Fecundity (egg per individuals)
1SW	45 %	3485
MSW	80 %	5569

Appendix 2.4. Sea age-specific females sex-ratio and fecundity per female (ONEMA, 2016)

```
model
{

######################################################################
#####################################################################
# 1/ HIERARCHICAL MODELING OF PRECISION

                                             #
######################################################################
#####################################################################
## Ntau : Total number of variability parameters
## tau[1] : tau_lgr, precision of river effect on log density
## tau[2] : tau_lgy, precision of year effect on log density

## tau[3] : tau_lgd, precision of density (log scale)

## tau[4] : tau_lgtrFSW, precision of river effect on FSW (logit scale)

## tau[5] : tau_lgtrFMSW, precision of river effect on FMSW (logit scale)

## tau[6] : tau_lgtFSW, precision of  FSW (logit scale)

## tau[7] : tau_lgtFMSW, precision of FMSW (logit scale)

## tau[8] : tau_lgdelta, precision of multiplication factor on SR (log
scale)
## tau[9:26] : tau_lgPARR[1:Nriver], precision of PARR production per
river (log scale)
######################################################################
#####################################################################

      mutau ~ dgamma(0.1,0.1)
      rate ~ dgamma(0.1,0.1)

      shape <- mutau*rate


      # Hierarchical modeling of every precision

      for (x in 1:Ntau)
      {
      tau[x] ~ dgamma(shape,rate)
      sigma[x] <- pow(tau[x],-0.5)
      }
######################################################################
#####################################################################
# 2/ ESTIMATION OF EGG DEPOSITION PER RIVER AND YEAR

######################################################################
#####################################################################
## t: year from 1 to Nyear=24 (1992:2015)
## r: river from 1 to Nriver=18
######################################################################
#####################################################################

######################################################################
#####################################################################
```

```
## DATA
## ---------------------------------------------------------------------------------------------------------------------------------#

## SRR[r,t]: Surface in riffle/rapid equivalent (unit:100m²) per river and per year.
## SRRSW[r,t] : Surface in riffle/rapid equivalent (unit:100m²) disponible during juvenile stage (SRR[r,t-2])
## SRRMSW[r,t] : Surface in riffle/rapid equivalent (unit:100m²) disponible during juvenile stage (SRR[r,t-3])
## SW[r,t]: Estimation of 1SW spawners from ORE DIApfc per river and year (only available for Scorff,1994:2015)
## SW.c[r,t] : Left-censored data of 1SW spawners per river and year. Disponible only for ELORN(2007-2015) and AULNE-DOUFFINE (1999-2015)
## is.SW.c[r,t] : Index matrix taken 0 if SW < || = SW.c and 1 if SW > || = SW.c
## PROPFEMSW : Female sex-ratio in 1SW cohort

## NBEGGSW : mean egg laid per 1SW Female

## MSW[r,t]: Estimation of MSW spawners from ORE DIApfc per river and year (only available for Scorff,1994:2015)

## MSW.c[r,t] : Left-censored data of MSW spawners per river and year. Disponible only for ELORN(2007-2015) and AULNE-DOUFFINE (1999-2015)#
## is.MSW.c[r,t] : Index matrix taken 0 if MSW < || = MSW.c and 1 if MSW > || = MSW.c

## PROPFEMMSW : Female sex-ratio in MSW cohort

## NBEGGMSW : mean egg laid per MSW Female
## Nriver[t] : Number of rivers sampled per year

## IND[Nriver[t],t] : Index matrix indicating the number of each river sampled per year
###############################################################################################################################################


##############################
#          Priors            #
##############################

#### Spawner density

## Mean of log density distribution

# River effect on mean log density

for (r in 1:Nriver[Nyear-1])
      {
      lg_river[r] ~ dnorm(0,tau[1])
      }

# Year effect on mean log density
mu_lgy ~ dunif(-10,10)           # Mean(lg_muy[r,t]) (log scale)

for (t in 1:(Nyear+1))
```

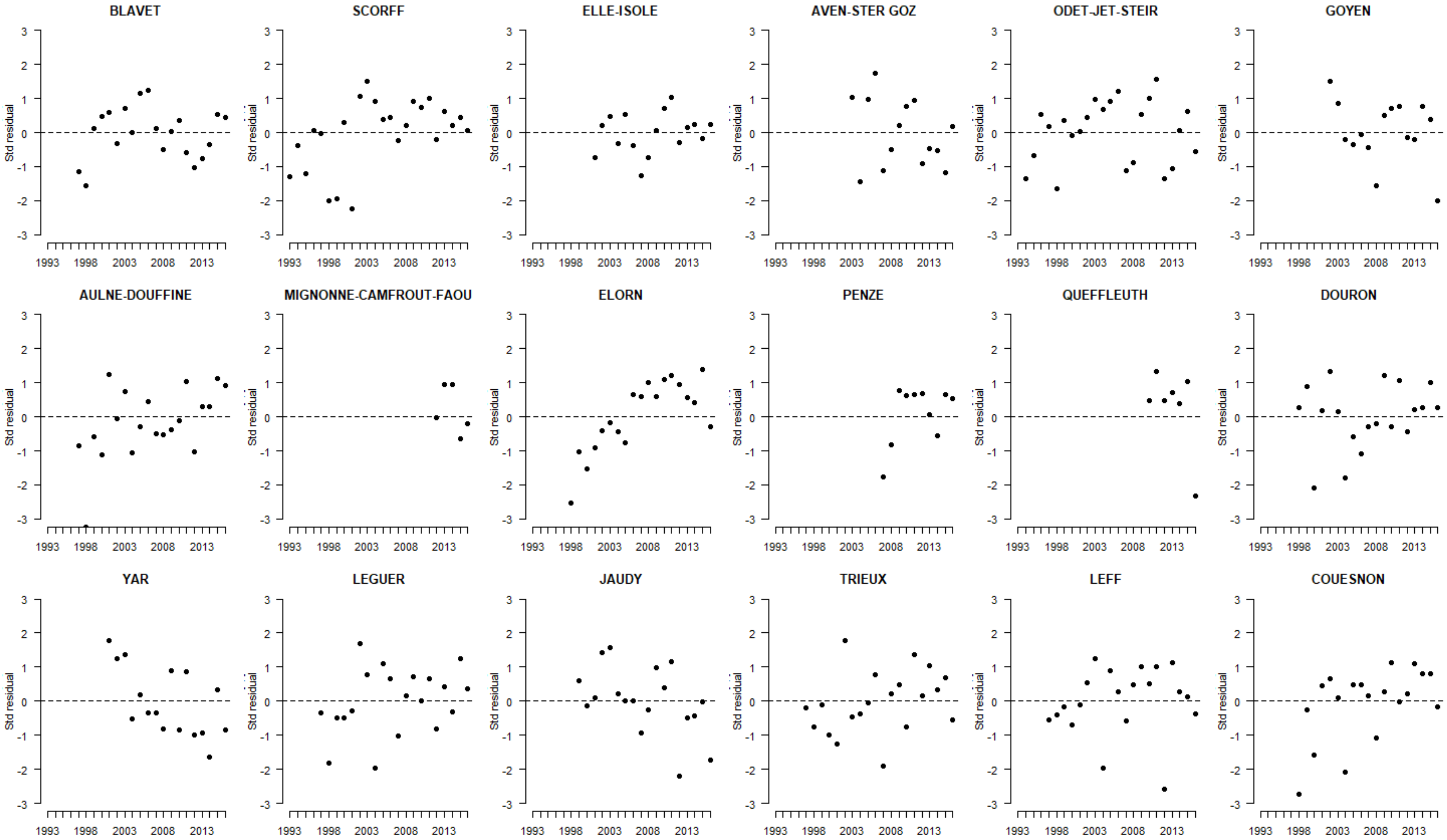
```
      {
      lg_year[t] ~ dnorm(mu_lgy,tau[2])
      }
## Density by sea age (SW and MSW)

# Reparametrization of propSW distribution

mupropSW ~ dbeta(1,1) #  Mean  proportion  of  1SW  in  the  population
lg_npropSW  ~ dunif(-10,10)
npropSW  <- exp(lg_npropSW )#  Sampling  size  of  Beta  distribution  on
propSW

# Switch to usual parametrization of beta distribution

alphaSW <- mupropSW*npropSW
betaSW <- npropSW - alphaSW
#### Exploitation rates

### 1SW exploitation rates


## Rivers effect on FSW (logit scale)

mu_lgtrFSW ~ dnorm(0,0.01) # Mean of river effect (logit scale)

# River effect
      for (r in 1:Nriver[Nyear])
      {
      lgt_riverFSW[r] ~ dnorm(mu_lgtrFSW,tau[4])
      mu_lgtFSW[r] <- lgt_riverFSW[r]
      }

### MSW exploitation rates

# Mean of river effect (logit scale)
mu_lgtrFMSW ~ dnorm(0,0.01)

# River effect
      for (r in 1:Nriver[Nyear])
      {
      lgt_riverFMSW[r] ~ dnorm(mu_lgtrFMSW,tau[5])
      mu_lgtFMSW[r] <- lgt_riverFMSW[r]
      }

###############################
# Modelling latents variables #
###############################


      for (t in 1:(Nyear+1)) # from 1991 to 2015 : year 1991 required to
determine dMSW for 1992
      {
            for (r in IND[1:Nriver[t],t])
            {

## Population density (Theorical density of salmon before freshwater
migration. 100% survival of MSW individuals)
```

```
                mu_lgd[r,t] <- lg_year[t] + lg_river[r]
# Hierarchical modeling on mean log density with year and river effects
                lgd[r,t]     ~    dnorm(mu_lgd[r,t],tau[3])#    Normal
distribution on log density
                d[r,t] <- exp(lgd[r,t])
          # Back to natural scale

                ## Population density per sea age (SW and MSW)

                propSW[r,t] ~ dbeta(alphaSW,betaSW)
      # Proportion of 1SW in the population. Hierarchical modeling without
neither year nor river effects
                dSW[r,t] <- d[r,t]*propSW[r,t]
      # Density of SW per 100m².
                dMSW[r,t+1] <- d[r,t]*(1-propSW[r,t])              #
Density of MSW per 100m². Density of MSW at year t+1 depend on d and
propSW of year t
          }
      }

      for (t in 1:Nyear)          # From 1992 to 2015

      {
          for (r in IND[1:Nriver[t],t])
          {
                ## Exploitation rates

                lgt_FSW[r,t] ~ dnorm(mu_lgtFSW[r],tau[6])
                lgt_FMSW[r,t] ~ dnorm(mu_lgtFMSW[r],tau[7])
                e.FSW.s[r,t] <- (lgt_FSW[r,t]-mu_lgtFSW[r])/sigma[6]
                e.FMSW.s[r,t] <- (lgt_FMSW[r,t]-mu_lgtFMSW[r])/sigma[7]

                FSW[r,t] <- ilogit(lgt_FSW[r,t])
                FMSW[r,t] <- ilogit(lgt_FMSW[r,t])

                ## Population abundance per sea age using censored and
uncensored data

                lambdaSW[r,t] <- dSW[r,t+1]*SRRSW[r,t]
      # Poisson parameter (mean and variance) define as the combination
of density and production surface
                is.SW_c[r,t] ~ dinterval(SW[r,t], SW_c[r,t])       #
Added ELORN & AULNE-DOUFFINE censored data
                SW[r,t] ~ dpois(lambdaSW[r,t])
          # SW abundance (Poisson distribution)
                e.SW.s[r,t]                <-                (SW[r,t]-
lambdaSW[r,t])/pow(lambdaSW[r,t],0.5)

                lambdaMSW[r,t] <- dMSW[r,t+1]*SRRMSW[r,t]
      # Poisson parameter (mean and variance) define as the combination
of density and surface
                is.MSW_c[r,t] ~ dinterval(MSW[r,t], MSW_c[r,t])
      # Added ELORN & AULNE-DOUFFINE censored data
                MSW[r,t] ~ dpois(lambdaMSW[r,t])
      # MSW abundance (Poisson distribution)
                e.MSW.s[r,t]               <-               (MSW[r,t]-
lambdaMSW[r,t])/pow(lambdaMSW[r,t],0.5)
```

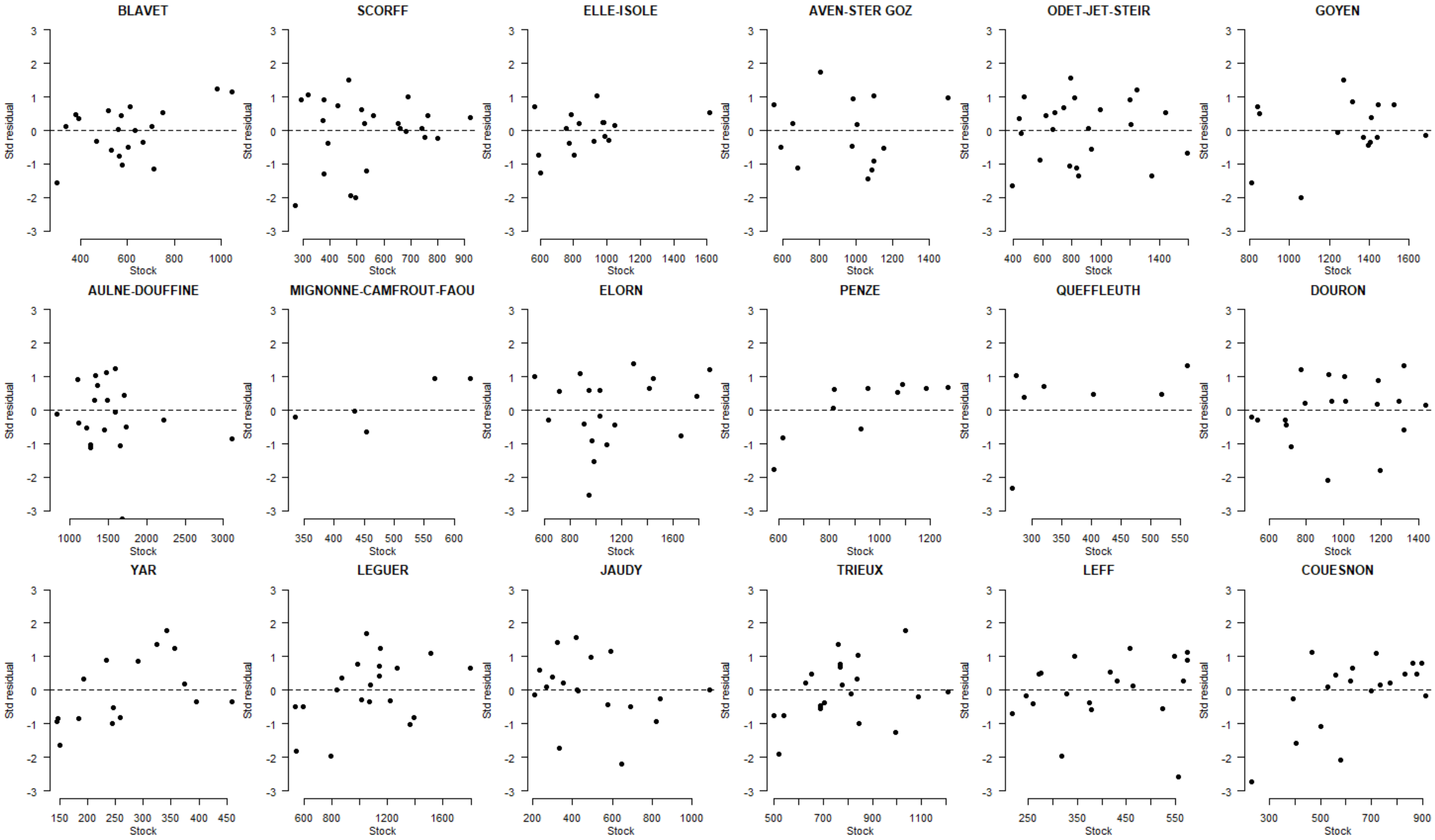
```
##############################
#    Likelihood on yield     #
##############################

                 YSW_n[r,t] ~ dbin (FSW[r,t],SW[r,t])
      # 1SW yield during open fishing periods
                 YMSW[r,t] ~ dbin (FMSW[r,t],MSW[r,t])

##############################
#         Eggs laid          #
##############################

                 EGG1[r,t]  <-  ((MSW[r,t]-YMSW[r,t])*PROPFEMMSW*NBEGGMSW
+                 (SW[r,t]-((1-IND_YSW[r,t])*YSW_n[r,t]              +
IND_YSW[r,t]*YSW_an[r,t]))*PROPFEMSW*NBEGGSW)/SRR[r,t]
                 EGG[r,t] <- max(EGG1[r,t],10^(-3))
            }
      }


########################################################################
##########################################
# 3/ MODELING SR RELATIONSHIP

########################################################################
##########################################
## t: year from 1 to Nyear=24 (1992:2015)
## r: river from 1 to max(Nriver)=22 (AULNE-DOUFFINE,AVEN-STER
########################################################################
##########################################

########################################################################
##########################################
## DATA

## PARR[r,t]: Production of 0+ parr estimate from model PARR (similar to
ORE-DIApfc model)                                  #
########################################################################
##########################################

##############################
#     Priors definitions     #
##############################

      ## BH parameters

      # Maximal survival rate : a

      mua <- 0.04042553                    # mean(a) = Maximal egg-to-
parr survival for SCORFF river
      na <- 2                              #  Sample  size  for  prior
distribution of parameter a
      alphaa <- mua*na
      betaa <- na - alphaa
      a ~ dbeta(alphaa,betaa)

      # Carrying capacity : Rmax
```

```
      lambda <- 1/19                          # Intensity parameter of
Rmax exponentielle distribution. E(Rmax)=1/lambda=19 the maximal parr
density observed in the Scorff
      Rmax ~ dexp(lambda)

      # SR multiplication factor

      mu_lgdelta ~ dunif(-10,10)

      for (r in 1:Nriver[Nyear-1])
      {
      lg_delta[r] ~ dlnorm(mu_lgdelta,tau[8])
      delta[r] <- exp(lg_delta[r])
      }
##############################
#     Likelihood on PARR     #
##############################

      for (t in 1:Nyear)          # From 1992 to 2015

      {
            for (r in IND[1:Nriver[t],t])
            {
                  mu_lgPARR[r,t]  <-  log(EGG[r,t]/((1/a)+(EGG[r,t]/Rmax))
* delta[r])
                  PARR[r,t] ~ dlnorm(mu_lgPARR[r,t],tau[8+r])
                  e.s[r,t] <- (log(PARR[r,t])-mu_lgPARR[r,t])/sigma[8+r]
            }
      }
}
```

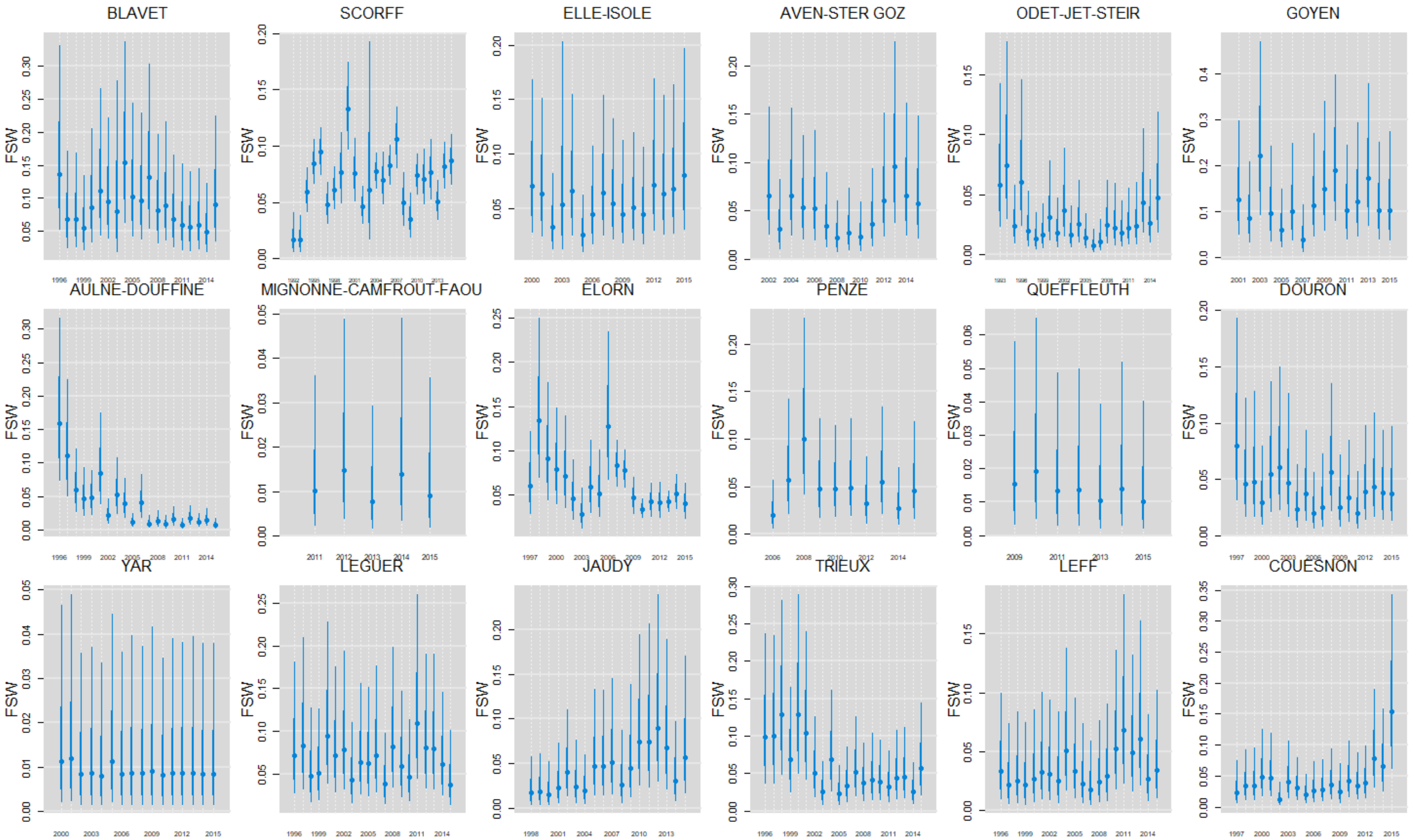
Appendix 2.5. Script of the model used in this study



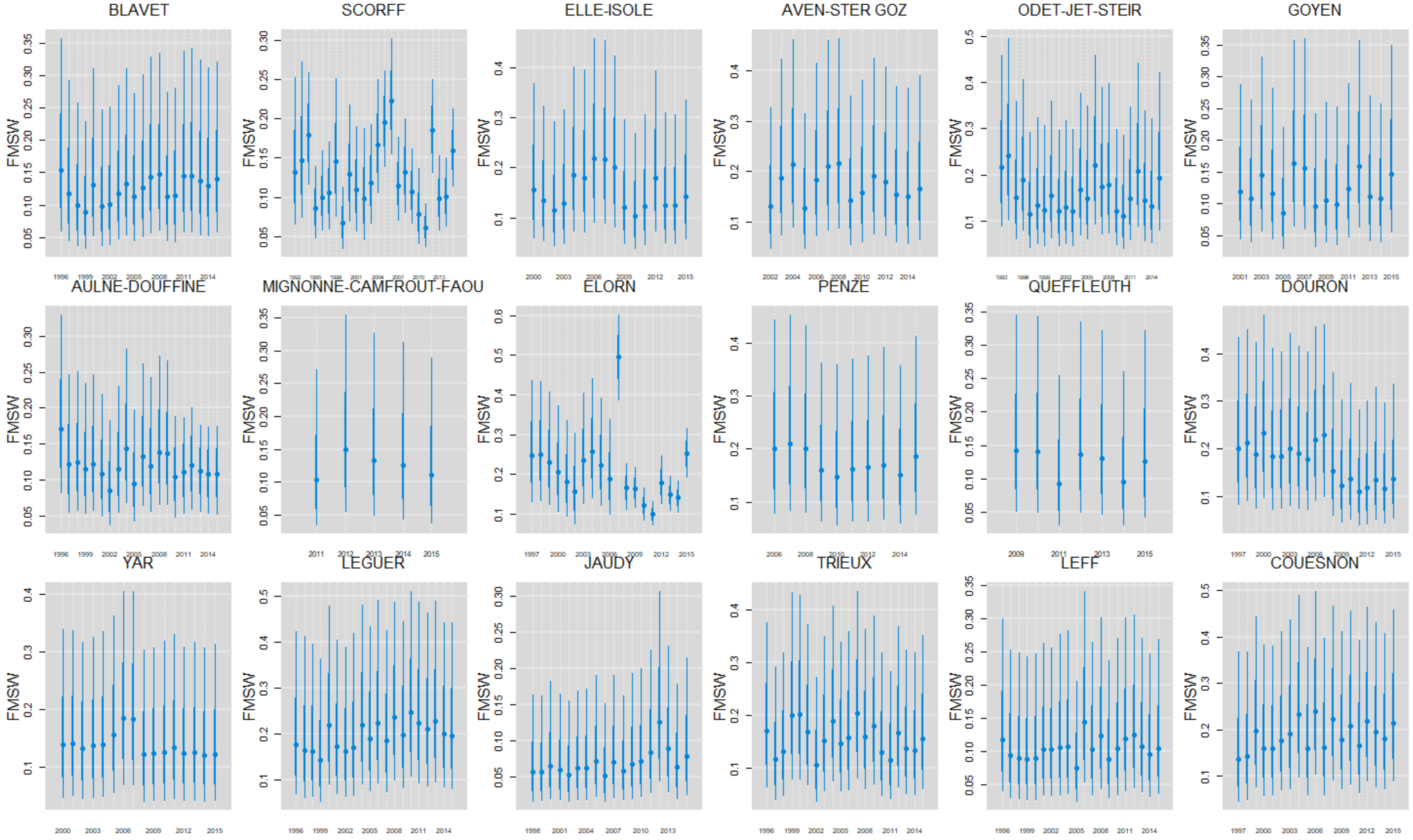
Appendix 3.1. Median standard residual trends over the time



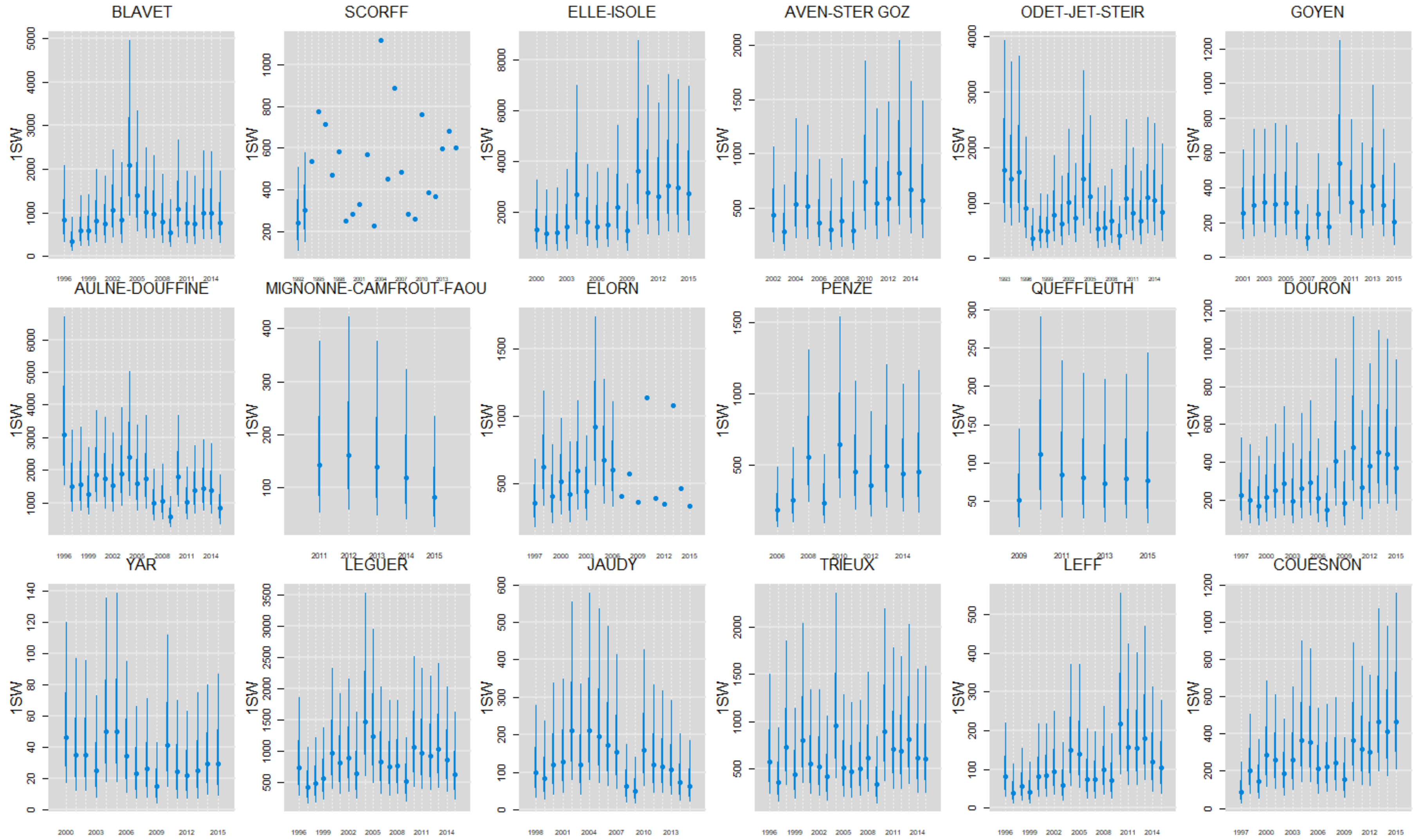
Appendix 3.2. Median standard residual trends in accordance to the stock levels



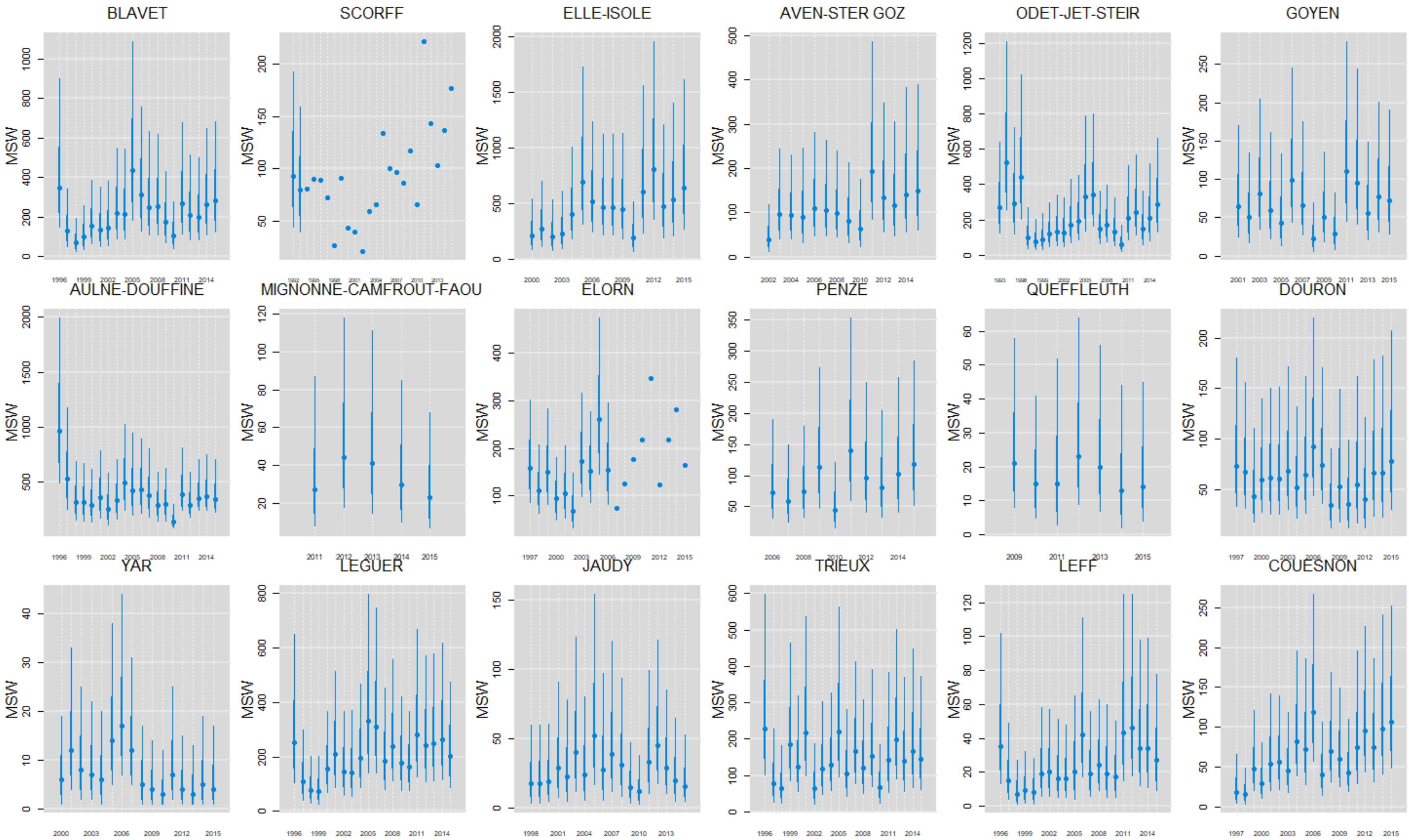
Appendix 3.3. Scatterplots of the 1SW exploitation rates estimates for each river and each year



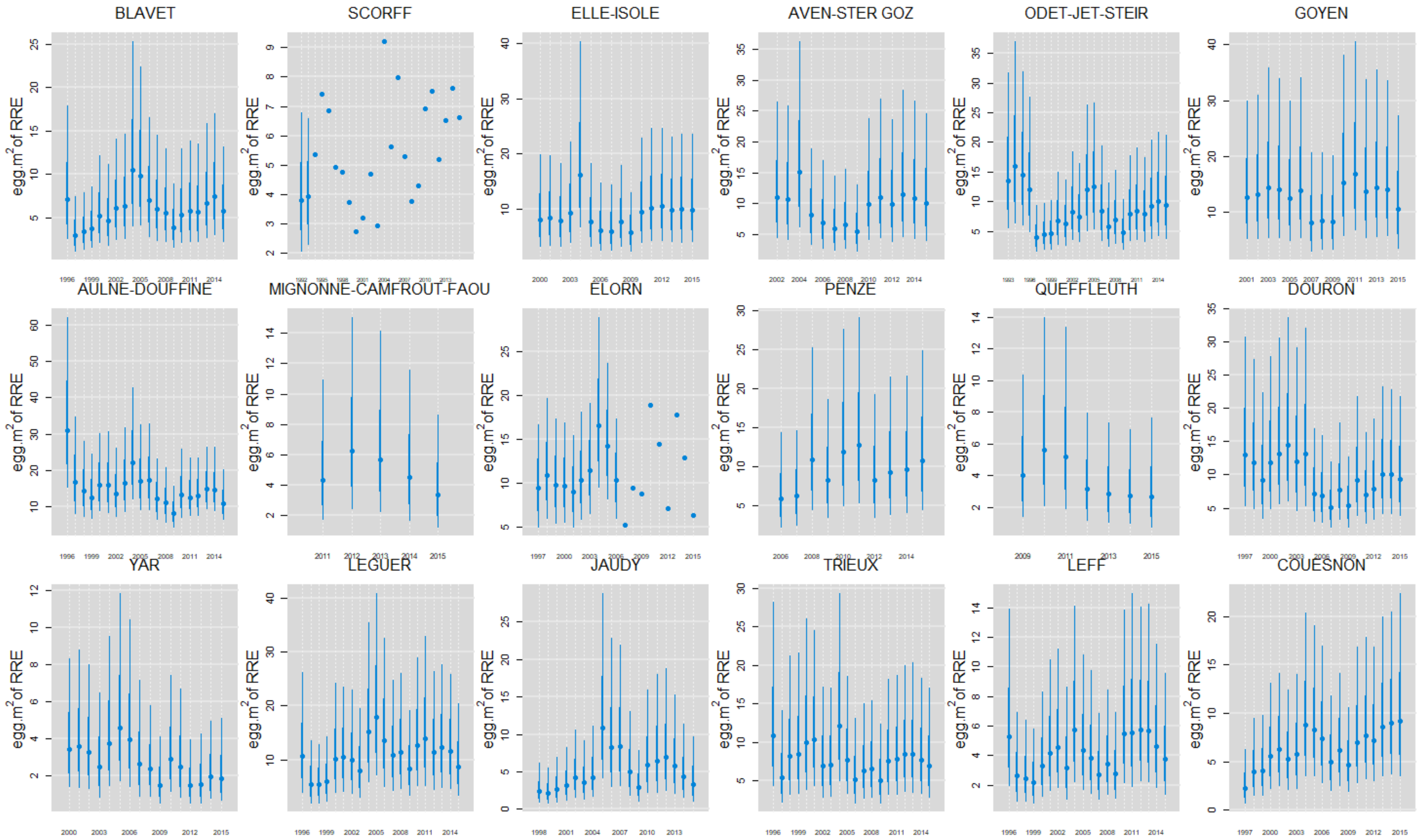
Appendix 3.4. Scatterplots of the MSW exploitation rates estimates for each river and each year



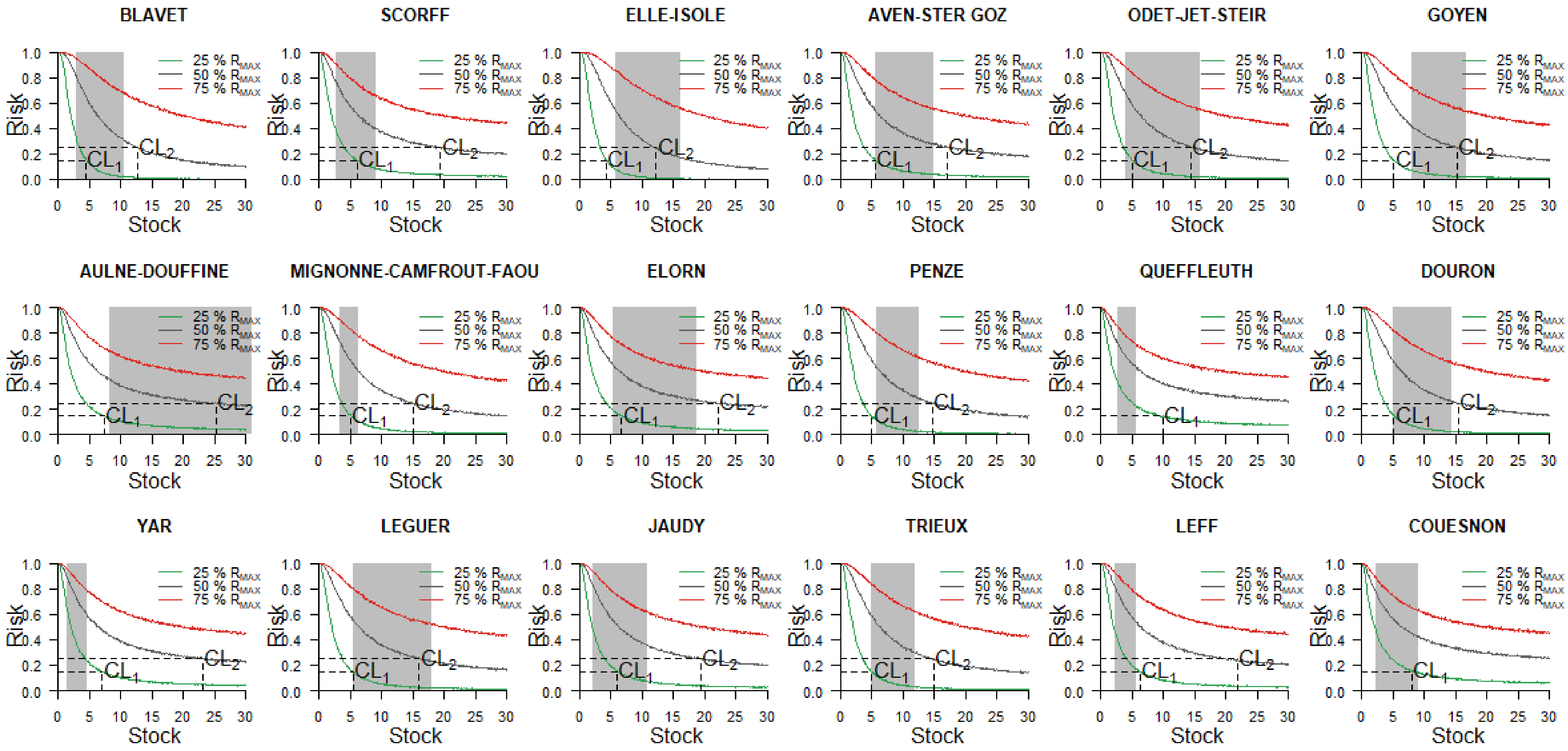
Appendix 3.5. Scatterplots of the 1SW return estimates for each river and each year



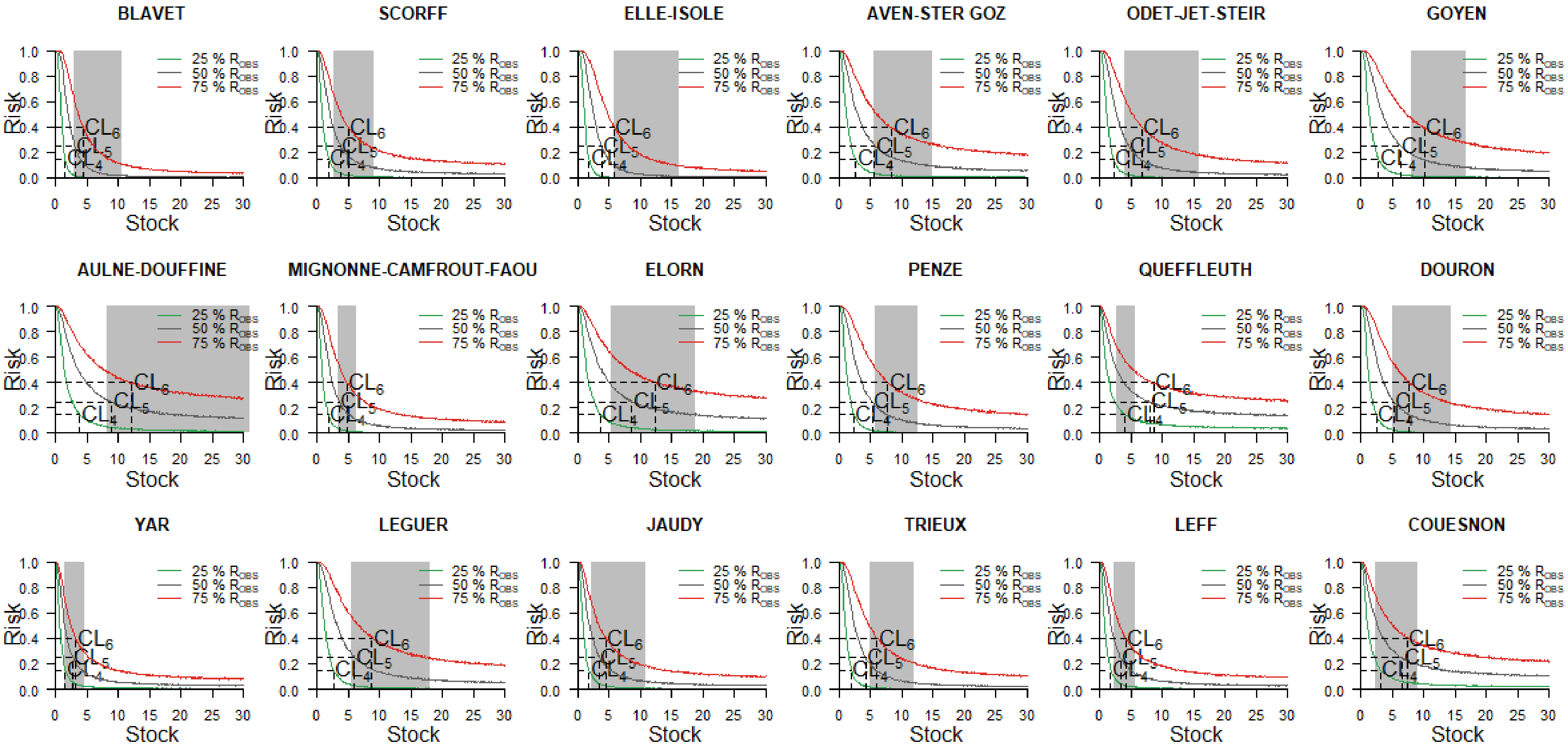
Appendix 3.6. Scatterplots of the MSW return estimates for each river and each year



Appendix 3.7. Scatterplots of the stock estimates for each river and each year



Appendix 3.8. Risk diagrams used to set CL related to R_{MAX}. Risk probability is expressed in the y-axis and stock level in the x-axis



Appendix 3.9. Risk diagrams used to set CL related to $R_{OBS.}$ Risk probability is expressed in the y-axis and stock level in the x-axis

Diplôme : Ingénieur Agronome

Spécialité : Sciences Halieutiques et Aquacoles

Spécialisation / option : Ressources et écosystèmes aquatiques

Enseignant référent : Etienne Rivot

Auteur(s) : LEBOT Clément

Date de naissance* : 17/07/1992

Nb pages : 30 Annexe(s) : 25

Année de soutenance : 2017

Organisme d'accueil : UMR EcoBiop

Adresse : D918

64310 Saint-Pée-sur-Nivelle

Maître de stage : Etienne Prévost

<u>Titre français:</u> Définition de nouvelles limites de conservation pour les populations de saumon atlantique (*salmo salar*) bretonnes

<u>Titre anglais</u> : Defining new conservation limits for Atlantic salmon (*Salmo salar*) populations of Brittany

Résumé (1600 caractères maximum) :

This study aims to set new CLs for the A. salmon populations of Brittany by shifting the management objective toward conservation rather than exploitation. Following the NASCO advices (2009), the theoretical framework used to define CLs leans on river specific data (catches and abundance indices of juveniles) and integrate the main sources of uncertainty. CL have been defined as the stock level corresponding to a low risk of low recruitment. Several limits have been considered by using different risks and references of recruitment. To assess the CL, we modeled freshwater SR relationships using a BHM. As the best-known population, Scorff population was set as a reference. The fitted SR relationships have made it possible for us to assess the different CL considered. Given the CL, the inter-river variability could be significant. We discuss about the possible bias induced on CL by the model used. Several prospects of improvement are presented. Finally, we discuss about the theoretical framework developed in this study and its possible application to different management strategies.

Abstract (1600 caractères maximum) :

La présente étude vise à élaborer de nouvelles limites de conservation pour les populations de saumon atlantique bretonnes en réorientant l’objectif de gestion, de l’exploitation vers la conservation. Comme le recommande la NASCO (2009), le cadre théorique utilisé pour définir ces nouvelles limites se base sur des données spécifiques à chaque population (captures et indices d’abondances de juvéniles) et intègre les sources d’incertitudes les plus importantes. Les limites de conservation ont été définies comme le niveau de stock correspondant à un risque faible de recrutement faible. Plusieurs limites de conservation ont été proposées, considérant différents risques et références de recrutement. Pour évaluer ces limites de conservation, des relations de stock-recrutement en eau douce ont été modélisés à l’aide d’un modèle hiérarchique bayésien. La population du Scorff ayant la dynamique la mieux renseignée, elle a été définit comme une référence dans le modèle utilisé. Les relations de stock-recrutement ajustées ont permis d’évaluer les différentes limites de conservation proposées. Selon la limite de conservation, les variations entre rivières peuvent être assez importantes. Cette étude nous a permis de discuter des possibles sources de biais affectant l’ajustement des relations de SR et donc la définition des limites de conservation. Plusieurs perspectives d’amélioration sont proposées. Enfin, nous discutons du cadre théorique développé ici et de son application à différente stratégie de gestion.

Mots-clés : Limites de conservation, densité-dépendance, Saumon Atlantique, Bretagne

Key Words: Conservation limits, density-dependence, Atlantique salmon, Bittany

* *Elément qui permet d’enregistrer les notices auteurs dans le catalogue des bibliothèques universitaires*