

Taking full advantage of the diverse assemblage of data at hand to produce time series of abundance: a case study on Atlantic salmon populations of Brittany

Lebot Clément ^{1,6}, Arago Marie-Andrée ², Beaulaton Laurent ^{3,4}, Germis Gaëlle ⁵, Nevoux Marie ^{6,7}, Rivot Etienne ^{6,7}, Prévost Etienne ¹

¹ Univ Pau & Pays Adour, E2s UPPA, INRAE, OFB, Inst Agro, ECOBIOP, Management Diadromous Fish, St Pee Sur Nivelle, France.

² OFB, Direct Bretagne, Rennes, France.

³ OFB, Serv Conservat & Gest Durable Espèces Exploitées, Direct Rech & Appui Sci, Rennes, France.

⁴ Univ Pau & Pays Adour, Management Diadromous Fish Their Environm, OFB, INRAE, Inst Agro, Rennes, France.

⁵ Bretagne Grands Migrateurs, Rennes, France.

⁶ INRAE, DECOD Ecosyst Dynam & Sustainabil, Inst Agro, IFREMER, Rennes, France.

⁷ Univ Pau & Pays Adour, Inst Agro, INRA, Management Diadromous Fish Their Environm, OFB, Rennes, France.

* Corresponding author : Clément Lebot, email address : clement.lebot@agrocampusouest.fr

Abstract :

Estimation of abundance with wide spatiotemporal coverage is essential to the assessment and management of wild populations. But, in many cases, data available to estimate abundance time series have diverse forms, variable quality over space and time and they stem from multiple data collection procedures. We developed a hierarchical Bayesian modelling (HBM) approach that take full advantage of the diverse assemblage of data at hand to estimate homogeneous time series of abundances irrespective of the data collection procedure. We apply our approach to the estimation of adult abundances of 18 Atlantic salmon (*Salmo salar*) populations of Brittany (France) from 1987 to 2017 using catch statistics, environmental covariates, and fishing effort. Additional data of total or partial abundance collected in four closely monitored populations are also integrated into the analysis. The HBM framework allows the transfer of information from the closely monitored populations to the others. Our results reveal no clear trend in the abundance of adult returns in Brittany over the period studied. Dans de nombreux cas, toutefois, les données disponibles pour l'estimation de séries chronologiques différentes procédures. Nous avons élaboré une approche de modélisation bayésienne hiérarchique (MBH) pour tirer pleinement parti de l'assemblage varié de données disponibles pour estimer des séries chronologiques homogènes d'abondance, quelle que soit la procédure de collecte de données. Nous appliquons l'approche à l'estimation de l'abondance d'adultes dans 18 populations de saumon atlantique (*Salmo salar*) de Bretagne (France) de 1987 à 2017, en utilisant des statistiques sur les prises, des covariables faisant l'objet d'une surveillance étroite sont aussi intégrées à l'analyse. Le cadre de MBH

permet le transfert d'information l'abondance des adultes de retour en Bretagne au cours de la période étudiée. [Traduit par la Rédaction]

60 INTRODUCTION

61 For assessing past and current conservation status of fish populations and providing fisheries
62 management advice, reliable time series of abundance are required. At a single spatio-
63 temporal unit, e.g. a population a given year, catch reflects abundance up to a scaling factor,
64 the proportion of adult removed by harvesting, also called the exploitation rate. Abundance
65 can be statistically inferred (i.e. estimated) from an observed catch under the premise the
66 latter results from a random process conditioned by the underlying abundance of the
67 harvestable population and the exploitation rate. Provided this process is explicitly modeled,
68 the accuracy and precision of the abundance estimate relies primarily, but not only, on our
69 ability to assess the exploitation rate. Information on changes in exploitation rates, resulting
70 for example from variations in harvesting effort, in the efficiency of catching gears or from
71 environmental factors, may be difficult to monitor. In the absence of such information,
72 abundance cannot be estimated from catch data without making strong assumptions on
73 exploitation rates, and even then, the estimates can be strongly biased if the assumptions are
74 wrong (Hilborn and Walters 1992; Arreguin-Sanchez 1996; Maunder and Punt 2004).
75 Abundance can also be estimated independently from catch. But catch statistics are often
76 more widely available over space and time than fisheries independent data. Hence, the
77 fisheries scientist often faces the dilemma of using abundance estimates from fisheries
78 independent data with limited spatio-temporal coverage versus potentially less reliable
79 estimates from fisheries catch but with a wider spatio-temporal coverage.

80 When abundance estimates, derived from fisheries independent data gathered under
81 controlled scientific protocols are simultaneously available with catch statistics offering a wider
82 spatio-temporal coverage, there can be a way out of this dilemma. Exploitation rate can be
83 estimated and extrapolated over other spatio-temporal units. To improve precision and
84 accuracy, this extrapolation may benefit from taking into account covariates that are correlated
85 with variations over space and time of exploitation rate or abundance. The value of the
86 Hierarchical Bayesian Modelling (HBM) framework (Gelman et al. 2013; Congdon 2014) in
87 such cases, where availability of data vary between observation units, has been well

88 established, especially in ecology (Clark 2003; Royle and Dorazio 2008; Cressie et al. 2009;
89 Parent and Rivot 2012). The HBM framework facilitates the joint treatment of heterogeneous
90 data sets: it allows the borrowing and transfer of information between data-rich and data-poor
91 spatio-temporal units, while accounting for the associated uncertainty (e.g. Prévost et al. 2003;
92 Brun et al. 2011). HBM also facilitates estimation for spatio-temporal units with missing data
93 (e.g. Clark and Bjørnstad, 2004) and prediction for new units with no observed data (e.g.
94 Prévost et al. 2003). In this paper, we show by means of a case study on Atlantic salmon how
95 HBM enables abundance estimation over a large set of spatio-temporal units from a
96 heterogeneous dataset made of fisheries catch, fisheries independent abundance data,
97 fishing effort and environmental covariates.

98 Atlantic salmon reproduce in freshwater, where juveniles grow before undertaking long-
99 distance migrations in the ocean to feeding areas. They return to their natal rivers to spawn
100 (after one or two years at sea, exceptionally three; Webb et al., 2007). Due to this homing
101 behavior, each river flowing into the ocean is usually considered as holding (at least) one
102 distinct salmon population. This specificity poses a special challenge to resource conservation
103 and management. Indeed, there are hundreds of Atlantic salmon populations (King et al.
104 2007), whose conservation status may vary greatly as a result of contrasted local
105 characteristics, even between neighboring rivers (NASCO 2019). The river scale is the
106 relevant and recommended spatial scale for the management of salmon stocks. But obviously,
107 even though salmon (Atlantic and Pacific) are among the most studied species (Prévost and
108 Chaput 2001), it is not conceivable to survey rigorously every individual river population. To
109 circumvent this difficulty, long term scientific population monitoring has targeted so-called
110 “index rivers” from which more precise knowledge on stock size, i.e. on abundance of adult
111 returns, can be obtained and ultimately transferred to unmonitored rivers. Atlantic salmon is a
112 species of great fishing interest (both commercial and recreational) and catch statistics are
113 often compiled on a river-by-river basis. These data provide an opportunity to tailor the
114 information brought by index rivers to other rivers in order to better appraise the abundance
115 of adult returns of any exploited population. The need to take the best advantage possible of

116 the data at hand for estimating abundance is particularly acute for Atlantic salmon. The
117 species has undergone a general decline of abundance during the last four decades (Chaput
118 2012; ICES 2019; Olmos et al. 2019). Many populations are impacted or threatened (if not yet
119 extirpated for a significant proportion) by human activities (e.g. damming, contamination,
120 fisheries), including through climate change (Piou and Prévost 2013; NASCO 2019).

121 Over the last twenty years, the HBM framework has been repeatedly used to estimate
122 abundance in Atlantic salmon (e.g. Rivot and Prévost 2002; Rivot et al. 2008; Brun et al. 2011;
123 Massiot-Granier et al. 2014; Dauphin et al. 2017, 2019). Among this now relatively wide
124 selection of papers, two are of more specific interest with regards to the question addressed
125 herein. Rivot et al. (2008) present a HBM to estimate juvenile salmon abundance over a set
126 of spatio-temporal units from successive removal data (i.e. catch by electrofishing). They
127 jointly treat units with two successive passes and others with only a single pass. They use
128 catch to estimate abundance and they extrapolate the probability of capture, analogous to an
129 exploitation rate, from units with two passes to units with one pass. But they make limited use
130 of covariates for explaining spatiotemporal variations (i.e. restricted to year and dichotomous
131 habitat type effects), and their data set is homogenous in terms of data collection procedure
132 (i.e. electrofishing census only). The more general HBM framework proposed by Brun et al.
133 (2011) allows to derive homogenous series abundance estimates from multiple data collection
134 procedures (DCPs). The homogeneity refers to the definition of the abundance time series
135 which is not contingent upon the various DCPs used. The key feature of Brun et al. (2011)
136 approach resides in the explicit modelling of each of the DCPs by which the observed data
137 stem from the unknown abundance. The DCPs may vary according to the spatio-temporal
138 units considered and they can be influenced by covariates. In the present paper, we take
139 inspiration from Brun et al. (2011) by considering fishing as a DCP that covers the full set of
140 spatio-temporal units of interest. Others DCPs (e.g. partial counting devices) may contribute
141 additional data on a subset. Finally, abundance may be fully known, an option not considered
142 by Brun et al. (2011), on another subset.

143 We demonstrate our approach with a case study on 18 populations of Atlantic salmon in
144 Brittany, France (Fig. 1). A complete set of 31 years (1987-2017) of angling catch is available
145 for each river. Fisheries independent DCPs provide additional information on abundance for
146 4 populations over part of the study period: the adult returns are known on the Scorff (1994-
147 2017) and the Elorn (2007-2017), while only partial counts are available for the Aulne (1999-
148 2017) and the Couesnon (1996-2015). Fishing effort data and environmental covariates (river
149 size and flow) are also used. All materials needed to run the model (data sets, model script,
150 etc) and to produce estimates, tables and figures presented in this paper are available at the
151 following link: <https://gitlab.com/clebot/abundance>.

152

Draft

153 MATERIALS AND METHODS

154

155 When catch statistics are available over wide set of spatio-temporal units together with fishery
156 independent abundance estimates covering only a restricted subset, estimating abundance
157 over the full set of spatio-temporal units can be undertaken by extrapolating over the units
158 where only catch statistics are available the information gained about the exploitation rates
159 from the units with both catch and fishery independent abundance estimates. To proceed to
160 this extrapolation, we propose a novel HBM approach which originality resides in a common
161 modeling of the relationship linking catch, exploitation rate and abundance, irrespective of the
162 fact the latter is fully unknown, estimated with error (i.e. partially observed) or directly observed
163 (i.e. fully known). The HBM setting allows for variations across spatio-temporal units, while
164 enabling the transfer of information between them. The use of this single catching process
165 model aims at facilitating the transfer of information from the data rich spatio-temporal units
166 (i.e. with abundance and catch) to the data-poor ones (i.e. with catch only) when proceeding
167 to statistical inference. The approach is further refined by including covariates, both
168 environmental or fishery related, that can help explaining spatio-temporal variations of
169 exploitation rate or abundance.

170 These modeling guidelines are quite general irrespective of the species or the spatio-temporal
171 setting of interest. We put them in practice on our case study on Atlantic salmon. We start by
172 describing the data at hand, followed by the modelling details, with first (i) the common
173 modelling of the catching process and next the hierarchical structure and the covariate effects
174 set on (ii) exploitation rate and (iii) abundance. The specification of prior distributions, the
175 implementation of the Bayesian inference and elements of evaluation of model performance
176 are subsequently presented.

177

178 1. Study site and fishing regulation

179 In France, freshwater fisheries targeting Atlantic salmon (mainly recreational angling by rod
180 and line) are regulated. A specific license is required and the regular fishing season is divided

181 in two periods; from mid-March to mid-June and from mid-June to mid-September. Fishing
182 dates are established every year at the river scale with some variations between rivers and
183 years. Multi-sea winter (MSW) fish return to rivers first and 89% of their catch is made during
184 the first fishing period. To limit the exploitation of MSW fish, their removal is not allowed
185 outside the first fishing period (i.e. no fish larger than 67 cm can be kept). The return migration
186 of one-sea winter fish (1SW) occurs later in the year, essentially after mid-June and 92% of
187 the 1SW catch is made after this date.

188 The declaration of salmon catches in rivers became mandatory in 1987 and nine years later,
189 river-specific annual Total Allowable Catches (TACs) were established (Prévost and Porcher
190 1996). In Brittany, TACs are defined for 26 rivers but only the main 18 rivers are considered
191 in this study (Fig. 1). These TACs are specific to each sea age category (i.e. MSW and 1SW).
192 They are updated on a multiannual basis according to available assessment data. The in-
193 season monitoring of catches is essential, allowing managers to close the fishery if the TAC
194 is reached before the prescribed end of the fishing period. As the 1SW TAC has never been
195 reached in any river to date, an extension of the second fishing period from mid-September to
196 mid-October (even late October in some circumstances) has also been established for some
197 rivers some years. We consider this extension as a third fishing period.

198

199 2. Data

200 a. Catch

201 Atlantic salmon catches are collated in a database managed by the “*Centre National*
202 *d’Interprétation des Captures de Salmonidés*” (CNICS,
203 [https://www6.rennes.inrae.fr/u3e_eng/ABOUT-US/Organisation/The-migratory-fish-](https://www6.rennes.inrae.fr/u3e_eng/ABOUT-US/Organisation/The-migratory-fish-hub/CNICS)
204 [hub/CNICS](https://www6.rennes.inrae.fr/u3e_eng/ABOUT-US/Organisation/The-migratory-fish-hub/CNICS)). We extracted time-series of annual catches by sea age category for our 18
205 salmon populations over the period from 1987 to 2017. Sea age is interpreted from the
206 analysis of fish scales samples that fishermen must provide for every fish caught when
207 declaring their catch.

208

209 b. Covariates of the exploitation rates

210 River angling catch is related to the number of returning adults through an exploitation rate,
211 which in turn depends on fishing effort. The number of fishing licenses issued annually and
212 the duration of fishing periods are the only information available on fishing effort. The number
213 of licenses is only known at the regional scale (i.e. Brittany) and cannot be allocated on a river
214 per river basis. This number varies minimally over time (coefficient of variation (CV): 11% over
215 the period of study) and preliminary analyses (not reported here) did not show it had an effect
216 on the variations of the exploitation rate estimates over time. Thus, the number of licenses
217 has been discarded from our analysis. The duration of the fishing periods is known for every
218 river every year. Hence, for each river and each fishing period, the time-series of fishing effort
219 from 1987 to 2017 corresponds to the number of days when fishing is allowed. Fishing effort
220 is considered separately by fishing period.

221 Rod and line catches of salmon can be correlated over time with river flows as they influence
222 angling success (Gee 1980). In Brittany, river flows are mainly driven by regional and seasonal
223 patterns of precipitations that are mostly common to all rivers. Three regional river flow indices,
224 one per fishing period, were derived using a subset of nine rivers for which flow measurements
225 were available for the period 1987 to 2017. For each river, we selected the gauging station
226 nearest to the estuary and computed annual indices by averaging the daily discharge
227 measurements across days and rivers for each fishing period.

228

229 c. Abundance of adult returns from monitored rivers

230 For the Scorff (Fig. 1), the total abundance of adult returns by sea age category (1SW and
231 MSW) have been estimated since 1994 using capture-mark-recapture techniques (Servanty
232 Royer and Prévost 2016; Buoro et al. 2019). Fish are marked at a trapping facility located at
233 the head of tide and, recaptures are made above this site and no angling catch occurs
234 downstream from it. Sea age is determined from interpretation of scales collected from
235 sampled fish.

236 On the Elorn (Fig. 1), direct counting of salmon has been undertaken since 2007 using a video-
237 recording unit located 2.5 km upstream from the head-of-tide. There are very few (if any) rod
238 and line catches below the counting facility. Total returns of 1SW and MSW adults are
239 determined based on the individual length (1SW fish are significantly shorter, more than 10
240 cm on average, than their MSW counterparts) and the date of observation of each fish
241 (Dartiguelongue 2017). Given the methods used to quantify adult returns on the Scorff and
242 the Elorn, the estimates of returns are considered to be known without error. The exception is
243 for the Elorn in 2007 when the video-counting was only set up in mid-April, after the beginning
244 of the period of river entry of MSW individuals. The number of MSW fish counted in 2007 is
245 thus considered as a partial count of the MSW returns.

246 Information on adult returns is also collected from counting devices on the Aulne (video
247 recording; Fig. 1) since 1999 and on the Couesnon since 1996 (acoustic recording and
248 trapping; Fig. 1). For both rivers, the characteristics of the facilities and the observation
249 procedures only provide partial counts. On the Aulne, the counting device is installed at a dam,
250 at the upstream end of the adjoining fishway. Under high flow conditions some fish may cross
251 the dam directly without using the fishway. On the Cousenon, the beam of the acoustic
252 recorder only covers part of the section of the river. At both sites, the distinction between 1SW
253 and MSW individuals is also based on length and date of observation.

254

255 d. River area

256 Abundance of Atlantic salmon populations are strongly dependent on the size of the home
257 river that supports the juvenile production (Prévost et al. 2001). The size can be quantified by
258 the water surface area that support juvenile production (i.e. productive area), expressed in
259 100 m² of riffle-rapid equivalent (RRE), with riffles and rapids being the preferred habitats for
260 juvenile salmon (Bagliniere and Champigneulle 1982; Prévost and Porcher 1996). For the
261 rivers of Brittany, habitat areas are derived from habitat cartography data and are regularly
262 updated.

263

264 3. Model overview

265 The simplified direct acyclic graph presented Fig. 2 describes the general conditioning
266 structure of the model (see also supplementary material A for the full DAG). At the bottom of
267 the graph are observed data, i.e. the catches, that are conditioned by other model quantities
268 but do not condition any other quantity. At the top of the graph are the model parameters ψ
269 and the observed covariates, i.e. the regional flow index Q , the river size S and the fishing
270 effort E ; that condition other model quantities but are not conditioned by any other quantity. In
271 between, are latent variables θ , i.e. intermediate quantities useful to conceptualize the process
272 giving rise to the data, and the quantities of ultimate interest to be estimated, i.e. the
273 exploitation rates u and the number of adult returns N , the latter being conditioned by river
274 size S . The catch C is assumed to depend on the adult return abundance N and the
275 exploitation rate u , also called the probability of capture. Part of the variations of the
276 exploitation rate is explained by two covariates, the regional flow index Q (i.e. environmental
277 conditions) and a river-specific measure of fishing effort E , i.e. the duration of the fishing
278 period. The parameters ψ govern the variations over time (year, t), space (river, r) and sea
279 age (a) of the latent variables θ and the quantities of ultimate interest in a hierarchical
280 structure. Most of the model parameters ψ are specific to the fishing period (p). Note that the
281 adult abundances are observed or unknown, according to the river and the year.

282

283 4. Model details

284 Observable quantities and covariates are denoted by capital Roman letters and unobservable
285 quantities by Greek or Roman lowercase letters. The notation $x|y \sim \text{distribution}(y)$ refers to the
286 conditional distribution of x given y . Subscripts indicate the year t , the river r (from 1 =
287 Couesnon to 18 = Blavet; Fig. 1), the sea age category a (1 for MSW and 2 for 1SW), and/or
288 the fishing period p (from 1 to 3). A superscript identifies the relationship between variables
289 within the hierarchical structure of the model, that is, μ^q is the mean of the distribution of the
290 quantity denoted q . In linear models, intercepts are denoted α and covariate coefficients or
291 effects are denoted β . These linear model parameters may also be numbered when

292 necessary. See also Tab. 1 for the definition of all model quantities.

293

294 a. Exploitation

295 The catch $C_{t,r,a}$ of sea age category a , in river r , in year t is assumed to result from a binomial
 296 draw in the total number of adult returns $N_{t,r,a}$ with a probability of capture $u_{t,r,a}$ (1) subsequently
 297 referred to as the exploitation rate.

298

299 (1) $C_{t,r,a}|N_{t,r,a}, u_{t,r,a} \sim \text{Binomial}(N_{t,r,a}, u_{t,r,a})$

300 The binomial distribution can accommodate variations in the probability of capture among
 301 individuals provided they are independent relative to the capture process (Mäntyniemi et al.
 302 2005). Angling tests fish individually, capture them one by one and we have no evidence
 303 showing that the catch of any given fish would change the behavior of its counterparts and
 304 render them more or less catchable. Independence therefore appears as a simple and
 305 reasonable default hypothesis in our case. Overdispersed alternatives to the binomial
 306 distribution (e.g. beta-binomial) could be used if warranted.

307 The survival to fishing $1 - u_{t,r,a}$, is modeled by means of three survival rates $s_{t,r,p}$ (2).

308

309 (2) $1 - u_{t,r,a} = \prod_{p=1}^3 (s_{t,r,p})^{I_{t,r,a,p}}$

310 where $s_{t,r,p}$ is the survival for MSW fish when $p=1$, for 1SW in the absence of third fishing
 311 period when $p=2$ and for 1SW during the third fishing period only when $p=3$. The index p of
 312 the fishing periods is used here because MSW fishing is only allowed during the first one and
 313 1SW fish are essentially caught during the second and the third. Note however that the very
 314 few (i) MSW individuals that may be caught and declared by mistake outside period 1 or (ii)
 315 1SW individuals caught prior to the beginning of the second period, are included in the catch
 316 data modeled at equation (1).

317 According to this formulation, the fishing survival probabilities $1 - u_{t,r,a}$ results from three
318 survival events, binary indicators ($I_{t,r,a,p}$) specifying which apply to each sea age category, in
319 any given year and river. For the MSW fish, the binary indicators $I_{t,r,1,1}$ equals 1 while the $I_{t,r,1,2}$
320 and $I_{t,r,1,3}$ are 0. Note however that, due to some exceptional fishery closures, $I_{t,r,1,1}$ may equal
321 0 in some years for some rivers (e.g. for the Yar in 2016 and 2017). For the 1SW fish, $I_{t,r,2,1}$
322 equals 0 and $I_{t,r,2,2}$ is almost always 1, while $I_{t,r,2,3}$ equals 0 or 1 according to whether the third
323 fishing period is allowed by managers. $I_{t,r,2,2}$ may exceptionally equal 0 to account for fishery
324 closures occurring the years where water levels were extremely low during summer. Under
325 this formulation, 1SW fish have to sequentially survive to a second exploitation event when
326 the third period is open.

327 The log-log scaled $s_{t,r,p}$ survival rate is related to fishing effort (number of days) and flow using
328 a linear-normal formulation (3 and 4). The log-log transformation is a standard link function
329 which converts the survival rates, varying between 0 and 1, into a quantity, denoted $v_{t,r,p}$,
330 varying from $-\infty$ to $+\infty$ and thus amenable to linear normal modeling (Congdon 2014). We
331 considered river flow as a covariate explaining part of the temporal variability of the exploitation
332 rates because it may influence the migration activity of the fish (Thorstad et al. 2008) and
333 ultimately angling success (Gee 1980). The flow and effort covariates are measured over the
334 fishing periods most relevant to the sea age category considered, i.e. the first one for MSW
335 and the second and third ones for 1SW. The linear model coefficients are assumed to vary
336 according to the river for each fishing period and between the fishing periods. Indeed, the
337 effects of fishing effort and flow on the exploitation rate potentially differ because fishing
338 practices and the behavior of the fish may change according to the season and the fish
339 characteristics (Gueguen and Prouzet 1994). In the first period, only MSW fish, which are
340 mostly females, are subject to exploitation. The second period corresponds to the peak of
341 1SW fish river entry, which are smaller and have a more balanced sex ratio (if not dominated
342 by males). In the third period, fishing only occurs on 1SW fish, but many have already spent
343 several weeks in freshwater without feeding and they are closer to spawning time. For

344 consistency with the linear-normal structure of the model, the flow ($Q_{t,p}$) and fishing effort
 345 ($E_{t,r,p}$) covariates, which are strictly positive in their natural scale, are log transformed.
 346 Centering of the log transformed covariates is undertaken thereafter using their empirical
 347 mean per fishing period ($M_p^{log(Q)}$ and $M_p^{log(E)}$) to facilitate inferences.

348

349 (3) $v_{t,r,p} | \mu_{t,r,p}^v, \tau_p^v \sim \text{Normal}(\mu_{t,r,p}^v, \tau_p^v)$

350 (4) $\mu_{t,r,p}^v = \alpha_{r,p}^v + \beta 1_{r,p}^v \times [\log(Q_{t,p}) - M_p^{log(Q)}] + \beta 2_{r,p}^v \times [\log(E_{t,r,p}) - M_p^{log(E)}]$

351

352 where τ_p^v is the precision of the normal distribution.

353 To account for variations among rivers, the intercepts $\alpha_{r,p}^v$ and the $\beta 1_{r,p}^v$ and $\beta 2_{r,p}^v$ coefficients
 354 are river specific and are hierarchically modeled assuming normal distributions with means ($\mu_p^\alpha, \mu_p^{\beta 1}, \mu_p^{\beta 2}$)
 355 and precisions ($\tau_p^\alpha, \tau_p^{\beta 1}, \tau_p^{\beta 2}$), respectively, specific to a period (5, 6 and 7).

356

357 (5) $\alpha_{r,p}^v | \mu_p^\alpha, \tau_p^\alpha \sim \text{Normal}(\mu_p^\alpha, \tau_p^\alpha)$

358 (6) $\beta 1_{r,p}^v | \mu_p^{\beta 1}, \tau_p^{\beta 1} \sim \text{Normal}(\mu_p^{\beta 1}, \tau_p^{\beta 1})$

359 (7) $\beta 2_{r,p}^v | \mu_p^{\beta 2}, \tau_p^{\beta 2} \sim \text{Normal}(\mu_p^{\beta 2}, \tau_p^{\beta 2})$

360

361 b. Adult returns

362

363 The number of adult returns $N_{t,r,a}$ is assumed to be Poisson distributed with a mean parameter
 364 $n_{t,r,a}$ defined for each year t , river r , and sea age category a (8). Overdispersed alternatives to
 365 the Poisson distribution (e.g. negative-binomial) could be used if warranted.

366

367 (8) $N_{t,r,a}|n_{t,r,a} \sim \text{Poisson}(n_{t,r,a})$

368

369 Adults returns are either observed as on the Scorff and the Elorn, partially observed as on the
 370 Couesnon and the Aulne (and the Elorn in 2007 for MSW fish), or unknown in any other
 371 instances (Fig. 1). On the Couesnon, available partial counts were most likely a minor fraction
 372 of the actual number and there was no additional knowledge about the proportion of counted
 373 fish. We opted for a mere data censoring, the observed count $NC_{t,r,a}$ being the lower bound of
 374 the corresponding Poisson distribution. On the Aulne (and the Elorn MSW in 2007), first trials
 375 using data censoring led to gross over estimation of adult returns, with unrealistically high
 376 values relative to the river size. In addition, the partial count is considered to be relatively close
 377 to the “true” value and there is additional expert knowledge about the proportion being
 378 counted. We thus chose to model these data differently from those of the Couesnon, and
 379 opted for modeling the partial counting process of adult returns by means of a binomial
 380 distribution, with the “true” abundances of adult returns $N_{t,r,a}$ corresponding to the total number
 381 of trials and a counting probability of adult returns $p_{t,r,a}$ (9).

382

383 (9) $NC_{t,r,a}|N_{t,r,a}, p_{t,r,a} \sim \text{Binomial}(N_{t,r,a}, p_{t,r,a})$

384

385 We used additional expert knowledge to constrain the counting probabilities. First, considering
 386 the *a priori* high efficiency of the counting device, we assumed that the counting probabilities
 387 of MSW returns were higher than MSW exploitation rates ($u_{t,r,1}$ in equation 1). Second, we
 388 further assumed that the counting probabilities are higher for 1SW compared to MSW fish.
 389 Lower river flow during the upstream migration window of 1SW fish (mostly in summer), with

390 fewer flood events, make the counting device more efficient than during MSW migration
 391 window (mostly in spring). Both hypotheses were implemented using left-truncated uniform
 392 distribution for the counting probabilities (10 and 11).

393

$$394 \quad (10) \quad p_{t,r,1} | u_{t,r,1} \sim \text{Uniform}(u_{t,r,1}, 1)$$

$$395 \quad (11) \quad p_{t,r,2} | p_{t,r,1} \sim \text{Uniform}(p_{t,r,1}, 1)$$

396 To assess the impact of these assumptions derived from available local expertise, we also
 397 used unconstrained uniform probability distribution for $p_{t,r,1}$ and $p_{t,r,2}$ (see supplementary
 398 material B).

399 In Atlantic salmon, population size is constrained by and positively dependent on river size
 400 (Prévost et al. 2001). Poisson parameter $n_{t,r,a}$ of the adult return distributions (8) is the mean
 401 number of adult returns per sea age category. Hence, it is computed as the product of the
 402 river size $S_{t,r}$ and the adult density $\delta_{t,r,a}$ per unit of river size (12). In accordance with common
 403 practice, the riverine wetted area that supports the juvenile production which the returning
 404 adults originates from is used as a measure of river size (e.g. Prévost et al. 2003). To avoid
 405 very low values of $\delta_{t,r,a}$ and facilitate inferences, unit of river size used was defined as 100 m²
 406 of riffles and rapids equivalents.

407

$$408 \quad (12) \quad n_{t,r,a} = \delta_{t,r,a} \times S_{t,r}$$

409

410 Densities of each sea winter category are computed as a proportion of the total density of
 411 adults returning to each river ($d_{t,r}$), 1SW and MSW combined (13).

412

$$413 \quad (13) \quad \delta_{t+a,r,a} = d_{t,r} \times q_{t,r,a}$$

414

415 The 1SW proportion $q_{t,r,1}$ ($q_{t,r,2} = 1 - q_{t,r,1}$ being the MSW proportion) is assumed exchangeable
 416 among years and rivers and modelled by a logit-normal distribution (14). Note sea-age
 417 proportion is considered by juvenile (i.e. smolt) migration year as it is expected to be less
 418 variable than by year of adult returns which combine two different juvenile cohort of potentially
 419 variable strength.

420

$$421 \quad (14) \quad \text{logit}(q_{t,r,1}) | \mu^q, \tau^q \sim \text{Normal}(\mu^q, \tau^q)$$

422

423 where μ^q and τ^q are the mean and the precision in the logit scale.

424 Despite standardization by river size, adult densities still vary according to year and river. The
 425 log scaled $d_{t,r}$ are thus assumed to be normally distributed with a common precision (τ^d) and
 426 a mean $\mu_{t,r}^d$ resulting from the sum of a grand mean $\alpha 1^d$ with additive year $\alpha 2_t^d$ and river $\alpha 3_r^d$
 427 random effects (15, 16, 17 and 18).

428

$$429 \quad (15) \quad \log(d_{t,r}) | \mu_{t,r}^d, \tau^d \sim \text{Normal}(\mu_{t,r}^d, \tau^d)$$

$$430 \quad (16) \quad \mu_{t,r}^d = \alpha 1^d + \alpha 2_t^d + \alpha 3_r^d$$

$$431 \quad (17) \quad \alpha 2_t^d | \tau^{\alpha 2} \sim \text{Normal}(0, \tau^{\alpha 2})$$

$$432 \quad (18) \quad \alpha 3_r^d | \tau^{\alpha 3} \sim \text{Normal}(0, \tau^{\alpha 3})$$

433

434 where $\tau^{\alpha 2}$ and $\tau^{\alpha 3}$ are the precisions of the year and river effects respectively.

435

436 5. Prior probability distributions and Bayesian inference

437 Independent prior probability distributions are assigned to the parameters of the model, i.e.
438 the quantities of the model not conditioned by any other quantity. No prior knowledge was
439 available to us regarding these parameters so we opted for vague priors probability
440 distributions (Tab. 2) to ensure that our posterior distributions reflect primarily the information
441 brought by the data. The structure of our model being essentially linear-normal, we stuck to
442 the standard choice of using normal distributions, with 0 mean and large variance, for the
443 parameters related to the coefficients of the linear relations and gamma distributions, with
444 small shape and inverse-scale for the precisions ($\tau_p^v, \tau_p^a, \tau_p^{\beta 1}, \tau_p^{\beta 2}, \tau^q, \tau^d, \tau^{\alpha 2}, \tau^{\alpha 3}$).

445

446 The joint posterior distribution of all unknown quantities was approximated using Markov chain
447 Monte Carlo (MCMC) sampling. All computations were carried out with the JAGS® software
448 (version 4.2.0.; Plummer 2003) running in rjags, Coda and Dclone packages of R (version
449 3.3.0, www.r-project.org). Three chains with contrasted starting points were run in parallel.
450 After an initial phase of 2,000 iterations for sampler adapting, 10^7 values were drawn for each
451 chain. The convergence of the MCMC sampling was evaluated using the Gelman–Rubin
452 (Rubin and Gelman 1992) diagnostics and Geweke stationarity tests as implemented in the
453 Coda R package. For all the model parameters, upper limits of the Gelman–Rubin statistics
454 were close to 1 (always lower than 1.1), indicating a good mixing of the MCMC chains, and
455 Geweke tests were successfully passed (i.e. Geweke statistics within its asymptotic 95%
456 probability interval). A subset of 12 000 values from the three chains (1 iteration out of 500 for
457 each chain) was used to approximate the posterior distributions. Running 5, 50 and 95
458 percentiles were examined graphically in order to verify they were stable at the end of the
459 MCMC sampling. This was done for all the quantities for which these quantiles are presented
460 in the Fig. 3 to 7 or in the text.

461

462 6. Posterior checking

463 The agreement between the model *a posteriori* and the observed data was assessed by
464 means of the χ^2 discrepancy measure according to the approach proposed by Gelman et al.
465 (1996). This was done separately for the catch data and the observed abundance on the Scorff
466 and the Elorn (see supplementary material C for more details).

467 Cross-validation was also conducted by five successive removals of a fifth of the years with
468 data from the observations of abundance collected on the Elorn (2008-2017) and on the Scorff
469 (1994-2017). The observations removed were compared with their posterior estimates (see
470 supplementary material D).

471

472 7. Sensitivity to the quality and quantity of fisheries independent data on abundance
473 We assessed the sensitivity of the posterior inferences to the availability and quality of
474 fisheries independent data on abundance by contrasting various hypothetical data scenarios.
475 The baseline scenario (S0) corresponds to the data as described in the Data section. In the
476 sequel, the others scenarios are described relative to S0, i.e. everything not mentioned
477 remains as in S0.

478 The scenarios S1x replace the abundance data on the Scorff (1994-2017) and the Elorn
479 (2007-2017) by estimates with random error, assumed normal around the values used in S0.
480 Indeed, considering the adult returns are fully known is oversimplifying. For the Scorff, they
481 are estimated from mark-recapture techniques. The average CV of the estimates are 0.15 for
482 MSW fish and 0.07 for the 1SW ones (see <http://doi.org/10.5281/zenodo.3275148> for details).

483 On the Elorn, the counting device operates almost all year round. Although there is a
484 correction made for the short periods of time when the counting device is off, there is no
485 quantification of the uncertainty associated to this correction procedure (Dartiguelongue
486 2017), in addition to some limited errors due to the ageing based on fish length and date of
487 observation. We used two levels of uncertainty applied equally to all the adult returns data:
488 the first corresponds to the average CV by sea age category observed on the Scorff (S1a)
489 and the second corresponds to its double (S1b).

490 The other scenarios vary the quantity of data available, with either reduction or augmentation.
491 The reduction scenarios S2x correspond to the removal of the observations of abundance
492 collected on the Elorn (S2a), the removal of every other year of observation on the Elorn and
493 on the Scorff (S2b) and the removal of the partial counting data from the Couesnon and the
494 Aulne (S2c). The last three scenarios S3x assume that more data were available, by using a
495 random draw in the posterior distribution under S0 as observed data. Scenario S3a considers
496 that the abundance was fully known for entire period of study on the Scorff and the Elorn.
497 Scenario S3b considers that in addition adult returns were also known on the Penzé and
498 scenario S3c adds the Aven to the observed abundance data (Fig 1).

499 All these scenarios were contrasted by examining the average standard deviation of the
500 posterior estimates they produced for both the abundance in log-scale and the exploitation
501 rates in log-log-scale. The average was calculated over data-poor (i.e. with catch data only)
502 spatio-temporal units as they are those of primary interest. To facilitate the comparison
503 between scenarios, the same subset of rivers was used to compute the average, i.e. the 12
504 rivers that were always data-poor whatever the scenario considered (thus excluding the Scorff,
505 the Elorn, the Aulne, the Couesnon, the Penzé and the Aven; Fig. 1).

506 RESULTS

507

508 Marginal posterior distributions of the model parameters have a lower dispersion and most
509 often modified means compared to those of their prior distributions (Tab. 2; supplementary
510 material E). The updating of the prior distributions is clear and indicates that our posterior
511 inferences are mostly reflecting the information brought by the data.

512 The *a posteriori* checking of standardized residuals of the exploitation rates reveal no clear
513 contradiction with the assumption of their normal *i.i.d.* distribution. The χ^2 discrepancies and
514 associated p values did not reveal any clear inconsistency between the observed catch or
515 abundance (Scorff and Elorn) and the same type of data predicted by the model *a posteriori*
516 (p-values from 0.490 to 0.726; supplementary material C). Cross-validation conducted on the
517 Scorff and Elorn observation of abundance show good agreement between the data removed
518 and their estimates (supplementary material D).

519 The precision of estimation of the abundance of the adult returns and of the exploitation rate
520 (Fig. 3) is little sensitive to the introduction of measurement errors for the Scorff or the Elorn
521 observations of abundance (scenarios S1a and S1b), or to the removal of every other
522 observation from the Scorff and the Elorn (scenario S2b) or to the removal of the partial counts
523 data from the Couesnon and the Aulne (scenario S2c). In contrast, the number of rivers with
524 observed data significantly influences the precision of estimation, especially that of
525 abundance. The removal of the Elorn observed data (scenario S2a) increases the uncertainty
526 of estimates while the addition of new rivers with observed data lead to a reduction (scenarios
527 S3b and S3c). Note that the mere completion of the data series of the Scorff and the Elorn
528 has little effect on the estimation precision (scenario S3a).

529 For the remainder of this paper, only the results obtained under the baseline data scenario S0
530 are presented.

531

532 1. Exploitation

533 During the first fishing period, there is an overall positive effect of river flow on the exploitation
534 rates (posterior probability of $\mu^{\beta_1} > 0$: 100%). At the river scale, the flow effect is significant
535 (i.e. posterior probability of being positive is above 90%) in 12 out of 18 cases, and for the 6
536 remaining rivers, posterior medians of effects are positive (Fig. 4). Fishing effort defined as
537 the length of the fishing season has an overall significant and positive effect on the exploitation
538 rate only during the second fishing period (posterior probability of $\mu^{\beta_2} > 0$: 99%). For this
539 period, the medians of the posterior estimates are positive for all rivers and the effects are
540 significantly positive (i.e. probability of being positive > 95%) for five rivers. There is no
541 general, significant and consistent effect of effort across rivers for the first and third fishing
542 periods. For the first period, there are some contrasted effects among rivers with significantly
543 positive and negative effects for six rivers whereas in the third period, there is only one river
544 with a significant and negative effect of effort, the Couesnon (Fig. 4).

545 The exploitation rate of MSW fish is estimated to be almost three times higher on average
546 (0.15) than that of 1SW fish (0.06) (probability the difference is positive: 92%; Tab. 3). The
547 decision to open a third fishing period increases the 1SW fishing mortality resulting in an
548 average exploitation rate of 0.08, compared to 0.03 when fishing is closed after the second
549 period. The precision of the exploitation rates estimates varies according to the quality of data
550 available. When abundances are observed, CVs of exploitation rate estimates are low and
551 equal to 18% and 16% on average for MSW and 1SW fish respectively. In contrast, the highest
552 average CVs are for spatio-temporal units where abundances are not observed (MSW: 45%;
553 1SW: 63%). Intermediate precision is obtained when abundances are partially observed (Tab.
554 3).

555 Times series of exploitation rates estimates by sea age category may exhibit contrasted
556 patterns through time according to the river. For the majority of the rivers it varies around the
557 mean without clear trend, as shown for the Penzé (Fig. 5.d and supplementary material F). In
558 contrast, the MSW exploitation rates of the Elorn (Fig. 5.a) and the Aulne (Fig. 5.b) decrease
559 whereas they increase for the Couesnon (Fig. 5.c). For 1SW individuals, two levels of

560 exploitation rates are generally observed depending on the opening vs closure of the third
561 fishing period. This is clearly visible for the Penzé (Fig. 5.h.) and the Couesnon (Fig. 5.g.). For
562 the Couesnon, exploitation rates increased dramatically in the last three years to a maximum
563 of 0.43 in 2015. The Aulne exhibits a very singular pattern with a strong rise of the 1SW
564 exploitation rate leading to a peak in 1996 followed by a decrease back to a level just above
565 that observed at the beginning of the time series (Fig. 5.f.).

566

567 2. Abundance of adult returns

568 The $\alpha 1^d$ posterior mean (-1.23; Tab. 2) corresponds to a mean density of 0.3 adult per 100
569 m² of productive area. The posterior distributions of the year effects show strong yearly
570 variations in the abundance of adults at the regional scale without any clear temporal trend
571 (Fig. 6.a). The lowest estimated abundance overall is in 2010 (median year effect = -0.62 in
572 the log scale): it corresponds to an average yearly density of adults reduced by half relative to
573 the overall mean. Conversely, the highest estimated abundance was in 1996 corresponding
574 to a yearly mean density 1.5 times higher than the overall mean. Most of the posterior medians
575 of the river effects are positive and less than 1 except for four small rivers, the Leff, the Jaudy,
576 the Yar and the Queffleuth, where they are negative (Fig. 6.b).

577 Associated with the precision of the exploitation rates, the precision of the abundance
578 estimates is dependent on the quality of the data available (Tab. 3). The CVs are null when
579 abundance is observed. The average CVs are almost 2 times lower when there are partial
580 observations of abundance than when there are no fishery-independent observations. In the
581 most common case of no fishery-independent data, the uncertainties of the annual abundance
582 estimate remain relatively high.

583 This lack of precision does not preclude the ability of improved understanding of temporal
584 patterns of variations in abundance. In the time series of abundance by sea age category of
585 the Elorn, the Aulne, the Couesnon and the Penzé presented for the sake of illustration (Fig.

586 7), posterior medians vary by a factor of 9 for MSW and of 7 for 1SW abundances. Good and
587 bad years are then clearly distinguished, as for instance the peak of abundance for the Aulne
588 in the mid-nineties (Fig. 7.b and Fig. 7.f). For the Couesnon, there is also a tendency of higher
589 adult abundance in recent years, especially for 1SW fish (Fig. 7.c and Fig. 7.g). These are
590 notable exceptions to the general absence of clear temporal patterns or trends for the other
591 rivers studied. (Fig. 7.d and Fig. 7.h; supplementary material G).

592

Draft

593 DISCUSSION

594

595 The ultimate goal of our work was to develop a statistical modelling approach to estimate
596 abundance time series by taking the fullest advantage of the diverse assemblage of data at
597 hand, namely in-river angling catch, total or partial counts of adult returns, environmental
598 covariates (i.e. river size and flows) and fishing effort. To do so, we drawn from the general
599 HBM framework proposed by Brun et al. (2011) to derive homogenous series of population(s)
600 abundance from multiple DCPs. We first considered fishing as a DCP that applies to the full
601 set of spatio-temporal units. We designed a model describing the process generating catch
602 from the underlying abundance. Its formulation is the same whatever the spatio-temporal unit
603 considered, irrespective of the availability of fisheries independent information on the
604 abundance of adult returns. Partial observations of abundance are additional DCPs, explicitly
605 modelled using two different techniques, i.e. binomial draw or data censoring, to account for
606 the local specificities of the counting facilities. But unlike Brun et al. (2011), we also considered
607 that abundance was known for a sub-set of the spatio-temporal units of interest. Finally, river
608 size, flows and effort measures were used as covariates conditioning abundance or
609 exploitation rate.

610 The joint treatment of our heterogeneous assemblage of data in a single HBM framework
611 allowed the transfer of information from data-rich to data-poor spatio-temporal units when
612 proceeding to the estimation of homogeneous time series of abundance for the full set of rivers
613 and years, while accounting for their associated uncertainty. As it is often the case, the data-
614 rich units were of limited spatio-temporal scope. Abundance was known, in addition to catch
615 and covariate data, only for the Scorff for most years of the time series and for the Elorn in
616 more recent years. This is insufficient for providing an overall view of the variations and
617 patterns of evolution of abundance for the full set of rivers and years. The data-poor units, for
618 which only catch and covariate data are available, make the bulk of the set of spatio-temporal
619 units of interest. Although these data are informative to some extent about abundance, they
620 are not sufficient for deriving meaningful estimates of abundance. An intermediate situation

621 occurs some years on the Aulne and the Couesnon when adult returns were partially counted.
622 When combined with the catch data by means of a consistent HBM framework that jointly
623 treats the full set of spatio-temporal units, the fisheries independent data on abundance
624 become more valuable. Indeed, they provide an opportunity to scale the catch to the
625 abundance and to fit the fishing process model. When proceeding to the statistical inference,
626 the information brought by the fisheries independent observations of abundance is conveyed
627 from the data rich units to the data-poor ones by the parameters of the catching process model
628 which are shared by all the spatio-temporal units. The strength of the data available
629 determines the uncertainty of the abundance estimates, as shown (i) when comparing the
630 units for which abundance is partially observed with the data-poor ones (Tab. 3) or (ii) by the
631 sensitivity of the estimation precision to the quantity of fully observed abundance data (Fig.
632 3). The quantity of abundance observations and the number of rivers over which they are
633 distributed, are also key for the accuracy of the estimation of the mean parameters governing
634 the hierarchical modelling of both the exploitation rate and the abundance, which in turn
635 influence more directly the inferences about the data-poor units than about the data-rich ones.
636 Ultimately, the more information is available, the less uncertain and the more accurate the
637 inferences are.

638 The quality of the observation data and their associated uncertainty, at least in our case study
639 and within the domain of situations tested in the present paper (i.e. up to a doubling of the
640 standard deviation of measurement errors observed on the Scorff), has a limited effect on the
641 precision of the estimation of abundance or exploitation rate. Hence, the simplification of
642 ignoring the uncertainty of the rather precise estimates of adult returns of the Scorff and the
643 Elorn appears justified. When the uncertainty of the estimates obtained for data-poor units is
644 high relative to that of the abundance observations, the complexification of the modelling
645 required for the explicit integration of the observation errors seems unwarranted.

646 In this paper, we present essentially one model formulation. Given the ultimate objective of
647 our work (i.e. the estimation of salmon abundance time series by taking the fullest advantage
648 of the diverse assemblage of data at hand including fisheries catch) and the illustrative

649 purpose of our case study, the testing of alternative hypotheses by means of alternative model
650 formulation was not of primary interest. Other formulations have been tried through the
651 process of elaborating the model version that is ultimately presented. Here as well we followed
652 Brun et al (2011) and adopted their step by step approach of increasing model complexity
653 guided by successive posterior model checking at each step. This approach was preferred to
654 multimodel inferences based on the averaging over various models according to some
655 weighting criterion. Although conceptually attractive, as it allows to incorporate model
656 uncertainty, multimodel inferences are practically difficult given the complexity of our model
657 and the associated computational burden, not to mention the choice of the weighing criterion
658 which is also a matter of debate (Gelman and Rubin 1995; Tenan et al. 2014; Ver Hoef and
659 Boveng 2015).

660 As it stands, our model does not acknowledge any sequential dependence (i.e.
661 autocorrelation) over time and/or space (i.e. between neighbouring rivers) in the abundance
662 or the exploitation rates of adult salmon. Explicit spatio-temporal modelling is certainly an
663 avenue for further work because spatio-temporal autocorrelation is widespread in ecological
664 processes and fisheries. It would increase the complexity of a model already quite complex
665 though. Caution is required to ensure the data needed to allow the posterior identification of
666 spatio-temporal autocorrelation, and in the end the provision of meaningful estimates of
667 abundance, are available. In our case study, this remains dubious as even with the model
668 currently used, the estimates of the quantities of ultimate interest, i.e. the abundances and to
669 a lesser degree the exploitation rates, are still fairly imprecise with the data at hand.

670 The relevance of our approach and the associated model is reinforced by the interest of the
671 results we obtained for population and fisheries management advice and their agreement with
672 additional knowledge and expertise not formally included in the model or the data. Without
673 any *a priori* assumptions introduced in our model, MSW exploitation rates are estimated to be
674 three times higher on average than 1SW exploitation rates. Such size-selective exploitation
675 toward larger individuals is common in both aquatic and terrestrial habitats (Fenberg and Roy
676 2008). It has been observed in other Atlantic salmon populations of Spain (Consuegra et al.

677 2005; Saura et al. 2010), UK (Gough et al. 1992; Quinn et al. 2006; Thorley et al. 2007) and
678 Finland (Borgström et al. 2010). Thorley et al. (2007) proposed three explanations for this
679 pattern: a longer upstream migration of MSW individuals, a possible higher catchability of
680 MSW individuals due to higher river flow and lower abundances (See Thorley et al. 2007 for
681 more details). In addition, the timing of the fishing season can contribute to size-selective
682 exploitation (Saura et al. 2010; Harvey et al. 2017), as for example being a consequence of a
683 longer MSW fishing period. Although the MSW fishing period used to be longer than 1SW
684 fishing period, in recent years this pattern has been reversed in Brittany. Still the MSW
685 exploitation rates remain higher, hence MSW selective exploitation rates in Brittany must be
686 defined by other factors than the timing of the fishing season. An explanation might reside in
687 the behaviour of anglers, who would preferentially target the larger MSW fish. In Brittany, data
688 on fishing effort allocation over time and space allowing to test this hypothesis are scarce.
689 Salanié et al. (2004) characterized the fishing effort applied on Atlantic salmon populations of
690 Brittany in 2002, a year when the duration of the fishing periods were similar for the two sea
691 age categories. They showed that anglers were selective on the sea age category with almost
692 60% of the fishing trips directed for MSW fish.

693 Overall positive effects of fishing duration and flow indices on exploitation rates were
694 estimated in this study. Such a result was expected based on the available literature (e.g. Gee
695 1980; Davidson et al. 1996; Quinn and Deriso 1999). But for each covariate, its effect was
696 detected for only one of the three fishing periods, namely the first fishing period for flow and
697 the second fishing period for fishing effort. The absence of a significant flow effect during the
698 second and third fishing periods might be a consequence of river flows generally being low
699 with too limited variation to observe an effect on exploitation rate during these periods. It may
700 also be due to the fact that the effect of river flow on salmon migration behaviour remains
701 somewhat elusive (Thorstad et al. 2008; Milner et al. 2012). The absence of a fishing effort
702 effect challenges the relevance of using the duration of fishing period as the fishing effort
703 index. Indeed, we suspect that the fishing period duration does not reflect the actual effort
704 resulting from anglers' activity. This lack of relevance of fishing period duration as an index of

705 fishing effort is reinforced by the apparently inconsistent variations in the intensity and
706 direction of its effect on exploitation rate between rivers (Fig. 4). There may be several reasons
707 for this lack of effect of fishing period duration. First, for a given fishing period duration, the
708 number of fishing trips may vary according to anglers' perception of catch opportunity, the
709 latter depending on both environmental conditions and perceived abundance of fish.
710 Redistribution of effort among rivers by anglers during the fishing season may also contribute
711 to blur its relationship with the exploitation rates. In addition, increased intensity of exploitation
712 may result in a more rapid attainment of the TAC and thus result in a shorter fishing period
713 duration in some instances.

714 Overall abundance of adult returns shows no clear trend over the last 30 years in Brittany (Fig.
715 6.a). This lack of trend applies to the vast majority of the rivers studied. It differs from the
716 general patterns reported elsewhere of a widespread North Atlantic decline in abundance over
717 the last four decades (Chaput 2012; ICES 2019). It may also appear surprising since the rivers
718 in France are at the southern edge of the distribution range of the species (Webb et al. 2007),
719 and as such would be expected to be negatively impacted by global warming (Lassalle and
720 Rochard 2009). But mere niche modelling approaches such as Lassalle and Rochard (2009),
721 designed to answer broad scale (continent wide) and long term (end of century) questions,
722 tells us little about shorter retrospective and localised impacts of ongoing climate change.
723 Moreover, Brittany is located significantly above the historical southern edge of the species
724 distribution area (in Portugal). So far, environmental conditions have likely not become
725 detrimental to Atlantic salmon in Brittany rivers (Piou and Prévost 2013; Bal et al. 2014). When
726 considered more carefully, the reported overall declining trend of abundance of Atlantic
727 salmon occurred mainly from the mid 70's to the beginning of the 90's (Chaput 2012). We
728 likely failed to detect this early decline because our study period starts in 1987. Still, recent
729 work from Olmos et al. (2019) suggests a downward trend in salmon returns for France even
730 over the period considered in our study. Abundance estimates from Olmos et al. (2019) are
731 derived from catch series and assumed exploitation rates (based on expert judgement) of
732 various fisheries, whereas in this study exploitation rates are estimated from multiple sources

733 of data. The apparent discrepancy between Olmos et al. (2019) and our results may also be
734 due to the fact they consider Brittany only. Although it is the region of France holding the
735 majority of the salmon rivers left in the country, the national scale declining pattern might be
736 driven by other regions.

737 The estimates of abundance for the Aulne and the Couesnon are exceptions to the general
738 stationary pattern of abundance. The Aulne has a unique pattern of adult returns in the mid
739 90's that are twice as high as for the rest of the study period. This sudden rise in the
740 abundances is most likely a consequence of massive juvenile stocking in this river in the early
741 90's. The revealing of this temporal pattern was not contingent on the hypotheses made
742 regarding the counting probabilities on this river (see supplementary material B). Although for
743 taking advantage of all the information available, the explicit consideration of local expert
744 knowledge is advisable for tailoring the best possible model to the situation at hand, it was not
745 key in our case study. In the Couesnon, the increasing trend of abundance is associated to
746 sustained efforts to enhance access and migration to spawning and nursery habitats, to
747 improvements in water quality, and possibly to the effects of some stocking as well. Again, the
748 ability of our HBM approach to reveal river specific patterns that make sense, relative to
749 ancillary information not a priori introduced in the modelling, supports its relevance.

750 Beside temporal patterns, river specific effects are also of interest. Most notably, lower
751 abundances, relative to the productive area available, are estimated for the Leff, the Jaudy,
752 the Yar and the Queffleuth (Fig. 6.b). The very low adult returns in the Queffleuth may at least
753 partly be a consequence of the severe impediments to upstream fish passage in its upper
754 estuary. For the three other rivers, there is no obvious explanation and further investigations
755 are needed to disentangle at least three potential causes, namely low juvenile production,
756 dispersion of adults to neighbouring rivers, or underestimation of adult returns due to
757 overestimation of angling exploitation. The last factor cannot be ruled out and is a potential
758 limitation of this modelling approach. Indeed, although the hierarchical structure of our model
759 is key to enable us to estimate the abundance of adult returns from catch data only, it tends
760 to homogenize average exploitation rates among rivers (so called "shrinkage" towards the

761 mean) when little river specific data are available for contrasting exploitation intensity between
762 rivers. This may result in an overestimation of the exploitation rates for rivers with low
763 exploitation intensity, which in turn leads to an underestimation of the abundance. This could
764 apply to the three rivers cited above which have very low reported catches and are bordered
765 by two bigger and potentially more attractive rivers for anglers, the Trieux and the Léguer.
766 Better river specific data on fishing effort or additional fisheries independent data on
767 abundance would certainly help to alleviate this concern.

768 The HBM approach we have proposed to offer a way out of the fisheries scientist dilemma
769 framed in the introduction of this paper. It essentially relies on the joint modelling of catch
770 statistics and fisheries independent data on abundance, potentially including direct
771 observation of the latter. Two key points are the disposal of catch statistics for the full set of
772 spatio-temporal units of interest and a single formulation of the process generating catch from
773 abundance, irrespective of the availability or not of fisheries independent data. The latter can
774 vary in nature (e.g. scientific surveys) as long as they lead to a measure of abundance which
775 is considered as a reference indicator which estimation is deemed relevant over a wider set
776 of spatiotemporal units. For the exploitation model, we proposed a version suited to our case
777 study, but other options may be warranted to adapt to other contexts. To do so, many of the
778 concepts and techniques found in classical fisheries science textbooks (e.g. Hilborn and
779 Walters 1992; Quinn and Deriso 1999) may be taken up. Beyond the details of the modelling
780 required to adapt to a given case study, the modelling guidelines we have put in practice are
781 quite general irrespective of the species considered. But undoubtedly, our HBM approach is
782 of special interest in salmon, be it Pacific or Atlantic.

783 Salmon species are both fragile and most wanted by fishermen, both commercial and
784 recreational. Their conservation is therefore a matter of great concern and the assessment of
785 their populations and fisheries is required. The singularity of salmon species resides, inter alia,
786 in their anadromy and their homing behaviour. From a population and fisheries assessment
787 perspective, anadromy is very advantageous. Any individual in a population may migrate twice
788 (even more for repeat spawners) in its life through a limited section of river or estuary, thus

789 providing great opportunity for direct observation of population abundance by various counting
790 techniques (e.g. trapping, video-recording) or by means of mark-recapture protocols. But at
791 the same time, the homing translates into a challenge as it leads to the structuring of the
792 species into a myriad of populations to be assessed separately. Despite the opportunity for
793 collecting very informative fisheries independent data on abundance, the required facilities
794 can only be deployed over limited numbers of populations, essentially for operational and
795 financial constraints. In the face this ambivalent situation, we propose to tap the fact that
796 salmon species are also fished in their natal rivers or estuaries and these fisheries are most
797 often surveyed. Indeed, fishing records with wide spatio-temporal coverage are available. Our
798 HBM approach has been designed to take the best advantage of catch statistics for
799 broadening the scope of abundance estimation well beyond the populations surveyed
800 according to fisheries independent protocols. Our case study on is an good illustration in this
801 respect.

802 In Atlantic salmon the need to expand the provision of abundance estimates of adults returns
803 stems also from the recommendations of the North Atlantic Salmon Conservation
804 Organization (NASCO) for the management of Atlantic salmon Fisheries (NASCO 2009). By
805 putting priority on conservation, NASCO conditions the exploitation of any salmon population
806 to its assessment relative to so-called conservation limits (CL). This assessment requires to
807 have both estimated abundance and determined a CL. The default approach recommended
808 by NASCO is to express the CL in terms of spawner abundance and to base its determination
809 on a stock-recruitment analysis. In Brittany, the salmon populations management attempts to
810 fulfill NASCO recommendations. CLs have been set to all populations, but the comparison
811 with the abundance of adult returns is only achieved for the Scorff. This type of situation is not
812 exceptional and, because of the general lack of estimates of adult returns at the river scale,
813 the comparison with CLs is conducted on a minority of rivers throughout the area of distribution
814 of the species (ICES 2019). Our proposed approach offers a good opportunity to enhance
815 both the assessment and the management of salmon populations in accordance with NASCO
816 guidelines. In Brittany, it will also contribute to a better definition of CLs. Juvenile recruitment

817 data are collected by electrofishing over the full set of rivers of our case study. Thanks to the
818 adult returns estimates derived from our HBM approach, they have been used in a regional
819 meta-analysis of stock-recruitment relationships which has led to the definition of new CLs.
820 At the international level, the status of Atlantic salmon is assessed at the scale of regional
821 stock complexes (6 in North American and 10 in Europe; Chaput 2012; ICES 2019). This
822 assessment is conducted under the auspices of the International Council for the exploration
823 of the sea (ICES) and is used to provide management advice for distant fisheries (at
824 Greenland and off the Faroes Islands) operating on mixed populations originating from both
825 sides of the Atlantic. Recently, new life-cycle models have been developed (Massiot-Granier
826 et al. 2014; Olmos et al. 2019, 2020). They not only improve over previous assessment
827 approaches but also open the door for a better understanding of the ecology of salmon at sea.
828 These new models assimilate aggregated series (i.e. at the scale of the regional stock
829 complexes) of in-river adult salmon returns. These series are currently produced by the
830 scientific experts of the ICES North Atlantic Salmon Working Group. The methods used are
831 diverse and still lack documentation and standardization. Our HBM approach offers a
832 possibility for improvement on these two aspects as it can be easily used for deriving regionally
833 aggregated estimates of abundance by summing over rivers.
834

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Notation	Definition	Equation	Type
t	Year from 1987 ($t=1$) to 2017 ($t=31$)		
r	River from the Couesnon River ($r=1$) to the Blavet River ($r=18$)		
a	Sea age category: MSW ($a=1$) and 1SW ($a=1$)		
p	Fishing period: MSW fishing period ($p=1$), 1SW fishing period ($p=2$) and extension of the 1SW fishing period ($p=3$)		

Exploitation

$C_{t,r,a}$	Catch of sea age category a made year t in the river r	(1)	Y
$u_{t,r,a}$	Exploitation rate of sea age category a made year t in the river r	(2)	θ
$I_{t,r,a,p}$	Binary indicator specifying which fishing period p must be applied to each sea age category a , in any given year t and river r	(2)	X
$v_{t,r,p}$	Complementary log-log scaled exploitation rate of the fishing period p for year t in river r	(3)	θ
$\mu_{t,r,p}^Y$	Mean of the linear-Normal model set on $v_{t,r,p}$	(3) and (4)	θ
τ_p^V	Precision of the linear-Normal model set on $v_{t,r,p}$	(3) and (19)	Ψ
$\alpha_{r,p}^Y$	Intercept of the linear-Normal model set on $v_{t,r,p}$	(4) and (5)	θ
$\beta 1_{r,p}^Y$	Flow coefficient of the linear-Normal model set on $v_{t,r,p}$	(4) and (6)	θ
$Q_{t,p}$	Flow index of fishing period p and year t	(4)	X
$\beta 2_{r,p}^Y$	Fishing effort coefficient of the linear-Normal model set on $v_{t,r,p}$	(4) and (7)	θ
$E_{t,r,p}$	Fishing effort expressed as the duration of the fishing period p , the year t in the river r	(4)	X
μ_p^α	Mean of $\alpha_{r,p}^Y$ Normal distribution	(5)	Ψ
τ_p^α	Precision of $\alpha_{r,p}^Y$ Normal distribution	(5) and (19)	Ψ
$\mu_p^{\beta 1}$	Mean of $\beta 1_{r,p}^Y$ Normal distribution	(6)	Ψ
$\tau_p^{\beta 1}$	Precision of $\beta 1_{r,p}^Y$ Normal distribution	(6) and (19)	θ
$\mu_p^{\beta 2}$	Mean of $\beta 2_{r,p}^Y$ Normal distribution	(7)	Ψ
$\tau_p^{\beta 2}$	Precision of $\beta 2_{r,p}^Y$ Normal distribution	(7) and (19)	Ψ

Adult returns

$N_{t,r,a}$	Number of adults of sea age category a returning to river r the year t	(8)	Y*
$n_{t,r,a}$	Mean of $N_{t,r,a}$ Poisson distribution	(8) and (14)	θ
$NC_{t,r,a}$	Partial count of adult returns of sea age category a in the Couesnon River from 1996 to 2015 and in the Aulne River from 1999 to 2017 (and the Elorn MSW in 2007)	(9)	Y
$p_{t,r,a}$	Counting probability of adult returns of sea age category a in river r the year t	(9), (10) and (11)	θ
$S_{t,r}$	River size of river r in year t expressed in as 100 m ² of riffles and rapids equivalents	(12)	X
$\delta_{t,r,a}$	Adult return density per unit of river size of sea age category a in river r the year t	(12) and (13)	θ
$d_{t,r}$	Total density of adults (1SW and MSW combined) returning to each river r in year t	(13) and (15)	θ
$q_{t,r,a}$	Proportion of sea age category a in river r the year t	(14)	Θ
μ^q	Mean of $q_{t,r,1}$ logit-Normal distribution	(14)	Ψ
τ^q	Precision of $q_{t,r,1}$ logit-Normal distribution	(14) and (19)	Ψ
$\mu_{t,r}^d$	Mean of the log-Normal linear model set on $d_{t,r}$	(15) and (16)	Θ
τ^d	Precision of the log-Normal linear model set on $d_{t,r}$	(15) and (19)	Ψ
$\alpha 1^d$	Intercept of the log-Normal linear model set on $d_{t,r}$	(16)	Ψ
$\alpha 2_t^d$	Additive random effect of the year for the log-Normal linear model set on $d_{t,r}$	(16) and (17)	Θ
$\alpha 3_r^d$	Additive random effect of the river for the log-Normal linear model set on $d_{t,r}$	(16) and (18)	Θ
$\tau^{\alpha 2}$	Precision of $\alpha 2_t^d$ Normal distribution	(17) and (19)	Ψ
$\tau^{\alpha 3}$	Precision of $\alpha 3_r^d$ Normal distribution	(18) and (19)	Ψ

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Tab. 1 Definitions of the model quantities.

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Type : Ψ : Parameters; θ : Latent variables; X: Covariates; Y: Observable random quantities.

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Parameter	Prior distribution			Marginal posterior distribution	
	distribution	mean	sd	mean	sd
Exploitation rates					
μ_1^{α}	Normal	0	10	-1.96	0.22
μ_2^{α}	Normal	0	10	-4.05	0.30
μ_3^{α}	Normal	0	10	-3.49	0.31
$\mu_1^{\beta 1}$	Normal	0	10	0.41	0.11
$\mu_2^{\beta 1}$	Normal	0	10	0.02	0.18
$\mu_3^{\beta 1}$	Normal	0	10	0.08	0.19
$\mu_1^{\beta 1}$	Normal	0	10	-0.04	0.24
$\mu_2^{\beta 2}$	Normal	0	10	0.70	0.30
$\mu_3^{\beta 2}$	Normal	0	10	-0.12	0.49
Abundances					
μ^{α}	Normal	0	10	1.30	0.07
$\alpha 1^{\alpha}$	Normal	0	10	-1.23	0.22
Precision parameters					
τ_1^{γ}	Gamma	1	3.16	14.50	4.46
τ_2^{γ}	Gamma	1	3.16	1.70	0.26
τ_3^{γ}	Gamma	1	3.16	3.87	1.43
τ_1^{α}	Gamma	1	3.16	5.67	4.36
τ_2^{α}	Gamma	1	3.16	1.41	0.81
τ_3^{α}	Gamma	1	3.16	1.93	1.47
$\tau_1^{\beta 1}$	Gamma	1	3.16	15.91	9.20
$\tau_2^{\beta 1}$	Gamma	1	3.16	8.58	6.81
$\tau_3^{\beta 1}$	Gamma	1	3.16	11	7.99
$\tau_1^{\beta 1}$	Gamma	1	3.16	1.94	1.27
$\tau_2^{\beta 2}$	Gamma	1	3.16	2.46	2.87

$\tau_3^{\beta^2}$	Gamma	1	3.16	0.78	0.83
τ^q	Gamma	1	3.16	9.61	1.63
τ^d	Gamma	1	3.16	4.07	0.60
τ^{α^2}	Gamma	1	3.16	11.61	3.56
τ^{α^3}	Gamma	1	3.16	3.43	2.48

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1028 **Tab. 2** Statistical summaries (mean and standard deviation) of prior and marginal posterior
 1029 distributions of the model parameters (see also supplementary material D)

Draft

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	Mean	CV			
		Abundance observed	Abundance partially observed	Abundance not observed	Combined
Exploitation rates					
MSW ($u_{t,r,1}$)	0.15	18%	31%	45%	43%
1SW ($u_{t,r,2}$)	0.06	16%	38%	63%	58%
Abundances					
MSW ($N_{t,r,1}$)	145	-	36%	55%	50%
1SW ($N_{t,r,2}$)	512	-	32%	52%	48%

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1032 **Tab. 3** Mean and CV of the posterior estimates of exploitation rates and abundances by sea
 1033 age category. Coefficients of variation (CV) of posterior distributions are averaged over the
 1034 full set of years and rivers and separately for three subsets according to the quality of the
 1035 information available on abundance (observed, partially observed and not observed).
 1036 Combined refers to the full set of rivers and years irrespective of their observation status.

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1038 **LIST OF FIGURES**

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1040 **Fig. 1** Rivers of Brittany considered in this study (Base map source: <https://www.data.gouv.fr>;
1041 map projection: RGF93). Rivers are figured in blue. Black lines outline the edges of the
1042 watershed associated to each river. A number from 1 to 18 is allocated to each river following
1043 a north-eastern to south-eastern rotation (1: Couesnon, 2: Trieux, 3: Leff, 4: Jaudy, 5: Léguer,
1044 6: Yar, 7: Douron, 8: Queffleuth, 9: Penzé, 10: Elorn, 11: Mignonne-Camfrou-Faou, 12: Aulne-
1045 Douffine, 13: Goyen, 14: Odet-Jet-Steir, 15: Aven-Ster Goz, 16: Ellé-Isole, 17: Scorff and 18:
1046 Blavet).

1047 **Fig. 2** Simplified Direct Acyclic Graph (DAG) showing the conditioning structure of the model.
1048 Model quantities are represented by circles or ellipses, except covariates which are
1049 represented by rectangles. They are filled with grey if the quantity is fully observed (known),
1050 in white if fully unknown and with stripes if only partly observed. The arrows represent
1051 conditioning and are pointing to the conditioned quantity. Frames represent a repetition of
1052 structure over the spatial (river, r) or temporal (year, t) units, sea age (a) and fishing period
1053 (p). See text for more detailed explanations.

1054 **Fig. 3** Uncertainty of the estimation of exploitation rate and abundance according to various
1055 data scenarios (see text; sub-section Sensitivity to the quality and quantity of fisheries
1056 independent data on abundance in the Materials and methods section). The average of the
1057 standard deviation of the posterior distributions of the exploitation rates (log-log scale) and of
1058 the abundances (log-scale) are calculated always for the same set of 12 rivers that are data-
1059 poor whatever the data scenario considered.

1060 **Fig. 4** Marginal posterior distributions of the covariate effects on the complementary log-log
1061 scaled exploitation rate (Equation 3, 4 et 5). For each fishing period, the hierarchical mean of
1062 the covariate effect is presented before the effect of every river. The median (dot) and the
1063 90% BCI (line) of the posterior distribution are displayed. Black: 0 is not included in the 90%

1064 BCI. Grey: 0 is included in the 90% BCI.

1065 **Fig. 5** Time series of annual posterior distributions of exploitation rates by sea age category
1066 (MSW and 1SW) from 1987 to 2017 for the Elorn (a and e), the Aulne (b and f), the Couesnon
1067 (c and g) and the Penzé (d and h). The median (dot) of coefficients and the 90% BCI (line) of
1068 the posterior distributions are displayed. The shade of grey indicates the quality of information
1069 available for population abundance: black when abundance is observed, light grey when
1070 abundance is not observed and dark grey when abundance is partially observed. For 1SW
1071 exploitation rates, empty dots are used when fishing was extended over a third period in
1072 autumn.

1073 **Fig. 6** Marginal posterior distributions of year (a) and river (b) effects of the adult density (log
1074 scale, equation 16, 17 and 18). The median (dot) of the effects and the 90% BCI (line) of their
1075 distributions are displayed. For river effects, the shade of grey indicates the quality of
1076 information available for population abundance: black when abundance is observed (for at
1077 least part of the study period), light grey when abundance is not observed and dark grey when
1078 abundance is partially observed.

1079 **Fig. 7** Time series of posterior distributions of yearly adult abundance by sea age category
1080 (MSW and 1SW) from 1987 to 2017 for the Elorn (a and e), the Aulne (b and f), the Couesnon
1081 (c and g) and the Penzé (d and h). The median (dot) and the 90% BCI (line) are displayed.
1082 The shade of grey indicates the quality of information available for population abundance:
1083 black when abundance is observed, light grey when abundance is not observed and dark grey
1084 when abundance is partially observed. When abundance is observed only a dot is displayed.

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