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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

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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]

INTRODUCTION

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

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

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

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

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

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

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

Draft

MATERIALS AND METHODS

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

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

1. Study site and fishing regulation

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

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

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

2. Data

a. Catch

Atlantic salmon catches are collated in a database managed by the “*Centre National d’Interprétation des Captures de Salmonidés*” (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 salmon populations over the period from 1987 to 2017. Sea age is interpreted from the analysis of fish scales samples that fishermen must provide for every fish caught when declaring their catch.

b. Covariates of the exploitation rates

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

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

c. Abundance of adult returns from monitored rivers

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

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

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

d. River area

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

3. Model overview

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

4. Model details

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

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

a. Exploitation

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

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

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

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

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

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

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

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

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

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

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 are river specific and are hierarchically modeled assuming normal distributions with means ($\mu_p^\alpha, \mu_p^{\beta 1}, \mu_p^{\beta 2}$) and precisions ($\tau_p^\alpha, \tau_p^{\beta 1}, \tau_p^{\beta 2}$), respectively, specific to a period (5, 6 and 7).

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

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

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

b. Adult returns

The number of adult returns $N_{t,r,a}$ is assumed to be Poisson distributed with a mean parameter $n_{t,r,a}$ defined for each year t , river r , and sea age category a (8). Overdispersed alternatives to 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

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

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

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

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

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

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

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

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

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

5. Prior probability distributions and Bayesian inference

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

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

6. Posterior checking

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

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

7. Sensitivity to the quality and quantity of fisheries independent data on abundance

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

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

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

RESULTS

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

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

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

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

1. Exploitation

During the first fishing period, there is an overall positive effect of river flow on the exploitation rates (posterior probability of $\mu_1^{\beta_1} > 0$: 100%). At the river scale, the flow effect is significant (i.e. posterior probability of being positive is above 90%) in 12 out of 18 cases, and for the 6 remaining rivers, posterior medians of effects are positive (Fig. 4). Fishing effort defined as the length of the fishing season has an overall significant and positive effect on the exploitation rate only during the second fishing period (posterior probability of $\mu_2^{\beta_2} > 0$: 99%). For this period, the medians of the posterior estimates are positive for all rivers and the effects are significantly positive (i.e. probability of being positive > 95%) for five rivers. There is no general, significant and consistent effect of effort across rivers for the first and third fishing periods. For the first period, there are some contrasted effects among rivers with significantly positive and negative effects for six rivers whereas in the third period, there is only one river with a significant and negative effect of effort, the Couesnon (Fig. 4).

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

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

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

2. Abundance of adult returns

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

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

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

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

Draft

DISCUSSION

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Salmon species are both fragile and most wanted by fishermen, both commercial and recreational. Their conservation is therefore a matter of great concern and the assessment of their populations and fisheries is required. The singularity of salmon species resides, inter alia, in their anadromy and their homing behaviour. From a population and fisheries assessment perspective, anadromy is very advantageous. Any individual in a population may migrate twice (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

Tab. 1 Definitions of the model quantities.
Type : Ψ : Parameters; θ : Latent variables; X: Covariates; Y: Observable random quantities.

Parameter	Prior distribution			Marginal posterior distribution	
	distribution	mean	sd	mean	sd
Exploitation rates					
μ_1^q	Normal	0	10	-1.96	0.22
μ_2^q	Normal	0	10	-4.05	0.30
μ_3^q	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^q	Normal	0	10	1.30	0.07
$\alpha 1^d$	Normal	0	10	-1.23	0.22
Precision parameters					
τ_1^v	Gamma	1	3.16	14.50	4.46
τ_2^v	Gamma	1	3.16	1.70	0.26
τ_3^v	Gamma	1	3.16	3.87	1.43
τ_1^q	Gamma	1	3.16	5.67	4.36
τ_2^q	Gamma	1	3.16	1.41	0.81
τ_3^q	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)

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	Mean	CV			
		Abundance observed	Abundance partially observed	Abundance not observed	Combined
<hr/>					
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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LIST OF FIGURES

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

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

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

Fig. 4 Marginal posterior distributions of the covariate effects on the complementary log-log scaled exploitation rate (Equation 3, 4 et 5). For each fishing period, the hierarchical mean of the covariate effect is presented before the effect of every river. The median (dot) and the 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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