



RESEARCH ARTICLE

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Key Points:

- We developed a simple, parsimonious outflux-influx model linking the number of salmon emigrating and returning to the same stream
- The model quantitatively accounts for the influence of the interannual variability of flow regime on the hydrological connectivity
- Results are compared against a detailed long-term hydroecological data set that includes annual fluxes of salmon and daily discharges

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A probabilistic approach to quantifying hydrologic thresholds regulating migration of adult Atlantic salmon into spawning streams

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Abstract Atlantic salmon is an economically and ecologically important fish species, whose survival is dependent on successful spawning in headwater rivers. Streamflow dynamics often have a strong control on spawning because fish require sufficiently high discharges to move upriver and enter spawning streams. However, these streamflow effects are modulated by biological factors such as the number and the timing of returning fish in relation to the annual spawning window in the fall/winter. In this paper, we develop and apply a novel probabilistic approach to quantify these interactions using a parsimonious outflux-influx model linking the number of female salmon emigrating (i.e., outflux) and returning (i.e., influx) to a spawning stream in Scotland. The model explicitly accounts for the interannual variability of the hydrologic regime and the hydrological connectivity of spawning streams to main rivers. Model results are evaluated against a detailed long-term (40 years) hydroecological data set that includes annual fluxes of salmon, allowing us to explicitly assess the role of discharge variability. The satisfactory model results show quantitatively that hydrologic variability contributes to the observed dynamics of salmon returns, with a good correlation between the positive (negative) peaks in the immigration data set and the exceedance (nonexceedance) probability of a threshold flow (0.3 m³/s). Importantly, model performance deteriorates when the interannual variability of flow regime is disregarded. The analysis suggests that flow thresholds and hydrological connectivity for spawning return represent a quantifiable and predictable feature of salmon rivers, which may be helpful in decision making where flow regimes are altered by water abstractions.

1. Introduction

Atlantic salmon (*Salmo salar*) is an economically and ecologically important fish species in North West Europe and North East North America [MacCrimmon and Gots, 1979; Mills, 1991; Maitland and Campbell, 1992]. Juvenile Atlantic salmon typically rear for 1–4 years in freshwater before migrating to sea where they grow for 1–3 years before returning as adults mostly to the stream system where they were born [Youngson and Hay, 1996; Klemetsen et al., 2003; Tetzlaff et al., 2005a; Bacon et al., 2005]. Spawning is a critical life stage to the recruitment and the maintenance of salmon populations. It usually occurs during autumn in headwater streams. Access to these streams may depend on flow exceeding some minimum thresholds [Tetzlaff et al., 2008; Cunjak et al., 2013]. Salmon usually remain in the main stem of the river network anticipating an increase in discharge that triggers the final upstream movement to the actual spawning site [Jonsson et al., 1990, 2007; Mitchell and Cunjak, 2007; Gibbins et al., 2008; Jonsson and Jonsson, 2009]. These minimum discharge requirements are usually unknown and difficult to quantify, yet they represent important components of flow regimes that need to be maintained to sustain salmon population. Since salmon rivers are subject to increasing abstraction and regulation for hydropower or water supply, identifying these thresholds is important to inform suitable management strategies [Gilvear et al., 2002].

General relationships between fish entry into spawning tributaries and flow variability have been shown by direct trapping of returning fish and tracking of radio-tagged adult salmon [Webb and Hawkins, 1989; Tetzlaff et al., 2008]. In years when flows are low, the size of the returning spawning population may be limited as access to suitable habitat may be restricted or even prevented [Moir et al., 1998; Gibbins et al., 2008]. Headwater areas can often be reached only under relatively high flows [Baxter, 1961; Vadas, 2000; Cunjak et al., 2013], and progressively higher discharges are needed for increasing fish sizes and more upstream

sites which are steep with high roughness [Moir *et al.*, 2004]. Large fish homing to small streams during periods of low flows may find it physically impossible to reach their destination when minimum depth requirement is not fulfilled [Youngson and Hay, 1996; Tetzlaff *et al.*, 2005b] or may be particularly vulnerable to predation in shallow water [Jonsson *et al.*, 2007]. The ascent of large salmonids at low flows in small streams is therefore often delayed compared to that of smaller ones [Jonsson *et al.*, 1990; Jensen and Aass, 1995; Jonsson *et al.*, 2007; Mitchell and Cunjak, 2007].

Although flow-related in-stream processes may act as an important control on salmon entry to spawning streams, its effects will be modulated by other factors. Density-dependent controls have been identified whereby the larger number of returning spawning fish will increase competition for spawning sites and add dispersive pressures on habitat utilization. Thus, simple flow effects can be confounded by the number of returning adults, which in turn depends on the number of out-migrating juveniles in the preceding years and their survival rates in the ocean. Marine mortality is often high (>95%) as a result of predation, commercial fishing, and variability of ocean food supplies. Moreover, the timing of the flow variability in the spawning migration can also have an important effect on discharge thresholds, with increasing the probability of fish trying to enter spawning tributaries on lower flows when ovulation becomes closer. Fish are more likely to cease waiting for higher flows as the autumn advances and spawning time approaches since they need to spawn promptly after ovulation, which in itself is temperature dependent and increasingly likely. However, it is also important to note that some studies have shown that in larger rivers with more stable flow regimes, discharge may have limited effects on the upstream migration of adult salmon, so effects may be most marked in headwaters [Thorstad and Heggberget, 1998; Lilja and Romakkaniemi, 2003; Thorstad *et al.*, 2003; Karppinen *et al.*, 2004].

Given these complexities, identifying the strength of flow influences on stream entry for spawning salmon remains an important fundamental and applied research question. The overall aim of this work is to use a novel probabilistic approach to quantifying the importance of the relationship between flows and the return of adult salmon to spawning streams whilst assessing the effect of associated biological factors. The specific objectives were to (1) develop a simple outflux-influx model linking the number of salmon emigrating and returning to the same stream, and explicitly accounting for the interannual variability of the hydrologic regime and (2) calibrate the model results against a detailed long-term hydroecological data set for an Atlantic salmon spawning stream in Scotland which gives robustness to the findings of this study. We also discuss the utility of the approach in other salmon streams and the potential for informing decision making.

2. Study Area and Data

The Scottish Highlands (UK) contain some of the least disturbed rivers in Europe and many form important spawning sites for Atlantic salmon [Gilvear *et al.*, 2002]. Among those is the River Dee, flowing in north-east Scotland from the Cairngorms to the North Sea at Aberdeen (2300 km²).

The Dee is the largest river in the UK that is not subject to the influence of river regulation by reservoirs and sustains an economically important salmon fishery. The Dee is particularly well known for its spring salmon—these are adult fish which return to freshwater habitat early in the year, allowing the fishing season to start early (in February). Genetic studies have shown that these fish mostly spawn in the high altitude headwater tributaries of the Dee [Youngson and Hay, 1996].

The Girnock Burn is one such relatively natural 9.5 km long tributary of the River Dee, draining a catchment of 30.3 km² with altitudes ranging between 230 and 862 m (Figure 1a) [Tetzlaff *et al.*, 2005a]. Various glacial and fluvio-glacial deposits cover the bedrock, which is composed of granite in the upper part of the catchment and dominated by schists and other metamorphic rocks in the lower parts [Moir *et al.*, 1998; Gibbins *et al.*, 2002; Soulsby *et al.*, 2005]. Land use is dominated by heather (*Calluna vulgaris*) moorland used for deer stalking.

The hydrology of the Girnock has been extensively studied. Daily discharge data were measured from 1972 to 2011 at the gauging station of Littlemill (grey circle in Figure 1a), which is located about 1 km upstream of the confluence between the Girnock and the Dee. Figure 1b shows the frequency distribution of streamflows recorded at Littlemill. Mean annual discharge is 0.55 m³/s, but flows can be smaller than 0.1 m³/s in June and August or larger than 50 m³/s during floods (usually in late autumn or early spring), implying a

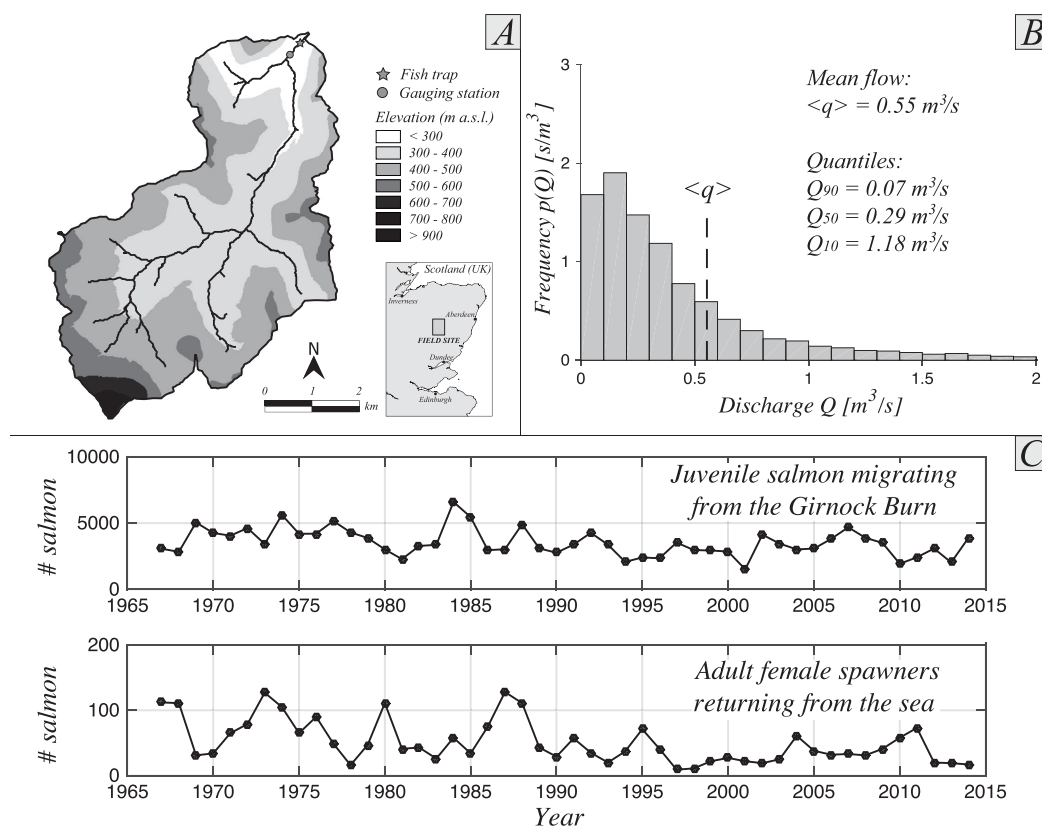


Figure 1. View of the (top) (a) Girnock Burn catchment with the location of the discharge gauging station and the fish trap and (b) probability density function of streamflows observed at the gauging station with mean flows and quantiles given; (c) annual number of (top) smolt and parr emigrating downstream of the juvenile fish trap in the Girnock and (bottom) adult females returning for spawning.

strong intraannual variability of streamflows [Moir *et al.*, 1998; Malcolm *et al.*, 2003]. Moreover, pronounced interannual flow variability is a distinctive feature of streamflow dynamics in the Girnock Burn [Moir *et al.*, 1998; Soulsby *et al.*, 2005].

Salmon population dynamics in the Girnock Burn have been monitored for a long period. The most relevant studies and data acquisition include geomorphic and hydrologic characterization of spawning habitats [Moir *et al.*, 2002], spawning observations within the river network [Moir *et al.*, 2004], and hydraulic modeling of spawning sites [Moir *et al.*, 2005].

In the mid-1960s, two fish traps were built by Marine Scotland Science Freshwater Laboratory (MSS-FL) staff a few hundred meters downstream of the discharge gauging station at Littlemill. One trap is set to catch juvenile salmon emigrating out of the Girnock during their journey to the sea (smolts in spring and parr in autumn). Trapped juveniles are counted, measured and their scales are taken for age determination. Juveniles are released in the stream downstream of the trap. Another trap is located just downstream of the juvenile trap to monitor the number of adult salmon returning from the ocean to spawn in the Girnock in autumn. The trap is temporary and is installed in the river only during the spawning season when adult salmon migrate from the River Dee into the Girnock. Adult female spawners and adult males undergo the same analysis as smolts and are released upstream of the traps.

The fish traps have continuously monitored emigration (smolt and parr) and immigration (adult female spawners) fluxes between the Girnock Burn and the River Dee since 1967 [Glover and Malcolm, 2015a, 2015b]. The emigrant database is subdivided into smolts and parr depending on the season when emigration takes place. Here we consider smolt and parr together, and the annual number of emigrants is the sum of all juveniles exiting the Girnock during spring and autumn of the same year. Comparative analyses were carried out which alternatively added each year autumn migrants to the previous and following cohort of smolts, with no significant influences on the modeled results. Unfortunately, the parr record exhibits some

missing data during 1980s (1982–1985 and 1988), and this is reflected in gaps in the total number of emigrants. This problem was circumvented by increasing the number of emigrating fish proportionally in these years (5 out of 40) to account for the missing parr data. However, annually emigrating smolt runs during recent decades were on average as twice as large as those for parr. Figure 1c shows the number of juveniles exiting the Girnock (top) and the number of females coming back for spawning (bottom) every year (1 January to 31 December) through the fish trap since 1967. The mean number of emigrating salmon and immigrating females is 3500 and 50 (1967–2014), respectively. In common with a number of other salmon rivers in the United Kingdom and elsewhere, the number of female spawners returning has shown a substantial decline over the past 50 years, with mean annual returning spawners falling from 70 (1967–1984) to 30 (1997–2014). Fish population studies in the Girnock indicate that an average of 30 spawning females are needed to maintain optimum habitat use and sustainable levels of productivity [Youngson and Hay, 1996].

3. Methods

The main goal of this work is to develop a probabilistic model for the estimate of adult female salmon returns for spawning to the Girnock Burn. The model explicitly accounts for the interannual variability of the hydrologic regime at the confluence between the Girnock and the River Dee. Female salmon returns are modeled based on the number of juveniles emigrated in previous years. Females are more important than males in determining subsequent juvenile recruitment because smolt and parr critically depend on the number of eggs deposited by female salmon. This is because each spawning female will produce approximately 5000 eggs which can be fertilized by relatively few adult males or sexually mature resident parr [Youngson and Hay, 1996].

The model incorporates a number of factors relevant to the salmon life cycle derived from previous empirical and/or theoretical studies. The number of emigrants is approximately 2 orders of magnitude higher than the number of immigrating females. Hence, the high mortality rate characterizing the marine life stage needs to be accounted for. Spawner age determination at the fish trap has demonstrated that most salmon return to the Girnock 2 or 3 years after they left it. Observations have also shown that peaks of emigrants are often reflected by peaks of immigrants with a delay of 2 or 3 years (e.g., immigrants from 1986 to 1997 reflect emigrants from 1983 to 1994 implying a delay of 3 years). In addition, the access to spawning sites in the Girnock strongly depends on the hydrologic regime in the river reaches connecting the stream with the Dee during the prespawning season, when females select spawning habitats [Moir et al., 1998]. Relatively dry spawning seasons reduce the probability of upstream migration and force females to spawn in the lower reaches of the Girnock. In such situations, uneven spawning distributions may result in suboptimal use of potential habitats and compromise subsequent juvenile production [Tetzlaff et al., 2005b].

Hence, the following factors are identified as the main drivers of the flux of females returning to the Dee: marine survival rates (μ), the delay (number of years) between emigration from and return to the native stream (τ), and the fish passage probability between the Girnock and the Dee (\bar{f}), which is driven by the underlying hydrologic regime. Other types of environmental factors possibly involved in the selection of the spawning site and migratory movements (chemical stresses, water temperature, etc.) have been neglected in order to produce a parsimonious model that could be transferable to other sites and is able to test whether hydrologic dynamics are a first-order control on fish migration.

3.1. Marine Survival Rates, μ

The marine survival rate $\mu(t)$ during year t defines the fraction of adult salmon emigrated during the t -th year that will survive to the year $t + 1$, and thus, will get a chance to return to the Girnock Burn for spawning. The survival rate $\mu(t)$ is therefore a dimensionless number that ranges between 0 (death of all emigrated salmon) and 1 (all emigrated salmon survive). The annual survival rate is known to have decreased with time. For this reason, salmon survival is defined as a linear function of time.

$$\mu(t) = \mu_0 + \frac{\mu_F - \mu_0}{t_F - t_0} \cdot (t - t_0). \tag{1}$$

According to equation (1), two parameters are needed to evaluate $\mu(t)$ during the entire model simulation: μ_0 , the survival rate for the first year of the simulation (t_0); μ_F , the survival rate for the last year of the simulation (t_F).

3.2. Delay Between Emigration and Return, τ

The number of years between emigration and returns (hereafter termed delay, τ) is considered as a discrete random variable with a probability density function (pdf), $p_{d,t}(\tau)$, where the subscript t refers to a specific emigration year. The distribution $p_{d,t}$ is assumed to hold positive values only for $\tau = 2$ and $\tau = 3$, since almost all salmon return 2 or 3 years after emigration. Hence, the model makes the simplifying assumption that salmon can return after 1 year only, or after more than 3 years. Under these assumptions, for any emigration year t , the definition of $p_{d,t}$ relies on one parameter, $\lambda \in [0, 1]$, representing the probability that $\tau = 2$. Accordingly, the probability of having $\tau = 3$ must be $(1 - \lambda)$.

Finally, in order to reduce the number of parameters, the probability distribution of delays between emigrations and returns has been considered to be the same for all years of the simulation (i.e., $p_{d,t}(\tau) = p_d(\tau) \forall t$). In this framework, a single parameter (λ) is needed to model delays between emigrations and immigrations throughout the simulation.

3.3. Fish Passage Probability

A time-variable average passage probability $\bar{f}(t)$ is introduced to quantify the probability for spawners to successfully migrate from the confluence of the Dee and the Girnock Burn to upstream spawning sites between September and November of year t . This component of the model explicitly accounts only for the observed hydrologic conditions immediately prior to spawning (i.e., September–November—as indicated by long-term observations). In this work, the average passage probability $\bar{f}(t)$ is considered as a seasonal measure of the local hydrological connectivity between the Dee and upstream spawning sites in the Girnock.

In the Girnock Burn, salmon spawning migrations have been found to be positively correlated with stream-flow [Moir et al., 1998; Tetzlaff et al., 2007]. In fact, adult females utilize discharges greater than the long-term spawning season median flow ($0.26 \text{ m}^3/\text{s}$) [Moir et al., 2004]. On the contrary, low discharges and associated reduced stages limit fish mobility and increase fish predation during immigration [Tetzlaff et al., 2008]. Hence, low discharges can be seen as a physical barrier impeding upstream migratory movements.

These factors have been incorporated into the model through a fish passage function f quantifying the probability of salmon to entering the Girnock Burn and accessing upstream spawning sites, and which is made dependent on the river discharge ($f(Q)$). An exponential fish passage function has been selected that relies upon two parameters (Figure 2).

$$f(Q) = \begin{cases} 0 & \text{if } Q \leq Q^* \\ 1 - \exp\left(-\frac{Q - Q^*}{\sigma}\right) & \text{if } Q > Q^* \end{cases} \quad (2)$$

In equation (2), Q^* represents a flow threshold that allows adult salmon movements while σ embeds the vulnerability of fishes to flow conditions when $Q > Q^*$. Units of Q^* and σ are the same as the unit of the discharge.

According to equation (2), the minimum threshold discharge, Q^* , separates two different situations (Figure 2): when $Q \leq Q^*$, salmon upstream movement is totally impeded by the physical limitation represented by low water stages; whereas if $Q > Q^*$, salmon are allowed to pass through and access the spawning stream.

However, for discharges higher than Q^* the connectivity increases with Q , and such increase depends on fish vulnerability σ . In particular, for $\sigma = 0$ (low vulnerability), $f(Q)$ becomes a step function always equal to 1 for $Q > Q^*$. In such circumstances, the probability of reaching upstream spawning sites is one whenever discharge is greater than the minimum threshold. Larger values of σ (higher vulnerability) imply an increased range of discharges where suboptimal connectivity ($f < 1$) is experienced by salmon. An exponential increase of $f(Q)$ above Q^* was chosen because it implies that a given discharge increment produces higher increases of $f(Q)$ for low streamflows. In fact, the relationship between river discharge and the relevant ecohydraulic variables controlling fish movement and predation (e.g., channel area, water level) is typically nonlinear [Leopold and Maddock, 1953; Ceola et al., 2014].

Note that in equation (2), any detrimental effect of high flows on fish movement is neglected because the exceedance probability of such high flows during an entire prespawning season is very small (e.g., $P[Q \geq 5 \text{ m}^3/\text{s}] \approx 10^{-2}$).

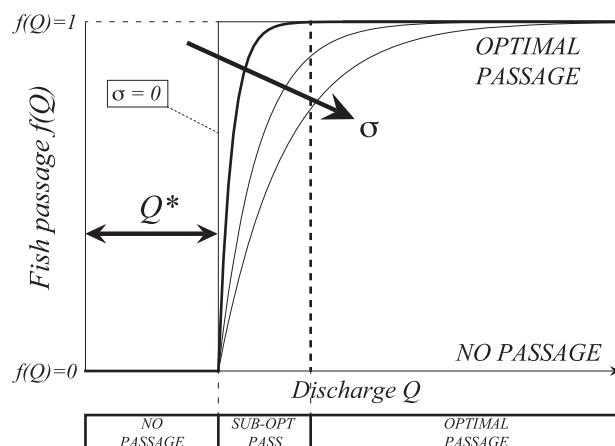


Figure 2. Exponential fish passage function f dependent on the river discharge (Q). The influence of the two parameters, namely the minimum threshold discharge (Q^*) and the fish vulnerability (σ), is also shown. For $\sigma = 0$ (low vulnerability), the movement toward upstream spawning sites is always allowed whenever discharge is greater than the minimum threshold (step fish passage function).

A complete lack of hydrological connectivity ($\bar{f}(t)=0$) occurs if the observed autumn streamflows are always lower than Q^* during year t . During such low flow, the considered river section represents an hydrological discontinuity for upstream migratory fluxes and thus salmon returning in year t have a null probability of entering the Girnock and reaching upstream spawning sites. Conversely, if the autumnal flow frequency distribution in year t only comprises discharges ensuring optimal fish passage conditions ($f(Q)=1 \forall Q$), hydrological connectivity in that year is optimal ($\bar{f}(t)=1$) and fish migration will not be limited by flow conditions. In general, most years, salmon experience hydrologic conditions that lie in between these two end-members.

Interannual variations of seasonal flows driven by climatic drivers such as rainfall and evapotranspiration [Zanardo et al., 2012; Botter et al., 2013; Botter, 2014] usually span a wide range of fish passage conditions $f(Q)$ and this leads to significant interannual variability in the average fish passage probability, \bar{f} .

3.4. Formulation of the Mathematical Model

Given the strong homing instinct of Atlantic salmon, with around 60–70% of returning fish having hatched in the Girnock [Youngson and Hay, 1996], adult females returning to the Girnock Burn in year t (Φ^{us}) can be expressed as a function of the number of juvenile females exiting the catchment during previous years (Φ^{ds}). The latter is estimated from the emigrants leaving the spawning site every year, assuming an even subdivision between males and females exiting the catchment.

$$\Phi^{us}(t) = \sum_{\tau=t_0}^{t-1} \Phi^{ds}(t-\tau) \left(\prod_{k=t-\tau}^{t-1} \mu(k) \right) p_d(\tau) \bar{f}(t), \quad (4)$$

where t_0 is the initial year of the simulation.

Equation (4) explicitly accounts for (i) marine survival rates (μ), (ii) the distribution of the delay between emigrations and immigrations ($p_d(\tau)$), and (iii) the annual fish passage probability (\bar{f}), as defined in sections 3.1–3.3. In particular, the overall survival rate in equation (4) is the product between survival rates of each year k , $\mu(k)$, spent by salmon in the sea. Therefore, the longer the duration of the period that a salmon spends at sea, the higher the mortality rate.

Fish passage probability reductions caused by loss of connectivity between the River Dee and the Girnock tributary, $\bar{f}(t)$, produce a similar effect, but only when female spawners return from the sea. Although salmon have been continuously monitored since 1966, the hydrological connectivity between the River Dee and spawning sites can be evaluated only from 1972, when discharge measurements began. Similarly, simulations must end in 2011 because streamflow data are no longer available afterward.

In this study, the annual number of females returning for spawning is assumed to depend on the seasonal average of the fish passage probability (\bar{f}) between the River Dee and the spawning sites located within the Girnock Burn. This can be defined as the integral over the entire range of experienced flows of the product between the fish passage function ($f(Q)$) introduced above and the streamflow distribution ($p_Q(Q)$) in the prespawning season (September–November).

$$\bar{f}(t) = \int_0^{\infty} f(Q) p_{Q,t}(Q) dQ, \quad (3)$$

where t identifies the t th year of the simulation. Note that in equation (3), the fish passage function $f(Q)$ is kept constant (i.e., parameters Q^* and σ are not dependent on t). Considering that $\int p_Q(Q) dQ = 1$ and $f(Q) \leq 1$, $\bar{f}(t) \in [0, 1]$.

Table 1. Minimum and Maximum Values for the Markov Chain Monte Carlo (MCMC) Calibration of Each Parameter of the Model^a

Parameter	Symbol	Units	Min	Max	Best
Minimum threshold discharge	Q^*	m^3/s	0	1	0.17
Fish vulnerability	σ	m^3/s	0	1	0.01
Marine survival rate (first year)	μ_0	–	0	1	0.37
Marine survival rate (last year)	μ_F	–	0	1	0.23
Probability of 2 years delay	λ	–	0	1	0.24

^aThe parameter set giving the highest performance of the model is also reported in the table (last column).

Note that in equation (4), μ depends on the year when salmon leave the Girnock ($t - \tau$), whereas \bar{f} is related to the year when salmon return for spawning (t). According to the model formulation proposed in sections 3.1–3.3, the model parameter vector (θ) is composed of five elements, namely marine survival rates for the first (μ_0) and last (μ_F) year of the simu-

lation, the probability of having females returning after 2 years in the sea (λ), the minimum flow allowing upstream movement (Q^*), and fish vulnerability to changes in flow (σ).

3.5. Model Calibration

Parameters are estimated through a Markov Chain Monte Carlo (MCMC) calibration procedure using *DREAM_{ZS}* [ter Braak and Vrugt, 2008; Vrugt et al., 2009] against observed annual salmon returns. Minimum and maximum values for model parameters during the MCMC calibration are reported in Table 1. Marine survival rates (μ_0 and μ_F) and the probability of having returns after 2 years in the sea (λ) can vary in their entire state space [0, 1]. Parameters of the average passage probability (Q^* and σ) are limited between 0 and 1 m^3/s (almost twice the long-term mean flow recorded at the gauging station of Littlemill). Model results are compared with the immigration data set (annual number of adult females returning to the Girnock across the fish trap).

Standard optimization techniques are based on the maximization of the Mean Squared Error (MSE) or the Nash-Sutcliffe Error (NSE). However, Gupta et al. [2009] showed that models calibrated maximizing the MSE or the NSE usually underestimate the observed variability of corresponding target outputs. They, thus, proposed an alternative criterion, namely the Kling-Gupta Efficiency ($KGE(\theta)$), which is adopted in this study as the objective function in the MCMC. The modeled mean m and standard deviation s (scaled with the same quantities observed in the data set), as well as the cross correlation r between model results and observations are considered as three independent objectives that need to be maximized. In particular, the following three components of the objective function can be defined: $\beta = m/m_{obs}$, $\alpha = s/s_{obs}$, and $r = Cov(mod, obs)/(s_{mod} s_{obs})$, where $Cov(mod, obs)$ represents the covariance between model results and observations. The optimal simulation is characterized by $\beta = 1$, $\alpha = 1$ and $r = 1$. The best simulation can thus be defined as the one for which the Euclidean distance (ED) from the optimal point (1,1,1) is the shortest. Accordingly, the Kling-Gupta Efficiency $KGE(\theta)$ is defined as

$$KGE(\theta) = 1 - ED(\theta) = 1 - \sqrt{(r(\theta) - 1)^2 + (\alpha(\theta) - 1)^2 + (\beta(\theta) - 1)^2}. \tag{5}$$

The KGE has been widely used in the hydrological literature to identify optimal parameter ranges [Formetta et al., 2014; Dick et al., 2015; Piccolroaz et al., 2015].

4. Results

Figure 3 (top) shows the comparison between observed and modeled annual salmon returns for spawning. The red dots of the simulation indicate the model results corresponding to the best simulation ($KGE_{max} = 0.65$), while the shadowed area represents the ensemble of simulations retained as behavioral performances (i.e., $KGE/KGE_{max} > 0.9$). Model results are generally in good agreement with the observations. The observed dynamic is not well reproduced at the beginning of the simulation (1972–1977) and only occasionally in the following years (1981–1982, 1985).

Figure 3b shows the annual average passage probability (\bar{f}) for the best model run in terms of the KGE . Important findings emerge from the comparison between the observed data and the corresponding seasonal average of the passage probability. In particular, positive peaks in the observed salmon returns (e.g., 1988, 1995, and 2004) are well captured by the model mainly because the average passage probability in those years approaches one (i.e., an optimal hydrological connectivity). Likewise, low values of the average

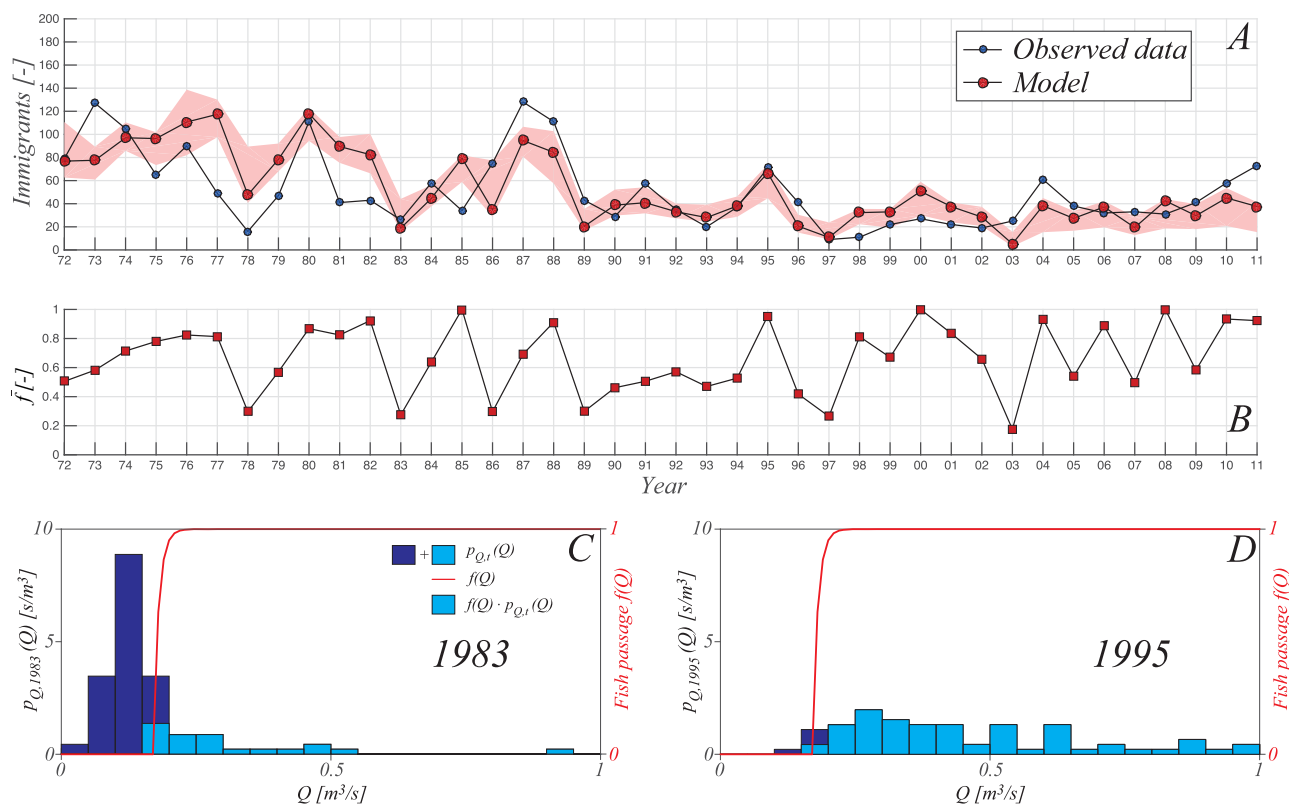


Figure 3. (a) The comparison between observed annual salmon returns (blue dots), model results corresponding to the best simulation (red dots), and the ensemble of simulation featured by acceptable performances (shadowed red area); (b) the annual average passage probability characterizing the best model run. (c, d) The annual average passage probability has been calculated by the model as the area of the product (light blue) between a fish passage function (red curve) and the flow regime annually observed in fall (dark blue). These plots refer to years characterized by relatively dry (1983, Figure 3c) or wet (1995, Figure 3d) hydrologic regimes, which gave $\bar{f}(1983)=0.24$ and $\bar{f}(1995)=0.96$.

passage probability induced by seasonal droughts allow the model to capture negative peaks of the observed data set (e.g., 1978, 1983, and 1997).

Figures 3c and 3d highlight the temporal variability of the annual average passage probability $\bar{f}(t)$. These examples refer to the flows observed between September and November of 1983 (Figure 3c) and 1995 (Figure 3d), that were the driest and wettest falls of the last 50 years, respectively. Red curves represent the shape of the fish passage function $f(Q)$ determined by parameters Q^* and σ giving best performances of the model (Table 1). The product between $p_{Q,t}(Q)$ (dark and light blue bars) and $f(Q)$ determines the light blue histogram which carries information about the occurrence probability of those flows that allow salmon to reach upstream spawning sites. The area underlying this histogram is the average passage probability $\bar{f}(t)$ during year t . The interannual variability of the flow regime produces different values for $\bar{f}(t)$, as shown by Figure 3b. In particular, arid years imply average passage probabilities approaching zero ($\bar{f}(1983)=0.24$) whereas higher flows ensure much higher fish passage probabilities ($\bar{f}(1995)=0.96$).

In the best simulation, salmon vulnerability σ is very low ($0.01 \text{ m}^3/\text{s}$). Therefore, the optimal fish passage function shown by Figures 3c and 3d is basically a step function rapidly increasing from 0 to 1 for $Q^* = 0.17 \text{ m}^3/\text{s}$. We have also tested a simplified version of the model in which fish vulnerability is assumed to be zero ($\sigma = 0$) and $f(Q)$ is a step function. Performances are quite satisfactory also in this case ($KGE_{max} = 0.64$), especially in view of the low number of parameters (see section 5).

Figure 4 shows the stationary posterior pdf of each parameter provided by the MCMC calibration. The vertical dashed line in each plot marks the parameter value giving the best model output (i.e., shown in the upper panel of Figure 3). The posterior pdf of the minimum threshold discharge (Q^*) ranges between 0 and $0.3 \text{ m}^3/\text{s}$, with a mean of $0.07 \text{ m}^3/\text{s}$. The posterior pdf of the fish vulnerability (σ) varies across the full range of values explored. However, higher probabilities characterize low vulnerabilities ($\sigma < 0.5 \text{ m}^3/\text{s}$). Marine survival rates in the first (μ_0) and last (μ_F) year of the simulation are both described by hump-shaped posterior

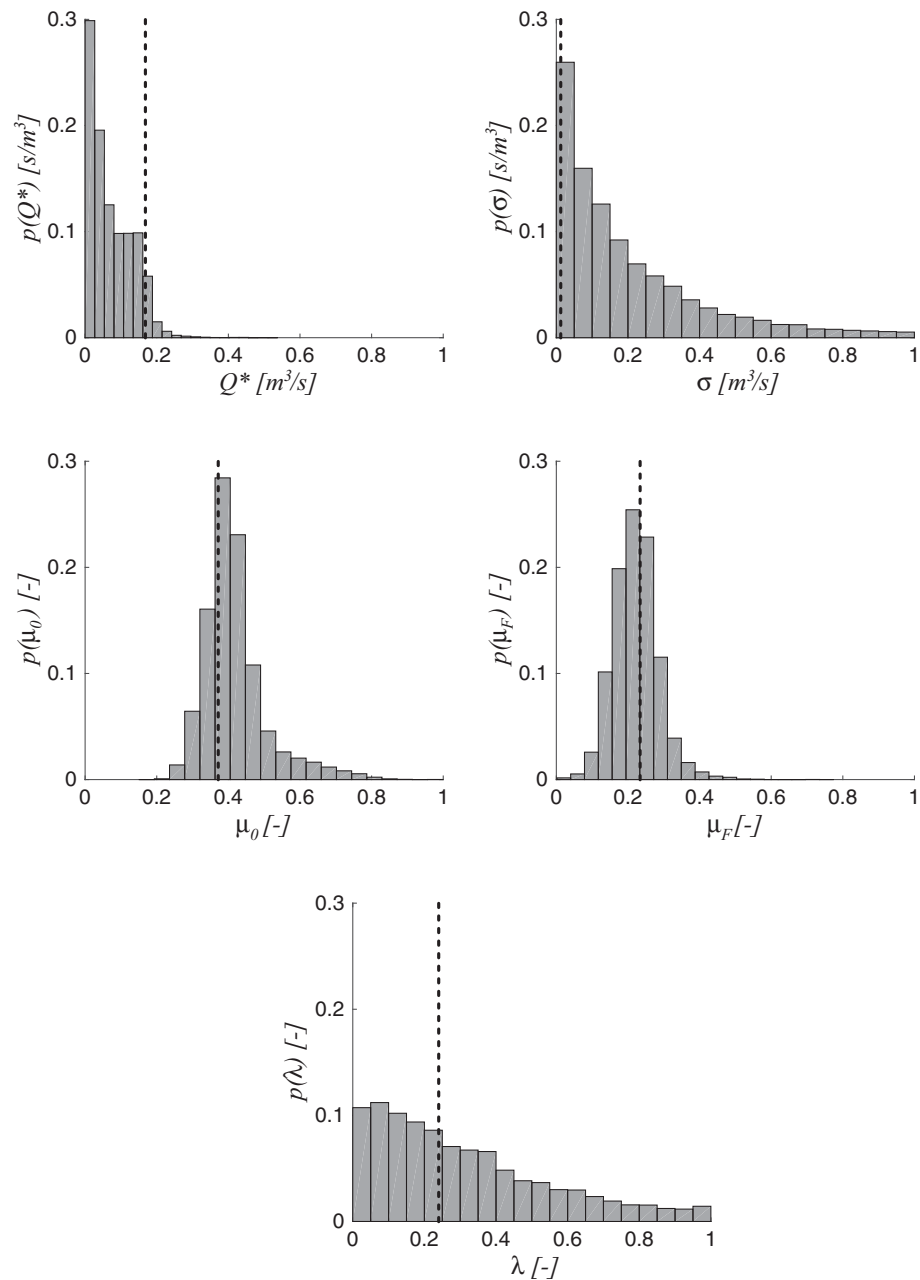


Figure 4. Stationary posterior frequency distribution of each parameter provided by the Markov Chain Monte Carlo calibration. Vertical dashed lines mark the value giving the best model output: $Q^* = 0.17 \text{ m}^3/\text{s}$, $\sigma = 0.01 \text{ m}^3/\text{s}$, $\mu_0 = 0.37$, $\mu_F = 0.23$, and $\lambda = 0.24$.

distributions with μ_0 ranging between 0.2 and 0.6, and μ_F ranging between 0.1 and 0.4. It is worth noting that the optimal survival rates decrease from 0.37 (first year) to 0.23 (last year). This confirms that mortality during the marine period has increased during the last 50 years [Chaput, 2012; Lacroix, 2014; Moore et al., 2014]. The posterior distribution of parameter λ is characterized by an enhanced variability. However, observed salmon returns seem to be better represented by low values of λ , which correspond to a preferential delay of 3 years. The value of λ giving best model results is 0.24. The corresponding average delay between emigration and immigration is larger than 2 years.

To better assess the relationship between the interannual variability of the hydrologic regime observed in the Girnock Burn and salmon migratory dynamics, we also compared the results obtained through equation

(4) (hereafter termed variable hydrological connectivity [VHC] model) and a modified version of the model where the annual fish passage probability is constant and independent on the observed streamflow regime (i.e., $\bar{f}(t)=1, \forall t$) (hereafter termed constant hydrological connectivity [CHC] model). Under the latter assumption, the CHC model parameter vector (θ) is composed of three elements $\theta=(\mu_0, \mu_F, \lambda)$.

Figures 5a and 5b compare the observed number of female spawners returning to the Girnock with the optimal simulations performed using both the VHC and CHC models. Green dots in Figure 5a indicate the best simulation obtained assuming a constant hydrological connectivity. Conversely, red dots in Figure 5b represent the optimal simulation when the annual average fish passage probability is seen as a function of the observed prespawning flow regime (VHC model).

Overall, model performances decline if the influence of the observed streamflow regime is no longer taken into account ($KGE_{VHC} = 0.65$ versus $KGE_{CHC} = 0.61$). In particular, the VHC model outperforms the CHC model in reproducing the mean and the standard deviation of the observed number of returning salmon ($m_{obs} = 51.0$ and $s_{obs} = 31.7$; $m_{VHC} = 52.8$ and $s_{VHC} = 30.9$ versus $m_{CHC} = 53.1$ and $s_{VHC} = 30.0$). In addition, the cross correlation between observed and modeled salmon returns is higher when adopting a variable hydrological connectivity ($r_{VHV} = 0.65$ versus $r_{CHV} = 0.62$).

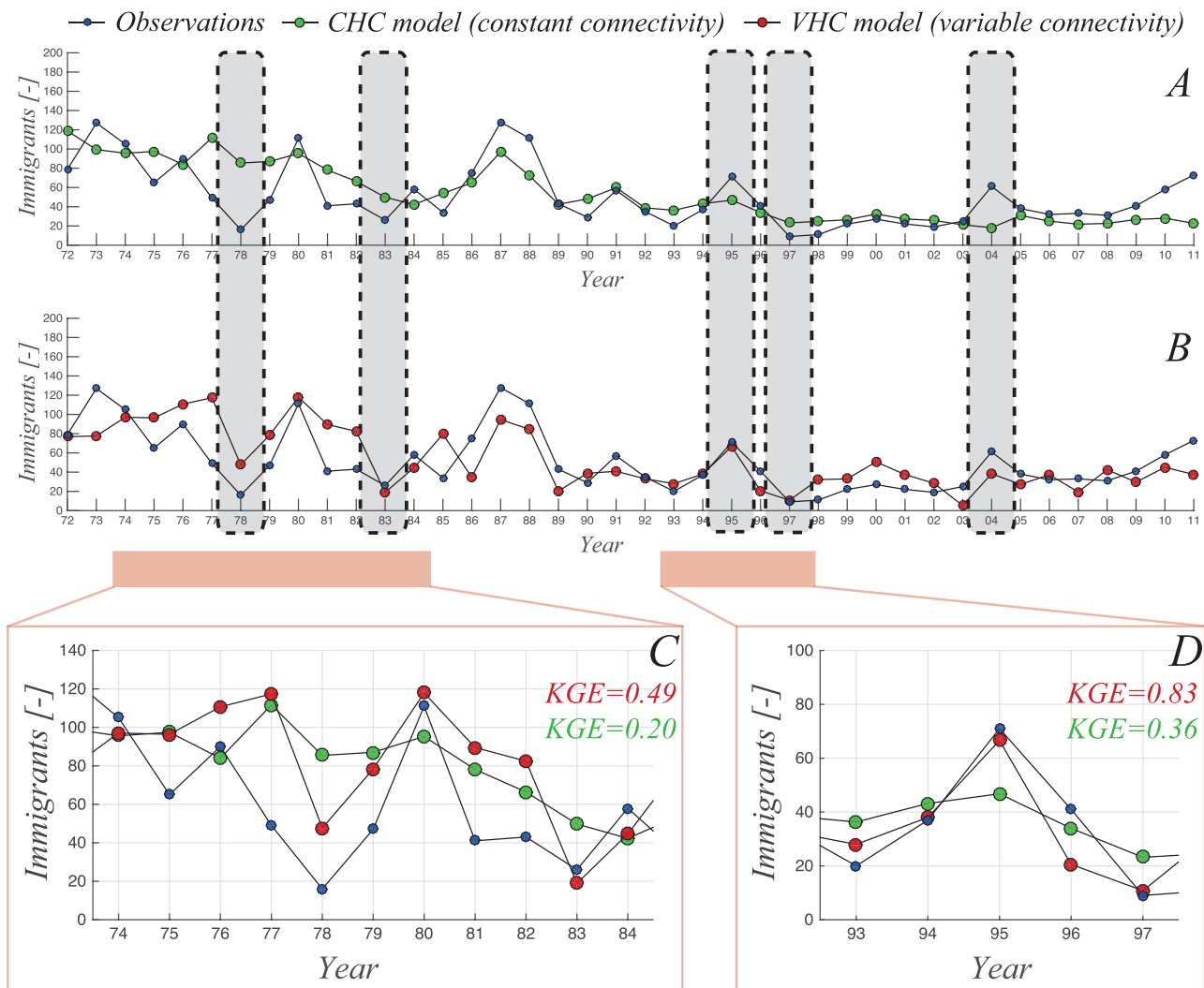


Figure 5. Comparison between the observed number of female spawners returning to the Girnock Burn and the optimal simulation performed using (a) the variable hydrological connectivity (VHC) model and (b) the constant hydrological connectivity (CHC) model. Shaded grey areas highlight years where the VHC model better reproduces positive and negative peaks in the observed data set. (c, d) Emphasize the reduced performances of the CHC model in 1974–1984 and 1993–1997 by showing VHC (red dots) and CHC (green dots) together against the observed data set (blue dots).

In those years highlighted by the shadowed grey areas, a time-variant connectivity allows the *VHC* model to better reproduce positive and negative peaks in the observed data set. This is not the case for the *CHC* model. For instance, the relative absolute error between observed and modeled salmon returns in 1978 is almost 2.5 times larger when the *CHC* is used. Similarly, in 1997 the error decreases from 160% to 20% if the influence of the observed flow regime on salmon migration is taken into account.

The importance of the interannual variability of the hydrological connectivity on salmon migratory dynamics is further emphasized in Figures 5c and 5d. The *CHC* best simulation (green dots) shows a poor agreement with the observed data in 1974–1984 and 1993–1997. When the hydrologic control is removed, the *KGE* of the model falls from 0.49 to 0.20 in 1974–1984 and from 0.83 to 0.36 in 1993–1997. The *CHC* model is strongly penalized by the different variability of the observed and modeled number of salmon returns ($s_{obs} < s_{mod}$) but also because the observed and *CHC*-modeled time series are poorly correlated (e.g., $r = 0.37$ in 1974–1984).

5. Discussion

Our results confirm that the interannual variability of hydrological connectivity helps explain the observed temporal pattern of salmon returns. Lack of hydrological connectivity can reduce the number of immigrating salmon by up to 80% of the potential value under optimal hydrologic condition (Figure 3b).

Interestingly, the value of minimum discharge required to guarantee the hydrological connectivity between the Girnock and the Dee ($Q < 0.30 \text{ m}^3/\text{s}$) suggested by our modeling exercise corresponds well with those found, in a more qualitative analysis, by Tetzlaff *et al.* [2008], who stated that only 30% of fish enter the Girnock on flows lower than the long-term median discharge during the spawning season ($0.25\text{--}0.30 \text{ m}^3/\text{s}$). Based on the stage-discharge relationship at the Girnock gauging station, this implies that the persistence of water stages lower than 0.28 m may inhibit salmon migration into the stream.

When fish vulnerability (σ) is set to zero, model performances are still satisfactory in the case study we examined. In this case, the minimum flow threshold (Q^*) becomes the only parameter required to define fish passage function ($f(Q)$). Whereas the physical underpinning of stepwise fish passage functions may be questioned, this simplified version of the model can be useful for management applications, where the impact of different minimum environmental flow requirements on hydrological connectivity could be easily assessed.

These findings, however, are case-specific as they depend on local characteristics of the considered river (e.g., bed morphology and flow regime) and calibration of parameters is unavoidable. Hence, the model has limited predictive potential in the absence of hydroecological data sets. Hence, stage and discharge thresholds identified in this work would be expected to be different from those of other rivers. However, this work sets a general and transferable quantitative framework that establishes causal relationship between salmon influx and outflux and helps to disentangle hydrological and ecological controls on fish migratory dynamics.

The specific model development and application carried out in this paper provides a new, objective way of identifying flow thresholds on salmon migration into the Girnock burn and, more importantly, the temporally varying strength of such influences in individual years. This advances our understanding of the observed migratory dynamics at the Girnock, a key monitoring site, and provides a potential tool to advance ecohydrological understanding of flow influences on fish migration in other salmon rivers.

Although the general influence of the hydrological connectivity on fish migratory dynamics has been already documented in the literature [Freeman *et al.*, 2007; Jonsson *et al.*, 2007; Mitchell and Cunjak, 2007; Gibbins *et al.*, 2008; Tetzlaff *et al.*, 2008; Cunjak *et al.*, 2013], quantitative assessment of ecologically relevant flow thresholds remains problematic. From this perspective, our study represents a proof of concept about how availability and variability of flows during the migration season could affect salmon returns for spawning. The modeling exercise also illustrates how the effect of seasonal flow regimes can be summarized by a synthetic index (\bar{f}) that expresses the average probability for fish to move across river networks during a given year/season.

The novelty of this work stems from the development of a simple and parsimonious model based on a probabilistic assessment of the hydrological connectivity to reproduce seasonal fish migratory dynamics.

The framework is quite general in the mathematical formulation and could be extended to include the effect of other environmental factors (e.g., temperature and density-dependent competition) and identify the hydrologic controls on spawning migrations in other rivers where sufficient data are available. Many other countries with rivers hosting Atlantic salmon populations have similar long-term monitoring sites like the Girnock [e.g., Kennedy and Crozier, 2010; Cunjak et al., 2013].

Many regions of the world are experiencing a significant exploitation of riverine water resources for anthropogenic uses [Jackson et al., 2001; Postel and Richter, 2003; Nilsson et al., 2005; Carlisle et al., 2011; Destouni et al., 2013; Lazzaro et al., 2013; Birkel et al., 2014; Lazzaro and Botter, 2015]. While the human exploitation of freshwater is introducing strong alterations of hydrologic conditions at multiple spatial and temporal scales, the ecological and morphological consequences of water abstractions are still poorly understood [Nilsson and Berggren, 2000; Rosenberg et al., 2000]. Hence, we propose that hydrological connectivity within river networks should be included in the planning of restoration and conservation initiatives aimed at preserving and revitalizing ecological services provided by streams and rivers. For instance, simple influx/outflux models of the type presented in this paper (if properly supported by extensive hydroecological data sets from other long-term monitoring sites) could be used to identify hotspots of connectivity [Fullerton et al., 2010; Nunn et al., 2010] for specific target species and to define flow requirements and policy rules that are deemed necessary to achieve target levels of connectivity in relation to critical ecological objectives.

6. Conclusions

This paper uses a detailed, long-term data set on Atlantic salmon migration and extensive numerical simulations with a probabilistic, parsimonious ecohydrological model to address the influence of the interannual variability of the natural flow regime on the migratory dynamics of salmon.

The model is tested in the River Dee catchment (Scottish Highlands, UK), an important spawning and rearing habitat site for Atlantic salmon. Results confirm that interannual variability of hydrologic conditions contribute significantly to the observed variability of salmon returns to the Girnock. Model output and immigration data recorded are indeed in good agreement. Moreover, positive (or negative) peaks in the data set are usually well correlated with the dynamics of the seasonal hydrological connectivity across different years.

Model simulations quantitatively demonstrate that salmon access to upstream spawning sites is limited at discharges lower than $0.3 \text{ m}^3/\text{s}$, consistent with thresholds identified more qualitatively in previous works on the same river [Tetzlaff et al., 2008]. Posterior pdfs of model parameters indicate that mortality in the sea has increased by 22% during last 50 years.

Model performances decline if the connectivity is assumed to be independent of available streamflows. In particular, the removal of the hydrologic control on connectivity strongly limits the model capability at reproducing the interannual variability of the observed number of salmon returning to the Girnock. The correlation between model output and observations is also strongly improved when the connectivity between the Girnock Burn and the River Dee is related to the observed flow regime during the prespawning season.

This work confirms that variations in streamflow regime bear ecologically meaningful and quantifiable impacts on salmon migratory dynamics for spawning.

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References

- Bacon, P. J., W. S. C. Gurney, W. Jones, I. S. McLaren, and A. F. Youngson (2005), Seasonal growth patterns of wild juvenile fish: Partitioning variation among explanatory variables, based on individual growth trajectories of Atlantic salmon (*Salmo salar*) parr, *J. Anim. Ecol.*, *74*, 1–11, doi:10.1111/j.1365-2656.2004.00875.x.
- Baxter, G. (1961), River utilisation and the preservation of migratory fish life, *P. I. Civ. Eng.*, *18*, 225–244.
- Birkel, C., D. Tetzlaff, G. Ali, and C. Soulsby (2014), Assessing the impacts of hydropower regulation on the flow characteristics of a large Atlantic salmon river system, *River Res. Appl.*, *30*, 456–475, doi:10.1002/irra.2656.
- Botter, G. (2014), Flow regime shifts in the Little Piney creek (US), *Adv. Water Resour.*, *71*, 44–54, doi:10.1016/j.advwatres.2014.05.010.
- Botter, G., S. Basso, I. Rodriguez-Iturbe, and A. Rinaldo (2013), Resilience of river flow regimes, *Proc. Natl. Acad. Sci. U. S. A.*, *110*(32), 12,925–12,930, doi:10.1073/pnas.1311920110.
- Carlisle, D. M., D. M. Wolock, and M. R. Meador (2011), Alteration of streamflow magnitudes and potential ecological consequences: A multi-regional assessment, *Frontiers Ecol. Environ.*, *9*, 264–270, doi:10.1890/100053.
- Ceola, S., E. Bertuzzo, G. Singer, T. J. Battin, A. Montanari, and A. Rinaldo (2014), Hydrologic controls on basin-scale distribution of benthic invertebrates, *Water Resour. Res.*, *50*, 2903–2920, doi:10.1002/2013WR015112.

- Chaput, G. (2012), Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality, *ICES J. Mar. Sci.*, *69*, 1538–1548, doi:10.1093/icesjms/fss013.
- Cunjak, R. A., T. Linnansaari, and D. Caissie (2013), The complex interaction of ecology and hydrology in a small catchment: A salmon's perspective, *Hydrol. Processes*, *27*(5), 741–749, doi:10.1002/hyp.9640.
- Destouni, G., F. Jaramillo, and C. Prieto (2013), Hydroclimatic shifts driven by human water use for food and energy production, *Nat. Clim. Change*, *3*, 213–217, doi:10.1038/nclimate1719.
- Dick, J. J., D. Tetzlaff, C. Birkel, and C. Soulsby (2015), Modelling landscape controls on dissolved organic carbon sources and fluxes to streams, *Biogeochemistry*, *122*(2–3), 361–374, doi:10.1007/s10533-014-0046-3.
- Formetta, G., A. Antonello, S. Franceschi, O. David, and R. Rigon (2014), Hydrological modelling with components: A GIS-based open-source framework, *Environ. Modell. Software*, *55*, 190–200, doi:10.1016/j.envsoft.2014.01.019.
- Freeman, M. C., C. M. Pringle, and C. R. Jackson (2007), Hydrologic connectivity and the contribution of stream headwaters to ecological integrity at regional scales, *J. Am. Water Resour. Assoc.*, *43*, 5–14, doi:10.1111/j.1752-1688.2007.00002.
- Fullerton, A. H., K. M. Burnett, E. A. Steel, R. L. Flitcroft, G. R. Pess, B. E. Feist, C. E. Torgersen, D. J. Miller, and B. L. Sanderson (2010), Hydrological connectivity for riverine fish: Measurement challenges and research opportunities, *Freshwater Biol.*, *55*, 2215–2237, doi:10.1111/j.1365-2427.2010.02448.x.
- Gibbins, C. N., H. Moir, J. Webb, and C. Soulsby (2002), Assessing discharge use by spawning Atlantic salmon: A comparison of discharge electivity indices and PHABSIM simulations, *River Res. Appl.*, *18*, 383–395, doi:10.1002/rra.685.
- Gibbins, C. N., J. Shellberg, H. J. Moir, and C. Soulsby (2008), Hydrological influences on adult salmonid migration, spawning, and embryo survival, *Am. Fish. Soc. Symp.*, *65*, 195–223.
- Gilvear, D. J., K. V. Heal, and A. Stephen (2002), Hydrology and the ecological quality of Scottish river ecosystems, *Sci. Total Environ.*, *294*(1–3), 131–159, doi:10.1016/S0048-9697(02)00060-8.
- Glover, R., and I. Malcolm (2015a), *Girnock and Baddoch: Emigrant Numbers by Year of Emigration*, Marine Scotland Science, Pitlochry, U. K., doi:10.7489/1017-1.
- Glover, R., and I. Malcolm (2015b), *Girnock and Baddoch: Adult Returns to the Traps*, Marine Scotland Science, Pitlochry, U. K., doi:10.7489/1588-1.
- Gupta, H. V., H. Kling, K. K. Yilmaz, and G. F. Martinez (2009), Decomposition of the mean squared error and NSE performance criteria: Implications for improving hydrological modelling, *J. Hydrol.*, *377*(1–2), 80–91, doi:10.1016/j.jhydrol.2009.08.003.
- Jackson, R. B., S. R. Carpenter, C. N. Dahm, D. M. McKnight, R. J. Naiman, S. L. Postel, and S. W. Running (2001), Water in a changing world, *Ecol. Appl.*, *11*, 1027–1045, doi:10.1890/1051-0761(2001)011<1027:WIACW>2.0.CO;2.
- Jensen, A. J., and P. Aass (1995), Migration of a fast-growing population of brown trout and water temperature, *Regul. River*, *10*, 217–228.
- Jonsson, B., and N. Jonsson (2009), A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow, *J. Fish Biol.*, *75*(10), 2381–2447, doi:10.1111/j.1095-8649.2009.02380.x.
- Jonsson, N., B. Jonsson, and L. P. Hansen (1990), Partial segregation in the timing of migration of Atlantic salmon of different ages, *Anim. Behav.*, *40*(2), 313–321, doi:10.1016/S0003-3472(05)80926-1.
- Jonsson, B., N. Jonsson, and L. P. Hansen (2007), Factors affecting river entry of adult Atlantic salmon in a small river, *J. Fish Biol.*, *71*(4), 943–956, doi:10.1111/j.1095-8649.2007.01555.x.
- Karppinen, P., J. Erkinaro, E. Niemela, K. Moen, and F. Økland (2004), Return migration of one-sea-winter Atlantic salmon in the River Tana, *J. Fish Biol.*, *64*, 1179–1192, doi:10.1111/j.0022-1112.2004.00380.x.
- Kennedy, G., and W. Crozier (2010), Evidence of changing migratory patterns of wild Atlantic salmon *Salmo salar* smolts in the River Bush, Northern Ireland, and possible associations with climate change, *J. Fish Biol.*, *76*(7), 1786–1805.
- Klemetsen, A., P. A. Amundsen, B. Dempson, B. Jonsson, N. Jonsson, M. O'Connell, and E. Mortensen (2003), Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): A review of their life histories, *Ecol. Freshwater Fish*, *12*, 1–59, doi:10.1034/j.1600-0633.2003.00010.x.
- Lacroix, G. L. (2014), Large pelagic predators could jeopardize the recovery of endangered Atlantic salmon, *Can. J. Fish. Aquat. Sci.*, *71*, 343–350, doi:10.1139/cjfas-2013-0458.
- Lazzaro, G., and G. Botter (2015), Run-of-river power plants in Alpine regions: Whither optimal capacity?, *Water Resour. Res.*, *51*, 5658–5676, doi:10.1002/2014WR016642.
- Lazzaro, G., S. Basso, M. Schirmer, and G. Botter (2013), Water management strategies for run-of-river power plants: Profitability and hydrologic impact between the intake and the outflow, *Water Resour. Res.*, *49*, 8285–8298, doi:10.1002/2013WR014210.
- Leopold, L. B., and T. Maddock (1953), *The Hydraulic Geometry of Stream Channels and Some Physiographic Implications*, U.S. Geol. Surv. Prof. Pap., *252*, 1–57.
- Lilja, J., and A. Romakkaniemi (2003), Early-season river entry of adult Atlantic salmon: Its dependency on environmental factors, *J. Fish Biol.*, *62*, 41–50, doi:10.1111/j.1095-8649.2003.00005.x.
- MacCrimmon, H. R., and B. L. Gots (1979), World distribution of Atlantic salmon, *Salmo salar*, *J. Fish. Res. Board Can.*, *36*(4), 422–457, doi:10.1139/f79-062.
- Maitland, P. S., and R. N. Campbell (1992), *Freshwater Fishes of the British Isles*, Harper Collins, London.
- Malcolm, I. A., A. F. Youngson, and C. Soulsby (2003), Survival of salmonid eggs in a degraded gravel bed stream: The role of groundwater-surface water interactions, *River Res. Appl.*, *19*(4), 303–316, doi:10.1002/rra.706.
- Mills, D. (1991), *Strategies for the Rehabilitation of Atlantic Salmon*, The Atl. Salmon Trust, Pitlochry, U. K.
- Mitchell, S. C., and R. A. Cunjak (2007), Relationship of upstream migrating adult Atlantic salmon (*Salmo salar*) and stream discharge within Catamaran Brook, New Brunswick, *Can. J. Fish Aquat. Sci.*, *64*, 563–573, doi:10.1139/f07-032.
- Moir, H. J., C. Soulsby, and A. F. Youngson (1998), Hydraulic and sedimentary characteristics of habitat utilized by Atlantic salmon for spawning in the Girnock Burn, Scotland, *Fish. Manage. Ecol.*, *5*, 241–254.
- Moir, H. J., C. Soulsby, and A. F. Youngson (2002), Hydraulic and sedimentary controls on the availability and use of Atlantic salmon (*Salmo salar*) spawning habitat in the River Dee system, north-east Scotland, *Geomorphology*, *45*(3–4), 291–308, doi:10.1016/S0169-555X(01)00160-X.
- Moir, H. J., C. N. Gibbins, C. Soulsby, and J. Webb (2004), Linking channel geomorphic characteristics to spatial patterns of spawning activity and discharge use by Atlantic salmon (*Salmo salar* L.), *Geomorphology*, *60*(1–2), 21–35, doi:10.1016/j.geomorph.2003.07.014.
- Moir, H., C. Gibbins, C. Soulsby, and A. F. Youngson (2005), Validation of PHABSIM predictions for simulating salmon spawning habitat, *River Res. Appl.*, *21*, 1–14, doi:10.1002/rra.869.
- Moore, J.-S., V. Bourret, M. Dionne, I. Bradbury, P. O'Reilly, M. Kent, G. Chaput, and L. Bernatchez (2014), Conservation genomics of anadromous Atlantic salmon across its North American range: Outlier loci identify the same patterns of population structure as neutral loci, *Mol. Ecol.*, *23*, 5680–5697, doi:10.1111/mec.12972.

- Nilsson, C., and K. Berggren (2000), Alterations of riparian ecosystems caused by river regulation: Dam operations have caused global-scale ecological changes in riparian ecosystems. How to protect river environments and human needs of rivers remains one of the most important questions of our time, *BioScience*, *50*(9), 783–792, doi:10.1641/0006-3568(2000)050<0783:AORECB>2.0.CO;2.
- Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga (2005), Fragmentation and flow regulation of the world's large river systems, *Science*, *308*(5720), 405–408, doi:10.1126/science.1107887.
- Nunn, A. D., G. H. Copp, L. Vilizzi, and M. G. Carter (2010), Seasonal and Diel patterns in the migrations of fishes between a river and a flood-plain tributary, *Ecol. Freshwater Fish*, *19*, 153–162, doi:10.1111/j.1600-0633.2009.00399.x.
- Piccolroaz, S., B. Majone, F. Palmieri, G. Cassiani, and A. Bellin (2015), On the use of spatially distributed, time-lapse microgravity surveys to inform hydrological modeling, *Water Resour. Res.*, *51*, 7270–7288, doi:10.1002/2015WR016994.
- Postel, S., and R. D. Richter (2003), *Rivers for Life: Managing Water for People and Nature*, Isl. Press, Washington, D. C.
- Rosenberg, D. M., P. McCully, and C. M. Pringle (2000), Global-scale environmental effects of hydrological alterations: Introduction, *BioScience*, *50*(9), 746–751, doi:10.1641/0006-3568(2000)050<0746:GSEEOH>2.0.CO;2.
- Soulsby, C., I. A. Malcolm, A. F. Youngson, D. Tetzlaff, C. N. Gibbins, and D. N. Hannah (2005), Groundwater-surface water interactions in upland Scottish rivers: Hydrological, hydrochemical and ecological implications, *Scot. J. Geol.*, *41*(1), 39–49, doi:10.1144/sjg41010039.
- ter Braak, C. J. F., and J. A. Vrugt (2008), Differential evolution Markov chain with snooker updater and fewer chains, *Stat. Comput.*, *16*, 239–249, doi:10.1007/s11222-008-9104-9.
- Tetzlaff, D., C. Soulsby, C. N. Gibbins, P. J. Bacon, and A. F. Youngson (2005a), An approach to assessing hydrological influences on feeding opportunities of juvenile Atlantic salmon (*Salmo salar*): A case study of two contrasting years in a small, nursery stream, *Hydrobiologia*, *549*(1), 65–77, doi:10.1007/s10750-005-4166-6.
- Tetzlaff, D., C. Soulsby, C. N. Gibbins, P. J. Bacon, and A. F. Youngson (2005b), An approach to assessing hydrological influences on feeding opportunities of juvenile Atlantic salmon (*Salmo salar*): A case study of two contrasting years in a small, nursery stream, *Hydrobiologia*, *549*(1), 65–77, doi:10.1007/s10750-005-4166-6.
- Tetzlaff, D., C. Soulsby, P. J. Bacon, A. F. Youngson, C. N. Gibbins, and I. A. Malcolm (2007), Connectivity between landscapes and river-scapes—A unifying theme in integrating hydrology and ecology in catchment science?, *Hydrol. Processes*, *21*(10), 1385–1389, doi:10.1002/hyp.6701.
- Tetzlaff, D., C. N. Gibbins, P. J. Bacon, A. F. Youngson, and C. Soulsby (2008), Influence of hydrological regimes on the pre-spawning entry of Atlantic salmon (*Salmo salar* L.) into an upland river, *River Res. Appl.*, *24*(5), 528–542, doi:10.1002/rra.1144.
- Thorstad, E. B., and T. G. Heggberget (1998), Migration of adult Atlantic salmon (*Salmo salar*): The effects of artificial freshets, *Hydrobiologia*, *372*, 339–346.
- Thorstad, E. B., F. Økland, B. O. Johnsen, and T. F. Næsje (2003), Return migration of adult Atlantic salmon, *Salmo salar*, in relation to water diverted through a power station, *Fish. Manage. Ecol.*, *10*, 13–22, doi:10.1046/j.1365-2400.2003.00324.x.
- Vadas, R. L., Jr., (2000), Instream-flow needs for anadromous salmonids and lamprey on the Pacific coast, with special reference to the Pacific south-west, *Environ. Monit. Assess.*, *64*, 331–358.
- Vrugt, J. A., C. J. F. ter Braak, C. G. H. Diks, B. A. Robinson, J. M. Hyman, and D. Higdon (2009), Accelerating Markov Chain Monte Carlo simulation by differential evolution with self-adaptive randomized subspace sampling, *Int. J. Nonlinear Sci. Numer. Simul.*, *10*(3), 273–290, doi:10.1515/IJNSNS.2009.10.3.273.
- Webb, J. H., and A. D. Hawkins (1989), The movement and spawning behaviour of adult salmon in the Girnock Burn, a tributary of the Aberdeenshire Dee, 1986, *Scot. Fish. Res. Rep.*, *40*, 1–41.
- Youngson, A., and D. Hay (1996), *The Lives of Salmon*, Swan Hill Press, Shrewsbury, U. K.
- Zanardo, S., C. J. Harman, P. A. Troch, P. S. C. Rao, and M. Sivapalan (2012), Intra-annual rainfall variability control on interannual variability of catchment water balance: A stochastic analysis, *Water Resour. Res.*, *48*, W00J16, doi:10.1029/2010WR009869.