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Modelling storage-driven connectivity between landscapes and riverscapes: towards a simple framework for long-term ecohydrological assessment

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Abstract:

The importance of conceptualizing the dynamics of storage-driven saturation area connectivity in runoff generation has been central to the development of TOPMODEL and similar low parameterized rainfall–runoff models. In this contribution, we show how we developed a 40-year hydrometric data base to simulate storage–discharge relationships in the Girnock catchment in the Scottish Highlands using a simple conceptual model. The catchment is a unique fisheries reference site where Atlantic salmon populations have been monitored since 1966. The modelling allowed us to track storage dynamics in hillslopes, the riparian zone and groundwater, and explicitly link non-linear changes of streamflows to landscape storage and connectivity dynamics. This provides a fundamental basis for understanding how the landscape and riverscape are hydrologically connected and how this regulates in-stream hydraulic conditions that directly influence salmonids. We use the model to simulate storage and discharge dynamics over the 40-year period of fisheries records. The modelled storage-driven connectivity provides an ecohydological context for understanding the dynamics in stream flow generation which determine habitat hydraulics for different life stages of salmon population. This new, long-term modelling now sets this variability in the riverscape in a more fundamental context of the inter-relationships between storage in the landscape and stream flow generation. This provides a simple, robust framework for future ecohydrological modelling at this site, which is an alternative to more increasingly popular but highly parameterized and uncertain commercial ecohydrological models. It also provides a wider, novel context that is a prerequisite for any model-based scenario assessment of likely impacts resulting from climate or land use change.

KEY WORDS ecohydrology; rainfall–runoff modelling; conceptual model; storage; Atlantic salmon

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INTRODUCTION

The last decade has seen increased consideration of explicit quantification of water storage dynamics as well as water fluxes in both empirical and modelling studies in catchment hydrology (McNamara *et al*., 2011). Of course, it is well established that storage dynamics influence non-linear connectivity between landscape units in catchments and regulate stream flow generation (Tetzlaff *et al*., 2014). Such concepts have been usefully embedded in the original TOPMODEL approach (Beven and Kirkby, 1979) and other well-known conceptual models such as HBV (Seibert and Vis, 2012). These concepts have been advanced in developments such as dynamic TOPMODEL (Beven and Freer, 2001). Traditionally, many modelling studies have focused on capturing the short-term dynamic storage changes that lead to successful simulation of storm events and the non-linearities of how rainfall–runoff transformations change with time (e.g. Troch *et al*., 1994; Cameron *et al*., 2000). Applications of models to long-term data sets are less common, but can provide valuable additional insights into catchment behaviour and function. In particular, they have the potential to characterize and contextualize how storage and connectivity are affected during extreme periods of wetness or drought and what 'memory effects' might occur (Beven, 2001; Nippgen *et al*., 2016). In addition, it has been shown that the 'dynamic storage' changes inferred from water balance considerations to explain the celerity of hydrological responses are inadequate for explaining the travel times of water molecules and tracers, which involve much larger 'total storage' inferred in catchment scale mixing processes (Beven, 2010; Soulsby *et al*., 2011). Thus, there has been a call for models to be able to address these issues if larger storages are important in the context of modelling objectives, such as simulation of water quality or assessing the resilience of catchments to the impacts of climatic and land use change (McDonnell and Beven, 2014).

Long-term evaluation of storage changes and their influence on rainfall–runoff relationships usually requires

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a modelling approach (Nippgen *et al*., 2016). Long-term data of soil moisture and groundwater levels are rarely available even in experimental catchments. Rainfall and streamflow records are usually all that is available for multi-decadal periods. Appropriate hydrological models can simulate stream flow on the basis of distributed storage-driven connectivity dynamics that link the landscape to the response of the stream channel network (Nippgen *et al*., 2015). Such model applications are increasingly incorporated in integrated ecohydrological assessment to understand how catchment-scale environmental change (e.g. climate or land cover change) might affect river flow regimes and in-stream aquatic habitats (e.g. Gore and Mead, 2008). Previously, such habitat assessment was mainly focused on instream hydraulics (Gore and Nestler, 1988), but the dependence of stream flows on catchment hydrological conditions is increasingly recognized, along with the importance of subtle non-linearities and hysteresis in storage–discharge relationships which may affect responses to environmental change (Capell *et al*., 2013). Often the hydrological modelling in such integrated studies involves complex, physically based models that are highly parameterized, such as MIKE SHE (e.g. Loinaz *et al*., 2014). The output from these models is then used as input to other models such as hydraulic models to assess preference/avoidance of aquatic species (Goode *et al*., 2013) or process-based water quality models for simulating water temperature or other parameters (Loinaz *et al*., 2013). Of course, there is danger that there may be error propagation through such a modelling chain that renders the final output highly uncertain (Refsgaard *et al*., 2007). More fundamentally, many such models have the risk that if the catchment hydrology is not appropriately conceptualized, flows can by simulated correctly for the ‘wrong’ reasons (Kirchner, 2006). This may then mean that the output from subsequent modelling steps is somewhat meaningless and potentially makes scenario analysis prone to erroneous interpretation (Kirchner, 2006). Thus, for many purposes it can be advantageous to use simpler conceptual runoff models in such ecohydrological investigations that have identifiable parameters and constrained uncertainty, but still capture the dominant hydrological connections between landscape and riverscape that regulate in-stream flows and habitat hydraulics (Weins, 2002).

For ecohydrological assessments, where freshwater species and populations may have multi-year or multi-decadal variability (e.g. Bacon *et al*., 2005; Cunjak *et al*., 2013), models need to be conditioned on long-term analysis to contextualize the potential ecological effects of both short term and long-term perturbations in the flow regime (e.g. Beecher *et al*., 2010; Jones *et al*., 2012). Modelling over the long-term usually involves data quality issues and the need to assess the degrees of information and disinformation in the data sets (Beven and Westerberg, 2011). This is because over prolonged periods of time (i.e. >10 years) instrumentation location, technology changes, operator competence, faults and breakdowns all have the potential to introduce errors into data sets that may not be identifiable (Levine *et al*., 2014). Thus, data sets need to be checked, and uncertainties and problems addressed or catalogued as a pre-requisite to modelling so that results can be interpreted with appropriate caution. This uncertainty then needs to be communicated to stakeholders if the modelling is to be used to guide land and water management and assess catchment sensitivity to change.

Here, we report on a study that used long-term (~40-year) data sets to model rainfall–runoff relationships in an upland catchment in Scotland. The conceptual model is based on a low parameter approach that captures the dynamics of hillslope–riparian interactions and simulated stream flow based on storage-based connectivity (Birkel *et al*., 2010). Moreover, the model evolution has been tracer-aided, and previous work has shown that the model can successfully simulate discharge as well as geochemical tracers that can differentiate the geographic sources of the dominant runoff processes (Birkel *et al*., 2011a). It has also been conditioned to simulate stable isotopes that can distinguish the temporal contribution of different sources to stream flow generation by constraining the storages involved in tracer mixing and damping (Soulsby *et al*., 2015). Analysis has shown that this is achieved with realistic estimates of storage changes indicated by soil moisture and groundwater dynamics (Birkel *et al*., 2014). The context of this longer term modelling is that the study site, the Girnock Burn, is a fisheries monitoring station (http://www.gov.scot/Topics/marine/Salmon-Trout-Coarse/Freshwater/Monitoring/Traps) where population dynamics of Atlantic salmon (*Salmo salar*) have been monitored since 1966 (Youngson and Hay, 1996). Atlantic salmon is a migratory fish species that reproduces in freshwater environments, typically upland headwater streams, where embryos hatch and juvenile fish typically spend 2–3 years maturing (Cunjak *et al*., 1998; Malcolm *et al*., 2012). The fish then out-migrate from their natal river to spend 1–3 years in a marine habitat in the North Atlantic where they grow (typically from <10 cm to >60 cm in length) before they return as adults to freshwaters – usually to their natal stream – to spawn (Mitchell and Cunjak, 2007; Gibbins *et al*., 2008). Annual numbers of emigrant juveniles and immigrant adults at the Girnock have been monitored since 1966, and electrofishing surveys have tracked the population densities and growth rates over juvenile fish within the river system over this period (e.g. Bacon *et al*., 2005; Gurney *et al*., 2008). Hydrological influences on various phases of the life cycles for different salmonids have been documented (Beechie *et al*., 2006). At the Girnock, these have included assessment of the effects of in-stream hydraulics on spawning behaviour (Moir *et al*., 2004, 2005) and juvenile feeding (Tetzlaff *et al*., 2005a,b) and the effects of hydrological variability on spawning return (Tetzlaff *et al*., 2008a). However, it has been recognized that there needs to be better understanding of the explicit linkages between landscape scale hydrological connectivity and in-stream ecological response for a more holistic understanding of long-term hydrological stressors on fish population dynamics (Tetzlaff *et al*., 2007a) and their sensitivity to future environmental change (Capell *et al*., 2013). Specifically, there is a need to understand how non-linearities in the catchment stream flow response relate to spatial variability in catchment storage dynamics, and how this may be affected by subtleties (e.g. hysteresis in the storage–discharge relationship; Tetzlaff *et al*., 2014). These processes have also implications for stream water quality (Dick *et al*., 2015).

Given this context, the aims of the work presented in this paper are (1) to collate long-term data sets of rainfall and runoff for the Girnock catchment since salmon monitoring commenced; (2) to use these data to calibrate and test a conceptual model that can track long-term storage changes over the period of record as a basis for understanding the landscape controls on connectivity that drive stream flow dynamics; (3) to demonstrate – via a simple meta-analysis – how such modelling-based understanding of catchment functioning can be helpful in providing an integrated framework for contextualizing ecohydrological influences on Atlantic salmon populations. The paper also reflects on the lessons learned from this exercise in terms of the limitations and uncertainties of the approach, as well as indicates how the modelling will guide future work.

STUDY SITE

The Girnock Burn is a montane tributary of the River Dee in north east Scotland (Figure 1). The area receives around 1000 mm per annum in precipitation and mean annual temperatures of ~6.5 °C. The Girnock drains a 30-km^2 catchment that ranges between 250 and 930 m, with a

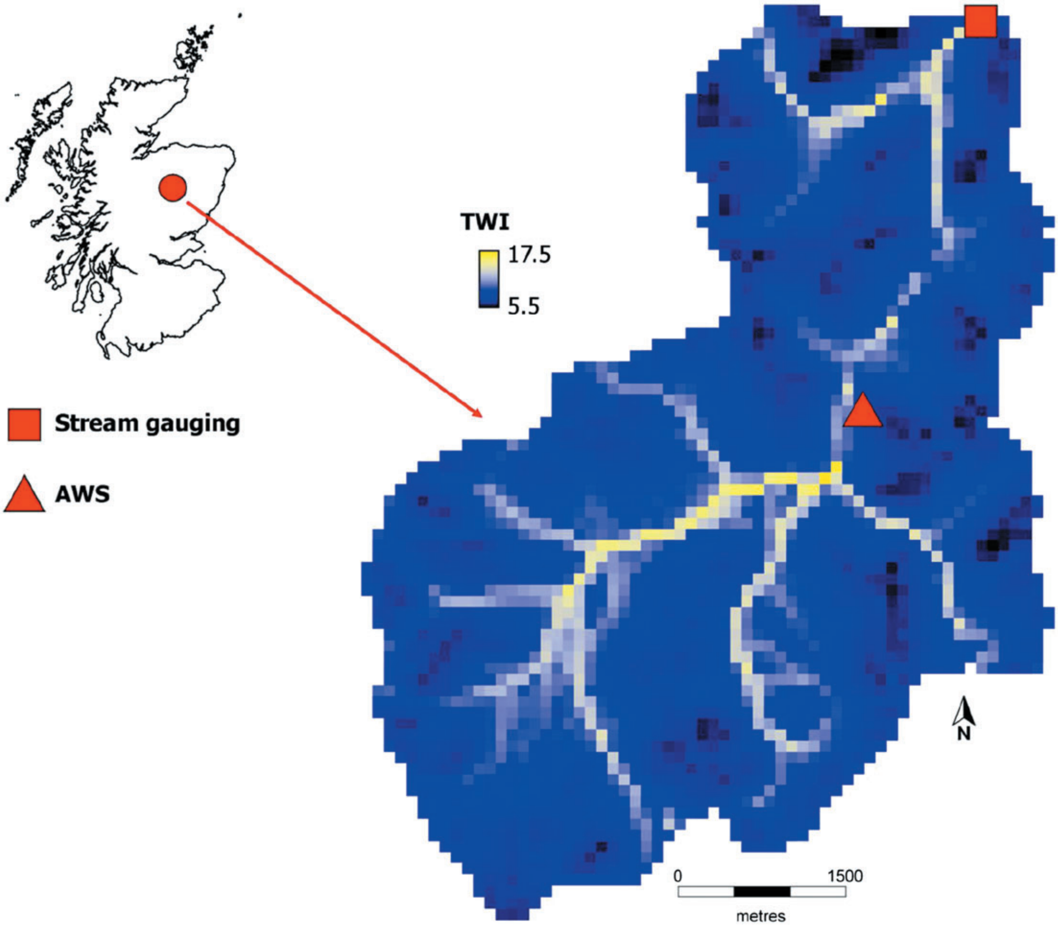

Figure 1. Topographic wetness index (TWI) and monitoring locations of the Girnock study catchment; shown in a regional context

median altitude of 410 m. The area has been glaciated, with steep slopes and the valley has a low gradient with a wide bottom and high Topographic Wetness Indices (TWI) (Figure 1). The geology is dominated by granite in the higher elevation areas contiguous with older metamorphic sediments (Soulsby *et al*., 2007). The soils range between podzols on the steeper hillslopes to peats and peaty gley soils in the valley bottom areas with higher TWIs (Tetzlaff *et al*., 2007b). These valley bottoms also correspond to relatively deep (up to 40 m) low permeability glacial drift deposits which create peat forming conditions (Blumstock *et al*., 2015). The podzols are dominated by heather moorland with *Calluna vulgaris* the most common species. The peats are dominated by *Spagnum spp* mosses, with purple moor grass (*Molina caerulea*) where the peats are influenced by minerogenic drainage. The area is managed for game shooting, mainly red deer (*Cervas elaphus*) and red grouse (*Lagopus lagopus*) and tree cover is low (<10% of the catchment).

The Girnock and its sub-catchment, the Bruntland Burn, have been a focus for hydrological research over the past decade. The hydrological regime of the catchment is responsive; precipitation events initiate a rapid stream flow reaction and a flashy hydrograph. The importance of riparian wetlands, indicated by the areas of high TWI in Figure 1 as the main sources of storm runoff generation, was identified by Tetzlaff *et al*. (2007b). The nature of heterogeneous groundwater inputs was characterized by Soulsby *et al*. (2007). More recent work has elucidated the characteristics of the storage dynamics of the different soils in the catchment, and how these control hydrological connectivity and runoff generation (Tetzlaff *et al*., 2014). This work has shown that around 75% of annual runoff is generated by near surface processes in the riparian peat soils and about 25% comes from groundwater. Runoff coefficients for individual events can vary between 2 and 60% depending on catchment wetness. Events are usually dominated (>80%) by old water (Tetzlaff *et al*., 2014).

Empirical insights into runoff generation have informed an iterative approach to conceptualizing dominant processes in rainfall–runoff models. Thus, the initial importance of riparian saturation zones in generating storm runoff was incorporated in an initial model by Tetzlaff *et al*. (2008b). Birkel *et al*. (2010) extended this with a tracer-aided model that parameterized the empirically validated dynamics of the expansion and contraction of saturated zones around the riparian wetlands. The algorithms used conceptualized how storage dynamics regulated this process to govern stream flow generation. This model was extended and used to simulate daily flows and weekly isotope ratios over the period 2003–2009 by differentiating both ‘dynamic’ and ‘total’ storage components (Birkel *et al*., 2015). This has shown that the ‘dynamic’ storage changes in the catchment annual water balance are around 150 mm, with changes most marked on the steeper hillslopes, corresponding broadly with empirical measurements of soil and groundwater storage dynamics (see Geris *et al*., 2015). However, the ‘total’ storage needed to account for tracer damping may exceed 2000 mm, resulting in stream water ages varying between a few months in events and >3 years in dry periods (Soulsby *et al*., 2015). However, to date, all of this modelling has been based on only up to 6 years of data at most. The present study meets the need for the longer-term analysis that is required to match the period of fisheries data collection and for use in ecohydrological applications.

DATA AND METHODS

Data quality issues

Although the Girnock salmon monitoring began in 1966 and flow measurements in 1969, the initiation of reliable flow records did not commence until the early 1970s. Initial problems dictated that 1972 was the first year of complete, consistent flow data. At first, only water level was recorded as a metric for use in fisheries data interpretation. In our analysis, the flow record is complete up until the end of 2011. Precipitation was not measured as part of the Girnock fisheries research, and thus, precipitation measurements within the catchment commenced only in 2001 when an Automatic Weather Station (AWS) was established (Figure 1); this has been subsequently supplemented by four additional AWS (Hannah *et al*., 2008). Estimating precipitation in upland catchments has the common issues of spatial variability and altitudinal influence. To produce the best possible precipitation time series, daily precipitation totals were derived from inverse distance-weighted averages from surrounding stations at Balmoral, Ballater, Aboyne and Braemar (which are all within 20 km of the catchment) and linearly corrected for altitude (Birkel *et al*., 2010). The altitudinal correction uses the mean annual precipitation-altitude relationship $y = 1.31x + 375$ with an $R^2 = 0.99$ derived for the Girnock. This relationship was calibrated for ranges from 170 m to 740 m and 672 to 1376 mm a^{-1}. The weighted and corrected Girnock catchment average showed R^2 from 0.72 to 0.86 if related to station data from the surrounding stations.

Potential evapotranspiration (PET) was estimated from the original AWS using the Penman Monteith Equation (2004 to 2011) with estimates checked for consistency with an upland Environmental Change Network (ECN) site at Glensaugh 20 km away, similar to Birkel *et al*. (2011a,b). Prior to 2004, PET estimates were ‘hindcast’ using air temperature (T(t)) records from Braemar (20 km away) going back to 1972 and the fixed (0.05) calibration (Seibert, 1997) parameter *Cet* based on the measured mean daily values (Tmean and PETmean) from the period 2004 to 2011:

$$\mathrm{PET}(t) = (1\text{–}\mathrm{Cet}((\mathrm{T}(t)\text{–}\mathrm{Tmean}))\mathrm{PETmean}. \quad (1)$$

The performance of the PET simulations from 2004 to 2011 had a NSE = 0.63 and $R^2 = 0.79$. PET was then adjusted prior to modelling using a scaling coefficient kET on an annual basis to match the water balance, which resulted in modifications between $0.94 < \mathrm{kET} < 1.09$. This was done with the premise to reduce measurement errors towards matching water balances for modelling purposes.

Streamflow data was quality controlled by re-constructing the rating curve using manual gaugings from the period 1997 to 2004 (Figure 2). Unfortunately, ratings prior to this period had not been archived. According to the 95% prediction bands of Figure 2, extrapolated high flows are less susceptible to errors compared to low flows. The channel at the gauging site has a plane bed, with a width of around 8 m and bank full depth of around 1 m. The bed is well-armoured and not prone to major change, but minor modification can affect the low flow rating. The highest measured discharge of 2.8 $m^3 s^{-1}$ corresponds to a 7 mm d^{-1} high flow and an extrapolated 10 $m^3 s^{-1}$ discharge event to a >5-year return period event with close to 30 mm d^{-1}. The latter is close to values with similar return periods for surrounding gauges. The flow time series includes the driest year (2003) on record in terms of mean annual precipitation and discharge (see Figure 3). It was assumed that flows lower than those recorded in the summer 2003 (which correspond to the lowest measured discharge values on the rating curve) were unlikely. Thus, any lower flows in the record from previous years were assumed to reflect rating curve errors and excluded from the model calibration (Beven and Westerberg, 2011). These corresponded to periods in August 1972 (3 days) and 1975 (4 days), July 1977 (16 days), August 1989 (10 days) and 1990 (5 days), September 1991 (7 days), June, July and August 1992 (18 days), July and August 1993 (9 days) and May and June 1994 (12 days) and 1 day in 2006 summing up to 90 rejected days in total. These generally coincided with times of budgetary constraints in the mid-1970s and early 1990s that resulted in less frequent flow gaugings.

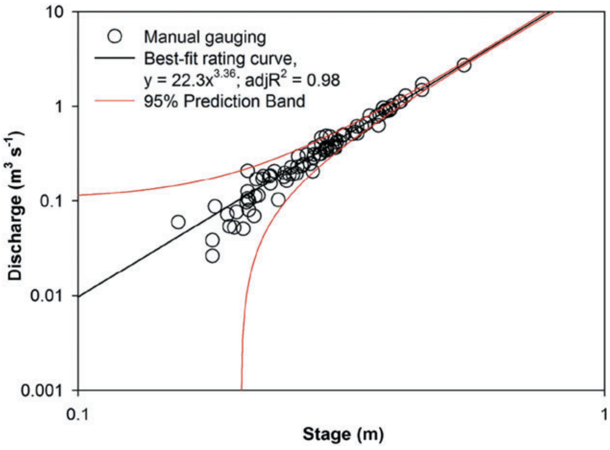

Figure 2. The reconstructed rating curve on a double logarithmic plot using manual gaugings between 1997 and 2004

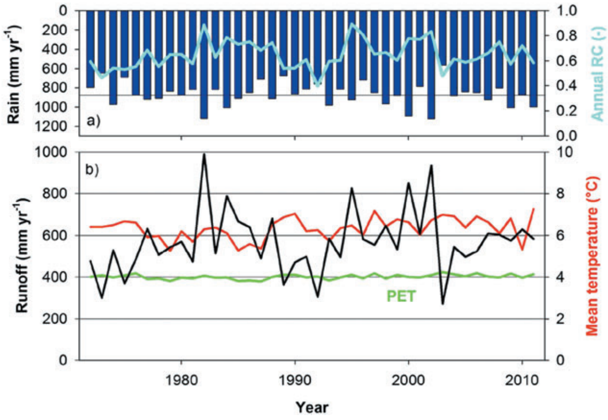

Figure 3. Mean annual values of observed hydrometeorological variables. a) Mean annual precipitation and runoff coefficients (RC) are given along with b) mean annual runoff, PET (related to left y-axis, in mm yr^{-1}) and air temperature

The corrected flow data was then used to construct daily flow distributions over the 40-year record. For a simple meta-analysis, we extracted the 1st and 99th flow percentile for each Julian day of the year as thresholds of flow outliers (high and low, respectively) that might affect two critically important ecohydrological periods in the Atlantic salmon lifecycle. We selected the 1st and 99th percentile as restrictive thresholds as a wider interval did not allow discriminating outliers. The first ecohydrologically important period is May/June in late spring/early summer when juvenile fish emergence occurs and small fish are vulnerable to the adverse effects of high flows either by limiting feeding opportunities or by washing out the year class (Crisp, 1988; Tetzlaff *et al.*, 2005). The second period is October/November in the autumn when adult fish return for spawning and require high flows to access the river and upstream spawning habitat (Welton *et al.*, 1999; Tetzlaff *et al.*, 2008a; Cunjak *et al.*, 2013).

Modelling approach

The dynamic saturation (Sat^d) area model was used to simulate daily discharge; the model is fully described by Birkel *et al.* (2010). It comprises three interacting landscape units: a dynamic saturation area, linked to a hillslope unit which can also recharge an underlying groundwater layer (Figure 4). Central to the model is capturing the non-linear streamflow response by conceptualizing the hydrological connectivity of the catchment. This links the dynamic

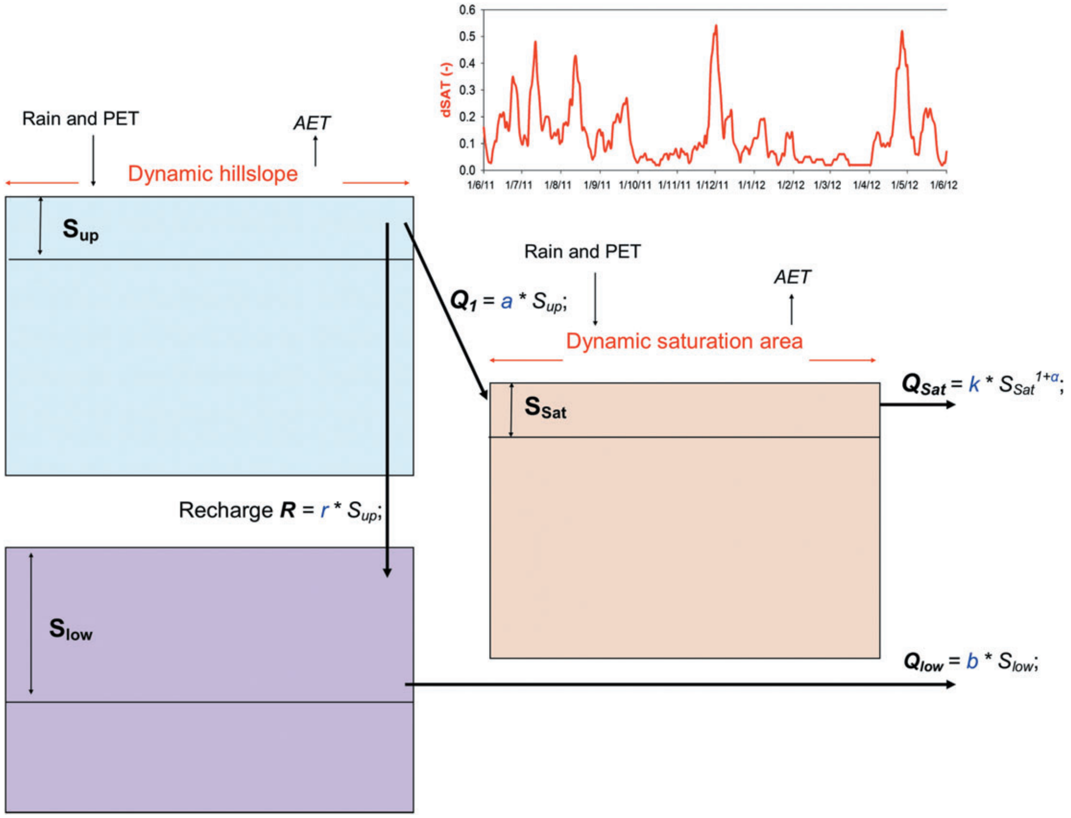

Figure 4. Conceptual diagram of the model with equations and calibrated parameters (in blue)

hillslope to the dynamic saturation area in the riparian zone and underlying groundwater. The approach connects the two upper storage units which conceptualize storage in the riparian peat soils (S_{sat}) and the freely draining podzols on the hillslopes (S_{up}). Direct mapping of the spatial extent of saturated soils in the valley bottom – that were hydrologically connected to the stream network during different wetness conditions (see Ali *et al.*, 2014) – allowed us to develop and fit a simple antecedent precipitation index-type algorithm which could explain around >90% of the variability (Birkel *et al.*, 2010). This algorithm was applied to create a continuous time series of the expanding and contracting daily saturation area extent (dSAT) (Figure 4). This dSAT time series was used as model input to dynamically distribute daily precipitation inputs between the storage volumes in the landscape-based (hillslope (S_{up}) and saturation area (S_{sat})) model structure (Soulsby *et al.*, 2015).

Like Birkel *et al.* (2015), we used reservoirs that could become unsaturated allowing storage deficits to occur. The riparian area is normally saturated (i.e. with positive storage), but can have small deficits following prolonged dry periods in summer. In the upper stores, water levels below a certain threshold can only be further depleted by transpiration and no lateral flow to the riparian area will be generated. Incoming precipitation fluxes are first intercepted and reduced by PET – if available. The remaining effective precipitation fills the uppermost storages and captures soil moisture-related threshold processes of runoff generation (Tetzlaff *et al.*, 2014). Consequently, S_{up} was often in deficit, but in wetter periods would fill and spill into S_{sat}, which usually has low or no deficit generating stream flow.

The storages S are state variables in the model, and we describe the following fluxes and calibrated parameters shown in Figure 4. The unsaturated hillslope reservoir S_{up} is drained (flux Q_1 in mm d^{-1}) by a linear rate parameter a (d^{-1}) and directly contributes to the saturation area store S_{sat}. The recharge rate R (mm d^{-1}) to groundwater storage S_{low} is linearly calculated using the parameter r (d^{-1}). The S_{low} store generates runoff Q_{low} (mm d^{-1}) contributing to total streamflow Q (mm d^{-1}) using the linear rate parameter b (d^{-1}). The runoff component Q_{sat} (in mm d^{-1}), which is generated nonlinearly from S_{sat}, conceptualizes saturation overland flow using the rate parameter k (d^{-1}) and the nonlinearity parameter α (—) in a power function-type equation (Figure 2). Q is simply the sum of Q_{sat} and Q_{low}. The use of linear or non-linear parameters was based on prior systematic tracer-aided multi-model testing for similar catchments in the Scottish Highlands (Birkel *et al.*, 2010; Capell *et al.*, 2012). In particular, the non-linear conceptualization of Q_{sat} has a physical basis in the dynamic expansion of the saturation area and fluxes that generate storm runoff. Likewise, the linear nature of Q_1 and R reflect the physical nature of the threshold-like response of the hillslope fluxes and the low aquifer drainage.

The basic rainfall–runoff model therefore uses only five calibrated parameters (*a*, *b*, *r*, *k* and *α*) shown in blue in Figure 4. The model is configured such that S_{up} does not contribute directly to stream flow as the steeper hillslopes are separated from the channel network by the riparian zone represented by S_{sat}. Furthermore, S_{sat} is not conceptualized to drain into S_{low} as the peat soils are saturated with lower subsoil permeability, limiting vertical drainage and promoting lateral flow (Tetzlaff *et al.*, 2014). As the modelling was carried out at daily time steps and the catchment is relatively small (30 km^2) and montane in nature, we did not need to include a channel routing parameter.

The model was initially calibrated using an evolutionary genetic algorithm for optimization applied to the complete data record. Model states resulting from this optimal solution were subsequently taken to initiate storage units for a Markov Chain Monte Carlo (MCMC) parameter sampling approach using 10^6 iterations. Prior parameter ranges were informed by previous tracer-based studies (using alkalinity as a tracer). The complete data record was split into roughly 5-year periods for calibration applying a split sample test. Five-year periods were chosen based on initial model tests allowing to capture enough inter-annual variability without compromising the ability of an exhaustive split sample test. Additionally, based on previous tracer-based hydrograph separations, only models reproducing a mean annual groundwater contribution between 0.26 and 0.51 (Birkel *et al.*, 2011a) were accepted for further analysis. We retained 10 000 parameter sets from the MCMC chain after convergence and randomly selected 1000 parameter sets for further analysis. From these 1000 retained parameter sets, uncertainty is represented at the 95% level and the posterior mean of simulations was used to assess model state dynamics. The total active catchment storage was calculated as the sum of model storage units S_{up}, S_{sat} and S_{low}. We ignored snow processes in the model due to the relatively low overall importance (<5%) on the water balance at the study site (Capell *et al.*, 2012).

RESULTS

Long-term hydrological data

The long-term precipitation record derived from the surrounding gauges had an annual mean of around 900 mm and limited variability ranging between ~600 mm and ~1100 mm in calendar years 2003 and 1982, respectively (Figure 3). Estimated PET was fairly constant at around 400 mm (range is 360 to 450 mm). Annual runoff totals generally tracked annual precipitation, with the annual runoff coefficient (RC) varying between >0.8 in wetter years to <0.5 in drier years. Annual water balance errors generally showed deficits most likely representing an underestimate of precipitation, given the lack of data from high altitude stations, and actual evapotranspiration being lower than PET.

Model results

The posterior parameter ranges from the retained parameter sets from the calibrated models for the 5-year periods are summarized in Table I. These show very similar mean values and ranges for each parameter across each 5-year block. The calibrated b parameter was low in 2000–2004 indicating lower rates of groundwater discharge, possibly reflecting the dry nature of this period (which included a 10-year return period drought in 2003/4). There is a suggestion of slight decreases in the *k* and *α* parameters, which regulate the nonlinearity of the saturation area runoff, which would suggest that the catchment response has been slightly less nonlinear since 1995. The hillslope contribution to the saturation area was calculated using the *a* parameter but this remained constant.

The model efficiencies for each calibrated period and the split-test application of each parameter set to the other 5-year periods as an independent test are shown in Table II. The mean efficiency statistics for the calibrated periods were reasonable with NSE and lnNSEs ~0.5 or greater. These remained stable over the period of modelling. The highest performance for individual wet years went up to NSE = 0.7, and the lnNSE showed similar values for the best models. This model performance was considered acceptable given uncertainties over high altitude precipitation inputs, potential routing effects of events spread over several days, occasional snowmelt influence and issues of data quality. Although the general dynamics were captured quite well, hydrograph peaks tended to be under-estimated and the initial phases of re-wetting after drier summers were often missed.

The model skill is shown at a higher resolution in Figure 5, which shows the ability of the retained model parameter sets to bracket the flow variability over the very wet winter period of 1982–1983 as well as distinct summer dry periods in the 3 years 1982, 1983 and 1984 (Figure 5a). At finer resolution, however, the model tended to under-estimate the highest peaks. The retained models also generally bracketed measured flows over the period 2002–2004, which was perhaps the period with the most marked hydroclimatic contrasts (Figure 5b). The catchment experienced a very wet autumn/winter over 2002–2003 (second wettest year on record) which transited into the driest, warmest summer of 2003 followed by a relatively dry winter and spring. The model performed quite well until autumn of 2003, where it over-anticipated

Table I. Prior and posterior parameter distributions (parameters a, b, R, k and α) applied to calibrate roughly 5 yr periods (ts70: 01/01/1972 to 31/12/1979; ts80: 01/01/1980 to 31/12/1984; ts85: 01/01/1985 to 31/12/1989; ts90: 01/01/1990 to 31/12/1994; ts95:01/01/1995 to 31/12/1999; ts00: 01/01/2000 to 31/12/2004 and ts05: 01/01/2005 to 31/12/2011)

	Priors	ts70		ts80		ts85		ts90		ts95		ts00		ts05	
		Mean	95th 5th	Mean	95th 5th	Mean	95th 5th	Mean	95th 5th	Mean	95th 5th	Mean	95th 5th	Mean	95th 5th
a	[0.1,0.9]	0.43	0.75	0.42	0.75	0.43	0.74	0.45	0.73	0.47	0.76	0.46	0.71	0.41	0.72
			0.13		0.15		0.16		0.17		0.16		0.16		0.15
b	[0, 0.5]	0.05	0.11	0.05	0.11	0.05	0.12	0.06	0.14	0.05	0.12	0.03	0.10	0.06	0.15
			0.005	0.61	0.003	0.49	0.003	0.56	0.01	0.56	0.004	0.58	0.002	0.49	0.003
r	[0.1, 1]	0.57	0.97		0.97		0.94		0.92		0.92		0.94		0.92
			0.15	0.11	0.15	0.09	0.15	0.13	0.18	0.09	0.16	0.08	0.18	0.07	0.15
k	[0,0.5]	0.11	0.3		0.29		0.24		0.32		0.28		0.20		0.20
			0.02		0.01		0.005		0.01		0.01		0.008		0.003
α	[0.1,0.9]	0.40	0.68	0.38	0.70	0.40	0.67	0.40	0.75	0.38	0.70	0.39	0.68	0.39	0.72
			0.14		0.12		0.15		0.12		0.13		0.14		0.12

Table II. Split sample test (NSE, lnNSE) of posterior mean parameter sets (in bold) applied to all periods as an independent model test

	Periods used for calibration (NSE, lnNSE)						
Test periods	ts70	ts80	ts85	ts90	ts95	ts00	ts05
ts70	**0.49, 0.56**	0.45, 0.54	0.49, 0.56	0.47, 0.52	0.48, 0.50	0.36, 0.49	0.46, 0.43
ts80	0.56, 0.59	**0.59, 0.61**	0.45, 0.58	0.43, 0.42	0.44, 0.45	0.46, 0.48	0.40, 0.42
ts85	0.49, 0.51	0.47, 0.47	**0.49, 0.51**	0.36, 0.37	0.39, 0.38	0.43, 0.49	0.34, 0.28
ts90	0.38, 0.37	0.37, 0.43	0.39, 0.38	**0.49, 0.46**	0.49, 0.51	0.40, 0.38	0.38, 0.48
ts95	0.45, 0.55	0.51, 0.53	0.45, 0.56	0.47, 0.41	**0.59, 0.59**	0.48, 0.57	0.40, 0.56
ts00	0.54, 0.65	0.53, 0.56	0.54, 0.66	0.54, 0.53	0.59, 0.57	**0.57, 0.59**	0.58, 0.47
ts05	0.46, 0.56	0.43, 0.49	0.57, 0.57	0.43, 0.41	0.47, 0.64	0.55, 0.62	**0.57, 0.64**

the initial phase of re-wetting. However, once again, as rewetting progressed in the autumn simulations improved before the highest flow peaks in early 2004 tended to be underestimated.

Tracking storage dynamics

The structure of the model allowed us to track dynamic storage changes in the catchment and three landscape components over the 40 years of record. From the wide range of hydroclimatic conditions experienced over such a long period, we were able to derive an average storage state on each day of the year (Figure 6). The plot shows that precipitation was fairly evenly distributed through the year, but the wettest days tended to fall between November and January. Stream flow reflected this seasonality, although summer low flows were mainly driven by the summer PET losses rather than lack of precipitation. The spatial distribution of storage dynamics was extracted from the model in terms of the three main model units. Thus, the model conceptualized the catchment storage transiting from winter positive storages (of around =40 mm) to a deficit from around mid-May. The deficits reached around −40 mm in June/July before being replenished and, on average, moving into a state of storage surplus in October. These spatial variations in water storage and summer deficits are broadly consistent with measured changes in soil moisture and groundwater in the catchment (Tetzlaff *et al.*, 2014; Geris *et al.*, 2015).

The modelled summer catchment storage deficits mainly reflected drying and disconnection of hillslope storage (S_{up}). The S_{low} and S_{sat} usually remained positive, reflecting a constant groundwater flux and the generally saturated conditions which prevail in the riparian wetland (Figure 6). However, the smoothed average curve showed marked variability in the storage conditions experienced on any given day. The faint lines in Figure 6 show the variability in catchment-scale storage for individual extreme years (wettest year 1982 and driest year 2003). The wettest years remained almost entirely in positive storage, whilst some of the drier years exhibited marked summer deficits. However, even in the driest years, re-wetting was generally complete by November; and almost always complete by the end of December. Carry-over storage deficits at the end of the calendar year were rare but did occur in 2003–2004, as well as 1973–2004, 1984–1985 and 1994–1995 (not shown in Figure 6).

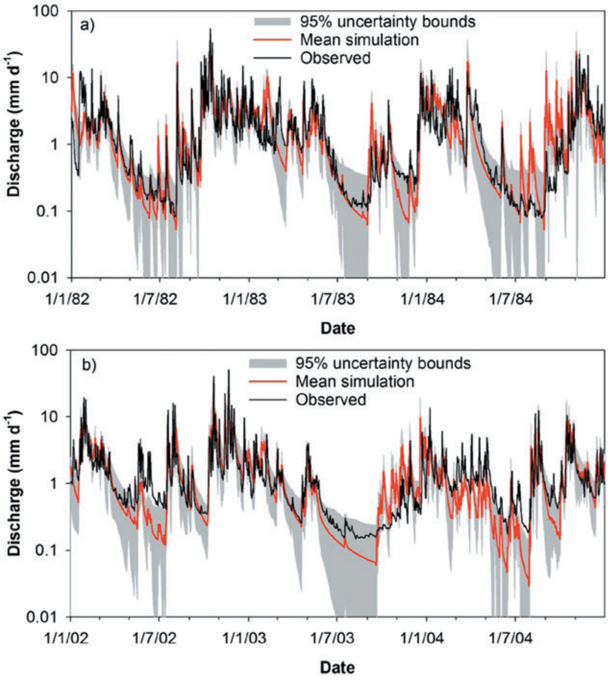

Figure 5. Discharge simulation results (log-scale) for the calibrated model during a) the wettest period on record during 1982 and b) the summer 2003 drought

More detailed inter-annual variation in modelled storage tracking is shown for the decade 2000–2011 (Figure 7). This includes the dry year of 2003 and the wet years of 2002, 2007 and 2009. In addition to 2003, the summers of 2005 and 2006 also showed quite large (ca −100 mm) deficits. The positive storage in winter was mainly the result of groundwater being recharged with a STOgw surplus of around 50 mm. In addition, the saturated area had a wide spatial extent and a high storage of up to around 30 mm. The groundwater store discharged slowly, whilst the riparian store discharged rapidly driving the storm response, as reflected in the *k* and *b* parameters in the model (Figure 4). Similar positive storages were evident in some of the wetter summers, such as 2002, 2007 and 2009. The bottom panel of Figure 7 shows how the storage dynamics link to the extent of the saturated area and the proportion of modelled stream flow derived from groundwater contributions.

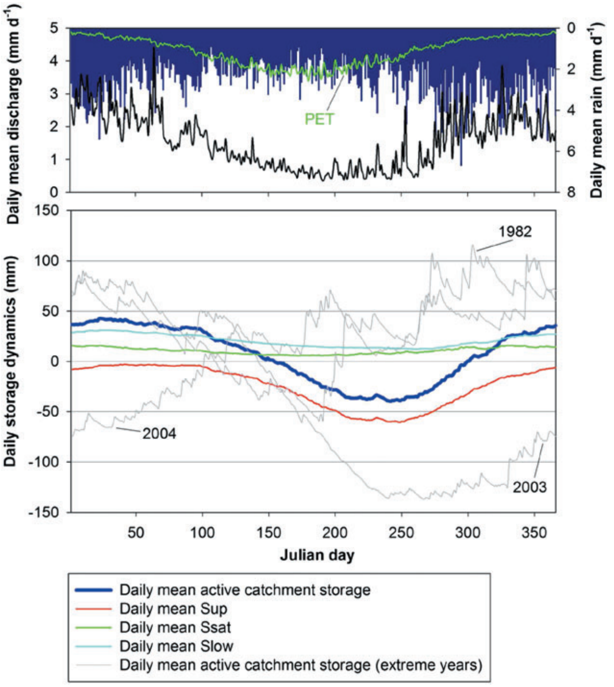

Figure 6. Modelled daily mean storage dynamics of the total active catchment storage plotted as well as the model storage components (S_{up}, S_{sat} and S_{low}) from 01 January to 31 December. Individual extreme years of 1982, 2003 and 2004 are plotted for comparison. Daily mean water balance components (rain, PET (related to right y-axis, in mm yr^{-1}) and discharge) are given for comparison purposes in the upper panel

Storage–discharge relationships

The modelled storage–discharge relationship for the Girnock shows the non-linearities of how hydrological connectivity links the landscape to the riverscape through runoff generation processes (Figure 8a). It also shows the nature of the hysteresis loops associated with modelled storage relative to the stream hydrograph. Generally, storage needs to be positive and the catchment very wet for the largest runoff events (>15 mm d^{-1}). However, substantial runoff events can still occur if the overall catchment storage is negative: if high precipitation occurs on saturated area. If the saturation area has a positive storage or even just a small deficit, then high stream flows can be generated even if the rest of the catchment is disconnected and the hillslope stores are in deficit. This is illustrated by the responses following the unusually dry period from summer 2003 to autumn 2004 where some moderate events occurred, despite significant catchment scale deficits (Figure 8b).

Hysteresis loops are evident in the storage–discharge relationships simulated by the model. As the catchment wets and dries, the hysteresis is generally clockwise, reflecting a rapid filling of stores, particularly in the riparian zone which drives the runoff response. This is then followed by slower drainage from the hillslope and groundwater stores sustaining the recession. These lags are more pronounced under drier conditions, with the hysteresis loops becoming shorter as the catchment gets wetter.

Influence of storage – discharge relationships on sensitive ecohydrological periods

The modelled storage-driven connections between the landscape and riverscape provides an ecohydological framework for understanding long-term dynamics in stream flow generation which determine habitat hydraulics for different life stages of the salmon population in the Girnock channel network. Hitherto, ecohydrological work in the catchment has looked most extensively at interactions between components of the Atlantic salmon population and

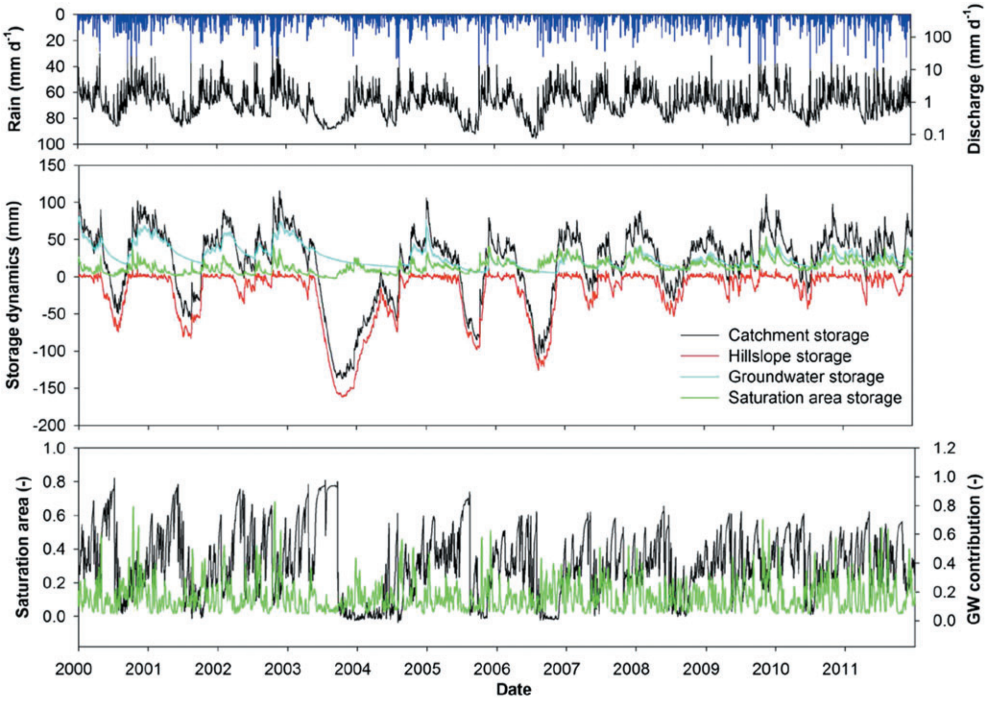

Figure 7. Daily precipitation and runoff (upper panel), modelled changes in the catchment and individual storage components (middle panel) and model derived groundwater (gw) contributions for selected 12-year period (2000–2012)

variability in stream flow or in-stream hydraulics. This new, long-term modelling now sets this variability in the riverscape in a more fundamental context of the inter-relationships between storage in the landscape and stream flow generation. This provides a wider, novel context that is a prerequisite for any model-based scenario assessment of likely impacts resulting from climate or land use change. A detailed analysis of the implications of this more fundamental context is the focus of ongoing work and beyond the scope of the current paper. However, a meta-analysis of hydrological influences on two important life stages of Atlantic salmon helps illustrating the potential value of the approach.

The long-term data set allowed us to examine when hydrological perturbations might disrupt in-stream hydraulics and riverscape functioning during biologically sensitive times. Figures 9 and 10 show daily low flow outliers below Q_{99} and greater Q_1, respectively, highlighting the time periods in autumn and early summer which are of critical importance for Atlantic salmon. The autumn spawning entry of fish to the river is fundamental to the recruitment to the next year's fish stocks and the early summer period is a key time immediately after embryos hatch and when juvenile salmon emerge into the river. The links between the flow regime during these critical periods, average catchment storage and the extent of the saturated area are clear from Figures 9 and 10. The autumn spawning entry period (Figure 9) clearly corresponds to the increase in autumn stream flows when the simulated dynamic storage changes indicated that the usual summer storage deficits are re-filled. Figure 9 shows periods when the flows during the spawning return window were $< Q_{99}$, representing periods when flows may have been too low to facilitate spawning entry to the river. These highlight the years of high autumn storage deficits such as 2003, but also 1989 and 2005. Likewise, the summer emergence timing (Figure 10) corresponds to the start of usual storage deficits and the summer low flows, which again were identified by the modelled, long-term storage–discharge relationships. Days when flows were higher than the Q_1 are shown in relation to this spring emergence period, when daily high flow outliers can potentially affect juvenile fish when storage is low. Again, wet summers like 2007, 2002 and 1983 are evident. Generally, the dry period outliers identified by Q_{99} seem to cluster over longer time periods compared to the more sporadic high flow events depicted by Q_1. The mean daily Q_{99} threshold time series was directly related to the modelled mean daily catchment storage, shown in Figure 6, and the relationship resulted in a correlation of $r = 0.72$ ($p < 0.01$). The mean daily Q_1 high flow threshold time series showed a significant relationship ($p < 0.05$) of $r = 0.33$ with the mean daily saturation area extent dSAT (Figure 9).

DISCUSSION

A conceptual model to track long-term storage and connectivity dynamics at the landscape scale

For many catchments around the world, the hydrological response to precipitation events reflects the funda-

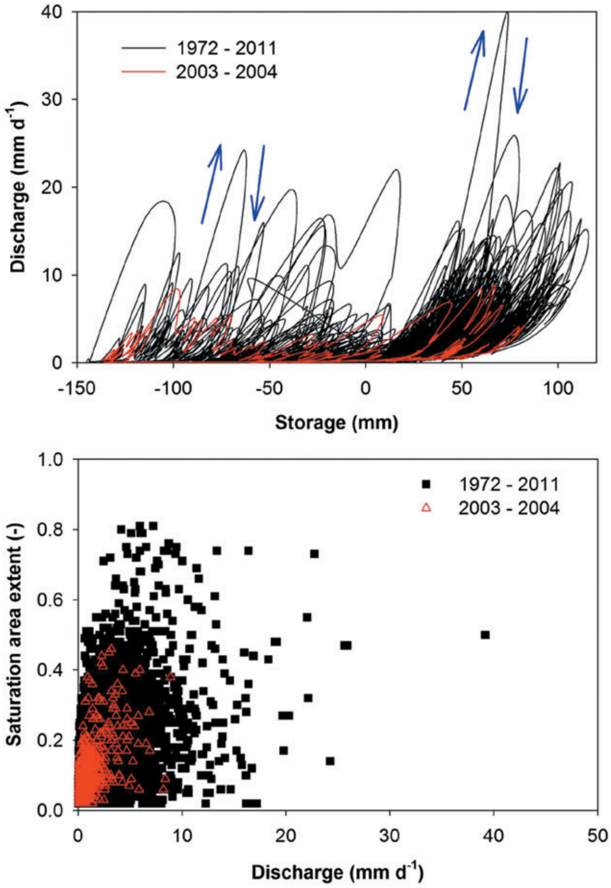

Figure 8. Model derived storage–discharge relationships. Blue arrows indicate direction of hysteresis loops, and the drought period 2003 to 2004 is highlighted in red (upper panel). The lower panel shows the relationship between the extent of the saturation area and daily discharge for the whole period and the dry year of 2003/4

mental importance of the connectivity between hillslopes, dynamic, riparian zone saturation areas in stream flow generation (e.g. Jencso *et al.*, 2010). The evolution of TOPMODEL (Beven and Kirkby, 1979) and similar approaches has shown how such processes can be conceptualized with low parameterization explicitly linking runoff generation to storage dynamics in main landscape units (e.g. Birkel *et al.*, 2010). Importantly, they have the potential for hindcasting catchment storage states providing a richer basis for understanding longer-term hydrological function at the catchment scale. By capturing dominant processes similar to Sivakumar (2004), such models have an increased likelihood of being ‘right for the right reasons’ (Kirchner, 2006). This, in turn provides a robust basis for projecting the possible impacts of climate or land use change (Capell *et al.*, 2013). Crucially, as well as being useful tools for predicting and understanding catchment function, such modelling approaches also have largely unrealized potential in providing a simple landscape hydrology context, based on storage-driven connectivity dynamics, for in-stream ecohydrological studies (Nippgen *et al.*, 2015). The advantage of this is that it allows us to track the state of catchment storage and contextualize high flows and wet periods in terms of the longevity of positive storages. Similarly, drier periods and low flows can be indexed according to storage deficits. In both cases, though particularly that of deficits, the ‘memory effects’ of more extreme system states is apparent. This then allows us to understand flow variability and in-steam hydraulics in terms of how the storage dynamics link to the extent of the saturated area and the proportion of stream flow derived from different water sources.

Such a perspective is important not only in terms of understanding long-term hydroclimatic influences on ecological variability (e.g. Gurney *et al.*, 2008), but also short term flow changes in terms of non-linearities in connectivity and storage – discharge hysteresis (Moir *et al.*, 2006). The long-term modelling undertaken here gives a reasonable representation of storage dynamics that is broadly consistent with recent spatially distributed empirical measurements (Tetzlaff *et al.*, 2014; Geris *et al.*, 2015). Stream flow dynamics are also captured reasonably well, though the limitations of a simple lumped model become apparent with the problems of capturing late summer re-wetting and event peaks. In part, these limitations may reflect errors in the precipitation estimates; however, they may also reflect the need for a more distributed model to capture more localized runoff sources that affected the re-wetting periods (Lessels *et al.*, 2016).

The study also needed to develop long-term data series of rainfall and runoff to underpin the modelling process. This raised issues of data quality and time periods of potential error (Beven and Westerberg, 2011). With awareness of the potential problems associated with such issues the re-construction of time series that provide the best estimates of data with the associated uncertainties can be used, with caution, to give a long-term perspective on hydrological function. We, however, did not explicitly account for data uncertainty similar to Westerberg and Birkel (2015). In contrast, we removed spurious low flow data from the time series following recommendations by Beven and Westerberg (2011) to avoid potential issues with dis-informative data for model calibration.

Linking modelling-based understanding of catchment hydrology to ecology in salmon spawning streams

Models that seek to capture the dominant processes of landscape-scale water partitioning, storage and fluxes, and how these processes governs stream flow generation, are being increasingly used in integrated ecohydrological studies (e.g. Goode *et al.*, 2013). These modelling studies seek to understand in-stream ecological processes which are influ-

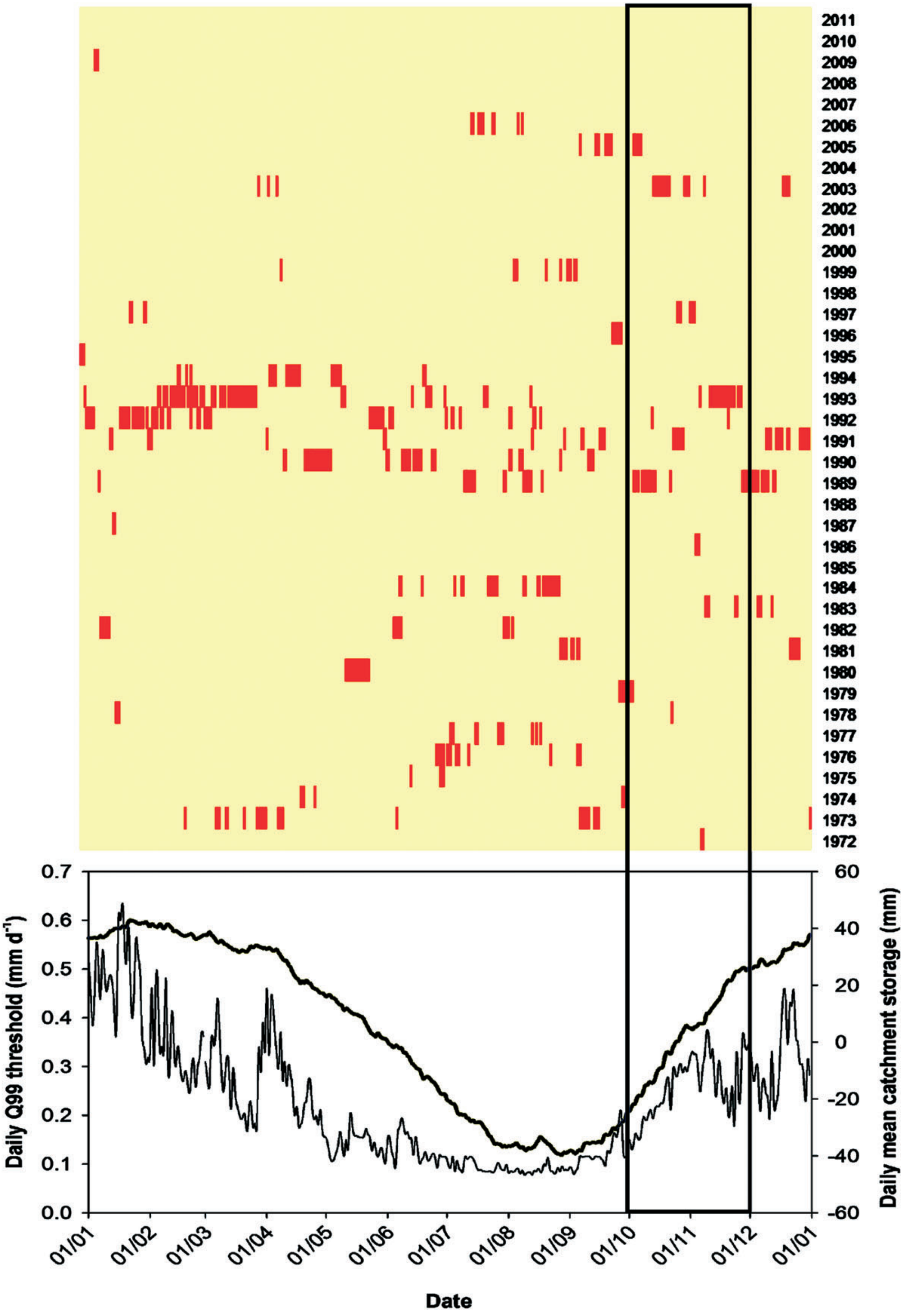

Figure 9. Daily low flow outliers below the Q_{99} were determined in relation to the Oct/Nov spawning return period for salmon in each year. This is plotted against the mean daily storage status for the catchment (bold black line)

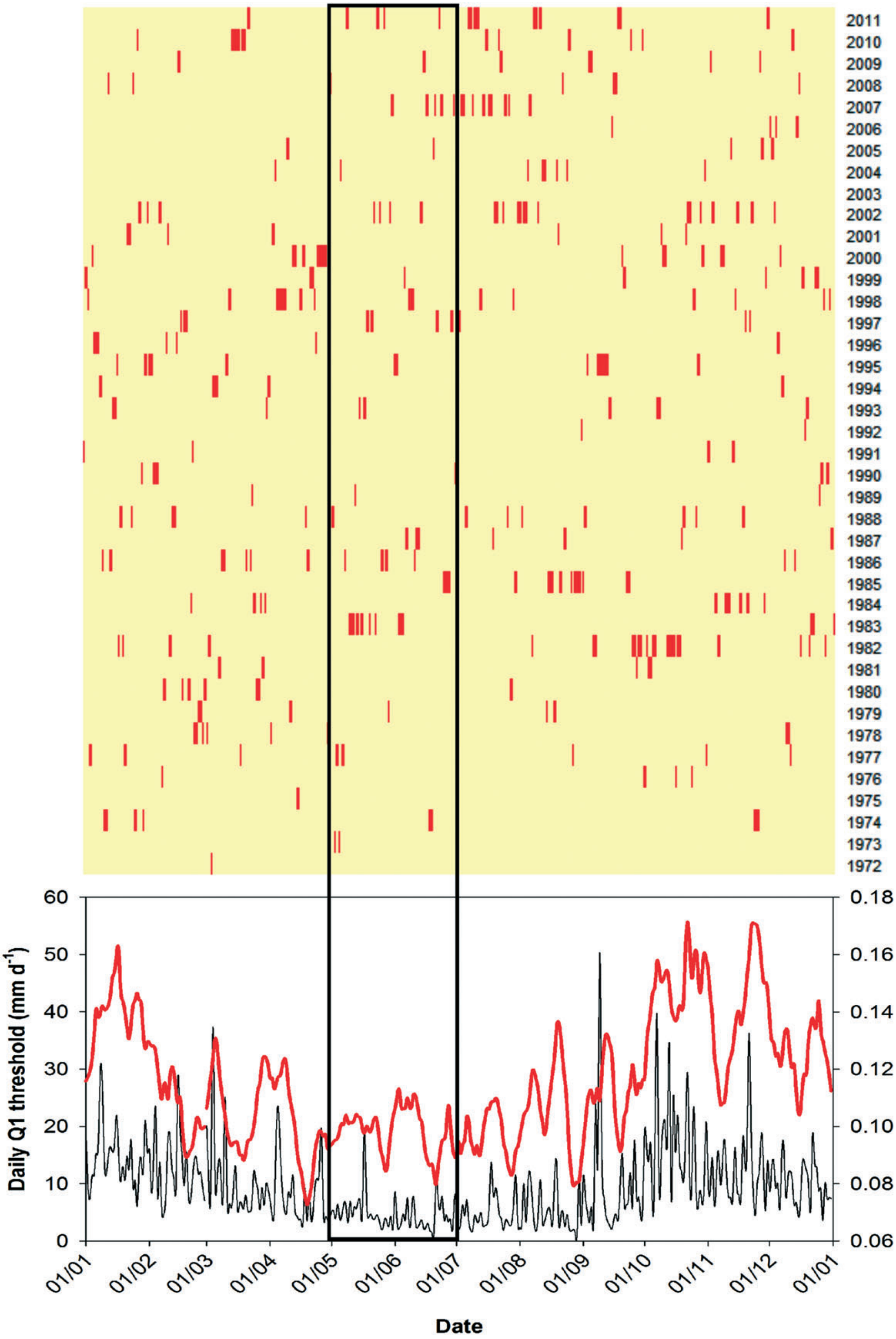

Figure 10. Daily high flow outliers greater than Q_1 were determined in relation to the May/June juvenile fish emergence period for each year. This is plotted against the mean extent of the saturation area for each day (bold red line)

enced by larger scale landscape hydrology, rather than simply in-stream hydraulics, such as the PHABSIM model (e.g. Moir *et al.*, 2005). Whilst there is a long-history of studies that look at the effects of flow regimes or local hydraulic interactions on in-stream biota in environmental flow assessment (e.g. see review in Gordon *et al.*, 2004), relatively few of these have a wider hydrological landscape context as advocated by Tetzlaff *et al.* (2007a). Recent work and the development of commercial software such as MIKE-SHE that allow such holistic studies have mainly used highly parameterized hydrological models (Loinaz *et al.*, 2014). However, such models have the risk of over-fitting and increased uncertainty which may render scenario assessment difficult and/or being potentially misleading (Beven, 2012). The advantage of simpler conceptual models such as applied here is that there can be increased confidence that the dominant processes are captured for further scenario analysis (Kirchner, 2006). Furthermore, the model results indicated that even extreme periods can be reasonably well simulated (Figure 5). Best-fit values of NSE = 0.7 for individual years were deemed satisfactory considering the data input uncertainties of the reconstructed long-term data record. As with most models, the initial late summer rewetting phase after prolonged dry periods posed a challenge to the $\mathrm{SAT}^{\mathrm{dyn}}$ model, though the flow sensitive periods for the two salmon life stages under consideration were quite good. In addition, our rigorous split sample test showed that the model coped well with the hydroclimatic variability of the data record (Table II) indicating a relatively minor non-stationarity issue of model parameters.

The use of the modelled data here to show how hydrological linkages provide the landscape context for understanding in-stream flow dynamics at different life stages of Atlantic salmon was a first step in this direction. Previous work in the Girnock has shown how flow variability and in-stream hydraulics are affecting the timing of spawning entry (Tetzlaff *et al.*, 2008a), spawning distributions at the local (Moir *et al.*, 2005) and catchment scale (Moir *et al.*, 1998) as well as the feeding patterns of juvenile salmon (Tetzlaff *et al.*, 2005). Whilst such work has elucidated some of the hydrological influences on salmon, these studies have typically focused on relatively short periods (i.e. individual years) and were based purely on flow metrics. These hydrologically influenced, ecologically important periods most likely reflect the long-term adaptation of the Girnock salmonid population to the prevailing flow regime and its hydroclimatic controls. However, these controls on the riverscape response are mediated through hydrological processes which occur in the landscape of the catchment and which govern the interrelationships between storage, connectivity and stream flow generation. Importantly for ecohydrological assessment such analytical framework can show the frequency and duration of flow perturbations and link them explicitly to catchment storage states which are likely receptors of land use and climatic change.

Current and future work will be using the model developed here along with long-term fisheries data to assess the effects of catchment hydrological conditions on stream flows and how landscape-riverscape connectivity affects both spawning entry and summer growth rates over multi-decadal time series. Our meta-analysis using daily dry and high flow thresholds allowed for a detailed assessment of potential hydrological disturbances to the salmon lifecycle. However, we presented this meta-analysis to simply discriminate situations which need thorough evaluation based on ecological data. Work to advance this agenda will involve a long-term analysis of annual and seasonal flow regimes in conjunction with fisheries data to examine how inter- and intra-annual flow regime variability explains variability in different components of the salmon population (Botter *et al.*, 2013). In addition, the long-term flow modelling will be used to downscale inputs to hydraulic models for spatially distributed reaches of the river that are important habitats for key life stages where long-term observational data are available (cf Goode *et al.*, 2013). The complex life cycle of Atlantic salmon renders such work extremely challenging as it needs to integrate conditions over 2 to 4 years of juvenile life spent in freshwaters with the 1–4 years spent at sea and associated density dependent controls on salmon populations (Gurney *et al.*, 2008). However, the analysis presented in this paper provides a landscape-scale hydrological context for understanding the strength of hydrological controls on various salmon life stages.

CONCLUSIONS

We have shown that a relatively simple rainfall–runoff model can give a reasonable representation of landscape-scale hydrology and the storage-driven connectivity between hillslopes and riparian wetlands which drives the catchment hydrological response. The modelling approach of low parameterization and capturing the dominant processes is very much in the spirit of TOPMODEL and other concepts developed by Keith Beven. Such models have unrealized potential in an ecohydrological context where models tend to be more highly parameterized with associated uncertainties and equifinality that could undermine use in environmental change scenarios. The modelling has also provided a plausible perspective on catchment storage conditions over the past 40 years, which provides an integrated context on landscape-riverscape linkages that will help understand hydrological influences on long-term Atlantic salmon population dynamics. It will also provide a more secure basis for future predictive modelling.

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