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Connectivity between landscapes and riverscapes—a unifying theme in integrating hydrology and ecology in catchment science?

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Integrating Hydrology and Ecology in Catchment Science—Moving from Multi-Disciplinarity to Interdisciplinarity

Developing the research interface between hydrology and ecology has been identified as a research frontier in catchment science (Bond, 2003). Yet, despite a history of research that integrates insights from the two fields (Bonell, 2002), it has been argued that the disciplines still operate somewhat independently with different philosophies, conceptual frameworks, terminology and experimental approaches (Hannah *et al.*, 2004). Facilitating greater integration is a prerequisite to more holistic understanding of how catchments function, which in turn is needed to inform sustainable river basin management (Petts *et al.*, 2006). In both sciences, progress towards such ends has been hampered by a focus on reductionist approaches at small spatial and temporal scales, because of the need for detailed observation to characterise processes adequately, together with logistic and resource constraints. For example, studies that seek to establish links between physical habitat and ecology have usually been carried out at reach scales (typically $< 10^2$ m), via the application of hydraulic models in order to understand the physical characteristics of aquatic habitats (e.g. Moir *et al.*, 2005). Examination of larger scale linkages have usually been implicit and limited to analyses of river flow regimes to identify parameters that might be ecologically meaningful in order to guide management decisions when setting environmental flow regimes (e.g. Olden and Poff, 2003; Tetzlaff *et al.*, 2005a; Beechie *et al.*, 2006). Often the lack of unifying themes and different disciplinary approaches results in ecohydrological studies that are multidisciplinary rather than interdisciplinary and which infer, rather than empirically measure, abiotic–biotic interactions.

Innovations in landscape ecology have resulted in the development of new paradigms in freshwater ecology, which provide an exciting opportunity for fruitful interdisciplinary research (Wiens, 2002). Viewing riverine ecosystems as 'riverscapes' which are closely connected with their catchment 'landscape', facilitates a more integrated perspective and a common conceptual framework for research (Fausch *et al.*, 2002). This provides an opportunity for hydrologists to develop ways of understanding catchment functioning in a more ecologically meaningful way (Stanford, 2006). The concept of 'connectivity' is emerging as an important theme in current approaches to understanding hydrology (e.g. Lane *et al.*, 2004) and catchment scale ecological processes (Pringle, 2003). In this commentary, we explore the utility of the concept of connectivity. We show how it has recently contributed to a more unified, interdisciplinary understanding of the influence of catchment-scale hydrological processes on the migratory movement of adult Atlantic salmon (*Salmo salar*) into a Scottish river system for spawning. We also share experiences on over a decade of interdisciplinary research between hydrologists and

ecologists and highlight some of the factors that have best facilitated holistic insight.

Landscape Connectivity—a Hydrological Perspective

Hydrological processes involve flows of matter and energy (water, nutrients, sediments, heat, etc.) between different landscape components. For example, the dynamics of runoff generation is intimately related to the hydrological connectivity between the channel network and the surrounding hillslopes (McDonnell *et al.*, in press). The spatial structure and temporal dynamics of the pathways of connectivity are usually driven by climatic factors and are mediated by catchment characteristics (Soulsby *et al.*, 2006a). Recent work has elucidated aspects of the complex spatial structure (e.g. Tetzlaff *et al.*, 2007) and threshold-like dynamics (e.g. Tromp Van Meerveld and McDonnell, 2006; Malcolm *et al.*, 2006) of such connections between hillslopes and channel networks; involving both surface and subsurface storm flows and groundwater discharges. However, such connectivity is usually most well understood at the scale of experimental hillslopes and small catchments, but not larger catchment scales where many ecological processes are evident and management decisions are needed (Soulsby *et al.*, 2006b).

Riverscape Connectivity—an Ecological Perspective

Increasingly, freshwater ecologists are conceptualising lotic ecosystems as riverscapes. In other words, they are viewing rivers as linear, spatially continuous, heterogeneous habitat patches (Schlosser, 1991) that are intimately linked to their catchment landscapes (Stanford, 2006). In this paradigm, the spatial arrangement of habitat patches within riverscapes is exploited by different species and different lifestages of individual species (Wiens, 2002). Importantly, the characteristics of different habitat patches are dynamic, altering with short-term hydrological variability and longer-term geomorphic and climatic change (Stanford, 2006). Crucially, the connectivity between different habitats is dynamically linked to hydrological connectivity, both between the landscape and riverscape and within the riverscape itself (Pringle, 2003).

Fausch *et al.* (2002) argue that the tendency to focus on small spatial scales (<200 m) and short timescales (<2 years) in ecohydrological research dictates that the importance of such connectivity has been underestimated in the past. They further suggest that there is a need for research to focus on intermediate scales—spatially (1–100 km stream segments) and temporally (5–50 years)—in order to understand the ecological integrity of riverscapes and how they connect with the catchment landscape and are affected by variability in hydroclimatological conditions.

Connectivity as a Unifying Theme in Catchment Science—an Example

As the hydrological connectivity of catchment landscapes governs the flux of matter and energy into the riverscape, this can influence the biological flux of organisms into and/or out of the riverscape, as well as along it. This provides a research interface, where focusing on connectivity is an area where hydrology and ecology can rapidly enhance mutual understanding.

The Girnock is a 30 km^2 experimental catchment in Scotland that forms a tributary of the river Dee, which drains 2300 km^2 (Figure 1a). The site has been monitored since the mid-1960s to understand the population dynamics of the Atlantic salmon. For over 15 years, we have been investigating salmon spawning at this site, and work has included characterisation of the spawning habitat (Moir *et al.*, 2002, Moir *et al.*, 2004), modelling spawning site preferences in relation to hydraulic conditions (Gibbins *et al.*, 2002; Moir *et al.*, 2005) and river flows (Webb *et al.*, 2001), and characterisation of the embryo survival in relation to hyporheic water quality (Malcolm *et al.*, 2003; Youngson *et al.*, 2004). This work has been interdisciplinary, and based on a riverscape perspective; but—as Fausch *et al.* (2002) note of many studies—one that largely ignored the connections with the catchment landscape, or connections with the larger riverscape of the Dee network.

Our most recent work on spawning has begun to look at these wider connections by considering the hydrological influences on spawning entry of adult fish into the Girnock Burn from the River Dee (Tetzlaff *et al.*, 2005b; Tetzlaff *et al.*, in press). Although adult salmon that will spawn in the Girnock return to the Dee from the sea throughout the year, they remain in the main stem of the river until shortly before spawning, which usually occurs in late October and November. Lack of refugia in deep pools in the Girnock preclude early entry, presumably reflecting risk of predation and higher metabolic costs in small, fast-flowing streams (Carss *et al.*, 1990; Bacon *et al.*, 2005). Analysis of fish trap data (which show the number of female fish entering the stream each day) over 37 years and corresponding flow records, show that fish enter the river in response to hydrological events, and the timing of entry reflects the antecedent and prevailing flow conditions. The combined physical and biological factors that trigger this migration are complex and incompletely understood, though hydrological events are clearly important as they facilitate access by drowning out 'barriers' such as gravel bars and help fish avoid predation. PCA and cluster analysis of hydrological parameters grouped the years into 15 dry, 10 wet and 12 intermediate (Tetzlaff *et al.*, in press). As Figure 1b and 1c show, hydrological conditions during the spawning 'window' have a critical influence on the timing of fish entry into the stream

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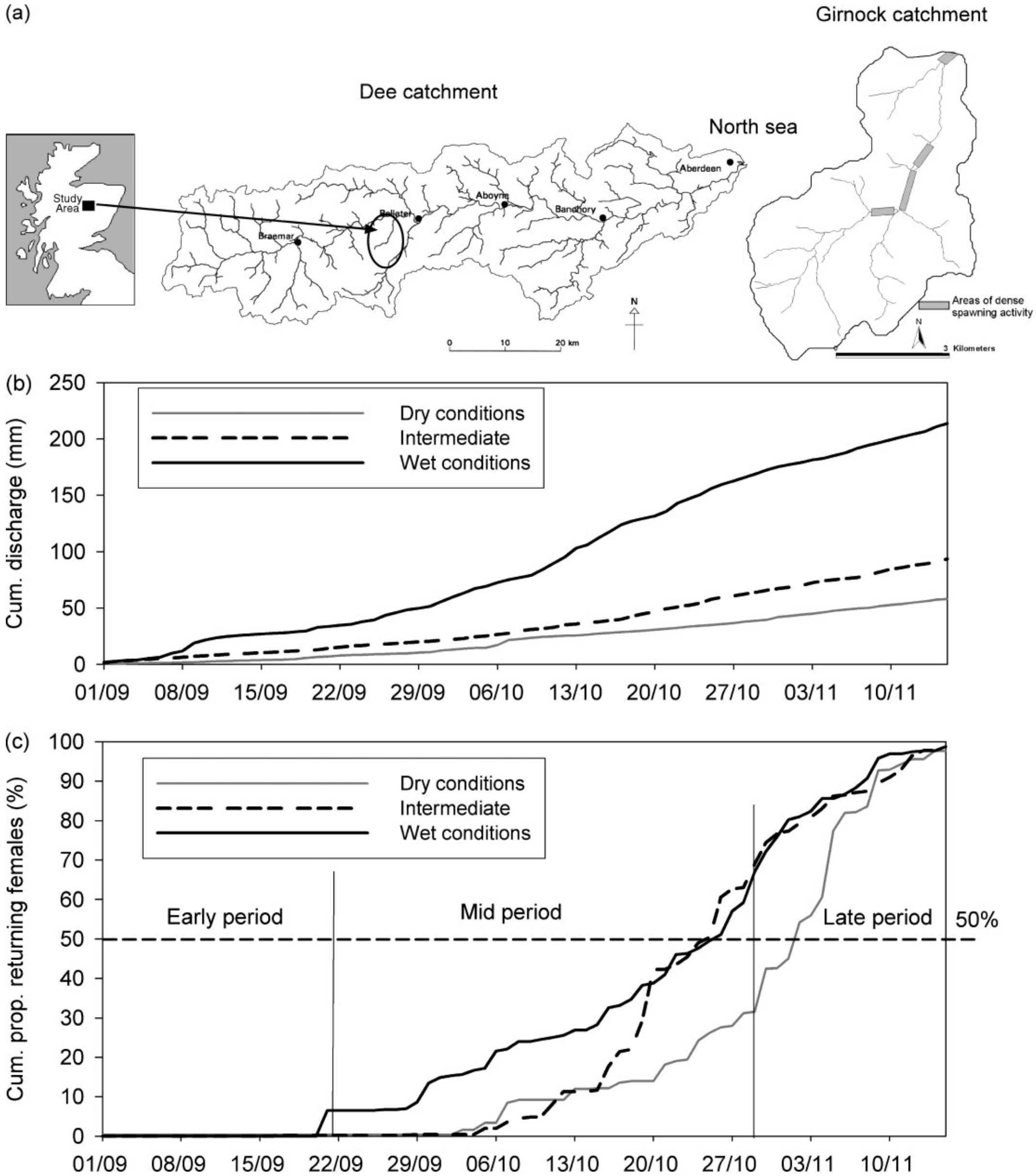

Figure 1. (a) Location of the Girnock catchment; (b) Cumulative discharge averaged for different flow regime types (dry, wet and intermediate); (c) Corresponding cumulative proportions of adult female fish arriving in the Girnock. Curves were calculated using overall values from each of the years forming respective groups, e.g. 60% of all the fish arriving in the years falling into the wet type regime arrived before 28th October (end of mid period)

which, in dry years, may be delayed by several weeks. Working at this larger spatial scale of analysis, with longer-term fish trap and hydrological records, provides a more integrated insight into how hydrological factors influence salmon's movement between different habitats in the riverscape, and how these are affected by climatic and hydrological variability.

Other recent work in the Girnock was carried out from a hydrological perspective to use hydrometric and tracer data, in conjunction with GIS analysis, to understand the catchment's hydrological response. This has helped elucidate aspects of the structure and dynamics of catchment scale connectivity in order to understand runoff generation (Tetzlaff *et al.*, 2007). Put simply, storm runoff in the Girnock catchment is mainly generated by saturation overland flow from the dominant peaty soils, while groundwater sustains base-flows. The catchment's hydrological behaviour is 'flashy', with approximately 70–75% of annual runoff being generated by rapid hydrological pathways emanating from the peaty soils, and groundwater contributing only 25–30%. The responsive hydrological pathways from acidic soils generate low pH (*ca* 5·0), low alkalinity runoff, while deeper groundwater is much more alkaline. Comparison of flow and alkalinity duration curves show close correspondence, which indicates that tracers can provide an insight into the degree to which the areas generating storm runoff are connected with the stream network (Soulsby *et al.*, 2004). Thus, as antecedent conditions become wetter and flows increase, the alkalinity falls and can be used as an index of connectivity.

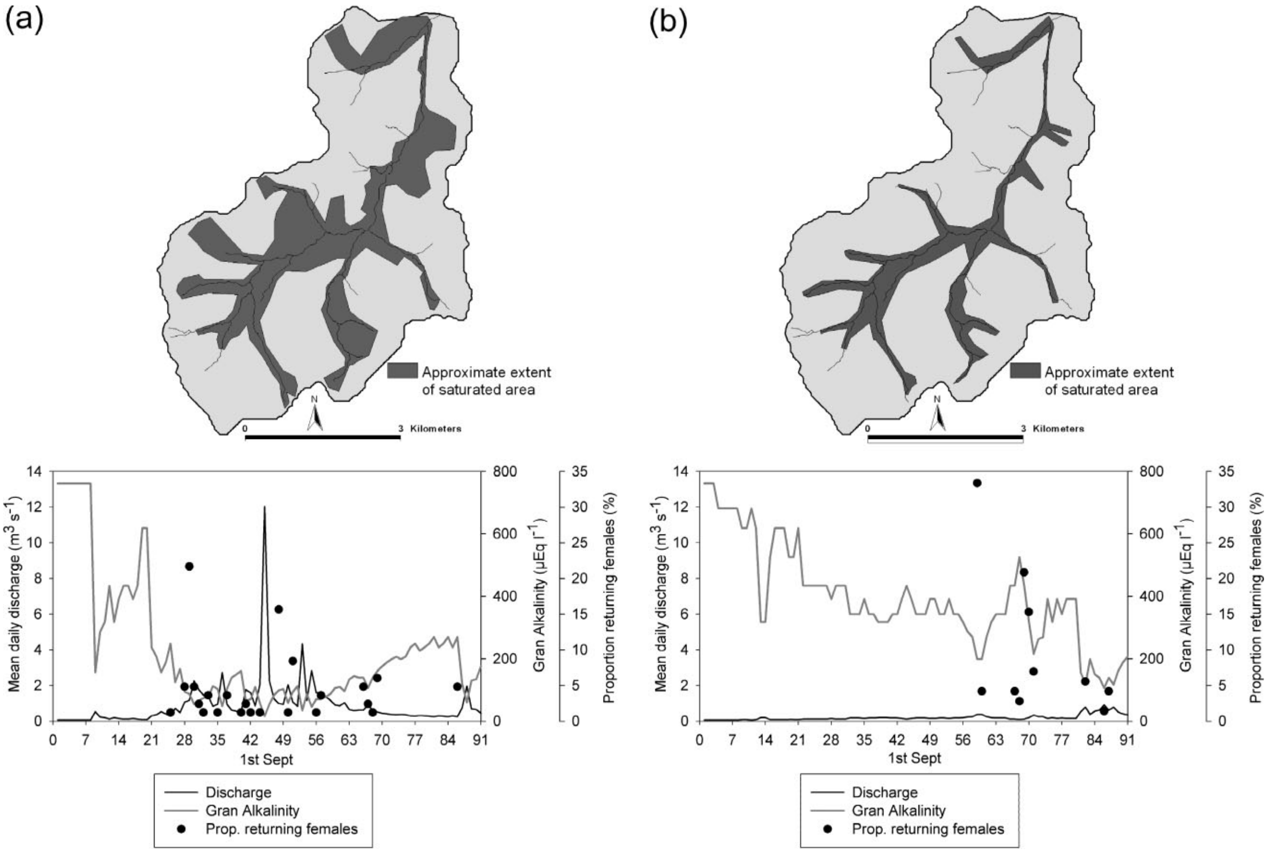

Figure 2. Fish pre-spawning entry in relation to stream flows and alkalinity data in a (a) wet year and (b) dry year which reflect the extent of field-mapped saturated areas prior to pre-spawning entry

These insights have allowed us to use tracers to link the connectivity of habitats in the spawning period riverscape to the hydrological connectivity of the catchment landscape. In wetter years, where wet antecedent conditions prevailed, saturated areas are extensive, providing a high degree of connectivity between the hillslope flow paths and channel network. This is reflected in the higher stream flows, which are characterised by low stream alkalinities (Figure 2a). This high connectivity along the Dee and between the Dee and Girnock facilitates early fish entry and maintains entry throughout the whole spawning period. This maximises the likelihood of an even distribution of spawners throughout the channel network, which optimises subsequent juvenile habitat utilisation. In contrast, when dry antecedent conditions prevail, spawning entry is often late and suboptimal flows are used, which minimises likelihood of even distribution of spawning (Figure 2b). The timing and distribution of spawning, together with subsequent winter climate, will determine the timing and distribution of juvenile emergence and may influence subsequent recruitment and wider processes in stream ecology.

Lessons Learned

As we move increasingly to such integrated approaches to understand the interactions between catchment hydrology and ecology, the concept of connectivity has obvious potential as a unifying theme where exchange of concepts and cross-fertilization of ideas can occur. Understanding ecological processes in the context of explicit catchment hydrological processes (rather than flow regime analysis) offers an exciting research frontier in catchment hydrology, which has the potential to provide many important insights. For example, in the same catchment, Malcolm *et al.* (2005, 2006) have carried out hillslope and catchment scale studies to show the spatial and temporal nature of groundwater connectivity with the hyporheic zone and its implications for embryo survival.

As Pringle (2003) notes, understanding the importance of connectivity in hydrological and ecological systems is important given the degree to which such connectivity has been severed or affected by human activities, such as river regulation or water abstraction. However, this makes elucidation of such interlinkages difficult in heavily managed riverscapes and landscapes. Thus, studies of relatively undisturbed systems like the Girnock Burn remain extremely important. Obviously, such insights will also be predicated on a commitment to sites where long-term data sets—both ecological and hydrological—will be collected. Such sites are of fundamental significance if meaningful predictions of the long-term effects of environmental change, such as climatic warming, are to be made.

A final aspect of 'connectivity' of such studies relates to the connections between hydrologists and ecologists in interdisciplinary research. Our informal group has a long history (*ca* 15 years) of successfully working within an interdisciplinary environment at the Girnock study site and elsewhere. Some of the new conceptual frameworks for researching ecohydrological issues in our study catchments are now providing a platform for some truly integrated perspectives on the physical, chemical and biological functioning of catchment systems. We are sometimes surprised to hear experiences of colleagues in hydrology (and ecology) who find working in an interdisciplinary environment—often in large, well-funded projects—difficult and sometimes unproductive. Indeed, as Hannah *et al.* (2004) note, many such studies often remain more multi-disciplinary than inter-disciplinary. As specialist hydrologists or ecologists, we have found working on issues of common interest—in an atmosphere of mutual respect and with a willingness to learn—has always proved intellectually stimulating as well as giving many insights into how catchments behave as integrated environmental systems.

References

Bacon PJ, Gurney WSC, Jones W, McLaren IS, Youngson AF. 2005. Seasonal growth patterns of wild juvenile fish: partitioning variation among explanatory variables, based on individual growth trajectories of Atlantic salmon (*Salmo salar*) parr. *Journal of Animal Ecology* 74: 1–11.

Beechie T, Buhle E, Ruckelshaus M, Fullerton A, Holsinger L. 2006. Hydrologic regime and the conservation of salmon life history diversity. *Biological Conservation* 130: 560–572.

Bond B. 2003. Hydrology and ecology meet–and the meeting is good. *Hydrological Processes* 17: 2087–2089.

Bonell M. 2002. Ecohydrology–a completely new idea? *Hydrological Sciences Journal* 47(5): 809–810.

Carss DN, Kruuk H, Conroy JWH. 1990. Predation on adult Atlantic salmon, *Salmo salar L.*, by otters, *Lutra lutra (L.)*, within the River Dee system, Aberdeenshire, Scotland. *Journal of Fish Biology* 37: 935–944.

Fausch KD, Torgersen CE, Baxter CV, Li HW. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *Bioscience* 52(6): 483–498.

Gibbins CN, Moir H, Webb J, Soulsby C. 2002. Assessing discharge use by spawning Atlantic salmon: a comparison of discharge electivity indices and PHABSIM simulations. *Rivers Research and Application* 18: 383–395.

Hannah DM, Wood PJ, Sadler JP. 2004. Ecohydrology and Hydroecology: a 'new paradigm'? *Hydrological Processes* 18: 3439–3445.

Lane SN, Brookes CJ, Kirkby AJ, Holden J. 2004. A network-index based version of TOPMODEL for use with high-resolution digital topographic data. *Hydrological Processes* 18(1): 191–201.

Malcolm IA, Youngson AF, Soulsby C. 2003. Survival of salmonid eggs in a degraded gravel bed stream: effects of groundwater–surface water interactions. *River Research and Applications* 19: 303–316.

Malcolm IA, Soulsby C, Youngson AF, Hannah DM. 2005. Catchment scale controls on groundwater-surface interactions in salmon spawning gravels. *Rivers Research and Application* 21: 977–989.

Malcolm IA, Soulsby C, Youngson AF. 2006. Dissolved oxygen in salmon spawning gravels with contrasting groundwater-surface water interactions: insights from monitoring at fine spatial and temporal scales. *Hydrological Processes* 20: 615–622.

McDonnell JJ, Sivapalan M, Vache K, Dunn SM, Grant G, Haggerty R, Hinz C, Hooper R, Kichner J, Roderick ML, Selker J, Weiler M. Moving beyond descriptions of watershed heterogeneity and process complexity: a new vision for watershed hydrology. *Water Resources Research* (in press).

Moir H, Soulsby C, Youngson AF. 2002. The hydraulic and sedimentary controls on the availability of Atlantic salmon spawning habitat in the river system NE Scotland. *Geomorphology* 45: 291–308.

Moir H, Gibbins CN, Soulsby C, Webb J. 2004. Linking channel geomorphic characteristics to spatial patterns of spawning activity and discharge use by Atlantic salmon (*Salmo salar L.*). *Geomorphology* 60: 21–35.

Moir H, Gibbins C, Soulsby C, Youngson AF. 2005. Validation of PHABSIM predictions for simulating salmon spawning habitat. *Rivers Research and Application* 21: 1–14.

Olden JD, Poff NL. 2003. Redundancy and the choice of hydrological indices for characterising streamflow regimes. *River Research and Applications* 19: 101–121.

Petts G, Morales Y, Sadler J. 2006. Linking hydrology and biology to assess the water needs of river ecosystems. *Hydrological Processes* 20: 2247–2251.

Pringle C. 2003. What is hydrologic connectivity and why is it ecologically important? *Hydrological Processes* 17(13): 2685–2689.

Schlosser IJ. 1991. Stream fish ecology: a landscape perspective. *BioScience* 41: 704–712.

Soulsby C, Tetzlaff D, Rodgers P, Dunn SM, Waldron S. 2006a. Runoff processes, stream water residence times and controlling landscape characteristics in a mesoscale catchment: an initial evaluation. *Journal of Hydrology* 325: 197–221.

Soulsby C, Tetzlaff D, Dunn SM, Waldron S. 2006b. Scaling up and out in runoff process understanding–insights from nested experimental catchment studies. *Hydrological Processes* 20: 2461–2465.

Soulsby C, Rogers P, Petry J, Hannah D, Dunn SM, Malcolm IA. 2004. Using tracers to upscale flow path understanding in mesoscale mountainous catchments: two examples from Scotland. *Journal of Hydrology* 291: 172–294.

Stanford JA. 2006. Landscapes and riverscapes. In *Methods in Stream Ecology*, Hauer RF, Lamberti GA (eds). Elsevier: Amsterdam; 3–21.

Tetzlaff D, Grottker M, Leibundgut C. 2005a. Hydrological criteria to assess changes of flow dynamic in urban impacted catchments. *Physics and Chemistry of the Earth (PCE)* 30(6–7): 426–431.

Tetzlaff D, Soulsby C, Youngson AF, Gibbins CN, Bacon PJ, Malcolm IA, Langan SJ. 2005b. Variability in stream discharge and temperature: a preliminary assessment of the implications for juvenile and spawning Atlantic salmon. *Hydrology and Earth Systems Sciences* 9: 193–208.

Tetzlaff D, Gibbins CN, Bacon PJ, Youngson AF, Soulsby C. Influences of hydrological regimes on the pre-spawning entry of Atlantic salmon (*Salmo salar L.*) into an upland river. *Rivers Research and Applications* (in press).

Tetzlaff D, Soulsby C, Waldron S, Malcolm IA, Bacon PJ, Dunn SM, Lilly A. 2007. Conceptualisation of runoff processes using GIS and tracers in a nested mesoscale catchment. *Hydrological Processes*. DOI: 10·1002/hyp.6309.

Tromp Van Meerveld I, McDonnell JJ. 2006. Threshold relations in subsurface stormflow 1: A 147 storm analysis of the Panola hillslope trench. *Water Resources Research* 42: 1–11. DOI:10·1029/2004WR003778.

Webb JH, Gibbins CN, Moir H, Soulsby C. 2001. Flow requirements of spawning Atlantic salmon in an upland stream: implications for water resource management. *Journal of the Chartered Institute of Water and Environmental Management* 15: 1–8.

Wiens JA. 2002. Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology* 47(4): 501–515.

Youngson AF, Malcolm IA, Bacon PJ, Soulsby C. 2004. Long-residence groundwater and mortality of salmonid eggs: low hyporheic DO limits natural recruitment of fry. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 2278–2287.