Hydrology and Earth System Sciences, 9, 193–208, 2005
www.copernicus.org/EGU/hess/hess/9/193/
SRef-ID: 1607-7938/hess/2005-9-193
European Geosciences Union

Hydrology and
Earth System
Sciences

Variability in stream discharge and temperature: a preliminary assessment of the implications for juvenile and spawning Atlantic salmon

D. Tetzlaff[1], C. Soulsby[1], A. F. Youngson[2], C. Gibbins[1], P. J. Bacon[2], I. A. Malcolm[2], and S. Langan[3]

[1]Department of Geography and Environment, University of Aberdeen, Aberdeen AB24 3UF, UK
[2]FRS Freshwater Laboratory, Faskally, Pitlochry, Perthshire, PH16 5LB, UK
[3]The Macaulay Institute, Craigiebuckler, Aberdeen, AB15 8QH, UK

Received: 14 March 2005 – Published in Hydrology and Earth System Sciences Discussions: 18 May 2005
Revised: 10 August 2005 – Accepted: 31 August 2005 – Published: 14 September 2005

Abstract. This study focuses on understanding the temporal variability in hydrological and thermal conditions in a small mountain stream and its potential implication for two life stages of Atlantic salmon (*Salmo salar*) – stream resident juveniles and returning adult spawners. Stream discharge and temperature in the Girnock Burn, NE Scotland, were characterised over ten hydrological years (1994/1995–2003/2004). Attention was focussed on assessing variations during particular ecologically "sensitive" time periods when selected life-stages of salmon behaviour may be especially influenced by hydrological and thermal conditions.

Empirical discharge data were used to derive hydraulic parameters to predict the Critical Displacement Velocity (CDV) of juvenile salmon. This is the velocity above which fish may no longer be able to hold station in the water column and thus can be used as an index of time periods where feeding behaviour might be constrained. In the Girnock Burn, strong inter- and intra-annual variability in hydrological and thermal conditions may have important implications for feeding opportunities for juvenile fish; both during important growth periods in late winter and early spring, and the emergence of fry in the late spring. Time periods when foraging behaviour of juvenile salmon may be constrained by hydraulic conditions were assessed as the percentage time when CDV for 0+ and 1+ fish were exceeded by mean daily stream velocities. Clear seasonal patterns of CDV were apparent, with higher summer values driven by higher stream temperatures and fish length. Inter-annual variability in the time when mean stream velocity exceeded CDV for 0+ fish ranged between 29.3% (1997/1998) and 44.7% (2000/2001). For 1+ fish mean stream velocity exceeded CDV between 14.5% (1997/1998) and 30.7% (2000/2001) of the time.

The movement of adult spawners into the Girnock Burn in preparation for autumn spawning (late October to mid-November) exhibited a complex relationship with hydrological variability with marked inter-annual contrasts. In years when discharge in the period prior to spawning was low, fish movement was increasingly triggered by suboptimal flow increases as spawning time approached. In contrast, wet years with numerous events allowed a much more even distribution of fish entry. Elucidating links between discharge/temperature variability and foraging opportunities and upriver migration of adult Atlantic salmon have the potential to contribute to the improvement of conservation strategies in both regulated and unregulated rivers.

1 Introduction

In river ecosystems the influences of discharge and temperature on aquatic organisms are often complex and interactive (Puckridge et al., 1998; Petts, 2000; Soulsby and Boon, 2001; Naiman et al., 2002). Aquatic organisms are generally adapted to a wide range of variability in stream discharge and temperatures (Allan, 1995); however, it is often difficult to define what "natural" variability is, given strong anthropogenic impacts on many rivers (Poff et al., 1997). Empirical studies that directly examine hydrological influences on aquatic organisms are still relatively scarce, and high quality, longer-term paired data sets of environmental and biological parameters are uncommon. Furthermore, very few studies have attempted to consider hydrological and thermal

---

Correspondence to: D. Tetzlaff
(d.tetzlaff@abdn.ac.uk)

variability simultaneously and explicitly link them to the functioning of aquatic ecosystems (Harris et al., 2000).

In many hydroecological studies, it is often assumed that averaged statistics (e.g. using monthly or weekly means) are sufficient to characterise flow and thermal regimes in ways that allow meaningful correlations with ecological functioning (Richter et al., 1996; Richter et al., 1998; Clausen and Biggs, 2000; Olden and Poff, 2003). But such analyses for coarser temporal scales are likely to underplay the fact that the biological effects of flow and temperature changes often occur much more rapidly (Stewardson and Gippel, 2003). In extreme cases, responses can occur over the course of individual hydrological events (Archer and Newson, 2002; Tetzlaff et al., 2005a), which can cause temporary, but substantial, changes in physical habitat and affect ecosystem functioning (Schlosser, 1995; Arndt et al., 2002). Our understanding of such short-term hydroecological interactions is poorly developed.

The Scottish Highlands contain some of the least disturbed rivers in Europe (Gilvear et al., 2002), and the region experiences highly variable flow conditions and marked annual ranges in stream temperatures, though the effects on ecosystem functioning are poorly understood (Gibbins et al., 2001). Many Highland rivers are internationally important as spawning and rearing habitats for Atlantic salmon (*Salmo salar*): particularly the early “spring” running fish which are of great economic, cultural and conservation importance. Salmon is often cited as a key higher order species and an indicator of wider ecosystem health, thus it is commonly a target species for instream flow studies aimed at providing an ecological basis for river management (Gibbins et al., 2002; Webb et al., 2002; Gordon et al., 2004; Moir et al., 2005). A number of Scottish salmon rivers are used for hydropower production and have regulated flow regimes that are only crudely relevant to the environmental requirements of salmon; and adverse impacts of flow regulation on salmon populations have been reported (Gilvear, 1994).

Understanding the hydrological and thermal requirements of Atlantic salmon at different life-stages is important for river management (Gilvear et al., 2002). Discharge influences in-stream hydraulics is thus one of the basic determinants of the amount of habitat space available in river systems for different life stages (Petts, 1980). A number of studies have investigated the influence of stream discharge on different phases of the salmon’s life-cycle (e.g. Økland et al., 2001; Jensen, 2003). For stream resident salmonids, discharge can exert a strong influence on general behaviour including foraging (e.g. Flodmark et al., 2004; Enders et al., 2005). In addition, discharge thresholds have been observed to trigger some life-stage specific activities, including upstream migration to spawning areas, spawning activity itself and the downstream migration of smolts (Youngson et al., 1983; Bunt et al., 1999; Gibbins et al., 2002). Likewise, temperature exerts a major influence on physiology reflected, for example, in the growth rate of stream-dwelling juveniles (e.g. Elliot, 1991; Arndt et al., 2002; Elliot and Hurley, 2003; Bacon et al., 2005). Temperature may also help trigger life-stage specific behaviours such as juvenile salmonid migration (Swansburg et al., 2004).

In the Girnock Burn, an upland tributary of the River Dee in Scotland, the Atlantic salmon population (adult spawner returns, smolt production, juvenile densities etc) has been routinely monitored since 1966. Therefore, a unique data set of long-term high resolution biological data is available. Alongside this, stream flows and temperatures have also been monitored, providing a rare longer-term hydroecological data set. Amongst other things, these data indicate two potentially important hydrological and thermal influences on the salmon population. Firstly, recent work using physiological and empirical models have suggested that much (ca. 85%) of the inter-annual variability in the growth rates of juvenile Atlantic salmon can be accounted for by variability in water temperatures (Bacon et al., 2005). It has been hypothesised that some of the unexplained variation in growth may be related to temporal differences in discharge regimes which may affect the availability of suitable hydraulic habitats when velocities are so high that fish are either unable to feed or when their prey capture success is reduced (Graham et al., 1996; Tetzlaff et al., 2005b). Secondly, the returning numbers of adult spawners has markedly declined over the part 2 decades, leading to concerns that insufficient fish may be returning to maintain a viable salmon population (Webb et al., 2001). Optimal juvenile fish distributions to maximise habitat utilization in spawning streams – and maximise smolt production – are considered to result from even distributions of spawning along approximately 8 km of the river system. However, in the past decade a number of dry autumns have been noted to delay spawning entry to the stream and focus spawning in the lower reaches of the river. In such situations, uneven spawning distributions may result in inadequate use of juvenile habitat and compromise smolt production (Gibbins et al., 2002).

To understand these issues better, the specific objectives of the study reported in this paper are: (i) To characterise hydrological and thermal conditions over 10 hydrological years (1994/1995–2003/2004) in the Girnock Burn, particularly during selected ecologically “sensitive” periods where flow and temperature variability might be expected to have a particular influence on certain salmon life stages. (ii) To examine the relationships between this variability in discharge and temperatures on the potential opportunities for foraging and food acquisition by juvenile fish via application of the concept of Critical Displacement Velocity (CDV) (Graham et al., 1996; Gibbins and Acornley, 2000) and (iii) To assess the influence of flows in the final phase of the upstream migration of adults during autumn, when they move into the Girnock Burn from the river Dee.

2 Study site

The Girnock Burn drains a catchment of 30.3 km^2 (Fig. 1) with altitude ranging from 230 m to 862 m. The upper part of the catchment is underlain by granite while the geology in the lower parts is dominated by schists and other metamorphic rocks (Soulsby et al., 2005b). Land use is dominated by heather (*Calluna vulgaris*) moorland used for deer stalking and grouse shooting, with smaller areas of abandoned rough grazing and forestry.

Extensive data sets have been compiled to characterise the hydrology, water quality and geomorphology of the Girnock Burn (e.g. Langan et al., 2001; Gibbins et al., 2002; Malcolm et al., 2003; Moir et al., 2004; Hannah et al., 2004). The stream is characterised by high inter- and intra-annual variability in discharge dynamics and thermal regimes (Moir et al., 1998; Malcolm et al., 2002; Soulsby et al., 2005a); though the effects of these on different salmon life-stages are not well-understood.

Average annual precipitation (1961–1990) is 1100 mm with the summer months (May–August) generally being driest. Discharge is calculated from stage measured in a calibrated section of the river at Littlemill using standard flow velocity cross-section methods (Fig. 1). Mean annual discharge is 0.52 m^3 s^{-1} (1969–2001), though discharges between June and August are often below 0.1 m^3 s^{-1} (Moir et al., 1998). However, instantaneous discharges have varied between ca. 0.04 m^3 s^{-1} in summer low flows (Malcolm et al., 2003) and $>$50 m^3 s^{-1} during floods. Most high discharge events occur between late autumn and early spring, though they can also occur in summer.

Mean annual stream temperature over the period 1968–1997 was ca. 7.0°C though Langan et al. (2001) noted that there was considerable inter-annual variation. For the winter months, variation of mean daily temperatures was constrained to 0.5–4.0°C but during summer mean daily temperatures varied between 11–13.5°C. Over the 30 year period examined there was no change in mean annual temperature with time, but an increase (ca. 1°C) in mean daily temperatures during winter and spring was observed (Langan et al., 2001).

The stream provides an important spawning and rearing habitat for Atlantic salmon and has been used as a research and monitoring site by the Scottish Executive's Freshwater Laboratory since 1966. A fish trap at Littlemill intercepts returning adult fish as they enter the stream close to spawning time. The growth of juveniles in the stream above the traps is monitored by electrofishing, marking and sizing resident fish at regular intervals throughout the year; most juveniles leave the stream at two or three years of age.

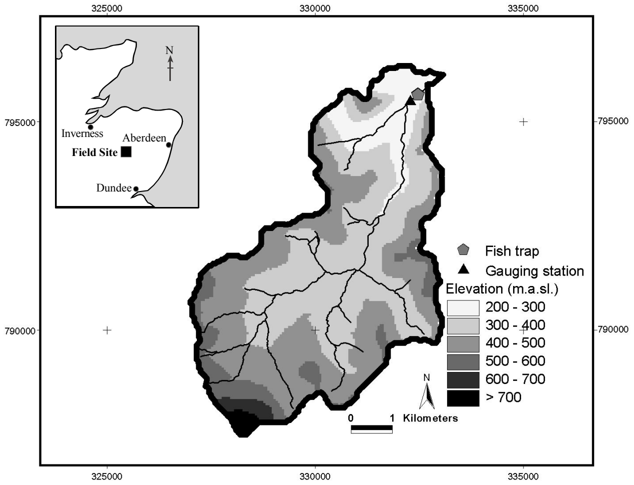

Fig. 1. The Girnock Burn catchment: location and topography showing gauging site at Littlemill and fish trap.

3 Methodology

3.1 Hydrology and hydraulic characteristics

Despite a 35 year data record of mean daily flows, quality controlled, high resolution discharge data (15 min) were only available for the ten most recent hydrological years (October–September) between 1994/1995 and 2003/2004. This was because the site was established for fisheries investigations where mean daily flow data were assumed to be adequate hydrological measurements. The flow data was used to derive flow duration curves and flow accumulation curves. The latter involved conversion of flow data from m^3 s^{-1} to mm.

Hydrological conditions are only an indirect measure of the hydraulic forces that aquatic organisms experience in the stream channel. To obtain more direct hydraulic data from the discharge measurements, a mean stream velocity (m s^{-1}) time series was derived. This used 89 existing calibration gaugings (1997–2004) at Littlemill; average velocities were measured across the gauged section from 26 points at the mean column velocity position (0.6×depth). From the gaugings, a total of 89 data points could be used to derive a discharge-mean velocity relationship for the gauged section. A power function best described the relationship (r^2=0.99) and was used to construct a mean velocity time series for each hydrological year (Tetzlaff et al., 2005b). Figure 2 shows the velocity distribution for the cross section at Littlemill for representative discharge; including those for the median (Q_{50}), high (Q_{10}) and low (Q_{95}) discharges. Low flow conditions (e.g. Q_{95}) generated uniformly low mean stream velocities but even at higher flows ($>Q_{50}$=0.52 m^3 s^{-1}) there remained areas of low stream velocity, which were potentially available as refugia for fish and other organisms.

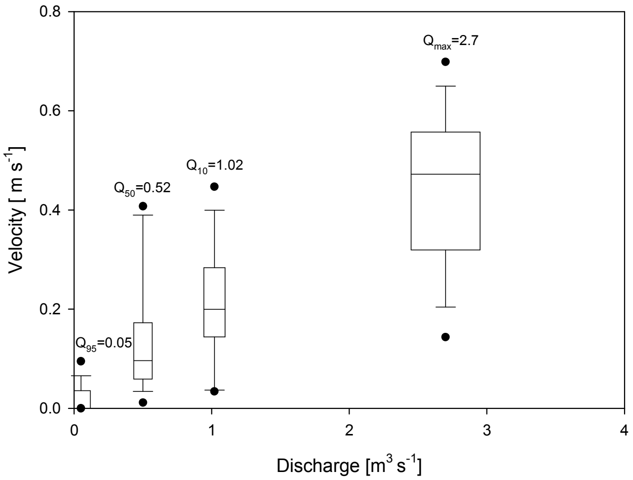

Fig. 2. Stream velocity for several discharges with median, 5th/95th percentiles (outlying points), 10th/90th percentiles (whiskers) and 25th/75 percentiles (box boundaries) at the cross-section at gauging site Littlemill ($Q_{\max}$ = maximum gauged flow; $Q_{95,50,10}$=95%, 50% (Median) and 10% exceedence during time period 1997–2004.).

Temporal variations in mean stream velocity at the gauged site were assumed to provide a meaningful index of the general temporal variation in stream velocities throughout the catchment. Obviously, it was recognised that different channel characteristics generate high spatial variability in velocity conditions at equivalent discharges in different stream channel types (Moir et al., 2002). Thus interpretations must be cautious. Nevertheless, in the absence of more spatially distributed long-term data sets, we can reasonably assume that the Littlemill data provide a meaningful indication of the temporal variability in velocity conditions throughout the catchment. In other words, when velocities are high at Littlemill, they are very likely to be high elsewhere in the catchment.

3.2 Stream temperature monitoring

Stream temperature data were available from 1968 at hourly resolution from a logging thermistor. Total error of a range of instruments used during this period is estimated at 0.6°C. When instruments were replaced – as new technologies became available – periods of parallel monitoring were used to check for no systematic errors (Langan et al., 2001). Temperature monitoring was carried near the Littlemill fish traps, where the stream is tree-lined. This was assumed to be a reasonable location of catchment-wide inferences as previous investigations have shown that stream temperatures exhibit little spatial variability under most conditions (Malcolm et al., 2004).

Data capture was 93%; the strong correlation between stream and air temperatures above 0°C facilitated the gaps in stream temperature time series being in filled using linear air-stream temperature relationships on an hourly basis for each month. Air temperature data were obtained on an hourly basis from the Meteorological Office observation station at Aboyne, about 20 km east of the catchment. A number of studies have discussed the limitations of such approximation (e.g. Webb and Nobilis, 1997; Mohseni and Stefan, 1999; Webb et al., 2003). However, this was the most convenient way of infilling the data record and high correlation coefficients for individual months indicated that the approach was reasonable. Degree days are a means of assessing the relationships between cumulative temperature measure sand ecological processes (Allan, 1995) and these values were calculated by summing all daily mean temperatures above 0°C.

3.3 Biological assessment for juvenile and spawning Atlantic salmon

To provide a framework for hydro-thermal analyses in the context of likely implications for Atlantic salmon, the following periods were identified on the basis of detailed observations at the site over a 35 year period. The 15 October–14 November (Period 1 in this paper) approximates the main period where Atlantic salmon enter the Girnock Burn for spawning. Spawning activity occurs during a more restricted time period, typically between 1 and 14 November (Webb et al., 2001). The winter period between 15 November–14 March (Period 2) represents a time of low biological activity and low growth for juvenile fish (Bacon et al., 2005). The spring period between 15 March–15 May (Period 3) represents the time of most rapid juvenile growth for fish that are one year of age or older (Bacon et al., 2005). During the final summer period until 31 August (Period 4) juvenile growth slows as a consequence of higher temperatures and higher metabolic costs prior to the end of the hydrological year (Bacon et al., 2005).

To assess the implication of variations in velocity dynamics for juvenile Atlantic salmon, Critical Displacement Velocity (CDV, Graham et al., 1996) was calculated. CDV is the maximum velocity against which a fish can hold station over sustained periods. When stream velocity exceeds CDV, it is assumed that fish will be unable to hold station and foraging opportunities are expected to be correspondingly constrained (Gibbins and Acornley, 2000), resulting in decreased growth rates or weight losses (Arndt et al., 1996). CDV is determined using relationships derived from flume experiments (Graham et al., 1996). Stream temperature and length data are input to a regression equation to calculate CDV ($\mathrm{m\,s^{-1}}$):

$$CDV=CDV_{BL}*L/100 \text{ with } CDV_{BL}=4.14 logT+1.74 \quad (1)$$

where CDV_{BL} is expressed in body lengths per second, T=water temperature (°C) and L is fish body lengths (cm). CDV's were estimated using date-specific mean fish length and mean daily stream temperature.

For estimating CDV's in the stream on any given day, the mean length of juveniles was derived from growth curves for the years 2002 and 2003 (described in detail in Tetzlaff et al., 2005b). The curves were derived from fish length data from electro-fishing surveys carried out in the Girnock at approximately monthly intervals. Data were available for 687 salmon fry (i.e. <1 year of age) and 1175 parr (between 1 and 2 years old). Best fit lines were fitted through size data using linear trend series filling so as to allow estimation of daily length increments. In the Girnock Burn, fry reach about 50 mm by the end of their first summer and about 100 mm a year later (Bacon et al., 2005).

To estimate CDV exceedence, and indicate the time periods when foraging may be adversely affected by high flows, the mean stream velocity at Littlemill was compared to the CDV's estimated for 0+ and 1+ fish. This analysis clearly involves several assumptions which need to be justified. First, it is assumed that the mean velocities at Littlemill are representative of velocity conditions throughout the Girnock. Second, it is assumed that mean velocity data (derived from mean column velocities) characterise the velocities that foraging salmon will experience. Thirdly, it assumed that CDV's derived from flume studies are representative for the responses of fish to changing velocities in complex natural channels. Whilst spatial variation in velocities at the catchment scale – given the diversity of channel types (Moir et al., 2004) – is likely to be even greater than the variability observed at the measured transect shown in Fig. 2, the temporal variation is likely to be indexed at Littlemill as noted above. Moreover, this is also likely to reflect temporal variations in more complex velocity fields in the water column. Thus, it is established that juvenile salmon can use refugia with hydraulically boundary layers near the stream bed at high flows (Armstrong et al., 2003). Nevertheless, at higher velocities when CDVs are exceeded, it is reasonable to assume that the total habitat available is likely to decline as fish movement will probably become more restricted. Whilst flume studies are unlikely to replicate conditions in the stream, empirically establishing the relationships between fish behaviour and flow variability in complex channels and spatially variable river systems is a major research undertaking and certainly beyond the scope of this study. Previous work has indicated that, although flume based, the CDV approach can have utility in understanding salmon responses to flow variability (Gibbins and Acornley, 2000). Thus, despite of these limitations, analysis of CDV can be a useful preliminary step towards linking velocity, temperatures and fish size. However, it is important to remember that when CDVs are predicted to be exceeded that foraging of fish will necessarily stop, or fish will be unable to survive, but simply show time periods when movement and feeding are most likely to be constrained. Indeed smaller flow increases may actually enhance drift and food sources (Kemp et al., 2003).

Relationships between hydrological and thermal variables and the numbers of returning spawning adults were investigated using data from the fish trap. The number of fish entering the stream is monitored daily during the relevant times of the year. Radio tagging studies have shown that returning adult salmon that spawn in the Girnock gradually move up the Dee throughout the year and in the months prior to spawning are found in holding pools a short distance down stream of the Girnock confluence. Movement into the Girnock represents the start of the final stage of the salmon life cycle. Since 1966 the mean annual number of adult salmon entering the Girnock Burn to spawn has been 125; with a range between 20 (2000) and 293 (1987). In general, females enter the stream ahead of males, at or before ovulation, and are expected to be more clearly responsive to abiotic factors than males, which respond additionally to pheromonal signals generated by females in spawning- or near-spawning condition (Moore and Waring, 1996). For the 10 years investigated, the number of returning females varied between 9 (1997/1998) and 71 (1995/1996, Fig. 3).

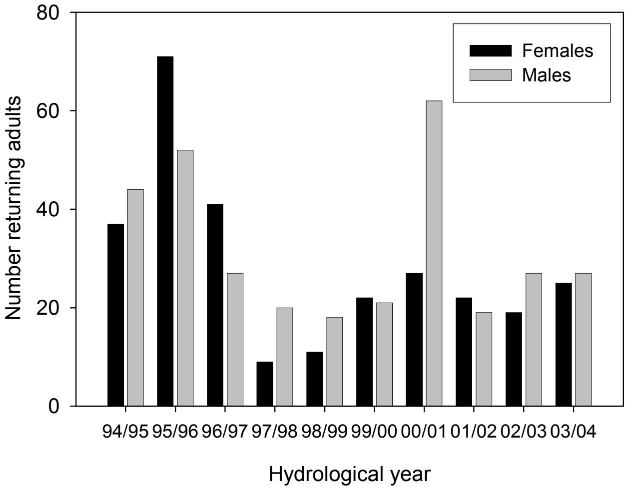

Fig. 3. Number of returning spawning adults entering the Girnock Burn during the ten hydrological years investigated.

4 Results

4.1 Characterisation of stream discharge

Marked inter-annual variability of discharge is evident in the range of the flow duration curves, whilst high intra-annual variability of discharge (e.g. in 1994/1995 and 2002/2003) is shown by steep flow duration curves (Fig. 4). For individual years, the Q_1 (1% exceedence) ranged between 8.63 $m^3 s^{-1}$ (1994/1995) and 2.82 $m^3 s^{-1}$ (2003/2004). The Q_{95} (95% exceedence) varied between 0.15 $m^3 s^{-1}$ (2001/2002) and 0.032 $m^3 s^{-1}$ (1998/1999). The long-term mean daily discharge of 0.52 $m^3 s^{-1}$ (1966–2003) was exceeded for 27% of the time on average; exceedence ranged between 19% (1996/1997) and 40% (2000/2001) in individual years.

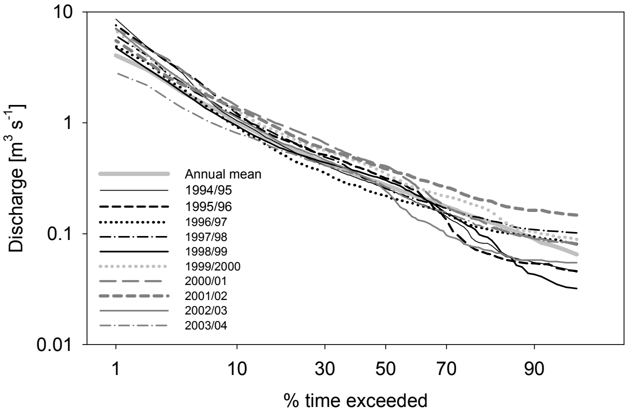

Fig. 4. Flow duration curves for the ten hydrological years investigated.

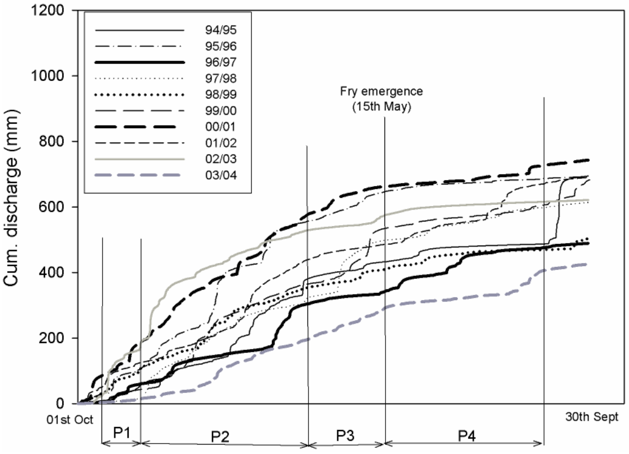

Fig. 5. Cumulative discharge curves showing ecological sensitive time periods: P1=Period 1, 15 October–14 November, Main time period where spawning salmon enter the Girnock Burn; P2=Period 2, 15 November–14 March, Winter period – low biological activity and low growth for juvenile fish; P3=Period 3, 15 March–15 May, Spring period – most rapid juvenile growth for fish that are one year of age or older; P4=Period 4, 15 May–31 August, Summer period – juvenile growth slows as a result of higher temperatures and higher metabolic costs.

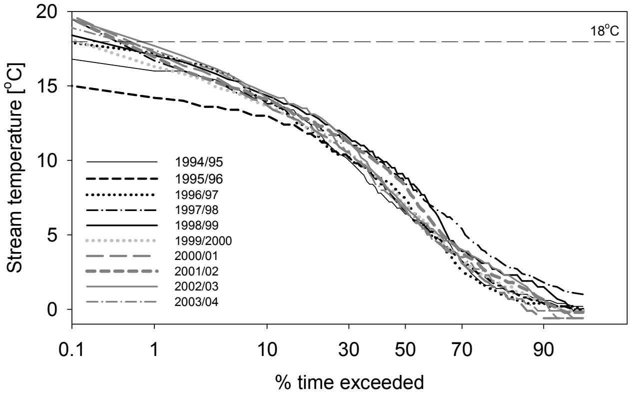

Fig. 6. Time of exceedence of stream temperatures showing benchmark temperature (optimum temperature) for Atlantic salmon growth (after Elliot and Hurley, 2003).

Focussing on the ecologically "sensitive" time periods where Atlantic salmon are potentially most susceptible to flow-related effects, the cumulative discharge curves show the magnitude and nature of flow variability within specific time periods for each year (Fig. 5). The winter period 2 (P2) was generally characterised by the most marked variability. The flattest period of flow accumulation (i.e. the lowest rate of change) was around the start of period 4 (P4), which coincides with the time of fry emergence.

In Table 1, selected discharge statistics are listed for the ten years and for each ecologically "sensitive" time period. Mean discharge varied between 0.48 (1996/1997) and $0.73\,\mathrm{m^3\,s^{-1}}$ (2000/2001). Principal Component Analysis (PCA) suggested that flow regimes differed between years principally in relation to their coefficients of variation and maximum flows.

The highest discharge generally occurred outside period 1 (i.e. when fish were moving into the burn), occurring four times during period 2 and three times during period 4. Only in 1997/1998 did the highest discharge occur in period 3. There was no consistent pattern in the timing of maximum discharge for different periods in individual years. This largely reflects the "flashy" hydrological regime of the Girnock Burn that even in summer high flow events can occur immediately after a period of low flow. Inter-annual variability in mean discharge, however, differed more markedly between designated periods. Period 1 had the greatest deviation between lowest and maximum value (93%), whilst period 2 showed the lowest variability (59%).

4.2 Characterisation of stream temperature

Stream temperatures in the Girnock Burn were characterised by less inter-annual variability than discharge (Fig. 6). Applying PCA to temperatures, inter-annual differences were characterised mainly by mean and median values. Mean temperatures ranged between 6.9°C (1995/1996) and 8.2°C (1997/1998, Table 2). The highest stream temperatures – exceeded for 1% of the time – ranged between 14.2°C (1995/1996) and 17.7°C (2002/2003). Stream temperatures in individual years varied between exceeding −0.6°C (2000/2001 and 2002/2003) and 1°C (1997/1998) for 95% of the time. Elliot and Hurley (2003) suggested a temperature of 18°C as the mid-point of an optimum temperature range for growth of Atlantic salmon based on growth model applications, with lower and upper temperatures for growth of 7.8°C and 24.6°C, respectively. However, Bacon et al. (2005) have shown that wild fish can probably grow well at temperatures below this lower limit. Stream

Table 1. Statistical values of discharge for ecologically sensitive time periods.

		Discharge ($m^3 s^{-1}$) 15 min time resolution				
Time period		Mean	Median	Max	Min	Coeff. of variation
Hydrological year	1994/1995	0.68	0.26	100.09 (09/09/1995)	0.04	3.86
	1995/1996	0.68	0.32	55.34 (08/01/1996)	0.04	2.63
	1996/1997	0.48	0.22	28.69 (19/02/1997)	0.07	2.14
	1997/1998	0.60	0.26	18.15 (05/04/1998)	0.06	2.07
	1998/1999	0.50	0.30	18.88 (20/09/1999)	0.03	1.83
	1999/20000	0.67	0.35	21.25 (22/12/1999)	0.06	1.96
	2000/2001	0.73	0.41	19.83 (10/10/2000)	0.06	1.79
	2001/2002	0.68	0.39	37.71 (31/07/2002)	0.12	1.72
	2002/2003	0.61	0.24	31.21 (21/11/2003)	0.05	2.8
	2003/2004	0.42	0.26	13.30 (11/08/2004)	0.06	1.46
Period 1 15 October–14 November Main time period where spawning salmon enter the Girnock Burn	1994/1995	0.64	0.34	13.87 (23/10/1994)	0.08	1.78
	1995/1996	0.93	0.4	30.62 (26/10/1995)	0.22	2.77
	1996/1997	0.65	0.34	10.33 (05/11/1996)	0.10	1.67
	1997/1998	0.15	0.11	1.01 (08/11/1997)	0.06	0.62
	1998/1999	1.03	0.57	10.50 (24/10/1998)	0.28	1.11
	1999/2000	0.45	0.27	04.61 (05/11/1999)	0.10	1.12
	2000/2001	1.28	0.71	16.90 (07/11/2000)	0.37	1.44
	2001/2002	0.98	0.54	07.75 (20/10/2001)	0.31	1.12
	2002/2003	1.93	0.72	26.84 (22/10/2002)	0.38	1.85
	2003/2004	0.14	0.11	0.81 (12/11/2003)	0.06	0.74
Period 2 15 November–14 March Winter period – low biological activity and low growth for juvenile fish	1994/1995	0.97	0.44	31.20 (10/03/1995)	0.11	2.03
	1995/1996	1.34	0.61	55.34 (08/01/1996)	0.16	1.93
	1996/1997	0.73	0.28	28.69 (19/02/1997)	0.09	2.01
	1997/1998	0.92	0.55	16.54 (18/11/1997)	0.13	1.39
	1998/1999	0.73	0.45	12.01 (02/01/1999)	0.17	1.45
	1999/2000	0.97	0.53	21.25 (22/12/1999)	0.16	1.65
	2000/2001	1.16	0.87	12.91 (23/01/2001)	0.21	1.18
	2001/2002	0.94	0.58	18.10 (01/02/2002)	0.24	1.37
	2002/2003	1.03	0.53	31.21 (21/11/2003)	0.15	2.06
	2003/2004	0.55	0.38	9.50 (08/01/2004)	0.06	1.13
Period 3 15 March–15 May Spring period – most rapid juvenile growth for fish that are one year of age or older	1994/1995	0.32	0.24	4.73 (23/04/1995)	0.11	1.24
	1995/1996	0.55	0.43	12.48 (23/04/1996)	0.16	1.36
	1996/1997	0.27	0.19	2.66 (04/05/1997)	0.08	0.95
	1997/1998	1.03	0.40	18.15 (05/04/1998)	0.14	2.08
	1998/1999	0.37	0.24	6.27 (20/04/1999)	0.09	1.49
	1999/2000	1.01	0.56	18.44 (26/04/2000)	0.17	1.75
	2000/2001	0.49	0.39	4.50 (31/03/2001)	0.11	1.02
	2001/2002	0.29	0.24	1.46 (22/03/2002)	0.13	0.64
	2002/2003	0.31	0.18	3.81 (02/05/2003)	0.09	1.28
	2003/2004	0.59	0.44	4.10 (19/04/2004)	0.23	0.80
Period 4 15 May–31 August Summer period – juvenile growth slows as a result of higher temperatures and higher metabolic costs	1994/1995	0.17	0.06	20.25 (01/06/1995)	0.04	3.53
	1995/1996	0.12	0.07	4.37 (23/07/1996)	0.04	1.58
	1996/1997	0.41	0.19	11.19 (18/05/1997)	0.07	1.92
	1997/1998	0.32	0.19	17.98 (07/06/1998)	0.09	1.97
	1998/1999	0.17	0.09	3.75 (06/06/1999)	0.03	1.75
	1999/2000	0.22	0.15	5.56 (29/07/2000)	0.06	1.35
	2000/2001	0.21	0.1	14.60 (19/08/2001)	0.06	3.3
	2001/2002	0.61	0.3	37.71 (31/07/2002)	0.14	2.21
	2002/2003	0.11	0.08	0.56 (21/05/2003)	0.05	0.83
	2003/2004	0.35	0.16	13.30 (11/08/2004)	0.07	2.20

Table 2. Statistics of stream temperature (* Percentage of missing data for given time period %.).

Time period		Stream temperature (°C) (hourly)				Coeff. of variation	Degree days (total at end of certain period)
		Mean	Median	Max	Min		
Hydrological year	1994/1995	6.9	6.4	17	−0.8	0.71	2570
	1995/1996	6.7	6.6	15	−0.8	0.68	2465
	1996/1997	7.0	7.4	18.8	−0.2	0.73	2568
	1997/1998	8.2	8.4	20.2	−0.6	0.55	2832
	1998/1999	8.1	8.8	19.1	−0.6	0.62	2610
	1999/2000	7.1	6.9	18.4	−1.0	0.69	2592
	2000/2001	6.9	6.7	20.2	−0.8	0.75	2453
	2001/2002	7.6	8.3	19.9	−0.4	0.65	2786
	2002/2003	7.5	6.9	19.8	−0.6	0.68	2769
	2003/2004	7.0	6.7	20.2	−0.6	0.74	2634
Period 1 15 October–14 November Main time period where spawning salmon enter the Girnock Burn	1994/1995	6.5	6.8	9.2	2.4	0.18	306
	1995/1996	6.9	6.8	12.2	2.6	0.30	352
	1996/1997	6.2	7.2	10.4	0.2	0.43	324
	1997/1998 (46%*)	6.8	6.4	10.6	4.4	0.21	327
	1998/1999	3.8	3.6	10.2	−0.1	0.51	224
	1999/2000	6.6	6.5	9.5	1.5	0.24	306
	2000/2001	4.8	4.6	9.1	0.7	0.36	260
	2001/2002	6.9	7.3	11.7	−0.2	0.40	356
	2002/2003	4.1	3.9	8.0	0.8	0.36	252
	2003/2004	4.7	4.4	9.1	0.3	0.38	244
Period 2 15 November–14 March Winter period – low biological activity and low growth for juvenile fish	1994/1995 (1.6%*)	2.1	1.4	8.8	−0.8	0.89	576
	1995/1996 (0.8%*)	2.0	1.6	7.8	−0.8	0.97	614
	1996/1997 (2.4%*)	1.6	1.0	7.4	−0.2	1.02	525
	1997/1998 (23%*)	3.5	3.2	9.2	0.2	0.62	798
	1998/1999 (54%*)	2.1	2.3	8.0	−0.6	0.91	459
	1999/2000	1.9	1.5	8.6	−1.0	1.06	549
	2000/2001 (10%*)	1.4	0.7	7.1	−0.8	1.54	445
	2001/2002	2.1	1.8	7.7	−0.4	0.93	612
	2002/2003	2.4	2.3	8.4	−0.6	0.95	554
	2003/2004	1.6	1.1	8.8	−0.6	1.26	451
Period 3 15 March–15 May Spring period – most rapid juvenile growth for fish that are one year of age or older	1994/1995	4.6	5.4	10.2	−0.8	0.63	905
	1995/1996	4.7	5.2	10.4	0.0	0.58	902
	1996/1997 (62%*)	6.1	5.8	12	2.6	0.29	927
	1997/1998 (27%*)	6.4	6.2	18.1	−0.6	0.63	1187
	1998/1999 (81%*)	9.9	9.5	15.1	7.3	0.17	881
	1999/2000	6.5	5.8	18.4	−0.6	0.60	946
	2000/2001	5.6	5.4	17.1	−0.2	0.64	788
	2001/2002	7.1	6.9	16.0	0.8	0.41	1052
	2002/2003	6.9	7.1	13.8	−0.6	0.37	981
	2003/2004 (56%*)	6.1	5.2	17	1.1	0.55	884

temperatures of 18°C were exceeded for 0.1% of the time during seven years (1997/1998–2003/2004). A temperature of 24.6°C was not exceeded at the site, though work on spatial distribution of Girnock temperatures has shown that more extreme temperatures in particularly hot summers occur in the upstream river network where riparian shading is absent (Malcolm et al., 2004).

The cumulative stream temperatures in degree-days relative to ecologically "sensitive" periods have shown clear differences in inter-annual variability (Fig. 7). The hydrological year 1997/1998 was most extreme, with the highest temperatures observed during each of the four periods. Degree days for the whole year varied between 2453 days (2000/2001) and 2832 days (1997/1998, Table 2); resulting in inter-annual variation of 13%.

Table 3. Time of exceedence when mean stream velocity exceeded Critical Displacement Velocity (CDV) (%) (* For January–April: assumption of a minimum fish length of 20 mm for 0+ fish; with fry emergence in mid May.).

0+ fish	1994–1995	1995–1996	1996–1997	1997–1998	1998–1999	1999–2000	2000–2001	2001–2002	2002–2003	2003–2004
October	3.2	9.7	6.5	0.0	32.3	0.0	22.6	16.1	35.5	0.0
November	6.7	36.7	46.7	23.3	33.3	13.3	56.7	13.3	33.3	3.3
December	32.3	54.8	71.0	22.6	51.6	96.8	77.4	67.7	51.6	45.2
January*	100	100	93.5	100	100	100	100	100	100	100
February*	100	100	96.4	46.4	100	100	100	100	100	100
March*	100	100	71.0	58.1	64.5	41.9	100	87.1	61.3	90.3
April*	26.7	96.7	0.0	93.3	30.0	100	76.7	0.0	10.0	80.0
May	6.5	25.8	45.2	3.2	16.1	19.4	0.0	22.6	32.3	29.0
June	3.3	0.0	10.0	6.7	6.7	0.0	0.0	0.0	0.0	0.0
July	0.0	0.0	6.5	0.0	0.0	0.0	0.0	6.5	0.0	0.0
August	0.0	0.0	0.0	0.0	0.0	0.0	6.5	6.5	0.0	12.9
September	26.7	0.0	0.0	0.0	6.7	6.7	0.0	0.0	0.0	0.0
Total time exceeded	33.4	43.4	37	29.3	36.2	39.6	44.7	34.8	35.1	38.5
1+ fish										
October	3.2	6.5	0.0	0.0	9.7	0.0	12.9	9.7	22.6	0.0
November	0.0	23.3	46.7	10.0	20.0	6.7	33.3	6.7	30.0	3.3
December	19.4	45.2	61.3	12.9	41.9	93.5	51.6	58.1	29.0	45.2
January	77.4	64.5	61.3	71.0	77.4	74.2	100	71.0	67.7	80.6
February	82.1	89.7	53.6	10.7	53.6	62.1	100	89.3	75.0	62.1
March	12.9	32.3	12.9	22.6	0.0	16.1	71.0	25.8	3.2	45.2
April	3.3	6.7	0.0	46.7	6.7	46.7	0.0	0.0	0.0	6.7
May	0.0	0.0	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
June	3.3	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
July	0.0	0.0	3.2	0.0	0.0	0.0	0.0	6.5	0.0	0.0
August	0.0	0.0	0.0	0.0	0.0	0.0	3.2	3.2	0.0	3.2
September	16.7	0.0	0.0	0.0	3.3	3.3	0.0	0.0	0.0	0.0
Total time exceeded	17.8	22.1	20.3	14.5	17.5	25.1	30.7	22.2	18.6	20.6

4.3 Effects of discharge and stream temperature on foraging behaviour of juvenile Atlantic salmon

To assess the times when the foraging behaviour of juveniles Atlantic salmon may be constrained by hydraulic conditions, the percentage of time when CDV was exceeded by mean daily stream velocity was determined for the fish age classes 0+ and 1+ (Table 3). As a result of the interaction between intra-annual changes in fish length and stream temperature, the CDV for each age class varied systematically throughout the year (Fig. 8). Clear seasonal patterns in CDV were apparent. The higher CDV values typical of the summer period, due to greater fish length and higher temperatures indicate that high discharges, are less likely to constrain feeding opportunities during this time. In addition, CDV was more stable (less day-to-day variability) during the summer than the winter. In general, CDV showed greater intra-annual than inter-annual variability due to strong seasonal patterns in stream temperature. However, clear differences were evident in the total percentage of the time for which mean velocities exceeded the CDV in the ten years, as a result of high inter-annual variability in discharge conditions (Table 3).

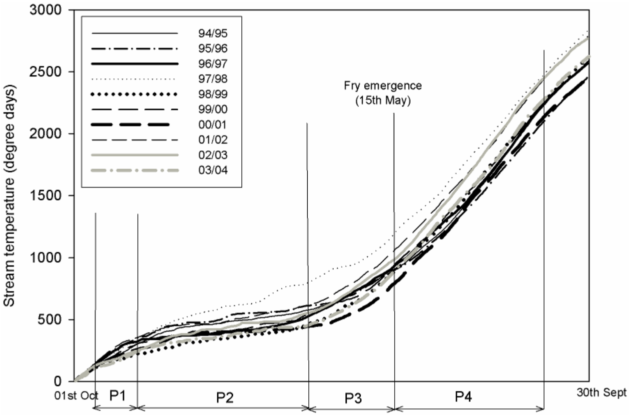

Fig. 7. Cumulative stream temperature curves as degree days showing ecological sensitive time periods: P1=Period 1, 15 October–14 November, Main time period where spawning salmon enter the Girnock Burn; P2=Period 2, 15 November–14 March, Winter period – low biological activity and low growth for juvenile fish; P3=Period 3, 15 March–15 May, Spring period – most rapid juvenile growth for fish that are one year of age or older; P4=Period 4, 15 May–31 August, Summer period – juvenile growth slows as a result of higher temperatures and higher metabolic costs.

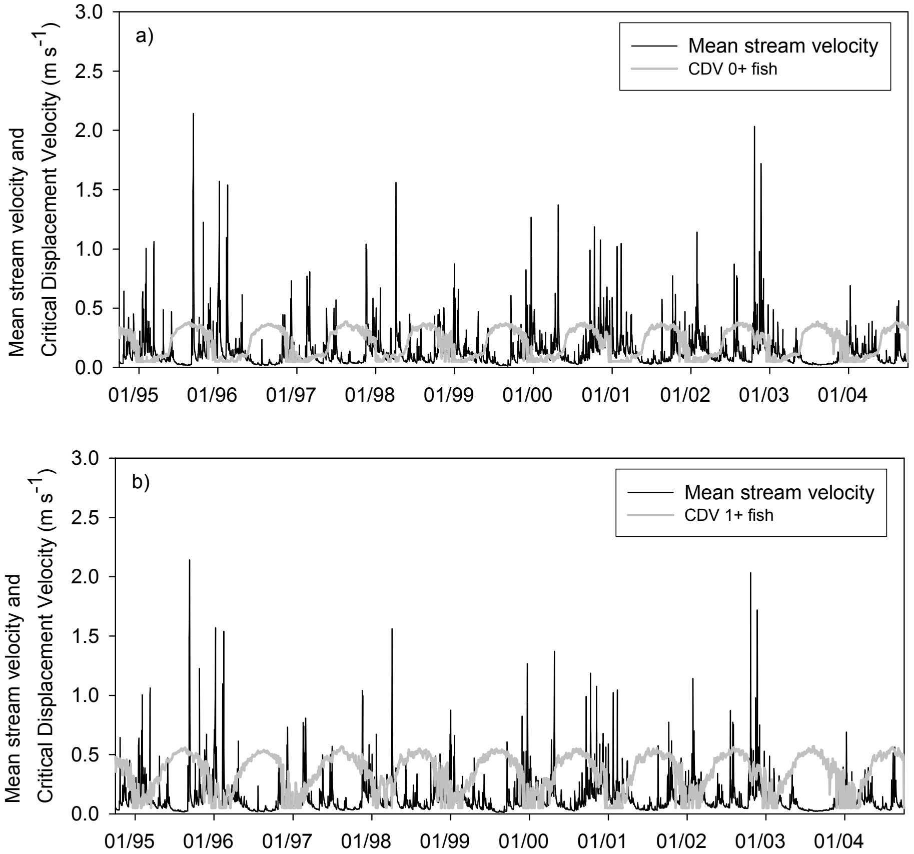

Fig. 8. Daily Critical Displacement Velocity (CDV) and daily mean stream velocity for **(a)** 0+ and **(b)** 1+ salmon over the ten years investigated.

The duration of periods when mean stream velocity exceeded CDV for salmon fry (0+) ranged between 29.3% (1997/1998) and 44.7% (2000/2001). CDVs are relatively high during the summer due to warmer stream temperatures and CDV was only occasionally exceeded. Although fry do not emerge from the streambed before ca. mid-May, CDV values were calculated for January to April months in order to examine the potential influence of CDV exceedence on foraging opportunities during this time. The winter months were characterised by an exceedence of CDV by stream velocity for fry by almost 100%. The earliest time at which hydraulic conditions are suitable for free swimming and foraging fry was May, close to the usual time of fry emergence in the Girnock.

For 1+ parr, mean stream velocity exceeded CDV between 14.5% (1997/1998) and 30.7% (2000/2001) of the time. Again, the highest percentages of exceedence time were generally reached in January/February. But because of the larger size of parr relative to fry, 100% exceedence in any month was only predicted in 2002/2003. During years with higher stream temperatures (e.g. 1997/1998, Table 2) and in summer, CDV values were relatively higher and exceedence values lower. This was because the potential constraints of high discharge on foraging were compensated for by the greater scope for fish mobility afforded by higher temperatures.

4.4 Effects of discharge and stream temperature on returning spawners

Simple linear correlation analyses were carried out as a preliminary assessment of influences of discharge and stream temperature on returning adult numbers (Table 4). Due to the extremely complex interactions between abiotic influences and biological controls on salmonids movement at spawning, it is unsurprising that the number of returning female spawners was not directly related to discharge for whole hydrological years ($P>0.1323$). However, focussing on ecologically "sensitive" time periods and providing a more biologically relevant temporal resolution for analysis improved regression results substantially.

Relatively strong correlations were observed between the coefficient of variation of discharge, which was used as an index of flow variability, during period 1 and returning numbers of female spawners (Table 4). Female salmon are observed to initiate spawning entry to the Girnock Burn; thus, it

Table 4. Pearson coefficients of correlation (r) and P-values between discharge variables and returning adults.

	Discharge value	Total fish		Total male		Total female	
		r	P	r	P	r	P
Total hydrological year	Mean	0.40	0.2552	0.32	0.1243	0.22	0.5424
	Max	0.51	0.1344	0.39	0.2589	0.51	0.1323
	Min	−0.25	0.4868	−0.29	0.4129	−0.17	0.6455
	SD	0.48	0.1637	0.47	0.1723	0.40	0.2584
	CV	0.40	0.2550	0.34	0.3417	0.38	0.2837
Period 1	Mean	0.15	0.6713	0.26	0.4667	0.03	0.9272
15th October–14 November	Max	0.66	0.0361	0.59	0.0751	0.61	0.0621
Main time period where	Min	0.08	0.8192	0.25	0.4824	−0.08	0.8320
spawning salmon enter	SD	0.43	0.2096	0.42	0.2275	0.37	0.2976
the Girnock Burn	CV	0.82	0.0038	0.61	0.0637	0.85	0.0018

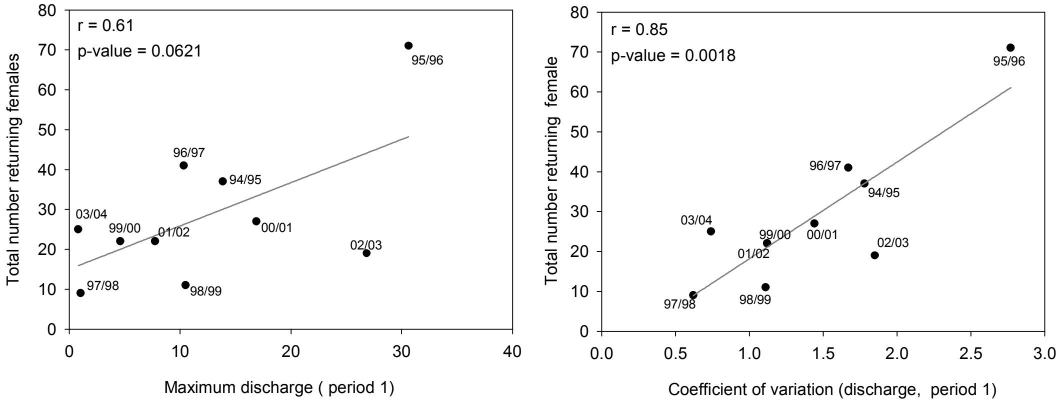

Fig. 9. Scatterplot showing relationships between selected discharge values during period 1 (15 October–14 November; main time period where spawning salmon enter the Girnock Burn) and returning females.

is unsurprising that there were weaker correlations between hydrological conditions and adult male numbers (Table 4). Correlation plots showing the relationships between maximum discharge and coefficients of variation and returning females are shown in Fig. 9 and indicate that the correlations were strongly influenced by the extreme conditions during 1995/1996 and 1997/1998.

For further understanding of relationships between hydrological conditions and returning female spawners, daily returning female spawners were plotted against hydrographs during period 1 (Fig. 10). Hydrological conditions differed substantially between the ten years examined and patterns of fish entry varied too. The entry of female fish was much more evenly distributed during years with regular flow pulses during the critical period. In most years, spawners could be shown to enter the stream coincident with hydrological events. For example, in 1994/1995, 1995/1996 and 1997/1998, the highest numbers of returns on one day occurred during the largest hydrological event. However, in other years, such as 1996/1997, 1998/1999, 1999/2000, 2000/2001, 2001/2002 and 2002/2003 fish entry was more evenly distributed over a range of smaller events. In contrast, 2003/2004 saw a sustained period of low discharges in the months prior to spawning, which resulted in all spawning females entering the burn in response to two very minor increases in stream discharge. Discharges below about $0.3\,\mathrm{m}^3\,\mathrm{s}^{-1}$ appeared to inhibit access to the stream.

5 Discussion

Inter- and intra-annual variability of discharges and temperatures clearly provide an important component of the habitat template of riverine ecosystems and can affect growth, behaviour and survival of Atlantic salmon both directly and indirectly (Swansburg et al., 2004). Long-term salmon monitoring sites such as the Girnock provide rare data sets that can yield important insights into the linkages between discharge, temperature and biological response (Gibbins et al., 2004; Hannah et al., 2004; Tetzlaff et al., 2005b). They suggest that the basic, underlying timing of certain salmon life stages has a strong heritable component suggesting that local

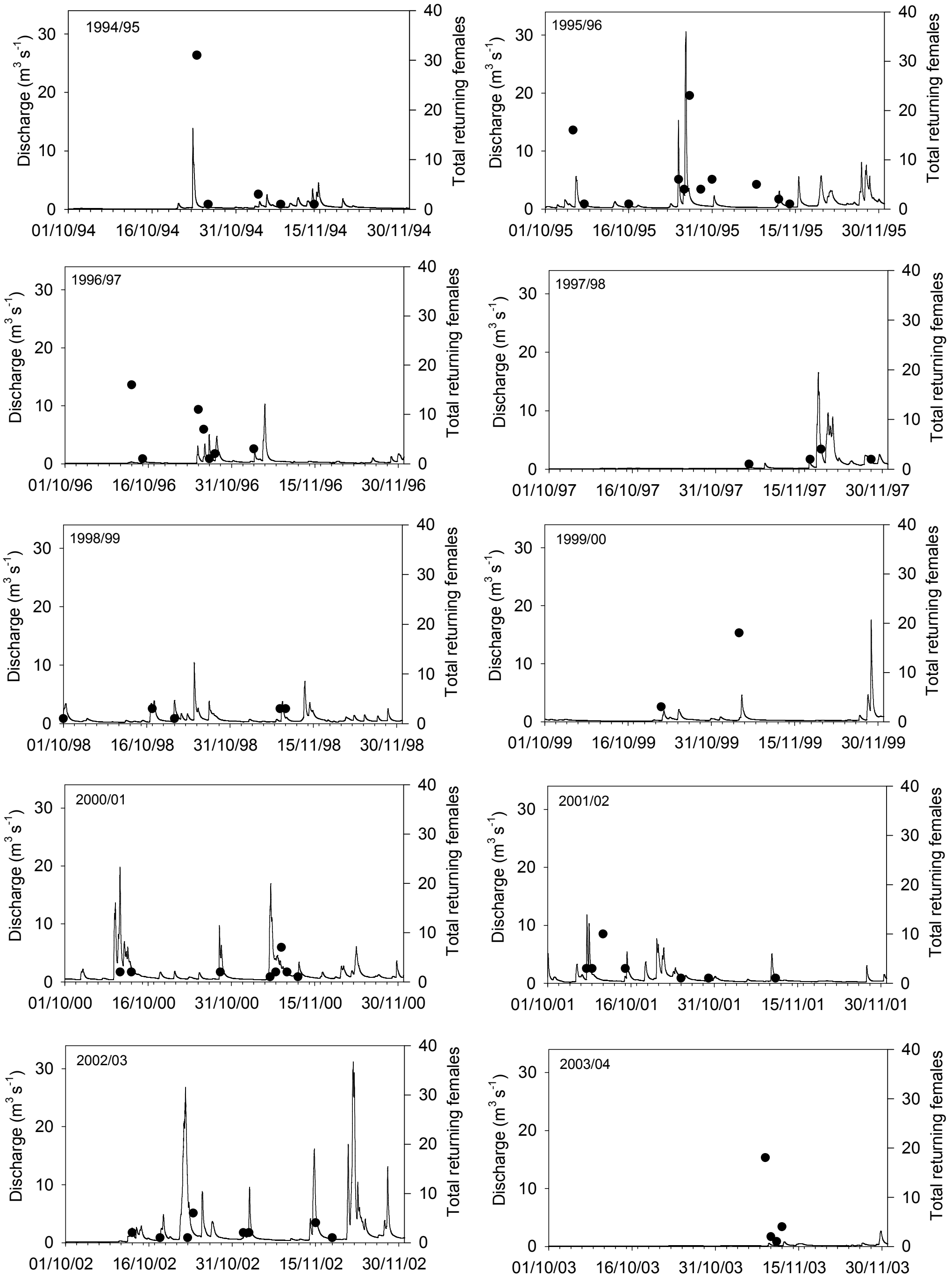

Fig. 10. Timing and number of returning spawning salmon in relation to hydrological conditions for the ten years investigated.

genetic adaptation may affect the timing of certain activities (Stewart et al., 2002). In the Girnock Burn, it has been shown that local genotype is a direct effect on growth performance (Jordan and Youngson, 1991), but, unsurprisingly, most of the variability in the growth of juvenile salmon (ca. 85%) can be accounted for by variability in stream temperatures (Bacon et al., 2005). In this context, the analysis of CDV applied in this study highlighted quite marked inter- and intra-annual variability in the potential feeding opportunities for juvenile salmon during critical growth time periods, a factor which may help account for unexplained variability in growth.

In the Girnock, recently hatched salmon fry tend to reach the emergence stage in May when discharge, temperature and CDVs are usually relatively low. This may be an adaptive response by fish mediated by differences in adult spawning time (Webb and McLay, 1996). Together with incubation temperature, this is likely to determine hatch and emergence dates, i.e. they emerge at a time when discharges are, on average, becoming lower and less variable (Heggberget, 1988). In the first few weeks after emergence, small 0+ fish have relatively low CDVs and consequent low ability to forage in faster flowing sections of the stream. When high discharges do occur soon after hatch time (e.g. in 1997/1998 and 1999/2000) there may be marked effects on recruitment, foraging and growth rates (Jensen, 2003).

In the Girnock, 1+ fish grow most markedly in the March-May period, prior to the emergence of 0+ individuals, probably because of the high seasonal prey abundance and low basal metabolic costs associated with lower temperatures (Gibbins et al., 2002; Elliot and Hurley, 2003; Gibbins et al., 2004; Bacon et al., 2005). The later emergence of the 0+ fish relative to this same period may reflect the overall fitness benefits of avoiding emergence when growth potential is high but hydraulic conditions are typically unfavourable for foraging.

The second key life stage examined in the present study was the entry of adult fish into the stream for spawning. This was also strongly influenced by event scale variation in discharge conditions. The timing of entry of females was more distributed during years with regular flow pulses during the critical period. During years with long periods of low flow the entry of spawners was delayed and minor flow pulses were apparently sufficient to cause fish to enter the stream, perhaps as sexual development and impending ovulation or actual ovulation increasingly demand entry even under suboptimal conditions. Many of the adults entering the Girnock Burn have been tagged there previously as smolts (Youngson et al., 1994). This suggests that fish originating in the stream are committed to spawning there rather than in other, more accessible locations. Yet, large fish in small streams are extremely vulnerable to predation for the duration of their stay there (Carss et al., 1990). Delaying final migration into the stream until shortly before spawning, and the increasing need to move upstream regardless of discharge magnitude, probably reflect play-offs between the likelihood of reaching preferred target locations for spawning, the energetic costs involved in doing so, and the discounted individual risk of predation before spawning can take place.

The study has also indicated significant positive correlations between coefficient of variation for discharge during spawning period 1 and number of returning females. This may emphasise the importance of regular discharge variation for ecological integrity (Fausch et al., 2002). Numerically, full juvenile recruitment to stream populations is dependent on a sufficient number of potential adult spawners reaching their targeted destinations throughout the usable reaches of the stream, so that juveniles are distributed throughout the useable habitat. Thus, qualitatively, effective population size and the maintenance of genetic diversity are critically dependent on spawner number in relatively small spawning populations such as those of the Girnock Burn (Ryman, 1991).

The entire range of variability in discharges and temperatures plays a crucial role in the maintenance of river ecosystems (e.g. Allan, 1995; Petts, 2000; Archer and Newson, 2002). This study has shown that short-term variability (e.g. at the event scale in relation to spawning or during critical growth period for juvenile fish) in discharge and temperatures can have important implications for certain life stages. Although the results represent only a first step in understanding such complex interactions, such information can provide insights for the management of fisheries resources (Fausch et al., 2002). For example, setting Ecologically Acceptable Flow regimes (EAFs) on regulated rivers for the benefit of target species such as Atlantic salmon need to incorporate the habitat requirements of different life-stages at a range of temporal scales. If freshet or compensation releases for fisheries benefit are to be made, variable regimes are needed during the period of maximum spring growth rates – to avoid potential CDV exceedence – and during the final phase of the spawning migration to facilitate passage (Jackson et al., 2004). This has implications for using tools such as the "Range of Variability" approach (Richter et al., 1997) in setting environmental flow targets in river systems, as they are generally based on timescales (i.e. weekly or monthly) that may not capture such subtle interactions between physical habitat conditions and biological activity (Stewardson and Gippel, 2003).

Moreover, whilst physical environmental effects on salmonids are most marked during extreme hydrological and thermal conditions (as shown in Fig. 9), the thresholds marking the difference between normal system behaviour and disturbances are uncertain. Thus it is clear that river systems are climatically-driven and need to be understood in the context of climatic variations (Harris et al., 2000). Additionally, the recognition that climatic effects on river systems are non-stationary needs to be considered, particularly at a time when the effects of marked climatic change are being predicted for many river systems (Fowler and Kilsby, 2003). Consequently, analysis of longer-term, discharge and temperature data, together with biological data, at those few sites where all are available is important in order to understand such mechanisms and controls on biological variables and contribute to the development of a more scientific basis for river management.

A clearer understanding of the relationships between discharge, species and life-stages is a major challenge in hydroecology. This study presents ways in which initial steps may be taken to elucidating such relationships. However, much more research is needed to provide a more robust ecological basis for the setting of flow regimes. For example in relation to the present study, further spatial validation is needed to investigate catchment-wide variations in hydraulic and thermal drivers which may result from contrasting channel habitat types. The use of mean cross-sectional velocity values as applied in this study, although useful for illustrating inter-annual variability in hydraulic conditions in relation to CDVs, masks differences in the absolute hydraulic conditions experienced by individual fish. Work by Webb et al. (2001) and Gibbins et al. (2002) has already shown how channel characteristics in different parts of the catchment affect the way in which spawning habitat varies with flow. On a finer scale, opportunities for individual fish to avoid locations where CDV is exceeded, by moving just a small distance to a refuge area are likely to exist, even at the gauge site (this is evident from velocity distribution presented in Fig. 2). Thus, more advanced hydraulic characterisation, either by field measurement and/or 3-D modelling, is needed to allow small spatial-scale variability in velocity to be factored into these types of analysis (Booker et al., 2004). In addition, the complex behavioural responses of juvenile fish to small scale velocity changes in natural channels need to be better understood (Holm et al., 2001).

More generally, studies at the larger spatial scales are needed to contextualise processes in small streams like the Girnock Burn. For example, the numbers of returning adult fish were used in this study to illustrate an ecological response which was potentially triggered by flow influences. However, the conditioning of the ways in which spawners exploit variable habitat conditions at particular times is probably conditioned over the long period of river life prior to stream entry (>8 months for many Girnock spawners). In addition, the connectivity of riverine habitats, and particularly the main river system – spawning stream continuum needs to be investigated further (Fausch et al., 2002). This might include an assessment of the connections between adult return to freshwaters and spawning in the autumn. It might also include a consideration of how spawners in mainstem river systems respond to differences in discharge and temperature variability that have their origin in different parts of the mainstem river or stream network. Clearly a major research effort is needed to underpin the implementation of policies aimed at more scientific approaches to the management of rivers over coming decades.

Acknowledgements. The authors are grateful to the support of DFG supporting DT on her research fellowship. The invaluable help of D. Fraser from the Scottish Environment Protection Agency (SEPA) in kindly providing the stage, discharge and velocity data is gratefully acknowledged. Thanks are also due to J. Thorley of the FRS Freshwater Laboratory for useful discussions. Three anonymous referees are thanked for pointing out numerous shortcomings in an earlier version of the paper.

Edited by: A. Ghadouani

References

Armstrong, J. D., Kemp, P. S., Kennedy, G. J. A., Ladle, M., and Milner, N. J.: Habitat requirements of Atlantic salmon and brown trout in rivers and streams, Fish. Res., 62, 143–170, 2003.

Allan, J. D.: Stream ecology, Chapman and Hall, 45–82, 1995.

Archer, D. and Newson, M.: The use of indices of flow variability in assessing the hydrological and instream habitat impacts of upland afforestation and drainage, J. Hydrol., 268, 244–258, 2002.

Arndt, S. K. A., Benfey, T. F., and Cunjak, R. A.: Effect of temporary reductions in feeding on protein synthesis and energy storage of juvenile Atlantic salmon, J. Fish Biol., 49, 257–276, 1996.

Arndt, S. K. A., Cunjak, R. A., and Benfey, T. J.: Effect of summer floods and spatio-temporal scale on growth and feeding of juvenile Atlantic salmon in two New Brunswick streams, Transactions of the American Fisheries Society, 131, 607–622, 2002.

Bacon, P. J., Gurney, W. S. C., Jones, W., McLaren, I. S., and Youngson, A. F.: 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, 2005.

Booker, D. J., Dunbar, M. J., and Ibbotson, A.: Predicting juvenile salmonid drift-feeding habitat quality using a three-dimensional hydraulic-bioenergetic model, Ecol. Modell., 177, 157–177, 2004.

Bunt, C. M., Cooke, S. J., Katopodis, C., and McKinley, R. S.: Movement and summer habitat of brown trout (*Salmo trutta*) below a pulsed discharge hydroelectric generation station, Regulated Rivers Research and Management, 15, 395–403, 1999.

Carss, D. N., Kruuk, H., and Conroy, J. W. H.: Predation on adult Atlantic salmon, *Salmo salar L.*, by otters, *Lutra lutra* (L.), within the River Dee system, Aberdeenshire, Scotland, J. Fish Biol., 37, 935–944, 1990.

Clausen, B. and Biggs, B. J. F.: Flow variables for ecological studies in temperate streams: groupings based on covariance, J. Hydrol., 237, 184–197, 2000.

Elliot, J. M.: Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*, Freshwater Biology, 25, 61–70, 1991.

Elliot, J. M. and Hurley, M. A.: Variation in the temperature preference and growth rate of individual fish reconciles differences between two growth models, Freshwater Biology, 48, 1793–1798, 2003.

Enders, E. C., Buffin-Belanger, T., Boisclair, D., and Roy, A. G.: The feeding behaviour of juvenile Atlantic salmon in relation to turbulent flow, J. Fish Biol., 66, 242–253, 2005.

Fausch, K. D., Torgersen, C. E., Baxter, C. V., and Li, H. W.: Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes, Bioscience, 52, 483–498, 2002.

Flodmark, L. E. W., Vollestad, L. A., and Forseth, T.: Performance of juvenile brown trout exposed to fluctuating water level and temperature, J. Fish Biol., 65, 460–470, 2004.

Fowler, H. J. and Kilsby, C. G.: A regional frequency analysis of United Kingdom extreme rainfall from 1961 to 2000, International Journal of Climatology, 23, 1313–1334, 2003.

Gibbins, C. N., Acornley, R. M.: Salmonid habitat modelling studies and their contribution to the development of an ecologically acceptable release policy for Kielder Reservoir, North-East England, Regulated Rivers Research and Management, 6, 203–224, 2000.

Gibbins, C. N., Dilks, C. F., Malcolm, R., Soulsby, C., and Juggins, S.: Relationships between invertebrates and hydrological variability in Cairngorm mountain streams, Hydrobiologia, 462, 205–219, 2001.

Gibbins, C. N., Moir, H. J., Webb, J., and Soulsby, C.: Assessing discharge use by spawning Atlantic salmon: a comparison of discharge electivity indices and PHABSIM simulations, Riv. Res. Appl., 18, 383–395, 2002.

Gibbins, C. N., Soulsby, C., Campbell, L., Scott, E., McEwan, I., and Malcolm, I.: Influence of channel hydraulics and sediment mobility on stream invertebrate drift. Hydrology: Science and Practice for the 21^{st} Century, Proceedings of the British Hydrological Society International Symposium, London, 2, 90–98, 2004.

Gilvear, D. J.: River flow regulation, in: The freshwaters of Scotland: a natural resource of international significance, edited by: Maitland, P. S., Boon, P. J., and McLuskey, D. S., Wiley, Chichester, 463–487, 1994.

Gilvear, D. J., Heal, K. V., and Stephen, A.: Hydrology and the ecological quality of Scottish river ecosystems, The Science of the Total Environment, 294, 131–159, 2002.

Gordon, N. D., McMahon, T. A., Finlayson, B. L., Gippel, C. J., and Nathan, R. J.: Stream hydrology – an introduction for ecologists, Wiley, 233–357, 2004.

Graham, D. W., Thorpe, J. E., and Metcalfe, N. B.: Seasonal current holding performance of juvenile Atlantic salmon in relation to temperature and smolting, Can. J. Fish. Aquat. Sci., 53, 80–86, 1996.

Gustard, A., Cole, G., Marshall, D. C. W., and Bayliss, A. C.: A study of compensation flows in the UK, Institute of Hydrology, report No. 99, Wallingford, 1987.

Hannah, D. M., Malcolm, I. A., Soulsby, C., and Youngson, A. F.: Heat exchange and temperature behaviour in a salmon spawning stream in the Cairngorms, Scotland: seasonal and sub-seasonal dynamics, Riv. Res. Appl., 20, 635–652, 2004.

Harris, N. M., Gurnell, A. M., Hannah, D. M., and Petts, G.: Classification of river regimes: a context for hydro-ecology, Hydrol. Processes, 14, 2831–2848, 2000.

Heggberget, T.: Timing of spawning in Norwegian Atlantic salmon (*Salmo salar*), Can. J. Fish. Aquat. Sci., 45, 845–849, 1988.

Holm, C. F., Armstrong, J. D., and Gilvear, D. J.: Investigating a major assumption of predictive instream habitat models: is water velocity preference of juvenile Atlantic salmon independent of discharge?, J. Fish Biol., 59, 1653–1666, 2001.

Jackson, H., Gibbins, C. N., Soulsby, C., McMullen, J. A., Casa Mulet, R., Malcolm, I. A., and Youngson, A. F.: Role of freshets in developing ecologically acceptable flow regimes for the river Lyon, Scotland. Proceedings of the 5th International Conference on Ecohydraulics, Madrid, Spain, 1, 723–729, 2004.

Jensen, A.: Atlantic salmon (*Salmo salar*) in the regulated River Alta: effects of altered water temperature on parr growth, Riv. Res. Appl., 19, 733–747, 2003.

Jordan, W. C. and Youngson, A. F.: Genetic protein variation and natural selection in Atlantic salmon, J. Fish Biol., 39 (Suppl. A), 185–192, 1991.

Kemp, P. S., Gilvear, D. J., and Armstrong, J. D.: Do juvenile Atlantic salmon parr track local changes in water velocity?, Riv. Res. Appls., 19, 569–575, 2003.

Langan, S. J., Johnston, L., Donaghy, M. J., Youngson, A. F., Hay, D. W., and Soulsby, C.: Variation in river water temperatures in an upland stream over a 30 year period, The Science of the Total Environment, 265, 195–207, 2001.

Malcolm, I. A., Soulsby, C., and Youngson, A. F.: Thermal regimes in the hyporheic zone of two contrasting salmon spawning streams; hydrological and ecological implications, Fisheries Management and Ecology, 9, 1–10, 2002.

Malcolm, I. A., Youngson, A. F., and Soulsby, C.: Survival of salmonid eggs in a degraded gravel bed stream: effects of groundwater – surface water interactions, Riv. Res. Appl., 19, 303–316, 2003.

Malcolm, I. A., Hannah, D., Donaghy, M., Soulsby, C., Youngson, A. F., and Bacon, P.: Influence of riparian woodland on water temperatures in an upland salmon stream, Hydrol. Earth Syst. Sci., 8, 449–459, 2004,
SRef-ID: 1607-7938/hess/2004-8-449.

Moir, H., Soulsby, C., and Youngson, A.F.: Hydraulic and sedimentary characteristics of habitat utilized by Atlantic salmon for spawning in the Girnock Burn, Scotland, Fisheries Management and Ecology, 5, 241–254, 1998.

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

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

Moir, H., Gibbins, C., Soulsby, C., and Youngson, A.F.: Validation of PHABSIM predictions for simulating salmon spawning habitat, Riv. Res. Appl., 21, 1–14, 2005.

Mohseni, O. and Stefan, H. G.: Stream temperature/air temperature relationship: a physical interpretation, J. Hydrol., 218, 128–141, 1999.

Moore, A. and Waring, C.P.: Electrophysiological and endocrinological evidence that F-series prostaglandins function as priming pheromones in mature male Atlantic salmon (*Salmo salar*) parr, J. Expl. Biol., 199, 2307–2316, 1996.

Naiman, R. J., Bunn, S. E., Nilson, C., Petts, G. E., Pinay, G., and Thompson, L. C.: Legitimizing fluvial ecosystems as users of waters, Environ. Manag., 30, 455–467, 2002.

Økland, F., Erkinaro, J., Moen, K., Niemelae, E., Fiske, P., McKinley, R. S., and Thorstad, E. B.: Return migration of Atlantic salmon in the River Tana: phases of migratory behaviour, J. Fish Biol., 59, 862–874, 2001.

Olden, J. D. and Poff, N. L.: Redundancy and the choice of hydrological indices for characterising streamflow regimes, Riv. Res. Appl., 19, 101–121, 2003.

Petts, G. E.: Long-term consequences of upstream impoundment, Environ. Conserv., 7, 325–332, 1980.

Petts, G. E.: A perspective on the abiotic processes sustaining the ecological integrity of running waters, Hydrobiologia, 422/423, 15–27, 2000.

Poff, N. L.: Why disturbances can be predictable: a perspective on the definition of disturbances in streams, J. North American Benthological Society, 11, 86–92, 1992.

Poff, N. L., Allan, D. J., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., Sparks, R. E., and Stromberg, J. C.: The Natural Flow Regime – A paradigm for river conservation and restoration, Bio-Science, 47, 769–784, 1997.

Puckridge, J. T., Sheldon, F., Walker, K. F., and Boulton, A. J.: Flow variability and the ecology of large rivers, Marine and Freshwater Res., 49, 55–72, 1998.

Resh, V. H., Brown, A. V., Covich, A., Gurtz, M. E., Hiram, W. L., Minshall, G. W., Reice, S. R., Sheldon, A. L., Wallace, J. B., and Wissmar, R. C.: The role of disturbance in stream ecology, J. North American Benthological Society, 7, 433–455, 1988.

Richter, B. D., Baumgartner, J. V., Powell, J., and Braun, D. P.: A method for assessing hydrologic alteration within ecosystems, Cons. Biol., 10, 1163–1174. 1996.

Richter, B. D., Baumgartner, J. V., and Braun, D. P.: How much water does a river need?, Freshwat. Biol., 37, 231–249, 1997.

Richter, B. D., Baumgartner, J. V., Powell, J., and Braun, D. P.: A spatial assessment of hydrologic alteration within a river network, Regul. Riv. Res. Managemt., 14, 329–340, 1998.

Ryman, N.: Conservation genetics considerations in fishery management, J. Fish Biol., 39 (Suppl. A), 211–224, 1991.

Schlosser, I. J.: Dispersal, boundary processes and trophic-level interactions in streams adjacent to beaver ponds, Ecology, 76, 908–925, 1995.

Soulsby, C. and Boon, P. J.: Freshwater Environments in Scotland: an Earth Science perspective on the natural heritage of Scotlands rivers, in: Earth Science and the Natural Heritage, edited by: Gordon, J. and Leys, K., Stationary Office, London, 82–104, 2001.

Soulsby, C., Malcolm, I. A., Youngson, A. F., Tetzlaff, D., Gibbins, C. N., and Hannah, D. M.: Groundwater – surface water interactions in upland Scottish rivers: hydrological, hydrochemical and ecological implications, Scottish Journal of Geology, 41, 39–49, 2005a.

Soulsby, C., Tetzlaff, D., van den Bedem, N., Malcolm, I. A., Bacon, P. J., and Youngson, A. F.: Inferring groundwater – surface water interactions in montane catchments from hydrochemical surveys of springs and streamwaters, J. Hydrol., in press, 2005b.

Stewardson, M. J. and Gippel, C. J.: Incorporating flow variability into environmental flow regimes using the flow event method, Riv. Res. Appl., 19, 459–472, 2003.

Stewart, D. C., Smith, G. W., and Youngson, A. F.: Tributary-specific variation in timing of return adult Atlantic salmon (*Salmo salar*) to fresh water has a genetic component, Can. J. Fish. Aquat. Sci., 59, 276–281, 2002.

Swansburg, E., El-Jabi, N., Caissie, D., and Chaput, G.: Hydrometeorological trends in the Miramichi River, Canada: Implications for Atlantic Salmon growth, North American Journal of Fisheries Management, 24, 561–576, 2004.

Tetzlaff, D., Uhlenbrook, S., Grottker, M., and Leibundgut, Ch.: Hydrological assessment of flow dynamic changes on an event-scale by storm water pipe outflows and combined sewer overflows in an urban river, Urban Water, in press, 2005a.

Tetzlaff, D., Soulsby, C., Gibbins, C., Bacon, P. J., and Youngson, A. F.: 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, 65–77, http://dx.doi.org/10.1007/s10750-005-4166-6, 2005b.

Townsend, C. R., Hildrew, A. G., and Schofield, K.: Persistence of stream invertebrate communities in relation to environmental variability, J. Animal Ecol., 56, 597–613, 1987.

Webb, B. W. and Nobilis, F.: A long-term perspective on the nature of the air-water temperature relationship: a case study, Hydrol. Processes, 11, 137–147, 1997.

Webb, J. H. and McLay, H. A.: Variation in the time of spawning of Atlantic salmon (*Salmo salar*) and its relationship to temperature in the Aberdeenshire Dee, Scotland, Can. J. Fish. Aquat. Sci., 53, 2739–2744, 1996.

Webb, J. H., Gibbins, C. N., Moir, H., and Soulsby, C.: 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, 2001.

Webb, B. W., Clack, P. D., and Walling, D. E.: Water-air temperature relationships in a Devon river system and the role of flow, Hydrol. Processes, 17, 3069–3084, 2003.

Youngson, A. F., Buck, R. J. G., Simpson, T. H., and Hay, D. W.: The autumn and spring emigrations of juvenile Atlantic salmon, *Salmo salar L.* from Girnock Burn, Aberdeenshire, Scotland: environmental release of migration, J. Fish Biol., 23, 625–639, 1983.

Youngson, A. F., Jordan, W. C., and Hay, D. W.: Homing of Atlantic salmon (*Salmo salar L.*) to a tributary stream in a major river catchment, Aquaculture, 121, 259–267, 1994.