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Variability in stream discharge and temperatures during ecologically sensitive time periods: a preliminary assessment of the implications for Atlantic salmon

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Abstract

This study focused on improving the understanding of the temporal variability in hydrological and thermal conditions and their potential influences on two life stages of Atlantic salmon (*Salmo salar)* – stream resident juveniles and returning adult spawners. Stream discharges and temperatures in the Girnock Burn, NE Scotland, a small nursery stream, were characterised over a time period of ten hydrological years (1994/95–2003/04). Frequency, magnitude, duration and timing of thermal, hydraulic and hydrological conditions were examined using data with a high temporal resolution (hourly and subhourly). Particular attention was focussed on assessing variations during ecologically sensitive time periods when salmon behaviour is most susceptible to environmental perturbations.

The Girnock Burn was characterised by a strong inter- and intra-annual variability in the hydrological and thermal regime. This has clear implications for the likely feeding opportunities for juvenile fish in winter and early spring and the emergence of fry in the late spring. The movement of adult spawners towards breeding areas showed a complex dependence on hydrological variability. If discharges were low, fish movement was increasingly triggered by suboptimal flow increases as spawning time approached. Elucidating links between discharge/temperature variability and salmon habitat availability and utilization at appropriately fine temporal scales is a prerequisite to the development of better conservation management strategies and more biologically meaningful flow regimes in regulated river systems.

1. Introduction

In aquatic ecosystems the effects of abiotic influences on biological processes are usually complex and highly interactive (Poff et al., 1997; Puckridge et al., 1998; Naiman et al., 2002). Stream discharge and temperatures are both key abiotic drivers that are characterised by strong spatial and temporal variability at a range of scales (Petts, 2000; Soulsby and Boon, 2001; Malcolm et al., 2002; Hannah et al., 2004). Variations in stream temperature have potentially major effects on all stream biota and are the primary abiotic driver of many ecosystem processes (Langan et al., 2001; Jensen, 2003). Discharge is also a key driver through its influence on in-stream hydraulics and one of the basic determinants of the amount of habitat space available in river systems for different species and life stages (Petts, 1980; Swansburg et al., 2004). Many hydro-ecological studies have provided evidence for the importance of extreme events, such as floods and droughts, in regulating stream community structure (e.g. Poff and Ward, 1989; Poff and Allan, 1995). The importance of physical disturbance in maintaining biological diversity and ecological functioning in aquatic ecosystems is formally recognised by disturbance theory (Resh et al., 1988; Townsend et al., 1987; Poff, 1992). Disturbance theory has been incorporated in the "natural flow" paradigm, which postulates that the "full range of natural intra- and inter-annual variation of hydrological regimes. . . are critical in sustaining. . . the integrity of aquatic ecosystems" (Richter et al., 1997). The paradigm is widely recognised as forming a basis for flow management in regulated rivers.

Aquatic organisms are generally adapted to a wide range of variability in stream discharge and temperature (Allan, 1995). However, it is often difficult to define what 'natural' variability is, given the wide range of anthropogenic impacts on many river systems. Moreover, empirical studies that directly examine the influences of physical variability on aquatic organisms are still relatively scarce. Thus, there remains a need to understand the habitat requirements of species and life-stages in terms of discharge and stream temperature, particularly in terms of variations and interplays in both. This knowledge is an essential prerequisite for the environmental assessment needed to underpin sustainable river management through, for example, Ecologically Acceptable Flow regimes (EAFs) (Gordon et al., 2004).

In order to specify flow regimes that are ecologically meaningful, the variability of hydrological conditions needs to be characterised in terms of its implications for ecosystem functioning or productivity. In many hydro-ecological studies based on the "natural flow" paradigm, it is assumed that monthly or daily means, which are often readily available, are sufficient to characterise parameters such as discharge, in ways that allow meaningful correlations with ecological data (Richter et al., 1996; Clausen and Biggs, 2000; Olden and Poff, 2003). This is probably not the case. In addition, few studies have attempted to consider hydrological and thermal variability simultaneously and to explicitly link them to the ecological functioning or productivity of aquatic ecosystems (Harris et al., 2000). Finally, analyses conducted for longer temporal scales, e.g. months or years (Richter et al., 1998), underplay the fact that the biological responses can occur much more rapidly. In extreme cases, responses can occur over the course of individual hydrological events (Archer and Newson, 2002; Stewardson and Gippel, 2003; Tetzlaff et al., 2005a). Short-term natural perturbations can cause temporary, but substantial, changes in physical habitat and affect ecological functioning (Arndt et al., 2002). Thus, for example, Schlosser (1995) found that nearly all the migratory movement of several juvenile fish species over four summers in a small Minnesota stream occurred in response to a single hydrological cue lasting for only a few days. Against this background, there is a need to develop analytical approaches that focus on the magnitude, duration, frequency and timing of physical events on fine temporal scales and that consider biological responses, particularly during ecologically sensitive periods.

The Scottish Highlands contain some of the least disturbed rivers in Europe and constitute an important reservoir of aquatic biodiversity (Gilvear et al., 2002). The region is subject to sub-arctic climatic conditions and experiences marked annual ranges in stream temperatures; it is also temperate and upland rivers consequently experience highly variable flow conditions (Gibbins et al., 2001). Many Scottish rivers originating in the region are internationally important as spawning and rearing habitats for Atlantic salmon (*Salmo salar*), which is a conservationally, culturally and economically important species. In addition, salmon is often cited as a key higher order species and an indicator of wider ecosystem functioning (Gordon et al., 2004). This status is given increased urgency as a consequence of the requirement to implement both Habitat Directive and the EU Water Framework Directive and to protect and enhance ecological status. Many Scottish rivers are used for hydropower production and have regulated flow regimes that are only crudely relevant to the biology of salmon (Gilvear, 1994). For example, many hydropower reservoirs reserve an allocation of water for freshet releases intended to benefit fisheries. However, their use is rarely scientifically based (Gustard et al., 1987; Jackson et al., 2004).

Understanding the hydraulic and thermal requirements of salmonids at different life-stages is correspondingly important (Gibbins et al., 2002; Gilvear et al., 2002). 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; Swansburg et al., 2004). For stream resident salmonids, discharge can exert a strong influence on general behaviour including foraging and feeding (e.g. Flodmark et al., 2004; Enders et al., 2005). In addition, discharge thresholds are observed to trigger some life-stage specific activities. These include 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; Moir et al., 2005). Likewise, temperature exerts a major influence on physiology reflected, for example, 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 trigger life-stage specific behaviours such as juvenile migration (Swansburg et al., 2004).

This study considers stream discharge and temperature data for the Girnock Burn in the eastern Cairngorms of Scotland. The stream's salmon population is routinely monitored throughout the year. The study assesses the effects of fine-scale environmental variation during two stream-based phases in the salmonid life-cycle – adult spawning and juvenile residence. These corresponding time periods are regarded as ecologically sensitive in the sense that fish are expected to be more susceptible to environmental influences or most responsive to environmental stimuli than at other times. The specific objectives of the study are firstly, to characterise hydrological and thermal conditions over the 10 hydrological years (1994/95–2003/04) using high resolution data (hourly and subhourly). Secondly, to examine the relationships between variability in discharges, temperatures and fish behaviour by focussing on two examples: (i) the potential opportunities for foraging and food acquisition by juvenile fish and (ii) the migration of sexually mature adults to spawning areas. The analyses are used to illustrate how hydrological data can be integrated at appropriate time-scales to consider the effects of temporally variable abiotic conditions at different life stages in a biologically realistic way. It is argued that such data are an essential prerequisite in assessment of EAF's.

2. Study site

The Girnock Burn (Fig. 1) is a sub-catchment of the River Dee in north-east Scotland, draining a catchment of 30.3 km^2. The altitude of the catchment ranges from 230 m to 862 m (Fig. 1). The upper part of the catchment is associated with granite while the geology in the lower parts is dominated by schists and other metamorphic rocks (Soulsby et al., 2005a). The average channel slope is 28.9 m km^{-1} (Moir et al., 1998). 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 for abiotic conditions including hydrology, water quality and geomorphology (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 variability in discharge dynamics and thermal regimes (Moir et al., 1998; Malcolm et al., 2002; Soulsby et al., 2005b). Averaged annual precipitation is 935 mm (1961–1991, Scottish Environmental Protection Agency SEPA) with the summer months (May–August) generally being driest. Discharge is calculated from a calibrated section of the river using standard flow velocity cross-section methods, monitored by SEPA. At the gauging station at Littlemill (Fig. 1), mean annual discharge is 0.52 m^3 s^{-1} (1969–2001) although discharges between June and August rarely exceeded 0.1 m^3 s^{-1} (Moir et al., 1998). However, instantaneous discharges have varied between ca. 0.04 $m^3 s^{-1}$ in the summer (Malcolm et al., 2003) and >50 $m^3 s^{-1}$ during floods. Most high discharge events occur between late autumn and early spring.

Mean annual stream temperature over the period 1968–1997 was ca. 7.0°C but with considerable inter-annual variation (Langan et al., 2001). 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 in mean daily maximum temperatures during winter and spring was observed (Langan et al., 2001).

The stream provides an important spawning and rearing habitat for 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 at intervals throughout the year; most juveniles leave the stream at two or three years of age.

The period from 15 October–14 November (Period 1 in this paper) approximates the main time period where spawning salmon enter the Girnock Burn. The main period of 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 period 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). These ecologically sensitive periods provided a framework for hydrothermal analyses presented in the paper in the context of likely ecological implications.

3. Data and methods

3.1. Hydrological and hydraulic data

High resolution discharge data (15 min) were available for ten hydrological years (1994/95–2003/04). Although discharges have been measured since 1969, 15 min data are only digitally archived since 1994. In order to derive hydraulically meaningful data from discharge measurements, velocity time series were constructed. 89 existing calibration gaugings (1997–2004) at Littlemill were used for this purpose. Average velocities were measured across the gauged section at 26 points at the mean column velocity position (0.6 × depth). Stream velocity conditions at the gauged site were assumed to be indicative of relative temporal variation in conditions throughout the catchment generally, although it is recognised that different channel characteristics generate spatially variable velocity conditions at equivalent discharges (Moir et al., 2002). 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 derive 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 discharges, including those for the median (Q_{50}), high (Q_{10}) and low (Q_{95}) discharges. Low flow conditions generated uniformly low mean stream velocities but even at higher flows there remained areas of low stream velocity, which were potentially available as refugia for fish and other organisms.

3.2. Stream temperatures

Water temperature data were available at hourly resolution from logging thermistors. Total error of these is 0.6°C. These were located near the Littlemill fish traps, where the stream is tree-lined. Data capture was approximately 93%. As there is a strong correlation between stream and air temperatures above 0°C, data gaps in the stream temperature time series were modelled by developing linear air-stream temperature relationships. A number of studies have discussed the limitations and complexities of this approach (e.g. Webb and Nobilis, 1997; Webb et al., 2003) but for monthly time scales, linear regressions, without incorporation of a time lag are found to be informative (Mohseni and Stefan, 1999). Air temperature data were obtained from the Meteorological Office observation station at Aboyne, about 20 km east of the study catchment. Degree days capture the relationships between cumulative temperature and ecological processes (Allan, 1995) and these values were calculated by summing all daily mean temperatures above 0°C.

3.3. Biological data

To assess the implication of variations in velocity dynamics for juvenile salmonids, Critical Displacement Velocity (CDV, Graham et al., 1996) was calculated. CDV is the maximum sustained velocity against which a fish can hold station over prolonged periods. When stream velocity exceeds CDV, fish are unable to hold station and foraging and feeding opportunities are expected to be correspondingly constrained (Gibbins et al., 2002), resulting in decreased growth rates or weight losses (Arndt et al., 1996). CDV is dependent on both fish size and stream temperature and is determined using relationships derived from flume experiments (see Graham et al., 1996). The value of CDV is that it is temperature dependent. Fish of average size have higher CDV if temperatures are higher (Gibbins et al., 2002). Thus, analysis of frequency and duration of CDV exceedence integrates both thermal and hydraulic constraints on feeding and hence, growth.

For estimating CDV's in the stream on any date, the mean length of juveniles was derived from growth curves for the years 2002 and 2003 (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).

Stream temperature and length data were input to the regression equation of Graham et al. (1996) to calculate CDV [m s^{-1}]:

$$CDV = CDV_{BL} * L/100 \quad \text{with} \quad CDV_{BL} = 4.14 \log T + 1.74 \tag{1}$$

where CDV_{BL} is expressed in body lengths per second, T = water temperature [°C] and L is fish body lengths [cm].

CDV's were calculated at daily resolution, using date-specific mean fish length and mean daily stream temperature.

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 routinely monitored on a daily basis during the relevant times of the year. 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) (Moir et al., 1998). In general, females enter the stream ahead of males 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 (1997/98) and 71 (1995/96, Fig. 3).

4. Results

4.1. Characterisation of stream discharge

The flow duration curves for the ten years investigated are shown in Fig. 4. Marked inter-annual variability of discharges is evident in the range of the curves, whilst high intra-annual variability of discharge (e.g. in 1994/95 and 2002/03) is shown by steep curves. For individual years, the Q_1 ranged between 8.63 m^3 s^{-1} (1994/95) and 2.82 m^3 s^{-1} (2003/04). The Q_{95} varied between 0.15 m^3 s^{-1} (2001/02) and 0.032 m^3 s^{-1}

(1998/99). For the entire study period, the long-term daily mean discharge of 0.52 m^3 s^{-1} (1966–2003) was exceeded for 27% of the time; exceedence ranged between 19% (1996/97) and 40% (2000/01) in individual years.

Focussing on the ecologically sensitive time periods where salmon are potentially most susceptible to flow related effects. The flow duration curves in Fig. 5 show more concisely the magnitude and nature of flow variability within specific time periods for each year. The winter period 2 (P2) was generally characterised by the most marked changes. Flattest period of flow accumulation was around start of period 4 (P4) , i.e. usually around 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 discharges varied between 0.48 (1996/97) and 0.73 mm^3 s^{-1} (2000/01). Inter-annual variability was especially apparent in maximum discharge: the highest maximum discharge is uncertain but close to 100 m^3 s^{-1} (1994/95) and the lowest maximum discharge 13.3 m^3 s^{-1} (2003/04). Minimum discharges varied between 0.12 m^3 s^{-1} (2001/02) and 0.03 m^3 s^{-1} (1998/99). The coefficient of variation, calculated as ratio between mean and standard deviation, was highest in 1994/95 (3.86) and lowest in 2003/04 (1.46).

The highest discharges generally occurred outside period 1 when fish were moving into the burn, occurring four times during period 2 and three times during period 4. Only in 1997/98 did the highest discharge occur in period 3.

Inter-annual variability (difference between lowest and maximum value of all ten years) was high in each period, ranging from 99% in period 4 to 78% in period 3. This largely reflects the “flashy” hydrological regime of the Girnock Burn – even in summer when 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 variability (93%), whilst period 2 showed the lowest variability (59%).

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4.2. Characterisation of stream temperatures

In common with discharge, stream temperatures in the Girnock Burn are also characterised by marked inter-annual variability (Fig. 6). Mean temperatures ranged between 6.9 °C (1995/96) and 8.2°C (1997/98, Table 2). However, the extremes of temperature were even more variable.

The highest stream temperatures exceeded for 1 % of the time ranged between 14.2°C (1995/96) and 17.7°C (2002/03). Stream temperatures in individual years varied between exceeding −0.6°C (2000/01 and 2002/03) and 1°C (1997/98) 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 those. Stream temperatures of 18°C were exceeded for 0.1% of the time during seven years (1997/98–2003/04). Exceedence of the lower temperature limit was more evenly distributed between all years, ranging between 40% (1994/95) and 55% (1998/99). The upper limit of 24.6°C was not exceeded at the site, though work on spatial distribution of Girnock temperatures has shown that higher summer temperatures occur in the upstream river network where shading from riparian trees is absent (Malcolm et al., 2004).

Cumulative stream temperatures in degree-days relative to ecologically important periods are shown in Fig. 7. Clear differences were observed in inter-annual variability. The hydrological year 1997/98 was most extreme, with the highest temperatures observed during each of the four periods. Degree days for the whole year varied between 2453 days (2000/01) and 2832 days (1997/98, Table 2); resulting in inter-annual variation of 13%.

4.3. Effects on foraging behaviour of juvenile salmon

To assess the times when foraging behaviour of juveniles 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). The mean stream velocities in 15 min resolution and the CDV for 1+ fish are shown in Fig. 8.

As a result of the interaction between intra-annual changes in fish length and stream temperature, the CDV for each age class varied throughout the year. However, clear seasonal patterns of CDV were apparent. The higher values typical of the summer period due to greater fish length and higher temperatures suggest 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 seasonal patterns in stream temperature. However, clear differences were evident in the duration 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 and temperatures (Table 3).

The duration of the time for which mean stream velocity exceeded CDV for salmon fry (0+) ranged between 29.3% (1997/98) and 44.7% (2000/01). CDVs are relatively high during the summer due to warmer stream temperatures and CDV was only occasionally exceeded at this time. 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 became 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% (1997/98) and 30.7% (2000/01) of the time. Again, the highest percentages of exceedence time were reached in January/February. But because of the larger size of parr relative to fry, 100% exceedence in any month was only predicted in 2002/03. During years with higher stream temperatures (e.g. 1997/98) and in summer, CDV values were relatively hogher and exceedence values lower. This was because the potential constraints of high discharge on foraging were compensated for by the greater scope for motor activity afforded by higher temperatures.

4.4. Effects on returning spawners

Table 4 shows the results of simple linear regression analysis carried out as a preliminary assessment of the hydrological influences on returning adult numbers. Due to the extremely complex interactions between abiotic influences and biological controls on salmonid movement at spawning, it is unsurprising that fish numbers were not directly correlated to discharge parameters for whole hydrological years. However, focussing on ecologically sensitive time periods and providing a more biologically relevant temporal resolution for analysis improved regression results substantially.

Strong correlations were observed between the coefficient of variation of discharge during period 1 and returning numbers of female spawners (Fig. 9). In general, female salmon are observed to initiate spawning entry to the Girnock Burn at or before ovulation and male fish generally follow the females into the system in response, probably, to pheromonal (Moore and Waring, 1996) as well as abiotic cues. Thus, it is unsurprising that there were weaker correlations with adult male numbers (Table 4). Regression plots showing the relationships between coefficients of variation and maximum discharges and returning females are shown in Fig. 9 and indicate that the high correlations were strongly influenced by the extreme conditions during 1995/96.

Figure 10 shows the daily resolution of returning female spawners in relation to the hydrological conditions during period 1. Hydrological conditions differed substantially between the ten years examined and patterns of fish entry varied too. In most years, spawners could be shown to enter the stream coincident with hydrological events. For example, in 1994/95, 1995/96 and 1997/98, the highest numbers of returns on one day occurred during the largest hydrological event. However, in other years, such as 1996/97, 1998/99, 1999/2000, 2000/01, 2001/02 and 2002/03 fish entry was spread more evenly over a range of smaller events. In contrast, in 2003/04 a prolonged period of low discharges resulted in all spawning females entering the burn in response to two very minor increases in stream discharge.

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). The relationship between "normal" variability and major "disturbance" events is recognised theoretically, but has rarely been defined in an empirical sense. 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 based on timescales (i.e. weekly or monthly) that may not capture subtle interactions between physical habitat conditions and biological activity (Stewardson and Gippel, 2003). Moreover, whilst physical environmental effects on salmon are most marked during extreme conditions, the thresholds marking the difference between normal system behaviour and disturbances are unclear. 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, high resolution discharge and temperature data, together with biological data, at those few sites where all are available is essential in order to understand mechanisms and controls on biological variables.

In Scotland, streams such as the Girnock Burn provide important habitat for Atlantic salmon and the data sets associated with the site have provided important insights into the linkages between discharge, temperature and biological activity (Gibbins et al., 2004; Hannah et al., 2004; Tetzlaff et al., 2005b). The basic, underlying timing of some of these activities has a strong heritable component suggesting that local genetic adaptation may affect some of the biological processes involved (Jordan and Youngson, 1991). In the Girnock Burn, genotype is a direct effect on growth performance (Youngson et al., 1994; Stewart et al., 2002) 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 likely feeding opportunities for juvenile salmon, a factor which may help account for unexplained variability in growth. In the Girnock Burn, recently hatched salmon fry tend to reach the emergence stage in May when discharge, variability in discharge and 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), which together with incubation temperature, determines hatch and emergence dates (Heggberget, 1988): i.e. they emerge at a time when discharges are, on average, becoming lower and less variable. 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 1997/98 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, 2004; Elliot and Hurley, 2003; 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 fine scale variation in discharge conditions. The entry of female fish was much more evenly distributed during years with regular flow pulses during the critical period. Discharges below about $0.3\,\mathrm{m^3\,s^{-1}}$ appeared to prevent access to the stream. 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 biological imperatives increasingly demand entry even under sub-optimal conditions. Many of the adults entering the Girnock Burn have been tagged there previously as smolts (Youngson et al., 1983). 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 (Carss et al., 1990) for the duration of their stay there. 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 when in a larger group for a shorter period.

The study has also shown strong 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; qualitatively, effective population size and the maintenance of genetic diversity is critically dependent on spawner number in relatively small breeding 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). This study has shown that for an ecologically meaningful analysis, data with a high temporal resolution has a number of advantages over averaged data, particularly if hydraulically meaningful parameters can be derived from the data set. In addition, focussing on ecologically sensitive time periods rather than averaged parameters over arbitrary, longer time periods allows temporal variability to be considered in terms of its implications for ecosystem processes (Archer and Newson, 2002). Such information can provide useful insights for the management of fisheries resources (Fausch et al., 2002). Setting EAFs for the benefit of target species such as Atlantic salmon in rivers affected by regulation ideally needs to incorporate the habitat needs of different life-stages at a range of temporal scales. For examples, if freshet releases for fisheries benefit are to be made, very different regimes are needed during the period of maximum spring growth rates – to avoid CDV exceedence – and during the final phase of the spawning migration to facilitate passage.

A clearer understanding of the relationships between discharges, species and life-stages is a major challenge in hydroecology. This study presents ways in which such relationships can be elucidated. However, much more research is needed. For example, 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 is useful for illustrating inter-annual variability in hydraulic conditions in relation to CDVs. However, this methodology 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 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). The requirement for measurements at high spatial and temporal resolution requires complementary approaches to sampling (Fausch et al., 2002).

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 (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 the WFD over the coming decade.

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Table 1. Statistical values of discharge for ten hydrological years and for ecologically sensitive time periods (in bold: maximum and minimum values for each parameter).

		Discharge [$m^3 s^{-1}$] 15 min time resolution				
Time period		Mean	Median	Max	Min	Coeff. Var.
Hydrological year	1994/95	0.68	0.26	**100.09 (09/09/95)**	0.04	3.86
	1995/96	0.68	0.32	55.34 (08/01/96)	0.04	2.63
	1996/97	0.48	0.22	28.69 (19/02/97)	0.07	2.14
	1997/98	0.60	0.26	18.15 (05/04/98)	0.06	2.07
	1998/99	0.50	0.30	18.88 (20/09/99)	**0.03**	1.83
	1999/2000	0.67	0.35	21.25 (22/12/99)	0.06	1.96
	2000/01	0.73	0.41	19.83 (10/10/00)	0.06	1.79
	2001/02	0.68	0.39	37.71 (31/07/02)	0.12	1.72
	2002/03	0.61	0.24	31.21 (21/11/03)	0.05	2.8
	2003/04	0.42	0.26	13.30 (11/08/04)	0.06	1.46
Period 1 15 Oct.–14 Nov. Main time period where spawning salmon enter the Girnock Burn	1994/95	0.64	0.34	13.87 (23/10/94)	0.08	1.78
	1995/96	0.93	0.4	**30.62 (26/10/95)**	0.22	2.77
	1996/97	0.65	0.34	10.33 (05/11/96)	0.10	1.67
	1997/98	0.15	0.11	1.01 (08/11/97)	0.06	0.62
	1998/99	1.03	0.57	10.50 (24/10/98)	0.28	1.11
	1999/2000	0.45	0.27	04.61 (05/11/99)	0.10	1.12
	2000/01	1.28	0.71	16.90 (07/11/00)	0.37	1.44
	2001/02	0.98	0.54	07.75 (20/10/01)	0.31	1.12
	2002/03	1.93	0.72	26.84 (22/10/02)	0.38	1.85
	2003/04	0.14	0.11	0.81 (12/11/03)	**0.06**	0.74
Period 2 15 Nov.–14 March Winter period – low biological activity and low growth for juvenile fish	1994/95	0.97	0.44	31.20 (10/03/95)	0.11	2.03
	1995/96	1.34	0.61	**55.34** (08/01/96)	0.16	1.93
	1996/97	0.73	0.28	28.69 (19/02/97)	0.09	2.01
	1997/98	0.92	0.55	16.54 (18/11/97)	0.13	1.39
	1998/99	0.73	0.45	12.01 (02/01/99)	0.17	1.45
	1999/2000	0.97	0.53	21.25 (22/12/99)	0.16	1.65
	2000/01	1.16	0.87	12.91 (23/01/01)	0.21	1.18
	2001/02	0.94	0.58	18.10 (01/02/02)	0.24	1.37
	2002/03	1.03	0.53	31.21 (21/11/03)	0.15	2.06
	2003/04	0.55	0.38	9.50 (08/01/04)	**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	1994/95	0.32	0.24	4.73 (23/04/95)	0.11	1.24
	1995/96	0.55	0.43	12.48 (23/04/96)	0.16	1.36
	1996/97	0.27	0.19	2.66 (04/05/97)	**0.08**	0.95
	1997/98	1.03	0.40	18.15 (05/04/98)	0.14	2.08
	1998/99	0.37	0.24	6.27 (20/04/99)	0.09	1.49
	1999/2000	1.01	0.56	**18.44 (26/04/00)**	0.17	1.75
	2000/01	0.49	0.39	4.50 (31/03/01)	0.11	1.02
	2001/02	0.29	0.24	1.46 (22/03/02)	0.13	0.64
	2002/03	0.31	0.18	3.81 (02/05/03)	0.09	1.28
	2003/04	0.59	0.44	4.10 (19/04/04)	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	1994/95	0.17	0.06	20.25 (01/06/95)	0.04	3.53
	1995/96	0.12	0.07	4.37 (23/07/96)	0.04	1.58
	1996/97	0.41	0.19	11.19 (18/05/97)	0.07	1.92
	1997/98	0.32	0.19	17.98 (07/06/98)	0.09	1.97
	1998/99	0.17	0.09	3.75 (06/06/99)	**0.03**	1.75
	1999/2000	0.22	0.15	5.56 (29/07/00)	0.06	1.35
	2000/01	0.21	0.1	14.60 (19/08/01)	0.06	3.3
	2001/02	0.61	0.3	**37.71 (31/07/02)**	0.14	2.21
	2002/03	0.11	0.08	0.56 (21/05/03)	0.05	0.83
	2003/04	0.35	0.16	13.30 (11/08/04)	0.07	2.20

Table 2. Statistics of stream temperature.

Time period		Stream temperature [°C] (hourly)				Coeff.	Degree days (total at
		Mean	Median	Max	Min	Var.	end of certain period)
Hydrological year	1994/95	6.9	6.4	17	−0.8	0.71	2570
	1995/96	6.7	6.6	15	−0.8	0.68	2465
	1996/97	7.0	7.4	18.8	−0.2	0.73	2568
	1997/98	8.2	8.4	20.2	−0.6	0.55	2832
	1998/99	8.1	8.8	19.1	−0.6	0.62	2610
	1999/2000	7.1	6.9	18.4	−1.0	0.69	2592
	2000/01	6.9	6.7	20.2	−0.8	0.75	2453
	2001/02	7.6	8.3	19.9	−0.4	0.65	2786
	2002/03	7.5	6.9	19.8	−0.6	0.68	2769
	2003/04	7.0	6.7	20.2	−0.6	0.74	2634
Period 1 15 Oct.–14 Nov. Main time period where spawning salmon enter the Girnock Burn	1994/95	6.5	6.8	9.2	2.4	0.18	306
	1995/96	6.9	6.8	12.2	2.6	0.30	352
	1996/97	6.2	7.2	10.4	0.2	0.43	324
	1997/98 (46%*)	6.8	6.4	10.6	4.4	0.21	327
	1998/99	3.8	3.6	10.2	−0.1	0.51	224
	1999/2000	6.6	6.5	9.5	1.5	0.24	306
	2000/01	4.8	4.6	9.1	0.7	0.36	260
	2001/02	6.9	7.3	11.7	−0.2	0.40	356
	2002/03	4.1	3.9	8.0	0.8	0.36	252
	2003/04	4.7	4.4	9.1	0.3	0.38	244
Period 2 15 Nov.–14 March Winter period – low biological activity and low growth for juvenile fish	1994/95 (1.6%*)	2.1	1.4	8.8	−0.8	0.89	576
	1995/96 (0.8%*)	2.0	1.6	7.8	−0.8	0.97	614
	1996/97 (2.4%*)	1.6	1.0	7.4	−0.2	1.02	525
	1997/98 (23%*)	3.5	3.2	9.2	0.2	0.62	798
	1998/99 (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
	2000/01 (10%*)	1.4	0.7	7.1	−0.8	1.54	445
	2001/02	2.1	1.8	7.7	−0.4	0.93	612
	2002/03	2.4	2.3	8.4	−0.6	0.95	554
	2003/04	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	1994/95	4.6	5.4	10.2	−0.8	0.63	905
	1995/96	4.7	5.2	10.4	0.0	0.58	902
	1996/97 (62%*)	6.1	5.8	12	2.6	0.29	927
	1997/98 (27%*)	6.4	6.2	18.1	−0.6	0.63	1187
	1998/99 (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
	2000/01	5.6	5.4	17.1	−0.2	0.64	788
	2001/02	7.1	6.9	16.0	0.8	0.41	1052
	2002/03	6.9	7.1	13.8	−0.6	0.37	981
	2003/04 (56%*)	6.1	5.2	17	1.1	0.55	884

* percentage of missing data for given time period %

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Table 3. Time of exceedence when mean stream velocity exceeded CDV [%].

0 +	1994–1995	1995–1996	1996–1997	1997–1998	1998–1999	1999–2000	2000–2001	2001–2002	2002–2003	2003–2004
Oct.	3.2	9.7	6.5	0.0	32.3	0.0	22.6	16.1	35.5	0.0
Nov.	6.7	36.7	46.7	23.3	33.3	13.3	56.7	13.3	33.3	3.3
Dec.	32.3	54.8	71.0	22.6	51.6	96.8	77.4	67.7	51.6	45.2
_Jan._*	100.0	100.0	93.5	100.0	100.0	100.0	100.0	100.0	100.0	100.0
_Feb._*	100.0	100.0	96.4	46.4	100.0	100.0	100.0	100.0	100.0	100.0
_Mar._*	100.0	100.0	71.0	58.1	64.5	41.9	100.0	87.1	61.3	90.3
_Apr._*	26.7	96.7	0.0	93.3	30.0	100.0	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
Aug.	0.0	0.0	0.0	0.0	0.0	0.0	6.5	6.5	0.0	12.9
Sep.	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+										
Oct.	3.2	6.5	0.0	0.0	9.7	0.0	12.9	9.7	22.6	0.0
Nov.	0.0	23.3	46.7	10.0	20.0	6.7	33.3	6.7	30.0	3.3
Dec.	19.4	45.2	61.3	12.9	41.9	93.5	51.6	58.1	29.0	45.2
Jan.	77.4	64.5	61.3	71.0	77.4	74.2	100.0	71.0	67.7	80.6
Feb.	82.1	89.7	53.6	10.7	53.6	62.1	100.0	89.3	75.0	62.1
Mar.	12.9	32.3	12.9	22.6	0.0	16.1	71.0	25.8	3.2	45.2
Apr.	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
Aug.	0.0	0.0	0.0	0.0	0.0	0.0	3.2	3.2	0.0	3.2
Sep.	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

* For January–April: assumption of a minimum fish length of 20 mm; with fry emergence in mid May

Table 4. Coefficients of determination r^2 between discharge variables and returning adults (positive trends).

	Discharge value	Total fish	Total male	Total female
Total hydrological year	Mean	0.16	0.27	0.05
	Max	0.26	0.16	0.26
	Min	0.06	0.09	0.03
	CV	0.16	0.11	0.14
Period 1	Mean	0.02	0.07	0.001
15 Oct.–14 Nov.	Max	0.44	0.34	0.37
Main time period where spawning	Min	0.01	0.06	0.01
salmon enter the Girnock Burn	CV	0.67	0.37	0.72

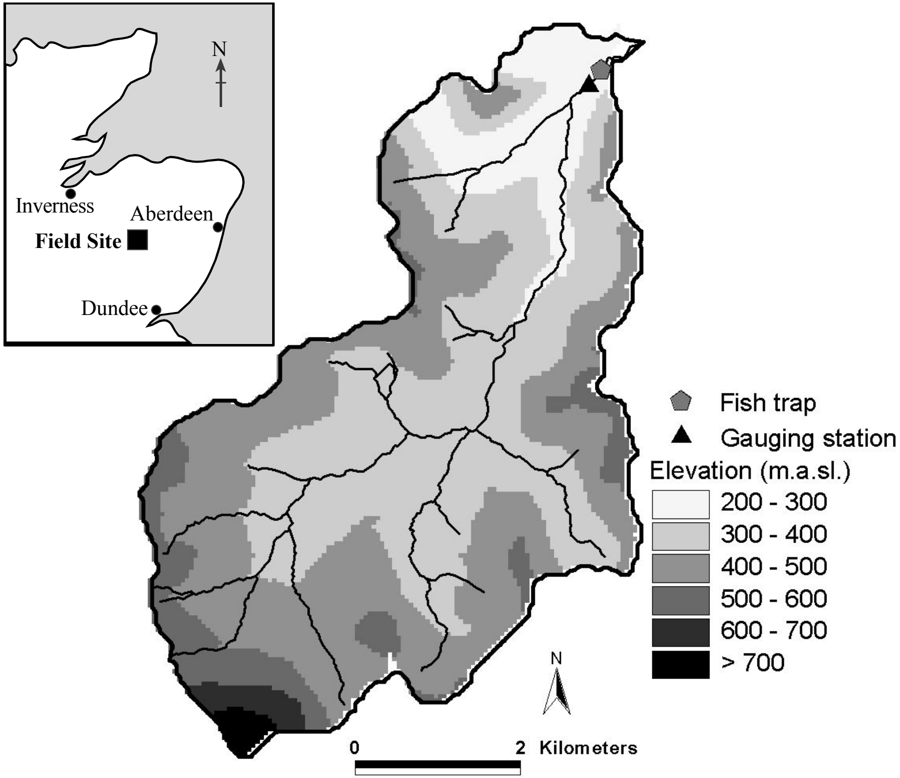

Fig. 1. The Girnock Burn catchment: topography and gauging site Littlemill.

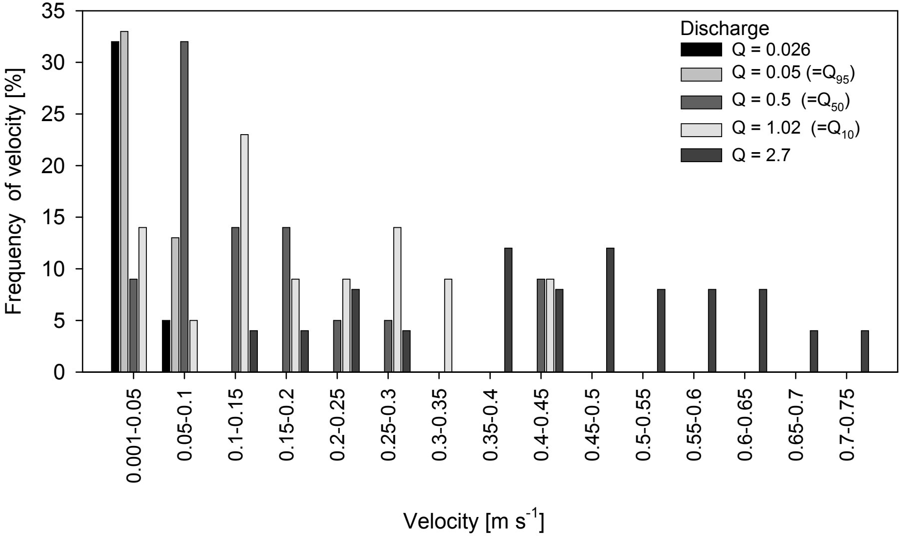

Fig. 2. Frequencies of stream velocity for several discharges (incl. Q_{95}, Q_{50}, Q_{10}) at the cross-section at gauging site Littlemill.

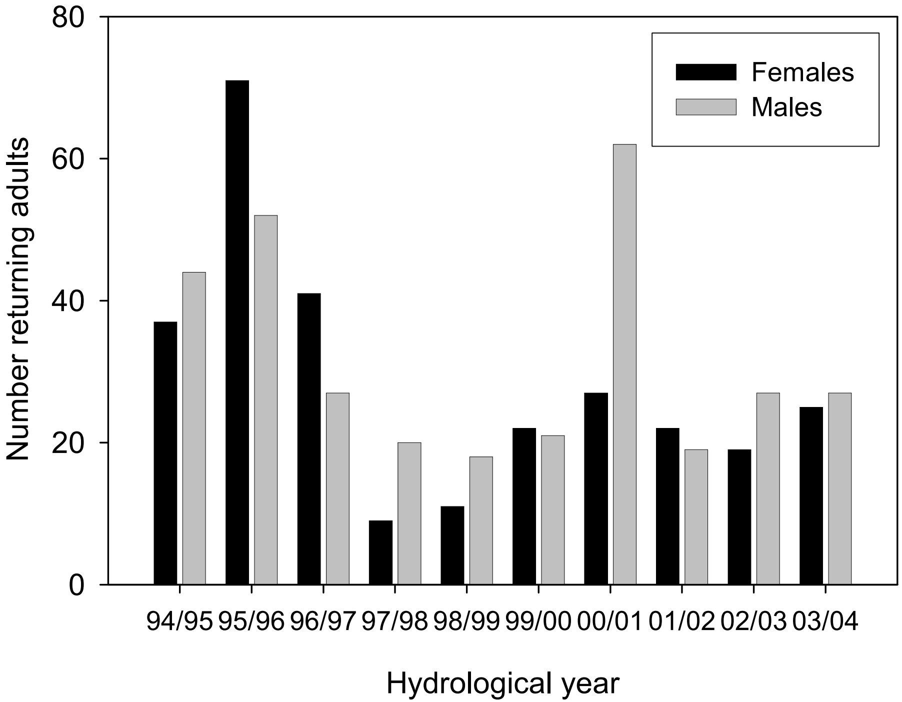

Fig. 3. Number of returning adults (autumn) used within the study.

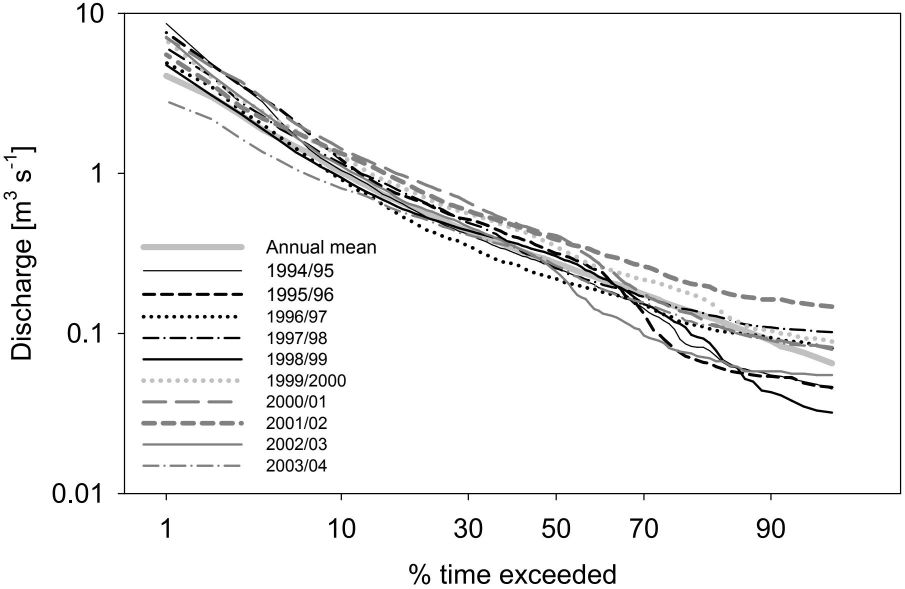

Fig. 4. Flow duration curves for the ten hydrological years investigated.

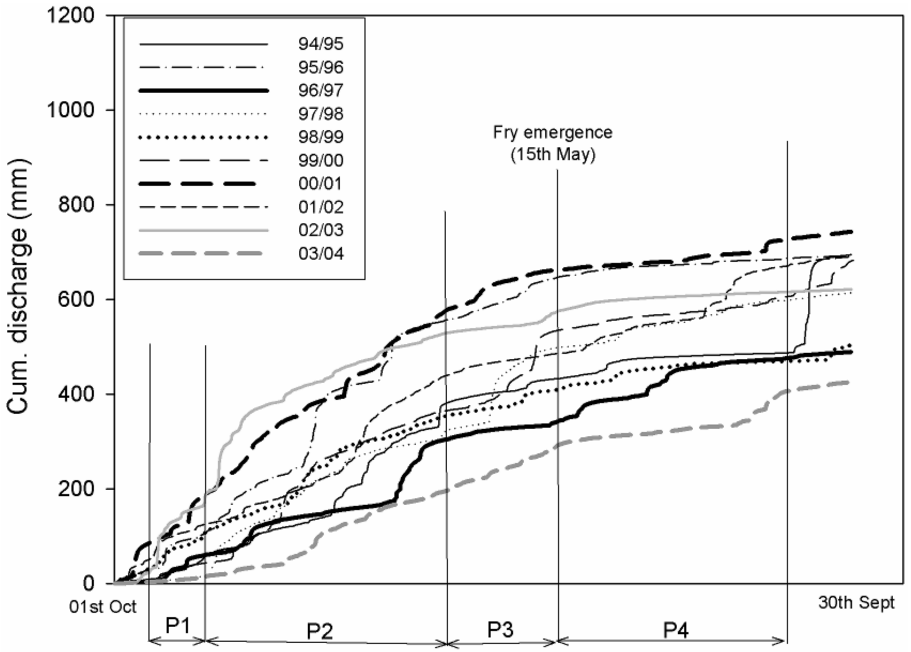

Fig. 5. Cumulative discharge curves showing ecological sensitive time periods.

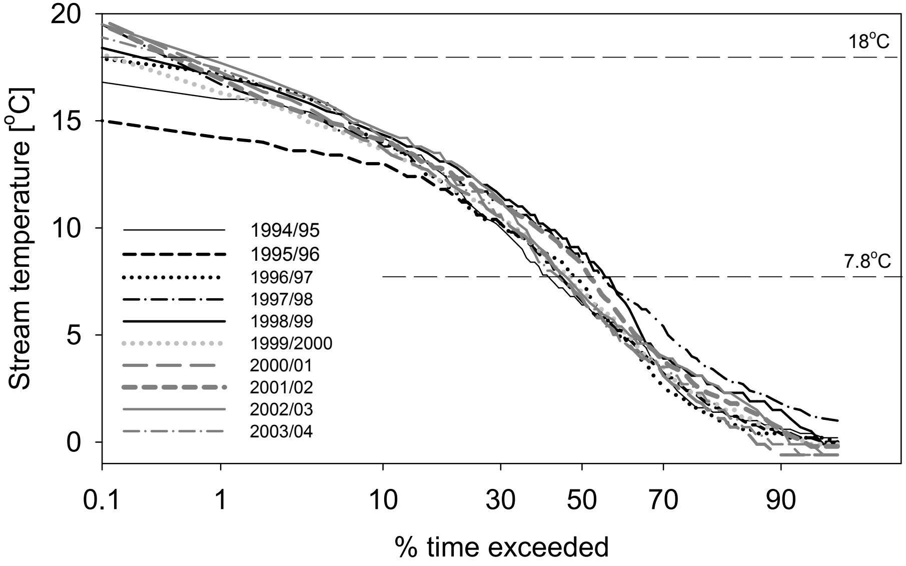

Fig. 6. Time of exceedence of stream temperatures showing optimum and lower limit temperatures for Atlantic salmon growth.

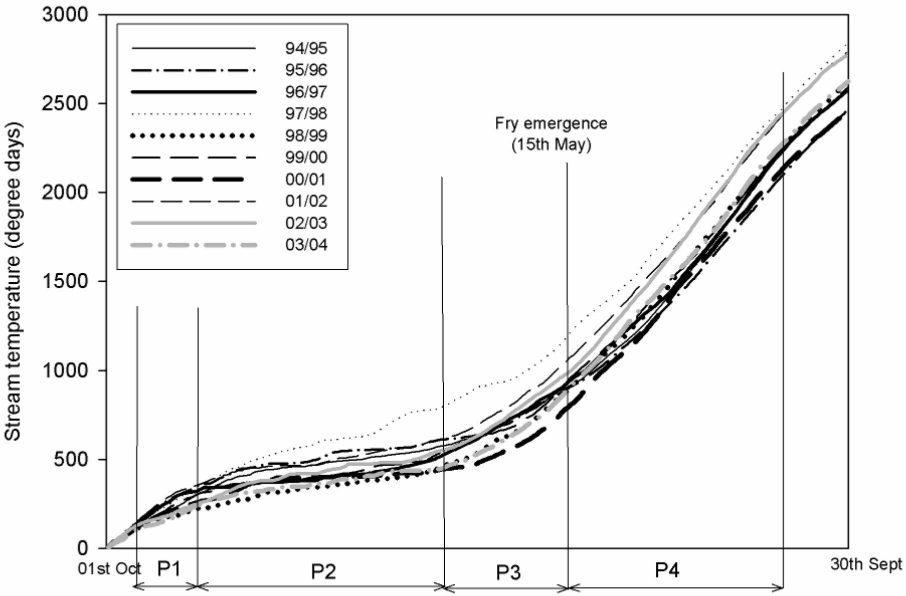

Fig. 7. Cumulative stream temperature curves showing ecological sensitive time periods.

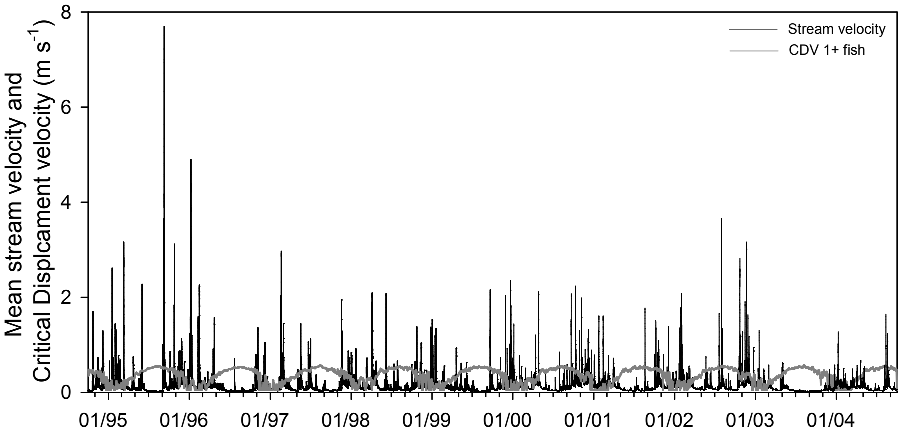

Fig. 8. Mean Critical Displacement Velocity CDV and mean stream velocity for 1+ salmon over the ten years investigated.

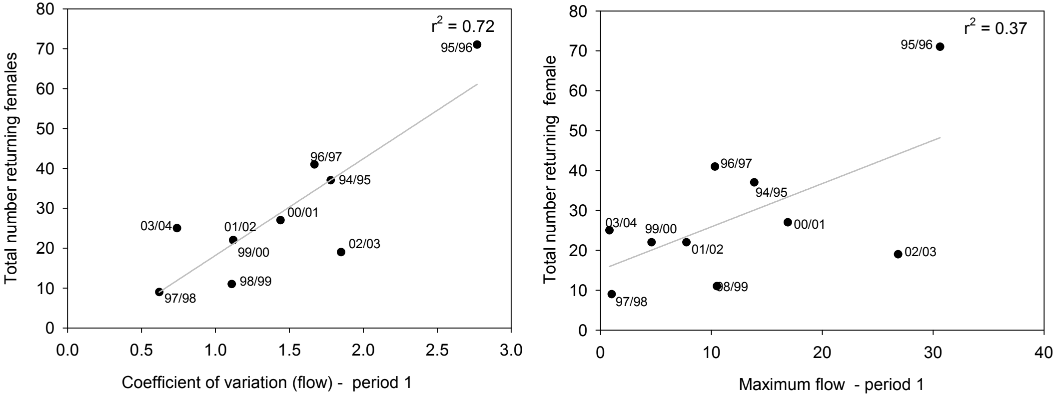

Fig. 9. Selected regression graphs showing dependence of returning females on exemplary hydrological variables.

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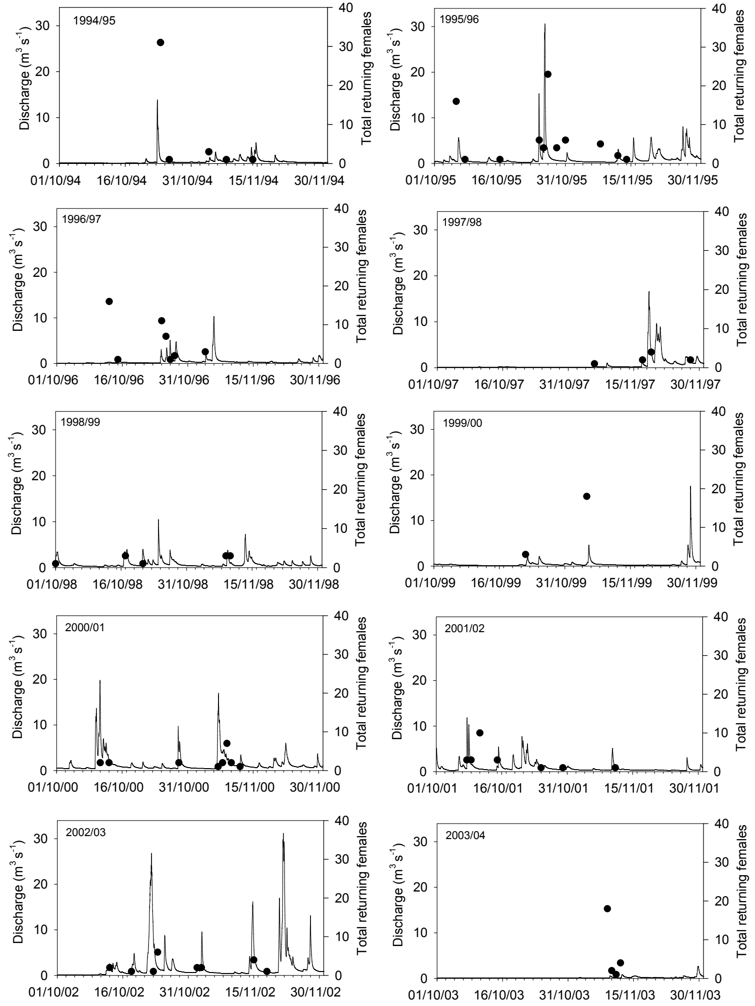

Fig. 10. Timing and number of returning spawning salmon in relation to hydrological conditions.