

INFLUENCE OF HYDROLOGICAL REGIMES ON THE PRE-SPAWNING ENTRY OF ATLANTIC SALMON (*SALMO SALAR L.*) INTO AN UPLAND RIVER

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ABSTRACT

The Girnock Burn is an Atlantic salmon (*Salmo salar*) spawning tributary of the river Dee, Aberdeenshire, Scotland. The dates, sexes and numbers of adult salmon entering the stream in the three months prior to spawning were determined between 1969 and 2005 using a permanent fish-trap. During this time, the number of fish returning to spawn varied markedly. Here we analyze the whole of this unique long term data set in order to characterize and classify the hydrologic regimes of the pre-spawning migration period and assess the extent to which these regimes help explain the timing and patterns of arrival of adult salmon into the stream. A range of flow parameters was calculated for the arrival period (September–November) for each of the 37 years. These parameters were used to ordinate and classify years according to their flow regimes. The analysis yielded six distinct groups or ‘flow regime types’ which separated principally in relation to flow magnitude and frequency parameters. The number of fish entering the burn on a given day was not significantly correlated to discharge on that day. However, patterns of arrival of fish differed markedly between years with different regime types, with the number of fish arriving on a given day related to patterns of discharge over the preceding part of the arrival period. Overall inter-annual variability in entry corresponded to the defined regime types. In wetter years, fish entry to the stream usually starts relatively early and continues throughout the pre-spawning period. In contrast, dry years may result in fish entry being delayed; this may result in lower numbers of spawning females entering the stream and sub-optimal utilization of juvenile habitat in the following spring. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: Atlantic salmon; pre-spawning river entry; flow regime types; discharge variability; hydrological influences

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INTRODUCTION

The importance of flow regimes in driving many facets of river and stream ecosystems is now well established (Petts, 2000). The natural flow paradigm—the view that natural discharge variability is central to maintaining river ecosystem integrity—is increasingly an implicit part of water resource legislation. For example, in Europe, the Water Framework Directive dictates that water resources management should, where possible, protect patterns of natural flow variability sufficiently well to maintain the ecological status of rivers. Numerous indices have been developed which aid the characterization of variability and identify ecologically important components of the natural hydrograph (e.g. Richter *et al.*, 1996; Harris *et al.*, 2000; Olden and Poff, 2003). Related tools can be used to estimate the availability of suitable habitat for target species or life stages at different discharges (e.g. PHABSIM; Bovee, 1982). Overall, these indices and flow assessment tools help emphasize the links between discharge, channel hydraulic conditions and habitat, and are now applied widely in flow assessment studies (Gordon *et al.*, 2004). However, the long-term biological data needed to explicitly link hydrological conditions to biological populations are rarely available.

Because of their ecological, economic and cultural importance, the Atlantic salmon (*Salmo salar*) and other salmonids have been the focus of many flow assessment studies. These studies have emphasized aspects of the complex, subtle and scale-dependent nature of how flow influences different life stages (e.g. Gilvear *et al.*, 2002; Jensen, 2003; Bacon *et al.*, 2005). River flows can have an important influence on salmon at various times in their

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life cycle. For example, there is evidence that juveniles select habitat patches where net energy gain is enhanced (Fausch, 1984), while adults select sites for spawning where depths and velocities can ease the process of nest (redd) cutting (Moir *et al.*, 2002). Over longer timescales, aspects of salmon life cycles have adapted to match local hydrological regimes (Beechie *et al.*, 2006). Juvenile emergence has been observed to occur at the time when winter spates become less frequent and so fish are statistically less likely to experience hydraulic conditions which cause downstream displacement or prevent adequate feeding (Tetzlaff *et al.*, 2005a). Consequently, subtle differences in the timing of life cycle events occur between different river systems in different regions with contrasting hydrological regimes (Beechie *et al.*, 2006; Gibbins *et al.*, in press).

There has been long-standing interest in the role that discharge plays in the entry of adult fish from the sea to their spawning river system and on their subsequent upstream movement to the spawning grounds (reviewed by Banks, 1969). The timing and duration of this pre-spawning migration varies from river to river, as a function of the distance from the sea to spawning areas and of the interaction between hydrologic regimes, stream temperatures and the geomorphology of the river network. In addition, the timing varies between salmon of different age classes, with multi-sea winter (MSW) fish returning earlier, with a longer upstream migration than one sea winter (1SW) fish (or grilse). In rivers whose geomorphic character produces deep pools close to spawning locations, fish move directly from the sea and spend the pre-spawning period (often several months) close to the spawning sites. In other cases where pools are lacking, fish spend the pre-spawning period some distance from their spawning locations and only move to these shortly before spawning.

The Gironck Burn is an upland tributary of the river Dee (NE Scotland) located approximately 70 km from the sea (Figure 1). Like many headwater spawning streams, there are no suitable holding pools in the stream, so Gironck spawners spend a protracted pre-spawning period (February–October) in the mainstem of the Dee where such pools exist. Consequently, adult fish only enter the stream in the period between early September and late November, immediately prior to spawning, which takes place from late October to early December in the Gironck. The Gironck salmon population has been routinely monitored since 1966, with data collected on the numbers of returning fish, juvenile densities and smolt production (Youngson *et al.*, 1994). Discharge and stream temperatures have been measured since 1969, providing rare long-term hydroecological data sets, which give an opportunity to

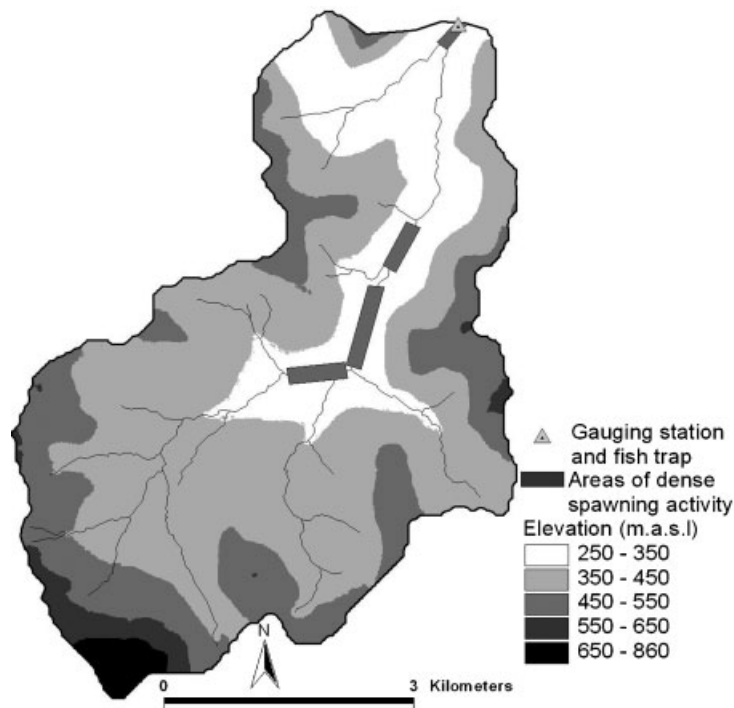


Figure 1. The Gironck catchment, showing topography, the location of the gauging station, fish trap at Littlemill and the main spawning areas

explore the interactions between flow regimes and various aspects of salmon lifecycles (Langan *et al.*, 2001). As in many areas across the species' range, it is evident from these records that the number of fish returning to the Girnock has declined markedly over the past two decades, leading to concerns that insufficient fish may be returning to maintain a viable population (Webb *et al.*, 2001). Furthermore, in the past decade, a number of dry autumns have been noted to delay spawning entry and restrict upstream migration, thus tending to concentrate spawning in the lower reaches of the burn. In such situations, uneven spawning distributions may result in sub-optimal use of juvenile habitat, with density dependent factors potentially compromising smolt production (Gibbins *et al.*, 2002).

The implication of the variation in patterns of upstream migration is that, in different rivers, different time periods are most relevant when assessing flow needs for different ecological objectives. The Girnock Burn is a typical upland spawning stream, characterized by a comparatively late returning period for females. The criticality of flows during this period relates both to entry to the stream from the Dee and the subsequent upstream movement of fish to spawning sites. Likewise, flow has a major effect on spawning distribution in the stream (Webb and Hawkins, 1989); Moir *et al.* (1998) have already shown that fish tend to penetrate further up the burn in years with higher median discharge during the spawning period. This is because higher flows are needed to 'drown out' physical obstructions to fish in the steeper, narrower upper channel, thus allowing access to the upper catchment (Webb *et al.*, 2001).

This paper focuses on how patterns of discharge variability influence the timing of the entry of fish into the Girnock burn. Using the unique 37-year data set, it assesses the role that intra- and inter-annual variability in discharge plays in influencing the pattern of entry during the immediate pre-spawning immigration period (late September to late November). The paper has three specific objectives:

- (1) to characterize the hydrologic regimes of the pre-spawning period using indices of flow variability;
- (2) using these indices, to objectively classify flow regimes and assess whether distinct regime types occur; and
- (3) to assess the extent to which different patterns of spawner entry reflect different regime types.

STUDY CATCHMENT

The Girnock Burn (Figure 1) is a third order upland stream with a catchment area of 30 km². The stream channel exhibits a high degree of naturalness: it has a River Habitat Survey Habitat Modification Score of 0 (Environment Agency, 1998), confirming a minimal human impact on the channel network. Average annual precipitation is 1100 mm with annual runoff about 700 mm (1961–1991, Scottish Environment Protection Agency, SEPA), with the summer months (May–August) generally being driest. Mean annual discharge is 0.52 m³ s⁻¹ (1969–2001). Previous hydrological studies have shown that the Girnock Burn is characterized by a high variability in discharge dynamics (Tetzlaff *et al.*, 2005a; Soulsby *et al.*, 2007). Instantaneous discharges vary between *ca.* 0.04 m³ s⁻¹ in the summer (Malcolm *et al.*, 2003) and > 30 m³ s⁻¹ during floods (Tetzlaff *et al.*, 2005b). Most high discharge events occur between late autumn and early spring, though they can occur throughout the year (Tetzlaff *et al.*, 2007a).

Flow exceedence values for the spawning period are typically higher than respective annual ones, particularly in the low flow range (Moir *et al.*, 1998). Mean discharge for the spawning period is 0.66 m³ s⁻¹ compared with 0.52 m³ s⁻¹ for the whole year. Spawning Atlantic salmon have been shown to utilize areas dominated by gravel sized (2–64 mm) substrate (Moir *et al.*, 2002). Such areas are distributed patchily in the Girnock, often separated by extensive areas of unsuitable sized sediment dominated by cobbles (64–256 mm) and/or boulders (>256 mm). Areas of suitable spawning substrate have been estimated to occupy <5% of the stream length (Webb *et al.*, 2001).

The catchment altitude ranges from 230 to 862 m above mean sea level. Along its 9.5 km length the stream has an average gradient of 17.4 m km⁻¹ and a mean width of 6.6 m (Moir *et al.*, 1998). Details of the climate, geology, landuse and hydrology of the Girnock have been described elsewhere (e.g. Moir, 1999; Soulsby *et al.*, 2005, 2007; Tetzlaff *et al.*, 2005a, b, 2007a). Briefly, the catchment has a complex geology, dominated by granite, calcareous schists and serpentine. Various glacial and fluvio-glacial deposits cover the solid geology. Soil cover is dominated by hydrologically responsive soils (peaty gleys, peats, thin alpine soils), supporting a moorland vegetation

dominated by *Calluna* and *Erica* sp. In its lower reaches the stream is bordered by rough pasture, with riparian vegetation consisting of unmanaged pine (*Pinus sylvestris*) birch (*Betula* sp.) and alder (*Alnus* sp.) woodland.

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. Over this period, there was no change in mean annual temperature, though an increase (*ca.* 1°C) in mean daily temperatures during winter and spring has been identified (Langan *et al.*, 2001).

DATA AND METHODOLOGY

Flows and female arrival patterns

The Girnock 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 close to the catchment outlet (*ca.* 800 m from the confluence with the Dee) intercepts returning adult fish as they enter the stream (Figure 1). Mean daily discharges for the Girnock have been calculated from continuously logged stage, measured at the gauging station just upstream of the fish trap at Littlemill (Figure 1). During the spawning period, the fish trap is monitored daily and fish are counted, sexed, measured and tagged before being placed upstream for spawning. Available data for both hydrological conditions and returning salmon covered the period 1969–2005 inclusive (a total of 37 years). In general, females enter the stream ahead of males, at or before ovulation. They tend to be more clearly responsive to abiotic factors than males, which mainly respond to pheromonal signals generated by females in spawning- or near-spawning condition (Moore and Waring, 1996). For this reason the data used in the current study concerned only patterns of returning female fish (Table I, Figure 2a). Although the components of the Girnock spawning run each year comprise variable age cohorts, from grilse (1SW) to MSW fish, for the purpose of this analysis, information on only the total number of female fish on a given day is used.

In addition, smolt tagging studies show that about 50% of the fish entering the stream are returning to their natal stream. The real value is likely to be higher (Youngson *et al.*, 1994) as some of the untagged fish that enter the trap may originate below the trap in the lower Girnock and some tagged fish may spawn below it. Additionally, the number of smolts leaving varies among years (Buck and Hay, 1984) and this will result in proportionate variations

Table I. Total numbers and entry dates for adult female salmon in the Girnock for the 37-year study period

Year	First entry	Final entry	Total no.	Year	First entry	Final entry	Total no.
1969	02/11	02/11	28	1988	07/10	03/11	100
1970	21/08	06/11	31	1989	28/10	12/11	26
1971	18/10	11/11	59	1990	07/10	29/10	27
1972	30/10	18/12	72	1991	03/10	04/11	52
1973	21/10	08/11	119	1992	01/09	10/11	31
1974	08/10	13/11	102	1993	03/10	09/11	20
1975	28/09	19/11	62	1994	24/10	14/11	35
1976	26/09	26/11	83	1995	29/09	12/11	65
1977	07/10	07/11	43	1996	13/10	04/11	39
1978	01/11	13/11	11	1997	06/11	28/11	9
1979	05/10	05/11	44	1998	01/10	10/11	9
1980	17/09	07/11	107	1999	22/10	05/11	18
1981	21/09	04/11	37	2000	21/09	12/11	17
1982	05/10	09/11	37	2001	08/10	11/11	18
1983	17/10	14/11	25	2002	13/10	18/11	20
1984	19/10	09/11	55	2003	09/11	12/11	18
1985	18/10	06/11	23	2004	04/10	08/11	61
1986	30/10	09/11	57	2005	11/10	11/11	38
1987	20/10	20/10	95				

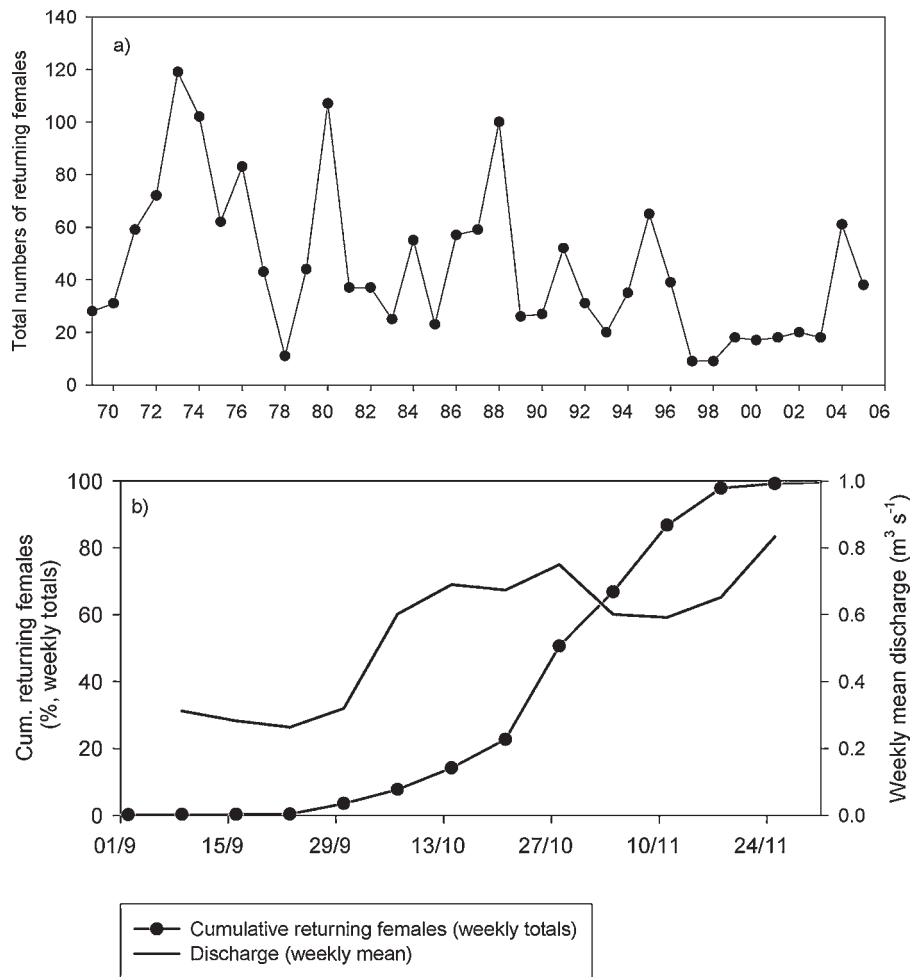


Figure 2. (a) Total numbers of returning females for the 37 years of data record, (b) mean cumulative percentage of adult female arrivals and mean weekly discharge (averaged over the 37-year data record) at the Girnock

in adult recruitment. Finally, by the time they reach adulthood, Girnock salmon have suffered natural marine mortality and human exploitation mortality in a sequence of fisheries (ocean, coastal, estuary and river) and all have varied grossly in their intensity over the period of this study. Physical environmental controls will therefore not be the only determinant of variation in the number of female salmon entering the stream to spawn. Furthermore, hydrological variability may not be the sole environmental control on the timing of entry to the stream. Salmon are poikilotherms and environmental temperature has profound effects on the physiological and biochemical processes which drive the processes associated with spawning (Webb and Hawkins, 1989). The key point addressed in the paper is whether—despite all these other influences—it is possible to detect effects of hydrological conditions on river entry.

To provide a framework for these hydrological analyses, the following sub-periods of the pre-spawning immigration period were identified on the basis of detailed observations at the site since 1966 (Figure 2b):

- (1) Early period (1st to 21st September): fish move up the Dee to near the Girnock confluence but only a small percentage of spawners enter the Girnock trap (<3% on average during the study period);
- (2) Mid arrival period (22nd September to 28th October): by the end of this period on average 50% of the eventual spawning population have entered the trap;

- (3) Late arrival period (29th October to 30th November): by the end of this period the remaining spawners have entered the trap.

Statistical analyses

For each of the 37 years, a number of indices of flow variability were calculated for the whole of the pre-spawning immigration period (1st September–30th November) and then for each of the three sub-periods separately (Table II). For each year, for the whole pre-spawning immigration period, a total of 21 indices were calculated. Selection was based on the work of Olden and Poff (2003) and Richter *et al.* (1996) (Table II). These have been argued to capture the ecologically meaningful characteristics of a flow regime while minimizing redundancy (Olden and Poff, 2003). Work by Gibbins *et al.* (2001) and Jackson *et al.* (2007) supported this, showing that these indices are ecologically relevant in Scottish streams. The use of these indices meant that each year was characterized by a series of values representing the ecologically important attributes of its discharge regime. Indices were then calculated separately for each of the three sub-periods. Because the sub-periods differed in length, it was not appropriate to compare some indices between sub-periods; thus, only a subset of 12 was used in the analysis of sub-period regimes (* in Table II).

Data were then ordinated (Principal Component Analysis (PCA)) using index values to represent the characteristics of each year. Two PCA ordinations were produced, one using index values for the whole immigration period and the second using the sub-period values. The second PCA ordinated years according to values of each index for each sub-period (i.e. using 36 (3×12) index values). The first PCA allowed the similarities/differences between years to be assessed with respect to the whole pre-spawning immigration period regime, where similarity/difference was determined by a set of values that captured important attributes of their flow regimes. The PCA also allowed the principal ways in which years differed to be identified (indices with the highest component loadings on Axes 1 and 2 were taken as those primarily responsible for between year differences). The second PCA provided an insight into which sub-period(s) was (were) responsible for any between-year differences observed.

A cluster analysis was used to objectively cluster years with similar flow regimes. A polythetic agglomerative cluster method was used as this allowed years to be grouped based on a number of attributes (the 21 and 12 index values for the whole pre-spawning period and sub-periods, respectively). The cluster analysis works by grouping individual samples (years) into successively larger groups, eventually producing a single group that contains all samples (years). As years are grouped into successively larger groups, information is lost; thus, there is a need to select an optimum number of groups. In the case of the whole pre-spawning period of the Gironck, which is shown as an example in Figure 3, the potential number of groups ranged from 37 (each year in its own group) to 1 (all years together in a single large group). The optimum number of groups was selected on the basis of parsimony. Six groups retained most (91%) of the information in the data (homogeneity within groups, variation between) and gave a manageable number of groups. Retaining more information required the use of appreciably more groups (e.g.

Table II. Indices of flow variability used to characterize the discharge regime during the pre-spawning migration period in the Gironck Burn

Mean* [$\text{m}^3 \text{s}^{-1}$]	Mean duration $Q > 0.1 \text{ m}^3 \text{ s}^{-1}$ [d]
Median* [$\text{m}^3 \text{ s}^{-1}$]	Max duration $Q > 0.1 \text{ m}^3 \text{ s}^{-1}$ [d]
Maximum discharge* [$\text{m}^3 \text{ s}^{-1}$]	Mean duration $Q > 0.3 \text{ m}^3 \text{ s}^{-1}$ [d]
Minimum discharge* [$\text{m}^3 \text{ s}^{-1}$]	Max duration $Q > 0.3 \text{ m}^3 \text{ s}^{-1}$ [d]
Coefficient variation* [-]	Mean duration $Q > 0.1 \text{ m}^3 \text{ s}^{-1}$ [d]
Skewness* [-]	Max duration $Q > 0.5 \text{ m}^3 \text{ s}^{-1}$ [d]
Pulse count $Q > 0.1 \text{ m}^3 \text{ s}^{-1}$ * [d]	25th-Perc* [$\text{m}^3 \text{ s}^{-1}$]
Pulse count $Q > 0.3 \text{ m}^3 \text{ s}^{-1}$ * [d]	75th-Perc* [$\text{m}^3 \text{ s}^{-1}$]
Pulse count $Q > 0.5$ (mean annual flow) $\text{m}^3 \text{ s}^{-1}$ * [d]	3xMedian* [$\text{m}^3 \text{ s}^{-1}$]
'Runnable' flow (pulse count days of $Q > 0.1 \text{ m}^3 \text{ s}^{-1}$, $12 \text{ m}^3 \text{ s}^{-1}$) [d]	Low flow count ($Q \leq 0.04 \text{ m}^3 \text{ s}^{-1}$) [d]
	Average low-flow duration [d]

*Are those calculated for both the whole migration period and sub-periods (see text for further details).

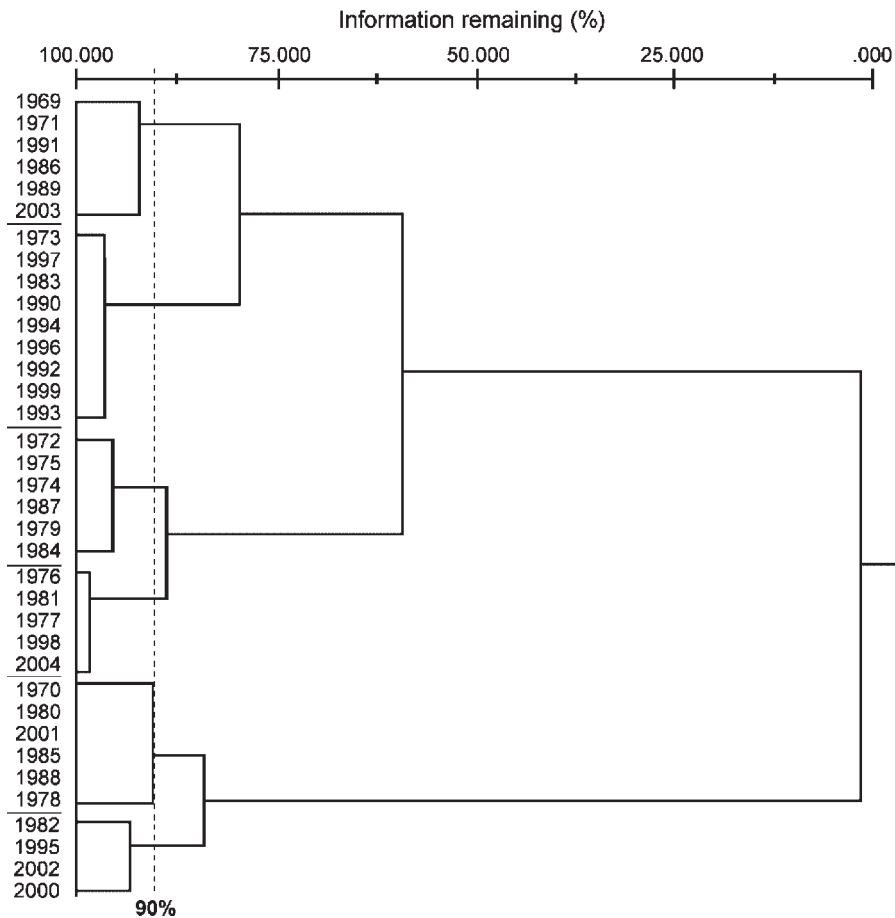


Figure 3. Cluster Analysis to objectively cluster years with similar flow regimes, shown for the analysis of the whole pre-spawning period

retaining 95% of the information required 12 groups) while the use of four groups meant that only 81% of the information was retained (Figure 3). In the case of the cluster analysis for the sub-periods (not shown), the optimum number of groups selected on the basis of parsimony applying the polythetic agglomerative cluster method was four. The Cluster and PCA analyses provided an objective grouping of years and information on the main hydrological differences between the groups. The timing and distribution of female spawner entry was compared between the defined groups for the whole pre-spawning period to determine whether arrival patterns differed.

RESULTS

Hydrology and flow regime types

There was marked inter-annual variability in the discharge statistics for the pre-spawning immigration period across 37 years investigated (Figure 4). This reflected antecedent and prevailing weather conditions. Median flow (Q_{50}) ranged from 0.07 (1969) to 1.10 (1982) $\text{m}^3 \text{s}^{-1}$; low flows (Q_{90}) during the same period varied between 0.02 (1969) and 0.37 (2000) $\text{m}^3 \text{s}^{-1}$ and high flows (Q_{10}) ranged from 0.20 (1969) to 4.47 (1982) $\text{m}^3 \text{s}^{-1}$. Years characterized by high flows and low flows occurred throughout the 37 year period showing no general decline or increase in flow conditions.

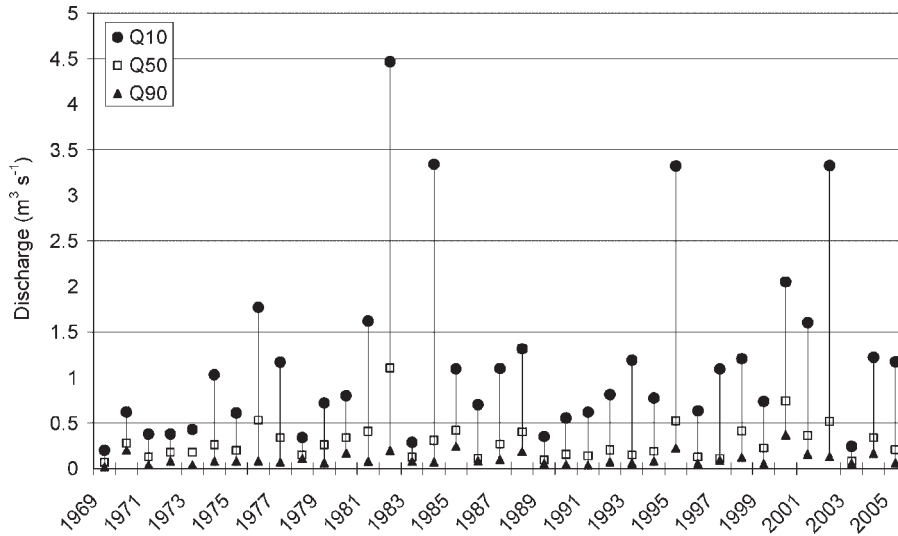


Figure 4. Variations in selected discharge percentiles (Q₁₀, Q₅₀, Q₉₀) for the period of pre-spawning immigration (September–November) for the 37 years of data record

The six flow regime types for the whole pre-spawning period—produced by the PCA and Cluster Analysis—separated principally with respect to Axis 1, an axis which reflected flow magnitude and frequency statistics (Figure 5). There was more overlap on Axis 2, with regime Type 5 the most distinct (higher coefficient of variation, skewness, maximum discharge).

In descriptive terms, the regime types can be characterized as:

- Type 1: years with and flows with little variability;
- Type 2: years with low flows and moderate variability;

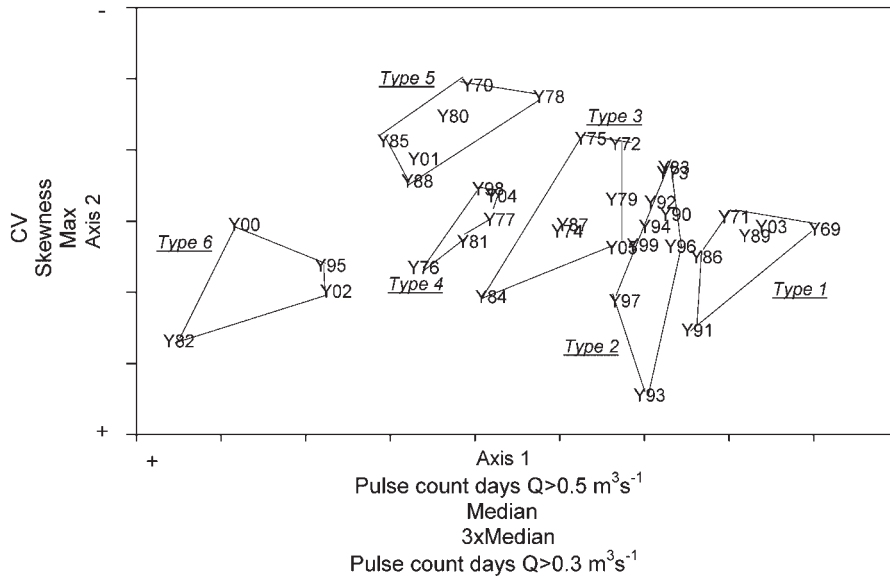


Figure 5. Principal Components Analysis (PCA) of pre-spawning immigration period hydrological regimes for each of the study years (e.g. Y82 = 1982). The regime for each year was characterized using a total of 21 indices (Table I), with index values then used to produce the PCA. Regime types (as identified using Cluster Analysis) are shown as polygons. Axis 1 explains 58% and Axis 2 a further 16% of variance in the data. The indices with the highest component loadings are shown adjacent to respective axes

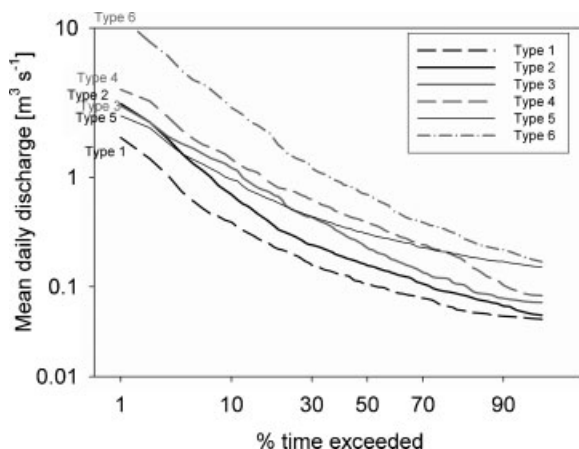


Figure 6. Flow duration curves for the six defined regime types of the whole pre-spawning period. Curves were calculated using values averaged across each of the years forming respective groups; for example the 90% exceedence value for Type 6 is the average 90 percentile flow for the years 1982, 1995, 2000 and 2002

- Type 3: years with moderate flow and moderate variability;
- Type 4: years with high flows and moderate variability;
- Type 5: years with moderate flows and low variability;
- Type 6: years with high flows and high variability.

Overall differences in pre-spawning hydrological conditions between the regime types are also evident from the respective average flow duration curves (Figure 6). Regime types 2, 3, 4 and 5 fall within the envelope created by

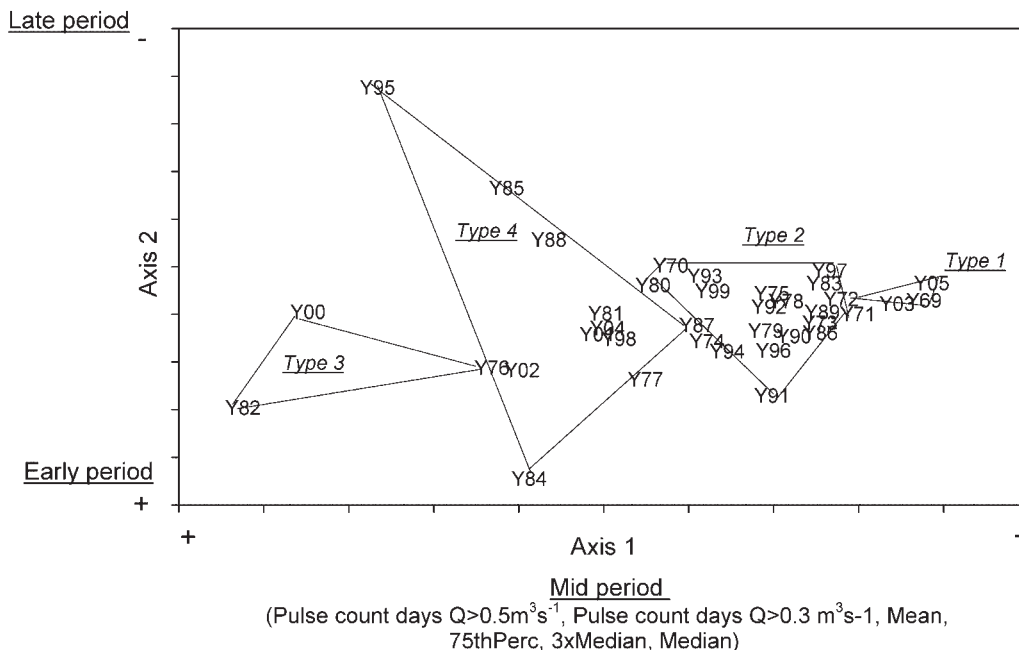


Figure 7. Principal Components Analysis (PCA) of annual pre-spawning immigration period hydrological regimes. Unlike Figure 5, each year was characterized using index values calculated separately for each of the three sub-periods. Regime types (as identified using Cluster Analysis) are shown as polygons. Axis 1 explains 40% and Axis 2 a further 19% of variance in the data

Types 1 and 6. The more variable regimes (e.g. Type 6) have relatively steep curves while the less variable ones (e.g. Type 5) have flatter curves.

The three sub-periods separated the years into four distinct clusters (Figure 7). The principal separation of clusters (Axis 1) was with respect to index values for the mid-period. Thus, the analysis suggests that the flow

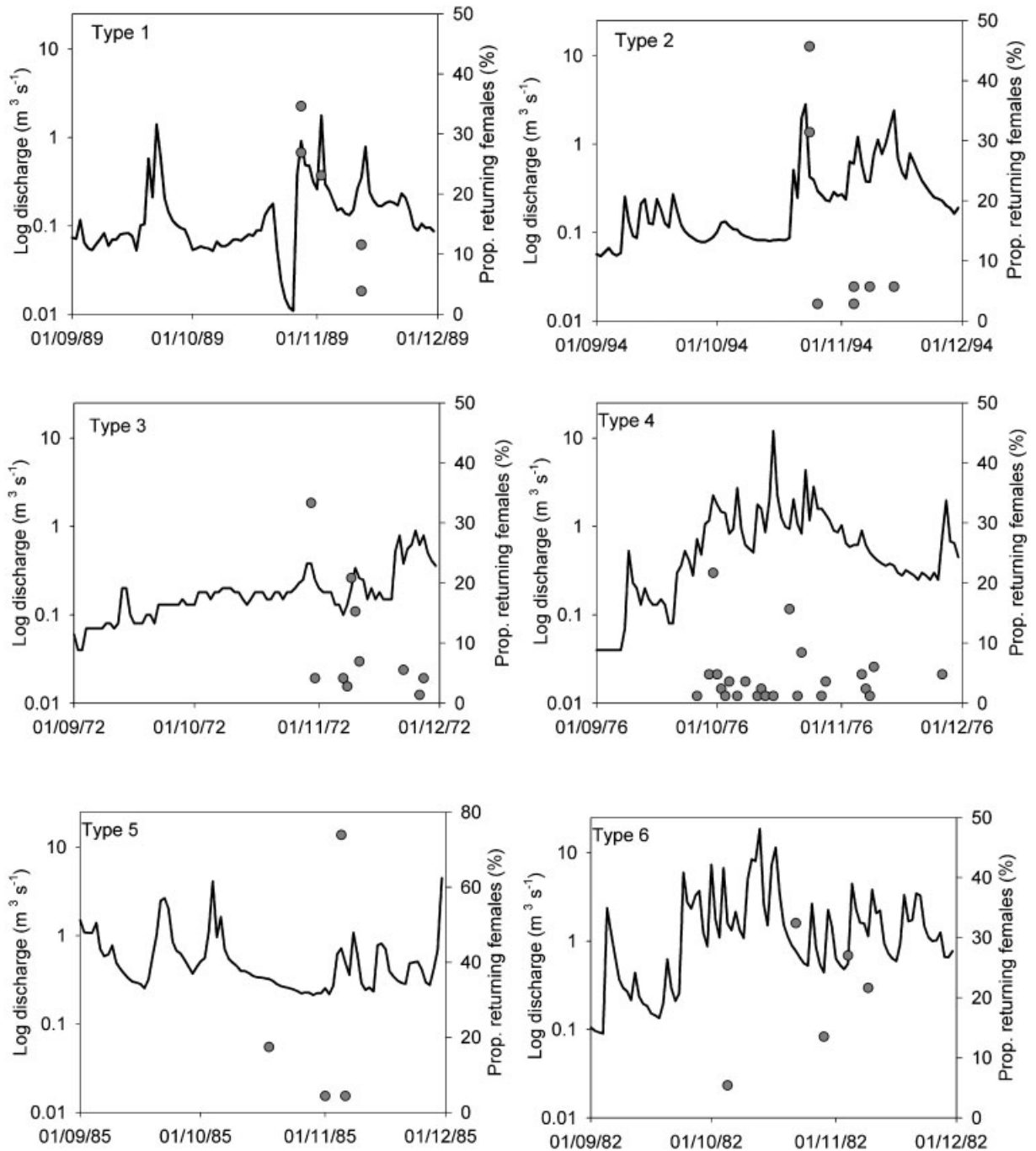


Figure 8. Example hydrographs (mean daily flows) for individual years from the six defined regimes types along with proportion and dates of returning fish. To standardize for the purpose of comparison between years, on each day the number of females is shown as a proportion of the eventual total for that year

differences between years are driven largely by differences in patterns of discharge in the mid-period, when the initial 50% of females usually arrive. There was no separation of clusters with respect to Axis 2.

Female arrival patterns in relation to discharge regimes

Since 1969 the annual number of adult female salmon entering the Girnock Burn has ranged from 9 (1997 and 1998) to 119 (1973) fish, with an average of 46 (Table I). The overall cumulative arrival curve (Figure 2b) masks considerable inter-annual variability in the precise timing and number of returning fish, as well as an overall decline in numbers. Therefore, for each year the hydrographs were grouped according to regime types and plotted against daily returning females.

Figure 8 shows patterns of entry for example years from each of the regime types which typify some of the differences in temporal distribution of female salmon entry. In most years, the timing of entry to the stream appears to be triggered by hydrological events. Entry was earlier and much more evenly distributed during years with regular flow pulses. This is evident in the patterns in 1982 and 1976, examples of regime Types 6 and 4, respectively. In years where flows were low, with low or moderate variability, a large proportion of fish entered the burn on rare, relatively small increments in discharge. The patterns of return in 1989 and 1994, which correspond to flow regime Types 1 and 2 respectively illustrate this. These years were characterized by low frequency of flow pulses and by sustained periods of low discharges in the months prior to spawning.

Between these two extremes, various patterns of entry can be seen. For example, in 1972 (Type 3) a number of medium sized spates occurred relatively late during the period and fish arrival was delayed to coincide to these events. In contrast, the large early spates which occurred in 1985 (Type 5) or 1982 (Type 6), did not appear to bring fish into the burn. This may reflect larger events discouraging or preventing upstream migration. In regime Type 3, as exemplified by 1972, most fish arrived on a spate which occurred at the end of October (35% of fish), with the remaining spawning population arriving on a number of events later in the period. As summarized in Figure 9, overall patterns of inter-annual variability of female entry distributions correspond to regime types, a pattern not evident from Figure 2b. Arrival in regime Types 4 and 6 starts in the early period, with approximately 60% of the spawners arriving by 28th October (the start of the late period). In contrast, less than 12% of spawners have arrived by this date in years with regime Type 1. Thus, hydrological conditions during the spawning 'window' appear to have a critical influence on the timing of fish entry into the stream which, in dry years, may be delayed by several weeks. It is clear that arrival timings differ appreciably between flow regime Types 1 and 4.

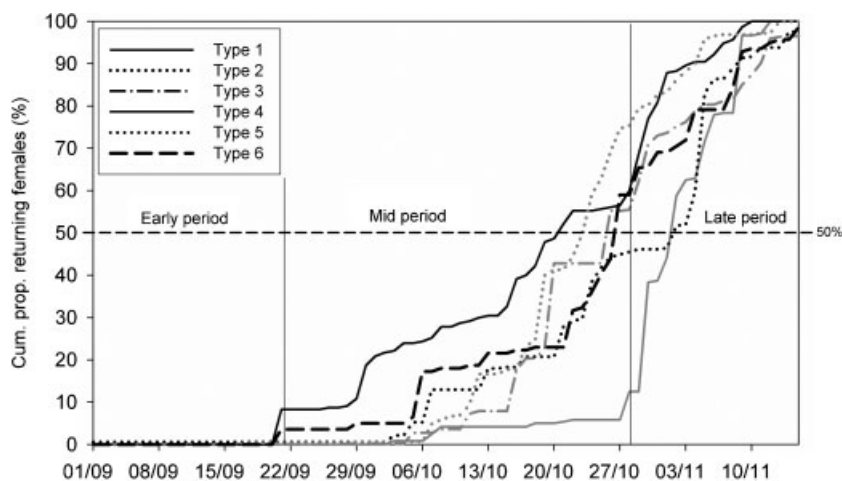


Figure 9. Average cumulative proportions of adult female fish arriving in the Girnock for each flow regime type. Curves were calculated using overall values from each of the years forming respective groups; for example 50% of all the fish arriving in the years falling into the Type 4 regime arrived before 21 October.

DISCUSSION

We sought to characterize the hydrologic regime of the pre-spawning migration period in an upland stream and assess the degree to which distinct regimes could be identified as a means of understanding inter-annual variability. We then assessed whether differences in entry patterns between years (timing and number of fish) corresponded to regime types. Such statistically based classifications of regime types are inevitably an imperfect representation of points along a continuum of natural variability. Nonetheless, the results of our analysis are clear and they represent a step towards a more quantitative understanding of how hydrological regimes contribute to the physical template of rivers and how, in turn, these influence spawning populations (Tetzlaff *et al.*, 2007b). The relationships between hydrological regime and the selection of life history traits, the response to flow events and patterns of migration will vary from river to river (Beechie *et al.*, 2006) and thus, the results are likely to be specific to the Gironck. However, the approach itself has potential in application to other rivers to evaluate the relationship between the variability of flow regimes and timing of spawner entry. Not only is such information needed to understand and predict how aquatic ecosystems function *per se*, but it has obvious practical implications in developing ecologically acceptable flow regimes in regulated systems.

Atlantic salmon are an important resource in NW Europe and NE North America and many aspects of flow management in regulated rivers are tailored to provide suitable habitat conditions for this species. There is also a long history of interest in the role of river flows in triggering the upstream movement of fish towards their spawning areas. Fishery managers generally consider that high discharge provides the stimulus which encourages upstream movement and in many regulated rivers freshet regimes have been designed with this purpose in mind (Gustard *et al.*, 1987; Jackson *et al.*, 2004). However, studies assessing the role of discharge as a trigger for upstream migration have yielded equivocal results. Fish have been observed to run on both high and low, stable and variable, rising and falling discharges (Gibbins *et al.*, in press). A number of studies have reported upstream movement being triggered by decreases in discharge (e.g. Stewart, 1969; Laughton, 1991). Huntsman (1948) found that fish began their ascent on the rising limb of a freshet but the principal ascent came on the descending limb. Trépanier *et al.* (1996) found that changes in discharge were important and that the number of migrants was generally higher in periods of decreasing discharge. Fish ascending the Tana River (Norway) were found to travel more quickly at high discharges than low discharges (Erkinaro *et al.*, 1999). This finding is counter-intuitive: higher discharges usually result in higher velocities, which might be expected to impede movement, or at least increase energy used for migration and so reduce that available subsequently for spawning. However, in another study in Tana river, Karppinen *et al.* (2004) found no significant correlation between discharge and migration. Thus, rather than assuming a consistent relation between discharge and upstream movement, there is a need to assess flow influences on a river-by-river basis. In the Gironck, it appears that flow increases are needed to trigger spawner entry, but the timing of these in relation to the hydrological characteristics of a given year may have a critical influence on the relationship between flow and female entry.

The data set for the Gironck Burn has provided a rare opportunity to assess patterns of arrival with respect to discharge over a long time period. The indices used to characterize the Gironck burn's hydrology show that distinct regime types occur for the pre-spawning immigration period, the period when female fish enter the stream. Our data indicated that the arrival pattern of adult female fish varies between years and—in general—corresponds to these regime types. However, over the 37-year data period, there was no significant relation between the number of fish entering the stream on a given day and discharge on that day ($R^2 = 0.02$). Thus, our analysis indicates that the hydrological template is important, but that it is necessary to recognize that this has a temporal dimension. Specifically, the pattern of entry into the Gironck on a given day depends on the patterns of discharge over the preceding period of days, weeks and months. For example, in dry years fish enter the burn on the back of late spates much lower in magnitude than those which act as stimuli in wet years. This suggests that, as might be expected, migratory drive increases in the final stages of sexual development in a way that results in the use of relatively low flows that would not be used in other years or earlier in the season. However, it remains unclear whether all the potential entrants to the fish trap are captured in years when Type 1 (low flow) conditions prevail as spawning may occur in the 0.5 km section between the confluence with the Dee and the fish trap because upstream movement is impeded. It also remains unclear precisely what cues fish are responding to when they enter and move up the stream.

Changes in water velocity, depth, as well as temperature and chemistry may all play a role, and most likely interact, and of course all are influenced by discharge.

Numerous studies have suggested that fish move upstream as long as a critical minimum discharge is exceeded (e.g. Welton *et al.*, 1999). Based on the data period 1994–2004, Tetzlaff *et al.* (2005b) concluded that discharges less than $0.3 \text{ m}^3 \text{ s}^{-1}$ inhibited access to the burn. The current analysis for a longer period showed minimum mean daily discharges for entry for each year ranging between 0.10 (1972) and $1.62 (1987) \text{ m}^3 \text{ s}^{-1}$. In regime Types 4 and 6 high flows may actually impede fish entry. However, the highest discharges fish have been observed to enter the burn on are $12 \text{ m}^3 \text{ s}^{-1}$ in (1976) and $5.7 \text{ m}^3 \text{ s}^{-1}$ (2000) in years with Type 4 and Type 6, respectively. Data for the Girnock suggest that the minimum discharge should not be viewed as static, particularly given that channel geometry may change and affect depths and velocities produced by a given discharge.

The two most extreme low flow regime types (Types 1 and 2) represent years with sustained low flows and low to moderate variability, respectively. As shown in Figure 9 this results in late entry of the main spawning population. In the first 19 years of record, only five years had hydrological regimes of these two types, whilst in the last 18 years, 10 years were characterized by these regimes. As this coincided with lower absolute numbers of returning salmon, the delay in spawning entry and the tendency of salmon to cluster in the lower parts of the river system, it may represent a sub-optimal uptake of juvenile habitat throughout the river network. This may have longer term implications for population viability. In addition, three of the last 18 years have been of Type 6 with high flows and high variability, contrasting with only one in the first 19 years. Thus, there are two patterns of arrival, linked to two extremes of flow, and which can be considered as sub-optimal, which have been more frequent in recent years.

Over the entire period of record, the final number of fish entering the burn in a given year is largely independent of discharge regime, but trends are masked due to declining number of salmon returns, which largely relates to poorer sea-survival in the past two decades. However, hydraulic conditions at particular discharges may play an important role in determining the fitness, fecundity and survival of spawners. Until such information is available—which is a major research task—conclusions as to the population impacts of flow variability will remain tentative.

There are a number of general points that can be drawn from the results presented in this paper. Natural river flow regimes, which provide part of the physical template for aquatic habitats, are vulnerable to change. In this context, our analyses suggest that arrival patterns may change if flow regimes in the Girnock are affected by future climate or landuse change. Gibbins *et al.* (2002) have already shown that afforestation in the Girnock will affect runoff and in turn, influence the availability of suitable conditions for spawning fish. In the Girnock, the vast majority of fish arrive in the narrow period of mid October to mid November on spates ranging in size between 2 and $4 \text{ m}^3 \text{ s}^{-1}$. Over the whole data record, it is notable that only 30% of fish have been observed to enter the Girnock on flows lower than the long term median discharge. Thus, while avoiding extremely low flows in the September to early October period would be desirable, maintaining higher flows in the mid-period seems to be particularly critical. As shown by the PCA of the sub-periods (Figure 7), this middle period is itself key to driving inter-annual differences in migration season hydrological regimes. Data also suggest large spates (or freshet releases in the case of regulated rivers) may not be essential; rather, in the mid-period, frequent medium sized spates may be more useful.

Overarching the impacts of flow regulation on discharge regimes are the likely consequences of long term climate change. If predicted changes in patterns of rainfall result in changes to river flow regimes, then there may be concomitant changes in patterns of spawner returns. Although extreme caution needs to be exercised when inferring the current downscaling predictions of climate change from Global Circulation Models (GCMs) to individual rivers, the most likely scenarios for the Girnock imply warmer, drier summers followed by higher and more intense rainfall in autumn and winter (Werrity, 2002). The increased occurrence of more extreme flow regime Types 1 and 2, and 5 and 6 in the second half of the data record might be consistent with such predicted trends. Although the ecological consequences of this are uncertain, it may be reasonable to anticipate a two-fold effect on flow regimes during the pre-spawning entry period in response to climatic change. It may be that the warmer, drier summers result in greater prevalence of low flow conditions, particularly early in the entry period, producing more Type 1 and 2 regime types. Conversely, moderate and higher flows later in the pre-spawning entry period may become more frequent after the catchment wets up and responds to the predicted higher and more intense autumn rainfall totals. Continuing long term monitoring of discharge and returning fish in the Girnock will provide the information necessary to understand how such changes affect salmon migration patterns.

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