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Primary Research Paper

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

D . Tetzlaff[1,*], C Soulsby[1], C. Gibbins[1], P.J. Bacon[2] & A.F Youngson[2]
[1]*Department of Geography and Environment, University of Aberdeen, AB24 3UF, Aberdeen, Scotland, UK*
[2]*FRS Freshwater Laboratory, Faskally, Pitlochry, PH16 5LB, Perthshire, Scotland, UK*
*(*Author for correspondence: E-mail: d.tetzlaff@abdn.ac.uk)*

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Abstract

This case study sought to examine how temporal variability in hydrological and hydraulic conditions might affect the feeding opportunities of juvenile Atlantic salmon in two hydrologically contrasting years of 2002 and 2003, which were characterised by high and low flows respectively. Firstly, measures of hydraulic influence were calculated to define what might be ecologically meaningful disturbance periods during high flows. Secondly, for identifying such periods, the parameter Critical Displacement Velocity (CDV) was derived from a river discharge time series as a first approximation of the amount of time in two hydrologically extreme years when fish foraging strategies for specific age classes of juvenile Atlantic salmon (*Salmo salar*) might be disrupted by flows. The CDV estimates the threshold velocity above which juvenile salmon are unable to hold station and it is dependent upon fish size and stream temperature. In the wet year 2002, the CDV was exceeded on 18% and 21% of days for 0+ and 1+ fish respectively. In 2003 these respective numbers fell to 6% and 15%. The data suggest that hydrological conditions during certain times of the year have the potential to affect foraging behaviour. This in turn might have implications for recruitment and growth rates for juvenile salmon in upland streams.

Introduction

The important role that in-stream hydrology plays in sustaining freshwater ecosystems is widely acknowledged (Poff et al., 1997; Bunn & Arthington, 2002; Olden & Poff, 2003). Although biotic factors, such as density dependent competition and predation, exert strong influences on the growth of individual fish and the dynamics of fish populations in general, complex physical controls such as water temperature can also be important (Conell, 1978; Arndt et al., 2002). Because of its influence on in-stream hydraulic conditions, discharge is also recognised as a key axis on the physical habitat template (e.g. Petts, 1980, 2000; Poff et al., 1997).

In recent years, many hydro-ecological assessment studies have attempted to identify ecologically meaningful hydrological parameters from readily available discharge data sets from gauging stations, with a view to restore natural patterns of discharge variability in managed rivers (e.g. Richter et al., 1996, 1998; Clausen & Biggs, 2000; Olden & Poff, 2003). Usually these parameters characterise the extremes and variability of flows – particularly floods and droughts – which may ‘disturb’ aquatic ecosystems. In those studies, it is assumed that such hydrological data are a meaningful proxy for in-stream hydraulic conditions which might affect individual organisms, populations and communities. However, there remains a general paucity of studies that have explicitly linked patterns of discharge variability to ecological conditions or processes. Such links are needed, to improve our understanding both of the factors that influence stream ecosystems and of the likely success of flow re-naturalisation programmes.

Upland rivers provide important spawning and rearing habitats for Atlantic salmon (*Salmo salar*). Such rivers are usually characterised by marked seasonal and inter-annual variability in discharge and channel hydraulics (Soulsby et al., 2001). In the Girnock Burn, an upland tributary of the River Dee in Scotland, physiological and empirical models have suggested that much (ca. 85%) of the variability in the growth of juvenile Atlantic salmon in different age classes can be accounted for by variability in water temperatures (Bacon et al., 2005). However, a significant amount of the variability in growth, and therefore the productivity of the stream's fishery, remains unexplained by current models. Some of the unexplained variation in growth rates may be related to natural variability in food supply e.g., timing of invertebrate cycle stages that may affect their availability for fish at key periods. However, some may also be related to temporal differences in discharge regimes which affect the availability of suitable hydraulic habitats for fish. Hydraulic conditions may affect fish growth when velocities are so high that fish are either unable to feed or when their prey capture success is reduced. Understanding how and when patterns of discharge variability may influence feeding opportunities is an important prerequisite to help understand inter-annual variability in fish growth and to contribute to more comprehensive models of the role of environmental controls.

One way of trying to develop an ecologically meaningful assessment from hydrological data is to use commonly available discharge data sets from routine monitoring to derive more sensitive hydraulic parameters that are more likely to be direct controls on ecosystem components. For example, a useful approach may be to derive velocity time series from discharge time series, and to assess the ecological implication of velocity dynamics. The approach builds on flume investigations with juvenile salmonids which have identified velocities above which fish feeding activity may be impeded (Graham et al., 1996).

The present study provides a preliminary example of how empirical data on stream temperature and discharge can be integrated via predictions of Critical Displacement Velocity (CDV) for juvenile fish to provide an insight into how differences in annual flow regimes might influence feeding opportunities. We present a case study of the two hydrologically contrasting years, 2002 and 2003, which were typified, respectively, by high and low flow compared to average years. For these years we assess the duration of time that discharge resulted in mean channel velocities that exceeded estimated CDVs for 0+ and 1+ fish.

Study area and conditions

The Girnock Burn (Fig. 1) drains 30.3 km^2 of the River Dee catchment in north-east Scotland. The stream has been used as a monitoring site for salmonid population dynamics and production by the Scottish Executive's Freshwater Laboratory since 1966.

The altitude of the catchment ranges from 230 m to 862 m (Gibbins et al., 2002a) and the channel has a mean slope of 28.9 m km^{-1} (Moir et al., 1998). 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 (Moir et al., 1998). Various glacial and fluvio-glacial deposits cover the solid geology (Gibbins et al., 2002a). Landuse is dominated by heather (*Calluna vulgaris*) moorland used for deer stalking and grouse shooting with smaller areas of abandoned rough grazing.

Since 1966 the mean annual number of adult salmon entering the Girnock Burn for spawning has been 125; with ranges between 20 (2000) and 293 (1987) (Moir et al., 1998). In comparison, smolt production is relatively constant: over the same period smolt numbers leaving the burn range between approximately 1400 and 4000. Spawning occurs in November and the ova typically hatch in April. 0+ fry reach about 50 mm by the end of their 0+ summer and approximately 100 mm by the end of their 1+ year (Bacon et al., 2005).

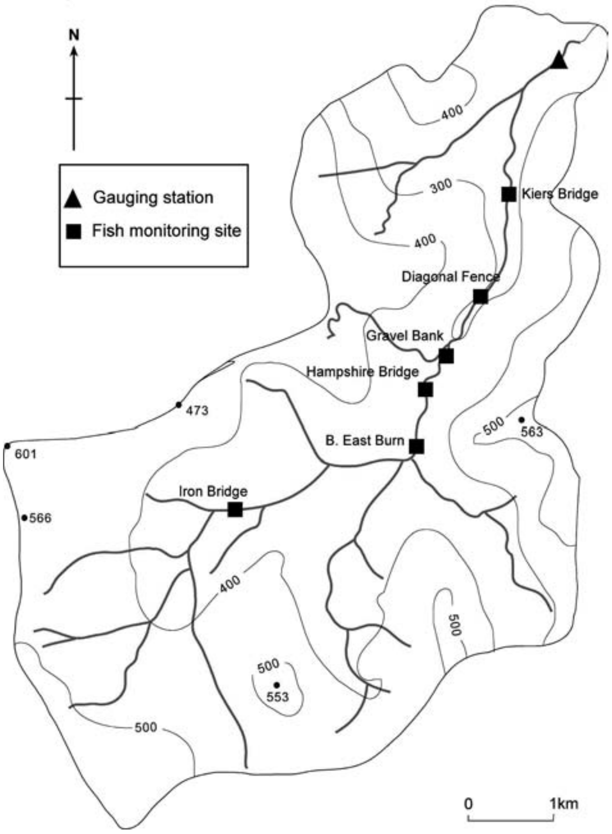

Figure 1. The Girnock Burn and monitoring sites.

Smolts leaving the burn are 1+, 2+ or 3+ years old, with 2+ being the modal age class. Prior to smolting the fish feed on invertebrates in the stream. The main growth period occurs between April and June. Salmon fry emerge from river gravel approximately mid-way through the period of peak achieved growth.

In recent years a number of studies have been conducted in the Girnock Burn catchment and an extensive data base for hydrological, hydraulic and geomorphological conditions and biological data is available (e.g. Gibbins et al., 2002b; Malcolm et al., 2003; Moir et al., 2004; Hannah et al., 2004). Additionally, the Girnock Burn is characterised by a high variability in flow dynamics and climate features (Moir et al., 1998; Soulsby et al., 2005). Averaged annual precipitation is 935 mm (1961–1991, Scottish Environmental Protection Agency) with the summer months (May–August) being driest. At the gauging station at Littlemill (Fig. 1), mean daily flow is 0.52 $m^3 s^{-1}$ (1969–2001) although flows between June and August rarely exceeded 0.1 $m^3 s^{-1}$ (Moir et al., 1998). However, mean daily flow varied between (0.4 $m^3 s^{-1}$ in the summer and ca. 100 $m^3 s^{-1}$ during floods (Malcolm et al., 2003). Most high flow events occurred between late autumn and early spring, including response to snowmelt in spring.

In the present study, two hydrologically extreme years were investigated. The flow duration curves of both 2002 and 2003 show clear deviations from the mean annual duration curve for previous years (1986–1994, Fig. 2), with a large number of sporadic flood events in 2002 and a prolonged uninterrupted period of low flow in 2003. The high variability of flow in 2002 is shown by the steeper flow duration curve compared to 2003. Mean discharge conditions were so markedly different (0.89 and 0.3 $m^3 s^{-1}$ respectively) that they provided an ideal basis for examining the effects of contrasting condition on productivity.

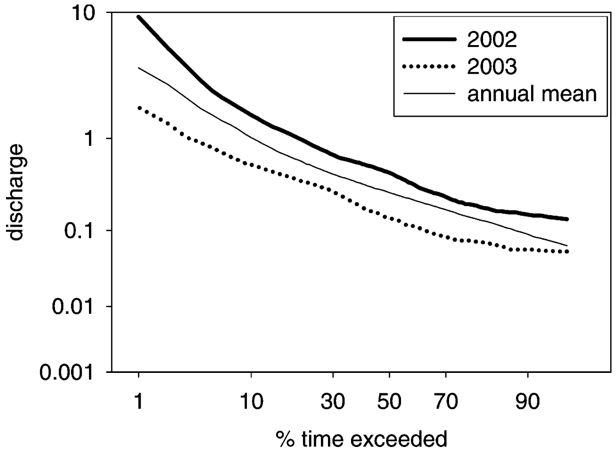

Figure 2. Flow duration curves for Littlemill: Annual mean (long-term average), 2002 and 2003.

Methods

If velocities exceed certain critical thresholds fish may be swept down downstream or feeding opportunities may be constrained (Gibbins et al., 2002a). CDV represents the maximum sustained velocity against which a fish can hold station. When stream velocity exceeds the CDV, feeding opportunities are likely to be constrained, resulting in decreased growth rates or weight losses (Arndt et al., 1996). Accordingly, the timing and duration of periods when the CDV is exceeded by channel velocities may provide useful insights into when foraging strategies are disrupted by flow conditions. Such information might aid subsequent modelling studies that seek to predict fish growth in response to environmental drivers. CDV is dependent on fish size and stream temperature and can be calculated using relationships derived from flume experiments (Graham et al., 1996). Clearly, such flume studies are likely to provide only a first approximation of the relationships in a complex river channel. However, they offer an empirical starting point for hydraulic assessment. The following sections detail the derivation of the stream velocity, fish size and temperature time series for the 2 years investigated and calculation of the CDV for the Girnock Burn.

In order to derive hydraulically meaningful data from the discharge data set, a velocity time series was constructed. For this, 89 separate gaugings (1997–2004) at Littlemill were used over a range of discharges. Average velocities were calculated across the gauged section based on up to 26 individual velocity measurements made at 0.6 × of the depth (i.e., at mean column velocity position). From these, 89 data points were used to derive a discharge–mean velocity relationship for the gauged section. A power function best described the relationship ($r^2 = 0.99$) (Fig. 3) and it was used to derive a mean velocity time series for both years. For safety reasons, high discharges were not gauged so the velocity time series are based on extrapolation for extremely high velocities. However, as calculated CDVs were relatively low (see later) and within the range of recorded velocities, the calculated duration of time that velocities exceeded the CDV was not affected by the lack of high flow data. Stream velocity conditions at the gauged site were regarded as more generally indicative of temporal variation in conditions throughout the catchment. It was recognised that different channel characteristics would give spatially variable velocity conditions throughout the river network (Moir et al., 2002). Moreover, it was recognised that such averaged velocity conditions would not be the same as those experienced at the microscale by fish in more local habitat units. Nevertheless, for the purpose of a preliminary analysis of potential influences on foraging, temporal variation was deemed most important and the data were considered adequate for this purpose. Figure 4 shows the median, range and percentiles of velocities at the gauged section for selected discharges, including those for the mean (Q50), high (Q10) and low (Q95) discharges.

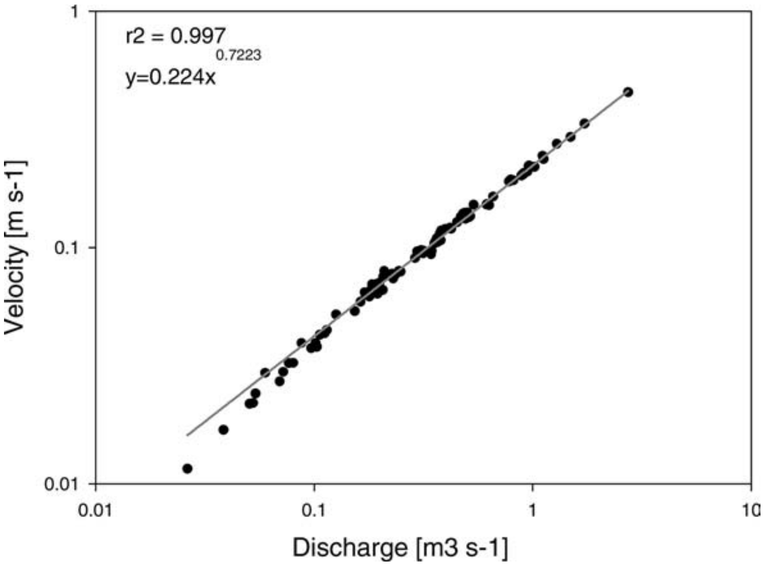

Figure 3. Discharge–velocity relationship (time period 1997–2004).

An equivalent time series for Froude number was constructed, using the derived velocity time series. Froude number is a useful initial habitat descriptor because it integrates velocity and depth as ratio of inertial to gravitational forces and describes the state of the flow relative to the critical velocity (Eq. 1). A Froude number of 1 is described as critical flow dividing a tranquil flow (Fr < 1, subcritical) from rapid flow (>1, supercritical) (Hornberger et al., 1998).

$$\mathrm{Fr} = u^2/(g * h) \qquad (1)$$

with Fr = Froude number [–], u = mean velocity (m s^{-1}), h = depth or stage (m) and gravitational acceleration g = 9.81 m s^{-2}.

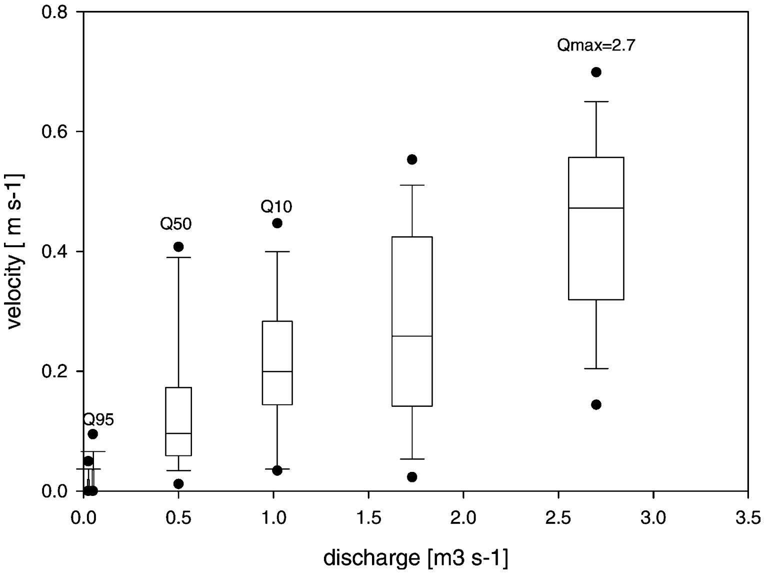

Figure 4. Velocity distribution for different discharges with median, 5th/95th percentiles (outlying points), 10th/90th percentiles (whiskers) and 25th/75th percentiles (box boundaries).

Water temperature data were available at an hourly resolution for the 2 years investigated (Malcolm et al., 2004a and b). Fish length values were available for six monitored sites within the stream (Fig. 1), based on approximately 1 month interval electrofishing surveys. The averaged fish lengths for the same aged individuals (as 0+, 1+ and 2+ salmon) for each monitoring site are shown in Fig. 5. In total, fish length data were available for 504 individual 0+ salmon and 1008 individual 1+ salmon in 2002. In 2003, data were more restricted with 183 individual 0+ salmon and 167 individual 1+ salmon (not shown). There were no significant differences in lengths at different monitoring sites throughout the catchment (Fig. 5). Given this similarity, spatially averaged fish length data for all sites were used to characterise fish sizes in the stream and these data were used to calculate CDVs.

Lines were fitted using linear trend series filling to allow estimation of daily length increments (Fig. 6). No 1+ salmon data were available after April 2003. However, because available fish lengths for February and March were comparable for 2002 and 2003, fish length distributions for 2002 were used for 1+ fish in 2003, beginning from March (Fig. 6). Fry emerge in mid-May in the Girnock Burn and it can be assumed that before this date no 0+ fish occur in the open water column. Subsequently, for both, 0+ and 1+ salmon, a relatively short period of maximum growth is observed. For 0+ salmon the time of growing is mainly in June–July, while for 1+ it is March–April.

Stream temperature and length data were input to the regression equation of Graham et al. (1996) to calculate CDV, where

$$\mathrm{CDV_{BL}} = 4.14 \log T + 1.74 \tag{2}$$

and where $\mathrm{CDV_{BL}}$ is expressed in body lengths per second and T = water temperature (°C).

This was then converted to CDV in unit m s^{-1} using the equation:

$$\mathrm{CDV} = \mathrm{CDV_{BL}} * L/100 \tag{3}$$

where L is fish body lengths (cm).

CDV's [m s^{-1}] were calculated at daily resolution, using date-specific mean fish length and stream temperature data (Fig. 8). To take into account the variability of individual fish lengths on any one date, additional upper and lower limits on CDV values were also estimated for each date. These used mean fish length values plus one standard deviation (i.e., larger fish) and minus one standard deviation (smaller fish) as input sizes for the CDV equation.

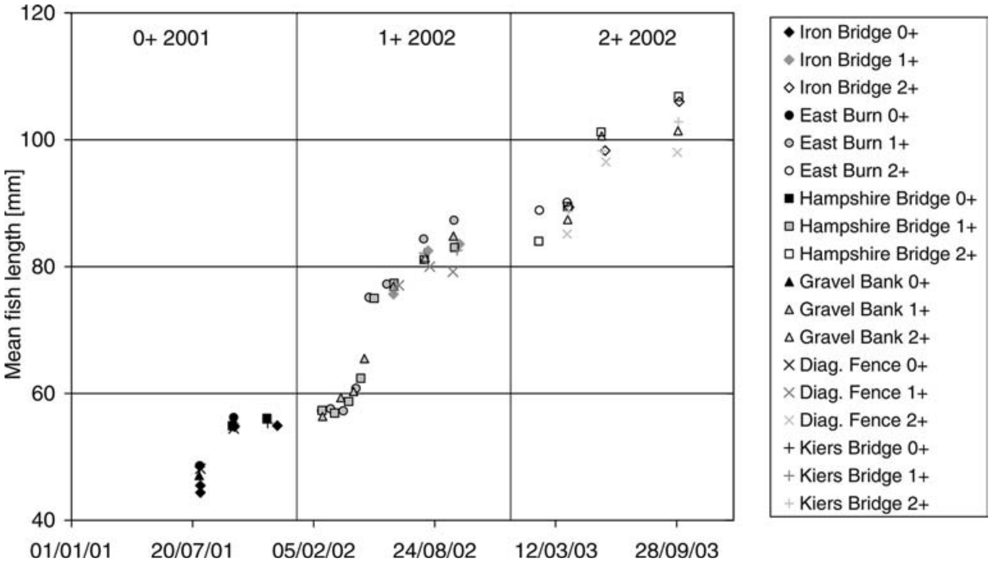

Figure 5. Fish length distribution for 0+, 1+ and 2+ ages (same individuals) at different monitoring sites.

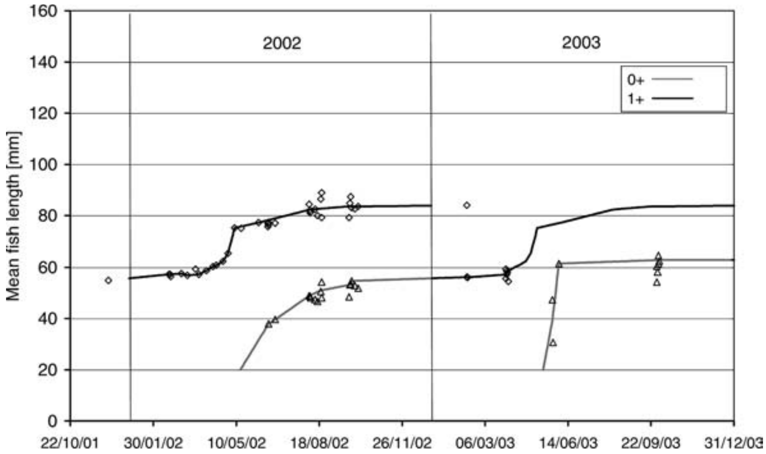

Figure 6. Calculated daily fish lengths for 0+ and 1+ fish for 2002 and 2003.

Results

Stream hydraulics and temperatures

The differences in the discharge time series for the two study years are readily apparent from Fig. 7. For 2002 the long-term daily mean flow (0.52 m^3 s^{-1}) was exceeded on 160 days. A particularly notable feature was the very wet summer and autumn of this year. In contrast, 2003 was characterised by very few high flow events and a long period of low flow between May and November, when the hydrograph shows virtually no response to precipitation. In total, 325 days had flows below the long-term daily mean flow in 2003. The velocity time series for the gauged site for both years are shown in Figure 8. Mean velocities regularly (13 events) exceeded 1 m s^{-1} in 2002, but exceeded this value only once in 2003.

The hydraulic parameters velocity, water depth and Froude number show clear differences between the 2 years (Table 1). The most notable differences concern the maximum values of each parameter in respective years. Maximum velocity in 2002 was +180% higher than 2003, while maximum water depth was 50% higher, although extrapolation of velocities beyond gauged flows needs to be treated cautiously. Coefficients of variation show that velocity was more variable in 2002. Froude number showed greatest variability with +530% in 2002 compared to 2003. The Froude number time series for both years (Fig. 7 a and b) show that only during one event (on 31/07/02) for a period of about 1 h a critical flow (Froude number = 1) was exceeded. Values of Froude number were more variable in 2002 (CV = 3.33) than 2003 (CV = 2.26).

Differences in daily mean stream water temperature (based on hourly values) were less extreme, with mean temperatures of 7.5 °C (2002) and 7.3 °C (2003), maximum temperatures of 19.9 °C and 19.8 °C respectively and minimum temperatures for both years indicating supercooling at −0.6 °C (Table 1, Fig. 9). In 2002, maximum mean monthly stream temperature was in August (14.3 °C); minimum in January (1.6 °C). In 2003, the maximum mean monthly stream temperature occurred in July (14.8 °C) and minimum mean monthly temperature in February (0.6 °C).

Critical displacement velocities

The CDV envelopes, together with stream velocities and precipitation, are shown in Fig. 9. CDV varied throughout the year, as a function of the interaction of changes in fish length and stream temperature. For 0+ fish in 2002, date-specific CDV ranged from 0.05 m s^{-1} (lowest point of envelope) to 0.36 m s^{-1} (highest point of envelope). In 2003, this min–max range extended from 0.05 and 0.45 m s^{-1}. For 1+ fish, CDV ranged between 0.05 and 0.60 (2002) and 0.05 and 0.61 m s^{-1} (2003). Clear seasonal patterns to CDV are apparent, with values higher during the summer in both age groups; thus, fish are less likely to

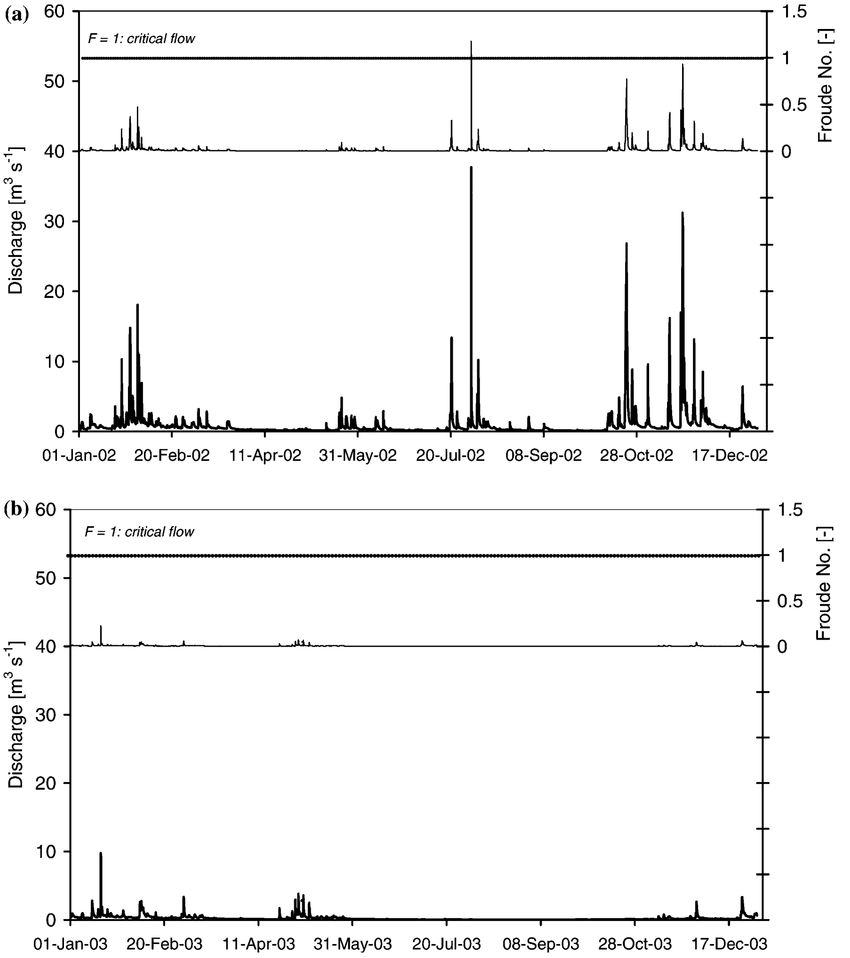

Figure 7. Discharge [m^3 s^{-1}] and Froude number [–] time series for the both investigated years, (a) 2002 and (b) 2003.

have their feeding opportunities constrained by high flows during this period. CDV was more stable (less day-to-day variability) during the summer than the winter.

There were clear differences in the duration of time that mean velocities exceeded the CDV in the two years (Table 2). In 2002, mean stream velocity exceeded the CDV for 0+ fish on 43 days and for 1+ fish on 77 days. These values equate to 18% of the year for 0+ fish and 21% for 1+ fish. The reason for lower percentage for 0+ salmon is that no CDV values were calculated before mid-May, as no 0+ fish occur in the open water column before this time. Apart from September, CDV were exceeded on at least one day each month for both 0+ and 1+ fish. Even though CDVs are higher during the summer (warmer stream temperatures), the extreme high flows during the summer of 2002 meant that CDVs were occasionally exceeded.

In 2003, periods of CDV exceedence were reduced to 14 days (6%) for 0+ and 56 days (15%) for 1+ fish. There were no CDV exceedence events during the period June–October in 2003, with periods where feeding opportunities likely to be constrained restricted primarily to January, February and December.

Discussion

Traditionally, freshwater biologists have focussed on water temperature as a primary abiotic driver in river ecosystems (Petts, 2000). Current studies

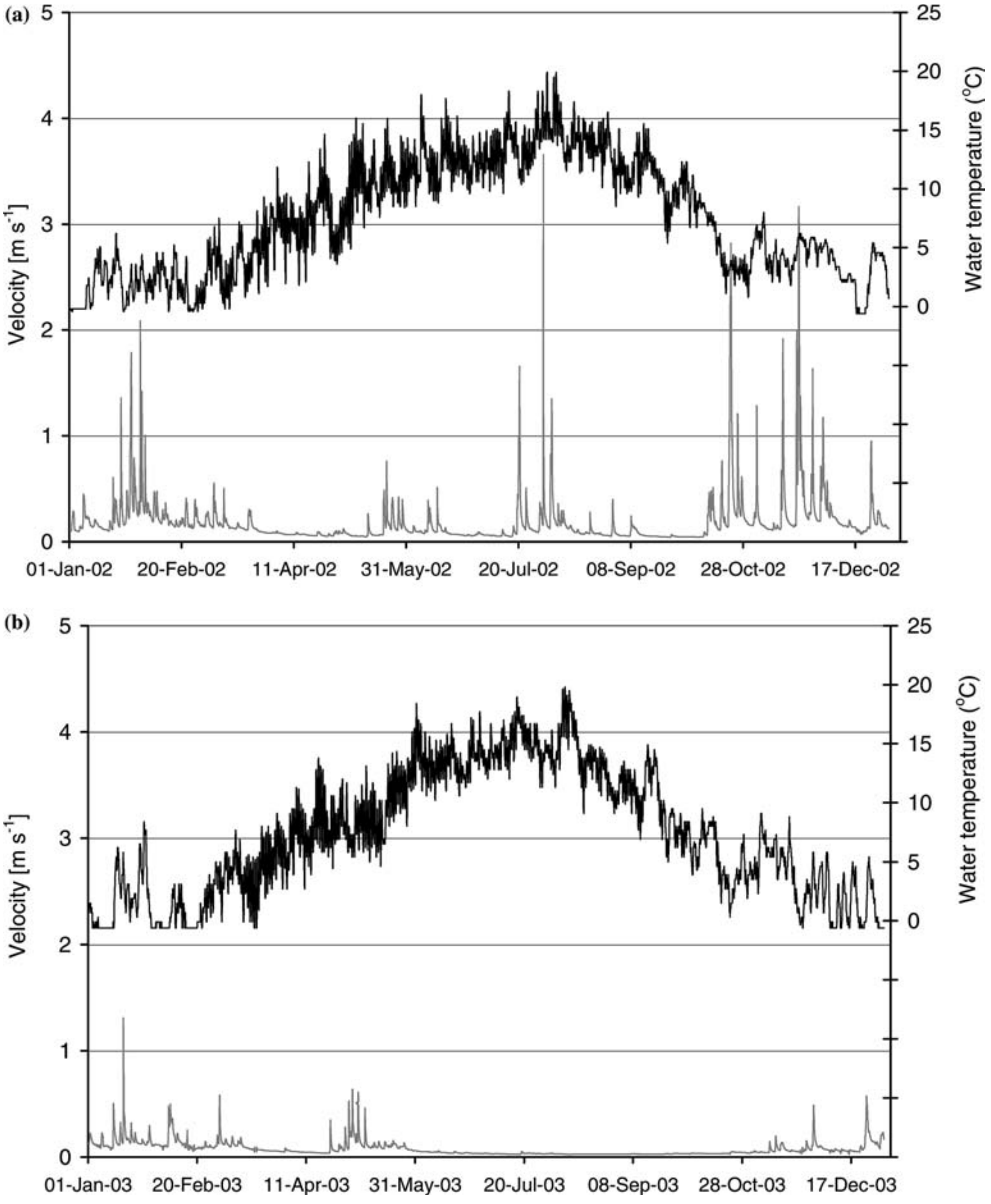

Figure 8. Water temperature and velocity, (a) 2002 and (b) 2003.

continue to show its importance; for example Bacon et al. (2005) in relation to juvenile salmonid growth at the site of the present study. However, rivers are characterised by important variations in hydrological conditions across a range of timescales (hourly, daily, seasonally, annually). While there is a general consensus that such variability is likely to be important, few studies have explicitly made the link between environmental variability and river biota. For example, Olden & Poff (2003) reviewed 171 flow variability assessment parameters, none of which had any explicit ecological context. In particular, there is a paucity of studies that have attempted to look for thresholds across the range of variability that potentially influence population parameters such as feeding opportunities or the growth of individual organisms.

Table 1. Statistical values (mean, maximum, minimum, standard deviation, coefficient of variability) for the hydraulic and biological parameters in the both investigated years

Parameter	2002	2003
Mean velocity (m s^{-1})	0.18	0.08
Max. velocity	3.66	1.31
Min. velocity	0.05	0.02
SD velocity	0.24	0.07
CV velocity	1.33	0.87
Mean water depth (m)	0.33	0.23
Max.	1.16	0.78
Min.	0.20	0.15
SD water depth	0.11	0.07
Mean Froude number [-]	0.015	3.1×10^{-3}
Max.	1.175	0.223
Min.	1.1×10^{-3}	3.9×10^{-4}
SD Froude	0.05	0.007
CV Froude	3.33	2.26
Mean water temperature (°C)	7.5	7.3
Max	19.9	19.8
Min	−0.6	−0.6
SD temperature	4.9	5.3

The seasonality in flow conditions with lower discharge in summer and higher in winter makes it difficult to define fixed hydrological thresholds that are ecologically meaningful. However, this study has shown how readily available gauging data sets can be used to provide an insight into hydraulic conditions at the catchment scale, which may have ecological importance. The value of the CDV approach is that it integrates flow and stream temperature data, two of the key physical controls on stream biota. While the approach requires further refinement and testing (as detailed below), it has allowed a preliminary insight into how inter-annual variability in hydrological conditions might influence feeding opportunities of juvenile salmonids.

Deriving hydraulic parameters from temporal high-resolution data allows subtle, short-term effects on biota to be examined. Such effects are often not captured by standard hydrological assessment approaches. In the present study, the indication of the potential ecological implications of velocity dynamics is possible by identifying

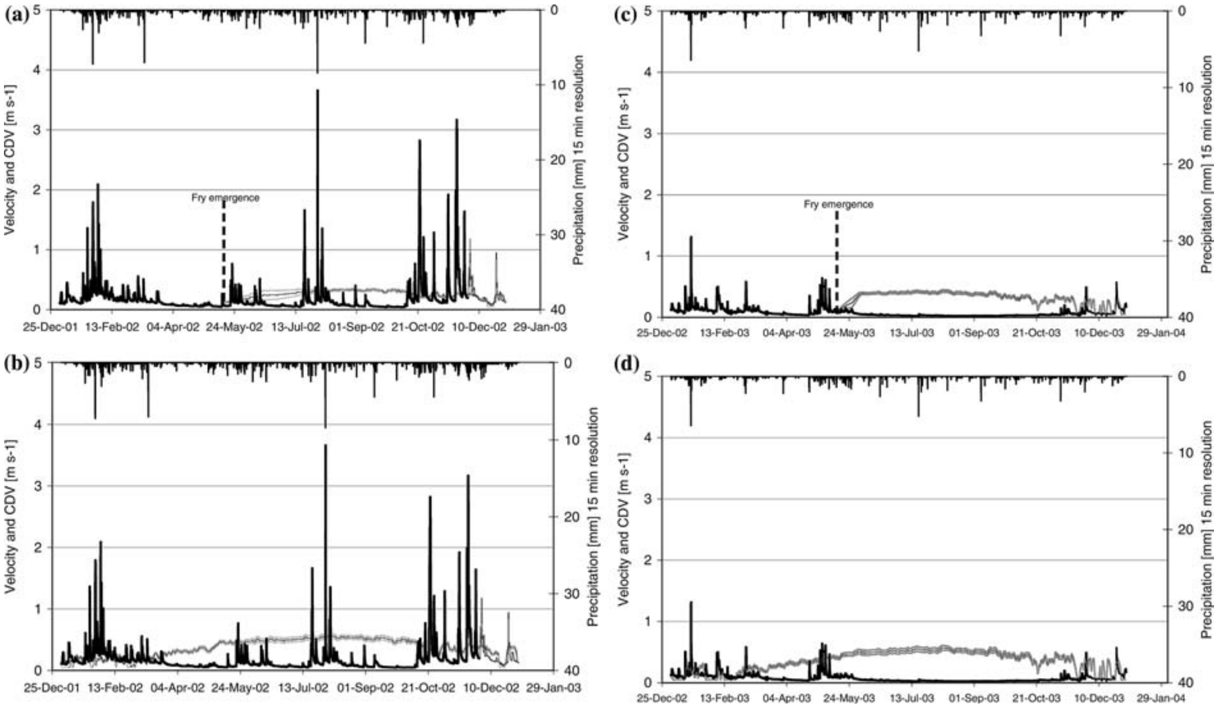

Figure 9. Mean CDV and envelope curves based on plus and minus one standard deviation for both years, (a) 2002 – 0+, (b) 2002 – 1+, (c) 2003 – 0+ and (d) 2003 – 1+.

Table 2. Monthly duration for mean stream velocity exceedence of CDV for 0+ and 1+ fish [d]

	2002		2003	
	0+	1+	0+	1+
Jan	–	21.5	–	20.6
Feb	–	23.5	–	20.3
Mar	–	8.0	–	0.6
Apr	–	0.0	–	0.2
May	4.4	0.3	0.0	0.6
Jun	0.9	0.1	0.0	0.0
Jul	2.6	1.2	0.0	0.0
Aug	1.5	0.9	0.0	0.0
Sep	0.0	0.0	0.0	0.0
Oct	10.3	5.7	0.0	0.0
Nov	9.6	7.0	1.3	1.0
Dec	13.5	8.6	12.8	12.5
Total days	240	365	240	365
Total days exceeded	42.8	76.7	14.1	55.8
% time exceeded	18%	21%	6%	15%

velocities above which fish feeding opportunities may be constrained. Most standard hydrological assessment tools (e.g. Petts, 1980; Jowett 1997) were not devised to describe flows in terms of their ability to sustain aquatic life. For the purpose of assessing habitat suitability, flow regime should be dissected into events that occur across a wide range of time scales (Gordon et al., 2004). Models such as PHABSIM, which simulate the relationship between streamflow and physical habitat for various life stages of species are complex and have well-known weaknesses (Gordon et al., 2004).

The timing and duration of periods when CDVs are exceeded potentially have important implications for fish populations. For example, in Scottish rivers salmon are adapted to emerge as 0+ fish in May when typically flows are relatively low. In the first few weeks after their emergence, 0+ fish have limited ability to swim and feed in faster flowing sections of the stream. Thus, their growth rates may be strongly affected by unusually high flows at this time. The critical nature of this period has been demonstrated in empirical studies (Jensen & Johnson, 1999). The CDV analysis highlighted differences between the two study years that may have implications for the growth of 0+ fish during this critical period. In the Girnock, fish aged 1+ grew most in the period prior to the emergence of 0+ individuals. This period presumably offers the greatest growth potential, possibly linked to seasonal patterns of food abundance (Elliot, 2002; Gibbins et al., 2002a; Gibbins et al., 2004). The emergence of the 0+ fish relative to this period may reflect the adaptive importance of avoiding a time when frequent high discharges result in sustained periods when hydraulic conditions are unfavourable (Arndt et al., 2002). The CDV analysis appears to be sensitive enough to show how, because of differences in size, hydraulic conditions might constrain 0+ fish at this time more than older (1+) individuals.

The data presented for the Littlemill site represent just one location in the Girnock, a stream which is known to have hydraulically contrasting channel types along its length (Moir et al., 2004). While the analysis presented here has been able to illustrate inter-annual variability in hydraulic conditions in relation to CDVs, further studies are needed to look for variation across the catchment that may be driven by the way in which different channel types respond differently (in terms of hydraulic changes) to changes in discharge. The use of mean cross-sectional velocity values, although useful for illustrating general utility of the CDV approach, masks differences in absolute hydraulic conditions experienced by individual fish. Opportunities for individual fish to avoid locations where CDV are exceeded by moving just a small distance to a refuge area are likely to exist at the gauge site (this is evident from data presented in Fig. 4). Thus, more advanced hydraulic characterisation, either by field measurement or modelling, is needed to allow small spatial-scale variability in velocity to be incorporated into calculation of the CDV time series. This would represent an important improvement to the approach. Finally there is a need to contextualise the two extreme years investigated in this study in terms of the longer flow record for the Girnock. In this way, it may be possible to link the long-term frequency–magnitude patterns of CDV exceedence to empirical data on productivity (e.g. growth and smolt run size) in the stream.

The approach outlined here is preliminary; further refinement, spatial validation and testing against empirical data on fish performance are now needed. Nonetheless, the study has shown how it is possible to link hydrologic variability to hydraulic (velocity) and other physical (temperature) measures that have ecological relevance. Potentially, it could be used to investigate the ecological consequences of natural variability in discharge regimes (e.g., between years or sites) or the effects of land-use change or river regulation schemes on fish. However, it is prudent to emphasise that the approach is perhaps best used to complement other flow assessment methods (e.g., PHABSIM (Reiser et al., 1989; Gibbins et al., 2002a; Moir et al., 2004), wetted perimeter (Stewardson & Gippel, 2003), Q basic, discharge utilisation indices (Gibbins et al., 2002a), and measures of hydrological variability (reviewed by Olden & Poff, 2002).

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