Science of the Total Environment 601–602 (2017) 1046–1059

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Hydraulic modelling of the spatial and temporal variability in Atlantic salmon parr habitat availability in an upland stream

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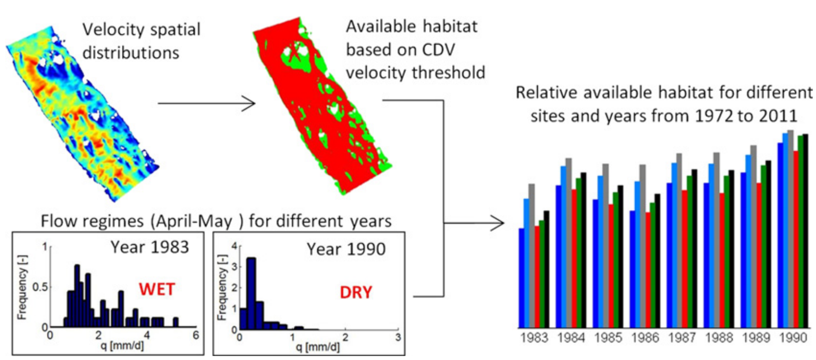
HIGHLIGHTS

- Habitat for salmon parr is strongly influenced by flow regime and bed morphology.
- High resolution modelling is essential to characterize upland stream hydraulics.
- Velocity is not a limiting factor for parr growth even in extreme years.
- Proportion of usable habitat and discharge per unit width are exponentially related.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 11 April 2017
Received in revised form 12 May 2017
Accepted 13 May 2017
Available online 9 June 2017

Editor: D. Barcelo

Keywords:
Salmon parr
Hydraulic models
Fish habitat
Flow regime
River bed morphology
Habitat restoration

ABSTRACT

We show how spatial variability in channel bed morphology affects the hydraulic characteristics of river reaches available to Atlantic salmon parr (*Salmo salar*) under different flow conditions in an upland stream. The study stream, the Girnock Burn, is a long-term monitoring site in the Scottish Highlands. Six site characterised by different bed geometry and morphology were investigated. Detailed site bathymetries were collected and combined with discharge time series in a 2D hydraulic model to obtain spatially distributed depth-averaged velocities under different flow conditions. Available habitat (AH) was estimated for each site. Stream discharge was used according to the critical displacement velocity (CDV) approach. CDV defines a velocity threshold above which salmon parr are not able to hold station and effective feeding opportunities or habitat utilization are reduced, depending on fish size and water temperature. An average value of the relative available habitat (<RAH>) for the most significant period for parr growth - April to May - was used for inter-site comparison and to analyse temporal variations over 40 years. Results show that some sites are more able than others to maintain zones where salmon parr can forage unimpeded by high flow velocities under both wet and dry conditions. With lower flow velocities, dry years offer higher values of <RAH> than wet years. Even though <RAH> can change considerably across the sites as stream flow changes, the directions of change are consistent. Relative available habitat (RAH) shows a strong relationship with discharge per unit width, whilst channel slope and bed roughness either do not have relevant impact or compensate each other. The results show that significant parr habitat was available at all sites across all flows during this critical growth period, suggesting that hydrological variability is not a factor limiting growth in the Girnock.

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http://dx.doi.org/10.1016/j.scitotenv.2017.05.112

1. Introduction

Atlantic salmon (*Salmo salar L.*) are an important natural resource with both high economic and conservation value in many rivers in North West Europe and North East America (Walsh and Kilsby, 2007; Winfield et al., 2004). Atlantic salmon are widely distributed in Scottish rivers where its populations are recognised as being of both national and international importance, accounting for 76% and 29% of the estimated UK and European salmon production (pre-fishery abundance), respectively (ICES, 2016). In recognition of the importance of Scotland's salmon populations, 17 rivers are designated as Special Areas of Conservation (SACs), while the economic benefit of angling, which is dominated by salmon and sea trout, is estimated to be worth ca. >£100 million per annum to the Scottish economy (Radford et al., 2004).

Salmon are an anadromous fish species with a complex life cycle requiring different habitat characteristics at different life stages. In freshwater, juvenile habitat quality depends on a complex range of interactive abiotic and biotic factors (Armstrong et al., 2003). Primary physical habitat characteristics include: water depth (Beecher et al., 2002; Geist et al., 2000; Guay et al., 2000; Kynard et al., 2000), water velocity (e.g. Geist et al., 2000; Kynard et al., 2000; Mallet et al., 2000), cover (e.g.Vadas and Orth, 2001) and substrate composition (e.g. Vadas and Orth, 2001). Hydraulic models, habitat models, and ecological indices (Hedger et al., 2005), can be combined to describe relationships between physical and hydraulic characteristics, and fish presence or abundance. They are some of several potential approaches for assessing the effects of bed morphology and hydrological dynamics on salmonid habitat at fine spatial scales (e.g. Ahmadi-Nedushan et al., 2006; Bacon et al., 2015; Dunbar et al., 2012; Millidine et al., 2012). Different channel characteristics produce spatially variable hydraulic conditions throughout the river network, these, in turn, vary temporally with flow (Millidine et al., 2012; Moir and Pasternack, 2008). The construction of dams and reservoirs for river flow regulation and the presence of vegetation on the river bed can also have substantial implications for the river hydraulics with direct and indirect (via alteration of other freshwater habitat for other organisms) effects on fish habitat (Santos et al., 2015). By combining hydraulic models with habitat models or indices it is therefore possible to assess spatial and temporal variability in habitat availability and quality.

Many of the upland streams used by Atlantic salmon for spawning are characterised by steep slopes and high roughness with coarse sediments dominating the bed morphology. In this context, variations of velocity over short distances can have a substantial impact on habitat quality, especially for juvenile fish that are sensitive to high water velocities. On the other hand, abiotic factors such as: competition and predation may also have considerable effects on juvenile abundance and distribution (Reinhardt et al., 2001; Volpe et al., 2001). Given the need to characterise habitats at the fine spatial scales appropriate for juvenile fish use and high levels of local habitat variability, high resolution 2D (vertically averaged) and 3D hydraulic models have become increasingly favoured for fish habitat evaluation (Mingelbier et al., 2008). In particular, there is considerable interest in the use of 2D hydraulic models for the prediction of instream habitat under complex hydraulic conditions as they offer a pragmatic compromise between good spatial representation and computational efficiency (Jowett and Duncan, 2012).

In this study, we use high resolution 2D hydraulic models in combination with a simple velocity based habitat index (Critical Displacement Velocity (CDV), (Graham et al., 1996; Tetzlaff et al., 2005)) to investigate spatio-temporal variability in available habitat (AH) for Atlantic salmon parr in an intensively monitored upland tributary of the River Dee, Scotland. Our investigation is based at the Girnock Burn, where Atlantic salmon populations have been monitored and assessed by Marine Scotland since 1966 (Bacon et al., 2015) and where a wide range of interdisciplinary ecohydrological research has been undertaken (Soulsby et al., 2016). We use detailed site bathymetries, high resolution meshes and discharge time series in a 2D hydraulic model to simulate the spatial distribution of velocities for six electro-fishing sites where salmon have been monitored for over 15 years. The study focuses on the critical spring time period between April and May, when Atlantic salmon parr in the Girnock Burn exhibit maximum growth associated with high food availability (Bacon et al., 2005) and low basal metabolic rate (Gurney et al., 2008), but where considerable discharge variability has the potential to impact feeding opportunities.

The specific objectives of the paper are to: (1) use high resolution Digital Terrain Models (DTMs) and computing meshes to capture depth-averaged velocity variability in upland rivers with very heterogeneous bathymetries; (2) quantify the capability of each site to provide refuge zones and potential suitable habitat for Atlantic salmon parr; (3) assess the effects of flow regime on AH over 40 years, particularly in extreme dry and wet years; (4) account for inter-site spatio-temporal variability in the provision of suitable habitat. The importance of characterising such spatial and temporal dynamics of salmon parr habitat in river systems is also discussed in the context of river management decisions for flow regulation, morphological alteration and building resilience to climate change to protect this important species (Ahmadi-Nedushan et al., 2006; Millidine et al., 2012; Radford et al., 2004).

2. Study site

The Girnock Burn is an upland tributary of the River Dee in the north-east Scotland well known to provide suitable habitat for salmon at any life stage and where Atlantic salmon populations have been monitored by Marine Scotland Science since 1966 (Bacon et al., 2015; Gurney et al., 2008) (Fig. 1). Average fry and parr density between 2001 and 2016 was estimated to range from 0.07–0.73 and from 0.13–0.47 fish per m^2 respectively – from a capture probability model based on electrofishing survey data (Millar et al., 2016)). Its catchment covers an area of about 31 km^2 and ranges in altitude from 230 to 862 m (Gibbins et al., 2002). The main stem of the river network is about 9 km long and the channel has a mean slope of 0.029 (Moir et al., 1998). The channel is mostly characterised by step-pool and plane-bed reaches and is armoured with abundant boulders from glacial lag deposits (Moir et al., 2006).

The catchment's land cover is characterised by heather moorland dominated by heather shrubs (*Calluna vulgaris* and *Erica tetralix*). Forest cover is dominated by Scot's Pine (*Pinus sylvestris*) and is limited to some steeper areas in the lower catchment. Average annual precipitation is ~1000 mm. This is distributed fairly evenly throughout the year, though the period November to March is usually the wettest. Mean annual air temperature is 6.3 °C and snow usually accounts for <10% of precipitation inputs. Stream flow has a mean daily discharge of 0.57 m^3 s^{-1}. Higher flows (>8 m^3 s^{-1}) are most common during winter and lowest flows tend to be concentrated in the summer period; though the flow regime is flashy and high flow events can occur throughout the year (Soulsby et al., 2016).

We investigated six sites that are used routinely for electrofishing surveys and juvenile assessment (Malcolm et al., 2016). These sites were intended to be more broadly representative of habitats in the Girnock Burn and cover the altitudinal range used by salmon. All the sites are known to support both fry and parr. Working from downstream to upstream the sites are: Forest Automatic Weather Station (FAWS), Mill of Cosh (MC), Diagonal Fence (DF), Hampshire's Bridge (HB), Below East Burn (BEB), and Iron Bridge (IB) (Fig. 2). FAWS and MC are bordered by semi-natural riparian woodland, while the other sites are characterised by moorland land use (Fig. 1).

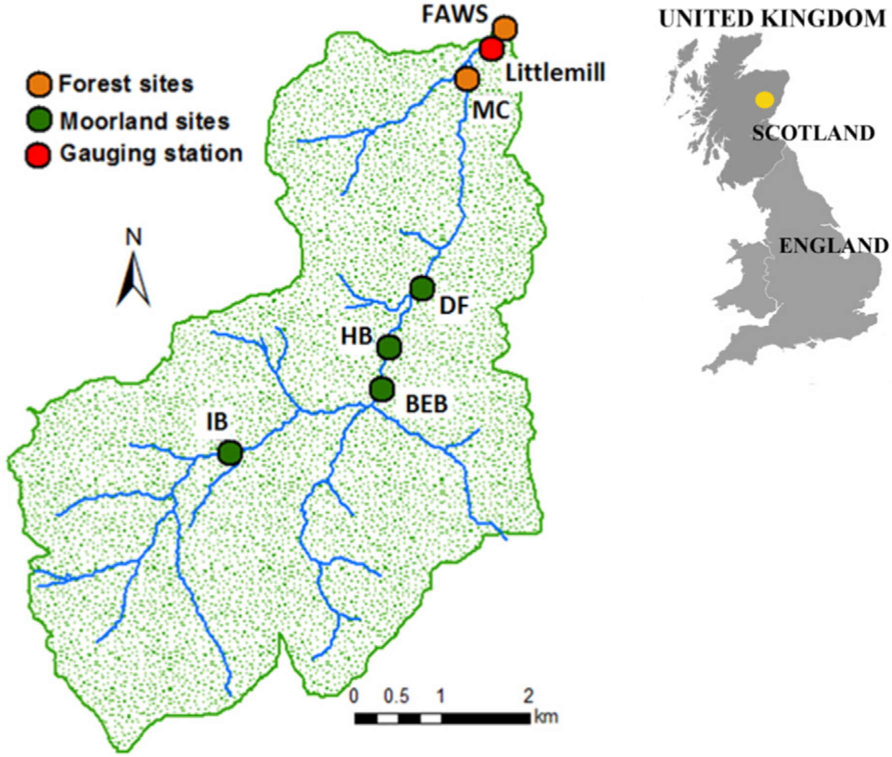

Fig. 1. On the right, location of the study catchment on the United Kingdom map (modified map from http://mapsopensource.com/). On the left, Girnock Burn catchment. Forest (brown dots) and moorland (green dots) investigated sites, and gauging station (red dot).

The sites have contrasting bed morphologies and channel geometries (Table 1). Substrate within each reach range from sand to boulders, though coarse sediment is abundant at all sites providing cover for fish in addition to undercut banking. Although all sites have features typical of a steep, high roughness upland stream, some marked differences are apparent. The most distinct sites in terms of channel morphology is FAWS, which is located in the lower part of the catchment close to the junction with the river Dee, and IB, which is located in the upper part of the catchment. The former has the lowest gradient and its morphology is dominated by a plane bed, though some boulders are present. The latter is the steepest and its morphology is characterised by the alternation of steps formed by large boulders and pools containing smaller substrate. The morphologies of MC, DF, HB and BEB lie between these more extreme sites and are dominated by plane beds, with abundant large boulders and coarse cobble/gravel bed sediments in patchy riffles and infrequently spaced pools. HB is characterised by a similar roughness and channel gradient to IB.

3. Material and methods

3.1. Field data collection

Detailed surveys of the stream bed bathymetry were carried out for each site using a robotic total station (Leica Geosystems TPS 1200) coupled with a 360° prism. For each site, a fixed length (from 16.2 to 76.3 m, in FAWS and IB respectively) of river channel was surveyed corresponding to the electrofishing reaches that were fished historically. The number of measurements collected varied according to the area and bed heterogeneity and ranged between 6696 at the smaller, more uniform FAWS site and 18,420 at the more complex IB site, with an average density of >50 measurements per square meter. Each site required about 6–8 person days of work to complete. The surveyed bathymetries were used to construct Digital Terrain Models (DTMs) of the bed elevation. Average bed slope was approximated from the average water surface slope and roughness was computed in ArcGIS as a detrended standard deviation of bed bathymetry using TopCAT tool (Olsen et al., 2012).

During the field surveys, river discharge, water surface elevations at the downstream cross section and extensive measurements of water velocities were taken and used as input for model calibration. Discharge was computed from the downstream section by current metering using the velocity-area method (Le Coz et al., 2012). We used an electromagnetic flow meter (Valeport, MODEL 801 Electromagnetic Flow Meter) at 0.6 times the water depth (from the water surface). Experiments were conducted optimising the time period needed to obtain stable average velocity measurements, given the local effects of turbulence; an interval of 1 minute was found to be sufficient. A graduated wading rod was used to measure water depth. Daily discharge at the catchment outlet (Littlemill) has been monitored since 1972 by a variety of organisations, most recently the Scottish Environment Protection Agency (SEPA) (Fig. 1). The discharge was then scaled for each site in proportion to the drainage area.

3.2. Hydraulic habitat modelling.

Detailed bathymetries were combined with scaled discharge as input for a 2D hydraulic model of each site. We used the model River2D (Steffler and Blackburn, 2002) which was developed at the University of Alberta specifically for natural stream and river applications. Several studies have used River2D to model fish habitats, among which: (Katopodis, 2003) modelled Walleye and Quillback habitats at different life stages in upland rivers; (Gard, 2009) compared spawning habitats for chinook salmon and steelhead trout in a Canadian river; (Millidine et al., 2012) assessed the impact of

Fig. 2. Study sites from downstream (FAWS) to upstream (IB). Pictures were taken from downstream to upstream.

Table 1
It reports the draining area, the slope (a mean value for each site), the roughness, the mean daily discharge (Q) from 1972 to 2011, the longitudinal length, the mean width (estimated under mean discharge), and the mean wetted area (estimated under mean discharge) for the investigated sites.

	FAWS	MK	DF	HB	BEB	IB
Draining area [km^2]	30.7	25.7	20.7	20.3	19.9	8.4
Slope [−]	0.003	0.016	0.011	0.021	0.008	0.022
Roughness [m]	0.068	0.108	0.078	0.112	0.072	0.124
Mean Q [m^3 s^{-1}]	0.57	0.48	0.38	0.38	0.37	0.15
Length [m]	16.2	19.3	17.5	30.5	26.6	76.3
Mean width [m]	7.0	7.2	7.8	6.8	6.2	3.2
Mean wetted area [m^2]	114	139	136	208	165	245

morphological alteration on brown trout habitats and (Millidine et al., 2016) assessed the transferability of hydraulic habitat models for juvenile Atlantic salmon. River2D is based on the two-dimensional depth averaged St. Venant equations representing the conservation of water mass and two components of the momentum vector. Model inputs required are the river bed DTM, discharge and the downstream water surface elevation (stage).

To overcome the limitation of a small number of stage-discharge observations, for each site we utilized the downstream cross-sectional geometry to construct a rating curve by fitting Manning's equation (for slope and roughness) to the available stage-discharge measurements collected during fieldwork days. This allowed us to extrapolate the corresponding stage directly from the rating curve for each modelled discharge. Model outputs were water depth and depth-averaged velocity spatial distributions. Given the bed heterogeneity and large number of roughness elements at each site, very fine mesh grids (triangular cells with an average area of 0.01 m^2) were utilized to capture small scale velocity variation.

Calibration was achieved by minimizing the mean square error between observed and simulated velocity for discharges measured in the field. Parameters used for calibration were Manning's coefficient representing resistance due to bed roughness, and eddy viscosity representing the resistance due to the turbulence. The spatial distributions of stream velocities and critical displacement velocity (CDV) for each cell were then combined to estimate the AH for Atlantic salmon parr.

The empirically-based equations for estimating the CDV provide a velocity threshold above which juvenile salmon are unable to hold station. Such conditions, thus, provide an objective index of whether a patch of habitat is likely to be useable or not for salmon parr. CDV is dependent upon fish size and stream temperature. For salmon parr, this relationship has been determined through laboratory flume experiments (Graham et al., 1996) as:

$$CDV = (0.39\,T + 31\,L)L \tag{1}$$

where T is water temperature [°C] and L is fish length [m]. (Garner et al., 2014) showed that, in the Girnock, there is limited variability in water temperature between moorland upstream and forest downstream sites for the months of April and May (usually <1 °C). There is limited information on the intra-annual spatial variability in fish size during the early part of the year where electrofishing data is more sparse. Therefore, for simplicity and to allow us to focus primarily on the hydraulic differences between the sites, we utilized values for T and L derived from the water temperatures for April and May (mean for this period based on 2007–11 data is 10 °C) at the HB site (Fig. 1) and the average length of parr (6.6 cm) caught in all the sites during spring electrofishing surveys, obtaining a CDV equal to 0.39 m s^{-1}. It follows that AH for each site can be defined as the area where mean column water velocity is below the CDV.

Given the high computational and data requirements of 3D models, we opted for 2D models in this study. We are aware of the limitations introduced by comparing depth-averaged current velocities, obtained from 2D model simulations, with an empirically derived CDV. Specifically, in free surface channels, velocity generally decreases exponentially with depth and consequently, even if average velocity is too high, fish may still find suitable habitat near to the bed substrate, only making short movements into the water column for feeding (Höjesjö et al., 2015). We recognise that CDV (as applied here) is likely to give a conservative estimate of available habitat, thereby identifying suitable habitat as unsuitable. Nevertheless, the approach still provides a consistent, biologically relevant velocity threshold that allows comparisons to be made between sites and years considering the effects of discharge, temperature and fish size and is thus, considered a useful metric for understanding the potential influence of higher flow conditions on the habitat of juvenile salmonids.

The study sites varied in size as they were pre-defined electrofishing sites, with mean wetted areas (wetted area under mean daily flow recorded from 1972 to 2011) ranging between 114 and 245 m^2. Considering AH depends on the size of the site, AH was expressed as a proportion of the wetted area (Table 1), giving a normalised measure of relative available habitat (RAH). For each year and site, we estimated an average value of the <RAH> for the April–May period that we used for subsequent comparisons. Through aggregation we obtained a 40 year time series of the <RAH> for each electrofishing site. Despite our study extending from 1972 to 2011, we assumed that channel morphology has remained similar over the period of record. Of course, this is a simplification, but given the armoured nature that plane and step-pool beds dominated by large boulders and coarse cobble commonly exhibit (Montgomery and Buffingtont, 1997) it is a reasonable assumption. To underpin this, also no substantial geomorphic variations were visually recognised when we visited the sites after the extreme event occurred on the 30th of December 2015 (the highest discharge recorded at the Dee since 1929 (Marsh et al., 2016)). Thus, we assumed that RAH provides a metric of available habitat and feeding opportunity that allows comparison among the sites and between years, with higher RAH values expected to result in more favourable conditions for salmon parr.

4. Results

Fig. 3 shows the spatial distributions of the depth-averaged velocity for three of the sites (FAWS, DF and HB) covering the range of observed channel gradients and roughness in the Girnock Burn under two different flow conditions: one relatively low (1 mm d^{-1} ~ Q_{40}) and one high (8 mm d^{-1} ~ Q_3) (quantiles are estimated based on the entire daily discharge time series). The DTMs and computational mesh resolution were adequate for simulating the effects of significant roughness elements on the current velocity under both high and low flow conditions.

The spatial distribution of roughness elements, topography and channel gradient controlled hydraulic heterogeneity and overall velocities across the three sites under lower flow conditions (Fig. 3a, c, e). At FAWS, higher velocity areas (>0.4 m s^{-1}) were largely restricted to the upstream end of the site and right bank. At DF, higher velocities were predominantly observed between emergent boulders at the upper and lower end of the site. HB is the steepest of the three sites and characterised by numerous and large emergent boulders that produced highly heterogeneous velocities across the site where high velocity areas were immediately bordered by low velocity areas.

Under higher flow conditions, velocities at DF became increasingly homogeneous as emergent boulders were drowned out and the distribution of roughness elements at the lower end of the site acted as a hydraulic control (Fig. 3d), but velocities generally remained below 1 m s^{-1}. Velocities at HB stayed highly heterogeneous with numerous large roughness elements remaining exposed even under high flow conditions (Fig. 3f). Velocities at FAWS (Fig. 3b) were generally higher than those observed at DF (frequently >1 m s^{-1}) and more homogeneous than observed under low flows.

The simulations for the remaining three sites (MC, BEB and IB) are shown in Appendix A (Fig. A.1). At higher flows these were most similar to DF in the sense that the roughness elements restricted higher velocities to very localised areas. However, at low flows, there were similarities to HB with many exposed roughness elements and highly heterogeneous hydraulic characteristics.

For each site these spatial patterns can also be summarised as velocity frequency distributions under low and high flows. Fig. 4 shows the frequency distributions of depth-averaged velocity for the three sites FAWS, DF and HB. As expected, mean flow velocity and wetted area increased at all sites with increasing discharge (Fig. 3, Fig. 4). Velocities at DF were generally lower than those observed at FAWS and HB, under both low and high flow conditions with lower mean and maximum velocities. The change in mean velocities between low and high flows was also smaller at DF (0.28 m s^{-1}) than observed at HB (0.35 m s^{-1}) or FAWSW (0.5 m s^{-1}). Additionally, DF was characterised by a unimodal velocity distribution under low flows, while FAWS and HB were characterised by bimodal distributions with velocities of <0.05 m s^{-1} being the most frequent class for both sites with secondary peaks at 0.3–0.4 m s^{-1} and 0.6–0.7 m s^{-1} for FAWS and HB, respectively. All sites were characterised by unimodal velocity distributions under high flows.

Appendix A (Fig. A.2) shows the velocity distributions for the remaining sites. At low flows, MC and BEB had bimodal distributions with slightly slower mean water velocity (0.24 m s^{-1}) than IB

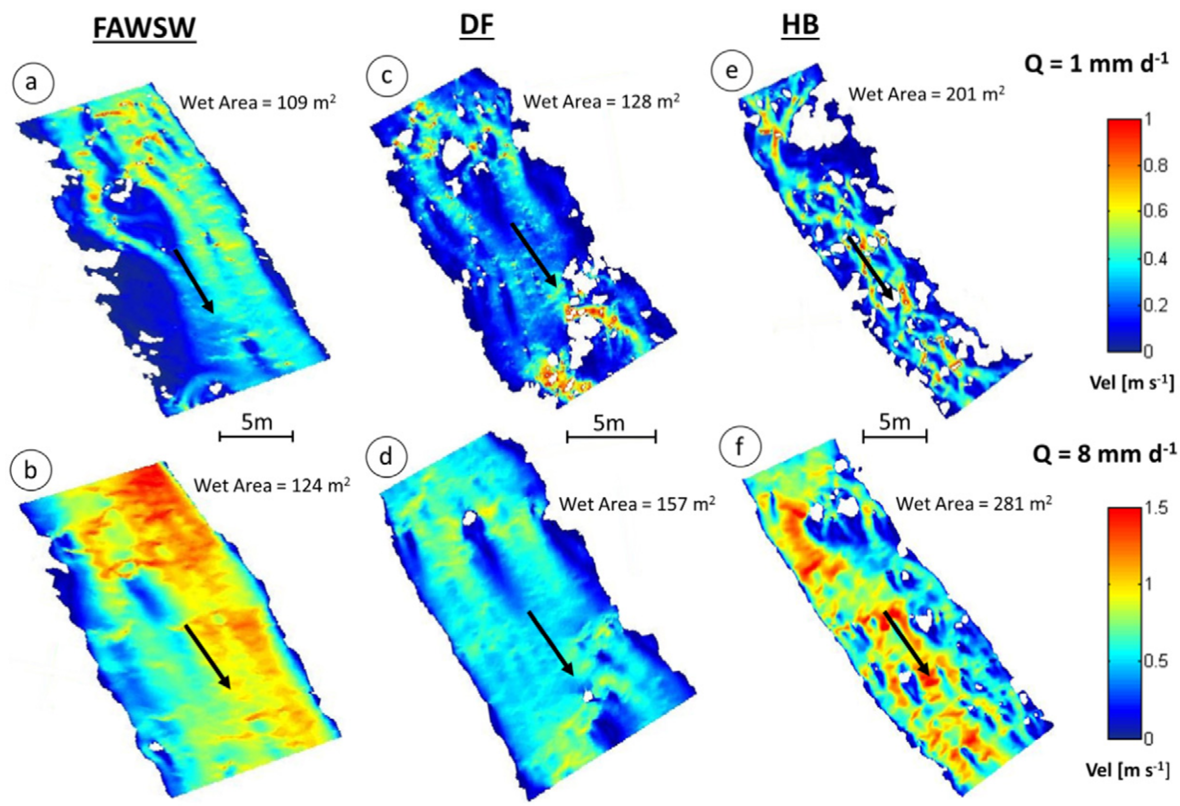

Fig. 3. Simulated spatial distribution of water velocity under two contrasting flow conditions: one low (1 mm d^{-1}) and one high (8 mm d^{-1}) for FAWS, DF, and HB sites.

(0.28 m s^{-1} - unimodal distribution). At higher flows, the three sites show similar unimodal distributions but with higher mean velocity in MC and IB (0.59 and 0.60 m s^{-1}, respectively) than in BEB (0.51 m s^{-1}).

The frequency distributions in Fig. 4 and the spatial maps in Fig. 5 show the distribution of the areas above and below the estimated spring CDV for salmon parr (0.39 m s^{-1}) for the three illustrated sites (FAWS, DF and HB), under low and high flow conditions. The remaining sites are shown in Appendix A (Fig. A.3) for comparison. It was clear that velocity was not a constraint on habitat use under lower flow conditions during drier periods with only a very small proportion of sites above CDV. Even under higher flows there were areas at all three sites where unconstrained habitat (below CDV) remained. However, it is also clear that there were substantial inter-site differences, both under low and high flow conditions with a greater proportion of AH in DF (87.2%) than HB (59.2%) and FAWS (77.1%), Fig. 5. At all three sites under high flow conditions, AH was mainly distributed along river banks or behind large roughness elements. Those sites with greater roughness elements therefore seemed to have greater proportions of AH. The same analysis was also carried out for the remaining sites (Appendix A, Fig. A.3). Under low flow conditions MC (82.3%) and BEB (81.2%) provided greater proportions of AH than IB (72.2%) while under high flow conditions MC provided higher proportions of AH.

The results of the daily simulations were integrated over the two-month spring growth period (April–May), to provide an average RAH (AH divided by wetted area under mean flow conditions) for each year (<RAH>). Fig. 6 summarises this information and compares the <RAH> of each sites as an integrated index of habitat availability between 1972 and 2011. Each site is represented by a box where the red line is the median value, the edges of the box are the lower (25$^{\text{th}}$ percentile) and the upper quartiles (75$^{\text{th}}$ percentile), the upper and lower whiskers are, respectively, the highest and the lowest values and red crosses represent outlier values. The sites are ordered from downstream (FAWS) to upstream (IB). Although all the sites provide a high proportion of usable habitat, median values suggest that for the period investigated, some sites are on average less constrained by high velocities and provide greater areas of flow refugia (retain higher AH). In particular, DF provides the greatest proportion of AH over time with a median value of 0.86, followed by MC (0.81) and IB (0.78). In contrast, FAWS, HB, and BEB which are characterised by generally higher velocities have lower median values of RAH 0.72, 0.67 and 0.75. Inter-annual variability in <RAH> is indicated by the vertical extent of the plots and was similar across sites with only DF characterised by notably more stable conditions. There was no evidence to suggest that upstream sites systematically provided more suitable habitat than downstream sites or vice versa.

Fig. 7 shows the inter-annual variability of <RAH> for each site over the period 1972 to 2011. Across all sites, <RAH> ranged between 0.48 (FAWS, 1983) and 0.96 (DF, 1990). It is evident that some sites provided more useable habitat, on average, than others (Fig. 6), but it is also useful to note that this was consistent between years (Fig. 7). Depending on the catchment antecedent wetness and hydroclimate, flow regime can vary markedly from one year to another. Fig. 7 also shows two examples of the discharge distribution for two contrasting years, one wet and one dry, emphasising the nature of hydrological variability. It demonstrated how dry years, at least inside the range of the flow regime investigated, potentially provide more stable and unconstrained habitat (greater <RAH>) than wet years, for all the sites investigated.

Bed slope and roughness are commonly recognised to be key factors affecting in-channel hydraulics and habitat suitability. Unfortunately, in this study, the two were strongly correlated (Fig. 8) with roughness increasing with slope following a quadratic relationship (see equation in Fig. 8), thus constraining assessments of

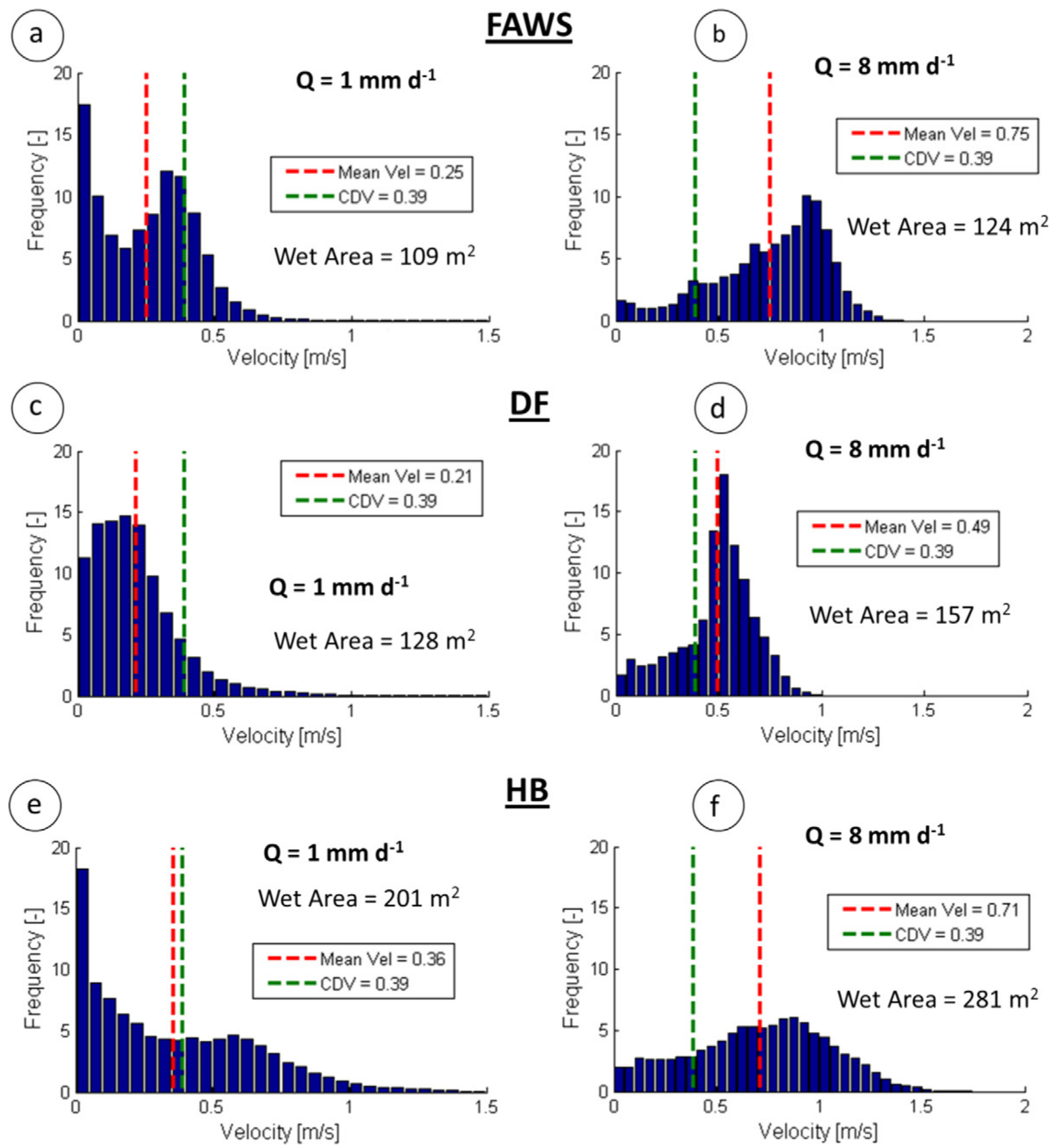

Fig. 4. Velocity distribution, wetted area and mean water velocity under two contrasting flow conditions: one low (1 mm d^{-1}) and one high (8 mm d^{-1}) for FAWS, DF, and HB.

their individual effects on velocity and thus AH. Nevertheless, Fig. 9 does not suggest any simple correlation between bed roughness or slope (Fig. 9) or their combination (not shown in this paper) and time averaged <RAH> at the scale of the Girnock Burn.

Fig. 10 shows a clear and strong relationship between the proportion of wetted area (this refers to the wetted area corresponding to each specific discharge) below CDV (AH/WA) and the discharge per unit width averaged over the reach (q [m^2 s^{-1}], computed by dividing the discharge [m^3 s^{-1}] by the mean wetted width for the reach [m]). This relationship can be described by a simple relationship ($y = a\exp(-b\,x) + c$) with 3 parameters (a, b, c – Table 2), which are site dependent. AH/WA (the proportion of the site below CDV) decreases exponentially with q, at a rate determined by parameters a and b until $q \approx 0.3$ m^2 s^{-1} after which AH/WA asymptotically tends to a threshold defined by the parameter c. Because the channel shape and absolute area of emergent roughness elements is implicitly included in the calculation of q, this result implies that the proportion of AH is also affected by the spatial distribution of the roughness elements. For example, very low values of discharge per unit width (averaged across the reach) are obtained when roughness elements are positioned in such a way as to suddenly reduce the channel width with consequent formation of pools or glides characterised by relatively low water velocity upstream of the restriction.

5. Discussion

This study investigated fine scale spatio-temporal variability in the hydraulic characteristics of six study reaches with contrasting channel morphologies and used this to assess the potential of high velocities (exceeding CDV) to influence habitat use and feeding by Atlantic

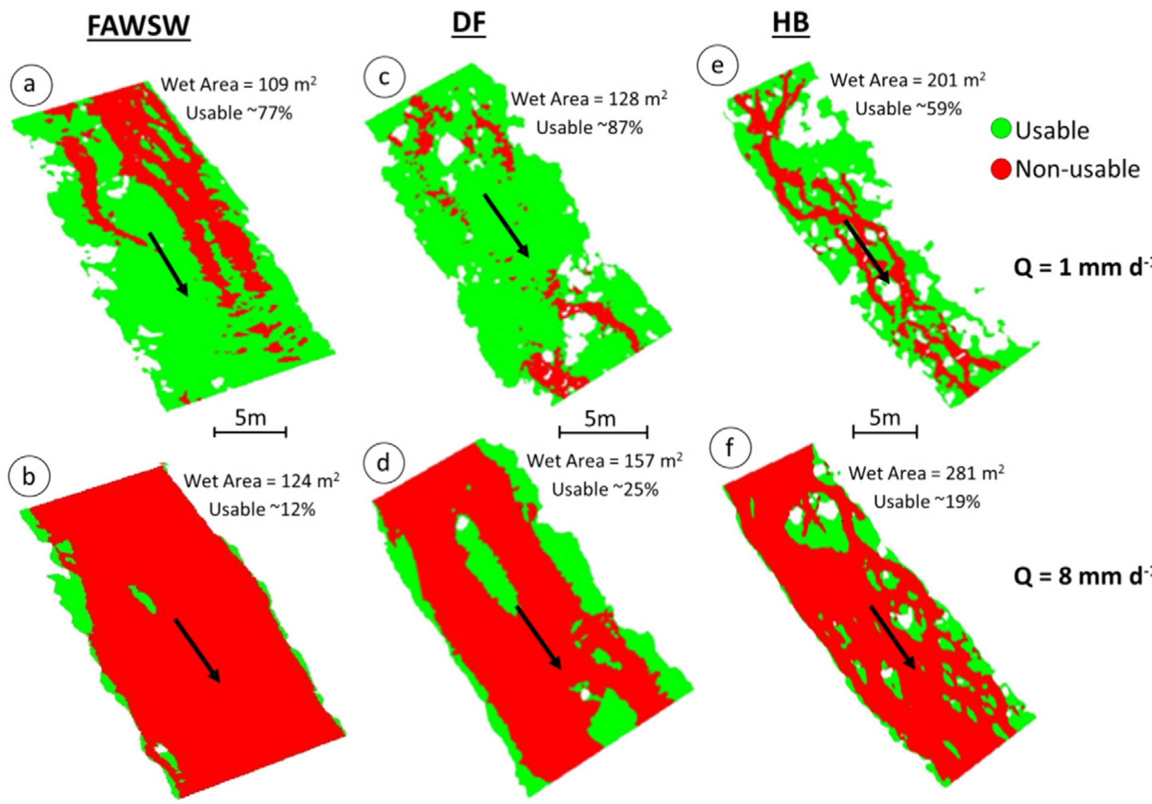

Fig. 5. Usable and non-usable habitat under two contrasting flow conditions: one low (1 mm d^{-1}) and one high (8 mm d^{-1}) for FAWS, DF, and HB.

salmon parr during the critical spring growth period over 40 years. As far as the authors are aware, such a long-term study of hydraulic habitat suitability has not been undertaken previously. The findings offer insights for understanding spatio-temporal variability in habitat conditions that may influence fish growth and for predicting the effects of channel modification on flow refugia.

5.1. Channel morphology and hydraulic characteristics

Spatio-temporal variability in hydraulic characteristics results from the interactions between bed morphology and flow regime. (Leopold and Maddock, 1953) were the firsts to empirically relate hydraulics (water depth and width) to flow (and therefore velocity) and river geometry. Since then, finding more accurate and physically based relations has been the focus of many researchers (Gleason, 2015). These relations have been employed in different types of applications including environmental and habitat quality assessment (Best et al., 2005; Huguet et al., 2008; Jowett et al., 2005; Lamouroux and Souchon, 2002; Saraeva and Hardy, 2009). In recent years, however, helped by the increase of computational performances, there has been a rapid increase on the use of hydraulic models potentially capable to represent the spatial variability of water depth and velocity (Millidine et al., 2016; Muñoz-Mas et al., 2012).

Nevertheless, in many hydraulic habitat studies the impact of small-scale elements is still neglected in favour of more readily generated, low resolution observations or simulations (Lee et al., 2010; Mouton et al., 2007) on the assumption that the variability of the velocity inside each cell can be ignored with respect to larger variations between the

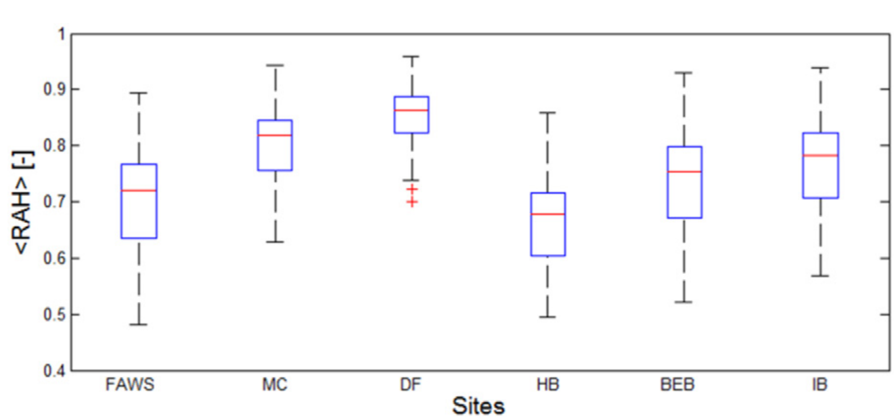

Fig. 6. Box-and-whiskers plots of yearly average (for the growth period, April–May) relative available habitat <RAH> from 1972 to 2011 for all six sites investigated.

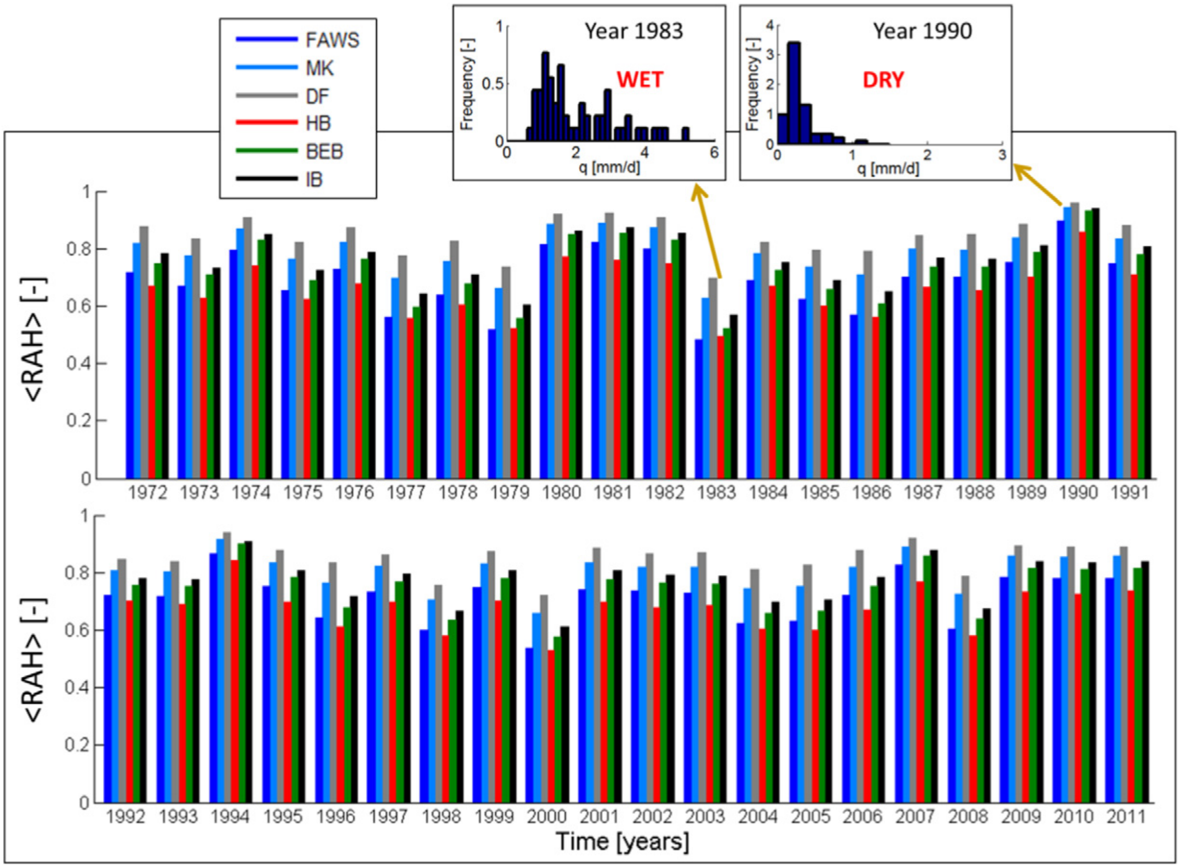

Fig. 7. <RAH> from 1972 to 2011 for all sites; and examples of two contrasting flow regimes providing greater (DRY) and lower (WET) < RAH>.

cells. In contrast, our work shows that water velocity can be highly heterogeneous at fine spatial scales and thus, that models based on low resolution data are unlikely to provide realistic assessments of hydraulic characteristics. This is particularly likely to be the case in many upland rivers, such as the Girnock, where channel bathymetries are usually very heterogeneous and complex with frequent presence of emergent cobbles and boulders.

Notwithstanding the importance of such small scale heterogeneity to in-stream hydraulics, this study also shows that aggregated effects at the reach-scale mean that some sites are more susceptible than others to rapidly changing and higher velocities under increasing discharge. This was not only related to simple reach scale parameters such as bed roughness and slope or their combinations, but also appeared to reflect the spatial distribution of individual roughness elements and how they alter local water surface gradients and reduce the discharge per unit width. This explains, for instance, why DF, even if not characterised by either very high roughness or very low slope, provides greater low velocity areas under high flow conditions than other sites. In fact, the high concentration and alignment of boulders acting as a cross-channel impediment to flow (Fig. 2) at DF's downstream cross section increases the water surface elevation and the wetted width at the lower end of the site, consequently reducing the discharge per unit width and thus, mean cross-sectional velocities. Even at sites such as FAWS, where average slope is quite low, the relative lack of roughness elements produced a greater proportion of area of higher velocities. Thus, it appears that the combination of overall roughness, the spatial distribution of roughness and channel gradient all affected the spatial distribution of high velocities.

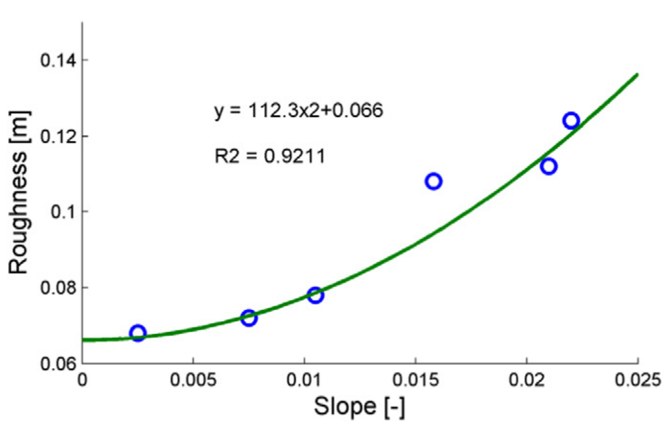

Fig. 8. Estimated slope vs. estimated roughness and corresponding fitting curve.

5.2. Water velocity and Atlantic salmon parr

Physical habitat requirements such as current speed and water depth vary substantially with species, life-stage, season and fish size (Nislow and Armstrong, 2012) and influence fish distribution, abundance and growth (Harvey et al., 2006; Inoue and Nunokawa, 2002; Jowett et al., 2005; Saraeva and Hardy, 2009). In the Girnock Burn, maximum growth rates for salmon parr are observed during a 10–12 week period starting abruptly in early April and centred around mid-May when food abundance is high and temperatures are relatively low resulting in low basal metabolic requirements (Bacon et al., 2005; Gurney et al., 2008). However, it could also

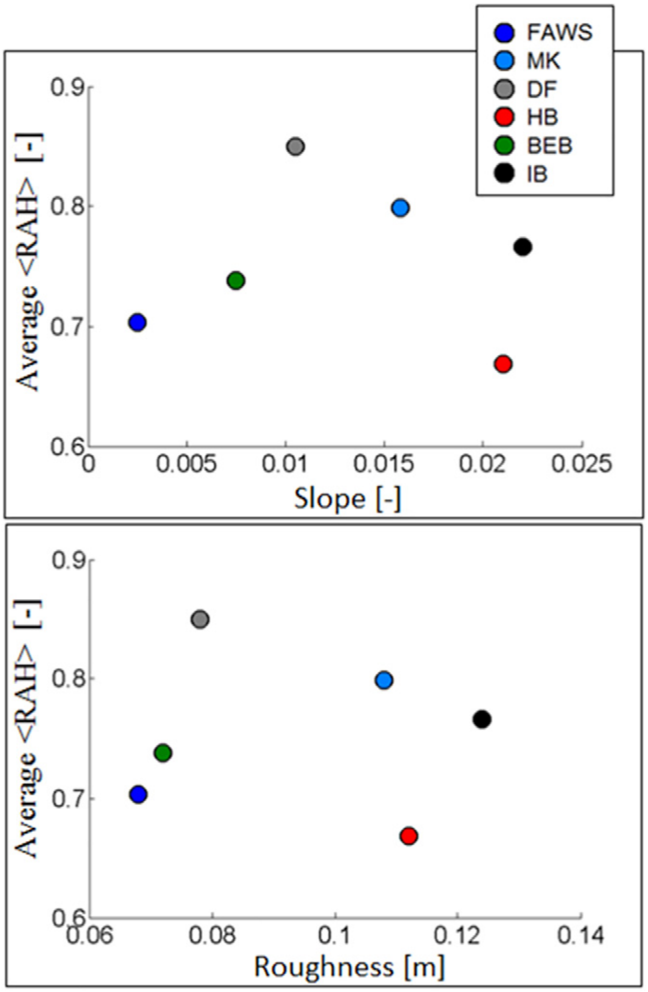

Fig. 9. Relationships between Mean <RAH> vs. stream slopes and roughness.

be anticipated that low river temperatures, smaller fish size, (early in the growing season) and a highly variable hydrological regime (frequently resulting in high velocities) could influence the usability of habitat and restrict feeding opportunities with consequences for growth. With this in mind, the current study focussed on the potential effects of high velocities using a simple, empirically derived, conservative velocity threshold.

Given the flashy nature of the Girnock flow regime (Soulsby et al., 2016), our initial expectations were that there was likely to be considerable inter-site and inter-annual variability in the proportion of wetted area where CDV was exceeded, with potential consequences for habitat use and growth. Inter-site differences in the proportion of habitat below CDV (AH) were observed, particularly under high flow conditions. However, substantial areas of AH remained at all sites even under high discharges. This is all the more surprising given the conservative nature of the CDV velocity threshold (see limitations below) which does not account for highly transient habitat utilization at short burst speeds (Höjesjö et al., 2015).

In terms of temporal variability, the analysis presented here suggests that relatively large areas of useable habitat (AH) are maintained in most years even under wet conditions and high flows. In general, inside the range of flow regimes investigated, drier spring periods provided greater proportional AH than wetter springs. These extreme dry years have been rare in the context of the Scottish climate, though scenarios for climate change may result in flow regimes with spring becoming characterised by less precipitation and lower flows (Capell et al., 2013). Even if higher discharges lead to higher averaged velocities, roughness elements such as boulders, pebbles, undercut banks and macro-vegetation can still provide low velocity areas for foraging and refuge (Beland et al., 2004).

5.3. Generalised habitat models

Given the financial and logistical costs of developing site specific hydraulic habitat models, there is increasing interest in combining models of hydraulic geometry with generalised habitat models (e.g. Lamouroux and Jowett, 2005). Such approaches potentially allow rapid assessment of habitat quality at new reaches with only limited (or no) field based data collection. In this study, it was observed that the relative proportion of the wetted channel below CDV could be predicted from the discharge per unit width of channel using a simple equation with 3 parameters. Discharge per unit width could be relatively rapidly obtained under various flow conditions using remote sensing techniques (e.g. Hedger et al., 2007). If the model parameters could then be predicted from other readily characterised reach scale descriptors (e.g. Booker, 2016), then this could provide a basis for predicting

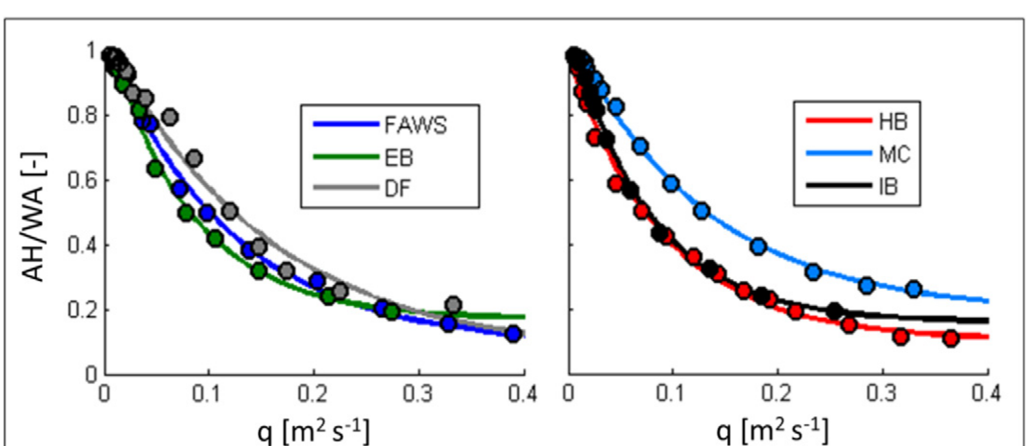

Fig. 10. Relationship between estimated available habitat proportions (AH/WA) and discharge per unit width (q) and respective fitting curves for the 6 study sites.

Table 2
Coefficients of the equation "$y = a\exp(-b\,x) + c$", describing the 6 investigated sites the proportion of available habitat (AH/WA) as a function of the discharge per unit width (q).

	FAWS	MK	DF	HB	BEB	IB
a	0.95	0.88	1.00	0.88	0.90	0.91
b	8.55	7.79	6.52	10.87	12.31	12.88
c	0.09	0.18	0.05	0.10	0.17	0.16

circumstances under which adequate flow refugia are not available. This information could be used to inform channel restoration efforts, for example where it is expected that channel modification could limit habitat quality (Millidine et al., 2012). Unfortunately (unlike in Lamouroux and Jowett, 2005), given the sites-specific nature of our study, we could not find any consistent relationship connecting the parameters to the site morphological characteristics due to the limited number of site investigated and therefore of data to fit.

5.4. Study limitations

Although this study has provided useful insights into the potential effects of channel morphology and variable hydrological regime on salmon habitat availability, it has necessarily used very simple habitat assessment tools and criteria. Water velocity is only one of a suite of complex inter-active controls that influences juvenile salmon abundance, distribution and growth. Furthermore, CDV is a relatively coarse and conservative metric of the upper threshold for habitat use (Tetzlaff et al., 2005). A number of studies have shown that salmon parr will make use of considerably higher velocities than used in this study for feeding. For example, Heggenes et al. (1999) suggested that parr prefer fast-flowing stream habitat with velocities ranging from 0.1 to 0.7 m s^{-1}, while Höjesjö et al. (2015) identified that parr will make use of high velocity areas, holding station near the bed using the pectoral fins (Arnold et al., 1991) before moving into the water column and moving downstream to capture prey items. In this context (Höjesjö et al., 2015) suggest that the upper velocity for habitat use may reflect burst swimming speeds of ca. 10 body lengths per second. This would give an effective upper velocity threshold of 0.66 m s^{-1}, a value that would increase the expected values of AH considerably.

Ignoring the specifics of any upper threshold, the quality of useable habitat also varies widely at lower velocities where it can also become unusable (Millidine et al., 2016). In this context, the finding that greater habitat availability is observed in dryer, lower flow years requires careful interpretation. While previous studies have shown that high flow can reduce growth (Arndt et al., 2002; Jensen and Johnsen, 1999), potentially through effects on metabolic costs (Arndt et al., 2002), other studies have suggested that higher flows increase food availability and thus, reduce the required duration of feeding with consequent benefits for reduced predation risk (Roy et al., 2013). Additionally, some long-term studies have shown that smolt production (which depends on parr production) increases with increasing minimum weekly discharge (Hvidsten et al., 2015). Taken together, this evidence suggests that intermediate discharges and velocities are likely to offer greatest benefits to parr. Based on these considerations habitat improvement could be achieved by partial flow regulation specifically designed to mitigate extreme events (both droughts and floods) whose frequency is due to increase according to climate change projections (IPCC, 2014) without limiting and impeding fish passage, and by adding roughness elements to the sites (e.g. boulders or wood - (Roni et al., 2002)), providing shaded refuge areas where fish can find refuge during flood events. Setting aside the issues over water velocity, other important physical habitat variables such as water depth, substrate and cover can also significantly influence on the suitability of salmonid habitat (Armstrong et al., 2003; Millidine et al., 2016, 2012). A wide range of biological interactions can also be highly influential. For example, the availability of food strongly affects habitat quality, carrying capacity and growth. This, in turn, reflects the nutrient status of the stream and the availability of allochthonous and autochthonous substrate for invertebrates to feed on. Similarly, the degree of density dependent competition and the presence or absence of predators will also be significant (Grant and Kramer, 1990; Imre et al., 2005) as behavioural characteristics which render responses to flow regime and hydraulics more complex then implied by simple hydraulic models. Finally, temperatures will affect fish mortality (Richter and Kolmes, 2005) and growth through seasonal influences on productivity and the trade of between increasing assimilation of food and metabolic costs as temperatures increases (Gurney et al., 2008; Marine and Cech, 2004; Sommer et al., 2001), as well as the capacity to move and resist current speed (partially explained by CDV expression) (Baker et al., 1995).

Such complex biological and physical data are now being incorporated into multi-variate fish habitat models that are seeking to explain spatial and temporal variation in fish abundance and growth for sites where historical electro-fishing data are available for fry and parr. This will hopefully result in a fuller understanding of the interactions between hydrology, in-stream hydraulics and salmon ecology. This remains an urgent requirement as global increases in river regulation for hydropower and water supply, along with climate change, have the potential for marked impacts on salmon populations (Zarfl et al., 2014). Such studies will be crucial to provide evidence–based management that may guide operational rules for regulated rivers, help develop strategies to build resilience to climate change or provide a basis for stocking strategies for restoration of fisheries in degraded rivers. In this context, working to capture the key findings of empirically-based studies such as this one in simpler, more probabilistic models is a key priority.

6. Conclusions

This paper used high resolution velocity fields obtained by 2D hydraulic models to estimate AH of several long-term electrofishing sites in an upland Scottish river. The combined effects of flow regime and bed morphology dictate that some sites are more able than others to provide and maintain useable habitat for Atlantic salmon parr during the critical spring growth period. Inter-annual variability in the flow regime can impact on the extent and duration of available habitat in individual years. In particular, lower and moderate flows provide more AH than higher flow regimes, though habitat is rarely – if ever – limiting for long periods. Discharge per unit width is a key factor to define the proportion of available habitat (AH/WA) and it is highly dependent on roughness distribution. Therefore from a management point of view, (at least when velocity may represent the dominating limiting factor) the work suggests that interventions aiming to moderate extreme events (e.g. partial flow regulation without altering fish passage), especially during very wet periods, and maintaining low value of the ratio AH/WA (morphological design) could have a positive impact and improve juvenile salmon habitat. Future work should seek to combine metrics of the accurate representation of the site hydraulics obtained here with more complex fish habitat models that can include the effects of other controlling factors and their interactions.

Acknowledgements

The authors would like to thank Marine Scotland Science and the University of Aberdeen for funding the PhD project and Marine Scotland Science for offering fieldwork assistance and providing discharge, water temperature and fish length data set.

Appendix A

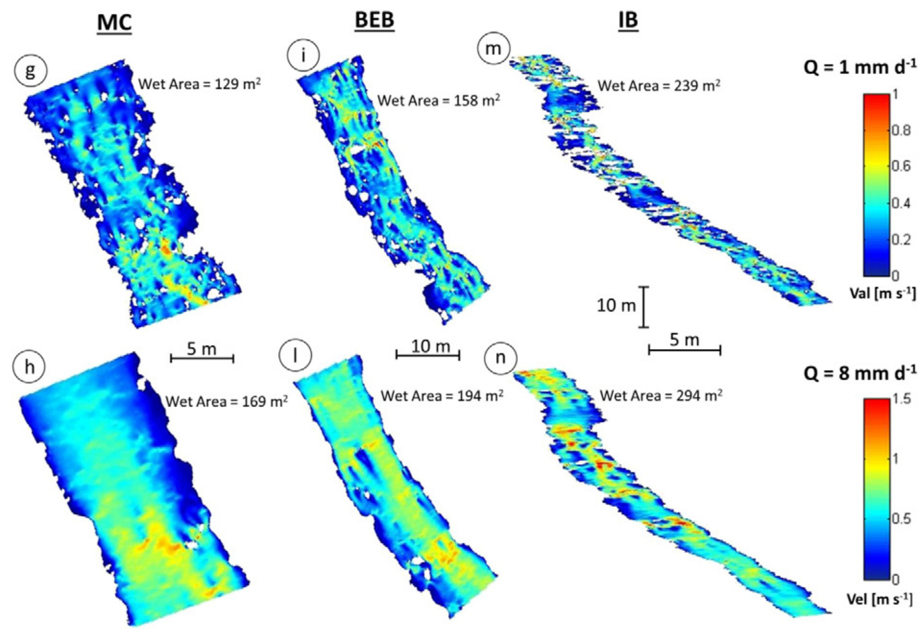

Fig. A.1. Simulated spatial distribution of water velocity under two contrasting flow conditions: one low (1 mm d^{-1}) and one high (8 mm d^{-1}) for MC, BEB, and IB sites.

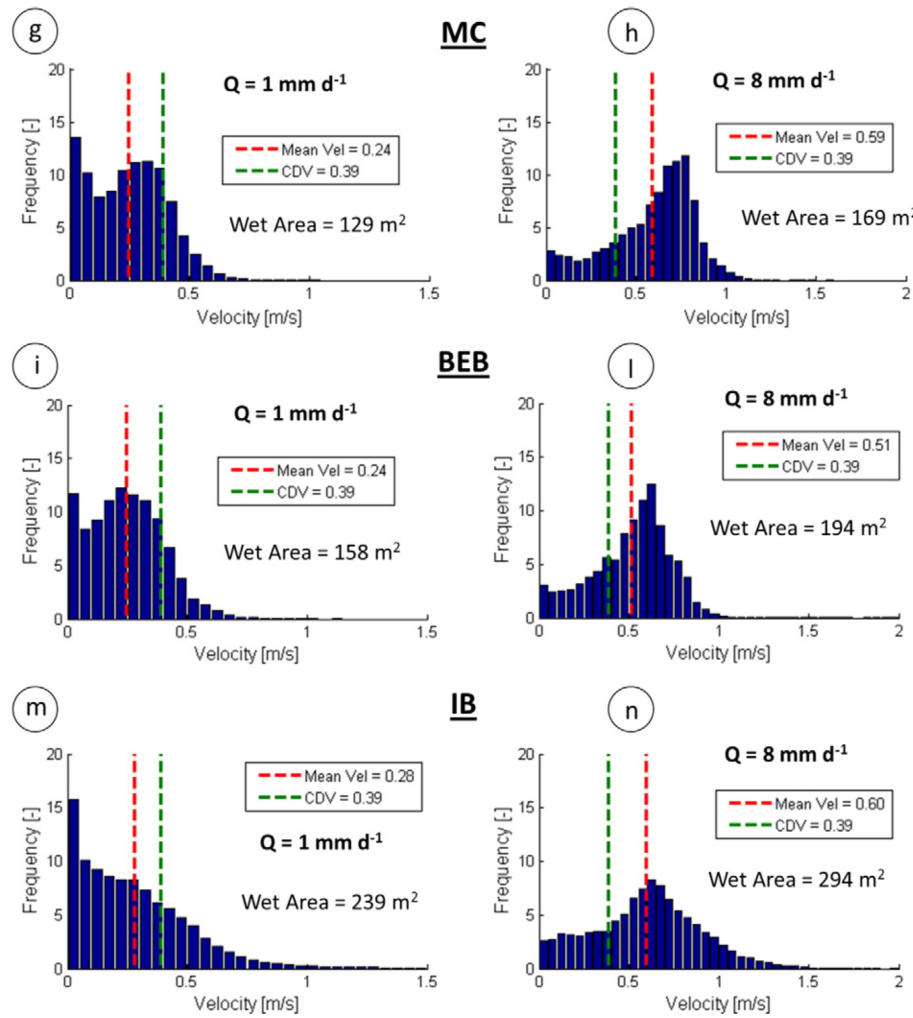

Fig. A.2. Velocity distribution, wetted area and mean water velocity under two contrasting flow conditions: one low (1 mm d^{-1}) and one high (8 mm d^{-1}) for MC, BEB, and IB.

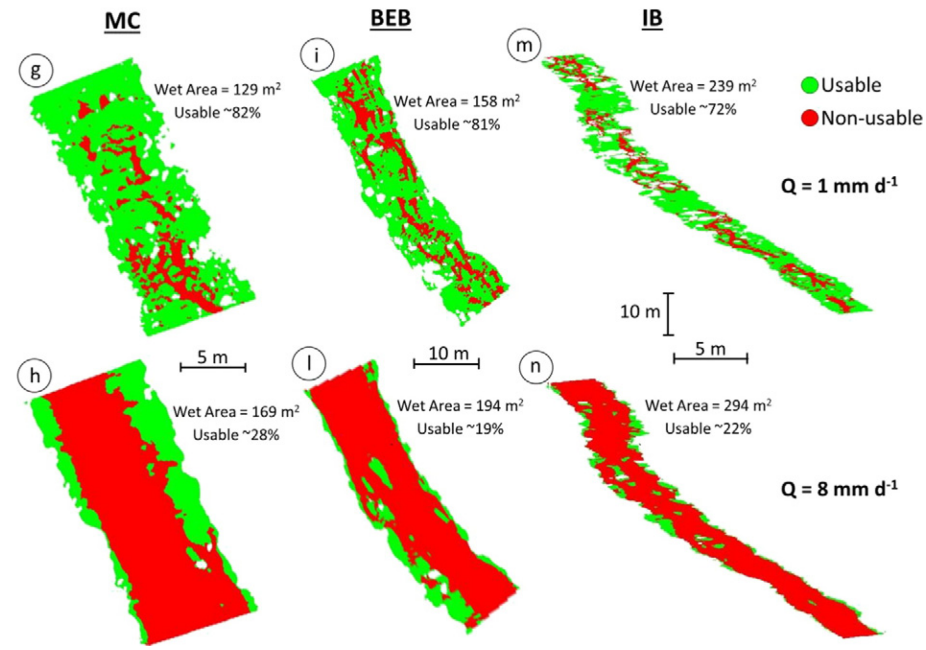

Fig. A.3. Usable and non-usable habitat under two contrasting flow conditions: one low (1 mm d^{-1}) and one high (8 mm d^{-1}) for MC, BEB, and IB.

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