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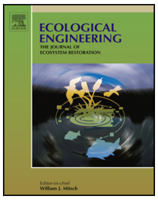

Importance of partial barriers and temporal variation in flow when modelling connectivity in fragmented river systems

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ABSTRACT

(1) The potential for catchment-scale connectivity modelling to help plan the restoration of connectivity in fragmented river systems is not yet well understood. In the present study the importance of two interrelated aspects of such modelling in determining predictions of connectivity are explored: (1) uncertainty in the passability of partial barriers (such as fish passes) and how the passabilities of series of partial barriers combine, and (2) temporal variation in connectivity due to flow.

(2) Connectivity for Atlantic salmon (*Salmo salar* L.) and European perch (*Perca fluviatilis* L.) are modelled under alternative restoration strategies in the heavily impounded Don Catchment UK using two different methods for simulating the combined passability of series of partial barriers. Catchment-scale hydraulic and connectivity modelling were integrated using a novel method to account for the effect of flow on connectivity, achieved by consideration of flow-fish pass efficiency relationships and the treatment of gaps between habitat patches as partial barrier.

(3) Modelled connectivity is very sensitive to uncertainty in barrier passability and the method used to simulate the combined passability of series of partial barriers. Flow also has a strong and complex effect on connectivity, with predicted temporal patterns being particularly dependent on how the combined impact of series of barriers is modelled. The sensitivity of the modelling constrains its capacity to predict the outcome of alternative connectivity restoration strategies. Nevertheless it does serve as a tool to think critically about connectivity restoration. If applied thoughtfully in full awareness of its limitations it can still be used assist in the planning and appraisal of alternative restoration options.

(4) The modelling also provides a number of important practical insights. It shows that series of fish passes may be ineffective unless they operate at very high efficiencies. Small changes to flow-fish pass efficiency relationships can have a large effect on temporal patterns in connectivity. Overall fish pass efficiency is comprised of attraction and passage efficiencies which may differ in the extent to which they are determined by random processes. This likely has significant implications for the nature of the combined passability of series of fish passes.

1. Introduction

River systems are prone to habitat fragmentation, with connectivity through these dendritic networks easily severed by common infrastructure such as dams and culverts (Fullerton et al., 2010). By constraining movement such barriers inhibit the feeding, breeding, sheltering and dispersal of riverine biota (Jungwirth et al., 2000). Populations isolated in habitat fragments become more vulnerable to random perturbations, are at risk of inbreeding depression, and are less likely to re-establish should they be extirpated (Morita and Yamamoto, 2002; Wiens, 2008). In extreme but not uncommon circumstances river barriers have caused significant population declines and even extinctions (Watters, 1996; Mallen-Cooper, 1999; Sheer and Steel, 2006).

As a consequence, river restoration often focuses on re-establishing river connectivity through barrier modifications such as fish pass installation, dam removal and deculverting. While these measures can bring about the dramatic recovery of impacted species (Meadows, 2001), numbers of barriers in river networks often far exceed the resources available for remediation. Decision

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makers must therefore prioritise the modification of barriers that will bring the most benefit (Bourne et al., 2011; Neeson et al., 2015; O'Hanley, 2011).

One approach to prioritising barriers for modification is the scoring-and-ranking method which scores the benefits (e.g. proportion of catchment upstream of barrier) and costs (e.g. financial outlay) associated with modification to individual barriers. However these approaches can be inefficient as they neglect important interdependencies between multiple barriers (O'Hanley and Tomberlin, 2005; Kemp and O'Hanley, 2010). Moreover their usefulness is limited as they provide little insight into the consequences of connectivity restoration (e.g. how interventions change habitat accessibility). As a result more sophisticated methods have been developed that account for barrier interdependencies at the catchment-scale by analysing river systems as spatial networks, calculating overall connectivity as a function of the connectedness of the river stretches that comprise the fragmented river network (Paulsen and Wernstedt, 1995; Kuby et al., 2005; O'Hanley and Tomberlin, 2005; Cote et al., 2009; Zheng et al., 2009; O'Hanley, 2011; McKay et al., 2013; Branco et al., 2014).

Although it is widely accepted that interactions between barriers should be accounted for when planning river connectivity improvements (Cote et al., 2009; Kemp and O'Hanley, 2010; Bourne et al., 2011; Segurado et al., 2013; Branco et al., 2014), doing so is far from simple. For pragmatic reasons a number of simplifications and assumptions are typically made, such as the treatment of the entire river network as having uniform habitat value, or the disregard of the dynamic nature of connectivity which varies temporally with flow as well as across species (Bourne et al., 2011; Branco et al., 2014). How such simplifications and assumptions determine the capacity of connectivity modelling to aid the planning of connectivity restoration is still poorly understood. In this paper we investigate the importance of two under-explored aspects of connectivity modelling at the catchment-scale: uncertainty in the passability of partial barriers and the interaction between them to determine catchment-scale connectivity, and how catchment-scale connectivity varies over time.

Many river barriers such as weirs and culverts are partial as a proportion of those individuals attempting to pass are successful. Just how passable partial barriers are, even with highly engineered connectivity enhancements such as fish passes, is often very uncertain (Bourne et al., 2011; Bunt et al., 2012; Noonan et al., 2012). Accordingly it is usually only possible to use rough estimates of partial barrier passability in connectivity modelling (e.g. McKay et al., 2013). There is also a lack of knowledge on how the passabilities of individual partial barriers combine to determine the total passability of a series of barriers (as might be traversed during migrations over longer distances), and how this should be represented in modelling (Kemp and O'Hanley, 2010). Commonly, this combined passability is calculated as the product of the individual barrier probabilities (e.g. Cote et al., 2009; Neeson et al., 2015; O'Hanley and Tomberlin, 2005; Padgham and Webb, 2010), and is an approach we term the 'cumulative method' (as the impact accumulates). However, Kemp and O'Hanley (2010) point out an alternative method could be to take the minimum barrier passability in a series of barriers, thereby assuming that all fish able to pass the most difficult barrier will have the swimming capability required to pass all subsequent barriers (termed the 'bottleneck method' in this paper).

Complicating matters further is the temporal dimension to connectivity (Bourne et al., 2011; Fullerton et al., 2010; Grantham, 2013). While this temporal variation has been neglected, especially at the catchment-scale, it is considered a significant research priority (Anderson et al., 2006; Fullerton et al., 2010; McKay et al., 2013; Stalnaker et al., 1996). Temporal variation in connectivity is often driven by flow (Fullerton et al., 2010; Grantham, 2013), which determines the distribution of habitat within river networks (Anderson et al., 2006), and also the passability of partial barriers such as weirs and fish passes (Armstrong et al., 2010; Ovidio and Philippart, 2002). Accounting for these relationships in connectivity modelling will help equip catchment managers with the ability to understand the consequences of different barrier modifications, flow manipulations and climate change.

The first objective of this paper is to investigate the significance of uncertainty in barrier passability and the use of the cumulative and bottleneck methods for modelling connectivity. Our second objective is to explore the importance of temporal variation in connectivity by making a novel modification to dendritic connectivity indices so that catchment-scale hydraulic modelling can be integrated with connectivity modelling. This enables us to examine flow mediated changes in connectivity and to consider the importance of doing so. Finally we discuss a number of important practical implications the modelling has for restoring connectivity in fragmented river networks.

2. Method

2.1. Case study catchment

The Don Catchment, north-east England, UK (Fig. 1) serves as the case study, in which we consider connectivity for Atlantic salmon (*Salmo salar* L.), an anadromous species; and European perch (*Perca fluviatilis* L.), a species which exhibits a degree of potamodromy (Lucas and Baras, 2008). The catchment covers about 1700 km^2, and includes the uplands of the Pennines in the west and lowlands in the east. At the downstream end the River Don flows into the River Ouse shortly before it discharges into the North Sea through the Humber Estuary. As the catchment is relatively small, daily rainfall variable, bedrock mainly sandstone, and rivers predominantly runoff fed, river flow can be quite flashy. The region's historical importance as a centre of metal working has resulted in the impoundment of the rivers by over 200 weirs (run-of-the-river low-head dams) which were mainly built to divert river water to water mills (Shaw, 2012). These structures are typically 1–3 m tall, with the incline of the downstream facing slope ranging from vertical to moderately steep (Shaw et al., 2016). By the 18th century impoundments and severe water pollution caused the extirpation of the formerly abundant salmon population (Firth, 1997). At the time of writing small numbers of adult salmon annually stray into the Don Catchment while attempting to return to their natal catchments, but are prevented by the weirs from completing spawning runs and potentially colonising the catchment. As water quality is now much improved, there is considerable interest in restoring connectivity in the catchment to facilitate the re-establishment of salmon and to increase the stability, abundance and distribution of populations of fish currently resident, such as perch. As is the case in many British catchments, weir removal is often not possible as those most downstream maintain water levels for river and canal navigation, and even redundant weirs retain heritage and other types of cultural value (for example some weirs are officially recognised as being of historical importance and are afforded protection from demolition (e.g. Historic England, 1985)). Furthermore removal is perceived as risking the disturbance of contaminated sediments and river bank collapse due to the loss of hydrostatic pressure that a reduction in river depth would bring. For these reasons the installation of fish passes is the preferred way to restore connectivity, with several passes already built on weirs and more planned.

2.2. Connectivity modelling

2.2.1. Overview

In common with a number of recent studies (e.g. Cote et al., 2009; McKay et al., 2013; Branco et al., 2014) we model the rivers in the Don Catchment as a dendritic ecological network

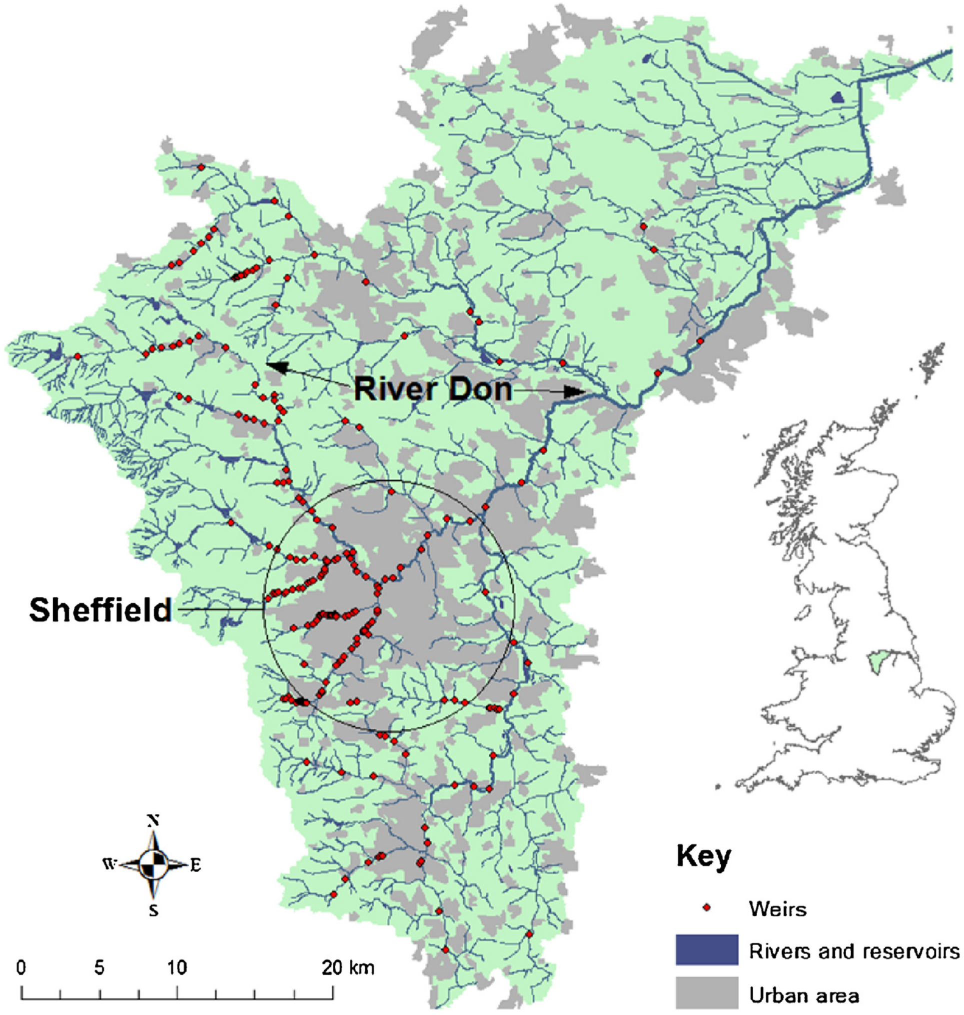

Fig. 1. Map of the Don Catchment showing the River Don, the city of Sheffield, and the distribution of weirs.

(DEN). Weirs, reservoirs, and culverts dissect the DEN into multiple subnetworks and pose complete or partial barriers to the movement of fish. The connectivity of the DEN is assessed through the calculation of two species-specific indices based on the mutual connectedness of these subnetworks for salmon and perch (Section 2.2.2). These subnetworks do not have equal habitat value so habitat is quantified using one-dimensional (1D) hydraulic modelling to map river area with potentially suitable flow conditions (Section 2.2.3). Barriers (including those with fish passes) are often partial as a proportion of fish attempting to pass fail due to intraspecific variation in swimming capability, heightened predation and competition at barriers, or the random chance that the best route to traverse a barrier happens to be taken (de Leaniz, 2008; Kemp and O'Hanley, 2010; Bourne et al., 2011). Hence barrier passability is represented as value between 0 (totally impassable) and 1 (all fish can pass) (Section 2.2.4). Connectedness of nonadjacent subnetworks is dependent on the combined passability of the series of barriers that separate them. This combined passability is modelled using the cumulative and bottleneck methods (Section 2.2.5). The connectivity indices are applied in a novel way to account for flow-mediated temporal variation in connectivity by relating river flow to barrier passability and the distribution of patches of habitat (Section 2.2.6). Insight is sought by exploring the modelling through alternative barrier modification scenarios in the Don Catchment (Section 2.2.7).

2.2.2. Connectivity indices

We define a salmon connectivity index that represents the proportion of the total spawning habitat in the Don Catchment that a migrating population of Atlantic salmon can access from the ocean (or indeed habitat accessibility in any dendritic network where access originates from a single point) as

$$\Omega = \frac{\sum_{i=1}^{n} c_i h_i}{\sum_{i=1}^{n} h_i} \times 100 \tag{1}$$

where i (1 to n) is the identifier of the subnetwork and of its bounding barrier immediately downstream, n is the number of subnetworks, h_i is the quantity of habitat within the subnetwork (and can be any measure as long as it is consistent), and c_i is the combined passability of barriers downstream of the subnetwork. The index produces a value between 0 and 100, which signifies the sum of all the habitat in the river network weighted by its accessibility, given as a proportion of the unweighted sum of all habitat, so that 0 and 100 indicate no and all habitat is accessible respectively. The equation is similar to the diadromous application of the Dendritic Connectivity Index (DCI_d) developed by Cote et al. (2009).

The little information that exists on the movement of perch through river systems suggests that the species exhibits a degree of migratory behaviour (Lucas and Baras, 2008). It is more difficult to assess the impact of barriers on sedentary and potamodromous fish, as often their connectivity requirements are less demanding and more flexible than diadromous fish. Consequently, rather than obviously preventing migration, the impact of habitat fragmentation can be more insidious; curtailing feeding, breeding, sheltering and dispersal, and increasing inbreeding (Jungwirth et al., 2000; Morita and Yamamoto, 2002). In such circumstances it is therefore appropriate to use a general metric of river connectivity. To assess connectivity in the Don Catchment for perch we use the potamodromous application of the Dendritic Connectivity Index (DCI_p) (Cote et al., 2009), which is a function of the connectedness of every potential pairing of the river subnetworks *i* and *j*:

$$DCI_p = \sum_{i}^{n}\sum_{j}^{n} c_{ij}\frac{h_i}{H}\frac{h_j}{H} \times 100 \qquad (4)$$

where H is the habitat weighted length of the river network, and c_{ij} is the combined passability of the barriers between subnetworks *i* and *j*.

2.2.3. Quantity of habitat (q_i)

Atlantic salmon spawn exclusively in high energy rivers (Fleming, 1997), while perch prefer to live in slower flowing rivers and lakes (Lucas and Baras, 2008). Potential habitat was mapped for spawning salmon and fully grown perch using a one-dimensional (1D) hydraulic–habitat model. While two-dimensional models can produce more detailed habitat maps, they require high resolution topographical data and longer run times which typically restricts their application to river reaches of only a few km in length (Jowett and Duncan, 2012), making their use infeasible at catchment-scales.

Habitat mapping followed the same principles applied in PHABSIM (Waddle, 2001). Validated 1D hydrodynamic models employed by the Environment Agency of England and Wales (EA) for flood modelling in the Don Catchment were run in the software HEC-RAS (Brunner et al., 2001) to produce estimates of velocity and depth at channel cross sections. These were typically spaced approximately 100 m apart, an adequate resolution as reach lengths of 500 m appear to be sufficient to map the spatial distribution of river habitat (Rivas Casado, 2006). The models consisted of 1388 river cross sections and covered the main rivers in the Don Catchment (see Fig. 2).

The 1D velocity and water level output of HEC-RAS were converted to depth and velocity profiles using the channel geometry and Manning's equation (Waddle, 2001). The width of river cross section with a velocity and depth of flow spawning salmon and adult perch have been observed to utilise (Fig. 3a; Bullock et al., 1991; Armstrong et al., 2003) could then be estimated (Fig. 3b). Habitat quantity (h) at each river reach was calculated as the mean width of habitat at the bounding cross sections multiplied by the reach length.

Fig. 2. Coverage of hydraulic models and expected distribution of unsuitable substrate for spawning.

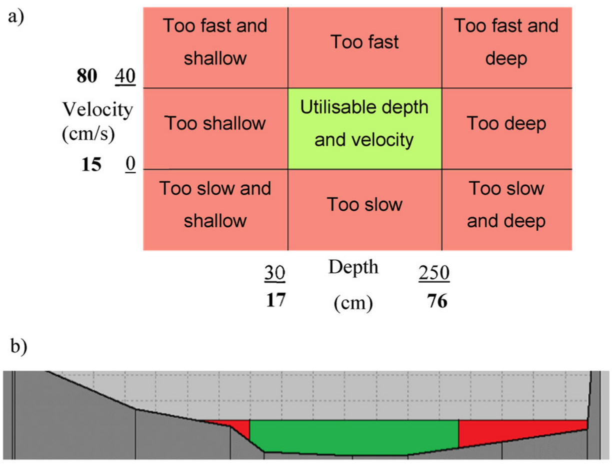

Fig. 3. (a) Reported flow conditions used by salmon for spawning (bold) and by adult perch (underlined) (Armstrong et al., 2003). (b) Width of a river cross section with flow conditions within the range salmon have been observed to utilise for spawning (in green). (For interpretation of the references to color in figure legend, the reader is referred to the web version of the article.)

Q10, Q20... to Q50 flows (the 10th, 20th... to 50th flow percentiles) were used to map salmon spawning habitat as spawning has been recorded to occur within this range of flows (Gibbins et al., 2002; Webb et al., 2001). Adult perch are found in rivers year round so habitat was mapped for Q10, Q20... to Q90 flows. Flow values were obtained from the CEH National River Flow Archive (http://www.ceh.ac.uk/data/nrfa/index.html) for five flow gauges in the Don Catchment. The two smallest rivers had no flow gauges and so flow was estimated using the ratios of spate flows between rivers calculated using Flood Estimation Handbook methods (JBA, 2007).

Further steps were taken to refine the mapping of potential salmon spawning habitat. Suitable flow conditions for spawning dissected by unsuitable mid-channel flow were discounted as salmon construct redds mid-channel (de Gaudemar et al., 2000). We also ruled out reaches where we had a high degree of certainty that the dominant substrate was unsuitable for salmon spawning (i.e. sand, silt or clay (Fig. 2)), as gravel beds are required for spawning (Armstrong et al., 2003; Hendry et al., 2003).

2.2.4. Barrier passability (z)

Before the recent installation of a fish pass the most downstream weir on the Don was known to be largely impassable to salmon as they were observed to congregate below the structure. At ~2 m the height of this weir is similar to many others in the Don Catchment and to those that were found to be largely impassable to salmonids by Ovidio and Philippart (2002) in tributaries of the Meuse River. Yet large salmonids can on occasion pass weirs of a similar height (Ovidio and Philippart, 2002) and there have been the odd anecdotal report of salmon being seen upstream of this barrier. It is impossible to assign an accurate passability value to all weirs without fish passes, but to acknowledge there is a small degree of permeability we treat weirs without fish passes as preventing all but 10% of migrating fish from passing.

The degree to which the installation of a fish pass will increase barrier passability is not well known (Bunt et al., 2012; Noonan et al., 2012). The mean of published efficiencies for fish passes used by salmonids in an upstream direction is 62%, but fish pass efficiencies can range from 0 to 100% (Noonan et al., 2012). Sensitivity of the connectivity modelling to uncertainty in fish pass efficiency was investigated for both the salmon and perch connectivity indices by assigning a range of passabilities from 10 to 100%. These are represented in the connectivity modelling by the term z, which is the species-specific passability score of each barrier, where the passability is rescaled to a value between 0 and 1. The perch DCI_p requires z values for the negotiation of barriers in both an upstream and downstream direction. While in reality these passabilities may well be very different, for the purpose of investigating sensitivity we assume symmetry.

2.2.5. Combined impact of consecutive barriers (c_i)

Atlantic salmon will need to traverse consecutive partial barriers during migration, and the combined effect of these barriers is represented in the modelling by the term c_i. How consecutive barriers combine to impact on migrating fish is unknown, and so we test the cumulative and bottleneck methods discussed in the introduction. The cumulative method treats each consecutive barrier as removing a proportion of the remaining population thereby expressing the chance some fish will fail to ascend a barrier (e.g. due to the random processes such as the chance that a fish happens to find the entrance to a fish pass) and not factors linked to variation amongst individual fish (e.g. maximum swimming speed, condition), so that:

$$c_i = \prod_{i=1}^{n} z_i \tag{2}$$

where z_i is the species-specific passability score of each barrier which represents with a number between 0 and 1 the proportion of all fish attempting to traverse a barrier that succeed. Consecutive barriers have been treated this way by Cote et al. (2009) to calculate c_{ij} for the DCI_p and by a number of other researchers (e.g. O'Hanley and Tomberlin, 2005; Nunn and Cowx, 2012). In contrast the bottleneck method represents intraspecific variation in ability of fish to pass a barrier (e.g. differences in maximum swim speed). It assumes that all fish capable of traversing a barrier of a certain difficulty to pass will be capable of passing all subsequent barriers of the same difficulty or less. Therefore the combined passability of a series of barriers is equal to the passability of the barrier most difficult to pass, so that (Cote et al., 2009; Kemp and O'Hanley, 2010):

$$c_i = \min(z_i) \tag{3}$$

2.2.6. Temporal variation

To explore the importance of accounting for temporal variation we modelled flow-mediated changes in daily connectivity for salmon and perch. Connectivity is dependent on flow as not only is it an important determinant of the distribution of habitat patches within a river network (and so the distance between them), but it is also a factor regulating the passability of weirs and the efficiencies of fish passes. As flow increases the head of a weir decreases as it 'drowns out', and the depth of water flowing over the face and at the foot of the weir increases, all of which can improve the ability of fish to pass (Keller, 2010; Ovidio and Philippart, 2002).

In the Don Catchment local opinion is that the larger weirs become passable to salmon during river spates, but not perch, which are slower swimmers (Webb, 1975). Table 1 presents a relationship we created to broadly represent how flow affects weir passability for salmon and perch. We include the impact of provision of fish pass, as pass efficiency also varies across flow. Though flow-fish pass efficiency relationships are currently something that cannot be accurately predicted (Noonan et al., 2012), fish passes can be designed to operate most effectively over certain flow conditions (Beach, 1984; Office of Technology Assessment, 1995). We created generalised flow-efficiency relationships for two hypothetical fish pass types: 'conventional' and 'high-flow' types. These relationships are approximations chosen to illustrate how potential fish pass designs can influence the effectiveness of different restoration strategies, as well as to explore how the flow-efficiency relationships determine temporal variation in connectivity.

The conventional type represents fish pass types such as Denil passes, where adequate flow is required to provide sufficient in-pass depth and velocity (Office of Technology Assessment, 1995). However, as flow increases so does velocity, which can overcome the swimming capacity of fish attempting to ascend the pass (Beach, 1984). For salmon the efficiency of the conventional fish pass is assumed to increase with flow between the Q90 and Q10 flows (which covers the EA recommended fish pass operational flows for salmon (Armstrong et al., 2010)) and converges with the weir passability when the fish pass is treated as drowning out. Efficiency also increases with flow for perch, but drops under higher flows due to the lower swim speeds of perch. To offer a contrast to the conventional type we include the high flow fish pass which increases the passability of a weir only above the Q30 flow (it could for example be positioned at a higher elevation so that it is wetted only during high flows). While these flow passability relationships are conceptual they allow us to show how fish pass design considerations affect temporal patterns in connectivity.

Accessibility of salmon spawning habitat and the perch DCI_p were calculated across a hydrograph of daily flows from 1976 to 1977 (years chosen to include a wide variation in flows). We used full annual hydrographs as salmon are known to enter many British river systems (e.g. the Tay and the Tweed) year round (Shearer, 1992). Accessibility of spawning habitat for salmon was calculated using both the cumulative and bottleneck methods. The status quo scenario represents the current situation, to which the Don scenario is contrasted using the conventional and high flow fish pass types. No other weir modification scenarios were examined as each will

Table 1
Flow-passability relationship used to specify passabilities of weirs.

Flow	Weir passability (z_i)					
	Salmon			Perch		
	Without fish pass	Conventional fish pass	High-flow fish pass	Without fish pass	Conventional fish pass	High-flow fish pass
Q10	0.9	0.9	0.98	0	0.1	0.3
Q20	0.5	0.9	0.95	0	0.4	0.6
Q30	0	0.9	0.9	0	0.6	0.1
Q40	0	0.7	0.3	0	0.8	0
Q50	0	0.6	0	0	0.7	0
Q60	0	0.5	0	0	0.6	0
Q70	0	0.3	0	0	0.5	0
Q80	0	0.3	0	0	0.4	0
Q90	0	0.3	0	0	0.3	0

produce the same temporal patterns in connectivity as all share the same flow-fish pass efficiency relationships.

We made two applications of the perch DCI_p: the 'weir application' where the status quo scenario was compared to the Don Scenario using conventional and high flow fish passes, and the 'habitat gaps application' where discontinuities in flow conditions utilised by perch served as partial barriers (i.e. lengths of river where flow conditions occur outside the depth and velocity ranges usually utilised as habitat by perch pose partial barriers to movement). The latter application includes a DCI_p calculated by treating only habitat gaps as barriers, and a DCI_p that counts habitat gaps and weirs as barriers. These applications illustrate how the effect of flow-mediated discontinuities in habitat on connectivity may be modelled at the catchment-scale.

Little is known about how discontinuities in habitat affect connectivity, though perch may be less inclined to travel large distances as there is some evidence that even natural habitat gaps in apparently well connected freshwater ecosystems can inhibit movement (Gerlach et al., 2001; Bergek and Björklund, 2009). We assume that most gaps in habitat pose less significant obstacles than weirs, and that passability declines gradually with gap length, more quickly at first and then more slowly. The following expression was chosen to reproduce these assumptions and assign a passability score to each habitat gap:

$$z = 0.99^{g_l/50} \tag{6}$$

where g_l is the length of the gap in meters. Other expressions can be used as research reveals how fish respond to habitat discontinuities.

2.2.7. Scenarios

To investigate whether uncertainty in barrier passability and the nature of the interaction between multiple barriers can affect the relative attractiveness of alternative management options, four scenarios to restore connectivity in the Don Catchment were compared. Rather than seeking to identify a specific barrier prioritisation strategy (which we would do if we were trying to find the most efficient approach to restoring connectivity), scenarios were chosen to correspond with local interest in restoration strategies (e.g. Don Catchment Rivers Trust, 2013), to fall within the area covered by the hydraulic modelling, and to offer contrasting numbers and location of barriers modified. In addition to the status quo scenario (Fig. 4a), which includes 13 fish passes already in existence, three other scenarios were analysed. The first was the installation of eight fish passes; two on weirs on the Don and six on the Rother (the Rother scenario; Fig. 4b), the second 19 fish passes on weirs up the Don and then on the Loxley (the Loxley scenario; Fig. 4c), and the third 30 fish passes on weirs on the Don (the Don scenario; Fig. 4d).

3. Results

3.1. Distributions of habitats

The hydraulic habitat assessment indicated that the majority of the potentially suitable spawning habitat for salmon is scattered around the upper reaches of the catchment, especially those draining uplands in the west (Fig. 5a). Potential habitat for adult perch (Fig. 5b) was also found to be widely spread, though the majority is located in the downstream half of the catchment.

3.2. Sensitivity to barrier passability

The output of the salmon connectivity modelling for the Don Catchment connectivity enhancement scenarios was found to be very sensitive to fish pass efficiency (Fig. 6), with the best result for the Don scenario being 29 times greater than the worst result. Furthermore sensitivity was greatest when the combined effect of the fish passes was treated as being cumulative, particularly when fish pass efficiencies were between 80% and 100%. Sensitivity is also dependent on the scenario, with the Don scenario greatly out performing all other scenarios when efficiencies are greater than 90%, but performing marginally worse than other scenarios under low efficiencies. In contrast, when the combined effect of fish passes are treated as being bottleneck then the Don scenario always performs the best regardless of pass efficiency.

The perch DCI_p is also sensitive to variation in fish pass efficiency, but to a lesser degree, with the best result for the Don scenario being twice as large as the worst result (Fig. 7). Again sensitivity was greater at higher fish pass efficiencies. While the Don and Status quo scenarios were consistently the best and worst respectively, differential sensitivity amongst the scenarios resulted in the Loxley scenario appearing the second best under high efficiencies and second worst under low efficiencies.

Fig. 8 shows the incremental gains in spawning habitat accessibility for each additional fish pass installed on the Don, starting at the downstream end and working up the river. It makes clear the strong effect multiple partial barriers can have if their combined impact is cumulative. When fish pass efficiency is 50% then there is almost no gain in habitat accessibility irrespective of the number of fish passes installed, while a fish pass efficiency of 90% brings good but diminishing returns, and 100% results in increasing returns. The use of the bottleneck method generates increasing returns for all fish pass efficiencies.

3.3. Temporal variability in connectivity

The accessibility of salmon spawning habitat varies greatly with flow (see Fig. 9). For both the status quo and the Don scenarios there are long periods of limited connectivity, interspersed with short spells of high connectivity associated with high flows. However the nature of the temporal variation is highly dependent on the combined effect of the barriers and the fish pass type.

When the combined effect of the barriers is simulated with the cumulative method and a conventional fish pass is used then there is almost no difference between the performance of the status quo scenario and the Don scenario. However the high-flow fish pass provides far better results, but only during the periods of high flow (see Fig. 9a).

A somewhat different result is produced when the combined effect of the barriers is simulated with the bottleneck method. The Don scenario performs marginally better than the status quo when the high-flow fish pass is used, but the conventional fish pass performs particularly well during low to intermediate flows (see Fig. 9b).

The perch DCI_p also varies greatly through time (see Fig. 9c). The Don scenario yields an improvement in connectivity compared to the status quo, but only when the conventional fish pass is used and during intermediate flows. When the Don scenario is implemented using the high flow fish pass (which involves treating existing fish passes as the high flow type) then for the majority of time connectivity is lower than the status quo scenario. There are however short periods associated with high flows when connectivity is greater than the other scenarios.

When the perch DCI_p is calculated (with gaps between river habitat with suitable flow conditions posing partial barriers) (see red line, Fig. 9d), patterns in connectivity emerge that are different to when weirs alone are treated as barriers (Fig. 9c). Indeed the highest connectivity occurs during periods of low flow. When habitat gaps and weirs are both treated as barriers (see blue line, Fig. 9d) then an intermediate result is produced, though the pattern is more similar to the weir only applications in Fig. 9c.

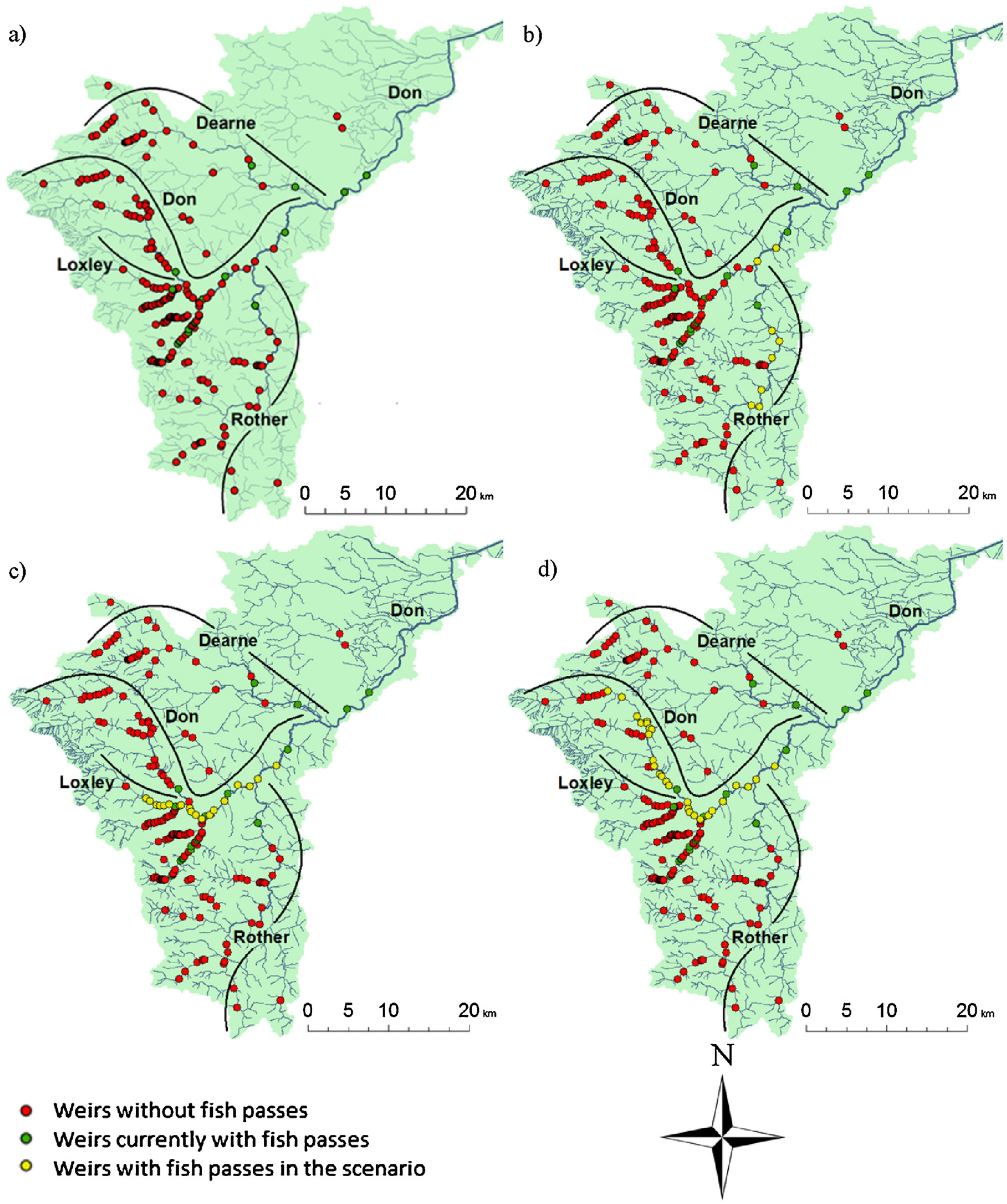

Fig. 4. The four weir modification scenarios used to explore the connectivity modelling. (a) The status quo scenario, (b) the Rother scenario, (c) the Loxley scenario, (d) the Don scenario.

4. Discussion

4.1. River connectivity modelling as an aid for planning connectivity restoration

Restoring connectivity in fragmented river networks is challenging. River barriers are often numerous and resources and options for mitigation limited. River connectivity modelling would provide a valuable tool if it could be used to explore what interventions are required to re-establish extirpated migratory fish alongside improving connectivity for resident species. However this study has demonstrated that the output of such modelling in the Don Catchment is very sensitive to uncertainty in barrier passability and how the impact of barriers combine. Both these

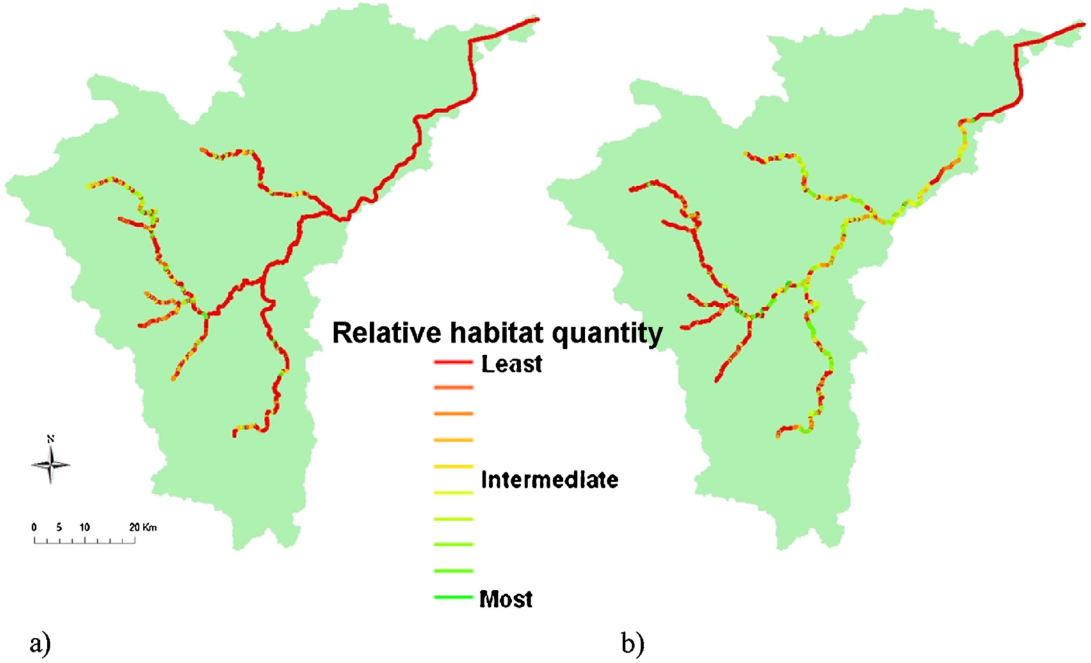

Fig. 5. Relative quantity of potential salmon spawning (a) and adult perch (b) habitat.

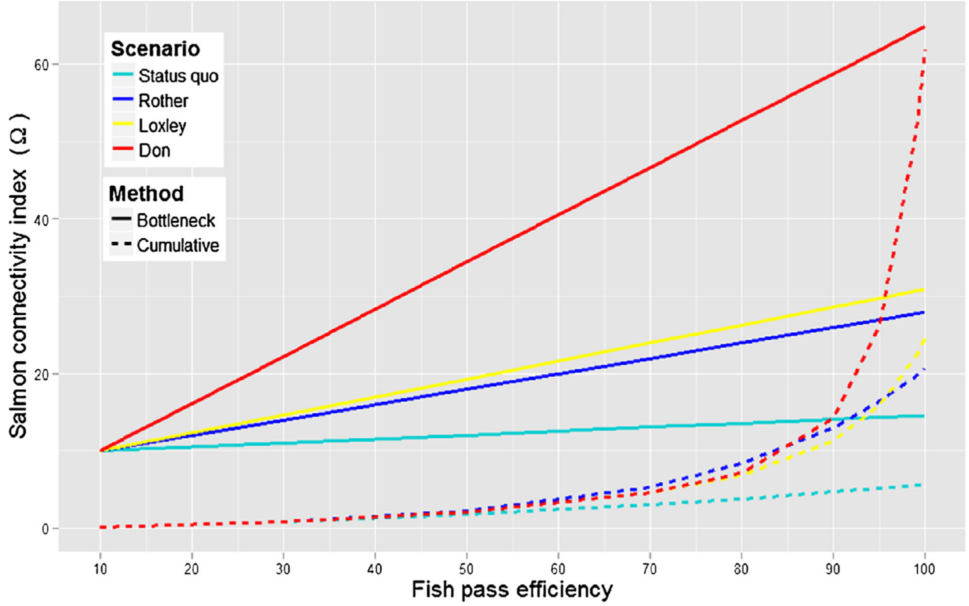

Fig. 6. Salmon connectivity index (Ω) calculated for the four weir modification scenarios when fish pass efficiencies are 10, 30, 50, 70, 80, 90, 95, 99, and 100%. The combined impact of consecutive barriers is modelled using both the cumulative and bottleneck methods.

modelling aspects are not understood well enough to be included with sufficient accuracy for us to confidently predict what barrier modifications are required to allow the re-establishment of salmon. In catchments like the Don that have series of partial barriers, even small changes to estimated barrier passability can determine which restoration strategy appears most attractive or whether the re-establishment of an extirpated species seems feasible or not.

Model sensitivity to barrier passability is dependent on the nature of the combined effect multiple partial barriers have on connectivity, with sensitivity being much greater when the combined impact is cumulative. It seems reasonable however to argue that series of partial barriers may in reality have an impact that is somewhere between the impacts simulated by the bottleneck and cumulative methods. The maximum swim speed of a fish is correlated with body length (Beach, 1984), and as there can be considerable intraspecific variation in body length in a cohort of migrating fish (Jonsson et al., 1991) so must there be in swim speed. Ovidio and Philippart (2002) observed that in tributaries of the Meuse River some barriers were only ascended by larger individuals. Therefore certain partial barriers do appear to selectively obstruct the weakest swimmers. Presumably the stronger swimmers that pass will on some occasions be able to negotiate subsequent barriers of a similar difficulty to pass. Yet some fish fail to ascend barriers due to factors not linked to swimming ability (e.g. whether a fish happens to find the entrance to a fish pass), and exhaustion due to repeated expenditure of energy traversing barriers. Both phenomena are known to occur during fish migrations (Booth, 1998; Armstrong et al., 2010; Bunt et al., 2012). Unless

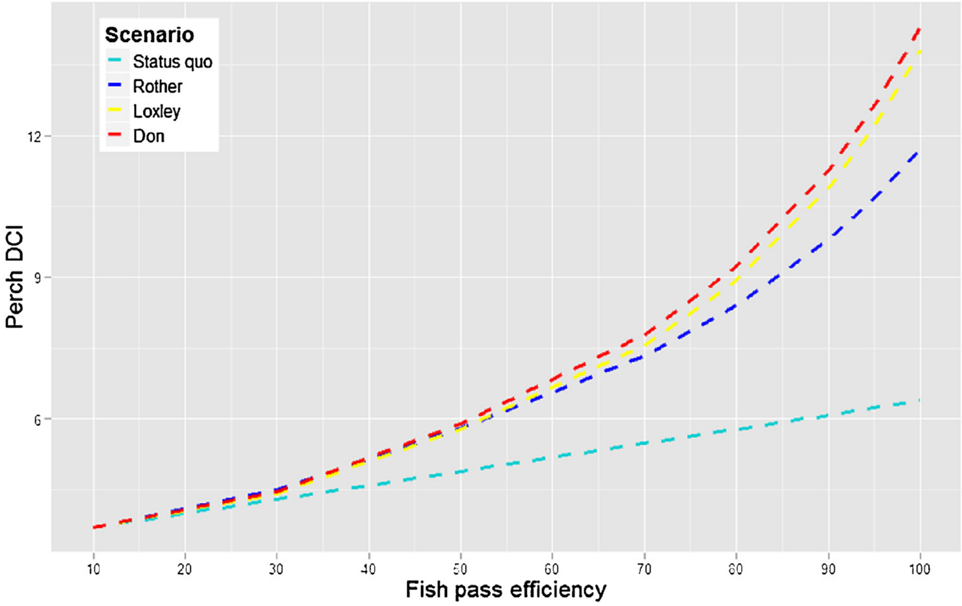

Fig. 7. Perch DCI$_p$ calculated for the four weir modification scenarios when fish pass efficiencies are 10, 30, 50, 70, 80, 90, 95, 99, and 100%.

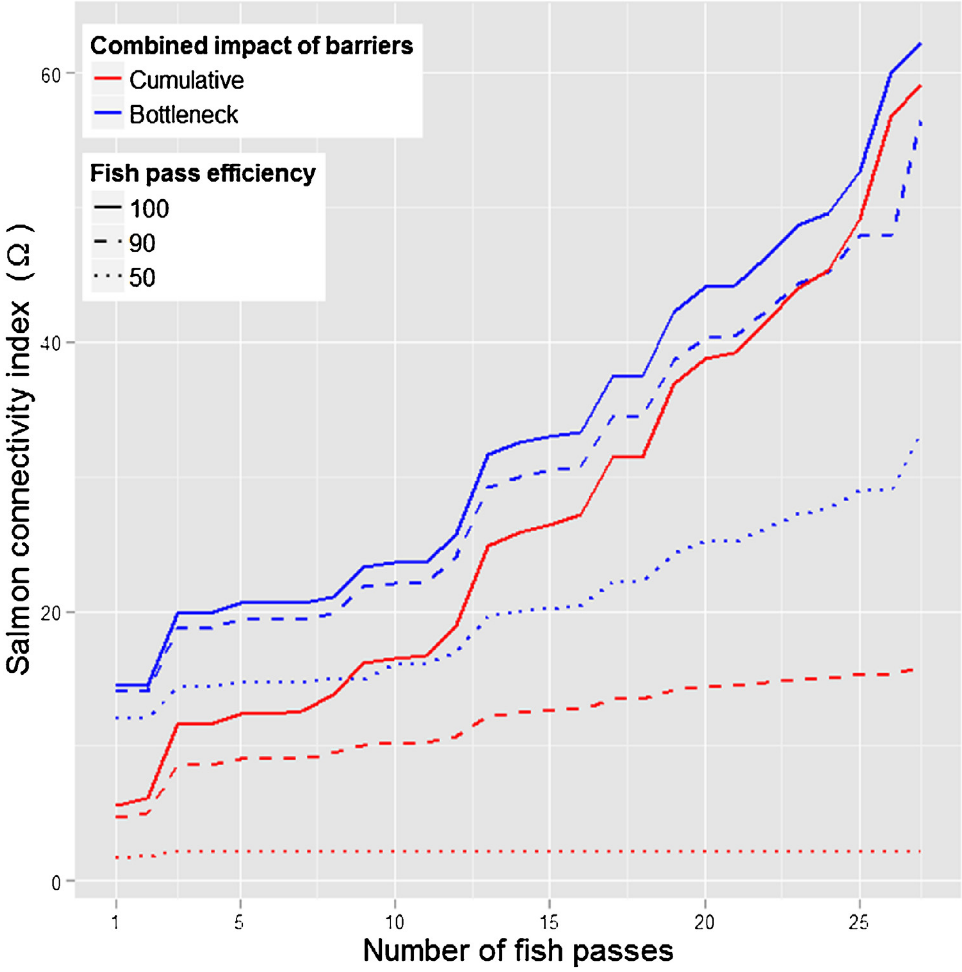

Fig. 8. Incremental increase in the salmon connectivity index (Ω) for each additional fish pass installed as part of the Don scenario, starting at the downstream end and working upwards. The index is calculated using fish pass efficiencies of 50, 90 and 100%, and combined impact of consecutive barriers is modelled using both the cumulative and bottleneck methods.

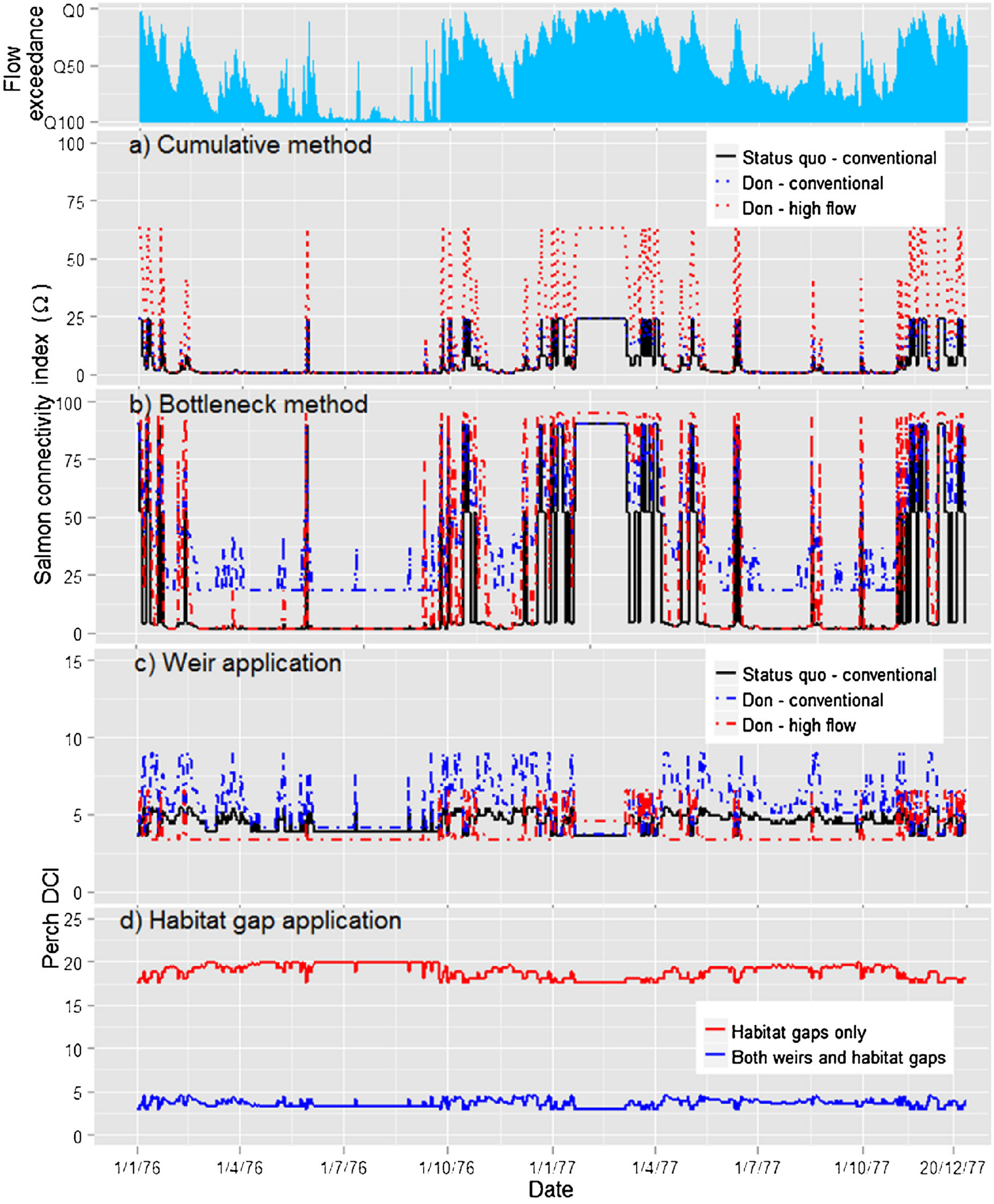

Fig. 9. Flow mediated temporal variation in the salmon connectivity index (Ω) and the perch dendritic connectivity index (DCI_p) for the years 1976 to 1977. The top panel shows flow exceedance. (a & b) The salmon connectivity index calculated using the cumulative and bottleneck methods of modelling the combined effect of consecutive weirs. Each shows the status quo scenario using the conventional fish pass and the Don scenario using both the conventional and high flow fish passes. (c) The perch DCI_p calculated for the status quo scenario using the conventional fish pass and the Don scenario using both the conventional and high flow fish passes. (d) The perch DCI_p calculated for the status quo scenario treating habitat gaps as barriers and weirs and habitat gaps as barriers.

this cumulative component of the combined impact is slight it is probable that any modelling of connectivity across series of partial barriers will be sensitive to uncertainty in barrier passability.

The degree to which sensitivity to uncertainty in barrier passability curtails the usefulness of connectivity modelling depends on context. The circumstances in which it can be used with confidence to plan the restoration of extirpated diadromous species include catchments where the series of partial barriers that must be traversed are short or do not have a significant cumulative effect, or where barriers can be removed. Unfortunately when more than a few partial barriers must be negotiated sensitivity becomes an issue, something which cannot currently be offset with the use of more accurate passability values for partial barriers such as culverts, weirs, and fish passes, due to our inability to accurately predict the passability of such structures (Ovidio and Philippart, 2002; Bourne et al., 2011; Noonan et al., 2012). Thus the capacity of connectivity modelling to differentiate between the value of alternative intervention strategies or to assess the viability of re-establishing extirpated species will often be limited.

The situation for potamodromous fish such as perch is somewhat different to diadromous species as these can have more flexible migratory requirements and many are able to persist in fragmented river networks. Some such as the European bullhead (*Cottus gobio*) are fairly sedentary, though even populations of this species have mobile individuals (Knaepkens et al., 2005). Partial migration is now recognised as widespread amongst fish, with populations frequently being comprised of both resident and migrant contingents (Chapman et al., 2012b). There appears to be a number of causes of partial migration, including temporal heterogeneity in predation pressure and competition for resources (Chapman et al., 2012a) and it is increasingly clear that fish exhibit diverse inter- and intraspecific connectivity needs (Chapman et al., 2012b). As a consequence both the fragmentation and restoration of connectivity in river networks can have species-specific ramifications that are hard to predict or quantify, such as by increasing gene flow or population stability. Given this complexity a simple index such as the potamodromous application of the DCI (Cote et al., 2009) may be an appropriate way to assess connectivity. Unlike the salmon connectivity index however, which is clearly linked to habitat accessibility, the DCI_p is more difficult to interpret in terms of what implications changes to the index have for the target species. This is apparent with the sensitivity of the DCI_p to uncertainty in barrier passability. While the sensitivity of the salmon connectivity index results in changes in the value of the index that clearly translate into different degrees of habitat accessibility for salmon, this is not the case for perch.

Numerous papers and guidance for fish passes have highlighted the importance of temporal variation in connectivity (Armstrong et al., 2010; Fullerton et al., 2010; Grantham, 2013). We present simple but novel applications of the connectivity indices to explore the significance of flow-mediated variation in connectivity. This was achieved by considering how the efficiency of fish passes and passability of weirs change with flow, and by utilising catchment-scale hydraulic modelling to identify gaps in habitat and treat them as partial barriers. Fish distributions are thought to be sometimes structured as metapopulations (Dunham and Rieman, 1999; Schtickzelle and Quinn, 2007; Fullerton et al., 2010), where patches of suitable river habitat can be colonised, and populations inhabiting patches can become extinct. Colonisation and extinction are both a function of patch size and its connectivity with other patches (Kareiva et al., 1990). Our approach offers a way by which these dynamics can be accounted for in modelling and could be developed further to advance the understanding of fish metapopulations.

The temporal modelling also demonstrates that flow can have complicated and significant effects on connectivity that need considering to help ensure connectivity restoration is effective. Our results show temporary periods of high connectivity that are strongly dependent on how barrier passability changes with flow. However, again our capacity to bring this temporal dimension into connectivity modelling is impaired by sensitivity to uncertainty in barrier passability and how the passabilities of multiple barriers combine. The two fish pass types produce very different results conditional on whether the cumulative or bottleneck methods are used to simulate the combined impact of the barriers. We found very little in the literature regarding how fish pass efficiency responds to flow, but this information is urgently required if catchment managers are to coordinate fish passes so that they provide simultaneous windows of high connectivity during periods of migration.

The different temporal patterns in connectivity that emerge when the perch DCI_p is calculated by treating habitat gaps rather than weirs as barriers shows how connectivity can be variable even without the presence of physical obstructions, and these patterns may be dissimilar to those produced by impoundments. While for the purposes of our modelling we assumed that gaps in habitat form a weak barrier to longitudinal movement through river networks, there is little information about how fish respond to such habitat discontinuities. Alternatively other flow attributes such as minimum depth (e.g. as Grantham (2013) used for steelhead trout (*Oncorhynchus mykiss*)), maximum flow velocity, or other forms of barrier produced by water chemistry, temperature, noise, illumination, or a lack of cover may be more appropriate. Again interpreting the significance of the variation in the perch DCI_p is difficult. More work is required to investigate how changes to such connectivity indices reflect real changes to fish distributions and population attributes. There is significant scope for the customisation of these indices to the connectivity needs of specific species or even population contingents, based for example on the size of habitat fragments, mobility of fish, or the degree of gene flow needed to avoid inbreeding.

Due to an absence of relevant information and the need for a pragmatic approach many simplifications must be made when modelling connectivity. This is especially the case in this study, where the objective was to investigate the importance of barrier passability and temporal variation rather than produce accurate predictions for the Don Catchment. Major simplifications include the treatment of all barriers as equal, and barrier passabilities as symmetrical in an upstream and downstream direction when calculating the perch DCI_p. The insensitivity of the modelling when using the cumulative method to changes in barrier passability below that are below 90% means that the assumption that weirs without fish passes have a passability of 10% is not of consequence. However, when the bottleneck method is used this assumption is more important as it sets the minimum potential value of an index (i.e. all DENs will have a value that is 10% or greater). The habitat mapping is another simplistic element of the modelling, but it served our purpose of producing a map that was approximately representative of the true distribution of habitat for salmon and perch. We believe we achieved this as the mapped habitat is consistent with knowledge that salmon spawn in fast flowing rivers (Armstrong et al., 2003) such as that in the poorly connected subnetworks in the upper parts of the Don Catchment, whereas perch prefer slower flows (Petts et al., 2016) such as those found in the lower parts of the catchment. It was not possible to validate the habitat maps as the salmon was extirpated hundreds of years ago and there is a paucity of data recording the distribution of perch. If decisions are to be made on the basis of connectivity modelling then serious consideration must be given to additional factors that determine habitat quality such as water and sediment quality, especially in a highly urbanised and formally industrial catchment like the Don. Another factor not accounted for but which probably strongly influences temporal variation in connectivity is water temperature, as this has a major role in determining fish swimming ability (Beach, 1984).

4.2. Practical implications

The modelling in the present study has a number of important implications for restoring connectivity in fragmented river networks. As discussed it is likely that series of partial barriers have to some degree a cumulative effect, and that unless very small this will rapidly diminish populations of migrating fish. Therefore programmes to restore connectivity for migrants that need to negotiate series of barriers must ensure that this cumulative impact is minimal. There is little scope for compromise. In the Don Catchment for example, even when fish passes are 95% efficient, if there is a cumulative impact where 5% of the migration is lost per weir then the accessibility of spawning habitat is half that when efficiency is 100%. When 10% or more of the population is lost per weir then results are very poor. Such a cumulative impact may be why efforts to restore Atlantic salmon populations on the US Atlantic coast have not yielded self-sustaining populations despite significant investment in fish passage (Brown et al., 2013). A review by Noonan et al. (2012) found that mean fish pass efficiency for salmonids moving upstream was only 61.7% showing that inefficient fish passes are common. Yet Noonan also notes that passes with efficiencies of 100% did exist, meaning it may be possible to avert the threat posed by inefficient passes. Nonetheless, simply removing barriers should be preferred over fish pass installation as this guarantees complete restoration of connectivity, though the scope for this is limited in many British river networks.

The results also have implications for fish pass choice and design. Overall fish pass efficiency can be divided into attraction efficiency and passage efficiency (Kemp and O'Hanley, 2010). The former is the percentage of fish that move close enough to a fish pass that they detect the entrance (Aarestrup et al., 2003), whereas passage efficiency is the percentage of fish attempting to negotiate a pass that succeed (Bunt et al., 2012). If, as we hypothesise, random chance rather than intraspecific variation in swimming ability drives fish success in finding the entrance to a fish pass, series of passes with attraction efficiencies less than 100% will have a cumulative impact. The review of fish pass efficiencies by Bunt et al. (2012) found that attraction efficiency was usually below and often much lower than 100%, so poor attraction efficiencies could commonly cause series of fish passes to have a cumulative impact. In comparison passage efficiency is likely to not only be dependent on random processes but also fish swimming ability, meaning efficiencies <100% could result in an impact intermediate between the cumulative and bottleneck impacts. This is because while some fish can become disorientated within fish passes (Haro and Kynard, 1997) (in which case successful negotiation may be down to luck), intraspecific variability in swimming ability can also be important (Kemp and O'Hanley, 2010). Both attraction and passage efficiencies vary widely within and across fish pass types, and there may even be a trade-off between them (Bunt et al., 2012). For example Bunt et al. (2012) noted that nature-like fish passes had high passage efficiencies but lower attraction efficiencies, possibly due to their low gradients which mean they are easy to ascend but do not draw large flows. Therefore an overall measure of fish pass efficiency can mask very important differences in attraction and passage efficiencies. Fish pass selection and design should prioritise the improvement of efficiency by attempting to minimise processes that cause passage failure at random, thereby reducing the potential for cumulative impacts. Catchment managers should also be aware of the negative impact certain types of river infrastructure (e.g. hydroelectricity schemes, Larinier, 2008) have on attraction efficiencies as the impact could be more detrimental than is currently recognised. Older fish passes often use less sophisticated designs and can have lower efficiencies (Larinier, 2008) and so it may also be necessary to review and replace existing fish passage facilities.

Another potential implication of the results regards the unassisted recolonisation by migratory species of rivers from which they have been extirpated. Every year the numbers of salmon that stray into the Don Catchment when attempting to return to their natal catchment are small, though it is hoped that when connectivity is restored such strays will spontaneously recolonise the catchment. However, if fish passes have more than a very small cumulative impact then it is possible that the population of immigrant fish will be depleted before it can reach good quality spawning habitat. In such circumstances stocking may be necessary to establish a viable population.

Further insight is provided by the temporal modelling. In the Don high flows provide a window of opportunity during which salmon can exploit increased connectivity. As a consequence decision makers must ensure that windows of high connectivity are sufficiently long to allow migration to occur. To do this it is necessary to consider how fish pass efficiency changes under low flows when attraction efficiency and the shallow depth of water running through a pass can become an issue, and also during spates when flow velocity can exceed burst swimming speeds and passes can be drowned out (Beach, 1984; Office of Technology Assessment, 1995). The hypothetical 'conventional' and 'high flow' fish passes used in this study demonstrate just how important the nature of the fish pass efficiency-flow relationship is and how it can lead to counterintuitive outcomes. Despite the conventional fish pass increasing weir passability by a greater amount over a wider range of flows, it provides much less benefit than the high-flow fish pass when series of passes are treated as having a cumulative impact. This is simply because it does not improve passability over the crucial range of 90–100% when connectivity switches from being almost absent to present. In contrast, when the bottleneck method is used it is the high-flow fish pass that provides little benefit relative to the conventional pass. The reason for this is that the bottleneck method translates any increase in barrier passability over the range of 0–100% proportionally into an increase in overall connectivity as long as no downstream barrier has a lower passability. Furthermore the nature of the improvements to connectivity provided by the conventional and high-flow passes differs. During the cumulative method application the high flow pass greatly increases connectivity, but only for short periods, amplifying connectivity which was already boosted by high flows. On the other hand, the conventional fish pass in the bottleneck application does not amplify the high connectivity windows associated with high flows but rather extends their duration. These results underscores the need for a greater understanding of the combined passability of series of partial barriers, as this information is essential to improving the design of fish passes and planning the restoration of riverine connectivity.

5. Conclusions

At first glance it may seem that it can be assumed that migratory fish will inevitably return to impounded catchments if connectivity enhancements are made at every barrier. However our results show there is a very real danger that efforts will fail unless serious thought goes into the passage efficiencies of the enhancements, how the impact of the barriers combine, and how all this varies through time. Unfortunately the capacity of connectivity modelling to aid the decision maker in this task and provide definitive predictions on the outcome of alternative restoration strategies is currently restricted due to the high degree of sensitivity to uncertainty in fish pass efficiencies and how the passability of series of fish passes combines. Even small changes to fish pass efficiency can make the difference between alternative restoration scenarios appearing more attractive, or even whether the re-establishment of species seems feasible. Dendritic connectivity indices for potamodromous fish are also sensitive to this uncertainty, but this measure is designed for species with more flexible migratory needs and as yet does not directly provide insight into how changes to connectivity affect focus species. As a consequence the significance of this sensitivity is less clear.

A novel application of a dendritic connectivity index allowed us to explore how flow drove temporal variation in connectivity. This was achieved by considering how flow determined fish pass efficiency and caused transient gaps between habitat patches that we treated as partial barriers. Connectivity varied greatly through time, but the nature of the temporal patterns was highly dependent on how the combined impact of series of barriers was modelled. The variation in the potamodromous application of the connectivity index was difficult to interpret and more work is needed to understand how such indices relate to actual population attributes. The consideration of how flow determines discontinuities in habitat across river networks could be important in understanding fish metapopulation dynamics.

A number of important practical implications can be drawn from the modelling. Overall fish pass connectivity is comprised of attraction and passage efficiencies, which differ in the extent to which they are determined by random processes. This likely has ramifications for whether series of fish passes have cumulative or bottleneck impacts on migrating fish. Designers and catchment managers need to prioritise the reduction of the cumulative impact as this is most detrimental. That two hypothetical fish pass types with different flow-efficiency relationships produced very different temporal patterns in connectivity shows that the nature of the flow-efficiency relationship is very important, and small modifications can have a counter-intuitive impact.

While the limitations of connectivity modelling is very apparent in this study, such modelling does serve as a tool to think critically about connectivity restoration, and provides important insight into the nature of connectivity. If applied thoughtfully in full awareness of its constraints it can still be used to plan and appraise alternative restoration options.

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