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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