

A Toolkit for Optimizing Fish Passage Barrier Mitigation Actions

Steven King,^a Jesse R. O'Hanley,^{b*} Lynda R. Newbold,^c Paul S. Kemp,^c Matthew W. Diebel^d

^a*UNEP World Conservation Monitoring Centre, 219 Huntingdon Road, Cambridge, CB3 0DL, UK*

^b*Kent Business School, University of Kent, Canterbury, CT2 7PE, UK*

^c*International Centre for Ecohydraulics Research, University of Southampton, Southampton, SO17 1BJ, UK*

^d*Wisconsin Department of Natural Resources, 2801 Progress Road, Madison, WI 53716, USA*

Running Title: Resident fish passage mitigation planning

Number of Words: total (6,638), Summary (269), Introduction (1,048), Materials and Methods (2,923), Results (951), Discussion (1,296), Acknowledgments (98), Data Accessibility (32), Supporting Information (21)

Number of Tables: 5

Number of Figures: 5

Number of References: 55

Keywords: fish passage barriers, dams, stream-road crossings, barrier mitigation, river connectivity restoration, rapid barrier assessment, optimization, mixed integer linear programming, regression.

*Correspondence email: j.ohanley@kent.ac.uk Tel: +44-1227-824286

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi:

10.1111/1365-2664.12706

This article is protected by copyright. All rights reserved.

Summary

1. The presence of dams, stream-road crossings, and other infrastructure often compromises the connectivity of rivers, leading to reduced fish abundance and diversity. The assessment and mitigation of river barriers is critical to the success of restoration efforts aimed at restoring river integrity.
2. In this paper, we present a combined modeling approach involving statistical regression methods and mixed integer linear programming to maximize resident fish species richness within a catchment through targeted barrier mitigation. Compared to existing approaches, our proposed method provides enhanced biological realism while avoiding the use of complex and computationally intensive population/ecosystem models.
3. To estimate barrier passability quickly and at low cost, we further outline a rapid barrier assessment methodology. The methodology is used to characterize potential passage barriers for various fish species common to the UK but can be readily adapted to different planning areas and other species of interest.
4. We demonstrate the applicability of our barrier assessment and prioritization approach based on a case study of the River Wey, located in south-east England. We find that significant increases in species richness can be achieved for modest investment in barrier mitigation. In particular, dams and weirs with low passability located on mid to high order streams are identified as top priorities for mitigation.
5. *Synthesis and applications.* Our study shows the benefits of combining a coarse resolution barrier assessment methodology with state-of-the art optimization modeling to cost-effectively plan fish passage barrier mitigation actions. The modeling approach can help inform on-the-ground river restoration decision making by providing a recommended course of action that best allocates limited resources in order to restore longitudinal connectivity and maximize ecological gains.

Introduction

Longitudinal connectivity is essential to the ecological integrity of river ecosystems (Pringle, 2003). However, human impacts have significantly reduced the connectivity of river systems worldwide through the construction of artificial barriers, such as dams, weirs, culverts, and other stream-road crossings (Nilsson et al., 2005). Anthropogenic fragmentation of river networks is well recognized as a significant threat to the occurrence, abundance, and persistence of many freshwater species (Bednarek, 2001; Bourne et al., 2011). River connectivity plays an important role for fish at the individual and population levels. For individuals,

physical obstructions limit movement, access to rearing and spawning habitat, and shelter from predation and disturbances (Lucas and Baras, 2001; Liermann et al., 2012). Artificial barriers also impact metapopulation dynamics by isolating local populations and restricting dispersal and genetic exchange (Stanford et al., 1996; Wofford et al., 2005; Minor and Urban, 2007). The result is that fragmented populations often face an increased risk of local extinction and a reduced chance of subsequent recovery because recolonization is no longer possible (Lucas et al., 2009).

There is sound evidence that removing artificial barriers is not only a cost-effective means of restoring hydrologic and river ecosystem processes (Roni et al., 2002), but that the benefits of such can be realized quickly (O'Connor et al., 2015). A number of studies have demonstrated significant increases in fish abundance and or diversity (Kanehl et al., 1997; Catalano et al., 2007; Gardner et al., 2013) and a rapid return to more natural flow conditions (East et al., 2015) following barrier removal. Unsurprisingly, there is growing support for and implementation of barrier mitigation schemes, particularly in the US, Canada, parts of the European Union (EU), and Australia. This is evidenced by legislative drivers, such as the EU Water Framework Directive, and by the funding of large-scale restoration programs, like the US National Fish Habitat Partnership, both of which emphasize the need to remove fish passage barriers.

Although headway is being made to restore river connectivity, the scale of the problem is nonetheless daunting. It is estimated, for example, that the North American Great Lakes basin is fragmented by no less than 7,000 dams and 268,000 road crossings (Januchowski-Hartley et al., 2013). To help direct barrier mitigation efforts, a variety of prioritization methodologies have emerged. Scoring and ranking is by far the most commonly employed approach (Kocovsky et al., 2009; Nunn and Cowx, 2012). A serious weakness with scoring and ranking is that barriers are considered independently. This can lead to a highly inefficient set of barriers being selected for mitigation (O'Hanley and Tomberlin, 2005). Optimization models, by comparison, provide an objective framework for decision making that guarantees maximum benefit given available resources. Coordinated planning is achieved (unlike with scoring and ranking) by considering the spatial relationships among barriers (i.e., their upstream/downstream positions) and the interactive effects that multiple barrier mitigation actions have on longitudinal connectivity.

In this paper, we present a novel optimization framework for cost-effectively targeting the mitigation of fish passage barriers in order to maximize resident fish species richness. Given the availability of fish survey data, statistical regression methods are used to capture relationships between fish species richness and river connectivity and then integrated into the optimization framework. We demonstrate the utility of our modeling approach with a case study of the River Wey located in south-east England. To estimate barrier passability quickly and at low cost, we further outline a rapid barrier assessment methodology. Although designed for

fish common to the UK, the methodology can be readily adapted to other planning areas and for other species of interest. We anticipate the techniques presented in this paper will be of direct use to practitioners involved in watershed management.

A number of features set our current model apart from barrier optimization models already proposed in the literature. For example, most existing models (Paulsen and Wernstedt, 1995; Kuby et al., 2005; O'Hanley and Tomberlin, 2005; Zheng et al., 2009; King and O'Hanley, 2016) are designed exclusively to facilitate passage of diadromous fish (e.g., salmon), which travel upstream from the sea into freshwater. This simplifies the modeling process in that the only dispersal paths that need to be considered are those from the river mouth to areas located above barriers. Our model, in contrast, focuses on potamodromous (aka resident) species fish, which exhibit more complex migration patterns involving internal movements from one area of a river network to another. The only existing studies dealing with resident fish dispersal to our knowledge are O'Hanley (2011) and O'Hanley et al. (2013b). Specifically, O'Hanley (2011) maximizes the single largest subsection of river unimpeded by barriers to promote undirected fish dispersal, while O'Hanley et al. (2013b) maximize river habitat connectivity according to the C metric proposed by Diebel et al. (2015), which accounts for the quality and accessibility of different river habitat types as well as travel distances between habitat areas. In the latter, dispersal paths between each and every pair of habitat patches are considered.

The most notable aspect of our model is the integration of statistical methods for the purpose of quantifying river connectivity impacts on fish species richness. This adds a degree of sophistication not normally seen with barrier optimization methods. The standard (simpler) approach is to maximize some form of habitat metric, as with O'Hanley (2011) or O'Hanley et al. (2013b). Two notable exceptions to the use of habitat metrics are Paulsen and Wernstedt (1995) and Zheng et al. (2009). Paulsen and Wernstedt (1995) propose a framework for selecting barrier mitigation and other in-stream habitat restoration actions at minimum cost which satisfy defined escapement and harvesting goals. Zheng et al. (2009), meanwhile, optimize multiple ecological and socioeconomic outcomes of dam removal, including fish productivity gains, adjusted fish biomass ratios, dam removal costs, and invasive species management costs. In both studies, impacts of barrier mitigation actions on fish abundance and community composition are modeled using complex population/ecosystem simulations. Simulation models normally require detailed knowledge of habitat use, demographic rates, and dispersal characteristics. This limits their applicability in most real-world settings, where reliable data of this kind are usually scarce or nonexistent.

Our proposed model strikes a good balance between realism and complexity. Maximizing species richness ostensibly has the advantage of being a more ecologically informed and managerially relevant planning goal. At the same time, data requirements are rather modest (i.e., the availability of fish survey data and wide-area

geographic information system data). Moreover, unlike the afore mentioned simulation-optimization based approaches, our proposed framework remains highly scalable and computationally efficient, meaning that problems involving large number of barriers still be solved relatively quickly.

In what follows, our aim is to give details of the proposed barrier optimization modeling framework, including a formal mathematical formulation of the problem, basic data needs, key statistical analyses required to parametrize the model, and an overview of the rapid barrier assessment protocol. For demonstration purposes, we use a case study of the River Wey catchment. This helps to achieve our second major aim, which is to show how our approach can be used to support smarter and more effective river barrier mitigation planning.

Materials and Methods

Case Study Background

The River Wey, located in the south-east of England, is a tributary to the River Thames and covers an area of approximately 900km² (Figure 1). The Wey is comprised of two main tributaries that meet approximately 15km to the west of Guildford and flows into the non-tidal portion of the Thames at Weybridge. There are three operational canal systems within the catchment: the Wey Navigation (between Guildford and Weybridge), the Godalming Navigation (between Guildford and Godalming), and Basingstoke Canal (heading west from Weybridge). Agriculture is the principal land-use in the south and west of the catchment, while the north is primarily urban (EA, 2008a).

The Environment Agency (EA) is the main public body in England with responsibility for managing river ecosystems. The EA's Fisheries Action Plan for the Wey catchment has identified the presence of physical obstructions as a key pressure on fish diversity and abundance (EA, 2008b). An inventory of barriers within the main reaches of the River Wey was prepared by merging three existing datasets:

1. The EA's obstruction database EA (2010b) containing natural and anthropogenic barriers across England and Wales, including waterfalls, dams, weirs, sluices, and locks (but not culverts).
2. The National Flood and Coastal Defense Database (NFCDD), a catalog of weirs, sluice gates, locks, and culverts.
3. Cross sections and longitudinal profiles of river reaches with labeled structures, including weirs and culverts (provided by the EA).

In total, 805 barriers were identified, including weirs, dams, sluices, culverts, locks, fords, bridge aprons, mills, and cascades. The location of each barrier was subsequently matched to the EA's detailed river network (DRN) using standard geographic information system (GIS) procedures.

To rationalize the river network for the River Wey catchment, all watercourses identified as a drain on the DRN were removed given their likely low ecological value.¹ Additionally, where man-made channels introduced braids into the system, these were terminated immediately before rejoining the main river stem in order to maintain a dendritic structure (Campbell Grant et al., 2007). Following these adjustments, the final barrier dataset employed in the analysis comprised 1,160km of waterway with 669 artificial and natural barriers (Figure 1).

Rapid Barrier Assessment

A coarse resolution rapid barrier assessment methodology for the UK that is suitable for multiple fish species and considers both up and downstream dispersal was devised by Kemp et al. (2008). This was later revised, following field trials, by the Scotland and Northern Ireland Forum for Environment Research (SNIFFER, 2010). The assessment method uses rule based criteria for fish morphology, behavior, and swimming and leaping ability to estimate barrier passability. Barrier passability represents the fraction of fish (in the range 0 to 1) that are able to successfully negotiate a given barrier in the upstream or downstream directions. Each barrier is assigned one of four passability levels as follows: 0 is a complete barrier to movement; 0.3 is a high impact partial barrier, passable to a small proportion of fish or passable only for short periods of time; 0.6 is a low impact partial barrier, passable to a high proportion of fish or for long periods of time; and 1 is a fully passable structure. Partial barriers are often created by fluctuating river discharge, which causes variation in water depth and velocity at the barrier, thereby impeding large fish at low flows or individuals with a weaker swimming performance at high flows. The methodology described in SNIFFER (2010) was used to evaluate adult brown trout (*Salmo trutta*) passability for a sample ($n = 63$) of the 669 barriers in our dataset based on a combination of in-field measurements and photographic analysis. Criteria used to assign upstream and downstream barrier passabilities are shown in Tables 1 and 2, respectively.

A remote based screening method was subsequently performed to identify any impassable structure. Hydraulic head data were extracted from the NFCDD and leveling surveys and used to determine which structures had head heights exceeding the 1m leaping ability of adult brown trout. Stepped weirs were also assumed to be impassable unless the total head height was less than 1m and the effective width was less than 2m (i.e., passable in a single leap). This was based on the finding that all stepped weirs surveyed in

¹Drains include any watercourse identified as a ditch, reen, rhyne, or drain on Ordnance Survey maps or by local EA staff.

the field had pool depths that were too shallow to allow adult brown trout to leap from one step to another. In all, 93 barriers were designated as impassable in the upstream direction due to excessive height or width and assigned an upstream passability score of 0. Navigation locks ($n = 35$) are not currently included in the rapid barrier assessment method due to limited research into their effects on fish migration. For our study, a provisional score of 0.3 was assigned to locks in each direction as they normally lack attraction flow and can remain empty for long periods of time. Their use without specific alterations to accommodate fish passage is thought to be largely accidental (Travade and Larinier, 2002). For all remaining barriers ($n = 478$), upstream/downstream passability was set to the median value of the same structural type. A cursory analysis showed relatively little variation in passability for barriers of a given structural type.

Fish Survey Dataset

The EA completed 145 fish surveys within the River Wey catchment between October 1989 and October 2011 as part of ongoing monitoring. Surveys were completed using electrofishing methods. The average length and area of river surveyed was approximately 120 m and 1,000 m², respectively. In total, 22 different species were identified, with an average of around 6 species and 96 individual fish identified per survey event.

All surveys in which one or zero fish species were recorded were removed from the dataset on the basis that such observations were due to sampling error, a temporal phenomenon, or indicative of highly localized pressures (e.g., pollution). In addition, all observations prior to 2002 (i.e., those from 1989, 1990, and 1991) were excluded in order to maintain a contemporary set of sampling data. This resulted in a final dataset of 121 survey observations spread across 29 locations (river reaches) to investigate the significance of subnetwork connectivity on species richness in the River Wey.

Habitat Connectivity

Formally, the area upstream of a barrier up to the next set of barriers or river terminus is termed a river *subnetwork*. Assuming that a river never diverges as it flows downstream (i.e., has a tree structure), each subnetwork can be identified by its bounding downstream barrier. Subnetwork A in Figure 2a, for example, is formed by the section of river between barriers A, B, and C.

In what follows, we take the overall passability p_j of a given barrier j (i.e., its *bidirectional* passability) as the product of the barrier's upstream and downstream passabilities. With respect to barrier B shown in Figure 2a, if passability in the upstream direction is 0.5 and passability in the downstream direction is 0.8, then $p_B = 0.5 \times 0.8 = 0.4$. The *cumulative passability* z_{jk} between an origin subnetwork j and destination

subnetwork k is equal to the product of all barrier passability values along the shortest path from subnetwork j to k . Cumulative passability is analogous to the notion of longitudinal connectivity, specifically between the origin and destination subnetworks of a given route. For instance, fish wanting to access habitat in subnetwork D starting from subnetwork C (Figure 2a) must negotiate barriers C, B, and D. Consequently, cumulative passability z_{CD} for this path is the product of the bidirectional passabilities of those three barriers (i.e., $z_{CD} = 0.3 \times 0.4 \times 0.2 = 0.024$).

With this in place, we use the C metric proposed by Diebel et al. (2015) to describe overall habitat connectivity within a watershed. Unlike simpler connectivity metrics (e.g., DCIP), the C metric takes into account access to different types of habitat (e.g., spring spawning in headwaters, summer feeding in mid-order streams, and over-wintering in larger rivers or lakes). Using the notation provided in Table 3, the C metric is constructed by first determining the total availability A_{jh} of habitat type h accessible from a given river subnetwork j as follows:

$$A_{jh} = \sum_{k \in J} D_{jk} v_{kh} z_{jk}$$

where cumulative passability is calculated as $z_{jk} = \prod_{\ell \in B_{jk}} p_{\ell}$, the product of all barrier passabilities along the path from subnetwork j to k . The baseline availability A_{jh}^0 of habitat type h accessible from subnetwork j assuming no barriers exist in the river network is similarly defined as:

$$A_{jh}^0 = \sum_{k \in J} D_{jk} v_{kh}$$

The term D_{jk} employed in the calculation of A_{jh} and A_{jh}^0 represents a distance decay factor for the journey between subnetworks j and k and is given by:

$$D_{jk} = \frac{1}{1 + \left(\frac{d_{jk}}{d_0}\right)^2}$$

The connectivity C_j for a given subnetwork j can then be calculated using the ratios of available and baseline habitat across all habitat types h or more specifically:

$$C_j = \frac{1}{m} \sum_{h=1}^m \frac{A_{jh}}{A_{jh}^0} \quad (1)$$

Note that in order to account for all habitat within a river system (specifically the stretch of river below the first set of barriers), a “dummy” barrier with passability equal to 1 must be introduced at the river mouth if no such structure exists (e.g., barrier M in Figure 2a). Accordingly, this results in a total of $\frac{n(n-1)}{2}$ unique subnetwork-to-subnetwork paths, where n is the total number of artificial/natural barriers present plus the dummy barrier.

Barrier Optimization Model

The aim of our model is to select barriers for repair or removal (i.e., mitigation) in order to maximize mean resident fish richness within a given study area. We assume that fish species richness R_j within a subnetwork j is determined, at least in part, by its connectivity status C_j . Given the availability of sufficient fish survey and potentially other relevant environmental data, the relationship between fish species richness R_j and connectivity C_j can be estimated empirically using standard statistical regression techniques.

We further assume that multiple mitigation options (e.g., removal, replacement, installing a fish pass, fitting baffles) may be available at any given barrier, which vary in terms of cost and passability improvement, but that only one of these can be implemented. In most practical situations, mitigation is restricted to artificial barriers (i.e., natural barriers like waterfalls cannot be mitigated). Besides producing an increase in passability, barrier mitigation potentially serves to increase the cumulative passability of each route passing through a treated barrier and, in turn, an increase in both the connectivity status C_j and fish species richness R_j of each river subnetwork. Lastly, there is assumed to be a budget b , which limits the total expenditure on river barrier mitigation actions.

To formalize this, we let p_j^0 denote the initial bidirectional passability of barrier j . The set of mitigation projects available at barrier j is given by S_j and indexed by i . Implementation of mitigation project i at barrier j costs an amount c_{ji} and results in an increase in passability of p'_{ji} . We also introduce the following decision variables.

$$x_{ji} = \begin{cases} 1 & \text{if mitigation project } i \text{ is implemented at barrier } j \\ 0 & \text{otherwise} \end{cases}$$

z_{jk} = cumulative passability between origin subnetwork j and destination k

C_j = connectivity status of river subnetwork j

R_j = mean fish species richness of river subnetwork j

With this in place, a nonlinear formulation of our optimization model is given below.

$$\max \frac{1}{V} \sum_{j \in J} v_j R_j \quad (2)$$

s.t.

$$R_j = f(C_j, \boldsymbol{\pi}_j) \quad \forall j \in J \quad (3)$$

$$C_j = \sum_{k \in J | k < j} w_{jk} z_{kj} + \sum_{k \in J | k \geq j} w_{jk} z_{jk} \quad \forall j \in J \quad (4)$$

$$z_{jk} = \prod_{\ell \in B_{jk}} \left(p_\ell^0 + \sum_{i \in S_\ell} p'_{\ell i} x_{\ell i} \right) \quad \forall j, k \in J | k \geq j \quad (5)$$

$$\sum_{i \in S_j} x_{ji} \leq 1 \quad \forall j \in J \quad (6)$$

$$\sum_{j \in J} \sum_{i \in S_j} c_{ji} x_{ji} \leq b \quad (7)$$

$$x_{ji} \in \{0, 1\} \quad \forall j \in J, i \in S_j \quad (8)$$

In the above model, the objective function (2) maximizes habitat weighted fish species richness across all subnetworks in the river system. Parameter $V = \sum_{j \in J} v_j$ is the total amount of habitat within the study area. Equations (3) specify that species richness R_j within a given subnetwork j is assumed to be some function $f(\cdot)$ of connectivity status C_j along with a set of additional environmental covariates $\boldsymbol{\pi}_j$ influencing species richness. Connectivity status C_j for any subnetwork j is determined by equations (4), where:

$$w_{jk} = \frac{1}{m} D_{jk} \sum_{h=1}^m \frac{v_{kh}}{A_{jh}^0}$$

Assuming that cumulative passability between subnetworks j and k is symmetric (i.e., $z_{jk} = z_{kj}$), it is straightforward to show that equations (1) and (4) provide equivalent expressions of the C metric. We also point out that other connectivity metrics could be used in place of the C metric. For example, the popular DCIP metric of Cote et al. (2009) computed at the individual subnetwork scale (referred to as DCIs by Mahlum et al., 2014b) could just as easily be integrated into our model by redefining parameter $w_{jk} = \frac{v_k}{V}$.

To continue, constraints (5) determine the cumulative passability z_{jk} between subnetworks j and k . This is equal to the product of all intervening barrier passabilities, where the passability of any barrier ℓ along the route is equal to initial passability p_ℓ^0 plus the increase in passability $p'_{\ell i}$ if mitigation project i is carried out

at the barrier (i.e., $x_{\ell i} = 1$). Constraints (6) ensure only one mitigation project i can be carried out at barrier j . This prevents the model from nonsensically selecting multiple types of mitigation for any given barrier (e.g., a barrier cannot be “repaired” and “removed” at the same time). Inequality (7) is the budget constraint, which stipulates that the total cost of barrier mitigation actions cannot exceed the available budget b . Lastly, constraints (8) impose binary restrictions on the x_{ji} barrier mitigation decision variables.

As detailed in the statistical analysis subsection below, rather than directly estimate species richness R_j , we employed the following model to evaluate the expected number of “missing” or absent species in subnetwork j .

$$\bar{R}_j = \exp(\beta'_j + \beta_1 C_j) \quad \forall j \in J \quad (9)$$

Equations (9) derive from the use of a generalized Poisson regression model, where β_1 is the coefficient for connectivity status C_j and β'_j is a parameter that aggregates the constant and other explanatory variables for species absence \bar{R}_j in subnetwork j . Expected species richness can, in turn, be determined by replacing equations (3) with:

$$R_j = R^{\max} - \bar{R}_j \quad \forall j \in J \quad (10)$$

where R^{\max} represents the total number of species found within the study area.

Note that inclusion of equations (9) invariably results in a nonlinear model, as does the multiplication of the x_{ji} decision variables in equations (5). Nonlinear optimization models are notoriously difficult to solve. Rather than resort to developing a heuristic or rely on some other specialized solution method, a preferable option, as recommended by O’Hanley (2009), is to try to linearize the problem. In an appendix (see Appendix S1 in Supporting Information), we first show how (5) can be transformed to into an equivalent set of linear constraints using the probability chain method of O’Hanley et al. (2013a). We subsequently detail an approach for approximating equations (9) as a piece-wise linear curve.

For our River Wey case study, the net amount of habitat in each subnetwork (v_j) was characterized as the net length of stream above a barrier up to the next set of barriers or the river terminus. Only a single habitat type was considered (i.e., $m = 1$) as over 75% of river stretches in the Wey are classified as primary river in the DRN. The dispersal distance for fish (d_0) was assumed to be 7.5km based on a preliminary analysis showing good statistical fit between species richness and the level of connectivity for this distance.

In total, there were 650 artificial barriers (out of the 669 total) that had bidirectional passabilities less than 1 and, therefore, were considered as candidates for mitigation action. For each of these barriers, a single mitigation project was considered. Barriers outside the middle and lower reaches of the main river stem and navigation sections were considered suitable candidates for complete removal, thereby restoring full passability in both directions (i.e., $p'_j = 1 - p_j^0$) at those locations. Such barriers are typically small, so there is generally little conflict or opportunity cost associated with their removal. Barriers associated with the middle and lower reaches of the main river stem were not considered suitable for removal due to the adverse effect on navigation in this part of the system. These barriers were considered candidates for the provision of fish passes. Fish passes were assumed to increase upstream passability to 0.75 and restore full passability in the downstream direction (i.e., $p'_j = 0.75 - p_j^0$). In our analysis, it was assumed that bidirectional passability at locks could be increased to 0.65 via investment in more regular or improved operations (i.e., $p'_j = 0.65 - p_j^0$). The costs of barrier mitigation were estimated on the basis of costs provided by the River Restoration Council (pers. comm.) for work at similar structures and from information published by the EA (EA, 2010a). The cost of mitigating all 650 candidate barriers within the River Wey was estimated to be £53,355,000.

The barrier optimization model was coded in the OPL modeling language using CPLEX studio version 12.5 (IBM, 2013). CPLEX is a state-of-art commercial software package that employs branch-and-cut methods to solve mixed integer linear programs (MILPs). All experiments were run on the same dual-core Toshiba Satellite Pro R850-15F laptop (Intel i3 processor, 2.10 GHz per chip) with 8GB of RAM.

Species Richness Statistical Analysis

To parametrize our optimization model, it is necessary to estimate the magnitude and confirm the significance of the effect of subnetwork connectivity on fish species richness. In the analysis that follows, we investigate the significance of the C metric in determining fish species absence (the complement to species richness) using the fish survey dataset for the River Wey described above. Estimation of species absence (\bar{R}_j) produced better fitting models than those in which species richness (R_j) was used as the dependent variable.

Our *a priori* expectation is that fish species absence is influenced by both subnetwork connectivity and size, with the later being quantified as the square root of total upstream river length ($\sqrt{USL_j}$). We also include dummy variables for time in the estimation procedure to control for temporal variation across survey years and to increase the accuracy of the parameter estimates. Consequently, our theoretical model of species absence for the River Wey takes the following form.

$$\log_e(\bar{R}_j) = \beta_0 + \beta_1 C_j^0 + \beta_2 \sqrt{USL_j} + \sum_{t=1}^T \beta_{2+t} year_{jt} \quad (11)$$

In the above equation, variable \bar{R}_j is the expected number of unobserved species during a survey event, β_0 is a constant, C_j^0 is the current connectivity status of subnetwork j with associated parameter β_1 , and $year_{jt}$, $t = 1, \dots, T$, are a series of dummy variables for the year fish surveys were undertaken (T being the total number of years) with associated parameters β_{2+t} .

We employ a Poisson regression model, rather than ordinary least squares (OLS), given the discrete nature of the dependent variable \bar{R}_j and the fact that it is not normally distributed. A good summary of Poisson regression is provided in Green (2008). The theoretical model specified in equation (11) was estimated using the LIMDEP version 10 software package (Green, 2012). To avoid the restriction of equal mean and variance (equidispersion), we rely on the generalized Poisson modeling approach proposed by Consul and Jain (1973). This generalized model relaxes the assumption of equidispersion by allowing the variance for the distribution of the dependent variable to be characterized as a function of the regression mean and an associated scaling factor θ . In adopting a generalized Poisson model, the regression equation for estimating species absence \bar{R}_j takes on the basic form given by (9), where $\beta'_j = \beta_0 + \beta_2 \sqrt{USL_j} + \sum_{t=1}^T \beta_{2+t} year_{jt}$.

Results

Regression Model Results

Results of the fish species richness statistical analysis are summarized in Table 4. The dummy variables for survey years are omitted from the table as their inclusion was purely to control for temporal variation. A conventional OLS regression reveals that approximately half the variation observed in missing fish species count \bar{R} is explained by the model ($R^2 = 0.46$) and that the key explanatory variables are significant at the 1 to 5% level. For the preferred generalized Poisson regression, the scale parameter θ is negative and significant at the 1% level, confirming underdispersion of the data. The likelihood ratio test confirmed that the explanatory variables are jointly significant at the 1% level. More importantly, the coefficient for variable C^0 (parameter β_1) is significant at the 1% level. This estimate is not directly comparable to the OLS estimate as it represents the effect on $\log_e(\bar{R})$ of a one unit increase in C^0 . However, a comparable *partial* effect (i.e., local gradient) can be calculated for C^0 by evaluating the effect this variable has on the expected value of \bar{R} by fixing each independent variable at its mean within the sample data. These results are reported in the

final column (dy/dx) of Table 4. The partial effect of -14.28 for C^0 is significant at the 5% level. Besides being close to the OLS estimate of -12.73, its magnitude indicates that potentially large reductions (gains) in species absence (richness) can be achieved with increased connectivity.

Optimization Model Results

Gains in mean species richness within the River Wey produced by the barrier optimization model are shown in Figure 3. An overall pattern of diminishing returns is observed, whereby increases in species richness become progressively smaller with increased budget. Given a budget of just £5M, for example, mean richness can increase by roughly 2.3 above the baseline value of 5.2 fish species. This represents close to a 50% increase in species diversity. To achieve nearly a doubling in species richness, however, requires a four-fold increase in the budget (i.e., £20M for an increase of 5.0 in species richness).

The spatial distribution of species richness for these two solutions as well as the baseline (£0 budget) are shown in Figure 4. At present (£0 budget), middle and lower portions of the River Wey are predicted to have comparatively higher richness (7-10 species), particularly along main stem river segments. Richness in most of the upper reaches is quite low (2-4 species), in part because of their smaller size but mostly do to limited connectivity. This is evident by looking at the species richness maps for the £5M and £20M solutions. Initial gains in species richness are primarily seen first in the upper reaches (£5M), followed by gains in the middle to lower sections of the river catchment (£20M).

In Table 5, we examine some of the basic characteristics of barriers that were selected for mitigation by our model. Dams/weirs and culverts are the dominant types of barriers in the Wey system, comprising 265 and 268, respectively, out of the 650 total candidate barriers. In spite of being roughly equally common, however, we find that dams/weirs are targeted for mitigation action much more often than culverts at lower budgets (\leq £25M). For instance, 57 structures are targeted for mitigation at a budget of £5M, 37 (65%) of which are dams/weirs but only 13 (23%) of which are culverts. No locks and relatively few screens are selected at lower budget levels. Locks, in fact, are almost never selected until the budget is large enough to remove nearly all barriers. Meanwhile, sluices and “other” barriers are comparatively over represented at lower budgets. Sluices and “other” barriers, for example, make up just 6% and 2% of all barriers, respectively, but account for 10% and 5% of selected barriers at the £20M budget.

Inspection of Table 5 further reveals that barriers on high order streams to be high priority targets. At a budget of £5M, almost no barriers on order 1-2 streams are selected. Even when the budget reaches as high as £25M, just 14% of selected barriers are located on order 1-2 streams. Figure 5, which displays the

£5M and £15M solutions spatially, shows that many of the barriers selected for mitigation are also in areas with high degrees of bifurcation, notably in the central portion of the river network between Weybridge and Guildford where several tributaries converge. In contrast, areas with limited bifurcation (e.g., to the west of Guildford and along stretches of river from Alton to Farnham) are not selected for mitigation.

Given all this, it comes as little surprise that barriers targeted for mitigation at lower budget levels (\leq £25M) tend to be large (\geq 1m head height), have lower than average initial passability, and are generally more costly to mitigate compared to barriers as a whole. These characteristics are all typical of barriers located on high order streams. Looking at Table 5, 43% of all large barriers are selected at a budget of £15M. Average passability of selected barriers is 0.10, slightly less than the overall average of 0.12. Further, the average cost of selected barriers is £98k, which is significantly higher than the £82k average for all barriers.

A final observation that can be made with respect to Table 5 is that at lower budget levels, the optimization model targets barriers with large upstream subnetworks. For example, the average length of river immediately above selected barriers (Net USL) goes from 7.5km at a budget of £5M to 3.3km at a budget of £25M. The average subnetwork size, in contrast, is only 1.7km. This suggests that at lower budget amounts, a simple rule of thumb may be to sequentially mitigate the barrier obstructing access between the two largest adjacent subnetworks until the budget is expended.

Discussion

The presence of river barrier infrastructure across the world has substantially reduced the longitudinal, lateral, and even vertical connectivity of fluvial ecosystems (Nilsson et al., 2005; Grill et al., 2015). The negative impacts that artificial barriers have on fish populations are well-known (Stanford et al., 1996; Bednarek, 2001; Pringle, 2003). There is now increasing interest amongst ecologists, river managers and policy makers to remove or otherwise mitigate these barriers in order to improve the ecological integrity of river environments. In this paper, we present a toolkit for the rapid assessment and cost-effective prioritization of resident fish passage barriers to restore longitudinal connectivity.

A large number of barrier passability assessment methods have been developed (Taylor and Love, 2003; WDFW, 2009; Gargan et al., 2011). Despite the varied impact that structures can have on different fish (Ovidio and Philippart, 2002; MacPherson et al., 2012), few methodologies account for multiple species and structure types and even fewer consider downstream movements (Kemp and O'Hanley, 2010). The rapid barrier assessment methodology proposed in SNIFFER (2010) and used in the current study is an exception. We apply this methodology on a catchment scale and demonstrate its potential in helping to prioritize barrier

mitigation work.

Although the passability values generated relate to flow conditions at the time of surveying, this compromise is necessary to create a rapid assessment tool for maximizing the number of structures that can be surveyed in the field. A good indication of barrier passability is obtained and more detailed surveys can be conducted if necessary. For barriers surveyed in the field, a mean of 5.7 barriers were evaluated each day using two surveyors and readily available equipment. Thus, the method can reduce the time and cost required to inventory river barriers compared to more detailed surveys. In situations where the number of barriers to be surveyed is prohibitive, a sampling procedure can be employed, as done in Januchowski-Hartley et al. (2014), whereby a subset of barriers are assessed for passability and the data used to build regression models for predicting passability at unsurveyed sites based on simple structural information combined with easy-to-obtain remote sensing data.

In our case study, the rapid barrier assessment was used to assess passabilities for adult brown trout (*S. trutta*). Normally, specification of a focal species can have a strong influence on the barrier prioritization process. A barrier to one species or life-stage may not be a barrier to another. Indeed, trout can typically pass barriers that fish with weaker swimming/jumping abilities cannot. This, in turn, can bias which barriers are selected for repair/removal. With our modeling approach, the choice of a focal species is largely arbitrary. Our main concern is overall species richness. To estimate this, a statistical analysis is performed to determine how species richness correlates with the connectivity status of a chosen focal species. Using a different focal species will invariably affect the raw level of connectivity being measured but only has a minor effect on predicted fish species richness due to the high degree of correlation in connectivity status for different species. Indeed, a statistical/optimization analysis using common carp (*Cyprinus carpio*) as the focal species (results not shown) produced qualitatively similar findings.

It is also worth noting that while the barrier assessment methodology is based on up-to-date fisheries research, it has not been validated against observed fish passage data. This is a common problem with most barrier assessment methods, which requires further attention in the literature. Consequently, it is important to bear in mind that inconsistencies between predicted and actual passability may lead to sub-optimal management decisions with resulting economic and ecological costs (Mahlum et al., 2014a).

It is vital for barrier prioritization methods, if they are to be applied in the real world, that they be capable of producing cost-effective solutions using easy to obtain data. Ideally, they should also be fairly easy to implement, computationally efficient, and flexible in meeting different planning goals. In this regard, the model we present here makes a valuable contribution to the growing literature on barrier optimization methods. Specifically, we propose an efficient and scalable model that can be implemented using off-the-shelf

Accepted Article
optimization software. The model is noteworthy for integrating statistical methods in order to maximize gains in mean species richness across a watershed. In this regard, it provides a simplified way of focusing on an ecologically relevant goal (species richness) without the need to integrate data hungry and computationally intensive population/ecosystem simulation models (Paulsen and Wernstedt, 1995; Zheng et al., 2009).

We demonstrate the applicability of our barrier optimization model using a dataset of 669 fish passage barriers from the River Wey in the UK. For the River Wey system, roughly a doubling in mean species richness can be achieved with a mitigation budget of £20M. Investments above £30M may not be cost-effective; approximately 85% of potential ecological improvements (equivalent to 6.23 additional species on average) can be obtained at this budget level. Beyond this point, one observes diminishing marginal returns. An analysis of the types of barriers selected for mitigation action under different budget scenarios indicates that it is the larger, low passability barriers located on mid to high order streams, particularly in areas of dense river branching, that are prioritized for action in the River Wey system. These results are generally in line with Cote et al. (2009) and O’Hanley et al. (2013b), which both found that it is the removal of barriers in the central portion of a river network that usually yield the largest connectivity gains for resident fish. In the case of the Wey, these barriers are far more likely to be dams/weirs, sluices, or “other,” rather than culverts, screens, or locks.

We believe that the methods presented here can be of direct use to decision makers involved in river ecosystem management. The optimization model readily generates prescriptive solutions for barrier mitigation action that maximize restoration gains given available resources. These solutions can, in turn, be implemented *in toto* or form the basis for more detailed modeling and fine-tuning later on. This is a distinct advantage compared to other barrier prioritization methods, such as scoring and ranking or graph theoretic approaches, which are either highly inefficient or merely descriptive (i.e., solutions proposed by an analyst can be evaluated but no recommended best course of action is provided).

Optimization models are especially useful for generating Pareto optimal trade-off curves, which reveal how environmental improvements vary with different levels of investment. They can also be useful in driving insightful economic analyses. For example, the economic benefit associated with barrier mitigation due to improvements in mean fish species richness (or other biophysical attributes) can be fairly easily estimated using established non-market valuation techniques (Morrison and Bennett, 2004; MacDonald et al., 2011). This suggests that our optimization model could be readily integrated into a bio-economic modeling framework to determine optimal levels of investment in barrier mitigation. Often used in cost-benefit analysis studies related to fisheries management (e.g., Adams et al., 1993), bio-economic models overlay economics with population modeling with the aim of assessing the monetary benefit of increased fish production derived from proposed management interventions (e.g., changes in harvesting rules or habitat conservation/restoration

activities) relative to the cost of the proposed interventions. Given the increasing use of cost-benefit analysis in environmental decision making, this is anticipated to be especially useful to government agencies involved in river management and policy. Research is ongoing in this regard.

With regard to other lines of future research, the optimization models presented here could be extended in a number of ways. For example, it is assumed in our model that the river network is strictly dendritic, meaning that there is only a single direct path between any two subnetworks. Moving away from this assumption would be useful, especially for the River Wey, which is heavily modified by man-made navigation channels that result in a braided river structure. Another interesting pursuit might be to consider different functional forms for describing the relationship between connectivity and fish species richness and then try to incorporate this into an optimization model. It is likely, if the resulting formulations were to involve complex, nonlinear functions, that specially designed heuristics would need to be developed to solve such problems.

Acknowledgments

S. King was supported by the Economic and Social Research Council (ESRC) via the South East Doctoral Training Centre (Grant No. ESJ500148/1). Funding for barrier assessment work in the River Wey catchment was provided to P. Kemp and L. Newbold by the Environment Agency. This support is gratefully acknowledged. We further thank Steve Sheridan and Lizzie Rhymes from the Environment Agency for the provision of data and general assistance. We also thank Stephanie Januchowski-Hartley, two anonymous referees, the associate editor, and the assistant editor, Alice Plane, for very helpful comments made on earlier drafts of the paper.

Data Accessibility

Fish sampling data, barrier data, and OPL optimization model code used in used in this study are available from the Dryad Digital Repository doi: 10.5061/dryad.46vf8 (King et al., 2016)

References

Adams, R., Berrens, R., Cerda, A., Li, H., P, K., 1993. Developing a bioeconomic model for riverine management: Case of the John Day River, Oregon. *Rivers* 4 (3), 213–226.

- Bednarek, A. T., 2001. Undamming rivers: A review of the ecological impacts of dam removal. *Environmental Management* 27 (6), 803–814.
- Bourne, C., Kehler, D., Wiersma, Y., Cote, D., 2011. Barriers to fish passage and barriers to fish passage assessments: The impact of assessment methods and assumptions on barrier identification and quantification of watershed connectivity. *Aquatic Ecology* 45, 389–403.
- Campbell Grant, E., Lowe, W., Fagan, W., 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters* 10 (2), 165–175.
- Catalano, M. J., Bozek, M. A., Pellett, T. D., 2007. Effects of dam removal on fish assemblage structure and spatial distributions in the Baraboo River, Wisconsin. *North American Journal of Fisheries Management* 27 (2), 519–530.
- Consul, P., Jain, G., 1973. A generalization of the Poisson distribution. *Technometrics* 15 (4), 791–799.
- Cote, D., Kehler, D. G., Bourne, C., Wiersma, Y. F., 2009. A new measure of longitudinal connectivity for stream networks. *Landscape Ecology* 24 (1), 101–113.
- Diebel, M., Fedora, M., Cogswell, S., O’Hanley, J. R., 2015. Effects of road crossings on habitat connectivity for stream-resident fish. *River Research and Applications* 31 (10), 1251–1261.
- EA, 2008a. The Wey catchment abstraction management strategy. Tech. rep., Environment Agency, Bristol, UK.
- EA, 2008b. The Wey Valley fisheries action plan. Tech. rep., Environment Agency, Bristol, UK.
- EA, 2010a. Environment Agency fish pass manual. Bristol, UK.
- EA, 2010b. Mapping hydropower opportunities and sensitivities in England and Wales: Final report. Tech. rep., Environment Agency, Bristol, UK.
- East, A., Pess, G., Bountry, J., et al., 2015. Large-scale dam removal on the Elwha River, Washington, USA: River channel and floodplain geomorphic change. *Geomorphology* 228, 765–786.
- Gardner, C., Coghlan, S., Zydlewski, J., Saunders, R., 2013. Distribution and abundance of stream fishes in relation to barriers: Implications for monitoring stream recovery after barrier removal. *River Research and Applications* 29 (1), 65–78.
- Gargan, P. G., Roche, W. K., Keane, S., King, J. J., Cullagh, A., Mills, P., Keeffe, J. O., 2011. Comparison of field- and GIS-based assessments of barriers to Atlantic salmon migration: A case study in the Nore catchment, Republic of Ireland. *Journal of Applied Ichthyology* 27 (s3), 66–72.

Green, W., 2008. *Econometric Analysis*, 6th Edition. Pearson Prentice Hall, Upper Saddle River, New Jersey.

Green, W., 2012. LIMDEP version 10. Econometric Software, Inc., Plainview, New York.

Grill, G., Lehner, B., Lumsdon, A., MacDonald, G., Zarfl, C., Liermann, C., 2015. An index-based framework for assessing patterns and trends in river fragmentation and flow regulation by global dams at multiple scales. *Environmental Research Letters* 10, 015001.

IBM, 2013. IBM ILOG CPLEX Optimization Studio V12.5.1 documentation. http://www-01.ibm.com/support/knowledgecenter/SSSA5P_12.5.1/maps/ic-homepage.html, accessed 16/11/2015.

Januchowski-Hartley, S., Diebel, M., Doran, P., McIntyre, P., 2014. Predicting road culvert passability for migratory fishes. *Diversity and Distributions* 20 (12), 1414–1424.

Januchowski-Hartley, S. R., McIntyre, P. B., Diebel, M., Doran, P. J., Infante, D. M., Joseph, C., Allan, D. J., 2013. Restoring aquatic ecosystem connectivity requires expanding inventories of both dams and road crossings. *Frontiers in Ecology and the Environment* 11 (4), 211–217.

Kanehl, P., Lyons, J., Nelson, J., 1997. Changes in the habitat and fish community of the Milwaukee River, Wisconsin, following removal of the Woolen Mills Dam. *River Research and Applications* 17 (2), 387–400.

Kemp, P. S., O'Hanley, J. R., 2010. Procedures for evaluating and prioritising the removal of fish passage barriers: A synthesis. *Fisheries Management and Ecology* 17 (4), 297–322.

Kemp, P. S., Russon, I. J., Waterson, B., O'Hanley, J. R., Pess, G. R., 2008. Recommendations for a "Coarse-Resolution Rapid-Assessment" methodology to assess barriers to fish migration and associated prioritization tools - Final report. Tech. rep., Scottish Environment Protection Agency, Stirling, UK.

King, S., O'Hanley, J. R., 2016. Optimal fish passage barrier removal - Revisited. *River Research and Applications* 32 (3), 418–4289.

Kocovsky, P. M., Ross, R. M., Dropkin, D. S., 2009. Prioritizing removal of dams for passage of diadromous fishes on a major river system. *River Research and Applications* 25 (2), 107–117.

Kuby, M. J., Fagan, W. F., ReVelle, C. S., Graf, W. L., 2005. A multiobjective optimization model for dam removal: An example trading off salmon passage with hydropower and water storage in the Willamette basin. *Advances in Water Resources* 28 (8), 845–855.

Liermann, C., Nilsson, C., Robertson, J., Ng, R., 2012. Implications of dam obstruction for global freshwater fish diversity. *Bioscience* 62 (6), 539–548.

Lucas, M., Baras, E., 2001. Migration of freshwater fishes. Blackwell Science, Oxford, UK.

Lucas, M., Bub, D., Minh-Ho, J., Kyong, H., Masters, J., 2009. Availability of and access to critical habitats in regulated rivers: Effects of low-head barriers on threatened lampreys. *Freshwater Biology* 54, 621–634.

MacDonald, D., Morrison, M., Rose, J., Boyle, K., 2011. Valuing a multistate river: The case of the River Murray. *The Australian Journal of Agricultural and Resource Economics* 55, 374–392.

MacPherson, L. M., Sullivan, M. G., Foote, A. L., 2012. Effects of culverts of stream fish assemblages in the Alberta foothills. *North American Journal of Fisheries Management* 32 (3), 480–490.

Mahlum, S., Cote, D., Wiersma, Y. F., Kehler, D., Clarke, K. D., 2014a. Evaluating the barrier assessment techniques derived from FishXing software and the upstream movement of brook trout through road culverts. *Transactions of the American Fisheries Society* 143 (1), 39–58.

Mahlum, S., Kehler, D., Cote, D., Wiersma, Y. F., Stanfield, L., 2014b. Assessing the biological relevance of aquatic connectivity to stream fish communities. *Canadian Journal of Fisheries and Aquatic Sciences* 71 (12), 1852–1863.

Minor, E., Urban, D., 2007. Graph theory as a proxy for spatially explicit population models in conservation planning. *Ecological Applications* 17 (6), 1771–1782.

Morrison, M., Bennett, J., 2004. Valuing New South Wales rivers for use in benefits transfer. *The Australian Journal of Agricultural and Resource Economics* 48 (4), 591–611.

Nilsson, C., Reidy, C. A., Dynesius, M., Revenga, C., 2005. Fragmentation and flow regulation of the world's large river systems. *Science* 308 (5720), 405–408.

Numm, A., Cowx, I., 2012. Restoring river connectivity: Prioritizing passage improvements for diadromous fishes and lampreys. *Ambio* 41, 402–409.

O'Connor, J., Duda, J., Grant, G., 2015. 1000 dams down and counting. *Science* 348 (6234), 496–497.

O'Hanley, J., 2009. Using the right tool to get the job done - Recommendations on the use of exact and heuristics methods for solving resource allocation problems in environmental planning and management. *Biological Conservation* 142 (4), 697–698.

O'Hanley, J. R., 2011. Open rivers: Barrier removal planning and the restoration of free-flowing rivers. *Journal of Environmental Management* 92 (12), 3112–3120.

- O'Hanley, J. R., Scaparra, P. M., Garcia, S., 2013a. Probability chains: A general linearization technique for modelling reliability in facility location and related problems. *European Journal of Operational Research* 230 (1), 63–75.
- O'Hanley, J. R., Tomberlin, D., 2005. Optimizing the removal of small fish passage barriers. *Environmental Modelling and Assessment* 10, 85–98.
- O'Hanley, J. R., Wright, J., Diebel, M., Fedora, M., Soucy, C., 2013b. Restoring stream habitat connectivity: A proposed method for prioritizing the removal of resident fish passage barriers. *Journal of Environmental Management* 125, 19–27.
- Ovidio, M., Philippart, J. C., 2002. The impact of small physical obstacles on upstream movements of six species of fish. *Hydrobiologia* 483, 55–69.
- Paulsen, C., Wernstedt, K., 1995. Cost-effectiveness analysis for complex managed hydrosystems: An application to the Columbia River basin. *Journal of Environmental Economics and Management* 28, 388–400.
- Pringle, C., 2003. What is hydrologic connectivity and why is it ecologically important? *Hydrological Processes* 17 (13), 2685–2689.
- Roni, P., Beechie, T. J., Bilby, R. E., Leonetti, F. E., Pollock, M. M., Pess, G. R., 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. *North American Journal of Fisheries Management* 22 (1), 1–20.
- SNIFFER, 2010. Trialling of the methodology for quantifying the impacts of obstacles to fish passage: Final report, WFD111 Phase 2a. Tech. rep., Scotland & Northern Ireland Forum for Environmental Research, Edinburgh, UK.
- Stanford, J. A., Ward, J., Liss, W. J., Frissell, C. A., Williams, R. N., Lichatowich, J. A., Coutant, C. C., 1996. A general protocol for restoration of regulated rivers. *Regulated Rivers: Research & Management* 12, 391 – 413.
- Taylor, R. N., Love, M., 2003. Part IX: Fish passage evaluation at stream crossings. California Department of Fish and Game, Sacramento.
- Travade, F., Larinier, M., 2002. Fish locks and fish lifts. *Bulletin Francais De La Peche et de la Pisciculture* 364 (1), 102–118.
- WDFW, 2009. Fish passage and surface water diversion screening assessment and prioritization manual. Washington Department of Fish and Wildlife, Olympia, WA.

Wofford, J., Gresswell, R., Banks, M., 2005. Influence of barriers to movement on within watershed genetic variation of coastal cutthroat trout. *Ecological Applications* 15 (2), 628–637.

Zheng, P. Q., Hobbs, B. F., Koonce, J. F., 2009. Optimizing multiple dam removals under multiple objectives: Linking tributary habitat and the Lake Erie ecosystem. *Water Resources Research* 45 (12), W12417.

Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. Linearization of the barrier optimization model.

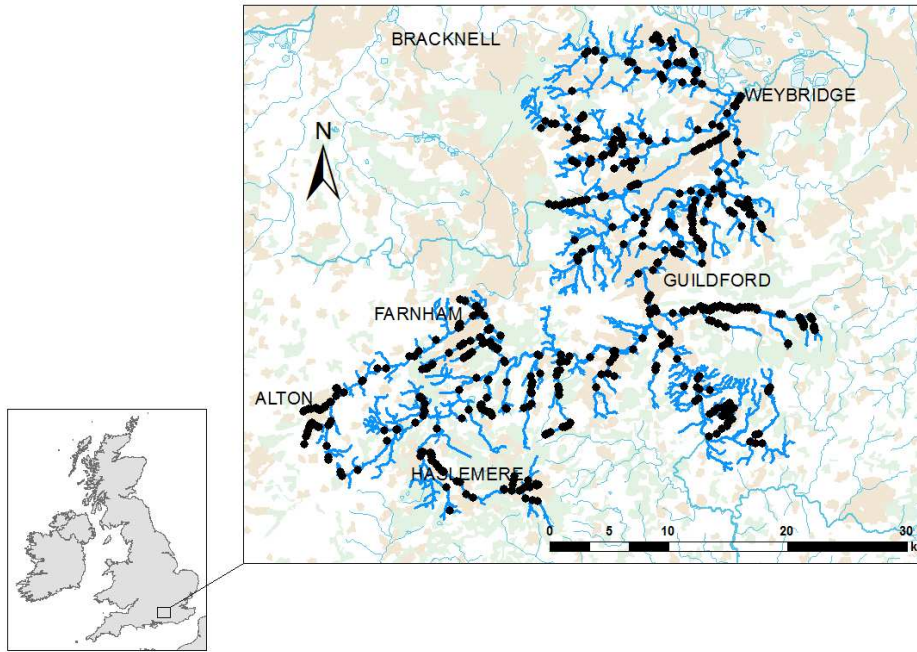


Figure 1: Location and extent of the River Wey catchment. Barriers are represented by black dots.

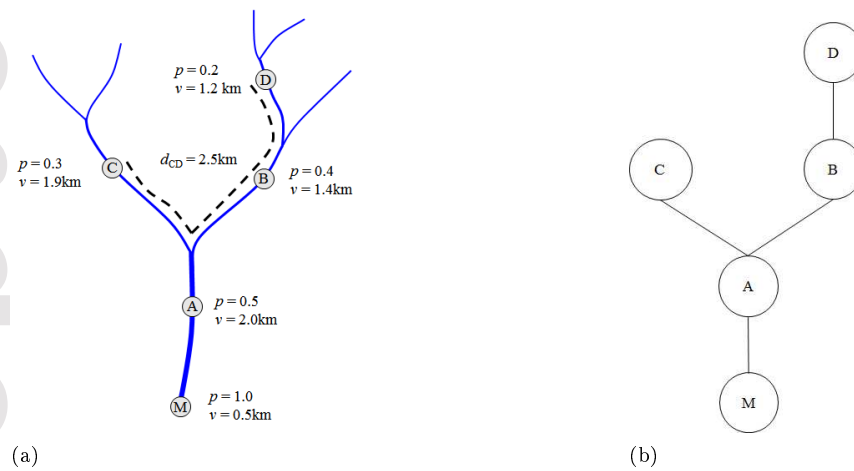


Figure 2: Example of a river barrier network represented spatially (a) and as an equivalent dendritic ecological network (DEN) (b). Note that barrier M is a dummy barrier located at the river mouth with initial passability 1 to ensure that all habitat in the river system is captured in the DEN. In (a), the bidirectional passability p of each barrier and the amount of river habitat v in the subnetwork above each barrier are provided. The value d_{CD} denotes the minimum distance from subnetwork C to D.

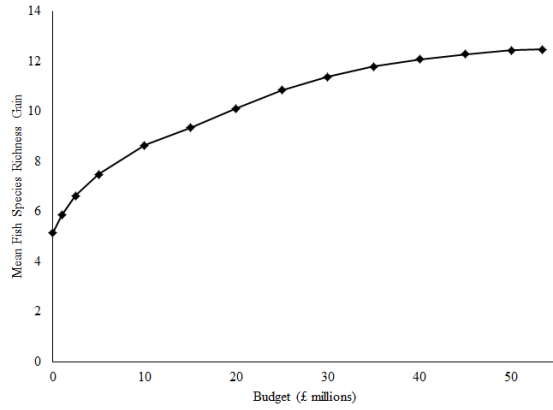
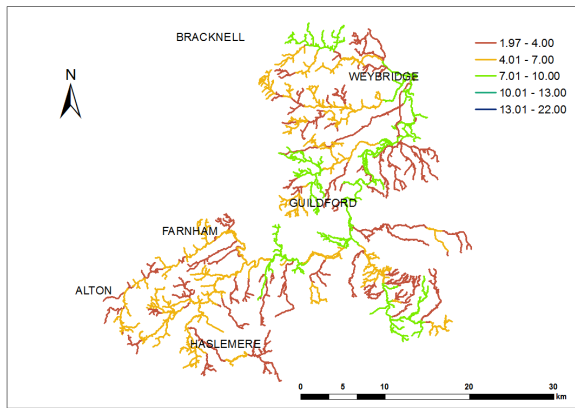
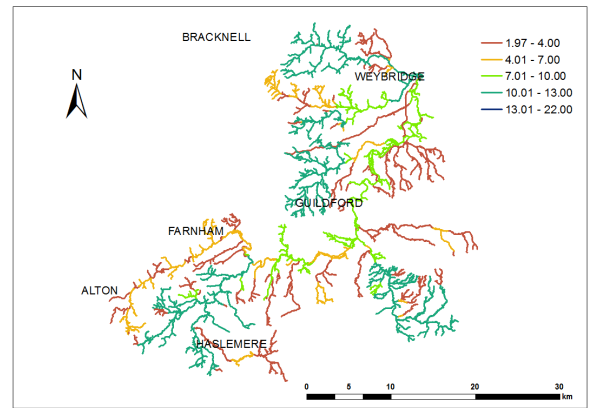


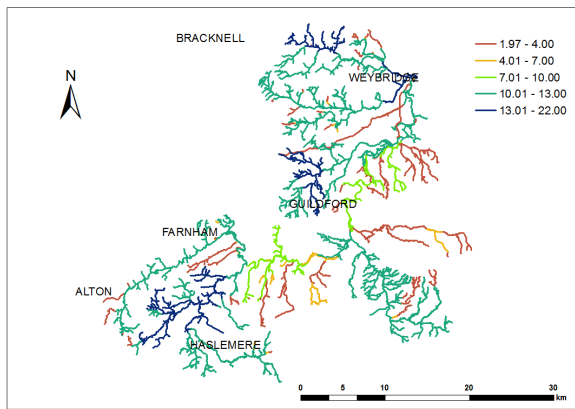
Figure 3: Mean species richness versus budget for the River Wey catchment.



(a)

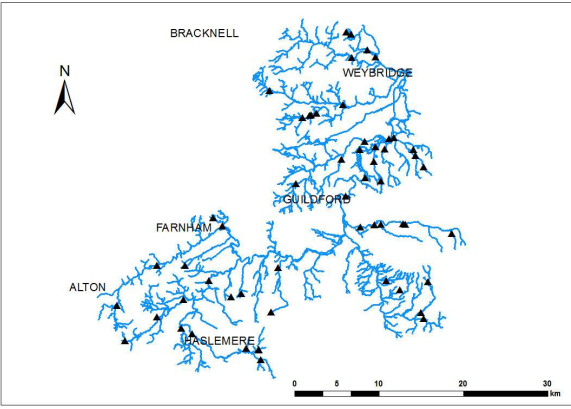


(b)

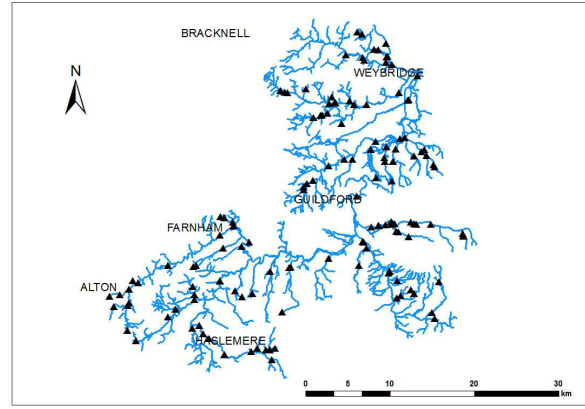


(c)

Figure 4: Distribution of species richness in the River Wey catchment at budgets of £0M (a), £5M (b), and £20M (c).



(a)



(b)

Figure 5: Barriers targeted for mitigation in the River Wey catchment at budgets of £5M (a) and £15M (b). Selected barriers are represented by black triangles.

Table 1: Barrier assessment criteria for assigning adult brown trout (*S. trutta*) upstream passability scores. Additional criteria used for determining passability scores not presented here include the availability of resting locations, level of turbulence, the presence of lips, standing waves, or debris, the gap width, and the minimum step length.

Assessment Criteria	Passability Score			
	1.0	0.6	0.3	0.0
All structures				
Water depth (m)	≥ 0.10	0.075 - 0.09	0.06 - 0.074	≤ 0.05
Velocity (m/s)	≤ 2	2.1 - 2.5	2.6 - 2.9	≥ 3
If leap barrier				
Hydraulic head (m)	≤ 0.40	0.41 - 0.60	0.61 - 0.99	≥ 1.0
Pool depth (% hydraulic head)	≥ 100	≥ 80	≥ 30	< 30
If slope/swim barrier				
Effective length (m)	≤ 10	11 - 30	31 - 99	≥ 100
Slope (%)				
If effective length $\leq 3\text{m}$	≤ 25	26 - 40	41 - 59	≥ 60
If effective length 4-9m	≤ 15	16 - 20	21 - 39	≥ 40
If effective length $\geq 10\text{m}$	≤ 5	6 - 10	11 - 14	≥ 15

Table 2: Barrier assessment criteria for assigning adult brown trout (*S. trutta*) downstream passability scores. Hazards include the presence of any features damaging to downstream migrants.

Assessment Criteria	Passability Score			
	1.0	0.6	0.3	0.0
Crest/inlet water depth (m)	≥ 0.1	0.075 - 0.09	0.06 - 0.074	≤ 0.05
Minimum gap width (m)	> 0.3	0.20 - 0.30	0.10 - 0.19	< 0.10
Hazards	Not present		Present	
Debris	Unrestricted passage	Restricted passage		Prevents passage

Table 3: Notation used in the C metric.

Symbol	Definition
J	Set of all natural and artificial barriers (aka subnetworks), indexed by j , k , and ℓ
m	The number of habitat types within the study area, indexed by h
v_{jh}	Amount of habitat type h in subnetwork j
v_j	Total amount of habitat in subnetwork j
p_j	Bidirectional passability of barrier j
B_{jk}	The set of barriers along the path from origin subnetwork j to destination subnetwork k
d_{jk}	Distance between subnetworks j and k
d_0	Dispersal distance of the focal fish species, taxa, guild, etc.

Table 4: Statistical model results for predicting fish species absence in the River Wey.

Parameter	OLS	Generalized Poisson	
	Est. (s.e.)	Est. (s.e.)	dy/dx (s.e.)
β_0	17.65 (0.90)**	2.89 (0.076)**	-
β_1	-12.73 (5.25)*	-0.93 (0.32)**	-14.28 (4.96)*
β_2	-0.0052 (6.2×10^{-4})**	-0.00037 (4.6×10^{-5})**	-0.0056 (6.7×10^{-4})**
θ	-	-0.035 (0.0025)**	
R ²	0.46	-	
pseudo-R ²	-	0.16	
AIC	510.6	509.6	

*Significant at the 5% level.

**Significant at the 1% level.

Table 5: Key attributes of barrier mitigation solutions at selected budget values. The column “All” provides a breakdown, by attribute, of the 650 artificial candidate barriers in the River Wey catchment. In the upper portion of the table, the number of selected barriers of a particular category is shown. The category “Other” comprises bridge aprons, mills, and a man-made cascade. In the middle portion of the table, the relative position (Strahler stream order) of targeted barriers within the river network is shown. In the lower portion of the table, selected attributes are provided. This includes the number of barriers with head differences $\geq 1\text{m}$ (Large), average initial passability (Passability), average cost of barrier mitigation (Cost), and the average net upstream length of river immediately above a barrier (Net USL).

Attribute	All	Budget (£M)										
		5	10	15	20	25	30	35	40	45	50	53.4
Dams / Weirs	265	37	55	80	106	121	134	160	178	220	253	265
Culverts	268	13	34	48	65	97	133	163	202	213	253	268
Sluices	41	3	7	14	20	25	27	31	32	37	39	41
Screens	30	1	3	3	7	8	9	12	19	23	30	30
Locks	34	0	0	0	0	0	0	2	4	4	5	34
Other	12	3	7	8	11	12	12	12	12	12	12	12
Total	650	57	106	153	209	263	315	380	447	509	592	650
Order 1-2	315	2	14	20	22	37	68	114	161	185	258	315
Order 3-4	278	42	64	96	148	183	200	209	229	267	277	278
Order 5-6	57	13	28	37	39	43	47	57	57	57	57	57
Large	67	7	17	29	36	42	59	59	62	67	67	67
Passability	0.12	0.06	0.11	0.10	0.10	0.10	0.11	0.11	0.12	0.12	0.12	0.12
Cost (£k)	82.1	87.6	93.8	97.7	95.6	95.0	95.2	92.1	89.5	88.4	84.4	82.1
Net USL (km)	1.7	7.5	5.7	4.6	3.8	3.3	3.0	2.6	2.3	2.1	1.8	1.7