Integration of juvenile habitat quality and river connectivity models to understand and prioritise the management of barriers for Atlantic salmon populations across spatial scales

Author details

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Abstract

Diadromous fish populations are strongly affected by in-stream barriers that cause river network fragmentation, constraining productivity or preventing completion of their lifecycle. Removal or reduction of barrier impacts is a restoration measure associated with unambiguous benefits. Management of barriers is therefore often prioritised above other restoration actions. Barrier management is prioritised at local and national scales depending on funding. However, barrier prioritisation is potentially sub-optimal because existing tools do not consider habitat quality. Furthermore, effects of partial barriers (those passable under certain conditions) are uncertain, depending on location and potential cumulative effects.

A framework is presented for assessing effects of impassable manmade barriers (IMBs) on longitudinal river network connectivity (percentage of upstream habitat accessible from the river mouth) for Atlantic salmon across spatial scales, using Scotland as an example. The framework integrates juvenile habitat quality and network connectivity models to (1) provide information necessary for local and national prioritisation of barriers, and (2) assess potential effects of passable manmade barriers (PMBs) within a sensitivity framework.

If only IMBs are considered, high levels of longitudinal connectivity are observed across most of Scotland's rivers. Barrier prioritisation is sensitive to habitat weighting: not accounting for habitat quality can lead to over- or underestimating the importance of IMBs. Prioritisation is also highly sensitive to the passability of PMBs: if passability drops to <97% (combined up- and downstream passability), the mean effect of PMBs becomes greater than IMBs at the national level. Moreover, impacts on catchment connectivity, and thus production (number of juvenile salmon produced by the river), could be severe, suggesting a better understanding of the passability of PMBs is important for future management of migration barriers. The presented framework can be transferred to other catchments, regions, or countries where necessary data are available, making it a valuable tool to the broader restoration community.

Key words: River connectivity; barriers to migration; restoration; barrier prioritisation; scalable; habitat quality

1 Introduction

River regulation and the construction of barriers for hydropower generation, irrigation, and drinking water supply has led to a global increase in the number of anthropogenically impacted water bodies (Grill *et al.* 2015). Fragmentation of river networks can increase the isolation of fish (sub)populations (Campbell Grant, Lowe & Fagan 2007; Schick & Lindley 2007), which are likely to be less robust to environmental perturbations (Freeman *et al.* 2001; Shrimpton & Heath 2003; Junge *et al.* 2014).

Diadromous species like Atlantic salmon (*Salmo salar)*, European eel (*Anguilla anguilla)* and migratory Brown trout (*Salmo trutta*, sea trout) are particularly sensitive to barriers, as juvenile and adult life stages must make extensive migrations across the freshwater environment (e.g., Thorstad *et al.* 2010). Barriers are therefore a potentially important constraint on production and population persistence where access to and from spawning and rearing habitats is limited (Holbrook, Kinnison & Zydlewski 2011; Brown *et al.* 2013), prevented (Gephard & McMenemy 2004), or delayed (Venditti, Rondorf & Kraut 2000; Anon 2009; Nyqvist *et al.* 2017a).

Atlantic salmon is a species of high economic and conservation value that occurs throughout the North Atlantic (Jonsson & Jonsson 2011) and is frequently the focus of fisheries management. Scottish salmon stocks are estimated to make up 74% and 29% of the UK and European pre-fishery abundance respectively (ICES 2017) and to be worth ca. £80 million per annum to the Scottish economy (PACEC 2017). Barriers to migration are also a frequent cause of ecological status downgrades under the Water Framework Directive (Water Framework Directive 2000/60/EC). Consequently, considerable funding is spent each year on barrier improvement works using both national (Scottish Environment Protection Agency Water Environment Fund) and local funding schemes. However, there is currently no consistent quantitative assessment of the benefits of barrier removal or modifications to fish and fisheries, which is scalable to allow both national and local management decisions.

Connectivity metrics are widely applied in landscape ecology to describe the spatial connections between key landscape elements (habitat patches) and inform conservation and management (Saura & Pascual-Hortal 2007; Galpern, Manseau & Fall 2011). Recently, similar approaches have been applied to rivers (linear networks) to investigate connectivity and identify the individual and cumulative effects of barriers to migration (Cote *et al.* 2009; McKay *et al.* 2013; Branco *et al.* 2014; Malvadkar, Scatena & Leon 2015; Rincón *et al.* 2017).

Despite increasing recognition of the importance of incorporating habitat quality and functional habitats into connectivity metrics (e.g., Branco *et al.* 2014; Van Looy *et al.* 2014; Buddendorf *et al.* 2017), most previous studies of river connectivity have focussed on more readily attainable metrics of river habitat such as length (Bourne *et al.* 2011; Mahlum *et al.* 2014), wetted area (Malvadkar, Scatena & Leon 2015), or volume (Grill *et al.* 2014). Furthermore, focus has been on the effects of impassable manmade barriers (hereafter IMBs), despite increasing evidence that passable manmade barriers (hereafter PMBs) can have substantial detrimental effects (Ovidio & Philippart 2002; Maynard, Kinnison & Zydlewski 2017; Birnie-Gauvin *et al.* 2018). In many cases this reflects the challenges posed in characterising the effects of PMBs which can be highly variable and uncertain (e.g., Bunt, Castro-Santos & Haro 2012; Noonan, Grant & Jackson 2012).

There is thus a need to develop a flexible scalable approach for assessing the effects of manmade barriers on longitudinal connectivity for Atlantic salmon, that considers the production potential of different habitats, the potential effects of PMBs under a range of passability values and provides the information necessary for local and national prioritisation of management resources.

The objectives of this study are to: 1) understand and illustrate the effects of IMBs on inter-catchment variability in habitat connectivity for Atlantic salmon using a recently derived landscape - habitat quality model (Malcolm *et al.* in press); 2) develop a scalable approach for prioritising barrier removal or easement at national and local scales based on the value of habitats for Atlantic salmon; 3) determine the effect of alternative habitat quality weightings (i.e., river length, wetted area, juvenile abundance) on the assessment of barrier impacts; and 4) explore the potential importance of PMBs for connectivity within a sensitivity framework.

2 Methods

2.1 Study site

Scotland has over >16000 individual river catchments draining to the sea (Jackson *et al.* 2018). Its climate is characterised by a North-South mean annual air temperature gradient ranging from 5.8 – 7.6˚C and East-West precipitation gradient of 700 - 4000mm (Soulsby *et al.* 2009; Jackson *et al.* 2018). For the purposes of this study, small coastal catchments (<10km^2) which are generally unproductive for salmon were excluded from the analysis leaving 628 so-called “baseline” catchments (Figure 1). It was not possible to obtain juvenile salmon density weightings for the Orkney and Shetland Islands due to a lack of electrofishing data (Malcolm *et al.* in press). Consequently, these areas were also excluded from the current analysis leaving a final set of 605 catchments, of which 221 contain manmade barriers to fish migration (Figure 1).

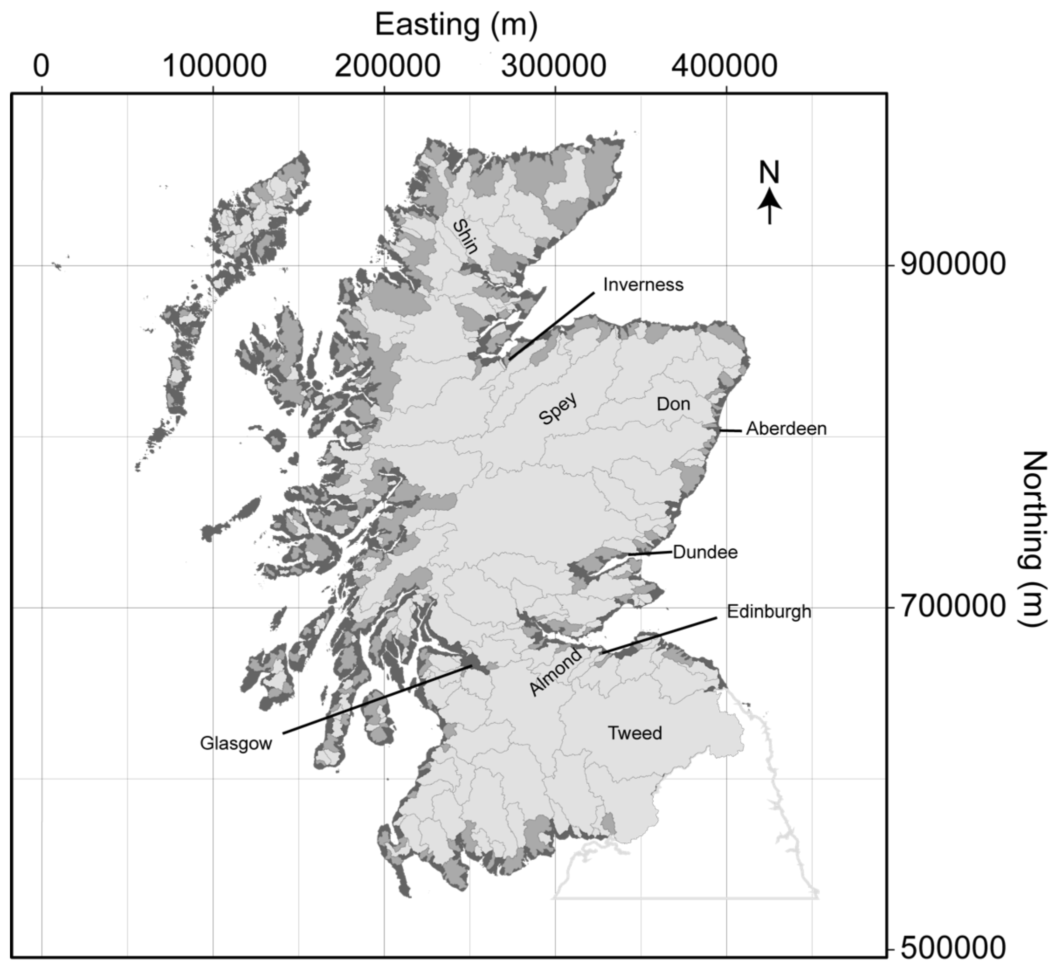


Figure 1: Map of Scotland. Light grey shows baseline catchments (>10km^2) with barriers to fish migration. Dark grey includes either coastal catchments or baseline catchments without barriers. River catchments mentioned in text are named. Larger urban areas are identified by a solid black line and associated text.

2.2 Spatial data

A detailed description of the spatial data and covariates used in this study is provided in Jackson *et al.* (2017). However, in brief, all analyses were performed on a topologically corrected version of the Centre for Ecology and Hydrology (CEH) digital river network (hereafter DRN). Prior to analysis, any standing waters or rivers above impassable natural barriers were assigned a zero weighting as these habitats are either inaccessible or considered to be of negligible value for juvenile salmon production. River widths were derived from the Ordnance Survey MasterMap Water Polygons dataset using the methods described by Jackson *et al.* (2017), but with a number of adjustments. These were implemented because small rivers (<2m) are represented as line features in the MasterMap dataset and cannot be automatically assigned a width. Furthermore, zero widths can be obtained where there is poor spatial agreement between the DRN and MasterMap data. Finally, rivers entering lochs (large polygons) can sometimes be characterised by exaggerated widths, taking information from the nearby lochs polygon. To address these constraints a pragmatic rule based system was used to ensure that all rivers were assigned realistic widths. Firstly, any river sections in Strahler river orders 2-8 with zero widths were assigned half the median width of all non-zero values for that order. Secondly, any order 1 rivers with zero widths were assigned half the median value of river order 2 rivers. This was because river orders 1 and 2 have been shown to have similar median widths (Hughes, Kaufmann & Weber 2011; Downing 2012). Finally, unrealistically high width values were removed by replacing any widths greater than the 90^{th} percentile with the 90^{th} percentile. The choice of the 90^{th} percentile was again pragmatic following visual assessment of the size distribution of width values.

2.3 Scottish barriers dataset

The passability of barriers was informed by the Scottish Obstacles to Fish Migration data set (see: https://www.sepa.org.uk/environment/environmental-data/, accessed 13-Aug-2018). The dataset contains information on the location of barriers on the river network, whether they are natural or manmade and whether they are impassable or passable under certain conditions. These data were initially collated in the 1980s by staff from Marine Scotland Science using information provided by District Salmon Fishery Boards, Fisheries Trusts and local angling clubs (Gardiner & Egglishaw 1986). A major update to the dataset was carried out in 2006 when the data were added to the CEH digital rivers network alongside information on salmon distribution (Anon 2009). Since 2008, the dataset has been maintained and updated by the Scottish Environment Protection Agency (SEPA, Table 1). In the dataset, barriers are considered “impassable” when <20% of fish are considered able to pass a barrier in an upstream direction.

For the purposes of this analysis, IMBs and impassable natural barriers were assigned a passability value of 0, hence these are full barriers to migration (Groups 1 and 3 in Table 1). Natural barriers that are passable under certain conditions were assumed to have a passability of 1, meaning they were assumed to be passable 100% of the time in an up- and downstream direction (Group 2 in Table 1). This is recognised as a simplification, but is a pragmatic approach where detailed local information is not available on the passability of individual barriers and natural barriers were not the focus of the study. PMBs were assumed to be fully passable except where the potential effects of changing passability were explored (Objective 4). The proportion of IMBs and PMBs were similar and make up ca. 20% and 27% of all barriers or ca. 43% and 57% of manmade barriers, respectively (Group 3 and 4, Table 1).

Table 1: Passability scores of barriers to fish migration. The scores result from the product for up and downstream passability.

Group	**Description of barrier passability in data set**	**Passability (up * down)**	**Passability range explored (up * down)**	**Percentage occurrence**
1	Impassable natural barrier	0	0	38
2	Passable natural barrier	1	1	15
3	Impassable manmade barrier	0	0	20
4	Passable manmade barrier	1	0.5 – 1	27

2.4 Juvenile salmon density

Atlantic salmon fry densities were predicted for each river segment using landscape covariates (upstream catchment area (UCA), river distance to sea, and altitude) and the national juvenile salmon density model for Scotland developed by Malcolm *et al.* (in press). This model predicts the benchmark densities for reaches of river, assuming habitat was fully stocked by spawners, in the absence of anthropogenic pressures. Because the national juvenile density model becomes increasingly uncertain for large rivers (>257km^2) where electrofishing data are sparse, biased or unreliable, all UCA values for density prediction in river segments where the UCA > 257km^2 were capped at 257km^2. In practice this prevents unrealistically high predictions of fish abundance in large mainstem rivers.

2.5 Dendritic Connectivity Index

Given the focus on a diadromous species, the Dendritic Connectivity Index (DCI) was used to assess the impacts of barriers on longitudinal connectivity (Cote *et al.* 2009). The standard index is denoted as DCI_d, where values returned are between 0 – 100%. A value of 100% would be in a river network with no barriers, where all potential habitat (i.e., rivers below natural impassable barriers) is accessible from the outflow. DCI_d is calculated as follows:

$$DCI_d = \sum_{i=1}^{n} \frac{l_i}{L} \left(\prod_{m=1}^{M} p_m^u p_m^d \right) \times 100$$

Where L = total river length (m); p_m^u and p_m^d = upstream and downstream passabilities of barriers m that exist between the downstream section (outlet) and section i (a river segment); l_i = summed river length (m) of reaches x within river section i.

Where information on habitat quality is available, this can be used to emphasise the ecological/functional importance of river segments, providing a more ecologically relevant measure of impact compared to basic measures of river length or wetted area. In these cases, the metric of habitat quality in each river reach can be used to replace (l_i) and the sum of the habitat quality metric replaces (L). The habitat weighting (L) used in this study was the total sum of national juvenile Atlantic salmon production, which was calculated as the product of the river length, channel width and density predictions from the national juvenile density model for Scotland (Malcolm *et al.* in press). This measure of DCI was scaled to (1) the total potential production of salmon fry in each catchment (DCI_{Catch}) and (2) the total potential production of salmon fry in Scotland (DCI_{Scot}) by varying L. The former approach provided an assessment of inter-catchment variability in connectivity and the latter provided an approach for ranking barrier impacts at both national and local scales and for assessing the potential impacts of PMBs.

2.6 Assessing the impacts of IMBs

For each river catchment, based on the number of times a barrier occurred on a shortest path between each river segment and the catchment outflow, barriers were "removed" by sequentially changing their passability value to 1 (i.e. fully passable), working in an upstream direction (i.e., working from high to low counts, where high counts are barriers that are encountered most) and recalculating the DCI.

The increase in connectivity associated with barrier removal was recorded as ΔDCI_{Scot}. This indicates the percentage increase in connectivity at a national level and thus provides a basis for ranking and prioritising the removal or easing of barriers to migration based on environmental gain at both local and national scales. ΔDCI_{Scot} assumes all downstream IMBs are also removed. Cumulative gain is calculated by summing the ΔDCI_{Scot} of the barrier of interest with the ΔDCI_{Scot} of downstream IMBs. The effect of alternative habitat weightings on barrier rankings was explored, by repeating the analysis, replacing salmon production with river length (ΔDCI_{ScotL}) and wetted area (ΔDCI_{ScotWA}). The change in barrier rankings with different habitat weightings was then summarised with individual examples to illustrate where large differences occurred.

2.7 Assessing the potential impact of PMBs

The potential effect of PMBs on connectivity was explored by sequentially reducing the passability of PMBs from 100% to 50% at 1% intervals. At each iteration, the effect of removing barriers was assessed by recording the ΔDCI_{Scot} for each barrier. Barriers were then ranked and the mean ΔDCI_{Scot}

for PMBs was compared to the mean ΔDCI_{Scot} for IMBs for each value of passability. This allowed the relative importance of IMBs (n = 513) and PMBs (n = 917) to be compared depending on the passability of PMBs. DCI_{Catch} was also calculated for each catchment and passability value to visualise the effects of changing PMB passability on catchment scale connectivity.

3 Results

3.1 Effects of IMBs on catchment scale connectivity

IMBs only had a small effect on connectivity in most catchments (Figure 2). Across Scotland 92% of catchments had a DCI_{Catch} value of >95%, while only ca. 3% of catchments had a DCI_{Catch} value of <25%. Catchments with low DCI_{Catch} values were typically small catchments, those situated in urban areas, or both (Figure 2, Appendix A).

Only 126 catchments contained IMBs. Of the top 20 impacted catchments, the DCI_{Catch} ranged from 0% - 52.3%, however, of these, 13 had an area <35km^2 (Table 2). There were three catchments where river access is prevented by an IMB at the outflow, resulting in a DCI_{Catch} value of 0%. The largest of these was the River Almond catchment (ca. 395km^2), which is located close to Edinburgh (Figure 2, Table 2). The largest catchment in the top 20 was the River Shin at ca. 583km^2 (Figure 2, Table 2) and is affected by a hydropower dam. A table showing the DCI for all catchments is provided in Appendix A.

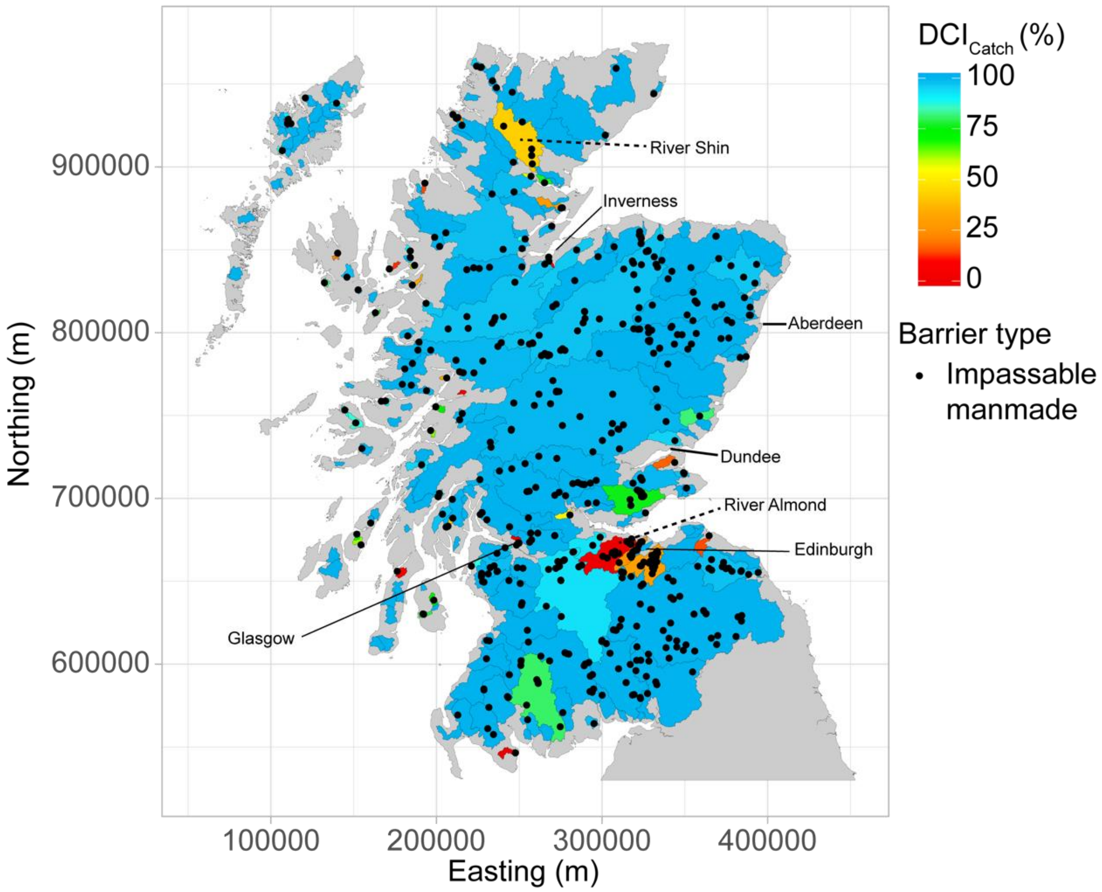


Figure 2: Map showing the effect of impassable manmade barriers on catchment connectivity. Blue colours indicate catchments where the impact of impassable manmade barrier barrier is low, red colours indicate catchments where impassable manmade barriers have a strong negative impact. Black dots show the location of impassable manmade barriers. Highlighted rivers and larger urban areas are identified by dashed and solid lines, respectively.

Table 2: Top 20 catchments most heavily impacted by impassable manmade barriers to migration. Area = total catchment area in km^2; N IMB= number of impassable manmade barriers; UCA IMB = maximum Upstream Catchment Area in km^2 affected by Impassable Manmade Barriers.

Catchment name	**DCI_{Catch}**	**Area (km^2)**	**N IMB**	**UCA IMB (km^2)**
Allt Nathrach	0	10.2	1	10.2
Duntocher Burn	0	18.8	3	18.4
Mill Burn	0	10.4	2	8.8

Dowalton Burn	0	33.7	1	31.1
River Almond	0	394.8	11	369.2
Clachan Burn	2.99	28.8	1	13.3
Abhainn Giosla	7.03	16.7	2	15.3
River Toscaig	12.67	13.9	1	13.2
Allt Bad an Luig	14.46	13.7	1	11.7
Biel Water	14.82	60.2	1	56.5
Motray Water	17.13	62.7	1	58.0
Allt Garbh	20.49	14.5	1	11.6
Oldany River	25.91	20.8	3	17.8
Water of Leith	26.37	117.4	13	109.7
Balnagown River	29.36	59.5	2	74.0
River Esk	31.26	323.4	17	152.6
Abhainn Sron a Chreagain	33.35	11.4	1	9.7
Allt Cleann Udalain	35.16	23.8	1	20.2
Glentarsan Burn	40.8	13.2	3	12.5
Lugton Water	42.13	57.1	1	42.4

3.2 Assessing and ranking the impacts of barriers to prioritise management action at national and local scales.

The impact of individual IMBs varied over 8 orders of magnitude, ranging from $5.8*10^{-9}$ to $2.27*10^{-1}$ (Figure 3). The greatest ΔDCI_{Scot} was for a weir on the River Almond near Edinburgh where removal resulted in an increase in DCI_{Scot} of 0.23% (Table 3, Figure 3). The second most important barrier was Shin dam at the lower end of Loch Shin which had a ΔDCI_{Scot} of 0.19% (Table 3, Figure 3). There were exceptional circumstances where catchments had a high DCI_{Catch} but also contained individual barriers with a high ΔDCI_{Scot}. For example, the River Spey has a DCI_{Catch} of 97.5% and the Spey dam has a ΔDCI_{Scot} of 0.17% (Table 3, Figure 3). This only occurred in the upper parts of larger catchments. A table showing the ΔDCI_{Scot} information for all IMBs is provided in Appendix B.

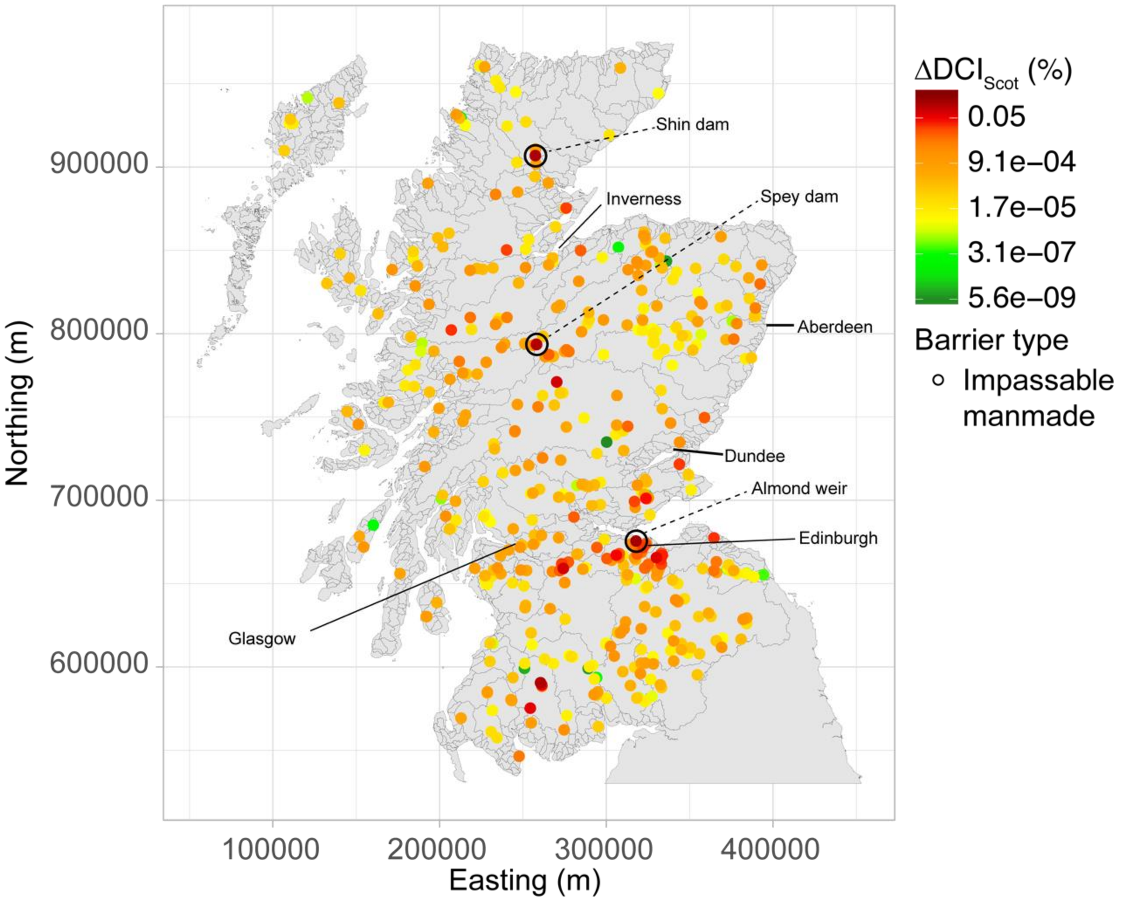


Figure 3: ΔDCI_{Scot} for impassable manmade barriers. Individually important barriers are highlighted in black circles and dashed lines; larger urban areas are identified by solid lines.

Table 3: Top 20 most important IMBs (ranked by ΔDCI_{Scot}). Barrier ID refers to the unique identifier used in the barrier dataset. Barrier type is provided where available. ΔDCI_{Scot} is the percentage increase in national connectivity where a barrier is removed. Passable Manmade Barriers/Impassable Manmade Barriers downstream are the number of passable/impassable manmade barriers downstream of a barrier. Cumulative gain is the sum of ΔDCI_{Scot} for the barrier of interest and all downstream impassable manmade barriers.

Catchment	**Barrier**	**Barrier**	**ΔDCI_{Scot}**	**PMBs**	**IMBs**	**Cumulative**

name	ID	type	(%)	downstream	downstream	gain
River Almond	20213	weir	0.228	0	0	0.228
River Shin	2727	dam	0.190	3	0	0.190
River Dee	20	dam	0.175	4	0	0.175
River Spey	2732	dam	0.168	0	0	0.168
River Tay	3602	dam	0.087	2	0	0.087
River Clyde	155	weir	0.085	2	2	0.103
River Esk	21235	weir	0.068	1	2	0.117
River Dee	20555	dam	0.067	4	0	0.067
River Dee	7	dam	0.060	3	0	0.060
River Almond	20217	weir	0.044	7	3	0.295
River Leven	3322	dam	0.037	12	6	0.047
River Esk	159	weir	0.034	1	0	0.034
Lugton Water	130	weir	0.033	0	0	0.033
River Esk	3337	weir	0.031	1	1	0.049
River Esk	3278	weir	0.031	1	1	0.064
River Ness	426	dam	0.029	4	0	0.029
Biel Water	164	weir	0.028	0	0	0.028
Water of Leith	20297	weir	0.026	3	3	0.053
Motray Water	3428	weir	0.025	0	0	0.025
River Clyde	20526	culvert	0.024	1	0	0.024

3.3 Effect of alternative habitat quality weightings on the assessment of barrier impacts

There were substantial differences in the impact rankings of individual barriers depending on the habitat weightings that were applied. The maximum differences in barrier rank between the salmon production and river length barrier assessment were -370 and 279. The maximum difference in barrier rank between the salmon production and wetted area weightings were smaller, but still substantial, ranging between -181 and 145. A comparison of all the barrier ranks across the three datasets suggests greater agreement between salmon production and wetted area (WA) weightings, than between salmon production and length weightings (Figure 4).

Assuming the production weighting provides the most appropriate prioritisation of barriers, overestimations of barrier rank occur where the WA (Fig. 5a) or length (Fig. 5c) upstream of an IMB is large but the production value (i.e. habitat quality) is small. Conversely, underestimates occur when WA (Fig. 5b) and length (Fig. 5d) upstream are small, but the production value is high.

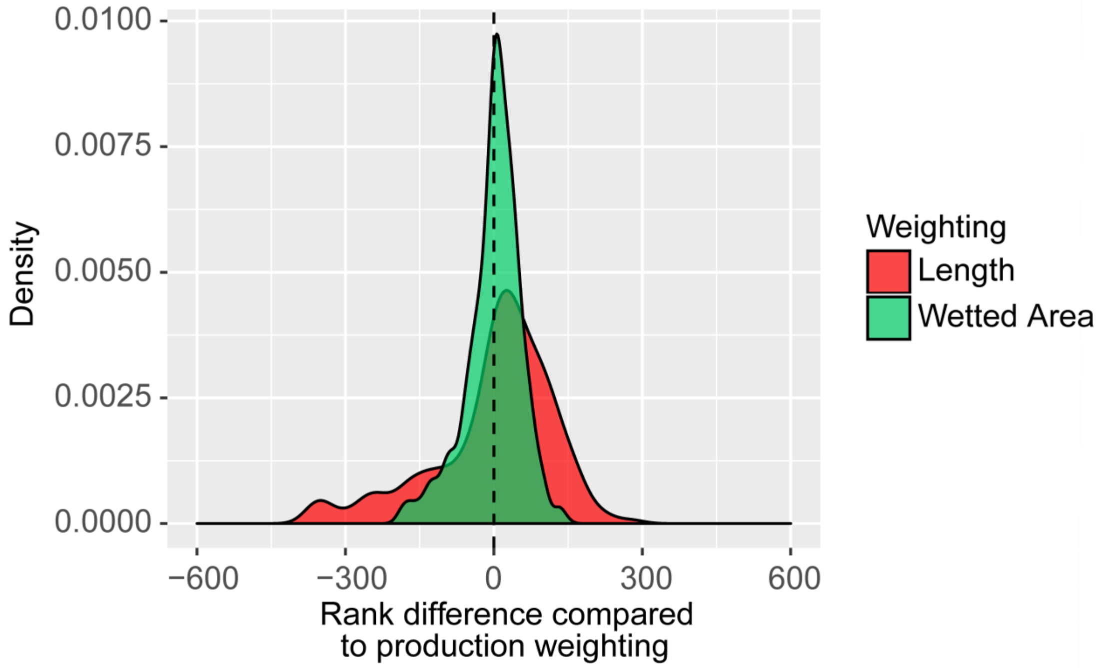


Figure 4: Density plots showing the difference in barrier rankings between scenarios where connectivity was weighted for salmon production and length (red) and for salmon production and wetted area (green). The dotted vertical line is the point where the rank of barriers is the same between the different weighting approaches.

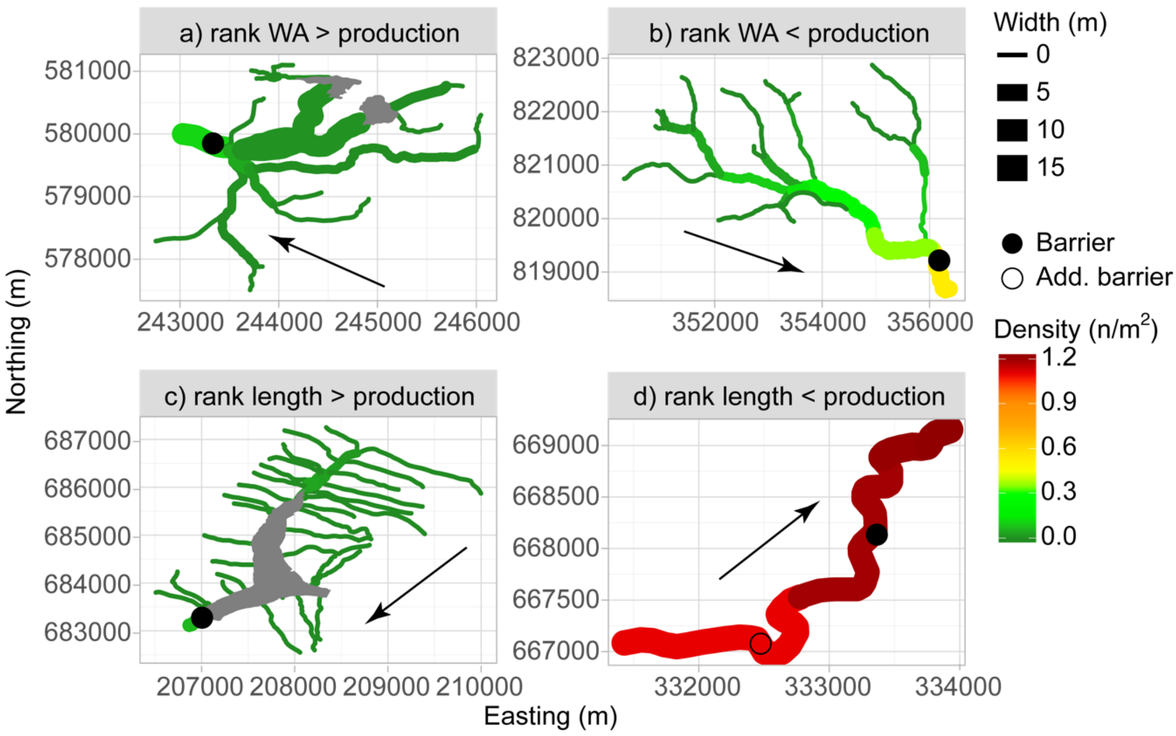


Figure 5: Example situations where a barrier's rank for an alternative connectivity weighting is markedly higher (">") or lower ("<") than for production weighting. Arrows in the subplots indicate the flow direction. Colours denote density predictions (production weighting); line thickness denotes river width; river length can be determined from the axis scales, note these differ between plots. Filled circles denote the barrier of interest, open circles show upstream IMBs. Lochs, which have no weighting values, are shown in grey.

3.4 Potential importance of PMBs for connectivity

The sensitivity analysis indicated that even small reductions in the passability of PMBs can have a substantial effect on river connectivity. Where the combined up- and downstream passability of PMBs was reduced by as little as 3%, the mean effects of PMBs would match those of current IMBs across Scotland (Figure 6). These effects can be seen in more detail in Figure 7, which shows density plots of the ΔDCI_{Scot} values for IMBs and PMBs when the passability of the latter was reduced from 100%, to 75% in 5% increments. The ΔDCI_{Scot} density plots are similar for IMBs and PMBs where passability of the latter is ca. 95%. However, at lower passability values the peak density curve for PMB increases markedly as PMBs begin to have notable effects. Changing the passability also has a marked effect on the DCI_{Catch} of particular catchments where PMBs are located close to the river mouth, for example on the Rivers Don or Tweed (Figure 7, see Figure 1 for locations).

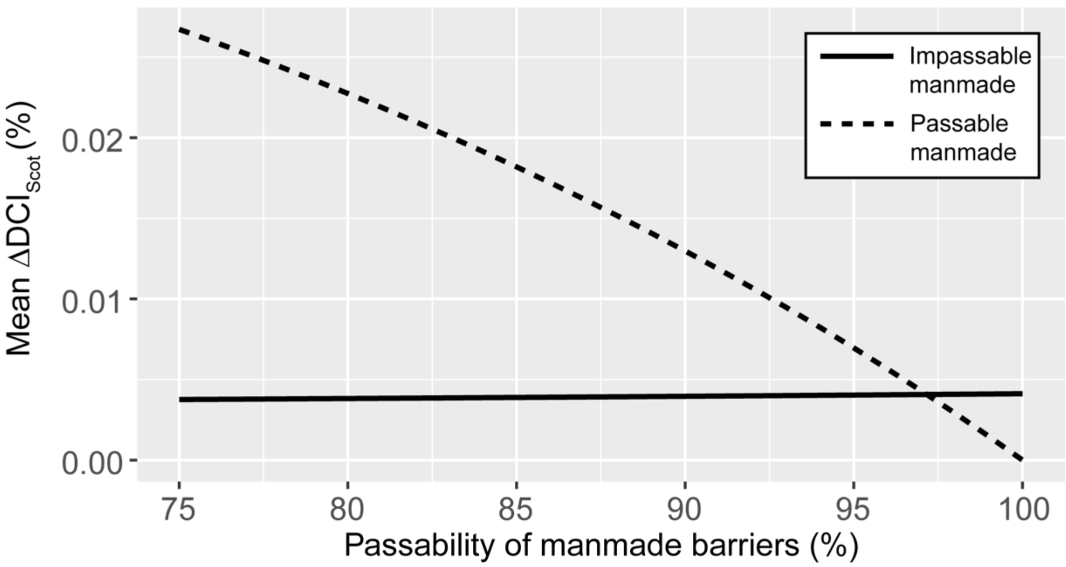
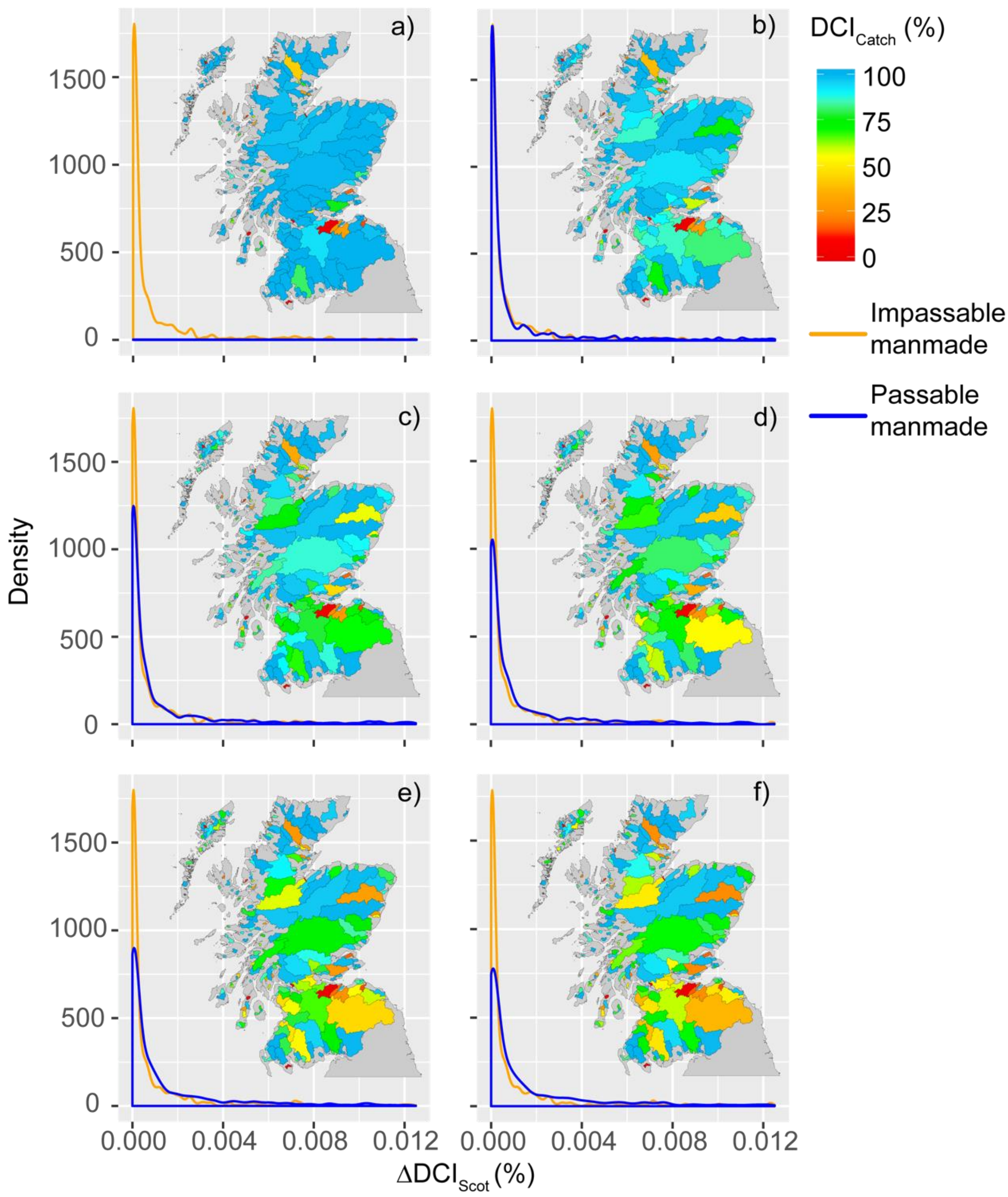


Figure 6: Mean ΔDCI_{Scot} as a function of passability values, in percentages, for passable (dotted line, n = 917) and impassable (solid line, n = 513) manmade barriers.



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305 Figure 7: Density plots of ΔDCI_{Scot} for impassable manmade barriers (yellow) and passable manmade

306 barriers (blue) where the passability of PMBs is 100%, 95%, 90%, 85%, 80%, and 75% in subplots a –

307 f, respectively. Insets a - f show the DCI_{Catch}, inset a is identical to Figure 2.

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4 Discussion

The removal of barriers to fish migration is often associated with substantial technical challenges and financial costs that are addressed through a variety of local and national funding mechanisms. It is therefore important that decision making is supported by a defensible, scalable, quantitative framework that can be used to prioritise management action across spatial scales from individual catchments to a whole country. The framework presented in this study used river connectivity models in combination with a recently developed national juvenile salmon density model to determine and rank the impacts of barriers on river connectivity. Through a simple re-ordering of this list it is possible prioritise barrier removal at both local and national scales. In combination with information of the number of downstream IMBs and PMBs, the allocation of resources can be optimised with respect to potential gains in habitat. Although previous studies have used a range of readily obtained river weightings (e.g., length and wetted area) to assess connectivity and the impact of barriers (Bourne *et al.* 2011; Pini Prato, Comoglio & Calles 2011; McKay *et al.* 2013; Rincón *et al.* 2017), relatively few have incorporated estimates of habitat quality (Branco *et al.* 2014; Shaw *et al.* 2016; Buddendorf *et al.* 2017; Erős *et al.* 2018). In this study, salmon fry production was used to infer the value and quality of habitat. Importantly, the current study suggests that the choice of weighting is important and that alternative weightings can result in substantially different assessments of barrier impacts and rankings and that this could result in sub-optimal management decisions.

The potential impacts of PMBs are often ignored, despite increasing recognition of the potential impacts they pose to migratory fish species (Gowans *et al.* 2003; Scruton *et al.* 2007; Perry *et al.* 2016; Nyqvist *et al.* 2017b; Ovidio *et al.* 2017). This likely reflects the high uncertainty that exists in defining the fish passage efficiency of particular passable barriers (Bunt, Castro-Santos & Haro 2012; Noonan, Grant & Jackson 2012). The current study explored the potential impact of PMBs by varying their passability over a range of values <100% and found that even small reductions in passability

(3%) can result in PMBs having as large an effect on connectivity as IMBs, with further compounding effects on catchment connectivity. To some extent this reflects the frequent occurrence of PMBs in large lower main-stem rivers. However, it can also reflect the presence of cumulative impacts, e.g., where there are multiple dams on a river with fish passes (Ovidio & Philippart 2002; Aarestrup & Koed 2003; Birnie-Gauvin *et al.* 2018). These findings support the view that there should be increasing focus on understanding the impacts of PMBs, by obtaining specific data on passage efficiency where barriers have the potential to substantially affect connectivity. Importantly the analytical framework used in this study can be readily updated to include more detailed knowledge on fish passage as it becomes available.

Scotland has a long history of industrial development that has affected the connectivity of its rivers through the construction of mill, weirs, lades and latterly hydropower infrastructure (Payne 1988). However, there is also a long history of fisheries management and river conservation that dates back to the formation of the River Tweed Commission in 1807, where the protection of fish passage was a primary driver. It is therefore reassuring to note that the combination of environmental protection and barrier removal in recent decades is reflected in high levels of river connectivity across most of Scotland's river catchments. Those catchments that remain heavily impacted are often small and of limited value to salmon fisheries or reflect the presence of major infrastructure that would be expensive to remove or improve (e.g., hydropower dams and infrastructure). Nevertheless, the analysis provided in the current study provides a framework for planning and funding further improvements.

4.1 Limitations and future work

The framework presented here represents a significant advance and provides a valuable management tool which can be improved as new information becomes available. It was facilitated by development of a topologically corrected DRN (Jackson *et al.* 2017), a new national juvenile density model (Malcolm *et al.* in press) and recently developed spatial data analysis packages in R.

As such, the analysis presented in this paper would not have been possible until very recently. Nevertheless, a number of limitations remain that warrant further discussion.

River width data are important to the current analysis. However, reliable river widths were not available for all rivers, particularly small rivers and those entering lochs. Furthermore, the size threshold at which width data were recorded varies between locations (e.g. 1m in urban areas and 2m in rural areas) (Ordnance Survey 2003). Finally, this analysis was completed using two complimentary datasets, the topologically corrected CEH DRN and MasterMap river polygons dataset. Because these two datasets do not show complete spatial agreement, this can generate further fine scale errors in the spatial data. Such issues are unlikely to substantially affect barrier rankings, but could affect precise DCI_{Catch} and ΔDCI_{Scot} values.

The barriers dataset used in this study is being constantly updated as barriers are added, altered or removed. However, not all barriers may be included. In particular, natural impassable barriers are likely to be underestimated. This could result in an overestimate of the availability of habitat above IMBs. In the future, improved characterisation of natural barriers will emerge from the National Electrofishing Programme for Scotland (NEPS 2018), where an understanding of salmon distribution and the presence of barriers informs the selection of sites for status assessments.

Our results show the importance of characterising the passability of barriers to reliably determine connectivity. To date, our analyses have focussed specifically on the effects of barriers on Atlantic salmon as that was the species for which the current barriers dataset was developed. Looking forwards there will need to be a re-assessment of the passability of barriers to other fish species for which management is proposed. It is recognised that this is a serious challenge as the passability of a barrier results from complex interactions between species, flow, the characteristics of the barrier and any fish passes that may be present. While obtaining this information will be a significant challenge, the current analysis framework could readily incorporate these data as they become available.

The national salmon fry density model used in this study was designed for salmon assessment purposes. Specifically, it was designed to provide a benchmark for healthy salmon populations against which electrofishing data could be compared. At present the model does not include “pressure” data in the predictions. As such it is possible that potential fish production would not be realised on removal of a barrier due to the presence of other pressures in the river system that affect production (e.g., acidification or abstraction). Future iterations of the national juvenile salmon density model will aim to incorporate the effects of hydrological and morphological pressures where these are recorded consistently at the national level thereby providing more realistic expectations of the benefits of barrier removal.

Finally, it is acknowledged that a formal cost-benefit analysis must be undertaken when prioritising barrier removal (Kuby *et al.* 2005; Kemp & O'Hanley 2010; Erős *et al.* 2018) and this is a key area of development that is not considered within the current framework. At present decision makers would need to complete a two-stage decision making process. First, this framework could be used to prioritise barriers for removal considering the presence of downstream barriers. Second, a cost benefit analysis could be undertaken which assesses the financial implications of barrier removal, while also considering the presence of other pressures and the likelihood of achieving expected benefits.

5 Conclusions

This paper presented a novel analytical framework for prioritising management action in relation to barriers at national and local scales. Atlantic salmon fry production in Scottish rivers was incorporated as the weighting for the assessment given the high economic and conservation value of the species. Comparisons to more readily available habitat weightings (length and wetted area) indicate that the use of weightings could result in poor resource allocation, although wetted area should be used in preference to river length. Finally, small changes in the passability of passable manmade barriers can result in large changes in connectivity comparable to the effects of impassable manmade barriers, emphasising the importance of improved understanding of the passability and effects of these barriers. The approach can be easily updated to account for barrier removals and improved knowledge on barrier passability. The analytical framework presented here is scalable and could be transferred to other catchments/regions/countries and species, providing the necessary spatial data, habitat and barriers datasets are available.

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