Not just a migration problem: Metapopulations, habitat shifts and gene flow are also important for fishway science and management

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Abstract

Worldwide, fishways are increasingly criticised for failing to meet conservation goals. We argue that this is largely due to the dominance of diadromous species of the Northern Hemisphere (*e.g.* Salmonidae) in the research that underpins the concepts and methods of fishway science and management. With highly diverse life histories, swimming abilities and spatial ecologies, most freshwater fish species do not conform to the stereotype imposed by this framework. This is leading to a global proliferation of fishways that are often unsuitable for native species. The vast majority of fish populations do not undertake extensive migrations between clearly separated critical habitats, yet the movement of individuals and the genetic information they carry is critically important for population viability. We briefly review some of the latest advances in spatial ecological modelling for dendritic networks to better define what it means to achieve effective fish passage at a barrier. Through a combination of critical habitat assessment and the modelling of metapopulations, climate change-driven habitat shifts and adaptive gene flow, we recommend a conceptual and methodological framework for fishway target-setting and monitoring suitable for a wide range of species. In the process, we raise a number of issues that should contribute to the ongoing debate about fish passage research and the design and monitoring of fishways.

Introduction

Structures designed to aid fish movement through river barriers, known as 'fishways' (including 'fish guidance systems' like screens and bypasses for downstream movement), are the preferred fish passage management solution worldwide. However, fishways are increasingly criticised for failing to meet conservation goals (Pompeu et al., 2012; Brown et al., 2013; McLaughlin et al., 2013; Pelicice et al., 2017). Even among those in agreement on the general utility of fishways, there is debate as to how designs should be developed and evaluated (Kemp, 2016; Williams & Katopodis, 2016; Bunt et al., 2016). A major part of the problem is that designs for single target species from the temperate Northern Hemisphere are promoted as solutions in diverse biogeographical settings worldwide (*e.g.* Quirós, 1989; Mallen-Cooper & Brand, 2007; Noonan et al., 2012; Bunt et al., 2016). However, the majority of freshwater fish exhibit vastly different life histories, swimming abilities and spatial ecologies (Winemiller, 1989; Humphries et al., 1999) to the iconic diadromous fish native to the north (*e.g. Salmo salar; Oncorhynchus* spp.).

By reviewing recent advances in spatial ecology, which we argue is presently under-represented in fishway science and management, our aim is to better define what it means to achieve effective passage at riverine barriers and to recommend a range of concepts and methods for fishway target-setting and monitoring that are applicable to a wide range of species. Our uniquely ecological perspective complements recent syntheses more firmly rooted in engineering (*e.g.* Williams et al., 2012; Silva et al., 2018).

Evaluating fishway effectiveness

Presently, the dominant framework for quantifying fishway effectiveness reduces the problem to a few simple metrics (Figure 1), often focusing only on the percentage of fish approaching from below the barrier that subsequently move upstream through the fishway ('overall fishway efficiency'; Larinier, 2008). This 'fishway efficiency' framework is highly biased towards obligate migratory populations that are strongly motivated to undertake directed movements between habitats clearly separated in space, for example diadromous salmonids (Roscoe & Hinch, 2010; Noonan et al., 2012; Bunt et al., 2016). The vast majority of freshwater fish species do not fit this definition and lack the motility or motivation to traverse hydraulic structures characterised by high mean velocities and turbulence intensities (*e.g.* spillways and fishways) or low mean velocities (*e.g.* reservoirs; Pelicice et al., 2015). Yet, in order to complete their life-cycle, all fish must undertake movements for reproduction and feeding, and to seek refuge from unfavourable conditions (Schlosser, 1991; Fausch et al., 2002). The distance of these movements for some populations may be restricted in terms of central tendency (*e.g.* <100 m; Rodríguez, 2002) but there is such variability involved that some have suggested that riverine fish should never be considered sedentary (Gowan & Fausch, 1996; Crook, 2004; Radinger & Wolter, 2014). For this reason, we prefer to use inverted commas when discussing 'non-migratory' species.

[Fig 1]

This population-level variability in dispersal distance is crucially important for processes occurring at a wide range of spatial and temporal scales (Figure 2), all of which may be impacted by anthropogenic barriers. These processes include: maintenance of gene flow (*e.g.* Frankham, 2015); recolonisation of habitats previously affected by physical disturbance and disease (*e.g.* Howell, 2006); and rescue of subpopulations otherwise bound for local extinction due to stochastic demographic processes (*e.g.* Stephens & Sutherland, 1999). Furthermore, as the climate changes, whole fish populations will need to shift distributions to adapt (Comte et al., 2014; Ruiz-Navarro et al., 2016; Radinger et al., 2017). In some cases, in-situ adaptive processes may be sufficient to adapt to climate change, but this would still require connectivity between diverse subpopulations from which genotypes can be selected (Sgro et al., 2011). At the longest timescales, species' distributions have been rebounding since the last glacial maximum and in response to orographic episodes (Consuegra et al., 2002; Zemlak et al., 2008).

[Fig 2]

Fishways must facilitate these processes, which may operate over timescales longer than those traditionally considered within the fishway efficiency framework (Figure 2). In other words, fishways must support the viability of fish populations. But how can fishway success be evaluated on this basis given the multitude of other processes, both natural and anthropogenic, acting on the community? In pondering this question, we find ourselves caught between the epistemologies of holism and reductionism (Hannah et al., 2007). Clearly, a single percentage (*e.g.* overall fishway efficiency) is tractable, easy to communicate to non-specialists and consistent with engineering traditions. Yet, equally clearly, it is challenging to reduce this complexity to a single number. Moreover, the fishway efficiency framework (Figure 1) begs the important practical question, *how much is enough*? Lucas and Baras' (2000) recommendation of 90-100% for overall fishway efficiency is often cited. However, the ecological basis for this target is restricted to only those populations with critical habitats clearly separated by the barrier in question

(Pompeu et al., 2012). More practically, in light of recent global syntheses, the target hardly seems achievable even for highly motivated migratory species (Noonan et al., 2012; Bunt et al., 2016; Wilkes et al., 2018a, b). In some instances, as we shall discuss, targeting such high efficiency may actually do more harm than good (Pompeu et al., 2012; Pelicice et al., 2017; Silva et al., 2017).

Setting ecologically realistic targets for fishway effectiveness

Alternatives to the fishway efficiency framework have been proposed and are gaining traction as operational tools. Castro-Santos and Perry (2012) proposed a time-to-event analysis that describes fish passage as a rate per unit time given environmental covariates (*e.g.* spilling regime, temperature). This is an improvement on the fishway efficiency framework and is applicable to larger-bodied migratory fish suitable for individual tracking using biotelemetry (Silva et al., 2018). Baumgartner et al. (2010) offered an alternative approach that can be applied to the whole fish community through a combination of biotelemetry (larger fish) and trapping at the fishway entrance and exit (all body sizes). However, the results of trapping campaigns are restricted to the species- and life stage- selectivity of fishways. Finally, Pompeu et al. (2012) proposed a new concept based on the occurrence of critical habitats on either side of a barrier, suggesting that even a highly 'efficient' fishway may not contribute to supporting population viability.

Whilst these alternatives represent progress over the fishway efficiency framework, they do not address all reasons why fish need to move (Figure 2). In particular, they do not cater for the needs of all fish populations to disperse in order to: (i) recolonise disturbed habitats and rescue subpopulations bound for local extinction; (ii) adapt to climate change through shifting distributions; and (iii) adapt through exchanging genetic information. Furthermore, they do not provide any quantitative mechanisms for setting targets against which the effectiveness of a fishway, in terms of its ability to support viable populations, can be evaluated. To address these gaps, we suggest the application of modelling frameworks based on: (i) metapopulation theory; (ii) species distributions and fish dispersal; and (iii) demo-genetics. Below, we identify recent advances in each of these areas and recommend approaches to specifying 'dispersal targets', *i.e.* the minimum number of individuals, as a function of population size, that fishways should pass in upstream and downstream directions to support population viability. We suggest that these targets are more realistic than the 90-100% typically targeted for migratory species with critical habitats clearly separated by barriers. We use the term 'realistic' because the targets are based on real ecological processes rather than a weak assumption that all fish must pass the barrier.

These modelling approaches may be applied to both 'non-migratory' and migratory species. However, in the latter case, the application must acknowledge that migratory species may require access to critical habitats found exclusively on either side of the barrier (Pompeu et al., 2012). As well as a minimum dispersal target, an upper limit may also be of interest, since demographic models of potamodromous fish suggest negative effects of highly 'efficient' fishways (Silva et al., 2017). In particular situations where upstream passage is favoured over downstream passage and there is a lack of suitable habitat upstream (Pompeu et al., 2012), overall fishway efficiencies of more than 10-30% have the potential to create damaging ecological sink behaviour (Pelicice & Agostinho, 2008; Silva et al., 2017). This risk is greater for high-head structures that are less likely to be drowned out during flood events, and also for structures that impound a larger body of water, thereby causing more drastic changes to habitat availability upstream.

Metapopulation theory

Fishways operate within a complex river network involving multiple habitat patches, barriers and stressors. However, with the exception of Pompeu et al. (2012), presently available conceptual frameworks for evaluating fishway efficiency focus on the immediate vicinity of a single structure. Metapopulation theory represents an appropriate foundation for better integration of the effects of large-scale spatial ecological processes, and the cumulative effects of multiple barriers and/or fishways. A metapopulation can be defined as a set of subpopulations within which local extinctions may be balanced by immigration and recolonisation (Levins, 1969). From this simple definition, it is possible to see immediately the relevance to connectivity - the viability of the metapopulation is contingent on dispersal. As yet, however, this idea has made little impact on fishway science and management. Better integration of metapopulation theory could help to define ecologically realistic dispersal targets for passage at the population level (Figure 3a-b), and across entire river networks.

[Fig 3]

Metapopulation modelling has a long history in two-dimensional terrestrial landscapes (Levins, 1969) and, although the geometry of dendritic networks precludes the direct transfer of terrestrial models to rivers (Fagan, 2002), its application to fragmented river basins has now matured to the extent that many are calling for its better integration into hydropower planning protocols (Jager et al., 2015; Hurd et al., 2016). The foundational work in metapopulation theory relied on patch occupancy models (Levins, 1969), reducing population processes within individual habitat patches to a simple statement of whether a patch is occupied (1) or not (0). Later, Stochastic Patch Occupancy Models (SPOMs) represented an advance in modelling, whereby presence-absence of a species in each suitable habitat patch was based on site-level colonisation and extinction probabilities (Hanski & Ovaskainen, 2003). This approach relies on the concept of *separability* of population (within patch) and metapopulation (among patch) processes (Drechsler & Wissel, 1997). The separability assumption supposes that because among-patch processes operate over such vastly longer temporal scales than within-patch population approaches, the latter can be safely ignored when modelling metapopulation responses. However, rivers are naturally much more connected than the mostly isolated populations first envisaged by metapopulation theory, and it would be difficult to argue separability of population and metapopulation processes.

With greater computing power, more recent efforts in modelling river network-scale metapopulations have included both within- and among-patch processes (*e.g.* Webb & Padgham, 2013), potentially providing a way forward (Erös & Campbell Grant, 2015). Under this 'graph theory' approach the river network is reduced to a series of 'nodes' (habitat patches containing subpopulations) and 'edges' (dispersal links between nodes), allowing the strength and direction of relationships between nodes to be represented (Webb & Padgham, 2013). The main benefit of this method is the ability to calculate summary statistics that define levels of connectedness for individual nodes and the entire network. For example, by parameterising the graph using alternative dispersal probabilities reflecting fishway effectiveness, a metric describing the independence (*I*) of each node (subpopulation *i*) in the network may be calculated as:

$$I_i = \sum_{j \neq i}^{n} \frac{s_{ii}}{s_{ii} + s_{j \to i}}$$

where s_{ii} is abundance of subpopulation *i*, and $s_{j \to i}$ is the number of fish emigrating from subpopulation *j* to subpopulation *i* (Schick & Lindley, 2007). By comparing *I* among different scenarios of connectivity ($s_{j \to i}$), the impact of a fishway permitting passage of a given number of fish on node independence (or 1-*I*, isolation) can be predicted.

The graph theoretical approach is conceptually simple in its application to dendritic networks but data intensive, requiring estimates of subpopulation abundances and baseline data on dispersal to compute the summary statistics. The latter could be estimated from stable isotope or genetic analyses, or predicted using existing fish dispersal models (Radinger et al., 2014; see below) if no direct empirical assessment is possible. Alternatively, modelling may be exploratory, for example focusing on the uncertainty of patch-level dispersal probabilities in order to assess the sensitivity of predictions (Fullerton et al., 2016). Graph theoretical models do not give explicit information on subpopulation viability, although more isolated subpopulations (i.e. with lower *I*) are expected to be at higher risk of local extinction, particularly if they are already small (Figure 3b). An appropriate target, therefore, would be to preserve dispersal at a level that maintains the pre-barrier values of patch- or network- scale connectivity.

Species distribution and fish dispersal

Observable shifts in species ranges are already occurring in response to climate change (Figure 3c; Walther et al., 2002; Parmesan & Yohe, 2003; Chen et al., 2011) and fish are predicted to be affected more severely than many terrestrial organisms (Comte et al., 2014). The ability of a population to keep pace with climate change is highly dependent on dispersal ability and connectivity (Radinger et al., 2017), raising obvious concerns about fish passage. Several recent applications of species distribution models (SDMs) have highlighted the severity of range shifts among numerous European fish taxa, often reporting upstream habitat shifts and the failure of populations to keep pace with the changes (Comte et al., 2014; Ruiz-Navarro et al., 2016; Radinger et al., 2017). It should be noted, however, that headwaters may be more resilient to climate change-driven habitat shifts due to topographic controls that limit the rapidity of water temperature increases (Isaak et al., 2016). As potential thermal refugia, retaining connectivity in such environments is nonetheless important.

In the context of climate change, a suitable modelling framework for predicting the sensitivity of a fish population to a new barrier is specified by Radinger et al. (2017). The framework can be applied directly to the problem of setting dispersal targets for fishways. The approach is based on SDMs constructed using boosted regression trees (BRTs) under past or present conditions or under scenarios describing climate change and management decisions. Indices quantifying the extent and direction (upstream, downstream) of habitat gains and losses are calculated for the scenarios of interest. A trait- and site- based model is then used to represent realistic fish dispersal using a leptokurtic dispersal function, i.e. a distribution of individual dispersal distances from each subpopulation (Radinger et al., 2014). The dispersal function is parameterised using empirical data on 62 riverine species showing that the form of the distribution can be predicted from fish body length, aspect ratio of the caudal fin and the stream order where the subpopulation occurs (Radinger & Wolter, 2014). Complete or partial barriers are represented in the model by restricting the passability of barriers, *i.e.* the proportion of fish approaching the barrier that subsequently traverse it. Indices derived from habitat gains and losses can then be compared under different scenarios (Radinger et al., 2018). In particular, the species-specific dispersal compensation index ($H_{dispersal:gain}$) is a useful quantity that describes the proportion of new habitat that can be reached through dispersal over a given time frame. Dispersal targets to support viable populations under climate change may be set by running the model for different values of barrier passability and focusing on a value that approaches a maximal $H_{dispersal:gain}$.

Demo-genetics

Whilst SDMs hold promise as the basis for setting dispersal targets in contexts where climate change is predicted to drive shifts into presently unoccupied habitats (Figure 3c), a different approach is required to support genotype selection for in situ adaptation of subpopulations (Figure 3d). It has long been known that barriers affect genetic variation within river networks, with isolated subpopulations found to suffer reduced genetic diversity, leading to genetic drift and loss of adaptive capacity (Wofford et al., 2005; Raeymaekers et al., 2008). This knowledge has provided the basis for demo-genetic modelling to set targets for population translocation, whilst controlling for outbreeding depression in the recipient subpopulation (*e.g.* Pavlova et al., 2017). As yet, however, the obvious application to setting targets for fishways has not been made. Below we outline a modelling procedure suitable for application to this problem.

The translocation model of Pavlova et al. (2017) was developed for *Macquaria australasica*, an endangered freshwater fish endemic to Australia. The species is threatened by range contraction and fragmentation in a landscape undergoing severe climate change. Thus, the example is highly analogous to the situation hypothesised in Figure 3d, whereby a barrier blocks gene flow between two or more populations that were previously connected via dispersal. In the modelling procedure, the outcomes of management scenarios (*e.g.* number of individuals passing a fishway) are simulated using an age-structured population model. The model performs individual-based simulations of population viability due to deterministic forces and stochastic demographic, environmental and genetic effects. Simulations proceed generation-by-generation based on observed markers, preferably from genomic regions under selection. At each time step, a number of simulations are performed (typically 500 to quantify uncertainty) and each offspring is randomly assigned one of the alleles from each parent. Several population-level metrics are reported, including probability of extinction over the modelled time period. With translocation of suitable genotypes, Pavlova et al. (2017) found that the probability of extinction in the smallest populations could be maintained at or near zero for 100 years, a substantial improvement on a 'do-nothing' scenario.

Using a similar approach, Vera-Escalona et al. (2018) found that a fixed percentage of gene flow (1%) at barriers would not be sufficient to conserve a *Galaxias platei* metapopulation in Pataogonia if hydropower development reduced population sizes by 90%. This underlines the importance of considering targets as a function of population size rather than a fixed percentage. It also reminds us that loss of connectivity is just one of the impacts that hydropower may have on fish populations, i.e. in addition to habitat quality and quantity.

Although the demo-genetic approach holds promise for setting quantitative fishway targets, there are instances where genetic connectivity is not required. In these instances, which may represent hotspots of speciation (Shelley et al., 2017) or populations bound for local extinction due to natural historical processes, intervention in the form of fishways is clearly not warranted. Only subpopulations among a wider metapopulation connected via dispersal should be considered as targets. If this is the case, a further consideration is genetic outbreeding, which must be mitigated for by: (i) only using source populations of the same karyotype as the recipient population; and (ii) ensuring that source and recipient populations have been isolated for <500 years (Frankham et al., 2011). In the context of fishways, these criteria would be met in all but the most extreme cases imaginable.

Towards diversified conceptual and methodological frameworks for fishway target-setting and monitoring

We recommend two alternative frameworks for monitoring (Figure 4). First, the classic fishway efficiency framework (see Figure 1) for the special case where critical habitats for different life-stages may only be accessed by traversing the barrier. Depending on the location of the barrier, this is likely to be the case for diadromous fish and some potamodromous populations. Consistent with our other recommendations, the population-level impacts of failing to achieve full fish passage in these circumstances should be assessed to determine whether 100% passage is truly necessary for long-term population viability. If critical habitats are found on only one side of the barrier, applications should consider if a fishway would be appropriate and, if so (*e.g.* to support fisheries), set upper limits for fishway efficiency (Silva et al., 2017). Second, the 'dispersal target' framework in situations where a barrier blocks the exchange of individuals and genetic information within a metapopulation, or prevents a distribution shift (Figure 3). This will be the case for many 'non-migratory' species, as well as potamodromous populations with access to critical habitats on both sides of the barrier (see Figure 2A of Pompeu et al., 2012). Habitat shifts are likely to be relevant for all life-histories (Comte et al., 2014; Ruiz-Navarro et al., 2016; Radinger et al., 2017).

[Fig 4]

The dispersal target framework is based on ecologically realistic targets describing the number of fish required to pass in order to support population viability, as a proportion of estimated population size. The target should be set at the maximum among the 95th percentiles of simulations performed under the three models, *i.e.* metapopulation, species distribution-fish dispersal and demo-genetics. The 95th percentile is recommended as a precautionary measure and should be based on population size estimates that account for any impacts of barriers on fish habitat independent of connectivity. This target is unlikely to exceed critical values triggering ecological sink behaviour, particularly if upstream and downstream passage are both managed effectively (Silva et al., 2017). This is to say nothing about when fish will be moving in response to environmental cues. The target, therefore, should be time-bounded based on prior knowledge of the population's movement patterns, which may include indigenous and local knowledge, or else managed adaptively depending on when fish arrive at the fishway once it is constructed. Adaptive management may also be called for if many fish are observed to be congregating near the barrier but not using the fishway, requiring alterations to the fishway and/or the attraction flow regardless of the dispersal target (Silva et al., 2012).

Whichever monitoring framework is considered appropriate (Figure 4), detail on the behaviour of fish in the vicinity of fishways and the delays associated with passage can be gained through applying time-to-event analysis if the characteristics of target species allow for the use of biotelemetry (Silva et al., 2018). In both cases, monitoring should recognise that upstream passage through a fishway is not necessarily an indicator of success if fish are trapped or disorientated in reservoirs upstream. If this is the case, methods should be in place to check that the fishway is supporting long-term population viability upstream of any impoundment, for example through stable isotope and genetic analyses. It is also important that downstream movement through reservoirs is given due consideration as drifting egg and larval stages may suffer high mortality rates due to long residence times (Pelicice et al., 2015).

We suggest the use of a range of methods to drive target-setting and monitoring (Table 1), going beyond previous recommendations exclusively limited to biotelemetry (Cooke & Hinch, 2013; Bunt et al., 2016; Silva et al., 2018), which is not feasible for a wide range of species and life-stages. For example, to implant a sufficient number of tags to detect rare, yet important dispersal events in ‘non-migratory’ species would be infeasible for large populations. Furthermore, some species and life-stages may be too small, too sensitive to handling or have unsuitable body morphologies to receive implanted tags without significant effects on growth, mortality and swimming performance, leading to bias in estimates of fishway effectiveness from tagged fish (*e.g.* Murchie et al., 2004; Moser et al., 2007). The extensive movements of dead fish may also confound results from biotelemetry studies, especially for quantifying downstream passage (Havn et al., 2017). Whilst a detailed discussion on each of the recommended alternative methods lies beyond the scope of this review, we do encourage readers to consult the original sources cited in Table 1.

Conclusions

Freshwater fish populations exhibit a wide range of life histories, swimming abilities and spatial ecologies. Despite this knowledge, the science and management of fishways has almost exclusively been dominated by concepts and methods well-suited to only a small fraction of species. For these few iconic species, whose critical habitats are clearly separated in space, the problem of passing fish at a barrier can be reduced to a set of simple metrics based on the assumption that 100% of the population must annually pass the barrier to reach critical spawning or feeding habitats on the other side. Yet a proportion of individuals of all fish populations must undertake movements of some magnitude to maintain population viability through the exchange of individuals and the genetic information they carry. These are ‘slower’ and less obvious processes than traditionally considered in fish passage research, so it seems understandable that they are only now being considered in greater detail. Fortunately, recent modelling advances now permit the setting of ecologically realistic targets for fishways to support viable populations and their adaptation to environmental change. Until now, however, such modelling approaches have remained somewhat disconnected from the concept of fishway effectiveness. It is time to embrace them as operational tools.

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Figure legends

Figure 1 Illustration of the present conceptual framework for fishway evaluations in which the ‘overall fishway efficiency’ is often taken as the product of attraction, entrance and passage efficiencies (Larinier, 2008). The turbine in this simplified example is represented as an Archimedes screw but the concept is applicable to any hydropower design.

Figure 2 The reasons why fish need to move are manifold and operate over vastly different spatial and temporal scales than traditionally considered in fish passage science and management.

Figure 3 Simplified examples of ways that barriers may affect fish populations, including qualitative targets for fishways and suitable modelling frameworks for setting quantitative targets. Nodes (open and grey circles) scaled to subpopulation size. To go from these crudely defined, qualitative targets to quantitative targets, a set of spatial ecological modelling approaches can be applied.

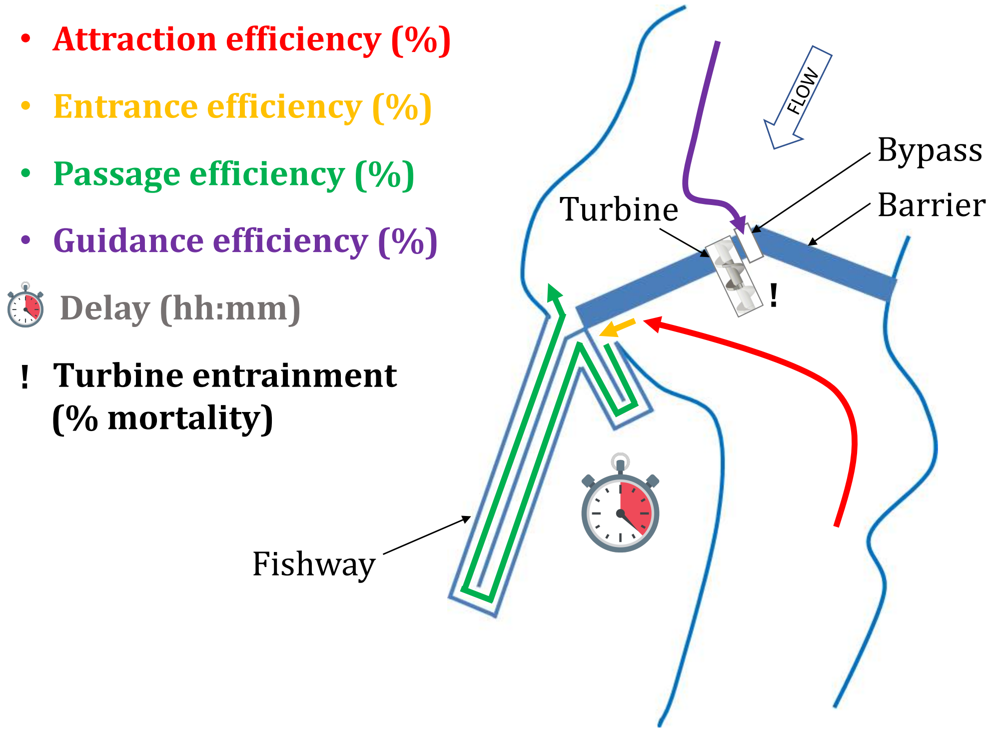
Figure 4 Recommended steps to identify dispersal targets and monitor fishways. Note that targets should describe the passage of fish through the total infrastructure, including reservoirs.

Table 1 A diverse set of field methods suitable for fishway target-setting and monitoring. Frameworks: metapopulation modelling (MM); species distribution-fish dispersal modelling (SDM); demo-genetic modelling (DG); fishway efficiency (FE) dispersal target (DT); and time-to-event (TE).

Method (example applications)	**Limitations**	**Application to fishway effectiveness**	**Target-setting frameworks**			**Monitoring frameworks**		
			MM	**SDM**	**DG**	**FE**	**DT**	**TE**
Fish sampling, e.g. electrofishing, netting, trapping (Wilkes et al. 2016)	Labour intensive to estimate fish occurrence, abundance or biomass over sufficient space and time scales but can be combined with modelling to fill gaps	Provides model parameters to drive ecologically realistic target-setting	x	x	x			
Stable isotope analysis (Cunjak et al. 2005)	Not all fish movements will be associated with strong isotopic signals. Requires access to suitable laboratory	Can be used to parameterise dispersal in metapopulation and species distribution models. Gives estimates of short-term	x				x	

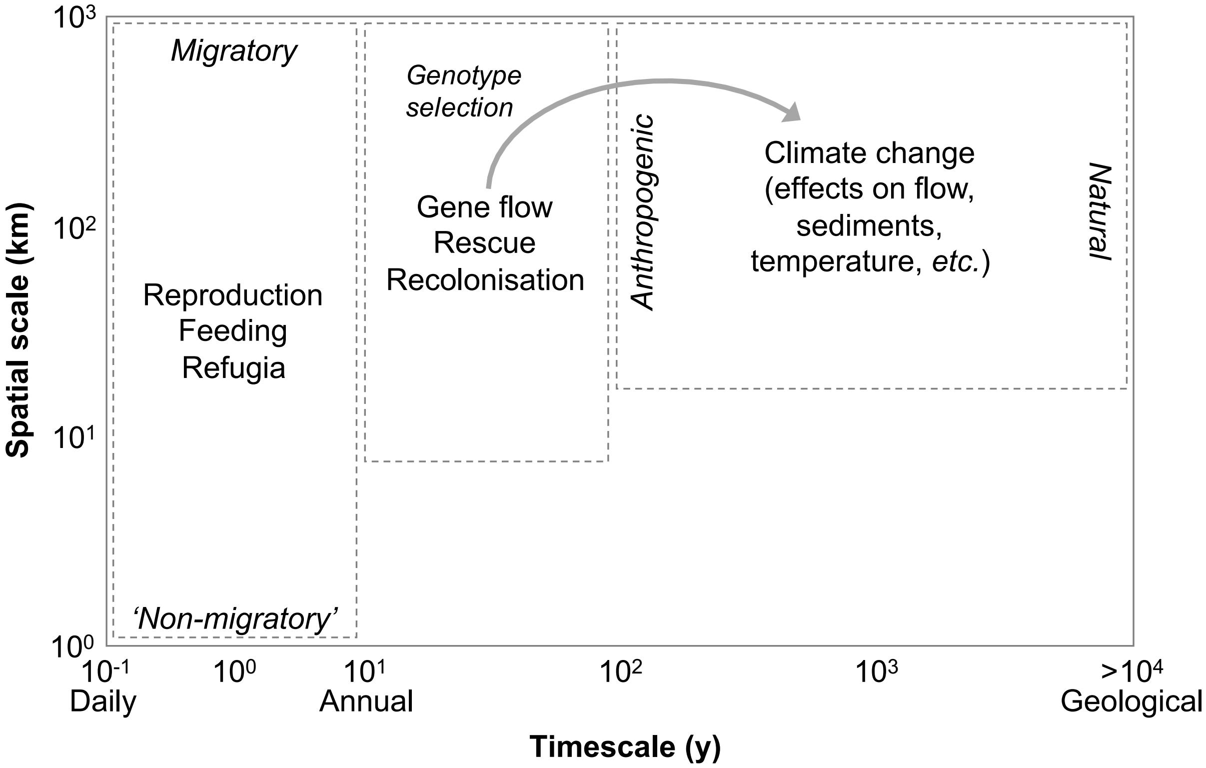
		(*e.g.* seasonal, generational) fish movements						
DNA sequencing (Ferreira et al. 2017)	May require may generations to detect barrier impact (e.g. up to 15; Landguth et al. 2010). Requires access to suitable laboratory	Baseline data can be used to set targets using demo-genetic modelling. Gives direct assessment of a fishway's ability to support viable populations through gene flow	x		x		x	
Biotelemetry (Calles & Greenberg 2009)	Unsuitable for many small bodied species. Impractical to tag sufficient 'non-migratory' fish to detect infrequent dispersal events. Cost and expertise required may be prohibitive	A useful method for assessing fishway efficiency for larger migratory species. Data can be used to parameterise metapopulation models.	x			x	x	x
Video and acoustic cameras (Kirk et al. 2015)	Limitations with smaller species (*e.g.* <50 mm TL) and in turbid rivers. Can be expensive and technically demanding	Can provide semi-automated species identification in suitable conditions and reveal reasons for success or failure in specific locations				x	x	

Stain and release (Amtstaetter et al. 2017)	Low recapture rate without ‘corralling’ fish in fishways	Useful to quantify passage efficiency for small fish and species sensitive to handling. Can identify specific sections of fishways where impediments exist				x	x	
Trapping in fishways (Baumgartner et al. 2010)	Cannot give quantitative estimates of fishway effectiveness	Can provide qualitative indicators of fishway effectiveness for upstream movement of a wide range of species and life-stages				x	x	
Ichthyoplankton surveys (Fuentes et al. 2016)	Many samples may be required in time and space. Identification of some taxa at egg and larval stages only possible through DNA barcoding	Directly evaluates the impacts of reservoirs and turbine mortality on entrained egg and larval life-stages				x	x	x



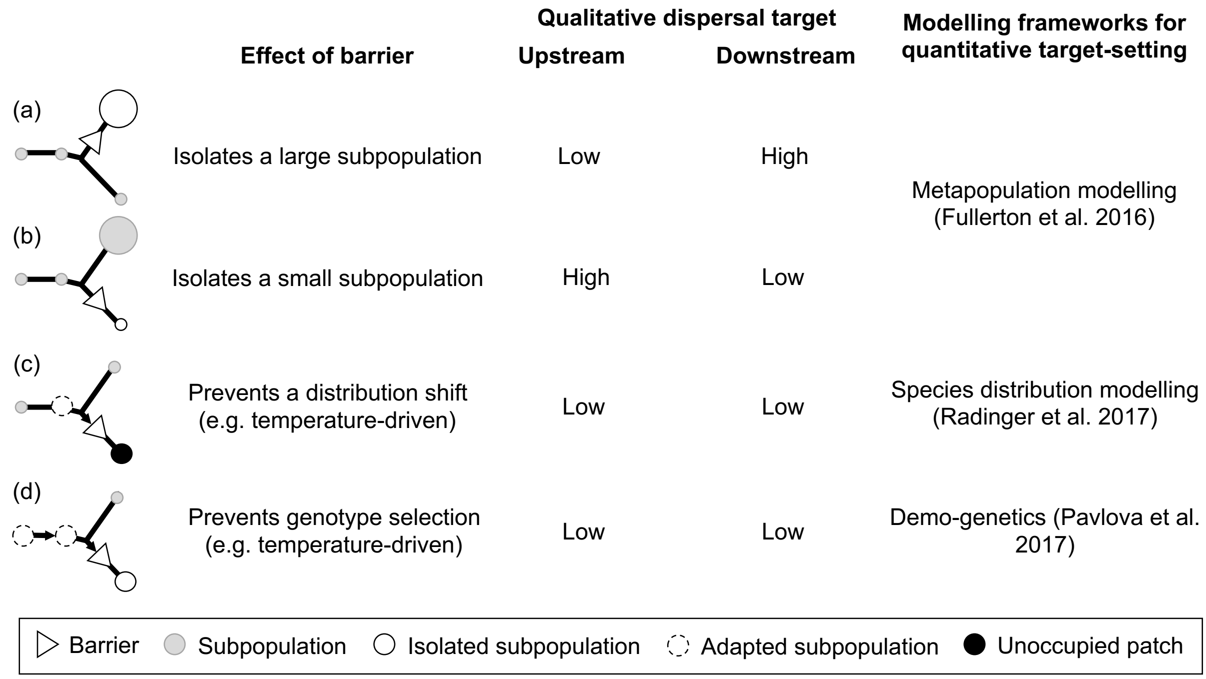
• Attraction efficiency (%)
• Entrance efficiency (%)
• Passage efficiency (%)
• Guidance efficiency (%)
⏱ Delay (hh:mm)
! Turbine entrainment (% mortality)
FLOW
Bypass
Barrier
Turbine
!
Fishway

[Fig 1]



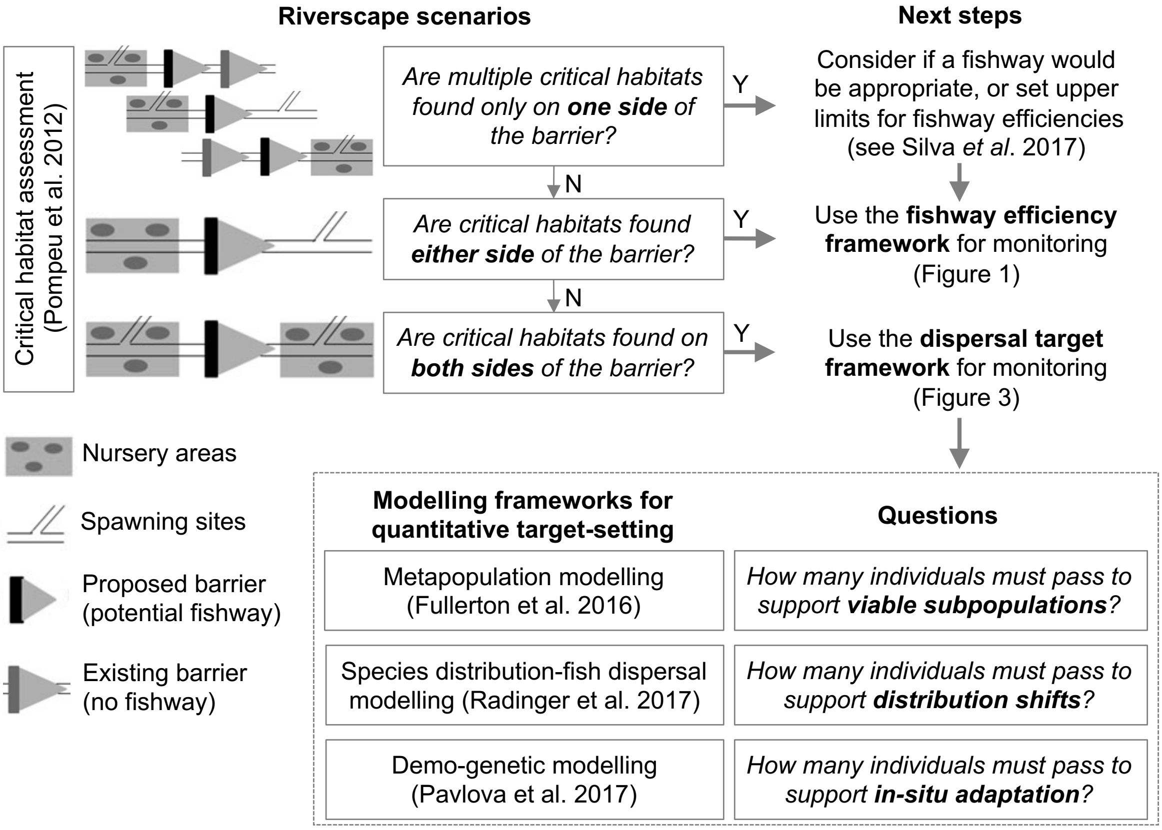
Spatial scale (km)
10^3
10^2
10^1
10^0
Migratory
Reproduction
Feeding
Refugia
'Non-migratory'
Genotype selection
Gene flow
Rescue
Recolonisation
Anthropogenic
Climate change (effects on flow, sediments, temperature, etc.)
Natural
10^-1 Daily
10^0
10^1 Annual
10^2
10^3
>10^4 Geological
Timescale (y)

[Fig 2]



	Effect of barrier	Qualitative dispersal target		Modelling frameworks for quantitative target-setting
		Upstream	Downstream	
(a)	Isolates a large subpopulation	Low	High	Metapopulation modelling (Fullerton et al. 2016)
(b)	Isolates a small subpopulation	High	Low	
(c)	Prevents a distribution shift (e.g. temperature-driven)	Low	Low	Species distribution modelling (Radinger et al. 2017)
(d)	Prevents genotype selection (e.g. temperature-driven)	Low	Low	Demo-genetics (Pavlova et al. 2017)

[Fig 3]


Riverscape scenarios
Next steps
Critical habitat assessment (Pompeu et al. 2012)
Are multiple critical habitats found only on one side of the barrier?
Y
Consider if a fishway would be appropriate, or set upper limits for fishway efficiencies (see Silva et al. 2017)
N
Are critical habitats found either side of the barrier?
Y
Use the fishway efficiency framework for monitoring (Figure 1)
N
Are critical habitats found on both sides of the barrier?
Y
Use the dispersal target framework for monitoring (Figure 3)
Nursery areas
Spawning sites
Proposed barrier (potential fishway)
Existing barrier (no fishway)
Modelling frameworks for quantitative target-setting
Questions
Metapopulation modelling (Fullerton et al. 2016)
How many individuals must pass to support viable subpopulations?
Species distribution-fish dispersal modelling (Radinger et al. 2017)
How many individuals must pass to support distribution shifts?
Demo-genetic modelling (Pavlova et al. 2017)
How many individuals must pass to support in-situ adaptation?

[Fig 4]