Unintended consequences and trade-offs of fish passage

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Abstract

We synthesized evidence for unintended consequences and trade-offs associated with the passage of fishes. Provisioning of fish passageways at dams and dam removals are being carried out increasingly as resource managers seek ways to reduce fragmentation of migratory fish populations and restore biodiversity and nature-like ecosystem services in tributaries altered by dams. The benefits of provisioning upstream passage are highlighted widely. Possible unwanted consequences and trade-offs of upstream passage are coming to light, but remain poorly examined and underappreciated. Unintended consequences arise when passage of native and desirable introduced fishes is delayed, undone (fallback), results in patterns of movement and habitat use that reduce Darwinian fitness (e.g. ecological traps), or is highly selective taxonomically and numerically. Trade-offs arise when passage decisions intended to benefit native species interfere with management decisions intended to control the unwanted spread of non-native fishes and aquatic invertebrates, or genes, diseases and contaminants carried by hatchery and wild fishes. These consequences and trade-offs will vary in importance from system to system and can result in large economic and environmental costs. For some river systems, decisions about how to manage fish passage involve substantial risks and could benefit from use of a formal, structured process that allows transparent, objective and, where possible, quantitative evaluation of these risks. Such a process can also facilitate the design of an adaptive framework that provides valuable insights into future decisions.

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Introduction

There is growing enthusiasm for fish passage at dams and culverts and, where possible, the removal of in-stream barriers to facilitate the free movement of fishes and restore more natural biodiversity and ecosystem services in rivers fragmented by dams (e.g. Jungwirth et al. 1998; Graf et al. 2002). Enthusiasm for fish passage has arisen, in part, from the development of landscape-level inventories of dams, coupled with a greater understanding of the effects of dams on fishes. Damming is one of the most widespread human alterations of riverscapes (Nilsson et al. 2005; Syvitski and Kettner 2011). Although the effects that dams have on fishes can be complex and vary with dam size, one of the most immediate effects common to a wide variety of dam sizes is the obstruction of fish movements and corresponding changes in the species and abundances of fishes found above and below a dam location (Gehrke et al. 2002; Katano et al. 2006). Consequently, dams and weirs have been implicated in the declines of many threatened freshwater fishes (Ingram et al. 1990; Hay-Chmielewski and Whelan 1997; Limburg and Waldman 2009). Enthusiasm for fish passage has also arisen, in part, from complementary evidence that riverine fishes move more extensively than appreciated historically and that these movements can be important for population persistence (Fausch and Young 1995; Schlosser and Angermeier 1995; Jungwirth et al. 1998). Even for sedentary species, long distance movements from one population to another, made by few individuals across unsuitable habitats and with substantial risk of failure, can have significant demographic and genetic consequences (Fausch and Young 1995; Schlosser and Angermeier 1995; Rieman and Dunham 2000). Lastly, enthusiasm for fish passage has arisen, in part, from case studies demonstrating that enhancing fish movement via fishways or dam removal can help restore key fish populations and the ecosystem services they provide (Kanehl et al. 1997; Bednarek 2001; Graf 2003).

This paper synthesizes evidence for unintended consequences and trade-offs associated with providing fish passage at dams, either through fishway construction or dam removal. Our aim is to help ensure that decisions regarding fish passage are logical, sound and scientifically defensible. Good decision-making requires thorough consideration of both the benefits and costs associated with the options available to managers. Our experience has revealed that while the benefits of fish passage and dam removal have been communicated effectively and are being accepted widely, the unintended effects of these decisions, and the trade-offs and uncertainties they create are understood less well and are often overlooked or underappreciated. Our synthesis is not intended to be a general argument against providing fish passage or removing dams. We feel these passage decisions should be considered widely and pursued wherever appropriate and possible. However, our experience also suggests that the benefits and costs of these options can vary from one dam location to another, making fish passage decisions context dependent, and frustrating to stakeholder groups and managers unfamiliar with the uncertainties surrounding decisions to provide fish passage or remove a dam. A synthesis of the unintended consequences and trade-offs associated with fish passage could increase awareness of these issues among fishery managers and scientists and help them communicate these concerns to the broader public.

Our synthesis consists of three parts. The first part examines the unintended effects associated with fishways and dam removal, the literature evidence for them and areas where additional research is needed. The second part demonstrates how these unintended effects can create trade-offs for fishery managers, between different environmental concerns and between different species of conservation concern or recreational or commercial value, with significant environmental and economic consequences. An example involving invasive sea lamprey (Petromyzon marinus, Petromyzontidae), walleye (Sander vitreus, Percidae), lake sturgeon (Acipenser fulvescens, Acipenseridae) and northern brook lamprey (Ichthyomyzon fossor, Petromyzontidae) at the Black Sturgeon dam in northern Lake Superior is provided to demonstrate how these uncertainties and trade-offs can complicate fish passage decisions. The third part briefly introduces structured approaches that can be used to explicitly evaluate the benefits and costs, and corresponding trade-offs, associated with fish passage and dam removal decisions.

Unintended consequences of fish passage and dam removal

Passage delays

Delay refers to the time required for a fish to move from one side of a dam location to the other side in the presence of a dam or barrier to movement, relative to the time required to traverse that distance in the absence of the dam or obstruction. A barrier can be defined as any structure or feature of an environment that reduces the rate at which individuals can move safely among locations within that environment. As such, the amount of delay associated with a barrier can be a fundamental quantity describing its severity (Castro-Santos and Haro 2003, 2010; Castro-Santos et al. 2009). Delays are usually considered for fishways at dams, but could be relevant to dam removal if habitat features that obstruct movement remain following removal of the dam (e.g. high flows, or thermal or predator barriers). Some dams have been built at small waterfalls or rapids that may have naturally challenged the movements of certain fishes. Delays can occur for both upstream and downstream movement. They can occur when fish attempt to locate the fishway entrance, navigate through the fishway proper or pass through any reservoir habitat above

a dam (Pon et al. 2006). Typically, delays are measured directly in hours or days (Table 1), although the time required to pass in the absence of the dam is usually considered negligible and not measured. Delays are also measured indirectly using the speed of movement in river sections with obstructions relative to river sections without obstructions (Raymond 1968). Measurement of delay can be challenging when more than one passage route is available, or when individuals fail to pass a structure, and methods of accommodating these challenges have been developed (Castro-Santos and Haro 2003; Castro-Santos et al. 2009).

There is ample literature evidence to suggest that delays represent a broad and significant concern, although individual estimates vary in quality owing to the challenges of measuring delays. Table 1 summarizes information from ten studies considering six fishes from four taxonomic families. Values quantified for the magnitude of delay within annual migrations are variable, suggesting that long delays occur consistently for at least some individuals within populations. Many of these values exceeded the magnitudes of 'allowable delay' published in management documents, e.g. 3 days (Bates 2000; Rowland et al. 2003), 3 days every 10 years (DFO 2007), 6 days (Bates 2000) or 7 days every 50 years (DFO 1996). Comparisons of migration rate (distance/day) also suggest that migration rates are slower in impounded rivers and river sections, than in unimpounded rivers and river sections (Raymond 1968). We did not find a study where the absence of delay was observed consistently.

There is growing theoretical justification and empirical evidence to suggest that delays of the magnitude typically reported are important to Darwinian fitness and population dynamics, but additional research explicitly measuring these consequences is required. At the point of passage, delays can force fish to congregate at high densities, possibly creating an attractive patch of prey for predators and facilitating the transfer of diseases and increased competition for space due to the close proximity of individuals (see below). While delayed, individuals may also encounter physiological challenges associated with unfavourable flows (Hinch and Bratty 2000), water temperatures (Bentley and Raymond 1976), saturation of nitrogen gas (Raymond 1979; Dauble and Mueller 1993) or ionic concentrations (Ebel 1977). These challenges can reduce an individual's ability to complete its migration to a spawning ground or new foraging

Table 1 Literature estimates for the magnitude of delay in migration reported for fishes at fishways.

habitat (Geist et al. 2000; Budy et al. 2002; Caudill et al. 2007; Roscoe et al. 2011). For spawning runs, such challenges can also mean that individuals arrive at spawning grounds with less energy for reproduction (Caudill et al. 2007; Schilt 2007) and arrive late, possibly creating a mismatch between offspring hatch and food availability (Cushing 1975). With iteroparous migratory species, the challenges could also reduce post-breeding survival and future reproductive effort. For example, the abundance of American shad (Alosa sapidissima, Clupeidae) in the Connecticut River initially soared following provision of upstream passage, but then declined dramatically. Delays in downstream migration appear to have reduced the post-breeding survival of adults, selecting against repeat spawning (iteroparity), and leading to a decline in shad abundances (Castro-Santos and Letcher 2010).

Fallback

Fallback occurs when a fish moving forward through a fishway reverses course either before or

after passing a barrier successfully. Our treatment here focuses on fallback after successful passage. Fallback is most pertinent to fish passage and is usually considered for upstream migration. Fallback can occur because, upon exiting the fishway, the fish is disoriented and moves in the wrong direction, is no longer motivated to swim upstream due to their experience in the fishway, is no longer physically capable of continuing their upstream migration due to the demands of using the fishway, or to innate tortousity in the fish's migration route as it explores different river branches. An individual may re-ascend the fishway at a later time.

Our survey of the literature suggests that fallback also occurs commonly. Table 2 summarizes estimates of the percentage of fish displaying fallback from nine studies considering eight fish species from five taxonomic families. Qualitatively, it appears that estimates of fallback differ among species and among fishway designs and locations. In some instances, the percentages of fish displaying fallback are surprisingly high (Table 2).

Table 2 Literature estimates for the percentage of passing fish that fallback at fishways. An observation represents an estimate made for a given year at a given fishway.

Fallback fosters concern in four ways. First, it can be an additional source of unwanted delays and their corresponding ecological consequences (Frank et al. 2009). Second, the experience of passing through a fishway could decrease energy reserves needed to re-ascend and pass an additional time (Cramer and Oligher 1964; Reischel and Bjornn 2003), particularly if the fishway is poorly designed. Third, repeated passage through a fishway could increase the probability of physical injury associated with using the fishway or from moving downstream over the dam through a spillway or turbine. During spawning migrations, such injuries could hinder the chances and timing of reproduction (Berg et al. 1986; Reischel and Bjornn 2003). Lastly, when fish are not marked individually, failure to consider fallback could bias estimates of the number and proportion of fish passed (Burke et al. 2004; Frank et al. 2009).

Ecological traps

The phrase 'ecological trap' is applied when an attractive environmental cue leads to animals selecting a habitat where their Darwinian fitness is relatively low, often due to human activities, over

an alternative habitat where their fitness is high. Its application to fishes at dams and fishways is recent and focused on upstream fish passage (Pelicice and Agostinho 2008).

Four conditions are required for fish passage to create an ecological trap (Pelicice and Agostinho 2008). First, there must be attractive forces (e.g. flows) that encourage fish to ascend a fishway. Second, the migratory movements of the fish must be unidirectional. Third, conditions above the dam must be poor for fish recruitment, while, fourth, conditions below the dam are good for recruitment. Under these conditions, individual fish can be drawn into poor quality habitats, where they experience reduced fitness, and population sizes can decline.

Whether ecological traps involving fishways occur remains uncertain. The most compelling examples to date come from the upper Paraná basin in Brazil, although quantitative support is limited (Pelicice and Agostinho 2008). The upper region of the basin has a sequence of three dams: Itaipu, Porto Primavera and Jupia. The fish lift and experimental ladder at the Porto Primavera dam successfully attract migrating fishes and pass them upstream, with little fallback (conditions 1 and 2). River reaches upstream of the Porto Primavera

dam to the Jupia dam lack spawning and nursery habitats required by the migratory species and surveys of fish eggs and larvae have revealed low reproductive activity (condition 3). Conversely, in river reaches below the Porto Primavera dam, many large migratory fishes reproduce successfully in the remaining floodplain habitat (condition 4). It remains uncertain whether the fishway at the Porto Primavera dam passes sufficient fish to deplete the downstream stocks and whether the poor reproduction below the Jupia dam is a consequence of flow regulation altering the timing and amount of floodplain habitat available for fish reproduction.

Some conditions for ecological traps have been observed for Chinook salmon (Oncorhynchus tshawytscha) in the western US (Boggs et al. 2004), Atlantic salmon (Salmo salar) in Finland (Jokikokko 2002) and brown trout (Salmo trutta, Salmonidae) in Denmark (Aarestrup and Jepsen 1998). In these systems, migrating adults sometimes 'overshoot' potential spawning habitat to pass upstream through a fishway, but then fallback below the dam to spawn. The condition for attractiveness of the fishway appears to be met. The conditions that spawning habitat below the dams is better than that above the dams remain to be demonstrated satisfactorily, but are suggested by the fish falling back below the dam to spawn. The condition of unidirectional movement is not met due to the fallback.

A different form of ecological trap can arise when adults passing through the fishway experience high mortality while migrating back downstream (Castro-Santos and Letcher 2010) or where adults spawn successfully above the dam, but their offspring experience low passage survival while migrating downstream (Smyth 2011).

Selective passage

Fishways are selective in terms of the species, and likely the phenotypes and genotypes within species, that pass them successfully. Selectivity at the species level is widely recognized; proportions of individuals passed at fishways are generally higher for salmonid fishes than for non-salmonid fishes (Mallen-Cooper and Stuart 2007; Bunt et al. 2012; Noonan et al. 2011). Evidence for selectivity at the phenotypic and genotypic levels is weaker; however, not all individuals pass at fishways (Bunt et al. 2012; Noonan et al. 2011) and there are examples where larger fish, with white muscle fibres of greater diameter, were more likely to pass

than smaller fish, with muscle fibres of lesser diameter (Mallen-Cooper and Stuart 2007; Volpato et al. 2009). Selectivity is expected because species and individuals within species will differ in their abilities to find fishway openings, to navigate successfully through the fishway and to persist in passing a barrier. It is also expected because the challenges faced by the fish will vary with local habitat features (e.g. flow, dam height) (Poff and Hart 2002; Pratt et al. 2009) and the type and operation of fishway provided (Pratt et al. 2009; Bunt et al. 2012; Noonan et al. 2011).

Selectivity can have important scientific and management implications at both species and individual levels. At the species level, selectivity can result in incomplete or new biotic communities upstream of the dam location. This might be considered acceptable if management objectives are focused on restoring a subset of valued species known to use the fishway, but could be troublesome if management objectives are focused on broader ecosystem restoration above the dam location. At the individual level, the consequences of selectivity are less clear, but two theoretical ideas warrant consideration when selective passage leads to differences in Darwinian fitness among genotypes: Darwinian debt and evolutionary suicide.

Darwinian debt refers to the evolutionary responses, and corresponding time lags, that can occur when a population exposed to a selective process created by human actions (e.g. fishing) is released from that process (Waples et al. 2007). Dams and fishways can create strong selective pressures operating over many generations, thereby selecting for genotypes with traits best suited for an environment with dams and fishways. If the dams and fishways are later removed, the population may have to undergo further evolution to restore the lost fitness associated with the change from a more fragmented to less fragmented river system (Waples et al. 2007).

Evolutionary suicide is an evolutionary process whereby a population adapts in a way that reduces long-term persistence (Gyllenberg and Parvinen 2001). Whether individuals of a population migrate is believed to be the outcome of the fitness benefits and costs of migration vs. the benefits and costs of remaining resident. Challenges presented by obstructions can increase the fitness costs of migration, potentially favouring resident genotypes or ecophenotypes of smaller body size and reproductive output (Morita and Takashima 1998), and living at lower population densities (Morita et al. 2000) with greater chance of local extinction due to demographic and environmental stochasticity (Gyllenberg et al. 2002). This can create the counterintuitive situation where adopting residency increases Darwinian fitness, but creates a local, resident population that is more prone to extinction (Gyllenberg and Parvinen 2001; Gyllenberg et al. 2002).

Species interactions at the dam location

One common consequence of migratory delay above and below barriers is that local densities of individuals increase because the rates at which fish pass the barrier are lower than the rates at which additional fish approach. Locations where this occurs can become hotspots for predation, disease transfer, and, to a lesser extent, interspecific and intraspecific competition for space. These hotspots are often attributed to dams. Here, we consider the notion of hotspots for fishways and sites of dam removal because the idea remains relevant if delays or fallback occur. Changes made to facilitate fish passage may not alleviate the crowding and its consequences. We also consider the notion of hotspots because we encounter the

idea widely, it seems logical, but empirical evidence is limited.

Evidence for predation hotspots is the strongest for salmonids in the western USA, and anecdotal for other taxa and locations (Table 3). On the Columbia River, predatory fishes and birds target downstream migrating, juvenile salmon at the base of dams (Rieman et al. 1991; Schreck et al. 2006; Waples et al. 2007). Determining the amount and importance of this predation to overall mortality has been complicated, because some predators may focus on prey that are dead or have been injured during passage (Mesa 1994). Authors of at least one study argued that the presence of a dam has increased predation over what it was in the past (Rieman et al. 1991). Predation of salmon at fishways during upstream migration by several species of pinniped is also becoming a concern in the western USA (Fryer 1998; Tackley et al. 2008). Both the salmon and the pinniped species are the focus of conservation efforts. The intensity and importance of this predation is still under investigation. At the Bonneville dam, the first dam on the Columbia River, the level of predation was considered great enough for the management agencies to place barred exclusion devices at the openings of fishways and to implement nonlethal 'hazing' programmes

Table 3 Literature sources where predation of fishes has been reported at dams and fishways. Qualitative is used for sources providing written descriptions that predation was observed, while quantitative is used for sources providing numerical estimates of numbers or percentages of prey species being attacked by predators.

to deter pinnipeds away from the tailrace of the dam (Tackley et al. 2008). Evidence for predation hotspots elsewhere is more limited. In a comparison of three fishway designs in the Lesser Slave River, Alberta, Schwalme et al. (1985) provided evidence that spottail shiners (Notropis hudsonius, Cyprinidae) were being eaten by northern pike (Esox lucius, Esocidae) immediately below or in the fishways. We have also encountered concerns about fishways becoming hotspots for anglers catching large fishes migrating upstream (Bunt 2001; McLaughlin et al. 2009; Bobrowicz 2010), although in some situations anglers may be catching large predatory fish feeding on small, juvenile fishes migrating downstream, possibly alleviating a predation hotspot for the small migrants.

Evidence of dams and fishways being disease or competition hotspots for fishes is even sparser. There is a significant literature addressing gas bubble disease in fishes, mainly salmonids in the western USA, which arises when fish are exposed to the supersaturation of dissolved gases caused by spilling large volumes of water over dams (Ebel and Raymond 1976; Weitkamp and Katz 1980; Lutz 1995). This condition can be hazardous to downstream migrants as they pass over or through dams. It can also be a problem to upstream migrating fish. When entry rates into a fishway are low, and fish get delayed and crowded downstream, prolonged exposure to supersaturated gases can increase the likelihood of stress and injury (Raymond 1979). Transfer of diseases among fish can also be facilitated when fish are crowded in fishways and near barriers (Bunt 2001), either because of physical proximity or stress-related immunodepression.

As for interspecific and intraspecific competition for space in fishways, we could not find any explicit, published evidence for such interactions. However, competitive interactions are a concern for the designs of fish lifts and for selective, trap-andsort fishways implemented when passage of invasive species is a concern (McLaughlin *et al.* 2007). Designs that do not adequately consider the size of spawning runs can result in periods where fishes are held at high densities and, with fish lifts, limited water and oxygen.

Unwanted introductions above the dam location

Fish passage and dam removal can allow unwanted movement of invasive and introduced species, and even native species, into upstream river reaches formerly isolated by the dam or barrier. These introductions can become the source of unwanted consequences from new predator-prey and competitive interactions, from hybridization and introgression within and between species, or between wild and hatchery fish, and from exposure to new diseases and contaminants (Table 4; see also Kiffney et al. 2009). Barriers to movement represent a recognized method of restricting invasions (Sharvo and Liebhold 1998). They are particularly attractive for non-jumping fishes in rivers (McLaughlin et al. 2007; Fausch et al. 2009). The barriers can be small in size, because of the narrow linear nature of rivers. They can be effective, because most fishes lack the physiological capabilities to leave water long enough to get around or over a barrier, although fish species that climb wetted inclined and vertical surfaces could be exceptions, e.g. some eels (genus Anguilla, Anguillidae) (D'Aguiar 2011), lampreys (genus Lampetra and Petromyzon, Petromyzontidae) (D'Aguiar 2011), climbing catfish (genus Lithogenes, Loricariidae) (Schaefer and Arroyave 2010), gobies (Sicyopterus stimpsoni, Gobiidae) (Schoenfuss and Blob 2003) and Galaxias spp., Galaxiidae (McDowall 2003).

The extent to which dams and other forms of barriers are being used to protect native biological communities is likely underappreciated, as evidenced by the minimal consideration of this topic in widely known treatises addressing fish passage and dam removal (Graf et al. 2002; Graf 2003; Stanley and Doyle 2003). Three examples of significant environmental and economic importance have become increasingly prominent. Electrical barriers are being used in the Chicago shipping canal as part of efforts to prevent Asian carp (Hypophthalmichthys spp., Cyprinidae) from invading the Laurentian Great Lakes (Stokstad 2003). Across the Great Lakes, a variety of in-stream barrier designs are used to restrict the upstream migration and reproduction of the invasive, parasitic sea lamprey (Lavis et al. 2003; McLaughlin et al. 2007; Pratt et al. 2009). The barriers represent part of an integrated control programme protecting large native and introduced fishes in the lakes from parasitism by juvenile sea lamprey. In the western US, instream barriers are being used or considered to protect highly valued populations of cutthroat trout (Oncorhynchus clarkia, Salmonidae) from introgression with introduced rainbow

Table 4 Examples where dams are being used purposely or incidentally to restrict upstream movement of introduced or undesirable native fishes, aquatic invertebrates, and contaminants. – indicates that specific target species have not been identified.

Table 4 Continued.

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trout (Oncorhynchus mykiss, Salmonidae) and competition with or predation by introduced brook trout (Salvelinus fontinalis, Salmonidae) (Novinger and Rahel 2003; Fausch et al. 2009).

Our literature survey revealed numerous other examples where barriers are being used, intentionally or unintentionally, or being considered as a method of restricting the movements of invasive fishes and crayfishes, and native predatory fishes, to protect biological communities upstream of the barrier (Table 4). Moreover, several fisheries management plans for watersheds within the Laurentian Great Lakes reveal how fishery managers are commonly, but quietly using dams and barriers to manage the distributions of fishes within watersheds to provide varied angling opportunities and to protect native fishes from invasive species (O.M.N.R. and C.V.C. 2002; O.M.N.R. and T.R.C.A. 2005). On the one hand, dams and barriers can be considered a temporary solution for addressing invasive species, to be abandoned once better control options become available, because these obstructions represent an impediment to restoring the native fishes that were impacted negatively following dam construction. On the other hand, consideration and use of dams and barriers as a management tool is likely to increase, particularly in ecosystems prone to problems with invasive species. Restoring native fishes in watersheds with a long history of fragmentation may not be practical because species sensitive to fragmentation have already been lost or remaining populations have changed irreversibly due to evolutionary

responses or alterations in ecosystem structure (Walters and Kitchell 2001; Waples et al. 2007).

Incomplete or unintended restoration outcomes

Broader consequences of the unwanted effects of fish passage and dam removal are restoration outcomes that are incomplete or unintended when compared to the management objectives set for the watershed or river. By incomplete restoration outcomes, we mean the realized outcome is similar in nature to the management objectives, but lower or higher in magnitude from what was expected when the fish passage decision was made (e.g. Doyle et al. 2005). Following fish passage decisions, studies comparing population- and community-level responses of fishes to management targets remain scarce. For fishways, progress is often considered incomplete because of low passage efficiency (Mallen-Cooper and Stuart 2007; Bunt et al. 2012). For dam removals, increases in fish abundance can be observed, but historical reference points or management targets are often lacking (Catalano et al. 2007; Burroughs et al. 2010), and restoration efforts in general often fall short of historical or reference conditions (Benayas et al. 2009). By unintended restoration outcomes, we mean the realized outcome is grossly different or counterintuitive in nature from the management objectives set when the fish passage decision was made. At the population level, for example, abundances of American shad in the Connecticut River initially increased dramatically following the provisioning of fish passage, but then decreased

dramatically, likely due to a change in age structure from older to younger fish as a consequence of reduced survival of adults during the downstream migration post spawning (Castro-Santos and Letcher 2010). At the community-level, American shad introduced on the Pacific coast has colonized the Columbia River and exploited fishways to move beyond hydroelectric facilities in the lower river reaches. The shad is a host for an Ichthyophonus sp. (Ichthyophonaceae), a Mesomycetozoean parasite of wild marine fishes that was likely endemic to the northeast Pacific. The range expansion by shad has amplified and transported Ichthyophonus into the Columbia River and created the risk for a freshwater Ichthyophonus life cycle and transfer of the parasite back to native fishes inhabiting the river (Hershberger et al. 2010).

Incomplete and unintended outcomes can be expected because some of the unwanted effects, such as introduction of invasive species, can create biological trade-offs between different ecosystem components (e.g. abundances of the fishes affected positively and negatively by any decision taken) and create corresponding management trade-offs between different restoration objectives (conserving native and valued non-native fishes by minimizing habitat fragmentation or using fragmentation to limit the harm caused by an invasive species) (e.g. Fausch et al. 2009; Pratt et al. 2009; Vélez-Espino et al. 2011). When fish passage or dam removal decisions are motivated by narrow interests, such as the enhanced angling opportunities for a specific species, the biological and management trade-offs can further reveal disagreements in how scientists, managers and stakeholders value the species that stand to benefit from the different management options available (value trade-offs) (Gregory and Keeney 2002; Gombu 2009). For example, on the Credit River near Toronto, Canada, the Credit River Anglers Association recently proposed to pass migratory rainbow trout beyond the lower reaches of the river. This elicited strong concern from the Izaak Walton Flyfishing Club, which fishes brown trout from the middle reaches of the river, over possible effects of interspecific competition between rainbow trout and brown trout (Gombu 2009).

Incomplete and unintended outcomes can also be expected because the probabilities of each of the unwanted effects identified above occurring, and their potential consequences, remain uncertain for any given dam location. This uncertainty exists because our understanding of the unwanted

effects remains limited, the responses of populations and ecosystems can be complex, and the uncertainties and responses can differ from one river system to another due to differences in geomorphology, climate, dam structure and operation, and the biota inhabiting river sections below and above individual dams (Power et al. 1996). In some situations, potential undesirable results of restoration efforts may not occur, at least initially (Stanley et al. 2007). In other situations, the desired results of restoration may not occur even when it seemed we understood the system well (Novinger and Rahel 2003; Doyle et al. 2005; Pine et al. 2009). For fish passage and dam removal decisions, the uncertainty and its consequences for the decision making process can be amplified further across river systems by differences in the objectives and clarity of watershed management plans and differences in the attitudes of stakeholder groups affected by any fish passage decision (Lavis et al. 2003).

An example: the Black Sturgeon Dam, Lake Superior, ON

We use a recent appeal to remove the dam on the Black Sturgeon River on the Canadian (north) shore of Lake Superior as an example where unwanted effects and trade-offs with fish passage and dam removal can create difficult challenges for resource managers. This example involves sea lamprey, a parasitic invader in the Great Lakes, walleye, a species of interest to commercial and recreational fishers, and lake sturgeon and northern brook lamprey, two species recommended for listing as threatened and special concern, respectively, within the basin under federal legislation by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). This example further highlights the value trade-offs between the large lake fishes (native and introduced) that benefit from sea lamprey control (lake trout, Salvelinus namaycush, Salmonidae; lake whitefish, Coregonus clupeaformis, Salmonidae; and introduced salmonids, Oncorhychus spp), the fishes that stand to benefit from improved fish passage (walleye and lake sturgeon) and the northern brook lamprey, which will be negatively affected by expanded, chemical control methods for sea lamprey should the dam be removed. Similar tradeoffs could arise at other dam locations within and outside of the Great Lakes.

The Black Sturgeon River is the seventh largest tributary to Lake Superior, with about 2000 linear km of river that empties in Black Bay on the north shore of Lake Superior. The Black Sturgeon dam is located approximately 17 km from the river mouth. It was built in 1959/60 as a water control structure and modified in 1966 for sea lamprey control. The dam prevents maturing sea lamprey migrating from Lake Superior into the Black Sturgeon River from accessing productive reaches of spawning habitat above the dam. The sea lamprey is the target of a basin-wide control programme managed by the Great Lakes Fishery Commission and its contract agents Fisheries and Oceans Canada and the US Fish & Wildlife Service. Spawning habitat below the dam is treated every 4–6 years with a lampricide, 3-trifluoromethy-4 nitrophenol (TFM) that kills sea lamprey ammocoetes and metamorphosing individuals. The Black Sturgeon River has the potential to be a major producer of sea lamprey in Lake Superior, due to its size and complexity, plus the presence of spawning sea lamprey below the dam and considerable sea lamprey spawning and rearing habitat, and large numbers of native northern brook lamprey, above the dam.

It is believed that the removal of the Black Sturgeon dam could greatly benefit walleye production (Furlong et al. 2006). From the late 1800s to mid 1960s, Black Bay supported the largest walleye population in the Canadian waters of Lake Superior, and a corresponding commercial fishery that crashed around 1968. Furlong et al. (2006) implicated the Black Sturgeon dam as the contributing factor. When the dam was constructed, it was thought that bay and river stocks of walleye existed below and above the dam location, respectively. Evidence collected since suggests Black Bay walleye were from a single, river-spawning stock where at least some individuals migrated to Black Bay (Wilson et al. 2007). Removal of the Black Sturgeon dam could also benefit lake sturgeon. Barriers to migration have been implicated in their decline. The Black Sturgeon River is one of seven tributaries along the Canadian shore of Lake Superior that supports a spawning population of lake sturgeon (Auer 2003).

There are five main options available to decision makers. One option is to leave the dam in its current location. A second option is to provide a selective, trap-and-sort fishway at the current dam location to remove sea lamprey and pass native fishes. A third option is to remove the existing dam and build a new dam (lacking fish passage) approximately 50 km upstream on the river mainstem to let native fishes access significantly more spawning habitat in the system, and chemically treat the larger section below the new dam to control sea lamprey. A fourth option is removal of the dam and control of the entire river system with chemical lampricides. A fifth option is to remove the dam and undertake no control of sea lamprey in the river system.

For the agencies responsible for sea lamprey control, dam removal or unselective passage of sea lamprey beyond the Black Sturgeon Dam are undesirable management options. The river system above the dam is extensive, dendritic, remote and difficult to access. Expanding the extent of chemical treatments to compensate for dam removal will increase control costs dramatically, risk reduction in treatment success, and expose large numbers of listed northern brook lamprey to negative effects of lampricide treatments. Building a trap-and-sort fishway where sea lamprey are removed, and native fishes passed, represents a potential compromise.

For the management agents and stakeholders favouring dam removal, maintaining the current dam location with or without selective fish passage is an undesirable option. They view walleye and lake sturgeon rehabilitation as being much more certain under dam removal (Furlong et al. 2006; Bobrowicz 2010). They question who will be responsible for fishway operation and whether a trap-and-sort fishway could pass enough walleye and lake sturgeon to achieve rehabilitation. Moving the dam upstream represents a potential compromise.

Perspectives regarding the suitability of the management options are complicated further by two additional issues. First, reductions in the effectiveness of sea lamprey control will be realized by the states and provinces across Lake Superior, because juvenile sea lamprey feed on large fishes throughout the lake (McLaughlin et al. 2003), whereas the benefits to walleye rehabilitation will be limited to Black Bay and the Black Sturgeon River region of Ontario. Second, the recovering populations of walleye and lake sturgeon could provide a prey source for sea lamprey in the lake (Becker 1983; Patrick et al. 2009).

Making decisions about fish passage

For many other systems, decisions regarding fish passage may be straightforward because invasive or nuisance species are not present and the unintended consequences of fish passage are considered acceptable. However, there will be systems like the Black Sturgeon River where arriving at good decisions about construction of or modifications to a dam to facilitate fish passage will be more difficult. The difficulty arises for two intersecting reasons. First, there are often conflicting values held by different stakeholders that appear to point to alternative choices – this leads to trade-offs. Second there is a high degree of uncertainty about the expected outcome of each choice. When uncertainties intersect values, the result is risk. There is a growing body of literature and practice in fisheries science that addresses the challenge of making decisions in the face of trade-offs and risks. We now provide a brief discussion of this emerging practice, broadly described as 'Structured Decision Making' (SDM) (Irwin et al. 2011). These approaches are starting to be applied to decisions involving barriers, fishways and dam removal (McLaughlin et al. 2008; Peterson et al. 2008), and scientists, managers and stakeholders involved with these decisions are often unfamiliar with SDM methods.

Structured decision making is a formal, strategic process with three essential elements (Irwin et al. 2011). It has to (i) involve stakeholders, (ii) explicitly consider the full range of management options and objectives that are relevant to the decisions being made and (iii) use models to forecast the expected consequence of each option in terms of its effect on the objectives. The use of models is vital to ensuring a process that is transparent to stakeholders, by making clear where expected outcomes of an option under consideration are well-understood, and where they are highly uncertain. There are many variations of this broad SDM approach. Some will be familiar $-$ by name $-$ to most readers. Others have been developed more recently. We highlight three examples: decision analysis, real options analysis and adaptive management.

Decision analysis

Decision analysis is a well-known example of an SDM process (Peterman and Peters 1998; Clemen 2001). Decision analysis was specifically developed to confront complex decision problems involving multiple objectives, significant uncertainty regarding the outcomes of decisions, expertise from multiple disciplines, value trade-offs and long time horizons (Keeney 1982; Peterman and Anderson 1999; Peterman 2004). Although its efficacy can decrease as problem complexity increases, it does so less rapidly than the efficacy of alternative approaches (Keeney 1982).

Peterman and Peters (1998) describe in detail the application of decision analysis to natural resource management. They outline eight key steps to a rigorous analysis, including identifying management objectives, available management options and uncertainties that make it difficult to determine which management option will best meet the management objectives. Simulation models are then used to incorporate uncertainty and forecast the outcomes of each management option with respect

Figure 1 A decision tree linking management options (left) and values $(V_{h,i})$ for outcome measures (i) of those options under different hypotheses (h) (right), via the uncertain states of nature (middle) that make it difficult to determine which management option is best for reaching the desired management outcomes.

to the management objectives. This process is often depicted visually using a decision tree linking the management options to performance measures that reflect the management objectives (Fig. 1). The outcome is a ranking of management options based on their expected performance at meeting objectives. By explicitly including uncertainty in the models, the ranking can address stakeholder views of risk tolerance as well as the expected benefits. Sensitivity analyses can be used to identify how robust the rankings are to assumptions made about the uncertainties and the weightings placed on the different management objectives (Dong and Chapman 2006). By explicitly addressing uncertainty, decision analysis can stimulate the imaginative thinking needed to identify more robust or informative policy options and help avoid reaching decisions using gut responses or rules of thumb shaped by earlier experiences, affect or cultural beliefs.

Real options analysis

Real options analysis is a relatively new innovation in structured decision making that applies to situations where a manager must decide whether to proceed with a new management option or stay with the management option in place (Fenichel et al. 2008). In addition to addressing situations where the outcome of the decision is uncertain, real options analysis applies when the consequences of the new management option are potentially irreversible. Most fish passage infrastructure decisions, such as removal of the Black Sturgeon dam, would meet this criterion. Under such situations, there can be value in delaying the decision until further information becomes available and the uncertainty is reduced. Real options analysis complements decision analysis by explicitly considering the benefits of delaying a decision (i.e. 'holding the option' of making the decision).

Real options analysis is based on the concept that when there is uncertainty about the outcome of a decision this introduces a cost of exercising the option (implementing the new management option) that is directly and quantitatively related to risk. The method involves calculating a precautionary adjustment (PA) that quantifies this risk and then specifying that the new option should be chosen when its expected benefit exceeds that of the status quo option plus the PA. The PA is estimated from simulation models that consider the expected change in net benefits over time (drift) and the vari-

ability about that change (volatility) for both the status quo and the new option. Like decision analysis, additional sensitivity analyses are used to assess how robust the estimate is to parameters used in the simulations. Real options analysis therefore provides a formal, objective basis for applying a precautionary approach, in contrast to making ad hoc precautionary decisions in the face of risk.

Adaptive management

Real options analysis recognizes that there may be benefits of delaying a decision until more is known about its consequences. Adaptive management (Walters 1986; Williams et al. 2009) is a more widely known form of SDM that takes this premise even further and elevates learning to the stature of a key management objective. Fish passage decisions are being made routinely in streams and rivers around the world, but comparatively little effort has been put into monitoring the consequences, particularly with respect to the potential effects discussed in this article. Specific fish passage tactics can be applied to multiple distinct (independent) lotic systems, creating compelling opportunities to design replicated management experiments that could provide valuable insights into the performance of these tactics at achieving management objectives. In turn these insights can then be applied to future decisions, improving the quality of these decisions and reducing the magnitude of precautionary adjustments that are required. This comparative approach has been applied successfully to determine the effect that small dams have on the species richness of fish assemblages (Dodd et al. 2003), explanations for imprecision in the size of that effect (Harford and McLaughlin 2007), mechanisms responsible for the effect (Porto et al. 1999; Dodd et al. 2003) and species sensitive to the presence of a dam (McLaughlin et al. 2006).

Many observers have noted that adaptive management, in practice, has failed to live up to its potential, in principle (McLain and Lee 1996; Walters 2007). One of the main reasons for this failure is the resistance to providing funds for adequate monitoring of the consequences of a decision. In the case of fish passage, there are frequently many stakeholders with strong interests in the outcome of decisions; by involving these stakeholders in an SDM process, especially one that includes an adaptive management component, managers may find themselves with a team of volunteers who are highly motivated to assist with the monitoring of consequences. In his early assessment of adaptive management from a human dimensions perspective, Lee (1993) argued that the establishment of 'epistemic communities', including key stakeholders, is vital to the success of an adaptive management enterprise. An epistemic community is a group that shares a common interest in knowing more about a system.

Conclusions

Our synthesis supports three main conclusions. First, there is sufficient evidence that decisions to increase or decrease the connectivity of river systems to facilitate or restrict the movements of fishes should consider the possibility of unintended consequences. Evidence for some of these unintended effects remains limited, and more information is needed, but a lack of evidence for a plausible effect is not grounds for ignoring that effect. It is unrealistic to expect the evidence regarding unintended effects of fish passage decisions to be thorough when the evidence for the intended consequences of these decisions remains inadequate (Roscoe and Hinch 2008; Kemp and O'Hanley 2010; Bunt et al. 2012) or incomplete (Stanley and Doyle 2003). Second, the importance of these effects, and the trade-offs they can create, can be meaningful and complex, costly economically and environmentally, and vary from system to system and dam to dam. For many systems, the unintended consequences could be minor and incomplete passage will be better than no passage. For some systems, like the Black Sturgeon River, unwanted consequences could be a much greater concern. Recognizing this variability reveals the need for a more nuanced, context-dependent perspective on dams, fishways and dam removal. Whether dams are bad, fishways ineffective and dam removals the solution depends on the management objectives for a river system. From this perspective, these options are better viewed as tools that managers can use to preserve biodiversity and services in ecosystems, or parts of ecosystems, largely unaffected by human actions, or to restore nature-like biodiversity and ecosystem services in systems heavily affected by human actions. The challenge is deciding which option from the set is best for a given river system or management region. Third, more rigorous and comprehensive assessments of the benefits and consequences of providing fish passage are needed

to assess the success of passage decisions. The assessments are needed to ensure that both benefits and consequences of the passage decisions, not just the former, are compared among different management options, and that these comparisons consider the uncertainties associated with the benefits and consequences (Fenichel et al. 2008). Decision and real options analysis provide structured ways of incorporating existing biological information and stakeholder values to determine which management option is expected to perform best over the long-term in a given circumstance. The outcomes of actual decisions on specific river systems can be unique to some degree, owing to uncertainty. Better monitoring methods can help determine what changes occurred following a specific decision and facilitate adaptive management of fish passage decisions. These structured decision making tools will be most valuable for situations where the passage options are controversial and the outcomes of each option uncertain. For situations where the appropriate passage decision is self evident and less controversial, decision or real options analyses will not be necessary but monitoring will remain valuable. The problem-scoping key provided by Williams et al. (2009) can be used to help determine when structured decision making is warranted.

A context-dependent approach to fish passage decisions need not be an impediment to the broader initiative to remove dams and restore populations of native fishes. Landscape inventories of dams reveal that river systems are fragmented by numerous potential barriers to fish movement (Nilsson et al. 2005; Syvitski and Kettner 2011). Given this, there should be ample opportunity to restore native fishes, while minimizing unwanted consequences, under a context-dependent approach. However, science-based methods of selecting dams for removal will need to become more sophisticated, comprehensive and widely employed (e.g. Kemp and O'Hanley 2010).

Although many of the unwanted consequences identified here are specific to fishways, we caution against using that information to argue for dam removal over provisioning of a fishway. This is not consistent with a context-dependent perspective. The history of use and evaluation of fishways is greater than that of dam removal, so there has been much more time for evidence of unwanted consequences of fishways to come to light. The enthusiasm for dam removal is more recent in origin, and the science supporting it has had less time to mature. At such an early stage, the study of dam removal could be open to confirmation bias, failure to publish negative results, and insufficient time for final outcomes of dam removals to be realized (Loehle 1987).

For river systems, tensions surrounding the pros and cons of enhanced or reduced connectivity are likely to heighten as human populations grow and the demands for the ecosystem services provided by rivers intensify. It will therefore be increasingly important to understand the unwanted effects of fish passage decisions. In some circumstances, one passage option may perform better than others in terms of meeting ecosystem objectives. The challenge will be to identify which option is best. In other circumstances, choosing between options may entail a trade-off between competing management objectives. The challenge here will be to seek new ways of reconciling the trade-off, to improve the overall management of fishes and the ecosystem services they provide.

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