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Turbine entrainment and passage of potadromous fish through hydropower dams: Developing conceptual frameworks and metrics for moving beyond turbine passage mortality

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Abstract

Potadromous fishes are vulnerable to involuntary entrainment through hydropower turbines. However, turbines can also provide a downstream passage route for potadromous fish. Here, we review evidence for turbine entrainment and passage in potadromous fish, and evaluate the effects of these processes on upstream and downstream populations. We develop conceptual frameworks and metrics to quantify vulnerability to turbine entrainment removals, and to quantify the efficiency of turbines as a downstream passage route. We highlight factors that influence these processes and provide case-studies demonstrating their applicability. We found that juvenile potadromous fish are being entrained through turbines at rates high enough to impact upstream populations. Given that juvenile passage survival is often high, we argue that turbines provide an important downstream passage route for potadromous fish. We show that entrainment vulnerability is likely a function of interactions between in-reservoir fish behaviour, habitat configuration and operations and thus not well captured by passage mortality estimates. Similarly, we show that while passage mortality can limit downstream passage efficiency, passage success is also dependent on reservoir and forebay navigation, along with survival and fitness in the downstream river. We advocate for a shift in focus away from estimates of passage mortality and injury, which have previously accounted for the majority of turbine passage research. Instead, we recommend an approach that focusses on quantification of the factors that influence downstream passage efficiency and entrainment vulnerability. Moreover, we highlight the need to better understand the broader scale impacts of these events on upstream and downstream populations.

KEYWORDS
connectivity, dams, downstream passage, freshwater fish ecology, hydropower, turbine entrainment

1 | INTRODUCTION

As global demand for electricity increases, construction of large hydropower dams (>10 m) is booming (Liermann, Nilsson, Robertson, & Ng, 2012; Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2014). However, investigations into the impacts of hydropower dams on the downstream movements of fish populations have focussed largely on anadromous and catadromous species (Calles & Greenberg, 2009; Nislow, Hudy, Letcher, & Smith, 2011; Schilt, 2007; Silva et al., 2017). Accordingly, the impacts of hydropower dams on the movements of potadromous fishes, that is, those fishes that complete their entire life cycle in freshwaters, have been largely overlooked. Potadromous fish populations are found in freshwaters across the globe and often have high ecological, economic and social value (Lynch et al., 2016), particularly in hydropower reservoirs (Hutt, Hunt, Steffen, Grado, & Miranda, 2013). However, many potadromous fish populations are critically endangered, extinctions are occurring at a rapid rate (Ricciardi, Rasmussen, Ricciardi, & Rasmussent, 1999), and hydropower dams have been implicated in the decline (Liermann et al., 2012). Accordingly, societies and governments throughout the world are recognizing the need for upstream passage facilities for potadromous fish at hydropower dams (Fukushima, Kameyama, Kaneko, Nakao, & Ashley Steel, 2007; Godinho & Kynard, 2009; Shi, Kynard, Liu, Qiao, & Chen, 2015). Nonetheless, global recognition of the need to provide downstream passage for potadromous fishes at hydropower dams has been slower (Liermann et al., 2012; Northcote, 1998; Pelicice, Pompeu, & Agostinho, 2015). Likewise, there has been little recognition of the potential impacts of involuntary displacement of fish into turbine intakes, a process known henceforth as turbine entrainment (Martins et al., 2013; Rytwinski et al., 2017), on populations of potadromous fish that often occur in hydropower reservoirs. In contrast to anadromous fishes, vulnerability to turbine entrainment, along with volitional downstream movement, dispersal or migration through turbines (henceforth termed *turbine passage*) of potadromous species, has rarely been considered in the design, operation and mitigation strategy of historical hydropower production (Agostinho, Gomes, Fernandez, & Suzuki, 2002; Katopodis & Williams, 2012). Thus, conceptual frameworks and metrics which can help us understand and parameterize the processes of turbine entrainment and turbine passage for potadromous fishes, and thus mitigate any potential hydropower dam impacts, are lacking.

Fishways are being constructed with increasing frequency at new and existing hydropower facilities (Mclaughlin et al., 2013), but at a global scale remain rare (Hatry et al., 2013; Noonan, Grant, & Jackson, 2012; Shi et al., 2015). In theory, fishways can accommodate both upstream and downstream movements. However, in practice there is little evidence to show that downstream movement occurs through these facilities (Agostinho, Pelicice, Marques, Soares, & de Almeida, 2011; Noonan et al., 2012). Facilities specifically designed to facilitate downstream passage, known as bypass facilities, have been constructed at a number of hydropower dams, particularly in the Pacific Northwest of the USA (Muir, Smith, Williams, & Sandford, 2001), but are not designed or operated with potadromous fish in mind (Noonan et al., 2012). In addition to passage and entrainment through turbine penstocks, passage and entrainment at hydropower dams can occur through a number of different structures, including spillways and pipes. Furthermore, a number of diverse routes of downstream passage and entrainment past hydropower are available at "run of the river" type dams. We acknowledge that enough knowledge gaps exist concerning the passage and entrainment of potadromous fish through such structures to warrant structure-specific reviews. Nonetheless, given the global abundance of large (>10 m head height) hydropower dams without fish passage facilities (Liermann et al., 2012), and the tendency for hydropower operators to minimize spillway use and maximize turbine flows, turbine passage and turbine entrainment have the greatest potential to impact potadromous fish populations. Accordingly, turbine passage and turbine entrainment are the focus of this manuscript.

Although historically thought of as sedentary (Gerking, 1959), potadromous fishes are now recognized as mobile, often displaying life histories that involve movements and migrations in both upstream and downstream directions (Gowan, Young, Fausch, & Riley, 1994; Rodríguez, 2002). Indeed, downstream movement is often necessary for potadromous fishes to access foraging, seasonal and spawning habitat (Fahrig, 2003) and important for the adult dispersive portion of stream fish populations which can be of disproportionate significance in the determination of fish community spatial dynamics (Fraser, Gilliam, Daley, Le, & Skalski, 2001; Harrison et al., 2015; Radinger & Wolter, 2014). Furthermore, downstream movement is particularly important for juvenile potadromous fishes, where dispersal is most commonly a rheophilic process (Kemp, Gessel, & Williams, 2008; Lechner et al., 2013; Schiemer, Keckeis, & Kamler, 2002). Nonetheless, despite the growing recognition of the importance of barrier-free downstream movement for potadromous fish (Silva et al., 2017), conceptual models and metrics designed to better understand and quantify the efficiency of turbines as downstream passage routes past dams are lacking.

Research into the impacts of hydropower dams on downstream movements has focussed on the fate of fish passing or being entrained through turbines and how mortality, injury and stressors differ among turbine types, hydropower operation and design, sites and species (reviewed in Pracheil, DeRolph, Schramm, & Bevelhimer, 2016). Turbine passage mortality, that is, the proportion of individuals that do not survive the passage past turbines, can lower or eliminate downstream movement, and is an important metric for understanding dam impacts (Colotelo et al., 2017). Indeed, turbine passage mortality and the traits which predict mortality have been extensively reviewed (Cada, 1990; Čada & Schweizer, 2012; Pracheil, McManamay, Bevelhimer, DeRolph, & Čada, 2016). This focus on turbine passage mortality may have occurred due to regulatory interest in high-value anadromous fish and an engineering focus on turbine design to reduce injury and mortality. Nonetheless, in systems where upstream passage is not possible, the impacts of involuntary entrainment on upstream populations are independent of the fate of entrained individuals. Indeed, in such systems the risk to upstream populations posed by turbine entrainment depends on the population's vulnerability to entry into turbine penstocks. Accordingly, conceptual models and metrics that allow for the testing of hypotheses concerning upstream population vulnerability to involuntary turbine entrainment are necessary to gauge the impacts of hydropower dams on upstream potadromous fishes.

Similarly, the effectiveness of turbines as a downstream passage route past hydropower dams for dispersing potadromous fish populations depends not just on survival past turbines, but also on successful navigation through the reservoir and successful navigation into turbine entrances, along with an ability to survive tailrace predation and chronic passage injury. Accordingly, there is a need to develop conceptual models and metrics that will enable a more holistic, quantitative assessment of turbine passage efficiency, and thus test hypotheses concerning the ability of turbine passage to act as a downstream connectivity route past hydropower dams.

In this manuscript, we begin by reviewing the evidence for the occurrence and impacts of involuntary entrainment and volitional passage through turbines in potadromous fish populations. Next, we develop conceptual frameworks and associated metrics to; better understand the factors that influence entrainment vulnerability and downstream passage efficiency in potadromous fish populations; and enable the quantification of the impacts of these processes on upstream and downstream fish populations. To illustrate the applicability of these two frameworks, we consider two case-studies. In case-study 1, we explore the impacts of involuntary turbine entrainment on an adult reservoir resident bull trout (*Salvelinus confluentus*, Salmonidae) population, through the quantification of entrainment vulnerability. In case-study 2, we investigate the ability of turbine passage to provide a downstream connectivity route for YOY kokanee salmon (*Oncorhynchus nerka*, Salmonidae) by estimation of turbine passage efficiency. We then conclude with a discussion of future directions for research and implications for management.

2 | REVIEW OF EVIDENCE FOR INVOLUNTARY TURBINE ENTRAINMENT AND IMPACTS ON UPSTREAM POPULATIONS

Research on turbine passage mortality and injury has been extensive (see Pracheil, DeRolph, et al., 2016 for a review, which includes both potadromous and anadromous populations). Nonetheless, we know much less about the numbers of potadromous fish that actually experience entrainment or passage through hydropower turbines (Silva et al., 2017). Indeed, where entrainment/passage has been quantified, the numbers of juvenile potadromous fish entrained/passing annually at individual facilities can often be very high, ranging from 80,000 to 4.47 million (Dawson & Parkinson, 2013; FERC, 1995; Janáč, Jurajda, Kružíková, Roche, & Prášek, 2013; Navarro, McCauley, & Blystra, 1996; Skaar, 1996). In contrast, we were able to find just two estimates of potadromous fish entrainment passage, where Spinelli (2010) estimated that 138,000 rainbow trout (*Onchorynchus mykiss*, Salmonidae) and 152,000 walleye (*Sander vitreus*, Percidae) were annually entrained through the Hauser Dam. However, because the values are not generally reported in comparison with upstream abundance, the impacts of these entrainment/passage events on upstream populations are not clear.

Given that the majority of hydropower dams do not have fishways for upstream passage that are effective for potadromous fish populations (Noonan et al., 2012), individuals that pass or are entrained through turbines represent a loss to the upstream population. Thus, if the rates of entrainment/passage removals exceed levels that the upstream population can maintain, potential exists for a decline in upstream abundance (Martins et al., 2013). This one-way passage means upstream populations, and life stages effectively lose access to downstream habitats potentially important for foraging, over-wintering or spawning (Nislow et al., 2011). Furthermore, reductions in upstream abundance can compound the genetic isolation that occurs in these populations that are cut off from the downstream gene pool (Vrijenhoek, 1998). Indeed, turbine entrainment/passage-induced upstream population declines have been recorded for rainbow smelt (*Osmerus mordax*, Osmeridae; Fincel, Radigan, & Longhenry, 2016), paddlefish (*Polyodon spathula*, Polyodontidae; Pracheil, Mestl, & Pegg, 2016), rainbow trout and kokanee (Baldwin & Polacek, 2002). In contrast, adult bull trout and burbot (*Lota lota*, Gadidae) were shown to be entrained/pass through turbines at an annual rate that was considered to likely to be sustainable for current upstream populations (see case-study 1), in Kinbasket Reservoir, British Columbia, Canada (Harrison et al., 2016; Martins et al., 2013). However, we were able to find no further empirical data, demonstrating impacts of turbine entrainment and passage on upstream potadromous fish abundance. Moreover, studies comparing upstream populations before and after dam construction that could be used to estimate entrainment/passage impacts have not generally occurred.

The lack of published empirical turbine entrainment and passage data and entrainment/passage impact data may in part reflect the difficulty in discriminating the direct effects of involuntary turbine entrainment removals from the more general ecological impacts of hydropower reservoir construction and associated population fragmentation (Fernando & Holčík, 1991). In general, fish assemblages above impassable anthropogenic barriers typically have reduced stream fish species richness and abundance (Guenther & Spacie, 2006). Indeed, Nislow et al. (2011) showed that species richness and abundance above impassable anthropogenic barriers were less than half the richness and abundance of stream sections below barriers. Luttrell, Echelle, Fisher, and Eisenhour (1999) demonstrated that two species of speckled chub (*Macrhybopsis aestivalis*, Cyprinidae) were extirpated above impoundments in the Arkansas River Basin. Similarly, several studies have reported increases in upstream species richness following dam removal (Catalano, Bozek, & Pellett, 2007; Magilligan, Nislow, Kynard, & Hackman, 2016). Subsequently, the relative role of entrainment removals on upstream populations, in comparison with general barrier effects, has yet to be quantified.

3 | REVIEW OF EVIDENCE FOR TURBINE PASSAGE AND IMPACTS ON DOWNSTREAM POPULATIONS

Turbine passage mortality has the potential to reduce recruitment from above the dam and thus negatively impact downstream populations (Winkle & Kadvany, 2003). High mortality associated with turbine passage has the potential to limit or even halt downstream movement (Cada, 1990; Pracheil, DeRolph, et al., 2016). However, turbine passage mortality estimates have been largely based on experimental turbine introductions or turbine passage simulations. Accordingly, data on the actual numbers of fish attempting turbine passage, and evidence for impacts on downstream vital rates, are lacking. Even in situations where mortality is reported as very high (e.g., 90%, Maiolie & Elam, 1996), we cannot be sure that this mortality has an impact on downstream passage of potadromous fish without knowledge of the actual numbers of fish entrained/passing. Moreover, adult turbine passage mortality is often <30% (Pracheil, DeRolph, et al., 2016). In such cases, it is hard to draw conclusions about the overall impacts of hydropower on downstream movement, without estimates of passage attempts or evidence of downstream impacts.

Avoidance of turbine intakes and reservoir forebays, or an inability to recognize or find turbine intakes during downstream passage, has the potential to disrupt or even halt volitional downstream passage (Coutant & Whitney, 2000), even if passage mortality is low or moderate. Reservoir impoundments change upstream conditions, and, the altered thermal and flow dynamics found in reservoirs can mask migration cues, such as velocity (Xu et al., 2017). Consequently, reservoir impoundments may be significant barriers to downstream dispersal (Agostinho et al., 2011; Pelicice et al., 2015). Even in cases where turbine passage mortality rates are experimentally estimated to be very high, mitigation measures cannot benefit downstream populations if potadromous fish avoid turbine passage.

Turbine passage survivors, which can often exceed 90% (Pracheil, DeRolph, et al., 2016), have the potential to contribute to downstream populations. For example, paddle fish, tube-nosed goby (*Proterorhinus semilunari*, Gobiidae) and white sturgeon (*Acipenser transmontanus*, Acipenseridae) on the Missouri, Danube and Snake rivers, respectively, have been shown to be subsidizing downstream populations, through downstream passage/entrainment through turbines (Jager, 2006; Janáč et al., 2013; Pracheil, Mestl, et al., 2016). Moreover, turbine entrainment/passage of kokanee through Mica Dam in British Columbia, Canada, is thought to provide recruitment for downstream reservoir populations, where access to spawning habitat is limited (see Dawson & Parkinson, 2013, and case-study 1). While we could find no further evidence demonstrating hydropower turbines can provide a successful downstream passage route, we suspect that this reflects a lack of research rather than an absence of successful passage. Indeed, we know downstream dispersal is important for potadromous fish (O'Hanley, Wright, Diebel, Fedora, & Soucy, 2013); we have shown in this review that large numbers of juvenile potadromous fish are likely being entrained; and we know that a large proportion of these juvenile entrained fish likely survive entrainment (Pracheil, DeRolph, et al., 2016). This juvenile entrainment/passage-based recruitment is potentially important for fish populations that occur downstream of hydropower facilities that can be negatively impacted by altered flow and temperature regimes (Olden & Naiman, 2010; Poff et al., 1997). Moreover, this entrainment/passage recruitment may be particularly important for downstream populations without access to spawning grounds. Furthermore, given the importance of downstream dispersal for larval and juvenile stream potadromous fish (Wolter & Sukhodolov, 2008), and the potentially low turbine passage mortalities of these life-history stages (Čada & Schweizer, 2012), turbine passage likely provides an important passage route for potadromous larval and juvenile stages.

4 | CONCEPTUAL MODEL OF VULNERABILITY OF POPULATIONS RESIDING UPSTREAM OF HYDROPOWER DAMS TO TURBINE ENTRAINMENT REMOVALS

We propose that in situations where upstream passage facilities are not available, the vulnerability of an upstream population to turbine entrainment/passage removals (Entrain_v) can be estimated as the product of the probabilities of reservoir entry (Res Entry_p), forebay entry (Fbay Entry_p) and fish entrainment zone (FEZ) entry FEZ Entry_p:

$$\text{Entrain}_v = \text{Res Entry}_p \times \text{Fbay Entry}_p \times \text{FEZ Entry}_p$$

All of the above entrainment/passage *entry* metrics use conditional denominator sample sizes based on the preceding factor; for example, Fbay Entry_p is expressed as a proportion of reservoir users that use the forebay, and FEZentry_p is expressed as the proportion

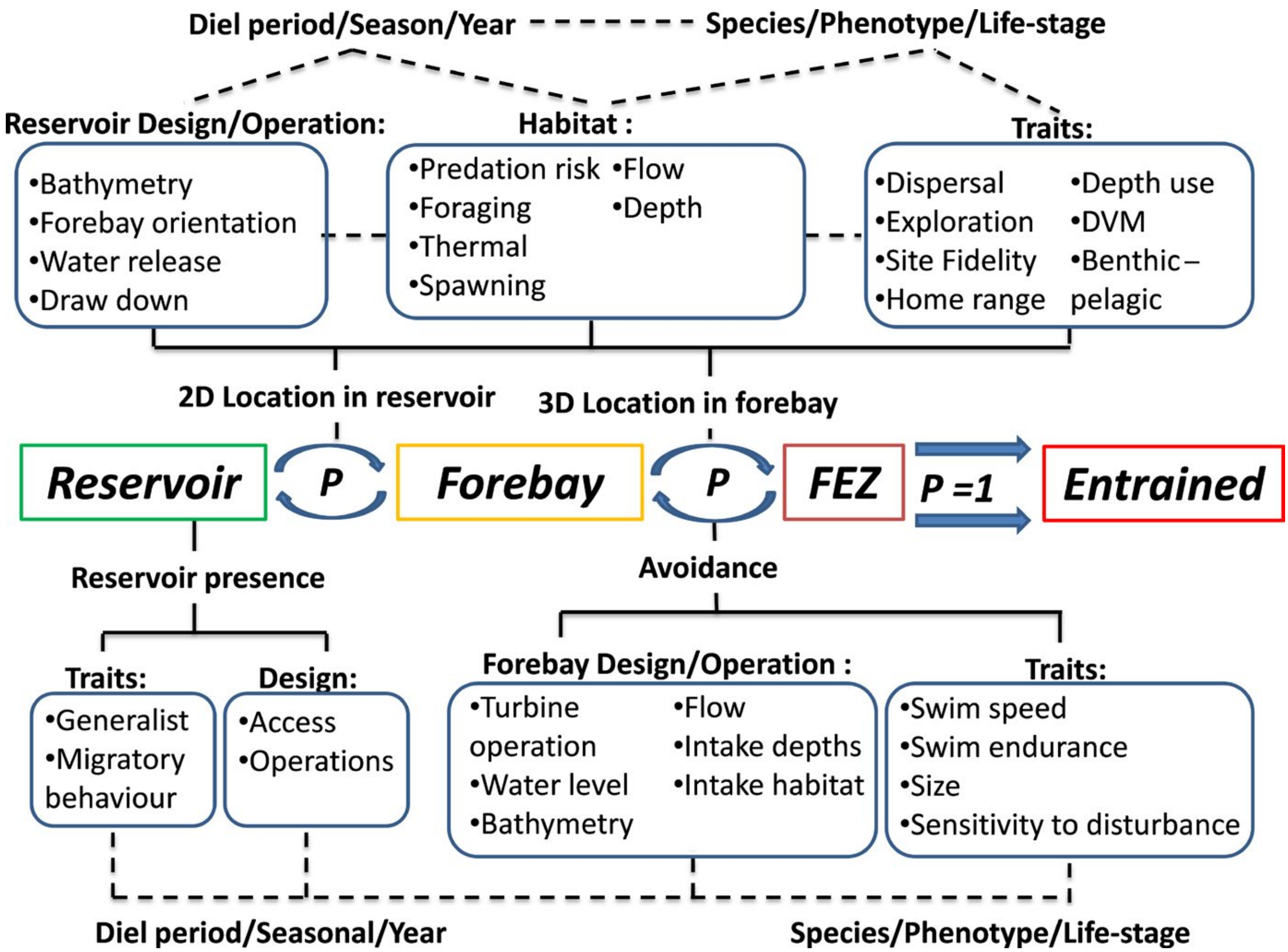

FIGURE 1 Conceptual model of involuntary entrainment vulnerability of potadromous fish populations residing upstream of hydropower dams, detailing traits, habitat and reservoir configuration that have potential to influence probability (*p*) of entry into each zone. Entrainment probability in the fish entrainment zone (FEZ) is defined as 1

of forebay users that enter the FEZ. Accordingly, the Entrain_v of a population, individual or life stage, can be simply estimated as the product of the constituent probabilities.

The estimation of FEZentry_p potentially requires the use of fine-scale fish tracking technology in the forebay (see, e.g., Johnson, Hedgepeth, Skalski, & Giorgi, 2004; Martins et al., 2014), which may not always be financially or technically feasible. However, in situations where broad-scale tracking technologies have been used to assess *entry* metrics, detections of entrained/passing fish at downstream (tailrace) receivers can be as a substitute for FEZentry_p (see case-study 1 for an example). That is, FEZentry_p may be replaced with the proportion of fish that enter the forebay that are detected downstream of the turbines, that is in the tailrace, which we term Tailrace Entry_p.

$$\text{Entrain}_v = \text{Res Use}_p \times \text{Fbay Use}_p \times \text{Tailrace Entry}_p$$

Thus, an Entrain_v value near zero would indicate a low vulnerability and values near 1 would indicate a high vulnerability. A schematic of the factors that influence these vulnerability metrics is given in Figure 1.

Understanding the broader impacts of turbine passage on upstream populations requires quantification of the impacts on upstream abundance. Thus Entrain_v is a key first step in understanding the impacts of turbine passage or entrainment on upstream potadromous fish populations (Martins et al., 2013). Entrain_v values lower than the maximum removal rates of upstream populations can sustain are necessary to ensure sustainable upstream populations (Martins et al., 2013). Accordingly, integration and comparison of Entrain_v with upstream population dynamics presents an opportunity to quantify impacts on upstream abundance. Moreover, even in cases where the vital rates of upstream populations are not known, high Entrain_v could potentially provide early warnings of negative upstream impacts. The proportional nature of the metric lends itself to tagging methods (see Table 1 and case-study 1), where assuming that the entrainment event detection efficiency is known, and vulnerability to entrainment is equal among tagged sample and equivalent populations, then the proportion of tagged fish entrained can be considered equal the proportion of population entrained. Furthermore, the proportional nature of the metric means that it is resilient to changes in upstream abundance, such as those that occur as a consequence of trophic upsurge which is common in newly constructed temperate reservoirs (Turgeon, Solomon, Nozais, & Gregory-Eaves, 2016). Alternatively, Entrain_v can also be calculated by comparison of Turb $\text{Entry}_{\text{count}}$, with upstream abundance estimates (see case-study 2). Details concerning the calculation of each constituent metric and current knowledge regarding the factors influencing each metric are provided in the following sections:

4.1 | Reservoir entry

Among potadromous fish populations occurring upstream of hydropower dams, occupancy of reservoir habitat ultimately determines vulnerability to involuntary turbine entrainment, because fish that never enter the reservoir cannot be entrained (Pracheil, McManamay, et al., 2016). Accordingly, we posit that estimation of reservoir occupancy probabilities (Res Entry_p), which we define as the proportion of the population that enters the reservoir, will be a useful first step in assessing entrainment vulnerability. In situations where, for example, the population in question is known to be reservoir resident, it may be more practical to assign probabilities, rather than design field studies to capture these probabilities (see case-study 1).

Given that reservoir habitats tend to be occupied by generalist species that can utilize both lentic and lotic habitats (Herbert & Gelwick, 2003), generalist species may carry an increased likelihood of reservoir entry in comparison with stream habitat specialists. Furthermore, species, individuals and phenotypes that perform longer migrations, or have larger home ranges, may have a higher risk of reservoir entry than more sedentary types (Hirsch, Thorlacius, Brodin, & Burkhardt-holm, 2016). However, the life history and ecology of many species of potadromous fish that occur in parts of the world where hydropower development is most rapid have yet to be documented (Winemiller et al., 2016). Moreover, even in well-studied potadromous fish species, the regional specific timing of reservoir entry may not be well documented (Martins et al., 2014). Consequently, quantification of the variables that influence Res Entry_p represents an important and necessary first step in understanding the potential for entrainment vulnerability.

4.2 | Forebay entry

For fish that are determined to use reservoirs (including permanent reservoir residents), vulnerability to involuntary turbine entrainment is further determined by entry into the forebay, defined broadly as the region immediately upstream of the dam (Martins et al., 2013). Thus, forebay entry probability Fbay Entry_p, which we define as the proportion of reservoir users that enter the forebay, can potentially provide an informative turbine entrainment vulnerability metric. Quantitative assessments of the factors that promote forebay use in potadromous fish are scarce. Accordingly, quantification of the parameters that influence Fbay Entry_p has good potential to increase our understanding of the factors that influence involuntary entrainment vulnerability.

From a conceptual viewpoint (see Figure 1 for a schematic), we hypothesize that spatial behavioural traits, such as movement/activity, exploration, dispersal, site fidelity and home-range size all have the potential to influence the two-dimensional (2D) location of a fish and thus may influence forebay use (Čada & Schweizer, 2012). Indeed, it seems likely that exploratory, mobile types, with large home ranges or dispersive tendencies, likely also carry greater risk of forebay entry (Harrison et al., 2015). Forebay use may also be influenced by ecological traits, such as littoral, benthic, pelagic habitat specializations, with risk of use dependent on the distribution of available habitats within and outside the forebay (Pracheil, McManamay, et al., 2016). Thus, individual, phenotypic, interspecific and life-history variation in these behavioural and ecological

TABLE 1 Methods with potential for estimating proposed involuntary turbine entrainment and volitional passage metrics

Method and examples	Entrainment applicable metrics	Passage applicable metrics	Advantages	Disadvantages
Presence–absence acoustic telemetry (Martins et al., 2013)	Res $Entry_p$ Fbay $Entry_p$ Tailrace $Entry_p$ $Entrain_v$	Turbine $Passage_s$ Turbine $Exit_S$ $Longterm_s$ Res $Entry_p$ Fbay $Entry_p$ Tailrace $Entry_p$	• Low receiver cost in comparison with positional arrays • Large receiver detection ranges in comparison with PIT tagging • Overlapping receiver ranges enable gates (Heupel, Semmens, & Hobday, 2006) • Can include a variety of sensors including depth, temp, predation (Cooke et al., 2004) • Sample can be used to estimate population entrainment rate without upstream abundance (Martins et al., 2013).	• Minimum fish size × transmitter size × battery life trade-offs. • Powerhouse noise can reduce detection efficiency (Kessel et al., 2014) • Not fine scale enough to estimate FEZ_p • Continued signal transmission after mortality complicates survival analysis (Skalski et al., 2014) • Need to account for tagging effects on survival
Positional acoustic telemetry (Martins et al., 2014)	FEZ $Entry_p$ $Entrain_v$ Fbay $Entry_p$	Tailrace $Entry_p$	• CDMI technology less sensitive to powerhouse noise than standard positional technologies (Deng et al., 2011) • Provides 3D positions with high precision	• Minimum fish size × transmitter size × battery life × pulse rate trade-offs • High costs mean small area can be covered
Fixed imaging (Johnson et al., 2004)	FEZ $Entry_p$ $Entrain_v$ (if upstream abundance is known)	Turb $Entry_{count}$	• Can provide raw counts of entrainment events (Deng et al., 2016) • Non-intrusive	• Requires concurrent net sampling to determine species compositions • Upstream abundance estimates required to estimate ER_r
Genetic methods (Neraas & Spruell, 2001)	NA	DSrec	Provides long-term picture of connectivity	Cannot distinguish between connectivity route in systems with spills

traits, along with diel, seasonal and climatic variation, all have the potential to influence two-dimensional (2D) location in the reservoir (Gido & Matthews, 2000) and thus potentially influence forebay entry probability.

The two-dimensional (2D) location of fish in the reservoir and thus forebay entry is also influenced by the distribution of competitors, predators and prey, and by availability of suitable thermal, reproductive habitat and shelter from predation (Prchalová et al., 2009). In turn, the configuration of the habitats within reservoirs is influenced by annual, seasonal and daily cycles. Reservoir location and forebay use are also potentially influenced by reservoir geography, such as bathymetry, which determines availability of suitable vertical habitat and substrate distribution (Gido et al., 2002). Furthermore, in-reservoir distribution of predators and prey can be influenced by the orientation of the reservoir in relation to prevailing wind directions (Gido & Matthews, 2000). Turbine operation and water release strategies influence both flow hydraulics and littoral habitat (Hirsch et al., 2017), which may potentially influence the suitability of forebay habitat for focal species and their predators and prey. These operational strategies are in turn influenced by diel, seasonal and annual variation in climate and demand for hydropower.

Where tracking technologies allow for estimations of the relative use of the forebay, we propose the additional calculation of continuous intensity of forebay use metrics such as Fbay Use_p, that is, the proportion of time (at large) spent in the forebay (see Martins et al., 2013 and case-study 1). Indeed, because the intensity or duration of forebay occupancy is likely to be correlated with turbine entrainment vulnerability, Fbay Use_p can potentially serve as a useful proxy metric for entrainment vulnerability, where sample sizes of entrained individuals are too low to allow for analysis of, for example, seasonal entrainment patterns.

4.3 | Fish entrainment zone entry

For fish that enter the forebay, involuntary entrainment vulnerability is determined by the probability of entering the fish entrainment zone, which surrounds the intakes. Accordingly, we propose the use of the metric ($FEZentry_p$), which can be estimated as the proportion of forebay users that enter the FEZ, has good potential for testing hypotheses surrounding accidental entrainment and turbine passage. The FEZ was defined by Johnson et al. (2004) as the three-dimensional (3D) zone in which fish that entered had a probability of entrainment into turbines exceeding 90%; however, for estimating $FEZentry_p$ we suggest the FEZ be defined at the 100% probability of entrainment zone.

Fish entrainment zone zones are thought to occur where flow velocities exceed the swimming capabilities of individuals (Čada & Schweizer, 2012). In addition, the areas of elevated velocity surrounding FEZ, which while not exceeding swimming capabilities, may also play a role in the involuntary entrainment process (Johnson et al., 2004). It is generally assumed that higher velocities promote avoidance responses in fish species that are not actively migrating (Coutant & Whitney, 2000). Consequently, traits related to swimming ability, and traits such as body size which determine swimming speed, are thought to be important for predictions of involuntary $FEZentry_p$ (Pracheil, McManamay, et al., 2016). Thus, species with lower swimming speeds and endurance are thought to have increased vulnerability (Pracheil, McManamay, et al., 2016). Similarly, life stages with lower swimming capabilities such as juvenile and larval fish, or the inability to swim such as planktonic life stages, carry an increased risk of involuntary entrainment in comparison with adults (Čada & Schweizer, 2012). Furthermore, species, which lack swim bladders and thus must constantly swim, may carry an increased risk of involuntary entrainment (Coutant & Whitney, 2000). Given that hydropower dams are relatively noisy, unnatural river features (Popper & Schilt, 2005), traits, such as sensitivity to noise or exploration in novel environments, may play a role in $FEZentry_p$ (Čada & Schweizer, 2012). We hypothesize that all the traits identified as relevant to reservoir 2D location above have potential to influence the finer scale 3D location of fish in the forebay and thus $FEZentry_p$. In particular, ecological traits such as littoral, pelagic, benthic habitat specializations are thought to influence the probability of involuntary entry into FEZ, with littoral types expected to carry a greater risk (FERC, 1995). Similarly, the distribution of habitats and forage within the forebay will influence fish location in the forebay and thus $FEZentry_p$. Moreover, the design of the forebay, and turbine intakes, including the relative depth of intakes, may influence $FEZentry_p$, with deeper intakes being riskier for benthic species and shallower intakes riskier for pelagic species (Pracheil, McManamay, et al., 2016). Water release and turbine operations change flow velocities in the forebay and influence FEZ size and $FEZentry_p$ (Johnson et al., 2004; Martins et al., 2014). FEZ volume estimations, therefore, provide an excellent opportunity for integration with forebay computational fluid dynamics models. Species, site and operation rate-specific estimations of FEZ volume and $FEZentry_p$ will be essential for a better overall understanding of involuntary turbine entrainment processes, and to guide mitigation strategies.

4.4 | Turbine entry counts

Counts and estimations of the numbers of fish entering turbine intakes provide important metrics for determining downstream passage and entrainment rates (FERC, 1995). Turbine entrainment and passage numbers can vary widely among seasons, among diel periods and in response to environmental and biotic variation (FERC, 1995). Accordingly, sampling strategies need to be designed to capture such variation. Among the few published examples of entrainment counts (FERC, 1995), a lack of reporting standardization makes comparisons among differing sized dams and turbines difficult. We propose the metric (Turb $Entry_{count}$), where entrainment is expressed as the annual number of fish entrained (see case-study 2 for an example). Moreover, we propose this metric can be standardized by cubic meter of flow, to allow for across-dam comparisons.

5 | CONCEPTUAL MODEL OF DOWNSTREAM PASSAGE EFFICIENCY FOR FISH POPULATIONS PASSING HYDROPOWER DAMS VIA TURBINES

We posit that the overall passage efficiency for potadromous fish populations using turbine routes to pass hydropower dams in a downstream direction (DS $Passage_{efficiency}$) can be considered a

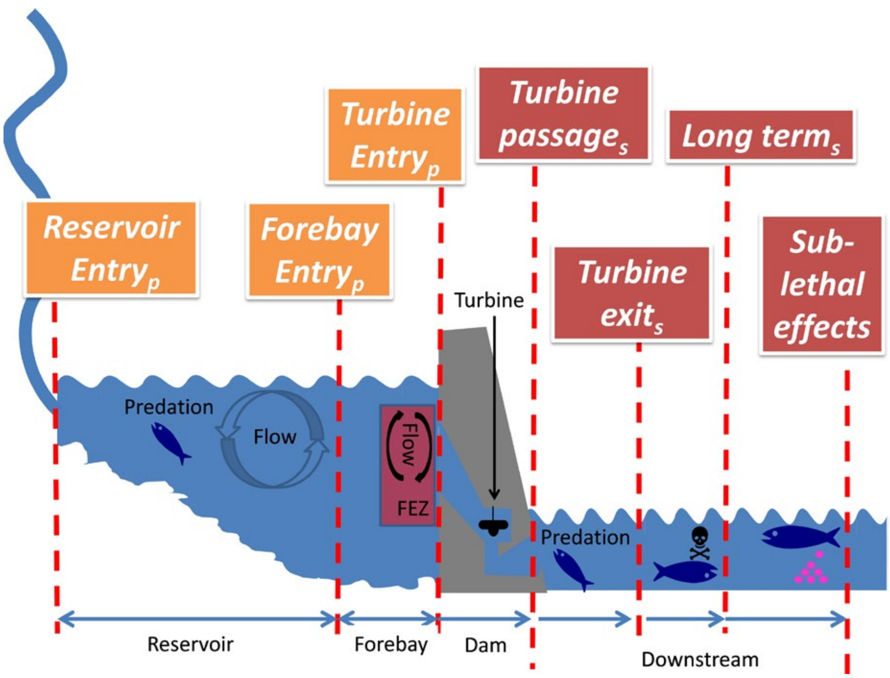

FIGURE 2 Conceptual schematic for the factors influencing the effectiveness of turbine passage as connectivity route for potadromous fish populations

product of the conditional probability of reservoir, forebay and turbine entry (Entrain_v), along with turbine passage survival, turbine passage exit survival, delayed survival and sub-lethal effects (see figure 2 for conceptual schematic). Again, because all metrics are based on a conditional denominator, the product of probabilities can be used to assess overall probability. Thus, values near zero are indicative of low efficiency of passage and values nearer 1 are indicative of high passage efficiency:

$$\text{DS Passage}_{\text{eff}} = \text{Res Entry}_p \times \text{Fbay Entry}_p \times \text{Tailrace Entry}_p \times \text{Turbine Passage}_s \times \text{Turbine Exit}_s \times \text{Longterm}_s \times \text{Sublethal effects}_p$$

We propose that the numbers of fish being recruited downstream as a consequence of turbine passage (DSrec) can be estimated as a product of turbine entry count and DS $\text{Passage}_{\text{eff}}$:

$$\text{DSrec} = \text{Turb Entry}_{\text{count}} \times \text{DS Passage}_{\text{eff}}$$

Such a metric has potential use for integration in downstream population dynamics models and thus may provide insight into the contribution of this passage on downstream populations. Details concerning the estimation of each metric are given below:

5.1 | Reservoir, forebay and turbine entry metrics for passage efficiency

Successful volitional turbine passage will first require entry into or use of the reservoir immediately upstream of hydropower facility. Accordingly, estimation of Res Entry_p can likely provide an early indication of reservoir access issues, which can be common in reservoirs with highly fluctuating water levels and shifting sediments (Langford, 2016). Moreover, low entry probabilities potentially provide an indicator of avoidance of the reservoir, which may be novel habitat for lotic fishes.

For dispersers that successfully enter reservoirs, passage efficiency is then modulated by the ability of individuals to successfully navigate through the reservoir to the dam forebay. Fbay Entry_p will capture the ability of dispersers to navigate the reservoir and avoid in-reservoir predation, which can be problematic in the reservoir fish assemblages which often differ from pre-construction assemblages (Herbert & Gelwick, 2003), often including non-native predators (Fernando & Holčík, 1991). Accordingly, Fbay Entry_p for dispersers is likely dependent on reservoir size and distance from entry point to forebay. Moreover, Fbay Entry_p can provide a measure of the ability of dispersers to navigate the novel flow and temperature regimes found in reservoirs, which often do not provide normal navigation cues (Agostinho et al., 2011; Xu et al., 2017).

Once dispersers enter the forebay, downstream passage efficiency will then be determined by the ability to locate and enter turbine entrances, which can be estimated using FEZ Entry_p. We are beginning to learn more about the forebay and reservoir hydraulic conditions that promote guidance for out-migrating anadromous species (Enders, Gessel, & Williams, 2009; Kemp, Gessel, & Williams, 2005; Scruton, McKinley, Kouwen, Eddy, & Booth, 2002; Scruton et al., 2008). In general, increased velocities tend to promote guidance for anadromous salmonids. Given that potadromous fish attempting to pass turbines are also actively migrating, it seems likely that high velocities will increase passage rates of potadromous dispersers (Coutant & Whitney, 2000). Moreover, passage efficiency for anadromous salmonids tends to decrease in relation to intake depth. However, the applicability of these findings to potadromous fish has yet to be demonstrated. Furthermore, avoidance of powerhouse noise, or forebay predators, has the potential to limit turbine entrance probability (Pracheil, McManamay, et al., 2016).

5.2 | Turbine passage survival

For individuals that enter the turbine penstocks, passage efficiency is determined by turbine passage mortality, which is usually estimated as the proportion of fish that enter the turbine that do not survive passage (Cada, 1990; Pracheil, DeRolph, et al., 2016). However, when estimating overall passage efficiency, it is more convenient to express this metric as turbine survival probability (Turbine Passage_s). Turbine passage survival is often difficult to estimate in situ; however, survival rates estimated by passage simulation techniques (e.g., Stephenson et al., 2010) can be substituted here (see case-study 2 for an example). Factors influencing turbine passage mortality have been extensively reviewed elsewhere (Pracheil, DeRolph, et al., 2016).

5.3 | Turbine exit survival

For individuals that survive turbine passage, passage efficiency may be determined by predation pressure in the turbine tailrace and in the area immediately downstream of the dam. Accordingly, we propose the estimation of turbine exit survival (Turbine Exit_S) as the proportion of alive fish exiting the turbine that remain alive for 1 week following turbine exit. Such a metric can likely capture predation in the tailrace and immediately below the dam which can be high, along with delayed mortality associated with turbine passage injury or stress, that was not immediately fatal (Budy, Thiede, Bouwes, Petrosky, & Schaller, 2002).

5.4 | Long-term post-passage survival

For individuals that survive the first week following turbine exit, passage efficiency can be further influenced by mortality that occurs as a function of more chronic passage injury. Moreover, turbine passage may delay migration in comparison with barrier-free movement and thus also impact survival. We propose estimation of the metric, long-term survival (Long term_s), that is, the difference between the survival rate of passage survivors and the survival rate of a downstream population control group. To eliminate any possible tagging effects on survival, downstream control survival can be estimated in tagged fish released downstream (Skalski, Buchanan, Townsend, Steig, & Hemstrom, 2009; Skalski, Townsend, Steig, & Hemstrom, 2010). Estimation of Longterm_s will require large numbers of tagged fish to experience entrainment and is thus logistically challenging in populations which display intra-specific variation in migratory behaviour. Nonetheless, we argue that the potential for Long term_s should be considered in entrainment management policy.

5.5 | Post-passage sub-lethal effects

Fishes that survive turbine passage may also suffer sub-lethal effects of downstream passage, such as injury or phenology disruption due to delayed passage, that can carry long-term fitness consequences (Budy et al., 2002). Accordingly, we propose that where fitness proxies can be quantified, sub-lethal effects ($\text{Sub lethal effects}_s$) can be estimated as the proportional difference between survivor fitness proxies and downstream control fitness proxies. We acknowledge that quantification of such a metric is challenging and potentially unrealistic with current technology. Nonetheless, we suggest a precautionary approach to management should recognize the existence of sub-lethal fitness effects. This is particularly important in jurisdictions where "harm" from entrainment in a regulatory context includes sub-lethal impacts and when considering the effects of turbine passage on fish welfare (see Schilt, 2007).

6 | CASE STUDIES

Here, we explore two case-studies concerning the entrainment and turbine passage efficiency of potadromous fish through Francis turbines at Mica Dam, illustrating the calculation of metrics, for two species of potadromous fish, in a well-studied system, Kinbasket Reservoir, British Columbia, Canada. Mica Dam currently provides no upstream passage routes. Accordingly, entrained fish are considered a loss to upstream populations. Moreover, while a spillway has been constructed at Mica Dam, the reservoir has been operated in such as way that the spillway is rarely used. Thus, turbine passage represents the only downstream connectivity route past Mica Dam.

6.1 | Entrainment vulnerability of bull trout

Bull trout, a species of high recreational value (Gutowsky, Harrison, Landsman, Power, & Cooke, 2011) are threatened throughout much of their western North American range (Post & Gow, 2012). Bull trout are often found in hydropower reservoirs of western Canada and the north-western USA. Indeed, in Kinbasket Reservoir populations of bull trout are sufficiently large to provide a popular sport fishery (Gutowsky et al., 2011). The potential vulnerability of the reservoir adult bull trout population to involuntary turbine entrainment had not previously been established and this provided the objectives for two studies in the system (Martins et al., 2013; Martins et al., 2014).

While mature bull trout perform adfluvial migrations into reservoir tributaries for spawning, the majority of their lives are spent in the reservoir. Given the research question was focussed on a reservoir resident population, it was practical to assume a reservoir entry (Res Entry_p) probability of 1.

Entrain_v and its components Fbay Entry_p, and Tailrace Entry_p were estimated using acoustic telemetry. For full methodological details, see Martins et al. (2013). Briefly, an array of seven acoustic telemetry receivers was deployed for two full years in Kinbasket Reservoir, with six in the forebay and one in the tailrace. A total of 187 adult bull trout were surgically implanted with acoustic telemetry transmitters. Annual estimates of Fbay Entry_p and Tailrace Entry_p were estimated using Kaplan–Meier time-to-event analysis (Table 2). Fbay Entry_p and Tailrace Entry_p were calculated at the season-by-year scale, to account for a seasonal and annual variation in the number of the tagged sample that occurs as a consequence of mortality and tag losses. Mean annual probability of an individual forebay entry event (Fbay Entry_p) was quite high (0.57, 95% CI [0.49, 0.64]). However, mean probability of entrainment among forebay users was relatively low (0.05, 95% CI [0, 0.10]), ensuring a low mean annual Entrain_v (0.03, 95% CI [0, 0.06]). Moreover, while the probability of forebay entrance was relatively high, calculation of Fbay Use_p metrics showed that relative use of the forebay was very low (3%), indicating that bull trout spend only a small proportion of their time within the forebay. The low Entrain_v indicates that the impacts on downstream populations are likely minimal, negating the need for estimation of turbine passage efficiency metrics. This case-study provides a good example of how a simple and relatively inexpensive telemetry array featuring just eight receivers can be used to determine entrainment vulnerability of a reservoir resident population.

6.2 | Turbine passage efficiency of 0+ kokanee

In addition to bull trout, Kinbasket reservoir also contains a large population of kokanee, the freshwater potadromous form of sockeye salmon, which were originally stocked to provide a pelagic forage fish for bull trout (Sebastian & Weir, 2016). While kokanee are abundant in Kinbasket reservoir, spawning opportunities for kokanee are limited in Revelstoke Reservoir, which is situated immediately below Mica Dam. Accordingly, managers sought to test the hypothesis that entrainment of 0+ aged kokanee through Mica Dam turbines was contributing to downstream populations in Revelstoke Reservoir.

0+ Kokanee abundance in the upstream reservoir was estimated using a roving hydroacoustic survey (see Sebastian & Weir, 2016, for full methodological details). The mean lake-wide abundance estimated over 17 annual kokanee surveys was 7.02 (5.56–8.47) million. 0+ kokanee entrainment data are not currently available for Kinbasket Reservoir. However, a fixed hydroacoustic survey that was used to quantify kokanee entrainment at the next dam downstream (Revelstoke Dam) provides a good example of how entrainment rates can be quantified in fish too small to tag with telemetry transmitters. Using a Biosonics TDX echosounder located at a turbine entry point, Dawson and Parkinson (2013) estimated an annual $\text{Turb Entry}_{count}$ of 2,081,879 for 0+ kokanee through Revelstoke Dam. For the sake of this case-study, we use this value for Mica Dam. Accordingly, we

TABLE 2 Summary of annual entrainment vulnerability metrics for bull trout, through Mica Dam, in Kinbasket Reservoir, British Columbia, Canada, based on data from Martins et al. (2013)

Year	Fbay $Entry_p$	Tailrace $Entry_p$	$Entrain_v$
1	0.64 (0.57, 0.70)	0.03 (0, 0.07)	0.02 (0, 0.04)
2	0.50 (0.41, 0.57)	0.06 (0, 0.12)	0.04 (0, 0.08)
Mean annual	0.57 (0.49, 0.64)	0.05 (0, 0.10)	0.03 (0, 0.06)

estimate an annual $Entrain_v$ of 0.30 for 0+ kokanee through Mica Dam, based on the proportion of the population that were entrained in a given year. Site-specific and general turbine passage survival estimates are not currently available for 0+ kokanee. However, in a meta-analysis based largely on YOY fish, Pracheil, DeRolph, et al. (2016) report general *Oncorhynchus* survival through Francis turbines at 0.74. Accordingly, we use this value for Turbine $Passage_s$.

Little is currently known about the survival of freshwater potadromous fish post-passage/entrainment, either at a species-specific or a general scale. Accordingly, rather than try to derive estimates from the scarce literature, we present Turbine $Exit_s$, $Longterm_s$, Sublethal $effects_p$ at low (0.9)-, moderate (0.5)- and high-risk (0.10) scenarios. The resulting passage efficiency metrics (DS $Passage_{eff}$) and downstream recruitment rates (DSrec; Table 3) vary largely across risk levels. This case-study highlights the important implications of post-passage survival on downstream recruitment, highlighting the need for research to better understand the impacts of turbine passage on downstream survival.

7 | CONCLUSIONS AND IMPLICATIONS FOR MITIGATION AND MANAGEMENT

7.1 | Involuntary entrainment vulnerability

We found that quantitative estimates of the numbers of potadromous fish being involuntarily entrained (or seeking passage) through hydropower turbines were scarce. Where entrainment and passage rates have been quantified, the estimates for juvenile fish were often high. Evidence for entrainment/passage of adult potadromous fish was rarer than for juveniles. However, sufficient evidence was found to suggest that adult entrainment/passage probabilities are not zero. Thus, we posit that quantification of standardized potadromous fish entrainment/passage metrics such as Turb $Entry_{count}$, at existing hydropower facilities for all adult and juvenile fishes, will be an important first step in assessing the ecological consequences of hydropower electricity production.

Given that we could find few published examples of entrainment event quantification, it is not surprising that research into the impacts of involuntary turbine entrainment on upstream populations was also lacking. We were able to find an abundance of evidence, demonstrating the negative impacts of connectivity barriers, on upstream populations. However, research that disentangles the impacts on entrainment/passage removals from the general effects of hydropower dam construction on upstream reservoir and river potadromous fish populations was lacking. Accordingly, we argue that estimates of our proposed entrainment/passage vulnerability metrics ($Entrain_v$) present an opportunity to generate an increased understanding of the magnitude of potadromous involuntary entrainment. Moreover, $Entrain_v$ offers an opportunity for integration into upstream population dynamics models and thus provides potential for assessment of population-level impacts. In the meantime we advocate a precautionary approach to involuntary entrainment management that assumes the impacts of entrainment removals on upstream populations are not zero.

Turbine entrainment research has focussed largely on passage mortality and does not adequately characterize the extent of the impacts of involuntary turbine entrainment on potadromous fish. Our framework highlights the need to better understand interactions among fish behaviour, reservoir habitat and operations that lead fish to enter reservoirs, hydropower forebays and turbine FEZs. While we have outlined and discussed factors that may influence vulnerability, estimation of our proposed entrainment vulnerability metric $Entrain_v$ and quantification of the factors that influence these metrics (Res $Entry_p$, Fbay $Entry_p$, FEZ $entry_p$) will be necessary in order to facilitate a traits-based approach to assessing vulnerability. Moreover, estimation of influence of the reservoir conditions and operation strategies on these vulnerability metrics will be essential for the design of effective mitigation.

In case-study 1, we provided a practical example of how entrainment vulnerability metrics can be estimated in a very large hydropower dam with a relatively simple acoustic telemetry array. We recognize that experimental assessment of each metric is likely not always practical, and accordingly, we provided a practical example of how prior ecological knowledge can be used to estimate some of the metrics that constitute $Entrain_v$. While we acknowledge that such

TABLE 3 Summary of kokanee annual downstream turbine passage efficiency and downstream recruitment through Mica Dam, British Columbia, Canada, based on data from Dawson and Parkinson (2013) and Sebastian and Weir (2016). Scenarios represent low, moderate and high, moderate and high post-passage survival estimates

Scenario	$Entrain_v$	Turbine $Passage_s$	Turbine $Exit_s$	Long $term_s$	Sub-lethal effects	DS $Passage_{eff}$	DSrec
Low risk	0.30	0.74	0.90	0.90	0.90	0.16	333,100
Moderate risk	0.30	0.74	0.50	0.50	0.50	0.03	62,456
High risk	0.30	0.74	0.25	0.25	0.25	0.003	7,222

acoustic telemetry arrays and associated tagging programmes carry an economic cost, and require some technical expertise to operate successfully, we argue that these costs are small in comparison with the value of electricity generation at large hydropower dams, and in comparison with the economic and social value of potadromous fishes.

7.2 | Volitional turbine passage

Given that large numbers of juvenile potadromous fish are potentially being entrained/passing through hydropower turbines and a high proportion of these fish potentially survive entrainment (Pracheil, DeRolph, et al., 2016), we argue that turbines likely provide an important downstream passage route for potadromous fish populations. While we were able to find a small number of studies, demonstrating that turbines provided effective passage for potadromous fish, research into this area was generally scarce. Accordingly, estimates of our proposed turbine passage efficiency metric DS Passage$_{efficiency}$ will be essential to test hypotheses concerning the impacts of hydropower on potadromous fish downstream connectivity. Furthermore, calculation of our proposed downstream entrainment recruitment metric (DSrec) has potential to provide a useful metric for incorporation into downstream population models.

In our second case-study, we provided a practical demonstration of how a combination of fixed and roving hydroacoustic surveys can be used to estimate passage efficiency for YOY fish which are too small for telemetry, and thus test hypotheses concerning the contribution of these fish to downstream populations. Again, while we acknowledge that these techniques will require significant economic and technical investment, we argue that these costs are modest in comparison with the value of electrical generation at similarly sized large hydropower facilities. In this case-study, we demonstrated how experimentally derived turbine mortality rates available from the literature can be incorporated, in recognition that site-specific experiments for each metric are likely not practical. Furthermore, our case-study which showed the high variation in DSrec that occurs in response to variation in post-passage efficiency metrics (Turbine Exit$_s$, Longterm$_s$, Sublethal effects$_p$) and highlighted the pressing need for experimental assessment of these metrics.

In North America, policy for potadromous fish has historically assumed that all downstream movement through turbines represents involuntary entrainment and therefore should be avoided or mitigated (Coutant & Whitney, 2000). We posit that in systems where no other downstream passage routes are available (which represent the vast majority of hydropower dams), the impacts of restricted passage also need to be considered in management plans. The importance of fish passage provisions for potadromous fish species is beginning to be recognized in policy in regions of the world where hydropower construction is booming, including Yangtze River (Shi et al., 2015; Wu, Huang, Han, Xie, & Gao, 2003), the Mekong Delta (Baumann & Stevanella, 2012), Congo basins (Winemiller et al., 2016) and the Amazon (Pelicice & Agostinho, 2008; Pompeu, Agostinho, & Pelicice, 2012). Nonetheless, fish passage facilities that are effective for downstream passage remain rare (Agostinho et al., 2011). Accordingly, a quantification of the efficiency of downstream passage through turbines will be essential to protect the important potadromous fish populations that occur in these areas of hydropower construction. Indeed, we argue that the risks to potadromous fish populations posed by hydropower disruptions to downstream connectivity, especially for larval and juvenile fish, have the potential to exceed the risks posed by accidental entrainment removals. Given the conservation concerns for many potadromous fish that live in hydropower impacted systems, further research on this topic is urgent to better inform mitigation and compensation needs.

Significant knowledge gaps concerning the spatial ecology and habitat requirements of river and reservoir potadromous fishes are currently hindering our ability to determine requirements for downstream connectivity through turbines (Cooke, Paukert, & Hogan, 2012; Gutowsky et al., 2016; Silva et al., 2017). Accordingly, a better understanding of the space use, dispersal patterns, habitat requirements and migratory behaviour of reservoir and river potadromous fish represents a priority for the management and mitigation of entrainment and turbine passage connectivity consequences, particularly in areas of the world where native fish populations are poorly understood. In the absence of detailed knowledge of the spatial ecology of potadromous fish, we suggest that a precautionary approach to passage management should assume that downstream connectivity through turbines is likely necessary for potadromous fish populations.

Our conceptual framework for downstream connectivity via turbines demonstrates that turbine passage mortality estimates alone cannot adequately capture the effectiveness of turbine passage as a connectivity route. Our framework shows that successful turbine passage is highly dependent on an ability to navigate through reservoirs and locate turbine entrances. As we currently know very little about the behavioural interactions with reservoir bathymetry and hydrology that facilitate effective navigation through reservoirs, estimation and parameterization of our proposed reservoir behaviour metrics (Res Entry$_p$, Fbay Entry$_p$, Turbine Entry$_p$) may facilitate an improved understanding of the factors that moderate downstream dispersal through turbines. Furthermore, our conceptual framework highlights the importance of tailrace predation and long-term survival and fitness impacts of passage into the novel downstream environment for effective connectivity. We acknowledge that field experiments for every metric described are likely not feasible. Nonetheless, we advocate for a holistic approach to management of turbine passage that acknowledges that each of these passage/entrainment stages can represent a connectivity bottleneck, with potential to reduce or even provide a complete barrier to connectivity.

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