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Updating the consensus on fishway efficiency: A meta-analysis

Henry Hershey [iD]

Auburn University, School of Fisheries, Aquaculture and Aquatic Sciences, Auburn, AL, USA

Correspondence
Henry Hershey, Auburn University School of Fisheries, Aquaculture and Aquatic Sciences, Auburn, AL, USA.
Email: hjh0027@auburn.edu

Abstract

To update the consensus on the effectiveness of fish passage mitigation structures or "fishways," I conducted a meta-analysis on the fish passage literature and synthesized attraction and passage efficiency estimates from 60 peer-reviewed articles. One hundred unique species were studied at 75 unique fishways of various designs and sizes yielding 210 and 252 estimates of attraction and passage efficiency, respectively. Following Bunt et al. (*River Research and Applications*, 28, 2012, 457), the fishways were grouped into five types: nature-like, denil, pool-and-weir, vertical slot or locks and lifts that were operated automatically. Generalized linear mixed effects models showed that fishway type was not a significant predictor of passage efficiency, although nature-like fishways had significantly lower attraction efficiency than other types. Neither fishway slope, nor elevation change was significant predictors of attraction or passage efficiency. Models comparing efficiency between ecological guilds of fishes (pelagic or benthic and rheophilic or limnophilic) showed that attraction and passage efficiency were highest for pelagic rheophiles and lowest for limnophiles. Models comparing migratory guilds of fishes (diadromous, potamodromous, facultative or non-migratory) showed that diadromous species outperformed other guilds, as expected. Fish that were captured inside or above fishways had significantly higher passage performance than fish that were naive to the fishway. Inconsistency in fishway evaluation methods was pervasive in the surveyed literature and made this meta-analysis challenging. When designing studies of fishway evaluations, researchers should conform to best practices so that their results are more generalizable and their conclusions of wider scope.

KEYWORDS

attraction efficiency, fish passage, fishway evaluation, passage efficiency

1 | INTRODUCTION

Dams and other human-constructed barriers disrupt aquatic ecosystems by altering habitat and fragmenting lotic systems. Loss of this connectivity can have negative effects on fish populations, particularly species that migrate (Nilsson et al., 2005). One solution to mitigate the effects of dams on migratory fishes is to retrofit them with fishways, which are structures built to assist fish migrating across barriers by providing alternate hydrologic channels or passive

transport over, around or through the barriers (Larinier, 2002). The rate of fishway construction has grown since its inception in the early 20th century, and now many dams in the Northern Hemisphere have one (if not more) (Castro-Santos et al., 2009). However, fishways have not always been designed to accommodate weak-swimming fish species or species of relatively low commercial value, for example non-salmonids, so there is increasing interest in modifying existing fishways to accommodate more species (Katopodis and Williams, 2012; Sanz-Ronda et al., 2016). Although conventions for fishway

design are not new (Katopodis, 1992; Osborn, 1987), conventions for *evaluation* are relatively novel (Castro-Santos et al., 2009; Cooke & Hinch, 2013).

Evaluating and monitoring the effectiveness of fishways are essential to understanding the ecology of migratory fish in dammed systems. Fishways can select for individuals with higher swimming performance, and filter out species that are incapable of passage (Keefer et al., 2013). Also, the stress of fishway passage can lead to delayed mortality and spawning failure upstream (Pon et al., 2009; Roscoe et al., 2011). Roscoe and Hinch (2010) identified historic biases in fishway evaluation and highlighted a lack of standardized methods for measuring their effectiveness. This flaw was widespread and proved to be a major challenge in synthesizing previous literature on passage efficiency at these structures.

To provide some consensus on the efficacy of fishways, two quantitative reviews of fish passage and attraction efficiency were performed by Noonan et al. (2012) and Bunt et al. (2012), Bunt et al. (2016). These quantitative reviews compared the efficiency of different fishway types, identified data gaps and highlighted similar biases as Roscoe and Hinch (2010). They identified problems with unstandardized evaluation methods, particularly with how efficiency was defined and measured, and how uncertainty in efficiency estimates was reported. They found a lack of data from the Southern Hemisphere, and for non-salmonid taxa. Cooke and Hinch (2013) made similar recommendations to improve the reliability of fishway efficiency estimation, but since these studies were published, there has been no re-evaluation of whether any sort of best practices has been identified and adopted, or if data gaps have been filled (Bunt et al., 2012; Noonan et al., 2012). Therefore, I used the definitions and methods outlined in Bunt et al. (2012) and performed an updated evaluation using meta-analytic techniques.

Meta-analysis is an excellent tool for synthesizing studies with variation in sample sizes and effect sizes (i.e. efficiency estimates), because it is a rigid framework with well-documented methodologies for identifying the sources of the variation (Gurevitch et al., 2018). Kemp (2016) warned that meta-analysis may not be an appropriate tool for synthesizing the fish passage literature because of the challenges associated with aggregating and comparing results from different studies over a range of spatial and temporal scales. While these challenges may be significant sources of variation between studies, meta-analysis includes techniques to quantify and account for that variation, as well as non-independence between effect sizes (Cheung, 2019).

To account for heterogeneity, generalized linear mixed effects models can estimate the relationship between variation in effect size and continuous or categorical predictor variables (Borenstein et al., 2010). A significant advantage of mixed effects models versus fixed-effect models is the ability to partition within-study estimation error from true variation in the effect size (i.e. passage efficiency). Between-study variance (the important source of heterogeneity) is estimated as t^2. Using this technique, more confident conclusions can be drawn about how variation in fishway efficiency is apportioned

to different variables while accounting for the "noise" created by within-study variation (an inherent result of the small sample sizes typical of many fishway evaluations).
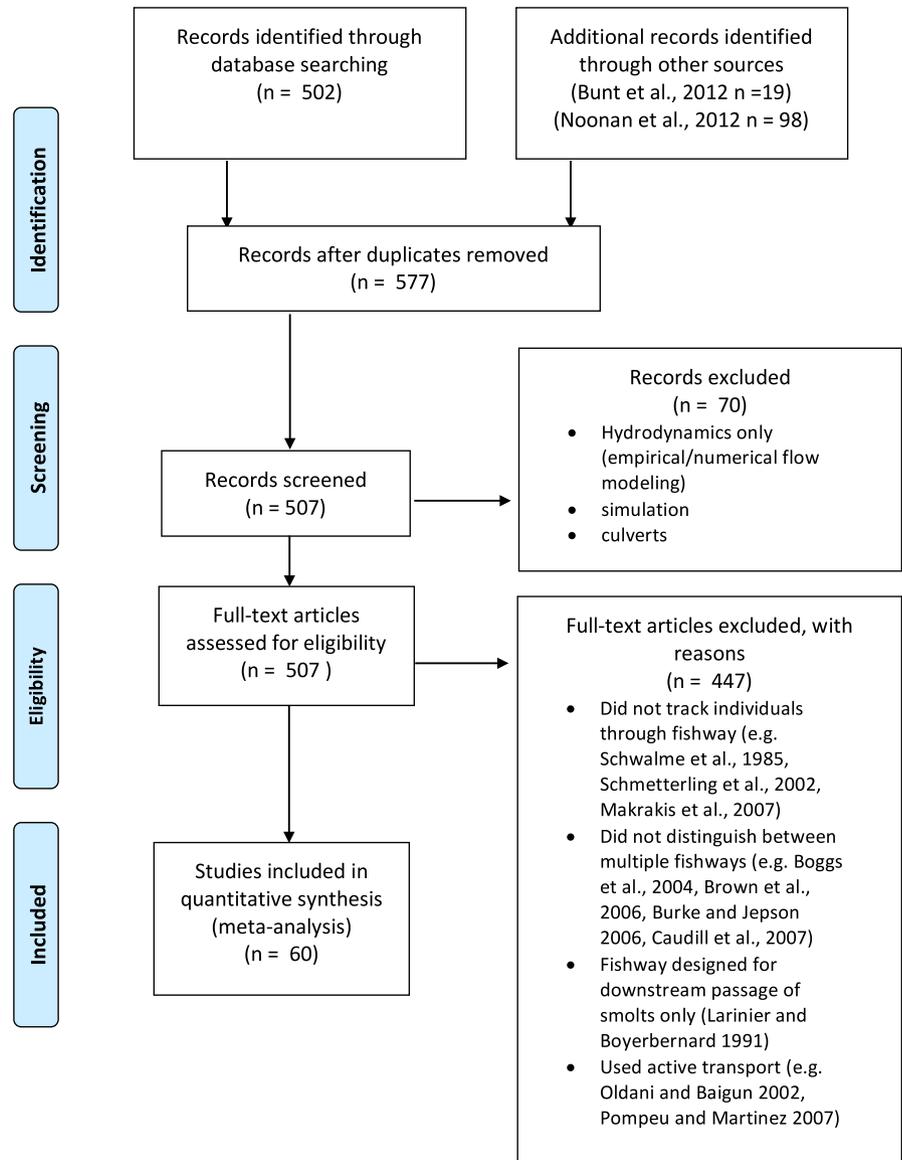
The main conclusion of previous meta-analyses was that too few efficiency evaluation studies have been performed to clearly justify recommendations for any particular type of fishway. They also showed that non-salmonid and non-diadromous taxa are underrepresented in the literature. Given that 8 years have passed since these meta-analyses were published, I set out to determine if their conclusions require updating, and whether recent publications strengthen our knowledge or add more uncertainty. The primary goal of this study is to compare new data to previous findings, as well as perform an updated meta-analysis that answers the following questions: (a) Do fishway evaluations published since 2012 change our understanding of the relative efficiency of fishway types? (b) Using all the available data (pre- and post-2012), can variation in fishway efficiency be explained by fishway type, species biology/ecology (i.e. habitat preference, migration strategy, size) or hydrodynamic characteristics? and (c) Have recent fishway evaluation studies adopted the best practices laid out by previous reviews or does methodological inconsistency persist?

2 | METHODS

2.1 | Literature search

In March 2020, I searched Web of Science for ("fish passage" OR "fish bypass" OR "fishpass" OR "fishway" OR "dam passage") AND ("evaluation" OR "efficiency" OR "success" OR "rate") and collected all the references made available online before 1 January 2020. I then added the references in Bunt et al. (2012) and Noonan et al. (2012) that were not found in my search (The most recent references used in these two meta-analyses were published in 2009 and 2011, respectively). In total, 530 unique studies were then filtered using the following exclusion criteria according to the PRISMA method (Moher et al., 2009) (Figure 1).

FIGURE 1 PRISMA diagram showing how papers were screened to ensure they met the search criteria. Some reasons for exclusion from the meta-analysis are provided [Colour figure can be viewed at wileyonlinelibrary.com]

Identification

Records identified through database searching
(n = 502)

Additional records identified through other sources
(Bunt et al., 2012 n =19)
(Noonan et al., 2012 n = 98)

Records after duplicates removed
(n = 577)

Screening

Records screened
(n = 507)

Records excluded
(n = 70)
- Hydrodynamics only (empirical/numerical flow modeling)
- simulation
- culverts

Eligibility

Full-text articles assessed for eligibility
(n = 507)

Full-text articles excluded, with reasons
(n = 447)
- Did not track individuals through fishway (e.g. Schwalme et al., 1985, Schmetterling et al., 2002, Makrakis et al., 2007)
- Did not distinguish between multiple fishways (e.g. Boggs et al., 2004, Brown et al., 2006, Burke and Jepson 2006, Caudill et al., 2007)
- Fishway designed for downstream passage of smolts only (Larinier and Boyerbernard 1991)
- Used active transport (e.g. Oldani and Baigun 2002, Pompeu and Martinez 2007)

Included

Studies included in quantitative synthesis (meta-analysis)
(n = 60)

While it is recommended that studies of fishway efficiency separate passage into three separate components: approach, entrance and passage (Castro-Santos et al., 2009), not enough studies make these distinctions to synthesize estimates for all three metrics. Attraction and entrance phases had to be combined in this study because of wide variation in the methods used to measure those phases (Bunt et al., 2012). Attraction efficiency was defined as the proportion of tagged fish being detected at or inside the fishway entrance (Bunt et al., 2012). Some studies reported the number of fish that "approached" the fishway, which was counted as attraction (Gowans et al., 1999). If a study reported both attraction and entrance efficiency, then the number of fish attracted to the fishway was used as the total from which the number of successful passages was divided, not the number of fish that entered. Passage efficiency was defined following Bunt et al. (2012) as the number of fish detected at or beyond a fishway exit divided by the number detected at or inside the fishway entrance. For example, say that in a hypothetical

study 100 fish were tagged and released below a fishway, 60 fish were detected at the entrance, 40 fish entered the fishway, and 30 were detected at the fishway exit. The attraction efficiency would be 60% (60/100), and the passage efficiency would be 50% (30/60). Fallback (the tendency of some fish to pass back downstream soon after a successful passage, resulting in ultimate failure) was ignored, although a few studies did report it, and it has been proposed as a best practice to adjust efficiency estimates accordingly (Boggs et al., 2004; Naughton et al., 2006).

Studies that did not track individual fish through the fishway were rejected from the analysis. This included mark-recapture studies (e.g. Schmetterling et al., 2011), studies that only sampled the number of fish present in a fishway or exiting a fishway (e.g. Makrakis et al., 2007; Schwalme et al., 1985), and studies that used paired sampling to infer passage rates from ratios of catch-per-unit-effort (e.g. Bice et al., 2017). Some studies assessed the effectiveness of fishways based on genetics (Lopes et al., 2007) and otolith microchemistry

(Lamson et al., 2006), which could not be used in this meta-analysis. Studies that used experimental fishways were also excluded (e.g. Monk et al. 1989; Santos et al. 2013).

Some studies report an "adjusted" passage efficiency; however, the definition of that metric is inconsistent. Raabe et al. (2019) adjusted their passage efficiency metric to reflect that imperfect detection efficiency probably led to underestimated passage efficiency. Ovidio et al. (2017) reported "overall passage efficiency" as the number of successfully passed fish divided by the total number released, and the "adjusted passage efficiency" as the number of successfully passed fish divided by the number that was attracted, which is actually how passage efficiency is defined for this meta-analysis. Only unadjusted metrics and data were used for this analysis.

2.2 | Data collection

For each study that met the search criteria, I recorded the number of fish tagged and released, the number detected downstream of the fishway, the number attracted to the fishway entrance, the number detected inside the fishway, and the number that were detected at or beyond the fishway exit. The passage efficiency metric was constructed by dividing the total number of successfully passed individuals by the number of fish available to pass. Due to differences in study design, the number of fish available to pass depended on where fish were released, and where fish were detected before completing passage. If the number of fish that entered the fishway was not recorded, then the number of tagged fish that were attracted to the entrance was used (e.g. Benitez et al., 2018). If that number was not available, then the number of tagged fish that were detected at any point downstream of the fishway was used. If tagged fish were never detected in the vicinity of the barrier or fishway, they were not included in the efficiency metric. For example, in Landsman et al. (2017), 276 rainbow smelt (*Osmerus mordax*, Osmeridae) were released below a nature-like fishway, but only 142 were detected, with 127 fish entering the fishway and 53 successfully passing. Therefore, the passage efficiency was 53/127 (41.7%). If fish were released into the fishway, rather than downstream of the entrance, then the number tagged was used as the total by which the number passed was divided (Pon et al., 2009). If fish were tracked at multiple fishways at successive barriers, then the number available to pass was the same as the number of fish that successfully passed the previous fishway (e.g. Franklin et al., 2012; Raabe et al., 2019). Some studies included an average estimate of passage efficiency for multiple cohorts of tagged fish (e.g. Nau et al., 2017; Silva et al., 2017). In these cases, the pooled passage efficiency was calculated from the data when available. If the data were not available, one attempt to contact the corresponding author was made.

To compare the fishway types described by Bunt et al. (2012), I recorded the type of fishway in each study as either pool-and-weir, vertical slot, lock/lift, denil or nature-like. Pool-and-weir

fishways included both bottom orifice (e.g. Sanz-Ronda et al., 2019) and spillover weirs (e.g. Landsman et al., 2018), as well as variants of the Ice-Harbour design (e.g. Ackerman et al., 2019). Vertical-slot fishways included any baffled or Hell's Gate style fishway (e.g. Sullivan, 2004). Lifts and locks included navigational locks, and automated lifts that passively moved fish upstream. Denil fishways are specially baffled chutes that are unique from other fishway types (Katopodis, 1992). Nature-like fishways included those that were deliberately designed to simulate natural substrates and flow. Trap and haul procedures were not included in this study, except for fishways that terminate in a trap or sorting facility such as the Brunswick fishway, Maine, USA (Weaver et al., 2019), and the vertical-slot fishways on Cobourg Brook and the Big Carp River, Ontario, CA (Pratt et al., 2009), which were designed to trap and sort out invasive sea-lamprey (*Petromyzon marinus*, Petromyzontidae) from native fish as they migrate upstream. When fishways of different types were combined in a series, each unique section was considered a separate fishway (e.g. Franklin et al., 2012). In these studies and those in which the same cohort of tagged fish was tracked attempting to pass multiple separate fishways in series (e.g. Columbia River hydropower dams; Naughton et al., 2005), the estimates of passage efficiency were treated as independent because while the *number* of fish successfully passing sequential dams is obviously autocorrelated, the *proportion* of fish successfully passing any fishway does not depend on the proportion of fish that successfully passed any preceding fishways. This may introduce some bias into the samples, since individuals that were unable to pass the first fishway in a sequence may have been able to pass subsequent ones.

To test the hypothesis that passage efficiency is related to biological factors, I recorded the species of fish used in each study and classified each species according to a modified ecological guild scheme based on Aarts and Nienhuis (2003), and Branco et al. (2013). Fish were classified as either benthic, benthopelagic or pelagic, and either rheophilic, limnophilic or eurytopic. If no information on the ecology of the species was given in the study, then I searched the species on FishBase (Froese & Pauly, 2019). I determined the orientation from the "Environment" section where each species is classified as demersal (benthic), benthopelagic or pelagic. I used information from the "Biology" section to determine whether it was found mostly in lotic systems (rheophilic), mostly in lentic systems (limnophilic) or both (eurytopic). Given that diadromous species inhabit the ocean, they were classified according to their habitat preferences during their freshwater phase. Even though this scheme may be simplistic, using a more complicated scheme with more guilds (e.g. Welcomme et al., 2006) would limit statistical power because not all guilds may be represented equally in the literature (Table 1).

To account for differences in migratory characteristics I grouped the species into four migratory classes (diadromous, potamodromous, facultative and non-migratory). Facultative species were ones that may make migrations to feed or spawn, but are not obligate migrants like many semelparous anadromous species. Given that large-bodied fishes have better swimming performance

TABLE 1 Ecological guilds and their members

Ecological guild	N (pooled)	Members
Pelagic rheophiles	16	Salmonids, Clupeids, American paddlefish (*Polyodon spathula*, Polyodontidae), Nase (*Pseudochondrostoma polylepys*, Cyprinidae) (Sanz-Ronda et al. 2019)
Benthopelagic rheophiles	13	Eastern perch (*Coreoperca herzi*, Sinipercidae), Sauger (*Sander canadensis*, Percidae), *Squalius* spp., *Barbus* spp.,
Benthic rheophiles	21	Lampreys (Petromyzontiformes), Suckers (*Moxostoma* spp., Catostomidae), Barbel (*Luciobarbus* spp., Cyprinidae; Sanz-Ronda et al. 2019), *Pseudogobio esocinus* (Nakajima & Onikura, 2016)
Pelagic eurytopic	2	Mooneye (*Hiodon tergisus*, Hiodontidae), Rudd (*Scardinius erythrophthalmus*, Cyprinidae)
Benthopelagic eurytopic	16	Bream (*Vimba vimba*, Cyprinidae), Rudd (*Scardinius erythrophthalmus*, Cyprinidae), *Leuciscus* spp.
Benthic eurytopic	18	Catfish (Siluriformes), Northern Pike (*Esox lucius*, Esocidae), Lake Sturgeon (*Acipenser fulvescens*, Acipenseridae)
Pelagic limnophiles	1	Zander (*Sander lucioperca*, Percidae)
Benthopelagic limnophiles	0	NA
Benthic limnophiles	8	Tench (*Tinca tinca*, Cyprinidae) Carp (*Carassius* spp), *Acheilognathus lanceolatus*, *Squalidus chankaensis*

Note: Limnophiles were grouped together, and pelagic eurytopic species were grouped with benthopelagic eurytopics.

than small ones, I split the diadromous and potamodromous classes by size to account for possible differences in swimming performance. Species were classified as "small" or "large" based on whether the maximum total length of the fish used in each study was smaller or larger than 400 mm. If size was not reported by the authors, I used the maximum total length reported on Fishbase (Froese & Pauly, 2019).

To test the hypothesis that passage efficiency is related to fishway design and abiotic factors, I recorded certain hydrodynamic variables about the fishways such as the mean discharge (m³/s), mean water velocity (m/s), head loss (m), length (m) and slope of the fishway (%) when available. In Keefer et al. (2013), entry and passage were reported in aggregate at McNary Dam, WA-OR, which has three fishway entrances, and two fishways. The five years of data in this study were pooled for the fishway type subgroup analysis given that both fishways were pool-and-weir, but they were excluded from the design analysis because of unknown differences between the fishways.

Finally, I recorded whether the study fish were naive to the fishway or not. Fish were considered naive if they were captured from downstream of the fishway, rather than inside it or upstream. Cooke and Hinch (2013) warned that researchers should consider the role of migratory motivation and experience, which could be large sources of variation in efficiency estimates. By capturing fish from inside or upstream of the fishway, researchers may hedge

against using unmotivated fish in their evaluations. However, they also may bias their results because fish that have already experienced the fishway may perform better than those that have not. Data for this meta-analysis are available in the Supporting Information.

2.3 | Data analysis

There has been some confusion about how variance (σ^2) in fish passage and attraction efficiency is measured and reported in the literature. Noonan et al., (2012) stated that a true meta-analysis of the fish passage literature would probably be impossible because "most studies reported the percentage of fish passing successfully through a facility without an estimate of variance." This is erroneous because the variance of any proportion can be calculated as $p*(1 - p)/n$ where p is the proportion of successes, and n is the sample size or number of fish attempting to pass (Wang, 2018). Meta-analytic techniques can be used for any study that reports fish passage efficiency as a proportion of a total number of fish available to pass, which according to this study can be either the number tagged, detected downstream or attracted, depending on what is reported. Studies need not report the variance to be included.

Fishways are so different in form and size that estimating an overall effect size metric across all studies (the goal of many
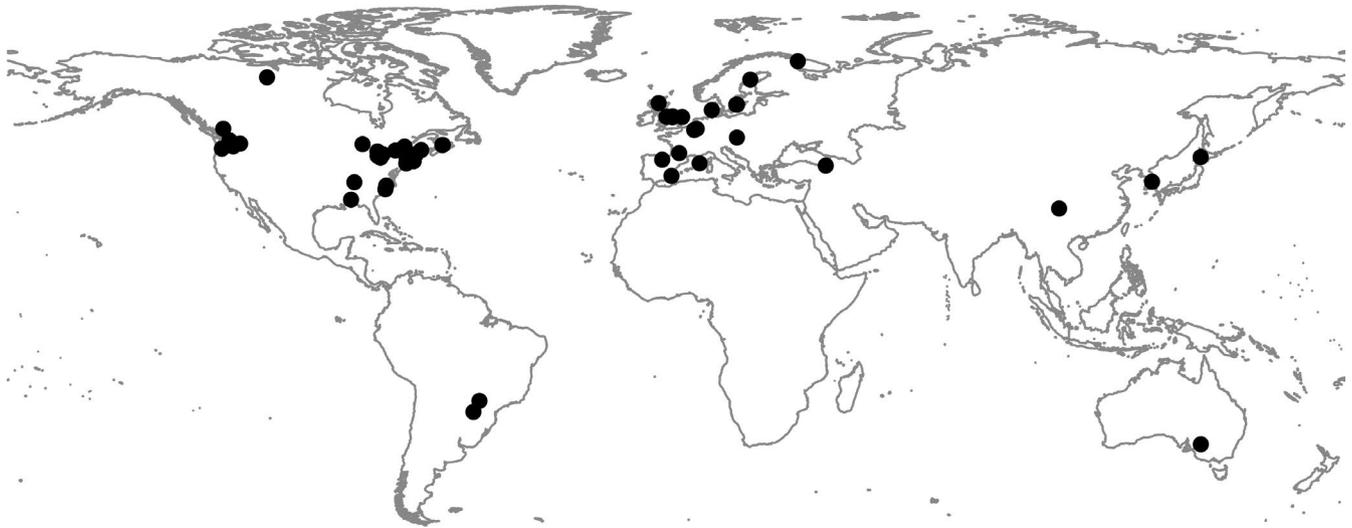
FIGURE 2 Global map showing the locations (black circles) of the fishways included in this study

meta-analyses) would not be informative, which is why I focused on subgroup analysis and meta-regression with generalized linear models. Fixed-effect linear models, such as the logistic regression used by Bunt et al. (2012), can be used to estimate a mean proportion across studies or for subgroups of studies that is weighted according to the within-study variance (Borenstein et al., 2010). However, fixed effects models assume each study is sampled from the same normally distributed population and thus cannot account for between-study variation. Rather, they assume that differences between studies are due to within-study variance alone. Random-effects models differ in that they estimate both the weighted mean and the between-study variance (τ^2). Results from random-effects models are more generalizable because the models assume that each study is a random sample from a *distribution* of true effect sizes, rather than a deviate from one *common effect size* that is only shared by the studies in the sample population. Because fixed-effect models assume that studies are functionally identical, and this is not usually the case, random-effects models are usually recommended for meta-analyses (Borenstein et al., 2010).

I estimated the weighted mean passage efficiency for each fishway type by fitting a generalized linear mixed effects model (a model with both fixed and random effects) to the proportion data with maximum likelihood. The efficiency estimates were transformed using the Tukey–Freeman double arc-sine transformation because it is a more appropriate method than the logit transformation for dealing with extreme proportions and low sample sizes (Lipsey & Wilson, 2001), which is true of many fishway evaluations where complete failure to pass by any species is not uncommon. The model was fit using the function meta-prop () from the package meta in R (Balduzzi et al., 2019; R Core Team, 2013). Confidence intervals for the weighted proportions were calculated using the Clopper–Pearson interval method (Agresti & Coull, 1998), and the between-study variance was calculated using restricted maximum likelihood, because the default estimator (Dersimonian and Laird) has the tendency to overestimate (τ^2) (Borenstein et al., 2010). This

model was first fit to the data from Bunt et al. (2016) to test their claims about the influence of fishway type on attraction and passage efficiency. Then, I refit the model with new data included from my own literature search to see whether the conclusions need to be updated. Because of debate over whether passage trials in different years within the same study can be considered independent sampling units, I present the results of the model fit to both pooled and unpooled data (Williams and Katopodis 2016). Estimates were pooled by fishway type within unique study/species/dam combination, eliminating interannual variation. I tested the sensitivity of the fishway type model results to excluding studies that contributed a disproportionate amount of data (i.e. > 10 independent estimates of efficiency: six studies).

I compared the passage performance of the ecological and migratory guilds using the same generalized linear mixed effects model design, but with a different pooling structure. Given that these models aim to account for between-species variation, each replicate must represent a unique species. So, efficiency estimates were pooled by species to account for sampling bias in overrepresented guilds and to remove within-species variation in efficiency. I also fit a model with slope (%) and elevation change (meters) as predictors. I pooled the efficiency estimates for each fishway so that fishways with multiple studies would not introduce pseudoreplication; each fishway constitutes an independent measure of the slope and elevation change variables. Locks and lifts were excluded from this model.

3 | RESULTS

In total, 60 unique papers met the criteria for use in this meta-analysis. Those studies yielded 252 estimates of passage efficiency and 210 estimates of attraction efficiency for 100 fish species at 75 fishways, in 18 different countries (Figure 2). Studies in the updated database were performed between 1995 and 2018 (Figure 3). Seventeen of the studies were previously analysed by Bunt et al.

(2016). For reference, Bunt et al. (2016) analysed 17 unique papers with 81 estimates of passage efficiency and 78 estimates of attraction efficiency from 24 distinct fishways in six countries. The last publication date reported in Bunt et al. (2016) was 2009. Only, three studies from Noonan et al. 2012 met my inclusion criteria. When I
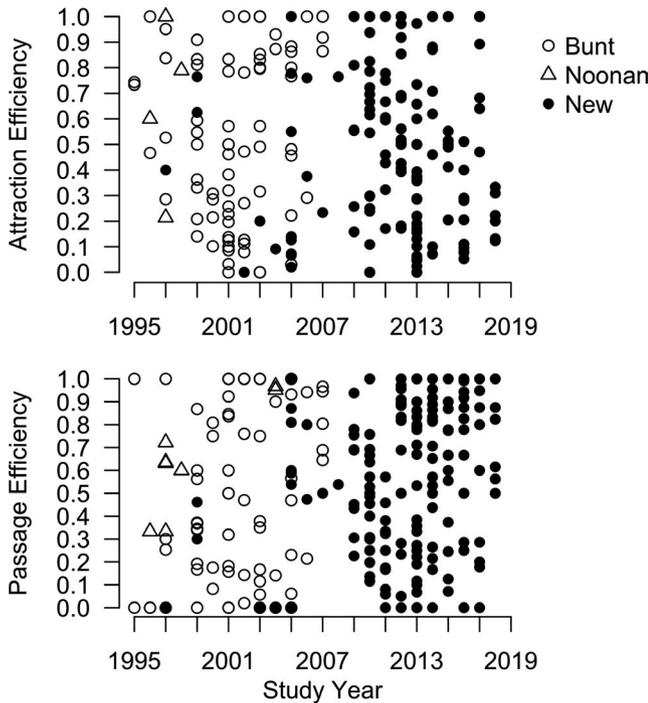

FIGURE 3 Scatterplot showing the variation and temporal spread of attraction (top panel) and passage efficiency (bottom panel) estimates used in this study. The points on the plot mark the year each study was completed, not published. Most of the new studies added by my literature search come from after 2007, when the last previously meta-analysed study was completed

re-analysed the data from Bunt et al. (2016), the model results for both the pooled (eliminating interannual variation within fishways) and unpooled attraction efficiency estimates showed no statistically significant differences between fishway types (Figure 4a) (pooled: number of studies (k) = 50, p = .6068, t^2 = 0.13; unpooled: k = 78, p = .4937, t^2 = 0.14). Between-study variance for each of the fishway types ranged from 0.11 to 0.17, and all four of the 95% confidence intervals overlapped. When I included the data from the updated literature search and refit the model, the results changed. With both pooled and unpooled attraction efficiency estimates, the updated models estimated that Denil fishways and locks and lifts performed significantly better than nature-like fishways. The overall between-study variance was slightly lower than it was when only references from Bunt et al., (2016) were included (pooled: k = 160, p = .0035, t^2 = 0.10; unpooled: k = 210, p = .0018, t^2 = 0.12) (Figure 4b).

Re-analysis of the passage efficiency estimates from Bunt et al. (2016) showed that differences between fishway types were marginally insignificant when pooled (k = 48, p = .0676, t^2 = 0.17). When the model was fit to the unpooled estimates, nature-like fishways significantly outperformed pool-and-weir and vertical slot fishways (k = 77, p = .0002, t^2 = 0.19) (Figure 5a). When I included the new data and refit the model, there were no significant differences between any of the fishway types (pooled: k = 182, p = .8098, t^2 = 0.13; unpooled: k = 252, p = .3622, t^2 = 0.14) (Figure 5b).

The six ecological guilds analysed in this study varied in their estimated attraction efficiency. The mixed effects models estimated that pelagic rheophiles were attracted to fishways more efficiently than limnophiles, while benthic rheophiles were more efficiently attracted than limnophiles and benthopelagic rheophiles (p = .0003, τ^2 = 0.11) (Figure 6a). No statistically significant differences in passage efficiency were found among ecological guilds (p = .30, τ^2 = 0.10), although the same general pattern was evident, with
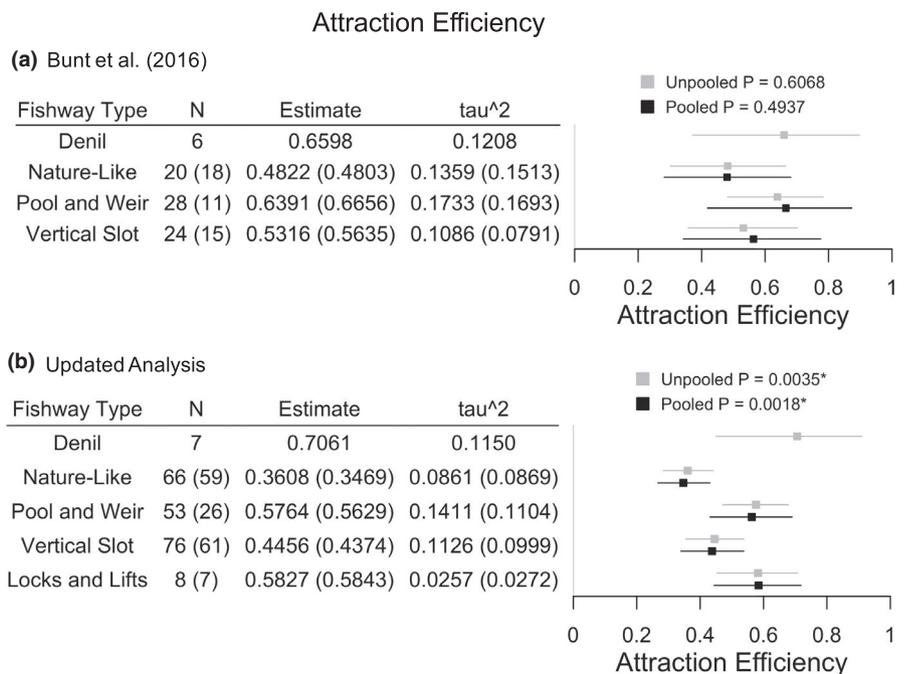
FIGURE 4 Forest plots showing the attraction efficiency of each fishway type as estimated by a mixed effects model fit to the pooled and unpooled data from Bunt et al. (2016) (top panel), and the pooled and unpooled data from this study's updated database (bottom panel). In each column, values in parentheses represent results from the pooled analysis. *N* is either the unpooled number of study estimates contributing to each group, or the number of study estimates when multiple years of data for a species at a fishway were pooled

Attraction Efficiency

(a) Bunt et al. (2016)

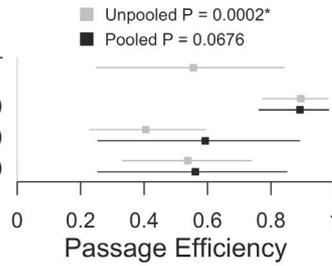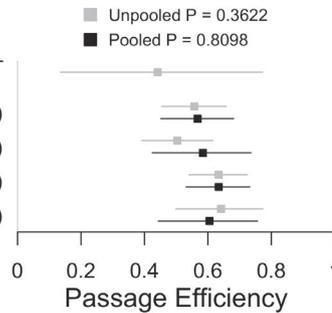| Fishway Type	N	Estimate	tau^2
Denil	6	0.6598	0.1208
Nature-Like	20 (18)	0.4822 (0.4803)	0.1359 (0.1513)
Pool and Weir	28 (11)	0.6391 (0.6656)	0.1733 (0.1693)
Vertical Slot	24 (15)	0.5316 (0.5635)	0.1086 (0.0791)

Unpooled P = 0.6068
Pooled P = 0.4937

(b) Updated Analysis

Fishway Type	N	Estimate	tau^2
Denil	7	0.7061	0.1150
Nature-Like	66 (59)	0.3608 (0.3469)	0.0861 (0.0869)
Pool and Weir	53 (26)	0.5764 (0.5629)	0.1411 (0.1104)
Vertical Slot	76 (61)	0.4456 (0.4374)	0.1126 (0.0999)
Locks and Lifts	8 (7)	0.5827 (0.5843)	0.0257 (0.0272)

Unpooled P = 0.0035*
Pooled P = 0.0018*

Passage Efficiency

(a) Bunt et al. (2016)

Fishway Type	N	Estimate	tau^2
Denil	7	0.5556	0.1512
Nature-Like	20 (18)	0.8940 (0.8913)	0.0488 (0.0516)
Pool and Weir	28 (11)	0.4052 (0.5927)	0.2361 (0.3130)
Vertical Slot	22 (12)	0.5373 (0.5613)	0.1607 (0.1763)

Unpooled P = 0.0002*
Pooled P = 0.0676

(b) Updated Analysis

Fishway Type	N	Estimate	tau^2
Denil	8	0.4417	0.2148
Nature-Like	76 (63)	0.5574 (0.5676)	0.1163 (0.1217)
Pool and Weir	63 (33)	0.5036 (0.5843)	0.1821 (0.1996)
Vertical Slot	78 (62)	0.6339 (0.6341)	0.1131 (0.1076)
Locks and Lifts	27 (16)	0.6413 (0.6050)	0.0955 (0.0866)

Unpooled P = 0.3622
Pooled P = 0.8098

FIGURE 5 Forest plots showing the passage efficiency of each fishway type as estimated by a mixed effects model fit to the pooled and unpooled data from Bunt et al. (2016) (top panel), and the pooled and unpooled data from this study's updated database (bottom panel). In each column, values in parentheses represent results from the pooled analysis. *N* is either the unpooled number of study estimates contributing to each group, or the number of study estimates when multiple years of data for a species at a fishway were pooled

Ecological Guilds

(a) Attraction Efficiency (P = 0.0003*)

Ecological Guild	N	Estimate	tau^2
Pelagic Rheophilic	17	0.5699	0.1687
Benthopelagic Rheophilic	13	0.2613	0.0435
Benthic Rheophilic	21	0.5663	0.0802
Benthopelagic Eurytopic	18	0.3208	0.1170
Benthic Eurytopic	20	0.4606	0.1030
Limnophilic	10	0.1818	0.0266
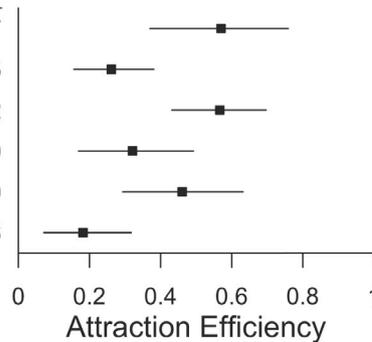
(b) Passage Efficiency (P = 0.1802)

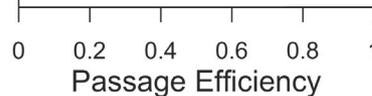| Ecological Guild	N	Estimate	tau^2
Pelagic Rheophilic	18	0.7253	0.1313
Benthopelagic Rheophilic	12	0.5303	0.1115
Benthic Rheophilic	21	0.4144	0.0810
Benthopelagic Eurytopic	18	0.4667	0.0906
Benthic Eurytopic	19	0.4949	0.0415
Limnophilic	8	0.3958	0.2538

FIGURE 6 Forest plot showing the attraction (a) and passage (b) efficiency of six ecological guilds estimated by a mixed effects linear model. *N* represents the number of unique species in each guild

pelagic rheophiles having the highest passage efficiency estimate of all the guilds (Figure 6b).

The six migratory guilds analysed in this study also varied in their estimated attraction and passage efficiency. The mixed effects models estimated that 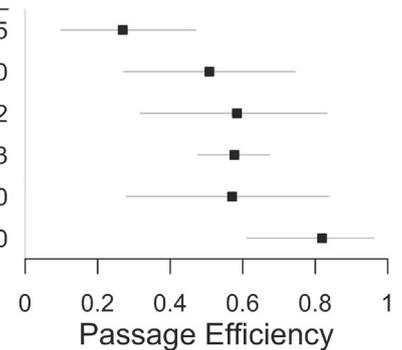large diadromous species were more efficiently attracted to fishways than small diadromous, small potamodromous and non-migratory species, which performed most poorly. Large potamodromous species were also more efficiently attracted to fishways than non-migratory species, but were comparable to other guilds. (k (number of estimates pooled by species) $= 99$, $p = .0006$, $\tau^2 = 0.11$)

Migratory Guilds

(a) Attraction Efficiency (P = 0.0006*)

Migratory Guild	N	Estimate	tau^2
Non-Migratory	23	0.2586	0.0479
Facultative	12	0.3358	0.1003
Potamodromous (small)	8	0.2437	0.0629
Potamodromous (large)	39	0.4871	0.0995
Diadromous (small)	4	0.3145	0.0503
Diadromous (large)	10	0.7682	0.1330
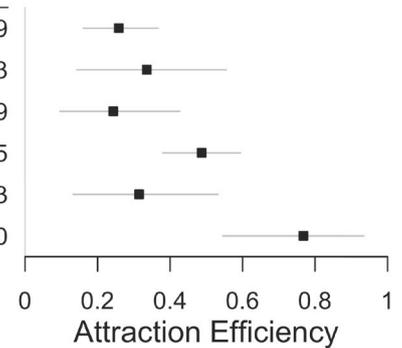
(b) Passage Efficiency (P = 0.0118*)

Migratory Guild	N	Estimate	tau^2
Non-Migratory	21	0.2694	0.1025
Facultative	11	0.5083	0.0550
Potamodromous (small)	8	0.5843	0.0662
Potamodromous (large)	38	0.5774	0.0733
Diadromous (small)	4	0.5709	0.0890
Diadromous (large)	10	0.8190	0.1270

FIGURE 7 Forest plot showing the attraction (a) and passage (b) efficiency of six migratory guilds estimated by a mixed effects linear model. *N* represents the number of unique species in each guild

Naiveté

(a) Attraction Efficiency (P = 0.036*)

Captured	N	Estimate	tau^2
Upstream	63	0.6204	0.1233
Downstream	148	0.4945	0.1311
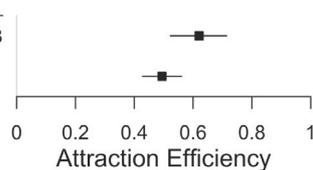
(b) Passage Efficiency (P < 0.0001*)

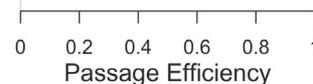| Captured	N	Estimate	tau^2
Upstream	60	0.7404	0.0704
Downstream	170	0.4805	0.1279

FIGURE 8 Forest plot showing the attraction (a) and passage (b) efficiency for fishway evaluations that used fishway naive versus non-naive test-fish. Fish were considered naive if captured downstream

(Figure 7a). Passage efficiency estimates for large diadromous and large potamodromous species were both statistically significantly higher than estimates for non-migratory species, but were similar to those of other guilds. The size groups were not different for either diadromous or potamodromous guilds ($k = 96$, $p = .012$, $\tau^2 = 0.098$) (Figure 7b).

Fishway slopes ranged from less than 1% (nature-like fishway, River Aire, Dodd et al., 2017) to almost 30% (steep pass, East River, Franklin et al., 2012). The change in elevation ranged from less than 1 m to 30 m (vertical slot fishway at ZTB Dam; Bao et al., 2019). Neither factor was a significant predictor of attraction or passage efficiency (attraction: $k = 50$, $p = .23$; passage: $k = 50$, $p = .87$).

In total, 35 unique studies reported 148 and 170 estimates of attraction and passage efficiency for tagged cohorts of "naive" fish that were captured from downstream of the fishway and presumably had not yet attempted to pass. Twenty-three unique studies reported 63 and 60 estimates of attraction and passage efficiency for tagged cohorts of "non-naive" fish that were captured upstream and then translocated back downstream of the fishway. The mixed effects models comparing these treatments showed that fish captured upstream were 13% more efficiently attracted to fishways than naive fish ($p = .036$) (Figure 8a). Fish captured upstream passed fishways 26% more efficiently than those captured downstream ($p < .0001$) (Figure 8b).

The only mixed effects model that accounted for more than 5% of the residual heterogeneity was the model comparing the translocation treatments ($I^2 = 95.7\%$). Such a high I^2 is a good indicator that most of the variation in attraction and passage efficiency is still unaccounted for (Higgins & Thompson, 2002).

Because single studies that contribute a lot of data to the meta-analysis can be a significant source of heterogeneity, I refit the fishway type models excluding the top 6 contributors, one at a time:

Raabe et al. (2019) (evaluation of passage at one nature-like fishway and two navigational locks by three species in the Cape Fear River, USA), Kim et al. (2016) (nature-like fishway evaluation in Korea with 18 species), Calles and Greenberg (2007) (11 species studied at a nature-like fishway in Sweden), Pratt et al. (2009) (eight species at two vertical slot fishways in Canada), Thiem, Binder, et al. (2013) (14 species at a vertical slot fishway in Canada) and Sullivan (2004) (4-year study of four sections of technical and nature-like fishways in Connecticut, USA). Removing Raabe et al. (2019) slightly lowered the passage efficiency estimate for locks and lifts and slightly improved it for nature-like fishways, but I^2 did not change and no new statistically significant differences among types were found. Removing Kim et al. (2016) slightly improved the passage efficiency estimate for nature-like fishways, but it was still not significantly higher than the other fishway types after re-analysis, and I^2 did not change. Removing Calles and Greenberg (2007) slightly lowered the passage efficiency estimate for nature-like fishways, but I^2 remained the same, and the differences remained insignificant. Removing Thiem, Binder, et al. (2013) slightly improved the passage efficiency estimate of vertical slot fishways, but did not improve I^2 or alter the significance. Finally, removing Sullivan (2004) slightly improved the passage efficiency estimate for pool-and-weir fishways, negligibly lowered I^2 and did not alter the significance. Therefore, none of these studies have a disproportionate influence over the conclusions drawn from the mixed effects models, nor do they contribute significantly to the heterogeneity of the metadata.

4 | DISCUSSION

Noonan et al., (2012) and Bunt et al. (2012) both published quantitative reviews of the fish passage literature. The ANOVA and PCA performed by Bunt et al. (2012) showed that although nature-like fishways and fishways with low slope generally had higher passage efficiency than any of the other types, the data available at the time did not justify recommendations for any particular fishway type. My analysis of the data available prior to 2012 align with the findings of Bunt et al. (2012); efficiency of nature-like fishways was statistically significantly higher than other types at the time. However, where the authors found that Denil fishways were the next most efficient, and my analysis found that pool-and-weir fishways were more efficient, and denil fishways performed most poorly, which was also the conclusion of Noonan (2012).

When I updated the data with more recent fishway evaluation studies, evidence that nature-like fishways outperformed any of the other fishway types went away. With 265 estimates of passage efficiency from 85 different fishways, there is no evidence that any particular design is favourable. Given that only one additional evaluation of a Denil fishway was added to the previously meta-analysed data, previous conclusions about their relatively poor performance remain unchanged. These results emphasize the point that there is no "one size fits all" solution to fish passage. Unfortunately, I was not able to account for design variation within fishway types. For

example, there is significant variation in how baffles in vertical-slot fishways are configured, and the weirs in pool-and-weir types can have submerged notches or bottom orifices that allow fish to pass without surfacing. Furthermore, fishways can have multiple entrances, resting pools and other modifications that are impossible to quantify for comparison among studies (Bravo-Córdoba et al., 2014; Bravo-Cordoba et al., 2018a, 2018b). Very few studies presented results from experimental modifications to fishways. Perhaps modular designs may be advantageous for optimizing fishway efficiency, especially in systems with diverse migratory fish communities.

The previous reviews found that salmonids and alosines outnumbered all other taxa in the fish passage literature. Out of the 210 estimates of passage efficiency compiled in this meta-analysis, 62 of them were for salmonid species. However, very few of the species that have been studied have more than one or two independent replicate trials. Of the 100 unique species represented in the literature, 91 have been studied only five times or fewer. The top nine most studied species were *Alosa sapidissima*, *Catostomus commersonii*, *Entosphenus tridentatus*, *Luciobarbus bocagei*, *Morone saxatilis*, *Oncorhynchus nerka*, *Pylodictis olivaris*, *Salmo salar* and *Salmo trutta*. Perhaps the increase in non-salmonid species represented in the literature reflects a shift in the values of fishway designers and operators towards biodiversity, or perhaps it reflects a trend towards globalization, where researchers from more continents (e.g. East Asia and South America) are evaluating fishways for endemic species.

As expected, attraction efficiency was highest for pelagic rheophilic species which probably respond better to flow cues at fishway entrances than limnophiles. Similarly, passage efficiency was highest for pelagic rheophiles and lowest for limnophiles, although there was too much variability to detect a true difference. Attraction efficiency was lower than expected for all of the migratory guilds, especially for small potamodromous and small diadromous species. Size could be a more limiting factor than their motivation to migrate if entering the fishway is a bigger challenge than finding the entrance. Passage efficiency was highest for large diadromous species, as expected. This is probably because of high migratory motivation (especially for semelparous species) or because of their relative size and increased swimming performance. Interestingly, passage efficiency tended to be higher than attraction efficiency across almost all of the ecological and migratory guilds, indicating that for most species, finding and entering fishways may be more challenging than actually passing them. More studies must distinguish between the attraction and entrance phases to determine which phase of fish passage is the biggest limiting factor.

Migratory motivation and experience were probably key factors in the analysis of naiveté. Given that non-naive test fish already experienced the fishway once before capture, a learning effect could positively bias efficiency estimates (Cooke & Hinch, 2013). Using naive test fish could negatively bias efficiency estimates when the proportion of tagged fish that are unmotivated is high, especially for facultative or potamodromous migratory species. If possible, researchers should determine what proportion of

their tagged fish are motivated with endocrine sampling to avoid biasing their fishway evaluation (Thiem et al., 2013b), especially whether it is known that the study species undergoes partial migration (Kaitala et al., 1993).

A potential source of heterogeneity in fishway efficiency that I was not able to account for is detection efficiency. Too few studies reported estimates of detection efficiency, and those that did used different methods to calculate it. Given that the configuration of telemetry arrays for detecting passing fish depends on the structure and design of the fishway, detection efficiency could be a major contributing factor to differences in observed passage and attraction efficiency at different fishway types. Until standardized methods for measuring and incorporating detection efficiency into fishway evaluations are adopted, this may remain a cryptic and insidious variable.

Perhaps the most important finding of the 2012 reviews was the lack of standardized methodologies for fishway evaluation (Kemp, 2016). The authors warned that if fishway evaluations are not standardized, then understanding the underlying causes of poor fishway performance may never be fully understood. Unfortunately, that seems to still be the case eight years later. I rejected dozens of recent peer-reviewed fishway evaluations that did not include standardized estimates of passage efficiency. In some cases, authors presented data that could be coerced into the standardized framework set forth by Bunt et al. (2012) but in other cases, authors totally redefined "passage efficiency."

The definition of passage efficiency used by Bice et al. (2017) was "Passage efficiency at each fishway was assessed by comparing the relative abundance (fish h^{-1} * trap event^{-1}) of the most abundant species (i.e. >200 individuals sampled over the study period) sampled at each fishway between entrance and exit samples." Kerr et al. (2015) and Sanz-Ronda et al. (2016) defined it as the total number of successful attempts divided by the total number of attempts made by fish in each trial. Differences in passage efficiency definitions are probably due to methodological limitations. Telemetry (acoustic and radio transmitters) can be prohibitively expensive, so that researchers who wish to measure passage efficiency may be constrained to other methods like mark recapture or stratified sampling. While these methods are not inherently flawed, and indeed they work well for single studies, they limit our ability to synthesize their findings because they do not conform to the existing definitions of useful passage metrics in the literature (Castro-Santos et al., 2009). If funds prohibit the use of telemetry, then PIT arrays should be used so that individuals can be marked and tracked through the fishway, and passage efficiency can be measured according to its accepted definition. Tracking individuals is also necessary to quantify other important and pervasively overlooked passage metrics such as time to passage (delay) and passage success *per-attempt*, rather than *per-individual*. Until more studies report these metrics, testing the effects of attempt rate or passage delay on passage performance with meta-analysis will be impossible.

In addition to reporting these overlooked passage metrics, more studies need to examine the endogenous mechanisms of passage failure. Studies such as Thiem et al. (2016) where lake sturgeon energy expenditure was measured during fishway passage with tri-axial accelerometers and Pon et al. (2009), where sockeye salmon passage efficiency was related to physiological, behavioral and energetic correlates, should serve as models for future studies in this field. Also, researchers should account for imperfect detection efficiency at fishways, but there should be conventions for how that is done to avoid further complicating the synthesis of the literature (Castro-Santos et al., 1996).

Future studies should be designed within the context of synthesis and meta-analysis. It is no longer enough to simply think about the generalizability of the results of a study. In an increasingly quantitative world, researchers should aim to provide sufficiently complete information that can be synthesized with robust statistical methods, and follow the conventions that previous researchers in their field have put forth. Hopefully, this large database of fishway evaluations will continue to grow in size and utility so that fish passage can be optimized around the world.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

ORCID

Henry Hershey https://orcid.org/0000-0002-9416-8589

REFERENCES

Aarts, B. G. W., & Nienhuis, P. H. (2003). Fish zonations and guilds as the basis for assessment of ecological integrity of large rivers. In K. Martens (Ed.), *Aquatic biodiversity* (pp. 157–178). Springer.

Ackerman, N. K., Pyper, B. J., David, M. M., Wyatt, G. J., Cramer, D. P., & Shibahara, T. M. (2019). Passage effectiveness at a pool-and-weir fishway designed to accommodate pacific lampreys. *North American Journal of Fisheries Management*, *39*(3), 426–440. https://doi.org/10.1002/nafm.10281

Agresti, A., & Coull, B. A. (1998). Approximate is better than "exact" for interval estimation of binomial proportions. *The American Statistician*, *52*(2), 119–126. https://doi.org/10.1080/00031305.1998.10480550

Balduzzi, S., Rücker, G., & Schwarzer, G. (2019). How to perform a meta-analysis with R: A practical tutorial. *Evidence-Based Mental Health*, *22*(4), 153–160. https://doi.org/10.1136/ebmental-2019-300117

Bao, J., Li, W., Zhang, C., Mi, X., Li, H., Zhao, X., Cao, N., Twardek, W. M., Cooke, S. J., & Duan, M. (2019). Quantitative assessment of fish passage efficiency at a vertical-slot fishway on the Daduhe River in Southwest China. *Ecological Engineering*, *141*, UNSP105597. https://doi.org/10.1016/j.ecoleng.2019.105597

Benitez, J.-P., Dierckx, A., Matondo, B. N., Rollin, X., & Ovidio, M. (2018). Movement behaviours of potamodromous fish within a large anthropised river after the reestablishment of the

longitudinal connectivity. *Fisheries Research*, *207*, 140–149. https://doi.org/10.1016/j.fishres.2018.06.008

Bice, C. M., Zampatti, B. P., & Mallen-Cooper, M. (2017). Paired hydraulically distinct vertical-slot fishways provide complementary fish passage at an estuarine barrier. *Ecological Engineering*, *98*, 246–256. https://doi.org/10.1016/j.ecoleng.2016.11.001

Boggs, C. T., Keefer, M. L., Peery, C. A., Bjornn, T. C., & Stuehrenberg, L. C. (2004). Fallback, reascension, and adjusted fishway escapement estimates for adult Chinook salmon and steelhead at Columbia and Snake River dams. *Transactions of the American Fisheries Society*, *133*(4), 932–949. https://doi.org/10.1577/T03-133.1

Borenstein, M., Hedges, L. V., Higgins, J. P. T., & Rothstein, H. R. (2010). A basic introduction to fixed-effect and random-effects models for meta-analysis. *Research Synthesis Methods*, *1*(2), 97–111. https://doi.org/10.1002/jrsm.12

Branco, P., Santos, J. M., Katopodis, C., Pinheiro, A., & Ferreira, M. T. (2013). Pool-type fishways: Two different morpho-ecological cyprinid species facing plunging and streaming flows. *PLoS One*, *8*(5), e65089. https://doi.org/10.1371/journal.pone.0065089

Bravo-Cordoba, F., Javier Sanz-Ronda, F., Ruiz-Legazpi, J., Valbuena-Castro, J., & Makrakis, S. (2018). Vertical slot versus submerged notch with bottom orifice: Looking for the best technical fishway type for Mediterranean barbels. *Ecological Engineering*, *122*, 120–125. https://doi.org/10.1016/j.ecoleng.2018.07.019

Bravo-Cordoba, F. J., Sanz-Ronda, F. J., Ruiz-Legazpi, J., Fernandes Celestino, L., & Makrakis, S. (2018). Fishway with two entrance branches: Understanding its performance for potamodromous Mediterranean barbels. *Fisheries Management and Ecology*, *25*(1), 12–21. https://doi.org/10.1111/fme.12260

Bravo-Córdoba, F. J., Sanz-Ronda, F. J., Ruiz-Legazpi, J., Fuentes-Pérez, J. F., & Salgado, V. (2014). Ecohydraulics monitoring and improvement of fish passes in the Duero Basin: The case of river Tormes in Santibáñez de Béjar (Salamanca). In *Proceedings of V Jornadas Ibéricas de Ictiología*, 24-27 June 2014, Lisboa, Portugal.

Brown, R. S., Geist, D. R., & Mesa, M. G. (2006). Use of electromyogram telemetry to assess swimming activity of adult Spring Chinook Salmon Migrating Past a Columbia River Dam. *Transactions of the American Fisheries Society*, *135*(2), 281–287. https://doi.org/10.1577/t05-223.1

Bunt, C. M., Castro-Santos, T., & Haro, A. (2012). Performance of fish passage structures at upstream barriers to migration. *River Research and Applications*, *28*(4, SI), 457–478. https://doi.org/10.1002/rra.1565

Bunt, C. M., Castro-Santos, T., & Haro, A. (2016). Reinforcement and validation of the analyses and conclusions related to fishway evaluation data from Bunt et al: 'Performance of fish passage structures at upstream barriers to migration'. *River Research and Applications*, *32*(10), 2125–2137. https://doi.org/10.1002/rra.3095

Burke, B. J., & Jepson, M. A. (2006). Performance of passive integrated transponder tags and radio tags in determining dam passage behavior of adult chinook salmon and steelhead. *North American Journal of Fisheries Management*, *26*(3), 742–752. http://dx.doi.org/10.1577/m05-138.1

Calles, E. O., & Greenberg, L. A. (2007). The use of two nature-like fishways by some fish species in the Swedish River Emån. *Ecology of Freshwater Fish*, *16*, 183–190. https://doi.org/10.1111/j.1600-0633.2006.00210.x

Castro-Santos, T., Cotel, A., & Webb, P. W. (2009). Fishway evaluations for better bioengineering: An integrative approach. *Challenges for Diadromous Fishes in a Dynamic Global Environment. American Fisheries Society, Symposium*, *69*, 557–575. https://www.researchgate.net/profile/Theodore_Castro-Santos2/publication/265050016_Fishway_evaluations_for_better_bioengineering_--_an_integrative_approach/links/55e5a3e808aede0b5736605a.pdf

Castro-Santos, T., Haro, A., & Walk, S. (1996). A passive integrated transponder (PIT) tag system for monitoring fishways. *Fisheries Research*, *28*(3), 253–261. https://doi.org/10.1016/0165-7836(96)00514-0

Caudill, C. C., Daigle, W. R., Keefer, M. L., Boggs, C. T., Jepson, M. A., Burke, B. J., Zabel, R. W., Bjornn, T. C., & Peery, C. A. (2011). Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: Delayed negative effects of passage obstacles or condition-dependent mortality? *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(7), 979–995. https://doi.org/10.1139/f07-065

Cheung, M.-W.-L. (2019). A guide to conducting a meta-analysis with non-independent effect sizes. *Neuropsychology Review*, *29*(4), 387–396. https://doi.org/10.1007/s11065-019-09415-6

Cooke, S. J., & Hinch, S. G. (2013). Improving the reliability of fishway attraction and passage efficiency estimates to inform fishway engineering, science, and practice. *Ecological Engineering*, *58*, 123–132. https://doi.org/10.1016/j.ecoleng.2013.06.005

Dodd, J. R., Cowx, I. G., & Bolland, J. D. (2017). Efficiency of a nature-like bypass channel for restoring longitudinal connectivity for a river-resident population of brown trout. *Journal of Environmental Management*, *204*, 318–326. https://doi.org/10.1016/j.jenvman.2017.09.004

Franklin, A. E., Haro, A., Castro-Santos, T., & Noreika, J. (2012). Evaluation of nature-like and technical fishways for the passage of alewives at two coastal streams in New England. *Transactions of the American Fisheries Society*, *141*(3), 624–637. https://doi.org/10.1080/00028487.2012.683469

Froese, R., Pauly, D. (2019). FishBase. World Wide Web electronic publication. www.fishbase.org (12/2019)

Gowans, A. R. D., Armstrong, J. D., & Priede, I. G. (1999). Movements of adult Atlantic salmon in relation to a hydroelectric dam and fish ladder. *Journal of Fish Biology*, *54*(4), 713–726. https://doi.org/10.1006/jfbi.1998.0910

Gurevitch, J., Koricheva, J., Nakagawa, S., & Stewart, G. (2018). Meta-analysis and the science of research synthesis. *Nature*, *555*(7695), 175–182. https://doi.org/10.1038/nature25753

Higgins, J. P. T., & Thompson, S. G. (2002). Quantifying heterogeneity in a meta-analysis. *Statistics in Medicine*, *21*(11), 1539–1558. https://doi.org/10.1002/sim.1186

Kaitala, A., Kaitala, V., & Lundberg, P. (1993). A theory of partial migration. *The American Naturalist*, *142*(1), 59–81. https://doi.org/10.1086/285529

Katopodis, C. (1992). *Introduction to fishway design* (p. 70). Freshwater Institute, Central and Arctic Region, Department of Fisheries and Oceans Canada.

Katopodis, C., & Williams, J. G. (2012). The development of fish passage research in a historical context. *Ecological Engineering*, *48*(SI), 8–18. https://doi.org/10.1016/j.ecoleng.2011.07.004

Keefer, M. L., Caudill, C. C., Clabough, T. S., Jepson, M. A., Johnson, E. L., Peery, C. A., Higgs, M. D., & Moser, M. L. (2013). Fishway passage bottleneck identification and prioritization: A case study of Pacific lamprey at Bonneville Dam. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(10), 1551–1565. https://doi.org/10.1139/cjfas-2013-0164

Kemp, P. S. (2016). Meta-analyses, metrics and motivation: Mixed messages in the fish passage debate. *River Research and Applications*, *32*(10), 2116–2124. https://doi.org/10.1002/rra.3082

Kerr, J. R., Karageorgopoulos, P., & Kemp, P. S. (2015). Efficacy of a side-mounted vertically oriented bristle pass for improving upstream passage of European eel (*Anguilla etaphor*) and river lamprey (*Lampetra fluviatilis*) at an experimental Crump weir. *Ecological Engineering*, *85*, 121–131. https://doi.org/10.1016/j.ecoleng.2015.09.013

Kim, J.-H., Yoon, J.-D., Baek, S.-H., Park, S.-H., Lee, J.-W., Lee, J.-A., & Jang, M.-H. (2016). An efficiency analysis of a nature-like fishway for freshwater fish ascending a large Korean river. *Water*, *8*(1), 3. https://doi.org/10.3390/w8010003

Lamson, H. M., Shiao, J.-C., Iizuka, Y., Tzeng, W.-N., & Cairns, D. K. (2006). Movement patterns of American eels (*Anguilla etaphor*) between salt- and freshwater in a coastal watershed, based on

otolith microchemistry. *Marine Biology*, *149*(6), 1567–1576. https://doi.org/10.1007/s00227-006-0308-2

Landsman, S. J., McLellan, N., Platts, J., & van den Heuvel, M. R. (2018). Nonsalmonid versus salmonid passage at nature-like and pool-and-weir fishways in Atlantic Canada, with special attention to rainbow smelt. *Transactions of the American Fisheries Society*, *147*(1), 94–110. https://doi.org/10.1002/tafs.10019

Landsman, S. J., Wilson, A. D. M., Cooke, S. J., & van den Heuvel, M. R. (2017). Fishway passage success for migratory rainbow smelt *Osmerus mordax* is not dictated by behavioural type. *River Research and Applications*, *33*(8), 1257–1267. https://doi.org/10.1002/rra.3176

Larinier, M. (2002). Pool fishways, pre-barrages and natural bypass channels. *Bulletin Francais De La Peche Et De La Pisciculture*, *364*, 54–82. https://doi.org/10.1051/kmae/2002108

Larinier, M., & Boyer-Bernard, S. (1991). Dévalaison des smolts et efficacité d'un exutoire de dévalaison à l'usine hydroélectrique d'Halsou sur la Nive. *Bulletin Français De La Pêche Et De La Pisciculture*, *321*, 72–92. https://doi.org/10.1051/kmae:1991009

Lipsey, M. W., & Wilson, D. B. (2001). *Practical meta-analysis* (pp. ix, 247). Sage Publications, Inc.

Lopes, C. M., de Almeida, F. S., Orsi, M. L., de Castro Britto, S. G., Sirol, R. N., & Koeblinger Sodre, L. M. (2007). Fish passage ladders from Canoas Complex—Paranapanema River: Evaluation of genetic structure maintenance of *Salminus brasiliensis* (Teleostei: Characiformes). *Neotropical Ichthyology*, *5*(2), 131–138. https://doi.org/10.1590/S1679-62252007000200006

Makrakis, S., Gomes, L. C., Makrakis, M. C., Fernandez, D. R., & Pavanelli, C. S. (2007). The canal da piracema at Itaipu Dam as a fish pass system. *Neotropical Ichthyology*, *5*(2), 185–195. https://doi.org/10.1590/S1679-62252007000200013

Moher, D., Liberati, A., Tetzlaff, J., & Altman, D. G. (2009). Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. *PLoS Med*, *6*(7), 1–6. https://doi.org/10.1371/journal.pmed.1000097

Monk, B., Weaver, D., Thompson, C., & Ossiander, F. (1989). Effects of flow and weir design on the passage behavior of American shad and salmonids in an experimental fish ladder. *North American Journal of Fisheries Management*, *9*(1), 60–67. https://doi.org/10.1577/1548-8675(1989)009<0060:EOFAWD>2.3.CO;2

Nakajima, J., & Onikura, N. (2016). Life history of pike gudgeon, *Pseudogobio esocinus* (Cypriniformes, Cyprinidae): Differences between the upper and lower reaches in a single river. *Ichthyological Research*, *63*(1), 46–52. https://doi.org/10.1007/s10228-015-0472-9

Nau, G. S., Spares, A. D., Andrews, S. N., Mallory, M. L., McLellan, N. R., & Stokesbury, M. J. W. (2017). Body size, experience, and sex do matter: Multiyear study shows improved passage rates for alewife (*Alosa pseudoharengus*) through small-scale Denil and pool-and-weir fishways. *River Research and Applications*, *33*(9), 1472–1483. https://doi.org/10.1002/rra.3215

Naughton, G. P., Caudill, C. C., Keefer, M. L., Bjornn, T. C., Peery, C. A., & Stuehrenberg, L. C. (2006). Fallback by adult sockeye salmon at Columbia River dams. *North American Journal of Fisheries Management*, *26*(2), 380–390. https://doi.org/10.1577/M05-015.1

Naughton, G., Caudill, C., Keefer, M., Bjornn, T., Stuehrenberg, L., & Peery, C. (2005). Late-season mortality during migration of radio-tagged adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(1), 30–47. https://doi.org/10.1139/F04-147

Nilsson, C., Reidy, C. A., Dynesius, M., & Revenga, C. (2005). Fragmentation and flow regulation of the world's large river systems. *Science*, *308*(5720), 405–408. https://doi.org/10.1126/science.1107887

Noonan, M. J., Grant, J. W. A., & Jackson, C. D. (2012). A quantitative assessment of fish passage efficiency. *Fish and Fisheries*, *13*(4), 450–464. https://doi.org/10.1111/j.1467-2979.2011.00445.x

Oldani, N. O., & Baigun, C. R. M. (2002). Performance of a fishway system in a major South American dam on the Parana River (Argentina-Paraguay). *River Research and Applications*, *18*(2), 171–183. https://doi.org/10.1002/rra.640

Osborn, J. F. (1987). Fishways – Historical assessment of design practices, p. 122–130. In M. J. Dadswell et al (ed.) *Proc. International Symposium, Common strategies of anadromous and catadromous fishes*. American Fisheries Society.

Ovidio, M., Sonny, D., Dierckx, A., Watthez, Q., Bourguignon, S., de le Court, B., Detrait, O., & Benitez, J. P. (2017). The use of behavioural metrics to evaluate fishway efficiency. *River Research and Applications*, *33*(9), 1484–1493. https://doi.org/10.1002/rra.3217

Pompeu, P. D. S. (2007). Efficiency and selectivity of a trap and truck fish passage system in Brazil. *Neotropical Ichthyology*, *5*(2), 169–176. https://doi.org/10.1590/S1679-62252007000200011

Pon, L. B., Hinch, S. G., Cooke, S. J., Patterson, D. A., & Farrell, A. P. (2009). Physiological, energetic and behavioural correlates of successful fishway passage of adult sockeye salmon *Oncorhynchus nerka* in the Seton River, British Columbia. *Journal of Fish Biology*, *74*(6), 1323–1336. https://doi.org/10.1111/j.1095-8649.2009.02213.x

Pratt, T. C., O'Connor, L. M., Hallett, A. G., McLaughlin, R. L., Katopodis, C., Hayes, D. B., & Bergstedt, R. A. (2009). Balancing aquatic habitat fragmentation and control of invasive species: Enhancing selective fish passage at sea lamprey control barriers. *Transactions of the American Fisheries Society*, *138*(3), 652–665. https://doi.org/10.1577/T08-118.1

R Core Team (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Raabe, J. K., Hightower, J. E., Ellis, T. A., & Facendola, J. J. (2019). Evaluation of fish passage at a nature-like rock ramp fishway on a large coastal river. *Transactions of the American Fisheries Society*, *148*(4), 798–816. https://doi.org/10.1002/tafs.10173

Roscoe, D. W., & Hinch, S. G. (2010). Effectiveness monitoring of fish passage facilities: Historical trends, geographic patterns and future directions. *Fish and Fisheries*, *11*(1), 12–33. https://doi.org/10.1111/j.1467-2979.2009.00333.x

Roscoe, D. W., Hinch, S. G., Cooke, S. J., & Patterson, D. A. (2011). Fishway passage and post-passage mortality of up-river migrating sockeye salmon in the Seton River. *British Columbia. River Research and Applications*, *27*(6), 693–705. https://doi.org/10.1002/rra.1384

Santos, J. M., Branco, P. J., Silva, A. T., Katopodis, C., Pinheiro, A. N., Viseu, T., & Ferreira, M. T. (2013). Effect of two flow regimes on the upstream movements of the Iberian barbel (*Luciobarbus bocagei*) in an experimental pool-type fishway. *Journal of Applied Ichthyology*, *29*(2), 425–430. https://doi.org/10.1111/jai.12043

Sanz-Ronda, F. J., Bravo-Cordoba, F. J., Fuentes-Perez, J. F., & Castro-Santos, T. (2016). Ascent ability of brown trout, *Salmo trutta*, and two Iberian cyprinids—Iberian barbel, *Luciobarbus bocagei*, and northern straight-mouth nase, *Pseudochondrostoma duriense*—In a vertical slot fishway. *Knowledge and Management of Aquatic Ecosystems*, *417*, 10. https://doi.org/10.1051/kmae/2015043

Sanz-Ronda, F. J., Bravo-Cordoba, F. J., Sanchez-Perez, A., Garcia-Vega, A., Valbuena-Castro, J., Fernandes-Celestino, L., Torralva, M., & Jose Oliva-Paterna, F. (2019). Passage performance of technical pool-type fishways for potamodromous cyprinids: Novel experiences in semi-arid environments. *Water*, *11*(11), 2362. https://doi.org/10.3390/w11112362

Schmetterling, D. A., Pierce, R. W., & Liermann, B. W. (2011). Efficacy of three Denil fish ladders for low-flow fish passage in two tributaries to the Blackfoot River, Montana. *North American Journal of Fisheries Management*, *22*(3), 929–933. https://doi.org/10.1577/1548-8675(2002)022<0929:EOTDFL>2.0.CO;2

Schwalme, K., Mackay, W., & Lindner, D. (1985). Suitability of vertical slot and Denil fishways for passing north-temperate, nonsalmonid fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*(11), 1815–1822. https://doi.org/10.1139/f85-227

Silva, S., Lowry, M., Macaya-Solis, C., Byatt, B., & Lucas, M. C. (2017). Can navigation locks be used to help migratory fishes with poor swimming performance pass tidal barrages? A test with lampreys. *Ecological Engineering*, *102*, 291–302. https://doi.org/10.1016/j.ecoleng.2017.02.027

Sullivan, T. J. (2004). *Evaluation of the turners falls fishway complex and potential improvements for passing adult American shad*. Master's thesis, University of Massachusetts Amherst, US.

Thiem, J. D., Binder, T. R., Dumont, P., Hatin, D., Hatry, C., Katopodis, C., Stamplecoskie, K. M., & Cooke, S. J. (2013). Multispecies fish passage in a vertical slot fishway on the Richelieu River, Quebec, Canada. *River Research and Applications*, *29*(5), 582–592. https://doi.org/10.1002/rra.2553

Thiem, J. D., Dawson, J. W., Hatin, D., Danylchuk, A. J., Dumont, P., Gleiss, A. C., Wilson, R. P., & Cooke, S. J. (2016). Swimming activity and energetic costs of adult lake sturgeon during fishway passage. *Journal of Experimental Biology*, *219*(16), 2534–2544. https://doi.org/10.1242/jeb.140087

Thiem, J. D., Hatin, D., Dumont, P., Van Der Kraak, G., & Cooke, S. J. (2013). Biology of lake sturgeon (*Acipenser fulvescens*) spawning below a dam on the Richelieu River, Quebec: Behaviour, egg deposition, and endocrinology. *Canadian Journal of Zoology*, *91*(3), 175–186. https://doi.org/10.1139/cjz-2012-0298

Wagner, R. L., Makrakis, S., Castro-Santos, T., Makrakis, M. C., Pinheiro Dias, J. H., & Belmont, R. F. (2012). Passage performance of long-distance upstream migrants at a large dam on the Parana River and the compounding effects of entry and ascent. *Neotropical Ichthyology*, *10*(4), 785–795. https://doi.org/10.1590/S1679-62252012000400011

Wang, N. (2018). How to conduct a meta-analysis of proportions in R: A comprehensive tutorial. John Jay College of Criminal Justice, CUNY. https://doi.org/10.13140/RG.2.2.27199.00161

Weaver, D. M., Brown, M., & Zydlewski, J. D. (2019). Observations of American Shad *Alosa sapidissima* approaching and using a vertical slot fishway at the head-of-tide Brunswick Dam on the Androscoggin River, Maine. *North American Journal of Fisheries Management*, *39*(5), 989–998. https://doi.org/10.1002/nafm.10330

Welcomme, R. L., Winemiller, K. O., & Cowx, I. G. (2006). Fish environmental guilds as a tool for assessment of ecological condition of rivers. *River Research and Applications*, *22*(3), 377–396. https://doi.org/10.1002/rra.914

Williams, J. G., & Katopodis, C. (2016). Commentary-incorrect application of data negates some meta-analysis results in Buntet al. (2012). *River Research and Applications*, *32*(10), 2109–2115. https://doi.org/10.1002/rra.3076

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