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Updating the consensus on fishway efficiency: A meta-analysis

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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 methodological 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 $\tau^2$. 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).
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 total 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...
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...
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 (m$^3$/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 ($\sigma^2$) 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

### TABLE 1  Ecological guilds and their members

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

Note: Limnophiles were grouped together, and pelagic eurytopic species were grouped with benthopelagic eurytopics.
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 \( \tau^2 \). 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 \( \tau^2 \) (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.
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 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 re-fit 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 re-fit 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 ($p = .0003, \tau^2 = 0.11$) (Figure 6a). No statistically significant differences in passage efficiency were found among ecological guilds ($p = .30, \tau^2 = 0.10$), although the same general pattern was evident, with

**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.

**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.
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, \( p = .0006, r^2 = 0.11 \)
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 ($k = 96, p = .012, r^2 = 0.098$) (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 it 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 it did not change. Removing Calles and Greenberg (2007) slightly lowered the passage efficiency estimate for nature-like fishways, but it 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 it did not improve it or alter the significance. Finally, removing Sullivan (2004) slightly improved the passage efficiency estimate for pool-and-weir fishways, negligibly lowered it 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 naïveté. Given that non-naïve test fish already experienced the fishway once before capture, a learning effect could positively bias efficiency estimates (Cooke & Hinch, 2013). Using naïve 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.

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

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REFERENCES


SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section.

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