Received: 20 March 2017 | Revised: 14 August 2017 | Accepted: 16 August 2017
DOI: 10.1002/rra.3215

WILEY

RESEARCH ARTICLE

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

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Funding information
Acadia University; Canada Research Chairs; Canadian Wildlife Service; Ducks Unlimited Canada; Irving Oil Ltd; Mitacs; Natural Sciences and Engineering Research Council of Canada; New Brunswick Environmental Trust Fund

Abstract

Alewife (*Alosa pseudoharengus*) passage through 3 fishways was assessed during the 2013–2016 spawning runs in 3 rivers of the Isthmus of Chignecto, Canada. From April 24 to June 10, 5,423 alewife with a mean ± *SD* fork length of 227 ± 18 mm were tagged with passive integrated transponders. During their tagging year, approximately half of individuals (40% to 64%) went undetected whereas those detected used fishways from April 16 to July 8. Detected alewife were significantly longer than those undetected. Attraction rates to fishway entrances in 2015 and 2016 ranged from 85% to 98%. Annual fishway passage rates for pooled fish tagged that year and returnees, varied from 64% to 97% for 2 Denil style fishways. A pool-and-weir fishway that was dysfunctional (2013), repaired (2014), and replaced (2015–2016) yielded 0.5%, 25%, 60%, and 73% annual pooled passage rates, respectively. Larger individuals, previously tagged returnees, and males compared to females of a similar size had higher passage success suggesting some fishways may apply population-level selective pressures. Alewife passage rates related to fishway style, design, and proper function, with greater passage for the 2 Denils than the pool-and-weir fishway in our study. Regular structural maintenance and fish passage reviews are essential management considerations to ensure fishway functioning and river connectivity. Replacement of a fishway with poor fish passage may be the best option to improve passage rates. Future research should address the effects of multiple anthropogenic instream obstructions, environmental variables, negative sublethal post-tagging effects, and the importance of returnees on fish passage rates in fishways.

KEYWORDS

alosids, attraction rate, Denil and pool-and-weir style fishways, passage rate, returnees, size-selectivity

1 | INTRODUCTION

Dams and impoundments pose a global threat to fishes by altering habitat, hindering migrations, changing river flow, and causing localized extinctions (Haro & Castro-Santos, 2012; Liermann, Nilsson, Robertson, & Ying, 2012; Roscoe & Hinch, 2010). To minimize these effects, fishways have been constructed to facilitate upstream passage. In northeastern North America, fishways have been installed primarily to enable passage of alewife (*Alosa pseudoharengus* Wilson, 1811), blueback herring (*Alosa aestivalis* Mitchill, 1814), American shad (*Alosa sapidissima* Wilson, 1811), sea lamprey (*Petromyzon marinus* L., 1758), and Atlantic salmon (*Salmo salar* L., 1758; Orsborn, 1987; Roscoe & Hinch, 2010).

The alewife, a commercially valuable, anadromous alosid, spawns in rivers from North Carolina to Newfoundland (Atlantic States Fisheries Management Commission, 2009; Scott & Scott, 1988). Depending on latitude, upstream migration lasts from early February to the end of June (Rulifson, 1994). Spawning occurs over rocky substrate in shallow lakes or low flow river pools. Alewife are iteroparous and after spawning return to the sea to feed along the continental shelf in depths less than 100 m (Neves, 1981; Scott & Scott, 1988). In the United States, intensive overfishing combined with obstruction of spawning habitat has severely reduced alewife abundance (Atlantic States Fisheries Management Commission, 2009; Castro-Santos & Vono, 2013) prompting a suggestion to list the species as "threatened" in an effort to prevent a total population collapse (Natural Resources Defense Council, 2011). In spite of overexploitation, alewife schools numbering in the thousands undertake annual spawning migrations. From 1960 to 1999, the Bay of Fundy (Figure 1) fishery annually harvested 860 tonnes to 6,700 tonnes of alewife and blueback herring combined. Since 1990, however, annual catches have been between 1,247 t and 1,745 t. The Isthmus of Chignecto (Figure 1) fishery reportedly harvests <100 t annually. Incomplete catch records and absence of biological data for most alewife stocks have encouraged river-specific management policies resulting in status quo or decreasing exploitation levels (Department of Fisheries and Oceans Canada (DFO), 2001).

The effectiveness of most fishways remains unstudied (Roscoe & Hinch, 2010) or has been studied inappropriately (Bunt, Castro-Santos, & Haro, 2012). The style, size, and flow dynamics of fishways are highly variable (Bunt et al., 2012; Haro & Castro-Santos, 2012). Studies on fish passage rates, the number of individuals successfully passing divided by the number of individuals attempting passage, have shown upstream passage rates decrease with increasing fishway slope, and positively correlate with river flow and fishway length (Noonan, Grant, & Jackson, 2012). Passage rate variability may also be influenced by light level and/or water temperature (Bunt et al., 2012; Roscoe & Hinch, 2010). Passage rate for one particular style fishway may be high for one species, yet completely impassible for others (Baumgartner, Boys, Stuart, & Zampatti, 2010; Noonan et al., 2012; Williams, Armstrong, Katopodis, Larinier, & Travade, 2012). Often only partial upstream passage success has been reported, even for strong swimming salmonids (Mallen-Cooper & Brand, 2007). Other than salmonids, there are few quantitative field studies involving other species passage through fishways (Bunt, Cooke, & McKinley, 2000; Bunt, Katopodis, & McKinley, 1999; Dominy, 1973; Franklin, Haro, Castro-Santos, & Noreika, 2012; Haro, Odeh, Castro-Santos, & Noreika, 1999; Noonan et al., 2012; Sullivan, 2004). Studies on herring species determined passage rates ranging from 10% to 40% (Haro et al., 1999; Haro,

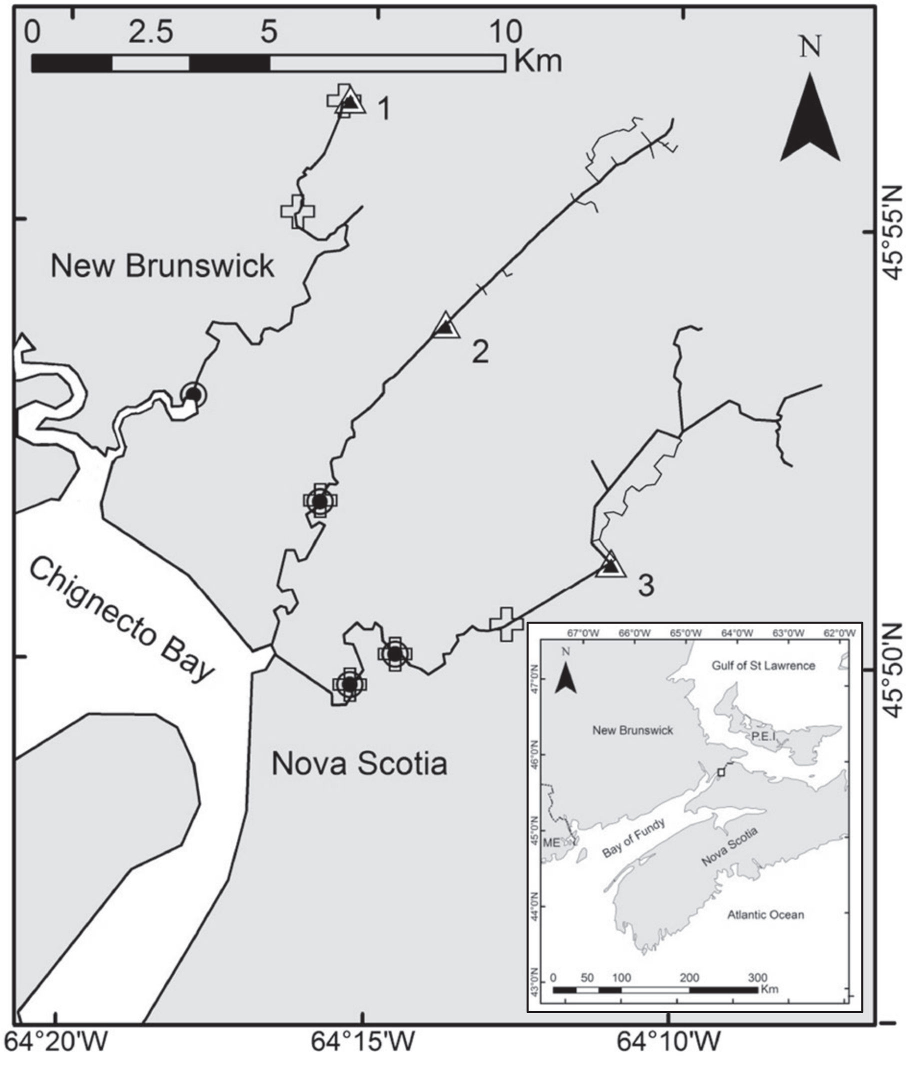

FIGURE 1 Location of the Isthmus of Chignecto (insert) and the LaCoupe (1), Missaquash (2), and LaPlanche (3) rivers and fishways (triangle) relative to tagging sites (cross) and tide gates (circle)

Franklin, Castro-Santos, & Noreika, 2008; Noonan et al., 2012). Even with effective fishways restoring river connectivity, anadromous fishes are still delayed during their migrations and consequently drain their energy reserves, negatively affecting survival during or after spawning runs (Castro-Santos & Letcher, 2010; Roscoe & Hinch, 2010).

Our objectives were to quantify passage of upstream migrating alewife through one fishway on each of three rivers during the 2013–2016 spawning runs. Passage rates were correlated to fish length, mass, sex, and number of years post-tagging. Fishway style and design were also examined relative to passage success, with an additional objective of assessing the pool-and-weir fishway that was modified and subsequently replaced during the study period.

2 | STUDY SITE

From 2013 to 2016, we monitored one fishway on each of the LaPlanche (LP), Missaquash (MS), and LaCoupe (LC) rivers on the Isthmus of Chignecto, Canada (Figure 1). Two fishways were Denil (LP & MS) and one was pool-and-weir style (LC; Figure 2), each with a length ≤17.2 m and a slope of 6° to 15° (Table 1). Following the 2014 spawning run, the LC fishway was replaced by a new pool-and-weir design. All fishways had an attached dam spillway; however, all river flow passed through the chute in the 2013–2014 LC pool-and-weir fishway (Figure 2c). Downstream of fishways to estuarine tide gates, the rivers were slow-moving, deeply incised, <2 m deep and <5 m wide, with numerous smaller agricultural ditches draining into the main channel. Upstream of fishways, rivers formed multiple branches characterized by bogs, lakes, man-made channels, marshes, and ponds.

3 | METHODS

3.1 | PIT antenna arrays

Alewife movements through fishways were quantified using passive integrated transponder (PIT) radio frequency identification (RFID) telemetry (Castro-Santos, Haro, & Walk, 1996). Each PIT antenna consisted of two turns of 10 AWG (5.26 mm, 7 or 19 strands, 600 V) copper wire protected within 2 cm diameter PVC pipe (Castro-Santos et al., 1996). Each fishway array had four antennas, two mounted on baffles or weirs at the downstream end and two mounted at the upstream end (Table 1). A separate array, referred to as the “downstream array,” consisted of one antenna or two antennas attached end-to-end that spanned the river cross-section within 60 to 150 m downstream of each fishway. Each antenna was connected to a tuner box linked with twin axial cable to a multi antenna half duplex (HDX) reader set at 14 scans per second (Oregon RFID Ltd). Each array was powered by two 12 volt, deep-cycle batteries (Nautilus, 800–900 A cranking/105–115 amp hr, 185–205 minimum reserve capacity) connected in parallel and replaced every 72 hr. Following antenna tuning, the detection range was tested in water and air approximately 20 to 30 cm from the antenna loop (Franklin et al., 2012).

FIGURE 2 Study site Denil fishways on the LaPlanche (a) and Missaquash (b) rivers during 2013–2016, and the 2013–2014 (c) and 2015–2016 (d) pool-and-weir fishways on the LaCoupe River, showing location of a passive integrated transponder tuning box (d) and an antenna loop located on a baffle (E) and a weir (F). Please note water level in photo was lower than during operation in LaCoupe pool-and-weir 2013–2014 fishway (c) as the photo was taken with the water flow temporarily blocked for passive integrated transponder antenna array installation. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Style, rise, and length (m), slope (°), number of baffles/weirs, # of resting pools and construction material of the LaPlanche, Missaquash, and LaCoupe fishways

River/fishway	Style	Rise (m)	Length (m)	Slope (°)	# of baffles/weirs	# of resting pools	Construction material	PIT antenna baffle/weir #
LaPlanche	Denil	1.9	13.5	8.0	22	—	Concrete with plywood baffles	1, 4, 19, 22
Missaquash	Denil	2.7	10.2	14.8	18	—	Concrete with plywood baffles	2, 5, 15, 18
LaCoupe[a]	Pool-and-weir	1.5	9.7	8.8	4	3	Concrete with wood stop logs	1, 2, 3, 4
LaCoupe[b]	Pool-and-weir	1.7	17.2	5.6	7	6	Concrete with wood stop logs	1, 3, 5, 7

Note. Passive integrated transponder (PIT) antennas were located on baffles or weirs indicated by Number 1 at the bottom and the highest number at the top.

[a] Fishway monitored during 2013–2014.

[b] Fishway monitored during 2015–2016.

Monitoring dates for 2013–2016 on all arrays varied annually due to water levels but ranged from April 9 to July 27. During 2013–2015, spawning runs were underway during array installation, but two fishways (LP & MS) were monitored before the spawning run in 2016. Downstream arrays were installed for attraction rate estimates of the LP and LC fishways in 2015, and MS was added in 2016. Detection efficiency, expressed as a percentage, was calculated for each antenna as the number of individuals detected by the antenna divided by the number of individuals detected further upstream (Franklin et al., 2012). Only "successful" individuals were used in these estimates to ensure antennas in a fishway were passed at least once (Castro-Santos et al., 1996). Detection efficiencies were not estimated for any Antenna 4 as no antennas were operating further upstream. Attraction rate was quantified as the percentage of individuals detected entering a fishway divided by the pooled number of individuals recorded on the fishway's downstream array and/or in the fishway (Franklin et al., 2012). Passage rate was quantified as the number of individuals successfully passing divided by the number of individuals entering the fishway. In 2015, flooding destroyed two of five arrays on June 23; however, the final detections were on June 20, suggesting the spawning run was finished or nearing completion.

3.2 | Tagging

From April to June, alewife were captured by dip netting or using fyke nets. In 2013–2014, all alewife were tagged and released at or near capture sites located 2.5 km (river km 8.9), 5.1 km (river km 5.5), and 220 m (river km 14.6) downstream of the LP (river km 11.4), MS (river km 10.6), and LC (river km 14.8) fishways, respectively. At the MS site, alewife were captured at the downstream outlet of the tide gate and transported in a water-filled bucket <35 m to be tagged and released at the upstream outlet of the tide gate to decrease chances of immediate capture by commercial fishers. In 2015, capture sites were relocated to 5.8 km (river km 5.6) and 2.9 km (river km 11.9 km) downstream of the LP and LC fishways. Similar to the MS capture site, tagging at the LP site in 2015 involved transport of captured alewife for tagging and release at the upstream outlet of the tide gate. In 2016, the LP site was again relocated immediately downstream of a new tide gate (river km 2.5), but the majority of alewife were released at the capture site to assess passage rate through the new tide gate. Fifty individuals, as controls, were transported to be tagged and released at the upstream outlet of the new tide gate.

Prior to tagging, captured alewife (n < 50 at a time) were held for no more than 30 min in a floating holding pen (60 cm × 90 cm × 45 cm) or cooler containing oxygenated river water. Each individual was measured for fork length (L_F) and total length (L_T) to the nearest millimeter, weighed to the nearest gram and simultaneously scanned with a PIT reader (Allflex Iso RFID model # RS20-3 or Oregon RFID datatracer FDX/HDX) to identify recaptures. Nonrecaptured individuals had four to five scales removed just posterior of the right pectoral fin and slightly dorsal of the ventral line where a puncture was made into the peritoneal cavity using a 3-mm-diameter biopsy needle. A 23-mm HDX PIT tag (3.65 mm diameter, 0.6 g, Oregon RFID) with known coded ID was inserted through the puncture by hand. In 2016, individuals were sexed, and the first 30 of each tagging session had scales collected for ageing. Handling time averaged <15 s per individual and release was immediate or delayed up to 25 min for recovery.

3.3 | Data management

PIT ID, corresponding timestamp, and antenna number were recorded by each reader box with downloads occurring every three 3 days. Tagged individuals were categorized as "undetected," "unsuccessful," or "successful." Undetected tagged individuals were not recorded by any array during their tagging year. Individuals detected within a fishway on any antenna with a 4-min lag following final detection on the antenna nearest the downstream entrance or upstream exit were defined as unsuccessful or successful, respectively (Castro-Santos & Perry, 2012).

3.4 | Analyses

Fork length and mass of tagged alewife were compared between the three rivers and undetected, unsuccessful, and successful groups using *t* tests or Mann–Whitney tests if data distributions did not approximate normality (tested with Kolmogorov–Smirnov tests). A generalized linear model with a binomial distribution was used to examine the probability of passing a fishway as a function of fish fork length and sex. Statistical results were considered significant at p < 0.05. All means are presented ± standard deviation. Fishway passage analyses were performed in the R statistical environment (R Core Team, 2013), using the following packages: ggplot2 (Wickham, 2009), dplyr (Wickham & Francois, 2014), plyr (Wickham, 2011), and lubridate (Grolemund and Wickham, 2011).

4 | RESULTS

4.1 | Tracking

From April to June in 2013 to 2016, we tagged 5,423 alewife with a mean fork length of 227 ± 18 mm (range 113 to 310 mm) and tag/body mass ratio of 0.4% ± 0.1% (range 0.2% to 0.9%). Pooled multi-year (2013–2016) comparisons between alewife tagged on each river revealed individuals tagged on the LC were significantly longer and heavier compared to alewife tagged on the LP and MS (Kruskal–Wallis; L_F $H_2 = 219.8$, M $H_2 = 60.6$; $p < .001$); however, there was no significant difference in fork length and mass of alewife tagged on the LP and MS (post hoc Dunn's method; $p > .05$). For each study year, inter-river comparisons of median fork lengths for tagged alewife revealed similar trends with longer individuals tagged on the LC compared to the LP and MS (Kruskal–Wallis; 2013 $H_2 = 105.5$, $p < .001$; 2014 $H_2 = 187.4$, $p < .001$; 2015 $H_2 = 12.8$, $p = .002$; 2016 $H_2 = 11.9$, $p = .003$). In 2013–2014, alewife tagged on the MS had median fork lengths 13 to 20 mm shorter than those tagged on the LC; however, this difference was only 2 mm L_F in 2015–2016. Larger individuals arrived earlier on spawning runs (Figure 3).

Calculated detection efficiencies for all antennas ranged from 21% to 100% depending on year, fishway and antenna placement. Detection efficiency generally decreased with antenna placement higher up a fishway. However, from 2015 to 2016, all antenna detection efficiencies were >89%, with most between 96% and 100% (Table 2). The mean percentage of undetected alewife during 2013–2016 was 50.3% ± 8.9% (range 40.1% to 64.4%; Table 3). Alewife were detected in fishways on May 3 to June 23, 2013; May 15 to July 8, 2014; May 16 to June 20, 2015; and April 16 to July 8, 2016. Detected individuals were significantly longer (t test, $t_{5229} = 16.6$, $p < .0001$) and heavier ($t_{5229} = 20.8$, $p < .0001$) than those undetetected (Table 4).

4.2 | Fishway attraction and passage

In 2015, we estimated attraction rates as 98% and 85% for the LP and LC fishways, respectively. In 2016, attraction rates were estimated at 98%, 87%, and 97% for the LP, MS, and LC fishways, respectively. Annual passage rates for pooled individuals newly and previous tagged varied from 64% to 97% for the two Denil style fishways. The pool-and-weir fishway yielded 0.5%, 25%, 60%, and 73% passage rates for each successive study year, relating to a dysfunctional (2013), repaired (2014), and replaced (2015–2016) structure, respectively. The LP fishway had the highest passage rates for newly tagged individuals in 2013–2016 (76% to 95%). At MS and LC fishways, greater passage success occurred for returnees, but for the LP, returnees exhibited

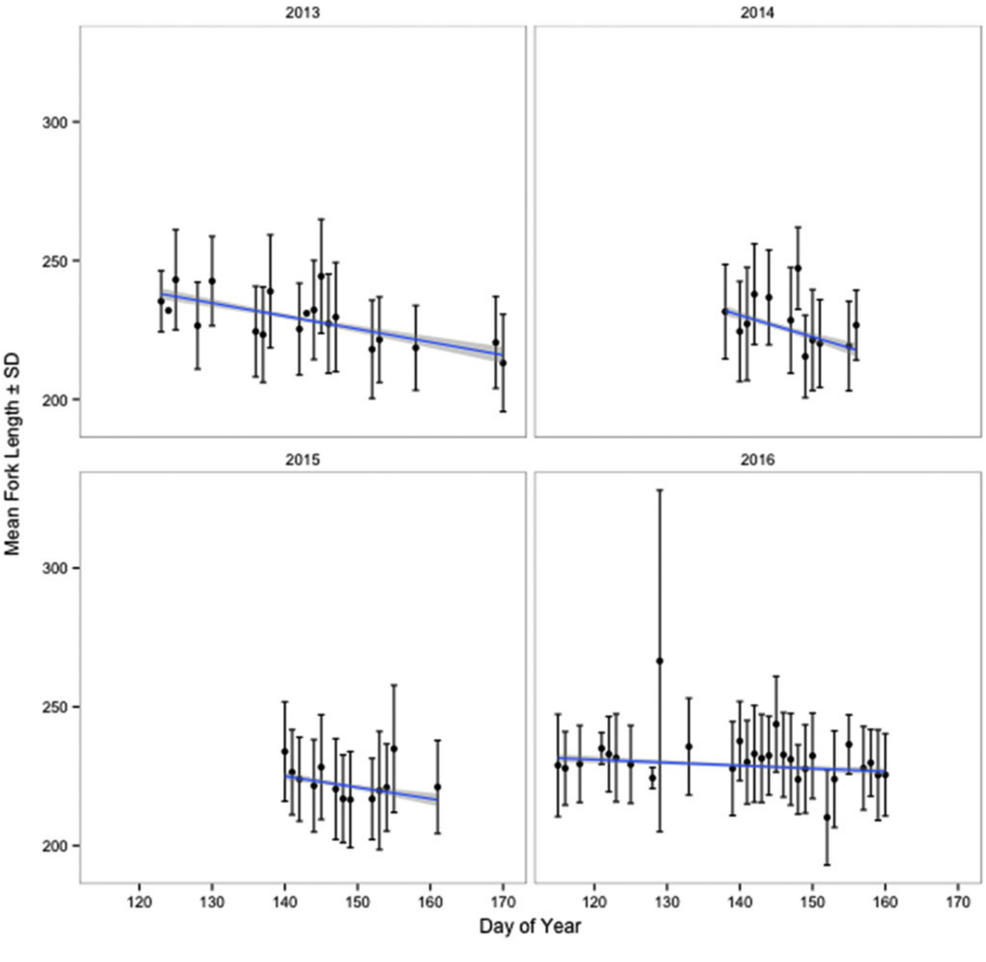

FIGURE 3 Daily mean ± *SD* fork lengths (mm) versus tagging day of year of alewife on 2013–2016 spawning runs in the Isthmus of Chignecto, Canada. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Detection efficiency (%) of Antennas 1–3 within each passive integrated transponder array installed at the LaPlanche (LP), Missaqaush (MS) and LaCoupe (LC) fishways during 2013–2016

	Detection efficiency (%)		
River/fishway	**Antenna 1**	**Antenna 2**	**Antenna 3**
2013			
LP	100	100	93
MS	99	63	51
LC	100	100	100
2014			
LP	100	64	21
MS	100	94	60
LC	100	84	56
2015			
LP	100	96	89
MS	100	99	98
LC[a]	98	100	96
2016			
LP	100	100	99
MS	99	99	99
LC[a]	100	99	99
mean ± *SD*	100 ± 1	92 ± 14	80 ± 26
Minimum	98	63	21
Maximum	100	100	100

Note. SD = standard deviation.

[a] New fishway installed in summer 2014.

no consistent pattern relative to newly tagged individuals, with passage rates ranging from 74% to 99% (Table 3).

Successful alewife had significantly longer fork length than unsuccessful individuals during 2013–2016 for both Denil and 2015–2016 pool-and-weir fishways (Table 4; Mann–Whitney, $p \leq .021$). In 2013, the pool-and-weir fishway had only one individual pass due to a shallow approach pool. In 2014, this structure had a deeper approach pool enabling more passage attempts, yet there was no significant difference in median fork length of successful and unsuccessful individuals (Table 4; Mann–Whitney, $p = .696$).

Probability of successful passage was positively correlated to fork length, except for the 2014 LC fishway (Figure 4). In 2016, males had a greater probability of passage success compared to females of the same fork length, yet this was fishway dependent (Figure 5). Returnees also had a higher passage success probability compared to newly tagged individuals at the LC and MS fishways during 2014–2016. The LP fishway had the same trend in 2016, but this reversed in 2014–2015 (Figure 6).

5 | DISCUSSION

Significantly longer alewife tagged in 2013–2014 on the LC compared to the LP and MS rivers may have favoured LC passage; however, results revealed no bias considering structural issues of the LC fishway and greater passage success for LP/MS alewife. Size differences between LC and LP/MS tagged alewife may have indicated distinct populations and/or varying fishing pressure. For example, gill netting occurred in the LP and MS estuaries in 2013–2016 but not on the LC. Statistically significant differences between median fork lengths of alewife tagged on each river in 2015–2016 was probably due to large sample sizes (n = 242 to 649) and measuring error, considering the small range (2 mm L_F).

Based on using successful migrants only, our detection efficiencies may not have been "true" estimates, as a subsample of tagged

TABLE 3 Number of alewife tagged and detected that year, returnees detected, and individuals successfully ascending a fishway, with passage rates (%; [lower, upper 95% CI]) for newly tagged, returnees and all individuals for the LaPlanche (LP), Missaquash (MS) and LaCoupe (LC) fishways during 2013–2016

River/fishway	*n* tagged	*n* undetected	*n* detected	Newly tagged passage	*n* returnees	Returnee passage	Pooled passage
2013							
LP	376	242	134	76 (72, 86)	-	-	-
MS	416	203	213	68 (63, 75)	-	-	-
LC	406	209	197	0.5 (0.0, 3)	-	-	-
2014							
LP	477	203	286	85 (81, 89)	155	81 (74, 87)	84 (80, 87)
MS	361	231	133	67 (57, 73)	57	77 (64, 87)	70 (63, 76)
LC	283	164	119	19 (13, 28)	162	29 (22, 37)	25 (24, 35)
2015							
LP	649	381	268	91 (86, 94)	128	74 (67, 83)	86 (85, 92)
MS	242	116	150	60 (52, 68)	103	76 (66, 84)	66 (70, 81)
LC[a]	379	162	217	47 (40, 53)	153	80 (73, 86)	60 (55, 65)
2016							
LP	594	251	361	95 (92, 97)	306	99 (98, 100)	97 (96, 99)
MS	635	273	352	59 (54, 64)	99	84 (75, 91)	64 (64, 73)
LC[a]	414	166	248	64 (58, 70)	166	86 (79, 91)	73 (68, 77)

[a] New fishway installed in summer 2014.

The hyphens represent information that is not applicable considering this was the first year of the study.

TABLE 4 Mean ± *SD* fork length (L_F, mm) and mass (M, g) of undetected, unsuccessful, and successful alewife tracked at the LaPlanche, Missaquash, and LaCoupe fishways during 2013–2016

River/fishway	Undetected	Unsuccessful	Successful
2013			
LaPlanche			
L_F	225 ± 17	239 ± 17	240 ± 19
M	145 ± 37	198 ± 48	202 ± 54
n	254	32	102
Missaquash			
L_F	220 ± 17	226 ± 14	230 ± 14
M	145 ± 37	163 ± 37	172 ± 38
n	194	70	147
LaCoupe			
L_F	235 ± 19	242 ± 19	258
M	170 ± 44	195 ± 50	236
n	209	196	1
2014			
LaPlanche			
L_F	219 ± 18	217 ± 15	230 ± 16
M	151 ± 42	145 ± 40	176 ± 42
n	203	42	244
Missaquash			
L_F	216 ± 15	220 ± 16	228 ± 18
M	148 ± 35	160 ± 41	177 ± 46
n	231	44	89
LaCoupe			
L_F	235 ± 16	245 ± 18	243 ± 17
M	174 ± 38	200 ± 49	199 ± 50
n	164	96	23
2015			
LaPlanche			
L_F	216 ± 15	218 ± 12	229 ± 15
M	143 ± 32	156 ± 32	174 ± 38
n	381	22	226
Missaquash			
L_F	216 ± 15	221 ± 15	224 ± 14
M	145 ± 32	155 ± 34	161 ± 33
n	116	60	90
LaCoupe[a]			
L_F	218 ± 17	223 ± 19	239 ± 19
M	145 ± 37	162 ± 45	198 ± 50
n	162	116	101
2016			
LaPlanche			
L_F	228 ± 16	215 ± 16	229 ± 16
M	183 ± 43	152 ± 43	185 ± 44
n	251	20	341
Missaquash			
L_F	226 ± 17	230 ± 15	231 ± 13
M	176 ± 39	190 ± 38	190 ± 37
n	273	145	207
LaCoupe[a]			
L_F	228 ± 14	229 ± 15	238 ± 17
M	165 ± 31	177 ± 40	206 ± 50
n	166	90	158

[a] New fishway installed in summer 2014.

individuals was used. Less than 100% detection efficiencies in our study were likely due to antenna placement, fish behaviour and/or fishway style. The duration a tagged alewife was present and the number of tagged individuals simultaneously present within an antenna's detection range likely influenced the probability of detection (Castro-Santos et al., 1996). Our highest detection efficiencies may have been due to alewife holding position. For example, all antenna 1 had detection efficiencies of 98% to 100%, probably due to individuals holding within the downstream entrances before an upstream passage attempt was made. Lower detection efficiencies for antennas located nearer the top of fishways may have related to alewife sprint swimming during the passage of these antennas. The lowest detection efficiencies occurred at MS Antennas 2 and 3 during 2013–2014 only, perhaps due to environmental conditions (i.e., greater water flow or debris) or poor electrical connections. These antenna loops were unaltered during the entire study period, so another possible cause for poor detection efficiencies may have been different researchers installing the electronics during 2013 and 2014. Considering detection efficiencies decreased with antenna placement further up a fishway, an Antenna 4 may have had the lowest detection efficiency. This may have resulted in our passage rates being underestimates. Better antenna detection efficiencies may have been calculated using test tags placed at known distances and orientations relative to each antenna's plane over specified periods and multiple sessions during monitoring each year; however, this approach to calculate detection efficiency would not account for fish behaviour.

Approximately half of migrants went undetected during their tagging year. Although others have reported and/or included undetected individuals in statistical methods (Castro-Santos & Haro, 2003; Castro-Santos & Perry, 2012; Franklin et al., 2012), none have determined their fate. Distance between tagging locations and fishways ranged from 0.2 to 8.9 km, yet undetected proportions were stable, implying tagging location may not be a contributing factor. One reason for undetected individuals may have been inadequate or distracting water flow at fishway entrances; however, the 2013–2014 LC fishway had all flow through the chute. Other possibilities included tag expulsion, delayed tagging mortality (Jepsen, Koed, Thorstad, & Baras, 2002), predation, or spawning downstream of fishways (Sheppard & Block, 2013). Delayed tagging, fishing, and natural predation mortality probably contributed; however, delayed tagging mortality and tag expulsion was 0% and <3.3%, respectively, of alewife held 24 hr to 14 days post-tagging in other studies (Castro-Santos & Vono, 2013; Smith et al., 2008). Spawning downstream of fishways may have occurred, but no spawning habitat and/or behaviour was observed.

Undetected alewife were smaller than detected individuals, suggesting river ascents may be size or age dependent. Based on

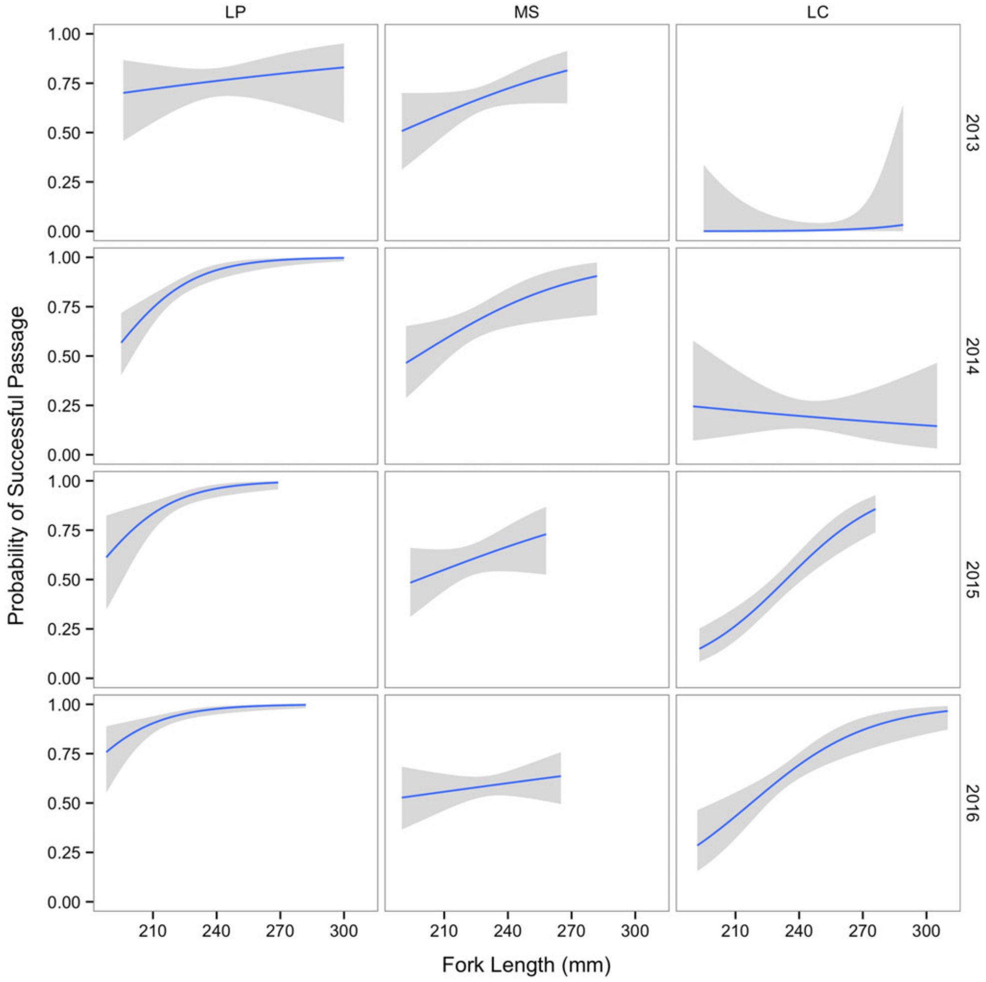

FIGURE 4 Probability of passage using a generalized linear model with binomial distribution based on fork length (mm) of alewife at the LaPlanche (LP) and Missaquash (MS) Denil-style, and LaCoupe pool-and-weir (LC) fishways during 2013–2016. [Colour figure can be viewed at wileyonlinelibrary.com]

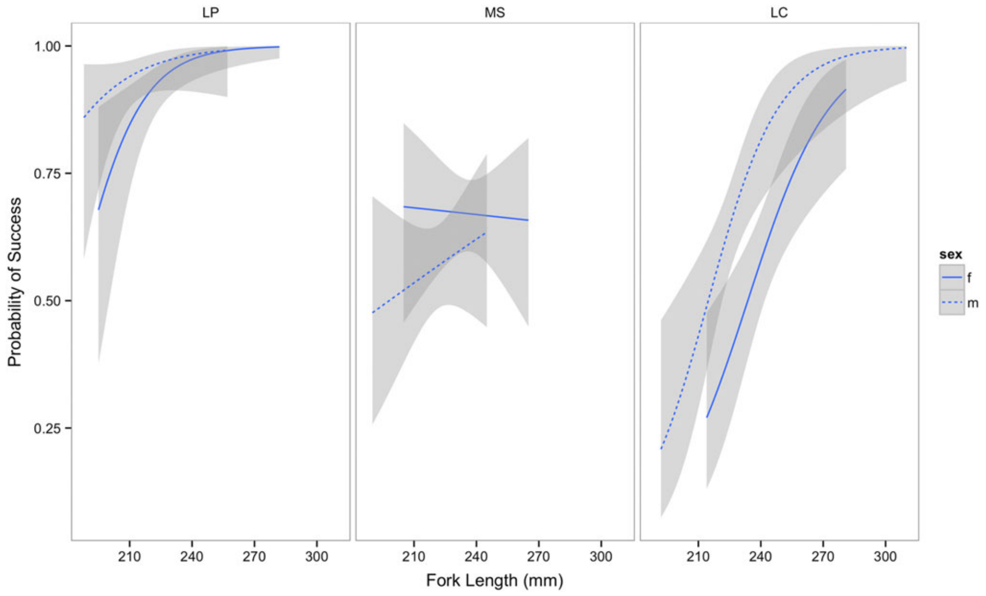

FIGURE 5 Probability of passage using a generalized linear model with binomial distribution based on fork length (mm) of male and female alewife at the LaPlanche (LP) and Missaquash (MS) Denil-style and the LaCoupe (LC) pool-and-weir fishways in 2016. [Colour figure can be viewed at wileyonlinelibrary.com]

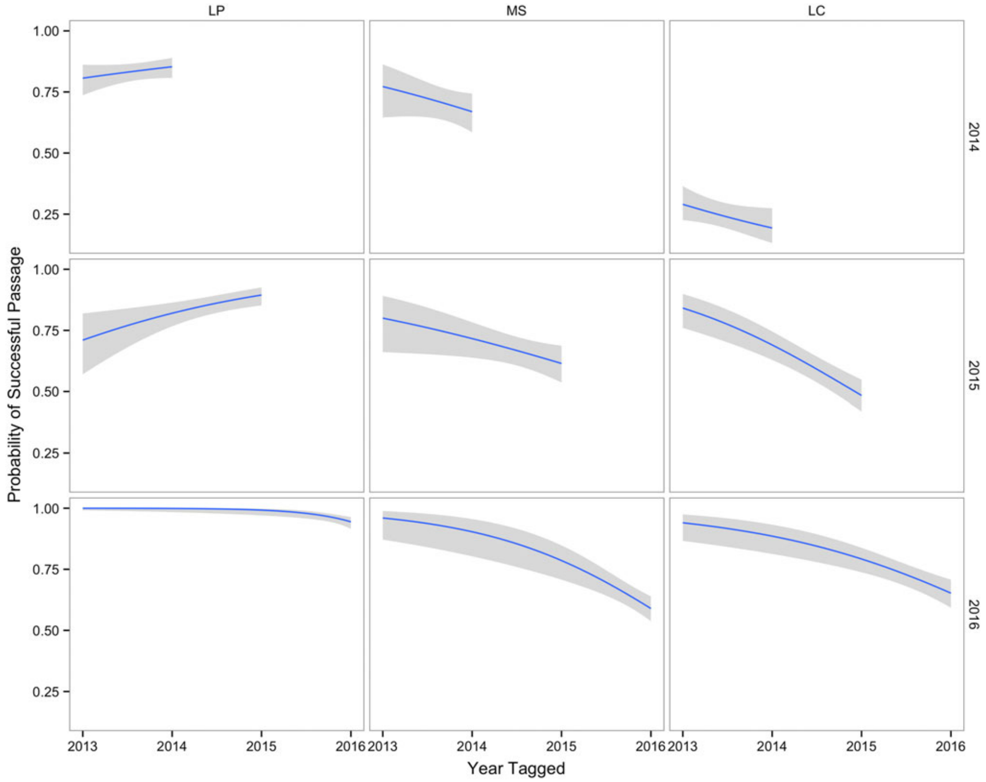

FIGURE 6 Probability of passage using a generalized linear model with binomial distribution based on tagging year for alewife at the LaPlanche (LP) and Missaquash (MS) Denil-style fishways, and LaCoupe (LC) pool-and-weir fishways during 2013–2016. [Colour figure can be viewed at wileyonlinelibrary.com]

sexing results in 2016, no immature individuals were captured, so undetected migrants were unlikely sexually immature. Overlap of mean lengths for detected and undetected groups suggested length may not be a key factor in detection but a contributing factor interacting with tagging stress and environmental variables. Smaller alewife arrive during the late spawning run (Stone, Jessop, & Parker, 1992), thus lower water levels and fishway attraction flow (Caudill et al., 2007) and rising water temperatures may deter these migrants; however, we found no relationship between tagging date and detection. Spawning migration behaviour may combine both up and downstream movements, where downstream movements ("fallback") are unassociated with injury or negative post-tagging effects (Frank et al., 2009; Naughton et al., 2006). We confirmed "fallback" as some individuals were detected in adjacent rivers, thus some undetected individuals may have "switched" to unmonitored rivers.

Our results highlighted three aspects of alewife passage through fishways. First, fishway style and design had significant effects on passage rates (Bunt et al., 2012; Haro et al., 1999). Hydraulic conditions within fishways may select for larger individuals (Haro, Castro-Santos, Noreika, & Odeh, 2004), which may be the case in our study. An example of the importance of fishway structure and proper function was observed at LC in 2013–2014 compared to 2015–2016. Offset weir notches were replaced by centre notches, weir number increased from four to seven and slope decreased from ~9° to ~6°, which corresponded to annual passage rate increases of 27% and 44% for newly tagged individuals, and 51% and 57% for returnees, comparing 2014 to 2015, and 2014 to 2016, respectively

The LP Denil and 2015–2016 LC pool-and-weir fishways had similar rise (~2 m) and entrances associated with the spillway's plunge pool <2 m depth, but different runs (14 & 17 m, respectively) and slopes (8° & 6°, respectively); thus, style could not be isolated as the changing condition. Comparing just the designs of these two styles, however, the 2015–2016 LC pool-and-weir would be expected to pass fish more effectively due to its longer length and lower slope (Noonan et al., 2012), but our results consistently revealed greater passage rates for the LP Denil fishway. Franklin et al. (2012) found two steeppass Denil designs (3-m length; 6° and 17° slopes) in their study were more effective for passing alewife (95% and 97%) than one pool-and-weir fishway (14-m length, 8° slope; 21% passage rate). Although lengths and slopes were not the same, the Denils, each with a lower and higher slope compared to the pool-and-weir, still passed more alewife (Franklin et al., 2012). This may have related to favourable hydraulics (Taguchi & Liao, 2011) in baffle-type designs that not only facilitate swimming, but also provide directed flow for fish to orientate upstream (Katopodis, 1992). We only monitored the 2015–2016 LC pool-and-weir for 2 versus 4 years for the LP Denil. Considering increasing passage rates over the study period for the LP Denil, the LC pool-and-weir passage rates may also increase over time.

Compared to the LP Denil and 2015–2016 LC pool-and-weir fishways, the MS Denil fishway had a shorter run (10 m), greater slope (15°) and an entrance with a shallower spillway plunge pool (<0.5 m depth), thus design specifics could be considered when comparing both Denil styles. For newly tagged and pooled alewife during 2013–2016 spawning runs, the LP fishway had consistently greater passage rates than MS (8% to 36%), suggesting a shorter run, ~7° greater slope and different entrance conditions decreased passage rates, concurring with other studies (Haro et al., 1999; Noonan et al., 2012). Returnees showed a similar pattern, but passage rates were similar in 2015 (LP 74% and MS 76%). The 2015–2016 LC pool-and-weir and MS Denil fishways had similar pooled passage rates (LC 60% in 2015 and 73% in 2016; MS 66% in 2015 and 65% in 2016). Although MS's Denil style may have conferred a passage advantage over LC's pool-and-weir style, the negative effects of MS's shorter run, greater slope, and shallower entrance may have nullified the effect of style.

Second, our results suggested fish length and number of years post-tagging positively correlate to passage success, with the exception of the LP fishway, where returnees had lower success during some years. Fish length and success may be linked to specific turbulence that affects fish posture control and swimming speed (Tritico & Cotel, 2010). Size and success may also be explained by variation in energy reserves or swimming ability between fish species (Haro et al., 2004; Peake, Beamish, McKinley, Scruton, & Katopodis, 1997; Roscoe, Hinch, Cooke, & Patterson, 2011). Considering our results, our fishways may impose size selectivity of migrants, and this would be a critical consideration for fisheries and fishway management, especially considering the additive effect of size selectivity by estuarine gill net fisheries in our study site. Males had a greater probability of successful passage than females of the same length, and this may have been related to relative muscle mass and not absolute size (Haro et al., 2004). In addition to increased body size, returnee passage success may be related to individual experience used to navigate obstacles differently than first-time spawners (Brown & Laland, 2003). Salmonid returnees used bypass surface flow outlets to navigate rivers with multiple anthropogenic obstructions, and indirect evidence showed return rates increased as more bypasses were installed (The Columbia Basin Bulletin, 2013). In heavily fished catch-and-release fisheries, veteran salmonids were often harder to catch, and may have learned from experience (Askey, Richards, Post, & Parkinson, 2006; Halttunen, 2011).

Third, sublethal post-tagging effects may change behaviour and decrease passage success. Alewife tagged in the year they were monitored were more likely to be unsuccessful. This may be due to adverse post-tagging effects, and/or fallback (Frank et al., 2009) triggered by traumatic tagging. Tagging stress may have a more negative effect on smaller migrants, and this may indirectly inflate success rates of larger individuals during their tagging year. Multi-year tracking studies, such as this one, enable more “natural” migration behaviour to be monitored by tracking returnees. Unfortunately, maiden spawners will always have tagging bias. Determining the relative importance of negative sublethal post-tagging and positive fish length and/or age effects on the probability of successful passage was difficult, especially when dealing with smaller migrants.

Migration delays due to obstacles, prolonged holding, and searching for passable routes deplete energy reserves (Hinch & Rand, 1998) and may have decreased passage success in our study. If upstream and downstream movements are considered (Frank et al., 2009; Naughton et al., 2006), a single obstacle may cause cumulative delay that drains energy and decreases success (Castro-Santos & Letcher, 2010). All our study rivers have a tide gate near their mouth, thus possible cumulative delay at these obstacles may have decreased fishway passage rates. In comparison to other alewife rivers in eastern North America, our study rivers were relatively short. The Penobscot River historically harvested alewife 322 km inland (Hall, Jordann, & Frisk, 2011) and other runs exceeding 90 km total travel distance did not exhaust migrant lipid stores to the point where protein was utilized (Crawford, Cusack, & Parlee, 1986). Considering the fishways in our study were <15 km from the head of tide, depletion of migrant energy reserves was likely not a major factor for passage success.

Caution should be taken comparing fishways and/or passage studies as each has differences in species' behaviour and morphology, fishway design and environmental conditions, and all may influence passage rates. To properly compare passage rates, it would be necessary to consider controlled laboratory experiments (Castro-Santos et al., 1996) or time- and distance-based functions (Castro-Santos & Letcher, 2010; Castro-Santos & Perry, 2012; Franklin et al., 2012), which we did not use. Alewife passage rates related to fishway style, design and proper function, with greater passage for the two Denils than the pool-and-weir fishway in our study. Regular structural maintenance and fish passage reviews are essential management considerations to ensure fishway functioning and river connectivity. Replacement of a fishway with poor fish passage may be the best option to improve passage rates. Future research should address the effects of multiple anthropogenic instream obstructions, environmental variables, negative sublethal post-tagging effects, and the importance of returnees on fish passage rates in fishways.

ACKNOWLEDGEMENTS

We acknowledge Acadia University, Ducks Unlimited Canada, Canadian Wildlife Service, Irving Oil Ltd, and New Brunswick Environmental Trust Fund for funding, field accommodation and project coordination. Thanks to A. Johnson and M. Dadswell for manuscript preparation. For field assistance, we thank A. Loder, C. Grove, C. McLauchlan, C. Buhariwalla, D. Sears, D. Bell, E. McConnell, F. Keyser, H. Dickinson, J. Beardsall, J. Hunt, L. Logan-Chesney, L. Millett, L. Cooper, L. Boudreau, M. Gregoire, M. Spares, N. Stewart, S. Landsman, S. Newell, S. Snow, T. Gregoire and others from Beaubassin. Research was conducted under DFO licence #338173, CWS permit NWATi-1, and Acadia Animal Care protocol #08-12R#2A#1. MITACS Accelerate and NSERC CGS-M programs funded ADS and GSN, respectively. MJWS and MLM were supported by NSERC and the Canada Research Chairs program. The authors have no conflict of interest to declare.

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How to cite this article: Nau GS, Spares AD, Andrews SN, Mallory ML, McLellan NR, Stokesbury MJW. 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 Res Applic*. 2017;1–12. https://doi.org/10.1002/rra.3215