

## Research Article

# River- and Sex-Specific Annual Survival Rates of Mature Anadromous Alewife (*Alosa pseudoharengus*)

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During multiple annual spawning runs from 2013 to 2021, over 9,000 mature anadromous alewife (*Alosa pseudoharengus* A. Wilson, 1811) were monitored with passive integrated transponders (PITs) in four rivers of the Chignecto Isthmus, Bay of Fundy, Canada. A subsample of 384 individuals tagged during 2016–2019 were aged from 3 to 6 years (mean  $\pm$  SD;  $4.2 \pm 0.7$  years,  $n = 232$ , males;  $4.5 \pm 0.7$  years,  $n = 152$ , females). Biotelemetry revealed that one unsexed individual survived seven years post tagging, possibly making it 10–13 years old. Return rates varied among the rivers, with the lowest rates in the most anthropogenically impacted river. Biotelemetry and ageing data were used to estimate apparent annual survival rates ranging from 0.25 to 0.50 depending on the river and the year. Based on capture-mark-recapture (CMR) analysis of biotelemetry data from the three less impacted rivers, the estimated overall annual survival was 0.396, total instantaneous mortality ( $Z$ ) was 0.93, and future life expectancy from time of release was 1.08 years. Frequency distribution of ages 4–6 for alewife pooled from all four study rivers estimated a lower annual survival rate of 0.301,  $Z = 1.20$ , and a future life expectancy of 0.83 years. The biotelemetry detection rates were 0.89–0.98 but varied depending on the river and the year, with the lowest rates in one river during 2017–2018 possibly related to a malfunctioning tide gate preventing upstream fish passage and subsequent detection. Based on CMR, males had a higher survival rate compared to females, which translated into an overall mean survival increase of 0.05. Alewife survivorship in our study highlighted that a limited ecosystem-based management period is required to mitigate river connectivity and mortality issues to avoid loss of population cohorts and decrease the risk of extirpation.

## 1. Introduction

Life history information incorporating the interdependence of oceanic and freshwater ecosystems is critical for the management and restoration efforts of anadromous fishes [1]. Studies on commercially valuable, anadromous alosines have been motivated in recent years due to declining

abundance [2–4]. The larger alosines, American shad (*Alosa sapidissima* Wilson, 811) [5] and Hickory shad (*Alosa mediocris* Mitchill, 1814) [6], have been studied more often than the smaller alewife (*Alosa pseudoharengus* A. Wilson, 1811) that is often studied collectively with blueback herring (*Alosa aestivalis* Mitchill, 1814) as “river herring” or “gaspereau” [2]. A recent literature review identified dams and

river connectivity as major factors contributing to declines and stressed estimates of survival were needed [2]. In the 1980s, a study that tagged nearly 19,000 river herring using external floy tags had low recapture rates (0.003) which precluded survival analyses [7]. Advances in biotelemetry since have estimated survival specific to life history or migratory phases of some anadromous fishes, such as Atlantic salmon (*Salmo salar* Linnaeus, 1758) postsmolts survival in estuaries while emigrating to sea [8] and postspawned adult survival of marine feeding to return to spawning rivers [9]. Acoustic tracking of emigrating postspawned alewife estimated survival through a river estuary and near-shore marine habitat in the Bay of Fundy [10]. Long-term mark-recapture and biotelemetry datasets have been used to determine the annual survival of fishes that demonstrate annual site fidelity [11, 12].

Anadromous alewife spawn annually during spring in rivers of the western North Atlantic Ocean from North Carolina, United States, to Newfoundland, Canada [13]. Spawning runs commence during February in southern latitudes [14] and during April–May farther north [13]. Alewives are iteroparous with a maximum age recorded as 9–11 years [15–18]. In the northern range of the species, first-time spawners were aged 3–6 years, averaging 4.5 years for males and 4.7 years for females. Total instantaneous mortality for male and female spawning alewives was 2.06 and 1.52 which corresponded to an annual mortality of 0.87 and 0.78, respectively [19]. After spawning, adults return to sea to forage in coastal waters <100 m depth during summer and along the continental shelf during winter [4, 13, 20, 21].

Along the eastern coast of the United States, the declining abundance of river herring triggered multiple states to impose moratoria on commercial and recreational fisheries. In Canada, however, abundance is considered stable and all commercial fisheries are active with no total allowable catch [4]. Of the 60 river populations of alewife in the Bay of Fundy, most fishing occurs in estuaries and rivers during annual spawning runs [22], with limited use of intertidal weirs in marine habitats [4, 7, 23]. Alewife bycatch associated with year-round midwater trawl fisheries for Atlantic herring (*Clupea harengus* Linnaeus, 1758) and Atlantic mackerel (*Scomber scombrus* Linnaeus, 1758) along the northwest Atlantic continental shelf is a considerable source of mortality [24, 25].

To address the knowledge gap in annual mature anadromous alewife survival, our study used biotelemetry to monitor alewife on annual spawning runs from 2013 to 2021 and an aged subsample of individuals captured during 2016–2019. We aimed to answer the following questions: (1) what are the apparent annual survival rates (the probability a marked individual survives the year and returns to the monitored rivers) and (2) does apparent annual survival vary by year, river, or sex?

## 2. Study Area

The La Coupe (LC), LaPlanche (LP), Missaquash (MS), and Tantramar (TM) rivers (45.84° N, 64.28° W) have their mouths situated <5 km straight-line distance apart along the

Chignecto Isthmus coast of the inner Bay of Fundy, Canada. Pairs of these rivers, the LC and TM and the LP and MS, share common mouths into Cumberland Basin (Figure 1). Estuarine riverbanks are dyked and the semidiurnal tides with a maximum tide range of 14 m [26] are blocked in each river's main channel by tide gates installed between river km (rkm) 2 and rkm 5. During the 2016 LP spawning run, a new periodically submerged tide gate was operational at rkm 2 with the original submerged tide gate operating at rkm 5 until its removal that autumn [27]. Commercial alewife fisheries operated during annual spawning runs immediately downstream of tide gates in the LP, MS, and TM rivers, with the most effort occurring in the TM using gill nets. Fishing ceased in the LP during 2016 and the effort varied depending on the year in the MS using dip, gill, and trap nets (pers. obs. A. Spares). Upstream of each river's tide gate, the main channel is slow moving, deeply incised, <2 m deep, and <5 m wide until reaching a small-scale technical fishway (rkm 10–14) connecting to an upstream watershed characterized by multiple river branches, bogs, lakes, ponds, and human-made wetlands [28]. Limited fishing also occurred upstream of tide gates at culverts and fishway outlets (pers. obs. A. Spares).

## 3. Materials and Methods

**3.1. Sampling and Tagging.** During 2013–2021, from April to June, mature alewife were captured, measured, weighed, sampled for scales to age, sexed, PIT tagged, and released according to methods in Nau et al. [28] and Spares et al. [27]. Due to COVID-19, tagging was suspended in 2020 and resumed in 2021, albeit limited to the LC, MS, and TM rivers (Table 1). Individuals were captured by dip netting immediately downstream of an obstruction (tide gates) or fyke netted in shallow sections of the main river channel. Captured individuals were scanned with a hand-held portable PIT reader (Allflex Iso RFID model # RS20-3 or Oregon RFID data tracer FDX/HDX) to identify individuals previously tagged. Any individual tagged during a previous year was noted as a “recapture” with body fork length ( $L_F$ ), body mass, sex, and PIT ID recorded before release. Scales were collected from the first 30 individuals captured during each tagging session in the four study rivers during 2016–2019. Subsamples of the collected scales were later mounted between two glass slides and annuli were read according to methods outlined in Devries and Frie [29] and Marcy [30] using a projection microscope by two readers.

Most individuals were released at capture sites; however, some were released immediately upstream of the tagging site obstruction to facilitate fish passage experiments further upstream. Tagging sites ranged from rkm 2 to 19 depending on environmental conditions, river, and year. Sites in the LC and LP rivers were relocated multiple times downstream during 2015–2021. Tagging sites in the MS and TM rivers were the same throughout the entire study (Table 1).

During the study, captured alewife from concurrent research fishing and subsamples of commercial fisheries catch were also counted and scanned for recaptures in the LC, MS, and TM rivers during May–June in 2016–2019

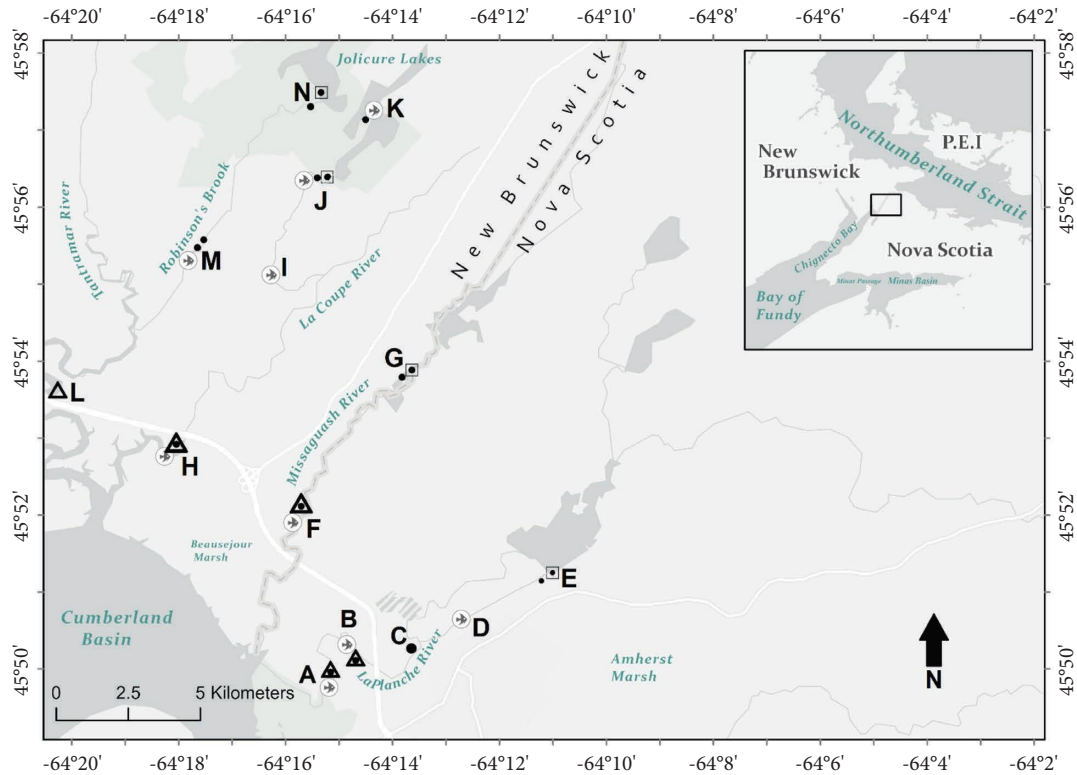


FIGURE 1: Chignecto Isthmus study area (open square in the insert map) showing PIT tracking antenna arrays (●) during 2013–2021 at fishways (□) and tide gates (Δ). The fish symbol in white circle indicates fishing and tagging sites during 2013–2021. LaPlanche tide gate (A); old LaPlanche tide gate (B); 2017 La Planche river cross-section array (C); 2013 LaPlanche river tagging site (D); LaPlanche river cross-section and fishway arrays (E); Missaquash tide gate (F); Missaquash cross section and fishway arrays (G); La Coupe tide gate (H); 2014–2018 La Coupe tagging site (I); La Coupe cross-section, fishway, and upstream arrays and 2013 tagging site (J); Tantramar tide gate (L); Robinson's Brook culvert (M); rockway/nature-like fishway (N); Prince Edward Island, P.E.I.

(Table 2). An individual recaptured and/or detected with RFID monitoring in the study area was considered present.

**3.2. Biotelemetry.** During 2013–2019, radio frequency identification (RFID) biotelemetry arrays monitored six consecutive annual spawning runs in the LC, LP, and MS rivers generating an encounter history to estimate detection and survival rates of mature alewife. PIT ID, corresponding timestamp, and antenna number were recorded by each array's reader box with data uploads occurring every three days or at the next opportunity. Two or more detections determined the presence of any individual, with PIT ID cross-referenced with known removals in previous years (commercial fishing captures) before an individual was marked as "present."

Depending on annual environmental conditions and deployments, arrays monitored from the head of tide (tide gate, [27]) to spawning sites (Long Lake, [31]) from April to July. Each river had a minimum and maximum of two and seven antennas, respectively, that individual alewife had to swim past to reach spawning sites (Table 3). Tide gates (rkm 2–5) were monitored only during 2015–2018 [27]. River channel cross-section arrays, consisting of one or two antennas arranged in a coplanar window, monitored <150 m downstream of each fishway in the LC, LP, and MS during

2015–2021. In 2017 only, the LP cross-section array was relocated to rkm 8. Fishways were monitored in the LC, LP, and MS during 2013–2019 and LC and MS in 2021, with each array consisting of four consecutive antennas monitoring baffle notches at and near the downstream outlet and upstream inlet of the fishway. Monitoring of the TM occurred in Robinson's Brook at a perched culvert (rkm 19; two consecutive antennas in 2018 and three consecutive antennas in 2019), a nature-like fishway (rkm 25; three consecutive antennas in 2018 and two consecutive antennas in 2019), and a river channel cross section (rkm 26; one antenna in 2019). In 2021, only the nature-like fishway array was operated (two antennas, Table 3). Detection of returnees by TM arrays enabled cumulative return rates for one to three years post tagging.

### 3.3. Analyses

**3.3.1. Morphometrics.** Shapiro–Wilk normality and Levene's tests on alewife body fork-length sample distribution and homoscedasticity, respectively, were used to determine parametric or nonparametric comparisons. Either a Student's *t*-test or Mann–Whitney *U*-test was used for male and female samples, and an ANOVA post hoc Tukey's or Kruskal–Wallis post hoc Dunn's tests for the four river

TABLE 1: Year, river, location (river kilometer, rkm) relative to river mouth (rkm 0), period and the number ( $n$ ) of alewife (*Alosa pseudoharengus*) tagged, or recaptured following one or more years at large, during 2013–2021 tagging sessions. The number of returning individuals detected (returnees) with RFID biotelemetry arrays in the LaPlanche (LP), La Coupe (LC), Missaquash (MS), and Tantramar (TM) rivers are presented for 2014–2019 and 2021. Fieldwork was suspended in 2020 due to COVID-19 restrictions.

Years	Rivers	Tagging (rkm)	Tagging periods	$n$ tagged	$n$ recaptures	$n$ returnees
2013	LC	14	10–27 May	406	—	—
2013	LP	9	3–27 May	376	—	—
2013	MS	5	8–27 May	416	—	—
2013	TM	19	1–19 Jun	191	—	—
2014	LC	14	18–28 May	283	5	161
2014	LP	9	18–31 May	477	0	100
2014	MS	5	29 May–5 Jun	361	1	92
2015	LC	12	20 May–4 Jun	379	4	167
2015	LP	5	21 May–10 Jun	649	2	104
2015	MS	5	22–28 May	242	0	130
2016	LC	12	30 Apr–6 Jun	414	3	181
2016	LP	2, 5	1 May–7 Jun	594	1	290
2016	MS	5	24 Apr–8 Jun	635	1	101
2017	LC	12	17 May–12 Jun	313	1	35
2017	LP	2	5 May–2 Jun	436	0	369
2017	MS	5	8–31 May	752	1	184
2018	LC	12	16–23 May	200	1	81
2018	LP	2	27 Apr–23 May	199	2	300
2018	MS	5	24 Apr–16 May	401	3	270
2018	TM	19	4–24 May	394	0	30 <sup>†</sup>
2019	LC	12, 3	17 May–6 Jun	203	2	25
2019	LP	2	5–29 May	204	0	152
2019	MS	5	1 May–4 Jun	386	3	166
2019	TM	19	9 May–25 Jun	359	0	22 <sup>‡</sup>
2021	LC	3	7 May–17 Jun	216	1	68
2021	MS	5	4–29 May	388	0	81
2021	TM	19	7 May–16 Jun	337	0	11 <sup>§</sup>
2013–2021			24 Apr–25 Jun	10,211	31	3,120

<sup>†</sup>Returnees were tagged in the LC ( $n=6$ ), LP ( $n=11$ ) and MS ( $n=13$ ) rivers during 2014–2017. <sup>‡</sup>Returnees were tagged in the TM during 2018 ( $n=18$ ) and in the LP ( $n=1$ ) and MS ( $n=3$ ) rivers during 2017 and 2018. <sup>§</sup>Returnees were tagged in the TM ( $n=11$ ) during 2018 and 2019.

TABLE 2: Recaptures of alewife (*Alosa pseudoharengus*,  $n=15$ ) by commercial or research fishing following one or more years at large post tagging showing the recapture year, river, location (river kilometer, rkm) relative to river mouth (rkm 0), sampling period (dd mmm), and the number of individuals sampled ( $n=13,044$ ) during 2016–2019 in the La Coupe (LC), Missaquash (MS), and Tantramar (TM) rivers on the Chignecto Isthmus, Canada.

Years	Rivers	rkm	Sampling periods	$n$ sampled	$n$ recaptures
2016	MS	5	11 May–12 Jun	2,691	0
2017	LC	17	4 Jun	15	1
2017	MS	5	14 May–2 Jun	4,567	4
2018	MS	5	1 May	1,398	8
2018	LC	17	10 May–27 Jun	202	0
2018	MS	5	25 Apr	30	0
2019	MS	5	5–23 May	2,124	2
2019	TM	7	22 May	2,017	0

populations [32]. Results were considered statistically significant at  $p < 0.05$ . All means were presented with  $\pm$ one standard deviation.

3.3.2. *Return Rates.* Return rates based on river or sex were estimated as  $r_{x+1}/n_x$ , whereas the number of individuals returning ( $r$ ) to be detected during subsequent spawning runs ( $x+1, \dots, x+6$ ) was divided by the number tagged ( $n$ ) during each cohort's spawning run ( $x$ ). The river where an

individual was tagged was assumed to be its natal river when estimating river-specific return rates.

3.3.3. *Capture-Mark-Recapture (CMR).* For the LC, LP, and MS rivers from 2013 to 2019, a period of consistent tagging and detections, we produced encounter histories, which are summaries for each fish representing the time when it was initially marked and the occasions of all subsequent detections. These encounter histories are simply a string of

TABLE 3: Monitoring periods using radiofrequency identification (RFID) biotelemetry arrays described by year, river, and river kilometer (rkm) location relative to river mouth (rkm 0) in the LaPlanche (LP), La Coupe (LC), Missaquash (MS), and Tantramar (TM) rivers during 2014–2021 on the Chignecto Isthmus, Canada.

Years	Rivers	River (km)	<i>n</i> antennas	Monitoring periods
2014	LP	11	4	15 May–19 Jul
2014	MS	11	4	28 May–19 Jul
2014	LC	15	4	15 May–19 Jul
2015	LP	11	6	18 May–27 Jul
2015	MS	11	4	19 May–27 Jul
2015	LC	15	5	16 May–27 Jul
2016	LP	2, 5, 11	7	9 Apr–11 Jul
2016	MS	6, 11	6	10 Apr–11 Jul
2016	LC	4, 15	6	19 Apr–11 Jul
2017	LP	8, 11	5	11 Apr–12 Jul
2017	MS	6, 11	6	11 Apr–12 Jul
2017	LC	15, 17	6	14 Apr–12 Jul
2018	LP	11	5	8 Apr–11 Jul
2018	MS	6, 11	6	7 Apr–12 Jul
2018	LC	15	5	9 Apr–11 Jul
2018	TM	19, 25	5	30 Apr–12 Jul
2019	LP	11	5	18 Apr–11 Jul
2019	MS	11	5	12 Apr–12 Jul
2019	LC	15	5	18 Apr–2 Aug
2019	TM	19, 25, 26	6	3 May–11 Jul
2021	LC	15	6	5 May–7 Jul
2021	MS	11	5	1 May–7 Jul
2021	TM	25	2	5 May–7 Jul

zeros and ones, where the length of the string is the number of occasions (years in this study) when captures/detections occurred [33, 34]. When a fish is marked or detected, it receives a 1 in the string and 0 if it is not detected. For example, an encounter history of 1011000 would indicate a fish marked in year 1 (2013 in this study), not detected in 2014, detected in 2015 and 2016, and not detected afterwards. Although this fish was last known to be alive in 2016, it may have survived much longer and was simply not detected in later years. Capture-mark-recapture (CMR) analyses account for this process by estimating detection rates from individuals known to be alive at specific time periods and then “correcting” survival rates for the lack of detection. All encounter histories are modeled as a joint multinomial likelihood, each with a probability based on combinations of time-specific survival and detection rates derived from the encounter history (see [35] for more details). Multiple detections in one year were ignored and were simply recorded as a single detection in that year. CMR analyses are predicated on discrete sampling occasions (short windows of time when all marking and detections occur) and intervals (the much longer periods between sampling occasions). Often the interval is one year (as it was with this study), especially when individuals are marked during specific life history events when they are vulnerable to capture, marking, and detection (spawning migration). Exposure period is therefore the interval, which is assumed to be one year in this study, regardless of exactly when an animal was marked or detected within a sampling occasion.

More formally, in CMR analyses, two parameters were estimated: the apparent survival rate ( $\phi$ ), defined as the probability of an animal surviving the preceding year and

returning to the study site and the detection rate ( $p$ ), which is the probability of detecting a marked individual given that an individual is alive and in the study area [35]. The RMark package [36] in R v 4.1.2 [37] which is based on the comprehensive CMR analysis program MARK [38] was used to fit models and obtain parameter estimates.

An underlying assumption of basic CMR analysis is that when individuals are first captured or last detected will not affect survival or detection rates, and this assumption was assessed using the package R2ucare [39]. We used R2ucare to examine capture histories to assess whether individuals demonstrated time since marking (tsm) effects (TEST.3sr), where survival in the first year after marking differed from survival in subsequent years. Furthermore, we used TEST.2ct to look for evidence of trap effects, which are differences in detection rates dependent on when the animal was last captured.

Following the general approach outlined in Lebreton et al. [35] a range of models with different parameterizations of  $\phi$  and  $p$  were fit to the data, including allowing both parameters to vary by year  $t$ , across the three rivers, and by the interaction between those variables. Additionally, if support for a time since marking effect was indicated by TEST.3sr,  $\phi$  was modeled with a tsm effect in the year immediately following marking. Time since marking effects are common in fishery tagging studies and generally reflect tagging-induced mortality [40]. Reduced parameter models in both  $\phi$  and  $\mathcal{P}$  were constructed, including additive effects between the year  $t$  and the river and only main effects.

The model with the lowest AIC value was selected for inference [41]. All parameters and effect sizes are presented

with 95% profile likelihood intervals. If highly parameterized models, such as multiplicative models, showed the best compromise between fit and numbers of parameters, annual means marginalized over the three study rivers and river-specific means marginalized over the years of study were calculated. These means were calculated by assuming that each river or year contributed equally to the overall mean. Total instantaneous mortality ( $Z = -\ln(\phi)$ ) and mean expectation of future life ( $1/\ln(\phi)$ ) were calculated for comparisons with other studies.

Sex was only recorded in the later years of the study (2016–2019) and was challenging to include in the initial model set because year  $t$  and sex were confounded. To examine whether there was an effect of sex on apparent survival, an additive effect of sex (including a third level of unknown for all fish tagged in 2013–2016) was added to the best fitting model selected by AIC.

**3.3.4. Total Instantaneous Mortality ( $Z$ ).** Total instantaneous mortality ( $Z$ ) of known-age alewife captured in the four rivers was estimated using a plot of  $\log_e$ -transformed number of individuals per year class by age according to Ricker [42].

$$Z = -\frac{(\log_e Nt_2 - \log_e Nt_1)}{t_2 - t_1}, \quad (1)$$

where  $\log_e Nt_2$  is the number of individuals of age  $t_2$ ,  $\log_e Nt_1$  is the number of individuals of age  $t_1$ , and  $t_2 - t_1$  is the period in years between the two age groups. A slope was generated by the analysis representing  $Z$  for the age distribution of pooled adults that were aged 4–6, excluding individuals at age 3 as age 4 represented 100% recruitment to the spawning run demographics.

## 4. Results

**4.1. Morphometrics and Biotelemetry.** From April to June in 2013–2021, alewife with a mean  $\pm$  SD body fork-length of  $230 \pm 18$  mm (range 175 to 310 mm;  $n = 10, 211$ ; Figure 2) were tagged in the four study rivers (Table 1). The tag/body mass ratio was  $0.4 \pm 0.1\%$  (range 0.1 to 0.9%;  $n = 8,991$ ). The mean body fork length of alewife tagged in the LC and TM rivers were significantly longer than those tagged in the LP and MS (ANOVA,  $F = 67.3$ ,  $df = 3$ ,  $p \leq 0.001$ ; Figure 2). Females ( $n = 2,480$ ) were significantly longer than males ( $n = 2,847$ ;  $t$ -test;  $df = 5,325$ ;  $t$ -stat =  $-36.04$ ,  $p \leq 0.001$ ; Figure 3).

In situ testing revealed that RFID monitoring detection fields were capable of detecting a PIT tag placed within 30 cm of the antenna wire loop and through an air and water interface. Coplanar window arrangements often simultaneously recorded a PIT tag held near two adjacent antennas.

**4.2. Recaptures.** Forty five alewife tagged in the previous years were recaptured during tagging sessions in 2014–2019 and 2021 and in the MS commercial fishery in 2016–2019. One individual was recaptured during two consecutive years in the LC following its tagging in the MS. Recaptures

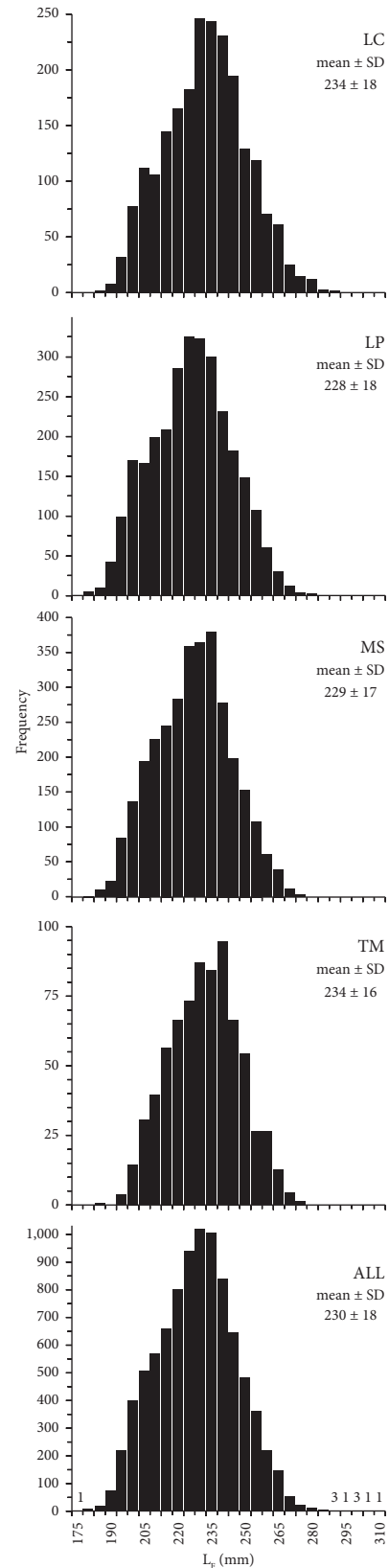


FIGURE 2: Fork length ( $L_f$ ; mm) histograms of adult alewife *Alosa pseudoharengus* tagged ( $n = 9,079$ ) during consecutive spawning runs in the La Coupe (LC;  $n = 2,198$ ), LaPlanche (LP;  $n = 2,933$ ), and Mis-saquash (MS;  $n = 3,195$ ) rivers during 2013–2019 and in the Tantramar river (TM,  $n = 753$ ) during 2018–2019, Chignecto Isthmus, Canada.

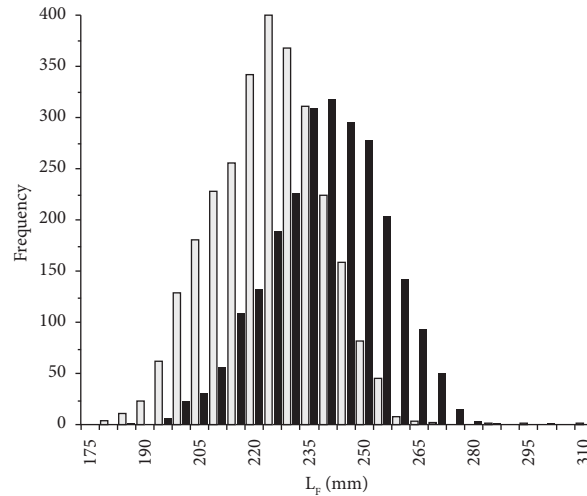


FIGURE 3: Fork length ( $L_F$ ; mm) histograms of male ( $\square$ ;  $n = 2,847$ ) and female ( $\blacksquare$ ;  $n = 2,480$ ) adult alewife *Alosa pseudoharengus* tagged during consecutive spawning runs in the La Coupe (LC), LaPlanche (LP), and Missaquash (MS) rivers during 2016–2019 and in the Tantramar river during 2018–2019, Chignecto Isthmus, Canada.

TABLE 4: Mature alewife *Alosa pseudoharengus* recaptured after one or more years-at-large during 2014–2022 following tagging in the La Coupe, LaPlanche, and Missaquash rivers during 2013–2019 and La Coupe and Missaquash rivers during 2021, Chignecto Isthmus, Canada.

PIT IDs	Tagging $L_F$ (mm)	$\Delta L_F y^{-1}$ (mm)	Years at large	Recapture rivers
<i>La Coupe</i>				
900228000279484 <sup>a</sup>	218	16	1	LC
900228000176290	220	21	1	LC
900228000176304	221	26	1	LC
181603055	225	24	1	LC
181626074	228	26	1	LC
900228000603849	230	8	1	LC
900228000275850	234	—	1	LC
181625865	239	6	1	LC
181603076	240	1	1	LC
181603017	240	4	1	LC
181625872	241	4	1	LC
181602983	245	5	1	LC
900228000707257	252	3	1	LC
900228000707201	255	5	1	LC
900228000279422	208	8	2	LC
181626071	220	7	2	LC
900228000574221	236	10	2	MS
900228000279478	213	6	5	LC
<i>LaPlanche</i>				
900228000290180	192	30	1	MS
900228000285878	230	3	1	MS
900228000290317	232	11	1	LP
900228000285864	233	12	1	MS
181626113	245	2	1	LP
181624610	213	13	2	LP
900228000279142	220	10	2	MS
900228000524311 <sup>b</sup>	225	—	2	LP
<i>Missaquash</i>				
900228000571530	189	17	1	MS
900228000574686	201	16	1	MS
181625008 <sup>c</sup>	203	16	1	LC
900228000040638	216	—	1	MS
900228000603627	225	17	1	MS

TABLE 4: Continued.

PIT IDs	Tagging $L_F$ (mm)	$\Delta L_F y^{-1}$ (mm)	Years at large	Recapture rivers
900228000279284	228	12	1	MS
181624694	232	-4	1	MS
900228000602832	232	19	1	MS
900228000290124	234	13	1	MS
900228000571891	235	10	1	MS
900228000290593	235	11	1	MS
900228000571699	238	15	1	MS
900228000602984	239	15	1	MS
900228000571989	245	15	1	MS
900228000290377	247	—	1	MS
900228000602864	255	6	1	MS
181625008 <sup>c</sup>	203	20	2	LC
181624787	217	10	2	LP
900228000279256	243	9	2	MS
900228000290086	251	5	2	MS

Note. <sup>a</sup>Individual tagged in the LC and recaptured one year later in the MS (24 May 2017) and LC (5 June 2017). <sup>b</sup>Individual tagged in the LP and recaptured two years later in the MS (2 May 2018) and LP (16 May 2018). <sup>c</sup>Individual tagged in the MS river and recaptured in the LC during the next two annual spawning runs, growth per year was calculated using measurements taken during each recapture event.

revealed movement between the study rivers during annual spawning runs and interannually (Table 4). The encounter history of one individual in the LC tagged during 2014 revealed it returned in 2015, 2016, and 2021.

**4.3. Return Rates.** Return rates for all tagged individuals decreased exponentially with increasing years-at-large. The pooled return rates in the LC, LP, and MS rivers decreased from 27% for one year-at-large to  $\leq 1\%$  for four or more years-at-large. The TM had a return rate of 5% for one year-at-large, with only 18 individuals detected in 2019 of the 394 individuals tagged in 2018. Compared to the LC, LP, and MS rivers, TM return rates were more than four times lower, with  $\leq 1\%$  return rates occurring after two years-at-large (Figure 4). Higher return rates were observed for males versus females after one year-at-large; however, this sex effect changed with increasing years-at-large. Return rates varied by rivers, with the TM, LC, MS, and LP ranked lowest to highest, respectively, in 2016–2019 (Figure 5).

**4.4. Capture-Mark-Recapture (CMR).** Goodness of fit testing supported a time since marking effect (TEST.3sr,  $\chi^2 = 69.9$ ,  $df = 5$ ,  $p \leq 0.001$ ), while there was no evidence of trap effects (TEST.2ct,  $\chi^2 = 6.6$ ,  $df = 5$ ,  $p = 0.16$ ). A tsm effect on  $\phi$  was therefore included in all models. Model  $\phi_{\text{tsm}+t*\text{river}}, p_{t*\text{river}}$  with an additive tsm effect and multiplicative effects of year  $t$  and river on  $\phi$ , and an interaction between year  $t$  and river on detection rate  $p$ , was highly supported with 99% of model weight. The tsm effect ( $\beta = 0.367$ , 95% PLI:  $-0.253$  to  $-0.480$ ) did not bound zero and amounted to a reduction in survival of 0.08 in the year following marking. Annual detection rates were generally high for the LP and MS rivers (0.89–0.98), while on the LC River, detection rates were high but more variable than the other rivers in 2014–2016 (0.76–1.00) and then declined to 0.17 and 0.37 in 2017 and 2018, respectively. Annual

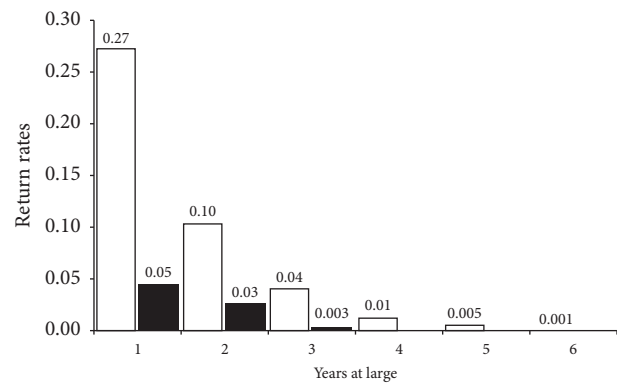


FIGURE 4: Cumulative return rates of mature, anadromous alewife *Alosa pseudoharengus* post PIT-tagging during 2013–2019 for the La Coupe, LaPlanche, and Missaquash rivers (□;  $n = 7,533$  tagged) and 2018–2021 for the Tantramar river (■;  $n = 394$  tagged 2018,  $n = 359$  tagged 2019), Chignecto Isthmus, Canada.

survival rates ranged from 0.25 to 0.50 depending on the river and year (Figure 6), with an overall annual survival based on all rivers and years of 0.396 (95% PLI: 0.367–0.425, Table 5). These discrete time survival rates convert to total instantaneous mortality rates ( $Z$ ) averaging 0.93, which leads to an expectation of future life averaging 1.08 years (or one additional spawning season, on average, Table 5). A sex effect on  $\phi$  was added to the model  $\phi_{\text{tsm}+t*\text{river}}, p_{t*\text{river}}$ , which included an unknown level for the years when fish were not sexed (2013–2015). Males had a higher survival rate compared to females ( $\beta = 0.205$ , 95% PLI: 0.068–0.342), which translated into an overall mean survival increase of 0.05.

**4.5. Ageing and Total Instantaneous Mortality.** A subsample of 384 individuals representing 7.0% of alewife tagged during 2016–2019 was aged from 3 to 6 years. The mean  $\pm$  SD age was  $4.2 \pm 0.7$  years and  $4.5 \pm 0.7$  years for



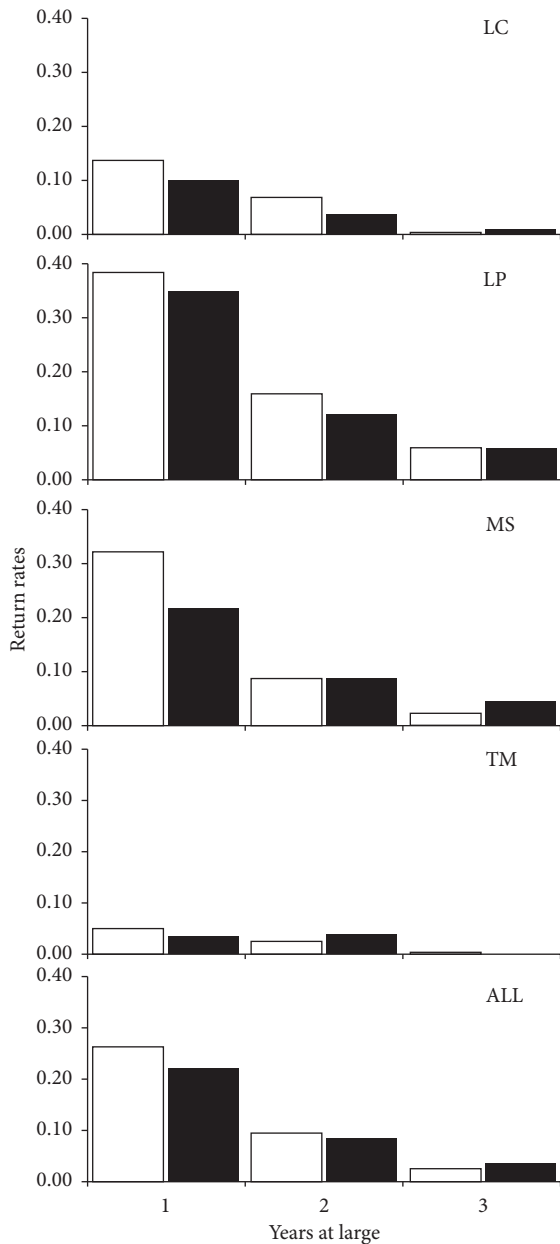


FIGURE 5: Cumulative return rates of mature male ( $\square$ ) and female ( $\blacksquare$ ) anadromous alewife *Alosa pseudoharengus* monitored for one to three years at large during 2016–2019 in the La Coupe (LC), LaPlanche (LP), and Missaquash (MS) rivers and in the Tantramar river during 2018–2019 and 2021 and cumulative for all four rivers during 2016–2021 on the Chignecto Isthmus, Canada.

males ( $n = 232$ ) and females ( $n = 152$ ), respectively, with males being younger than females ( $t$ -test,  $t = -3.6$ , and  $p < 0.001$ ; Figure 7). First-time spawners ( $n = 321$ ) were 3–5 years old. Females were significantly longer at age compared to males ( $p < 0.01$ , Figure 8). Estimated  $Z$  based on the frequency distribution of ages 4–6 for alewife pooled from all four study rivers was 1.20 ( $r^2 = 0.81$ , Figure 9), resulting in an estimated annual survival rate of

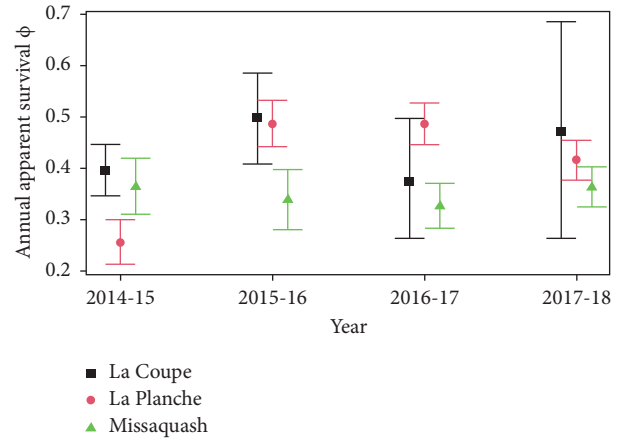


FIGURE 6: Capture-mark-recapture estimates of apparent annual survival ( $\phi$ ) during 2014–2018 for mature alewife *Alosa pseudoharengus* in the La Coupe ( $\blacksquare$ ), LaPlanche ( $\bullet$ ), and Missaquash ( $\blacktriangle$ ) rivers on the Chignecto Isthmus, Bay of Fundy, Canada.

0.301 and future life expectancy of 0.83 years from time of release.

## 5. Discussion

**5.1. Annual Life History Survival.** In general, survival and the ability of fish to avoid predators increases with size [43]. Considering the size range (135 mm) of alewife in our study, mature adults would most likely experience similar natural predation, such as Striped bass (*Morone saxatilis* Walbaum, 1792) in estuaries [27] or Atlantic bluefin tuna (*Thunnus thynnus* Linnaeus, 1758) in continental shelf waters [44]. Anthropogenic-related mortality caused by fisheries or river obstructions may be size-selective for adult alewife [24, 25, 27, 28]. Opposing size selection of these two mortality vectors may mute a cumulative survival effect, such as smaller individuals may possibly swim through a gill net mesh size targeting larger individuals [45] and fail to pass more difficult anthropogenic obstructions resulting in delayed mortality [46, 47].

CMR analysis detected a reduction in survival (0.08) in the year after tagging, which is possibly an indication of tagging-induced mortality and/or tag expulsion [48]. There was still a notable decrease in return rates and survival following one year-at-large, suggesting an age effect. Unfortunately, based on the relatively small subsample of individuals in this study, age was not incorporated into CMR analyses.

Spawning survival was based on the limited analysis of newly tagged alewife during 2013 in the LP and MS, and in 2018 and 2019 in the TM, and varied from 0.72 to 0.94 ([49]; unpublished data Aaron Spares). Marine mortality most likely affects populations equally [50] as stocks are well mixed while at sea [4]. Acoustic tracking of post-spawned alewife revealed tidal displacements increasingly separated individuals moving from the Gaspereau River mouth

TABLE 5: Apparent annual survival rates ( $\phi$ ), total instantaneous mortality ( $Z$ ), and mean expectation of future life (years) with 95% lower (LCL) and upper (UCL) confidence limits estimated using capture-mark-recapture analyses for adult alewife *Alosa pseudoharengus* PIT tagged and monitored during consecutive spawning runs from 2013–2019 in the La Coupe (LC), LaPlanche (LP), and Missaquash (MS) rivers, Chignecto Isthmus, Canada.

	$\phi$	$\phi$ LCL	$\phi$ UCL	$Z$	$Z$ LCL	$Z$ UCL	Future life (years)	LCL	UCL
LC	0.434	0.371	0.500	0.83	0.69	0.99	1.20	1.01	1.44
LP	0.343	0.228	0.403	1.07	0.91	1.48	0.93	0.68	1.10
MS	0.348	0.320	0.377	1.06	0.98	1.14	0.95	0.88	1.03
2014	0.336	0.304	0.370	1.09	0.99	1.19	0.92	0.84	1.01
2015	0.441	0.399	0.483	0.82	0.73	0.92	1.22	1.09	1.37
2016	0.394	0.347	0.442	0.93	0.82	1.06	1.07	0.94	1.22
2017	0.417	0.341	0.496	0.87	0.70	1.08	1.14	0.93	1.43
OVERALL	0.396	0.368	0.425	0.93	0.86	1.00	1.08	1.00	1.17

Note. Marginal means, treating each river, year or both as contributing equally to the overall mean.

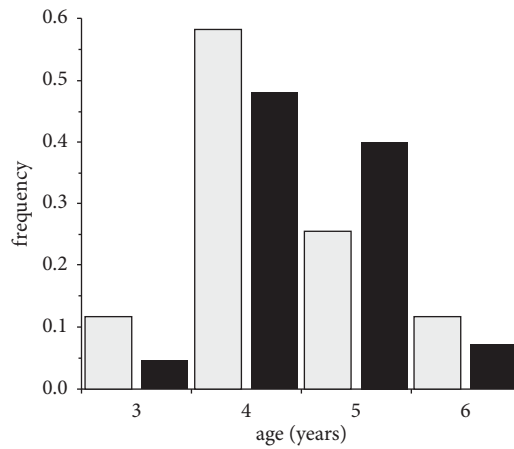


FIGURE 7: Age (years) histograms of male ( $\square$ ;  $n = 232$ ) and female ( $\blacksquare$ ;  $n = 152$ ) adult alewife *Alosa pseudoharengus* captured during spawning runs in the La Coupe (LC), LaPlanche (LP), Missaquash (MS), and Tantramar (TM) rivers during 2016–2019 on the Chignecto Isthmus, Canada.

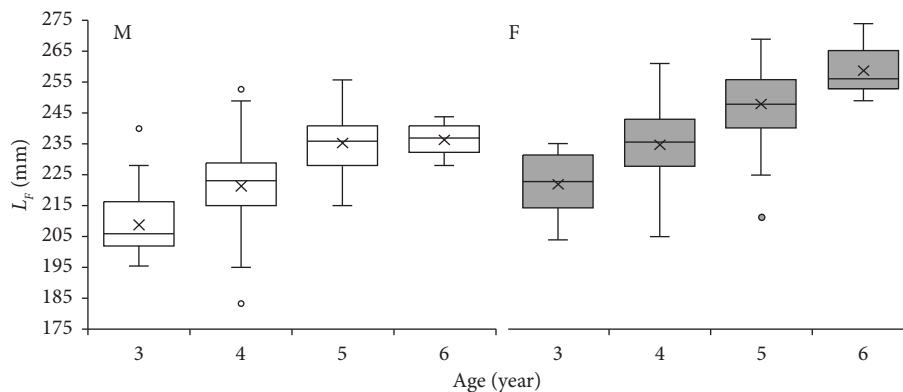


FIGURE 8: Mean ( $x$ ) and median ( $-$ ) fork length ( $L_f$ , mm) at age 3–6 years for male ( $\square$ ;  $n = 232$ ) and female ( $\blacksquare$ ;  $n = 152$ ) adult alewife *Alosa pseudoharengus* captured during spawning runs in the La Coupe (LC), LaPlanche (LP), Missaquash (MS), and Tantramar (TM) rivers during 2016–2019 on the Chignecto Isthmus, Canada. Box ends ( $\square$ ) and whiskers ( $\Upsilon$ ) represent interquartile range and minimum and maximum values, respectively. Outliers are denoted by  $\circ$ .

towards the outer Bay of Fundy (Figure 1; [10]). Apparent survival during a relatively short distance ( $\sim 7.5$  km) one-day downstream migration from the river tagging site to the

Gaspereau River mouth was 0.76 [10]. Once in the marine environment, survival decreased a further 35% for an apparent survival of 0.41 for alewife detected in Minas Passage,

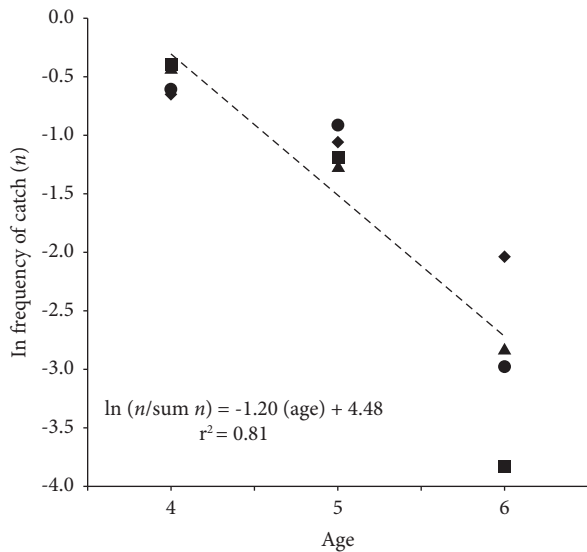


FIGURE 9: The  $\log_e$ -transformed ( $\ln$ ) frequency of catch at age (years) for adult alewife  $n = 363$ ,  $\ln(n/\text{sum } n) = -1.20(\text{age}) + 4.48$ ,  $r^2 = 0.81$ , ----) sampled during 2016–2019 in the La Coupe ( $n = 46$ , ■), LaPlanche ( $n = 137$ , ●), Missaquash ( $n = 134$ , ▲), and Tantramar ( $n = 46$ , ◆) rivers of the Chignecto Isthmus, Bay of Fundy, Canada. Total instantaneous mortality of  $Z = 1.20$  for fish aged four–six years.

a distance of 30 km from the river mouth [10]. If one assumes high survival and tag retention for alewife post surgery [48, 51], spawning and early summer marine migration survival rates may be 0.31–0.53 ([10, 49]; unpublished data Aaron Spares). These survival estimates agree with our annual survival results (0.25–0.50); however, there is no accounting for survival from autumn to spring, which may include fishery-related mortality in the ocean and estuaries [4, 7, 22–25]. It is unclear exactly where the inner Bay of Fundy alewife populations overwinter [50] and what natural and/or fishery-related mortality they may experience [24, 25].

**5.2. Maximum Age and Iteroparity.** The maximum age of alewife has been recorded as greater than 10 years [16]. In our study, one unsexed individual tagged in 2014 and detected in 2021 revealed that eight spawning runs may have been undertaken if this individual was tagged as a first-time spawner. If tagged as a first-time spawner at 6 years old [19], this individual would have been 13 years old. Aging in our study, however, revealed first-time spawners were 3–5 years old, and the tagging  $L_F$  of 225 mm suggested that this individual was <5-years-old at tagging, thus seven years post-tagging would age this individual at 10 or 11 years.

Repeat spawners were reported as dominating spawning runs in a Connecticut, USA, study during the 1960s but have since been replaced by mostly first-time spawners [52]. Heavily impacted stocks have shown spawning runs with <10% repeat spawners, such as the Gaspereau River, Bay of Fundy, where up to 89% of the spawning run has been

exploited [19]. In our study, most migrants were first-time spawners, but approximately 37% were repeat spawners in the LP and MS rivers (aged 4–6 years old, unpublished data Aaron Spares) which supported our return rate results and observations that these two rivers were less impacted.

**5.3. River-Specific Survival.** Return rates were notably different between rivers in our study. When accounting for detection, apparent survival rates during 2014–2018 across the LC, LP, and MS rivers indicated an overall mean of 0.396, but with both annual and inter-river variation. Interestingly, the pattern of annual variation was not consistent among rivers, which suggested temporal and river-specific drivers. For example, in the LP, the consistently higher apparent annual survival from 2016 onwards may have been related to the mitigation of the new tide gate and cessation of estuarine fishing [27]. In the MS, commercial fishing occurred throughout the study period, and this likely was related to the lower, consistent apparent annual survival rates. Lower return rates in the LC during the later years of our study were confirmed by CMR analysis and the large decrease in detection rates was most likely related to a malfunctioning tide gate preventing upstream passage of returning migrants. This was further supported by an individual tagged in 2014 that went undetected during 2017–2019 before last detected in 2021.

The low return rates of the TM population were concerning, yet not surprising considering the fishery is the largest in the study area. Periodic closure of the TM tide gate may have increased the chance of capture as upstream-moving migrants would be delayed in the estuary until opening of the gate (pers. obs. Aaron Spares). Considering the gill net fishery, periodically closed tide gate and other anthropogenic obstructions in the TM, such as the perched culvert in Robinson's Brook (pers. obs. Aaron Spares), higher mortality would be expected compared to the other three study river populations. Another factor to consider with lower TM return rates is that returning tagged individuals may have used the main river branch and its spawning habitat during subsequent runs instead of returning to Robinson's Brook where they were tagged.

The estimated annual survival rate of 0.301 based on the frequency distribution of ages 4–6 for alewife pooled from all four study rivers during 2016–2019 concurred with return rates. CMR analysis provided apparent survival estimates higher than return rates obtained from the cohort decay and frequency distribution of age analyses. CMR rates are likely a closer approximation of true survival considering the monitoring period for CMR spanned 2013–2019 whereas ageing spanned 2016–2019, a period that corresponded to decreased return and detection rates. CMR excluded the TM, whereas ageing analysis included this river, which may account for the lower estimated annual survival. If one considers active commercial fisheries and the cumulative negative effects of anthropogenic obstructions, river-specific return rates and apparent annual survival should mirror the most to the least impacted rivers. Our results agreed with

this as the TM, LC, MS, and LP rivers, respectively, had the lowest to highest return rates and apparent annual survival. Compared to the heavily exploited Gaspereau River in the Bay of Fundy ( $Z=1.51-2.06$ ; [19]), the pooled total instantaneous mortality result (0.93) for the LC, LP, and MS rivers in our study suggested lower exploitation.

**5.4. Sex-Related Survival.** Sex-related annual survival rates were lower for male alewife than females in the Gaspereau River, Bay of Fundy [19]. However, in our study, male survival was consistently higher than females. Greater survival of males may be related to the higher passage success of anthropogenic obstructions for males relative to similarly sized females [28]. Also, the larger mean length of spawning females may have increased the chance of capture in the gill net fisheries ([45]; pers. obs. Aaron Spares). During lake spawning in our study area, both sexes fed; however, males maintained their body condition as in estuaries during the start of the spawning run, whereas female body condition decreased by 9.4% because of egg release from their larger ripe gonads [31]. This decrease in body condition of females during spawning runs may have accounted for some of the difference in apparent annual survival between the sexes.

**5.5. Sources of Error.** Our estimates may have incorporated many factors influencing mature alewife survival from release following tagging to detection during subsequent monitored spawning runs. For example, if an individual alewife survived tagging during its upstream spawning run migration to be detected during the next year's spawning run, life history events such as upstream migration, spawning, downstream emigration, marine feeding, and homing to spawning rivers and anthropogenic factors such as commercial fishing [4, 24] or plastic ingestion while feeding [31], may be included.

The authors acknowledge varying number of deployed RFID antennas and monitoring periods may have altered the probability of detection and this may have influenced return rates and survival estimates. However, detection rates were accounted for as part of the CMR analysis. Also, during the estimation period, monitoring was relatively consistent with any individual alewife reaching potential spawning sites needing to swim through 4–7 antennas deployed in each of the three rivers used for the analysis. In 2021, only two antennas were deployed in the TM upstream of a perched culvert known to delay and prevent upstream passage (17% passage rate, unpublished data Aaron Spares), thus returnees may not have been as likely to be detected compared to six antennas in 2019 with one antenna monitoring immediately downstream of the culvert. This known obstacle may have decreased the detection of returnees and consequently, return rates. However, considering similar numbers of alewife were tagged in the TM during 2018 and 2019 ( $n = 394$  and  $n = 359$ ,

respectively), and based on the number of returnees detected downstream and/or upstream of the culvert in 2019 following one year at large ( $n = 18$ ), the 10 individuals returning after two years and 1 individual returning following three years at large post tagging seemed reasonable as an exponential decrease in the number of returnees during subsequent years at large was demonstrated by consistent monitoring in the other three rivers.

Location of tagging sessions and RFID monitoring arrays may have also influenced survival estimates. For example, tagging locations in estuaries interrupted most individuals starting their upstream spawning migration; thus, these individuals still had to survive possible estuarine fishing, multiple anthropogenic obstacles, and spawning before returning to sea, whereas an individual tagged while finishing their spawning run would most likely have returned to sea following release. Monitoring arrays deployed at the upstream inlet of tide gates at rkm 2–6 may have had a higher probability of detecting returning individuals compared to monitoring arrays located further upstream as some individuals may have returned but died before reaching these upstream sites. However, once passing tide gates, upstream migration to subsequent arrays was usually accomplished by individuals within hours to days ([27]; unpublished data Aaron Spares). Most spawning migration mortality would have likely occurred downstream of tide gates in estuaries due to predation and commercial fisheries [27, 53, 54].

## 6. Conclusion

River herring populations have demonstrated a moderate to strong tendency to recolonize rivers within 100 to 200 km of a viable population [55]. In our study area, most interannual straying events occurred between the tagging river and the closest adjacent river [56]. Thus, recolonization of any one river population would most likely occur via the other populations.

Efforts to improve river connectivity in our study area occurred during 2014–2019, with LP tide gate mitigation [27], new LC and MS fishways ([28]; unpublished data Aaron Spares), and an improved rockway/nature-like fishway in the TM (unpublished data Aaron Spares). Without the cooperation of all stakeholders in a river system, efforts may yield minimal improvements for overall fish passage, spawning success, and survival. In the TM, for example, lower return rates may have been related to the cumulative negative impacts of anthropogenic obstructions (closed tide gate and perched culvert) and mortality vectors (estuarine gill net fishery <400 m downstream of the tide gate) when compared to the other study rivers. Alewife survivorship in our study highlighted that a limited ecosystem-based management period is required to mitigate river connectivity and mortality issues to avoid the loss of population cohorts and decrease the risk of extirpation [57].

## Data Availability

The data used to support the findings of this study are available from the corresponding author upon request.

## Conflicts of Interest

The authors declare that they have no conflicts of interest.

## Authors' Contributions

Aaron Spares, Nic McLellan, and Michael Stokesbury conceived and designed the protocol for data collection. Aaron Spares, Rachelle Vincent, Nic McLellan, and Michael Stokesbury performed the fieldwork. Aaron Spares, Gregory Robertson, Anna Calvert, Sarah Gutowsky, David Fifield, and Rachelle Vincent analyzed the data. Aaron Spares, Gregory Robertson, and Michael Dadswell wrote the manuscript. Nic McLellan and Michael Stokesbury secured the funding. All authors provided editorial advice.

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