Animal Biotelemetry

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Migration and apparent survival of post-spawning alewife (*Alosa pseudoharengus*) in Minas Basin, Bay of Fundy

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Abstract

The anadromous alewife is a commercially fished clupeid in Atlantic Canada, whose oceanic migration is poorly understood. Migration of alewives is presently investigated from the lower reaches of Gaspereau River into Minas Basin, Bay of Fundy. Seventy-five post-spawning adults were tagged on their downstream migration; within two days of being tagged, most alewives had left Gaspereau River and 57 entered into the Southern Bight of Minas Basin. Thirty-one alewives were detected in Minas Passage and their average time from tagging to final detection was 28 days with standard deviation of 11 days. None of the alewives were detected in Minas Passage until day 20 after the start of tagging. After day 20, the residence timescale in Minas Basin was only 8.8 days with 95% CI of 8.4–9.3 days. Fast tidal currents prevail in much of the study area, and alewives travelled many large tidal excursions in Minas Basin and Minas Passage. Separation distances between pairs of alewives increased greatly after day 20, indicating tidal mixing over large distances within the study area. Offshore movement was associated with seasonal warming, with alewives moving down the spatial temperature gradient and into deeper waters. Offshore, larger tidal displacements widely dispersed tagged alewives through Minas Basin and to Minas Passage. During transit of Gaspereau River, 18 ± 2 alewives were lost with corroborating evidence of mortality for 4 of these. By day 20, the apparent mortality within Minas Basin was ≤ 10 alewives. Individual alewives were observed to make many transits through Minas Passage during their migration, where they may become exposed to in-stream tidal turbines.

Keywords: Telemetry, Tracking, Survival, *Alosa*, Tidal energy, Bay of Fundy

Background

Alewives (*Alosa pseudoharengus*) are a pelagic forage fish in the family *Clupeidae* that are widely distributed along the Atlantic coast of North America, from the Gulf of St. Lawrence to North Carolina [53]. Collectively with blueback herring (*Alosa aestivalis*), they are known as river herring, and the two species overlap throughout much of their range. Alewives are dominant in many rivers of Maritime Canada and the eastern United States, supporting lucrative commercial and recreational fisheries throughout those regions [21, 33]. They are ecologically important as a prey species in both the marine and freshwater environments, and can serve as vectors for marine nutrient transport into inland waters [13, 52]. While some landlocked populations exist [7, 37, 38], most alewives are anadromous, and undertake seasonal spawning migrations cued by water temperature around 5–10 ˚C, returning to their natal rivers [12, 26]. Historically, alewives have been abundant across their range, but declining trends in run size have been observed in many rivers over the last decade, and average commercial landings today are less than 3% of the late 1960's peak [2, 21].

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Alewives are thought to feed in the continental shelf waters [35], but little is known about estuarine and oceanic movements during the juvenile and adult phases. The few studies that have described the migration of anadromous alewives focused on upstream, in-river movement [14, 32, 34]. This is in part due to their small body size and the perception that Clupeid fishes may be susceptible to stress, damage, and behavioral changes as a result of invasive handling procedures associated with acoustic tagging [16, 23, 44]. The journey from spawning rivers to the ocean is fraught with challenges, such as in-river damming [20] and bycatch in pelagic fisheries [5]. Tracking alewife migration is therefore of interest to improving management and answering pertinent research questions, such as passage efficiency around hydroelectricity dams [17].

One important freshwater habitat for alewives is Gaspereau River in the province of Nova Scotia, Canada. Gaspereau River is part of the Black River watershed and supports two hydroelectric generating stations, which are equipped with fish ladders and bypasses to allow upstream and downstream movement [26]. The status of the Gaspereau River alewife stock has been assessed intermittently since the early 1980s, and is currently managed based on estimates of escapement from a commercial fishery that targets fish in tidal waters at the start of their spawning run [17, 33]. In 2002, a 5-year management plan was implemented to address overexploitation from the 1980s and 1990s. This plan included reductions in fishing mortality and improvements in fish passage at the ladders, and the stock is now meeting the target escapement level of 400,000 spawners per season. There is no evidence that management efforts have increased longevity or incidences of repeat spawning [19, 33]. As of the latest stock assessment, this population has a mean annual run size (5-year average) of 594,918 individuals, and depends primarily on first-time spawners (age 4 and 5) [33]. This may be indicative of low post-escapement and/or post-spawning survival, and causes continued concern for the population.

Along with several large rivers in Nova Scotia, Gaspereau River drains into the Minas Basin—a broad macrotidal estuary at the head of the Bay of Fundy (Fig. 1). Minas Basin is linked to the rest of the Bay of Fundy by the relatively narrow (~ 5 km width) Minas Passage. Tidal current speeds during flood tide can reach 6 m/s in this area, making it of interest for the extraction of renewable energy [28]. In 2009, the Fundy Ocean Research Centre for Energy (FORCE) was established near the northern side of Minas Passage as a facility for the testing and development of in-stream tidal turbines. The FORCE site represents a small area within the Minas Passage (< 20% of the passage width) and the size of a single turbine is ~ 100 m^2 [40]. The Canada Fisheries Act requires that marine animals not be harmed when turbines are installed [15]. Several species have been documented using Minas Passage as a migratory corridor and feeding area [41, 48], however the present acoustic tracking study is the first for local Clupeid fishes. The volitional swimming speed of alewives, estimated around 5 body lengths/s against fixed flow velocities of 1.5–3.5 m/s, is not within an order of magnitude of typical flood and ebb currents in this region [9, 22], so it is possible for fish–turbine encounters to occur if alewives overlap spatially and temporally with the FORCE test site (Fig. 1).

The present project measures a portion of the journey that an alewife from the Gaspereau River must undertake to return to the ocean after spawning. Migration was measured from the base of a downstream fish ladder on the Gaspereau River into Minas Basin and Minas Passage. We aimed to assess post-spawning survival of fish in the river, as well as provide a baseline description of the migration in relation to the large semidiurnal tides that prevail in the Bay of Fundy.

Methods

Animal capture and handling

Between June 17 and 22, 2019, post-spawned alewives were captured at the White Rock Fish Ladder, located ~ 7.5 km above the head of the tide. Fish were captured by dip netting and transferred to a holding tank (270 L capacity). River water was pumped from the fish ladder into the tank to create a circular flow and promote the alewives' natural swimming behavior. Alewives were anesthetized with tricaine methanesulfonate (MS-222) at a concentration of 2 g/10 L, buffered with sodium bicarbonate ($NaHCO_3$) at a 1:2 ratio, until loss of vertical equilibrium and response to tactile stimulus (tail grab) was observed. Fork length (mean 247 mm, SD 8.9 mm) and sex (40 males, 35 females) were recorded prior to tagging (sexing was done by abdominal massage). Fish were then transferred to a tagging cradle and supplied with orally delivered anesthetic at a concentration of 1 g/10 L of MS-222 to maintain sedation during surgery.

Alewives were tagged with V5-2H, high residency (HR) acoustic transmitters manufactured by VEMCO/InnovaSea (Bedford, Nova Scotia, Canada). An incision just large enough to insert the tag was made vertically between the ribs, and the tag was pushed into the peritoneal cavity to a position above the pyloric caeca. Incisions were closed with two simple interrupted sutures (Ethicon monofilament nylon sutures, reverse cutting 4–0, 1.5 metric, 45 cm, PS-2 18 mm, 3/8 circle needle). Each alewife was also fitted with a Floy dart tag (Floy Tag & Manufacturing Inc., Seattle, Washington) at the base of dorsal fin to help identify tagged individuals if subsequently caught by

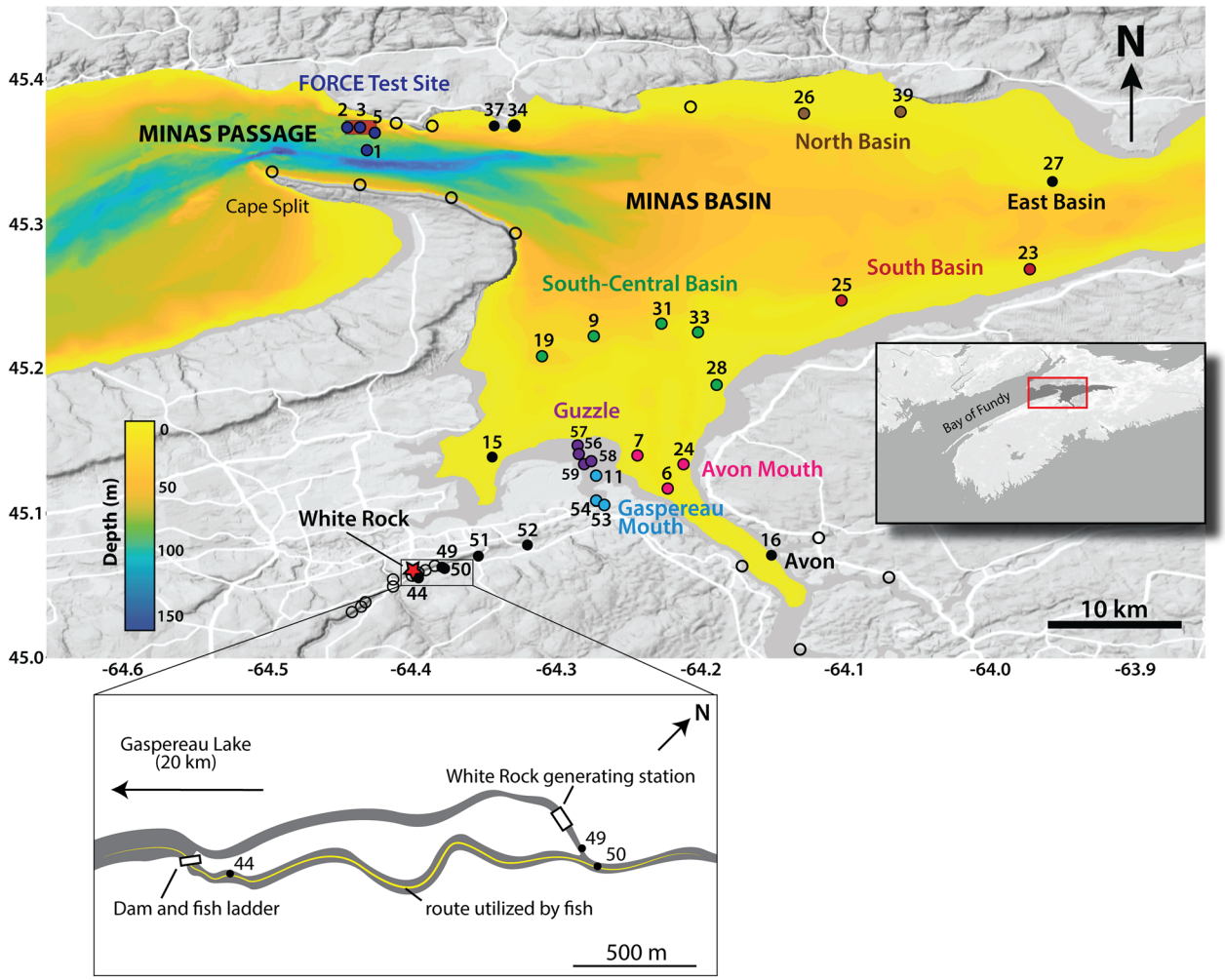

Fig. 1 Map of study area showing positions of moored acoustic receivers. Open circles show receivers that did not detect alewife. Groups of receivers are named and color coded. A shaded red box corresponds to the FORCE test site in Minas Passage. Bathymetry below mean sea level was obtained from the model used by Karsten et al. [28]. Outset shows layout of the White Rock generating station and fish bypass (yellow). Tagged alewives were released near the fish ladder

fisheries. After surgery, fish were transferred to a recovery tank with several untagged (control) individuals—an alewife was considered recovered when its swimming behavior was indistinguishable from that of the untagged fish. After tagging, all fish were released as a group at the base of the fish ladder near the White Rock dam.

Receiver deployment

Acoustic tags were set to transmit 170 kHz HR signals at an average interval of 1.5 s, and 180 kHz pulse position modulation (PPM) signals at an average interval of 20 s. An array of HR2 receivers was deployed in the faster flowing waters of Minas Passage. HR2 receivers detect both PPM signals and the more frequent HR signals to ensure highest chance of detection while a tagged alewife is within detection range. In Minas Basin the currents are slower, and VR2W receivers were sufficient to detect the less frequently transmitted PPM signals. A combination of HR2 and VR2W receivers was used in Gaspereau River. VR2W receivers have a battery life of 15 months, with an expected maximum detection range of 150–200 m for V5 tags (VEMCO/InnovaSea Ltd.). HR2 receiver batteries last approximately 6 months, with a detection range of ~ 210 m, based on V9 tags [45].

Ideally, receivers would continuously monitor the entire study area in order to always track tagged animals as they moved by some combination of swimming and tide. As a compromise to limited resources, receivers were deployed in a clumped fashion, with groups of receivers (color coded in Fig. 1) providing better coverage

of a few locations that serve as migration milestones. Separation between groups of stations was commensurate with tidal excursion. An array of 4 receivers was used at the Guzzle where previous work [40] indicated high abundance of striped bass (*Morone saxatilis*).

On 3 May 2019, four moorings were deployed at stations 1, 2, 3, and 5 in Minas Passage (Fig. 1). Each mooring consisted of a customized streamlined subsurface buoy (SUB; Open Seas Instrumentation, Musquodoboit Harbour, NS) with an acoustic release and steel anchor chain connected to anchor links [41]. An HR2 receiver was attached near the tail of the SUB float. The instrument load of each SUB also included a VEMCO/InnovaSea VR2W-69 kHz receiver and a Chelonia C-POD, but those instruments were not used for the present study. SUBs were retrieved on 14 August 2019 for battery changes, and recovered on 13 December 2019 and 14 January 2020. Data examined in this study span from June 2019 through December 2019, although no tagged alewives were detected after 14 August.

Preferably, a receiver array using SUB moorings would monitor the middle of Minas Basin (east of Minas Passage) because that area is tidally coupled to Minas Passage (Fig. 1). Availability of mooring equipment and appropriate boat time limited the present project to monitoring nearer shore (North Basin, South Basin and East Basin) by piggy-backing upon other projects.

A rigid mooring design was used for shallow sites in Minas Passage and throughout Minas Basin, consisting of rebar set in a cement weight with a float tethered to the top of the rebar. Most of these moorings supported VR2W receivers. HR2 receivers were used at 5 shallow stations along the northern bank of Minas Passage, but only one of these (station 37) detected tagged alewives (Fig. 1). Receivers were deployed between 12 April 2019 and 17 May 2019.

In Gaspereau River, receivers were deployed between Gaspereau Lake and the river mouth using an anchor with a float or with a ground line running to shore. Several receivers were attached directly to surface floats (booms) deployed above the White Rock generating station between 30 April 2019 and 17 May 2019. Migration associated with river flow from White Rock to the mouth of Gaspereau River was monitored by stations 44, 49, 50, 51, and 52. Tidal influence begins at site 52, and good signal reception at this location, combined with limited spatial extent, enabled effective monitoring with a single receiver. Given tidal excursion, the next logical monitoring site was the mouth of Gaspereau River, where 3 receivers were deployed to cover its spatial extent.

HR2 receivers measure both instrument temperature and water temperature at 10-min intervals. Hourly water temperature measurements were also obtained from HOBO Pendant temperature loggers at Minas Basin stations 6, 16, 23, 24, 25, and 28 (Fig. 1). Hourly atmospheric temperature and precipitation were obtained from the Kentville weather station (45° 04′ N, 64° 29′ W).

Data analysis

Analysis was done in R (version 3.6.1) and MATLAB (version 9.2.0.538062, R2017a). The distribution of travel times in Gaspereau River was obtained, and time scales for displacement of alewives were assessed in view of swimming behavior and mortality. Movements in Minas Basin and Minas Passage were examined in relation to tidal displacement, diel period, and seasonal warming. The presence of tagged alewives within a group of receivers (Fig. 1) was typically condensed into 10-min detection-positive events, such that all detections of the same animal within that timeframe were collapsed to a single data point. Ten minutes is sufficiently long for a tagged alewife to pass through receiver detection range when tide is running, but shorter than the time required to move into a new group of receivers. The time of each event was assigned as the average time at which detections belonging to it were made. For example, if 2 receivers in a group jointly obtain 20 detections of the same individual within a 10-min span, this was recorded as a single detection event, with the time defined by the average time of all 20 detections. Given that receiver detection ranges can be several hundreds of meters, a 10-min detection-positive event more closely approximates an independent estimate of an alewife location than do the individual detections.

To understand mechanisms associated with migration where tidal excursion is large, it is useful to quantify how migrating alewives become spread out as they migrate through the study area. Richardson [42] was first to evaluate turbulent mixing (dispersal) by measuring the separation distance between pairs of particles and determining how pair separation varied with time. Mixing (dispersal) of tagged alewives can similarly be studied. In order to measure the separation between a pair of alewives, it is necessary to know both their positions at the same time. Obviously, this is only possible to within an approximation because position is only known to the scale of the detection range (~ 100 m) and detection times are intermittent. Pair separation is, therefore, calculated as follows. Detections of a tagged alewife at a specific receiver site were grouped into 20-min windows (detection positive 20 min) so that they represent where that tagged animal was (the receiver group) at the average time of detections within that window of time. A pair separation then becomes the distance between two sites that detect different tagged alewife within the same time window. Many pair separations can be obtained

by considering all possible combinations of tagged alewives and stations over all detection positive time windows. Position is only known to within detection range and the distance of travel during 20 min, but pair separation distances usually become large compared to such uncertainty.

Departure of alewives from the study area was analyzed as a function of time since tagging. The nature of such time dependence, in concert with the nature of pair separation, provides an indication of the extent to which migration out of the study area is consistent with a simple mixing model.

Environmental predictors

Estimates of tidal current and sea-surface elevation were obtained at various times and locations throughout the study area based on a hydrodynamic model that had previously been configured for the Bay of Fundy and adjacent continental shelf [28]. Previously, the model was run from August to November 2011, and simulated currents and tidal elevation were stored at 30-min intervals for all model grid points throughout the Bay of Fundy. To obtain current and elevation data at sites and times relevant to the present study, model results were interpolated to obtain 2011 time series at sites of interest. These time series were used to fit amplitudes and phases of tidal constituents, which were used to reconstruct tidal currents and elevations at the sites and times of interest [10]. This process involves a variety of approximations associated with imperfectly fitting amplitudes and phases, the impact of which is expected to increase with the time elapsed since the model simulation. Few measurements are available for error checking, but comparisons with unpublished 2018 drifter tracks in Minas Passage suggest the projected currents were 10–15% too slow. Comparison with unpublished April 2021 tidal elevation measurements at the FORCE Test Site indicated that projected tide had a 30-min phase error. No attempt was made to correct for such errors, and error might have been different for other parts of the Minas Passage/Basin system.

For examining the diel presence of alewives at measurement sites, daylight was defined as the interval when the solar zenith angle was less than 90°, and the proportion of alewives present during daylight hours (pDAY) was calculated for each receiver group. Sun position data were obtained from the R package GeoLight [31]. Proportions of alewives detected during daylight were tabulated for sites across Minas Basin and Minas Passage.

Comparing water temperature measurements at the FORCE site with contemporaneous values in Minas Basin showed a spatial temperature gradient associated with increased spring warming of shallow Minas Basin water relative to deeper waters in Minas Passage and beyond. Thus, with some interpolation, temperature can be estimated at times and locations for individual alewives when they were detected. Temperature local to migrating alewives was compared with seasonal change. Seasonal and tidal changes in water temperature were diagnosed by fitting amplitudes and phases of the M2, S2, N2, K1, M4 and O1 tidal constituents to time series of temperature measurements. One can then reconstruct the temperature signal associated with tidal advection of spatial temperature gradient. Subtracting the temperature change due to tidal advection from measured time series leaves an estimate of the seasonal signal of water temperature. Seasonal temperature relates more naturally to the temperature experienced by an alewife because an alewife that moves with the water mass does not experience temperature changes caused by tidal advection.

Survival estimates in Gaspereau river

Here, we estimate the survival of tagged alewives as they migrate from the White Rock tagging site, down Gaspereau River and into Minas Basin. As previously discussed, receivers had a clumped distribution so that more measurement power could be obtained from groups of receivers at particular sites (Fig. 1).

Survival is considered to be the number of tagged alewives M_i that pass site i at any time during their migration. Measurements directly give the number of tagged alewives N_i that are detected by the group of receivers at site $i \in \{1, 2, 3, \ldots, I\}$ where there are I monitoring sites downstream of the release site $i = 0$. $N_0 = 75$ is the number of tagged alewives that are known to have been released. Receiver arrays are not perfect, so N_i will be an underestimate of M_i. A better estimate for M_i would be the number of tagged alewives that are detected at i or beyond ($N_{k \geq i}$), but this will still be an underestimate for imperfect receiver arrays.

Better estimates of M_i require that we first determine the probability p_i that the receiver array at site i will detect a tagged alewife that is known to pass by. Measurements directly give two quantities that enable an estimation of p_i. First, the number of tagged alewives $N_{k>i}$ that are detected at all sites k that are further along the migration route than site i. These $N_{k>i}$ tagged alewives are known to have passed by. Second, the number of tagged alewives $N_{i\&k>i}$ that are detected both at site i and beyond site i. The proportion of passing alewives that are detected at site i is

$$p_i = \frac{N_{i\&k>i}}{N_{k>i}}, \tag{1}$$

and, given the categorical nature of the data, the standard error is

$$se(p_i) = \sqrt{p_i(1-p_i)/N_{k>i}}. \quad (2)$$

Values of p_i are intrinsically interesting because they quantify how well each site is monitored, and what measures would be required to improve subsequent experiments. By definition, the number of alewives that are expected to be detected at site i will equal p_i multiplied by the number that pass site i. It follows, therefore, that

$$M_i = \frac{N_i}{p_i}, \quad (3)$$

with standard error

$$se(M_i) = \frac{N_i}{p_i^2} se(p_i). \quad (4)$$

As anticipated above, $M_i \geq N_i$. Given that M_i is the number estimated to pass site i, then the number that did not pass (were lost) is

$$L_i = N_0 - M_i, \quad (5)$$

and this has the same standard error as M_i. Corroborating evidence is desirable before considering loss to be mortality. The above methodology can be used to establish the effectiveness of monitoring at sites in Minas Basin, but large-scale tidal mixing restricts interpretation of M_i.

Animal weight, length, handling time, and water temperature at tagging were compared for individuals that made it out of the Gaspereau River and those that were lost using multivariate analysis of variance (MANOVA) and the Wilcoxon signed-rank test.

Results

Tagged alewives were not detected at nearshore sites indicated by open circles in Fig. 1. Notably, alewives were not detected in the shallow, upper reaches of the Avon River and its tributaries. In contrast, alewives were commonly detected by receivers in shallow waters at the Guzzle and near the mouth of Avon River. VR2W receivers near the southern shore of Minas Passage (Fig. 1) did not detect tagged alewives, but this result is inconclusive because those receivers only operated until 3 July 2019 and also because VR2W receivers can have low detection efficiency in fast currents [45]. With the minor exception of a few detections at station 37 (a deeper site), HR2 receivers failed to detect tagged alewives near the shallow, nearshore waters of the northern shore of Minas Passage.

Overall movement of individual alewives is broadly illustrated by grouping stations into several areas of interest, and by grouping detections into detection-positive 3-h windows so that location and time are resolved graphically and the Nyquist–Shannon sampling theorem ensures that the tidal timescale is also resolved. Figure 2 shows sequential locations of the 31 individuals that were ultimately detected in Minas Passage (and thus assumed to continue on their oceanic migration). Animals are plotted in order of release time, and vertically separated when plotted at a given location, such that all points within a grey band are for the same location, and individual animals can be graphically resolved even if some are detected at the same location at the same time. The plots tabulate the last detection day for each tag number.

Figure 2 illustrates many features of the migration. Migration from the tagging site to the mouth of Gaspereau River is fast. For 20 days from the start of tagging, alewives are mostly detected within Avon River with excursions to the Guzzle and into South-central Basin, which indicates alewives are tidally displaced by the current. After 20 days, alewives begin to be detected in Minas Passage, and the first detections in both East Basin and North Basin were also on 7 July. It seems that after day 20, the alewives become widely dispersed throughout the study area, being detected from Minas Passage to the Guzzle, and sometimes even at the mouth of Gaspereau River. These qualitative results guide more quantitative analysis.

The last group to be tagged (panel D, Fig. 2) was among the first to depart the study area. Time of migration $t_{\text{migration}}$ from tagging to last detection in Minas Passage is related to tagging time t_{tagging} relative to the beginning of tagging t_0 by:

$$t_{\text{migration}} = a + b\left(t_{\text{tagging}} - t_0\right), \quad (6)$$

where linear regression gives $a = 34d, 95\text{CI}[30-44]$ and $b = -2.8, 95\text{CI}[-4.8\text{to}-0.9]$. The expectation is that the first alewives tagged would migrate through the study area in about 37 days, whereas the last alewives tagged would take only 23 days. There is a good deal of variability about this trend because the regression only explains 24% of the variance. Nevertheless, it does raise a possibility that departure from the study area might be related to some environmental factors like seasonal warming of the water.

Travel times down the Gaspereau River were fast, and most alewives exited the river within a day or two after being tagged (Table 1). Flow is riverine upstream of station 52, and median travel time for the 69 alewives recorded over this 7.6-km leg was 14.0 h, with quartile range 6.9–36.5 h. River flow might have been faster in 2019 than in most years; larger than average precipitation was recorded from 1 April to the last day of tagging (407 mm as compared with an average of 235 mm,

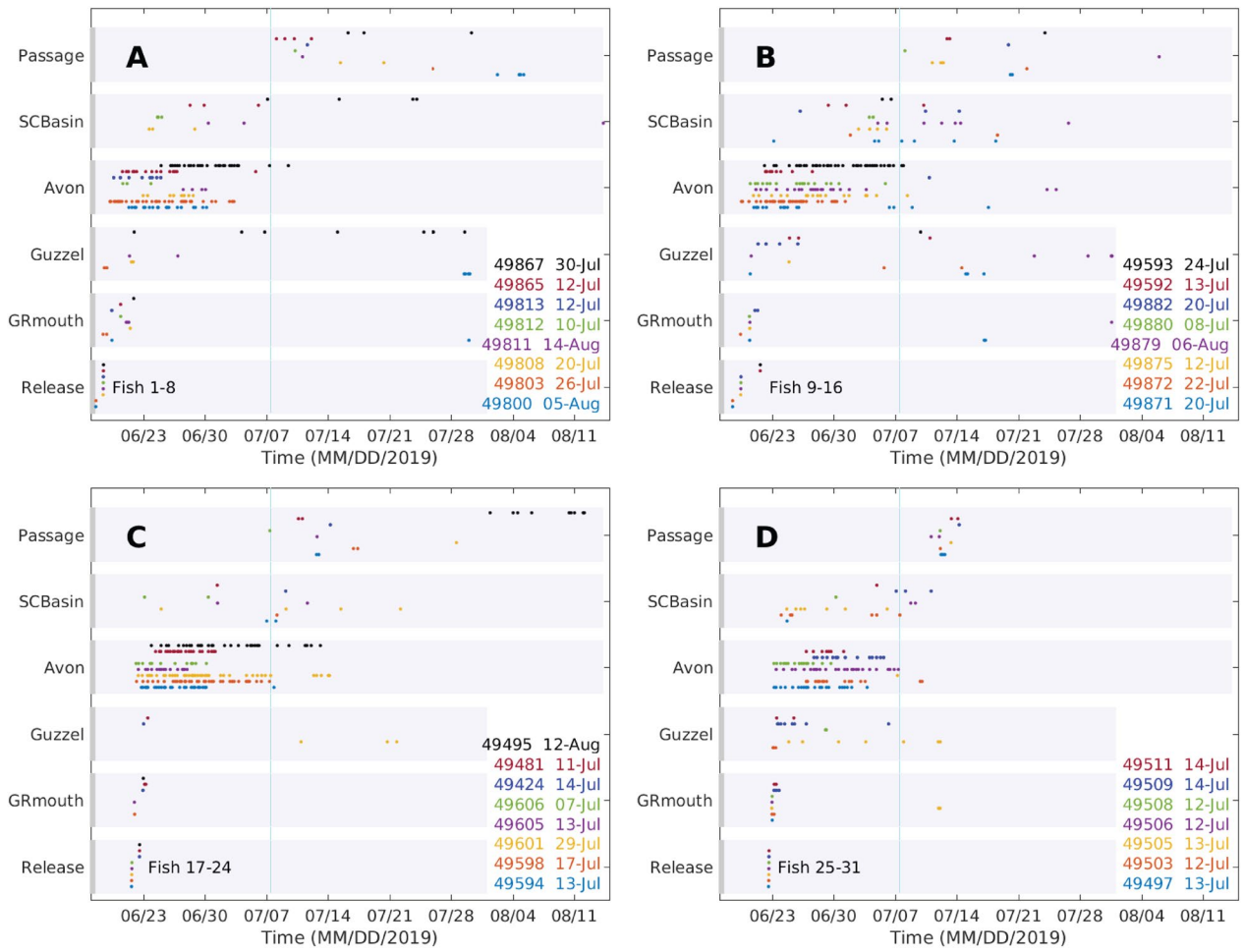

Fig. 2 Locations and times when tagged alewives were detected. Locations correspond to groups of stations: "Release" is the release site; "GRmouth" are stations 11, 53, 54; "Avon" are Avon River stations 6, 7, 16, 24; "SCBasin" are South-central Basin stations 9, 19, 31, 33, 28; "Passage" are Minas Passage stations 1, 2, 3, 5. Cyan lines mark 20 days from the first day of tagging, corresponding to when fish first enter Minas Passage

Table 1 Travel times of tagged alewives from the release site to station 52 and to the mouth of Gaspereau River

Travel time (days)	Station 52 (# alewives)	River mouth (# alewives)
0–1	38	31
1–2	15	14
2–3	8	5
3–4	1	2
Total	62	52

SD 52 mm, for the 5 previous years) and was associated with observations that the White Rock generating station was spilling water and flooding the nearby forest area. It is noteworthy that fish were released immediately downstream of the fish ladder (Fig. 1) and the current in that part of the route was influenced by water spilling from the head pond. In that current, 10 tagged alewives were only briefly detected by the receiver at station 44, but one fish was detected many times during a 6-h timespan and another during a 4-h timespan. Although slow to start, both those fish survived the migration to Minas Basin. It is possible that down-river migration might be slower in years when there is less discharge from the head pond of the White Rock generating station.

Station 52 (Fig. 1) represents a hydraulic discontinuity, with the river bed steeply rising up river and sloping gently down river. From station 52 to the mouth of the Gaspereau is tidal, and median travel time for the 49 fish recorded over this 9.2 km leg was 2.3 h, with quartile range 1.9–8.2 h. At station 52 the river flow slows and is counteracted by the rising tide, making this an efficient monitoring site, which detected 45 of the 57 tagged alewives (79%) that were subsequently detected in Minas Basin. For these 45 alewives, time elapsed from their first

to last detection at station 52 was < 1 h for 34 and ≤ 8 h for all 45. This indicates active downstream swimming in the tidal portion of Gaspereau River that is usually sufficient to prevent being returned by the tide and always sufficient to prevent being returned by a second tide. Of the 18 not detected beyond the river mouth, 10 were detected at station 52. For 4 of those 10 alewives, time elapsed from their first to last detection at station 52 was > 1 day, which indicates no active swimming and might be considered to be corroborating evidence of mortality.

Qualitatively, Fig. 2 indicates that tagged alewives were distributed within Avon River to South-central Basin for the 20 days after the beginning of tagging, and became more widespread after day 20. The scale of spreading suggests examination of the redistribution of tagged alewives by the tidal excursion. Tidal sea-surface elevation serves as a convenient proxy, with high tide representing the limit of flood-tide excursion and low tide the limit of ebb-tide excursion. Figure 3 shows the ebb–flood distribution of detection-positive 10-min events for the 57 alewives detected in Minas Basin. Alewives were observed to reach the mouth of Gaspereau River (panel B, Fig. 3) at all phases of the tide during the tagging period, but after clearing the Gaspereau River, alewives were infrequently observed at the river mouth, and only at high tide.

For the first two weeks following tagging, alewives were detected at the Avon Mouth site at all phases of the tide (panel C Fig. 3), consistent with them entering the Avon at all phases of the tide and becoming distributed over the scale of the tidal excursion about the mouth of the Avon River. Consistent with the flood tide excursion, alewives were only detected nearer the head of the Avon River (panel A, Fig. 3) near high tide, but they did not remain and were not found at nearby shallow-water stations (Fig. 1). The alewives distributed about Avon

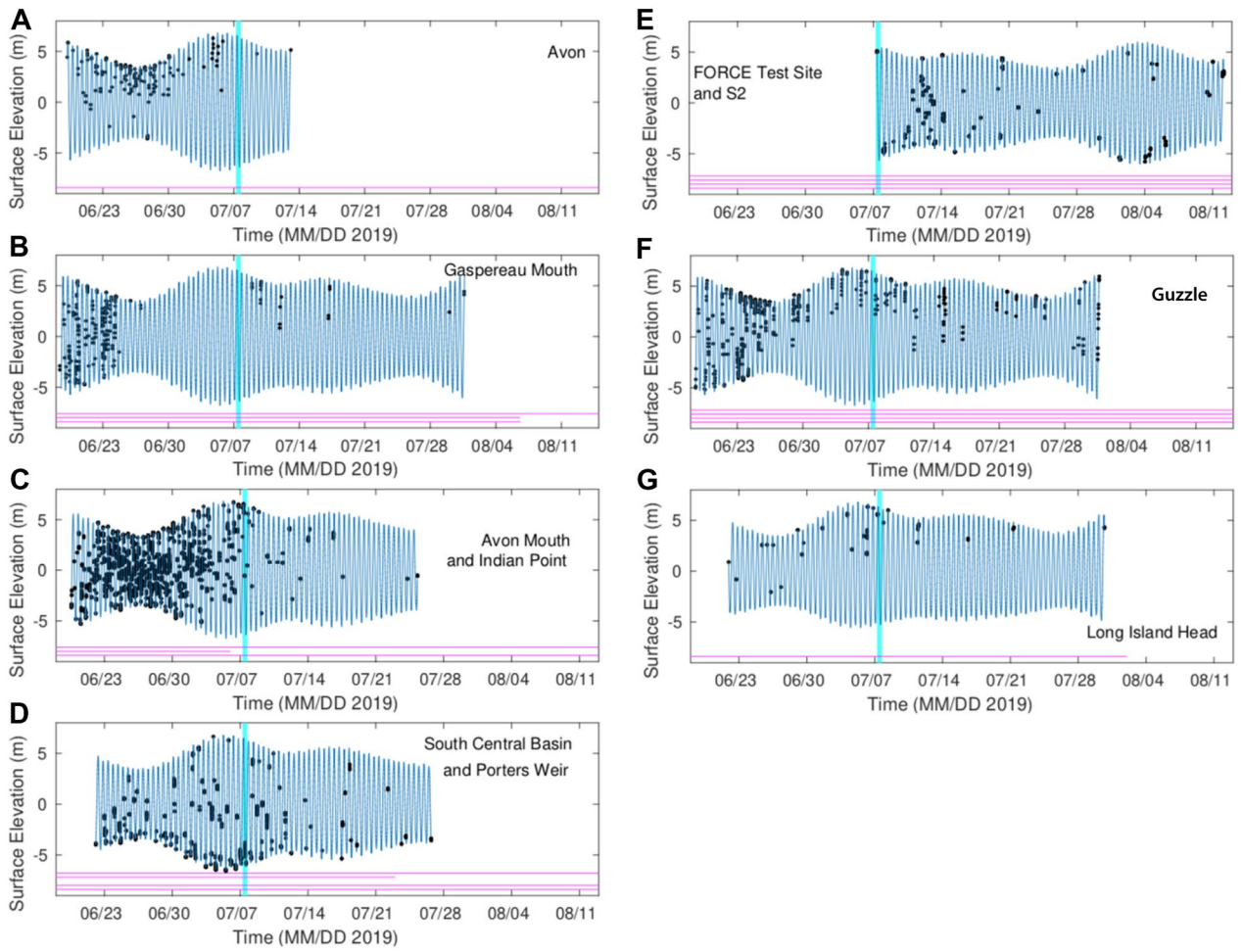

Fig. 3 Sea surface elevation at times that tagged alewives were detected. Black dots show detection-positive 10-min intervals. Magenta lines indicate times that receivers were operating at each location. Cyan lines indicate 20 days after the beginning of tagging

Mouth were observed in South-central Basin (panel D, Fig. 3) near low tide, consistent with displacement by the ebb current. This pattern applies generally for the first 2 weeks from the start of tagging.

In the third week, alewives are still displaced to the Avon site near high tide (panel A Fig. 3) but they are now unlikely to be found at Avon Mouth near low tide (panel C Fig. 3). Also, although alewives are still more likely to be detected in South-central Basin at low tide, they are more often detected there at other phases of the tide than during the first 2 weeks (panel D Fig. 3). Thus, with the onset of spring tides, the distribution of alewives spreads in the long-stream sense and is displaced northwards (seawards).

Shortly following the peak spring tide, 20 days after the start of tagging, alewife detections began to occur in Minas Passage (panel E, Fig. 3), where they were detected at all phases of the tide. During this time, it was mostly near high tide that alewives were observed at the mouth of the Gaspereau River, at the Guzzle and Long Island Head (station 15 in Fig. 1) (panels F and G, Fig. 3). This pattern of detections indicates that tidal currents are transporting alewives over large distances, consistent with measurements of large tidal excursion through Minas Passage [46].

The connectivity between receiver groupings can be examined in relation to tidal excursions. Blue lines in Fig. 4 show the number of alewife movements between receiver groups within a 6.2 h interval, representative of movement over either a flood or ebb tide. The Avon River mouth was the most heavily trafficked location, with the highest number of detection events and multiple connections to other stations. Connectivity was strongest between Avon mouth and the Avon station 16, with 27 flood-tide movements from Avon Mouth to Avon, and 30 ebb-tide movements from Avon to Avon Mouth. No alewives were detected going further upstream into the Avon or the connecting rivers.

For the present purposes, station 28 (Porter Weir) has been split off from the South-central Basin group in order to resolve a bathymetric split in the channel. Within the 6.2 h time scale, Fig. 4 shows 8 ebb transits from Avon Mouth to Porter Weir, and 3 flood transits from Porter Weir to Avon Mouth. This is not much different from the 9 ebb transits and 3 flood transits between Avon Mouth and the large receiver array of South-central Basin.

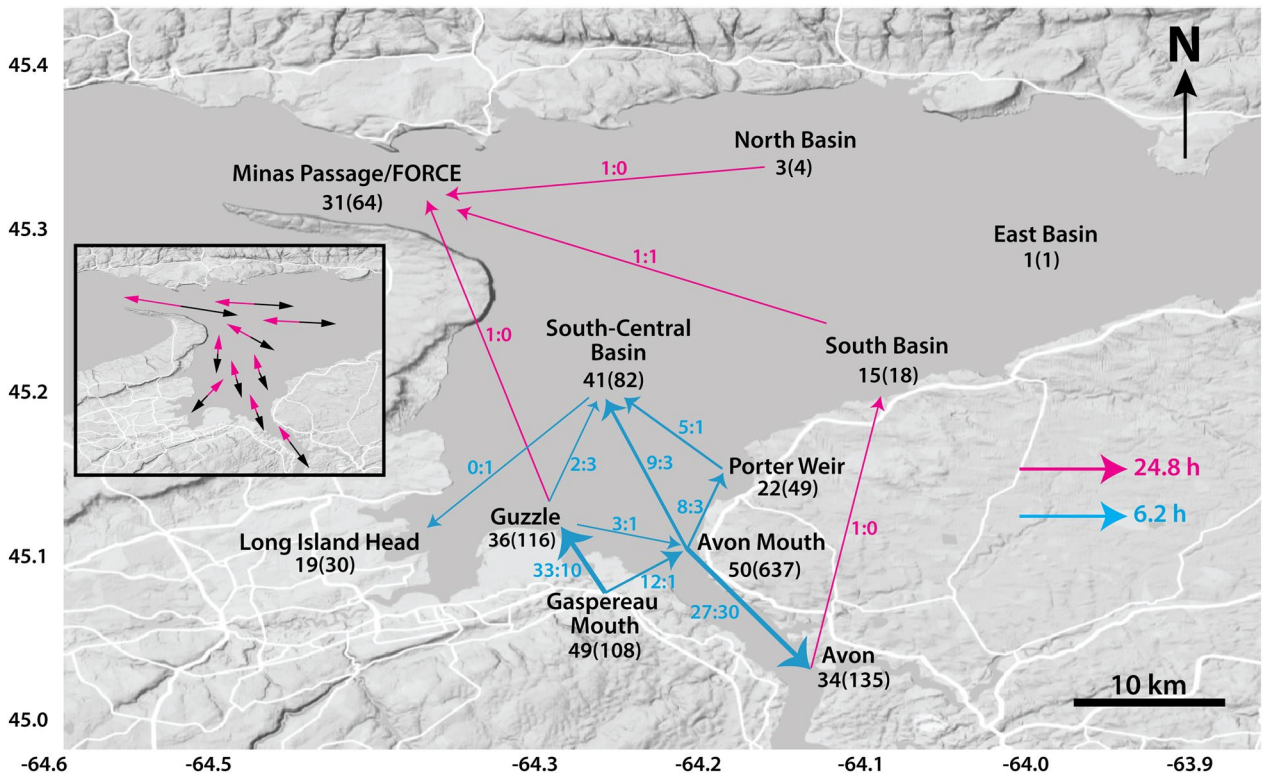

Fig. 4 Record of alewife presence at and movement between locations in Minas Basin. The number of tagged individuals detected at each location is shown, with the total number of presence events in brackets. Blue arrows indicate movement from one location to another within a 6.2-h time span. Pink arrows indicate movement within a 24.8-h time span. The notation nf:nb associated with each arrow indicates the number of movements in the arrow direction (nf) and in the opposite direction (nb). Inset illustrates flood–ebb tidal currents

Within the 6.2-h time scale, movement was always between neighboring sites, such as between the South-central basin and the mouth of the Avon River. To find transits over larger distances we considered a 24.8-h interval (pink arrows in Fig. 4), representative of movement within a full diurnal tide cycle. Presently, we only consider transits between Minas Passage and any other site, and transits between Avon (station 16) and South Basin, or North Basin, or East Basin. Figure 4 shows that Minas Passage has connectivity with North Basin and South Basin, consistent with drifter studies [46]. Minas Passage also has connectivity with the Guzzle. Surprisingly, no connectivity of alewife detections was found between Minas Passage and South-central Basin. Given the shorter interval connectivity between Avon and Avon Mouth and between Avon Mouth and Porter Weir, it was not surprising to find longerterm connectivity between Avon and South Basin.

For graphical clarity, we did not consider all possible longer term connections when calculating Fig. 4, but there are others. For example, within a 24.8-h interval, alewives were found to travel longer distances, such as from the Gaspereau mouth to Minas Passage (~52 km). Large-scale movements were not observed until 6 July, whereas 50% of the small-scale movements happened before 25 June, and 80% before 1 July. This is consistent with migration and the timing of spring tides, which are expected to cause larger excursions of alewives into Minas Basin and Minas Passage.

The above results (Figs. 3, 4) indicate that tides are dispersing alewives. Separation distance between pairs of alewives provides a means to quantify such dispersion. Pair separations were calculated from all possible combinations of tagged alewives and receivers over detection-positive 20-min intervals (Fig. 5). Each point represents the distance between a pair at the time they were both detected. The range of pair separation values increased with time since tagging. There appeared to be two times of discontinuity: at 2.5 days, and at 20 days post-tagging. Averaging pair separations within time intervals defined by these discontinuities shows a much higher value beyond 20 days. The apparent jump at 2.5 days is probably an artifact of tagging being done over a 6-day period, so the arrival times of alewives in Minas Basin varied. After 20 days, corresponding to when alewives are first detected in Minas Passage, pair separations increased, having greater maximum values and fewer small values. This is a clear demonstration that the tagged alewives had become more widely dispersed through the study area.

The average time from tagging to final detection in Minas Passage was 28 days with standard deviation 11 days, a result obtained only from those 31 alewives that were detected in Minas Passage. How alewives depart

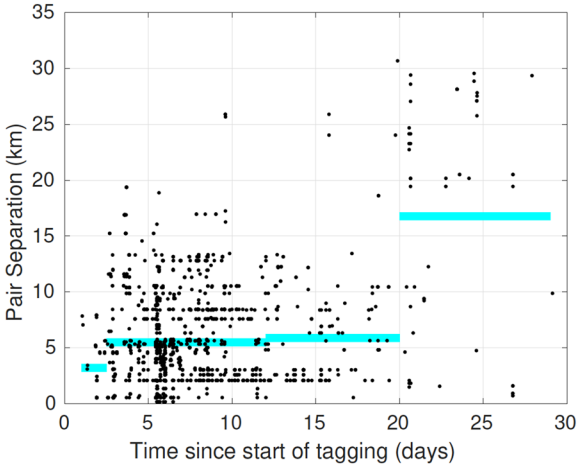

Fig. 5 Pair separation between tagged alewives that were detected by different receivers within a 20-min interval. Cyan lines show averages over four time spans: < 2.5 days, 2.5–12 days, 12–20 days, > 20 days, based on apparent times of discontinuity

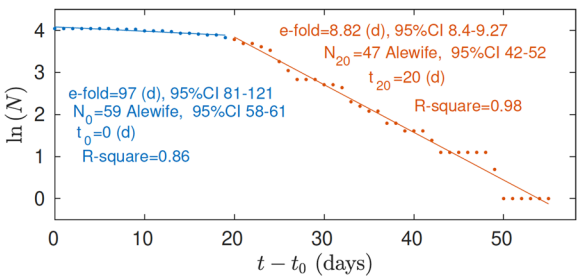

Fig. 6 The decline in the number of tagged alewives that are subsequently detected by the entire receiver array (Gaspereau River, Minas Basin and Minas Passage) as a function of time since tagging. All tagged fish are considered

as a function of time might be gleaned from Fig. 6, which shows the number of tagged alewives that are deemed to remain in our study area by virtue of being subsequently detected. For the first 20 days the decline is slow, but afterwards becomes much faster. Piecewise exponential models were fitted to these data. The first piecewise fit showed slow decline in the number of remaining alewives over the first 19 days. The second piecewise fit gives a value of $N_{20}=47$ tagged alewife on day 20, after which the number of remaining tagged alewives declines with e-folding time scale of 8.8 days. Given that alewives are not observed in Minas Passage until day 20, a lower limit on the number that survive is 47, corresponding to an upper limit for mortality of 28 alewives by day 20. Given the large pair separation after day 20, Minas Basin and Minas Passage can be approximated as a well-mixed water volume which exchanges with the ocean beyond Minas Passage. As such, and

setting aside any mortality after day 20, the 8.8 days e-folding time becomes the residence time beyond day 20. Thus, once alewives disperse to Minas Passage, they more quickly leave the study area.

Tidal currents are strongest and collimated in Minas Passage [46]. Less dispersive mixing is expected where flow is a one-dimensional oscillation than where spatial variation is in two dimensions. For purposes of understanding both migration and alewife–turbine interaction, it is of interest to make a more detailed examination of the transit of alewives through Minas Passage. 31 tagged individuals were detected in Minas Passage, of which 16 were detected on only one transit. A transit constitutes one occurrence of a fish being swept past the receivers in the passage, and there are two possible transits for each tidal cycle: flood and ebb tide. It is expected that many transits were not detected because the receiver array (stations 1, 2, 3, 5) could not monitor the entire width of Minas Passage. Nevertheless, one alewife was detected on 10 transits that were made over a 12 days period. Another alewife was detected on only 3 transits, but those transits happened over a time span of 15 days. This might be considered as 3 transits being detected out of a total of 58 possible transits, or it might have been that the alewife spent several days at a time in either Minas Basin or Minas Channel before returning to be detected in Minas Passage. Measurements are not conclusive, but they indicate that migration through Minas Passage can take many days, and often involves multiple transits back and forth.

Alewife–turbine interaction is more likely of concern for passing events when tide is running fast. One passing event is when signals from one tagged fish are detected as it passes a single station. Of the passing events documented in Table 2, it is the flood/ebb passing events that are of interest for potentially harmful alewife–turbine interaction. At the turbine test area (stations 2, 3, 5) there were 25 passing events during flood/ebb tide, and 23 at station 1 in the middle of Minas Passage.

Table 2 Passing events of tagged alewives at stations in Minas Passage during different stages of the tide

Station	Number of passing events				Number of fish detected
	Flood	Ebb	High	Low	
1	8	16	4	7	21
2	4	12	1	1	14
3	8	10	3	1	15
5	8	5	0	2	11

Station 1 is located in the mid-channel, and the other stations are at the FORCE test site

Environmental predictors of alewife behavior and movement

Alewife spawning runs are cued by 5–10 °C water temperature. It is reasonable, therefore, to investigate any association that water temperature might have with post-spawning migration. Water temperature at the tagging site had a median value of 14 °C during tagging, with a quartile range from 13 to 15 °C. Declining presence of tagged alewives in the study area over time coincided with seasonal warming. Water temperatures in Minas Basin and Minas Passage showed seasonal warming with tidal variation caused by advection (inset of Fig. 7).

For visual clarity, Fig. 7 shows temperature trends with most of the tidal variation removed. Detections at each site/time are scattered over similar temperature range for the first 20 days after the beginning of tagging. This happens because tagged alewives were at the hotter site (Avon) when tides advect cooler water there, and at the cooler site (South-central Basin) when tides advect hotter water there. A 4-day running average of temperatures at times/sites of detection is about 14 °C (black line). The temperatures at times/sites of detection are consistent with the following causation: that alewives move towards deeper (cooler) water when temperature rises above ∼14 °C. Once they have moved into deeper waters of Minas Basin, strong tidal effects move alewives through a wider range of temperatures, but still generally

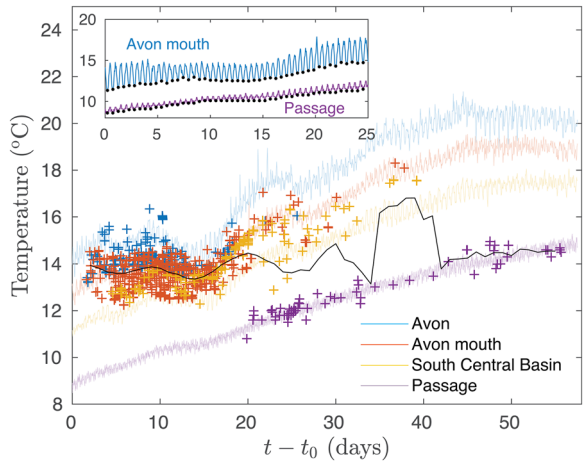

Fig. 7 Temperature at four locations in the study area. Colored lines show temperature after removing variation associated with tidal constituents. Corresponding to times of detection-positive 10-min intervals, actual temperatures at each location are indicated with colored crosses. Inset shows temperature variation at the mouth of Avon Channel and in Minas Passage (station 1), with black dots indicating temperatures were lowest at high tide

centered near 14 °C. Water temperature during the 2019 study period is likely typical for other years, given that 2019 monthly averaged air temperatures at Kentville were within 0.5 °C of the 2001–2018 averages for April through August, except for May, which was 3 °C cooler than usual.

The day–night cycle seemed to influence presence at some locations in the Minas Basin. The proportion of alewife presence during daylight (pDAY) was calculated for receiver groups (Table 3). As this study was conducted during summer, a value of $E(p\text{DAY}) = 0.642$ was expected if alewife presence was equally likely during daylight and nighttime. We found that tagged alewives were more likely to be present at the Guzzle during daylight, and at Minas Passage and the South-central Minas Basin during nighttime.

Survival estimates in Gaspereau river

The number of tagged alewives detected at site i depends upon the detection efficiency of the receiver array that monitors the site, as well as how much time a tagged alewife spends at that site. Equation (1) enables probabilities p_i that receivers at various sites will detect tagged alewives at any time during the post-spawning migration run (Table 4). Such probabilities enable a best estimate of the number of tagged alewife that are lost L_i before reaching site i (Table 4). Fast river flow causes probability of detection to be very low at the upper Gaspereau site (station 51), so the local calculation of losses is not statistically meaningful at that site. One VR2W receiver was sufficient at the first tidal site (station 52) to give a high probability of detecting tagged alewives as they passed by. 18 ± 2 losses occurred within the Gaspereau River, with 11 ± 4 lost in the tidal portion of the river and 7 ± 3 lost in the river flow upstream of station 52. Corroborating evidence for mortality has been noted for 4 of those losses. Making the assumption that all losses are due to mortality enables an estimate of the apparent probability of survival of 0.76 ± 0.03 from tagging to the mouth of Gaspereau River.

To within measurement uncertainty, 57 tagged alewives survived migration down Gaspereau River to Minas Basin. Given the high probabilities of detection at Gaspereau mouth and lower Minas Basin, it is likely that most of the 18 alewives that were never detected in either Minas Basin or Minas Passage were actually lost. Factors that might influence survival in Gaspereau River are best studied, therefore, by comparing those 18 undetected alewife with the other 57.

Table 3 Daytime proportion of tagged alewives that are present at locations in Minas Passage

Location (station #s)	*p*DAY	SE (*p*DAY)	#Events
Gaspereau mouth (11, 53, 54)	0.58	0.05	108
Guzzle (56, 57, 58, 59)	**0.77**	0.04	116
Avon mouth (6, 7)	0.66	0.02	637
Avon River (16)	0.68	0.04	135
South-central Basin (9, 19, 31, 33)	**0.50**	0.06	82
Minas Passage (1, 2, 3, 5)	**0.44**	0.06	64

Statistically meaningful values (more than 2 standard errors from 0.642) are in bold font

Differences between live and lost fish

A Shapiro–Wilk's test of normality, as well as visual inspection of density and Q–Q plots, was conducted for the relevant variables (length, weight) prior to the MANOVA analysis in order to confirm the assumption of multivariate normality. Both variables were shown to be normally distributed ($W = 0.98$, $P = 0.16$; $W = 0.99$, $P = 0.77$, respectively). The mean fork length of the 35 tagged females was 250.7 mm (SD 8.6 mm) and for the 40 males it was 243.7 mm (SD 8.0 mm). A two-sided t-test rejected the null hypothesis that length of females is not different from that of males ($P < 0.05$). However, there was no significant difference (MANOVA, $P > 0.05$) between fish that successfully exited the river and those that failed to do so based on length ($F1, 71 = 0.597$, $P = 0.443$) or weight ($F1, 71 = 0.093$, $P = 0.761$).

Handling time and water temperature at tagging were not expected to be normally distributed as these values are not representative of a random sample—tagging was conducted during a small portion of the season with limited temperature fluctuations, and all animals underwent the same procedure expected to take about ~ 5 min.

Table 4 Estimates of number surviving M_i, number lost L_i, and detection probability p_i at sites within Gaspereau River, Minas Basin, and Minas Passage

Site (stations)	N_i	$N_{k>i}$	$N_{i\&k>i}$	$p_i \pm SE$	$N_{k\geq i}$	$M_i \pm$ SE	L_i
Gaspereau upstream, $i = 1$ (station 51)	8	67	8	0.12 ± 0.04	67	67 ± 22	–
Gaspereau tidal, $i = 2$ (station 52)	62	57	52	0.91 ± 0.04	67	68 ± 3	7
Gaspereau mouth, $i = 3$ (Stations 11, 53, 54)	52	57	52	0.91 ± 0.05	57	57 ± 2	18
Minas Basin, $i = 4$	57				57		

Numbers of tagged alewives detected at and beyond each site are given

Therefore, the differences between fish that made it out of the river and those that did not were compared using the two-samples Wilcoxon test, with both groups showing no significant difference in handling time ($W=460$, $P=0.093$) or tagging temperature ($W=370$, $P=0.778$). All alewives had effectively the same chances of suffering loss during migration from the tagging site to Minas Basin.

Discussion

This study provides one of few cases of acoustic tracking of alewives, and the first examination of coastal movement in Maritime Canada. Results indicate that behavior coupled with a variety of physical processes are relevant to different stages of the migration from the tagging site in Gaspereau River, into Minas Basin, and through Minas Passage. We observed rapid downstream migration from the release site, followed by a period of nearshore residency before dispersal into the upper reaches of Minas Basin, and subsequent disappearance from the study site. Apparent in-river survival was around 76%, with higher mortality in the lower portion of the river. Time to migrate through the study area averaged 28 ± 2 days. Strong tidal currents contributed to migration of alewives in Minas Basin, and fast, collimated tides advected alewives back and forth through Minas Passage before they left the system.

Alewives spent little time (1.1 ± 0.1 days) in the Gaspereau River following tagging. This is consistent with observations of post-spawned alewives and blueback herring emigrating from the Hudson River, New York [14], and is generally not surprising, as downstream movement is assisted by the current flow. In the riverine portion of Gaspereau River the median migration speed was 0.28 m/s with quartile range 0.06–0.31 m/s. It is likely that in 2019 the post-spawn migrating alewives were subject to higher river flow than for most years. River flow is not monitored and is subject to operational requirements for power generation. Nevertheless, average precipitation from 1 April to the last day of tagging was larger than for the 5 previous years, and was associated with observations of the White Rock generating station to spilling water at a high rate and flooding of the nearby forest area. The lower 9.2 km of Gaspereau River is tidal and median migration speed of alewives was 1.11 m/s with quartile range 0.31–1.35 m/s. Most alewives exited from lower Gaspereau within one tide, indicating active swimming.

About 18 tagged alewives were lost between the tagging site and the mouth of Gaspereau River. Four were observed in the tidal portion of Gaspereau River for more than a day, which we consider to be corroborating evidence of mortality as the fish showed no active swimming. One of these fish was detected at station 52 for several months, which is a clear indication of a lost or shed tag. There were 7 losses in the riverine portion and 11 in the tidal portion of Gaspereau River, which is similar to previous findings on the survival of Atlantic salmon smolts (*Salmo salar*) in this system [18]. Some of these losses might be due to natural mortality; Minas Basin is a known habitat of striped bass (*Morone saxatilis*) (ex: [40], with the Guzzle area near the mouth of Gaspereau River being a popular angling site. This species is an important predator in the area, and adults would be expected to prey on adult alewives.

Tagging conditions and size did not differ between tagged fish that successfully left the river and those that did not. Tag burden (0.3–0.7%) was lower than in previous tagging work on Clupeids [14, 32]. Based on a previous study of short-term tagging effect in this population [51], as well as tagging trials in Pacific herring, a closely related Clupeid (e.g., [47], tagging procedures may influence mortality of alewife, but are not expected to be a primary cause of mortality.

Beyond Gaspereau River, tidal excursion limits the interpretation of one site relative to another. An alternative calculation (Fig. 6) was done by summing over sites in order to examine the number that remain in the study area as a function of time. At 20 days after the start of tagging, 47 alewives were estimated to remain (Fig. 6), corresponding to a total of 28 lost. No tagged alewives were observed in Minas Passage before that time, so losses are not attributed to migration out of the study area. Assuming all 28 losses are due to mortality, this corresponds to mortality of 10 tagged alewives subsequent to migration out of Gaspereau River. The rate of attrition is much lower in Minas Basin than in Gaspereau River, but repeat spawning would become extremely rare if similar rates of mortality persisted beyond Minas Basin.

Groups of alewives that were tagged on the same day exhibited similar patterns of migration, and most fish spent the first two weeks post-tagging in the coastal zone near the mouths of the Gaspereau and Avon rivers. During this time, there were frequent movements between the mouth of Gaspereau River and the Guzzle (Fig. 4), and between the Gaspereau and Avon rivers. At low tide, alewives were swept northward, where they were detected by the array in the South-central basin. At high tide, alewives were detected further inland on the Avon. The black lines in Fig. 8 illustrate how the above patterns of detection might result from nearly cyclical tidal excursions, as calculated for this area from modeled currents during neap and spring tides. The black lines illustrate a passive particle starting from station 9 at the beginning of a flood tide, being swept southward during the flood tide, and then returned close to its starting point by the subsequent ebb tide. For the first 2-week post-tagging,

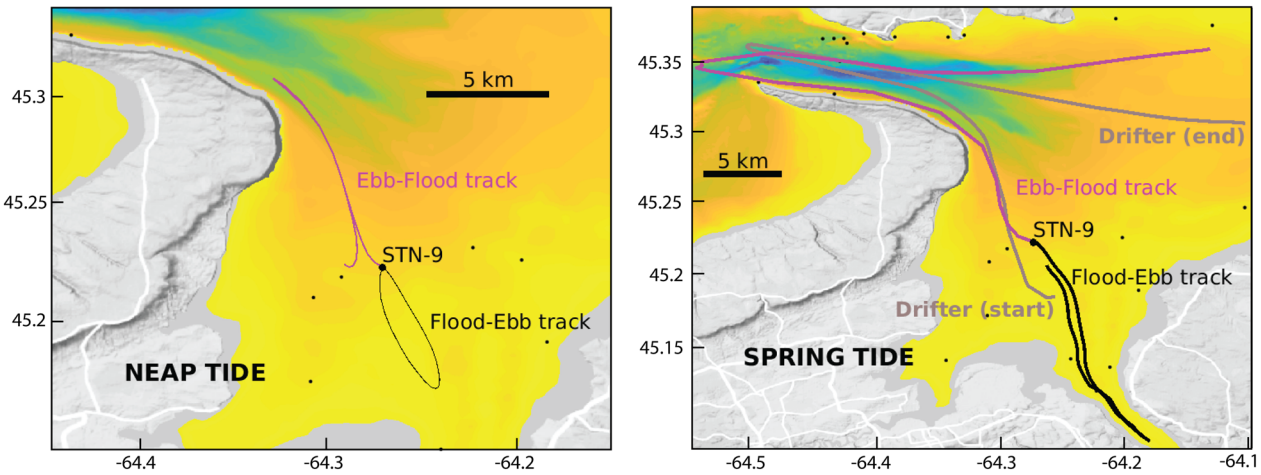

Fig. 8 Flood–ebb (black) and ebb–flood (magenta) tracks begin at station 9 and are computed from modeled currents. Left panel shows tracks during a neap tide and the right panel during a spring tide. The grey line shows an unpublished measurements of an ebb–flood drifter track over a tidal cycle on 20 October 2020 during a spring tide

detections of alewives are compatible with simulated tracks along nearly periodic paths in response to the periodic tide. Telemetry studies on other fish species in the Bay of Fundy have found substantial fish movements associated with the periodic nature of tides. Keyser et al. [29] found tide assisted motion of striped bass (*Morone saxatilis*) in Minas Passage. Sanderson et al. [46] used a drifter-mounted receiver to track a kelt Atlantic salmon (*Salmo salar*) as it moved with the tides in Minas Channel. Lacroix et al. [30] observed ebb–flood displacements of post-smolt Atlantic salmon in the Inner Bay of Fundy.

At sites in Fig. 4 there are far more independent detection events than there are recorded trajectories to another site. This is an expected consequence of less than perfect receiver coverage, $p_i < 1$, at most sites. Simulated trajectories in Fig. 8 raise a prospect that careful hydrodynamic simulation might extend the utility of present measurements by extrapolating all detection events to become paths taken over a time scale commensurate with the tidal cycle.

Beyond 20 days from the start of tagging, alewives were detected more widely over the Minas Basin and Minas Passage, and pair separations indicated that individuals become separated by similarly large spatial scales. At this stage, alewives are lost more rapidly from the study area with an e-folding time scale of 8.8 days. Some of the loss might be attributed to predation by Atlantic harbor porpoise (*Phocoena phocoena*) and striped bass which are commonly found in the vicinity of Minas Passage [1, 29], but most of the loss is expected to reflect departure through Minas Passage and out of the monitored area. Once offshore, nearer the juncture of Minas Basin and Minas Passage, alewives are in water that is both deeper and has faster currents. Now larger tidal excursions can be expected to pass through locations over which the spatial structure of tidal currents varies in substantial ways. These are the conditions required for Lagrangian chaos [43] and some trajectories should be expected to become aperiodic, causing substantial dispersal of tagged alewives throughout Minas Basin and Minas Passage (Figs. 2, 5). Again, the idea can be illustrated by calculating trajectories of passive particles from modeled currents (Fig. 8). During spring tides, a particle released at station 9 at the start of the ebb tide is carried into the more collimated currents in Minas Passage and the subsequent flood tide carries the particle into the center of Minas Basin, far from its starting position (magenta line, right panel, Fig. 8). Irregular, aperiodic paths have also been measured in the vicinity of Minas Passage [46] and a drifter track (right panel of Fig. 8) shows large net displacement over a tidal period.

Alewives were sometimes observed to move great distances over short time scales (as much as 52 km in a day) which seems unlikely by swimming alone. Over longer time scales, movement of American shad (*Alosa sapidissima*) [11] and post-smolt Atlantic salmon [30] have been associated with tidal residual current [8]. The present study is the first biotelemetry indication that large-scale tidal mixing (Lagrangian chaos) plays a substantial role in the migration of alewives within Minas Passage and Minas Basin.

Even though the receiver array could only monitor a small portion of the width of Minas Passage, individual alewives were observed to make up to 10 transits back and forth through Minas Passage, taking as long as 15 days from first entering Minas Passage to final

departure. Currents in Minas Passage reach upwards of 6 m/s [27], so it is unlikely that alewives could control their swimming behavior. Fast currents and multiple passes are expected to increase the likelihood of alewives encountering in-stream tidal turbines at the FORCE test site (Fig. 1). Surface flotsam is well known to pass back and forth through Minas Passage over many tidal cycles [6]. Current-assisted movement in this area has also been shown for tagged striped bass, with movements into the Minas Basin on the flood tide, and into the Minas Channel on the ebb tide [29]. Flow through Minas Passage will exit as a turbulent jet [50], whereas the return tide will enter more like broad flow into a point sink [4]. Thus there are conditions favorable for both chaotic and stable trajectories through Minas Passage [46], the combination of which are hypothesized to at least partially determine paths taken by alewives through this area. The present results would be consistent with alewives being more likely to pass to the south of the FORCE test site, as was also found for striped bass [29] and drifter tracks [46]. With further measurements to determine the effective area monitored by receivers at the FORCE test site, the presently reported work could be extended to quantify the probability that tagged alewives encounter a tidal turbine.

It is interesting that post-spawning fish remain near the mouth of Avon channel for so long, when they could depart sooner with only a modest swimming effort. This raises a possibility that banks associated with the Gaspereau and Avon rivers could be used as feeding sites. A study conducted on the northern coast of Minas Basin showed evidence of alewives foraging in the nearshore habitats at a time that would coincide with the end of their spawning runs [49]. Based on those data, alewives feed on a diverse range of both pelagic and benthic prey that are abundant in the Minas Basin, such as *Eurytemora herdmani*—a species of planktonic calanoid copepod that has been shown to be a principle food item for planktivorous estuarine fishes found in Minas Basin during spring and early summer [24]. Female *E. herdmani* carry clutches of eggs that remain viable following ingestion and evacuation but make the female vulnerable to visual predation [39]. It is conceivable that post-spawning adults pause near the mouth of their spawning river to rebuild energy reserves before continuing their migration to the outer Bay of Fundy, where adult alewives have also been demonstrated to feed [25]. The dominant daytime presence of alewives at the Guzzle (Table 3) is consistent with visual feeding, but no sampling of feeding alewives are available to test this hypothesis.

Large-scale dispersion by tidal currents plays a significant role in alewife migration, but it is not inevitable. Such chaotic trajectories over large distances might be largely avoided with a small swimming effort to remain in shallow waters. Factors that induce alewives to move into deeper waters are, therefore, of fundamental importance. Presently we observed that alewives followed 14 °C water as they migrated down Gaspereau River and through Minas Basin. Measurements showed that water temperature increased seasonally, fluctuated with tidal advection, and increased from deeper, offshore to shallower, nearshore waters. For the first 20 days post-tagging, alewife detections fell along a 14 °C average across all sites, with detections at shallow-water sites occurring primarily during the cooler high tides. Shortly after a rapid temperature rise ~ day 15, alewives begin to be detected in the cooler, deeper waters of Minas Passage, after which detections decline rapidly throughout the study area until no alewife remain by mid-August. Alewives were not observed further towards the head of the Avon than station 16, probably because water temperature there was already too high by the time they had migrated to the mouth of the Gaspereau River. As seasonal heating continued, alewives moved offshore, into deeper water. Consistent with avoidance of warmer nearshore waters, alewives that were tagged later spent less time in the area than those tagged earlier. However, alewives were not observed at nearshore sites in Minas Passage even though temperature there was low; this was likely because, having moved into deeper water, alewives were mostly moved by tidal transport, and only a very small proportion of the tidal transport through Minas Passage would be adjacent to the shore. Overall, our observations of alewife presence in the study area were congruent with catches from fishing weirs in Minas Basin, which show alewives having high abundance in late June but subsequently decreasing in number in July to early August [3]. Early studies on American shad found that oceanic migration along the coast occurs via "migration corridors" where water temperatures are 3–15 °C, with a preferred range of 7–13 °C [36]. We might similarly expect alewives to exhibit a temperature preference as they leave the freshwater environment.

The uneven distribution of stations and sampling effort across the study area introduces certain limitations to this study. The concentration of sampling stations was lower in northern Minas Basin, with fewer stations dispersed over a greater area compared to inshore. Therefore, fish trajectories are undersampled throughout most of the study area. There were relatively few individuals detected and few presence events at the North, South, and East Basin locations, but this does not mean that alewives are not common in those general areas. Alewives may have become greatly dispersed by the time they moved North, and large East–West tidal excursions are expected to sweep them into the central part of Minas Basin, where

there are no receivers monitoring. Receiver stations were too sparse to define detailed fish trajectories, but at some locations within Minas Basin measurements were sufficient to demonstrate spatial connectivity within tidal time scales. Given that tides play an important role in defining alewife movement, there is every reason to expect that accurate hydrodynamic modeling could be used to interpolate more detailed tracks between connections obtained from acoustic telemetry. There is also the possibility that tracks of acoustically tagged alewives might be directly measured in Minas Basin by mounting VR2W receivers to current-following drifters [46].

Conclusion

The short in-river residence time post-spawning observed in this study is consistent with findings by Eakin [14] from the Hudson River, New York. Losses were high during the brief down-river migration, probably reflecting mortality associated with predation and environmental challenges, while mortality rate was less within Minas Basin. Movement in Minas Basin was strongly influenced by tidal currents, with the first 2 weeks spent nearshore, followed by some offshore dispersion. Offshore alewife movement was consistent with moving to cooler offshore waters in order to avoid seasonal warming above 14 °C. Once offshore within Minas Basin, alewives were widely dispersed by tidal currents and mixed out of the study area. Tides carried alewives through many transits of Minas Passage during their post-spawning migration.

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