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ARTICLE

Adult Sea Lamprey approach and passage at the Milford Dam fishway, Penobscot River, Maine, United States

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Abstract

Objective: Sea Lamprey *Petromyzon marinus* provide important ecological services within their native range, such as nutrient cycling, and can also act as a prey source for other species. Adult Sea Lamprey must access freshwater rivers to spawn, and because of this they are susceptible to changes in river connectivity. Human-made structures, such as dams, can exclude them from usable habitat. Sea Lamprey dam passage has not been extensively studied in Maine, despite Maine being within the native range of this species. The goals of this study were to evaluate upstream passage efficiency at the Milford Dam on the Penobscot River, Maine, and to provide comprehensive information about adult Sea Lamprey passage at five other dams throughout the Penobscot River watershed.

Methods: In 2020–2021 we captured and tagged 150 Sea Lamprey at the Milford Dam, the lowest dam in the Penobscot River, Maine, and displaced them downstream to assess passage efficiency at this dam and five upstream dams. In 2020, 50 Sea Lamprey were released on the east shore of the river downstream of Milford Dam; in 2021, the east shore release was repeated with an additional 50 fish and another 50 fish were released on the west shore.

Result: Between 70–82% of Sea Lamprey were observed passing Milford Dam again after mean delay times of 9–11 days. The release location did not affect dam passage success or the amount of time that was required to locate and use the passage structures. Sea Lampreys from both release groups were equally likely to approach the entrance to the fishway upon returning to Milford Dam, despite the fishway being located against the eastern shore of the river. However, high flows shortly after release may have resulted in higher attraction to the fishway in 2020. Passage success at dams upstream of Milford was highly variable. All Sea Lamprey were able to successfully navigate past West Enfield Dam (100% passage, $n = 63$), whereas Brownsmill Dam apparently acted as a complete barrier to further migration (0% passage, $n = 7$). Fish from all years and release groups together had a median upstream migration distance of 38.8 km after fish had passed Milford Dam, and a maximum observed upstream travel distance of approximately 100 km, indicating that most tagged Sea Lamprey ended their migration in the vicinity of a dam.

Conclusion: The results of this study indicate that Sea Lamprey have high passage efficiency at the Milford Dam and highlight areas within the Penobscot River basin—such as the Brownsmill Dam—where passage facilities are currently inadequate for Sea Lamprey.

KEYWORDS
dam passage, Maine, Penobscot River, Sea Lamprey

INTRODUCTION

Diadromous fishes migrate between marine and freshwater habitats to spawn and grow, and are therefore particularly vulnerable to river alterations that impede movement between these two ecosystems (Moring 2005). An analysis by Limburg and Waldman (2009) of diadromous fish abundances in the North Atlantic indicated that most of the populations in their study declined by over 90% between early surveys (late 19th to the early 20th centuries) and those conducted more recently (late 20th to early 21st centuries). The authors attributed these declines largely to dams preventing migratory fishes from accessing all potential spawning reaches (Limburg and Waldman 2009).

Sea Lamprey *Petromyzon marinus*, which are native to the east coast of North America and northern Europe and the Mediterranean (Beamish 1980; Hansen et al. 2016), have declined throughout their range, likely because of the damming of free-flowing rivers that Sea Lamprey rely on for spawning and rearing (Moring 2005). Sea Lamprey spawn in rivers, after which all adults die (Saunders et al. 2006). Juveniles (also known as ammocoetes) spend up to 8 years in their natal streams acting as burrowing filter feeders before undergoing a metamorphosis during which they acquire eyes and rasping mouth parts (Beamish 1980). Juveniles then emigrate to saltwater and parasitize fish and other animals before maturing and returning to freshwater to complete their life cycle. Unlike other anadromous species such as the Pacific salmon *Oncorhynchus* spp., Sea Lamprey do not necessarily return to their natal streams to spawn and die (Waldman et al. 2008). Thus, an abundance of free-flowing rivers within the Sea Lamprey's range is necessary for this species to successfully reproduce. When free-flowing rivers are interrupted, such as occurs when dams are constructed, upstream migrating Sea Lamprey may experience migratory delays or even abandon migration altogether (Castro-Santos et al. 2017).

The Sea Lamprey is ecologically important within its native range. Larval Sea Lamprey can achieve mean densities of over 22 individuals/m^2 in the sediment of their natal streams (Pajos and Weise 1994), making them an abundant food source in areas where high densities occur. A study of fish predation on larval Pacific Lamprey *Entosphenus tridentatus* on the west coast of North America found that larvae were readily eaten by a variety of fish species, including Chinook Salmon *Oncorhynchus tshawytscha* and Coho Salmon *O. kisutch*, respectively (Arakawa and Lampman 2020). Because larval lamprey are slender and lack bones, even large larvae can be easily consumed by fish predators (Arakawa and Lampman 2020).

> **Impact statement**
>
> Sea Lamprey are an ecologically important species in their native range. Although they contribute to nutrient cycling and serve as prey for other species, little is known about how damming has affected them. We studied migratory movements of adult Sea Lamprey in the Penobscot River, Maine, a heavily dammed coastal river system.

Sea Lamprey also act as a conduit for marine derived nutrients into upstream river reaches through the deposition of their carcasses (Weaver et al. 2016), and their spawning activities condition substrate for other species, such as federally endangered Atlantic Salmon *Salmo salar* by removing fine sediments during nest building (Saunders et al. 2006; Nislow and Kynard 2009; Sousa et al. 2012). Studies in spawning streams in Maine indicate that the nutrient subsidies provided by adult Sea Lamprey carcasses benefit both larval Sea Lamprey and macroinvertebrates (Weaver et al. 2016, 2018). Sea Lamprey in a small tributary of the Connecticut River (Massachusetts, USA) contributed up to 20% of the stream's total annual phosphorus budget through the decomposition of their carcasses after spawning (Nislow and Kynard 2009). This contribution was contingent on the successful passage of Sea Lamprey at a downstream main-stem dam (Nislow and Kynard 2009).

Despite their ecological importance and observed declines, little is known about Sea Lamprey movements and interactions with dams in the Penobscot River, Maine. At over 22,000 km^2, the Penobscot River watershed is the largest watershed in the state of Maine. The main-stem Penobscot River has an extensive history of damming in the basin (Walburg and Nichols 1967), but throughout the past decade restoration projects including dam removals and fish passage improvements have been implemented (Opperman et al. 2011; Trinko Lake et al. 2012). The Veazie (river kilometer [RKM] 48) and

Great Works (RKM 58) dams were removed and the Howland Dam (RKM 99) bypassed with a nature-like fishway from 2012 to 2016. However, there are still six dams in our study area, which does not include all of the dams that are present on the main-stem Penobscot River or its major tributaries (Figure 1). Trinko Lake et al. (2012) estimated that even after the Veazie, Great Works, and Howland dams were no longer barriers to migration, Sea Lamprey would still only have access to approximately 53% of their historic range. Their estimate was based on historic records of distribution and life history characteristics of the species concerned, and they specifically did not take into account passage efficiencies at dams that were expected to remain in the system (Trinko Lake et al. 2012). We did not evaluate the amount of habitat that was available to Sea Lamprey, but as of the time of this study, fishway effectiveness for Sea Lamprey had still not been evaluated.

There were two goals of this study: (1) evaluate upstream passage efficiency of adult Sea Lamprey at the Milford Dam and whether direction of approach (approaching from immediately downstream of the fish way or not) affected passage and (2) provide comprehensive information about adult Sea Lamprey passage at five additional dams in the Penobscot River watershed to shed light on the migratory extent of this species and where additional passage barriers my occur. Regarding the first goal, we hypothesized that Sea Lamprey that were released on the east bank of the Penobscot River, directly downstream of the fishway, would approach the dam near the fishway and pass the dam more quickly than Sea Lamprey that were released on the west bank.

METHODS

Study site

Milford Dam is the first dam that anadromous adult fishes encounter on their upstream spawning migration in the Penobscot River (Figure 1). The dam structure is 6 m high, approximately 630 m wide, and the powerhouse approximately 145 m wide. Milford Dam has a single fishway that is located on the eastern shore of the Penobscot River, equipped with an automated fish lift (Figure 2, inset). This lift was installed in 2014 at the same time that the Denil fishway that had previously provided passage at Milford was decommissioned (Penobscot River Restoration Trust 2018). The Denil fishway is reopened when maintenance at the dam requires that the fish lift be shut down for extended periods. During our study period in both years (2020 and 2021), only the fish lift was in use; the Denil fishway remained closed while our tagged fish were in the river.

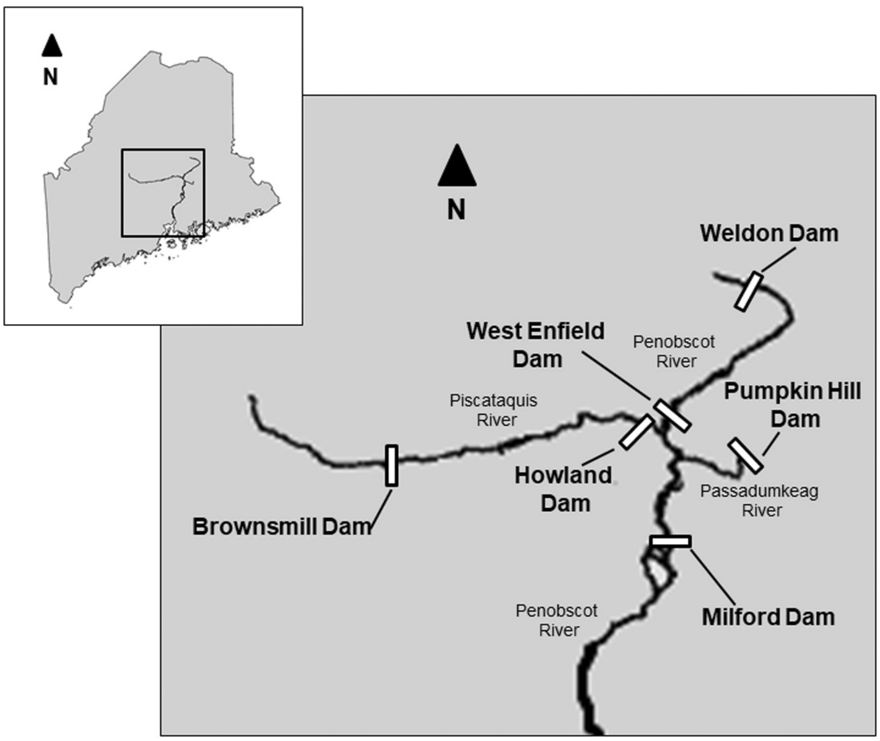

FIGURE 1 Location of six dams where the passage rates of radio-tagged Sea Lamprey were recorded on the main-stem Penobscot River and its major tributaries. The location of the Penobscot River within the state of Maine is outlined in the inset.

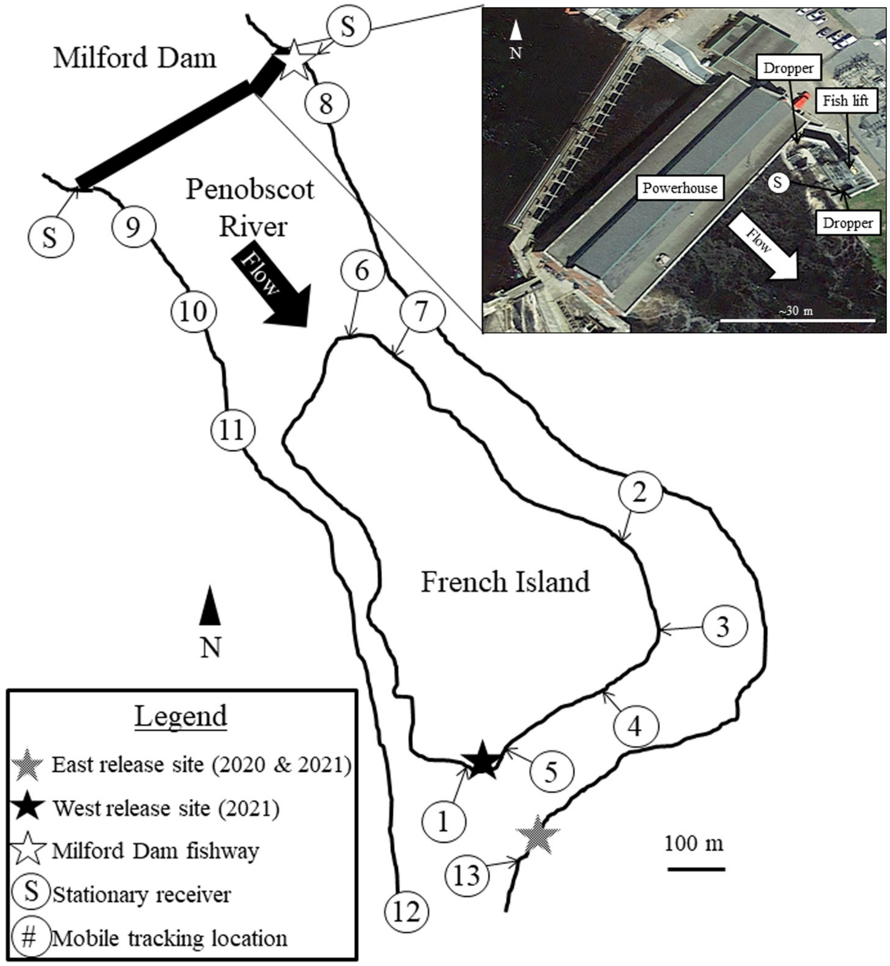

FIGURE 2 The Penobscot River immediately downstream of the Milford Dam. Release sites are indicated by stars: The east release site (shaded) was used in both 2020 and 2021, and the west release site (black) was used in 2021. The white star indicates the location of the Milford fishway. The stationary radio receiver locations for 2020–2021 ($n=2$) are shown in circles that are marked with the letter "S." Numbered circles ($n=13$) indicate locations where daily mobile tracking took place in 2021. The inset is an aerial view of the Milford Dam powerhouse on the east side of the river showing the locations of the two dropper antennas relative to the fish lift. The "S" within the inset indicates the position of the stationary radio receiver and associated Yagi antenna.

Hereafter, "fishway" refers to the fishway leading to the fish lift, rather than the Denil fishway.

To access the fish lift, fish enter the fishway opening on the east side of the river and navigate around a 180° bend before encountering the trap. Gates at the entrance of the trap hopper (a large container with the ability to open at the bottom) controlled entry and exit to the trap. The gates could be opened and closed automatically on a timer or operated manually from a control panel (E. Peterson, personal observation). Fish that were retained in the trap were lifted approximately 6 m and dumped into the upper fishway. From there, they could swim through the upper fishway into the Milford Dam headpond or they could be intercepted at a smaller, secondary hopper associated with a fish-sorting facility that is operated by staff from the Maine Department of Marine Resources.

Sea Lamprey capture and tagging

In 2020 and 2021 we collected adult migratory Sea Lamprey at the Milford Dam fish sorting facility. In 2020, 50 Sea Lamprey were captured, tagged, and released 1 km downstream of the dam on the eastern shore of the river. Tagging was repeated in 2021, with an additional 50 Sea Lamprey that were released at the 2020 release site (hereafter, "east release"), along with 50 Sea Lamprey that were released on the western side of the channel ("west release") directly across from the east release site (Figure 2).

Capture, tagging, and release took place on June 1 and June 3 in 2020 and May 25–26 in 2021. The Sea Lamprey that were judged to be in good condition (i.e., did not have any visible wounds) and were placed in MS-222 solution (buffered 20 MM Na_2CO_3, pH = 7.0) until they lost the ability to orient and became unresponsive to touch stimuli.

The Sea Lamprey were then measured (mm) and tagged using internal radio tags. The radio tags (MST 820; Lotek Wireless, Inc., Newmarket, Ontario, Canada) measured 8×20 mm and weighed 2.1 g, with a 2.5-s ping rate. The tags were split equally among five frequencies (the maximum number of frequencies that could be programmed into the radio receivers) to minimize signal collisions. A passive integrated transponder (PIT) tag (12 mm, APT12, Biomark, Boise, Idaho) was attached to each radio tag by using a cyanoacrylate adhesive. This added approximately 2 mm to the diameter of the tag and allowed the fish to be detected on a PIT antenna array that was located near the exit of the Milford Dam fishway. The Sea Lamprey were wrapped in a wet towel during the surgeries, which took approximately 90 s. First, a small incision just large enough to accommodate the radio tag was made in the peritoneal cavity. The radio tag antenna was threaded through a 14-gauge septum needle, passed through the incision, and pushed through the skin a few centimeters behind the incision. The tag was then guided into the incision manually while gently drawing on the antenna. The incisions were closed using two or three Vicryl sutures (Ethicon 4–0 RB-1; Molina-Moctezuma et al. 2021), and the Sea Lamprey were then allowed to recover in freshwater before release. The Sea Lamprey were considered recovered when they could orient in an upright position and were observed swimming in the recovery tank.

The Sea Lamprey were transported by truck to their respective release sites in a tank of aerated river water, with a maximum of 50 fish in the tank. Both release sites were less than 2.5 km from Milford Dam by road, and once the truck left the dam site, transport time to each release site was approximately 5 min. The fish were transferred into nets or buckets and carried to the edge of the water, where they were released near to the shore. They were monitored after release to ensure that they swam into deeper water.

Postrelease monitoring

The arrival of Sea Lamprey to Milford Dam was monitored by stationary radio receivers that were positioned at either end of the dam (Figure 2) that detected radio signals in the area extending about 280 m downstream of the dam. The antenna on the west side of the dam was located on a platform at the edge of the dam structure and pointed about 45° downstream of the dam structure. The eastern antenna was mounted on a railing overlooking the entrance to the fishway and pointed straight across the river. Two PIT antennas in the upper part of the fishway near the exit to the headpond were used to detect Sea Lamprey that were passing through the fish lift. The radio receiver stations consisted of a four-element Yagi antenna associated with a scanning receiver (Lotek SRX-800D, SRX-DL, or SRX-1200D). The receiver station on the eastern side of Milford Dam was also equipped with dropper antennas that were placed (1) inside the fishway near the entrance and (2) behind the fish-lift hopper (Figure 2) to monitor entrance to the fishway and entrance to the trap, respectively. The droppers were made from coaxial cable with a single connector pin at the end and submerged using weights attached to the cable. The PIT antennas were built following the methods described in Kazyak and Zydlewski (2012). Both antennas were pass-through antennas that were mounted to plastic barriers on the walls and floor of the fishway. The plastic barriers prevented the antennas from touching the concrete because the rebar within the concrete can cause interference when the antennas are directly in contact with the concrete.

Daily mobile tracking was carried out in the vicinity of Milford Dam during the time that stationary receivers were operational from May 27, 2021, to July 16, 2021, a period that should cover the entire immigration period of adult Sea Lamprey (Saunders et al. 2006). Personnel that were equipped with a portable radio receiver (Lotek SRX-400) and a handheld Yagi antenna visited 13 locations from the southern tip of French Island to Milford Dam on foot (Figure 2). At each location, tag codes and the signal strength of detections were recorded at a consistent gain setting. Mobile tracking above and below Milford Dam from canoes or motorized boats took place opportunistically throughout the summer during 2020 and 2021.

Approach to Milford (2021)

The relationship between detection signal strength and distance from a given antenna was established using a test tag (Lotek MCFT3-L) and a handheld GPS unit (Garmin eTrex 20×). The test tag and GPS were either carried or placed on a remote-controlled boat within the reach extending approximately 450 m downstream of Milford Dam and spanning the width of the river (approximately 300–350 m). Transects were either walked or floated with the remote-controlled boat while the GPS was set to actively track and record its location. After the transects were completed, the GPS tracks were downloaded and the data from the stationary radio receivers at Milford were collected. The data from both stationary receivers were pooled because an outage in the western receiver early in the season caused that receiver to have an incomplete detection record of real tags, and limited its usefulness during the time tagged Sea Lamprey were present.

Using the timestamps associated with the points on the GPS track and those associated with the detection of the test tag on the Milford receivers, it was possible to estimate the location of the test tag when detections occurred. The signal strength of the test tag could then be related to the tag's distance from the receiver at the time of the detection. Because the timestamp on the GPS was only accurate to the minute (i.e., it did not include a reading of seconds within each minute), the GPS coordinates and the detection signal strengths were averaged for each minute. Visual analysis in ArcGIS Pro showed that averaging the coordinates on this timescale did not meaningfully change the location that was associated with the detection. The data from all minutes with both a GPS location and an estimated signal strength were retained for further analysis.

The data set consisting of timestamp, coordinates (in decimal degrees), and average signal strength were processed and analyzed using Program R (R Core Team 2021). The coordinates were converted to Universal Transverse Mercator units, and then the Pythagorean theorem was used to calculate the distance in meters between the stationary receiver, which had a fixed location, and the location of the GPS unit. Using signal strength as a predictor variable and distance as the response variable, we derived the following relationship:

$$y = 301.97 - 0.367x, \quad (1)$$

where y is the distance in meters from a given receiver set to a gain of 50 and x is the signal strength of the detected tag ($R^2 = 0.72$). Although the test tag was on the surface of the water (on the deck of the remote controlled boat), we assumed that changes in bathymetry would make little difference in the signal strength of tags that were located underwater, as the majority of the area surveyed is wadeable.

For each detection of a radio tag from a live Sea Lamprey, equation (1) was used to compute the distance in meters between the tag (and therefore, the Sea Lamprey) and the stationary or mobile receiver on which it was recorded. Circular buffers were then created around the location of the receiver on which the detection was recorded using the computed distance from the receiver as the radius of the circle, using ArcGIS Pro. Sea Lamprey location was estimated on a daily basis as the intersection point of two or more buffers. When a Sea Lamprey was detected more than once from the same location, the calculated distances that were recorded from that location were averaged. Given that mobile tracking took place over only a few hours each day, the estimated location was assumed to be representative of the Sea Lamprey's location during that period.

The estimated location where each Sea Lamprey initially approached Milford Dam was taken to be the first assigned location after release that was upstream of French Island (i.e., within approximately 450 m downstream of the dam). This area coincided with the area where signal strength mapping took place. If Sea Lamprey were initially located downstream of the powerhouse, they were considered to be approaching the "east side" of the dam. Sea Lamprey that initially approached the dam structure itself were approaching the "west side" of the dam. It was clear from aerial imagery and on-the-ground observations that the influence of the attraction flow coming out of the fishway was restricted to the eastern side of the channel and likely did not extend beyond the width of the powerhouse.

For Sea Lamprey that approached Milford Dam, we obtained the time of entry (night vs. day) to the fishway and the time of dam passage. Time of fishway entrance was assigned to the timestamp of the first detection of a lamprey on either of the dropper antennas. Passage time—the time at which the fish successfully passed upstream of the dam—was assigned using either the timestamps from detection on the Milford PIT array or detections on the stationary radio receiver immediately upstream of Milford Dam. Passage time could also be inferred as the time when Sea Lamprey that were known to pass the dam disappeared from the Milford radio antennas, and their next detection was upstream of the dam. In 2021, entry times to the fishway were recorded as the timing of the final fishway entry prior to successful passage. This was because the intensive mobile tracking that took place in that year made it possible to determine if Sea Lamprey had entered and exited the fishway multiple times prior to passage (i.e., Sea Lamprey were detected entering the fishway by the dropper antennas and subsequently located outside of the fishway in the main stem). Night was defined as the period between the beginning of civil twilight on the evening of a given day and the end of civil twilight on the morning of the following day (Time and Date AS 2021).

Upstream movements (2020 and 2021)

Movements upstream of Milford Dam were described based on radio and PIT detections above the dam in both years. Stationary, shore-based radio receivers were located throughout the Penobscot River main stem and the Piscataquis and Passadumkeag rivers, which are major tributaries to the Penobscot River entering the main stem at RKM 99 and 92.3, respectively (Figure 1). Also, PIT arrays that were similar to the one at Milford Dam were deployed in the fishways at four dams upstream of Milford: West Enfield Dam (Penobscot River, RKM 100, vertical-slot fish ladder), Weldon Dam (also known as Mattaceunk Dam, Penobscot River, RKM 150.2, pool-and-weir fish ladder), Brownsmill Dam (Piscataquis River, RKM 163, Denil fishway), and Pumpkin Hill Dam (also known as Lowell Tannery Dam, Passadumkeag River, RKM 112.7, Denil fishway). Passage at West Enfield Dam was inferred by a radio receiver located <1 RKM downstream of the dam and the PIT array; Weldon Dam and Brownsmill Dam had upstream- and downstream-facing receivers as well as the PIT array, and Pumpkin Hill Dam had only a PIT array. Last, Howland Dam, which is located on the Piscataquis River at its confluence with the Penobscot (RKM 99) is circumvented by a nature-like fish bypass that became operational in 2016 (Opperman et al. 2011). This site was monitored by stationary radio receivers that were located at the upstream and downstream ends of the nature-like fish bypass during our study. In addition, there were four shore-based radio receivers that were located between Milford Dam and West Enfield Dam, including one that was immediately upstream of Milford Dam and another that was within 2 RKM upstream of Milford Dam. Downstream of our study area, there were 5–6 additional shore-based radio receivers in an array extending ~30 RKM downstream of the dam.

Because the Sea Lamprey were sampled within only a few days in each year and because they are assumed to represent a random sample of all the Sea Lamprey that passed Milford on those days, there was no reason to believe that observed behaviors after successfully passing the dam would differ between release groups. Therefore, the 2021 release site was not considered in the analysis of upstream movements. We recorded the maximum observed distance that tagged Sea Lamprey traveled upstream of their release sites and whether they approached and/or successfully passed any of the dams upstream of Milford Dam. There were no dropper antennas in any fishways upstream of Milford Dam, so approach was determined by a detection on a downstream-facing radio antenna or detection in a fishway via the PIT array. Successful passage was recorded when Sea Lamprey were detected on a radio antenna facing upstream of a given dam or when they were detected on a PIT antenna located near the exit of a fishway.

River discharge

Discharge records that covered the week that tagged Sea Lamprey were released in each year (June 1, 2020, to June 8, 2020, and May 25, 2021, to June 1, 2021) were taken from the U.S. Geological Survey gauge at West Enfield, Maine (USGS 01034500 [USGS WaterWatch, https://waterwatch.usgs.gov/]). The gauge records discharge (ft^3/s [0.0283 m^3/s]) every 15 min.

River discharge on the first release date in 2020 was approximately 3000 ft^3/s (~85 m^3/s) higher than the discharge on the first release date in 2021 (Figure 3). However, the 2020 discharge dropped steadily until 3 days postrelease (May 27, 2020), at which time it eclipsed the

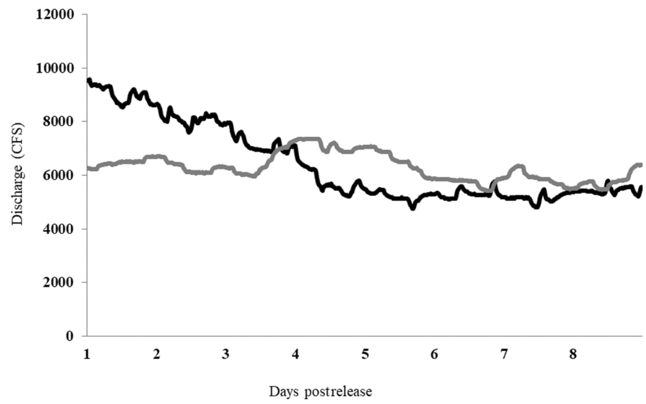

FIGURE 3 Discharge measured in ft^3/s (0.0283 m^3/s) at the U.S. Geological Survey gauge in West Enfield, Maine (USGS 01034500), beginning on the day of release of tagged Sea Lamprey and continuing for 1 week. The record for 2020 (black line) spans from June 1 to June 8, and the record for 2021 (gray line) spans from May 25 to June 1.

2021 flow record (3 days postrelease in 2021 was June 3, 2021). For the remaining 5 days that flow records were compared, discharge was higher in 2021. Discharge data were not used in any further analyses.

Data analysis

Sea Lamprey from the two release groups in 2021 were categorized as either approaching the Milford Dam fishway after release or not approaching the fishway after release. Approach was defined as detection by one or both stationary receivers or detection within approximately 450 m downstream of the dam during mobile tracking (the receivers could reliably detect tags within ~280 m). Sea Lamprey that did not approach the fishway after release included individuals that approached the western half of the dam (the side without passage facilities) and those that reversed direction downstream after being returned to the river. Reversal was assigned when the first detection following release was received greater than 1 RKM downstream of the release site, confirmed either by mobile tracking or by radio receivers from another related project that were located further downstream. Although Sea Lamprey that reversed direction after release were considered to not have approached the dam, the overall approach and passage timing for these fish was still considered in other analyses. The time between approach to the dam and passage (or abandonment of migration) was termed "delay."

We hypothesized that there may be a difference in the location of approach to Milford Dam between the east and west release groups in 2021. We therefore tested the null hypothesis that Sea Lamprey from both release groups were equally likely to approach the eastern half of the dam (thus, the Milford Dam fishway) as they were to approach the western half of the dam or to reverse direction after release. The counts of tagged individuals from each group that initially approached the eastern/fishway half of the dam after release were compared using a χ^2 test.

For those Sea Lamprey that approached the Milford Dam at any location, the time to approach and the delay time below the dam (the time elapsed from approach to passage or abandonment of upstream movements) were recorded, as well as whether or not that Sea Lamprey successfully passed the dam. Sea Lamprey that initially reversed direction were also included in these calculations. The time of approach was defined as the time of the first detection of a tagged lamprey on any of the stationary radio receivers located at Milford Dam or the first detection of the tagged lamprey within 450 m downstream of the dam via mobile tracking. Lamprey successfully passed the dam when they were detected at the PIT antenna in the upper part of the Milford Dam fishway or when they were detected on the stationary radio receiver that was located immediately upstream of the dam. Migratory abandonment was assigned when Sea Lamprey were no longer detected at Milford Dam but there was no evidence that they had passed the dam. Approach time, delay time, and passage success were compared between the two groups with a Welch two-sample *t*-test, which does not require the assumption that variance between sample populations is equal (Nicholas School of the Environment 2022). All statistical analyses were performed in Program R (R Core Team 2021), with values considered significant at $\alpha = 0.05$.

RESULTS

The mean sizes of the Sea Lamprey that were tagged in each year were similar among years and release sites (Table 1). The transmitter from one Sea Lamprey in the west release was never detected after release and was not included in any analyses. Assigning sex based on morphology was possible for 22 Sea Lamprey and was confirmed by the observation of gonads during tagging. Therefore, we know that six tagged Sea Lamprey in 2020 were females; during 2021, six females and four males were in the east release, and six females were in the west release. These sample sizes were too small to be able to include sex in any of our analyses.

Milford Dam passage and delays (2020)

Every tagged Sea Lamprey from the 2020 release was detected in the Milford Dam fishway at some point after release, with no reversal behavior documented between release and approach to the fishway. Overall observed passage success was 82% (41/50, Table 1). Forty-eight Sea Lamprey (96% of all fish tagged) were detected on a dropper antenna in the Milford Dam fishway, on the Milford Dam PIT array, or on a stationary receiver just upstream of Milford Dam within 24 h of release. Of the remaining two Sea Lamprey, one was detected entering the fishway within 36–48 h of release (the exact time of entry was unknown) and the other was not detected at Milford Dam but was detected in the vicinity of Howland Dam (RKM 99) approximately 48 h after release. This observation could be the result of imperfect detection by the radio and PIT receivers at Milford Dam but raises the possibility that Sea Lamprey could be using alternate passage routes to pass Milford Dam, such as climbing up the dam face.

The average time spent below Milford Dam between approach and successful passage was 2 days ($n = 40$; Table 1). One lamprey spent approximately 15 days (the exact date of passage was unknown) searching for passage. Among

TABLE 1 Numbers of tagged Sea Lamprey released at each study site on the Penobscot River, Maine. The values for mean length of Sea Lamprey (mm) and length range (parentheses) are reported, as well as the number and percentage (passage success) that passed Milford Dam. Delay time is the time spent between approach to the Milford Dam and either successful passage or migratory abandonment. Maximum delay times are displayed in parentheses. One Sea Lamprey from the west release group was excluded because it was never detected after release. Refer to Figure 1 for the locations of the release sites.

		2021	
	2020	East	West
Number released	50	50	49
Mean length (mm)	743 (650–810)	737 (650–820)	743 (630–850)
Number passed	41	35	36
Passage success	82%	70%	73%
Mean delay before successful passage (Max.)	2 days (~15)	3.4 days (12)	4.2 days (13)
Mean delay before abandoning migration (Max.)	8 days (15)	11 days (44)	9 days (27)

the nine Sea Lamprey that eventually abandoned migration, the mean time spent searching for passage was 8 days and the maximum was 15 days (Table 1).

The timing of fishway entrance in 2020 was skewed toward the hours between sunset and sunrise, with 31/45 (69%) of Sea Lamprey for which entry times could be determined first detected in the fishway during dark. The exact time of successful passage of Milford Dam was only known for 26 individuals that were detected on the PIT antennas in the upper end of the fishway, and 16 (62%) passed the dam during dark (Figure 4). The detection efficiency of the PIT antennas in 2020 was 63% (33/41 successful passers were detected on the PIT array). However, when detections from radio receivers were also used to confirm passage time, detection efficiency increased to 88%. The remaining Sea Lamprey could not be assigned to an exact date or time of passage because of detection gaps between the Milford radio receivers and radio receivers upstream of Milford.

Milford Dam passage and delays (2021)

The majority of Sea Lamprey for which approach time was known approached Milford Dam on the day of release. This was consistent between both release groups, with 40/49 (82%) Sea Lamprey from the east release approaching on the same day and 47/48 (98%) from the west release approaching on the same day. The remaining 10 Sea Lamprey approached the dam the day after release (overall return rate of 98%). Passage success rates between the two release groups were similar to but less than the overall passage success observed in 2020 (35/50 [70%] for the east release vs. 36/49 [73%] for the west release; Table 1). Only 25 Sea Lamprey from the east release and 26 Sea Lamprey from the west release had known entry times to the fishway, and of these 12 (48%) and 8 (31%) entered the fishway between sunset and sunrise, respectively. Among Sea Lamprey for which individual passage times could be determined, 17/33 Sea Lamprey (52%) from the east release and 12/31 (39%) Sea Lamprey from the west release successfully passed Milford Dam at night (Figure 4). There were several periods of outages for the Milford PIT antennas in 2021, but 64/71 Sea Lamprey (90%) could still be assigned to the correct date of passage and general time (i.e., day or night) of passage because of high volumes of detections from the radio receivers at Milford and directly upstream of Milford.

Time to pass after approach was not different between Sea Lamprey from the two release groups. On average, the Sea Lamprey from the east release required 3 days to pass Milford Dam after approach and Sea Lamprey from the west release required 4 days (Welch two-sample t-test: $t = -0.96357$, df = 68.797, $p = 0.339$; Table 1). The maximum number of days that any Sea Lamprey was delayed below Milford before passing the dam was 12 for the east release and 13 for the west release. Overall, 35 Sea Lamprey from the east release and 36 Sea Lamprey from the west release were successful in reascending Milford Dam. Of the Sea Lamprey that abandoned migration, delays averaged 10 days (11 days for the east release and 9 days for the west release; Table 1). Maximum delay time was 44 days experienced by one Sea Lamprey from the east release. The longest delay for any Sea Lamprey from the west release was 27 days (Table 1).

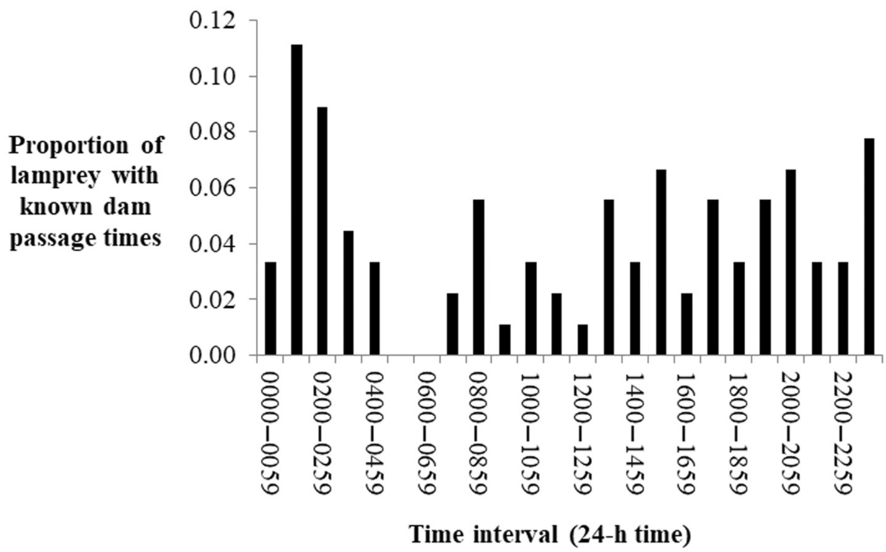

FIGURE 4 Time of dam passage for 90 Sea Lamprey at the Milford Dam. Passage time is binned by hour using 24-h time.

Approach to Milford (2021)

The movement tracks from 67 Sea Lamprey were used to determine the location of approach to Milford Dam. These 67 fish were detected from multiple locations in the days following release, and maps of their movements made it evident that these fish were alive and actively swimming. The initial locations of 31 Sea Lamprey from the east release and 36 Sea Lamprey from west release are shown in Figure 5. Only four Sea Lamprey from each release group approached the fishway side of the dam. The proportion of Sea Lamprey from the east release that did approach the fishway (13%) was higher than the proportion approaching from the west release (11%), but the difference was not significant (two-proportion *z*-test, $\chi^2 = 2.2 \times 10^{31}$, df = 1, $p = 1.0$). The remaining Sea Lamprey for which an approach location could be determined approached the dam away from the fishway.

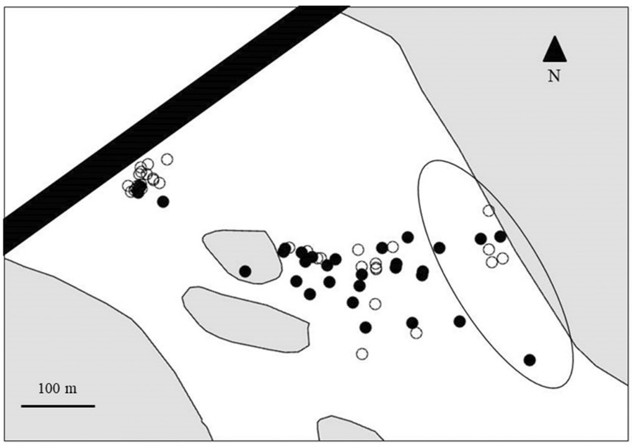

FIGURE 5 Initial location of 31 Sea Lamprey released from the east release (filled circles) and 36 Sea Lamprey released from the west release (open circles) in 2021, upon approach to the Milford Dam. The Sea Lamprey within the oval approached on the "east side" of the dam, near the fishway. The shaded areas represent land—the shaded areas within the river indicate islands that are above the surface at low flows. These islands remained mostly submerged during our study period in each year.

Upstream movements (2020 and 2021)

The majority of Sea Lamprey that passed Milford Dam in 2020 were also observed to approach and pass West Enfield Dam at RKM 100 (29/41, 71%). In both years, all tagged Sea Lamprey (29 in 2020, 34 in 2021) that approached West Enfield Dam were successful passers (Table 2; Figure 6). Similarly, 100% (7/7) Sea Lamprey approaching Howland Dam passed in 2020, and a slightly lower proportion (72%) was successful in 2021. Of the 29 Sea Lamprey that passed West Enfield in 2020, three traveled an additional 50 RKM upstream to Weldon Dam, two of which passed Weldon Dam. This is in contrast to 2021, when six Sea Lamprey approached Weldon Dam and none of them passed (Table 2; Figure 6). No tagged Sea Lamprey that approached Brownsmill Dam passed (one approached in 2020, six approached in 2021). The median distance that was traveled upstream of the release site was similar in both years (39.8 RKM in 2020; 38.8 RKM in 2021), with the Sea Lamprey approaching Brownsmill Dam accounting for the detections farthest upstream of Milford.

DISCUSSION

Overall, passage success of tagged Sea Lamprey at the Milford Dam seems to be much higher and more efficient (i.e., shorter delays) than in other major systems on the East Coast. Passage through four fishways on the Connecticut River is only as high as 55%, with passage success dropping below 30% at one fishway (Castro-Santos et al. 2017). These results were similar to those observed in Pacific Lamprey attempting passage at the Bonneville Dam on the Columbia River in Washington State (41–57% passage efficiency; Keefer et al. 2013). In contrast, 98% of the tagged Sea Lamprey returned to Milford Dam after release, and passage success was 70% or greater for all three release groups.

The high passage success for Sea Lamprey in our study may be attributed to several factors. First, the Sea Lamprey that we tagged were not naïve to Milford Dam. The Sea Lamprey that were tagged by Castro-Santos et al. (2017) were released immediately upstream of the dam where they were captured, and their movements were tracked

TABLE 2 Numbers of tagged Sea Lamprey approaching (App.) and passing (Pass.) dams throughout the Penobscot River watershed, Maine, USA. The maximum observed (max. dist.) and median distances (med. dist.) are the distances in kilometers traveled upstream of Milford Dam (RKM 61.3). BRO, Brownsmill Dam; HOW, Howland Dam; MIL, Milford Dam; PHI, Pumpkin Hill Dam; WEL, Weldon Dam; and WEN, West Enfield Dam. The locations of these dams can be found in Figure 1.

Year	App. MIL	Pass. MIL	App. HOW	Pass. HOW	App. WEN	Pass. WEN	App. WEL	Pass. WEL	App. BRO	Pass. BRO	App. PHI	Pass. PHI	Max. dist.	Med. dist.
2020	50	41	7	7	29	29	3	2	1	0	0	0	100.5	39.8
2021	97	71	25	18	34	34	6	0	6	0	0	0	102.8	38.8

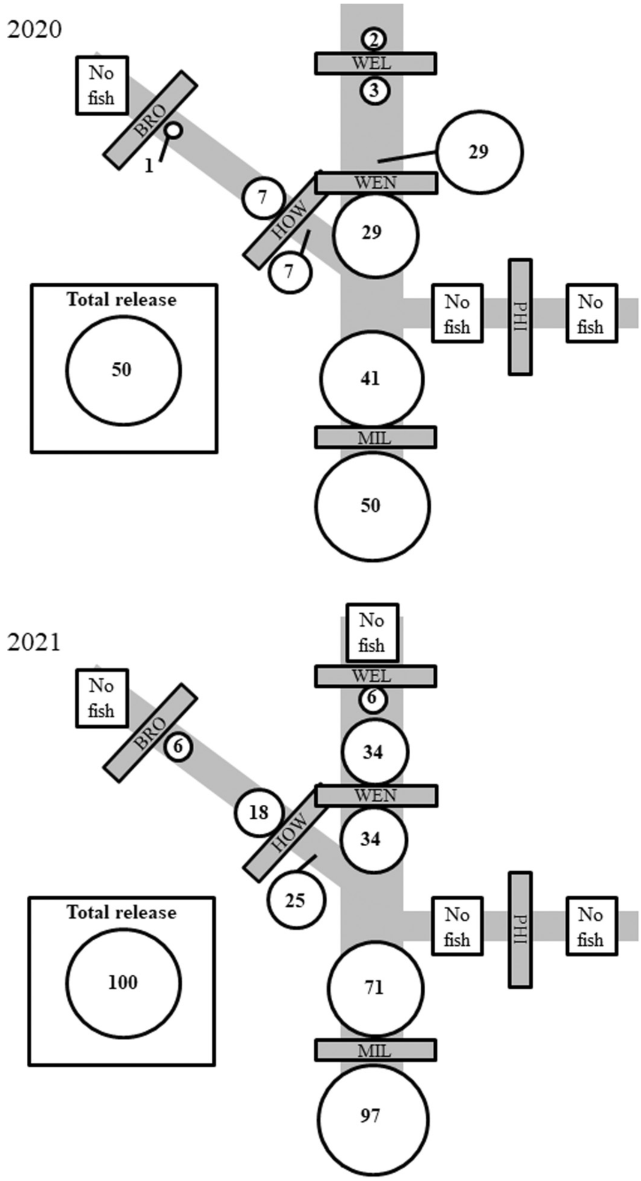

FIGURE 6 Number of tagged Sea Lamprey that approached and passed each dam in the Penobscot River watershed, Maine, USA, which was being monitored by PIT and/or radio arrays in 2020 (above) and 2021 (below, release groups combined). The number within each circle is the total number of Sea Lamprey, and the sizes of the circles are relative to the size of the release, shown in the inset. The circles that are immediately downstream of a given dam represent approach, and the circles immediately upstream represent passage. MIL, Milford Dam; HOW, Howland Dam; WEN, West Enfield Dam; WEL, Weldon Dam; BRO, Brownsmill Dam; and PHI, Pumpkin Hill Dam.

thereafter, whereas we released Sea Lamprey within 2 km downstream of the Milford Dam, which they had all already successfully passed. The fact that these Sea Lamprey had experienced the Milford Dam fishway at least once before could lead to a positive bias in future passage attempts (Hershey 2021). However, given the size and complexity of the Penobscot River downstream of Milford Dam, obtaining Sea Lamprey in this area would be difficult without the aid of the Milford Dam sorting facility. We believe that experience with Milford Dam is unlikely to be the only factor leading to high rates of passage success because high passage success was observed elsewhere in the Penobscot River as well. Notably, passage was 100% at the West Enfield Dam, located 40 RKM upstream of Milford Dam, suggesting that the particular types of fishways at these dams (fish lift and vertical slot) are conducive to Sea Lamprey passage and also that the Sea Lamprey that were used in our study were motivated to move upstream.

The findings in the above paragraph are in line with a meta-analysis by Noonan et al. (2012) that found that vertical-slot fishways and nature-like fishways tended to result in greater passage rates for all types of fishes compared with Denil fishways. Interestingly, their analysis also found that pool-and-weir fishways were among the most effective fishway types for passing fishes upstream, and yet we only saw 2/9 tagged Sea Lamprey that approached a dam with this type of fishway (Weldon Dam) pass successfully. Sea Lamprey have difficulty navigating most traditional fish passage structures, which are typically designed for other species such as salmonids (Keefer et al. 2010; Moser et al. 2010) and feature areas of high water velocity that Sea Lamprey cannot negotiate (Keefer et al. 2010). Fish lifts such as the one currently providing the majority of fish passage at the Milford Dam can pass many species regardless of swimming ability, provided that the fish can locate the entrance to the lift and are retained in the trap (Haro and Castro-Santos 2012).

Compared with other migratory species in the Penobscot River, such as Atlantic Salmon, migratory abandonment in Sea Lamprey was triggered by relatively short delays. Atlantic Salmon that were tagged at Milford Dam and transported ~20 km downstream had a passage success rate of 92% among fish that approached the dam after release, even with delays lasting as long as 155 days (E. Peterson and colleagues, unpublished data). This phenomenon may be at least partially explained by the differences in the life history and habitat requirements of Sea Lamprey compared with other anadromous species on the east coast. First, there is suitable spawning habitat for Sea Lamprey downstream of Milford Dam (e.g., Weaver et al. 2015), so Sea Lamprey do not need to pass the dam to spawn. Sea Lamprey also do not necessarily return to their natal steams to spawn but instead migrate up any suitable river when they are ready to spawn (Waldman et al. 2008). This behavioral divergence from other diadromous fishes may be a result of parasitism—Sea Lamprey are dispersed throughout the ocean by their host species, in no particular pattern—and is evidenced by high rates of genetic diversity within populations that are collected in the same freshwater locations (Waldman et al. 2008). Because they are not returning to a specific natal stream, some Sea Lamprey may have less motivation for dam passage and may seek downstream spawning habitat instead of continuing to search for upstream passage.

Perhaps the most likely reason that Sea Lamprey abandoned migration after a relatively short amount of time is that they are semelparous. Unlike Atlantic Salmon and many other diadromous fishes in their native range, all Sea Lamprey die after spawning (Beamish 1980). Therefore, lifetime fitness for Sea Lamprey is contingent on migratory motivation in a single season. McConnachie et al. (2012) correctly predicted that semelparous Pink Salmon *O. gorbuscha* reproduction would not be affected by acute stressors because of the necessity for these fish to spawn before dying at the end of their freshwater migration period. Likewise, semelparous Sockeye Salmon *O. nerka* did not alter their migratory speeds after being subjected to handling and tagging (Cook et al. 2014). It makes logical sense that semelparous species would resist a certain amount of stress in favor of completing their life cycle, such as Pacific salmon seem to do (Wingfield and Sapolsky 2003). However, chronic stress can negatively affect reproductive success (McConnachie et al. 2012), and this could be why the tagged Sea Lamprey in our study sought other spawning opportunities when they were not able to pass Milford Dam relatively quickly. The behavior of the tagged Sea Lamprey was unlikely to be negatively influenced by handling and tagging because the Sea Lamprey were held until they had recovered from anesthesia—sometimes for several hours—and our surgical methods followed those found in other studies (i.e., Bouletreau et al. 2020).

Delays of any magnitude, including the delays that we observed for tagged individuals, could be biologically meaningful for Sea Lamprey. Like most anadromous fishes, Sea Lamprey do not feed after entering freshwater (Beamish 1979). Energy concentration decreases significantly in adult Sea Lamprey as they reach maturation during their spawning migration, and a considerable amount of the total energy of both males and females is required for spawning activities (Beamish 1979). Araujo et al. (2013) reported decreases in the lipid content of over 12% (~51% down to ~38%) for Sea Lamprey that were migrating 65 km up a river on the Iberian Peninsula. We did not investigate the energy expenditures that were incurred by the Sea Lamprey in our study or quantify delays at dams upstream of Milford Dam, but it is likely that delays did occur and that the time spent engaged in search behavior throughout the system could result in higher-than-normal energy losses compared with a situation where Sea Lamprey were allowed to migrate upstream unimpeded. It is possible that if Sea Lamprey do experience significant energy losses at Milford Dam, their subsequent behavior and passage success at upstream dams could be affected. Future researchers of Sea Lamprey in an impounded system may be interested in measuring energetic losses through a mark–recapture study at multiple dams.

We know that Sea Lamprey use olfactory cues, particularly pheromones excreted by larvae, to locate suitable spawning reaches (Bjerselius et al. 2000), and we thought that olfaction may also direct Sea Lamprey to the Milford Dam. Specifically, we hypothesized that olfactory cues from the fishway would guide Sea Lamprey that were released on the east side of the river back to the fishway more quickly than Sea Lamprey that were released on the west side of the river. However, there was no evidence that release site during the 2021 season affected the ability of Sea Lamprey to find or use the fish passage at Milford Dam. Intensive mobile tracking from 2021 indicated that Sea Lamprey from both release groups did not directly approach the entrance to the fishway when first approaching Milford Dam. This lack of direct approach may be due to spill coming over the dam, causing Sea Lamprey to be attracted to areas other than the fishway entrance. Other researchers have observed Sea Lamprey seeking upstream paths that offer the lowest water velocities regardless of the location along the river channel (Holbrook et al. 2015), so it is possible that the Sea Lamprey that we tracked were not migrating strictly along the shoreline, as we assumed they may have been doing.

River discharge may have contributed to the marked differences that were observed in approach time and location between 2020 and 2021. In 2020, 96% of the tagged Sea Lamprey returned to the Milford Dam fishway or passed the dam within 24 h of release, whereas we did not see any Sea Lamprey entering the fishway so soon after release in 2021. Because there was no intensive mobile tracking below Milford Dam in 2020, it is possible that we missed the fine-scale movements of the Sea Lamprey in that vicinity and Sea Lamprey could have been approaching near the western end of the dam. However, it is more likely that high flows in the days following the 2020 releases may have enhanced attraction flow into the Milford Dam fishway. This conclusion would be consistent with other studies that noted that adult Sea Lamprey displayed decreased retreat (reversal) rates under high-flow conditions (Davies et al. 2022).

The maximum upstream extent that we recorded for any tagged Sea Lamprey was approximately 160 km upstream from the ocean (they reached Milford Dam at RKM 61.3 and then proceeded ~100 RKM upstream to Brownsmill Dam), which is similar to the distance traveled by Sea Lamprey in other studies where dams inhibited upstream migration (e.g., 140 km, reported by Beamish 1979). However, Sea Lamprey are capable of traveling even greater distances before spawning (e.g., Castro-Santos et al. 2017; Kynard and Horgan 2019), suggesting that the tagged Sea Lamprey in our study could have migrated farther upstream if not impeded by dams. Davies et al. (2022) also noted that Sea Lamprey in the River Severn, UK, tended to terminate their upstream migration directly downstream of a passage barrier. They suggest that the presence of impassable barriers is the main factor inhibiting the upstream movement of Sea Lamprey (Davies et al. 2022). We did not evaluate the presence or quality of spawning habitat in the areas where the tagged Sea Lamprey were last detected, but it is possible that the Sea Lamprey spawned before attempting to pass upstream dams. The distribution of Sea Lamprey spawning habitat in the Penobscot River and its tributaries was not treated in the current study but could be an avenue for further research.

Without adequate passage, Sea Lamprey cannot provide nutrient cycling or habitat conditioning services to upstream portions of the river (Saunders et al. 2006; Sousa et al. 2012). The loss of Sea Lamprey therefore has ecological ramifications, especially for other fishes that share parts of their native range, such as the Atlantic Salmon. The ecological services that are provided by Sea Lamprey make understanding patterns of dam approach and passage in Sea Lamprey important not just for this species but for the preservation of a functioning ecosystem.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest in this article.

DATA AVAILABILITY STATEMENT

At the time of publication, data were not publicly available from Danielle Frechette (Maine Department of Marine Resources, danielle.frechette@maine.gov).

ETHICS STATEMENT

This work was conducted under Institutional Animal Care and Use Committee protocols A2017-01-09 and 2020_05_02 approved by the Institutional Animal Care and Use Committee at the University of Maine.

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