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# Migratory behavior of adult Sea Lamprey and cumulative passage performance through four fishways

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## Abstract

This article describes a study of PIT-tagged Sea Lamprey (*Petromyzon marinus*) ascending 4 fishways comprising 3 designs at two dams on the Connecticut River, USA. Migration between dams was rapid (median migration rate = 23 km $d^{-1}$). Movement through the fishways was much slower, however (median = 0.02 - 0.33 km $d^{-1}$). Overall delay at dams was substantial (median =13.6 - 14.6 d); many fish failed to pass (percent passage ranged from 29% - 55%, depending on fishway), and repeated passage attempts compounded delay for both passers and failers. Cox regression revealed that fishway entry rates were influenced by flow, temperature, and diel cycle, with most lampreys entering at night and at elevated flows, but with no apparent effect of sex or length. Overall delay was influenced by slow movement through the fishways, but repeated failures were the primary factor determining delay. These data suggest that although some lamprey were able to pass fishways they did so with difficulty, and delays incurred as they attempted to pass may act to limit their distribution within their native range.

## INTRODUCTION

The Sea Lamprey (*Petromyzon marinus*) is a widely distributed anadromous fish that occupies both coasts of the North Atlantic Ocean. It spawns in lotic freshwater habitat, and in many cases access to spawning habitat is obstructed by dams. Although fishways can provide access to habitat, the effectiveness of these structures for sea lampreys is poorly studied (Noonan et al. 2012).

Sea lampreys are semelparous, and in their native range can be an important source of marine derived nutrients into freshwater (Nislow and Kynard 2009). During spawning they construct extensive redds, contributing to bed load transport and benthic restructuring (Sousa et al. 2012). During their juvenile stage (typically 5-6 years) they are abundant filter feeders. When these juveniles migrate to sea they can also act as an important source of nutrient transport, providing forage for marine predators as they convey terrestrial nutrients out of freshwater ecosystems. As they enter their marine phase they become parasitic, feeding on large pelagic fishes for about 2 years, after which they return to rivers to spawn and die (Beamish 1980; Larsen 1980; Riley et al. 2011). These characteristics, along with their local abundance, make Sea Lampreys an important part of their ecosystem wherever they occur.

Sea Lampreys are also opportunistic invaders and have established landlocked populations in the Laurentian Great Lakes. There, the parasitic phase has been problematic, causing, or at least contributing to precipitous declines in important freshwater fisheries (Koonce et al. 1993).

Recent efforts to control Sea Lampreys in the Great Lakes have included construction of dams and similar barriers (McLaughlin et al. 2007). These obstruct movements of adult Sea Lampreys, preventing them from accessing spawning habitat. Problematically, they also obstruct movements of native species, and any fishways that might provide passage for natives might also be passed by lamprey, negating the purpose of the dams (McLaughlin et al. 2007; 2012). This creates a conundrum: there is a need to design fishways that pass native species but that invasive lamprey cannot pass.

In the Sea Lamprey's native range, dams have been constructed for various reasons, and access to habitat has been greatly restricted (Beamish and Northcote 1989; Beamish and Northcote 1989; Lucas et al. 2009). Fishways have been constructed at many dams, but typically these have been designed for anadromous teleosts, and few data are available that describe the effectiveness of these structures for passing Sea Lampreys.

Analogous data from the Pacific Coast of North America suggest that these fishways may perform poorly. There, Pacific Lampreys (*Entosphenus tridentatus*), which serve ecological functions similar to *P. marinus*, are unable to effectively pass fishways that were originally designed to pass native salmonids. Passage performance was so poor that new fishway designs were developed exclusively for Pacific lamprey (Moser et al. 2011). Although preliminary results suggest these new fishways are effective at passing lampreys, their deployment and maintenance is costly. For conservation purposes, it is important to understand whether existing fishway designs effectively pass Sea Lampreys along with other species. Conversely, if existing fishways are effective for passing native species but constitute a barrier for lampreys, this might hold valuable information for Sea Lamprey control in their invasive range.

The Connecticut River (northeastern USA; Fig. 1) supports a large spawning population of native Sea Lamprey (20,000 – 50,000 adults are counted annually passing the first dam at Holyoke; U.S. Fish and Wildlife Service Connecticut River Coordinator's Office, pers. Comm.). These numbers have remained stable since construction of fishways on the mainstem dams between 1976 and 1987 (Gephard and McMenemy 2004). This consistency has been interpreted as evidence that the fishways are performing well, although no formal evaluation has ever been performed (Haro and Kynard 1997).

A growing consensus indicates that fishway performance cannot be evaluated based on numbers of fish passing, but should instead be measured in terms of rates, differentiating at minimum between proportions that enter from those that pass (Bunt et al. 2012; Castro-Santos et al. 2009; Noonan et al. 2012). It is also important that these rates be quantified with respect to time required to pass. This is because failure is not an instantaneous event, but rather a process that occurs over time (Castro-Santos and Haro 2003; Castro-Santos and Perry 2012), and failure to pass a fishway may be caused as much by the condition and behavior of the migrants as by fishway hydraulics (Wagner et al. 2012).

In addition to its value as a metric for quantifying passage performance at fishways, the time required to pass has broader biological relevance. Migration is often a time-limited process: various time-driven functions such as energetics, maturation, disease and mortality risks, and even time spent migrating itself can all act to terminate migration (Dingle 1996; Castro-Santos and Letcher 2010). Because of this, any time spent attempting to pass a barrier constitutes migratory delay, whether or not the animal ultimately is successful in passing the barrier. Indeed, the delay itself can cause migratory termination, and so is a key metric of passage performance.

Here we describe a study of anadromous Sea Lamprey ascending four fishways at two dams on the Connecticut River. We assessed passage performance-- quantifying both overall percent passage and percent passage per unit time--and rates of movement, and compared these quantities with analogous movements between dams. In addition we tested for effects of diel patterns and of discharge, temperature, sex, and length on entry and passage performance. Finally, we quantified migratory delay that was incurred by both passers and failers, and considered the implications of this delay for passage success and species range.

## MATERIALS AND METHODS

### Study Area

The Connecticut River is the longest river in New England, draining 29,200 $km^2$ from Canada to Long Island Sound (Fig. 1). Its indigenous fauna includes 10 diadromous species of which the Sea Lamprey is among the most abundant (Gephard and McMenemy 2004). The first three barriers on the mainstem are Holyoke Dam (rkm 135), the Turners Falls Dam complex (rkm 190.5–194), and Vernon Dam (rkm 227; Fig. 1, Table 1). Passage at Holyoke is provided by dual fish lifts.

Between Holyoke and Turners Falls the river is primarily free-flowing: a natural gorge caused by the Holyoke Range restricts the impoundment to the lower 3 km of this reach. Flows and velocities upstream of this point are governed by hydrology and upstream hydroelectric operations (Castro-Santos and Letcher 2010).

At Turners Falls, a 3 km long power canal separates the primary hydroelectric station (‘Cabot Station’) from the dam (Fig. 2). The fishway adjacent to this powerhouse (‘Cabot’) is the primary ascent route for anadromous species (Sullivan 2004; Haro and Castro-Santos 2012; Moffitt et al. 1982; Rideout et al. 1985). Fish that ascend Cabot must enter and navigate the power canal, at which point they must enter another fishway (‘Gatehouse’) via one of two entrances.

Parallel to the power canal is the original riverbed, or ‘bypassed reach’ of the river. During the migratory season dam operators maintain a minimum flow in this channel of 11.3 $m^3s^{-1}$. During freshets, however, discharge that exceeds the canal’s capacity (>510 $m^3s^{-1}$) is diverted through the bypassed reach. A separate fishway (‘Spillway’) was constructed at the dam to pass fish that ascended the bypassed reach. Spillway fishway connects directly with Gatehouse fishway. This connection occurs adjacent to, and at the same level as the upstream end of the power canal. The Spillway-Gatehouse connection provides a direct route from the bypassed reach to the river upstream of the dam, but it is also possible for fish to fall back into the power canal via the Gatehouse entrance, in which case fish must re-enter Gatehouse via one of the canal entrances described above. Both Cabot and Spillway fishways are modified Ice Harbor type pool-and-weir designs; Gatehouse fishway is a double-Hell's Gate, vertical slot design, capable of accommodating varying headpond and canal levels. Note that each fishway has different structural and hydraulic characteristics, with Gatehouse fishway having the least elevation gain of all the fishways tested (Table 1).

Once past Gatehouse, fish return to the open river above the dam and are able to migrate unimpeded to Vernon Dam, where a single fishway provides access to the upper river. Fishway design specifications are detailed in Table 1 and Fig. 2.

Spawning habitat is available both upstream and downstream of these three barriers, with about one-third of total available habitat occurring above Vernon Dam, one third between Holyoke and Vernon, and one-third below Holyoke. Active spawning and recruitment is known to occur in each of these areas, although most of the best quality habitat is upstream of Holyoke (Fig. 1).

### Collection, tagging, and monitoring

Lampreys were collected at the Holyoke Dam fish lift (Fig. 1), fish were measured (total length) to the nearest millimeter, and surgically implanted with a uniquely coded 23-mm glass-encapsulated HDX-PIT tag (134.2 kHz; Texas Instruments, Dallas, Texas. Castro-Santos and Vono 2013). The tags were inserted through a small (0.4 cm long) incision in the body cavity along the ventral midline. To minimize stress and handling time, no anaesthesia was used during the tagging or handling. Once tagged, fish were immediately released to the exit channel of the fish lift, with free access to the river upstream of Holyoke Dam. Total handling time was 30 -45 s per fish. Lamprey movements were monitored with pass-through HDX-PIT tag interrogation antennas (Castro-Santos et al 1996). PIT antennas were installed at entrances and exits at Cabot, Spillway, Gatehouse, and Vernon fishways (Fig. 1). Five additional antennas were placed in the slots and channels of Gatehouse Fishway. Two antennas were installed on downstream bypass structures at Holyoke Dam and adjacent to Cabot Station to identify any fish that passed downstream using those routes. A PIT antenna at the release location recorded the initial time each fish was released, and also monitored for any fish that fell back downstream and subsequently passed. Final detection at the Holyoke fish lift antenna was considered the time of entry into the study—throughout this article we refer to this as ‘self-release time’. All antennas were interrogated at 10 Hz using a custom-built multi-reader system, with each antenna being interrogated by a separate reader, and all readers at a given location interfaced to a single computer with a common clock (Castro-Santos et al. 1996; Haro et al. 2004). Individual exposures to antennas were identified by series of sequential reads separated by < 1 s. Each of these series was considered a single ‘presence’ in our analyses. Detection zones for all antennas covered the entire opening, to a distance of 0.5 - 1 m from the opening Monitoring began before the first release and continued through the end of fishway operation (15 July).

River and canal discharge were monitored and recorded on 15-minute intervals. Water temperature was monitored in the Turners Falls power canal and recorded hourly.

## Data analysis

For each route of passage, we calculated (1) overall percent entry (%$E_O$: 100 * number entered/number released); (2) fishway and dam-specific percent passage (%$P_D$: 100 * number passed/number entered; and (3) overall percent passage (%$P_O$: 100 * number passed/number released)).

The first detection of a fish at a fishway entrance represented arrival time. Although it was possible for fish to be detected without having physically passed the plane of a fishway entrance, the range of these antennas was small enough to assume that any detected fish were either within the strongest flow of the entrance jet or attached immediately adjacent to the fishway entrance. In either case, any fish that was detected was effectively within the influence of the fishway, and for the purposes of this paper will be considered as having entered. Travel time and speed through each reach were estimated as the time of last detection at a downstream location to the time of first detection at the next barrier upstream. For each reach-specific travel time, the corresponding migration speed (m $s^{-1}$) and relative migration speed (BL $s^{-1}$, BL= body length) were calculated.

Effects of individual and environmental variables on entry rates into Cabot and Spillway fishways were estimated using Cox's proportional hazards regression with time-varying covariates. This is a theoretically-robust method for estimating event rates that allows for unequal exposure to riverine conditions as well as for competing risks or censoring, e.g. such as occurs when fish enter via alternate routes. Under this framework rates are calculated as the proportion of the available population that experiences an event on a given time interval; importantly, the number available decreases as fish pass by any route or abandon the effort (Cox 1972; Castro-Santos and Haro 2003; Castro-Santos and Perry 2012). Time to enter was measured as elapsed time between one day following release at Holyoke and entry into either Cabot or Spillway fishways. The one day lag constitutes a 'guarantee time', representing a theoretical minimum time required to traverse the river between Holyoke and Turners falls (see Results). We used AIC to select the best model(s), considering any model with ΔAIC < 2 as having sufficient evidence for consideration among the best models.

Because the antennas at the fishway entrance could only identify presence and not whether fish were ascending or descending the fishway on a given detection, we used interval analysis to differentiate among attempts. This approach identifies individual attempts to pass each fishway by calculating lags between detections at the fishway entrances (Castro-Santos 2004; Castro-Santos and Perry 2012). Ninety nine percent of the intervals between presences at fishway entrances were < 1 h. However, we were unable to determine with certainty whether these intervals represented fish dropping out of a fishway or new entry events. To avoid overestimating the number of distinct attempts to ascent the fishway, we grouped all presences at fishway entrances within 24 hours of each other into single attempts, with longer intervals indicating new attempts.. The 24 h threshold was based on the minimum time required to pass the longer fishways, and this approach ensured that we did not overestimate the number of times individual fish attempted to pass a given fishway.

Transit times through each fishway were calculated as the time elapsed between the last detection at the bottom of a fishway to the last detection as a fish exited the top. By using the last detection at the fishway entrance this method eliminates bias caused by repeated and/or failed attempts to enter and pass the fishway. Transit times were only calculated for those attempts where fish were detected at both the bottom and top of the fishway.

Total delay at each dam and fishway was estimated as the time elapsed between first detection at that barrier to the last detection anywhere at that site. Note that this method overestimates actual arrival time because lampreys presumably must spend some time searching before they are able to locate and enter the fishway entrance. This means that the methods described here underestimate both migration rate and delay..

## Results

### Percent Entry and Passage

We tagged 97 lampreys (53 female, 44 male) from May 10 – June 3, 2013 (Table 2). Males were slightly shorter than females (mean ± SD: 698 ± 44 mm vs. 712 ± 47 mm) but this difference was not significant (t-test; P= 0.157). After tagging, several fish fell back downstream, but subsequently re-entered the Holyoke fish lifts. This can be inferred from the time elapsed between tagging and entry into the Holyoke impoundment ('self-release time'): for 84 lampreys the elapsed time was < 24 h (range = 0 – 22.4 h); for the remaining fish the elapsed time ranged from 41.5 – 548.7 h (Fig. 3). Fallbacks were assumed to have dropped over the dam crest or through the turbines because none were detected on the bypass antenna. Moreover, because re-entry was probably less than 100%, the actual number that fell back downstream was probably greater than what we report here.

Fifty-three lampreys (54.6%) were detected at Turners Falls. Of these, 8 (6 at Cabot and 2 at Spillway) were only detected at the upstream end of the fishways (i.e. they were not detected at the bottom of either fishway). Estimates of percent entry were adjusted for missed detections by dividing detections at the top by percent passage (see below).

There were two principal causes of missed detections: 1) brief outages of the PIT systems at Cabot entry (total down-time = 3.18 d) and Spillway (total downtime = 0.52 d); and 2) prolonged attachment by tagged lamprey within the detection zones of the entrance antennas of Cabot and Spillway fishways-- when more than one tag is present within the detection field of a PIT antenna it can often prevent other tags from being detected (signal collision). Given the timing of the outages it is likely that most of the missed detections at Cabot were caused by outages and those at Spillway by signal collisions. This, combined with the fact that there was no evidence of missed detections at antennas further upstream, means that available data were sufficient to estimate number of missed detections at the Cabot and Spillway fishway entrances. Although some data were lost, overall coverage was good (98.6% of total time).

Percent passage (%$P_D$; Table 2) was calculated only for those individuals that were detected entering each fishway. At Cabot, 31 lampreys were detected at the entrance; of these 12 passed (38.7%). Similarly, 29 lampreys were detected at the Spillway entrance, of which 9 passed (31.0%).Taken together, 45 lampreys were detected entering either Cabot or Spillway, and 21 of these passed, yielding combined passage percentage to the level of the Turners Falls Canal of 46.7%. Note that this value is greater than either fishway alone. This is because 15 of the 45 lampreys detected at the entrances entered both fishways, and so had additional opportunities to pass. As indicated above, however, 8 lampreys were detected exiting the tops of the fishways that were not detected at either entrance (6 in Cabot, 2 in Spillway). Including these individuals, a total of 29 lampreys were detected passing one or the other of these fishways. Dividing this value by the combined passage rate yields an adjusted estimate of entry into Turners Falls of 62.1 individuals, or 64.1% of those tagged at Holyoke. Given that several lampreys fell back downstream below Holyoke after release, it is also likely that not all tagged fish re-ascended the lifts. This means that actual percentage entering was even greater, and 64.1% is a conservative estimate.

Because Spillway fishway is directly connected to the Gatehouse fishway, all 11 of the lampreys that passed Spillway were detected at Gatehouse. Only six of these

(54.5%) passed Gatehouse successfully, however. This was a similar passage proportion to what was observed for Cabot passers that entered Gatehouse (17 of 18 Cabot passers entered (94.4%), but only 10 passed, or 58.8% of entrants).

Of the 16 lampreys detected at the exit of Gatehouse fishway, 4 were detected at Vernon Dam fishway antennas (25% of available lampreys, and 4% of the total, Table 2). This was a significantly lower proportion than those that entered Turners Falls (Logistic regression, P=0.0115). Of these 4 entrants, 2 passed Vernon fishway (50% of entrants; 2% of the total). There were no differences in percent entry between the sexes or by length (logistic regression, P>0.1 in all cases), except for Cabot, where longer fish were slightly more likely to pass (risk ratio: 1.6% $mm^{-1}$; P = 0.059).

### Rates of migration and entry, transit times, and delay

More lampreys entered Cabot than Spillway (Logistic P=0.085; Table 2). Accounting for missed detections, 74.8% of those that arrived entered Cabot and 57.0% entered Spillway. Fifteen (33.3%) of the 45 lampreys detected entering the fishways entered both fishways, and all of these entered Cabot first. This may be in part because the fishways are arranged sequentially along the migration corridor, and fish must first pass by Cabot in order to reach Spillway (Fig. 1).

Overall transit time from Holyoke to Turners Falls was rapid (median=1.97 d; distance =54.5 km), but was correspondingly shorter for lampreys that entered Cabot (median=1.41 d) than those that entered Spillway (median=2.72 d; P=0.0267, Fig. 4).

Given a migration distance of 54.5 km, these data indicate that the actual median migration speed was greater than 0.45 m $s^{-1}$ or 0.63 BL $s^{-1}$ (Fig. 4). Because our PIT system did not detect lampreys until they actually entered a fishway and do not account for time required to locate and enter it, actual travel times must have been shorter than what we report here, and rates were accordingly faster. Any tortuosity to the migratory path would also increase the groundspeeds required to produce these arrival times. This means that migration speeds reported here are conservative, even when based only on lampreys that entered Cabot.

The differences in time to enter Cabot and Spillway were likely the result of differing rates of discovery and entry of the two fishways once fish arrived at Turners Falls. To test for this while controlling for diurnal effects and effects of flow and temperature (Fig. 3) we used Cox’s proportional hazards regression with a guarantee time set to 1 d (Castro-Santos and Haro 2003; Hosmer and Lemeshow 1999). This was slightly less than the minimum observed transit time (1.02 d). Applying a guarantee time removes some bias caused by variation in travel time, while still allowing for least-biased estimation of covariate effects on the actual rate of entry into each fishway from the pool of available fish.

This approach confirmed the difference in entry rates: accounting for other effects lampreys entered Cabot more than twice as quickly (exp(0.697)=2.01-fold) as they did Spillway (Cox’s proportional hazards regression with time-varying covariates, Table 3).

There was a strong diel pattern, with most entries (64%) occurring at night at both fishways. This effect was strongest at Cabot, where entry rates were exp(3.195), or 24.4-times greater during the night than during the day. Discharge was also important and positively correlated with entry rate at both fishways. For lampreys that first entered Cabot, increased discharge appeared to have the greatest effect during the day (Table 3: exp(0.734), meaning entry rate increased by 2.1-fold per 100 $m^3s^{-1}$ flow increase). Bypass flows dominated movement of lampreys that first entered at Spillway, increasing entry rate by 11.6-fold per 100 $m^3s^{-1}$. Both these results indicate that increased flows had a strong influence on orientation, improving attraction to both fishway entrances; with bypass flows being particularly important for attracting lamprey to Spillway fishway (Table 3 and Fig. 3).

One important caveat here is that no lamprey entered during high-flow events (Fig. 3). Owing to the rapid migration and entry rates, very few fish were available to enter during these freshets (Holyoke fish lift was closed during periods when flows exceeded 857 $m^3$ $s^{-1}$). We point this out because although the data here suggest that elevated flow stimulated fishway entry, this was based primarily on observations of fish exposed to only low to moderate flows, and there are insufficient data with which to evaluate effects of the full range of flows on fishway entry.

Importantly, temperature was inversely correlated with flow (Fig. 2; described by regression: TempC= 19.6 - 0.0043 * $Q_{Tot}$, R-square = 0.47, N=89 day/night intervals;

$P<0.001$; TempC=temperature (°C); $Q_{Tot}$=total river discharge). Given the relatively steady temperatures during the 2013 spring migration, coupled with a negative effect on entry rate (Table 3), it is possible that the observed response includes some confounding effects between temperature and discharge. This does not appear to be the case, however: the positive effect of flow on the model remained even when temperature was removed. Taken together these data strongly suggest that discharge was an important factor in motivation and/or orientation.

As mentioned above, 17 of the 18 Cabot passers entered Gatehouse, and transit time through the canal was rapid (median time to enter Gatehouse: 0.703 d). Although this is a shorter time than from Holyoke to Turners Falls, the distance is also much less (3.3 km), meaning that migration velocity was reduced relative to the open river (.054 m $s^{-1}$ or 0.077 BL $s^{-1}$). Again, however, it is not possible to distinguish migration rate from time required to find and enter the fishways. For those lampreys that did enter Gatehouse from the Canal entry was again largely nocturnal, with 76% entering at night (Table 3). In contrast to the arrival timing to Cabot and Spillway, rates of entry into Gatehouse were reduced at elevated discharge, an effect that was strongest at night (Table 3). The effect of temperature was also opposite to its effect on arrival timing, with entry rate increasing with temperature (Table 3). The canal passage data occurred over a much more constrained time period, however (13 of 17 entry events occurred between 18-23 May), and it is possible that unequal exposure to environmental conditions influenced the model results.

Transit times from Turners Falls to Vernon ranged from 2.7 d – 18.6 d, but with only 4 lampreys entering Vernon it was not possible to make meaningful comparisons with the Holyoke-Turners Falls reach.

Rates of movement through the fishways were much slower than through the open-river and canal reaches (Fig. 5). Median transit times varied among fishways (Cabot: 18.3 h; Spillway: 8.2 h; Gatehouse: 0.9 h). The two lampreys that passed Vernon exhibited similar rates of movement through that fishway (mean = 7.9 h). The apparent difference among passage time can largely be explained by differences in fishway length (Table 1), although movement rate through Cabot (0.40 cm $s^{-1}$ or 0.0057 BL $s^{-1}$) does appear to have been slightly slower than through Spillway (0.61 cm $s^{-1}$ or 0.0086 BL $s^{-1}$ (Kruskal-Wallis P = 0.0826)). Movement through Gatehouse was much more rapid than through the other fishways (3.26 cm $s^{-1}$ or 0.0462 BL $s^{-1}$ (P = 0.0056)), but was still an order of magnitude slower than through the open-river reach. One consequence of this rate of movement through the fishways is that most (26 of 40, or 65%) passage events occurred during daylight hours, despite lampreys having entered mostly at night.

While transit times describe the maximum rate of movement through each fishway, this metric fails to capture the total delay incurred as fish often made repeated failed attempts to pass (Figs. 5 and 6). Fish staged more attempts through Gatehouse (average=6.6 attempts) than through Cabot (average=1.8 attempts) or Spillway (average=2.9 attempts; $P < 0.0001$), although the value for Cabot is probably biased low owing to the antenna outage there. On average passers staged 55% more attempts than failers, but this difference was significant only at Spillway (Kruskall-Wallis test, $P = 0.0024$; Cabot: $P = 0.1115$; Gatehouse: $P = 0.2143$). If failed attempts were included in $\%P_D$ actual success rate would be seen to be much lower than reported above, particularly for Gatehouse.

The location of failures was not clear for Cabot and Spillway fishways because antennas were only present at the entrance. For Gatehouse, however, a more extensive array monitored movement through the fishway—there, all but one failed attempt ended with fish making no progress past the fishway entrance. A similar pattern was observed at Vernon. Furthermore, 99% of presences at all fishway entrances were separated intervals by less than one hour, suggesting that failed passage was largely associated with rapid rejection of fishways near the entrances.

The combined effects of transit times and repeated failures meant that total delay incurred at each fishway was extensive (Fig.s 5 and 6). Patterns differed by fishway, with passers experiencing the greatest delays at Cabot (mean = 8.3 days) and Gatehouse (mean = 8.0 d); Spillway passers had a mean delay of 4.1 d. Fish that failed to pass experienced similar delays at Gatehouse (mean =8.3 d), but reduced delays at Cabot (mean = 2.8 d) and increased delays at Spillway (mean = 5.9 d). Maximum delay ranged from 19.4 d (Spillway) to 26.2 d (Cabot; Fig. 6).

These delays accumulated as fish ascended sequential fishways. Mean total delay of lampreys that passed Turners Falls was 12.1 d (N=11; range = 0.5 – 22.0 d), which was similar to the delay of lampreys that failed to pass (N=35; mean = 10.5 d, range = 0 - 29.8 d; Kruskal-Wallace P > 0.4). For the four fish that arrived at Vernon mean delay was 9.9 d (passers: 0.2 – 29.1 d; failers: 3.6 – 6.8 d; Fig. 5).

The effect of these delays on migratory range are evident from the competing rates of passage and failure at Turners Falls, where failure rates exceeded passage rates throughout their residence time (Fig. 6). Both rates began to increase after about a week of effort, with failure rate increasing more rapidly than passage rate. This implies that overall likelihood of passage continued to increase for lampreys that were retained within the system. It also indicates, however, that the competing probability of failure also increases, and is direct evidence that the incurred delays act to limit migratory range. The fact that the curves in Fig. 6b are nearly parallel is also important—it explains why we do not necessarily expect percent failure to increase with increased delay. The two rates are independent and change with the passage of time, but when they are parallel as occurred here, we expect the overall proportion passing and failing to remain similar, regardless of the duration of effort.

## DISCUSSION

Our results indicate that more than half of the lampreys tagged at Holyoke Dam successfully traversed 54.5 km of river and entered the Turners Falls Complex. This is similar to what has been observed for Pacific lamprey: Studies performed at the Bonneville and McNary dams on the Columbia River detected 67% and 61% entry, respectively (Johnson et al. 2012; Keefer et al. 2013a; 2013b). There, however, lampreys were released just 3 km (Bonneville) and 1 km (McNary) downstream of the dams, with minimal spawning habitat between the release sites and the fishways (Keefer et al. 2013a).

In our study, most lampreys bypassed extensive spawning habitat, both in the mainstem and in several 2nd-5th order tributaries between Holyoke and Turners Falls. Given the short transit times, movements must have been both rapid and highly directed. Sea Lampreys are known to respond to pheromones, and presence of ammocoetes is thought to be an important cue driving motivation and orientation (Vrieze et al. 2010; 2011). Those cues are available in the habitat below Turners Falls: based on fishway counts, the long-term average proportion of Holyoke-lifted lampreys that pass Turners Falls is 23.9% (SD= 21.4%; U.S. Fish and Wildlife Service Connecticut River Coordinator's Office, pers. Comm), leaving 76.1% to spawn between Holyoke and Turners Falls. Given that there is ample habitat and more reproduction it is likely that there are more juveniles present in this reach of river. The fact that >60% of lamprey bypassed these cues and entered Turners Falls indicates that other factors, such as discharge and other hydraulic cues are probably more important. It is also possible that lampreys possess an innate trigger that causes them to attempt to maximize distance. Such triggers are common among migratory animals (Dingle 1996), and may act as a mechanism for distributing spawning effort across as much habitat as possible. This phenomenon may well be present among lampreys, which are not philopatric (Waldman et al. 2008)—it may also play an important role in their ability to colonize and invade new habitat (Hogg et al. 2013).

Only 4% of tagged lamprey entered the fishways at Vernon (25% of those that passed Turners Falls), which was a significant decrease compared with the Holyoke-Turners Falls reach, despite the fact that the distance between Turners Falls and Vernon was only half that of the lower reach. It is worth noting that although the sample size was small, the proportion of lampreys that passed Turners Falls that also passed Vernon (12.5%) was consistent with fishway counts data from those dams (14.7% from 2011-2015). Similar attrition was observed on the Columbia River, where passage of Pacific lamprey at 3 sequential dams was about 50% each, but dropped to 25% each at the fourth and fifth dams (Keefer et al. 2009a). There is abundant spawning habitat between Turners Falls and Vernon (although less than was present between Holyoke and Turners Falls) and it is likely that lampreys terminated their migration in this reach in order to spawn. It is also possible, however, that the reduction in entry at Vernon was caused by poor guidance to or attraction into the fishway there. Because of the limitations of PIT technology we are unable to distinguish among possible fates and further work will be required to resolve this ambiguity. Nevertheless, the extensive delays, attrition, and timing of failure at the Turners Falls fishways, coupled with low entry rates at Vernon suggest that passage at Vernon is likely being at least partially constrained by migratory delays downstream.

Taken together, the rapid movement and high entry rates at Turners Falls fishways suggest that the capture and handling techniques must have had negligible effect on condition or motivation of the fish. Mesa et al. (2003) found that tagged lamprey had reduced swimming performance compared with untagged lamprey. They used larger tags and more invasive surgery, however, and our results, while not as comprehensive, do confirm that PIT telemetry is an appropriate technique for monitoring migration and passage performance of this species (Keefer et al. 2009b).

The rapid movement between Holyoke and Turners Falls suggests that lamprey may seek to optimize cost of transport (Trump and Leggett 1980; Ware 1975; Ware 1978). The rates we observed (0.63 BL $s^{-1}$) were slightly greater than has been observed elsewhere (0.43-0.55 BL $s^{-1}$; Andrade et al. 2007; Almeida et al. 2002)). It is also greater than what has been reported for many anadromous migrants (Bernatchez and Dodson 1987). Importantly, however, Bernatchez and Dodson (1987) based much of their analyses on mark-recapture data, which can greatly underestimate travel times. Even so, our study also underestimates travel time because PIT telemetry fails to account for time required to find and enter fishways. Here again, radio- or acoustic telemetry studies could help improve accuracy of actual migration speeds, which will help improve understanding of migratory energetics.

Energetics may be particularly important in the context of fishway performance. Lampreys were significantly delayed by reduced rates of movement through the fishways, but the repeated failed passage attempts and associated overall delay more than doubled the time required to pass each dam. Given that time to pass and time to fail were similar it seems likely that energetic costs of migratory delay were as important as physiological capacity in determining whether or not an individual that encountered a fishway ultimately passed it. Similar processes have been proposed for other species (Castro-Santos and Letcher 2010; Rand and Hinch 1998; Caudill et al. 2007). This is consistent with recommendations that passage performance be measured in units of time and rates of movement rather than just numbers or percentages (Castro-Santos et al. 2009; Castro-Santos and Letcher 2010; Castro-Santos and Perry 2012).

The cause of the repeated failures, followed by eventual passage remain unclear. It did appear that failure was concentrated at or near the fishway entrances, suggesting that the transition between the open river environment and the highly artificial environment of the fishways may itself have posed an impediment to passage. Previous studies have shown that lampreys undergo repeated ascent and descents wihin fishways and often have difficulty passing individual weirs (Haro and Kynard 1997; Keefer et al. 2013b). Weir geometry has been shown to be problematic for Pacific Lamprey (Keefer et al. 2010), and it may be that similar issues acted to limit passage in this study.

The rates-based approach also helps explain the observed benefit of the second fishway at Turners Falls. Not only did the Spillway fishway offer an additional passage route for lamprey that bypassed the first fishway at Cabot, repeated attempts and movement between the fishways meant that overall probability of passage increased as a result (Castro-Santos 2004).

In this study we have differentiated between overall delay and transit time. This differs with some earlier studies (e.g. Moser et al. 2002; Pratt et al. 2009) that have calculated transit time as the time between first detection at a dam and passage (equivalent to our delay metric). The striking differences between transit times and delays described here highlight the importance of using both metrics, with transit times describing performance within the fishways, and delays incorporating rates of entry and re-entry as well as passage. Segregating these processes has important implications for our understanding of fishway effectiveness and for optimizing design solutions for facilitating passage.

This study has shown that existing structures pose a substantial impediment to passage of Sea Lamprey on the Connecticut River. Given that the fishway designs described here are in widespread use (Clay 1995) it is likely that similar issues exist elsewhere. The reduced migratory rates experienced near dams contrasts dramatically with what was observed in the open river, and the collective evidence suggests that the delays incurred may be as important as fishway hydraulics in limiting the range of this species (Wagner et al. 2012). This has important implications, not only for improving conservation and passage of lampreys, but also for control measures in their native range. If barriers or fishways can be developed that allow for expedited passage of native species, but that impose delays to lampreys, then migratory range and access to habitat can be restricted without necessarily resorting to trapping and sorting (McLaughlin et al. 2013; McLaughlin et al. 2007).

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**Table 1:** Fishway design specifications. Cabot, Spillway, and Vernon fishways are all modified Ice Harbor designs; Gatehouse is a Hells Gate double vertical slot design (Clay 1995). Volume and Energy Dissipation Factor (EDF) are calculated per pool, following Towler et al. 2015.

| | **Cabot** | **Spillway** | **Gatehouse** | **Vernon** |
|---|---|---|---|---|
| **River km** | 190 | 194.5 | 195 | 227.5 |
| **Length (m)** | 263.7 | 179.8 | 70.1[1] | 204.2 |
| **Height (m)** | 20.1 | 10.7 | 0.30-2.13 | 8.8 |
| **Active pools** | | | | |
| **Number** | 67 | 35 | 8 | 43 |
| **Volume ($m^3$)** | 27.11 | 16.76 | 54.9-110.2 | 26.04 |
| **EDF ($W\ m^{-3}$)** | 113.85 | 105.28 | 21.5-263.3 | 120.57 |
| **Resting pools** | | | | |
| **Number** | 6 | 3 | 0 | 3 |
| **Volume ($m^3$)** | 76.8 | 42.7 | --- | 62.5 |
| **EDF ($W\ m^{-3}$)** | 40.2 | 41.32 | --- | 50.21 |
| **Slope** | 1:10 | 1:10 | 1:18 | 1:10 to 1:25 |

1. This dimension is from the left-bank entrance; including the right-bank entrance and the Spillway exit the mean length of the entire fishway is 82.6 m

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**Table 2**. Number of fish released and detected at each fishway, grouped by release. Numbers represent detections anywhere in each fishway, including those that were only detected at the exits. TL is mean total length ± 1 SD; 'Combined' refers to the combined entry of both Cabot and Spillway fishways, and includes 15 fish that entered both. Percent passage are presented as % (95% CI), where the CI is calculated from the binomial distribution.

| | | | Detected (N) | | | | |
|---|---|---|---|---|---|---|---|
| | | | Turners Falls complex | | | | |
| Release | N | TL | Cabot | Spillway | Combined | Gatehouse | Vernon |
| 10 May | 18 | 709±29 | 8 | 6 | 10 | 4 | |
| 17 May | 51 | 705±53 | 24 | 16 | 33 | 19 | 3 |
| 3 June | 28 | 706±43 | 5 | 9 | 10 | 7 | 1 |
| Total | 97 | 706±46 | 37[1] | 31[1] | 53[1] | 28 | 4 |
| Percent Entry[2] | | | 47.9% | 36.5% | 64.1% | 28.9% | 4.1% |
| (%$E_O$) | | | (38.2-57.8) | (27.6-46.4) | (54.6-73.4) | (21.1-38.9) | (1.7-10.2) |
| Number Passed | | | 18[1] | 11[1] | 29[1] | 16 | 2 |
| Percent Passage | | | 38.7% | 31.0% | 46.7% | 57.1% | 50.0% |
| (%$P_D$) | | | (24.6-57.8) | (18.0-50.8) | (33.8-62.1) | (40.6-75.5) | (19.5-93.2) |
| Cumulative Passage | | | 18.6% | 11.3% | 29.9% | 16.5% | 2.1% |
| (%$P_O$) | | | (12.3-27.7) | (6.6-19.3) | (22.0-40.0) | (10.6-25.4) | (0.7-12.2) |

1. 8 individuals were detected at the fishway exits but not the entrances: 6 at Cabot and 2 at Spillway. Also, 15 fish were detected entering both fishways; the total number of fish detected entering Cabot and/or Spillway was 45.
2. Values for Cabot, Spillway, and Turners Falls Combined are adjusted for missed detections at Cabot and Spillway entrances (see text for details).

**Table 3**. Effect of environmental variables on entry rates at the Turners Falls fishway complex. Data are AIC best-fit proportional hazards models and describe effect on ln(entry rate). Effect of discharge (Q) is presented per $10^2$ $m^3$ $s^{-1}$ for total river flow ($Q_{Tot}$), discharge through Cabot Station ($Q_{Cabot}$), and discharge through the bypassed reach ($Q_{Bypass}$). Day/Night is coded Day (1) and Night (0). Canal models describe rates of entry into Gatehouse fishway of fish that passed Cabot Fishway and ascended the canal. For these models, $Q_{tot}$ and $Q_{Cabot}$ terms both refer to total discharge within the canal only. Coefficients not included in best models are indicated by '---'. 'Events' indicates entry events; 'Censored' observations occurred whenever a time-varying covariate changed for a given fish.

| **Parameter** | **Turners Falls** | **Cabot** | **Spillway** | **Canal** |
|---|---|---|---|---|
| **Fishway (Cabot)** | 0.697 ± 0.355 | --- | --- | --- |
| | P = 0.0497 | | | |
| **Day/Night** | -0.869 ± 0.369 | -3.195 ± 1.271 | --- | -4.8707 ± 1.9914 |
| | P = 0.0022 | P = 0.0120 | | P = 0.0137 |
| **$Q_{Tot}$** | 0.626 ± 0.174 | --- | --- | -0.0748 ± 0.0353 |
| | P = 0.0022 | | | P = 0.0342 |
| **$Q_{Cabot}$*Day/Night[1]** | --- | 0.734 ± 0.371 | --- | 0.0919 ± 0.0509 |
| | | P = 0.0478 | | P = 0.0712 |
| **$Q_{Bypass}$** | --- | --- | 2.455 ± 0.681 | --- |
| | | | P = 0.0003 | |
| **Temp (°C)** | -0.355 ± 0.173 | --- | --- | 0.828 ± 0.325 |
| | P = 0.0405 | | | P = 0.0109 |
| **Nevents** | 45 | 31 | 14 | 17 |
| **Ncensored** | 220 | 234 | 251 | 51 |

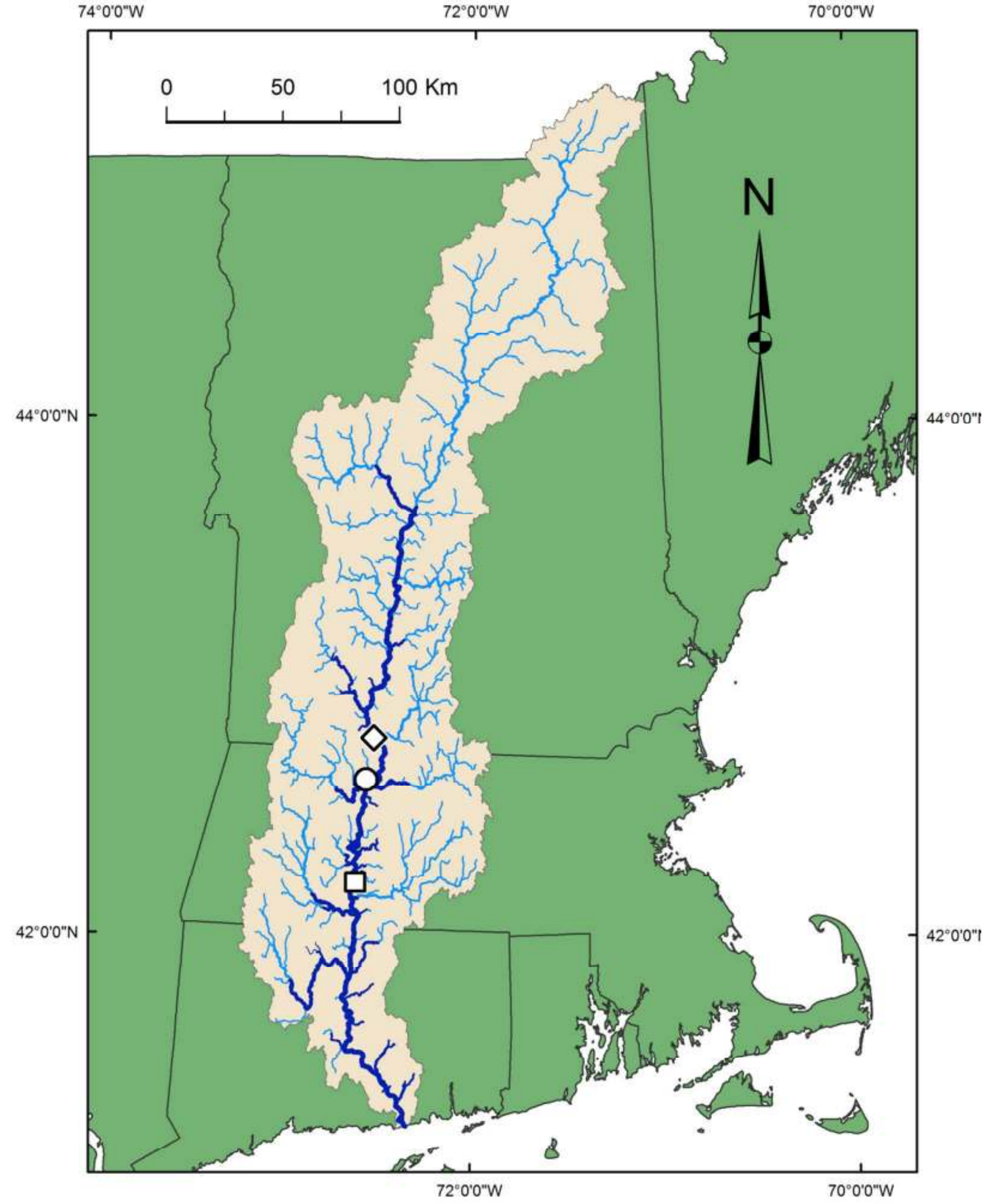


**Fig. 1**. Map of the Connecticut River watershed, showing the three lower mainstem dams (Holyoke: □;Turners Falls: ○; and Vernon Dam:◇). Dark blue lines indicate current range of Sea Lamprey within the basin.

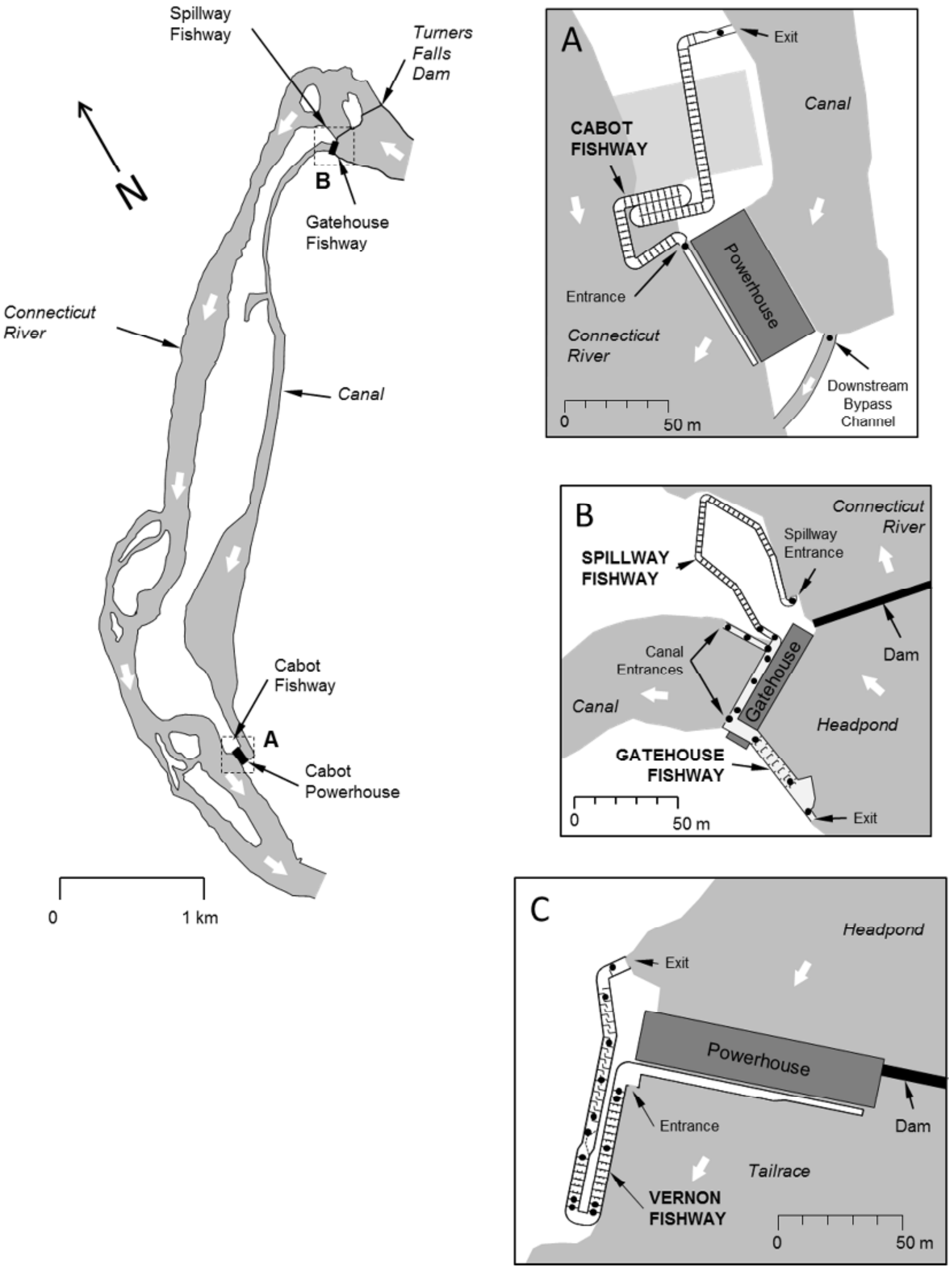
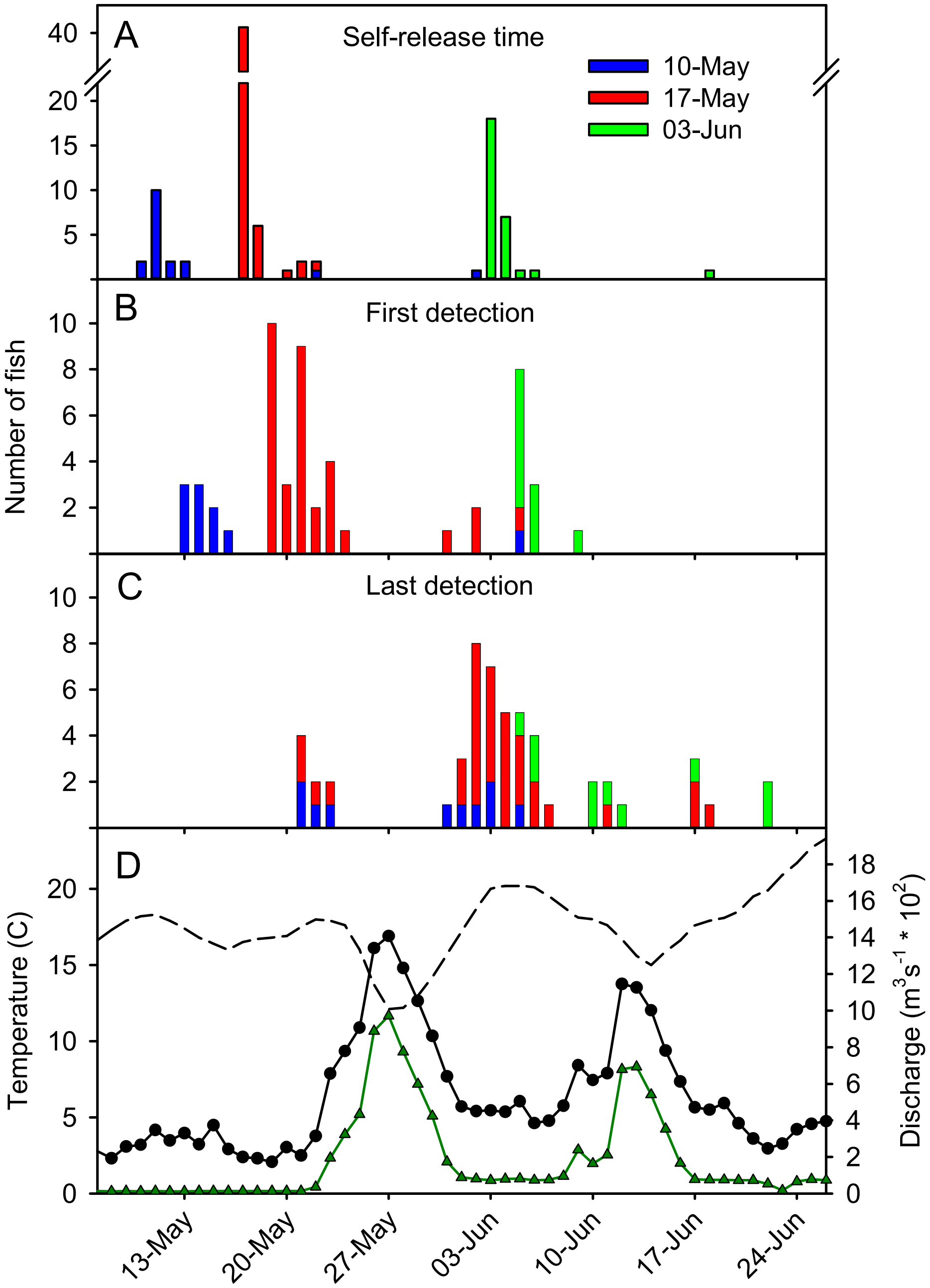


**Fig 2.** Map of Turners Falls reach of the Connecticut River showing hydropower canal complex and locations of Cabot and Gatehouse fishways. Dashed boxes are areas shown

in Insets A & B. White arrows indicate direction of river flow. (A) Plan view of Cabot fishway and downstream bypass channel; (B) Plan view of Gatehouse and Spillway fishways--note multiple fishway entrance locations; Black circles indicate locations of PIT antennas; (C) Plan view of Vernon fishway (Fig. 1; not shown on map to left).



757

758 **Fig. 3.** The distribution of self-release times ('river entry; panel A), arrival time at

759 Turners Falls complex (Panel B), last detection at Turners Falls or Vernon Dam (panel C),

and discharge and water temperature during the monitoring period (Panel D). Discharge is presented as total discharge at Turners Falls (dots) and bypassed reach discharge (triangles); temperature is represented by a dashed line.

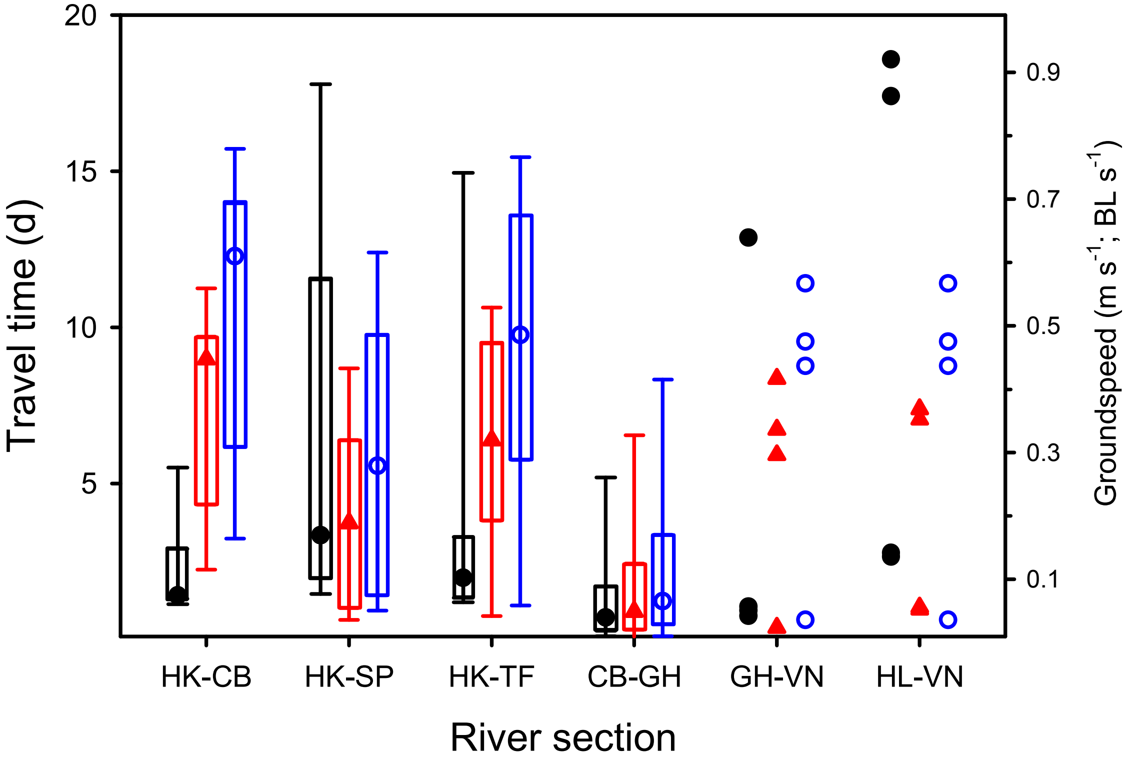


**Fig. 4.** The travel time (in days; ●) and migration rate of lampreys (in m s$^{-1}$ (▲) and BL s$^{-1}$(○)) by river reach. Dams are Holyoke (HK), Turners Falls (TF), and Vernon (VN); Fishways are Cabot (CB), Spillway (SP), Gatehouse (GH) and Vernon (VN). Data are presented as median (point), interquartile range (box) and 5th-95th percentile range (whiskers). Points for GH-VN and HL-VN reach represent individual fish.

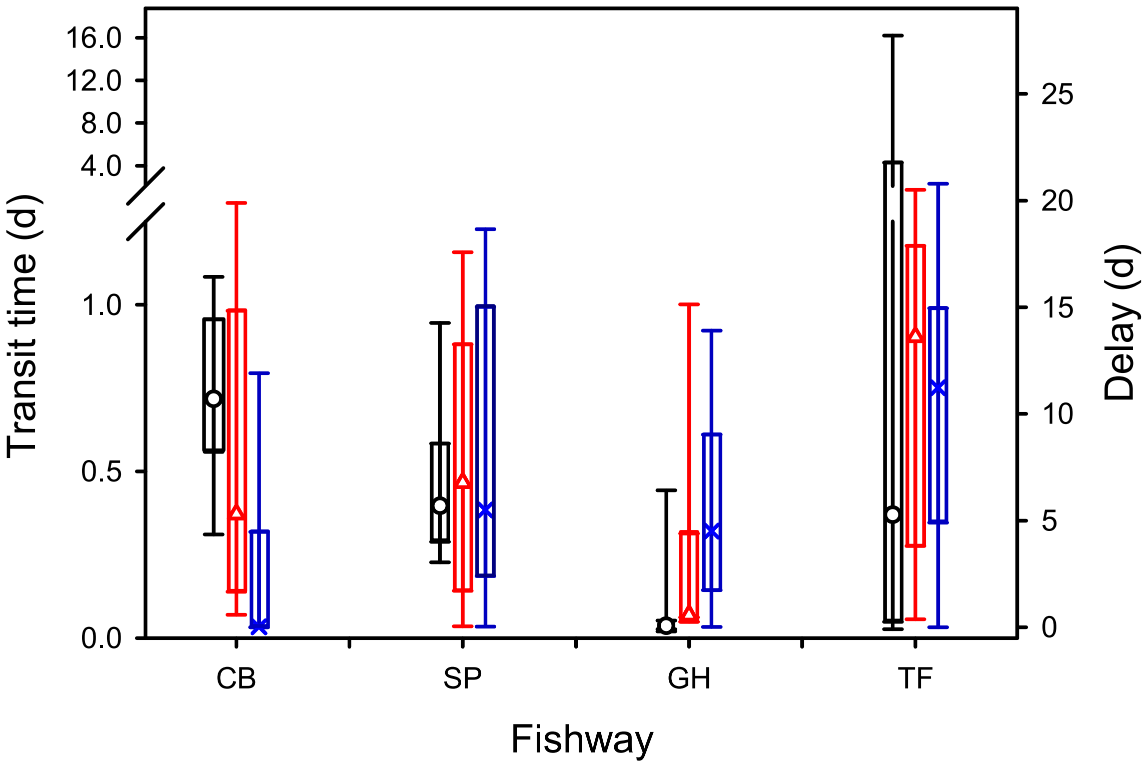
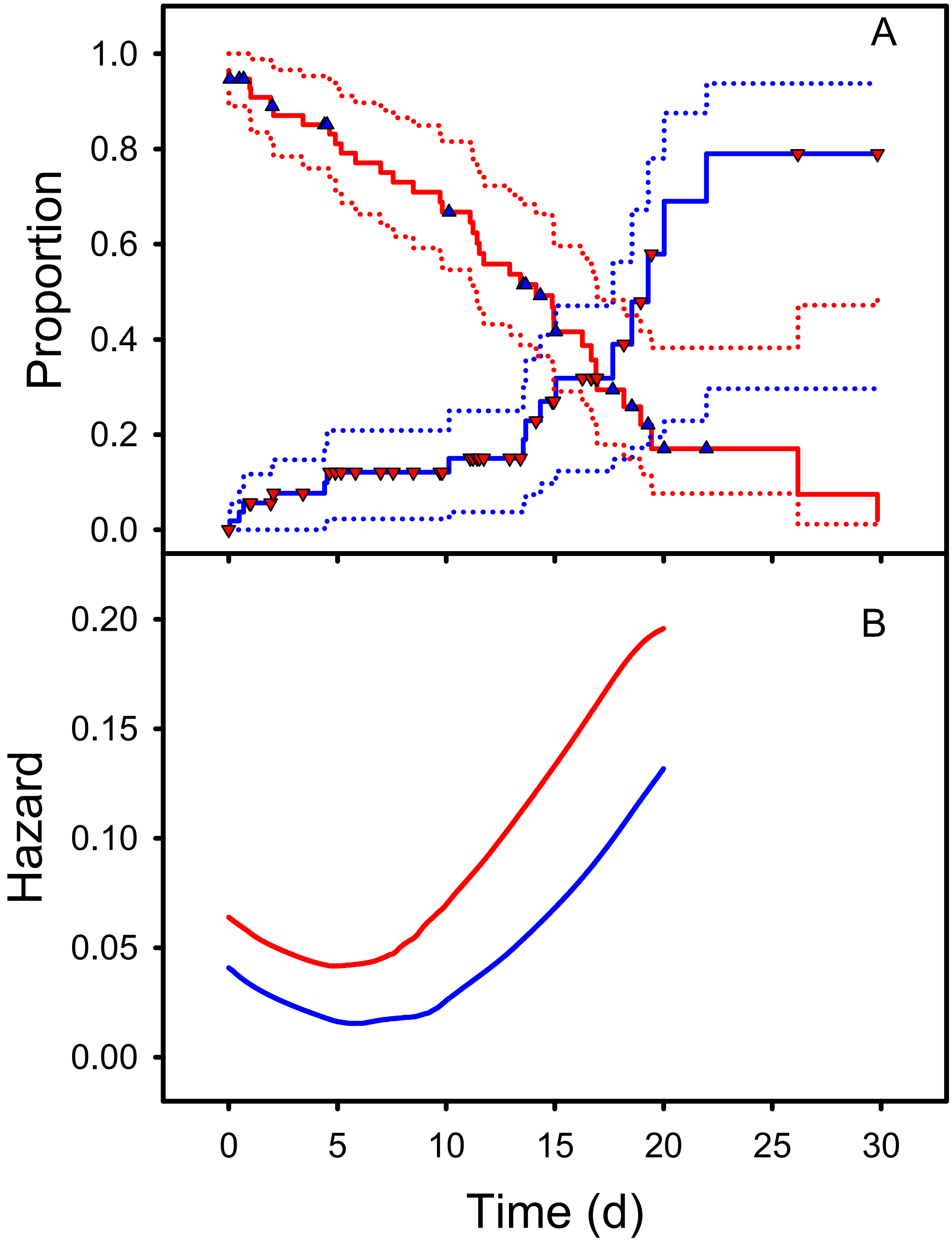


**Fig. 5**. The transit time and delay (d) of lampreys at each fishway (Cabot (CB), Spillway (SP), Gatehouse (GH)) and combined data for Turners Falls (TF). Data are presented as transit time (○, left axis), and overall delay (right axis) of fish that passed (△) or failed (x).


A
B
Proportion
0.0
0.2
0.4
0.6
0.8
1.0
Hazard
0.00
0.05
0.10
0.15
0.20
0
5
10
15
20
25
30
Time (d)

779

780

**Fig. 6.** Time to pass (blue curves and points) vs. time to fail (red curves and points) for lampreys attempting to pass Turners Falls Fishways. (A) Upper panel are Kaplan-Meier curves (KM) for failure and their complement (1 – KM) for passage (solid lines) and their 95% confidence intervals (dotted lines). Each curve describes the expected cumulative passage or failure probability, based on all the fish remaining in the system until a given event time. Observations are censored with respect to passage at the last detection for a fish that failed to pass (red triangles), and are censored with respect to failure at passage time (blue triangles). (B) Lower panel are smoothed hazard functions for the same data, showing the change in passage and failure rates over time. Hazard smooths are restricted to the first 20 d.