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Long-term studies on restoration of Connecticut River anadromous sea lamprey, *Petromyzon marinus* Linnaeus 1758: Trend in annual adult runs, abundance cycle, and nesting

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Abstract

This study is the first to evaluate the results of 60 years of restoring anadromous sea lamprey, *Petromyzon marinus*, to historical spawning and rearing habitats using fish passage at barrier dams in the Connecticut River, USA. We obtained counts of pre-spawning adult *P. marinus* annually passed upstream at Holyoke Dam (river km 140), Connecticut River, MA, during 37 years (1978–2014), and we counted *P. marinus* nests during 25 years (1986–2010) in the Fort River, a tributary upstream of Holyoke Dam. These two data sets were used to study relationships between adult passage and subsequent nesting and to study nesting timing and ecology. During the 37 years, annual adult *P. marinus* abundance at Holyoke Dam ranged from 15,000 to 95,000, but regression analysis found no trend ($p = .50$) for increasing annual adult abundance with years. However, during the 37 years, adults gained access via fish passage at dams to an estimated double the amount of spawning and rearing habitat upstream compared to the 1970s. The lack of a trend for increased adult abundance is consistent with a hypothesis of non-natal river homing by adults. However, the lack of a trend in adult abundance, when many more larvae are likely present in the watershed compared to the 1970s, is inconsistent with the hypothesis that greater numbers of larvae (and greater concentration of larval pheromone) results in greater number of adults attracted to a river. Instead of an abundance trend of adults with years, we found a rare life history phenomenon occurs in anadromous adult *P. marinus* — an abundance cycle with peaks at 6 year intervals (autocorrelation analysis, $p = .04$). Comparison of passage timing with nesting timing found passage did not affect nesting initiation or duration ($p = .61$). Annual date of nesting initiation strongly affected the duration of nesting with earlier nesting resulting in longer nesting ($p = .001$). Time series comparing Fort River temperature and discharge with nesting found these factors did not clearly predict annual initiation of nesting. This suggests a role for day length (photoperiod) as the trigger for nesting initiation (most nesting began annually during 1–14 June, all year mean, 7 June), regardless of river conditions. However, river discharge may affect nesting ecology because most nesting occurred during decreasing discharge when variability in daily discharge was small (stable discharge). The present research on passage and nesting contributes to a new Connecticut River restoration program for *P. marinus*, which is a keystone fish species in the watershed.

1 | INTRODUCTION

Research on anadromous sea lamprey, *Petromyzon marinus*, is rare in North America, although the species spawns in many Atlantic coast rivers from Labrador, Canada, to Florida, USA (Beamish, 1980). In Canada, life history research on *P. marinus* studied larvae, juveniles, and pre-spawning migrating adults in several rivers (Beamish, 1980; Beamish & Potter, 1975; Potter, 1980). In the USA, *P. marinus* in the Connecticut River and tributaries in Massachusetts and Connecticut have been studied for adult demography and migration (CRASC, 2018; Steir & Kynard, 1986a, 1986b), adult nesting timing and ecology (present study; Kynard and Horgan, unpubl. data), larval age structure (Aarrestad, 1985; CRASC, 2018; Kynard and Horgan, unpubl. data), and juvenile migration and behaviour (CRASC, 2018; Kynard, unpubl. data).

The Connecticut River has the largest documented run of adult anadromous *P. marinus* on the Atlantic coast (CRASC, 2018; Steir & Kynard, 1986a). Annual runs of pre-spawning adult *P. marinus* at Holyoke Dam, Holyoke, MA (river km = rkm 140) passed upstream of the dam by fish lifts has increased from tens in 1958 to tens of thousands beginning in 1975, after the second fish lift (spillway lift) was installed at the dam (Moffitt, Kynard, & Rideout, 1982; Steir & Kynard, 1986a). Previous studies on migrant adults at Holyoke Dam found sex ratio was skewed toward males, but the percent of males was only different from a 50:50 sex ratio during 1982 (1981%–56% males; 1982%–62% males; Steir & Kynard, 1986a). The skewed abundance toward males is typical of a stable land-locked population (Potter, Beamish, & Johnson, 1974; Smith, 1971). Also, males and females at Holyoke Dam in 1981–1982 did not differ for TL (range, 60–85 cm; mean, 71 cm for both sexes; Steir & Kynard, 1986a). Radio-tagged pre-spawning adults in the Connecticut River moved at night (early in the run) both day and night (later in the run) and swam upstream at a daily mean ground speed, including rest periods, of 1.01 km/day ± 0.75 (*SD*) with migrants moving the fastest (2 km/hour) during the migration peak (Steir & Kynard, 1986b).

Migration timing of the adult run relative to water temperature at Holyoke Dam was 10.5–15.5°C (Steir & Kynard, 1986a). This temperature range is similar to temperatures during migration of adult pre-spawning landlocked *P. marinus* (Applegate, 1950; Applegate & Smith, 1950) and adult pre-spawning anadromous *P. marinus* in Canadian rivers (Beamish & Potter, 1975). These results indicate a key role for water temperature affecting migration timing.

Land-locked *P. marinus* in North America's Great Lakes are a parasite on freshwater sport fish and are classified an undesirable species by many agencies (Johnson & Anderson, 1980). To restrict access of pre-spawning migrant adults to spawning and rearing habitats, adults are trapped below dams and not passed upstream. Additionally, land-locked populations are artificially controlled by chemically killing larvae (Smith & Tibbles, 1980), so all aspects of adult runs (abundance trends, abundance cycles, run timing, etc.) are affected by humans. Land-locked *P. marinus* have been studied for many aspects of nesting and larval biology (Applegate, 1950; Applegate & Smith, 1950; Manion & Hanson, 1980). However, there is an absence of long-term studies on restoring *P. marinus* to rivers or on the effect of riverine factors on nesting. More research on nesting ecology of all lampreys was called for in a recent book on North American lampreys (Brown, Chase, Mesa, Beamish, & Moyle, 2009).

North American fisheries agencies have recently characterized the two anadromous lamprey species (*P. marinus* on the Atlantic coast and Pacific lamprey, *Entosphenus tridentata*, on the Pacific coast) as keystone species that contribute in many important ways to stream fish communities and watershed ecology (Nislow & Kynard, 2009; https://www.fws.gov/pacific/fisheries/sphabcon/lamprey/lampreyRP.html, 2016; CRASC, 2018). *Petromyzon marinus* has no federal protection, but *E. tridentata* is classified as a Species of Concern by the U.S. Fish and Wildlife Service (USFWS). Restoration of *E. tridentata* to rivers has begun on the Pacific coast of the USA (Moyle, Browm, Chase, & Quinones, 2009) and the USFWS and five western states initiated the Pacific Lamprey Conservation Initiative in 2016 (https://www.fws.gov/pacific/fisheries/sphabcon/lamprey/lampreyRP.html, 2016). In 2018, the USFWS and the four state fisheries agencies bordering the Connecticut River watershed will consider a restoration program for anadromous *P. marinus* to their historical range in the river (CRASC, 2018). *Petromyzon marinus* in the Connecticut River are not harvested, and although dams may affect all life stages (block adult migrations, control river discharge and fate of eggs and larvae, kill larvae during dam-canal drawdowns, and harming seaward migrant juveniles passing through turbines), *P. marinus* may be mainly affected by natural environmental factors. The Connecticut River restoration program identified priority research needs as passage of adult *P. marinus* at dams and riverine factors that affect nesting ecology. Research in the present report addresses these information needs.

The present report uses fish count data from 1978–2014 of anadromous adult *P. marinus* passed upstream at Holyoke Dam, Connecticut River, and also, nesting count data on some of these adults, that after passing upstream of Holyoke Dam, migrated to spawn in the Fort River, an unregulated tributary located 15 rkm upstream from the dam. Using these two data sets, we tested six hypotheses: two hypotheses on the adult run (adult abundance trend and abundance cycle), two hypotheses involving both data sets (passage timing effect on nesting initiation and duration, and correlation between annual adult counts at the dam and annual nest counts), and two hypotheses on nesting (density of nests in lower versus headwater reaches; effect of annual nesting timing on nesting duration. Further, nesting ecology in the Fort River was investigated the relationships between nesting and river temperature and discharge. Hypotheses tested are listed in the Methods section.

2 | MATERIALS AND METHODS

2.1 | Study areas

Location of Holyoke Dam, Connecticut River, MA, the lowermost mainstem dam, is shown in Figure 1. The dam is 28-m high and was

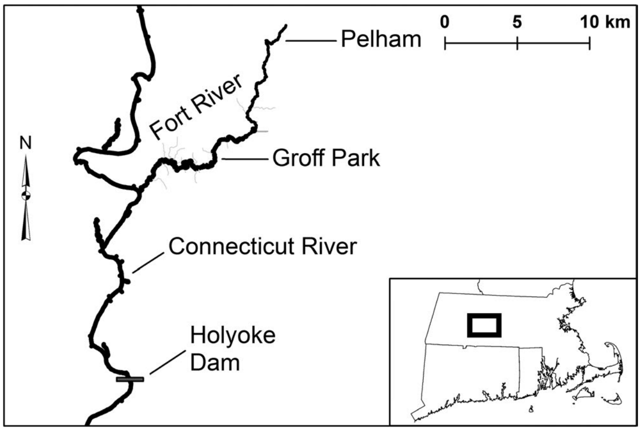

FIGURE 1 Map showing (a) the reach of the Connecticut River, MA, with Holyoke Dam, where adult migrant *Petromyzon marinus* were counted in the fish lift system, and (b) the Fort River, where some *P. marinus* passed over Holyoke Dam nested in two reaches (lower reach = Groff Park; headwater reach = Pelham)

completed in 1849. Thus, the dam blocked access of all anadromous fish from 1849 until the first fish lift was installed at the dam in the 1950s. A multi-state-federal restoration program for anadromous fish in the Connecticut River basin resulted in construction of two fish lifts (tailrace lift, built in 1955; spillway lift, built in 1975; Moffitt et al., 1982) at Holyoke Dam to pass anadromous fish to upstream spawning and rearing habitats. The fish lifts were designed for Atlantic salmon, *Salmo salar*, and American shad, *Alosa sapidissima*; however, adult blueback herring, *A aestivalis*, *P. marinus*, and other anadromous and riverine fishes entered the lifts and were passed upstream (USFWS, Region Five Office, Connecticut River Anadromous Fish Coordinator, Sunderland, MA (USFWS, CRAFC).

Location of the Fort River, where nesting of *P. marinus* was studied in the Groff Park and Pelham reaches, is shown in Figure 1. The lower 13 rkm of the river is low gradient with a sandy bottom and rare rocky nesting habitat required for *P. marinus* (Kynard and Horgan, unpubl. data). Groff Park (a 375-m-long stream reach with pool, run, and riffle habitats and abundant gravel-rubble substrate) begins 14 rkm from the river mouth and is the lower-most reach where abundant rocky substrate exists and mass nesting occurs (Kynard and Horgan, unpubl. data). In this reach, slope increases and gravel-rubble rocks are exposed. Nesting was also studied in a headwater reach (Pelham, a 335-m-long reach) that begins at rkm 29.5 and has pool, run, and riffle habitats and abundant gravel-rubble substrate.

2.2 | Counts of adults passed at Holyoke Dam

Pre-spawning adult *P. marinus* were annually trapped and lifted over Holyoke Dam by the two fish lifts and deposited into an escape flume that exited into the reservoir upstream of the dam. As *P. marinus* swam upstream in the escape flume, they were visually counted at a viewing window (see picture of counting window in Moffitt et al., 1982). Daily and annual counts of anadromous fish species included *P. marinus*. Counts were done by staff from several agencies who reported fish counts to the USFWS, CRAFC, who provided the run count data used for the present study. We used annual counts of *P. marinus* from 1978–2014 for most passage analyses, exceptions are noted under specific hypotheses in Methods.

2.3 | Nesting in the Fort River

Most hypotheses on nesting used nest count data collected for 25 years (1986–2010). Years during 1986–2010 when data on water temperature and discharge were available are noted under Nesting ecology in Methods.

We identified the annual nesting period of males as the date when the first nest was started to the date the last new nest was started. We began daily visual surveys for nesting males at Groff Park and Pelham reaches in mid to late-May, before nesting began, to identify the date nesting began. Nest surveys continued daily during the nesting period and extended several days after nesting ended to identify the date the last nest was started. New nests (starter nests by solitary males) were marked daily on a map of each reach and each nest site was marked in the river by a colored and numbered flag mounted on a wire inserted near the nest (to reduce duplicate counts of nests and to identify new nests on a previously used site). However, only enlarged nests (constructed by a male plus one or more females) were counted as a nest, because many starter nests do not result in a female spawning with the male and enlarging the male's starter nest. At the end of the annual nesting period, the timing of nesting (beginning and end dates of nesting) and the total number of nests on the map was tabulated for Groff Park and Pelham reaches.

2.4 | Data analyses and null hypotheses tested

All data sets on counts of adults at Holyoke Dam or nests in the Fort River were evaluated with Shapiro-Wilk tests to determine if the assumption of a normal distribution was violated. All data sets were normal, except for *P. marinus* counts at Holyoke Dam, which were transformed by natural logs for analyses. A null hypothesis (of no difference or effect of factors) was rejected if alpha was ≤0.05.

2.4.1 | H_O 1 = annual number of adults at Holyoke Dam has no trend with years

To determine if there was a significant trend in annual counts of *P. marinus* with years, annual counts for 1978–2014 were analyzed with linear regression.

2.4.2 | H_O 2 = annual adult abundance at Holyoke Dam has no abundance cycle

Annual counts of adults were analyzed using autocorrelation analysis of yearly abundance with time lags through 12 years to look for evidence of a cycle in run size. Time lag correlations were significant with linear regression at alpha = 0.05. Instead of using the annual number of *P. marinus*, autocorrelation analysis used population growth rates between consecutive years: ln (N_t/N_{t-1}) where t is year, in case of underlying trends in run size.

2.4.3 | H_O 3 = adult passage timing and duration at Holyoke Dam does not affect nesting timing and duration in the Fort River

We used daily counts of *P. marinus* at Holyoke Dam for 1981–2008 to examine run timing (beginning and end of the run) at Holyoke Dam. First and last passage dates were characterized as the dates that ≥10 adults were counted. We used the annual count data to calculate the mean first and last passage dates, as well as, the date on which 50% of all *P. marinus* were counted.

We used passage timing and nesting timing data during 1990–2008 and regression analysis to test the null hypothesis that run timing at Holyoke Dam has no effect on nesting timing or nesting duration in the Fort River. Specifically, we tested whether the date when 50% of adults passed Holyoke was related to either the first or last dates of nesting in the Fort River. Further, we graphed annual run timing versus nesting timing for 1990–2008 to visually examine the annual overlap between passage duration and initiation and duration of nesting.

2.4.4 | H_O 4 = annual adult passage counts at Holyoke Dam and annual nests counts in the Fort River are not correlated

We used regression analysis to examine the relationship between annual run counts and annual nest counts in the Fort River (combined Groff Park + Pelham nests) during 1986–2010.

Also, using a sex ratio of 59% for males passed at Holyoke Dam (Steir & Kynard, 1986a), we also estimated the number (and percent) of the total adults passed annually at Holyoke Dam during 1986–2010 that nested in the Groff Park and Pelham reaches in the Fort River.

2.4.5 | H_O 5 = nesting density at Groff Park and Pelham are not different

Annual nest counts during 25 years (1986–2010) were used for analysis. The Groff Park reach is longer than the Pelham reach, so we normalized nest number to reflect nest abundance per 100 m of river length. A paired *t*-test compared mean nest density (number of nests per 100-m river length) between the Groff Park and Pelham reaches.

2.4.6 | H_O 6 = initial nesting date does not affect nesting duration

Analysis used the combined annual nesting counts at Pelham and Groff Park for 26 years (1986–2012). Regression analysis examined the relationship between annual initial nesting date and nesting duration (number of days).

2.4.7 | Nesting ecology

The relationships between initiation of nesting and Fort River discharge and temperature was examined using a time series of 7 years (1990–1996). Discharge data were from the U.S. Geological Survey (USGS) gage #01171300 located mid-distance between the Groff Park and Pelham reaches. Temperature data were from a temperature logger we installed at Groff Park to record temperature every 2 hr, 24 hr per day. We made a set of seven annual descriptive plots to show the annual nesting period (dates from first to last new nest), mean daily river discharge ($m^3 \cdot s^{-1}$), and daily high and low temperatures (°C) from 24 May (pre-nesting period) to 1 July (end of the nesting period).

Another time series examined the relationship between temperature and discharge and nesting timing by regressing daily median low and high temperatures (°C) for 8 years (1992–2008), and daily mean discharge ($m^3 \cdot s^{-1}$) for 16 years (1979–1982 and 1985–1996) against three time periods relative to nesting timing: the week (7 days) before nesting, the nesting period, and the week (7 days) after nesting. Temperature was from a logger at Groff Park; discharge was from the U.S. Geological Survey (USGS) gage #01171300 located mid-distance between Groff Park and Pelham.

Finally, another time series examined relationships between Fort River daily discharge and daily Coefficient of Variation (CV) and nesting timing. The time series began on 15 May (pre-nesting) and ended on 15 July (post-nesting). For 16 years (1979–1982; 1985–1996), we plotted the daily median discharge, the daily CV, to show the river discharge and CV before, during, and after nesting.

3 | RESULTS

3.1 | H_O 1 = annual number of adults counted at Holyoke Dam has no trend with years

Annual abundance of adult *P. marinus* at Holyoke Dam from 1978–2014 is shown in Figure 2a. Annual counts ranged from 15,000 to 95,000.

There was no trend in abundance in the log-transformed number of adults (r^2 = 0.014, p = .50). However, there were 4 years in the second half of the series in which the count exceeded the highest year (1981:53550) in the first one-half of the series (Figure 2a). We accept the null hypothesis of no significant trend in abundance of the adult run.

3.2 | H_O 2 = annual adult abundance at Holyoke Dam has no abundance cycle

Autocorrelation analysis of the time series of annual run size during 1978–2014 found significant correlations at two time lags (Figure 2b). There was a negative correlation at a 1-year time lag

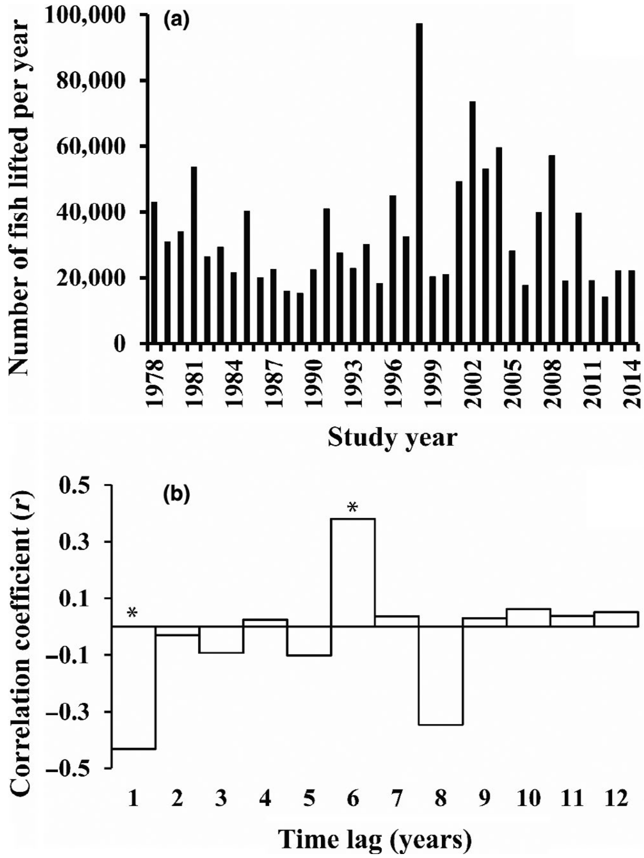

FIGURE 2 Annual number of adult migrant *Petromyzon marinus* counted at Holyoke Dam, 1978–2014 (panel a). Panel b shows the autocorrelation results for between-year changes in counts; correlations at time lags significant for alpha = 0.05 are indicted by an asterisk. Analysis shows one significant positive peak at 6 years

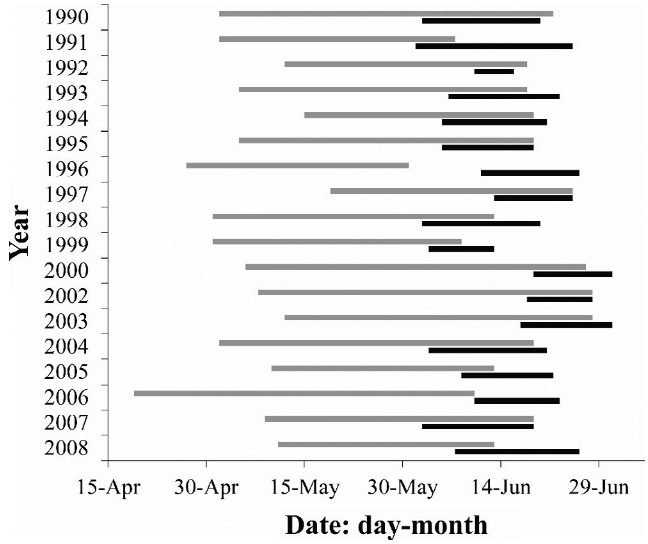

FIGURE 3 Relationship between the annual passage timing of *Petromyzon marinus* at Holyoke Dam (minimum daily count = ≥10 adults; horizontal gray bars) and the annual nesting period of adults in the Fort River (black bars), 1990–2008

(r = −0.43, p = .01, 33 df), which likely reflects the large number of single year peaks (Figure 2a,b). The other significant correlation was positive (r = +0.38, p = .04, 28 df) and occurred at a 6-year time lag (Figure 2b). We reject the null hypothesis—there is an abundance cycle with peaks at 6-year intervals.

3.3 | H_O 3 = adult passage timing at Holyoke Dam does not affect nesting initiation or duration in the Fort River

Annual counts of *P. marinus* runs at Holyoke Dam during 1990–2008, shows the first date that ≥10 adults were counted occurred during 19 April-21 May (average, 7 May; Figure 3). The last date on which ≥10 adults were counted occurred during 31 May-28 June (average date, 17 June). Thus, the duration (number of days) for annual runs at Holyoke Dam was 30–52 days (mean = 41 days, SD = 6.6 days).

Nesting duration in the Fort River during 1981–2008 was 6–24 days (mean = 14.8 days, SD = 4.3 days; Figure 3). Nesting began between 1–22 June, with an average start date of 7 June. Nesting ended on 13 June-1 July (average date for all years, 23 June).

From 1990 to 2008, nesting began an average of 33 days after the run began at Holyoke Dam (range, 21–52 days; Figure 3). In 16 of 18 years, some adults began nesting in the Fort River while other adults were still passing Holyoke Dam. In only 2 years (1996 and 2006) did passage at Holyoke Dam end before nesting in the Fort River began. In 6 years, adults were still being counted at Holyoke Dam on or after the final day of nesting in the Fort River. Regression analysis found no relationship between the annual duration of the adult run (number of days) at Holyoke Dam and annual nesting duration in the Fort River (number of days adults nested; r^2 = 0.02, p = .61, 18 years).

Also, the date that 50% of the adults were counted at Holyoke Dam did not predict either the first or last date of nesting in the Fort River (first date: r^2 = 0.14, p = .12, 18 years; last date: r^2 = 0.13, p = .12, 19 years). We accept the null hypothesis that passage timing at Holyoke Dam does not affect nesting initiation or duration in the Fort River.

3.4 | H_O 4 = annual adult counts at Holyoke Dam and annual nest counts in the Fort River are not correlated

Annual run size at Holyoke Dam (ln-transformed count) was significantly positively correlated with the annual total nest counts (Groff Park + Pelham reaches) during 1986–2010 (nests = 39*ln(count) − 316; r^2 = 0.32, p = .003). We reject the null hypothesis that annual counts of adults at Holyoke Dam are not correlated with annual nest counts.

Assuming 59% males and one male + one female per nest, the number of nesting adults observed comprised <1% of the lifted adults at Holyoke Dam in every year (mean, 0.5%; range among years, 0.2%–0.9%) in the two Fort River reaches we monitored.

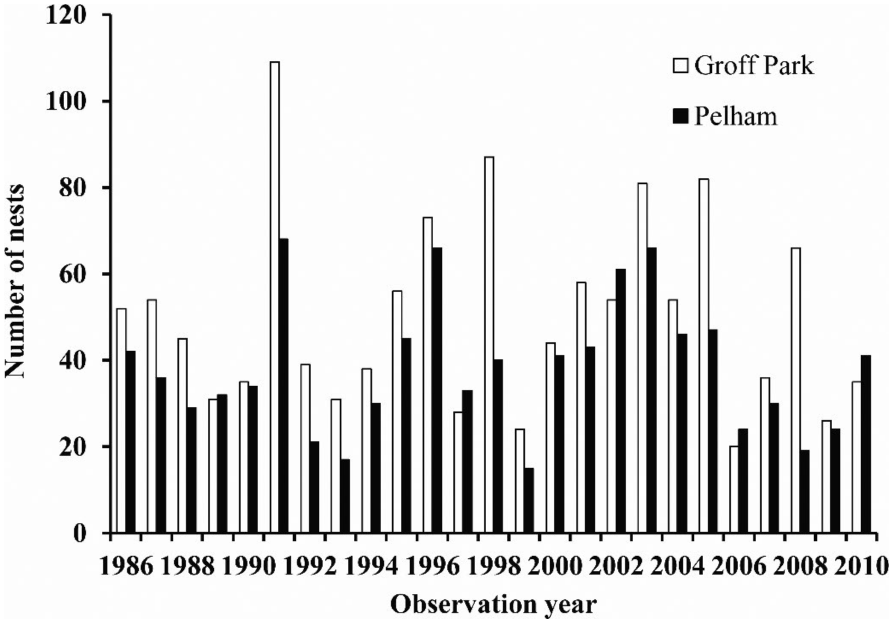

FIGURE 4 Annual number of *Petromyzon marinus* nests at Groff Park and Pelham reaches in the Fort River, 1986–2010

3.5 | H_O 5 = nesting density at Groff Park and Pelham are not different

During 1986–2010, we observed 1,258 nests at Groff Park and 950 nests at Pelham (Figure 4). At Groff Park, annual nest abundance was 20–109 nests (mean = 50, *SD* = 22); at Pelham, annual nest abundance was 15–68 nests (mean = 38, *SD* = 15).

Per 100 m of river length, the mean nest density at Groff Park was 13.4 nests and 11.3 nests at Pelham. Nest density over 25 years was significantly greater at Groff Park (paired *t*-test; $t = 2.34$, 24 *df*, $p = .028$). We reject the null hypothesis that nesting density at Groff Park and Pelham are not different.

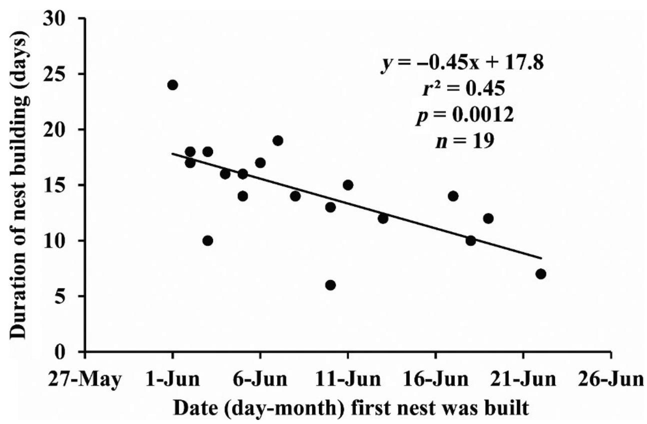

FIGURE 5 Relationship between date of annual *Petromyzon marinus* nesting initiation and duration of the nesting period (number of days) in the Fort River, 1981–2008

3.6 | H_O 6 = annual initial nesting date does not affect annual nesting duration

Regression analysis showed annual nesting initiation date significantly affected annual nesting duration (the total number of days nests were built each year; $r^2 = 0.45$; $p = .0012$; Figure 5). For years when the first nest was built after 11 June, duration of nest building was short, ≤14 days; whereas, in years when nesting began the first week in June, duration of nesting was ≥14 days. We reject the null hypothesis.

3.7 | Nesting ecology

The annual time series plots of nesting timing and Fort River discharge and temperature for 7 years (1990–1996) showed no clear pattern that either factor affected initiation or duration of nesting (Figure 6). For example, in some years nesting began many days after peak discharge, and in other years, nesting began only 1–2 days after a peak discharge. The 4 years that included river temperature also showed great variation in temperature when nesting began or ended.

Time-series analysis of Fort River temperature and discharge in 1990–1996 showed nesting occurred during decreasing mean river discharge and increasing median daily low and high temperatures (Figure 7). The values of temperature and discharge just before and during nesting varied greatly among years, and also, the values of temperature and discharge overlapped among years between the week before nesting and the nesting period, as well as, between the nesting period and the week after nesting (Figure 7). River temperature and discharge had no clear relationship with nesting.

However, the time-series analysis using 16 years of data on Fort River discharge plotted to show median daily discharge and daily CV before nesting (15–31 May), during nesting (1 June-1 July), and after nesting (2–15 July) showed the nesting period occurred during a period of declining discharge when variability in daily discharge (CV) was low (Figure 8).

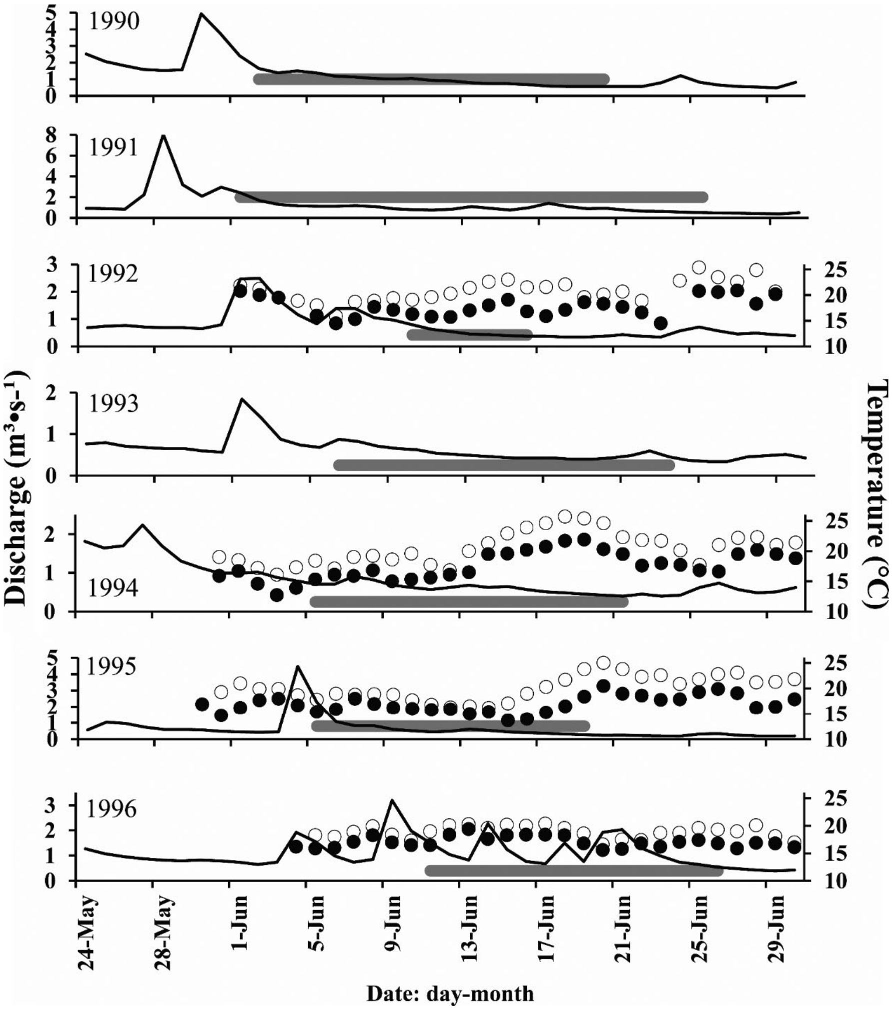

FIGURE 6 Time series of 7 years (1990–1996) showing the daily low and high temperatures (°C) and the mean daily discharge ($m^3 \cdot s^{-1}$; USGS station 01171300) in relation to annual *Petromyzon marinus* nesting time in the Fort River. Discharge = solid line with peaks above the x-axis; daily temperatures = high (white circles) and low (black circles). The annual nesting period is shown by the solid horizontal gray bar above the x-axis

4 | DISCUSSION

4.1 | Counts of adults in the fish lifts at Holyoke Dam

The number of adult migrant *P. marinus* counted in the fish lift system at Holyoke Dam is not the total run into the Connecticut River. Each year, some adults enter tributaries downstream of Holyoke Dam where several thousand are counted at passage facilities in three tributaries (CRASC, 2018). An unknown number of adults spawn in the mainstem and in other tributaries, where they are uncounted. Dams remain on many tributaries that block access of adult *P. marinus* to spawning and rearing habitat (CRASC, 2018). Although the annual count of adults at Holyoke Dam excludes some adults that do not swim to Holyoke Dam, the counts at Holyoke Dam are likely a good index measurement for annual run abundance to the river (although accuracy of the counts has not been measured).

The annual schedule of fish lift operation at Holyoke Dam includes the time before and after migrant adult *P. marinus* occur at the dam; thus, the entire annual 30–52 day long run is able to enter the fish lifts and no adults are omitted from being counted. The fish lifts begin annual operation on 1–7 April and end operation on 9–18 July (USFWS, CRAFC), which encompasses the total *P. marinus* run timing at Holyoke Dam during any year (Figure 3). Thus, all migrant *P. marinus* reaching Holyoke Dam have the opportunity to enter a fish lift and be counted. The daily lifting schedule is restricted to daylight hours and migrant *P. marinus* move upstream mostly at night, particularly early in the run (Steir & Kynard, 1986b). Some early migrants may not enter the fish lifts during the day. Lifting or unfavorable river conditions for passing *P. marinus* could minimize passage on a particular day or for several days, but no factor likely affects the total annual number of *P. marinus* lifted.

4.2 | Abundance of adult migrant *P. marinus* in the Connecticut River

Prior to the anadromous fish restoration program in the Connecticut River using fish passage at mainstem and tributary dams, adult *P. marinus* entered the Connecticut River and spawned in the mainstem and tributaries downstream of Holyoke Dam (CRASC, 2018). After the tailrace fish lock, and later, fish lift was installed at Holyoke Dam beginning in 1955, counts of adults annually passed over the dam in 1955–1974 show zero-537 adults were

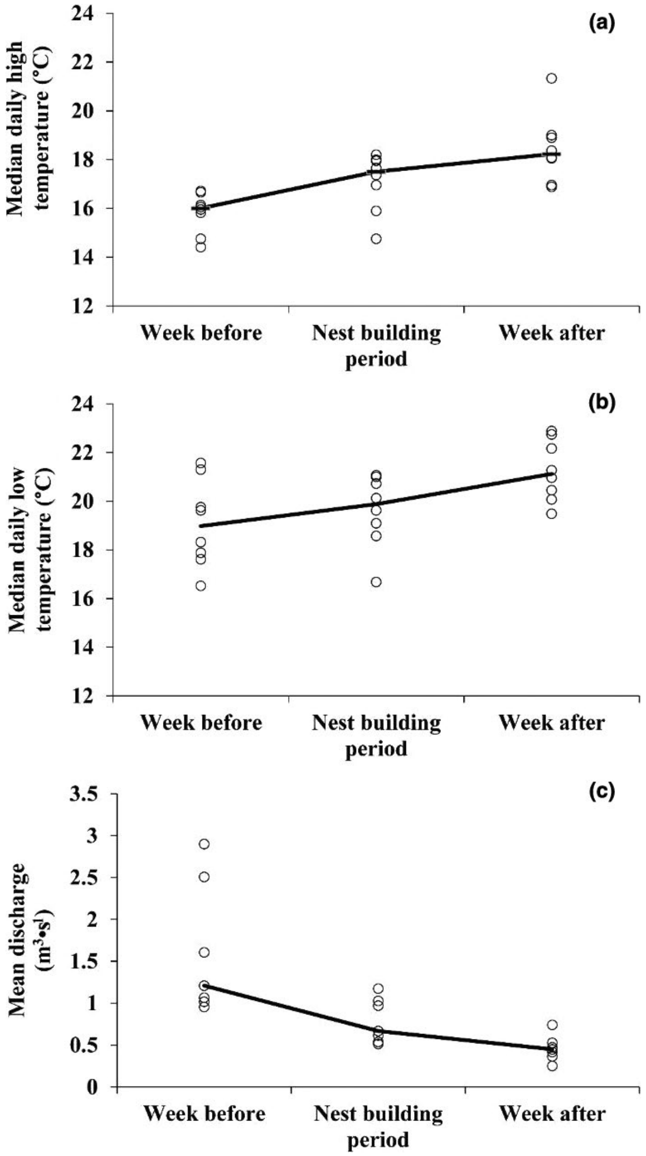

FIGURE 7 Time series showing relationships between Fort River temperature and discharge and three time periods relative to nesting (week before nesting, during nesting, and week after nesting). Temperature data are from 8 years between 1992 and 2008. For the three nesting timing, panel a shows the median high temperature (°C), panel b shows the median low temperature, and panel c shows the mean river discharge ($m^3 \cdot s^{-1}$; USGS station 01171300). Discharge data were used from 16 years (1979–1982 and 1985–1996). Lines connect the median values of the three time periods

passed upstream (although adults were not counted for 7 years; Moffitt et al., 1982). Thus, few adults were passed upstream of Holyoke Dam until the spillway fish lift began operation in 1975. However, annual counts of adult *P. marinus* in the Holyoke fish lifts during the first 5 years of spillway lift operation (1975–1979) was 23,000 (1975), 32,000 (1976), 52,000 (1977), 43,000 (1978), and 32,000 (1979; Moffitt et al., 1982; present study, Figure 2). Thus, before the fish passage program began passing significant numbers of adults upstream of Holyoke Dam, there was an annual

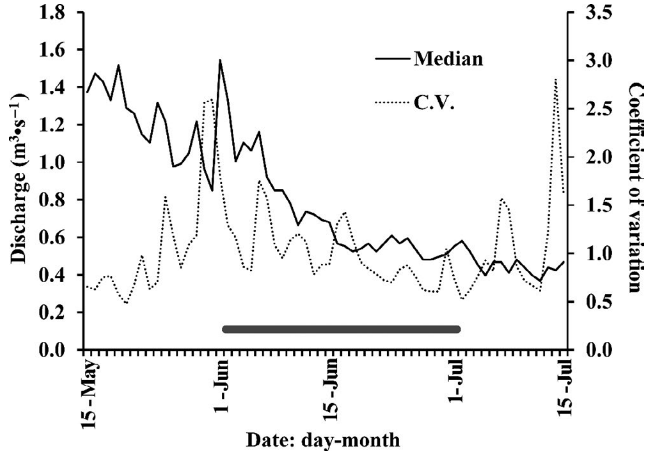

FIGURE 8 Time series showing the relationship between Fort River discharge, daily discharge coefficient of variation, and *Petromyzon marinus* nesting. Daily median Fort River discharge ($m^3 \cdot s^{-1}$; USGS station 01171300) and daily CV are from 15 May (pre-nesting) to 15 July (post-nesting) during 16 years (1979–1982, 1985–1996). Nesting period is indicated by the dark solid horizontal line above x-axis. Mean date of annual nesting initiation was 7 June. Solid jagged line = daily median discharge; dashed jagged line = daily CV

run into the Connecticut River in excess of tens-of-thousands of adults.

Beginning in 1975, adults annually gained access to increased historical spawning and rearing range in the watershed using the new tailrace fish lift at Holyoke Dam and also, using fish passage at three mainstream dams upstream from Holyoke Dam (dam name, first operation year, rkm: Turners Falls Dam, 1980, rkm 198; Vernon Dam, 1981, rkm 228; and Bellows Falls Dam, 1983, rkm 280; Moffitt et al., 1982). In all cases, tens-hundreds of adult *P. marinus* passed upstream in fish passage facilities the first year of operation. Imprinting to upstream river reaches was not required for adults to have the behavioral drive to migrate farther upstream. In recent years, hundreds to tens of thousands of adults pass upstream at the three dams upstream of Holyoke Dam (USFWS, CRAFC). Fish passage has given adult *P. marinus* access to an estimated double the amount of spawning and larval rearing habitat compared to the habitat available before 1975 (CRASC, 2018).

Even if increased access to spawning and rearing habitats produced twice as many larvae, juveniles, and adults, adult run size into the Connecticut River might only see a slight or no increase (as we found in the present study for 1978–2014). Recent genetic studies found anadromous *P. marinus* lack natal stream homing (Waldman, Grunwald, & Wirgin, 2008). This life history pattern was found previously in land-locked *P. marinus* (Bergstedt & Seelye, 1995). Thus, a Connecticut River population of *P. marinus* with adults returning to spawn in their natal river does not exist. Instead, the species uses a strategy of entering a river to spawn based on a most suitable river strategy. All evidence suggests the most suitable river is one with a strong pheromone attractant produced by larvae (Bjerselius et al., 2000).

Although pheromones from rearing larvae attract land-locked adults (Bjerselius et al., 2000), it is not known if there is a positive relationship between abundance of larvae (and pheromone concentration) and abundance of adults attracted into a river. The lack of a positive trend in adult abundance at Holyoke Dam during 1978–2014, when larval distribution (and likely abundance) greatly increased throughout the Connecticut River watershed, does not support the idea of a positive relationship between larval abundance and abundance of adults attracted into the Connecticut River. Data are lacking on larval abundance in the Connecticut River, but all surveys found larva in the mainstem and tributaries upstream of Holyoke Dam where few or no larvae existed prior to 1975, suggesting larval abundance has greatly increased since 1975 (CRAC, 2018; Kynard, unpubl. data).

The Connecticut River fish passage program's goal is to restore anadromous fish to their historical range in a watershed segmented by damming. The present case study of restoration of anadromous *P. marinus* in the Connecticut River provides a conceptual model for restoration expectations of anadromous lampreys in other rivers with an existing large run of adults (thousands to tens-of-thousands) to the river. For the other anadromous fish species in the Connecticut River, abundance and distribution of adults is a good indication of program success. However, program success for *P. marinus* in the Connecticut River watershed cannot be measured solely by annual run size and distribution of the nesting and rearing. Instead, success should be viewed in larger ecological and spatial contexts that include the distribution of all life stages throughout the watershed and marine environments, their role in freshwater and in marine food-web systems, and the contribution of marine-derived nutrients and minerals to freshwater-riparian systems from dead adults. All adults die after spawning and their bodies contribute marine-derived nutrients, minerals, and materials to the watershed, usually the only source of marine minerals in tributary headwaters (CRASC, 2018; Nislow & Kynard, 2009).

4.3 | Abundance cycle

A recent book on North American lamprey species does not mention abundance cycles for any species (Brown et al., 2009). Abundance cycles of lampreys are poorly studied in North America, although land-locked *P. marinus* had a 3-year peak in abundance during 10 years (1986–1995) in the Brule River, Wisconsin *P. marinus* trap (L. Drews, Wisconsin Department of Natural Resources, unpubl. data). No explanation for this cycle was provided. An explanation for the abundance cycle of land-locked *P. marinus* would be difficult to discover because of the annual variation in larval mortality (and the resulting abundance of adults) created by killing larvae with a lampricide (Smith & Tibbles, 1980; Wells, 1980).

Even when there are long-term data on annual abundance from *P. marinus* fisheries catch data in Europe (Maitland, 1980) or annual counts of adult *P. marinus* at barrier fences (Applegate & Smith, 1950), or counts at dams of adult Pacific Lamprey, *E. tridentatus* (Negrea, Thompson, Juhnke, Fryer, & Loge, 2014) analyses to discover abundance cycles have not been done. Pre-spawning adult counts at fish passage facilities at dams provide an excellent opportunity to examine adult runs for an abundance cycle for any lamprey species.

There are no fisheries for anadromous *P. marinus* in the United States; thus, the 6-year-cycle should be controlled by natural factors. Further, because adults entering the Connecticut River are natal to many rivers (Waldman et al., 2008), the abundance cycle is not likely related to freshwater conditions in the Connecticut River (or other rivers). Instead, the cycle is likely related to marine factors where juveniles and adults from all rivers are subject to common factors, like marine prey abundance for parasitic juveniles and adults. Further, adults produced by spawning and rearing in the Connecticut River that do not return to the Connecticut River to spawn likely enter other Atlantic coast rivers, and perhaps, expand distribution of the species.

A recent review of information needs for lamprey conservation in North America by (Mesa and Copeland 2009) failed to mention the need for long-term data sets to document natural run abundance and cycles. Long-term data sets can identify natural trends (and abundance declines from human causes) and abundance cycles. Long-term data sets on critical life behaviors, like run size, nesting abundance, and nesting timing, are particularly important as the climate becomes directionally warmer with time.

4.4 | Nesting

Passage timing of *P. marinus* at Holyoke Dam had no significant effect on nesting timing in the Fort River. Although the fish lifts operate only in daytime, which is an artificial schedule for nocturnal early-migrant *P. marinus* (Steir & Kynard, 1986b), annual lift operations had no effect on annual nesting timing. Delays of migrant *P. marinus* adults at the Mactaquac Dam fish lift on the St. John River, New Brunswick, Canada, was suggested by Beamish (1980), but the study did not evaluate whether delays affected nesting timing.

An important management finding of the present study was that annually counting nests in a target reach of river or tributary provides data to monitor trends of the total abundance of adults in the entire river. Thus, trends in adult abundance in a large river without fish counts at a dam could be monitored by a relatively small effort counting nests in a small reach of a tributary. Adult counts and nest abundance were also used to monitor abundance of adult *E. tridentata* for 2 years in the Coquille River, OR, USA (Brumo, 2009). Like the significant relationship we found for 25 years between annual run counts at Holyoke Dam and nest counts in the Fort River, there was good agreement between these two methods in the Coquille River, suggest this methodology is suitable for other rivers and other species of lampreys.

Time-series analyses of nesting timing and river discharge and temperature found no clear relationship between river discharge or temperature and initiation of annual nesting (Figures 6, 7). Day length (photoperiod) is the proximate environmental factor triggering spawning timing in Connecticut River shortnose sturgeon, *Acipenser brevirostrum* (Kieffer & Kynard, 2012). During 17 years of observations, shortnose sturgeon spawned within a 26 day window. Day length may also trigger nesting initiation by *P. marinus* in the Fort River. *P. marinus* initiated nesting in a 21 day window (1–20 June). During 15 of 18 years (1990–2008) nesting began during a short 15 day window (1–14 June).

Timing of larvae to metamorphose is mainly controlled by water temperature (Holmes, Beamish, Seelye, Sower, & Youson, 1994). Thus, if day length triggers spawning, different environmental factors control important events during *P. marinus* life history.

Most *P. marinus* nesting in the Fort River occurred when river discharge was decreasing, low, and variation among years was relatively stable (Figure 8). The results suggest males may delay spawning until the period of low, stable discharge. The advantages associated with nesting during this discharge regime may be related to the effect of water velocity on egg fertilization, egg and early larval survival, or both.

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