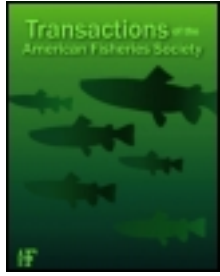


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Robert Hogg^a, Stephen M. Coghlan Jr.^a & Joseph Zydlewski^b

^a Department of Wildlife Ecology, University of Maine, 5575 Nutting Hall, Orono, Maine, 04469, USA

^b U.S. Geological Survey, Maine Cooperative Fish and Wildlife Research Unit, University of Maine, 5575 Nutting Hall, Orono, Maine, 04469, USA

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ARTICLE

Anadromous Sea Lampreys Recolonize a Maine Coastal River Tributary after Dam Removal

Robert Hogg* and Stephen M. Coghlan Jr.

Department of Wildlife Ecology, University of Maine, 5575 Nutting Hall, Orono, Maine 04469, USA

Joseph Zydlewski

U.S. Geological Survey, Maine Cooperative Fish and Wildlife Research Unit, University of Maine, 5575 Nutting Hall, Orono, Maine 04469, USA

Abstract

Sedgeunkedunk Stream, a third-order tributary to the Penobscot River, Maine, historically supported several anadromous fishes, including the Atlantic Salmon *Salmo salar*, Alewife *Alosa pseudoharengus*, and Sea Lamprey *Petromyzon marinus*. However, two small dams constructed in the 1800s reduced or eliminated spawning runs entirely. In 2009, efforts to restore marine–freshwater connectivity in the system culminated with removal of the lowermost dam, thus providing access to an additional 4.6 km of lotic habitat. Because Sea Lampreys utilized accessible habitat prior to dam removal, they were chosen as a focal species with which to quantify recolonization. During spawning runs of 2008–2011 (before and after dam removal), individuals were marked with PIT tags and their activity was tracked with daily recapture surveys. Open-population mark–recapture models indicated a fourfold increase in the annual abundance of spawning-phase Sea Lampreys, with estimates rising from 59 ± 4 ($\bar{N} \pm SE$) before dam removal (2008) to 223 ± 18 and 242 ± 16 after dam removal (2010 and 2011, respectively). Accompanying the marked increase in annual abundance was a greater than fourfold increase in nesting sites: the number of nests increased from 31 in 2008 to 128 and 131 in 2010 and 2011, respectively. During the initial recolonization event (i.e., in 2010), Sea Lampreys took 6 d to move past the former dam site and 9 d to expand into the furthest upstream reaches. Conversely, during the 2011 spawning run, Sea Lampreys took only 3 d to penetrate into the upstream reaches, thus suggesting a potential positive feedback in which larval recruitment into the system may have attracted adult spawners via conspecific pheromone cues. Although more research is needed to verify the migratory pheromone hypothesis, our study clearly demonstrates that small-stream dam removal in coastal river systems has the potential to enhance recovery of declining anadromous fish populations.

Dams are ubiquitous throughout the world, providing hydroelectric power generation, flood control, municipal water supplies, and recreational opportunities. Historically, dams were built without forethought of their ecological impacts, and some early dams have outlived their utility. Dams constructed without fish passage systems have blocked anadromous fish migrations and are a leading cause of fish declines in Maine and around the world (Limburg and Waldman 2009). Dams contribute to declines in the biodiversity and productivity of stream system fauna (Freeman et al. 2003), and dam removal may provide rapid (<1 year) ecosystem responses if high-water events move

the impounded sediment downstream (Hart et al. 2002; Gardner et al. 2013).

The Penobscot River is Maine's largest river, and the watershed once supported as many as 11 co-evolved diadromous species (Saunders et al. 2006). However, 113 dams throughout the watershed have severed marine–freshwater connectivity and have led to declines in all sea-run fishes (PRRT 2012). Efforts to restore marine–freshwater connectivity along the Penobscot River are underway, with main-stem dam removal projects anticipated to occur from June 2012 to November 2013 (PRRT 2012).

*Corresponding author: hogg.robert.s@gmail.com

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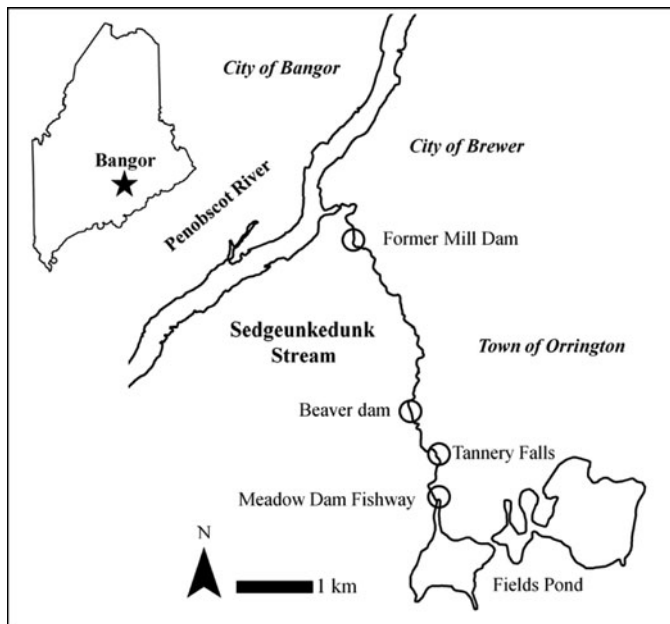


FIGURE 1. Locations of Sedgeunkedunk Stream (Penobscot County, Maine), Fields Pond, barriers that were removed as part of the Sedgeunkedunk Stream Restoration Project (e.g., former Mill Dam), and natural landmarks that were identified as potential barriers to Sea Lamprey range expansion.

Sedgeunkedunk Stream, a small tributary to the Penobscot River below head of tide, typifies the small streams in Maine that have been impacted by dams (Figure 1). Recent restoration efforts in Sedgeunkedunk Stream have provided opportunities to assess fish community responses to dam removal, and the system provides ideal conditions for predicting the recovery of other upstream tributaries that are influenced by main-stem Penobscot River dam removals (Gardner et al. 2012, 2013). Sedgeunkedunk Stream is one of only three major tributaries flowing into the Penobscot River downstream of the lowermost main-stem dam (i.e., Veazie Dam), which is slated for removal during 2013–2014 (PRRT 2012). Therefore, recovery of anadromous species in Sedgeunkedunk Stream may provide a glimpse of predicted restoration outcomes on the main-stem Penobscot River.

Efforts to restore marine–freshwater connectivity in Sedgeunkedunk Stream culminated in August 2009 with the removal of the lowermost dam, Mill Dam, at stream kilometer 0.7 (Figure 1), allowing access to an additional 4.7 km of high-quality spawning and rearing habitat for Sea Lampreys *Petromyzon marinus* and federally endangered Atlantic Salmon *Salmo salar*. Additionally, the removal of Mill Dam, coupled with construction of a rock–ramp fishway that bypassed the remnants of the former Meadow Dam, provided a corridor for migrating Alewives *Alosa pseudoharengus* to access lentic spawning habitat in Fields Pond (Figure 1). Previous studies within Sedgeunkedunk Stream indicated the annual occurrence of Sea Lamprey spawning runs, which were limited to the lower 700 m of stream below Mill Dam (Gardner et al. 2012). The Sea Lamprey was the

only anadromous species known to consistently spawn in Sedgeunkedunk Stream prior to dam removal and now serves as a focal species for evaluating the short-term efficacy of restoration efforts.

Anadromous Sea Lampreys begin their life history in freshwater streams and rivers, where fertilized eggs settle into gravel and cobble nests. Embryos incubate for 3–8 d before the larvae (ammocoetes) emerge, drift downstream, settle in silty substrate, and filter feed for as many as 8 years (Beamish 1980). After this prolonged period of larval filter feeding, ammocoetes undergo a suite of behavioral, physiological, and morphological changes as they prepare to leave the freshwater environment. This transformation is likely triggered by maturation to a minimum body length of 120 mm, body mass of 3 g, and condition factor of 1.5, in combination with the accumulation of sufficient lipid reserves to ensure survival during the 10–11-month non-trophic metamorphosis period (Jones 2007). These transformers (or macrophthalmia) develop large eyes, an oral disk, and salt-water tolerance as they exit freshwater and become parasitic in the open ocean. Sea Lampreys are parasitic in the Atlantic Ocean for 2–3 years, after which they cease feeding and migrate back into freshwater rivers to spawn (Beamish 1980).

Anadromous lampreys select spawning streams by cueing on temperature and flow (Andrade et al. 2007; Keefer et al. 2009; Binder et al. 2010), but chemical compounds released by the ammocoetes are extremely influential (Wagner et al. 2009; Vrieze et al. 2010). The observed reliance upon chemical and environmental cues in selection of spawning habitat—instead of philopatry as exhibited by Atlantic Salmon (Hansen and Quinn 1998) or Alewives (Jessop 1994)—suggests that Sea Lampreys may recolonize newly accessible habitat more rapidly than the other historically cohabiting anadromous species of Sedgeunkedunk Stream. The rapid expansion of Sea Lampreys into the upper Laurentian Great Lakes during the 1930s after the construction of navigation channels further demonstrates the species' ability to exhibit rapid colonization (Smith and Tibbles 1980).

Because Sea Lampreys in the upper Great Lakes parasitize valuable sport fishes, research in North America has largely been driven by mitigating negative impacts upon recreational and commercial fisheries (Christie and Goddard 2003). However, within their native range, anadromous Sea Lampreys are a focus of concern due to decreasing runs. Declines and local extirpations of Sea Lampreys in Europe have been documented (Renaud 1997), and the species has received conservation attention on both sides of the Atlantic Ocean (Maitland 2003; CRASC 2011). Additionally, in recognition of the unique ecological functions that anadromous species may perform, current restoration efforts have shifted away from single-species approaches to more-community-based and ecosystem-based approaches. Operating under this community-based paradigm, resource managers have recognized that Sea Lampreys may be an ecologically important constituent of stream ecosystems and that the Sea Lamprey's recovery may therefore be critical to

restoration of native anadromous fish assemblages in Maine (Saunders et al. 2006).

Sea Lampreys are semelparous and die within days after spawning (Beamish 1980). Postspawning mortality typically occurs during periods of declining discharge and increasing summer temperatures, thereby translating into rapid carcass decomposition. Therefore, Sea Lamprey carcasses may provide pulses of marine-derived nutrients in otherwise oligotrophic headwater streams at a favorable time to support instream production (Nislow and Kynard 2009; Guyette 2012). Sea Lamprey spawners use their suctorial disk mouths to rearrange gravel and cobble substrate during nest construction. Essentially, they excavate rocks from the tails of pools and deposit them slightly downstream to form pit-and-mound nest structures. Pairs of male and female individuals spawn from a remnant “anchor rock” in the pit, where they vibrate vigorously against one another and release gametes. Finally, the fertilized eggs settle downstream; although only approximately 15% of these eggs are ultimately deposited in the mound, a high proportion of the mound-deposited eggs (85–90%) survive to hatch (Smith and Marsden 2009). Spawning-related activities detach fine sediments from coarser substrates (Kircheis 2004), and these modifications to streambed topography may reduce substrate armoring and embeddedness, similar to the effects of redd-building Pacific salmon *Oncorhynchus* spp. (Montgomery et al. 1996). Hence, nest construction and spawning activities by Sea Lampreys may “condition” the spawning habitat for Atlantic Salmon (Kircheis 2004; Saunders et al. 2006), provide prey in the form of displaced eggs and dislodged benthic invertebrates (Scott and Crossman 1985), and potentially create physical structure for drift-feeding fishes.

The present study expands on previous research conducted prior to dam removal (Gardner et al. 2012) and serves to quantify the efficacy of dam removal as a restoration tool. The primary focus of this study was the hypothesized expansion of Sea Lampreys into previously inaccessible habitat of Sedgeunkedunk Stream. Our project goal was to compare and contrast the abundance, distribution, and behavior of spawning Sea Lampreys before and after dam removal. Specifically, our objectives were to (1) provide annual estimates of spawning-phase Sea Lampreys by using mark–recapture data; (2) quantify and compare the distributions and abundances of nesting sites before and after dam removal; (3) characterize attributes, behaviors, and movement patterns of spawning-phase Sea Lampreys in response to dam removal; and (4) describe annual patterns in timing of the Sea Lamprey spawning run as related to stream temperature and discharge.

STUDY AREA

Sedgeunkedunk Stream is a third-order tributary to the Penobscot River (Penobscot County, Maine) and flows through the town of Orrington and the city of Brewer (Figure 1). Sedgeunkedunk Stream drains Fields Pond at the Meadow Dam

Fishway (44°44′05″N, 68°45′56″W) and flows 5.3 km downstream to the confluence of the Penobscot River near head of tide at river kilometer (rkm) 36.5 (44°46′08″N, 68°47′06″W). The lower 90-m reach of Sedgeunkedunk Stream experiences tidal fluctuations due to its proximity with the Penobscot River head of tide. The Sedgeunkedunk Stream watershed drains approximately 5,400 ha and includes several ponds in the headwaters. The watershed is mostly forested, but some urban and industrial development exists, primarily in downstream reaches. The relatively low-gradient stream has a median bank-full width of approximately 5 m, with a peak discharge of 5 m³/s immediately after early spring ice-out and a base flow discharge of 0.1 m³/s during late summer. The lowermost dam (Mill Dam; 44°45′55″N, 68°46′47″W) was located 700 m upstream of the Penobscot River confluence and 610 m upstream of head of tide. Although the Meadow Dam Fishway provides marine–freshwater connectivity between the Atlantic Ocean and Fields Pond, access through the fishway is inconsequential for Sea Lampreys because their spawning requirements limit them to lotic habitats. Therefore, this study was focused on the 5.2-km reach of lotic habitat from the Meadow Dam Fishway downstream to the Sedgeunkedunk Stream head of tide. However, we note that a 4-m-high natural waterfall (Tannery Falls) located at rkm 4.8 may be a substantial barrier to Sea Lamprey migration, especially during low-flow years (Figure 1).

METHODS

Mark–Recapture Surveys

Sea Lamprey capture and tagging.—Our methods were similar to those of Gardner et al. (2012). As migrating Sea Lampreys entered Sedgeunkedunk Stream, they were captured with an Indiana-style trap net (fyke net) anchored 90 m upstream from the confluence with the Penobscot River. The 2.5-m-long fyke net was constructed of 3-mm square mesh, with a 1.3- × 1.6-m (height × width) mouth and a 1-m-diameter cod end. The trap was centered longitudinally in the 0.8-m-deep thalweg (±0.2 m, dependent on tidal cycle and discharge), and the wings of the trap spanned the entire 4.5-m width of the stream (±0.5 m, dependent on tidal cycle and discharge). We deployed the fyke net from 15 May to 26 June 2010 and from 22 May to 6 July 2011. Two submersible light-emitting diode (LED) lamps were sewn into the entrances of the fyke net during 2011 to increase trap efficiency (Purvis et al. 1985).

Upon capture, each Sea Lamprey received two tags. A full-duplex (12- × 2-mm) PIT tag was implanted within the dorsal musculature via a hypodermic injector, and an externally visible t-bar anchor tag (uniquely coded) was inserted into the dorsal musculature on the opposite side to assess PIT tag retention on future dates. We recorded the mass, length, and sex of each Sea Lamprey before release. Fully mature Sea Lampreys exhibit sexual dimorphism, and males are accurately identified by the presence of a thickened dorsal ridge, or “rope” (Hardisty and Potter 1971). However, this dorsal characteristic may not

be fully developed in early arriving males. Therefore, to verify sex, we used a suite of primary and secondary sexual characteristics, including the gentle expression of gametes, female post anal fin development, and presence of the male genital papilla or “penis,” in addition to the dorsal rope (Percy et al. 1975). If we lacked confidence in sex determination based on all of these characteristics, we recorded the sex of the individual as unconfirmed. Out-of-water processing generally took less than 40 s, and individuals were allowed to re-acclimate in live wells for at least 15 min prior to their release back into the stream. No adverse effects were witnessed after the tagging process, and recently tagged fish were often observed building nests within hours of tagging.

Spawning surveys.—We conducted daily surveys on foot to track the activity of tagged individuals and to identify Sea Lamprey nests along the entire reach of stream from the fyke net to the Meadow Dam Fishway. Foot surveys were performed by two crews: one crew worked upstream from the fyke net, and the other worked downstream from the fishway. Surveys generally began shortly after dawn and no later than 0700 hours. Surveys were completed by 1800 hours. We captured nontagged individuals with dip nets or by hand and processed them as described previously. A portable PIT tag antenna coupled with a battery-powered reader was used to identify previously tagged individuals without repeated handling (Hill et al. 2006), thus minimizing the disruption of spawning activity (Gardner et al. 2012). Upon each Sea Lamprey encounter, we recorded the individual’s identity (unique tag code), tag retention, condition (live or dead; carcass recoveries were recorded as “losses on capture”), behavior, nest attendance, and location.

Nest surveys.—We marked each nest location with a coded stake driven into the streambank and recorded Universal Transverse Mercator (UTM) coordinates with a handheld GPS device (eTrex Legend H; Garmin, Inc.). All UTM waypoints were ground-truthed at a later date and were found to be within 5 m of the respective nest locations. Many Sea Lampreys exhibit photophobic, nocturnal behavior and abandon nests in favor of sheltered areas during daylight hours (Kelso and Gardner 2000). Furthermore, male lampreys typically initiate nest construction, but a male will often abandon a particular nest if he is not joined promptly by a receptive female (Manion and Hanson 1980). Therefore, nest identifications were based on obvious substrate disturbances in addition to direct observations of spawning activity.

Spawning Run Timing: Temperature and Discharge

We adopted the remote stream gauging methodology of Lundquist et al. (2005) and deployed a combination pressure and temperature sensor (Solinst Levelogger Junior; www.solinst.com), which was encased in a protective polyvinyl chloride standpipe anchored to a concrete bridge in Sedgeunkedunk Stream at rkm 0.6. We programmed the levelogger to record temperature and water level continuously at 1-h intervals from May to November (the expected onset of winter icing)

during 2010 and 2011. The bridge location provided ideal conditions, with relatively uniform depth across a fixed stream width of 4.2 m. We used a propeller-driven current velocity meter (Swoffer Model 2100) and a U.S. Geological Survey (USGS) top-set wading rod to gauge the stream at minimum 1-week intervals. Individual gauging measurements were regressed to average daily water levels to estimate a continuous daily discharge record. A third-order polynomial ($R^2 = 0.998$, $P < 0.001$) was used to build an average daily discharge curve for 2010. Because the standpipe was damaged by ice scour in 2011 and was subsequently replaced, a second-order polynomial ($R^2 = 0.984$, $P < 0.001$) was used for that year.

Data Analysis

Data set.—Unless otherwise stated, we incorporated archived 2008 pre-dam-removal data from Gardner et al. (2012) to perform direct post-dam-removal comparisons. We note that due to flood conditions throughout the month of June in 2009, no Sea Lamprey spawning activity was observed during the 2009 pre-dam-removal season (Gardner et al. 2012). Therefore, we report no data from 2009. All means are reported with SEs, and statistical tests were conducted using the Statistical Analysis Systems version 9.2 (SAS 2010) at the significance level α of 0.05 unless otherwise noted.

Abundance estimates.—We estimated abundance of spawning Sea Lampreys in Sedgeunkedunk Stream for 1 year before dam removal (2008) and 2 years after dam removal (2010 and 2011) by using a Jolly–Seber population analysis (POPAN) model developed for open populations (Arnason and Schwarz 1999) in program MARK (White and Burnham 1999). We recorded carcasses as losses on capture (Schwarz et al. 1993), and after enumeration, carcasses were removed from the analyses. The POPAN model is appropriate for estimating the abundance of spawning Sea Lampreys in Sedgeunkedunk Stream because the following assumptions were likely met: (1) animals retained their tags throughout the duration of the studies; (2) tags were read properly; (3) sampling was consistent with daily encounter histories (sampling was not instantaneous, but model developers claim that departures of less than 2–3 d are small enough to avoid violation; Schwarz et al. 1993); (4) the study area was held constant; and (5) constant trap and survey efforts provided equal catchability between marked and unmarked animals at each sampling occasion (Pledger and Efford 1998). We used Akaike’s information criterion corrected for small sample sizes (AIC_c) to evaluate and select the best candidate models for each spawning run (Burnham and Anderson 2002). Candidate models included the following as parameters: the probability of capture (p_{cap}), probability of apparent survival (Φ), and probability of entering the study system (p_{ent}). Parameters were set to vary at daily time steps or to remain constant, but because models incorporating time-dependent capture parameters are inherently unable to estimate abundance at the first or last sampling occasion (Schwarz et al. 1993), we limited p_{cap} to a constant value in all model iterations.

Nesting site distributions.—In the context of newly available habitat, we expected a relatively slow rate of Sea Lamprey range expansion due to their purported reliance upon conspecific chemical cues (ammocoete pheromones) for selection of spawning habitat. We anticipated comparatively fewer nests upstream of the former Mill Dam during the first year of recolonization (2010), but we expected to observe an increase in upstream nesting sites during 2011 after larval recruitment from the prior year. To test these hypotheses, we conducted chi-square (χ^2) goodness-of-fit tests for 2010 and 2011; the null hypotheses stated that nesting site selection would be proportionately equivalent to the habitat available in the historically accessible reach downstream of the former Mill Dam and in the newly accessible upstream reach.

We used the following rationale for setting up the χ^2 analyses. Sea Lampreys accessed approximately 3,000 m² (610-m length \times 5-m median width) of lotic habitat prior to the August 2009 removal of Mill Dam. Restoration efforts provided an additional 23,000 m² (4.6 km of stream length) of available lotic habitat for Sea Lampreys, but 2010 drought conditions confined Sea Lampreys to habitat below a beaver dam located near rkm 4.0 (Figure 1). Therefore, Sea Lampreys accessed 17,000 m² (3.4 km of stream length), and the return to a more typical flow regime during 2011 resulted in an additional 1,000 m² of habitat ending at Tannery Falls (Figure 1). We note that although the distance between the beaver dam and Tannery Falls is approximately 800 m in stream length, the beaver dam impoundment renders approximately 600 m of stream unsuitable for spawning.

Sea Lamprey capture, biological measures, and behavior.—We surmised that individual Sea Lampreys that were captured in the fyke net would be heavier than those that were tagged further upstream. Additionally, we anticipated that the 2011 addition of LED lights at the fyke net entrance would increase the trap efficiency. Therefore, we employed two-way ANOVA models incorporating the year \times trap interaction as a factor to investigate differences in size distributions of males and females separately. Furthermore, we questioned whether the sex ratio would be skewed toward exploratory males during recolonization after dam removal, so we used χ^2 goodness-of-fit tests to determine whether there were differences in gender distributions. If recolonization was driven by the exploratory behavior of males, we would expect to see more male-initiated instances of nest construction. Therefore, we organized active nest observation data into categories of single, paired, or communal nesting behaviors. For the 2010 and 2011 spawning seasons, we used χ^2 goodness-of-fit tests to compare the observed gender of a single Sea Lamprey against an expected equal probability of the individual being male or female. Additionally, χ^2 tests were used to compare the observed genders of paired Sea Lampreys against expected equal probabilities that pairs were engaged in either male–female courtship or same-sex nest construction.

To quantify individual movements, successive detections were organized chronologically and minimum pathway distances traveled between detections were estimated with the

measurement tool in ArcGIS version 9.3 (ESRI, Inc., Redlands, California). In total, we observed 57% (2008: $n = 27$), 48% (2010: $n = 63$), and 49% (2011: $n = 76$) of tagged Sea Lampreys after the initial capture date; although most of the tagged individuals were subsequently detected only once, some were detected as many as six times after the tagging date. We observed a small percentage of same-day repeat detections (<5%) and found that most of those individuals fell back relatively short distances downstream (range = 12–242 m). For consistency, we removed all same-day fallback distances and used only the furthest upstream daily detection in analyses. Because initial capture locations were so variable, we limited statistical analysis of movement patterns to detections of maximum upstream distances (Max rkm) for individuals that were encountered at least two times. A two-factor ANOVA on ranked Max rkm data incorporating the year \times gender interaction was used to explore differences in movement patterns. We did not include the 2008 Max rkm data in statistical analysis because the presence of Mill Dam limited the potential for Sea Lamprey movements to downstream reaches below rkm 0.7 (Gardner et al. 2012). However, we do report gender-specific 2008 medians and ranges of Max rkm for pre- and post-dam-removal comparisons. Furthermore, we simply plotted gender-specific point measurements of upstream and downstream movements for individuals that were detected more than once to elucidate the gender-specific movement patterns that occurred after dam removal.

Spawning run timing: temperature and discharge.—To detect interannual stream temperature variation, we used a one-way ANOVA with year as the factor and average daily temperature during the Sea Lamprey spawning period as the response variable. Additionally, a Student's t -test assuming unequal variances was employed to detect interannual variation in stream discharge. The use of Student's t -test was appropriate because we only estimated discharge during the 2010 and 2011 spawning runs.

We used generalized least-squares (GLS) regression models to explore how run timing was related to both temperature and discharge. Daily counts of initial Sea Lamprey captures in the study system were used as the response variable. Mean daily discharge, change in discharge from the previous day, mean daily temperature, and change in temperature from the previous day were used as predictor variables. Generalized least-squares modeling offers an alternative to ordinary linear regression by accounting for correlative, non-independent residuals (Trépanier et al. 1996) and has been used for comparable time series migration data (Anderson and Quinn 2007). We followed the GLS modeling protocol of Anderson and Quinn (2007) by specifying the error structure as a first-order autoregressive process, and we utilized maximum likelihood techniques for parameter estimation (R Development Core Team 2010). Reported GLS P -values are from t -tests of each environmental predictor variable, and reported R^2 values were calculated by comparing the log-likelihood of each fitted model to the log-likelihood

TABLE 1. Total number of Sea Lampreys captured, number captured in the fyke-net trap (percentage of annual captures is shown in parentheses), count of nests identified, number of males (M), number of females (F), number of individuals with unconfirmed gender (U), observed gender ratio (M:F), run duration, mean average daily temperature, and mean average daily discharge during annual spawning runs before dam removal (2008) and after dam removal (2010 and 2011) in Sedgeunkedunk Stream, Maine. Means are presented with SEs; variables that are significantly different at $\alpha = 0.05$ are in bold italics. No Sea Lampreys were observed in the system during 2009 due to flood conditions.

Year	Captures		Nests	M	F	U	M:F	Days	Temperature ($^{\circ}$ C)	Discharge (m^3/s)
	Total	Trap								
2008	47	16 (34%)	31	26	21	–	1.24	10	19.3 ± 0.6	–
2009	0	0 (0%)	–	–	–	–	–	–	–	–
2010	131	39 (30%)	128	72	50	9	1.44	24	19.0 ± 0.4	<i>0.21 \pm 0.02</i>
2011	156	72 (46%)	131	86	67	3	1.28	20	19.9 ± 0.4	<i>0.28 \pm 0.02</i>

of the null (intercept-only) model (Nagelkerke 1991). Sea Lamprey spawning runs in Maine are extremely abbreviated and usually last between 3 and 6 weeks (Kircheis 2004). Therefore, to pinpoint discharge and temperature influences on daily counts of immigrating spawners, we limited our analyses to a period extending from 1 week before the initial detection to the date of the final detection for both the 2010 and 2011 spawning runs ($n = 31$ d in 2010; $n = 33$ d in 2011).

RESULTS

Sea Lamprey Capture and Abundance Estimates

We observed a considerable increase in the number of Sea Lampreys captured and the duration of spawning runs after the removal of Mill Dam (Table 1). Post-dam-removal captures were 2.8 times greater (in 2010) and 3.3 times greater (in 2011) than the 2008 pre-dam-removal captures (Table 1). Spawning run durations in Sedgeunkedunk Stream more than doubled after the removal of Mill Dam (Table 1). We note that a female Sea Lamprey was captured in the trap net on 10 June 2011, but it was a victim of snapping turtle *Chelydra serpentina* predation upon capture (fyke-net bycatch). Therefore, we considered the 2011 spawning run duration to be a 20-d period because no subsequent evidence of spawning was observed in the system until 16 June 2011. The 2011 trap efficiency increased by 12% and 16% in comparison with 2008 and 2010, respectively (Table 1). The number of males was greater than the number of females in all 3 years, but 2010 was the only spawning run in which a statistically significant gender bias was observed ($p = 0.046$; Table 1).

The POPAN models incorporating a constant probability of capture $\{p_{cap}(\cdot)\}$, a constant probability of apparent survival $\{\Phi(\cdot)\}$, and a time-dependent probability of entering the system $\{p_{ent}(t)\}$ consistently had the most support among the candidate models based on AIC_c and model weighting (w_i) scores (Table 2). The $\{p_{cap}(\cdot), \Phi(\cdot), p_{ent}(t)\}$ models estimated annual spawning run sizes of 59 ± 4 (mean \pm SE) in 2008, 223 ± 18 in 2010, and 242 ± 16 in 2011 (Figure 2). The $\{p_{cap}(\cdot), \Phi(\cdot), p_{ent}(t)\}$ models reasonably estimated a fourfold increase in an-

ual run size abundances based on approximately threefold increases in the number of individuals tagged during both of the years after dam removal (Figure 2).

Nesting Site Distributions

Evidence of Sea Lamprey nesting was not observed upstream of the former Mill Dam until the sixth day of the 2010 spawning run, when we observed a previously tagged male engaged in solitary nest construction less than 100 m beyond the remnant structure. Sea Lampreys penetrated further upstream at a pace of approximately 400 m/d until exhibiting a burst of activity on the ninth day of the 2010 spawning run. On that day, we marked multiple nests in newly colonized habitat, including a nest that was located slightly downstream of a beaver dam near rkm 4 (Figure 1). This nest marked the extent of Sea Lamprey range expansion during the 2010 spawning run (Figure 3). Whereas Sea Lampreys took 9 d to access a 4-km extent of linear stream habitat during the 2010 spawning run, they expanded their range 800 m further to Tannery Falls at rkm 4.8 (Figure 3) in just 3 d during the 2011 spawning run.

Post-dam-removal abundances of Sea Lamprey nesting sites increased over 400% relative to the 2008 pre-dam-removal count. Nest counts rose from 31 in 2008 to 128 and 131 in 2010 and 2011, respectively (Table 1). Sea Lamprey nesting sites were predominately located in historically accessible habitat downstream of the former Mill Dam during both 2010 and 2011. Forty-eight (38%) of the 128 nests observed during 2010 and 39 (30%) of the 131 nests observed during 2011 occurred in approximately 15% of the available habitat during both years (Figure 3). The χ^2 analyses revealed that a Sea Lamprey nest was more likely to be observed downstream of the former Mill Dam than in newly accessible upstream reaches ($p < 0.001$ for both years).

Sea Lamprey Biological Measures and Behavior

There were no discernible differences in Sea Lamprey length between genders or among years, but body mass was comparatively lighter during the 2010 spawning run than during the other years (Table 3). The two-way ANOVA for body mass of males indicated a difference among years ($p = 0.047$),

TABLE 2. Akaike’s information criterion corrected for small sample sizes (AIC_c), Akaike difference (ΔAIC_c ; difference in AIC_c value between the i th model and the best model), Akaike weight (w_i ; the relative probability that the i th model is the best model), number of parameters (K_i), and abundance estimates ($\hat{N} \pm SE$) for candidate models used to estimate annual Sea Lamprey spawning run sizes in Sedgeunkedunk Stream. Candidate models are defined by three distinct probabilities: the probability of capture (p_{cap}), probability of apparent survival (Φ), and probability of entering the study system (p_{ent}), where individual probabilities are set either to vary by daily time step (t) or to remain constant throughout the annual study period (\cdot). The $p_{cap}(\cdot)$ and $\Phi(\cdot)$ parameter values ($\pm SE$) are given for the best-fit models. No Sea Lampreys were observed in the system during 2009 due to flood conditions.

Model	AIC_c	ΔAIC_c	w_i	K_i	$\hat{N} \pm SE$	$p_{cap}(\cdot)$	$\Phi(\cdot)$
2008 (before dam removal)							
$p_{cap}(\cdot), \Phi(\cdot), p_{ent}(t)$	296.82	0.00	0.99	12	59 ± 4	0.63 ± 0.06	0.80 ± 0.04
$p_{cap}(\cdot), \Phi(t), p_{ent}(t)$	306.85	10.03	0.01	21	56 ± 4		
$p_{cap}(\cdot), \Phi(t), p_{ent}(\cdot)$	7,013.71	6,716.89	0.00	11	361 ± 111		
$p_{cap}(\cdot), \Phi(\cdot), p_{ent}(\cdot)$	7,022.70	6,725.88	0.00	3	144 ± 20		
2010 (after dam removal)							
$p_{cap}(\cdot), \Phi(\cdot), p_{ent}(t)$	676.84	0.00	1.00	21	223 ± 18	0.30 ± 0.03	0.79 ± 0.03
$p_{cap}(\cdot), \Phi(t), p_{ent}(t)$	703.98	27.14	0.00	43	226 ± 21		
$p_{cap}(\cdot), \Phi(t), p_{ent}(\cdot)$	12,031.93	11,355.09	0.00	20	2,722		
$p_{cap}(\cdot), \Phi(\cdot), p_{ent}(\cdot)$	17,586.68	16,909.84	0.00	2	3,081 ± 438		
2011 (after dam removal)							
$p_{cap}(\cdot), \Phi(\cdot), p_{ent}(t)$	654.00	0.00	0.98	17	242 ± 16	0.41 ± 0.04	0.76 ± 0.03
$p_{cap}(\cdot), \Phi(t), p_{ent}(t)$	662.15	7.92	0.02	37	326 ± 153		
$p_{cap}(\cdot), \Phi(\cdot), p_{ent}(\cdot)$	3,471.69	2,817.46	0.00	2	4,414 ± 261		
$p_{cap}(\cdot), \Phi(t), p_{ent}(\cdot)$	Non-estimable						

but no effects were detected at the trap level ($p = 0.512$) or for the interaction between year and trap ($p = 0.825$). Post hoc comparisons revealed that a gender-specific difference in the mass of males existed only between the 2008 and 2010 spawning runs ($p = 0.05$; Table 3). Likewise, the two-way ANOVA for body mass of female Sea Lampreys indicated a difference among years ($p = 0.04$), but no effects were detected at the trap level ($p = 0.323$) or for the trap × year interaction

($p = 0.951$). Post hoc comparisons revealed that a gender-specific difference in mass of females existed only between the 2010 and 2011 spawning runs ($p = 0.039$; Table 3).

We observed active Sea Lamprey nests on 84 and 90 separate occasions during 2010 and 2011, respectively. It was common to observe Sea Lampreys engaging in communal nesting behavior. Communal nest attendance ranged between three and eight individuals, with a maximum of three males or seven females at a given nest. Of the active nests that were observed during 2010 and 2011, 25% ($n = 22$) and 29% ($n = 26$), respectively, were communal (Figure 4). The χ^2 analyses for the 2010 season revealed that if only a single Sea Lamprey was observed on a nest, that individual was more likely to be a male ($p = 0.008$); if we observed a pair, they were more likely to be engaged in strictly male–female courtship ($p = 0.003$; Figure 4). However, χ^2 analyses for the 2011 season revealed that if only one Sea Lamprey was observed on a nest, it was just as likely to be a male as to be a female; if a pair was observed, this did not necessarily translate into strict male–female courtship (Figure 4).

Female Sea Lampreys that were detected at least once subsequent to the initial tagging procedure penetrated further upstream than their male counterparts during both post-dam-removal years, as indicated by median Max rkm values ($p = 0.025$; Table 4). As mentioned previously, no evidence of spawning activity beyond remnants of the former Mill Dam (rkm 0.610) was observed during the first several days of the 2010 recolonization event, and exploratory plots of all detected upstream and downstream movements aid in illustrating this phenomenon (Figure 5). Upstream movements increased

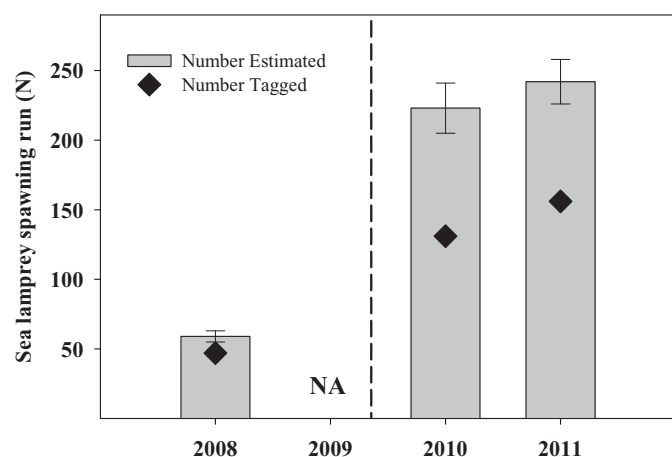


FIGURE 2. Sea Lamprey spawning run size ($\pm SE$; gray bars) per year in Sedgeunkedunk Stream, as estimated from mark–recapture encounter histories of tagged individuals (black diamonds). Dashed vertical line represents the August 2009 removal of Mill Dam. Sea Lampreys were not observed in the system during the 2009 spawning season.

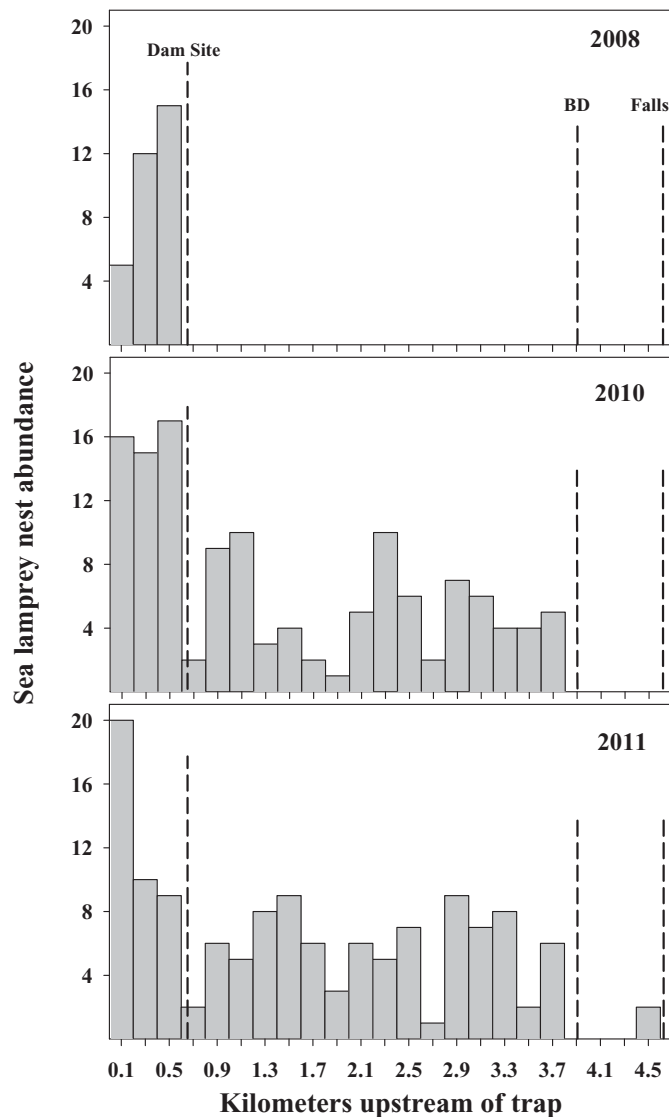


FIGURE 3. Distributions of Sea Lamprey nesting sites in Sedgeunkedunk Stream, as observed before dam removal (2008: $n = 31$) and after dam removal (2010: $n = 128$; 2011: $n = 131$). Dashed vertical lines demark the former Mill Dam (Dam Site), the beaver dam (BD), and Tannery Falls (Falls). No Sea Lampreys were observed in the system during the 2009 (pre-dam-removal) spawning season due to flood conditions.

rapidly after 7 June 2010; interestingly, females appeared to move upstream at a faster rate than males (Figure 5). Downstream movements were not prevalently detected in the system until after nesting was observed in the upstream reaches directly below the beaver dam (located near rkm 4) on 9 June 2010. Early movements during the 2011 spawning run did not appear to follow the pattern observed during the previous year. Instead, there were multiple movements greater than 0.6 km/d detected within the first week of the 2011 spawning run (Figure 5). Additionally, most of the rapid upstream movements during the second week of the 2011 spawning run were detected from females

(Figure 5). These patterns coincide with the statistical difference observed between the Max rkm values for males and females.

Spawning Run Timing: Temperature and Discharge

Spawning run timing was variable among years and did not appear to be influenced by the presence or absence of Mill Dam. Annual spawning runs began as early as 1 June in 2010 and as late as 18 June in 2008. Spawning run duration, however, did appear to be affected by the dam and was at least 10 d longer in both post-dam-removal years (Table 1). There was no discernible difference in average daily water temperature during pre- and post-dam-removal spawning runs (Table 1). However, average daily discharge was comparatively greater during the 2011 spawning run than during the 2010 run ($p = 0.024$; Table 1). Although GLS models revealed no significant relationships linking daily Sea Lamprey counts with temperature, change in temperature, discharge, or change in discharge during the 2010 and 2011 spawning runs ($p > 0.05$), the 2011 discharge model indicated that a descending limb in the hydrograph had marginal explanatory power ($R^2 = 0.27$, $P = 0.055$) in describing the arrival of Sea Lampreys into Sedgeunkedunk Stream during the 2011 spawning run.

DISCUSSION

Abundance Estimates

The primary objective of this study was to document abundance patterns of spawning-phase Sea Lampreys as they responded to the August 2009 removal of Mill Dam in Sedgeunkedunk Stream. The spring of 2010 was the first opportunity in over a century for migrating adult Sea Lampreys to access historic spawning habitat beyond the former Mill Dam. Sea Lampreys responded rapidly to this opportunity by recolonizing approximately 3.3 km of newly accessible habitat during 2010 and expanding their range by an additional 0.8 km in 2011 (Figure 3). In correspondence with an approximate sixfold increase in available habitat, our most well-supported POPAN models estimated a nearly fourfold increase in the abundance of migrating adult Sea Lampreys: from 59 fish in 2008 before dam removal to 223 fish in 2010 and 242 fish in 2011 after dam removal (Figure 2).

Our POPAN estimates of annual Sedgeunkedunk Stream spawners were biologically plausible given the seasonally predictable and semelparous nature of Sea Lamprey spawning events. First, the constant p_{cap} parameters were plausible given that our survey protocols were extremely consistent within and among years; traps were set in advance of all spawning runs, and daily foot surveys were conducted at regular hours in advance of and throughout the entire duration of each spawning run. Although there was considerable interannual variation among the p_{cap} parameters (Table 2), this variation was expected given the increased amount of survey habitat after dam removal and the increased trap efficiency during 2011. The p_{cap} was greatest in 2008 (0.63; Table 2), when surveys were limited to 0.610 km of

TABLE 3. Mean body length (mm) and mass (g) of Sea Lampreys that were tagged in Sedgeunkedunk Stream during annual spawning runs in 2008–2011. Means are presented with SE (*n* is given in parentheses); asterisks indicate variables that were significantly different from one another at $\alpha = 0.05$. No Sea Lampreys were observed in the system during 2009 due to flood conditions.

Year	Trap-captured fish		Upstream-captured fish		All captured fish	
	Length (mm)	Mass (g)	Length (mm)	Mass (g)	Length (mm)	Mass (g)
Males						
2008	607 ± 21 (10)	750 ± 60 (8)	631 ± 12 (16)	740 ± 60 (11)	622 ± 11 (26)	740 ± 40 (19)*
2010	634 ± 9 (27)	640 ± 60 (27)	622 ± 6 (44)	590 ± 30 (44)	627 ± 5 (71)	610 ± 30 (71)*
2011	636 ± 7 (43)	670 ± 30 (43)	632 ± 7 (39)	650 ± 20 (39)	634 ± 5 (82)	660 ± 20 (82)
Pooled	632 ± 5 (80)	670 ± 30 (78)	627 ± 4 (99)	630 ± 20 (94)	629 ± 3 (179)	650 ± 20 (172)
Females						
2008	600 ± 19 (5)	700 ± 70 (4)	614 ± 16 (13)	680 ± 60 (8)	610 ± 12 (18)	680 ± 50 (12)
2010	602 ± 13 (12)	630 ± 50 (12)	610 ± 7 (37)	590 ± 30 (37)	608 ± 6 (49)	600 ± 20 (49)*
2011	636 ± 8 (27)	720 ± 30 (27)	618 ± 7 (38)	660 ± 20 (38)	625 ± 6 (65)	690 ± 20 (65)*
Pooled	622 ± 7 (44)	700 ± 30 (43)	614 ± 5 (88)	630 ± 20 (83)	617 ± 4 (132)	650 ± 20 (126)

accessible habitat, but p_{cap} declined precipitously in 2010 (0.30; Table 2), when available habitat increased by nearly 600% and trap efficiency was at its lowest level (30%). Probability of capture rose to an intermediate level in 2011 ($p_{cap} = 0.41$; Table 2), and this increase may be explained by the greater trap efficiency (46%). Secondly, the constant Φ parameters were plausible given the semelparous nature of spawning Sea Lampreys; spawning-related mortality typically occurs within a week upon

arrival to the spawning grounds, and the observed similarity between interannual Φ values (range = 0.76–0.80) reflected this phenomenon (Table 2). Finally, the time-dependent p_{ent} parameters were plausible given the observed daily variation in the number of individuals tagged within and among years.

Historical Sea Lamprey abundance data for the Penobscot River and its tributaries are lacking (Kircheis 2004; Saunders et al. 2006), so we do not know whether the observed fourfold increase in spawning Sea Lampreys in Sedgeunkedunk Stream after dam removal represents a return to historic levels. Sea Lamprey spawning runs in Lake Ontario tributaries with comparable discharge (mean annual discharge < 1.0 m³/s) were estimated over the course of 8 years (1997–2004) to range between 207 ± 30 individuals ($\hat{N} \pm SE$) in a 1.22-km reach of Port Britain Creek and 798 ± 98 individuals in a 0.55-km reach of

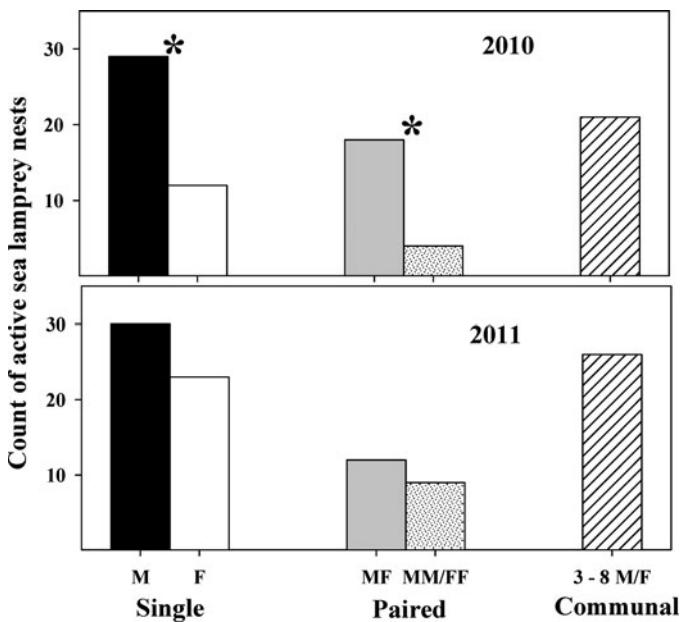


FIGURE 4. Abundances of active Sea Lamprey nests observed during the 2010 and 2011 annual spawning runs in Sedgeunkedunk Stream. Nests are categorized by the gender and number of individuals in attendance (M = males; F = females; Single = solitary individual; Paired = two individuals; Communal = three or more individuals). Asterisks indicate distributions that are significantly different from 1:1 at $\alpha = 0.05$.

TABLE 4. Gender-specific medians (range in parentheses) of observed maximum upstream movements (Max river kilometer [rkm]) by tagged Sea Lampreys that were detected in Sedgeunkedunk Stream at least once after the initial tagging procedure. Sea Lampreys tagged during 2008 were excluded from statistical analysis because the presence of Mill Dam limited their movements to the lower 0.610 km of stream. Asterisks indicate gender-specific median values that were significantly different from one another at $\alpha = 0.05$.

Year	Max rkm detected
Males	
2008 (<i>n</i> = 14)	0.341 (0.146–0.529)
2010 (<i>n</i> = 34)	0.875 (0.000–3.865)
2011 (<i>n</i> = 39)	0.407 (0.000–3.737)
2010–2011 (<i>n</i> = 73)	0.621 (0.000–3.865)*
Females	
2008 (<i>n</i> = 13)	0.381 (0.146–0.529)
2010 (<i>n</i> = 28)	2.232 (0.056–3.690)
2011 (<i>n</i> = 36)	2.049 (0.000–3.725)
2010–2011 (<i>n</i> = 64)	2.050 (0.000–3.725)*

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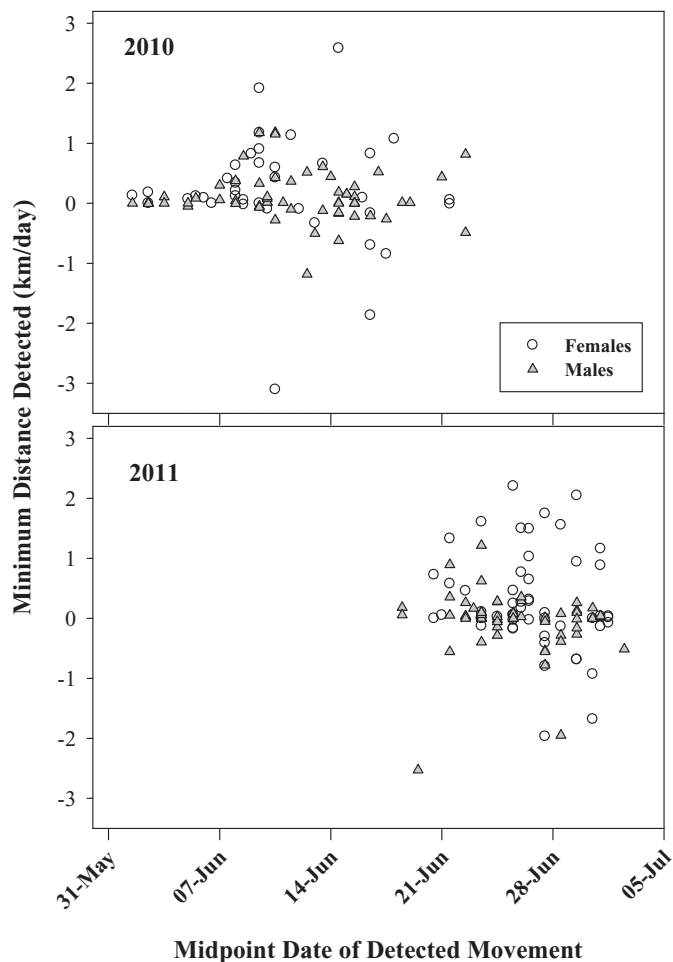


FIGURE 5. Detected minimum pathway distances of tagged Sea Lampreys in Sedgeunkedunk Stream during the 2010 (upper panel) and 2011 (lower panel) spawning runs. Point measurements were standardized to kilometers per day by using the midpoint day of successive observations; positive values represent upstream movements, and negative values represent downstream movements.

Shelter Valley Creek (Binder et al. 2010). Port Britain Creek, which has a mean annual discharge of $0.5 \text{ m}^3/\text{s}$ (Binder et al. 2010), appears to be somewhat comparable to Sedgeunkedunk Stream. Given that Port Britain Creek regularly hosts spawning Sea Lamprey densities of approximately $0.03 \text{ fish}/\text{m}^2$, one may anticipate comparable densities in Sedgeunkedunk Stream after the system experiences multiple year-classes of ammocoete recruitment. Therefore, an annual spawning run of over 500 Sea Lampreys may be realistic for the $18,000 \text{ m}^2$ of lotic habitat that are presently available in Sedgeunkedunk Stream.

Nesting Site Distributions

The observed number of Sea Lamprey nests increased more than fourfold during the 2 years after the removal of Mill Dam, essentially mirroring the nearly fourfold increase in our POPAN abundance estimates. An interesting pattern was uncovered after combining the raw nest count data with the corresponding POPAN estimates in the development of annual Sea Lamprey

per nest ratios. Annual number of Sea Lampreys per nest displayed minimal variation, ranging from a high of 1.9 in 2008 to a low of 1.7 in 2010, with a median value of 1.8 calculated for the 2011 data. The consistent relationship between raw nest counts and POPAN estimates ($R^2 = 0.998$; $P = 0.001$) suggests that nest enumeration may provide a proxy for abundance estimates when mark–recapture studies are cost prohibitive.

Sea Lampreys in Sedgeunkedunk Stream continued to predominantly select nesting locations downstream of the former Mill Dam in both years after dam removal. However, the 2011 nesting site distribution trended towards a more equitable longitudinal distribution of nesting sites. Nest abundances downstream of the former Mill Dam declined from 48 nests (38%) in 2010 to 39 nests (30%) in 2011, and 20 (15%) of the nests observed in 2011 were in the lowermost 200 m of stream. With the exception of those 20 nests, the 2011 longitudinal distribution of Sea Lamprey nesting sites was more evenly dispersed than the 2010 distribution (Figure 3).

Sea Lamprey Capture, Biological Measures, and Behavior

Our fyke-net trap was not as effective as we had anticipated, but the addition of waterproof LED lights sewn into the entrance during 2011 did improve trap performance. Our study was not designed with the intention of statistically examining the effectiveness of illuminated traps, but we did desire to improve trap efficiency as a means of intercepting Sea Lampreys as they entered the system, thereby reducing the disturbance of spawning activities. Additionally, a standardized tagging location could have potentially improved our ability to investigate movement patterns. For these purposes, we report limited success in Sea Lamprey capture by use of illuminated trap entrances.

Variation in trap efficiency may explain the observed differences in 2010 gender-specific body masses compared with the other 2 years. Although trap efficiency was comparable in 2008 and 2010 (34% and 30%, respectively), the body mass of males in 2010 was lower than that in 2008, and this discrepancy may have resulted from the striking difference in total captures between the 2 years. Masses were recorded upon initial capture, which sometimes occurred far upstream of the trap (maximum distance from trap = 4 km) for 45 males in 2010, whereas in 2008 only 13 males were initially captured at a maximum distance of just 0.6 km. The analysis had low discriminatory power at the trap level (10%) and for the trap \times year interaction (8%). Therefore, the disparity in male body mass between 2008 and 2010 may simply be a reflection of the small sample size in 2008 combined with variable capture locations in both years.

Accompanying the overall rise in trap efficiency between 2010 and 2011 (30% and 46%, respectively), the number of ripe female Sea Lampreys that were initially captured in the trap more than doubled: from only 12 females in 2010 to 28 females in 2011. Females that were initially captured upstream of the trap were usually intercepted after bouts of spawning and likely experienced some degree of decreased body mass due to the release of gametes and due to starvation. The absolute increase

in captures of prespawning females from the trap may explain why the body mass of females was greater in 2011 than in 2010, but again the analysis had low discriminatory power at the trap level (17%) and for the trap \times year interaction (6%).

Sea Lamprey range expansion into previously inaccessible habitat during the 2010 spawning run appeared to be driven by the exploratory behavior of males. Male Sea Lampreys are sensitive to a larval migratory pheromone that serves as a conspecific cue, drawing migrants toward tributaries with habitats that are adequate for offspring rearing (Wagner et al. 2009). In turn, females are sensitive to the male mating pheromone, a bile acid compound released by spermiating males that attracts females toward the vicinity of potential mates (Siefkes et al. 2005). This conspecific pheromone communication system may explain why Sea Lampreys took 6 d to move just 0.65 km past the former dam site in 2010. The lack of ammocoetes and associated larval migratory pheromone signals from newly accessible upstream reaches likely provided little motivation for spawning males to venture into the previously inaccessible habitat. However, males display antagonistic behavior during the establishment of nesting territory (Manion and Hanson 1980); therefore, range expansion may have resulted from brief exploratory searches for vacant spawning habitats.

Whereas it took Sea Lampreys 6 d to expand their range beyond the former Mill Dam and an additional 3 d to penetrate the furthest upstream reaches during 2010, activity extended throughout the system up to the Tannery Falls boundary in only 3 d during 2011. Perhaps a cohort of 1-year-old ammocoetes that were spawned during the 2010 run settled into rearing habitats upstream of the former Mill Dam, subsequently releasing larval pheromones that cued the 2011 adult migrants immediately to the furthest upstream reaches. Prior lines of evidence from Sea Lamprey studies in the Great Lakes suggested that adult spawning runs were extremely responsive to ammocoete populations. Moore and Schleen (1980) reported that the removal of ammocoetes from a stream reduced the number of spawning adults in subsequent migrations. Additionally, Sorensen and Vrieze (2003) found that streams with relatively large ammocoete populations attracted larger adult spawning runs than neighboring streams with smaller larval populations. Therefore, the increased activity observed in the upstream reaches of Sedgeunkedunk Stream during the early stages of the 2011 spawning run may have resulted from the prior year's establishment of ammocoete recruits and the subsequent release of larval conspecific chemical cues. Although we lack ammocoete data with which to confirm the larval migratory pheromone hypothesis for Sedgeunkedunk Stream, the subtle differences between the 2010 and 2011 nesting site distributions provide indirect support.

The male-biased sex ratio and the observed prevalence of active nests occupied by single males during the 2010 spawning run further support the contention that range expansion was driven by the exploratory behavior of males. We also detected a prevalence of shorter maximum upstream movements (Max rkm) among males in comparison with females, and this subtle

gender-specific difference provides additional support. In describing the reproductive life histories of anadromous Pacific salmon populations, Morbey (2000) defined protandry as "the earlier arrival of males to the spawning grounds than females." Morbey (2000) argued that protandry is a valuable reproductive strategy for male salmon because they are semelparous, and intraspecific competition for access to spawning females is fierce due to the semelparous life history. Sea Lampreys share many mating system attributes with Pacific salmon, so it follows that protandry may be an equally valuable strategy for them as well. Our data suggest that Sea Lampreys exhibited protandry during the 2010 recolonization event and that the phenomenon of protandry provides a parsimonious explanation for the male-biased sex ratio, a statistical preponderance of solitary males at nesting sites, and a relatively slow progression of movement into previously unoccupied habitats.

Spawning Run Timing: Temperature and Discharge

Our intensive monitoring of Sea Lamprey spawning runs in Sedgeunkedunk Stream revealed that in all years studied, spawning-phase migrants arrived at least 2–4 weeks later in this stream than in most streams of the lower Penobscot River watershed (O. Cox, Maine Department of Marine Resources, Bangor, personal communication). Additionally, the 2009 spawning season appeared anomalous, as Gardner et al. (2012) were unable to detect Sea Lampreys entering Sedgeunkedunk Stream at all, even though Sea Lampreys were found in neighboring tributaries. The lack of detections in 2009 could be attributable to the extreme precipitation events throughout the month of June, when unusually high discharge in the lower portion of Sedgeunkedunk Stream may have inhibited spawning activities. Regardless, the initiation of spawning activity in Sedgeunkedunk Stream was extremely variable among years, occurring as early as 1 June during 2010 and as late as 18 June during 2008.

Sea Lamprey spawning activities in Maine typically occur during late May and early June, when mean daily water temperatures range between 17°C and 19°C (Kircheis 2004). However, our data show that in all 3 years, Sedgeunkedunk Stream temperatures exceeded this range for periods of days to weeks prior to the arrival of spawning-phase Sea Lampreys. Mean daily temperatures were 19°C or greater during all three spawning runs (Table 1), thus suggesting additional or alternative environmental cues to migration in Sedgeunkedunk Stream. Perhaps the observed difference in stream discharge between the 2010 and 2011 spawning runs (Table 1) can partially explain some of the variability in run timing.

Binder et al. (2010) found significant stream-dependent differences in the relative importance of environmental variables as predictors of Sea Lamprey spawning runs in six Lake Ontario tributaries. Although water temperature was the best predictor among all six streams, water level—a surrogate measure for stream discharge—was an equally reliable explanatory variable but only in the two smallest streams, Port Britain Creek and Shelter Valley Creek (Binder et al. 2010). As alluded to earlier,

these two streams compare well with Sedgeunkedunk Stream, and results from our GLS modeling exercises support the findings of Binder et al. (2010) regarding the importance of water level in relation to Sea Lamprey migratory activity. Our GLS results, although not significant at an α level of 0.05, indicated that stream discharge during 2011 had some explanatory power in describing the arrival of spawning migrants to Sedgeunkedunk Stream.

Perhaps temperature and discharge must reach a combination of threshold levels before Sea Lampreys enter the spawning grounds. Close inspection of Sedgeunkedunk Stream hydrographs in relation to daily Sea Lamprey counts offers a simplistic explanation regarding the observed variation in timing of the annual spawning runs. Mean daily temperatures throughout the peak of the 2010 spawning run (1–14 June) were within the 17–19°C range reported for Maine streams (Kircheis 2004), while discharge was consistently below 0.45 m³/s during the same period. In contrast, the 2011 hydrograph was vastly different. The 2011 mean daily discharge was above 1.0 m³/s until midway through the first week of June and did not decline below 0.45 m³/s until 12 June. Consequently, the peak of the 2011 spawning run (21 June–1 July) was delayed in comparison with 2010, and mean daily temperatures were consistently above 20°C during that period. The complete absence of spawning Sea Lampreys in Sedgeunkedunk Stream during the flood of 2009 and the relative delay in 2011 run timing are not surprising given that high-discharge events have inhibited migratory activity in other anadromous (Masters et al. 2006) and potamodromous lampreys (Malmqvist 1980).

Additionally, because Sedgeunkedunk Stream converges with the Penobscot River near head of tide, late-arriving migrants may display phenotypic plasticity in their migratory behavior as a response to a relatively short (36.5-km) upstream migration distance. Quinn and Adams (1996) reasoned that anadromous fishes that spawn shortly after entering freshwater are more likely than long-distance migrants to have evolved adaptations in response to fluctuating temperature because fish that migrate short distances likely experience the same conditions as developing larvae. Whereas spawning Sea Lampreys enter the Fort River (tributary to the Connecticut River at rkm 159) consistently earlier in the season (Nislow and Kynard 2009), late migrants to Sedgeunkedunk Stream may be displaying an adaptation that favors arrival at the spawning grounds consistent with temperatures that are optimal (18.4°C; range = 15.5–21.1°C) for embryonic development (Smith et al. 1968).

Conclusions

Our study has clearly demonstrated that restorative dam removal projects have the potential to enhance recovery of declining anadromous fish populations by providing access to habitats that are necessary for the completion of migratory life histories. The Sea Lampreys' rapid response to dam removal in Sedgeunkedunk Stream may produce a multitude of beneficial effects by providing sorely missed ecological services. The

semelparous life history of the Sea Lamprey translates into consistent delivery of marine-derived nutrients at a crucial time of the year when many aquatic organisms are at the peak of their growing seasons. Additionally, the nest-building activities of Sea Lampreys have the potential to condition habitat that has been degraded by decades of increased sedimentation. The literature is replete with evidence suggesting that redd-digging Pacific salmon improve the quality of riverine habitats by sweeping fine sediments downstream, coarsening the stream bed, and reducing cobble embeddedness (Montgomery et al. 1996). Sea Lamprey nest construction may produce similar effects in coastal New England systems, and ongoing research in Sedgeunkedunk Stream is currently addressing these questions. Very little is understood regarding the community-level effects of recurring Sea Lamprey spawning disturbances, and this study provided us with the impetus to explore their role as streambed "conditioners." The daily spawning surveys conducted during this study allowed us to catalog exact nesting locations and to return to those sites periodically to measure microhabitat characteristics that are influenced by Sea Lamprey spawning disturbances. The synergistic interactions of multiple co-evolved diadromous and freshwater fishes may be a necessary ingredient for the recovery of high-functioning aquatic ecosystems throughout Maine and northern New England (Saunders et al. 2006), and this study provides a platform with which to begin addressing the potentially overlooked role played by anadromous Sea Lampreys within their native range.

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