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Distribution and Abundance of Anadromous Sea Lamprey Spawners in a Fragmented Stream: Current Status and Potential Range Expansion Following Barrier Removal

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Abstract - Dams fragment watersheds and prevent anadromous fishes from reaching historic spawning habitat. Sedgeunkedunk Stream, a small tributary to the Penobscot River (Maine), has been the focus of efforts to reestablish marine-freshwater connectivity and restore anadromous fishes via the removal of two barriers to fish migration. Currently, *Petromyzon marinus* (Sea Lamprey) is the only anadromous fish known to spawn successfully in the stream downstream of the lowermost dam. Here, we describe the distribution and abundance of a spawning population of Sea Lamprey in Sedgeunkedunk Stream, prior to and in anticipation of habitat increase after the completion of one barrier removal. In 2008, we estimated the abundance of Sea Lamprey and its nests using daily stream surveys and an open-population mark-recapture model. We captured 47 Sea Lamprey and implanted each with a PIT tag so that we could track movements and nest associations of individual fish. The spawning migration began on 18 June, and the last living individual was observed on 27 June. We located 31 nests, distributed from head-of-tide to the lowermost dam; no spawners or nests were observed in the tidally influenced zone or upstream of this dam. Mean longevity in the stream and the number of nests attended were correlated with arrival date; early migrants were alive longer and attended more nests than later migrants. Males were more likely to be observed away from a nest, or attending three or more nests, than were females, which attended usually one or two nests. We observed a negative association between nest abundance and substrate cover by fine sediment. Based on their observed movements in the system, and the extent of their habitat use, we anticipate that spawning Sea Lamprey will recolonize formerly inaccessible habitat after dam removals.

Introduction

Many rivers and ponds in Maine once harbored spawning runs of anadromous fishes, including *Salmo salar* L. (Atlantic Salmon), *Alosa pseudoharengus* Wilson (Alewife), *Petromyzon marinus* L. (Sea Lamprey), and *Osmerus mordax* Mitchill (Rainbow Smelt) (Saunders et al. 2006). These fishes likely transported marine-derived nutrients and energy (MDNE) into otherwise oligotrophic freshwater ecosystems (West et al. 2010) and enhanced the biomass of several trophic levels, similar to the effects exerted by *Oncorhynchus* salmonines in Pacific Northwest waters (Bilby et al. 1996, Scheuerell et al. 2007, Wipfli et al. 1998). As dams have severed such marine-freshwater connections, anadromous species have experienced worldwide decline (Limburg and Waldman 2009), and freshwater systems have become more oligotrophic (Stockner et al. 2000).

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Sedgeunkedunk Stream, a small tributary to the Penobscot River below head-of-tide (Fig. 1), typifies small streams in Maine impacted by dams. Current restoration offers an opportunity to assess how the structure, function, and resilience of the fish community responds to long-term disturbance by, and then relief from, habitat fragmentation from multiple dams (Gardner et al. 2011). Runs of anadromous fishes in Sedgeunkedunk Stream either disappeared or were reduced after the construction of three dams; the lowermost dam has existed, in some form, for more than two centuries (Steve Shepard, Aquatic Science Associates, Inc., Brewer, ME, pers. comm.). Declines in anadromous fishes in Sedgeunkedunk Stream mirror those in the entire Penobscot watershed, which contains 116 dams (Penobscot River Restoration Trust 2011).

Sedgeunkedunk Stream is an ideal system in which to study the effects of dam removal for two reasons. First, it is one of only three major tributaries that enter the Penobscot River downstream of the lowermost mainstem dam (i.e., Veazie Dam) and contains a remnant population of Sea Lamprey, whereas this fish does not occur in most tributaries upstream. Second, recovery of anadromous fishes in Sedgeunkedunk Stream should precede that in tributaries upstream in the watershed when two mainstem dams on the Penobscot are removed as part of the Penobscot River Restoration Project, anticipated to proceed in 2012 (Penobscot River Restoration Trust 2011). Atlantic Salmon in Sedgeunkedunk Stream and most of the Penobscot watershed is federally listed as endangered (74 Fed. Reg. 29344, 19 June 2009), and Alewife, Sea Lamprey, and Rainbow Smelt abundances are at historic low levels (Saunders et al. 2006). No other Lamprey species occurs in the study area, and the word Lamprey herein always refers to the Sea Lamprey. Likewise, hereafter, Sedgeunkedunk always refers to the Stream.

As part of a collaborative restoration project that ended in 2009, fish passage was created or restored in Sedgeunkedunk at the location of two former dam sites between Fields Pond and the confluence with the Penobscot (Fig. 1). The lowermost dam (Mill Dam) was removed in August 2009 after this study was completed; the middle dam (Meadow Dam) was bypassed by a rock-ramp fishway, and it is not considered further here because its presence or removal does not impact Lamprey migrations. A third dam farther upstream in the watershed (Brewer Lake Dam) is not scheduled for removal and likely has little or no impact on anadromous fishes, and is not shown on Figure 1. Gardner et al. (2011) provide a detailed description of barriers and barrier removals in the system.

Prior to and during this study, Sedgeunkedunk received a small run of Lamprey, the only anadromous fish known to spawn reliably in the stream. It is parasitic on fishes in the Atlantic Ocean and returns after two to seven years to spawn in fresh water (Beamish 1980). Unlike many anadromous species, it does not home to natal streams (Bergstedt and Seelye 1995, Waldman et al. 2008, but see Wright et al. 1985), and may select spawning streams based on flow, temperature (Andrade et al. 2007), or chemical compounds released in fresh water by ammocoetes (larval Lamprey) and sexually mature males (Li et al. 2002, Vrieze et al. 2010). This behavior should foster more rapid colonization of new habitats than by anadromous species with strong homing tendencies (e.g., Atlantic Salmon). The rapid expansion of Lamprey throughout the upper Great Lakes is strong evidence of its colonization ability (Smith and Tibbles 1980), and this ability makes it likely to benefit immediately from restoration of Sedgeunkedunk.

In North America, research on Lamprey is focused on the Great Lakes. The species is invasive upstream of Niagara Falls, but probably is native in the Lake Ontario and Lake Champlain watersheds (Waldman et al. 2004, 2006; but see Eshenroder 2009). Such invasion has devastated valuable recreational and commercial fisheries (Lawrie 1970). Because of its highly visible parasitism on popular sport fish, it has acquired a negative public image not only in the Great Lakes region, but also in its native range (Brown et al. 2009). However, the roles of native Lamprey on the Atlantic coast and invasive Lamprey in the upper Great Lakes may be very different (Clemens et al. 2010).

Lamprey may be an ecologically significant member of stream ecosystems, and thus its recovery may be a critical step in the restoration of native anadromous fish assemblages in Maine (Saunders et al. 2006). It is selemparous, and dies in early summer after it spawns. Therefore, the adults may be sources of MDNE in small oligotrophic streams during mid-summer, an important combination of time and place for nutrient subsidies in Maine (Nislow and Kynard 2009). Further, adults build nests in riffles or the tails of pools by moving cobbles to create a pit with a mound on its downstream edge; spawning occurs in the pit. Nest building and spawning activities clear fine sediment from coarse substrate (Kircheis 2004) and perhaps reduce substrate armoring and embeddedness, similar to the effects of spawning by Pacific salmonines (Montgomery et al. 1996). Thus, Lamprey nest building and spawning may "condition" spawning habitat for Atlantic Salmon (Kircheis 2004, Saunders et al. 2006) and provide prey (eggs and dislodged invertebrates) and physical structure for drift-feeding stream fishes (S.M. Coghlan, Jr., pers. observ.). Finally, ammocoetes are filter feeders and sequester nutrients from the water column, and in turn are a prey of other species (Applegate 1950).

This study provides a baseline assessment of the status of Lamprey in Sedgeunkedunk, where we predict restoration will make the watershed more accessible to it and other anadromous fishes. Specifically, our objectives are to: 1) quantify the abundance and movements of Lamprey in Sedgeunkedunk before the removal of Mill Dam; 2) quantify the distribution and abundance of Lamprey nests in this stream before the removal of Mill Dam; and 3) describe patterns in Lamprey run timing and nest attendance. This work represents the first step in a long-term monitoring of the response of Lamprey to this restoration, and on its anticipated subsequent influence in the Sedgeunkedunk ecosystem.

Field Site Description

Sedgeunkedunk Stream is a third-order tributary of the Penobscot River, Penobscot County, ME (Fig. 1), flowing through the town of Orrington and the city of Brewer. The watershed is mostly forested, but light development exists in its downstream portion near its confluence with the Penobscot. Several ponds

(Fields Pond, Brewer Lake, and Thurston Pond) are located in the headwaters. Median stream width is approximately 4 m. The lowermost dam (Mill Dam: 44°45'55.35"N, 68°46'47.53"W) was located 700 m upstream of the stream confluence with the Penobscot River and 610 m upstream of head-of-tide. The removal of this barrier in August 2009 provided for subsequent presumed unimpeded access from the Atlantic Ocean into 6 km of lotic habitat within Sedgeunkedunk, via the lower Penobscot River. However, for this paper, we present only pre-removal data, collected in summer 2008. Our study is focused on the stream reach downstream of Mill Dam and upstream of the head-of-tide. We ignore two other barriers in the system (Meadow Dam, which was bypassed by a rock-ramp fishway in fall 2008, and Brewer Lake Dam, which is not scheduled for removal) as both were upstream of Mill Dam and thus beyond the distributional limits of Lamprey in Sedgeunkedunk during this study.

Methods

Sea Lamprey population estimate and behavioral evaluation

We captured Lamprey in one Indiana-style trap net that spanned the width of Sedgeunkedunk, placed 90 m upstream of the confluence with the Penobscot River (river km 36), approximately at head-of-tide. The net consisted of 3-mm-

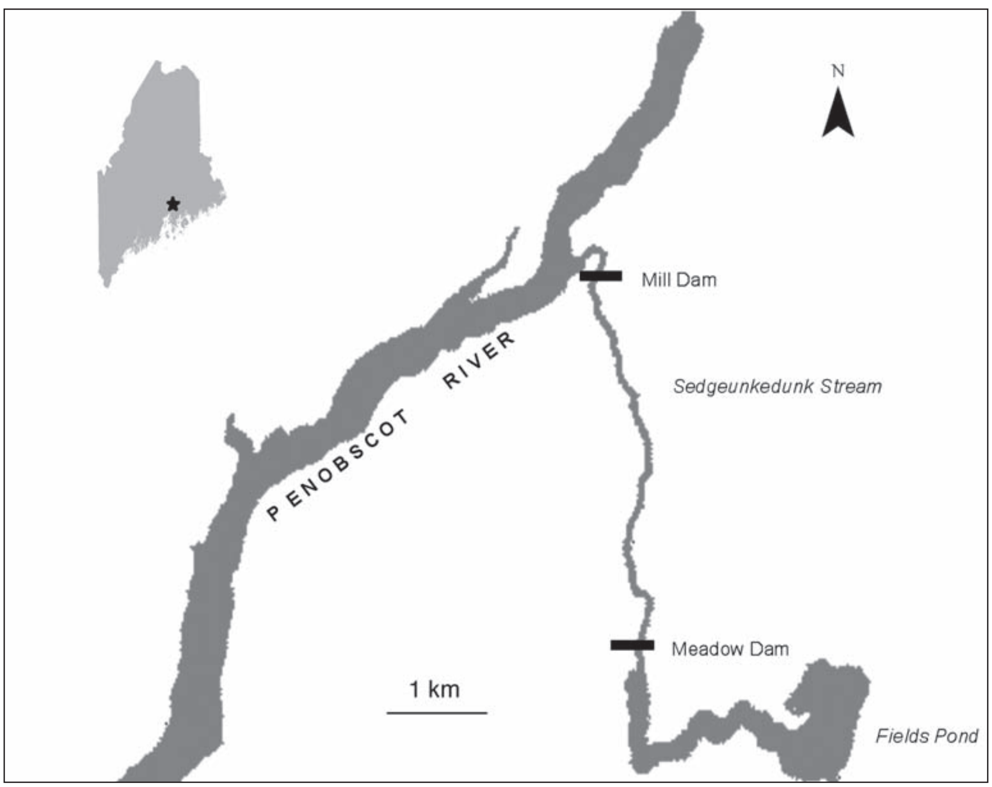

Figure 1. Location of Sedgeunkedunk Stream, Fields Pond, and dams present during the study but later removed as part of the Sedgeunkedunk Stream Restoration Project, Penobscot County, ME.

square mesh, with 1.3-m x 1.6-m rectangular mouth and 1-m-diameter circular cod end, and was 2.5 m in length, with wings that extended the width of the stream (4.0 m at time of deployment). We deployed the net from 15 May to 1 July 2008. At deployment, channel depth was 0.8 m, but water depth varied with stream discharge and tidal cycle. During the first five sampling days (18–22 June), high water rendered the net ineffective, but a lack of deep pools and in-stream structure, combined with low turbidity and high visibility, facilitated hand capture of Lamprey that had evaded the net. We tagged each Lamprey with both an internal passive integrated transponder (PIT) tag and an external floy tag. Mass, length, and sex were recorded for each Lamprey before release. Mature Lamprey are sexually dimorphic; males were identified by the presence of a thickened dorsal ridge, or "rope" (Hardisty and Potter 1971). Initial sex determination was verified when we relocated spawning fish and examined them for physical and behavioral sexual differences. In all cases, our initial determination of sex was correct. No mortality due to the tagging process was apparent, and in several cases, we observed newly tagged fish building nests within hours of tagging.

During the Lamprey run, stream surveys for adults and for nests were conducted once daily. We surveyed the 610-m reach from the trap net upstream to Mill Dam, with the stream divided into 25-m-long sections. Surveys began by 0800 hours and usually were completed by 1600 hours, depending on the level of activity encountered. We also surveyed the first 2 km upstream of Mill Dam thrice weekly to verify impassability. We captured any non-tagged Lamprey with a hand net and processed it as described previously. Previously tagged fish were identified using a portable PIT tag wand and reader (or "PIT pack"), thus eliminating secondary handling (Hill et al. 2006).

On each encounter with a Lamprey, we recorded sex, identity (if tagged previously), status (dead or alive), the stream reach, behavior, and nest attendance (i.e., which nest was used and which other individual Lamprey were present). We estimated abundance of adult Lamprey in the stream using a POPAN Jolly-Seber open population model (Arnason and Schwarz 1995) in the program MARK (White and Burnham 1999). An "open" population model allows for new individuals to enter the system continuously.

Nest surveys and abundance estimation

Each nest location was recorded and marked on the stream bank with flagging visible to upstream observers only (so that downstream observers walking upstream would need to re-sight the nest itself and not the flagging). Maximum length, width, and depth/height were recorded for both the upstream pit and the downstream mound of each nest, and any Lamprey on a nest was identified. Nest abundance was estimated using a Cormack-Jolly-Seber mark-recapture method in the program MARK. Nest abundance was recorded for each 25-m section. We recorded substrate size along a random transect, running perpendicular to the stream bank, in each stream reach, to quantify its relation with nest abundance. Substrate was sampled by walking heel to toe along the transect and visually classifying the size class (modified

Wentworth scale) of the substrate component at each step to yield an estimate of fine substrate (<2 mm) proportional coverage.

Results

In 2008, the spawning run of Lamprey in Sedgeunkedunk began on 18 June and ended on 27 June. We did not observe any live Lamprey after 27 June. During that period, 47 Lamprey (21 female and 26 male) were captured and tagged (two of these were observed dead in the trap net on 28 June, so could not be recaptured subsequently), 16 of which were collected in the trap net. The mark-recapture model estimated a total abundance (n ± 2 SE) of 47 ± 0. Of those Lamprey that evaded the trap net, the mean point of capture was 345 ± 52 m upstream of the net, and five Lamprey were captured initially in a pool directly below Mill Dam. No Lamprey was observed upstream of Mill Dam. Males and females were similar in size (mean length of males was 625 ± 23 cm, and mean mass was 750 ± 100 g; mean length of females was 612 ± 22 cm, and mean mass was 700 ± 100 g). There was no detectable correlation in size or sex with arrival date in the stream. Lamprey entered the stream at a relatively steady rate throughout the period (Table 1).

Individual Lamprey were active in the stream for an average of 2.5 ± 0.5 days (range = 1–6 days), and were observed on average 2.3 ± 0.4 times (range = 1–5 observations). Based on successive observations of individuals, the average linear distance travelled was 103 ± 48 m; minimum and maximum daily means were 89 ± 55 m and 138 ± 50 m, respectively. Daily distances traveled ranged from 0 m (i.e., individuals found on the same nest on consecutive days, n = 3) to 255 m. Each living tagged individual was observed alive again at least once. Of the 45 live fish captured, we later observed 17 carcasses. Carcasses were found only in the wetted stream channel, and, on average, 116 ± 71 m downstream of the point of last live observation. We did not observe any additional downstream movement of carcasses after first sighting.

Table 1. Number of Sea Lamprey captured for the first time on each day of the sampling period (by sex), mean daily water temperature, mean number of days that Sea Lamprey entering on that day were observed active in the stream, and mean number of nests that Sea Lamprey entering on that day used before they died, during the 2008 spawning run. Means are presented with ± 2 SE.

Date	Number	Male	Female	Cumulative total	Temp (°C)	Days active	Nests used
6/18	5	1	4	5	16.9	4.4 ± 1.0	1.8 ± 1.2
6/19	9	5	4	14	16.5	3.3 ± 1.0	2.0 ± 0.7
6/20	3	3	0	17	16.9	4.0 ± 2.0	3.3 ± 1.3
6/21	7	4	3	24	18.8	2.1 ± 0.5	1.4 ± 0.7
6/22	4	2	2	28	19.5	3.0 ± 2.2	2.8 ± 1.7
6/23	5	2	3	33	19.5	1.4 ± 0.8	0.8 ± 0.6
6/24	3	1	2	36	20.9	2.0 ± 2.0	0.3 ± 0.3
6/25	5	4	1	41	20.9	1.2 ± 0.4	0.2 ± 0.2
6/26	3	2	1	44	20.8	1.0	0.3 ± 0.3
6/27	1	1	0	45	21.9	1.0	0.0
6/28	2	1	1	47	-	-	-
Total	47	26	21	-	-	2.5 ± 0.5	1.4 ± 0.4

Mean water temperature increased every day during the run, starting with 16.9 °C and reaching 21.9 °C on the last day. Lamprey that arrived in the stream earlier, regardless of sex, were able to spend more days in the stream and, on average, were associated with more total nests (Table 1). Mean number of days active was related negatively to date entering the stream (Pearson's correlation coefficient = -0.91; $P = 0.0002$), as was mean number of nests used (Pearson's correlation coefficient = -0.77; $P = 0.008$). Females were more likely than males to be observed on only one or two nests, whereas males were more likely than females to be observed away from a nest or to be seen on three or more nests (Fig. 2; $\chi^2 = 3.13$, $P = 0.077$).

During stream surveys, 31 nests were identified, and all were downstream of Mill Dam, verifying that Mill Dam was a barrier to upstream migration. The mark-recapture model estimated total nest abundance ($n \pm 2$ SE) of 31 ± 0. Nests were present in 52% (13 of 25 stream sections) of the stream and were distributed throughout the stream upstream of head-of-tide to immediately downstream of Mill Dam, wherever the substrate contained a low percentage of fine sediment (<2 mm) (Fig. 3). The number of nests present in 25-m-long reaches was correlated negatively with the abundance of fine sediment in that reach (Pearson's correlation

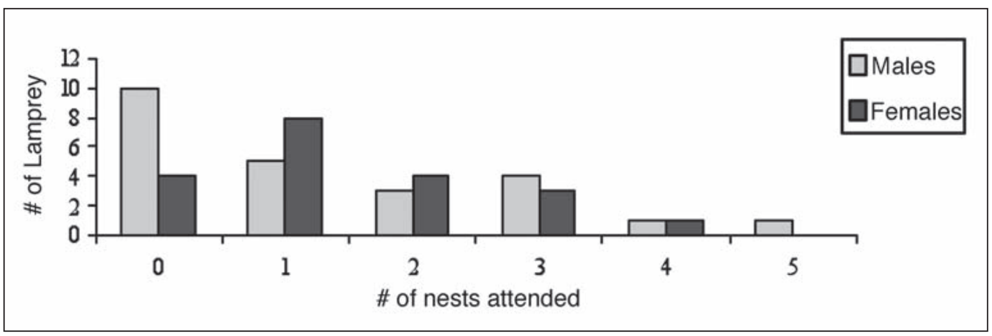

Figure 2. Frequency of the number of nests individual Sea Lamprey of each sex attended during the duration of their activity in Sedgeunkedunk Stream during the 2008 spawning run.

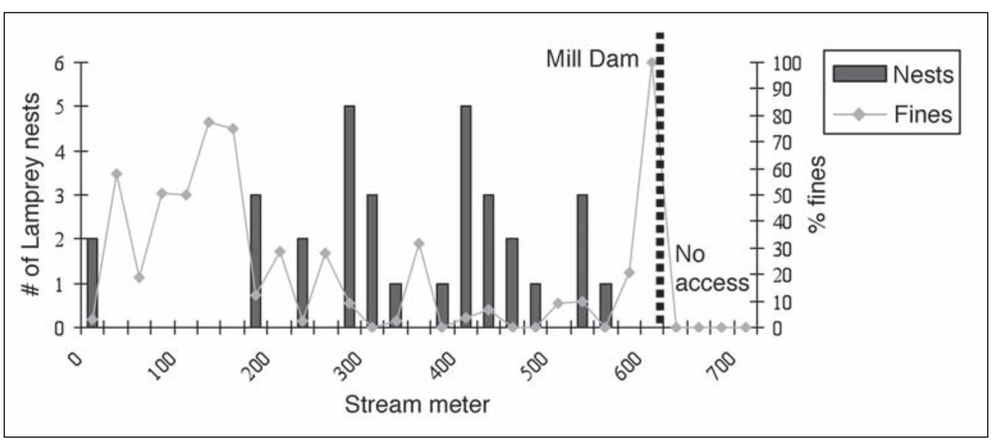

Figure 3. Distribution of Sea Lamprey nests, and proportion of substrate cover composed of fines (<2 mm) along the stream gradient in Sedgeunkedunk Stream from head-of-tide to Mill Dam, during the 2008 spawning run.

coefficient = -0.57; $P = 0.003$); no nests were found in reaches where fine sediment cover exceeded 25%, and all reaches with fine sediment relative abundance below 10% contained at least one nest. No nests were found below head-of-tide or above the dam. Mean nest dimensions included a pit that was 75 cm long, 56 cm wide, and 20 cm deep, and a mound that was 62 cm long, 57 cm wide, and 8 cm high (Table 2). Number of individuals attending nests at one time ranged from 0 to 6 Lamprey. Observed nests never hosted more than two males or four females, with a mean attendance of 1.7 ± 0.4 individuals. Each nesting female was associated with, on average, 0.9 ± 0.3 males and 0.8 ± 0.4 other females. Each nesting male was associated, on average, with 0.2 ± 0.2 other males and 0.7 ± 0.4 females. A male was less likely to attend a nest with another male and more likely to attend a nest with a female, whereas a female was equally likely to attend a nest with either a male or another female present ($\chi^2 = 7.00$, $P = 0.008$). On several occasions, we observed an interloping male attempt to occupy a nest attended by a spawning pair, upon which the attendant male expelled the interloper.

Discussion

In 2008, Lamprey arrived in Sedgeunkedunk two to four weeks later than in most streams in the lower Penobscot watershed, and peak spawning occurred here after most mortality had occurred downstream and carcasses were observed in nearby watersheds (O. Cox, Maine Department of Marine Resources, Bangor, ME, pers. comm.). In Maine, Lamprey spawning was reported from late May and early June when the water temperature reaches 17–19 °C (Kircheis 2004). By the time Lamprey arrived, the mean daily water temperature in Sedgeunkedunk had exceeded 20 °C for most of early June. The Lamprey run might have been triggered by temperatures dropping below 17 °C on 17 June, and then recovering to 20 °C over nine days (Binder and McDonald 2008). This decrease in temperature coincided with an increase in discharge, which has been shown to initiate migration (Almeida et al. 2002). This period of lower temperatures was short, so individuals that arrived early had more opportunity to take advantage of a brief period of favorable spawning conditions. In contrast, Lamprey begin to arrive in the lower Connecticut River in early April, and spawning there is usually completed by May (S. Gephard, Connecticut Department of Environmental Protection, Old Lyme, CT, pers. comm.), but Nislow and Kynard (2009)

Table 2. Smallest, largest, and mean sizes of Sea Lamprey nests, and the maximum number of associated Sea Lamprey observed, in Sedgeunkedunk Stream during the 2008 spawning run. Measurements are in cm. Mean of the maximum number of Sea Lamprey for all nests is shown with ± 2 SE. Smallest and largest nests determined by area.

	Pit length	Pit width	Pit depth	Mound length	Mound width	Mound height	Max. # of Lamprey
Smallest	42	40	23	37	35	11	0
Largest	126	101	23	128	101	9	6
Mean	75 ± 11	56 ± 9	20 ± 2	62 ± 14	57 ± 8	8 ± 1	1.8 ± 0.4

report a spawning period of late May through late June in a small tributary of the Connecticut River 20 km upstream of the Holyoke Dam. Although the mouth of Sedgeunkedunk is located near head-of-tide, Lamprey enter this stream relatively late, and in a state of sexual maturity, as evidenced by their apparent sexual dimorphism. Other anadromous species (e.g., Atlantic Salmon) are characterized by late-running individuals that spawn in the lower reaches of a watershed and early-running individuals that penetrate into the headwaters (Saunders 1967). If this pattern holds true for Lamprey, it is not surprising that Sedgeunkedunk receives a late run of mature fish.

We saw no evidence of nest fidelity in either male or female Lamprey. In fact, we observed that Lamprey moved often in the system and attended multiple nests, with individuals on as many as five nests and travelling as much as 255 m between nest sites in consecutive days. This finding is consistent with what has been observed in other lamprey species (Moser et al. 2007). Thus, a single Lamprey may modify the substrate in several reaches of the same stream, and multiple Lamprey may build and expand upon a communal nest. Males initiate nest building (Kircheis 2004), and typically were associated with multiple nests. Males were more likely to be observed away from a nest than were females, perhaps from their tendency to move among multiple nests, and possibly to avoid sharing nests with other males.

Despite the relatively short reach of Sedgeunkedunk accessible to anadromous fishes, Lampreys did spawn there. Our methods of capture and survey for both Lamprey and their nests were successful, and our models of abundance indicated that we were able to capture every Lamprey in the system and record each nest. Our use of PIT packs was effective in identifying individuals without apparent disruption of their behavior, and we were able to record the location and activity of individuals on a daily basis.

The historic abundance of Lamprey in Maine is unknown (Kircheis 2004). Therefore, we do not know whether 47 Lamprey in Sedgeunkedunk represents a run of spawners that is persistent in the system despite the limited available habitat, or one that is in decline. During a 20-year study on the Fort River, MA (a tributary to the Connecticut River similar in size to Sedgeunkedunk), a mean of 80 spawners per year entered the stream (Nislow and Kynard 2009). Tributaries to Lake Ontario with less than 1 km of available stream habitat below a dam can support runs of up to 800 Lamprey (Binder et al. 2010).

Lamprey may provide important ecological functions in stream ecosystems, particularly ones that have lost other anadromous components. Its semelparous life history makes it a potential source of MDNE. We observed 17 carcasses in Sedgeunkedunk, which suggests that the other Lamprey left before death, that carcasses were removed by scavengers, or that carcasses were washed downstream into the Penobscot. Most Lamprey carcasses decompose within 1–2 weeks (Nislow and Kynard 2009), such that MDNE addition could occur in Sedgeunkedunk before high discharge events wash the carcasses downstream. We did not observe downstream movements of intact carcasses, but did witness their rapid disintegration.

The nest-building behavior of Lamprey has the potential to act as a substrate conditioner for Atlantic Salmon, especially in a system that does not currently support reliable spawning of that species. Lamprey nest abundance was related negatively to fine sediment coverage; this could indicate that Lamprey select a substrate of coarse particles and avoid a substrate of fine particles, or that the nest-building activities themselves function to coarsen the substrate, or both. Nests as large as we observed could have a substantial impact on the substrate composition of a relatively small stream. If the abundance and distribution of the spawning run increases with restoration, as we expect, this creates potential for Lamprey to affect the substrate of a large portion of Sedgeunkedunk. Repeated mass spawning by Pacific salmonines can coarsen substrate, reduce armoring, and increase the quality of nest habitats in a positive feedback mechanism (Montgomery et al. 1996). A similar effect of Lamprey in our study area is yet to be determined, but is the focus of ongoing research. The synergism among a suite of anadromous species could be an important factor in the recovery of each species as barriers are removed in Maine streams (Saunders et al. 2006).

Conclusion

Now that Mill Dam has been removed and most of the lotic habitat within the watershed is presumably accessible to anadromous fishes, what happens next will help us to determine the viability of the Lamprey spawning run in this stream. In Portugal, Sea Lamprey has been shown to use previously inaccessible habitat after connection is restored (Almeida et al. 2002). It is likely there will be an immediate expansion of Lamprey spawning area in Sedgeunkedunk. We believe that only Mill Dam blocked upstream spawning migration, and that suitable habitat upstream should be colonized quickly now that Mill Dam has been removed. After dam removal, we expect a positive feedback mechanism for population increase initially, whereby adults penetrate farther upstream and spawn over a greater distance, and a resultant increased density of ammocoetes later that provides a stronger pheromone cue to attract even more adults.

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