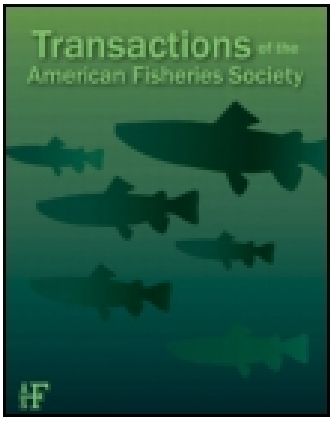

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ARTICLE

Fish Community Response to a Small-Stream Dam Removal in a Maine Coastal River Tributary

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Abstract
Sedgeunkedunk Stream, a third-order tributary to the Penobscot River in Maine, historically has supported several anadromous fishes including Atlantic Salmon *Salmo salar*, Alewife *Alosa pseudoharengus*, and Sea Lamprey *Petromyzon marinus*. 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 in removal of the lowermost dam (Mill Dam) providing access to 4.7 km of lotic habitat and unimpeded passage into the lentic habitat of Fields Pond. In anticipation of these barrier removals, we initiated a modified before-after-control-impact study, and monitored stream fish assemblages in fixed treatment and reference sites. Electrofishing surveys were conducted twice yearly since 2007. Results indicated that density, biomass, and diversity of the fish assemblage increased at all treatment sites upstream of the 2009 dam removal. No distinct changes in these metrics occurred at reference sites. We documented recolonization and successful reproduction of Atlantic Salmon, Alewife, and Sea Lamprey in previously inaccessible upstream reaches. These results clearly demonstrate that dam removal has enhanced the fish assemblage by providing an undisrupted stream gradient linking a small headwater lake and tributary with a large coastal river, its estuary, and the Atlantic Ocean.

Human societies have had intimate connections to the natural resources provided by river ecosystems since time immemorial (Vitousek et al. 1997), and the construction of dams and weirs has enabled the manipulation of rivers for the purposes of maximizing resource acquisition while minimizing the associated dangers (Erickson 2000). Dam construction in the United States proliferated following the European settlement of North America and projects have provided municipal and agricultural water supplies, flood control, navigation, and hydroelectric power generation (Benke 1990). Historically, many dams were built without forethought of ecological impacts. Recently, scientists began comparing impounded rivers with free-flowing ones to quantify those ecological impacts (Hart et al. 2002). Dams can cause changes to hydrological flow regimes (Richter and Thomas 2007), temperature regimes (Poole and Berman 2001), sediment loadings (Petts 1980),

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pollution levels (Köster et al. 2007), and connectivity within and among ecosystems (Northcote 1998). Dams constructed with poor or absent fish passage systems have blocked anadromous fish migrations and are a leading cause of fish declines worldwide (Limburg and Waldman 2009). Furthermore, dams have a finite lifespan, and many dams constructed in the 19th century have outlived their utility (Poff and Hart 2002).

With the emergent recognition that environmental costs associated with dams may outweigh the economic benefits, society has begun to view dam removal as a means to restore ecologically degraded rivers (Babbitt 2002). Restorative dam removal projects in the United States have increased in response to the 1994 Federal Energy Regulatory Commission (FERC) relicensing policy mandating that dam owners either address environmental concerns or proceed with decommission and removal (Bednarek 2001). As of 2010, 888 dams have been removed in the USA nationwide, and 450 of these removals have taken place since 1999 (American Rivers 2010). Though removals are generally justified by invoking ecological benefits, less than 5% of all removals were coupled with published biomonitoring studies as of 2002 (Hart et al. 2002).

The Penobscot River is Maine's largest river (560 km) and the watershed (22,300 km^2) once supported as many as ten coevolved anadromous species (Saunders et al. 2006). However, 113 dams throughout the watershed have severed marine–freshwater connectivity, which has led to declines in populations of all anadromous fishes (PRRT 2014). Sedgeunkedunk Stream, a small tributary to the Penobscot River below head-of-tide (Figure 1), typifies small streams in Maine impacted by dams and subsequent dam removal. Sedgeunkedunk Stream is one of only three major tributaries flowing into the Penobscot River downstream from the lowermost main-stem dam (i.e., Veazie Dam), which was recently removed (PRRT 2014). 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 main-stem Penobscot River dam removal impacts (Gardner et al. 2012, 2013; Hogg et al. 2013).

Little is known regarding the interactions between recolonizing anadromous species and resident species in river ecosystems (Kiffney et al. 2009), and the response of ecosystems to dam removal is also poorly characterized (Dufour and Piégay 2009). Dams are known to impact the distribution and abundance of resident fish communities by fragmenting habitat (Winston et al. 1991; Pringle 1997). Habitat fragmentation can prevent some resident fish species from accessing habitats necessary for the completion of their life histories (Schlosser 1995). Though the impetus for dam removal projects on Sedgeunkedunk Stream was the restoration of declining anadromous runs, dam removals may also benefit resident freshwater communities. Studies have demonstrated that anadromy contributes to species richness and possibly structures riverine fish communities by facilitating recovery through colonization after environmental perturbations (McDowall 1998).

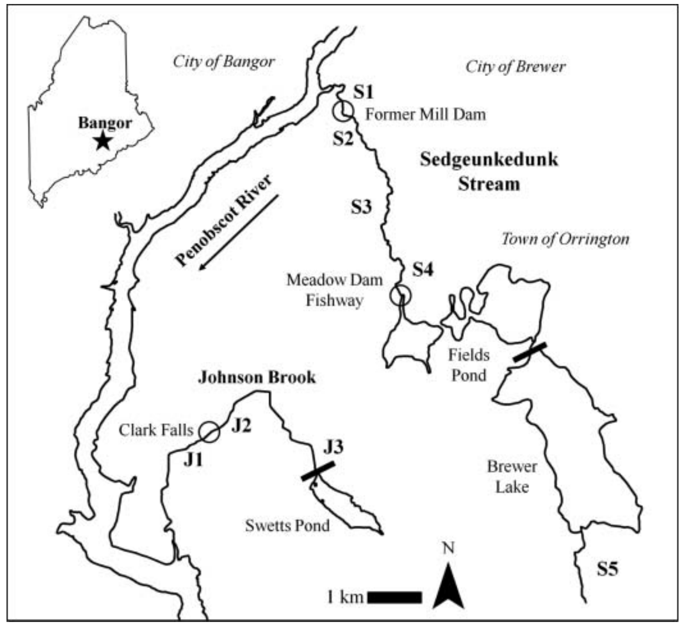

FIGURE 1. Study sites in Sedgeunkedunk Stream (S1–S5) and Johnson Brook (J1–J3), Penobscot County, Maine, 2007–2011. Open circles represent restored dam sites in Sedgeunkedunk Stream and a natural waterfall barrier in Johnson Brook that is functionally analogous to the former Mill Dam. Filled rectangular bars represent Brewer Lake and Swetts Pond lake outlet dams.

Efforts to restore marine–freshwater connectivity in Sedgeunkedunk Stream culminated in August 2009 with the removal of the lowermost Mill Dam (Figure 1), allowing Sea Lampreys *Petromyzon marinus* and endangered Atlantic Salmon *Salmo salar* access to an additional 4.7 km of high-quality spawning and rearing habitat. Additionally, construction of the Meadow Dam Fishway provided migrating Alewives *Alosa pseudoharengus* access to spawning and nursery habitat in Fields Pond (Figure 1). Gardner et al. (2013) provide a comprehensive description of barriers and restorative barrier removals in the system.

Longitudinal and temporal patterns of the Sedgeunkedunk Stream fish assemblage were relatively consistent during the 2 years of this study prior to dam removal (Gardner et al. 2013), which allowed for the detection of immediate disturbance effects associated with the 2009 removal of the Mill Dam. This predam removal consistency also enabled us to evaluate the efficacy of recent restoration efforts in relation to the primary project goal of characterizing resilience and recovery of resident and anadromous fishes in small coastal systems impacted by dams. Immediately following the 2009 dam removal, the Sedgeunkedunk Stream fish community response suggested that the presence of the Mill Dam disrupted the natural longitudinal gradients in density, biomass, species richness, and diversity (Gardner et al. 2013). Prior to dam removal, these fish community metrics were maximized in the reach downstream from the dam, minimized in the reach upstream from the dam, and were intermediate in the two most upstream reaches.

Immediately following the dam removal, Gardner et al. (2013) documented a longitudinal redistribution of resident fishes and noted the recolonization of juvenile Atlantic Salmon into habitat previously rendered inaccessible by the Mill Dam. We continued the monitoring protocols established by Gardner et al. (2013) with the specific objectives of quantifying the distribution and abundance of fish species in Sedgeunkedunk Stream during a 2-year, postdam removal period. We sought to assess spatial and temporal changes in fish community metrics with a focus on responses by anadromous species. Specifically, we hypothesized that anadromous fishes would recolonize and successfully reproduce in previously inaccessible spawning and nursery habitats, while the resident fish community in the former dam impoundment would transition from lentic to lotic species dominance.

STUDY AREA

Sedgeunkedunk Stream is a third-order tributary to the Penobscot River, Penobscot County, Maine, that flows through the town of Orrington and the city of Brewer. The watershed drains approximately 5,400 ha including Brewer Lake and Fields Pond in the headwaters (Figure 1). Sedgeunkedunk Stream flows from Fields Pond at the Meadow Dam Fishway (44°44′05″N, 68°45′56″W), an historical dam site that was rehabilitated with the installation of a rock-ramp fishway in August 2008. From the Meadow Dam Fishway, the stream flows 5.3 km to the confluence of the Penobscot River at river kilometer (rkm) 36.5 near the head of tide (44°46′08″N, 68°47′06″W). The Sedgeunkedunk Stream watershed is mostly forested, but some urban and industrial development exists primarily in downstream reaches. This relatively low-gradient stream has a median bank-full width of approximately 5 m, with peak discharge of 5 m^3/s immediately following early spring ice-out, and a base-flow discharge of 0.1 m^3/s during late summer. The lowermost dam (Mill Dam: 44°45′55″N, 68°46′47″W) was located 700 m upstream from the Penobscot River confluence and was demolished in August 2009. A third dam located at the outlet of Brewer Lake remains with no plans to modify or remove it (Figure 1).

Johnson Brook is a neighboring third-order tributary that flows 7.4 km from the Swetts Pond lake outlet dam (44°42′18″N, 68°47′10″W) into the Penobscot River near rkm 24 (44°42′08″N, 68°49′50″W; Figure 1). The Johnson Brook system includes a natural barrier (Clark Falls, near stream kilometer 3.7) that we considered functionally analogous to the former Mill Dam in Sedgeunkedunk Stream. Because of its proximity and hydrological similarities, Johnson Brook satisfied the assumptions of our modified before-after-control-impact (BACI) study design (Stewart-Oaten et al. 1986; Kibler et al. 2011; Gardner et al. 2013) and was therefore chosen as a "control" reference system.

METHODS

Study design.—Our methods were similar to those of Gardner et al. (2013) and were expanded to include the "after" portion of the modified BACI study design. The modified BACI study design was expected to account for naturally occurring temporal and spatial variation not related to dam removal. Instead of limiting our before-and-after monitoring efforts to sites specifically impacted by the dam and its subsequent removal, we included multiple reference sites not likely to be affected by the dam removal. If changes occurred at impacted sites but not at the reference sites, then we could attribute those changes to the dam removal. We established eight fixed monitoring sites throughout the Sedgeunkedunk Stream and Johnson Brook watersheds as part of the modified BACI study design (Figure 1). Four sites (S1–S4) impacted by dam removal were selected longitudinally from downstream of the former Mill Dam upstream to the Meadow Dam Fishway in Sedgeunkedunk Stream, and are hereafter referred to as "treatment" sites. Four "reference" sites (J1–J3 and S5) were selected from neighboring Johnson Brook and a disjointed headwaters site upstream from Brewer Lake (Figure 1).

Site S1 was located immediately downstream from the former Mill Dam and was the only treatment site accessible to anadromous fishes prior to restoration efforts. Site S2 was located immediately upstream from the former Mill Dam, and site S3 was located approximately midway between the former Mill Dam and the Meadow Dam Fishway. Site S4 was located immediately downstream from the Meadow Dam Fishway.

Site S5 served as a reference site because it was isolated from the treatment sites by the Brewer Lake outlet dam. Site S5 was located approximately 8.2 stream kilometers upstream from the Meadow Dam Fishway. The remaining three references sites were located in Johnson Brook and were chosen because they were functionally analogous to Sedgeunkedunk Stream treatment sites. Site J1 was located immediately downstream from Clark Falls, a likely natural barrier to upstream movement of most fishes with exception of American Eel, *Anguilla rostrata*. Site J2 was located immediately upstream from Clark Falls, and site J3 was located immediately downstream from the Swetts Pond lake outlet dam. All sample sites ranged between 50 and 100 m in stream length and were characterized by riffle and glide mesohabitats with coarse substrates.

Electrofishing surveys.—We sampled the five sites within the Sedgeunkedunk watershed in July 2007 and started a biannual sampling regime at all eight locations beginning in May 2008. Locations were sampled immediately following high spring run-offs when logistically feasible. Sampling episodes usually occurred in mid to late May and once again during summer low-flow conditions usually in late July to mid-August. Gardner et al. (2013) completed their sampling in August of 2009, 7 d after the removal of Mill Dam. We continued the biannual sampling of all sites beginning in May of 2010 and finishing in August 2011. We allowed no more than 10 d to elapse between sampling of the first and last sites within a season.

We used backpack electrofishing techniques to collect fish and maintained consistent unit settings throughout the duration of episodic sampling events. Barrier nets with 3-mm mesh were deployed at the upstream and downstream boundaries of each site to prevent immigration and emigration during surveys. All captured fish were identified to species, and TL (mm) and mass (nearest 0.1 g) were measured for the first 300 individuals of a species at a given site. All captured fish were retained in aerated live wells throughout the duration of sampling episodes and returned alive to approximate capture locations. Incidental mortality was low ($<2\%$ for all sampling episodes) and biannual electrofishing was assumed relatively inconsequential to the fish community (Latimore and Hayes 2008).

Abundance estimates.—We employed three-pass depletion electrofishing techniques (Zippin 1958) for estimating abundance and associated variance during most sampling episodes except under the following conditions. Two-pass depletions were conducted at all Sedgeunkedunk watershed sites during July 2007 sampling. Two-pass depletions were also conducted if the second pass yielded a 75% or greater reduction in total captures compared with the first pass, and two-pass abundance and variance estimates were generated using the formulae of Seber and LeCren (1967). Four-pass depletions were conducted on rare occasions (three occasions only for site S4) when the third pass yielded a 50% or less reduction in total captures compared with the second pass. When four passes were conducted, we consolidated the data structure to be mathematically equivalent to a two-pass depletion estimate, in which the first two passes were condensed into a single pass (pass 1 + pass 2 = pass A) and the third and fourth passes were condensed into a single pass (pass 3 + pass 4 = pass B). The Seber and LeCren (1967) two-pass depletion formula was then applied to passes A and B to generate abundance estimates.

Stream width was measured at 10-m-long intervals from the downstream net to the upstream net at each sampling reach and the sample area was estimated as the product of mean width and reach length. Sampled areas were used in estimates and associated variances of total fish density (number/m^2) and subsequently combined with mean mass to generate estimates of biomass density (g/m^2; Hayes et al. 2007). We plotted density and biomass in sampled reaches over time and inspected for overlap in the 95% CIs to determine if statistically and biologically meaningful differences existed. There has been considerable debate regarding the effectiveness of traditional hypothesis testing in environmental and ecological monitoring (Stewart-Oaten et al. 1986; Reichardt and Gollob 1997), and inspection of overlapping 95% CIs provides an alternative in making conservative estimates regarding the significance and magnitude of differences in ecological monitoring (Payton et al. 2003; Bradford et al. 2005).

Young-of-the-year (age 0) minnows (Cyprinidae) less than 35 mm TL captured during late summer sampling episodes were excluded from analyses because of their incomplete recruitment to our electrofishing gear and their inherent low winter survival (typically ~5% annually; see Freeman et al. 1988). Similarly, Alewives, Rainbow Smelt *Osmerus mordax*, and Sea Lampreys were excluded from density measures because their presence was sporadic during seasonal migrations and they were not included in predam removal analyses. Additionally, we excluded "glass eels" (juvenile American Eel migrants $<$ 65 mm TL; see Hardy 1978) from quantitative analyses because they were observed passing through the 3-mm mesh of our barrier nets, demonstrating incomplete recruitment to our gear. Furthermore, mass measurements were not recorded consistently for American Eels prior to dam removal, so American Eels were excluded from biomass estimates.

Assemblage assessment.—We used two species diversity indices to characterize temporal and longitudinal changes in the fish assemblages. These indices included species richness and the Shannon diversity index (H'). Species richness was determined by noting the presence or absence of each species at a given site over time, followed by calculation of H' scores.

Comparisons of species richness and H' scores within each site over time were made using a Friedman test with Tukey multiple comparisons (Zar 2010). Finally, changes to the fish assemblage structure (i.e., the species present and their relative abundances) in response to dam removal were examined with nonparametric multidimensional scaling (NMDS: PC-ORD 4.0, MjM Software, Gleneden Beach, Oregon; McCune and Grace 2002) based on a Sorensen distance matrix derived from estimated density of each species across all sample sites. The NMDS scores were plotted for greater ease in the interpretation of similarities and differences among sites and to better visualize trajectories within each site over time (Taylor 2010).

RESULTS

Fish Density and Biomass

Before dam removal, total fish densities in Sedgeunkedunk Stream were always highest or second highest at site S1 and lowest at sites S2 and S5 (Figure 2). After dam removal, total fish densities increased at all treatment sites upstream from the dam but remained lowest at reference site S5 (Figure 2). Immediately following dam removal in August 2009, treatment sites S1 and S2 changed the most dramatically. Whereas total fish densities at sites S3 and S4 were consistently

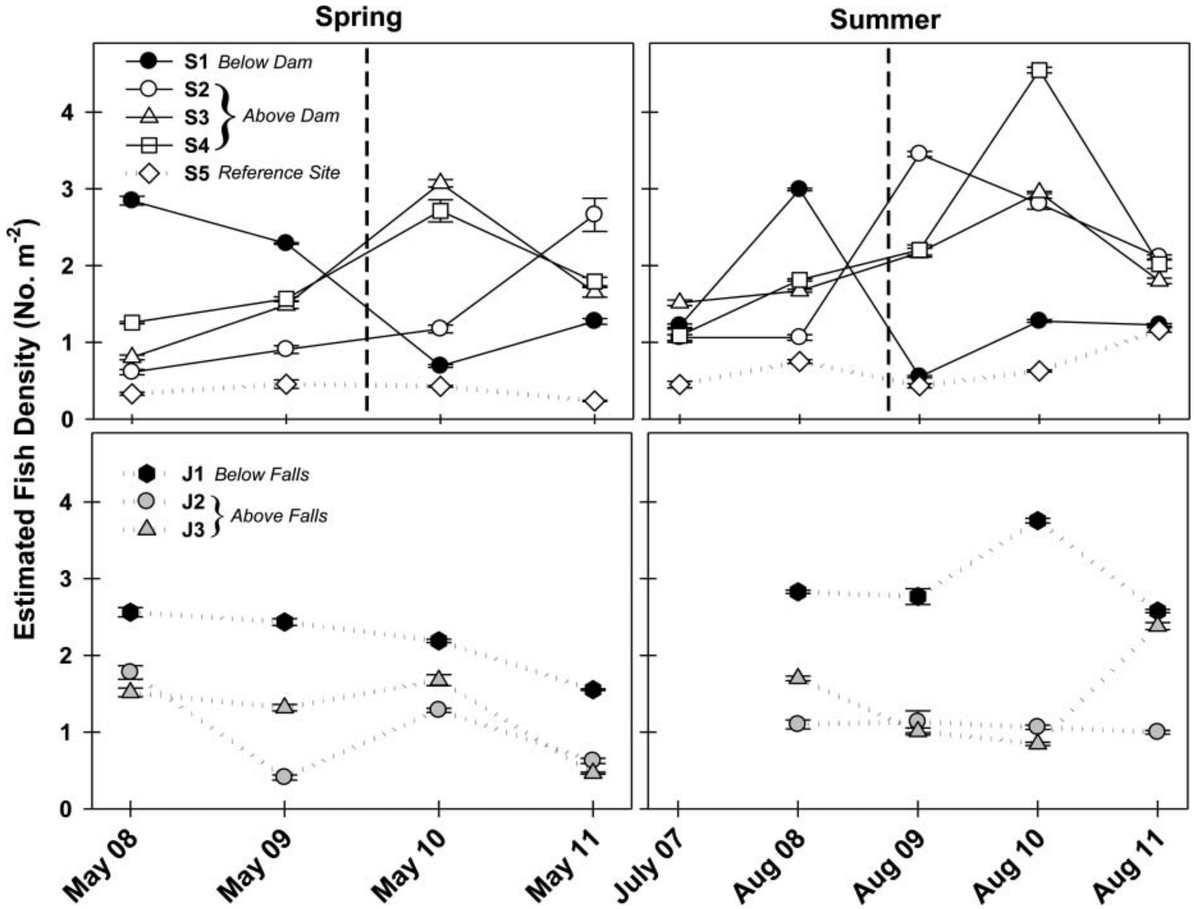

FIGURE 2. Estimated fish densities (number/m^2) at sampling sites (S1–S5) in Sedgeunkedunk Stream (upper panels) and at sampling sites (J1–J3) in Johnson Brook (lower panels) during course of the 5-year study period, 2007–2011. Left panels represent spring seasonal samples and right panels represent summer sampling. Black symbols represent lowermost downstream sites presumably accessible to anadromous species regardless of restoration efforts. Error bars represent the 95% CI of each estimate. Symbols connected by solid lines are representative of treatment sites affected by restoration efforts and symbols connected by broken lines are representative of reference sites not affected by restoration efforts. Dashed vertical lines represent the August 2009 removal of the Mill Dam in Sedgeunkedunk Stream.

intermediate to sites S1 and S2 prior to dam removal, they increased to their highest levels during 2010 before converging towards values comparable with those of the downstream sites in August 2011 (Figure 2). Although all four treatment sites in Sedgeunkedunk Stream displayed variability in total fish densities during postdam removal sampling episodes, their values approached one another during the final sampling episodes in August 2011 (Figure 2).

Total fish densities in Johnson Brook displayed a relatively consistent pattern throughout the duration of the study irrespective of the Sedgeunkedunk Stream dam removal. Total fish densities in Johnson Brook were always highest at site J1 and lower at sites J2 and J3 upstream from the Clark Falls barrier (Figure 2). Throughout the study period, total fish densities at site J1 were similar to those at site S1 prior to the 2009 dam removal in Sedgeunkedunk Stream (Figure 2). Likewise, most total fish densities at sites J2 and J3 were similar to those at Sedgunkedunk Stream sites upstream of the dam prior to the 2009 removal (Figure 2).

Predam removal biomass estimates from site S1 were usually somewhat intermediate to all the other Sedgeunkedunk Stream sites, whereas postdam removal estimates were always lowest at site S1 (Figure 3). Following the 2009 dam removal, biomass estimates from the upstream treatment sites increased and remained greater than at site S1 throughout the duration of the study (Figure 3). However, biomass estimates at the reference site S5 during May 2010 and May 2011 far exceeded all others in both time and space due to the presence of spawning-phase White Suckers *Catostomus commersonii* with individuals in excess of 1 kg (Figure 3). Excluding these exceptionally high estimates from reference site S5, patterns in biomass were similar to patterns observed in total fish density, where biomass estimates at upstream treatment sites approached one another yet remained greater than the estimate from site S1 during August 2011 sampling (Figure 3).

Biomass patterns at the Johnson Brook reference sites remained consistent throughout the duration of the study period regardless of the dam removal in Sedgeunkedunk

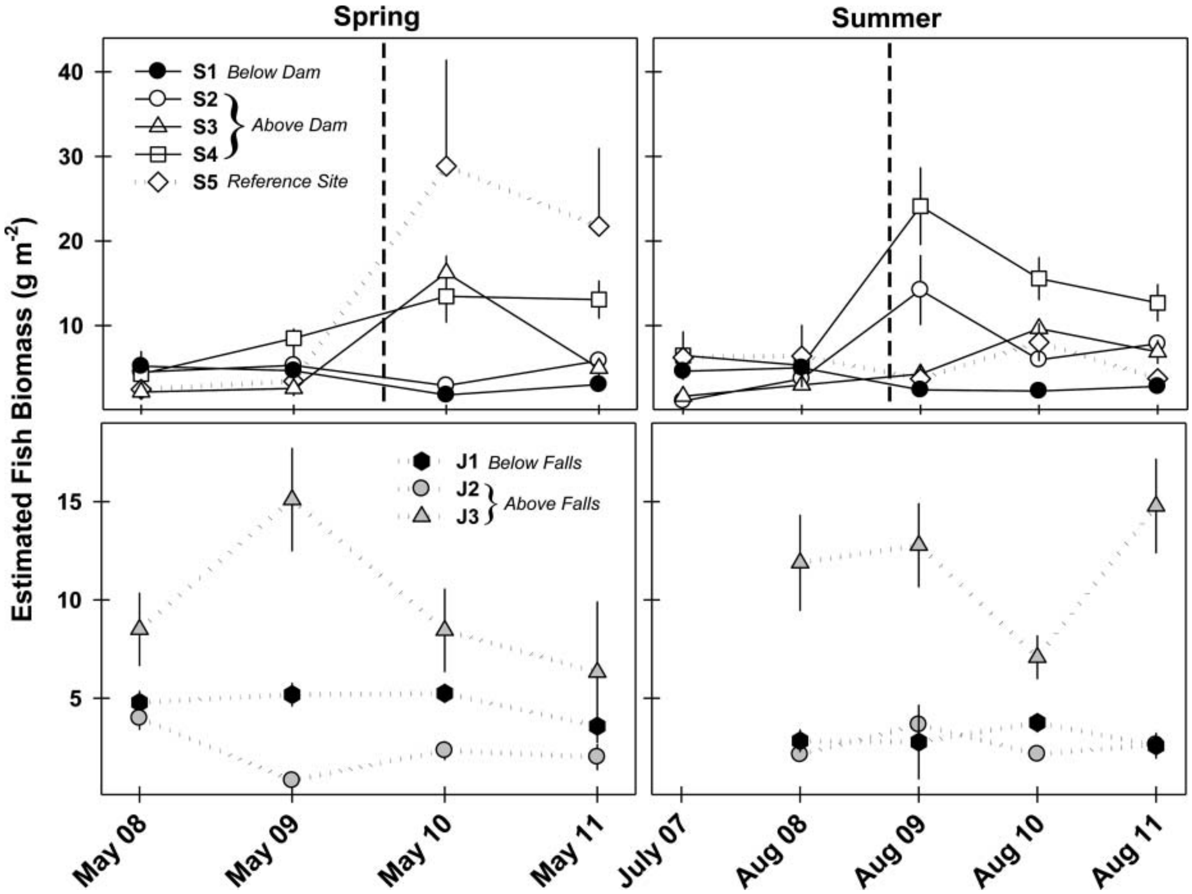

FIGURE 3. Fish biomass (g/m^2) estimated at sampling sites (S1–S5) in Sedgeunkedunk Stream (upper panels) and at sampling sites (J1–J3) in Johnson Brook (lower panels; note *y*-axes scale differences) during course of the 5-year study period, 2007–2011. Left panels represent spring seasonal samples and right panels represent summer sampling. Black symbols represent lowermost downstream sites presumably accessible to anadromous species regardless of restoration efforts. Error bars represent the 95% CI of each estimate (note: error bar caps and some lower bars are omitted for clarity). Symbols connected by solid lines are representative of treatment sites affected by restoration efforts and symbols connected by broken lines are representative of reference sites not affected by restoration efforts. Dashed vertical lines represent the August 2009 removal of the Mill Dam in Sedgeunkedunk Stream.

Stream. Reference site J2, upstream from the Clark Falls barrier, always had the lowest biomass estimate, while reference site J3, located slightly downstream from the Swetts Pond lake outlet dam, generally had the highest biomass estimate (Figure 3). Biomass estimates at reference site J1 were generally intermediate between sites J2 and J3 (Figure 3).

Assemblage assessment.—We encountered 26 species distributed throughout both streams during the 5-y study period (Table 1). Individual species that were ubiquitous over time and space in both streams included Blacknose Dace, White Sucker, American Eel, and Common Shiner (Table 1). Fallfish were ubiquitous in Sedgeunkedunk Stream but virtually absent in Johnson Brook, which contained the closely related Creek Chub (Table 1).

While anadromous species were encountered only at site S1 prior to dam removal, juvenile Atlantic Salmon were observed consistently at upstream Sedgeunkedunk Stream treatment sites thereafter. We surmise that we encountered multiple age-classes of juvenile Atlantic Salmon ranging from age 0 to age 2 based on TL measurements at time of capture (Figure 4). We also encountered migrating adult Alewives sporadically at upstream treatment sites both years after dam removal during May sampling. In August 2011 we serendipitously found that the upstream barrier net at site S4 had been impeding a large school of juvenile Alewives from their downstream migration. The observation of this school prompted us to investigate the upstream plunge pools of the Meadow Dam Fishway where we subsequently witnessed hundreds of juvenile Alewives (~100 mm TL) descend from the Fields Pond outlet into Sedgeunkedunk Stream. Furthermore, we encountered a single Sea Lamprey ammocoete at site S3 during August 2011 sampling. No anadromous species were encountered at any of the reference sites throughout the 5-year duration of this study, although some or all Brook Trout collected at site J1 may have been anadromous in origin.

A difference in species richness among Sedgeunkedunk Stream sites prior to dam removal was detected ($P < 0.05$). Although species richness values at site S1 were numerically

TABLE 1. List of species captured in Sedgeunkedunk Stream and the reference tributary Johnson Brook in Maine over the 5-year period between 2007 and 2011 with the relative occurrence of each species broken down into pre- and postdam removal categories. Relative occurrence is calculated as a percentage of categorical samples that contained the species. Categorical samples are based on biannual spring and late summer electrofishing sampling of five Sedgeunkedunk Stream sites beginning summer of 2007 and three Johnson Brook reference sites beginning spring of 2008 Each site and season represents a single sample, and the Mill Dam in Sedgeunkedunk Stream was removed prior to August 2009 sampling.

	Relative occurrence (%)			
	Sedgeunkedunk Stream		Johnson Brook (reference)	
Species	Preremoval ($n = 20$)	Postremoval ($n = 25$)	Preremoval ($n = 9$)	Postremoval ($n = 18$)
Blacknose Dace *Rhinichthys atratulus*	100	100	100	100
White Sucker *Catostomus commersonii*	100	100	100	100
American Eel *Anguilla rostrata*	100	96	89	100
Common Shiner *Luxilus cornutus*	75	72	89	100
Fallfish *Semotilus corporalis*	90	92	56	33
Creek Chub *Semotilus atromaculatus*	30	20	100	100
Redbreast Sunfish *Lepomis auritus*	70	76	56	44
Golden Shiner *Notemigonus crysoleucas*	50	56	67	61
Brown Bullhead *Ameiurus nebulosus*	60	48	44	39
Fathead Minnow *Pimephales promelas*	25	24	33	50
Pumpkinseed *Lepomis gibbosus*	55	40	11	17
Northern Redbelly Dace *Phoxinus eos*	20	4	44	33
Brook Trout *Salvelinus fontinalis*	15	0	22	39
Atlantic Salmon *Salmo salar*	10	48	0	0
White Perch *Morone americana*	0	4	33	17
Ninespine Stickleback *Pungitius pungitius*	10	4	11	28
Chain Pickerel *Esox niger*	10	12	11	17
Smallmouth Bass *Micropterus dolomieu*	0	8	22	11
Yellow Perch *Perca flavescens*	15	16	0	0
Black Crappie *Pomoxis nigromaculatus*	5	8	0	0
Alewife *Alosa pseudoharengus*	0	12	0	0
Finescale Dace *Phoxinus neogaeus*	5	0	0	6
Bluntnose Minnow *Pimephales notatus*	5	4	0	0
Largemouth Bass *Micropterus salmoides*	5	0	0	0
Rainbow Smelt *Osmerus mordax*	5	0	0	0
Sea Lamprey *Petromyzon marinus*	0	4	0	0

greater than most other Sedgeunkedunk Stream sites prior to dam removal, post hoc comparisons revealed that sites S1 and S2 were the only two that differed from one another ($P = 0.014$) during the predam removal time period (Table 2). The species richness at site S1 decreased precipitously to a low of five species in May of 2010, 9 months after the dam removal, but recovered to levels comparable with other treatment sites by August of 2011 (Table 2). No differences in species richness among treatment sites were detected after dam removal. Species richness at Johnson Brook reference sites remained somewhat predictable throughout the course of the study irrespective of the dam removal in Sedgeunkedunk Stream.

Patterns in H' scores in Sedgeunkedunk Stream were similar to the patterns in species richness described above. Prior to dam removal, the H' scores in Sedgeunkedunk Stream were always greatest at sites S1 and S5 ($P < 0.01$; Table 3). Post hoc comparisons revealed that H' scores at sites S1 and S5 were indistinguishable yet both were greater than those at S2 ($P = 0.007$), S3 ($P < 0.001$), and S4 ($P = 0.016$) prior to dam removal (Table 3). Following the dam removal in August 2009, we observed a trend of numerically increasing H' scores within sites S2, S3, and S4, but no difference among treatment sites was detected for that time period ($P = 0.092$). Although the H' score at site S1 decreased precipitously following dam removal in May 2010, that metric recovered to values consistent with the other treatment sites by August 2011. There were no discernible trends in Johnson Brook H' scores coincident with the dam removal in Sedgeunkedunk Stream.

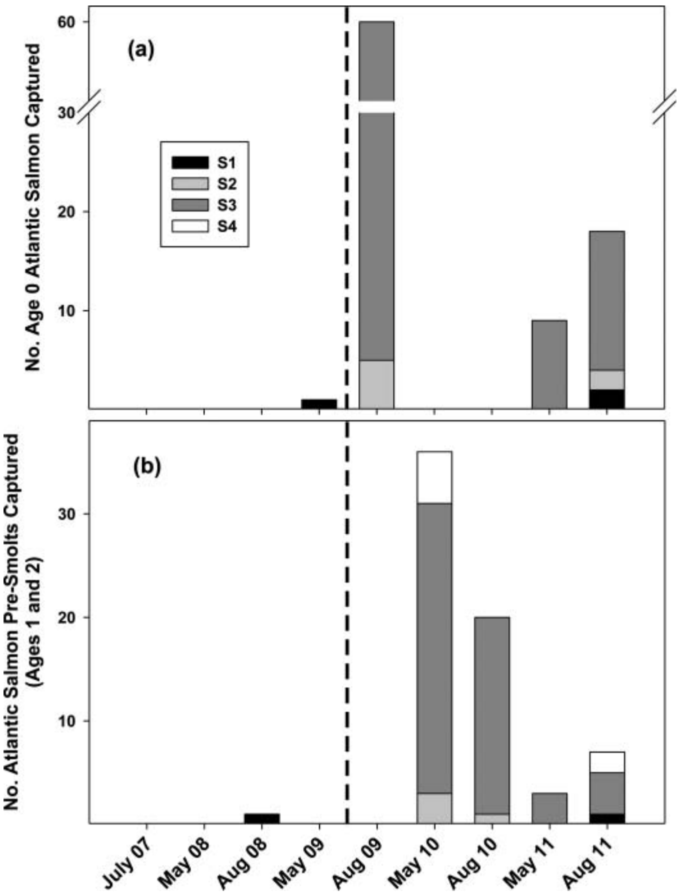

FIGURE 4. Numbers of (**a**) age-0 Atlantic Salmon and (**b**) Atlantic Salmon presmolts (ages 1 and 2) captured at treatment sites (S1–S4) in Sedgeunkedunk Stream, Penobscot County, Maine, 2007–2011. Dashed vertical lines represent removal of the Mill Dam in 2009.

The NMDS ordination generated a stable two-dimensional solution with an acceptable stress value of 0.15 that explained 87% of the variance in species density among all sites during the 5-year study (axis 1, $R^2 = 0.51$; axis 2, $R^2 = 0.36$; Figure 5). The lower-left quadrant of the NMDS ordination was dominated primarily by the presence of native Blacknose Dace, White Suckers, Fallfish, and juvenile Atlantic Salmon. The upper-left quadrant was dominated by just a single nonnative species, the Black Crappie, which is typically associated with lentic systems. The upper-right quadrant of the ordination solution was dominated by lentic, pool-dwelling, native species, which included Pumpkinseed, Redbreast Sunfish, Chain Pickerel, and White Perch. The lower-right quadrant of the ordination was dominated primarily by native stream-dwelling and migratory species. Dominant species associated with the lower-right quadrant included native Creek Chub, Common Shiner, Brook Trout, and Northern Redbelly Dace as well as migratory American Eel and Ninespine Stickleback.

The predam removal ordination score of site S1 originated in the lower-left quadrant (space dominated by native lotic species) but trended strongly positive on both axes into the upper-right quadrant (space dominated by native lentic species) immediately after the dam was removed in 2009 (Figure 6). Subsequently, site S1 ordination scores followed negative trajectories in both dimensions trending back towards the predam removal score that was more closely associated with native lotic species (Figure 6). The ordination scores of sites S3 and S4 remained relatively consistent in two-dimensional space and were located in the lower-left quadrant (space dominated by native lotic species) throughout the study period (Figure 6). The predam removal ordination score of site S2 was distinctly separated from all the neighboring Sedgeunkedunk Stream treatment sites in two-dimensional space but was closest to the isolated headwater reference site S5 in the upper-left quadrant; ordination space that was associated most closely with nonnative lentic species (Figure 6). However, immediately following dam removal, site S2 trended negatively on both axes where it approached sites S3 and S4 in the lower-left quadrant (Figure 6). Site S5 remained consistent in

TABLE 2. Pre- and postdam removal species richness values at sampling sites (S1–S5) in Sedgeunkedunk Stream and at sampling sites (J1–J3) in Johnson Brook by month and year during the course of the 5-year study period, 2007–2011 Stream-specific mean values within pre- and postdam removal periods that share letters in common are not statistically different at α = 0.05.

	Predam removal					Postdam removal					
Sites	Jul 07	May 08	Aug 08	May 09	Mean	Aug 09	May 10	Aug 10	May 11	Aug 11	Mean
S1	8	14	14	15	13z	10	5	8	10	8	8 z
S2	7	5	7	6	6 y	8	8	7	9	11	9 z
S3	9	7	6	9	8 zy	8	10	7	9	8	8 z
S4	7	11	9	9	9 zy	9	8	9	10	9	9 z
S5	7	9	7	8	8 zy	7	8	10	7	8	8 z
J1		11	8	11	10 z	10	13	7	9	11	10 z
J2		6	6	4	5 y	5	9	7	8	6	7 y
J3		12	10	13	12 x	12	11	9	11	10	11 zyx

TABLE 3. Shannon index (H') values for pre- and postdam removal at sampling sites (S1–S5) in Sedgeunkedunk Stream and at sampling sites (J1–J3) in Johnson Brook by month and year during course of the 5-year study period, 2007–2011 Stream-specific mean values within pre- and postdam removal periods that share letters in common are not statistically different at $\alpha = 0.05$.

	Predam removal					Postdam removal					
Sites	Jul 07	May 08	Aug 08	May 09	Mean	Aug 09	May 10	Aug 10	May 11	Aug 11	Mean
S1	1.18	1.63	1.22	1.40	1.36 z	1.44	0.61	0.90	1.10	0.92	0.99 z
S2	1.03	0.66	0.77	0.43	0.72 y	0.82	0.76	0.92	1.14	1.19	0.97 z
S3	0.51	0.67	0.60	0.41	0.55 y	0.69	0.86	0.95	0.91	1.05	0.89 z
S4	0.82	1.16	0.65	0.77	0.85 y	0.56	0.49	0.68	1.29	0.97	0.80 z
S5	1.58	1.67	1.04	1.32	1.40 z	1.06	1.50	1.56	1.21	1.25	1.32 z
J1		1.12	1.06	1.36	1.18 z	1.41	1.74	1.3	1.75	1.48	1.53 zy
J2		1.40	1.38	1.15	1.31 z	1.24	1.74	1.26	1.44	1.32	1.40 y
J3		1.88	1.92	1.58	1.79 z	2.22	2.05	2.08	1.46	1.84	1.93 z

the upper-left quadrant (space dominated by nonnative lentic species) throughout the duration of the study but trended more towards the Sedgeunkedunk treatment sites in 2011 (Figure 6). The Johnson Brook reference sites remained relatively consistent in ordination space throughout the study. Site J1 occupied space in the lower-right quadrant, which was correlated with migratory American Eel and native lotic species, and sites J2 and J3 occupied space more closely associated with native lentic species (Figure 6).

DISCUSSION

Anadromous Species

Barrier removals in Sedgeunkedunk Stream reestablished an unimpeded migratory corridor between the Atlantic Ocean and Fields Pond for three species of andromous fishes. Juvenile Atlantic Salmon responded immediately to the 2009 dam removal by colonizing previously inaccessible upstream sections of the stream (Gardner et al. 2013). We did not detect streambed disturbances associated with Atlantic Salmon redds during the two spawning seasons following the removal of the Mill Dam in 2009, but sizes and locations of Atlantic Salmon captured during electrofishing surveys provided direct evidence of successful reproduction. Whereas all of the parr captured during our sampling efforts in 2010 represented a single age-class of 1-year-old presmolts based on size (McCormick and Saunders 1987), the parr captured in May 2011 distinctly represented a minimum of two age-classes. At site S3, which was 2.5 km upstream from the Penobscot River confluence, we captured nine newly emerged Atlantic Salmon fry with TL averaging 31 ± 1 mm (mean ± SD) and three larger parr averaging 179 ± 12 mm TL. Again, we did not detect evidence of Atlantic Salmon spawning during the autumn of 2010, but the presence of emergent fry this far upstream in the watershed provided compelling evidence of natural reproduction, as median dispersal distance from redds for Atlantic Salmon fry is generally less than 100 m (Einum and Nislow 2005).

In addition to Atlantic Salmon, our electrofishing surveys afforded us the opportunity to document recolonization and successful reproduction by anadromous Alewives. Migrating adults were captured in previously inaccessible reaches during springtime spawning runs both years after dam removal. We subsequently encountered juvenile Alewives at the farthest upstream treatment site (S4) during the August 2011 sampling episode. Additionally, the August 2011 electrofishing capture of a 20-mm (TL) ammocoete at site S3 confirmed successful Sea Lamprey reproduction upstream from the former Mill Dam. Collectively, these observations provided clear evidence that three anadromous species responded to restoration efforts in less than 2 years by spawning successfully in habitats from which they had been excluded for over a century.

Resident Species

Beyond restoring connectivity to spawning and rearing habitats for anadromous fishes, barrier removals in Sedgeunkedunk Stream had marked effects on the resident fish community. We observed general increasing trends in fish community metrics at all treatment sites following the Mill Dam removal. Moreover, most metric values at treatment sites were more similar to one another than they had previously been by May 2011. By August 2011, most values approached one another with the narrowest ranges recorded both before and after removal. The closeness of community metrics in August 2011 suggested that the Sedgeunkedunk Stream fish assemblage was becoming more homogenous among reaches 2 years following the dam removal disturbance and these data may provide a baseline for assessing whether the system transitions into an alternative stable state (Hobbs and Cramer 2008).

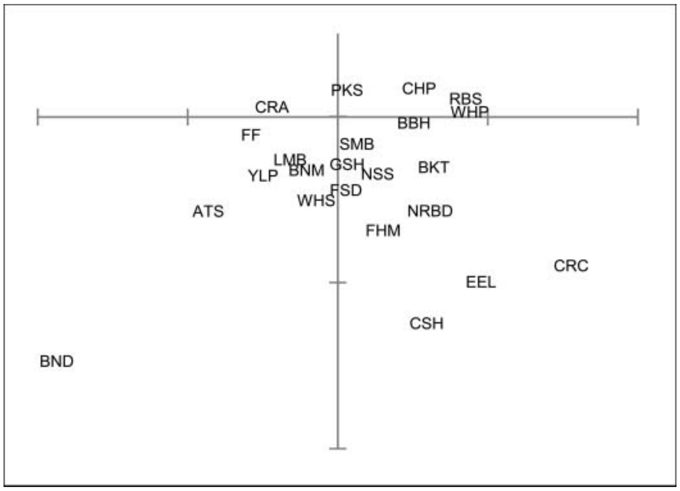

FIGURE 5. Fish species ordinations on first two nonmetric multidimensional scaling axes. Species abbreviations: ATS = Atlantic Salmon, BBH = Brown Bullhead, BKT = Brook Trout, BND = Blacknose Dace, BNM = Bluntnose Minnow, CHP = Chain Pickerel, CSH = Common Shiner, CRA = Black Crappie, CRC = Creek Chub, EEL = American Eel, FF = Fallfish, FHM = Fathead Minnow, FSD = Finescale Dace, GSH = Golden Shiner, LMB = Largemouth Bass, NRBD = Northern Redbelly Dace, NSS = Ninespine Stickleback, PKS = Pumpkinseed, RBS = Redbreast Sunfish, SMB = Smallmouth Bass, WHP = White Perch, WHS = White Sucker, YLP = Yellow Perch.

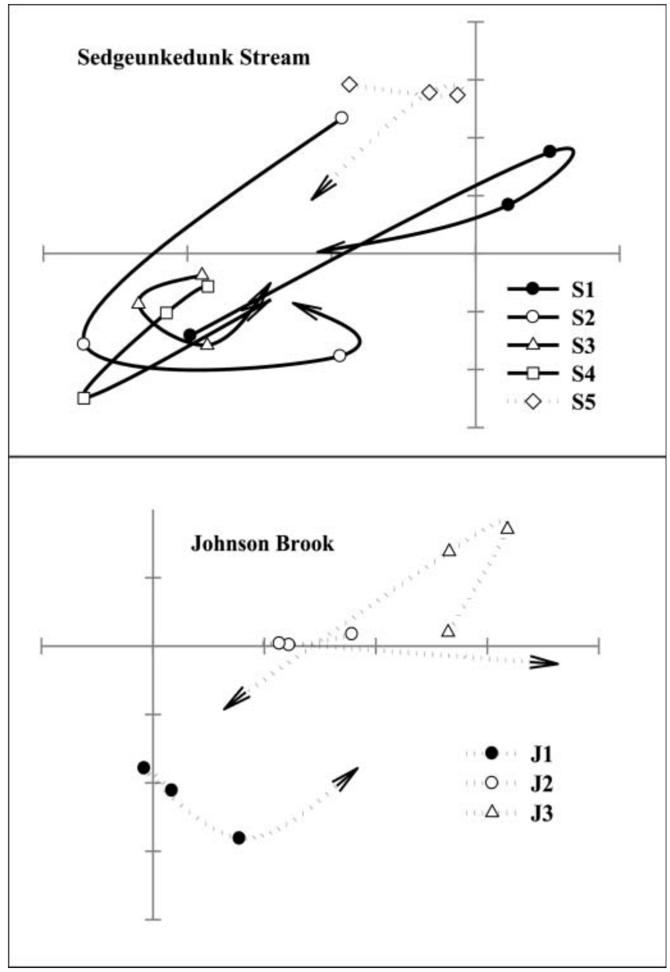

FIGURE 6. Ordinations of the first two nonmetric multidimensional scaling (NMDS) axes scores for fish density data in Sedgeunkedunk Stream (upper panel) and Johnson Brook (lower panel) within each site over time (2008–2011; limited to August sampling for consistency and clarity). Arrows illustrate trends over time beginning August 2008 before the removal of Mill Dam. Arrowheads represent two-dimensional location of data from final sampling episodes (August 2011). Solid lines are representative of treatment sites affected by restoration efforts and broken lines represent reference sites not affected by restoration efforts. Axis orientations differ between panels for clarity.

The observed changes at treatment sites were more likely due to dam removal rather than regional environmental fluctuations. Fish community metrics at the reference sites were consistent throughout the entire course of this study with the exception of standing stock of fish biomass at the isolated reference site S5. The striking biomass increases observed during the spring sampling episodes in 2010 and 2011 at site S5 were attributed to the presence of relatively few large-bodied spawning White Suckers migrating from Brewer Lake (Figure 1). Mass measurements of some spawning-phase White Suckers were an order of magnitude greater than that of the heaviest of fishes captured at all other sites. In relation to the treatment sites, total fish density at site S5 was always lowest and species richness was moderately low throughout the duration of this study.

Prior to dam removal, the farthest downstream sites on Sedgeunkedunk Stream (S1) and Johnson Brook (J1) were the only sites accessible to migrating fish from the Penobscot River (Gardner et al. 2013). Connectivity to larger river networks provides for a more diverse pool of colonizing fish species (Smith and Kraft 2005; Thomas and Hayes 2006). Therefore the increased abundance, species richness, and diversity observed at sites S1 and J2 were likely explained by connectivity with the Penobscot River. Following dam removal, the upstream treatment sites (S2–S4) consistently displayed greater diversity, richness, and abundance values than those observed before the dam was removed. These increased values at treatment sites were clearly due to restored connectivity to the Penobscot River. In contrast, metric values at the upstream reference sites (J2–J3) remained lower than those at site J1 throughout the study because the Clark Falls barrier restricted connectivity to the Penobscot River.

The treatment site located immediately upstream from the dam (S2) arguably was most affected by the presence of the Mill Dam. Fragmentation resulted in a fish assemblage that was distinct from the other treatment sites (Gardner et al. 2013). Although all of the species found at site S2 were found elsewhere in the system, the predam removal assemblage at this site consisted primarily of Fallfish, White Suckers, Brown Bullheads, and Redbreast Sunfish (Gardner et al. 2013), all of which may benefit from the deeper pools associated with dam impoundments (Petts 1980; Swink and Jacobs 1983). Not only was site S2 dominated by larger-bodied, pool-dwelling fishes more typically associated with lentic systems, but the site had fewer fish and lower species richness and diversity, and was more dissimilar to neighboring Sedgeunkedunk Stream sites (Gardner et al. 2013). Following dam removal, the fish assemblage at site S2 transitioned towards lotic species dominance with community metric values in accordance with neighboring treatment sites. By August 2011, 2 years after the removal of Mill Dam, resident fish assemblages at all Sedgeunkedunk Stream treatment sites were dominated by native lotic species.

Conclusion

The fish community assessments presented here have demonstrated that barrier removals in Sedgeunkedunk Stream restored connectivity along the stream gradient. This connectivity is ecologically important because anadromous fishes have demonstrated the ability to penetrate into headwaters, thereby providing marine-derived nutrients and energy subsidies to otherwise oligotrophic freshwater systems (Mitchell and Cunjak 2007; Flecker et al. 2010). Barriers disrupting such connectivity also have effects on freshwater communities. Complex interactions between resident and migratory species likely play important roles in the restoration of riverine fish communities following environmental perturbations (McDowall 1998). For example, postglacial colonization of the Matamek River, Quebec, resulted in a modern freshwater fish community that included 54% anadromous and 8% catadromous species, while the remaining 38% of species were likely derived from diadromous species (McDowall 1996).

The Mill Dam removal also restored important but often overlooked ecological services. A companion study in Sedgeunkedunk Stream revealed that spawning-phase Sea Lampreys acted as ecosystem engineers with their nest-building behaviors influencing the macroinvertebrate and resident fish communities (Hogg et al. 2014). Spawning surveys monitoring Sea Lamprey recolonization (Hogg et al. 2013) also gave us the opportunity to witness direct effects of behaviors on resident fish. We routinely observed Blacknose Dace and Common Shiners feeding on drifting eggs in the plumes of spawning Sea Lampreys. Again, removal of the Mill Dam barrier allowed Sea Lampreys to spawn in newly accessible reaches and thereby provided an additional prey source for resident drift-feeding fishes.

In conclusion, this study has demonstrated that dam removal enhanced the fish assemblage in Sedgeunkedunk Stream by providing an undisrupted stream gradient linking a small headwater lake and a small headwater tributary to a large coastal river and estuary, and ultimately the Atlantic Ocean. The restoration goal of returning the Sedgeunkedunk Stream watershed back into spawning and rearing habitat for anadromous fishes has been demonstrated. Barrier removals in this system also provided a model for large-scale restoration projects like the Penobscot River Restoration Project (PRRP). A before–after study design was initiated at main-stem Penobscot River sites downstream and upstream from two dams that were recently removed and a third that was retrofitted with an improved fish passage system (Kiraly et al. 2015). Restoration outcomes in Sedgeunkedunk Stream are of importance to the PRRP because fish passage improvements in the main-stem Penobscot River allow both anadromous and resident fishes access to dozens of tributaries similar in size and function to Sedgeunkedunk Stream. The modified BACI study in Sedgeunkedunk Stream also provides management agencies with empirical information for making difficult decisions regarding whether it is appropriate to stock anadromous fishes in restored systems or allow natural colonization (Pess et al. 2014). Finally, the empirical information gathered from this study fills a critical knowledge gap in the science of small-stream dam removal.

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