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Dam Removal and Fish Passage Improvement Influence Fish Assemblages in the Penobscot River, Maine

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Abstract

Dams and their impoundments disrupt river habitat connectivity to the detriment of migratory fishes. Removal of dams improves riverine connectivity and lotic habitat, which benefits not only these fishes but also resident fluvial specialist species. Restoration efforts on the Penobscot River, Maine, are among the largest recently completed in the United States and include the removal of the two lowermost dams and improvements to fish passage at several remaining barriers. We assessed fish assemblages in the main-stem river and several major tributaries before (2010–2012) and after (2014–2016) dam removal using boat electrofishing surveys and a stratified random sampling design. In total, we sampled 303 km of shoreline and captured 107,335 individual fish representing 39 species. Similarity indices and rarefaction curves indicated that significant changes in fish assemblage composition occurred in reaches that underwent both habitat and connectivity changes (i.e., directly above removed dams). The newly connected reaches became more similar in fish assemblage composition, as demonstrated by an average increase of 31% in similarity scores. The changes in similarity score in these reaches were driven by increasing access for anadromous fishes and decreasing abundances of slow-water specialist species. For example, we observed a marked reduction in lacustrine species in former impoundments. These assemblage shifts were further illustrated by nonmetric multidimensional scaling in which sites directly above former dams exhibited the largest ordinal shifts immediately following dam removal. We also found all anadromous species in greatest abundance below the lowermost dam during each respective sampling period, though we did find some anadromous species above the lowermost dam during postremoval sampling. Our results demonstrate the potential for large dam removal projects to restore both fluvial and anadromous fish assemblages.

Dams fundamentally alter the flow, temperature, sediment dynamics, and connectivity of rivers, which results in changes to aquatic and riparian biota (Petts 1980; Poff et al. 1997). Such biotic changes include reduced biodiversity in impoundment habitat (Santucci et al. 2005; Guenther and Spacie 2006; Slawski et al. 2008), reduction in

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habitat quality for riverine fishes (Santucci et al. 2005), and shifts in fish assemblage structure (Hayes et al. 2008). The impoundments created by dams convert riverine habitat from lotic to lentic, which favors fluvial generalist fish species (Guenther and Spacie 2006) and facilitates the establishment of invasive species (Graf 2003).

An obvious impact of barriers is reduced connectivity in riverine systems through the introduction of both physical and physiochemical barriers, which restrict the movements of diadromous and potamodromous fishes (reviewed by Pringle et al. 2000). This can ultimately impede the flow of organisms, energy, and nutrients from areas of high to relatively low productivity (Hall 1972) and increase the likelihood of localized extirpation of fish (e.g., as described by Winston et al. 1991 for several fish species in a prairie stream after dam construction).

The migrations of diadromous fish populations are greatly impeded by the presence of dams (see review by Freeman et al. 2003). Such situations are especially prevalent in the eastern United States where mill dams are common (Walter and Merritts 2008) and diadromous fishes are currently at historically low abundances (Limburg and Waldman 2009). In New England states, many local populations of migratory fish, including Alewife *Alosa pseudoharengus* and Blueback Herring *A. aestivalis* (collectively known as river herring), American Shad *A. sapidissima*, and Atlantic Salmon *Salmo salar*, have been extirpated from their natal rivers by the construction of dams in the 19th and 20th centuries (Brown et al. 2013; Mattocks et al. 2017). Similar problems have been created by the construction of dams throughout the world.

Dam removals have immediate and often profound impacts on riverine fish communities. These changes have been studied recently in, for example, Pine River in Michigan (Burroughs et al. 2010), Baraboo River in Wisconsin (Catalano et al. 2007), Rappahannock River in Virginia (Hitt et al. 2012), Eightmile River in Connecticut (Poulos et al. 2014), and Sedgeunkedunk Stream in Maine (Gardner et al. 2013; Hogg et al. 2015). These studies and others have highlighted changes common among many dam removals such as recolonization of diadromous fishes in newly available habitat (Hitt et al. 2012; Weigel et al. 2013; Hogg et al. 2015), increased fish diversity upstream from former dams (Burroughs et al. 2010; Hogg et al. 2015), and the incorporation of newly available marine-derived nutrients and energy in stream food webs (Tonra et al. 2015). Information gathered from such case studies are important for describing commonalities among dam removals and can be used in the development of similar projects in the future (Bednarek 2001; Poff and Hart 2002).

The Penobscot River Restoration Project (PRRP) is one of the largest river restoration efforts recently completed in the United States (Trinko Lake et al. 2012). The goal of this project was to restore the connectivity of the watershed through both dam removal and enhanced fish passage at remaining barriers (see review by Opperman et al. 2011). Most of the 11 species of diadromous fishes once abundant in the Penobscot River watershed before dams were constructed in the 19th and early 20th centuries are currently at historically low levels (Saunders et al. 2006). The PRRP is anticipated to greatly increase the ability of these diadromous species to access critical habitat (Trinko Lake et al. 2012). It is important to remember that although we describe these actions as a "restoration project," the resulting assemblages will almost certainly be different than those that existed before the anthropogenic perturbation of dam construction (i.e., a new "state" sensu Dufor and Piegay 2009).

Prior to the PRRP, multiple years of electrofishing surveys were completed to characterize baseline metrics of species richness, relative abundance, and assemblage structure. The results from those surveys include finding distinct assemblages associated with lentic habitat in former impoundments and evidence of habitat fragmentation between dammed sections of the river (Kiraly et al. 2014a).

The objective of this study was to describe immediate changes to fish assemblages at the watershed scale associated with the PRRP. Specifically, we asked: (1) Has the PRRP resulted in immediate changes to species occurrence and richness in areas of the watershed both above and below current and former dams? (2) Did changes in connectivity associated with dam removal and fish passage improvement result in different distributions of migratory fishes? (3) To what extent did conversion of river conditions from lentic to lotic in former impoundments result in changes to resident fish assemblages?

METHODS

Study area and river modification.— The Penobscot River watershed is the largest in Maine and the second largest in New England, draining approximately 22,455 km^2 and containing more than 8,800 km of riverine habitat (Opperman et al. 2011). There are seven dams on the main-stem river (Table 1) and the Milford Dam is the farthest downstream, located on a natural falls at river kilometer (rkm) 63. Four of the dams constitute the Marsh Island hydropower complex, where water flows either through the Milford Dam and into the main-stem Penobscot River or through a flow-control dam into the Stillwater Branch, through two hydroelectric dams, and then into the main-stem river (Figure 1). Though water is diverted into the Stillwater Branch, there is a minimum flow requirement through Milford Dam of 3,800 ft^3/s or natural inflow, whichever is less (FERC 2012). These three hydroelectric dams have been retrofitted with increased

generation capacity to compensate for the removal of two hydroelectric dams lower on the main-stem river (Opperman et al. 2011). Great Works Dam (rkm 60) and Veazie Dam, formerly located at the head of tide (rkm 48), were removed in 2012 and 2013, respectively. In 2014 a new fish lift, intended to accommodate all upstream migrating fishes, was completed and operational at Milford Dam, the new lowermost main-stem dam. Also, in 2016 a rock-ramp fishway was completed and operational at the Howland Dam (rkm 100), located at the mouth of the Piscataquis River, a major tributary. Before fish passage modification, there was either a vertical slot or denil fishway at each of these dams, which were used by some anadromous species such as Atlantic Salmon, but were largely impassible to others such as alosine fishes (Opperman et al. 2011; Grote et al. 2014).

Sampling design.— We established and tested our sampling design prior to dam removals (described in detail by Kiraly et al. 2014a, 2014b). We adhered to this design during postremoval surveys and review it here briefly to provide context for our analyses. Our sampling design included both fixed sites and sites selected randomly. Fixed sites on the main-stem river were located either directly adjacent to former and present dams or areas that contained a variety of suitable fish habitats. We used a stratified random sampling design to account for large-scale habitat heterogeneity on the main-stem river (Kiraly et al. 2014b). Kiraly et al. (2014b) determined that sampling both fixed and random sites were sufficient to describe over 90% of the species richness in the main-stem Penobscot River, as long as a minimum of 5 km of total main-stem shoreline was sampled during each sampling season. We also sampled eight fixed sites on major tributaries to the Penobscot River. Tributaries were classified as "lower" if they joined the main-stem river in the Argyle stratum and "upper" if they joined the main-stem upstream

of that stratum. No tributaries were sampled below the Argyle stratum for this study.

For the randomly selected main-stem sites, we first divided our sampling efforts among four sections (strata) of the main-stem river (Figure 1) described here from upstream to downstream: (1) The Argyle stratum, which consisted of 32 km of main-stem river between West Enfield Dam and Milford Dam. (2) The Milford stratum, which consisted of 3 km of main-stem river located between Milford Dam and the former Great Works Dam. (3) The Orono stratum, which consisted of 9 km of main-stem river between the former Great Works Dam and former Veazie Dam at the head of tide. (4) The Tidal stratum, which consisted of 15 km of main-stem river below the head of the tide and above the area of saltwater intrusion. Because strata varied greatly in length, most were further divided into reaches that reflect their location relative to dams (former and existing) and general accessibility. Longer strata (i.e., Argyle, Tidal) were divided into three reaches, whereas shorter strata (i.e., Orono, Milford) were composed of fewer reaches (two and one, respectively). Accessible shoreline in each reach was then delineated into 500-m transects using ArcGIS 9.3 (ESRI, Redlands, California), from which two to four transects were chosen randomly for sampling in each season. Transects were located in the field using a handheld GPS, and starting and ending coordinates were recorded at the time of sampling. In a few instances, transects were not samplable (i.e., large rapids) after dam removal, in which case we randomly chose alternate transects. We report results at the stratum level here for the sake of simplicity.

We sampled twice annually in both spring (late May–early July) and fall (September–October) from the spring of 2010 until the summer of 2012 and again from the spring of 2014 until the summer of 2016, resulting in a

TABLE 1. Information regarding dams in the lower Penobscot River watershed, Maine, including river kilometer (rkm), location, and upstream extent of former impoundments. Dam type: H = hydroelectricpower, F = flow control, D = decommissioned hydropower. Dam location: M = main-stem Penobscot River, SB = Stillwater Branch, P = Piscataquis River. Alteration: R = removed, U = upgraded hydropower capacity, F = upgraded fishway, N = no action.

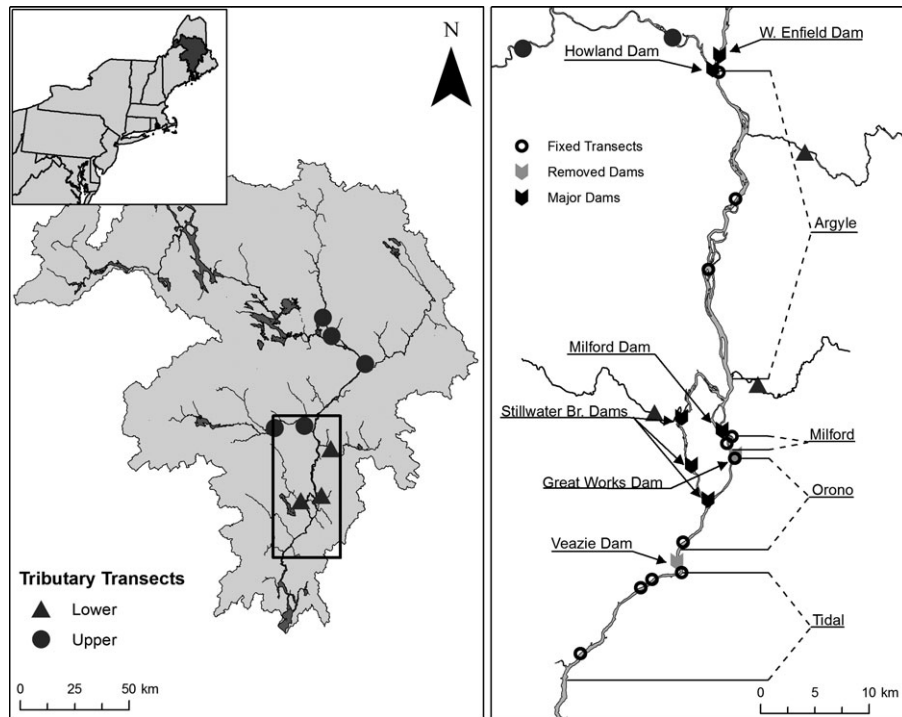| Dam	Dam type	Dam location	Dam height (m)	Dam length (m)	rkm	Extent of former impoundment (rkm)	Alteration	Year passage completed
Veazie	H	M	6	327	48	54.1	R	2013
Great Works	H	M	6	435	60	62.7	R	2012
Milford	H	M	6	427	63		U, F	2014
Orono	H	SB	8	343	54		U	
Stillwater	H	SB	6	539	58		U	
Gillman Falls	F	SB	5	187	64		N	
Howland	D	P	6	201	100		F	2016
West Enfield	H	M	7	296	101		U	

FIGURE 1. The Penobscot River watershed, Maine, and fixed tributary transects (left panel), the main-stem Penobscot River (inset), major main-stem dams, removed main-stem dams, locations of fixed transects (circles), and strata (lines) on the main-stem Penobscot River.

total of 10 sampling seasons (Table 2). The dams of interest were removed during the interim between these pre- and post-sampling periods (2012–2013).

Sampling via boat electrofishing.— We used the same electrofishing equipment and sampling approach described in detail by Kiraly et al. (2014a), and we briefly review the details here. In all possible sampling situations, we deployed a 5.5-m-long Lowe Roughneck (Lebanon, Missouri) aluminum boat equipped with a Smith Root 5.0 GPP (Vancouver, Washington) electrofishing system and two anode droppers. In situations where boat access was not possible (most tributary sites), we deployed a 4.3-m-long Sea Eagle (Port Jefferson, New York) inflatable raft with a Smith Root 2.5 GPP electrode fishing system and a custom single-boom anode dropper. We initiated sampling at the upstream boundary of each transect, positioned the vessels parallel to shore, and operated at the same rate or slightly faster than the velocity of stream flow, proceeding in a downstream direction. Where feasible, we returned to all accessible structures (e.g., woody debris, boulder fields, vegetation) and pocket water areas contained in each transect and systematically sampled these areas thoroughly by probing them with the anode boom arrays.

We identified all captured fish to species, measured mass to the nearest 0.1 g, and returned the fish to near the point of capture after all sampling was complete. Any fish that were difficult to identify were euthanized in a buffered tricaine methanesulfonate (MS-222) solution, preserved in a 10% solution of formalin, and brought back to the lab for confirmation. Because of permitting restrictions, adult Atlantic Salmon, Shortnose Sturgeon *Acipenser brevirostrum*, and Atlantic Sturgeon *A. oxyrhinchus* were not netted, but sightings were considered a "capture," noted, and their size was visually estimated. We estimated the mass of these fishes using the procedures described by Kiraly et al. (2014a).

Catch and mass per unit effort and occurrence.— We used both CPUE (n) and mass (kg) per unit effort (MPUE) to describe the structure and changes to fish assemblages. Effort was defined by the length (km) of each transect, which was determined using field GPS coordinates recorded at the start and end points for each transect and measured using orthoimagery in ArcGIS 10.2 (ESRI). We evaluated the correlation (R^2) between catch standardized by transect length compared with standardization by total sampling time to determine the extent to which changing river conditions (i.e., lentic to lotic) could bias our measures of relative abundance. We also evaluated this relationship for biomass to determine potential sources of bias for MPUE measures.

We used the package doBy 4.5-15 (developed by S. Højsgaard and U. Halekoh, available at CRAN.R-project.org/package=doBy) to calculate the mean and SE values

TABLE 2. Distance of shoreline sampled (km) in each stratum of the Penobscot River, Maine, during each sampling period from 2010 to 2016.

Stratum	Before dam removal					After dam removal				
	Spring 2010	Fall 2010	Spring 2011	Fall 2011	Spring 2012	Spring 2014	Fall 2014	Spring 2015	Fall 2015	Spring 2016
Tidal	10.0	5.4	10.4	5.6	10.5	7.6	8.6	9.4	8.0	8.7
Orono	4.0	4.0	4.2	4.2	7.0	4.4	4.3	6.3	3.9	5.2
Milford	3.1	2.8	3.1	1.6	2.7	2.6	3.5	3.5	2.9	3.5
Argyle	7.8	7.3	9.6	4.9	4.9	4.7	9.0	10.6	7.7	9.9
Lower Tributary	2.2	2.9	2.7	3.1	3.1	3.6	1.8	3.0	2.9	2.3
Upper Tributary	3.3	3.3	3.4	4.8	2.3	2.9	3.7	5.2	3.9	5.2

for these indices in both sampling seasons (e.g., spring 2010) and sampling periods (e.g., before dam removal) in Program R 3.2.3 (R Core Team, available at www.r-project.org). We calculated the mean and standard errors of CPUE and MPUE for each species, within each stratum, and for each sampling season (e.g., fall 2014) and each sampling period (i.e., preremoval and postremoval). We also calculated mean catch for each sampling season and sampling period for use in the analyses described here. Finally, we calculated percent occurrence in each sampling period to describe the ubiquity of species throughout the sampled area and species incidence data to describe changes in the observed distribution of commonly occurring species.

Rarefaction.— Because we captured different numbers of individuals in each sampling period, we used rarefaction to examine differences in species richness by stratum. We used sample-based rarefaction to calculate the expected number of species when a subset of samples are drawn at random without replacement as this preserves spatial heterogeneity in the samples (Gotelli and Colwell 2011). We calculated sample-based rarefaction curves for each stratum in each sampling period using 100 sample randomizations using the program EstimateS 9.1.0 (developed by R. K. Colwell, available at viceroy.eeb.uconn.edu/EstimateS/). We then plotted rarefaction curves with the x-axis scaled to individual abundance, which allows for comparisons of species richness, as suggested by Gotelli and Colwell (2001). Finally, we evaluated differences in species richness in each stratum between sampling periods by assessing the overlap of 95% CIs at the largest number of samples common between two sampling periods (Gotelli and Colwell 2011).

Indices of similarity.— We used both the Sørensen index and the Morisita–Horn index to compare similarity between different strata within each sampling period (i.e., before or after dam removal) and to compare the same stratum between sampling periods. Both indices possess the three properties necessary for valid ecological comparison (i.e., density invariance, replication invariance, and

monotonicity; Jost et al. 2011), are commonly used in dam removal studies, and result in a value on a scale from 0 to 1, where 0 indicates no similarity and 1 indicates compositionally identical assemblages. Furthermore, the Morisita–Horn index is relatively insensitive to unequal sampling effort, insensitive to rare species, and provides an indicator of functional differences between assemblages (Jost et al. 2011). The Sørensen index is relatively more sensitive to rare species and unequal sampling effort.

Chao et al. (2008) found that these indices are also both formulations of a general overlap measure, C_{qN}, where N is the number of assemblages and q essentially determines the sensitivity of the measure to relative abundance of species. We used the C_{02} measure and species incidence frequency data (equivalent to the Sørensen index) to examine differences in species composition and the C_{22} measure (equivalent to the Morisita–Horn index) to examine differences in assemblage composition using average species catch data in each sampling period. We used the program SpadeR (Chao et al. 2016) to calculate similarity index values, SE values, and the 95% CI for each estimate based on 300 bootstrap replications (Chao et al. 2008). Unless otherwise noted, all results of similarity indices are reported as mean ± 2SE.

Nonmetric multidimensional scaling.— We analyzed catch data from each sampling season with nonmetric multidimensional scaling (NMDS) using Bray–Curtis dissimilarity to graphically examine changes in assemblage composition over time. For this analysis, we used the metaMDS routine in package vegan 2.4-6 (Oksanen et al. 2018) in Program R 3.2.3 (R Core Team). We transformed average sampling season catch values by taking the fourth root, which reduces the influence of abundant species and better reflects differences in the entire assemblage (Clarke 1993). The metaMDS function posteriorly rotates the NMDS axes using principle component analysis so that axis 1 reflects the primary sources of variation followed by axis 2 (Oksanen et al. 2018). Finally, we plotted the site results from spring and fall samples separately

to remove the effect of seasonal variation and ease interpretation.

Indicator species and composition by habitat and origin.— We chose to examine changes in average CPUE and MPUE for all fish by stratum and sampling season. We also calculated average CPUE and MPUE for each stratum in both pre- and postremoval sampling periods to illustrate the magnitude of change in the Milford and Orono strata. Unless otherwise noted, all estimates of relative abundance and biomass are reported as mean ± 1SE.

We examined patterns of CPUE and MPUE by sampling period for several indicator species identified from the Tidal and Orono strata during preremoval surveys (Kiraly et al. 2014a). Indicator species analysis identifies species that are representative of a particular group (in this case, stratum) relative to other groups and is used to describe differences among groups (Dufrene and Legendre 1997). Kiraly et al. (2014a) found that Alewife was a significant indicator species in the Tidal stratum, and Smallmouth Bass and Pumpkinseed were both significant indicator species in the Orono stratum. We also examined the spatial distribution of American Eel *Anguilla rostrata* due to its status as a species of concern and its ubiquity in the watershed.

Finally, to determine the effect of dam removal on species groups of interest, we examined percent composition by mass of species grouped by origin (e.g., percent native fish biomass). We also grouped species by habitat preferences that we would anticipate to be characteristic of a free-flowing river (e.g., percent riverine and anadromous fish biomass, combined), as designated in Table 3. We chose to present these percentages by sampling season to examine potential changes over time and in terms of mass because MPUE was more consistent between sampling seasons than was CPUE. We only present data from main-stem strata here for simplicity.

RESULTS

Species Abundance, Occurrence, and Richness

We captured a total of 107,335 individuals representing 39 species through all years of electrofishing surveys. During preremoval surveys we captured 69,393 individuals from 38 species. During postremoval surveys we captured 37,942 individuals from 35 species. The distance of shoreline sampled in each stratum was roughly equal between periods (Table 1), which facilitated the comparison of observed species occurrence and richness.

Twelve species occurred frequently (>40% relative occurrence) in our samples during both periods (Table 3). Of the frequently observed species, four exhibited large decreases (>20%) in relative occurrence between sampling periods. These were species associated with slow-water

habitats, and we observed the largest decrease in their relative abundances in former impoundments. Sea Lamprey was the only one of these frequently captured species to exhibit an increase in relative occurrence, although there was only a 6% increase. Among the species that were less frequently observed in our samples (<30% relative occurrence) only Banded Killifish exhibited a large decrease (20%) in relative occurrence. In contrast, the frequency of occurrence for two of these less common species, Alewife and Largemouth Bass, increased moderately (9% and 11%, respectively).

Rarefaction curves suggest that richness remained largely consistent between both preremoval and postremoval sampling periods, despite differences in catch. We observed the highest observed richness in the Tidal stratum during both sampling periods, which is also evident in rarefaction curves for that stratum (Figure 2). Rarefaction curves also suggest that there was a significant increase in species richness in the Milford stratum. Observed species richness in this stratum increased from a preremoval total of 16 species, which was also the asymptote of the rarefaction curve, to a total of 22 species observed during postremoval sampling, despite far fewer individuals being captured in this reach. Also, richness may have increased minimally in other strata (e.g., Orono, Lower Tributary), but estimated CIs overlapped extensively, which indicates that any changes to observed richness were likely not significant. Finally, the preremoval rarefaction curve estimated for the Upper Tributary stratum indicates that we likely did not sample enough individuals to allow for estimation of asymptotic richness in this stratum. This has implications for incidence-based similarity measures (Sørensen index) and is likely due to sampling across different tributaries and a large spatial scale (see Figure 1).

Similarity Indices

Patterns of assemblage composition analyzed using the Sørensen and Morisita–Horn indices suggest that assemblages within each stratum remained largely similar between sampling periods (i.e., preremoval versus postremoval), with a few notable exceptions. Strata that were determined to be least similar between sampling periods were those directly upstream from former dams (i.e., Orono and Milford). In contrast, other main-stem strata (i.e., Tidal, Argyle) exhibited largely similar assemblages between sampling periods.

Sørensen index estimates from comparisons between sampling periods for the same stratum indicate that the Milford, Orono, and Upper Tributary strata varied significantly from identity (Table 4). Upper Tributary had the lowest estimated species composition similarity (0.54 ± 0.29), likely due to smaller sample sizes and samples taken in a variety of tributaries. Milford was estimated to have

TABLE 3. Fish species caught during electrofishing surveys and their relative occurrence in all electrofishing surveys. Species information: abbreviations, habitat, origins, and relative occurrence in electrofishing samples before and after dam removal in the Penobscot River, Maine. Each species is listed in order of its preremoval relative occurrence. The number of samples (*n*) is reported for each sampling period. Habitat designations follow Werner (2004) and Yoder et al. (2008): R = riverine, L = lacustrine, G = freshwater habitat generalist, E = estuarine, A = anadromous, C = catadromous. Origin: N = native, I = introduced.

Species	Abbreviation	Habitat	Origin	Relative occurrence (%) Preremoval ($n = 202$)	Postremoval ($n = 226$)
Smallmouth Bass *Micropterus dolomieu*	SMB	G	I	96	93
Redbreast Sunfish *Lepomis auritus*	RBS	G	N	92	69
Fallfish *Semotilus corporalis*	FF	R	N	88	85
American Eel *Anguilla rostrata*	EEL	C/G	N	85	75
White Sucker *Catostomus commersonii*	WS	R	N	74	69
Common Shiner *Luxilus cornutus*	CSH	R	N	69	52
Pumpkinseed *Lepomis gibbosus*	PS	L	N	68	30
Chain Pickerel *Esox niger*	CHP	L	I	61	41
Golden Shiner *Notemigonus crysoleucas*	GSH	L	N	52	23
Yellow Perch *Perca flavescens*	YP	L	I	49	40
Brown Bullhead *Ameiurus nebulosus*	BBH	L	N	45	34
Sea Lamprey *Petromyzon marinus*	LAM	A	N	44	50
Banded Killifish *Fundulus diaphanus*	BKF	G	N	27	7
Burbot *Lota lota*	CSK	R	N	23	21
Alewife *Alosa pseudoharengus*	ALE	A	N	15	24
Blueback Herring *Alosa aestivalis*	HER	A	N	11	15
Largemouth Bass *Micropterus salmoides*	LMB	L	I	9	21
Atlantic Salmon *Salmo salar*	ATS	A	N	9	10
Creek Chub *Semotilus atromaculatus*	CRC	R	N	9	11
White Perch *Morone americana*	WP	L/A	N	9	8
Eastern Silvery Minnow *Hybognathus regius*	ESM	L	I	6	3
Black Crappie *Pomoxis nigromaculatus*	CRA	L	I	5	0.4
Blacknose Dace *Rhinichthys atratulus*	BND	R	N	3	3
Mummichog *Fundulus heteroclitus*	MUM	E	N	3	1
American Shad *Alosa sapidissima*	SHD	A	N	2	4
Threespine Stickleback *Gasterosteus aculeatus*	TSS	E	N	2	0.4
Ninespine Stickleback *Pungitius pungitius*	NSS	R	I	2	0
Fathead Minnow *Pimephales promelas*	FHM	R	I	1	3
Northern Redbelly Dace *Phoxinus eos*	RBD	L	N	1	2
Longnose Sucker *Catostomus catostomus*	LNS	R	N	1	1
Blacknose Shiner *Notropis heterolepis*	BNS	R	N	1	0
Spottail Shiner *Notropis hudsonius*	STS	L	I	1	0
Brook Trout *Salvelinus fontinalis*	BKT	R/A	N	1	2
Sturgeon *Acipenser* spp.	SGN	A	N	1	0
Finescale Dace *Phoxinus neogaeus*	FSD	L	N	0.5	4
Striped Bass *Morone saxatilis*	STB	A	N	0.5	3
Central Mudminnow *Umbra limi*	CMM	L	I	0.5	2
Slimy Sculpin *Cottus cognatus*	SSC	R	N	0.5	2
Atlantic Tomcod *Microgadus tomcod*	ATC	E	N	0	1

the lowest similarity in the main-stem river (Table 4), primarily due to the new detection of anadromous fish in the postremoval sampling period. The Tidal stratum had the highest similarity score (0.93 ± 0.32), which reflected the consistent detection of over 30 species of fish in this area in both sampling periods (Figure 3).

Sørensen index comparisons between strata within each sampling period indicate that, in several cases, strata that
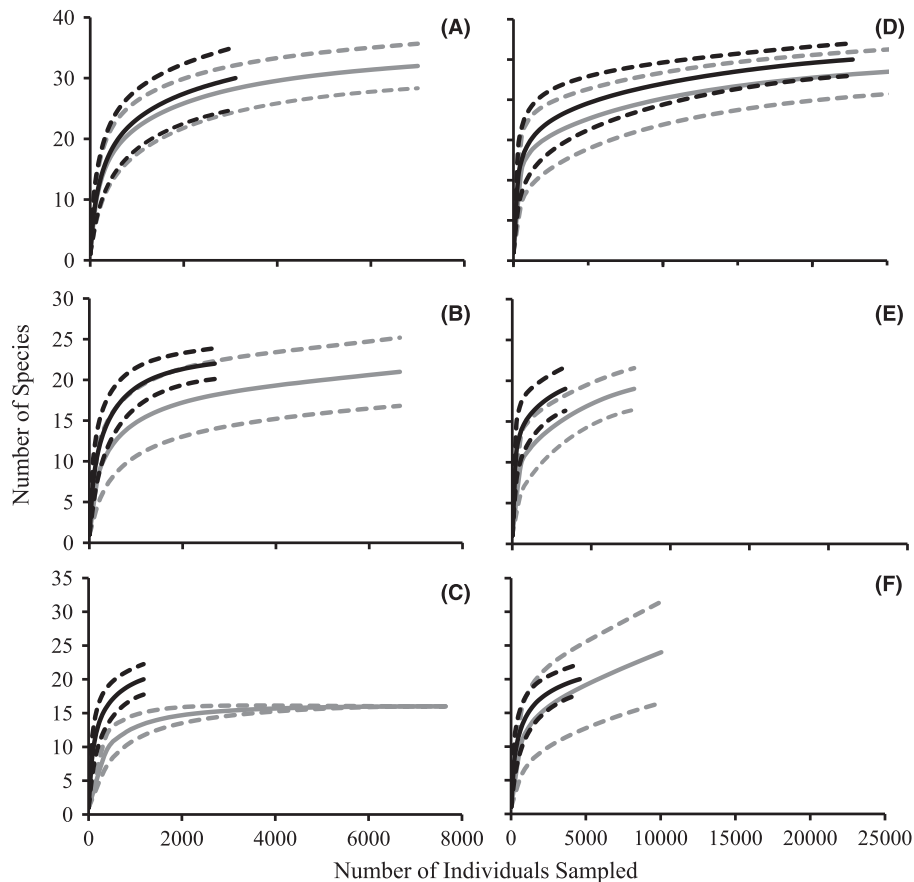
FIGURE 2. Sample-based rarefaction curves for the (**A**) Tidal, (**B**) Orono, (**C**) Milford, (**D**) Argyle, (**E**) Lower Tributary, and (**F**) Upper Tributary strata calculated before (gray) and after dam removal (black) and rescaled to the number of individuals captured in each stratum. Dashed lines indicate limits to 95% CIs.

TABLE 4. Similarity index values calculated for each stratum during preremoval versus postremoval periods and their associated 95% CI (lower limit, upper–limit). Confidence intervals that do not overlap a value of 1 indicate significant differences from identity.

Stratum	Sørensen index	Morisita–Horn index
Tidal	0.93 (0.62, 1)	0.73 (0.70, 0.75)
Orono	0.83 (0.67, 0.99)	0.88 (0.86, 0.89)
Milford	0.70 (0.56, 0.84)	0.44 (0.41, 0.47)
Argyle	0.87 (0.65, 1)	0.99 (0.98, 1)
Lower Tributary	0.92 (0.67, 1)	0.71 (0.69, 0.74)
Upper Tributary	0.54 (0.26, 0.82)	0.93 (0.92, 0.94)

were different (i.e., significantly different from a value of 1) in preremoval samples were significantly different than other strata from the postremoval sampling period (Figure 3). Species composition in the three lowermost strata became more similar, and the Tidal and Argyle strata also became more similar. The relatively large 95% CI around each Sørensen index estimate reflects the influence of rare species on this index.

The Morisita–Horn similarity index values were also relatively high when the same stratum was compared between sampling periods (Table 4). The most notable exception was the Milford stratum for which similarity was 0.45 ± 0.03. This suggests that this stratum underwent the largest assemblage composition change associated with its change from a lentic impoundment to a lotic habitat (Table 1) and because of the increasing connectivity for migratory fish. This change was not evident in the Orono stratum likely due to the occurrence of both impoundment and free-flowing river reaches present in this stratum prior to dam removal. The highest Morisita–Horn index value (0.99 ± 0.01) occurred in the Argyle stratum, which was the only stratum not significantly different from identity when compared between sampling periods.

When the similarity between strata within each sampling period was compared, the largest shifts in the Morisita–Horn similarity index were observed among the mainstem strata, of which Milford exhibited the largest shifts (Figure 3). Similarity increased significantly between the Milford stratum and the Orono and Tidal strata, whereas
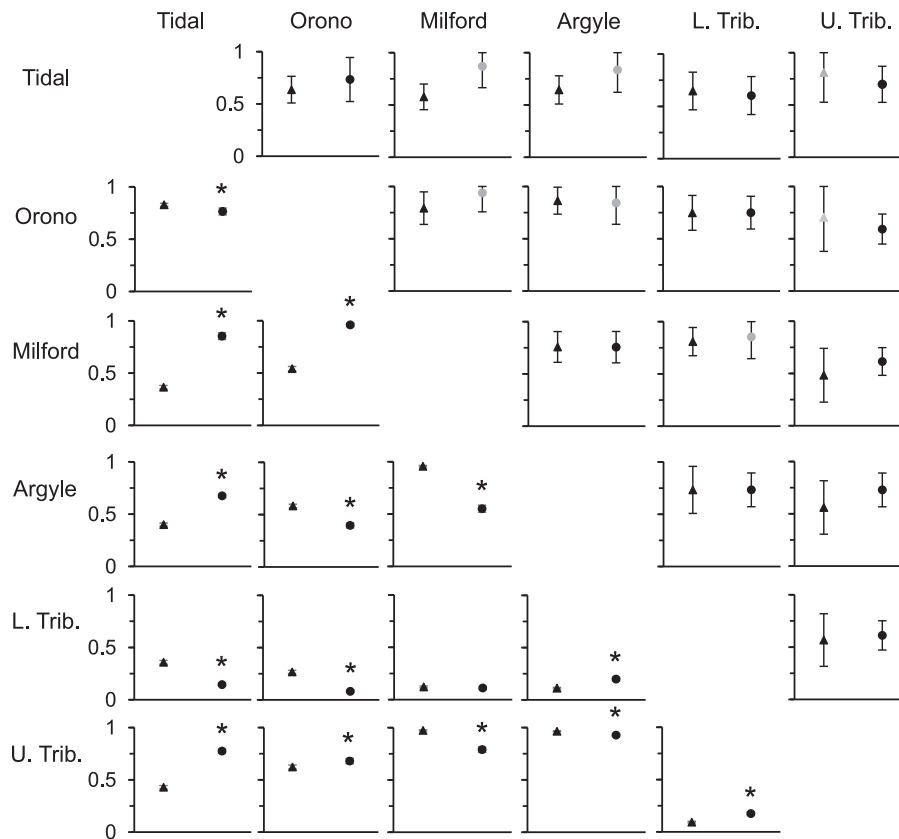
FIGURE 3. Sørensen (upper, right) and Morisita–Horn (lower, left) similarity index values calculated between strata during the sampling periods before (triangle) and after (circle) dam removal. The bootstrapped 95% CI is included for each value. Confidence intervals that do not contain a value of 1 (black) are significantly different from identity. Postremoval CIs that do not overlap preremoval CIs (*) are significantly different between before and after dam removal sampling periods. L. Trib. = Lower Tributary, U. Trib. = Upper Tributary.

values decreased significantly between the Argyle stratum and the Orono and Milford strata. The Argyle and Milford strata were estimated to be near identity (0.96 ± 0.01) during preremoval surveys and exhibited relatively low similarity (0.55 ± 0.03) during postremoval surveys. Conversely, similarity increased between the Milford and Orono strata from 0.54 ± 0.02 to 0.96 ± 0.02. The Lower Tributary stratum exhibited consistently low similarity to all other strata, likely due to the dominance of lacustrine fishes in these low-gradient sites.

Collectively, the similarity indices suggest that although the assortment of species (Sørensen index) in each stratum remained largely consistent between sampling periods, there have been some notable changes regarding the relative abundance of different species (Morisita–Horn index), especially in the Milford stratum. Both indices indicated that there was little relative change in the similarity among strata above the current lowermost dam between sampling periods (i.e., Argyle and tributaries). For example, The Morisita–Horn similarity index remained high between the Argyle and Upper Tributary strata between pre- (0.97 ± 0.01) and postremoval (0.93 ± 0.01) sampling

periods. Also, Morisita–Horn similarity values remained low in the Lower Tributary stratum indicating that, despite exhibiting similar species composition (Sørensen index) to that of other strata, lacustrine species continued to dominate in terms of relative abundance.

Nonmetric Multidimensional Scaling

The NMDS ordination represented the data adequately in two dimensions (final stress = 0.15). Values < 0.2 indicate that the data are well described in the chosen number of axes (Clarke 1993). Axis 1 ordinated with positive values associated with anadromous and estuarine species (e.g., Atlantic Tomcod) to negative values associated with species only found upstream (e.g., Ninespine Stickleback) or only in slack-water reaches (e.g., Golden Shiner). Axis 2 ordinated with positive values associated with species only found in slack-water habitats (e.g., Central Mudminnow) and with negative values associated with species mainly found in fast-water reaches (e.g., Slimy Sculpin), though we did not observe consistent shifts along this axis.

Ordination results were consistent with Morisita–Horn similarity index results, though the influence of relatively
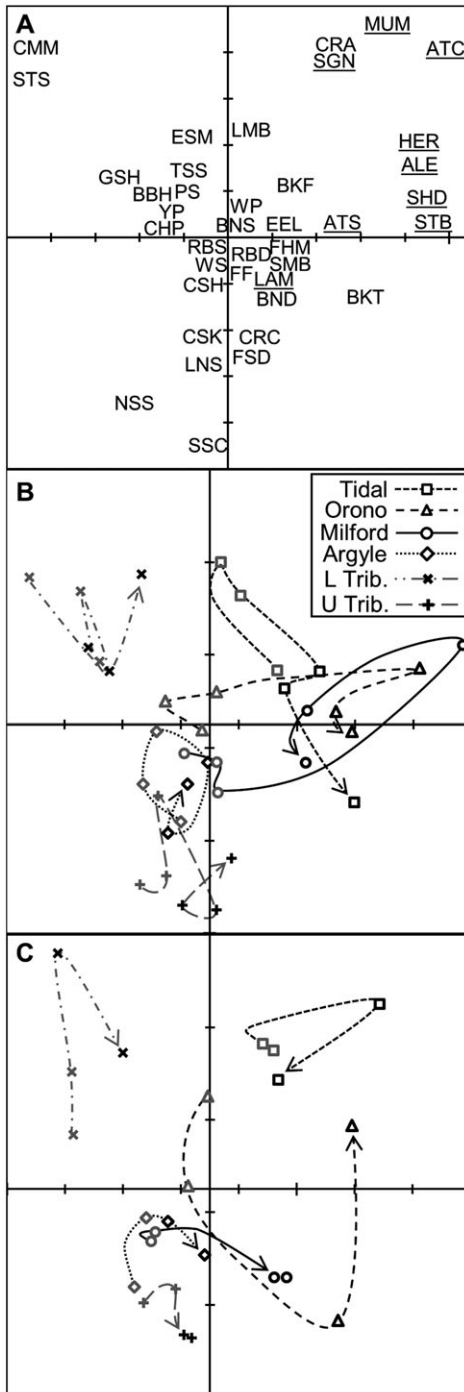
FIGURE 4. Nonmetric multidimensional scaling ordination including (**A**) species leverages and site ordinations from (**B**) spring and (**C**) fall sampling periods using seasonal catch from each stratum from 2010 to 2016. Curved lines indicate shifts over time from the first sampling event in the respective season through the last (arrow), where preremoval points are displayed in gray and postremoval points are displayed in black. Species abbreviations can be found in Table 2 and underlined abbreviations indicate anadromous species. Some species leverage labels were removed or shifted slightly for clarity.

rare fish was more pronounced in this analysis. We observed a consistent increase in axis 1 values across post-removal sampling seasons in strata below the new lower-most dam, with the most pronounced shifts in the strata evident immediately above the removed dams (Figure 4). This is a result of increasing occurrences of anadromous fish upstream from the former Veazie Dam in both spring and fall surveys and a decrease in impoundment specialist species. The Milford stratum exhibited the largest shift relative to other strata followed by the Orono stratum, and we observed the largest single shift in these strata in the sampling season immediately following dam removal (spring 2014). Interestingly, the ordination of three strata (Tidal, Orono, and Milford) downstream from the new lowermost dam shifted to more positive axis 1 values and grouped more closely across postremoval spring surveys, indicating increasing similarity, increasing influence of anadromous fish, and decreasing lentic specialist fishes in all three strata. The three strata upstream from these areas ordinated relatively close to their preremoval values, which further suggests little change in assemblages upstream from the new lowermost dam.

Distribution of Selected Species

Patterns of cumulative relative abundance (CPUE, all species included) suggest that dam removal likely caused decreasing fish density in strata directly above former dams. For example, in the Milford stratum (i.e., former Great Works Impoundment), CPUE decreased from an average of 631 ± 133 fish/km to an average of 101 ± 11 fish/km. This change was associated with decreasing capture of young of the year (age-0) centrarchids (e.g., Redbreast Sunfish) and slow-water specialists (e.g., Golden Shiner) in this stratum. Furthermore, this observation was consistent across postremoval sampling seasons (Figure 5).

Patterns of cumulative relative biomass (MPUE, all species included) in the main-stem Penobscot River for all species of fish were similar between both sampling periods. We frequently found the highest average fish biomass in the Orono stratum, relative to other main-stem strata. Average MPUE in this stratum ranged from 15.5 ± 2.1 kg/km during preremoval sampling to 12.4 ± 1.8 kg/km during postremoval sampling. These similarities reflect the persistence of adult macrohabitat generalist species (e.g., Smallmouth Bass) and riverine species (e.g., White Sucker), which continue to dominate the biomass in the main-stem Penobscot River.

When we examined patterns of relative mass and abundance for selected species, we found patterns associated with increasing connectivity for migratory fishes and decreasing relative abundance of macrohabitat generalist species. For example, we observed a decrease in the relative abundance of Smallmouth Bass in the Orono stratum
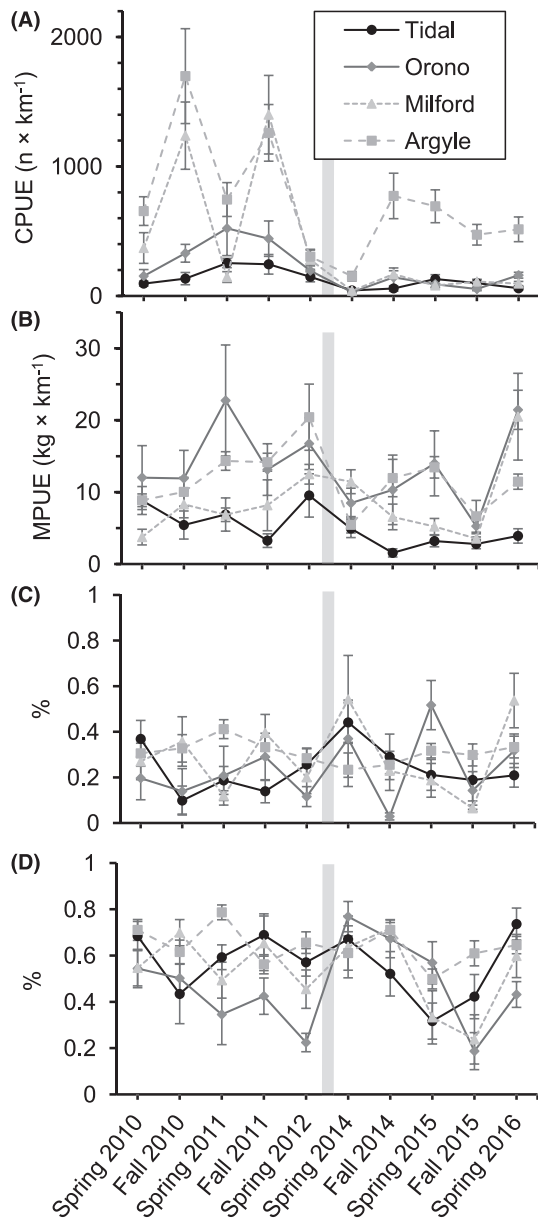
FIGURE 5. Average (**A**) CPUE and (**B**) MPUE observed in the main-stem strata of the Penobscot River, Maine, in each sampling season from 2010 to 2016. Also included is the average percent by biomass of (**C**) anadromous and riverine species combined and (**D**) native fish species in each sampling season. The vertical gray bar in each panel indicates the period in which dam removals and fish passage improvement at the current lowermost dam occurred.

from 110 ± 86 fish/km during preremoval surveys to 45 ± 9 fish/km during postremoval surveys (Figure 6). This decline in CPUE was not also observed in MPUE, which indicated that the decreases in abundance were largely due to low CPUE of age-0 Smallmouth Bass. We observed a similar trend for another common generalist species, Redbreast Sunfish, and we present Smallmouth Bass as a representative example. In contrast, both the

relative abundance and biomass of Alewife, a preremoval indicator species in the Tidal stratum, shifted upstream after dam removal (Figure 6). Only one Alewife was captured in the Orono stratum, immediately upstream from the Veazie Dam prior to its removal. In contrast, we found the highest average relative abundance of Alewives in this stratum during postremoval surveys (8 ± 3 fish/km). We also captured adult Alewives while sampling one of the Lower Tributary fixed transects in 2016 and age-0 Alewives in the Argyle stratum each year, indicating that successful reproduction occurred upstream from Milford, the new lowermost dam.

American Eel, the only catadromous species present in the Penobscot River watershed, exhibited relatively little change in longitudinal patterns of CPUE and MPUE between sampling periods (Figure 6). There was, however, a slight decrease in their mean relative abundance in the Tidal stratum from 22 ± 5 fish/km to 10 ± 2 fish/km. Overall, we observed a more even distribution of this species throughout the sampled transects during the postremoval sampling period.

Lacustrine species, of which Pumpkinseed was representative, exhibited large declines in relative abundance in the strata adjacent to removed dams. In the Orono stratum, for example, CPUE decreased from an average of 32 ± 12 fish/km to 0.1 ± 0.07 fish/km. This decline is associated with the loss of impoundment habitat upstream from the former Veazie Dam. Similar declines were observed in other slow-water fishes (e.g., Golden Shiner). We did not observe such declines in the Lower Tributary stratum, where lacustrine species were found in the highest biomass during both sampling periods.

Finally, the percent composition by mass of native and riverine fish was highly variable across sampling seasons, and we noted no consistent changes in the main-stem Penobscot River between sampling periods. When we examined percent biomass of riverine and anadromous fishes combined, we found they generally comprised less than 40% of the biomass in all main-stem strata (Figure 5C), with the exception of spring sampling seasons during the postremoval sampling period in which anadromous fish contributed substantially to the total biomass. This indicates that generalist species, primarily Smallmouth Bass, continued to dominate the fish biomass of the main-stem Penobscot River immediately following dam removal. Similarly, we did not observe a consistent change in biomass of native species after dam removal (Figure 5D) and attributed this to the continuing presence of Smallmouth Bass.

DISCUSSION

Our collective results suggest that dam removal has caused the most pronounced changes to fish assemblage
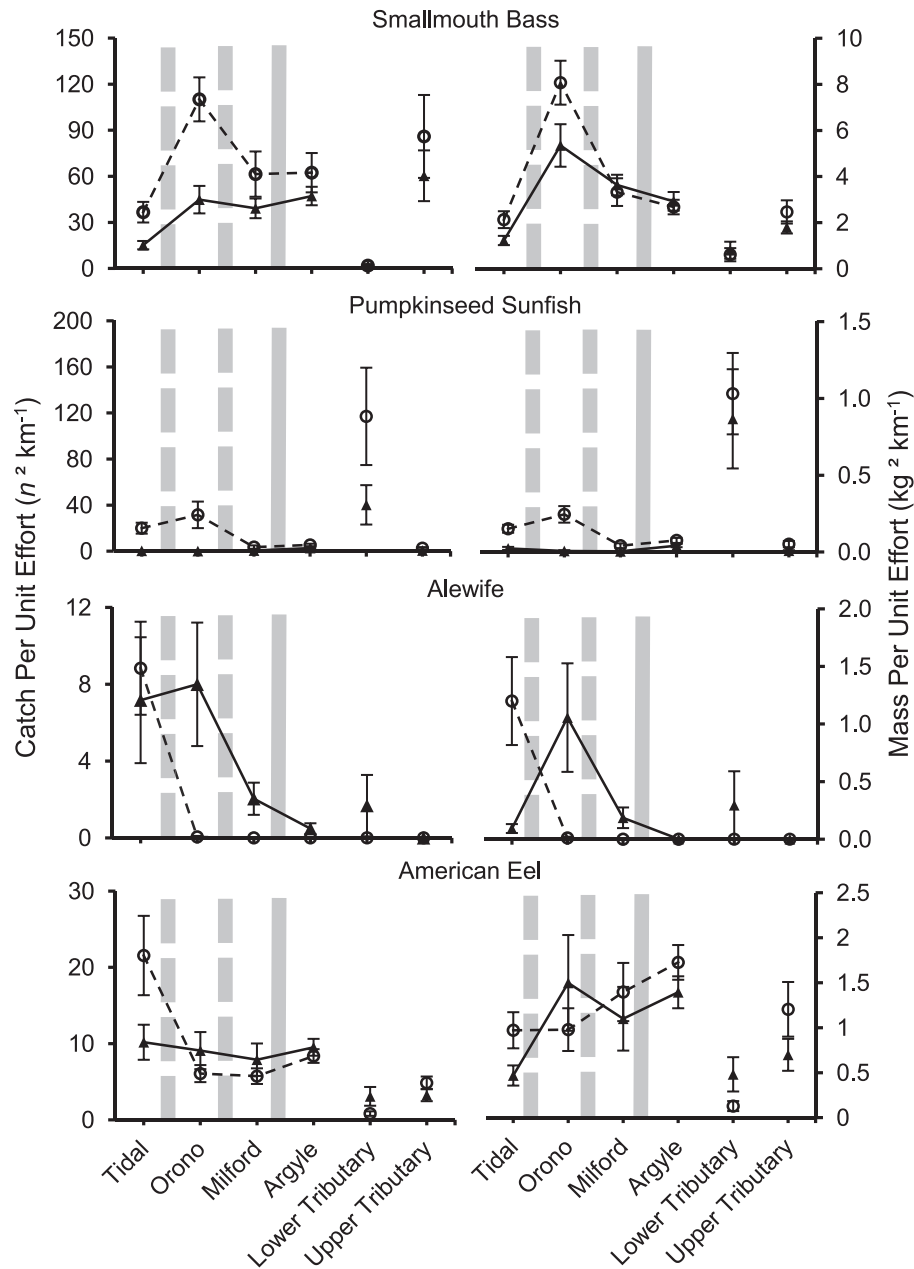
FIGURE 6. Mean CPUE (*n*/km ± 1SE) and MPUE (kg/km ± 1SE) for preremoval (open circle, dashed line) and postremoval (triangle, solid line) sampling periods for three indicator species (Smallmouth Bass, Pumpkinseed, and Alewife) and American Eel. Values are presented from downstream to upstream along the *x*-axis. Vertical gray bars indicate the relative location of removed dams (dashed) and existing dams (solid).

composition within strata in the immediate vicinity of removed dams and that the new lowermost dam (Milford) still causes fragmentation within the main-stem Penobscot River. Patterns of species occurrence and richness remained largely consistent between sampling periods, as indicated by observed richness values and the Sørensen similarity index. The only exception was the Milford stratum, in which more anadromous species were present during postremoval sampling compared with preremoval sampling.

Collective patterns of relative abundance and biomass, as measured by the Morisita–Horn similarity index, indicate that the assemblages were most changed in former impoundments and that strata in the lower river became more similar in composition during the postremoval period. This increasing similarity downstream was due to a shift in the longitudinal distribution of certain fish species. Anadromous species have shifted upstream, whereas the relative abundance of slow-water specialist species has

decreased substantially in former impoundments. Strata above the new lowermost dam (Milford) exhibited largely similar assemblage composition and will provide a valuable baseline for future studies to examine potential future changes including possible effects of the new fish passage structures.

We observed large differences in relative abundance between sampling periods despite relatively equal effort, and there are likely many causes for this. These differences were primarily driven by decreases in capture of age-0 fish, especially in the former impoundments (i.e., Milford and Orono strata) and below (i.e., Tidal stratum) during postremoval surveys compared with preremoval surveys. We also note that MPUE did not show a similarly noticeable reduction during postremoval sampling, which further suggests that changes to CPUE were driven by differences in age-0 fish abundance. It is possible that changing river conditions (i.e., impoundment to river in some strata) could have potentially affected fish detection; however, indices of relative abundance (CPUE) and biomass (MPUE) standardized by both time and transect length were highly correlated ($R^2 = 0.91$ and 0.81, respectively). This indicates that differences described here were primarily driven by changes in relative abundance and biomass rather than changes to capture efficiency associated with altered habitats.

Collectively, our results indicated that there is greater connectivity among the lowest three strata following dam removal and that Milford Dam still acts as a barrier to the movement of fish in the Penobscot River main stem. We observed a significant increase in diversity in the Milford stratum, which became more connected to areas downstream after dam removal and is bounded on the upstream end by the new lowermost dam. Other studies (e.g., Dodd et al. 2003; Stoller et al. 2016) have described similar peaks in fish species richness below dams resulting from restrictions in upstream movement. Conversely, we did not observe large shifts in assemblage structure between sampling periods in the strata above the Milford Dam. The acute effects of dam removal were localized to areas immediately adjacent to former dams in the Penobscot River, and future surveys will be required to determine whether increased fish passage has ramifications for the assemblages above Milford Dam.

We used both the Sørensen and the Morisita–Horn similarity indices because changes in connectivity and, in some cases, habitat in each stratum may result in differences in species composition (Sørensen index), proportional species abundance (Morisita–Horn index), or both aspects of the assemblage composition. These indices have also been used in previous studies examining the impact of connectivity on fish assemblages (e.g., Dodd et al. 2003; Hayes et al. 2008; Gardner et al. 2013; Stoller et al. 2016), and their use here facilitates comparison across

studies. For example, Hayes et al. (2008) found that when comparing fish assemblages in upstream and downstream reaches, 23 streams without dams in the Laurentian Great Lakes basin had average Sørensen and Morisita–Horn similarity scores of 0.69 and 0.75, respectively. We consider this to be a threshold level for similarity observed over a large spatial scale, and note that, with the exception of the Lower Tributary stratum, many of our estimates of similarity between strata not divided by dams are above those thresholds.

The NMDS ordination (Figure 4) corroborated results from the Morisita–Horn similarity indices by demonstrating increasing similarity between strata where connectivity was improved through dam removal. The two formerly impounded strata (Orono and Milford) displayed the largest ordinal shifts, which indicates a greater influence of diadromous fishes and a reduction in relative abundance of lacustrine fishes. These two adjacent strata ordinated closely to each other during both sampling periods. However, during preremoval surveys they grouped more closely with the Argyle and Upper Tributary strata, and during postremoval surveys they exhibited scores associated with diadromous fish ordination. These ordinal shifts along with the Morisita–Horn index suggest that the removal of the dams made these two strata more similar to areas downstream (e.g., Tidal stratum) and less similar to areas upstream (e.g., Argyle stratum). These results are consistent with other dam removal studies (e.g., Poulos et al. 2014; Hogg et al. 2015) that have shown increasing ordinal similarity in sites where connectivity has been restored. Despite changes evident at the assemblage level, we did not find consistent evidence of changes to the composition of assemblages by guilds (i.e., native and riverine species), which may be explained by the persistence of Smallmouth Bass, a nonnative generalist species. The lack of a consistent response by the riverine fish guild here and elsewhere (e.g., Catalano et al. 2007) may reflect the persistence of riverine fish within run-of-river impoundments that are subjected to seasonal flow differences.

The relative abundance and relative biomass data collected for this study reflect high annual assemblage variability, heterogeneous shoreline habitats, and variable sampling conditions. As such, it is important to note that there are limitations to the inferences one can draw from these data. Unfortunately, it was impractical to generate estimates of true abundance for each species in each sample. However, the magnitude of changes relative to average preremoval abundance and biomass for several species was greater than the variability observed in the data, suggesting the observed signals were a result of the PRRP rather than a result of annual, seasonal, or sampling variability. Similarly, Catalano et al. (2007) observed high variability in the index of biotic integrity (IBI) scores following dam removal, though the magnitude of changes in

former impoundments were well above the observed magnitude of annual variability.

Our survey indicates that anadromous fishes, notably Alewife, were able to access areas upstream from Milford Dam, although they were not observed in high relative abundance in those strata, and the largest changes were observed below this dam. We observed an increase in the number of age-0 river herring during the postremoval period, most noticeably in the Tidal stratum. We also captured both adult and juvenile river herring above Milford Dam in both the Argyle stratum and several lower tributaries during the postremoval surveys (Figure 6). Notably, in the final sampling season for this study (spring 2016) we captured several adult river herring in Sunkhaze Stream (Lower Tributary) where they had not been previously detected. It is important to note that 2 years before the first dam removal (2010), a program was initiated whereby several lakes within the watershed were annually stocked with adult river herring that were trapped and trucked from the Kennebec and Union rivers in Maine (M. Simpson, Maine Department of Marine Resources, personal communication). Similar efforts occurred prior to the dam removal on the Kennebec River in Maine (Pess et al. 2014). Such preemptive stocking confounds our ability to attribute new upstream occurrences of river herring solely to increased connectivity, but regardless, our sampling documented successful reproduction either from new colonizers or previously stocked spawners. It is difficult to assess the impact of these restoration actions on other anadromous species of interest found in the Penobscot River (i.e., Atlantic Salmon and American Shad) because they were not commonly encountered in our surveys and would likely be slower to respond due to them maturing at older ages. However, American Shad were not actively stocked before dam removal, and we did note evidence of successful recolonization of this species including the detection of adults throughout the main-stem study area and the capture of one age-0 individual during fall 2014 sampling surveys.

While alosine fishes exhibited the most pronounced changes, postremoval distributions of other migratory fishes also changed. We found evidence that upstream movements of juvenile American Eels may have been hindered by the former Veazie Dam, and their relative abundance decreased below this dam following its removal. Other studies have also observed higher abundances of small eels below dams (Goodwin and Angermeier 2003) and upstream movements of small eels after dam removal (Hitt et al. 2012). While American Eels were found above several dams during preremoval surveys, we note that the removal of barriers increases access to additional habitat without requiring the passage around large dams.

Based on the observed changes after their removals, the former dams on the Penobscot River seem to have influenced resident fish assemblage composition in several ways. First, localized absence of lacustrine fishes (e.g., Golden Shiner, Pumpkinseed, Banded Killifish) during postremoval surveys likely indicates that impoundments provided artificial habitat suitable for these fishes. Similarly, we rarely observed age-0 centrarchids (Redbreast Sunfish, Pumpkinseed, and Smallmouth Bass) during our fall surveys after dam removal in the former impoundments, which suggests that these habitats no longer provide suitable spawning habitat for these species. We also observed a decline in relative biomass of adult Smallmouth Bass in the Orono stratum (Figure 6), which may indicate that the former Veazie Dam impoundment served as local winter refugia habitat for adult fish, as was suggested by Kiraly et al. (2014a). The factors associated with these observed changes to resident fish assemblages are complex and likely associated with impoundments reverting to lotic habitats; however, we made no empirical measure of habitat change, and without such a measure, it is impossible to determine the specific mechanisms that drove the observed differences.

Several studies (e.g., Quinn and Kwak 2003; Kruk et al. 2016) have illustrated that the effects of river modification on fish assemblages are revealed over long time scales (i.e., >10–20 years), and initial observations may be specific to the period immediately following the dam removal. However, long-term studies associated with dam removals are rare. In this study, the most substantial fish assemblage changes immediately (<3 years) after dam removal occurred in former impoundments. While we found evidence that connectivity has been enhanced for migratory fishes throughout much of the Penobscot River watershed, these ramifications will likely be revealed over longer timescales (i.e., several generations of fish) than those described here. Our characterization of fish assemblages found in the strata above the new lowermost dam, while not discussed extensively here, will serve as a valuable baseline for future studies examining the changes associated with increasing passage for migratory fish.

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