

## ARTICLE

# Fish Assemblages in the Penobscot River: A Decade after Dam Removal

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## Abstract

The Penobscot River Restoration Project in Maine was a large river rehabilitation project that culminated in the removal of the two lowermost dams and improvements to fish passage on several remaining dams. Fish assemblages were surveyed for 3 years prior to rehabilitation, 3 years after rehabilitation, and 8 years after rehabilitation. Approximately 475 km of shoreline were sampled via boat electrofishing, yielding 133,394 individual fish of 41 species. The greatest shifts in assemblage structure occurred immediately after dam removal in formerly impounded sections, with an increased prevalence of riverine and migratory species. Long-term sampling documented changes within tributaries and tidally influenced river segments, where large schools of adult and young-of-the-year alosines increased in abundance. Upstream of the lowermost dam, the river remains dominated by lacustrine species, while adult anadromous fishes continue to be most abundant immediately downstream of the lowermost dam. Our results provide increased evidence that dam removals result in altered fish assemblages, which are now dominated by riverine and anadromous

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**species in previously impounded habitats. Alosines in the Penobscot River have exhibited the greatest long-term response to river restoration efforts.**

Rivers have long been an integral component for the success of civilizations, as they provide a source of water, sustenance, transportation, and power generation (Roy et al. 2018). Human reliance on river systems remains evident in the landscape today through damming for water supply, flood control, power generation, and recreational purposes. In the United States, there are more than 91,000 dams, 7% of which are used for hydroelectric power generation (National Inventory of Dams 2021). In Maine, there are 581 active dams, with 39% used for hydroelectric power generation. The average age of dams in Maine is 104 years—twice the national average (National Inventory of Dams 2021). As these structures continue to age, opportunities to remove these dams and reconnect watersheds may arise, potentially representing a tradeoff between societal benefits and environmental costs (Song et al. 2020).

Dams and the impoundments they create fundamentally alter biophysical processes within rivers by disrupting flow, temperature, sediment transport, and overall connectivity (Poff et al. 1997; Petts et al. 2006). Dams often reduce the habitat quality for native riverine fishes (Santucci et al. 2005; García et al. 2011) and favor the establishment of nonnative, slow-water generalist fishes (Han et al. 2008). In coastal rivers, dams disrupt migration for diadromous (sea-run) fishes. These fish require connectivity between marine and freshwater ecosystems to complete their complex life cycles. Many of these species have experienced substantial population declines due to dams (and other threats) and now persist at greatly diminished levels (Greene et al. 2009; Limburg and Waldman 2009; Waldman and Quinn 2022). Dams and other barriers may directly influence survival for downstream migrants (Mensing et al. 2021; Molina-Moctezuma et al. 2021), delay the movement of upstream migrants (Castro-Santos and Letcher 2010; Babin et al. 2021), and restrict access to historical spawning habitat (Opperman et al. 2011; Zydlewski et al. 2021). In addition, they may provide habitat for introduced piscivorous species (e.g., Kiraly et al. 2014a), promoting predation on riverine and diadromous species that pass through impounded areas.

Within Maine, diadromous fishes have suffered substantial population declines (Saunders et al. 2006) due to the loss of accessible habitat (Trinko-Lake et al. 2012) in conjunction with overfishing, pollution, climate change, and competition with introduced species. In an effort to rehabilitate these fish populations, the Penobscot River Restoration Project was undertaken, representing a multi-million-dollar collaborative effort. The project focused on

diadromous fisheries restoration through dam removal while mitigating the loss of hydropower production (Opperman et al. 2011). Beginning in 2012, the Great Works Dam was removed, followed by the removal of the Veazie Dam in 2013, opening roughly 15 km of main-stem river access (Figure 1). In addition to dam removals, a fish lift was incorporated into the Milford Dam (the lowermost remaining dam) to increase upstream passage for migratory fishes. In 2016, the Howland Bypass, a nature-like fishway, was constructed around the Howland Dam, which allowed for passage to the Piscataquis River (a major tributary to the Penobscot River) without changing the impoundment.

Returning sea-run fish were counted at passage facilities from 1978 up until 2013 at the lowermost dam (Veazie Dam) on the Penobscot River and have since been recorded at the Milford Dam fish lift, beginning in 2014, following restoration efforts. Eight of the 12 diadromous fishes that are native to the Penobscot River have used the new fish lift at the Milford Dam to pass upriver since the lift's construction. Of these diadromous fishes, alosines have responded the most positively after dam removal and upgraded fish passage (together with initial translocation programs). Annual counts of river herring (*Alewife Alosa pseudoharengus* and Blueback Herring *Alosa aestivalis*) prior to fish passage upgrades averaged 556 fish (range = 0–12,708) returning annually from 1978 to 2012. Counts for river herring exceeded 180,000 the first year after dam removal (2014), and within 4 years (2018) the count reached 2.3 million fish (Maine DMR 2021).

In addition to river herring, counts of American Shad *Alosa sapidissima* and Sea Lamprey *Petromyzon marinus* at the Milford Dam fish lift have increased since the dam removals and upgraded fish passage. Prior to restoration efforts, Sea Lamprey peaked at 2,125 individuals, while American Shad peaked at only 7 individuals. Counts in the most recent year (2021) reached 6,647 Sea Lamprey and 11,363 American Shad. While the abundances of several anadromous species have generally increased, Atlantic Salmon *Salmo salar* continue to persist at low abundance (<2,000 individuals annually) since the restoration efforts took place (Maine DMR 2021). Although the counts for migratory fish may reflect changes in relative abundance over time, the relative abundances of resident species cannot be inferred from these counts.

To assess how fish assemblages as a whole have responded to restoration efforts, a biomonitoring approach was taken using both pre-dam-removal (2010–2012) and post-dam-removal (2014–2016) data (Kiraly

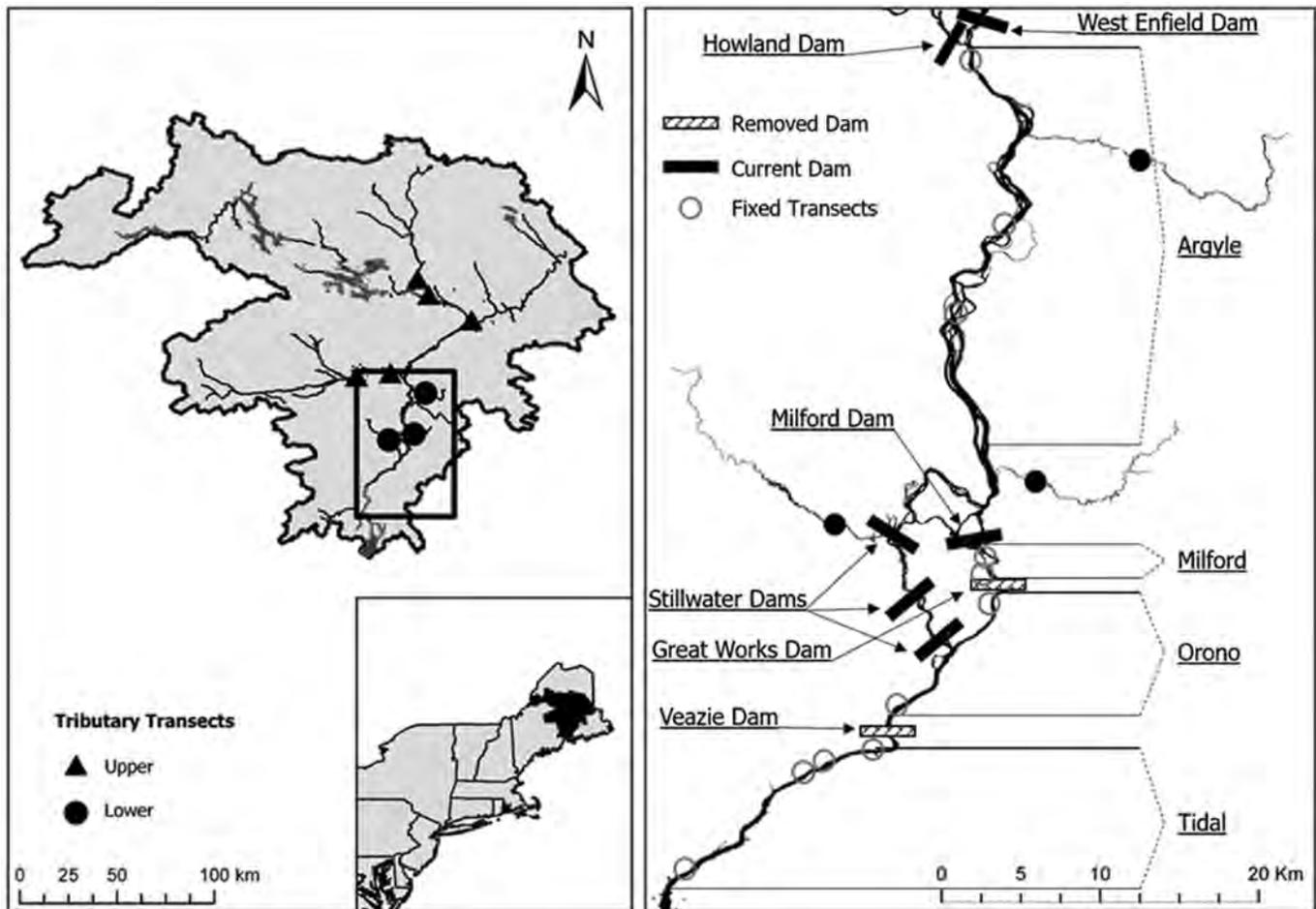


FIGURE 1. The Penobscot River watershed, with both Upper and Lower Tributary fixed sampling transect locations (left panel), and fixed main-stem Penobscot River sampling locations along with stratified river sections (right panel). Current and former dam locations within the study area are marked with solid black rectangles (current dams) or hatched rectangles (removed dams).

et al. 2014a; Watson et al. 2018). Pre-dam-removal fish assemblage data indicated that dams and their impoundments presented distinct fish assemblages, with most migratory fishes being restricted downstream of the Veazie Dam (Király et al. 2014a). Immediately after dam removal, shifts in fish assemblages occurred in newly free-flowing reaches, with slow-water generalist fishes declining in abundance while anadromous fishes began to occupy reconnected reaches (Watson et al. 2018).

The long-term effects from large-scale dam removal are poorly studied (Griffith and McManus 2020), with only 5% of 139 dam removal studies in the United States documenting responses beyond 5 years post-removal (Bellmore et al. 2017). Although major biophysical responses can be observed immediately after dam removal, significant changes may be revealed over a longer time frame (>5 years; Quinn and Kwak 2003; Kruk et al. 2016). For this study, we specifically focused on comparing surveys completed both before and immediately after dam removal

with surveys completed later (>5 years after removal; hereafter, “extended period surveys”) to describe the long-term implications of this river restoration approach for resident and diadromous fish assemblages.

## METHODS

### Study area

The Penobscot River watershed is the largest watershed in Maine, with over 8,800 km of riverine habitat within a 22,455-km<sup>2</sup> watershed (Opperman et al. 2011). This river system is fragmented by over 125 dams, with six major dams present on the main-stem river within 100 km of its confluence with the Gulf of Maine (Maine DIFW 2020). Prior to restoration efforts, fish passage was focused on Atlantic Salmon, whereas appropriate passage measures for alosines were not available (Grote et al. 2014). As a result, most diadromous fishes were restricted to the lower

50 km of riverine habitat. After dam removals, a total of 15 km of riverine habitat was reconnected, and upgraded fish passage allowed for an additional 465 km of potential upstream access. While connectivity was increased in a short period of time, the degree to which both migratory and resident fish would respond over the long term was unknown. Biomonitoring of assemblages over the long term allows the relative success of restoration projects to be revealed, providing critical information for those looking to increase connectivity within watersheds.

### Sampling design

**Fixed-site design.**—Sampling designs were established prior to dam removals (Király et al. 2014a, 2014b) but are reviewed here briefly to provide context for this study. We employed both fixed and random transects. Fixed sites were selected opportunistically prior to the beginning of this study and were used as a reference for areas of particular interest. Sampling consisted of 11 shoreline transects on the main-stem Penobscot River along with 8 sites within major tributaries (Figure 1). Fixed transects were 1 km long and located approximately 500 m above and below current or former dams. Several sites further from removed dams were also selected to serve as reference sites. Tributary sites were identified as “lower” if they were above only one dam (Milford Dam) after dam removals and as “upper” if they were above more than one dam (Figure 2).

**Stratified random design.**—To account for habitat heterogeneity within the main-stem river, a stratified random sampling design was implemented alongside the fixed-site design. The lower Penobscot River was split into four major strata (Tidal, Orono, Milford, and Argyle) based on the presence of current and/or former dams (Figure 1). The lowermost stratum (Tidal) consisted of 15 km of tidally influenced freshwater beginning at the salt wedge up to the head of the tide. The Orono stratum was 10 km long, beginning at the downstream portion of the former Great Works Dam and ending at the upstream portion of the former Veazie Dam. The Milford stratum was the shortest, spanning 3 km from the downstream portion of the Milford Dam to the upstream portion of the former Great Works Dam. The Argyle stratum was the largest reach, covering 32 km of main-stem river from the Howland Dam down to the Milford Dam.

Within each stratum, 500-m shoreline transects were delineated in areas that were accessible by boat. Several (2–6) transects were selected randomly and sampled within each stratum during each sampling season. Sampling was conducted during late spring and early fall to account for both adult and young-of-the-year (age-0) migratory fish. We followed the guidance of Király et al. (2014b) to sample a minimum of 5 km of shoreline during each sampling season; this was expected to document 90% of the species

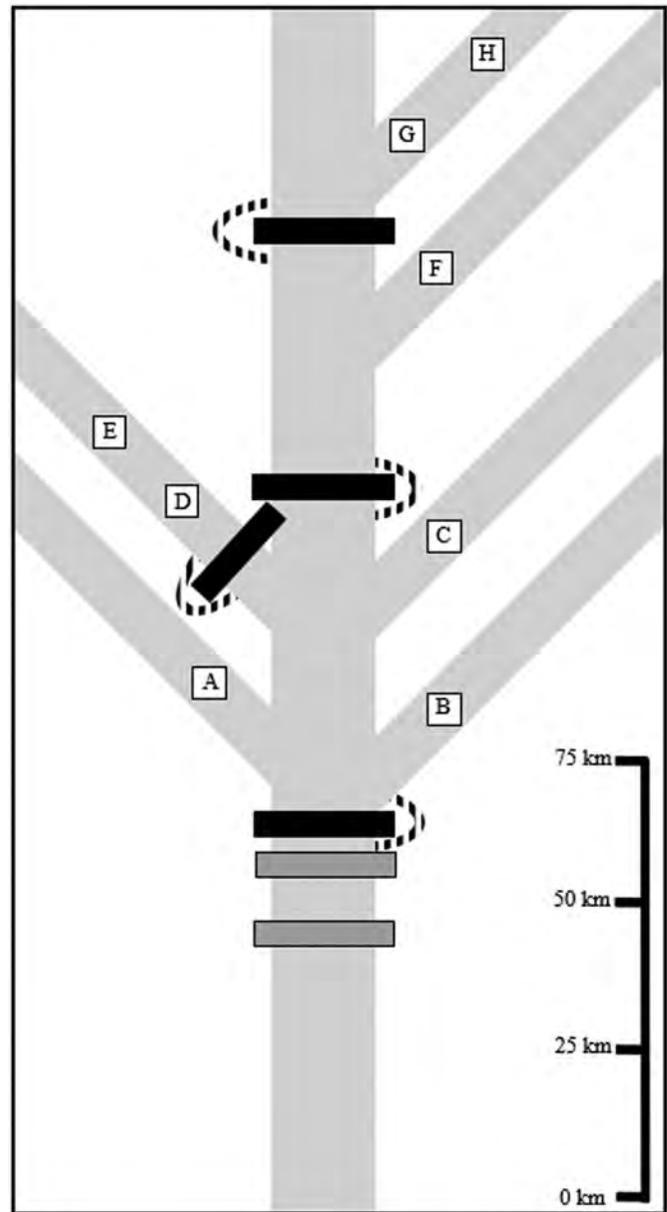


FIGURE 2. Simplified graphic of the lower Penobscot River watershed sampling area. Removed dams (Veazie, river kilometer [rkm] 48; Great Works, rkm 60) are represented as gray bars, current dams (Milford, rkm 63; Howland, rkm 100; West Enfield, rkm 101; Weldon, rkm 149) are represented as black bars, and structures allowing fish passage around dams are shown as dashed lines (fish lift, rkm 63; vertical slot, rkm 101; nature-like bypass, rkm 100; pool/weir, rkm 149). Lower Tributary sites (A = Pushaw Stream; B = Sunkhaze Stream; C = Passadumkeag River) and Upper Tributary sites (D and E = Piscataquis River; F = Mattawamkeag River; G and H = East Branch of the Penobscot River) are depicted as white squares with corresponding letters.

present. Since no significant differences between the fixed-site and random sampling designs were found when assessing species richness during pre-removal (2010–2012) surveys, data from both sampling designs have been and

continue to be combined in analyses to achieve a greater sample size (Kiraly et al. 2014b).

### Data collection

The same sampling gear used by Kiraly et al. (2014a) and Watson et al. (2018) was used for the extended sampling period (2019–2021). A 5.5-m-long Lowe Roughneck aluminum boat (Lowe, Lebanon, Missouri) outfitted with a Smith-Root 5.0 GPP (Generator-Powered Pulsator) electrofishing system (Smith-Root, Vancouver, Washington) with two anode dropper arrays was implemented for main-stem sampling. Two netters were positioned at the bow of the boat while an operator positioned the boat perpendicular to the shoreline, navigating in a downstream direction. For tributary sites (Figure 2) or when main-stem flows prevented navigation with the larger aluminum boat, we used a 4.3-m Sea Eagle inflatable raft (Sea Eagle Boats, Port Jefferson, New York) equipped with a Smith-Root 2.5 GPP electrode fishing system with a single-boom anode dropper array, and one netter was positioned at the bow.

Sampling was first conducted beginning in spring 2010 and was repeated again for two additional spring seasons and two fall seasons, ending in 2012 (Kiraly et al. 2014a). After dam removals in 2012 and 2013, sampling was initiated in the spring of 2014 and again repeated for an additional two spring seasons and two fall seasons (Watson et al. 2018). For the extended monitoring, sampling methods were repeated beginning in the spring of 2019 and continued into the spring of 2021 (Figure 3). Each spring, sampling was initiated in the Tidal reach, working

upstream to follow migrating adult anadromous fishes. Sampling was then repeated in the fall, beginning higher in the watershed and moving downstream.

For each transect, start and stop coordinates were recorded using a GPS unit. All fish captured were placed in an onboard live well, and after survey completion the fish were identified to species. We also recorded the TL (mm) and mass (g) of each fish. Fish were then released to the nearest point of capture. Due to permitting restrictions, adult Atlantic Salmon, Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus*, and Shortnose Sturgeon *Acipenser brevirostrum* (listed as endangered under the U.S. Endangered Species Act) were observed but not netted. Encounters were infrequent, and sampling was terminated following the observation of these species to prevent further contact. Size and mass were visually estimated using the methods outlined by Kiraly et al. (2014a). Data analyses for this study were conducted in R version 4.0.3 (RStudio Team 2021).

### Catch per unit effort and relative occurrence

For each species, the CPUE (number of fish per meter of shoreline) was assessed to determine potential changes in relative abundance for all fishes encountered throughout the study. Catch data were standardized by distance of shoreline (m) sampled rather than by time (s) due to differences in flow throughout the river and between sampling periods. Shoreline distance was determined using start and stop waypoints that were uploaded to ArcGIS Pro (ESRI, Redlands, California, USA) to measure the total distance sampled. In addition, we calculated the

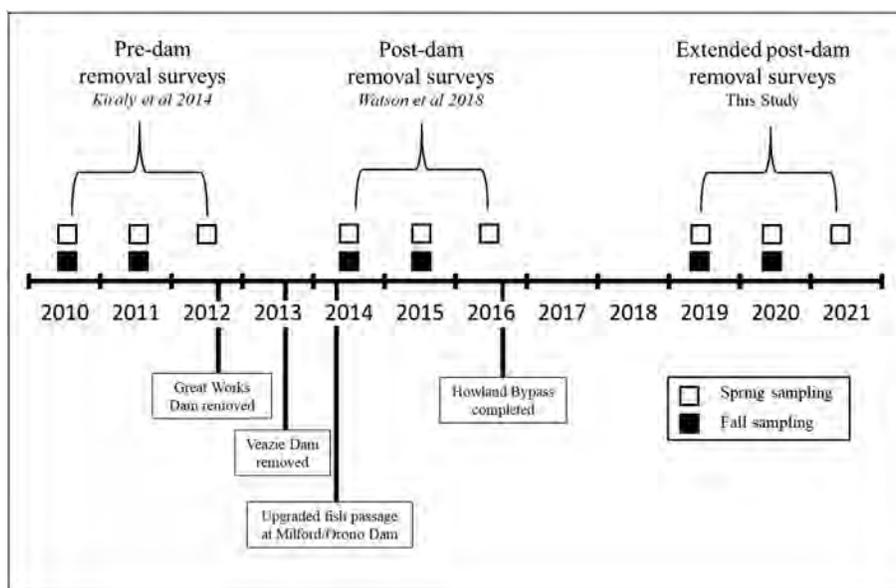


FIGURE 3. Timeline of fish assemblage assessment surveys (top), with associated large-scale river modifications that were implemented as part of the Penobscot River Restoration Project (listed below the timeline). Solid black squares indicate fall surveys, while open squares indicate spring surveys.

relative occurrence, expressed as a percentage that each species was present within surveys for the respective sampling periods. This allowed us to assess potential changes in species presence throughout our study area.

### Diversity: richness and evenness

Species richness was compared between sampling periods for each stratum. Due to differences in effort (total transects sampled) among strata and across sampling periods, species richness among randomly selected transects was compared by constructing species accumulation curves using the BiodiversityR package (Kindt and Coe 2005). This method allows for comparison of species richness at equivalent levels of effort (i.e., number of sites sampled) between each period of sampling. To assess species evenness, we used the vegan package (Oksanen et al. 2020) to calculate the Simpson diversity index (Simpson 1949) for each sampling event and we compared median scores across sampling years for each river stratum. Using this index, we accounted for both presence and abundance of a species within a sample while measuring the probability that two individuals randomly selected from a sample will belong to the same species. In addition, the index accounts for species dominance by giving more weight to common species. Values range from 0 to 1, with 0 representing no diversity and 1 representing the greatest sample diversity.

### Similarity/Hierarchical clustering

To assess the similarity of species composition between sampling periods for each river stratum, we calculated the Morisita–Horn similarity index, as it accounts for both presence and abundance between two or more sampling events (Jost et al. 2011). Due to differences in capture efficiency between operators, we chose to use proportional abundance data, with the abundance of each species expressed as its percentage contribution to the total catch within a given sampling period. These data were then analyzed with the Divo package (Rempala and Seweryn 2013) to obtain the percent similarity of each stratum between sampling periods with bootstrapped 95% confidence intervals. We also assessed similarity among all strata across each sampling period by using hierarchical clustering analysis within the Divo package. Clustering was performed using 50 iterations and then examined to identify clusters based on the similarity of assemblage composition.

### Nonmetric multidimensional scaling

To assess overall shifts in fish assemblages between sampling periods, we analyzed proportional abundance data using nonmetric multidimensional scaling (NMDS; Faith et al. 1987) with the Bray–Curtis dissimilarity index in the vegan package (Oksanen et al. 2020). Prior to analysis, rare species (relative occurrence <5% within a sampling period) were removed since NMDS can be overly

sensitive to rare species (Poos and Jackson 2012). A single ordination was conducted, providing both species and site scores and accounting for all sampling events in a two-dimensional solution. Site scores were then organized based on sampling season (fall/spring) and plotted separately from species scores to show seasonal differences in composition. Rather than plotting all sampling events, the centroid for each stratum within a given period was calculated and plotted for greater ease of interpretation. Centroids were then connected with a line in the order in which they occurred to clearly show shifts in species composition over time (sensu Hogg et al. 2015).

## RESULTS

### Sampling Effort and Catch

Total shoreline sampled (km) among river strata was largely consistent between sampling periods (Table 1). Overall, 133,394 individual fish representing 41 species were captured from 2010 to 2021 during boat electrofishing surveys (Table 2). Pre-dam-removal surveys (2010–2012) accounted for 69,393 individual fish from 38 species, immediate post-dam-removal surveys (2014–2016) yielded 37,942 individuals from 35 species, and extended period surveys (2019–2021) yielded 26,059 individual fish representing 34 species. Median CPUE estimates for fish less than 150 mm (Figure 4) were notably higher during the pre-dam-removal surveys across all main-stem river strata and steadily declined in later years. The median CPUE estimate for fish greater than 150 mm was initially highest within the impounded Argyle stratum (61 fish/km), but after rehabilitation efforts the median CPUE was highest in the free-flowing Milford stratum (119 fish/km; Figure 5). The CPUE for larger fish (>150 mm) captured in the Milford stratum during the most recent year of sampling primarily consisted of adult anadromous alosines (Alewife, Blueback Herring, and American Shad), while larger fish captured in the Argyle stratum

TABLE 1. Total number of fish species (*n*) sampled and total shoreline (km) sampled per Penobscot River stratum grouped by sampling period (pre-dam removal [Pre]: 2010–2012; post-dam removal [Post]: 2014–2016; extended [Ext]: 2019–2021).

Stratum	Total species			Shoreline sampled (km)		
	Pre	Post	Ext	Pre	Post	Ext
Tidal	32	31	27	42.0	42.3	45.4
Orono	21	21	23	23.3	24.1	26.5
Milford	16	22	22	13.3	15.9	15.6
Argyle	24	25	21	34.4	41.8	49.3
Lower Tributary	20	19	18	14.1	13.7	12.5
Upper Tributary	24	20	22	17.1	20.9	22.8

TABLE 2. Species encountered during electrofishing surveys, with associated common and scientific names, species abbreviation code, life history (R = resident; C = catadromous; A = anadromous), and origin (I = introduced; N = native to the watershed). Species relative occurrence is grouped by sampling period and presented as a percentage of occurrence for all sampling events (*n*) within each period; “S” denotes spring survey percent occurrences, while “F” denotes results from fall surveys.

Species	Abbreviation	Life history	Origin	Relative occurrence (%)					
				2010–2012		2014–2016		2019–2021	
				All events ( <i>n</i> = 202)	(S, F)	All events ( <i>n</i> = 226)	(S, F)	All events ( <i>n</i> = 247)	(S, F)
Alewife <i>Alosa pseudoharengus</i>	ALE	A	N	14.9	(16, 13)	24.3	(20, 32)	42.9	(40, 44)
Sea Lamprey <i>Petromyzon marinus</i>	LAM	A	N	44.1	(44, 44)	49.6	(45, 57)	35.6	(32, 38)
Blueback Herring <i>Alosa aestivalis</i>	HER	A	N	11.4	(16, 3)	15.5	(15, 16)	30.4	(37, 14)
American Shad <i>Alosa sapidissima</i>	SHD	A	N	2.5	(4, 0)	4.0	(6, 1)	14.2	(17, 7)
Atlantic Salmon <i>Salmo salar</i>	ATS	A	N	9.4	(11, 7)	10.2	(15, 2)	11.7	(16, 2)
Striped Bass <i>Morone saxatilis</i>	STB	A	N	0.5	(1, 0)	2.7	(4, 0)	1.6	(2, 0)
Atlantic Tomcod <i>Microgadus tomcod</i>	ATC	A	N	0.0	(0, 0)	1.3	(0, 3)	0.8	(0, 2)
Sturgeon spp. (Acipenseridae)	SGN	A	N	1.0	(1, 1)	0.0	(0, 0)	0.4	(0, 1)
White Perch <i>Morone americana</i>	WP	A/R	N	8.9	(8, 10)	8.4	(5, 14)	4.5	(4, 7)
Brook Trout <i>Salvelinus fontinalis</i>	BKT	A/R	N	1.0	(2, 0)	2.2	(2, 2)	1.6	(2, 0)
American Eel <i>Anguilla rostrata</i>	EEL	C	N	85.1	(87, 82)	75.2	(80, 68)	84.6	(85, 82)
White Sucker <i>Catostomus commersonii</i>	WS	R	N	73.8	(73, 75)	69.5	(74, 63)	67.6	(71, 61)
Redbreast Sunfish <i>Lepomis auritus</i>	RBS	R	N	92.1	(91, 94)	68.6	(71, 65)	64.8	(62, 72)
Fallfish <i>Semotilus corporalis</i>	FF	R	N	88.1	(85, 94)	84.5	(83, 86)	63.6	(66, 59)
Common Shiner <i>Luxilus cornutus</i>	CSH	R	N	68.8	(65, 77)	52.2	(52, 52)	40.1	(42, 36)
Brown Bullhead <i>Ameiurus nebulosus</i>	BBH	R	N	44.6	(49, 36)	33.6	(37, 28)	28.3	(28, 29)
Golden Shiner <i>Notemigonus crysoleucas</i>	GSH	R	N	52.0	(56, 44)	23.0	(28, 15)	21.9	(25, 17)
Pumpkinseed <i>Lepomis gibbosus</i>	PS	R	N	67.8	(65, 74)	29.6	(25, 38)	21.5	(17, 30)
Banded Killifish <i>Fundulus diaphanus</i>	BKF	R	N	27.2	(23, 35)	6.6	(2, 14)	10.1	(11, 8)
Burbot <i>Lota lota</i>	CSK	R	N	22.8	(23, 23)	20.8	(17, 26)	8.5	(7, 11)

TABLE 2. Continued.

Species	Abbreviation	Life history	Origin	Relative occurrence (%)					
				2010–2012		2014–2016		2019–2021	
				All events ( <i>n</i> = 202)	(S, F)	All events ( <i>n</i> = 226)	(S, F)	All events ( <i>n</i> = 247)	(S, F)
Creek Chub <i>Semotilus atromaculatus</i>	CRC	R	N	8.9	(12, 3)	11.1	(14, 7)	6.5	(5, 8)
Longnose Sucker <i>Catostomus catostomus</i>	LNS	R	N	1.5	(2, 1)	0.9	(1, 0)	1.2	(2, 0)
Northern Redbelly Dace <i>Chrosomus eos</i>	RBD	R	N	1.5	(2, 0)	1.8	(3, 0)	0.8	(1, 0)
Finescale Dace <i>Chrosomus neogaeus</i>	FSD	R	N	0.5	(1, 0)	3.5	(6, 0)	0.0	(0, 0)
Slimy Sculpin <i>Cottus cognatus</i>	SSC	R	N	0.5	(1, 0)	1.8	(1, 2)	0.0	(0, 0)
Blacknose Shiner <i>Notropis heterolepis</i>	BNS	R	N	1.5	(2, 0)	0.0	(0, 0)	0.0	(0, 0)
Threespine Stickleback <i>Gasterosteus aculeatus</i>	TSS	R	N	2.5	(3, 1)	0.4	(1, 0)	0.0	(0, 0)
Blacknose Dace <i>Rhinichthys atratulus</i>	BND	R	N	3.0	(3, 3)	2.7	(4, 0)	0.0	(0, 0)
Mummichog <i>Fundulus heteroclitus</i>	MUM	R	N	3.0	(3, 3)	0.9	(0, 2)	0.0	(0, 0)
Smallmouth Bass <i>Micropterus dolomieu</i>	SMB	R	I	95.5	(95, 96)	93.4	(96, 90)	94.7	(95, 93)
Yellow Perch <i>Perca flavescens</i>	YP	R	I	48.5	(48, 49)	40.3	(39, 42)	32.8	(36, 25)
Chain Pickerel <i>Esox niger</i>	CHP	R	I	60.9	(64, 55)	41.2	(40, 43)	32.0	(29, 38)
Largemouth Bass <i>Micropterus salmoides</i>	LMB	R	I	9.4	(7, 15)	20.8	(10, 38)	13.0	(5, 29)
White Catfish <i>Ameiurus catus</i>	WCF	R	I	0.0	(0, 0)	0.0	(0, 0)	9.3	(8, 10)
Eastern Silvery Minnow <i>Hybognathus regius</i>	ESM	R	I	6.4	(5, 9)	2.7	(1, 5)	3.2	(4, 2)
Central Mudminnow <i>Umbra limi</i>	CMM	R	I	0.5	(1, 0)	2.2	(2, 2)	2.4	(2, 2)
Northern Pike <i>Esox lucius</i>	NP	R	I	0.0	(0, 0)	0.0	(0, 0)	1.2	(1, 2)

TABLE 2. Continued.

Species	Abbreviation	Life history	Origin	Relative occurrence (%)					
				2010–2012		2014–2016		2019–2021	
				All events ( <i>n</i> = 202)	(S, F)	All events ( <i>n</i> = 226)	(S, F)	All events ( <i>n</i> = 247)	(S, F)
Fathead Minnow <i>Pimephales promelas</i>	FHM	R	I	1.5	(2, 0)	3.1	(4, 1)	0.4	(1, 0)
Ninespine Stickleback <i>Pungitius pungitius</i>	NSS	R	I	2.5	(3, 2)	0.0	(0, 0)	0.4	(1, 0)
Black Crappie <i>Pomoxis nigromaculatus</i>	CRA	R	I	5.0	(7, 1)	0.4	(0, 1)	0.4	(0, 1)
Spottail Shiner <i>Notropis hudsonius</i>	STS	R	I	1.5	(1, 3)	0.0	(0, 0)	0.0	(0, 0)

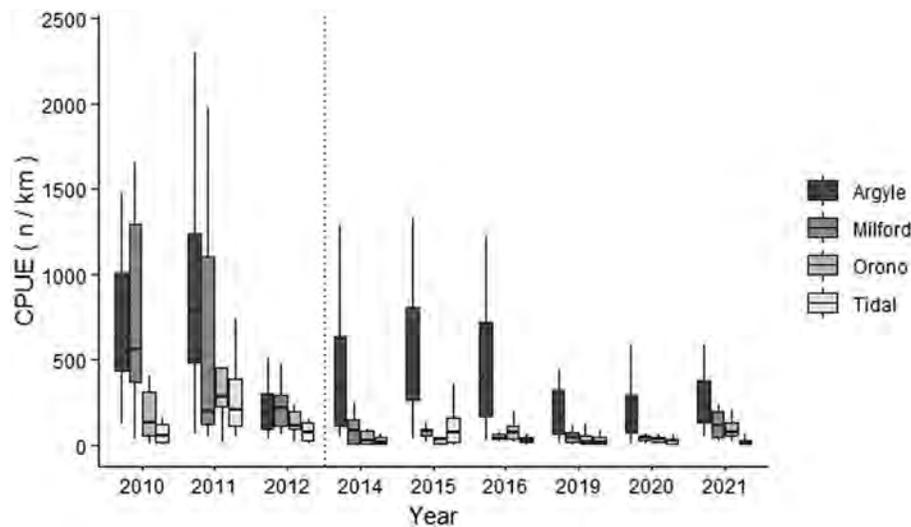


FIGURE 4. Median CPUE estimates (number of fish/km; horizontal black bars within boxes) for 150-mm and smaller fish in each main-stem Penobscot River stratum (Argyle, Milford, Orono, and Tidal). Boxes indicate the upper and lower quartile range, while whiskers indicate minimum and maximum values. The vertical dotted line indicates the period in which dam removals occurred.

consisted of resident species (Smallmouth Bass, Chain Pickerel, and White Sucker).

### Occurrence and Species Richness

During the extended sampling effort, alosines experienced the most notable change in their relative occurrence, with an increase of greater than 10% when compared to immediate post-dam-removal surveys. Alewife and Blueback Herring occurrence increased by 54% and 46%, respectively, within the Lower Tributary stratum. American Shad occurrence increased the most within the Orono (+23%) and Milford (+26%) strata, but this species still experienced

low occurrence (<10%) in the Argyle stratum, with no captures in either Upper Tributary or Lower Tributary sites. Atlantic Salmon were infrequently observed and exhibited little to no change in their relative occurrence throughout the study area. American Eel were detected frequently (>75% occurrence) within the study area throughout all sampling periods (Appendix Table A.1).

Species richness among main-stem strata and tributary sites was similar between the post-dam-removal and extended period surveys (Figure 6). We detected no significant difference in species richness during the extended sampling period in comparison with the post-dam-removal

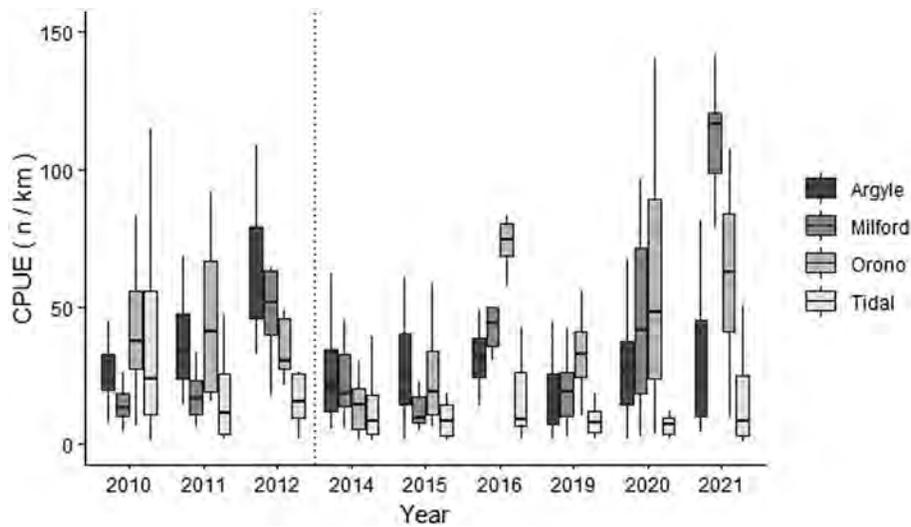


FIGURE 5. Median CPUE estimates (number of fish/km; horizontal black bars within boxes) for 150-mm and larger fish in each main-stem Penobscot River stratum (Argyle, Milford, Orono, and Tidal). Boxes indicate the upper and lower quartile range, while whiskers indicate minimum and maximum values. The vertical dotted line indicates the period in which dam removals occurred.

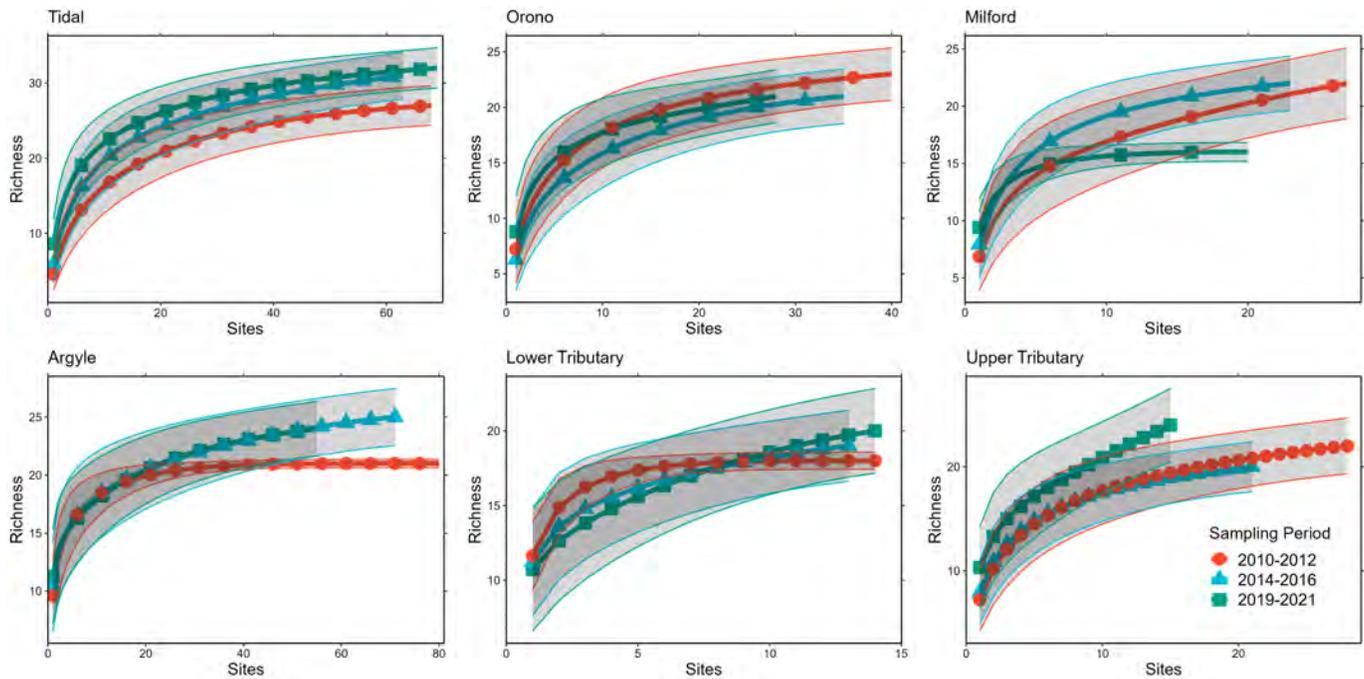


FIGURE 6. Species accumulation curves for all Penobscot River strata grouped by sampling period (pre-dam removal: 2010–2012; post-dam removal: 2014–2016; extended sampling: 2019–2021). Shaded areas represent 95% confidence intervals around mean richness (number of species) estimates.

surveys. Five species (Blacknose Dace, Fathead Minnow, Finescale Dace, Mummichog, and Threespine Stickleback) occurred in both pre- and post-dam-removal surveys within the Tidal reach but were not detected during the extended period surveys. It is important to note that these species were relatively rare (<5% occurrence) in post-dam-removal surveys. Two recently introduced species, White Catfish and Northern Pike, were detected during the

extended period but had not been detected in previous sampling periods. White Catfish were detected in the Orono, Tidal, and Milford strata during extended surveys, while Northern Pike were only detected in Pushaw Stream.

Anadromous species, including American Shad, Alewife, Blueback Herring, Sea Lamprey, and Atlantic Salmon, were all detected above the Milford Dam, thus demonstrating successful passage, although we cannot infer passage

efficiencies from this study. These species were observed in relatively low abundance within the 32 km of riverine habitat above the dam, whereas most of these fish were encountered in greatest abundance immediately below the Milford Dam. Of these species, Alewife and Blueback Herring had not been previously detected in the Upper Tributary stratum, but they were detected there during the extended period surveys. These detections included both adult and age-0 river herring in the Piscataquis and Mattawamkeag rivers, with no detections occurring in the East Branch of the Penobscot River (see Figure 2 for relative locations). During the extended sampling period, we detected age-0 Alewife, Blueback Herring, and American Shad above the Milford Dam in low relative abundance. The relative abundance of age-0 alosines was greatest in the lowermost strata (Orono and Tidal), where schools ( $n > 100$ ) of outmigrating fish were encountered.

### Diversity

The Simpson index indicated similar temporal patterns for reconnected main-stem river strata in the most recent years of sampling. After restoration efforts, diversity in previously impounded reaches declined, as slow-water generalist species (Pumpkinseed, Redbreast Sunfish, and Chain Pickerel) were encountered less frequently. Diversity rebounded in recent years as slow-water generalist species were replaced by riverine and anadromous species (Figure 7). The Lower Tributary stratum exhibited the highest median Simpson index (0.85) in our most recent year of sampling (2021; Figure 7). Prior to dam removal, Lower Tributary samples were dominated by lacustrine species without the presence of anadromous species. Aside from Northern Pike, much of the resident assemblage remained similar, with a strong presence of slow-water generalist species. The addition of Alewife and Blueback Herring further contributed to both the increased diversity and evenness within the samples. Similarly, the Milford stratum exhibited the greatest median Simpson index (0.79) during the most recent sampling years as result of several introduced resident species coupled with an increased relative abundance of anadromous species.

### Similarity and Hierarchical Clustering

The Morisita–Horn similarity index and NMDS ordination indicated that fish assemblages among main-stem river strata remained largely unchanged from the post-dam-removal surveys to the extended period surveys. The Lower Tributary and Tidal strata exhibited the greatest changes in similarity, while the strata above the lowermost dam (Upper Tributary, Argyle, Milford, and Orono) exhibited little to no difference in similarity (Figure 8). Hierarchical clustering revealed three main break points in fish assemblages based on species composition (Figure 9). The most dissimilar grouping was the Lower Tributary

stratum during all three sampling periods, which consisted of a high abundance of cyprinid species and a low abundance of riverine species. The two other, larger groups were primarily split between free-flowing and impounded river stratum fish assemblage structure (Figure 9).

### Nonmetric Multidimensional Scaling

The NMDS analysis demonstrated a strong influence of estuarine species and riverine species, with the Milford reach being the most clearly influenced. Results adequately represented the overall fish assemblages, with a stress value less than 0.20 (stress = 0.19) indicating that the data were well described within two axes (Bradfield and Kenkel 1987). Axis 1 explained the most variance, ordinated positively with resident species (e.g., Chain Pickerel), and ordinated negatively with estuarine species (e.g., Atlantic Tomcod). Axis 2 ordinated positively with resident riverine species (e.g., Smallmouth Bass) and ordinated negatively with slower-water species (e.g., Largemouth Bass; Figure 10A). Spring surveys (Figure 10B) revealed that the greatest shifts in species composition between post-dam-removal and extended period surveys occurred in the Tidal, Argyle, and Lower Tributary strata. These strata exhibited a greater influence of anadromous and riverine species relative to other strata during this period. Although the Lower Tributary and Argyle strata showed some influence by riverine and anadromous species, the relative scores still indicated that lacustrine species (e.g., Brown Bullhead and Yellow Perch) remained dominant. Shifts in the Orono, Milford, and Upper Tributary strata were greatest between the pre- and post-dam-removal surveys as compared to the post-dam-removal and extended period surveys, demonstrating that the greatest shifts occurred immediately after dam removals.

Fall surveys (Figure 10C) revealed a similar pattern in that the greatest shifts in species composition between the post-dam-removal and extended period surveys occurred in the Tidal and Upper Tributary strata, while minimal shifts occurred in the Orono, Argyle, and Milford strata. The Tidal stratum remained largely represented by anadromous species, while the Lower Tributary stratum was comprised of lacustrine and/or resident riverine species. The shift exhibited in the Upper Tributary sites is largely attributable to the presence of age-0 river herring, which were encountered in high abundance in the Piscataquis River during fall surveys.

### DISCUSSION

Collectively, our results demonstrate that the greatest changes in fish assemblages were observed immediately after dam removal and remained consistent over an extended time frame. With the Milford Dam being the lowermost dam in the river system, we still observed much of

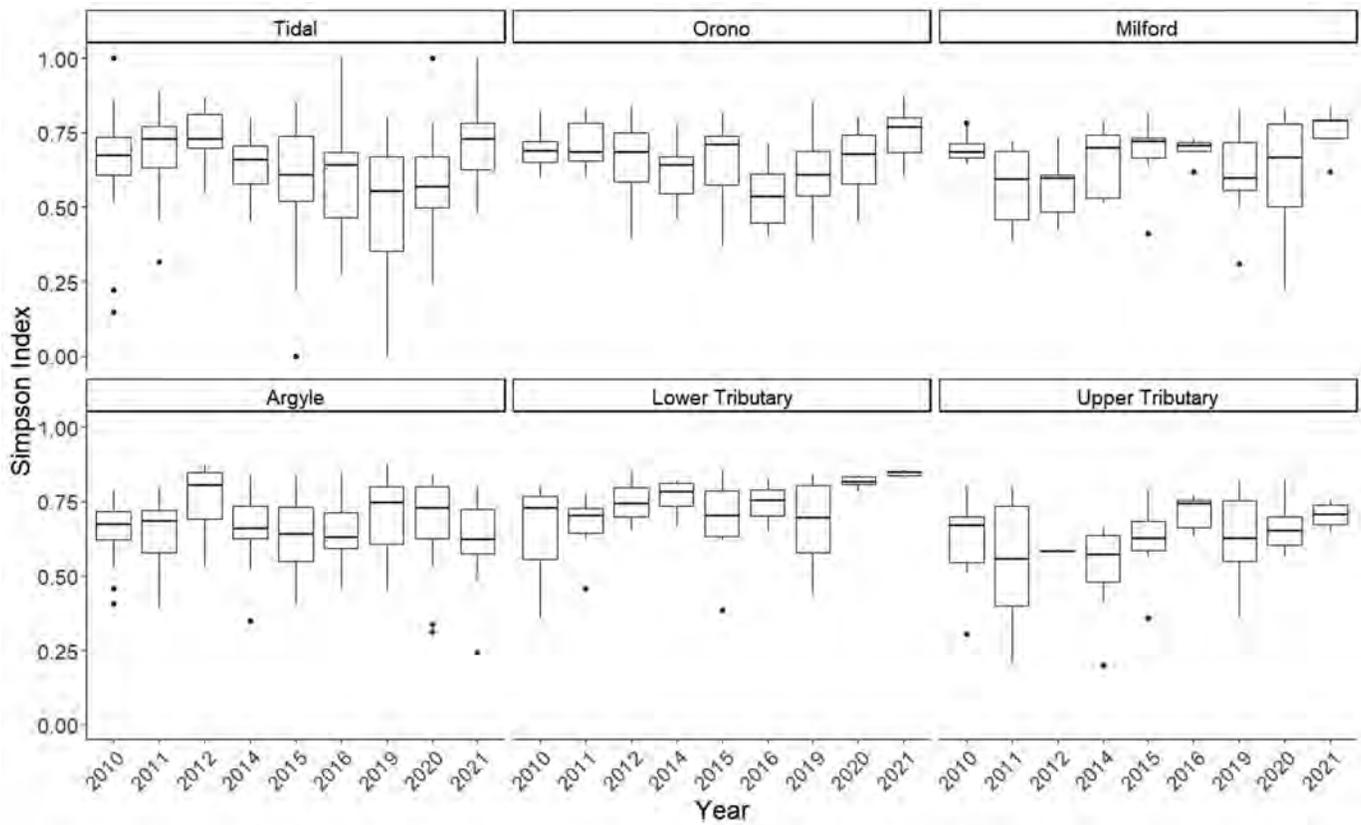


FIGURE 7. Median estimates of the Simpson diversity index for each Penobscot River stratum by sampling year. Horizontal black bars within boxes indicate median values, boxes indicate 25% and 75% quantiles, whiskers represent the minimum and maximum range, and outliers are shown as points.

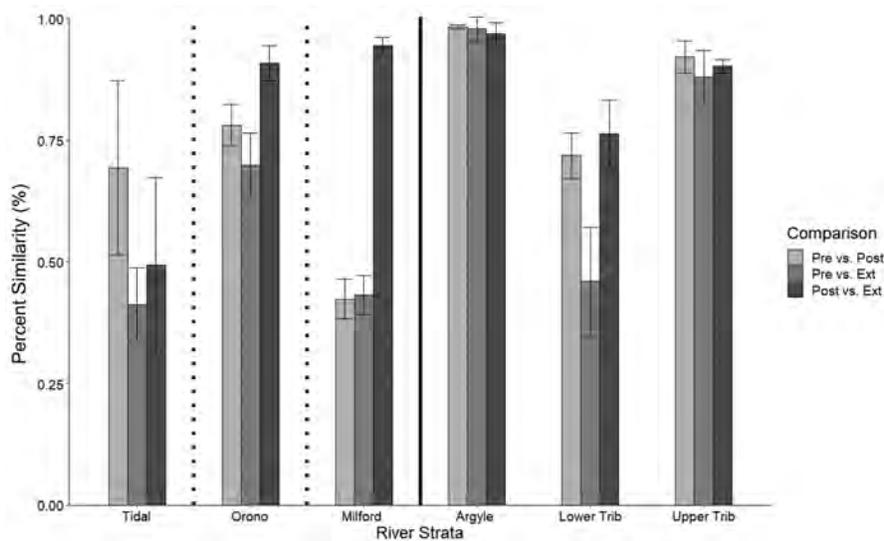


FIGURE 8. Percent similarity of species composition between pre-dam-removal (Pre; 2010–2012), immediate post-dam-removal (Post; 2014–2016), and extended (Ext; 2019–2021) periods for each Penobscot River stratum (Trib = Tributary). Similarity was measured using relative occurrence data and is shown with 95% bootstrapped confidence intervals. The vertical dotted lines represent dams that were removed as part of the Penobscot River Restoration Project and their relative locations with respect to the river strata. The solid black vertical line represents the current Milford Dam.

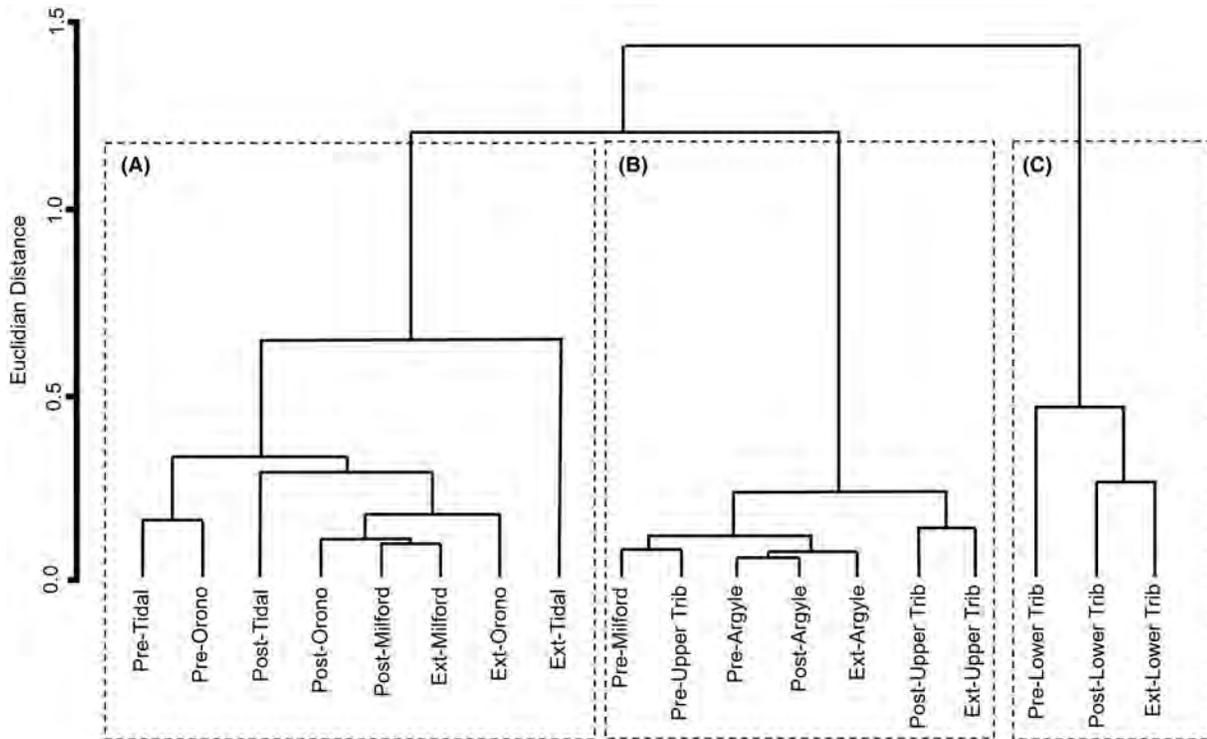


FIGURE 9. Hierarchical clustering dendrogram using pairwise similarity derived from the Morisita–Horn similarity index using relative occurrence data among Penobscot River strata across pre-dam-removal (Pre; 2010–2012), immediate post-dam-removal (Post; 2014–2016), and extended (Ext; 2019–2021) sampling periods. Three major clusters are labeled, representing (A) impounded habitat, (B) free-flowing habitat, and (C) Lower Tributary sampling events.

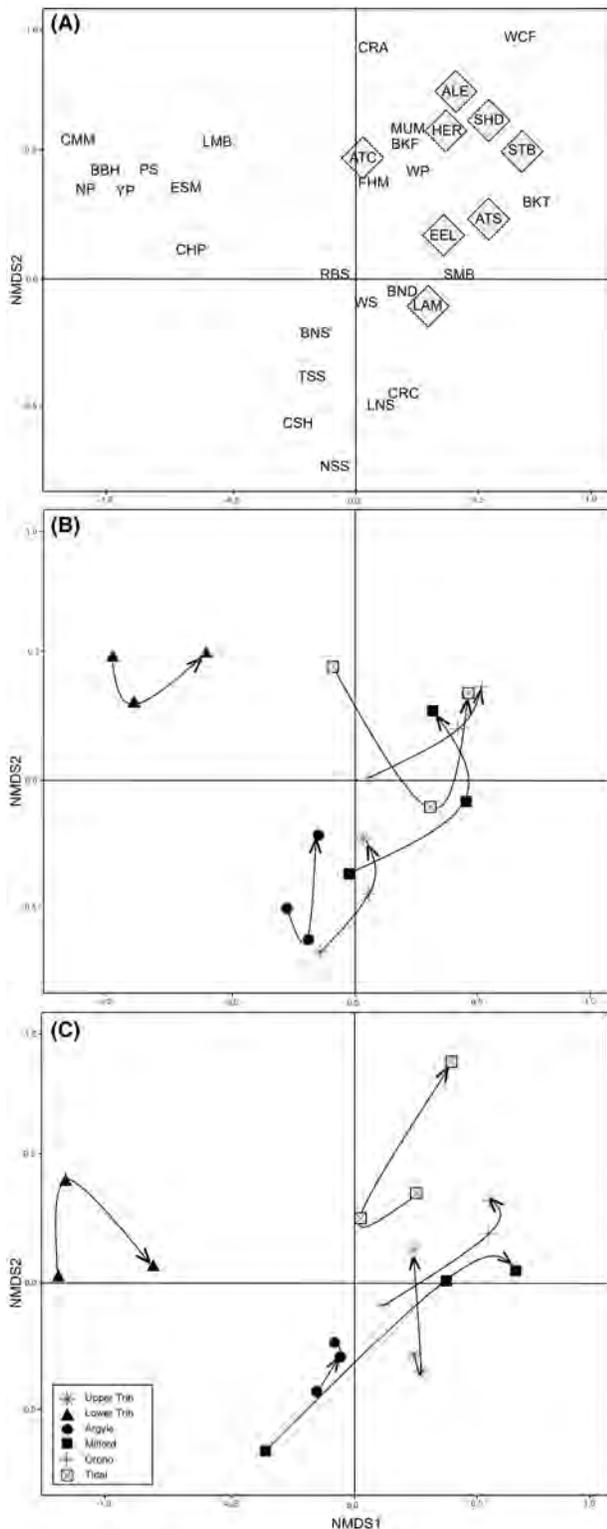
the migratory catch restricted below the dam, while lacustrine species remained in relatively high abundance above the dam. This pattern in catch as a result of dams is consistent within the watershed (Gardner et al. 2013; Kiraly et al. 2014a; Hogg et al. 2015; Watson et al. 2018), within other impounded Atlantic coastal riverine systems (Holcomb et al. 2016; Magilligan et al. 2016), and even on a global scale for impounded river systems (Anderson et al. 2006; Katano et al. 2006; Liu et al. 2019).

Although the intent was to replicate the same sampling methods previously used in pre- and post-dam-removal surveys, there were clear differences in the capture efficiency for smaller fish ( $\leq 150$  mm) between sampling periods. We would expect this to occur in habitat that has been converted from impounded to free flowing, but we also saw this same pattern occur in habitat that remained impounded after the dam removals. One reason for this decline in capture efficiency could be the condition of our gear, which potentially influenced our ability to effectively sample smaller fish. During electrofishing, smaller fish absorb less power than larger fish and have a smaller voltage gradient across the length of their body (Borgström and Skaala 1993; Anderson 1995; Dauwalter and Fisher 2007). If any diminution in the electrical field

around the boat occurred as a result of over a decade of using the gear, the greatest impact would likely occur on the ability to capture smaller fish.

Additional differences in capture efficiency can be due to differences in sampling crews, river discharge, and overall time spent surveying various habitats within a transect. Although capture efficiency differences were clear for small fish, the capture efficiency of larger fish ( $\geq 150$  mm) remained relatively consistent across sampling periods (Figure 5). The highest median CPUE for larger fish was observed in the most recent year of sampling within the Milford stratum and was the direct result of a greater abundance of adult migratory species, such as Alewife, Blueback Herring, and American Shad.

Shifts in the Lower Tributary stratum during the extended sampling period were the result of adult Alewife and Blueback Herring captured in higher abundance, along with the detection of Northern Pike, which had not been detected in the previous surveys. Although the Northern Pike is new to our study, it was previously documented by the Maine Department of Inland Fisheries and Wildlife during extensive monitoring of the species' range expansion. We did not detect Northern Pike within the main-stem Penobscot River during this study, although



they have been observed using the Milford Dam fish lift. Aside from several new species that were encountered in the Lower Tributary sites, much of the resident assemblage structure remained similar. Significant changes in

FIGURE 10. Nonmetric multidimensional scaling (NMDS) of proportional abundance data for fishes encountered during electrofishing surveys, including (A) species scores, (B) spring surveys, and (C) fall surveys in pre-dam-removal (Pre; 2010–2012), immediate post-dam-removal (Post; 2014–2016), and extended (Ext; 2019–2021) sampling periods. Points are connected in the order that they occurred to show the long-term shifts in assemblage (Pre → Post → Ext) grouped by river stratum. Diadromous species are identified with gray diamonds in panel A. Species abbreviations are defined in Table 2.

similarity within the Tidal stratum were the result of encountering schools ( $n > 100$ ) of age-0 alosines during the extended fall surveys. Additional drivers for assemblage shifts in the Tidal stratum include the increased occurrence of White Catfish coinciding with the decrease in occurrence of lacustrine species, such as Brown Bullhead, Chain Pickerel, Pumpkinseed, and Redbreast Sunfish.

Variation in the occurrence of diadromous fishes at our Upper Tributary sites is likely a result of variability in upstream passage constraints between sampling locations. The presence of both adult and age-0 river herring in the Piscataquis River can be attributed to the recently constructed nature-like rock-ramp fishway around the Howland Dam. These nature-like fishways improve connectivity for migratory fish but do not necessarily fully restore conditions to the level observed for free-flowing rivers (Stoller et al. 2016); hence, we observed high similarity in fish assemblages between sampling periods for the Upper Tributary sites (Figure 8).

The highest Upper Tributary site (East Branch of the Penobscot River) lacked the presence of alosines, which can likely be explained by additional passage constraints to reaching this site. The absence of alosines can be attributed to the additional dams (Weldon Dam, river kilometer [rkm] 149; West Enfield Dam, rkm 101) as well as the types of upstream fish passage incorporated into these dams. The Weldon Dam is 13.7 m in height (FERC 2018) and is 6 m taller than the six dams that are downstream. In addition to height, fish passage structures at Weldon Dam (pool and weir) and West Enfield Dam (vertical slot) are likely more species selective than fish elevator systems, such as that used at the Milford Dam (Bunt et al. 2012). As a result, Atlantic Salmon were the only anadromous fish detected at the site but remained in low relative abundances due to additional population pressures, including increasing water temperatures and predation from introduced species. In addition, a significant proportion of the sea-run adults are removed from the Milford Dam fish lift and are brought to a hatchery for artificial spawning, which contributes to their absence higher in the watershed. Occurrence of American Eel, the only catadromous species, remained high across sampling periods, demonstrating relatively successful passage prior to restoration, likely due to their ability to ascend various barriers.

Dams can restrict further upstream range expansions of nonnative fish in rivers (Sharov and Liebhold 1998; Lavis et al. 2003; Pratt et al. 2009; McLaughlin et al. 2013) to prevent unwanted predator–prey or competitive interactions with native fishes (Kiffney et al. 2009). Although the Penobscot River Restoration Project had clear benefits associated with increased connectivity for native diadromous fishes, there were also unintended consequences that ultimately led to the range expansion of an invasive species, the White Catfish. Thought to be previously restricted below the Veazie Dam in low abundance (J. Vallerie, Maine Department of Marine Resources, personal communication), White Catfish were not detected during our pre- or post-dam-removal boat electrofishing surveys. However, during extended period surveys, the species was detected in all river strata below the Milford Dam, indicating not only an expansion in its range but also an increase in relative abundance. When contemplating the use of dam removal as a conservation approach, managers may need to consider how enhanced passage may influence nonnative species (Cooper et al. 2021).

Impounded riverine reaches within the Penobscot River continue to provide habitat that is conducive to a higher relative abundance of cyprinid species while also supporting a higher relative abundance of top predators, such as Chain Pickerel and Largemouth Bass. Although upgraded passage has allowed anadromous species to attain greater upstream ranges, much of the community structure above the lowermost dam has remained largely similar. As a result, any age-0 anadromous migrants above these dams likely encounter these piscivores when moving downriver. Downstream migrants, such as Atlantic Salmon smolts, have exhibited migration delays at impounded locations in the Penobscot River (Molina-Moctezuma et al. 2021), which may provide additional opportunity for predation from these reservoir species.

Our assessment of relative abundances for all fishes and at the individual species level revealed high annual and seasonal variability. This is due to variation in the timing of sampling, river discharge, and heterogeneous shoreline habitats as well as changes in true population status. Despite these confounding factors, the strong sampling design and consistent sampling methods provide data that have a strong relationship to underlying changes in fish relative abundance. Therefore, these data are useful in evaluating the response of the fish assemblage to dam removal and improved fish passage. Large-scale rehabilitation projects like the Penobscot River Restoration Project can be used to inform future river restoration projects around the world. With many diadromous species continuing to decline as a result of dams that reduce access to freshwater environments, we provide evidence that dam removal and upgraded fish passage constitute an effective conservation approach to rehabilitating runs of migratory fishes.

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**Appendix: Relative Occurrence within Each Stratum**

TABLE A.1. Relative occurrence (%) for each fish species within each Penobscot River stratum grouped by sampling period (pre-dam removal [Pre]: 2010–2012; post-dam removal [Post]: 2014–2016; extended [Ext]: 2019–2021).

Species	Relative occurrence (%)																	
	Tidal			Orono			Milford			Argyle			Lower Tributary			Upper Tributary		
	Pre	Post	Ext	Pre	Post	Ext	Pre	Post	Ext	Pre	Post	Ext	Pre	Post	Ext	Pre	Post	Ext
Alewife	41	32	43	4	49	70	0	43	52	0	8	30	0	15	69	0	0	7
Atlantic Tomcod	0	5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atlantic Salmon	4	5	6	21	23	18	15	43	37	9	3	5	7	0	0	7	0	14
Brown Bullhead	20	11	6	36	11	18	45	39	4	76	58	54	100	100	100	7	10	14
Banded Killifish	44	21	16	21	3	0	35	0	7	18	1	15	0	0	0	7	0	0
Brook Trout	1	2	1	0	6	8	0	4	0	0	0	0	0	0	0	7	5	0
Blacknose Dace	7	5	0	0	0	0	0	0	0	2	1	0	0	0	0	0	10	0
Blacknose Shiner	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0
Chain Pickerel	41	25	10	36	6	0	70	0	7	85	76	70	100	100	92	60	38	18
Central Mudminnow	0	0	0	0	0	0	0	0	4	0	0	0	7	38	38	0	0	0
Black Crappie	14	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Creek Chub	6	2	3	14	0	5	0	9	0	9	21	6	0	0	0	33	33	25
Common Shiner	34	19	6	68	9	10	85	57	22	96	92	78	93	62	69	87	81	64
Burbot	0	0	0	4	3	0	25	13	4	47	41	16	14	15	0	80	57	29
American Eel	83	59	56	86	83	95	85	78	89	91	87	96	57	69	100	100	71	89
Eastern Silvery Minnow	6	6	3	11	0	0	0	4	4	5	0	0	21	8	38	0	0	0
Fallfish	73	76	31	96	63	58	100	91	74	98	97	86	79	85	62	100	95	79

TABLE A.1. Continued.

Species	Relative occurrence (%)																	
	Tidal			Orono			Milford			Argyle			Lower Tributary			Upper Tributary		
	Pre	Post	Ext	Pre	Post	Ext	Pre	Post	Ext	Pre	Post	Ext	Pre	Post	Ext	Pre	Post	Ext
Fathead Minnow	4	6	0	0	0	3	0	0	0	0	3	0	0	0	0	5	0	
Finescale Dace	0	2	0	0	0	0	0	0	0	2	8	0	0	0	0	5	0	
Golden Shiner	49	16	15	64	0	8	60	17	4	38	32	34	93	85	85	47	19	21
Blueback Herring	33	24	25	0	31	63	0	26	30	0	3	21	0	8	54	0	0	4
Sea Lamprey	24	22	6	36	49	30	35	52	37	84	86	63	14	23	23	47	24	32
Largemouth Bass	14	17	18	14	29	13	0	17	0	4	21	13	14	54	46	7	0	4
Longnose Sucker	0	0	0	4	0	3	0	0	0	2	0	0	0	0	0	7	10	7
Mummichog	9	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Northern Pike	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	0	0	0
Ninespine Stickleback	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	13	0	4
Pumpkinseed	69	17	3	71	9	20	55	30	7	67	42	30	93	77	77	53	29	32
Northern Redbelly Dace	1	5	0	0	0	0	0	0	0	4	1	0	0	0	0	0	0	7
Redbreast Sunfish	84	56	40	96	60	65	95	48	59	100	94	85	100	100	100	80	38	64
Sturgeon spp.	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
American Shad	7	2	10	0	3	25	0	22	48	0	3	6	0	0	0	0	0	0
Smallmouth Bass	99	84	90	100	100	98	100	100	100	98	97	99	50	77	77	100	100	96
Slimy Sculpin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	19	0
Striped Bass	1	3	3	0	6	3	0	9	4	0	0	0	0	0	0	0	0	0
Spottail Shiner	1	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0
Threespine Stickleback	4	2	0	0	0	0	0	0	0	0	0	0	7	0	0	7	0	0
White Catfish	0	0	13	0	0	18	0	0	26	0	0	0	0	0	0	0	0	0
White Perch	10	13	6	4	9	5	10	4	0	7	8	6	7	8	0	20	0	4
White Sucker	43	40	35	68	63	75	85	70	48	100	89	89	100	100	100	93	86	79
Yellow Perch	26	14	4	25	17	18	40	13	19	76	66	59	100	100	92	60	62	32