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FEATURED PAPER

Recovery of Diadromous Fishes: A Kennebec River Case Study

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Abstract

The lack of safe, timely, and effective fish passage at dams remains a major impediment to the restoration of diadromous fish species to their historic range and abundance. Because fish passage facilities are often ineffective, dam removal has increasingly been used to restore diadromous species. However, few quantitative studies have assessed the response of fishes to dam removal. This paper documents the long-term response of multiple fish species in the Kennebec River, Maine, to the removal of two hydropower dams and the installation of upstream fish passage facilities that restored access to historic habitat. Edwards Dam was removed in 1999, and Fort Halifax Dam was removed in 2008. Counts of river herring (Alewife *Alosa pseudoharengus* and Blueback Herring *A. aestivalis*), American Shad *A. sapidissima*, and Striped Bass *Morone saxatilis* at upstream dams confirmed that these species quickly recolonized the 27-km, free-flowing segment of the Kennebec River that became accessible after Edwards Dam was removed. Average counts of river herring increased by 228% after the removal of Edwards Dam and by 1,425% after the removal of Fort Halifax Dam. However, access to a substantial amount of habitat in the Kennebec River is blocked by ineffective passage at the lowermost dam.

Diadromous fish species once supported large commercial fisheries along the U.S. East Coast, but they have experienced dramatic declines, with many stocks currently at historically low or depleted levels (Department of the Interior 1967; Moring 2005; Limberg and Waldman 2009; NMFS and USFWS 2009; NMFS 2012a, 2012b; ASMFC 2017, 2020). In addition to providing food for human consumption, diadromous fish are an important link between marine, estuarine, and freshwater ecosystems. Adult anadromous fish on their spawning migration deliver marine-derived nutrients to estuarine and freshwater ecosystems (Durbin et al. 1979; Kline et al. 1990; Garman and Macko 1998). Diadromous species, both juveniles and adults, are an important source of food for birds (Dalton et al. 2009), marine mammals (Cairns and Reddin 2000; Marston et al. 2002), and other fishes (Moring and Mink 2002; Davis et al. 2012). The decline of diadromous populations in the northeastern United States has largely been attributed to human activity, including the damming of rivers, overfishing, and pollution (Moring 2005).

The Kennebec River, Maine's second-largest drainage, historically was inhabited by 11 native diadromous species: Alewife *Alosa pseudoharengus*, American Shad *Alosa sapidissima*, Blueback Herring *Alosa aestivalis*, Striped Bass *Morone saxatilis*, Atlantic Salmon *Salmo salar*, Shortnose Sturgeon *Acipenser brevirostrum*, Atlantic Sturgeon *Acipenser oxyrinchus*, Rainbow Smelt *Osmerus mordax*, Sea Lamprey *Petromyzon marinus*, Atlantic Tomcod *Microgadus tomcod*, and American Eel *Anguilla rostrata*. The commercial fisheries they supported began to decline substantially in the 1800s (Atkins 1887). In 1867, the governor of Maine appointed two commissioners of fisheries under a legislative resolve to restore anadromous fish to the rivers and inland waters of the state. The commissioners surveyed the fisheries in Maine's major river systems and concluded that the decline of anadromous species was caused by impassable dams, overfishing, and pollution of the water (Foster and Atkins 1867).

Foster and Atkins (1867) and Atkins (1887) described the historical range of seven anadromous species in the

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Kennebec River drainage, which collectively encompassed approximately 250 km of the Kennebec River and five major tributaries (Figure 1). The five tributaries and the river kilometer (rkm) where they enter the Kennebec River are as follows: Cobbosseecontee Stream (rkm 64), Seven Mile Stream (rkm 84), the Sebasticook River (rkm 101), the Sandy River (rkm 153), and the Carrabassett River (rkm 166). Atlantic Salmon ascended the Kennebec River to rkm 250 and also utilized spawning habitat in the Carrabassett and Sandy rivers. Alewife and American Shad historically ascended the Kennebec River to Norridgewock Falls (rkm 156), migrated an unspecified distance up the Sandy River, migrated approximately 70 km up the Sebasticook River, and used the Cobbosseecontee Stream drainage. Foster and Atkins (1867) and Atkins (1887) did not describe the range of Blueback Herring; however, this species likely accessed the same areas as Alewife and American Shad given their comparable

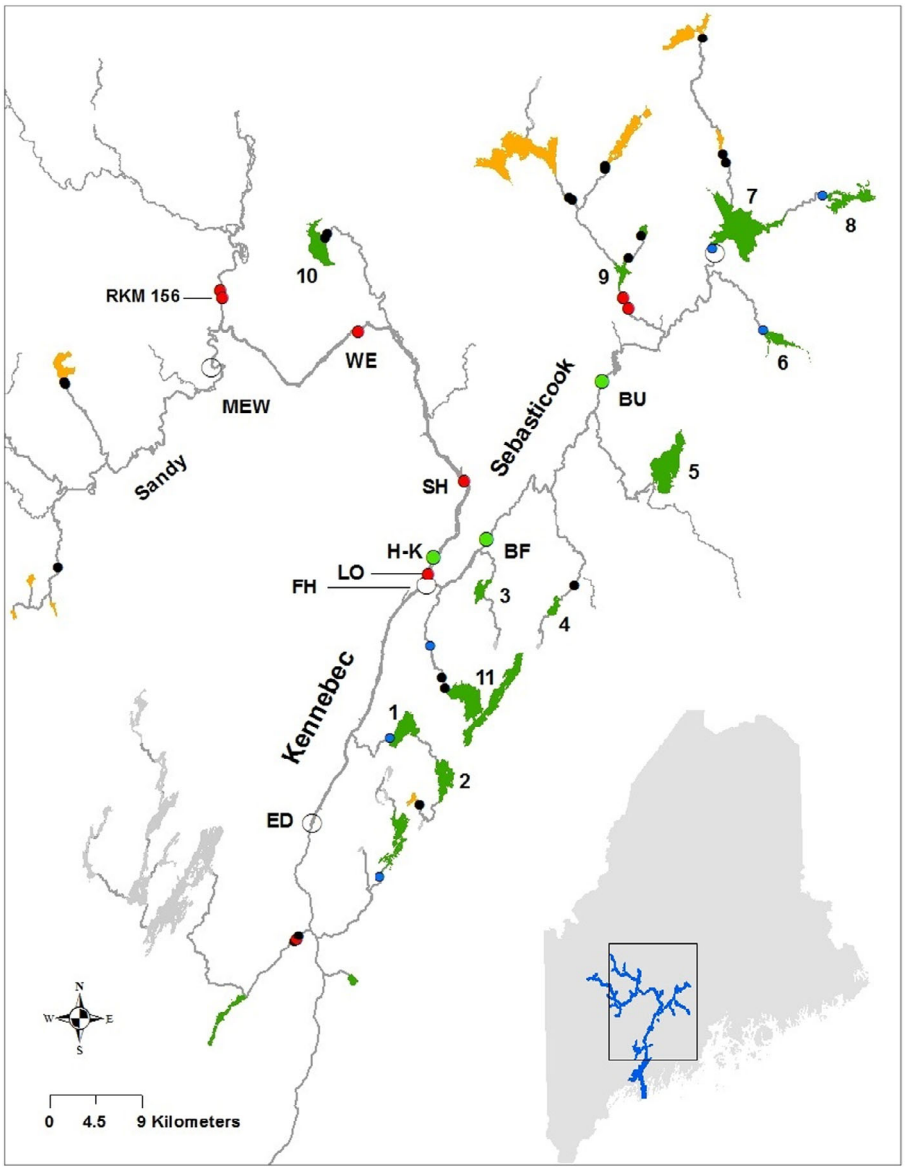

FIGURE 1. Map showing the extent of historic habitat utilized by Alewife, Blueback Herring, American Shad, and Striped Bass in the Kennebec River watershed, Maine, and locations of barriers, including dams that have been removed (open circles), hydropower dams with upstream passage (green circles), hydropower dams without upstream passage (red circles), and nonhydropower dams (black circles). Hydropower projects of note include Edwards (ED), Hydro-Kennebec (H-K), Shawmut (SH), Weston (WE), Madison Electric Works (MEW), Fort Halifax (FH), Benton Falls (BF), and Burnham (BU). Green polygons represent lakes/ponds that are accessible (1–3, 5–8) or that are being stocked prior to passage (4, 9–11). Orange polygons represent inaccessible habitat. Inset shows the location of mapped habitat in Maine.

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swimming abilities and spawning habitat requirements. Shortnose Sturgeon, Atlantic Sturgeon, and Striped Bass did not migrate beyond Taconic Falls (rkm 101) on the main stem, and Striped Bass ascended an unspecified distance up the Sebasticook River (Foster and Atkins 1867; Atkins 1887). Hall et al. (2011) estimated that by 1792, dam construction in the Kennebec River watershed had reduced lake area to 4.8% and stream habitat to 14.8% of what had been historically accessible, and stream habitat was further reduced to 6.9% when Edwards Dam was completed at the head of tide in 1837.

Efforts to restore anadromous species in the Kennebec River began in the mid-1980s and were triggered by four major events: (1) water quality in the river had improved significantly because of the Clean Water Act; (2) the State of Maine filed a petition with the Federal Energy Regulatory Commission (FERC) for installation of a fishway at Edwards Dam; (3) the licensees of the Lockwood, Hydro-Kennebec, Shawmut, Weston, Fort Halifax, Benton Falls, and Burnham hydropower projects (Figure 1) formed the Kennebec Hydro Developers Group (KHDG); and (4) the Maine Department of Marine Resources (MDMR) completed a fisheries management plan for the Kennebec River and began stocking a limited number of Alewife in spawning habitat above Edwards Dam. After extensive negotiations between the state and KHDG, a 10-year settlement agreement (1986 Agreement) was signed that contained a schedule for upstream and downstream fish passage at the seven KHDG dams and provided funds to MDMR for restoration efforts. The funding allowed MDMR to expand its stocking program the following year.

The federal license for the Edwards Project expired in 1993 and resulted in a coordinated effort between the State of Maine, the Kennebec Coalition (American Rivers, Atlantic Salmon Federation, Natural Resources Council of Maine, Trout Unlimited, and Trout Unlimited–Maine Chapter), the U.S. Fish and Wildlife Service, and the National Marine Fisheries Service to decommission and remove Edwards Dam (Crane 2009). On November 25, 1997, FERC ordered the decommissioning of the Edwards Project and the removal of Edwards Dam. This was the first time in FERC's history that it refused to renew a hydropower license for environmental reasons. Specifically, FERC concluded that (1) Edwards Dam blocked the upstream passage of multiple anadromous species, (2) the resulting negative impacts could not be completely mitigated by existing technologies, and (3) dam removal was the only alternative that would allow anadromous species, including those not known to use fishways, to migrate to historic spawning habitat. The following year, a multi-party settlement agreement (1998 Agreement) was signed by the State of Maine, KHDG, Kennebec Coalition, U.S. Fish and Wildlife Service, and National Marine Fisheries Service; the agreement included new schedules or triggers for upstream and downstream fish passage at the seven KHDG projects and provided additional funds for restoration efforts. Edwards Dam was removed in the summer and fall of 1999, which restored the Edwards Project impoundment into a 27-km-long, free-flowing segment of the Kennebec River.

In part, the 1998 Agreement required upstream fish passage at the Fort Halifax Project by May 1, 2003; passage at the Lockwood Project by May 1, 2006; and passage at the Benton Falls and Burnham projects within 2 years of the MDMR providing upstream passage at three nonhydropower dams (Figure 1; Sebasticook Lake, Guilford, and Plymouth Pond dams). By 2003, MDMR and its partners had removed Guilford Dam and installed technical fishways at Sebasticook Lake Dam (pool-and-chute fishway) and Plymouth Pond Dam (Alaskan steeppass fishway). The Lockwood, Benton Falls, and Burnham projects each began operating a new fish lift in spring 2006. Passage at the latter two was delayed by 1 year, primarily due to changes in ownership. Upstream passage at the Fort Halifax Project was further delayed due to local opposition to the licensee's desire to decommission and remove the dam. Fort Halifax Dam was finally removed in the summer and fall of 2008.

More than 1,300 barriers in the United States have been removed since 1999 (AR 2020), but few studies have documented the response of fish populations to dam removal (Brewitt 2016; Griffith and McManus 2020), and all have been of limited duration. The longest study of dam removal to date lasted for 11 years. In that study, Burroughs et al. (2010) documented the response of fish communities to the gradual removal of Stronach Dam on the Pine River, Michigan, for 7 years during removal and 4 years after removal. This paper is the first comprehensive, long-term assessment (34 years) of the response of multiple species to the removal of a large dam (7.32 m high; 279.5 m long) and installation of fish passage facilities on a large river system.

METHODS

Stocking.— Sexually mature, prespawn river herring (primarily Alewife) were stocked annually into 10 lakes and ponds above Edwards Dam (Figure 1; Table 1), at a rate of no more than 15 fish/surface hectare, when the habitat was inaccessible; stocking ceased when the habitat became accessible. The ponds provided the maximum area of suitable spawning habitat located upstream of relatively few existing barriers, in total representing approximately 55% of the historic spawning habitat. River herring for stocking initially were obtained from other river systems (1985–1993) but subsequently were collected at Edwards Dam until its removal (1994–1999), at Fort Halifax Dam

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TABLE 1. Location, amount of historical lake/pond or riverine/impoundment habitat, and number of hydropower (H) and nonhydropower (N) dams located downstream of the habitat in 1986. Habitat is located in Seven Mile Stream, Sebasticook River, Kennebec River, or Sandy River. Numbered lakes and ponds correspond to locations depicted in Figure 1. Lakes/ponds 1–3 and 5–8 were stocked with river herring until 2006, when they became accessible; stocking of inaccessible lakes and ponds (4 and 9–11) is ongoing. Edwards–Lockwood habitat is the post-dam-removal value; Fort Halifax–Benton Falls is the preremoval value.

Habitat	Surface area (ha)	Years stocked	Dams (H)	Dams (N)
Seven Mile Stream				
1. Webber Pond	507	1997–2008	1	1
2. Three Mile Pond	436		1	1
Three Cornered Pond	79		1	2
Spectacle Pond	56		1	2
Sebasticook River				
11. China Lake	1,587	2014–2019	2	6
3. Pattee Pond	288	1987–2005	2	0
4. Lovejoy Pond	131	1987–2019	3	1
5. Unity Pond	1,023	1989–2005	3	
6. Plymouth Pond	194	1986–2005	3	1
7. Sebasticook Lake	1,735	1985–2005	4	2
8. Stetson Pond	311	1987–2005	4	3
Wassookeag Lake	430		6	1
9. Douglas Pond	213	1986–2010	6	
Big Indian Pond	401		6	2
Little Indian Pond	58		6	1
Great Moose Lake	1,450		6	1
Mouth–Fort Halifax	3		2	
Fort Halifax–Benton Falls	152		2	
Benton Falls–Burnham	223		3	
Burnham–Sebasticook Lake	275		4	
Sandy River				
Norcross Pond	46		5	
Clearwater Pond	322		5	
North Pond	70		5	
Parker Pond	42		5	
Sandy River (125 km)	356		6	
Kennebec River				
10. Wesserunsett Lake	568	1996–2019	4	2
Edwards–Lockwood	575		1	
Lockwood–Hydro Kennebec	22		2	
Hydro Kennebec–Shawmut	212		3	
Shawmut–Weston	512		4	
Weston–Abenaki	415		5	

until its removal (2000–2008), and at Lockwood Dam (2006–2019). Because five lakes and ponds became accessible in 2006 when upstream passage became operational at the Benton Falls and Burnham projects, the majority of fish returning to the Fort Halifax Dam were sluiced into the headpond between 2006 and 2008.

Three life stages of American Shad were stocked into the Kennebec River above Edwards Dam between 1987 and 2007 (Table 2). From 1987 to 1997, sexually mature, prespawn adults, primarily obtained from the Connecticut River (Holyoke, Massachusetts), were released into the Edwards Project impoundment. Beginning in 1993, adult stocking was replaced by the stocking of fry and fingerlings that were raised at the privately owned Waldoboro Shad Hatchery. The hatchery initially utilized fertilized eggs but transitioned to collecting eggs from adults that spawned in tanks at the hatchery. Fertilized eggs or prespawn adults were primarily obtained from the Connecticut and Merrimack rivers (Lowell Project, Massachusetts), with lesser contributions from the Saco River (Maine).

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TABLE 2. Number of American Shad adults, fry, and fingerlings stocked into the Kennebec River (KE) or the Sebasticook River (SE) between 1987 and 2007. Adults were obtained from the Kennebec, Narraguagus, Connecticut, Saco, or Merrimack River.

Year	Source river	Adults released	Fry released (KE)	Fry released (SE)	Fingerlings released
1987	Kennebec	16			
1987	Narraguagus	183			
1988	Connecticut	616			
1989	Narraguagus	174			
1989	Connecticut	444			
1989	Kennebec	1			
1990	Narraguagus	36			
1990	Connecticut	568			
1991	Connecticut	639			
1992	Connecticut	994			
1993	Connecticut	880	186,000		16,000
1994	Connecticut	898	51,000		15,600
1995	Connecticut	1,518	388,000		27,841
1996	Connecticut	462	599,990	320,000	3,070
1997	Connecticut	420	1,484,908	474,313	60,261
1997	Saco		459,241		
1998	Connecticut		1,348,937	725,420	27,907
1999	Connecticut		2,020,838	839,068	13,141
2000	Connecticut		3,346,727	500,004	27,685
2001	Merrimack		1,489,913	618,879	6,671
2002	Merrimack		5,671,856	1,034,207	
2003	Merrimack		5,989,358	1,857,184	
2004	Merrimack		4,931,174	510,962	
2005	Merrimack		1,105,343		
2006	Connecticut		262,131		
2007	Merrimack		7,937,841	422,518	
Total		7,849	37,273,257	7,302,555	198,176

Over the 20-year period, MDMR released 7,849 adults, 198,176 fingerlings, and more than 37 million fry into the Kennebec River and more than 7 million fry into the Sebasticook River (Table 2).

Counts of returning fish.— Adult anadromous fish were counted at the first barrier they encountered on their upstream migration, but fish that were removed by commercial harvest were not included. Individuals were counted at the Edwards, Fort Halifax, Lockwood, and Webber Pond dams as they were transferred by net from an upstream passage facility to a stocking truck or as they swam through an upstream passage facility. Due to the large number of migrants at the Benton Falls Project, river herring were counted electronically with a Smith-Root fish counter (Model SR-1601) as they passed through an array of 16 counting tubes installed in the exit flume of the fish lift. The counting tubes were cleaned, calibrated, and monitored daily during the passage season. At the peak of the migration from 2017 to 2019 (≥200,000 fish/d), the counting tubes were removed to reduce the risk of excessive mortality, and the number of fish was estimated from the number of lifts made and the average number of fish per lift in the preceding days.

Changes in the counts of river herring were compared among major phases of restoration in three regions of the watershed. Major phases for the Sebasticook River were (1) initial stocking of habitat in the Sebasticook River (1985–1993); (2) returns to Edwards Dam before its removal (1994–1999); (3) returns to Fort Halifax Dam before its removal (2000–2008); and (4) returns to Benton Falls Dam (2009–2019). Counts at Fort Halifax Dam included the 6 years when broodstock river herring were trucked to upstream spawning habitat and the 2 years (2007–2008) when fish were passed into the Fort Halifax headpond because spawning habitat was accessible. The Fort Halifax counts were not normally distributed (Shapiro–Wilk test: $P < 0.01$); therefore, a Kruskal–Wallis rank-sum test was used to assess whether differences in fish returns were significant, and a pairwise Wilcoxon rank-sum test was used to determine whether returns varied significantly by dam. For the Kennebec River, changes in counts before (2000–2005) and after (2006–2019) the

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installation of the fish passage facility at Lockwood Dam were compared with a *t*-test. Similarly, for Webber Pond, changes in counts before (1997–2005) and after (2006–2019) fish passage at Webber Pond Dam were compared with a *t*-test. Counts at Webber Pond Dam included 3 years (2006–2008) before passage was constructed, when returning fish were dipnetted over the dam to reduce the possibility of mortality.

Biological data.— Approximately 50 river herring were sacrificed weekly from the Fort Halifax Project (2000–2008), Benton Falls Project (2006–2018), Lockwood Project (2008, 2010, 2013–2019), and Webber Pond (2005–2013, 2015–2017) to estimate the proportion of Alewife and Blueback Herring in the sample and obtain information on size distribution, sex ratio, and age structure. Individuals were weighed to the nearest 0.1 g, measured to the nearest 0.1 mm, and identified to species by using the criteria described in Collette and Klein-MacPhee (2002). Sex was determined from visual inspection of the gonads. The weekly samples were used to estimate the annual returns of Alewife and Blueback Herring at the Benton Falls and Lockwood projects. The proportion of the two species was assumed to change linearly between samples. In 2019, daily samples of river herring were taken during most of the migration period and simply identified to species.

Scale aging followed protocols developed by the Atlantic States Marine Fisheries Commission (ASMFC 2014). Scale samples were removed ventrally of the dorsal fin, were cleaned with soap and water, and were blotted dry with paper towels. Three to four scales were mounted between glass slides and viewed with a microfiche reader. Two readers independently aged each sample. If the readers disagreed on an age, they both examined the sample and attempted to determine a consensus age. If consensus was not reached, the sample was not included.

Early life stages.— Plankton nets were used from 2000 to 2002 to capture American Shad eggs and document the presence of spawning areas. The 4.3-m-long plankton nets were constructed of 800-μm mesh or 1,600-μm mesh and had a 1-m-diameter mouth opening. The mouth of each net was attached to a D-shaped, stainless-steel frame to which a Danforth anchor was attached. The "D-nets" were set on the bottom and fished for approximately 15 h. The samples were sorted in the laboratory under a dissecting microscope, and suspected American Shad eggs were identified using guidelines given by Jones et al. (1978). The majority of the putative American Shad eggs were preserved, but 50 were hatched and examined to verify the identification.

A beach seine survey was initiated in 2000 to monitor the annual presence of young-of-year (age-0) fish in the free-flowing segment of the Kennebec River that became accessible after the removal of Edwards Dam. The eight fixed sampling sites were located at the few places in the river where the substrate was sand or mud, water depth was less than 2 m, and water velocity was sufficiently low to allow the net to be deployed. A single seine haul, which swept an area of approximately 415 m^2, was taken at each site biweekly from late July to mid-October. Few or no samples were taken after 2007 when high discharge made sampling unsafe or low discharge made sites inaccessible. All fish were identified and enumerated, and as many as 50 individuals of the target species (Alewife, Blueback Herring, American Shad, and Striped Bass) were measured. The CPUE index was calculated by dividing the number of individuals caught at each station by the number of seine hauls at that station.

RESULTS

Counts

River herring.— The counts of river herring in the Sebasticook River increased in stages as dams were removed and as upstream fish passage became more efficient (Kruskal–Wallis test: $P < 0.001$). From 1985 to 1994, MDMR annually stocked 25,749 ± 5,088 river herring (mean ± SE) into 10 lakes and ponds to prepare for future passage improvements (Table 1; Figure 2A). By 1993, wild returns had increased substantially, and after 1994 only river herring returning to the Kennebec River were used for broodstock. From 1993 to 1999, MDMR annually captured 83,184 ± 10,777 river herring at the Edwards Dam (Figure 2A), a nonsignificant increase relative to the initial stocking (Wilcoxon rank-sum test: $P = 0.074$), and the majority were stocked upstream. Subsequent counts of river herring at Fort Halifax Dam were higher compared to the years before Edwards Dam was removed (Wilcoxon rank-sum test: $P = 0.005$). The mean counts at Fort Halifax Dam (189,900 ± 47,404 river herring) were 228% greater than the counts at Edwards Dam. From 2000 to 2005, the majority of fish collected at Fort Halifax Dam were trucked to spawning habitat, but from 2006 to 2008 more than 400,000 river herring were passed into the headpond via a temporary sluice (Figure 2B). The stocking of Pleasant Lake, Sebasticook Lake, Plymouth Pond, and Unity Pond ceased in 2006 because upstream fish passage had restored access to spawning habitat for anadromous alosines. Counts of river herring at the Benton Falls Dam were higher compared to the years before the Fort Halifax Dam was removed (Wilcoxon rank-sum test: $P < 0.001$). The average count of river herring at the Benton Falls Dam for the period 2009–2019 (2,706,352 ± 358,619) was 1,425% greater than the average count at Fort Halifax Dam (Figure 2B).

The counts of river herring in the years after fish passage became operational at Lockwood Dam were significantly greater than in the years preceding passage (*t*-test: $P < 0.001$). Upstream spawning habitat in Wesserunsett Lake

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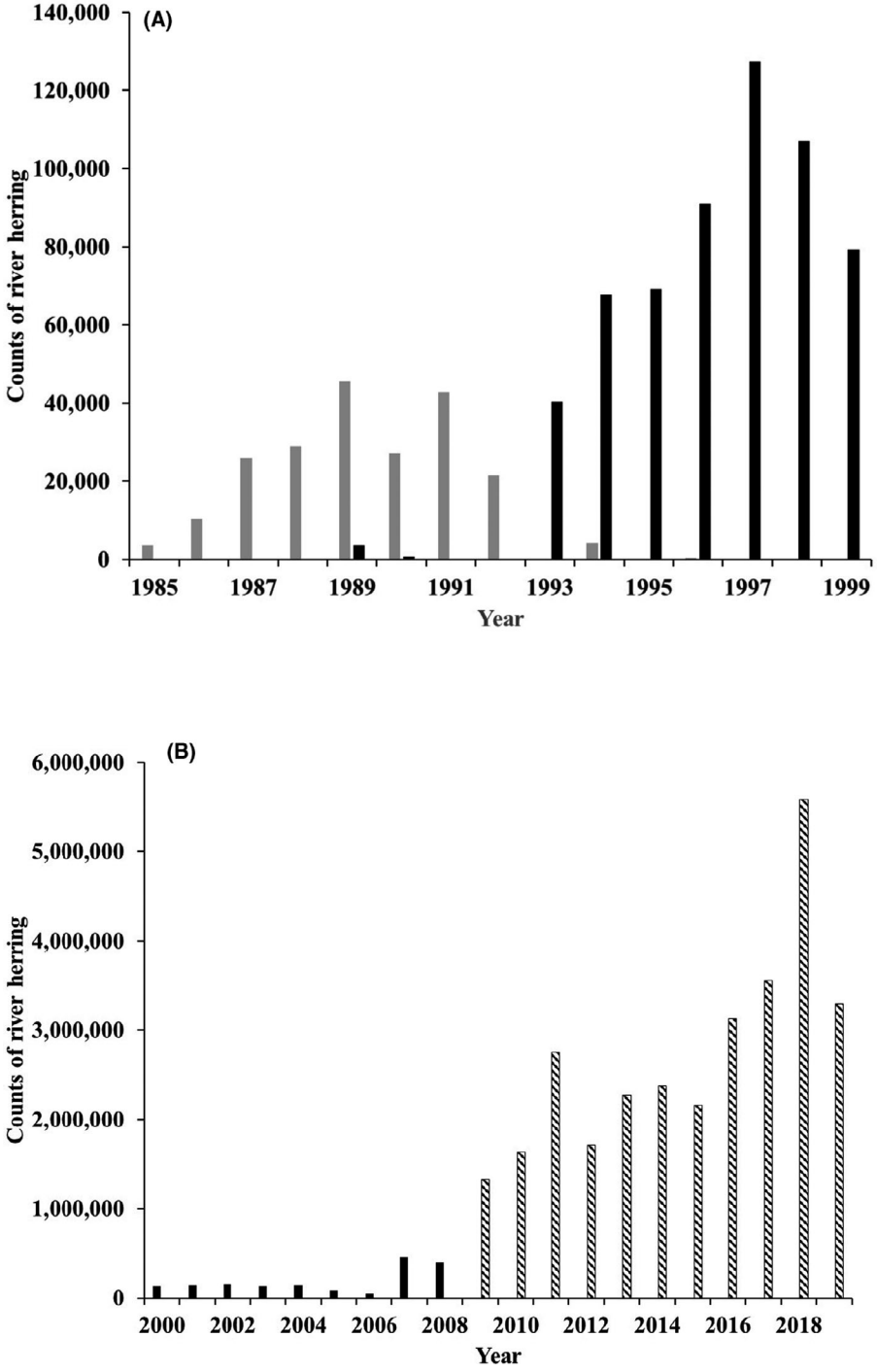

FIGURE 2. **(A)** Annual counts of river herring stocked into historic spawning habitat above Edwards Dam (gray bars) on the Kennebec River, Maine, and wild returns of river herring collected at Edwards Dam (black bars); and **(B)** annual counts of wild returns collected at Fort Halifax Dam (black bars) and passed upstream at Benton Falls (hatched bars) on the Kennebec River. Note the change in magnitude of the *y*-axis.

was stocked with 8,731 ± 21 river herring (mean ± SE) from 2000 to 2005. From 2006 to 2019, an average of 113,089 ± 21,881 river herring was counted annually—an increase of 1,295% compared to years before passage was operational. Because the Lockwood Dam fish lift is an interim facility with no connection to the impoundment, MDMR annually stocks the majority of fish into upstream habitat.

The counts of Alewife in the years after the fish passage facility was installed at Webber Pond Dam were significantly greater than those in the years before fish passage

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was constructed (*t*-test: $P < 0.001$). Webber Pond was stocked annually with 8,263 ± 1,543 fish (mean ± SE) from 1997 to 2005. From 2006 to 2008, before the fish passage facility became operational, MDMR netted returning fish and passed them upstream to reduce the risk of excessive mortality. Counts of returning Alewife averaged 221,328 ± 36,903 fish from 2006 to 2019, an increase of 2,378% compared to pre-passage years (Figure 3).

American Shad.— American Shad quickly recolonized spawning habitat in the free-flowing segment of the river after Edwards Dam was removed, as evidenced by the presence of early life stages, but few adults have used the upstream fish passage facilities (Table 3). Sampling for eggs and larvae confirmed the presence of spawning American Shad near the confluence of the Sebasticook and Kennebec rivers. In 2001, two D-nets that were set approximately 500 m downstream of the Lockwood Project on two dates caught 25.6 eggs/h. In the following year, a D-net that was set in the same location and a second net that was set approximately 480 m downstream of the Fort Halifax Project caught 33.2 eggs/h. Beach seine sampling confirmed the presence of age-0 American Shad at a site 6.6 km downstream of the confluence of the two rivers in multiple years. The average CPUE (mean ± SE) for the years 2000–2007 was 274.6 ± 165.7. Despite the confirmed presence of adults within 500 m of Lockwood Dam, only 1,104 American Shad have been captured at the Lockwood Dam fish lift over the 13 years from 2006 to 2019, and 499 have successfully passed Benton Falls over 9 years (2009–2019).

Striped Bass.— Striped Bass have naturally recolonized the restored free-flowing Kennebec River, and fish passage facilities may be allowing them to expand beyond their historical range—the falls where the Lockwood and Benton Falls projects are located. Between 2006 and 2019, 662 Striped Bass were lifted at the Lockwood Project fish lift and 553 were lifted at the Benton Falls Project (Table 3). Fish are passed upstream at the Benton Falls Project, whereas those lifted at the Lockwood Project are sluiced downstream and may be recaptured in the fish lift multiple times.

Commercial and Recreational Fisheries

River herring are commercially harvested at the Benton Falls and Webber Pond sites, and the counts of fish at these locations do not include the harvest. In 2009, the Atlantic States Marine Fisheries Commission approved Amendment 2 to the Interstate Fishery Management Plan for Shad and River Herring (ASMFC 2009), which prohibited commercial fisheries in state waters beginning in 2012 unless a state or jurisdiction developed and submitted for approval a sustainable management plan by 2010. The State of Maine submitted a plan, which included mandatory reporting of catch, and the harvest at Benton Falls, Webber Pond, and 22 other sites was deemed sustainable. Because Maine's commercial landings are confidential by statute, the data must be pooled in order to be

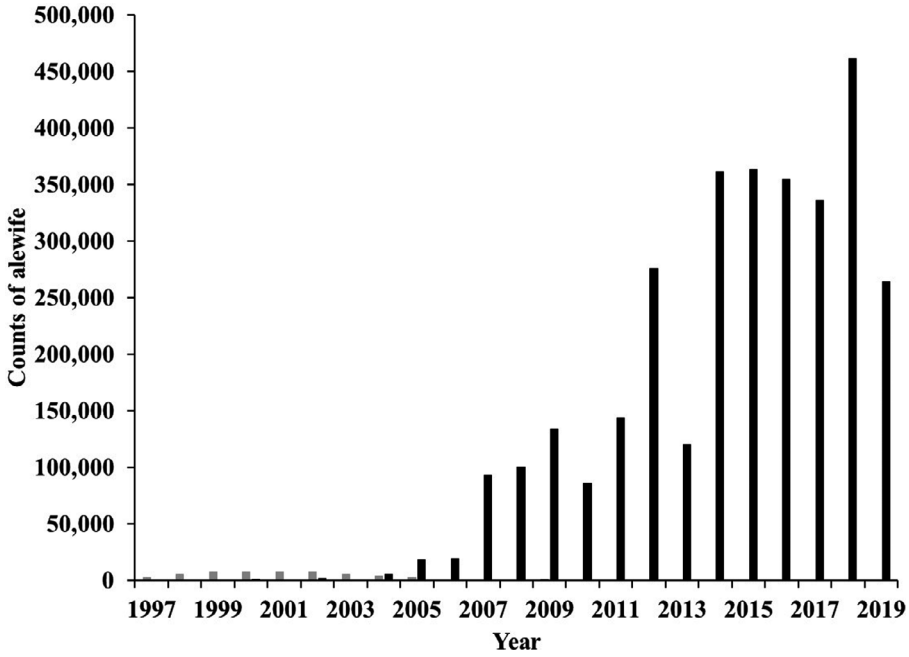

FIGURE 3. Annual counts of Alewife stocked into historic spawning habitat in Webber Pond (gray bars) and counts of wild returns of Alewife (black bars) that were dipnetted upstream (2000–2008) or that used the upstream fish passage facility (2009–2018) at Webber Pond Dam.

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TABLE 3. Total counts of river herring, American Shad, and Striped Bass passed upstream at the Fort Halifax, Benton Falls, and Lockwood projects, and estimated number of river herring that were Alewife or Blueback Herring.

Year	River herring	Alewife	Blueback Herring	American Shad	Striped Bass
			Fort Halifax Project		
2000	137,658	137,658			
2001	142,845	142,155	690		
2002	151,574	150,743	831		
2003	131,633	131,616	17		
2004	143,697	143,663	34		
2005	81,576	81,265	311		
2006	46,960	43,865	3,095		
2007	458,491	457,464	1,027		
2008	401,059	388,692	12,367		
			Benton Falls Project		
2009	1,327,861	1,263,015	64,846	9	
2010	1,628,187	1,201,559	426,628	3	4
2011	2,751,473	2,537,226	214,247	54	
2012	1,703,520	1,499,216	204,304	163	1
2013	2,272,027	1,964,613	307,414	113	14
2014	2,379,428	1,784,425	595,003	26	22
2015	2,158,419	1,725,165	433,254	48	3
2016	3,128,753	2,131,789	996,964	18	3
2017	3,547,698	2,339,419	1,208,279	65	314
2018	5,579,901	4,201,838	1,378,063	26	3
2019	3,287,701	2,086,545	1,201,156	114	169
			Lockwood Project		
2006	3,152				83
2007	4,534			30	
2008	90,940	89,121	1,819		
2009	45,428				10
2010	75,072	59,363	15,709	28	4
2011	31,066				8
2012	156,428				11
2013	95,314				31
2014	108,256	73,883	34,373	1	22
2015	89,496	55,433	34,063	26	33
2016	206,941	88,463	118,478	830	214
2017	238,481	73,595	164,886	201	137
2018	238,953	145,267	93,686	275	109
2019	182,987	118,921	64,066	22	

reported. The commercial harvest at four sites in the Kennebec River, each near a dam, removed $18.2 \pm 5.1\%$ (mean $\pm$ SD) of the total river herring population from 2009 to 2019.

A recreational fishery for American Shad and Striped Bass in the restored Kennebec River quickly became established after the removal of Edwards Dam. The most accessible area (by small boat or along the shore) is the reach that extends downstream from Lockwood Dam to the mouth of the Sebasticook River. No landings data are available for these fisheries.

Species Composition

Few Blueback Herring were stocked upstream of Edwards Dam, but the number returning to the Sebasticook River increased from a few thousand fish, representing no more than 7% of all river herring returns to Fort Halifax in 2006, to over 2 million fish, approximately 36% of all returns to Benton Falls in 2018 (Table 3). The number of Blueback Herring that were passed at Lockwood Dam increased from approximately 2,000 fish to nearly 164,000 fish in 2017 (Table 3), an increase from 2.0% to 69.1% of all wild returns. The count of adults passing the

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remaining dams provides some indication of the magnitude of adult returns to the lower reaches of the river that were accessible after dam removal.

Migration Timing

The timing of the capture or passage of river herring has changed as capture location, fish passage method, and species composition have changed (Table 4). The mean capture date of the first river herring was 11 d earlier at Fort Halifax and 20 d earlier at Benton Falls compared to Edwards Dam, and half of the run passed 11–12 d earlier at Fort Halifax and Benton Falls compared to Edwards Dam. In contrast, the last date of river herring capture has occurred later in the season as the proportion of Blueback Herring has increased. In the Sebasticook River, the Alewife migration typically begins and peaks approximately 1 week earlier than the Blueback Herring migration, but the two species can overlap for a considerable period (Figure 4).

Alewife Size, Age, and Sex Ratio

The MDMR collected biological data (TL, weight, and sex) from 9,705 Alewife sampled on their spawning migrations at Fort Halifax, Benton Falls, Lockwood, and Webber Pond dams; age was determined for a subsample of 1,491 females and 1,800 males (Tables 5, 6). Mature females were on average 10 mm longer than mature males (mean ± SD = 280.7 ± 14.8 mm versus 270.6 ± 14.8 mm) and 24 g heavier than mature males (188.7 ± 33.3 g versus 164.5 ± 28.9 g). Approximately 95% of the females and males were 3–5 years old. Eighteen percent of females and 20% of males were repeat spawners. The sex ratio varied among samples at all sites and in all years without a discernable trend. Females accounted for 44.7 ± 0.9% (mean ± SE) of the sampled fish at Fort Halifax Dam, 49.5 ± 1.9% at Benton Falls Dam, 45.8 ± 2.4% at Lockwood Dam, and 43.0 ± 1.1% at Webber Pond Dam.

Blueback Herring Size, Age, and Sex Ratio

Biological data (TL, weight, and sex) were collected for 1,993 Blueback Herring sampled on their spawning migration at Fort Halifax, Benton Falls, and Lockwood dams, and age was determined for a subsample of 295 females and 385 males (Tables 5, 6). Blueback Herring were not identified in samples from Webber Pond Dam, and only 31 females and 46 males were sampled at Fort Halifax Dam. Mature female Blueback Herring were on average 11 mm longer than mature males (mean ± SD = 252.8 ± 12.0 mm versus 241.7 ± 13.8 mm) and 20 g heavier than males (132.1 ± 22.4 mm versus 112.4 ± 21.0 mm). More than 96% of the females and males were 3–5 years old. Nineteen percent of females and 20% of males were repeat spawners. The sex ratio varied among samples at all sites and in all years without a discernable trend. Females accounted for 45.2 ± 8.3% (mean ± SE) of the sampled fish at Fort Halifax Dam, 40.5 ± 2.5% at Benton Falls Dam, and 46.4 ± 4.1% at Lockwood Dam.

DISCUSSION

This is the first study describing ecological conditions in the Kennebec River before and after the removal of three dams and the installation of multiple technical fishways. When the Kennebec River Diadromous Fish Restoration Project began, 13 hydropower project dams and 23 non-hydropower dams had blocked anadromous fish from approximately 9,958 ha of lake/pond habitat and 2,508 ha of previously unimpounded riverine habitat for 150 years. Removal of the Edwards Dam in 1999 converted 524 ha (20.9%) of impounded water to free-flowing river. Removal of the Fort Halifax Dam in 2008, preceded by the construction of seven technical fishways and two dam removals, made 4,625 ha (46%) of historic of lake/pond habitat and an additional 489 ha (19.5%) of mostly unimpounded river accessible. Despite this progress, approximately 60% of historical alosine habitat above the Lockwood Project and 54% of the lake/pond habitat primarily in the Sebasticook River remain inaccessible.

Alewife and Blueback Herring showed a very strong response to the removal of dams and the installation of technical fishways. This restoration effort has allowed for the establishment of what is likely the largest contemporary spawning population of river herring on the U.S. East Coast (ASMFC 2017). Unimpeded access to spawning habitat in the Sebasticook River and Webber Pond since 2009 has resulted in annual returns (not including those taken in the sustainable commercial harvest) of Alewife reaching 4.2 million adults and Blueback Herring reaching nearly 1.4 million adults. Restoration of Alewife to spawning habitat in the West Branch of the

TABLE 4. Capture timing of river herring (Alewife and Blueback Herring) at four locations in the Kennebec River, 1994–2019.

Location	Years	First day	25% passed	50% passed	75% passed	Last day
Edwards	1993–1999	May 21	May 26	May 30	Jun 1	Jun 12
Fort Halifax	2000–2008	May 10	May 14	May 19	May 25	Jun 7
Benton Falls	2009–2019	May 1	May 13	May 19	May 26	Jul 9
Lockwood	2006–2019	May 11	May 22	May 27	May 31	Jun 18

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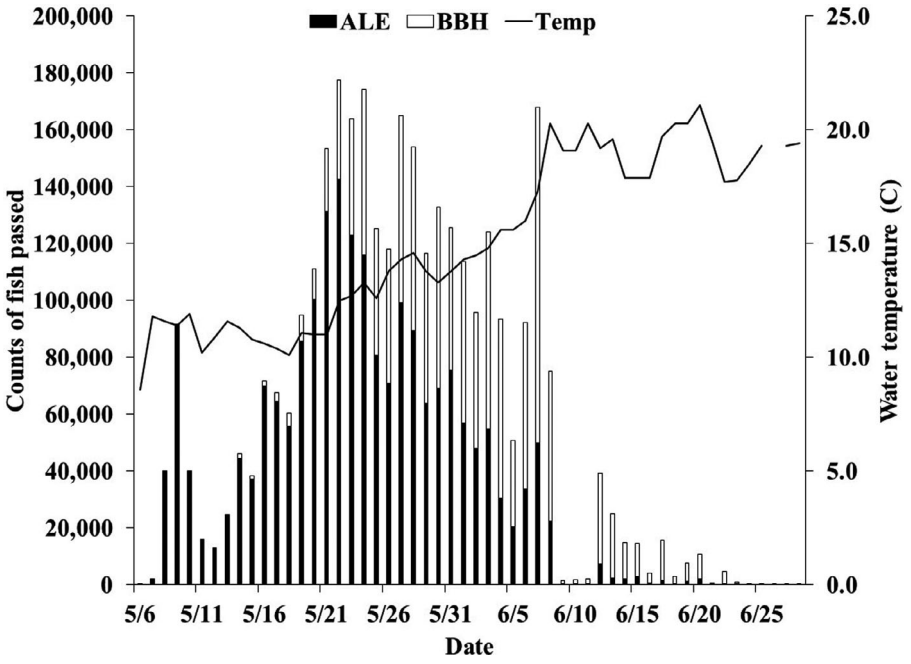

FIGURE 4. Water temperature (°C; black line) and counts of Alewife (black bars) and Blueback Herring (unfilled bars) that were passed daily at the Benton Falls Dam fish lift in 2019.

TABLE 5. Summary of TL and weight (WT) for female (F) and male (M) Alewife (ALE) and Blueback Herring (BBH) sampled at Fort Halifax, Benton Falls, Lockwood, and Webber Pond dams. Means are presented with SDs.

Species, sex	*N*	Mean TL (mm)	TL range	Mean WT (g)	WT range
ALE, F	4,110	280.3 ± 14.8	231–331	188.0 ± 33.3	105.6–336.0
ALE, M	5,106	270.4 ± 14.9	217–316	164.2 ± 29.1	79.0–292.8
BBH, F	719	251.2 ± 11.4	213–289	129.0 ± 20.6	78.0–223.5
BBH, M	930	240.0 ± 13.9	196–277	110.2 ± 21.1	54.6–195.1

Sebasticook River is hampered by the limited capacity of the fish lifts at the Benton Falls and Burnham projects and the presence of two more hydropower projects and five nonhydropower dams that will require fish passage. Restoration into China Lake and Outlet Stream, which joins the Sebasticook River below the Benton Falls Project, is ongoing. To date, MDMR and its partners (Maine Rivers, Sebasticook Regional Land Trust, China Region Lakes Alliance, China Lake Association, The Nature Conservancy in Maine, and the U.S. Fish and Wildlife Service) have removed two of the six dams on the stream and installed technical fishways at two other dams.

American Shad responded quickly to the removal of Edwards Dam. Spawning was documented near the confluence of the Kennebec and Sebasticook rivers 2 years after the dam was removed, and the capture of age-0 American Shad throughout the free-flowing segment in multiple years demonstrates the continued use of this historic spawning habitat. This rapid response was similar to that reported after the removal of a low-head dam on the Neuse River (Beasley and Hightower 2000; Burdick and Hightower 2006). Despite this promising beginning, few American Shad have utilized the Lockwood Project fish lift. Radiotelemetry studies conducted by the licensee in 2015 found that American Shad were rarely detected within approximately 60 m of the fishway entrance (Brookfield White Pine Hydro 2016). Poor passage of American Shad at technical fishways is a common problem in many East Coast river systems, including the Androscoggin River, Maine; the Merrimack River, Massachusetts; the Connecticut River, Connecticut–Massachusetts; and the Susquehanna River, Maryland–Pennsylvania (Sprankle 2005; Haro and Castro-Santos 2012; Kahnle and Hattala 2012; Aunins et al. 2013; Brown et al. 2013; Weaver et al. 2019). Minimal upstream passage in the Kennebec River not only precludes adult American Shad from reaching the 1,495 ha of historic spawning habitat, but also has impeded the conversion of

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TABLE 6. Age structure (%) of female and male Alewife and Blueback Herring sampled at the Fort Halifax (FH), Benton Falls (BF), Lockwood (LO), and Webber Pond (WP) dams.

	Females				Males			
Age (years)	FH	BF	LO	WP	FH	BF	LO	WP
Alewife								
2							0.5	
3	5.4	7.8	8.9	7.0	9.5	14.7	20.3	14.9
4	65.7	69.1	52.7	47.3	63.0	65.3	50.3	48.3
5	25.7	19.6	33.1	39.9	24.6	16.3	24.6	28.8
6	3.1	3.3	5.3	4.9	2.6	3.5	3.7	7.6
7		0.3		0.7	0.3	0.2	0.5	0.4
Blueback Herring								
2						1.5	2.5	
3	9.1	23.8	51.5		8.3	25.9	61.9	
4	54.5	56.9	39.8		75.0	58.7	30.6	
5	36.4	18.2	7.8		16.7	11.9	4.4	
6		1.1				1.5		
7			1.0			0.5	0.6	

the Lockwood Dam fish lift to a swim-through facility pursuant to the 1998 Settlement Agreement.

Four additional native diadromous species likely benefited from the removal of Edwards Dam. Acoustic telemetry studies have verified that the endangered Shortnose Sturgeon and the threatened Gulf of Maine Distinct Population Segment of Atlantic Sturgeon now have access to all of their historical spawning habitat in the Kennebec River, and spawning has been documented in the newly accessible free-flowing segment (Wippelhauser et al. 2015, 2017). The capture of Striped Bass in upstream passage facilities at the Lockwood and Benton Falls projects confirms that this species now has access to its historical habitat in the Kennebec River. Removal of Edwards Dam likely increased the distribution and abundance of American Eel in the Kennebec River. In a postremoval study, the relative abundance of American Eel weighing 10–500 g was highest in the free-flowing reach (208.4 eels/km electrofished), intermediate in the downstream tidal freshwater (51.8 eels/km), and lowest above three (9.22 eels/km) or four (4.67 eels/km) main-stem dams (Yoder et al. 2006). The greatest decline was seen at the first barrier, where relative abundance dropped from 127.5 eels/km downstream of Lockwood Dam to 43 eels/km upstream of the dam.

Other studies of the effect of total dam removal on diadromous and freshwater fishes have found that species previously excluded from habitat above a dam quickly recolonized the newly accessible habitat after dam removal and often showed substantial increases in abundance. Burdick and Hightower (2006) reported spawning activity by American Shad, Hickory Shad *Alosa mediocris*, and Striped Bass 5–6 years after upstream habitat was made accessible by the removal of Quaker Neck Dam on the Neuse River, North Carolina. Two to 3 years after the removal of Embry Dam on the Rappahannock River, Virginia, the abundance of American Eel, particularly individuals smaller than 300 mm, increased significantly in headwater streams (Hitt et al. 2012). Poulos et al. (2014) observed significant shifts in fish relative abundance over 3 years in response to the removal of Zemko Dam on the Eightmile River, Connecticut. Gardner et al. (2012) and Hogg et al. (2015) documented an increase in fish density and biomass and the recolonization and successful reproduction of Atlantic Salmon, Alewife, and Sea Lamprey in a previously inaccessible reach 2 years after the removal of a dam on Sedgeunkedunk Stream, Maine. Magilligan et al. (2016) documented the presence of four species of fish, including Sea Lamprey, in Amethyst Brook, Massachusetts, which were not present above a dam prior to its removal. For 9 of 16 dam removal projects in California, Oregon, and Washington, anadromous salmonids *Oncorhynchus* spp. recolonized upstream habitat from which they had previously been excluded (Brewitt 2016). After the removal of Condit Dam on the White Salmon River, Washington, Pacific Lamprey *Entosphenus tridentatus* utilized spawning habitat that had been inaccessible for nearly 100 years (Jolly et al. 2018). Scherelis and Zydlewski (2020) reported a threefold increase in mean fish abundance in the Penobscot River, Maine, after dam removal; however, they noted that stocking had occurred in upriver habitat prior to removal. In the Baraboo River, Wisconsin, 10 of 11 freshwater species that were rarely found above four dams recolonized new sites upstream

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within 2 years after dam removals (Catalano et al. 2007). In the Pine River, Michigan, 8 of 11 freshwater species recolonized upstream habitat within 4 years of the removal of Stronach Dam (Burroughs et al. 2010).

The Kennebec River Restoration Project has been successful in its first 34 years, but restoration efforts are ongoing. Of particular concern are hydropower dams on the main-stem Kennebec River that block access to nearly 100% of Atlantic Salmon spawning habitat, 60% of American Shad and Blueback Herring spawning habitat, and 11% of Alewife spawning habitat.

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REFERENCES

AR (American Rivers). 2020. ARDamRemovalList_figshare_Feb2020 [online data set]. AR, Washington, D.C. Available: https://doi.org/10.6084/m9.figshare.5234068. (June 2019).

ASMFC (Atlantic States Marine Fisheries Commission). 2009. Amendment 2 to the Interstate Fishery Management Plan for Shad and River Herring (river herring management). ASMFC, Arlington, Virginia.

ASMFC (Atlantic States Marine Fisheries Commission). 2014. 2013 River Herring Ageing Workshop report. ASMFC, Arlington, Virginia.

ASMFC (Atlantic States Marine Fisheries Commission). 2017. River herring stock assessment update: volume I (coastwide summary) and volume II (state-specific reports). ASMFC, Arlington, Virginia.

ASMFC (Atlantic States Marine Fisheries Commission). 2020. 2020 American Shad benchmark stock assessment and peer review report. ASMFC, Arlington, Virginia.

Atkins, C. G. 1887. The river fisheries of Maine. Pages 673–728 *in* G. B. Goode, editor. The fisheries and fishing industries of the United States, section V, volume 1. U.S. Government Printing Office, Washington, D.C.

Aunins, A. W., B. L. Brown, M. Balazik, and G. C. Garman. 2013. Migratory movements of American Shad in the James River fall zone, Virginia. North American Journal of Fisheries Management 33:569–575.

Beasley, C. A., and J. E. Hightower. 2000. Effects of a low-head dam on the distribution and characteristics of spawning habitat used by Striped Bass and American Shad. Transactions of the American Fisheries Society 129:1316–1330.

Brewitt, P. K. 2016. Do the fish return? A qualitative assessment of anadromous Pacific salmonids' upstream movement after dam removal. Northwest Science 90:433–449.

Brookfield White Pine Hydro. 2016. Diadromous fish passage report for the lower Kennebec River watershed during the 2015 migration season. Brookfield White Pine Hydro, Lewiston, Maine.

Brown, J. J., K. E. Limburg, J. R. Waldman, K. Stephenson, E. P. Glenn, F. Juanes, and A. Jordaan. 2013. Fish and hydropower on the U.S. Atlantic coast: failed fisheries policies from half-way technologies. Conservation Letters 6:280–286.

Burdick, S. M., and J. E. Hightower. 2006. Distribution of spawning activity by anadromous fishes in an Atlantic slope drainage after removal of a low-head dam. Transactions of the American Fisheries Society 135:1290–1300.

Burroughs, B. A., D. B. Hayes, K. D. Klomp, F. Jonathan, and J. Mistak. 2010. The effects of the Stronach Dam removal on fish in the Pine River, Manistee County, Michigan. Transactions of the American Fisheries Society 139:1595–1613.

Cairns, D. K., and D. G. Reddin. 2000. The potential impact of seal and seabird predation on North American Atlantic Salmon. Canadian Science Advisory Secretariat Research Document 2000/12.

Catalano, M. J., M. A. Bozek, and T. D. Pellett. 2007. Effects of dam removal on fish assemblage structure and spatial distributions in the Baraboo River, Wisconsin. North American Journal of Fisheries Management 27:519–530.

Collette, B. B., and G. Klein-MacPhee, editors. 2002. Bigelow and Schroeder's fishes of the Gulf of Maine. Smithsonian Institution Press, Washington, D.C.

Crane, J. 2009. Setting the river free: the removal of the Edwards Dam and the restoration of the Kennebec River. Water History 1:131–148.

Dalton, C. M., D. Ellis, and D. M. Post. 2009. The impact of double-crested cormorant (*Phalacrocorax auritus*) predation on anadromous Alewife (*Alosa pseudoharengus*) in south-central Connecticut, USA. Canadian Journal of Fisheries and Aquatic Sciences 166:77–186.

Davis, J. P., E. T. Schultz, and J. C. Vokoun. 2012. Striped Bass consumption of Blueback Herring during vernal riverine migrations: does relaxing harvest restrictions on a predator help conserve a prey species of concern? Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 4:239–251.

Department of the Interior. 1967. Native fish and wildlife: endangered species. Federal Register 32:48(11 March 1967):4001.

Durbin, A. G., S. W. Nixon, and C. A. Oviatt. 1979. Effects of the spawning migration of the Alewife spawners, *Alosa pseudoharengus*, on freshwater ecosystems. Ecology 60:8–17.

Foster, N. W., and C. G. Atkins. 1867. First report of the Commissioners of Fisheries of the state of Maine. Owen and Nash, Augusta, Maine.

Gardner, C., S. M. Coghlan, and J. Zydlewski. 2012. Distribution and abundance of anadromous Sea Lamprey in a fragmented stream: current status and potential range expansion following barrier removal. Northeastern Naturalist 19:99–110.

Garman, G. C., and S. A. Macko. 1998. Contribution of marine-derived organic matter to an Atlantic coast, freshwater, tidal stream by anadromous clupeid-fishes. Journal of the North American Benthological Society 17:277–285.

Griffith, M. B., and M. G. McManus. 2020. Consideration of spatial and temporal scales in stream restorations and biotic monitoring to assess restoration outcomes: a literature review, part 2. River Research and Applications 36:1398–1415.

Hall, C. J., A. Jordaan, and M. C. Frisk. 2011. The historical influence of dams on diadromous fish habitat with a focus on river herring and hydrologic longitudinal connectivity. Landscape Ecology 26:95–107.

Haro, A., and T. Castro-Santos. 2012. Passage of American Shad: paradigms and realities. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 4:252–261.

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Hitt, N. P., S. Eyler, and J. E. B. Wofford. 2012. Dam removal increases American Eel abundance in distant headwater streams. Transactions of the American Fisheries Society 141:1171–1179.

Hogg, R. S., S. M. Coghlan Jr., J. Zydlewski, and C. Gardner. 2015. Fish community response to a small-stream dam removal in a Maine coastal river tributary. Transactions of the American Fisheries Society 144:467–479.

Jolley, J. C., G. S. Silver, J. E. Harris, and T. A. Whitesel. 2018. Pacific Lamprey recolonization of a Pacific Northwest river following dam removal. River Research and Applications 34:44–51.

Jones, P. W., F. D. Martin, and J. D. Hardy Jr. 1978. Development of fishes of the Mid-Atlantic Bight: an atlas of eggs, larval, and juvenile stages, volume 1. Acipenseridae through Ictaluridae. U.S. Fish and Wildlife Service FWS/OBS-78/12.

Kahnle, A., and K. Hattala. 2012. Relative sensitivity of New England American Shad to fishing, discard mortality, and dam passage failure or mortality. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 4:294–301.

Kline, T. C. Jr, J. J. Goering, O. A. Mathisen, P. H. Poe, and P. L. Parker. 1990. Recycling of elements transported upstream by runs of Pacific salmon: I. $\delta^{15}N$ and $\delta^{13}C$ evidence in Sashin Creek, southeastern Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47:136–144.

Limburg, K. E., and J. R. Waldman. 2009. Dramatic declines in North Atlantic diadromous fishes. BioScience 59:955–965.

Magilligan, F. J., K. H. Nislow, B. E. Kynard, and A. M. Hackman. 2016. Immediate changes in stream channel geomorphology, aquatic habitat, and fish assemblages following dam removal in a small upland catchment. Geomorphology 252:158–170.

Marston, B. H., M. F. Willson, and S. M. Gende. 2002. Predator aggregations during Eulachon *Thaleichthys pacificus* spawning runs. Marine Ecology Progress Series 231:229–236.

Moring, J. R. 2005. Recent trends in anadromous fishes. Pages 25–42 *in* R. Buchsbaum, J. Pederson, and W. E. Robinson, editors. The decline of fisheries resources in New England: evaluating the impact of overfishing, contamination, and habitat degradation. Massachusetts Institute of Technology. Sea Grant College Program, Publication 05-5, Cambridge.

Moring, J. R., and L. H. Mink. 2002. Anadromous Alewives, *Alosa pseudoharengus*, as prey for White Perch, *Morone americana*. Hydrobiologia 479:125–130.

NMFS (National Marine Fisheries Service). 2012a. Threatened and endangered status for distinct population segments of Atlantic Sturgeon in the Northeast Region. Federal Register 77:24(6 February 2012):5879–5912.

NMFS (National Marine Fisheries Service). 2012b. Final listing determinations for two distinct population segments of Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) in the Southeast. Federal Register 77:24(6 February 2012):5913–5982.

NMFS (National Marine Fisheries Service) and USFWS (U.S. Fish and Wildlife Service). 2009. Endangered and threatened species; determination of endangered status for the Gulf of Maine distinct population segment of Atlantic Salmon. Federal Register 74:117(19 June 2009):29343–29387.

Poulos, H. M., K. E. Miller, M. L. Kraczkowski, A. W. Welchel, W. R. Heineman, and B. Chernoff. 2014. Fish assemblage response to a small dam removal in the Eightmile River system, Connecticut, USA. Environmental Management 54:1090–1101.

Scherelis, C., and G. B. Zydlewski. 2020. Using hydroacoustics to relate fluctuations in fish abundance to river restoration efforts and environmental conditions in the Penobscot River, Maine. River Research and Applications 36:234–246.

Sprankle, K. 2005. Interdam movements and passage attraction of American Shad in the lower Merrimack River main stem. North American Journal of Fisheries Management 25:1456–1466.

Weaver, D. M., M. Brown, and J. D. Zydlewski. 2019. Observations of American Shad *Alosa sapidissima* approaching and using a vertical slot fishway at the head-of-tide Brunswick Dam on the Androscoggin River, Maine. North American Journal of Fisheries Management 39:989–998.

Wippelhauser, G. S., J. Sulikowski, G. B. Zydlewski, M. Kieffer, and M. T. Kinnison. 2017. Movements of Atlantic Sturgeon of the Gulf of Maine inside and outside the geographically defined DPS. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 9:93–107.

Wippelhauser, G. S., G. B. Zydlewski, M. Kieffer, J. Sulikowski, and M. T. Kinnison. 2015. Shortnose Sturgeon in the Gulf of Maine: use of spawning habitat in the Kennebec system and response to dam removal. Transactions of the American Fisheries Society 144:742–752.

Yoder, C. O., B. H. Kulik, J. M. Audet, and J. D. Bagley. 2006. The spatial and relative abundance characteristics of the fish assemblages in three Maine Rivers, 2002 and 2003. Midwest Biodiversity Institute, Technical Report MBI/12-05-1, Columbus, Ohio.

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