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Authors: Lake, Tara R. Trinko, Ravana, Kyle R., and Saunders, Rory

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Evaluating Changes in Diadromous Species Distributions and Habitat Accessibility following the Penobscot River Restoration Project

Tara R. Trinko Lake,* Kyle R. Ravana, and Rory Saunders
National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Maine Field Station, 17 Godfrey Drive, Suite 1, Orono, Maine 04473, USA

Abstract
The Penobscot River basin, covering approximately 22,265 km^2, is the largest river wholly within Maine and the second largest river system in New England. The Penobscot River Restoration Project (PRRP) is a multimillion-dollar endeavor that aims to restore native sea-run fish through the removal of two main-stem dams and improved fish passage at a third dam on the Penobscot River. We used geographical information systems, accounts of historic ranges, and barrier survey data to estimate species-specific distributions and habitat accessibility for 11 diadromous species before and after the proposed restoration. We predict a range of outcomes in terms of expected distribution and accessibility that are largely based on habitat use and life history differences. For 4 out of 11 species (Atlantic sturgeon *Acipenser oxyrinchus*, shortnose sturgeon *A. brevirostrum*, Atlantic tomcod *Microgadus tomcod*, and striped bass *Morone saxatillis*), the PRRP is anticipated to provide access to 100% of their historic freshwater habitat. However, for alewives *Alosa pseudoharengus*, approximately 69% of the historic spawning and rearing habitat will remain inaccessible due to the presence of other passage barriers. Our results demonstrate that the PRRP is an important step toward ecosystem recovery in the Penobscot River basin but that other restoration activities will be needed to realize the full potential of the PRRP, particularly for alosines. Further, our results provide the first spatial analysis of diadromous fish distribution and access following the PRRP and serve as the baseline for developing a guiding image for expected diadromous fish population responses following the dam removals.

Diadromous fish populations are important to humans through both commercial and recreational fisheries, but also to ecosystems (Willson and Halupka 1995) through such mechanisms as the delivery of marine-derived nutrients to terrestrial ecosystems (Durbin et al. 1979; Kline et al. 1990); the provision of prey for many species of terrestrial vertebrates (Cederholm et al. 1989), birds (Wood 1986), marine mammals (Cairns and Reddin 2000), and other fish (Schulze 1996); and potential reductions in the predation risks for less abundant fish species (Saunders et al. 2006). The declines of many diadromous fish populations in the Northwest Atlantic are documented (Limburg and Waldman 2009), yet the ecological ramifications of these declines are poorly understood.

In the northeastern United States, the decline of the native suite of diadromous fish has been attributed to dams, overfishing, and pollution (Moring 2005). Marine survival has also become more widely recognized as an important influence in population dynamics, particularly for Atlantic salmon *Salmo salar*. A substantial decline (i.e., regime shift) in the productivity of the marine environment since the early 1990s is correlated with Atlantic salmon population declines throughout their range (Chaput et al. 2005). The historic declines and consequent low abundances in contemporary diadromous populations (particularly for Atlantic salmon in Maine) are largely attributable to the construction and operation of dams (Cutting 1959; NRC 2004; Gephard 2008).

Subject editor: John Waldman, Queens College, Flushing, New York, USA

*Corresponding author: tara.trinko@noaa.gov
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In response to the declines in diadromous fish populations, both small-scale (e.g., fishway installations; see Havey 1961) and large-scale restoration efforts (e.g., the removal of Edwards Dam; see Casper et al. 2006) have been undertaken to enhance stocks in the Northeast. However, assessing the success of these projects has been difficult for two key reasons. First, few restoration projects incorporate monitoring ecological changes (Hart et al. 2002). As a result, many projects are touted as "highly successful" without evidence. Also, Stanley and Doyle (2003) highlight the paucity of data supporting even the most basic results from dam removals: enhanced migratory fish access. Stanley and Doyle (2003) noted that as of that time no studies had documented changes in the population size of migratory fish attributable to dam removal. Second, there has been a lack of consensus regarding what constitutes a successful river restoration project. The five criteria proposed by Palmer et al. (2005) and responses by Jansson et al. (2005) and Gillilan et al. (2005) have greatly advanced progress toward refining standards of evaluation. The first criterion for a successful river restoration project, introduced by Palmer et al. (2005), is the idea of a "guiding image" that allows for a more precise evaluation of project success and failure. The other four criteria are ecosystem improvement, increased resiliency, no lasting harm, and ecological assessment.

The Penobscot River Restoration Project (PRRP) is among the largest and most ambitious river restoration projects currently under way in the United States. The Penobscot River is the second largest river basin in New England, covering approximately 22,265 square kilometers, and drains most of central Maine. Historically, the Penobscot River held significant numbers of diadromous fish species, including alewives *Alosa psuedoharengus*, American eels *Anguilla rostrata*, American shad *A. sapidissima*, Atlantic salmon, Atlantic sturgeon *Acipenser oxyrinchus*, Atlantic tomcod *Microgadus tomcod*, blueback herring *A. aestivalis*, rainbow smelt *Osmerus mordax*, sea lamprey *Petromyzon marinus*, shortnose sturgeon *Acipenser brevirostrum*, and striped bass *Morone saxatillis*. Throughout much of the 19th century, the estimated annual commercial harvest of alosines in the Penobscot River numbered in the millions (Foster and Atkins 1869). Presettlement abundance estimates of anadromous Atlantic salmon spawners range from 40,000 (Baum 1983) to 100,000 (Foster and Atkins 1869).

Many diadromous fish populations are presently at all-time lows in Maine. River herring populations are well below historical estimates, and alewife and blueback herring are listed as a species of concern by the National Marine Fisheries Service (NMFS). There is no longer a commercial fishery for American shad in Maine due to dwindling stocks, and the species has been extirpated from many rivers in the state. Atlantic salmon and shortnose sturgeon are listed as endangered (USOFR 1967, 2009) under the U.S. Endangered Species Act (1973). Additionally, in 2012 Atlantic sturgeon were listed as threatened within the Gulf of Maine distinct population segment (USOFR 2012). The current low abundance of diadromous fish has served as the main impetus for the restoration of the Penobscot River.

The PRRP, which is managed by the nonprofit Penobscot River Restoration Trust, centers on the removal of the two lowermost dams on the Penobscot River (Veazie Dam at rkm 48 and Great Works Dam at rkm 60; Figure 1) and the decommissioning of the power plant at Howland Dam (rkm 100) and installation of a fish bypass system there. The planned dam removals will leave Milford Dam (rkm 62) as the lowest dam on the mainstem Penobscot River. Designs for a new fish lift at Milford Dam are scheduled to be completed in 2012 and construction is anticipated in the summer of 2012.

Both dam removals and the provision of fish bypass systems have been shown to have a positive effect on diadromous fish species by restoring passage through migration corridors (Burdick and Hightower 2006). It is important to note that there are other aspects that will influence restoration outcomes when undertaking a project of this nature. For example, the PRRP could allow invasive species to colonize new areas. In addition, other barriers may continue to impede migration and access to essential habitats. In the case of the Penobscot River, there are hundreds of barriers (culverts, dams, etc.) to fish passage that will affect the restoration outcomes of the PRRP. Passage efficiencies at the remaining dams must be taken into consideration because the proportion of migrating fish successfully passing heavily obstructed waterways may remain low (Power and McCleave 1980; Keefer et al. 2004; Calles and Greenberg 2005; Holbrook 2007) and fishways are never 100% efficient (Moring 2005). Often fishways are engineered for upstream passage and little consideration is given to downstream passage. Consequently, there may be a high level of mortality when iteroparous fish attempt to return to the sea after spawning (Oldani et al. 2007). Given the lack of information about restoration outcomes following a dam removal (Bernhardt et al. 2005; Palmer et al. 2005) and the increased use of dam removals as a fisheries restoration tool (NRC 2004), there is a need to make accurate estimates of what can be expected from these efforts.

In the following sections of this article, we predict the changes to distribution and habitat accessibility for native diadromous species that will follow implementation of the PRRP. The purpose of this analysis is to provide a starting point for the development of an unbiased guiding image for the Penobscot River after the implementation of the PRRP. This effort aims to estimate habitat gains for 11 species of diadromous fish in the Penobscot River basin in an attempt to better understand the potential restoration outcomes and to identify additional restoration needs subsequent to this large-scale dam removal effort.

METHODS

We used life history characteristics (Flescher and Martini 2002; Klein-MacPhee 2002a, 2002b; Munroe 2002; Musick 2002) and historic accounts of the Penobscot River (Saunders

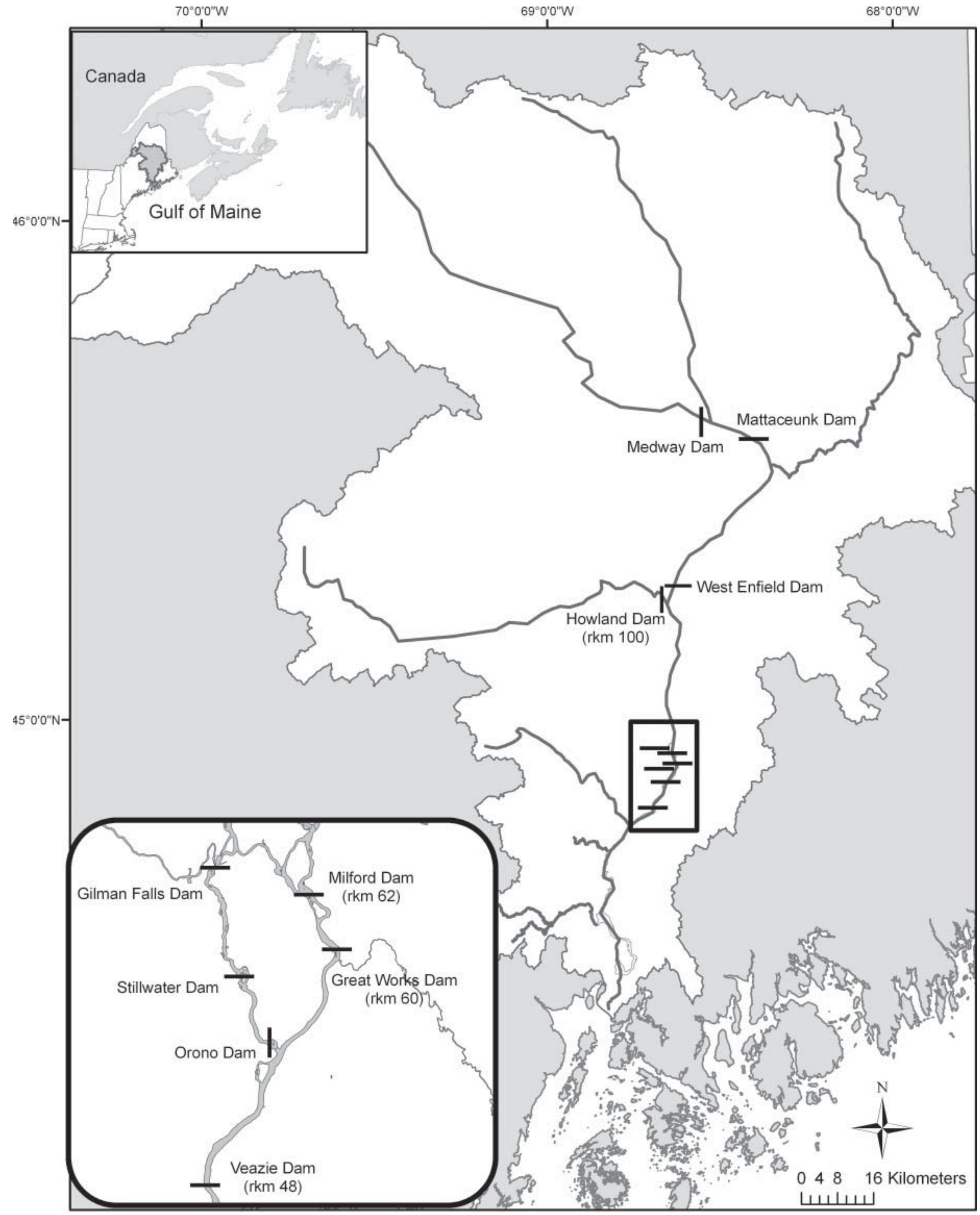

FIGURE 1. Map of the Penobscot River watershed showing the locations of the major hydropower dams. Future projects include the removal of Veazie and Great Works dams, the installation of a fish lift at Milford Dam, and the installation of a bypass channel at Howland Dam.

et al. 2006; Houston et al. 2007) to divide the 11 diadromous species into the following four groups: lower-river, middle-river, upper-river, and lake spawners. Lower-river species are characterized by their use of main-stem river habitat that roughly coincides with the head of tide; historically their migrations extended upstream to Milford Falls (the current site of Milford Dam; Figure 1). Lower-river species include Atlantic sturgeon, shortnose sturgeon, Atlantic tomcod, rainbow smelt, and striped bass. Middle-river species are also main-stem river spawners, but they have been documented to move well above the head of tide. These species do not migrate into headwater reaches and include American shad and blueback herring. Upper-river species' migrations extend well into headwater streams; these species include Atlantic salmon, sea lampreys, and American eels. Alewives comprise the final group, lake spawners. They utilize slow water for both spawning and rearing, but in Maine they have primarily been documented spawning in lake habitat.

Distribution.—Diadromous fish distributions from Saunders et al. (2006) and Houston et al. (2007) were digitized using ArcGIS 9.3 software by stream reach from the medium-resolution National Hydrography Dataset. The current, predicted, and historic distributions of diadromous fish were estimated using previously reported distributions, the National Inventory of Dams database, fishway locations (N. Dube, Maine Department of Marine Resources, personal communication), culvert surveys (Abbot 2008; A. Abbot, U.S. Fish and Wildlife Service, unpublished data), and life history characteristics. Distribution is solely presented as species occurrence (i.e., presence/absence); therefore, distribution does not include demographic considerations such as passage inefficiencies at individual dams, species-specific swimming performance, or localized habitat suitability. For the purposes of this analysis, we assume that existing fishways and the proposed Milford Dam fish lift will pass the species under consideration. Thus, the analysis portrays a "best-case" scenario in terms of expected distributional changes.

We calculated the predicted distribution gain as the potential number of river kilometers that could become newly occupied as a direct result of the PRRP. We calculated the percent gain post-PRRP as follows:

$$\%\ \text{Gain PostPRRP} = ([\text{predicted distribution} - \text{current distribution}]/\text{historic distribution}) \times 100.$$

For alewives, we quantified the lake hectares historically available compared with current availability and predicted the availability post-PRRP. Atlantic salmon were not included in the habitat gain calculations due to current state and federal stocking programs throughout the watershed (USASAC 2009). American eels and sea lampreys were also omitted from this calculation because of current passage at existing project dams and current distribution throughout the watershed (Kulik 2008; MDMR 2009).

Access.—Two additional metrics were used to categorize the habitat gains or improvements in habitat accessibility post-PRRP. First, we calculated Penobscot River basin habitat accessibility pre- and post-PRRP using the 12-digit U.S. Geological Survey hydrologic unit code (HUC12) subwatershed area. Using existing fishway information and the National Inventory of Dams database for the pre– and post–dam removal conditions, each HUC12 in the Penobscot River basin ($n = 258$) was coded with the number of fishways that a fish would be required to pass in order to reach the subwatershed. HUC12s that had more than a 50% inaccessible area due to complete passage blockages were coded as inaccessible. Second, for species that historically migrated above Milford Falls, we binned the river kilometers above Veazie Dam into the following categories: 0 fishways, 1 fishway, 2 fishways, 3 fishways, 4 fishways, and 5–7 fishways. The bins were determined by the number of fishways each species would be required to traverse to access the habitat pre- and post-PRRP.

RESULTS

Distribution

Our results show that diadromous fish distributions in the Penobscot River will range from 53% to 100% of historic ranges post-PRRP (Table 1; Figure 2). Lower-river species are expected to gain access to roughly 100% of their historical range (Table 1). Middle-river species will have access to 93% of their historic distributions. The current distribution of upper-river species is slightly more than half of the historic distribution (53%). We predict no changes in the distributions for Atlantic salmon, American eels, and sea lampreys following the PRRP due to the species' occurrence above project dams and the lack of additional dam removals in upper watershed areas. Alewives currently have access to 14 lakes, or 8% of the total lake hectares historically available for spawning. Post-PRRP, we predict that alewives will have improved access to an additional 39 lakes. Approximately 69% of the total amount of historic spawning habitat (56 lakes) will remain inaccessible due to the presence of other passage barriers, such as dams at the outlets of lakes.

Access

The removal of Great Works and Veazie dams and the installation of the new fishways will improve river access by decreasing the number of barriers to migration. However, we estimated that the PRRP will provide unimpeded access (0 fishways) to only one additional subwatershed (Figure 3; Table 2), or 14 km of main-stem river. Subwatersheds with unimpeded access account for only 6% of the total watershed area before dam removal and will account for 7% of the total watershed area after dam removal. Subwatersheds considered inaccessible ($n = 103$) due to lack of fish passage account for 41% of the total watershed area before and after the PRRP dam removals.

TABLE 1. Historical, current, and predicted accessible river kilometers for 11 species of diadromous fish following the Penobscot River Restoration Project (PRRP). Asterisks denote alewife habitat (ha) from lakes >4 ha.

Migratory extent	Species	Current distribution (km)	Predicted distribution (km)	Predicted distribution gain (km)	Historical distribution (km)	% Gain post-PRRP	% Habitat accessible post-PRRP
Lower river	Atlantic tomcod	52	52	0	52	0	100
	Atlantic sturgeon	51	73	22	73	31	100
	Shortnose sturgeon	51	73	22	73	31	100
	Rainbow smelt	76	98	21	103	21	95
	Striped bass	64	86	22	86	26	100
Middle river	American shad	177	730	552	786	70	93
	Blueback herring	177	730	552	783	70	93
Upper river	American eel	6,162	6,162	[a]	11,569	[a]	53
	Atlantic salmon	6,162	6,162	[a]	11,569	[a]	53
	Sea lamprey	6,162	6,162	[a]	11,569	[a]	53
Middle river/lake	Alewife*	3,002	12,140	9,137	39,425	23	31

[a]Atlantic salmon were not included in the habitat gain calculations due to stocking throughout the watershed. American eel and sea lamprey were also omitted because of current passage at existing project dams and current distribution throughout the watershed.

We predict that the PRRP will improve access for diadromous fish on a basinwide scale. After the restoration project, 50% of the watershed area (130 of 258 subwatersheds) will have improved accessibility. Of subwatersheds with improved access, 15% of the watershed area will be above one or fewer fishways and 85% above two or more. Accessibility to subwatersheds above Milford Dam is predicted to improve, shifting from a maximum of seven fishways to five fishways (Figure 4). Middle-river species are predicted to have unimpeded access (0 fishways) to an additional 22 km of river and approximately 35% of their historic range by migrating through up to one fishway (Table 3). If American shad and blueback herring can successfully traverse up to three dams post-PRRP, they will have access to 529 km of historic habitat. Upper-river species will gain unimpeded access to 49 km of habitat following the PRRP. Of the improved-access reaches for upper-river species, 12% are above 1 or fewer fishways while over three-quarters (4,729 km) are above two or more fishways following the implementation of the PRRP. There are no additional unimpeded access lakes for alewives post-PRRP, and 39 lakes will have improved access post-PRRP, with five of those (1,117 ha) accessible through one fishway.

DISCUSSION

This study provides the first comprehensive spatial analysis of diadromous fish distribution and access for the PRRP. We expect to observe a range of outcomes in terms of habitat gains for the diadromous fish community post-PRRP. Lower-river species (e.g., sturgeon) will experience gains in both predicted distributional shifts and in terms of accessibility to historic habitat. These species are now limited to the area below Veazie Dam; following implementation of the PRRP, they will have unimpeded access to roughly 100% of their entire historic range in the Penobscot River basin. The PRRP, therefore, represents a complete cessation of all passage impediments to lower-river species in Maine's largest river. Middle-river species (e.g., American shad) are predicted to have access to over 90% of their historic habitat, assuming that they are able to successfully pass the new Milford Dam fishway and several other existing fishways. Therefore, the implementation of the PRRP will allow them to access vital spawning grounds, the vast majority of which have been inaccessible for at least the last 50 years. The distributions of upper-river species (e.g., American eels) will not change because these species can successfully navigate most main-stem fishways. These species will, however, have greatly improved

TABLE 2. Penobscot watershed habitat accessibility by subwatershed (HUC12) area (km^2). Habitat accessibility is represented by the number of fishways a hypothetical fish would need to navigate in order to access each subwatershed.

	Number of fishways						
Stage	0	1	2	3	4	5–7	Inaccessible
Pre-PRRP	1,404 (17)	500 (6)	302 (3)	1,499 (19)	6,459 (74)	2,992 (36)	9,146 (103)
Post-PRRP	1,493 (18)	1,967 (24)	6,638 (76)	1,683 (20)	770 (8)	605 (9)	9,146 (103)

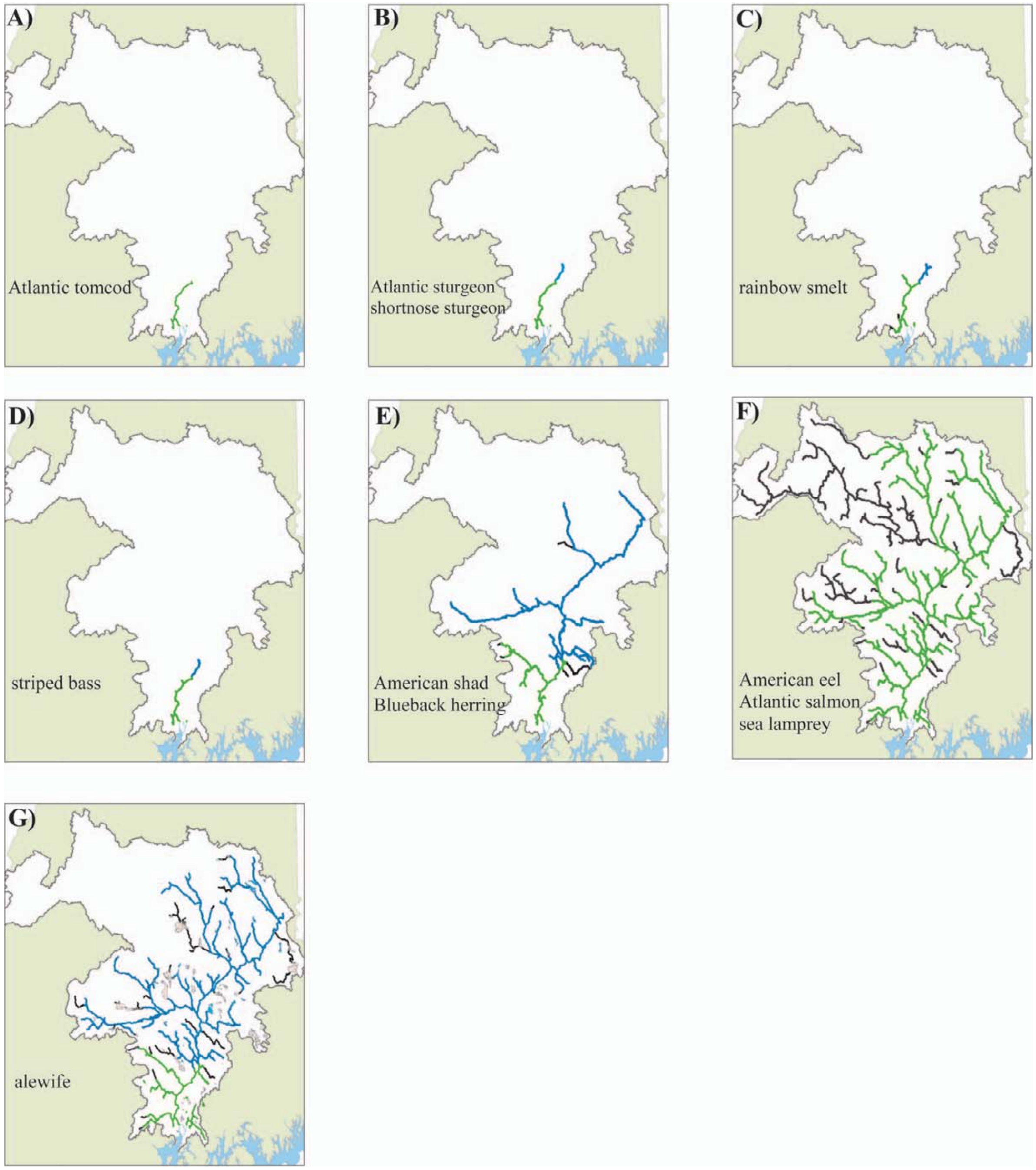

FIGURE 2. Spatial distribution of current (green), predicted (postrestoration; blue), and historic (black) habitat in the Penobscot River for the lower-river species **(A)** Atlantic tomcod, **(B)** Atlantic and shortnose sturgeon, **(C)** rainbow smelt, and **(D)** striped bass; the middle-river species **(E)** American shad and blueback herring; and the upper-river species **(F)** Atlantic salmon, American eel, and sea lamprey and **(G)** alewives. For clarity, only rivers and streams with a stream order of three or more are shown.

access to freshwater habitats as a result of the PRRP. The demographic effects of upstream and downstream passage inefficiency can be quite severe for these species (McCleave 2001).

Predicted distributions and accessibility are slightly different for alewives because they require access to slow moving water often in the form of lakes and ponds to complete their life history. Historically, alewives migrated hundreds of kilometers up the Penobscot River to reach spawning habitats (Foster and Atkins 1867) and were an important component of the ecosystem. Alewives may have served as a prey buffer for other fish species, such as Atlantic salmon (Saunders et al. 2006), as well as a source of marine-derived nutrients (Durbin et al. 1979;

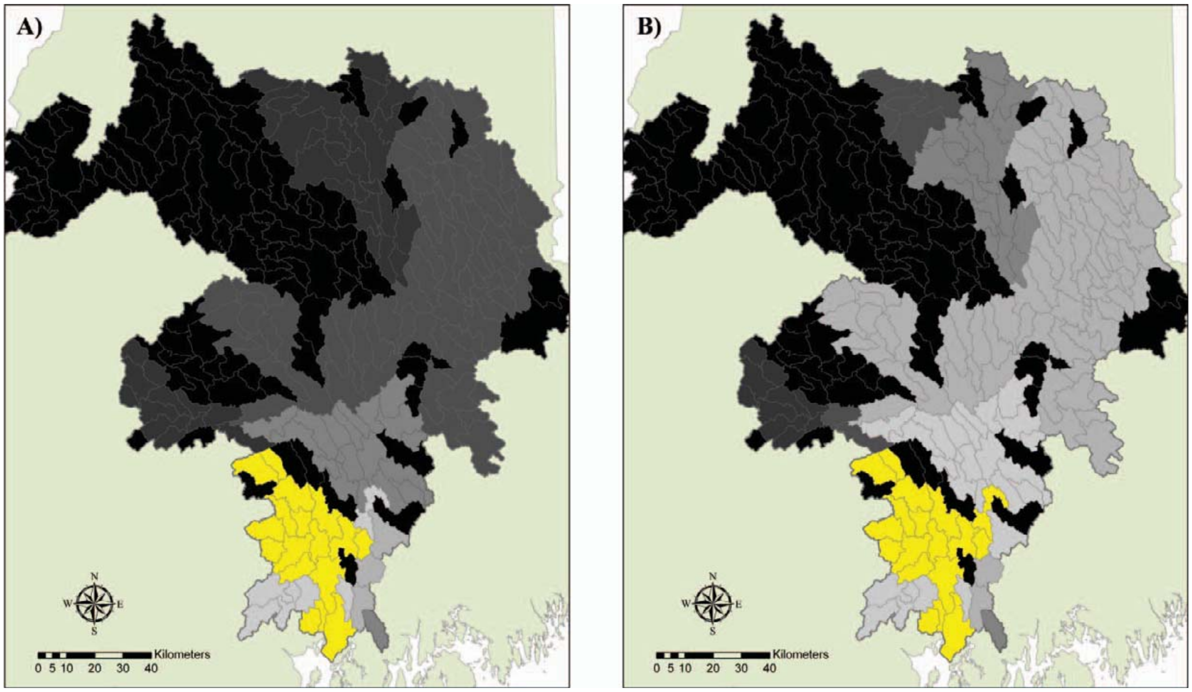

FIGURE 3. Subwatershed (12-digit HUC) accessibility **(A)** before and **(B)** after Penobscot River restoration. Subwatersheds with open access (no fishways) are denoted by the color yellow. The various shades of gray represent the different numbers of fishways that must be navigated to access the different subwatersheds, from the lightest shade (1 fishway) to the darkest (5–7 fishways). Subwatersheds that are more than 50% inaccessible are denoted by the color black.

Walters et al. 2009) in the Penobscot River. These migratory depositions of marine-derived nutrients have the potential to enhance the river's biological and ecological production capabilities (Flecker et al. 2010), as has been demonstrated in the western United States with Pacific salmon *Oncorhynchus* spp. (Schudt and Hershey 1995; Wipfli et al. 1998; Johnston et al. 2004). Currently, alewife distributions do not extend past Milford Dam (Kulik 2008; Gail Wippelhauser, Maine Department of Marine Resources [MDMR], personal communication). Due to the widespread distribution of small dams throughout the watershed (Hall et al. 2011), we predict that little lake habitat will be made available to alewives post-PRRP; thus, the various ecosystem services performed by alewives will not be restored unless additional lake habitat is made available.

Thus, we predict a range of outcomes in terms of habitat accessibility following the implementation of the PRRP and suggest that the PRRP is a necessary first step in increasing access to valuable diadromous species spawning habitats; however, it is not the only step that needs to be undertaken to achieve recovery of sustainable populations of diadromous fish in the Penobscot River. The analysis in this paper is an intermediate step toward creating a guiding image for the PRRP in terms of diadromous fish recovery potential and conceptual model development for the success of the project. The lack of a guiding

TABLE 3. Habitat accessibility (river kilometer) above Veazie Dam before and after the PRRP for species that historically migrated above Milford Falls. Asterisks denote alewife habitat (ha) from lakes >4 ha.

	Pre-PRRP by number of fishways						Post-PRRP by number of fishways					
Species	0	1	2	3	4	5–7	0	1	2	3	4	5–7
American shad and blueback herring	0	19	5	0	0	0	22	178	280	49	13	27
American eel, Atlantic salmon, and sea lamprey	0	46	43	553	3,002	1,726	49	593	3,002	1,045	366	316
Alewife*	0	0	495	0	0	0	0	1,117	8,232	352	0	11
Number of lakes			1					5	30	3		1

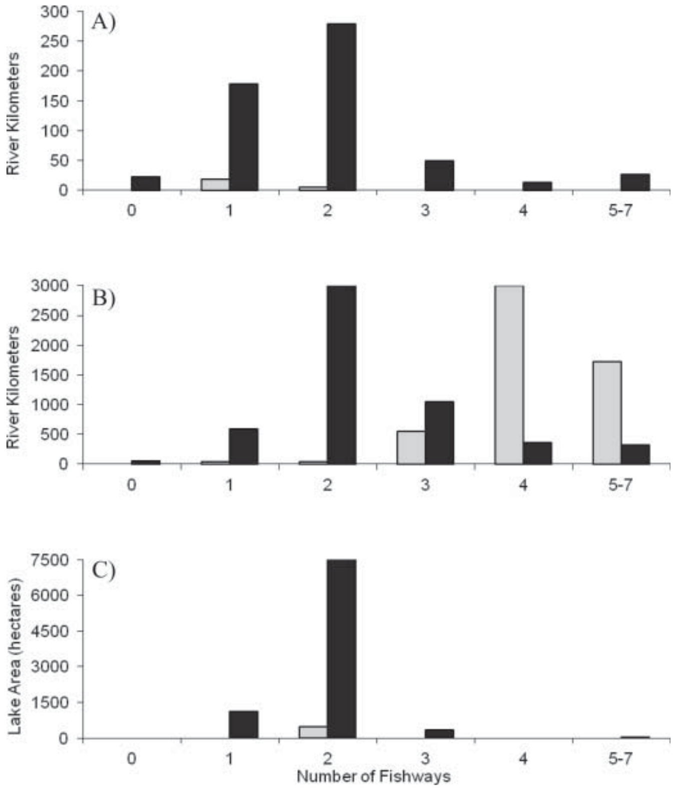

FIGURE 4. Habitat availability above Veazie Dam before (gray bars) and after (black bars) Penobscot River restoration, by number of fishways, for **(A)** American shad and blueback herring; **(B)** Atlantic salmon, sea lampreys, and American eels; and **(C)** alewives.

image, or "guiding image drift" (Gillilan et al. 2005), is a significant threat to the success of restoration projects, including the PRRP. Other dam removal projects, such as that of the Elwha River in the Pacific Northwest, have developed such conceptual models (Woodward et al. 2008) and used historic information and empirical models to predict fish distributions pre– and post–dam removal (Brenkman et al. 2008). Now that this information is available for the Penobscot River, a next step would be the development of conceptual models and hypotheses that can be tested in an adaptive-management context. Preliminary work on this front has been done by the Nature Conservancy and the MDMR. However, a comprehensive guiding image or definition of "success" for the PRRP has not yet been agreed to by all parties (the Penobscot River Restoration Trust, state agencies, federal agencies, tribal nations, and the public). In particular, consideration of the possible risks associated with the potential spread of exotic species (similar to the northern pike *Esox lucius* risk assessment; MDMR 2009, appendices J and K) should be explicitly included into the development of the guiding image for the PRRP.

Several aspects of the analyses presented in this article could be further refined by additional scrutiny of the historic and predicted species distributions, habitat suitability and population demographics, and upstream and downstream passage rates at existing dams. With respect to species distributions, many of the historic distributions used in our analysis are based on fishery reports from the late 1800s. Reports such as these should be viewed carefully (Swetnam et al. 1999); reference to these historic accounts is not intended to make a case for returning to historic conditions but rather to establish a baseline to guide restoration work. The potential distributions used in our analyses are based on contemporary barrier surveys that may be incomplete (Abbot 2008). Therefore, it is likely that we overestimated the species distributions in some instances and underestimated them in others. With respect to habitat suitability and population demographics, we believe that population modeling could inform restoration target development. However, data limitations may preclude meaningful demographic modeling for many species, though some initial efforts have been made (MDMR 2009). Finally, with respect to upstream and downstream passage rates, our assumptions for fish upstream passage at existing and future fish passage facilities in the Penobscot River are very optimistic, especially given the lack of studies confirming the passage of alosines at fishways upstream of Milford Dam. Information such as the above would greatly enhance the scientific rigor of demographic projections and thus substantially refine the overall guiding image for the PRRP.

Although additional analysis is clearly warranted, our analyses do clarify the importance of the remaining barriers in terms of the restoration potential of diadromous fish following the implementation of the PRRP, particularly for middle-river species and alewives. If middle-river species are able to effectively use the fish lift at Milford, the nature-like fishway at Howland, and the existing fishways at West Enfield and Mattaceunk dams, they will have potential access to nearly 93% of their historical habitat in the Penobscot River basin. However, if (for example) the proposed fish lift at Milford Dam does not effectively pass middle-river species such as American shad, the recovery outlook for these species would remain bleak. Even state-of-the-art fishways may be problematic if site-specific considerations are not adequately addressed (Moring 2005). For example, Sprankle (2005) noted the lack of effective passage (roughly 10%) at a Merrimack River fish lift in 2002. The lack of effective fish passage precludes passage to roughly 70% of the remainder of the Merrimack River basin (Sprankle 2005).

In addition, the cumulative effects of and downstream passage inefficiencies at the remaining dams are vital, particularly given the iteroparous life history of American shad (Castro-Santos and Letcher 2010). While our analyses show that the PRRP will provide access to an additional 552 rkm for shad, 63% of them are above two or more fishways. There is evidence that shad primarily spawn during their downstream migration (Maltais et al. 2010). Demographically speaking, these new habitats could have little influence on the overall population growth of the species if the effect of downstream passage on the survival of repeat spawners and out-migrating juveniles is not taken into account.

In conclusion, we believe that the prospects for success are quite high for the PRRP. For the PRRP to live up to its potential, however, we suggest that each of the five criteria suggested by Palmer et al. (2005) require additional attention. In particular, the analyses presented in the previous sections of this article are intended as an important first step toward the completion of the guiding image. Steps toward implementing the other four criteria are now under way as well. For example, the removal of Great Works Dam is preceding the removal of Veazie Dam largely to ensure that Atlantic salmon broodstock can be collected at the Veazie fishway until the Milford fish lift is fully operational. This ensures that no lasting harm will be inflicted upon the genome of the Penobscot River population of Atlantic salmon. In addition, substantial prerestoration monitoring efforts have already begun, including fish community assessment, hydrologic and hydraulic evaluations, water quality surveys, and riparian and wetland surveys, among others. This serves to meet the fifth criterion of conducting and publicizing pre- and postassessments. Thus, with minimal additional effort directed at conceptual model and guiding image development, the likelihood of an ecologically successful outcome could be substantially heightened.

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