Landscape Ecol
DOI 10.1007/s10980-010-9539-1

RESEARCH ARTICLE

The historic influence of dams on diadromous fish habitat with a focus on river herring and hydrologic longitudinal connectivity

Carolyn J. Hall · Adrian Jordaan · Michael G. Frisk

Received: 23 February 2010 / Accepted: 1 October 2010

Abstract The erection of dams alters habitat and longitudinal stream connectivity for migratory diadromous and potamodromous fish species and interrupts much of organismal exchange between freshwater and marine ecosystems. In the US, this disruption began with colonial settlement in the seventeenth century but little quantitative assessment of historical impact on accessible habitat and population size has been conducted. We used published surveys, GIS layers and historical documents to create a database of 1356 dams, which was then analyzed to determine the historical timeline of construction, use and resultant fragmentation of watersheds in Maine, US. Historical information on the anadromous river herring was used to determine natural upstream boundaries to migration and establish total potential alewife spawning habitat in nine watersheds with historic populations. Dams in Maine were constructed beginning in 1634 and by 1850 had reduced accessible lake area to less than 5% of the virgin 892 km^2 habitat and 20% of virgin stream habitat. There is a near total loss of accessible habitat by 1860 that followed a west-east pattern of European migration and settlement. Understanding historic trends allows current restoration targets to be assessed and prioritized within an ecosystem-based perspective and may inform expectations for future management of oceanic and freshwater living resources.

Keywords Historical Ecology · Gulf of Maine · Habitat fragmentation · Alewife · Blueback herring · Forage fish · Ecosystem · Energy flux · Restoration targets

Electronic supplementary material The online version of this article (doi:10.1007/s10980-010-9539-1) contains supplementary material, which is available to authorized users.

C. J. Hall (✉) · A. Jordaan · M. G. Frisk
School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, NY 11794-5000, USA
e-mail: cjhall29@me.com; info@gomher.org

Introduction

Widespread species loss and large-scale environmental change over the past 400 years has been well documented (Foster et al. 2002; Lotze et al. 2006; Jackson 2008). One prominent environmental change has been the fracturing of coastal watersheds by man-made obstructions (Dynesius and Nilsson 1994; Humphries and Winemiller 2009). Damming of waterways alters the aquatic environment and surrounding landscape through sedimentation, channelization, flooding and temperature changes (Poff et al. 1997; Poff and Hart 2002; Walter and Merritts 2008). Passage of aquatic migratory species between feeding and spawning sites is interrupted, as is the exchange of nutrients among ecosystems (Kline et al. 1990; Bilby et al. 1996; Walters et al. 2009). Subsequent habitat and population loss leads to alteration of foodwebs, loss of biodiversity, species decline and extirpation

Published online: 04 November 2010

(Pringle et al. 2000; Jackson et al. 2001; Pess et al. 2008; Morita et al. 2009). An understanding of the historical condition of ecosystems before significant anthropogenic impact is required to assess restoration targets, yet landscape studies and ecological baselines are often lacking historical perspective or use incomplete data (Wu et al. 2003). Historical data is needed to empirically evaluate the loss of habitat connectivity in relation to species presence and ecosystem function over centuries to effectively apply conservation and restoration methods (Haila 2002).

In the northeastern U.S., concentrated commercial fishing, forestry, agriculture and damming of riverways began altering the condition of river ecosystems with the arrival of European colonists in the seventeenth century. Unfortunately, reliable records of watershed conditions and fish harvests were not kept until the formation of Federal and State Fish Commissions in the 1860s (Atkins and Foster 1868; Judd 1997). Previous to these records were numerous mentions of colonial mill dams obstructing the migration of spawning fishes including river herring [collectively alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*)], shad (*Alosa sapidissima*), Atlantic salmon (*Salmo salar*) and Atlantic sturgeon (*Acipenser oxyrinchus*) (Anonymous 3/26/1798; Moody 1933, pp 445–446). After the construction of the first saw mill dam in Maine in 1634 (Pope 1965, p. 219), hundreds of small dams appeared statewide wherever natural waterfalls and topography provided an area of impoundment and the vertical height required to generate mechanical energy (Moody 1933, p. 332; Clark 1970, p. 336). In 1829 it was estimated that 1,686 principal manufacturing establishments, primarily mills, depended upon water-power (Greenleaf 1829, p. 451). Forty years later, over 3,100 sites in use or potentially suitable for harnessing water-power were documented in Maine (Wells 1869).

The species listed above are diadromous, crossing the ocean-freshwater boundary to complete spawning, and provided abundant resources to historical local diets and commercial fisheries along the Gulf of Maine's coastal and inland ecosystems (Atkins and Foster 1868; Mullen et al. 1986). They also provided a rich forage base for valuable coastal predators and game fish including Atlantic cod (*Gadus morhua*) (Baird 1872; Graham et al. 2002). Decline of coastal cod populations has been linked to the loss of the nutritious and predictable food source these species provided (Baird 1883; Ames 2004). By 1870, State Fish Commissioners concluded that dam construction was the principal cause of migratory fish extinction from Maine's waterways (Atkins and Foster 1868) and 20 years later estimated that only 10% of original habitat remained available for spawning (Atkins 1887). Current diadromous species' populations are at historic lows with some at less than 1% of early nineteenth century estimations (Lotze and Milewski 2004; Saunders et al. 2006). Presently, river herring and Atlantic sturgeon are listed as species of concern and Atlantic salmon as an endangered species (Federal Register 2006). Thus, efforts to provide long-term solutions through population and watershed restoration are of immediate importance, yet no comprehensive attempts have been made to assess virgin habitat baselines or thoroughly document the long-term scale of habitat destruction these species have endured.

Historical records of dam construction can present a timeline of stream and landscape alteration and physical impediment of spawning diadromous species. Here we estimate the loss of accessible freshwater habitat within Maine from 1600 to 1900 due to dam obstruction. First, we present a spatial and temporal analysis of dam construction from the seventeenth through the nineteenth century. Second, we quantitatively present an analysis of accessible migratory and spawning area, both stream and lake habitat, impacted by the erection of dams over time with river herring as our example "species." Current river herring habitat status and coastal watersheds will be evaluated in light of the historical baseline determined for the state of Maine and related to restoration of stream networks and ecosystem connectivity.

Materials and methods

River herring life history

River herring are a mid-trophic level species that prey primarily on zooplankton (Bigelow and Schroeder 1953). River herring reach reproductive maturity in 3–5 years and are iteroparous, or capable of spawning for multiple years, returning to spawn in natal Maine streams between late April and early July (MDMR 1982). Alewives historically migrated over 300 km to spawning areas in quiet freshwaters of Maine, primarily lakes and ponds but also slow sections of streams;

bluebacks prefer riverine habitat up to or near head of tide with moving water. Both species will spawn below head of tide provided that appropriate habitat is available (Bigelow and Schroeder 1953; MDMR 1982). For the purpose of this study, measured stream habitat is defined broadly as accessible habitat for both species but is not included in measurable alewife spawning habitat which is limited to lakes and ponds, and thus an underestimate of total potential area.

Study area

Dams throughout Maine were documented, but analysis was limited to nine historical river herring watersheds, approximately 60% of our estimated historical range, that were divided amongst three categories: (1) primary river watersheds with extensive tributaries totaling a stream distance of 1000 km or greater; (2) secondary watersheds with few tributaries totaling less than 1000 km; (3) bay watersheds composed of multiple small rivers and coastal waterways (Fig. 1). Primary (category 1) watersheds are the Androscoggin, Kennebec and Penobscot Rivers. Secondary (category 2) watersheds are the Mousam, Sheepscot, St. George, Union and Dennys Rivers. The Casco Bay watershed with the Presumpscot River was used as the example for tertiary (category 3) watersheds. Watershed analysis

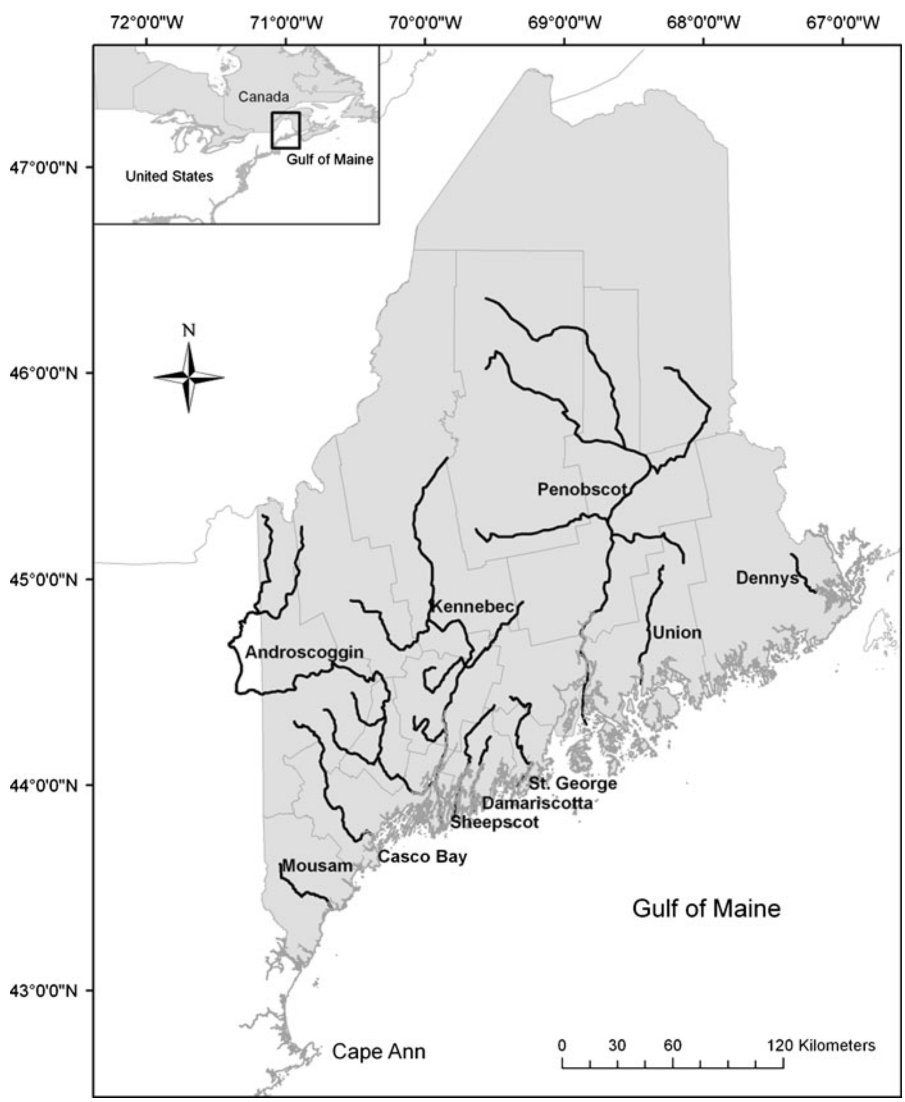

Fig. 1 State of Maine highlighted with historical river herring watersheds assessed in this study for temporal spawning habitat changes from 1600 to 1900

was constrained to within the State of Maine. The Damariscotta River watershed is also referenced in this study.

Methodology

We followed a 6-step procedure to document and map locations of dams, natural boundaries and upstream limits of diadromous fish migration, and determine the historical timeline of use and main stem blockage by dams.

1. Determination of current dam locations

The Maine Geographic Information Systems (MEGIS) Impound database completed in 2006 by the US Fish and Wildlife Service Gulf of Maine Coastal Program (MEGIS 2006) served as our initial database and includes full demographics of still functional dams including waterway, latitude and longitude, ownership, year of completion of the most recent dam at the location (not the original configuration), structural height, and limited information about recent breaches or removals. The database was developed from data collected in the U.S. Army Corp of Engineers (USACE) 1987 Dam Survey, Maine Department of Environmental Protection (MDEP), Bureau of Land and Water Quality (BLandWQ) staff for use with BLandWQ projects. The Maine Emergency Management Agency (MEMA) reviewed all point locations against existing orthophotography or digital raster graphic base layers. Point locations of dams, levees, and impoundments in Maine are at 1:24000 scale. Inventories of removed dams, potentially removable dams and currently active dams listed by MDEP (2009) were an additional source.

2. Determination of historic dams and timeline of use

The most comprehensive reference for historic dams was *The Water-power of Maine*, a hydrographic survey with water resource demographics from the 1860s (Wells 1869). Not all dams reported in Wells (1869) were included in this study. Omitted dams were: (1) not located due to an historic name or no precise location mentioned; (2) upstream of alewife migrations; (3) on tributaries above head of tide with no pond area for alewife spawning; or (4) one of many already surveyed dams on a short stretch of waterway (under 3 miles).

Nineteenth and twentieth century governmental reports were also used to identify and date original construction of dams. These included Maine Commissioner of Fisheries (COF) reports spanning from 1868 to 1899 (Atkins and Foster 1868, 1869; Atkins and Stillwell 1874; Atkins 1887; Smith 1899), and alewife fisheries reports and collections of Atlantic Sea-Run Salmon Commission river surveys and management reports through the 1980s (Rounsefell and Stringer 1945; Supplementary Materials I).

Dates and locations of dams constructed prior to Wells (1869) were found in wills, historical magazines and journals, town histories, eighteenth and early nineteenth century newspaper articles and records of early nineteenth century Maine Legislative Records containing legislative acts and petitions held at the Maine State Archives (Supplementary Materials I). Hand drawn maps labeled with early settlements included in historical publications gave clear references to location of mills and date of existence. For a full list of references used to date and locate mills and dams see Supplementary Materials I. In historical literature, mills are documented more consistently than dams, therefore it was assumed the presence of a mill indicated the presence of a dam.

3. Determination of main stem blockage

Main stem blockage, particularly dams at head of tide, was determined from historical reports by Atkins (1887) and other publications that stated the year of full obstruction and were only considered migration obstacles beginning on sourced dates.

4. Determination of natural barriers and limits to upstream alewife migration

Natural barriers and limits of anadromous species upstream passage, particularly alewives, were determined using Maine COF reports, alewife fishery and Atlantic Sea-Run Salmon Commission river survey and management reports (Atkins and Foster 1868, 1869; Atkins and Stillwell 1874; Atkins 1887; Smith 1899; Rounsefell and Stringer 1945; Supplementary Materials I). Because of historical omnipresence of alewives in Maine ponds with connection to the ocean (Atkins 1887; Mullen et al. 1986), all water bodies below natural barriers within known migration distances were considered potential spawning sites. Thus, we assumed presence of fish unless we found evidence to the contrary. Town histories were instrumental in further determining presence or absence of alewives. For example, in *The History of Sanford Maine 1661–1900* (Emery 1901, pp. 169–170) litigation regarding fish passage for salmon, alewives and shad at mills within the town of Sanford on the Mousam River is discussed. This indicates alewives surmounted the considerable falls downstream of Sanford. Our approach possibly overestimates alewife lake and pond spawning habitat and requires further water body sediment and artifact research to empirically determine historical presence.

5. GIS mapping

All dams, natural obstructions and migratory limits were mapped using ESRI® ArcGIS™ v.9.3. Map base layers in 1:24000 scale of watersheds, counties and coastline were obtained from the MEGIS database (MEGIS 2004). Latitude and longitude in decimal degrees were geo-referenced using the Geographic Coordinate System North America 1983.

6. Error checking

Latitude and longitude in decimal degrees for existing and historical dam sites were confirmed or determined using the 26th (2003) and 30th (2007) editions of the DeLorme Maine Atlas and Gazetteer™ and Google Earth 5.0 during the period of January to July 2009. Additionally, personal site visits were conducted throughout the state of Maine in 2008 and 2009 to ground-truth over 90 dams with GPS and obtain information, photographs and meet with current owners and local residents.

Analysis

Virgin spawning habitat was dated in year 1600, pre European colonization. Historical river herring migratory and spawning habitat was estimated using stream and lake demographics from MEGIS (2004). Streams categorized as perennial on the MEGIS database that led to ponds within the estimated range of alewife migration were used to calculate potential stream migration distance whereas streams categorized as intermittent or not connected to water bodies above head of tide were not included. Perennial streams below or to head of tide but without connection to water bodies were included for potential blueback migratory and spawning habitat.

Let m be the river mouth and n_v the historical natural limit of migration; virgin habitat for alewife spawning (V_A), and blueback and alewife migration ($V_{BB,A}$), is the sum of all suitable lake (L, in km^2) and stream (S, in km) habitat, respectively, such that:

$$V_A = \sum_m^{n_v} L; \quad V_{BB,A} = \sum_m^{n_v} S,$$

Accessible habitat (h_A, $h_{BB,A}$) was then calculated chronologically from 1600 to 1900 each year a new obstruction occurred within the defined virgin habitat area, where n_x is the year specific upstream migration boundary:

$$h_A = \sum_m^{n_x} L; \quad h_{BB,A} = \sum_m^{n_x} S$$

Changes in accessible habitat (H_A, $H_{BB,A}$) resulting from dam construction was calculated using:

$$H_A = V_A - h_A; \quad H_{BB,A} = V_{BB,A} - h_{BB,A}$$

Then change from virgin conditions in percent (R_A, $R_{BB,A}$) since 1600 was calculated:

$$R_A = \frac{H_A}{V_A}100; \quad R_{BB,A} = \frac{H_{BB,A}}{V_{BB,A}}100$$

Results

Dam timeline

A total of 1356 historical and current dams were documented in the state of Maine from the Piscataqua/Salmon Falls River in the west to the St. Croix River in the east and all inlets and islands along the coast (Table 1). A comprehensive database with the history of each dam including use, dates of construction and reconstruction, owners, fish passage capability, hydrology, etc. can be viewed at the Gulf of Maine Historical Ecology Research website: www.GOMHER.org. Dams were grouped according to watershed access to coastal regions divided into western, central and eastern. Earliest construction of dams in the three regions was 1634, 1640 and 1763 for western, central and eastern, respectively. Of the

Table 1 Summary of historical and current dams in Maine by region and watershed[a]

Coastal region	Watershed	Total dams constructed 1600-present	Year of earliest documented dam construction	Number of dams still on watershed as of 2006[b]
Western	Piscataqua/Salmon Falls River	29	1634	12
	York River	12	1634	6
	Mousam River	24	1672	12
	Kennebunk River	10	1749	1
	Saco River	72	1648	42
	Fore River	6	1674	2
	Presumpscot River	68	1732	30
	Royal River	10	1722	4
Central	Kennebec River	226	1754	128
	Androscoggin River	145	1716	79
	Sheepscot River	47	1664	15
	Damariscotta River	8	1726	2
	Pemaquid River	6	1640	3
	Medomak River	12	1797	5
	St. George River	35	1647	18
	Penobscot River	283	1768	116
Eastern	Union River	36	1766	11
	Narraguagus River	15	1773	4
	Pleasant River	9	1765	2
	Machias River	13	1763	6
	East Machias River	12	1765	4
	Orange River	6	1828	4
	Dennys River	19	1787	8
	Pennamaquan River	18	1823	7
	St. John River	77	1811	48
	St. Croix River	48	1780	20
General	Coastal Waterways	110	1651	45
	Total	1356		634

[a] Includes dams that could not be assigned latitude and longitude

[b] Dams still present in 2006 at completion of the MEGIS impoundment database. Includes dams with fish passage and those more recently removed or breached

1356 dams documented in this study, 47% (634 dams) were still present on the waterways as of 2006. Not all of the locations of dams were identified clearly enough in the literature for exact, or estimated, latitude and longitude; therefore a total of 1333 dams were assigned coordinates and are presented in Fig. 2a.

Accumulation of dams across the state on all watersheds is mapped in four time periods: 1630–1750 (Fig. 2b), 1630–1800 (Fig. 2c), 1630–1850 (Fig. 2d) and 1630–1900 (Fig. 2e). A total of 43, 164, 187 and 521 dams were completed in each of the four time periods, respectively, for a total of 915 dams. Between 1750 and 1800, dam completion more than tripled and by 1900, increased 20-fold.

Dam development remained localized in the southwest of the state until northeast expansion in the mid 1700s (Fig. 2b, c). The rate of expansion to the east was more rapid than northern, or inland, but by 1850 the maximum range was reached in both directions while the density of dams continued to increase through the present (Fig. 2).

Historical habitat analysis

The Penobscot watershed had the most virgin habitat with 5332 km of streams and 327.7 km^2 of lake area whereas the Mousam watershed was the smallest with 183.5 km of streams and 10.7 km^2 of lake area (Table 2). From 1720 to 1846, impassable dams were

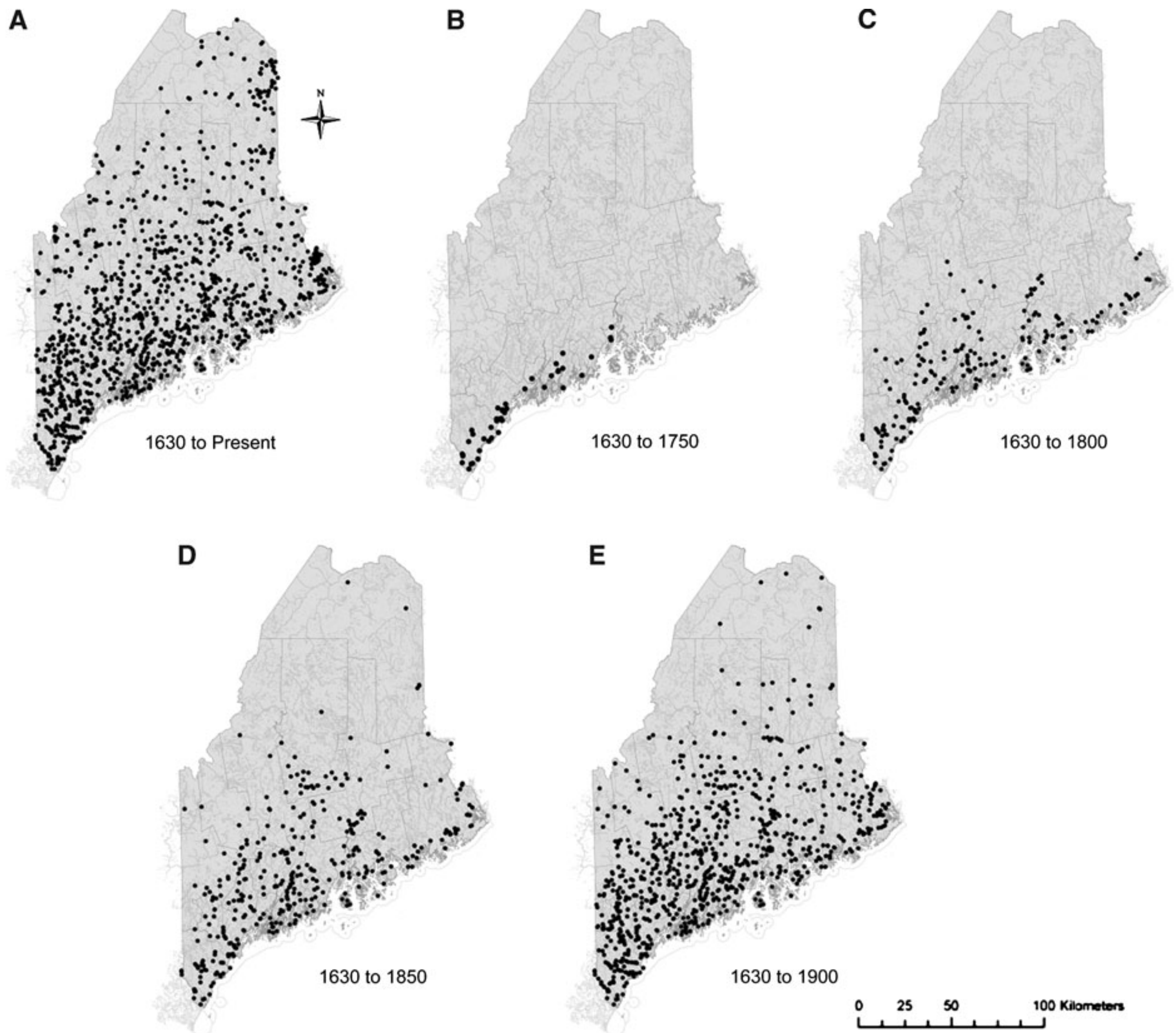

Fig. 2 Temporal and spatial accumulation of dams in Maine for which latitude and longitude were determined. Each dot represents a dam. **a** comprehensive of all dams completed through 2008. **b** all dams constructed by 1750. **c–e** the cumulative increase of completed dams in 50-year increments from 1750 to 1900

constructed at or near head of tide on the main stem of our nine historical river herring watersheds (Table 2). Head of tide dams alone reduced accessible stream distance and lake area to between 7–59% and 0–33%, respectively, having the greatest impact on the Kennebec, Mousam and Casco Bay watersheds with less than 1% of virgin lake surface area remaining after construction.

A representative watershed for each category is used to illustrate chronological changes in available spawning habitat. The Kennebec, St. George and Casco Bay represent primary, secondary and bay watersheds. See Supplementary Material II for remaining watersheds. On the Kennebec watershed, considerable reductions in stream and lake habitat first occurred in 1754. Stream habitat declined to 65.4% and lake area to 53.6% (Fig. 3a). Dam construction in 1760 reduced lake area to 25.6% of virgin habitat and in 1792 further reduced habitat to 14.8% of streams and 4.8% of lake area. In 1837 the Edwards Dam was built at head of tide which reduced stream habitat to 6.9%. The last dams to have a measurable impact on the Kennebec watershed were completed in 1867 and left 4.9% and 0.4% of stream and lake area available, respectively.

Table 2 Nine focus watersheds with total virgin stream distance (SD) and lake surface area (LSA) in year 1600 for potential accessible river herring habitat, year of head of tide dam construction and percent remaining stream and lake habitat after full obstruction at head of tide[a]

Category	Watershed	Virgin SD (km)	Virgin LSA (km^2)	Year	% SD	% LSA
1	Androscoggin	906.2	45.9	1807	14.9	4.4
1	Kennebec	2392.3	197	1837	7.3	0.5
1	Penobscot	5332	327.7	1835	18.6	8.2
2	Mousam	183.5	10.7	1720	8.1	0
2	Sheepscot	558	19.4	1762	58.2	32.4
2	St. George	549.2	31.7	1840s	20.5	6.8
2	Union	480.9	93.2	1800	21.5	5.2
2	Dennys	230.1	30.1	1846	31.9	1.9
3	Casco Bay	862.1	136.1	1819	20.9	0.1

[a] Percent calculated based on presence of head of tide dam only. Habitat loss from other dams built on watersheds previous to above years or below head of tide not considered for this estimate

On the St. George watershed, the first notable reductions in available habitat occurred in 1777 resulting in 82.7% of stream and 72.2% of lake area remaining (Fig. 3b). Obstructed at head of tide in 1785, habitat was reduced to 18.9% stream and 4.9% lake area. The last dam to have a measurable impact on accessible spawning habitat was completed in 1867 leaving 13% stream and 0% lake habitat available.

Changes in available spawning habitat in Casco Bay were quite different between streams and lakes. Stream distance decreased 9.5% in fairly regular intervals until 1762 while lake area remained above 99% (Fig. 3c). Construction of a main stem dam on the Presumpscot River in 1762 reduced lake habitat to 3% and stream habitat to 57.8%. The Presumpscot River provides access to 116.4 km^2 Sebago Lake, the principal lake of the Casco Bay watershed. By blocking access to Sebago Lake, the dam obstructed nearly 97% of the watershed lake habitat but only about a third of the accessible stream habitat.

For an overall picture of Maine, the nine analyzed watersheds were combined (Fig. 3d). Remaining stream and lake habitat both decreased to below 50% by 1800 and were further reduced to 16.22% and 2.42% by 1900, respectively.

Discussion

This study provides the first comprehensive temporal and spatial analysis of dam construction as it relates to historical watersheds in Maine and determination of virgin baselines for diadromous river herring habitat. We illustrate the early history of anthropogenic fracturing of northeastern U.S. coastal ecosystems and consequent statewide loss of longitudinal connectivity and diadromous spawning habitat accessibility. From 1634 to 1850 mill dam construction on tributaries and small watersheds reduced Maine's river herring lake habitat by more than 95%. Large dams on primary rivers at head of tide led to a near total loss of accessible habitat by the 1860s. Legacy land use has diminished hydrologic connectivity within and among coastal ecosystems resulting in shifts to ecological form and function that must be recognized and incorporated explicitly into restoration.

Implications for restoration and management

While restoration and trending towards pre-colonial habitat have occurred since the American Civil War (Foster 2002), obstruction of waterways, especially at head of tide, has meant that waterways and diadromous fish are not experiencing the same trend. In light of our results, Atkins' (1887) underestimated lost habitat by an order of magnitude, and even the dire estimate of 1% remaining at present (Lotze and Milewski 2004) fails to identify that this baseline was reached 150 years ago, before industrial pollution and human-induced climate change had become widespread concerns. Historically, alewife migrated 193 km and 322 km inland on the Kennebec and Penobscot Rivers, respectively (Atkins and Foster 1868), but completion of head of tide dams restricted

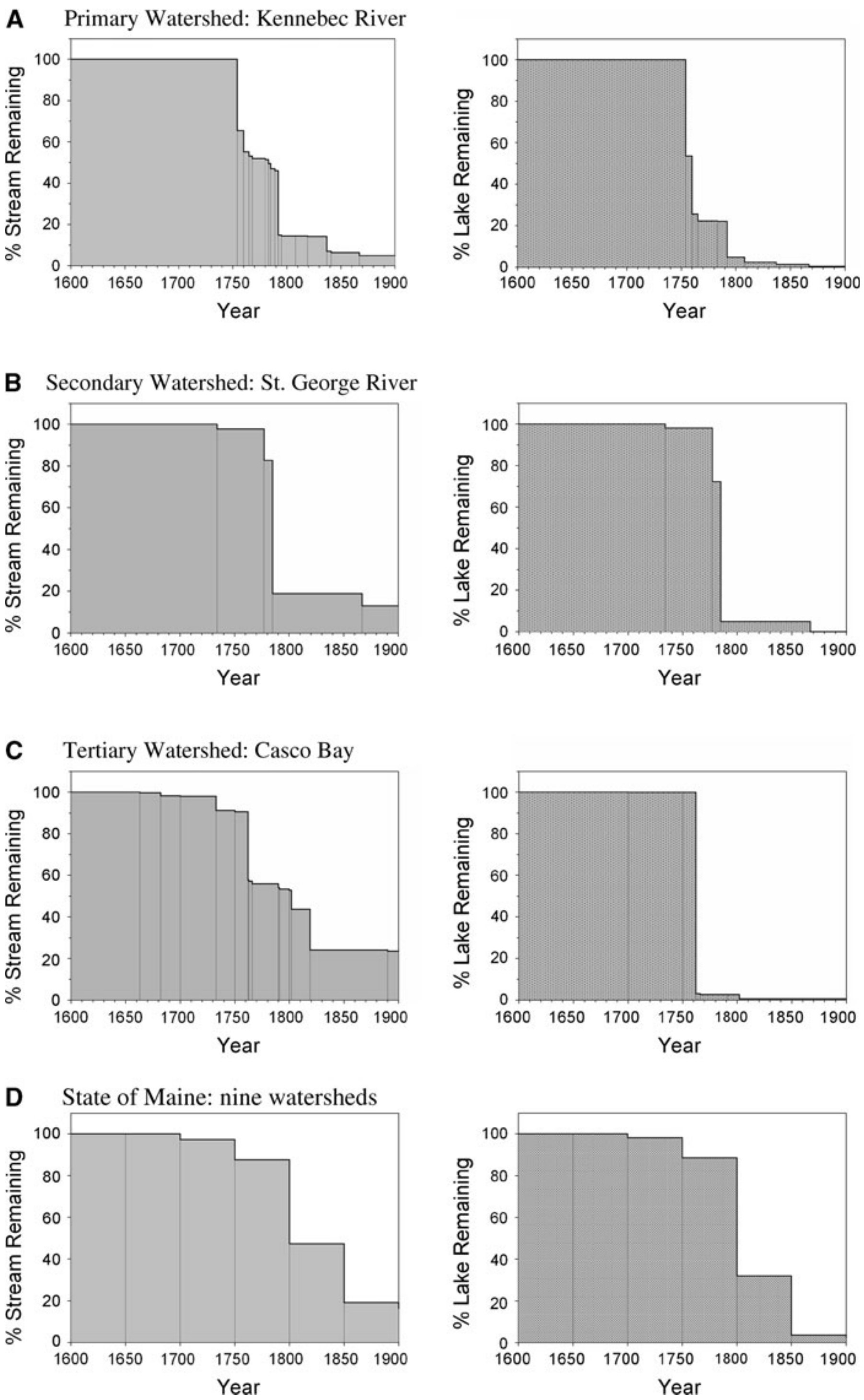

Fig. 3 Percent virgin habitat. Percent stream distance remaining (*on left*) and percent lake surface area remaining (*on right*) for representative watersheds of three categories and all nine assessed watersheds combined to represent the state: **a** primary rivers represented by the Kennebec River, **b** secondary rivers represented by the St. George River, **c** tertiary bay systems represented by Casco Bay and **d** state of Maine. Vertical drop down lines in each graph indicate year of dam construction that resulted in a measurable loss of potential spawning habitat

migration to less than 8% and 19% virgin habitat. Penobscot historical alewife catch declined from 1 million individuals in 1867 (Atkins 1887) to 230,283 in 1943 (Maine Department of Marine Resources unpublished data), documenting species decline due to habitat fragmentation and other factors. The extent of habitat loss during the 1800s left little spawning habitat accessible to wild populations along the Maine coast with the Damariscotta River serving as the only consistent documented refuge for river herring (Maine Secretary of State 1804–1893). As a result, Damariscotta fish were likely responsible for repopulating other watersheds through straying and restocking efforts as habitat re-opened during the 1900s (Rounsefell and Stringer 1945). Increased population biocomplexity, where population structure includes access to a greater variety of spawning sites, improves species resilience in the face of environmental changes (Hilborn et al. 2003). Genetic and spatial variability of spawning populations would have been reduced from numerous discrete groups to as few as one, potentially endangering the resiliency of the species and possibly contributing to its current depleted status.

Over 100 years before recognition of the dramatic impacts of species loss, and advent of the Endangered Species Act, river herring were already at critically low population levels experiencing habitat conditions linked to genetic bottlenecks. The current IUCN Red List criteria for listing a species as "vulnerable" includes a 30% or greater loss of historic Area of Occupancy or Extent of Occurrence (IUCN Standards and Petitions Working Group 2008). Our study is far from global and does not conform to regional Red List guidelines' definition of a state or province (IUCN 2003). Yet, if our analysis can be assumed to represent the entire State, continued presence of migration barring dams contributing to 70% or greater loss of accessible habitat per watershed would merit a listing of "regionally endangered". Disruption of habitat-use and spawning migrations occurred during colonial development along the entire U.S. Atlantic coast (ASMFC 2009). An IUCN evaluation of river herring in watersheds throughout the greater Gulf of Maine, from Bay of Fundy in the north to Cape Cod in the south, would include numerous extirpated historical runs where the species is "regionally extinct" (IUCN 2003, p. 10). Subpopulation watershed loss could be the most important conservation parameter on a regional scale. Incorporation of assessments at watershed and subpopulation levels into regional river herring management efforts is critical and should be required.

Fortunately, alewives are ideal candidates for restoration because they rapidly populate reopened spawning habitat within 3–5 years, roughly equivalent to the species age of maturity (Atkins and Foster 1868; Pardue 1983; Lichter et al. 2006). Some progressive state management plans have implemented individual watershed restoration programs (Brown et al. 2008; MDMR 2008; Brady 2009) and currently there are numerous efforts in Maine to restore stream connectivity and diadromous fish habitat access through fish passage construction, dam removal and stocking with varying success. Fish passage over the head of tide Brunswick Dam in 1981 provided access to 53.8% of historical lake habitat for the Androscoggin watershed (Brown et al. 2008). Removal of the head of tide Edwards Dam in 1999, without unblocking additional upstream dams, allowed access to only 1% of potential lake habitat within the Kennebec watershed (MDMR 2008). Yet, removal of Fort Halifax Dam in 2008 at the mouth of the Sebasticook River provided access to 45% of the original lake habitat. Opening of these two dams potentially provided access to 46% of the Kennebec watershed's virgin lake habitat. Finally, planned removal of the main stem Great Works and Veazie Dams on the Penobscot would restore 37% of the Penobscot watershed's historical lake habitat (MBSRFH 2007; MDEP 2009), which with the already accessible Orland River would make 42% of historic lake habitat available. We propose that habitat is the best indicator of restoration success and efforts to reopen historical spawning habitat and apply management per watershed, in addition to larger coastal regions, is an important step towards restoring Gulf of Maine river herring.

Landscape and ecosystem impacts

Understanding the consequences of diadromous species' loss of access to spawning habitat is relatively straightforward compared to assessing their contribution to Gulf of Maine ecosystems, including as a nutrient vector between freshwater and marine environments. Extensive research on anadromous and semelparous (death after single spawning) Pacific salmon (*Oncorhynchus* spp.) has shown significant transport of marine derived nutrients to freshwater spawning sites and incorporation into aquatic and terrestrial food webs (Kline et al. 1990; Bilby et al. 1996; Schindler et al. 2003). River herring along the Atlantic coast could be equally important but differ from Pacific salmon by not providing as substantial an influx of nutrients through mortality. However, by returning to the marine environment multiple times, iteroparous river herring provide repeated exchange between fresh and marine aquatic systems. Shortterm research on small watersheds shows evidence of marine derived nutrient incorporation into freshwater ecosystems (MacAvoy et al. 2000; Walters et al. 2009). Long-term studies of river herring reintroduction and nutrient transport are needed to understand greater ecosystem impacts (Schindler et al. 2003).

Small-scale natural and human induced change to watershed morphology was not accounted for in our four-century analysis. To assess large-scale obstruction, we assumed stream distance and lake area remained consistent with values obtained from MEGIS (2004). As mentioned in the introduction, long-term presence of dams seriously affects water body characteristics and biological habitat availability (Poff and Hart 2002; Wu et al. 2004; Walter and Merritts 2008). Accurate estimates of these changes are difficult to obtain (Petts 1989; Poff et al. 1997) and require quantitative analyses of historical maps and sediment profiles to determine river width, depth and lake surface area over time. Also, small-scale natural (i.e: beaver dams) and human induced (i.e: road culverts) fragmentation was not assessed here. Inclusion of this work is necessary to improve understanding and management of localized landscape changes.

We have focused on the long-term destruction of river herring habitat. Substantial impacts on other diadromous species, including salmon, American eel (*Anguilla rostrata*) and shad, and their contributions to freshwater and coastal ecosystems were not considered. Consideration of all species implies a devastating loss of diadromous biomass from coastal food webs, as suggested for over 100 years (Baird 1872; Ames 2004). While trophically important river herring also potentially provide prey buffering for juvenile salmon from fish and bird predators (Fay 2003), restoration efforts have suffered because of perceived competition with sport fisheries (Willis 2006). Further, river herring as bycatch in marine fisheries such as Atlantic herring (*Clupea harengus*) is increasingly considered an impediment to successful restoration (Kritzer and Black 2007). Thus, recovery of one species does not occur in a vacuum.

While diadromous fish are impacted by obstructions to a greater degree than potamodromous species (Cote et al. 2009), fragmentation of rivers, isolation of lake and stream habitat, rapid increase of impoundments combined with deforestation and other land-use changes that accompanied dams, have altered landscape ecology and affected all species (Foster et al. 2003). Fragmentation, land clearance and conversion to pasture land co-occurred with mill development. Thus, the documentation of damming is an indicator of regional changes to the landscape, including loss of foundation species (Ellison et al. 2005), shifts in species and habitats, nutrient composition, soil and sediment structure, presence of woody debris and overall flora and fauna (Foster et al. 2003). When the scale of alteration is considered (Walter and Merritts 2008) in relation to hydrologic connectivity and the relative strengths and directionality of hierarchal processes (Poole 2002), a dramatic shift from habitat continuum to discontinuum, not only within stream networks, but across the freshwater-oceanic boundary, has occurred. Further, punctuated discontinuities across the landscape together with homogenization of forests at the regional scale (Foster et al. 1998) have shifted the biotic structure and nutrient flux of Maine's ecosystems. Today, the terrestrial, riverine and marine landscape of Maine favors shorter-lived rapid growing species compared to pre-colonial ecosystems (Foster et al. 2002). A systematic and comprehensive plan is required to determine minimum habitat connectivity and species restoration targets, with multi-level involvement from individual watersheds to coast-wide management. Finally, by comparing current watershed restoration results to baseline habitat and productivity estimates we can determine the effectiveness of proposed actions towards regaining ecological connectivity after centuries of watershed obstruction.

Acknowledgments This work has benefited from conversations with Robert M. Cerrato, William Leavenworth, Karen Alexander, Theodore Willis, Michele Dionne, Gail Wippelhauser and Tom Squiers. We are indebted to the staff of The Maine Historical Society, The Maine State Archives, The Fogler Library Special Collections at the University of Maine Orono, and The Bangor Public Library Local History/Special Collections. We would like to thank J Wu, G Poole, D Cote and 1 anonymous reviewer for comments that improved this manuscript. We also thank undergraduate researchers Jaime Wright and Veronica Scorcia. This research was funded by a 2007 Mia J. Tegner Memorial Research Grant in Marine Historical Ecology and Environmental History (awarded to Adrian Jordaan) and NOAA award NA07NMF4550320.

References

Ames EP (2004) Atlantic Cod stock structure in the Gulf of Maine. Fisheries 29:10–28

Anonymous (1798) Legislature of Massachusetts. The Eastern Herald and Gazette of Maine [Portland] 26 March, 1798

ASMFC (2009) Amendment 2 to the Interstate Fishery Plan for shad and river herring (river herring management). Atlantic States Marine Fisheries Commission

Atkins CG (1887) The river fisheries of Maine. In: Goode BG (ed) The fisheries and fishery industries of the United States, Section V, vol. 1, pp 673–728

Atkins CG, Foster N (1868) First Report of the Commissioners of Fisheries of the State of Maine, 1867. Owen and Nash, Printers to the State, Augusta, ME

Atkins CG, Foster N (1869) Second Report of the Commissioners of Fisheries of the State of Maine, 1868. Owen and Nash, Printers to the State, Augusta, ME

Atkins CG, Stillwell EM (1874) Obstructions to the upward movement of fishes in streams, and the remedy In: US Commission of Fish and Fisheries, Part II, Report of the Commissioner for 1872 and 1873. Appendix E; Sections XXIII and XXIV. Government Printing Office, Washington, DC, pp 589–621

Baird ST (1872) Letter to Maine Commissioner of Fisheries on the diminution of the supply of food-fishes. In: Atkins CG (ed) 1872 Sixth Report of the Commissioners of Fisheries of the State of Maine, 1872. Owen and Nash, Augusta, ME, pp 7–10

Baird ST (1883) US Commission of Fish and Fisheries Report of the Commissioner for 1883. Government Printing Office, Washington, DC

Bigelow HB, Schroeder WC (1953) Fishes of the Gulf of Maine. US Fish and Wildlife Service Fishery Bulletin #74, vol 53. US Government Printing Office, Washington, DC, 577 pp

Bilby RE, Fransen BR, Bisson PA (1996) Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Can J Fish Aquat Sci 53:164–173

Brady PD (2009) Marine fisheries to work with local river herring officials on sustainable management of Massachusetts River Herring. DMF News 30: 9. Massachusetts Department of Marine Fisheries, Boston, MA

Brown ME, Maclaine JE, Flagg L (2008) Anadromous fish restoration in the Androscoggin River Watershed. 2007 report on the operation of the Brunswick fishway. FERC #2284, Maine Dept of Marine Resources. PL 89-304, 28 pp

Clark CE (1970) The Eastern Frontier: the settlement of Northern New England 1610–1713. Alfred A Knopf, New York, 419 pp

Cote D, Kehler DG, Bourne C, Wiersma YF (2009) A new measure of longitudinal connectivity for stream networks. Landscape Ecol 24:101–113

Dynesius M, Nilsson C (1994) Fragmentation and flow regulation of river systems in the Northern third of the World. Science 266(5186):753–762

Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, Mohan J, Orwig DA, Rodenhouse NL, Sobczak WV, Stinson KA, Stone JK, Swan CM, Thompson J, Von Holle B, Webster JR (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front Ecol Environ 3(9):479–486

Emery E (1901) In: Emery WM (ed) The history of Sanford Maine 1661–1900. Fall River, ME, 537 pp

Fay C (2003) Biological and ecological role of alewives. Maine Rivers annual conference 2003, September 27–28, 2003 Indian Island, ME

Federal Register (2006) Vol 71, No 200/Tuesday, October 17, 2006/Notices, pp 61022–61025

Foster DR (2002) Thoreau's country: a historical-ecological perspective to conservation in the New England landscape. J Biogeogr 29:1537–1555

Foster DR, Motzkin G, Slater B (1998) Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. Ecosystems 1:96–119

Foster DR, Motzkin G, Bernardos D, Cardoza J (2002) Wildlife dynamics in the changing New England landscape. J Biogeogr 29:1337–1357

Foster DR, Swanson FJ, Aber JD, Burke I, Brokaw N, Tilman D, Knapp A (2003) The importance of land-use legacies to ecology and conservation. Bioscience 53:77–88

Graham J, Engle S, Recchia M (2002) Local knowledge and local stocks: an atlas of groundfish spawning in the Bay of Fundy. The Centre for Community-based Management, Extension Dept., St. Francis Xavier University, Antigonish, NS, Canada

Greenleaf M (1829) A survey of the State of Maine: In: Reference to its geographical features, statistics and political economy. Shirley and Hyde, 460 pp

Haila Y (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. Ecol Appl 12(2):321–334

Hilborn R, Quinn TP, Schindler DE, Rogers DE (2003) Biocomplexity and fisheries sustainability. Proc Natl Acad Sci 100:6564–6568

Humphries P, Winemiller KO (2009) Historical impacts on river fauna, shifting baselines, and challenges for restoration. Bioscience 59(8):673–684

IUCN (2003) Guidelines for application of IUCN Red List criteria at regional levels: version 3.0. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK, ii + 26 pp

IUCN Standards and Petitions Working Group (2008) Guidelines for using the IUCN Red List categories and criteria. Version 7.0. Prepared by the Standards and Petitions Working Group of the IUCN SSC Biodiversity Assessments Sub-Committee in August 2008. Downloadable from http://intranet.iucn.org/webfiles/doc/SSC/RedList/RedListGuidelines.pdf

Jackson JBC (2008) Ecological extinction and evolution in the brave new ocean. Proc Natl Acad Sci 105(Suppl 1): 11458–11465

Jackson JBC, Kirby M, Berger W, Bjorndal KA, Botsford L, Bourque BJ, Bradbury RH, Cooke RG, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange C, Lenihan H, Pandolfi JM, Peterson C, Steneck R, Tegner MJ, Warner RR (2001) Historical overfishing and the collapse of coastal ecosystems. Science 293:629–638

Judd RW (1997) Common lands, common people. Harvard University Press, Cambridge, MA, 335 pp

Kline TC, Goering JJ, Mathisen OA, Poe PH, Parker PL (1990) Recycling of elements transported upstream by runs of Pacific salmon I $\partial^{15}N$ and $\partial^{13}C$ evidence in Sashin Creek, southeastern Alaska. Can J Fish Aquat Sci 47:136–144

Kritzer J, Black P (2007) Oceanic distribution and bycatch of river herring. An analysis of federal fishery-independent and fishery-dependent data. Progress report. October 2007. Environmental Defense

Lichter J, Caron H, Pasakarnis TS, Ridgers SL, Squiers TS Jr, Todd CS (2006) The ecological collapse and partial recovery of a freshwater tidal ecosystem. Northeastern Nat 13(2):153–178

Lotze HK, Milewski I (2004) Two centuries of multiple human impacts and successive changes in a North Atlantic food web. Ecol Appl 14(5):1428–1447

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312(5781): 1806–1809

MacAvoy SE, Macko SA, McIninch SP, Garman GC (2000) Marine nutrient contributions to freshwater apex predators. Oecologia 122:568–573

Maine Secretary of State. Fish Inspector Records (1804–1893) Boxes 1–9. Maine State Archives. Augusta, ME

MBSRFH (2007) Draft strategic plan for the restoration of diadromous and resident fishes to the Penobscot River. Maine Bureau of Sea-Run Fisheries and Habitat, Department of Marine Resources, Augusta, ME

MDEP (2009) January 1, 2009 status reports: hydropower projects in Maine, DEPLW0363-H2009, and Dam Removals in Maine and Dams Subject to Regulated Minimum Flow Releases. Maine Department of Environmental Protection

MDMR (1982) Statewide river fisheries management plan. Maine Department of Marine Resources, Maine Department of Inland Fisheries and Wildlife, and Atlantic Sea Run Salmon Commission. State of Maine Augusta, ME

MDMR (2008) Kennebec River anadromous fish restoration Annual progress report—2007. Maine Department of Marine Resources, Bureau of Sea-Run Fisheries and Habitat, 131 pp

MEGIS (2004) Watershed, county line and coast base layers. Maine Geographic Information Systems (comp, ed), United States Geological Survey. Last accessed April 2009 at http://megismainegov/catalog/

MEGIS (Maine Geographic Information Systems) (comp, ed), Army Corp of Engineers (USACE), Maine Emergency Management Agency (MEMA), Maine Department of Environmental Protection (MEDEP)(comp, ed) (2006) Impound database. Last accessed August 2008 at http://megismainegov/catalog/catalogasp?state=2andextent=cover

Moody RE (1933) The Maine Frontier 1607–1763. Yale University, New Haven, CT, 462 pp

Morita K, Morita SH, Yamamoto S (2009) Effects of habitat fragmentation by damming on salmonid fishes: lessons from white-spotted charr in Japan. Ecol Res 24(4):711–722

Mullen DM, Fay CW, Moring JR (1986) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic)—alewife/blueback herring U S Fish Wildl Serv Biol Rep 82(1156) U S Army Corps of Engineers, TR EL-82-4, 21 pp

Pardue GB (1983) Habitat suitability index models: alewife and blueback herring. USFWS, FWS/OBS-82/10.58, 22 pp

Pess GR, McHenry ML, Beechie TJ, Davies J (2008) Biological impacts of the Elwha River dams and potential salmonid reasons to dam removal. Northwest Sci 82(Sp Iss SI):72–90

Petts GE (1989) Perspectives for ecological management of regulated rivers. In: Alternatives in regulated river management by JA Gore and GE Petts. CRC Press, pp 3–24

Poff NL, Hart DD (2002) How dams vary and why it matters for the emerging science of dam removal. Bioscience 52(8):659–668

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC (1997) The natural flow regime: a paradigm for river conservation and restoration. Bioscience 47(11):769–784

Poole G (2002) Fluvial landscape ecology: addressing uniqueness within the river discontinuum. Freshw Biol 47:641–660

Pope CH (1965) The pioneers of Maine and New Hampshire 1623 to 1660. Originally published Boston, 1908. Geneological Pub Co, Baltimore, MD, 252 pp

Pringle CM, Freeman MC, Freeman BJ (2000) Regional effects of hydrologic alterations on riverine macrobiota in the New World: tropical-temperate comparisons. Bioscience 50:807–823

Rounsefell GA, Stringer LD (1945) Restoration and management of the New England alewife fisheries with special reference to Maine. US Department of the Interior, Fish and Wildlife Service. Trans Am Fish Soc 73:394–424

Saunders R, Hachey MA, Fay CW (2006) Maine's diadromous fish community: past, present, and implications for Atlantic salmon recovery. Fisheries 31(11):537–547

Schindler DE, Scheuerell MD, Moore JW, Gende SM, Francis TB, Palen WJ (2003) Pacific salmon and the ecology of coastal ecosystems. Front Ecol Environ 1(1):31–37

Smith HM (1899) Notes on the extent and condition of the alewife fisheries of the United States in 1896. In: US Commissioner of Fish and Fisheries Report part XXIV for the year ending June 30, 1898. Government Printing Office, Washington, DC, pp 31–43

Walter RC, Merritts DJ (2008) Natural streams and the legacy of water-powered mills. Science 319:299–304

Walters AW, Barnes RT, Post DM (2009) Anadromous alewives (*Alosa pseudoharengus*) contribute marine-derived nutrients to coastal stream food webs. Can J Fish Aquat Sci 66:439–448

Wells W (1869) The Waterpower of Maine Hydrographic Survey of Maine Sprague. Owen and Nash, Printers to the State, Augusta, ME, 526 pp

Willis TV (2006) St. Croix River alewife—smallmouth bass interaction study. Final Report to Maine Rivers, Hallowell, Maine

Wu J, Huang J, Han X, Zongqiang X, Gao X (2003) Three Gorges Dam—experiment in habitat fragmentation? Science 300:1239–1240

Wu J, Huang J, Han X, Gao X, He F, Jiang M, Jiang Z, Primack RB, Shen Z (2004) The Three Gorges Dam: an ecological perspective. Front Ecol Environ 2(5):241–248