



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

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Received: 23 February 2010 / Accepted: 1 October 2010
Springer Science+Business Media B.V. 2010

Abstract The erection of dams alters habitat and trends allows current restoration targets to be assessed longitudinal stream connectivity for migratory diadromous and potamodromous fish species and interrupts and may inform expectations for future management of much of organismal exchange between freshwater and oceanic and freshwater living resources.

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 We used published surveys, GIS layer targets and historical documents to create a database of 1356 dams, which was then analyzed to determine the historical timeline of construction, use and resultant fragmentation of watersheds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. **Keywords** Historical Ecology Gulf of Maine Blueback herring Forage Fish Ecosystem Energy flux Restoration

Introduction 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. One prominent environmental change had reduced accessible lake area to less than 5% of the virgin 892 km² 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 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

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

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.

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(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 (Hail 2002).

In the northeastern U.S., concentrated commercial fishing, forestry, agriculture and damming of rivers 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 1968; 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 (Green 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 1968; 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 rely on in lakes and ponds but also slow sections of streams; 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 1968) 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

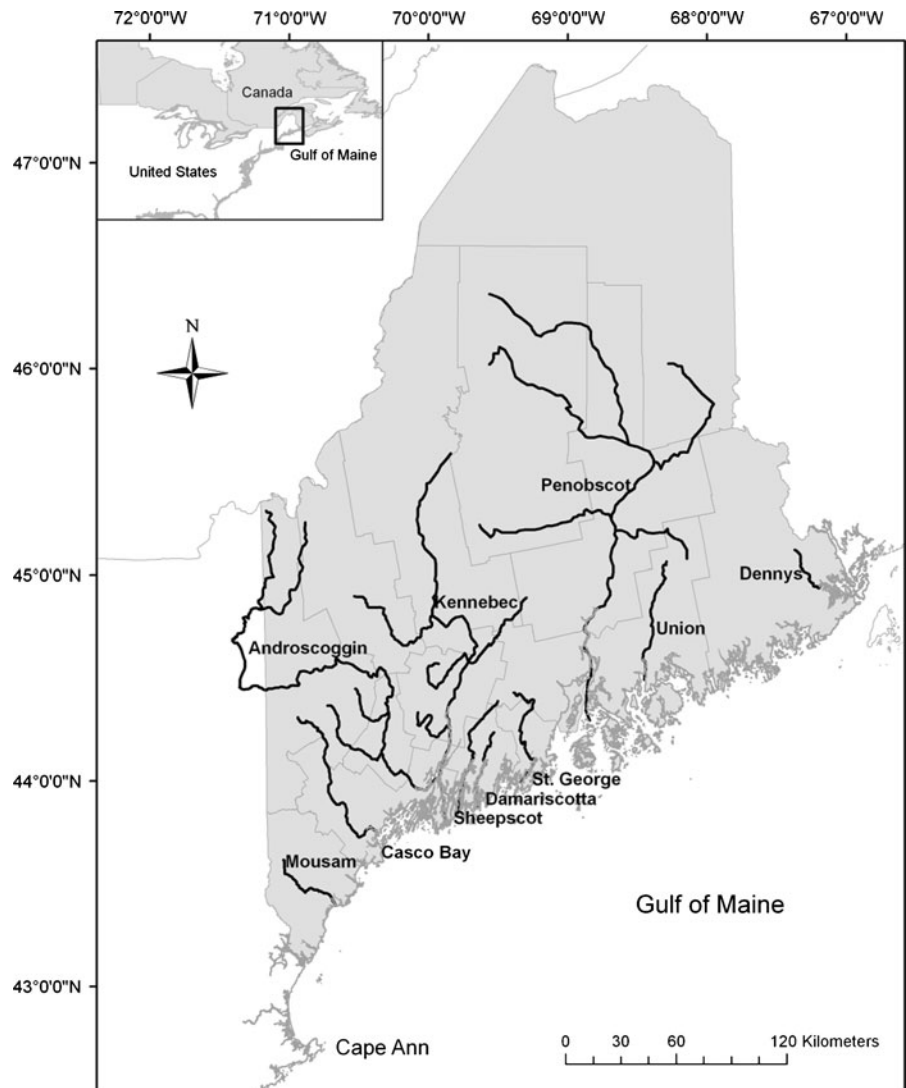
River herring are a mid-trophic level species that prey primarily on zooplankton (Bigelow and Schroeder 1953). River herring reach reproductive maturity in 3–5 years and are iteroparous, or capable of spawning for multiple years, returning to spawn in natal streams between late April and early July (MDMR 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 watersheds, approximately 60% of our estimated tide with moving water. Both species will spawn below historical range, that were divided amongst three head of tide provided that appropriate habitat is 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 species but is not included in measurable watersheds composed of multiple small rivers and spawning habitat which is limited to lakes and ponds, coastal waterways (Fig.). 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 tertiary (category 3) watersheds. Watershed analysis and thus an underestimate of total potential area.

Study area

Dams throughout Maine were documented, but Presumpscot River was used as the example for analysis was limited to nine historical river herring spawning habitat changes from 1600 to 1900

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 (MEGIS2006) 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. Intermittent or not connected to water bodies above. Thus, we assumed presence of psh unless we found head of tide were not included. Perennial streams evidence to the contrary. Town histories were below or to head of tide but without connection to instrumental in further determining presence or water bodies were included for potential blueback absence of alewives. For example, *The History of Sanford Maine 1661-1900* (Emery 1901, pp. 169-170) litigation regarding psh passage for natural limit of migration; virgin habitat for alewife salmon, alewives and shad at mills within the town of Sanford on the Mousam River is discussed. This indicates alewives surmounted the considerable falls and stream 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

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

$$V_A = \sum_{m}^{n_v} L_i; \quad V_{BB,A} = \sum_{m}^{n_v} S_i$$

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

$$h_A = \sum_{m}^{n_x} L_i; \quad h_{BB,A} = \sum_{m}^{n_x} S_i$$

Changes in accessible habitat ($H_{BB,A}$) 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:

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

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, psh 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

Coastal region	Watershed	Total dams constructed 1600-present	Year of earliest documented dam construction	Number of dams still on watershed as of 2008
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
General	St. John River	77	1811	48
	St. Croix River	48	1780	20
	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. 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 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. By 1850 the maximum range was reached in both directions while the density of dams continued to increase through the present (Fig 2).

Accumulation of dams across the state on all watersheds is mapped in four time periods: Historical habitat analysis 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. The Penobscot watershed had the most virgin habitat with 5332 km of streams and 327.7 km² of lake area whereas the Mousam watershed was the smallest with 183.5 km of streams and 10.7 km² of lake area (Table 2). From 1720 to 1846, impassable dams were

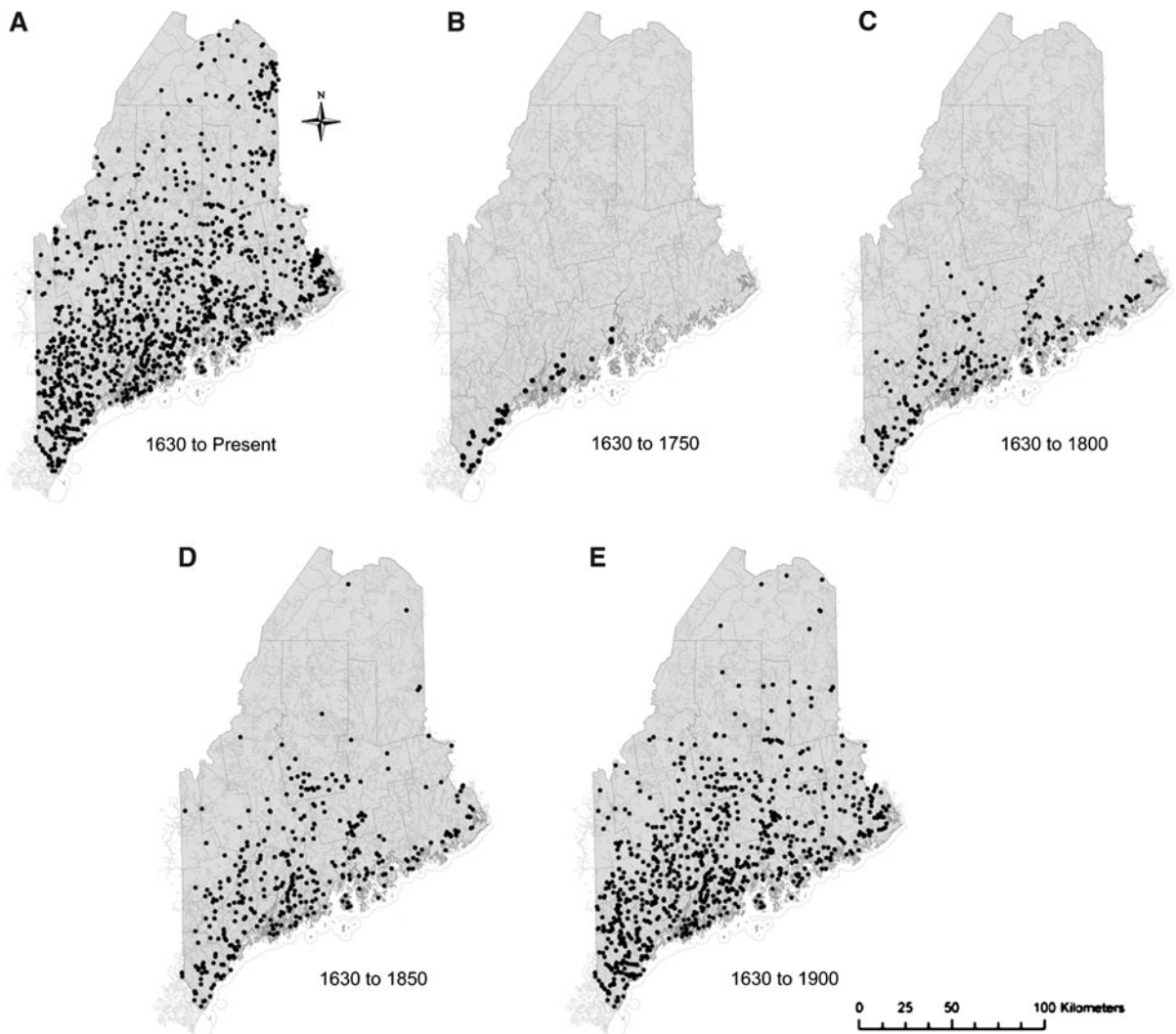


Fig. 2 Temporal and spatial accumulation of dams in Maine through 2008. **a** all dams constructed by 1750. **b** the cumulative increase of completed dams in 50-year increments from 1750 to 1900

constructed at or near head of tide on the main stem remaining watersheds. On the Kennebec watershed, of our nine historical river herring watersheds considerable reductions in stream and lake habitat (Table 2). Head of tide dams alone reduced accessible stream distance and lake area to between 7.5% and 53.6% (Fig. 2). Dam and 33%, respectively, having the greatest impact on the Kennebec, Mousam and Casco Bay watersheds/virgin habitat and in 1792 further reduced habitat to with less than 1% of virgin lake surface area 14.8% of streams and 4.8% of lake area. In 1837 the remaining after construction.

A representative watershed for each category is reduced stream habitat to 6.9%. The last dams to used to illustrate chronological changes in available have a measurable impact on the Kennebec spawning habitat. The Kennebec, St. George and Casco Bay represent primary, secondary and bay and 0.4% of stream and lake area available, watersheds. See Supplementary Material II for 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

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 virgin baselines for diadromous river herring habitat. reductions in available habitat occurred in 1777. We illustrate the early history of anthropogenic resulting in 82.7% of stream and 72.2% of lake area fracturing of northeastern U.S. coastal ecosystems remaining (Fig. 3b). Obstructed at head of tide in 1785, and consequent statewide loss of longitudinal connect-habitat was reduced to 18.9% stream and 4.9% laketivity and diadromous spawning habitat accessibility. area. The last dam to have a measurable impact onFrom 1634 to 1850 mill dam construction on tributary-accessible spawning habitat was completed in 1867ies and small watersheds reduced Maine's river herring leaving 13% stream and 0% lake habitat available. lake habitat by more than 95%. Large dams on primary

Changes in available spawning habitat in Casco rivers at head of tide led to a near total loss of Bay were quite different between streams and lakes. accessible habitat by the 1860s. Legacy land use has Stream distance decreased 9.5% in fairly regular diminished hydrologic connectivity within and among intervals until 1762 while lake area remained above coastal ecosystems resulting in shifts to ecological 99% (Fig. 3c). Construction of a main stem dam on form and function that must be recognized and the Presumpscot River in 1762 reduced lake habitat incorporated explicitly into restoration. to 3% and stream habitat to 57.8%. The Presumpscot

River provides access to 116.4 km² Sebago Lake, the principal lake of the Casco Bay watershed. By

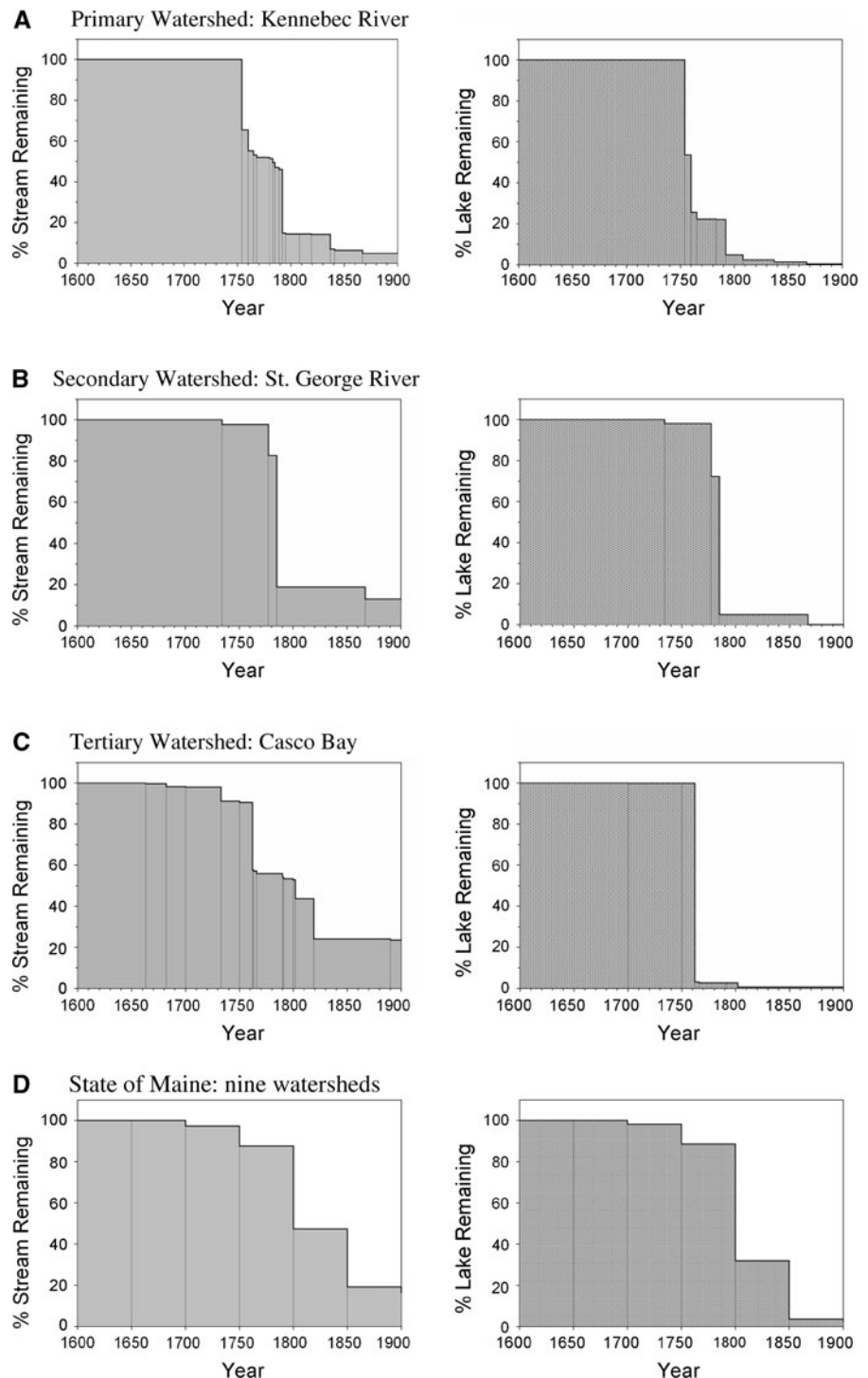
blocking access to Sebago Lake, the dam obstructedWhile restoration and trending towards pre-colonial nearly 97% of the watershed lake habitat but only habitat have occurred since the American Civil War about a third of the accessible stream habitat. (Foster2002), obstruction of waterways, especially at

For an overall picture of Maine, the nine analyzed head of tide, has meant that waterways and diadro- watersheds were combined (Fig. 4). Remaining mous fish are not experiencing the same trend. In stream and lake habitat both decreased to below light of our results, Atkins (1887) underestimated 50% by 1800 and were further reduced to 16.22% and lost habitat by an order of magnitude, and even the 2.42% by 1900, respectively. dire estimate of 1% remaining at present (Lotze and Milewski 2004) fails to identify that this baseline was

Discussion

This study provides the first comprehensive temporal 193 km and 322 km inland on the Kennebec and and spatial analysis of dam construction as it relates Penobscot Rivers, respectively (Atkins and Foster to historical watersheds in Maine and determination of 1868), but completion of head of tide dams restricted

Fig. 3 Percent virgin habitat. Percent stream distance remaining (left) and percent lake surface area remaining (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 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 1893). As a result, Damariscotta Psh 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 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 p. 10).

Subpopulation watershed loss could be the most important conservation parameter on a regional scale. Incorporation of assessments at watershed and sub-watershed population 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 1983; 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 Psh habitat access through Psh 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. Short-

term research on small watersheds shows evidence of fragmentation, land clearance and conversion to pasture land co-occurred with mill development. 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). 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 bora 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 hierarchical 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 Wipfelhauser 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.

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