Damming of Maine Watersheds and the Consequences for Coastal Ecosystems with a Focus on the Anadromous River Herring (*Alosa pseudoharengus* and *Alosa aestivalis)*: A Four Century Analysis

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The Graduate School

Carolyn Jean Hall

We, the thesis committee for the above candidate for the

Master of Science degree, hereby recommend

acceptance of this thesis.

Michael G. Frisk – Thesis Advisor
Assistant Professor in Marine Environmental Sciences

Adrian Jordaan – First Reader
Marine Ecologist in Marine Environmental Sciences

Darcy J. Lonsdale – Second Reader
Professor in Marine Environmental Sciences

Marah J. Hardt – Third Reader
Marine Ecology Researcher, Writer and Creative Consultant

This thesis is accepted by the Graduate School

Lawrence Martin
Dean of the Graduate School

Abstract of the Thesis

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The anadromous river herring, collectively alewives (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*), were historically abundant in most northeastern U.S. coastal river systems and were an important resource for humans as well as fish and bird predators. Colonial dam construction is considered the earliest principal cause of migration pathway disruption and reduced population productivity. In order to comprehensively examine the effect of dams on river herring spawning site access and historical abundance in Maine watersheds, I created a timeline of dam construction from 1600 through the present.

I used published surveys, GIS layers and historical documents to create a database of 1356 dams, which was then analyzed to determine date of construction, dam use and resultant fragmentation of watersheds. Information regarding movement and catches of anadromous fish were used to determine upstream limits of migration and establish total potential spawning habitat in nine watersheds with historic river herring populations. Subsequent loss of spawning habitat throughout 1600-1900 was then estimated. The results demonstrate impassable dam construction at head of tide on all Maine rivers by 1850 and a near total blockage of riverine and lake spawning habitat by the 1860s.

Between 1840 and 1880, alewife harvests shifted from primary rivers and multiple watersheds along the entire Maine coast to three mid-coast secondary rivers. From changes in available spawning area, I estimated annual alewife productivity per watershed and for the state of Maine. I calculated a range of annual alewife productivity using five potential production values: two based on harvest and percent escapement as adult returns/lake area and three calculated by applying a cumulative frequency distribution to virgin recruits as recruits/lake area. Across the nine watersheds, I found maximum annual production losses ranging from 1 to 29 million alewives/year during 300 years, 1600 to 1900. Over the same period, I estimated a state-wide total maximum production loss of 6.5 billion alewives. Today, annual alewife counts on three watersheds with restoration efforts are at 2 – 6% of my maximum annual virgin production estimates.

This evaluation of historical watershed habitat access provides the first comprehensive estimates of pre-colonial river herring populations in Maine and has implications for our understanding of coastal rivers and the consequences of the loss of a large and reliable forage base used by humans and other animals in both freshwater and marine ecosystems. Also, the erection of dams eliminated much of the exchange of organisms between freshwater and marine ecosystems long before any data is available, thus altering habitat connectivity for diadromous species. This study begins to confront current restoration goals including habitat restoration, baseline population targets, species diversity and ecosystem resiliency in the face of changing environments and ecosystem-based management of interdependent oceanic and freshwater living resources.

Dedication

I dedicate this work to my parents, Harry and Jean Hall, who whole-heartedly supported my endeavors all along and to my husband, Kelly AuCoin, who has been my constant companion and source of encouragement throughout this journey.

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Chapter 1: An Introduction to the Historical Relationship Between River Herring and the Development of Water Power in the State of Maine.

> "We are informed that some Time since a Man living in Haverhill, being a great lover of Fish, sat down and eat upwards of a Hundred Alewives in the space of two Hours & half."
> Boston Gazette, December 22, 1747

Much has been written on the history of the State of Maine – its abundant natural resources, the tenacity and independence of the early settlers, the disappearance of indigenous peoples and the long term exploitation of fish and forests through early fishery, timber and shipbuilding industries (Carlton, 1983; Whitten, 1990; Duncan, 1992; O'Leary, 1998; Paine, 2000; Wilson, 2001). By focusing on colonists' early use of Maine waterways, two conflicting feats of ingenuity become evident: the harnessing of water power by mill dams and sustenance and profit from those rivers in the form of harvested diadromous and coastal wild fish populations (Cronon, 1983; Judd, 1997). These early practices began a legacy of resource depletion that has resulted in severely diminished river herring populations and current efforts to manage and restore this species and their coastal ecosystems (ASMFC 2009).

Life history of river herring

Diadromous fishes (anadromous and catadromous) divide their life cycles by migrating between freshwater and ocean systems. Anadromous species mature and live as adults at sea but return to freshwater habitat to spawn whereas catadromous species have the reverse migration pattern (Bigelow & Schroeder 1953). The model species of this thesis, the anadromous river herring (collectively alewife, *Alosa pseudoharengus*, and blueback herring, *Alosa aestivalis*), were once found in most North American rivers along the Atlantic coast from Newfoundland to North Carolina (MDMR et al. 1982). In Maine, the iteroparous alewives and bluebacks spend three to five years reaching reproductive maturity before returning to natal bays and estuaries for spawning between late April and early July. The return is thought to be triggered by lengthening daylight and increases in water temperature, with a preference for spawning in freshwater of 14^{o}-15.5^{o} C (Baird 1874; MDMR et al. 1982; ASMFC 2009). Alewives historically migrated over 300 km past steep waterfalls and ledges to reach spawning areas in the quiet waters of Maine's lakes and ponds; bluebacks prefer riverine habitat near head of tide with moving water (Atkins & Foster 1868; MDMR et al. 1982). Both are deterred by high velocity flows and primarily migrate in daylight navigating along the shoreline (Atkins & Foster 1868). Post-spawning adults return to sea within days and juveniles begin their seaward migration one to two months after hatching. These fish provide an important link between inland and marine environments, supplying nutrients from each to the other. They are mid-trophic level species that prey primarily on zooplankton and are foraged upon by numerous upper-trophic level bird and fish predators including osprey (*Pandion haliaetus)* and Atlantic cod (*Gadus morhua)* (ASFMC 2009).

Maine, anadromous fishes and industry

The historically abundant populations of anadromous species including salmon (*Salmo salar*), sturgeon (*Acipenser oxyrhinchus*), striped bass (*Morone saxatilis*), shad (*Alosa sapidissima*), smelt (*Osmerus mordax mordax*) and river herring that returned annually to Maine's coastal watersheds provided a reliable, sustainable food source for indigent inhabitants (MDMR et al. 1982; Cronon 1983; Paine 2000). The importance of these fishes to Maine Indians is reflected in local place names: *Skowhegan*: a place to watch for fish/salmon; *Madamiscomtis* (Blackman Stream): plenty of alewives; *Cabbasaconteag* (Cobbosseecontee Stream): where the sturgeon is found and *Madamaswok* (Cold Stream in Enfield): alewife stream (Hanson, 1852; Trefts, 2006). Before the arrival of European colonists, river herring, along with salmon and shad, were a staple in the diets of indigenous peoples who caught them with dipnets, weirs and spears as they made their way upstream to spawn (Josselyn & Lindholt 1988; Paine 2000). These fishes soon became important resources for early 17th century European settlers in territories that would later become the New England states. European explorers and naturalists in the 16th and 17th centuries made numerous references to the surprisingly large numbers of coastal and river fishes and other wildlife in their reports:

> "Sturgeon, salmon, herrings, eels, smelts: all in great abundance…Besides there are such infinite flocks of Fowle, and Multitudes of fish both in the fresh waters, and also on the Coast, that the like hath not else where bin discovered by any traveler."
> Morton 1637: 89, 95

Not only were alewives and bluebacks fine fishes for human consumption – easy to preserve by smoking, pickling or salting – they were also good bait for coastal and off-shore fishing and good fertilizer for crops (Morton 1637; Baird 1883). As a result, river herring were valuable in their own right for local consumption and commercial harvest in addition to being a valuable forage fish for economically important coastal game fish that came inshore to feed on the schools returning during spring spawning (Baird 1883).

The same rivers that provided these bountiful fish were seen as a potential source of power for mills from the fall of water over ledges and the rushing of tide into coves.

With colonial settlement quickly came dams and mills to grind grain, saw timber, make gunpowder and weave cloth (Dwight, 1821; Wells, 1869; Moody, 1933; Carlton, 1983; Whitten, 1990). The abundance of tall trees for masts and shipbuilding encouraged timber harvesting and the building of more dams to control river water levels enabling transport of logs over ledges (Wells, 1869; Moody, 1933; Wilson, 2001).

Construction of dams on large and small waterways through the 17th, 18th and 19th centuries obstructed access for river herring, salmon and shad to upstream spawning grounds. With decreased passage came an increasingly noticeable decline in the presence of these valuable anadromous species. Declines in coastal marine species that fed on the millions of spawning anadromous fishes soon followed. Notable among these predators was the Atlantic cod that constituted the oldest, largest and most economically important fishery in the new territories (Innis, 1940). The decline of this fishery and the blow to local economies created a strong desire to restore productive populations, including a demand to restore cod's anadromous forage base.

> "…the reduction in the cod and other fisheries, so as to become practically a failure, is due, to the decrease off our coast in the quantity, primarily, of alewives; and secondarily, of shad and salmon, more than to any other cause."
> Baird 1874: xii

The implications of the loss of anadromous and coastal fishes created legal battles between those who relied on fish harvests for their livelihood and those who relied on mills and water power. Petitions from both sides were submitted from towns on many of Maine's rivers including the Mousam, Presumpscot, Penobscot, Kennebec, St. George, and St. Croix. Coastal and inland fishermen demanded passage of anadromous fishes over mill dams be made mandatory to maintain longstanding fisheries while mill owners argued logging and mill industries were more economically important than local fisheries and fish passages would significantly injure water power and production (Emory 1901). The Commonwealth of Massachusetts followed by the state government of Maine began passing laws to prohibit obstruction of upstream passage of alewives, salmon and shad in the 18th century but often mill owners were granted exceptions or the laws were not enforced so blockage remained.

Current stock status

Today, reduction of access to spawning sites for anadromous species, as well as waterway pollution and overfishing has had serious effects on the conditions of the stocks. In the Gulf of Maine, the National Oceanic and Atmospheric Administration (NOAA) river herring landings show significant declines in the fishery over the last 30 years, with a collapse in the 1990s (Figure 1.1). The Atlantic States Marine Fisheries Commission (ASMFC) reported a 93% decline in river herring commercial landings from over 13 million pounds in 1985 to under 1 million pounds in 2007 (ASMFC 2009). Despite policies passed to protect and restore the species including mandatory fish passage on hydropower dams, fishery closures and improved monitoring (MDMR et al. 1982; ASMFC 2009), the severity of the stock condition led to NOAA Fisheries listing river herring as a species of concern in 2006 (NOAA 2006).

Application of historical ecology and the objective of this thesis

> "Out of monuments, names, words, proverbs, traditions, records, fragments of stone, passages of books, and the like, we recover somewhat from the deluge of time."
> Merrill 1891: frontispiece

The extirpation of economically important fishery stocks and the failure of management policies based on 20th century landings and trawl data has led to an increased application of historical ecology research to evaluate long-term abundance, fishing effort and population biology for species of concern. Using both quantitative and qualitative historical data and anecdotes, the goal is to provide more accurate estimates of former population abundance before heavy exploitation so management baselines can be adjusted to create more realistic expectations of recovery (Pauly 1995; Jackson et al. 2001). This has been done with success in New England and elsewhere across the globe for many ecosystems. For instance, Rosenberg et al. (2005) analyzed fishery logs of Canada's Scotian Shelf and other local fishery documents from the mid 19th-century for historical Atlantic cod stock assessment. The paper demonstrated that estimated abundance in 1852 may have been three times greater than the highest Atlantic cod biomass estimates of the last 30 years. In another approach, Ames (2004) used fishery data and surveys of retired fishermen from 1920 to reconstruct and map historic spawning grounds, migration patterns and stock movement of cod in coastal Gulf of Maine. He used current cod egg presence to identify active spawning grounds as compared to areas of historic or lost spawning grounds illustrating the significant decline of inshore cod spawning populations. Ames concluded that Gulf of Maine coastal cod spawning grounds from 50 to 70 years ago have been reduced by nearly 50 percent.

Yet another study, by Lotze and Milewski (2004), expanded the application of historical research techniques to examine 200 years of human impacts on the components of the food web in the Quoddy Region of the Bay of Fundy coastal ecosystem just north of the Gulf of Maine. As with Rosenberg et al. (2005) and Ames (2004), they used historical data (anecdotal reports and archeological studies) and recent catch data to assess abundance from the mid-1800s to present. Especially relevant to this thesis is the evaluation of diadromous fishes in the St. Croix River, particularly gaspereau (called river herring in the U.S.). Potential historic abundance estimates were calculated based on reduction of available habitat due to human degradation. Current abundance estimates of gaspereau were reported to be less than one percent of the estimated abundance before 1825. They attributed this decline to long-term effects of dam construction, pollution from mills and effluents from industrial activities and sewage (Lotze & Milewski 2004).

It has been suggested that Gulf of Maine coastal cod populations would follow and feed on the formerly large spawning populations of river herring returning to coastal watersheds and loss of this important forage fish contributed to the decline of inshore cod populations (Shaw & Allen et. al. 1824; Baird 1874; Graham et al. 2002; Ames 2004). In order to further investigate this predator-prey relationship, a historical assessment of river herring is needed to compare to historical cod analyses. This research initiates this investigation by examining one principal anthropogenic mechanism that contributed to the decline of anadromous species over 400 years of development on Maine's watersheds: the proliferation of dam construction for water power.

This study seeks to establish a timeline of dam construction on Maine's waterways from 1600 to present and to explore the landscape-level effect early obstructions had on the passage and abundance of spawning anadromous fish, specifically river herring. In chapter two, a temporal and spatial analysis of accessible spawning habitat was conducted to illustrate the impact of dam obstruction on river herring as settlements and industry expanded throughout the state. In chapter three, results of the spawning site analysis were used to calculate estimates of alewife production as access to spawning habitat was reduced by waterway obstructions. Historical estimates are compared to current records of production and catch data to illustrate shifts in productivity baselines. Also investigated were changes in watershed contribution to alewife harvests from 1800 to the present. Finally, the research results are summarized and implications for Gulf of Maine ecology, conditions and management of watershed ecosystems, including the impact on coastal cod populations, are discussed.

This research presents an approach to utilizing existing historical data and anecdotes to analyze former species abundance that can potentially be applied to other species and ecosystems. It also will help further understanding of the profound effect European colonial settlement and development had on anadromous and coastal marine fish populations in the Gulf of Maine and its river systems, and how best to tackle restoration efforts.

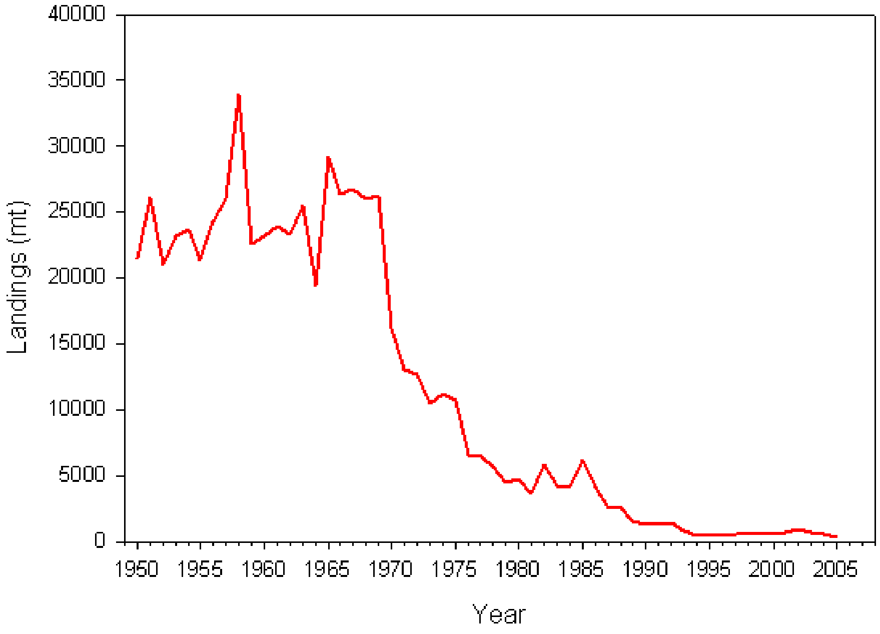

Figure 1.1. Gulf of Maine river herring commercial landings 1950-2005 from NOAA website: www.nefsc.noaa.gov/sos/spsyn/af/herring/

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Chapter 2: Estimating a historic habitat baseline for diadromous species with a focus on river herring

Introduction

Widespread losses of species, and large-scale environmental degradation over the past 400 years have been well documented (Lotze et al. 2006; Jackson 2008). Studies have identified estuaries, coastal seas, coral reefs, large predators, marine mammals, valuable shellfish and diadromous species as those particularly harmed. Effective restoration requires an understanding of the historical condition of ecosystems and the wildlife they sustained before significant anthropogenic alteration (Jackson et al. 2001). Unfortunately, standardized records of watershed conditions and fish harvests in the U.S. were not kept until the 1860s when the Federal and State Fish Commissions were formed (Atkins & Foster 1868; Judd 1997). Yet, concentrated commercial fishing, damming of riverways, forestry and agriculture had been altering the condition of river ecosystems since the arrival of European colonists in the 17th century. Data evaluation from this 200-year gap is required to avoid the “shifting baseline syndrome” or the practice of basing management and restoration policies on recent data from heavily exploited systems instead of data from eras of former abundance and more pristine conditions (Pauly 1995).

The fracturing of coastal watersheds by human-made obstructions has been occurring worldwide for thousands of years (Dynesuis & Nilsson 1994; Larinier 2000). Damming of waterways not only drastically alters the aquatic environment and surrounding landscape through sedimentation, channelization, flooding and temperature changes (Poff et al. 1997; Poff & Hart 2002; Walter & Merritts 2008), it also prevents the passage of migratory species and exchange of nutrients between marine and inland freshwater ecosystems (Kline et al. 1990; Bilby et al. 1996; MacAvoy et al. 2000; Walters et al. 2009). Such anthropogenic habitat reduction and isolation leads to population decline and extirpation of species (Pess et al. 2008; Morita et al. 2009). The resulting impact can be alteration of food web structure and reduction of watershed biodiversity, not only in freshwater systems, but cascading effects are felt along coastal ocean environments (Jackson et al. 2001). For example, Atlantic cod (*Gadus morhua*) fed on alewife (*Alosa pseudoharengus*), blueback herring (*Alosa aestivalis*) and shad (*Alosa sapidissima*) while these forage species undertook migrations between freshwater spawning sites and offshore overwintering grounds (Shaw & Allen et al. 1824; Baird 1872; Graham et al. 2002). The decline of coastal cod populations (and the loss of millions of dollars and hardship for dozens of communities) forced commercial fisheries to increase offshore effort and has been linked to the loss of the nutritious and predictable food source these forage species provided (Baird 1883; Ames 2004).

Diadromous species of the region – those that cross the ocean-freshwater boundary to complete spawning – include the anadromous alewife and blueback herring (collectively river herring), American shad, Atlantic salmon (*Salmo salar*), Atlantic sturgeon (*Acipenser oxyrinchus*), rainbow smelt (*Osmerus mordax*), striped bass (*Morone saxatilis*), the often-estuarine shortnose sturgeon (*Acipenser brevirostrum*) and the catadromous American eel (*Anguilla rostrata*). These species were historically abundant supporting commercial fisheries and serving as a staple in not only local human consumption, but as food for other fish and birds along the Gulf of Maine’s coastal and inland ecosystems (Atkins & Foster 1868; Baird 1872; Mullen et al. 1986). Other parasitic and sympatric species were also linked through dependence on these migratory fish. River herring and Atlantic sturgeon are presently listed as species of concern and Atlantic salmon and shortnose sturgeon are endangered species (NOAA 2006; http://www.maine.gov/IFW/wildlife/species/endangered_species/state_federal_list.htm). Thus, efforts to provide long-term solutions through population and watershed restoration are of immediate importance.

Historic accounts demonstrated higher abundances compared to the present-day, but exact censuses are not available. For example, in 1674 naturalist John Josselyn noted that over ten thousand alewives were taken by two men in two hours without a weir (Josselyn & Lindholdt 1988). A century later, historian J.W. Hanson wrote of 1780s seine fishing on the Kennebec watershed where "incredible numbers of shad, [river] herring, salmon and sturgeon, were taken every spring" (Hanson 1874: 155). However, by the mid 18th century, decline of this previously abundant resource led to laws authorizing the "preservation of the Fish called Salmon, Shad and Alewives" (Anon. 3/26/1798; Moody 1933) and creation of fish warden positions due to concern over dams blocking upstream migration (Wheeler & Wheeler 1878; Cushman 1882). By the late 1800s these ecologically and economically important species were in decline in many of Maine's rivers and had been extirpated from some (Atkins & Foster 1868; Bigelow & Schroeder 1953). After their first comprehensive evaluation of Maine watersheds, Maine Commissioners of Fisheries, Atkins and Foster (1868), concluded the construction of dams was "sufficient to account for the entire extinction of the migratory fishes in all waters above these obstructions" and 20 years later estimated that only 10% of the original habitat remained available for spawning (Atkins 1887). Efforts to regulate harvests and re-introduce populations occurred throughout the 19th and 20th centuries (Atkins & Stillwell 1874; Atkins 1887; Rounsefell & Stringer 1942; MBSRFH 2007), yet despite those efforts, present populations are at historic lows with some at less than 1% of early 19th century estimations (Lotze & Milewski 2004; Saunders et al. 2006). Still, no systematic comprehensive attempts have been made to assess former population sizes of these important ecological links between freshwater and marine environments.

European colonists began damming waterways in the 17th century primarily to power grist and saw mills (Moody 1933; Clark 1970; Smith 2002). As settlements and towns spread across Maine’s coast and up rivers to forested inland areas, hundreds of mill dams (Figure 2.1) were constructed wherever natural waterfalls, ledges and topography provided an area of impoundment and the vertical height (head pressure) required to generate mechanical energy (Clark 1970). The earliest recorded water-powered saw mill in Maine was built near the Maine-New Hampshire border on a tributary of the Piscataqua/Salmon Falls River in 1634 (Pope 1965). By 1665 more than 20 saw mills had been constructed within the Piscataqua River watershed (Clark 1970) increasing to 70 by 1706 (Paine 2000). Statewide accounts in 1829 estimated that 1,686 principal manufacturing establishments depended upon water-power including grist, saw, cotton, fulling and other mills (Greenleaf 1829). Only 40 years later, the number had expanded to over 3,100 water-power privileges both impounded and unimproved (Wells 1869). Throughout the 19th century, larger scale logging and mill operations were being developed with improved technology enabling dam construction to span large rivers at the head of tide (Atkins & Stillwell 1874; Judd 1997; Wilson 2001).

Here I attempt to discern the loss of spawning site access from 1600-1900 due to these obstructions. My model species is the river herring, a mid-trophic level anadromous fish that chiefly feed on zooplankton (Bigelow & Schroeder 1953) and an important forage fish for lake and ocean predators (Pardue 1983; Mullen et al. 1986; Fay 2003). River herring use both rivers (bluebacks) and lakes (alewives) for spawning and alewives were historically known to migrate over 300 km (Atkins & Foster 1868). The first objective is to present a spatial and temporal analysis of obstructions within Maine from early mill dams of the 17th and 18th centuries and logging industry dams of the early 19th century to the introduction of hydroelectric dams in the late 19th century. The second objective is to quantitatively present an analysis of accessible spawning area affected by the erection of dams over time using river herring as an example species. The final objective is to evaluate the current status of alewife populations in light of the historical baseline determined from objective 1 and 2 for the state of Maine, and discuss the application of this analysis to restoration efforts in these impacted coastal watersheds.

Materials and Methods

Study area

Dams throughout Maine were documented, but analysis of river herring spawning habitat was limited to nine watersheds referenced as having historical alewife populations (Figure 2.2). These watersheds were placed into three categories 1) primary river watersheds with extensive tributaries totaling a stream distance (main stem river plus tributaries) of 1000 km or greater 2) secondary watersheds with few tributaries totaling less than 1000 km and 3) bay-based watersheds composed of multiple small rivers and coastal waterways. Category 1 watersheds are the Androscoggin, Kennebec and Penobscot Rivers. Category 2 watersheds are the Mousam, Sheepscot, St. George, Union and Dennys Rivers. The Casco Bay watershed with the Presumpscot River comprises category 3. Note: the Androscoggin River was only researched for stretches lying within the Maine state border. Also included is the Damariscotta River secondary watershed referenced in this study.

Determination of dam location and original construction

Two comprehensive databases served as primary references to locate and identify currently standing or recently removed dams. 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) and the Trails.com publicly available U.S. Geological Survey (USGS) quad topographic maps of Maine (Trails.com April 2009). The MEGIS database 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. It was developed from data collected in the U.S. Army Corp of Engineers (USACE) 1987 Dam Survey, Maine Department of Environmental Protection (MEDEP), Bureau of Land & Water Quality (BL&WQ) staff for use with BL&WQ 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. The Trails.com database is organized by county and searchable by specific features including dams. It provides a corresponding map with nearest town, elevation, latitude and longitude for each dam. Additionally, inventories of removed dams, potentially removable dams and dams subject to regulated minimum flow releases listed by the Maine Department of Environmental Protection (MDEP) were referenced as a third source for current dams (MDEP 2009).

The most comprehensive historic reference for dams is *The Water-power of Maine*, a hydrographic survey of Maine from the 1860s (Wells 1869). Initial results of surveys conducted in 1867 were published in 1868 (Wells 1868) with a complete return of surveys and water resource demographics published in 1869. Not all dams reported in Wells' comprehensive hydrological survey (1869) were included in this study. Omitted dams fell into four categories: 1) not located due to an historic name or no precise location mentioned, 2) upstream of alewife migrations, 3) on tributaries with no pond area considered suitable for alewife spawning, or 4) one of many already surveyed dams on a short stretch of obstructed waterway (under 3 miles).

Nineteenth and 20th century governmental reports were also used to identify and date dams. These included Maine Commissioner of Fisheries (COF) reports from 1868 to 1899 (Atkins & Foster 1868, 1869; Atkins & Stillwell 1874; Atkins 1887; Smith 1899) and alewife fisheries reports and river survey and management reports through the 1980s (Rounsefell & Stringer 1943; MDIFG 1955-1967; ASRSC 1982-1983).

Dates and locations of dams constructed before Wells' 1867 survey were found in numerous popular and legislative historical sources. In historical literature, mills are documented much more consistently than the dams used to power them – it was assumed the presence of a mill indicated the presence of a dam. Such sources included wills, historical magazines and journals, town histories, 18th and early 19th century newspaper articles and records of early 19th century legislative acts and petitions from the Maine State Archives (Maine Legislative Records 1821-1830). Hand drawn maps labeled with early settlement buildings including mills were sometimes included in popular publications and gave clear references to location and date of existence (Figure 2.3). For a full list of references used to date and locate mills and dams see Appendix 2.1.

Locations and latitude and longitude in decimal degrees for existing and historical dam sites were confirmed or determined using the twenty-sixth (2003) and thirtieth (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, photographs and conversations with current owners and local residents.

The spatial pattern in dam construction was investigated by plotting the latitude and longitude of the dam site against the year of original construction.

Determination of natural barriers to alewife upstream migration

Natural, or non-anthropogenic, barriers to upstream passage of anadromous species, particularly those of alewives, were determined using the Maine COF reports, alewife fishery reports and river survey and management reports referenced in the previous section (Atkins & Foster 1868, 1869; Atkins & Stillwell 1874; Atkins 1887; Smith 1899; Rounsefell & Stringer 1943; MDIFG 1955-1967; ASRSC 1982-1983). Natural barrier location and latitude and longitude in decimal degrees were determined using the twenty-sixth (2003) and thirtieth (2007) editions of the DeLorme Maine Atlas and Gazetteer™ and Google Earth 5.0 during the period of January to July 2009.

Mapping of dams and natural barriers

Obstructions 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.

Temporal analysis of historical spawning habitat; stream distance and lake surface area

> "No stream seems to be too small for [alewives] if its waters are derived from a pond, and there can have been hardly an accessible pond in the whole state they did not visit."
> Atkins 1887: 687

Because of historical omnipresence of alewives in Maine ponds and lakes with connection to the ocean (Atkins 1887; Mullen et al. 1986), all water bodies below natural barriers within known alewife migration distances were considered potential spawning sites. Documentation or discussion of maximum upstream alewife migration not determined by natural barriers was found in Maine COF reports, alewife fisheries and river survey and management reports (Atkins & Foster 1868, 1869; Atkins & Stillwell 1874; Atkins 1887; Smith 1899; Rounsefell & Stringer 1943; MDIFG 1955-1967; ASRSC 1982-1983).

Town histories were instrumental in determining presence or absence of alewives. For example, *The History of Sanford Maine 1661-1900* (Emery 1901) discusses litigation regarding fish passage for salmon, alewives and shad at mills within the town limits of

Sanford on the Mousam River. This provides evidence that alewives were able to surmount the considerable falls downstream of Sanford. In cases such as the Mousam River, popular literature provides the only evidence that alewives existed in this waterway because alewives were extirpated by the time fishery reports and watershed analyses were made (Atkins & Foster 1868, Rounsefell & Stringer 1943).

Streams categorized as perennial in the MEGIS database (MEGIS 2004) that led to ponds within alewife migration ranges were used to calculate stream migration distance whereas streams categorized as intermittent were not included. Reports that bluebacks will migrate to and somewhat above head of tide to spawn in moving water (MDMR et al. 1982) determined the inclusion of perennial streams without connection to water bodies within the distance of head of tide.

Virgin, or unobstructed, potential spawning habitat, was estimated using river and lake demographics from MEGIS 2004 to calculate total stream distance (km), composed of main stem river and all accessible tributaries, and total lake surface area (km^2) to maximum upstream alewife migration imposed by natural barriers. For this study, virgin spawning habitat was dated in year 1600, pre European colonization.

Changes in accessible stream distance and lake surface area resulting from dam construction were calculated chronologically at the year of dam construction from 1600 through 1900. In the case of large river main stem blockage, particularly dams at head of tide, historical reports from Atkins (1887) and other publications stated the year of full obstruction to anadromous fishes, therefore main stem dams were not considered obstacles until sourced dates. Inaccessible stream distance and lake area upstream of the completed dam were subtracted initially from the virgin total and from remaining distance and area totals subsequently. Percent stream distance (SD) or lake surface area (LSA) still available was then calculated using

$$\% \text{ remaining spawning habitat} = \frac{\text{SD or LSA available}}{\text{virgin SD or LSA}} * 100$$

Percent remaining spawning habitat was calculated each year a dam was completed that impacted accessible habitat. Dams built upstream of an already accounted for obstruction were not included in this assessment.

Results

Dam timeline

A total of 1356 historical and current dams were documented across all waterways in the state of Maine from the Piscataqua/Salmon Falls in the southwest to the St. Croix River in the northeast and all inlets and islands along the coast (Table 2.1A). 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 (Table 2.1B). The western Maine coastal region includes, from west to east: the Piscataqua/Salmon Falls, York, Mousam, Kennebunk, Saco, Fore, Presumpscot and Royal Rivers (Table 2.1A). A total of 400 dams were documented in this region with the earliest dam constructed in 1634. The central region includes, from west to east: the Kennebec, Sheepscot, Damariscotta, Pemaquid, Medomak, St. George and Penobscot

Rivers. A total of 637 dams were documented in this region with the earliest dam constructed in 1640. The eastern region includes from west to east the Union, Narraguagus, Pleasant, Machias, East Machias, Orange, Dennys, Pennamaquan, St. Croix and St. John Rivers. A total of 319 dams were documented in this region with the earliest dam constructed in 1763. Of the 1356 dams documented in this study, 47% (634 dams) were still present on the waterways as of 2006 (Table 2.1B). Not all dam locations were identified clearly enough in the literature for exact, or estimated, latitude and longitude; a total of 1333 dams were assigned coordinates and are presented in Figure 2.4A.

Accumulation of dams across the state on all watersheds is mapped in four time periods: 1630 – 1750 (Figure 2.4B), 1630-1800 (Figure 2.4C), 1630-1850 (Figure 2.4D) and 1630-1900 (Figure 2.4E). A total of 43, 164, 187 and 521 dams were completed between 1630-1750, 1751-1800, 1801- 1850 and 1851-1900, respectively. A total of 915 dams were completed by 1900. Between 1750 and 1800, dam completion had more than tripled and by 1900 had increased 20-fold.

Dam development remained mostly localized between 43.0^{o} to 44.2^{o} latitude and -71.0^{o} to -69.0^{o} longitude until northeast expansion in the mid 1700s (Figure 2.4B, C) as indicated by the plot of latitude and longitude against year of original construction (Figure 2.5). The rate of expansion to the east was more rapid than to the north, or inland, but by 1850 maximum range was reached in both directions while the density of dams continued to increase through to the present (Figure 2.4, 2.5).

Spawning habitat analysis

From 1720 to 1846, dams impassable to river herring were constructed at or near head of tide on the main stem of all Maine watersheds (Table 2.2). Head of tide dams alone reduced accessible stream distance 42-93% and lake area 67-100% (Table 2.3). Head of tide dams had the greatest impact on the Kennebec, Mousam and Casco Bay watersheds with less than 1% of virgin lake surface area remaining after construction (Table 2.3).

Substantial virgin spawning habitat for blueback herring (stream distance in km) and alewives (lake surface area in km^2) existed before dams were constructed on the nine focus watersheds (Table 2.4). The Penobscot watershed had the most virgin habitat in Maine with 5332 km of streams and 327.7 km^2 of lake area. The Mousam watershed is the smallest examined in this study with 183.5 km of streams and 10.7 km^2 of lake area. The Androscoggin River total virgin stream distance is less than 1000 km, the requisite distance for a category 1 watershed, limited by natural barriers to alewife migration within the lower Androscoggin and the borders of present day Maine (Figure 2.2).

A representative watershed for each category is used to illustrate chronological changes in available spawning habitat. The Kennebec represents primary river watersheds (Table 2.5, Figure 2.6). The St. George represents secondary river watersheds (Table 2.6, Figure 2.7). Casco Bay represents bay watersheds (Table 2.7, Figure 2.8). Only dams that changed available stream or lake habitat were included in figures. See Appendices 2.2 and 2.3 for remaining watersheds.

On the Kennebec watershed, considerable reductions in stream and lake habitat first occurred in 1754 with the construction of the Fort Halifax Dam. Stream habitat declined to 65.4% and lake area to 53.6% of virgin spawning area (Table 2.5, Figure

2.6A, B). The Foot of Falls Dam, built in 1760, reduced lake area to 25.6% of virgin habitat and in 1792, the Milstar Dam 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.

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 (Table 2.6, Figure 2.7A, B). The Warren Dam, completed in 1785, obstructed the St. George River at head of tide and reduced habitat to 18.9% stream and 4.9% lake area. The Mill Stream Dam, completed in 1867, was the last dam to have a measurable impact on accessible spawning habitat 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 to 90.5% in fairly regular intervals until 1762 while lake area remained above 99% (Table 2.7, Figure 2.8A, B). Construction of the Cumberland Mills 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 (Figure 2.9). By blocking access to Sebago Lake, the Cumberland Mills Dam obstructed nearly 97% of the watershed lake habitat but only about a third of the accessible stream habitat.

By 1760 dams were beginning to reduce spawning habitat in the Kennebec, St. George and Casco Bay watersheds and by 1800 (over 60 years before the first COF report) each watershed's available lake habitat was reduced to less than 5% virgin lake area (Tables 2.5-7, Figure 2.6-8).

Discussion

To fully understand alterations to an ecosystem, the origin and scope of all historical anthropogenic changes need to be evaluated individually and then collectively integrated in order to establish the most accurate baseline conditions and potential productivity of a system (Dayton et al. 1998; Rosenberg et al. 2005). This study provides the first comprehensive temporal and spatial analysis of dam construction as it relates to spawning habitat availability for diadromous species. It provides estimated virgin baseline spawning habitat before European colonization for blueback herring, measured in stream distance, and alewives, measured in lake area. Dams constructed across Maine beginning in 1634 increasingly diminished Maine's river herring habitat from the earliest colonial settlements through continued efforts to harness hydropower. The historical impact of damming waterways is a near total loss of accessible habitat by the 1860s and removal of trophically important diadromous species from coastal ecosystems. Future restoration efforts for diadromous species must be guided by evaluation of current conditions in comparison to historical habitat to have a chance of restoring genetic and spatial resiliency to Maine's ecosystems.

History of anthropogenic alterations of the Maine landscape

Socio-politically driven expansion of saw and grist mills and the resulting reductions in diadromous passage occurred spatially and temporally from western to eastern Maine. Expansion across coastal Gulf of Maine waters was initiated by mid 17th century from southwest of Cape Ann where it had already impacted diadromous species and other important fish stocks (Leavenworth 2008). By 1675, Maine had a population of 6000 people scattered from the New Hampshire border to Penobscot Bay mostly within a few of miles of the coast (Josselyn & Lindholdt 1988; Sylvester 1909). The earliest dam construction dates for the western and central coastal regions, 1634 and 1640, respectively, reflect the synchronous settlement of these areas. A series of French-Indian Wars from 1675 to 1764 slowed the pace of early settlement expansion (Moody 1933). Homes, businesses and dams built before 1720 in coastal towns west of the Penobscot were repeatedly destroyed in these wars causing settlement efforts to stagnate (Atkins 1887). Yet the lure of profitable fisheries and timber harvest encouraged settlers to rebuild year after year (Moody 1933; Paine 2000).

The conclusion of the wars allowed for expansion east of the Penobscot River and by 1763, the first dam was constructed in the eastern region (Smith 2002). The next 100 years of northeast and inland expansion was Maine's era of a rapidly developing timber industry and an increased rate of dam construction resulting in 394 dams completed by 1850. Between 1850 and 1900, 521 additional dams were completed reaching a total of 915 dams. During this time, the Fish Commission was created to address decreasing numbers of riverine and marine fish species. This period also witnessed notable changes to water-power use. The timber industry was shifting from individual or partnership businesses to mass production associations, the pulp and paper industry was established and hydroelectric dams were introduced late in the 19th century (Isaacson 1970).

The impact of dams on spawning habitat accessibility for diadromous fish is obvious when presented along a temporal scale. The three representative watersheds from each category, the Kennebec, the St. George and Casco Bay, show reduction of available spawning habitat beginning by 1760 with less than 5% lake habitat still accessible by 1800. All historical alewife rivers had full obstruction at head of tide by 1846. Over 100 years would have to pass, however, before these species received official designation of declines under the Endangered Species Act.

Main stem or major tributary dams had the greatest impact on accessible habitat, yet those built on smaller tributaries, especially those with access to ponds, also had a diminishing effect. For smaller rivers and tributaries, I assumed the construction of a dam created an obstruction for migrating alewives. Supporting this assumption are the records of numerous petitions from towns that harvested alewives on smaller rivers in the 1700s protesting the construction of dams and the reduction of anadromous species spawning upstream (Shaw & Allen et al. 1824; MLR 1821-1830). A steady construction of dams from 1663 to 1750 on the Casco Bay watershed reduced availability of stream habitat by 9.5% before dams were constructed on the main stem of the Presumpscot River. Also, on the St. George River watershed, the Mill Stream Dam on a small tributary just below head of tide obstructed the last 4.9% of accessible lake spawning habitat in 1867. Because alewives are opportunistic, they potentially used any and all accessible ponds as spawning areas. It is therefore important to not overlook smaller tributaries that could contribute to the total productivity of a watershed.

The susceptibility of early timber and stone dams to seasonal freshets resulting from rain or snowmelt could indicate smaller dams did not provide consistent obstruction. Other factors, such as destruction of dams during wars, also could have allowed passage. Yet, as mentioned above, dams were typically rebuilt within the year, often within two or three months (Smith, 2002). Also, original dam constructions were frequently updated or replaced when more stable construction or advanced technology, such as hydroelectricity, was developed; thus, interruption of obstruction was fairly minimal and many original obstructions became permanent elements of the landscape.

Uncertainties in estimated historical river herring habitat

An assumption that should be further examined is the historical presence of river herring in all rivers, streams, lakes and ponds used to calculate total virgin spawning habitat. Because documentation of natural barriers and final destinations of alewife upstream migration is scarce and debated for several Maine watersheds, I opted for the longest potential migration. But evidence of historical occupation of inland lakes and ponds is still being sought. Isotopic studies of sediment in upstream lakes can be used to assess historical transport of marine derived nutrients (Peterson & Fry 1987). Also, the identification and analysis of fish bones and scales preserved in watershed sediments has been used to confirm presence of anadromous fish in upstream habitat (Flagg 2007). Such analyses are needed to confirm the extent of anadromous fish inland migration – then more accurate virgin spawning habitat estimates can be made for each watershed.

Additionally, analyses of specific aspects of habitat suitability and water hydrology for individual watersheds are needed that were not covered in this study. First, tributary streams included in virgin spawning habitat were not assessed for elevation grade or hydrological flow. Alewives resist entering streams with high flows of water

(Atkins & Foster 1868) and therefore each watershed needs to be assessed regarding which potential streams have too high of a flow to allow alewife migration. Second, depth, food availability, competitors, predators or average temperature during the April to July spawning season and juvenile growth period (Pardue 1983) for each water body were not considered. These factors could determine alewife spawning preference and recruitment success and therefore require examination in future analyses. Third, distance of a water body from the coast and the biological or reproductive cost imposed by longer distance migrations, and the evolutionary consequences, were not considered (Kinnison et al. 2001). No water body was excluded within known or estimated migration boundaries, but spawning efficiency related to distance from the ocean could be an important consideration in restoration efforts. This is especially pertinent to restoration funding since the number of dams in need of fishways or removal, and hence the economic cost, would presumably also increase with distance from the coast.

Also of concern, the MEGIS data used to calculate stream distance and lake surface area consists of measurements of the current morphology of Maine’s waterways. Yet, morphology of rivers and lakes would have changed over 400 years both naturally and by human manipulation through deforestation and damming. Various studies have shown that the long-term presence of dams can affect waterway hydrology, water body dimensions, sedimentation, branching and channelization, water temperature, and biological habitat availability (Poff et al. 1997; Poff & Hart 2002; Walter & Merritts 2008). Thorough and accurate estimations of these changes are difficult to obtain (ASRSC, Fletcher & Meister 1982; Petts 1989; Poff et al. 1997) requiring quantitative analyses of historic maps and sediment profiles to determine river width, depth and lake surface area over time. The objective of this study was to present a broad overview and timeline of loss of virgin spawning habitat, but such analyses would be necessary to give precise estimates of historically available spawning habitat and species productivity as affected by dams over time.

Finally, because of the alewife's migratory range, river herring represent a middle ground of spawning migration distance for diadromous species. Salmon and eels are known to have migrated longer distances and scaled steeper waterfalls than alewives to reach their destinations while sturgeon and striped bass were limited earlier in their migrations by their inability to ascend as many barriers (Atkins & Foster 1868; Bigelow & Schroeder 1953). Therefore, my migration distance assessment would be conservative for salmon and eels and a more thorough survey of upstream and non-pond tributary dams is recommended for salmon and eel spawning site studies to include their longer-distance migrations and different spawning site condition requirements. However, main stem head of tide dam construction would have been a decisive blow to all these species.

Implications for Restoration and Conclusion

My dam construction timeline and baseline habitat estimates provide quantitative and comprehensive data that can be used to evaluate where it would be most beneficial and cost effective to re-establish diadromous fish passage by defining the habitat range of historic river herring populations. With further research, historic and future river herring productivity within Maine's watersheds and the species' contribution to greater ecosystem productivity can be produced. Most importantly, these methods of historical evaluation demonstrate the dire consequences dams had on habitat availability for migratory species and the consequent economic and ecological impacts of removal from coastal watersheds.

The estimates of lost spawning habitat in this study are more severe than those presented in the past. Atkins' prediction of 10% remaining habitat (Atkins 1887) is an underestimate by up to an order of magnitude compared to my alewife spawning habitat estimates of less than one percent remaining by the late 1880s. Even the Lotze & Milewski (2004) dire estimate of 1% habitat remaining at present fails to identify that this baseline was probably reached over 100 years ago, before any effects of industrial pollution and human-induced climate change. Economically, dam blockage of the two largest watersheds in Maine, the Penobscot and Kennebec, has directly impacted harvests. Historically, alewife migrated 193 km and 322 km inland on the Kennebec and Penobscot, respectively, serving as food for local residents far from the ocean (Atkins & Foster 1868). These two watersheds historically provided harvests of up to one million alewives in the 1800s (Atkins 1887). Fisheries harvests for 2007 included 100,000 fish from the Orland River, 30 km upstream on the Penobscot watershed, and no harvest from the Kennebec (Gail Wippelhauser, MDMR, personal communication 2008); ten percent of historic harvests on these two already exploited waterways. The extensive system of dams on watersheds fractured the river ecosystems thereby decimating diadromous species' fisheries and presumably any coastal fisheries that depended on them.

Ecologically, we need to assess what these diadromous species historically contributed to the overall watershed food web of the Gulf of Maine. For instance, at their baseline abundance, what was river herring's energetic contribution to predators? What was the historical connectivity and exchange from watershed to watershed and freshwater to coastal marine systems? Extensive research on the anadromous and semelparous Pacific salmon species (*Oncorhynchus* spp.) has shown a significant ecosystem contribution to all trophic levels through transport of marine derived nutrients to freshwater spawning sites (Kline et al. 1990; Bilby et al. 1996). Salmon-derived nitrogen and carbon are incorporated into freshwater biota from riparian plants to secondary predators, are important contributors to juvenile fish growth and have been found in most trophic levels of adjacent terrestrial food webs (Bilby et al. 1996; Schindler et al. 2003). River herring along the Atlantic coast could be equally important but are iteroparous and therefore differ from Pacific salmon as nutrient vectors by not providing as substantial an influx of nutrients through mortality. By returning to the marine environment as adults multiple times, river herring potentially provide repeated exchange of nutrients between fresh and marine aquatic systems, and as a forage species, also the predators of each system. Short-term research on small watersheds shows evidence of incorporation of marine derived nutrients into freshwater ecosystems via excretion, mortality and eggs (MacAvoy et al. 2000; Post & Walters 2009; Walters et al. 2009). As with Pacific salmon, long-term studies of river herring reintroduction and nutrient transport need to be conducted to understand greater ecosystem impacts (Schindler et al. 2003).

For a complete analysis of what dam obstruction did to historical nutrient and energy exchange within coastal ecosystems we have to account for not only lost river herring populations but those of salmon, eel, sturgeon, shad and other diadromous fish prevented from migrating to their spawning habitat. If habitat was reduced to 10% of baseline totals by 1850, we can assume biomass was similarly reduced and in turn contributed to reductions of coastal game fish including cod and mackerel as has been suggested for over one hundred years (Baird 1872, Ames 2004). Also to consider, river herring potentially provide prey buffering for Atlantic salmon from fish and bird predators (Fay 2003), thus restoration of river herring populations may assist efforts to restore salmon. Yet, because habitat reduction and overfishing have decimated diadromous populations for centuries, the bigger question is: has resiliency of river herring and interdependent species been evolutionarily lost and impaired the ability of systems to buffer against future environmental changes?

The good news is opportunistic and highly fecund (60,000 to 300,000 eggs per female) alewives have rapidly populated reopened spawning areas in short time spans (Atkins & Foster 1868; Bigelow & Schroeder 1953; Pardue 1983). For example, in 1800 there were no alewives present in Damariscotta Lake. In 1803, transporting of adult spawners to the lake commenced a run that was thereafter "naturally" sustained with the completion of a fish ladder providing passage in 1809 and by 1821 required regulation of the highly productive fishery (Maine Legislative Records 1821; Cushman, 1882). Further rapid repopulation has also been demonstrated in the past two decades where dams have been removed or fish passage has been provided (Lichter et al. 2006; David Lamon, Executive Director, Somes-Meynell Wildlife Sanctuary, personal communication 2008).

Currently, there are numerous large-scale restoration efforts underway to restore access to diadromous fish habitat by removal, restored passage, or plans for future removal of main stem dams. Assessing the objectives of these dam removal and passage projects in comparison to my baseline spawning habitat estimates can help evaluate progress towards restoring historic levels of diadromous fishes. For example, the opening of the Brunswick Dam on the Androscoggin provided access to 53.8% of estimated historic lake habitat within the watershed (Brown et al. 2007). Opening the main stem Edwards Dam on the Kennebec watershed without unblocking the upstream main stem Milstar (Lockwood) Dam, or dams on tributaries like the Fort Halifax Dam, allows access to only 1% of estimated potential lake habitat (MDMR 2008; MDEP 2009). Yet, the opening of Fort Halifax Dam at the mouth of the Sebasticook River, assuming free passage of alewives upstream to all potential spawning area, provides access to 45% of lake habitat (MDMR 2008). In total, the opening of these two dams provides access to 46% of the Kennebec watershed’s virgin lake habitat for alewives. Finally, opening of the Great Works and Veazie Dams on the Penobscot River would allow access to 37% of my estimate of the watershed’s historical lake habitat (MBSRFH 2007). Today the Orland River is accessible to alewives, thus a total 42% of historical lake habitat would be made available. A forty percent increase in habitat access is a considerable step towards recovery, but species recruitment and resiliency studies need to be conducted to know how percent available habitat translates to population recovery.

The above restoration efforts have also brought river herring and other diadromous fish back to historical habitat primarily through stocking programs, fish pumps and fish ladders. With such assistance, it is difficult to estimate natural population limitation, watershed carrying capacity and energetic exchange between freshwater and marine ecosystems. Monitoring programs at the Brunswick Dam and Fort Halifax Dam on the Androscoggin and Kennebec watersheds are providing valuable time series information on spawning and recruitment (Brown et al. 2007; MDMR 2008). Such data can be used to understand the current contribution of diadromous fish to coastal ecosystems. The next step towards effective restoration is to conduct energy exchange studies on productive systems with assisted passage and stocking efforts. Similar research can then be conducted on watersheds as dams are removed to assess energetic contribution and carrying capacity from naturally accessible habitat systems. Finally, with current assisted passage and natural passage contribution values, my baseline spawning habitat estimates can be used to estimate total carrying capacity if all watersheds were opened to natural access. With knowledge of potential production and energetic contribution to the greater coastal ecosystems based on this historical data, we can begin to understand the magnitude of loss created by nearly 400 years of diadromous species habitat obstruction in the watersheds of Maine. Then, we can more realistically address management objectives including minimum percent accessible spawning habitat and maximum sustainable yields to create sustainable fisheries and restore the health and diversity of the Gulf of Maine coastal ecosystems.

Table 2.1A. Summary of historical and current dams in Maine by watershed.*

Watershed	**Total dams constructed 1600-present**	**Year of earliest documented dam construction**	**Number of dams still on watershed as of 2006****
Androscoggin River (Maine only)	145	1716	79
Coastal Waterways	110	1651	45
Damariscotta River	8	1726	2
Dennys River	19	1787	8
East Machias River	12	1765	4
Fore River	6	1674	2
Kennebec River	226	1754	128
Kennebunk River	10	1749	1
Machias River	13	1763	6
Medomak River	12	1797	5
Mousam River	24	1672	12
Narraguagus River	15	1773	4
Orange River	6	1828	4
Pemaquid River	6	1640	3
Pennamaquan River	18	1823	7
Penobscot River	283	1768	116
Pleasant River	9	1765	2
Saco River	72	1648	42

Piscataqua/Salmon Falls River	29	1634	12
Presumpscot River	68	1732	30
Royal River	10	1722	4
Sheepscot River	47	1664	15
St. Croix River	48	1780	20
St. George River	35	1647	18
St. John River	77	1811	48
Union River	36	1766	11
York River	12	1634	6
TOTAL	1356		634

*Includes dams that could not be assigned latitude and longitude.

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

Table 2.1B. Summary of historical and current dams in Maine by coastal region and associated river watersheds.*

Coastal Region	Total dams constructed 1600-present	Year of earliest documented dam construction	Number of dams still on watershed as of 2006**
Western	400	1634	196
Central	637	1640	299
Eastern	319	1763	139
TOTAL	1356		634

*Includes dams that could not be assigned latitude and longitude.

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

Table 2.2. Head of tide main stem dams on rivers with historical river herring runs and year of complete obstruction to upstream migration.

River	Dam	Town	Year	Source
Androscoggin	Brunswick Dam	Brunswick/ Topsham	1807	Brown et al. 2008
Dennys	Dennysville (Lincoln) Dam	Dennysville	1846	Atkins 1887, Atkins & Foster 1868 &1869
East Machias	Bangor Hydro Dam	East Machias	1784	Atkins & Foster 1868, Drisko 1904
Kennebec	Edwards Dam	Augusta	1837	Atkins 1887
Mousam	Kesslen Dam	Kennebunk	1720	Emery 1901, Atkins 1887
Narraguagus	Cherryfield Dam	Cherryfield	1820	Porter 1885-1886 & 1890-1891, Atkins 1887
Orange	Whiting Dam	Whiting	1828	Atkins & Foster 1868
Orland	Orland Village Dam	Orland	1836	Ames & Bray 2000
Pennamaquan	Lower River Dam (Iron Forks)	Pembroke	1828	Atkins 1874, MDIFG (Havey) 1956
Penobscot	Veazie Dam	Veazie	1835	Atkins 1887
Pleasant	Columbia Falls Dam	Columbia	1830s	Atkins 1887
Presumpscot	Presumpscot Falls - Smelt Hill Dam	Portland	1739, 1802	Willis 1831, Atkins & Foster 1868, Atkins 1887, MEGIS 2004
Sheepscot	Head Tide Dam	Head Tide	1762	Atkins 1874, MEGIS 2004
St. Croix	Union Mills Dam	Calais	1825	Atkins 1887
St. George	Upper Falls (Knox Falls) Dam	Warren	1840s	Atkins 1887, MDIFG (Foye) 1956
Union	Ellsworth Dam	Ellsworth	1800	Atkins 1887, Porter 1890-1891

Table 2.3. Percent remaining stream and lake habitat accessible to river herring resulting from full obstruction at head of tide dam on nine focus watersheds.*

Category	**Watershed**	**Year**	**% Stream Distance Remaining**	**% Lake Surface Area Remaining**
1	Androscoggin (Maine only)	1807	14.9	4.4
1	Kennebec	1837	7.3	0.5
1	Penobscot	1835	18.6	8.2
2	Mousam	1720	8.1	0
2	Sheepscot	1762	58.2	32.4
2	St. George	1840s	20.5	6.8
2	Union	1800	21.5	5.2
2	Dennys	1846	31.9	1.9
3	Casco Bay	1819	20.9	0.1

*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.

Table 2.4. Nine focus watersheds with total virgin stream distances and lake surface areas for potential river herring spawning habitat.

Category	**Watershed**	**Virgin stream distance (km)**	**Virgin lake surface area (km^2)**
1	Androscoggin (Maine only)	906.2	45.9
1	Kennebec	2392.3	197
1	Penobscot	5332	327.7
2	Mousam	183.5	10.7
2	Sheepscot	558	19.4
2	St. George	549.2	31.7
2	Union	480.9	93.2
2	Dennys	230.1	30.1
3	Casco Bay	862.1	136.1

Table 2.5. Category 1 Watershed: Kennebec River percent remaining stream and lake potential river herring spawning habitat based on chronological completion of dams with measurable impact before 1900.*

Year	Dam(s)	% Stream Distance Remaining	% Lake Surface Area Remaining
1600	None	100.0	100.0
1754	Fort Halifax Dam, Dresden Bog Dam	65.4	53.6
1760	Foot of Falls Dam	55.1	25.6
1765	Lower Togus Pond Dam	53.2	22.4
1768	Searles Mill Dam	51.9	22.3
1780	Pittston Mill Dam	51.4	22.3
1783	Temple Stream Dam	49.5	22.1
1785	Drummore Sawmill Dam	47.0	22.1
1789	Fall Brook (Buswell’s Mill) Dam	46.0	22.1
1792	Milstar (Lockwood) Dam, Union Gas Dam	14.8	4.8
1795	Winnegance Causeway Dam	14.4	4.8
1808	Rogers Neck Pond Dam	14.4	2.4
1819	Whiskeag Creek Dam	14.2	2.4
1837	Edwards Dam, Parker Head Dam	6.9	1.4
1841	Bond Brook Dam	6.3	1.4
1867	Nequasset Lake Dam, Vaughn Brook Dam	4.9	0.4

*Repeated values for percentages indicate no change in available area for either stream distance or lake surface area with construction of dam.

Table 2.6. Category 2 Watershed: St. George River percent remaining stream and lake potential river herring spawning habitat based on chronological completion of dams with measurable impact before 1900.*

Year	Dam(s)	% Stream Distance Remaining	% Lake Surface Area Remaining
1600	None	100.0	100.0
1734	Tollman Dam	97.7	98.0
1777	Crawford Outlet Dam	82.7	72.2
1785	Warren (Knox Falls) Dam	18.9	4.9
1867	Mill River Dam	13.0	0.0

*Repeated values for percentages indicate no change in available area for either stream distance or lake surface area with construction of dam.

Table 2.7. Category 3 Watershed: Casco Bay percent remaining stream and lake potential river herring spawning habitat based on chronological completion of dams with measurable impact before 1900.*

Year	Dam(s)	% Stream Distance Remaining	% Lake Surface Area Remaining
1600	None	100.0	100.0
1663	Libby River Dam	99.7	100.0
1682	Nonesuch Mill Dam	98.2	100.0
1700	Mill Brook Dam	98.1	100.0
1733	Stroudwater Dam	91.2	100.0
1750	Capisic Pond Dam	90.5	99.9
1762	Cumberland Mills Dam	57.8	3.0
1763	Shaw Mills Dam	57.2	3.0
1766	Runaround Pond Dam	56.0	2.6
1790	Long Creek Pond Dam	54.0	2.6
1791	Mayall Mills Dam	53.4	2.6
1800	Randall Mill Privilege Dam	53.0	2.6
1802	Smelt Hill Dam	43.7	0.6
1819	Bridge Street Dam	24.1	0.6
1890	Milliken Mill Pond Dam	23.6	0.6

*Repeated values for percentages indicate no change in available area for either stream distance or lake surface area with construction of dam.

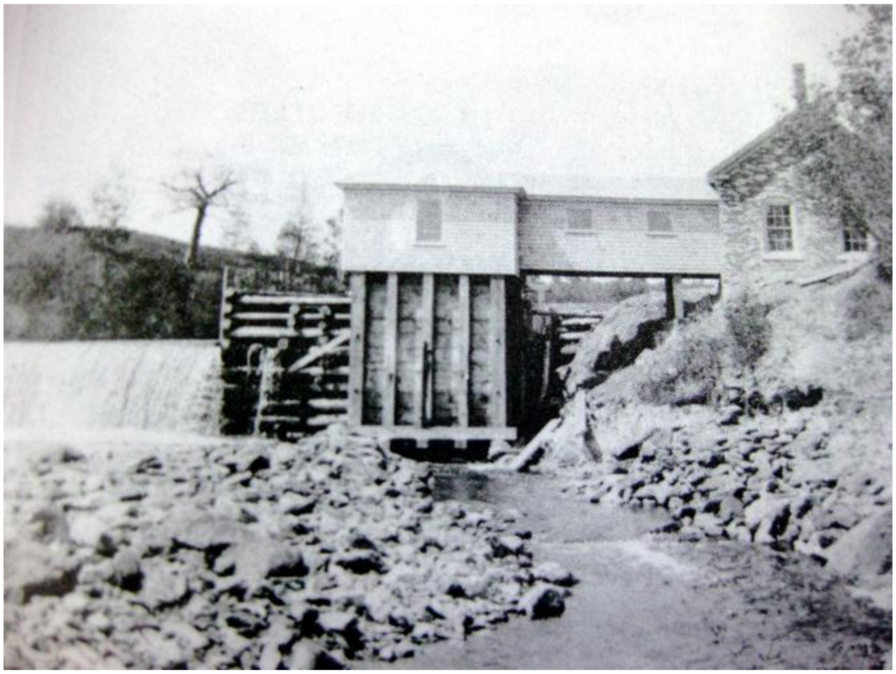

Figure 2.1. Dam and power house on St. George River circa early 1900s. From Whitten, 1990: 213. Courtesy, Edwin Boggs, Sr.

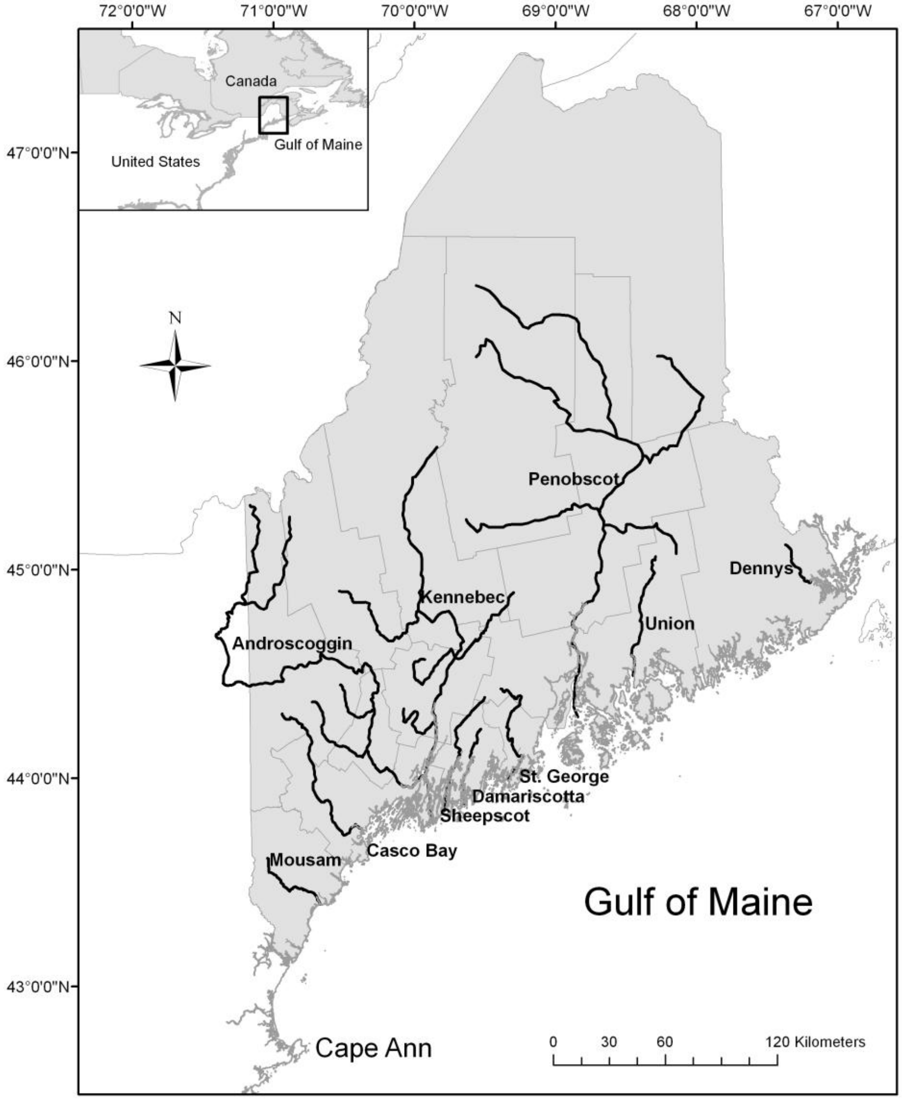

Figure 2.2. State of Maine with historical river herring watersheds assessed in this study for temporal spawning habitat changes from 1600 – 1900.

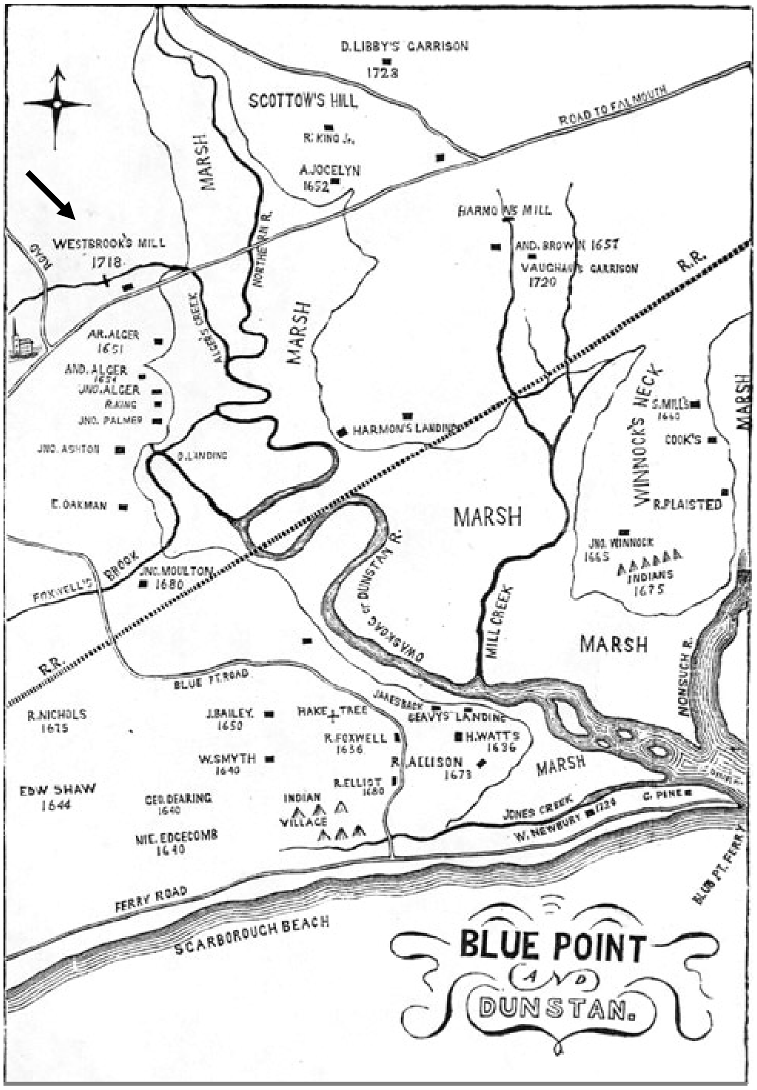

Figure 2.3. Map of Blue Point, Maine drawn by H.G. Storer between 1830 and 1880. Building and dam locations, owners and dates are labeled. The arrow indicates Westbrook's mill of 1718 with associated dam. From Southgate, 18--: frontispiece.

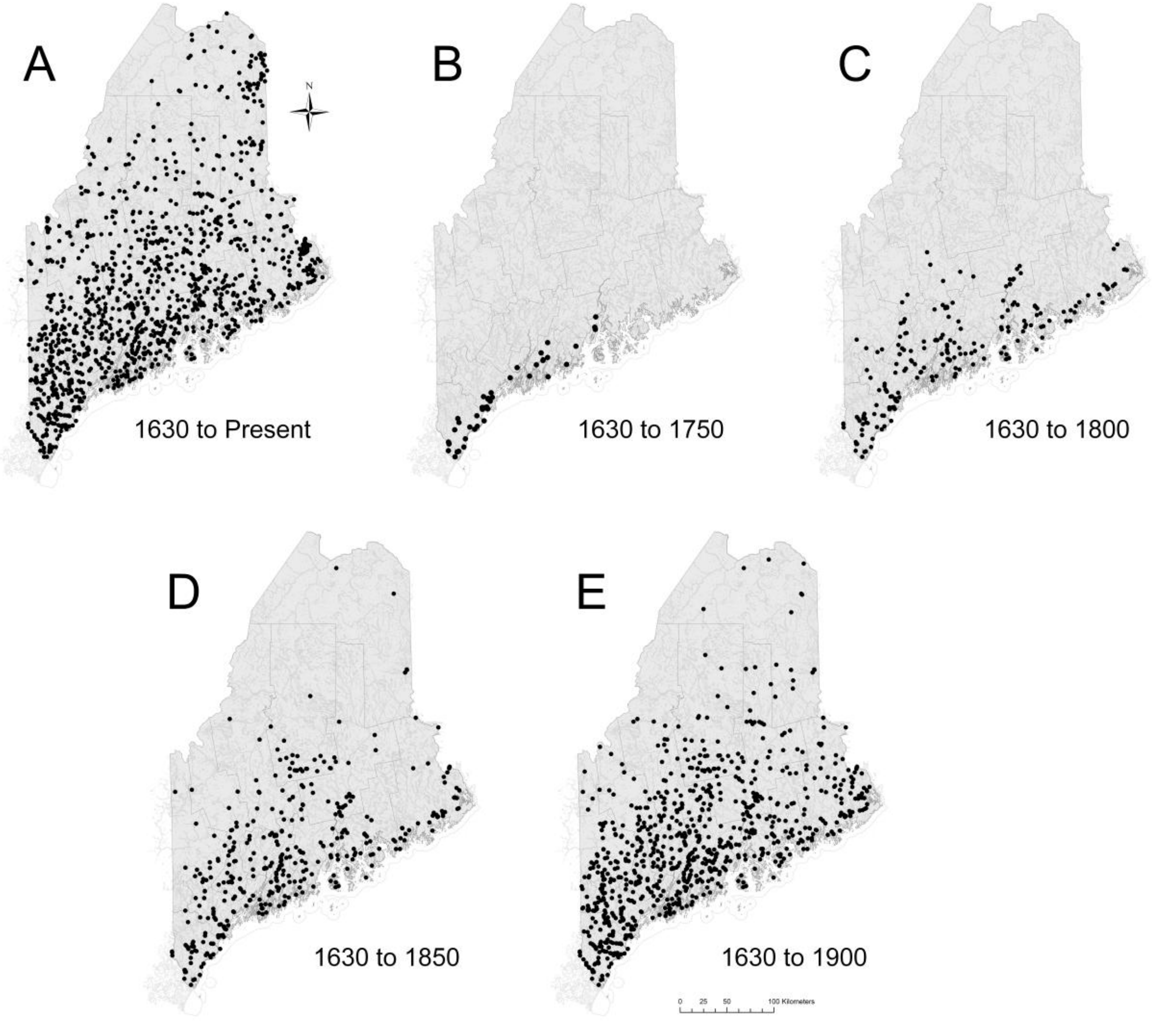

Figure 2.4. Temporal and spatial accumulation of dams in Maine for which latitude and longitude were determined. Each dot represents a dam. Map A: comprehensive of all dams completed through 2008. Map B: all dams constructed by 1750. Maps C – E: the cumulative increase of completed dams in 50-year increments from 1750 to 1900.

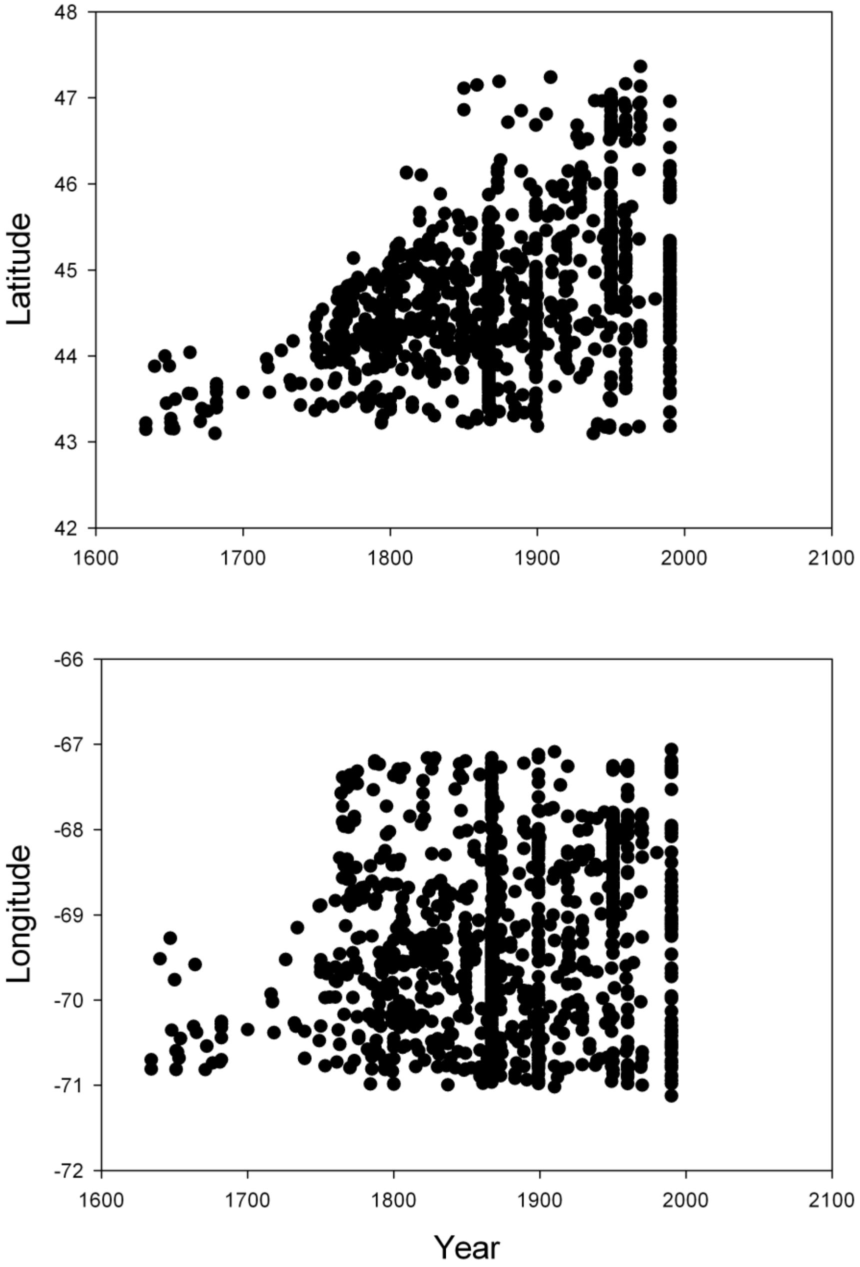

Figure 2.5. Temporal and spatial distribution of dam latitude (top) and longitude (bottom) in Maine from 1600 to 2000.

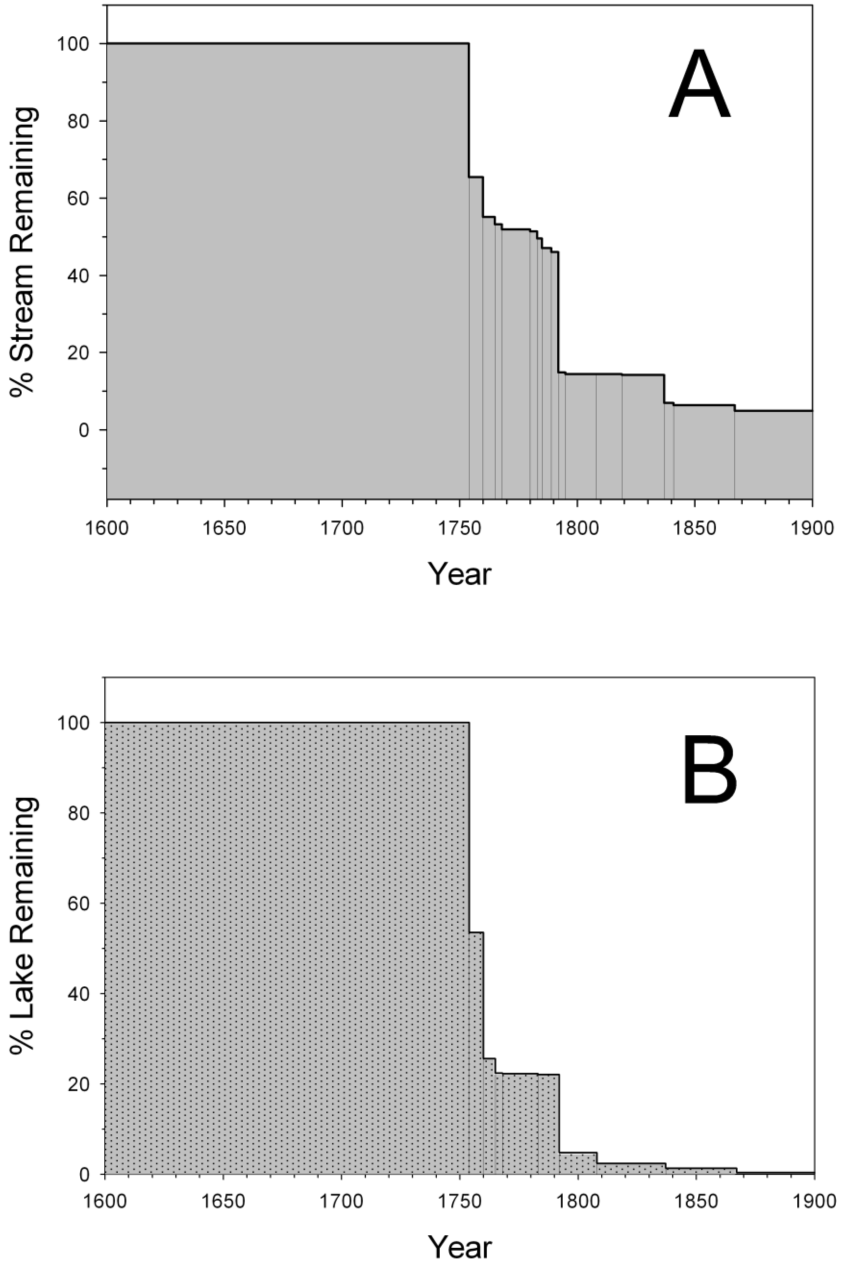

Figure 2.6. Category 1 Watershed: Kennebec percent virgin habitat. A) Percent stream distance remaining and B) percent lake area remaining from 1600-1900. Vertical drop down lines in each graph indicate year of dam construction that resulted in a measurable loss of virgin spawning habitat.

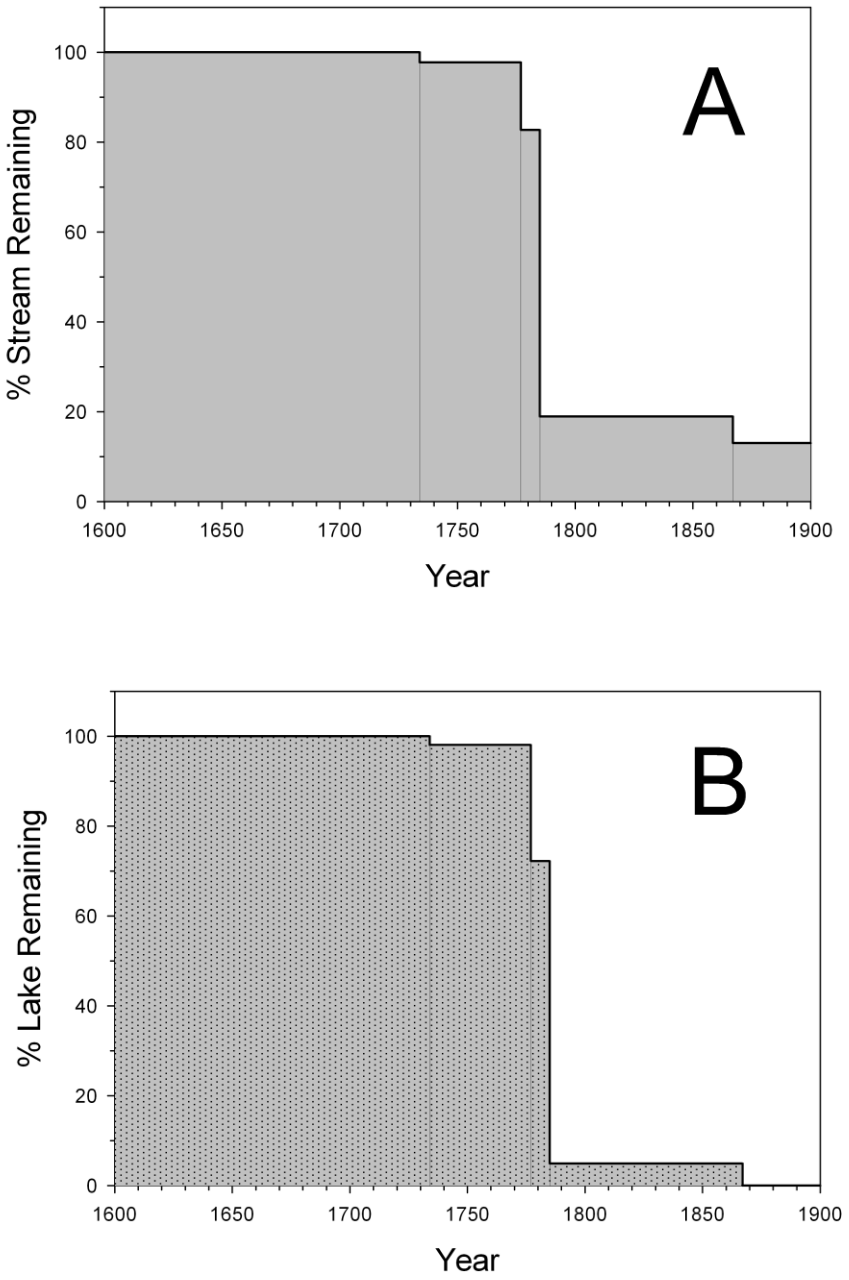

Figure 2.7. Category 2 Watershed: St. George percent virgin habitat. A) Percent stream distance remaining and B) percent lake area remaining from 1600-1900. Vertical drop down lines in each graph indicate year of dam construction that resulted in a measurable loss of virgin spawning habitat.

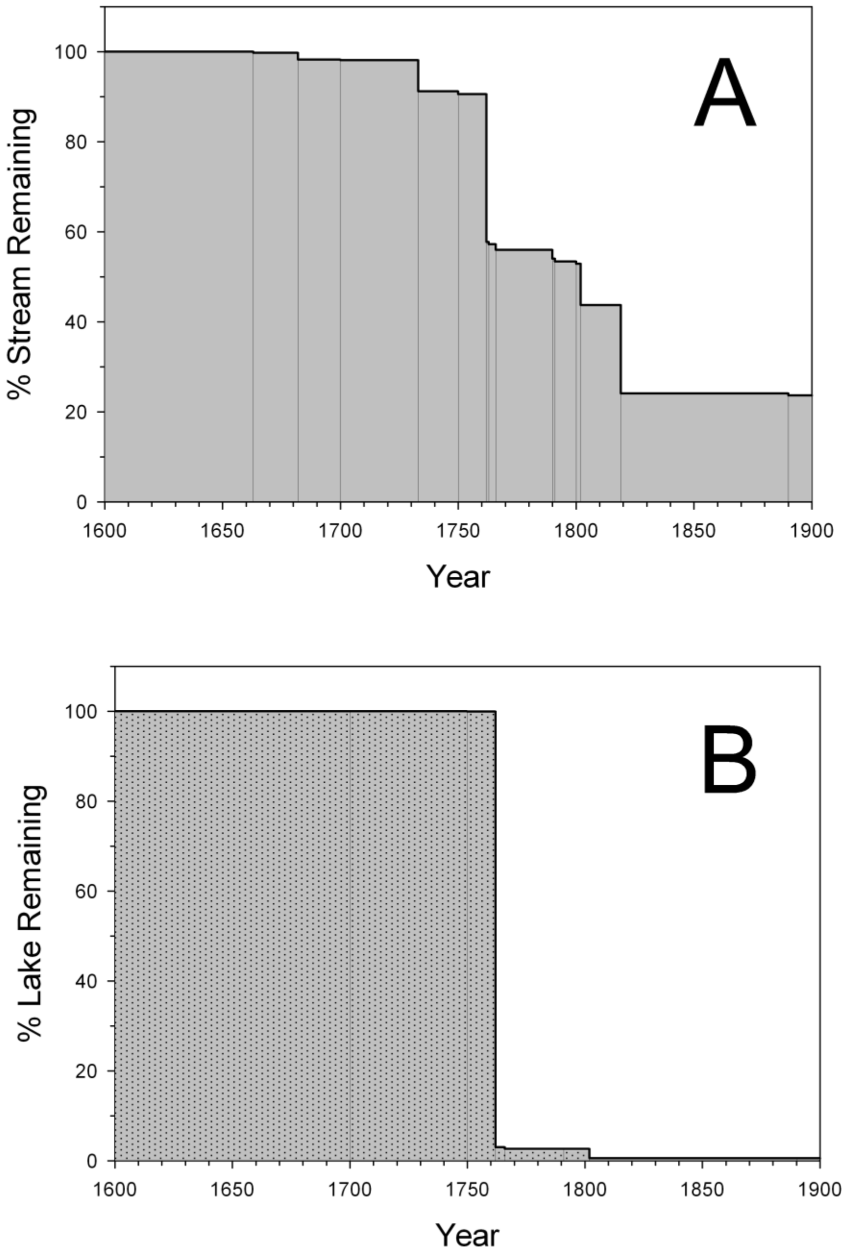

Figure 2.8. Category 3 Watershed: Casco Bay percent virgin habitat. A) Percent stream distance remaining and B) percent lake area remaining from 1600-1900. Vertical drop down lines in each graph indicate year of dam construction that resulted in a measurable loss of virgin spawning habitat.

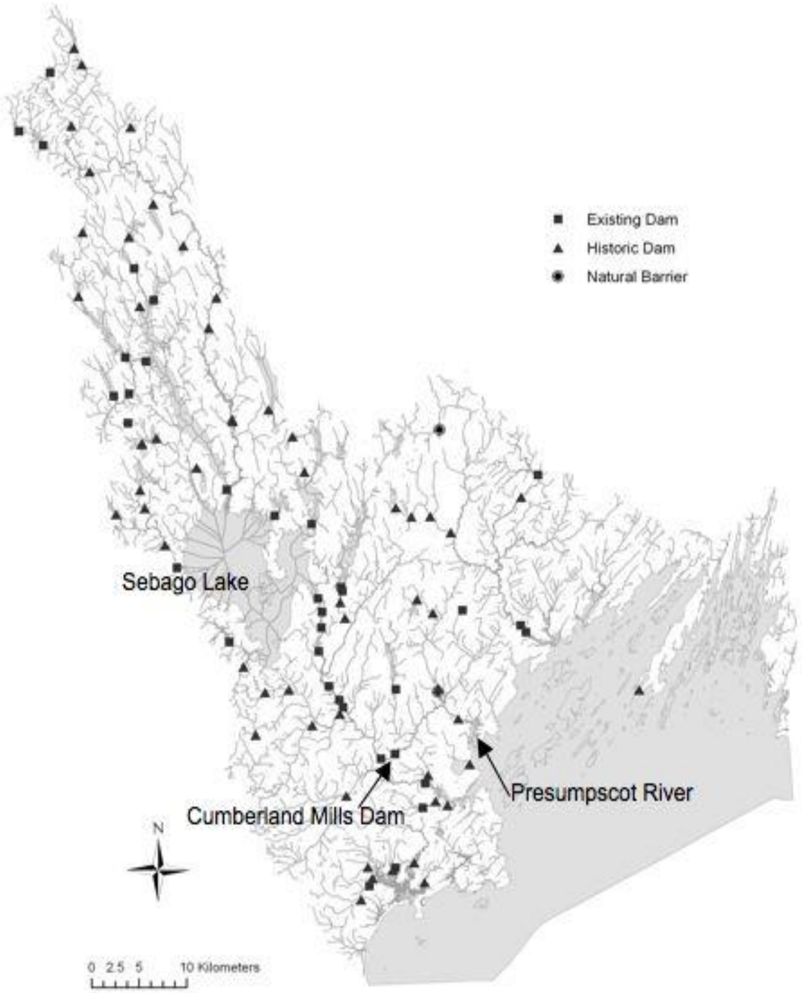

Figure 2.9. Casco Bay watershed with all dams constructed 1600 to 2008.

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Chapter 3: Watershed obstruction and the anadromous alewife: loss of ecological productivity in the Gulf of Maine.

Introduction

Of growing interest to the construction of natural ecosystem models and restoration efforts is the application of historical data, both qualitative and quantitative (Pitcher & Pauly 1998). Historical data can be used to adjust baseline estimates for species and ecosystem productivity to pre-exploitation conditions, which for targeted fish populations in the northeastern United States were 400 years ago. Current U.S. regional fisheries status and stock assessments are typically based on state and federal landings and abundance data or state fishery data from the last century (NCDENR 2000; AMSFC 2009). Without information pre-dating 1900, management is only informed by highly impacted systems to estimate potential productivity, and recovery, of native ecosystems.

Historical ecology studies have used diaries, ships' logs, naturalist publications, and other records from the 19th century and earlier to compile estimates of species abundance and ecosystem shifts across diverse fauna and ecosystems, from temperate to tropical. Qualitative descriptions include 16th and 17th century species diversity and populations of whales, turtles, oysters and fishes in the Gulf of California far beyond modern population sizes (Saenz-Arroyo et al. 2006). Quantitative historical studies have estimated a greater than 3-fold decrease in individual Atlantic cod sizes (Jackson et al. 2001), a 99% reduction of river herring populations in the St. Croix River from the early 19th century (Lotze & Milewski 2004) and a reduction of Scotian Shelf Atlantic cod biomass from 1.26 million mt in 1852 to less than 50,000 mt in 2004 (Rosenberg et al. 2005). Although these estimates may seem extreme, such historical studies are often conservative: for instance the cod and river herring studies ignore the first 200 years of human impacts. In this chapter, I focus on 400 years of human impacts to Maine watersheds in order to provide a context and establish a realistic historical baseline of pre-impact diadromous fish populations.

Diadromous species, those that migrate between marine and freshwater ecosystems during their life cycles, have long been important resources for coastal communities. Both economically and ecologically valuable, decline of these populations due to anthropogenic impacts have had myriad consequences to their native watersheds (Baird 1883; Schindler et al. 2003; Morita et al. 2009). In the Gulf of Maine, river herring, collectively alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*), has been a principal bait fish for numerous commercial fisheries including Atlantic cod (*Gadus morhua*), Atlantic mackerel (*Scomber scombrus*), striped bass (*Morone saxatilis*) and American lobster (*Homerus americanus*) (Baird 1872; ASMFC 2009). Settlers also valued it for consumption as a preferred food fish, locally and for export (Atkins & Foster 1868, Baird 1874). An anadromous species, river herring spend most of their adult lives in the ocean, returning annually to freshwater sites to spawn. During spawning runs, especially at sites of constricted passage, river herring are easy and predictable targets for fishermen and were historically caught by a variety of gear including dipnets, pound nets, weirs and seines (Smith 1899).

Seventeenth century European settlers described an astonishing abundance of alewives in most of the northeastern United States coastal waterways. In 1634 colonist

William Wood stated that alewives "…[came] up to the fresh Rivers to spawne, in such multitudes as is almost incredible, pressing up such shallow waters as will scarce permit them to swime..." (Wood 1634: 56). In an alewife account on a Kennebec River tributary in the 1700s, historian J.W. Hanson reported "… alewives were so plenty there at the time the country was settled, that bears, and later, swine, fed on them in the water. They were crowded ashore by thousands." He followed with testimony of a single woman catching seven barrels of alewives in one day with a dipnet on the same tributary (Hanson 1852: 186). The alewife was so abundant as to be almost a nuisance. As unwanted bycatch in fisheries for the more favorable Atlantic salmon (*Salmo salar*), they were "left to decay in heaps upon [the river] banks, in mere wantonness" (Loring 1880: 23).

As settlements developed in Maine, two significant – and often conflicting – anthropogenic pressures increased on anadromous populations: direct exploitation via fishing and indirect effects of dam construction to spawning habitat access. Reduction of these economically important anadromous species, as well as that of coastal fish that relied on them for foraging, led to town petitions and state laws meant to lessen the impact of dams on the shrinking populations as early as the late 1700s (Reed et al. 1821, Shaw & Allen et al. 1824). Atkins (1887) reported a total of 161 legislative acts passed in reference to anadromous fishes from 1800 to 1880. A majority of these were focused on how to preserve the supply of fish attempting to balance demands of river fisheries and water-power dependent industries. In 1868, the first Maine Commissioners of Fisheries listed impassable dams as the most damaging of anthropogenic impacts on anadromous fish, followed by overfishing and pollution (Atkins & Foster, 1868).

Despite long-term awareness of human impact on anadromous populations, Maine alewife landings from 1880 to 2005 vary considerably reaching historic lows in the 1990s (Figure 3.1). Periodic increases in landings may reflect changes in fishing effort and/or natural variability (Chaput & Atkinson 2001), but in general, increases in alewives correspond to and follow periods of renewed focus on fish passage installation. These passage efforts have occurred multiple times throughout the late 19th and 20th centuries: in the 1870s after the Fish Commissioners were established (Atkins & Stillwell 1874); in the 1920s to increase salmon populations (MCOIFG 1922); in the 1940s to improve alewife fisheries (Rounsefell & Stringer 1943); during the 1960s after extensive river reports on anadromous species (MDIFG 1955-1967); and during recent restoration efforts in the 1980s and 1990s. But the variability also reflects failure to maintain rebounding populations. Increased fishing pressure on improving stocks probably contributed to failed recovery as well as poor fishway construction, monitoring and maintenance (Decker 1967). In 1990, the Atlantic States Marine Fisheries Commission (ASMFC) conducted a stock analysis including eleven New England river herring rivers with restoration programs that consisted primarily of establishing dam fish passages (Crecco & Gibson 1990). All populations were at least partially exploited with one significant alewife river in Maine, the Damariscotta, severely overfished.

The remaining river herring populations continued to decline after the 1990 stock analysis, with Atlantic coast commercial landings decreasing from 6.2 million kg in 1985 to less than half a million kg in 2007 (AMSFC 2009). With the populations showing little sign of recovery, NOAA Fisheries listed river herring as a species of concern in 2006 (NOAA 2006). Yet in 1887, Charles Atkins estimated the productive capacity of all rivers in Maine to have been reduced by 90% due to dam construction (Atkins 1887). This means over one hundred years before becoming a species of concern, the 1887 alewife catch of 1.15 million kg or over 5 million fish may have been only 10% of potential fisheries productivity.

Much time and money has been spent on multiple efforts to restore declining populations, all without any realistic knowledge of what levels equate with "successful" restoration. This study provides a rigorous analysis of historic and current alewife harvests in Maine over the period of 1800 to present day in order to help provide this much-needed estimate of pre-colonial abundance. Estimates of changes in total productivity from 1600 to 1900, based on changes in watershed habitat (due to dam construction) and how loss of habitat contributed to declines in alewife populations are presented. Finally, the findings provide a more realistic baseline for evaluating anthropogenic impact on watershed ecology, and effectively and accurately assessing the progress of restoration attempts.

Materials and Methods

Study area

River herring harvest research was conducted on all Maine watersheds. Nine watersheds with referenced historical river herring presence were then assessed for changes in access to spawning habitat and estimated productivity due to dam construction from 1600 to 1900 (Figure 3.2). These watersheds represent three categories of coastal watersheds in Maine: 1) principal rivers with numerous tributaries, 2) secondary rivers with few tributaries and 3) bay-system watersheds with multiple coastal waterways.

Watersheds are shown with associated dams documented in this study (see Results). Also included is the Damariscotta River from which spawner-recruit data is used for analysis.

Historic and current alewife harvest sources

The earliest harvest records are Commonwealth of Massachusetts and State of Maine Fish Inspector reports beginning in 1804 (Maine Secretary of State 1804-1893). Reports were from fishery and shipping towns along the length of the Maine coast from Casco Bay to Cobscook Bay (Figure 3.2) and contain barrels of pickled fish and boxes of smoked fish according to town and species. Although inconsistent, they provide the only regular harvest records for the early 19th century.

Of the two river herring species, alewives were the predominant fish reported historically and are therefore the focus of this study. To compare “barrel” and “boxed” quantities to later harvest data units, all quantities were converted to number of fish. Conversions were found in individual fish inspector reports (Maine Sec. of State 1804-1893). With an average of 90.72 kg alewives per barrel, at an average weight of 0.227 kg per alewife (Rounsefell & Stringer 1943; Bigelow & Schroeder 1953), alewives averaged 400 fish per barrel. For boxes, 220,000 smoked alewives were packed into 3200 boxes equaling 69 fish per box. It is important to note that all of these conversions are calculated based on 19th and early 20th century averages of alewife size across Maine.

Later 19th century harvest reports included the first Maine Commissioner of Fisheries (COF) report (Atkins & Foster 1868), subsequent Maine COF reports (MCOFG 1888, 1889-1890), and special reports on river and alewife fisheries (Atkins 1887; Smith 1899). Mid-twentieth century annual harvests were found in Rounsefell & Stringer’s

(1943) alewife fishery report. Town harvests from 1943 to 2007 provided recent landings per watershed and represent ninety percent of all Maine harvests (Gail Wippelhauser, MDMR, personal communication 2008).

Harvests reported by town in Fish Inspector records were assigned watersheds according to the nearest river or water body. Harvests designated by county (Rounsefell & Stringer 1943) were assigned according to waterways specified in the text of the report. Where multiple towns or tributaries within a single watershed had harvests, proportions of harvest were estimated based on river-specific yields from other years.

Watershed fishery productivity index

Historic and current fishery reports were quantitatively evaluated for percent contribution of individual watersheds to total alewife harvest. Spanning from 1804 to 2007, this provides snapshots representing which watersheds had the most productive historical alewives harvests. A proportional watershed fisheries productivity index (WFPI) is calculated as percent contribution of an individual watershed (IW) to the total Maine harvest (TH) over a chosen time interval, t.

$$\mathrm{WFPI}_{(t)} = \frac{\mathrm{IW}_{(t)}}{\mathrm{TH}_{(t)}} * 100$$

Identification of dams and natural barriers to spawning migration

The principal database referenced for still present and recently removed dams was 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). It lists over 800 dams with information on waterway, owner, latitude and longitude, and year of completion. No dam completion years from this source dated before the 1800s. Earlier dates of dam presence required historic literature surveys. The most comprehensive historical reference was *The Water-power of Maine*, based on an 1867 hydrographic survey of Maine (Wells 1869).

Nineteenth and twentieth century government reports were used to identify and date dams on river fishery watersheds and determine natural barriers to upstream passage of alewives. COF reports from 1868 to 1899 included accounts of anadromous fish populations and obstructions that impeded migration to spawning habitats (Atkins & Foster 1868, 1869; Atkins & Stillwell 1874; Atkins 1887; Smith 1899). Twentieth century sources included alewife fisheries reports, river surveys and management reports (Rounsefell & Stringer 1943; MDIFG 1955-1967; ASRSC 1982-1983).

Dates and locations of dams constructed before Wells' 1867 survey were found in numerous popular and legislative historical sources including wills, historical magazines and journals, town histories, 18th and early 19th century newspaper articles and records of early 19th century legislative acts and petitions (Maine Legislative Records 1821-1830). These sources were also instrumental in determining presence or absence of alewives in rivers where anadromous species were already extirpated before 19th century fishery and watershed reports. See Chapter 2, Appendix 2.1 for a comprehensive listing of sources.

Latitude and longitude in decimal degrees for dams and natural barriers were determined using the twenty-sixth (2003) and thirtieth (2007) editions of the DeLorme Maine Atlas and Gazetteer™ and Google Earth 5.0 during the period of January to July 2009. Obstructions 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 were geo-referenced using the Geographic Coordinate System North America 1983.

Definition of historical alewife spawning habitat

Alewives spawn in still water so all lakes or ponds below natural barriers or within known alewife migration distances were considered potential spawning habitat. Documentation of maximum alewife migration not limited by natural barriers was found in the Maine COF reports, alewife fisheries and river survey and management reports referenced above. Streams categorized as perennial in the MEGIS database (MEGIS 2004) that led to water bodies within the estimated range of migration were used to calculate stream migration distance whereas streams categorized as intermittent or not connected to water bodies were not included. Perennial streams within distance of head of tide but without connection to water bodies were included for potential blueback spawning habitat. Inclusion is based on reports that bluebacks will migrate to and somewhat above head of tide to spawn in flowing water (MDMR et al. 1982).

Quantifying habitat

To estimate pre-colonial (hereafter referred to as “virgin”) alewife spawning habitat, river and lake demographics from MEGIS 2004 were used to calculate total stream distance in kilometers (km), composed of main stem river and accessible tributaries, and total lake surface area in squared kilometers (km^2) up to natural barriers or maximum alewife migration. Virgin spawning habitat was dated 1600, pre European colonization. Changes in accessible stream distance and lake area resulting from dams were calculated chronologically at the year of dam construction from 1600 through 1900. Inaccessible stream distance and lake area upstream of the completed dam was subtracted initially from the virgin total and from remaining habitat totals subsequently.

Historical productivity estimates

Two approaches were taken to find alewife productivity estimates. The first uses Lewis Flagg's two estimates for adult alewife returns of 29.0 x 10^3 and 58.1 x 10^3 adults per lake surface km^2 based on annual harvest yields plus one day/week, or 15%, spawning escapement (Flagg 2007). The yield values were from Damariscotta and St. George River harvests from the recent past (post 1990) when the fisheries were at historic lows (Figure 3.1) making even the upper estimate highly conservative. The value of 58.1 x 10^3 adults per km^2 is currently used as the standard production estimate for Maine (Flagg 2007; Rory Saunders NOAA, NMFS Maine, personal communication 2009).

A second approach used a longer time series to give productivity values from a potentially less exploited system. A spawner-recruit time series from the Damariscotta River was used in the 1990 ASMFC river herring and shad stock assessment report to which the authors fit a Shepherd S-R model and determined the parent-recruit relationship to be density dependent (Crecco & Gibson 1990). I fit thirty-five years of this data, 1949-1983, to a Beverton-Holt spawning stock-recruitment curve by minimizing the sum of squared residuals. A Gauss-Newton non-linear analysis was completed using SAS™ v. 9.3 to determine the Beverton-Holt model significance and 95% confidence intervals. A segmented regression with a breakpoint analysis was performed on recruitment against time to identify significant changes in annual recruitment using Bayesian Information Criterion (BIC). This analysis was performed with the "strucchange" 145 package in R. The recruitment values were then normalized and ordered to provide 25th, 50th and 75th percentiles within a cumulative frequency distribution to establish a range of recruits and then divided by the surface area of Damariscotta Lake (18.87 km^2, MEGIS 2004) to give three estimated production values in terms of first time recruits/km^2. For the analysis, parents were treated as fish that escaped harvesting and made it to spawning grounds and recruits were calculated as the sum of first time spawning 3-6 year old fish from the entire run (Crecco & Gibson 1990).

Historical productivity per watershed over time was calculated with total productivity of a particular watershed in year t, $TP_{w(t)}$, as a product of the accessible lake habitat in year t, $AH_{w(t)}$, and a productivity estimate in fish per km^2, P.

$$TP_{w(t)} = (AH_{w(t)}) * (P)$$

This calculation was done with each of the five production potential estimates described above on all nine watersheds through changes in accessible habitat from 1600 (virgin) to 1900. Total productivity was calculated each year a dam was completed on the watershed that had a measurable impact on accessible habitat.

A total productivity for Maine based on the nine watersheds was calculated by summing all watershed productivity estimates at fifty-year increments from 1600 to 1900

$$TP_{Me(t)} = \sum_{i=1}^{n=9} (AH_{w(t)})_i * (P)$$

where $TP_{Me(t)}$ is the total estimated productivity for Maine in year t.

Current production estimates

Current estimates of river herring production on three watersheds were provided by watershed restoration and restocking programs that conduct annual fish counts at weirs or dams. Count and stock data was collected for the Androscoggin (Brown et al. 2008; Gail Wippelhauser, MDMR, personal communication 2009), Kennebec (MDMR & MASC 2007; MDMR 2008) and Dennys (Gail Wippelhauser, MDMR, personal communication 2009). These were then compared to the maximum virgin production estimates calculated using the 75th percentile production value to illustrate the greatest potential loss of production.

Results

Watershed contribution to harvest

Watersheds contributing 90% or greater of state alewife harvest are presented across twelve harvest periods from 1804 to 2007 (Table 3.1). Harvest periods were determined based on single year comprehensive records or multi-year periods representative of all watersheds producing during a focused time frame of consistent harvest reporting. Four principal watersheds, the combined Androscoggin/Kennebec, the Damariscotta, the St. George and the Penobscot, provided regular yields for 10 to 11 of the 12 harvests. During the first period, 1804 – 1820, five watersheds spanning the coast from Casco Bay in the west to eastern-most Cobscook Bay contributed 98% of the harvest (Figure 3.3). The next period from 1833 to 1840 also had five main watersheds with replacement of the St. George by the Damariscotta. The Damariscotta was a regular contributor to Maine's harvest from the 1830s to the present (Table 3.1). By the late 1880s, three watersheds, Damariscotta, Medomak and St. George, were the only watersheds with recorded yields. All three are located in the center of the coast and are category 2, smaller secondary river watersheds (Figure 3.3). Harvests re-expanded along the coast in the 20th century, including Casco Bay and the Dennys River in 1896 and 1942, respectively, but became more centrally focused again by the 1950s. From the 1970s through the 2000s, 90 percent of the state's harvest was taken consistently from the Androscoggin/Kennebec, Sheepscot, Damariscotta, St. George, Penobscot, Union, Narraguagus and East Machias watersheds. Town records from the 1950s through the 2000s specified harvests on primary rivers were all taken below head of tide (Table 3.1).

Watershed fishery productivity index

The watersheds from Table 3.1 are presented with percent contribution to Maine's alewife fishery productivity as an index across fourteen intervals with 89.6% or greater of state harvest represented by the contributing watersheds (Table 3.2). The western-most watershed Casco Bay contributed 23% in the earliest interval, 1804-1810, which dropped to 3.3% in the 1840s and reached a high of 27% in 1896 before decreasing to and remaining at zero. Cobscook Bay, the eastern-most watershed, contributed 16.2% from 1804-1810, dropped to 2.4% the next decade and reached a high for the state of 57.5% in the 1840s (Figure 3.4) before decreasing to zero for the rest of the index. The Androscoggin/Kennebec watershed was fairly consistent and contributed to 11 of the 14 intervals across the index ranging from a low of zero to a high of 18.4% with an average of 7.1%. All contributions from the Androscoggin/Kennebec watershed were from habitat below head of tide after the 1820s (Table 3.1). Starting in 1887, the St. George became a consistent contributor through the 2000s ranging from 6.4% to 28.1% and an average of 18% for the 10 intervals between 1887 and 2007.

The Damariscotta and the Penobscot are the two watersheds that contributed the most to harvests, 11 and 12 times, respectively, and had the highest values in the index, both 86.7% occurring before 1900. An index replacement occurred around mid-century with the Penobscot having the highest values through the 1840s supplanted by the Damariscotta by the 1880s (Table 3.2, Figure 3.4). Also in the 1880s, the St. George began to replace the contribution of the two bay systems, the Casco and Cobscook Bays (Figure 3.4). The Sheepscot, Union, Narraguagus and East Machias watersheds became regular contributors to the index from the 1970s to 2007 with the Union having the highest average of 19.5%. The contribution of the Damariscotta and Penobscot watersheds decreased to 7.7% and 10.7% percent, respectively, in the 2000s, with the St. George providing 24.4% percent. Notable among the index values, the Penobscot watershed had contributed over 86% to alewife production from 1811-1820, disappeared completely by the 1880s, and today contributes less than 11 percent.

Dams on waterways and historical alewife spawning habitat

A total of 908 dams were documented between 1600 and 2009 on the nine historical river herring watersheds (Figure 3.2). The Mousam, Sheepscot and Union watersheds had main stem dams constructed by 1800 and all watersheds had main stem obstruction at head of tide by 1846 (Table 3.3). The primary river system watersheds, the Androscoggin, Kennebec and Penobscot, had the most dam construction with 145, 226 and 283 dams documented, respectively. The secondary river system watersheds had between 19 and 47 documented dams and 93 dams were documented for Casco Bay. 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.

Virgin spawning habitat in stream distance (km) and lake surface area (km^2) for the nine watersheds are listed in Table 3.3. The Penobscot River watershed has the most virgin habitat in Maine with 5332 km stream and 327.7 km^2 lake habitat. The Mousam River watershed is the smallest examined in this study with 183.5 km stream and 10.7 km^2 lake habitat. The potential habitat for the state of Maine based on virgin totals of these nine watersheds is 11,494.3 km of streams and 891.9 km^2 of lake area.

Damariscotta River Stock-Recruitment data 1949-1983

A Beverton-Holt S-R model was fit to the alewife spawner-recruit data from the Damariscotta River fishery with the equation of $R = (2354.3)\ S/\ 85.59 + S$ ($n = 35$, $F = 183.67$, $p < 0.0001$) (Figure 3.5). A breakpoint analysis of the recruits shows three significant regressions separated by two breakpoints at 1953 and 1967 (Figure 3.6). These demarcate an initial period of increasing recruitment to a decline from 1953 through 1967 before a brief increase and return to a decline through 1983. Recruitment at 25th, 50th and 75th percentiles of the cumulative frequency distribution was estimated at 1210.2 x 10^3 recruits, 1418.8 x 10^3 recruits, and 1727.1 x 10^3 recruits, respectively. Each of these values divided by the total surface area of Damariscotta Lake, 18.87 km^2, gave annual production potentials of 64.13 x 10^3 recruits/km^2, 75.15 x 10^3 recruits/km^2 and 91.53 x 10^3 recruits/km^2 (Table 3.4). These estimates combined with those calculated by Flagg

(2007) give five values for estimated historical production ranging from 29.0 x 10^3 adults/km^2 to 91.53 x 10^3 recruits/km^2. My estimates of recruits/km^2 does not include all returning adults as Flagg (2007) did for his estimates, thus my production estimates are comparatively conservative.

Total historical productivity potential for Maine and per watershed

On the Kennebec watershed, estimated virgin annual productivity ranged from 5.7 million alewives/year to over 18 million alewives/year (Table 3.5, Figure 3.7B). Significant reductions in available lake habitat occurred in 1754, 1760 and 1792 decreasing accessible spawning area from 197.0 km^2 to 9.4 km^2 in less than 40 years (Table 3.5, Figure 3.7A). By 1792, potential production was reduced to a range of 271,788 to 857,819 alewives/year – a loss of at least 85%. The last dams to have a measurable impact on the Kennebec were completed in 1867 and left a total of 0.7 km^2 or 0.4% virgin lake habitat – production estimates decreased to a range of 20,474 to 64,620 alewives/year. Comparing the maximum production potential estimates, the loss of Kennebec annual alewife productivity from 1600 to 1867 would be over 17 million fish.

On the St. George watershed, annual productivity estimated in 1600 ranged from 920,170 to over 2.9 million alewives/year (Table 3.6, Figure 3.8B). Significant reductions in available lake habitat occurred in 1777 and 1785 decreasing lake area from 31.7 km^2 to 1.6 km^2 (Table 3.6, Figure 3.8A) and with 5% of lake habitat available in 1785, potential annual production ranged from 45,240 to 142,787 alewives/year. After dams obstructed access to all lake habitat, the St. George potentially lost annual alewife productivity of nearly 3 million alewives/year by 1867.

For Casco Bay, available lake spawning habitat remained near its unobstructed total of 136.1 km^2 in 1600 until the construction of the Cumberland Mills Dam in 1762 which reduced lake habitat to 4.1 km^2 or 3% of the virgin watershed (Table 3.7, Figure 3.9A). This dam obstructed the Presumpscot River that provides access to 116.4 km^2 Sebago Lake, the principal lake of the Casco Bay watershed (See Chapter 2, Figure 2.7). Virgin annual productivity ranged from 3.9 million to over 12 million alewives/year (Table 3.7, Figure 3.9B), but with the loss of Sebago Lake, potential annual production decreased to a range of 117,943 to 372,253 alewives/year. By 1890, continued damming reduced lake habitat to 0.8 km^2 and annual productivity declined to 22,939 – 72,400 alewives/year with a maximum annual potential loss of over 12 million alewives.

By 1760, dams were having a significant impact on alewife access to lake spawning habitat in the Kennebec, St. George and Casco Bay watersheds and by 1800 these watersheds had individually lost annual alewife productivity in the range of 2 to 17 million fish/year. See Appendices 3.1 and 3.2 for additional analyzed watersheds.

Virgin lake habitat calculated for the state of Maine from the nine watersheds was 891.9 km^2 (Table 3.8) and annual productivity estimates in 1600 ranged from 25.9 million to over 81 million alewives/year (Table 3.8, Figure 3.10A). From 1600 to 1700 there was little change in accessible lake habitat, but from 1700 to 1750 the area was reduced to 880.4 km^2 and by 1800 lake area decreased to 367.2 km^2, 42% of the virgin habitat. By 1850 17.6 km^2 remained, a decrease of 98% and in 1900, lake area was reduced to 6.5 km^2 (0.7% of virgin habitat). With two percent of the total lake habitat remaining in 1850, annual production potentials decreased to between 510,000 – two million alewives/year. In 1900, estimated productivity was reduced to 190,000 – 700,000 alewives/year. Percent annual virgin production for Maine declined to less than 50% by 1800 and less than 1% by 1900 (Figure 3.10B). If all virgin lake area of the nine watersheds had been accessible, total alewife production for 1600 through 1900 would have equaled 24.5 billion fish. With reduced spawning site access, estimated total productivity was 18 billion fish. This gives an estimated loss of 6.5 billion alewives from the Maine ecosystem over 300 years – or an average loss of 21.6 million alewives/year.

Comparison of virgin to present production

Current annual river herring counts for the Androscoggin, Kennebec and Dennys watersheds are compared to maximum annual production estimates from 1600 calculated with the potential production value of 91.5 x 10^3 recruits/km^2 (Figure 3.11). The 2008 count of river herring on the Androscoggin with 18.86 km^2 lake habitat was 92,359 fish/year or 2% of the virgin annual production of 4.2 million fish/year. The 2007 count on the Kennebec with approximately 65 km^2 lake area accessible was 551,636 fish/year or 3% of the virgin estimate of 18 million fish/year. The 2009 count on the Dennys over 24 days was 167,226 fish/year or 6% of the virgin estimate of 2.7 million fish/year.

Discussion

Since the 18th century, concern regarding anthropogenic interruption of natural passage to spawning sites for diadromous species has led to mostly failed attempts to solve the conflict between development and natural ecosystems (Baird 1872; Emery 1901; Judd 1997). In the watersheds of Maine, my estimated loss of one species, alewives, amounts to over six billion fish in 300 years. This vastly underestimates the full loss caused by watershed obstruction when other diadromous species including salmon, shad, sturgeon and eels and the predators that depended upon them for sustenance, are considered. The shift in productivity from primary river watersheds to secondary rivers with much less spawning habitat, as well as dependence upon human efforts to maintain spawning populations, further indicates how dramatically the Gulf of Maine ecosystem has been transformed from abundant bounty to a depleted ecosystem. My pre-colonial alewife production estimates on Maine watersheds can be applied to natural ecosystem models of productivity and nutrient exchange such as Ecopath and Ecosim (Christensen & Walters, 2004) to better focus watershed restoration efforts.

Watershed contribution

As stated in the beginning of this study, Atkins (1887) estimated river production capacity to be 10% of potential virgin capacity. In light of my research, he was overly conservative. My estimated production of historically accessible alewife watersheds dropped from two percent in 1850 to 0.7 percent in 1900, not including the Damariscotta. During this period the Penobscot watershed was replaced by the Damariscotta. In 1887, the Damariscotta watershed produced 73% of the state's alewife yield. Adding the Damariscotta's lake surface area (18.9 km^2) to the remaining surface area of the nine analyzed watersheds in 1850 (18.6 km^2), there would have been 37.5 km^2 available to spawning alewives. The proportion of available lake spawning habitat to the total available virgin surface area, 911.8 km^2, (including Damariscotta Lake) would be 4% in 1850, making Atkins' estimate of a 90% capacity reduction in 1887 an underestimate and the situation even more severe. This emphasizes the significance of lost total production due to the replacement of primary watershed contribution by secondary watershed contribution, particularly the Penobscot by the Damariscotta.

The decline of the Penobscot watershed contribution to alewife harvest from over 80 percent in the 1820s to none in the 1880s coincides with the completion of the Veazie Dam on the main stem at the head of tide in 1835. Within one decade of its construction, the Penobscot's productivity decreased nearly 70%. In contrast, the Damariscotta watershed began to register as a regular contributor to alewife production after the Penobscot habitat was diminished. Being close in proximity along the mid-coast, it is possible the Damariscotta fishery benefited from the reduction of available lake spawning habitat in the Penobscot as returning alewives searched for appropriate lake habitat in the vicinity of Penobscot Bay and found the fishway-accessible Damariscotta Lake. The mid-coast became the principal area for alewife harvest during the 1880s composed of secondary rivers with most dipnet harvesting occurring at the head of tide dams and in weirs downstream in the estuaries (Atkins 1887). The Medomak River became important during this time as the larger watersheds had all been made impassable by head of tide dams by the 1840s. It too, most likely benefited from straying alewives seeking appropriate pond spawning habitat. How much of the Penobscot population could find spawning refuge in smaller watersheds is questionable. Looking at total lake spawning habitat, Damariscotta Lake, 18.9 km^2, is only 5.8% of the 327.7 km^2 virgin Penobscot habitat. The addition of the Damariscotta harvests, and those of other secondary river watersheds, helped to keep the alewife fishery alive but considering the percent contribution to overall state production by the Penobscot watershed alone, the replacement of primary river systems by secondary river watersheds would have accommodated only a small portion of the displaced alewife population.

Another notable trend is the loss of the western- and eastern-most watershed contributions to alewife harvest in the mid 1800s. This could be a result of remaining spawning alewife populations condensing into areas of accessible habitat or harvesting efforts consequently being concentrated in the most reliable areas for efficiency and profit. From 1800 to 1850 the available lake spawning habitat for the nine historical alewife watersheds decreased by 349.6 km^2 to a total of 17.6 km^2. By 1846 all watersheds were obstructed at head of tide with the exception of the artificially accessible Damariscotta Lake. This supports the concentration of production centering at Damariscotta River and proximal mid-coast watersheds.

It is also possible that as fish ladders were introduced on formerly productive rivers in the late 19th and early 20th centuries, the mid-coast populations provided spawners for reopened western and eastern areas through straying. In addition, artificial transport of adult alewives from Damariscotta, as well as the Orland River below head of tide on the Penobscot, was used to provide stock for nearby watersheds as late as the 1930s and 40s (Rounsefell & Stringer 1943). Hypothetically, dependence on one or two populations with reduced habitat type to restock all watersheds could have built an expanded population with less genetic diversity and adaptive resilience than the naturally distributed population and could have contributed to the crash of river herring stocks in the later 20th century.

Historical and current productivity

The difference between Maine's potential annual production estimate today and that from virgin spawning habitat based on the 75th percentile calculation from historical data is 30 million alewives per year – such discrepancy has considerable implications for restoration policies. These two annual production values result in a range of total alewives potentially produced from 21.2 to 33.5 billion fish between 1600 and today – a difference of 12 billion fish over 410 years.

In order to more effectively restore river herring populations, more data on the current abundance of river herring from more watersheds in Maine needs to be collected. Presently, there is no statewide estimate of river herring abundance, thus we cannot calculate how much of the potential capacity is being used.

Current annual productivity on three watersheds with restoration efforts is 2-6 % of my maximum virgin production estimates. If this is indicative of progress towards restoration of river herring production in Maine, there is much work to be done not only to benefit harvests, but also to restore historical biodiversity and productivity to coastal ecosystems as a whole.

There are several caveats to the methods employed to determine these historical abundances, and thus, the current percent decline. The S-R data used for my production estimates is not ideal: it is from the 20th century, potentially includes harvesting of first year spawners, and in addition to periods of increase, includes two periods of decline in recruitment. The data therefore is not representative of pre-exploitation conditions and barely predates the 1990 assessment that the Damariscotta alewife stock was overfished (Crecco & Gibson 1990). Also, the Damariscotta alewife run was started with stocking in 1803 (Atkins 1887) and therefore is not a pre-colonial alewife watershed. But, due to the long-term maintenance of the Damariscotta fishway (constructed 1809) and the lack of dam construction upstream, the run is essentially the only Maine alewife fishery that has had self-sustained access to a consistent spawning habitat area for 200 years. All other historic alewife river systems were subject to increased damming during the 19th and 20th centuries. Therefore, the harvest records from this system provide the data most likely limited by density dependent environmental variables such as spawning area and food availability (Haddon 2001). Ideally, Damariscotta alewife fishery data from the mid 1800s with a well-established fish ladder and not yet heavily impacted stock would be used to estimate productivity, but such data is not available. For the above reasons, the maximum production potential based on the 75th percentile gives us a highly conservative estimate for a healthy population and is likely underestimated.

In order to refine these production values, more data to help groundtruth the assumptions of fishery escapement estimates and distance to spawning habitat would be helpful. Productivity based on harvest depends on percent escapement, or non-harvested days per week, and reproductive cost of migration distance. Escapement for the potential production value currently used in Maine is assumed to be one day or 15%. This was not consistent over the history of the fisheries with periods of no harvest and in-season closures varying from 4 days to none differing from watershed to watershed and dependent on gear type (Maine Legislative Records 1821-1830; Atkins & Foster 1869; Rounsefell & Stringer 1943). Also 15% escapement towards production is based on coastal runs on secondary watersheds and may be less for spawners that migrate much further distances to historical spawning habitat on primary watersheds (MDMR & MASC

2007). Further adjustment of production values should be done per watershed to represent distinct conditions contributing to recruitment over time.

Finally, off-shore fisheries bycatch of alewives can potentially have a large impact on spawning populations (Kritzer & Black 2007) and sea temperature changes have been shown to affect alewife and other estuarine and marine species' productivity (Dow 1977). These were not considered in this study and would need to be factored in as parameters for ecological modeling of abundance over time, especially considering future plans for off-shore fishery monitoring and projections for climate change.

Future Directions and Conclusion

> "Ecological changes since approximately 1900 have been described, but most likely underestimate the full impact of river regulation due to the lack of quantitative baseline data."
> Petts 1989: 12

It is impossible to know how far present day ecosystems are from historical productivity without pre-exploitation baseline estimates. The difficulty lies in finding historical data to calculate and estimate these baseline values. My baseline estimates for pre-colonial alewife lake spawning habitat and potential production on obstructed watersheds in Maine provide new values that incorporate anthropogenic alteration for over 400 years. As current baseline values are replaced by estimates from historical data, ecological modeling can more accurately predict the effect restoration and management policies will have on ecosystems (Rosenberg et al. 2005).

As a result of the dramatic decline of river herring stocks in the late 20th century numerous state commercial river herring fisheries were closed, including Massachusetts, Rhode Island, Connecticut, Virginia and North Carolina (ASMFC 2009). Maine fared better keeping its fishery open with a much-reduced harvest despite the official assessment of the Damariscotta river herring fishery as overfished. True success of restoration efforts requires long-term monitoring and analysis of the impact of multiple factors on river herring populations, including: distance from ocean; distance from stock population; habitat condition; similarity of new habitat to source habitat; size of stock population; stray rate of stock population; adjustment to new habitat; and interaction with resident fish populations (Pess et al. 2008). In addition, management programs need to encompass estimates of current river herring abundance and watershed capacity from more locations so models can more accurately determine requirements of what is needed to restore watersheds to productive and profitable levels. Such models would provide better analysis of how resilient the population remains after four centuries of obstruction and exploitation. We can then apply such estimates to predict future abundance and evaluate effects on predator and prey species. This will be a necessary step for creating fisheries policies that follow ecosystem-based management approaches.

For example, can restoration of fifty percent of historical river herring productivity provide enough of an inshore forage base to bring back coastal Atlantic cod spawning populations? Ames (2004) found that up to 50% of coastal cod spawning grounds in the Gulf of Maine were lost between 1920 and the present, with many of the spawning areas located along the Maine coast. During this time, Maine river herring were restricted to below head of tide spawning areas and annual production was most likely less than one percent of historical potential. Energetic studies of cod growth and reproductive health with river herring and other diadromous forage fish as primary food sources compared to other prey would allow us to estimate the gains or losses spawning cod populations would experience with reintroduction of these migrating species. Also, returning diadromous fish populations would restore a large component of lost nutrient exchange between freshwater and marine ecosystems thereby affecting the entire trophic landscape from inland ecosystems to open ocean.

For a complete picture of anthropogenic impact, estimates of truly virgin baselines would need to be produced from not just pre-colonial data, but from evidence of population size before the appearance of indigenous peoples. Such archaeologically based work has been conducted successfully in several marine ecosystems based on food refuse piles (middens) and paleontological data (Wing &Wing 2001).

However, even without more refined calculations, the estimates of historic productivity and potential population size of alewives presented here will allow for much more accurate and realistic evaluation of current recovery initiatives and help guide more effective future management programs. Incorporating these historic baselines into models that analyze the trophic cascade of nutrient exchange and interdependent species abundance within extended terrestrial-aquatic ecosystems can not only tell us how the ecology has been changed but in what ways can it most realistically be restored.

Table 3.1. Watershed contribution based on alewife harvest records throughout the 19th and 20th centuries. Total is the number of times each watershed contributed to harvests. Watersheds are listed as they occur along the coast from west to east.

Watershed	**1804-1820**[a]	**1833-1840**[a]	**1867**[b]	**1887-1890**[c,d]	**1896**[e]	**1942**[f]	**1950-1955**[g]	**1960-1966**[g]	**1970s**[g]	**1980s**[g]	**1990s**[g]	**2000-2007**[g]	**Total**
Casco Bay	X	X			X								3
Androscoggin/ Kennebec	X	X[8]	X		X	X[2]		X[1]	X[2]	X[2]	X[2]	X[2]	10
Sheepscot									X	X	X	X	4
Damariscotta		X	X	X	X	X	X	X	X	X	X	X	11
Medomak				X									1
St. George	X		X	X	X	X	X	X	X	X	X	X	11
Penobscot	X	X[8]	X		X	X[3]	X[3]	X[3]	X[3]	X[3]	X[3]	X[3]	11
Union									X[4]	X[5]	X[6]	X[6]	4
Narraguagus									X	X		X	3
East Machias			X			X			X	X		X	5
Dennys			X			X							2
Cobscook Bay	X	X											2
% Maine harvest from watersheds	98	91		"mainly"	90	90[7]	90	90	90	90	variable	90	

a. Maine Sec. of St. Fish Inspector Reports 1804-1840
b. Atkins & Foster 1868
c. Maine Comm. of Fish. & Game Report 1888
d. Maine Comm. of Fish. & Game Report 1889-1890
e. Smith 1899
f. Rounsefell & Stringer 1943
g. Town Harvests from MDMR 2008

1. Nequasset Lake only, below Kennebec River head of tide
2. Nequasset and Winnegance Lakes only, below Kennebec River head of tide
3. Orland River only, below Penobscot River head of tide
4. Patten Pond Stream only, below Union River head of tide
5. Patten Pond Stream and main stem of Union River
6. Main stem of Union River only, no harvest from Patten Pond Stream
7. Estimated from accessible spawning area
8. Harvested below river-obstructing head of tide dam

Table 3.2. Watershed fisheries productivity index. Percent contribution of watershed to total recorded production over 14 periods of alewife harvest records from 1800-2007. Timeline gaps indicate periods of missing or incomplete quantitative harvest records.

Watershed	**1804-1810**[a]	**1811-1820**[a]	**1833-1840**[a]	**1841-1850**[a]	**1887**[b]	**1889**[c]	**1896**[d]	**1938**[e]	**1950-1959**[f]	**1960-1969**[f]	**1970-1979**[f]	**1980-1989**[f]	**1990-1999**[f]	**2000-2007**[f]
Casco Bay	23.0	6.3	5.4	3.3	0	0	20.7	0	0	0	0	0	0	0
Androscoggin/ Kennebec	12.6	2.3	0	18.4	0	0	8.2	2.9	3.2	7.5	8.4	15.1	8.8	11.8
Sheepscot	0	0	0	0	0	0	0	0	0	1.1	7.9	7.9	3.1	4.4
Damariscotta	0	0	0	10.0	73.8	86.7	41.0	33.5	51.4	44.5	28.1	13.8	4.3	7.7
Medomak	0	0	0	0	7.0	6.9	0	0	0	0	0	0	0	0
St. George	1.5	0	0	0	19.1	6.4	11.4	13.0	22.4	21.8	20.7	12.6	28.1	24.4
Penobscot	43.6	86.7	78.0	9.0	0	0	9.1	12.0[g]	13	14.1	15.9	18.5	8.7	10.7
Union	0	0	0	0	0	0	0	0	0	0	3.9	18.1	33.8	22.2
Narraguagus	0	0	0	0	0	0	0	0	0	0	2.1	2.8	1.8	6.5
East Machias	0	0	0	0	0	0	0	22.6[h]	0	1	3.0	1.2	1.4	2.3
Dennys	0	0	0	0	0	0	0	5.6[h]	0	0	0	0	0	0
Cobscook Bay	16.2	2.4	7.7	57.5	0	0	0	0	0	0	0	0	0	0
% total Maine harvest	96.9	97.7	91.1	98.1	99.9	100	90.4	89.6	90	90	90	90	90	90

a. Maine Sec. of St. Fish Inspector Reports 1804 –1850
b. Maine Comm. of Fish. & Game Report 1888
c. Maine Comm. of Fish. & Game Report 1889-1890
d. Smith 1899
e. Rounsefell & Stringer 1943
f. Town Harvests from MDMR 2008
g. Estimated contribution of Orland River
h. Estimated based on 1942 harvest proportions

Table 3.3. Nine focus river herring watersheds with total number of dams constructed from settlement to present, the year of full obstruction by dam at head of tide and total virgin stream and lake spawning habitat. Numbers in parentheses by watersheds indicate categories of primary river (1), secondary river (2) or bay system (3).

Watershed	Dams constructed 1600 – present	Head of tide dam: year	Virgin stream distance (km)	Virgin lake surface area (km^2)
Mousam River (2)	24	1720	183.5	10.7
Casco Bay (3)	93	1802	862.1	136.1
Androscoggin River (1) (Maine only)	145	1807	906.2	45.9
Kennebec River (1)	226	1837	2392.3	197
Sheepscot River (2)	47	1762	558	19.4
St. George River (2)	35	1840s	549.2	31.7
Penobscot River (1)	283	1835	5332	327.8
Union River (2)	36	1800	480.9	93.2
Dennys River (2)	19	1846	230.1	30.1
TOTAL	908		11,494.3	891.9

Table 3.4. Summary of recruitment cumulative frequency distribution results based on Damariscotta River fishery data, 1949-1983 (Crecco & Gibson 1990).

Percentile	**Estimated recruits ($N \times 10^3$)**	**Production potential $\times 10^3$ (recruits/km^2)**
25th	1210.2	64.13
50th	1418.8	75.15
75th	1727.1	91.53

Table 3.5. Category 1 Watershed: Kennebec watershed remaining lake habitat and five estimates of annual alewife productivity based on chronological completion of dams with measurable impact before 1900. Fish (adults or recruits) per km^{2} is abbreviated as f/km^{2}.

Year	**Lake surface area (km^{2})**	**Production (# of fish) at**				
		29.0 x 10^{3} f/km^{2}	**58.1 x 10^{3} f/km^{2}**	**64.1 x 10^{3} f/km^{2}**	**75.2 x 10^{3} f/km^{2}**	**91.5 x 10^{3} f/km^{2}**
1600	197.0	5,713,870	11,447,443	12,635,534	14,806,805	18,034,156
1754	105.5	3,059,462	6,129,474	6,765,632	7,928,227	9,656,296
1760	50.4	1,461,890	2,928,821	3,232,793	3,788,312	4,614,027
1765	44.1	1,278,320	2,561,048	2,826,850	3,312,612	4,034,642
1768	43.9	1,272,665	2,549,719	2,814,345	3,297,958	4,016,794
1783	43.5	1,260,688	2,525,723	2,787,859	3,266,921	3,978,992
1792	9.4	271,788	544,513	601,026	704,306	857,819
1808	9.4	271,324	543,584	600,000	703,103	856,355
1837	2.7	77,024	154,314	170,329	199,598	243,104
1867	0.7	20,474	41,019	45,276	53,056	64,620

Table 3.6. Category 2 Watershed: St. George watershed remaining lake habitat and five estimates of annual alewife productivity based on chronological completion of dams with measurable impact before 1900. Fish (adults or recruits) per km^2 is abbreviated as f/km^2.

Year	**Lake surface area (km^2)**	**Production (# of fish) at**				
		29.0 x 10^3 f/km^2	**58.1 x 10^3 f/km^2**	**64.1 x 10^3 f/km^2**	**75.2 x 10^3 f/km^2**	**91.5 x 10^3 f/km^2**
1600	31.7	920,170	1,843,513	2,034,845	2,384,510	2,904,247
1734	31.1	901,813	1,806,736	1,994,251	2,336,940	2,846,308
1777	22.9	664,303	1,330,897	1,469,026	1,721,461	2,096,678
1785	1.6	45,240	90,636	100,043	117,234	142,787
1867	0	0	0	0	0	0

Table 3.7. Category 3 Watershed: Casco Bay watershed remaining lake habitat and five estimates of annual alewife productivity based on chronological completion of dams with measurable impact before 1900. Fish (adults or recruits) per km^2 is abbreviated as f/km^2.

Year	**Lake surface area (km^2)**			**Production (# of fish) at**		
		29.0 x 10^3 f/km^2	**58.1 x 10^3 f/km^2**	**64.1 x 10^3 f/km^2**	**75.2 x 10^3 f/km^2**	**91.5 x 10^3 f/km^2**
1600	136.1	3,945,624	7,904,854	8,725,271	10,224,608	12,453,206
1700	136.0	3,944,290	7,902,181	8,722,321	10,221,152	12,448,995
1750	136.0	3,943,043	7,899,683	8,719,564	10,217,920	12,445,060
1762	4.1	117,943	236,293	260,817	305,635	372,253
1766	3.6	104,023	208,405	230,034	269,563	328,318
1791	3.6	103,385	207,126	228,623	267,910	326,304
1802	0.8	23,548	47,177	52,074	61,022	74,322
1890	0.8	22,939	45,957	50,727	59,444	72,400

Table 3.8. State of Maine remaining lake habitat, five estimates of annual alewife productivity recorded as number of fish (N) and percent (%) of total historical abundance in fifty-year increments. Fish (adults or recruits) per km^2 is abbreviated as f/km^2.

Year	Lake surface area (km^2)	Production (N x 10^6) at					%
		29.0 x 10^3 f/km^2	58.1 x 10^3 f/km^2	64.1 x 10^3 f/km^2	75.2 x 10^3 f/km^2	91.5 x 10^3 f/km^2	
1600	891.8	25.87	51.82	57.20	67.03	81.64	100
1650	891.8	25.87	51.82	57.20	67.03	81.64	100
1700	890.2	25.82	51.72	57.09	66.90	81.48	99.8
1750	880.4	25.53	51.15	56.46	66.16	80.58	98.7
1800	367.2	10.65	21.33	23.55	22.60	33.61	41.2
1850	17.6	0.51	1.02	1.13	1.32	1.61	2.0
1900	6.5	0.19	0.38	0.41	0.49	0.59	0.7

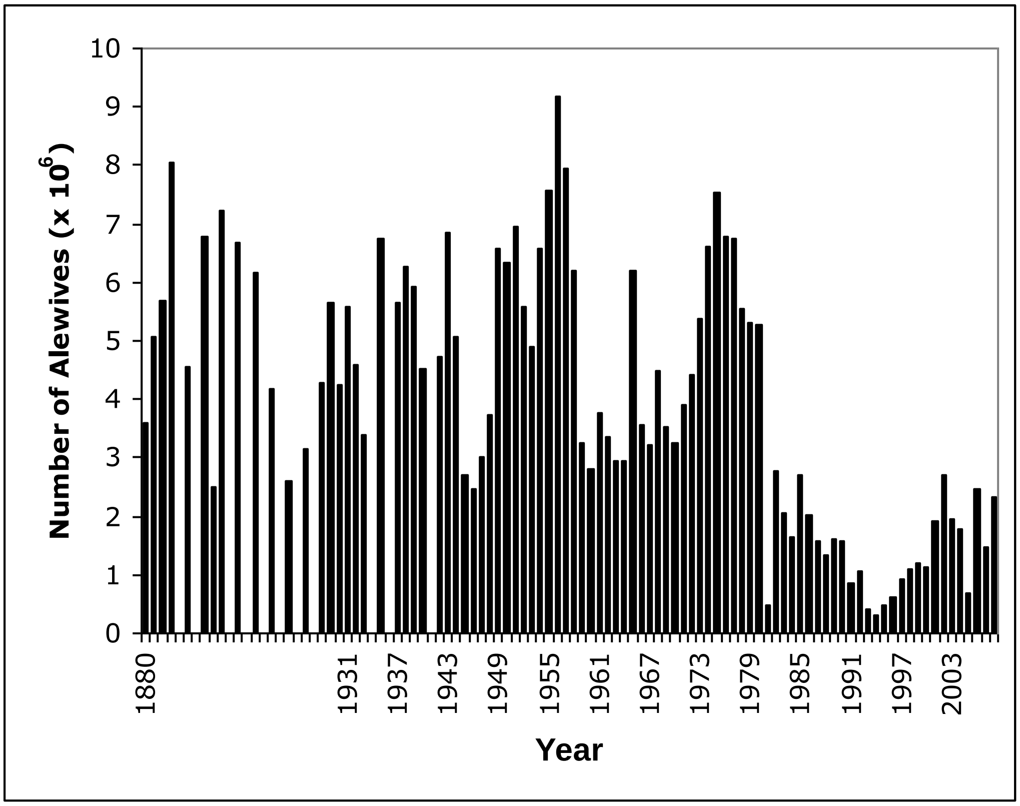

Figure 3.1. Maine Landings compiled 1880 – 2007. Data from Smith 1899, Flagg 1979, and MDMR website last accessed August 2009 at: http://www.maine.gov/dmr/commercialfishing/documents/alewife.tbl.pdf

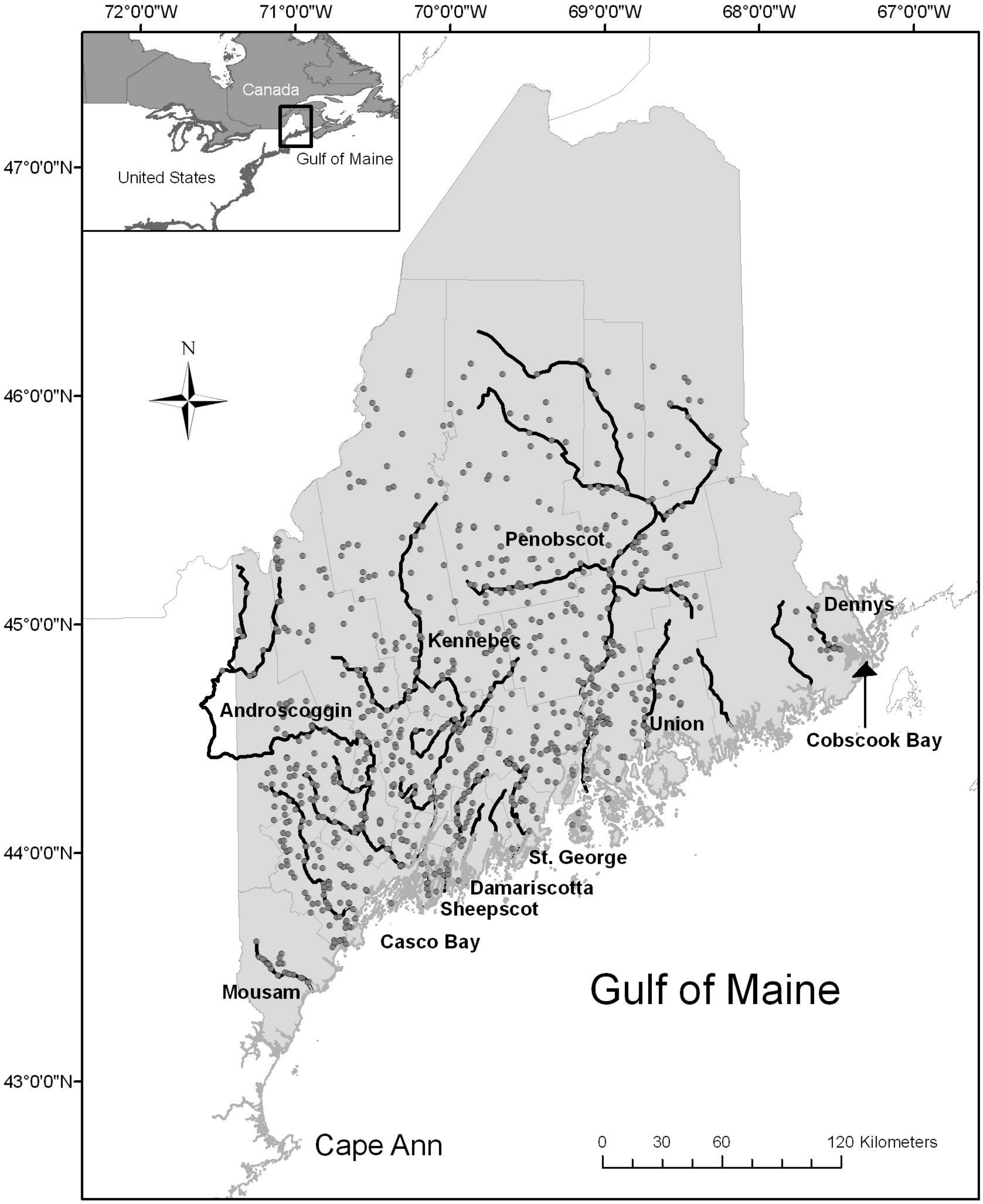

Figure 3.2. State of Maine with historical river herring watersheds assessed in this study demarcated by associated documented dams along each watershed.

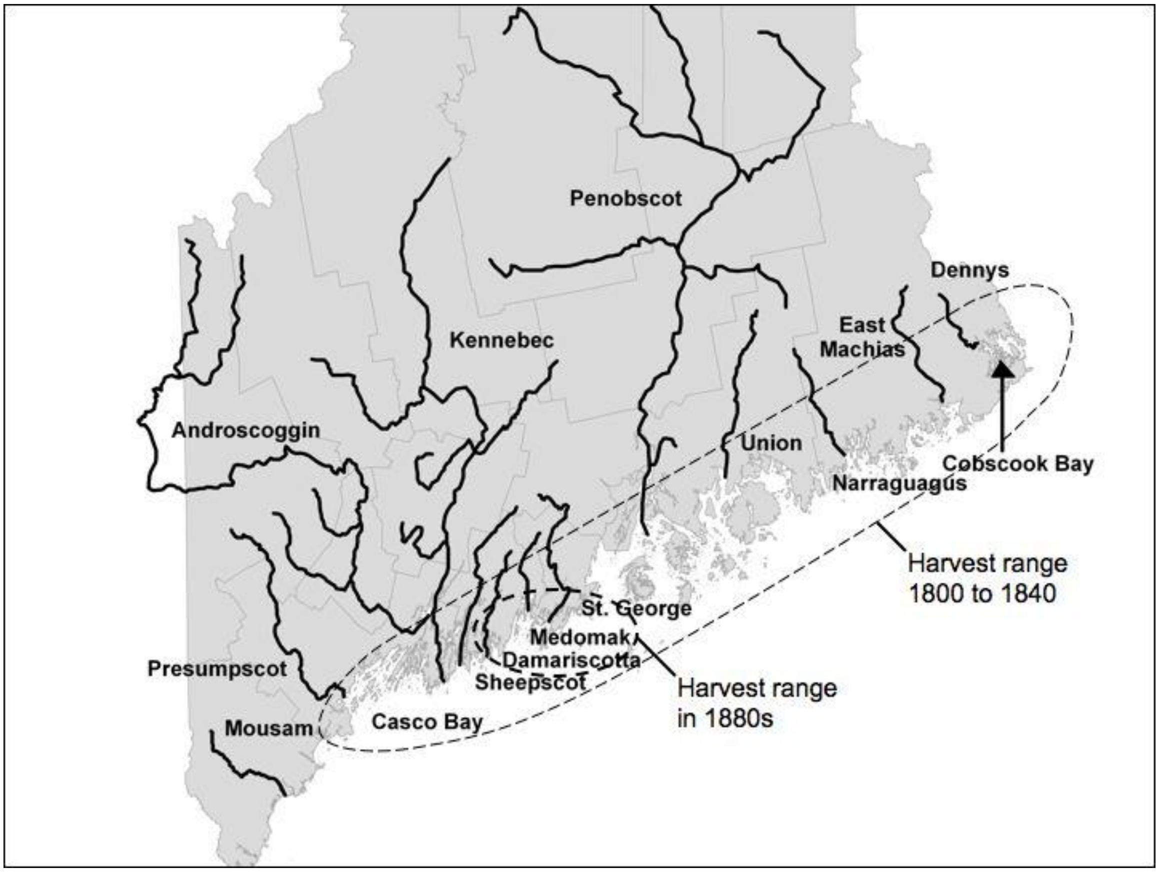

Figure 3.3. Detail of Maine coast with all watersheds identified that contributed to harvests 1800-2007. Harvest ranges of 1800 to 1840 (thin dashed circle) and 1880s (thick dashed circle) indicated.

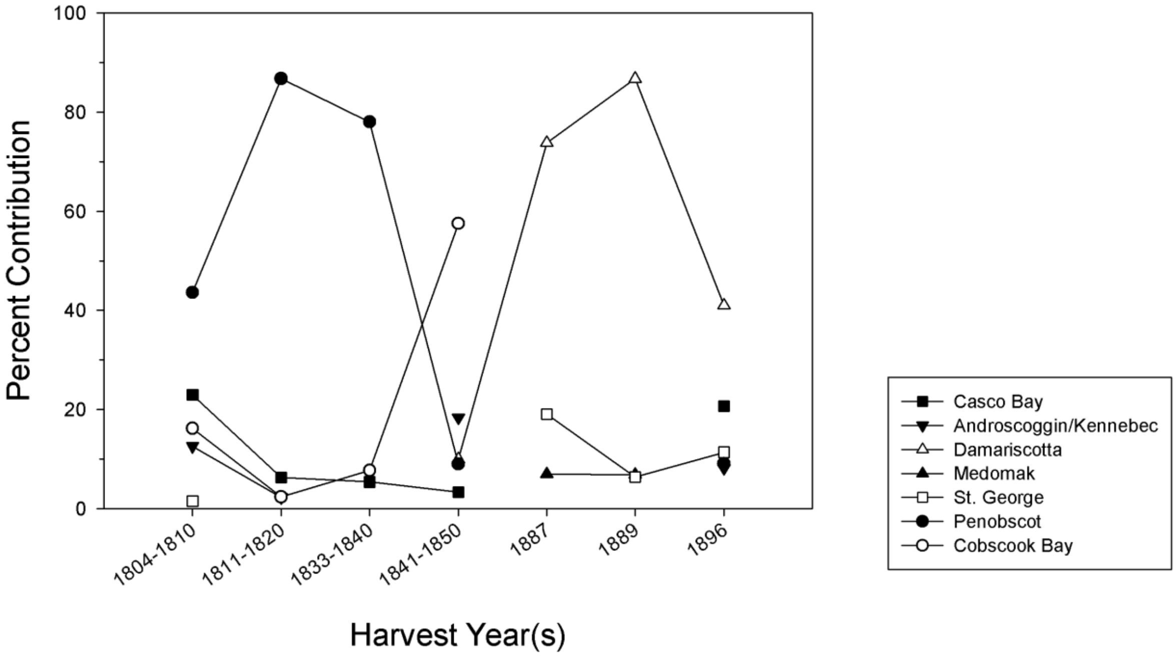

Figure 3.4. Watershed harvest contribution 1800 – 1900. Changes in percent contribution to alewife productivity per watershed reported during the 19th century. Harvest periods chosen by watershed specific harvest data availability.

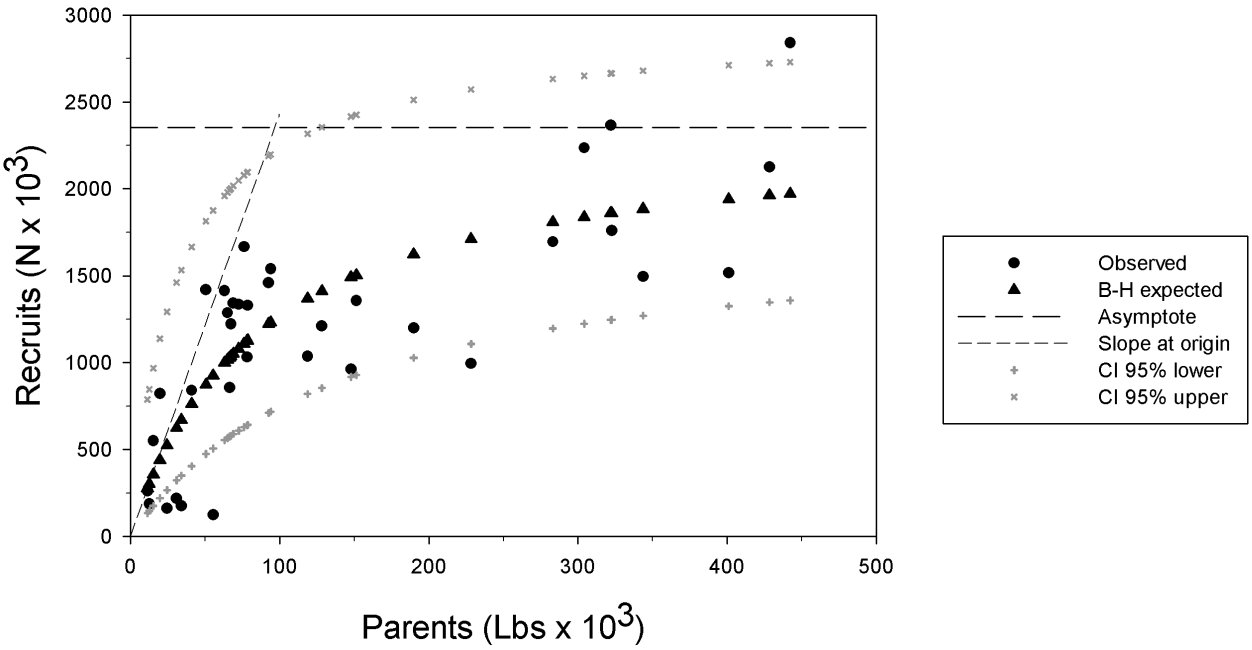

Figure 3.5. Damariscotta alewife fishery spawner – recruit curve. Beverton-Holt model fit to observed data from 1949 – 1983 (n = 35, R = (2354.3) S/ 85.59 + S, F = 183.67, $p < 0.0001$). Asymptote at 2354 x 10^3 recruits, slope at origin = 24.3. Best fit bracketed by 95% confidence intervals with upper parameters of a = 2920, b = 30.85, and lower parameters of a = 1788.6, b = 140.3.

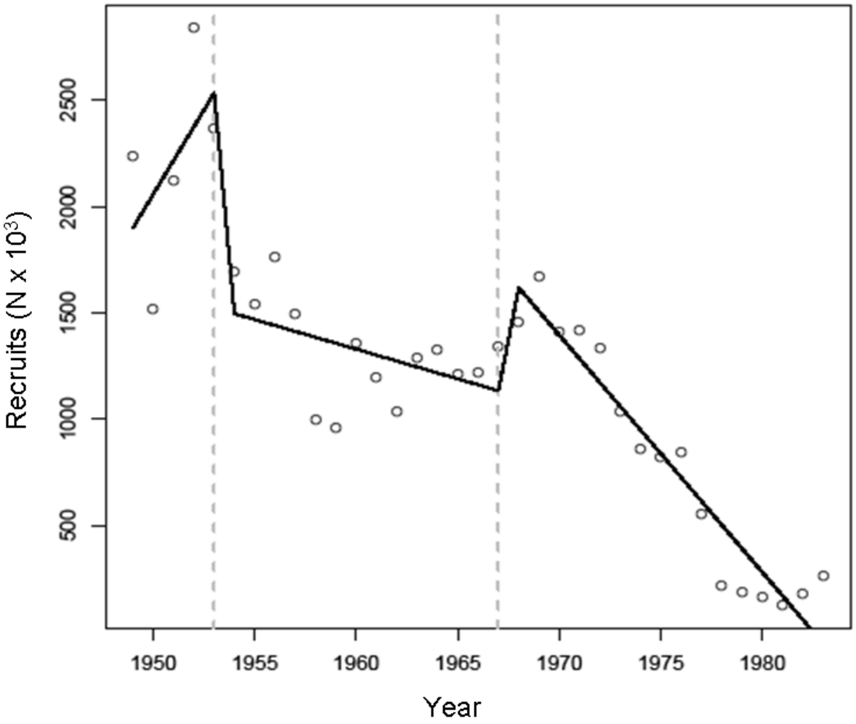

Figure 3.6. Breakpoint analysis of observed recruits from Damariscotta River alewife fishery data 1949-1983. Three significant regressions were found with breakpoints at 1953 and 1967.

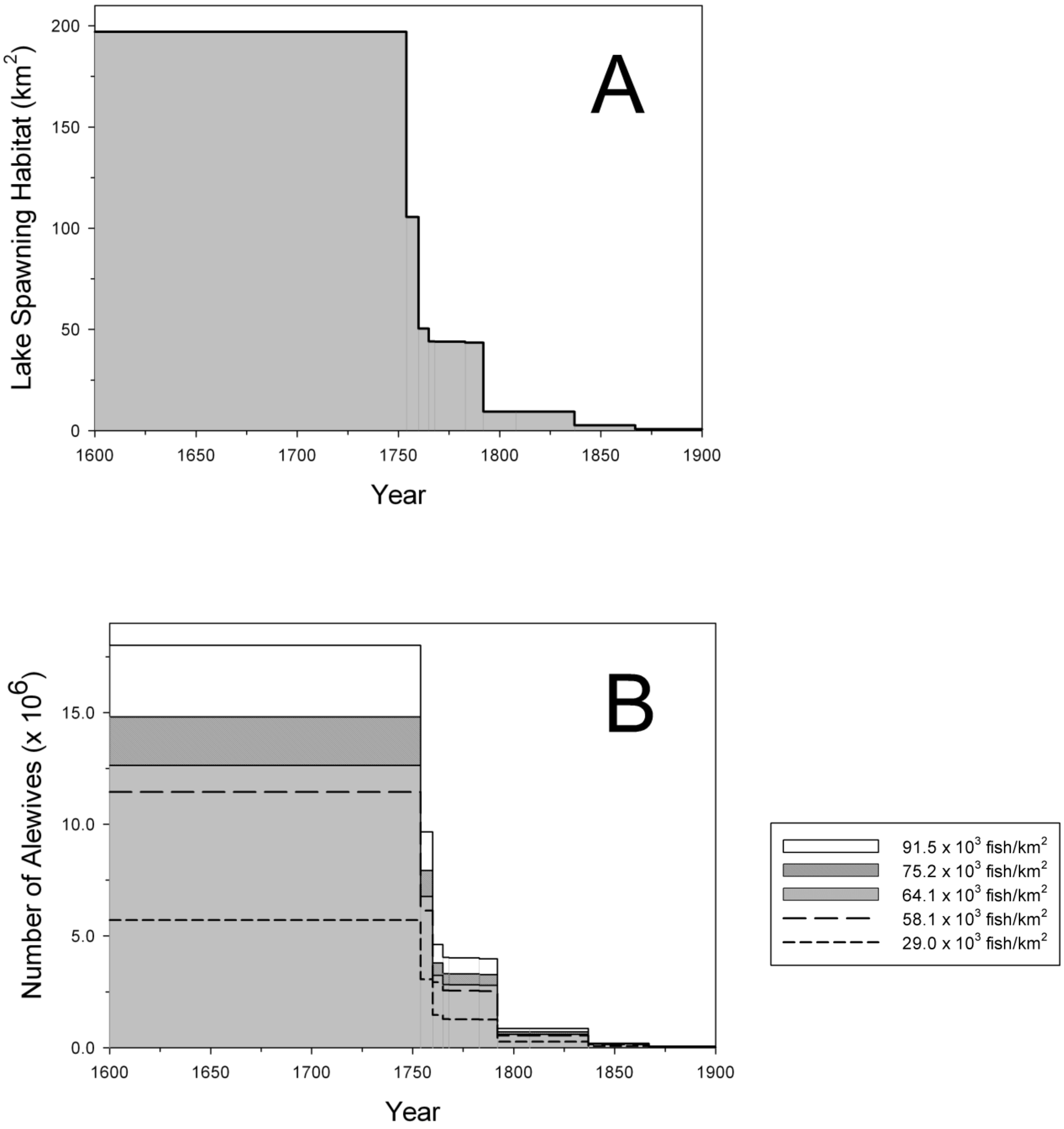

Figure 3.7. Category 1 Watershed: Kennebec River. A) lake surface area remaining in km^2 and B) five annual productivity estimates over years 1600 – 1900 in number of alewives. Vertical drop down lines in each graph indicate year of dam construction that resulted in a measurable loss of virgin spawning habitat.

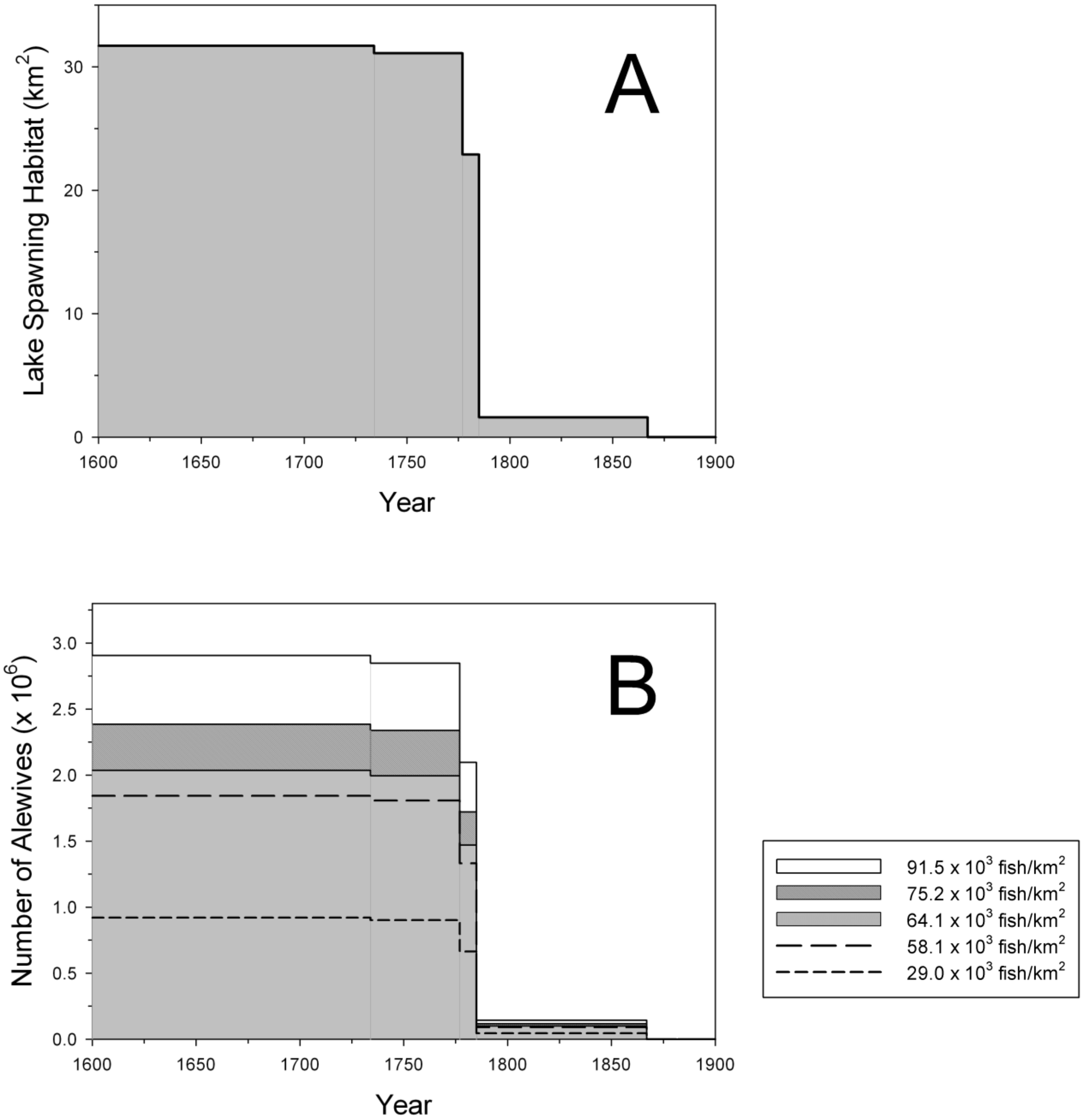

Figure 3.8. Category 2 Watershed: St. George River. A) lake surface area remaining in km^2 and B) five annual productivity estimates over years 1600 – 1900 in number of alewives. Vertical drop down lines in each graph indicate year of dam construction that resulted in a measurable loss of virgin spawning habitat.

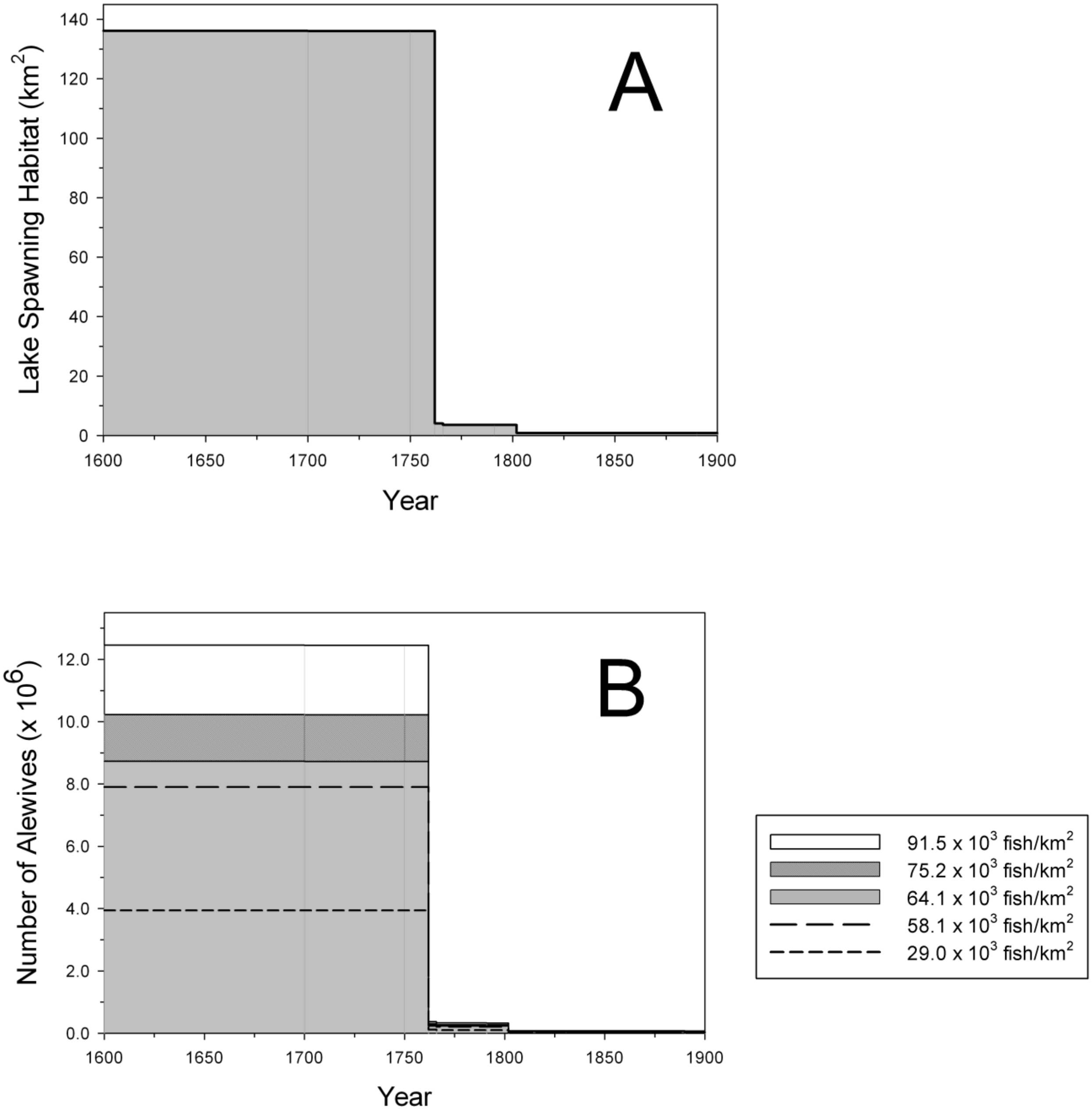

Figure 3.9. Category 3 Watershed: Casco Bay. A) lake surface area remaining in km^2 and B) five annual productivity estimates over years 1600 – 1900 in number of alewives. Vertical drop down lines in each graph indicate year of dam construction that resulted in a measurable loss of virgin spawning habitat.

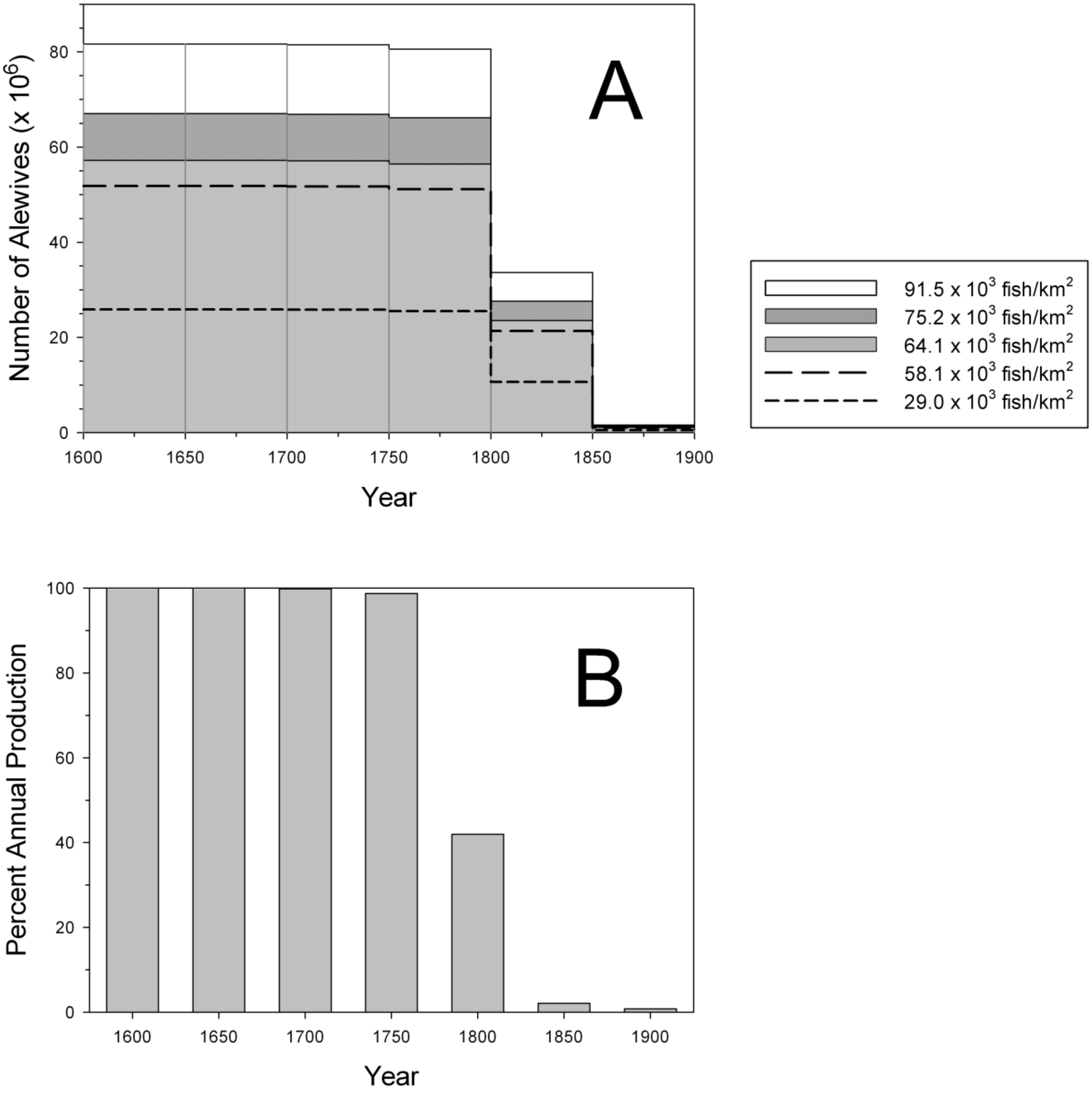

Figure 3.10. State of Maine A) Five annual productivity estimates from nine focus watershed totals. Vertical drop down lines correspond to fifty-year increments. B) Chronological presentation of changes in percent annual virgin productivity over fifty-year increments.

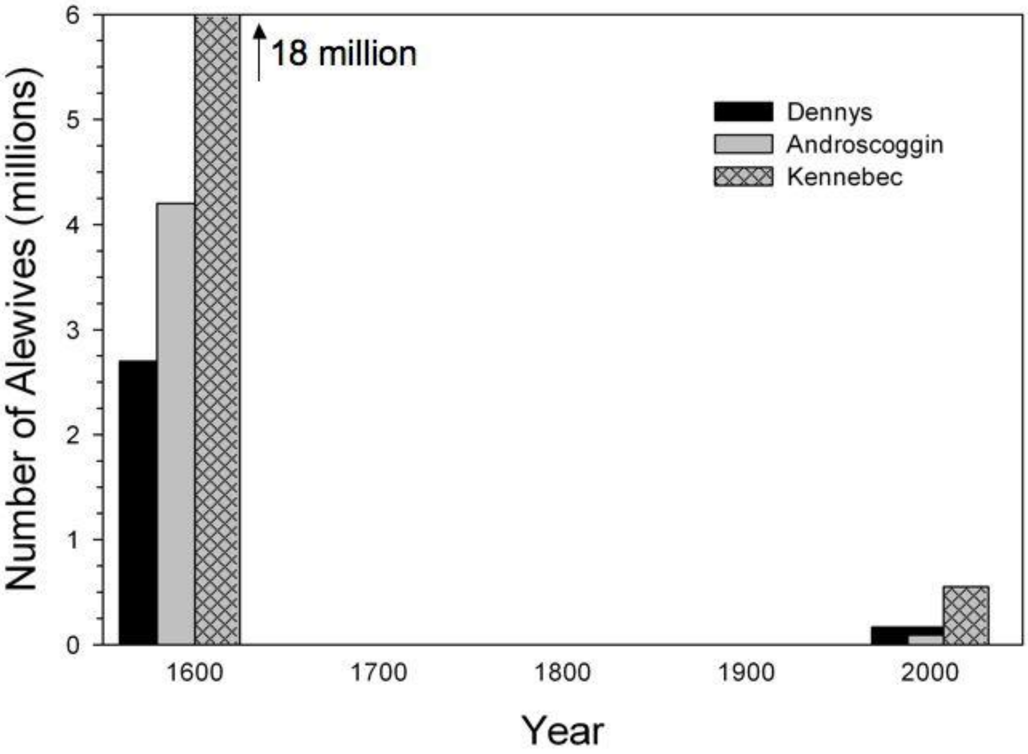

Figure 3.11. Comparative annual alewife production in the Dennys, Androscoggin and Kennebec watersheds. Virgin production estimates in 1600 calculated using productivity value of 95.1 x 10^3 recruits/km^2, arrow and number in top left indicate virgin production estimate for Kennebec. Current production fish count data from Dennys in 2009 (Gail Wippelhauser, MDMR, personal communication 2009), Androscoggin in 2008 (Brown et al. 2008; Gail Wippelhauser, MDMR, personal communication 2009) and Kennebec in 2007 (MDMR & MASC 2007; MDMR 2008).

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Chapter 4: Summary

Over the last four centuries, loss of diadromous fish populations due to overfishing and other human impacts on the watersheds they inhabit has led to costly stock and watershed restoration efforts (Jackson 2008). Despite such efforts, many of these commercially and ecologically valuable species, and the predators that relied on their former abundance, have been extirpated or have declined to unsustainable levels today (Lotze et al. 2006, Saunders et al. 2006). Restoring these species and their historical watersheds in the northeastern U.S. to pre-colonial conditions is not necessarily desirable. However, successful recovery defined in terms of healthy ecosystem functioning and sustainable fisheries requires an understanding of how current conditions compare to past potentials. In other words, we have to know where the system has come from in order to know what we can expect and manage for in the future.

Missing from current management efforts is a thorough assessment of the individual factors leading to population decline for the complete history of anthropogenic ecosystem alteration (Pitcher & Pauly 1998; Jackson et al. 2001). This thesis provides the first comprehensive historical analysis of the impact of colonial industry in the form of dam construction on watersheds and the diadromous species dependent upon them for survival in the state of Maine. Although this study focused on river herring, the methods and conclusions can be applied to all migration and spawning habitat requirements for mid-trophic level diadromous species. Despite uncertainties and assumptions included in this study, the broad trends regarding damming of Maine waterways, including loss of river herring access to spawning habitat, shifts in watershed importance for alewife fisheries, and estimates of lost alewife production, comprehensively illustrate the enormous magnitude of harm caused by anthropogenic obstruction of fish migration.

The cumulative effect of 915 dams constructed between 1600 and 1900, and 1356 dams in total today, is state-wide obstruction of all Maine watersheds from the coast to deep inland and the loss of over 6 billion fish in 300 years. Following the advancement of colonial settlements, mill, logging and finally hydroelectric dam construction spread from the southwest to the northeast resulting in damming of all river herring watersheds at head of tide by 1846, thus restricting migration distance on most rivers to less than 32%. Depending on watershed size, the timeline of dam construction differed in that one dam could reduce lake habitat to 3%, as in the Casco Bay watershed, whereas three dams in 40 years reduced Kennebec lake habitat to 4.8% with both reductions occurring before 1800. Even with these differences, the 19th century began with lake spawning habitat less than 5% of its pre-disturbed size on most watersheds. By 1860, nearly all historically available habitat – stream and lake – was no longer accessible.

Records of alewife harvest through the 1800s documented changes in watershed contribution to fisheries productivity during a peak century of dam construction. The range of watersheds used for alewife harvest in the first half of the 19th century spanned nearly the entire coast from western Casco Bay to the eastern Canadian border. Over 80% of the harvest came from a primary river watershed, the Penobscot, during this time. By mid century, fishery production occurred only from spawning sites below head of tide on all watersheds. In the 1880s, harvests were restricted to three secondary river watersheds all situated in the center coast and the artificially stocked Damariscotta watershed replaced the Penobscot, producing over 80% of the harvest.

A quantitative assessment of alewife productivity as dams obstructed waterways was conducted using five potential annual production values based on data from the mid 20th century through the 1990s. These values ranged from 29 x 10^3 adult returns per km^2 to 91.5 x 10^3 recruits per km^2. As dams obstructed access to lake area, annual productivity decreased on all watersheds with a maximum loss of 1 to 29 million alewives per year from 1600 to 1900 (see Chapter 3, Appendix 3.1). Current annual alewife counts on three watersheds with restoration efforts are just 2 – 6% of the virgin annual production estimates calculated with the 75th percentile value based on mid 20th century data. Percent annual production for Maine, calculated by summing annual production of all nine analyzed historic watersheds, remained near 100% or virgin annual productivity through 1700. By 1750, productivity was beginning to decrease. Productivity was only 50% by 1800 and less than 1% by 1900. If all virgin lake area had been accessible from 1600 to 1900, the total production calculated using the 75th percentile, or the maximum of my estimated range, would have been 24.5 billion alewives. With documented obstructions, the total production equaled 18 billion giving a total loss of 6.5 billion alewives over 300 years, or a quarter of the potential production.

The 75th percentile value was estimated from 20th century data, and therefore provides a conservative adjustment of production values to reflect less-altered watersheds. Even with mid 20th century data, the results show a 30,000 alewives/km^2 difference in virgin annual potential production between the historic value and the current Maine standard. This emphasizes the importance of determining an historic baseline abundance based on longer term and earlier population data. Historical analysis of sea turtle populations in the Caribbean supports the notion that short-term data series often fail to detect declines in populations (McClenachan et al. 2006). Setting maximum sustainable yields and restoration goals based on more historically realistic baselines can help address not only the decline of one species, but also the impact that lost biomass had on the ecosystem as a whole. Future ecosystem modeling and energy exchange studies that incorporate historical estimates can better determine how the disappearance of over 6 billion alewives might have contributed to the loss of other important species in the Gulf of Maine including the commercially valuable coastal Atlantic cod (Baird 1874, Ames 2004). Multi-species analyses can also help answer critical management questions such as, what is the likelihood of Atlantic salmon reintroduction success without migrating alewives serving as a prey buffer for juvenile salmon (Fay 2003, Saunders et al. 2006)?

A comprehensive understanding of long-term human influence on diadromous species requires historical research incorporating pollution, overfishing and changes in river channelization and pond formation spanning the 17th, 18th and 19th centuries in the U.S. – and even further back for watersheds in countries with earlier development. Only with all elements of anthropogenic alteration represented can we fully appreciate the magnitude of ecosystem change European colonists set into motion in North America four hundred years ago. Even so, the historical analysis presented here can be immediately applied to current restoration and management initiatives, helping to determine the most cost-effective and beneficial dam removal or fish ladder restoration projects. These results will help determine how removal of these barriers will affect recovery of river herring, as well as other interdependent coastal species, and move us one step closer to a more realistic recovery of a once-bountiful ecosystem.

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Appendices

Appendix 2.1. List of sources used to date and locate mills and dams.

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Appendix 2.2. Additional tables for analyzed watersheds showing percent remaining stream and lake river herring spawning habitat based on chronological completion of dams with measurable impact before 1900.*

A) Category 1 Watershed: Androscoggin River

Year	Dam(s)	% Stream Distance Remaining	% Lake Surface Area Remaining
1600	None	100.0	100.0
1716	Topsham Mill Dam	96.1	99.7
1790	Little River Dam	86.9	99.2
1799	Taylor Pond Upper Dam	85.7	93.5
1800	Thompson Lake Dam, Rayville Dam	79.9	53.8
1807	Brunswick Dam	11.1	4.1
1872	Kendall Mill Dam	9.6	4.1

*Repeated values for percentages indicate no change in available area for either stream distance or lake surface area with construction of dam.

B) Category 1 Watershed: Penobscot River

Year	Dam(s)	% Stream Distance Remaining	% Lake Surface Area Remaining
1600	None	100.0	100.0
1768	Grist Mill Dam	99.0	98.7
1771	Brewer Cove Dam, Mill Street Dam	98.2	96.7
1772	Penjejawock Dam	98.1	96.7
1773	Orland Village (Lower Falls) Dam	95.5	91.7
1775	Odam’s Mill Stream Dam	95.4	91.4
1778	Stillwater Dam	95.3	91.4
1780	Kenduskeag Head of Tide Dam	88.4	91.2
1787	Marsh River Dam	85.3	90.9
1795	Orono Waterworks Dam	84.1	87.9
1804	Sebec Dam	79.9	75.2
1806	Pleasant River/Brownville Dam	72.4	75.2
1807	Lower Dover-Foxcroft Dam, Atkinson Mills Dam	60.7	70.0
1820	Lovejoy Dam	59.4	61.3
1823	Milo Dam	59.1	61.3
1826	Howland Dam, Lee Dam	50.0	39.2
1830	Boyd Lake Village Dam	49.8	37.9
1831	Great Works Dam	7.8	0.9
1832	Great Works Stream Dam	6.7	0.9
1835	Veazie Dam, Phillips’ Cove Dam	5.0	0.8
1868	Silver Lake Dam	5.0	0.0

*Repeated values for percentages indicate no change in available area for either stream distance or lake surface area with construction of dam.

C) Category 2 Watershed: Mousam River

Year	Dam(s)	% Stream Distance Remaining	% Lake Surface Area Remaining
1600	None	100.0	100.0
1682	Littlefield River Dam	77.9	84.6
1720	Kesslen Dam	8.1	0.0
1867	Rogers Fibre Mill Dam	8.1	0.0

*Repeated values for percentages indicate no change in available area for either stream distance or lake surface area with construction of dam.

D) Category 2 Watershed: Sheepscot River

Year	Dam(s)	% Stream Distance Remaining	% Lake Surface Area Remaining
1600	None	100.0	100.0
1750	Head Mill Dam	95.8	100.0
1768	Head Tide Dam	58.2	32.4
1779	Hilton Pond Dam	56.6	32.4
1820	Westport Saw Mill Dam	55.9	32.4
1828	Georgetown Dam	55.3	32.4
1850	Boynton-Trask Dam, Marsh Bridge (Sherman Lake) Dam	50.7	15.9
1867	Dyer Dam, Dyer Dam 2	48.32	15.9

*Repeated values for percentages indicate no change in available area for either stream distance or lake surface area with construction of dam.

E) Category 2 Watershed: Union River

Year	Dam(s)	% Stream Distance Remaining	% Lake Surface Area Remaining
1600	None	100.0	100.0
1766	Millken Dam	99.6	100.0
1799	Card Mill Dam	96.7	100.0
1800	Ellsworth Dam	27.5	5.2
1899	Lower Patten Pond Dam	20.7	0.0

*Repeated values for percentages indicate no change in available area for either stream distance or lake surface area with construction of dam.

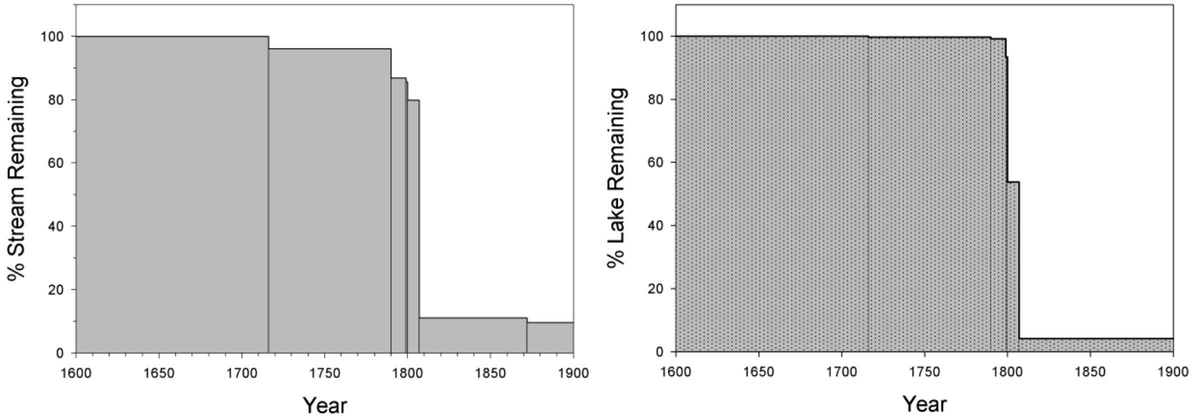
F) Category 2 Watershed: Dennys River

Year	Dam(s)	% Stream Distance Remaining	% Lake Surface Area Remaining
1600	None	100.0	100.0
1787	Hobart Stream Dam	88.6	98.1
1790	Cathance Stream Dam	83.2	95.6
1846	Dennysville Dam 2	20.5	0.0
1867	Wilson Stream Dam	12.8	0.0

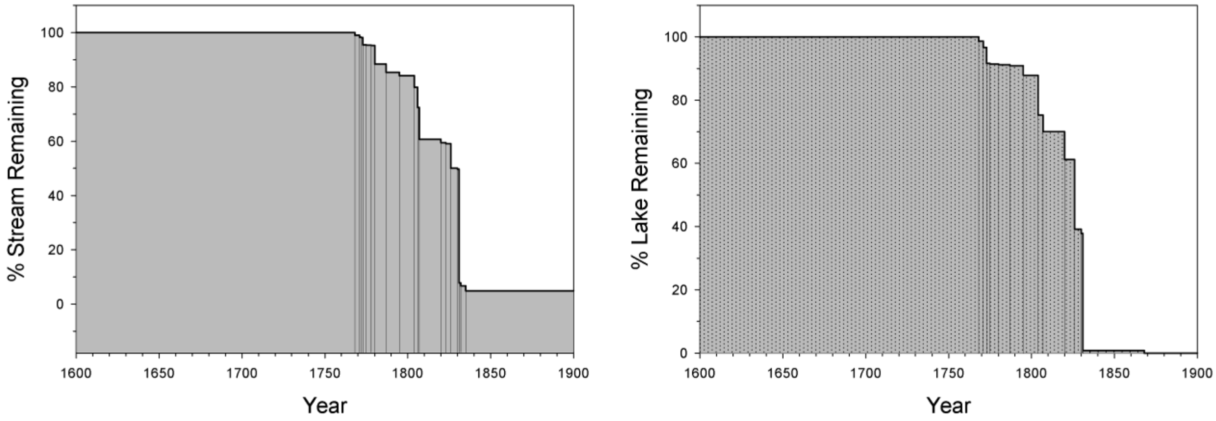
*Repeated values for percentages indicate no change in available area for either stream distance or lake surface area with construction of dam.

Appendix 2.3: Additional analyzed watersheds for percent stream distance remaining (on left) and percent lake area remaining (on right). Drop down lines in each graph indicate year of dam construction that resulted in a measurable loss of potential spawning habitat.

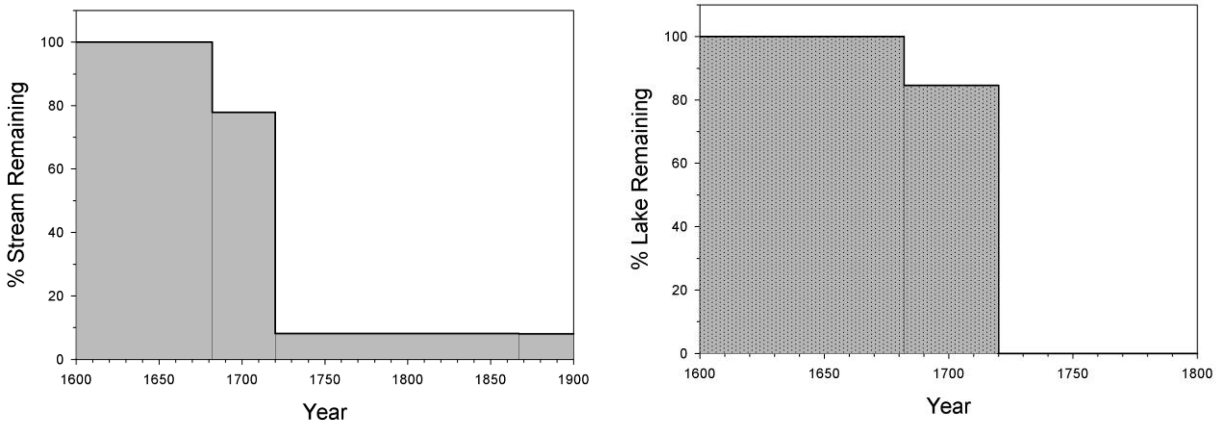
A) Category 1 Watershed: Androscoggin River



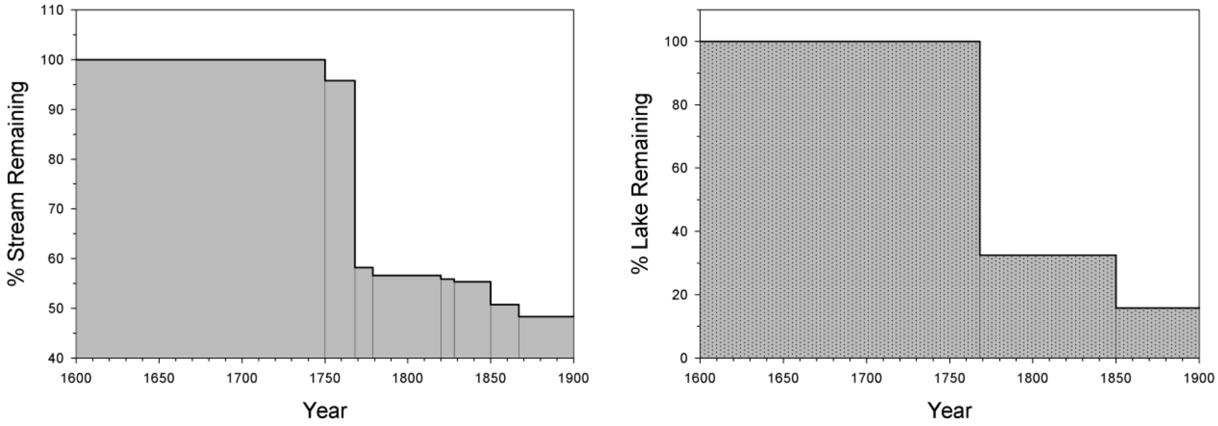
B) Category 1 Watershed: Penobscot River



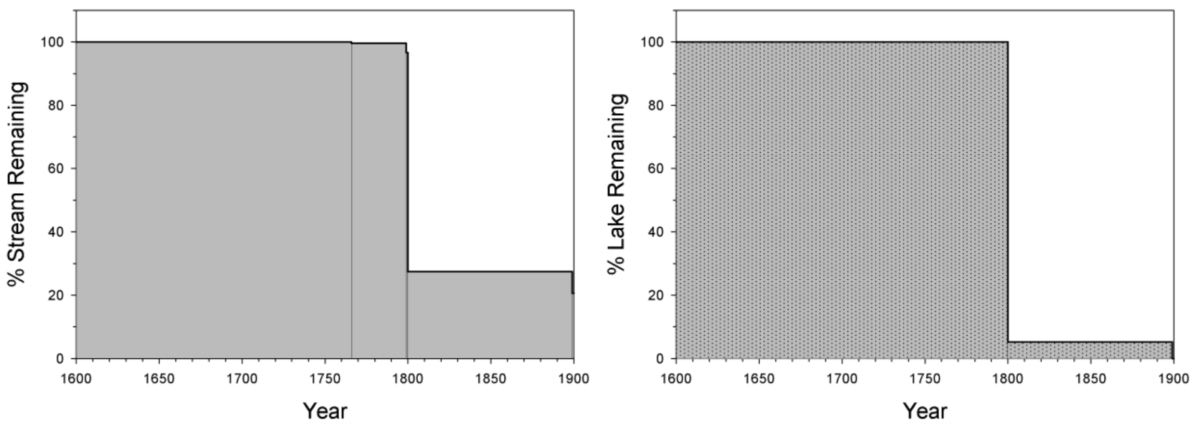
C) Category 2 Watershed: Mousam River



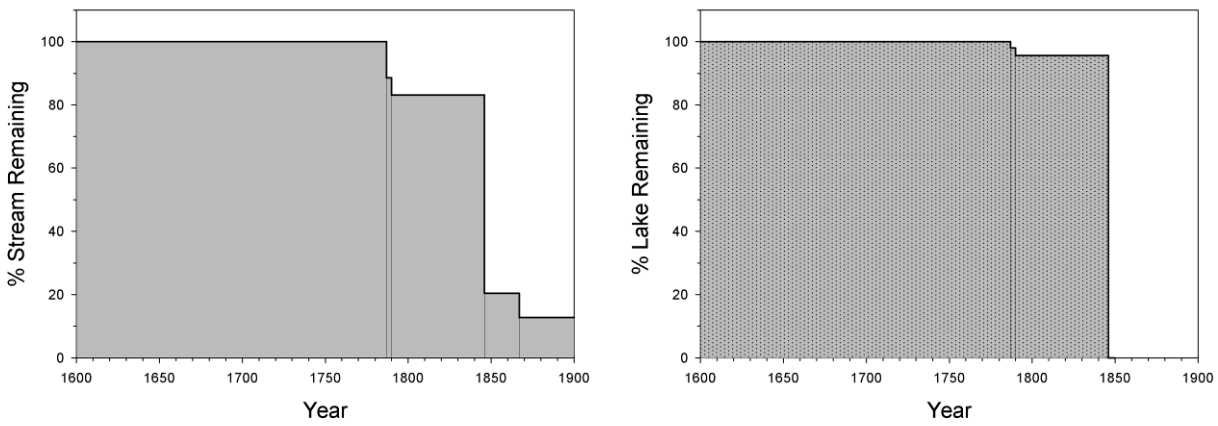
D) Category 2 Watershed: Sheepscot River



E) Category 2 Watershed: Union River



F) Category 2 Watershed: Dennys River



Appendix 3.1. Additional tables for analyzed watersheds showing remaining alewife lake spawning habitat and five estimates of annual productivity based on chronological completion of dams with measurable impact before 1900. Fish (adults or recruits) per km^2 is abbreviated f/km^2.

A) Category 1 Watershed: Androscoggin River

Year	**Lake surface area (km^2)**			**Production (# of fish) at**		
		29.0 x 10^3 f/km^2	**58.1 x 10^3 f/km^2**	**64.1 x 10^3 f/km^2**	**75.2 x 10^3 f/km^2**	**91.5 x 10^3 f/km^2**
1600	45.9	1,332,202	2,668,988	2,946,004	3,452,241	4,204,705
1716	45.8	1,328,751	2,662,084	2,938,372	3,443,298	4,193,813
1790	45.6	1,321,588	2,647,733	2,922,532	3,424,736	4,171,205
1799	42.9	1,245,028	2,494,349	2,753,229	3,226,340	3,929,566
1800	24.7	716,648	1,435,767	1,584,781	1,857,107	2,261,889
1807	1.9	54,868	109,925	121,334	142,184	173,175

B) Category 1 Watershed: Penobscot River

Year	**Lake surface area (km^2)**	**Production (# of fish) at**				
		29.0 x 10^3 f/km^2	**58.1 x 10^3 f/km^2**	**64.1 x 10^3 f/km^2**	**75.2 x 10^3 f/km^2**	**91.5 x 10^3 f/km^2**
1600	327.8	9,504,750	19,042,275	21,018,608	24,630,413	29,998,958
1768	323.5	9,381,500	18,795,350	20,746,055	24,311,025	29,609,955
1771	316.9	9,189,230	18,410,147	20,320,873	23,812,781	29,003,111
1773	300.5	8,713,630	17,457,307	19,269,141	22,580,321	27,502,019
1775	299.7	8,689,850	17,409,665	19,216,555	22,518,698	27,426,965
1780	298.8	8,664,910	17,359,699	19,161,403	22,454,069	27,348,249
1787	297.8	8,637,070	17,303,923	19,099,838	22,381,925	27,260,380
1795	288.1	8,353,740	16,736,286	18,473,288	21,647,709	26,366,132
1804	246.6	7,150,530	14,325,717	15,812,534	18,529,736	22,568,552
1807	229.4	6,653,470	13,329,883	14,713,346	17,241,665	20,999,728
1820	200.8	5,822,620	11,665,318	12,876,021	15,088,617	18,377,393
1826	128.5	3,727,080	7,467,012	8,241,988	9,658,278	11,763,436
1830	124.2	3,602,090	7,216,601	7,965,587	9,334,382	11,368,941
1831	2.8	82,070	164,423	181,488	212,675	259,030
1835	2.8	80,040	160,356	176,999	207,414	252,623
1868	0	0	0	0	0	0

C) Category 2 Watershed: Mousam River

Year	**Lake surface area (km^2)**	**Production (# of fish) at**				
		29.0 x 10^3 f/km^2	**58.1 x 10^3 f/km^2**	**64.1 x 10^3 f/km^2**	**75.2 x 10^3 f/km^2**	**91.5 x 10^3 f/km^2**
1600	10.7	310,155	621,380	685,870	803,729	978,913
1682	9.0	262,305	525,515	580,056	679,732	827,889
1720	0	0	0	0	0	0

D) Category 2 Watershed: Sheepscot River

Year	**Lake surface area (km^2)**	**Production (# of fish) at**				
		29.0 x 10^3 f/km^2	**58.1 x 10^3 f/km^2**	**64.1 x 10^3 f/km^2**	**75.2 x 10^3 f/km^2**	**91.5 x 10^3 f/km^2**
1600	19.4	561,353	1,124,642	1,241,364	1,454,679	1,771,746
1768	6.3	182,120	364,868	402,736	471,942	574,808
1850	3.1	89,001	178,309	196,815	230,635	280,906

E) Category 2 Watershed: Union River

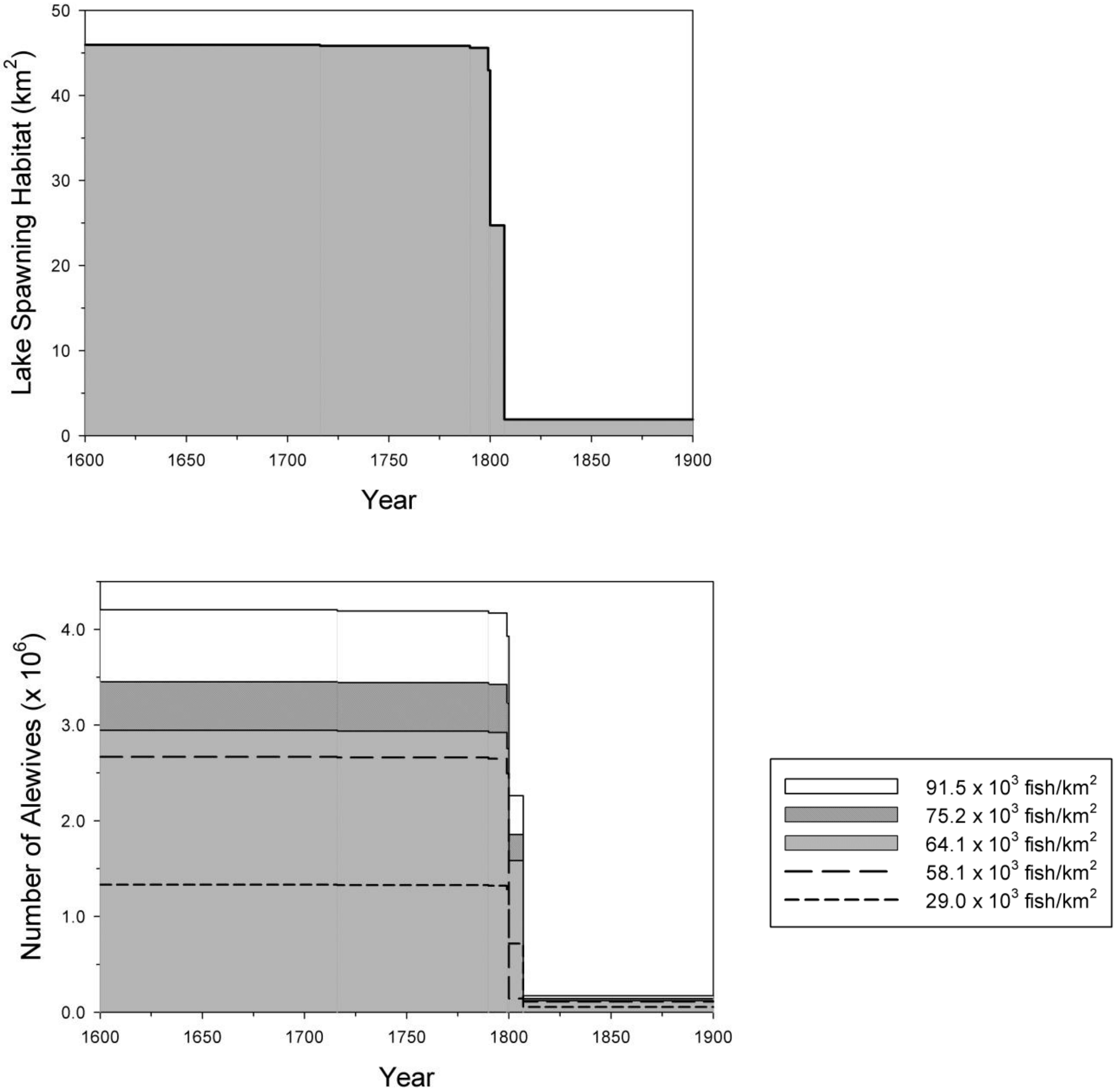
Year	**Lake surface area (km^2)**	**Production (# of fish) at**				
		29.0 x 10^3 f/km^2	**58.1 x 10^3 f/km^2**	**64.1 x 10^3 f/km^2**	**75.2 x 10^3 f/km^2**	**91.5 x 10^3 f/km^2**
1600	93.2	2,702,452	5,414,223	5,976,146	7,003,078	8,529,498
1800	4.8	140,360	281,204	310,389	363,726	443,005
1899	0	0	0	0	0	0

F) Category 2 Watershed: Dennys River

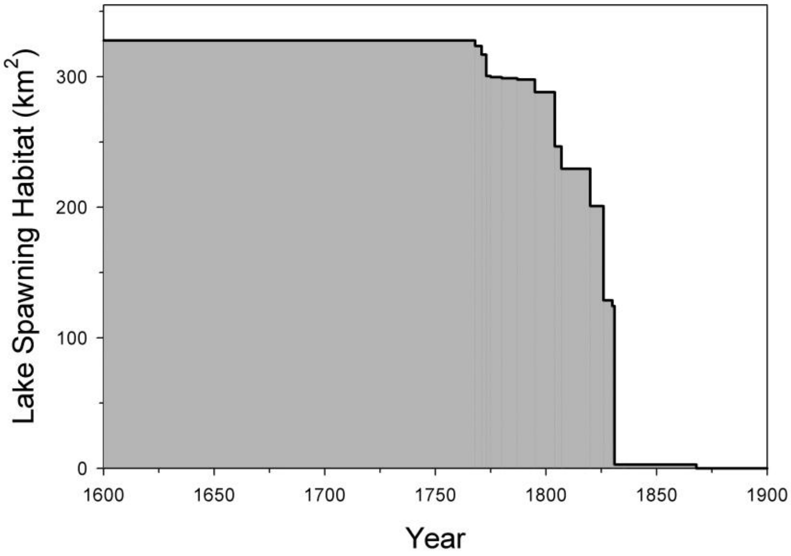
Year	**Lake surface area (km^2)**	**Production (# of fish) at**				
		29.0 x 10^3 f/km^2	**58.1 x 10^3 f/km^2**	**64.1 x 10^3 f/km^2**	**75.2 x 10^3 f/km^2**	**91.5 x 10^3 f/km^2**
1600	30.1	873,654	1,750,321	1,931,980	2,263,969	2,757,433
1787	29.5	856,863	1,716,681	1,894,849	2,220,457	2,704,437
1790	28.8	835,490	1,673,861	1,847,585	2,165,072	2,636,979
1846	0	0	0	0	0	0

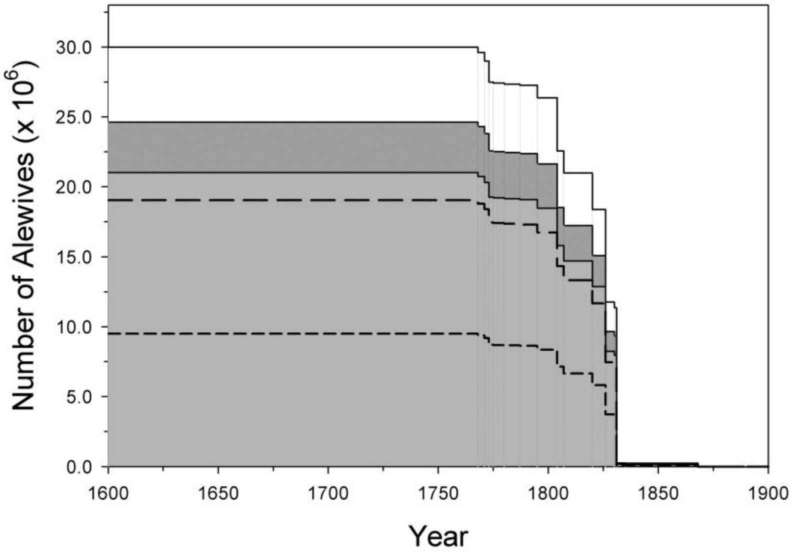
Appendix 3.2. Additional watersheds analyzed over years 1600 – 1900 for lake surface area remaining (top) and five annual productivity estimates (bottom). Vertical drop down lines in each graph indicate year of dam construction that resulted in a measurable loss of potential spawning habitat.

A) Category 1 Watershed: Androscoggin River

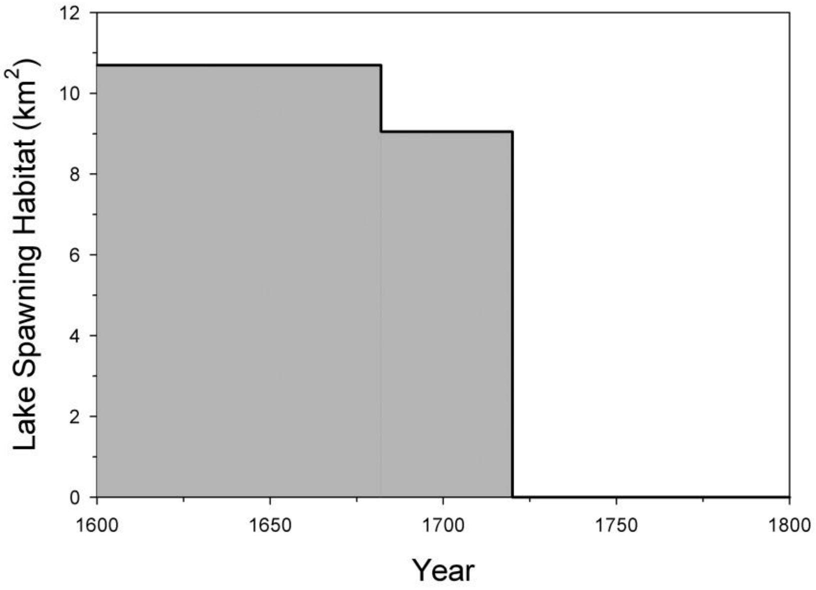


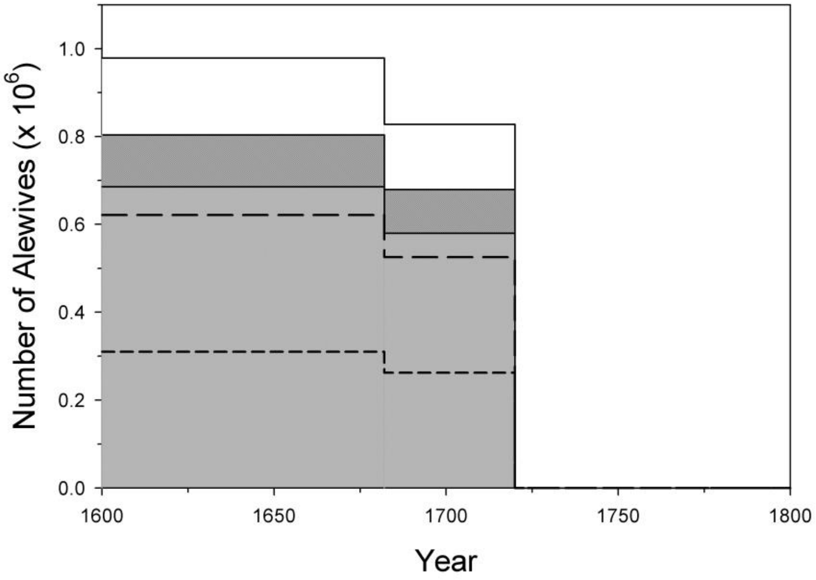
B) Category 1 Watershed: Penobscot River



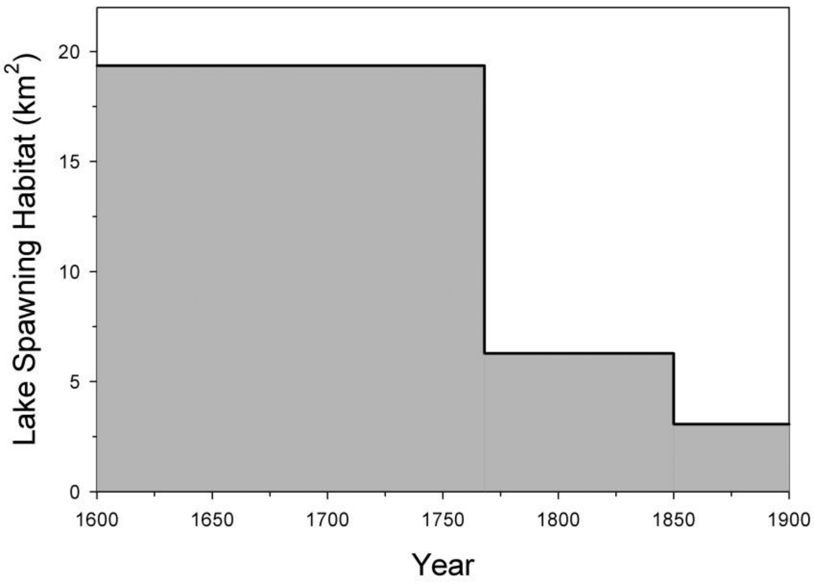


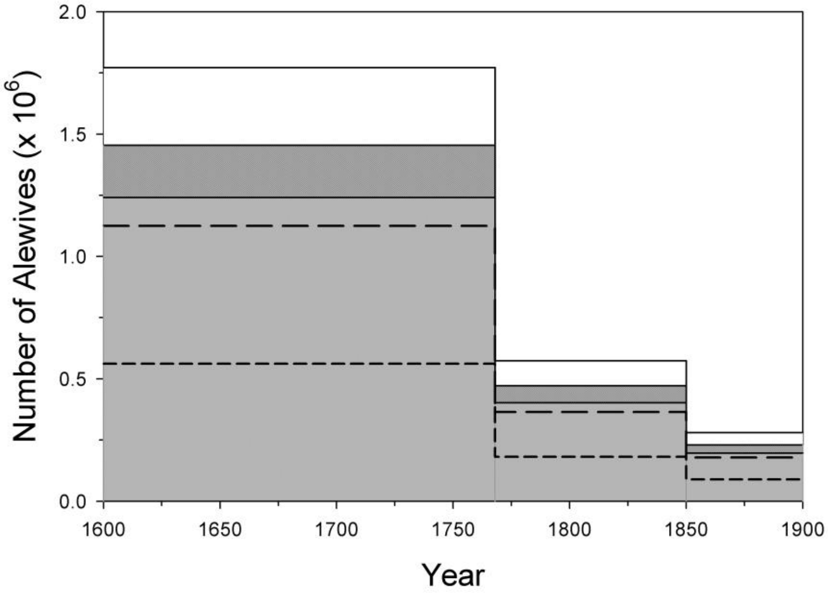
C) Category 2 Watershed: Mousam River



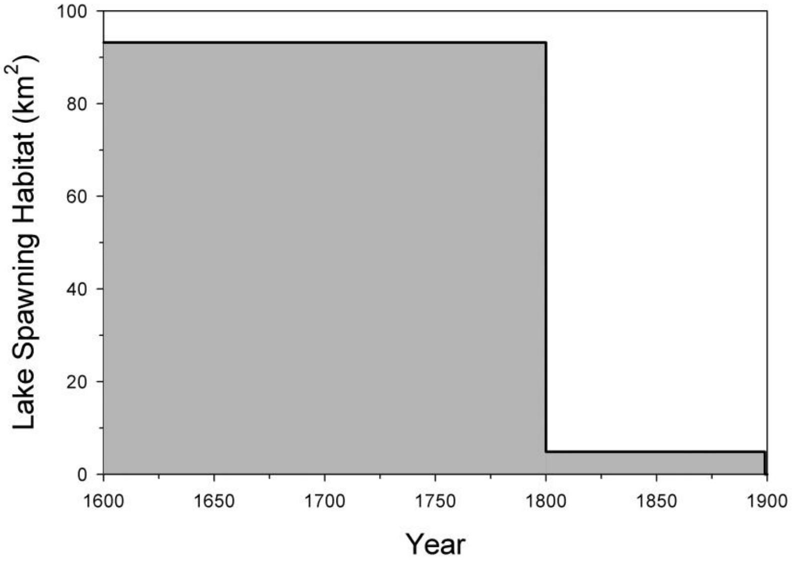


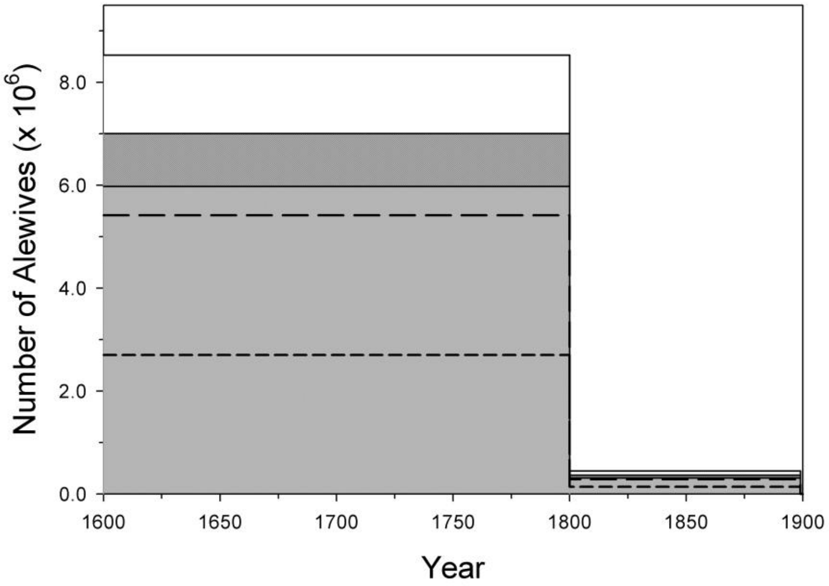
D) Category 2 Watershed: Sheepscot River





E) Category 2 Watershed: Union River





F) Category 2 Watershed: Dennys River