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Author(s): Carolyn J. Hall, Adrian Jordaan and Michael G. Frisk
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Centuries of Anadromous Forage Fish Loss: Consequences for Ecosystem Connectivity and Productivity

CAROLYN J. HALL, ADRIAN JORDAAN, AND MICHAEL G. FRISK

Lost biomass of anadromous forage species resulting from the seventeenth to nineteenth century damming of waterways and from overharvest in the northeastern United States contributed to significant changes in coastal marine–terrestrial ecosystems. Historic alewife populations in Maine for the years 1600–1900 were assessed using analyses of nineteenth and twentieth century harvest records and waterway obstruction records dating to the 1600s. Obstructed spawning access in nine watersheds reduced the annual alewife productivity per watershed to 0%–16% of virgin estimates, equaling a cumulative lost fisheries production of 11 billion fish from 1750 to 1900. Including preharvest production, our estimates suggest a lost flux of anadromous forage fish increasing from 10 million fish per year in 1700 to 1.4 billion annually by 1850. Our results suggest a realignment of current restoration goals is needed to recognize oceanic and freshwater ecosystem interdependence and the gap between current targets and potential productivity.

Keywords: applied ecology, history, coastal ecosystems, fisheries, dams

Recognition of a shifting baseline in natural resource policy and science (Pauly 1995) has resulted in increasing application of historical data to understand preexploitation conditions (Swetnam et al. 1999, Jackson et al. 2001, Alexander et al. 2009). Anadromous fish species require migration from marine to freshwater habitat to spawn and to complete their life cycle. This predictable annual appearance of spawning individuals has resulted in those species' long history as important resources for coastal communities. A paucity of baseline productivity estimates of northeastern US rivers has obscured the role that anadromous species played in precolonial coastal ecosystems. Many North Atlantic anadromous populations have presently been afforded *endangered* and *threatened* status, and several appear to have declined 90%–99% since the early twentieth century (Limburg and Waldman 2009). In systems that have large anadromous fish populations, the marine–terrestrial connection is important for ecological functioning (Schindler et al. 2003, Walters et al. 2009), which suggests that lost connections between land and sea result in impaired ecosystems. Furthermore, a number of the declining anadromous species are important forage fish, whose loss may leave only a small portion of the original prey base and may limit nutrient exchange between freshwater and marine habitats.

Limburg and Waldman (2009) analyzed 35 long-term anadromous species harvest and abundance data sets for the North Atlantic, but only 8 included data from the nineteenth century, and only 1 contained data collected prior to 1880. The pre-1880 data series, for American shad (*Alosa sapidissima*), indicated that catches from the early 1800s were around an order of magnitude higher than those of a century later. The loss of anadromous fish resulted from anthropogenic impacts and large-scale changes to coastal ecosystems throughout the Industrial Revolution, during which rapid increases in natural-resource use occurred (Bolster 2008, Alexander et al. 2009, Hall et al. 2011).

Ecosystem services

Alewives (*Alosa pseudoharengus*), one of two river herring species, undergo substantial coastal ocean migrations (Neves 1981), returning annually to spawn in lakes and slow-flow sections of rivers (Bigelow and Schroeder 1953). During spawning runs—especially at sites of constricted passage—alewives are easy and predictable targets for human, fish, and bird predators (Lindholdt 1988, Bolster 2008). European colonists described an abundance of spawning alewives in most northeastern coastal waterways "in such multitudes as is almost incredible, pressing up such shallow waters as will scarce permit them to swime [sic]" (Wood 1977, p. 56).

The harvest of alewives created economic opportunities throughout the northeastern United States as a principal bait in the current American lobster (*Homarus americanus*) and

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historical Atlantic cod (*Gadus morhua*) fisheries (Baird 1874, ASMFC 2009), for local consumption (Baird 1874), and as an export to the West Indies to feed slaves and laborers (Perley 1852). But beginning in the seventeenth century, dams constructed to power saw- and gristmills began blocking access to anadromous freshwater spawning sites. Efforts to prevent the continuing reduction of Atlantic salmon (*Salmo salar*), alewife, and shad populations resulted in 161 legislative acts passed in the state of Maine from 1800 to 1880 (Atkins 1887).

Alewife current status: A past problem?

Despite repeated efforts to restore alewives throughout the twentieth century, directed and nondirected fishing pressure, dam obstruction, pollution, and poor fishway construction and maintenance contributed to the ongoing population depletion (Rounsefell and Stringer 1945, Decker 1967). In a 1990 river herring (alewife and blueback herring) stock analysis including 11 New England rivers, Crecco and Gibson (1990) found that all populations were at least partially exploited and that 1 significant alewife river in Maine—the Damariscotta—was severely overfished. River herring populations continued to decline after the 1990 stock analysis, with Atlantic coast commercial landings decreasing from 6.2×10^6 kilograms (kg) in 1985 to less than 5.0×10^5 kg in 2007 (ASMFC 2009). River herring were federally listed as a species of concern in 2006 (NOAA 2006) and are currently undergoing a formal review of population status and trends for potential listing under the US Endangered Species Act.

The population decline of river herring is not a recent phenomenon. In 1868, impassable dams were identified in the first Maine Commissioner of Fisheries Report as the most damaging of anthropogenic impacts on anadromous species (Atkins and Foster 1868). Therefore, although the widespread decline of anadromous fish populations can be attributed to a multitude of anthropogenic effects, including pollution, overfishing, and changes to native watersheds (Köster et al. 2007, Limburg and Waldman 2009), the damming of waterways predates all other significant impacts (Perley 1852, Atkins and Foster 1868, Hall et al. 2011). In 1887, Fish Commissioner Atkins estimated that the productive capacity of Maine rivers had been reduced by 90% because of dam construction (Atkins 1887), suggesting that the 1887 alewife catch of 1.15×10^6 kg, or over 5 million fish, may have been only 10% of the potential fisheries production. Establishing goals and targets for restoration depends on the current distribution and abundance of the species but also on the historical capacity of populations. Here, we present two analyses to estimate the lost capacity of dammed rivers in the northwest Atlantic. First, we present a reconstruction of changes in the relative contribution of individual watersheds to alewife harvest in Maine. Second, we include estimates of historical alewife production per square kilometer based on twentieth century harvest records applied to accessible spawning area prior to the construction of dams to show lost watershed productivity during the period of 1600–1900.

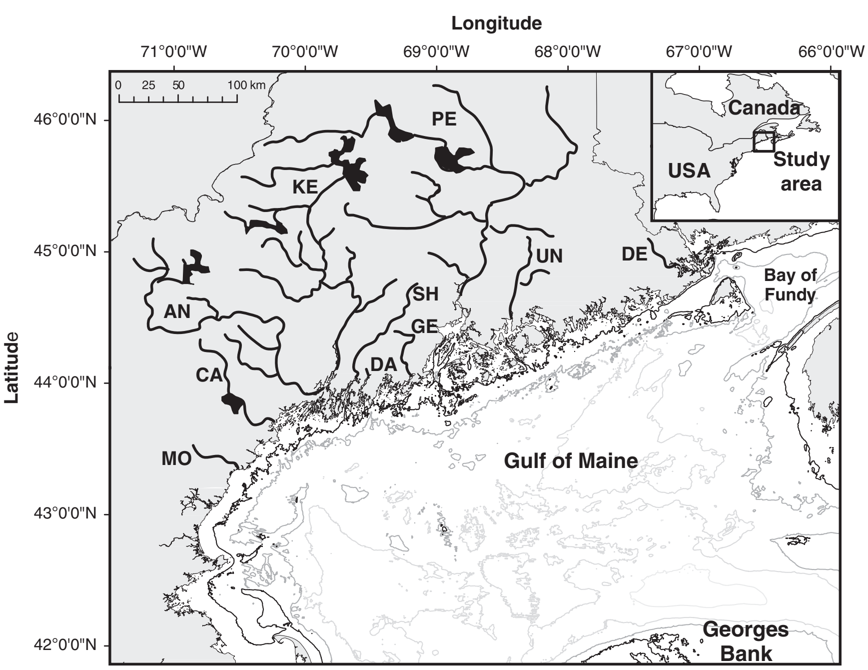

Figure 1. State and Gulf of Maine with historical river herring watersheds assessed for lost habitat due to damming: the Mousam River (MO), the Presumpscot River and Casco Bay (CA), the Androscoggin River (AN), the Kennebec River (KE), the Sheepscot River (SH), the Damariscotta River (DA), the St. George River (GE), the Penobscot River (PE), the Union River (UN), and the Dennys River (DE). Depth contours for the Gulf of Maine at 100, 200, 300, and 400 meters are also shown. The inset map displays the study location. Abbreviation: km, kilometers.

Historical fluctuations in Maine alewife harvest

Alewives were historically harvested from large and small watersheds along the entire Maine coast (figure 1). The earliest recorded alewife landings are in the Commonwealth of Massachusetts and State of Maine Fish Inspector reports, beginning in 1804 (Maine Secretary of State 1804–1893). The reports are from fishery and shipping towns along the length of the Maine coast and contain records of pickled-fish barrels and smoked-fish boxes intended for export, listed by town and species. The fish inspector records contain less information for entire river systems than later Fish Commissioner and Maine Department of Marine

Resources records because reporting was not enforced for each harvester in each town, nor was it replicated year to year, and it also did not account for local consumption. Although these records are inconsistent, they are the only regular Maine harvest records for the early nineteenth century and provide an estimate of the geographic range of harvest.

To compare barrel and box quantities to contemporary units, all quantities were converted to number of fish on the basis of values found in individual fish inspector reports. With an average weight of 90.72 kg of alewives per barrel and 0.227 kg per alewife (Rounsefell and Stringer 1945, Bigelow and Schroeder 1953), the number of alewives was determined to be 400 fish per barrel. For the boxes, 220,000 smoked alewives were packed into 3200 boxes, equaling 69 fish per box. All of these conversions were calculated on the basis of the average size of alewife captured in Maine during the late nineteenth and early twentieth centuries. Later nineteenth century landings reports included the first Maine Commissioner of Fisheries (MCOF) report (Atkins and Foster 1868), subsequent MCOF reports (MCOFG 1888, 1890), and special reports on river and alewife fisheries (Atkins 1887, Smith HM 1899). Mid-twentieth century annual landings were found in Rounsefell and Stringer's (1945) alewife fishery report. Town reports from 1943 to 2007 provided recent alewife catches per watershed and represented 90% of all of Maine's harvest (Gail Wippelhauser, Marine Resources Scientist, Maine Department of Marine Resources, personal communication, 28 August 2008).

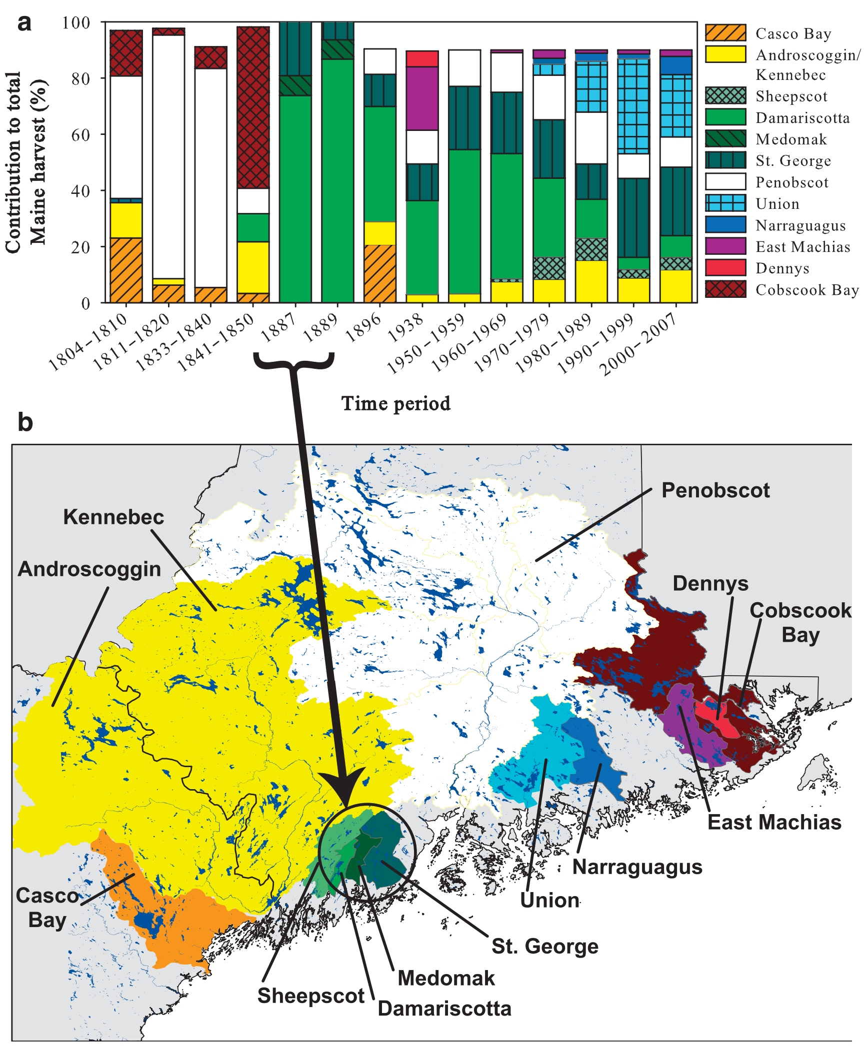

Figure 2. (a) Watershed harvest contribution: changes in individual watershed percentage contribution to state alewife landings reported between 1800 and 2007. Watersheds are displayed in the legend from west (top) to east (bottom). The harvest periods were determined from available watershed landings data. (b) Geographic shift of watersheds contributing to 1800s alewife harvest. The Maine watersheds are color coded to the legend in panel (a). The harvest watersheds of the 1880s are circled to illustrate when the landings were restricted to sites within the midcoast region, in contrast to the harvests of 1800–1840, when reported landings were distributed coastwide.

The historical and current fishery landings reports were evaluated to detect changes in watershed contribution to statewide landings. Spanning 1804–2007, these evaluations provide snapshots representing watershed alewife productivity and geographic shifts in historical habitat over time. A watershed fisheries productivity index was calculated as the percentage contribution of an individual watershed to the total Maine landings for each time interval. Although using landings data to calculate productivity shifts can result in bias because of other factors, such as unaccounted natural fluctuations, the behavior of harvesters, and changes in demand, they have been used to document declines in species productivity over long time periods (Myers and Worm 2003, Limburg and Waldman 2009). The landings were standardized across time by presenting each watershed as a percentage contribution rather than in weight or in the number of fish. A comparison of total alewife landings over the years is not provided here because, as a result of the inconsistencies stated above, the fish inspector data do not permit a reliable calculation of the total landings prior to 1880.

Harvest intervals were determined from single-year comprehensive records or multiyear periods representative of all watersheds harvested during a focused time frame and resulted in 14 time intervals from 1804 to 2007 (figure 2a). During the first part of the nineteenth century (1804–1840), five watersheds spanning the coast from Casco Bay in the west to easternmost

Cobscook Bay contributed over 90% of the state harvest (figure 2a). These five watersheds include the greatest-area watersheds in the study, with the Penobscot—the largest in Maine and second largest in New England—contributing the greatest portion (figure 2). By the late 1880s, only three watersheds—the Damariscotta, the Medomak, and the St. George—recorded yields. All three are located in the center of the coast and are significantly smaller watersheds than the Penobscot or Kennebec and Androscoggin Rivers (figure 2b). Harvests reexpanded along the coast in the twentieth century, including in Casco Bay and on the Dennys River in 1896 and 1938, respectively, but became more centrally focused again by the 1950s (figure 2). In addition, town records from the 1950s through the 2000s specified that all harvests were taken below the *head of tide*, or the most upstream reach of marine tidal waters (Gail Wippelhauser, Marine Resources Scientist, Maine Department of Marine Resources, personal communication, 28 August 2008). Therefore, the alewife harvest moved from large watersheds and the use of inland locations to an entirely coastal fishery that was focused on rivers with vastly lower potential capacities (Hall et al. 2011).

The Damariscotta and the Penobscot watersheds contributed the most to state landings in 11 and 12 time intervals, respectively, and constituted 86% of the state landings for one interval each prior to 1900. A replacement occurred in the mid-nineteenth century, with the Penobscot having the highest contribution through the 1840s, supplanted by the Damariscotta by the 1880s (figure 2). The Penobscot River system has 327.8 square kilometers (km^2) of potential lake habitat, compared with only 18.9 km^2 in the Damariscotta. In the 1880s, the St. George (24.3 km^2) also began to replace the contribution of the Casco (136.1 km^2) and Cobscook Bay systems (figure 2). The Damariscotta and Penobscot watershed contributions decreased to 7.7% and 10.7%, respectively, in the 2000s, and the St. George provided 24.4%. Notable among the percentage harvest values is the continuous shift from large to small river systems, often spanning orders-of-magnitude reductions in potential capacity.

Harvest-based estimates of productivity per unit area

Potential alewife production was calculated as the estimated adult (spawner escapement), recruit (first-time spawners), and harvest (annual fishery landings) median weight per area (in kilograms per square kilometer [kg/km^2]) for the Damariscotta River. Harvest data were available for 1949–2007. Adult and recruit estimates were available for 1949–1989 and 1949–1983, respectively (Crecco and Gibson 1990). Rather than focus on the span of overlapping years for the three population components (1949–1983), we analyzed all of the data in such a way that we fully utilized all of the available time series.

The estimated number of recruits was based on age-structure and abundance data and, in this case, is the sum of those returning to the river (the fishery) for the first time (Crecco and Gibson 1990). The number of adults is the estimated escapement (those allowed to pass to spawning habitat), which is based on the number of days without harvest (Crecco and Gibson 1990). For example, if 1 day of passage were permitted, the parents would be estimated as 16.7% of the harvested biomass. These data do not permit any sophisticated population modeling, so we provide the median and 25th and 75th percentiles as estimates for each population component and use box plots to display these with their extreme values. Landings data were also available from four other systems that were associated with a defined spawning region for which the area could be calculated. These are the Orland River (1943, 1949–1955, 1960–1969, 1971–1994, 1998–2007), Nequasset Lake (1943, 1958–1969, 1971–1989, 1992–1994, 1996–2004, 2006), Winnegance Lake (1943, 1969, 1971–1989, 1991, 1993–1994, 1998–2007), and the Dyer River (1973–1980, 1982–1986, 1988, 1993, 2000–2007). We applied the same technique and estimated the median value of harvest production per square kilometer for each of these systems. A statewide average median harvest production per square kilometer was calculated using the five rivers.

The estimated productivity of recruits and harvest per unit area using data available for the Damariscotta are 3.0×10^4 kg/km^2 and 2.5×10^4 kg/km^2, respectively (figure 3). The harvest estimate generated from the Damariscotta data is almost identical to the five-river state average harvest median value of 2.5×10^4 kg/km^2 (figure 4). The harvest estimates ranged from 6.6×10^3 kg/km^2 using Dyer River data to 5.0×10^4 kg/km^2 for Winnegance Lake (figure 4). These are not much different from two estimates for adult alewife returns currently used—2.9×10^4

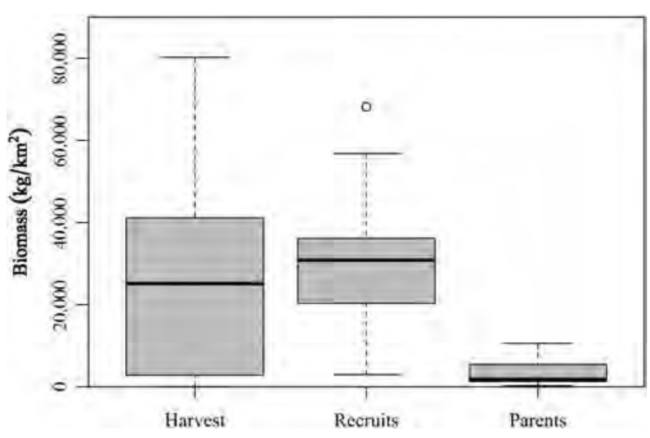

Figure 3. Damariscotta River production estimates are shown for the biological metrics of recruits, parents, and fisheries productivity per area (in kilograms per square kilometer [kg/km²]). The box plots show the median (the dark line); 25th and 75th percentiles (the ends of each box); the maximum value or 1.5 times the interquartile range, whichever is smaller (the error bars); and outliers (the open circles). Time series for the recruits represented the period from 1949 to 1983, that for the parents was from 1949 to 1989, and that for the harvest was from 1949 to 2007.

and 5.8 × 10[4] adults per area of lake—which are also based on annual harvest yields (Flagg 2007).

Historical alewife habitat availability and productivity
Estimating historical productivity is made difficult by a lack of abundance data and a paucity of landings data between

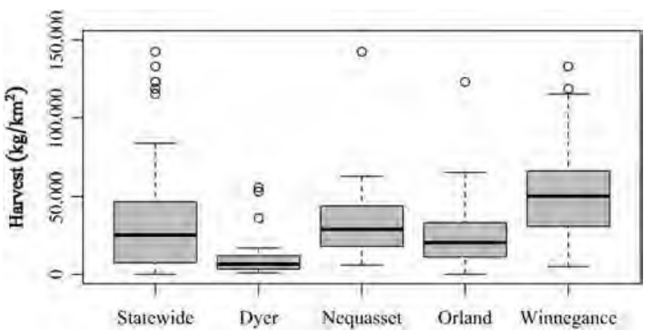

Figure 4. Harvest production estimates for a statewide average and for the Dyer River, Nequasset Lake, the Orland River, and Winnegance Lake. The time series represented the Orland River for 1943, 1949–1955, 1960–1969, 1971–1994, and 1998–2007; that for Nequasset Lake was for 1943, 1958–1969, 1971–1989, 1992–1994, 1996–2004, and 2006; that for Winnegance Lake was for 1943, 1969, 1971–1989, 1991, 1993–1994, and 1998–2007; and that for the Dyer River was for 1973–1980, 1982–1986, 1988, 1993, and 2000–2007. The statewide values are an average of the five watersheds with harvest-data time series. The open circles represent outliers. Abbreviation: kg/km², kilograms per square kilometers.

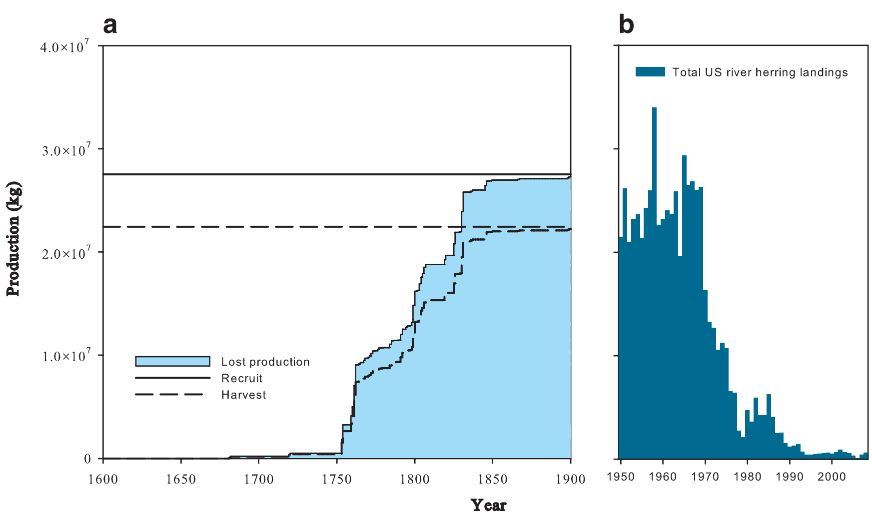

Figure 5. (a) Cumulative lost annual production of alewives from nine Maine watersheds for the time period of 1600–1900. The Damariscotta average production estimates (figure 3) were used to generate values for the recruits and harvest. (b) Total US river herring landings, which ranged between 1.8 × 10⁷ and 2.9 × 10⁷ kilograms (kg) per year from 1950 to 1970, are included to add perspective to the estimated lost production. The data were generated using the Atlantic Coastal Cooperative Statistics Program (www.accsp.org).

1600 and the present. We calculated lost historical alewife production (in kg) and the number of fish using available alewife habitat (km^2) altered by damming from 1600 to 1900 (Hall et al. 2011) and the Damariscotta data estimate of fisheries productivity (kg/km^2) detailed above. Our analysis is based on twentieth century data of watershed productivity and does not take into account anthropogenic and ecological changes over time to individual watersheds, such as eutrophication. However, it does provide the first baseline estimates of anadromous forage populations and illustrates how one key ecosystem change greatly affects productivity.

Historical alewife recruit, adult, and harvest productivity were calculated by applying the per-area productivity estimates from the Damariscotta to historically available alewife spawning habitat. The results demonstrate the near-complete loss of potential production well before 1900, with the majority of the loss occurring between 1750 and 1850 (figure 5a). As a comparison with contemporary population productivity, the total annual US river herring harvest during the 1950–2000 time period is also included (figure 5b), which demonstrates that the virgin alewife harvest productive capacity of nine Maine watersheds is equivalent to the average US river herring (alewife and blueback herring) harvest between 1950 and 1970, when stocks were considered healthy. Many of those “healthy” populations were maintained through assistance by trucking and stocking. In our estimates, we have not accounted for lost annual production of the other river herring species, blueback herring, which coexists in much of the same habitat as the alewife and is also a major contributor to the US Atlantic Coast river herring fisheries (Limburg and Waldman 2009). Therefore, the pre-1900 loss of alewives being comparable to the total US river herring landings from 1950 to 1970 is alarming, because the production of a single species in a handful of watersheds equaled that of the coastwide harvests of both species.

The annual productive capacity of the nine Maine rivers declined from 1600 to 1900 at least by 5.8×10^6 kg (using Dyer River data), at most by 4.4×10^7 kg (using Winnegance Lake data), and by 2.4×10^7 kg using the state average (figure 6). Therefore, regardless of the productivity estimates, dammed northeastern rivers appear to have lost at least six orders of magnitude in production capacity compared to their virgin, or undammed, potential. Assuming the average weight of adult fish applies, the result is the aggregate loss of 11.8 billion fish from harvest. As was stated earlier, Atkins estimated that the 1887 harvest of 5 million alewives was 10% of the undammed-waterway productivity potential. By his calculations, the annual

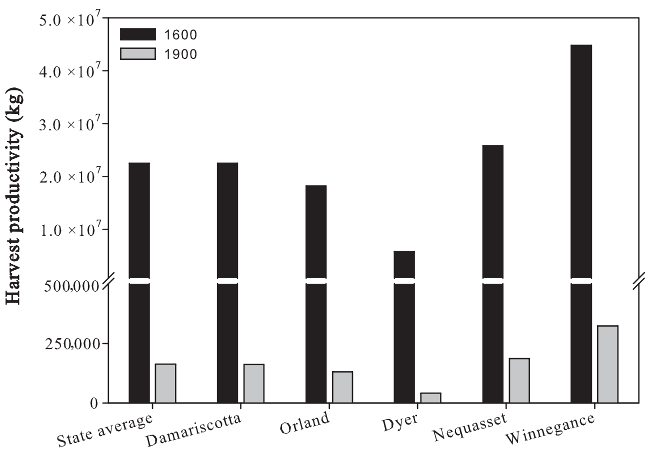

Figure 6. Lost alewife production: A comparison of 1600 to 1900. Lost production estimates using the statewide harvest data productivity estimate (figure 4) are combined with lost habitat for the nine study rivers (figure 5).

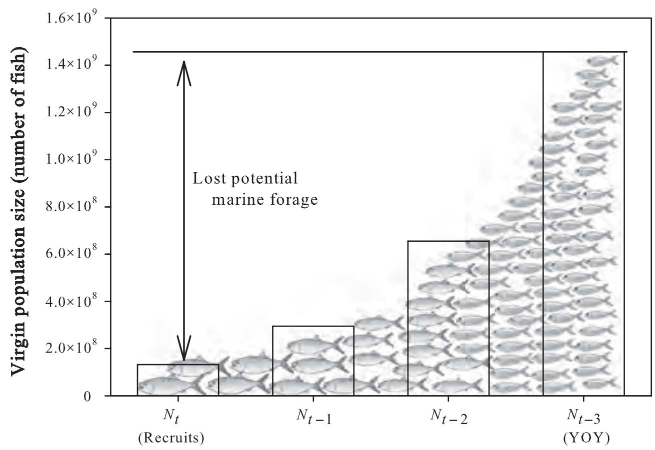

*Figure 7. After estimating the number of 4-year-old fish in 1880, assuming an average adult weight of 0.204 kilograms, the theoretical population sizes were back calculated to year 1 using an instantaneous mortality rate of 0.8. This provides an indication of the lost marine forage base supplied into the Gulf of Maine from the nine study rivers. Abbreviation: YOY, young of the year. The fish images are used courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (***http://ian.umces.edu/symbols***).*

harvest could have been 50 million fish. Our retrospective analysis indicates that in 1880, according to harvest productivity estimates and lost habitat, the nine river systems were 109 million fish short of their unobstructed potential—twice what Atkins surmised was the statewide condition.

Although the above estimates provide a measure of potential fisheries productivity, harvest-based metrics (including the number of recruits) vastly underestimate the true number of fish generated in each area, because the data were collected after a 4–6-year marine growth phase. To back calculate an estimated number of fish at age 1–3 years, we used the projection form of the exponential equation (Gotelli 1998) to account for natural mortality losses. It was assumed that all recruiting fish were 4 years old, weighed 0.204 kg, and experienced a natural instantaneous mortality rate of 0.8, or 55% mortality in one year (Crecco and Gibson 1990). Using the cumulative weight of recruits (2.93×10^9 kg) that were lost between 1600 and 1900 based on Damariscotta productivity estimates, 14 billion returning 4-year-old fish were absent from returning spawning runs. Annually, this translates into a missing 203,081 kg in 1700, which increased to 27,327,452 kg in 1900. Assuming a modest natural instantaneous mortality rate of 0.8, we estimate that from 1700 to 1800, the lost forage base from the Gulf of Maine increased from 10 million to 795 million juvenile fish per year. By 1850, the annual loss totaled 1.4 billion juvenile fish, as is displayed in the schematic demonstrating the back calculation of juvenile numbers in figure 7. The changes reflect the period of lost production concentrated from 1750 to 1850.

Setting a baseline

River herring stock status is frequently judged on the basis of performance relative to the annual US landings of the 1950s to the 1970s. However, our pre-1900 estimate of alewives from nine Maine rivers indicates that this mid-twentieth century reference represents a population that is at a level considerably reduced from baseline conditions and demonstrates the need for the application of historical data. In historical ecology studies, commercial harvest data of northwest Atlantic fish populations, ships' logs, and naturalist publications have been used to document dramatic declines in both body size (Jackson et al. 2001) and abundance (Lotze and Milewski 2004, Rosenberg et al. 2005) of the primary historical predator Atlantic cod (*Gadus morhua*) and 99% reductions of anadromous fish (Lotze and Milewski 2004). Although these estimates seem extreme, such studies are often conservative, are restricted to data from the nineteenth century, and do not incorporate the first 200 years of northwest Atlantic colonial exploitation. Our historical alewife population baseline determined from landings records, productivity estimates, and a time series of available habitat from 1600 to 1900 illustrates another such population in decline—in this case, a highly migratory anadromous forage fish.

Lost forage and ecosystem processes

The most significant implication of the lost forage base is the impact on coastal trophic relationships—in particular, as it relates to restoration goals and ecosystem-based management. After being heavily overfished until federal law required restrictive management and moratoriums on commercial fishing in 1984, the Atlantic coastal stocks of striped bass (*Morone saxatilis*) are at or near former twentieth century population highs (Hartman and Margraf 2003). The case of the striped bass is a single-species restoration success story, but it points to a larger issue for ecosystem approaches.

Because striped bass are generalist predators, enabling recovery without a concomitant increase in prey resources is now having negative impacts on salmon and other anadromous fish through predation (Grout 2006). Hudson River estimates of striped bass predation on alosines, which are considered a critical prey item, exceeded biomass in recent years, indicating that prey resources are limiting (Hartman 2003). Not only have prey populations decreased, but striped bass themselves have exhibited declining condition and decreased growth rates (Griffin and Margraf 2003, Hartman 2003, Uphoff 2003, Walter et al. 2003). Therefore, the restoration of single species cannot be viewed independently, and ecosystem-based management requires that forage fish be included in predator restoration planning.

Lost production from alosine species also intersects with the management of other forage species, such as the Atlantic herring (*Clupea harengus*), the largest Gulf of Maine commercial fishery, which shares habitat with river herring in coastal waters (Jordaan et al. 2010). It is not possible to reasonably conjecture on the historical interplay among forage species in the Gulf of Maine; however, it is clear that current management must consider the migrations and habitat overlap of forage species, particularly if active fisheries are involved. For example, bycatch of alewives in the Atlantic herring fisheries can have a large impact on populations (Cieri et al. 2008). The lost production of alewives because of obstructed rivers has left reduced population sizes susceptible to overharvest even if only as bycatch. As a result, harvest thresholds for maintaining sustainable commercial fisheries will have to be reduced to alleviate additional river herring mortality. Therefore, restoring forage species biodiversity requires not only harvest controls but also consideration of the interdependence of species, many of which are federally managed, in a comprehensive management plan.

Management implications

Management reaction to the dramatic decline of river herring stocks in the late twentieth century resulted in the closure of numerous Atlantic state commercial river herring fisheries or in much-reduced harvests (ASMFC 2009). The legacy of removing watersheds from harvest followed the temporal and spatial pattern of obstructions to New England's rivers. In Maine, as alewife habitat was dammed (Hall et al. 2011), harvest intensity was focused on fewer and fewer rivers. In 1835, the completion of the Veazie Dam on the main stem of the Penobscot River at the head of tide (Hall et al. 2011) essentially eliminated the historically significant level of harvest in the state of Maine. Within one decade of the dam's construction, the Penobscot's contribution to state landings decreased nearly 70%. In contrast to the diminishing Penobscot contribution, the Damariscotta began to register as a regular contributor to alewife harvest. Midcoast Maine became the principal alewife fishing region during the 1880s and fishing was focused on watersheds of significantly less spawning habitat than the Penobscot, with most harvest occurring at head of tide dams and downstream estuarine weirs (Atkins 1887). By 1846, all watersheds were obstructed at the head of tide, except the artificially accessible Damariscotta Lake (Hall et al. 2011), and annual statewide fishery potential productivity dropped 98%. The result of landscape changes is a dramatic shift in ecosystems long forgotten by society, with former connected and productive systems lost to impounded recreational ponds and hydropower dams.

Restoring access to geographically diverse historical spawning sites would result in increased population biocomplexity and improved species resilience in the face of environmental changes (Hilborn et al. 2003). Restored access would also reestablish missing marine–terrestrial nutrient exchange and a forage base for a vast number of predators. Alewife are an ideal candidate for restoration efforts, with high fecundity and straying rates that allow for rapid colonization of reopened spawning habitat within 3–5 years (Atkins and Foster 1868, Bigelow and Schroeder 1953, Pardue 1983). This has been demonstrated where dams have been removed or successful fish passages installed (Lichter et al. 2006). In addition to improving the resilience of alewife populations and nutrient exchange, the restoration of alewives will have profound impacts on other species. The alewife floater (*Anodonta implicata*), a freshwater mussel dependent on alewives for life cycle completion (Davenport and Warmuth 1965), has undergone a range expansion because of dam removal and the restoration of alewife populations (Smith DG 1985). Atlantic salmon smolt could benefit from increased alewife spawning populations that may provide critical prey protection from aquatic and terrestrial predators (Fay 2003). Numerous coastal predators, many of which are also at low population levels, would benefit from the additional influx of forage. For example, the restoration of striped bass demonstrated that any increase in coastal predator populations such as Atlantic cod, which have lost numerous spawning populations (Ames 2004), would require the reestablishment of a large and varied forage base. The anadromous river herrings link the management of local-scale habitat restoration, freshwater and oceanic predators, and open-ocean fisheries. In the case of alewife, removing obstructions would result in a natural reintroduction from nearby stocks that would benefit the greater Gulf of Maine ecosystem.

Native American cultures, ecosystems of the past, and alewives

The significance of the impacts of precolonial river herring harvest and river obstruction in Maine is uncertain. Although river herring were certainly used by Native American cultures, there is a lack of any evidence of the restriction of herring access to spawning habitat. River herring remains have been found in midden sites in Maine around Damariscotta, but they appeared not to be a major component of the diet. Instead, larger fish, including cod, flounder, sculpin, swordfish, striped bass, and sturgeon, represented the majority of the bones recovered (Spiess and Lewis 2001). It is possible that native cultures of North America used alewives for agricultural fertilizer (Goode 1880). However, the reality of this practice is debated (Clifton 2007), and at the very least, the quantities of alewife used were not likely to be significant compared with the species' abundance in precolonial times.

As in all historical studies, there are several caveats to the methods employed here to determine abundances. Out of necessity and for the reasons described above, production estimates were not recorded during precolonial conditions; instead, we utilized values from the twentieth century derived from harvested watersheds. However, because the time period used encompasses a significant population decline, the likelihood that our production estimates are conservative is high. It would be ideal to have pre-twentieth century data or data representing out-emigrating young alewives to understand watershed productivity without depending on returning-age adults (4 years old or older). However, even without more refined calculations, the estimates of historic alewife productivity presented here allow for a more robust and realistic evaluation of current ecosystem recovery initiatives and can help guide more effective management programs in the future.

Restoration and dam construction: A cautionary note for ecologists and managers

In the United States, a change in coastal river and anadromous species restoration is under way with the removal of numerous dams and a noted increase in fishway construction (Opperman et al. 2011). In Pacific systems, fish passage success has been examined (Ferguson et al. 2011) and has been subject to judicial review (Service 2011). After over 100 years of intensive fishway efforts, little progress has been made to integrate anadromous fishes into a holistic view of ecosystem restoration (Katopodis and Williams 2011). As the United States struggles to balance current hydropower and fish-restoration policy, China, the Lao People's Democratic Republic, and Cambodia are on the verge of constructing 200, including 11 mainstem, dams in the Mekong River (Ferguson et al. 2011, Grumbine and Xu 2011). The Mekong River is the second most biodiverse freshwater system, currently hosts the world's most productive inland fisheries (Ferguson et al. 2011), and is relied on by 2.1 million people (Grumbine and Xu 2011). The present study offers a cautionary tale for the future, suggesting that losing the connections and ecosystem services provided by anadromous species will have lasting ecosystem-wide impacts that may not be compensated through fish passage technology. Furthermore, these changes are rarely accounted for by contemporary ecologists evaluating structure and processes in North America and Europe.

It is impossible to fully appreciate how far present-day ecosystems have shifted structurally and productively without pre-exploitation baseline estimates. The challenge lies in finding historical data with which to calculate and estimate those baseline values. In our approach, we combined an extensive analysis of historical records spanning 300 years to estimate available river habitat with productivity estimates to determine the loss of historical anadromous fish populations from Maine's ecosystems. Although the project was limited to alewives, the findings indicate that billions of forage fish are missing annually from coastal ecosystems and potential harvests. If similar methods were applied globally, with many regions having much longer timelines of human river obstruction than the northeastern United States, it is hard to imagine the magnitude of lost productivity and exchange between marine and freshwater ecosystems. The implications of this magnitude of change for our current understanding of system connectivity and wildlife management, developed primarily over the past 50 years, will require integration into policy decisions in order for restoration actions to be made with an ecosystem-based perspective.

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Carolyn J. Hall (cjhall29@me.com), Adrian Jordaan, and Michael G. Frisk are affiliated with the School of Marine and Atmospheric Sciences at Stony Brook University, in Stony Brook, New York. Adrian Jordaan is also affiliated with the Department of Environmental Conservation at the University of Massachusetts, in Amherst.