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A successful day of Atlantic salmon fishing on the Penobscot River in 1926.

FEATURE: ENDANGERED SPECIES

Maine's Diadromous Fish Community: Past, Present, and Implications for Atlantic Salmon Recovery

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ABSTRACT: Co-evolved diadromous fishes may play important roles in key life history events of Atlantic salmon (*Salmo salar*) in northeastern U.S. riverine ecosystems. We reviewed available information on the historic and current abundance of alewives (*Alosa pseudoharengus*), blueback herring (*Alosa aestivalis*), American shad (*Alosa sapidissima*), rainbow smelt (*Osmerus mordax*), and sea lamprey (*Petromyzon marinus*) for several rivers in Maine. Historically, these diadromous fishes were substantially more abundant and were able to travel much farther inland to spawning and rearing areas in comparison to contemporary conditions. At historic abundance levels, these diadromous fishes likely provided several important functions for Atlantic salmon such as providing alternative prey for predators of salmon (i.e., prey buffering), serving as prey for juvenile and adult salmon, nutrient cycling, and habitat conditioning. Restoring the co-evolved suite of diadromous fishes to levels that sustain these functions may be required for successful recovery of the last native Atlantic salmon populations in the United States.

INTRODUCTION

Maine is now the southern terminus of the range of native Atlantic salmon (*Salmo salar*). By the late 1800s, native populations in the Connecticut, Merrimack, and Androscoggin Rivers had been completely extirpated, shifting the southern terminus of the species' range approximately 2 degrees north in latitude and 4 degrees east in longitude (Colligan et al. 1999). Current restoration efforts in Maine depend on substantial hatchery supplementation. Even with supplementation, however, their demographic status is far from secure (Legault 2005).

The life history of the Atlantic salmon is a complex process that requires unobstructed access between freshwater, estuarine, and marine environments. In these variable ecosystems, an intricate set of events is required for salmon to successfully complete their life cycle. When properly functioning, freshwater ecosystems provide spawning habitat and thermal refuge for adult Atlantic salmon; overwintering and rearing areas for eggs, fry, and parr; and migration corridors for smolts and adults (Bardonnet and Bagliniere 2000). The eggs hatch in late March or April. At this stage, they are referred to as alevin or sac fry. Alevins remain in the redd for about six more weeks and are nourished by their yolk sac until they emerge from the gravel in mid-May. At this time, they begin active feeding and are termed fry. Within days, the fry enter the parr stage, indicated by vertical bars (parr marks) on their sides that act as camouflage. Atlantic salmon parr are territorial; thus, most juvenile mortality is thought to be density dependent and mediated by habitat limitation (Gee et al. 1978; Legault 2005). In particular, suitable overwintering habitat may limit the abundance of large parr prior to smoltification (Cunjak et al. 1998). Smoltification usually occurs at age 2 for most Atlantic salmon in Maine (Colligan et al. 1999). Morphologically, smolts lose the vertical bars on their sides, become silver in color, and develop streamlined shape and a distinct fork in their tail (Kocik and Friedland 2002). Physiologically, changes to osmoregulatory function, olfactory receptiveness, vision, and metabolism occur allowing smolts to survive in marine environments (McCormick et al. 1998). The smolt emigration period is rather short and lasts only 2 to 3 weeks for each individual. During this brief emigration window, smolts must contend with rapidly changing osmoregulatory requirements (McCormick et al. 1998) and predator assemblages (Mather 1998). The freshwater stages in the life cycle of the Atlantic salmon have been well studied; however, much less information is available on Atlantic salmon at sea (Klemetsen et al. 2003).

Maine Atlantic salmon migrate vast distances in the open ocean to reach feeding areas in the Davis Strait between Labrador and Greenland, a distance over 4,000 km from their natal rivers (Danie et al. 1984; Meister 1984). During their time at sea, Atlantic salmon undergo a period of rapid growth until they reach maturity and return to their natal river. Most Atlantic salmon (about 90%) from Maine return after spending 2 winters at sea; usually less than 10% return after spending 1 winter at sea; roughly 1% of returning salmon are either repeat spawners or 3-sea-winter salmon (Baum 1997).

Clearly, Atlantic salmon have an extremely complex life history. Many environmental conditions must fall within suitable ranges for any individual salmon to complete its life cycle. Surprisingly little is known about the ecological interactions between Atlantic salmon and the co-evolved suite of diadromous fishes in Maine. Historically, Atlantic salmon shared the rivers of Maine with at least 11 other species of diadromous fish including the alewife (*Alosa pseudoharengus*), American eel (*Anguilla rostrata*), American shad (*Alosa sapidissima*), Atlantic sturgeon (*Acipenser oxyrinchus*), Atlantic tomcod (*Microgadus tomcod*), blueback herring (*Alosa aestivalis*), brook trout (*Salvelinus fontinalis*), rainbow smelt (*Osmerus mordax*), sea lamprey (*Petromyzon marinus*), shortnose sturgeon (*Acipenser brevirostrum*), and striped bass (*Morone saxatilis*).

The life histories of these diadromous fishes are quite variable. Alewives, blueback herring, and American shad adults all return to rivers to spawn in late spring or early summer (Table 1). In Maine, post-spawn mortality for adult alewives ranges from 41 to 91% (Havey 1961, 1973). For American shad, spawning mortality decreases, and the percentage of repeat spawners increases at higher latitudes (Weiss-Glanz et al. 1986); although, precise estimates of post-spawn mortality of American shad are not available for populations in Maine. These juvenile clupeids emigrate to the ocean in late summer or early fall (Mullen et al. 1986). The anadromous rainbow smelt is primarily an inshore species. Smelt move into estuaries and rivers during autumn and remain there throughout the winter (McKenzie 1964) until they spawn in the spring. Spawning migrations for smelt are usually quite short, with upstream migration often ceasing near the head of tide (Scott and Crossman 1973). The life history of sea lampreys is unique for East Coast anadromous fish. Adult lampreys spawn in late spring, range in weight from 1 to 2 kg, and experience 100% post-spawning mortality on spawning grounds (semelparous). All other anadromous fishes native to the eastern United States experience some degree of iteroparity.

At historic abundance levels, several of these diadromous species may have provided ecological functions that benefited Atlantic salmon at key life history events. In the following sections of this article, we describe the historic and current abundance levels of several of these diadromous fishes. We also present four distinct lines of reasoning describing how the diminishment of these diadromous populations, and the ecological functions they perform, may be partly responsible for the currently low returns of Atlantic salmon in Maine. From each set of ecological linkages, future investigators could develop and test falsifiable hypotheses in an adaptive management framework. We conclude that such an effort would substantially advance Atlantic salmon restoration efforts in Maine.

HISTORICAL ABUNDANCE AND DISTRIBUTION OF DIADROMOUS FISHES IN MAINE

> *The Penobscot fairly swarmed with the finest fish…salmon, shad, and alewives were taken in quantities that now seem almost incredible.*
>
> *—Ford 1882*

Historical distribution and abundance estimates of the diadromous fishes are quite limited for most rivers of the state of Maine. Maine's two largest rivers, the Penobscot and Kennebec, have the most available information. Most historical accounts come from the writings of Charles G. Atkins, one of the first commissioners of fisheries for Maine. Even in these cases, the only information available pertains to fisheries for each species. Therefore, historical abundance for each species can only be roughly inferred, since formal surveys and quantitative population estimation techniques had not yet been developed.

Atlantic salmon—There is more historic information pertaining to Atlantic salmon than any other diadromous fish. Historically, 34 rivers and streams in Maine had naturally reproducing Atlantic salmon populations

Table 1. Generalized life history of several anadromous fish in Maine.

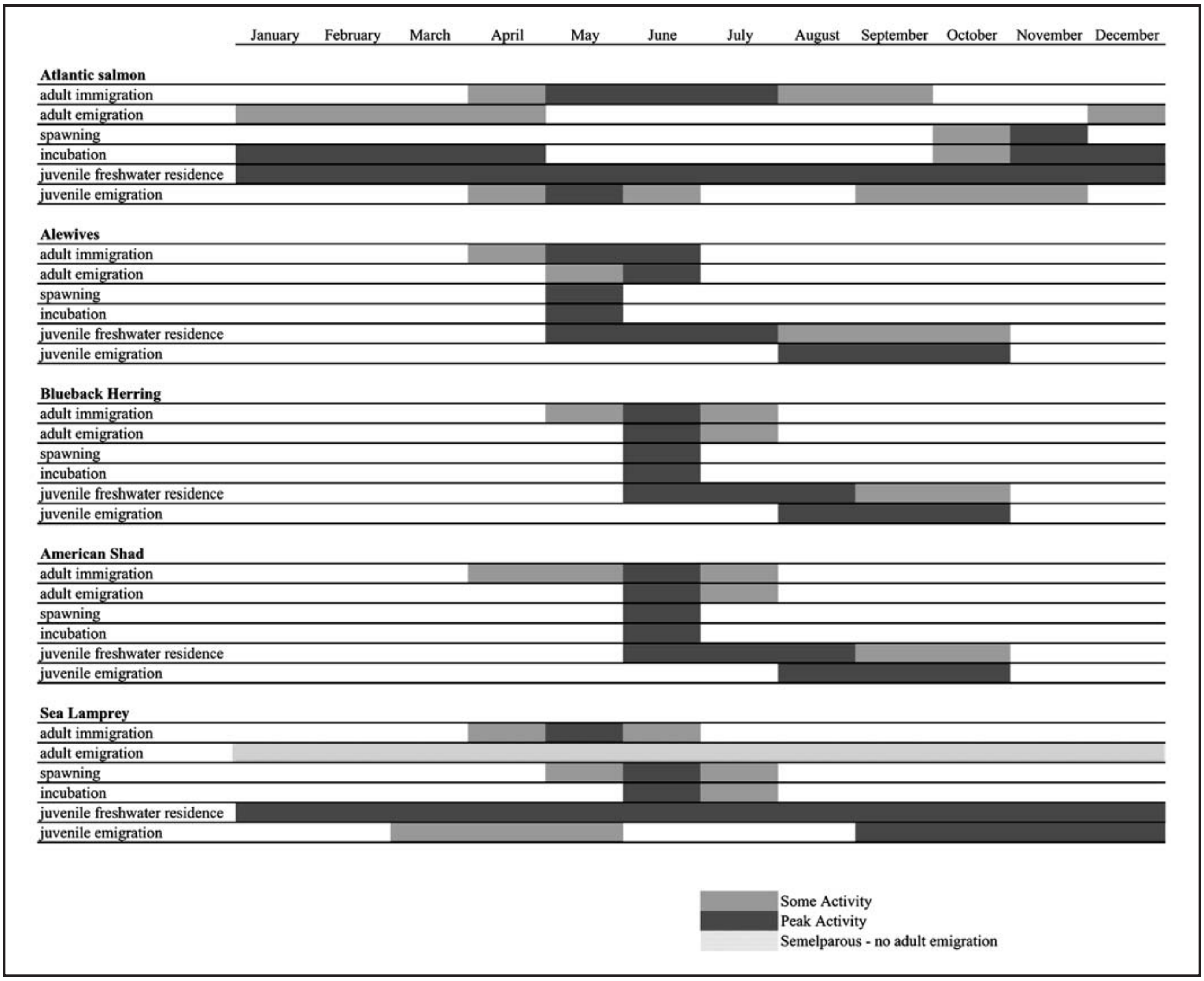


Table 2. Summary of historic and present commercial catch (estimates converted to individuals) of Atlantic salmon, American shad, and river herring on certain rivers in Maine.

	Atlantic salmon		American shad		River Herring	
River	**Historic**	**Present**[1]	**Historic**	**Present**[2]	**Historic**	**Present**
Penobscot	100,000[3]	0	2,000,000[3]	0	1,000,000[3]	0
Kennebec	216,000[4]	0	251,000[5]	0	unknown	unknown
Sebasticook	unknown	0	unknown	0	1,200,000[4]	unknown
Dennys	1,000[6]	0	unknown	0	160,000[7]	unknown
East Machias	unknown	0	unknown	0	160,000[8]	84,700[9]
Machias	unknown[10]	0	unknown	0	unknown	0
Pleasant	unknown[11]	0	9,000	0	12,000	0
Orland	0	0	0	0	1,000,000[4]	127,500[9]
Narraguagus	unknown[12]	0	unknown	0	unknown	90,500[9]
Damariscotta	0	0	0	0	2,472,000[8]	112,800[9]
St. George	unknown	0	unknown	0	686,000[8]	322,700[9]
Sheepscot	unknown	0	1,000	0	unknown	19,500[9]

1 Closed to commercial and recreational fishing.
2 Closed to commercial fishing.
3 Foster and Atkins 1869
4 Foster and Atkins 1867
5 Stevenson 1899
6 Atkins 1874
7 Smith 1899
8 Atkins 1887
9 Based on 6 year averages (2000 to 2005) of commercial catches
10 Foster and Atkins 1867 note that 60/day dip-net for salmon before the construction of the dam at the falls in Machias village.
11 Atkins 1887 notes that 12/day dip-net for salmon before the construction of the dam at Columbia falls.
12 Atkins 1874 notes that 3 men in the early 1800s dipped 40 salmon in one morning before the construction of dams.

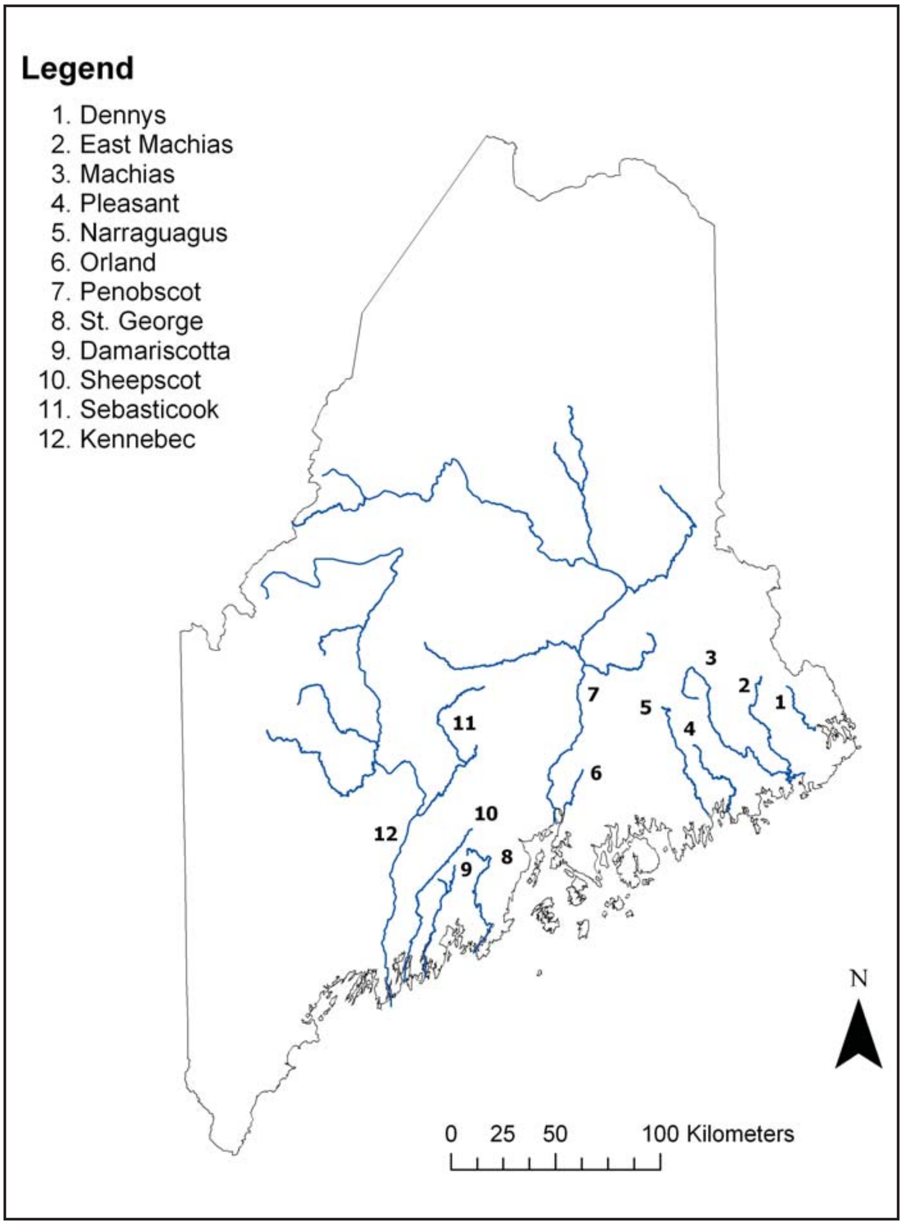
(Beland 1984). In the Penobscot River, Foster and Atkins (1869; Table 2) suggested that the average annual "yield" of Atlantic salmon could not have been less than 100,000 individuals, based on catch data that preceded the construction of the Old Town, Great Works, and Veazie Dams in the 1830s. Similarly, Foster and Atkins (1867) estimated that at least 68,000 and perhaps as many as 216,000 salmon returned to the Kennebec each year before 1820. Many of the smaller rivers and streams in Maine also had substantial runs of Atlantic salmon (Colligan et al. 1999; Figure 1). For example, Atkins (1874) estimated the total catch of Atlantic salmon from the Dennys River was 1,000 fish in 1873. Clearly, Atlantic salmon were very abundant in large and small rivers alike.

Before the construction of dams in the early 1800s, the upstream migrations of salmon extended well into the headwaters of large rivers unless a naturally impassable waterfall existed. Thus, vast amounts of habitat in the headwaters of the Penobscot and Kennebec Rivers were used for spawning and rearing. For example, Atlantic salmon were found throughout the West Branch of the Penobscot as far as Penobscot Brook, a distance over 350 km inland (Atkins 1870; Figure 2). Upstream migration in the Kennebec River was also substantial, with Atlantic salmon ranging as far inland as the Kennebec River Gorge and Grand Falls on the Dead River, 235 km inland (Foster and Atkins 1867; Atkins 1887). Anadromous Atlantic salmon may have also been found in the Moose River above Moosehead Lake (Foster and Atkins 1867); however, these reports are scarce and most evidence suggests they did not ascend further than Kennebec River Gorge near Indian Pond.

Alewife and blueback herring—Many rivers in Maine also historically produced enormous runs of alewife and blueback herring (collectively called river herring). Before the construction of dams on the Penobscot, alewives were very abundant at the Old Town falls, and "as many were taken as would supply the demand" (Foster and Atkins 1869:6). Foster and Atkins (1869) estimated that in 1867 the catch of alewives was 1,000,000 fish for the Penobscot River alone. On the Kennebec River and its tributaries, alewives were highly profitable. In one tributary of the Kennebec River near the town of Clinton, the alewife catch approached 3,000 bushels (roughly 1,200,000 alewives) per year in the early 1800s (Foster and Atkins 1867). The total catch of the river herring fishery on the Kennebec River in 1880 was 1,075,000 fish, of which roughly 400,000 were blueback herring (Atkins 1887). In 1896, the total catch of alewives was about 2,472,000 fish for the Damariscotta River (Smith 1899). Before the construction of dams, alewives migrated great distances to inland spawning areas: up to 320 km inland on the Penobscot River (Foster and Atkins 1867) and 190 km inland in the Kennebec River (Atkins 1887; Figure 3).

American shad—Historically, American shad were also very abundant, especially in the larger rivers in Maine. Foster and Atkins (1869) estimated that the catch on the Penobscot River may have been 2,000,000 fish before the construction of dams in the 1830s. Foster and Atkins (1867) reported that 4 men dipped 6,400 large American shad at the falls in

Figure 1. Selected rivers of Maine with important diadromous fisheries.

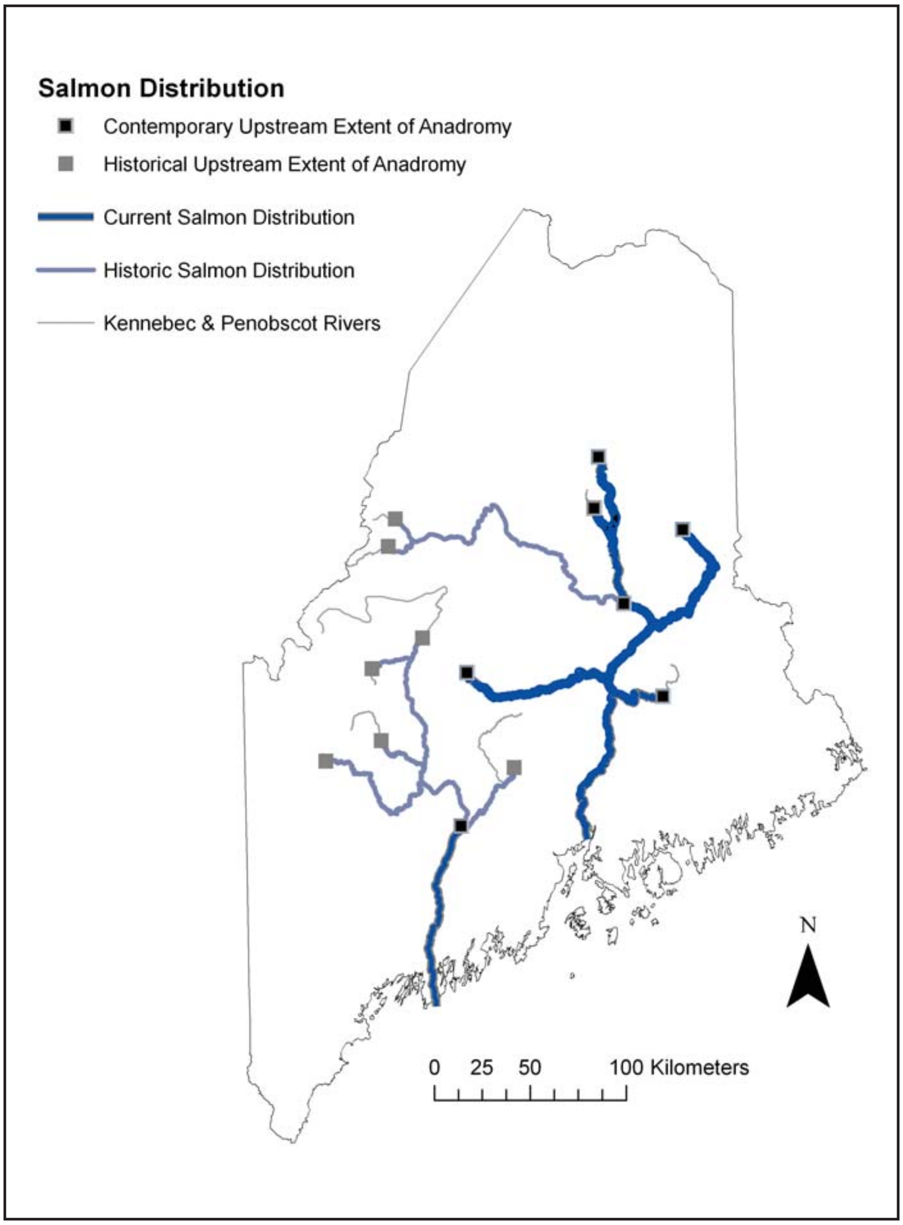


Waterville in 1 day before the construction of dams on the Kennebec River. American shad historically could ascend the Kennebec River as far inland as Norridgewock Falls on the mainstem, the town of Farmington on the Sandy River, and the town of Newport on the Sebasticook River (Foster and Atkins 1867; Atkins 1887; Figure 4). In the Penobscot drainage, American shad migrated inland to Grand Falls in the Passadumkeag River, to Shad Pond in the West Branch near Millinocket (Stillwell and Smith 1879), and to Wassataquoik Stream on the East Branch (Foster and Atkins 1867).

Rainbow smelt—Rainbow smelt were also historically very abundant, and fisheries for them were economically important. In the mid to late 1800s, the rainbow smelt fishery was the second most important fishery in the Penobscot River (Atkins 1887). In 1887, the rainbow smelt fishery for the entire Penobscot River was estimated at around 121,000 kg with another 45,000 kg caught in the Bagaduce River and areas near the town of Brooksville (Atkins 1887). The Kennebec River rainbow smelt fishery for the 1879 to 1880 season produced at least 53,000 kg from only three of the many fishing areas of the lower river (Atkins 1887). Atkins (1887) also reported total catch of rainbow smelt in the year 1880 for the Sheepscot River (10,000 kg), Pleasant River (13,000 kg), Damariscotta River (32,000 kg), and St. George River (43,000 kg).

Sea lamprey—Information on the historical abundance and distribution of sea lampreys in the rivers of Maine is essentially nonexistent. The sea lamprey was considered a delicacy when Europeans first settled North America, and commercial fisheries for sea lamprey existed on many rivers in Europe (Scott and Crossman 1973; Flescher and Martini 2002). In Maine, the commercial fisheries never targeted the sea lamprey during the 1800s. Atkins (1887) referred to them as a "neglected species" that inhabits most of the rivers in the state.

Figure 2. Historic and current distribution of Atlantic salmon in the Penobscot and Kennebec Rivers.



PRESENT ABUNDANCE AND DISTRIBUTION OF DIADROMOUS FISHES AND FACTORS FOR DECLINE

Currently, many diadromous fish populations in Maine are at, or near, historical lows. In fact, several species are either currently listed as endangered or being considered for listing under the Endangered Species Act (ESA).

The Atlantic salmon and shortnose sturgeon are both listed as endangered under the ESA. The shortnose sturgeon has been listed throughout its range since 1967. Surprisingly little is known about the shortnose sturgeon's current distribution and abundance in Maine. Atlantic salmon are listed as endangered throughout the range of the Gulf of Maine Distinct Population Segment. Fewer than half of the 34 historic "salmon rivers" in Maine now have Atlantic salmon returning to them. For each river except the Penobscot, adult returns are currently less than 25 fish annually (USASAC 2005). The Penobscot River continues to produce the highest annual adult Atlantic salmon returns in Maine, with returns fluctuating around 1,000 individuals annually (USASAC 2005).

Several other species of diadromous fish in Maine are at historic lows but not federally protected. The Atlantic sturgeon and rainbow smelt are both listed as species of concern by NOAA's National Marine Fisheries Service (NMFS). The U.S. Fish and Wildlife Service is currently conducting a status review for American eel to assess whether the species warrants listing under the ESA. While not listed as endangered or threatened, blueback herring and alewife both remain well below historical levels. A dramatic decline in spawning habitat in the Gulf of Maine has occurred in the last two centuries (Munroe 2002), and river herring stocks have suffered a recent decline in landings since the 1960s (Kocik 2000). American shad now only inhabit four or five rivers in Maine. No commercial fisheries for American shad are allowed on the rivers of Maine, and annual returns are estimated at 2,000 fish or less in rivers with remnant American shad populations (N. Gray, Maine Department of Marine Resources, pers. comm.). These runs still support a small recreational fishery in the spring and early summer. Striped bass stocks declined dramatically in the 1970s, but have rebounded substantially (Field 1997). Little information is available to assess the present status of sea lampreys in Maine (Kircheis 2004). During the 1970s and 1980s, the sea lamprey became an important specimen for biological and medical research, and a fishery was developed on the Sheepscot River with catches averaging about 8,000 adult fish per year (Meister 1982; Kircheis 2004).

Many factors have contributed to the currently low abundance of each of the diadromous species in Maine. However, dams, overfishing, and pollution are the three most often cited for the past precipitous declines that occurred beginning in the early 1800s (see Moring 2005 for a detailed review).

Our review of historical fisheries above presents abundance data for several species that exceed those observed today by several orders of magnitude. However, many fisheries had already declined substantially before Charles Atkins began his observations. For example, in 1821, the chiefs of the Penobscot Nation petitioned the legislature of the state of Maine to outlaw the use of weirs in the Penobscot River because the "fish grow more scarce every year" (Neptune 1821). By 1868, the abundance of American shad had declined to only 5,000 fish for the Penobscot River (Foster and Atkins 1869).

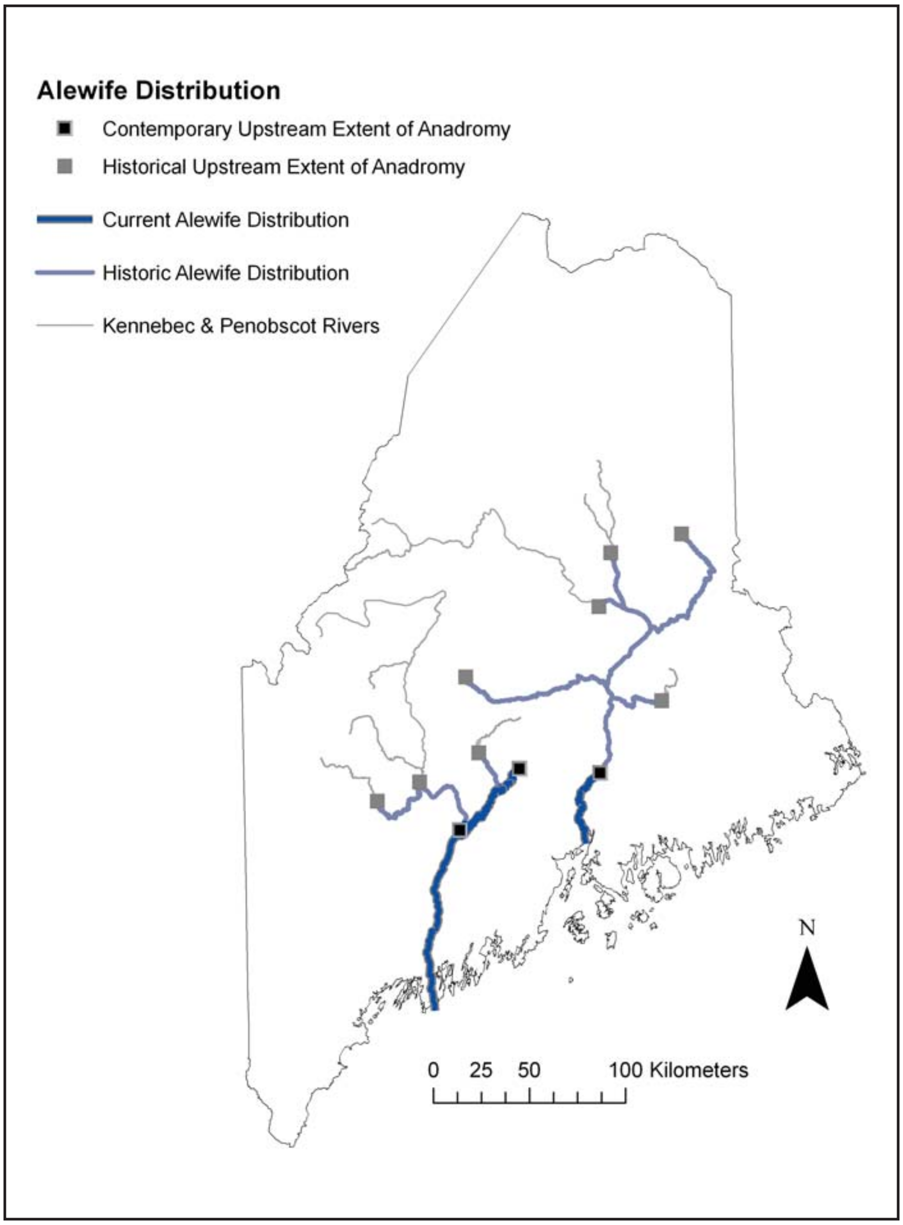
ROLES OF DIADROMOUS FISHES AND THEIR IMPORTANCE TO ATLANTIC SALMON

The diadromous fish communities that exist in Maine today are quite different than those that existed historically when Atlantic salmon were abundant. At historic abundance levels, the co-evolved diadromous fishes likely provided several important ecological functions for Atlantic salmon in Maine. Below, we identify four broad categories of interactions that likely benefited Atlantic salmon historically and may benefit salmon in localized areas today where given populations remain somewhat stable.

Prey Buffering

Historically, large populations of clupeids, such as shad, alewife, and blueback herring, used these river systems as migratory corridors, spawning grounds, and juvenile nursery habitat.

Figure 3. Historic and current distribution of alewives in the Penobscot and Kennebec rivers. Note: Veazie Dam is not a complete barrier to upstream migration of alewives in the Penobscot River.

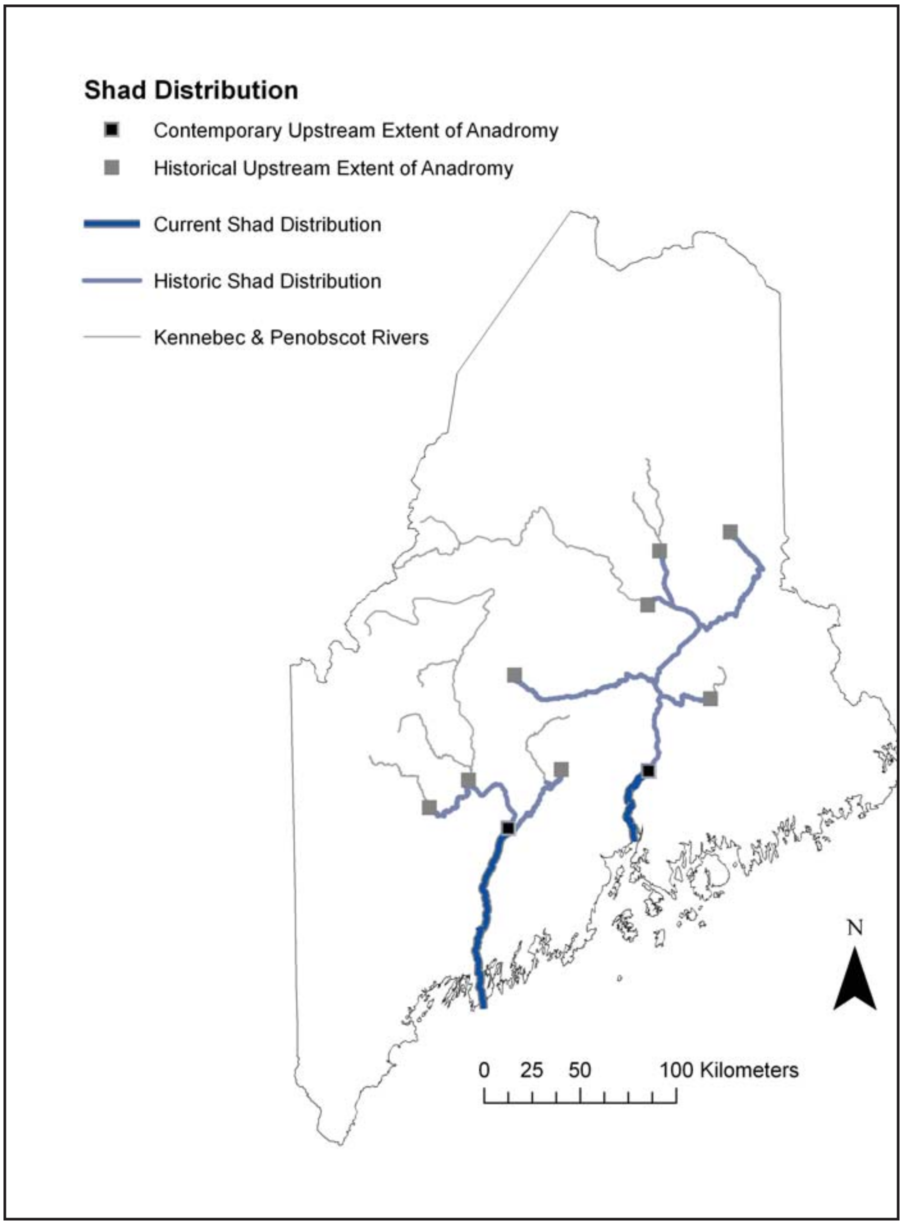


These species likely provided a robust alternative forage resource (i.e., prey buffer) for opportunistic native predators of salmon during a variety of events in the salmon's life history. While many of the following relationships still require further testing, they are each supported by optimal foraging theory (see Smith 1996), empirical observations (e.g., Svenning et al. 2005), or parallel relationships observed or modeled with other species (see Taylor 1990).

First, pre-spawn adult alewives overlap in time and space with Atlantic salmon smolts. With similar body size, numbers that exceeded salmon smolt populations by several orders of magnitude (Smith 1899; Munroe 2002), and a higher caloric content per individual (Schulze 1996), alewives were likely a substantial prey buffer that protected salmon smolts from native predators such as double-crested cormorants (*Phalacrocorax auritus*), river otters (*Lontra canadensis*), and ospreys (*Pandion haliaetus*) within sympatric migratory corridors (Mather 1998; USASAC 2004).

Svenning et al. (2005) recently described an analogous series of interactions, whereby lesser sandeel (*Ammodytes marinus*) served as a prey buffer for marine and estuarine piscivorous fish that may otherwise feed on Atlantic salmon smolts. In a survey of nearly 500 cod (*Gadus morhua*), pollock (i.e., saithe; *Pollachius virens*), whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*), and sea trout (*Salmo trutta*) in the estuary of the River Tana, Svenning et al. (2005) found no remains of Atlantic salmon in the diets of these fishes during the entire smolt emigration period. Svenning et al. (2005) consider the high abundance of lesser sandeel a key factor in the maintenance of the River Tana as one of the world's most productive Atlantic salmon rivers.

Figure 4. Historic and current distribution of American shad in the Penobscot and Kennebec Rivers.



Second, adult American shad likely provided a similar prey buffer toward potential predation on Atlantic salmon adults by river otters, harbor seals (*Phoca vitrulina*), and perhaps odontocete cetaceans. Pre-spawn adult shad would enter these same rivers and begin their upstream spawning migration at approximately the same time as adult salmon. Historically, shad runs were considerably larger than salmon runs (Foster and Atkins 1869; Stevenson 1899). Thus, native predators of medium to large size fish in the estuarine and lower river zones could have preyed on these 1.5 to 2.5 kg size fish readily.

Third, juvenile American shad and blueback herring may have represented a substantial prey buffer from potential predation on Atlantic salmon fry and parr by native opportunistic predators such as mergansers (*Mergus* spp.), great blue herons (*Ardea herodias*), mink (*Mustela vison*), and fallfish (*Semotilus corporalis*). Large populations of juvenile American shad (and blueback herring, with similar life history and habitat preferences to shad) would have occupied main stem and larger tributary river reaches through much of the summer and early fall. Juvenile shad and river herring would ultimately emigrate to the ocean in the late summer and fall. Recognizing that the range and migratory corridors of these juvenile clupeids would not be precisely sympatric with juvenile salmon habitat, there nonetheless would have been a substantial spatial overlap amongst the habitats and populations of these various juvenile fish stocks. Even in reaches where sympatric occupation by juvenile salmon and juvenile clupeids may have been low or absent, factors such as predator mobility and instinct-driven energetic efficiency (i.e., optimal foraging theory) need to be considered since the opportunity for prey switching would have been much greater than today. The opportunity for prey switching may produce stable predator-prey systems with coexistence of both prey and predator populations (Krivan 1996).

Prey for Salmon

Atlantic salmon are significant predators during most of their life stages. Salmon parr may opportunistically consume juvenile alewives and other small fish to supplement their primary foraging base of macroinvertebrates (Baum 1997). The historical abundance of other diadromous species (e.g., larval blueback herring) probably represented significant supplemental foraging resources for juvenile salmon in sympatric habitats.

In addition, anadromous rainbow smelt are a favored spring prey item of Atlantic salmon kelts (Cunjak et al. 1998). A 1995 radio tag study found that Miramichi River (New Brunswick, Canada) kelts showed a net upstream movement shortly after ice break-up (Komadina-Douthwright et al. 1997). This movement was concurrent with the onset of upstream migrations of rainbow smelt (Komadina-Douthwright et al. 1997). In addition, Moore et al. (1995) suggested that the general availability of forage fishes shortly after ice break-up in the Miramichi could be critical to the rejuvenation and ultimate survival of kelts as they prepared to return to sea. Kelts surviving to become repeat spawners are especially important due to higher fecundity and as a naturally selected legacy of virgin spawners (Baum 1997; NRC 2004). The historical availability of anadromous rainbow smelt as potential kelt forage in lower river zones may have been important in sustaining the viability of this salmon life stage. Conversely, the broad declines in rainbow smelt populations may be partially responsible for the declining occurrence of repeat spawners in Maine's salmon rivers.

Nutrient Cycling

The dynamics and ecological significance of nutrient cycling by anadromous fish species assemblages has been well established amongst co-evolved Pacific salmon species in West Coast ecosystems (e.g., Bilby et al. 1996). However, the scientific basis and biological significance (to Atlantic salmon or otherwise) of any parallel nutrient cycling role that co-evolved clupeids, sea lamprey, or Atlantic salmon themselves, might assume in East Coast salmon rivers is less well studied or understood at this time (Garman and Macko 1998; MacAvoy et al. 2000; Nislow et al. 2004). The presently low abundance of the other diadromous species could only reduce the net benefits that Atlantic salmon may derive. However, this ecological function was likely important in explaining the tremendous production potential of Maine's Atlantic salmon rivers.

Historically, upstream migrations of large populations of adult clupeids, along with adult salmon themselves, provided a conduit for the import and deposition of biomass and nutrients of marine origin into freshwater environments. Mechanisms of direct deposition included discharge of urea, discharge of gametes on the spawning grounds, and deposition of post-spawn adult carcasses (Durbin et al. 1979). Thus, the decomposition of post-spawn adult carcasses as well as the release of gametes and excretion by river herring and shad may provide a considerable influx of marine-derived nutrients into receiving waters (Durbin et al. 1979; Garman 1992; Garman and Macko 1998). These nutrient subsidies may be as large, or larger, than those observed in Pacific salmon ecosystems (Durbin et al. 1979). Migrations and other movements of mobile predators and scavengers of adult carcasses likely resulted in further distribution of imported nutrients throughout the freshwater ecosystem. Conversely, juvenile outmigrants of these sea-run species likely represented a substantial annual outflux of forage resources for Gulf of Maine predators, while also completing the cycle of importing base nutrients back to the ocean environment.

Sea lampreys also likely played a role in nutrient cycling. Lampreys prefer spawning habitat that is very similar to that used by spawning Atlantic salmon (Kircheis 2004). Their semelparous life history results in the deposition of marine-origin nutrients at about the same time that salmon fry would be emerging from redds and beginning to occupy adjacent juvenile production habitats. These nutrients would likely have enhanced the primary production capability of these habitats for weeks or even months after initial deposition, and would gradually be transferred throughout the trophic structure of the ecosystem, including those components most important to juvenile salmon (e.g., macroinvertebrate production).

Habitat Conditioning

Sea lampreys likely provide an additional benefit to Atlantic salmon spawning activity in sympatric reaches. In constructing their nests, lamprey carry stones from other locations and deposit them centrally in a loose pile within riffle habitat and further utilize body scouring to clean silt off stones already at the site (Kircheis 2004). Ultimately, a pile of silt-free stones as deep as 25 cm and as long as 1 meter is formed (Leim and Scott 1966; Scott and Scott 1988), into which the lamprey deposit their gametes. The stones preferred by lampreys are generally in the same size range as those preferred by spawning Atlantic salmon. Thus, lamprey nests can be attractive spawning sites for Atlantic salmon (Kircheis 2004). Kircheis (2004) also notes the lamprey's silt-cleaning activities during nest construction that may improve the "quality" of the surrounding environment with respect to potential diversity and abundance of macroinvertebrates, a primary food item of juvenile salmon; however, empirical data to support this assertion are lacking at this time.

CONCLUSION

Maine Atlantic salmon evolved to cope with freshwater, estuarine, and marine ecosystems that are substantially different than those that exist today. In particular, we argue that diadromous fish communities have been drastically altered in most rivers in Maine, and several of the co-evolved diadromous fishes may have provided substantial benefits to Atlantic salmon at key life history events. Foster and Atkins (1867) and Moring (2005) largely attributed the historical loss of diadromous fish in the rivers of Maine to impassable dams, overfishing, and pollution. These mechanisms are still affecting many rivers in Maine today and, in some cases, prevent the opportunity to restore the co-evolved diadromous fishes to a portion of their historical abundances.

Several native diadromous species show remarkable resilience, however. For example, Havey (1961) reported a highly successful restoration of alewives to Long Pond, Maine. In Long Pond, dams prevented alewives from reaching suitable spawning areas for decades until 1951 when local citizens built fishways in four remaining low head dams. By providing passage and stocking ripe adults, Havey (1961) and his cooperators quickly re-established a substantial alewife run. Similarly, American shad now inhabit the Kennebec River above the site of the former Edwards Dam (N. Gray, Maine Department of Marine Resources, pers. comm.), and anadromous rainbow smelt now inhabit the Penobscot River above the site of the former Bangor Dam (NMFS unpublished data).

We suggest that restoration of the native suite of diadromous fishes may provide several important ecological functions that may benefit Atlantic salmon at important life history events. Many of the linkages discussed above clearly remain untested hypotheses; however, testing these hypotheses (e.g., alewives buffering predation on migrating smolts) in an adaptive management framework could substantially advance restoration efforts for Atlantic salmon in Maine. In the case of predator-prey interactions, the framework provided by Mather (1998) provides clear direction in terms of such hypothesis development and testing. Restoring the last native Atlantic salmon populations in the United States is clearly a daunting challenge; however, a multi-species approach guided by rigorous hypothesis development and testing should improve the probability of success.

ACKNOWLEDGMENTS

With the passing of Clem Fay in October 2005, the fisheries community in Maine lost a remarkable character. Clem not only cared deeply for the fisheries resources he managed, but also for the people he worked with. Clem was genuinely concerned for the well-being of others and for the future condition of the fisheries resources of the Penobscot Nation.

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REFERENCES

Atkins, C. G. 1870. Fourth Report of the Commissioner of Fisheries of the state of Maine for the year 1870. Sprague, Owen and Nash, Printers to the State, Augusta, Maine.

____. 1874. On the salmon of eastern North America, and its artificial culture. Pages 226-337 *in* United States Commission of Fish and Fisheries, Part II: Report of the Commissioner for 1872 and 1873. Government Printing Office, Washington, DC.

_____. 1887. The river fisheries of Maine. Pages 673-788 *in* G. B. Goode and a staff of associates, eds. The fisheries and fishery

industries of the United States, Volume I Section V. History and methods of the fisheries. Government Printing Office, Washington DC.

Bardonnet, A., and **J. L. Bagliniere.** 2000. Freshwater habitat of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 57:497-506.

Baum, E. T. 1997. Maine Atlantic salmon: a national treasure. Atlantic Salmon Unlimited, Hermon, Maine.

Beland, K. F. 1984. Strategic plan for management of Atlantic salmon in the state of Maine. Atlantic Sea Run Salmon Commission, Bangor, Maine.

Bilby, R. E., B. R. Fransen, and **P. A. Bisson.** 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 53(1): 164-173.

Colligan, M. A., J. F. Kocik, D. C. Kimball, J. Marancik, J. F. McKeon, and **P. R. Nickerson.** 1999. Status review for anadromous Atlantic salmon in the United States. National Marine Fisheries Service/ U.S. Fish and Wildlife Service Joint Publication. Gloucester, Massachusetts.

Cunjak R. A., T. D. Prowse, and **D. L. Parrish.** 1998. Atlantic salmon (*Salmo salar*) in winter: "the season of parr discontent"? Canadian Journal of Fisheries and Aquatic Sciences 55 (supplement 1):161–180.

Danie, D. S., J. G. Trial, and **J. G. Stanley.** 1984. Species profiles: life histories and environmental requirements of coastal fish and invertebrates (North Atlantic): Atlantic salmon. FWS/OBS-82/11.2, TR EL-82-4. U.S. Fish and Wildlife Service and U.S. Army Corps of Engineers.

Durbin A. G., S. W. Nixon, and **C. A. Oviatt.** 1979. Effects of the spawning migration of the alewife, *Alosa pseudoharengus*, on freshwater ecosystems. Ecology 60:8–17.

Field, J. D. 1997. Atlantic striped bass management: Where did we go right? Fisheries 22(7): 6-8.

Flescher, D., and **F. H. Martini.** 2002. Lampreys. Order Petromyzontiformes. Pages 16-19 *in* B.B. Collette and G. Klein-MacPhee, eds. Bigelow and Schroeder's fishes of the Gulf of Maine. Third Edition. Smithsonian Institution Press, Washington and London.

Ford, H. A. 1882. History of Penobscot County, Maine. Williams, Chase and Company, Cleveland, Ohio.

Foster, N. W., and **C. G. Atkins.** 1867. Report of Commission on Fisheries. *In* Twelfth annual report of the Secretary of the Maine Board of Agriculture. Stevens and Sayward Printers to the State, Augusta, Maine.

_____. 1869. Second report of the Commissioners of Fisheries of the state of Maine 1868. Owen and Nash, Printers to the State, Augusta, Maine.

Garman, G. C. 1992. Fate and potential significance of postspawning anadromous fish carcasses in an Atlantic coastal river. Transactions of the American Fisheries Society 121:390–394

Garman, G. C., and **S. A. Macko.** 1998. Contribution of marine-derived organic matter to an Atlantic coast, freshwater, tidal stream by anadromous clupeid fishes. Journal of the North American Benthological Society 17(3):277–285.

Gee, A. S., N. J. Milner, and **R. J. Hemsworth.** 1978. The effect of density on mortality in juvenile Atlantic salmon (*Salmo salar*). Journal of Animal Ecology 47:497-505.

Havey, K. A. 1961. Restoration of anadromous alewives at Long Pond, Maine. Transactions of the American Fisheries Society 90:281–286.

_____. 1973. Production of juvenile alewives, *Alosa pseudoharengus*, at Love Lake, Washington County, Maine. Transactions of the American Fisheries Society 102:434–437.

Kircheis, F. W. 2004. Sea lamprey *Petromyzon marinus* L. 1758. F. W. Kircheis L.L.C., Carmel, Maine.

Klemetsen, A., P. A. Amundsen, J. B. Dempson, B. Jonsson, N. Jonsson, M. F. O'Connell, and **E. Mortensen.** 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish 12:1-59.

Kocik, J. F. 2000. River herrings. in S. H. Clark, ed. Status of fishery resources off the northeastern United States for 1998. National Oceanic and Atmospheric Administration Technical Memo NMFS-NE-115.

Kocik, J. F., and **K. D. Friedland.** 2002. Salmons and trouts. Order Salmoniformes. Pages 170-181 *in* B.B. Collette and G. Klein-MacPhee, eds. Bigelow and Schroeder's fishes of the Gulf of Maine. Third Edition. Smithsonian Institution Press, Washington and London.

Komadina-Douthwright, S. M., D. Caissie, and **R. A. Cunjak.** 1997. Winter movement of radio-tagged Atlantic salmon (*Salmo salar*) kelts in relation to frazil ice in pools of the Miramichi River. Canadian Technical Report of Fisheries and Aquatic Sciences 2161. Department of Fisheries and Oceans, Maritime Region, Science Branch, Diadromous Fish Division. Moncton, New Brunswick, Canada.

Krivan, V. 1996. Optimum foraging and predator-prey dynamics. Theoretical Population Biology 49: 265-290.

Legault, C. M. 2005. Population viability analysis of Atlantic salmon in Maine, USA. Transactions of the American Fisheries Society 134:549–562.

Leim, A. H. and **W.B. Scott.** 1966. Fishes of the Atlantic coast of Canada. Fisheries Research Board of Canada: 21-22.

MacAvoy, S. E., S. A. Macko, S. P. McIninch, and **G. C. Garman.** 2000. Marine nutrient contributions to freshwater apex predators. Oecologia 122(4):568-573.

Mather, M. E. 1998. The role of context-specific predation in understanding patterns exhibited by anadromous salmon. Canadian Journal of Fisheries and Aquatic Sciences 55(Supplement 1):232–246.

McCormick, S. D., L. P. Hansen, T. P. Quinn, and **R. L. Saunders.** 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55(1):77-92.

McKenzie, R. A. 1964. Smelt life history and fishery in the Miramichi River, New Brunswick. Bulletin Fisheries Research Board of Canada 144, Ottawa.

Meister, A. L. 1982. The Sheepscot River: an Atlantic salmon river management report. Atlantic Sea-Run Salmon Commission and Maine Inland Fish and Game, Augusta, Maine.

_____. 1984. The marine migrations of tagged Atlantic salmon (*Salmo salar* L.) of USA origin. C. M. 1984-M:27. Anadromous and Catadromous Fish Committee, International Council for the Exploration of the Sea, Copenhagen, Denmark.

Moore, D., G. J. Chaput, and **P. R. Pickard.** 1995. The effect of fisheries on the biological characteristics and survival of mature Atlantic salmon (*Salmo salar* L.) from the Miramichi River. Canadian Special Publication Fisheries and Aquatic Sciences 123: 229-247.

Moring, J. R. 2005. Recent trends in anadromous fishes. *In* R. Buchsbaum, J. Pederson, W. E. Robinson, eds. The decline of fisheries resources in New England: evaluating the impact of overfishing, contamination, and habitat degradation. MIT Sea Grant College Program, Cambridge, Massachusetts, MITSG 05-5.

Mullen, D. M., C. W. Fay, and J. R. Moring. 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic) alewife/blueback herring. U.S. Fish and Wildlife Service Biological Report 82(11.56). U.S. Army Corps of Engineers, TR EL-82-4.

Munroe, T. A. 2002. Herrings. Family Clupidae. Pages 111-160 *in* B. B. Collette and G. Klein-MacPhee, eds. Bigelow and Schroeder's fishes of the Gulf of Maine. Third Edition. Smithsonian Institution Press, Washington and London.

Neptune, J. 1821. Petition to the Maine State Legislature. Reprint courtesy of the Maine State Archives, Augusta, Maine.

Nislow, K. H., J. D. Armstrong, and **S. McKelvey**. 2004. Phosphorus flux due to Atlantic salmon (*Salmo salar* L.) in an oligotrophic upland stream: effects of management and demography. Canadian Journal of Fisheries and Aquatic Sciences 61: 2401-2410.

NRC (National Research Council). 2004. Atlantic salmon in Maine. Committee on Atlantic Salmon in Maine, Ocean Studies Board, Division of Earth and Life Sciences. National Academy Press, Washington, DC.

Schulze, M. B. 1996. Using a field survey to assess potential temporal and spatial overlap between piscivores and their prey and a bioenergetics model to examine potential consumption of prey, especially juvenile anadromous fish, in the Connecticut River estuary. Master's thesis. University of Massachusetts, Amherst.

Scott, W. B., and **E. J. Crossman.** 1973. Freshwater fishes of Canada. Bulletin 184. Fisheries Research Board of Canada, Ottawa 69-75.

Scott, W. B., and **M. G. Scott.** 1988. Atlantic fishes of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences 219.

Smith, H. M. 1899. Notes on the extent and condition of the alewife fisheries of the United States in 1896. Pages 31-34 *in* U.S. Commission of Fish and Fisheries. Report of the Commissioner for the year ending June 30, 1898 Part XXIV. Government Printing Office, Washington, DC.

Smith, R. L. 1996. Ecology and field biology, fifth edition. HarperCollins College Publishers, New York.

Stevenson, C. H. 1899. The shad fisheries of the Atlantic coast of the United States. Pages 101-269 *in* U.S. Commission of Fish and Fisheries: report of the Commissioner for the year ending June 30, 1898 Part XXIV. Government Printing Office, Washinton, DC.

Stilwell, E. M., and **E. Smith.** 1879. Report of the Commissioner of Fisheries of the state of Maine for the year 1879. E.F. Pillsbury and Company, State Printers, Augusta, Maine.

Svenning, M. A., R. Borgstrøm, T. O. Dehli, G. Moen, R. T. Barrett, T. Pedersen, and **W. Vader.** The impact of marine fish predation on Atlantic salmon smolts (*Salmo salar*) in the Tana estuary, North Norway, in the presence of an alternative prey, lesser sandeel (*Ammodytes marinus*). Fisheries Research 76: 466–474

Taylor, A. D. 1990. Metapopulations, dispersal, and predator-prey dynamics: an overview. Ecology 71(2): 429-435.

USASAC (United States Atlantic Salmon Assessment Committee). 2004. Annual report of the U.S. Atlantic Salmon Assessment Committee Report 16—2003 Activities. Annual Report 2004/16. Woods Hole, Massachusetts.

_____. 2005. Annual Report of the U.S. Atlantic Salmon Assessment Committee Report 17—2004 Activities. Annual Report 2005/17. Woods Hole, Massachusetts.

Weiss-Glanz, L. S., J. G. Stanley, and **J. R. Moring.** 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic)—American shad. U.S. Fish and Wildlife Service Biological Report 82(11.59). U.S. Army Corps of Engineers, TR EL-82-4.