# Dramatic Declines in North Atlantic Diadromous Fishes

KARIN E. LIMBURG AND JOHN R. WALDMAN

*We examined the status of diadromous (migratory between saltwater and freshwater) fishes within the North Atlantic basin, a region of pronounced declines in fisheries for many obligate marine species. Data on these 24 diadromous (22 anadromous, 2 catadromous) species are sparse, except for a few high-value forms. For 35 time series, relative abundances had dropped to less than 98% of historic levels in 13, and to less than 90% in an additional 11. Most reached their lowest levels near the end of the observation period. Many populations persist at sharply reduced levels, but all species had suffered population extirpations, and many species are now classified as threatened or endangered. Habitat loss (especially damming), overfishing, pollution, and, increasingly, climate change, nonnative species, and aquaculture contributed to declines in this group. For those diadromous fishes for which data exist, we show that populations have declined dramatically from original baselines. We also discuss the consequences of these changes in terms of lost ecosystem services.*

*Keywords: diadromous fishes, overfishing, dams and other threats, habitat loss, shifting baselines*

**W**e examined the status of North Atlantic diadromous fishes, that is, those species that migrate between marine waters and continental watersheds to complete their life cycles. The North Atlantic basin receives the drainage of major rivers such as the St. Lawrence, the Mississippi, and the Rhine, and hundreds of smaller rivers, all of which host diadromous fishes. Diadromy occurs in two primary forms: anadromy, in which spawning takes place in freshwater, and catadromy, in which reproduction occurs at sea. Diadromous fishes comprise less than 1% of world fish fauna, but their value to humans far exceeds this portion. Many diadromous fishes such as salmons, sturgeons, and shads are not only economically important, but they also serve as crucial links for energy flow between fresh and marine environments (Helfman 2007).

Recent analyses have shown major declines in many North Atlantic obligate marine fishes (Christensen et al. 2003). For these species, declines generally take the form of population reductions to the level of commercial extinction, but not extirpation (Casey and Myers 1998). Unlike many marine fishes that have few but large, geographically widespread populations, most anadromous fishes have numerous but smaller river-specific populations (Powles et al. 2000). This renders them more susceptible to population-level extirpations, and, if these extirpations occur serially, species extinction may occur.

Diadromy as a life-history strategy has evolved in phylogenetically diverse fish groups (McDowall 1997). It appears to offer the benefits of lessened predation in early life stages, access to increased food resources in marine environments for individuals, and the potential for demographic and morphological sculpting to the particulars of each population's migratory circuit (McDowall 2001). These habitat-switching life histories may have evolved in response to geographic differentials in marine and freshwater productivity, with anadromous species dominating the higher latitudes where marine productivity far exceeds that of inland waters (Gross et al. 1988). But these more complicated life histories come with costs, including osmoregulatory and energetic demands for movement between two distinctly different environments. Moreover, occurrence both in freshwater and in the sea exposes populations to the uncertainties of environmental conditions in two realms.

Recent work has shown that migratory movements of diadromous fishes are far more complex than originally thought (e.g., Secor and Rooker 2000, Limburg et al. 2001). Many display spectacular long-distance migrations not only at sea but also as they traverse thousands of kilometers inland and ascend hundreds of meters in elevation. Because the spawning aggregations of diadromous fishes often place them within easy reach of humans, these runs have been particularly important sources of protein.

"Ecosystem goods and services" is a recently derived paradigm (Daily 1997, Ruffo and Kareiva 2009) used to demonstrate the value and benefits to humans of the natural world. Ecosystem services are defined as natural ecological functions

or properties that support human well-being either directly or indirectly. In this paradigm, diadromous fishes have four special roles, although we will show that their importance in these functions has diminished greatly as a result of their population declines. First, provisioning of protein and other products is a primary ecosystem service of diadromous fishes because of their (historic) vast abundances, the high predictability of these runs, and the ease of their capture as they aggregate near or on their spawning grounds (Bolster 2008). Second, these fishes link continental and marine ecosystems, transporting embodied productivity from one to the other. Semelparous anadromous fishes (those that spawn once and then die) may act as keystone species (Willson and Halupka 1995): They have a major impact in their ecological communities because their carcasses are consumed directly by wildlife or stream infauna, or they decompose and release their nutrients to the water or riparian zones. Garman (1992) estimated that the nontidal James River, in Virginia, may have received annual biomass input from anadromous alosines of 1.55 kilograms (kg) per hectare (ha) (representing 3.6 million individuals in the run, with 70% mortality) before dams blocked their movements. Garman (1992) determined mean decomposition rates on the order of 10 days. These subsidies of "marine-derived nutrients" often serve as critical additions of energy and nutrients that fuel food webs well beyond the streams in which they died (Gende et al. 2002).

A third ecosystem service generated by diadromous species is the support of marine food chains through the addition of fish that emigrate from natal rivers to the sea, again transporting energy and nutrients, but in the reverse direction. At northern temperate latitudes, these fluxes are composed mainly of young fishes emigrating seaward. Nineteenth-century reports noted that the voluminous outpourings of young anadromous fishes provided important forage for marine species such as cod, *Gadus morhua,* tightly coupling inland production to coastal food webs (Stevenson 1899); today, such continental-marine linkages are broken to a large extent in the North Atlantic basin. This coupling also enabled fishers to harvest marine predators closer to shore without having to venture onto the high seas (Stevenson 1899).

Finally, diadromous species have played important roles for both indigenous and nonindigenous peoples. Because these fishes could supply great amounts of food after long periods with little to eat, they enjoyed high cultural status. For many coastal Native American communities, Atlantic sturgeon (*Acipenser oxyrinchus*), American eel (*Anguilla rostrata*), and other diadromous fishes had enormous practical and totemic importance (Bolster 2008). In modern American society, coastal communities still celebrate the return of American shad (*Alosa sapidissima*), hickory shad (*Alosa mediocris*), river herring (alewife, *Alosa pseudoharengus*, and blueback herring, *Alosa aestivalis*) (Waldman 2003), although these runs, and celebrations thereof, have diminished greatly.

## Metrics of change

We synthesized information on the current status of North Atlantic diadromous fishes using these metrics: the number of original populations versus extant populations (table 1), temporal changes in population abundances or harvests (table 2, figure 1), and official conservation status (table 1). We identified 24 diadromous fishes in the North Atlantic. Of these, 12 are restricted to North America, 9 to Europe and Africa, and 3 are common to both shores. Each coast has only one strongly catadromous species, American eel and European eel (*Anguilla anguilla*). Information about the survival status of populations of diadromous fishes was obtained from the broadest and most recent sources available. The conservation status listed also was from the broadest possible listing identified.

Time-series data sets were collected mostly from published literature; two sets (European eel recruitment in Swedish rivers, and Atlantic salmon [*Salmo salar*] catches in the River Dee) were obtained from scientists in their respective fields of expertise (see the acknowledgments). Because few species have long time series of fisheries-independent data, catch statistics were the most commonly found time series. While fishery data are often subject to biases due to factors such as markets, fads, and misreporting (Ocean Studies Board 2000), in general, the species in our survey were in demand throughout most of the periods of observation.

We analyzed the time series in two ways. First, because of the variety of response variables (abundances, tons, catches per unit effort, recruitment indices), as well as the differences in absolute magnitudes of the variables, we normalized the time series so that the maximum value equals one and the minimum equals zero. These transformed data were then plotted (figure 1) for visual comparisons of trends. Second, because of the uncertainty about the meaning of individual data points (i.e., a peak in a time series in a particular year probably does not correspond to a peak in abundance or even to peak catch per unit effort expended), the untransformed data were smoothed by running averages corresponding to a particular species' generation time, thereby lessening the importance of individual points and emphasizing the trends over the time frame of the data. The slopes of the log transformation of these smoothed time series were computed and used to calculate the percentage change in relative abundance over the period of observation (table 2).

We had an especially rich and long set of American shad landings from the Atlantic States Marine Fisheries Commission (ASMFC 2007) that could be examined for evidence of multiple shifting baselines. These were normalized to the number of river kilometers available for spawning within each river system along the eastern US coast (ASMFC 2007).

## Numbers of populations

For many species, data on historical and present numbers of populations are deficient; the availability of information appears positively associated with their commercial importance. Of the 14 anadromous species for which comparisons

*Table 1. The original reproductive range of North Atlantic diadromous fish species, numbers of original and extant populations, and current highest institutional-level species conservation status.*

| Common name | Latin name | Original reproductive range | Number of original populations | Number of extant populations | Conservation status |
|---|---|---|---|---|---|
| **Western Atlantic** | | | | | |
| Sea lamprey | *Petromyzon marinus* | Florida to New Brunswick | 116 (Beamish 1980) | DD | LC (IUCN 2008) |
| Shortnose sturgeon | *Acipenser brevirostrum* | Florida to New Brunswick | > 20 (NMFS 1988) | About 20 (NMFS 1988) | VU (IUCN 2008) |
| Atlantic sturgeon | *Acipenser oxyrinchus* | Mississippi to Quebec | > 35 (Waldman and Wirgin 1998) | About 35 (Waldman and Wirgin 1998) | NT (IUCN 2008) |
| Alewife | *Alosa pseuodharengus* | South Carolina to Newfoundland | DD | DD | SC (NMFS 2009) |
| Blueback herring | *Alosa aestivalis* | Florida to Nova Scotia | DD | DD | SC (NMFS 2009) |
| Hickory shad | *Alosa mediocris* | Florida to Maine | DD | DD | Status unknown[a] |
| Skipjack herring | *Alosa chrysochloris* | Texas to Florida | DD | DD | Stable (Warren et al. 2000) |
| American shad | *Alosa sapidissima* | Florida to Quebec | 138 (Limburg et al. 2003) | 68 (Limburg et al. 2003) | Lowest in history (ASMFC 2007) |
| Alabama shad | *Alosa alabamae* | Louisiana to Florida | DD | 7 (Mettee and O'Neil 2003) | EN (IUCN 2008) |
| Atlantic whitefish | *Coregonus huntsmani* | Nova Scotia | 2 | 1 | VU (IUCN 2008) |
| Arctic char | *Salvelinus alpinus* | Newfoundland to the Arctic Ocean | DD | DD | LC (IUCN 2008) |
| Atlantic salmon | *Salmo salar* | Connecticut to Quebec | 600 (of which 398 are DD; WWF 2001) | 135 of 202 (WWF 2001) | LR/lc (IUCN 2008); needs updating |
| Rainbow smelt | *Osmerus mordax* | Delaware to Labrador | DD | DD | SC[a] |
| American eel | *Anguilla rostrata* | Brazil to Greenland | 1 (panmictic) | 1 (panmictic) | Highly depleted in Great Lakes drainage |
| Striped bass | *Morone saxatilis* | Louisiana to Quebec | About 50 (Fruge et al. 2006) | < 50 (Fruge et al. 2006) | Not overfished[a] |
| **Eastern Atlantic** | | | | | |
| Sea lamprey | *Petromyzon marinus* | Greenland/Norway to the western Mediterranean | DD | DD | Declining regionally |
| River lamprey | *Lampetra fluviatilis* | Finland to the western Mediterranean | DD | DD | DD (IUCN 2008) |
| European sea sturgeon | *Acipenser sturio* | Baltic Sea to the Black Sea | > 18 (Elvira et al. 2000) | 1 (Elvira et al. 2000) | CR (IUCN 2008) |
| Allis shad | *Alosa alosa* | Spain to Germany | 29 (Bagliniere et al. 2003) | 16 (Bagliniere et al. 2003) | LC (IUCN 2008) |
| Twaite shad | *Alosa fallax* | Morocco to Lithuania | About 35 (Aprahamian et al. 2003) | About 30 (Aprahamian et al. 2003) | LC (IUCN 2008) |
| European eel | *Anguilla anguilla* | Morocco to Scandinavia | 1 (panmictic) | 1 (panmictic) | CR (IUCN 2008) |
| European whitefish | *Coregonus lavaretus* | Arctic Ocean to Denmark | DD | DD | VU (IUCN 2008) |
| Houting | *Coregonus oxyrinchus* | England to Germany | About 4 (Freyhof and Schöter 2005) | 0 (Freyhof and Schöter 2005) | EX (IUCN 2008) |
| Arctic char | *Salvelinus alpinus* | Arctic Ocean to Sweden | DD | DD | See above |
| Atlantic salmon | *Salmo salar* | Portugal to Greenland | 2015 (of which 206 are DD; WWF 2001) | 1809 (of which 1572 are DD; WWF 2001) | See above |
| Sea trout | *Salmo trutta* | Russia to Portugal | DD | DD | LC (IUCN 2008) |
| European smelt | *Osmerus eperlanus* | France to Russia | DD (21 England) (Maitland 2003) | DD (14 England) (Maitland 2003) | LC (IUCN 2008) |

CR, critically endangered; DD, data deficient; EN, endangered; EX, extinct; LC, least concern; LR, lower risk; LR/lc, lower risk taxa that do not qualify for conservation-dependent or near-threatened status; LR/nt, lower risk taxa close to qualifying as vulnerable; NT, near threatened; SC, species of concern; VU, vulnerable.

a. Agency designations by the National Marine Fisheries Service and the Atlantic States Marine Fisheries Commission.

*Note*: Populations are assumed to be reproducing; multiple tributary populations in a single drainage are considered part of one population.

could be made, all have reduced numbers of populations (table 1). Strongly managed North American fishes such as Atlantic sturgeon, shortnose sturgeon (*Acipenser brevirostrum*), and striped bass (*Morone saxatilis*) had lost few populations. Where data allow cross-continental comparisons, Atlantic salmon in Europe have suffered relatively fewer population extirpations (13%) than in North America (33%). Alosine herrings have lost moderate numbers of populations on both sides of the Atlantic, but as much as nearly half for American shad and allis shad (*Alosa alosa*). Anadromous whitefishes

*Table 2. Characteristics of time series data for selected diadromous fishes.*

| Species | Unit of measurement | Maximum value | Year of maximum | Minimum value | Year of minimum | Period of record | Location | Slope | R² of slope | Percentage increase or decrease or (fitted) | Long-term increase or decline | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Eastern Atlantic** | | | | | | | | | | | | |
| Alosa alosa | Abundance | 277,637 | 1886 | 0 | 1933 | 1880–1934 | Rhine River, Netherlands | –0.1519 | 0.87 | –99.94 | D (E) | Bagliniere et al. 2003 |
| Alosa alosa | Abundance | 115,974 | 1925 | 120 | 1988 | 1914–1990 | Minho River, Portugal | –0.0710 | 0.82 | –99.48 | D | Bagliniere et al. 2003 |
| Alosa alosa | Metric tons | 860.7 | 1967 | 0 | 1992 | 1961–1993 | Oued Sebou, Morocco | –0.1326 | 0.92 | –98.13 | D (E) | Bagliniere et al. 2003 |
| Alosa alosa | Abundance | 106,706 | 1996 | 2979 | 2007 | 1985–2007 | Garonne River, France | –0.2195 | 0.93 | –95.37 | D | Migado (www.migado.fr) |
| Alosa fallax | Abundance | 1,174,137 | 1938 | 283 | 1947 | 1893–1950 | Rhine River, Netherlands | –0.5669 (*) | 0.85 | –99.80 | D | de Groot 2002 |
| Anguilla anguilla | Abundance | 48,615 | 1976 | 375 | 2004 | 1975–2005 | Imse River, Norway | –0.1139 | 0.93 | –91.84 | D | EIFAC/ICES 2006 |
| Anguilla anguilla | Kilograms | 8011 | 1953 | 30 | 1998 | 1950–2005 | Swedish eel rivers | –0.0554 | 0.97 | –92.60 | D | EIFAC/ICES 2006 |
| Anguilla anguilla | Kilograms | 6215 | 1960 | 5 | 1997 | 1951–2005 | Ems and Vidå River, Denmark | –0.0673 | 0.72 | –95.48 | D | EIFAC/ICES 2006 |
| Anguilla anguilla | Metric tons | 49.37 | 1979 | 0.88 | 2005 | 1960–2005 | British Isles | –0.0588 (*) | 0.96 | –65.30 | D | EIFAC/ICES 2006 |
| Anguilla anguilla | Number per haul | 138 | 1963 | 0.58 | 2001 | 1950–2005 | Den Oever River, Netherlands | –0.0625 | 0.79 | –94.70 | D | EIFAC/ICES 2006 |
| Anguilla anguilla | Kilograms | 946 | 1974 | 0.831 | 2004 | 1964–2005 | Ijzer River, Belgium | –0.1612 | 0.93 | –99.51 | D | EIFAC/ICES 2006 |
| Anguilla anguilla | Metric tons | 1137 | 1979 | 10.86 | 2005 | 1950–2005 | French rivers | –0.0902 (*) | 0.96 | –88.52 | D | EIFAC/ICES 2006 |
| Anguilla anguilla | Metric tons | 88.89 | 1981 | 0.51 | 2004 | 1953–2005 | Iberian Peninsula | –0.1085 (*) | 0.98 | –90.81 | D | EIFAC/ICES 2006 |
| Anguilla anguilla | Metric tons | 11 | 1975 | 0.02 | 2002 | 1975–2005 | Tiber River, Italy | –0.2121 | 0.82 | –99.06 | D | EIFAC/ICES 2006 |
| Acipenser sturio | Metric tons | 58 | 1950 | 0.11 | 1966 | 1891–1980 | Eider, Gironde, and Guadalquivir Rivers, Europe | –0.2372 (*) | 0.93 | –99.31 | D | Williot et al. 2002 |
| Acipenser spp. | Metric tons | 765.3 | 1927 | 0.5 | 1991 | 1920–1999 | Danube River | –0.0416 | 0.78 | –93.58 | D | Williot et al. 2002 |
| Acipenser spp. | Metric tons | 32,000 | 1977 | 2 | 2002 | 1913–2002 | Ponto–Caspian | –0.077 (*) | 0.92 | –72.99 | D | Williot et al. 2002, Pikitch et al. 2005 |
| Lampetra fluviatilis | Metric tons | 44 | 1890–1899 | 0.6 | 1980–1989 | 1887–1999 | Southern Baltic Sea | –0.0343 | 0.45 | –96.29 | D | Thiel et al. 2005 |
| Petromyzon marinus | Metric tons | 130,252 | 1897 | 84 | 1979 | 1887–1999 | Southern Baltic Sea | –0.0375 | 0.50 | –97.98 | D | Thiel et al. 2005 |
| Lamprey | Scaled relative abundance | 2.2 | 2004 | –0.95 | 1994 | 1986–2005 | Garonne and Adour Rivers, France | 0.0758 | 0.73 | +230 | I | Beaulaton et al. 2008 |
| Salmo salar | Abundance | 5707 | 1928 | 552 | 2000 | 1928–2004 | River Dee, Wales | –0.0206 | 0.69 | –77.31 | D | Aprahamian et al. 2008 |
| Salmo salar | Abundance | 104,000 | 1885 | 0 | 1957 | 1863–1957 | Rhine River, Netherlands | –0.0526 | 0.70 | –98.97 | D | de Groot 2002 |
| Salmo salar | Metric tons | 3032 | 1967 | 912 | 1997 | 1960–2005 | North Europe | –0.0217 | 0.79 | –62.34 | D | WGNAS 2006 |
| Salmo salar | Metric tons | 4604 | 1973 | 778 | 2005 | 1960–2005 | South Europe | –0.0397 | 0.86 | –83.25 | D | WGNAS 2006 |
| Salmo salar | Metric tons | 160 | 1971 | 9 | 2002 | 1960–2005 | Faroes and Greenland | –0.1736 (*) | 0.89 | –99.81 | D | WGNAS 2006 |
| Salmo trutta | Abundance | 25,244 | 2004 | 5096 | 1987 | 1987–2007 | Iceland | 0.0439 | 0.93 | +220 | I | Gudbergsson 2007 |

**Table 2. (continued)**

| Species | Unit of measurement | Maximum value | Year of maximum | Minimum value | Year of minimum | Period of record | Location | Slope | R² of slope | Percentage increase or decrease or (fitted) | Long–term increase or decline | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Western Atlantic** | | | | | | | | | | | | |
| Acipenser oxyrinchus | Metric tons | 3294 | 1888 | 6 | 1924 | 1880–1994 | North America | −0.0239 | 0.28 | −91.05 | D | Kahnle et al. 2007 |
| Alosa sapidissima | Metric tons | 22,408 | 1814 | 18 | 1892 | 1814–2005 | North America | −0.0189 | 0.67 | −97.14 | D | ASMFC 2007 |
| Alosa pseudo-harengus | Metric tons | 16,148 | 1958 | 7.5 | 2006 | 1950–2006 | North America | −0.0829 | 0.86 | −98.76 | D | NOAA Fisheries statistics |
| Alosa aestivalis | Metric tons | 23,800 | 1969 | 109.9 | 2006 | 1950–2006 | North America | −0.0963 | 0.90 | −99.39 | D | NOAA Fisheries statistics |
| Alosa mediocris | Metric tons | 303.8 | 1952 | 5.6 | 1990 | 1950–2006 | North America | −0.0323 | 0.36 | −81.95 | D | NOAA Fisheries statistics |
| Anguilla rostrata | Metric tons | 1792.6 | 1979 | 290.9 | 2002 | 1950–2006 | North America | −0.0533 (*) | 0.99 | −72.20 | D | NOAA Fisheries statistics |
| Osmerus mordax | Metric tons | 163 | 1966 | 0.1 | 1997 | 1950–2004 | North America | −0.0852 | 0.67 | −99.08 | D | NOAA Fisheries statistics |
| Salmo salar | Metric tons | 2864 | 1967 | 132 | 2005 | 1960–2005 | North America | −0.0736 | 0.82 | −96.36 | D | WGNAS 2006 |
| Morone saxatilis | Metric tons | 6704 | 1973 | 100 | 1989 | 1950–2006 | North America | 0.1635 | 0.85 | +1,368 | I | NOAA Fisheries statistics |

D, decline; E, extirpated; I, increase.
*Note:* Slopes were calculated from normalized data that had been smoothed with running averages corresponding to generation times, and then log-transferred. Generation times: alosines, salmons, and brown trout, 4 years; smelt, 2 years; striped bass, 6 years; lampreys, 9 years; eels, 10 years; sturgeons, 15 years. Slopes with an asterisk (*) indicate that they were calculated after a clear peak or nadir (e.g., after a "fishing up" period or following a collapse and subsequent recovery). Percentage increase or decrease is calculated with the fitted slope, and include the most recent years in the time series. Type of record was catch for all species except *Alosa alosa* (fish passage), *Anguilla anguilla* (recruitment index), and lamprey (fishery).

(*Coregonus* spp.) are in perilous condition: Only a small and now purposely landlocked population of *Coregonus huntsmani* persists in Nova Scotia and a European species, *Coregonus oxyrinchus*, has become extinct (Freyhof and Schöter 2005). Also, sea sturgeon (*Acipenser sturio*), once found in as many as 18 major rivers over much of Europe, now verges on extinction, remaining only as a small, struggling population in France's Gironde River (Williot et al. 2002).

## Abundances of populations

Although some anadromous species have suffered numerous extirpations, the predominant pattern among these fishes has been for continuation of runs, but at drastically reduced levels that may be trending to inviability, as low as about 100 individuals for shortnose sturgeon in two populations (Kynard 1997). These declines have also been manifested—often profoundly so, especially with many long-exploited fish populations—in reduced biomass, age distributions, age at maturity, and maximum size and growth (Law 2007).

The length and quality of time series data sets vary, but the trend is nearly always the same: Diadromous fishes have declined, often to historic lows (figure 1, table 2). Of the 35 species or stocks for which we were able to obtain time series data sets, 32 had declined and only 3 had increased (table 2). Where long-term records exist, losses from baseline levels are often dramatic. American shad offers a good example, as data on the Potomac River date back to 1814, but the baseline for restoration efforts is derived from US Fisheries Commission records, which began in 1887 (figure 2a). The highest catch (51,136,364 kg) occurred in 1832 (figure 2b; Massman 1961). The Potomac could produce more than 22 million shad (3 kg in weight and 0.9 meters [m] in length, on average, versus approximately 1.8 kg and 0.5 m today) "in a good year" (Tilp 1978); today, only a minor recreational fishery persists there. Time series of American shad landings (normalized to kilometers of available river or estuary) for 10 major producing areas show a long-term exponential decline with a slope of −0.035 per year with all the data ($R^2 = 0.33$, $p < 10^{-5}$), or −0.033 per year if the early Potomac landings are excluded ($R^2 = 0.26$, $p < 10^{-5}$).

Comparisons of landings between diadromous fish taxon pairs from both sides of the Atlantic often show similar patterns (figure 1). These include moderate to sharp declines in the 1900s (some with occasional short-term recoveries), followed by low harvests or a mandated cessation of fishing, that continue to the present. Not only do most diadromous species exhibit precipitous declines over time, but the differences between maximum levels and recent
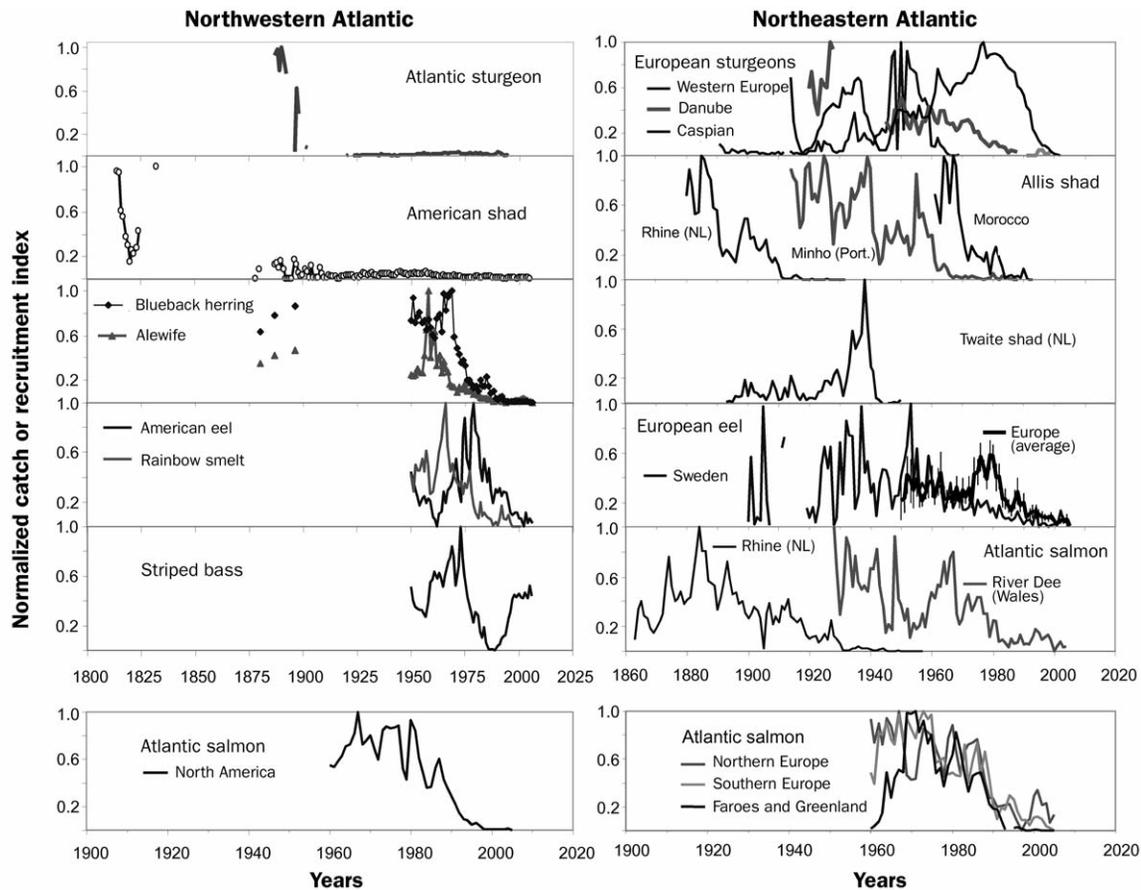
*Figure 1. Normalized time series of indices of abundance of selected north Atlantic diadromous species. European eel includes standard errors of means for nine regions. The lower two panels compare Atlantic salmon. For type of index, maxima, minima, percentage change, and data sources, see table 2. Unless otherwise stated, northwestern Atlantic data are US summary statistics.*

ones are even greater than what has been observed in many obligate marine species. Thirteen of the 35 time series in table 2 had declined by more than 98%; another 11 had declined by more than 90%. The few exceptions include the coastal migratory stock of striped bass, northern European populations of Atlantic salmon, and Icelandic populations of sea-run brown trout (*Salmo trutta*). This last example shows a marked increase in records over the smoothed observation period (1991–2007), and may be attributable to a true increase in population or an increase in sport fishing, or both (Gudbergsson 2007).

## Conservation status

We believe the conservation status of anadromous fishes integrates knowledge of population persistence, abundance, and threats. Of the 12 exclusively North American species, the International Union for the Conservation of Nature (IUCN) Red List classifies 1 as endangered and 2 as vulnerable; the National Marine Fisheries Service lists 3 others as species of concern; and the ASMFC rates 1 more as having its lowest abundance in history, and is in the process of assessing 2 more species that are also likely at historic lows. Of the

9 eastern Atlantic species, 1 has gone extinct, 2 are now critically endangered (including the once abundant European eel), 1 is vulnerable, and 2 are listed by the IUCN as data deficient (table 1). At least one (*A. alosa*) appears to be in serious decline, although noted as "least concern" by the IUCN. Of the pan-Atlantic salmonids (Atlantic salmon and arctic char, *Salvelinus alpinus*), wild *S. salar* is at historic lows in North America, and overall, its status is in need of updating (IUCN 2008).

## Threats

North Atlantic diadromous fishes must navigate a gauntlet of threats. The primary triad that affects most taxa is damming of rivers, overfishing, and pollution. However, there are now a host of threats beyond the three that have long been considered primary.

**Dams and other habitat losses.** Industrialization depended on rivers for water power, and many waterways became multiply dissected with dams. Dams often block access to historical spawning reaches, causing population reductions and extirpations. Few larger rivers remain undammed: It is estimated
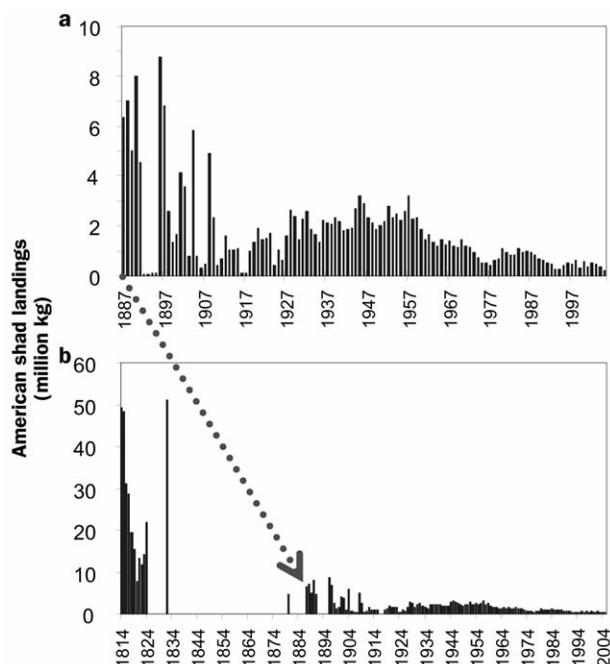
*Figure 2. Example of how baselines shift. (a) Baseline for American shad restoration is typically referenced to 1887, when the US Fishery Commission began to collect statistics. (b) Earlier data show that levels for the 1887 baseline are considerably lower than they were in the past. Source: ASMFC (2007).*

that in the United States alone, there are more than 80,000 dams of 6 feet in height or more, and perhaps as many as 2,000,000 of all sizes (Graf 2003). For example, within the Hudson River watershed there are 797 registered dams (Swaney et al. 2006); that figure does not include small dams (< 0.6 m tall), which also can hinder migration. In Spain, some dams have blocked fish movements continuously since the 2nd century, and the nations of Europe together have about 7000 large (more than 15 m) dams, most of which are situated on Atlantic drainages. Engineered solutions to fish passage in the form of ladders and lifts have been fitted to some dams, but generally passage is species specific, and the number of fish traveling through them is far fewer than it would be in the absence of dams; these dams also inhibit downstream migration of young. One useful metric of the effect of dams is the number of kilometers of river they occlude to migrants. For American shad, approximately 4000 of an original 11,200 km of spawning habitat have been lost to dams (Limburg et al. 2003); these dams have similar effects on other anadromous species.

Dams also have numerous other ecological effects on rivers, many of which may affect diadromous fishes directly or indirectly. Among these are the blocking of normal movements and changes in the community composition of resident fishes that interact with diadromous fishes; microevolution of populations isolated by barriers; pronounced alterations of water temperatures upriver and downriver; retention of

nutrients and sediments; and, even where fish passage is successful, the imposition of the need to cross sometimes large, unnatural stillwater habitats (Helfman 2007). Dams that are operated for hydropower also cause direct mortality (death by turbines) and may radically alter water discharges (Helfman 2007)—and hence, habitat availability (water or no water)—on daily or even hourly timescales.

In addition to the large habitat changes wrought by dams, dredging and channelization may cause short-term stresses while these activities occur and, more important, long-term diminution of habitat quality through the changes they create. Culverts impede fish movements by species such as river herring in smaller systems. Gravel and water removals reduce habitat in many waterways. Because many anadromous fishes use rivers as nurseries, reductions in the extent and quality of marshes and other shallow water habitats may lessen productivity and, therefore, recruitment.

**Overfishing.** Harvest has strongly compromised diadromous fish populations. Atlantic sturgeon were taken at an extraordinary rate during the international caviar craze of the 1890s (Secor and Waldman 1999); with continued fishing and their low intrinsic rate of increase, many populations have shown little subsequent recovery, despite greater protection. In the Delaware River, the chief US fishery for Atlantic sturgeon, landings in 1901 were only 6% of their 1889 peak of more than 2000 metric tons (Secor and Waldman 1999). Atlantic sturgeon remain so scarce in the Delaware that it is not known whether any reproduction still occurs there.

Overfishing is a major factor in the nearly complete demise of the once-widespread European sea sturgeon (Williot et al. 2002). Extirpations led to a range contraction to just the Gironde estuary in France, and even when fishing was halted there in 1982, the population continued to decline. Despite regulatory protection, accidental bycatch threatens sturgeons on both the American and European coasts.

Alewives were once so numerous in northeastern US rivers that they were likened to "passenger pigeons of the sea" (Bolster 2006); their numbers have since plummeted, and several states have banned any takings. Runs in several large rivers from Maine to the Chesapeake Bay have declined by 99.9%; for example, at the Holyoke Dam on the Connecticut River, counts went from approximately 630,000 in 1985 to 21 in 2006. Bycatch at sea is one likely contributor, as subadults are taken along with the targeted Atlantic herring (*Clupea harengus*) fisheries. Another alosine that appears to be undergoing a similar collapse because of recruitment overfishing is the allis shad; juvenile recruitment in the Gironde, the center of its range, has been negligible for the past few years.

Extensive analysis of decadal trends in eel fisheries suggests that exploitation is a major factor in European eel decline (Dekker 2004), with many fisheries collapsed. Eels are targeted not only as immature (yellow phase, in lakes and running waters) or adolescent (silver phase, migrating toward the Sargasso Sea to spawn) but also as postlarval glass eels entering continental waters. The highly lucrative glass eel fishery is

driven by demand in Southeast Asia, where imported American and European glass eels are pond-reared to market size. Glass eel fisheries sometimes harvest all available individuals at a particular locale, but in general the harvest has been 80% to 95% (Dekker 2004), which is still an alarming statistic.

**Pollution.** Water pollution also has reduced runs of diadromous fishes. Some river systems received so much raw or lightly treated human sewage—which induced low oxygen levels—that they became equivalent to "chemical dams" blocking spawning migrations. Examples include the Thames in the United Kingdom and the Delaware River in the United States (Chittenden 1971); however, both rivers have shown dramatic improvements as a result of new laws and management actions. Over the past few decades, shortnose sturgeon has made an unusually robust recovery in the Hudson River not only because of its placement on the US endangered species list but also because the population's original spawning location near the head of tidewater was reoxygenated through measures to control sewage, which stemmed from the Clean Water Act of 1972 (Waldman 2006). However, late 20th-century exurbanization (sprawl development) has led to more impervious surface cover in many drainage basins, further altering water quantity and quality.

Contaminants such as polychlorinated biphenyls (PCBs), polycyclic aromatic hydrocarbons, and heavy metals may induce difficult-to-quantify sublethal effects in fishes in riverine environments. Highly biomagnified levels of PCBs in boreal regions are causing concerns for Artic char. Laboratory experiments with Arctic char have shown that these compounds impair hypo-osmoregulatory ability and reduce growth rate and survival upon transfer to seawater (Jørgensen et al. 2004). Also, European and American eel reproduction may be compromised by fat-soluble, teratogenic organic compounds (Palstra et al. 2006), which are translocated into developing embryos from maternal lipid stores.

Acidification from atmospheric deposition of contaminants has been devastating for some Atlantic salmon stocks. In Norway, 18 populations are extirpated and 8 more are threatened, with others sustained only by liming rivers to raise pH (Sandøy and Langåker 2001).

**Climate change.** Climate change is altering species distributions. The boreal rainbow smelt *Osmerus mordax,* which in the 1880s ran in US rivers as far south as the Delaware, was extirpated from the Hudson in the 1990s (Waldman 2006) and is becoming scarce everywhere south of Maine. Meanwhile, gizzard shad (*Dorosoma cepedianum*), a euryhaline clupeid of no commercial value and uncertain ecological effects, has been colonizing rivers northward, establishing in large numbers in the Hudson in the 1970s and recently reaching as far as Maine (Waldman 2006).

Warming also appears to be shifting the phenologies of anadromous fishes towards earlier spawning runs. Monitoring in Maine revealed that the median capture date for Atlantic salmon in the Penobscot River advanced by 1.3 days per year

between 1986 and 2001, and by 1.2 days per year between 1983 and 2001 for alewife in the Androscoggin River (Huntington et al. 2003). The consequences of such acceleration are unknown, but the rapidity of the change has the potential to disrupt these fishes' established ecological relationships at various life history stages.

In the future, warming may intensify the severity of floods and droughts, lessening the frequency of successful annual reproduction for anadromous fishes. In Europe, models predict that, collectively, 22 species will lose 336 suitable catchments and gain only 113 as a result of the most likely climate change scenario (Lassalle and Rochard 2009). The Gulf sturgeon (*Acipenser oxyrinchus desotoi*) depends on limited numbers of cool thermal springs to survive hot summer temperatures in Gulf of Mexico rivers (Carr et al. 1996); warming may impose even greater stresses on this scarce and federally threatened subspecies.

Warming will also impose complex and difficult-to-forecast shifts in the relationships between freshwater and saltwater habitats. Both American and European eels have evolved to capitalize on the transport and trophic resources of the Gulf Stream. However, the recent effects of climate change on this current may be contributing to the declines seen in both eel species in freshwaters (Wirth and Bernatchez 2003). In Arctic regions, warming may increase the productivity of inshore marine habitats used by anadromous fishes, but this may be counterbalanced by decreased flows in spawning rivers. Increased productivity of inland waters may also reduce facultative anadromy for plastic species such as Arctic char, with higher proportions of populations opting for freshwater residency (Reist et al. 2006).

### Other threats

Electric generating plants and other facilities that withdraw water from rivers may kill high numbers of early life stages of diadromous fishes through entrainment and by impinging larger individuals against intake screens; power plants may also alter local temperature regimes though discharges of warm water (Barnthouse et al. 1988). Disease, competition, and genetic introgression with escapees from aquacultured Atlantic salmon threaten wild stocks in northeastern North America and Scandinavia (Naylor et al. 2005). Progeny of Atlantic sturgeon used in experimental culture have been opportunistically stocked in the wild (St. Pierre 1999) while ignoring protocols for the maintenance of appropriate effective population sizes. Similarly, research-culture escapees of a nonnative sturgeon species now compete in the Gironde with the few remaining sea sturgeon (Maury-Brachet and Rochard 2008). Many invasive and nonnative species also disrupt lotic ecology. Introduction of black bass (*Micropterus* spp.) and other piscivores increased the predation regime for juvenile alosines and other young diadromous fishes in US rivers. Invasive zebra mussels (*Dreissena polymorpha*) have altered the Hudson River's spring production cycle, to the detriment of its alosines (Strayer et al. 2004).

## Conclusions

Few of the North Atlantic's diadromous fishes face any of the abovementioned threats in isolation; rather, it is likely that reasons for the losses we have outlined are multifactorial, and possibly synergistic. Many of these declines have been steady and insidious, fitting well into the "shifting baselines" paradigm, whereby new generations of managers accept that recent environmental conditions and levels of species reflect historical conditions and levels, and set restoration goals accordingly (Humphries and Winemiller 2008, Waldman 2008). Loss of historical baselines contributes to marginalization of the species, as social customs relating to bygone (collapsed) fisheries also perish, and ecosystems unravel at rates that go unnoticed.

Especially troublesome is the outright loss of many populations and their genetic legacies in the face of changing environments. The high phylogenetic diversity of these 24 species and the differences in life histories, geographic ranges, and commercial values conspire to make generalized solutions impossible. There is a strong need for better information on the population-specific status of many species of low commercial interest. Harvests of some species have been reduced and moratoria have even been applied, but usually not until abundances had become dangerously low. Atlantic coast populations of migratory striped bass are one of the few successful recoveries for an anadromous species, but the severe measures needed to generate this recovery were not taken until the stock fell to crisis levels (Richards and Rago 1999). Even with moratoria, populations may fail to recover (e.g., *A. sturio* in the Gironde, *A. sapidissima* in Chesapeake Bay), suggesting changes occurring systemwide are collectively hindering recovery.

Fishermen and other stakeholders need to elevate their long-term interests in a species' welfare over their own short-term economic interests, with the understanding that the more the populations are fished, the less the likelihood of recovery (and the lengthier the period of recovery), and hence the more damage to the future sustainability of the fishery. A laudatory example of an early intervention is the moratorium imposed in late 1997 on Atlantic sturgeon fishing in US waters in response to indications that some populations were rapidly declining because of suddenly increased fishing pressure (Waldman 2006). Almost exactly a century after the international caviar craze left many US stocks sharply reduced or decimated, the few remaining commercial Atlantic sturgeon fishermen acquiesced to an ambitious protection plan that prohibits their take for up to 40 years—two generations for this slowly maturing species.

The environmental movement has resulted in a reduction of new sources of pollution in the United States and Europe, but many rivers still have a legacy of contaminants produced from the Industrial Revolution through the mid-1900s. Although cleanup actions have been helpful for some species in some places, the single broadest and most useful recovery action has been to remove dams wherever possible. This is especially true for large mainstem dams. For example, when the Edwards Dam on Maine's Kennebec River was removed in 1999, the benefits to the full suite of this river's diadromous fishes were almost immediately visible as the fishes reoccupied their historical spawning grounds. Where dams cannot be removed, it is far preferable to install fish passage devices, despite their flaws, than to impede the movements of all diadromous fishes in a river. Research to enable passage of anadromous species that shun conventional fish ladders, such as sturgeons, should also be encouraged.

Viewed collectively, North Atlantic diadromous species underwent similar sequences of events that led to their declines (figure 3). Although quantitative data are largely lacking, anecdotal evidence from diaries, journals, and other historical accounts suggests that pristine populations of diadromous fishes were staggering in their plenitude (Waldman 2008), and formed the basis of important fisheries. Gradually, some populations became extirpated, but the pace of extirpations through the mid-20th century was slow enough to forestall great alarm (but note that overfishing of American shad in the 19th century spurred concerted management efforts).

The cumulative impacts resulted in declines, but these declines in themselves have had another unintended consequence: namely, a loss of standing or "saliency" among issues considered important by society at large. As species became scarce, fisheries declined, and often demand dropped off. Other watershed uses gained prominence. As demand dwindles and constituencies are lost, it becomes increasingly difficult to motivate and secure funding for adequate management and restoration measures. This downward spiral of
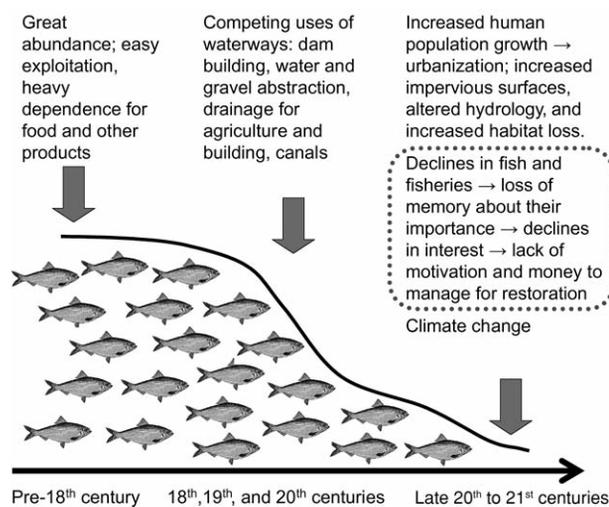


*Figure 3. Conceptual diagram of the general history and factors leading to declines in North Atlantic diadromous species. Most species were heavily exploited before industrialization and physical alteration of waterways; further watershed alterations due to human population expansion and climate change increased habitat loss. Gradually, the declines also led to the loss of institutional and societal memory about past abundance and importance (outlined for emphasis).*

events lacks a term, but we suggest that it is a kind of *ecosocial anomie,* a breakdown both of expectations of what species should be present in healthy populations, and societal loss of interest. The result is not only the loss of populations and species but also the loss of services the species provided when their inland ecosystems were more intact.

The stories of individual stocks that perished or are commercially extinct are numerous, but it is clear that the diminishment of diadromous fishes, taken as a group, represents one of the greatest corruptions of the ecological connections between North American and European watersheds and the North Atlantic ecosystem. Although management needs to consider the specifics of each species and population, the causes of decline we have outlined appear to be general and widespread. If there is to be a future for this group, societies must make difficult decisions concerning the trade-offs between maintaining healthy populations within healthy ecosystems and taking actions that degrade and imperil those systems. The emerging field of ecosystem service quantification may provide a means to enhance restoration, since it highlights those services that depend on ecosystem function as well as provisioning services. If ecosystem service quantification becomes mainstreamed (Cowling et al. 2008), local and regional decisionmaking would have an alternative to conventional cost-benefit schemes. These alternatives would support ecosystem and habitat restoration. It may take decades to bring back diadromous species, but restoring the watersheds and their connectivity with coastal marine ecosystems is a critical first step in that direction.

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*Karin E. Limburg (klimburg@esf.edu) is an associate professor at the College of Environmental Science and Forestry, State University of New York, Syracuse. John R. Waldman (john.waldman@qc.cuny.edu) is a professor of biology at Queens College, City University of New York, Flushing.*