

ARTICLE

A Review of River Herring Science in Support of Species Conservation and Ecosystem Restoration

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Abstract

River herring—a collective name for the Alewife *Alosa pseudoharengus* and Blueback Herring *A. aestivalis*—play a crucial role in freshwater and marine ecosystems along the Eastern Seaboard of North America. River herring are anadromous and return to freshwater habitats in the tens to hundreds of millions to spawn, supplying food to many species and providing nutrients to freshwater ecosystems. After two and a half centuries of habitat loss, habitat degradation, and overfishing, river herring are at historic lows. In 2013, National Oceanic and Atmospheric Administration Fisheries established the Technical Expert Working Group (TEWG) to synthesize information about river herring and to provide recommendations to advance the science related to their restoration. This paper was composed largely by the chairs of the TEWG subgroups and represents a review of the current state of knowledge of river herring, with an emphasis on identification of threats and discussion of recent research and management actions related to understanding and reducing these threats. Important research needs are then identified and discussed. Finally, current knowledge is synthesized, considering the relative importance of different threats. This synthesis identifies dam removal and increased stream connectivity as critical to river herring restoration. Better understanding and accounting for predation, climate change, and fisheries are also important for restoration. Finally, there is recent evidence that the effects of human development and contamination on habitat quality may be more important threats than previously recognized. Given the range of threats, an ecosystem approach is needed to be successful with river herring restoration. To facilitate this ecosystem approach, collaborative forums such as the TEWG (renamed the Atlantic Coast River Herring Collaborative Forum in 2020) are needed to share and synthesize information among river herring managers, researchers, and community groups from across the species' range.

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Socioecological Setting

River herring are intertwined with the human experience along the Atlantic seaboard of North America as a result of their historically high abundance, wide distribution, and anadromous life history (Waldman 2013; Bassett 2015). The term “river herring” refers to two species that are similar in appearance and ecology: the Alewife *Alosa pseudoharengus* and Blueback Herring *Alosa aestivalis*. Adults of both species undertake coastwide marine migrations and return to freshwater to spawn in the spring (Loesch 1987; Figure 1).

These two species contribute to a number of important ecosystem services (Figure 2), which are defined as the benefit people derive from functioning ecosystems (Costanza et al. 2017). The Millennium Ecosystem Assessment (2005) delineated four categories of benefit: provisioning, cultural, regulating, and supporting; river herring contribute to all four. Provisioning services are material benefits from ecosystems. Fisheries for river herring have supported human populations for hundreds of years, providing food, fertilizer, and bait (Goode 1880; Waldman 2013). Cultural services are nonmaterial benefits from ecosystems, including aesthetic and spiritual value. River herring are culturally important to a number of Native American tribes (Bassett 2015), and runs of adults into freshwater spawning habitats are celebrated in communities along the East Coast of North America (Hay 1959; Waldman 2013). Public engagement in conservation

activities also provides an appreciation for the role of river herring in ecosystems (Frank et al. 2009), and these activities can have value on par with provisioning services from marine resources (Roman et al. 2018). Regulating services influence or control ecosystem processes. As predators, river herring can exert control over prey populations in freshwater and potentially marine environments and therefore regulate food web structure and function (Brooks and Dodson 1965; Pothoven et al. 2007; Palkovacs and Post 2009). Supporting services allow an ecosystem to provide the other three services. River herring are important prey species and, thus, support other species—fish, mammals, and birds—and the ecosystem services these species provide (Yako et al. 2000; Ames and Lichter 2009; Jones et al. 2010). In addition, river herring may act as a predator buffer for the endangered Atlantic Salmon *Salmo salar*, supporting conservation goals for another species (sensu LaCroix et al. 2009). River herring also serve as a conduit for nutrients between freshwater and marine environments (Walters et al. 2009; Barber et al. 2018; Samways et al. 2018).

The concept of ecosystem services facilitates explicit consideration of trade-offs among various human activities, which is a central element of ecosystem-based management (Dolan et al. 2016). Throughout the 18th, 19th, and 20th centuries, dam building, habitat degradation, and overfishing contributed to the decline of river herring (Belding 1921; Waldman 2013); the impacts of these

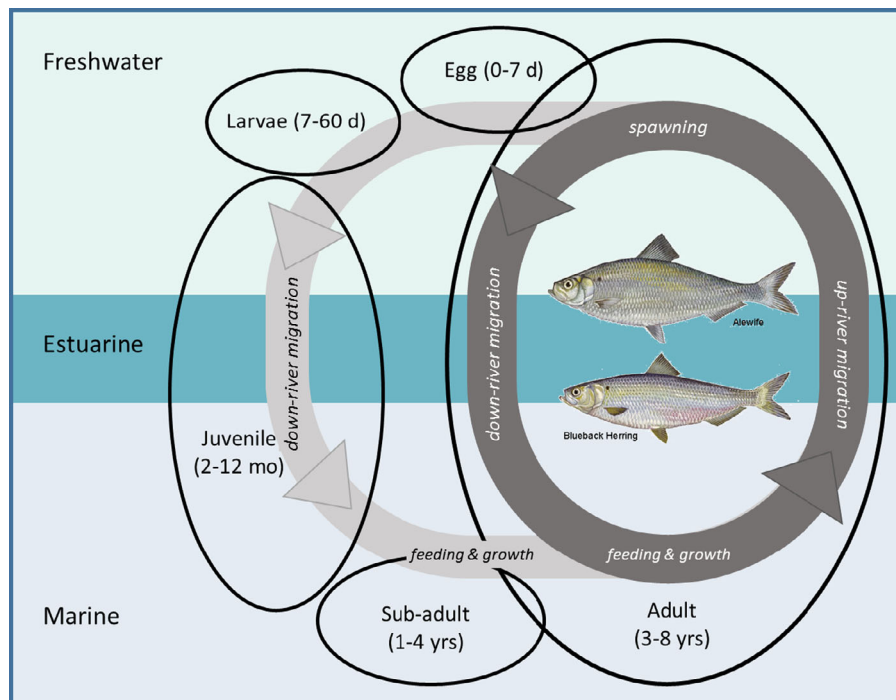


FIGURE 1. Conceptual life history of river herring, showing life stages, life stage durations, major life events, and habitats used.

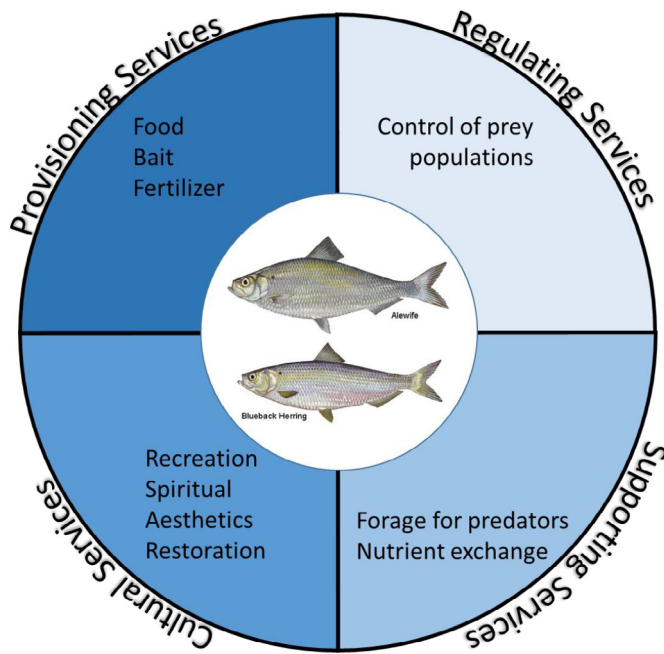


FIGURE 2. River herring from an ecosystem services perspective.

declines on the provisioning services of harvest were well recognized, while the impacts on other ecosystem services provided by river herring were unknown or not considered. In the 21st century, we recognize—but do not always value—ecosystem services beyond provisioning. Recent work, for example, suggests that the non-use value of river herring restoration related to ecosystem health exceeds the value of direct benefits, such as improved fishing opportunities (Johnston et al. 2011, 2012). However, it is still difficult to include the range of ecosystem services in management decisions (Holmlund and Hammer 1999; Johnston et al. 2017).

Management Setting

Most, if not all, anadromous species in eastern North America have declined in abundance since European colonization (Limburg and Waldman 2009). This multispecies, coastwide pattern suggests that large-scale, pervasive factors are responsible for the declines, including dams, habitat degradation, and overfishing. These factors have long been recognized, and states and localities began enacting management measures as early as the 1700s (Belding 1921; ASMFC 2017a, 2017b).

Federal fisheries management started in 1976 with the passage of the Magnuson–Stevens Fisheries Management and Conservation Act. The act established a 370-km (200-nautical mile) Exclusive Economic Zone that excluded foreign fishing fleets, which had been catching large amounts of many species, including river herring (Saila et al. 1972). Management actions directed at river herring started in

1985, with the implementation of the fishery management plan for American Shad *Alosa sapidissima* and river herring by the Atlantic States Marine Fisheries Commission (ASMFC 1985). Even with these management actions, river herring continued to decline, and in 1994 the ASMFC determined that the existing fishery management plan was no longer adequate for protecting or restoring the remaining river herring stocks. Amendment 1 to the fishery management plan was adopted in 1998 and recommended fishery-dependent and fishery-independent monitoring programs for river herring to improve stock assessment capabilities (ASMFC 1999).

Fisheries management efforts intensified in the 2000s. Several state-specific closures of targeted fisheries were initiated in the early 2000s, and in 2009 the ASMFC approved Amendment 2 to the shad and river herring fishery management plan (ASMFC 2009), which prohibited targeted commercial and recreational fisheries in state waters beginning on January 1, 2012, unless a state or jurisdiction had an approved sustainable management plan (ASMFC 2009). Amendment 2 also required states to implement fisheries-dependent and fisheries-independent monitoring programs and contained recommendations to conserve, restore, and protect important river herring habitat. Despite these actions, stocks generally remain at historically low levels.

At the U.S. federal level, the National Marine Fisheries Service (National Oceanic and Atmospheric Administration [NOAA] Fisheries) included the Alewife and Blueback Herring as species of concern in 2006 (NMFS 2006). This designation signals attention to the status of and threats to river herring but does not carry the procedural or substantive protections given to species formally listed under the Endangered Species Act. Several threats were identified that most likely contributed to the decline of river herring in the species of concern determination, including fishing, the construction of dams or other impediments to anadromous migrations, habitat degradation, and increased predation due to increasing populations of Striped Bass *Morone saxatilis*.

In 2011, NOAA Fisheries was petitioned under the Endangered Species Act to list river herring as threatened species throughout all or part of the species' range (NMFS 2011). A status review conducted by NOAA Fisheries determined that listing was not warranted (NMFS 2013). As a follow-up to the listing determination, NOAA Fisheries partnered with the ASMFC in forming the River Herring Technical Expert Working Group (TEWG) to better address the complexity of issues affecting river herring in the USA and Canada. The information identified by the TEWG and the public informed the initial River Herring Conservation Plan, which was released by NOAA Fisheries and ASMFC in May 2015. The goal of the conservation plan is to increase public awareness and foster

cooperative research and conservation efforts to restore river herring along the Atlantic coast. The TEWG continues to meet on a biannual basis to bring together diverse river herring interests, support the exchange of information, and promote collaboration. To better reflect its present-day function, the TEWG was renamed the Atlantic Coast River Herring Collaborative Forum in 2020.

The 2013 listing decision was challenged, and NOAA Fisheries was court-ordered to conduct a new Blueback Herring status review and determination. National Oceanic and Atmospheric Administration Fisheries initiated a second status review for both Alewives and Blueback Herring (NMFS 2017). The status review identified four Alewife distinct population segments (DPSs): Canada, Northern New England, Southern New England, and Mid-Atlantic (NMFS 2019c). Three Blueback Herring DPSs were also identified: Canada/Northern New England, Mid-Atlantic, and Southern Atlantic. Based on the best scientific information available, NOAA Fisheries found that listing was not warranted for either species or for any of the identified DPSs (NMFS 2019a). This decision has been challenged by the plaintiffs, and NOAA Fisheries filed its answer to the complaint on July 13, 2020.

In addition to the considerations under the Endangered Species Act, efforts have also been made at the Regional Fishery Management Councils to conserve river herring during the operation of fisheries in federal waters. The councils operate under the Magnuson–Stevens Fishery Management and Conservation Act, and proposals have been made to include river herring as a “stock in a fishery,” which would result in direct management in federal waters like other Regional Fishery Management Council-managed species. River herring have not been added as a “stock in a fishery”; both the New England and Mid-Atlantic Fishery Management Councils have decided that primary management by the ASMFC is appropriate. However, both councils have established combined incidental catch limits of river herring, American Shad, and Hickory Shad *Alosa mediocris* in the Atlantic Herring *Clupea harengus* and Atlantic Mackerel *Scomber scombrus* fisheries (NMFS 2014a, 2014b).

There have been similar concerns about the status of river herring in Canada, where the two species are harvested together as “gaspereau” (Gibson et al. 2017). Declines in river herring harvest in the Gaspereau River in the late 1970s prompted stock assessments and management actions. The declines abated, but the populations have not increased (McIntyre et al. 2007). A decrease in exploitation rates has been the primary management action used to address the observed population declines (Gibson et al. 2017). The status of river herring in the Canadian Maritimes is not well known and has not been regularly assessed (Gibson et al. 2017). Neither species of river

herring is currently listed under the Canadian Species at Risk Act. Canadian river herring fishery management is a consultative process involving advisory committees, formal science advice, and input from Indigenous groups. Regulations are variable by region and consist of limited entry, seasonal and intra-week closures, gear restrictions, and area restrictions. Key Canadian fishery management concerns include enforcement, over-capacity in some areas, demands for increased access for bait from fishers holding licenses for other species (e.g., lobsters and groundfish), and addressing Indigenous rights to fishing (Gibson et al. 2017).

The factors determining the dynamics of river herring abundance are complex and still being researched despite a long history of cultural importance, harvest, and study. Numerous threats and issues across multiple scales affect river herring population dynamics (Table 1). Fisheries management (e.g., incidental catch caps; harvest limits) focuses on the provisioning services of fishing and balancing harvest with the sustainability of the resource. Listing under the Endangered Species Act or the Species at Risk Act and other processes (e.g., focused efforts, such as the TEWG) recognize intrinsic value: in an ecosystem services context, protection may yield more value than alternatives (Costanza et al. 2017). Given the complexity of the anadromous life cycle, the diversity of threats, and the numerous contributions to ecosystem services, there is a need for comprehensive science and management to restore and maintain healthy river herring populations. Efforts are needed across the freshwater, estuarine, and marine continuum, entailing local, state, tribal, federal, and international coordination. Furthermore, there is a clear need for additional research into the factors that affect population abundance and there is a need to synthesize what is known. New research and synthesis of existing research can be used to inform future management.

Objectives

Our purpose here is threefold: (1) to synthesize current knowledge of the status and trends of anadromous river herring in a holistic-ecosystem context, (2) to identify research needs relative to river herring ecology and restoration, and (3) to synthesize the information related to threats in an ecosystem context. Our focus is on research that has been completed since the development of the TEWG in 2013, but we include informative earlier studies. Our emphasis is on river herring in New England and the mid-Atlantic USA, where much of the recent river herring work has been completed. Where available, we include research in Canada and the southeastern USA as well as research on related species when it is seminal and relevant. Finally, we include information on landlocked populations when relevant to the status of, trends in, and threats to anadromous river herring.

TABLE 1. Qualitative ranking of threats for Alewives and Blueback Herring rangewide from the 2019 status review (NMFS 2019c). Threats were scored by status review team members using five likelihood points in the following bins: 1 = very low, 2 = low, 3 = medium, 4 = high, and 5 = very high. Values represent the mean of scores provided by the status review team. Threats with scores over 2.5 for one or both species are shaded to emphasize more significant threats.

Listing factor	Threat	Alewife	Blueback Herring
The present or threatened destruction, modification, or curtailment of habitat or range	Climate variability	2.4	2.1
	Climate vulnerability	2.6	2.5
	Dams/other barriers	2.9	3.1
	Dredging/channelization	1.5	2.2
	Water quality	2.8	2.9
	Water withdrawal	3.2	2.9
	Overutilization for commercial, recreational, scientific, or educational purposes	Directed commercial harvest	1.7
Incidental catch		2.5	2.4
Recreational harvest		1.5	1.5
Scientific research		1.0	1.0
Educational		1.0	1.0
Disease or predation	Disease	1.5	1.7
	Predation	1.8	1.8
Inadequacy of existing regulatory mechanisms	International regulations	2.1	2.0
	Federal regulations	2.6	2.6
	State regulations	2.5	2.7
Other natural or man-made factors	Competition	1.4	1.5
	Artificial propagation	1.2	1.3
	Hybrids	1.1	1.0
	Landlocked populations	1.0	1.0

The TEWG consisted of multiple subgroups. The Stock Status subgroup considered the status of stocks rangewide and discussed methodologies to quantitatively assess river herring populations (e.g., consider data-poor approaches; identify data needs). The Fisheries subgroup considered impacts from state and federal fisheries. The Genetics, Hybrids, and Landlocked Populations subgroup considered issues related to population stock structure, possible

effects from hybridization, effects of stocking on genetic diversity, and impacts that landlocked populations may have on anadromous forms. The Habitat subgroup considered impacts from various factors affecting river herring habitat, including but not limited to connectivity (e.g., fish passage), water quality/quantity, and appropriate habitat characteristics (e.g., thermal habitat and spawning habitat). The Species Interactions subgroup considered issues surrounding the interactions between river herring and other components of the ecosystems they occupy, including trophic interactions and ecosystem services in freshwater, estuarine, and marine environments. The Climate Change subgroup considered the current and potential future impacts of climate change on river herring in both marine and freshwater habitats. Topics were discussed with the entire TEWG membership to promote full participation and a coastwide approach. Finally, the Ecosystem Integration subgroup, mostly comprising subgroup chairs and co-chairs, ensured communication among the subgroups. All of the subgroup chairs are authors of this article.

The *Current State of Knowledge* section mirrors the TEWG subgroup structure, with the goal of summarizing recent research. These summaries include identification of threats to river herring and recent research and management actions related to these threats. The *Research Needs* section draws from the summary of recent research and focuses on stock status and fisheries; life history, habitat use, and population dynamics; and ecosystem approaches to restoration. The *Synthesis* section compares threats to river herring, with a goal of informing and facilitating collaborative and integrative science across issues. Identifying connections and trade-offs among various issues is important for considering river herring ecosystem services holistically and providing direction for future science and management efforts.

CURRENT STATE OF KNOWLEDGE

Stock Status

The term “stock” is used in fisheries management to represent a group of fish that can be defined and managed as discrete from other groups; the definition is similar to but not equivalent to the ecological definition of a population (Cadrin et al. 2013). Traditionally, each river containing river herring has been considered a separate stock, with management occurring at the river scale and broader scales (e.g., individual states or the entire USA). Assessment of river herring stocks is difficult owing to the morphological similarities between the two species, the complex stock structure of both species, and their anadromous life history. Thus, many data collection programs and most management actions combine both species and

combine fish from different rivers and different regions. The fate of river-specific stocks during marine migrations is still largely unknown, as is the river-specific stock composition of river herring that are incidentally caught in ocean fisheries. These complexities, combined with great variation in the amount, types, and quality of data collected by numerous different agencies, make assessment of population status a daunting task and limit the types of stock assessment methods that can be applied.

Despite these challenges, a benchmark stock assessment was completed by the ASMFC in 2012 (ASMFC 2012), and a stock assessment update was completed in 2017 (ASMFC 2017a, 2017b). Both assessments concluded that river herring were depleted and near historic lows. The 2012 benchmark stock assessment conducted a full analysis of the status of the two species in U.S. waters, focusing on new data sources and improved assessment methods. Although the assessment was considered coastwide, most of the analyses were completed by examining abundance and age trends in specific river systems. Data were included from 52 distinct river systems between Maine and Florida. Data collected for many rivers by a variety of agencies and organizations resulted in a diversity of collection techniques, data elements, data quality, and time series lengths. As a result, the benchmark assessment used data-limited approaches—primarily analyses of abundance trends and estimates of total mortality from age distributions of adults returning to spawn. The assessment made three general conclusions: (1) river herring are severely depleted (the term “depleted” is used to reflect low levels of abundance, though it is unclear whether fishing mortality is the primary cause for reduced stock size), (2) establishing abundance trends over the preceding 10 years was difficult, and (3) total mortality exceeded sustainable levels in all rivers where it could be calculated. The assessment was not able to evaluate river- or region-specific stocks or to distinguish between the two species, thus limiting understanding.

The 2017 assessment update, which incorporated data through 2015, used the same approaches as developed in the 2012 benchmark assessment. Conclusions of the 2017 assessment update indicated that river herring remained severely depleted. However, 16 rivers showed positive abundance trends compared to 2 rivers in the 2012 benchmark assessment (Table 2). Decreasing trends were detected in three rivers in the 2017 assessment compared to decreasing trends in five rivers in the 2012 benchmark assessment. Mortality estimates in the 2017 assessment update exceeded sustainable levels in all but two rivers, whereas in the 2012 benchmark assessment, mortality estimates exceeded sustainable levels in all rivers (Table 2). Additionally, declines in size continued in four of nine rivers for Alewives and in six of nine rivers for Blueback Herring. Larger and older fish are more fecund (Ganias

et al. 2015; Sullivan et al. 2019) and have higher reproductive success (Marjadi et al. 2019); thus, the high mortality and declining size continue to limit the productivity of the two species (Hixon et al. 2014). Although the increase in the number of rivers with increasing abundance trends from 2012 to 2017 is a positive sign, it is clear that river herring remain near historic lows and total mortality remains high.

In Canada, the Department of Fisheries and Oceans has completed river herring stock assessments for several specific rivers, which are sites with commercial fishing and hydroelectric power generation (DFO 2007; Bowlby and Gibson 2016). Data used in the assessments included catch, run counts, and escapement estimates. In these rivers, escapement was below target levels and exploitation was at or above target levels. In 2017, the Department of Fisheries and Oceans completed a framework for the assessment of river herring in Canadian waters (Gibson et al. 2017). It is difficult to compare assessments between the USA and Canada because Canadian assessments are river specific and include both fishing and escapement targets, whereas the U.S. assessment is coastwide and includes abundance trends and total mortality estimates from specific rivers where data are available. However, the existence of commercial Alewife and Blueback Herring

TABLE 2. Summary of stock status indicators from the 2012 benchmark assessment (ASMFC 2012) and the 2017 update assessment (ASMFC 2017a, 2017b). Included are summaries of a trends analysis and a mortality analysis. The trends analysis includes 55 combinations of rivers and species from 2012 and 54 combinations from 2017. The difference in number of combinations is a result of changes in reporting at the species level and the river herring level in some rivers (Table 1 in ASMFC 2017c). Mortality analysis includes 18 combinations of rivers and species from 2012 and 17 combinations from 2017. The difference in number of combinations is due to a lack of mortality estimates available for one species in one river (Table 2 in ASMFC 2017a).

Stock status metric	Specific metric	2012 benchmark assessment	2017 update assessment
Trend of abundance by river/species combinations	Increasing trend	1	16
	Decreasing trend	5	3
	Stable/no trend	9	18
	Unknown trend	40	17
Measured mortality (Z) compared to mortality reference points	$Z > Z_{40\%}$	12	13
	$Z_{40\%} > Z > Z_{20\%}$	6	2
	$Z < Z_{20\%}$	0	2

fisheries throughout Atlantic Canada indicates that in comparison to U.S. stocks, Canadian stocks are currently more abundant, albeit lower than historical levels.

Fisheries

Directed river herring fisheries have existed for hundreds of years (Hay 1959; Brennessel 2014; Bassett 2015). In the USA, consolidated landings records extend back to 1887, but overall harvest was likely underestimated because landings were not recorded consistently until 1950 (ASMFC 2012). Domestic landings increased to a peak of approximately 61,000 metric tons in 1969 (Figure 3). Foreign fishing became a large component of landings in the mid-1960s but diminished after implementation of the U.S. Exclusive Economic Zone in 1977, and there have been no reported foreign landings since 1990 (Figure 3). In comparison to these historical landings, domestic commercial landings in 2015 were 1.9% of peak domestic landings and just 1.0% of peak foreign and domestic landings (Table 3). Recreational fishing and subsistence fishing for river herring occur in the USA but are not well documented due to a lack of surveys in the upriver areas where they typically occur (ASMFC 2017a). River herring landings in the Canadian Atlantic also have decreased over time but not to the extent that U.S. landings have decreased (Table 3; Gibson et al. 2017).

The principal fishing gears used in the historic inshore and in-river fisheries were fish weirs, pound nets, lift nets, haul seines, and gill nets (Belding 1921; ASMFC 2009). Canadian in-river commercial fisheries generally use traps or lift nets (Gibson et al. 2017). Domestic and foreign fishing by ocean trawlers and purse seiners increased in the

TABLE 3. Landings for specific fisheries and specific years, illustrating the range in landings over the period of record (1897–present).

Category	Landings		Source
	Year (s)	(metric tons)	
U.S. landings	1887	9,957	ASMFC 2017b (Table 2.1)
Peak U.S. landings	1958	31,903	ASMFC 2017b (Table 2.1)
Peak foreign landings	1969	36,244	ASMFC 2017b (Table 2.2)
Peak foreign and U.S. landings	1969	61,634	ASMFC 2017b (Table 2.2)
U.S. landings	2015	610	ASMFC 2017b (Table 2.1)
Canadian landings	1970s	9,167	DFO 2001 (page 2, gaspereau landings table)
Canadian landings	1980s	7,914	DFO 2001 (page 2, gaspereau landings table)
Canadian landings	1990s	6,427	DFO 2001 (page 2, gaspereau landings table)

1960s and 1970s (ASMFC 1985). Currently, a substantial portion of river herring catch occurs as directed in-river commercial catch and secondarily as incidental catch in

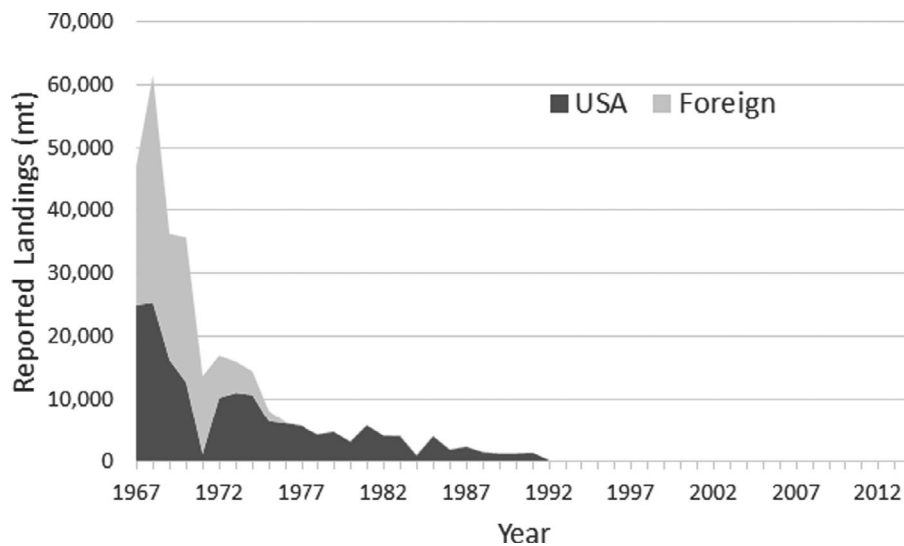


FIGURE 3. Reported landings (metric tons) of river herring in International Commission for the Northwest Atlantic Fisheries/Northwest Atlantic Fisheries Organization Areas 5 and 6 by country (ASMFC 2017) from 1967 to 2015. Landings in the USA from 2006 to 2015 averaged 76 metric tons.

the marine bottom trawl and midwater trawl fisheries targeting Atlantic Herring and Atlantic Mackerel.

As concerns over the status of river herring increased in the 1990s, states limited directed fishing and numerous national- to local-level entities attempted to address habitat access and habitat quality issues. Declines continued despite these efforts, and the focus on incidental catch in marine fisheries increased. Analysis of federal observer data from 2005 to 2015 indicated that on average approximately 373 metric tons of river herring were caught annually in ocean fisheries, primarily midwater and small-mesh bottom trawls targeting Atlantic Herring and Atlantic Mackerel (ASMFC 2017a). Some of the incidental catch is counted in domestic landings data, but some is either discarded or caught in mixed bait fisheries and not reported (ASMFC 2017a). Less is known about current incidental catch in state fisheries, which are only partially covered by federal observers.

Recognizing that incidental catch of river herring in these fisheries represents a threat (Table 1) and potentially undermines ongoing efforts at river herring restoration, the New England and Mid-Atlantic Fishery Management Councils instituted combined river herring and American Shad incidental catch caps in both the Atlantic Herring and Atlantic Mackerel fisheries in 2014 (MAFMC 2013; NEFMC 2013). The incidental catch caps cover both midwater trawl and small-mesh bottom trawl components of these fisheries (Table 4). The caps are tracked in real time and can close all or part of these fisheries (GARFO 2020). The caps were set based on relatively recent catches (not on biological criteria). In 2017, the incidental catch cap represented approximately one-third of the commercial in-river landings of river herring in 2017 (ASMFC 2018; GARFO 2020). Seasonal progress toward these caps is monitored by extrapolating the species composition of kept catch using data collected by NOAA Fisheries at-sea observers. Until recently, observers covered approximately 5% of trips, and they attempted to sample the species composition of all on-boarded hauls.

Incidental catch levels may undetectably exceed the cap because of discards arising from “slippage.” In this practice, a midwater trawler does not bring the entire catch onboard but instead releases part or all of the catch into the water (i.e., slips the net), thereby preventing observers from sampling the catch and potentially biasing estimates of river herring incidental catch. Slippage is a standard part of trawl operations and involves a partial or full release of catch prior to the catch being brought onboard. Slippage can occur for a number of reasons, including an inability to pump the remainder of fish onto the vessel, detection of a prohibited species, or safety concerns regarding equipment or weather. An analysis of slippage indicated that it is currently a relatively infrequent event (Wealti et al. 2018), and both the New England and Mid-

TABLE 4. River herring and American Shad incidental catch caps for 2020. The New England and Mid-Atlantic Fishery Management Councils implemented caps in 2014 as a conservation measure. The Greater Atlantic Regional Fisheries Office tracks incidental catch in the Atlantic Mackerel and Atlantic Herring fisheries (GARFO 2020) and closes the fisheries if the incidental catch cap is exceeded.

Fishery, region, year	Incidental catch cap (metric tons)	Source
Atlantic Mackerel, coastwide, 2020	89–152	NMFS 2019b
Atlantic Herring, Cape Cod midwater trawl, 2020	32.4	NMFS 2019b
Atlantic Herring, Gulf of Maine midwater trawl, 2020	76.7	NMFS 2019b
Atlantic Herring, Southern New England/Mid-Atlantic midwater trawl, 2020	129.6	NMFS 2019b
Atlantic Herring, Southern New England/Mid-Atlantic midwater bottom trawl, 2020	122.3	NMFS 2019b

Atlantic Fishery Management Councils have instituted measures designed to discourage slippage. In collaboration with the midwater trawl fleet, NOAA Fisheries has demonstrated that electronic monitoring can successfully detect slippage events. Similar to any observation technique, electronic monitoring has strengths and weaknesses (van Helmond et al. 2020). In 2017, the New England Fishery Management Council approved an Industry Funded Monitoring Amendment for Atlantic Herring, requiring that 50% of trips be monitored either by a human observer or a combination of electronic monitoring and portside sampling (NEFMC 2017); the final rule was approved by NOAA Fisheries in 2020 (NMFS 2020). These programs will improve precision in discard estimates and provide stakeholders more confidence that slippage is not introducing bias into incidental catch estimates.

Efforts are also underway to document patterns in incidental catch to help fishers avoid areas of high overlap between river herring and target species. Incidental catch of river herring in the Atlantic Herring fishery occurs mostly during January–April and September–December, primarily in southern New England and northern Middle Atlantic Bight waters (Cournane et al. 2013). In these areas, incidental catch is primarily a mix of juveniles, pre-spawning adults, and migratory adults (Bethoney et al. 2014). Farther north, in the Gulf of Maine, incidental catch is composed primarily of migratory mature or near-mature adults. The efficacy of real-time voluntary

avoidance has been recently evaluated. University of Massachusetts Dartmouth's School for Marine Science and Technology implemented a voluntary bycatch ("bycatch" is another term used for incidental catch) avoidance program using at-sea and portside observations (SMAST 2020). Consistent communication facilitated by the avoidance program positively influenced fishing habits and played a role in an approximately 60% decrease in total incidental catch and a 20% decrease in the incidental catch ratio observed during the program (Bethoney et al. 2017). However, the ability to reduce incidental catch by moving a set distance from large incidental catch areas (e.g., a move-along strategy) varied greatly in different areas and years. Species distribution modeling also has been coupled with ocean model forecasts to predict areas of increased probability of incidental catch (Turner et al. 2016). Subsequent testing of the models revealed some marginal ability to predict areas of higher incidental catch (Turner et al. 2017a, 2017b). Efforts are currently underway to combine the two approaches. Recently, the New England Fishery Management Council approved Amendment 8, which prohibits midwater trawling in inshore federal waters from the U.S.–Canadian border to the Rhode Island–Connecticut border. This amendment is intended to decrease local depletion of Atlantic Herring and may decrease the incidental catch of river herring.

Genetics, Hybridization, and Landlocked Populations

Genetic techniques have a long history of informing fisheries biology (Ryman and Utter 1987) and have provided powerful tools for the conservation and management of anadromous fishes (Hasselman et al. 2013; Bradbury et al. 2015; Hess et al. 2015). However, genetic techniques have only recently been used to aid river herring conservation and management. Microsatellite and single-nucleotide polymorphism-based genetic studies have provided valuable insights into (1) spatiotemporal scales of population structure, (2) stock origins of river herring incidental catch in commercial marine fisheries, (3) range-wide extent of hybridization between Alewives and Blueback Herring, and (4) the impacts of stocking programs on population genetic structure.

Resolving the spatiotemporal distribution of intraspecific genetic variation is an important step in identifying the spatial scale of population genetic structure and defining conservation and management units. Four population genetic studies have been completed since 2014. Palkovacs et al. (2014) used microsatellites and sampled rivers from Maine to Florida. McBride et al. (2014) used microsatellites and examined the spatial genetic structure of Alewives and Blueback Herring from the Canadian portion of the species' ranges. Ogburn et al. (2017) used microsatellites and examined genetic structure among rivers flowing into the Chesapeake Bay.

Reid et al. (2018) used a panel of single-nucleotide polymorphisms developed by Baetscher et al. (2017) to examine population structure from Florida to Newfoundland. Two main conclusions come from these studies: most spawning populations (e.g., rivers) are genetically distinct, even on relatively small scales (e.g., across Chesapeake Bay); and spawning populations can be grouped into distinct regional stocks. The specific boundaries vary to some degree among studies, but in general four and five regional stocks have been identified for Alewives and Blueback Herring, respectively. For Alewives, these regional stocks are Canadian, Northern New England, Southern New England, and Mid-Atlantic. For Blueback Herring, these regional stocks are Canadian, Northern New England, Southern New England, Mid-Atlantic, and South Atlantic (Figure 4). Palkovacs et al. (2014) concluded that the Southern New England and Mid-Atlantic stocks for both species were of highest conservation priority based on trends in abundance and body size.

An important challenge in river herring management is identifying which stocks are subjected to mortality from incidental catch in marine fisheries. Hasselman et al. (2016) determined the genetic stock composition of river herring taken as incidental catch in commercial fisheries using the previously identified genetic stocks of Palkovacs et al. (2014). Incidental catch of Alewives and Blueback Herring was disproportionately assigned to the stocks identified as the highest conservation priority by Palkovacs et al. (2014). For Alewives, 70% of assignments were to the Southern New England stock (Figure 5A); for Blueback Herring, 78% of assignments were to the Mid-Atlantic stock (Figure 5B). Hasselman et al. (2016) supported the contention by Palkovacs et al. (2014) that incidental catch may be negatively impacting restoration efforts for spawning populations in this region. Further, this study provides a tool for subsequent stock assignments from mixed-stock fisheries.

The results of genetics studies have implications for understanding extirpation and recolonization of rivers by river herring. Gene flow via straying among proximate rivers promotes local admixture and recolonization (Reid et al. 2018). Genetic subdivision at larger spatial scales indicates that gene flow and straying are restricted among regions, thereby reducing the likelihood of across-region recolonization (Reid et al. 2018). Distance similarly influences genetic population structure in a European congener, the Allis Shad *Alosa alosa*, with more straying between rivers in closer proximity and less straying between rivers further apart (Martin et al. 2015). The factors that contribute to the regional stock boundaries are unknown but could include environmental and habitat differences or migratory breaks that decrease movement among regions.

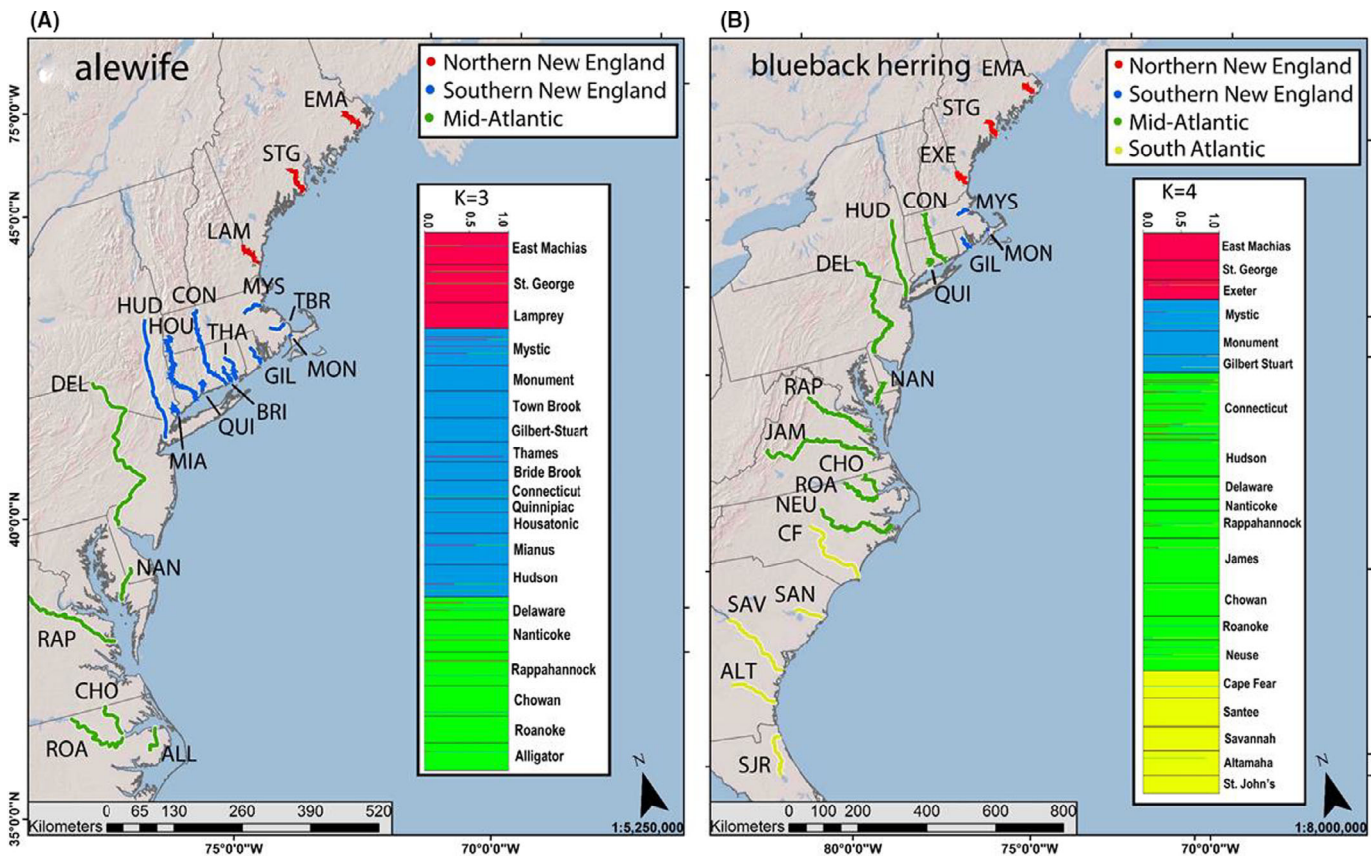


FIGURE 4. Map depicting the genetic clustering of (A) Alewife populations and (B) Blueback Herring populations defined from Palkovacs et al. (2014). The populations are color coded to match the genetic stocks (see legend; top right) inferred from Bayesian analyses. The inset panel shows the admixture proportions, with individual specimens indicated by a thin horizontal line that is partitioned into K colored segments representing a specimen's estimated assignment fraction to each of K clusters. Analyses identified the most likely number of clusters as $K=3$ for Alewives and $K=4$ for Blueback Herring. (Used with permission from Hasselman et al. 2016.)

Recent studies have documented hybridization between Alewives and Blueback Herring and have identified anthropogenic habitat alteration as a factor that increases the rate of hybridization. Hasselman et al. (2014) conducted a rangewide assessment of hybridization between Alewife and Blueback Herring populations. They found that the incidence of hybridization between sympatric anadromous populations was generally low (0–8%; Figure 6); they concluded that reproductive isolation was maintained by differences in phenology and habitat preferences. These results were supported by Kan et al. (2017), who found approximately 5% hybrids among fish collected in the southern Gulf of Maine, and by McBride et al. (2014), who found approximately 6% hybrids among fish collected in the Gulf of Maine, Nova Scotia, and the Gulf of St. Lawrence. Much higher hybridization rates were found in the Kerr Reservoir (Hasselman et al. 2014), which was formed when the Roanoke River was dammed in 1953. Hasselman et al. (2014) hypothesized that the absence of fish passage prevented the immigration of Alewives and

Blueback Herring, and introgressive hybridization facilitated the formation of a hybrid swarm between divergent species that naturally occur in sympatry. McBride et al. (2014) also found rates of hybridization as high as 30% in the Petitcodiac River (Bay of Fundy), suggesting that similarities between species in run timing and human alterations to river ecosystems are possible factors contributing to hybridization potential.

The legacy effects of historical stocking activities (i.e., supportive breeding and stock transfers) can influence the spatial patterns of genetic structure and present a challenge to conservation and management goals. Although stocking programs are frequently deemed successful when spawning stock biomass increases (Hasselman and Limburg 2012), they can jeopardize the genetic integrity and fitness of wild populations, with negative consequences for population persistence and species' evolutionary potential (Hindar et al. 1991; Araki et al. 2007; Valiquette et al. 2014). These consequences frequently extend beyond the jurisdiction of the agency conducting the stocking

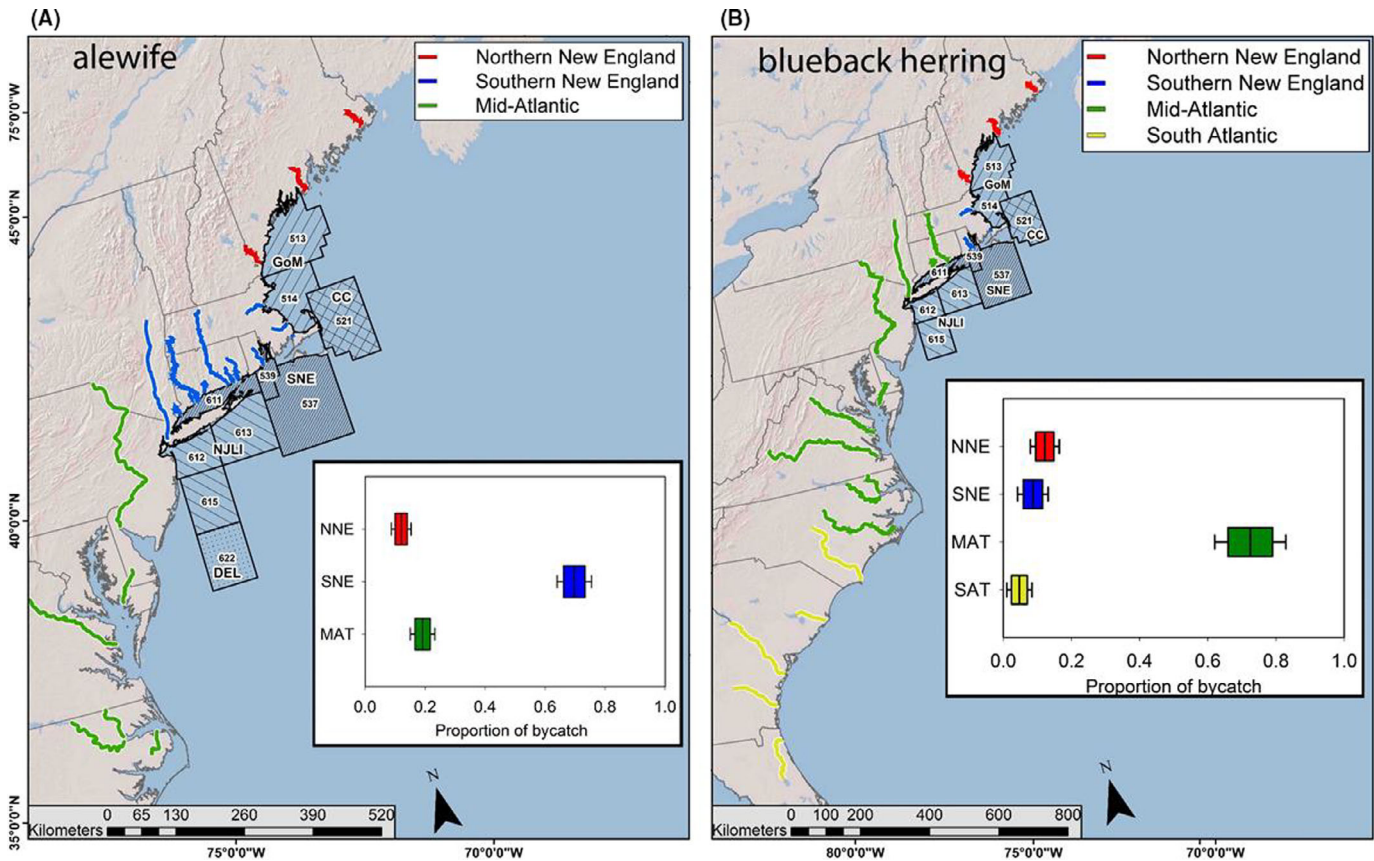


FIGURE 5. Map depicting the genetic assignment of (A) Alewife incidental catch and (B) Blueback Herring incidental catch examined by Hasselman et al. (2016). The populations are color coded to match the genetic stocks (see legend; top right) inferred from Bayesian analyses in Palkovacs et al. (2014). National Oceanic and Atmospheric Administration statistical areas where incidental catch was sampled are indicated on the map and are grouped by region (i.e., GoM = Gulf of Maine; CC = Cape Cod; SNE = Southern New England; NJLI = New Jersey/Long Island; DEL = Delaware) using various degrees of shading. The inset panel provides box plots showing the proportion (posterior median, with 10th, 25th, 75th, and 95th percentiles of the posterior distribution) of overall bycatch assignment to genetic stock. Genetic stock designations are Northern New England (NNE), Southern New England (SNE), Mid-Atlantic (MAT), and South Atlantic (SAT). (Used with permission from Hasselman et al. 2016).

program. For instance, clarification of the spatial distribution and mixing of Alewife populations at sea hinges on the extent to which distinct spawning populations can be identified from mixed-stock assemblages. McBride et al. (2015) examined the spatiotemporal genetic structure of Alewife populations from Maine that had experienced stock transfers of various intensities. They observed a highly significant decline in among-population genetic differentiation as the extent of interbasin stocking activity increased. Hence, historical stock transfers have apparently homogenized the genetic structure of some Alewife populations in Maine and may have inadvertently hindered the use of genetic stock identification as a fishery management tool to inform conservation. Genetic parentage-based tagging is being evaluated as a means of assessing hatchery contribution to river herring populations (Evans et al. 2017). This method will allow detection of hatchery fish but will not prevent the subsequent

introgression of hatchery fish with wild fish. Contemporary stocking programs used by some agencies in river herring restoration should fully consider, prior to implementation, the genetic consequences of proposed restoration activities and the impact of local-scale actions on the long-term success of broad-scale conservation objectives.

Habitat

Habitat use.—River herring are anadromous and use a variety of marine, estuarine, and freshwater habitats during their life cycle (Loesch 1987; Figure 1). Adults migrate to freshwater systems in the spring to spawn. They remain in spawning habitats for several weeks to several months before returning to sea. Alewives enter rivers earlier in the spring and typically spawn in lentic habitats (i.e., still water), whereas Blueback Herring enter later and typically spawn in lotic habitats (i.e., flowing water; Greene et al. 2009). Generally, both species are thought to return to

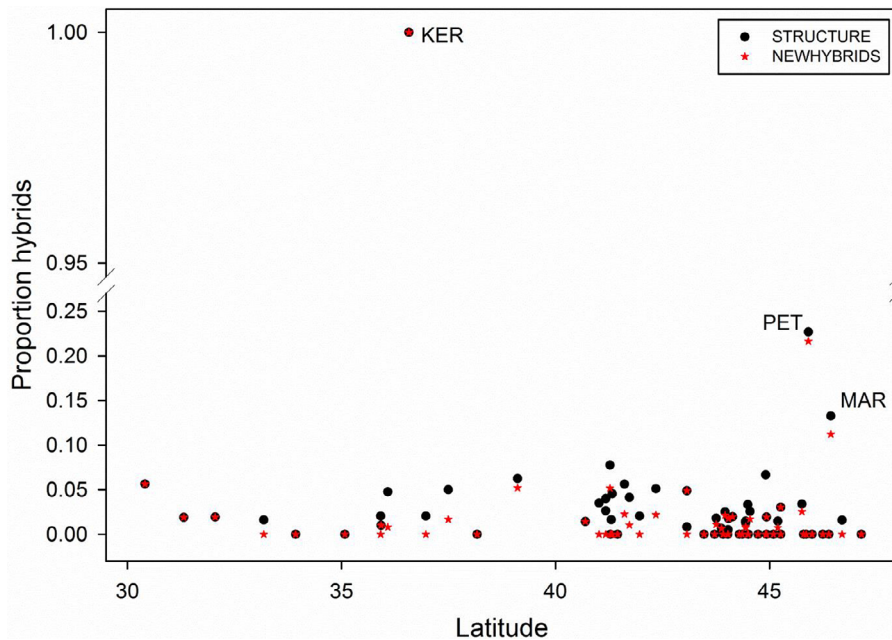


FIGURE 6. Spatial distribution of the proportion of river herring hybrids identified using two Bayesian clustering analyses (STRUCTURE and NewHybrids). The Margaree River, Nova Scotia (MAR), Petitcodiac River, New Brunswick (PET), and Kerr Reservoir, North Carolina (KER), are denoted because they exhibited a substantially greater proportion of hybrids than other sampling locations. (Used with permission from Hasselman et al. 2014).

natal sites for spawning, although straying does occur and is a mechanism for readily colonizing new habitats. Eggs, larvae, and juveniles develop in freshwater, and then juveniles move into estuarine systems during the late spring and summer; juveniles emigrate to the sea in summer and early fall. Juveniles and adults spend the remainder of their life cycle in marine habitats, generally north of Delaware Bay, and move offshore to overwinter. Water temperature influences temporal and spatial patterns in river herring at-sea distributions (Neves 1981; Stone and Jessop 1992), and warming temperatures have affected distributions (Nye et al. 2009; Kleisner et al. 2016).

Recent studies have demonstrated greater diversity in habitat use than previously known. River herring have been viewed as obligate freshwater spawners. In laboratory experiments, DiMaggio et al. (2016) found that embryonic Alewife survival was high at salinities up to and including 10‰, while Blueback Herring embryos displayed a wide salinity tolerance throughout the range from 2‰ to 30‰. Embryos of both species exhibited high survival even when exposed to fluctuating salinities used to simulate tides. The ecological implication of these salinity tolerance studies for the definition of spawning habitats is unclear but suggests that survival of eggs in brackish and estuarine waters is possible.

A number of studies also have revealed complex patterns of habitat use during the juvenile stage. Otolith microchemistry has shown variable individual migration

histories, with some fish migrating into seawater well before the end of the first year and others staying longer in freshwater or low-salinity habitats (Payne Wynne et al. 2015). Blueback Herring were found in freshwater nurseries approximately 8% more frequently than Alewives, and Alewives used a combination of freshwater and estuarine nurseries approximately 9% more frequently than Blueback Herring. Estuarine nursery use was more common in populations at lower latitudes (Turner and Limburg 2016). Gahagan et al. (2012) described high movement rates across salinity boundaries for age-0 Alewives and Blueback Herring in systems where movement between river and estuary habitats was unrestricted. These studies indicate that the emigration of juveniles from freshwater systems is more complex than simply a unidirectional movement in the late summer or fall.

Understanding of adult habitat use during spawning has also improved. Rosset et al. (2017) used fishway counts and otolith-derived hatch dates to determine that spawning continued for 13–48 d after adults stopped migrating into freshwater and that the duration of spawning was 43–76 d. Using acoustic tags, Eakin (2017) found that adult Alewives and Blueback Herring had in-river residence times of 2–3 weeks. These estimates agree with prior studies but are at the individual level. Tagging also demonstrated that adults move into and out of spawning habitats multiple times over the course of weeks rather

than performing a simple migration to and from spawning habitats (McCartin et al. 2019).

The use of species distribution models has enhanced the understanding of marine habitat use (Lynch et al. 2015; Turner et al. 2016). In the spring (March–April), Alewives are found in deeper and warmer waters than Blueback Herring (Lynch et al. 2015). In the fall, both species are found in the northern Gulf of Maine (Lynch et al. 2015). Hasselman et al. (2016) found stock structure at sea, with approximately 70% of the individuals caught in the U.S. midwater trawl fisheries originating from the Mid-Atlantic stock. Rulifson and Dadswell (2020) documented temporal patterns in length, gonadal stage, condition factor, and fat deposits in migrating Alewives and Blueback Herring in Bay of Fundy weir fisheries. Taken together, these results indicate that fish from specific regions are grouped together at sea, but the at-sea migration patterns of fish from individual rivers or from regional stocks are still unclear.

Habitat-related threats.—There are two general habitat-related threats to river herring: loss of habitat connectivity and habitat degradation. The first restricts the ability of river herring to move among habitats during their life history, and the second decreases the quality of habitats relative to the requirements of river herring. Loss of connectivity to spawning habitats and degradation of spawning and early life stage habitats have played important roles in historical declines and extirpations of river herring and other diadromous species across the entire North Atlantic basin and represent critical and large-scale threats to river herring populations (Limburg and Waldman 2009; Mattocks et al. 2017).

The presence and operation of dams constituted the top threat identified in the notice of listing determination for Alewife and Blueback Herring (NMFS 2013, 2019c). There are more than 14,000 dams from Virginia to Maine (Figure 7; Martin and Apse 2011). In the Connecticut River watershed alone, 1,422 dams have been documented. Dams disrupt river herring migrations during the adult spawning migration, in-river movements, adult out-migration, and juvenile out-migration. They deplete energy stores, cause mortality, and reduce iteroparity (Castro-Santos and Letcher 2010).

The effect of dams on river herring access to spawning habitats is well documented in the state of Maine. Obstructed access for Alewives to just nine watersheds in Maine is estimated to have resulted in lost production of 11×10^9 fish from 1750 to 1900 (Hall et al. 2012). Mattocks et al. (2017) analyzed eight New England watersheds from 1630 to 2014 and estimated the annual lost biomass of freshwater forage, marine forage, and adult return spawners due to dams as 18,229, 6,250, and 1,576 metric tons, respectively. Based on the number of returning mature fish, the authors estimated that Alewife abundance

is 6.7–39.0% of historical biomass. An interesting perspective represented in the Mattocks et al. (2017) study is that there is greater abundance of river herring at sea than returning to the rivers since the at-sea population represents immature and mature fish, while the returning population represents only mature fish. The result of this recognition is that the capture of migrating fish in rivers is not directly equivalent to the incidental catch of fish at sea, and thus catches cannot be directly compared.

The most common method of mitigating the negative effects of dams is to construct fishways that allow fish to pass the barrier. Fishways are structures created to facilitate safe and timely fish movement past an obstacle (Silva et al. 2018). One of the first fishways was built in Pawtucket, Rhode Island, in 1714 (Kulik 1985), and in the 19th century, fishways emerged as a mitigation effort to facilitate the bidirectional movement of fish around barriers. A number of different approaches are currently used, including technical structures (e.g., Denil baffled fishways), natural structures (e.g., replicating natural flows), and specialized structures (e.g., fish lifts and fish ladders; Turek et al. 2016; Silva et al. 2018).

Despite the widespread use of fishways, the performance of passing fish through these structures remains low: on average, nonsalmonids experience 20% passage efficiency upstream and 40% passage efficiency downstream (Noonan et al. 2012; see also Brown et al. 2013). Stich et al. (2019) indicated that high rates of survival for upstream and downstream passage are necessary for supporting restoration and management goals. Relatively high passage rates (>70%) can be achieved with appropriate fishway design, regular structural maintenance, and adaptive management (Turek et al. 2016; Nau et al. 2017; Birnie-Gauvin et al. 2019; USFWS 2019).

Managing water releases is another method for mitigating the downstream effects of dams. In a modeling study, Song et al. (2019) found that by adjusting water releases, adult downriver survival could increase spawner abundance by approximately 500%, while 65% of power generation could be preserved. However, owing to the diversity of diadromous fishes in a watershed, a water release plan that is optimized for one species can have negative consequences for another species (Zarri et al. 2019).

Dam removal is becoming an accepted strategy for mitigating the effects of dams. For example, the Chesapeake Bay Program has a goal of and tracks progress on increasing access to habitat in the Chesapeake Bay watershed (CBP 2019); this goal is implemented through dam removals and fish passage improvements. In the northeastern USA, 127 dams were removed between 1990 and 2013, re-connecting approximately 3% (3,770 river kilometers) of the regional river network (Magilligan et al. 2016). A database of dam removals lists less than 20 dam

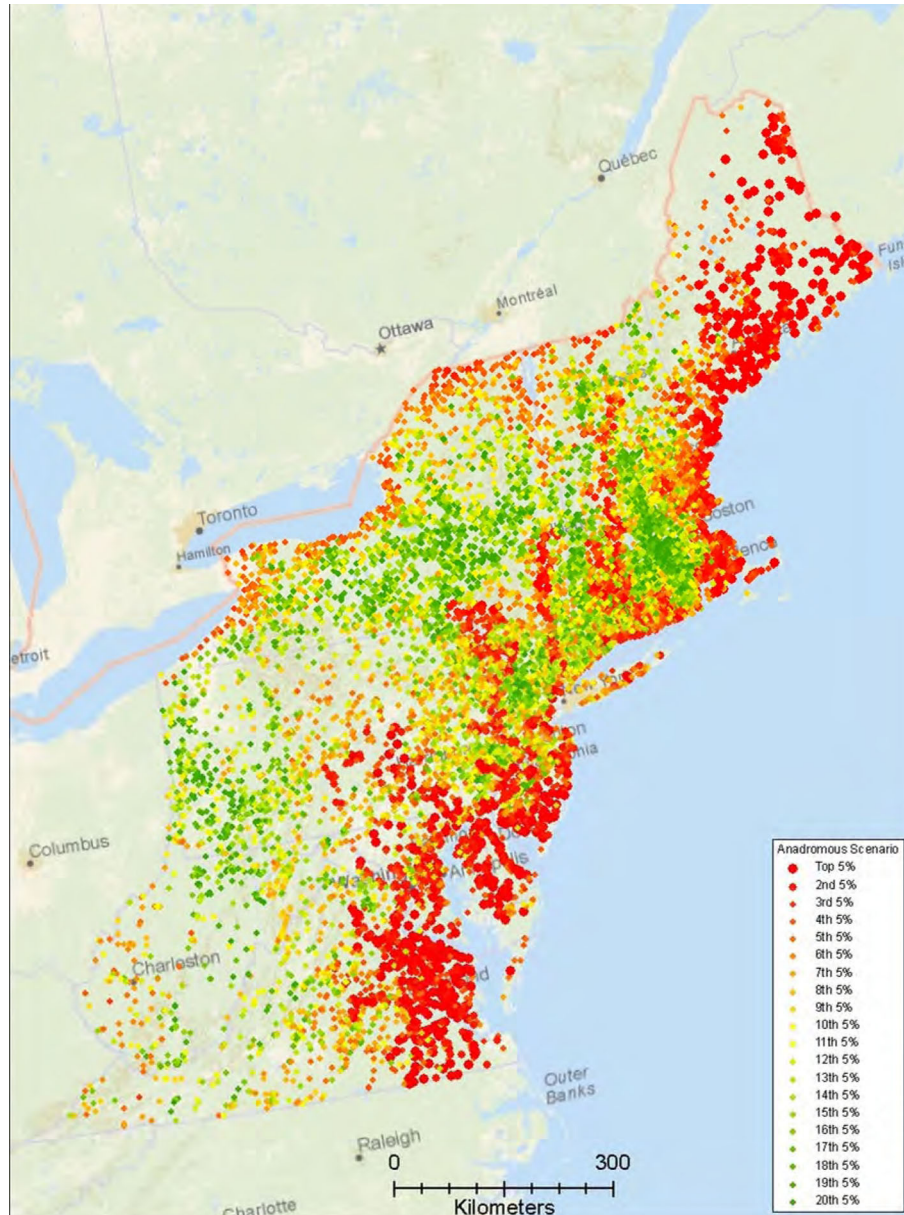


FIGURE 7. Map of dams in the U.S. Northeast, totaling 13,835 dams among the 13 states. The color scale indicates the value of dam removal to restore anadromous fish habitat (used with permission from Martin and Apse 2011). Color indicates the value of removal for anadromous species (red = high value; yellow = medium value; green = low value). Sixteen metrics were used in ranking the benefits of dam removal; the top-three metrics were the presence of anadromous fish habitat in a dam's downstream functional river network, the length of functional river network upstream of a dam, and the number of impassable dams below a given dam. The results for the anadromous fish benefits scenario demonstrate an intuitive pattern of relative high rankings for dams along the coastal zone (anadromous fish habitat downstream of a dam and relatively few impassable dams downstream) and up major rivers (greater length of functional river network upstream of a dam).

removals (American Rivers 2019) in the Connecticut River watershed (~1–2% of existing dams). Thus, despite the significant costs of past dam removal efforts, dams remain a significant threat. Monitoring protocols and analyses should be developed and implemented to determine river herring population responses to restoration efforts; targets should be developed for rivers undergoing restoration

(dam removals, fishways, supplemental stocking, etc.), and efforts are needed to quantify and improve fish passage efficiency.

Increases in river herring abundance have been documented following dam removals (Watson et al. 2018), contributing to the large body of evidence demonstrating that dams have had a major impact on river herring and that

access to spawning habitats is a critically important limiting factor for river herring populations. For example, in a modified before–after–control–impact design study, Hogg et al. (2015) found clear evidence that Alewives responded to a dam removal in less than 2 years by spawning successfully in habitats from which they had been excluded for over a century. There is also a number of river herring runs that have increased after dam removals, indicating a positive response from dam removals. For example, following the removal of the Edwards Dam in 1999 and the Fort Halifax Dam in 2008, river herring returns to the Kennebec and Sebasticook rivers increased 228% and 1,425%, respectively (Wippelhauser 2021). Recent dam removals in Maryland (Bloede Dam) and Massachusetts (Holmes Dam) and future dam removals provide the opportunity to further test this hypothesis. These studies also indicate that river herring are readily able to colonize new habitats, which implies a relatively high degree of straying from natal spawning locations.

Prioritization tools have been developed to support effective restoration coastwide. General themes for restoration needs across all watersheds included addressing upstream and downstream fish passage barriers, water quality, water quantity and flow alteration, and excessive predation (especially related to passage barriers; Martin et al. 2020). The Nature Conservancy developed a subwatershed prioritization to help identify areas of high diadromous fish conservation potential along the U.S. East Coast. A suite of metrics was calculated for each 12-digit hydrologic unit code (HUC12) to measure population and habitat factors that are relevant for river herring and American Shad. A subset of these metrics was then selected and assigned relative weights to develop prioritizations for Alewives, Blueback Herring, and American Shad. The high-priority subwatersheds in these results are areas where conservation activities to support diadromous fish could have the greatest impact (Martin and Apse 2011). Many prioritization/conservation approaches focus on enhancing species resilience by identifying and focusing conservation and restoration investment on a network of core populations, stratified by biologically relevant regional stock units proposed for river herring (Bowden 2013; Palkovacs et al. 2014) and for a suite of anadromous fish (Waldman et al. 2016).

At a broader scale, the Atlantic Coastal Fish Habitat Partnership is a U.S. coastwide collaborative effort that seeks to accelerate the conservation of habitat for native Atlantic coastal, estuarine-dependent, and diadromous fishes. The partnership consists of resource managers, scientists, and professionals representing 33 different state, federal, tribal, nongovernmental, and other entities. The species–habitat matrix developed by the partnership evaluates the relative importance of coastal, estuarine, and freshwater habitat types in terms of their value for the

major life stages of over 100 fish species, including river herring (Kritzer et al. 2016).

Although dam removals represent a high-profile effort to improve the connectivity of river systems, the reality is more complicated. Road crossings and culverts can also create barriers to fish migration (Gibson et al. 2005). Culverts are structures placed beneath roadways to allow water to flow under the road. Detailed studies of barriers to fish passage provide a clear picture of the challenges faced to improve the situation for river herring. In six small river systems (~16.1 km [~10 mi] long) on the south shore of Long Island, 42 barriers to fish migration were identified (NYSDS 2008). In Massachusetts, a similar assessment of the Taunton River watershed (1,456 km² [562 mi²]) found 32 severe and significant barriers to fish passage and another 108 moderate barriers (Audubon 2017). The state of Maine has developed guidance for transportation improvements that include culvert redesigns (Gates 2009), and the North Atlantic Aquatic Connectivity Collaborative and the Southeast Aquatic Resources Partnership have developed databases of barriers to fish passage, which can be used to prioritize restoration efforts (UMASS 2020).

Just as passage barriers can disconnect habitats, poor water quality can impede or reduce survival within habitats and delay movements among habitats. Decreases in water quality can occur through many mechanisms. River flow—a “master variable” in river herring life history (Poff 1997)—ensures the proper habitat, substrate, temperature, depth, velocity, biological cues, and other conditions required by aquatic species. Many mitigated flow regimes are designed to ensure favorable conditions for upriver adult migration. However, out-migration of young-of-the-year (age-0) river herring is also dependent on river flow and water temperature (Henderson and Brown 1985; Rulifson 1994; Gahagan et al. 2010). Early summer river flow and temperature had the greatest influence on age-0 recruitment in five river systems; spring or fall conditions were also important determinants of survival in some of the systems studied (Tommasi et al. 2015). An observed correlation between the abundance of returning river herring and the flow that occurred 3 years prior suggests that flow during the fall out-migration period may be a primary driver of year-class strength (Nelson et al. 2011). Groundwater and surface water withdrawals for public water supply can result in portions of streams becoming dry, serving as another mechanism disconnecting river habitats during the fall out-migration period.

High levels of impervious surface have also been linked to decreases in river herring habitat quality. One component is less infiltration of water into the ground, which leads to reduced groundwater recharge and lower summer base flows. A second component is increased runoff, which causes flash flooding and carries pollutants into

water bodies. When impervious cover levels are at 5%, the number of Alewife eggs and larvae may be reduced by as much as 50%; at 10% impervious cover, there may be almost 100% mortality of eggs and larvae (Limburg and Schmidt 1990). Zhou and Wang (2007) estimated that as of 2004, 10% of the state of Rhode Island was covered with impervious surfaces; urban areas were over 30% and coastal towns averaged 14%. These statewide estimates indicate the potential for broad-scale decreases in habitat quality. Increases in the amount of impervious surface and decreases in dissolved oxygen levels have severely limited suitable fish habitat in Chesapeake Bay (Uphoff et al. 2011). There have been many episodes since 2000 in which dissolved oxygen in portions of the Delaware River estuary has dropped below 3.5 mg/L, creating conditions that are lethal to some life stages of river herring (Martin et al. 2020 and references therein). Degree of urbanization is also linked to lower length, weight, and condition of juvenile Alewives in Massachusetts and Maine, which could lead to lower survival and productivity (Monteiro Pierce et al. 2020).

Contaminants are also a concern regarding water quality and river herring biology, particularly eggs and larvae in freshwater systems and juveniles in urbanized estuaries. Wastewater and runoff add contaminants to aquatic ecosystems, including a wide range of chemicals, such as pharmaceuticals, personal care products, and industrial compounds. In general, there are limited data on the occurrence, environmental fate, and toxicity of these compounds. There are also very few studies on the individual- and population-level effects of contaminants. However, studies have identified “contaminants of emerging concern” in northeastern U.S. river systems (Cantwell et al. 2018) and the risks posed by these contaminants in the Northeast are among the highest in the world (Oldenkamp et al. 2019).

Studies on salmon from the West Coast are suggestive that contaminants could negatively impact river herring, particularly in urbanized areas of the Northeast. Pesticides remain a risk and are potentially impacting the conservation of Pacific salmon *Oncorhynchus* spp. (Macneale et al. 2010). Meador (2014) and Meador et al. (2016) detected contaminants of emerging concern in Puget Sound water and fish tissue at concentrations that may cause adverse effects, such as altered growth, behavior, immune function, and antibiotic resistance as well as reproductive impairment. Juvenile Chinook Salmon *O. tshawytscha* bioaccumulated contaminants of emerging concern, and some of the lowest survival rates for this species were seen in estuaries with wastewater treatment plants discharging into rearing habitats. Salt pollution is also affecting freshwater systems, particularly in the densely populated eastern USA (Kaushal et al. 2018, 2021). Exposure to road salt may decrease egg and larval survival (Mahrosh et al.

2014, 2018). Stormwater runoff and its collection of chemicals caused impacts to the development of the sensory system in fish (Young et al. 2018). In a recent study, a ubiquitous tire rubber-derived chemical was found to cause acute mortality in Coho Salmon *O. kisutch* and die-offs were linked to the chemical- and stormwater-impacted waterways (Tian et al. 2021). Although these studies have not investigated river herring, they are strongly suggestive of a major negative impact of contaminants and runoff on river herring populations, especially in the portions of the Eastern Seaboard with a higher degree of urbanization.

Habitat quality is also directly impacted by habitat alteration. Riparian wetland complexes, which likely provide important spawning, nursery, and refuge habitat for river herring, have been altered or removed in many large river systems by shoreline development and dredging. For example, a study of the upper Hudson River estuary found that total water area decreased by 30% from the early 1900s to the present (Collins and Miller 2012). This loss of habitat was primarily driven by filling secondary channels and other backwater areas. Habitat restoration and restoring riparian buffers are a priority in the region, as is recreating lost habitat.

An emerging issue related to habitat use by river herring is energy development in the marine environment, including offshore oil and gas, offshore wind, and tidal energy. As of 2011, the Bureau of Ocean Energy Management estimated that the undiscovered, technically recoverable oil and gas resources in the Atlantic planning area amounted to 4.72×10^9 barrels of oil-equivalent (BOEM 2014). No offshore oil or natural gas production currently takes place in U.S. Atlantic waters; the last lease sale was in 1983. There is oil and gas production in Canadian Atlantic waters offshore of eastern Nova Scotia and offshore of Newfoundland and Labrador (CER 2017); the environmental impacts of these projects are monitored (DeBlois et al. 2014). The environmental impacts of fracking on watersheds—and, more specifically, diadromous species—are largely unknown (Burton et al. 2014; Entekin et al. 2015). Although fracking has been banned or is not economical in most Eastern Seaboard states, there is a number of fracking operations in Pennsylvania (Meng 2015).

To replace fossil fuels, many U.S. states and Canadian provinces have set renewable energy goals. For example, New York state has a goal of 50% renewable electricity by 2030 (NYS 2015). Nova Scotia had set a target of 40% renewable electricity by 2020 (NSDE 2010). There are several sources of renewable energy, including hydro, tidal, and wind. Hydropower development is linked to the above discussion of dams. Tidal kinetic power is completely predictable, unlike riverine hydropower and wind; the Minas Basin at the head of the inner Bay of Fundy has the

largest tidal range in the world. Dadswell et al. (1986) and Dadswell and Rulifson (1994, 2021) expressed significant concerns over potential widespread impacts of tidal energy turbines leading to significant declines in fish abundance. Autopsies of dead fish downstream of the tidal barrage at Annapolis Royal, Nova Scotia (built between 1980 and 1984), indicated that the deaths were caused by mechanical strike, pressure change, shearing, and cavitation (Dadswell et al. 1986; Stokesbury and Dadswell 1991). New tidal energy projects using seafloor-mounted devices rather than tidal barrages (which are similar to dams) are in development in the Gulf of Maine and the Bay of Fundy. Pilot-scale projects are being monitored, with particular attention to measuring (1) direct contact with turbine blades and subsequent injury or mortality and (2) indirect effects on behavior and use of migratory routes (Viehman and Zydlewski 2015, 2017; Stokesbury et al. 2016). Another renewable energy source is wind, and the northeastern U.S. region is on the verge of large-scale offshore wind energy development. Approximately 2,000 fixed turbines are planned for the region from Cape Cod to Cape Hatteras by 2030. These activities will be undergoing environmental review over the next several years (Methratta et al. 2020). The impacts on diadromous species in general and river herring specifically are largely unknown.

Species Interactions

River herring are forage fish species: “small or intermediate-sized pelagic species ... that are the primary food source for many marine predators” (Pikitch et al. 2014). Forage fish play an important role in linking zooplankton prey to piscivorous predators (Figure 8). The links may be sufficiently strong so as to control the abundance of populations at multiple trophic levels. For instance, predators may exert top-down control on river herring populations (Davis et al. 2012; Smith et al. 2016). Conversely, river herring abundance may influence the success of predator year-classes or may have had such influence historically (Ames and Lichter 2013; McDermott et al. 2015; Willis et al. 2017). River herring also are drivers of zooplankton population dynamics and have selective influences on zooplankton life history, evolution, and morphology (Walsh and Post 2011, 2012; Walsh et al. 2014). Conversely, zooplankton may exhibit bottom-up control on river herring populations—either early life stages or adults—although evidence for this interaction is lacking (see Castonguay et al. 2008 for an example based on Atlantic Mackerel). The complexity of river herring life history means that the importance of trophic interactions can vary in time and space. Nonetheless, the success of river herring conservation efforts depends critically on understanding the interactions among river herring and their prey and predators. Furthermore, some of the benefits of river herring restoration will be realized through

these trophic linkages to supporting ecosystem services, such as increasing abundance of prey for piscivorous predators.

Species that are primary producers and decomposers benefit from nutrients transported by migrating river herring and other anadromous fishes, particularly in freshwater, where migrating adults import marine-derived nutrients through their excretion, carcasses, and eggs. Samways et al. (2018) found that a large run of Alewives in New Brunswick, Canada, generated pulses of excreted marine carbon and nitrogen that were rapidly assimilated by primary producers in the biofilm and transferred to grazers, filter feeders, predatory benthic insects, and resident fishes (Atlantic Salmon parr and Brook Trout *Salvelinus fontinalis*). The carbon and nitrogen signals of marine-derived nutrients were strongest 2–3 weeks after the Alewife spawning period and remained evident into the autumn. Samways et al. (2018) estimated that resident fishes relied on marine sources for roughly one-fifth to one-quarter of their carbon and nitrogen inputs.

An additional flux of nutrients must be taken into account to understand trophic effects of anadromous fish runs in freshwater because out-migrating juveniles export nutrients as they depart their natal grounds. Barber et al. (2018) modeled the import and export of nitrogen and phosphorus in a watershed with Alewife spawning habitat. They incorporated nutrient content of carcasses, excreta, and gametes into an age-structured population projection model that included a Beverton–Holt stock–recruitment relationship, as net transport of nutrients (the balance between import and export) depends critically on how many juveniles leave the watershed for every spawning adult. When adult spawner abundance is low, the process of juvenile export of nutrients dominates the fluxes and there is a net export of nutrients, which shifts to a net import of nutrients as a run rebuilds to more fully use the spawning habitat. The population size marking the transition from export to import depends on freshwater productivity, fishing mortality, and fish passage efficiency. Barber et al. (2018) noted that in some Alewife populations, particularly in the south where reproduction is more semelparous, freshwater systems may receive greater marine-derived nutrients through species feeding on carcasses, whereas the northern Alewife populations import nutrients primarily via excretion that is taken up by primary producers in the biofilm and periphyton.

Despite their low abundance relative to historical levels, river herring can be a substantial component of a piscivore’s diet. River herring predators include demersal and pelagic marine fishes, birds (Markham and Watts 2008; Dalton et al. 2009; Jones et al. 2010), marine mammals (Smith et al. 2015; Toth et al. 2018), and freshwater fishes (Yako et al. 2000; Mattocks et al. 2017; Schmitt et al. 2019). Predators on Alewife juveniles in lentic nursery

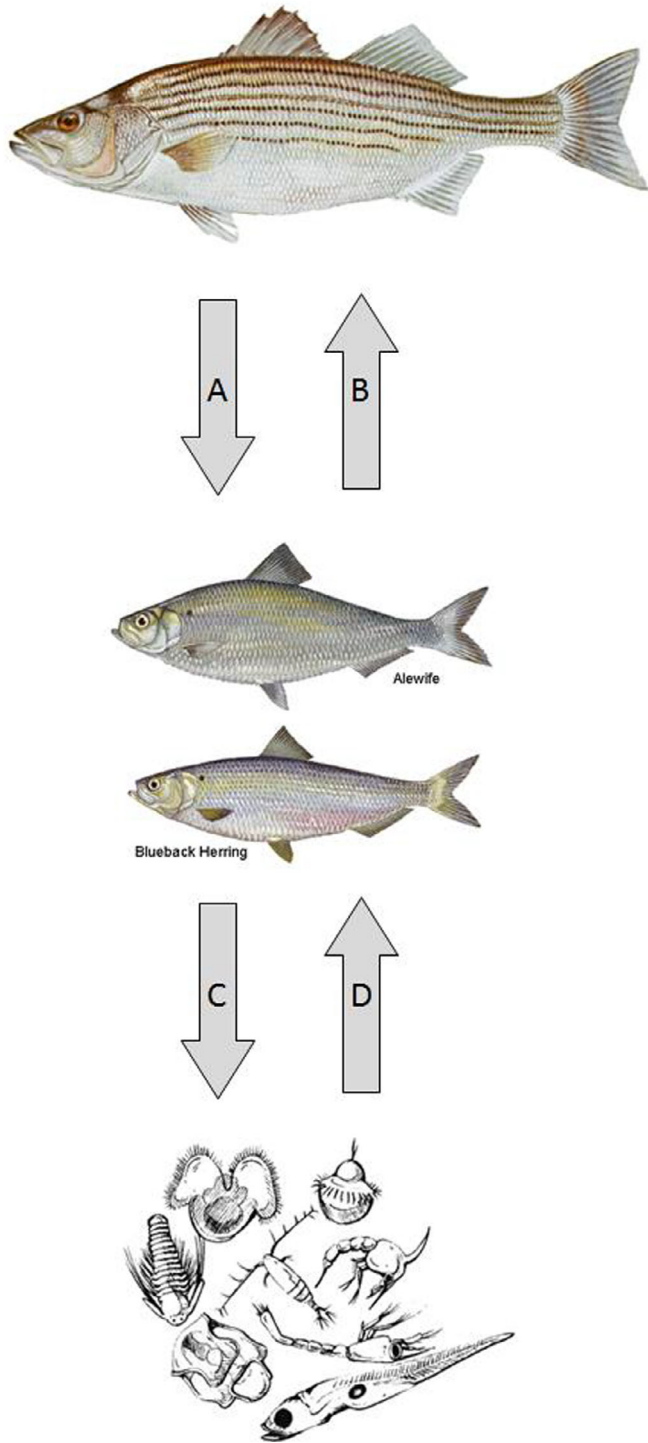


FIGURE 8. Schematic of the role of river herring as a link between zooplankton prey and piscivorous predators. Arrows A and C represent top-down effects (i.e., the upper trophic level controls the abundance of the lower trophic level). Arrows B and D represent bottom-up effects (i.e., the lower trophic level controls the abundance of the upper trophic level).

habitats can be ecologically diverse. In one study of lakes in eastern Massachusetts (Mattocks et al. 2017), Alewives constituted 20% or more of the diet for Brown Bullhead *Ameiurus nebulosus*, White Perch *Morone americana*, Black Crappie *Pomoxis nigromaculatus*, and Smallmouth Bass *Micropterus dolomieu*.

When local concentrations of river herring are high, particularly in inshore or riverine habitats, migratory predators will feed nearly exclusively on them. The extent to which the predator is cued to the appearance, as well as the duration of the interaction, may vary substantially. Striped Bass predictably feed on Blueback Herring during the spring spawning migrations into the Connecticut River (Davis et al. 2012). In a recent 3-year period, the gut contents of about 20% of large Striped Bass (650–999 mm TL [~25–39 in]) included at least one river herring. In contrast, Ferry and Mather (2012) found that river herring had a minor contribution to the diet of Striped Bass feeding in estuaries of Massachusetts, demonstrating the spatial variability in predator–prey interactions or low predation on river herring when populations are low. Dams can also concentrate both migrating adults and early life stages of river herring and can thereby increase predation (Schmitt et al. 2017; Able et al. 2020). Predator migrations may be mismatched with river herring migration; perhaps for that reason, clupeids (Atlantic Herring and river herring) were a negligible dietary component for groundfish species in Gulf of Maine embayments during two study years but constituted one-third of the diet in one year (Willis et al. 2017), again demonstrating the spatial and temporal variability in predator–prey interactions.

Striped Bass predation may have a significant impact on river herring populations (Hartman 2003; Savoy and Crecco 2004; Grout 2006; Heimbuch 2008). Davis et al. (2012) focused on the period when Striped Bass are preying on river herring during their spring spawning migration. River herring life history was represented via age- and stage-dependent transition probabilities and was parameterized using the best available estimates for fecundity and mortality rate. In the absence of Striped Bass predation, the simulated river herring population increased from low abundance. Incorporating rates of Striped Bass predation that are estimated to occur in the Connecticut River, the Blueback Herring population crashed. This analysis corroborates Savoy and Crecco's (2004) suggestion that Striped Bass can be a primary cause for local collapse of the Blueback Herring. The strength of the conclusion is critically dependent on estimates of predator abundance, how prey abundance affects predation rate, and prey life history traits that determine the sensitivity of the prey population to changes in predation rate. Similar

top-down effects (Figure 8, interaction A) have been found in a mass-balanced food web model of a Gulf of Maine estuary in which Striped Bass and piscivorous ducks had a modest negative effect on river herring (Smith et al. 2016). Recent declines in Striped Bass abundance could provide a natural experiment revealing the impact of coastwide Striped Bass abundance on river herring abundance (NEFSC 2019); the prediction would be an increase in river herring in response to a decrease in Striped Bass. The abundances of a number of predators have changed along the Eastern Seaboard; for example, seal abundance has increased (Gilbert et al. 2005). Similar to Striped Bass, if the magnitude of predation is relatively large, these changes in predator abundance can affect the population dynamics of river herring (see O'Boyle and Sinclair 2012 for an Atlantic Cod *Gadus morhua* example).

Conversely, changes in river herring abundance may affect the abundance and production of their predators (Figure 8, interaction B). A bottom-up effect of river herring on their predators was indicated in a spatial analysis of Gulf of Maine fishing records in the 1920s (Ames and Lichter 2013). Multiple gadids exhibited migratory movements and overlapping inshore areas of high abundance that coincided with Alewife runs. Over subsequent decades, the gadids in these areas have declined as the Alewife runs decreased in abundance. Atlantic Cod reproduction and recruitment in the Gulf of Maine may partially depend on the availability of river herring runs that remain (Willis et al. 2017). However, energy flow to higher trophic levels within a Gulf of Maine estuary is driven by marine planktivores, such as Atlantic Herring and sand lances *Ammodytes* spp., rather than juvenile river herring (Figure 9). A recent study concluded that restoration of river herring populations could result in a moderate increase of marine predators, including groundfish, sharks, seabirds, and marine mammals (Dias et al. 2019).

Anadromous river herring have relatively well-understood ecological and evolutionary effects on their prey (Figure 8, interaction C). Alewife juveniles in nursery habitats predictably decimate their preferred prey (Brooks and Dodson 1965; Post et al. 2008; Demi et al. 2012; Howeth et al. 2013) and have a strong selective influence on zooplankton species (Walsh and Post 2011, 2012). The top-down effect of river herring on their prey can have indirect effects on primary producers. Such a trophic cascade was evident in a time series of three trophic levels in a tidal river: the collapse of river herring was followed by an increase in zooplankton abundance and a decrease in primary producers (phytoplankton; Ensign et al. 2014). Phytoplankton community composition is also shaped by river herring through top-down control on zooplankton (Weis and Post 2013).

Similarly, the feeding ecology of Alewives has imposed competitive pressures on coexisting fish species. Through

common-environment comparisons and comparative field studies, Huss et al. (2014) demonstrated that Bluegill *Lepomis macrochirus* coexisting with landlocked and anadromous Alewives have evolved differences in prey selectivity and gill raker morphology; Bluegill coexisting with landlocked Alewives are more effective at feeding on small zooplankton. Interestingly, these changes in Bluegill parallel the evolutionary changes that occur in Alewives upon landlocking and are opposite to the processes of resource partitioning and character displacement that would be predicted by classical competition theory. In contrast to the Bluegill coexisting with landlocked Alewives, those living in lakes without Alewives do not differ from those coexisting with anadromous Alewives. Competitive interactions in the marine environment are possible, as the diets of Alewives and Blueback Herring overlap with each other and with those of other planktivores, such as Atlantic Mackerel, in the marine environment (Suca et al. 2018).

The potential for food limitation of river herring should be evaluated (Figure 8, interaction D). Juvenile river herring are voracious zooplanktivores but will also consume benthic and epiphytic invertebrates. Jones and Post (2013) indicated that the shift from zooplankton to littoral prey resources corresponded to the depletion of zooplankton prey; the magnitude of this shift was linked to the density of the juvenile population. Both observational and experimental evidence confirms the long-standing idea that density is a key driver of juvenile growth (Gibson and Myers 2003; Jones and Post 2013; Devine et al. 2021). Given the observed depletion of lentic resources by juveniles, it seems possible that availability of preferred prey could influence the growth and survival rate of Alewives in nursery habitat, competency to out-migrate, and consequently year-class success. In contrast, analysis of the spatiotemporal overlap between larval alosines and their prey base in a North Carolina estuary suggested that there is no food limitation, which may be a function of the productivity of the environment (Binion et al. 2012). In the north-west Atlantic, Alewives and Blueback Herring feed heavily on calanoid copepods in the spring, and Alewives show a particular fondness for large and lipid-rich *Calanus*, seasonally switching in the fall to krill when copepods are less abundant (Suca et al. 2018). There is evident regional, seasonal, and long-term temporal variability in the diet of river herring in marine ecosystems, raising the possibility of complex bottom-up effects.

Approaches to managing the top-down and bottom-up species interactions have been included in river herring restoration plans. Planners of river herring restoration in the mid-Atlantic states are concerned with the impact of invasive Blue Catfish *Ictalurus furcatus* and Flathead Catfish *Pylodictis olivaris*. In Virginia tidal rivers flowing into Chesapeake Bay, river herring have been prominent

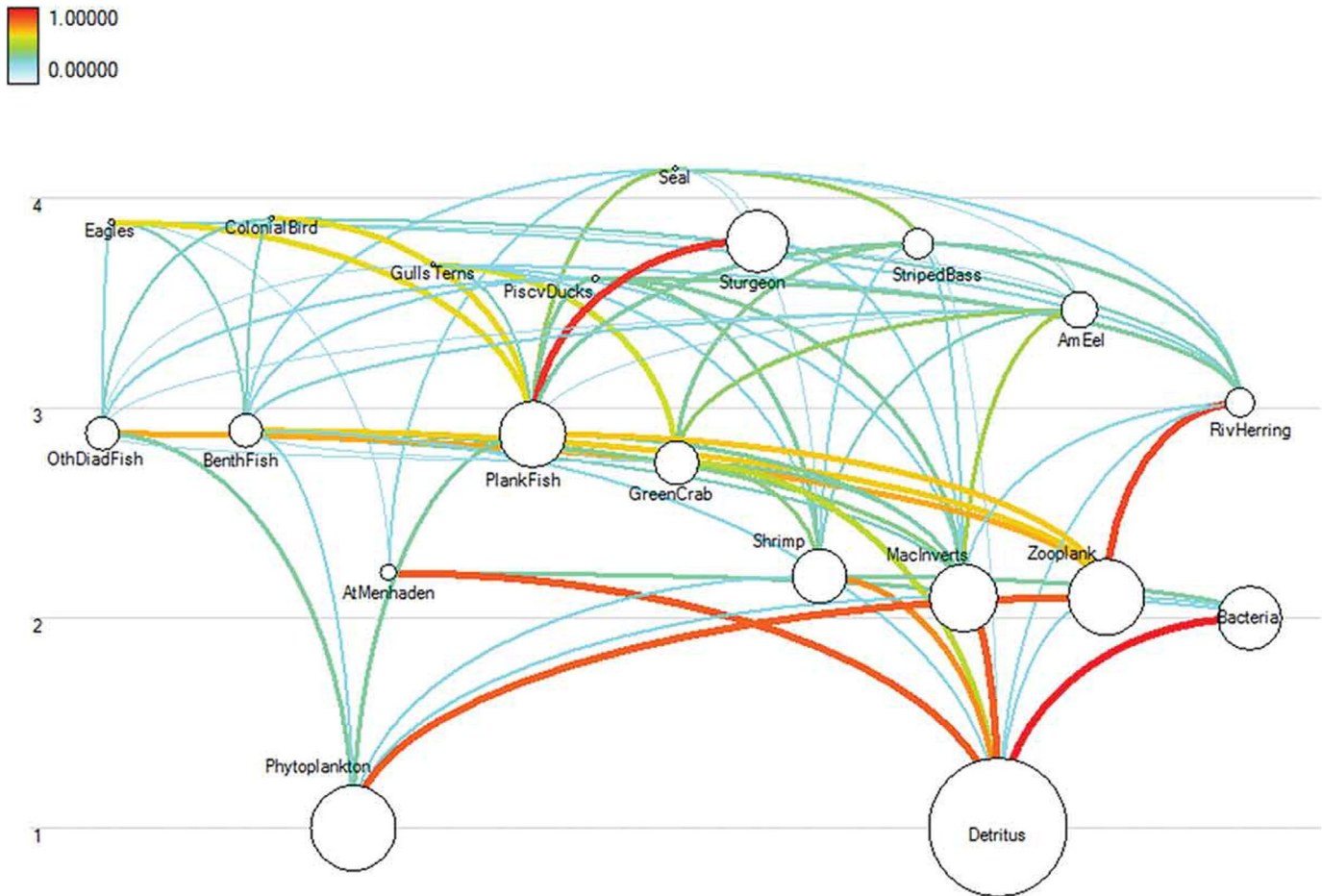


FIGURE 9. Food web of a Gulf of Maine estuary. Trophic exchange is represented by nodes, comprising species or functional groups of taxa (PiscvDucks = piscivorous ducks; AmEel = American Eel *Anguilla rostrata*; RivHerring = river herring; OthDiadFish = other diadromous fishes; BenthFish = benthic-feeding fishes; PlankFish = planktivorous fishes; MacInverts = macroinvertebrates; Zooplank = zooplankton; AtMenhaden = Atlantic Menhaden *Brevoortia tyrannus*), and edges between nodes represent energy flow. Node area indicates its biomass, and edge color and thickness represent importance in terms of the amount of energy flow. Nodes are arranged by trophic level along the vertical dimension of the plot. (Used with Creative Commons License from Smith et al. 2016).

components of the gut contents of invasive Blue and Flathead catfish (Moran et al. 2016). In Maryland tidal rivers, river herring were the second-most frequent prey of White Catfish *Ameiurus catus* (Aguilar et al. 2017). Suggestions to mitigate the impact of these piscivores include developing a commercial market that would support a more robust fishery for catfish, regulations that would require harvest rather than release of a caught catfish, and a public education program on the impact of invasive catfishes on the ecosystem (Schloesser et al. 2011).

The state of Connecticut provides one example of action that was explicitly designed to promote river herring restoration through management of species interactions. After electrofishing surveys and diet analysis revealed that Striped Bass feeding in the Connecticut River were smaller than the minimum legal size of 71.12 cm (28 in) at the time, the state of Connecticut established

an experimental “bonus fishery” for 55.88–71.12-cm (22–28-in) Striped Bass within the Connecticut River (Davis et al. 2012). The program was ended in 2020 (CTDEEP 2020) as a result of the 2018 Striped Bass stock assessment (NEFSC 2019), which concluded that the stock is overfished and experiencing overfishing.

Climate Change

River herring have been identified as highly vulnerable to climate change based on expert opinion, with high biological sensitivity to climate stressors and very high exposure to climate change in the northeastern USA (Hare et al. 2016). The high sensitivity for river herring was related to the complexity in reproduction, the relatively narrow spawning season, and the exposure to a number of other stressors, many of which are described above. Other studies have also concluded that river herring may be

especially vulnerable to climate change because they migrate between marine, estuarine, and freshwater habitats, exposing them to many stressors and to many different management agencies and approaches (Crowder et al. 2006).

In terms of exposure to climate change, numerous studies have described the importance of temperature for influencing river herring physiology, growth, migration timing, and survival (see Tommasi et al. 2015; Alexander et al. 2020). Recent work with American Shad found that growth rates and natural mortality rates were linked to temperature, indicating that population dynamics are influenced by climate change (Gilligan-Lunda et al. 2021); similar work has not been completed for river herring. In North Carolina, increases in temperature are linked to earlier spawning migrations, earlier adult out-migration, and shorter durations on the spawning grounds (Lombardo et al. 2020). In Maine, river herring arrival on spawning grounds has occurred earlier as a result of earlier warming in the marine environment (Cobb 2020). Changes in marine distributions have also been linked to warming temperatures (Nye et al. 2009; Kleisner et al. 2017) and to changes in the timing of the fall transition (Henderson et al. 2017). Species distribution models based on temperature indicate that northward shifts in river herring will likely continue as ocean temperatures warm (Lynch et al. 2015). However, the loss of suitable marine habitat in the northeastern U.S. shelf ecosystem may be balanced by a gain of suitable habitat further north on the Scotian Shelf and in the Gulf of Saint Lawrence (see Shackell et al. 2014). The effect of climate-driven changes in phenology and distribution on abundance and productivity is still unclear but will likely vary latitudinally as thermal habitat shifts or extends northward, population productivity changes, and seasonal migration cues change.

River flow is another critical factor that affects river herring, mediating the movement of adults upriver and downriver to spawn and return to the ocean in the spring and the movement of juveniles downriver in the fall (Crecco and Savoy 1984; Kosa and Mather 2001). Hare et al. (2016) did not consider river flow in their vulnerability assessment, which was based on large-scale global climate models that do not capture changes in the regional magnitude and timing of river flow. River-specific studies have found a relationship between river flow and population productivity. The fit of stock–recruitment models was consistently improved by including environmental variables in five river systems spanning the coastwide distribution of both species in the USA (Tommasi et al. 2015). Early summer river flow and temperature had the greatest influence in most systems, but spring or fall conditions were also important determinants of survival, suggesting river flow and temperature effects on survival of early life stages and egress of juveniles from freshwater nursery

habitats (Tommasi et al. 2015). Furthermore, temperature and river flow affect the timing of the river herring spawning migration such that adult ingress has advanced by 2–6 d/decade in three rivers examined (Androscooggin, Connecticut, and Monument rivers; Tommasi et al. 2015). Thus, changes in both temperature and river flow will likely have large impacts on river herring populations and restoration efforts, and again these impacts will likely vary spatially.

Assessing the vulnerability of river herring to climate change requires understanding not only the environmental influences on population dynamics but also the probability that the species will experience such climate changes in the future. The North American Regional Climate Change Assessment Program (Mearns et al. 2009, 2012) is an ensemble of simulations in which regional climate models with higher resolution (~50 km²) are embedded within global climate models over North America. The program is designed to study climate change processes and provide climate change projections at finer resolution than nearly all current global climate models. Simulations for the current/historical period span 1971–1999, while the future simulations are representative of the middle of the 21st century and span 2041–2069. Greenhouse gas projections for the future climate simulations are based on the A2 scenario within the *Special Report on Emissions Scenarios* (Nakićenović et al. 2000). Annual mean air temperature is expected to increase by at least 2°C or more across the range of river herring (Figure 10A); air temperature is closely linked to temperatures in freshwater habitats (Morrill et al. 2005; van Vliet et al. 2011). Annual mean precipitation and runoff are expected to increase by mid-century, while warmer temperatures are expected to reduce the snow water equivalent (Figure 10B–D).

Given the seasonal nature of river herring movements, seasonal trends in these environmental conditions are critical for assessing how climate will impact each river herring run. Daily climatologies of temperature, precipitation, and snow water equivalent for the Canadian portion of the river herring range and the three major watersheds or HUCs along the U.S. Atlantic coast (shown in white on Figure 10A) indicate that temperature increases occur fairly uniformly across seasons for all HUCs, whereas total runoff and precipitation increases occur in winter months, with a concomitant decrease in snowfall. Surface temperatures over much of the Atlantic Ocean are projected to increase by 1.6–1.8°C by mid-century (Hare et al. 2010). Four regional model projections using the RCP8.5 (RCP = representative concentration pathway) carbon emission scenario indicated increases of 1.1–2.4°C in the Gulf of Maine mean sea surface temperature and increases of 1.5–2.1°C in bottom temperature (Brickman et al. 2021). Projections based on higher-resolution ocean models have indicated a greater magnitude of warming in the

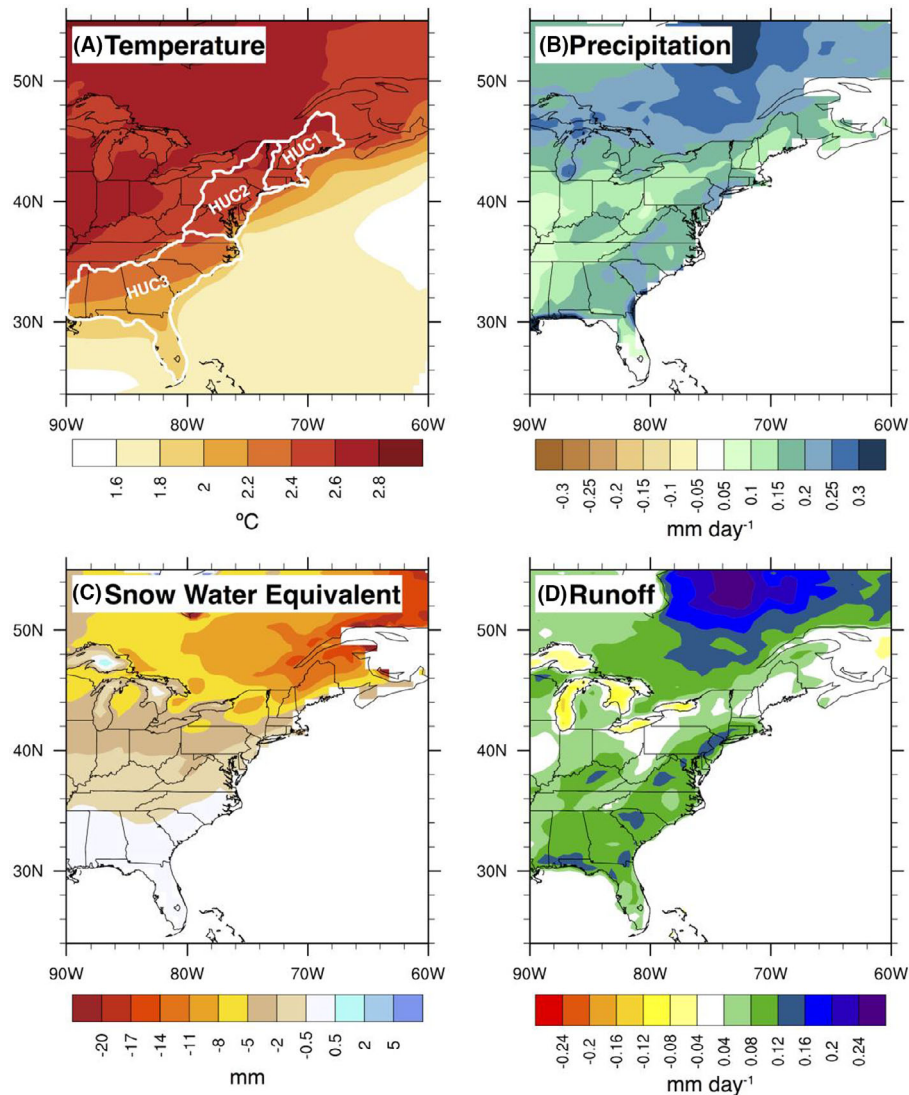


FIGURE 10. Mean mid-century climate change projections (from the North American Regional Climate Change Assessment Program's ensemble of regional climate models) for annual mean (A) temperature ($^{\circ}\text{C}$), (B) precipitation (mm/d), (C) snow water equivalent (mm), and (D) runoff (mm/d). Climate changes are calculated by taking the difference between the future time period simulations and the historical simulations. The three hydrologic units (outlined in white; HUC = hydrologic unit code) are identified in panel A.

Gulf of Maine: 1.5–2.5 $^{\circ}\text{C}$ in mean sea surface temperature and 4.5–5.5 $^{\circ}\text{C}$ in mean bottom temperature (Saba et al. 2016). Relative to changes in ocean temperatures, changes in surface air temperature over the land are higher, ranging from 2.0–2.2 $^{\circ}\text{C}$ over the southeastern USA (HUC3; see Figure 10A) to 2.4–2.5 $^{\circ}\text{C}$ over the northeastern USA (HUC1 and HUC2). Optimal nursery temperatures for river herring vary across systems but typically range between 20 $^{\circ}\text{C}$ and 22 $^{\circ}\text{C}$ (Tommasi et al. 2015). Summer temperatures in the southeastern USA have already exceeded these optima and are projected to further increase by 2 $^{\circ}\text{C}$. Blueback Herring recruitment in the Chowan River in the Southeast is already affected by

relatively warm temperatures in May and June (Tommasi et al. 2015). Stream shading may enhance survival in southeastern estuaries (Ouellet et al. 2020).

Annual precipitation is projected to increase across the entire Atlantic coast, which will increase river flows (Figure 10B). However, relative to temperature, there is much more uncertainty in the simulations of precipitation, as evident by the larger spread in the current and projected future changes (Figure 10B). Across the Atlantic coast, precipitation is projected to increase in the fall, winter, and spring but to decrease in the summer. Snowfall accumulation is projected to decrease by 30–60%, and spring snowmelt is projected to occur 15–30 d earlier in spring

(McCrary and Mears 2019). Summer flow does not appear to have a large influence on river herring recruitment, but spring and fall flows were important for all river runs of Blueback Herring and the northern river runs of Alewives (Tommasi et al. 2015). In New England, earlier snowmelt and enhanced rainfall relative to snow will lead to earlier runoff (Figure 11), which may impact river herring spawning runs. Although the effects of climate change on river herring in the northeastern USA are largely negative, these negative impacts can be mitigated by rebuilding robust populations (Lynch et al. 2015). Furthermore, if or when river herring extend or shift northward in the Canadian part of the species' range, developing management to support robust populations will also mitigate negative effects in the southern part of the range.

RESEARCH NEEDS

There are numerous research needs related to river herring conservation and restoration. These are summarized in Table 5 and expanded upon below. We encourage future research on river herring to be framed in the broader ecosystem context presented here.

Stock Status and Fisheries

Over the past decade, a number of research and monitoring needs have been identified to improve river herring assessments. The 2012 benchmark assessment (ASMFC 2012) identified several priorities for better understanding river herring fisheries. First and foremost is improved reporting of catch by water body and gear type. This includes differentiation of the two species, which is challenging due to the highly distributed nature of river herring harvest along the East Coast. Efforts to improve historical catch data are also needed, as our perspective of the current state of river herring fisheries is based on a comparison to historical data. A better understanding of recreational and subsistence river herring fisheries is also needed. Much recent effort has been devoted to improving the monitoring of incidental catch in the marine fisheries. The increase in human observer coverage, the use of electronic monitoring, and portside sampling will address this need. Efforts to develop tools to help the fishing industry avoid river herring have shown promise and should continue. Finally, as river herring populations are restored, interactions with other fisheries will increase, creating new challenges for fisheries and fisheries management in the region (Turner et al. 2017c); tools and strategies will be needed to address these challenges.

The 2012 benchmark assessment (ASMFC 2012) also recommended the importance of reducing uncertainty in age determination. An aging workshop was conducted following the benchmark assessment to evaluate and provide a baseline of error among laboratories (ASMFC 2013),

but continued efforts to standardize aging protocols among laboratories are necessary. Continued aging work is also needed for river-specific growth and age information (Carroll Schlick and de Mutsert 2019).

Another major issue identified in the benchmark assessment was the variety of data available for the assessment: different collection techniques, data elements, data quality, and time series lengths. In many river systems, there are efforts to address the recommendations of the River Herring Data Collection Standardization Workshop held in 2016 (ASMFC 2016), which reviewed fishery-independent monitoring programs and biological data collection in both the USA and Canada. Details of each monitoring program were documented, and recommendations were developed for increased standardization among programs. Recommendations included documenting changes to sampling over time, developing standardized training for volunteer observers, validating electronic or acoustic counting methods, and recording abiotic variables. In addition to improving assessments in the USA, data standardization would also improve the ability to compare status in both U.S. and Canadian rivers. Genetic methods could be integrated with monitoring programs and support future stock assessments and restoration efforts. Rangelwide estimates of effective population size could provide a standardized metric of relative abundance to complement annual census counts. Similarly, environmental DNA methods are being developed to detect river herring and potentially quantify distribution and abundance (Plough et al. 2018; Antognazza et al. 2019).

A better understanding of stock structure is needed, including tools for stock identification in mixed-stock and non-directed fisheries. Regional stock areas have been defined using population genetics (McBride et al. 2014; Palkovacs et al. 2014; Reid et al. 2018). New techniques, including genetic (Plough et al. 2018), acoustic (Grote et al. 2014; Ogburn et al. 2017), and optical approaches, have the potential to provide new perspectives on river herring abundance and trends. Future assessments incorporating new methodologies can be used to track stock status and the impacts of restoration efforts in the region. Genetic data from river herring sampled from fisheries-independent surveys (e.g., trawl surveys) will provide valuable data on the marine distribution and ecology of river herring. Genetic data should be integrated with (1) other natural tags (e.g., otolith microchemistry; Turner et al. 2015) for insight into the origins of river herring taken in mixed-stock assemblages and (2) other types of data (morphology and growth) to provide information about life history variation and demography.

Life History, Habitat Use, and Population Dynamics

There remain important gaps in our understanding of river herring life history, habitat use, and population

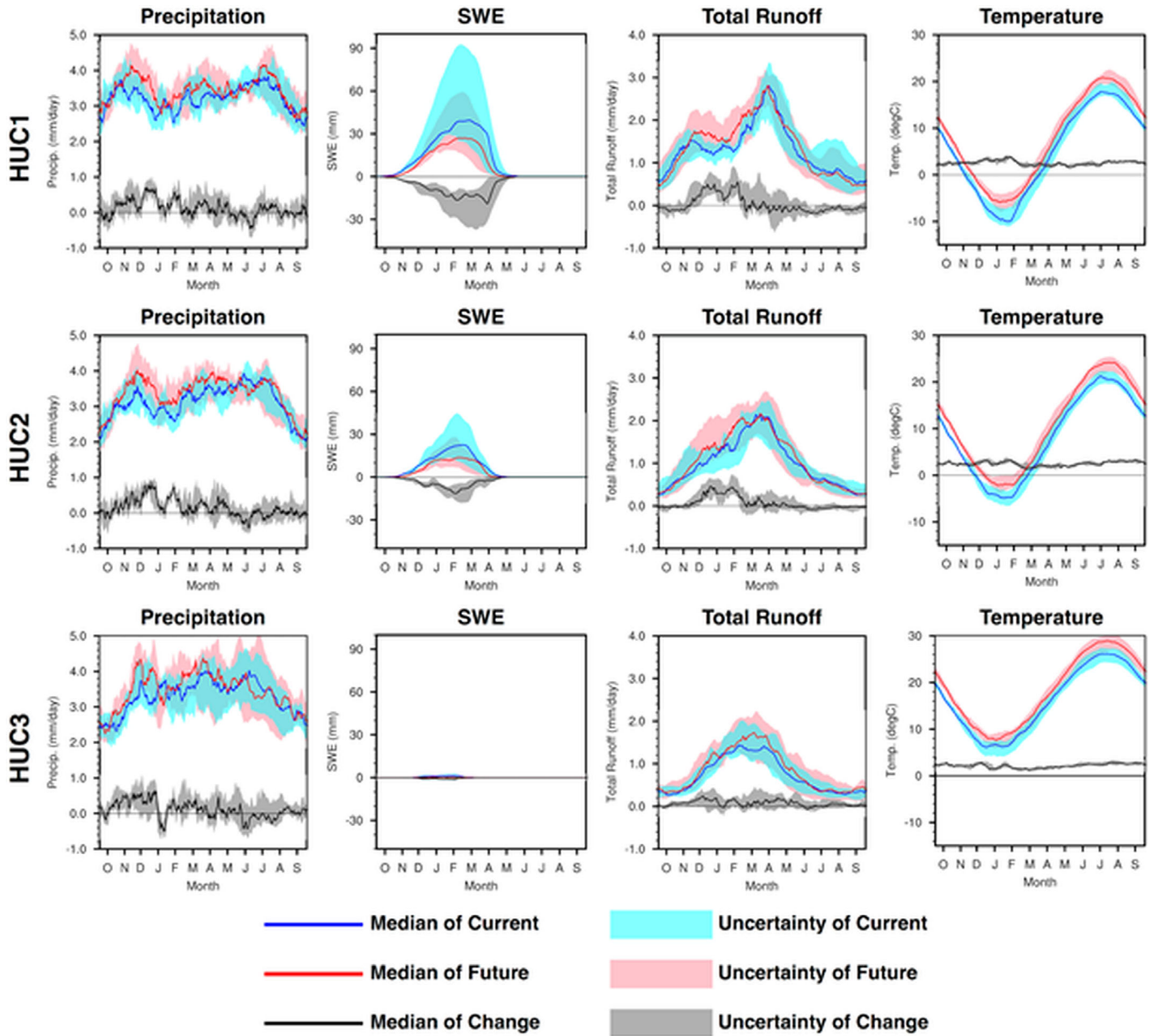


FIGURE 11. The median and uncertainty range from the North American Regional Climate Change Assessment Program models of the daily annual cycle of precipitation (mm/d), snow water equivalent (SWE; mm), total runoff (mm/d), and temperature (°C) averaged over each hydrologic unit code (HUC; HUC1 = New England [top row]; HUC2 = Mid-Atlantic [middle row]; HUC3 = South Atlantic Gulf [bottom row]) from the current period (blue) and future period (red). A 15-d running average was applied to the daily model climatologies to generate a smooth seasonal cycle.

dynamics. The life history is defined as iteroparous anadromy—repeated annual returns to freshwater spawning grounds from marine waters by adults, with early life stages developing in freshwater and transitioning to marine waters during the late juvenile and early adult stages (Figure 1). Adults are thought to return to their natal rivers to spawn, yet recolonization of newly opened habitat occurs quickly (e.g., after dam removal). Improved

understanding of the spatial scale of gene flow and improved estimates of philopatry and straying rates are needed to improve both management and restoration efforts. Similarly, an improved understanding of mixing and movements at sea is needed.

Recent work has shown variation in the general life history and habitat use of river herring; this variation needs to be better documented, and the importance to

TABLE 5. Summary of research needs for river herring restoration categorized by topic area.

Topic area	Research need
Stock assessment	<p>Monitoring river-specific population status and trends (use the 2012 benchmark assessment [ASMFC 2012] as a template)</p> <p>Improved catch estimates: commercial, incidental catch, and recreational catch</p> <p>Standardization of monitoring methods to improve comparability among rivers and regions</p> <p>Continued aging and efforts to standardize aging among laboratories</p> <p>Better quantify the sources of natural mortality (e.g., predation) and develop metrics of trend in natural mortality</p> <p>Development of new population monitoring methods, including optical, acoustic, and genetic estimates</p> <p>Stock structure studies and monitoring of mixed-stock dynamics at sea, in estuaries, and in rivers</p>
Life history	<p>Natal homing and straying rates and controlling factors</p> <p>At-sea migrations and degree of mixing of river herring from different rivers and regions</p> <p>Timing and cues of adult upstream and downstream movement</p> <p>Spawning and spawning habitats (including spatial extent)</p> <p>Timing and cure of juvenile downstream movement</p> <p>Ecological and evolutionary aspects of hybridization</p> <p>Role of human activities in hybridization and affecting timing and scale of movements</p> <p>Role of life history variability in metapopulation dynamics and effect of human activities on metapopulation dynamics</p>
Ecosystem approaches to restoration	<p>Measure and improve fish passage</p> <p>Conduct dam removals with intent of documenting effect on river herring abundance (and other diadromous fishes)</p> <p>Development of approaches to avoid incidental catch should also continue, along with ways to measure the effectiveness of fishery management measures</p> <p>Improved measuring and modeling of predation</p> <p>Role of predation in population dynamics</p> <p>Physiological responses and tolerances across life stages in a multi-stressor approach</p> <p>Investigating local adaptation in response to changing environment</p> <p>Project, forecast, and predict the effect of changing climate conditions on river herring</p> <p>Improved understanding of interaction between climate change, other threats, and restoration efforts</p> <p>Impact of urbanization and contaminants on river herring populations</p>

population dynamics needs to be better understood. In particular, studies are needed on adult upstream migration, adult and juvenile downstream migration, and adult and juvenile estuarine habitat use. There is a range of upstream migration and downstream migration timing; the effects of this variability on population dynamics are largely unknown but important for designing management that supports restoration (e.g., fish passage; incidental catch avoidance). Similarly, otolith chemistry research has shown a diversity of patterns in estuarine habitat use, but the importance of these patterns for river herring ecology needs to be resolved. The development of acoustic tagging techniques (Tsitrin et al. 2020) will likely lead to new insights regarding

individual-scale movements of adults and, potentially, juveniles.

Investigation of the ecological and evolutionary consequences of hybridization between Alewives and Blueback Herring for population dynamics is also needed. Hybridization is high in systems that are dammed; Hasselman et al. (2014) found 100% hybrids in the Kerr Reservoir, which was blocked from anadromous forms in 1953. In river systems where anadromous Alewives and Blueback Herring occur sympatrically, hybridization rates range from 0% to 8% (Hasselman et al. 2014). These rates are similar to those from hybridization studies of European alosines (Jolly et al. 2011) and consistent with the documented hybridization in multiple marine fish taxa

(He et al. 2019). A number of questions arise regarding hybrid fitness, contribution to population dynamics, and the factors leading to hybridization in natural systems. Furthermore, there are questions about the importance of dam removal in maintaining species integrity.

The overall role of life history variability in river herring population dynamics is largely unknown. Work with anadromous Pacific salmon has documented variability across a range of life history traits, including age and size at maturity, the seasonal timing of upriver migration, the seasonal timing of spawning, spawning habitat, and energy allocation within a spawning period. Research indicates that this variability across different stocks and rivers contributes to the resilience of the aggregated metapopulation. For example, the Bristol Bay Sockeye Salmon *O. nerka* stock complex, consisting of several-hundred discrete spawning populations with diverse life history characteristics and local adaptations, has exhibited sustained productivity despite major changes in climatic conditions affecting individual populations (Hilborn et al. 2003; Schindler et al. 2010).

Ecosystem Approaches to Restoration

The dramatic declines in river herring are not unique; all diadromous fish species in eastern North American rivers have declined over the past century (Limburg and Waldman 2009). This pattern points to large-scale and pervasive impacts, particularly from barriers to upstream and downstream fish passage caused by dams, road crossings, and ineffective fish passage designs (Limburg and Waldman 2009). Coordinated restoration and management efforts and the development of management tools show promise for advancing the enhancement of river herring stocks. Foremost, where improvements in river connectivity have been made, river herring abundance has increased. The U.S. Fish and Wildlife Service's fish passage design criteria, as well as improvements in the understanding of passage survival and monitoring technology, should improve the overall effectiveness of fish passage facilities. Prioritization tools have been developed to inform future efforts to improve fish passage (Martin et al. 2020). In Europe, the FITHydro Consortium (<https://www.fithydro.eu/>) is developing decision support tools for the commission and operation of hydropower plants while avoiding individual fish damage and negative impacts on fish populations; large-scale coordinated efforts in North America should be encouraged. In the future, pre- and postproject monitoring should be conducted to test the importance of specific migration barriers for limiting river herring populations and to evaluate designs and methods for improving the effectiveness of projects (see Trinko Lake et al. 2012; Hogg et al. 2015). Since barriers to passage likely limit many diadromous species, these monitoring and evaluation studies should include more than river

herring; therefore, removal of barriers to migration represents an ecosystem-based approach to management for the suite of diadromous species (Hare et al. 2019). Metrics of success, such as basin-specific connectivity indices (Barbarossa et al. 2020), should also be developed and tracked to evaluate restoration progress. Similarly, reviewing and coordinating conservation plans developed for other anadromous species may prove instructive for developing strategies that preserve Alewives and Blueback Herring as well as other anadromous fishes.

Fishing is also a large-scale effect and has contributed to the decline of diadromous fishes. As stated above, efforts to continue to improve catch data are needed in commercial and recreational fisheries. Specifically, efforts to improve monitoring of catch and incidental catch are needed, including self-reporting, human observers, and electronic monitoring. Development of approaches to avoid incidental catch should also continue, along with ways to measure the effectiveness of fishery management measures. The evaluation of the voluntary bycatch avoidance program is novel in this respect (Bethoney et al. 2017).

Predation has widespread implications for river herring restoration, but the magnitude likely varies spatially and temporally as the distribution of predators and prey changes seasonally, across habitats, and with life stage. Studies evaluating predation as a source of mortality are typically site or species specific and have rarely been put into a coastwide ecosystem framework. Measuring and modeling of predation in estuarine and marine systems are challenging. Traditional fishery stock assessments assume a constant rate of natural mortality, which includes predation. Long-term increases in predator abundance (e.g., Striped Bass) and increases in temperature will likely raise predation rates (Petersen and Kitchell 2001; Biro et al. 2007). There are data-intensive methods for estimating absolute consumption of fish prey by predators (e.g., Davis et al. 2012); there are also simpler methods that develop an index of predation based on predator abundance (Richards and Jacobson 2016). A multispecies assessment model has been developed for Atlantic Menhaden (Chagaris et al. 2020), and a similar approach could be evaluated for river herring. These methods and others should be explored in detail to better understand the role of predation in river herring restoration. In addition, the details of the predator-prey interaction should be studied with the goal of informing (1) the large-scale understanding of predation's role in determining river herring abundance and (2) river herring restoration efforts. These studies would also address a recommendation from the 2012 benchmark assessment (ASMFC 2012) to improve estimates of natural mortality.

A better understanding of how species interactions affect the benefits and/or efficacy of river herring

restoration will require more attention to variability arising from geography, migration, and density dependence. The range of river herring spans a diversity of predator fields from Florida into Atlantic Canada and from lakes and streams to the continental shelf. While the predator field in some regions (e.g., Gulf of Maine) is relatively well understood, the predator field in other areas (e.g., Canada and Chesapeake Bay) has been less studied. Furthermore, predator fields are changing with climate change and with the increase of introduced species, namely catfishes. The possibility and practicality of facilitating river herring restoration by increasing the harvest of these catfish deserve particular attention. The potential increase in predation pressure by Striped Bass in Maine and Canadian rivers may also pose challenges for river herring restoration (see Dugdale et al. 2018).

Changing climate conditions are also occurring on a large scale and will affect diadromous species across their range. Changes in climate conditions will also impact other species using freshwater and marine habitats throughout the range of river herring, potentially affecting phenology, life history connectivity, species interactions, and human interactions. The impact of these changes on diadromous species is likely to be negative, particularly in the southern extent of the range (Rougier et al. 2015; Hare et al. 2016). Future work should better define the physiological tolerances of river herring across life stages in a multi-stressor approach (Gunderson et al. 2016). The potential for local adaptation should also be investigated (*sensu* Crozier and Hutchings 2014; Merilä and Hendry 2014; Carim et al. 2017). Finally, modeling should continue to project, forecast, and predict the effect of changing climate conditions on river herring. Advances in dynamical and statistical downscaling global climate models for estuaries (Chesapeake Bay) and for the northeastern USA have been made in the last 5 years (Muhling et al. 2018; Alexander et al. 2019), and these should be applied to river herring. The outlook for making mechanistic, whole-life-cycle projections (Rougier et al. 2015) of river herring productivity and distribution is promising.

Importantly, climate change interacts with all aspects of conservation. For instance, efforts to increase freshwater connectivity or freshwater habitat quality may be impacted by climate change. Dam removal may be more effective in some rivers than others depending on how climate change impacts temperature and precipitation in each system. Climate change is also likely to shift the marine distribution of river herring, which may result in increased straying from natal rivers and affect the population structure of river herring. Climate change may also cause changes in predator and prey populations, thereby affecting river herring through species interactions. Ecosystem models coupled with physical models can be used to understand the relative importance of trophic

interactions, fishing, and climate for restoring river herring populations (Ihde and Townsend 2017).

A number of unknowns remain regarding nearly ubiquitous threats: water quality, contaminants, and habitat alterations. In most cases, there is evidence of widespread exposure to threats (e.g., contaminants of emerging concern; road salt application) and some evidence to suggest that these threats could have significant negative effects on fish (Tian et al. 2021). However, scientific studies focused on river herring are rare, as are efforts to understand the population-level effect of lethal and sublethal exposure to these common threats. Given the link between these emerging threats and urbanization, research related to river herring is urgently needed to understand and potentially mitigate the effects of human development along the U.S. East Coast on river herring restoration and conservation (Limburg and Schmidt 1990; Monteiro Pierce et al. 2020).

SYNTHESIS

Despite the many areas where additional information is needed, much progress has been made in the past 10 years to better understand the status of river herring, the threats to the two species, and the next steps to promote restoration. The methods developed in the 2012 benchmark assessment (ASMFC 2012) were used in 2017 (ASMFC 2017a, 2017b) to re-examine the status of river herring, providing metrics for the coastwide evaluation of restoration efforts. These metrics can now be followed through time. Even though river herring remain severely depleted, there were signs of improvement from the 2012 assessment to the 2017 assessment, with 16 of 54 rivers exhibiting increasing trends in 2017 compared to 2 of 54 rivers exhibiting increasing trends in 2012.

Throughout this paper, we have identified the various threats facing river herring. Comparing the magnitude of these threats is difficult but possible, at least as a first-order approach (Table 6). The reduction in spawning habitat by dams is the primary large-scale disturbance that significantly impacts river herring production. Dams, however, are not the only barriers to fish passage: culverts and road crossings also contribute. This primary threat will need to be alleviated if the restoration goal is to increase abundance while allowing for other anthropogenic sources of mortality to continue, such as incidental catch, predation, and passage over dams (Mattocks et al. 2017). In addition to the decreases in life history connectivity due to dams, predation is a large source of mortality and past increases in predators (e.g., Striped Bass) have likely increased predation on river herring. Directed fisheries are removing river herring, and the removals are reasonably well quantified by fishery monitoring programs; the magnitude of removals is smaller than that

caused by barriers to fish passage and predation. Similarly, incidental catch in nondirected fisheries is well quantified and less than the effect of dams, predation, and the directed fishery.

The list of quantified threats (Table 6) is incomplete because of limited knowledge regarding the effects of other factors—particularly the changing climate, freshwater habitat quality, and stocking activities. These known threats have been evaluated qualitatively (NMFS 2019c), but quantifying their impact on river herring populations is difficult. Furthermore, this examination of threats does not take into account spatial heterogeneity in river herring population structure or spatial heterogeneity in the impact of these different factors. For example, commercial fisheries occur in specific rivers and under management plans. Nondirected fisheries impact predominantly river herring from southern New England, where commercial fisheries are closed (Hasselman et al. 2016). Similarly, the effects of predation will likely vary across rivers and in relation to time of year. Thus, while the magnitude of these factors is smaller than that of dams and the loss of river connectivity, the impact on river herring in specific regions or rivers may be greater.

A major step in an integrated understanding of river herring dynamics was recently made by Nelson et al. (2020). They developed a mechanistic, spatially explicit, full-life-cycle simulation model that can be used to explore population responses of Alewives to various exogenous drivers. The authors used the model to evaluate three hypotheses regarding trends in river herring size, run

timing, and abundance from 1960 to the present: (1) in-river harvest only, (2) in-river Striped Bass predation and harvest, and (3) ocean incidental catch in the Atlantic Herring fishery and in-river harvest. Comparing modeled and observed trends from Massachusetts and Rhode Island rivers, Nelson et al. (2020) concluded that hypotheses 2 and 3 were best supported by the model output: that is, additional mortality above directed fishing is contributing to recent declines in river herring size and abundance. The authors also discussed how the new model could be used to address other threats, including climate change, and identified areas where additional information and data could improve the model.

River herring remain at historical lows along the East Coast of North America. Restoration of these species is a goal held by a number of management agencies and interest groups. The NOAA Fisheries' and ASMFC's coordinated River Herring Conservation Plan seeks to "inform efforts to help restore river herring throughout much of their Atlantic coastal range." The ASMFC's goal for river herring management is "to achieve stock restoration and maintain sustainable levels of spawning stock biomass" (ASMFC 2009). Many individual states also have goals for river herring management. For example, the goal of the North Carolina fishery management plan (NCDMF 2000) "is to restore and manage River Herring ... in a manner that is biologically, economically, and socially sound while protecting the resource, the habitat, and its users." These management goals extend beyond restoring river herring for fishing and include the range of

TABLE 6. Estimates of annual loss of river herring biomass from select threats (Table 1). Returning adults and marine forage are listed separately, as the total biomasses of these two life stages differ, with more age-classes and biomass in the marine forage component than in the returning adult component. The spatial scale over which these estimates are made differs.

Threat	Returning adults (metric tons)	Marine forage (metric tons)	Spatial scale	Species	Source
Lost biomass resulting from dam construction, annual average, 1630–2014	1,576	6,250	Eight watersheds in New England	Alewife	Mattocks et al. 2017
Predation estimate, 2008	58 ^a	173 ^b	Connecticut River	Blueback Herring	Davis et al. 2012
Commercial catch, annual average, 2016–2018	1,031	3,077 ^b	Coastwide	Alewife and Blueback Herring	ASMFC 2017d, 2018, 2019
Incidental catch in Atlantic Herring and Atlantic Mackerel fisheries, annual average, 2016–2018	66 ^b	198	Northeast	Alewife and Blueback Herring	GARFO 2020

^a370,582 individual Blueback Herring consumed (Davis et al. 2012), with an average individual weight of 0.159 kg (0.35 lb; ASMFC 2012).

^bDenotes an estimate based on Mattocks et al. (2017), who estimated that returning fish biomass is equivalent to 33% of marine forage biomass. Returning fish represent mature age-classes only, while marine forage biomass represents all age-classes.

ecosystem services: provisioning, cultural, regulating, and supporting (Figure 2).

The recent advances and remaining questions point to the need for continued development of a holistic approach to river herring restoration, one that considers the range of threats, the ecosystem goods and services connected to these threats, and the ecosystem goods and services related to river herring. Furthermore, a holistic approach should iteratively and collaboratively improve data, tools, and understanding. The benefits of river herring restoration are reasonably well described (Figure 2). The ecosystem costs of not restoring river herring are less well quantified. Financial costs can be developed for a given project, but the nonmarket-based services that are impacted by river herring restoration or lack of restoration can be the hardest to estimate. Dam removal on a stream where landowners prefer an impoundment is one example. This also argues for more efforts connecting humans to river herring so that the role of river herring in the ecosystem is understood and appreciated. In a very important sense, apathy toward river herring restoration is also a limitation, and continued outreach and education using the best scientific information available are critical components of the conservation plan (see Liebich et al. 2018). Taking a lesson from Maine, Alewife restoration has catalyzed a suite of direct and indirect social benefits, including a reversal of the “shifting baselines syndrome” and a motivation to manage fisheries sustainably, diversification of local economies and fisheries, community building and an increased sense of local pride, a demographic broadening of the conservation community, and identification of a positive feedback between economic benefits and other social benefits, with revenue earned from Alewife fisheries enhancing community engagement and providing motivation for further restoration (McClenachan et al. 2015).

The present synthesis of knowledge and evaluation of threats were made possible by the TEWG, a collaborative framework representing experts from a diversity of backgrounds established to identify and better define threats, identify and fill data gaps, and identify and consider research needs and management approaches. The TEWG also formed a community interested in the continued improvement of river herring science and the encouragement of new research and understanding. Furthermore, chairs and co-chairs of the TEWG subgroups developed this paper to summarize recent scientific advancements related to river herring. Taking the example from the TEWG, collaborative, co-learning structures appear to be effective for improving the situation for river herring. We recommend that these approaches continue for river herring and that the approaches be considered for other species and conservation management issues in the region. While the ultimate long-term success of overall river herring restoration is still an open question, the current

approaches have fostered substantial improvements in scientific understanding as documented in this review, which will support long-term effective management.

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