Transactions of the American Fisheries Society, 2026, 00, 1–13
https://doi.org/10.1093/tafafs/vnag005
Published: 10 March 2026
Article

An approach to identify dam passage performance standards for American Shad in four Maine rivers

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ABSTRACT

***Objective*: Diadromous fishes make crucial connections across ecosystems and require adequate habitat connectivity to complete their life history, a necessity that has become more difficult in many river systems with the construction of dams. We assessed the fish passage performance standards at Federal Energy Regulatory Commission-licensed dams required to meet two hypothetical restoration scenarios for American Shad *Alosa sapidissima* on the Penobscot, Kennebec, Androscoggin, and Saco rivers in Maine.**

***Methods*: We modified an existing stochastic life-history-based model to estimate the impact of poor dam passage on American Shad abundance and to identify the upstream and downstream performance standards required to achieve two hypothetical restoration scenarios, which were based on achieving target abundances in historic American Shad habitat above the upstreammost dam in each river.**

***Results*: A range of performance standards were required to meet both hypothetical restoration scenarios, but in general, high upstream passage (>80%) and downstream survival (>75%) was required.**

***Conclusion*: Incorporation of performance standards required to meet identified management objectives into decision-making processes at hydroelectric dams may promote recovery of American Shad in Maine rivers, potentially leading to the restoration of a wide suite of ecosystem services.**

KEYWORDS: American Shad, dams, fish passage, performance standards

LAY SUMMARY

Northeast U.S. populations of American Shad have declined due to dam construction among other factors. New modeling tools provide methods to determine fish passage performance standards at dams to promote population recovery.

INTRODUCTION

The migration of animals is a complex strategy to maximize productivity by varying habitat use over time (Dingle & Drake, 2007). The migration of sea-run or diadromous fish species is driven by differences in potential productivity and mortality risk between marine and freshwater habitats (Gross et al., 1988). Given their migrations between systems, diadromous fish provide key connections and broad ecosystem services across the watershed–ocean continuum (Ouellet et al., 2022). Diadromous fish communities support many ecological services, including predatory interactions, potential prey buffering (LaCroix et al., 2009), and nutrient cycling (Barber et al., 2018), that span aquatic, avian, and terrestrial environments (Ouellet et al., 2022). Many diadromous species also support the traditional lifeways of Indigenous peoples (Daigle et al., 2019) and other cultural and provisioning services as fundamental sources of food (Atlantic States Marine Fisheries Commission, 2017), recreation (Atlantic States Marine Fisheries Commission, 2019), and preferred bait in other valuable fisheries (McClenachan et al., 2015).

Received: July 18, 2025. **Revised:** November 24, 2025. **Accepted:** January 21, 2026

The abundance of many diadromous fishes is at historic lows across the North Atlantic (Limburg & Waldman, 2009), and the delivery of ecosystem services has been greatly diminished or eliminated. Despite decades of effort, restoration of diadromous fishes still faces several obstacles (Waldman & Quinn, 2022). The construction and operation of dams impairs habitat connectivity, reducing diadromous fish productivity, abundance, and distribution (Limburg & Waldman, 2009; Waldman & Quinn, 2022; Zydlewski et al., 2023). Installing engineered upstream and downstream fish passage facilities at dams can reduce impacts to migratory species, but low passage effectiveness has broadly limited their success for certain species at large hydroelectric dams (Brown et al., 2013). "Passage effectiveness" refers to a facility's ability to safely and effectively transport fish up- or downstream in a timely manner and is commonly reported as a percentage (e.g., percent, percent per season, percent per day).

Generally, upstream passage facilities exhibit reduced effectiveness at two points: (1) fish fail to locate the fishway entrance due to limited attraction effectiveness or (2) fish abort passage attempts while inside the fishway due to inadequate internal effectiveness (Katopodis & Williams, 2012). These structural or operational issues prevent fish from passing quickly, which can cause delay. Rates of both passage effectiveness and delay can vary throughout the season based on environmental, biological, and operational conditions. Fish passage delays can result in increased predation rates and impose high energetic costs on diadromous fish (Castro-Santos & Letcher, 2010; Rubenstein et al., 2023; Zydlewski et al., 2023). Furthermore, significant delay may cause fish to arrive at spawning locations or return to the ocean at suboptimal times. Diadromous species are also subject to impacts associated with dams during their downstream migration, including direct injury and mortality from hydropower turbines or other man-made structures (Larinier, 2008), impoundment mortality, and passage delays (Ohms et al., 2022). Furthermore, it is challenging to engineer upstream and downstream passage solutions that work for all species given the large variation in morphology, swimming ability, and migratory strategies of diadromous fishes. Facilities that have less than 100% upstream passage will result in some portion of the population being unable to migrate upstream, with those individuals remaining in lower, potentially less desirable, habitat. Where downstream survival of out-migrants through dams is not sufficiently high, dams can create ecological traps and result in reduced population productivity (Ohms et al., 2022; Stich et al., 2019). Perhaps there are no engineered solutions that are 100% effective for all species; however, designing facilities for species that are highly sensitive to passage conditions may provide the greatest benefit for the greatest number of species.

Safe, timely, and effective passage for diadromous species is often required for hydroelectric projects regulated by the Federal Energy Regulatory Commission (FERC). These measures may be unilaterally required by FERC or drafted by resource agencies pursuant to the Federal Power Act (Lake et al., 2024). Within the FERC licensing process, safe, timely, and effective is a qualitative metric, which does not identify clear, measurable standards for practitioners. However, resource management agencies can define specific fish passage performance standards that would be required to achieve predefined management objectives. This information could help hydropower practitioners define alternatives, including fishways and associated infrastructure or operational modifications or dam removal that would be necessary to achieve species-specific objectives.

The American Shad *Alosa sapidissima* is an anadromous fish species native to the east coast of North America (Limburg et al., 2003). American Shad populations once supported valued commercial, recreational, subsistence, and sustenance fisheries (Atlantic States Marine Fisheries Commission [ASMFC], 2020; Limburg et al., 2003) but have collapsed across their range due largely to pollution, overexploitation, and reduced connectivity through dam construction (Hasselman & Limburg, 2012; Limburg & Waldman, 2009). Fish passage facilities designed to resolve upstream passage issues have a history of low effectiveness for this species relative to design standards (Brown et al., 2013; Haro & Castro-Santos, 2012; Sprankle, 2005; Weaver et al., 2019). Low passage effectiveness coupled with delays accrued at fishways inflict significant energetic costs on American Shad that can reduce survival and the rate of iteroparity (Castro-Santos & Letcher, 2010), an important life history strategy in the northern part of their range (Carscadden & Leggett, 1975; Grote et al., 2014; McBride et al., 2016). Under natural conditions, northern populations of American Shad may spawn five or more times, achieving similar lifetime reproductive potential as semelparous conspecifics in the southern portion of their range (McBride et al., 2016), which may help to buffer against years of poor recruitment (Carscadden & Leggett, 1975). Chronically reduced survival and repeat spawning can result in truncated mean size and age of American Shad (Leggett et al., 2004), thus further reducing productivity. In fact, dam construction is estimated to have reduced coastwide production potential of American Shad by 39% and theoretical spawning populations would only be increased by 4% if "current" upstream passage (40%) and downstream survival rates (80% adult, 95% juvenile) could be achieved at all dams (Zydlewski et al., 2021). While the "current" passage rates were meant to reflect the most optimistic assessment of American Shad passage at existing facilities (Zydlewski et al., 2021), advances in fish passage engineering and our understanding of fish behavior may improve future effectiveness. Clearly "current" rates are not enough, and higher upstream passage and downstream survival rates through or around dams is crucial to the recovery of this species (Stich et al., 2019). While managing toward highly effective upstream and downstream passage of American Shad is intuitive, that goal is complicated by multiple competing interests and difficulty defining performance standards that balance achieving fisheries management objectives with other societal needs.

Recent developments in life history modeling frameworks (Nieland et al., 2015; Stich et al., 2019; Zydlewski et al., 2021) provide tools managers can use to identify species- and site-specific fish passage performance standards at dams. The *anadrofish* package for R (Stich et al., 2025) is a set of population-modeling tools that can be used to assess the responses of fish populations to dam passage and fisheries. The R package

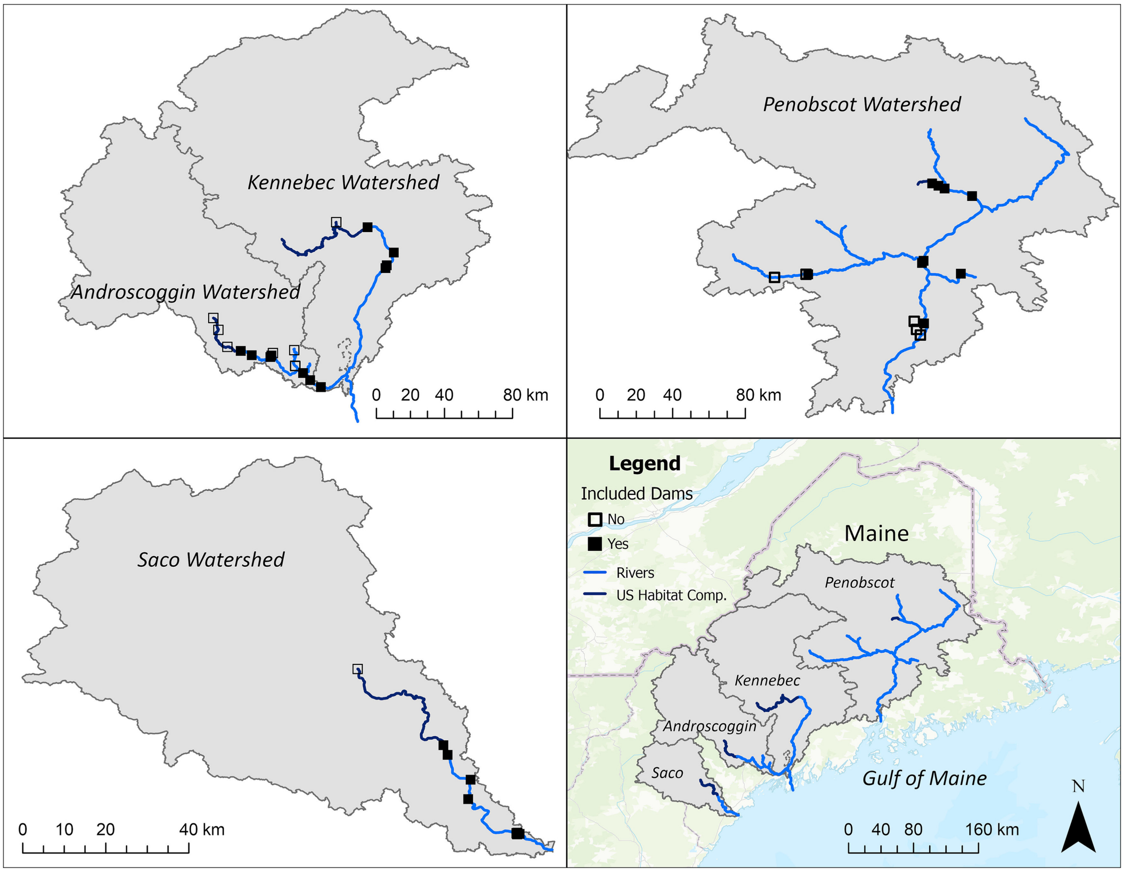

Figure 1. A map of the four watersheds (gray polygons) modeled during the study. Black squares indicate dams within historical American Shad habitat in each watershed and are either open (not included) or closed (included) based on whether they were included as barriers in the models. Dams were excluded either because they were not regulated by the Federal Energy Regulatory Commission or because they were not within historic habitat. Light blue lines indicate historical American Shad habitat that is specifically identified in Maine Department of Marine Resources management plans. Dark blue lines indicate the upstream habitat component in each river system.

hosts stochastic population models for anadromous species that use an age-structured approach to migratory dynamics. The models were originally parameterized for American Shad in 167 Atlantic coastal rivers from Florida to Québec (Zydlewski et al., 2021), concurrent with the most recent ASMFC benchmark stock assessment (ASMFC, 2020). The model and additional information can be accessed from the original publication (Zydlewski et al., 2021) or the GitHub repository for the R package (https://github.com/danStich/anadrofish).

We applied the *anadrofish* model to compare theoretical American Shad abundance using the "current" passage scenario as defined by Zydlewski et al. (2021) (i.e., 40% upstream passage, 95% downstream juvenile survival, and 80% downstream adult survival) with hypothetical restoration scenarios for four large rivers in Maine: the Penobscot (22,265-km^2 drainage area), Kennebec (15,263-km^2 drainage area), Androscoggin (9,143-km^2 drainage area), and Saco (4,395-km^2 drainage area; Figure 1). American Shad are native to each of these rivers, and adults typically return to spawn in mid to late May and leave the system by the end of July (Maine Department of Marine Resources [MDMR], unpublished data; Grote et al., 2014). Spawning adults range in age from 4 to 9, with high rates of repeat spawning (75–95%) compared with other geographic regions, albeit this estimate does not account for dam impacts (Grote et al., 2014). Juveniles begin to hatch in May and have typically emigrated to the ocean by the end of November (Saunders et al., 2006). Each of the four river systems contain a number of hydroelectric dams, and we have identified a range of upstream and downstream fish passage performance standards that would be required to achieve hypothetical restoration scenarios in each river. The Penobscot and Kennebec rivers have been the targets of large-scale habitat restoration and dam removal efforts in the recent past. A 1988 settlement agreement on the Kennebec River resulted in the removal of two dams in the lower river and fish passage improvements at multiple other projects (Wippelhauser, 2021). The Penobscot River Restoration Project involved the removal of the two lowermost dams on the Penobscot River, the decommissioning of a third dam coupled with construction of a nature-like fishway, and numerous passage improvements at the remaining dams throughout the system (Trinko Lake et al., 2012). In response to these dam removals and modifications coupled with additional habitat restoration work, American Shad populations have increased in abundance in both rivers (Watson et al., 2018; Wippelhauser, 2021). The Androscoggin and Saco rivers have not seen the same level of habitat restoration, and dams remain at the head of tide in both rivers. Regardless, habitat upstream of dams on all four rivers remains relatively inaccessible to American Shad due to the difficulty of upstream passage for this species, coupled with the cumulative impacts of multidam passage.

METHODS

Model inputs

The American Shad population model within the *anadrofish* R package was used to stochastically simulate populations in each of our four study rivers 1 million times. Each simulation was run for 50 years, which provided an estimate of stable population size for a given management scenario with variability in biological parameters incorporated by sampling them randomly during each simulation. Thus, this model does not forecast over time within a given simulation but rather provides an estimate of abundance given input variables. We simulated a starting population of American Shad from a negative binomial distribution with the overdispersion parameter (μ) equal to 400,000 and the shape parameter (θ) equal to 1, which ensured that the starting population did not influence stabilized population abundance. A sex ratio from a beta distribution ($a = 100$ and $b = 100$) was inputted for each simulation. It was assumed that all spawning habitat was of the same quality and, in the absence of dams, that spawners distributed throughout the river system proportional to habitat availability. For example, if 15% of habitat is in river reach A, then 15% of upstream migrating American Shad would be expected to spawn in that reach in the absence of dams. Upstream passage and downstream survival rates at each dam were sampled from a sequence with values from 0 to 1 (0.05 increments). We make the distinction between "passage" and "survival" here because failure to pass upstream is not indicative of mortality, while fish that fail to pass downstream are treated as mortalities. Downstream survival for the adult and juvenile life stages were allowed to vary independently during each simulation. Upstream passage and downstream survival rates were consistent among dams within a single simulation. A detailed table of additional life history parameters used in the model is available in Zydlewski et al. (2021, Table 1), along with their associated references. Given the focus on Maine rivers, parameters associated with the Northern Iteroparous ecoregion were used in this manuscript. A complete description of the *anadrofish* R package, including multiple examples detailing real-world performance, is available on GitHub (https://github.com/danStich/anadrofish).

Inclusion of American Shad habitat and dams

All model runs incorporated habitat estimates generated by the MDMR rather than default habitat estimates included in the model (Androscoggin River: MDMR, unpublished data; Kennebec River: Maine State Planning Office, 1993; Penobscot River: MDMW & Maine Department of Inland Fisheries and Wildlife [MDIFW], 2008; and Saco River: U.S. Fish and Wildlife Service [USFWS] et al., 1987). In some cases, MDMR habitat delineation included multiple dams, so they were adjusted to estimate habitat above each individual dam based on the ratio of habitat upstream of each dam in the default model estimates. Available habitat between the river outlet and the first dam is also included and is based on default estimates in the *anadrofish* R package. Total habitat ranged from 7.6 km^2 in the Saco River to 65.7 km^2 in the Penobscot River (Table 1). A table of habitat estimates for each drainage from MDMR data is included in the Supplementary Materials (Supplementary Table 1).

The built-in habitat data set in the *anadrofish* package includes all documented dams within historical American Shad habitat in the four study rivers (Stich et al., 2025), but for our analysis, we only included hydroelectric dams regulated by FERC. We limited the current analysis to include dams regulated by FERC, as the agency's regulatory process provides a direct pathway for the establishment and implementation of performance standards. Non-FERC dams are not typically held to the same legal requirements, and there is not a clear path to establishing, monitoring, and enforcing performance standards. While the impacts of these non-FERC dams were absent from our analyses, historical habitat upstream of these structures was retained. The number of dams retained ranged from four on the Kennebec River to nine on the Penobscot River (Table 1; Supplementary Table 1).

Finally, previous work has demonstrated that predicted abundance from similar models is sensitive to assumed carrying capacity (e.g., Stich et al., 2019, 2025). Carrying capacity is enforced within the *anadrofish* models through a density-dependent Beverton–Holt stock–recruitment relationship (Stich et al., 2025; https://danstich.github.io/anadrofish/reference/beverton_holt.html). Therefore, we explored sensitivity of predicted spawner abundance to changes in this parameter in addition to changes in habitat availability (Supplementary Table 2; Supplementary Figure 1 [see online Supplementary Material]).

Passage scenarios and seasonal performance standards

Predicted abundances resulting from varying combinations of upstream passage and downstream survival rates were compared with the estimated abundance levels resulting from a "current" passage scenario and two hypothetical restoration scenarios. The "current" passage scenario (as defined by Zydlewski et al., 2021) was the resulting abundance reached with seasonal passage rates of 40% upstream passage, 95% downstream juvenile survival, and 80% downstream adult survival at each hydroelectric dam in the watershed. We investigated "Maine" and "Connecticut" hypothetical restoration scenarios, which were based on current real-world management objectives specified within the Penobscot, Kennebec, and Connecticut River management plans (Connecticut River Atlantic Salmon Commission [CRASC], 2020; Maine State Planning Office, 1993; MDMR & MDIFW, 2008, 2009). We consider these "hypothetical" restoration scenarios because the 2020 Connecticut River plan (CRASC, 2020) has not been used to inform Maine management objectives, the Androscoggin River does not have a final management plan, and the authors of this manuscript are not responsible for interpreting or assigning management goals in their current role. American Shad management goals in the current Maine

Table 1. The number of dams regulated by the Federal Energy Regulatory Commission, total amount of historical American Shad habitat, and size of the upstream habitat component within each modeled river system. Mean predicted abundance of American Shad in the upstream habitat component for the "current" passage scenario and estimated minimum abundances for the upstream habitat component of each river system for both hypothetical restoration scenarios are also shown.

River	Dams	Total habitat (km^2)	Upstream habitat component (km^2)	"Current" passage scenario	Connecticut restoration scenario	Maine restoration scenario
Saco	7	7.6	3.9	37	78,803	107,920
Androscoggin	7	12.1	1.9	34	37,892	51,893
Kennebec	4	33.3	7.7	6,119	156,228	213,953
Penobscot	9	65.7	0.6	46	12,405	16,988

plans are based on the original Connecticut River management plan (CRASC, 1992) and are calculated by multiplying 2.75 American Shad/100 m^2 (27,500 American Shad/km^2; we convert to square kilometers to align with units in *anadrofish*) by the subset of historical habitat targeted for restoration (MDMR & MDIFW, 2008). This number (27,500 American Shad/km^2) was the average unit production of American Shad that passed upstream of the Holyoke Dam on the Connecticut River (Knight, personal communication, as cited in Maine State Planning Office, 1993). The Connecticut River management plan was updated in 2020 and now contains an objective to sustain 203 American Shad/hectare (20,263 American Shad/km^2) in main-stem habitats (CRASC, 2020). This updated estimate (20,263 American Shad/km^2) represents the highest number of American Shad returning to the CRASC (1992) divided by the number of hectares of available main-stem habitat to the presumed historic extent of American Shad migration in the river (CRASC, 2020). These two objectives (20,263 American Shad/km^2 and 27,500 American Shad/km^2) form the basis of the Connecticut and Maine hypothetical restoration scenarios and are used to assess passage standards required to meet target abundances in each river.

Abundance comparisons between the two scenarios focused on the historic habitat above the upstreammost dam in each river (henceforth, referred to as the "upstream habitat component"). We only focused on the upstream habitat component because it would likely be the most difficult to restore due to fish having to pass all preceding downstream dams. The size of the upstream habitat component ranged from 0.61 km^2 on the Penobscot River to 7.71 km^2 on the Kennebec River (Table 1). American Shad populations in each river successfully achieved each hypothetical restoration scenario once predicted abundance surpassed the American Shad per square kilometer ratio multiplied by the amount of habitat in the upstream habitat component. Calculated hypothetical restoration scenario abundance targets within the upstream habitat component ranged from 12,405 American Shad on the Penobscot River to 213,953 on the Kennebec River (Table 1). The range of upstream passage and downstream survival rates that resulted in estimated abundance levels that exceed the targets identified for each hypothetical restoration scenario were deemed representative of the seasonal performance standards that would be required at each dam. Seasonal rates can readily be transformed into daily or incremental rates by assuming nominal time frames for upstream and downstream migration seasons as follows:

$$\left\{\text{daily passage} = 1 - \left[1 - \text{seasonal passage}^{\left(\frac{1}{\text{season length}}\right)}\right]\right\}.$$

In the absence of those data, we elected to use seasonal rates for this example following the default implementation in *anadrofish* rather than converting to time-based rates. However, where data are available or assumptions about spawning and migration durations can be made, the seasonal rates from our study could be used to directly inform time-based passage performance standards for empirical assessment of fish passage performance.

RESULTS

The mean predicted abundance in the upstream habitat component under the "current" passage scenario represented <1% of the calculated abundance under either hypothetical restoration scenario for all rivers except the Kennebec River, where it was 2.9% and 3.9% for the Connecticut and Maine scenarios, respectively. The Androscoggin River had the lowest upstream mean abundance (34 American Shad) under the "current" passage scenario, and the Kennebec River had the highest (6,119 American Shad; Table 1). Despite having the smallest upstream habitat component and most downstream dams, the Penobscot River had the second highest mean abundance (46 American Shad) in the "current" passage scenario (Table 1).

Estimated abundance levels in the upstream habitat component exceeded the targets associated with both hypothetical restoration scenarios across a range of upstream and downstream passage efficiencies for each river (Figures 2–5). In general, increasing one standard (i.e., upstream adult passage, downstream juvenile or downstream adult survival) reduced the requirements for the other two standards. While many combinations of performance standards resulted in abundance estimates that exceeded each hypothetical restoration scenario, we focused on the minimum upstream adult and downstream juvenile survival that achieved each scenario across a range of downstream adult survival (75–100%) for simplicity and ease of interpretation when paired with

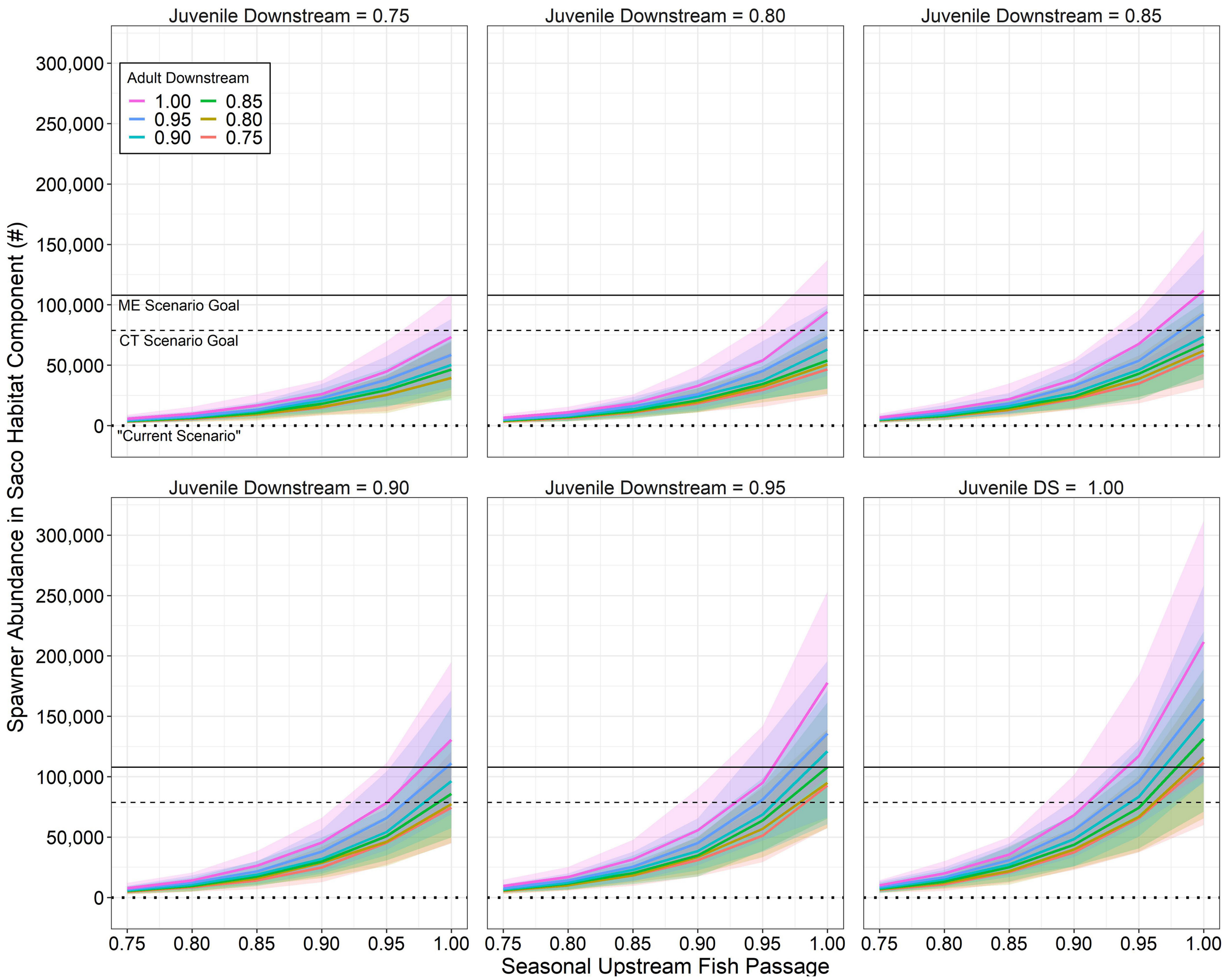

Figure 2. Modeled spawner abundance of American Shad within the upstream habitat component in the Saco River across a range of seasonal upstream fish passage conditions (0.75–1.00) at hydroelectric dams. Estimated abundance was low and no hypothetical restoration scenarios were achieved when upstream passage, juvenile downstream survival, or adult downstream survival was below 75%, so our results are limited to a range of 75–100% for those parameters. Solid colored lines indicate the 50th percentile of spawners across model runs, with colors representing different levels of downstream adult survival (0.75–1.00). Ribbons indicate 95% confidence intervals of model predictions for each passage combination. Panels represent different levels of downstream juvenile survival (0.75–1.00). The dotted, dashed, and solid black lines represent the "current" passage and Connecticut-based (CT) and Maine-based (ME) hypothetical restoration scenarios, respectively.

the relevant figures. River-specific performance standards are detailed below.

Saco River

The predicted mean spawner abundance in the upstream habitat segment on the Saco River did not exceed either hypothetical restoration scenario unless upstream passage was greater than 90% and juvenile downstream survival was greater than 75% (Figure 2). With juvenile downstream survival set to 95%, the mean spawner abundance exceeded the Connecticut scenario across a range of adult downstream survival (75–100%) and upstream passage rates (94–100%). Mean spawner abundance exceeded the Maine scenario across a range of adult downstream survival (75–100%) and upstream passage rates (93–100%) but only with juvenile downstream survival of 100%.

Androscoggin River

The predicted mean spawner abundance in the upstream habitat segment on the Androscoggin River did not exceed either hypothetical restoration scenario unless upstream passage was greater than 90% (Figure 3). With juvenile downstream survival set to 90%, the mean spawner abundance exceeded the Connecticut scenario across a range of adult downstream survival (75–100%) and upstream passage rates (92–100%). Mean spawner abundance exceeded the Maine scenario across a range of adult downstream survival (75–100%) and upstream passage rates (92–100%) but only with juvenile downstream survival of 100%.

Penobscot River

The predicted mean spawner abundance in the upstream habitat segment on the Penobscot River did not exceed either

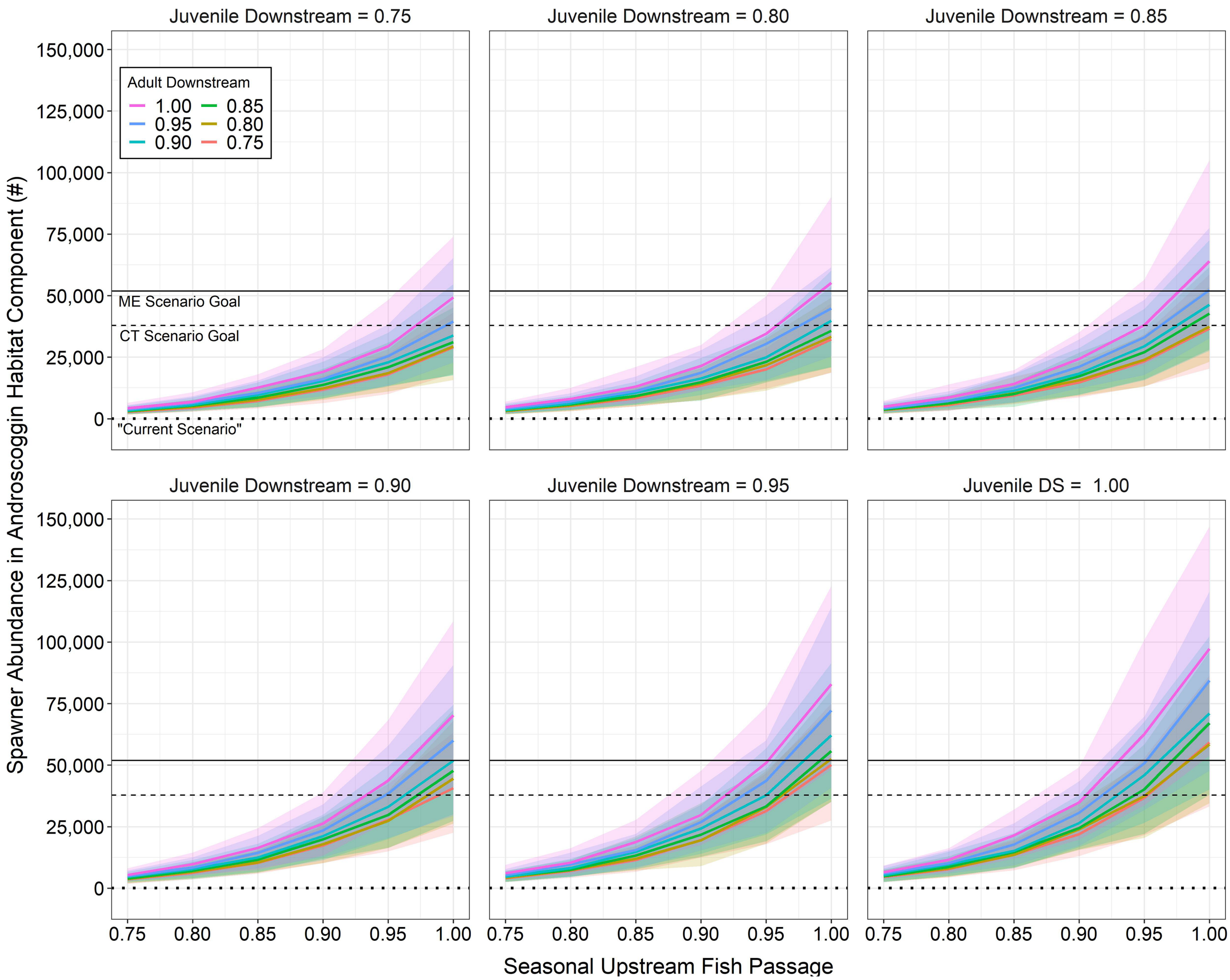

Figure 3. Modeled spawner abundance of American Shad within the upstream habitat component in the Androscoggin River across a range of seasonal upstream fish passage conditions (0.75–1.00) at hydroelectric dams. Estimated abundance was low and no hypothetical restoration scenarios were achieved when upstream passage, juvenile downstream survival, or adult downstream survival was below 75%, so our results are limited to a range of 75–100% for those parameters. Solid colored lines indicate the 50th percentile of spawners across model runs, with colors representing different levels of downstream adult survival (0.75–1.00). Ribbons indicate 95% confidence intervals of model predictions for each passage combination. Panels represent different levels of downstream juvenile survival (0.75–1.00). The dotted, dashed, and solid black lines represent the "current" passage and Connecticut-based (CT) and Maine-based (ME) hypothetical restoration scenarios, respectively.

hypothetical restoration scenario unless upstream passage was greater than 85% (Figure 4). With juvenile downstream survival set to 75%, the mean spawner abundance exceeded the Connecticut scenario across a range of adult downstream survival (75–100%) and upstream passage rates (91–100%). Mean spawner abundance exceeded the Maine scenario across a range of adult downstream survival (75–100%) and upstream passage rates (92–100%), with juvenile downstream survival of at least 85%.

Kennebec River

The predicted mean spawner abundance in the upstream habitat segment on the Kennebec River did not exceed either restoration scenario unless upstream passage was greater than 80% (Figure 5). With juvenile downstream survival set to 75%, the mean spawner abundance exceeded both the Connecticut scenario and the Maine scenario across a range of adult downstream survival (75–100%) and upstream passage rates (85–100%; depending on the scenario).

DISCUSSION

Implementing performance standards at dams is a difficult task. There are many combinations of upstream and downstream performance standards that may lead to achievement of chosen management objectives; thus, the challenge lies in determining what combination to implement. While we have not identified specific performance standards, we have demonstrated that the *anadrofish* package and similar tools can assist in quantifying expected increases or decreases in population abundance under different passage combinations. We compared American Shad abundances in the upstream

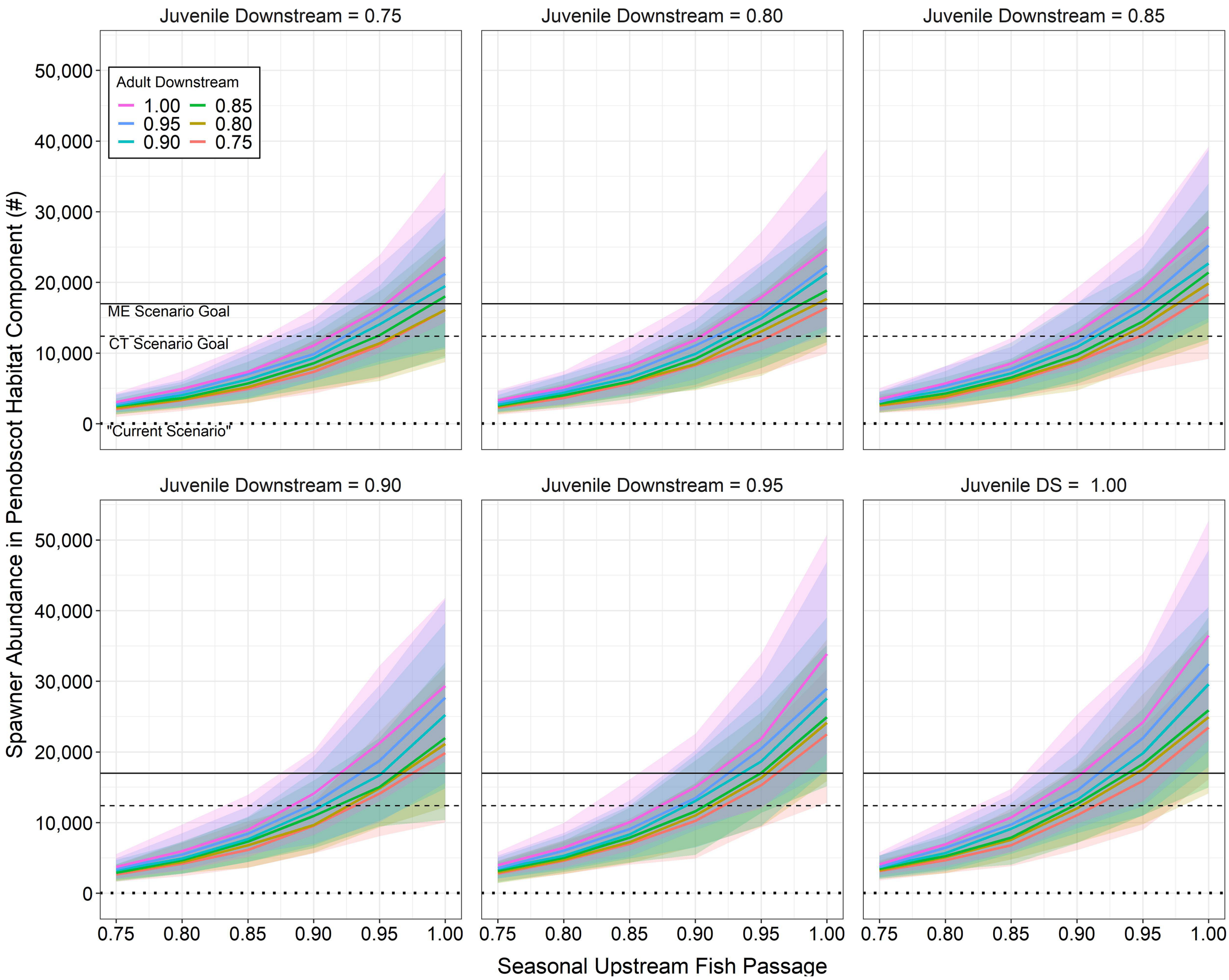

Figure 4. Modeled spawner abundance of American Shad within the upstream habitat component in the Penobscot River across a range of seasonal upstream fish passage conditions (0.75–1.00) at hydroelectric dams. Estimated abundance was low and no hypothetical restoration scenarios were achieved when upstream passage, juvenile downstream survival, or adult downstream survival was below 75%, so our results are limited to a range of 75–100% for those parameters. Solid colored lines indicate the 50th percentile of spawners across model runs, with colors representing different levels of downstream adult survival (0.75–1.00). Ribbons indicate 95% confidence intervals of model predictions for each passage combination. Panels represent different levels of downstream juvenile survival (0.75–1.00). The dotted, dashed, and solid black lines represent the "current" passage and Connecticut-based (CT) and Maine-based (ME) hypothetical restoration scenarios, respectively.

habitat component under a "current" passage scenario with two hypothetical restoration scenarios on four major rivers containing multiple, federally regulated hydroelectric projects in Maine. We also identified a range of fish passage performance standards that would be required for abundance levels that exceeded the targets associated with both hypothetical restoration scenarios. Similar to the results of Zydlewski et al. (2021), American Shad abundances in the upstream habitat component under the "current" passage scenario were a fraction (i.e., <4%) of the threshold abundances calculated under either hypothetical restoration scenario. This passage scenario was previously deemed optimistic compared with what is often achieved in reality (Haro & Castro-Santos, 2012; Zydlewski et al., 2021). In particular, low upstream passage effectiveness has been documented for American Shad in Maine and elsewhere, with 0% passage being documented at the first dam on the Androscoggin River (Weaver et al., 2019) and only 16 adults passing the first dam (subsequently removed) on the Penobscot River from 1978 to 2012 (MDMR, unpublished data). In addition to poor upstream passage of American Shad at existing fishways, several of the dams included in the models lack any upstream passage infrastructure, so passage into the upstream habitat component is currently impossible. That combined with the removal of non-FERC dams from our analysis adds a significant amount of optimism to our estimates (i.e., including more dams would increase performance standards required to achieve restoration scenarios). Thus, considerable improvements to fish passage infrastructure and passage effectiveness would be needed to achieve these two hypothetical restoration scenarios in the upstream habitat components of these river systems.

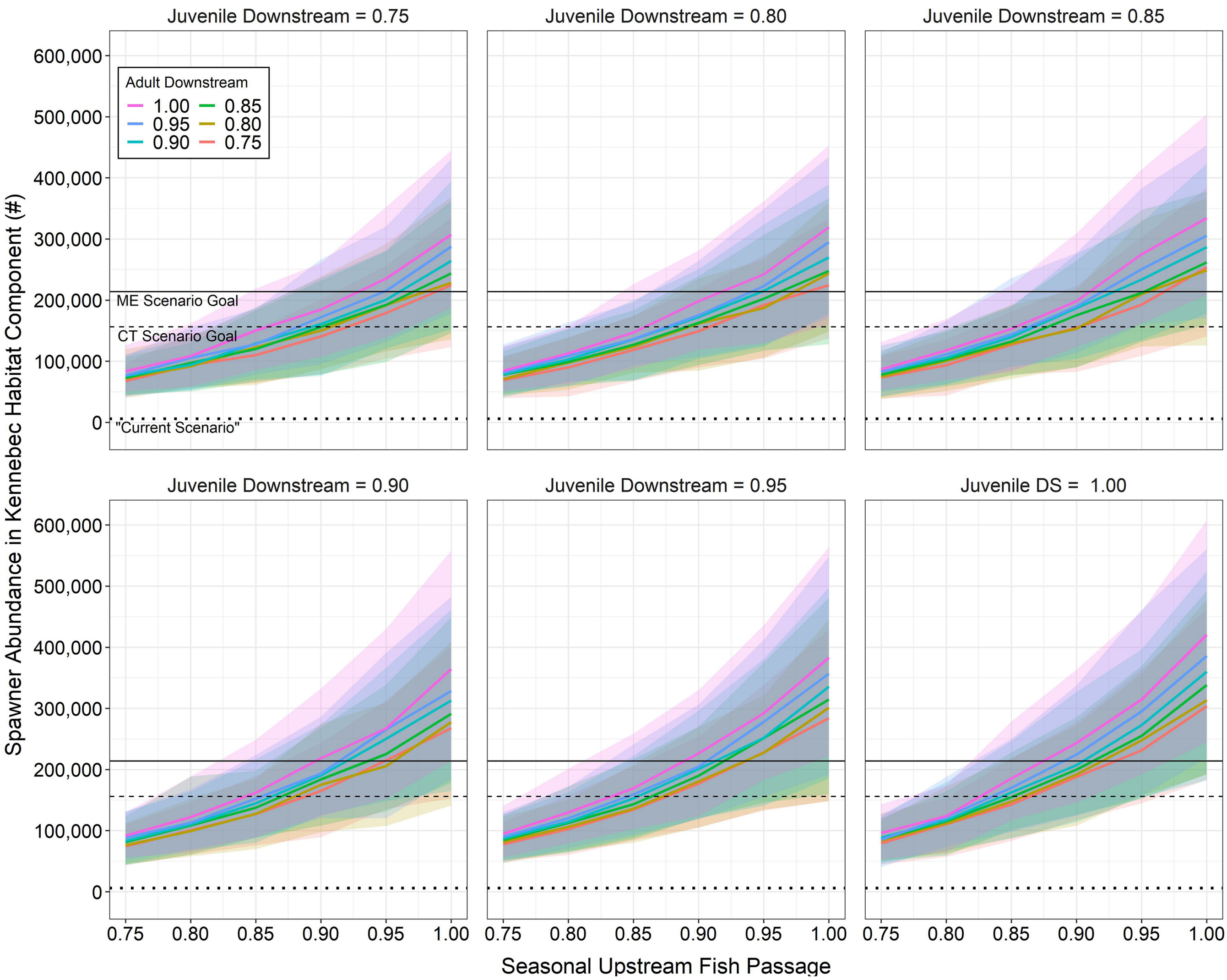

Figure 5. Modeled spawner abundance of American Shad within the upstream habitat component in the Kennebec River across a range of seasonal upstream fish passage conditions (0.75–1.00) at hydroelectric dams. Estimated abundance was low and no hypothetical restoration scenarios were achieved when upstream passage, juvenile downstream survival, or adult downstream survival was below 75%, so our results are limited to a range of 75–100% for those parameters. Solid colored lines indicate the 50th percentile of spawners across model runs, with colors representing different levels of downstream adult survival (0.75–1.00). Ribbons indicate 95% confidence intervals of model predictions for each passage combination. Panels represent different levels of downstream juvenile survival (0.75–1.00). The dotted, dashed, and solid black lines represent the "current" passage and Connecticut-based (CT) and Maine-based (ME) hypothetical restoration scenarios, respectively.

Given the clear need for passage improvements, we have identified a range of seasonal upstream and downstream performance standards that could meet two different hypothetical restoration scenarios (assuming 100% passage and survival at non-FERC dams), which were informed by management targets on the Connecticut (CRASC, 2020), Kennebec (Maine State Planning Office, 1993), and Penobscot (MDMR & MDIFW, 2008, 2009) rivers. System-specific variation in performance standards required to exceed the abundance targets associated with both scenarios are likely related to differences in the number of dams, total habitat, and the juxtaposition and size of the most upstream habitat component assessed. This is unsurprising because in the absence of dams, the model calculates fish distribution based on habitat size in the model. Of the three passage metrics considered (i.e., upstream adult passage and downstream adult and juvenile survival), upstream passage appeared to be the most immediately limiting to populations. If upstream passage was <80%, neither restoration scenario could be achieved, regardless of the combination of downstream survival rates input into the model. This is logical, as downstream survival does not matter if fish do not pass upstream in the first place. However, as upstream passage improves and adults reach upriver spawning habitats, downstream survival becomes more important (Castro-Santos & Letcher, 2010; Stich et al., 2019), particularly for juveniles (Stich et al., 2019, 2024). Highly effective upstream passage of American Shad has historically been difficult to achieve (Brown et al., 2013; Weaver et al., 2019), and increased downstream survival rates may be necessary to offset this challenge. However, our collective knowledge of fish behavior and fish passage engineering continue to improve, and some facilities have achieved high upstream passage effectiveness for American Shad (e.g., >90% Safe Harbor Dam, Susquehanna River; Groux et al., 2015; Normandeau Associates, 2021). Fishways on the Columbia River routinely pass millions of American Shad, though their performance has never been rigorously evaluated for this species (Haro & Castro-Santos, 2012). While engineered passage facilities can work, dam removal addresses both upstream and downstream passage challenges and may be the most effective solution for restoration of this species (Waldman & Quinn, 2022). In addition to providing more effective fish passage, dam removal may offer a reduced initial capital expenditure when compared to the installation of technical fishways (Magilligan et al., 2016; Nieminen et al., 2017). The *anadrofish* model is easily updated with new information; therefore, incorporating future changes such as dam removals, improved passage efficiency estimates, updated life history parameters, or updated management objectives could potentially alter the necessary performance standards at remaining dams.

Migration delays (both upstream and downstream) are an important aspect of performance standards at dams (Castro-Santos & Letcher, 2010; Stich et al., 2019). A recent study using similar models in the Penobscot River suggested that increasing passage delays from 24 to 48 h increases the percentage of fish that need to pass and thus the performance standards required to achieve management goals for American Shad on the Penobscot River (Stich et al., 2019). Delay or other time-based components of passage are treated as part of the seasonal rates within the *anadrofish* R package, just as mechanisms for fish passage (e.g., fish ladder or fish lift) are not considered individually. In cases where subseasonal, time-based rates are needed for prescriptions, those rates can be derived from our results by assuming upstream or downstream migration durations or delays incurred therein. However, future research and monitoring are needed to reliably parameterize delay standards that are sufficient to understand and mitigate biological impacts.

The model results presented herein are dependent upon multiple assumptions, many of which have been discussed previously (Zydlewski et al., 2021). The model we used currently relies on the assumption that fish distribute throughout the river proportional to habitat availability, although in theory, it maintains flexibility for incorporating alternative approaches that could be explored in the future. In reality, some riverine habitats are likely to be more productive than others and American Shad may preferentially distribute to those habitats. However, proportional distribution to habitat is a common assumption for herrings (*Alosa* spp.) (e.g., Barber et al., 2018; Zydlewski et al., 2021) and is appropriate considering the lack of river-specific habitat quality data. Similarly, the model assumes static river conditions and does not explicitly account for potential changes in thermal or hydrologic conditions in rivers that may be associated with climate change. However, other models are available to more directly assess the impacts of climate change on American Shad populations (Gilligan-Lunda et al., 2021; Stich et al., 2019), which can be used in combination with the *anadrofish* model to inform the questions at hand. While this tool does not consider in-river conditions or climate-related changes, it can be used to model predicted changes in population abundance based on observed passage rates or life history parameters derived empirically from climate-related impacts. If, for example, coastwide instantaneous natural mortality was expected to increase due to climate change (Gilligan-Lunda et al., 2021), the impacts of increased mortality on predicted population abundance could be modeled using the *anadrofish* package. The model is also reliant upon assumptions of carrying capacity. An assumed carrying capacity of ~24,710 American Shad/km^2 is used as the default in the *anadrofish* package (ASMFC, 2020; Stich et al., 2025), but alternative values can be specified by the user (see Supplementary Material 2). This value is between the production potential estimates targeted within the Connecticut River (20,263 American Shad/km^2) and Maine (27,500 American Shad/km^2) management plans (CRASC, 2020; Maine State Planning Office, 1993; MDMR & MDIFW, 2008, 2009). Sensitivity analysis of the carrying capacity parameter indicated that model results were indeed sensitive to changes in carrying capacity. Thus, future applications of these models should utilize system-specific carrying capacity estimates as opposed to the default parameter where possible.

Our study also assumes that the two hypothetical restoration scenarios derived from the Connecticut River and Maine management plans are appropriate for the rivers assessed. The value obtained from the Maine management plans (2.75 American Shad/m^2) currently forms the basis for numeric targets in a subset of historical habitat in the Penobscot and Kennebec drainages (Maine State Planning Office, 1993; MDMR & MDIFW 2008, 2009). The value has also been used to estimate the production potential on the Saco River, again, only for a subset of historical habitat (USFWS et al., 1987). This value was calculated in the early 1990s based on empirical data (i.e., fish counts at Holyoke Dam) collected from the Connecticut River (Maine State Planning Office, 1993) and used within the previous Connecticut River American Shad management plan (CRASC, 1992). Circa 2020, an updated goal of 203 American Shad/ha was set and used to support management on the Connecticut River (CRASC, 2020). Given this history, we suggest that both numbers provide appropriate estimates of American Shad production potential in the northeastern United States and therefore may be reasonable starting values for assessing performance standards for our study rivers.

We have demonstrated the utility of the *anadrofish* package (Stich et al., 2025) as one tool to aid in identifying dam passage performance standards for American Shad that meet predefined river-specific management objectives. This tool covers the native range of American Shad along the eastern coast of North America, and it is flexible enough to estimate the impacts of all or a specific subset of dams. As the connectivity landscape changes with ongoing habitat restoration efforts or as new information is collected (e.g., demonstrated passage efficiencies, river-specific carrying capacities, life history parameters), the tool can be easily updated to operate with the best available information. A critical requirement for identifying upstream and downstream performance standards in support of FERC licensing efforts is the identification and documentation of predefined management objectives. For our study rivers, the Penobscot, Kennebec, and Saco have management plans with predefined management objectives. Given quantifiable, spatially explicit objectives, this tool could be used to identify performance standards that would be required to meet these objectives. Development of operative performance standards for American Shad passage on our study rivers can be guided by this tool, but ultimately, these decisions lie with fisheries managers, hydropower practitioners, and FERC during the licensing process.

Broadly, we have modeled the impacts of poor passage of American Shad at dams and the unrealized potential in the upstream habitat component of four large rivers in Maine. While we focus specifically on the upstream extent of habitat, losses due to the presence of dams are evident throughout entire river systems coastwide (Zydlewski et al., 2021). These four rivers exemplify the conclusion put forth by Zydlewski et al. (2021). Low numbers of American Shad return on an annual basis to each river (2013–2024 mean abundance passed above the first dam: 180 [Androscoggin], 155 [Kennebec], 5,548 [Penobscot], and 4,581 [Saco]), which is a fraction of their production potential in the absence of dams (MDMR, 2024; MDMR & MDIFW, 2008; USFWS et al., 1987). Dams, therefore, are limiting the ecosystem services that may be provided by robust runs (Brown et al., 2013; Weaver et al., 2019). Poor passage and mortality of American Shad and other diadromous fish at dams is akin to an in-river fishery, which removes biomass through direct mortality and lost production, but without the benefits typically associated with a fishery. The continued existence of dam-related mortality and its effect on American Shad populations is preventing the development of an actual fishery (ASMFC, 2020) while also eliminating the delivery of a host of other ecosystem services that would benefit communities and adjacent ecosystems (Ouellet et al., 2022). Widespread improvements in passage effectiveness are needed to increase the abundance of American Shad in these river systems to enable the restoration of the wide suite of ecosystem services that they may deliver.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Transactions of the American Fisheries Society* online.

DATA AVAILABILITY

The *anadrofish* R package is available on GitHub (https://github.com/danStich/anadrofish). The authors will make data and code available upon publication of the manuscript.

ETHICS STATEMENT

This study did not involve any animal subjects and therefore did not require ethics review.

FUNDING

None declared.

CONFLICTS OF INTEREST

The authors have no conflicts of interest.

ACKNOWLEDGMENTS

We thank MDMR staff Sean Ledwin, Casey Clark, Michael Brown, and Danielle Frechette, the National Oceanic and Atmospheric Administration internal review team, and the anonymous reviewers who reviewed and provided suggestions to improve the quality of this manuscript.

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