4-2020

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Julie L. Nieland

Timothy F. Sheehan

Northeast Fisheries Science Center Reference Document 19-16

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by Julie L Nieland[1] and Timothy F Sheehan[2]

[1] Integrated Statistics, 16 Sumner Street, Woods Hole, MA 02543
Under contract to
National Oceanic and Atmospheric Administration, National Marine Fisheries Service,
Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543

[2] NOAA Fisheries Service, Northeast Fisheries Science Center,
166 Water Street, Woods Hole, Massachusetts 02543 USA

US DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northeast Fisheries Science Center
Woods Hole, Massachusetts

April 2020

Northeast Fisheries Science Center Reference Documents

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Information Quality Act Compliance: In accordance with section 515 of Public Law 106-554, the Northeast Fisheries Science Center completed both technical and policy reviews for this report. These predissemination reviews are on file at the NEFSC Editorial Office.

This document may be cited as:

Nieland JL, Sheehan TF. 2020. Quantifying the effects of dams on Atlantic Salmon in the Penobscot River Watershed, with a focus on Weldon Dam. NEFSC Ref Doc 19-16; 90 p. Available from: https://www.fisheries.noaa.gov/new-england-mid-atlantic/northeast-center-reference-document-series

TABLE OF CONTENTS

ABSTRACT

Dams are a major contributor to the decline and current low abundance of Atlantic salmon in the United States. We conducted a population viability analysis to assess the effects of dams on Atlantic salmon, focusing on hydroelectric dams and the population in the Penobscot River watershed in Maine. We simulated the life cycle of Atlantic salmon, tracking the number and origin of salmon through their various life stages, especially during the smolt and adult stages when salmon directly interact with dams. This modeling approach was previously used to assess potential management actions during Federal Energy Regulatory Committee licensing activities at 5 hydroelectric dams on the Penobscot River in 2012 and to address questions about recovering the population. We have updated the model to reflect changes in the watershed and to include recent data. We estimated adult abundance and distribution to evaluate the effects of survival at dams. In addition to dam-related scenarios, we ran scenarios to look at how hatchery supplementation, including changes in the number of smolts stocked and stocking location, and increased survival in the egg-to-smolt and marine life stages affected the population. Finally, we ran a series of scenarios focused on the Mattaceunk Project, which includes Weldon Dam and is being considered for relicensing in 2019. In these scenarios, we estimated adult abundance and distribution and smolt survival and mortality. Modeled results projected the number of adults in the Penobscot River watershed and the proportion of adults located in the upper areas of the watershed to generally increase as survival at dams increased or dams were removed. Abundance declined to zero when smolts were not stocked, and survival was low during the egg-to-smolt and marine life stages. However, adult abundance increased even without hatchery supplementation when survival increased during egg-to-smolt and marine life stages. The number and location of adults varied greatly with changes in stocking location and survival during the egg-to-smolt and marine life stages. Changes in survival at Weldon Dam did not affect the number and location of adults when survival was low during egg-to-smolt and marine life stages and when most smolts were stocked low in the watershed. However, adult abundance, including above Weldon Dam, did increase with increases in survival at Weldon Dam when survival was higher during the egg-to-smolt and marine life stages and smolt stocking numbers and locations were altered. The survival of smolts above Weldon Dam also increased as dam-related mortality decreased. Our findings indicate that Atlantic salmon abundance can increase as survival at dams increases, but hatchery supplementation will be necessary to sustain the population when survival is low in egg-to-smolt and marine life stages. Increases in survival during both of these life stages will likely be necessary to attain a self-sustaining population, especially if hatchery supplementation is reduced or discontinued.

1. INTRODUCTION

In North America, Atlantic salmon (*Salmo salar*) were historically found in rivers from northeastern Labrador to the Housatonic River in Connecticut (Kocik and Friedland 2002) and supported sustenance, commercial, and recreational fisheries (Day 2006; Goode 2006). However, abundance has declined and populations, especially those in the southern range of the species, are at or near historical lows (Moring 2005; Saunders et al. 2006). Today the only remaining Atlantic salmon populations in the United States are found in Maine. The largest of these populations is located in the Penobscot River (Figure 1.1), which on average accounted for 74% of US returns from 2007 to 2016 (USASAC 2018). Atlantic salmon in the Penobscot River are part of the Gulf of Maine Distinct Population Segment (GOM DPS) and are listed as endangered under the US Endangered Species Act (USOFR 2009b).

Multiple factors have contributed to the decline, including decreased marine survival, predation, habitat degradation, overfishing, bycatch, aquaculture, pollution, climate change, and installation of dams (NRC 2004; Moring 2005; Fay et al. 2006; Limburg and Waldman 2009). Of these factors, marine survival and dams are considered the 2 biggest threats to Atlantic salmon in the GOM DPS (NRC 2004; Fay et al. 2006) and are the primary drivers of abundance (USOFR 2009b). Mortality in the marine environment cannot be reliably influenced by human intervention in the short term (i.e., 1–2 generations), with the exception of limiting marine exploitation, but several anthropogenic sources of freshwater mortality can be addressed in the short to medium term (NRC 2004). As such, management actions have focused on increasing freshwater survival of Atlantic salmon (Windsor et al. 2012), including attempts to limit mortality from dams.

Dams affect Atlantic salmon through various direct and indirect mechanisms. Dams kill and injure fish migrating upstream and downstream (USOFR 2009b). They also prevent or impede fish passage and degrade the productive capacity of habitats upstream by inundating formerly free-flowing rivers, reducing water quality, and altering fish communities (Ruggles 1980; NRC 2004; USOFR 2009b; Pess et al. 2014).

Mortality from dams can be divided into direct and indirect categories as well. Direct mortality results from injury during passage through turbines, over fishways, or through fish bypasses that leads to death during dam passage or immediately thereafter (Cada 2001; Amaral et al. 2012). Indirect mortality can occur because of a wider range of mechanisms and over a longer period of time. For example, increased predation risk in modified habitats; increased health risk from sublethal injuries; and the additive effects of stress, injury, and delay associated with passing 1 or more dams can lead to indirect mortality (Cada 2001; Budy et al. 2002; Amaral et al. 2012; Stich et al. 2015c). Indirect effects may be realized in freshwater (i.e., indirect cumulative mortality) or long after passage (i.e., indirect latent mortality occurring in the estuary or ocean, also known as delayed mortality and delayed hydrosystem mortality; Budy et al. 2002; Schaller and Petrosky 2007; Haeseker et al. 2012). Direct and indirect mortality are both detrimental to salmon productivity (Nieland et al. 2015; Stevens et al. 2019).

The effects of dams can be mitigated in many ways, but a structured analysis should be completed before a management action is chosen. A structured analysis can support the development of management goals and actions, prioritize restoration objectives, and give realistic and quantitative expectations of outcomes (Palmer et al. 2005; Kemp and O'Hanley 2010; Nunn and Cowx 2012). Population models are an example of structured analysis, and these models are important tools for evaluating management strategies and risks (Morris and Doak 2002; McGowan and Ryan 2009; McGowan and Ryan 2010). Population viability analysis (PVA) is a way to quantitatively assess the viability of a species, especially a threatened or endangered species, and to explore the effects of management actions on those species (Beissinger and McCullough 2002).

We developed a PVA called the Dam Impact Analysis (DIA) model to simulate the effects of various sources of mortality, especially mortality caused by dams, on the endangered population of Atlantic salmon in the Penobscot River watershed. We simulated the interactions of Atlantic salmon with Federal Energy Regulatory Commission (FERC)-licensed hydroelectric dams (Figure 1.1). We used a life-history modeling approach to estimate abundance and distribution of Atlantic salmon within the watershed and at different life stages, including the smolt and adult stages when salmon interact with dams.

The DIA model was first used in FERC licensing activities at 5 hydroelectric dams in the Penobscot River in 2012 (NMFS 2012). We have updated inputs from that model version (Nieland et al. 2013, 2015) to reflect changes in the watershed and to incorporate recent data. We are now using the model for the relicensing of the Mattaceunk Project, which includes Weldon Dam, on the Penobscot River in 2019. The objective of this document is to describe the current version of the model and present results for model scenarios that included changes in dam survival, hatchery supplementation, and survival during marine and early life stages. In several of the scenarios with changes in dam survival, we focused on evaluating how changes in survival at Weldon Dam affected productivity of the Penobscot River Atlantic salmon population.

2. MODEL OVERVIEW

The Penobscot River watershed includes much of the east central portion of Maine and drains approximately 22,000 km^2 (Figure 1.1). Many diadromous species, including Atlantic salmon, are found in the watershed, but hundreds of barriers (e.g., dams and culverts) block or impede the migrations of these species (Trinko Lake et al. 2012). When building the DIA model, we only included FERC-licensed hydroelectric dams within Atlantic salmon occupied critical habitat (USOFR 2009a). We used those hydroelectric dams to divide the watershed into sections called production units (PUs). We estimated Atlantic salmon abundance and distribution as they migrated from spawning and rearing habitat, through the PUs and the northwestern Atlantic Ocean, and then back.

We divided the Atlantic salmon life cycle into 5 discrete stages: female spawners, eggs, smolts, post-smolts, and female returns (Figure 2.1). We used a simple age distribution for the smolt and adult life stages based on known characteristics of this population. Smolts were modeled as age-2 fish exclusively because the majority (80%) of naturally reared Maine Atlantic salmon emigrate as age-2 fish (relatively small proportions are age-1 and age-3; NRC 2004; USASAC 2018). Adults were modeled as 2 sea-winter (2SW) females exclusively because more than 98% of females return to the Penobscot River after 2 winters at sea (Justin Stevens, Integrated Statistics under contract to the National Marine Fisheries Service (NMFS), personal communication) and because egg deposition is a primary limiting factor for this population (Chaput et al. 2005; Fay 2006; USASAC 2018). Kelts (i.e., potential repeat spawners) were not included in the model because of limited quantitative information for model inputs and the limited number of kelts in the present-day Penobscot population (USASAC 2018).

One life cycle for Atlantic salmon occurred over 5 years in the model. In year 1, 2SW females (both wild-origin and hatchery-origin) were seeded into PUs. The number of females was multiplied by the number of eggs produced per female to estimate the number of eggs in that same year. Eggs were considered wild fish regardless of parentage because all eggs were spawned in the river rather than in a hatchery. The number of eggs was multiplied by the egg-to-smolt survival rate to estimate the number of smolts in year 4. The number of wild smolts in each PU was limited by the amount of rearing habitat. Therefore, if the number of wild smolts in a PU exceeded the amount of habitat available to support them, a smolt production cap was applied, reducing the number of wild smolts to the maximum allowed for that PU to ensure that estimates of smolt abundance remained biologically reasonable. Hatchery supplementation also occurred at the smolt stage. Multiple life stages of Atlantic salmon are stocked in the Penobscot River, but we focused on smolt stocking. A smolt production cap was not applied to hatchery smolts because we assumed these smolts began downstream migration soon after being stocked and, therefore, habitat was not considered to be a limiting factor (Aprahamian et al. 2003).

Wild and hatchery smolts migrated from their initial PU through subsequent downstream PUs, over dams, and to Verona Island in year 4. Wild and hatchery smolts experienced the same natural and dam-related mortality during this migration. Smolts migrating through a PU experienced natural mortality first and then dam-related mortality just before exiting the PU and entering another. To account for natural mortality, the number of smolts in a PU was multiplied by a distance-specific, in-river, survival rate. Then 3 types of dam-related mortality were applied to smolts: impoundment, direct, and indirect cumulative mortality. Impoundment mortality occurred immediately upstream of a dam, and the number of smolts that survived in-river mortality was multiplied by the impoundment survival rate. This mortality was applied at Weldon Dam only. Direct and indirect cumulative mortality were accounted for by using dam-specific smolt survival estimates. The number of smolts remaining after impoundment mortality was multiplied by these smolt survival estimates. Smolts were subjected to in-river and dam-related mortality in their initial PU and through subsequent downstream PUs until they reached the southern end of Verona Island.

During downstream migration, smolts can migrate through 1 of 2 pathways in the lower river: the Stillwater branch (to the west of Indian Island) or the mainstem of the Penobscot River (to the east of Indian Island). The number of smolts upstream of the Stillwater/mainstem split was multiplied by the proportion of smolts that chose the Stillwater path. Those smolts experienced in-river and dam-related mortality specific to the Stillwater branch. Smolts that did not use the Stillwater branch migrated down the mainstem and experienced in-river and dam-related mortality specific to that part of the river. Smolts that survived migration through these 2 paths were summed at the confluence of the Stillwater branch and mainstem and continued migration to Verona Island.

The number of smolts that successfully migrated to the southern end of Verona Island was considered the number of post-smolts entering the marine environment. Another type of dam-related mortality, indirect latent mortality, occurred during the post-smolt life stage, which was also in year 4. The amount of indirect latent mortality that post-smolts experienced was based on the number of dams encountered during downstream migration. Therefore, post-smolts originating from different areas of the watershed may have experienced different amounts of indirect latent mortality. For post-smolts that originated in each PU, the indirect latent mortality rate was multiplied by the number of dams that were passed to reach the marine environment, subtracted from 1, and then multiplied by the number of post-smolts that had reached the southern end of Verona Island.

A discount could be applied to hatchery smolts in the post-smolt phase. Although wild and hatchery smolts were treated the same during downstream migration, hatchery smolts typically experience lower survival than wild smolts. So, a hatchery discount factor was developed to adjust the number of hatchery smolts to wild equivalents before they entered the marine environment. The number of hatchery smolts would be divided by the hatchery discount to give the wild-equivalent number of post-smolts. This discount was not used because origin-specific marine survival rates were available, and, therefore, the lower survival rate of hatchery smolts was accounted for.

The remaining post-smolts were both male and female, but the number of female post-smolts was needed to estimate the number of adult female returns. We assumed an equal male-to-female ratio at the post-smolt life stage. Consequently, the number of post-smolts was halved to convert the number to female post-smolts.

Female post-smolts entered into the marine environment in year 4 and returned to the Penobscot River as 2SW females in year 6. To estimate the number of 2SW female returns, the number of female post-smolts was multiplied by the origin-specific marine survival rates, as noted above.

We assumed a 100% homing rate to the Penobscot River, so all surviving 2SW females returned to the watershed. Homing within the river to a specific PU, however, is likely less than 100%. In-river straying of 2SW females was incorporated by assigning a target PU based on estimated straying rates. The number of 2SW females from a natal PU was multiplied by the proportion estimated to stray to each target PU. This process was repeated for each natal PU. The number of 2SW females in a target PU equaled the sum of all 2SW females assigned from all natal PUs. Straying rates were not differentiated based on whether the fish were wild-origin or hatchery-origin.

As 2SW females attempted to migrate upstream from Verona Island in year 6, most fish had to pass at least 1 dam to reach their target PU. Therefore, where appropriate, the number of 2SW females below a dam was multiplied by the dam-specific upstream passage efficiency rate. The 2SW females that passed the dam continued their upstream migration, whereas those that were unable to pass the dam died, returned to the ocean without spawning, or strayed and spawned in a downstream PU. These 3 outcomes were known as "upstream dam passage inefficiency." The number of 2SW females that did not pass the dam was multiplied by the corresponding proportion for each type of upstream dam passage inefficiency. Of the 2SW females that strayed because of unsuccessful upstream passage, that number was multiplied by the proportion assigned to stray to each downstream PU. In-river morality was not applied during upstream migration because we assumed freshwater mortality in free-flowing stretches of river would be low for adult Atlantic salmon.

For 2SW females that successfully migrated past Milford Dam, 150 of those fish, regardless of origin, were removed for hatchery broodstock collection. The 2SW females were removed from the population proportional to their relative abundance. The 2SW females that did not die, return to the ocean, or become part of the hatchery broodstock spawned and produced eggs in year 6, which was the first year of the next life cycle. Life cycles continued for a total of 75 years, or 15 generations.

Numbers, locations, and origin of fish were tracked at each life stage. The initial number of adults used to seed the model in generation 1 was based on estimated adult escapement, and adults were assigned to an initial location based on smolt stocking locations and straying rates by using a multinomial distribution. Numbers of fish were rounded rather than binomially assigned in all subsequent abundance calculations. Rounding the abundance maintained whole numbers of fish but minimized computation time. Monte Carlo simulations were used to incorporate stochastic variation in the life processes (Goodman 2002). Year-specific and iteration-specific random draws were made from model input distributions. The length of 1 iteration was 75 years, and 10,000 iterations were run for each model scenario unless otherwise noted. The model was built in Microsoft® Excel® with the @RISK® add-on.

We estimated smolt survival and mortality and adult abundance and distribution within the watershed and compared these metrics across different modeling scenarios to evaluate changes in the productivity of the population. The model was not meant to predict absolute abundance but was intended to project relative change in abundance and distribution under different scenarios.

3. MODEL INPUTS

Many of the model inputs differ from the model version used in the relicensing of 5 hydroelectric dams in the Penobscot River in 2012 (NMFS 2012; Nieland et al. 2013, 2015). We have updated inputs to reflect changes in the watershed and to include recent data and best available information. The following descriptions represent the baseline conditions for each input, but the inputs can be adjusted for different model scenarios.

3.1 Production Units

Using FERC-licensed hydroelectric dams, we divided the watershed into PUs (Figure 1.1). In each PU, the upstream boundary was either the headwaters of a tributary or a dam, and the downstream boundary was a dam, except at the mouth of the river (PU 14), where the boundary was the southern end of Verona Island, or the marine environment (Table 3.1.1). This spatial scheme helped isolate the locations where salmon and dams interacted in the model.

Nieland et al. (2013, 2015) modeled 15 FERC-licensed hydroelectric dams. Through the Penobscot River Restoration Project (PRRP; Day 2006), 2 of those dams were removed (Great Works Dam in 2012 and Veazie Dam in 2013), and another was decommissioned and a bypass was built (Howland Dam in 2016; Figure 1.1). We combined the 2 PUs that were delineated by Great Works and Veazie dams with the lowest PU in the watershed because the removal of those dams made 1, continuous river segment (PU 14). We did not change the PUs delineated by Howland Dam because the dam structure still exists and is assumed to affect downstream migration.

Estimated stream lengths were also important characteristics of the PUs (Table 3.1.1). The longest segment length was the longest straight-path distance that a fish could migrate in a PU, and the partial segment length was the distance that a smolt would migrate when traversing from 1 PU to another (e.g., a smolt leaving PU 2 would migrate from Weldon Dam to West Enfield Dam in PU 3; Figure 1.1). Therefore, a PU with 1 or more partial segment lengths indicated that smolts could enter the PU from multiple locations. Longest and partial segment lengths were updated from the last model version to correct minor errors in the distance calculations. We also added hatchery segment length, which was the distance that stocked smolts would migrate in the PU where they were stocked. The hatchery segment length was estimated by using stocking location or the mean of stocking locations. Several PUs had not been stocked previously, and we used expert opinion to estimate the likely stocking location in those PUs (Justin Stevens, Integrated Statistics under contract to NMFS, personal communication).

Habitat units were also used to describe each PU (Table 3.1.2). The total number of Atlantic salmon habitat units (in 100 m^2) in each PU was calculated by using a model that estimated spawning and rearing habitat (Wright et al. 2008). The number of accessible habitat units demonstrated the amount of habitat that Atlantic salmon could access because of conditions at hydroelectric dams.

Atlantic salmon are unable to access the habitat in several areas of the Penobscot River. For example, the West Branch of the Penobscot River (PU 1; Figure 1.1) contains 26.6% of high value (and historically accessible) habitat in the watershed (Table 3.1.2; Wright et al. 2008), but no salmon are able to access this area of the river because of a lack of adult passage at Medway Dam. This dam marks the lower boundary of the West Branch and has no formal upstream or downstream passage facilities for Atlantic salmon. Although we included the West Branch in the model, this PU did not contribute to the Atlantic salmon population because of the lack of passage at Medway Dam. The West Branch has the potential to contribute significantly to future recovery efforts if Atlantic salmon are able to migrate into and out of this area.

3.2 Seeding the Model

We seeded the model with adults in generation 1. In previous versions of the model, the number of seeded 2SW females was based on the number of adults returning to the Penobscot River, but some of those returns were removed for use as broodstock and did not spawn in the river. Using estimated escapement instead of the number of adult returns would more accurately represent the contemporary Penobscot River population by accounting for the number of adults removed for broodstock purposes. Therefore, in the current version of the model, we based the number of seeded 2SW females on estimated escapement to more accurately reflect reality. Previously, all 2SW females were seeded into the model as wild-origin fish. However, in the current model version, we seeded both wild- and hatchery-origin 2SW females based on the proportions of naturally reared and hatchery-origin 2SW female returns. The seeding locations were previously based on the amount of Atlantic salmon habitat available in each PU, but many salmon are not able to reach habitat higher in the watershed because of migration barriers, such as dams. In the current version of the model, we used smolt stocking locations and adult straying rates to estimate where smolts would return as adults and seeded 2SW females into those locations.

The number of 2SW females seeded in generation 1 was based on Penobscot River escapement, but actual escapement into the river is not easily tallied because of the complex management of broodstock transported to and from Craig Brook National Fish Hatchery. To estimate escapement for the past 10 years, we first estimated the number of 2SW returns by using adult return data from the fishway trap above Veazie Dam (2008–2013) and the fish lift at Milford Dam (2014–2017; MDMR 2018). The Maine Department of Marine Resources (MDMR) estimated sea age by using scale samples collected from a subset of returning adults each year. Scales were collected from each fish taken for broodstock and all fish on sample days, which encompassed roughly 30% of the days the trap was scheduled for operation each year. (The trap at Veazie Dam operated May 1–October 30, and the fish lift at Milford Dam operates April 15–November 15.) Fish sampled for length but not age in each year were assigned an age by using an annual age-length key constructed from fish that were sampled for both length and age. Generally, the lengths of 1 sea-winter and 2SW fish overlap very little, so all of the fish in a length class were usually assigned to 1 age class. The sex of each fish was assigned at the trap or fish lift based on external morphological characteristics. For fish that were taken to the hatchery, sex was confirmed based on gametes observed during spawning, and, when necessary, corrections were made to the data. However, the number of corrections was not tracked, so we assumed sex determination accuracy was consistent for both broodstock and released fish. From these data, we calculated the mean of the total number of 2SW female returns from 2008 to 2017 and then subtracted 150, which was the target number of 2SW females removed from the Penobscot River each year to support the smolt stocking program (Fay et al. 2006). The mean total number of 2SW female returns was 487, and so we seeded the model with 337 2SW females.

We also designated the seeded 2SW females as wild-origin or hatchery-origin fish. The MDMR assigned origin by inspecting fish for fin clips at the fishway trap or fish lift or by analyzing scale samples from the subset of returning adults (MDMR 2018; MDMR fishway trap database, 2018 version). Any fish without a fin clip or with natural growth patterns on the scale (i.e., multiple freshwater annuli) was assigned as naturally reared, whereas any fish with a fin clip or hatchery growth patterns on the scale was assigned as a hatchery-origin fish. Fish that were not subsampled were assigned as naturally reared or hatchery-origin based on the annual proportions of each origin as calculated by using the scale samples. We calculated the proportions of naturally reared and hatchery-origin 2SW females from 2008 to 2017. The proportions were then multiplied by the number of 2SW females seeded in the model to estimate the number of naturally reared and hatchery-origin fish in generation 1. These estimates were rounded to maintain whole numbers of fish. Of the 337 2SW females seeded in the model, 31 were wild-origin and 306 were hatchery-origin fish.

We seeded the 2SW females into PUs based on smolt stocking locations and adult straying rates. Because the majority of returning 2SW females from 2008 to 2017 were hatchery-origin fish, we used a submodel to track where 1 generation of hatchery smolts would be estimated to return as 2SW females and used those locations to seed adults in the model in generation 1. We seeded 545,000 smolts only (i.e., no adults) into PUs based on the mean of the number of stocked smolts and their stocking locations from 2008 to 2017 (Table 3.2.1; USASAC 2018). We tracked the numbers and locations of smolts through the submodel as they migrated downstream to the ocean and then back upstream 2 years later as adults. A portion of returning 2SW females strayed from the PUs where they were stocked (Table 3.2.2), resulting in adults occupying PUs where they were not seeded. We ran 10,000 iterations and used the median number of 2SW females in each PU in generation 2 to calculate the proportion of adults in each PU. Adults were randomly assigned to PUs according to a multinomial distribution based on the proportion of adults in each PU (Table 3.1.2). No adults were seeded in PUs 1, 7, 8, and 11 because of the lack of upstream dam passage at the downstream boundaries.

3.3 Eggs per Female

Atlantic salmon spawn at multiple ages, with older females typically producing more eggs (Baum 1997). We used fecundity data from Penobscot River female returns to estimate the number of eggs that would be produced by a 2SW female. In the model, we applied the fecundity rate to 2SW female returns in each PU to estimate the number of eggs produced in the same year.

Each year, Atlantic salmon returning to the Penobscot River are collected for hatchery broodstock purposes and spawned at Craig Brook National Fish Hatchery. Fecundity is estimated annually, and we used the 1997–2010 estimates to create a distribution for the number of eggs produced per 2SW female (Denise Buckley, US Fish and Wildlife Service [USFWS], personal communication). The data were primarily (greater than 98%) from 2SW females, but a small number of older females were also spawned each year. We fit a distribution to the mean annual number of eggs per female by using a combination of characteristics of the data and goodness of fit tests in @RISK®. The data were best described by a normal distribution with mean $\mu = 8{,}304$ and standard deviation $\sigma = 821$ defined on the interval (4,000, 12,000) (Figure 3.3.1). We did not have a minimum or maximum for the distribution in previous model versions, but we felt these bounds would help keep the number of eggs produced per 2SW female in a realistic range. Year-specific and iteration-specific values were drawn from this distribution for the baseline fecundity values.

3.4 Egg-to-Smolt Survival

Atlantic salmon reside in rivers from the time they are eggs until they migrate to the ocean as smolts. This period includes the egg, fry, parr, and smolt life stages. We did not simulate Atlantic salmon abundance in all of these life stages but instead estimated an egg-to-smolt survival rate. We applied this survival rate to the number of eggs in a year to estimate the number of smolts that would survive 3 years later (i.e., age-2 smolts) and be available to initiate downstream migration to the ocean.

We updated the egg-to-smolt survival distribution provided by Legault (2004) with contemporary studies (Aprahamian et al. 2004; Millard 2005). Survival rates for egg to fry, fry to parr0+, parr0+ to parr1+, and parr1+ to smolt life stages were obtained from the literature and combined by using a process that would account for uncertainty in each study (Legault 2004). In order to combine the survival rates for a particular life stage, the rates were standardized to the same time interval. The standardized mean, minimum, and maximum values were used to generate a triangular distribution for each study. The distributions were added together to form a new distribution of the probability of survival for that life stage. This probability distribution function was converted to a cumulative distribution function, and the 10th and 90th percentiles were used as the limits of a uniform distribution. The uniform distribution was used to describe the uncertainty in survival for each life stage.

Combining the survival rates across these life stages produced a possible range of 0.10–5.88% for the egg-to-smolt survival rate (Table 3.4.1). The egg to fry, fry to parr0+, parr0+ to parr1+, and parr1+ to smolt distributions were each sampled 10,000 times, and the life stage survival values from each iteration were multiplied together to calculate an egg-to-smolt survival rate. The sum of random values from the egg to fry, fry to parr0+, parr0+ to parr1+, and parr1+ to smolt distributions was approximately normal by the central limit theorem, and egg-to-smolt survival could be expressed as the sum of the natural logs of each survival rate (Hilborn and Walters 1992; Legault 2004). Therefore, egg-to-smolt survival approximated a lognormal distribution. The distribution was described by $\mu = 1.31\%$ defined on the interval (0.10%, 5.88%) with a 90% confidence interval between 0.5 and 2.4%. We previously used these parameters to estimate the egg-to-smolt survival distribution. In the current model version, we fit a lognormal distribution with these parameters. Egg-to-smolt survival was best described by a lognormal distribution with $\mu = 0.0133$ and $\sigma = 0.0086$ defined on the interval (0, 0.23) (Figure 3.4.1). Year-specific and iteration-specific values were drawn from this distribution for the baseline egg-to-smolt survival values.

3.5 Smolt Production Cap

The number of smolts that are able to survive in an area is in large part related to how much habitat is available. We limited the number of wild smolts in each PU with a smolt production cap, which was the maximum number of smolts allowed per habitat unit (in 100 m^2).

Meister (1962) estimated that the Penobscot River could produce 3 smolts per 100 m^2. Previous versions of the model used a smolt production cap of 10 smolts per 100 m^2, which may be too high. A literature review was conducted to look at the numbers of Atlantic salmon smolts produced in various rivers (Table 3.5.1). We did not consider rivers in Europe to be comparable to the Penobscot River because of the large geographic expanse between the eastern and western Atlantic and differences in freshwater habitat types. Therefore, we removed data from European rivers. We also removed data from 3 North American rivers because Atlantic salmon in these rivers exhibit different life history traits than Atlantic salmon in Maine. The remaining rivers were located in the northeastern United States and Nova Scotia, and a maximum of 4.10 smolts per 100 m^2 were observed (Meister 1962; Orciari et al. 1994; McMenemy 1995; Whalen et al. 2000; Bowlby et al. 2013). We increased the smolt production cap to 6 smolts per 100 m^2 to allow for the possibility that high quality habitat might produce more smolts than the observed maximum (Table 3.1.2). This cap was similar to the average maximum production (5 smolts per 100 m^2) for age 2+ smolts estimated by Symons (1979) and prevented biologically unrealistic outputs from being produced via stochastic sampling.

3.6 Stocking

Hatchery-origin fry, parr, and smolts are stocked annually into the Penobscot River. These fish supplement wild production and therefore play an important role in the recovery of the Atlantic salmon in the Penobscot Bay Salmon Habitat Recovery Unit (SHRU). We included hatchery supplementation in the model to convey this importance. We did not include stocking from all 3 life stages but focused on smolts because approximately 90% of adult returns to the Penobscot River originated from smolt stocking (USASAC 2018).

We simulated stocking 545,000 smolts annually to mimic the mean number and distribution of smolts stocked in the Penobscot River watershed from 2008 to 2017 (Table 3.2.1; USASAC 2018). Stocking location and the distance stocked smolts would have to migrate downstream through each PU were estimated based on the historical stocking sites and expert opinion (Table 3.1.1; Justin Stevens, Integrated Statistics under contract to NMFS, personal communication). We used expert opinion to estimate the stocking location in PUs that had not been stocked previously because we wanted to have the ability to run model scenarios with stocking in any PU. The smolt stocking number, distribution, and migration distances were all updated from previous model versions (Nieland et al. 2013, 2015). Hatchery smolts migrated with their wild conspecifics. The smolt production cap was not applied to hatchery smolts because we assumed these smolts began their downstream migration soon after being stocked, and so habitat was not considered to be a limiting factor.

Smolt stocking could be turned on or off on an annual basis in the model. When smolt stocking was turned on, 545,000 smolts were stocked and 2SW females were removed for use as broodstock (Section 3.17). Smolts were stocked annually regardless of the number of 2SW females removed for broodstock because we assumed shortages in broodstock would be covered by backup sources. When smolt stocking was turned off, no smolts were stocked and no 2SW females were collected for use as broodstock.

3.7 In-river Mortality

Smolts experience natural mortality as they migrate downstream. In the model, we referred to this type of mortality as in-river mortality and applied it based on the distance that a smolt migrated. In-river mortality occurred in free-flowing stretches of the river, and therefore, dam-related mortality during downstream migration was separate. In-river mortality can be an important source of mortality for smolts, especially those migrating long distances (Stevens et al. 2019).

We developed an in-river mortality distribution from telemetry data collected in undammed sections of the Penobscot River from 2005 to 2006 and 2009 to 2010 (Stich et al. 2015a). We reexamined the methods that we used to develop the distribution (Nieland et al. 2013, 2015) because a recent estimate of the mean in-river mortality in the Penobscot River (0.005 per km; Stich et al. 2015a) was an order of magnitude greater than the mean of the in-river mortality distribution that we used previously (0.000203 per km; Nieland et al. 2015).

Wild-origin and hatchery-origin smolts were tagged and released at various locations throughout the Penobscot River watershed (Holbrook et al. 2011). Mortality estimates between successive telemetry receivers/arrays for each year-specific and origin-specific release group were standardized to compare mortality among river segments of different lengths. While reviewing our methods, we discovered that mortality per km was calculated differently for the 2005–2006 data than for the 2009–2010 data. This error was corrected, and the mean mortality rate per km for both data sets was estimated as the survival in a segment to the power of the inverse length subtracted from 1. Only fish that survived to the first receiver/array were included to eliminate potential bias associated with tagging-related mortality. Mortality estimates from successive telemetry receiver/array pairs that spanned a hydroelectric facility were excluded because dam-related mortality was estimated separately. Sixty-four estimates of mortality per km were available, but 11 were removed from the analysis because of concerns that they were biased by effects from tagging-release, small river segment length (< 1 km), or 2 dams flanking the river segment. The remaining mortality-per-km estimates ranged from 0 to 0.0293 per km, and the data were used to create a cumulative frequency distribution with $\mu = 0.00329$ and $\sigma = 0.00459$ defined on the interval (0, 0.02928) (Figures 3.7.1 and 3.7.2). The 2 largest mortality-per-km values were unintentionally excluded from the previous cumulative frequency distribution (Nieland et al. 2013, 2015) but were included in this version. An in-river mortality-per-km value was randomly drawn from this distribution for each PU, year, and iteration.

The mean of our new distribution is comparable to that of Stich et al. (2015a). Our mean is likely different because we used telemetry data from 2005 to 2006 and 2009 to 2010, whereas Stich et al. (2015a) used telemetry data from 2005 to 2006, 2009 to 2010, and 2011 to 2014. We also excluded 11 mortality-per-km estimates from river segments that we considered biased, but Stich et al. (2015a) included estimates from all free-flowing segments.

We used our in-river mortality-per-km distribution to estimate the number of wild and hatchery smolts that survived downstream migration through each PU. The starting location of wild smolts in their natal PUs was unknown. Therefore, we assumed these fish migrated half of the longest straight-path distance in each PU (Table 3.1.1). The number of wild smolts that survived migration through their natal PU equaled in-river mortality per km to the power of half of the longest straight-path distance subtracted from 1. Historical stocking data and expert opinion were used to estimate the starting location of stocked smolts (Table 3.1.1; Justin Stevens, Integrated Statistics under contract to NMFS, personal communication). The number of stocked smolts that survived migration through their initial PU equaled in-river mortality per km to the power of stocking distance subtracted from 1.

In subsequent PUs, we assumed smolts swam directly from dam to dam (or from the dam to Verona Island in the case of PU 14) when traversing from 1 PU to the next (Table 3.1.1). Survival of smolts through these PUs equaled in-river mortality per km to the power of the distance subtracted from 1.

3.8 Impoundment Mortality

Before smolts attempt to pass a dam, they must migrate through the impoundment. The impoundment is the area immediately upstream of a dam and typically has more lacustrine than riverine habitat because of the water that is being stored by the dam. Impoundments can be areas of high mortality for smolts, mainly because of increased mortality from fish and bird predators (Jepsen et al. 1998; Okland et al. 2016). We added impoundment mortality in this model version, and smolts would be subjected to this mortality after in-river mortality but before dam-related mortality. At this time, we have only included impoundment mortality at Weldon Dam in the model.

We used estimates of survival per km through the Weldon impoundment (Stich et al. 2015a, online supplementary material, Table S3; https://www.nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0573/suppl_file/cjfas-2014-

0573suppl.docx) and the mean in-river survival-per-km estimate (0.995 per km; Stich et al. 2015a) to estimate mortality through the impoundment. We used these survival estimates to compare survival through the Weldon impoundment to survival through a free-flowing stretch of the river of the same length. The Weldon impoundment was composed of 3 river segments delineated by the location of the acoustic telemetry receivers. Survival over the 3 segments was estimated as the product of each segment-specific survival rate per km to the power of the associated segment-specific length. The in-river survival estimate was the mean in-river survival-per-km estimate to the power of the summed length of the 3 Weldon impoundment segments. We calculated the mean annual differences between Weldon impoundment and in-river survival from 2012 to 2014 and found survival through the Weldon impoundment was 0.072 less than survival through a free-flowing segment of the same length. Therefore, we set Weldon impoundment mortality at 0.072. We estimated the number of smolts that survived through the Weldon impoundment as the product of the number of smolts in PU 2 after in-river mortality and the impoundment mortality subtracted from 1.

3.9 Downstream Dam Survival Rates

Hydroelectric dams affect Atlantic salmon through various mechanisms with a wide range of effects. They reduce habitat productivity by inundating formerly free-flowing rivers, reducing water quality, and altering fish communities; prevent and impede fish passage; and injure and kill fish (Ruggles 1980; NRC 2004; USOFR 2009b; Pess et al. 2014).

Mortality from dams can be divided into 2 categories: direct and indirect. Direct mortality results from injury during passage through turbines, over fishways, or through fish bypasses that leads to death during dam passage or immediately thereafter (Cada 2001; Amaral et al. 2012). Indirect mortality occurs through several mechanisms, such as increased predation risk in modified habitats and increased health risk from sublethal injuries (Cada 2001; Amaral et al. 2012). We classify these indirect effects as indirect cumulative mortality, and they occur in freshwater. Another type of indirect mortality (i.e., indirect latent mortality) exists but occurs in the estuary or ocean (Section 3.10).

3.9.1 Desktop Survival Analysis and Downstream Flow Correlation

Because of the range of effects and multiple types of mortality that hydroelectric dams can have on Atlantic salmon, we wanted site-specific estimates of smolt survival for the dams included in the model. To account for direct and indirect cumulative mortality, smolt survival rates for May were estimated based on river flow and how operations at the dams were predicted to change with flow (Figure 3.9.1.1; Amaral et al. 2012; Nieland et al. 2013). Data from each dam (e.g., turbine type, revolutions per minute, head, and presence of fishways), fish characteristics, and hydrological records were used to estimate the smolt survival rates. Survival was estimated for May because the majority of smolt migration occurs in that month. Smolt survival rates at low flow were a function of dam configuration and operation (e.g., whether fish passed over spillways, through bypasses, or through turbines and when individual turbines came online; Amaral et al. 2012) and, therefore, did not always increase with flow (Figure 3.9.1.1).

Generally, survival of smolts migrating past hydroelectric dams is positively correlated with river flow. Flow within the Penobscot River watershed is highly correlated among sections of the watershed as well (correlation coefficient $\mu = 0.901$ for mean April–June flow rates in the Penobscot River watershed from 1935 to 2009; Nieland et al. 2013; http://waterdata.usgs.gov/nwis). For example, if 1 dam on the Penobscot River is experiencing high flows, and consequentially high smolt survival, all dams are likely experiencing similar high flows and high smolt survival. To mimic the correlation of flow within the Penobscot watershed and determine subsequent smolt survival, we selected independent year-specific and dam-specific uniform random variables defined on the interval (-0.1695, 0.1695) (Nieland et al. 2013). Then we added a year-specific uniform random variable common to all dams defined on the interval (0, 1) to each year-specific and dam-specific random variable to determine the cumulative flow probabilities and approximate the same level of correlation as the Penobscot River flow time-series data. We used the same cumulative flow probability for dams located less than 15 km apart because no difference in flow is expected given the short distance between these dams. The cumulative flow probabilities were used to find the corresponding smolt survival rates for each dam, year, and iteration (Figure 3.9.1.1).

We did not follow the process above for smolt survival at several dams but instead set survival at a specific value for all years and iterations. We set smolt survival at Medway Dam at zero because this dam lacks downstream passage. At Upper Dover Dam, no turbine entrainment occurs and no downstream bypass is available, so baseline smolt survival was set at 0.9215 (i.e., the product of 0.97 spillway survival and 0.95 indirect cumulative survival). In contrast to previous model versions, we set baseline smolt survival at Great Works, Veazie, Howland, West Enfield, Milford, Stillwater, and Orono dams to reflect conditions after the PRRP and a species protection plan (SPP) were put in place. Through the PRRP, Great Works and Veazie Dam were removed. We "removed" these dams in the model by setting their downstream survival rates as 1 in all model scenarios. Howland Dam was also decommissioned as part of the PRRP, and a nature-like bypass was built around the dam. We did not "remove" Howland Dam from the model because the dam structure still exists, and we assumed the structure could affect downstream migration. However, because of fish passage improvements at Howland Dam, recent smolt survival was estimated as 1 (Joseph Zydlewski, US Geological Survey (USGS)/University of Maine, personal communication). Although the bypass seems to be passing fish effectively, the survival estimate was based on 1 year of data (2016), and natural mortality that occurs in the bypass has not been accounted for. However, given the short distance in the bypass, any mortality is likely negligible, and we consider our results to be robust. Therefore, we set the baseline smolt survival for this dam at 1. Future studies will further inform the estimate of downstream survival at Howland Dam. In 2012, a SPP was put in place for Atlantic salmon during the FERC-relicensing process for 5 dams on the Penobscot River (NMFS 2012). The SPP called for 0.96 smolt survival at West Enfield, Milford, Stillwater, and Orono dams, and NMFS expected this rate to be achieved at each dam (NMFS 2012). Multiple downstream passage studies conducted at each dam suggested most dams achieved this survival goal under an intentional spill program (Brookfield 2017). Therefore, we set baseline smolt survival at 0.96 for these 4 dams.

Whether the smolt survival rate was drawn from a distribution or was a constant rate, we estimated smolt survival the same way. The number of smolts immediately before a dam (i.e., the number after in-river mortality or Weldon impoundment mortality) was multiplied by the smolt survival rate to estimate the number of smolts that survived migration passed the dam.

3.9.2 Downstream Path Choice

One of the features of the Penobscot River is a 17-km long side channel located in the lower river, called the Stillwater branch (Figure 1.1). Smolts that originated upriver of the Stillwater branch can migrate downstream via this branch or the mainstem of the river and likely experience different survival through the 2 routes because of local environs and differences in the number, configuration, and operation of hydroelectric dams. Therefore, the proportion of smolts that use the Stillwater branch was estimated from telemetry studies in the Penobscot River from 2005 to 2006 and 2009 to 2010 (Stich et al. 2014). Stich et al. (2014) contains additional years of data. However, we did not change this input from the previous model version. A triangular distribution defined on the interval (0.044, 0.259) with the most likely value = 0.259 was fit to the data (Figure 3.9.2.1). Stillwater branch use is also positively related to river flow (Holbrook 2007; Holbrook et al. 2011). Because of this relationship, we correlated Stillwater branch use with river flow in the same manner as the smolt survival estimates. The cumulative flow probabilities were used to find the corresponding Stillwater use rate for each year and iteration. The number of smolts migrating through the Stillwater branch was the product of the Stillwater use rate and the number of smolts in PU 9 that would migrate downstream. The remaining smolts migrated through the mainstem.

3.10 Indirect Latent Mortality

As smolts complete the freshwater portion of their migration and begin their marine migration, they transition to the post-smolt stage. We considered the estimated number of smolts that successfully migrated through PU 14 to be the number of post-smolts entering the marine environment.

Post-smolts are affected by an additional type of indirect mortality: indirect latent mortality. This mortality, also known as delayed mortality and delayed hydrosystem mortality, occurs in the early marine phase of Atlantic salmon life history and is due to the effects of stress and injury associated with passing 1 or more dams (Budy et al. 2002; Schaller and Petrosky 2007; Haeseker et al. 2012). These effects may extend beyond the estuary, but at this time, we do not have data to inform this theory.

We updated our indirect latent mortality rate to 0.06 per dam passed to align with a recent Penobscot River-specific estimate (Stich et al. 2015c). The indirect latent mortality rate was applied based on the number of dams that fish passed. The product of the indirect latent mortality rate and the number of dams passed was subtracted from 1. The resulting survival rate was multiplied by the number of post-smolts that had passed that number of dams. This process was repeated for the different number of dams that fish passed to estimate the number of post-smolts that survived indirect latent mortality.

3.11 Hatchery Discount

Wild-origin and hatchery-origin smolts experience the same types of mortality, but hatchery-origin smolts typically experience lower survival. Because of this difference in survival, we developed a discount factor to adjust the number of hatchery-origin smolts to wild equivalents before they entered the ocean. Survival rates from the smolt to adult life stage were estimated to be 1.18–8.20 times greater for wild fish than for hatchery fish (Jonsson et al. 1991, 2003; Crozier and Kennedy 1993; Jonsson and Fleming 1993; Jutila et al. 2003; Kallio-Nyberg et al. 2004, 2011; Saloniemi et al. 2004; Jokikokko et al. 2006; Peyronnet et al. 2008). We fit estimates from these studies to a log-logistic distribution, with $\gamma = 1$, $\beta = 1.4271$, $\alpha = 1.9922$, and maximum = 12 (Figure 3.11.1). The mean from this distribution was 3.25, which suggested that approximately 3 hatchery-origin fish were equivalent to 1 wild-origin fish. The proportion of hatchery-origin post-smolts at Verona Island (after the indirect latent mortality rate was applied) was divided by the year-specific and iteration-specific hatchery discount to estimate the number of wild-equivalent post-smolts.

Hatchery-origin fish also likely have a lower marine survival rate than wild-origin fish, and so we fit separate marine survival distributions for fish from the 2 origins. The distribution for hatchery-origin fish was developed by using smolt data from the Penobscot River because the majority of those smolts were hatchery-origin fish. So, the marine survival distribution for hatchery fish included their lower survival rate, and these fish would be penalized twice if we used both the hatchery discount and the marine survival distribution for hatchery-origin fish. Therefore, as in the previous model version, the hatchery discount was set to 1 (i.e., no hatchery discount) for all model runs.

3.12 Sex-ratio Discount

Female post-smolts were needed to estimate the number of adult female returns. To convert the total number of post-smolts to females only, we halved the remaining number of post-smolts, assuming an equal male-to female ratio in this life stage. We did not have new data to update this model input, and so the sex ratio was not changed from the previous model version.

3.13 Marine Survival

US Atlantic salmon spend their marine phase in the Labrador Sea, and 2SW fish are assumed to migrate to the coast of Greenland to feed during their second summer at sea before returning to natal rivers to spawn (Renkawitz et al. 2015). We applied a marine survival rate to the number of female post-smolts to estimate the number of 2SW female returns that would successfully migrate to Greenland and back to the Penobscot River 2 years later. We previously used 1 marine survival distribution for all fish. However, we estimated different marine survival distributions for hatchery-origin and wild-origin fish in this model version because they likely survive at different rates. The 2SW females that survive the marine phase then initiate upstream migration to natal spawning grounds.

3.13.1 Hatchery Marine Survival

Marine survival for hatchery-origin fish was estimated by using data from the Penobscot River. Penobscot River adult return rates are available for hatchery smolts from 1969 to the present and can be used as a proxy for marine survival. However, these return rates include in-river and dam-related mortalities, which we already accounted for in the model. We built a submodel to remove in-river and dam-related mortalities to estimate a more accurate marine survival distribution.

In the submodel, we first estimated the number of smolts at the mouth of the Penobscot River. We multiplied the total annual number of smolts stocked (USASAC 2018) by the proportion of smolts that survived to the river mouth to adjust for in-river and dam-related mortalities. Smolt survival to the river mouth was estimated by using smolt survival data from telemetry studies in the Penobscot River from 2005 to 2006 and 2009–2010 (Stich et al. 2015a, 2015c). Stich et al. (2015a, 2015c) contain additional years of data from those that we used. We fit the survival estimates to a beta distribution with $\mu = 0.6921$ and $\sigma = 0.1738$ defined on the interval (0, 1). Year-specific values were sampled from this distribution to estimate the number of smolts that would survive from stocking to the Penobscot River mouth.

We then calculated year-specific marine survival rates for 2SW adults by dividing the estimated annual number of 2SW returns (MDMR fishway trap database, 2018 version) by the estimated number of stocked smolts at the mouth of the Penobscot River. We used estimates of the total numbers of adults and smolts rather than estimates for females only because we assumed 2SW return rates would not differ between sexes. We ran 10,000 iterations, where the number of smolts that would survive from stocking to the river mouth was a stochastic process (as described above). We capped the maximum marine survival rate at 25% and fit a lognormal distribution to the 1991–2017 marine survival estimates. Because of the abrupt decline in marine survival in the early 1990s (Chaput et al. 2005) and continued low adult return rates, we considered marine survival estimates from this recent time-series to be a better representation of future marine survival rates than estimates from the whole time-series. The lognormal distribution was defined on the interval (0, 0.25) with μ = 0.0021 and σ = 0.0015 (Figure 3.13.1.1). Year-specific and iteration-specific values were sampled from this distribution for the marine survival rate for hatchery-origin fish.

3.13.2 Wild Marine Survival

Marine survival for wild-origin fish was estimated by using data from the Narraguagus River, a small coastal Gulf of Maine river located approximately 105 km northeast of Penobscot Bay. Narraguagus River adult return rates are available from 1997 to the present (USASAC 2018), and these rates were once again used as a surrogate for marine survival. Although the Narraguagus River is stocked, data from smolt monitoring and the adult trap can be used to estimate the return rate of naturally reared adults, which we used as a proxy for wild adults. The number of smolts was estimated near the mouth of the river, and so adult return rates did not include in-river mortality. No FERC-licensed hydroelectric dams are located on the Narraguagus River, and therefore, we assumed dam-related mortality was minimal.

We fit a lognormal distribution to the 1999–2014 marine survival estimates for 2SW adults. We capped the maximum marine survival rate at 25%. The lognormal distribution was defined on the interval (0, 0.25) with μ = 0.0080 and σ = 0.0057 (Figure 3.13.1.1). Year-specific and iteration-specific values were sampled from this distribution for the marine survival rate for wild-origin fish.

3.14 Straying

Maine Atlantic salmon return to their natal river to spawn with high fidelity (98–99%; Baum 1997), and so we assumed 100% of the surviving 2SW females homed to the Penobscot River. Less is known about within-river migration, but this behavior could be driven by many factors, including habitat (Kocik and Ferreri 1998), the presence of conspecifics, and environmental cues (Fleming 1996). Still, homing to a specific river reach is likely less than 100%. Field studies conducted within the Penobscot River watershed (Power and McCleave 1980; Shepard 1995; Gorsky 2005; Gorsky et al. 2009; Holbrook et al. 2009; MDMR fishway trap database, 2011 version), recommendations by a panel of experts (NMFS 2012), and local knowledge (Justin Stevens, Integrated Statistics under contract to NMFS, personal communication) were used to develop a set of rules about homing and straying within the Penobscot River watershed.

- Homing rates to headwater areas (i.e., PUs 1–8, 13, and 15) would be 90%.
- Homing rates to the mainstem (i.e., PUs 9, 11, and 14) would be 70%.
- Of the proportion of fish that strayed, 90% would go upstream and 10% would go downstream.

- Upstream straying would be assigned equally to adjacent PUs.
- Downstream straying would be assigned to the downstream PU.

We made several exceptions to the rules based on unique attributes of PUs.

- PUs 1 and 2 are in the upper drainage, and straying fish would likely stop in multiple lower PUs (i.e., all straying fish were not confined to straying into the immediate downstream PU).
- Some fish from PUs 4, 5, and 6 would likely stray into PUs 7 and 8 (i.e., lateral straying).
- Similar to PUs 1 and 2, straying fish from PUs 7 and 8 would likely stop in multiple lower PUs (i.e., all straying fish were not confined to straying into the immediate downstream PU).
- PUs 9 and 11 contain lower quality spawning habitat compared to adjacent PUs. Therefore, a higher rate of straying into adjacent PUs containing higher quality spawning habitat was assumed (i.e., lateral straying).
- PU 13 is a self-contained drainage in the lower river, and all straying was assumed to be upstream because of a lack of suitable habitat downstream.
- PU 14 is mostly mainstem habitat with only a small amount of suitable habitat in tributaries. All straying was assumed to be upstream because of a lack of suitable habitat downstream.
- PU 15 is a self-contained drainage in the lower river. Straying was assumed to be primarily downstream, with a small amount of straying upstream.

These rules were developed into homing and straying rates for each PU, and 2SW females were assigned to a PU based on these rates (Table 3.2.2).

Straying rates for PU 14 needed to be updated from the previous model version because this PU now encompasses the area from Milford Dam to the southern end of Verona Island. Straying rates from other PUs to PU 14 were calculated as the sum of straying rates from Milford Dam to the southern end of Verona Island (Table 3.2.2). Straying rates from PU 14 to all other PUs were calculated as the habitat area weighted mean straying rates among the river reaches between Milford Dam to the old site of Great Works Dam, the old site of Great Works Dam to the old site of Veazie Dam, and the old site of Veazie Dam to the southern end of Verona Island. These weighted means were normalized to sum to 1 among all PUs (other than 14). The normalized weighted means were multiplied by 0.3, which was the proportion of 2SW females that strayed from PU 14.

3.15 Upstream Dam Passage Rates

3.15.1 Upstream Passage Efficiency

During their upstream migration, most returning adults must pass at least 1 dam to access spawning grounds. We generated upstream passage efficiency estimates for each dam. Great Works and Veazie dams were removed as part of the PRRP, and so the inputs at these dams were updated from the previous model version. We set the upstream passage rate at both dams to 1 for all model scenarios to simulate removal of the dams. We set baseline upstream passage to zero at Medway, Milo, Sebec, and Orono because these dams do not have any upstream passage facilities, meaning adults were not able to migrate into PUs 1, 7, 8, or 11, respectively. Subsequently, no smolts originated in these PUs, and no 2SW females would home to them. However, adults were allowed to attempt to stray to these PUs, although their attempts would be unsuccessful because of the lack of passage at the facilities at the lower boundary of the PU. These adults would then die, return to the ocean without spawning, or stray and spawn in a downstream PU (Section 3.16). Upstream passage efficiency rates were also updated for Howland, West Enfield, Milford, and Weldon dams. The baseline upstream passage at Howland Dam was set to 0.95, which is the best available estimate based on telemetry studies at this dam and its bypass (also part of the PRRP; Joseph Zydlewski, USGS/University of Maine, personal communication). The estimate of 0.95 is an uncertain value as it was based on a relatively small sample size from 1 year of data (2016). Revising this estimate of upstream passage at Howland Dam is a topic of continued research. The SPP called for upstream passage rates of 0.95 at West Enfield and Milford dams. Telemetry studies conducted at these 2 dams suggested that both were achieving the upstream passage efficiency goal of 0.95, although the majority of adults at Milford Dam took longer than the passage standard of 48 hours (Brookfield 2017). However, we still set baseline upstream passage at 0.95 for both dams because we assumed action would be taken in the near future to reduce adult delay at Milford. Upstream passage was studied at Weldon Dam in the 1980s, and the passage rate was estimated as 0.90 (NMFS 2013). Therefore, we set the baseline upstream passage at Weldon Dam to 0.90. Dam-specific upstream passage estimates were not available for the 5 remaining dams (i.e., Upper Dover, Browns Mill, Lowell Tannery, Stillwater, and Frankfort), so we adopted generalized estimates used in previous modeling efforts (USFWS 1988). We developed a uniform distribution defined on the interval (0.8875, 0.9525) and sampled year-specific and iteration-specific values from the distribution for each of the 5 remaining dams.

Only dam-related mortality was applied to migrating adults because we assumed freshwater mortality in free-flowing stretches of river to be low. Therefore, no in-river mortality was applied to adults.

3.15.2 Upstream Path Choice

The Stillwater branch and mainstem of the Penobscot River also offer 2 different routes for adults to migrate upstream. However, Orono Dam, which is the downstream endpoint of PU 11 and the Stillwater branch, has no upstream fish passage facilities. Therefore, all adults that attempted to migrate upstream of the confluence of the Stillwater branch and the mainstem were forced to migrate through the mainstem. We set upstream path choice for the mainstem to 1 for all model scenarios, which was the same as in previous model versions.

3.16 Upstream Dam Passage Inefficiency

Upstream fishways rarely pass 100% of migratory fish, including Atlantic salmon. Very few data are available concerning the fate of adult Atlantic salmon that are unsuccessful in locating or negotiating upstream fishways at dams. In the model, we assumed that adults that were unable to pass a dam would die, return to the ocean without spawning, or stray and spawn in a downstream PU (Table 3.16.1). These probabilities were determined by an expert panel (NMFS 2012) and were updated to incorporate changes in the configurations of dams and PUs. The number of 2SW females that did not pass a dam was multiplied by the probability for these 3 outcomes. Adults that died or returned to the ocean without spawning were removed from the population. For adults that strayed and spawned in a downstream PU, the number of strays was multiplied by the probability for each destination PU, and the fish were redistributed to the appropriate PUs.

3.17 Broodstock Collection

Returning adults are collected from the fish lift at Milford Dam for potential use as broodstock. To simulate the annual collection of broodstock, we removed 150 2SW females from the system. This number reflects the minimum amount of adults needed to meet smolt production goals (Fay et al. 2006). In previous model versions, broodstock were collected after they passed Veazie Dam. However, because of the removal of Veazie Dam, we updated the collection location to occur after broodstock passed Milford Dam. Adult returns to PUs 13 and 14 were unaffected because those 2 PUs are below Milford Dam. The number of fish removed from other PUs was based on the relative fraction of fish available in each PU. We only removed 2SW females in years when stocking was turned on. If 150 or fewer 2SW females were present above Milford Dam, all of the fish were removed for use as broodstock. A total of 545,000 smolts were stocked annually regardless of the number of 2SW females removed for broodstock because we assumed shortages in broodstock would be covered through backup sources. If stocking was turned off, no smolts were stocked, no 2SW females were collected for broodstock, and all 2SW females that successfully migrated above Milford Dam proceeded upriver.

3.18 Model Scenarios

3.18.1 Base Model Runs

We ran 4 model scenarios to evaluate the effects of dams and hatchery supplementation on the population of Atlantic salmon. Model inputs related to survival at dams (i.e., impoundment mortality at Weldon Dam only, downstream dam survival rates, and upstream dam passage rates) and hatchery supplementation (i.e., stocking and broodstock collection) were varied in these scenarios (Table 3.18.1.1), but all other inputs were set to baseline conditions. In the first scenario (Dams On Hatch On), all inputs were set to baseline conditions, including survival at dams and hatchery supplementation. Baseline downstream dam survival rates and upstream dam passage rates mirrored the Existing scenario conditions in Table 3.18.1.2. In the second scenario (Dams On Hatch Off), dam survival rates were also set to baseline conditions, but no smolts were stocked and no adult females were removed for use as broodstock. The third scenario (No Dams Hatch On) simulated removing all dams in the watershed, except Medway Dam, where survival rates were set at zero. Downstream and upstream dam survival rates were set at 1 at all other dams, and impoundment mortality was set at zero at Weldon Dam. Hatchery supplementation was set to baseline conditions. In the fourth scenario (No Dams Hatch Off), impoundment mortality was set at zero at Weldon Dam, downstream and upstream dam survival rates were set at 1 at all dams except Medway Dam, no smolts were stocked, and no adult females were removed for use as broodstock. These scenarios were run for 75 years, or 15 generations.

3.18.2 Whole System Model Runs

We ran model scenarios to explore the effects of changes in survival at dams and stocking, including stocking location, across the whole Penobscot River watershed. We were also interested in comparing the effects of baseline verses increased egg-to-smolt and marine survival rates, so we ran scenarios that combined changes in egg-to-smolt survival, marine survival, dam survival, and stocking.

3.18.2.1 Whole System Dam Analysis

We ran model scenarios to evaluate how adult abundance changed with varying dam, egg-to-smolt, and marine survival rates when hatchery supplementation was not used to support the population. Three model scenarios (low, medium, and high) were run with different levels of dam survival (Tables 3.18.2.1.1 and 3.18.2.1.2). We set these levels as 0.80, 0.90, and 1 for downstream survival and 0.90, 0.95, and 1 for upstream survival. We used the lowest median survival rates from dams in the model for the low level, a survival rate of 1 for the high level, and the mean of the low and high levels for the medium level. For each of the 3 scenarios, most dams were set at the same deterministic rate. Sebec, Milo, and Orono dams were set at this rate as well to simulate hypothetical upstream passage at these dams. Only Howland and Medway dams were not set at the same survival rates as the other dams. Given the decommissioned status and nature-like fishway bypassing Howland Dam, downstream and upstream survival rates were set at 1. Both survival rates were set at zero for Medway Dam because of the lack of fish passage at this dam and others in the West Branch of the Penobscot River.

We also ran model scenarios with a range of egg-to-smolt and marine survival rates. These 2 survival rates were varied independently and were increased by a factor of 1–3, which was selected randomly from a uniform distribution defined on the interval (1, 3). For both egg-to-smolt and marine survival, the distribution was increased by multiplying a randomly selected factor from the uniform distribution and μ from the baseline distribution, and the product was used as μ in the egg-to-smolt or marine survival distribution.

The model scenarios did not include hatchery supplementation. Therefore, no smolts were stocked, and no adults were collected for broodstock. We ran 40,000 iterations for each scenario, and each iteration was 75 years.

3.18.2.2 Whole System Stocking Location Analysis

We ran model scenarios to estimate the effects of different stocking locations on the Atlantic salmon population. Smolts were stocked only in PU 14, immediately below Milford Dam (Below Milford); by using the baseline stocking strategy (Baseline); or only in PU 2, upstream of Weldon Dam (Above Weldon; Table 3.18.2.2.1). We ran 6 scenarios: 3 with these stocking locations and baseline egg-to-smolt and marine survival rates, and another 3 with these stocking locations and increased egg-to-smolt and marine survival rates. Egg-to-smolt and marine survival were increased by a factor of 2.2 and 1.8, respectively. These increases in egg-to-smolt and marine survival rates were the same as those used in the Weldon Model Runs Phase 3 Recovery Analysis (Section 3.18.3.2). These scenarios were run for 75 years, or 15 generations.

3.18.3 Weldon Model Runs

We ran model scenarios designed to provide information for the FERC relicensing of the Mattaceunk Project. These scenarios included model inputs that reflect baseline conditions in egg-to-smolt and marine survival rates (while highlighting survival and recovery potential; Survival and Phase 2 Recovery Analyses) as well as increased egg-to-smolt and marine survival rates that would help facilitate the recovery of Atlantic salmon in the Penobscot River watershed (Phase 3 Recovery Analysis). Dam survival rates, especially those at Weldon Dam, were also varied to reflect possible management scenarios.

3.18.3.1 Survival and Phase 2 Recovery Analyses

The Survival and Phase 2 Recovery Analyses were designed to reflect contemporary conditions for Atlantic salmon in the Penobscot River watershed. Therefore, model inputs for this analysis included baseline egg-to-smolt and marine survival rates, baseline stocking numbers and locations, and removal of 2SW females for use as broodstock (Table 3.18.3.1.1). We ran 5 model scenarios to evaluate the effects of varying dam survival rates, especially at Weldon Dam (Table 3.18.1.2). The model scenarios reflect existing conditions at Weldon Dam (Existing); proposed conditions at Weldon Dam with impoundment mortality present (Proposed w/ Impound); proposed conditions at Weldon Dam without impoundment mortality (Proposed); Weldon Dam removed (Weldon Removed); and all hydroelectric dams in the watershed removed, except those in the West Branch (No Dams). Iterations for these scenarios were run for 40 years, or 8 generations, to replicate a likely term-length of a new license for the Mattaceunk Project that is expected to be issued by FERC in 2019.

3.18.3.2 Phase 3 Recovery Analysis

The Phase 3 Recovery Analysis focused on estimating the effects of dams on a recovering population of Atlantic salmon in the Penobscot River watershed. Scientists and managers are striving for the delisting of this population (i.e., recovery and removal from endangered status under the Endangered Species Act), which would include increasing the abundance, distribution, and productivity of wild Atlantic salmon and transitioning from dependence on hatchery supplementation to wild smolt production. Delisting criteria for Atlantic salmon in the GOM DPS include, but are not limited to, escapement of 2,000 wild adults annually in each SHRU (Penobscot Bay is 1 of 3 SHRUs that compose the GOM DPS), at least 30,000 units of habitat in each SHRU that are accessible and suitable for spawning and rearing, and a population growth rate greater than 1 in each SHRU for the 10-year period preceding delisting (USFWS and NMFS 2018). We set a goal of reaching 2,000 wild adult returns in the Penobscot Bay SHRU for this analysis. To reach this goal, we altered model inputs related to hatchery supplementation and increased egg-to-smolt and marine survival rates (Table 3.18.3.2.1).

We changed the number and location of smolts stocked and the number of broodstock collected to reflect a plausible future management scenario under recovery conditions. We expected managers would monitor abundance for several years or a few generations after the initial detection of increased abundance to confirm that the increase was not a 1-year or 1-cohort event. We waited 3 generations to ensure that abundance was increasing, and then began changing smolt stocking numbers and locations and the number of broodstock collected. Baseline smolt stocking numbers and locations were used in generations 1–3, reduced numbers of smolts were stocked in altered stocking locations in generations 4–7, and no smolts were stocked in generations 8–15 (Figures 3.18.3.2.1 and 3.18.3.2.2). Starting in generation 4, the number of smolts stocked was reduced by 20% of the original number stocked. We continued this 20% reduction in every generation until no smolts were stocked in generation 8. Smolt stocking locations were also changed to areas of higher quality spawning and rearing habitat that were underutilized in the current (i.e., baseline) stocking strategy. Removal of 2SW females for use as broodstock occurred only in generations 1–7 because no broodstock were needed when smolt stocking ceased (Figure 3.18.3.2.3). These changes in model inputs reflected possible changes in management actions as the management strategy transitioned from attempting to recover the Atlantic salmon population to sustaining a recovered population.

To estimate the increase in egg-to-smolt and marine survival rates needed to reach 2,000 wild adults, we ran a base case scenario with variable increases in egg-to-smolt and marine survival rates and the previously mentioned changes in the number and locations of smolts stocked and the number of 2SW females removed for use as broodstock (Table 3.18.3.2.1). Egg-to-smolt and marine survival were varied independently and were increased by a factor of 1–3. The factor was selected randomly from a uniform distribution defined on the interval (1, 3). For both egg-to smolt and marine survival, the distribution was increased by multiplying a randomly selected factor from the uniform distribution and μ from the baseline distribution. The product was used as μ in the egg-to-smolt or marine survival distribution. Because the baseline egg-to-smolt and marine survival rates were not equal, the same proportional changes to those rates do not imply the same absolute effect on the population (Nieland et al. 2015). Many combinations of egg-to-smolt and marine multipliers could result in 2,000 wild adults. We selected a combination where the multipliers were approximately the same because we lacked information to determine if increases to either survival rate would be more likely. We ran 100,000 iterations, selecting random draws from the uniform distributions. We reviewed the results for combinations of multipliers that were approximately equal and would result in the median wild adult abundance estimate that was closest to and greater than 2,000. We narrowed down the uniform distributions and again ran 100,000 iterations, selecting random draws from a uniform distribution defined on the interval (1.7, 2.2). From this set of iterations, we selected the combination of multipliers that were approximately equal and resulted in the median number of wild adults closest to and greater than 2,000. The resulting multipliers for the increased egg-to-smolt and marine survival rates were 2.2 and 1.8, respectively.

We used the increased egg-to-smolt and marine survival rates starting in generation 1 and again ran 5 model scenarios to evaluate the effects of varying dam survival rates, especially at Weldon Dam (Table 3.18.3.2.1). The model scenarios were the same 5 that were run for the Survival and Phase 2 Recovery Analyses but were run for 75 years, or 15 generations. Seventy-five years was selected to be consistent with the projected timeframe needed to recover Atlantic salmon in the GOM DPS (USFWS and NMFS 2018).

3.18.3.3 Smolt Mortality Analysis

We ran model scenarios to investigate smolt mortality from 3 difference sources (in-river, impoundment, and dam mortality) to estimate a common currency of smolts killed at or upstream of Weldon Dam by the various mortality sources. To focus on the mortality that occurred in PU 2 and at Weldon Dam, we stocked 1,000 smolts into PU 2 and tracked their mortality and survival through only PU 2 and Weldon Dam for part of a single generation. Therefore, these scenarios used only a small part of the model and focused on a very specific portion of the Atlantic salmon life cycle. We ran the same 5 scenarios as in the Survival and Phase 2 Recovery Analyses, which included changes in impoundment mortality and survival at Weldon Dam (Table 3.18.3.3.1).

3.19 Performance Metrics

We reported performance metrics for adult abundance and distribution, as well as smolt survival and mortality. All performance metrics were calculated across all iterations.

We examined adult abundance in the Base, Whole System, and Weldon model runs. In the model, adults were 2SW females only. However, we converted 2SW female abundance to total adult abundance for the performance metrics because we wanted estimates of adult abundance to include all ages and sexes. We estimated the ratio of total adult returns (including all ages and sexes) to 2SW female returns annually from 2008 to 2017 (MDMR 2018; MDMR fishway trap database, 2018 version). We then calculated the mean of the ratios (μ = 2.45) and used the mean as the conversion factor. Total adult abundance was estimated as the product of 2SW female abundance and the conversion factor. The mean; median; and 5th, 25th, 75th, and 95th percentiles were calculated across all PUs. We also estimated total adult abundance for only PU 2 and the probability of zero adults in PU 2. Total adult abundance in PU 2 was estimated as the product of 2SW female abundance in PU 2 and the conversion factor. The probability of zero adults in PU 2 was estimated as the proportion of the 10,000 iterations in which the number of 2SW females in PU 2 equaled zero.

We explored the adult distribution in the Base, Whole System, and Weldon model runs as well. Distribution of adults was separated into 3 areas of the Penobscot River watershed: the upper Penobscot (i.e., above West Enfield Dam, PUs 1–3), the Piscataquis (i.e., the Piscataquis River watershed, PUs 4–8), and the lower Penobscot (i.e., below West Enfield Dam, PUs 9, 11, and 13–15; Figure 3.19.1). We assessed distribution by estimating the median proportion of adults in each of the 3 areas of the watershed. Adults in these 3 areas were specified further as wild-origin or hatchery-origin.

We reported smolt survival and mortality in the Weldon model runs. We calculated the median numbers and proportions of the 1,000 smolts stocked in PU 2 that survived or were killed by in-river, impoundment, and dam mortality in PU 2 and at Weldon Dam. The numbers of smolts killed by these 3 types of mortality were estimated as described above (Sections 3.7–3.9).

4. RESULTS

4.1 Base Model Runs

Median adult abundance in the Penobscot River watershed was highest in the scenario with no dams and hatchery supplementation turned on, was lower in the scenario with dams and hatchery supplementation on, and decreased to zero in scenarios without hatchery supplementation (Figures 4.1.1 and 4.1.2). The decrease in adult abundance from generation 1 to generation 2 was a product of the number and location of adults seeded in generation 1 and low survival under baseline conditions (Figure 4.1.1). In the scenarios without hatchery supplementation, adult abundance continued to decrease after generation 2 and equaled zero by generation 5. In the scenarios with hatchery supplementation, the 90% probability interval was wider in the No Dams scenario than in the Dams On scenario in generation 15 (Figure 4.1.2).

When adult abundance in the watershed was greater than zero, the greatest proportion of adults in generation 15 was located in the lower Penobscot area, but the distribution of adults to the Piscataquis and upper Penobscot areas increased with decreasing numbers of dams (Figure 4.1.3). In scenarios with hatchery supplementation, the majority of adults were distributed in the lower Penobscot area, but the proportion of adults in this area decreased when no dams were in the watershed (0.88 in the Dams On Hatch On scenario and 0.81 in the No Dams Hatch On scenario). Small proportions of adults were located in the Piscataquis and upper Penobscot areas, and the proportions of adults in these areas increased slightly when no dams were in the watershed (Piscataquis: 0.09 in the Dams On Hatch On scenario and 0.14 in the No Dams Hatch On scenario; upper Penobscot: 0.03 in the Dams On Hatch On scenario and 0.05 in the No Dams Hatch On scenario). Adult abundance equaled zero in scenarios without hatchery supplementation.

The median proportions of wild-origin adults in generation 15 were similar in each area when the number of dams was decreased (Figure 4.1.3). In scenarios with hatchery supplementation, the proportion of wild-origin adults ranged from 0.19 to 0.20 in the lower Penobscot, from 0.18 to 0.20 in the Piscataquis, and from 0.22 to 0.25 in the upper Penobscot. In scenarios without hatchery supplementation, adult abundance of wild-origin (and hatchery-origin) fish equaled zero regardless of the number of dams.

4.2 Whole System Model Runs

4.2.1 Whole System Dam Analysis

Adult abundance increased as marine and egg-to-smolt multipliers and dam survival increased (Figure 4.2.1.1). In all 3 scenarios, adult abundance was lowest when the egg-to-smolt and marine survival multipliers equaled 1 (i.e., equaled the baseline survival rate). A combination of increased egg-to-smolt and marine survival was needed to have more than 1,000 adults. Adult abundance increased as these 2 survival rates increased and was greatest when the multipliers both equaled 3. Adult abundance increased further when dam survival rates increased. No hatchery supplementation occurred in these scenarios, so all adults were wild-origin fish.

4.2.2 Whole System Stocking Location Analysis

Median adult abundance in the Penobscot River watershed was highest when smolts were stocked lower in the watershed (either all below Milford Dam or using the baseline stocking locations) and was lowest when all smolts were stocked higher in the watershed (above Weldon Dam; Figures 4.2.2.1 and 4.2.2.2). In the scenarios with baseline egg-to-smolt and marine survival rates, adult abundance increased when all smolts were stocked below Milford Dam but decreased when smolts were stocked by using the baseline stocking locations or above Weldon Dam (Figure 4.2.2.1). Adult abundance was lowest when all smolts were stocked above Weldon Dam. The 90% confidence interval was widest when all smolts were stocked below Milford Dam and was narrowest when all smolts were stocked above Weldon Dam (Figure 4.2.2.2). Adult abundance increased in all 3 scenarios with increased egg-to-smolt and marine survival rates, but abundance increased more when all smolts were stocked below Milford Dam or in baseline stocking locations than when all smolts were stocked above Weldon Dam (Figures 4.2.2.1). Adult abundance and the 90% probability interval were similar in the Milford and Baseline scenarios. The 90% probability interval was narrowest when all smolts were stocked above Weldon Dam (Figure 4.2.2.2).

Median adult abundance in PU 2 was lower when all smolts were stocked below Milford Dam or using the baseline stocking locations than when all smolts were stocked above Weldon Dam (Figure 4.2.2.3). Adult abundance in PU 2 equaled 12 in generation 1 in all scenarios because those adults were seeded into the PU. In the scenarios with baseline egg-to-smolt and marine survival rates, adult abundance in PU 2 decreased to zero in generation 2 when all smolts were stocked below Milford Dam or in baseline stocking locations (Figure 4.2.2.3). When all smolts were stocked above Weldon Dam, adult abundance in PU 2 increased in generation 2, decreased from generation 2–5, and was similar in generations 5–15. Adult abundance in PU 2 increased in all 3 scenarios with increased egg-to-smolt and marine survival rates (Figure 4.2.2.3). Abundance was highest when all smolts were stocked above Weldon Dam and was similar when all smolts were stocked below Milford Dam or in baseline stocking locations.

The probability of having zero adults in PU 2 was highest when all smolts were stocked below Milford Dam and was lower when smolts were stocked in baseline stocking locations or above Weldon Dam (Figure 4.2.2.4). In the scenarios with baseline egg-to-smolt and marine survival rates, the probability was close to zero in generation 1 in all scenarios because of the adult seeding strategy, then increased in generation 2, and was similar in generations 3–8 as the model stabilized (Figure 4.2.2.4). By generation 15, the probability of having zero adults in PU 2 was highest when all smolts were stocked below Milford Dam and was lowest when all smolts were stocked above Weldon Dam. In the scenarios with increased egg-to-smolt and marine survival rates, the probability was close to zero in generation 1 in all scenarios because of the adult seeding strategy, then increased in generation 2, decreased for several generations, and was similar for at least the last half of the time series as the model stabilized (Figure 4.2.2.4). By generation 15, the probability of having zero adults in PU 2 was near zero in all scenarios.

The median proportion of adults in generation 15 was greatest in the lower Penobscot area in every scenario, but the distribution of adults to the Piscataquis and upper Penobscot areas increased when smolts were stocked in PUs above Milford Dam (Figure 4.2.2.5). In the 3 scenarios with baseline egg-to-smolt and marine survival rates, adults were only distributed in areas where smolts were stocked or in the lower Penobscot area (Figure 4.2.2.5). Adults were located only in the lower Penobscot area (1) when all smolts were stocked below Milford Dam. When all smolts were stocked above Weldon Dam, adults were located in the upper Penobscot (0.27) and lower Penobscot (0.73) areas but not in the Piscataquis area. When smolts were stocked in all 3 areas, as in the baseline stocking strategy, adults were located in all 3 areas (lower Penobscot: 0.88, Piscataquis: 0.09, upper Penobscot: 0.03). In the scenarios with increased egg-to-smolt and marine survival rates, adults were distributed to all 3 areas regardless of the stocking strategy (Figure 4.2.2.5). The greatest proportion of adults was located in the lower Penobscot area in all 3 scenarios but decreased as more smolts were stocked above Milford Dam (0.80 in the Milford scenario, 0.70 in the baseline scenario, and 0.50 in the Weldon scenario). The proportion of adults in the Piscataquis area was the greatest in the baseline scenario when smolts were stocked in the Piscataquis area (0.22), decreased when all smolts were stocked below Milford Dam (0.14), and was the least when all smolts were stocked above Weldon Dam (0.11). The proportion of adults in the upper Penobscot area was the greatest when all smolts were stocked in this area above Weldon Dam (0.38), decreased when smolts were stocked using the baseline stocking locations (0.08), and was the least when all smolts were stocked below Milford Dam (0.06).

The median proportion of wild-origin adults in generation 15 depended on stocking location and egg-to-smolt and marine survival rates (Figure 4.2.2.5). In the scenarios with baseline egg-to-smolt and marine survival rates, the proportion of wild-origin adults was the same in the lower Penobscot area in all 3 scenarios (0.20; Figure 4.2.2.5). Adults were present in all 3 areas only in the scenario with baseline stocking locations, and the proportion of wild-origin adults was similar among the areas (ranged from 0.19 to 0.25). The proportion of wild-origin adults in the upper Penobscot area was highest in the scenario with all smolts stocked above Weldon Dam (0.39). In the scenarios with increased egg-to-smolt and marine survival rates, the proportion of wild-origin adults was lowest in the areas where the majority of smolts were stocked (Figure 4.2.2.5). When all smolts were stocked below Milford Dam, the lower Penobscot had the lowest proportion of wild-origin adults of the 3 areas (0.62 in the lower Penobscot, 0.86 in the Piscataquis, and 0.83 in the upper Penobscot). The majority of smolts were stocked in the lower Penobscot in baseline stocking scenario, and that area had the lowest proportion of wild-origin adults (0.71 in the lower Penobscot, 0.78 in the Piscataquis, and 0.80 in the upper Penobscot). When all smolts were stocked above Weldon Dam, the lowest proportion of wild-origin adults was in the upper Penobscot area (0.96 in the lower Penobscot, 0.92 in the Piscataquis, and 0.43 in the upper Penobscot).

4.3 Weldon Model Runs

4.3.1 Survival and Phase 2 Recovery Analyses

Median adult abundance in the Penobscot River watershed was highest in the scenario with no dams and was similar in all other scenarios, which included changes in survival at Weldon Dam and in the impoundment (Figure 4.3.1.1). Adult abundance decreased from generation 1 to generation 2. This drop in abundance was a product of the number and location of adults seeded in generation 1 and low survival under baseline conditions.

Median adult abundance in PU 2 decreased to zero in all scenarios (Figure 4.3.1.2). Changes in survival at Weldon Dam, in the impoundment, and at all dams in the watershed did not affect the number of adults in PU 2. In generation 1, adult abundance in PU 2 equaled 12 in all scenarios because those adults were seeded into the PU. Adult abundance decreased to zero in generation 2.

The probability of having zero adults in PU 2 was lowest in the scenario with no dams but was similar in all other scenarios (Figure 4.3.1.3). The probability equaled zero in generation 1 in all scenarios because of the adult seeding strategy, then increased in generation 2, and was similar in generations 3–8 as the model stabilized (0.53–0.54 in the No Dams scenario and 0.66–0.67 in the other 4 scenarios).

The greatest proportion of adults in generation 8 was located in the lower Penobscot area in all scenarios, but the distribution of adults to the Piscataquis and upper Penobscot areas increased when no dams were in the watershed (Figure 4.3.1.4). The distribution of adults was the same in the scenarios with existing conditions and with changes in survival in the impoundment and at Weldon Dam (0.88 in the lower Penobscot, 0.09 in the Piscataquis, and 0.03 in the upper Penobscot). In the scenario with no dams, the proportion of adults decreased in the lower Penobscot (0.81) and increased in the Piscataquis (0.14) and upper Penobscot (0.05) areas.

The median proportion of wild-origin adults in generation 8 was similar for each area across all scenarios (Figure 4.3.1.4). The proportion of wild-origin adults ranged from 0.19 to 0.20 in the lower Penobscot, from 0.18 to 0.20 in the Piscataquis, and from 0.22 to 0.25 in the upper Penobscot.

4.3.2 Phase 3 Recovery Analysis

Median adult abundance in the Penobscot River watershed was highest in the scenario with no dams and was similar in all other scenarios, which included changes in survival at Weldon Dam and in the impoundment (Figure 4.3.2.1). In scenarios with existing conditions and changes in survival in the impoundment and at Weldon Dam, adult abundance increased from generations 1 to 4 while baseline stocking conditions were used and then decreased as the number of smolts stocked was reduced and stocking locations were altered. Abundance was similar among these 4 scenarios. In the scenario with no dams, adult abundance increased from generations 1 to 6, which included the period of baseline stocking conditions as well as 2 generations of reduced smolt stocking and altered stocking locations. Adult abundance decreased from generations 6 to 15 in this scenario.

Median adult abundance in PU 2 increased as survival in the impoundment and at Weldon Dam increased and was highest in the scenario with no dams (Figure 4.3.2.2). Adult abundance in PU 2 remained low while baseline stocking conditions were in place, increased as smolts were stocked higher in the watershed (including in PU 2), and then decreased as the number of smolts stocked decreased to zero.

The probability of having zero adults in PU 2 decreased as survival in the impoundment and at Weldon Dam increased and was lowest in the scenario with no dams (Figure 4.3.2.3). The probability increased from generation 1 to 2 because of the adult seeding strategy used in generation 1, and then decreased and remained near zero because of the smolt stocking higher in the watershed (including in PU 2). After smolt stocking was ceased, the probability of having zero adults in PU 2 increased in all scenarios but was lowest in the scenario with no dams. In generation 15, the probability of having zero adults in PU 2 was less than 0.01 in the No Dams scenario and ranged from 0.07 to 0.11 in the other 4 scenarios.

The greatest proportion of adults in generation 15 was located in the lower Penobscot area in all scenarios, but the distribution of adults to the Piscataquis and upper Penobscot areas increased when no dams were in the watershed (Figure 4.3.2.4). The distribution of adults was similar in the scenarios with existing conditions and with changes in survival in the impoundment and at Weldon Dam (equaled 0.73 in the lower Penobscot, ranged from 0.18 to 0.19 in the Piscataquis, and ranged from 0.08 to 0.09 in the upper Penobscot). In the scenario with no dams, adults were distributed more evenly (0.48 in the lower Penobscot, 0.36 in the Piscataquis, and 0.15 in the upper Penobscot).

The median proportion of wild adults in generation 15 was 1 for all areas in all scenarios (Figure 4.3.2.4). No smolts were stocked from generation 9 on, so all of the fish in the watershed were wild-origin.

4.3.3 Smolt Mortality Analysis

The majority of the 1,000 smolts stocked into PU 2 survived in all scenarios, but more smolts survived as impoundment mortality and mortality at Weldon Dam decreased (Figure 4.3.3.1). The greatest number of smolts was killed in the scenario with existing conditions, with Weldon Dam killing more smolts than the other 2 types of mortality combined (24 smolts killed by in-river mortality, 70 smolts killed by impoundment mortality, and 181 smolts killed by dam mortality). Dam mortality was reduced in the 2 scenarios with proposed conditions at Weldon Dam (ranged from 36 to 39 smolts killed). Impoundment mortality remained the same in the Proposed with Impoundment scenario. In the scenarios with Weldon Dam removed and all dams removed, in-river mortality was the only mortality on smolts. In these 5 scenarios, in-river mortality was only tracked through PU 2 and did not change. Therefore, the number of smolts killed by this type of mortality was the same in all scenarios. Results for the proportions of smolts that survived and were killed followed the same patterns.

5. DISCUSSION

Adult Atlantic salmon abundance generally increased as the survival at hydroelectric dams increased or dams were removed. Our results are consistent with previous studies of the effects of dams on Atlantic salmon in the Penobscot River (Nieland et al. 2013, 2015) where greater connectivity throughout the watershed led to increases in abundance. Dams not only cause direct and indirect mortality on migratory fishes, including Atlantic salmon, but they can also have numerous ecological effects on rivers that negatively affect native resident and migratory fishes (Limburg and Waldman 2009). These effects are compounded when multiple dams are present in the river (Ward and Stanford 1983), greatly increasing the negative consequences on ecological and migratory processes.

Our results show that hatchery supplementation is necessary to keep the population from going extinct during times of low (i.e., baseline) survival. This conclusion is in line with a recent analysis of hatchery supplementation in the Penobscot River (Nieland et al. 2015), as well as a PVA of 8 other rivers in the GOM DPS (Legault 2005). However, if increased levels of survival in early freshwater (i.e., egg-to-smolt) and subsequent marine life stages can be attained, our results demonstrate that long-term hatchery supplementation may not be necessary to sustain the population. Increases in both of these survival rates will likely be needed to achieve increased numbers of Atlantic salmon in the Penobscot River watershed before hatchery supplementation should be reduced and eventually ceased. However, there is some urgency to reduce the population's dependence on this management tool because the artificial selection effects of long-term hatchery supplementation are likely a risk to the population as well (NRC 2004).

Increases in both marine and early-life-stage survival rates will be important for recovery of Atlantic salmon in the Penobscot River. Survival in the marine environment is 1 of the biggest threats to Atlantic salmon in the GOM DPS (NRC 2004; Fay et al. 2006). Salmon populations have been shown to go through periods of increased and decreased productivity, as cycles in marine survival have been documented in Pacific salmon (Johnson 1988; Beamish and Bouillon 1993; Francis and Hare 1994; Wells et al. 2006) and suggested in Atlantic salmon (Beaugrand and Reid 2003; Friedland et al. 2003). The current low productivity period for US Atlantic salmon populations (USASAC 2018) could be the low point in a cycle, which would mean that an increase in marine survival could be plausible. Increases in marine survival may lead to larger increases in adult abundance in the Penobscot River than increases in egg-to-smolt survival would (Nieland et al. 2015), and so evaluating these survival rates separately can be beneficial and may lead to targeted management actions. Michel (2019) found that although outmigration (freshwater and estuarine) survival for Sacramento River Chinook salmon (*Oncorhynchus tshawytscha*) ranged from 2.6% to 17% and marine survival ranged from 4.2% to 22.8%, most year-to-year variability in survival from the smolt-to-adult life stage was explained by outmigration survival. Options currently exist for improving survival in freshwater in the short term (NRC 2004), and scientists and managers are continually working to increase freshwater productivity and survival with the goal of increasing the number of smolts that reach the estuary. Furthermore, decreasing sources of mortality in the river and estuary may also buffer the effects of mortality in the ocean (Stich et al. 2015c), which is important as management options to reduce marine mortality in the short term appear limited (NRC 2004). Regardless, our results confirm that a combination of increased survival in early life stages and in the marine environment will likely be necessary to attain a sustainable population of Atlantic salmon in the Penobscot River.

Marine survival rates for wild and hatchery fish were quite different in the model, and this difference highlights limitations of hatchery supplementation. For example, every effort is made to preserve genetic diversity within existing GOM Atlantic salmon stocks, but those processes do not equate to natural selection on critical life history traits. The effects of artificial selection, although associated with reduced marine survival, are unavoidable while the population is dependent on hatchery supplementation. A much higher proportion of the population will likely need to become wild in order to provide long-term resilience when confronted with changing ocean conditions.

Stocking location also has substantial effects on abundance. Adult Atlantic salmon abundance was lower when smolts were stocked above Weldon Dam than when smolts were stocked lower in the watershed, even when survival rates for early life stages and the marine phase were increased. Smolts stocked higher in the watershed migrated longer distances and encountered more dams than smolts stocked lower in the watershed, meaning lower in-river and dam-related survival for smolts stocked above Weldon Dam. Although watershed-level adult abundance was higher when smolts were stocked lower in the watershed, few adults occupied the upper watershed because of the combination of little or no stocking in that area and dam mortality.

We performed analyses to support managers in their evaluation of the Mattaceunk Project for the FERC-relicensing process. To isolate the individual effects of Weldon Dam, we ran model scenarios with varying conditions at the dam and evaluated the survival and recovery potential of the Penobscot River Atlantic salmon population. Adult abundance at the watershed level was not affected by increased survival at Weldon Dam or its impoundment when early-life-stage and marine survival rates were low. Current stocking locations have been set to minimize the negative effects of dams, such as Weldon Dam, and therefore, no smolts are stocked high in the watershed. From 2008 to 2017, an average of 48% of smolts were stocked below all dams in the watershed, and less than 5% of smolts were stocked into the upper Penobscot drainage (as defined in Figure 3.19.1; USASAC 2018). From 2014 to 2017, 100% of smolts were stocked below all dams in the watershed. Few or no fish are located in the upper watershed because of these management decisions, and so few fish are affected by changes at Weldon Dam. However, in scenarios where the population was recovering under increased survival rates and the stocking strategy had been modified, our results showed further increased abundance when survival at Weldon Dam and its impoundment increased. Atlantic salmon were located above Weldon Dam in these scenarios, and so increased survival at the dam and impoundment did benefit the population.

As presently constructed, the model does not account for potential differences in habitat quality across subwatersheds. Higher quality habitat would likely produce more smolts than lower quality habitat, and the upper watershed contains higher quality habitat than does the lower watershed (NMFS 2009). Therefore, the upper watershed (i.e., PU 2) may produce more smolts than does the lower watershed, which could counter-balance the lower in-river and dam-related survival experienced by smolts coming from the upper watershed. To allow Atlantic salmon to reach higher quality habitat, survival would need to be increased at dams from the lower to the upper watershed. Increased survival at dams in the upper watershed, such as Weldon Dam, would be essential for getting fish to areas of higher quality habitat. Still, the potential benefits of increased habitat quality are not quantifiable at this time, as the information needed to ascribe higher potential smolt production in a given subwatershed is currently lacking. This type of information is routinely used in watershed prioritization exercises for Pacific salmon in the northwest United States (Beechie et al. 2008; Hendrix et al. 2014), including in evaluating the consequences of effects of climate change in Pacific salmon recovery efforts (Mantua et al. 2010), and would be beneficial for managers working toward Atlantic salmon restoration.

Given the potential importance of habitat quality on Atlantic salmon populations, future efforts should be made to quantify the biological response of Atlantic salmon to different habitat qualities and evaluate the effects of changing habitat conditions on Atlantic salmon productivity given a changing climate. These analyses should be conducted for the entire range of US Atlantic salmon populations and cover freshwater and marine habitats from headwaters to Greenland. Coupling information about current habitat conditions with Atlantic salmon habitat needs and preferences will allow researchers to identify areas where salmon would survive and thrive and to quantify the effects of productivity in a changing climate. These results will allow for a data-driven assessment of the future productivity of US Atlantic salmon and will allow managers to develop realistic recovery goals while prioritizing restoration efforts in areas with the greatest potential future productivity.

When considering habitat where Atlantic salmon could be most productive, areas that are currently inaccessible to Atlantic salmon should not be dismissed. For example, the West Branch of the Penobscot River represents a significant portion of the high quality habitat in the watershed, but Atlantic salmon are not able to access this branch because of the multiple impassable dams in their migration path. Therefore, we do not know how much the West Branch could contribute to the productivity of the population. This habitat could be critical for salmon in the Penobscot River. Although our current model structure accurately represents contemporary dynamics, all hydroelectric dams in the West Branch would need to be modeled to evaluate the effects of dams in the entire Penobscot River watershed. A modeling exercise including dams in the West Branch could be done in the future.

We developed the model and updated inputs with the best available information from a combination of field studies, expert opinion, and local knowledge. However, advancements to the model should be made where possible. We suggest further research related to egg-to-smolt survival, indirect latent mortality, impoundment mortality, delay at dams, and adult straying patterns. Egg-to-smolt survival estimates in the model were obtained from the literature. Several of these studies were conducted in New England, including 3 in Maine, and so we assumed that our distribution of egg-to-smolt survival included survival rates that salmon would experience in the Penobscot River. We would prefer to have survival estimates from within the Penobscot River to verify our distribution. A Penobscot River-specific estimate of indirect latent mortality was available (Stich et al. 2015c) and was used to estimate this type of mortality in post-smolts. Stich et al. (2015c) accounted for indirect latent mortality in the estuary. However, this mortality likely extends to post-smolts in the ocean as well. An estimate of the portion of post-smolt marine mortality that is caused by indirect latent mortality would be useful for differentiating dam-related mortality from mortality caused by marine environment-related factors. Impoundment mortality was another source of dam-related mortality included in the model. This mortality was only modeled at Weldon Dam but should be expanded to the other dams in the watershed to more accurately reflect the amount of mortality on Atlantic salmon. Dams can also cause significant migration delays for smolts (Stich et al. 2015b) and adults (Gorsky et al. 2009; Holbrook et al. 2009). In smolts, these delays can cause increased predation risk (Poe et al. 1991; Blackwell and Juanes 1998) and mismatch of physiological traits with timing of ocean entry (Stich et al. 2015c). In adults, these delays may result in fallback to the estuary without spawning (Holbrook et al. 2009) and reductions in survival and energetic reserves used for spawning (Dauble and Mueller 1993; Gowans et al. 2003). Future research quantifying the effects of these delays, especially on adults, would be beneficial. Adult straying patterns also affect the distribution of Atlantic salmon in the Penobscot River watershed. Although we used the best available information for adult straying rates and locations, these rates were mostly based on expert opinions and local knowledge. Directed studies of adult straying rates within the watershed would be beneficial for predicting the migration paths of adults and identifying obstructions. Knowing the eventual distribution of spawning adults could also be useful for restoration efforts. The model should be updated as new data become available.

6. CONCLUSIONS

The DIA model is a useful tool to understand the dynamics of an Atlantic salmon population in a dammed watershed. We used the best available data and information to build this stochastic model and simulated the effects of changes in dam survival rates, egg-to-smolt and marine survival rates, and hatchery supplementation on Atlantic salmon abundance and distribution in the Penobscot watershed. The model and results can be used to evaluate and support informed management decisions and set realistic expectations of outcomes.

The Penobscot River population of Atlantic salmon is currently stable at a low abundance level but is heavily dependent on hatchery supplementation to avoid extinction. Low survival rates in early life stages and in the ocean are contributing to low abundance, as are hydroelectric dams, which are prevalent in the watershed. Given the number of dams in the Penobscot watershed and an increased understanding of the negative effects of dams on Atlantic salmon productivity through altered ecological functions, the approach to managing the population has changed. For example, stocking locations have been moved to lower in the watershed to maximize adult return rates. Although more salmon are returning to the river, focusing the population in the lower watershed also means Atlantic salmon, including potential spawners, are occupying lower quality habitat, which could minimize their production. Another consequence of focusing the population in the lower watershed is that increasing survival rates at dams, especially those in the upper watershed (e.g., Weldon Dam), have little effect on salmon abundance and distribution. We may be missing important population recovery opportunities by concentrating Atlantic salmon in lower quality habitat. As highlighted by the difference between marine survival rates of wild- and hatchery-origin fish, artificial selection effects of long-term hatchery supplementation may negatively affect recovery as well.

In order for Atlantic salmon in the Penobscot River to recover, increases in marine, early-life-stage, and dam survival rates will be necessary, along with reduced dependency on hatchery supplementation. Increasing marine and early-life-stage survival will likely require minimizing a range of natural and anthropogenic effects. Identifying and addressing the range of possible effects will require additional study. Increased survival at dams from the lower to the upper watershed will also be needed so that if marine and early-life-stage survival rates do increase, returning salmon can access habitat throughout the watershed. Survival rates at lower watershed dams will need to be increased to allow salmon access to upper watershed dams and higher quality habitat. Survival rates at upper watershed dams will need to be increased to allow salmon to access the highest quality habitat. Hatchery supplementation will need to be reduced as well if the population begins to increase. The decrease in hatchery-origin fish and increase in wild-origin fish will allow natural selection processes to resume. Using tools such as this model, scientists and managers can work together to better understand and characterize threats to Atlantic salmon in the Penobscot River and develop more efficient management and restoration strategies.

7. ACKNOWLEDGEMENTS

We have many people to thank for their roles in updating the DIA model and completing this document. Jeff Murphy, Rory Saunders, Dan Tierney, Matt Buhyoff, and Dan Kircheis (NMFS) provided management guidance. Chris Legault, Jon Deroba, and Dan Hennen (NMFS) participated in many helpful discussions of statistical distributions. Justin Stevens, Tara Trinko Lake, Graham Goulette, Audrey Dean, Doug Sigourney, and John Kocik (NMFS); Dan Stich and Joseph Zydlewski (University of Maine); and Denise Buckley (USFWS) provided data and insight to help improve model inputs. Dan Stich, Jon Deroba, and Dan Hennen assisted in coding contour plots. Graham Goulette, Justin Stevens, and Audrey Dean contributed Table 3.5.1. Justin Stevens contributed Figures 1.1 and 3.19.1. Rory Saunders, Jeff Murphy, Dan Tierney, Matt Buhyoff, Justin Stevens, Jon Deroba, and Sean Hayes provided helpful reviews and comments that greatly improved this document. As is evident from this document, Justin Stevens made a tremendous number of contributions to this project. Reference herein to any specific commercial product, process, or service by trade name, trademark, manufacturer, or otherwise is for descriptive purposes only and does not imply endorsement, recommendation, or favoring by the United States government or any agency thereof.

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9. TABLES

Table 3.1.1. Descriptions of production unit (PU) boundaries with corresponding metrics of longest segment length, partial segment length, and hatchery segment length (in km). Longest segment length is the longest straight-path distance that a fish could migrate in each PU. One or more partial segment lengths indicate that smolts could enter a PU from multiple locations, and the lengths represent the migration distance from various starting locations. Hatchery segment length is the distance that stocked smolts would migrate in their initial PU.

PU	Upstream boundaries	Downstream boundaries	Longest segment length	Partial segment length	Hatchery segment length
1	West Branch Penobscot headwaters	Medway Dam	309	NA	19
2	East Branch Penobscot headwaters, Medway Dam	Weldon Dam	139	11	12
3	Mattawamkeag River headwaters, Weldon Dam	West Enfield Dam	208	48	41
4	Pleasant River headwaters, Milo Dam, Browns Mill Dam	Howland Dam	125	42, 65	45
5	Dunham Brook headwaters, Upper Dover Dam	Browns Mill Dam	10	1	1
6	Piscataquis River headwaters	Upper Dover Dam	78	NA	8
7	Sebec Dam	Milo Dam	12	NA	12
8	Sebec River headwaters	Sebec Dam	59	NA	21
9	Lowell Tannery Dam, Howland Dam, West Enfield Dam	Stillwater Dam, Milford Dam	61	56, 44	35
11	Stillwater Dam	Orono Dam	4	NA	4
13	Marsh Stream headwaters	Frankfort Dam	54	NA	4
14	Kenduskeag Stream headwaters, Frankfort Dam, Orono Dam, Milford Dam	Southern end of Verona Island	121	18, 54, 62	61
15	Passadumkeag River headwaters	Lowell Tannery Dam	49	NA	6

Table 3.1.2. Total number of habitat units and accessible habitat units (in 100 m^2) to Atlantic salmon (*Salmo salar*), the proportion of adults seeded, and the smolt production cap (i.e., the maximum number of wild-origin smolts) in each production unit (PU). Habitat in PUs 1, 7, 8, and 11 is inaccessible to Atlantic salmon because of the current conditions at Medway, Milo, Sebec, and Orono dams. Therefore, the baseline habitat units and smolt production cap values were set as zero for these PUs. Figure 1.1 identifies the PU locations.

PU	Total habitat units	Accessible habitat units	Proportion of adults	Smolt production cap
1	84,287	0	0	505,722
2	44,250	44,250	0.0153	265,503
3	56,450	56,450	0.0586	338,697
4	42,849	42,849	0.1353	257,091
5	284	284	0	1,703
6	21,782	21,782	0.0084	130,692
7	1,733	0	0	10,400
8	13,922	0	0	83,532
9	17,860	17,860	0.1925	107,160
11	940	0	0	5,642
13	4,801	4,801	0.0070	28,808
14	23,656	23,656	0.5621	141,935
15	3,601	3,601	0.0209	21,606

Table 3.2.1. Mean proportion and number of hatchery-reared smolts stocked into each production unit (PU) from 2008 to 2017.

PU	Proportion stocked	Number stocked
1	0	0
2	0	0
3	0.0486	26,490
4	0.1851	100,869
5	0	0
6	0.0188	10,258
7	0	0
8	0	0
9	0.2616	142,561
11	0	0
13	0	0
14	0.4859	264,822
15	0	0
Total	1	545,000

Table 3.2.2. Adult homing and straying rates by production unit (PU). The natal PU identifies where a fish was reared, and the final destination PU identifies where a fish attempted to migrate as a prespawning adult. Homing rates are bolded and listed in the diagonal row. A zero indicates no straying from the natal PU into the final destination PU.

	Final destination PU												
Natal PU	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**11**	**13**	**14**	**15**
1	**0.900**	0.080	0.009	0.005	0	0	0	0	0.005	0	0	0	0.001
2	0.070	**0.900**	0.009	0.010	0	0	0	0	0.010	0	0	0	0.001
3	0	0.010	**0.900**	0.050	0.010	0.010	0	0	0.010	0	0	0	0.010
4	0	0	0.010	**0.900**	0.001	0.049	0.020	0.020	0	0	0	0	0
5	0	0	0	0.010	**0.900**	0.080	0.004	0.004	0.002	0	0	0	0
6	0	0	0	0.080	0.010	**0.900**	0.005	0.005	0	0	0	0	0
7	0	0	0	0.020	0	0	**0.900**	0.080	0	0	0	0	0
8	0	0	0	0.020	0	0	0.080	**0.900**	0	0	0	0	0
9	0	0.010	0.040	0.080	0	0	0	0	**0.700**	0.010	0	0.060	0.100
11	0.010	0.020	0.040	0.020	0	0	0	0	0.100	**0.700**	0.020	0.080	0.010
13	0	0	0.040	0.020	0	0	0	0	0.030	0	**0.900**	0.010	0
14	0	0	0.041	0.074	0	0	0	0	0.163	0.018	0.004	**0.700**	0
15	0	0.010	0.010	0	0	0	0	0	0.060	0.010	0	0.010	**0.900**

Table 3.4.1. Summary of the life stage survival percentage rates used to develop the egg-to-smolt survival distribution.

Life Stage		Survival		
Begin	**End**	**Minimum**	**Maximum**	**Mean**
Egg	Fry	15	35	25.0
Fry	Parr 0+	31	60	45.5
Parr 0+	Parr 1+	13	56	34.5
Parr 1+	Smolt	17	50	33.5
Egg	Smolt	0.10	5.88	1.31

Table 3.5.1. Smolt production values per habitat unit (in 100 m^2) from the literature. Highlighted entries were used in setting the smolt production cap.

Author	Region	River	Years of data	Mean	Minimum	Maximum
Meister 1962	Maine	Cove Brook	3	3.59		
Elson 1975	New Brunswick	Pollett	19		0.24	6.57
Egglishaw and Shackley 1977	Scotland	Shelligan Burn			1.00	6.00
Gee et al. 1978	Wales	Wye	2	2.00	0.50	4.30
Garnas and Hvidsten 1985	Norway	Orkla	1	4.10		
Gibson et al. 1987	Newfoundland	Highlands			0.60	5.30
Shackley and Donaghy 1992	Scotland	five rivers	1		1.97	7.02
Kennedy and Crozier 1993	Northern Ireland	Bush	16		3.00	8.90
Orciari et al. 1994	Connecticut	Sandy Brook	7		1.00	4.10
McMenemy 1995	Vermont	West	8	4.00		
Matthews et al. 1997	Ireland	Burrishoole		0.13		
Cunjak and Therrien 1998	New Brunswick	Catamaran	7		0.44	2.06
Jonsson et al. 1998a	Norway	Imsa	19		3.97	27.51
Jonsson et al. 1998b	Norway	Imsa	22	13.40	0.30	31.00
Whalen et al. 2000	Vermont	Utley	3	0.76	0.55	0.96
Whalen et al. 2000	Vermont	Rock	3	1.18	0.78	1.58
Whalen et al. 2000	Vermont	Wardsboro	3	1.13	0.51	1.74
Bagliniere et al. 2002	France	La Roche Brook		5.20		20.10
Bagliniere et al. 2005	France	Oir	18	2.10	0.17	5.70
Bowlby et al. 2013	Nova Scotia	LaHave	15		0.20	0.98
Bowlby et al. 2013	Nova Scotia	St. Mary's	5		0.43	1.48
Hvidsten et al. 2015	Norway	Orkla	27	6.20	3.40	10.80

Table 3.16.1. The fate of adult spawners that do not successfully migrate above each hydroelectric dam. Unsuccessful fish died, returned to the ocean without spawning, or remained downstream and spawned in a different production unit (PU). Fish that remained downstream were redirected to a downstream PU according to the proportions under the destination PU. A zero in the destination PU indicates no fish were redirected to that PU. The dashes in the rows for Great Works and Veazie dams indicate that Atlantic salmon (*Salmo salar*) do not encounter upstream passage inefficiency because these dams have been removed.

				Destination PU												
Dam failed to pass	**Proportion dying**	**Proportion returning to sea**	**Proportion remaining downstream**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**11**	**13**	**14**	**15**
Medway	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Weldon	0.01	0	0.99	0	0	1	0	0	0	0	0	0	0	0	0	0
West Enfield	0.02	0	0.98	0	0	0	0.6	0	0	0	0	0.4	0	0	0	0
Upper Dover	0.02	0	0.98	0	0	0	1	0	0	0	0	0	0	0	0	0
Browns Mill	0.02	0	0.98	0	0	0	1	0	0	0	0	0	0	0	0	0
Sebec	0	0	1	0	0	0	0.1	0	0	0.9	0	0	0	0	0	0
Milo	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Howland	0.02	0	0.98	0	0	0.4	0	0	0	0	0	0.6	0	0	0	0
Lowell Tannery	0.01	0	0.99	0	0	0.01	0.01	0	0	0	0	0.98	0	0	0	0
Milford	0.03	0.15	0.82	0	0	0	0	0	0	0	0	0	0	0.1	0.9	0
Stillwater	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Great Works	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Orono	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Veazie	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Frankfort	0.02	0.1	0.88	0	0	0	0	0	0	0	0	0	0	0	1	0

Table 3.18.1.1. Model inputs for 4 model scenarios in the Base Model Runs evaluating the effects of dams and hatchery supplementation. Dams were either set at baseline survival rates (Dams On) or 100% survival (No Dams). Hatchery supplementation was either set to the baseline stocking strategy (Hatch On) or no stocking occurred (Hatch Off).

Input	Dams On Hatch On	Dams On Hatch Off	No Dams Hatch On	No Dams Hatch Off
Adult seeding	Baseline	Baseline	Baseline	Baseline
Eggs per female	Baseline	Baseline	Baseline	Baseline
Egg-to-smolt survival	Baseline	Baseline	Baseline	Baseline
Smolt production cap	Baseline	Baseline	Baseline	Baseline
Stocking	Baseline	None	Baseline	None
In-river mortality	Baseline	Baseline	Baseline	Baseline
Impoundment mortality	Baseline	Baseline	0	0
Downstream dam survival rates	Baseline	Baseline	1 at all dams	1 at all dams
Indirect latent mortality	Baseline	Baseline	Baseline	Baseline
Hatchery discount	Baseline	Baseline	Baseline	Baseline
Sex-ratio discount	Baseline	Baseline	Baseline	Baseline
Marine survival	Baseline	Baseline	Baseline	Baseline
Straying	Baseline	Baseline	Baseline	Baseline
Upstream dam passage rates	Baseline	Baseline	1 at all dams	1 at all dams
Upstream dam passage inefficiency	Baseline	Baseline	Baseline	Baseline
Broodstock collection	Baseline	None	Baseline	None

Table 3.18.1.2. Median survival or passage rates (downstream, upstream) for hydroelectric dams on the Penobscot River in 5 model scenarios with changes in dam conditions for the Weldon Model Runs.

Dam	Existing	Proposed w/ Impound	Proposed	Weldon Removed	No Dams
Medway	(0, 0)	(0, 0)	(0, 0)	(0, 0)	(0, 0)
Weldon	(0.80, 0.90)	(0.96, 0.95)	(0.96, 0.95)	(1, 1)	(1, 1)
West Enfield	(0.96, 0.95)	(0.96, 0.95)	(0.96, 0.95)	(0.96, 0.95)	(1, 1)
Upper Dover	(0.92, 0.92)	(0.92, 0.92)	(0.92, 0.92)	(0.92, 0.92)	(1, 1)
Browns Mill	(0.85, 0.92)	(0.85, 0.92)	(0.85, 0.92)	(0.85, 0.92)	(1, 1)
Sebec	(0.87, 0)	(0.87, 0)	(0.87, 0)	(0.87, 0)	(1, 1)
Milo	(0.88, 0)	(0.88, 0)	(0.88, 0)	(0.88, 0)	(1, 1)
Howland	(1, 0.95)	(1, 0.95)	(1, 0.95)	(1, 0.95)	(1, 1)
Lowell Tannery	(0.87, 0.92)	(0.87, 0.92)	(0.87, 0.92)	(0.87, 0.92)	(1, 1)
Milford	(0.96, 0.95)	(0.96, 0.95)	(0.96, 0.95)	(0.96, 0.95)	(1, 1)
Stillwater	(0.96, 0.92)	(0.96, 0.92)	(0.96, 0.92)	(0.96, 0.92)	(1, 1)
Great Works	(1, 1)	(1, 1)	(1, 1)	(1, 1)	(1, 1)
Orono	(0.96, 0)	(0.96, 0)	(0.96, 0)	(0.96, 0)	(1, 1)
Veazie	(1, 1)	(1, 1)	(1, 1)	(1, 1)	(1, 1)
Frankfort	(0.94, 0.92)	(0.94, 0.92)	(0.94, 0.92)	(0.94, 0.92)	(1, 1)

Table 3.18.2.1.1. Model inputs for 3 model scenarios in the Whole System Dam Analysis evaluating the effects of dam, egg-to-smolt, and marine survival rates and no hatchery supplementation. The model scenarios reflect low, medium, and high levels of downstream and upstream survival at dams in the model.

Input	Low	Medium	High
Adult seeding	Baseline	Baseline	Baseline
Eggs per female	Baseline	Baseline	Baseline
Egg-to-smolt survival	Range	Range	Range
Smolt production cap	Baseline	Baseline	Baseline
Stocking	None	None	None
In-river mortality	Baseline	Baseline	Baseline
Impoundment mortality	Baseline	Baseline	Baseline
Downstream dam survival rates	0.80	0.90	1
Indirect latent mortality	Baseline	Baseline	Baseline
Hatchery discount	Baseline	Baseline	Baseline
Sex-ratio discount	Baseline	Baseline	Baseline
Marine survival	Range	Range	Range
Straying	Baseline	Baseline	Baseline
Upstream dam passage rates	0.90	0.95	1
Upstream dam passage inefficiency	Baseline	Baseline	Baseline
Broodstock collection	None	None	None

Table 3.18.2.1.2. Survival or passage rates (downstream, upstream) for hydroelectric dams on the Penobscot River in 3 model scenarios for the Whole System Dam Analysis. The model scenarios reflect low, medium, and high levels of downstream and upstream survival at all dams in the model (including Milo, Sebec, and Orono), with 2 exceptions. Downstream and upstream survival were set at 1 for Howland Dam because of the Penobscot River Restoration Project, and both survivals were set at zero for Medway Dam because of the lack of fish passage at this dam and others in the West Branch of the Penobscot River.

Dam	Low	Medium	High
Medway	(0, 0)	(0, 0)	(0, 0)
Weldon	(0.80, 0.90)	(0.90, 0.95)	(1, 1)
West Enfield	(0.80, 0.90)	(0.90, 0.95)	(1, 1)
Upper Dover	(0.80, 0.90)	(0.90, 0.95)	(1, 1)
Browns Mill	(0.80, 0.90)	(0.90, 0.95)	(1, 1)
Sebec	(0.80, 0.90)	(0.90, 0.95)	(1, 1)
Milo	(0.80, 0.90)	(0.90, 0.95)	(1, 1)
Howland	(1, 1)	(1, 1)	(1, 1)
Lowell Tannery	(0.80, 0.90)	(0.90, 0.95)	(1, 1)
Milford	(0.80, 0.90)	(0.90, 0.95)	(1, 1)
Stillwater	(0.80, 0.90)	(0.90, 0.95)	(1, 1)
Great Works	(1, 1)	(1, 1)	(1, 1)
Orono	(0.80, 0.90)	(0.90, 0.95)	(1, 1)
Veazie	(1, 1)	(1, 1)	(1, 1)
Frankfort	(0.80, 0.90)	(0.90, 0.95)	(1, 1)

Table 3.18.2.2.1. Model inputs for 6 scenarios in the Whole System Stocking Location Analysis estimating the effects of stocking location and increased egg-to-smolt and marine survival rates. Smolts were stocked only in production unit (PU) 14, immediately below Milford Dam; with the baseline stocking strategy; or only in PU 2, upstream of Weldon Dam. Scenarios were run with these 3 stocking locations and baseline egg-to-smolt and marine survival rates as well as increased egg-to-smolt and marine survival rates.

	Baseline survival			Increased survival		
Input	**Below Milford**	**Baseline**	**Above Weldon**	**Below Milford**	**Baseline**	**Above Weldon**
Adult seeding	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Eggs per female	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Egg-to-smolt survival	Baseline	Baseline	Baseline	Increased	Increased	Increased
Smolt production cap	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Hatchery stocking	All below Milford	Baseline	All above Weldon	All below Milford	Baseline	All above Weldon
In-river mortality	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Impoundment mortality	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Downstream dam passage survival	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Indirect latent mortality	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Hatchery discount	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Marine survival	Baseline	Baseline	Baseline	Increased	Increased	Increased
Straying	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Upstream dam passage survival	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Upstream dam passage inefficiency	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Broodstock collection	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline

Table 3.18.3.1.1 Model inputs for 5 scenarios evaluating the effects of varying dam survival, especially at Weldon Dam, for the Survival and Phase 2 Recovery Analyses. The model scenarios reflect existing conditions at Weldon Dam (Existing); proposed conditions at Weldon Dam with impoundment mortality present (Proposed w/ Impound); proposed conditions at Weldon Dam without impoundment mortality (Proposed); the removal of Weldon Dam (Weldon Removed); and the removal of all hydroelectric dams in the watershed, except those in the West Branch (No Dams).

Input	Existing	Proposed w/ Impound	Proposed	Weldon Removed	No Dams
Adult seeding	Baseline	Baseline	Baseline	Baseline	Baseline
Eggs per female	Baseline	Baseline	Baseline	Baseline	Baseline
Egg-to-smolt survival	Baseline	Baseline	Baseline	Baseline	Baseline
Smolt production cap	Baseline	Baseline	Baseline	Baseline	Baseline
Stocking	Baseline	Baseline	Baseline	Baseline	Baseline
In-river mortality	Baseline	Baseline	Baseline	Baseline	Baseline
Impoundment mortality	Baseline	Baseline	0%	0%	0%
Downstream dam survival rates	Baseline	96% at Weldon	96% at Weldon	100% at Weldon	100% at all dams
Indirect latent mortality	Baseline	Baseline	Baseline	Baseline	Baseline
Hatchery discount	Baseline	Baseline	Baseline	Baseline	Baseline
Sex-ratio discount	Baseline	Baseline	Baseline	Baseline	Baseline
Marine survival	Baseline	Baseline	Baseline	Baseline	Baseline
Straying	Baseline	Baseline	Baseline	Baseline	Baseline
Upstream dam passage rates	Baseline	95% at Weldon	95% at Weldon	100% at Weldon	100% at all dams
Upstream dam passage inefficiency	Baseline	Baseline	Baseline	Baseline	Baseline
Broodstock collection	Baseline	Baseline	Baseline	Baseline	Baseline

Table 3.18.3.2.1. Model inputs for a base case scenario to estimate increased egg-to-smolt and marine survival rates and 5 scenarios evaluating the effects of varying dam survival, especially at Weldon Dam, for the Phase 3 Recovery Analysis. The 5 model scenarios with varying dam survival reflect existing conditions at Weldon Dam (Existing); proposed conditions at Weldon Dam with impoundment mortality present (Proposed w/ Impound); proposed conditions at Weldon Dam without impoundment mortality (Proposed); the removal of Weldon Dam (Weldon Removed); and the removal of all hydroelectric dams in the watershed, except those in the West Branch (No Dams).

Input	Base Case	Existing	Proposed w/ Impound	Proposed	Weldon Removed	No Dams
Adult seeding	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Eggs per female	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Egg-to-smolt survival	Range	Increased	Increased	Increased	Increased	Increased
Smolt production cap	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Stocking	Changed over time	Changed over time	Changed over time	Changed over time	Changed over time	Changed over time
In-river mortality	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Impoundment mortality	Baseline	Baseline	Baseline	0%	0%	0%
Downstream dam survival rates	Baseline	Baseline	96% at Weldon	96% at Weldon	100% at Weldon	100% at all dams
Indirect latent mortality	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Hatchery discount	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Sex-ratio discount	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Marine survival	Range	Increased	Increased	Increased	Increased	Increased
Straying	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Upstream dam passage rates	Baseline	Baseline	95% at Weldon	95% at Weldon	100% at Weldon	100% at all dams
Upstream dam passage inefficiency	Baseline	Baseline	Baseline	Baseline	Baseline	Baseline
Broodstock collection	Changed over time	Changed over time	Changed over time	Changed over time	Changed over time	Changed over time

Table 3.18.3.3.1. Model inputs for 5 scenarios in the Smolt Mortality Analysis evaluating the effects of in-river, impoundment, and dam mortality that occurred in production unit 2 and at Weldon Dam. The model scenarios reflect existing conditions at Weldon Dam (Existing); proposed conditions at Weldon Dam with impoundment mortality present (Proposed w/ Impound); proposed conditions at Weldon Dam without impoundment mortality (Proposed); the removal of Weldon Dam (Weldon Removed); and the removal of all hydroelectric dams in the watershed, except those in the West Branch (No Dams).

Input	Existing	Proposed w/ Impound	Proposed	Weldon Removed	No Dams
Stocking	1,000 smolts in PU 2	1,000 smolts in PU 2	1,000 smolts in PU 2	1,000 smolts in PU 2	1,000 smolts in PU 2
In-river mortality	Baseline	Baseline	Baseline	Baseline	Baseline
Impoundment mortality	Baseline	Baseline	0%	0%	0%
Downstream dam survival rates	Baseline	96% at Weldon	96% at Weldon	100% at Weldon	100% at all dams

10. FIGURES

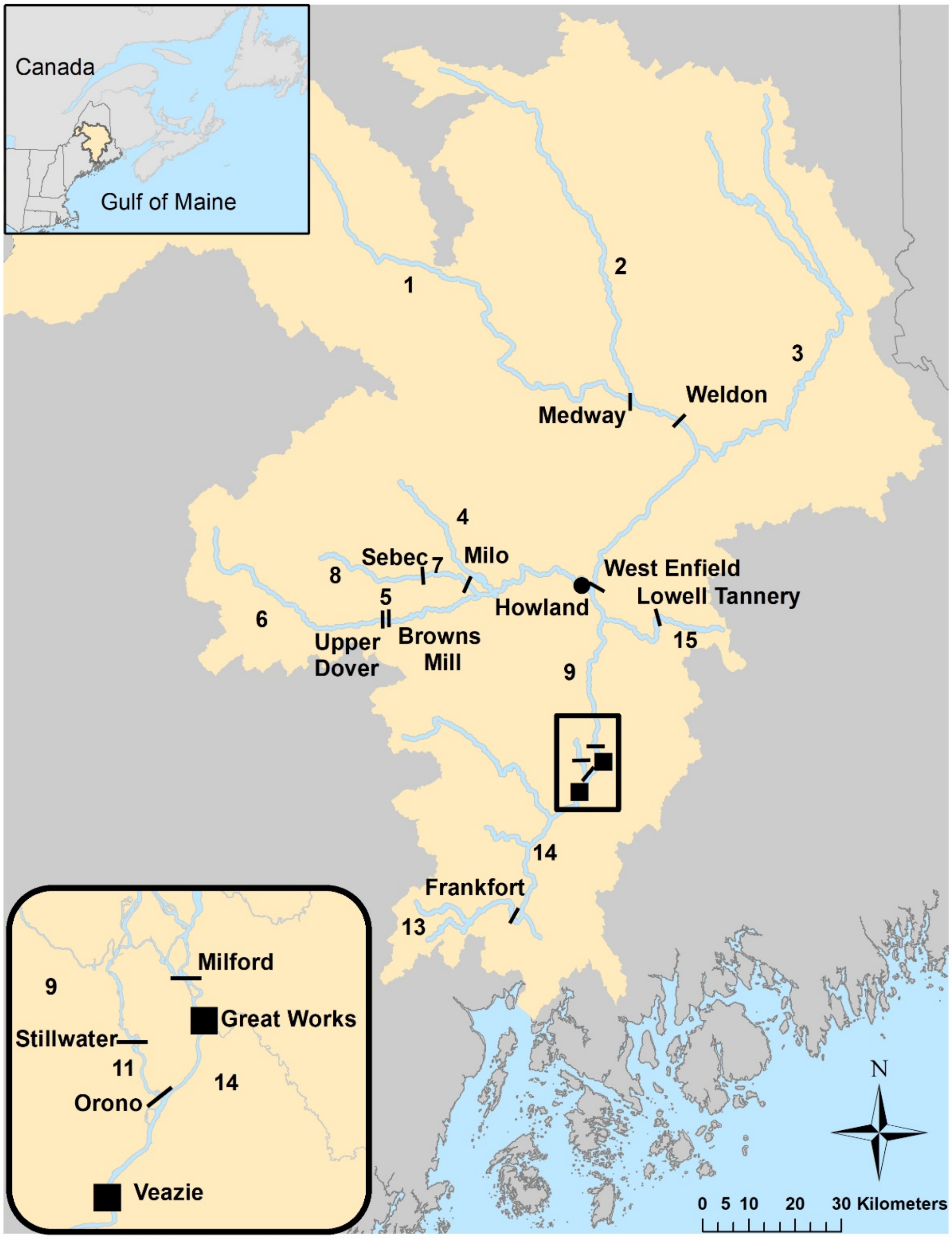

Figure 1.1. The Penobscot River watershed divided into production units (numbered). Locations of modeled hydroelectric dams are denoted by the name of each dam and a dash (–) for dams that are present and active, a filled square (■) for dams that have been removed, and a filled circle (●) for dams that have been bypassed. The insets show the Penobscot River watershed within the northeastern United States and southeastern Canada (upper map) and the mainstem and Stillwater branches of the Penobscot River (lower map).

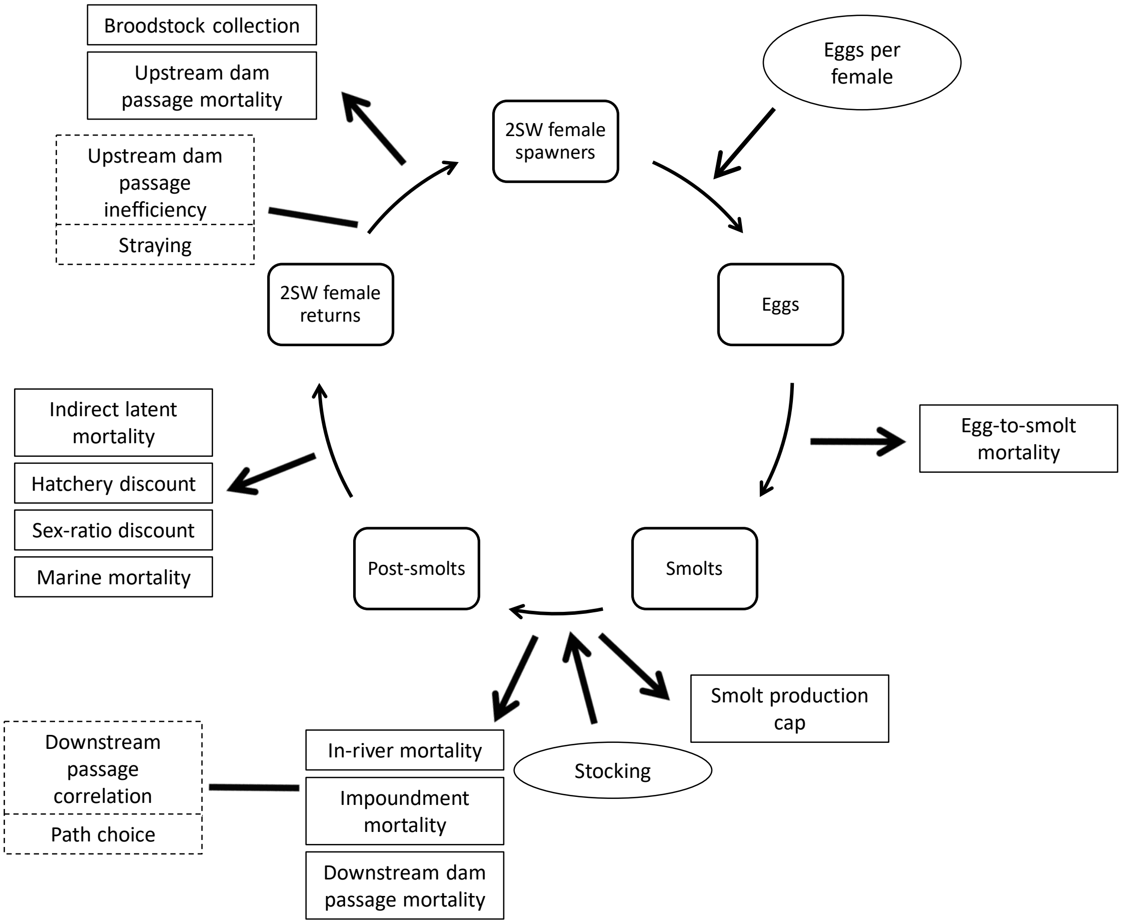

Figure 2.1. Schematic of the Atlantic salmon (*Salmo salar*) life cycle detailed within the model. Rounded rectangles indicate life cycle stages, ovals indicate additions to the population, and rectangles indicate subtractions from the population. Dashed rectangles are neither additions to nor subtractions from the population but represent dynamics incorporated into the model. Adult Atlantic salmon were modeled as 2 sea-winter (2SW) fish.

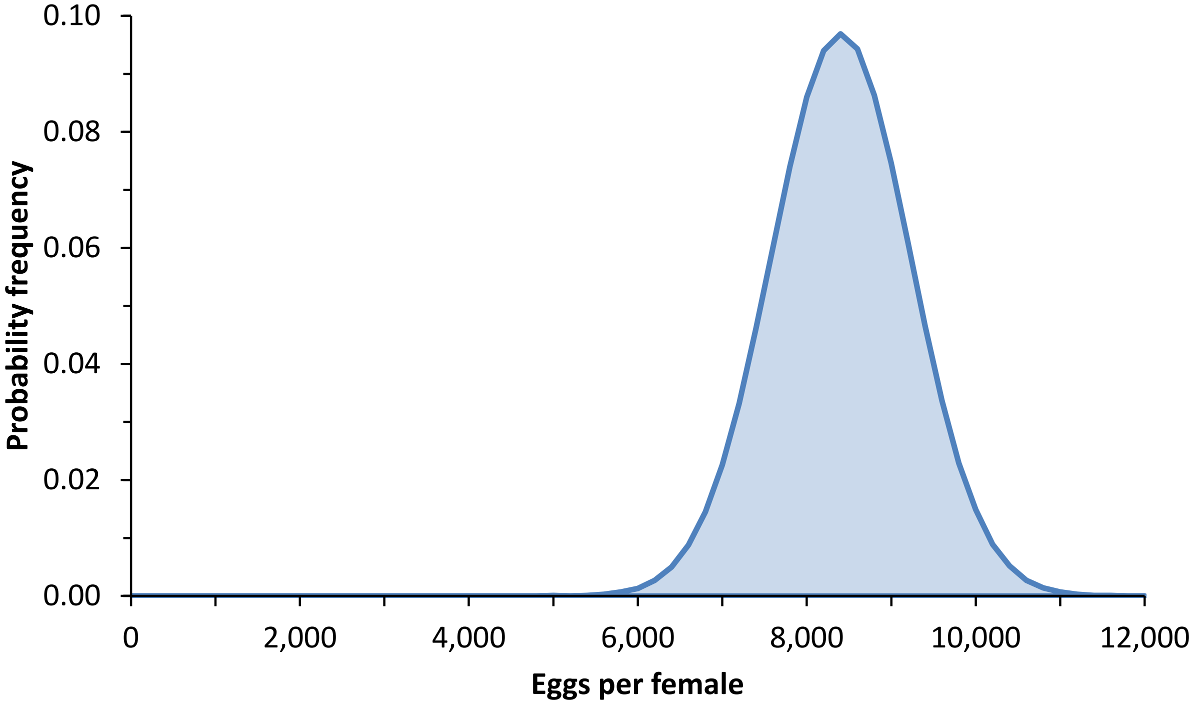

Figure 3.3.1. Distribution of the number of Atlantic salmon (*Salmo salar*) eggs produced per 2 sea-winter female generated from mean annual fecundity estimates for Penobscot River sea-run females spawned at Craig Brook National Fish Hatchery from 1997 to 2010.

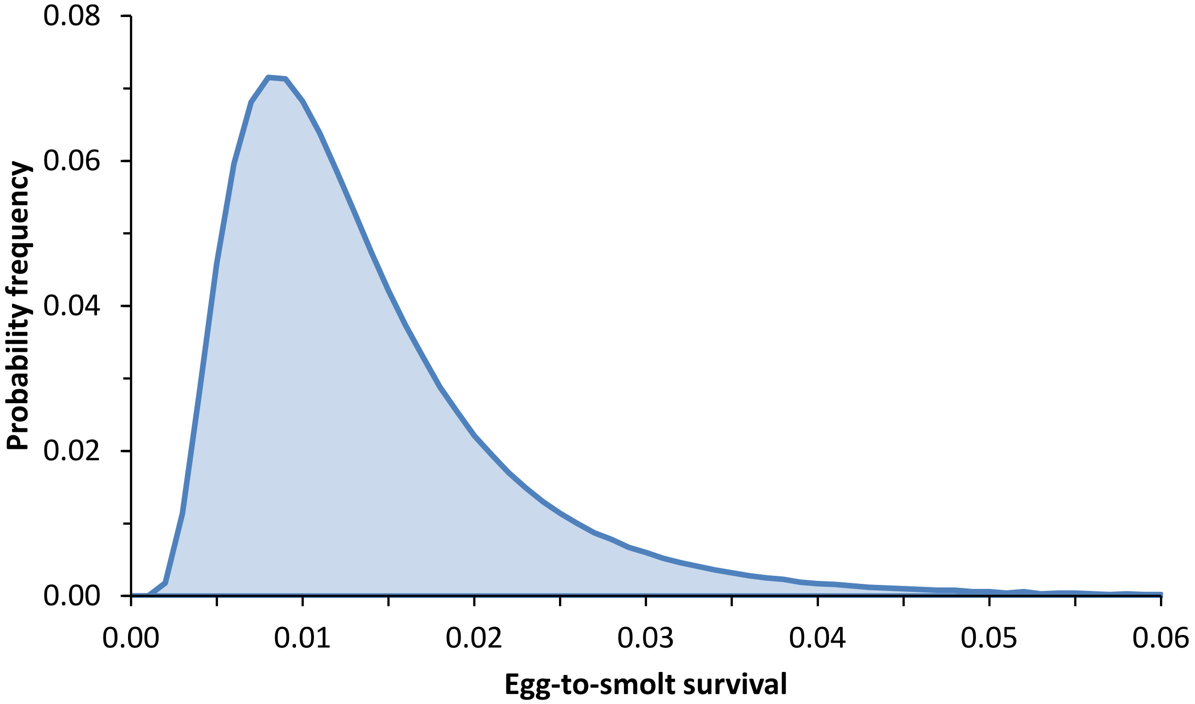

Figure 3.4.1. Distribution of the Atlantic salmon (*Salmo salar*) egg-to-smolt survival rate generated from survival estimates of egg to fry, fry to parr0+, parr0+ to parr1+, and parr1+ to smolt life stages in the literature.

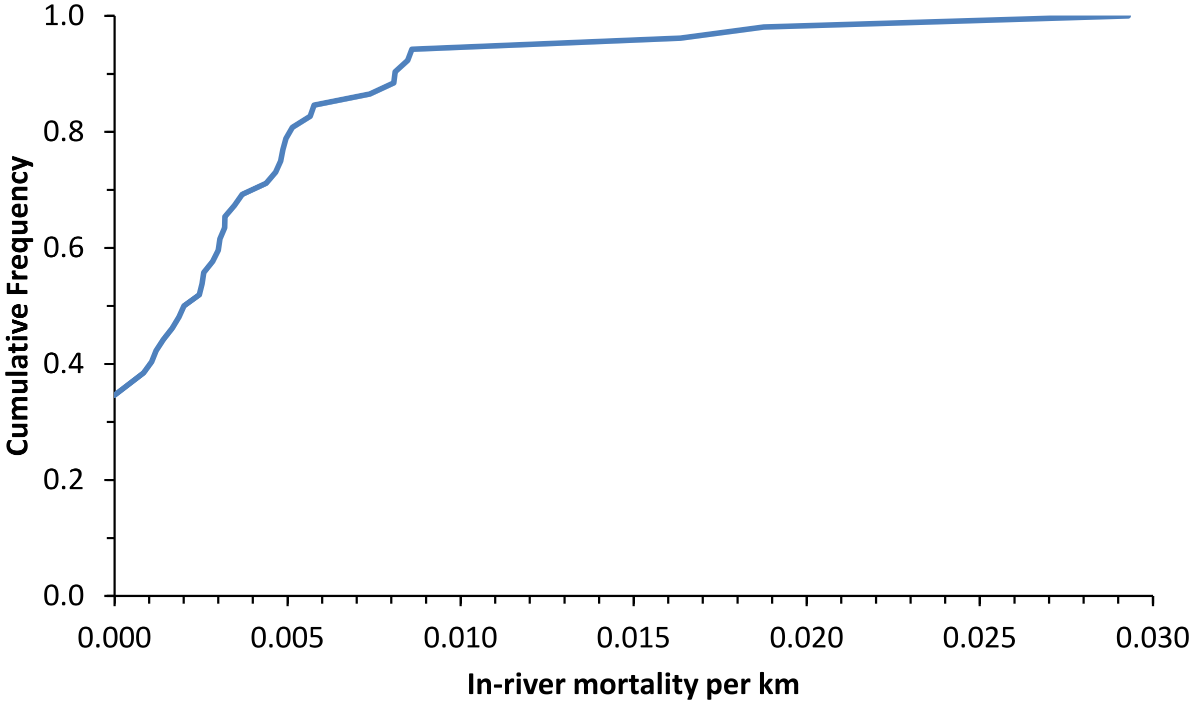

Figure 3.7.1. Cumulative frequency distribution of natural, in-river mortality per km for Atlantic salmon (*Salmo salar*) smolts migrating downstream. Mortality-per-km estimates did not include dam-related mortality.

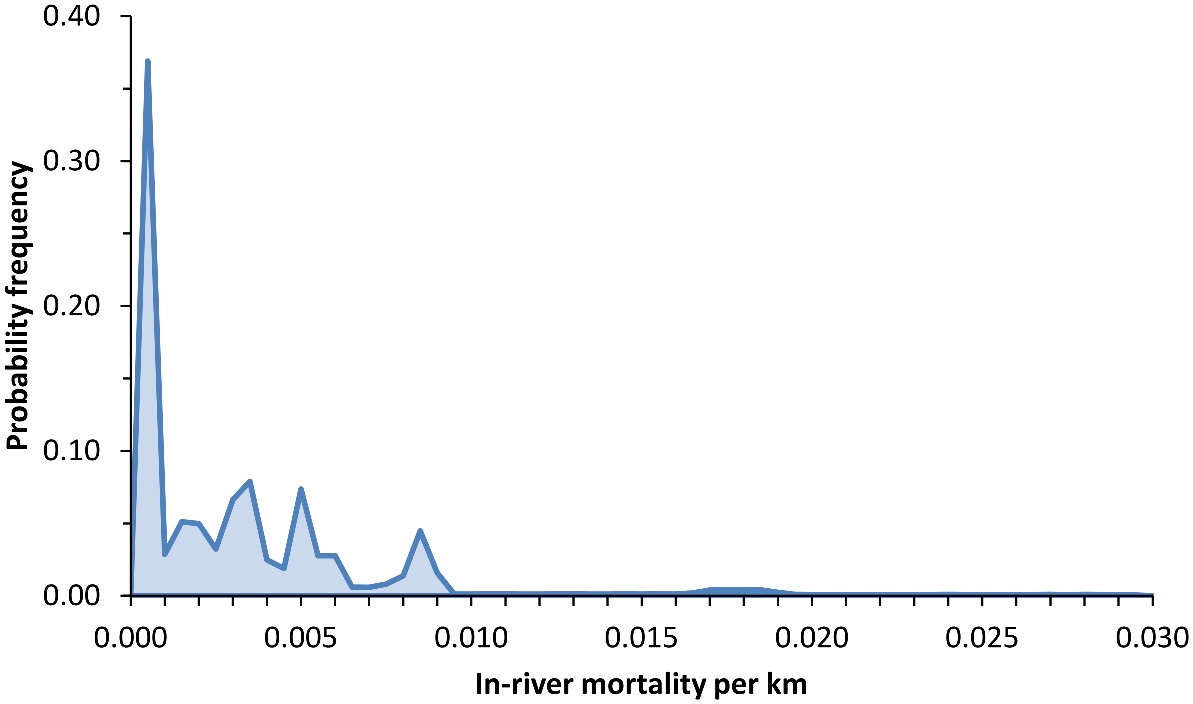

Figure 3.7.2. Probability frequency distribution of natural, in-river mortality per km for Atlantic salmon (*Salmo salar*) smolts migrating downstream. Mortality-per-km estimates did not include dam-related mortality.

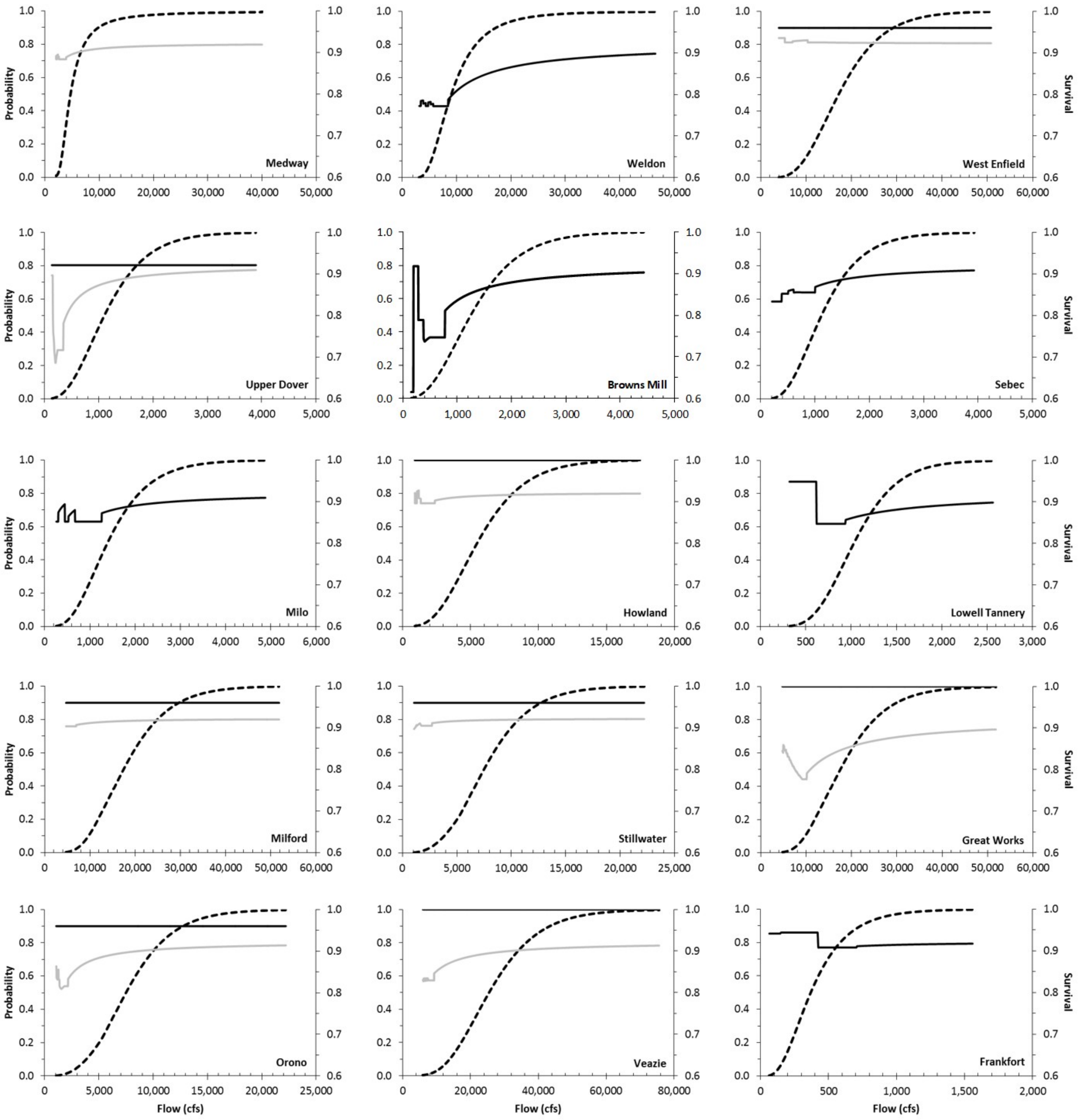

Figure 3.9.1.1. Cumulative flow probability functions (dashed line) and Atlantic salmon (*Salmo salar*) smolt survival (solid line) for 15 Federal Energy Regulatory Commission-regulated hydroelectric dams on the Penobscot River. For 6 of the dams, survival was modeled by flow (dams with only a solid black line; in cubic feet per second [CFS]). For the other 9 dams, smolt survival by flow is shown (solid gray line), but survival was modeled at a constant value (solid black line) based on current conditions. The constant value is not shown for Medway Dam because survival equaled zero. Note that the x-axes are dam-specific.

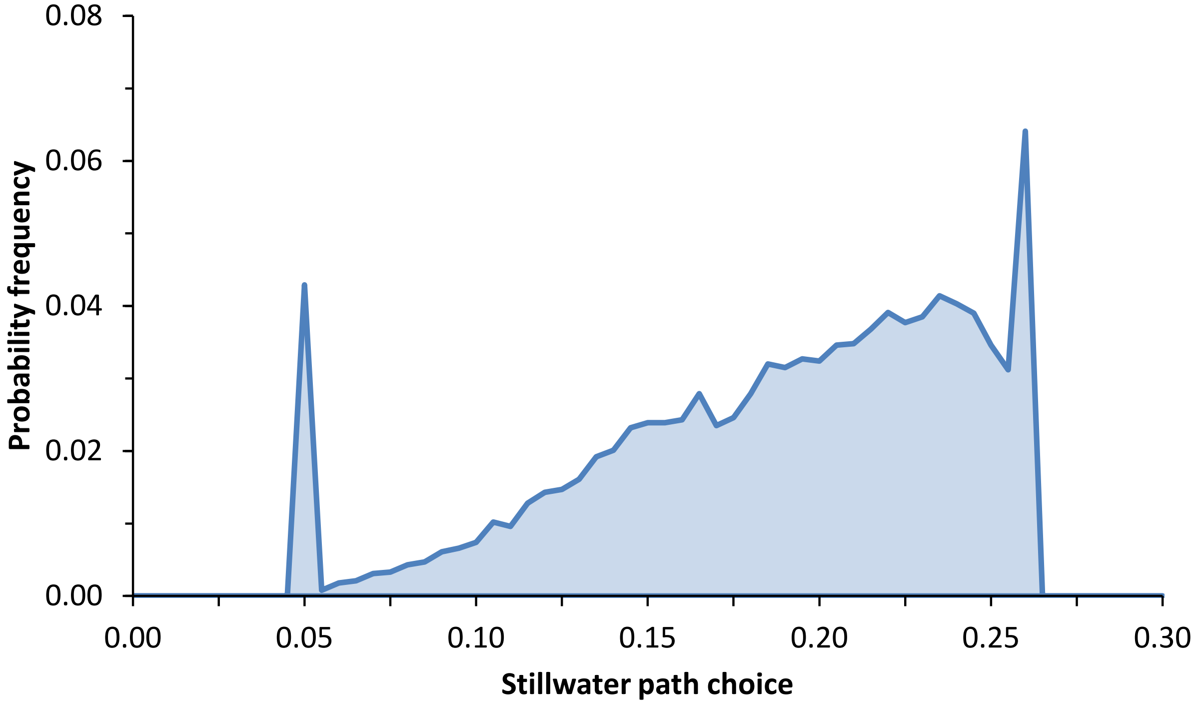

Figure 3.9.2.1. Probability frequency distribution of smolt path choice for Atlantic salmon (*Salmo salar*) in the Stillwater branch of the Penobscot River.

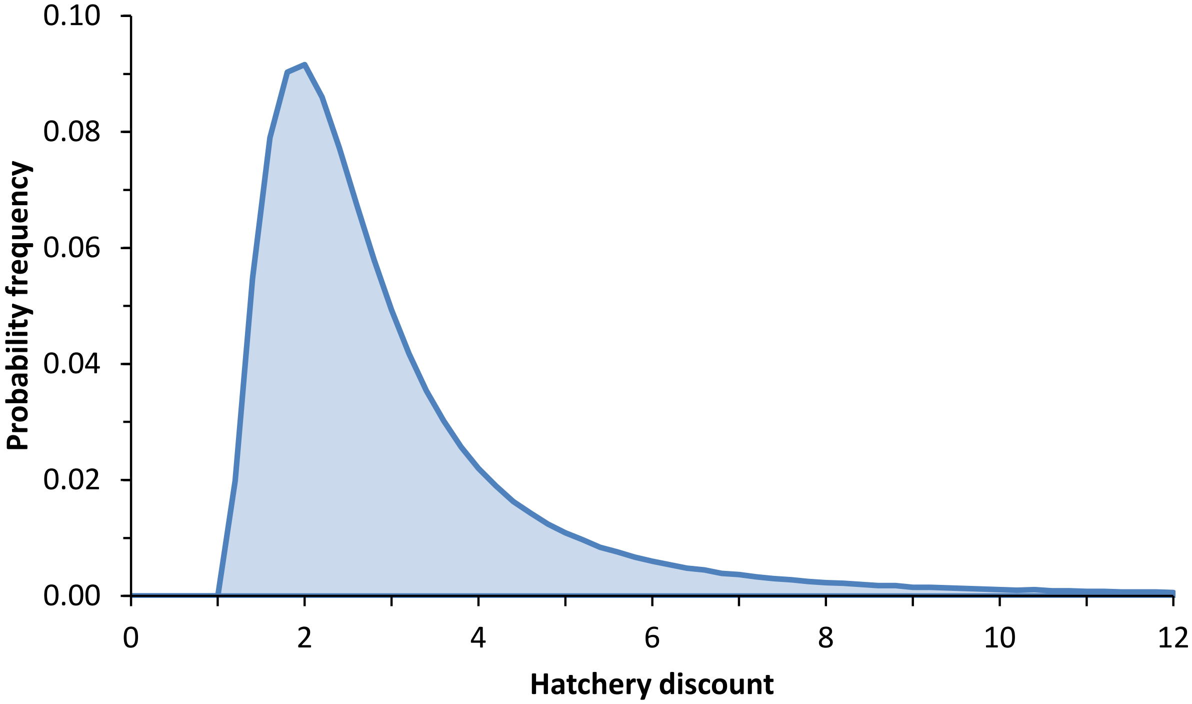

Figure 3.11.1. Probability frequency distribution of the discount on Atlantic salmon (*Salmo salar*) hatchery smolts to adjust to the equivalent number of wild smolts.

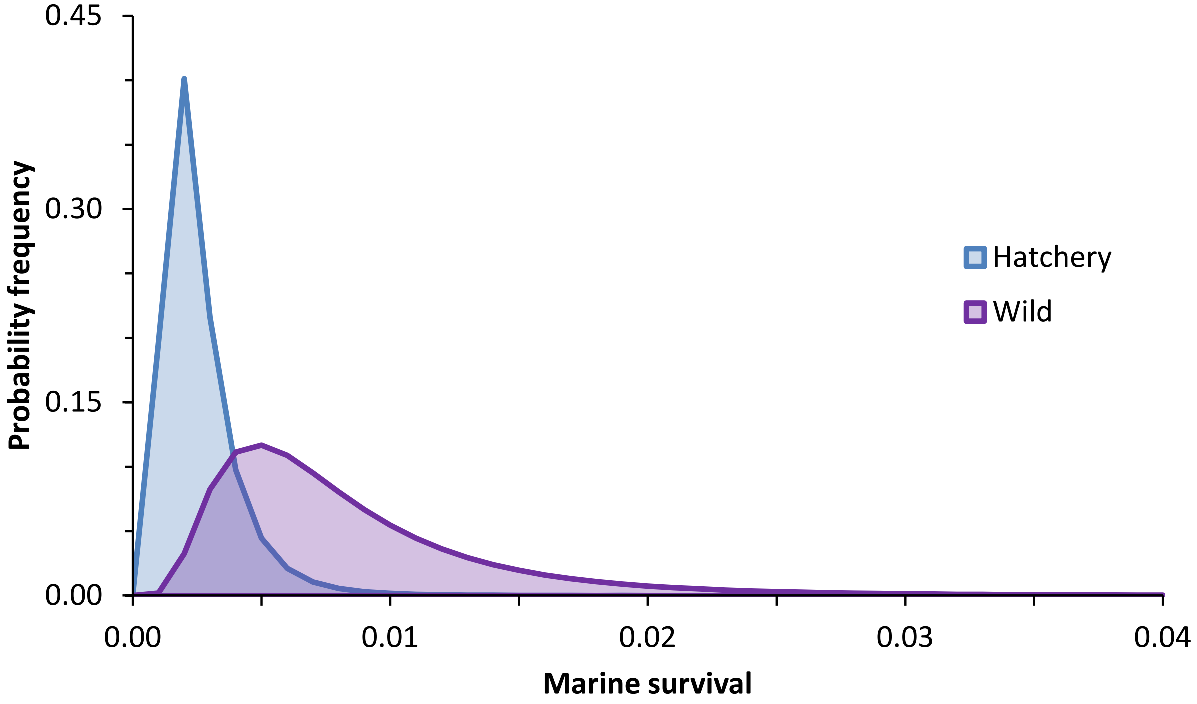

Figure 3.13.1.1. Probability frequency distributions of marine survival for hatchery-origin and wild-origin Atlantic salmon (*Salmo salar*).

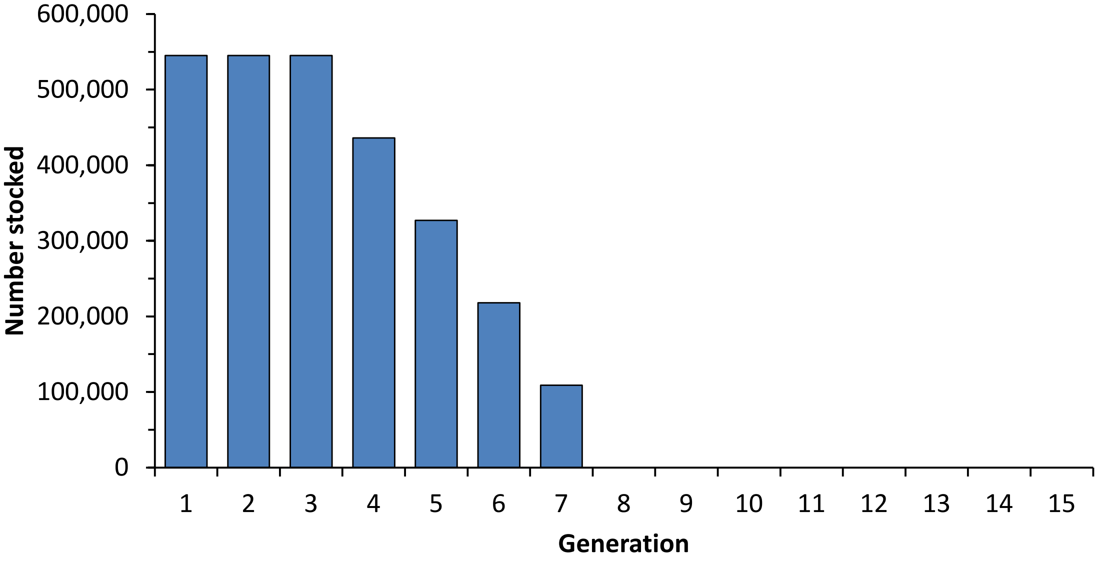

Figure 3.18.3.2.1. Number of Atlantic salmon (*Salmo salar*) smolts stocked in the Penobscot River watershed in generations 1–15 in the Phase 3 Recovery Analysis.

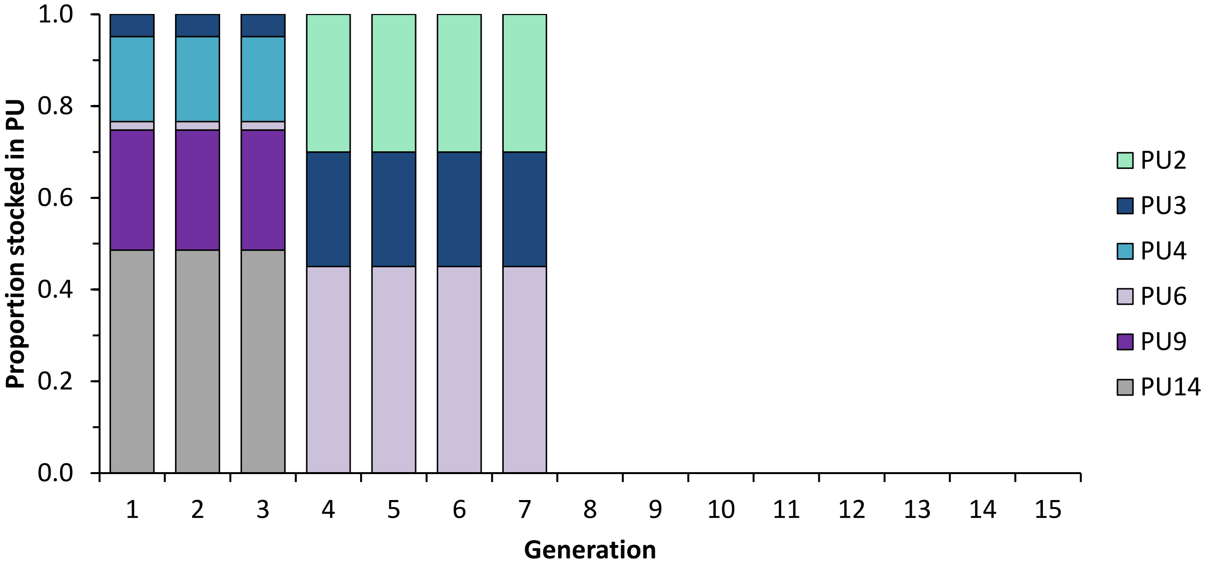

Figure 3.18.3.2.2. Smolt stocking locations for Atlantic salmon (*Salmo salar*) in the Penobscot River watershed in generations 1–15 in the Phase 3 Recovery Analysis.

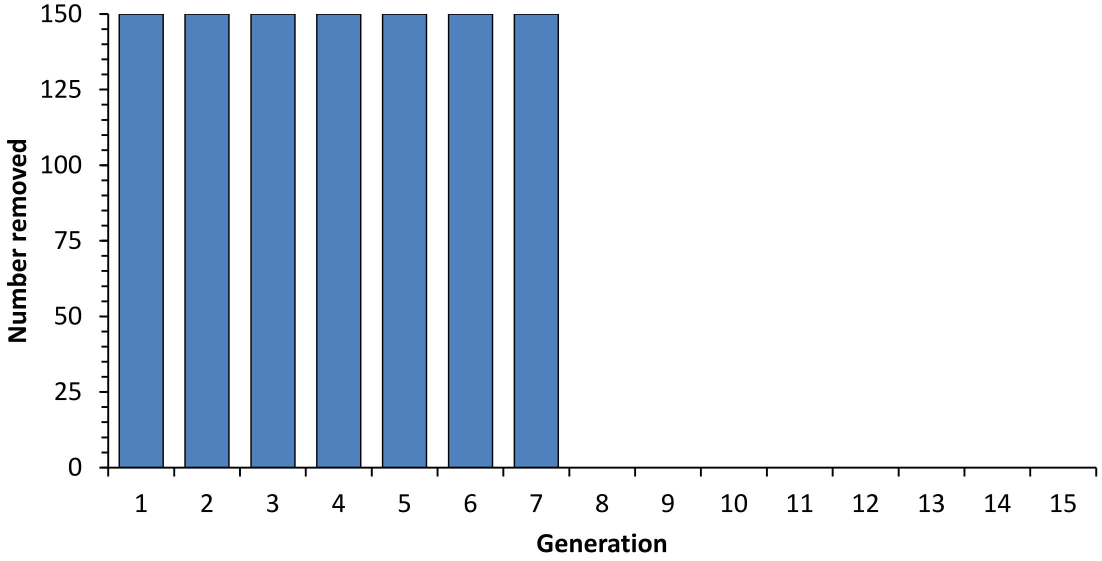

Figure 3.18.3.2.3. Number of 2 sea-winter Atlantic salmon (*Salmo salar*) females removed for use as broodstock in the Penobscot River watershed in generations 1 – 15 in the Phase 3 Recovery Analysis. In generation 1, the removal of 150 2 sea-winter females was included in the calculation of the initial number of adults.

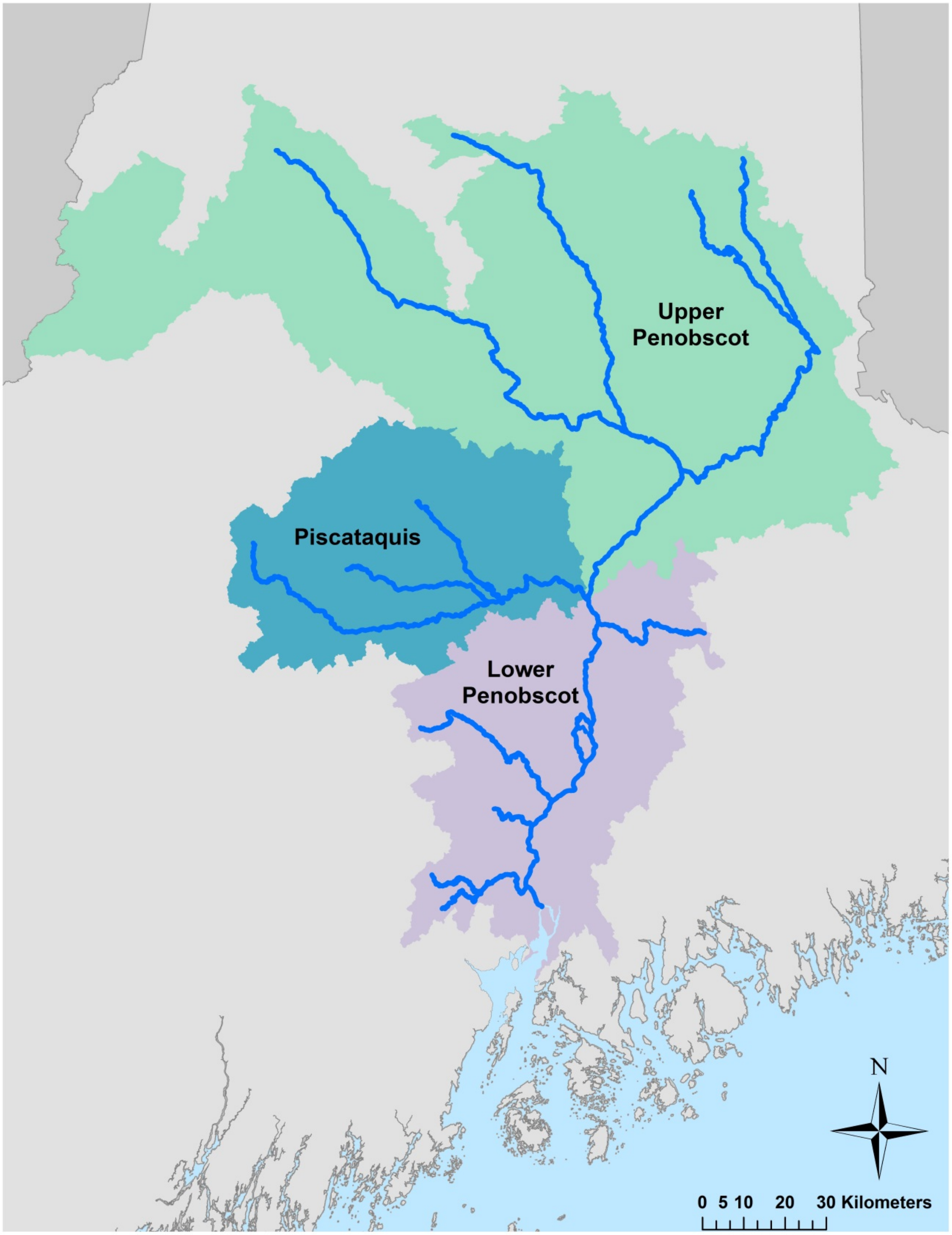

Figure 3.19.1. The Penobscot River watershed divided into 3 areas. The upper Penobscot area included the portion of the watershed above West Enfield Dam, the Piscataquis area included the Piscataquis River watershed, and the lower Penobscot area included the portion of the watershed below West Enfield Dam.

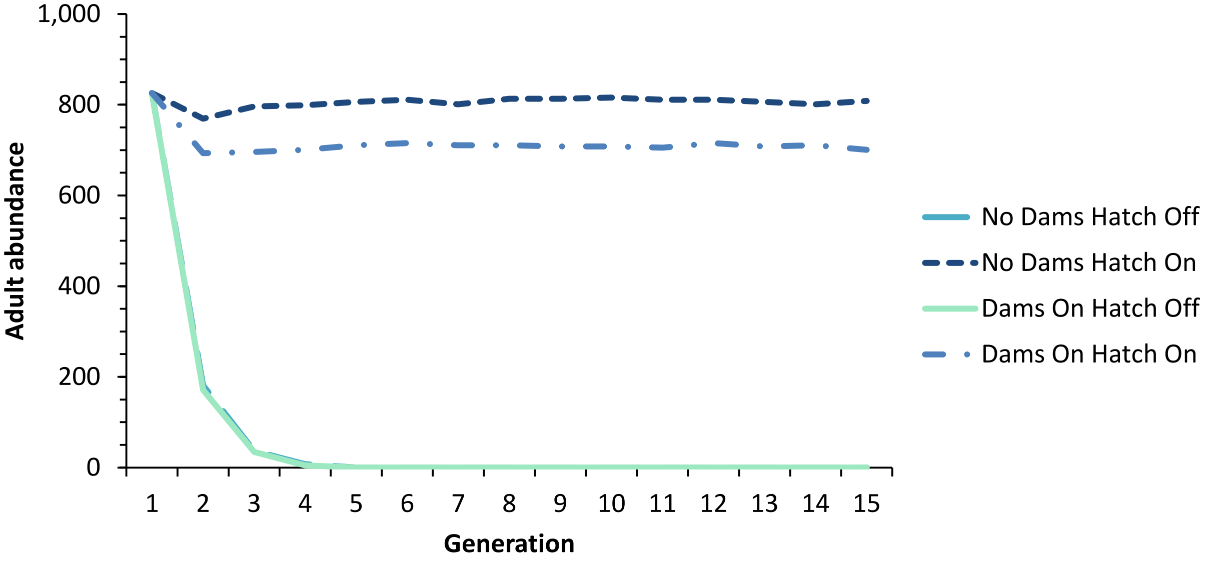

Figure 4.1.1. Median adult abundance of Atlantic salmon (*Salmo salar*) in the Penobscot River watershed in generations 1–15 for 4 model scenarios evaluating the effects of dams and hatchery supplementation in the Base Model Runs. Dams were either set at baseline survival rates (Dams On) or 100% survival (No Dams). Hatchery supplementation was either set to the baseline stocking strategy (Hatch On) or no stocking occurred (Hatch Off). Results overlap in Hatch Off scenarios.

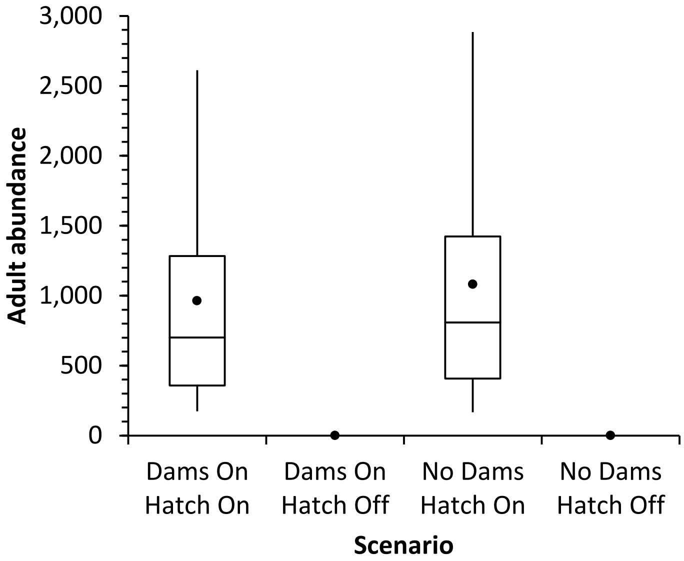

Figure 4.1.2. Mean (dot), median (center line), 25th and 75th percentiles (box), and 5th and 95th percentiles (whiskers) of Atlantic salmon (*Salmo salar*) adult abundance in the Penobscot River watershed in generation 15 for 4 model scenarios evaluating the effects of dams and hatchery supplementation in the Base Model Runs. Dams were either set at baseline survival rates (Dams On) or 100% survival (No Dams). Hatchery supplementation was either set to the baseline stocking strategy (Hatch On) or no stocking occurred (Hatch Off).

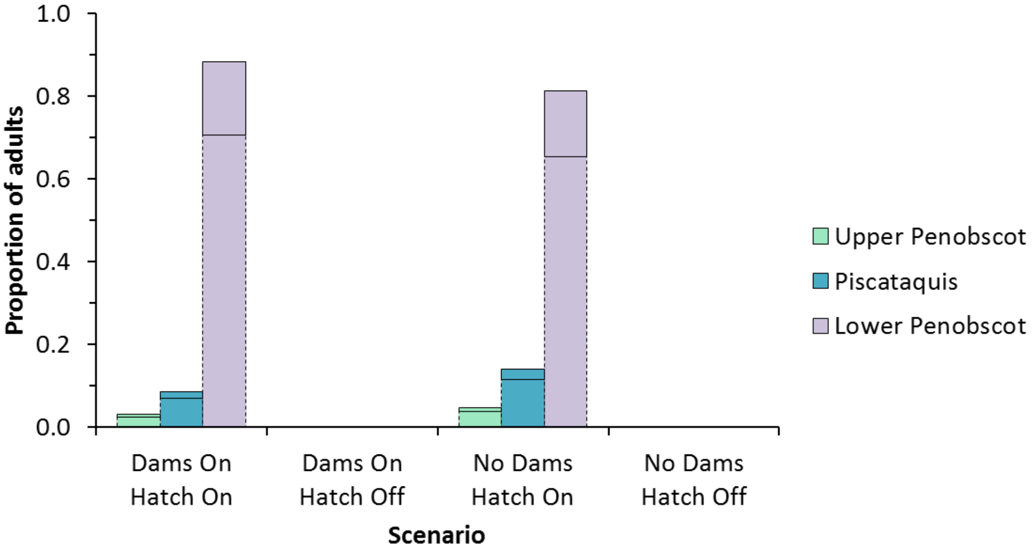

Figure 4.1.3. Median proportion of wild-origin (solid borders) and hatchery-origin (dashed borders) Atlantic salmon (*Salmo salar*) adults in the upper Penobscot, Piscataquis, and lower Penobscot areas of the Penobscot River watershed in generation 15 for 4 model scenarios evaluating the effects of dams and hatchery supplementation in the Base Model Runs. Dams were either set at baseline survival rates (Dams On) or 100% survival (No Dams). Hatchery supplementation was either set to the baseline stocking strategy (Hatch On) or no stocking occurred (Hatch Off).

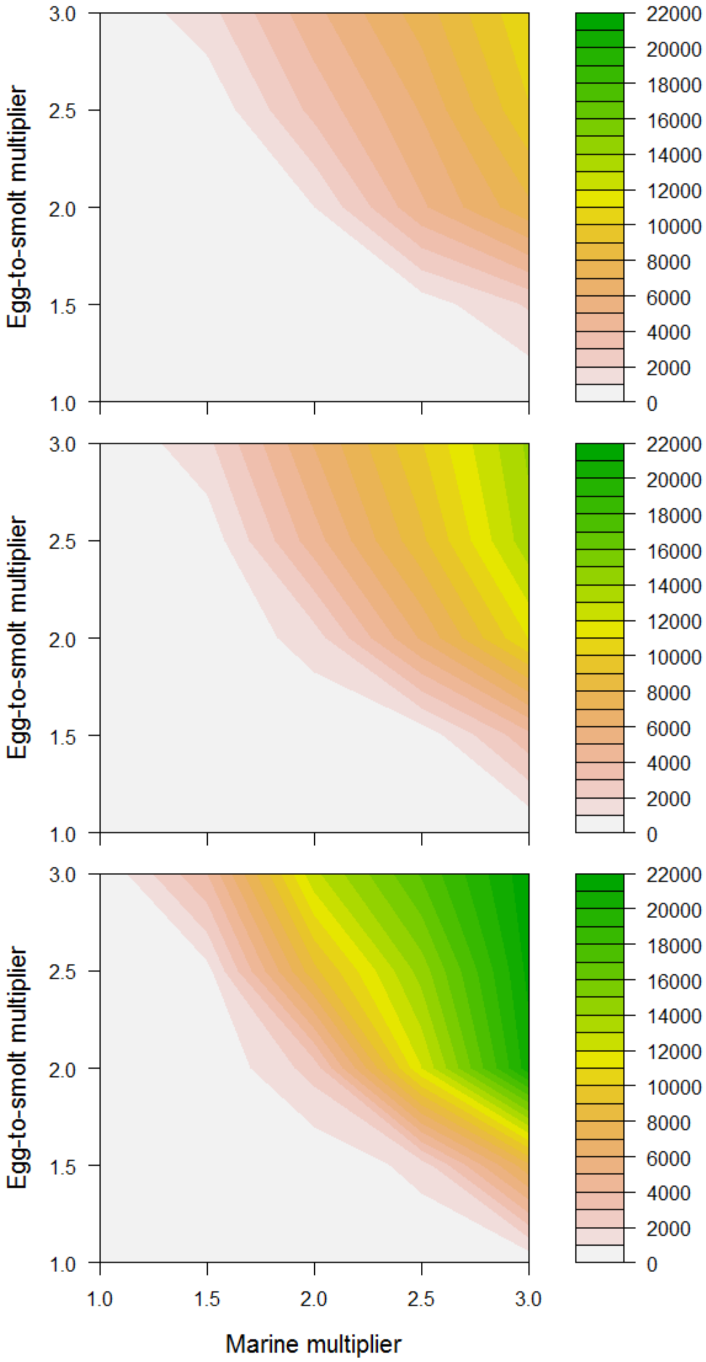

Figure 4.2.1.1. Median Atlantic salmon (*Salmo salar*) adult abundance in the Penobscot River watershed in generation 15 for 3 model scenarios evaluating the effects of varying dam, egg-to-smolt, and marine survival rates in the Whole System Dam Analysis. Egg-to-smolt and marine survival were increased by a factor of 1–3. Downstream and upstream dam survival rates were set at low (0.80, 0.90; top panel), medium (0.90, 0.95; middle panel), and high (1, 1; bottom panel) levels at all dams in the watershed, except Howland (1, 1) and Medway (0, 0) dams. No hatchery supplementation occurred in these scenarios.

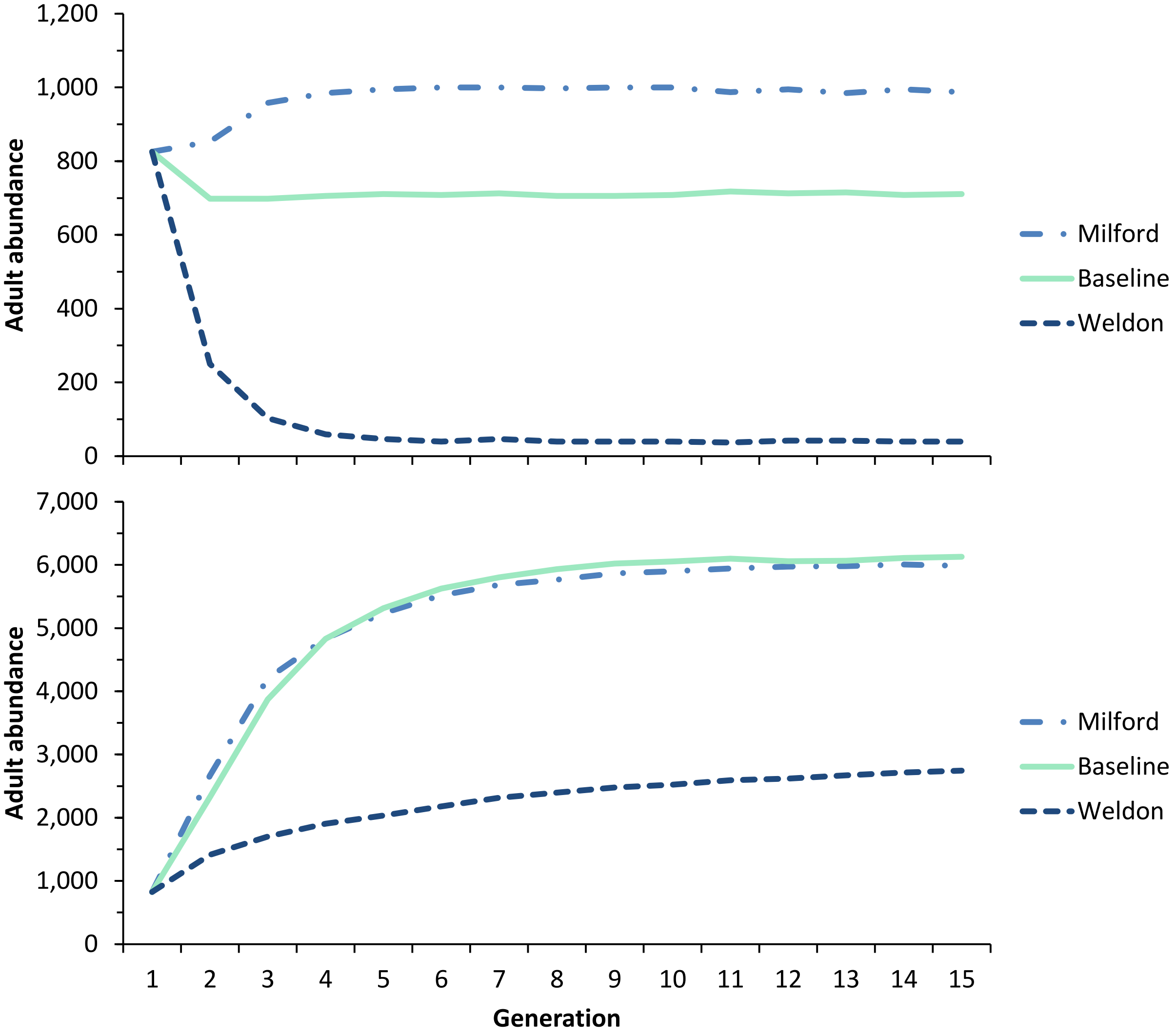

Figure 4.2.2.1. Median Atlantic salmon (*Salmo salar*) adult abundance in the Penobscot River watershed in generations 1–15 for 3 model scenarios evaluating the effects of stocking location in the Whole System Stocking Location Analysis. The model scenarios reflect all smolts stocked in production unit (PU) 14, immediately below Milford Dam (Milford); the baseline stocking strategy (Baseline); and all smolts stocked in PU 2, upstream of Weldon Dam (Weldon). Egg-to-smolt and marine survival were set at the baseline rates (top panel) and increased (bottom panel; egg-to-smolt survival was increased by a factor of 2.2, and marine survival was increased by a factor of 1.8).

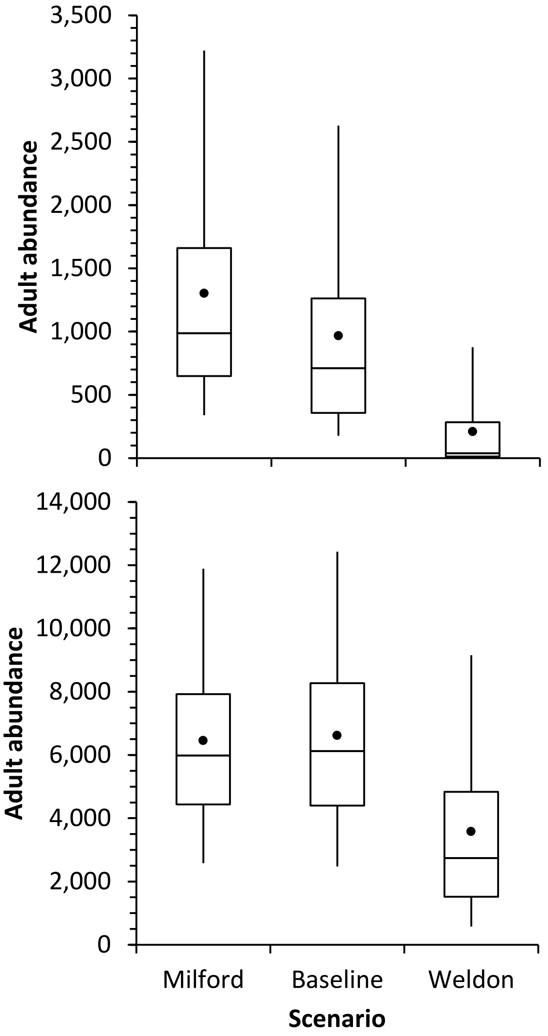

Figure 4.2.2.2. Mean (dot), median (center line), 25th and 75th percentiles (box), and 5th and 95th percentiles (whiskers) of Atlantic salmon (*Salmo salar*) adult abundance in the Penobscot River watershed in generation 15 for 3 model scenarios evaluating the effects of stocking location in the Whole System Stocking Location Analysis. The model scenarios reflect all smolts stocked in production unit (PU) 14, immediately below Milford Dam (Milford); the baseline stocking strategy (Baseline); and all smolts stocked in PU 2, upstream of Weldon Dam (Weldon). Egg-to-smolt and marine survival were set at the baseline rates (top panel) and increased (bottom panel; egg-to-smolt survival was increased by a factor of 2.2, and marine survival was increased by a factor of 1.8).

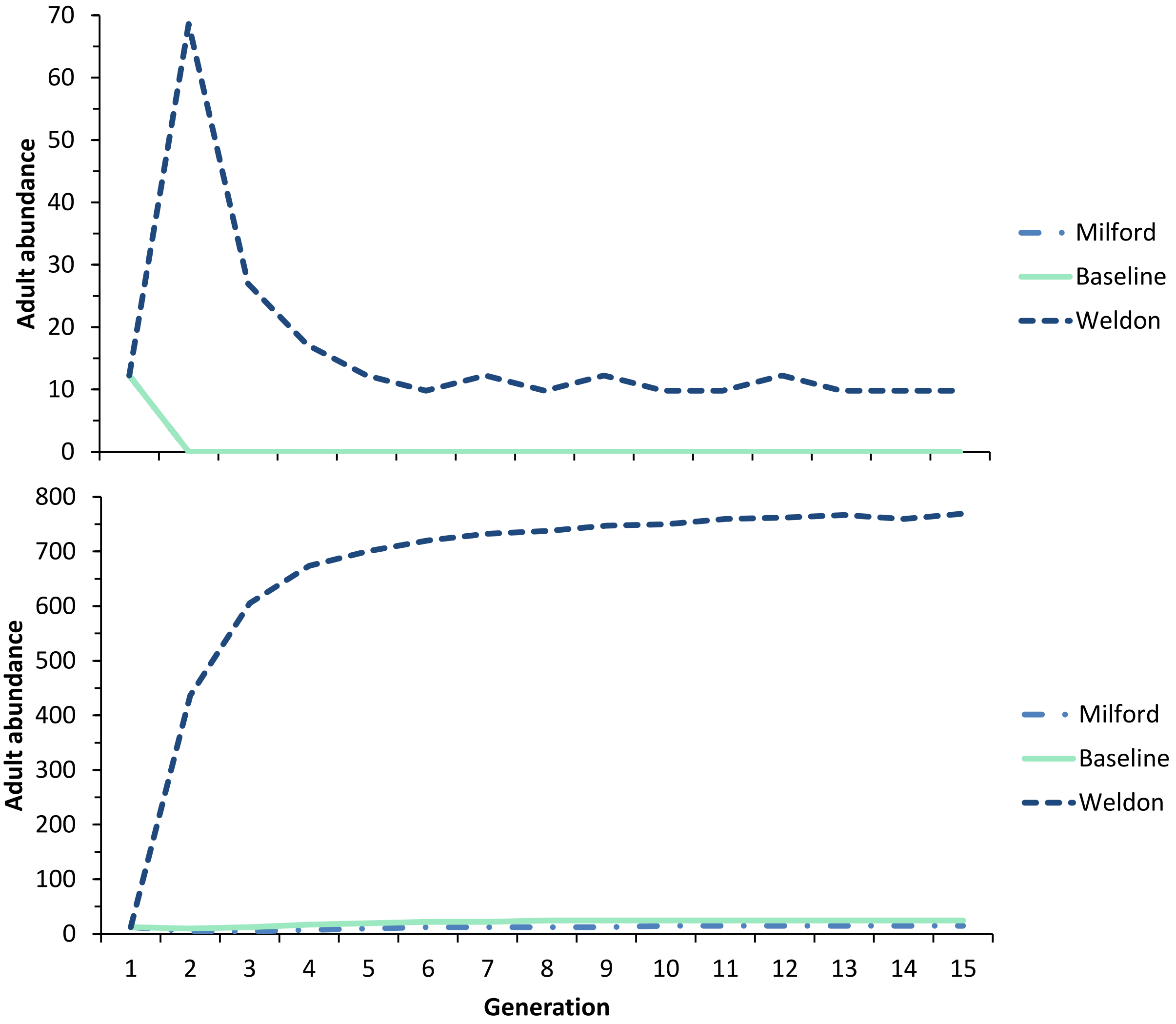

Figure 4.2.2.3. Median Atlantic salmon (*Salmo salar*) adult abundance in production unit (PU) 2 in generations 1–15 for 3 model scenarios evaluating the effects of stocking location in the Whole System Stocking Location Analysis. The model scenarios reflect all smolts stocked in PU 14, immediately below Milford Dam (Milford); the baseline stocking strategy (Baseline); and all smolts stocked in PU 2, upstream of Weldon Dam (Weldon). Egg-to-smolt and marine survival were set at the baseline rates (top panel) and increased (bottom panel; egg-to-smolt survival was increased by a factor of 2.2, and marine survival was increased by a factor of 1.8). Results overlap in Milford and Baseline scenarios in top panel.

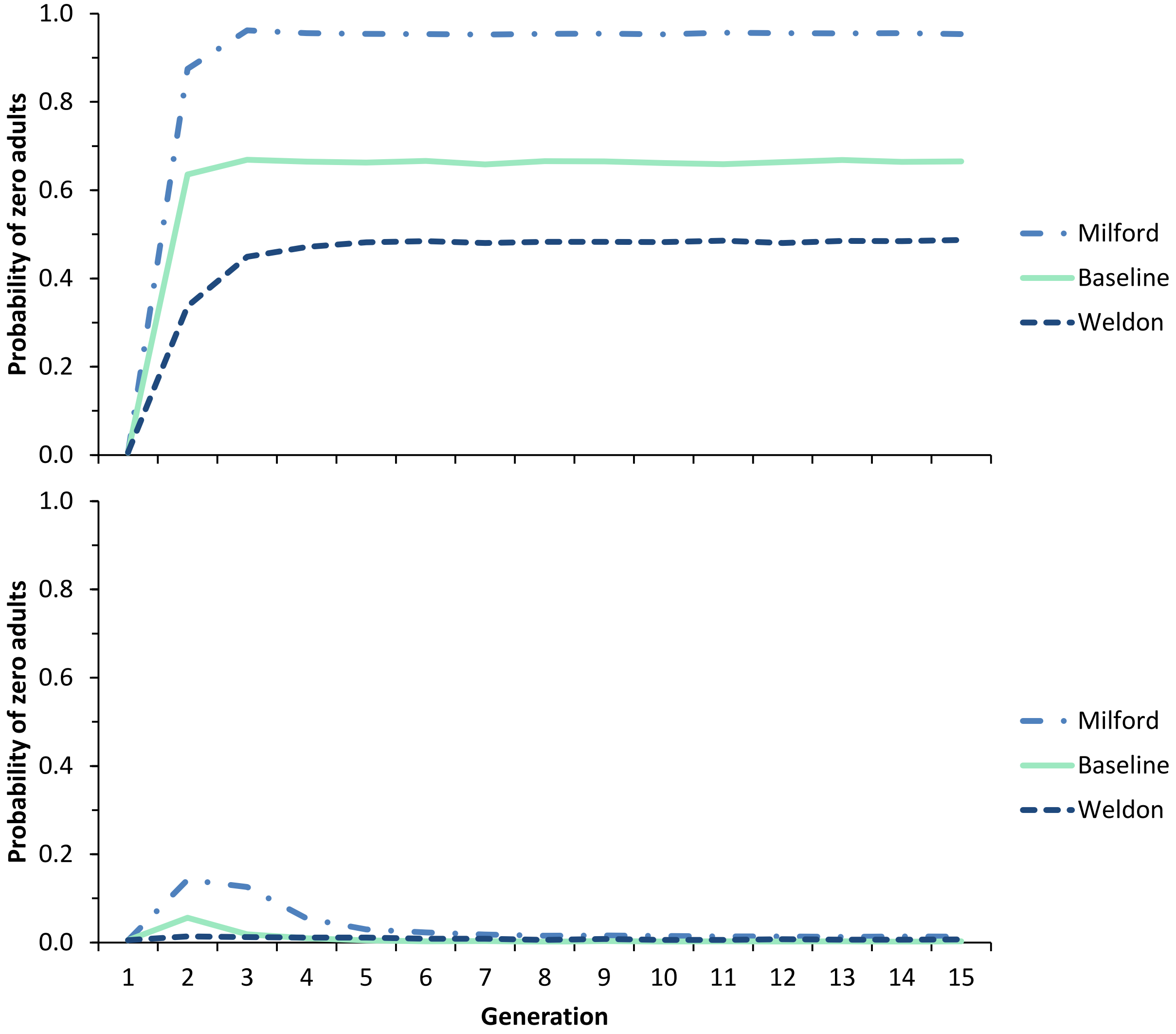

Figure 4.2.2.4. The probability of having zero Atlantic salmon (*Salmo salar*) adults in production unit (PU) 2 in generations 1–15 for 3 model scenarios evaluating the effects of stocking location in the Whole System Stocking Location Analysis. The model scenarios reflect all smolts stocked in PU 14, immediately below Milford Dam (Milford); the baseline stocking strategy (Baseline); and all smolts stocked in PU 2, upstream of Weldon Dam (Weldon). Egg-to-smolt and marine survival were set at the baseline rates (top panel) and increased (bottom panel; egg-to-smolt survival was increased by a factor of 2.2, and marine survival was increased by a factor of 1.8).

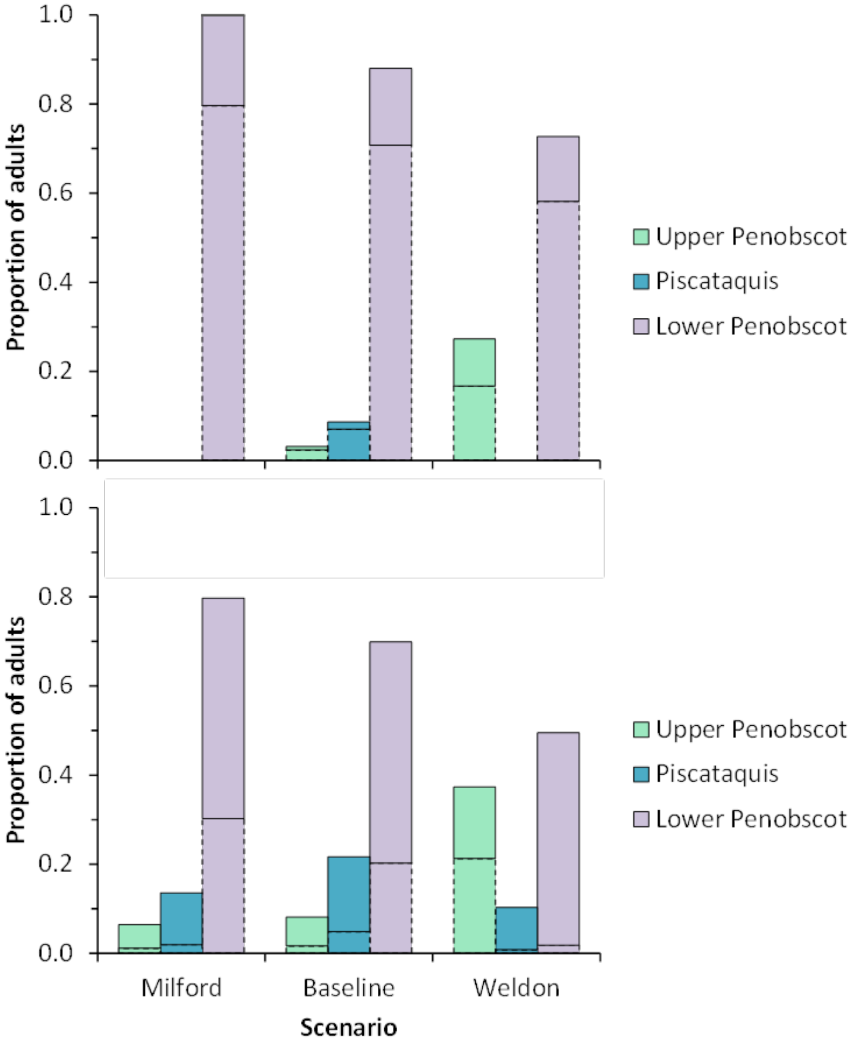

Figure 4.2.2.5. Median proportion of wild-origin (solid borders) and hatchery-origin (dashed borders) Atlantic salmon (*Salmo salar*) adults in the upper Penobscot, Piscataquis, and lower Penobscot areas of the Penobscot River watershed in generation 15 for 3 model scenarios evaluating the effects of stocking location in the Whole System Stocking Location Analysis. The model scenarios reflect all smolts stocked in production unit (PU) 14, immediately below Milford Dam (Milford); the baseline stocking strategy (Baseline); and all smolts stocked in PU 2, upstream of Weldon Dam (Weldon). Egg-to-smolt and marine survival were set at the baseline rates (top panel) and increased (bottom panel; egg-to-smolt survival was increased by a factor of 2.2, and marine survival was increased by a factor of 1.8).

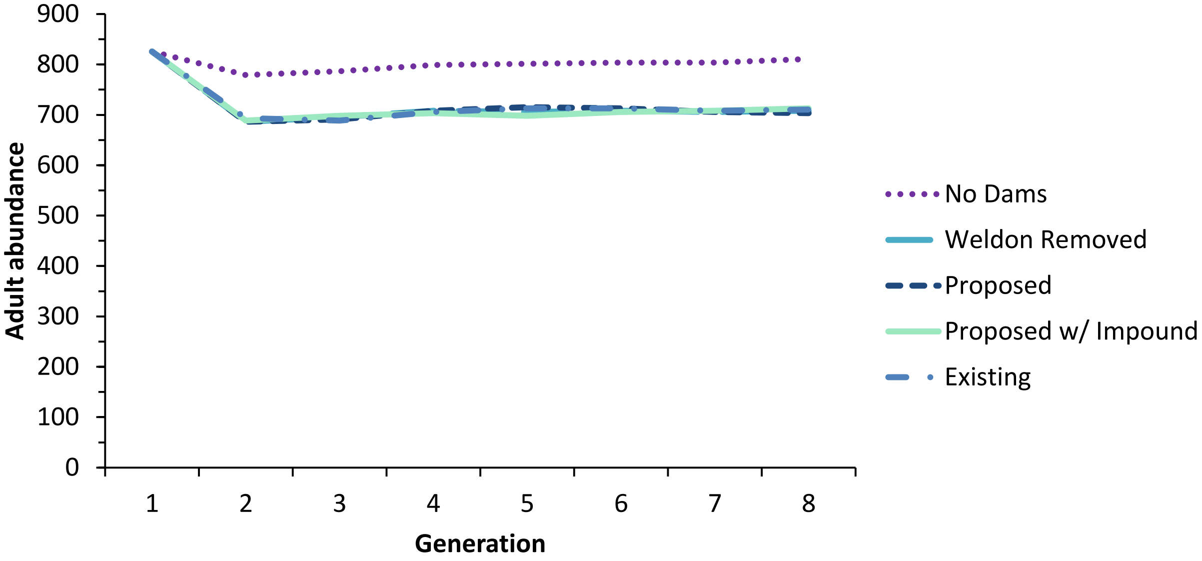

Figure 4.3.1.1. Median Atlantic salmon (*Salmo salar*) adult abundance in the Penobscot River watershed in generations 1–8 for 5 model scenarios evaluating the effects of varying dam survival, especially at Weldon Dam, in the Survival and Phase 2 Recovery Analyses. The model scenarios reflect existing conditions at Weldon Dam (Existing); proposed conditions at Weldon Dam with impoundment mortality present (Proposed w/ Impound); proposed conditions at Weldon Dam without impoundment mortality (Proposed); the removal of Weldon Dam (Weldon Removed); and the removal of all hydroelectric dams in the watershed, except those in the West Branch (No Dams). Smolt stocking numbers and locations were set at baseline conditions. Results overlap in Existing, Proposed w/ Impound, Proposed, and Weldon Removed scenarios.

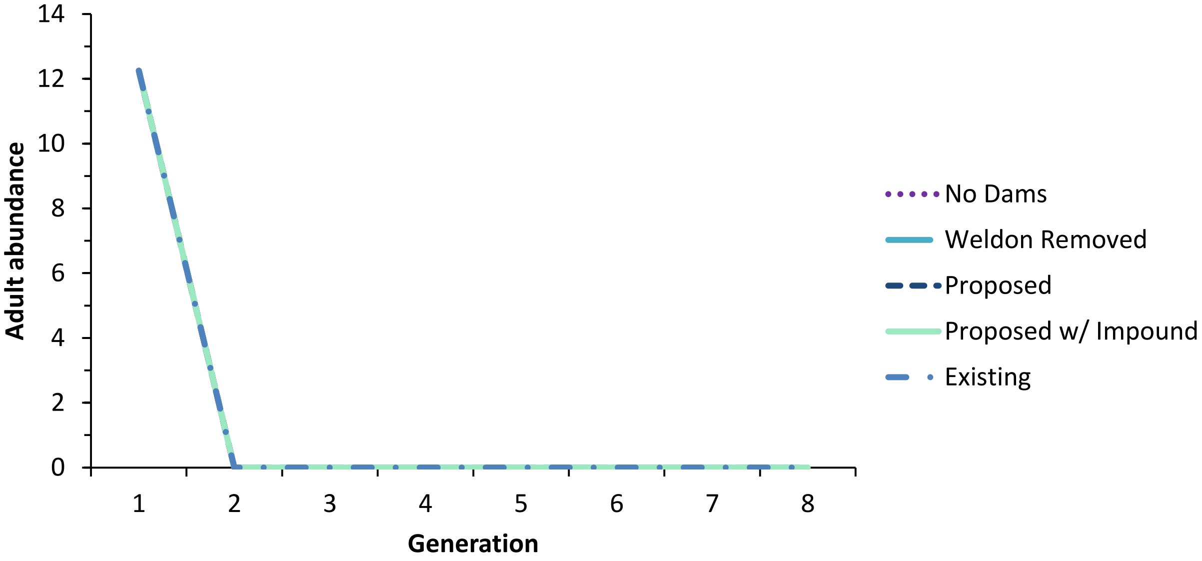

Figure 4.3.1.2. Median Atlantic salmon (*Salmo salar*) adult abundance in production unit 2 in generations 1–8 for 5 model scenarios evaluating the effects of varying dam survival, especially at Weldon Dam, in the Survival and Phase 2 Recovery Analyses. The model scenarios reflect existing conditions at Weldon Dam (Existing); proposed conditions at Weldon Dam with impoundment mortality present (Proposed w/ Impound); proposed conditions at Weldon Dam without impoundment mortality (Proposed); the removal of Weldon Dam (Weldon Removed); and the removal of all hydroelectric dams in the watershed, except those in the West Branch (No Dams). Smolt stocking numbers and locations were set at baseline conditions. Results overlap in all scenarios.

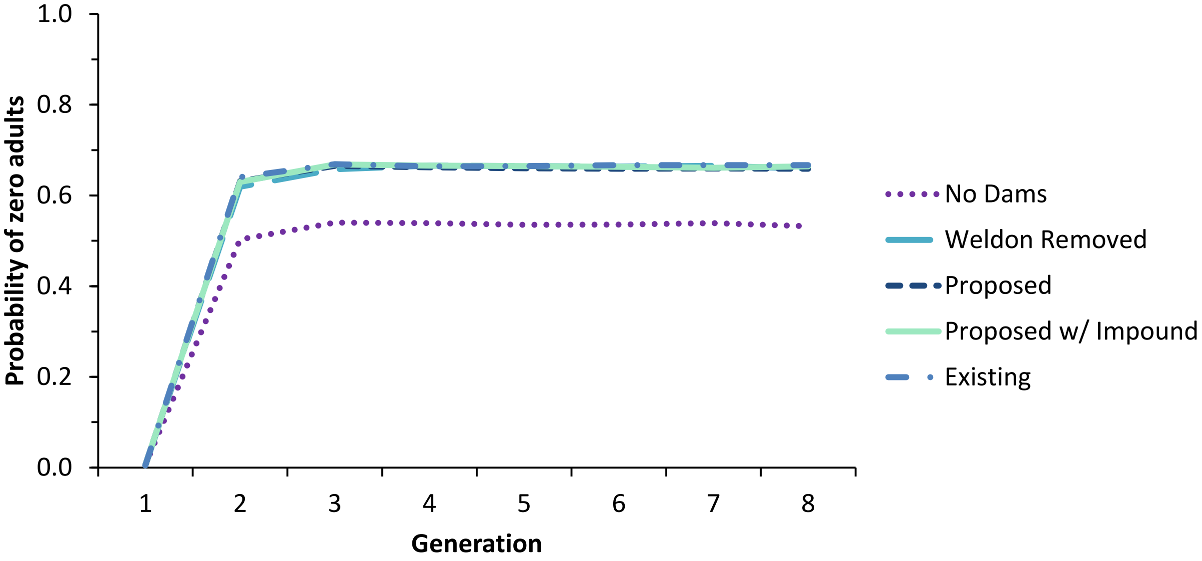

Figure 4.3.1.3. The probability of having zero Atlantic salmon (*Salmo salar*) adults in production unit 2 in generations 1–8 for 5 model scenarios evaluating the effects of varying dam survival, especially at Weldon Dam, in the Survival and Phase 2 Recovery Analyses. The model scenarios reflect existing conditions at Weldon Dam (Existing); proposed conditions at Weldon Dam with impoundment mortality present (Proposed w/ Impound); proposed conditions at Weldon Dam without impoundment mortality (Proposed); the removal of Weldon Dam (Weldon Removed); and the removal of all hydroelectric dams in the watershed, except those in the West Branch (No Dams). Smolt stocking numbers and locations were set at baseline conditions. Results overlap in Existing, Proposed w/ Impound, Proposed, and Weldon Removed scenarios.

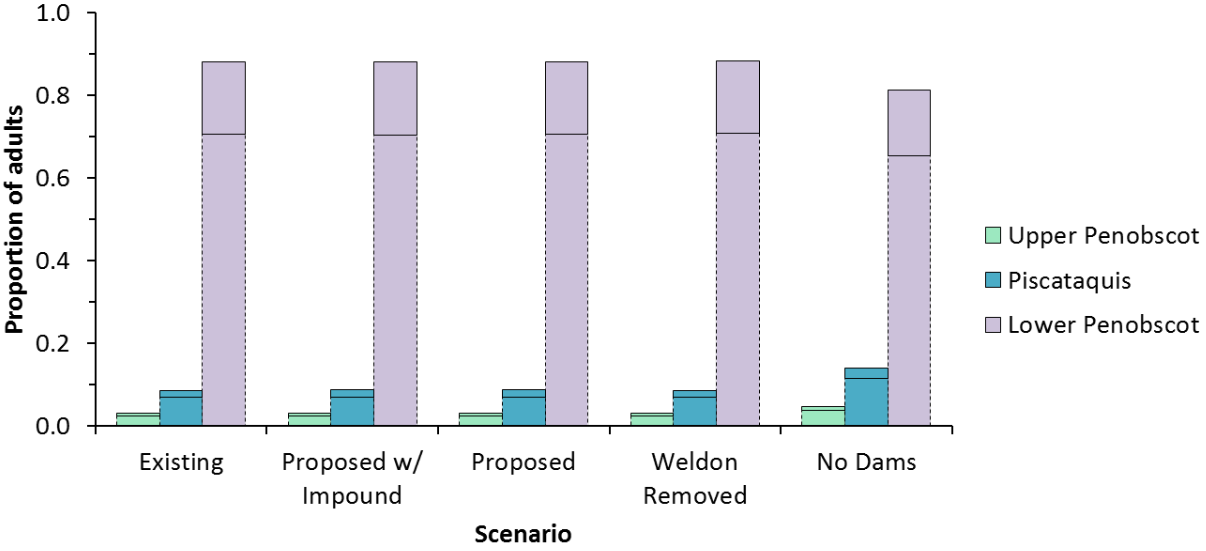

Figure 4.3.1.4. Median proportion of wild-origin (solid borders) and hatchery-origin (dashed borders) Atlantic salmon (*Salmo salar*) adults in the upper Penobscot, Piscataquis, and lower Penobscot areas of the Penobscot River watershed in generation 8 for 5 model scenarios evaluating the effects of varying dam survival, especially at Weldon Dam, in the Survival and Phase 2 Recovery Analyses. The model scenarios reflect existing conditions at Weldon Dam (Existing); proposed conditions at Weldon Dam with impoundment mortality present (Proposed w/ Impound); proposed conditions at Weldon Dam without impoundment mortality (Proposed); the removal of Weldon Dam (Weldon Removed); and the removal of all hydroelectric dams in the watershed, except those in the West Branch (No Dams). Smolt stocking numbers and locations were set at baseline conditions.

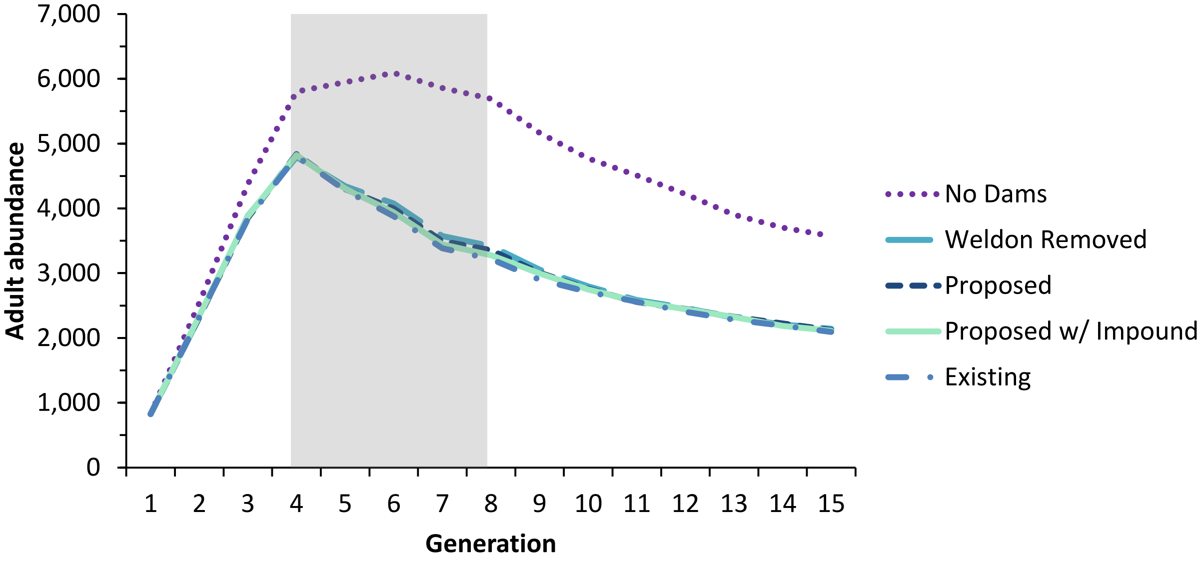

Figure 4.3.2.1. Median Atlantic salmon (*Salmo salar*) adult abundance in the Penobscot River watershed in generations 1–15 for 5 model scenarios evaluating the effects of varying dam survival, especially at Weldon Dam, in the Phase 3 Recovery Analysis. The model scenarios reflect existing conditions at Weldon Dam (Existing); proposed conditions at Weldon Dam with impoundment mortality present (Proposed w/ Impound); proposed conditions at Weldon Dam without impoundment mortality (Proposed); the removal of Weldon Dam (Weldon Removed); and the removal of all hydroelectric dams in the watershed, except those in the West Branch (No Dams). The gray box highlights the period of changes in smolt stocking numbers, stocking locations, and removal of 2 sea-winter females for use as broodstock.

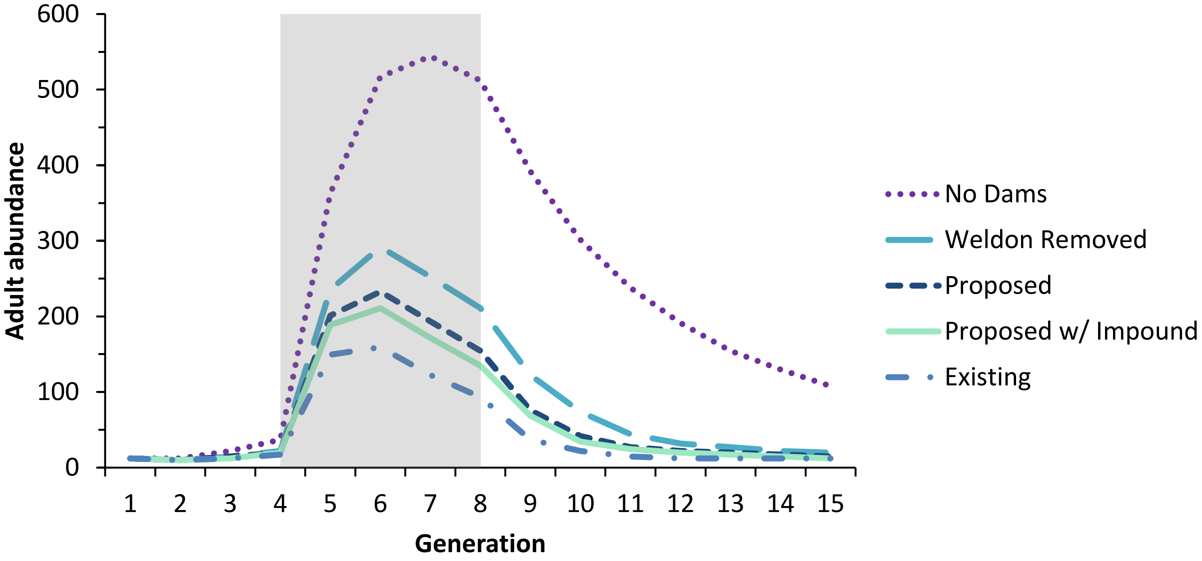

Figure 4.3.2.2. Median Atlantic salmon (*Salmo salar*) adult abundance in production unit 2 in generations 1–15 for 5 model scenarios evaluating the effects of varying dam survival, especially at Weldon Dam, in the Phase 3 Recovery Analysis. The model scenarios reflect existing conditions at Weldon Dam (Existing); proposed conditions at Weldon Dam with impoundment mortality present (Proposed w/ Impound); proposed conditions at Weldon Dam without impoundment mortality (Proposed); the removal of Weldon Dam (Weldon Removed); and the removal of all hydroelectric dams in the watershed, except those in the West Branch (No Dams). The gray box highlights the period of changes in smolt stocking numbers, stocking locations, and removal of 2 sea-winter females for use as broodstock.

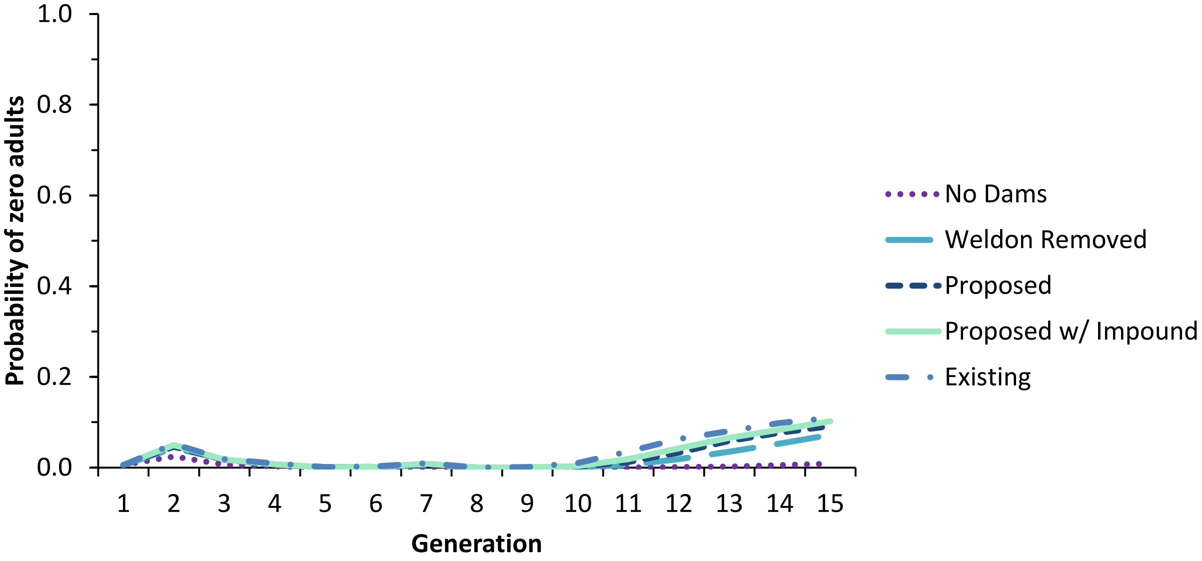

Figure 4.3.2.3. The probability of having zero Atlantic salmon (*Salmo salar*) adults in production unit 2 in generations 1–15 for 5 model scenarios evaluating the effects of varying dam survival, especially at Weldon Dam, in the Phase 3 Recovery Analysis. The model scenarios reflect existing conditions at Weldon Dam (Existing); proposed conditions at Weldon Dam with impoundment mortality present (Proposed w/ Impound); proposed conditions at Weldon Dam without impoundment mortality (Proposed); the removal of Weldon Dam (Weldon Removed); and the removal of all hydroelectric dams in the watershed, except those in the West Branch (No Dams).

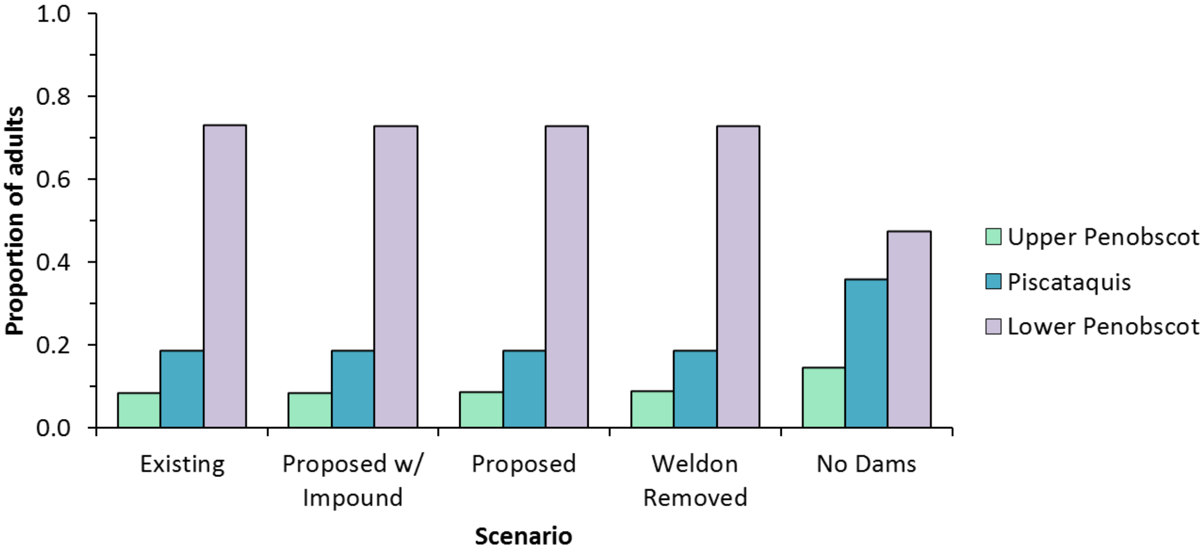

Figure 4.3.2.4. Median proportion of wild-origin (solid borders) and hatchery-origin (dashed borders) Atlantic salmon (*Salmo salar*) adults in the upper Penobscot, Piscataquis, and lower Penobscot areas of the Penobscot River watershed in generation 15 for 5 model scenarios evaluating the effects of varying dam survival, especially at Weldon Dam, in the Phase 3 Recovery Analysis. The model scenarios reflect existing conditions at Weldon Dam (Existing); proposed conditions at Weldon Dam with impoundment mortality present (Proposed w/ Impound); proposed conditions at Weldon Dam without impoundment mortality (Proposed); the removal of Weldon Dam (Weldon Removed); and the removal of all hydroelectric dams in the watershed, except those in the West Branch (No Dams).

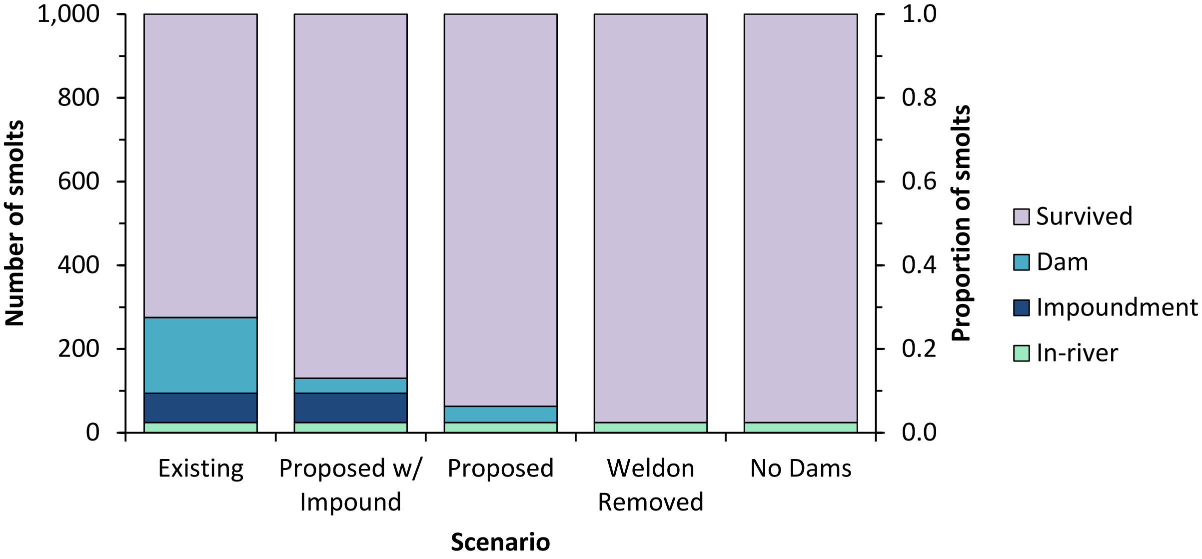

Figure 4.3.3.1. The numbers and proportions of Atlantic salmon (*Salmo salar*) smolts that survived and were killed by in-river, impoundment, and dam mortality in production unit (PU) 2 and at Weldon Dam for 5 model scenarios evaluating the effects of 3 types of mortality in the Smolt Mortality Analysis. The model scenarios reflect existing conditions at Weldon Dam (Existing); proposed conditions at Weldon Dam with impoundment mortality present (Proposed w/ Impound); proposed conditions at Weldon Dam without impoundment mortality (Proposed); the removal of Weldon Dam (Weldon Removed); and the removal of all hydroelectric dams in the watershed, except those in the West Branch (No Dams).

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The CRD series uses the American Fisheries Society's guides to names of fishes, mollusks, and decapod crustaceans, the Society for Marine Mammalogy's guide to names of marine mammals, Integrated Taxonomic Information System guidance on scientific and common names for all other species, the Biosciences Information Service's guide to serial title abbreviations, and the ISO's (International Standardization Organization) guide to statistical terms.

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Publications and Reports of the Northeast Fisheries Science Center

The mission of NOAA's National Marine Fisheries Service (NMFS) is "stewardship of living marine resources for the benefit of the nation through their science-based conservation and management and promotion of the health of their environment." As the research arm of the NMFS's Northeast Region, the Northeast Fisheries Science Center (NEFSC) supports the NMFS mission by "conducting ecosystem-based research and assessments of living marine resources, with a focus on the Northeast Shelf, to promote the recovery and long-term sustainability of these resources and to generate social and economic opportunities and benefits from their use." Results of NEFSC research are largely reported in primary scientific media (*e.g.*, anonymously-peer-reviewed scientific journals). However, to assist itself in providing data, information, and advice to its constituents, the NEFSC occasionally releases its results in its own media. Currently, there are three such media:

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