Spring 5-10-2019

Assessing Migrations and Habitat Connectivity for two Anadromous Species Following a Major Restoration Effort in the Penobscot River, Maine

George A. Maynard
University of Maine, galphonsemaynard@gmail.com

Follow this and additional works at: https://digitalcommons.library.umaine.edu/etd
Part of the Aquaculture and Fisheries Commons, and the Evolution Commons

Recommended Citation
https://digitalcommons.library.umaine.edu/etd/3028

This Open-Access Thesis is brought to you for free and open access by DigitalCommons@UMaine. It has been accepted for inclusion in Electronic Theses and Dissertations by an authorized administrator of DigitalCommons@UMaine. For more information, please contact um.library.technical.services@maine.edu.
ASSESSING MIGRATIONS AND HABITAT CONNECTIVITY FOR TWO ANADROMOUS SPECIES FOLLOWING A MAJOR RESTORATION EFFORT IN THE PENOBSCOT RIVER, MAINE

By

George Alphonse Maynard

B.S. University of Connecticut, 2009

M.S. State University of New York, College at Plattsburgh, 2013

A DISSERTATION

Submitted in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy (in Wildlife Ecology)
The Graduate School
The University of Maine

May 2019

Advisory Committee:

Joseph Zydlewski, Professor of Wildlife Ecology, Advisor

Erik Blomberg, Assistant Professor of Wildlife Ecology

Michael Kinnison, Professor of Evolutionary Applications

Joan Trial, Retired from Maine Department of Marine Resources

Gayle Zydlewski, Associate Professor of Marine Sciences
ASSESSING MIGRATIONS AND HABITAT CONNECTIVITY FOR TWO ANADROMOUS SPECIES FOLLOWING A MAJOR RESTORATION EFFORT IN THE PENOBSKOT RIVER, MAINES

By George Alphonse Maynard

Dissertation Advisor: Dr. Joseph Zydlewski


May 2019

The construction of industrial dams across major rivers in New England began in the early 1800s with textile mills in Massachusetts. Because of its legacy of mill dams and log driving dams, New England has the highest density of dams anywhere in North America, averaging one dam for every 44 km$^2$ of drainage area. By the early 1900s, these dams drastically limited migrations by diadromous fishes, resulting in declines in populations of migratory fishes, including Atlantic salmon Salmo salar and American shad Alosa sapidissima. Since that time, different fishway designs and river management plans have been tried around the region in an attempt to balance hydropower generation, water storage, flood control, and fish passage.

The Penobscot River, in Maine, USA, is the second largest river in New England, with a drainage area of 22,000 km$^2$, and presents an ideal opportunity for understanding fish passage and migratory movements in a heavily-modified river system. Historically, the river contained runs of eleven species of diadromous fishes including alewife Alosa pseudoharengus, American shad, blueback herring A. aestivalis, Atlantic salmon, sea lamprey Petromyzon marinus, American eel Anguilla rostrata, rainbow smelt Osmerus mordax, Atlantic tomcod Microgadus
tomcod, striped bass *Morone saxatilis*, brook trout *Salvelinus fontinalis*, Atlantic sturgeon *Acipenser oxyrinchus*, and Shortnose Sturgeon *A. brevirostrum*, many of which supported subsistence and commercial fisheries prior to dam construction. The Penobscot River Restoration project (initiated in 2004), decommissioned three hydroelectric dams, upgraded fish passage at four dams, and increased generation capacity at three dams, theoretically opening much of the watershed to migratory fishes. We used a combination of telemetry methods, historic data, and modeling to assess the potential for fishways to select for certain traits with enough power to cause evolutionary change in migratory fish populations and evaluate the ability of migratory fish to use newly available habitat in the Penobscot River watershed.

The primary fishway design used in New England for many years was the Denil fishway, which uses angled baffles to reduce water velocity while maintaining high volume and thus, high attraction flow. In order to reach their spawning grounds in the headwaters of the Penobscot River watershed, in-migrating Atlantic salmon have had to navigate between five and seven (mostly Denil) fishways at different dams. Six years of PIT telemetry data were used to evaluate passage success at fishways on the second, third, and fourth dams in the system (Great Works Dam, Milford Dam, and either Howland Dam or West Enfield Dam, depending on path choice) as a function of water temperature, flow, migratory timing, and fish length. At the lower two fishways (Great Works and Milford Dams), fish length was a significant predictor of passage success, with a 91-cm salmon 21%–27% and 12%–16% less likely to pass than a 45-cm salmon, at Great Works and Milford Dams, respectively. Additionally, we analyzed thirty-four years of escapement data and found that the slow-maturing and iteroparous individuals that represented the largest salmon size classes were essentially lost from the population during that time, and that Penobscot River fish have shorter fork lengths at maturity (45 – 91 cm) than Atlantic salmon in
undammed systems (45 – 110 cm). Both of these results indicate that selective pressure towards smaller sizes at maturity (exerted by fishways) may be driving evolutionary responses in Atlantic salmon in the Penobscot River.

Size at maturity and age at maturity are heritable in salmonids and have ramifications for population stability over time, as body size is an important predictor of an individual salmon’s egg quality and quantity. To test whether the selection against large-bodied fish exerted by fishways was substantial enough to elicit an evolutionary response from a population of Atlantic salmon over many years, we developed a computer simulation of an Atlantic salmon population, which was primarily informed by research done in the Penobscot River as well as other rivers in Maine and rivers in Atlantic Canada. Using an individual based model, we allowed a population of Atlantic salmon to evolve over a 100-year period of exposure to between zero and five dams, using different narrow-sense heritability values for age at maturity and size at maturity. This necessitated 150 different combinations of heritability values and dams, each of which was simulated 1000 times. Populations without dams present never went extinct, but 7.2% of populations exposed to one dam, 63.2% of populations exposed to two dams, and > 85% of populations exposed to three or more dams went extinct more than 30 years before the end of the simulation. Coefficient of Variation of size at maturity decreased over time when dams were present, indicating that dams may be a source of stabilizing or directional selection.

Little is known about the survival of hatchery-spawned kelts that are released into the natural environment. As the Penobscot River population of Atlantic salmon is primarily captured and spawned out in captivity, managers are faced with a decision of whether to release the post-spawn adults (kelts) in the estuary (downstream of the dams) or upstream of the dams in freshwater habitat. We released radio-tagged kelts at two sites (upstream of Milford Dam and in
the Penobscot River estuary) in the late fall to evaluate overwinter survival and successful outmigration from each release location. Unexpectedly, 71% of tagged kelts made upstream movements after release, but were blocked by dams with fishways that had been shuttered for the season. Overwinter survival was low (23.6%) and neither survival nor behavior differed between release locations. Low overwinter survival may have contributed to the precipitous decline in iteroparous spawners in this population over the past four decades.

Another potentially iteroparous species in the Penobscot River assemblage is the American shad. Thought to have been extirpated from the system until fairly recently, a spawning population was recently documented near the head of tide. However, with the removal of the first two dams in the system and passage improvements at upstream dams, American shad should have access to up to 93% of its historic spawning habitat. To assess habitat use by these fish, we gastrically tagged 265 American shad at the head of tide between 2015-2017 and monitored their movements from the time of tagging until the end of summer (mid-September) each year. Additionally, we collected scales and used them to estimate the age and spawning history of each tagged fish. Few tagged fish moved upstream beyond the previously documented spawning grounds. Those that did were all virgin spawners, indicating that repeat spawners may be less likely to overshoot known spawning areas. Additionally, none of the tagged fish that approached the dam successfully used the new fishway there. However, several thousand untagged fish used the fishway each year during our study.
ACKNOWLEDGEMENTS

This work would not have been possible without financial and logistical support from numerous agencies, individuals, and organizations. Financial support for this work was provided by the American Recovery and Reinvestment Act through the Penobscot River Restoration Trust. Logistical support was provided by the U.S. Geological Survey, the Maine Department of Marine Resources, Brookfield Renewable Energy, and Kruger Inc. Special thanks to Mitch Simpson, Peter Ruksznis, and Jason Valliere at the Department of Marine Resources for their invaluable assistance capturing and tagging fish and collecting data. Kevin Bernier, Robert Brochu, Gary Crane, Tom Deshane, Richard Dill, Stephen Farrington, Chris Hale, Dave Harvey, Dan Hesseltine, Roy Jordan, Adam Keefe, Lance McComber, Keith Oullette, Glen Sherman, and Pete Spooner of Brookfield Renewable Energy, and Donny Durant of Kruger Inc. provided a range of help at the hydroelectric stations from planning safe operations to fabricating and installing new hardware and lending a little extra horsepower for moving gear around. Randy Spencer and the Maine Warden Service provided airborne telemetry of the Penobscot River watershed during the winter of 2016. The Penobscot Indian Nation graciously allowed us to deploy acoustic and radio receivers on tribal lands and waterways. Thank you also to BNW Variety Store of Passadumkeag, the City of Old Town, the Eddington Salmon Club, Hamlin’s Marina, the Town of Orono, R&K Property Management of Bangor, the Carlisle Family, the Chandler Family, the Clark Family, the Hagstrom Family, the Hart Family, the Homola Family, and the Pate Family for allowing us access to their property for this research.

I would also like to thank the faculty, staff, graduate students, undergraduate technicians, and volunteers at the University of Maine for their help throughout this process. Rena Carey, Katherine Goodine, and Molly-Jean Langlais-Parker worked incredibly hard to ensure that all of
our logistics needs were met. Meg Begley, Bayu Broto, Aubrey Curley, Tyler Davis, Berlynna Heres, Silas Ratten, and Jonathon Watson provided support in the field or the workshop. Karla Boyd, Heather Brinson, Cory Gardner, Tal Kleinhouse-Goldman, Joe Kocik, and Josh Kocik spent countless hours lugging gear and tracking fish in all weather. Ann Grote, Dmitry Gorsky, Chris Holbrook, Andrew O’Malley, and Douglas Sigourney made substantial contributions to this project before and during my time at the University of Maine. Lisa Izzo, Kevin Job, Alejandro Molina Moctezuma, Daniel Stich, and Daniel Weaver provided hours of fieldwork help, statistical support, code debugging, and a healthy dose of motivation. My thesis committee, Erik Blomberg, Michael Kinnison, Joan Trial, and Gayle Zydlewski provided valuable feedback, mentoring, and encouragement throughout this process. My advisor, Joe Zydlewski was incredibly helpful and encouraging both at work and outside, and helped broaden my experience in Maine. Thank you for pushing me outside of my comfort zone and helping me grow.

I would be remiss if I didn’t also thank my friends and family including my in-laws Ellen Hayes and Dale Pontius and my siblings Emily and Sam Gordon, Thomas Maynard, and Griffin Hayes-Pontius, for all of their support and care through this process. Their visits to Maine for candlepin bowling, family dinners, fishing trips, board games, snowshoeing, canoeing, and hiking helped make my time living in this great state a truly wonderful experience. My parents Marc and Margaret Maynard helped me find enjoyment in learning, tinkering, and exploring outdoors from an early age, and without their constant encouragement and support I wouldn’t be where I am today. I would also like to thank my daughter Beatrice Hayes-Maynard, whose arrival helped extend my dissertation writing experience. Finally, I cannot ever thank my wife and best friend Erin Hayes-Pontius enough for the support, patience, and love she has shown me throughout our time together.
# TABLE OF CONTENTS

ACKNOWLEDGEMENTS ........................................................................................................ ii

LIST OF TABLES .................................................................................................................. viii

LIST OF FIGURES .............................................................................................................. ix

1 SIZE SELECTION FROM FISHWAYS AND POTENTIAL EVOLUTIONARY RESPONSES IN A THREATENED ATLANTIC SALMON POPULATION ......................... 1

1.1 Abstract .......................................................................................................................... 1

1.2 Introduction .................................................................................................................... 2

1.3 Study Site ...................................................................................................................... 5

1.4 Methods ....................................................................................................................... 9

1.5 Results .......................................................................................................................... 14

1.5.1 Great Works Dam .................................................................................................... 15

1.5.2 Milford Dam ............................................................................................................. 19

1.5.3 West Enfield and Howland ..................................................................................... 19

1.5.4 Composite Model ................................................................................................... 19

1.5.5 Evolutionary Rates ................................................................................................. 20
<table>
<thead>
<tr>
<th>Section</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.6</td>
<td>Discussion</td>
<td>24</td>
</tr>
<tr>
<td>1.6.1</td>
<td>Size Selection</td>
<td>24</td>
</tr>
<tr>
<td>1.6.2</td>
<td>Environmental Variables</td>
<td>26</td>
</tr>
<tr>
<td>1.6.3</td>
<td>Evolutionary Trends</td>
<td>27</td>
</tr>
<tr>
<td>1.7</td>
<td>Conclusions</td>
<td>29</td>
</tr>
<tr>
<td>2</td>
<td>DEMOGRAPHIC AND EVOLUTIONARY IMPACTS OF SIZE SELECTION AT FISHWAYS ON ATLANTIC SALMON</td>
<td>31</td>
</tr>
<tr>
<td>2.1</td>
<td>Abstract</td>
<td>31</td>
</tr>
<tr>
<td>2.2</td>
<td>Introduction</td>
<td>32</td>
</tr>
<tr>
<td>2.3</td>
<td>Methods</td>
<td>35</td>
</tr>
<tr>
<td>2.3.1</td>
<td>Overview</td>
<td>35</td>
</tr>
<tr>
<td>2.3.2</td>
<td>Demography</td>
<td>37</td>
</tr>
<tr>
<td>2.3.3</td>
<td>Heritability</td>
<td>39</td>
</tr>
<tr>
<td>2.3.4</td>
<td>Simulation</td>
<td>40</td>
</tr>
<tr>
<td>2.3.5</td>
<td>Analysis</td>
<td>42</td>
</tr>
<tr>
<td>2.4</td>
<td>Results</td>
<td>43</td>
</tr>
<tr>
<td>2.4.1</td>
<td>Extinction</td>
<td>43</td>
</tr>
<tr>
<td>2.4.2</td>
<td>Evolutionary Change</td>
<td>45</td>
</tr>
<tr>
<td>2.5</td>
<td>Discussion</td>
<td>52</td>
</tr>
</tbody>
</table>
3  THE FATE OF HATCHERY-SPAWNED ATLANTIC SALMON KELTS RELEASED
   INTO THE PENOBSCOT RIVER, MAINE ................................................................. 58

3.1  Abstract ............................................................................................................. 58

3.2  Introduction ....................................................................................................... 59

3.3  Methods ............................................................................................................. 64

3.3.1  Study Area ..................................................................................................... 64

3.3.2  Fish Capture and Tagging ............................................................................. 65

3.3.3  Radio Tracking ............................................................................................... 66

3.4  Results ............................................................................................................... 67

3.5  Discussion .......................................................................................................... 74

4  FRESHWATER MOVEMENTS OF MIGRATING ADULT AMERICAN SHAD IN THE
   PENOBSCOT RIVER, MAINE FOLLOWING TWO DAM REMOVALS .................... 79

4.1  Abstract ............................................................................................................. 79

4.2  Introduction ....................................................................................................... 79

4.3  Methods ............................................................................................................. 82

4.3.1  Capture and Tagging ................................................................................. 85

4.3.2  Telemetry / Tracking .................................................................................. 86

4.3.3  Defining Behavior ....................................................................................... 87

4.3.4  Age Estimation ............................................................................................ 88

4.3.5  Milford Dam ................................................................................................ 88
LIST OF TABLES

Table 1.1. Fishway descriptions

Table 1.2. Detection probabilities

Table 1.3. Fish passage candidate models

Table 1.4. Measures of dispersion in length over time

Table 1.5. Best fitting passage model for each dam

Table 2.1 Extinction modeling

Table 2.2 Fish length modeling

Table 3.1. Kelt summary statistics

Table 3.2. Kelt mortality

Table 4.1 Shad summary statistics

Table 4.2. Shad tagging summary

Table 4.3. Shad mortality summary

Table 4.4. Shad ages and spawning history
LIST OF FIGURES

Figure 1.1. Schematic of the influence of hatchery stocking........................................... 6
Figure 1.2. Map of the study reach of the Penobscot River........................................... 8
Figure 1.3. Schematic of example detection histories of fish at a particular passage facility ..... 11
Figure 1.4. Length-frequency histograms of Atlantic salmon in this study........................... 15
Figure 1.5. Probability of successfully using the fishways as a function of length............... 18
Figure 1.6. Boxplot of lengths of Atlantic salmon returning to the Penobscot River........... 21
Figure 1.7. Boxplot of response to selection using different generation times...................... 22
Figure 1.8. Measures of dispersion of length over time .................................................. 23
Figure 1.9. Bar graphs showing Penobscot River escapement over time............................ 24
Figure 2.1. Schematic representation of the IBM model.................................................... 37
Figure 2.2. Starting distributions of salmon lengths for the simulation............................... 41
Figure 2.3. Surface plot of extinction probability after 100 years..................................... 44
Figure 2.4. Coefficient of variation of fork length over time ........................................... 48
Figure 2.5. Length over time............................................................................................. 50
Figure 2.6. Proportion of eggs produced by different age classes....................................... 51
Figure 3.1. Map of the study area within the State of Maine............................................ 62
Figure 3.2. Representative tracks from four tagged kelts.................................................. 69
Figure 3.3. Timing of outmigration.................................................................................... 70
Figure 3.4. Example tracks of kelts showing upstream movement .................................... 71
Figure 4.1. Map of study reach inset from State of Maine................................................ 84
Figure 4.2. Length-frequency histogram of shad sampled in each of three study years......... 90
Figure 4.3. Representative example tracks......................................................................... 93
CHAPTER 1

1 SIZE SELECTION FROM FISHWAYS AND POTENTIAL EVOLUTIONARY RESPONSES IN A THREATENED ATLANTIC SALMON POPULATION

1.1 Abstract

The evolutionary effects of harvest on wild fish populations have been documented around the world; however, sub-lethal selective pressures can also cause evolutionary changes in phenotypes. For migratory fishes, passage facilities may represent instances of non-lethal selective pressure. Our analysis of six years of passage data suggests that certain fish passage facilities on the Penobscot River have been exerting selective pressure against large-bodied, anadromous Atlantic salmon (Salmo salar). At the second and third dams in the river, a 91 cm salmon was 21%-27% and 12%-16% less likely to pass than a 45 cm salmon, respectively. Fish size positively influences egg survival and number, and is a heritable trait. Therefore, in a wild-reproducing population, exclusion of large fish from spawning areas may have population-level impacts. In the Penobscot River, most returning adults derive from a hatchery program that collects its broodstock after passing the first dam in the river. Analysis of fork lengths of salmon returning to the Penobscot River from 1978-2012 provided mixed support for evolution of size at maturity in different age classes in a pattern that may be expected from interactions with conservation hatchery operations. Additionally, slow-maturing and iteroparous individuals that represent the largest salmon size classes were essentially lost from the population during that time, and Penobscot River fish have shorter fork lengths at maturity than Atlantic salmon in undammed systems.
1.2 Introduction

Fishing exploitation has resulted in well-characterized selection including decreases in size at maturation (Kuparinen and Merilä 2007) and shifts in age-structures (Allendorf and Hard 2009). Other anthropogenic influences create unnatural selection through sub-lethal pressure, including catch and release angling (Cooke et al. 2007) and fishways at dams (Haugen et al. 2008). Atlantic salmon *Salmo salar* in impounded systems have lower reproductive success than their conspecifics in natural systems (Lundqvist et al. 2008) due to reduced fecundity from in-river delays (Thorstad et al. 2008) and exclusion from spawning grounds (Caudill et al. 2007). However, the potential for fishways to act as selective filters against certain classes of fishes has only recently begun to be explored (Mallen-Cooper and Stuart 2007; Haugen et al. 2008), and literature characterizing the evolutionary impacts of fishways is limited (Haugen et al. 2008; Waples et al. 2008).

Characterizing the impact of fish size on passage success can be difficult because of the suite of variables involved. Flow, temperature, season, and fish size can influence passage success. For example, river flows that are too low may prevent large fish from using fishways, and flows that are too high may prevent fish from locating fishways (Jensen and Aass 1995). High flows may also result in increased migratory costs through energetic expenditures (Jonsson et al. 2007). Water temperature can affect swimming ability of salmonids (Taylor et al. 1996; Ojanguren and Brana 2000). For example, adult Brown Trout *Salmo trutta* experience difficulty ascending obstacles at temperatures below 5°C (Jensen and Aass 1995), and other salmonids have difficulty navigating fishways below 10°C (Rodríguez et al. 2006). Thus, there is an optimal range for passage, with declining passage rates as temperatures depart from that range (Quinn et al. 1997; Salinger and Anderson 2006). To add further complexity, river entry and
migratory movements may be more tied to circannual rhythms than instantaneous environmental variables (Lilja and Romakkaniemi 2003), likely because of photoperiod and physiological changes in adult migrants (Keefer et al. 2004).

There is also great variability in the design of fishways that can influence passage success and its potential selectivity. Many fishways are explicitly designed to have hydraulic features optimized for particular species and sizes of fish, and variability in the configuration of Denil and vertical slot fishways may thus substantially alter the size classes of fish that are able to successfully use them (Rodríguez et al. 2006; Mallen-Cooper and Stuart 2007). Installation of a fishway on the River Gulbrandsdalslågen in Norway caused rapid evolution towards smaller body sizes in Brown Trout (Haugen et al. 2008). Recently, a short-term tagging study provided evidence that size-selection on adult Atlantic salmon occurs at some fishways on the Penobscot River, USA (Sigourney et al. 2015). In this study, passage success at upper dams of fish trucked around the lowest dams in the river was compared with passage success of fish that were allowed to volitionally migrate through the entire system in 2010 and 2011. The average fork length for volitionally moving fish decreased by 5.9% from release to successful passage at the upper dams and that of trucked fish decreased by 1.2%. However, the limited spatial and temporal scope of data in this study makes it unclear how general this pattern has been.

These findings illustrate the potential that dams and fishways have to exert selection on a population of migratory fish, but also that such selection can vary with respect to species, river conditions and the design of fishways themselves. Hence, an evaluation in a given year, at a given dam, for a given species may not be particularly representative of the net effects of passage throughout a system with multiple passage facilities or the long-term consequences of selective passage. Understanding selection at fishways and its potential evolutionary consequences is thus
best conducted in a holistic fashion that considers the combined effects of multiple fishways in a given river system and multiple years of potential passage patterns.

Over many generations, even moderate selective pressure against large fish can accrue population-level effects. Female Atlantic salmon may invest up to 25% of their body weight into egg production (Fleming 1996). Such investments are expressed as increased egg number or egg size (Fleming and Gross 1990), which is correlated with higher survival from egg to alevin and larger fry size (Beacham and Murray 1985). Larger fry have higher survival to smoltification and outmigration (Quinn and Peterson 1996), and larger smolts have higher survival to maturity than their smaller conspecifics (Saloniemi et al. 2004). Heritability of length-at-age (0.0 - 1.0) is estimated to be up to 0.5 in salmonids (Carlson and Seamons 2008). Loss of large, spawning fish has been a concern for fisheries managers since the early 1900s, with managers believing it may lead to an increase in the proportion of fish populations made up of smaller, younger fish (Rutter 1903), reduce the overall adult size (Smith et al. 1920) and compromise the recruitment and recovery of populations by undermining the important fecundity contributions of large old fish (Begley 2016). These hypotheses have been born out in computer simulations (Hard 2003) with Chinook salmon *Oncorhyncus tshawytscha*, laboratory experiments (Conover et al. 2009) with Atlantic Silversides *Menidia menidia*, and field observations of Atlantic Cod *Gadus morhua* (Swain et al. 2007) and Plaice *Pleuronectes platessa* (Law 2007).

Cross-river dams have been present in Maine, for over a century. Regionally, over that time, runs of Atlantic salmon have declined over 98% (Fay et al. 2006). With extensive multi-year datasets available for both length-at-maturity and passage success at dams, the Penobscot River provides an opportunity to address the following questions: 1) Do passage structures in the Penobscot River system impose size selection across multiple years of data? 2) Has the size-at-
age or age structure of Penobscot salmon changed over time in a manner consistent with potential responses to size selectivity?

1.3 Study Site

The Penobscot River is located entirely within the State of Maine and contains the last viable run of Atlantic salmon in the United States. The current run of salmon, numbering only 381 to 2,115 in the last decade, is more than 95% composed of hatchery-produced fish (National Research Council (U.S.) 2004). Broodstock for this program are captured following passage through a fishway at the first dam on the river. In recent years 50-100% of trapped salmon have been taken for broodstock. Remaining fish are released to the river and must traverse fishways at between three and six additional dams before reaching spawning habitat (Figure 1.1). Historically, when salmon returns were much greater, a larger proportion of returning salmon were released to migrate further up river.
Figure 1.1 Schematic of the influence of hatchery stocking. Schematic showing the influence of hatchery spawned fish on the Penobscot River population. Adults from hatchery smolts account for ~95% of returns to the river. The remaining returns are “wild” adults, which include fish stocked out as fry or eggs from the hatchery as well as natural reproduction. In any given year, ~50% of the returning adults are taken to the hatchery for use as brood stock. The majority of those taken are MSW fish, and the majority of those allowed to continue upstream are grilse (1SW males).

The main stem of the Penobscot River has been fragmented by dams since the 1800s. Fishways were present on the river for much of that time (Everhart and Cutting 1968). Historic records indicate that in the 1800s, fishways often were not opened because of threats against fish wardens (Buck 1838), and even when opened, they may not have functioned well (Feyler 1932). The fishways that currently exist throughout the study area were constructed after 1965. Our study area included a 100 km stretch of the Penobscot River from Veazie Dam (rkm 48) to Weldon Dam (rkm 148) containing five dams (Figure 1.2), three of which were included in the
Howland Dam, at the confluence of the Penobscot and Piscataquis Rivers was also included (Table 1.1). Three of the four dams analyzed had Denil fishways, and the fourth (West Enfield) had a vertical slot fishway. Denil fishways are rectangular channels with evenly spaced baffles angled 45° against the flow that allow water to pass through the center of the channel. The typical slope for this fishway style is ~20% (Katopodis et al. 1997), but the Denil fishways in the lower Penobscot River all had slopes of 12.5%. Vertical slot fishways consist of rectangular channels with baffles at 90° to the flow. Water passes through a vertical slot in the baffle, dissipating energy while leaving low-flow areas to either side of the slot. The recommended slope for these fishways is between 6-10% (Rodríguez et al. 2006), and the vertical slot fishway at West Enfield Dam has a slope of 6.7%. Veazie Dam had little data available for passage, as fish were tagged at the upstream end of its fishway. Weldon Dam was the farthest upstream site, and many unmonitored tributaries with suitable habitat exist between Weldon Dam and the next dam downstream, making detection probability inestimable at that site. The Penobscot River has recently been the focus of a major restoration effort that included removal of the Veazie and Great Works Dams (in 2013 and 2012, respectively) and the construction of new passage facilities (a fish lift and a bypass channel) at Milford and Howland Dams (in 2014 and 2016, respectively).

Table 1.1. Fishway descriptions. Description of fishways at each dam including distance from the mouth of the river (rkm), style, year built, length (m), and slope (%). Great Works Dam had two nearly identical fishways.

<table>
<thead>
<tr>
<th></th>
<th>rkm</th>
<th>Style</th>
<th>Year Built</th>
<th>Length (m)</th>
<th>Slope (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Great Works</td>
<td>59</td>
<td>2 Denils</td>
<td>1968</td>
<td>68.8</td>
<td>12.5</td>
</tr>
<tr>
<td>Milford</td>
<td>61</td>
<td>Denil</td>
<td>1968</td>
<td>72.5</td>
<td>12.5</td>
</tr>
<tr>
<td>West Enfield</td>
<td>100</td>
<td>Vertical Slot</td>
<td>1988</td>
<td>173.7</td>
<td>6.7</td>
</tr>
<tr>
<td>Howland</td>
<td>99</td>
<td>Denil</td>
<td>1965</td>
<td>76.8</td>
<td>12.5</td>
</tr>
</tbody>
</table>
Figure 1.2. Map of the study reach of the Penobscot River. Veazie Dam (represented by a star) was the release point for the passage portion of this study. It was also historically the location of brood stock collection. The Stillwater Branch dams have no upstream passage facilities.
1.4 Methods

From 2002-2004 (Gorsky et al. 2009) and 2010-2012 (Sigourney et al. 2015), adult Atlantic salmon were collected at the Veazie Dam trap. All fish not kept for broodstock were measured, marked with PIT tags and released into the headpond. Fish movements were monitored using PIT antennas located at the entrance and exit of each fishway. Detection probability was modeled using a Cormack-Jolly-Seber mark-recapture framework for each antenna, during each year (Table 1.2; Cooch and White 2014). Fish were assumed to be motivated to move continually upstream through the study area because more than 80% of spawning habitat in the system exists upriver of the study area (Fay et al. 2006).

Table 1.2. Detection probabilities. Range of detection probabilities ($p_d$) at each dam’s entrance and exit antennas over the study period (± 1SD). A * mark indicates a significant difference ($p < 0.05$) between the detection probabilities of grilse and multi-seawinter (MSW) fish.

<table>
<thead>
<tr>
<th>Dam</th>
<th>Antenna</th>
<th>Grilse $p_d$</th>
<th>MSW $p_d$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Great Works</td>
<td>Entrance</td>
<td>0.758 ± 0.109</td>
<td>0.738 ± 0.104</td>
</tr>
<tr>
<td></td>
<td>Exit</td>
<td>0.907 ± 0.074</td>
<td>0.921 ± 0.036</td>
</tr>
<tr>
<td>Milford</td>
<td>Entrance</td>
<td>0.782 ± 0.091</td>
<td>0.902 ± 0.047</td>
</tr>
<tr>
<td></td>
<td>Exit</td>
<td>0.774 ± 0.124</td>
<td>0.834 ± 0.078</td>
</tr>
<tr>
<td>West Enfield</td>
<td>Entrance</td>
<td>0.821 ± 0.189</td>
<td>0.899 ± 0.671</td>
</tr>
<tr>
<td></td>
<td>Exit*</td>
<td>0.984 ± 0.241</td>
<td>0.905 ± 0.037</td>
</tr>
<tr>
<td>Howland</td>
<td>Entrance</td>
<td>0.991 ± 0.150</td>
<td>0.992 ± 0.014</td>
</tr>
<tr>
<td></td>
<td>Exit</td>
<td>0.926 ± 0.019</td>
<td>0.962 ± 0.075</td>
</tr>
</tbody>
</table>

Passage success was modeled as a Bayesian logistic regression of water temperature ($T$ and $T^2$), discharge ($F$ and $F^2$), fork length (L), and days at large (D; Table 1.3). All continuous variables were z-standardized to make the effect sizes ($\beta$-values) comparable. The binary variable used to represent passage success was informed by combining detection histories of each fish with detection probabilities at each antenna (Figure 1.3. Schematic of example detection histories of fish at a particular passage facility. Fish 1 (♦) was detected at the entrance and exit of a passage facility, and detected again at an upstream facility. Therefore, it must have
passed successfully, and is given an upstream movement probability of 1. Fish 2 (■) was detected at the entrance and exit of a passage facility, but was never detected upstream. Therefore, it could have passed successfully and evaded detection upstream with a probability of 1 – the probability of detection upstream, or it could have failed to pass and fallen back to the lower river. Fish 3 (●) was detected only at the entrance of a fish passage facility. It was next detected at another facility downstream. Therefore, it was confirmed to have failed to pass and fallen back into the lower river.). Each fish was only counted once per dam to avoid repeated measures sampling (i.e. if the fish ever passed, it was counted as a success, regardless of the number of attempts taken). We used linear and quadratic terms for discharge data as a surrogate for flow in our models. Discharge data was not available from a single, consistent source for the duration of the study period. Thus, discharge (cubic feet per second) in the lower river was estimated using a regression ($R^2 = 0.967$) based on data collected at the US Geological Survey gauge on the Penobscot River from 1980 to 2014 when necessary.

Table 1.3. Fish passage candidate models. Candidate model set divided up into models run at individual dams and in the all dam set (top) and models run only for the all dam set (bottom). Variables tested included fork length (L), days at large (a surrogate for delay, D), water temperature (linear T and quadratic $T^2$), discharge (a surrogate for flow, linear F and quadratic $F^2$), number of dams (N), and an interaction between water temperature and fork length (LT).

<table>
<thead>
<tr>
<th>Individual Dams and All Dams</th>
<th>All Dams</th>
</tr>
</thead>
<tbody>
<tr>
<td>I. $\beta_0 + \beta_L$</td>
<td>I. $\beta_0 + \beta_NN$</td>
</tr>
<tr>
<td>II. $\beta_0 + \beta_L + \beta_D D$</td>
<td>X. $\beta_0 + \beta_NN$</td>
</tr>
<tr>
<td>III. $\beta_0 + \beta_T + \beta_T^2 T^2$</td>
<td>XI. $\beta_0 + \beta_L + \beta_NN + \beta_D D$</td>
</tr>
<tr>
<td>IV. $\beta_0 + \beta_F F + \beta_F^2 F^2$</td>
<td></td>
</tr>
<tr>
<td>V. $\beta_0 + \beta_T + \beta_T^2 + \beta_F F + \beta_F^2 F^2$</td>
<td></td>
</tr>
<tr>
<td>VI. $\beta_0 + \beta_T + \beta_T^2 + \beta_D D$</td>
<td></td>
</tr>
<tr>
<td>VII. $\beta_0 + \beta_T + \beta_T^2 + \beta_D D + \beta_L L$</td>
<td></td>
</tr>
<tr>
<td>VIII. $\beta_0 + \beta_T + \beta_T^2 + \beta_L L + \beta_{LT} LT$</td>
<td></td>
</tr>
</tbody>
</table>
Figure 1.3. Schematic of example detection histories of fish at a particular passage facility. Fish 1 (♦) was detected at the entrance and exit of a passage facility, and detected again at an upstream facility. Therefore, it must have passed successfully, and is given an upstream movement probability of 1. Fish 2 (■) was detected at the entrance and exit of a passage facility, but was never detected upstream. Therefore, it could have passed successfully and evaded detection upstream with a probability of 1 - the probability of detection upstream, or it could have failed to pass and fallen back to the lower river. Fish 3 (●) was detected only at the entrance of a fish passage facility. It was next detected at another facility downstream. Therefore, it was confirmed to have failed to pass and fallen back into the lower river.

Temperature data was compiled from a variety of sources (including USGS gages on the Penobscot River, the St. Croix River ($R^2 = 0.97$), and the Androscoggin River ($R^2 = 0.95$)), as no one source was available for the entire time-period of interest. We incorporated delay in our models through a “days at large” term. This term was simply the ordinal date minus the date of initial capture at the Veazie Dam.

The models were run in two sets. The first set treated each dam as an individual entity. The second set was made up of system-wide models that incorporated the number of dams.
passed by each fish as a factor that could influence passage success. In both sets of models, possible $\beta$ values were drawn from uninformed prior distributions. We used JAGS (Just Another Gibbs Sampler) version 3.4.0 (Plummer 2003) in the R2jags environment (Plummer and Stukalov 2014) to sample the parameter distributions using Markov Chain Monte-Carlo methods. Each model was run for 3000 burn-in steps to tune the sampler. Each chain was then run for 50,000 saved steps before assessing each model’s potential scale reduction factor ($\hat{R}$) to determine if more sampling was necessary. Most-supported models were identified using deviance information criterion (DIC) scores.

In order to assess goodness of fit, the most-supported models were tested against bootstrapped passage data by resampling 1,000 individual passage attempts out of the data set and comparing the results of those attempts to the simulated results generated from the models (Clough 2012). The results of each simulation (1,000 pass-fail trials) were recorded as the ratio of the number of simulated passage successes over the number of actual passage successes. These simulations were conducted 1,000 times for each dam, and the proportion of the 1,000 results above the 1:1 line (Bayesian p-value) were recorded. A value of $p \approx 0.5$ would indicate that the model represents the data well (Gelman 2014).

We also used a long-term data set of returning Penobscot salmon length frequencies from 1978 – 2012 to explore potential patterns in body-size of returning Atlantic salmon. Length-frequency data was collected from Atlantic salmon captured at the Veazie Dam trap by Maine Department of Marine Resources personnel.

In the Penobscot River, salmon may return to spawn at 1 seawinter (SW), 2SW, or 3SW, and some returning fish are iteroparous. We used a chi-squared ($X^2$) test to determine whether the
distribution of individuals between these different life history strategies changed from 1978 to 2012. Additionally, we calculated response to selection on fork length for multi-seawinter adults (MSW) and 1SW grilse, varying generation time between 4 and 6 years to account for possible differences between hatchery and wild generation time.

We also calculated rates of evolutionary change in fork length in haldanes (Equation 1.1; Hendry and Kinnison 1999). Using haldanes provides a metric that is comparable across traits and species because change is measured in standard deviations per generation.

\[ r = \frac{X_2 - X_1}{S_p - t_g} \]

Equation 1.1

\( r = \) Evolutionary rate (haldanes)

\( X_1 = \) the log mean trait value for the parents

\( X_2 = \) the log mean trait value for the offspring

\( S_p = \) the pooled standard deviation of the populations

\( t_g = \) the time between samples (generations)

In addition to calculating rate of evolutionary change, we calculated standard deviations (\( \sigma_{sy} \)) and coefficients of variation (\( CV = \sigma_{sy}/\text{mean}_{sy} \) where \( \text{mean}_{sy} = \) the mean fork length for a given sex and year) for fork lengths over time to test whether length-at-spawning distributions remained stable (Haugen et al. 2008). Both evolutionary rate and measures of dispersion were calculated separately for each life history strategy (Table 1.4).
Table 1.4. Measures of dispersion in length over time. Changes in measures of dispersion over time. β values represent the slope of the regression line ± σ. The value t36 represents the total change over the time series.

<table>
<thead>
<tr>
<th></th>
<th>CV</th>
<th>P</th>
<th>Standard Deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>β</td>
<td>t36</td>
<td>P</td>
</tr>
<tr>
<td>Female MSW</td>
<td>-0.064</td>
<td>1.282</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>±0.015</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male MSW</td>
<td>-0.067</td>
<td>0.881</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>±0.015</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grilse</td>
<td>-0.058</td>
<td>2.788</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>±0.011</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Finally, we used linear regressions to explore changes in size at age over time for all in-migrating adult Atlantic salmon for with ages estimated from scale samples or visible tags (i.e. Carlin tags, VIE tags) affixed prior to stocking. Data to perform this analysis was provided as a collaborative effort between the Maine Department of Marine Resources and NOAA. The total number of Atlantic salmon included in this analysis was 25,141.

1.5 Results

The full data set for the passage portion of the study included 3,517 individuals with fork lengths that ranged from 45 cm to 91 cm. The distribution of \( L \) was bi-modal, with grilse (1SW) averaging 54.2 cm (\( \sigma = 2.45 \)) and multi-seawinter adults averaging 73 cm (\( \sigma = 3.52 \); Figure 1.4). The full data set for the evolutionary portion of the study included 40,069 individuals with fork lengths that ranged from 40 cm to 104 cm. Grilse averaged 54.4 cm (\( \sigma = 3.06 \)) and multi-seawinter adults averaged 73.1 cm (\( \sigma = 4.64 \)).
Figure 1.4. Length-frequency histograms of Atlantic salmon in this study. The dark bars in the back represent all fish captured at the Veazie trap from 1978-2012 and were used for the evolutionary rates analysis. The light bars in the front represent a subset of fish captured at the Veazie trap in 2002-2004 and 2010-2012 and were used for the passage selectivity analysis.

1.5.1 Great Works Dam

At Great Works Dam, passage success was best modeled with the inclusion of $L$, $D$, $T$, and $T^2$ (}
Table 1.5). Effect sizes of $L$, $T$, and $T^2$ were all significant (had 95% high density intervals (HDI) that did not include zero). The variable with the largest effect was $L$. When $T$, $T^2$, and $D$ were held constant at their mean values, a 45 cm salmon was 21% – 27% more likely to pass the dam successfully than a 91 cm salmon (Figure 1.5). The model had a Bayesian p-value of 0.489 (~0.5 indicates a good fit).
Table 1.5. Best fitting passage model for each dam. Best fitting model, scored by DIC value for each dam as well as for the All Dam model set (left), and ΔDIC values for all other candidate models (right). 95% credible intervals for the best fitting model’s $\beta$ values are displayed, along with the median $\beta$ value for each coefficient.

<table>
<thead>
<tr>
<th>Great Works</th>
<th>$LLP = \beta_0 + \beta_D D + \beta_T T + \beta_L L$</th>
<th>Model</th>
<th>ΔDIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Factor</td>
<td>95% C.I. ((\beta))</td>
<td>Mean ((\beta))</td>
<td>DIC</td>
</tr>
<tr>
<td>Days at Large (D)</td>
<td>$-0.327 &lt; \beta &lt; 0.264$</td>
<td>-0.256</td>
<td>5534</td>
</tr>
<tr>
<td>Temperature (T)</td>
<td>$-0.315 &lt; \beta &lt; -0.026$</td>
<td>-0.098</td>
<td></td>
</tr>
<tr>
<td>Quad. Temp. (T$^2$)</td>
<td>$-0.152 &lt; \beta &lt; -0.024$</td>
<td>-0.088</td>
<td></td>
</tr>
<tr>
<td>Fork Length (L)</td>
<td>$-0.379 &lt; \beta &lt; -0.055$</td>
<td>-0.236</td>
<td></td>
</tr>
</tbody>
</table>

| Milford | $LLP = \beta_0 + \beta_L L + \beta_D D$ | Model | ΔDIC |
| Factor      | 95% C.I. (\(\beta\)) | Mean (\(\beta\)) | DIC |
| Days at Large (D) | $-0.145 < \beta < -0.025$ | -0.084 | 5819 |
| Fork Length (L) | $-0.25 < \beta < -0.028$ | -0.095 | |

| West Enfield | $LLP = \beta_0 + \beta_F F + \beta_F F^2 + \beta_T T + \beta_T T^2$ | Model | ΔDIC |
| Factor      | 95% C.I. (\(\beta\)) | Mean (\(\beta\)) | DIC |
| Discharge (F) | $-0.928 < \beta < -0.627$ | -0.777 | 5431 |
| Quad. Disc. (F$^2$) | $0.104 < \beta < 0.162$ | 0.132 | |
| Temperature (T) | $-0.047 < \beta < 0.306$ | 0.129 | |
| Quad. Temp. (T$^2$) | $0.161 < \beta < 0.305$ | 0.233 | |

| Howland | $LLP = \beta_0 + \beta_D D + \beta_T T + \beta_T T^2$ | Model | ΔDIC |
| Factor      | 95% C.I. (\(\beta\)) | Mean (\(\beta\)) | DIC |
| Days at Large (D) | $0.198 < \beta < 0.687$ | 0.443 | 2676 |
| Temperature (T) | $0.079 < \beta < 0.241$ | 0.159 | |
| Quad. Temp. (T$^2$) | $-0.238 < \beta < -0.011$ | -0.125 | |

| All Dams | $LLP = \beta_0 + \beta_D D + \beta_L L + \beta_T T + \beta_T T^2$ | Model | ΔDIC |
| Factor      | 95% C.I. (\(\beta\)) | Mean (\(\beta\)) | DIC |
| Days at Large (D) | $0.073 < \beta < 0.153$ | 0.113 | |
| Fork Length (L) | $-0.252 < \beta < -0.188$ | -0.219 | 22243 |
| Temperature (T) | $0.155 < \beta < 0.314$ | 0.235 | |
| Quad. Temp. (T$^2$) | $0.072 < \beta < 0.129$ | 0.1 | |
Figure 1.5. Probability of successfully using the fishways as a function of length. Probability of successfully using the fishway (y-axis) modeled as a function of fork length (x-axis) for Great Works Dam (a) and Milford Dam (b). The dotted lines represent the 95% credible interval. Associated \( \beta \) values can be found in Table 1.5.
1.5.2 Milford Dam

At Milford Dam, passage success was best modeled by a combination of $L$ and $D$. Both were significant. Again, $L$ had the largest effect, and when $D$ was held constant at its mean value, a $45 \text{ cm}$ salmon was $11.9\% – 16.2\%$ more likely to pass the dam successfully than a $91 \text{ cm}$ salmon. The model had a good fit (Bayesian p-value = 0.528).

1.5.3 West Enfield and Howland

At West Enfield Dam, passage success was best modeled as a function of $F$, $F^2$, and $T$. There was no evidence of size selection at this dam. The model had a Bayesian p-value of 0.516. At Howland Dam, passage success was best modeled as a function of $D$, $T$, and $T^2$. There was no evidence of size selection at this dam. The model had a Bayesian p-value of 0.488. A Kruskal-Wallis test comparing size distributions of fish approaching each dam in this study shows the distribution of fish approaching Howland Dam was significantly different from that approaching West Enfield Dam ($p = 0.022$), Milford Dam ($p = 0.013$), and Great Works Dam ($p < 0.001$), with smaller fish approaching Howland.

1.5.4 Composite Model

In the composite model set, the most supported model included $L$, $D$, $T$, and $T^2$. The factor with the largest effect size was $T$, closely followed by $L$. $D$ and $T^2$ had effects that were approximately half as large as the other two factors. The effect size for $T$ was positive, and the effect size for $L$ was negative (larger fish were less likely to successfully pass). The model had a Bayesian p-value of 0.492.

1.5.5 Evolutionary Rates

Overall, average fork length of Atlantic salmon returning to the Penobscot River did not increase or decrease from 1978 – 2012, (Figure 1.6). Response to selection showed no consistent
direction bias in short-term responses in length at maturity for grilse or MSW adults (Figure 1.7). Annual evolutionary rates measured in haldanes ranged from -2.8 to 2.6 for MSW males, -2.3 to 2.4 for MSW females, and -3.0 to 3.1 for 1SW grilse. Dispersion in length-at-spawning significantly decreased over time using either measure (Figure 1.8), indicating reduced phenotypic variability. Likewise, the $X^2$ test revealed that the numbers of Atlantic salmon in the 1SW, 2SW, 3SW, and iteroparous groups differed significantly over time ($X^2 = 5002$, df = 105, $p < 0.001$), with 3SW and iteroparous fish nearly absent from the run in recent years (Figure 1.9). Linear regressions of trait change over the full period did not indicate consistent changes in size-at-age for 2SW and 3SW fish. However, there was support for a modest decrease in size-at-age for 1SW fish ($p < 0.001$; $R^2 = 0.011$). The net evolutionary rate of change in mean size of 1SW fish over the full period was -0.987 haldanes.
Figure 1.6. Boxplot of lengths of Atlantic salmon returning to the Penobscot River. Boxplot showing the distribution of fork lengths (cm) of Atlantic salmon MSW females (a), MSW males (b), and grilse (c) returning to the Penobscot River from 1978 to 2012.
Figure 1.7. Boxplot of response to selection using different generation times. Boxplot showing response to selection ($\Delta$cm) on fork length (cm) for generations of Atlantic salmon 1SW grilse (white) and MSW adults (gray) captured at the Veazie trap between 1978-2012 using different generation times.
Figure 1.8. Measures of dispersion of length over time. Coefficient of variation (%), left and standard deviation (cm, right) of fork lengths of MSW males (a), MSW females (b), and grilse (c) returning to the Penobscot River from 1978 to 2012.
Figure 1.9. Bar graphs showing Penobscot River escapement over time. Bar graphs showing the proportion (top) and number (bottom) of Atlantic salmon returning to the Penobscot by seawinter (SW; RPT = repeat spawner > 3SW) from 1978 to 2012.

1.6 Discussion

1.6.1 Size Selection

The data demonstrate that fork length is a significant predictor of passage success at two of the lowermost dams in the Penobscot River, with larger fish being less likely to succeed.

When dams were modeled together with a factor to account for the number of dams already
passed, temperature and fork length were both significant, and again, the relationship between size and passage success was negative.

In the individual dam model set, the dams that exhibited size selection (Great Works and Milford Dams) shared two characteristics; both dams were in the lower portion of the river (rkm 59 and rkm 61 respectively) and both had Denil fishways of similar age, dimensions, and slope. These dams are ~40 rkm downriver of the other two modeled dams. The average slope of Denil fishways in use around the world is 14.5 ± 1.47%, meaning the fishways on the Penobscot River have a slightly below average slope. However, this slope is still relatively high compared to other styles of fishway, and a recent review suggests that Denil fishways perform poorly for some size classes of fishes (both salmonids and non-salmonids) for this reason (Noonan et al. 2012). West Enfield Dam has a comparatively new vertical slot fishway with a lower slope and longer length than others in the system. Both decreased slope and increased length of fishways have been associated with increased fish passage in other studies (Mallen-Cooper and Stuart 2007; Noonan et al. 2012).

There may have also been an issue of design criteria mismatch at fishways in the lower Penobscot. Denil fishways in use at the Great Works and Milford Dams fell within the slope and width values recommended for use in the northeastern United States (Marmulla et al. 2002). However, these dimensions are designed to be effective for fish ranging from 250 to 740 mm (Mallen-Cooper and Stuart 2007). Multi-seawinter Atlantic salmon returning to the Penobscot River since 1978, average 728 mm (female) and 739 mm (male), putting them at the upper threshold of fishway design. Thus, it is not surprising that larger fish had lower chances of success at these dams. The potential design mismatch between these fishways and the size of returning Atlantic salmon that they were built for may be an issue throughout the northeastern
United States and Atlantic Canada, where Denil fishways predominate on dams < 3m or on smaller streams (Franklin et al. 2012).

No size selection was detected at Howland Dam, which had a Denil fishway with dimensions like those of Milford and Great Works Dams. Howland Dam is located on a tributary rather than on the main stem Penobscot River. With more flow and historically greater amounts of spawning habitat available, the main stem attracts larger fish than the Piscataquis River. This is consistent with studies from the Pacific Northwest that document larger size salmon spawning in larger river systems with more flow (Taylor 1991). Because only smaller fish approached the dam to begin with, size selection would be difficult to detect here. Moreover, the opportunity to observe size selection at this fishway would also be expected to be lower due the fact that fish reaching this dam are a subset that already passed selective fishways lower in the river system.

1.6.2 Environmental Variables

Aside from the consistent, negative coefficients associated with fork length, there were no noticeable trends in environmental variables. Temperature (in both linear and quadratic forms) was a significant predictor of passage success at Great Works Dam, Howland Dam, and in the All Dams model. Both Great Works and Howland had negative coefficients for quadratic temperature, indicating that passage was highest in a particular “optimum” range. Linear temperature had a negative coefficient at Great Works and a positive coefficient at Howland, indicating that the for passage at Great Works was likely lower than that at Howland.

The difference in optimum temperature between Howland and Great Works could be explained in two ways. First, before removal, Great Works Dam was at rkm 59. Howland Dam is 40 km upriver. Thus, fish would arrive at Great Works earlier in the season, when water temperatures were lower. Secondly, even within a river-specific strain of salmon, optimal
swimming performance temperatures exist over a range, with as much as a $10^\circ C$ difference between the minimum and maximum values (Lee et al. 2003). Because only a subset of our fish that approached Great Works also approached Howland, it is possible that the mean optimal swimming performance temperature was higher for the subset approaching Howland.

River flow was only a significant factor in passage success at West Enfield Dam. There, extreme high discharges were negatively associated with passage; additionally, the quadratic discharge term was positive, indicating high likelihood of passage across a range of values, rather than a particular optimum.

### 1.6.3 Evolutionary Trends

We did not detect trends in size at age for MSW adults; both evolutionary rate and response to selection varied through time with no clear positive or negative responses. We did find modest support for evolution of reduced size in 1SW fish over the full time period of monitoring, with a net evolutionary rate of -0.987 haldanes. While we did not find evidence for size at age responses in MSW fish, 3SW (slow maturing) and iteroparous salmon all but disappeared from the population during this time. This mixed evidence of evolutionary responses, however, may make sense considering the management of salmon in this system.

Since the early 1970s, hatchery-raised smolts are estimated to have accounted for more than 50% of Atlantic salmon returns to the Gulf of Maine DPS. The long-term average since then is $81.6\% \pm 7.8\%$ of returns originating from hatchery smolts, with the balance made up from a combination of fry stocking and wild reproduction. Considering both stocking of smolts and fry, $\approx 95\%$ of returns have been hatchery origin in recent years (National Research Council (U.S.) 2004). Importantly, broodstock collection has long occurred at a facility located above the first fish passage structure in the river, and selection of broodstock at this facility has consistently
favored collection and spawning of MSW fish of perceived wild origin. Hence, while all returning fish might be exposed to some size selectivity at the lowest passage facility, this pattern of management suggests that hatchery operations may impede responses to selection in size at age of MSW fish by limiting the number of dams such phenotypes pass and inflating their future contributions via hatchery production. However, this same management would be expected to facilitate greater opportunity for responses to size selection in 1SW fish by exposing much larger proportions of those phenotypes to passage at multiple fishways in a greater total number and proportion of generations. Our ability to detect a modest trend in size at age for 1SW fish but not MSW fish is consistent with these expectations.

Despite only modest evidence of directional changes in average size at age over time, changes in dispersion of fork length were very evident in all three age groups of Atlantic salmon (Figure 1.8), indicating a population under potentially strong stabilizing or fluctuating selection (Haugen et al. 2008). To our knowledge, this is only the second paper to document decreased trait variance that may be attributable (at least in part) to fish passage facilities. Given the opposing effects of selective passage disfavoring larger fish and natural and broodstock disfavoring small fish, loss of size variation might be expected over time. Moreover, such loss of variation might be apparent in this system given its history. Supplementation of the Penobscot River Atlantic salmon run has occurred at some level since the 1870s. Until the 1920s, most eggs fertilized in the hatcheries came from Penobscot River stock, but from 1920 to 1974, eggs for supplementation often came from out-of-river sources, such as the Miramachi and Saguenay Rivers in Canada (Fay et al. 2006) and the Narraguagas and Machias Rivers in Maine. Penobscot River eggs once again became the primary source for supplementation starting in 1974, just before the start of our dataset. While genetic analyses suggest that past stockings did not replace
the Penobscot lineage, this supplementation history could have inflated phenotypic variation in
the Penobscot population by the 1970s, after which selection would have had greater opportunity
to reduce it.

Finally, we think it is important to reiterate that changes in size at age are not necessarily
the most probable outcome from size-selective fish passage. Age at maturity and repeat
maturity, account for a much larger proportion of total variation in salmon size than does size
variation within age classes (Jonsson et al. 1991). Moreover, age at maturity is under strong
genetic control in salmonids (Carlson and Seamons 2008; Barson et al. 2015). We observed that
the age structure of the Penobscot population has changed dramatically over time, such that 3SW
and repeat spawning salmon have been nearly eliminated from the population during a period
when hatchery operations might have been favoring these phenotypes. While we cannot exclude
other agents of selection, or effects of changing marine or freshwater conditions on age at
maturation, the strong selection against passage by large fish could certainly contribute to such a
trend.

1.7 Conclusions

Our study documents selection against large, run of the river Atlantic salmon migrating in
the Penobscot River caused by Denil fishways at two dams. Although the Penobscot River
Restoration Project effectively removed all Denil fishways from the main stem of the river, there
are still three Denil fishways of similar dimensions and age that fish must navigate to access
spawning habitat in the Piscataquis River, and one Denil fishway that Atlantic salmon must
navigate to access spawning habitat in the Passadumkeag River. A fish elevator was also
installed at the lower most dam. While such structures are presumed to be less size selective, no
data have been collected at this facility to verify that assumption.
Additionally, although we found no evidence of a sustained, negative trend in Atlantic salmon size over the past thirty-four years, there was strong evidence of a sustained decrease in size variability within MSW fish and grilse. Such a decrease in variability is evidence of a population under stabilizing selection, with different forces driving the phenotype (in this case, size) towards an optimum. If restoration of a wild spawning population of Atlantic salmon to the Penobscot River system, or other anthropogenically altered systems, is to succeed, the potential for fishways to exert size-selective pressure and possibly contemporary evolution in a naturally spawning population, may need to be considered.
CHAPTER 2

2 DEMOGRAPHIC AND EVOLUTIONARY IMPACTS OF SIZE SELECTION AT FISHWAYS ON ATLANTIC SALMON

2.1 Abstract

The migratory routes of Atlantic salmon have been fragmented throughout their range by damming. Efforts to restore connectivity often include construction of fishways. Empirical studies indicate that these structures create unforeseen obstacles to restoration over time by imposing selective pressures against large-bodied individuals. To determine whether selection at dams can drive evolution of Atlantic salmon, we used an individual-based model under selective pressure previously documented in the Penobscot River to simulate a population of Atlantic salmon in a simplified, relatively small river (~89 rkm) system and followed it over a 100-year period. We varied the number of dams present in the system as well as narrow-sense heritability of length at maturity and age at maturity and tested 150 combinations of these variables 1000 times each. Our results indicate that the probability of extinction increases dramatically when more than one dam is present in the system. Populations never went extinct without dams, but 7.2% went extinct with only a single dam in the system and 63.2 % went extinct with two dams in the system. Additionally, the selective pressure at fishways is strong enough to have observable impacts on the distribution of life history strategies and lengths across a range of heritability values. Coefficient of Variation in length decreased over time across all life history strategies with at least one dam present in the system, but did not change in free-flowing systems. Egg production in free-flowing systems was dominated by 2 seawinter fish. The proportion of eggs contributed to the population by multiseawinter (large, slow-growing) fish was highest in two dam systems, which, coupled with low populations in these systems, is
indicative of populations under stress. These data indicate that restoration practitioners may wish
to pay particular attention to the length-frequency of fish ascending fishways in addition to the
number of fish using the structures. Population-level impacts modeled here could complicate
efforts to restore populations of migratory salmonids.

2.2 Introduction

Atlantic salmon *Salmo salar* are a species of salmonid that exist in the North Atlantic
Ocean and its freshwater drainages. Adult Atlantic salmon migrate into headwater streams to
spawn, and their arrival on the spawning grounds may be delayed or stopped by the presence of
dams (Gowans et al. 1999; Bradford et al. 2011; Izzo et al. 2016). Throughout their range, the
inability to move upstream of these structures has resulted in population declines (Saunders
1960; Parrish et al. 1998; Lundqvist et al. 2008). Attempting to balance the requirements of fish
passage with the desire to generate electrical power or manage river flows, many dams include
fishways (e.g., ladders or elevators) to provide an avenue for upstream movement (Opperman et
al. 2011). However, fishway performance rarely, if ever, matches movement in a natural system.

Even dams with fishways may have passage success rates below 20% if environmental
conditions are not within an optimal range (Gorsky 2005; Holbrook et al. 2009; Maynard et al.
2017). These obstacles may also present migratory delays of several days to several months
(Laine et al. 2002; Izzo et al. 2016). Failed passage attempts at dams can eventually lead to fall
back and return to the sea (or lake, in the case of freshwater residents) without spawning
(Holbrook et al. 2009). Thus, dams can exclude certain fish from the spawning grounds (Caudill
et al. 2007), and the exclusion is not random (Maynard et al. 2017). Passage efficiency studies at
dams generally involve the evaluation of exogenous factors influencing passage success, such as
environmental (Gorsky 2005), structural (Mallen-Cooper and Stuart 2007), or behavioral (Monk
et al. 1989) factors; however, relatively few studies incorporate endogenous factors such as fish size or physiology (Roscoe and Hinch 2010).

Recent research has found that fish size can be a strong predictor of passage success in Denil fishways for multiple non-salmonid species (Mallen-Cooper and Stuart 2007), brown trout *S. trutta* (Haugen et al. 2008), sockeye salmon *Onchorhynchus nerka* (Roscoe et al. 2011), and Atlantic salmon (Sigourney et al. 2015; Maynard et al. 2017). Denil fishways are the most common style of fishway used for alosine and salmonid passage in the Northeastern United States (Mallen-Cooper and Stuart 2007), and fish migrating through many rivers in the region face a gauntlet of multiple Denil fishways in series (Sigourney et al. 2015). Counterintuitively, in each of the salmonid examples mentioned previously, larger body sizes were associated with lower probabilities of successfully passing dams via Denil fishways, as well as longer delays below dams equipped with Denil fishways. The reduced success rates of larger bodied individuals may reflect a size mismatch in the design of Denil fish ladders. Throughout the United States and Europe, the slope and width of Denil fishways are generally optimized for salmonids with fork lengths between 250 mm and 740 mm (Baras et al. 1994; Haro et al. 1999; Mallen-Cooper and Stuart 2007; Noonan et al. 2012). Adult multiseawinter salmon returning to the Penobscot River in Maine averaged 731 mm over the past four decades (Maynard et al. 2017), multiseawinter adults tagged for a passage study on the River Tummel in Scotland averaged 764 mm (Gowans et al. 1999), and a survey of 17 Norwegian rivers in the late 1980s found multiseawinter adults averaged between 715 mm and 1028 mm depending on the river (Jonsson et al. 1991). Therefore, this mismatch between Denil construction and fish size may have been prevalent across the range of Atlantic salmon throughout much of the 20th century.
In addition to influencing passage success, the length of salmonids also influences the amount of energy that an individual fish can store for migration and reproduction (Jonsson et al. 1997), with the energy content of an individual nearly doubling as length increases from 710 mm to 830 mm. Such exponential increases in energy content with length also translate to higher egg quantity (Heinimaa and Heinimaa 2004) and higher egg quality (i.e., more energy stores available to offspring; Fleming and Gross 1990; Fleming 1996). With more energy stores available, juveniles hatched from larger eggs have higher post-emergence survival (Beacham and Murray 1985). It is also well-documented that length at maturity is heritable in salmonids, with narrow-sense heritability ($h^2$) values (i.e., the proportion of phenotypic variability attributable to additive genetic values) ranging from 0 – 0.55 (Carlson and Seamons 2008). Length at maturity is also influenced by the timing of when a fish matures. Atlantic salmon can mature after 1 – 3 winters at sea, and the time at which a fish matures is linked to growth rate. Faster growing individuals tend to mature earlier and at smaller sizes than their slower growing conspecifics (Friedland and Haas 1996). Additionally, individuals that mature after one seawinter (hereafter, “grilse”) are predominantly male, whereas individuals that mature at two or three seawinters are predominantly female (Niemela et al. 2000).

Given the relationships between body size, growth, and maturity, the interaction of passage probability with size may be consequential at a population level. In order for evolution by selection to occur, a trait must vary, confer a fitness benefit, and be heritable (Godfrey-Smith 2007). Length at maturity and speed of growth in Atlantic salmon meet all three conditions. Thus, it is possible that selection on size from fishways could drive evolution of these traits in a population of Atlantic salmon. Similar phenomena have been observed under size-selective harvest regimes, in which large individuals are harvested prior to reproduction (Allendorf and
Hard 2009) and in aquaculture breeding programs in which the spawning population is artificially constricted (Heath 2003). Such selection can drive a population towards smaller length at maturity (Kuparinen and Merilä 2007) and shift the population’s age structure towards a narrow range of optimal values (Gjerde 1984). Sublethal selection such as what occurs during fishway passage (Haugen et al. 2008; Sigourney et al. 2015; Maynard et al. 2017) and catch-and-release angling (Philipp et al. 1997; Cooke et al. 2007) may also have negative impacts on demography, life history, ecology, and long-term persistence of populations (Fenberg and Roy 2008).

Fish species that are particularly vulnerable to decreases in average size and age due to anthropogenic selective forces share five important characteristics, of which Atlantic salmon have three: length at maturity > 250 mm, age at maturity > 3 years, and a spawning period > 7 months (Anderson et al. 2008); the two characteristics they do not have off the list are a low trophic level and high interannual variability in abundance. Selection at fishways for smaller, younger spawning migrants could potentially reduce the number and quality of eggs produced in a given river system, which has serious implications for population restoration. Given the concerns about the possible long-term impacts of selection at fishways, we sought i) to test whether the documented selective pressure exerted by fishways in the Penobscot River is sufficient to elicit an evolutionary response in length at maturity of Atlantic salmon, and ii) to assess the sensitivity of demographic parameters to such selection under multiple scenarios.

2.3 Methods

2.3.1 Overview

We used an individual-based model (Sections 0, 0, and 0) to simulate the demographic and evolutionary impacts of size-selective passage at dams on an Atlantic salmon population in a
short, simplified river system over a 100-year period (Figure 2.1). Upstream passage success of adult salmon and downstream survival of outmigrating kelts and smolts were modeled using empirical data from recent studies of dams on the Penobscot River (Stich et al. 2014; Maynard et al. 2017, 2018). Each fish had values for sex (female or male), maturity state (true or false), size-at-maturity (cm), age, age at maturity, and a series of heritable “threshold” values to determine maturity status. Population-level parameters that were tracked over the course of the simulation included male to female ratio, number of grilse, two seawinter (2SW), and multiseawinter (MSW) fish (combined 3SW maturing fish and repeat spawners), the average and standard deviation of lengths for grilse, 2SW, and MSW adults (separately), and the average maturity threshold values for grilse and 2SW fish. To define carrying capacity through the delineation of available spawning habitat, the physical habitat parameters of the system were based on the Narraguagus River in Maine, USA (USASAC 2015), a well-characterized small river system typical of coastal systems in eastern Maine. As such, the in-river migratory distance (mouth to headwaters) was set at 89 km, and available wetted habitat was set at 502,763 m². Habitat was assumed to be saturated when egg deposition reached 3.01 million (~ 6 eggs / m²; Jonsson et al. 1998).
Figure 2.1. Schematic representation of the IBM model. Schematic representation of the individual based salmon evolution model. Beginning at the egg stage, salmon are subjected to a survival probability \( R \) based on a latitude-specific Ricker curve. The parr – smolt transition is governed by a survival probability taken from the literature (Legault 2005). Smolt \( P_{\text{out}} \) (probability of surviving outmigration) is drawn from empirical studies of the Penobscot River, Maine, USA. Each year at sea, survival is assessed using a probability of 0.24. After maturing at sea, adults cross back into freshwater, passing dams with a probability \( (P_{\text{pass}}) \) based on empirical studies in the Penobscot River and governed by each individual’s size at maturity. Finally, post-spawn fish survive with a probability of 0.63 (no dams) or 0.43\( ^d \) (if dams are present), again, based on empirical studies of the Penobscot River. Heritability \( (H^2) \) influences the characteristics of each egg (calculated as the mid-parent values plus some variability) and the time at which a fish matures (transitions from post-smolt to adult migrant). Size \( (S) \) influences the probability of successful upstream passage at dams \( (P_{\text{pass}}) \), mate choice, and egg number.

2.3.2 Demography

The demographic model calculated total egg production (Equation 2.1) as the sum of the size-specific egg production of each female spawner (Heinimaa and Heinimaa 2004).

\[
S = \sum_i e^{3.07 \times \log(L_i) - 4.46}
\]

Equation 2.1
Total egg production ($S$) was fed into a latitude-specific Ricker model for 45°N (Equation 2.2), calculated from Prevost et al. (2003) using the Solver extension (Walsh and Diamond 1995) in Excel (Microsoft 2010) to estimate $\alpha$ and $\beta$, where $R$ is the number of successful hatchings and $S$ is total egg production from Equation 1. For this model, $\alpha$ was fixed at 0.42 and $\beta$ was fixed at $5.01 \times 10^{-7}$.

$$R = S \times e^{\alpha - \beta S}$$

Equation 2.2

The freshwater life history of parr was accounted for by multiplying the output of the Ricker model by 0.041, the mean freshwater survival from parr to smolt used in Legault (2005). Each spawning female was assigned a male partner using a size advantage mating system, in which 2SW and 3SW males were twice as likely to be selected as grilse males, based on observations in natural systems that indicate 2SW and 3SW males have a lifetime reproductive success 1.92 times that of grilse (Garant et al. 2003). If more females than males were present, selection of mates by male fish was random (Vladic and Petersson 2016). Using these pairs, a matrix of possible offspring was produced, and surviving smolts were drawn randomly from that matrix. All fish that survived to smolting spent just over two years in freshwater before outmigrating to the sea (Jutila et al. 2006). Probability of surviving outmigration ($P_{out}$) was calculated based on a per river kilometer survival rate of 0.99 for free-flowing stretches of river and 0.95 per kilometer encompassing a dam, (Equation 2.3; Stich et al. 2014).

$$P_{out} = 0.99^{(rkm-d)} \times 0.95^d$$

Equation 2.3

A binomial draw using this probability was conducted for each smolt to determine whether it reached the sea. Annual marine survival was held constant at 0.24 (Chaput 2012), and again, a binomial draw using this probability was conducted for each fish to determine whether it
survived the year at sea. After maturing at sea, adults returned to the river to spawn. In the absence of dams, adult survival during in-migration to the spawning grounds was assumed to be 1 (Finstad et al. 2005; Richard et al. 2014). When dams were present, probability of successful passage for each individual at each dam ($P_{pass}$) was calculated as shown in Equation 2.4, where $L_i$ is the length of the fish, all $\beta$ values for each fish are drawn from distributions developed by Maynard et al. (2017), and the value $D$, drawn from U(0, 30), represents the number of days the fish is delayed below the dam.

$$P_{pass} = e^{\beta_1 + \beta_2 \times \frac{(L_i-65.711)}{9.945} + \beta_3 D}$$

Equation 2.4

Fish were required to pass all dams in the system to reach the spawning grounds. Post-spawning survival probability was held at 0.63 with no dams or $0.43^d$ (where $d$ is the number of dams) if dams were present (Maynard et al. 2018). Fish that survived spawning and outmigration returned to sea for one year (subject to the annual marine mortality of 0.76 described above) before rejoining the spawning run in the subsequent year. All fish that survived at sea were assigned growth between 1 cm and 5 cm U(0,5) based on at sea growth rates reported by Izzo and Zydlewski (2017). No artificial age limit was imposed on the population, as previous research in undammed systems observed some kelts returning for up to six repeat spawning events (Ducharme 1969), and the probability of returning beyond that time in this model was 0.00006.

2.3.3 Heritability

A simple heritability component was added to the demographic model to allow length at maturity and age at maturity to evolve (Carlson and Seamons 2008). Narrow sense heritability ($h^2$) was kept static for both traits throughout a single (100-year) run of the model. Length at maturity was z-standardized based on life-history specific von Bertalanffy curves for grilse and
multi-seawinter fish (Allen et al. 1972). Age at maturity was inherited as a series of three z-scores. Each offspring inherited a “threshold value” for maturity at both one and two seawinters along with a “maturity value”. Each year, the program checked subadult maturity values against the appropriate maturity threshold (e.g., if the fish had been at sea for one winter, that fish’s maturity value was checked against its 1SW threshold). If the maturity value exceeded the threshold, the fish was counted as mature and joined the spawning migration. All subadults remaining at sea after two seawinters matured at three seawinters. For all traits, inherited values for each offspring were calculated using the z-standardized mid-parent value, $h^2$, and a random draw from $U(-2.5, 2.5)$ to encompass any trait variability not captured by additive genetic variation (Equation 2.5). The value $U(-2.5,2.5)$ was chosen because it represents ~99% of the possible values in a $Z$ distribution. $Z$ standardization was accomplished using mean and standard deviation values of the starting distribution selected at the beginning of the simulation (i.e., the larger-sized ‘historic’ distribution or the smaller-sized ‘modern’ distribution). All offspring from a given set of parents are given the same $(Z_M+Z_F)/2$ value, but the random draw ensures offspring are not identical to one another.

$$Z_o = \left(\frac{Z_M + Z_F}{2}\right) \times h^2 + U(-2.5, 2.5) \times (1 - h^2)$$

Equation 2.5

2.3.4 Simulation

Starting lengths of fish were drawn from the modern (1979-2015) distribution of sizes present in the spawning escapement Penobscot River (Figure 2.2). Run proportions of each age group (grilse, 2SW, MSW) started off using the proportions in Downeast Maine salmon rivers reported by Izzo and Zydlewski (2017) and were allowed to evolve over time.
Figure 2.2 – Starting distributions of salmon lengths for the simulation. The hatched bars are a modern distribution (1979-2015) measured at the Veazie Dam fish ladder. The solid bars are a historic distribution back-calculated from Atlantic salmon weights (whole fish) measured at the Bucksport, ME fish market in 1879.

Narrow sense heritability was varied separately for the two traits (length at maturity and age at maturity) from 0.1 to 0.5 (Carlson and Seamons 2008) by steps of 0.1. The number of dams in the system was varied from 0 to 5 by steps of 1. This totaled 150 possible combinations of parameters. Each combination was simulated 1000 times. Each simulation began with a 50-year model stabilization period with no dams. After the stabilization period, the population was tested to ensure it met the following criteria: 1) the estimated $h^2$ values for each trait had to be within 0.05 of the $h^2$ values specified at the beginning of the simulation run, and 2) the spawning escapement needed to be between 300 and 800 individuals, consistent with the estimated productivity of the Narraguagus River (USASAC 2015). If the population failed either test, the
simulation was discarded and rerun. If the population passed both tests, the simulation was run out for another 100 years with the appropriate number of dams. The simulation code was written in R x64 v3.2.3 (R Core Team 2012) and used the following packages: truncnorm (Trautmann et al. 2015), FSA (Ogle 2017), broom (Robinson et al. 2017), and nlstools (Baty et al. 2015).

To ensure the model was not unduly influenced by some of the assumptions that were made, we also conducted several four additional 100 simulation test runs of the model, holding $h^2$ of growth and size at maturity constant at 0.2. In the first test run, we reduced the mating advantage of 2+SW males over grilse from 1.92 to 1.46 (so 2+SW fish were only 1.48 times as likely to be drawn from the pool of potential mates as grilse were). Next, we eliminated the mating advantage entirely, so that mate selection was random. The third test run kept the mating advantage of 2+SW fish at 1.92 while eliminating the random variability added into heritability (effectively, setting $H^2 = h^2$). Finally, we kept the mating advantage at 1.92, $h^2$ at 0.2, and started the simulation with large sized salmon. This larger distribution was based on weight data of live salmon reported by Atkins (1874) on the Penobscot River from which lengths were back calculated using salmon growth curves from less impacted rivers in the Canadian Maritimes (DFO 2018), and was selected to test whether beginning with a less impacted size distribution gave different results than start with a size distribution of a run that had already experienced ~100 years of selection at dams and hatcheries.

2.3.5 Analysis

We used logit-link generalized linear models to explore the relationship between the probability of population extinction at the end of 100 years, narrow-sense heritability of traits, and the number of dams present in the system. Generalized liner models were used to compare
outcomes on continuous scales (e.g., length and escapement) at the end of the 100-year simulation across a number of dams and ranges of both heritabilities. Models were compared using AICc scores and Akaike weights as calculated by the qcpR package in R (Spiess 2018). Any models with a ΔAICc value ≤ 2 were counted as competing candidate models, and any with ΔAICc values > 10 were considered irrelevant.

Evolutionary change in length was calculated in haldanes (Hendry and Kinnison 1999; Equation 1.1). Finally, we used Wilcoxon rank sum tests to evaluate differences in proportional egg production within a life history group from the beginning of the simulation to the end of the simulation. All statistical analyses were performed in R x64 v3.2.3 (R Core Team 2012) and used an α value of 0.05 to determine significance.

2.4 Results

2.4.1 Extinction

Very few (< 2.5%) of the simulations were discarded after failing the stabilization tests; however, many simulations were unable to complete the full 100-year run because of the presence of dams. Although we initially intended to simulate the system with up to five dams, all model runs with more than two dams had escapements of fewer than 15 fish by the end of the simulation, and more than 85% of all runs with three or more dams ended in extinction well before 100 years. Because of these low sample sizes, we present data from simulations with no more than two dams for all subsequent analysis. No populations in undammed streams went extinct within 100 years. However, across all heritability values, 7.2% of populations went extinct with one dam, and 63.2% of populations went extinct with two dams (Figure 2.3).
Figure 2.3. Surface plot of extinction probability after 100 years. Extinction probability (z-axis) plotted over heritability of age at maturity (y-axis) and number of dams in the system (x-axis). Darker shades represent a lower probability of extinction.

The average number of years post-damming before extinction with two dams was 70.8 (± 21.0), and with one dam 95.7 (± 7.5). There were two candidate models to predict extinction. Both included the number of dams in the system and the heritability of age at maturity, and both predictors were significant (Table 2.1), although the effect size of the number of dams was substantially larger than the effect size of heritability of age at maturity (Figure 2.3). The second candidate model also included heritability of length at maturity as a predictor, but its $\beta$ value was not significant. The effect of the heritability of age at maturity was positive (i.e., higher heritability of age at maturity decreased the probability of extinction) and the effect of the number of dams was negative (i.e., more dams increased the probability of extinction). The heritability of age at maturity and the number of dams present in the system were the most important predictors of measures directly related to extinction such as the number of eggs produced, and escapement numbers across all three life history strategies (grilse, 2SW, MSW).
2.4.2 Evolutionary Change

The rate of evolutionary change was not steady in any one direction over time. That is, with every possible combination of heritability values and dams, the range of rates across all simulations included zero. Length at the end of 100 years was best modeled using heritability of size-at-maturity and number of dams for grilse, heritability of age-at-maturity and number of dams for 2SW fish, and dams alone for MSW fish (Table 2.2). However, in all of these models, the only significant (non-zero) $\beta$ values were those associated with the number of dams, and they were all negative. That is, the only non-zero predictor of fish size across all life history strategies was the number of dams, and more dams resulted in smaller fish at the end of the simulation. As evidenced by their absence from the list of significant $\beta$ values in Table 2.2, heritability of length at maturity and heritability of age at maturity were not significant predictors of the size of fish present in the population after 100 years. Additionally, the comparative effect size of dams was strong enough to swamp out any influence of $h^2$ values in predicting probability of extinction (Figure 2.3).

Regardless of the initial starting distribution of sizes used (modern or historic), the presence of dams caused significant decreases in CV of length over time. The reduction was most pronounced in slower maturing fish (MSWs) with more dams present and indicates a gradual loss of phenotypic variability not seen in simulations of undammed river systems.

Modern starting size

When heritability of size at maturity and growth were both set at 0.2, and no dams were present, the coefficient of variation in length was steady over time for grilse, 2SW, and MSW salmon with no significant change over the course of the simulation (Figure 2.4). With one dam, there was an average decrease of 0.23% in grilse CV ($p < 0.001$), a 0.65% decrease in average
2SW CV (p < 0.001), and a 3.36% decrease in average 3SW CV (p < 0.001). The decrease in CV was steeper with two dams, declining 4.72% in grilse (p < 0.001), 3.78% in 2SW (p < 0.001), and 8.52% in MSW fish (p < 0.001).

**Historic starting size**

There was no significant change in CV of length across all types of salmon when no dams were present (Figure 2.4). With one dam, there was an average decrease of 0.28% in grilse CV (p < 0.001), a 0.61% decrease in average 2SW CV (p < 0.001), and a 3.19% decrease in average 3SW CV (p < 0.001). Once again, there was a more substantial decrease in CV when two dams were present, with a 5.25% decrease in 1SW CV (p < 0.001), a 3.29% decrease in 2SW CV (p < 0.001), and a 10.91% decrease in CV of MSW lengths (p < 0.001).

Table 2.1 Extinction modeling. Summary table for logit-link GLMs modeling extinction (E) by the end of 100 years using the number of dams (D), the heritability of fork length at maturity (S), and heritability of age at maturity (G) as predictor variables. The "weight" column shows the Akaike weight of each model.

<table>
<thead>
<tr>
<th>Model</th>
<th>ΔAICc</th>
<th>Weight</th>
<th>Residual df</th>
</tr>
</thead>
<tbody>
<tr>
<td>(E \sim G+D)</td>
<td>0</td>
<td>0.53</td>
<td>7497</td>
</tr>
<tr>
<td>(E \sim S+G+D)</td>
<td>0.2</td>
<td>0.47</td>
<td>7496</td>
</tr>
<tr>
<td>(E \sim D)</td>
<td>159.9</td>
<td>0</td>
<td>7498</td>
</tr>
<tr>
<td>(E \sim S+D)</td>
<td>160.2</td>
<td>0</td>
<td>7497</td>
</tr>
<tr>
<td>(E \sim G)</td>
<td>3533.4</td>
<td>0</td>
<td>7498</td>
</tr>
<tr>
<td>(E \sim S+G)</td>
<td>3534.3</td>
<td>0</td>
<td>7497</td>
</tr>
<tr>
<td>(E \sim S)</td>
<td>3633.8</td>
<td>0</td>
<td>7498</td>
</tr>
</tbody>
</table>
Table 2.2 Fish length modeling. Summary table for GLMs modeling the average length \((L)\) of fish in each maturity class by the end of 100 years using the number of dams \((D)\), the heritability of length at maturity \((S)\), and the heritability of age at maturity \((A)\) as predictor variables. The “W” column shows that Akaike weight of each model. The values in the \(\beta\) column are labeled with a * if the \(\beta\) was significant. Only models with \(\Delta AIC < 10\) are shown.

<table>
<thead>
<tr>
<th>Model</th>
<th>1SW</th>
<th>2SW</th>
<th>MSW</th>
<th>β</th>
<th>ΔAIC</th>
<th>W</th>
<th>β</th>
<th>ΔAIC</th>
<th>W</th>
<th>β</th>
<th>ΔAIC</th>
<th>W</th>
</tr>
</thead>
<tbody>
<tr>
<td>L~S+D</td>
<td>S</td>
<td>-0.26</td>
<td>0.35</td>
<td>0.24</td>
<td>1.61</td>
<td>0.16</td>
<td>0</td>
<td>1.99</td>
<td>0.18</td>
<td>L~D</td>
<td>D</td>
<td>-0.13*</td>
</tr>
<tr>
<td>L~D</td>
<td>D</td>
<td>-0.13*</td>
<td>0.23</td>
<td>0.31</td>
<td>-0.33*</td>
<td>0.73</td>
<td>0.25</td>
<td>-1.0*</td>
<td>0</td>
<td>L~S+D</td>
<td>S</td>
<td>-0.26</td>
</tr>
<tr>
<td>L~S+A+D</td>
<td>A</td>
<td>-0.14</td>
<td>1.41</td>
<td>0.39</td>
<td>-0.33</td>
<td>-0.33</td>
<td>-0.99*</td>
<td>1.38</td>
<td>0.23</td>
<td>L~A+D</td>
<td>D</td>
<td>-0.13*</td>
</tr>
<tr>
<td>L~A+D</td>
<td>A</td>
<td>-0.14</td>
<td>0.39</td>
<td>0</td>
<td>0.36</td>
<td>-0.33</td>
<td>0.96</td>
<td>0.01</td>
<td></td>
<td>L~S</td>
<td>S</td>
<td>-0.25</td>
</tr>
</tbody>
</table>
Figure 2.4. Coefficient of variation of fork length over time. Coefficient of variation (%) of fork length (y-axis) over time (simulated years, x-axis) for grilse (light gray), 2SW (dark gray), and MSW (black) salmon with zero dams (AX), one dam (BX), or two dams (CX) present in the system. The left column (Y1) represents simulations beginning with the modern size distribution, and the right column (Y2) represents simulations beginning with the historic size distribution. For consistency, only simulations with $h^2$ of growth set at 0.2 and $h^2$ of size at maturity set at 0.2 are shown.
The proportion of eggs contributed by individuals at each life history strategy remained stable over the 100-year simulation period in undammed systems (Figure 2.6). The proportional contribution of grilse was expectedly low, as this life history strategy is primarily associated with males. The majority of eggs in undammed systems were produced by 2SW spawners (0.41 – 0.76), with the remainder coming from MSW fish (0.21 – 0.55). Both life histories produced an amount of eggs proportional to their presence in the population. With the addition of one dam to the system, proportional egg production by grilse remained low. Proportional egg production by 2SW fish increased slightly, but significantly \((W = 1894000, p = 0.042)\) to an average of 0.63, and proportional egg production by MSW fish decreased slightly, but significantly \((W = 2035600, p = 0.034)\) to an average of 0.32. With two dams in the system, grilse produced a higher proportion of eggs, and the proportion of eggs produced by 2SW and MSW fish declined. However, the proportional importance of 2SW fish declined further than that of MSW fish when two dams were present.

When \(h^2\) was increased to 1.0 for both traits (growth and size-at-maturity), clear evolutionary trends emerged over time (Figure 2.5). When no dams were present and heritability was set high, all three groups of salmon (1SW, 2SW, and MSW), increased in size over time. The presence of dams caused declines in size over time across all life history groups, with two dams causing steeper declines than one.
Figure 2.5. Length over time. Length (cm, y-axis) over time (years, x-axis) for 1SW (top row), 2SW (middle row), and MSW (bottom row) spawners with $h^2$ set at 0.2 (left column) and 1.0 (right column). Red dots represent simulations with no dams, blue dots had one dam, and black dots had two dams. For consistency, only simulations with starting size distributions based on modern Penobscot River sizes are shown.
Figure 2.6. Proportion of eggs produced by different age classes. Proportion of eggs produced (y-axis) plotted along proportion of female escapement (x-axis) for grilse (light gray), 2SW (dark gray), and MSW (black) individuals with no dams present, one dam present, or two dams present. Mean values for each group of fish are shown by the dashed lines in corresponding colors. All results plotted here used an $h^2$ value of 0.2 for growth and size at maturity.
2.5 Discussion

Atlantic salmon face threats associated with dams during spawning migrations throughout their native range (Parrish et al. 1998). Traditional passage assessments focused on the number or proportion of fish able to ascend fishways may unintentionally mischaracterize the threat dams pose to Atlantic salmon by ignoring the effect of fish size on passage probability. This can be important to recovery efforts due to the difference in spawning potential of larger fish vs. smaller fish. There is clear data from the United States (Sigourney et al. 2015; Maynard et al. 2017) and Norway (Haugen et al. 2008) that fishways impose size selection pressure on migratory salmonids. Our simulation study bore out the well-known impact of dams (Nicola et al. 1996; Limburg and Waldman 2009; Hall et al. 2011; Liermann et al. 2012): localized extirpation of migratory fish. Additionally, we demonstrated the possibility that realistic levels of non-lethal selection on length at maturity and age at maturity (both heritable traits) by fishways could reduce the variability in life history strategies and length at maturity in a population of migratory salmonids over a 100-year period.

A major caveat that should inform all results from our simulation is that one simplification we used was to keep the environment static. For example, the same amount of wetted habitat was available to spawners each year, which is not necessarily the case, as interannual changes in rainfall strongly impact freshwater habitat availability (Mantua et al. 2010). Additionally, at-sea mortality was fixed for the duration of the simulation, although marine survival of salmonids actually varies based on a number of factors at both the individual and ecosystem level including parasite load (Vollset et al. 2016), river of origin (Lacroix 2008), climate (Peyronnet et al. 2008), and individual growth rate (Duffy and Beauchamp 2011). We also assumed consistent operations at any dams in the simulated system, while in reality, changes
in dam operations to account for changes in river conditions may result in wildly different experiences for fish approaching the same structure at different times (Sinokrot et al. 1995; Young et al. 2011). Additionally, dam operations may change over time, resulting in changes to passage-related delays and mortality (Ferguson et al. 2007; Izzo et al. 2016).

Increasing the number of dams in the system resulted in a sharp increase in the likelihood of extinction for the population. Dams, unlike more slow-moving, natural selective forces (e.g., changes in a river channel over time), can be thought of as acute influences on fish populations. When such strong selective forces are abruptly introduced into a system (e.g., dam construction over several years) the impact may be too rapid to allow for any sort of response to selection to occur (Chevin et al. 2010). Rather, the population would simply go extinct. Extinctions of migratory fishes caused by dams are well documented in the literature (Nicola et al. 1996; Musick et al. 2000; Hall et al. 2011; Lawrence et al. 2016, etc.). Additionally, research from terrestrial ecology demonstrates that severe habitat fragmentation can reduce migratory ability (Collingham and Huntley 2000) and cause declines in biodiversity via localized extinction (Fahrig 2003). The history of Atlantic salmon in New England provides a real-world look at how dams can extirpate populations of fish. With over 4,000 documented dams in the region (average age ~100 years; U.S. ACE 2018) many rivers in New England have been dammed for over a century, and New England is the most heavily dammed region in the country. Two distinct population segments (DPSs) of anadromous Atlantic salmon (Long Island Sound and Central New England) have been completely extirpated, while the Gulf of Maine DPS has remnant populations in fewer than half of its rivers, and total returns of fewer than 100 fish annually (USASAC 2015). Further work in this area may wish to simulate the addition and removal of
dams over time to better reflect the changes in water management that have characterized many salmon rivers over the past several centuries (Hall et al. 2011).

Although the simulations did not show evolution towards smaller length at maturity or younger age at maturity, they did indicate a reduction in the coefficient of variation in length over time, indicating that the real-world selective pressure of fishways against large-bodied individuals is enough to result in stabilizing selection over time. We did not see directional selection towards smaller lengths in our simulations. However, the coefficient of variation decreased markedly over time in simulations that included the presence of dams across all life history strategies. A similar phenomenon has been documented in studies of migratory fish populations exposed to Denil fishways in the United States (Maynard et al. 2017) and Norway (Haugen et al. 2008). Decreasing variation may be the result of fluctuating selection pressures (e.g., non-directional environmental changes; Hallsson and Björklund 2012), or stabilizing selection (Quinn et al. 2001; Neff 2004). In our simulations, we had four pressures acting on length. First, larger fish took longer to mature at sea, subjecting them to a higher probability of marine mortality (directional selection against large fish). Larger fish produced more eggs than their smaller conspecifics, and also had a better chance of spawning when mate availability was a limiting factor (directional sexual selection against small fish). Finally, the introduction of dams into the system created directional selection against large fish by reducing their likelihood of entering the spawning population. With the exception of the number of dams (which varied from 0 to 2, but kept constant within an individual simulation), the other selective pressures were kept constant across all simulations, removing the possible explanation of fluctuating selection. Thus, the presence of size-selective fishways appears to cause stabilizing selection by acting as a counterweight to the natural advantages conferred by increased body size. Similar balances of
selective forces have been observed in natural systems, for example where large body size increases reproductive capability, but also increases vulnerability to stranding on gravel bars and predation by bears (Carlson and Quinn 2007). In these systems, streams with lower bear predation risk had larger bodied spawning salmon. Additionally, the standard deviation of salmon body lengths in rivers exposed to heavy depredation by bears was 6 mm smaller than in rivers without heavy depredation, indicating reduced phenotypic variability.

To our knowledge, few studies have assessed the existence of size-selective passage at dams (Mallen-Cooper and Stuart 2007; Haugen et al. 2008; Sigourney et al. 2015; Maynard et al. 2017). Those that have showed reduced success rates of larger bodied individuals, and primarily assessed Denil fishways. The equations used for passage probability in this study were taken directly from a multi-year study of one particular Denil fishway in central Maine, USA (Maynard et al. 2017). As mentioned before, the slope and width of Denil fishways are generally optimized for salmonids with lengths between 250 mm and 740 mm, a range which does not include many 2SW and MSW salmon in North America (Chadwick et al. 1978; Maynard et al. 2017) or Europe (Jonsson et al. 1991; Gowans et al. 1999). In addition to concerns about slope optimization, Denil fishways may also have difficulty attracting larger fish to begin with. Because of the turbulent flow throughout the fishway and the low water velocity at the base of the water column (Katopodis 1992), attraction flow dissipates rapidly downstream of Denil fishways (Nieminen et al. 2017). Milling and poor passage of MSW fish at such facilities is documented and can be mitigated by converting from Denil fishways to other designs (Laine et al. 2002).

The existence of dams, particularly dams in series, is known to negatively impact migratory success (Sigourney et al. 2015) and impair populations of migratory fishes (Parrish et al. 1998). Simulations indicating this problem are not surprising, given the well-documented
impacts of hundreds of years of damming around the world (Gowans et al. 1999; Bednarek 2001; Caudill et al. 2007; Hall et al. 2011). However, the fact that the simulations were able to bear out this history lend some credence to the methods we used. As in dammed rivers throughout their range, the proportion of Atlantic salmon that returned as 3SW fish declined over time during our simulations with one or more dams from an average of 0.17 to 0.15 over a 100-year period. On the Penobscot River (Maine, USA), a decline from 0.01 MSW to 0 MSW was documented during a 30 year period (Maynard et al. 2017); however, dams were present for over 60 years before that data series was collected. On the River Dee (Wales, UK), the decline in MSW proportion went from 0.28 to 0.01 over a 70 year period that included increases in water temperature along with the construction of major impoundments (Aprahamian et al. 2008). It is difficult to partition how much of the decline was due to each factor. Regardless, these declines in MSW proportion caused by the presence of dams coincided with steep declines in the numbers of fish present in both simulated and natural systems. Thus, an additional consequence of the presence of dams beyond the reduction of MSW fish in the simulated systems was a substantially higher risk of extinction compared with undammed systems.

A contributing factor to the higher risk of extinction is the increased importance of large MSW salmon to spawning populations (measured by their proportional contribution to the number of eggs produced) in systems with small populations. Through heavy reliance on a few individual to provide the bulk of the eggs, these systems are more at risk of extinction than systems where egg production is spread across multiple size classes and life history strategies. In our simulated systems without dams, large, 2SW fish dominated egg production. Similarly, 2SW fish provided an average of 64% and up to 90% of egg deposition in the Miramachi River (Randall 1989) and an average of 64% and up to 99% of egg deposition in nine rivers across the
Canadian Maritimes (Chaput et al. 2015). Despite producing a smaller fraction of the total number of eggs than their 2SW conspecifics, large MSW fish are thought to play an important role by providing buffers against years of poor recruitment in natural systems (Niemelä et al. 2017) because of their high reproductive capacity. Thus, their elimination from spawning runs corresponds with a rapid, non-linear increase in probability of extinction, and may be of concern for managers and restoration practitioners. Our simulation characterized the relative effect sizes of $h^2$ variation and the number of dams on the size of salmon in a small river population over 100 years. We found that the presence of dams causes a reduction in the number of fish present in the population, a reduction in the range of fish sizes present in the spawning population, and an increased probability of extinction for that population. Large, MSW fish play an outsized role in propping up struggling populations, but are also the fish likely to be excluded from spawning by size selection at fishways. The effect of multiple dams in series quickly drove the population to extinction. Mathematically, this effect would scale up with the system, so long as system characteristics remained the same. However, if some spawning habitat were available between dams (i.e., not all fish have to pass through all fishways to spawn), a remnant population may be able to persist in that available habitat.
CHAPTER 3

3 THE FATE OF HATCHERY-SPAWNED ATLANTIC SALMON KELTS
RELEASED INTO THE PENOBSCOT RIVER, MAINE

3.1 Abstract

The Penobscot River is home to the last major run of Atlantic salmon in the United States. For over one century, the river has been stocked intensively. Since the late 1970s, most kelts are released to the Penobscot River estuary following hatchery spawning. Over time, the proportion of the run made up of iteroparous individuals has declined to < 1%. These fish are typically large and produce more eggs than virgin spawners. We radio-tagged 55 kelts that were artificially spawned at a Federal hatchery in 2015 and released them at two locations (head of tide and ~50 km upstream) to assess 1) when hatchery-spawned kelts leave the river, 2) whether release location influences river exit timing, and 3) if kelts from the upper river could outmigrate through the lower Penobscot River’s hydroelectric complex. The kelts were tracked from November 2015 to July 2016. Although some fish from both release groups were documented leaving the system within one month, the majority of fish (84%) overwintered in freshwater habitat. Many (71%) of those kelts that overwintered in the Penobscot River made directed, upstream movements in November and December. However, there was no difference in upstream movement rates, timing of outmigration, or survival between the release groups. Survival to outmigration was 23.6%, which is considerably lower than survival documented in Canadian and European rivers. Low survival to outmigration may have contributed to the disappearance of iteroparous individuals from the Penobscot River run of Atlantic salmon over the last four decades.
3.2 Introduction

Atlantic salmon *Salmo salar* populations in the United States have declined precipitously over the last several decades, with the only remaining population segment listed as endangered under the U.S. Endangered Species Act (Fay et al. 2006). The Penobscot River historically supported spawning runs of more than 100,000 individuals (Saunders et al. 2006), but recent returns average only around 1,000 fish annually (Oliver Cox, Maine Dept. of Marine Resources, *pers. comm.*). The U.S. Government has identified restoration of the Gulf of Maine distinct population segment (GOM DPS) as a high priority (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2005). However, Atlantic salmon face a variety of threats because of their anadromous and iteroparous life history (Legault 2005; Maynard et al. 2017), including overfishing, pollution, and the presence of dams (Parrish et al. 1998; Nieland et al. 2015). While many stages of Atlantic salmon life history have been well studied (Klemetsen et al. 2003), comparatively little is known about the survival and movements of kelts (post-spawn adults) following successful spawning. Because repeat spawners have outsized reproductive influence in salmonine populations (Kusterle et al. 2013; Trammell et al. 2016), ensuring survival of kelts could be valuable to restoration efforts.

Many anadromous salmonines can spawn multiple times during their life cycle, returning to sea after each spawning event to recondition (Klemetsen et al. 2003). Survival following spawning can be high in Atlantic salmon (~80%; Chadwick et al. 1978; Jonsson et al. 1990). However, a much smaller proportion of fish survive to spawn again (Ducharme 1969). Broadly, the outmigration of kelts takes place in two stages. A small proportion of individuals migrate directly to the sea, while the majority overwinter in the river before outmigrating to the marine environment the following spring (Ruggles 1980). For those fish that overwinter in-river,
survival to outmigration has been reported in a small number of studies as >50% (Gray et al. 1987; Downton and Reddin 2004). Across systems (North American and European rivers) and species (Atlantic salmon and steelhead *Onchorhynchus mykiss*), downstream kelt migrations in spring are generally over by July (Halttunen et al. 2010; Marston et al. 2012; Lacroix 2013). Once at sea, the time needed to rebuild energy stores varies according to several factors, including the amount of time previously spent in freshwater (Niemelä et al. 2006), migratory distance to marine feeding areas (Lacroix 2013), and fish condition post-spawning (Jonsson et al. 1991).

The ability of kelts to survive a return migration to the sea, a year or more of reconditioning, and a return migration to the spawning grounds affects the proportion of repeat spawners, which varies from 0 to 26% for Atlantic salmon populations (Fleming and Reynolds 2003; Niemelä et al. 2006). However, spawning runs composed of >40% repeat spawners have been reported in undammed systems in Canada that are not subject to commercial exploitation (Jessop 1976; Saunders and Schom 1985). The number of broods a fish has is also variable in salmonines. In Steelhead nearly all iteroparous individuals spawn no more than twice in their lifetime (Seamons and Quinn 2010). Atlantic salmon have been documented returning for as many as eleven spawning runs during their lives (Ducharme 1969; Saunders and Schom 1985; Hutchings and Morris 1985), but with at-sea kelt survival <10% (Jonsson and Jonsson 2004), multiple returns is likely the exception rather than the rule.

It is unknown how recent changes to the Penobscot River (Opperman et al. 2011) may affect migration of naturally-spawned kelts from the upper reaches of the river, particularly because the downstream bypasses at all dams are closed for much of the winter, and thus may not be operational during the post-spawning period. Kelts outmigrating down the upper mainstem
Penobscot River must pass two dams to reach the middle portion of the river (upstream of the Marsh Island hydropower complex, and downstream of the Piscataquis River confluence (Figure 1)), while kelts moving through the Piscataquis River must pass three dams to reach the same location. Once reaching the confluence of the Piscataquis and Penobscot rivers, kelts may travel downstream via the main stem Penobscot River to the estuary (passing Milford Dam), or migrate through the Stillwater Branch of the river through Gilman Falls Dam, Stillwater Dam, and Orono Dam (Figure 3.1).
Figure 3.1. Map of the study area within the State of Maine. Black rectangles represent functioning hydroelectric dams that have no operable upstream fish passage from November 15 to April 15. Open rectangles represent water control dams that are passable under certain conditions. Gray triangles represent the location of stationary radio arrays, and the release sites are represented by circles. River kilometer zero is located at the southwest tip of Verona Island (516414E 4927755N, UTM Zone 19N).
The Penobscot River has been the focus of hatchery supplementation efforts based on sea-run broodstock since the late 1800s (Spidle et al. 2001). Current broodstock management practice dictates collection of mature adults from a trap at the terminus of the first fishway on the river (currently, Milford Dam) by the Maine Department of Marine Resources (MEDMR). These fish are transported to the USFWS Craig Brook National Fish Hatchery in Orland, ME, where they are held for up to five months before being artificially spawned in late October or early November. Following spawning, kelts are released into the Penobscot River just downstream of the head of tide (rkm 43.5). This release point is thought to minimize spatial and temporal overlap with naturally-spawning salmon and maximize survival by expediting return to the sea (Bartron et al. 2006), although neither of these assumptions have been tested. Because of record low returns in 2013 and 2014, an average of 56% (18-98%) of all salmon returning to the Penobscot has been taken to the hatchery as broodstock (USASAC 2015). Coinciding with decreased returns to the Penobscot River has been a reduction in the percentage of the run made up of repeat spawners from an average of 1.7% in the 1980s to an average of 0.6% in recent years (Maynard et al. 2017).

Although the absolute number of repeat spawners in the Penobscot River has been low for several decades, their contribution to the total number of eggs produced in the system was likely important, historically. A review of salmon egg production in New England from the early 1980s to 2011 indicates that, on average, repeat spawners produced 2,300 more eggs per female than virgin spawners in the Connecticut River, 3,000 more eggs/female in the Sheepscot River, and 3,100 more eggs/female in the Merrimack River (USASAC 2015). Similarly, research from the River Teno, Finland, found that although iteroparous Atlantic salmon numerically comprised an average of 5% of the run, they accounted for an average of 7% of the total mass of salmon.
caught in the river (Niemelä et al. 2006). In Pacific river systems, female, iteroparous Steelhead have lifetime reproductive success (LRS) 1.3 times higher than semelparous individuals, and iteroparous males have an LRS that is 2.8 times higher than semelparous individuals (Seamons and Quinn 2010), indicating that this life history strategy allows some salmonines to produce more offspring than semelparity would. Previously spawned individuals may also provide an important buffer against years with low escapement (Saunders and Schom 1985) because of their high fidelity to their natal rivers (Hansen and Jonsson 1994) and high reproductive potential.

Research on kelt movements and survival is relatively sparse, however, (Hubley et al. 2008), compared with literature on other life history stages of salmonines. This is especially true in the context of hatchery spawned individuals. Because nearly all kelts in the Penobscot River system are the product of artificial spawning at hatcheries (i.e. the fish are anesthetized and stripped of gametes prior to release), a better understanding of post-release movements may allow for targeted selection of release sites to match overwintering habitat needs, and thus improve survival to outmigration.

Our study goals were 1) to compare the post-release movement and exit timing of kelts released at two sites in the Penobscot River (~head of tide and upstream of the Marsh Island hydropower complex) and 2) to evaluate differences in outmigration success between fish released upstream of the hydropower complex and those released downstream, in the free-flowing estuary.

3.3 Methods

3.3.1 Study Area

The Penobscot River, Maine, USA, is the second largest watershed in New England (22,000 km²) and has been dammed in multiple locations since the late 1800s (Opperman et al. 2011). It
is also currently the largest remaining run of Atlantic salmon in the United States and is
dependent on hatchery stocking. Since the 1970s, an average of 82% of returning adult Atlantic
salmon have originated from hatchery smolts (USASAC 2015), and in recent years, the number
is > 95%.

Our study area (Figure 3.1) included a 66 km section of the Penobscot River from
Orrington, ME (rmk 33) to the West Enfield Dam (rmk 99) as well as a 67 km stretch of the
Piscataquis River from Howland Dam (rmk 98) to Brown’s Mill Dam (rmk 165). There are six
dams in the study area. Howland Dam has a newly constructed bypass channel that is operational
in the winter months. Stillwater Dam is impassable in an upstream direction, and the remaining
four dams (Orono, Milford, West Enfield, and Brown’s Mill) have upstream passage facilities
that are not operated between November 15 and April 15. Downstream passage facilities at
Stillwater Dam, Orono Dam, and Milford Dam are closed between December 31 and April 1
because of ice, but passage may still be possible via the spillways or when water overtops the
dams.

3.3.2 Fish Capture and Tagging
Throughout the 2015 upstream migration, adult Atlantic salmon were collected at the Milford
Dam lift and trap facility (rmk 61) by MEDMR personnel. Following collection, the fish were
transported to Craig Brook National Fish Hatchery, approximately 56 km south of the dam, on a
different river system. There, fish were held until fall spawning. During the spawning process,
fork length, mass, and sex were collected for each fish. We used the residuals of log(Mass)
regressed on log(Total Length) to calculate body condition (Halttunen et al. 2013). On
November 17, 2015, following several days of recovery from the artificial spawning procedure,
55 fish were anaesthetized using MS-222 and surgically implanted with model MCFT2-3L radio
transmitters (Lotek Wireless, Inc. Newmarket, Ontario). An incision was made offset from the ventral line and posterior to the pelvic fin girdle on the ventral side of the fish as close to the tag diameter as possible (16 mm) to enable closure with two or three size 4-0 vicryl sutures. Tags had an air mass of 25.0 g and a water mass of 11.0 g, ensuring that they were < 1% of the estimated body mass of the study fish, which ranged from 3.3 kg to 5.9 kg (median = 4.4 kg). Transmitters had a 2.5 second burst rate and a < 170 day tag life, due to their reuse from a previous study. Of the 55 fish, 27 were released at the Brewer boat launch (rkm 43.5, a 26 mile drive from the hatchery), just downstream of the head of tide, and 28 were released at the Passadumkeag boat launch (rkm 92, a 53 mile drive from the hatchery). All releases took place within five hours of surgery on November 17, 2015.

### 3.3.3 Radio Tracking

We monitored fish movements over a seven-month period from mid-November 2015 to mid-June 2016, primarily via mobile tracking with a portable receiver (Lotek SRX-800). These trips took place between Orrington (rkm 33) and Medway (rkm 149) on a weekly basis, with more frequent trips (two or three per week) before ice-in (late December) and after ice-out (late April). Once per month, mobile tracking occurred along the Piscataquis River to detect any fish that moved upstream through the Howland Dam bypass. All mobile tracking was conducted using cars with omnidirectional antennas traveling alongside the river on ME-116, U.S. Highway 2, and ME-178 at an average distance of 0.332 km (min 0.037 km, max 0.965 km), and an average speed of 40 mph. We also employed an array of three stationary receivers (Lotek SRX-DL) equipped with unidirectional Yagi antennas and located between Orrington (rkm 33) and Indian Island (rkm 62; Figure 3.1). One aerial survey with a mobile receiver was used to cover the
mainstem Penobscot River, the Penobscot estuary, and the Piscataquis River on January 25, 2016.

As a study using similar tagging methods found no tag loss in Atlantic salmon smolts (Stich et al. 2014), we assumed no tag loss, and fish that remained in the same position throughout the winter, spring, and into the summer of 2016 were presumed dead. We used $X^2$ tests to test for differences in survival, successful migration, and behavioral differences between the upper and lower release groups. Only fish that were detected at the most downstream receiver or fish that were detected in-river over the duration of the study were included in the survival analysis. Mann-Whitney-Wilcoxon tests were used to compare condition factor between groups of fish with different movements or survival outcomes. For the purposes of this study, we considered overwinter survival to take place between November – late April (ice-out); any movements after this were considered to take place during the spring, and we stopped tracking fish in early July 2016.

3.4 Results

We collected and tagged 55 fish from the hatchery, including 53 females and two males (Table 3.1). All fish were multi-seawinter (i.e. no grilse were tagged, limiting the number of males available for the project). Total lengths ranged from 720 mm to 850 mm (median = 770 mm). Fish masses ranged from 3.3 kg to 5.9 kg (median = 4.4 kg), and the body condition index ranged from -0.33 to 0.16 (median = 0.01).
Table 3.1. Kelt summary statistics. Minimum, median, and maximum values of total length (mm), mass (g), and body condition for kelts released at the upstream and downstream sites.

<table>
<thead>
<tr>
<th></th>
<th>Downstream</th>
<th></th>
<th></th>
<th>Upstream</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min</td>
<td>Med</td>
<td>Max</td>
<td>Min</td>
<td>Med</td>
<td>Max</td>
</tr>
<tr>
<td>Total Length</td>
<td>72</td>
<td>76</td>
<td>85</td>
<td>73</td>
<td>77</td>
<td>81</td>
</tr>
<tr>
<td>Mass</td>
<td>3900</td>
<td>4481</td>
<td>5901</td>
<td>3338</td>
<td>4454</td>
<td>5561</td>
</tr>
<tr>
<td>Body Condition</td>
<td>-0.03</td>
<td>0</td>
<td>0.13</td>
<td>-0.13</td>
<td>0</td>
<td>0.16</td>
</tr>
</tbody>
</table>

Of the 55 fish released, 30 were detected at least once on the stationary radio array, and 49 were detected at least once during mobile tracking. Only three fish were never detected. Over half of all fish (56%) were tracked for more than 100 days (median = 46 days). Based on detection histories (as described in the Methods section) 19 fish from the upstream release and 20 fish from the downstream were included in the survival analysis.

Broadly, movement could be classified into two major groups: overwintering in-system or rapid (within one month) downstream movement to the estuary (Figure 3.2). Most of the tagged kelts (n = 46) overwintered in the Penobscot River, and only six rapidly exited the system (Figure 3.3). Of the six that rapidly exited the system, four were initially released at the downriver site (rkm 43.5) and two were released at the upriver site (rkm 92). Many of the fish (n = 36) that remained in the river over the winter made directed upstream movements (Figure 3.4). Fish that overwintered in the system did so between rkm 33 and rkm 99, depending on where they were stocked (i.e. under most river conditions Milford Dam at rkm 61 impeded movement upstream). Of these, 15.4% of the fish were downstream of the head of tide (~rkm 48), 34.6% were between the head of tide and the first dam, and the remainder of our tagged fish (50%) overwintered between the first and second dams on the main stem of the river.
Figure 3.2. Representative tracks from four tagged kelts. Representative tracks from four tagged kelts with pie charts to show the proportion of fish that exhibited each behavior (gray = upstream release at rkm 92, black = downstream release at rkm 43.5). Panel A shows the track of a fish that overwintered in freshwater and then migrated to the estuary in the spring. Panel B shows an apparent overwinter mortality. Panel C shows a rapid outmigration following release, and Panel D shows an apparent initial mortality. River kilometer is on the y-axis, and time is on the x. The dotted lines represent the locations of hydroelectric dams on the main stem of the river. River kilometer 30 was our lowest antenna in the system, so detection at that point was considered successful outmigration.
Figure 3.3. Timing of outmigration. Timing of outmigration (in months since release) of kelts in the upriver (light gray, rkm 92) and downriver (dark gray, rkm 43.5) release groups.
Figure 3.4. Example tracks of kelts showing upstream movement. Example tracks of kelts showing upstream movement from both release sites in the first month after release. River kilometer is on the y-axis, and date is on the x-axis. The dotted lines represent dams located at rkm 61 and rkm 99 on the main stem of the river.

A total of 23 fish moved upstream to the next dam up from their release location. Of these fish, nine made repeated approaches to the dams over a period of days or weeks, indicating that the dams likely impeded their upstream movement. Apparent overwinter survival was below 50%, with 26 kelts presumed dead in the river system and an additional 16 fish with unknown fates (eight from each release group).
The apparent survival for kelts released upriver was 43%. The maximum distance the 28 upper release fish could have moved upstream was 7 km before reaching the West Enfield Dam. Further movement was possible into the Passadumkeag River for up to 17 km before reaching the Pumpkin Hill Dam, although due to the absence of roads, this area was not mobile tracked, except during our one flight. Thirteen fish moved upstream from the release site (eleven during the first month following release), and ten of those approached the dam. Half of the fish (14 / 28) released upstream moved downstream past the Milford Dam. Most fish that successfully passed the dam did so before March, with only one fish descending from the upper river in May. Four of the fish in this release group were documented leaving the system through the estuary, including two of those that initially moved upstream (Figure 3.3). Of the sixteen presumed mortalities in the upriver release group, six initially moved upstream, eight initially moved downstream, and two remained within 1 rkm of the release site, indicating no relationship between initial movement choice and survival. Six of the presumed mortalities occurred after the fish had moved downstream over the Milford Dam. For the purposes of these analyses, mortality and movement are not mutually exclusive (i.e. a fish that was counted as moving upstream could also be counted as a mortality).

The maximum distance that the 27 lower release fish could have moved upstream from the Brewer release point was 17.5 km before reaching Milford Dam. Twenty-three fish moved upstream from the release site; thirteen of those approached the dam, and one passed the dam during a period of extreme high water in mid-December 2015, when river discharges were more than twice the historic median (113-year time series). All upstream movements originating from the downriver release site took place before the end of January. Nine of these fish were eventually documented leaving the system, including five that initially moved upstream (Figure
An additional ten fish in this release group were presumed dead. Of these fish, six moved upstream initially, and three remained within 1 rkm of the release site.

A larger proportion of kelts released downstream were observed making directed upstream movements than those kelts released at the upstream location (85% vs. 46%, $X^2=7.498$, df=1, $P=0.006$). There was no difference in apparent survival to the estuary between the upstream and downstream release groups (14% and 33% respectively, $X^2=1.8084$, df=1, $P=0.179$). Apparent mortality over the course of the study and apparent initial mortality (fish that remained within 1 rkm of the release site for the duration of the study) were not different between the upstream and downstream groups (Table 3.2). There was no difference in body condition index between the fish that were documented successfully leaving the system, and fish that were presumed dead ($W=367$, $P=0.899$). There was also no difference in body condition index between the fish that made directed movements upstream and those that moved downstream ($W=343$, $P=0.566$).

Table 3.2. Kelt mortality. Presumed mortality of kelts released at the upstream and downstream sites. Fish presumed to be initial mortalities are those that remained within 1 km of their release site for the duration of the study. Fish presumed to be overwinter mortalities are those that remained at a fixed location in the river for several months, including the end of the study in late June 2016. Total presumed mortality includes both initial mortalities and overwinter mortalities. Mortality between the two release sites was compared using a chi-squared test.

<table>
<thead>
<tr>
<th>Mortality</th>
<th>Upstream (n = 28)</th>
<th>Downstream (n = 27)</th>
<th>$X^2$</th>
<th>df</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial</td>
<td>2 (0.071)</td>
<td>3 (0.111)</td>
<td>0.002</td>
<td>1</td>
<td>0.966</td>
</tr>
<tr>
<td>Overwinter</td>
<td>14 (0.500)</td>
<td>7 (0.259)</td>
<td>2.432</td>
<td>1</td>
<td>0.119</td>
</tr>
<tr>
<td>Total</td>
<td>16 (0.571)</td>
<td>10 (0.370)</td>
<td>1.496</td>
<td>1</td>
<td>0.221</td>
</tr>
</tbody>
</table>
3.5 Discussion

The results of this study suggest that the majority (88%) of kelts released into the Penobscot River overwinter in freshwater, regardless of where they are released. This finding is consistent with research from the River Teno, where about one third of individuals (35%) moved directly out to sea (Halttunen et al. 2010). Unlike Halttunen et al. (2013), we found no differences in condition factor between fish that emigrated quickly and fish that overwintered in the Penobscot River. However, our data set of outmigrating fish was considerably smaller (n=13 vs. n=166), entirely hatchery spawned, and entirely female.

Research from European rivers suggests that females are generally in better condition than males post-spawn, likely due to low instances of aggression between female fish (Halttunen et al. 2013). Because their condition is generally better post spawn, it may be more advantageous for females to remain in the low-productivity, low-risk freshwater environment through the winter (Halttunen et al. 2013), to keep risk of mortality low for those months, while males must enter the marine environment sooner to recondition. In our study, both males were presumed dead. Previous research has also documented low post-spawn survival among males, leading to a higher proportion of iteroparous fish being female (Niemelä et al. 2006; Halttunen et al. 2010). However, given that the sex-ratio of our study fish was so heavily skewed towards females, it is possible that our results are applicable only to female fish. With only two male fish (both released at the upriver release, and both mortalities) we were unable to capture the full range of male post-spawn behavior.

Unlike several other studies of kelt movements (Baglinière and Porcher 1994; Komandina-Douthwright et al. 1997; Cunjak et al. 1998), many fish in our study made directed, upstream movements following release. However, in our study, kelts were released downstream...
of where they would naturally spawn if not taken to the hatchery. This provides at least two possible reasons for why fish would move upstream: habitat conditions and complexity and life-history stage.

Further study is needed to clarify the causes of upstream movements, such as those we observed in hatchery-spawned kelts. One possible explanation for upstream movement centers on habitat availability. Estuarine habitat may be most desirable for kelts during severe winters (Cunjak et al. 1998) because of the absence of frazil ice in that area. However, the winter of 2015-16 was unusually mild, which may have contributed to kelts overwintering farther upstream in the watershed during our study. Additionally, studies in other systems (Saunders 1960; Komandina-Douthwright et al. 1997; Cunjak et al. 1998) have found that habitat complexity (e.g. lakes, large pools, islands, and other structure) was positively correlated with higher instream survival of post-spawn fish and higher usage of freshwater habitat instead of marine or estuarine. The first 38 rkm of the Penobscot River are commercially navigable, and relatively few islands (natural or artificial) exist downstream of rkm 48. In contrast, the reach between rkm 48 – rkm 61 is filled with artificial islands built for log drives as well as several large, natural islands. Therefore, for fish released at the downstream site, most of the complex habitat exists upriver of their release point. However, because the habitat between rkm 61 – rkm 99 is mostly complex, braided channel with many small islands, upstream migration would not be necessary for fish released at the upstream location to reach suitable overwintering habitat.

Another possible explanation for upstream migration following release is physiological. In our study, most of the fish in the lower release group and nearly half of the fish in the upper release group made directed movements upstream following release. However, other researchers have found that kelts move downstream after spawning (Baglinièare and Porcher 1994). Upstream
movements late in the spawning season, as documented here, have only been documented in fish that were still ripe (Komandina-Douthwright et al. 1997). Because all of the fish used in our study were artificially spawned in a hatchery, many still had gametes in the abdominal cavity when we surgically implanted tags. Physiological mechanisms to motivate upstream migration prior to spawning have been noted in previous studies (Bendall et al. 2012), so it is possible that our kelts were behaving more like ripe adults than post-spawn adults, given that gametes were still present. The majority (95.3%) of upstream movements in individuals from both release sites ceased within a month of release. Thus, without further knowledge of the physiology of each fish, it is difficult to determine a trigger for upstream movement.

Regardless of the mechanism behind upstream movement, the fact that kelts continue to move throughout the fall and early winter may be of concern to river managers. During this time of year, fish passage structures (in both upstream and downstream directions) are typically shut down to avoid damage from ice and debris (M. Simpson, Maine Dept. of Marine Resources, pers. comm.). Keeping these facilities operational in the winter may require substantial expenditures of effort and capital, but may also provide an opportunity for better survival outcomes, particularly for kelts moving in a downstream direction.

Due to the logistics of maintaining the receiver array, we were unable to place receivers on the Stillwater Branch of the river. Because of this gap in coverage, we were unable to determine what the predominant path choice around Marsh Island (rkm 56-63) was for fish outmigrating from the upriver release. In the future, securing access to sites along this portion of the river could help determine whether path choice around the island influences mortality in the lower river. Previous research on Atlantic salmon smolts has shown that downstream passage at hydroelectric facilities has delayed impacts on survival farther downriver (Stich et al. 2015).
Because path choice influences the number of dams passed (e.g. there is one dam on the east side of the island and three on the west, Figure 1), it may be also be linked to survival. Just as smolts are at risk of descaling, movement delays, and depredation at dams, these sites may also pose risks to downstream migrating kelts.

In both release groups, eight tags were lost to the radio network, and we were unable to ascertain their disposition. The lack of transmissions from these tags could be due to a number of factors. First and foremost, the tags were all repurposed from an earlier study of upstream migrating Atlantic salmon, so their batteries had already been depleted. Additionally, some tags may have been removed from the watershed either by poachers or wildlife (e.g. birds of prey). Finally, the most downstream receiver in the system covered a portion of the river that is inundated with salt water at high tide. Salt water can interfere with radio signals and likely reduced the probability of detection at that receiver during certain time periods.

Survival of kelts released to the Penobscot River was relatively low, compared with European rivers, which may contribute to the observed declines in the number of multi-spawn individuals in the population (Maynard et al. 2017). Apparent initial mortality (fish that remained within 1 km of release for the duration of the study) was < 15% in both release groups. There was no significant difference in apparent overwinter mortality between the groups. Apparent survival to outmigration was at least 23.6% (n = 13/55), which is considerably lower than documented survival to outmigration in the River Imsa (65-85%; Jonsson et al. 1990) in Norway and the Burrishoole River in Ireland (40%; Piggins 1990). Because 2015-16 was an unusually warm winter, an absence of ice cover on the river may have contributed to low survival, as kelts are known to use ice for refuge from aerial predators (Cunjak et al. 1998) such as bald eagles (Willson and Halupka 1995). Since the initiation of the Penobscot River Restoration Project, the
proportion of bald eagle diets made up of marine-derived nutrients has been increasing (Call 2015). Although survival to repeat spawning varies among river systems (2-25% Jonsson et al. 1991), multi-spawn returns to the Penobscot River averaged 0.04% in the past decade. This is below even reports from degraded rivers in France where multi-spawn individuals made up 0.5-3% of spawning runs (Bardonnet and Baglinière 2000).

The majority of kelts released into the Penobscot River overwintered in freshwater or the estuary rather than making a rapid exit to the marine environment. There was no measurable difference in migratory timing between fish released downstream of the head of tide vs. those released ~50 km upstream, and some fish stocked upstream were able to successfully migrate to the ocean through one or two hydroelectric facilities. Survival rates were comparable between the two release groups, but were lower than expected. Additionally, the majority of tagged fish exhibited directed, upstream movements more characteristic of ripe fish than spent fish. Survival and movement patterns may have been influenced by an unusually mild winter. Future research may benefit from a longer time-series of data as well as better quantification of the reproductive status of the fish. Additionally, this study documents the possibility of adult Atlantic salmon requiring passage both upstream and downstream at dams in the Penobscot River during time periods when these facilities traditionally are non-operational.
CHAPTER 4

4  FRESHWATER MOVEMENTS OF MIGRATING ADULT AMERICAN SHAD IN THE PENOBSCOT RIVER, MAINE FOLLOWING TWO DAM REMOVALS

4.1 Abstract

The American shad population in the Penobscot River, Maine, was decimated by damming in the early 1900s. However, an apparently small population persisted by using spawning areas below the most seaward dam. Through the Penobscot River Restoration Project a series of dam removals and passage redesigns at remaining dams in the system were designed to allow this population access to 93% of its historical habitat. We tagged and tracked 269 American shad over a three year period to understand their use of this newly available habitat. Scales were used to determine the spawning history and age of tracked fish. Few tagged fish moved upstream beyond known spawning areas in the lower river, and none of the fish that reached the first dam successfully passed it. However, several thousand untagged American shad passed the fishway in each year of the study. Of the tagged fish that approached the dam, most were virgin spawners, suggesting that repeat spawners may be less likely to overshoot known spawning grounds in search of new habitat. We discuss the potential implications of this project for the Penobscot River population of American shad and future research on fish passage in this system.

4.2 Introduction

American shad *Alosa sapidissima* are the largest, anadromous clupeid native to eastern North America, and they play an important role in coastal and riverine ecosystems throughout their range. Migrating adults provide an influx of marine-derived nutrients to freshwater systems (Garman and Macko 1998; MacAvoy et al. 2000), and recently hatched juveniles are food for other game fishes including Bluefish *Pomatomus saltatrix* and Striped Bass *Morone saxatilis*
In the Northeastern United States, American shad spawning runs historically brought adult fish as far inland as Millinocket, Maine (174 river kilometers; rkm), Bellows Falls, Vermont (204 rkm), and Binghamton, New York (513 rkm). These migrations supported large, commercial fisheries on many east coast rivers until the late 1800s (Stevenson 1896). However, the construction of cross-river dams in the late 1800s and early 1900s drastically reduced the availability of spawning habitat throughout their range (Buchsbaum et al. 2005).

The Penobscot River (Maine, USA) supported a large commercial fishery for American shad, with annual landings of up to two million fish (Foster and Atkins 1869; Saunders et al. 2006) prior to the construction of mainstem dams at Bangor (rkm 41.5) and Veazie (rkm 48). By 1900, the species was considered “commercially extinct” (Vickers 2004), and by 1950, the U.S. Fish and Wildlife Service classified the Penobscot River as “a former shad stream” (Taylor 1951), attributing the absence of the species solely to dam construction. The Bangor Dam was abandoned and naturally breached during the mid-1970s, leaving the Veazie Dam with its vertical slot fishway as the most downstream obstacle for migrating American shad over the last several decades.

Constructing fishways that American shad will reliably use has historically been difficult (Stevenson 1896; Barry and Kynard 1986; Sprankle 2005; Haro and Castro-Santos 2012; Grote et al. 2014b). This challenge is likely due to American shad avoidance of slight changes in shadows, turbulence, and entrained air (Haro and Castro-Santos 2012), coupled with their reluctance to use submerged orifices or leap over obstacles (Pess et al. 2014). The fishway at Veazie Dam was no exception (Haro et al. 1999), passing an average of one shad per year from 1978 to 2013 (Mitch Simpson, Maine Dept. of Marine Resources pers. comm.), leaving it unclear
if passage was extremely poor, or if the fish were absent. However, large aggregations of American shad were documented below the Veazie Dam in 2011 and 2012 using DIDSON and electrofishing surveys (Grote et al. 2014a, 2014b), and spawning was documented in the reach upstream of the former Bangor Dam (Grote et al. 2014a), indicating that the Penobscot River population was potentially not as small as previously believed. Throughout that time, the existing population was limited to ~6.5 rkm of suitable spawning habitat between the former Bangor Dam and the head of tide at Veazie Dam.

In 2013-14, as part of the Penobscot River Restoration Project, Veazie Dam and Great Works Dam (rmk 59) were removed, and a new fish lift was constructed at Milford Dam (rmk 61), which is now the most seaward dam on the Penobscot River. If passage through the new fish lift at Milford Dam is effective, American shad would have access to 93% of their historic spawning habitat in the Penobscot River (Opperman et al. 2011). However, several factors could influence the success of this restoration effort. To reach Milford Dam, American shad must navigate through a series of obstacles that represent potential delays in migration, including the remnants of the Veazie and Great Works Dams, as well as the confluence of the Stillwater Branch (rmk 53) with the mainstem Penobscot River (Izzo et al. 2016). The Stillwater Branch’s mouth is blocked by the Orono Dam, and no volitional upstream passage is provided at that site. Additionally, as documented by Grote et al. (2014a), some amount of spawning habitat is available below the former site of the Veazie Dam.

It is unclear what encourages fish with access to newly available stretches of river to expand into previously inaccessible habitat. The density of adult American shad present on the spawning grounds may play a role in determining whether fish move upstream or not. If the existing spawning habitat is not fully saturated, fish may be less likely to continue moving
upstream (Huntsman et al. 2017). Additionally, the presence of residual structures from the dams and resulting areas of altered flow may impede American shad movements (Raabe and Hightower 2014).

Another unknown is whether these fish would be able to effectively use the habitat, given the (less severe) impediments that remain. Restoration of upstream passage can be a double-edged sword (Castro-Santos and Letcher 2010), as it increases both spawning opportunities and energy expenditures (Burdick and Hightower 2006), potentially resulting a reduction in iteroparity. Downstream passage through hydroelectric dams may cause descaling (McComas et al. 2010) and disorientation (Dawley et al. 1993), both of which can contribute to migrant mortality (Amaral 2001). Few changes were made to downstream passage throughout the Penobscot River for adult American shad; currently downstream passage is accomplished primarily via log sluices, and outmigrating American shad that ascend the Milford Dam fishway will encounter 1 to 3 dams on their return to the sea, depending on path choice.

Given the presence of a spawning population of American shad that may have been habitat-limited and previous research documenting habitat use in the available reach (Grote et al. 2014a), the Penobscot River Restoration Project provides a unique opportunity to observe American shad response to increased habitat access. The goals of this study were to assess American shad movement patterns in the newly accessible stretch of river between the Veazie Dam remnants (rkm 48) and the Milford Dam fish lift (rkm 61). Additionally, we hoped to characterize the effectiveness of the new fish lift at Milford Dam for passing American shad.

4.3 Methods

Our study area (Figure 4.1) included the lower portion of the Penobscot River from Verona Island (rkm 0) to the Milford Dam (rkm 61). From Verona Island to the City of Bangor (rkm 41),
the river is characterized by a deep channel with a silty bottom that experiences tidal changes of over 8 m. The stretch of river between Bangor and the former site of the Veazie Dam contains a series of ledge outcroppings and rapids at low tide that are inundated and become flatwater at high tide. A natural fall line at the former Veazie Dam site blocks any tidal influence upstream of that point. From Veazie to the Milford Dam, the river is characterized by stretches of fast, shallow water (depth < 3 m) broken up by four large rapids. Milford Dam is a 6 m high concrete dam with an additional 1.4 m of flashboards installed seasonally. The station has a generating capacity of 8 MW. For the past five decades, fish passage was provided by a 229 m Denil fishway with a 12.5% slope. In 2014, a new fish lift opened on the eastern shore of the river, and the Denil fishway was decommissioned. The entrance to the lift is a 3.05 m wide 180° turn. Water to increase attraction flow is pumped into the entrance via grates in the floor of the 180° turn. After entering and navigating the turn, migrating fish pass through a V-shaped gate that traps them in a hopper, which is lifted and emptied every 20-30 minutes from 0400 h to 2200 h between mid-April and mid-November. After exiting the hopper, fish transit a concrete flume through the base of the powerhouse. To exit the flume into the river, fish must pass through a series of hydraulic gates (used to sort fish for broodstock programs and invasive species management) or be lifted into a second hopper and passed through a steep chute from the sorting deck into the headpond.
Figure 4.1. Map of study reach inset from State of Maine. Stationary receivers are represented by black triangles (radio receivers) or Xs (acoustic receivers). Dams are indicated by black rectangles (hydroelectric dams), open rectangles (water control dams), or open ellipses (removed dams / dam remnants).
4.3.1 Capture and Tagging

To evaluate American shad movement patterns, we used gastrically inserted radio transmitters (Lotek Wireless Inc. Newmarket, Ontario, Canada) and acoustic transmitters (Vemco, Bedford, Nova Scotia Canada). Adult American shad were captured via boat electrofishing (Model MBS, ETS Electrofishing LLC., Madison, WI) at the Bangor Dam remnants (n = 20) or Eddington Bend (rkm 47; n = 245). A small number (n = 4) of American shad were captured via angling in the Milford Dam tailrace. Each year from 2015-2017, sampling began within two weeks of the first American shad arriving at the Milford Dam fishway and continued until all available tags were deployed. Tidal cycles constrained sampling efforts below rkm 48, so all electrofishing was conducted within three hours of high tide at Bangor (~4.25 m; NOAA 2017). Fish were stunned, netted, and allowed to briefly recover in an aerated livewell filled with river water at ambient temperature. Each fish was gastrically tagged using a plastic straw following the methods of Bailey et al. (2004) and Grote et al. (2014a). Radio antennas were left trailing out of the fish’s mouths (Hightower and Sparks 2003). After tagging, we collected scales and measured each individual’s fork length. No more than five fish were held in the aerated livewell at any time, and the handling time for each fish was < 60 seconds. When the livewell was emptied of fish (i.e. following tagging of 1 to 5 individuals), the livewell water was discharged into the river and replaced. As long as fish could actively swim and were not exhibiting reflex impairment, they were released immediately within 300 m of their original capture location.

In 2015-2016, all tagged individuals received a Lotek MST-820 coded transmitter (8 mm x 20 mm, 2.1 g) operating between 148-152 MHz. In an effort to increase the detectability of tags, larger radio tags with a stronger signal output (+10 dB) were used in 2017. In that year, 69
individuals were tagged with Lotek MST-930 coded transmitters (9.5 mm x 26 mm, 4 g). Radio transmitters in all years were programmed with a 2.5 second burst rate. In 2015 and 2016, five frequencies were used (no more than 20 fish per frequency), and in 2017, three frequencies were used (23 fish per frequency). In 2017, 30 additional fish were gastrically tagged with VEMCO V9 acoustic transmitters (9 mm x 21 mm, 1.6 g) operating at 69 kHz. All tag sizes were within the range of sizes used in similar studies of American shad movements (Bailey et al. 2004; Grote et al. 2014a) and were less than 1% of the estimated body weight for all individuals (Wigley et al. 2003).

4.3.2 Telemetry / Tracking

Radio-tagged American shad were tracked on an array of stationary receivers (Lotek models SRX400, SRX800, or SRX-DL) positioned between rkm 24 and rkm 62 (Figure 4.1). In 2015, there was one receiver at Eddington Bend (where the majority of fish were tagged), four receivers upstream of Eddington, and one receiver downstream. In 2016, the number of downstream receivers was increased from one to three, and in 2017, the number of upstream receivers increased from four to five and the number of downstream receivers increased from three to four. When fish were detected, stationary radio receivers recorded a timestamp, the unique frequency / code combination of the transmitter, and the strength of the radio signal.

The range of stationary receivers was tested using a GPS and radio transmitter attached to a remote controlled boat. The radio transmitter was attached to the boat by a 1 m line and was driven past the receivers at different distances, and we calculated the proportion of expected pings per minute (based on burst rate) that were recorded by the receiver. Detection rates averaged 0.63 within 200 m of the receivers (range 0.31 – 0.97, median 0.67), decreasing to an average of 0.4 between 200 – 250 m (range 0.31-0.52, median 0.43).
Radio-tagged fish were also actively tracked twice per week using a car-mounted Lotek SRX800 with an omnidirectional antenna traveling in a loop around the lower river. The driving loop traveled along U.S. Highway 2 and ME-178 at an average distance of 0.332 km from the mid-point of the river (range 0.037 – 0.965 km) and an average speed of 64.4 kmph. Each year, these radio tracking trips occurred from the time of the first tagging until the middle of September. Fish were also opportunistically tracked by boat during sampling events for other research projects. Acoustically tagged fish in 2017 were exclusively tracked on a stationary array of VEMCO VR2-W receivers positioned from rkm 13.1 to rkm 99. Acoustic receivers were omnidirectional and typically have a minimum detection range of 500 m in this system (Holbrook et al. 2009).

4.3.3 Defining Behavior

We used several rules to interpret detection data. Tags were assumed to be regurgitated or mortalities if they were continuously relocated within the same river kilometer for over two weeks and were not subsequently detected at any other station. We counted any fish that made a directed downstream movement of > 5 rkm from the tagging site in the 36 hour period following tagging as a “fallback” (Shrimpton et al. 2001; Grote et al. 2014a). Outside of this window, movements were assumed to be unimpaired by tagging. False detections by radio receivers were defined as when multiple detections occurred within a short time frame over an unrealistically wide geographic area (e.g., 10 detections between 1100h and 1130h over a 30 km distance) or only one ping was detected in a five minute period. These points were considered unresolvable for the purposes of data analysis if no other temporally relevant data was available to assist in determining the likely location of the fish.
4.3.4 **Age Estimation**

At least three scales were collected from the left side of each fish, medial and slightly posterior to the dorsal fin. All scales for an individual fish were cleaned with deionized H₂O and mounted on a single microscope slide prior to review on an electronic microfiche reader. Two experienced readers reviewed scales following the methods of Elzey et al. (2014) to estimate ages and spawning history. When differences in estimates occurred, scales were reread to reach consensus on age and spawning marks.

4.3.5 **Milford Dam**

Biologists from the Maine Department of Marine Resources operate a counting and sorting facility at the Milford Dam fish lift. Daily tallies from this facility were used to compare the run timing at the most-seaward mainstem dam to the timing of tagging in the lower river. Additionally, all mortalities from this facility that could be safely collected were collected by employees of Brookfield Renewable Energy and measured to provide a sample of the size distribution of fish approaching the dam.

4.3.6 **Analyses**

We used a Kruskal-Wallis test to compare date distributions of fish tagged each year, two-sided Fisher’s exact tests with the Freeman-Halton extension (Freeman and Halton 1951) to compare binomial proportions among years (e.g., fallbacks, stationary tags), and a Wilcoxon rank sum test to compare length distributions of fish sampled at different locations (tagging site vs. Milford Dam fishway) within year. Fork lengths and estimated ages were compared across years using ANOVA. All statistical tests used an α value of 0.05 and were conducted using the R Project for Statistical Computing (R Core Team 2012).
4.4 Results

During the project, we tagged 269 American shad (Table 4.1), 479 mortalities were recovered from Milford Dam, and 13,536 American shad successfully used the fish lift at Milford Dam. As would be expected given our sampling design, in all three years, the distribution of tagging dates was earlier than the distribution of fish tallied at Milford Dam (Table 4.2). The mean fork length of fish captured over the course of the study was 41.9 cm (SD = 3.3 cm) and did not differ ($F_{1, 246} = 0.46, P = 0.498$) between years (Table 4.1). In 2015, the fork length of American shad mortalities at Milford Dam was less than the fork length of fish tagged in our study (Table 4.3). In 2016 and 2017, there was no difference in fork lengths between fish captured in our study and mortalities recovered from Milford Dam.

Table 4.1 Shad summary statistics. Summary statistics for distributions of fork lengths of fish sampled each year. Residence time was calculated as the number of days between tagging and final detection at the lowermost receiver that the fish was detected on. Only fish that were successfully detected more than twice were included in the residence time calculation. Tags that were assigned to the Stationary column were assumed to be regurgitated or mortalities based on continuous detection at one location and no subsequent detections at other locations. Stationary tags were not included in the residence time calculations.

<table>
<thead>
<tr>
<th>Year</th>
<th>n Fish</th>
<th>Mean FL (cm)</th>
<th>Std. Dev. FL (cm)</th>
<th>Mean Res. Time (d)</th>
<th>Std. Dev. Res. Time (d)</th>
<th>Stationary</th>
</tr>
</thead>
<tbody>
<tr>
<td>2015</td>
<td>71</td>
<td>42.5</td>
<td>3.5</td>
<td>5.7</td>
<td>5.6</td>
<td>0</td>
</tr>
<tr>
<td>2016</td>
<td>99</td>
<td>41.2</td>
<td>3.3</td>
<td>19.1</td>
<td>15.2</td>
<td>3</td>
</tr>
<tr>
<td>2017</td>
<td>99</td>
<td>42.1</td>
<td>2.9</td>
<td>18.1</td>
<td>12.0</td>
<td>17</td>
</tr>
</tbody>
</table>

Table 4.2. Shad tagging summary. Sample sizes and Kruskal-Wallis test statistics comparing the distribution of tagging dates and average tagging date for study fish to the distribution and average approach date of American shad passed through the Milford Dam fish lift each year. Our goal was to sample earlier in the season to allow fish time to migrate upstream. In all three years, the distribution of tagging days skewed earlier than the distribution of passing days at the fish lift.

<table>
<thead>
<tr>
<th>Year</th>
<th>Tagged</th>
<th>Counted</th>
<th>$X^2$</th>
<th>df</th>
<th>p</th>
<th>Days Earlier</th>
</tr>
</thead>
<tbody>
<tr>
<td>2015</td>
<td>71</td>
<td>1806</td>
<td>15.925</td>
<td>1</td>
<td>&lt; 0.001</td>
<td>5</td>
</tr>
<tr>
<td>2016</td>
<td>99</td>
<td>7862</td>
<td>217.83</td>
<td>1</td>
<td>&lt; 0.001</td>
<td>14</td>
</tr>
<tr>
<td>2017</td>
<td>99</td>
<td>3868</td>
<td>292.38</td>
<td>1</td>
<td>&lt; 0.001</td>
<td>16</td>
</tr>
</tbody>
</table>
Table 4.3. Shad mortality summary. Sample size, mean (cm), range, and Kruskal-Wallis test statistics comparing the distribution of sizes for study fish to the distribution of sizes of American shad mortalities at Milford Dam.

<table>
<thead>
<tr>
<th>Year</th>
<th>Tagged n</th>
<th>Tagged Mean</th>
<th>Tagged Range</th>
<th>Mortalities n</th>
<th>Mortalities Mean</th>
<th>Mortalities Range</th>
<th>$X^2$</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>2015</td>
<td>71</td>
<td>42.5</td>
<td>36 – 51</td>
<td>104</td>
<td>41.1</td>
<td>34 – 50</td>
<td>5.034</td>
<td>1</td>
<td>0.025</td>
</tr>
<tr>
<td>2016</td>
<td>99</td>
<td>41.2</td>
<td>35 – 49</td>
<td>282</td>
<td>41.3</td>
<td>31 – 53</td>
<td>0.338</td>
<td>1</td>
<td>0.561</td>
</tr>
<tr>
<td>2017</td>
<td>99</td>
<td>42.1</td>
<td>35 – 49</td>
<td>88</td>
<td>42.5</td>
<td>33 – 51</td>
<td>1.107</td>
<td>1</td>
<td>0.293</td>
</tr>
</tbody>
</table>

Figure 4.2. Length-frequency histogram of shad sampled in each of three study years.
In 2015, we were only able to successfully track 20% (n = 14) of the tagged fish for between 1 – 16 days post tagging. This low percentage was likely due to the limited number of receivers located downstream of the release site. No fish were believed to be lost due to regurgitation or tagging mortality. The remaining 80% of fish were detected fewer than two times post-tagging or had a substantial number of unresolvable false detections. In 2016, we successfully tracked 80% (n = 79) of our tagged fish for between 1 – 50 days post tagging. In 2017, 68% (n = 67) of tagged fish were tracked for between 1 – 42 days post tagging. The proportion of fish with stationary tags vs. moving tags was higher (P = 0.001) in 2017 (17:67) than in 2016 (3:78) or 2015 (0:16). There was no difference in fork length between fish that were stationary and fish that moved (X^2 = 0.025, df = 1, P = 0.873). Mean residence time for non-stationary fish was lowest in 2015 (5.7 days), but was nearly three weeks in 2016 (19.1 days) and 2017 (18.1 days; Table 4.1).

Of the 169 fish we were able to successfully track, we observed 43.7% (n = 74) exhibiting fallback behavior likely associated with tagging. There was no difference (P = 0.449) in the proportion of fish exhibiting fallback behavior between 2015 (9:7), 2016 (32:46), and 2017 (33:34). Fish that fell back were similar in size to fish that held position or moved up (X^2 = 3.508, df = 1, P = 0.061). Of the fish that fell back, 31.1% (n = 23) made upriver movements following fallback. About half (n = 13) of the fish that reascended the river reached their original capture location, and four fish moved upstream of the capture location after falling back to the estuary. None of the fish that fell back approached Milford Dam over the course of the study.

Of the fish that were tagged in the lower river and did not fall back (n = 95), only 3.2% (n = 3) approached the Milford Dam fish lift at rkm 61. None of these fish were detected upstream of the dam. Two were detected moving back downstream, while the other was not detected at all
after being logged on the dam receivers. Both fish that were detected moving back downstream were repeat spawners, while the third fish was a virgin spawner. All three fish that were tagged in the lower river and later approached the dam were tagged in 2017. Two were 4 years old, and one was 5 years old. Over the course of the study, 28 American shad were observed spending multiple (> 5) days between rkm 40 and rkm 50, just downstream of the tagging area, sometimes returning to the estuary for several days before reascending the river to between 40 rkm and 50 rkm (Figure 4.3). Additionally, some of the acoustically-tagged shad were observed traveling through the estuary timed with tidal movements in the river.
Figure 4.3. Representative example tracks of several behaviors observed during this study and the percentage of fish exhibiting them. Time is on the x-axis and river kilometer is on the y-axis. Very few (1.8%) successfully tracked fish moved upriver and approached the Milford Dam (A). 16.6% of successfully tracked fish spent several days between rkm 40 and 50, a known spawning area for American shad in the Penobscot River (B). Just under one third of successfully tracked fish exited the system rapidly (C), exhibiting fallback behavior that is common among tagged clupeids. 7.4% of all tagged fish either regurgitated the tags or were counted as a “stationary” fish because they were detected in the exact, same location for several weeks (D).

To document shad behavior in the tailrace of Milford Dam, we angled and tagged four fish there in 2016. All four fish were virgin spawners and ranged in age from 3 to 5 years. Two of these fish fell back. One fallback returned to Milford Dam and spent eight days in the tailrace before turning back downstream. Of the two American shad that did not fall back, one remained in the tailrace for three days before traveling to the lower river. It later returned to the tailrace for
two additional days then moved downstream again. The other fish was detected moving in and out of the tailrace for two days post-tagging, but was not subsequently detected.

Age estimates derived from scales ranged from 3 to 6 years old, with most fish (53.8%) estimated to be four years old (Table 4.4). There was no significant difference in age distributions between years ($F_{1, 246} = 0.41, P = 0.52$). The mean age in all three years was between 3.9 and 4.1 years old. The number of spawning checks identified on scales from tagged fish ranged from 0 to 2 (Table 4.4), with most fish (52.6%) estimated to have spawned once before. There was no significant difference in the number of repeat spawners (virgin vs. repeat) among years ($F_{1, 246} = 1.47, P = 0.23$), and the mean number of spawning checks for all fish was 0.61 (SD = 0.57).

Table 4.4. Shad ages and spawning history. Number of American shad tagged each year in each estimated age and number of repeat spawning events category denoted as “Age / Spawning Events”.

<table>
<thead>
<tr>
<th>Age / Spawning Events</th>
<th>2015</th>
<th>2016</th>
<th>2017</th>
</tr>
</thead>
<tbody>
<tr>
<td>3/0</td>
<td>13</td>
<td>24</td>
<td>14</td>
</tr>
<tr>
<td>3/1</td>
<td>1</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>4/0</td>
<td>12</td>
<td>24</td>
<td>16</td>
</tr>
<tr>
<td>4/1</td>
<td>19</td>
<td>24</td>
<td>38</td>
</tr>
<tr>
<td>5/0</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>5/1</td>
<td>7</td>
<td>11</td>
<td>21</td>
</tr>
<tr>
<td>5/2</td>
<td>1</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>6/1</td>
<td>3</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>6/2</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

4.5 Discussion

Of the 265 American shad tagged in the lower river, only three migrated far enough upstream to encounter Milford Dam and the new fish lift facility following tagging. Such a low number of upstream migrants seems contradictory to the statements that 1) the population of American shad in the Penobscot River was characterized as containing “a few hundred
individuals” as recently as 2011 (Opperman et al. 2011), and 2) between 1,800 and 7,800 American shad passed through the Milford Dam fish lift annually over the course of our study (J. Valliere, Maine Dept. of Marine Resources, _pers. comm._). The obvious question is – why did so few tagged fish reach the dam? We propose four possible explanations – i) The fish we tagged were not motivated to move upstream due to some intrinsic factor. ii) Our handling process may have prevented fish from moving upriver, a common problem in other studies of American shad (Chittenden Jr. 1973; Leonard and McCormick 1999; Shrimpton et al. 2001; Bailey et al. 2004). iii) Sufficient spawning habitat exists in the lower portion of the Penobscot River that upstream migrations were not necessary for fish arriving earlier in the run. iv) All fish returning to the river during the study period were spawned in the river prior to dam removals, and a majority of them (58%) had spawned in previous years in impounded sections of the river. So, these fish may have been homing back to spawning sites or natal reaches. We consider each of these explanations below.

Given that our sampling took place in the earlier portion of the Penobscot River shad migration each year, it is possible that we did not adequately capture the variability in the run (e.g. the full range of ages, sizes, and spawning histories). In many species of anadromous fish, certain demographic groups tend to enter rivers earlier than others. For example, in some populations of Atlantic salmon _Salmo salar_, age determines migratory timing (Jonsson et al. 1990). Similarly, Hightower and Sparks (2003) found American shad that migrated the farthest upriver in a dammed system were generally repeat spawners, while those that remained lower in the river were virgin spawners.

Few of our study fish approached the dam, and combined with the collection of mortalities from the fishway, no clear picture emerges. There were no clear differences in size
between years or between fish we tagged and fish that died at the fish lift with the exception of 2015, when dam mortalities were slightly smaller than tagged fish. In 2016, all four fish that approached the dam had been angled and tagged in the tailrace. These fish were all virgin spawners. In 2017, however, the fish that approached the dam were all tagged in the lower river. Two of these fish were repeat spawners, and one was a virgin spawner. Given the low sample sizes, it is difficult to draw any meaningful inferences from these results, but the proportion of virgin spawners to repeat spawners between the two years approaching the dam (5:2) vs. the overall sample of fish tagged during the study (107:141) suggests that virgin spawners may be more likely to move farther upstream than repeat spawners in this system. Because all of our study fish hatched when Veazie Dam was still present in the river, in order to reach Milford Dam they would need to “overshoot” their natal spawning grounds. Overshoot has been documented in other species of migratory fish, and depending on the river system may include 1 – 75% of available spawners (Keefer et al. 2008). Given their previous success in spawning below rkm 48, repeat spawners may have had little motivation to continue moving upstream. More rigorous scale sampling of fish approaching Milford Dam may provide additional insight into this trend.

It is also possible that the process of handling and tagging fish may have influenced their behavior. Migration is a metabolically demanding behavior for American shad (Leonard and McCormick 1999; Shrimpton et al. 2001). Handling fish results in an increase in stress (Heisey et al. 1992). Migrating clupeids generally, and American shad in particular, are notorious for displaying fallback behavior following tagging (Frank et al. 2009). This behavior may be a response to stress that enables fish to return to saltwater quickly. A return to saltwater may be beneficial to the fish, as cortisol levels reach higher peaks in freshwater and decline faster in saltwater (Shrimpton et al. 2001). Additionally, the return to saltwater relieves the additional
osmotic burden created by transitioning from a saltwater environment to a freshwater environment. As noted in many studies of American shad movement (Hightower and Sparks 2003; Bailey et al. 2004; Frank et al. 2009; Grote et al. 2014a), fallback behavior associated with stress can make movement analysis problematic. We followed the definition of Grote et al. (2014a) and attributed any downstream movement within 48 h of tagging to handling stress. Using this definition, our incidence of fallback was just below 44% across the entirety of the study. This is lower than rates of fallback reported in similar studies (Bailey et al. 2004; Grote et al. 2014a). Although Grote et al. (2014a) did not document upstream migration of tagged fish, that finding was likely due to poor passage performance of the Veazie Dam fishway (< 1 shad per year successfully passed from 1979 – 2015), not handling effects. However, Bailey et al. (2004) was able to successfully document upstream movement of fish, despite rates of fallback that were similar to our study. It is important to note that definitions of fallback vary (Frank et al. 2009), so our proportion of fallbacks is not directly comparable with many other studies of American shad migration. The lower proportion of fallbacks compared with Grote et al. (2014a) in the same system, using the same definition of fallback indicates that we were likely not influencing American shad behavior in a way that would preclude fish from moving up the river, as both studies documented over half of all tagged fish maintaining position or moving upstream post-tagging.

Our incidence of “stationary” tags, likely caused by mortality or regurgitation (7.5%) was similar to the value (9%) reported by Grote et al. (2014a), and lower than the value (13.6%) reported by Bailey et al. (2004). Our tagging methods and handling times were based on the work of Grote et al. (2014a) and Bailey et al. (2004), and total handling time averaged under one minute per fish. Given this information and the fact that our tags were well within the range of
external dimensions and masses used in similar studies, it seems unlikely that handling stress and fallback behavior could be the primary cause of most tagged fish not moving upstream.

Prior to the Penobscot River Restoration Project, it is unlikely that sufficient spawning habitat existed below the most downstream dams in the Penobscot River for the American shad population to grow to historic levels. However, NOAA surveys documented the presence of juvenile American shad in the Penobscot River estuary before the removal of the Veazie Dam (Lipsky et al. 2016), which should not be surprising, given the range of habitats that American shad can use for spawning. A coast-wide assessment of American shad from the 1960s indicates that shad can spawn over multiple bottom types throughout a range of depths (Walburg and Nichols 1967). More recent research suggests that American shad prefer wide, shallow, mid-river sections with moderate current for spawning (Ross and Bennet 1993). Furthermore, large sediment size and high incidences of overhang and large woody debris correlate well with American shad egg deposition (Bilkovic et al. 2002) and a wide range of water column velocities are suitable for spawning (Hightower and Sparks 2003).

Of the fish in this study that were successfully tracked and did not fall back, 29.5% spent longer than five days between rkm 40 and rkm 50. This portion of the river marks a transition zone from the deep, muddy estuary to shallower habitat with larger substrate (Haefner Jr. 1967). This area of river is also characterized by a wide range of flows including a steep section near the former Veazie Dam site (rm 50) and a gentler gradient farther downstream. Throughout, the flow is punctuated by rocky ledges and artificial islands left over from log drives. In 2015 and 2016, American shad spawning behavior was observed throughout this stretch of river during sampling as part of a concurrent project assessing sturgeon migrations (Johnston 2016).
If the population is truly recovering from a much smaller, remnant population of American shad, it is possible that spawning habitat in the lower river has not been saturated yet, so fish are less motivated to continue moving upstream. Density dependent migration has been documented in other fish species such as Chinook salmon *Oncorhynchus tshawytscha* (Huntsman et al. 2017), but such density dependence may require more territorial spawning behavior than that associated with American shad. Research from both the Connecticut River (Leggett 1977) and the Columbia River (Hinrichsen et al. 2013) suggest that upstream migration of American shad may also be strongly influenced by environmental conditions, such as water temperature and flow. However, the Connecticut River research also suggests that extremely high densities of American shad spawning (such as those levels seen below dams without adequate fish passage) may cause significant reduction in juvenile growth and survival, irrespective of temperature or flow. Thus, spawning at low densities may confer a selective advantage to an individual’s offspring.

Unlike Grote et al. (2014a), we did not document any spawning fish older than age 6. Additionally, the average number of spawning checks was substantially lower (0.61, SD = 0.57) in our study than in Grote et al. (2.2, SD = 1). The difference in ages could be due to a change in methodology (e.g. if Grote et al. over-estimated ages or we under-estimated ages). However, the age difference would not likely impact the number of spawning checks observed. The decline in the average number of spawning checks may be indicative of age truncation and reduction in the number of lifetime spawning events for the Penobscot River population, or could represent an increase in the proportion of the run made up of virgin spawners (perhaps due to strong year classes post-dam-removal). The mechanisms behind such a change are not determinable based on our data; however, as described by Castro-Santos and Letcher (2010), increasing upstream
passage success may be a double-edged sword for American shad if careful consideration is not paid to downstream passage. If the population is habitat limited, increasing upstream passage and providing additional habitat will likely increase the number of fish spawned each year (Stich et al. 2018). However, if downstream passage is not upgraded simultaneously, spawning fish above the remaining obstacles may find their downstream migration delayed. Since American shad do not feed during their spawning migration (Leggett 1972), such delays can cause fatal losses of energy reserves, removing those fish from the subsequent year’s spawning class. Further research into survival to outmigration of American shad in the Penobscot River system may elucidate whether mortality-inducing delays during downstream migration are cause for concern.

We were able to document behavior patterns similar to those observed before the removal of Veazie Dam such as tidally influenced migratory movements in the lower river and potential spawning behavior at sites first documented by Grote et al. (2014a). Whatever their reason for not moving upstream, this study was unable the characterize the upstream passage efficiency of the Milford Dam fish lift for American shad, which is vitally important to understanding the potential for American shad restoration in the Penobscot River. Future research into passage at this location may require tagging fish closer to the dam to ensure that they are motivated to move upstream beyond the known lower-river spawning area and / or tagging fish at the dam to assess their movement upstream of the fish lift. Additionally, a better understanding of the population size of American shad in the Penobscot River may assist in determining what proportion of the spawning population even approaches the fishway. Finally, further investigation of downstream passage success may provide insight into the potential for age and iteroparity truncation in this population of American shad.
WORKS CITED


Begley, M. A. 2016. Understanding the impact of commercial harvest on white suckers (Catostomus commersonii) in Maine. M.S., University of Maine, Orono, ME.


Buck, D. 1838. Petition of the inhabitants of Bucksport.


Call, E. 2015. River birds as indicators of change in riverine ecosystems. The University of Maine, Orono, ME.


Foster, N. W., and C. G. Atkins. 1869. Second report of the Commissioners of Fisheries of the State of Maine. Maine Department of Inland Fisheries and Wildlife, 35, Augusta, ME.


Katopodis, C. 1992. Introduction to fishway design. Fisheries and Oceans Canada, Winnipeg, MB.


Microsoft. 2010. Excel. Microsoft, Redmond, WA.


Rutter, C. 1903. Natural history of the Quinnat salmon.


APPENDIX A: INDIVIDUAL-BASED MODEL CODE “HEADER.R”

The following code was written and run in R v3.4.2 “Short Summer”.

```r
# Set working directory
setwd(choose.dir())
# Set size heritability (between 0 and 1)
sheritability=0.2
# Set growth heritability (between 0 and 1)
gheritability=0.2
# Set number of dams
nDams=0
# Set the number of simulations to run
simNum=100

# Set the advantage for >=2SW males in the mating scheme. If mating is "2",
# then 2+SW males are twice as likely to be drawn from the pool as grilse.
# If mating is "3", they are three times as likely, etc.
mating=1.92

# Set the number of years to simulate
nYears=100
# Set the burn-in length (years)
maxBurn=100

# Parameterize the river length (km) and wetted habitat area (m2). These values
# were taken from the description of the Narraguagus River in USASAC (2015)
rm=89 #Length (kilometers)
W=502763 #Wetted habitat (square meters)

# Parameterize the Ricker curve (Prevost et al. 2003)
A=0.42025011
B=0.0000005

# Set the starting distributions for fish size (modern or historic)
# "modern" sizes are based on fish measured by Maine Dept. of Marine Resources
# at the Veazie Dam trap from 1979-2015.
# "historic" sizes are lengths back-calculated from weights measured by
# U.S. Commission on Fish and Fisheries Agents at the Bucksport fish market
# in 1879. Lengths were back-calculated using the average of three Atlantic
# Salmon length/weight curves (DFO Canada, Icelandic Institute for Freshwater
# Science, and the River Tweed Commission (Scotland)).
startSize=" historic"
```
## Set survival values
freshwaterSurvival=0.041426 #hatching to smolt survival (Legault 2005)
damSurvive=0.95 #per rkm survival of smolts at dams (Stich et al. 2014)
marineSurvival=0.24 #annual survival at sea (Chaput 2012)
if(nDams==0){
  keltSurvival=0.63
} else {
  keltSurvival=0.429^nDams
} #outmigration survival for kelts (Maynard et al. 2018)

## At sea growth
## Annual growth at sea for adults is assumed to be between 0 and 5 cm (Izzo
## and Zydlewski 2018)
maxGrowth=5

### Read in beta values for passage modeling and remove any empty cells from
### the csv file (Maynard et al. 2017)
betas=read.csv("MFBetas.csv", sep=',')
betas=na.omit(betas)

### Set the starting simulation number at 1
s=1

### Load necessary packages
library(truncnorm)

### Loop over multiple simulations
### Create a matrix to store simulation results
Results=matrix(nrow=simNum*nYears,ncol=19)
colnames(Results)=c("SimNum","nDams","gHerit","sHerit","M:F","Year",
  "n1SW","n2SW","nMSW","FL1SW","FL2SW","FL3SW",
  "sd1SW","sd2SW","sd3SW","mGrowth","mGrilse","m2SW","eggs")
for(i in 1:simNum){
  source('burnin.R')
  source('simulation.R')
  s=s+1
}

write.csv(Results,file=paste("g",gheritability*10,"s",sheritability*10,
  "Results",nDams,"Dams.csv",sep=""),row.names=FALSE)
APPENDIX B: INDIVIDUAL-BASED MODEL CODE “BURNIN.R”

The following code was written and run in R v3.4.2 “Short Summer”.

```
# SET UP
## Clear workspace
rm(list=setdiff(ls(), c("betas","Results","sheritability","gheritability","nDams","simNum","mating","nYears","maxBurn","rkm","W","A","B","startSize","freshwaterSurvival","damSurvive","marineSurvival","keltSurvival","maxGrowth","s","i"))
## Create a progress bar
bpb=txtProgressBar(min=0,max=1,initial=0,char=paste(".",s,".",sep=''),style=3)

# Set a starting number of eggs based on a carrying capacity of 6 eggs/m² of wetted habitat (Jonsson et al. 1998)
S=6*W

if(startSize=="modern"){
  m1=55.5 ; sd1=4.0
  m2=76.6 ; sd2=5.7
  m3=91.9 ; sd3=7.6
}
if(startSize=="historic"){
  m1=75 ; sd1=6.59
  m2=83 ; sd2=4.51
  m3=99 ; sd3=2.07
}

## Produce parr based on the number of eggs
Parr0=round(S*exp(A-B*S)*freshwaterSurvival,0)
Parr1=Parr0
Parr2=Parr1

## Calculate the number of juveniles based on smolt survival and at sea survival
Juveniles1=round(Parr2*0.99^(rkm-nDams)*damSurvive^nDams*marineSurvival^2,0)
Juveniles2=round(Parr2*0.99^(rkm-nDams)*damSurvive^nDams*marineSurvival^3,0)
Juveniles3=round(Parr2*0.99^(rkm-nDams)*damSurvive^nDams*marineSurvival^4,0)

## The number of spawning adults is set at the upper limit of the estimated run size of the Narraguagus River (USASAC 2015)
Adults=800

## The number of reconditioning adults is based on the number of kelts and marine survival
Recon=round(Adults*keltSurvival*marineSurvival,0)

## The number of repeat spawn adults is based on the number of reconditioning...```
## adults and marine survival

Repeats=round(Recon*marineSurvival,0)

## Create a matrix to store each life history stage. These matrices will have
## eight columns as follows:
## 1) Sex (0=Male, 1=Female)
## 2) Size (measured in cm)
## 3) Age (in years)
## 4) Growth coefficient (z distribution, lower number = slower growing)
## 5) Individual threshold to become a grilse (z distribution)
## 6) Individual threshold to become a ZSW (z distribution)
## 7) Seawinters at maturity
## 8) Prior spawns

### Reconditioned Spawners

Recon=matrix(ncol=8, nrow=Recon)

## The growth coefficient is a random draw from a z distribution
Recon[,4]=rnorm(nrow(Recon),0,1)

## Fish in the upper 10% of the distribution are grilse to match the sea age
## proportions in Izzo and Zydlewski (2017)
Recon[,7]=2
Recon[,7]=ifelse(Recon[,4]>=1.28,1,Recon[,7])

## Fish in the lower 3% of the distribution are MSW to match the sea age
## proportions in Izzo and Zydlewski (2017)
Recon[,7]=ifelse(Recon[,4]<(-1*1.87 ),3,Recon[,7])

## Set sizes of fish based on the distribution selected and at sea growth
Recon[,2]=ifelse(Recon[,7]==1,rnorm(nrow(Recon),m1,sd1),Recon[,2])
Recon[,2]=ifelse(Recon[,7]==2,rnorm(nrow(Recon),m2,sd2),Recon[,2])
Recon[,2]=ifelse(Recon[,7]==3,rnorm(nrow(Recon),m3,sd3),Recon[,2])
Recon[,2]=Recon[,2]+sample(maxGrowth,nrow(Recon),replace=TRUE)

## Set sex of fish based on life history (i.e., most grilse are male and most
## ZSW and MSW are female)
Recon[,1]=ifelse(Recon[,7]==1,rbinom(nrow(Recon),1,0.015),Recon[,1])
Recon[,1]=ifelse(Recon[,7]>=2,rbinom(nrow(Recon),1,0.55),Recon[,1])

## Set maturity thresholds based on life history
Recon[,c(5,6)]=0
Recon[,5]=ifelse(Recon[,7]>=2,rtruncnorm(nrow(Recon),Recon[,4],10000,0,
1),rtruncnorm(nrow(Recon),-10000,Recon[,4],0,1))
Recon[,6]=ifelse(Recon[,7]==3,rtruncnorm(nrow(Recon),-10000,Recon[,5],0,
1),Recon[,6])
Recon[,6]=ifelse(Recon[,7]==2,rtruncnorm(nrow(Recon),-10000,Recon[,4],0,
1),Recon[,6])
Recon[,6]=ifelse(Recon[,7]==1,rtruncnorm(nrow(Recon),Recon[,4],10000,0,1),Recon[,6])

## Each Reconditioned Spawner is assumed to have one prior spawn for model
## initialization
Recon[,8]=1

### Repeat Spawners

Repeats=matrix(ncol=8, nrow=Repeats)

## The growth coefficient is a random draw from a z distribution
Repeats[,4]=rnorm(nrow(Repeats),0,1)

## Fish in the upper 10% of the distribution are grilse
Repeats[,7]=2
Repeats[,7]=ifelse(Repeats[,4]>=1.28,1,Repeats[,7])
## Fish in the lower 3% of the distribution are MSW

Repeats[,7]=ifelse(Repeats[,4]<(-1*1.87),3,Repeats[,7])

## Set sizes of fish based on the distribution selected and at sea growth

Repeats[,2]=ifelse(Repeats[,7]==1,rnorm(nrow(Repeats),m1,sd1),Repeats[,2])
Repeats[,2]=ifelse(Repeats[,7]==2,rnorm(nrow(Repeats),m2,sd2),Repeats[,2])
Repeats[,2]=ifelse(Repeats[,7]==3,rnorm(nrow(Repeats),m3,sd3),Repeats[,2])

Repeats[,2]=Repeats[,2]+sample(maxGrowth,nrow(Repeats),replace=TRUE)

## Set sex of fish based on life history (i.e., most grilse are male and most

## 2SW and MSW are female)

Repeats[,1]=ifelse(Repeats[,7]==1,rbinom(nrow(Repeats),1,0.015),Repeats[,1])
Repeats[,1]=ifelse(Repeats[,7]>=2,rbinom(nrow(Repeats),1,0.55),Repeats[,1])

## Set maturity thresholds based on life history

Repeats[,c(5,6)]=0

Repeats[,5]=ifelse(Repeats[,7]==2,rtruncnorm(nrow(Repeats),Repeats[,4],10000,0,1),rtruncnorm(nrow(Repeats),-10000,Repeats[,4],0,1))
Repeats[,6]=ifelse(Repeats[,7]==3,rtruncnorm(nrow(Repeats),-10000,Repeats[,5],0,1),rtruncnorm(nrow(Repeats),-10000,Repeats[,4],0,1))
Repeats[,6]=ifelse(Repeats[,7]==1,rtruncnorm(nrow(Repeats),Repeats[,5],0,1),Repeats[,6])

## Each Repeat is assumed to have one prior spawn for model initialization

Repeats[,8]=1

## Virgin Adults

Virgins=Adults-Repeats

Virgins=matrix(ncol=8, nrow=Virgins)

## The growth coefficient is a random draw from a z distribution

Virgins[,4]=rnorm(nrow(Virgins),0,1)

## Fish in the upper 10% of the distribution are grilse

Virgins[,7]=2

Virgins[,7]=ifelse(Virgins[,4]>=1.28,1,Virgins[,7])

## Fish in the lower 3% of the distribution are MSW

Virgins[,7]=ifelse(Virgins[,4]<(-1*1.87),3,Virgins[,7])

## Set sizes of fish based on the distribution selected and at sea growth

Virgins[,2]=ifelse(Virgins[,7]==1,rnorm(nrow(Virgins),m1,sd1),Virgins[,2])
Virgins[,2]=ifelse(Virgins[,7]==2,rnorm(nrow(Virgins),m2,sd2),Virgins[,2])
Virgins[,2]=ifelse(Virgins[,7]==3,rnorm(nrow(Virgins),m3,sd3),Virgins[,2])

## Set sex of fish based on life history (i.e., most grilse are male and most

## 2SW and MSW are female)

Virgins[,1]=ifelse(Virgins[,7]==1,rbinom(nrow(Virgins),1,0.015),Virgins[,1])
Virgins[,1]=ifelse(Virgins[,7]>=2,rbinom(nrow(Virgins),1,0.55),Virgins[,1])

## Set maturity thresholds based on life history

Virgins[,c(5,6)]=0

Virgins[,5]=ifelse(Virgins[,7]==2,rtruncnorm(nrow(Virgins),Virgins[,4],10000,0,1),rtruncnorm(nrow(Virgins),-10000,Virgins[,4],0,1))
Virgins[,6]=ifelse(Virgins[,7]==3,rtruncnorm(nrow(Virgins),-10000,Virgins[,5],0,1),rtruncnorm(nrow(Virgins),-10000,Virgins[,4],0,1))

## virgin spawners by definition have no prior spawning events

Virgins[,8]=0
## 3SW Juveniles

```r
Juveniles3 <- matrix(ncol=8, nrow=Juveniles3)
Juveniles3[,4] <- rtruncnorm(nrow(Juveniles3), -10000, -1.87, 0, 1)
Juveniles3[,5] <- rtruncnorm(nrow(Juveniles3), Juveniles3[,4], -1.87, 0, 1)
Juveniles3[,6] <- rtruncnorm(nrow(Juveniles3), Juveniles3[,5], Juveniles3[,4], 0, 1)
Juveniles3[,7] <- 3
Juveniles3[,3] <- 5
Juveniles3[,2] <- rnorm(nrow(Juveniles3), m3, sd3)
Juveniles3[,1] <- rbinom(nrow(Juveniles3), 1, 0.55)
Juveniles3[,8] <- 0
```

## 2SW Juveniles

```r
Juveniles2 <- matrix(ncol=8, nrow=Juveniles2)
Juveniles2[,4] <- rtruncnorm(nrow(Juveniles2), -10000, 1.28, 0, 1)
Juveniles2[,5] <- rtruncnorm(nrow(Juveniles2), Juveniles2[,4], 1.28, 0, 1)
Juveniles2[,6] <- rtruncnorm(nrow(Juveniles2), Juveniles2[,5], Juveniles2[,4], 0, 1)
Juveniles2[,3] <- 4
Juveniles2[,2] <- ifelse(Juveniles2[,7] == 2, rnorm(nrow(Juveniles2), m2, sd2), Juveniles2[,2])
Juveniles2[,2] <- ifelse(Juveniles2[,7] == 3, rnorm(nrow(Juveniles2), m3, sd3), Juveniles2[,2])
Juveniles2[,1] <- rbinom(nrow(Juveniles2), 1, 0.55)
Juveniles2[,8] <- 0
```

## 1SW Juveniles

```r
Juveniles1 <- matrix(ncol=8, nrow=Juveniles1)
Juveniles1[,4] <- rnorm(nrow(Juveniles1), 0, 1)
Juveniles1[,7] <- ifelse(Juveniles1[,4] >= 1.28, 1, Juveniles1[,7])
Juveniles1[,7] <- ifelse(Juveniles1[,4] > -1.87 & Juveniles1[,4] < 1.28, 2, Juveniles1[,7])
Juveniles1[,7] <- ifelse(Juveniles1[,4] < (1 - 1.87), 3, Juveniles1[,7])
Juveniles1[,3] <- 3
Juveniles1[,2] <- ifelse(Juveniles1[,7] == 1, rnorm(nrow(Juveniles1), m1, sd1), Juveniles1[,2])
Juveniles1[,2] <- ifelse(Juveniles1[,7] == 2, rnorm(nrow(Juveniles1), m2, sd2), Juveniles1[,2])
Juveniles1[,2] <- ifelse(Juveniles1[,7] == 3, rnorm(nrow(Juveniles1), m3, sd3), Juveniles1[,2])
Juveniles1[,1] <- ifelse(Juveniles1[,7] == 1, rbinom(nrow(Juveniles1), 1, 0.015), Juveniles1[,1])
Juveniles1[,1] <- ifelse(Juveniles1[,7] == 2, rbinom(nrow(Juveniles1), 1, 0.55), Juveniles1[,1])
Juveniles1[,6] <- ifelse(Juveniles1[,7] == 3, rtruncnorm(nrow(Juveniles1), Juveniles1[,4], Inf, 0, 1), Juveniles1[,6])
Juveniles1[,6] <- ifelse(Juveniles1[,7] == 2, rtruncnorm(nrow(Juveniles1), -Inf, Juveniles1[,4], 0, 1), Juveniles1[,6])
Juveniles1[,6] <- ifelse(Juveniles1[,7] == 1, rtruncnorm(nrow(Juveniles1), 2.6520698, Juveniles1[,4], 0, 1), Juveniles1[,6])
Juveniles1[,5] <- ifelse(Juveniles1[,7] == 2, rtruncnorm(nrow(Juveniles1), Juveniles1[,4], Inf, 0, 1), rtruncnorm(nrow(Juveniles1), Juveniles1[,6], Juveniles1[,4], 0, 1))
Juveniles1[,8] <- 0
```

## 2 year Parr

```r
```
Parr2 = matrix(ncol = 8, nrow = Parr2)
Parr2[,4] = rnorm(nrow(Parr2), 0, 1)
Parr2[,7] = ifelse(Parr2[,4] >= 1.28, 1, Parr2[,7])
Parr2[,7] = ifelse(Parr2[,4] < (1 - 1.87), 3, Parr2[,7])
Parr2[,3] = 2
Parr2[,2] = ifelse(Parr2[,7] == 1, rnorm(nrow(Parr2), m1, sd1), Parr2[,2])
Parr2[,2] = ifelse(Parr2[,7] == 2, rnorm(nrow(Parr2), m2, sd2), Parr2[,2])
Parr2[,2] = ifelse(Parr2[,7] == 3, rnorm(nrow(Parr2), m3, sd3), Parr2[,2])
Parr2[,1] = ifelse(Parr2[,7] == 1, rbinom(nrow(Parr2), 1, 0.015), Parr2[,1])
Parr2[,1] = ifelse(Parr2[,7] >= 2, rbinom(nrow(Parr2), 1, 0.55), Parr2[,1])
Parr2[,6] = ifelse(Parr2[,7] == 2, rtruncnorm(nrow(Parr2), Parr2[,4], Inf, 0, 1), Parr2[,6])
Parr2[,6] = ifelse(Parr2[,7] == 3, rtruncnorm(nrow(Parr2), Parr2[,4], Inf, 0, 1, , Parr2[,6])
Parr2[,5] = ifelse(Parr2[,7] >= 2, rtruncnorm(nrow(Parr2), Parr2[,4], Inf, 0, 1), rtruncnorm(nrow(Parr2), Parr2[,6], Parr2[,4], 0, 1))
Parr2[,8] = 0

## 1 year Parr #################################################################
Parr1 = matrix(ncol = 8, nrow = Parr1)
Parr1[,4] = rnorm(nrow(Parr1), 0, 1)
Parr1[,7] = ifelse(Parr1[,4] >= 1.28, 1, Parr1[,7])
Parr1[,7] = ifelse(Parr1[,4] > 1.87 & Parr1[,4] < 1.28, 2, Parr1[,7])
Parr1[,7] = ifelse(Parr1[,4] < (1 - 1.87), 3, Parr1[,7])
Parr1[,3] = 1
Parr1[,2] = ifelse(Parr1[,7] == 1, rnorm(nrow(Parr1), m1, sd1), Parr1[,2])
Parr1[,2] = ifelse(Parr1[,7] == 2, rnorm(nrow(Parr1), m2, sd2), Parr1[,2])
Parr1[,2] = ifelse(Parr1[,7] == 3, rnorm(nrow(Parr1), m3, sd3), Parr1[,2])
Parr1[,1] = ifelse(Parr1[,7] == 1, rbinom(nrow(Parr1), 1, 0.015), Parr1[,1])
Parr1[,1] = ifelse(Parr1[,7] >= 2, rbinom(nrow(Parr1), 1, 0.55), Parr1[,1])
Parr1[,6] = ifelse(Parr1[,7] == 2, rtruncnorm(nrow(Parr1), Parr1[,4], -Inf, Parr1[,4], 0, 1), Parr1[,6])
Parr1[,6] = ifelse(Parr1[,7] == 3, rtruncnorm(nrow(Parr1), Parr1[,4], -Inf, Parr1[,4], 0, 1, Parr1[,6])
Parr1[,5] = ifelse(Parr1[,7] >= 2, rtruncnorm(nrow(Parr1), Parr1[,4], -Inf, Parr1[,4], 0, 1), rtruncnorm(nrow(Parr1), Parr1[,6], Parr1[,4], 0, 1))
Parr1[,8] = 0

## YoY #######################################################################
Parr0 = matrix(ncol = 8, nrow = Parr0)
Parr0[,4] = rnorm(nrow(Parr0), 0, 1)
Parr0[,7] = ifelse(Parr0[,4] >= 1.28, 1, Parr0[,7])
Parr0[,7] = ifelse(Parr0[,4] > 1.87 & Parr0[,4] < 1.28, 2, Parr0[,7])
Parr0[,7] = ifelse(Parr0[,4] < (1 - 1.87), 3, Parr0[,7])
Parr0[,3] = 0
Parr0[,2] = ifelse(Parr0[,7] == 1, rnorm(nrow(Parr0), m1, sd1), Parr0[,2])
Parr0[,2] = ifelse(Parr0[,7] == 2, rnorm(nrow(Parr0), m2, sd2), Parr0[,2])
Parr0[,2] = ifelse(Parr0[,7] == 3, rnorm(nrow(Parr0), m3, sd3), Parr0[,2])
Parr0[,1] = ifelse(Parr0[,7] == 1, rbinom(nrow(Parr0), 1, 0.015), Parr0[,1])
Parr0[,1] = ifelse(Parr0[,7] >= 2, rbinom(nrow(Parr0), 1, 0.55), Parr0[,1])
Parr0[,6]=ifelse(Parr0[,7]==3,rtruncnorm(nrow(Parr0),Parr0[,4],Inf,0,1),
                   Parr0[,6])
Parr0[,6]=ifelse(Parr0[,7]==2,rtruncnorm(nrow(Parr0),-Inf,Parr0[,4],0,1),
                   Parr0[,6])
Parr0[,6]=ifelse(Parr0[,7]==1,rtruncnorm(nrow(Parr0),2.6520698,Parr0[,4],0,1),
                   Parr0[,6])
Parr0[,5]=ifelse(Parr0[,7]>=2,rtruncnorm(nrow(Parr0),Parr0[,4],Inf,0,1),
                   rt
runcnorm(nrow(Parr0),Parr0[,6],Parr0[,4],0,1))
Parr0[,8]=0

for(b in 1:maxBurn){ #For each year of burn-in
  ## Pull together all in-migrating adults
  Adults=rbind(Virgins,Repeats)
  ## In the burn-in, there are no dams, so all Adults are spawners and there
  ## are no fallbacks
  Spawners=Adults
  ## Select which Juveniles will mature and which will remain in salt water
  J1=which(Juveniles1[,3]-2>=Juveniles1[,7])
  J2=which(Juveniles2[,3]-2>=Juveniles2[,7])
  ## Create a new matrix of virgin spawners for next season
  Virgins=rbind(Juveniles3,Juveniles2[J2,],Juveniles1[J1,])
  ## Progress the rest of the fish
  Juveniles3=matrix(Juveniles2[-J2,],ncol=8)
  Juveniles3=matrix(Juveniles3[which(rbinom(nrow(Juveniles3),1,marineSurvival)==1),],ncol=8)
  Juveniles2=matrix(Juveniles1[-J1,],ncol=8)
  Juveniles2=matrix(Juveniles2[which(rbinom(nrow(Juveniles2),1,marineSurvival)==1),],ncol=8)
  Smolts=matrix(Parr2[which(rbinom(nrow(Parr2),1,0.99^(rkm-0)*
                     damSurvive^0)==1),],ncol=8)
  Juveniles1=matrix(Smolts[which(rbinom(nrow(Smolts),1,marineSurvival)==1),],
                     ncol=8)
  ## Year 1 and Year 0 parr are older
  Parr2=Parr1
  Parr1=Parr0
  ## Clean up unused matrices
  rm(Parr0)
  rm(Smolts)
  rm(Adults)
  ## Separate out female and male spawners
  if(nrow(Spawners)>1){
    fSpawners=matrix(subset(Spawners,Spawners[,1]==1),ncol=8)
    mSpawners=matrix(subset(Spawners,Spawners[,1]==0),ncol=8)
    ## If there are more female spawners than male spawners, randomly assign
    ## mates
    if(nrow(fSpawners)>nrow(mSpawners)){
      a=sample(nrow(fSpawners),nrow(mSpawners),replace=FALSE)
      fSpawners=matrix(fSpawners[a,],ncol=8)
    }
    ## If there are more male spawners than female spawners, assign mates based
    ## on the advantage given to large 2+SW males in variable "mating"
    if(nrow(fSpawners)<nrow(mSpawners)){

mateProb = ifelse(mSpawners[,7]==1, 1, mating)
mateProb = mateProb / sum(mateProb)
a = sample(nrow(mSpawners), nrow(fSpawners), replace=FALSE, prob=mateProb)
mSpawners = matrix(mSpawners[a,], ncol=8)

fFL = vector(length=nrow(fSpawners))
mFL = vector(length=nrow(mSpawners))
fFL = ifelse(fSpawners[,7]==1, (fSpawners[,2]-55.5)/4, fFL)
fFL = ifelse(fSpawners[,7]==2, (fSpawners[,2]-76.6)/5.7, fFL)
fFL = ifelse(fSpawners[,7]==3, (fSpawners[,2]-91.9)/7.6, fFL)
fFL = ifelse(is.na(fFL)==TRUE, 0, fFL)
mFL = ifelse(mSpawners[,7]==1, (mSpawners[,2]-55.5)/4, mFL)
mFL = ifelse(mSpawners[,7]==2, (mSpawners[,2]-76.6)/5.7, mFL)
mFL = ifelse(mSpawners[,7]==3, (mSpawners[,2]-91.9)/7.6, mFL)
mFL = ifelse(is.na(mFL)==TRUE, 0, mFL)

## Calculate the number of eggs produced by each spawning pair based on
## female size (Heinimaa and Heinimaa 2004)
S = sum(na.omit(round(exp(3.07*log(fSpawners[,2])-4.46), 0))))
#points(S=b, pch=16)
spawn = round(exp(3.07*log(fSpawners[,2])-4.46), 0)
Spawners = rbind(mSpawners, fSpawners)

} else {
## If there are no spawning fish (or only one sex is present), spawning
## cannot occur, so the number of eggs produced is 0
S = 0
spawn = 0

} # If there is at least one female and one male fish
if(exists("fSpawners")*exists("mSpawners")==TRUE & nrow(fSpawners)*nrow(mSpawners)>0){
## Pair off adults
if(sheritability! = 0){
  Sizes = c(fFL, mFL)
  Sizes = Sizes*sheritability + runif(length(Sizes), -2.5, 2.5)*(1- sheritability)
  spawnProb1 = rep(spawn/sum(spawn), 2)
}
if(gheritability! = 0){
  Growth = c(fSpawners[,4], mSpawners[,4])
  Growth = Growth*gheritability + runif(length(Sizes), -2.5, 2.5)*(1-gheritability)
  tGrilse = na.omit(c(fSpawners[,5], mSpawners[,5]))
  tGrilse = tGrilse*gheritability + runif(length(Sizes), -2.5, 2.5)*(1-gheritability)
  t2SW = na.omit(c(fSpawners[,6], mSpawners[,6]))
  t2SW = t2SW*gheritability + runif(length(Sizes), -2.5, 2.5)*(1-gheritability)
  spawnProb2 = rep(spawn/sum(spawn), 2)
}
Spawners = rbind(fSpawners, mSpawners)
## All spawners get one spawning season added to their total
Spawners[,8] = Spawners[,8] + 1
}
## Any reconditioned fish at sea prepare to join the next spawning migration
Repeats = matrix(Recon[,1:8], ncol=8)
Repeats[,2] = Repeats[,2] + sample(maxGrowth, nrow(Repeats), replace=TRUE)
rm(Recon)
## Any surviving kelts return to the sea to recondition
Recon=matrix(Spawners[which(rbinom(nrow(Spawners),1,0.63*marineSurvival)==1),
1:8],ncol=8)
Recon=matrix(Recon[1:8],ncol=8)
rm(Spawners)
## A new YoY Parr matrix is built
Parr0=matrix(ncol=8,nrow=round(S*exp(A-B*S)*freshwaterSurvival,0))
if(nrow(Parr0)>0){
  ## Assign each Parr0 a sex
  Parr0[,1]=rbinom(nrow(Parr0),1,0.5)
  ## Assign each Parr0 a z-standardized length (inherited from parents)
  Parr0[,2]=sample(Sizes,nrow(Parr0),spawnProb1,replace=TRUE)
  ## All parr0 are 0 years old
  Parr0[,3]=0
  ## Assign each Parr0 a growth parameter (inherited from parents)
  Parr0[,4]=sample(Growth,nrow(Parr0),spawnProb2,replace=TRUE)
  ## Assign each Parr0 maturity thresholds (inherited from parents)
  Parr0[,5]=sample(tGrilse,nrow(Parr0),spawnProb2,replace=TRUE)
  Parr0[,6]=sample(t2SW,nrow(Parr0),spawnProb2,replace=TRUE)
  ## Compare thresholds to growth parameter and assign a value for SW at
  ## maturity
  Parr0[,7]=ifelse(Parr0[,4]<Parr0[,6],3,Parr0[,7])
  Parr0[,7]=ifelse(Parr0[,4]>Parr0[,5],1,Parr0[,7])
  Parr0[,7]=ifelse(is.na(Parr0[,7])==TRUE,2,Parr0[,7])
  ## Calculate size at maturity using SW at maturity, z-standardized growth,
  ## and size at maturity values from Allen 1972
  Parr0[,2]=ifelse(Parr0[,7]==1,Sizes*4.01+55.5,Parr0[,2])
  Parr0[,2]=ifelse(Parr0[,7]==2,Sizes*5.74+76.6,Parr0[,2])
  Parr0[,2]=ifelse(Parr0[,7]==3,Sizes*7.7+92,Parr0[,2])
  Parr0[,1]=ifelse(Parr0[,7]==1,rbinom(nrow(Parr0),1,0.015),Parr0[,1])
  Parr0[,1]=ifelse(Parr0[,7]==2,rbinom(nrow(Parr0),1,0.55),Parr0[,1])
  while(sum(Parr0[,6]>Parr0[,5])>0){
    Parr0[,6]=ifelse(Parr0[,6]>Parr0[,5],Parr0[,6]-0.1,Parr0[,6])
  }
  Parr0[,8]=0
}
## Increase the ages of all fish except YoY
x=rbind(Repeats)
x[,3]=x[,3]+1
Repeats=x;rm(x)
x=rbind(Recon)
x[,3]=x[,3]+1
Recon=x;rm(x)
x=rbind(Juveniles1)
x[,3]=x[,3]+1
Juveniles1=x;rm(x)
x=rbind(Juveniles2)
x[,3]=x[,3]+1
Juveniles2=x;rm(x)
x=rbind(Juveniles3)
x[,3]=x[,3]+1
Juveniles3=x;rm(x)
x=rbind(Parr2)
x[,3]=x[,3]+1
Parr2=x;rm(x)
\begin{verbatim}
x=rbind(Parr1)
x[,3]=x[,3]+1
Parr1=x;rm(x)
setTxtProgressBar(bpb,b/maxBurn)
}\end{verbatim}
APPENDIX C: INDIVIDUAL-BASED MODEL CODE “SIMULATION.R”

The following code was written and run in R v3.4.2 “Short Summer”.

```r
# Create a progress bar
pb=txtProgressBar(min=0,max=1,initial=0,char=paste("\*",s,"\*",sep=''),style=3)

# SIMULATION
for(b in 1:nYears){ #For each year of simulation
  Adults=rbind(Virgins,Repeats)
  if(nDams==0){
    Spawners=Adults
    MF=nrow(subset(Spawners,Spawners[,1]==0))/nrow(subset(Spawners,Spawners[,1]==1))
    Fallbacks=matrix(nrow=0,ncol=8)
  } else {
    sBetas=betas[sample(nrow(betas),nrow(Adults),replace=TRUE),]
    Passage=exp((sBetas[,1]+sBetas[,2]*(Adults[,2]-65.711)/9.945)+sBetas[,3]*runif(nrow(Adults),0,30))
    Passage=ifelse(Passage>1,1,Passage)
    Passage=rbinom(nrow(Adults),nDams,Passage)
    Spawners=matrix(Adults[which(Passage>=nDams),],ncol=8)
    MF=nrow(subset(Spawners,Spawners[,1]==0))/nrow(subset(Spawners,Spawners[,1]==1))
    Fallbacks=matrix(Adults[which(Passage<nDams),],ncol=8)
  }
  if(nrow(Adults)>0){
    sBetas=betas[sample(nrow(betas),nrow(Adults),replace=TRUE),]
    Passage=exp((sBetas[,1]+sBetas[,2]*(Adults[,2]-65.711)/9.945)+sBetas[,3]*runif(nrow(Adults),0,30))
    Passage=ifelse(Passage>1,1,Passage)
    Passage=rbinom(nrow(Adults),nDams,Passage)
    Spawners=matrix(Adults[which(Passage>=nDams),],ncol=8)
    MF=nrow(subset(Spawners,Spawners[,1]==0))/nrow(subset(Spawners,Spawners[,1]==1))
    Fallbacks=matrix(Adults[which(Passage<nDams),],ncol=8)
    Virgins=rbind(Juveniles3,Juveniles2[,J2,],Juveniles1[,J1,])
    Juveniles3=matrix(Juveniles2[-J2,],ncol=8)
    Juveniles3=matrix(Juveniles3[which(rbinom(nrow(Juveniles3),1,marineSurvival)==1),],ncol=8)
    Juveniles2=matrix(Juveniles1[-J1,],ncol=8)
    Juveniles2=matrix(Juveniles2[which(rbinom(nrow(Juveniles2),1,marineSurvival)==1),],ncol=8)
  } else {
    Virgins=rbind(Juveniles3,Juveniles2[,J2,],Juveniles1[,J1,])
    Juveniles3=matrix(Juveniles2[-J2,],ncol=8)
    Juveniles3=matrix(Juveniles3[which(rbinom(nrow(Juveniles3),1,marineSurvival)==1),],ncol=8)
    Juveniles2=matrix(Juveniles1[-J1,],ncol=8)
    Juveniles2=matrix(Juveniles2[which(rbinom(nrow(Juveniles2),1,marineSurvival)==1),],ncol=8)
  }
}
```

129
marineSurvival==1),[,ncol=8)
Smolts=matrix(Parr2[which(rbinom(nrow(Parr2),1,0.99^(rkmdamSurvive^0)==1),[,ncol=8)
Juveniles1=matrix(Smolts[which(rbinom(nrow(Smolts),1,marineSurvival)==1),[,ncol=8)
## Year 1 and Year 0 parr are older
Parr2=Parr1
Parr1=Parr0
## Clean up unused matrices
rm(Parr0)
rm(Smolts)
rm(Adults)
## If the spawner or fallback matrices don't exist, make an empty placeholder
if(exists("Spawners")==FALSE){
  Spawners=matrix(nrow=0,ncol=8)
}
if(exists("Fallbacks")==FALSE){
  Fallbacks=matrix(nrow=0,ncol=8)
}
## Separate out female and male spawners
if(nrow(Spawners)>1){
  fSpawners=matrix(subset(Spawners,Spawners[,1]==1),ncol=8)
  mSpawners=matrix(subset(Spawners,Spawners[,1]==0),ncol=8)
  ## If there are more female spawners than male spawners, randomly assign
  ## mates
  if(nrow(fSpawners)>nrow(mSpawners)){
    a=sample(nrow(fSpawners),nrow(mSpawners),replace=FALSE)
    fSpawners=matrix(fSpawners[a,],ncol=8)
  }
  ## If there are more male spawners
  ## than female spawners, assign mates based
  ## on the advantage given to large 2+ SW males in variable "mating"
  if(nrow(fSpawners)<nrow(mSpawners)){
    mateProb=ifelse(mSpawners[,7]==1,1,mating)
    mateProb=mateProb/sum(mateProb)
    a=sample(nrow(mSpawners),nrow(fSpawners),replace=FALSE,prob=mateProb)
    mSpawners=matrix(mSpawners[a,],ncol=8)
  }
  fFL=vector(length=nrow(fSpawners))
  mFL=vector(length=nrow(mSpawners))
  fFL=ifelse(fSpawners[,7]==1,(fSpawners[,2]-55.5)/4,fFL)
  fFL=ifelse(fSpawners[,7]==2,(fSpawners[,2]-76.6)/5.7,fFL)
  fFL=ifelse(fSpawners[,7]==3,(fSpawners[,2]-91.9)/7.6,fFL)
  fFL=ifelse(is.na(fFL)==TRUE,0,fFL)
  mFL=ifelse(mSpawners[,7]==1,(mSpawners[,2]-55.5)/4,mFL)
  mFL=ifelse(mSpawners[,7]==2,(mSpawners[,2]-76.6)/5.7,mFL)
  mFL=ifelse(mSpawners[,7]==3,(mSpawners[,2]-91.9)/7.6,mFL)
  mFL=ifelse(is.na(mFL)==TRUE,0,mFL)
  ## Calculate the number of eggs produced by each spawning pair based on
  ## female size (Heinimaa and Heinimaa 2004)
  S=sum(na.omit(round(exp(3.07*log(fSpawners[,2])-4.46),0))))
  spawn=round(exp(3.07*log(fSpawners[,2])-4.46),0)
  Spawners=rbind(mSpawners,fSpawners)
  n1=nrow(subset(Spawners,Spawners[,8]==0&Spawners[,7]==1))
  n2=nrow(subset(Spawners,Spawners[,8]==0&Spawners[,7]==2))
  nm=nrow(subset(Spawners,Spawners[,8]==0&Spawners[,7]==3))
nm=nm+nrow(subset(Spawners,Spawners[,8]>0))
f1=mean(subset(Spawners,Spawners[,8]==0&Spawners[,7]==1)[,2])
f2=mean(subset(Spawners,Spawners[,8]==0&Spawners[,7]==2)[,2])

fm=mean(c(subset(Spawners,Spawners[,8]==0&Spawners[,7]==3)[,2],subset(Spawners,Spawners[,8]>0)[,2]))
s1=sd(subset(Spawners,Spawners[,8]==0&Spawners[,7]==1)[,2])
s2=sd(subset(Spawners,Spawners[,8]==0&Spawners[,7]==2)[,2])

sm=sd(c(subset(Spawners,Spawners[,8]==0&Spawners[,7]==3)[,2],subset(Spawners,Spawners[,8]>0)[,2]))
mgrowth=mean(Spawners[,4])
mgrilse=mean(Spawners[,5])
m2SW=mean(Spawners[,6])
}
else {
## If there are no spawning fish (or only one sex is present), spawning
## cannot occur, so the number of eggs produced is 0
S=0
spawn=0
n1=0
n2=0
nm=0
f1=NA
f2=NA
fm=NA
s1=NA
s2=NA
sm=NA
mgrowth=NA
mgrilse=NA
m2SW=NA
Spawners=matrix(nrow=0, ncol=8)
}
## If there is at least one female and one male fish
if(exists("fSpawners")&&exists("mSpawners")&&!nrow(fSpawners)*
nrow(mSpawners)>0){
## Pair off adults
if(sheritability!=0){
Sizes=c(fFL,mFL)
Sizes=Sizes*sheritability+runif(length(Sizes),-2.5,2.5)*(1-sheritability)
spawnProb1=rep(spawn/sum(spawn),2)
}
if(gheritability!=0){
 Growth=c(fSpawners[,4],mSpawners[,4])
 Growth=3.4*gheritability+runif(length(Sizes),-2.5,2.5)*(1-gheritability)
 tGrilse=na.omit(c(fSpawners[,5],mSpawners[,5]))
 tGrilse=tGrilse*gheritability+runif(length(Sizes),-2.5,2.5)*(1-gheritability)
 t2SW=na.omit(c(fSpawners[,6],mSpawners[,6]))
 t2SW=t2SW*gheritability+runif(length(Sizes),-2.5,2.5)*(1-gheritability)
 spawnProb2=rep(spawn/sum(spawn),2)
}
Spawners=rbind(fSpawners,mSpawners)
## All spawners get one spawning season added to their total
Spawners[,8]=Spawners[,8]+1
}
## Any reconditioned fish at sea prepare to join the next spawning migration
Repeats=matrix(Recon[,1:8],ncol=8)
Repeats[,2]=Repeats[,2]+sample(maxGrowth,nrow(Repeats),replace=TRUE)
rm(Recon)
## Any surviving kelts return to the sea to recondition
if(nDams==0){
  Recon=matrix(Spawners[which(rbinom(nrow(Spawners),1,0.63*marineSurvival)==1),1:8],ncol=8)
  Recon=matrix(Recon[,1:8],ncol=8)
} else {
  Recon=matrix(Spawners[which(rbinom(nrow(Spawners),1,0.429^nDams*marineSurvival)==1),1:8],ncol=8)
  Recon=matrix(Recon[,1:8],ncol=8)
  Recon=rbind(Recon,Fallbacks[which(rbinom(nrow(Fallbacks),1,0.429^nDams*marineSurvival)==1),1:8])
}
rm(Spawners)
rm(Fallbacks)
## A new YoY Parr matrix is built
Parr0=matrix(ncol=8,nrow=round(S*exp(A-B*S)*freshwaterSurvival,0))
if(nrow(Parr0)>0){
  ## Assign each Parr0 a sex
  Parr0[,1]=rbinom(nrow(Parr0),1,0.5)
  ## Assign each Parr0 a a z-standardized length (inherited from parents)
  Parr0[,2]=sample(Sizes,nrow(Parr0),spawnProb1,replace=TRUE)
  ## All parr0 are 0 years old
  Parr0[,3]=0
  ## Assign each Parr0 a a growth parameter (inherited from parents)
  Parr0[,4]=sample(Growth,nrow(Parr0),spawnProb2,replace=TRUE)
  ## Assign each Parr0 maturity thresholds (inherited from parents)
  Parr0[,5]=sample(tGrilse,nrow(Parr0),spawnProb2,replace=TRUE)
  Parr0[,6]=sample(t2SW,nrow(Parr0),spawnProb2,replace=TRUE)
  ## Compare thresholds to growth parameter and assign a value for SW at maturity
  Parr0[,7]=ifelse(Parr0[,4]<Parr0[,6],3,Parr0[,7])
  Parr0[,7]=ifelse(Parr0[,4]>Parr0[,5],1,Parr0[,7])
  Parr0[,7]=ifelse(is.na(Parr0[,7])==TRUE,2,Parr0[,7])
  ## Calculate size at maturity using SW at maturity, z-standardized growth, and size at maturity values from Allen 1972
  Parr0[,2]=ifelse(Parr0[,7]==1,Sizes*4.01+55.5,Parr0[,2])
  Parr0[,2]=ifelse(Parr0[,7]==2,Sizes*5.74+76.6,Parr0[,2])
  Parr0[,2]=ifelse(Parr0[,7]==3,Sizes*7.7+92,Parr0[,2])
  Parr0[,1]=ifelse(Parr0[,7]==1,rbinom(nrow(Parr0),1,0.015),Parr0[,1])
  Parr0[,1]=ifelse(Parr0[,7]==2,rbinom(nrow(Parr0),1,0.55),Parr0[,1])
  while(sum(Parr0[,6]>Parr0[,5])>0){
    Parr0[,6]=ifelse(Parr0[,6]>Parr0[,5],Parr0[,6]-0.1,Parr0[,6])
  }
}
Parr0[,8]=0
## Increase the ages of all fish except YoY
x=rbind(Repeats)
x[,3]=x[,3]+1
Repeats=x;rm(x)
x=rbind(Recon)
x[,3]=x[,3]+1
Recon=x;rm(x)
x=rbind(Juveniles1)
x[,3]=x[,3]+1
Juveniles1=x;rm(x)
x=rbind(Juveniles2)
x[,3]=x[,3]+1
Juveniles2=x;rm(x)
x=rbind(Juveniles3)
x[,3]=x[,3]+1
Juveniles3=x;rm(x)
x=rbind(Parr2)
x[,3]=x[,3]+1
Parr2=x;rm(x)
x=rbind(Parr1)
x[,3]=x[,3]+1
Parr1=x;rm(x)
setTxtProgressBar(pb,b/nYears)
Results[(s-1)*nYears+b,]=c(s,nDams,gheritability,sheritability,MF,b,n1,n2,nm,
f1,f2,fm,s1,s2,sm,mgrowth,mgrilse,m2SW,S)
rm(n1,n2,nm,f1,f2,fm,s1,s2,sm,mgrowth,mgrilse,m2SW)
BIOGRAPHY OF THE AUTHOR

George Alphonse Maynard was born in Manchester, Connecticut on November 9, 1988. He grew up fishing the rivers and mill ponds of northern Connecticut, dreaming of the day he would get to be on a boat. He graduated from Stafford High School in 2006 and studied Natural Resource Management with a focus in fisheries at the University of Connecticut, where he earned his Bachelor of Science in 2009. After graduation, George worked on research projects and invasive species monitoring around irrigation reservoirs for the Nebraska Cooperative Fish and Wildlife Research Unit. Distressed by the absence of trees and thin-crust pizza on the Great Plains, George moved back east to Plattsburgh, NY, where he earned a Master of Science in Natural Sciences through SUNY Plattsburgh’s Lake Champlain Research Institute in 2013. Currently, George works as the Research Director for the Cape Cod Commercial Fishermen’s Alliance. George is a candidate for the Doctor of Philosophy degree in Wildlife Ecology from the University of Maine in May 2019.