BEHAVIOR AND SURVIVAL OF MIGRATING ATLANTIC SALMON
(SALMO SALAR) IN THE PENOBSCOT RIVER AND ESTUARY,
MAINE: ACOUSTIC TELEMETRY STUDIES
OF SMOLTS AND ADULTS

By
Christopher Michael Holbrook
B.S. University of Maine, 2004

A THESIS
Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Science
(in Zoology)

The Graduate School
The University of Maine
August 2007

Advisory Committee:
Michael T. Kinnison, Associate Professor of Biology, Co-advisor
Joseph Zydlewski, Assistant Professor in Wildlife Ecology, Co-advisor
John F. Kocik, NOAA National Marine Fisheries Service
LIBRARY RIGHTS STATEMENT

In presenting this thesis in partial fulfillment of the requirements for an advanced degree at The University of Maine, I agree that the Library shall make it freely available for inspection. I further agree that permission for "fair use" copying of this thesis for scholarly purposes may be granted by the Librarian. It is understood that any copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Signature:

Date:
Acoustic telemetry was used to evaluate passage success, survival and behavior of migrating Atlantic salmon (Salmo salar), at both the smolt and adult stages, through the Penobscot River and Estuary, Maine. Survival and behavior of migrating hatchery (n=493) and naturally-reared (n=133) smolts were evaluated in 2005 and 2006. Mortality, movement rates, and use of a secondary migration path (the Stillwater Branch) were quantified, and related to rearing, release history, and migratory condition (gill Na⁺,K⁺-ATPase activity and condition factor). River sections containing three mainstem dams (Howland, Milford and West Enfield dams) accounted for 43% and 60% of total losses for 2005 and 2006, respectively, though these sections accounted for only 16% and 6% of monitored reaches. Survivorships through individual sections with dams ranged from 95-100% and 71-100% in 2005 and 2006, respectively. Movement rates were significantly slower at dams compared to free-flowing reaches, and smolts arriving at
dams during the day experienced longer delays than smolts arriving at night. Hatchery smolts released in April were not ready to migrate at time of release, but migrated earlier than wild smolts in both years. Gill Na\textsuperscript{+},K\textsuperscript{+}-ATPase activity was positively associated with movement rate to the estuary in both years. Further, gill Na\textsuperscript{+},K\textsuperscript{+}-ATPase activity for wild smolts was similar to hatchery smolts that were released 29-26 days earlier in 2005 and 2006, respectively. Hatchery smolts released in May showed similar freshwater survival compared to both wild smolts and hatchery smolts released in April, but behavior was more similar to wild smolts than earlier-released hatchery smolts. Use of the Stillwater Branch by individual release groups ranged from 0-26\% and 0-19\% in 2005 and 2006, respectively, and was positively related to discharge. Smolts released in the Pleasant River at Milo used the Stillwater Branch at a significantly lower rate than smolts released in the mainstem. These results indicate that fundamental differences exist between hatchery and naturally reared smolts, and may help managers determine which rearing and release protocols best meet the goals of the restoration program.

Acoustic telemetry was used to quantify riverine behavior and passage success for pre-spawn adult Atlantic salmon in the lower Penobscot River, Maine in 2005 (N=10) and 2006 (N=25). Passage success was extremely poor in both years. Only 38\% (3/8) and 8\% (2/25) of tagged salmon successfully passed the fourth upstream dam in 2005 and 2006, respectively. In 2005 and 2006, 100\% (3/3) and 74\% (17/23) of unsuccessful migrants fell back into the estuary and few successfully re-ascended. Water temperature in the mainstem exceeded 27\°C in both years, and fallback behavior was common when temperatures exceeded 22\°C. A small stream provided thermal refuge during morning hours only and was warmer than the mainstem during afternoon hours. Results from this
pre-removal assessment indicate that insufficient upstream passage at dams in the lower Penobscot River can severely limit migratory success in this system.

As part of the Penobscot River Restoration Project (PRRP), the planned removal of two dams (Great Works and Veazie dams) is expected to enhance passage through the mainstem corridor for salmon and other migratory fish. Results from this study suggest that removal of these lower river dams will improve migratory success for adult salmon. However, this study highlights the need to improve downstream passage for smolts at dams that will remain in place (Milford, Howland and West Enfield dams).
ACKNOWLEDGEMENTS

I would like to thank members of the Kinnison and Zydlewski labs (past and present) for all of their help and contributions. Mike Kinnison and Joe Zydlewski were encouraging mentors throughout this process and I am thankful for their support. Thank you also to John Kocik, who added an invaluable third point of view and crucial insight into this project.

I would like to thank my family for their support, which helped make this project possible. Thank you for providing me with a background that allowed me to see this process through, and for always offering an open door when I needed a break. Thank you also to my wife, Lauren, who not only participated in the field and laboratory, but lended moral support throughout the process.

Lastly, I would also like to thank all of the different people and organizations that contributed to this project in one form or another, without which this project would not have met success. Thank you to the Maine Atlantic Salmon Conservation Fund of the National Fish and Wildlife Foundation for generously supporting this work. Additional commitments of support from the University of Maine (Biology Department, Dean of Natural Sciences, Forestry and Agriculture, Vice President of Research); the West Enfield Fisheries Mitigation Fund; the Maine Cooperative Fisheries and Wildlife Research Unit; and Vemco Inc. made this work possible. The expertise of many individuals contributed to the success of this project, including Ed Hastings, Rory Saunders, Jeff Murphy, Christine Lipsky, Jim Hawkes, Ruth Haas-Castro, Graham Goulette, Paul Music and Trent Liebach (NOAA Fisheries Service); Dr. Jim Gilbert (University of Maine); Gordon Russell, Scott Craig, Fred Trasko and Carl Burger (U. S.
Fish and Wildlife Service); Joan Trial, Richard Dill, Mitch Simpson, Kevin Dunham, Norm Dube and Randy Spencer (Maine Atlantic Salmon Commission); Clem Fay, John Banks and the Land Use Committee (Penobscot Nation); Dave Miller, Bob Sweeney, Nell Halse (Atlantic Salmon of Maine); Mike Pietrak (Maine Aquaculture Association); Kevin Bernier (Great Lakes Hydro); Scott Hall (Pennsylvania Power and Light, Maine) and a myriad of students from the University of Maine. Invaluable field support was contributed by Cory Gardner, Timothy Coombs, Allan Roberts, David Pert, Lauren Holbrook, Kevin Lachapelle, Michael Bailey, Stephen Fernandes, Eric Ham, Casey Jackson, Leif Whitman, Luke Whitman, Dimitry Gorsky, Paul Kusnierz, Nate Wilke, Wendy Michaud and many others.
TABLE OF CONTENTS

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

LIST OF TABLES.......................................................................................................................... ix

LIST OF FIGURES.......................................................................................................................... x

Chapter

1. ATLANTIC SALMON (Salmo salar) IN THE PENOBSCOT RIVER, MAINE: HISTORY OF RESTORATION EFFORTS AND THE NEED FOR EVALUATION................................................................................................................................. 1
   Introduction..................................................................................................................................... 1
   Hatchery Supplementation Practices............................................................................................. 2
   Effects of Dams on Migration......................................................................................................... 3
   The Penobscot River Restoration Project......................................................................................... 4
   Acoustic Telemetry as a Tool........................................................................................................... 5
   Project Goals................................................................................................................................. 6

2. EFFECTS OF HYDROELECTRIC DAMS ON SURVIVAL AND BEHAVIOR OF MIGRATING ATLANTIC SALMON (Salmo salar) SMOLTS IN THE PENOBSCOT RIVER, ME................................................................................. 7
   Abstract......................................................................................................................................... 7
   Introduction...................................................................................................................................... 9
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Materials and Methods</td>
<td>13</td>
</tr>
<tr>
<td>Field Methods</td>
<td>13</td>
</tr>
<tr>
<td>Tagging and release of hatchery and wild smolts</td>
<td>13</td>
</tr>
<tr>
<td>The acoustic array</td>
<td>14</td>
</tr>
<tr>
<td>Active searches for unsuccessful migrants</td>
<td>15</td>
</tr>
<tr>
<td>Collection of environmental data</td>
<td>15</td>
</tr>
<tr>
<td>Statistical Analyses</td>
<td>16</td>
</tr>
<tr>
<td>Parameter estimation</td>
<td>16</td>
</tr>
<tr>
<td>Movement rates</td>
<td>16</td>
</tr>
<tr>
<td>Path choice</td>
<td>17</td>
</tr>
<tr>
<td>Results</td>
<td>19</td>
</tr>
<tr>
<td>Parameter Estimation</td>
<td>19</td>
</tr>
<tr>
<td>Movement Rates</td>
<td>20</td>
</tr>
<tr>
<td>Use of the Stillwater Branch</td>
<td>20</td>
</tr>
<tr>
<td>Active Searches</td>
<td>24</td>
</tr>
<tr>
<td>River Discharge and Flashboard Installation Dates</td>
<td>25</td>
</tr>
<tr>
<td>Discussion</td>
<td>26</td>
</tr>
<tr>
<td>Locations of Mortality and Potential Causes</td>
<td>26</td>
</tr>
<tr>
<td>Dams</td>
<td>26</td>
</tr>
<tr>
<td>Release site</td>
<td>28</td>
</tr>
<tr>
<td>Movement Rates, Predation, and Physiological Impairment</td>
<td>29</td>
</tr>
<tr>
<td>Use of the Stillwater Branch</td>
<td>30</td>
</tr>
<tr>
<td>Implications for Restoration</td>
<td>31</td>
</tr>
</tbody>
</table>
3. COMPARATIVE CONDITION AND MIGRATORY PERFORMANCE

OF HATCHERY AND WILD ATLANTIC SALMON (*Salmo salar*)

SMOLTS IN THE PENOBScot RIVER, MAINE................................. 33

Abstract.................................................................................. 33

Introduction............................................................................. 35

Materials and Methods............................................................ 39

Field Methods......................................................................... 39

The acoustic array.................................................................. 39

Tagging and release of hatchery and wild smolts.................... 39

Laboratory Methods................................................................. 41

Statistical Analyses................................................................. 42

Survival estimation................................................................. 42

Movement rates....................................................................... 43

Results.................................................................................... 44

Survival Near the Release Site.................................................. 44

Comparing Hatchery and Wild Smolts.................................... 44

Freshwater and estuarine survival......................................... 44

Smolt condition and migration timing.................................... 44

Comparing Among Hatchery Groups...................................... 46

Freshwater and estuarine survival......................................... 46

Behavioral synchrony and time in freshwater....................... 48

Smolt condition and relation to behavior............................... 48
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Discussion</td>
<td>50</td>
</tr>
<tr>
<td>Comparison of Hatchery and Wild Smolts</td>
<td>50</td>
</tr>
<tr>
<td>Comparative Survival and Behavior for Various Stocking Strategies</td>
<td>52</td>
</tr>
<tr>
<td>4. MOVEMENTS OF PRE-SPAWN ATLANTIC SALMON (Salmo salar)</td>
<td>56</td>
</tr>
<tr>
<td>NEAR HYDROELECTRIC DAMS IN THE LOWER PENOBSCOT</td>
<td></td>
</tr>
<tr>
<td>RIVER, MAINE</td>
<td>56</td>
</tr>
<tr>
<td>Abstract</td>
<td>56</td>
</tr>
<tr>
<td>Introduction</td>
<td>57</td>
</tr>
<tr>
<td>Materials and Methods</td>
<td>61</td>
</tr>
<tr>
<td>Field Methods</td>
<td>61</td>
</tr>
<tr>
<td>The acoustic array</td>
<td>61</td>
</tr>
<tr>
<td>Tagging and release of salmon</td>
<td>62</td>
</tr>
<tr>
<td>Environmental data collection</td>
<td>63</td>
</tr>
<tr>
<td>Passage Analyses</td>
<td>63</td>
</tr>
<tr>
<td>Temperature Analyses</td>
<td>64</td>
</tr>
<tr>
<td>Results</td>
<td>66</td>
</tr>
<tr>
<td>2005 Passage Success</td>
<td>66</td>
</tr>
<tr>
<td>2006 Passage Success</td>
<td>69</td>
</tr>
<tr>
<td>River Temperature, Flow and Fallback Behavior</td>
<td>69</td>
</tr>
<tr>
<td>Discussion</td>
<td>73</td>
</tr>
<tr>
<td>REFERENCES</td>
<td>78</td>
</tr>
</tbody>
</table>
BIOGRAPHY OF THE AUTHOR

87
LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Table 2.1</td>
<td>Descriptive statistics for smolt release groups</td>
<td>14</td>
</tr>
<tr>
<td>Table 2.2</td>
<td>CJS survival estimates through river sections containing dams</td>
<td>19</td>
</tr>
<tr>
<td>Table 2.3</td>
<td>Use of the Stillwater Branch</td>
<td>23</td>
</tr>
<tr>
<td>Table 3.1</td>
<td>Descriptive statistics for smolt release groups</td>
<td>41</td>
</tr>
<tr>
<td>Table 4.1</td>
<td>Descriptive statistics for tagged adult salmon</td>
<td>62</td>
</tr>
</tbody>
</table>
# LIST OF FIGURES

| Figure 1.1 | Atlantic salmon life cycle | 1 |
| Figure 2.1 | Smolt monitoring map | 11 |
| Figure 2.2 | Smolt survival trajectories | 21 |
| Figure 2.3 | Movement rates, time of arrival and presence of dams | 22 |
| Figure 2.4 | Flows upon arrival at Marsh Island and use of the Stillwater Branch | 24 |
| Figure 2.5 | Discharge and cumulative arrival at Marsh Island | 25 |
| Figure 3.1 | Smolt survival through Release, Freshwater and Estuary | 45 |
| Figure 3.2 | Median detection date at each monitoring site | 47 |
| Figure 3.3 | Gill Na+,K+-ATPase activity versus movement rate to the estuary | 49 |
| Figure 4.1 | Adult salmon monitoring and release sites | 60 |
| Figure 4.2 | Monitoring sites near Great Works Stream | 61 |
| Figure 4.3 | Selected tracks for adult salmon | 67 |
| Figure 4.4 | Passage success at the Milford, Great Works and Veazie Dams, 1987-2006 | 68 |
| Figure 4.5 | Flow, temperature and fallback behavior | 70 |
| Figure 4.6 | Great Works Stream as a thermal refuge | 72 |
Chapter 1

ATLANTIC SALMON (*Salmo salar*) IN THE PENOBSCOT RIVER, MAINE:

HISTORY OF RESTORATION EFFORTS AND THE NEED FOR EVALUATION

**Introduction**

The Atlantic salmon (*Salmo salar*) is an iteroparous anadromous species that typically spends two to three years in freshwater and one to three years in the marine environment (Figure 1.1). While the majority of this life cycle takes place in either freshwater rearing habitats or adult feeding grounds at sea, rivers and estuaries serve as critical migration corridors. Successful migration through these corridors at both the smolt and adult stages is essential for perpetuation of a salmon population (Cutting 1963; NRC 2004; Fay et al. 2006;).

![Figure 1.1. Atlantic salmon life cycle.](image-url)
Historically, the Atlantic salmon (*Salmo salar*) was an important economic and cultural resource in the northeastern United States (Baum 1997). However, populations experienced precipitous declines throughout the 19th and 20th centuries, culminating in Endangered Species Act listing of populations in eight Maine rivers in 2000 (NRC 2004). Initial declines were caused by overfishing, pollution, and dams (Foster and Atkins 1867; Baum 1997) and many populations were likely extirpated during this time. Restoration efforts began as early as 1871, when the first hatchery was built to supplement declining runs (Moring 2000). However, more than 140 years after this hatchery was built, Maine salmon populations are at all-time low levels.

Today, the Penobscot River hosts the largest returning run of adult Atlantic salmon in the United States (USASAC 2005), yet total adult returns have fallen below 600 fish in recent years (USASAC 2004; Fay et al. 2006; Baum 1997). The continuing decline of wild stocks and the failure of hatcheries to stem declines have been attributed to persistence of many of the above problems, as well as to complications from more modern concerns surrounding agriculture, sylviculture, hatchery practices and oceanic regime changes (NRC 2004).

**Hatchery Supplementation Practices**

Hatchery supplementation has been a critical component of Atlantic salmon restoration in Maine, and is thought to have played a key role in preventing extinction. The smolt-stocking program appears to be more successful than other programs, since the majority of adult salmon returning to the Penobscot in recent years are of smolt-stocked origin (USASAC 2004). However, the smolt-to-adult return rate has declined steadily
over the past 30 years (Moring et al. 1995; USASAC 2005), indicating increased mortality in the river or at sea.

Studies in other systems have shown that hatchery-reared salmon incur higher mortality than their wild counterparts (Collis et al. 2001; Fresh et al. 2003; Johnsson et al. 2003). Behavioral or physiological differences that are critical to successful dam passage, predator avoidance, or seawater entry may be the cause of survival differences (Alvarez and Nicieza 2003; Fuss and Byrne 2002; Hockett 1994; Shrimpton et al. 1994). Thus, restoration smolts may be more vulnerable to predation, osmoregulatory impairment, or dam-induced injury than their wild counterparts.

Recent concern for the genetic and ecological effects of hatchery fish on extant wild populations has led to the development of guidelines for conservation-oriented hatcheries (Flagg and Nash 1991). Flagg and Nash recommend that conservation hatcheries define quality standards, and set clear goals for production, based on characteristics of wild populations. Thus, it is critical that restoration programs seek to quantify, and understand the basis for, variation in hatchery and wild smolt performance if they are to use the tool of hatchery supplementation effectively. The relative performance and behavior of hatchery and wild smolts in the Penobscot River may allow direct evaluation of hatchery smolt performance relative to wild smolts in this system.

**Effects of Dams on Migration**

Dams have been identified as one of the most acute impediments to salmon restoration in Maine (NRC 2004). As complete or partial barriers to upstream migration, dams effectively reduce the use of upstream spawning and rearing habitats (Fay et al.
2006). These effects are commonly mitigated by hatchery supplementation, trapping and transportation, and the installation of upstream fish passage devices (NRC 1996; Flagg and Nash 1999).

Although dams rarely exclude all juvenile migrants from reaching downstream river sections, dams are known to be a site of impact through direct injury and migratory delay during downstream passage (NRC 2004, Nettles and Gloss 1987). Direct injuries can be caused by contact with dam structures or pressure changes during turbine entrainment (Cada 2000). Delays may further increase predation risk (Nettles and Gloss 1987) or cause poor synchrony of physiological tolerance to salinity (Whalen et al. 1999; McCormick et al. 1999).

Nearly all of the high-quality rearing habitats in the Penobscot River are located upstream of four hydroelectric dams (Fay et al. 2006). To complete its life cycle, nearly every sea-run individual must successfully pass all of these dams, both during juvenile seaward migration and adult upriver migration. Even when losses at individual dams are small, the cumulative losses (both direct and indirect) at several dams can be substantial.

**The Penobscot River Restoration Project**

Previous studies in the Penobscot River have suggested that significant mortality occurs between upriver release sites and marine entry (Shepard 1991b; Spicer et al. 1995). Mortality may be attributed to predation (Blackwell 1995) or entrainment at hydroelectric dams (USASAC 2004). The Penobscot River Restoration Project (PRRP) provides some hope for ameliorating some of these negative effects through dam removal and decommissioning (PPL Maine et al. 2004). However, hydroelectric generation lost by
these efforts will be recovered by increased generation at other projects within the drainage, some in an alternative migratory passage route (e.g., Stillwater Branch). The costs or benefits of planned hydro-system alterations will thus depend on the relative influences of different dams and passage routes after implementation of the PRRP.

**Acoustic Telemetry as a Tool**

Previous fish passage and behavior studies on the Penobscot River have been limited to specific dam facilities or sections of river (e.g., estuarine or freshwater only), because methods were restricted to labor-intensive mobile telemetry, or passive telemetry at only a few fixed sites. The recent development of miniature acoustic transmitters and self-contained, continuously monitoring receivers, now allows researchers to track individual fish using a fixed array of stationary receivers in both freshwater and marine environments (Voegeli et al. 1998; Clements et al. 2005).

In the studies presented here, an extensive time-stamped series of detections was used to quantify (1) survival, (2) movement rates, and (3) path choice over more than 200 km of the Penobscot River and estuary. The large number of stationary monitoring sites provided high spatial precision and parameter estimation (e.g., survival and detection probabilities) approaches that were not attainable with prior methods. Moreover, such an extensive tracking network afforded the ability to provide perspective on the relative importance of various sections, management actions and restoration targets within the larger migratory challenges faced by these fish.
**Project Goals**

This thesis presents a direct characterization and quantification of pre-removal conditions, as they pertain to both downstream (Chapter 2) and upstream (Chapter 4) passage at hydroelectric dams. Further, a comparative assessment of migratory condition, behavior, and survival among hatchery release groups, as well as between hatchery and wild-reared smolts is presented (Chapter 3). This information would help managers determine which rearing and release practices best meet the goals of the restoration program. Such baseline information is necessary to design restoration approaches and evaluate the relative costs and benefits of restoration efforts, including hatchery supplementation and the PRRP.
Chapter 2

EFFECTS OF HYDROELECTRIC DAMS ON SURVIVAL AND BEHAVIOR
OF MIGRATING ATLANTIC SALMON (Salmo salar) SMOLTS
IN THE PENOBSCOT RIVER, MAINE

Abstract

Survival and behavior of migrating hatchery (n=493) and naturally-reared (n=133) Atlantic salmon (Salmo salar) smolts were evaluated in 2005 and 2006 through the Penobscot River and estuary in Maine using acoustic telemetry. Mortality, movement rates, and use of a secondary migration path (the Stillwater Branch) were quantified. River sections containing three mainstem dams (Howland, Milford and West Enfield dams) accounted for 43% and 60% of total losses for 2005 and 2006, respectively, though these sections accounted for only 16% and 6% of monitored reaches. Survivorships through sections with dams ranged from 85-100% and 71-100% in 2005 and 2006, respectively. Movement rates were significantly slower at dams compared to free-flowing reaches, and smolts arriving at dams during the day experienced longer delays than smolts arriving at night. Use of the Stillwater Branch by individual release groups ranged from 0-26% and 0-19% in 2005 and 2006, respectively; was significantly lower for groups released in a tributary compared to the mainstem; and was positively associated with river discharge. As part of the Penobscot River Restoration Project, the planned removal of two dams is expected to enhance passage through the mainstem corridor for salmon and other migratory fish. However, this study demonstrates that the two dams scheduled for removal (Great Works and Veazie dams) had little affect on
smolt survival and highlights the need to improve passage at the Milford, Howland and West Enfield dams, as well as at facilities in the Stillwater Branch, which will likely be passed by more smolts after hydro-system changes are implemented.
Introduction

Juvenile anadromous fishes require uninterrupted passage through riverine habitats in order to successfully reach the marine environment. During migration, immediate or delayed mortality may result from predation or direct injury from turbines or other dam-related structures (Ruggles 1980; NMFS 2000). Migratory delays caused by physical or behavioral barriers may further increase predation risk (Nettles and Gloss 1987; Blackwell and Krohn 1997) or cause poor synchrony of physiological tolerance to salinity (McCormick et al. 1999), possibly increasing estuarine mortality (Budy et al. 2002; Ferguson et al. 2006). Identifying and mitigating such artificial mortality is thus an important component of programs that seek to maintain or restore anadromous salmonid populations.

Atlantic salmon (Salmo salar) populations throughout New England have experienced precipitous declines. Populations in eight Maine rivers were listed as Endangered under the Endangered Species Act in 2000 (NRC 2004). While the causes of decline are numerous, the National Research Council (2004) identified dams as one of the greatest and most acute impediments to Atlantic salmon restoration in Maine.

The Penobscot River hosts the largest population of adult Atlantic salmon in the U. S. (USASAC 2004). Restoration efforts include the release of hatchery-reared fry, parr and smolts throughout the Penobscot Drainage (Moring et al. 1995; Baum 1997). Although most adults returning in recent years are of smolt-stocked origin (USASAC 2004), the smolt-to-adult return rate has steadily declined since 1970 (Moring et al. 1995; USASAC 2005), indicating increased mortality in the river or at sea.
Earlier studies have suggested that survival of migrating smolts through the mainstem is low (Spicer et al. 1995) and that dams may be responsible for some of these losses (USASAC 2004). In the Penobscot River, an estimated 76% of spawning and rearing habitats are located upstream of the four lowermost hydroelectric dams (Fay et al. 2006). Losses at these dams effectively reduce the productivity of upstream rearing habitats and the efficacy of hatchery supplementation. However, only two of the 24 hydroelectric dams in the Penobscot River watershed are equipped with downstream passage facilities designed specifically for smolts (West Enfield and Weldon; see USASAC 2005). Despite these efforts, studies have demonstrated an overall effectiveness for these facilities ranging from only 8-59% (see USASAC 2005; Fay et al. 2006). Downstream passage at all other dams occurs via spill (i.e., in water passing over the dam) or through turbines or sluiceways (USASAC 2005), with unassessed or questionable effectiveness.

Information on Atlantic salmon smolt survival through the mainstem of the Penobscot River is limited to studies conducted by Shepard (1991a) and Spicer et al. (1995). These two studies present a wide-range of survival estimates (Fay et al. 2006) due to small sample sizes and technological limitations (i.e., few monitoring sites; high tag failure rates; low or unknown detection probabilities). Thus, the extent of loss and delay at most dams, particularly those in the lower river, has been poorly characterized.

The need for such data has been recently heightened due to the Penobscot River Restoration Project (PRRP); wherein, Pennsylvania Power and Light Maine (PPL Maine) has agreed to sell three hydroelectric dams in the Penobscot Drainage for eventual
Figure 2.1: Smolt monitoring map. Map of the Penobscot River with dams, acoustic monitoring sites, and release sites near the towns of Milo (R1), Howland (R2), Mattawamkeag (R3) and below the Weldon Dam (R4).
removal (Veazie and Great Works dams; Figure 2.1) and/or decommissioning (Howland Dam). While these measures are anticipated to ameliorate some effects of the hydroelectric dams on Penobscot River salmon, conditions will change at other facilities; PPL Maine will be able to install additional turbines at three dams (Milford, Stillwater and Orono dams) and raise head pond levels at two others (West Enfield and Stillwater dams). These developments will likely change the passage risks associated with the remaining facilities. Additionally, PPL Maine will be allowed to alter flows in order to utilize increased hydroelectric generation capacity in the Stillwater Branch (PPL Maine et al. 2004). Changes in flow regime may alter the path taken by downstream migrants. Without concurrent downstream passage improvements, these activities stand to increase threats to smolts, particularly for fish utilizing the Stillwater Branch, and may offset, to some degree, the benefits of restoration.

Shepard (1991a) estimated that 20-41% of smolts use the Stillwater Branch, though this estimate had considerable uncertainty. A robust estimate of use of the Stillwater Branch versus the mainstem path is necessary to assess usage under the current flow regime and to predict changes following PRRP efforts. Evaluation of passage improvements or costs associated with the PRRP requires the direct characterization and quantification of pre-removal conditions.

In this study, acoustic telemetry was used to assess path choice, transit times and losses (assumed mortality) for both hatchery and wild smolts through the Penobscot River and estuary (Figure 2.1). Survival, delays at dams, and path choice are reported for 2005 and 2006.
Materials and Methods

Field Methods

Tagging and release of hatchery and wild smolts

Hatchery-reared smolts were obtained from Green Lake National Fish Hatchery and transported in a 760 L tank, with aeration, to release sites (Figure 2.1). At each release site, each smolt was anesthetized with buffered MS-222 (100 mg·L⁻¹, NaC₃O₃, pH=7.0), length and weight were measured, and a non-lethal gill biopsy was collected for gill Na⁺,K⁺-ATPase analysis. The relationship between these condition-related characters and smolt survival and movement is discussed in the next chapter.

Acoustic transmitters (V7-2L and V9-6L, Vemco Ltd., Halifax, Nova Scotia, in 2005 and 2006, respectively) were surgically implanted into each smolt through a ventral incision, which was subsequently sutured with 5-0 coated Vicryl absorbable sutures (Ethicon, Inc., Somerville, New Jersey). Smolts were held in an aerated holding tank for a minimum of 30 minutes post-surgery. V7 transmitters were 7 mm in diameter, 18.5 mm long, weighed 1.6 g in air (0.75 g in water) and had an estimated tag life of 80 days. V9 transmitters were 9 mm in diameter, 20 mm in length, weighed 3.3 g in air (2.0 g in water) and had an estimated tag life of 70 days. Each transmitter emitted a unique pattern of acoustic pulses on a random interval ranging from 20 to 60 seconds.

Groups of 40-76 hatchery-reared smolts (Table 2.1) were released in April to coincide (within one day) with scheduled GLNFH releases of 15,000 to 40,000 smolts at three locations in 2005 (Figure 2.1); the Pleasant River near the town of Milo (Site 1), the Penobscot River near the town of Howland (Site 2), and the Mattawamkeag River near the town of Mattawamkeag (Site 3). In 2006, tagged hatchery smolts were released in
April at Milo and Weldon (in the Penobscot River below the Weldon Dam; Site 4) to coincide with GLNFH releases, and in May at Weldon to coincide with the release of tagged wild smolts.

In both years, wild smolts were collected at the Weldon Dam smolt bypass trap in May, surgically implanted with acoustic tags, and released at Weldon (Table 2.1). In 2006, scale samples were collected to determine age of wild smolts.

The acoustic array

An array of up to 117 stationary acoustic receivers (VR2, Vemco) was deployed and maintained, in cooperation with NOAA National Marine Fisheries Service (NOAA Fisheries), from April through November, 2005 and 2006 in the Penobscot River, estuary and bay (Figure 2.1). Receivers contained omni-directional hydrophones, monitored continuously at 69 kHz, and were deployed to cover the entire width of the system at up

Table 2.1: Descriptive statistics for smolt release groups. Year, origin, release site, release date, number (N), fork length (FL, in mm), weight (W, in g) for groups of hatchery (H) and wild (W) smolts released in 2005 and 2006.

<table>
<thead>
<tr>
<th>Year</th>
<th>Origin</th>
<th>Site</th>
<th>Date</th>
<th>N</th>
<th>FL (Range)</th>
<th>W (Range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>H</td>
<td>Matt</td>
<td>14-Apr</td>
<td>40</td>
<td>185 (154-220)</td>
<td>68.7 (41.2-113.7)</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Howl</td>
<td>19-Apr</td>
<td>74</td>
<td>185 (156-212)</td>
<td>69.9 (40.5-112.0)</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Milo</td>
<td>21-Apr</td>
<td>40</td>
<td>190 (159-217)</td>
<td>74.5 (43.6-114.7)</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Howl</td>
<td>27-Apr</td>
<td>76</td>
<td>192 (175-214)</td>
<td>80.4 (57.8-117.6)</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Milo</td>
<td>27-Apr</td>
<td>45</td>
<td>193 (173-214)</td>
<td>79.9 (58.0-114.1)</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>Weld</td>
<td>26-May</td>
<td>60</td>
<td>178 (148-227)</td>
<td>52.3 (28.5-107.9)</td>
</tr>
<tr>
<td>2006</td>
<td>H</td>
<td>Weld</td>
<td>12-Apr</td>
<td>73</td>
<td>190 (166-216)</td>
<td>76.7 (49.0-115.8)</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Milo</td>
<td>24-Apr</td>
<td>72</td>
<td>196 (169-225)</td>
<td>86.6 (53.3-136.4)</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Weld</td>
<td>8-May</td>
<td>73</td>
<td>209 (184-233)</td>
<td>97.3 (64.5-137.2)</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>Weld</td>
<td>8-May</td>
<td>73</td>
<td>189 (170-215)</td>
<td>61.9 (45.2-99.1)</td>
</tr>
</tbody>
</table>
to 38 sites per year. In some instances (e.g., wide river sections or islands) several acoustic receivers were necessary for complete coverage. Detections on these receivers were pooled and treated as a single site. Additionally, all receivers in Penobscot Bay (beyond Fort Point) were pooled and treated as a single site. Receivers were moored on the bottom of the river at freshwater and estuarine sites, and approximately 10 m below the surface in the bay. Data were downloaded at least monthly throughout the period of smolt migration.

Active searches for unsuccessful migrants

In 2006, active searches were conducted from canoes using a mobile acoustic receiver (VR-100, Vemco) with an omni-directional hydrophone. Five searches were conducted between the Great Works and Veazie dams throughout July. Date, time and location were recorded for each detection using a handheld geographic positioning system.

Collection of environmental data

Daily river discharge at the United States Geological Survey’s (USGS) gauging station for the Penobscot River at West Enfield was obtained from the USGS Water Data website (www.waterdata.usgs.gov). Specific data on dam operations (e.g. flashboards installation dates) were provided by PPL Maine.
Statistical Analyses

Parameter estimation

Survivorship ($\Phi$) and detection ($\rho$) probabilities were estimated between monitoring sites using the Cormack-Jolly-Seber (CJS) release-recapture model (Cormack 1964; Jolly 1965; Seber 1965). Parameters were estimated from complete capture histories (Burnham et al. 1997) at up to 24 sites, with removals in Program MARK (White and Burnham 1999). We used the full CJS model, where both $\Phi$ and $\rho$ are site-dependent, for each release group. Although no tagged fish were physically removed by researchers during the study, fish detected in the Stillwater Branch were removed from analyses at the last detection upstream of the Stillwater confluence. Thus, parameter estimates downstream from this point (~65 km upstream of the river mouth) represent fish that passed the Milford and Great Works dams, as opposed to Stillwater and Orono dams.

Movement rates

Because movement rates between individual monitoring sites were only calculated for the 2006 study, low detection efficiencies during the 2005 study period did not provide adequate sample sizes for calculation of site-to-site movement rates. To provide direct comparison among river sections, the movement rate ($R_{ij}$; Eqn. 1) was calculated for each smolt between any two monitoring sites,

$$R_{ij} = D_{ij} \times (T_j - T_i)^{-1}$$

Eqn. 1.
where $D_{i,j}$ is the distance (in km) between upstream site $i$ and downstream site $j$, and $T_j$ and $T_i$ represent date and time of first detection at sites $j$ and $i$, respectively. Similar detection range at each site is assumed.

Movement rates through each section containing a dam were compared to a reference section (i.e., free-flowing section) using a Wilcoxon paired samples test (Zar 1999). Reference sections selected for the West Enfield, Howland, and Milford dams were located immediately upstream of sections containing those dams. A single reference section was used for both the Great Works and Veazie dams, and was located between the two dams. The movement rate for each fish through each of these sections was expressed relative to the median rate through the corresponding reference section at night. A Kruskall-Wallis test was conducted to determine if relative movement rates differed significantly among smolts arriving during the day (between sunrise and sunset) and night and through river sections with and without dams. When significant differences were detected, a nonparametric multiple comparisons test (Zar 1999) was conducted to determine if differences were associated with arrival time (day versus night) and/or the presence of dams. The significance level for all tests was set at 0.05.

Path choice

The proportion of smolts passing through the Stillwater Branch was compared to the proportion passing through the mainstem around Marsh Island. Based on detections in the vicinity of Marsh Island and farther downstream, smolts were identified as having passed via the Stillwater Branch, the mainstem, or unknown routes (i.e., not detected but known to have passed). It was assumed that undetected passage through the Stillwater
Branch was unlikely (see Discussion) and smolts with unknown routes were attributed to mainstem passage.

To determine if proportional use of the Stillwater Branch was significantly different between any two groups, a G test (i.e., log-likelihood ratio test) was conducted with Yates correction (Zar 1999). Additionally, a two-sample Kolmogorov-Smirnov test and Kruskall-Wallis tests were performed to determine if discharge upon arrival or date of arrival at Marsh Island, respectively, were significantly different between hatchery smolts released in the mainstem (Howland or Weldon) and at Milo. When significant differences in date of arrival were detected among groups, a non-parametric multiple comparisons test was used to determine which groups differed.
**Results**

Parameter Estimation

Mean detection probabilities within each release group ranged from 52-54% and 95-96% in 2005 and 2006, respectively.

Survivorships through sections containing dams were generally lower in 2006 than in 2005 (Table 2.2). Losses ranged from 3-72% among release groups near the release site (between release and the second receiver downstream; Figure 2.2) and were minimal in the upper estuary. Losses occurring in river sections containing the Howland, West Enfield and Milford dams accounted for 43% and 60% of all losses (excluding losses within two monitoring sites downstream of release) in 2005 and 2006, respectively. The sections containing these three dams represented 16% and 6% of the total study region (by river km) in 2005 and 2006, respectively. Sections were similar in

**Table 2.2: CJS survival estimates through river sections containing dams.**

Survivorship probabilities for all groups through sections of river containing dams in 2005 and 2006. ID denotes insufficient data (n<10). Standard errors (SE) represent theoretical sampling error from the CJS model.

<table>
<thead>
<tr>
<th>Year</th>
<th>Release</th>
<th>Origin</th>
<th>Site</th>
<th>Date</th>
<th>Howland (SE)</th>
<th>West Enfield (SE)</th>
<th>Milford (SE)</th>
<th>Great Works (SE)</th>
<th>Veazie (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>H</td>
<td>Matt</td>
<td>14-Apr</td>
<td>ID</td>
<td>1.00 (0.00)</td>
<td>1.00 (0.00)</td>
<td>1.00 (0.00)</td>
<td>1.00 (0.00)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Howl</td>
<td>19-Apr</td>
<td></td>
<td>0.96 (0.22)</td>
<td>0.89 (0.08)</td>
<td>1.00 (0.00)</td>
<td>1.00 (0.00)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Milo</td>
<td>21-Apr</td>
<td></td>
<td>0.87 (0.06)</td>
<td>1.00 (0.00)</td>
<td>1.00 (0.00)</td>
<td>1.00 (0.00)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Howl</td>
<td>27-Apr</td>
<td></td>
<td>0.85 (0.10)</td>
<td>0.88 (0.08)</td>
<td>0.92 (0.07)</td>
<td>1.00 (0.00)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Milo</td>
<td>27-Apr</td>
<td></td>
<td>0.86 (0.09)</td>
<td>0.92 (0.08)</td>
<td>1.00 (0.00)</td>
<td>1.00 (0.00)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>Weld</td>
<td>26-May</td>
<td></td>
<td>0.80 (0.06)</td>
<td>0.81 (0.07)</td>
<td>0.96 (0.04)</td>
<td>0.96 (0.04)</td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>H</td>
<td>Weld</td>
<td>12-Apr</td>
<td></td>
<td>0.81 (0.07)</td>
<td>0.96 (0.04)</td>
<td>1.00 (0.00)</td>
<td>1.00 (0.00)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Milo</td>
<td>24-Apr</td>
<td></td>
<td>0.71 (0.06)</td>
<td>0.84 (0.05)</td>
<td>1.00 (0.00)</td>
<td>1.00 (0.00)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Weld</td>
<td>8-May</td>
<td></td>
<td>0.89 (0.05)</td>
<td>0.75 (0.08)</td>
<td>1.00 (0.00)</td>
<td>1.00 (0.00)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Weld</td>
<td>8-May</td>
<td></td>
<td>0.87 (0.07)</td>
<td>0.85 (0.10)</td>
<td>0.91 (0.09)</td>
<td>1.00 (0.00)</td>
<td></td>
</tr>
</tbody>
</table>
length between years (Figure 2.2), except that sections containing the West Enfield and Howland dams were longer (~16 and 18 km, respectively) in 2005 compared to 2006 due to receiver placement and failure. The proportion of smolts using the Stillwater Branch did not provide a sufficient sample size for estimating survivorship through reaches containing the Stillwater, Orono, or Gilman Falls dams separately. However, in 2005 and 2006, 96% (26/27) and 100% (8/8) of smolts detected in the Stillwater were detected in the estuary. Over both years combined, only one of these failed to reach Verona Island, approximately 50 km downstream.

Movement Rates

Movement rates were significantly lower through the segments containing dams versus reference reaches (Wilcoxon paired sample tests, α=0.05, p≤0.009). For all release groups, rates of passage were significantly lower through sections containing dams compared to sections lacking dams for fish arriving to the section in the day (Figure 2.3). Conversely, no such differences were observed for fish arriving at night. For sections containing dams, the movement rate of fish arriving in the day was significantly lower than the movement rate of those arriving at night, for three of the four release groups (Figure 2.3b-d).

Use of the Stillwater Branch

Proportional use of the Stillwater Branch ranged from 0-26% and 0-19% among release groups in 2005 and 2006, respectively (Table 2.3). In 2005, proportional use of the Stillwater Branch was not significantly different between early and late released
Figure 2.2: Smolt survival trajectories. Estimated survival for individual release groups from release (~99, 143 and 149 km) to Fort Point (~ -3.9 km) in (a, b) 2005 and (c, d) 2006. Solid vertical lines represent dams. The first dam encountered is the West Enfield Dam (~102 km) for smolts released at (a, c) Howland, Weldon or Mattawamkeag, and the Howland Dam (~100 km) for smolts released at (b, d) Milo. Other dams are the Milford (~63 km), Great Works (~60 km), and Veazie (~48 km) dams.
Figure 2.3: Movement rates, time of arrival and present of dams. Relative movement rates for fish arriving during the day (unshaded boxplots) or night (shaded boxplots) at sections with and without dams, for hatchery smolts released on (a) April 12, (b) April 24, (c) May 8, and wild smolts released (d) May 8. Different italicized letters indicate significant differences (non-parametric multiple comparisons test, Q > 2.639, p < 0.05).
groups at either Milo or Howland (G test, G≤0.534, df=1, p≥0.465). In both years, smolts released at Milo used the Stillwater Branch at a significantly lower rate than hatchery or wild smolts released in the mainstem (G test, G≥7.70, df=1, p≤0.006). In 2005, date of arrival at Marsh Island was significantly different among the four groups released at Milo and Howland (Kruskal-Wallis test; df=3; H=15.48; p = 0.001). Significant differences were associated with timing of release (i.e., “early” vs. “late”; non-parametric multiple comparisons test; Q≥2.75, p<0.05) and not release location (Q≤0.57, p>0.50).

Proportional use of the Stillwater Branch tended to increase with increasing discharge at West Enfield in 2005 (Figure 2.4b), although the proportions are not significantly different among discharge bins due to small sample sizes. There was no difference in discharge at arrival between smolts released at Milo and the mainstem within either year (Figure 2.4a). A higher proportion of smolts arrived at lower flows in 2006 compared to 2005.

Table 2.3: Use of the Stillwater Branch. Proportion and number of hatchery (H) and wild (W) smolts using the Stillwater Branch as a migration path in 2005 and 2006.

<table>
<thead>
<tr>
<th>Year</th>
<th>Origin</th>
<th>Release Site</th>
<th>Date</th>
<th>Frequency</th>
<th>Use of Stillwater (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Stillwater</td>
<td>Mainstem</td>
</tr>
<tr>
<td>2005</td>
<td>H</td>
<td>Matt</td>
<td>14-Apr</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Howl</td>
<td>19-Apr</td>
<td>10</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Milo</td>
<td>21-Apr</td>
<td>1</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Howl</td>
<td>27-Apr</td>
<td>7</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Milo</td>
<td>27-Apr</td>
<td>0</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>Weld</td>
<td>26-May</td>
<td>7</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>ALL</td>
<td></td>
<td>27</td>
<td>107</td>
</tr>
<tr>
<td>2006</td>
<td>H</td>
<td>Weld</td>
<td>12-Apr</td>
<td>4</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Milo</td>
<td>24-Apr</td>
<td>0</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>Weld</td>
<td>8-May</td>
<td>1</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>Weld</td>
<td>8-May</td>
<td>3</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>ALL</td>
<td></td>
<td>8</td>
<td>122</td>
</tr>
</tbody>
</table>
Figure 2.4: Flows upon arrival at Marsh Island and use of the Stillwater Branch. (a) Cumulative proportions of smolts reaching Marsh Island at various discharge levels in 2005 and 2006 for hatchery smolts released in the main stem (Howland or Weldon) and at Milo in April. (b) Proportional use of the Stillwater Branch by smolts released at Howland in 2005. Error bars represent binomial standard errors.

Active Searches

A total of 11 acoustic transmitters were found between the Great Works and Veazie dams in 2006. All transmitters were found stationary near a cable suspended across the river approximately 2.7 km downstream of Great Works Dam. All release groups were represented by transmitters detected at this site (N=2, 3, and 5 for hatchery smolts released at Weldon on 4/12, Milo on 4/14, and Weldon on 5/8; N=1 for wild smolts released at Weldon on 5/8). Detection histories from stationary receivers indicate that all 11 smolts were last detected at receivers in the Milford head pond (6.55 km upstream), but none were detected in the Great Works head pond (3.27 km upstream), despite 100% detection probability in the Great Works head pond for all release groups.
These transmitters represent 45.8% (11/24) of all fish lost at the Milford Dam, and the cable is a known cormorant roosting site (Blackwell 1995).

River Discharge and Flashboard Installation Dates

In 2005, most hatchery smolts reached Marsh Island at flows between 250 and 1,250 m$^3$s$^{-1}$ (Figure 2.5). In 2006, most smolts reached Marsh Island at flows between 300 and 550 m$^3$s$^{-1}$. Thus, most smolts moved at lower flows in 2006 compared to 2005. Peak mean daily discharge at West Enfield in April was approximately 2,860 and 1,175 m$^3$s$^{-1}$ in 2005 and 2006, respectively.

![Figure 2.5: Discharge and cumulative arrival at Marsh Island.](image)

**Figure 2.5: Discharge and cumulative arrival at Marsh Island.** Daily mean discharge at West Enfield and cumulative relative frequency of arrival at Marsh Island for hatchery and wild smolts in (a) 2005 and (b) 2006.
Discussion

Locations of Mortality and Potential Causes

Dams

A substantial proportion of all losses (43 and 60% in 2005 and 2006, respectively) occurred in the vicinity of the West Enfield, Howland and Milford dams. Estimated survivorship at these dams ranged from 80-89%, 71-96%, 75-100%, respectively, among years. Although these data do not definitively reveal sources of mortality, these losses are likely attributable to the direct and indirect effects of the dams (e.g., physical injury, predation). Physical injury during passage can occur during turbine entrainment (Cada 2001) or during passage via spill or bypass structures (Ruggles 1980; Coutant and Whitney 2000).

The rate of entrainment mortality depends on two probabilities; the probability that fish will enter a turbine bay (entrainment) and the probability they will suffer mortality as a result of turbine passage, which varies with turbine types and fish size (EPRI 1992; Coutant and Whitney 2000). Previous studies have revealed that turbine entrainment at the Milford and West Enfield dams ranged from 38-44% (Shepard 1991a) and 38-92% (Shepard 1991b; Shepard 1991c; BPHA 1993a; Shepard 1993), respectively, in the early 1990s.

In the only empirical study of actual turbine mortality for Penobscot River dams, Bangor-Pacific Hydro Associates (BPHA; 1993a) estimated acute turbine mortality to be 2.3%. No other such studies have been conducted in the Penobscot Drainage, but model-based turbine mortality estimates for the Weldon, Milford and Veazie dams range from 5-9% per dam (USASAC 2005). Recent assessments by NOAA Fisheries have shown that
many smolts captured in the lower Penobscot River possessed injuries consistent with
turbine entrainment (USASAC 2004). Further, mortality and injury were more frequent
in the lower Penobscot River compared to a smaller river (Narraguagus River) lacking
hydroelectric dams (USASAC 2004). Injured and disoriented smolts may become more
vulnerable to predators after passage (Raymond 1979; Riemann et al. 1991, Mesa 1994).
Even when mortality at individual dams is low, cumulative losses over dams can be
substantial (Coutant and Whitney 2000).

While the installation of downstream fishways and bypass structures may offer
some hope for ameliorating the potential negative effects of increased hydroelectric
generation, such measures should be given careful consideration. Only two dams in the
Penobscot River are equipped with formal downstream bypass facilities (West Enfield
and Weldon; USASAC 2005; Fay et al. 2006). The effectiveness of these facilities has
ranged from 2-22% (Shepard 1991b, Shepard 1991c, BPHA 1993a, Shepard 1993) and
17-59% (GNP 1998, GNP 1999), respectively, in the early 1990s, and modifications to
these structures have ultimately failed to improve collection efficiencies (BPHA 1993b;
Brown and Bernier 2000). These studies have shown that existing downstream bypass
structures at Penobscot River dams perform poorly and efforts to improve bypass
efficiency have had little success. Fortunately, bypasses have been successful at small
hydroelectric dams in other systems (Simmons 2000).

Estuarine survival was high in both years (Figure 2.2), particularly through the upper
estuary, indicating that delayed mortality was probably not a significant factor, at least
for lower river dams. However, delayed mortality may not be apparent until after marine
entry (Budy et al. 2002).
Entrainment rate, bypass efficiency, and proportional spill are often directly related to flow conditions at dams (Coutant and Whitney 2000). Flow conditions are largely determined by river discharge and dam operations. Low river discharge in 2006 (Figure 2.5) allowed installation of flashboards at the West Enfield and Howland dams during the period of smolt emigration (Scott Hall, PPL Maine, personal communication). During this time, all but a short section of the Milford Dam contained flashboards (Holbrook, personal observation). Conversely, flashboards were not installed at dams with better smolt passage—the Veazie or Great Works dams. The effects of flashboard installation may have compounded the effects of low flows in contributing to higher observed mortality in 2006 than 2005.

**Release site**

All hatchery and wild release groups, with the exception of the Milo release group in 2006, exhibited substantial losses (range 2-72%) near the release site in both years (Figure 2.2). Similarly, high rates of tag loss near the release site were observed by Spicer et al. (1995) and Bangor-Pacific Hydro Associates (BPHA 1993a). Similar losses for both hatchery and wild smolts suggest that these losses may be attributable to indirect effects of pre-release handling (e.g., transport, anesthesia, surgery). Results from the dummy-tagging studies in 2005 revealed that the handling and tagging process does not cause direct mortality (Holbrook, unpublished data), but other factors could compound the effects of tagging after release (i.e., predation, turbulence, etc.).
Movement Rates, Predation, and Physiological Impairment

This study and others (BPHA 1993a) have shown that migratory delays most often occur during the day, rather than at night (Figure 3.4). Delays can increase exposure to predators (Blackwell and Krohn 1997; Riemann et al. 1991; Venditti et al. 2000) or cause physiological loss of osmoregulatory capacity (McCormick et al. 1999). Blackwell and Krohn (1997) reported that double-crested cormorants (*Phalacrocorax auritus*), which mainly feed during daylight hours, were observed feeding in headponds, under spillways and in tailraces. Specifically, the Milford, West Enfield, Howland and Great Works dams were identified as regular feeding sites for cormorants. Further, the site where 11 smolt tags were discovered in 2006 had been previously identified as a cormorant roosting site (Blackwell 1995). Daytime migratory delays could increase exposure of smolts to feeding cormorants (a visual predator) and may have been responsible for losses at dams in 2005 and 2006. Blackwell (1995) estimated that cormorants annually consumed approximately 7% of all hatchery smolts in the Penobscot River. Although predation by cormorants may be considered a natural source of mortality, the influence of dams on water velocities and smolt behavior likely increases the rate of predation.

During the study period, we suspected that most smolts would reach seawater between the north tip of Verona Island (river km ~7.0) and the marine site at Fort Point (river km ~3.9). Some groups (e.g., smolts released at Milo on April 27, 2005; Figure 2.2c) did show depressed survival through this region. These losses could be due to predation or physiological impairment. However, physiological desmolting would likely require more prolonged exposure to the temperatures observed in the Penobscot River.
during the migration period (McCormick et al. 1999). At this time, we do not know the degree to which detection and survival probabilities contribute to low recovery rates at the most downstream estuarine site. Further evaluation of survival through the estuary and bay is currently being conducted in collaboration with NOAA Fisheries and will be presented in a future publication.

Use of the Stillwater Branch

These results indicate that hatchery and wild smolts used the Stillwater Branch (Table 2.3) as a migration corridor, particularly at higher flows (Figure 2.4b). Lower flows in 2006 are likely responsible for lower use of the Stillwater during that year compared to 2005. The upper range of observed rates of use of the Stillwater Branch (0-26%) in 2005 is similar to that reported by Shepard (1991a). Qualitative assessments of conditions in the Stillwater revealed a more favorable environment for high detection probabilities (e.g., lower velocity, deeper channel) compared to the mainstem. Thus, it was assumed that very few smolts passed through the Stillwater Branch undetected, warranting allocation of smolts with unknown passage to the mainstem route.

Smolt path choice is generally considered to be determined by bulk flow, although the relationship between flow and path choice is likely not linear and deviations do exist (Coutant and Whitney 2000). Thus, greater proportional use of the Stillwater Branch is expected to accompany increased discharge through the Stillwater hydrosystem. That said, our results indicate significant variation in use of the Stillwater Branch at similar flows among release groups, suggesting that release location may have stronger effect on path choice than relative discharge between paths. Low use of the Stillwater
Branch by smolts released at Milo, compared to those released at Howland, was not related to differences in timing of migration or discharge at arrival to the point of path choice. If this perceived behavioral difference is real, it raises an important consideration for future migration studies and salmon management in this system. Stocking at Milo, for example, may ensure optimal sample sizes for future downstream passage assessments at the Milford or Great Works dams and reduce the number of smolts that migrate through the larger number of dams in the Stillwater once the PRRP is completed.

Implications for Restoration

The PRRP offers great hope for improving fish passage (upstream and downstream) for Atlantic salmon and other diadromous fishes in the Penobscot River. However, the two dams scheduled for removal (Veazie and Great Works) had the least apparent effects on emigrating smolts under the conditions studied in 2005 and 2006. Of course, these dams may impose greater risk to passing smolts under different conditions (i.e., when flashboards are installed).

The Howland Dam showed the highest mortality (29%) of any dam in either year. If these losses were attributed to entrainment, decommissioning of the Howland Dam should increase smolt escapement in the Piscataquis River. However, if losses were attributable to delays in the head pond (i.e., predation) or impingement during spill, decommissioning alone may not effectively eliminate these threats, and removal may be warranted. Poor survival at the Milford and West Enfield dams should be of particular concern to fishery managers, since hydroelectric generation will be increased at these dams following PRRP efforts.
Increased flow and hydroelectric generation capacity in the Stillwater Branch present a mixed set of potential outcomes. We have shown that the Stillwater Branch is used as a migration pathway, particularly at higher flows. In general, survival was high through the Stillwater Branch during this study, however, conditions are likely to change after planned hydroelectric upgrades. Without concomitant improvements to downstream passage, these activities may increase the risk of turbine entrainment and/or migratory delay at the Stillwater and Orono dams. Adequate downstream passage may thus remain an important consideration in the Stillwater Branch and other parts of the Penobscot system even after implementation of the PRRP.
Chapter 3

COMPARATIVE CONDITION AND MIGRATORY PERFORMANCE OF HATCHERY AND WILD ATLANTIC SALMON (*Salmo salar*) SMOLTS IN THE PENOBSCOT RIVER, MAINE

Abstract

Acoustic telemetry was used to compare migratory condition (gill Na\(^+\),K\(^+\)-ATPase activity and condition factor) and performance (survival and behavior) among hatchery (N=493) and naturally-reared (N=133) Atlantic salmon (*Salmo salar*) smolts in the Penobscot River, Maine, during 2005 and 2006. An array of acoustic telemetry receivers was used to quantify migratory performance at up to 38 sites per year. Measures of migratory performance were related to rearing and release history, as well as condition. Estimated freshwater survival was 13-30% higher for smolts released 99 km, versus 143 km upstream of the river mouth in 2005. Hatchery smolts released in April were not ready to migrate at time of release, but migrated earlier than wild smolts in both years. Gill Na\(^+\),K\(^+\)-ATPase activity was positively associated with movement rate to the estuary in both years. Further, gill Na\(^+\),K\(^+\)-ATPase activity for wild smolts was significantly different than for hatchery smolts released on the same date in 2006, but similar to hatchery smolts that were released 29-26 days earlier in 2005 and 2006, respectively. Hatchery smolts released in May showed similar freshwater survival compared to both wild smolts and hatchery smolts released in April, but behavior was more similar to wild smolts than earlier-released hatchery smolts. These results indicate that fundamental differences exist between hatchery and naturally reared smolts. These data may help
managers determine which release protocols best meet the goals of the restoration program, and to establish hatchery production goals based on characteristics of the wild population.
Introduction

Hatchery supplementation, particularly at the smolt stage, is the cornerstone of efforts to restore endangered Atlantic salmon (Salmo salar) populations in the United States (NRC 2004). However, hatchery-reared salmon have been shown to incur higher mortality than their wild counterparts in many systems (Collis et al. 2001; Fresh et al. 2003; Johnsson et al. 2003; Metcalf et al. 2003). Documented differences may be associated with behavioral or physiological mechanisms that are critical to successful dam passage, predator avoidance (Hockett 1994; Alvarez and Nicieza 2003), or seawater entry (Shrimpton et al. 1994; Fuss and Byrne 2002). The underlying causes of these differences may be phenotypic plasticity or differential patterns of selection acting in the natural and hatchery environments (Einum and Fleming 2001). Recent concern for the genetic and ecological effects of hatchery fish on extant wild populations has led to the establishment of guidelines for conservation-oriented hatcheries (Flagg and Nash 1999). Flagg and Nash (1999) recommend that conservation hatcheries define quality standards, and set clear goals for production, based on characteristics of wild populations. Thus, it is critical that restoration programs seek to quantify, and understand the basis for, variation in hatchery and wild smolt performance if they are to use the tool of smolt supplementation effectively.

The parr-smolt transition (PST) is a critical transitional stage in the life history of Atlantic salmon, and many other anadromous salmonids, when a territorial, stream-dwelling parr transforms into a migratory sea-bound smolt, under the influence of endogenous rhythms (Hoar 1976; Eriksson and Lundqvist 1982) and environmental cues (e.g., photoperiod, temperature, turbidity, flow; McCormick et al. 1998). This transition
includes preparatory development of smolt characteristics (morphological, physiological and behavioral changes) that are advantageous in a marine environment (McCormick and Saunders 1987). Successful transition into the marine environment is thought to occur during a “window of opportunity,” when physiological condition is optimal for survival (McCormick and Saunders 1987). Misalignment of migration with the physiological window may result in mortality in the estuary (McCormick et al. 1999) or at sea (Virtanen et al. 1991; Staurnes et al. 1993).

During the PST, migrating smolts utilize riverine and estuarine habitats as migration corridors between rearing habitats and the sea. During this migration, smolts can incur significant direct or indirect mortality from dams (Ruggles 1980; Coutant and Whitney 2000), predation (Larsson 1985; Jepsen et al. 1998), or other factors. The severity and presence of these factors may be directly or indirectly associated with environmental conditions during migration (McCormick et al. 1998). Further, the timing of wild smolts migration may itself provide an indicator of the optimal “environmental window” within a given system. Indeed, studies have shown that survival of hatchery smolts may be maximized if hatchery releases coincide with the emigration of wild smolts (Hvidsten and Johnsen 1993; Heinimaa 2003). As such, restoration programs may use a suite of wild smolt parameters, including migration timing and physiological condition, as benchmarks for hatchery production and determination of smolt quality.

The Penobscot River hosts the largest returning run of adult Atlantic salmon in the U. S. Nonetheless, populations in this and neighboring systems have experienced precipitous declines, despite extensive supplementation efforts dating back to the late 1800’s (Baum 1997; NRC 2004). Recent hatchery practices include the release of
salmon fry, parr and smolts, yet the majority of adult salmon returning to the Penobscot in recent years are of smolt-stocked origin (USASAC 2004). Further, smolt-to-adult return rates have steadily declined since 1970 (Moring et al. 1995; USASAC 2005), indicating increased mortality in the river or at sea.

Variability in survival and migration patterns among stocking locations may be attributable to habitat differences (mainstem versus tributary) or distance from the estuary, where smolts released farther upstream encounter more threats (e.g., dams, predators) than smolts stocked in the lower river. Quantifying smolt survival relative to stocking location is important because smolts stocked in the lower river tend to home to the lower river (Power and McCleave 1980; Gorsky 2005), where successful spawning is improbable. Current stocking protocols seek to balance quantity (i.e., higher adult returns) associated with lower river releases with quality (i.e., higher probability of homing to spawning habitat) associated with upper-river releases. Understanding survival differences among release sites can help managers determine which release sites best suit the needs and goals of the restoration program.

To examine the effects of rearing or release history on smolt performance, an array of acoustic telemetry receivers was used to provide an extensive time-stamped series of detections for both hatchery and wild smolts over more than 200 km of the Penobscot River and estuary (Figure 2.1). Specifically, we measured migration speeds and survival, and related these to various measures of smolt condition, including gill Na\(^+\),K\(^+\)-ATPase activity, and condition factor. We describe the relative success of stocking strategies (varied by release location and timing) by quantifying migratory performance (survival and migration speeds) for smolts stocked at tributary and
mainstem locations. Further, we provide a side-by-side evaluation of hatchery and wild
smolt performance and condition during migration. Such information may provide
managers with some indication of smolt quality (as defined by Flagg and Nash 1999),
and will help determine which release sites best match the needs and goals of the
restoration program.
Materials and Methods

Field Methods

The acoustic array

An array of up to 117 stationary acoustic receivers (VR2, Vemco) was deployed and maintained, in cooperation with NOAA National Marine Fisheries Service (NOAA Fisheries), from April through November, 2005 and 2006 in the Penobscot River, estuary and bay (Figure 2.1). Receivers contained omni-directional hydrophones, monitored continuously at 69 kHz, and were deployed to cover the entire width of the system at up to 38 sites per year. In some instances (e.g., wide river sections or islands) several acoustic receivers were necessary for complete coverage. Detections on these receivers were pooled and treated as a single site. Additionally, all receivers in Penobscot Bay (beyond Fort Point) were pooled and treated as a single site. Receivers were moored on the bottom of the river at freshwater and estuarine sites, and approximately 10 m below the surface in the bay. Data were downloaded at least monthly throughout the period of smolt migration.

Tagging and release of hatchery and wild smolts

Hatchery-reared smolts were obtained from the Green Lake National Fish Hatchery (GLNFH) and transported (via truck) with aeration to release sites in the Penobscot River drainage. Tank water temperature was measured prior to departure from GLNFH and upon arrival at the release site. At each release site, each smolt was anesthetized with tricaine methansulphonate (MS-222) and photographed for assessment of smolt characteristics and morphology (silvering, fin darkening, scale loss, etc.). Length and weight were recorded, and a gill biopsy was collected for measurement of gill
Na\textsuperscript{+},K\textsuperscript{+}-ATPase activity (see McCormick 1993). The acoustic transmitter (V7-2L and V9-6L, Vemco, in 2005 and 2006, respectively) was surgically implanted into each smolt through a ventral incision, which was subsequently sutured with 5-0 coated Vicryl absorbable sutures. V7 transmitters were 7 mm in diameter, 18.5 mm long, weighed 1.6 g in air (0.75 g is water) and had an estimated tag life of 80 days. V9 transmitters were 9 mm in diameter, 20 mm in length, weighed 3.3 g in air (2.0 g in water) and had an estimated tag life of 70 days. Each transmitter emitted a unique pattern of acoustic pulses on a random interval ranging from 20 to 60 second. Proper operation of each transmitter was confirmed prior to surgery, and each smolt was held in an aerated holding tank for a minimum of 30 minutes between surgery and release.

Tagged smolts were released at four locations (Figure 2.1), including the Pleasant River near the town of Milo (Site 1), the Penobscot River near the town of Howland (Site 2), the Mattawamkeag River near the town of Mattawamkeag (Site 3) and the Penobscot River below the Weldon Dam (Site 4). These sites were 143, 99, 144 and 149 km upstream of the river mouth (at the south tip of Verona Island), respectively. Batches of 40-76 hatchery-reared smolts (Table 3.1) were released in April to coincide (within one day) with GLNFH releases of 15,000 to 40,000 smolts at each site. Naturally-reared (hereafter referred to as “wild”) smolts were collected at the Weldon Dam smolt bypass trap in May, surgically implanted with acoustic tags as described, and released below the dam. In 2006, scale samples were collected to determine age of wild smolts. Additionally, 73 hatchery smolts (from GLNFH as described above) were tagged and released below the Weldon Dam on the same day as wild smolts in 2006.
Table 3.1: Descriptive statistics for smolt release groups. Year, release site, release date, number of tagged smolts (N), fork length (FL), condition factor (K), gill Na⁺,K⁺-ATPase activity (ATPase) and age for hatchery (H) and wild (W) smolts released in the Penobscot River in 2005 and 2006. Mean, SE in parentheses for FL and K. Median, semi-interquartile range in parentheses for ATPase. Different superscripts represent significant differences (p < 0.05) among groups within years; Non-parametric multiple comparisons post-hoc test for ATPase; Tukey’s post-hoc test for K.

<table>
<thead>
<tr>
<th>Year</th>
<th>Origin</th>
<th>Release Group</th>
<th>Site</th>
<th>Date</th>
<th>N</th>
<th>FL</th>
<th>K</th>
<th>ATPase</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>H</td>
<td>Matt</td>
<td>14-Apr</td>
<td>40</td>
<td>185 (1.88)</td>
<td>1.08 (0.011)²</td>
<td>6.15 (1.15)²,c</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>-</td>
<td>Howl</td>
<td>19-Apr</td>
<td>74</td>
<td>185 (1.28)</td>
<td>1.09 (0.007)³,b</td>
<td>5.45 (1.27)²</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>-</td>
<td>Milo</td>
<td>21-Apr</td>
<td>40</td>
<td>190 (1.82)</td>
<td>1.08 (0.009)²</td>
<td>7.25 (1.06)²,c</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>-</td>
<td>Howl</td>
<td>27-Apr</td>
<td>76</td>
<td>192 (1.09)</td>
<td>1.12 (0.007)³,b</td>
<td>7.44 (1.09)³</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>-</td>
<td>Milo</td>
<td>27-Apr</td>
<td>45</td>
<td>193 (1.57)</td>
<td>1.10 (0.008)³,b</td>
<td>8.54 (1.00)³</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>W</td>
<td>Weld</td>
<td>26-May</td>
<td>60</td>
<td>178 (2.35)</td>
<td>0.91 (0.012)³,c</td>
<td>9.07 (1.36)³</td>
<td>2-3</td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>H</td>
<td>Weld</td>
<td>12-Apr</td>
<td>73</td>
<td>190 (1.29)</td>
<td>1.10 (0.006)³,a</td>
<td>3.68 (1.13)³,a</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>-</td>
<td>Milo</td>
<td>24-Apr</td>
<td>72</td>
<td>196 (1.33)</td>
<td>1.14 (0.007)³,a</td>
<td>4.96 (0.83)³</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>-</td>
<td>Weld</td>
<td>8-May</td>
<td>73</td>
<td>209 (1.49)</td>
<td>1.06 (0.008)³,a</td>
<td>5.66 (1.04)³,c</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>W</td>
<td>Weld</td>
<td>8-May</td>
<td>73</td>
<td>189 (1.05)</td>
<td>0.85 (0.008)³,b</td>
<td>4.08 (0.61)³,a</td>
<td>2-3</td>
<td></td>
</tr>
</tbody>
</table>

Laboratory Methods

Gill Na⁺,K⁺-ATPase activity was determined using a modification of the microplate method described by McCormick (1993). Gill samples were thawed immediately prior to assay and homogenized in 200 µL of 0.1% sodium deoxycholate in SEI buffer. The homogenate was centrifuged to remove insoluble material. Specific activity of Na⁺,K⁺-ATPase was determined in triplicate by measuring ATPase activity with and without 0.5 M ouabain in a solution containing 4 U/mL lactate dehydrogenase, 5 U/mL pyruvate kinase, 2.8 mM phosphoenolpyruvate, 0.7 mM adenosine triphosphate (ATP), 0.22 mM nicotinamide adenine dinucleotide (reduced NADH), 50 mM imidizole, 45 mM NaCl, 2.5 mM MgCl₂, 10 mM KCl, pH = 7.5. Kinetic analysis of ATP
hydrolysis was measured at 25°C by monitoring [NADH] at 340 nm using a 96 well plate reader. Protein concentration of the gill homogenate was determined in triplicate using the bicinchoninic acid (BCA) method (Smith et al., '85; BCA Protein kit, Pierce, Rockford, IL, USA) using bovine serum albumen as standard. Activity of gill Na⁺,K⁺-ATPase is expressed as μmol ADP·mg protein⁻¹·hr⁻¹.

Statistical Analyses

Survival estimation

Separate survivorship and detection probabilities (Φ and ρ, respectively) were estimated between monitoring sites using the Cormack-Jolly-Seber (CJS) release-recapture model (Cormack 1964; Jolly 1965; Seber 1965). Parameters were estimated from complete capture histories (Burnham et al. 1997) in Program MARK (White and Burnham 1999). For each release group, we used the full CJS model where both Φ and ρ are site-dependent. Capture histories for the CJS models included up to 24 sites, including release.

Total survival was estimated through three broad regions of the study system. These were from release to the second downstream receiver, 25-32 km downstream; from the second downstream receiver to the first receiver below head of tide, at river km 45; and from the head of tide to the monitoring site at Fort Point, 4 km downstream of the river mouth. We refer to these regions as Release, Freshwater and Estuary, respectively. We estimated total survival through each region as the product of survival estimates from the CJS model for each section within each region.
**Movement rates**

To compare movement rates among release groups, median detection dates were calculated among fish within each group at each site, using the date and time of first detection (i.e., arrival date) at each site for each tagged fish. Smolts released at Mattawamkeag in 2005 were excluded because sample sizes were small (N<10) for most sites. Arrival dates were compared among groups at an estuarine site 10 km upstream of the river mouth using a Kruskall-Wallis test and non-parametric multiple comparisons post-hoc test (Zar 1999).

The movement rate (R) was calculated for each smolt between release and the estuarine site 10 km upstream of the river mouth using

\[ R = |D| \times |T|^{-1} \]

where D is the distance (in km) between sites, and T is the difference between release and Julian date and time of first detection at the estuarine site. The mean rate and associated standard error for each release group was calculated and compared to physiological condition using linear regression.

Gill Na⁺,K⁺-ATPase activities were compared among release groups using a Kruskall-Wallis test with a non-parametric multiple comparisons post-hoc test. Condition factor (K) was compared among groups using a single-factor ANOVA with Tukey’s post-hoc test. A significance level of 0.05 was used for all statistical tests.
Results

Survival Near the Release Site

Over the two-year study period, survival near the release site ranged from 28-97% and 33-53% among hatchery and wild groups, respectively. Survival in this region did not seem to be related to date of release (Figure 3.1). Further, we found no evidence that survival was dependent upon size or condition (K, gill Na⁺,K⁺-ATPase) in this or any other region.

Comparing Hatchery and Wild Smolts

Freshwater and estuarine survival

In 2005, estimated freshwater survival for wild smolts was 6-8% higher than for hatchery smolts released at Milo, but 7-21% lower than hatchery smolts released at Howland. Freshwater survival was similar among all groups in 2006, with a maximum difference of 3%. In general, freshwater survival was lower in 2006 compared to 2005 for both hatchery and wild smolts (Figure 3.1).

In 2005, estuarine survival for wild smolts was 12% lower than for hatchery smolts released at Milo on April 27, but similar (max. difference of 5%) to other hatchery groups. In 2006, estuarine survival for wild smolts was 5-12% lower than for hatchery groups (including those released in May) in 2006.

Smolt condition and migration timing

In 2005, gill Na⁺,K⁺-ATPase activity for wild smolts released on May 26 was not significantly different than hatchery smolts released 29 days prior (Table 3.1). In 2006,
Figure 3.1: Smolt survival through Release, Freshwater and Estuary. Estimated survival from (a, b) release to the second downstream monitoring site, from (c, d) the second downstream monitoring site to the first monitoring site below head of tide, and from (e, f) head of tide to the monitoring site at Fort Point (~ 4 km below river mouth), for hatchery (gray bars) and wild (white bars) smolts released in 2005 and 2006.
gill Na\(^+\),K\(^+\)-ATPase activity for wild smolts released on May 8 was significantly lower than for hatchery smolts released on the same day, but was not significantly different than hatchery smolts released 26 days prior. Condition factor was significantly lower for wild smolts compared to all hatchery groups in both years (Table 3.1).

Once released, naturally-reared smolts moved rapidly through the system in both years (Figure 3.2). Nearly all hatchery smolts released in April had passed through the estuary before any naturally reared or May-released hatchery smolts were detected. Hatchery smolts released in May 2006 exhibited similar patterns of movement to naturally reared smolts released on the same date (Figure 3.2).

**Comparing Among Hatchery Groups**

*Freshwater and estuarine survival*

Estimated freshwater survival ranged from 67-97% and 51-54% for hatchery groups released in April 2005 and 2006, respectively. Freshwater survival was more variable among release groups in 2005 compared to 2006 (Figure 3.2). Smolts stocked at Milo in 2005 showed 13-30% lower freshwater survival than smolts stocked at Howland. Smolts stocked at Mattawamkeag showed substantially lower survival (41-71%) than other groups. Smolts released at Howland showed the highest survival in 2005. Freshwater survival was only 1% different between hatchery smolts released at Weldon 26 days apart (on April 12 and May 8) in 2006.

Estuarine survival was similar among most groups in 2005, with the exception of smolts released at Milo on April 27, which showed 13-17% lower estuarine survival than other groups. In 2006, estuarine survival was 6% lower for smolts released at Milo
Figure 3.2: Median detection dates at each monitoring site. Median detection dates at each monitoring site (shown here by river km) for hatchery (H) and wild (W) release groups released in (a) 2005 and (b) 2006.
compared to both groups released at Weldon. Estuarine survival was only less than 1% different between hatchery smolts released at Weldon 26 days apart (on April 12 and May 8) in 2006.

*Behavioral synchrony and time in freshwater*

For both years, earlier-released smolts spent more time in freshwater compared to later-released smolts (Figure 3.2). Although release dates in 2005 differed by up to 8 days among hatchery groups, median detection dates in the estuary were not significantly different among groups. In 2006, median detection dates for hatchery groups released 12 days apart in April converged near river km 70 and median detection dates in the estuary were again not significantly different between these groups. However, the date of estuarine arrival was significantly different between hatchery smolts released in April and May in 2006.

*Smolt condition and relation to behavior*

In general, gill Na$^+$,K$^+$-ATPase activity at release was positively associated with release date and was significantly different among hatchery groups (Table 3.1). Conversely, condition factor was not significantly different among any hatchery groups. Movement rates between release and the estuary were positively associated with mean gill Na$^+$,K$^+$-ATPase activities among hatchery release groups in both years (Figure 3.3).
Figure 3.3: Gill Na\textsuperscript{+}, K\textsuperscript{+}-ATPase activity versus movement rate to the estuary. Relationship between mean gill Na\textsuperscript{+}, K\textsuperscript{+}-ATPase activity at release and mean movement rate between release and an estuarine site (10 km above the river mouth) for hatchery release groups in (a) 2005 and (b) 2006. Error bars represent standard errors.
Discussion

Comparison of Hatchery and Wild Smolts

These results indicate that fundamental differences exist between restoration hatchery smolts (stocked by GLNFH in April) and wild smolts reared in the upper Penobscot River. Specifically, hatchery-reared smolts from GLNFH seemed to undergo accelerated smolting relative to naturally-reared smolts. The younger, larger hatchery smolts in this study exhibited downstream migratory behavior earlier than naturally-reared smolts, with nearly all April-released hatchery smolts migrating through the system before wild smolts were captured at the bypass trap (Figure 3.2). Late migration timing of wild smolts may indicate that the environmental window of opportunity occurs later than hatchery-reared smolts are currently migrating. Further, the physiological condition (gill Na$^+$,K$^+$-ATPase activity) of naturally reared smolts was comparable to hatchery smolts released 29 and 26 days earlier in 2005 and 2006, respectively (Table 3.1). Thus, hatchery smolts showed advanced development of behavioral and physiological PST-related characters, relative to naturally reared smolts. Premature smolting in hatchery fish (relative to wild fish in this system) may cause misalignment of migration with natural environmental windows.

Despite these developmental differences, stocking in May did not significantly reduce or improve the overall survival of hatchery smolts during the seaward migration. However, unlike smolts released in April, hatchery smolts released in May displayed immediate and uninhibited downstream migratory behavior, more like wild smolts. This may indicate that these smolts were either within the physiological/behavioral “smolt window,” or that the optimal migration time had passed. These smolts also exhibited
higher gill Na\(^+\),K\(^+\)-ATPase activities than those released in April (Table 3.1), suggesting that they were physiologically “more ready” for seawater entry at the time of release. However, estuarine mortality was similar between these late-released smolts and earlier-released smolts (Figure 3.1). This suggests that physiological impairment was not a factor for late-released hatchery smolts, although mortality may not occur until long after marine entry. Regardless, these data indicate a clear difference between readiness for seawater entry between hatchery and wild smolts.

As suggested by Flagg and Nash (1999) and Stefansson et al. (2003), the current restoration program may benefit from rearing smolts that develop and migrate in synchrony with wild smolts. Using wild smolts as a benchmark for hatchery smolt production standards, smolt quality (as defined by Flagg and Nash 1999) may be improved by delaying stocking and peak migration for hatchery smolts until mid-May. Zydlewski et al. (2005) have shown that the onset of smoltification may be delayed by altering water temperatures experienced by developing smolts.

One important difference is that naturally-reared smolts used in this study were captured by a passive gear (downstream bypass trap) and were thus already exhibiting downstream migratory behavior upon capture. We do not know if the naturally-reared smolts tagged in this study correspond temporally with the peak migration of natural smolts in the study year, but peak migration has typically been observed in late May in previous years (GNP 1997) while peak migration of hatchery smolts typically occurs earlier (Christine Lipsky, NOAA Fisheries, personal communication).

It is not known if the wild fish used in this study were of fry-stocked origin, or if they were truly the product of reproduction in the wild. Since natural reproduction
remains extremely low in the Penobscot River and the majority of successful returning adults are the progeny of the smolt stocking program, these adults have not been exposed to natural selection at the early (egg to pre-smolt) or late (freshwater adult) life stages. Studies in other salmonid systems have shown that PST-specific traits (e.g., initiation of migratory behavior, timing of preparatory physiological changes) differ among salmon populations and even families (Orciari and Leonard 1996, Nemeth et al. 2003; Olsen et al. 2004). Unfortunately, homogenized breeding of the Penobscot salmon in a single hatchery program may have already substantially mixed stream- or reach-adapted sub-populations within and among drainages. Thus, development and migratory performance of the wild smolts used in this study may have been affected by a long history of hatchery supplementation.

**Comparative Survival and Behavior for Various Stocking Strategies**

All hatchery and wild release groups, with the exception of the Milo release group in 2006, exhibited substantial losses (2-72%) near the release site in both years. Similarly, high rates of tag loss near the release site were observed by Spicer et al. (1995) and Bangor-Pacific Hydro Associates (BPHA 1993a). It is not known if this mortality was exclusive to acoustically-tagged smolts, or if untagged hatchery smolts (i.e., restoration smolts) experience a similar rate of mortality near the release site. Similar losses for both hatchery and wild smolts suggest that these losses may be attributable to indirect effects of pre-release handling (e.g., transport, anesthesia, surgery). Results from the dummy-tagging studies in 2005 revealed that the handling and tagging process does not cause direct mortality (Holbrook, unpublished data), but other factors could compound the
effects of tagging after release (i.e., predation, turbulence, etc.). Nonetheless, these losses do not seem to be related to time in freshwater.

Hatchery smolts released in April were likely not ready for migration upon release. Following release, these smolts did not immediately display downstream migratory behavior, but remained in the river for some time, exhibiting either station holding or slowed movement rates (Figure 3.2). This behavior has been documented for hatchery smolts in the Penobscot (Spicer et al. 1995) and other systems (Tytler et al. 1978; Lacroix and McCurdy 1996; Aaerstrup et al. 1999). Stocking of hatchery smolts prior to the development of strong migratory behavior may prolong exposure to freshwater predators, because earlier-stocked smolts spend more time in freshwater (Koed et al. 2002). However, our results suggest (except for the Mattawamkeag site) that early stocking does not significantly reduce survival (Figure 3.1). This may be because predators in this system are spatially-aggregated in specific locations and prey on smolts as they arrive or migrate past these locations, rather than actively searching for prey throughout the river. Indeed, Blackwell and Krohn (1997) reported that double-crested cormorants favored specific regions (typically near dams) and waited for smolts to arrive at those sites. Thus, the effect of predation on survival depends on the behavior and distribution of predators relative to the spatial distribution of stocking sites and smolt “holding” reaches.

Among hatchery groups, Na⁺,K⁺-ATPase activities were a good predictor of smolt migratory impetus. Results showed that hatchery release groups with higher mean gill Na⁺,K⁺-ATPase activities moved more quickly to the estuary compared to groups with lower gill Na⁺,K⁺-ATPase activities (Figure 3.3). Thus, groups with higher gill Na⁺,K⁺-ATPase activities are likely further along in the development of smolt characteristics.
Hatchery managers may be able to use gill Na\(^+\),K\(^+\)-ATPase activity or similar measures of sea-water tolerance (e.g., plasma osmolality) to determine optimal stocking times within years.

One motivation for earlier releases may be to expose hatchery smolts to natural selection prior to migration. However, the release sites currently used for restoration smolt stocking do not coincide with contemporary rearing habitat. Thus, selective pressures and environmental cues may be quite different between current stocking sites and rearing habitats inhabited by wild smolts. For example, in some systems, “pre-smolts” exhibit a fall movement out of low-order rearing habitats and into higher-order reaches (see McCormick et al. 1998). This behavior may be necessary for survival in rearing habitats with high over-winter mortality, but there is no evidence that wild smolts move to the sites used for smolt stocking or experience the types of selection that fosters such complex behavior.

Meister (1962) observed that most pre-smolts left Cove Brook, a small tributary in the Penobscot River estuary, in the fall. We are not aware of any other studies that have documented these behaviors in the Penobscot Drainage. However, smolt collection facilities at the Weldon Dam (downstream bypass trap) and on the Pleasant River (rotary screw traps) are located upstream of all hatchery smolt release sites, suggesting that initiation of naturally-reared smolt migration occurs upstream of these reaches in the spring. Further, no smolts are released upstream of these sites although strong olfactory imprinting likely occurs during smoltification (McCormick et al. 1998). Previous studies with Atlantic salmon and steelhead trout suggest that salmon return to the specific place within the river they were stocked (see Quinn 1993). In the Penobscot system, sufficient
evidence suggests that hatchery-reared smolts home to their respective stocking sites (Power and McCleave 1980; Gorsky 2005). Thus, stocking in upriver habitats may be critical to the successful homing and the reestablishment of natural reproduction and patterns of selection in this system.

Smolts stocked lower in the system (at Howland) in 2005 showed higher survival than smolts stocked at upper river sites (Weldon or Milo) sites (Figure 3.1). Very low survival for smolts released at Mattawamkeag are consistent with adult returns for smolts stocked at this site in previous years (Richard Dill, Maine Atlantic Salmon Commission, personal communication), although the cause of mortality is largely unknown. Smolts released at Howland had the shortest travel distance, with one fewer dam to pass than smolts released at other sites and may explain why freshwater survival was higher for this group. Indeed, losses at hydroelectric dams have likely accounted for a substantial proportion of mortality in both years (see Chapter 1). These results suggest that stocking lower in the system may increase survival from release to marine entry.

Stocking of smolts in lower river habitats may provide higher returns to the lower river, increasing the effective hatchery population. However, the reduced probability of successful spawning and natural reproduction suggests that lower river stocking would best fall short of conservation standards that target future wild production and adaptation. Considering the currently low levels of natural reproduction, and the necessity for hatchery propagation in the Penobscot system, the best management practice may include some combination of upper and lower river stocking.
Chapter 4

MOVEMENTS OF PRE-SPAWN ADULT ATLANTIC SALMON

(Salmo salar) NEAR HYDROELECTRIC DAMS IN THE

LOWER PENOBSCOT RIVER, MAINE

Abstract

Acoustic telemetry was used to quantify riverine behavior and passage success for pre-spawn adult Atlantic salmon (Salmo salar) in the lower Penobscot River, Maine in 2005 (N=10) and 2006 (N=25). Only 38% (3/8) and 8% (2/25) of tagged salmon successfully passed the fourth upstream dam in 2005 and 2006, respectively. In 2005 and 2006, 100% (3/3) and 74% (17/23) of apparently unsuccessful migrants fell back into the estuary and few successfully re-ascended. Water temperature in the mainstem exceeded 27°C in both years, and fallback behavior was common when temperatures exceeded 22°C. A small stream provided thermal refuge during morning hours only and was warmer than the mainstem during afternoon hours. Results from this pre-removal assessment indicate that insufficient upstream passage at dams in the lower Penobscot River can severely limit migratory success in this system.
Introduction

The establishment of sustainable, naturally-reproducing populations is the ultimate goal of fisheries restoration programs. Hatchery supplementation is often considered necessary to prevent extinction of imperiled species and bolster restoration efforts (Flagg and Nash 1999). However, hatchery supplementation can have adverse genetic effects on the wild populations they attempt to restore (Reisenbichler and Rubin 1999). To mitigate these effects, naturally-reared individuals that have experienced selection in the wild should be incorporated into hatchery programs (Flagg and Nash 1999). Although many traditional hatchery programs are successful at increasing population sizes, few restoration programs are successful without active removal or abatement of limiting factors (Miller 1990).

Dams have been identified as one of the most acute impediments to restoration of Atlantic salmon in the United States (NRC 2004). Atlantic salmon populations in Maine have declined and remain low, despite extensive supplementation efforts dating back to the late 1800’s (Baum 1997). In the Penobscot River, which hosts the largest remaining run of adult Atlantic salmon in the U.S. (USASAC 2005), all high quality rearing habitats currently available are located upstream of the four lowest hydroelectric dams (Fay et al. 2006). Three of these dams (Veazie, Great Works and Milford) are located within 15 km of the head of tide, and the fourth (Howland or West Enfield, depending on route) is approximately 52 km above head of tide. Successful upstream passage through this complex of dams is necessary for most natural reproduction.

Despite the presence of upstream fishways at all mainstem dams, previous studies have revealed that passage success is highly variable among years and sites. Upstream
passage success was determined at several dams between 1987 and 2004 using radio (Shepard 1989, Shepard and Hall 1991, Shepard 1995) and passive integrated transponder (PIT) telemetry (Gorsky 2005). Results from these studies indicate that passage success at individual dams ranged from 38-100% among years (reviewed by Fay et al. 2006; D. Gorsky, University of Maine, unpublished data). However, it is not clear from these results if poor passage was caused by inadequate upstream fishways or other factors (e.g., predation, angling mortality, flow, temperature, etc.).

As complete or partial barriers to migration, dams cause delays that may reduce the probability of survival or spawning success for returning salmon (Dauble and Miller 1993). Okland et al. (2001) suggested that in the absence of barriers, Atlantic salmon migration consists of three behavioral phases: directed upstream movement toward spawning grounds; slow searching behavior in the vicinity of spawning grounds; and long periods of station-holding near spawning grounds. Delays in lower river habitats may increase exposure to predators, deplete energy reserves, or increase exposure to sub-optimal water quality.

High summer temperatures have been shown to sufficiently reduce movement rates (Shepard 1995; Gorsky 2005) and may be responsible for substantial mortality during migration through the lower Penobscot River (Shepard and Hall 1991). Migrating salmonids are known to seek refuge in cooler tributaries or springs during periods of high temperatures in the Penobscot (Gorsky 2005) and other systems (Keefer et al. 2004; Goniea et al. 2006). Such behavioral thermoregulation may be necessary for survival during exceptionally warm periods. However, the availability of cool-water tributaries may be limited between dams in the lower Penobscot River (Gorsky 2005). Inadequate
upstream passage at these dams may thus inhibit timely access to critical cool-water tributaries upstream and further reduce the probability of successful migration or survival for salmon in this system.

It was the goal of this study to evaluate upstream passage success at dams in the lower Penobscot River, and to describe the behavior of successful and unsuccessful migrants relative to mainstem dams and one small tributary (Great Works Stream). In 2005, a study was conducted to determine if an array of acoustic telemetry receivers could provide detailed information on fish behavior between dams. In 2006, this technique was employed to track the movements of pre-spawn adult salmon over more than 200 km of the Penobscot River, estuary, and tributaries (Figure 4.1). Data were used to determine passage success at dams and to illustrate the combined effects of migratory delays and high temperatures on behavior and passage success of migrating salmon.

As part of the Penobscot River Restoration Project (PRRP) engineers will remove the two most downstream dams (Veazie and Great Works) and improve passage at others (PPL Maine et al. 2004; Fay et al. 2006). The findings of the present research thus provide an important baseline to predict and assess the outcomes of future hydro-system modifications.
Figure 4.1: Adult salmon monitoring and release sites. Map of the Penobscot River with acoustic monitoring and release sites.
Materials and Methods

Field Methods

The acoustic array

An array of up to 117 stationary acoustic receivers (VR2, Vemco) was deployed and maintained from April through November, 2005 and 2006 in the Penobscot River, estuary and bay (Figure 4.1). Receivers contained omni-directional hydrophones, monitored continuously on a single frequency (69 kHz), and were deployed to cover the entire width of the system at up to 40 sites. Some receivers were only used in the 2006 study. These were located above and below the Dover and Browns Mills dams in the Piscataquis River; in the Pleasant River; in Great Works and Otter streams (Figure 4.2); near the mouth of the Stillwater River; and in the mouth of the Kenduskeag River. In some instances (e.g., wide river sections or islands) several acoustic receivers were necessary for complete coverage. Detections on these receivers were pooled and treated as a single site. Additionally, all receivers in Penobscot Bay (beyond Fort Point) were pooled and treated as a single site. Receivers were moored on the bottom of the river at freshwater and estuarine sites, and approximately 10 m below the surface in the bay. Data were downloaded at least monthly throughout the period of smolt migration.

Figure 4.2: Monitoring sites near Great Works Stream. Close-up of acoustic monitoring sites in Great Works Stream, Otter Stream and in the mainstem below Great Works Dam.
Table 4.1: Descriptive statistics for tagged adult salmon. Age, number (N), mean fork length (FL, in cm) release dates and release sites for tagged male salmon in 2005 and 2006.

<table>
<thead>
<tr>
<th>Year</th>
<th>Age</th>
<th>N</th>
<th>FL (Range)</th>
<th>Release Dates</th>
<th>Release Site</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>2SW</td>
<td>5</td>
<td>74.2 (71.0-77.0)</td>
<td>6/20-6/21</td>
<td>Penobscot Bay</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>2SW</td>
<td>74.0 (71.0-77.0)</td>
<td>6/21</td>
<td>Veazie head pond</td>
</tr>
<tr>
<td>2006</td>
<td>2SW</td>
<td>19</td>
<td>76.5 (72.0-79.0)</td>
<td>6/2-6/7</td>
<td>Veazie head pond</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>1SW</td>
<td>54.5 (50.0-58.0)</td>
<td>6/3-6/5</td>
<td>Veazie head pond</td>
</tr>
</tbody>
</table>

Note: 2SW indicates return after two winters at sea; 1SW indicates one winter at sea

Tagging and release of salmon

Returning adult Atlantic salmon (N=10 and 25 in 2005 and 2006, respectively) of hatchery origin (as determined by scale evaluation or appearance of external tags at time of capture) were collected at an upstream fishway trap operated by the Maine Atlantic Salmon Commission at the Veazie Dam (Table 4.1). Length and sex (as determined by morphology) were recorded at time of capture. Fish were anesthetized in tricaine methanosolfonate solution (100 mg·L⁻¹, NaC0₃, pH=7.0) and surgically implanted with 69-kHz acoustic transmitters (V9P-2L and V13TP-1H, Vemco). V9 transmitters were used in 2005, were 46 mm in length, 9 mm in diameter, weighed 5.2 g in air (2.6 g in water), had an estimated transmission life of 253 days, and provided an estimate of depth at detection. V13 transmitters were used in 2006, were 45 mm in length, 13 mm in diameter, weighed 12.0 g in air (6.0 g in water), had an estimated transmission life of 184 days, and provided estimates of both depth and internal temperature at detection. Each transmitter emitted a unique code on random intervals ranging from 30 to 90 seconds, and was functioning properly prior to implantation. Transmitters were surgically implanted in anaesthetized salmon through a ventral incision approximately 3 cm long that was subsequently sutured with coated Vicryl 3-0 absorbable sutures.
In 2005, five salmon were transported (via truck) with aeration approximately 100 km downstream and released in Penobscot Bay (Figure 4.1) and five were transported approximately 5 km upstream and released in the Veazie Dam head pond. In 2006, all 25 salmon were held for a minimum of 30 minutes post-surgery and released approximately 200 m upstream of the Veazie Dam. All salmon received an external t-bar anchor tag and adipose punch for future identification by trap personnel.

Environmental data collection

River discharge was measured for the Penobscot River at West Enfield by the U.S. Geological Survey (USGS) and obtained through the USGS Water Data website (http://waterdata.usgs.gov). Water temperatures were recorded on 30 to 60 min intervals by temperature loggers (WaterTemp Pro, Onset) located on the bottom of the river in the Great Works head pond (mainstem) and Great Works Stream.

Passage Analyses

Passage success was defined as the number of fish detected upstream of a given dam, relative to the number of fish known to occur between that dam and the next downstream dam, when one existed. Migratory success was defined as the proportion of all fish released that were detected upstream of the West Enfield or Howland dams. Passage times at individual dams represent the number of days between initial approach (first detection at immediate downstream receiver) and successful passage (first detection at immediate upstream receiver). Fallback behavior is defined as a detectable downstream movement greater than 5 km.
**Temperature Analyses**

To compare the temperature of Great Works Stream to that of the mainstem, the temperature of the mainstem was subtracted from the temperature of Great Works Stream at each hourly interval between July 1 and 31, 2006. The month of July was separated into early (July 1-15) and late (July 16-31) time periods. For each time period, the among-day mean temperature difference (between mainstem and stream) and associated standard error were calculated at each hourly interval.

To determine if tagged salmon were effectively utilizing Great Works Stream for behavioral thermoregulation, the temperature obtained from salmon tags was compared to that of the mainstem temperature logger during early and late July. Detection and fish temperature data were pooled for the three receivers in the vicinity of Great Works Stream (including receivers in Otter Stream, Great Works Stream, and in the mainstem near the confluence of these streams; Figure 4.2). The mean temperature for each fish was first calculated within each hourly bin during the time period, and then the among-fish mean was calculated for each hourly bin. Mainstem temperatures were subtracted from among-fish temperatures for each bin. For each time period, the among-day mean temperature difference (between mainstem and fish) was calculated at each hourly interval with the associated standard error.

The occurrence of tagged salmon in Great Works Stream was compared to the mainstem by comparing frequencies of fish detected at each receiver within hourly bins. It was assumed that the receiver in the mainstem could detect fish in Great Works or Otter streams, but the receiver in Great Works Stream could not detect fish in the mainstem. To determine the mean frequency in the mainstem, the among-day mean
frequency per hourly bin in Great Works Stream was subtracted from the among-day mean frequency from both receivers combined.
Results

2005 Passage Success

The acoustic array provided detailed tracks for eight of the ten salmon that were tagged and released (Figure 4.3). Only 38% (3/8) of all tagged fish successfully passed the Howland or West Enfield dams.

Of the 5 fish released in Penobscot Bay, 4 approached the Veazie Dam (2 successfully passed) and 1 was never detected. Additionally, two fish released in the Veazie head pond fell back over Veazie Dam and eventually re-ascended. Though inferences from these results are limited by small sample sizes, 67% (4/6) passage success was observed for the Veazie Dam (Figure 4.4). Individual passage times ranged from 2.9 to 88.5 days (median 30.6 days; n=4).

Passage success for Great Works Dam was 50% (3/6). One fish was excluded from analyses because it was never detected after release into the Veazie head pond. All other fish that either passed Veazie Dam or were released in the Veazie head pond were known to approach the Great Works Dam. Successful passage occurred when discharge ranged from 166 to 261 m$^3$·s$^{-1}$, and individual passage times ranged from 1.9 to 25.4 days (median 13.1 days; n=3).

Passage success was 100% (3/3) at the Milford Dam and successful passage occurred within 0.3 to 3.7 days of passing the Great Works Dam.
Figure 4.3: Selected tracks for adult salmon. Selected tracks for individual fish in 2005 and 2006. Horizontal lines represent dams.
Figure 4.4: Passage success at the Milford, Great Works and Veazie dams, 1987-2006. Historic passage success for the Milford (a), Great Works (b), and Veazie (c) dams, as determined by a radio (Shepard and Hall 1991), passive integrated transponder (PIT; D. Gorsky, unpublished data) and acoustic telemetry studies between 1987 and 2006. Numbers on bars denote initial sample sizes.
2006 Passage Success

The acoustic array provided detailed tracks for all 25 salmon tagged and released in the Veazie Dam head pond (Figure 4.3). Only 8% (2/25) of tagged fish successfully passed the Howland or West Enfield dams.

Although no fish were released below the Veazie Dam in 2006, 11 fish released in the Veazie Dam head pond fell back over the dam prior to October 1 (Figure 4.5). Of these, 7 re-approached the dam and 3 of these successfully re-ascended. The remaining four fish either became stationary in the estuary or left the study region. Overall, I observed 43% (3/7) passage success for the Veazie Dam. Individual passage times ranged from 2.1 to 58.4 days (median 6.84 days; n=3).

Passage success for Great Works Dam was 12% (3/25) in 2006. All fish released in the Veazie Dam head pond were known to approach the Great Works Dam. Successful passage occurred prior to flashboard installation in 2006 and at discharge between 795 and 938 m$^3$.s$^{-1}$. Individual passage times ranged from 8.6 to 12.5 days (median 8.7 days; n=3).

Passage success at the Milford Dam was 67% (2/3) and successful passage occurred within 2.2 to 2.3 days of passage at the Great Works Dam.

River Temperatures, Flow and Fallback Behavior

Mean daily temperatures were inversely related to flow during the months of June and July, and reached a maximum of 27ºC in both years (Figure 4.5). All three unsuccessful migrants in 2005 exited freshwater (two passed downstream over Veazie Dam; one passed downstream to Veazie Dam head pond and was never again detected) as
Figure 4.5: Flow, temperature and fallback behavior. Temperature and discharge for the Penobscot River in (a) 2005 and (b) 2006, with (c) daily fallback frequencies (stacked bars) for fish located between the Great Works and Veazie dams June-Sept. 2006 (with mean daily river temperature—solid line).
the result of fallback during the months of June and July. In 2006, 74% (17/23) of unsuccessful migrants exhibited at least one fallback during the months of June, July and August (Figure 4.5). Fourteen fish left freshwater (11 passed downstream over Veazie Dam; 3 passed downstream to the Veazie Dam head pond and were never again detected) as a result of fallbacks prior to October 1. All fallbacks (except one in late September) occurred when mean daily mainstem river temperature exceeded 22ºC.

Great Works Stream, a small tributary located 200 m downstream of Great Works Dam, reached a maximum temperature of 29.5ºC during the summer months, and fluctuated as much as 7ºC daily. On average, the stream was cooler than the mainstem during morning hours and warmer than the mainstem during afternoon hours (Figure 4.6). Mean fish body temperatures in the vicinity of the confluence of Great Works Stream, Otter Stream, and the mainstem reached a minimum at 8:00 hrs for both early and late July. Fish body temperatures were more similar to stream temperatures during morning hours and mainstem temperatures during afternoon hours. In early July, a greater proportion of fish were present in the stream (compared to the mainstem) between 4:00 and 12:00 hours (Figure 4.6).
Figure 4.6: Great Works Stream as a thermal refuge. (a) Mean temperature (± standard error) of Great Works Stream (water temperature on the bottom) and for tagged salmon detected near the Great Works Stream confluence, relative to the temperature of the mainstem Penobscot River (Great Works head pond); and (b) mean number of fish detected during hourly intervals (stacked bars) at the Great Works Stream confluence and in the Great Works Stream for the periods July 1-15, 2006.
Discussion

Overall, migratory success in 2006 was severely limited by failure of upstream fishways at Great Works Dam to operate without flashboards that are installed to raise head pond levels and increase hydroelectric generation. Timely flashboard installation is critical because migration typically peaks in mid-June in the Penobscot River (Baum 1997; Gorsky 2005). Unfortunately, upstream fishways at this dam are only functional with flashboards installed and these boards were not installed until August 14, 2006 (compared to June 13 in 2005 - Scott Hall, PPL Maine, personal communication). Given that all successful migrants passed the Great Works Dam within a two-day window and at high flows, we suspect that these few successful migrants passed up over the spillway, rather than through the upstream fishway.

These data reveal that the Great Works Dam can be a severe impediment to upstream migration of Atlantic salmon, particularly when fishway operation is delayed well beyond the peak of upstream salmon migration. Fishway functionality at the Great Works Dam depends upon the date of flashboard installation, which varies with hydrologic conditions among years. Although the high water conditions observed in June and July of 2006 (Figure 4.5) may be infrequent, they are within the observed range of variation and may be expected to occur in the future. A single year of poor passage can have dramatic effects on natural reproduction and future recruitment and may even represent a lost opportunity for recovery given that prolonged higher flow conditions may be favorable to upstream migration in the absence of dams. If managers wish to minimize the potential for such losses, efforts should be taken to ensure adequate passage
at a range of flows. Such measures may include transport around dams, fishway renovation, or dam removal, as planned with the PRRP.

Upstream passage at the Veazie Dam has historically showed substantial inter-annual variation (Figure 4.4). The upstream fishway trap at the Veazie Dam serves as the sole facility for collection and enumeration of Penobscot River Atlantic salmon. If observed low upstream passage rates at Veazie Dam are representative of passage rates for naïve fish, a substantial proportion of the population may never be handled or passed upstream. Observed low passage success at the Veazie Dam may be confounded by the fact that these fish had all previously passed through the upstream fishway when they were initially collected. Studies in the Columbia River have shown that fish generally take longer to pass a dam on a second attempt after fallback compared to the first (Bjornn et al. 1999). Thus, actual passage rates for naïve salmon may be higher than for tagged salmon captured at the Veazie Dam fishway trap.

The high incidence of fallback reported in this (Shepard 1995) and other systems (Gowans et al. 1999; Dauble and Mueller 2000; Keefer et al. 2006; Naughton et al. 2006) may further reduce the number of spawners from expectations based on trap counts. Fallback has been observed by researchers immediately after tagging and/or handling (Bernard et al. 1999; Bailey et al. 2004). In this study, however, all fallbacks occurred after fish had approached the Great Works Dam, a minimum of 14 days after release. Thus, fallbacks were probably attributed to factors such as inadequate upstream passage and high temperatures, rather than the direct effects of tagging and handling.
Nearly all of the tagged salmon in this study showed long delays in the lower river that were not consistent with typical migratory behavior in an unimpounded river (see Okland et al. 2001). Long delays and frequentfallbacks in the lower river have been observed in other studies of Penobscot River salmon (Power and McCleave 1980, Shepard 1995, D. Gorsky, unpublished data). Prior authors have attributed such behaviors to a number of factors, including homing to lower river stocking sites; lack of homing motivation due to hatchery rearing; high water temperatures; and the presence of hydroelectric dams. Results from this study suggest that rapid upstream movement was initially impeded by the presence of dams, and further impeded by high water temperatures.

River temperature is usually inversely related to discharge in the summer. Thus, ideal hydrological conditions (low flows) for dam passage in this system can also bring about threatening temperatures. Thermal refugia are likely found in low order tributaries upstream. However, upstream migration has been shown to slow or cease when temperatures exceed 23°C in the Penobscot River (Shepard 1995). Mortalities have been observed at temperatures greater than 26°C (Shepard and Hall 1991).

In 2006, Great Works Stream provided thermal refuge below the Great Works Dam, but only during the morning hours. During the evening hours, tagged salmon showed a preference for the mainstem over the tributary, yet mainstem temperatures exceeded 27°C in both study years. When temperatures rise, upstream passage is limited, and thermal refugia are not readily accessible, fallback may be an important mechanism for seeking thermal refuge in the estuary.
To avoid abandonment of spawning for the year or ascent of another coastal river, a successful fallback strategy requires both downstream passage and subsequent re-ascent of lower river dams. Downstream passage, however, exposes salmon to alternative risks of turbine entrainment or impingement during spill. Furthermore, high temperatures are often coupled with low flow conditions that are generally considered less optimal for downstream passage. Dams may impede downstream movement into the estuary under such conditions. In addition to the risk of injury or mortality, such behavior may deplete the energy available for successful migration and spawning. Pacific salmon exhibiting fallback behavior at dams in the Columbia River (reviewed by Dauble and Mueller 2000) can experience direct injury, mortality or fatigue as a result of fallback (Reischel and Bjornn 2003). Removal of the Veazie Dam, or head of tide dams in other salmon systems, may allow salmon to quickly return to the estuary to seek thermal refugia and more efficiently return upstream when temperatures decline.

When passage at several dams is required for successful migration, the cumulative effects of even slightly reduced passage at several dams can be substantial. Results from this and previous studies (Figure 4.4) indicate that 1) successful upstream passage at lower Penobscot River dams is dependent upon hydrological conditions and shows substantial inter-annual variation; and 2) migrants often exhibit fallback behavior at high temperatures that effectively reduces the run size if fallback and re-ascent are not successful. Through removal of the Veazie and Great Works dams, PRRP efforts should enhance the Penobscot River salmon population by improving accessibility to spawning habitats and upper-river thermal refugia, and by minimizing the risks to migrants exhibiting fallback behavior during high summer temperatures. In the absence of such
efforts, managers may want to consider transporting fish around these dams to hasten migration upriver to sites that provide more optimal thermal refugia during periods of high temperatures.
REFERENCES


BIOGRAPHY OF THE AUTHOR

Christopher Michael Holbrook was born in Norway, Maine in March, 1982. He grew up in Norway with his parents Dan and Laura as well as his older brother, Shawn. After graduating from Oxford Hills Comprehensive High School, Chris moved west to Northland College in Wisconsin. Although he greatly enjoyed the hunting and fishing that northern Wisconsin offered, he ultimately decided that to pursue his dream of becoming a fisheries biologist, he should transfer to the University of Maine. During his second semester (May 2002) at The University of Maine, Chris was hired as a Biological Science Technician at NOAA Fisheries’ Maine Field Station in Orono. During his time with NOAA, he assisted with smolt assessments on the Penobscot River; genetic comparisons of landlocked and anadromous Atlantic salmon; summarized historic fish passage in the Penobscot and Kennebec rivers; and gained valuable knowledge of acoustic telemetry systems and the Penobscot River watershed. It was through these experiences that he decided to pursue a master’s degree in Zoology at the University of Maine.

In his final year as an undergraduate at the University of Maine, Chris worked with Dr. Michael Kinnison on a diet analysis study of Atlantic salmon and other fishes in Shorey Brook, Maine. He gained valuable research experience from this opportunity and also found one of his two future graduate advisors. Chris graduated with a B.S. in Zoology in December, 2004 and soon after began graduate school in the Department of Biological Sciences at the University of Maine in January, 2005. He was co-advised by Michael Kinnison and Joseph Zydlewski.
Chris was an active participant in the Student Conservation Association (SCA) from 1998-2001. He worked on trail crews in Portland, Maine; Grand Teton National Park, Wyoming; and Denali National Park, Alaska. In his final year with SCA, Chris was a Conservation Intern working with Chinook salmon in the Metolius River, Oregon.

When taking a break from writing his thesis, Chris prefers to be fishing for stripers or brook trout. He also enjoys hunting, writing and traveling with his wife, Lauren. Christopher is a candidate for the Master of Science degree in Zoology from the University of Maine in August, 2007.