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Exploring the Threats of Dams and Ocean Conditions: In-River Movements and Ocean Growth of Atlantic Salmon (Salmo salar) from Maine's Rivers

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EXPLORING THE THREATS OF DAMS AND OCEAN CONDITIONS: IN-RIVER MOVEMENTS AND OCEAN GROWTH OF ATLANTIC SALMON (*SALMO SALAR*) FROM MAINE'S RIVERS

By

Lisa K. Izzo

B.S. Rutgers University, 2012

A THESIS

Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Science
(in Wildlife Ecology)

The Graduate School
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August 2016

Advisory Committee:

Joseph Zydlewski, Professor of Fisheries Science, Advisor

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THESIS ACCEPTANCE STATEMENT

On behalf of the Graduate Committee for Lisa K. Izzo I affirm that this manuscript is the final and accepted thesis. Signatures of all committee members are on file with the Graduate School at the University of Maine, 42 Stodder Hall, Orono, Maine.

Joseph Zydlewski, Professor of Fisheries Science	Date

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EXPLORING THE THREATS OF DAMS AND OCEAN CONDITIONS: IN-RIVER MOVEMENTS AND OCEAN GROWTH OF ATLANTIC SALMON (*SALMO SALAR*) FROM MAINE'S RIVERS

By Lisa K. Izzo

Thesis Advisor: Dr. Joseph Zydlewski

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
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Substantial declines of anadromous Atlantic Salmon *Salmo salar* have occurred throughout the range of the species, with many populations at the southern extent of the distribution being extirpated or endangered. While Maine is the last state in the country where adult Atlantic Salmon return to rivers each year to spawn, numbers have decreased dramatically in recent decades, with typically less than 2,000 spawners returning to all Maine's rivers combined. The complex life history of this species, which involves a juvenile freshwater phase followed by a marine phase that can last one to five years before returning to freshwater to spawn has exposed Atlantic Salmon to a series of threats that have contributed to their continued decline. These threats include, among others, dams and changing ocean conditions that can influence marine mortality. This thesis focuses on those two threats by using radio telemetry to assess upstream passage of adult salmon in the lower Penobscot River and scale analysis to interpret ocean growth patterns in relation to ocean conditions.

The Penobscot River Restoration Project (PRRP), completed in 2016, involved an extensive plan of dam removal, increases in hydroelectric capacity, and fish passage modifications to increase habitat access for diadromous species. As part of the PRRP, Great Works (rkm 59) and Veazie (rkm 46) Dams were removed, making Milford Dam (rkm 61) the first impediment to federally endangered Atlantic Salmon and other diadromous species. In 2014 and 2015, a total of 73 adult salmon were radio-tagged to track their upstream movements through the Penobscot River to assess potential delays at 1) the dam remnants, 2) the confluence of the Stillwater Branch and the main stem of the Penobscot River below the impassable Orono Dam, and 3) the Milford Dam fish lift (installed in 2014). Movement rates through the dam remnants and the Stillwater confluence were comparable to open river reaches. Passage efficiency of the fish lift was high in both years (95 and 100%). However, fish experienced long delays at Milford Dam, with approximately 1/3 of fish taking over a week to pass in each year. Telemetry indicates most fish locate the fishway entrance within 5 hours of arrival and were observed at the entrance at all hours of the day. These data indicate that overall transit times through the lower river were comparable before and after changes to the Penobscot River due to the substantial delays seen at Milford Dam fish lift. The results of this study show that while adult Atlantic Salmon locate the new fish lift entrance quickly, passage of these fish was significantly delayed under 2014-2015 operations.

Prior to returning to spawn, Maine's Atlantic Salmon typically spend one or two years at sea feeding. While both one sea winter (1SW) and two sea winter (2SW) spawner numbers for the North American stocks have declined since the 1950s, the decline has been most severe in 2SW spawners. The first months at sea are considered a

period of high mortality. However, early ocean mortality alone cannot explain the more pronounced decline of 2SW spawners, suggesting that the second year at sea may be more critical than previously thought. Angler and state agency collected scales from 1946 to 2013 from the five eastern Maine rivers were used to estimate smolt age and ocean age of returning adults. Additionally, seasonal growth rates of maiden 2SW spawners were estimated using intercirculi measurements and linear back-calculation methods. Generalized linear models (Gaussian family, log link function) were used to investigate the influence of average sea surface temperature (SST), accumulated thermal units (ATUs), the Atlantic Multidecadal Oscillation (AMO) and North Atlantic Oscillation (NAO) indices, smolt age, smolt length (FL), and post-smolt growth on growth rate during the oceanic migration of North American Atlantic Salmon. Results suggest that different factors influence salmon growth throughout their oceanic migration, and previous growth can be a strong predictor of future size. Growth was negatively impacted by the phase of the AMO, which has been linked to salmon abundance trends, in the late winter and early spring following the post-smolt period. This is likely when the 1SW and 2SW stock components separate and these results suggest that this period could play a role in the disproportionate decline in 2SW spawners.

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CHAPTER 1

UPSTREAM MOVEMENTS OF ATLANTIC SALMON IN THE LOWER PENOBSCOT RIVER FOLLOWING TWO DAM REMOVALS AND FISH PASSAGE MODIFICATIONS

Abstract

The Penobscot River Restoration Project (PRRP), completed in 2016, involved an extensive plan of dam removal, increases in hydroelectric capacity, and fish passage modifications to increase habitat access for diadromous species. As part of the PRRP, Great Works (rkm 59) and Veazie (rkm 46) Dams were removed, making Milford Dam (rkm 61) the first impediment to federally endangered Atlantic Salmon *Salmo salar* and other diadromous species. Upstream habitat access for Atlantic Salmon is dependent upon successful and timely passage at Milford Dam, as nearly all suitable spawning habitat is located upstream. In 2014 and 2015, a total of 73 adult salmon were radio-tagged to track their upstream movements through the Penobscot River to assess potential delays at 1) the dam remnants, 2) the confluence of the Stillwater Branch and the main stem of the Penobscot River below the impassable Orono Dam, and 3) the Milford Dam fish lift (installed in 2014). Movement rates through the dam remnants and the Stillwater confluence were comparable to open river reaches. Passage efficiency of the fish lift was high in both years (95 and 100%). However, fish experienced long delays at Milford Dam, with approximately 1/3 of fish taking over a week to pass in each year, well below the FERC passage standard of 95% within 48 hours. Telemetry indicates most fish locate the fishway entrance within 5 hours of arrival and were observed at the entrance at all

hours of the day. These data indicate that overall transit times through the lower river were comparable before and after changes to the Penobscot River due to the substantial delays seen at Milford Dam fish lift. The results of this study show that while adult Atlantic Salmon locate the new fish lift entrance quickly, passage of these fish was significantly delayed under 2014-2015 operations.

Introduction

Currently populations of Atlantic Salmon *Salmo salar* in the United States are dramatically below historic levels, with runs of the species declining to 500 to 2,000 fish in all Maine rivers combined by the mid-1990s. This led to the listing of the Gulf of Maine distinct population segment (GOM DPS), which included eight rivers in Maine, as federally endangered in 2000 (Fay et al. 2006). The Penobscot River was not included in the original listing, as it has the largest return of Atlantic Salmon in the United States, however after continued declines this run was added to the endangered GOM DPS in 2009. Despite conservation efforts, adult returns have decreased in recent decades and fluctuated at low levels (generally less than 2,000 returning adults). The GOM DPS has been identified as a high priority for recovery by the National Marine Fisheries Service (NMFS), as while the species is at a high risk of extinction, the primary threats facing Atlantic Salmon are well understood (NMFS 2016).

Multiple factors, including overfishing, habitat loss, dams, and pollution, have contributed to Atlantic Salmon declines (Parrish et al. 1998, NRC 2004). Of these factors, dams have been identified as a major threat because they obstruct both the downstream migration of juveniles as well as the upstream and downstream migrations of iteroparous adults (NRC 2004). A large number of dams have restricted adult salmon access to upstream spawning habitats on the Penobscot River since the 1820s (Opperman et al. 2011). Until recently, 100% of high quality rearing habitat was located above at least four dams (Fay et al. 2006). The cumulative negative effects of dams on upstream migration and spawning success have been well documented for Atlantic Salmon (Gowans et al. 2003) as well as Pacific salmonids (Naughton et al. 2005; Caudill et al. 2007; Roscoe et al. 2010). As a result, dam removal is being considered as a tool in multiple recovery plans across the United States, including the Elwha River (Wunderlich et al. 1994) and the Klamath River (Gosnell and Kelly 2010). Additionally, NMFS, as part of the 2016 Atlantic Salmon 5-Year Action Plan for recovery of the species, has identified the need to reconnect the Gulf of Maine with headwater streams and reduce the effects of dams that prevent or delay Atlantic Salmon passage (NMFS 2016).

Over the past decade, steps have been taken in the Penobscot River to decrease the negative impacts of dams on Atlantic Salmon. The Penobscot River Restoration Project (PRRP), set to be completed in 2016, involved an extensive plan of dam removal, increases in hydroelectric capacity, and fish passage modifications. In the summers of 2012 and 2013, the Great Works and Veazie Dams, respectively, were removed from the main stem of the Penobscot River (Figure 1.1). Upstream passage success for Atlantic Salmon at both dams was annually variable and often poor prior to removal (43-100% at Veazie Dam, 12-95% at Great Works Dam, Holbrook et al. 2009), so the demolition of these two dams was anticipated to be a significant step in improving upstream passage for adult salmon in the system.

Concurrent with the removal of the Great Works Dam and Veazie Dam on the main stem of the Penobscot River, hydropower generation was increased at facilities on the Stillwater Branch, a section of river that moves around a large island in the lower river, in order to offset losses in energy production (Opperman et al. 2011). Generation increases included changes to the Orono Dam, which is located at the confluence of the Stillwater Branch and the main stem of the Penobscot River. A trap was put in place at the base of the Orono Dam to capture upstream migrants that may enter the Stillwater Branch, which are then trucked upstream and released on the main stem of the Penobscot River. This trapping and trucking operation was not designed to handle large numbers of upstream migrants, as passage is provided via the Milford Dam fishway on the main stem. Following these changes, adult upstream migrating salmon may be attracted to increased flow coming from the Stillwater Branch, leading adult salmon to the Orono Dam, which lacks an upstream fishway. While the Orono Dam lies close to the confluence (~200 meters upstream), attraction to the area below the dam could cause a delay in upstream migration.

After the removal of the Great Works and Veazie Dams, Milford Dam has become the lowest dam on the main stem of the Penobscot River and the first barrier for upstream migrating anadromous fish. Passage success at Milford Dam through a Denil fishway was relatively high prior to the PRRP (>80%, Holbrook et al. 2009) and delays were short compared to the other dams in the lower river (< 1 day, Shepard 1989; < 4 days, Holbrook et al. 2009). In April of 2014, a new fish lift and handling facility designed to pass not only Atlantic Salmon but also Sea Lamprey *Petromyzon marinus*, Alewife *Alosa psuedoharengus* and Blueback Herring *A. aestevalis* (collectively referred to as river herring), and American Shad *A. sapidissima* was completed at Milford Dam. With effective passage at the Milford Dam fish lift, as well as a natural bypass that opened at the Howland Dam (~40 km upstream of Milford Dam) in 2016, Atlantic Salmon are anticipated to have access to 60% of their historic range (Opperman et al. 2011). However, this increase depends on passage success at Milford Dam. Efficient passage at the lift is therefore a critical component of Atlantic Salmon recovery in the Penobscot River.

Upstream migration of adult Atlantic Salmon in unimpounded rivers can be broken down into three phases prior to spawning: (1) steady progress upriver with periods of swimming alternating with periods of rest, (2) searching with movements up and down river close to the spawning area, and finally (3) a long residence period in the spawning area (Økland et al. 2001). In a natural environment, migrating adults face many challenges that may alter their migration patterns, including changes in physiological conditions, changes in water flow (Thorstad et al. 2008), and high temperatures (Shepard 1995). However, dams can have considerable effects on upstream progress. Fishways primarily designed for Atlantic Salmon passage have been installed at many dams in Maine, but adult Atlantic Salmon can experience delays before successful passage despite the addition of fishways (Gowans et al. 1999, Thorstad et al. 2008, Holbrook et al. 2009). Substantial delays at fishways can lead to decreased energy reserves, which can cause decreases in reproductive success and survival (Dauble and Mueller 1993; Geist et al. 2000). For this reason, the Federal Energy Regulatory Commission (FERC) licensing regulations include both passage and delay criteria. These criteria are set in coordination with the state and federal regulatory fisheries agencies, and specify that 95% of adult salmon must pass Milford Dam within 48 hours after coming within 200 meters of the dam (NMFS 2012).

The goals of this study were to investigate movements of adult Atlantic Salmon in the lower Penobscot River after the dam removals and fish lift installation. Specifically I sought to determine if migrating adults were being delayed at: 1) the remnants of the Veazie Dam and the Great Works Dam, 2) the confluence of the Stillwater Branch and the main stem of the Penobscot River below the Orono Dam, and 3) the Milford Dam fish lift (installed in 2014), both in general and in the context of FERC licensing requirements. Lastly, this assessment of current movements was used to compare transit times of adult Atlantic Salmon in the lower Penobscot River before and after the dam removals and addition of the Milford Dam fish lift.

Study Area

The Penobscot River watershed is the largest in Maine, and drains an area of approximately 22,200 km^2 throughout the state (Opperman et al. 2011). The river contains multiple dams that impede the migrations of Atlantic Salmon and other diadromous species. The Great Works Dam, which was located at river kilometer (rkm) 59 and was removed in 2012, included two Denil fishways for upstream passage. The Veazie Dam (rkm 46), removed in 2013, included a vertical slot fishway (FERC 2009). Adult Atlantic Salmon upstream passage at both dams was annually variable (43-100% at Veazie Dam, 12-95% at Great Works Dam, Holbrook et al. 2009) prior to removal. Milford Dam (rkm 61), now the lowermost dam on the main stem of the Penobscot River, is approximately 6.1 m high and included a Denil fishway for upstream passage, which is

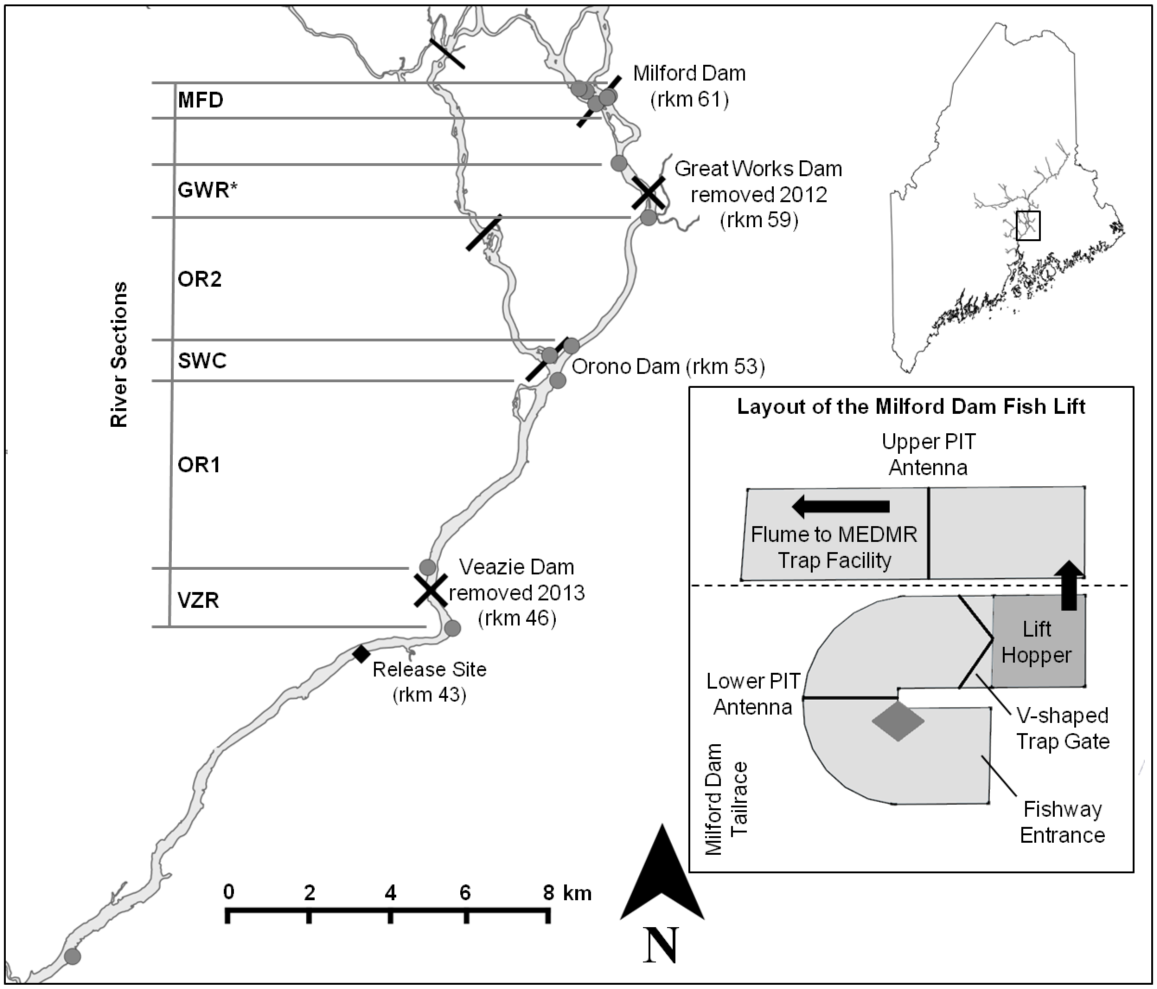


Figure 1.1: Lower Penobscot River study area map. Stationary radio receivers indicated by gray circles, and release site for tagged fish indicated by a black diamond. River sections used in upstream movement calculations shown as VZR (Veazie Dam remnants), OR1 (Open river 1), SWC (Stillwater confluence), OR2 (Open river 2), GWR (Great Works remnants), and MFD (Milford Dam). Inset shows a schematic of the Milford Dam fish lift (fishway is 3.05 meters across). Gray diamond represents the location of the dropper antenna. *Note: Upstream receiver in GWR added in 2015, upstream movement speed calculations in 2014 included unlabeled section between GWR and MFD.

located on the western side of the powerhouse (NMFS 2012). As part of the PRRP, a new fish lift was installed on the eastern shore, and the Denil fishway was left intact to be used on occasion during scheduled shut downs or lift failures. The lift became operational in April of 2014, and includes a horseshoe-shaped entrance (3.05 meters across) which leads to a V-shaped gate that traps fish in a lift hopper (Figure 1.1). After being lifted, migrants are dumped into an upper flume which leads to the trap and handling facility operated by the Maine Department of Marine Resources (MEDMR). The lift operates on a 30 minute cycle, with greater frequency during the peak of the alosine runs, from 0400 hours to 2200 hours from mid-April to mid-November.

The Orono Dam (rkm 53) is just upstream of the confluence of the Stillwater Branch and the main stem of the Penobscot River. The dam is 7.6 m high, and previously contained four turbines with a total hydroelectric capacity of 2.3 MW. A new powerhouse with three additional turbines was added to the project as part of the PRRP, increasing the total capacity to 6.0 MW. While no upstream passage for anadromous species exists at the Orono Dam, a fish trap was installed at the base of the dam to capture upstream migrants (including Atlantic Salmon, Sea Lamprey, American Shad, and river herring) that are transported to the main stem of the river above the Milford Dam (NMFS 2012). Before the restoration project, up to 30% of total discharge in the lower Penobscot River was directed through the Stillwater Branch. With the addition of new powerhouses on the Stillwater Branch at both the Orono Dam and the Stillwater Dam (rkm 60), that percentage can be increased to 40% of total river discharge (FERC 2004). This study focused on the lower section of the Penobscot River (Figure 1.1), from Orrington, ME (rkm 32) to Milford, ME (rkm 61). This area includes the Orono Dam, the Milford Dam, and the remnants of the former Veazie and Great Works Dams.

Methods

Tagging and Release

Adult Atlantic Salmon were collected from either the trap and handling facility at Milford Dam (rkm 61, operated by MEDMR, n=71) or the trap at the base of the Orono Dam (rkm 53, operated by Brookfield Renewable Energy, n=2). Fork length (FL) and sex (as determined by morphology) were recorded at time of capture. When possible, sex was validated after recapture closer to spawning at U.S. Fish and Wildlife Service (USFWS) Craig Brook National Fish Hatchery. A total of 22 multi-sea-winter (MSW, > 63 cm) adult salmon were tagged in 2014 from May 24 to June 30, with one additional salmon tagged on September 19. In 2015, MSW fish (n=46) and 1SW fish (grilse, ≤ 63 cm, n=4) were tagged from May 6 to June 19 (Table 1.1). In both years tagging was halted when river temperature reached 23˚C as a condition of permitting.

Fish were held in tanks of ambient river water prior to tagging and were not anesthetized. Salmon were tagged with gastrically implanted coded radio transmitters (Lotek Wireless, Inc. Newmarket, Ontario, Canada). Tags used for MSW fish were 16 mm x 73 mm and weighed 25.0 g in air (11.0 g in water; Lotek MCFT2-3L). Tags used

Table 1.1: Summary of salmon radio tagging. Number, tagging date, location, median fork length, life stage, and sex (as determined by morphology) of adult Atlantic Salmon radio-tagged in the Penobscot River in 2014 and 2015.

			Tagging location			Life stage		Sex	
Year	n	Tagging date	Milford	Orono	FL (cm, range)	MSW	1SW	M	F
2014	23	5/24 - 9/19	21	2	77.0 (67 - 89)	23	0	16	7
2015	50	5/6 - 6/19	50	0	74.5 (52 - 81)	46	4	29	21

for 1SW fish were 14 mm x 53 mm and weighed 10.0 g in air (4.3 g in water; Lotek MCFT2-3EM). Weights were not recorded for tagged fish, however based on the length-to-weight relationship found in Lear and May 1972, tags used weighed less than 1% of the body weight of the smallest fish in both age classes. Both tag types were set to a 2.5 second burst rate. Each tag was wrapped with one livestock castration band (Ideal Instruments, Inc., Schiller Park, IL, U.S.A.) to decrease the risk of regurgitation (R. Spencer, MEDMR, personal communication; Keefer et al. 2004b). Each salmon also received a 23 mm Passive Integrated Transponder (PIT) tag (Biomark, Boise, ID, U.S.A.), implanted in the dorsal muscle, which was used to track the fish on the existing PIT array in the Penobscot River (Gorsky et al. 2009; Sigourney et al. 2015). During the gastric tagging procedure, two experienced salmon handlers held the fish upside-down against the side of the tank while the tagger opened the mouth of the fish to insert the tag (via flexible plastic tubing) into the esophagus of the fish. Total handling time for tagging and measurements was less than 2 minutes, with fish out of water for no more than 30 seconds during tagging. After tagging, fish were moved to an aerated tank of ambient river water and transported 18 km downstream to the release point at the Brewer boat launch (rkm 43). Total transit time was less than 30 minutes.

Stationary and Active Radio Telemetry

An array of 11 shore-based stationary radio receivers (Lotek SRX400 or SRX-DL) was maintained in the lower Penobscot River from May through October of 2014 (Figure 1.1). In 2015, two additional stationary receivers (Lotek SRX800), located in the middle of Milford Dam and above the Great Works Dam remnants, were added to the array, which was in operation from May to October. Most receivers were connected to one Yagi antenna. The east side of Milford Dam had two antennas, with one facing into the tailrace and the other facing downstream. In the second year of the study (2015), one dropper antenna was added into the Milford Dam fishway, and two Yagi antennas were added on the west side of the powerhouse. The underwater dropper antenna was able to detect fish within the lower flume of the fishway as well as fish within 3 meters of the fishway entrance. Based on locations of stationary receivers, the lower river was divided into six sections that were assessed for upstream movement rates. Potential delay regions included the Veazie Dam remnants (VZR), the area of the Stillwater confluence (SWC), the Great Works Dam remnants (GWR), and the area below Milford Dam (MFD). Two open river sections were also included, which were located between potential delay reaches (Figure 1.1).

In addition to stationary sites, tagged salmon were monitored by active tracking using a portable radio receiver (Lotek SRX400). Fish were not tracked above Milford Dam, as 67 out of 73 of the study fish were recaptured at Milford Dam and taken to USFWS Craig Brook National Fish Hatchery for use as sea-run broodstock for the Penobscot River. Active tracking surveys were conducted 1-3 times per week from May until all fish had either been recaptured or left the study system. The majority of active tracking took place by car and on shore, augmented with trips by canoe in the upper section of the study site (Milford, rkm 61, to Brewer, rkm 43) and by boat in the lower section (Brewer to Orrington, rkm 32). Active tracking utilized both omnidirectional and Yagi antennas to locate tagged salmon.

Environmental Data

In 2014, temperature at the Milford Dam fish lift was obtained from MEDMR. In 2015, a temperature logger was placed in the lower flume at the Milford Dam fish lift. Discharge from the U.S. Geological Survey gauge at West Enfield (rkm 100) was used as a proxy for discharge in the lower portions of the river.

Lower River Movements

Positions from both stationary and active tracking detections were plotted for each individual fish to look for patterns in movement throughout the study season. In addition, upstream movements were used to investigate if fish were moving through the lower river while the Milford Dam fish lift was not operational (2200 hours to 0400 hours). Upstream movements were assessed from the last detection on a downstream receiver to the first detection on an upstream receiver. Upstream movements through the dam remnants and open river sections (VZR, GWR, OR1, and OR2, Figure 1.1) were classified into three groups based on period of initiation and period of completion: 1) "night" initiated and completed movements, 2) "night" initiated movements that were completed during daytime hours, and 3) daytime initiated and completed movements. For these classifications, "night" is defined as between 2200 hours and 0400 hours (based on the hours of operation of the Milford Dam fish lift). If both the last detection downstream and the first detection upstream were during daytime hours, but the interval contained a night, the fish was classified as daytime only movement since it is possible that it could have ceased movement at night.

Upstream Movement Speeds

For this study, upstream movement speeds based on stationary receiver detections were calculated as:

$$\frac{D - 1.0}{t_{first\ upstream} - t_{last\ downstream}}$$

where *D* represents the distance between two receivers (in rkm), and *t* indicates time of detection. These calculations represent a minimum upstream movement speed. Subtraction of 1.0 rkm was added to account for the range of the tags (~0.5 km from the receiver, based on range testing conducted for this study). Speeds through the Stillwater confluence were calculated based on the first detection at the downstream receiver and last detection at the upstream receiver, along with a +1.0 rkm correction, due to the two receivers being <1 rkm apart. For the purpose of this analysis, the lower river was divided into six sections (Figure 1.1). Movement speeds from the release point (rkm 43) to the first upstream stationary receiver (Eddington Bend, rkm 46) were not included in analysis as movement up to Eddington Bend was taken as re-initiation of migration following tagging and transport.

Due to small sample sizes and non-normal distributions, non-parametric methods were used for statistical analysis throughout this study, and central tendencies are reported as medians. A paired sample Wilcoxon signed rank test was used to test for differences in upstream movement speeds among potential delay reaches (Veazie Dam remnants - VZR, Stillwater Branch confluence - SWC, Great Works Dam remnants - GWR, Milford Dam - MFD) and unobstructed reaches - OR1 and OR2. All possible pairwise comparisons, with a Bonferroni correction included to account for multiple comparisons, were performed on sections of the lower river. If a fish made multiple movements upstream after dropping downstream, only the initial upstream attempt was used in movement speed comparisons. Significance for all tests was assessed at a level of $\alpha = 0.05$. Statistical analyses were performed using Program R (R Core Team 2015).

Milford Dam Delays

Overall delay times at Milford Dam were calculated as the time from the first detection on any of the antennas in the Milford Dam array until successful passage, which is defined as when the fish was recaptured at the trap and handling facility at the top of the Milford Dam flume. This was used as a measure of successful passage since tagged fish were taken to the USFWS Craig Brook National Fish Hatchery after recapture and did not continue upstream after passing Milford Dam. In addition, delay times were calculated in terms of the FERC passage standard for the Milford project, which specifies that 95% of adult Atlantic Salmon that come within 200 meters of the face of the dam must utilize the lift within 48 hours (NMFS 2012). For the FERC standard, successful passage is defined as when the fish has used the lift and been moved to the upper flume (Figure 1.1). This measure of successful passage ignores the amount of time that salmon spend in the upper flume, as this is influenced by the operation of the Milford Dam trap and handling facility and not the fish lift. Delay times in terms of the FERC passage standard were not calculated for fish that were first detected at Milford Dam during either a lift shutdown or when temperatures were greater than or equal to 23˚C (the legal limit for assessment, based on the thermal tolerance of Atlantic Salmon (Jonsson and Jonsson 2009)) so that estimates reflect only a fully functioning system.

We used a conservative estimate to look at delay times in terms of the FERC passage standard since tag strength and noise from the hydropower project made it difficult to determine when a fish was 200 meters from Milford Dam. In 2014, these delays were calculated based on first detection in the tailrace to the last detection in the tailrace (~50 m range) before being recaptured. In 2015, the addition of a PIT antenna in the upper flume allowed for detection of fish immediately or shortly after they exited the lift hopper. Delays in 2015 were calculated from the first detection on the dropper antenna at the fishway entrance to the first detection on the PIT antenna in the upper flume. If a detection on the upper PIT antenna was not available, delays were calculated based on the last detection on the dropper antenna before recapture, indicating when the fish had left the lower flume, as a conservative estimate.

Fishway Visits

The addition of a dropper radio antenna in the Milford fishway in 2015 allowed for investigation of fish use of the lower entrance. Number and duration of visits to the fishway entrance were calculated for each fish detected at the entrance. A visit was defined as multiple detections that occurred until a fish left the area for more than 30 minutes. If a fish was not detected at the entrance for 30 minutes, a new visit began when the fish returned. Additionally, if a single detection occurred both 30 minutes after the last detection and 30 minutes prior to the next detection, that observation was excluded from analysis of fishway visits. The interval of 30 minutes was chosen due to the operation of the fish lift, which was operated on a 30 minute cycle. An absence time of 30 minutes would represent when a fish had missed at least one lifting of the hopper. Based on these visit calculations (number and duration), the proportion of time individual fish spent near the fishway was calculated for each day. Spearman's rank correlation was used to investigate relationships between the proportion of time spent near the fishway and mean daily flow and mean daily temperature.

To investigate diel patterns of detections at the fishway entrance, detections on the dropper antenna for each individual fish during its entire time period spent near Milford Dam were binned into hourly observations. If multiple detections occurred during an hourly bin, the fish was considered present during that hour of the day. The frequency of hours present at the fishway, on a 24 hour cycle, was calculated for each fish, and then standardized to proportion to determine if fish were approaching the fishway while the lift was not operational. A Kruskal-Wallis multiple comparisons test (R package: asbio, Aho 2015) was used to test for differences among hours of the day.

Comparisons of Transit Times Before and After Changes to the Lower Penobscot River

Data previously collected via the PIT array in the Penobscot River from 2002-2004 (Gorsky et al. 2009) and 2010-2012 (Sigourney et al. 2015) allowed for comparisons between transit times (in days) of adult Atlantic Salmon before and after changes to the lower river. The Penobscot River PIT array included PIT tag antennas constructed in the fishway entrances and exits at each hydroelectric dam (see Gorsky et al. 2009; Sigourney et al. 2015 for detailed methods). Prior to the dam removals, adult salmon were PIT tagged after capture at the top of the Veazie Dam fishway and released into the headpond following tagging. Transit times from Veazie Dam to Milford Dam were calculated from release into the Veazie Dam headpond to detection exiting the

Milford Dam fishway, indicating successful passage at Milford Dam. Transit times from Great Works Dam to Milford Dam were calculated from detection exiting one of the Great Works Dam fishways to detection exiting the Milford Dam fishway. In comparing transit times from Great Works Dam to Milford Dam, 2010, 2011, and 2012 were not included in analysis since the PIT array was not operating at Great Works Dam in those years.

For current work, transit times for this study from the former Veazie Dam to Milford Dam were calculated from first detection on the radio receiver located in the area of the former Veazie Dam headpond to time the fish was handled at the trap and handling facility at Milford Dam, as this would approximate successful passage at Milford Dam. For consistency between years, transit times from the former Great Works Dam to Milford Dam were calculated from the last detection on the receiver located right below the Great Works remnants to successful passage at Milford Dam since a receiver was not located in the Great Works headpond in 2014 (Figure 1.1). I felt this would not influence the transit time comparisons, as movement between the two Great Works receivers in 2015 often occurred in less than two hours. Transit times were compared among years for each reach using a Kruskal-Wallis multiple comparisons test (R package: asbio, Aho 2015).

Results

Lower River Movements

After release in 2014, 22 of 23 salmon were detected on the stationary antenna array in multiple locations. One fish likely regurgitated its radio tag soon after release and was later recaptured without a radio tag at the trap at the base of the Orono Dam. It is unknown if this fish ever approached Milford Dam. All other fish were detected approaching Milford Dam. Tag retention in 2014 was 83% (4 tags regurgitated). In 2015 all radio-tagged salmon (n = 50) were detected on multiple stationary radio receivers and tag retention was 100% for the duration of the study. All fish were detected approaching Milford Dam in 2015.

Tagged salmon displayed three general movement patterns (Figure 1.2) during the two study years: (1) directed upstream movement followed by holding in the area below Milford Dam for more than 48 hours, (2) directed upstream movement followed by rapid passage at Milford Dam (within 48 hours), or (3) fallback of greater than 4 rkm from Milford Dam followed by upstream and downstream movements greater than 4 rkm. The threshold of 4 rkm was chosen due to the placement of stationary receivers, and represents when fish had dropped back past the next receiver downstream of Milford Dam. Fish that displayed the third movement pattern either eventually returned to Milford Dam to successfully pass or moved downstream and left the system. For both years (n=72), the most common movement pattern was holding in the area below Milford Dam for more than 48 hours (58.3%). About one third (33.3%) of tagged fish passed Milford Dam quickly (<48 hours), while a small subset of fish (8.3%) made downstream and upstream movements after reaching Milford Dam. Most fish were moving upstream during the hours that the Milford fish lift was operational, however a small percentage completed upstream movements between 2200 hours and 0400 hours (GWR = 10.9%, VZR = 2.3%, OR1 = 2.4%, OR2 = 5.4%). Additionally, some fish initiated upstream movement during these hours (GWR = 9.1%, VZR = 0.0%, OR1 = 2.4%, OR2 = 1.8%)

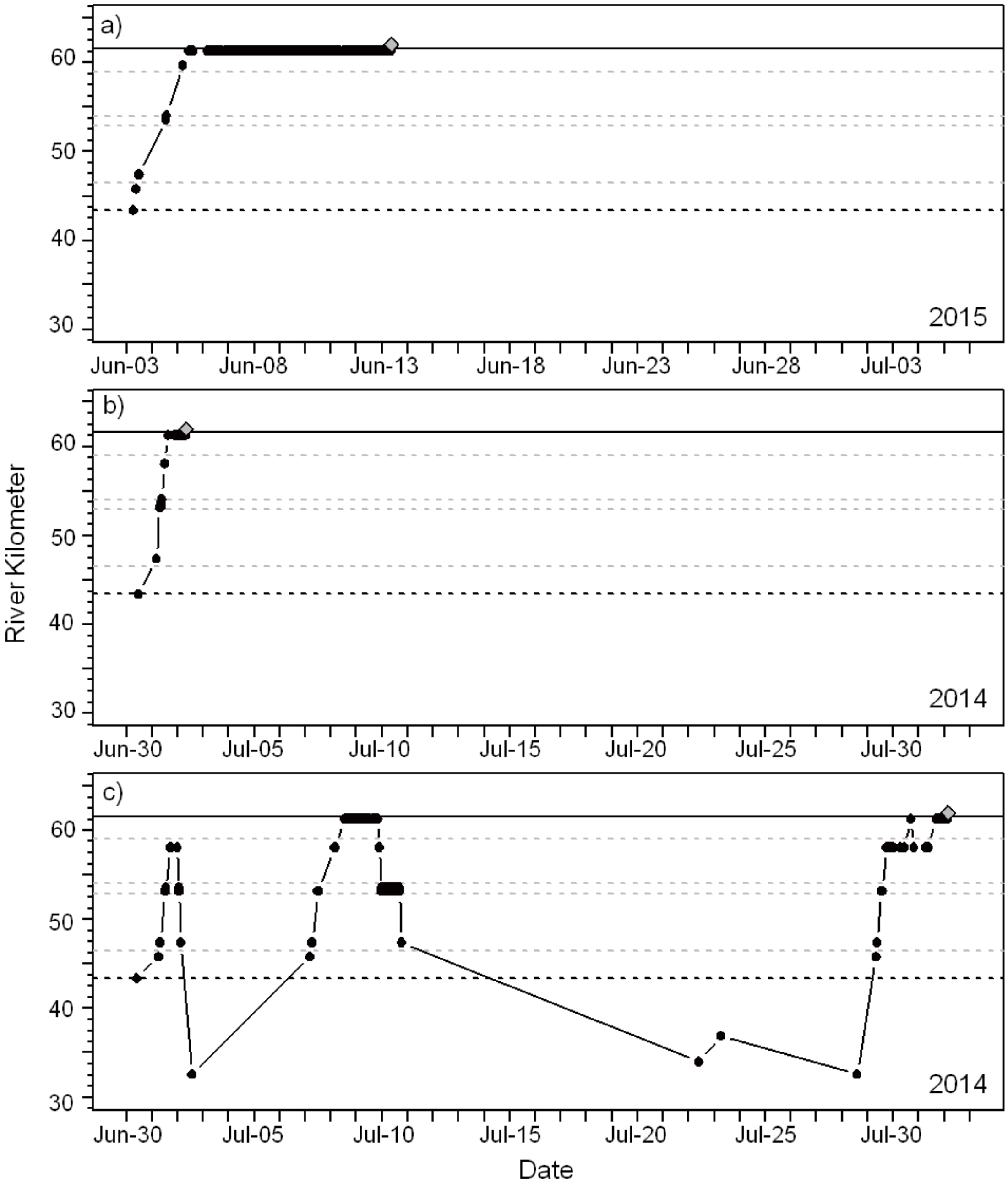


Figure 1.2: Upstream movement patterns of tagged salmon. Characteristic migration tracks of radio-tagged salmon throughout the study: (a) fish holding below Milford Dam, (b) fish passing Milford Dam in less than 48 hours, and (c) fish making upstream and downstream movements after reaching Milford Dam. Dashed gray lines represent the former Veazie Dam (rkm 46), the Stillwater confluence (rkm 53), and the former Great Works Dam (rkm 59). The dashed black line represents the release point (rkm 43), and the solid line represents Milford Dam (rkm 61). Successful passage is indicated by a gray diamond.

Upstream Movement Speeds

Upstream movement speeds in 2014 in the reaches downstream of Milford Dam were variable, ranging from 0.04 to 2.4 km/h (1.0 to 57.1 km/day), with a median of 1.0 km/h. Salmon moved at speeds from 0.02 to 2.0 km/h (0.5 to 47.0 km/day) before reaching Milford Dam (median of 0.5 km/h) in 2015. In both years, speeds through the potential delay reaches of the Veazie and Great Works Dam remnants as well as the Stillwater confluence were comparable to speeds through unobstructed reaches of river (Figure 1.3). While no differences were detected in upstream movement through the Stillwater confluence, an increase in detections was observed in 2014 from July 8 to July 11, when two tagged fish were consistently detected below the Orono Dam. Main stem temperatures during this period (20 - 23˚C) were in the upper critical range for Atlantic Salmon (Jonsson and Jonsson 2009). Although salmon moved through dam remnants and open river sections at similar speeds, movement through Milford Dam was often over 100 times slower than both unobstructed and potential delay river sections, and median upstream speed in the area of Milford Dam was only 0.006 km/h (0.001 to 0.096 km/h) in 2014 and 0.005 km/h (0.001 to 0.050 km/h) in 2015.

Milford Dam Passage Success and Delays

In 2014, 95.5% (21/22) of tagged fish that were detected on the Milford array successfully passed Milford Dam. The one fish that was not able to pass was detected on the PIT antenna inside the fishway entrance on July 1, and the tag was recovered on July 22 in the mouth of Sedgeunkedunk Stream (rkm 35). Of the fish that successfully passed Milford Dam, all used the new fish lift except for one, which may have passed over the

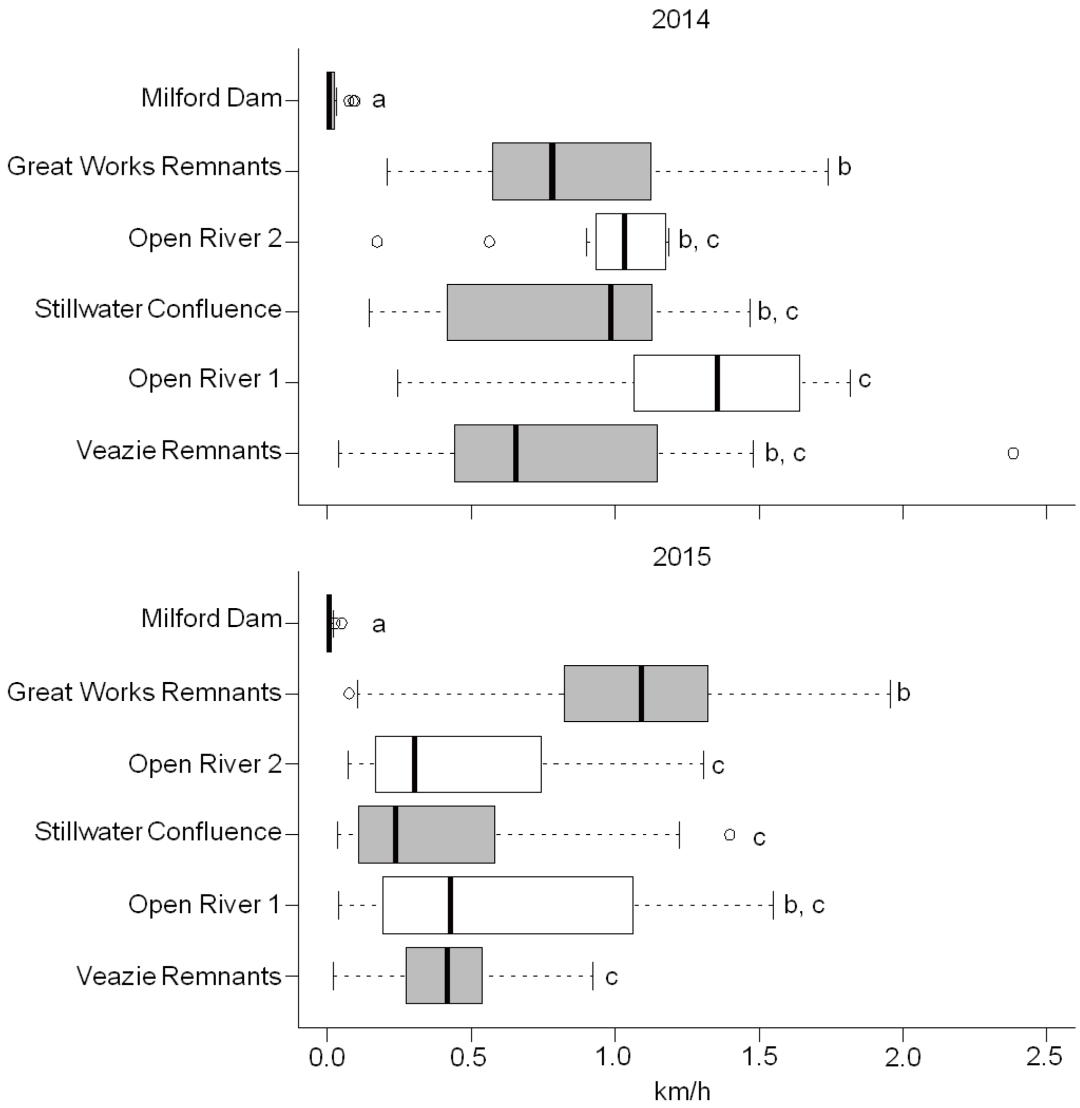
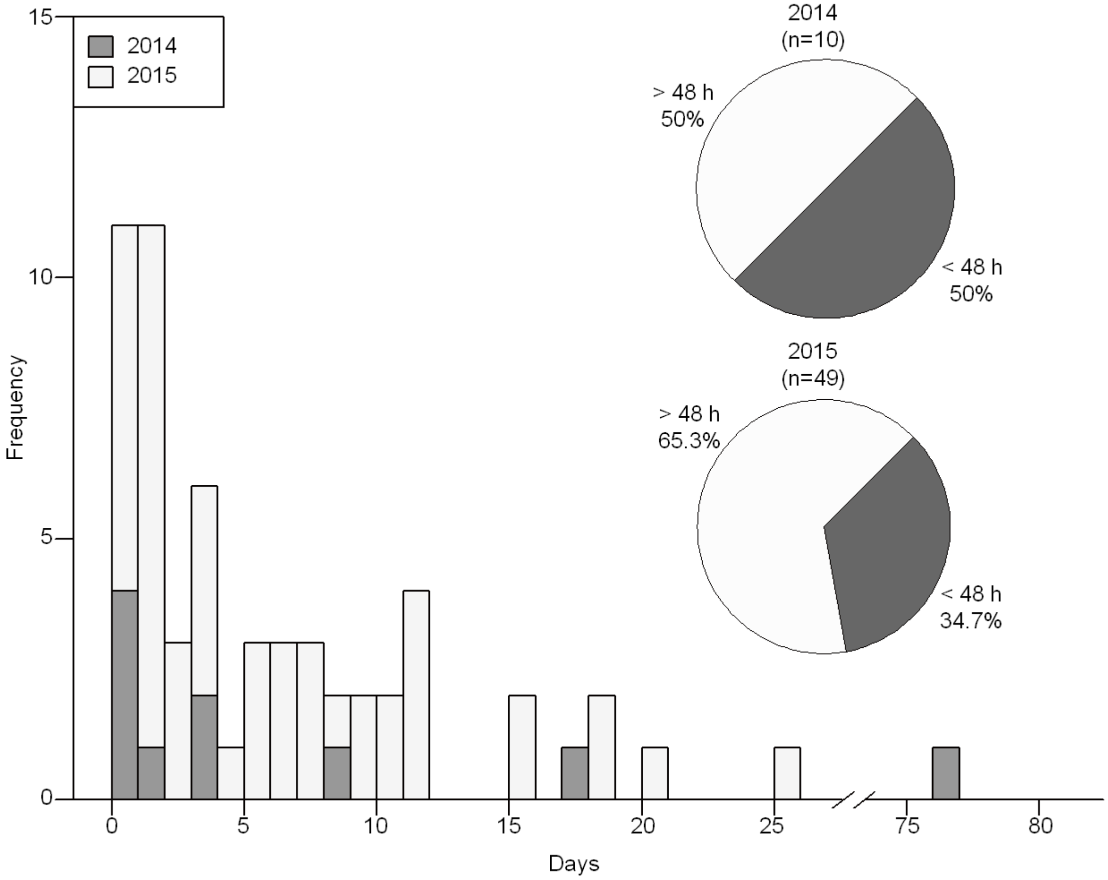


Figure 1.3: Upstream movement speeds. Upstream movement speeds of radio-tagged Atlantic Salmon through unimpounded (open) and potential delay (gray) reaches of the lower Penobscot River. Differences from Wilcoxon signed rank test with multiple comparisons denoted by different letters.

spillway before the flash boards were installed. Delay times from first detection on the Milford antenna array to recapture at Milford Dam ranged from 0.03 to 78.4 days (median=3.0). After reaching Milford Dam, 36% (8/22) of fish dropped back more than 3 rkm, with 4 of those fish falling back past the release site (rkm 43). After being detected downstream of Milford Dam (~500 m), 67% of fish were detected in the tailrace in less than 24 hours, and 71% in less than 48 hours. Despite this, only 55% passed within 48 hours of being detected in the tailrace.

In 2015, 100% of tagged fish successfully passed Milford Dam, all using the fish lift. One radio-tagged salmon did fall back after using the Milford fish lift, possibly through a tube at the back of the upper flume as it was never seen at the trap and handling facility. The initial approach of this fish was used in FERC passage standard delay calculations (hours), although it was continually tracked through the summer until successfully passing Milford Dam at the beginning of October before falling back a second time. This fish was not included in general delay time calculations (days) since it was never recaptured or seen at the MEDMR trap and handling facility when it was initially lifted in June. Delay times ranged from 0.4 to 26.9 days (median=4.3) from first detection on the Milford array to recapture. As in 2014, some fish displayed small downstream movements after reaching Milford Dam, with 26% (13/50) dropping back over 3 km, and one fish (2%) dropping back past the release site (rkm 43). The addition of the dropper antenna indicated that 78% of fish were approaching the entrance to the fishway within 5 hours of being detected on the Milford array. All fish that were detected on the dropper antenna (n=49) had approached the fishway entrance within 24 hours of detection elsewhere on the Milford array. One fish was not detected on the dropper antenna due to an antenna malfunction later in the season.

Figure 1.4: Milford Dam delay times. Histogram of FERC delay times of Atlantic Salmon approaching Milford Dam in 2014 and 2015. Pie charts represent percentage of fish in each year that met the passage standard of utilizing the fish lift in less than 48 hours (shown in dark gray).



Delays in the Context of the FERC Standard

In 2014, the lift was shut down from June 15 to 26, as well as from September 21 to 29. Two tagged fish arrived at Milford Dam during these shut downs, and are not included in the FERC delay time analysis. Additionally, main stem river temperatures reached 23˚C on July 1. Tagged fish that arrived at Milford Dam on this date or the day before (n=8) are also not included in the FERC delay analysis since these temperatures are the legal limit for assessment. Removing these fish leaves 10 tagged salmon that were detected in the tailrace before passing Milford Dam. Two of these tagged fish were present at Milford Dam during the June lift shut down, however they had arrived more than 48 hours prior so they had already failed to meet the standard. Of these 10 fish, 50% passed within the 48 hour window. Delay times ranged from 1.2 hours to 76 days, with 70% of tagged fish passing Milford Dam within one week. Tagged fish were not affected by lift shut downs or high river temperatures in 2015. Delay times ranged from 7.4 hours to 26 days, with 34.7% of fish passing within the 48 hour window and 63.2% passing within one week (Figure 1.4).

Fishway Visits

Based on the criteria for a visit described above, individual fish made between 1 and 47 visits to the entrance of the Milford Dam fishway (median=11) in 2015 before passing, with fish that spent more days at Milford Dam making the most visits overall. More than half (53%) of these visits were less than 90 minutes in length. Across all days of the study season, individual tagged fish spent on average 27% of a day (6.5 hours) visiting the fishway (0.1% to 84%). The proportion of time fish spent near the fishway entrance in a day was not significantly correlated with mean daily flow (Spearman's rank correlation, $p = 0.23$) or mean daily temperature (Spearman's rank correlation, $p = 0.22$). The number of visits that an individual fish made per day ranged from 1 to 12 (median of 2). Tagged fish were detected on the dropper antenna at all hours of the day, and no diel patterns were observed in fishway approach (Figure 1.5). This observation was supported by the results of the Kruskal-Wallis multiple comparisons test, which failed to detect differences between hours for all but the following pairs: 1400 and 0100, 1400 and 0200, 1400 and 2100, 1400 and 2200, 1400 and 2300, and 1600 and 0200.

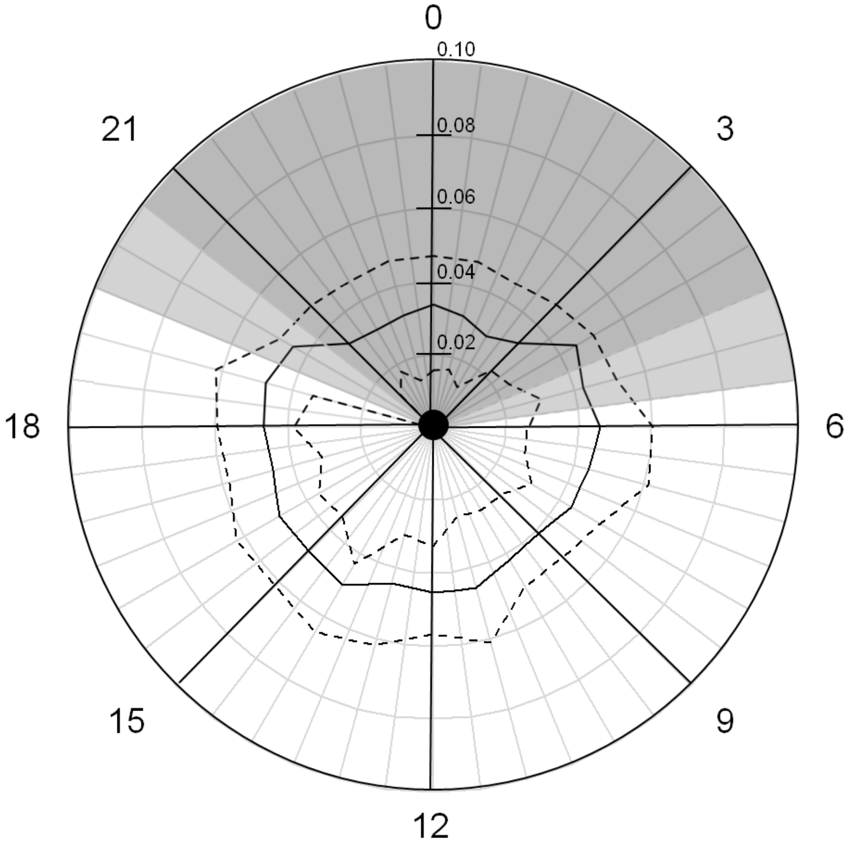


Figure 1.5: Diel patterns of fishway visits. Radial plot showing the median (solid line) proportion of hourly observations that occurred during hours thoughout the day for individual fish, with 25% and 75% percentiles indicated by dashed lines. Dark gray shading indicated hours of darkness, while light gray shading indicates the approximate time of shifting sunrise and sunset times throughout the study period in May and June of 2015.

Comparisons of Transit Times Before and After Changes to the Lower Penobscot River

In 2014, transit times from the former Veazie Dam headpond to successful passage at Milford Dam ranged from 1 to 80 days, with a median of 4 days. Similarly, transit times from the Great Works Dam headpond to successful passage at Milford Dam ranged from less than a day to 79 days, with a median of 4 days. In 2015, Veazie Dam headpond to successful passage at Milford Dam transit times ranged from 3 to 33 days

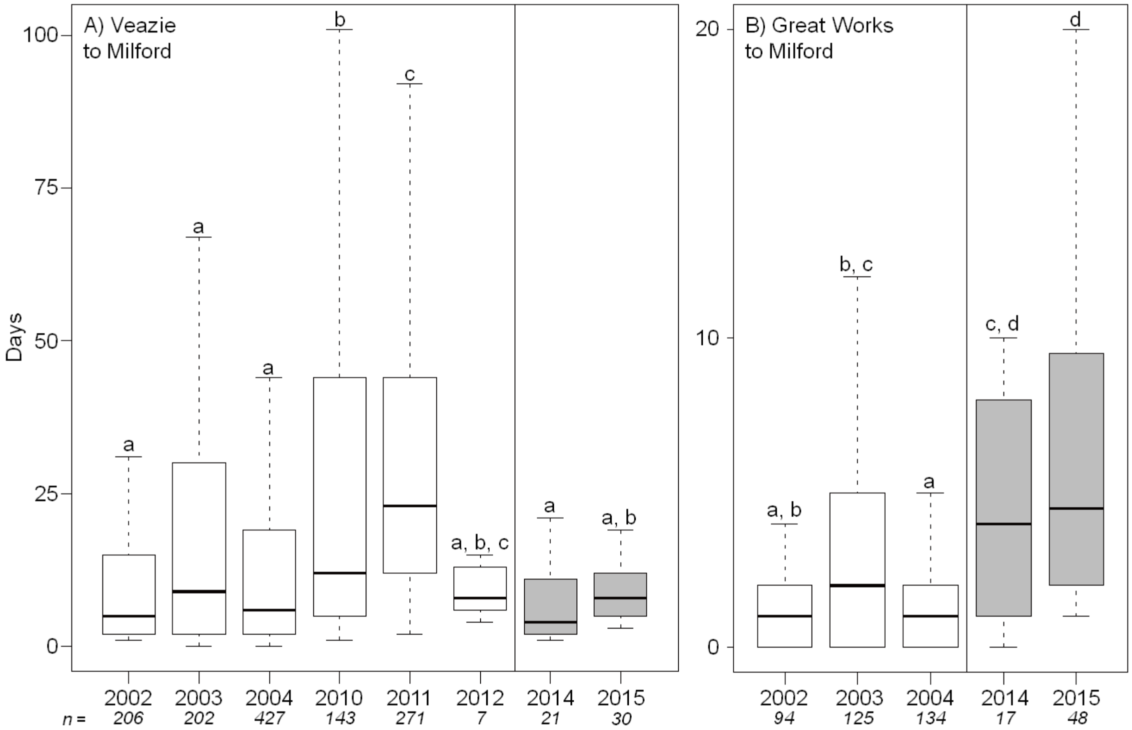


Figure 1.6: Adult salmon lower river transit times. Transit times of adult Atlantic Salmon in days in the years before (open) and after (gray) the removal of the Great Works Dam and the installation of the new Milford fish lift. Transit times are calculated from passage at Veazie or Great Works to passage at Milford Dam. Data collected from 2002 - 2004 and 2010 - 2012 utilized PIT telemetry; data collected in this study (2014 - 2015) utilized radio telemetry. Outliers are excluded from this plot for simplicity. Sample size denoted below each year, and differences indicated by lettered group membership above bars.

with a median of 8 days, and Great Works Dam headpond to successful passage at Milford Dam transit times were between 1 and 27 days with a median of 4.5 days. Across all years prior to changes to the lower river, transit times for adult salmon from the Veazie Dam headpond to successful passage at Milford Dam ranged from less than a day to 172 days, with median values between 5 and 23 days. Transit times from the Great Works Dam headpond to successful passage at Milford Dam prior to modifications ranged from less than a day to 103 days, with median values of 1 to 2 days.

There was no difference between transit times in 2014 and 2015 for both movement from the former Veazie Dam headpond to Milford Dam passage and from the former Great Works Dam headpond to Milford Dam passage. Transit times from the Veazie Dam headpond to Milford Dam passage before and after the changes in the Penobscot River were comparable in most years; however 2014 and 2015 did have lower median transit times than 2010 and 2011. Differences in Great Works Dam headpond to Milford Dam passage transit times were detected in multiple years. Median transit time in days from the Great Works Dam headpond to successful passage at Milford Dam was higher in 2014 and 2015, after the installation of the new fish lift, than in 2002-2004, when the Denil fishway was still in use. Differences are summarized by lettered group membership in Figure 1.6.

Discussion

These results show that upstream migrating adult Atlantic Salmon are not being delayed at the dam remnants after the removal of the Veazie and Great Works Dams. Tagged salmon were also not delayed at the modified Orono Dam just upstream of the confluence of the Stillwater Branch and the main stem of the Penobscot River. Movement rates through these sections were similar to other nearby open river sections and were within the range reported for upstream movements of Atlantic Salmon in other studies in the Penobscot River and elsewhere (Økland et al. 2001; Gorsky 2005; Thorstad et al. 2005, 2008). Prior to the dam removals, migrating adults spent significant time in the lower river due to delays experienced at Veazie and Great Works Dams, and passage at these dams was often highly variable (Shepard 1989; Holbrook et al. 2009). The removal of the lower main stem dams has greatly increased the rate of salmon movement from tidal reaches to the base of Milford Dam, despite the increased flow on the Stillwater Branch.

The removal of Veazie and Great Works Dams on the Penobscot River likely allows migrants better access to cool water during high summer temperatures. A small number (n=3) of tagged salmon made downstream movements after reaching Milford Dam during the months of July and August when water temperature was high (up to 26˚C). Two of these fish re-ascended the river and successfully passed Milford Dam after spending time in the lower river. During summer months fish were located in the mouth of the Stillwater Branch, and the mouths of Great Works and Sedgeunkedunk Streams. At least one fish exited the study area and moved into the estuary. This behavior is consistent with increased use of tributaries observed in the Columbia and Snake Rivers during high temperatures (Keefer et al. 2004a; Goniea et al. 2006), as well as past work in the Penobscot River, which documented that adult salmon use Great Works Stream as thermal refuge (Holbrook et al. 2009). Prior to the removal of Great Works and Veazie Dams, little thermal refugia existed between the two lowermost dams, and fish that successfully passed Veazie Dam were then often trapped below Great Works Dam during the summer (Holbrook et al. 2009). While few fish were tracked during high temperatures in this study, this behavior suggests that the removal of the two lower main stem dams may allow adult salmon access to more cool water refugia in stream mouths or access to the estuary during thermally stressful temperatures.

After upstream migration through the lower portion of the Penobscot River, almost all tagged salmon were able to eventually pass Milford Dam. Since Milford Dam is now the first dam on the main stem of the Penobscot River that migrating Atlantic

Salmon face on their journey upstream, successful passage at the new fishway is critical to recovery. In previous studies, fishway function has often been looked at in terms of attraction and passage efficiency. Attraction efficiency can be defined as the proportion of tagged fish released that are located within 3 m of a fishway entrance (Bunt et al. 1999) or near enough to a fishway entrance for a fish to detect the attraction flow (Aarestrup et al. 2003). Passage efficiency can be defined as the proportion of fish detected at the fishway entrance that are then detected at the fishway exit (Bunt et al. 1999; Aarestrup et al. 2003). In terms of passage efficiency, between 95 and 100% of tagged fish that were detected near or inside the lower fishway entrance successfully used the lift during the two study years. Attraction efficiency at the fish lift is also high, as all fish that reached Milford Dam were detected inside the fishway entrance at some point during the study. Notably, in 2015 all fish were detected near the fishway entrance within 24 hours of reaching the dam. While the tailrace detections from 2014 have a lower percentage of fish in the tailrace in less than 24 hours (67%), I believe this was an artifact of poor detection efficiency on the tailrace antenna, as fish that were detected repeatedly on the lower PIT antenna inside the fishway were often not detected on the tailrace antenna.

While the detection data from the Milford Dam radio telemetry array indicate that the Milford fish lift has a high attraction efficiency and passage efficiency, tagged fish experienced substantial delays prior to successful passage. The current regulatory passage standard of 95% passage within 48 hours was not met in either year of this study, and my estimates fall well below the target value (50% in 2014 and 34.7% in 2015, Figure 1.4). Few studies have examined Atlantic Salmon behavior at fish lifts. Reported passage efficiencies range from 47% (Croze et al. 2008) to 87% (Larinier et al. 2005) at lifts located on European rivers. In the study conducted by Croze et al. (2008) on the River Garonne, France, mean delay time at the fish lift was 12.5 days. On the Gave de Pau River, France, a median delay time of 9 days was reported at the Baigts hydroelectric plant (Larinier et al. 2005). While delay times differed across systems, behavior of tagged salmon in this study was similar to the behavior of Atlantic Salmon seen at the fish lifts in Europe. Authors reported tagged fish rapidly approaching the entrance to the fish lift after arriving at the dam (74% in less than 24 hours, Larinier et al. 2005; 79% within one hour, Croze et al. 2008), and then making multiple visits to the entrance before successfully being trapped and lifted. In the second year of this study, tagged salmon located the fishway rapidly, but made multiple visits, often over many days (or weeks), before successful passage. It should also be noted that the number of visits per fish in this study may represent a conservatively low estimate based on the criteria chosen for this analysis (30 minutes between visits), and fish may be making more frequent passage attempts. Future focus on behavior near and inside the fishway entrance would be beneficial in regards to determining frequency of passage attempts.

Despite an increase in movement rates through the regions of Veazie and Great Works Dams after the dam removals, overall transit times through the lower river were similar after changes to the lower Penobscot River due to the extensive delays incurred at Milford Dam. As demonstrated by the PIT data from 2002 to 2004, transit time from the Great Works Dam headpond to the area below Milford Dam was often short, and delay times at Milford Dam were low compared to the other dams in the lower section of the system. Other telemetry studies in the Penobscot River showed similar results, with most

Atlantic Salmon using the Denil fishway at Milford Dam within a day after being detected below the dam (Shepard 1989). Additionally, all tagged fish that successfully passed Great Works Dam in 2005 and 2006 were able to pass Milford Dam in 3.7 days or less (Holbrook et al. 2009). While the transit times from the former Great Works Dam headpond to the base of the Milford Dam in this study were short, delay times at the Milford Dam fish lift were markedly higher than those seen at the Denil fishway in previous years. Median delay times in this study were lower than those previously seen at the now removed Great Works and Veazie Dams; however between 30 and 40% of adult Atlantic Salmon over the two study years were delayed longer than a week before successfully passing.

In terms of migratory transit times through the lower Penobscot River, these results suggest that the benefits of dam removal have the potential to be offset by the lack of timely passage at the Milford Dam fish lift. While overall passage success at Milford Dam remains high, improving passage time would be beneficial to the recovery of Atlantic Salmon in the system. Considerable delays in upstream progress could have multiple impacts on the overall migration success of adult Atlantic Salmon in the Penobscot River. Extensive delays at dams have been shown to decrease energetic reserves needed for spawning success and lower the probability of survival (Dauble and Mueller 1993; Geist et al. 2000). Additionally, long delays before passage at Milford Dam could result in adults being exposed to poor passage conditions at dams further upstream that would have been avoided otherwise. Passage success at both Howland and West Enfield Dams on the Penobscot River (rkm 100) are reduced by high temperatures and low flows (Gorsky 2005; Maynard et al. 2015, *in review*). Because the peak of the

Penobscot River run typically occurs in June, long delays at Milford Dam would cause fish to be exposed to high river temperatures during migration. This was observed in both 2014 and 2015.

It is unlikely that the regulatory standard will be met and delays decreased at the Milford fish lift without modifications that increase the probability of capturing adult salmon in the lift hopper. The fishway is currently operated primarily during daytime hours, however data from this study showed that salmon did move upstream during the hours that the lift was not operational and approached the fishway entrance at all hours. The river reach with the highest percentage of movement at night was the Great Works Dam remnants, which also represents one of the shortest reaches in this study, so it is possible that more fish were moving at night in other reaches but were not detectable due to the distance between receivers. This is consistent with other studies that have documented upstream migration of salmonids at night (Gowans et al. 1999; Rivinoja et al. 2001). While there were nocturnal movements of salmon around the fishway entrance, analysis of the PIT detections indicated a peak in detections in the late morning (Maynard, University of Maine, unpublished data). Similar trends have been noted at other fishways (Gowans et al. 1999; Thiem et al. 2012; Keefer et al. 2013), suggesting that entrance and use of multiple styles of fishways may be dependent on visual cues. However, since Atlantic Salmon are approaching the fishway entrance at all hours of the day, continuous operation of the lift is an untested method that may increase trapping efficiency.

Since the tagged salmon are in the area of the fishway, there is the potential that the delays observed are due to an unknown factor inside the lower fishway entrance. One potential factor that could influence these delays is the highly aerated attraction flow in the lower entrance, which can discourage fish from entering or moving through the fishway (Clay 1995). It is unclear how many of the visits to the fishway included salmon entering the lower fishway entrance, or if fish were remaining a short distance away from the fishway. When fish do enter the fishway, another potential influential factor is suboptimal operation of the V-shaped gate at the hopper entrance. Previous studies have documented low probabilities of passing through V-shaped entrances to lift holding pools for Atlantic Salmon (0.15 in Larinier et al. 2005; 0.17 in Croze et al. 2008), and have additionally documented that up to 40% of entries through a V-shaped gate can result in salmon returning to the area outside of the fish lift (Croze et al. 2008). Both hesitation to enter and frequent return back through the V-shaped gate could be contributing to the delays observed at the Milford Dam fish lift. Further investigation into behavior near the V-shaped gate would be valuable for optimizing the design and operation of the lift.

Previous studies in the Penobscot River have attributed migration delays and poor passage rates at dams to poor attraction at fishways (Shepard 1989), flow and temperature influences (Gorsky 2005, Holbrook et al. 2009), and lack of migration motivation due to homing to lower river stocking sites (Shepard 1989). The data from this study suggests that attraction at the fishway entrance is likely not the limiting factor at Milford Dam, as all fish in 2015 were detected near the fishway entrance within 24 hours of reaching the dam. Additionally, fish made multiple visits to the fishway entrance before successful passage, further supporting the contention that the attraction flow was effective. I was not able to detect any relationships between proportion of the day spent near the fishway entrance and environmental factors. However this may have been due to the limited scale of this study.

While the origin of the study fish is unknown, it is unlikely that homing to lower river stocking sites contributed to the delays seen at the Milford Dam fish lift. The majority (69/73) of fish used during the study were MSW fish, spending two to three years at sea. The Penobscot River has a large smolt stocking program, and in the smolt years of interest all fish were stocked in multiple locations that were at least 10 rkm upstream of Milford Dam (USFWS, unpublished data). In addition, the movements that tagged fish displayed below Milford Dam were not consistent with the searching phase described by Økland et al. (2001), which included erratic upstream and downstream movements in river stretches that averaged 7.7 to 14.9 km over two study years as salmon homed to spawning areas in the River Tana in Norway. In previous studies in the Penobscot River, Atlantic Salmon stocked in the main stem of the river near the head of tide made more downstream movements than fish stocked in tributaries near spawning grounds (Power and McCleave 1980). In contrast, most tagged fish in this study moved directly upstream and then remained in the area below Milford Dam for multiple days or weeks before passing. The number and duration of visits to the fishway entrance suggest that tagged salmon were actively seeking a way upstream since they were often moving towards and away from the dam. As such, it is unlikely that tagged salmon had entered a natural resting period during the migratory phase.

Prior to and during the years of this study, adult returns were at historic lows in the Penobscot River, and the best method to capture adults for tagging was via the Milford Dam trap and handling facility, requiring fish to be transported and released downstream. After release and recovery from tagging, all fish displayed directed upstream movement that is consistent with the first phase of Atlantic Salmon upstream migration, the "migratory phase", described by Økland et al. (2001). The effects of gastric tagging and displacement downstream on my study fish were likely minimal, as the majority of salmon resumed upstream migration within 24 hours of release. Additionally, while all but two (captured at the Orono Dam trap in 2014) tagged fish used in this study were not naive to the fish lift at Milford Dam, it is unlikely that long delay times were due to fish having experienced the fishway once before. Studies have not been designed to specifically test the effects of using non-naive fish to study passage time, however a previous study with Atlantic Salmon on the River Nidelva showed no differences in migratory speed or length of stay at a tunnel outlet between fish captured downstream of a power station and fish collected at the fish passage facility (Thorstad et al. 2003). Similarly, researchers conducting a study of anadromous Brown Trout *S. trutta* found no differences in attraction or passage efficiency of a nature-like bypass between fish initially captured upstream and downstream of the bypass weir (Aarestrup et al. 2003). In this study, the two fish that were initially captured at the Orono Dam trap (and therefore had not experienced the Milford fish lift) were delayed 4 and 21 days below the dam, supporting the conclusion that delays longer than 48 hours are not due to fish having experienced the fishway before.

Overall recovery of Atlantic Salmon in the Penobscot River is highly dependent on the effectiveness of the new fishway installed at Milford Dam. The most recent action plan for Atlantic Salmon in the Gulf of Maine has identified dams as a major threat, and have made reducing the effects of dams that prevent or delay Atlantic Salmon passage a priority in the recovery of the species (NMFS 2016). All high quality rearing habitat for Atlantic Salmon within the Penobscot River watershed is located upstream of the Howland and West Enfield Dams (Fay et al. 2006), which are just upstream of the confluence of the Piscataquis and the main stem of the Penobscot River (rkm 100). After successful use of the Milford Dam fish lift, adults must travel almost 40 rkm upstream and pass at least one more dam to reach ideal spawning habitat. As shown in this study, passage efficiency at the new Milford Dam fish lift is high. However, these results show that while adult Atlantic Salmon are able to locate the new fish lift entrance quickly, and make multiple visits to the lift, passage of these fish is significantly delayed under the operational conditions in 2014 and 2015. With Atlantic Salmon often present near the fishway, efforts to improve passage time at the fish lift would likely benefit from focusing on behavior inside the fishway entrance to increase the probability of capturing adult migrants in the lift hopper.

CHAPTER 2

RETROSPECTIVE ANALYSIS OF SEASONAL OCEAN GROWTH RATES OF TWO SEA WINTER ATLANTIC SALMON IN EASTERN MAINE USING HISTORIC SCALES

Abstract

Substantial declines of anadromous Atlantic Salmon *Salmo salar* have occurred throughout its range, with many populations at the southern extent of the distribution being extirpated or endangered. While both one sea winter (1SW) and two sea winter (2SW) spawner numbers for the North American stocks have declined since the 1950s, the decline has been most severe in 2SW spawners. The first months at sea are considered a period of high mortality. However, early ocean mortality alone cannot explain the more pronounced decline of 2SW spawners, suggesting that the second year at sea may be more critical than previously thought. Angler and state agency collected scales from 1946 to 2013 from the five eastern Maine rivers were used to estimate smolt age and ocean age of returning adults. Additionally, seasonal growth rates of maiden 2SW spawners were estimated using intercirculi measurements and linear back-calculation methods. Generalized linear models (Gaussian family, log link function) were used to investigate the influence of average sea surface temperature (SST), accumulated thermal units (ATUs), the Atlantic Multidecadal Oscillation (AMO) and North Atlantic Oscillation (NAO) indices, smolt age, smolt length (FL), and post-smolt growth on growth rate during the oceanic migration of North American Atlantic Salmon. Results suggest that different factors influence salmon growth throughout their oceanic

migration, and previous growth can be a strong predictor of future size. Growth was negatively impacted by the phase of the AMO, which has been linked to salmon abundance trends, in the late winter and early spring following the post-smolt period. This is likely when the 1SW and 2SW stock components separate and results suggest that this period could play a role in the disproportionate decline in 2SW spawners.

Introduction

Anadromous Atlantic Salmon *Salmo salar* are native to multiple countries in both Europe and North America, but substantial declines have occurred throughout the range of this once abundant species. On both sides of the Atlantic Ocean, southern runs have declined more extensively, with many populations currently extirpated (Parrish et al. 1998). In Maine, 28 to 34 rivers had populations of this species at one time (Fay et al. 2006). By the mid-1990s, runs of the species had declined to 500 to 2,000 fish in all Maine rivers combined, leading to listing of the Gulf of Maine distinct population segment (DPS) as federally endangered in 2000 (Fay et al. 2006).

The complex life history of this species, which involves a juvenile freshwater phase followed by a marine phase that can last one to five years before returning to freshwater to spawn (Webb et al. 2007), has exposed Atlantic Salmon to a series of threats that have contributed to their continued decline, including pollution, dams, and overfishing (Parrish et al. 1998; NRC 2004). The continued declines of Atlantic Salmon across populations from multiple rivers supports the hypothesis that common events operating in the marine environment are at least partially responsible for population declines (Hutchinson and Mills 2000; Mills et al. 2013). Atlantic Salmon juveniles complete an extensive migration from their natal rivers to reach ocean feeding grounds. For North American stocks, juveniles enter the ocean environment as smolts and travel to the southern coasts of Nova Scotia and Newfoundland to feed during the summer as "post-smolts" (Friedland et al. 2014) and spend their first winter in the Labrador Sea (Reddin 1988). These juveniles are considered "post-smolts" until their first winter at sea. Following this first winter, some will mature as one sea winter (1SW) fish and return to their natal rivers to spawn. The majority of salmon from the United States' rivers will remain in the ocean at least one more year. These fish migrate to the west coast of Greenland to feed from June to September of their second year (Hansen and Jacobsen 2000) and then return to the southern Labrador Sea to overwinter (Figure 2.1). Most adults, then known as two sea winter (2SW) fish, will return to rivers to spawn after their second winter at sea (Mills et al. 2013).

The initial time in sea water is a period of high mortality, and therefore has a large influence on the success of a year class (Hansen and Quinn 1998). In Europe, return rates in multiple rivers have been linked to sea surface temperature (SST) and post-smolt growth (Friedland et al. 1993, 2000, 2005; McCarthy et al. 2008; Todd et al. 2008). While data suggests that growth mediated mortality during the post-smolt period has been important for recruitment of European Atlantic Salmon stocks, this trend has not been observed in North American stocks. Climatic factors experienced in the early post-smolt period (the first few months at sea) have been linked to stock abundance (Friedland et al. 2003, 2014), however post-smolt growth of both hatchery- and wild-origin fish from North American rivers has not been clearly linked to stock abundance (Friedland et al. 2005, 2009b; Hogan and Friedland 2010). These results suggest that growth during the

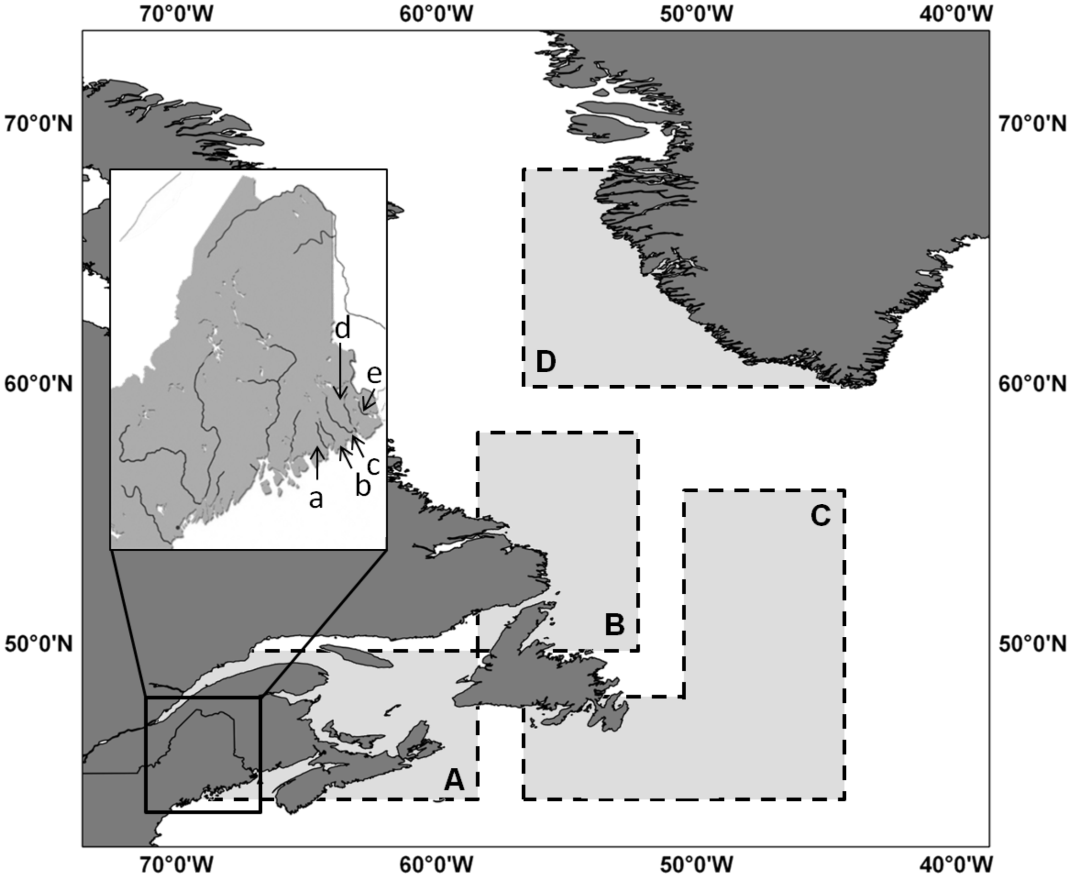


Figure 2.1: Salmon oceanic migration area map. Map of areas used during the oceanic migration of Atlantic Salmon from rivers in eastern Maine. Rivers used for analysis include: a) Narraguagus River, b) Pleasant River, c) Machias River, d) East Machias River, and e) Dennys River. Light gray boxes represent areas used for temperature analysis during A) the early post-smolt migration period, B) the post-smolt fall nursery, C) the overwintering area, and D) the 2SW summer feeding grounds.

post-smolt period may not be a primary driver of marine survival in North American stocks.

While both 1SW and 2SW spawner numbers for the North American stock have declined since the 1950s, the decline has been most severe in 2SW fish, especially since the 1980s (Chaput et al. 2005; Mills et al. 2013; Friedland et al. 2014). It is unclear whether the more pronounced decline in 2SW spawners is due to climate and ecosystem conditions that influence salmon throughout their entire period at sea, having a greater cumulative impact on 2SW fish, or conditions that influence mortality following the first winter at sea when the maturing and non-maturing portions of the stock separate (Mills et al. 2013). Multiple biological and physical factors have been linked to Atlantic Salmon abundance and productivity trends, including SST, the Atlantic Multidecadal Oscillation (AMO), and capelin *Mallotus villosus* size and energy content (Mills et al. 2013; Renkawitz et al. 2015). Decreased energy density of prey could have important implications for growth, condition, survival, and overall recruitment of 2SW spawners. The question remains as to whether changes in growth during the second year at sea are noticeable since the 1950s. Furthermore, which factors influence the ocean growth of Atlantic Salmon during different phases of their oceanic migration could elucidate factors that are playing a role in the continued decline of the species in North American rivers.

Multiple Atlantic Salmon runs have been monitored during the latter half of the 20th century as conservation efforts have attempted to mitigate declines. Included in these efforts was the collection of scales from returning adults that have been used to estimate age and determine the rearing origin (hatchery or wild) of these fish. Scales can also be used to estimate size-at-age and ocean growth of individuals, and have often been used in the past to examine growth during the post-smolt period (Friedland et al. 2000, 2005, 2006). However, little emphasis has been placed on growth during the second year at sea, a period which may play an important role in recruitment. During their oceanic migration, 2SW spawners span a large area of the ocean, making it possible that different factors are influencing the overall growth of salmon during different times of the year. The objective of this study was to use Atlantic Salmon scales from five eastern Maine rivers (Narraguagus, Pleasant, Machias, East Machias, and Dennys) to evaluate changes in seasonal growth rates of maiden (first-time) 2SW spawners from the 1950s to the 2000s in order to evaluate factors influencing growth during the oceanic phase of these individuals.

Methods

Capture, Length, and Scale Collection

Adult Atlantic Salmon scales were obtained from the Maine Department of Marine Resources (MEDMR). Scales were from returning adults captured in the Narraguagus, Pleasant, Machias, East Machias, and Dennys Rivers in eastern Maine (Figure 2.1) from 1946 to 2013. Samples were from both angler collected scales as well as scales collected during state monitoring efforts. Fork lengths (FL, mm) and total lengths (TL, mm) at capture were obtained from MEDMR. Prior to the 1980s, most lengths for returning adults were reported as total lengths, with lengths from later years reported as fork lengths. A subset of these samples (n=94) contained both TL and FL for each individual. The relationship of TL to FL for these fish was linear ($R^2 = 0.97$), so any total lengths were converted to fork length using the equation:

$$FL = 0.9302*TL + 15.776$$

Scale Processing and Age Estimation

Scales were cleaned with water and then mounted between two glass microscope slides. Each scale was viewed using 25x magnification on a Zeiss Axioplan microscope and imaged with a microscope-mounted digital camera (SPOT Insight 2 MP Color

Mosaic; Sterling Heights, MI). Each sample was viewed by at least two trained scale readers to estimate both smolt age and ocean age (ICES 2011). If ages from the two initial readers were not in agreement, a third reader aged the sample to resolve conflicting readings by majority rule.

Scale Measurements for Growth Analysis

During aging, "high quality" scales from maiden 2SW spawners were identified for measuring. Scales that were eroded, cracked, or had broken circuli or regenerate centers were excluded from measurement analysis. One scale was measured from each fish. For each smolt year (year at emigration), I attempted to find 50 quality samples for measurement (Table 2.1). This goal was met in many years in the 1960s and 1970s when salmon were more abundant, however in later years sample numbers are low due to the low numbers of returning adults.

Scale images were measured using ImagePro Premier software (Media Cybernetics, www.mediacy.com). Total radius was measured from the focus of the scale along the anterior axis to the margin of the scale (ICES 2011). The end of the freshwater growth zone was marked along this axis, indicated by the end of closely spaced circuli pairs. Circuli in the ocean growth zone (starting at the first circuli following the freshwater zone) were counted on each scale, and distance between circuli pairs was measured (Friedland et al. 1993). For each fish, I calculated a mean circuli spacing index for each pair by taking the average intercirculi distance of the indicated pair, the two pairs before the indicated pair, and the two pairs following the indicated pair. This

Table 2.1: Summary of scales used for measurement. Sample sizes, by river, of scales used for growth analysis

Smolt Year	Dennys	East Machias	Machias	Narraguagus	Total
1950	0	0	0	2	2
1951	0	0	0	26	26
1952	0	1	1	8	10
1953	2	0	2	5	9
1954	4	0	0	14	18
1955			MISSING		
1956	1	0	4	2	7
1957	12	3	0	35	50
1958	6	2	5	6	19
1959	4	3	23	0	30
1960	10	1	24	0	35
1961	5	0	2	43	50
1962	0	0	1	49	50
1963	0	1	25	1	27
1964	0	0	12	38	50
1965	0	0	50	0	50
1966	0	0	50	0	50
1967	0	0	50	0	50
1968	0	0	21	29	50
1969	0	0	50	0	50
1970	0	0	50	0	50
1971	0	0	0	50	50
1972	0	0	2	48	50
1973	0	3	1	46	50
1974	0	9	6	15	30
1975	0	10	2	38	50
1976	0	9	10	31	50
1977	0	1	9	17	27
1978	9	5	8	28	50
1979	2	11	5	31	49
1980	1	4	13	32	50
1981	0	1	1	26	28
1982	2	10	4	23	39
1983	0	8	4	26	38
1984	2	0	1	21	24
1985	0	2	1	15	18
1986	0	2	2	7	11
1987	2	5	1	13	24
1988	7	5	2	22	36
1989	4	0	0	42	46
1990	0	0	0	18	18
1991	1	0	0	49	50
1992			MISSING		
1993	5	0	0	25	30
1994	2	0	0	32	34
1995	0	0	0	4	4
1996	0	0	0	13	13
1997-1999			MISSING		
2000	0	0	0	1	1
2001	0	0	0	13	13
2002	0	0	0	8	8
2003	0	0	0	2	2
2004	1	0	0	2	3
2005	0	0	0	4	4
2006	0	0	0	10	10
2007	4	0	0	3	7
2008	1	0	0	26	27
2009	1	0	0	1	2
2010	0	0	0	12	12
Total	88	99	442	1012	1641

index was used to avoid misidentification of important growth points on the scale due to the high variability in intercirculi spacing (Friedland et al. 2009b). The first winter annulus was estimated by identifying the minimum of the mean circuli spacing index that was within the first 3/4 of the total marine circuli on the scale and after pair 15. I focused on pairs greater than 15 to avoid misidentification of the winter minimum due to growth checks observed on some scales during the first year at sea.

Growth Sections

Marine circuli pairs prior to the first winter annulus were used to measure the post-smolt growth increment. Using methods similar to Friedland et al. (2009b) and Hogan and Friedland (2010), the post-smolt growth increment was divided into seven equal sections by circuli count to approximate growth during the months of June to December in the smolt year. Growth in the second year at sea was investigated by extracting circuli pairs laid down after the first winter annulus for analysis. The minimum value of the mean circuli spacing index for the last five circuli pairs was used to designate the second winter minimum, as some scales were used from fish that exhibited "plus growth" after their second winter as sea, indicated by an increase in circuli spacing near the edge of the scale. Additionally, the second sea year growth increment was divided into twelve equal sections by circuli count to estimate monthly growth during the second year at sea.

To avoid a mismatch of monthly growth zones with environmental conditions, monthly increments were combined into seven sections that represented different periods of adult growth during the first and second years at sea. These sections were chosen based on circuli spacing patterns and general known locations of Atlantic Salmon during their time at sea, and are indicated by year (Y1 or Y2, based on a calendar year system) and season (Winter, Spring, Summer, Fall). During the first year at sea, the estimated months of June and July were combined to represent the initial summer growth during the post-smolt period (Y1-Summer). Y1-Fall consisted of August, September, and October during the post-smolt period, when post-smolts have been located in the "fall nursery" in the Labrador Sea north of Newfoundland (Reddin and Short 1991). Y1-Winter consisted of November and December before the first winter annulus, when fish have moved into the overwintering area in the Labrador Sea (Figure 2.1). The months of January, February, and March were combined to represent the first growth period following the winter annulus in the Labrador Sea (Y2-Winter). The months of April and May were combined to represent spring growth, indicated by increasing intercirculi spacing (Y2-Spring). The months of June, July, August, and September were combined to represent summer growth when fish are feeding in West Greenland (Y2-Summer). The last months of October, November, and December were combined to represent the final growth section of the second year, when adults move back to the Labrador Sea to overwinter (Y2-Fall). An example of these growth zones is indicated by Figure 2.2.

Back-Calculated Lengths

Dahl-Lea proportional back-calculation (Lea 1910), the recommended method for Atlantic Salmon scales (Friedland et al. 2000; Heidarsson et al. 2006; Kuparinen et al. 2009), was used to estimate smolt length (FL) and length after the first winter at sea (FL) for each individual. Smolt length was calculated based on the end of the freshwater growth zone, and length after the first winter at sea was calculated based on the identified

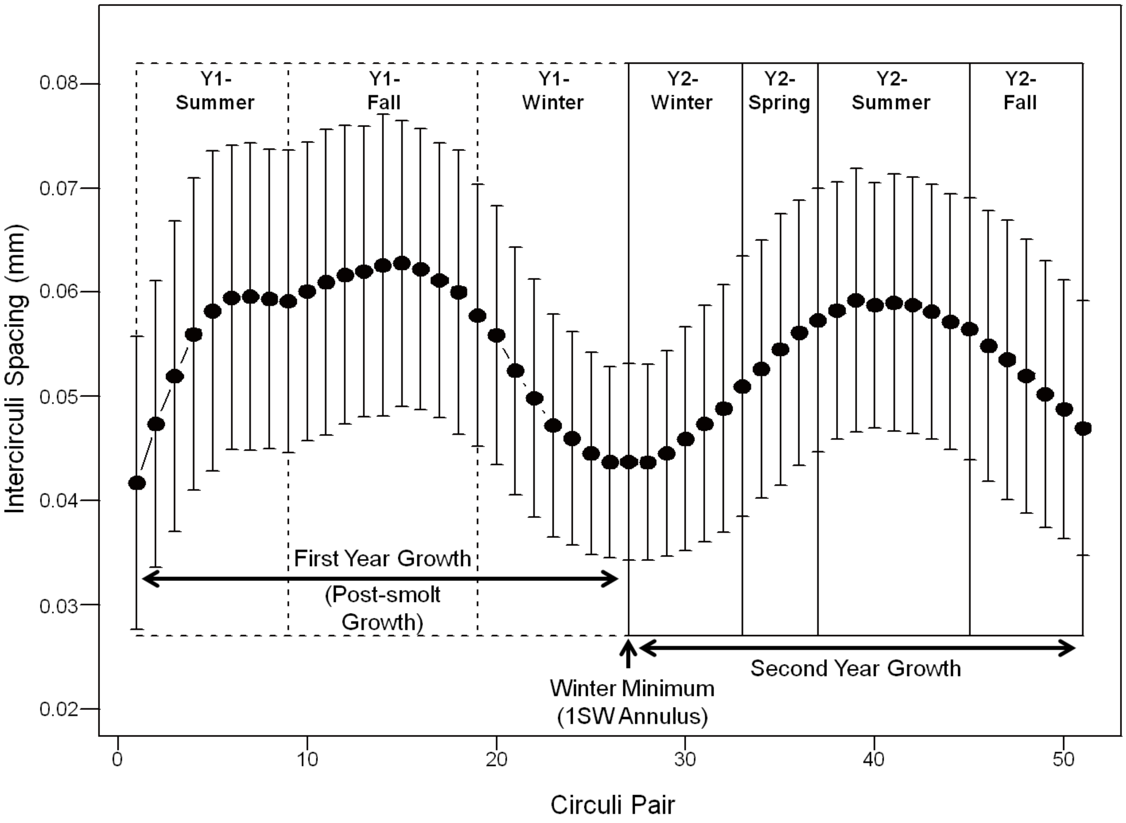


Figure 2.2: Scale seasonal growth sections. Example of growth sections used in regression analysis based on mean intercirculi spacing (± SD) patterns from Atlantic Salmon scales collected from adults returning to Maine's eastern rivers. Closely spaced circuli represent decreased growth during winter periods, while increased spacing represents increased growth during summer and fall seasons.

winter annulus. The post-smolt growth increment was calculated by subtracting estimated smolt length from estimated length after first winter at sea. Additionally, estimates of monthly growth rates were calculated for each growth section for use in regression analysis. Back-calculation methods, as described above, were used to calculate the growth of the fish (in mm) during each growth section. I then divided the calculated growth increment by the number of months corresponding to that growth section (see above) to obtain growth rates in mm/month. While it is unlikely that growth during each section is entirely linear, the assumption of linear growth allowed me to investigate growth during the same interval for different individual fish.

Growth Rate Correlations

Spearman's rank correlation coefficients were calculated between each growth increment and the previous growth increment in the year for individual fish. This analysis was used to investigate if faster growing fish sustain rapid growth throughout their entire time at sea, and if not to identify time periods where the reverse relationship (a negative correlation) occurs, as this could indicate a shift in resource allocation or utilization. Significance was assessed at a level of $\alpha = 0.05$.

Environmental Variables

Sea surface temperature (SST) data were obtained from the Extended Reconstructed SST (ERSST) version 4 (Huang et al. 2015). A series of 2˚ latitude x 2˚ longitude grids (Figure 2.1) was chosen for the presumed post-smolt migration area, fall nursery in the Labrador Sea (Reddin and Short 1991; Friedland and Todd 2012), overwintering area in the southern Labrador Sea, and the west coast of Greenland, the presumed summer feeding grounds for 2SW spawners (Mills et al. 2013). Averages for the months corresponding to each growth section were calculated based on monthly averages for the entire area of each location. Accumulated thermal units (ATUs) were calculated by summing the monthly accumulated thermal units (number of days in the month * average temperature for that month) for the months corresponding to each growth section.

The smoothed Atlantic Multidecadal Oscillation (AMO) Index (detrended to remove the influence of anthropogenic climate change) and the North Atlantic Oscillation (NAO) Index (normalized using the 1981-2010 base period monthly means and standard deviations) were used to examine the influence of large scale climatic factors on growth (NOAA 2016b; NOAA 2016a). The AMO operates on 60 to 80 year time scales, and is a measure of the SST variability across the entire North Atlantic, which is believed to be driven by the strength of global thermohaline circulation (Drinkwater et al. 2013). While the AMO index describes temperature variability, and regional effects can vary throughout the Atlantic Ocean, this multidecadal forcing also influences currents and sea ice, phytoplankton and zooplankton abundance, and recruitment dynamics and growth of fishes (Drinkwater et al. 2013; Mills et al. 2013; Nye et al. 2014) . The NAO index describes the pressure difference between the subtropical atmospheric high-pressure zone (the Azores) and the low-pressure zone (Iceland) in the North Atlantic and often occurs at shorter than decadal time scales (Ottersen et al. 2001). This climate forcing is strongest in the winter, and has been shown to influence the distribution of major water masses and currents in the Atlantic Ocean, climate variability in the Labrador Sea, sea ice extent, phytoplankton biomass, and recruitment, growth, and distribution of higher trophic levels (Ottersen et al. 2001; Mills et al. 2013) . For the purposes of this study, I used the AMO and the NAO to attempt to capture more broad-scale ecosystem effects that could influence Atlantic Salmon growth. Both of these data sets contained monthly values for these indices. The average value was taken for the months corresponding to each growth section.

Regression Analysis

Generalized linear models (Gaussian family, log link function) were used to investigate the influence of average SST, ATUs, the AMO and NAO indices, smolt age, smolt length, and the post-smolt growth increment on monthly growth rate during each growth section. The post-smolt growth increment was only used in models pertaining to the second year at sea, as this increment was calculated based on length after the first year at sea, and all other predictors were used for both years. I developed a set of 21 *a priori* models for each growth section during the post-smolt period (Y1 sections), and a set of 24 *a priori* models for each of the four growth sections in the second year at sea (Y2 sections). These models are reported in Table 2.2, and the basis for the included predictors is explained below.

Table 2.2. List of *a priori* growth models. *A priori* developed for growth rates during the first (a) and second (b) years at sea. All models included River as a factor. Predictors include average temperature (AVT), accumulated thermal units (ATU), smolt age (SMA), smolt length (SML), the post-smolt growth increment (PSI), the Atlantic Multidecadal Oscillation Index (AMO), and the North Atlantic Oscillation Index (NAO).

A Priori Models (Response = Estimate Growth Rate in mm/month)	
(a)	(b)
AVT + AVT^2	AVT + AVT^2
AVT + AVT^2 + SMA	AVT + AVT^2 + SMA
ATU	ATU
ATU + SMA	ATU + SMA
SML	PSI
SML + SMA	PSI + SMA
SML + SMA + (SML * SMA)	PSI + SMA + (PSI * SMA)
AVT + AVT^2 + SML	SML
ATU + SML	SML + SMA
AVT + AVT^2 + SML + SMA	SML + SMA + (SML * SMA)
ATU + SML + SMA	AVT + AVT^2 + PSI
AMO	ATU + PSI
AMO + SML	AVT + AVT^2 + PSI + SMA
AMO + AVT + (AMO * AVT)	ATU + PSI + SMA
AMO + ATU + (AMO * ATU)	AMO
AMO + SML + (AMO * SML)	AMO + PSI
NAO	AMO + AVT + (AMO * AVT)
NAO + SML	AMO + ATU + (AMO * ATU)
NAO + AVT + (NAO * AVT)	AMO + PSI + (AMO * PSI)
NAO + ATU + (NAO * ATU)	NAO
NAO + SML + (NAO * SML)	NAO + PSI
	NAO + AVT + (NAO * AVT)
	NAO + ATU + (NAO * ATU)
	NAO + PSI + (NAO * PSI)

For models for Y1-Summer, temperatures calculated from the post-smolt migration area were used, and for models for Y1-Fall temperatures from the fall nursery area in the Labrador Sea were used. Temperatures from the southern Labrador Sea were used for models regarding Y1-Winter, Y2-Winter, Y2-Spring, and Y2-Fall. Lastly, temperatures from the west coast of Greenland were used for models regarding Y2-Summer. Continuous predictors were z-standardized prior to use in regression models. Average SST was included as a quadratic term when used, as I expected there to be an optimal relationship between average temperature and growth (Handeland et al. 2003). Smolt length and the post-smolt growth increment were included to investigate the hypothesis that previous size would influence future growth. Smolt age was included as a factor with 3 levels (wild-origin 2 year smolts, wild-origin 3 year smolts, and smolts determined to be of hatchery origin) to investigate if differences in freshwater rearing had an influence on growth throughout the oceanic period. To attempt to capture more broad-scale ecosystem changes that could influence salmon ocean growth, climate indices (NAO and AMO) were included in these models.

For each growth section, competing models were compared using Akaike's Information Criterion (AIC). Models that had a ΔAIC ≤ 2 were considered to be competitive. Preliminary analysis revealed that adding river as a factor improved the AIC score of models, even though it was often not significant, so river was included in all *a priori* models. Samples from four rivers (Narraguagus, Machias, East Machias, and Dennys) were used in models for ocean growth analysis. The Pleasant River was not included in this analysis because the samples from this river consisted primarily of kelts, which show considerable scale erosion after overwintering in rivers and were therefore not suitable for measurement. Previous work has documented synchronization in ocean growth from rivers that are in close proximity to one another (Jensen et al. 2011). Additionally, Hogan and Friedland (2010) found that post-smolt growth of salmon from the Machias and Narraguagus Rivers was not different. As such, I determined that using samples from multiple rivers would have little effect on the results. Regression models were constructed using Program R v3.0.2 and AICc tables were computed using R package MuMIn (Barton 2015). Additionally, likelihood ratio based psuedo-R^2 values for the top models for each growth section were calculated using R package MuMIn (Barton 2015).

Results

Age Composition

The samples from the Narraguagus, Pleasant, Machias, East Machias, and Dennys Rivers consisted primarily of wild-origin age 2 smolts (80% of all samples aged). The proportion of hatchery-origin smolts increased from the 1970s until the end of the time series, with the majority of returning adults in the late 2000s being of hatchery origin. Returning adults consisted primarily of maiden 2SW spawners (90% of all samples aged). The proportion of maiden 1SW spawners remained low and relatively consistent throughout the majority of the time series (< 10% per year), however this proportion increased from the early 1990s (generally > 20% per year). The proportion of repeat spawners showed a slight decrease beginning in the 1970s. The apparent increase in repeat spawner proportion after the 1990s may be due to the comparatively low sample sizes for those years. The proportion of maiden 3SW spawners was low (only 2% of all samples aged) and these adults were often absent in many of the years in the series, particularly in the last 19 years (Figure 2.3).

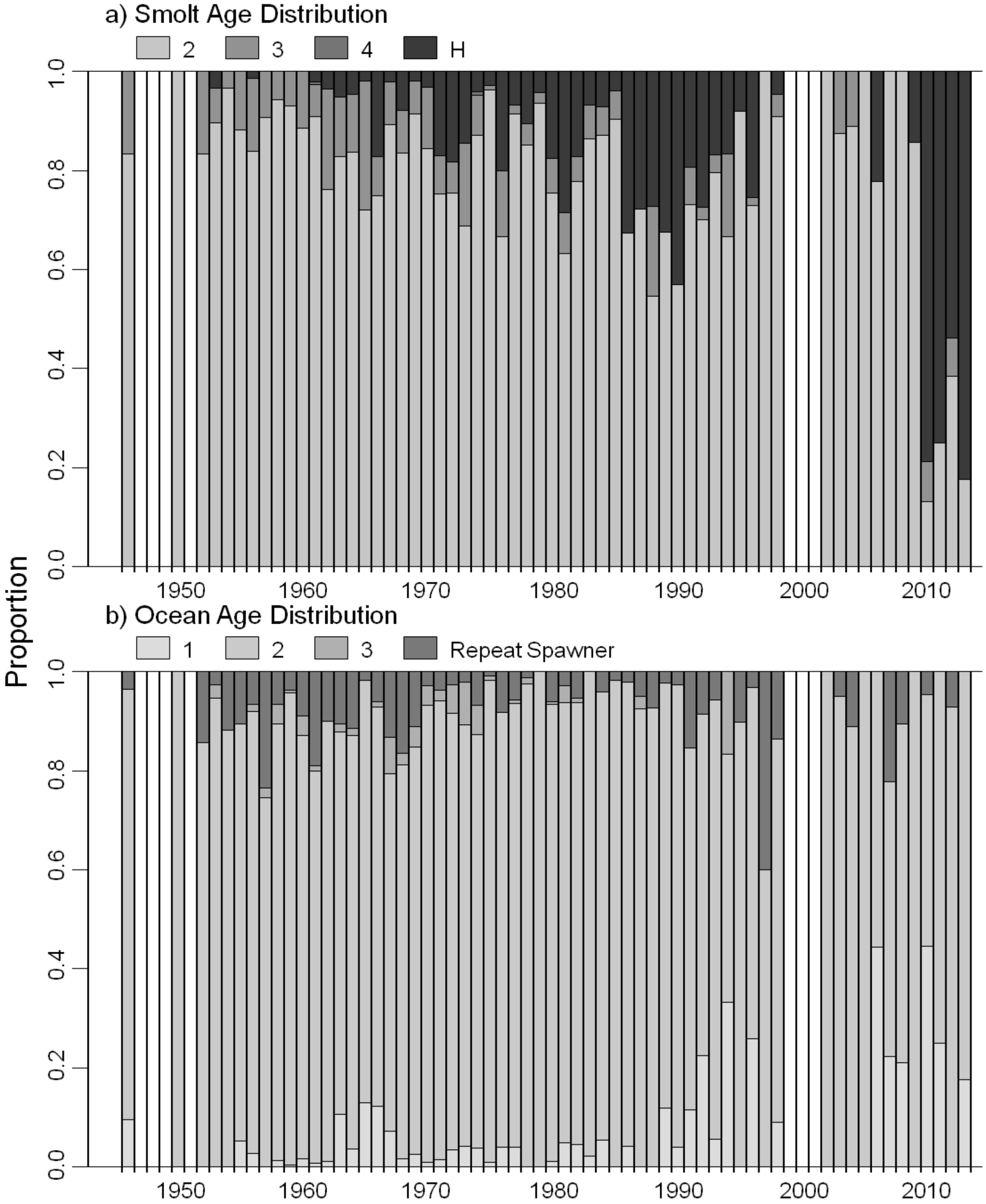


Figure 2.3: Age distribution. Smolt age and ocean age distribution by return year of Atlantic Salmon from the Narraguagus, Pleasant, Machias, East Machias, and Dennys rivers from 1946 to 2013. H = smolts of hatchery origin.

Back-Calculated Lengths

Back-calculated smolt fork lengths from all samples across years had a mean of 152 mm (± 27 mm), and back-calculated fork lengths for the post-smolt growth increment had a mean of 274 mm (± 41 mm). Both smolt length and the post-smolt growth increment fluctuated throughout the time series with no obvious trends. Throughout the time series, growth trends in the second year at sea were similar in the four growth sections that were investigated. A peak in growth in all three sections appears in 1973 (which corresponds to smolt year 1972), but overall growth in the second year at sea oscillated over time with no obvious trends (Figure 2.4).

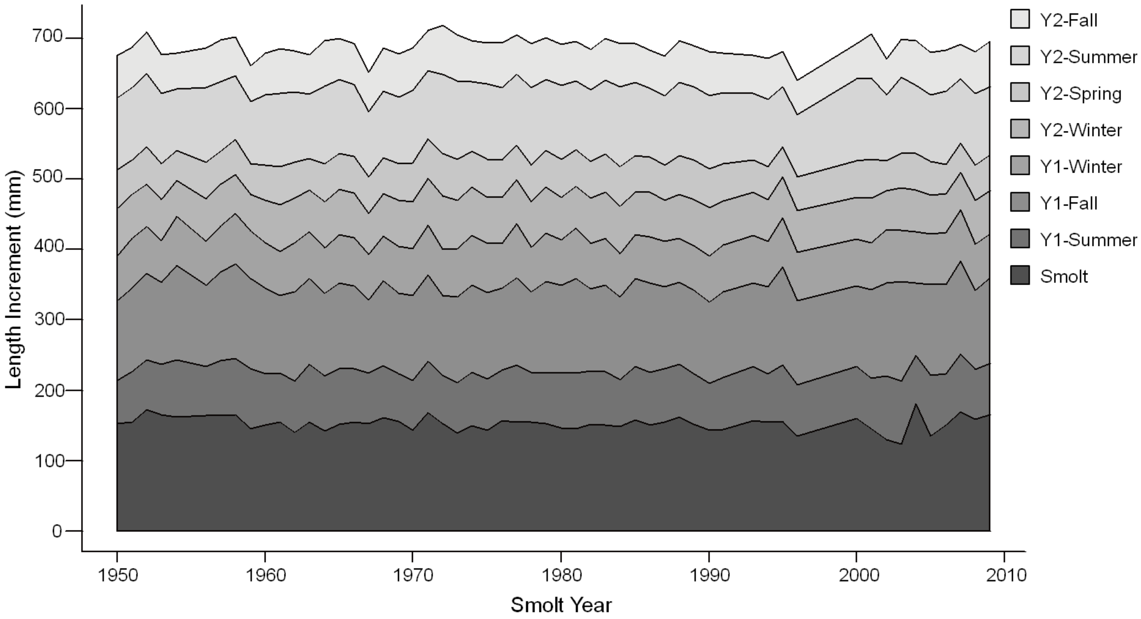


Figure 2.4: Seasonal growth time series. Stacked plot showing mean smolt length and mean growth increments during each growth section over the time series. Note: Growth data was not available for 1955, 1992, and 1997-1999. (Smolt) Smolt fork length at emigration, (1) Y1-Summer, (2) Y1-Fall, (3) Y1-Winter, (4) Y2-Winter, (5) Y2-Spring, (6) Y2-Summer, (7) Y2-Fall.

Growth Rate Correlations

Observed growth rates followed the expected pattern of high summer growth followed by minimal winter growth during both years at sea (Figure 2.2). During the first year at sea, correlation coefficients were moderately positive and significant ($\rho = 0.49$ - 0.45). The correlation between monthly growth rate during the Y1-Winter and Y2-Winter is also significant ($p < 0.01$), yet was negative and weak ($\rho = -0.09$). Correlations between growth sections in the second year at sea were also positive and significant, and were slightly stronger ($\rho = 0.56$ - 0.60) than those during the first year at sea. These relationships are illustrated in Figure 2.5.

Regression Analysis

AIC tables for each growth section are reported in Table 2.3 and a summary of the top models for each growth section is reported in Figure 2.6. Growth during the summer in the first year at sea was high, and AIC analysis identified four competitive models (with a $\Delta\text{AIC} \leq 2.0$). All four had a very poor fit (psuedo-$R^2 = 0.04$) and included a significant, negative relationship with the back-calculated smolt length. The highest ranked model additionally included smolt age and accumulated thermal units (Figure 2.6a), with the following models including: the additive model of the NAO index and smolt length, the interactive model of the NAO index and smolt length, and the additive model of average temperature (as a quadratic term), smolt age, and smolt length. Six other models had a ΔAIC value of less than 7.

During fall and winter of the first year at sea, growth began to slow. A single top model was identified for both Y1-Fall (Figure 2.6b) and Y1-Winter (Figure 2.6c), which

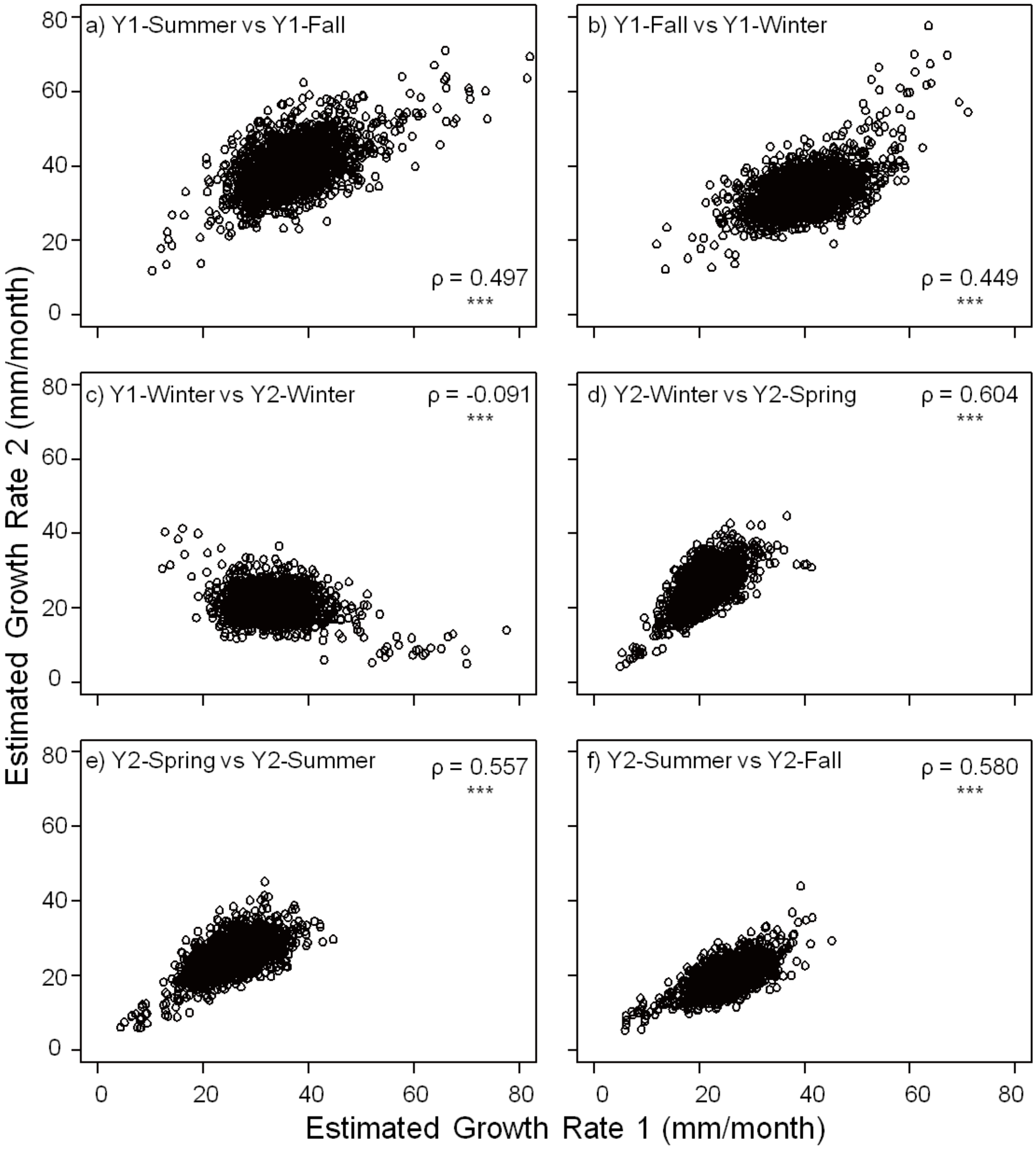


Figure 2.5: Seasonal growth correlations. Scatter plots representing the correlations between successive estimated monthly growth rates over the time that Atlantic Salmon spend at sea. Spearman's rho reported for each correlation (*** denoting p = 0.000).

both had a slightly better fit than the models from the initial growth section (psuedo-R^2 = 0.10 for Y1-Fall, psuedo-R^2 = 0.11 for Y1-Winter). In these models, smolt length was a negative predictor and average temperature had a negative quadratic relationship. The

Table 2.3. Top growth model AICc tables. AICc tables for competitive models of each growth section (ΔAIC < 2), which the next highest ranked model also reported. Predictor abbreviations references in Table 2.2. Full AICc tables are reported in Appendix B.

Model	Log-likelihood	k	AIC_c	ΔAIC_c	Akaike Weight	Psuedo-R^2
Y1-Summer						
ATU + SML + SMA	-5628.2	9	11274.5	0.00	0.294	0.041
NAO + SML	-5630.5	7	11275.1	0.52	0.226	0.038
NAO + SML + (NAO * SML)	-5630.0	8	11276.1	1.61	0.131	0.039
AVT + AVT^2 + SML + SMA	-5628.1	10	11276.4	1.83	0.118	0.041
AMO + SML	-5631.3	7	11276.7	2.13	0.101	0.037
Y1-Fall						
AVT + AVT^2 + SML + SMA	-5404.6	10	10829.4	0.00	0.953	0.102
AVT + AVT^2 + SML	-5410.7	8	10837.5	8.14	0.016	0.099
Y1-Winter						
AVT + AVT^2 + SML	-5184.1	8	10384.2	0.00	0.790	0.106
AVT + AVT^2 + SML + SMA	-5183.7	10	10387.6	3.39	0.145	0.106
Y2-Winter						
AMO + PSI	-4392.9	7	8799.8	0.00	0.732	0.231
AMO + PSI + (AMO * PSI)	-4392.7	8	8801.8	2.01	0.268	0.231
AVT + AVT^2 + SMA	-4405.8	10	8831.7	31.84	0.000	0.220
Y2-Spring						
AMO + PSI + (AMO * PSI)	-4783.0	8	9582.0	0.00	0.532	0.222
AMO + PSI	-4784.1	7	9582.3	0.26	0.468	0.221
AVT + AVT^2 + SMA	-4804.3	10	9628.8	46.75	0.000	0.202
Y2-Summer						
ATU + PSI + SMA	-4517.7	9	9053.4	0.00	0.544	0.319
AVT + AVT^2 + PSI + SMA	-4517.1	10	9054.3	0.89	0.348	0.320
PSI + SMA	-4520.5	8	9057.1	3.64	0.088	0.318
Y2-Fall						
PSI + SMA	-4267.3	8	8550.8	0.00	0.495	0.267
ATU + PSI + SMA	-4267.2	9	8552.6	1.83	0.199	0.267
PSI + SMA + (PSI * SMA)	-4266.5	10	8553.1	2.31	0.156	0.267

model for Y1-Fall additionally included smolt age as a factor. The next highest ranked models for both Y1-Fall and Y1-Winter were not competitive.

Growth remained low during the months following the first winter annulus (Y2-Winter), until increasing in the spring months (Y2-Spring). The models produced for growth during the second year at sea had a better fit than those during the first year at sea.

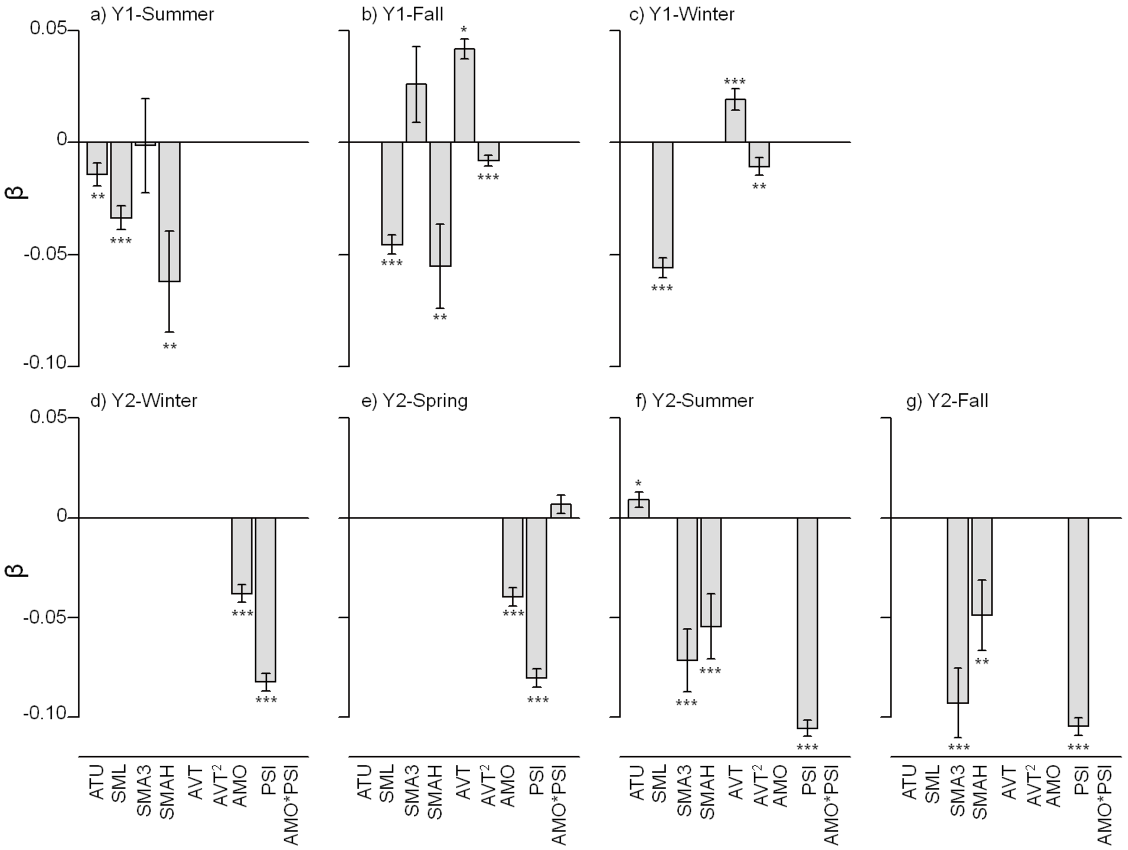


Figure 2.6: Standardized regression coefficients. Summary of standardized coefficients for the top model in each growth section (+ SE). Significance of coefficients denoted as: p = 0.000 ***, p < 0.001 **, p < 0.05 *. Betas included for accumulated thermal units (ATU), smolt length (SML), wild-origin age 3 smolts (SMA3), hatchery-origin smolts (SMAH), average temperature (AVT) and average temperature^2 (AVT^2), the Atlantic Multidecadal Oscillation Index (AMO), the post-smolt growth increment (PSI), and the interaction of the AMO and the post-smolt growth increment (AMO*PSI).

The top model for both Y2-Winter (Figure 2.6d, psuedo-R^2 = 0.23) and Y2-Spring (Figure 2.6e, psuedo-R^2 = 0.22) contained a negative relationship with the post-smolt growth increment and a weak negative relationship with the AMO Index. For Y2-Winter, the additive model was ranked the highest, followed by the interactive model (ΔAIC = 2.01). Y2-Spring showed the opposite trend, with the interactive model ranking the highest followed closely by the additive model (ΔAIC = 0.26). For both of these sections, the interaction term in these models was not significant ($p = 0.92$ and $p = 0.15$ respectively). The next highest ranking models for Y2-Winter and Y2-Spring were definitively non-competitive (ΔAIC = 31.84 and ΔAIC = 46.75, respectively).

Growth rates were high during the Y2-Summer period. The two top models for Y2-Summer also contained a significant, negative relationship with the post-smolt growth increment ($\beta = -0.105$, $p = 0.0$, Figure 2.6f). These models additionally included smolt age as a significant factor, as well as a temperature variable. The highest ranked model included accumulated thermal units as a weak predictor ($\beta = 0.009$, $p < 0.05$), and the next competitive model (ΔAIC = 0.89) included average temperature ($\beta = 0.011$, $p < 0.01$), although the quadratic term was not significant ($\beta = 0.003$, $p = 0.29$). The psuedo-R^2 for both of the top models was 0.32. The next two models were not considered competitive, and also included smolt age as a factor, but did not include a temperature variable.

During the final growth section (Y2-Fall), growth once again began to slow as fish approached the second winter minimum. Two top models were identified for Y2-Fall (psuedo-R^2 = 0.27). Once again the highest ranking model included a significant, negative relationship with the post-smolt growth increment ($\beta = -0.105$, $p = 0.0$), as well as smolt age as a factor (Figure 6g). In contrast to the results from previous growth sections, this model did not include any temperature or climatic variables. The next competitive model additionally included accumulated thermal units (ΔAIC = 1.83). However, this predictor was not significant. The next model was considered non-competitive, and included the interaction of the post-smolt growth increment and smolt age, but no temperature or climatic variables.

Discussion

The majority of samples aged for the Narraguagus, Pleasant, Machias, East Machias, and Dennys Rivers over the times series consisted of 2SW spawners, which is the most common life history strategy for Maine's Atlantic Salmon (NRC 2004). Unlike the Penobscot River, Maine's largest river which has been a primarily hatchery-origin stock (Friedland et al. 1996), the eastern rivers over the past six decades consisted of primarily wild-origin age 2 smolts. It is possible that some of the fish that were classified as wild origin were, in fact, stocked as fry. Managers used fry stocking as a primary recovery tool in these rivers especially after 1990 (Hogan and Friedland 2010; Maynard and Trial 2014). Hatchery-origin stocked fry would be indistinguishable from wild-spawned fish based on scale readings, so it is unclear what percentage of fish in these samples were entirely wild. An increase in the proportion of hatchery-origin fish, which would have been stocked as smolts, is seen beginning in 2010. The number of samples from these last 4 years in this time series is limited (only 100 individuals), with most from the Narraguagus River. While stocking practices in this river prior to 2007 consisted of primarily fry stocking, an increased number of hatchery smolts were stocked beginning in 2008 (USASAC 2012), which explains the increase in hatchery-origin fish observed at the end of the time series.

Examination of seasonal growth in this study did not reveal any obvious trends in smolt size, post-smolt growth, or growth during the second year at sea. This is in agreement with other work examining both wild- and hatchery-origin stocks from North America (Friedland et al. 1996, 2009b; Hogan and Friedland 2010), which have not shown clear trends in the growth of Atlantic Salmon in the second half of the 20th century despite declines in abundance across the range of the species. Individually, estimated seasonal growth followed the expected pattern of a rapid increase in growth in the first few months at sea, followed by decreasing growth prior to the winter minimum. High growth once again occurs during the second summer at sea, when 2SW spawners are presumably on the feeding grounds off of West Greenland for up to four months. Finally, growth slows during the second winter at sea prior to fish migrating back to their natal rivers to spawn. This pattern of intercirculi spacing has been utilized in prior studies to investigate post-smolt monthly growth increments in both European and North American salmon (Friedland et al. 2009a, 2009b; Hogan and Friedland 2010), and is a useful way to estimate seasonal growth patterns and evaluate those patterns during different times of year and locations along the oceanic migration of the species.

Due to the large geographic range of migrating post-smolts and adult Atlantic Salmon in the ocean, this analysis shows that different factors influence growth at different time periods throughout the two years spent at sea. Based on a review of previous work, Hayes and Kocik (2014) hypothesized that Atlantic Salmon are being influenced by both top-down and bottom-up factors at different points in their oceanic migration. These results support this hypothesis, with both biological and physical factors appearing in top models for salmon growth during different seasons at sea, and these predictors shifting depending on season and presumed location. While this study focused on growth, and did not investigate top-down processes over spatial-temporal scales, it appears that the factors regulating bottom-up drivers in Atlantic Salmon populations change as these fish migrate across the oceanic environment.

Multiple factors, expressed in various competitive models, had an influence on growth during the initial months that post-smolts spent at sea. Despite multiple competitive models that attempted to describe early ocean growth, the fit of these models was extremely poor. The growth of post-smolts in their first months at sea is likely influenced by many factors such as migration corridors and timing, availability of prey, and optimal temperatures. The poor fit of these models suggests that the available environmental datasets were not able to fully capture the ecosystem variables that affect early marine growth. This may be due to the broad area selected to represent temperatures during the post-smolt migration, which could have masked smaller scale variations in coastal habitats that could have a greater influence on post-smolt growth. Atlantic Salmon are believed to migrate along narrow coastal bands during their journey to the summer feeding grounds (Hayes and Kocik 2014). Additionally, smolts typically migrate over approximately a 4 to 5 week period from Maine's rivers (Kocik et al. 2009), causing individual fish to potentially be experiencing different conditions which could influence their growth during this period.

Following the early ocean growth period, temperature does appear to be an important predictor in the fall and early winter of the first year at sea. This result is to be expected as growth in salmonids is temperature dependent (Handeland et al. 2008). However, during the second year at sea, temperature on its own disappears from the best models in favor of biological factors such as smolt age and previous size, as well as the Atlantic Multidecadal Oscillation, one of the climate indices investigated to examine the effects of broad-scale ecosystem changes on adult salmon growth (Condron et al. 2005; Mills et al. 2013; Friedland et al. 2014).

The large and complex migration of Atlantic Salmon at sea at times makes it difficult to isolate specific factors influencing their growth. However, investigating the influence of broad-scale climate forcing can give an indication of potential ecosystem effects as drivers. While other authors have noted that the NAO index correlates with Atlantic Salmon abundance trends (Friedland et al. 2003; Mills et al. 2013), this predictor was not in the top models in this study except for the initial months at sea, suggesting that the factors influencing recruitment and survival related to the NAO are likely not growth related. The AMO, on the other hand, did appear as a predictor in the late winter and spring after the post-smolt period. In this case, the results indicate a weak, negative relationship between salmon growth rate and the AMO during this time period. Interestingly, the AMO has also been noted as a dominant climate forcing affecting Atlantic Salmon abundance on both sides of the Atlantic Ocean, and it has been hypothesized that the influence of the AMO operates through both thermal stress and ecosystem changes (Condron et al. 2005; Mills et al. 2013; Friedland et al. 2014). As the AMO replaced temperature in best supported models during the late winter and early spring, these results support the conclusion that ecosystem changes as a response to climate-related variation are more important than the direct influence of temperature during this time period.

Mature 1SW adults from United States rivers migrate south at some point after their first winter at sea to reach natal rivers in the spring. At the same time, immature adults that will return as maiden 2SW spawners move northward from the overwintering area, following the receding ice cover and associated isotherms to eventually reach the west coast of Greenland to feed in the summer and early autumn (Friedland and Todd 2012). Friedland et al. (2014) reported that the AMO was strongly correlated with pre-fishery abundance of the immature (2SW) portion of the North American stock but was weakly correlated with the maturing (1SW) portion of the North American stocks, and that the North American stocks appear to be in opposite phase to the AMO. While the effect of the AMO detected in this study is very slight, growth in maiden 2SW spawners in the late winter and early spring is also in opposite phase with the AMO. This time period likely coincides with when the mature and immature portions of the stock are beginning to separate. Based on these results, it is possible that ecosystem variables and ongoing climate-related changes that are affecting adult growth and condition during this time period are playing a role in the disproportionate decline of 2SW fish of North American origin.

By the time 2SW fish have reached the west coast of Greenland to feed, these results suggest that climate and physical factors play very little role in their overall growth. The absence of the AMO in the top models for the second summer at sea is consistent with the effects of this climate regime on regional SST anomalies. While the phase of the AMO correlates with SST anomalies near Newfoundland and the Grand

Banks in the winter, it does not correlate significantly with the waters off of Greenland in the summer (Condron et al. 2005). It is possible that the abundance and accessibility of prey are stronger drivers of growth during the second summer at sea than physical factors. Recent work has shown that the size of capelin, the primary prey for Atlantic Salmon, in the northwest Atlantic Ocean is highly correlated with salmon abundance trends (Mills et al. 2013). In addition to an overall decrease in size, the energy density of capelin has decreased by over 30% since 1990 and currently adult salmon feeding off of West Greenland are consuming fewer capelin and seeking alternate prey sources (Renkawitz et al. 2015). My analysis did not reveal a specific decrease in second year growth after 1990 during summers off of the west coast of Greenland. However, utilizing salmon scales only gave access to estimated lengths and not condition factor, which may provide more evidence to support an energy deficit in 2SW spawners. During the final winter at sea, once again climate and physical factors did not play a role in top models. By this time, 2SW adult salmon have achieved a large size and are likely preparing to return to natal rivers to spawn, so external factors are having little influence on overall growth rates.

While different factors can influence salmon growth at different periods at sea, overall previous size seems to play a significant role in growth of an individual. The data from this study are generally consistent with previous work examining post-smolt growth on the Narraguagus and Machias Rivers, which observed an increase in the post-smolt growth increment in the early 1990s despite a continued decline in stock abundance (Hogan and Friedland 2010). With the addition of the East Machias and Dennys Rivers, I also observed a slightly increasing trend in the 1990s in the post-smolt growth increment.

The post-smolt growth increment began to decline again after 2000 in this time series. Hogan and Friedland (2010) also found that maximum growth during the post-smolt period was positively correlated with growth in the first month at sea. Similarly, I observed that fish that initially experience high growth rates continue to experience high growth rates throughout their first year at sea.

In contrast to previous work on Atlantic Salmon from eastern Maine, which found that there was no relationship between first and second year growth (Hogan and Friedland 2010), results from this study suggested a negative relationship between smolt length and the post-smolt growth increment, as well as the post-smolt growth increment and growth during the second year at sea. Similar relationships were reported for Atlantic Salmon from the River Narcea in Northern Spain, where the first marine growth period and the second marine growth period (following the first winter at sea) were negatively correlated (Nicieza and Brana 1993). Further investigation of estimated growth rates in this study revealed that this change in pattern occurs sometime during the first winter at sea. The observed relationship could point to compensatory growth in smaller individuals after the first winter at sea, while larger individuals do not need to sustain high growth rates. Compensatory growth has been suggested for Atlantic Salmon at multiple points in their life cycle (Nicieza and Brana 1993; Hogan and Friedland 2010) indicating that years of poor post-smolt growth have the potential to be mitigated by high growth in the second year at sea.

The decline of North American Atlantic Salmon has involved multiple factors that span both the freshwater and the marine environment. Despite steps that have been taken to reduce the human-induced causes of salmon declines, the continued low abundance of these populations points to the influence of large-scale effects acting throughout the range of the species. Previous work has suggested that the first winter at sea is a critical period for North American Atlantic Salmon (Friedland et al. 1993; Condron et al. 2005). While the post-smolt period is often considered the primary source of Atlantic Salmon mortality, mortality during the post-smolt period cannot fully explain the decline of North American salmon, as the decline of 2SW fish has been more severe than that of 1SW fish. As these portions of the stock separate after the first winter at sea, this suggests that factors acting throughout the entire marine period are cumulatively affecting 2SW spawners, increasing their decline, or that factors operating on salmon after their first winter at sea are responsible for the disproportionately low numbers of maiden 2SW spawners. The models in this study have shown that slightly different factors are acting on the growth of 2SW Atlantic Salmon throughout their time at sea. During the late winter and early spring, salmon growth is negatively impacted by the phase of the AMO, which has also been linked to salmon abundance. The factors influencing the decline of this highly migratory species are complex, however more emphasis on migration patterns, growth, and condition during the second year at sea could be advantageous for future management of the North American Atlantic Salmon stocks.

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APPENDIX A: SCALE AGING AND MEASUREMENT

Figure A.1. Example of scale from a 2SW spawner from the Narraguagus River (1963). Estimated age is 2:2 - 2 years in freshwater, 2 years at sea. Freshwater (a) and ocean growth (b) indicated as marked, with annuli identified by horizontal lines.

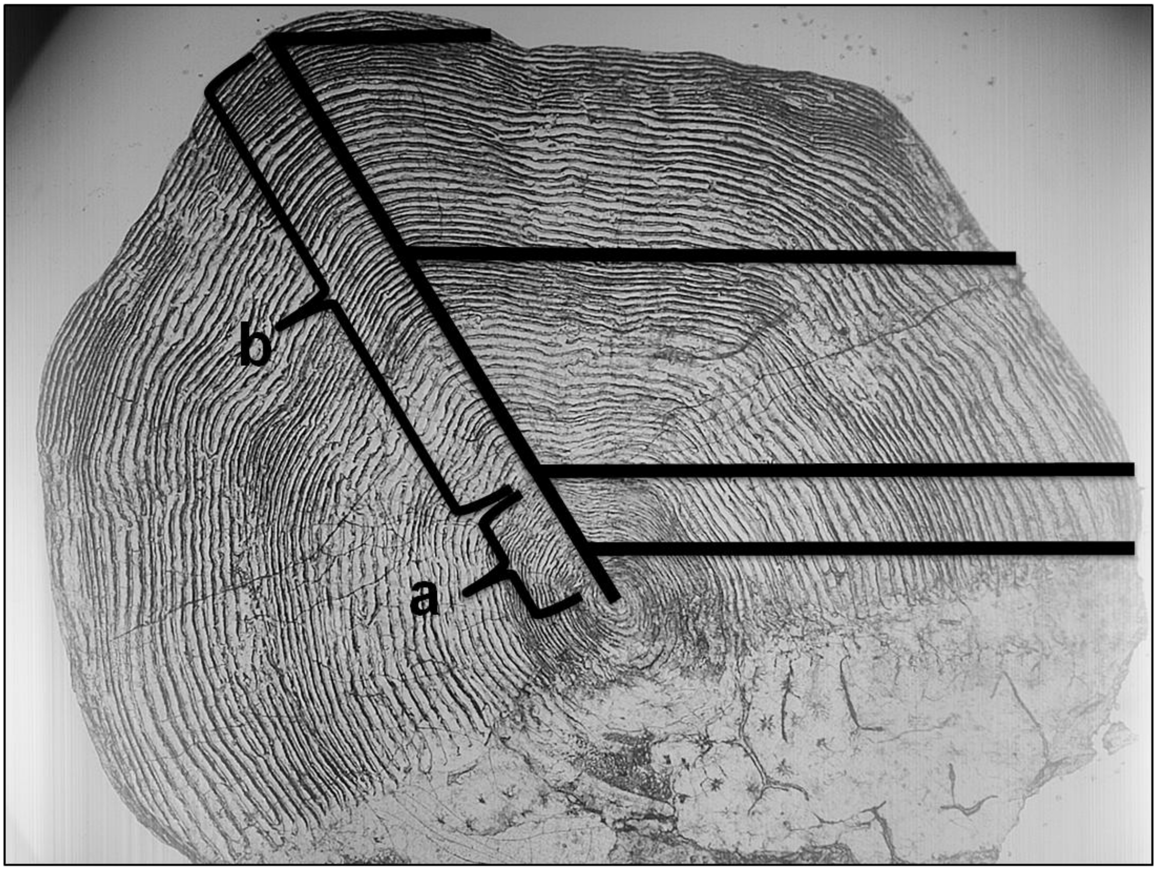


Figure A.2. Example of scale from the East Machias River (1988) identified as a hatchery-origin smolt, indicated by consistent freshwater growth (circled).

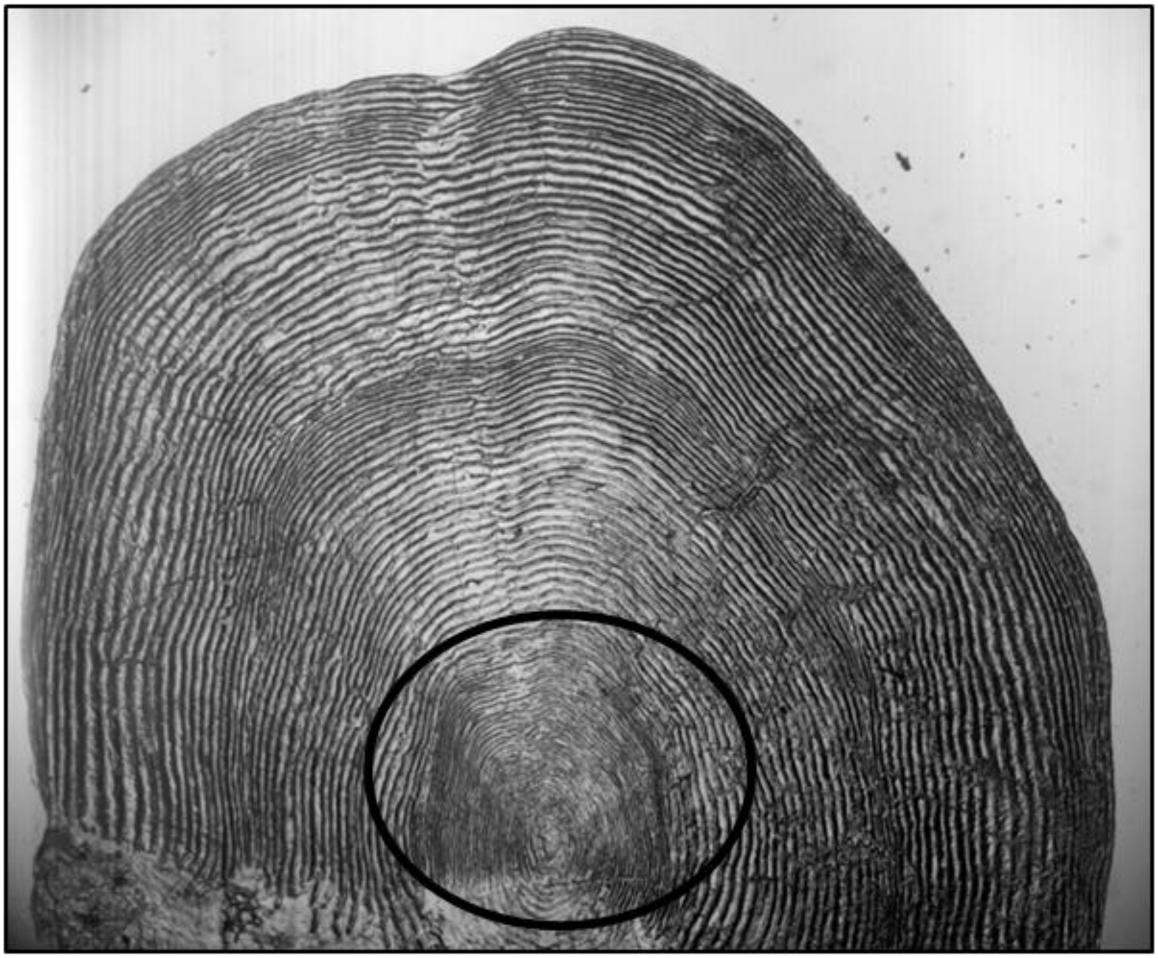
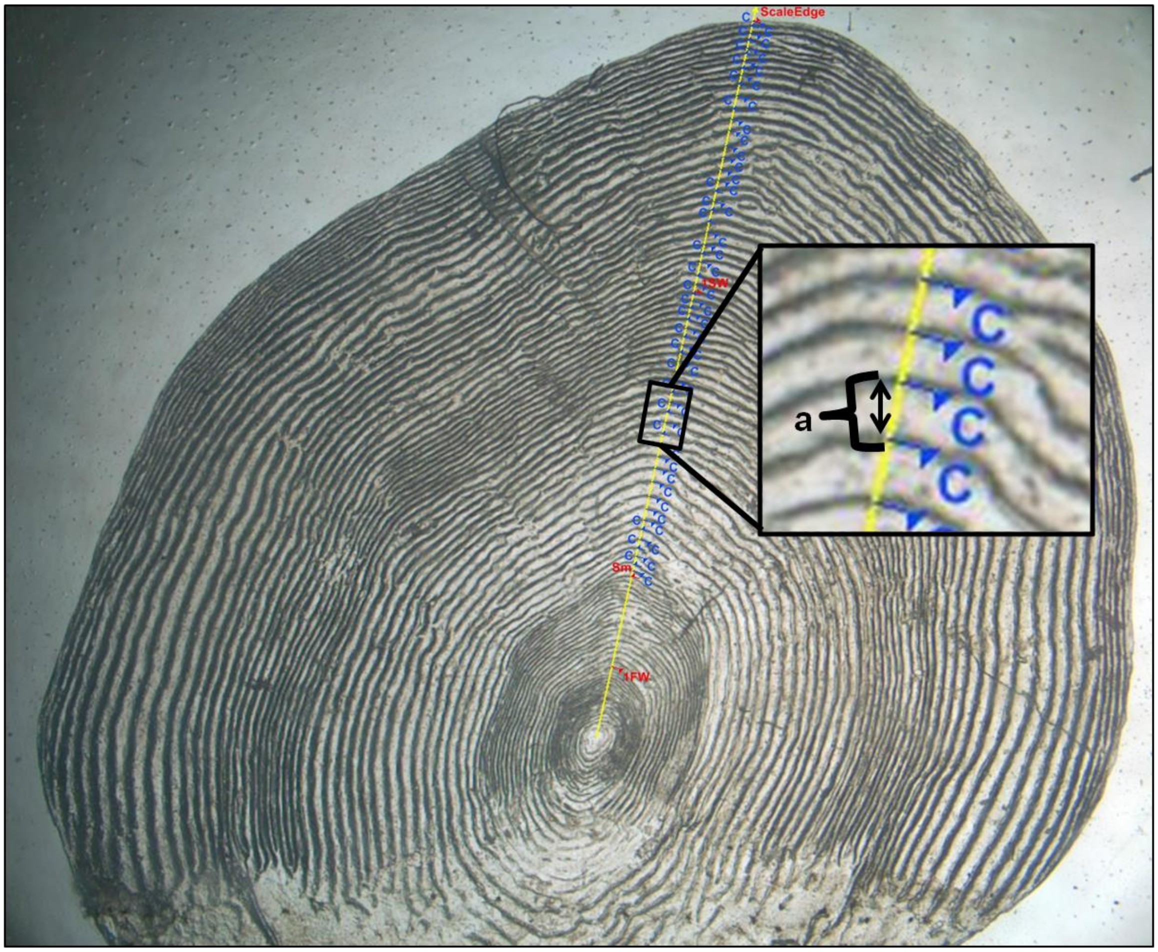


Figure A.3. Example of scale from the Machias River (1969) identified as a repeat spawner. Scale erosion (circled) is indicative of time spent in freshwater during the spawning migration.

Figure A.4. Example of measured 2SW spawner scale. Scales were measured using ImagePro Premier software (Media Cybernetics, www.mediacy.com). Indicated letters represent: (C) - Marine circuli, (1FW) - First winter in freshwater, (Sm) - Smolt mark or emigration from freshwater, (1SW) - First marine winter annulus, (ScaleEdge) - End of scale. Inset shows zoomed view of marine circuli, (a) - intercirculi distance between a pair of circuli.



APPENDIX B: COMPLETE AIC$_c$ TABLES

Table B.1. Full AICc tables for Y1-Summer growth section. Note: River included as a factor in all models.

Model	Log-likelihood	k	AIC$_c$	ΔAIC$_c$	Akaike Weight
ATU + SML + SMA	-5628.2	9	11274.5	0.00	0.294
NAO + SML	-5630.5	7	11275.1	0.52	0.226
NAO + SML + (NAO * SML)	-5630.0	8	11276.1	1.61	0.131
AVT + AVT^2 + SML + SMA	-5628.1	10	11276.4	1.83	0.118
AMO + SML	-5631.3	7	11276.7	2.13	0.101
ATU + SML	-5632.2	7	11278.5	3.91	0.041
AMO + SML + (AMO * SML)	-5631.3	8	11278.6	4.07	0.038
SML + SMA	-5632.0	8	11280.0	5.48	0.019
AVT + AVT^2 + SML	-5632.1	8	11280.4	5.85	0.016
SML + SMA + (SML * SMA)	-5630.2	10	11280.6	6.02	0.015
SML	-5636.8	6	11285.7	11.17	0.001
ATU + SMA	-5647.8	8	11311.7	37.21	0.000
AVT + AVT^2 + SMA	-5647.7	9	11313.6	39.07	0.000
ATU + AMO + (ATU * AMO)	-5652.0	8	11320.1	45.57	0.000
AMO + AVT + (AMO * AVT)	-5652.1	8	11320.2	45.66	0.000
ATU + NAO + (ATU * NAO)	-5653.5	8	11323.0	48.48	0.000
NAO + AVT + (NAO * AVT)	-5653.5	8	11323.1	48.58	0.000
ATU	-5655.9	6	11323.9	49.33	0.000
AMO	-5656.6	6	11325.2	50.62	0.000
NAO	-5656.7	6	11325.4	50.89	0.000
AVT + AVT^2	-5655.9	7	11325.8	51.31	0.000

Table B.2. Full AICc tables for Y1-Fall growth section. Note: River included as a factor in all models.

Model	Log-likelihood	k	AIC$_c$	ΔAIC$_c$	Akaike Weight
AVT + AVT^2 + SML + SMA	-5404.6	10	10829.4	0.00	0.953
AVT + AVT^2 + SML	-5410.7	8	10837.5	8.14	0.016
NAO + SML	-5412.2	7	10838.4	8.98	0.011
ATU + SML + SMA	-5410.6	9	10839.4	10.02	0.006
NAO + SML + (NAO * SML)	-5411.7	8	10839.4	10.05	0.006
SML + SMA	-5412.1	8	10840.2	10.83	0.004
SML + SMA + (SML * SMA)	-5410.5	10	10841.2	11.82	0.003
AMO + SML + (AMO * SML)	-5414.4	8	10844.8	15.47	0.000
SML + AMO	-5417.1	7	10848.3	18.89	0.000
SML	-5420.3	6	10852.6	23.27	0.000
ATU + SML	-5420.1	7	10854.2	24.84	0.000
AVT + AVT^2 + SMA	-5468.8	9	10955.7	126.32	0.000
ATU + SMA	-5474.6	8	10965.3	135.88	0.000
ATU + AMO + (ATU * AMO)	-5477.6	8	10971.2	141.83	0.000
AMO + AVT + (AMO * AVT)	-5477.6	8	10971.2	141.84	0.000
AVT + AVT^2	-5479.4	7	10972.8	143.47	0.000
ATU + NAO + (ATU * NAO)	-5480.7	8	10977.4	148.03	0.000
NAO + AVT + (NAO * AVT)	-5480.7	8	10977.4	148.04	0.000
NAO	-5482.8	6	10977.7	148.36	0.000
AMO	-5488.6	6	10989.2	159.80	0.000
ATU	-5490.4	6	10992.9	163.48	0.000

Table B.3. Full AICc tables for Y1-Winter growth section. Note: River included as a factor in all models.

Model	Log-likelihood	k	AIC$_c$	ΔAIC$_c$	Akaike Weight
AVT + AVT^2 + SML	-5184.1	8	10384.2	0.00	0.790
AVT + AVT^2 + SML + SMA	-5183.7	10	10387.6	3.39	0.145
ATU + SML	-5187.8	7	10389.7	5.48	0.051
ATU + SML + SMA	-5187.4	9	10392.8	8.63	0.011
NAO + SML + (NAO * SML)	-5190.4	8	10397.0	12.74	0.001
SML	-5193.0	6	10398.0	13.76	0.001
NAO + SML	-5192.9	7	10399.8	15.54	0.000
AMO + SML	-5192.9	7	10399.8	15.61	0.000
SML + SMA	-5192.6	8	10401.2	16.97	0.000
AMO + SML + (AMO * SML)	-5192.9	8	10401.8	17.56	0.000
SML + SMA + (SML * SMA)	-5192.2	10	10404.5	20.26	0.000
AVT + AVT^2 + SMA	-5257.7	9	10533.5	149.29	0.000
AVT + AVT^2	-5262.2	7	10538.4	154.21	0.000
ATU + SMA	-5262.8	8	10541.7	157.49	0.000
ATU + AMO + (ATU * AMO)	-5264.2	8	10544.5	160.29	0.000
AMO + AVT + (AMO * AVT)	-5264.2	8	10544.6	160.35	0.000
NAO	-5268.3	6	10548.6	164.43	0.000
AMO	-5266.5	8	10549.2	164.95	0.000
NAO + AVT + (NAO * AVT)	-5266.6	8	10549.2	164.99	0.000
NAO	-5272.7	6	10557.5	173.30	0.000
AMO	-5272.8	6	10557.6	173.36	0.000

Table B.4. Full AICc tables for Y2-Winter growth section. Note: River included as a factor in all models.

Model	Log-likelihood	k	AIC_c	ΔAIC_c	Akaike Weight
AMO + PSI	-4392.9	7	8799.8	0.00	0.732
AMO + PSI + (AMO * PSI)	-4392.9	8	8801.8	2.01	0.268
AVT + AVT^2 + PSI + SMA	-4405.8	10	8831.7	31.84	0.000
ATU + PSI + SMA	-4407.1	9	8832.3	32.53	0.000
ATU + PSI	-4412.8	7	8839.7	39.88	0.000
AVT + AVT^2 + PSI	-4411.9	8	8839.8	39.96	0.000
PSI + SMA	-4425.3	8	8866.7	66.91	0.000
PSI + SMA + (PSI * SMA)	-4425.3	10	8870.7	70.92	0.000
PSI	-4431.0	6	8874.1	74.24	0.000
NAO + PSI	-4430.3	7	8874.7	74.91	0.000
NAO + PSI + (NAO * PSI)	-4430.2	8	8876.6	76.76	0.000
AMO + ATU + (AMO * ATU)	-4552.3	8	9120.7	320.91	0.000
AMO + AVT + (AMO * AVT)	-4552.5	8	9121.2	321.36	0.000
AMO	-4566.6	6	9145.3	345.50	0.000
AVT + AVT^2	-4583.3	7	9180.6	380.79	0.000
AVT + AVT^2 + SMA	-4581.6	9	9181.2	381.41	0.000
ATU	-4586.2	6	9184.5	384.70	0.000
ATU + SMA	-4584.4	8	9184.9	385.05	0.000
NAO + ATU + (NAO * ATU)	-4585.7	8	9187.5	387.65	0.000
NAO + AVT + (NAO * AVT)	-4585.8	8	9187.6	387.82	0.000
SML	-4597.1	6	9206.2	406.37	0.000
SML + SMA	-4595.9	8	9207.9	408.12	0.000
SML + SMA + (SML * SMA)	-4595.3	10	9210.7	410.92	0.000
NAO	-4602.1	6	9216.4	416.56	0.000

Table B.5. Full AICc tables for Y2-Spring growth section. Note: River included as a factor in all models.

Model	Log-likelihood	k	AIC$_c$	ΔAIC$_c$	Akaike Weight
AMO + PSI + (AMO * PSI)	-4783.0	8	9582.0	0.00	0.532
AMO + PSI	-4784.1	7	9582.3	0.26	0.468
AVT + AVT^2 + PSI + SMA	-4804.3	10	9628.8	46.75	0.000
ATU + PSI + SMA	-4806.5	9	9631.1	49.12	0.000
AVT + AVT^2 + PSI	-4811.8	8	9639.7	57.69	0.000
ATU + PSI	-4814.3	7	9642.6	60.57	0.000
PSI + SMA	-4814.0	8	9644.0	62.03	0.000
PSI + SMA + (PSI * SMA)	-4814.0	10	9648.0	66.03	0.000
PSI	-4821.9	6	9655.9	73.88	0.000
NAO + PSI	-4821.4	7	9656.9	74.94	0.000
NAO + PSI + (NAO * PSI)	-4821.2	8	9658.6	76.56	0.000
AMO	-4946.0	6	9904.0	321.95	0.000
AMO + AVT + (AMO * AVT)	-4944.0	8	9904.1	322.05	0.000
AMO + ATU + (AMO * ATU)	-4944.0	8	9904.1	322.11	0.000
AVT + AVT^2 + SMA	-4969.6	9	9957.2	375.20	0.000
ATU + SMA	-4972.2	8	9960.6	378.57	0.000
SML + SMA	-4972.6	8	9961.4	379.34	0.000
AVT + AVT^2	-4973.8	7	9961.7	379.71	0.000
SML	-4975.9	6	9963.8	381.84	0.000
SML + SMA + (SML * SMA)	-4972.5	10	9965.1	383.05	0.000
ATU	-4976.5	6	9965.1	383.11	0.000
NAO + AVT + (NAO * AVT)	-4975.9	8	9967.9	385.85	0.000
NAO + ATU + (NAO * ATU)	-4975.9	8	9967.9	385.85	0.000
NAO	-4983.3	6	9978.8	396.76	0.000

Table B.6. Full AICc tables for Y2-Summer growth section. Note: River included as a factor in all models.

Model	Log-likelihood	k	AIC$_c$	ΔAIC$_c$	Akaike Weight
ATU + PSI + SMA	-4517.7	9	9053.4	0.00	0.544
AVT + AVT^2 + PSI + SMA	-4517.1	10	9054.3	0.89	0.348
PSI + SMA	-4520.5	8	9057.1	3.64	0.088
PSI + SMA + (PSI * SMA)	-4520.0	10	9060.1	6.70	0.019
AMO + PSI + (AMO * PSI)	-4530.3	8	9076.6	23.21	0.000
AMO + PSI	-4531.5	7	9077.1	23.66	0.000
ATU + PSI	-4533.3	7	9080.7	27.26	0.000
AVT + AVT^2 + PSI	-4533.0	8	9082.1	28.72	0.000
PSI	-4536.0	6	9084.1	30.63	0.000
NAO + PSI	-4535.4	7	9084.8	31.35	0.000
NAO + PSI + (NAO * PSI)	-4534.6	8	9085.3	31.90	0.000
AMO + AVT + (AMO * AVT)	-4808.1	8	9632.4	578.94	0.000
AMO + ATU + (AMO * ATU)	-4808.1	8	9632.4	578.95	0.000
SML	-4811.0	6	9634.0	580.57	0.000
SML + SMA	-4809.9	8	9635.8	582.40	0.000
SML + SMA + (SML * SMA)	-4809.6	10	9639.3	585.87	0.000
AMO	-4815.8	6	9643.7	590.29	0.000
ATU + SMA	-4817.4	8	9650.9	597.53	0.000
NAO + ATU + (NAO * ATU)	-4818.3	8	9652.6	599.18	0.000
NAO + AVT + (NAO * AVT)	-4818.3	8	9652.6	599.21	0.000
AVT + AVT^2 + SMA	-4817.3	9	9652.8	599.34	0.000
ATU	-4820.9	6	9653.8	600.39	0.000
AVT + AVT^2	-4820.8	7	9655.7	602.27	0.000
NAO	-4822.0	6	9656.0	602.54	0.000

Table B.7. Full AICc tables for Y2-Fall growth section. Note: River included as a factor in all models.

Model	Log-likelihood	k	AIC_c	ΔAIC_c	Akaike Weight
PSI + SMA	-4267.3	8	8550.8	0.00	0.495
ATU + PSI + SMA	-4267.2	9	8552.6	1.83	0.199
PSI + SMA + (PSI * SMA)	-4266.5	10	8553.1	2.31	0.156
AVT + AVT^2 + PSI + SMA	-4266.5	10	8553.2	2.42	0.148
AMO + PSI	-4274.3	7	8562.6	11.87	0.001
AMO + PSI + (AMO * PSI)	-4273.7	8	8563.5	12.78	0.001
NAO + PSI	-4282.9	7	8579.9	29.13	0.000
PSI	-4284.6	6	8581.2	30.43	0.000
NAO + PSI + (NAO * PSI)	-4282.8	8	8581.6	30.86	0.000
ATU + PSI	-4284.4	7	8582.9	32.17	0.000
AVT + AVT^2 + PSI	-4283.8	8	8583.6	32.86	0.000
AMO + AVT + (AMO * AVT)	-4502.3	8	9020.7	469.92	0.000
AMO + ATU + (AMO * ATU)	-4502.3	8	9020.7	469.92	0.000
AMO	-4505.1	6	9022.3	471.54	0.000
SML + SMA	-4507.8	8	9031.7	480.95	0.000
SML	-4511.0	6	9033.9	483.18	0.000
SML + SMA + (SML * SMA)	-4507.8	10	9035.6	484.88	0.000
AVT + AVT^2 + SMA	-4509.3	9	9037.3	486.54	0.000
ATU + SMA	-4511.9	8	9039.9	489.18	0.000
NAO + AVT + (NAO * AVT)	-4512.8	8	9041.7	490.98	0.000
NAO + ATU + (NAO * ATU)	-4512.9	8	9041.8	491.04	0.000
AVT + AVT^2	-4515.2	7	9044.4	493.68	0.000
ATU	-4517.5	6	9047.1	496.34	0.000
NAO	-4517.5	6	9047.1	496.37	0.000

BIOGRAPHY OF THE AUTHOR

Lisa Izzo was born in Flemington, New Jersey, on August 8, 1990. She grew up first in New Jersey, and then in southeastern Pennsylvania, spending time each summer exploring the coast of New Jersey. Lisa's love of the coastal environment led her to attend Rutgers University, where she graduated with a Bachelor of Science in Marine Sciences (Biological Oceanography) and a minor in Ecology and Evolution in 2012. Through a series of internships, classes, and volunteer activities that included activities from genetic analysis of cyanobacteria to growth of juvenile clams to trawling for estuarine fishes, Lisa pinpointed her interests on fisheries ecology. During her search for a master's program, she moved from the marine environment into freshwater to work with Atlantic Salmon in Maine. Lisa is a candidate for the Master of Science degree in Wildlife Ecology from the University of Maine in August 2016.