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**ENERGETIC IMPACTS OF PASSAGE DELAYS IN MIGRATING ADULT ATLANTIC
SALMON**

By

Sarah R. Rubenstein

B.S. Cornell University, 2015

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Wildlife Ecology)

The Graduate School

The University of Maine

August 2021

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By Sarah R. Rubenstein

Thesis Advisor: Dr. Joseph Zydlewski

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
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August 2021

For any migratory organism, habitat connectivity is critical for population stability. Structures that impede movement between necessary habitats can be damaging to population persistence. In riverine systems, dams act as migratory barriers, altering ecosystems and delaying, injuring, or otherwise impairing migratory fish movement into essential habitat. Critically endangered Atlantic salmon (*Salmo salar*) populations in Maine have been on the decline since the 1800s. Because most Atlantic salmon rivers are now highly dammed systems, hydropower dams have been cited as causal to the decline in returning adult populations. Previous studies have demonstrated that Atlantic salmon experience substantial delays below dams while moving upstream, but current state of knowledge with respect to metabolic costs and fitness outcomes for delayed Atlantic salmon provides no clear quantification of risk associated with this delay.

I sought to understand consequences of delay in the context of an increased thermal experience below dams. With my collaborators, I have documented that water temperatures below surface-release dams remain several degrees warmer throughout peak summer months than water temperatures in upstream sections of river. Thus, adult Atlantic salmon experiencing delays below dams will be subject to warmer thermal experiences than if they had moved

rapidly to upstream sections of river. As ectotherms, ambient water temperatures directly impact physiological processes, but salmonids generally have a narrow optimum temperature range. As waters warm to outside that range, metabolic processes become more energetically costly. That excess energy use might manifest itself in reduced individual reproductive success, or in the case of Atlantic salmon, a decrease in population iteroparity rates.

In Chapter 1, we quantified the energetic cost of dam-mediated delays of adult migrating Atlantic salmon using HOBO temperature loggers, temperature-logging radio tags, and a Distell Fish Fatmeter as a noninvasive surrogate for full-body energy estimation. On the Penobscot River and Kennebec Rivers of central Maine, we tagged fish, released them a short distance below the dams, and tracked their movements back upstream, taking a Fatmeter measurement first at tagging and then after ascending the fish way at the respective dams. We found that Atlantic salmon experienced delays of two to three weeks on average while attempting to pass dams on their respective rivers. At that time, these fish lost between 11.1 and 19.4% of their starting endogenous fat reserves. Using the temperature-logging radio tags, we documented the individual thermal experience of each study salmon and determined that the thermal experience did indeed predict fat loss. Our results suggest that dams cause delays, not only extending migration times but also exposing adult Atlantic salmon to warmer water temperatures, compounding energetic impacts of dams and depleting available energy reserves.

In Chapter 2, we utilized a bioenergetic model to further understand energy allocation of migrating adult Atlantic salmon in the context of delays at dams and corresponding water temperatures. Atlantic salmon can survive after spawning to be iteroparous, engaging in multiple reproductive life cycles over the course of a lifetime. Iteroparity is thought to be important to the conservation of this federally endangered species through greater population recruitment but currently, repeat spawners in Maine populations have been nearly eliminated.

We modeled five different Atlantic salmon spawning runs in five different hypothetical rivers with either zero, one, two, three, or four dams presenting as migration barriers causing delays and subjecting salmon to warmer water temperatures. The results of our model showed that as the number of dams on a river increased, the number of post-spawn surviving Atlantic salmon decreased. On the unimpeded river, 6.3% of the run survived after spawning but on a river with four dams, only 2.8% of the returning salmon run survived. We also found that the number of salmon able to complete the single reproductive event decreased and the number of salmon that died before spawning increased as dams were added to the modeled system. Our results from Chapter 2 suggest that rapid movement through warmer downstream sections of rivers to upstream, cooler waters is key to increasing iteroparity rates in spawning populations and overall reproductive success.

ACKNOWLEDGEMENTS

This research received financial and logistical support from numerous agencies, individuals, and organizations. Financial support for this work was provided through Anson and Abenaki and the National Oceanic and Atmospheric Administration, grant NA17NMF4720195. I am greatly appreciative of the logistical support provided by the Maine Department of Marine Resources and Brookfield Renewable Energy. A special acknowledgment to Paul Christman for his unwavering enthusiasm and effort on the Kennebec River. Paul was critical to the success of this project. Thank you to Jennifer Noll, Cassidy Bigos, Jason Valliere, Mitch Simpson, and Peter Ruksznis at the Maine Department of Marine Resources for their assistance with capturing and tagging fish and data collection. Thank you to Richard Dill and the rest of the Brookfield Renewable Energy team for coordination, planning, and telemetry station maintenance help. Thank you to Denise Buckley, and her team at Craig Brook National Fish Hatchery, for assistance and accommodations at the hatchery. I would also like to express my gratitude to the multiple landowners allowing us access to their property for this research. In-kind support was provided by the USGS Maine Cooperative Fish and Wildlife Research Unit.

The faculty, staff, and students at the University of Maine have made this project possible and my time at the University so enjoyable. I would like to thank all the members, past and present, of the Zydlewski lab that I was lucky enough to work alongside: Sarah Vogel, Betsy Barber, Andy O'Malley, Kevin Job, Alejandro Molina-Moctezuma, Dan Weaver, Matt Mensinger, Kory Whittum, Kathryn Sloan, and Cory Gardner. A special thank you to Erin Peterson who was instrumental in assuring a smooth field season and who made tagging fish for hours so much fun, and to Cody Dillingham, without whom I would have been overwhelmed by telemetry maintenance and data.

Being a part of the Department of Wildlife, Fisheries, and Conservation Biology and surrounded by such inspiring and encouraging peers and mentors was so special. Thank you to every graduate student I came to know – you each made my time in Maine extraordinary and I have been continually impressed by each of you. I would also like to extend a special thank you to Rena Carey, Katherine Goodine, and Molly-Jean Langlais-Parker for unwavering logistical assistance within the department.

I want to thank my advisor, Joe Zydlewski, for his continuous support and encouragement both professionally and personally. I cannot fully express how much I have enjoyed working with you and learning from you. Thank you also to my committee, Nishad Jayasundara and Stephen Coghlan, Jr., for valuable feedback and insights.

Finally, thank you to my friends and family for all of your support through this process. To Stephanie Shea, Megan Hess, and Sarah Vogel: I am eternally grateful for that one night at Marsh. Thank you for being one of my strongest support systems. To Juliet Jacobson, Eliana Jacobson, and Sarah Khalil: you have always managed to cheer me on, even from afar. Lastly, thank you to my parents, Barney Rubenstein and Sandra Scroggins, and my brother, Ethan Rubenstein, for your constant care and support through all of my adventures, including this one. I wouldn't be here today if you hadn't believed in me from the very beginning. Thank you.

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CHAPTER 1

ENERGETIC CONSEQUENCES TO MIGRATING ATLANTIC SALMON (*SALMO SALAR*) DELAYED BELOW DAMS

ABSTRACT

Dams contribute to the decline of endangered Atlantic salmon runs in the United States. Atlantic salmon return to natal rivers every spring and summer for a long, arduous journey upstream to engage in spawning. The entire migration process is energetically costly and consequently, excessive use of energy during any one portion of the migration may impact the probability of successful reproduction and survival. Rivers that hold Atlantic salmon runs are highly dammed, and previous studies have shown that Atlantic salmon are often delayed below dams while migrating upriver. Because Atlantic salmon are ectotherms highly sensitive to the environmental temperature the warmer water often found below surface release dams translates to an increase in metabolic cost. The objectives of this research were to quantify the energetic cost of dam-mediated delays in migrating adult Atlantic salmon. Our study systems were the Penobscot River and Kennebec River of central Maine. We used HOBO temperature loggers, temperature-logging radio tags, and a Distell Fish Fatmeter as a noninvasive surrogate for full-body energy estimation of salmon as a function of their environmental temperature. We demonstrated that water temperature below the first dam on each river was regularly warmer than upstream river temperatures throughout the summer months. We tagged fish, released them a short distance below the dams, and tracked their movements back upstream, taking a Fatmeter measurement first at tagging and then after ascending the fish way at the respective dams. We found that Atlantic salmon experienced delays of 16 to 19 days on average while attempting to pass dams on their respective rivers, and in that time, lost between 11.1 and 19.4% of their starting endogenous fat reserves. Using regressions, we found that the thermal experience of a salmon was the best model to describe that fat loss, though delay length was also competitive.

Recovery of Atlantic salmon populations in Maine depends on the ability of Atlantic salmon to maintain sufficient energetic supply during upstream migrations to invest in successful reproduction and survival. However, our results show that dams cause delays while also exposing upstream migrating Atlantic salmon to warmer thermal experiences, compounding energetic impacts of dams and depleting available energy reserves.

INTRODUCTION

For any migratory organism, habitat connectivity is a critical part of individual fitness and long-term population stability and persistence. In fluvial ecosystems, structures that impede the movement of diadromous fish between habitats essential for spawning and rearing (e.g., dams) may negatively impact these populations (Kemp and O’Hanley 2010). Dams change river systems, impacting downstream ecosystems by altering flow and temperature regimes, degrading water quality, and delaying, injuring or otherwise impairing migratory fish movement into essential habitat (Opperman et al. 2011; Haro et al. 2004), and consequently, have been cited as causal to the decline of fish populations (Caudill et al. 2007; Limburg and Waldman 2009). Fish ways and fish lifts/elevators installed at river barriers may partially restore connectivity and aid with both upstream and downstream fish migration (Noonan et al. 2012; Bunt et al. 2012), but for a passage structure to work effectively, fish must rapidly find entrances and hydraulics must allow fish to enter and ascend (Williams et al. 2012). Critically endangered Atlantic salmon (ATS) populations in Maine have severely felt the impacts of dams as barriers to migration (U.S. Fish and Wildlife Service and NMFS 2018).

Successful spawning and recruitment is important to the preservation of this species. ATS are anadromous, beginning life in freshwater and migrating to the ocean as juveniles to grow in a nutrient rich environment before returning to spawn in natal streams as mature adults. ATS return to natal rivers from late spring throughout the summer, many months before the onset of

spawning in the fall. The migration begins with a directed movement upstream from the mouth of the river to a suitable spawning location, lasting for weeks to more than a month in an undisturbed system with individual fish traveling between 2 and 31 kilometers per day (Thorsad et al. 2008). Adults returning to coastal watersheds are thought to cease consumption upon commencing the freshwater stay of the spawning migration (Kadri et al. 1995), ensuring that energetic stores developed during the marine phase of an ATS's life become essential to survival and spawning success. Endogenous stores of energy are invested in freshwater migrations, including gamete production, upstream migration, development of secondary sexual traits, spawning, courtship, redd building, guarding, and intersexual competition (Jonsson and Jonsson 1991; Fenkes et al. 2016). Although ATS experience high mortality after they have completed spawning, post-spawn adults (kelts) may survive to return to the sea, some to return to spawn at least once more during their lifetime (Maynard et al. 2018). After spawning, surviving kelts will either migrate directly to the sea or over-winter in the river before out migrating to the marine environment in the following spring (Ruggles 1980). The same individual may spawn in up to four different years. These larger, multi-year fish are critical components of their populations with an increased reproductive potential as female Atlantic ATS may invest up to 25% of their body weight into egg production (Fleming 1996). However, these repeat spawners have been nearly eliminated from Maine populations, as less than 1% of anadromous spawning adults survive, return to sea, and migrate again to their natal river to spawn (Maynard et al. 2017; Board and NRC 2004). The entire migration process is long and arduous, necessitating the need for conservation of energy stores, particularly when considering the potential for kelt survival. Excessive use of energy during one portion of the migration may reduce the energy available for the remaining migration process (Fenkes et al. 2016; Bowerman et al. 2017) and impact the probability of survival.

As ectotherms, ambient water temperature directly controls and limits growth and metabolism of ATS (Lennox et al. 2018). Salmonines are sensitive to environmental temperatures and have a range of optimum temperatures at which aerobic scope is greatest (Elliott and Elliott 2010). Outside their range of optimal temperatures (estimated near 15-18°C in juveniles, Elliott and Elliott 2010), a critical point is reached when aerobic scope is minimal, leading to a metabolic deficit and dependence on anaerobic processes (Farrel et al. 2008). Once the lethal temperature limit is reached (estimated near 28°C in juveniles but likely lower for adults, Elliott and Elliott 2010) ATS become thermally stressed, reducing long-term survival unless access to cooler water becomes available (Frechette et al. 2018). While over-summering in rivers awaiting seasonal maturation, ATS are often subjected to temperatures that approach or reach the upper lethal level. Non-lethal effects of high temperatures begin as temperatures move beyond optimum and towards the upper limit; higher temperatures increase basal metabolism, increasing the depletion rates of available energy stores. Because pre-spawn ATS are relying solely on endogenous reserves (without consumption) power available to fuel the remaining migration and costly spawning efforts is reduced (Martin et al. 2015). To avoid stress and to maintain sufficient energy stores for spawning and survival, adult ATS must access cool thermal refugia (Frechette et al. 2018; Holbrook et al. 2009; Todd et al. 2011).

Dams delay upstream passage for migratory salmonids (Noonan et al. 2012; Izzo et al. 2016). A delay below a dam may draw down critical energy reserves of migrants by exposing them to a longer migration period and increased thermal experiences during peak summer temperatures (Fenkes et al. 2016). Consequences may manifest as pre-spawn mortality or as non-lethal effects, such as increased energy loss (Hinch et al. 2012; Caudill et al. 2007; Nadeau et al. 2010; Jonsson et al. 1997; Berg et al. 1998; Kinnison et al. 2001), longer exposure to freshwater parasites (Hari et al. 2006), or reduced gamete production (Vladić and Järvi 1997). For iteroparous species, there is the added risk of increased post-reproductive mortality. Glebe and

Leggett (1981) suggested that iteroparous fish must invest less than 60% of their total energy in migration in order to conserve enough energy to survive post-spawning, return to the sea, and recondition. Post-spawning survival rates have been shown to correlate significantly with estimated energy expenditures during spawning (i.e., post-spawning survival of ATS increases with decreasing energy expenditure; Jonsson et al. 1997). Thus, additional energetic costs of dams may provide a strong source of stress if delays influence energetic stores.

ATS populations in Maine have been on the decline since the 1800s. The historic distribution of ATS in the United States ranged from the Housatonic River in western Connecticut to the St. Croix River in northern Maine. ATS were native to nearly every major river north of the Hudson River (Atkins 1874; Kendall 1935). The annual ATS spawning run returning to U.S. rivers was estimated to be up to 500,000 adults, with the largest runs occurring in the Connecticut, Merrimack, Androscoggin, Kennebec, and Penobscot Rivers (Beland 1984; DeRoche 1967; Baum 1983). The Penobscot River alone (Maine) supported an estimated 100,000 adult ATS every year (Atkins and Foster 1867). Beginning in the late 1800s, ATS populations began to experience severe declines attributed to overfishing, marine survival, dams, and habitat degradation (Fay et al. 2006). Now, ATS runs in the United States are limited to only Maine rivers. Among those, the Penobscot River continues to support the largest numbers of adults although numbers have dropped to between 500 and 2,000 fish annually (Fay et al. 2006). In 2009, the National Marine Fisheries Service and the U.S. Fish and Wildlife Service listed the Gulf of Maine Distinct Population Segment, including the Penobscot and Kennebec rivers of central Maine, of ATS as Endangered under the Endangered Species Act, listing dams and marine survival as key causes of their current demographic decline (NOAA Fisheries 2016).

ATS in Maine have to navigate highly dammed systems. The Penobscot River and the Kennebec River of central Maine are home to the largest remaining runs of ATS adults. The

Penobscot River watershed is the second largest river basin in New England and encompasses over 8800 km of main stem and mapped tributary habitat. The Penobscot River itself is interrupted by numerous dams, but over recent years has undergone substantial restoration efforts via the Penobscot River Restoration Project (PRRP; Opperman et al. 2011). Fish passage improvements, decommissioning of dams, and dam removal have all been part of restoration efforts. Great Works dam (river kilometer [rkm] 59) and Veazie dam (rkm 48) were removed in 2012 and 2013, respectively, making Milford Dam (rkm 61) the most downstream barrier to ATS migrating upstream on the main stem of the Penobscot River (Trinko Lake et al. 2012). Successful upstream and downstream passage at Milford Dam has been identified as a critical component of ATS restoration since a 2006 survey by the ATS Biological Review Team found that less than 20% of suitable spawning habitat in the Penobscot River is located below Milford Dam (Fay et al. 2006).

On the Kennebec River, Lockwood Dam (rkm 101) is the first substantial main stem barrier after the removal of Edwards Dam in 1999. Upstream of Lockwood Dam, there are three other main stem dams – Hydro-Kennebec, Shawmut, and Weston – that prevent unimpeded upstream movement. Currently, none of the dams on the Kennebec have functioning upstream fish passage. Instead, Maine Department of Marine Resources (MEDMR) implement trap and haul methods to move adult ATS from Lockwood Dam to high quality upstream spawning habitats located in the Sandy and Carrabassett Rivers. Thus, most in-migrating adults must pass through Milford Dam or Lockwood Dam.

It has been well documented that upstream migrating fish are regularly delayed below dams with negative repercussions (Bunt et al. 2012), but what remains unclear is the relative cost these delays have on the performance and fitness of adult ATS as a consequence to increased thermal exposure. We sought to quantify the energetic cost of dam-mediated delays of adult

migrating ATS. Our objectives in this study were to (i) characterize the thermal experience of salmon below dams, (ii) empirically assess the energetic costs of delays, and (iii) quantify energetic changes in the context of thermal experience.

METHODS

Capture – Both Milford Dam and Lockwood Dam operate a fish lift and fish sorting facility on the turbine side of the dams. The lifts have a horseshoe-shaped entrance leading to a V-shaped gate to trap fish within a hopper. The hopper is lifted, and fish are released either directly into a trap (Lockwood) or an upper flume guiding them to a trap and handling facility (Milford) operated by the Maine Department of Marine Resources (MEDMR). The lifts are generally operated from mid-April to mid-November (for details, see Izzo et al. 2016). Fish collection for this research occurred in both 2018 and 2019. Adult ATS were collected from the traps at Milford Dam (2018, $n = 49$; 2019, $n = 50$) and at Lockwood Dam (2018, $n = 6$; 2019, $n = 20$) on the Penobscot and Kennebec Rivers, respectively. Following MEDMR protocol, at time of capture, a scale sample was taken from each salmon (for later identification of age and origin) and fork length and sex (assessed by morphological metrics) were recorded. The origin of salmon in either river falls into one of two categories: wild-reared or hatchery. In the Penobscot river, the majority of adults are of hatchery smolt-stocked origin and rarely of wild spawned eggs. Adults of hatchery origin were released into their respective rivers as fry or as smolts, just before the out-migration period. All ATS in the Kennebec river are wild reared. Salmon of wild-reared origin are from naturally spawned eggs or artificially planted eggs. Prior to tagging, fish were held in tanks of ambient river water without anesthesia.

Tagging – Captured ATS were gastrically tagged with either standard Lotek radio tags or temperature logging Lotek archival radio tags (MCFT3-L; 30g and 16x85mm; 2.5-s burst rate). The fish was manually held against the side of the tank while the tagger inserted the tag into the

esophagus of the salmon via flexible tubing. Each tag was wrapped with one livestock castration band to decrease the risk of regurgitation (Izzo et al. 2016). Each fish on the Penobscot River also received a 22-mm passive integrated transponder (PIT) tag (Biomark) implanted in the dorsal muscle which was used for secondary identification and for tracking on an existing PIT array. Tagging of salmon started in late May to early June and continued throughout the summer until the target number of fish was reached on each river. To abide by permitting and avoid excessive stress to the fish, tagging took place only at river temperatures below 23°C. After tagging, salmon recovered in an aerated tank of ambient river water and, post-recovery, fish were transported downstream on their respective rivers for release. On the Penobscot, salmon were released at Brewer Boat Launch, approximately 18 km downstream from Milford Dam (Figure 1.1). On the Kennebec River, salmon were released at the Sydney Boat Launch, approximately 14 km downstream from Lockwood Dam (Figure 1.2).

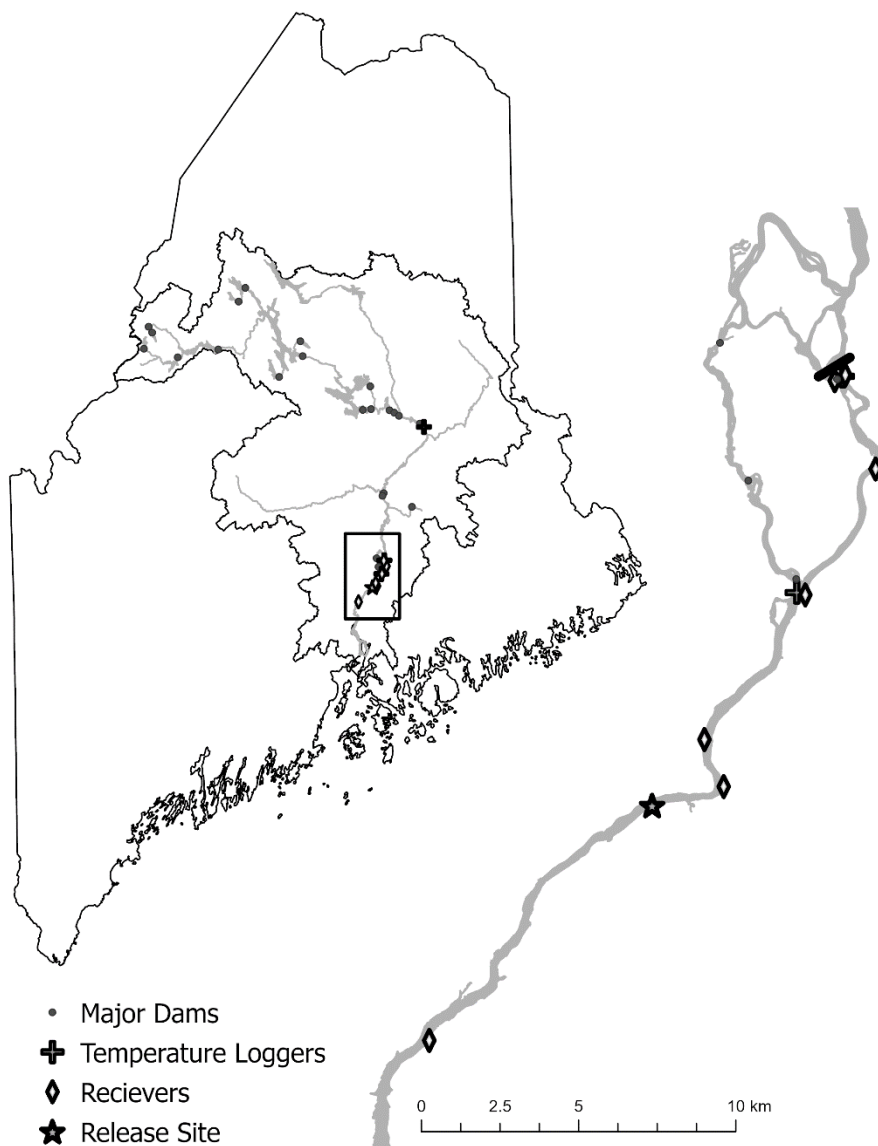


Figure 1.1. Map of the study area within the Penobscot River system with major dams, temperature loggers, stationary radio receivers, and the release site.

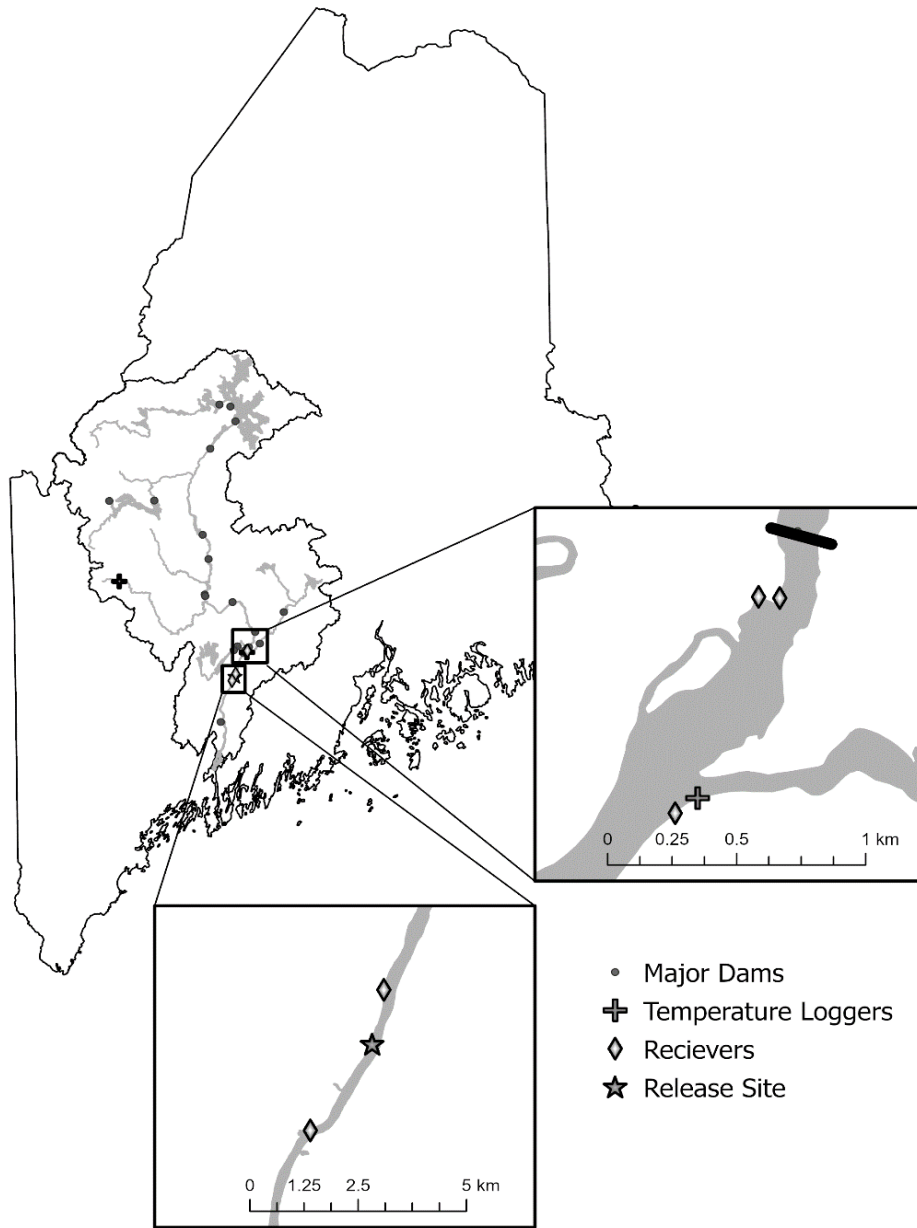


Figure 1.2. Map of the study area within the Kennebec River system with major dams, temperature loggers, stationary radio receivers, and the release site.

Energetic assessment– We used a Distell Model 692 Fish Fatmeter (Distell Inc., West Lothian, Scotland) to estimate whole-body energy concentrations based on indirect lipid assessments. This is a cordless, handheld unit that uses a microwave oscillator (frequency 1.975 GHz; power 1 mW) that interacts with water in the fish’s tissue. The sensor transmits a microwave signal

through the skin of the fish and into the flesh. Depth of penetration of the microwave signal is dependent upon the water content as the signal is reduced by the amount of water in the sample. There is an inverse relationship between fat and water – the lower the percentage of water, the greater the relative lipid content and higher energy content of the fish (Jonsson et al. 1997). The unit is used to take measurements of four body positions along the flank on both sides of the salmon, and these data provide an energy estimate based on the lipid content of somatic tissues derived from established calibration curves for ATS. This method has proven effective (lipid and somatic energy values determined through whole-carcass proximate analysis showed a strong relationship to fat meter readings; Crossin and Hinch 2005). Fat measurements of Penobscot River and Kennebec River salmon were taken at their first and second captures at Milford Dam and Lockwood Dam, respectively, in order to estimate energy use between captures.

Telemetry - In-river movements of radio tagged fish from release site back upstream to respective dams were monitored using stationary Lotek SRX-DL and SRX-800 receivers with high-gain YAGI antennas from May until November of both 2018 and 2019. In the Penobscot River, we had antennas located on Milford Dam to allow us to determine fish presence in the spillway and additional receivers and antennas between the release site at Brewer Boat Launch and the dam (Figure 1.1). Similarly, on the Kennebec River, we had antennas on Lockwood Dam and additional receivers and antennas placed between the release site at Sydney Boat Launch and the dam (Figure 1.2).

Recapture - Tagged salmon that re-ascended the dam and were recaptured at Milford were transported to the USFWS Craig Brook National Fish Hatchery to be part of the Penobscot brood stock. A second measurement of fat content was carried out with the Distell Fish Fatmeter prior to transportation. Tags were either removed immediately following the second

measurement or at the hatchery later in the season (to avoid pre-spawn handling stress). Salmon recaptured on the Kennebec River at Lockwood Dam were measured for a second fat content and subsequently had their radio tags removed. Kennebec River salmon were then trucked upstream to the Sandy River by the MEDMR and released. The end result of the tagging and two fat measurements is summarized by Figure 1.3. Between two time points, initial capture (t_0) and recapture (t_1), we chronicled the fish's thermal experience from radio tags and measured a change in relative lipid stores from Distell Fish Fatmeter readings.

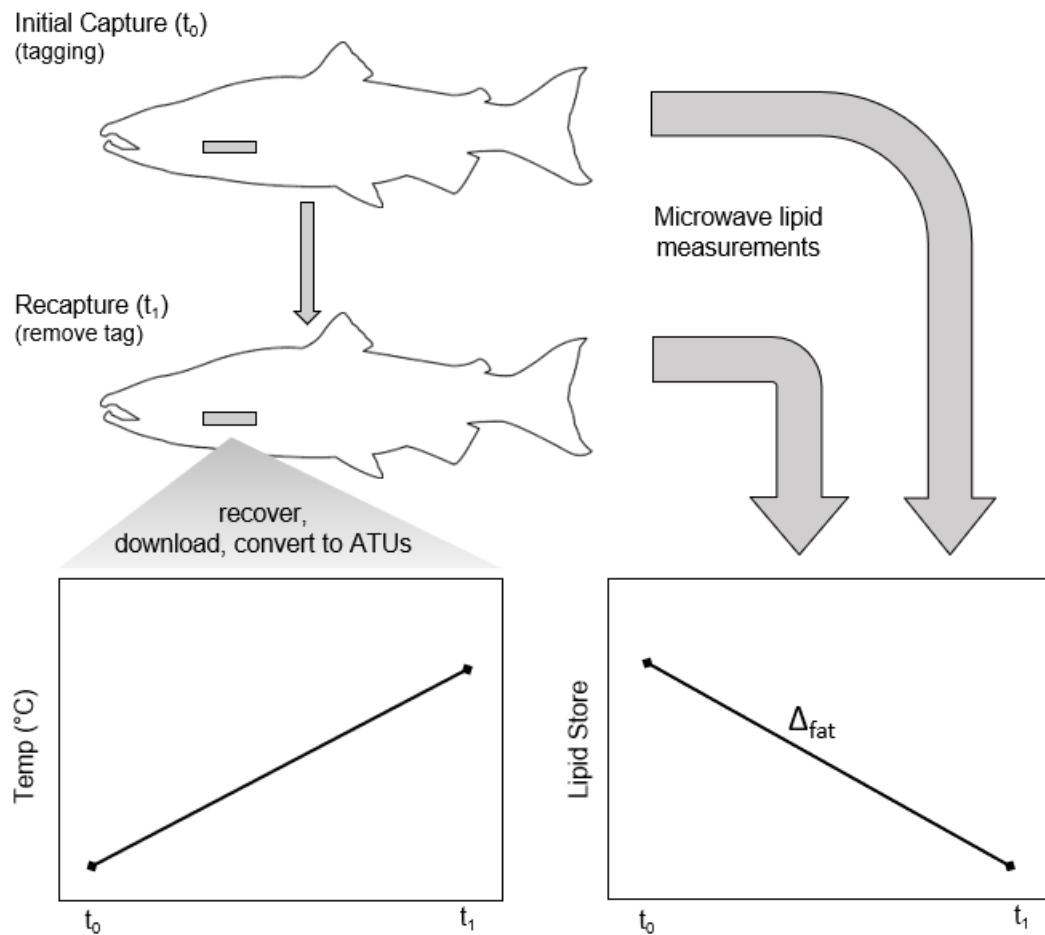


Figure 1.3. Methods figure summarizing capture, recapture, thermal experience, and fat loss. At first capture (t_0), salmon are tagged with a temperature-logging radio tag and measured with a Distell Fish Fatmeter. At second capture (t_1), the radio tag is removed and downloaded and a second Fatmeter reading is performed. The result is the thermal experience and relative loss of fat between two time periods.

Thermal experience – To characterize the range of thermal experiences that adult ATS may experience during upstream migrations, we deployed temperature loggers (Hobo Water Temperature Pro v2 Data Loggers (resolution of 0.02°C at 25°C and an accuracy of 0.21° from 0 to 50°C) within the Kennebec and Penobscot River watersheds in early May of 2018 and 2019 (Figures 1.1 and 1.2). Loggers were placed at sites thought to be of known use to ATS for holding or spawning. Loggers stayed in the river from May until the start of ice formation in late November or early December.

Analyses – Stationary radio detections were used to determine movement patterns between captures, described in days in two different categories: approach to dam and delay. Approach to the dam was calculated as the time from release to the time of first detection on any of the stationary radio antennas on the dam (approximately 14-18 rkm). Delay time at both dams was calculated as the time from first detection on any of the antennas at the dams until successful passage (i.e., entry and recapture at the trap and handling facilities at either dam).

Temperature data collected from the HOBO temperature loggers was averaged per day and plotted throughout the season to calculate the differences in temperatures between upstream and downstream locations on the rivers. Both average daily temperatures from HOBO temperature loggers and average daily thermal data from individual salmon with temperature logging radio tags were converted to accumulated thermal units (ATUs), the cumulative daily water temperature in degrees Celsius per day. Using ATUs, we performed several comparisons between actual salmon thermal experience (from loggers being carried by fish) and the ambient water temperatures at the upstream and downstream locations (recorded by temperature loggers), which we treated as potential upstream experiences if given unimpeded access to

cooler upstream waters (upstream temperatures) and if holding consistently below the respective dams (downstream temperatures).

Fat loss was simply the percentage of fat at second capture subtracted from initial fat percentage measured at first capture. The percent of initial fat lost was calculated as

$$\Delta_{fat} = \frac{fat_1 - fat_2}{fat_1} \times 100$$

with fat_1 and fat_2 as first and second fat measurements, respectively. A multiple linear regression with R^2 and AIC model selection was used to predict the outcome of the proportion of initial fat lost during delays (for temperature logging tagged salmon only). Explanatory variables included accumulated thermal units and the length of delay. Independent Welch t-tests were performed to determine the effect of salmon sex and salmon origin on the proportion of initial fat lost.

To determine if fat lost is proportional, we used a second regression between the ratio of fat lost, calculated as:

$$ratio = \frac{fat_1}{fat_2},$$

and accumulated thermal units.

RESULTS

Upstream movements and delays – On the Penobscot river in 2018, 42 of 49 tagged and released salmon (16/20 archival tags, 26/29 standard tags) returned to Milford Dam for recapture. In 2019, 46 of 50 tagged and released salmon (18/20 archival tags, 28/30 standard

tags) returned for recapture (Table 1.1). On the Kennebec River, all tagged fish were tagged with temperature logging archival tags. In 2018, only 6 fish were tagged due to very low total run numbers. Four of those fish returned for recapture. In 2019, 9 of 20 tagged salmon returned to Lockwood Dam for recapture (Table 1.1). The salmon that did not return were detected on radio antenna arrays eventually falling back from the dam and moving downstream (Figure 1.4).

Table 1.1. A summary of radio tagging data. Archival tags are the temperature logging radio tags. Standard tags are radio tags without the temperature logging capacity. FL is fork length. Origin is either hatchery (HO) or wild reared (WR). Stage indicates either first spawning migration (2SW) or repeat spawner (RPT). The number of recaps indicates fish that we tagged, released, and successfully recaptured.

	Year	n	Tagging date	Tag Type		FL (cm, range)	Sex		Origin		Stage		No. recaps	% recapped
				Archival	Standard		Male	Female	HO	WR	2SW	RPT		
<i>Milford Dam</i>	2018	49	May 21 - Jun 1	20	29	76.7 (67 - 92)	24	25	40	9	47	2	42	86%
	2019	50	Jun 7 - Jun 9	20	30	73.1 (61 - 85)	26	24	40	10	50	0	46	92%
<i>Lockwood Dam</i>	2018	6	May 31 - Jun 6	6	-	71.7 (68 - 74)	3	3	0	6	6	0	4	67%
	2019	20	Jun 3 - Jun 18	20	-	69.0 (61 - 73)	12	8	0	20	20	0	9	45%

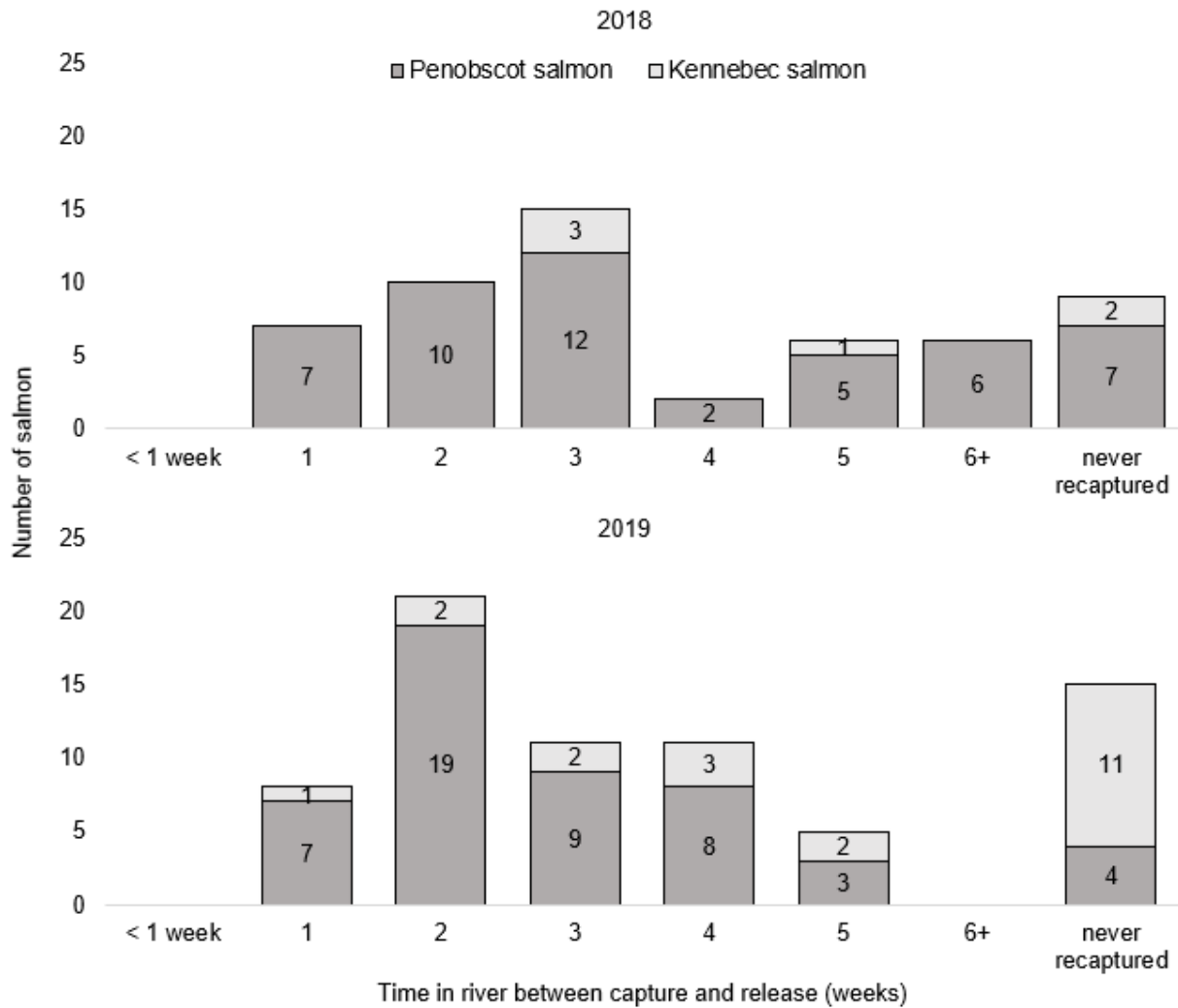


Figure 1.4. A summary of the time between captures for salmon tagged in 2018 (top panel) and 2019 (bottom panel) for both the Penobscot (dark gray) and Kennebec (light gray) rivers.

Most tagged salmon displayed directed upstream movement after recovery and release post-tagging, approaching the base of their respective dams within a relatively short window.

However, the time to enter the fish way, ascend, and pass the dam was much longer (Figure 1.5). In 2018, the average approach time to Milford Dam was 4.0 days (n = 48; median = 3; range 1-28 days) in contrast to the 23.1 days salmon spent on average delayed below the dam (n = 41; median = 12; range 2-155 days). In 2019, approach time to Milford Dam was 4.0 days

(n = 49; median = 3; range 0-12 days) while delay time was 11.0 days (n = 45; median = 8; range 0-30 days). Similarly, in 2018, approach time to Lockwood Dam was just 4.0 days (n = 6; median = 3; range 3-8 days) but delay length was 18.8 days on average (n = 4; median = 16; range 13-10 days). In 2019, approach to Lockwood was 6.9 days (n = 19; median = 3; range 1-42 days), and delay length was 16.1 days (n = 9; median = 18; range 2-31 days).

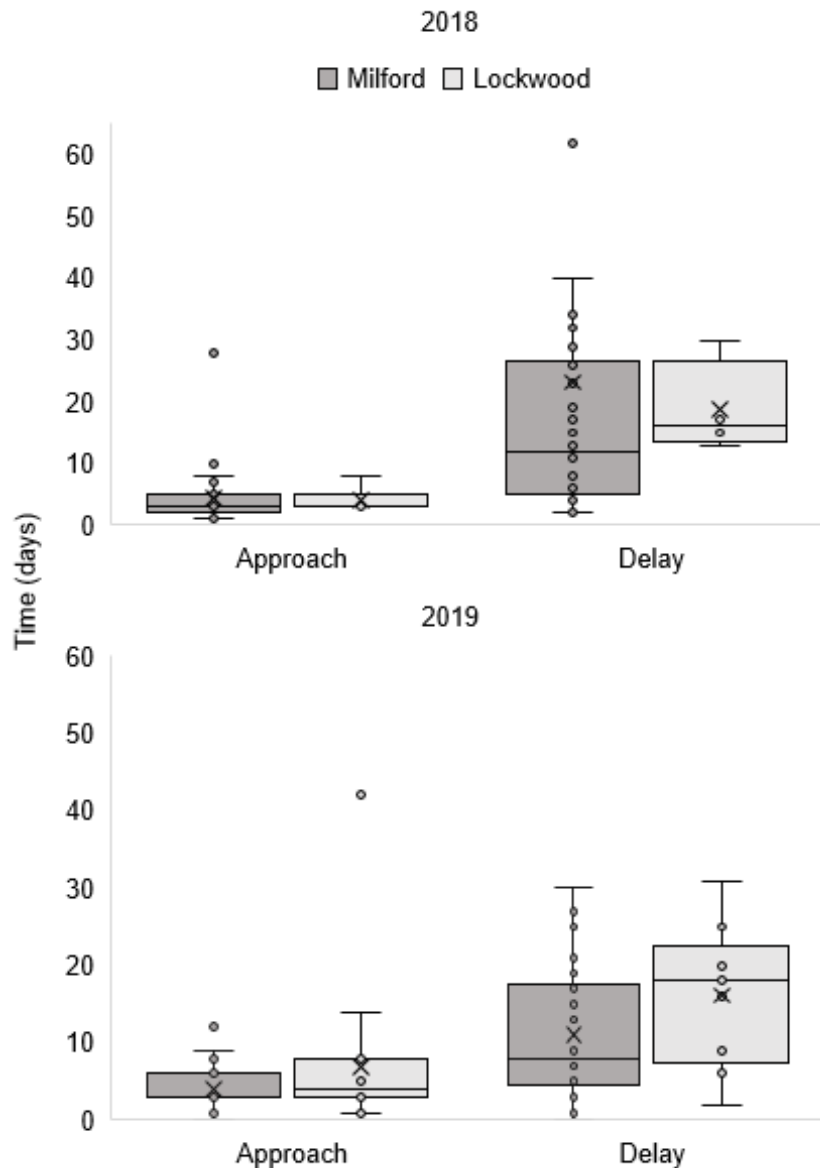


Figure 1.5. A comparison of the time taken (in days) for a fish to first approach the dam and then to ascend the dam after first approach for 2018 (top panel) and 2019 (bottom panel). Approach was measured as the time since release to first detection on a dam stationed radio array. Delay was measured as the time taken from first detection on a dam stationed radio array to successful recapture at the respective dam fish sorting facility. Note: 2018 Penobscot delay outliers at 91, 150, and 155 days.

Thermal data – Downloaded thermal data from our HOBO temperature loggers showed that upstream temperatures, where ATS might hold before spawning if allowed unimpeded access throughout the river, were regularly cooler (over 5°C) than downstream temperatures found below dams, especially during peak summer months (Figure 1.6).

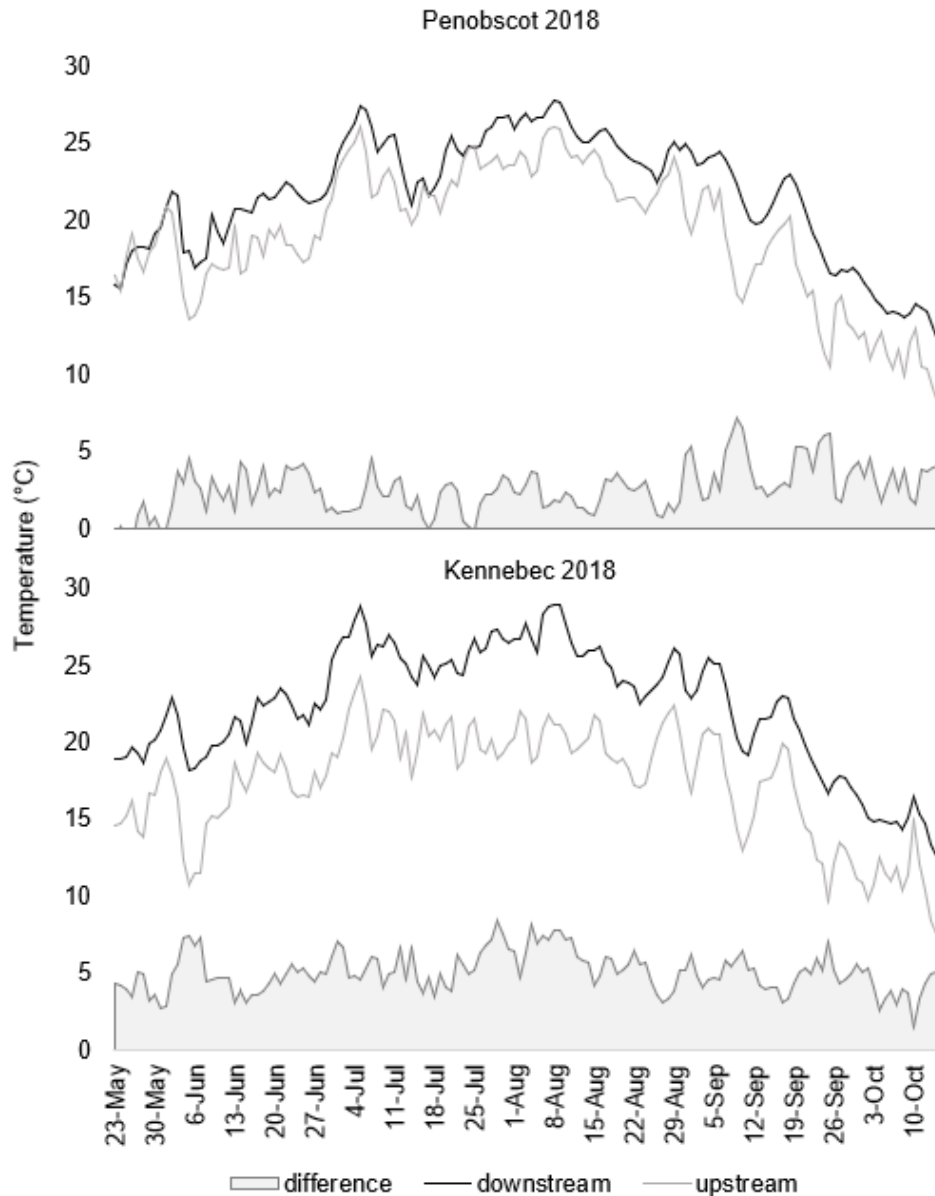


Figure 1.6. The temperature ranges throughout the summer in downstream (black) and upstream (gray) sections of each river. The downstream locations are just below each dam, and the upstream locations are from upstream tributaries. The shaded grey area is the difference in temperatures throughout the summer.

The thermal experience of migrating salmon was retrieved from temperature logging radio tags recovered from recaptured salmon. After accounting for tags that were not recovered from fish that either spit their tags in-river ($n = 4$) or did not return to the dam ($n = 21$) and tags that failed to log temperature while in the field ($n = 12$), we had thermal experiences from 9 of the 2018 Penobscot fish, 12 of the 2019 Penobscot fish, 3 of the 2018 Kennebec fish, and 5 of the 2019 Kennebec fish. The reported range of ATU values from salmon below dams was 54.0 to 662.5 during the period of release to recapture.

In Figure 1.7 we show the thermal experience of our fish, in ATUs (solid line), plotted against an upstream thermal experience (ATUs) if given unimpeded access to cooler upstream waters (dashed line) and against a downstream thermal experience (ATUs) if holding consistently below the respective dams (dotted line). The pattern of the actual thermal experience of the fish presented in either one of two ways, as illustrated by two individual examples in Figure 1.7. In the top panel, the salmon's thermal experience was almost identical to the thermal experience of the downstream logger, indicating a lack of behavioral thermoregulation. In the bottom panel, the salmon thermal experience was slightly lower than the thermal experience of the downstream logger, indicating an ability to locate and utilize thermal refugia during delay. Of our tagged Penobscot fish, 41% exhibited patterns of likely behavioral thermoregulation, (maintaining internal temperatures lower than that of the main-stem river). Of our Kennebec fish, 63% exhibited clear behavioral thermoregulation.

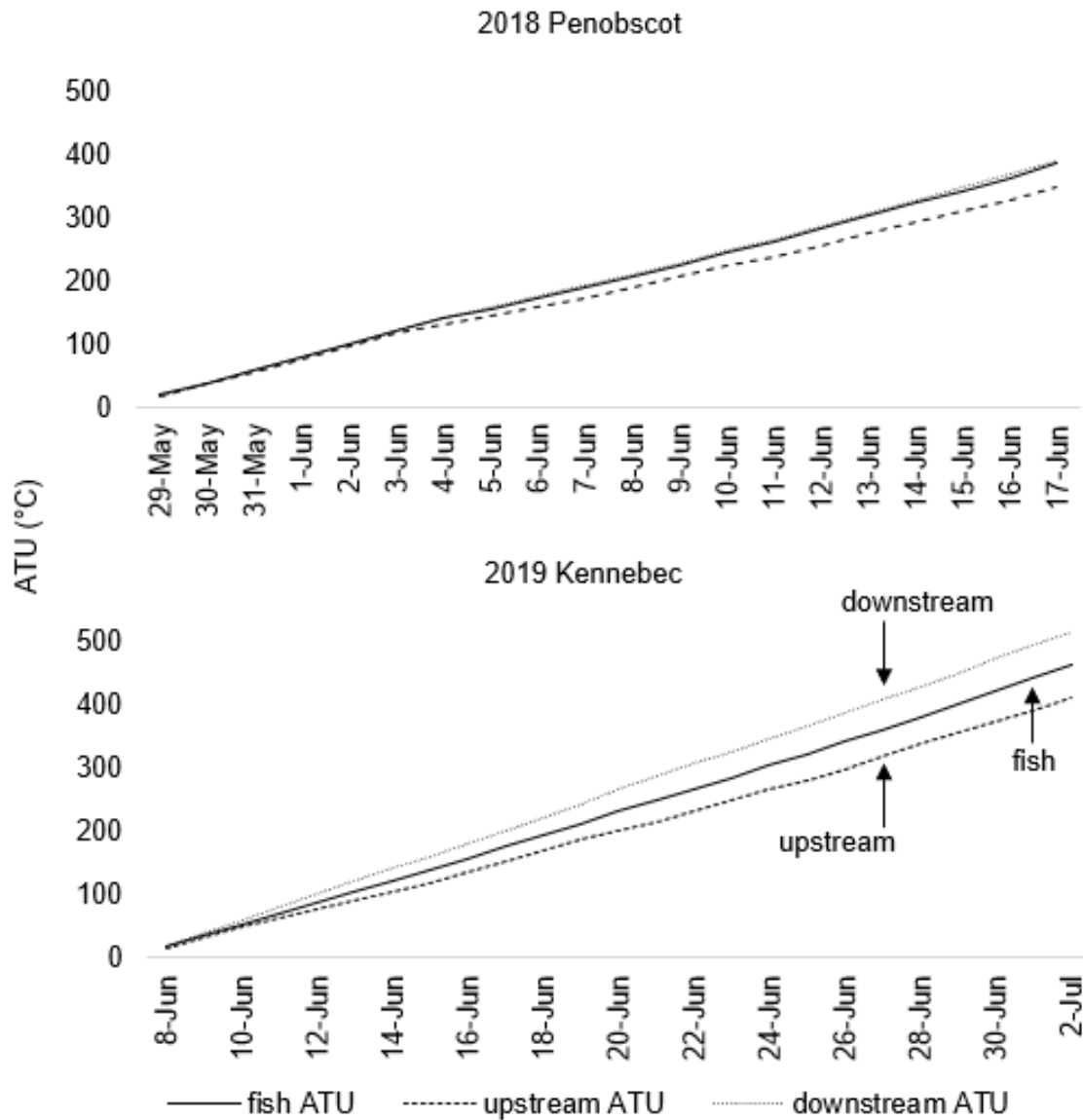


Figure 1.7. Accumulated thermal units (°C) of archival radio tagged Atlantic salmon (solid line) alongside potential ATUs of a salmon holding for the same period in cooler upstream waters (dashed line) and potential ATUs salmon holding in warmer waters directly below respective dams (dotted line).

Fat loss – The average initial fat percentage from the Distell Fish Fatmeter for salmon at first capture ranged between 5.4% and 6.0% (Table 1.2). Fish that were subsequently recaptured via the fish lifts and successfully measured with the Fatmeter lost a range of 0.7% to 1.6% relative fat (Table 1.2). We converted fat percentage lost in the field to the percent of initial body

Table 1.2. The initial fat content, change in fat content between captures, and the percent of initial fat content lost between captures for Atlantic salmon on the Penobscot and Kennebec Rivers for both 2018 and 2019.

	<i>Year</i>	<i>Initial Fat</i>	<i>Change in Fat</i>	<i>% of Initial Fat Lost</i>
<i>Penobscot</i>	<i>2018</i>	5.8% (n = 49; range 2.6 - 9.6)	1.0% (n = 39; range -0.6 - 4.6)	16.9% (n = 39; range -10.7 - 65.8)
	<i>2019</i>	6.0% (n = 50; range 1.9 - 11.3)	1.2% (n = 46; range -0.5 - 4.2)	19.4% (n = 46; range -3.1 - 57.7)
<i>Kennebec</i>	<i>2018</i>	6.0% (n = 6; range 4.3 - 8.0)	1.6% (n = 4; range -0.6 - 2.7)	21.7% (n = 4; range -14.1 - 38.3)
	<i>2019</i>	5.4% (n = 20; range = 2.6-8.4)	0.7% (n = 9; range -0.1 - 2.5)	11.1% (n = 9; range -2.1 - 30.1)

fat lost. We found that in the time between release and recapture, salmon lost between 11.1% and 19.4% of their original endogenous fat reserves (Table 1.2).

Some recaptured fish were measured to have gained fat between first capture and second capture. We attribute this to the accuracy of the fat meter. The fish that exhibited this were generally fish that experienced relatively short delays (range 4-33 days; median 8 days), so a substantial change in fat would not have been expected. The accuracy of the Fatmeter ranges in uncertainty approximately plus or minus 1% fat in readings ranging from 2-15%, so without a substantial change in fat content, that error is likely to have presented itself more clearly.

The simple linear regression model (Figure 1.8) is based on 21 points for Penobscot River salmon and 8 points for Kennebec River salmon and explained 64% of the variance ($R^2 = 0.64$). Using AIC, the best-fit model, carrying 46% of the model weight, to describe fat loss was accumulated thermal units (Table 1.3). However, ATUs in combination with the days in river (AIC Wt = 29%), and days in river alone (AIC Wt = 26%), were both competitive models, as well. There was no significant difference ($p > 0.05$) in fat lost between hatchery origin (mean = -13.5; SD = 13.7) or wild reared (mean = -22.8; SD = 20.0) salmon, and there was no significant

difference ($p > 0.05$) in fat lost between male (mean = -17.9; SD = 15.9) or female (mean = -16.3; SD = 18.6) salmon.

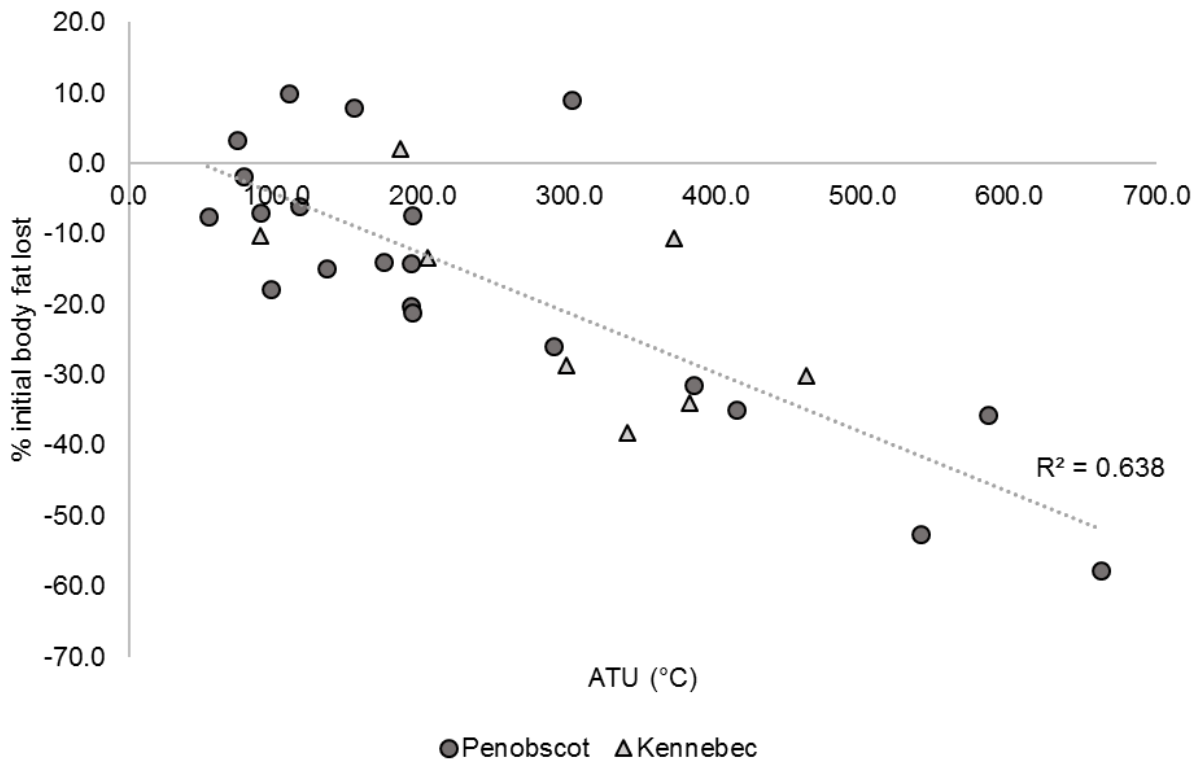


Figure 1.8. A simple linear regression of accumulated thermal units (°C) of archival radio tagged Atlantic salmon from the Penobscot (N = 21) and the Kennebec (N = 8) against the percent of initial body fat lost between first capture and second capture.

Table 1.3. An AIC model selection to parse out the fit of accumulated thermal units or time spent in the river to describe percentage of fat lost during delay. Linear regressions were used, and all three models were competitive with ATUs as top model.

<i>Model</i>	R^2	K	AIC	ΔAIC	$AIC Wt$
<i>ATU</i>	0.64	3	224.61	0.00	0.46
<i>ATU + days in river</i>	0.66	4	225.53	0.93	0.29
<i>days in river</i>	0.62	3	225.77	1.16	0.26

The regression between the ratio between fat readings and ATUs was based on the same 29 points (21 Penobscot fish, 8 Kennebec fish) as the previous models (Figure 1.9). The regression explained 70% ($R^2 = 0.70$) of the variance, supporting a proportional loss of fat in individual salmon.

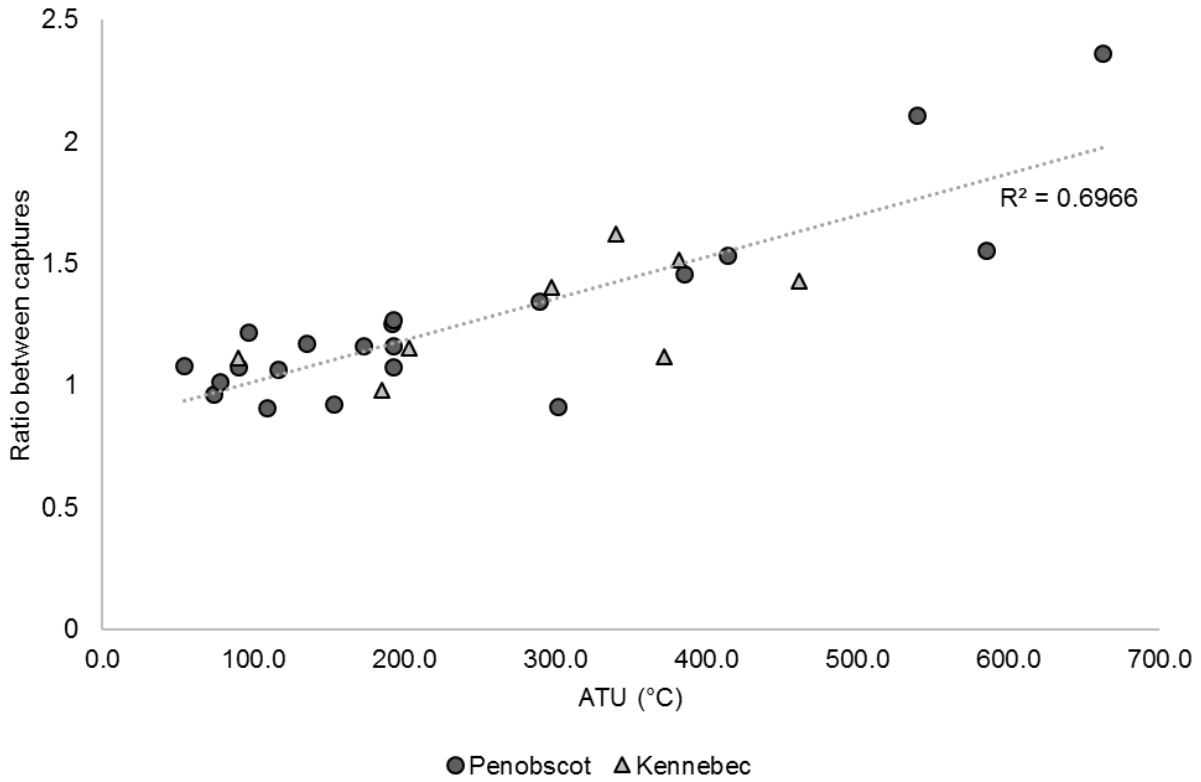


Figure 1.9. A simple linear regression of accumulated thermal units (°C) of archival radio tagged Atlantic salmon from the Penobscot ($n = 21$) and the Kennebec ($n = 8$) against the ratio between fat measurements (initial fat/recapture fat). A strong linear trend indicates a proportional loss of fat.

DISCUSSION

Delays at dams during upstream spawning migrations have been well documented for both Pacific salmon and ATS. As evidenced by our work (Figures 1.4 and 1.5), and has been documented by other studies, corresponding consequences of delays at dams include slowed migration times, high energy expenditure during extended periods of burst swimming,

decreased passage rate dropping the number of reproducing individuals, and reduced subsequent survival following passage (Gowans et al. 2003; Naughton et al 2005; Caudill et al. 2007; Roscoe et al. 2011; Izzo et al. 2016). Our results from the radio tagging and tracking demonstrated that the majority of our ATS exhibited a clear and directed movement upstream from release site, but dams did, in fact, impede migration. The time, on average, from release to arrival at respective dams ranged from 4.0 to 6.9 days, a clear contrast to the 11.0 to 24.0 days on average it took the same ATS to find and utilize fish passage. Because of the extended period of time that delays force ATS to remain in downstream waters, ATS delayed below dams will endure increased thermal experiences during peak summer temperatures than they might if allowed unimpeded access to cooler, upstream waters.

We showed that delay was directly linked to thermal experience and energy loss. The upstream spawning migration and the following reproductive effort of ATS is already a long and grueling journey requiring high energetic input, with individuals expending a substantial part of their somatic energy reserves to complete the process (Brett 1995). Any excessive energy loss depletes the finite energy budget with which a fish entered freshwater, consequently exhausting any reserves that might be allocated to post-spawn survival. Glebe and Leggett (1981) have suggested that fish investing more than 60% of their total energy in migration and spawning would be semelparous, whereas those investing less were iteroparous. Adding dams and corresponding delays along the migration path can simulate a longer, more demanding migration, resulting in the expense of more energy, likely surpassing that 60% semelparous/iteroparous threshold (Jonsson et al. 1997). The kelts that survive and return to natal rivers a following year, especially females, contribute more to the production of the next generation than a first-time spawner does. Repeat spawners tend to be larger with increased egg numbers and egg sizes, which has been correlated with higher survival from egg to fry (Johnston and Leggett 2002; Fleming 1996; Christie et al. 2018). Therefore, in order to ensure

higher percentages of repeat spawners in endangered ATS populations to increase population productivity, rapid passage to alleviate energy expenditure at dams is essential.

To a species with a narrow optimal temperature range, like the ATS, exploiting even slight differences in water temperature can be key to survival (Todd et al. 2011). Thermal experience further compounds the effects of delays at dams on ATS, as warmer temperatures increase metabolic rates. Our temperature loggers deployed on both the Penobscot and the Kennebec Rivers very clearly showed a substantial temperature differential between upstream and downstream sections of river. Upstream sections of river remained cooler throughout the summer than sections of river below dams, which often approached the 28°C estimated lethal temperature for adult ATS (Elliott and Hurley 2003). The thermal experience of our temperature-logging tagged ATS compared to the below-dam river temperature (from the downstream temperature loggers) in two different ways (see Figure 1.7). In some cases, an individual ATS's thermal experience was slightly lower than that of the river temperature, indicating that that individual ATS was able to locate and utilize thermal refugia during their delay below the dam. Of our Penobscot fish, 41% exhibited patterns of behavioral thermoregulation, maintaining internal temperature lower than main stem river temperature. Of our Kennebec fish, 63% exhibited clear thermoregulation. The remaining 59% of our tagged Penobscot fish and 37% of our tagged Kennebec fish endured a thermal experience that very closely mirrored that of the downstream logger, indicating that thermal refugia might be quite limited. Frechette et al. (2018) found that adult ATS in a Quebec river engaged in behavioral thermoregulation at river temperatures as low as 17 to 19°C, temperatures significantly cooler than the below dam temperatures that we documented. Frechette et al. (2018) also reported that, using refuges, ATS maintained body temperatures within a narrow range of 16-20°C, indicating that temperatures above 20°C are likely inducing thermal stress in adult ATS. This has been previously supported by Wilke et al. (1997) in a study that saw only 70% of adult ATS

recovering from exhaustion at 23°C, again a temperature lower than the peak summer temperatures we saw in our study rivers. The fact that our tagged ATS exhibit a thermal experience less than that of the downstream loggers indicate that finding thermal refugia plays an important role in mitigating the thermal stress of delays below dams. However, despite behavioral thermoregulation abilities, internal temperatures of tagged ATS below both Milford and Lockwood regularly approached and exceeded 20°C, supporting the need for rapid passage through dams in warm, downstream sections of river to upstream cooler temperatures. Moreover, a linear regression of each individual ATS's accumulated thermal units during their delay and the percent of relative energy lost in that same time period strongly supports the conclusion that increased temperatures contribute to greater energy expenditure.

The Distell Fish Fatmeter was an effective way to generate measures of lipid level percentages in our study fish (Crossin and Hinch 2005; Bayse et al. 2018). Similar to other anadromous fish species, salmon first draw energy predominantly from lipid reserves as they migrate upstream (Bayse et al. 2018). We measured our ATS to have lost, on average, 11 to 22% (ranging up to 66%; Table 1.2) of relative energy stores during the time spent below either Milford Dam or Lockwood Dam. This is a substantial portion of available energy reserves being directed to one portion of spawning requirements when they must also be allocated to gonadal investment, development of secondary sexual traits, redd building and guarding, courtship and competition, and spawning (Jonsson and Jonsson 1991; Fenkes et al. 2016). Rivers home to ATS are disturbed by an incredible number of dams (Opperman et al. 2011) so an ATS is likely to encounter several migration barriers during their journey, both natural and anthropogenic (Newton et al. 2018). If we use Glebe and Leggett's (1981) estimate of 60% or less energy expenditure to preserve an iteroparous life history, the fat loss we documented at one dam will contribute to reduced energy substrate available to meet this threshold if applied to cumulative delay experiences.

As might be expected, the relationship we found between accumulated thermal units and percent of fat lost during delay was closely mirrored by the relationship between the time spent in the river and percent of fat lost. Model selection indicated that accumulated thermal units best described fat loss, but the time spent in the river, either as the only variable or in addition to accumulated thermal units were competitive models (see Table 1.3). In order to gain a clearer understanding of the direct role thermal experience plays on energy expenditure in migrating adult ATS, further studies that more deeply parse out the difference between thermal experience and time between captures would be useful.

While we have focused on fish that were delayed, but ultimately successful in passing a dam, it is important to note the number of ATS we captured once but did not pass after approaching the dams. It was surprising to see such a high percentage of tagged fish (14%, 8%, 33%, or 55%; Table 1.1) fail to pass the dam after a first capture. Every fish displayed recovery after tagging and was documented approaching the dams for a second time. The distances from release site to the dams were short (14 and 18 km) and our radio telemetry data indicated that all fish were motivated to move back up river after release and reached the dam within a few days. Though some ATS may have been deterred from re-ascending the fish lift after an experience deemed impassable, all fish displayed directed upstream movement consistent with upstream migration patterns as described by Oakland et al. (2001). Because delay length was significantly longer than approach times, we can assume that some ATS eventually made the decision to forgo passage attempts to either spawn downstream or return to the ocean to spawn again another year. This finding is consistent with many additional studies that have also documented poor dam passage rates of ATS, ranging from 0% (Thorstand et al. 2003) to 63% passage (Gowans et al. 2003; Lundqvist et al. 2008; Karppinen et al. 2002).

Interestingly, we did not find any statistical difference in days spent in river or percentage of fat lost between hatchery reared or wild reared fish. Previous studies have shown that hatchery-reared fish that have been deprived of natural river life as juveniles differ from wild fish in their freshwater migration pattern, typically displaying erratic within-river movement (Thorstad et al. 2011). Because of this, we would have expected that our hatchery reared fish might have exhibited longer times between captures. However, both hatchery and wild fish displayed similar upstream motivation, suggesting that fish stocked as smolts have behavioral potential to reach natural spawning grounds. It would be remiss, however, not to note that our power to detect any difference is hampered by small sample sizes.

Remaining populations of endangered ATS in the United States exist almost entirely in highly dammed rivers, so understanding the impact that dams have on ATS survival and reproduction can be key to the future conservation of the species. Recovery of ATS in Maine depends on the ability of ATS to move upstream quickly during spawning migrations, maintaining sufficient energetic supply to invest in post-spawn survival and potential iteroparity. However, despite restoration efforts, dams continue to be a source of delay. When a dam impedes upstream movement, adult ATS expend a significant portion of their limited available energy on just one of potentially several obstructions to migration. We have shown that delays also expose upstream migrating ATS to warm, downstream waters that can compound energetic impacts of dams, and that there is a strong relationship between a fish's thermal experience and energy loss.

Currently, protection of the species on the Penobscot River is centered on hatchery production and the collection of broodstock rather than the establishment of natural reproduction. ATS are captured at Milford Dam and moved to US FWS Craig Brook National Fish Hatchery. On the Kennebec River, a focus on natural reproduction is supported by a trap and truck fish passage. In the current recovery plan for Maine ATS (U.S. Fish and Wildlife Service and NMFS 2018), there is little focus on ensuring conditions for natural reproduction and post-spawning survival

(and the associated benefits of iteroparity). We know that increasing access to quality habitat benefits diadromous fish species (Wippelhauser 2021). Accordingly, restoration efforts focused on improving rapid access to upstream habitats in highly dammed systems are likely to promote moving fish quickly to cooler waters, thereby reducing the depletion of adult energetic stores, and increasing spawning and post-spawning success.

CHAPTER 2

DAMS MAY FORCE SEMELPARITY IN ATLANTIC SALMON

ABSTRACT

Anadromous Atlantic salmon can survive after spawning to be iteroparous, engaging in multiple reproductive migrations over the course of a lifetime. Iteroparity is thought to be important to the conservation of this critically endangered species, as older females are often larger, with greater fecundity, resulting in greater juvenile recruitment. Currently, repeat spawners on the Penobscot River of Maine (the river with the largest population of returning adult Atlantic salmon in the United States) have been nearly eliminated. By utilizing a bioenergetic model, we sought to understand how delays at dams and corresponding exposure to increased water temperatures may contribute to the loss of iteroparity in spawning populations of Atlantic salmon. We modeled five different Atlantic salmon spawning runs in five hypothetical rivers with either zero, one, two, three, or four dams presenting as migration barriers causing delays in warmer downstream water. We drew data from the Penobscot River for run timing, fish length and observed passage delays. Temperature data were based on observations both in upstream and downstream sites in the Penobscot and Kennebec Rivers. Our results of the model showed that as the number of dams on a river increased, the number of post-spawn surviving Atlantic salmon decreased. Compared to a river without a dam, fish in a river with four dams showed a 56% decrease in survival after spawning, a 53% decrease in the number of one-time spawners, and a 50% increase in the number of salmon that died before having a chance to spawn even a single time. Our results suggest that rapid movement through warmer downstream sections of rivers to upstream, cooler waters is key to successful reproduction and survival in spawning Atlantic salmon.

INTRODUCTION

Atlantic salmon (ATS) populations in the United States are critically endangered. The species that once returned to nearly every major river north of the Hudson River in numbers approaching 500,000 are now only found in Maine rivers at numbers as low as 500 to 2,000 fish annually (Fay et al. 2006). Dams have been identified as one of the major causes of this demographic decline (NOAA Fisheries 2016). It is likely that insufficient energy at spawning might be one repercussion of dams contributing to the decline of ATS in Maine rivers. Understanding the constraints of energy allocation may help managers evaluate the extent to which increased energetic costs might limit successful reproduction in vulnerable salmonid populations (Bowerman et al. 2017).

Anadromous salmon begin their lives in freshwater, hatching from eggs deposited in cold headwater streams. These fish later transition to the marine environment at the “smolt” stage, where they grow to sexual maturity for a number of years before homing back to their natal streams to spawn, lay eggs, and begin the cycle again. Following spawning, adult ATS can survive to be iteroparous, a life history strategy characterized by multiple reproductive cycles over the course of a lifetime (Fleming 1996).

Upstream migrations of adult ATS in unimpounded rivers can conceptually be divided into three stages prior to spawning. First, an initial freshwater entry starts a steady progress upriver until reaching a spawning area. Second, upon reaching the spawning area, ATS will engage in searching movements up and downriver, likely scouting for natal spawning grounds or thermal refugia (Økland et al. 2001). Lastly, the migration period concludes with a long, over-summering residence period in or near the spawning area until environmental cues commence active spawning (Økland et al. 2001). The entirety of the spawning process, including upstream migrations, is energetically costly. ATS are thought to cease feeding in freshwater. Therefore, all

of the energy required for migrations must be derived from reserves stored in somatic and visceral tissue while at sea. During the initial upstream migration, fish may travel between 2 and 31 km per day for a period ranging from as short as a week to more than a month for individual fish (Thorstad et al. 2011). Energetic constraints detrimental to reproduction may occur when the energy expended during migrations exceeds the energy stored (Bernatchez and Dodson et al. 1987). Energy must be allocated among demanding requirements of migration: gonadal maturation, spawning behaviors, and (in the case of Atlantic salmon) a potential return-to-ocean, downstream migration (Nadeau et al. 2010). As such, the upstream movement phase of spawning is long, arduous, and costly, and any excess energy use during any one process will cause energy allotments to other essential processes to suffer.

Migrating adults in an undisturbed river face many challenges that may alter their migration patterns including natural barriers, environmental circumstances, and physiological conditions (Thorstad et al. 2008; Shepard 1995). Anthropogenic changes, including the presence of dams, can compound these challenges. Delays at dams during ATS upstream movements have been widely documented (Izzo et al. 2016, Thorstad et al. 2003; Gowans et al. 2003; Lundqvist et al. 2008; Karppinen et al. 2002). Substantial delays as ATS locate and ascend fish ways can lead to decreased energy reserves through consequences such as extended migration periods (Bowerman et al. 2017) and exposure to increased water temperatures (Rubenstein, Chapter 1). During peak summer months, when most ATS are engaging in their upstream migrations, water temperatures just below surface-release dams have been documented to be significantly warmer than upstream waters in the same river, a pattern persisting for long distances downstream of the dam (Zaidel et al. 2021).

Because ATS are ectotherms, ambient water temperature directly reflects thermal experience, impacting every biological process including the rates of enzymatic, metabolic, and cardiac

processes (Lennox et al. 2018). ATS have a temperature optimum range (estimated near 15-18°C in juveniles) at which point aerobic scope is greatest. Outside that optimum range, aerobic scope decreases until a lethal thermal limit is reached, estimated near 28°C in juveniles but likely lower for adults (Elliott and Elliott 2010; Frechette et al. 2018). At these higher water temperatures, an increasing proportion of available energy is diverted to maintenance of metabolism, reducing the energy available for remaining migration needs and spawning activities (Martin et al. 2015). This sensitivity to high temperatures is heightened with additional metabolic demand, stemming from the need to ascend fish passage structures. The ability to repeatedly swim at burst speeds and the ability to recover are crucial for migrating adult salmon navigating demanding sections of river characterized by natural and anthropogenic barriers, but burst swimming abilities and recovery are compromised at higher temperatures (Brett 1995; Wilkie et al. 1997). As temperatures exceed the optimum range for ATS, the tissue demands for oxygen increase, but the capacity to deliver that oxygen decreases, thus warm waters become energetically taxing (Lennox et al. 2018).

Previous research of ATS delayed below dams has shown that time spent below dams exposes fish to warmer thermal experiences than if those salmon were allowed rapid, efficient passage to cooler upstream waters (Rubenstein, Chapter 1), translating to increased energy expenditure over time. ATS delayed below only a single dam sometimes experienced losses exceeding 60% of initial lipid stores (Rubenstein, Chapter 1). This loss is a considerable fraction of available energy reserves being directed to one small portion of a long migration and numerous spawning activities. In fact, Glebe and Leggett (1981) estimated that anadromous fish engaging in iteroparity must expend 60% or less of endogenous energy from freshwater entry to post-spawning in order to survive and return to the ocean to recondition. In contrast, it has been reported in semelparous Pacific salmon that energy estimates post-spawning (i.e., at death) range from 80 to 92% (Bowerman et al. 2017). Spawning behaviors alone (i.e., holding, digging,

competition, spawning, etc.) can represent greater than 50% of expenditure of initial energy reserves (Bowerman et al. 2017). Given the potential for iteroparity in ATS, reducing the percentage of energy stores spent during migration may have profound implications for individual reproductive success as well as population demographics (Maynard et al. 2017).

Many ATS rivers are highly dammed systems so adults are likely to encounter several migration barriers (and therefore delays), both natural and anthropogenic, during their upstream journey. These encounters can extend migration period or trap fish in suboptimal habitat. Either case exposes fish to warmer water temperatures, thereby multiplying energetic losses attributed to delays and thereby risking energy depletion that exceeds the iteroparous/semelparous threshold (Newton et al. 2018; Ferguson et al. 2011). By utilizing a bioenergetic model, we intend to increase understanding of energy allocation in the context of delays at dams and corresponding water temperatures in ATS spawning migrations. We also performed field validation of our model using a Distell Fish Fatmeter as a metric of lipid stores in Penobscot River, Maine, salmon. Our objectives in this study were to (i) document the difference in thermal regimes between upstream sections of river and below dam sections of river, (ii) model ATS loss of energetic stores during upstream migrations on dammed rivers, and (iii) use in-field energetic metrics to validate the model.

METHODS

Overview – We modeled five different ATS spawning runs in five different rivers. 20,000 fish were allowed to ascend each modeled river that had either zero, one, two, three, or four dams presenting as migration barriers. Freshwater entry dates, ATS length, and ATS mass varied for each individual. Anytime an ATS approached a dam during its migration, it was subjected to a delay of varied length, keeping the fish downstream in warmer waters. Once a salmon passed every dam on its river, it was allowed to hold in cooler upstream waters until the start of active

spawning. During migration, every fish underwent a daily energetic loss, informed by fish size and environmental temperature. At the end of the model, we were left with remaining energetic status after completing an upstream spawning run.

Bioenergetics modeling – To estimate the theoretical amount of energy lost during an upstream spawning migration, we used equations derived from Lennox et al. (2018) to model adult ATS migrating up a river with zero, one, two, three, or four dams. Using hatchery ATS, Lennox et al. (2018) generated an oxygen consumption equation for salmon moving slowly (0.3 body lengths [bl]/s; Bernatchz and Dodson 1987 estimated an average swim speed of 0.1 bl/s for ATS migrating from river mouth to spawning grounds), returned in $\text{mg O}_2 \text{ kg}^{-1} \text{ min}^{-1}$:

$$(1) \text{mgO}_2 \text{kg}^{-1} \text{min}^{-1} = 0.45 \times e^{0.07 \times T},$$

where T is the ambient water temperature ($^{\circ}\text{C}$). By multiplying that equation by body mass (kg) and 1,440 (min/day) we converted the output to $\text{O}_2 \text{ day}^{-1}$. We then converted respiration rate into joules (J) by using standard oxycaloric values ($14.1 \text{ J mgO}_2^{-1}$) as reported by Hein and Keirsted (2012). The final equation to describe the change in energy per day (in joules), with T as ambient water temperature ($^{\circ}\text{C}$) and W as body mass (kg) was:

$$(2) \Delta E_D = 0.45 \times e^{0.07 \times T} \times W \times 1440 \times 14.1.$$

This equation was applied to individual fish for each day spent in the river to calculate a change in energy content per day.

The model was initiated for each fish on an entry date (i), or the day of year that the salmon entered freshwater, randomly selected from an array of dates compiled from average catch numbers per day of the year at Milford Dam (Penobscot River, Maine) from 2014 to 2019. Milford Dam, at river kilometer 61, is the most downstream barrier to ATS migrating upstream on the main stem Penobscot (Figure 2.1). Milford Dam operates a fish lift and fish sorting facility on the turbine side of the dam. The lift traps fish within a hopper that is lifted to release the fish into an upper flume guiding them to a trap and handling facility operated by the Maine Department of Marine Resources (MEDMR). The lift is operated from mid-April to mid-November (Izzo et al. 2016). Late season salmon arriving after the bulk of the run had passed through the dam were emitted from the array because we could not assume that they were representative of fresh ocean fish (could have been fish that ascended the dam once and had fallen back, had approached the dam but had not passed, etc.). A spawning date was arbitrarily assigned as a day in early November, selected based on the artificial, but temperature informed, spawning schedule of adult ATS at the US Fish and Wildlife Service, Craig Brook National Fish Hatchery in East Orland, Maine. The model stopped on that spawning date (day “ s ”). Total energy expended (E_{lost} in joules) was simply the sum of daily energy losses (ΔE_D) for the length of time spent in the river (from entry date [i] to spawning date [s]):

$$(3) E_{lost} = \sum_i^s \Delta E_D$$

ATS catch data from Milford Dam includes total lengths. We used length/mass tables from Fisheries and Oceans Canada (Canada 2021) and River Tweed Commission (Commission n.d.) to calculate an average regression equation,

$$(4) W = 0.0015L^2 - 0.0398L - 0.419$$

with W = mass (kg) and L = total length (cm), allowing us to convert known length data from Penobscot River salmon to kilograms to inform our bioenergetic equation.

The result of the bioenergetic model was a proportion of initial energy lost during the upstream, freshwater portion of the spawning migration. The energy content (in joules) of each modeled salmon as it first entered freshwater ($E_{initial}$) was calculated by an equation from Lennox et al. (2018):

$$(5) E_{initial} = e^{0.044 \times L + 6.99} \times 100$$

and, after the model completed, final energy content (in joules) was simply

$$(6) E_{final} = E_{initial} - E_{lost}$$

The proportion of initial energy lost was

$$(7) E_{proportion} = \frac{E_{initial} - E_{final}}{E_{initial}}$$

Each iteration of the model (from zero dams to four dams) was run for 20,000 fish. For each of the five simulated rivers, we calculated the proportion of fish that could be assumed to have spawned and survived (energy loss < 0.60), spawned and died (energy loss > 0.60 and < 0.80), or died before spawning (energy loss > 0.80) based on the physiological thresholds of 60% and 80% energy loss as proposed by Glebe and Leggett (1981) and Bowerman et al. (2017). We used those thresholds to break the modeled spawning populations into three categories: 1)

finished the migration with enough remaining energy to survive post spawn, 2) finished the migration with enough energy to spawn but not to survive post spawning, or 3) could not complete the migration or suffered mortality before spawning.

Temperature experience – We used two temperatures to inform the temperature variable in Equation 2. In 2018 and 2019 we deployed sets of temperature loggers (Hobo Water Temperature Pro v2 Data Loggers; resolution of 0.02°C at 25°C and an accuracy of 0.21° from 0 to 50°C) in the Penobscot River of central Maine. We had one logger below Milford Dam, where delays are known to occur during upstream movements (Izzo et al. 2016), and one logger in an upstream tributary of the Penobscot River where a salmon might over-summer pre-spawning if given unimpeded access to the river (Figure 2.1). Loggers remained in the river from early May until the start of ice formation (late November/early December).

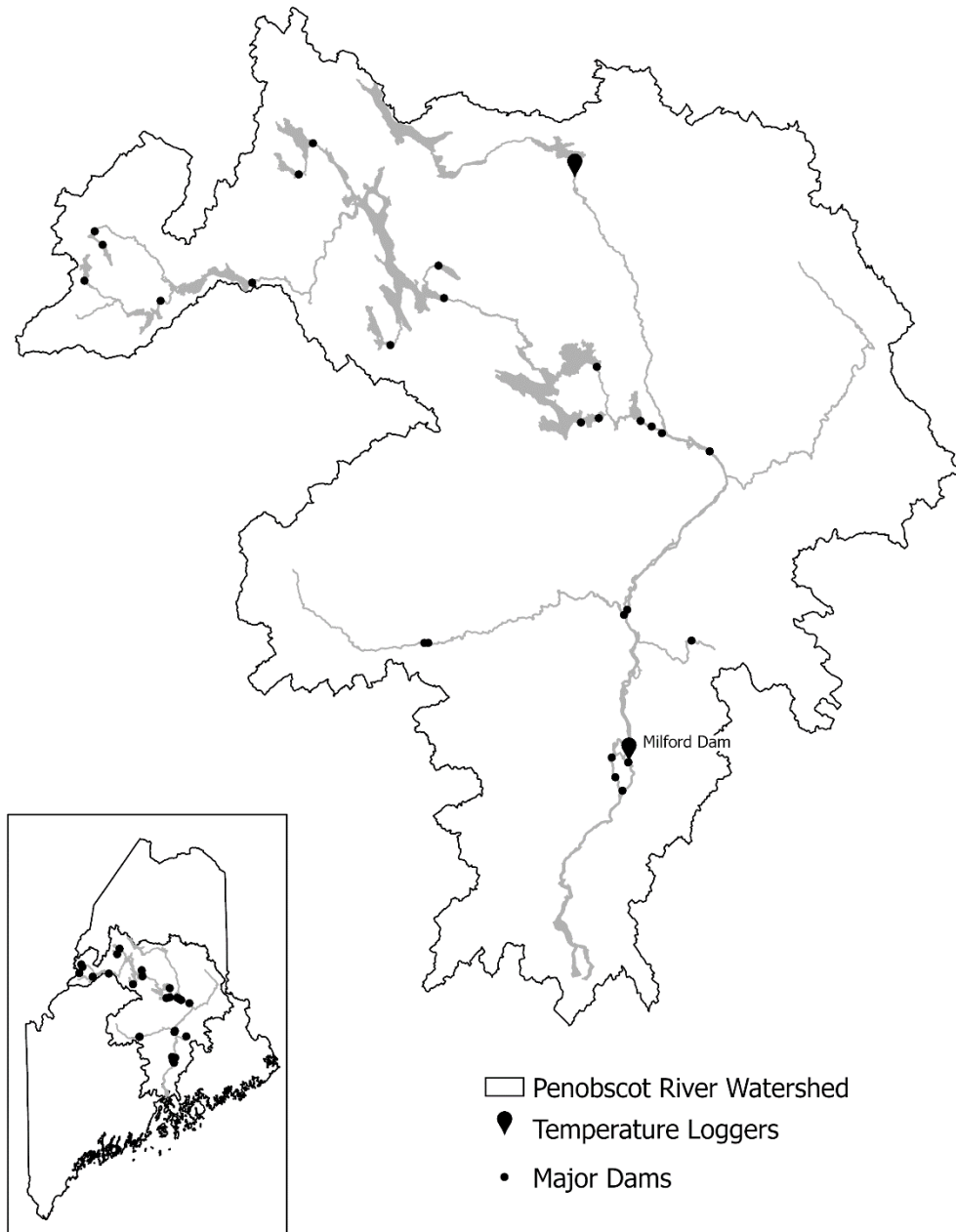


Figure 2.1. Map of the Penobscot River with Milford Dam at river kilometer 61. Other lower stem dams and our upstream and downstream temperature loggers are shown.

Delay experience at dam – The temperature used in the bioenergetic equation (either below dam or upstream temperature) was dependent on whether a fish was considered delayed or not while in the model. For each fish at each dam in a simulation, a random length of delay was selected from an array of delays of previously studied salmon on the Penobscot River at Milford

Dam, from 2014 to 2019. During the length of that delay, the below dam temperature was applied to the equation for each day. Once that fish was considered to have passed the dam (i.e., after the length of delay was complete), the upstream temperature was applied to the equation. On the river with zero dams, each fish was considered to have been delayed for only one day to represent the time spent moving through the lower river before reaching lower temperatures. After that initial day at below dam temperatures, all fish on the unimpeded river experienced upstream temperatures for the remainder of their stay in freshwater. On rivers with multiple dams, a length of delay was selected for each fish. Those delays were totaled and the below dam temperature was applied for the entirety of all delays. A summary of the model is represented by Figure 2.2.

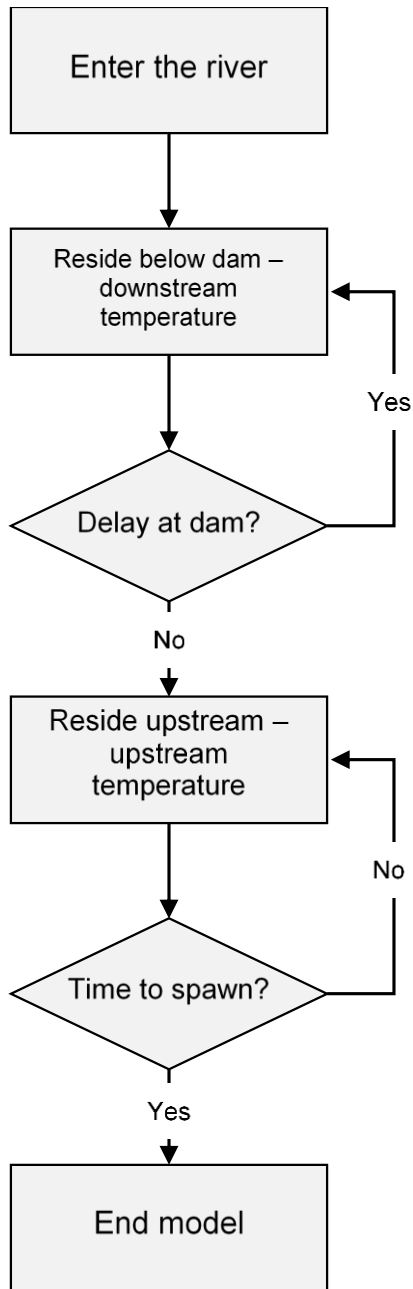


Figure 2.2. A flow chart of the model for each theoretical system. A fish enters the river, resides below the dam at the downstream temperature for a period of delay before moving up river to reside at upstream temperatures until active spawning begins.

Field validation – Our in-field measurements came from ATS on the Penobscot River, Maine. As described in Chapter 1, adult ATS were collected from the Milford Dam trap in 2019. Each individual was measured for a total length and gastrically tagged with a temperature logging

Lotek archival radio tag (MCFT3-L; 30g and 16x85mm; 2.5-s burst rate). An initial estimation of whole-body energy concentration was determined using a Distell Model 692 Fish Fatmeter (Distell Inc, West Lothian, Scotland). After tagging and measurements, salmon recovered in an aerated tank of ambient river water and, post-recovery, were transported back downstream for release, approximately 18 km below Milford Dam. Tagged salmon navigated their way back upstream to Milford Dam and re-ascended the fish lift. A second fat content measurement was made with the fatmeter, the tag was removed from the fish, and the thermal data was downloaded. The end result was two fat measurements (providing a change in relative lipid content) and a thermal experience across a period of time spent below the dam.

A simple linear regression was performed between total modeled energetic loss (joules) and the proportion of fat lost (fat meter %) to evaluate the bioenergetic equation derived from Lennox et al. (2018). The energy lost per day (in joules) was calculated for the field measured fish during their associated delays using Equation 2. Temperature input came from the average daily temperature logged from the temperature-logging radio tags. The results for each day were added together for a total energetic loss during residence below Milford Dam. The proportion of fat lost was defined simply as

$$(5) \Delta_{fat} = \frac{fat_1 - fat_2}{fat_1}$$

with fat_1 and fat_2 as first and second fat measurements, respectively.

RESULTS

Model inputs – River temperatures downloaded from the Hobo temperature loggers placed in the upper and lower reaches of the Penobscot River very clearly exemplify the difference

between thermal environments. On average, the upstream section of the Penobscot River remained more than 3°C cooler than the lower river below the dam. The maximum summer temperature reached below the dam was 27.6°C. Conversely, the maximum summer temperature reached upstream was 25.2°C (see Figure 2.3).

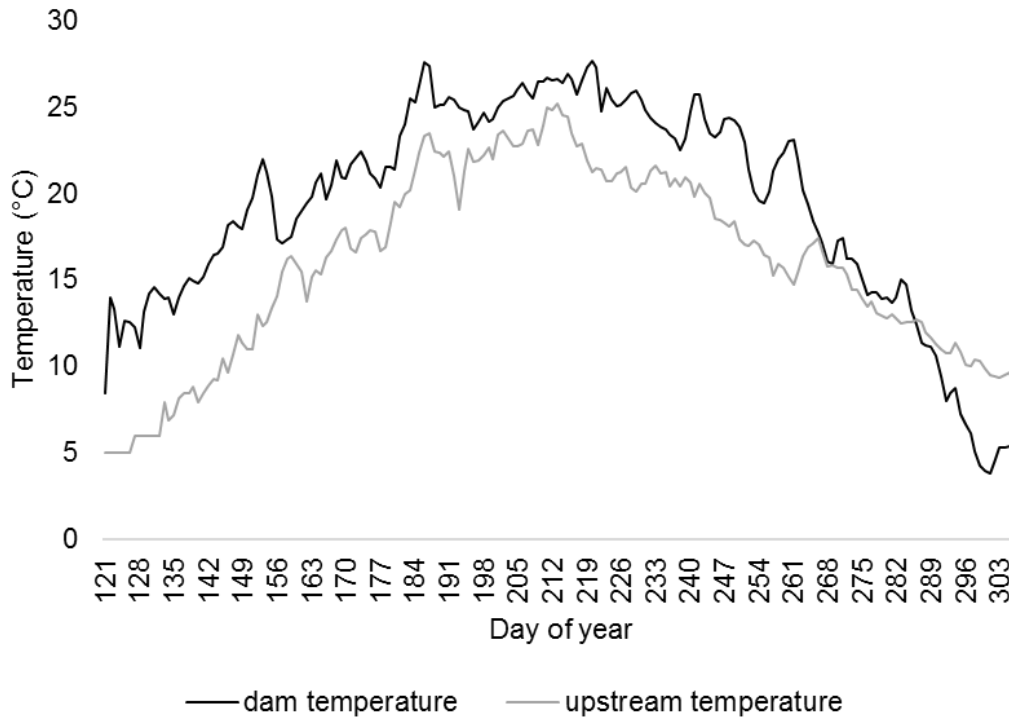


Figure 2.3. The Penobscot River temperature ranges throughout the summer just below Milford Dam (black) and in an upstream (gray) section of river

Data to inform the bioenergetic model, including river entry date, total length (and corresponding mass), and delay length, was composed from historical data of previously studied ATS returning to Milford Dam on the Penobscot River from 2014 to 2019. Entry dates ranged from day 125 to day 310 (average = day 189) to represent the bulk of the summer return (Figure 2.4). Salmon total lengths, from 222 ATS, ranged from 52 to 92 cm with an average of 75 cm. Delay lengths below Milford Dam, from 159 previously studied salmon, ranged from no delay (i.e., 0 days) to 155 days (average = 12 days).

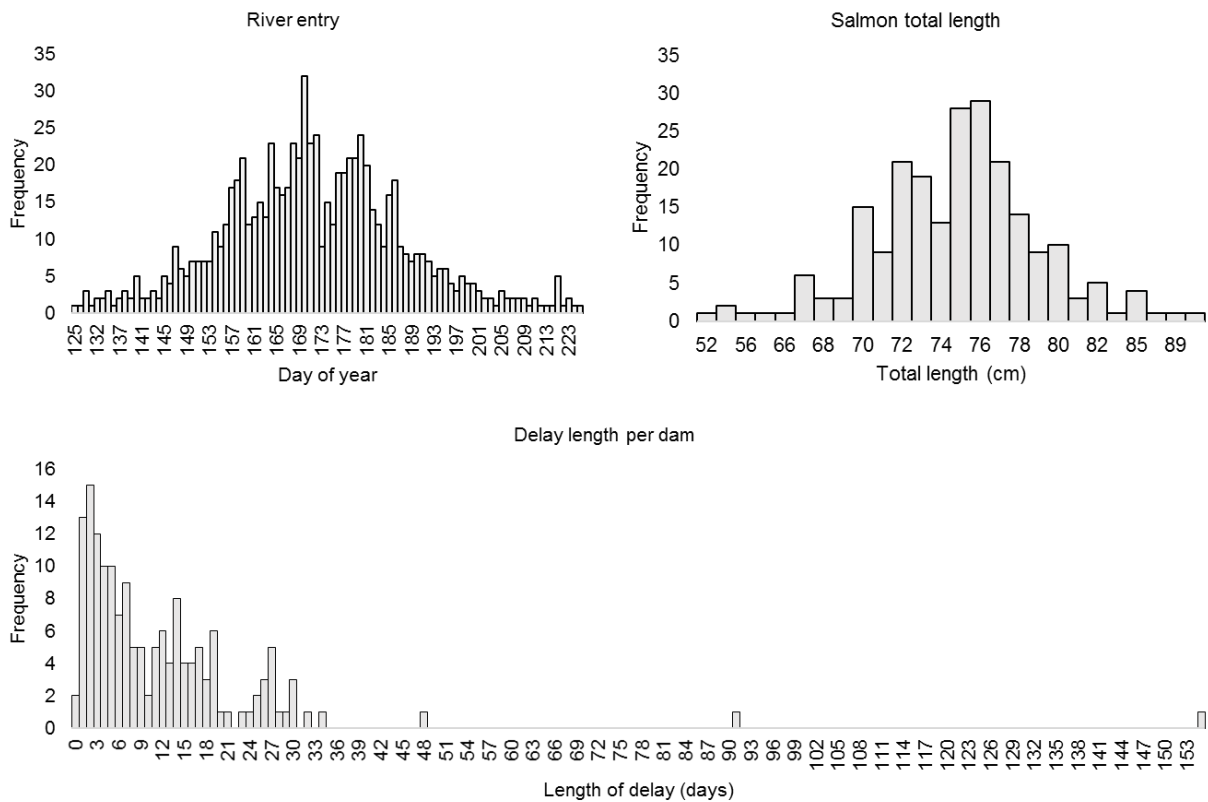


Figure 2.4. Histograms of historical data of salmon total lengths, delay lengths, and entry dates on the Penobscot River that were used to inform the bioenergetic model.

Energetics – Results of the model found that as the number of dams on a river increased, so did the proportion of the salmon run that died before spawning. On an unimpeded river, 6.3% of the returning run should have enough energy to survive after spawning, 59.2% of the run would have enough energy to spawn once (for a total of 65.5% of the spawning run completing successful reproduction), and 34.6% of the run suffering premature mortality before engaging in active spawning (see Figure 2.5). Alternatively, on a river with four dams, 2.8% of the returning salmon run have the opportunity to survive after spawning, 27.9% of the run have the remaining energy to spawn and die (for a total of only 30.7% of the run able to reproduce), and 69.3% of the run do not have sufficient energy reserves after the upstream migration to spawn at all (Figure 2.5). This pattern of decreasing post-spawn survival, decreasing successful

reproduction, and increasing pre-spawn mortality was consistent as dams were added to the modeled river systems.

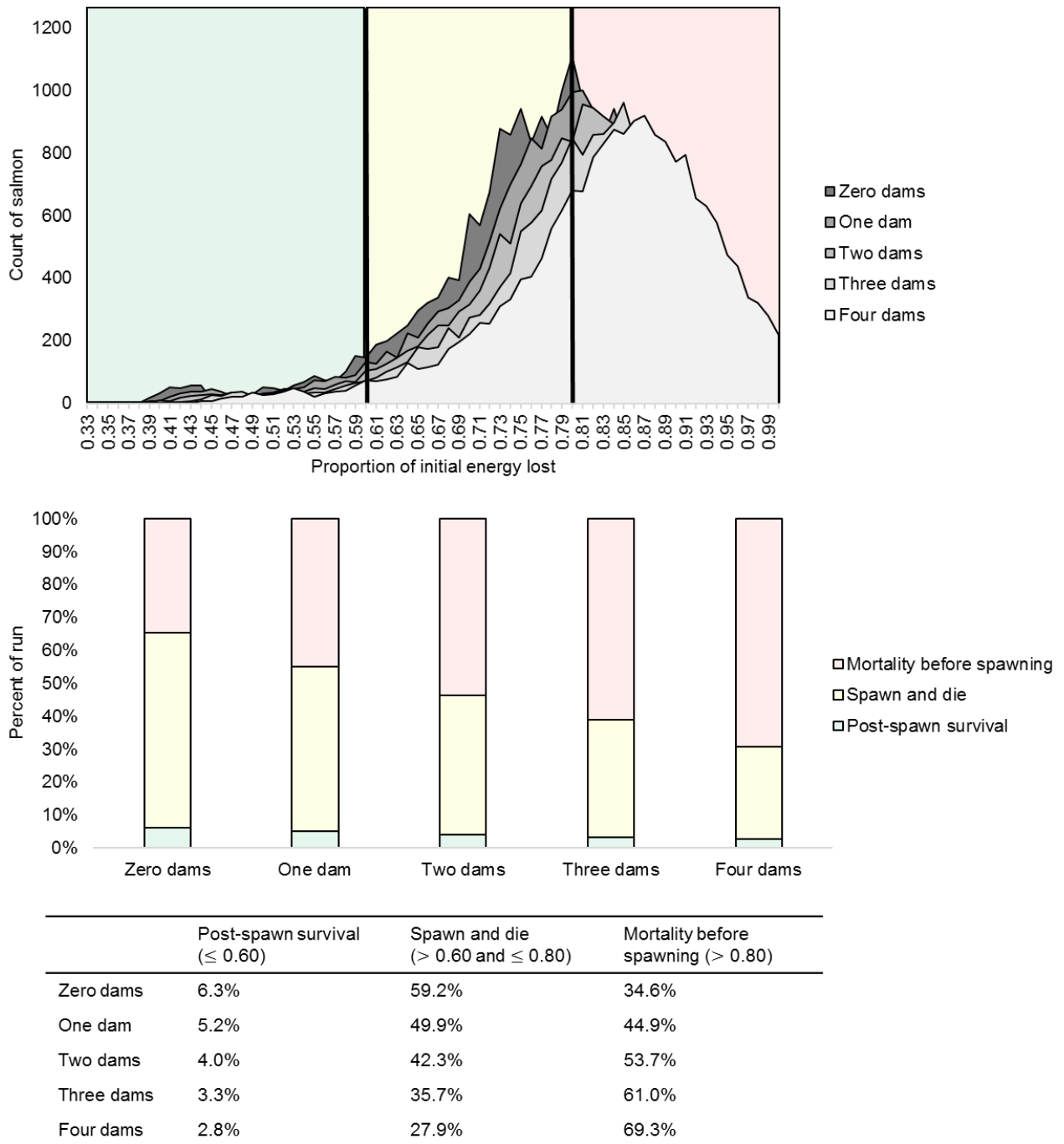


Figure 2.5. The results of the bioenergetic model using Penobscot River temperatures: the top panel shows a histogram of the proportion of initial energy lost for every modeled salmon on each of the five river scenarios (zero, one, two, three, and four dams). The solid black lines at 0.60 and 0.80 represent the cut-offs for the potential to survive post-spawning (green) or to die pre-spawning (red), respectively. The middle panel shows the percent of the run on each river that either dies pre-spawning (red), is able to spawn but dies afterward (yellow), or has enough remaining energy to survive post-spawning (green). The bottom panel is a table with the percent of the run that falls into each category.

The post-spawn survival percentages on a river with no dams (6.3%) seemed low in comparison to previous literature reports of 11% of spawning adults, on average, surviving after spawning (Ducharme 1969). The Penobscot River reaches warm summer temperatures, even in upstream sections of river. After running the model with Penobscot River temperatures, we repeated the model keeping everything the same but using river temperatures from the Kennebec River of central Maine. The Kennebec River remains slightly cooler throughout peak summer months (see Figure 2.6). The maximum summer temperature below the dam reached 26.3°C while the summer temperature in upstream sections of river reached a maximum of 24.2°C. The differences in maximum temperatures between the two rivers was only 1.3°C below the dams and 1.0°C upstream.

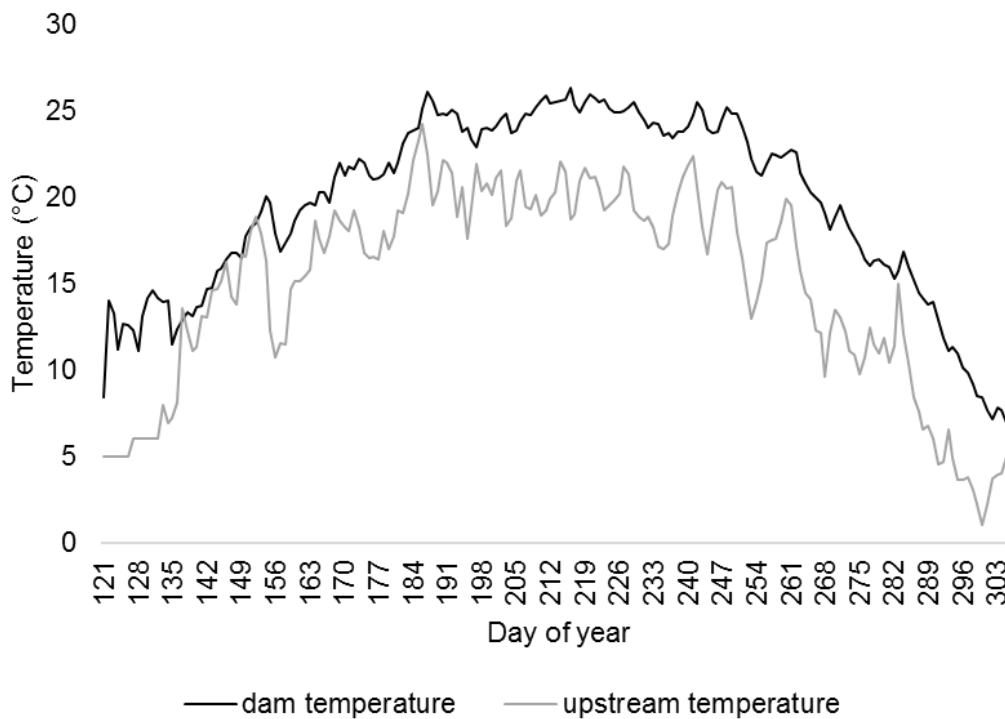
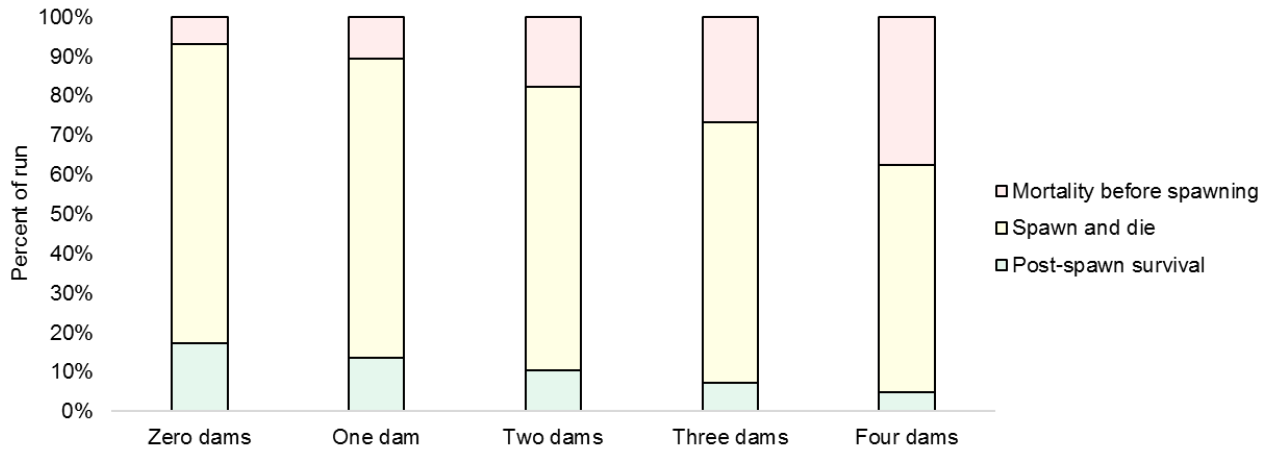


Figure 2.6. The Kennebec River temperature ranges throughout the summer just below Lockwood Dam (the first passage barrier to upstream migrating salmon on the Kennebec River; black) and in an upstream (gray) section of river

Results of the model using the cooler river temperatures followed the same pattern (decreased post-spawn survival, decreased spawning success, and increased mortality before spawning with the addition of dams) as the previous model for all scenarios. However, the overall proportion of the runs with the potential to survive post-spawn and to achieve at least one successful reproductive event increased while the proportion of mortalities before spawning decreased (Figure 2.7). On a river with no dams, 17.4% of the returning run should have enough energy to survive after spawning (in contrast to the 6.3% using slightly warmer water temperatures), 75.6% of the run should have enough energy to spawn once (for a total of 93.0% of the spawning run completing successful reproduction), and only 7.0% of the run (34.6% in the previous model) is predicted to suffer a mortality before engaging in active spawning (see Figure 2.7). On a river with four dams, 4.9% of the returning adults might survive after spawning, 57.7% of the run have the remaining energy to spawn and die (for a total of 62.6% of the run able to spawn at least once), and only 37.4% of the run was predicted to not have sufficient energy reserves after the upstream migration to spawn at all.



	Post-spawn survival (≤ 0.60)	Spawn and die (> 0.60 and ≤ 0.80)	Mortality before spawning (> 0.80)
Zero dams	17.4%	75.6%	7.0%
One dam	13.6%	75.9%	10.5%
Two dams	10.4%	72.0%	17.6%
Three dams	7.2%	66.1%	26.7%
Four dams	4.9%	57.7%	37.4%

Figure 2.7. The results of the bioenergetic model using Kennebec River temperatures: the top panel shows the percent of the run on each river that either dies pre-spawning (red), is able to spawn but dies afterward (yellow), or has enough remaining energy to survive post-spawning (green). The bottom panel is a table with the percent of the run that falls into each category.

Field validation – we collected in-field thermal experience and fat measurements for 11 adult ATS in the 2019 field season. Each of those fish was captured at Milford Dam on the same day (June 7) but experienced different lengths of delays (average 15.3 days; range 4-33 days, Table 2.1) between captures. Using the fat percentages collected at capture (initial) and recapture (final) of the salmon, we were able to determine a change in fat percentage that was lost during the delay (see Table 2.1). We performed a simple linear regression between the percent fat change measured by the Fatmeter and a percent energy change as determined from the bioenergetic equation outlined from Lennox et al. (2018). Results of the regression established the bioenergetic equation as a good predictor of the fat changes measured in the field, validating the equation for the model ($R^2 = 0.85$; Figure 2.8).

Table 2.1. Atlantic salmon from the Penobscot River that were handled in-field and used for Distell Fish Fatmeter readings to compare to our model equation.

Fish	Capture date	Recapture date	Days delayed	Capture fat (%)	Recapture fat (%)	Change in fat (%)	Proportion of fat lost (change/capture)
ATS – 1	June 7	June 11	4	5.4	5.3	0.1	0.02
ATS – 2	June 7	June 17	10	6.2	4.9	1.3	0.21
ATS – 3	June 7	June 17	10	6.8	6.2	0.6	0.09
ATS – 4	June 7	June 12	5	5.8	4.8	1.0	0.17
ATS – 5	June 7	July 6	29	6.4	4.1	2.3	0.36
ATS – 6	June 7	June 14	7	1.9	1.6	0.3	0.16
ATS – 7	June 7	June 17	10	7.0	6.0	1.0	0.14
ATS – 8	June 7	June 17	10	7.8	7.2	0.6	0.08
ATS – 9	June 7	June 30	23	6.0	4.5	1.5	0.25
ATS – 10	June 7	July 4	27	4.6	2.2	2.4	0.52
ATS – 11	June 7	July 10	33	7.3	3.1	4.2	0.58

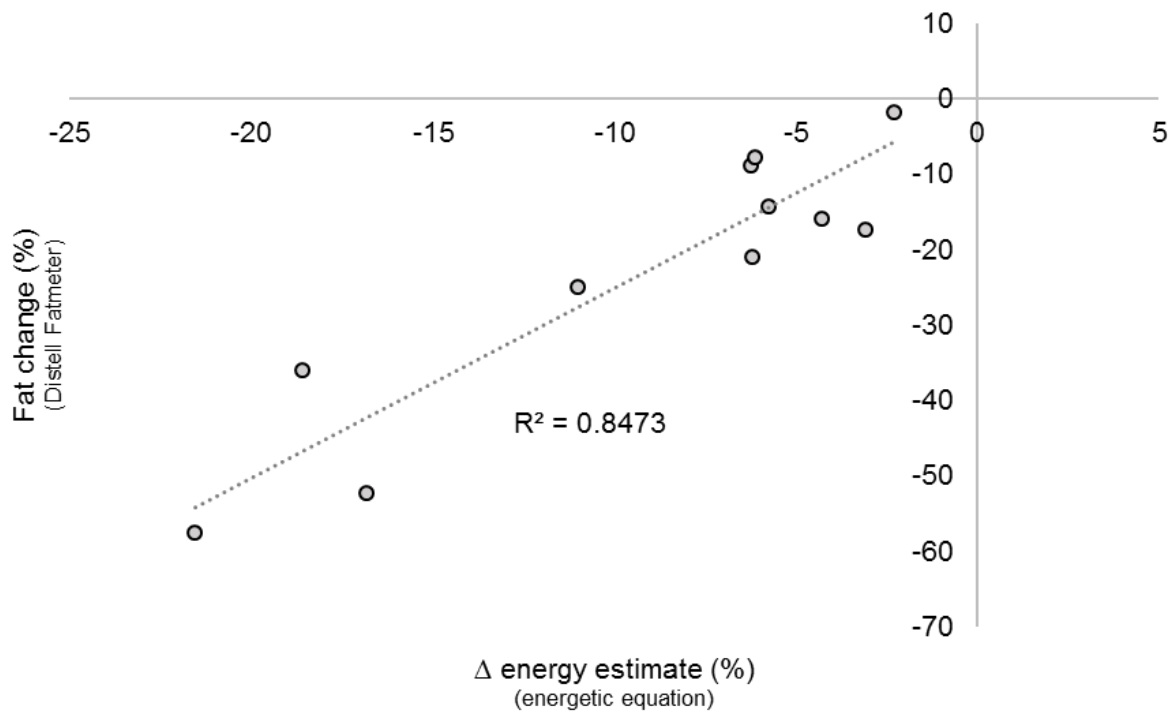


Figure 2.8. A simple linear regression to compare the in-field energetic depletions with modeled energetic depletions.

DISCUSSION

The energy loss during ATS upstream migrations comprises a significant portion of endogenous reserves (Jonsson and Jonsson 1997), and the longer a fish is in the river, either from distance to spawning grounds or delays, the greater the energy use will be (Mesa and Magie 2006). We modeled a spawning population migrating up an undisturbed river and found that most (~60%) of the individuals used between 60 and 80% of initial energetic reserves, a finding consistent with other energetic estimates of spawning ATS (Jonsson and Jonsson 1997). Based on literature of semelparous Pacific salmon, increasing that proportion of energetic beyond 80% puts ATS at risk for pre-spawning mortality (Bowerman et al. 2017). As such, in order to ensure a successful reproductive event, ATS must move quickly to upstream spawning grounds and minimize any excessive energy expenditure.

Remaining ATS populations in the United States exist almost entirely in highly dammed systems. Several studies have emphasized the detrimental impact of dams through, including delay, on the freshwater migration portion of the ATS spawning run (Bunt et al. 2012; Roscoe et al. 2011; Ferguson et al. 2011; Caudill et al. 2007; Izzo et al. 2016). Literature has also outlined that dams cause changes to the thermal environment of rivers (Zaidel et al. 2021; Chapter 1), creating stark temperature differences between free-flowing upstream sections of river and below-dam sections of river. We were also able to support this with evidence from our temperature loggers placed within the river. Consequently, when dams cause delays to upstream migrating fish, those fish are subjected to warmer thermal experiences for longer than if they had moved quickly upstream.

ATS are ectotherms with a range of optimum temperatures, so warmer thermal experiences outside of that range will have negative energetic consequences (Frechette et al. 2018). Our model focused on the impact of an increased thermal experience caused by dams to migrating

ATS populations and found that on a river with zero dams, almost 35% of the population is at risk of pre-spawning mortality. If one dam is added to the system and adds a delay that keeps ATS in warmer temperatures for longer, that number increases to 45% of the spawning population dying before reproduction. Suggesting that ATS will encounter only one dam is conservative, because migrating fish in Maine will likely encounter several dams in their journey upstream (Figure 2.2). If two, three, or four dams are added to our modeled river, the percent of the spawning population at risk of pre-spawn mortality increases to 54%, 61%, and almost 70%, respectively, of the population. Unless egg and juvenile survival is exceptionally high, increased pre-spawning mortality rates in ATS are likely to have a substantial negative effect on conservation efforts (Keefer et al. 2010).

Another consequence of dams and cumulative delay experiences is the loss of iteroparity from the spawning population and a decrease in egg fitness. ATS must preserve enough energy after spawning for a return to the ocean where it can begin reconditioning for another migration and reproduction event. Literature has suggested that ATS populations display various degrees of iteroparity ranging from 1-43% (average: 11%) of returning adult runs (Fleming 1998). However, despite their relatively low occurrence, repeat spawners make considerable contributions to annual reproduction. Multi-year fish are often majority female (Niemela et al. 2000; Halttunen 2011) and older, which generally corresponds to larger body sizes and translates into high fecundity (i.e., greater fitness), thereby contributing a greater proportion of population recruitment (Maynard et al. 2018; Hixon et al. 2014; Fleming 1996). Presently, the number of repeat spawners on the Penobscot River of Maine has been nearly eliminated, last estimated at 0.6% of the returning adult run (Maynard et al. 2017). Our model using Penobscot River temperatures predicted only 6.3% of the returning ATS run on an unimpeded river would be able to survive post-spawn and return a following year. That number is at a lower percentage than the average rate of iteroparity in other populations (Fleming 1998), and continuous to drop

severely with each dam added as a barrier on the river. At four dams, we estimated the rate of iteroparity to drop to only 2.8% of the returning run. As the number of dams increases on the river, the amount of energy expended for each individual ATS during migration increases, and that excess cost becomes manifested in decreased post-spawn survival and iteroparity rates. This decline in iteroparity rates is likely to express itself in poor recruitment rates.

Recent studies have shown that even at relatively low numbers to the rest of the spawning population, female repeat spawners produce a high number of larger eggs (Hixon et al. 2014; Bordeleau et al. 2019). Female age and size has been linked to energy reserves (Hixon et al. 2014), so iteroparous ATS have more resources to apply to reproduction, often resulting in greater embryo and fry fitness. In effect, Reid and Chaput (2012) noted that female ATS spawning in multiple consecutive years had smaller eggs than females that missed a year of spawning, seemingly to allow for an acquisition of more endogenous energy, supporting the correlation between high energy content and fitness. This effect is pronounced even more so during periods of low first-time spawner returns and of low post-smolt survival and recruitment, with multi-year fish accounting for 11.9-18.5% of all spawners but contributing 18.2-35.3% of all eggs (Bordeleau et al. 2019). Larger iteroparous individuals have the potential to become a vital defense against poor recruitment and act as mitigation to some threats to ATS persistence (Bordeleau et al. 2019; Niemela et al. 2006; Saunders and Schom 1985).

Notably, the second model (Model 2), using the cooler Kennebec River temperatures, resulted in substantial shifts in spawning population percentages for post-spawn surviving adults, for single spawning events followed by mortality, and for mortalities before spawning. On a river interrupted by four dams, Model 2 with cooler temperatures resulted in a 75% increase in survival after spawning, a 107% increase in the number of one-time spawners, and a 46% decrease in the number of salmon that died before having a chance to spawn even a single

time. The temperature differential between upstream and below-dam sections of river during peak summer months was greater and sustained longer in the Kennebec River than in the Penobscot River. There are two relevant conclusions to draw from this: (1) ATS benefit from even slight temperature differences when sustained over a period of time, and (2) rapid ascent into cooler waters provides greater survival up to and through spawning, as well as a greater probability of surviving to return to the ocean for potential repeat spawning.

The losses we see to the spawning population from both iterations of the model are representative of thermal effects only. Warm impoundment waters directly above a dam result in warmer temperatures immediately downstream (Zaidel et al. 2021) in areas where ATS reside during the length of a delay below a fish way (Izzo et al. 2016). We confirmed this pattern in our study area with our two temperature loggers placed in upstream and downstream sections of river; upstream waters were consistently cooler during the peak summer temperatures corresponding with the salmon run. In order to explore only thermal impacts of delays at dams, temperature was the only environmental variable we altered in our model. However, this could suggest that the energetic losses we predicted for our theoretical study ATS might actually be an underestimation. ATS are likely to experience various other energy intensive challenges, both physical and environmental, as they navigate the freshwater portion of their migration, including injury and post-passage consequences from fish ways and dam passage, water discharge and quality, natural migration barriers, intraspecific competition, freshwater diseases, etc. (Thorstad et al. 2008; Roscoe et al. 2011). Any additional challenges will further amplify energetic expenditure during the freshwater migration and compound the effects on the viable reproducing population. Additionally, our equation (Equation 2) derived from Lennox et al. (2018) was for slow moving ATS (swimming at 0.3 bl/s), but fish below a dam are engaging in daily searches for thermal refugia (Frechette et al. 2018) and are navigating and ascending a

passage structure so are likely to periodically engage in burst swimming behavior, further amplifying energy expenditure.

We modeled the impact of dams on spawning ATS populations in the exclusive context of thermal experience on energetic cost, and showed not only the detrimental impact of a single dam added to a system, but also the cumulative effects of multiple dams. Our projected numbers are likely underestimations for two reasons: (1) the energetic equation was intended for ATS at slow speeds, and (2) other energetic constraints that might occur in freshwater are not considered (i.e., disease, competition, etc.). Additionally, ongoing increases in summer temperature in future years may signify an increasingly energetically demanding freshwater migration. Most remaining ATS habitat in the United States exists solely on highly dammed systems. More than 90% of rivers and streams supporting the current population of migrating ATS remain constrained by dams with over 400 dams existing along these waterways (NOAA Fisheries 2016). In fact, only 8% of the Gulf of Maine distinct population segment of ATS historic spawning and rearing habitat is unimpeded. Our model predicts a biologically substantial decrease in reproductive potential as dams were added to the system and fish experienced longer delays in warmer environments. Conversely, effective fish passage that expedites migration times to cool upstream waters during migratory periods is predicted to increase reproductive success and would improve recovery efforts.

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Sarah Rubenstein was born in Cambridge, New York, on May 17, 1993. She grew up in Shushan, New York, and graduated from Cambridge Central High School in 2011. She attended Cornell University, where she began her research career studying Black-throated Blue Warblers with the Cornell Lab of Ornithology. Sarah graduated in 2015, earning a Bachelor of Science in Science of Natural and Environmental Systems with a Distinction in Research and with a Development Sociology minor. Following graduation, Sarah moved around the country working various fisheries positions, living in Alaska, Nevada, California, and Yellowstone. In the spring of 2017, after almost three years of traveling, she moved back east to Maine and entered the Wildlife Ecology graduate program at The University of Maine. Currently, Sarah works for U.S. Fish and Wildlife Service in Vermont, applying her studies to Atlantic salmon conservation in Lake Champlain. After receiving her degree, she will continue pursuing a career as a fish biologist. Sarah is a candidate for the Master of Science degree in Wildlife Ecology from the University of Maine in August 2021.