

# Adult Atlantic salmon (*Salmo salar*) delayed below dams rapidly deplete energy stores

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## Abstract

Atlantic salmon (*Salmo salar*) return to rivers in spring for an energetically costly upstream migration for spawning. These fish are often delayed in the lower river below dams, subjecting them to warmer waters than occur in upstream sections of river, that may increase metabolic costs. We sought to quantify the energetic cost of dam-mediated delays in migrating adults in the Penobscot and Kennebec rivers, ME. We radio-tagged fish at the lower most dams, released them downstream (18 and 14 km), and tracked their movements back upstream. We used a Distell Fish Fatmeter as a noninvasive measurement of full-body energy at tagging and then again after re-ascending the fish-way at the dams. We found that adults ( $n = 99$ ) experienced average delays of 16–23 days at dams, losing 11%–22% of initial fat reserves. Using linear regressions, we showed thermal experience as a strong predictor of fat loss. Delay time was also a contributing factor. Extensive delays at dams expose migrating Atlantic salmon to warmer temperatures and increase the depletion rate of energy reserves required for spawning and post-spawn survival.

**Key words:** temperature effects, Atlantic salmon, dams, energetics

## Introduction

For any migratory organism, habitat connectivity is a critical contributor to individual fitness and long-term population stability and persistence. Structures that inhibit movement of diadromous fish between habitats essential for different life stages (e.g., dams) may negatively impact these populations (Kemp and O’Hanley 2010). Dams also change river systems, impacting downstream ecosystems by altering flow and temperature regimes, degrading water quality, and delaying, causing injury, or otherwise impairing migratory fish movements into essential habitat (Haro et al. 2004; Opperman et al. 2011). Consequently, dams have been cited as being causal to the decline of many migratory fish populations (Caudill et al. 2007; Limburg and Waldman 2009). Critically endangered Atlantic salmon (ATS; *Salmo salar*) populations in Maine have been severely impacted by dams as barriers to migration through both delays and mortality (U.S. Fish and Wildlife Service and NMFS 2018).

ATS are anadromous, beginning life in fresh water and migrating to the ocean as juveniles (smolts) to grow in a nutrient rich environment before returning in the fall to spawn in natal streams (Thorstad et al. 2011). It is notable that ATS return to fresh water in late spring and throughout the summer, often many months before the start of spawning. The migration typically entails a directed movement upstream from the mouth of the river to a suitable holding location

near spawning habitat. This movement may last weeks to more than a month in an undisturbed system, with individual fish traveling between 2 and 31 km per day before resting for months prior to spawning (Thorstad et al. 2003). Adults returning to coastal watersheds are thought to cease consumption upon freshwater entry (Kadri et al. 1995) making the energetic stores accrued during the marine phase likely the sole source of energy for survival during the upstream migration and spawning activities. Stored energy is invested in freshwater migration, gamete production, development of secondary sexual traits, and spawning (courtship, redd building, guarding, and intersexual competition; Jonsson et al. 1991; Fenkes et al. 2016). Although ATS experience high mortality after completing spawning, post-spawn adults (kelts) may survive to return to the sea (Maynard et al. 2018). These kelts may migrate directly to the sea or over-winter in the river before out migrating to the marine environment in the following spring (Ruggles 1980; Maynard et al. 2017). A single fish may spawn in as many as five different years (Fleming 1996). These larger, multi-year fish are a critical component of the population, with an increased reproductive potential. Female ATS may invest up to 25% of their body mass into egg production (Fleming 1996). However, 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). Because energy usage during one portion of the migration may reduce the energy available for the remaining migration process (Fenkes et al. 2016; Bowerman et al. 2017), energy loss likely influences the probability of post-spawn survival and may be causal to reduced repeat spawning.

Ambient water temperature directly controls and limits growth and metabolism of ectotherms such as ATS (Lennox et al. 2018). Salmonids are sensitive to environmental temperatures and have an optimum thermal range at which aerobic scope is greatest (Elliott and Elliott 2010). Outside this range (estimated near 15–18 °C in juveniles (Elliott and Elliott 2010) but likely lower for adults), aerobic scope is reduced, leading to a metabolic deficit and dependence on anaerobic processes (Farrel et al. 2008). ATS may become thermally stressed, and without access to cooler water, long-term survival is reduced (Elliott and Elliott 2010; Frechette et al. 2018). While over-summering in rivers and awaiting seasonal maturation, ATS may be subjected to temperatures that approach or reach the upper lethal level (>28 °C; Elliott and Elliott 2010). ATS that do not access thermal refuge are therefore likely to experience a gradation of impacts. As temperatures increase, routine metabolism will increase due to  $Q_{10}$  effects, and beyond a certain thermal limit, stress responses are elicited, eventually leading to mortality. The increase in basal and routine metabolism increases the depletion rates of available energy stores. Because pre-spawn ATS are relying solely on stored energy reserves (without food consumption), power available to fuel the remaining migration and costly spawning effort may be reduced by residence in elevated temperatures (Martin et al. 2015). To avoid stress and to maintain sufficient energy stores for spawning and survival, adult ATS may actively seek out relatively cool thermal refuge (Holbrook et al. 2009; Todd et al. 2011; Frechette et al. 2018).

Dams delay upstream passage for migratory salmonids (Noonan et al. 2012; Izzo et al. 2016), potentially depleting critical energy reserves of migrants by exposing them to a longer migration period and increased thermal experiences during summer temperatures (Fenkes et al. 2016). Consequences of increases in energy loss may manifest as pre-spawn mortality (Jonsson et al. 1997; Berg et al. 1998; Kinnison et al. 2001; Caudill et al. 2007; Nadeau et al. 2010; Hinch et al. 2012), longer exposure to freshwater parasites (Hari et al. 2006) and reduced gamete production (Vladić and Järvi 1997). For iteroparous species, there is the added risk of increased post-spawning mortality. Glebe and Leggett (1981) suggested that iteroparous fish must invest no more than 60% of their total energy in migration to conserve enough energy to survive post-spawning, return to the sea, and recondition. This assessment is consistent with the observation that post-spawning survival rates correlate with estimated energy expenditures during spawning; post-spawning survival of ATS increases with decreasing energy expenditure (Jonsson et al. 1997). Thus, in addition to the well documented risks of stress and mortality, excess energetic costs caused by dams are likely to reduce energetic stores, and influence both the reproductive performance and survival of ATS.

These influences may be important to the critically endangered ATS population of Maine. Once common to nearly every

major river north of the Hudson (Atkins 1874; Kendall 1935), ATS populations have experienced severe declines since the 1800s attributed to overfishing, poor marine survival (due to predation, starvation, disease/parasites, and abiotic factors), dams, and other habitat degradation (Fay et al. 2006). Now, ATS returns in the United States are limited to only Maine. Among those, the Penobscot River supports the largest numbers of adults at an estimated 500 to 2000 fish annually (Fay et al. 2006). In 2009, the National Marine Fisheries Service and the U.S. Fish and Wildlife Service (USFWS) listed the Gulf of Maine Distinct Population Segment (including the Penobscot and Kennebec rivers) as Endangered under the Endangered Species Act, highlighting dams and marine survival as key causes of current demographic decline (NOAA Fisheries 2016).

ATS in the Penobscot and Kennebec rivers must navigate highly dammed systems to reach the majority of high-quality spawning habitat. On the Penobscot River, less than 20% of suitable spawning habitat is located below Milford Dam (rkm 61), the most downstream barrier to ATS migrating upstream (Fay et al. 2006). Successful upstream and downstream passage at Milford Dam has been identified as a critical component of ATS restoration. On the Kennebec River, Lockwood Dam (rkm 101) is the first main-stem barrier to upstream migrating fish. Upstream of Lockwood Dam, there are numerous other main-stem dams that prevent upstream movement, none of which have functioning upstream fish passage. Less than 10% of the habitat in the Kennebec River is fully accessible (Fay et al. 2006). Maine Department of Marine Resources (MEDMR) implements a trap and haul method to move adult ATS from Lockwood Dam to high quality upstream spawning habitats located in the Sandy and Carrabassett rivers (i.e., trap ATS at the Lockwood Dam fish lift, and haul via truck and tank to an upstream to release site).

It has been well documented that upstream migrating fish are regularly delayed below dams with negative repercussions (Bunt et al. 2012; Izzo et al. 2016). What remains unclear is the relative cost these delays have on the performance and fitness of adult ATS as a consequence of increased thermal exposure. This research sought to quantify the energetic cost of dam-mediated delays (defined as the time spent below the dam before successful passage) of adult migrating ATS. The objectives in this study were to (i) characterize the thermal experience of ATS delayed below Milford and Lockwood 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 (Penobscot River, FERC project number p-2534) and Lockwood Dam (Kennebec River, FERC project number p-2574) operate a fish lift and fish sorting facility on the turbine side of the dams. The Milford Dam lift has a horseshoe-shaped entrance leading to a V-shaped gate to trap fish within a hopper. The entrance to the Lockwood Dam lift is 90 degrees to the river flow. The hoppers are 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 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 each ATS was scanned for a previous PIT tag (indicating a likely repeat spawner if present), a scale sample was taken (for later identification of age and origin by MEDMR) and fork length and best assessment of sex (note that sex was deduced by morphological appearance by MEDMR, but ATS were captured close to the ocean and sexually dimorphism was often not obvious) were recorded. The origin of ATS in either river falls into one of two categories: wild-reared or hatchery-reared. In the Penobscot River, the majority of adults are of hatchery-reared origin and rarely of wild-reared eggs. Adults of hatchery-reared origin were released into their respective rivers as smolts, just before the out-migration period. All ATS in the Kennebec River are wild-reared, either from naturally spawned eggs or artificially planted eggs ([Annual Report of the U.S. Atlantic Salmon Assessment Committee 2021](#)).

## Tagging

Prior to tagging, fish were held in tanks of ambient river water and were handled without anesthesia. Captured ATS were gastrically tagged with either Lotek radio-tags (see [Table 2](#)) or temperature logging Lotek archival radio-tags (MCFT3-L; 30 g and 16 mm  $\times$  85 mm; 2.5-s burst rate). Each fish was manually held against the side of the tank while the tagger inserted the tag into the esophagus of the ATS 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) injected into the dorsal musculature. This tag was used for secondary identification and for tracking on an existing PIT array (E. Peterson, S.R. Rubenstein, G. Maynard, and J. Zydlewski, unpublished data). After tagging, ATS recovered in an aerated tank of ambient river water. Post-recovery, fish were transported downstream on their respective rivers for release. On the Penobscot River, ATS were released at Brewer Boat Launch, approximately 18 km downstream from Milford Dam ([Fig. 1](#)). On the Kennebec River, ATS were released at the Sydney Boat Launch, approximately 14 km downstream from Lockwood Dam ([Fig. 1](#)). Tagging of ATS started at the beginning of the respective runs in late May to early June as ATS began to show up in the fish lifts. Every available ATS was tagged as they came into the trap provided researchers were on station and the fish was a mature adult in good health (i.e., showing no obvious signs of illness or injury). Tagging continued until the target number of fish was reached on each river (50 on the Penobscot and 20 on the Kennebec). To abide by permitting and avoid excessive stress to the fish, tagging took place only at river temperatures below 23 °C.

## Energetic assessment

A Distell Model 692 Fish Fatmeter (Distell Inc., West Lothian, Scotland) was used to noninvasively estimate whole-body energy status 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 (as defined by [Distell.com 2022](#)) along the flank on both sides of the ATS (for a total of eight), and these data provide an average energy estimate based on the lipid content of somatic tissues derived from established calibration curves for ATS ([Distell.com 2022](#)). Lipid and somatic energy values determined through whole-carcass proximate analysis has shown a strong relationship to fat meter readings ([Crossin and Hinch 2005](#); [Bayse et al. 2018](#)). Total measurement time takes approximately 30 s per fish. Fat measurements of Penobscot River and Kennebec River ATS were taken at their first and second captures at Milford Dam and Lockwood Dam, respectively, to estimate energy use between captures.

To validate the reliability of taking a single fatmeter estimate at each capture, the fatmeter was first tested on six, recently culled, full-body ATS from the National Cold Water Marine Aquaculture Center in Franklin, Maine. Following the Distell Fatmeter protocols, each ATS was consecutively measured for ten fat estimates per fish. An analysis of the variability in the measurements was conducted.

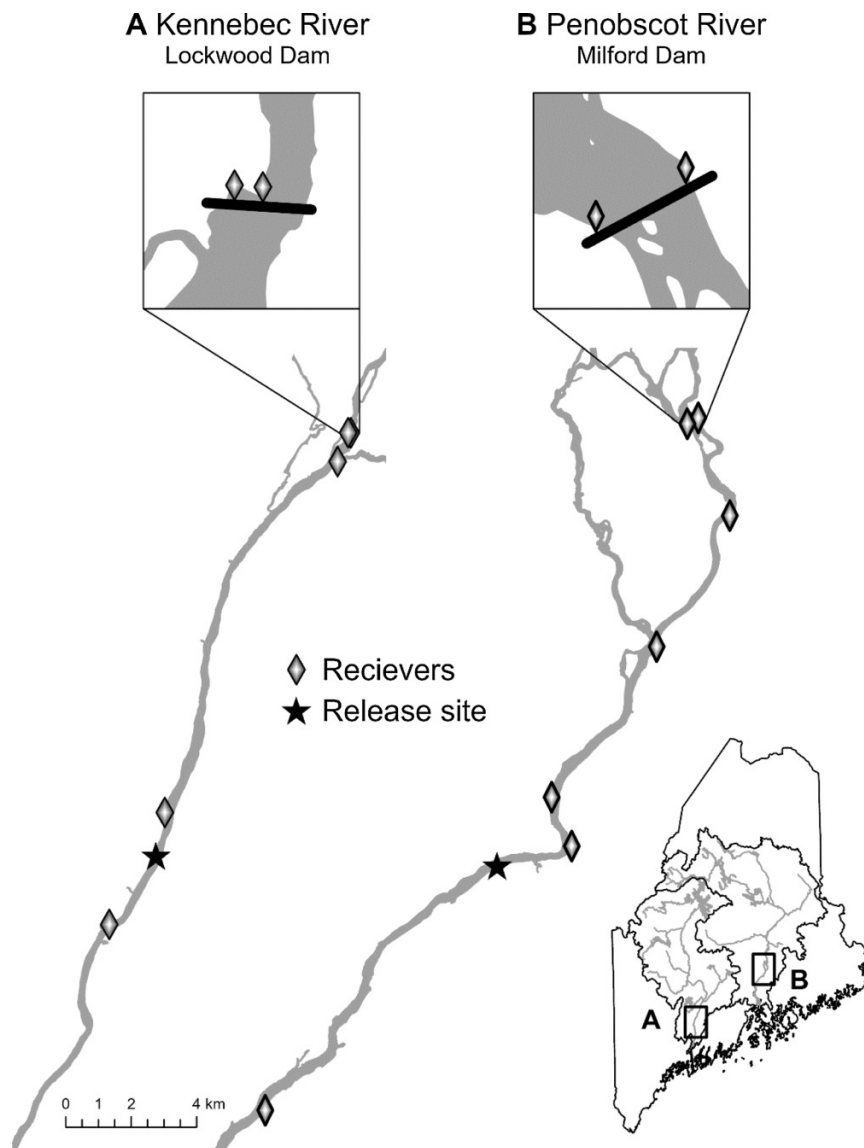
## Telemetry

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, antennas were located on Milford Dam to allow a detection of fish presence in the spillway, and additional receivers and antennas were set up between the release site at Brewer Boat Launch and the dam ([Fig. 1](#)). Similarly, on the Kennebec River, antennas were set up on Lockwood Dam, and additional receivers and antennas were placed between the release site at Sydney Boat Launch and the dam ([Fig. 1](#)).

## Recapture

Tagged ATS that re-ascended the dam and were recaptured at Milford Dam were transported to the USFWS Craig Brook National Fish Hatchery to be part of the Penobscot River brood stock. A second estimate of fat content was measured 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 minimize pre-spawn handling stress). ATS recaptured on the Kennebec

**Fig. 1.** Maps of the study areas along the Kennebec (A) and Penobscot (B) rivers (U.S. Geological Survey 2020). The black solid lines in the callouts are Lockwood and Milford dams, with the diamonds as radio receiver locations, and the stars as release sites of tagged Atlantic salmon. Temperature loggers were placed just below each dam and in upstream tributaries (see Table 1). NAD83, UTM19N.



River at Lockwood Dam were measured for a second fat estimate and immediately had their radio-tags removed. ATS were then trucked upstream, past three additional dams, to the Sandy River by the MEDMR and released. For temperature logging radio-tags, the result of the tagging and two fat measurements was thermal experience and a change in relative fat stores between initial capture ( $t_0$ ) and recapture ( $t_1$ ); summarized in Fig. 2).

### Thermal experience

To characterize the range of thermal experiences that adult ATS may have experienced during upstream migrations, either below dams or upstream, temperature loggers were deployed (HOBO Water Temperature Pro v2 Data Loggers, resolution of 0.02 °C at 25 °C and an accuracy of 0.21 °C from 0 to

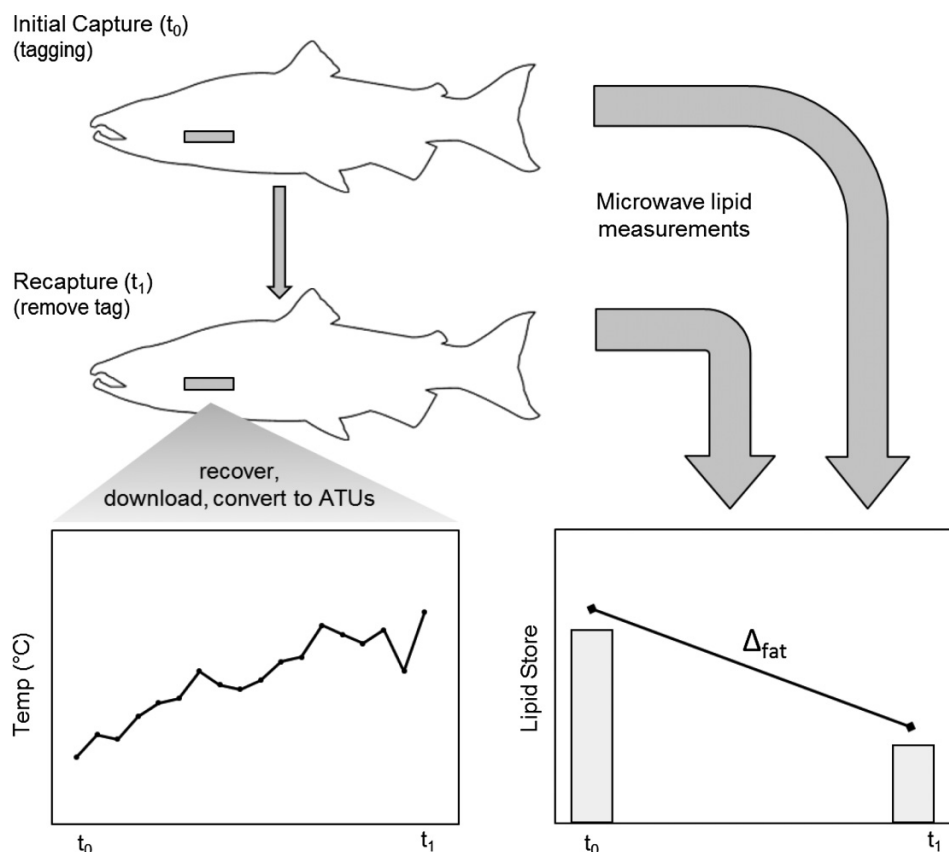
50 °C) within the Kennebec and Penobscot river watersheds in early May of 2018 and 2019 (Table 1). Loggers were placed at sites of known use to ATS for holding or spawning (MEDMR, Pete Ruksznis, personal communication, January 2018). Loggers stayed in the river from May until the start of ice formation in late November or early December.

### Analyses

Stationary radio detections were used to determine movement patterns between captures to describe time to approach the lowermost 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, a distance of approximately 14 or 18 rkm. Delay time at both dams was calculated as the time from first detection on any of the



**Fig. 2.** Summarization of methods: capture, recapture, thermal experience, and fat loss. At first capture ( $t_0$ ), Atlantic salmon were tagged with a temperature-logging radio-tag and measured with a Distell Fish Fatmeter. At second capture ( $t_1$ ), the radio-tag was removed and downloaded and a second fatmeter reading was performed. The result was the thermal experience and relative loss of fat between two time periods. ATUs, accumulated thermal units.



**Table 1.** Approximate locations (region 19) of temperature loggers in the Penobscot and Kennebec rivers of Maine, in decimal degrees.

	Penobscot River	Kennebec River
Downstream	44.879606, -68.664485	44.538114, -69.632014
Upstream	45.554314, -68.382639	44.853581, -70.405389

**Note:** One logger was placed downstream, below each dam, and one was placed in an upstream reach of each river (Fig. 1).

antennas at the dams until successful passage (i.e., entry and recapture at the trap and handling facilities at either dam). Independent Welch's *t*-tests were used to test the differences in approach and passage times.

Data collected from the HOBO temperature loggers was converted to daily averages to calculate the differences in temperatures between upstream and downstream locations on the rivers. Average daily temperatures from HOBO temperature loggers and average daily temperatures from individual ATS with logging radio-tags were converted to accumulated thermal units (ATUs), the cumulative daily water temperature in degrees Celsius per day. Several comparisons between actual ATS thermal experience (from loggers being

carried by fish,  $n = 29$ ) and the ambient water temperatures at the upstream and downstream locations (recorded by temperature loggers; Penobscot  $n = 2$ ; Kennebec  $n = 2$ ) were conducted.

Fat loss was the whole-body percentage of fat at second capture subtracted from initial fat percentage measured at first capture. The percentage 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 Akaike information criterion (AIC) model selection was used to predict the outcome of the proportion of initial fat lost during delays (for temperature logging tagged ATS only) using maximum likelihood estimation and the number of predictor variables. Explanatory variables included ATUs, the time between captures (days in river), fish fork length, and capture date. Independent Welch's *t*-tests were performed to determine the influence of sex, origin (hatchery vs. wild-reared), year, or river on the proportion of initial fat lost.

To assess whether or not fat lost was proportional to starting fat percentages, a second regression using ratio of fat lost

(rather than  $\Delta_{\text{fat}}$ ) was calculated as

$$\text{ratio} = \frac{\text{fat}_1}{\text{fat}_2}$$

## Results

### Upstream movements and delays

On the Penobscot River in 2018, 42 of 49 tagged and released ATS (16/20 archival tags, 26/29 non-archival tags) returned to Milford Dam for recapture. In 2019, 46 of 50 tagged and released ATS (18/20 archival tags, 28/30 non-archival tags) returned for recapture (Table 2). On the Kennebec River, all ATS were tagged with temperature logging archival tags. In 2018, only 6 ATS were tagged due to low total run numbers. Four of those fish returned for recapture. In 2019, 9 of 20 tagged ATS returned to Lockwood Dam for recapture (Table 2). The ATS that were not recaptured were detected on the radio antenna arrays before eventually falling back from the dam and moving downstream (Fig. 3).

All but one tagged ATS (a 2019 Kennebec fish never detected moving past the most downstream receiver) displayed directed upstream movement after release post-tagging, approaching the base of respective dams within days. However, the time to enter the fishway, ascend, and pass the dam was much longer (Fig. 4). In 2018, the average approach time to Milford Dam was 4.6 days ( $n = 48$ ; median = 3 days; range = 1–28 days), significantly different than the 23.1 days ATS spent on average delayed below the dam ( $n = 41$ ; median = 12 days; range 2–155 days;  $p < 0.05$ ). In 2019, approach time to Milford Dam was 4.0 days ( $n = 49$ ; median = 3 days; range = 0–12 days), a significant difference from the delay time of 11.0 days ( $n = 45$ ; median = 8 days; range 0–30 days;  $p < 0.05$ ). Similarly, in 2018, approach time to Lockwood Dam was 4.0 days ( $n = 6$ ; median = 3 days; range = 3–8 days), significantly less than the average delay length of 18.8 days ( $n = 4$ ; median = 16 days; range = 13–30 days;  $p < 0.05$ ). In 2019, approach to Lockwood was 7.7 days ( $n = 19$ ; median = 5 days; range = 1–42 days), and delay length was significantly different at 15.1 days ( $n = 9$ ; median = 18 days; range = 2–25 days;  $p < 0.05$ ).

### Thermal data

Upstream temperatures recorded by HOBO temperature loggers were regularly cooler (over 5 °C) than downstream temperatures recorded below dams (Fig. 5). Between 23 May and 15 October, the maximum upstream temperature on the Penobscot River was 26.0 °C in 2018 and 25.2 °C in 2019. The maximum downstream temperature on the Penobscot River was 27.8 °C in 2018 and 27.1 °C in 2019. The maximum upstream temperature on the Kennebec River was 24.2 °C in 2018 and 23.9 °C in 2019. The maximum downstream temperature on the Kennebec River was 28.9 °C in 2018 and 27.5 °C in 2019. The thermal experience of migrating ATS was retrieved from temperature logging radio-tags recovered from recaptured ATS. After accounting for tags that were not recovered from ATS (due to either an in-river loss of tag ( $n = 4$ ) or to a failure to recapture ( $n = 21$ )) and tags that failed to

log temperature while in the field ( $n = 12$ ), there were thermal experiences from nine of the 2018 and 12 of the 2019 Penobscot River fish, and three 2018 and five 2019 Kennebec River fish. The range of ATU values from ATS below dams was 54.0–662.5 °C (mean = 253.6 °C; median = 192.5 °C) during the period of release to recapture (Fig. 6 shows examples of raw temperature data (panels C and D) and corresponding ATU conversions (panels A and B)).

The ATUs from ATS temperature logging tags mirrored the below-dam river temperatures in 59% of Penobscot River fish and in 37% of Kennebec River fish (an example of this pattern is shown in Fig. 6A; fish ATU = 385.1 °C, downstream ATU = 390.6 °C, upstream ATU = 347.0 °C). In the remaining tagged ATS, the thermal experience of the fish resulted in fewer ATUs than the ATUs collected by the below-dam logger (Fig. 6B; fish ATU = 461.4 °C, downstream ATU = 514.8 °C, upstream ATU = 320.3 °C). This pattern indicates that some ATS delayed below the dam were able to locate and utilize locations with lower temperatures than our temperature logger. These potential thermal selections were reflective of minor temperature differentials (<1–4 °C) that were markedly lower than the upstream/downstream temperature logger differential (<1–8 °C).

### Fat loss

The validation of the repeated fatmeter readings from aquaculture ATS resulted in 10 different average fat estimates for each of the six fish. The calculated variances for the repeated measurements ranged from 0.03 to 0.11 (mean = 0.08; median = 0.08). The standard deviations ranged from 0.18 to 0.34 (mean = 0.28; median = 0.29). The low measures of variability indicated support for the single fatmeter measurement taken at the initial time of capture and at the time of recapture.

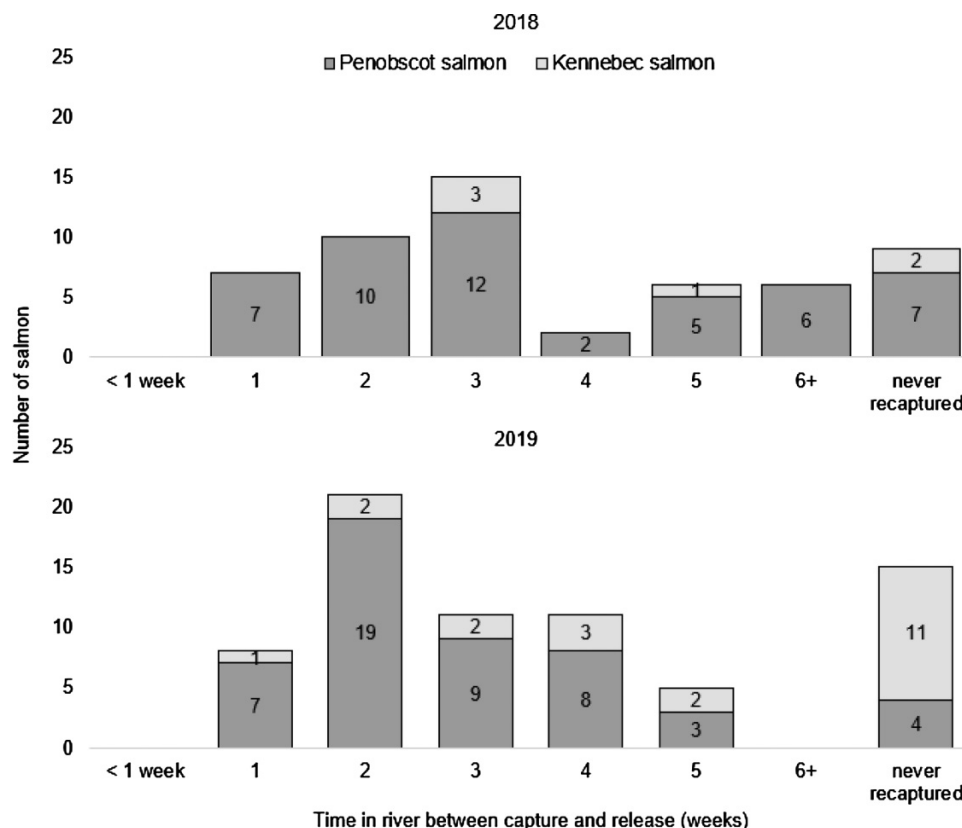
The average measured initial fat percentage from the Distell Fish Fatmeter for ATS at first capture ranged between 5.4% and 6.1% (among years and rivers; Table 3). The average fat percentage measured for ATS that were subsequently recaptured via the fish lifts ranged between 4.6% and 5.2% (among years and rivers; Table 3). Fat percentage lost in the field was converted to the percentage of initial body fat lost. In the time between release and recapture, ATS lost between 10.7% and 21.6% of original stored fat reserves (Table 3).

Using AIC, the best-fit model (carrying 44% of the model weight) to describe fat loss included only ATUs (Table 4). A simple linear regression (Fig. 7A) based on 21 Penobscot River ATS and 8 Kennebec River ATS explained 64% of the variance ( $R^2 = 0.64$ ). However, ATUs in combination with the days in river (AIC Wt = 27%), and days in river alone (AIC Wt = 24%), were both competitive models (e.g.,  $\Delta\text{AIC} < 2.0$ ). ATS fork length, maximum average daily temperature, and average daily thermal experience had no measured effect on fat loss (Table 4). There was no difference ( $p > 0.05$ ) in the percentage of initial fat lost between hatchery origin ( $n = 17$ ; mean = –13.5; SD = 13.7) and wild-reared ATS ( $n = 12$ ; mean = –22.8; SD = 20.0;  $t = 1.33$ ;  $p = 0.20$ ), between male ( $n = 16$ ; mean = –17.9; SD = 15.9) and female ATS ( $n = 13$ ; mean =

**Table 2.** A summary of Atlantic salmon (*Salmo salar*) radio-tagging data on the Penobscot and Kennebec rivers, Maine (Figure 1).

	Year	n	Tagging date	Tag type		FL (cm, range)	Sex		Origin		Stage		No. of recaptures	% recaptured
				Archival	Standard		Male	Female	HO	WR	2SW	RPT		
Milford Dam	2018	49	21 May – 1 June	20	29	76.7 (67–92)	24	25	40	9	47	2	41	84%
	2019	50	7 June – 9 June	20	30	73.1 (61–85)	26	24	40	10	50	0	46	92%
Lockwood Dam	2018	6	31 May – 6 June	6	—	71.7 (68–74)	3	3	0	6	6	0	4	67%
	2019	20	3 June – 18 June	20	—	69.0 (61–73)	12	8	0	20	20	0	9	45%

**Note:** Archival tags are the temperature logging radio-tags. Standard tags are radio-tags without the temperature logging capacity. 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 were tagged, released, and successfully recaptured. FL, fork length.

**Fig. 3.** A summary of the time between captures for Atlantic salmon tagged in 2018 (top panel) and 2019 (bottom panel) for both the Penobscot (dark gray) and Kennebec (light gray) rivers, Maine.

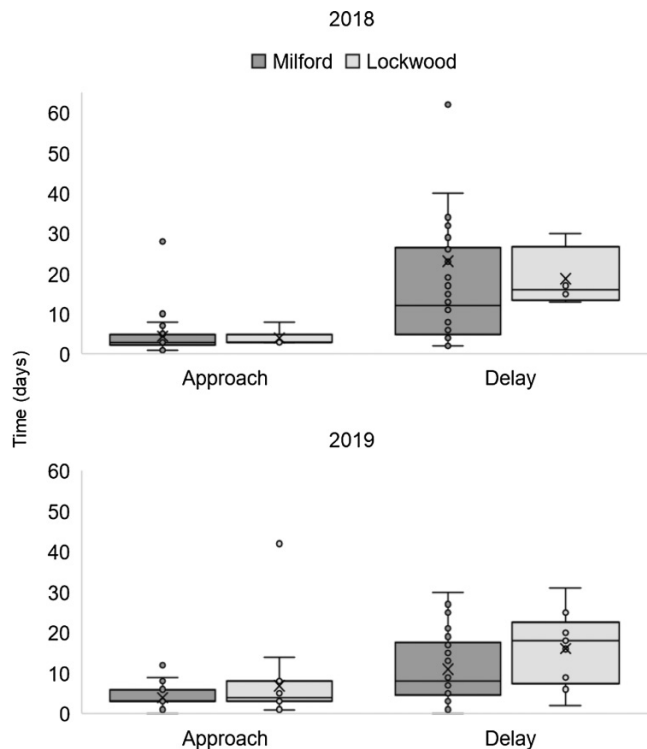
–16.3; SD = 18.6;  $t = 0.19$ ;  $p = 0.85$ ), between Penobscot River ( $n = 21$ ; mean = –16.2; SD = 18.3) and Kennebec River ATS ( $n = 8$ ; mean = –20.4; SD = 13.3;  $t = -0.65$ ;  $p > 0.05$ ) or between 2018 ( $n = 12$ ; mean = –14.2; SD = 16.4) and 2019 ATS ( $n = 17$ ; mean = –19.6; SD = 17.3;  $t = 0.81$ ;  $p > 0.05$ ). It is important to note that sample sizes for these tests were small, therefore the ability to resolve differences is poor. The linear regression to test the effect of ATUs on the ratio of fat lost between readings explained 70% ( $R^2 = 0.70$ ) of the variance, supporting a proportional loss of fat between captures in individual ATS.

## Discussion

Delays at dams and poor passage during upstream spawning migrations have been well documented for ATS

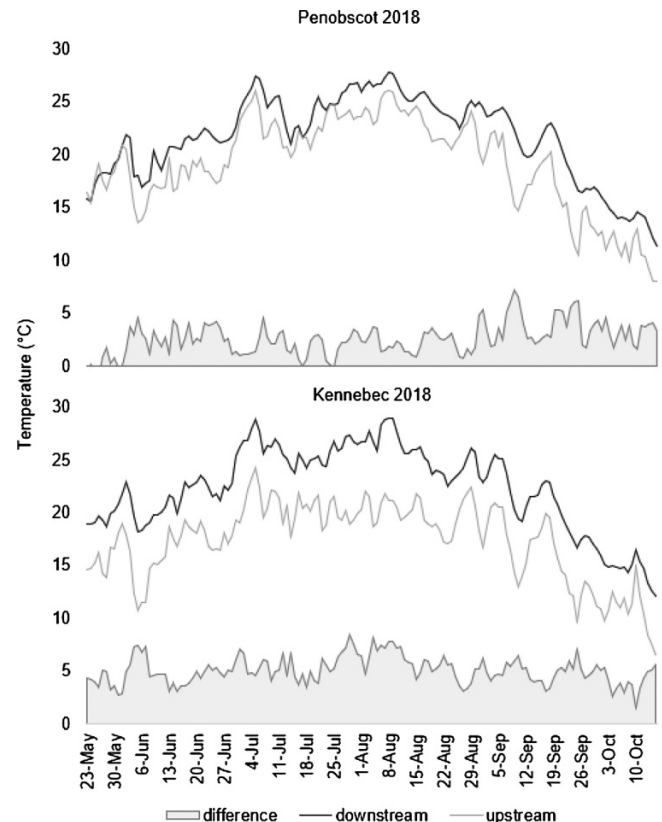
(Karppinen et al. 2002; Gowans et al. 2003; Thorstad et al. 2003; Lundqvist et al. 2008). The slowed migration times as a consequence of delays at dams may have biologically significant effects (Gowans et al. 2003; Naughton et al. 2005; Caudill et al. 2007; Roscoe et al. 2011; Izzo et al. 2016). Results from this study showed that the majority of the radio-tagged ATS exhibited a clear and directed movement upstream from release site, but encountering dams impeded migration. The time, on average, from release to arrival at respective dams ranged from 4.0 to 7.7 days, a clear contrast to the 11.0 to 23.1 days on average it took to find and utilize fish passage after approach. Because the extended delays force ATS to remain in downstream waters, delayed ATS endured greater exposure to warm summer temperatures than they would experience if allowed unimpeded access to cooler, upstream waters.

**Fig. 4.** A comparison of the time to approach (in days) the dam and then to ascend and pass the dam after first approach for 2018 (top panel) and 2019 (bottom panel). Each circle represents one individual Atlantic salmon. The “X” is the mean value. 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 are not shown.



This research shows evidence that delay was directly causal to thermal experience and energy loss. The upstream spawning migration and the following reproductive effort of ATS is already a long journey requiring high energetic input. Individuals expend a substantial part of their energy reserves to complete the process (Brett 1995). Additional energy loss depletes the finite energy stores with which an ATS entered fresh water, consequently exhausting any reserves that might contribute to post-spawn survival. Glebe and Leggett (1981) have suggested that fish investing more than 60% of their total energy in migration and spawning are more likely to die after spawning, whereas those using less have a higher potential of surviving post-spawn and reconditioning. Delays along the migration route, like those documented for ATS on the Penobscot and Kennebec rivers, increase migration duration and demand, resulting in the expense of more energy, increasing the potential to surpass that proposed 60% semelparous/iteroparous threshold (Jonsson et al. 1997). The ATS in this study lost an average of 11%–22% (ranging up to 66%; Table 3) of energy stores during the time spent below either Milford Dam or Lockwood Dam. This is a large share of stored energy that is directed to one portion of spawning require-

**Fig. 5.** 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 (refer to Fig. 1 for mapped locations of the temperature loggers). The shaded grey area is the difference in temperatures throughout the summer.

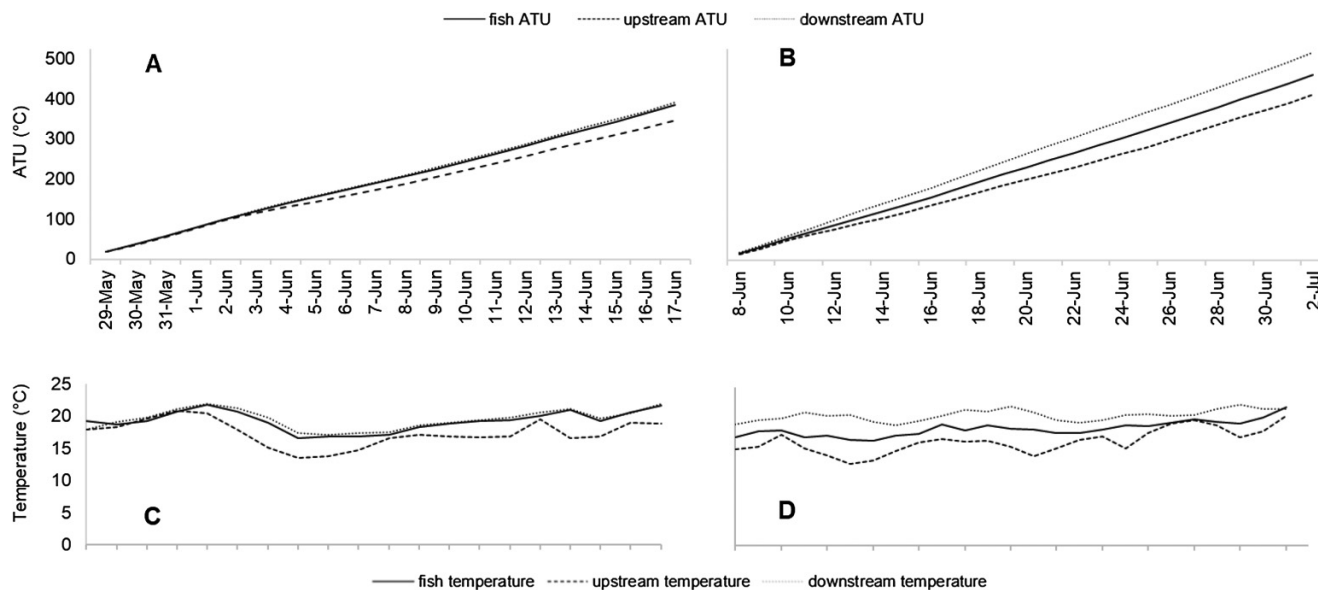


ments when that energy must also be allocated to gonadal investment, development of secondary sexual traits, redd building and guarding, courtship and competition, and spawning (Jonsson et al. 1991; Fenkes et al. 2016). Encountering multiple dams along a migratory route that each cause this level of loss increases the likelihood of a cumulative loss of more than 60% of energy stores (Glebe and Leggett's (1981) threshold for post-spawn survival). Such a scenario is realistic as ATS in the Penobscot and Kennebec rivers encounter numerous migration barriers during their journey, both natural and anthropogenic (Opperman et al. 2011; Newton et al. 2018).

Thermal experience further compounds the effects of delays at dams on ATS, as warmer temperatures increase metabolic rates. Temperature loggers deployed on both the Penobscot and the Kennebec rivers 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). To a species with a narrow optimal temperature range, occupying habitat with even slight differences in ambient water temperature may be key to survival (Todd et al. 2011). The thermal experience



**Fig. 6.** (A and B) Accumulated thermal units (ATUs; °C) of archival radio-tagged Atlantic salmon (solid line) alongside upstream and downstream temperature loggers. (C and D) The corresponding raw temperature data from archival radio-tags and the upstream and downstream temperature loggers.



**Table 3.** The average initial fat content, change in fat content between captures, and the percentage of initial fat content lost between captures for Atlantic salmon (*Salmo salar*) on the Penobscot and Kennebec rivers, Maine, for both 2018 and 2019.

	Year	Initial fat	Change in fat	Recapture fat	% of initial fat lost
Penobscot	2018	5.8% (n = 49; range = 2.6%–9.6%)	1.0% (n = 39; range = –0.6%–4.6%)	4.9% (n = 39; range = 1.9%–9.1%)	17.2% (n = 39; range = –9.7%–66.1%)
	2019	6.0% (n = 50; range = 1.9%–11.3%)	1.2% (n = 46; range = –0.5%–4.2%)	4.7% (n = 46; range = 1.6%–7.2%)	19.3% (n = 46; range = –8.3%–57.5%)
Kennebec	2018	6.1% (n = 6; range = 4.3%–8.0%)	1.6% (n = 4; range = –0.6%–2.7%)	4.6% (n = 4; range = 3.9%–5.3%)	21.6% (n = 4; range = –14.0%–37.1%)
	2019	5.4% (n = 20; range = 2.6%–8.4%)	0.7% (n = 9; range = –0.1%–2.5%)	5.2% (n = 9; range = 3.3%–6.8%)	10.7% (n = 9; range = –2.9%–30.1%)

**Table 4.** Akaike information criterion (AIC) model selection to explore the fat lost during delay.

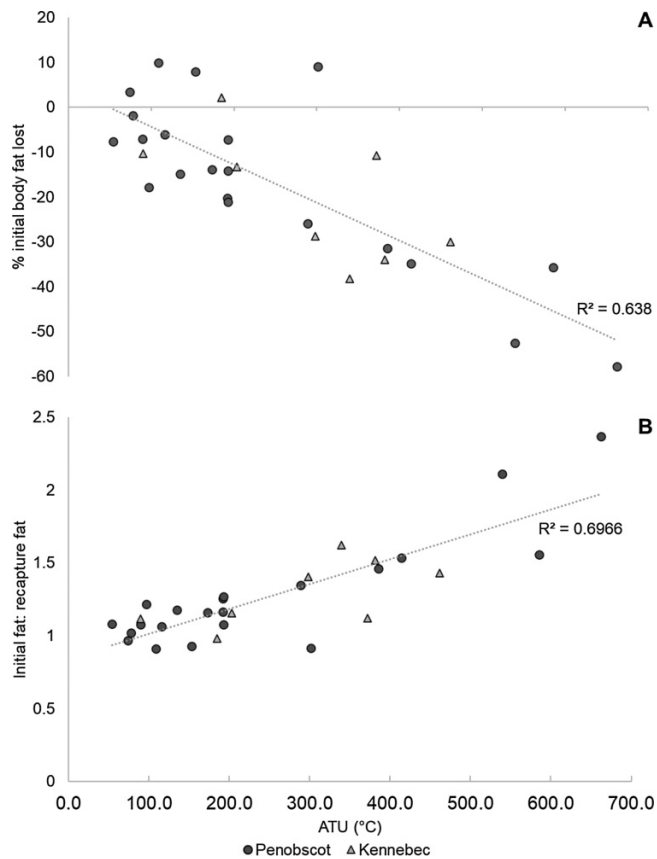
Model	R <sup>2</sup>	K	logLik	AIC	ΔAIC	AIC Wt
ATU	0.64	3	–108.8	224.6	0.00	0.44
ATU + days in river	0.66	4	–108.0	225.5	0.93	0.27
Days in river	0.62	3	–109.4	225.8	1.16	0.24
Initial fat + day of capture + ATU	0.64	5	–108.7	23.0	5.40	0.29
Initial fat + day of capture + days in river	0.63	5	–109.2	231.1	6.50	0.17
Max. T encountered	0.38	3	–116.7	240.3	15.70	0.17
Average T encountered	0.35	3	–117.3	241.6	17.00	0.89
Minimum T encountered	0.38	3	–123.0	253.0	28.37	0.30
FL	0.88	3	.123.6	254.8	29.48	0.17

**Note:** Linear regressions were used, and the top three models were competitive ( $\Delta\text{AIC} < 2.00$ ) with accumulated thermal units (ATUs) as the best predictor of fat loss. FL, fork length.

of the temperature-logging ATS was often lower than ambient river temperatures measured below-dams (using temperature loggers), providing evidence of preferential selection of cooler waters. Frechette et al. (2018) found that adult ATS in

the Rivière Sainte-Marguerite Nord-Est in Quebec, Canada, engaged in behavioral thermoregulation at river temperatures as low as 17–19 °C (temperatures cooler than the below dam temperatures logged in this study) often maintaining

**Fig. 7.** (A) A simple linear regression of accumulated thermal units (ATUs) ( $^{\circ}\text{C}$ ) of archival radio-tagged Atlantic salmon (ATS) from the Penobscot ( $n = 21$ ) and the Kennebec ( $n = 8$ ) rivers, Maine, against the percentage of initial body fat lost between first capture and second capture. (B) A simple linear regression of ATUs ( $^{\circ}\text{C}$ ) of archival radio-tagged ATS from the Penobscot ( $n = 21$ ) and the Kennebec ( $n = 8$ ) rivers against the ratio between fat measurements (initial fat/recapture fat). A strong linear trend indicates a proportional loss of fat.



body temperatures within a narrow range of 16–20  $^{\circ}\text{C}$ . These data may indicate that temperatures above 20  $^{\circ}\text{C}$  are likely inducing some level of thermal stress in adult ATS. This is congruent with work by Wilkie et al. (1997) who reported that only 70% of adult ATS successfully recovered from exhaustion at 23  $^{\circ}\text{C}$ . Note that 20  $^{\circ}\text{C}$  is far lower than the peak summer temperatures recorded in the Penobscot or Kennebec rivers (documented reaching almost 29  $^{\circ}\text{C}$ ). The high summer temperatures found in Maine rivers suggests that even for fish that find thermal relief of a few degrees, passage delays through lower river sections are not without substantial cost. Though this research did not attempt to identify cold water refuge sites, a thorough survey of thermal habitats downstream of the dams may be useful to understand ATS ability to mitigate warm summer temperatures.

A minority of measurements resulted in a greater fat measurement upon recapture compared to first capture. This might be attributed to the influence of variability in the fat meter measurements taken over short time frames, thereby resulting in spurious calculations. The fish that exhibited this

increase in fat content 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 precision of the fatmeter ranges in uncertainty (approximately plus or minus 0.5%–1%) in readings ranging from 2% to 15% (Distell.com 2022). The negative net changes in fat for fish measured over a short period of time reflects the variability of whole-body measurements.

As might be expected, the relationship found between ATUs and percentage of fat lost during delay was closely mirrored by the relationship between the time spent in the river and percentage of fat lost. Model selection indicated that ATUs best described fat loss in delayed ATS, but the time spent in the river, either as the only variable or in addition to ATUs, also had statistical support (see Table 4). To gain a clearer understanding of the direct role thermal experience plays on energy expenditure in migrating adult ATS, a study of the fat lost in ATS moving or over-summering in cooler upstream waters might provide a helpful comparison to the warmer thermal experiences of this research.

No difference was found in the days spent in river or in the 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 more erratic within-river movement (Thorstad et al. 2011). Because of a potentially less direct upriver migration pattern, it might have been expected that the hatchery-reared fish would have exhibited longer times between captures. However, both hatchery and wild-reared fish displayed similar initial river entry behaviors and upstream motivation. It would be remiss, however, not to note that the power to detect any difference is hampered by small sample sizes.

Remaining populations of endangered ATS in the USA exist almost entirely in highly dammed rivers. Understanding the impact that dams have on ATS survival and reproduction may 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 repeat spawning potential. However, despite restoration efforts, dams continue to be a source of delay. Effective fishway passage requires successful attraction and passage (Bunt et al. 1999). When these two fundamentals are not met and 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. This study has 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.

Although the recent recovery plan for the ATS in Maine identifies the importance of ensuring a self-sustaining wild population, protection has not specifically prioritized post-spawn survival (U.S. Fish and Wildlife Service and NMFS 2018) as essential to conservation. The limited attention to post-spawn survival is largely a result of the current state of returns that has been, and remains, low (U.S. Fish and Wildlife

Service and NMFS 2018). Returning spawning runs on the Penobscot River are heavily reliant on hatchery production, requiring collection of sea-run broodstock (rather than on the establishment of natural reproduction). ATS are captured at Milford Dam and moved to USFWS Craig Brook National Fish Hatchery for artificial spawning (U.S. Fish and Wildlife Service and NMFS 2018). On the Kennebec River, a trap and truck fish passage program is implemented to move fish that ascend Lockwood Dam to spawning habitat in the Sandy River. A large focus of recovery has been on ensuring this assisted movement and artificial spawning rather than on ensuring habitat and passage conditions for natural reproduction and post-spawning survival. However, it is known that increasing access to quality habitat benefits diadromous fish species through all life history stages (Wippelhauser 2021). Fine-scale monitoring of ATS behavior below dams and near fishway entrances, a survey of lower river thermal refuge availability, and follow-up studies of reproductive consequences of excess energy expenditure may lend insight into understanding ATS conservation needs. Accordingly, restoration efforts focused on improving rapid access to high quality, upstream habitats in highly dammed systems are likely to promote the rapid movement of fish to cooler waters, thereby reducing the depletion of adult energetic stores, and increasing spawning and post-spawning success.

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## Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Formal analysis: SRR, EP, JDZ

Investigation: SRR, EP, PC, JDZ

Methodology: SRR, PC, JDZ

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## Competing interests

The authors declare there are no competing interests.

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