THE LONG-TERM IMPACT OF DAM REMOVALS ON PENOBSCOT RIVER MIGRATORY FISHES

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An Abstract of the Dissertation Presented
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Dams interrupt river connectivity and disrupt fish migrations. We used telemetry to study the migratory movement patterns of adult American shad, sea lamprey, and Atlantic salmon on the Penobscot River, Maine after dam removals and other passage improvements had occurred. We also studied scale formation of marine-stage Atlantic salmon raised in marine net pens, the findings from which could be relevant to captive rearing efforts.

American shad now have access to the majority of their historic spawning habitat, contingent on passage the first main-stem dam (Milford Dam). We found that habitat upstream of dams was infrequently accessed, and first time spawners were most likely to pass Milford, suggesting that passage motivation may be related to downstream spawning habitat saturation. Sea lampreys provide important ecological services within their native range. Passage success of tagged lampreys at Milford was relatively high, but passage success at upstream dams was variable. The insights provided by this study are an important first step towards ensuring that lampreys will persist in their native habitats.

Although fish passage exists at Milford Dam, it does not appear to be efficient for Atlantic salmon. Most salmon experienced extended delays at Milford Dam. Salmon also had low passage efficiencies when approaching dams elsewhere in the system. Most adults in the Penobscot are hatchery-origin fish stocked into the river as smolts, and current stocking practices release smolts downstream of Milford. This may prevent smolts from imprinting on upstream waters. We also found that fish that searched for passage at Milford near the fishway entrance experienced shorter delays compared to fish that searched throughout the river channel. Many study fish passed the dam on the same day as entering the fishway, suggesting that attraction to the fishway is a major factor leading to delays.

The rate at which scale circuli are formed can yield valuable information about fish growth. Scales were collected from Atlantic salmon raised in marine net pens to characterize circulus deposition and scale growth in relation to time and water temperature during the early marine phase. Deposition and growth rates were variable through time and when related to temperature.

DEDICATION

This dissertation is dedicated to my lab mates.

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This dissertation is dedicated to my lab mates, past and present, because they are simply the best group of people anyone could be fortunate enough to work with. Anthony, Camille, Josh, Rex, Silvia, and Zach provided support as undergraduate technicians and as collaborators. Alejandro, Betsy, Dan, Ernie, George, Kathryn, Kevin, Kory, Lara, Matt, Melissa, Rylee, Sarah R., and Sarah V. all shared part of their UMaine graduate experience with me, and I am a better person for it. Cody Dillingham deserves special thanks for being there with me through all of my field seasons and beyond. It has been a pleasure to work with you, and I can honestly say that I could not have done it without you.

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CHAPTER 1

AMERICAN SHAD (*ALOSA SAPIDISSMA*) MIGRATION, DAM PASSAGE MOTIVATION, AND DEMOGRAPHICS IN THE PENOBSCOT RIVER, MAINE

ABSTRACT

Two centuries of dam construction have drastically reduced the abundances of migratory fishes in the Penobscot River. Two recent dam removals and significantly modified fish passage structures (2012-2016) have made it possible for American shad to access the majority of their historic spawning habitat, contingent on successful passage the first main-stem dam (Milford Dam). We sought to characterize resulting changes in the movement patterns and population demography of this species in response to increased access. We used a combination of radio, acoustic, and PIT telemetry to track 755 adult shad during their spawning migration from 2014-2021. Demographic data was collected from a total of 951 fish including tagged (live) and opportunistically collected mortalities (445) at the Milford Dam during the same time period. Spawning history based on scales was determined for all fish (via scales) and age estimates from mortalities were made using otoliths. Habitat upstream of dams in the system was infrequently accessed by fish tagged downstream, and only 10 percent even approached the dam. Fish that did successfully ascend the dam generally did not move far upstream. First time spawners were more likely to pass the Milford Dam than fish with more spawning experience, suggesting that passage motivation may be related to downstream spawning habitat saturation. The population is currently dominated by 4, 5 and 6 year old fish with rates of iteroparity ranging between 35-55 %

among years and sexes. This work serves as a baseline for future monitoring of this population to describe the effects of increased habitat access.

INTRODUCTION

The American shad (*Alosa sapidissima*) is native to the watersheds of the eastern United States and Canada, ranging from the Gulf of St. Lawrence to as far south as the St. John's River, Florida (Walburg and Nichols 1967, Limburg et al. 2003). It is anadromous and also the largest member of the herring family. The American shad (hereafter, "shad") once supported an important commercial fishery in northern New England (Walburg and Nichols 1967). However, extensive damming throughout its range has drastically reduced its abundance to the point that commercial fisheries in some rivers have disappeared (Taylor 1951, Trinko-Lake et al. 2012).

Dams have been cited as one of the leading causes in population decline for anadromous species on the Atlantic Coast (Limburg and Waldman 2009) including American shad (Zydlewski et al., 2021). In fact, the total number of dams impeding migratory fishes in New England may be grossly underestimated (Magilligan et al. 2016). A combination of damming (Moring 2005) and overfishing (Limburg et al. 2003) led to precipitous declines in shad populations. Beyond just physically blocking the upstream movements of adults searching for spawning habitat and the subsequent downstream outmigration of juveniles, the presence of dams, especially in tidal rivers, may alter estuarine habitats occupied by migrating shad by changing rates of freshwater influx and sediment delivery (Deegan and Buchsbaum 2005).

Recent focus on migratory fishes such as the shad and the iconic–and federally Endangered–Atlantic salmon (*Salmo salar*), has resulted in dam removal becoming an important method for restoring rivers (Opperman et al. 2011). Although dam removal and the re-connection of river corridors are known tobenefit both migratory and resident fishes (Magilligan et al. 2016), the effects of removal are not always quantified (Casper et al. 2006, Magilligan et al. 2016). We sought to characterize the short-term influence of dam removal and increased connectivity on Penobscot River shad by describing the migratory extent of this species following restoration actions. We also examined size and spawning experience as factors that influence dam passage motivation.

The Penobscot River is the largest watershed in the state of Maine and the second largest in New England, after the Connecticut River (Trinko-Lake et al. 2012, Connecticut River Conservancy 2020). The river has been extensively dammed since European colonization began in the region, to support log drives, mills, and hydropower (Day 2006). Dams devastated shad populations in the Penobscot River (Atkins and Foster 1869 *in* Opperman et al. 2011, Taylor 1951). The Veazie Dam at river kilometer (rkm) 48 was the first dam that upstream migrants encountered after it was completed in ca. 1835 (Taylor 1951 [Figure 1]). While a population persisted in the lower river, the Veazie Dam passed only one shad every two years (Grote et al. 2014a).

Restoration efforts on the Penobscot River culminated in the removal of Veazie Dam (2013) and the dam immediately upstream of it, the Great Works Dam (rkm 58, removed in 2012). The Howland Dam, located on the Piscataquis River at the confluence with the Penobscot River (rkm 99), was bypassed in 2016 as part of the same restoration program. Fish passage at the Milford Dam (rkm 61) was enhanced through the addition of a fish lift in 2014 (PRRT 2018), as this was now the most seaward dam on the main-stem Penobscot River (Figure 1.1). Assuming that the Milford Dam fish lift provided safe and efficient passage for shad, these combined efforts restored access to 529 km (67%) of the shad's historic range in the river (Opperman et al. 2011).

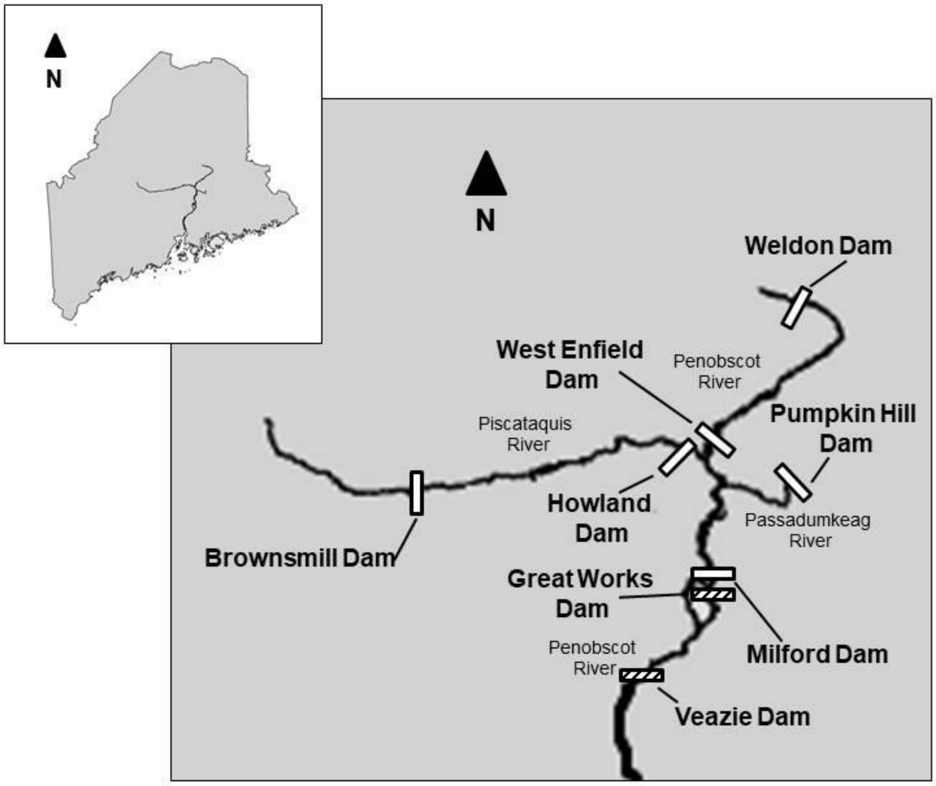


Figure 1.1. Location of study dams on the Penobscot River, Maine, and its major tributaries. Extant dams are shown in white triangles. Dams that have been removed are shown in cross-hatched triangles. Milford Dam was the most seaward dam for the majority of this study.

There is a distinct trend in the iteroparity (repeat spawning) rates of shad populations that varies along a latitudinal gradient. Southern populations, such as that in the St. Johns River, Florida, (the most southern shad population in its range) to the Cape Fear in North Carolina, experience 100% post-spawn mortality (Leggett and Carscadden 1978; ASMFC 2020).

However, iteroparity rates increase heading north, with adult populations in Virginia made up of 23% repeat spawners, and runs in Canada, the northernmost end of the shad's range, having iteroparity rates over 70% (Leggett and Carscadden 1978). Evolutionarily, the more unpredictable conditions of northern latitude rivers may make an iteroparous life history advantageous to shad returning there in contrast to more climatically stable rivers in the southern part of their range (Leggett and Carscadden 1978). Therefore, it is advantageous for shad in northern populations to expend less energy on upstream migrations so they might retain enough energy to return to the ocean, recondition, and spawn the following year (Glebe and Leggett 1981). Repeat spawning may be a bet-hedging strategy to increase fitness.

These trends in iteroparity rates–and the mechanisms behind them–are important in the context of river restoration because it raises the possibility that population demographics could change as a result of the increased migratory distance afforded by increased connectivity (Grote et al. 2014a). Leggett et al. (2004) propose that reduced rates of iteroparity in American shad returning to the Connecticut River may be the result of dam removals and more efficient fish passage at existing dams. They even go so far as to suggest that managers restrict the numbers of adult shad passed above dams to maintain high iteroparity rates in the population. A model of shad migratory energetics by Castro-Santos and Letcher (2010) could lend support to this hypothesis. However, the loss of repeat spawners is likely not an unintended consequence of improved upstream passage, but rather a consequence of insufficient downstream passage and delays under adverse thermal conditions (Stich et al., 2019). Regardless of the mechanism, increased passage may lead to lower post-spawn survival and cause demographic shifts in a population over time. In the Penobscot River, even though shad have been observed in increasing numbers (with nearly 12,000 fish passed in 2021) the effectiveness of fish lifts such as the one at Milford Dam for passing shad is thought to be moderate at best (ME DMR 2014).

The goal of the current study is threefold. First, we use an eight-year telemetry dataset (2014-2021) to describe shad migratory movements in the Penobscot River after the removal of Veazie and Great Works Dams, and their use of the habitat upstream of the Milford Dam that was made more accessible by the installation of a fish lift. Next, we use size, spawning history and age to explore if population demographics have changed since river connectivity was increased. Our third and final objective was to model the variables–iteroparity and total length (as surrogate for age)–that may explain individual passage motivation at the Milford Dam for 2014-2021.

METHODS

Fish Collection

Electrofishing.--The majority of fish captured for telemetry were captured during their upstream spawning migration in all years via electrofishing (Table 1.1). All fish captured via electrofishing were collected, tagged and released downstream of dams to assess upstream movements, approach and passage. Boat electrofishing was conducted downstream of the old Veazie Dam site from 2014-2020 (rkm 43-48). In 2021, all shad were captured and released approximately one kilometer downstream of the Milford Dam (rkm 60.3).

Table 1.1. Number of tags released each year by capture location and method. Tag distribution refers to the number and type of tags released at each location. +PIT indicates that a PIT tag was attached to either a radio or acoustic tag. For capture locations, Veazie Dam in the area downstream of the old Veazie Dam (rkm 45.8), Milford Dam refers to fish tagged at the dam and released upstream (rkm 61.3), Milford Dam tailrace refers to fish angled immediately downstream of Milford Dam and tagged and released in place (rkm 61.3), and French Island is located at rkm 60.3.

Year	Number	Capture location	Capture method	Tag distribution
2014	29	Veazie Dam	Boat electrofishing	29 radio+PIT
	11	Milford Dam	ME DMR sorting facility	11 PIT*
2015	71	Veazie Dam	Boat electrofishing	69 radio+PIT, 2 PIT-only
2016	95	Veazie Dam	Boat electrofishing	95 radio
	4	Milford Dam tailrace	Angling	4 radio
2017	99	Veazie Dam	Boat electrofishing	69 radio, 30 PIT
2018	95	Veazie Dam	Boat electrofishing	66 radio+PIT, 29 acoustic
	60	Milford Dam	ME DMR sorting facility	50 radio+PIT, 10 acoustic
	5	Milford Dam tailrace	Angling	4 radio+PIT, 1 acoustic
2019	70	Veazie Dam	Boat electrofishing	55 radio+PIT, 15 acoustic+PIT
	30	Milford Dam	ME DMR sorting facility	15 radio+PIT, 15 acoustic+PIT
2020	70	Veazie Dam	Boat electrofishing	70 radio+PIT
	30	French Island	Angling	30 acoustic+PIT
2021	43	Milford Dam	ME DMR sorting facility	43 radio+PIT
	22	French Island	Angling	22 radio+PIT
	21	French Island	Boat electrofishing	21 radio+PIT

*There is no indication of where these fish were released; none of them recorded any data, however

Boat electrofishing crews consisted of one driver and two netters who also acted as lookouts. The crew electrofished moving downstream under minimal power. Shad that were captured during a drift were placed in an aerated live well. Each drift typically ended when 4-5 shad were in the live well, or when the boat reached a pre-determined turnaround spot. The crew then took the shad upstream for tagging and release. Sampling in the vicinity of the old Veazie Dam was limited to daylight hours 90 minutes before and after high tide, both for safe boating conditions and because shad have been observed to move upstream on flood tides (Grote et al. 2014a). The number, length, and exact location of each drift were not recorded because the purpose of these drifts was to obtain shad for tagging and not calculate a catch per unit effort or other abundance estimates.

Angling.--A minority of fish captured for telemetry (64) were captured by rod and reel (Table 1.1). A small number (n=9) of shad were captured and release in the Milford Dam tailrace in 2016 and 2018. In 2020, 30 fish used for surgical implantation of acoustic tags were captured and released approximately one kilometer downstream of the Milford Dam. In 2021 approximately half of the radio tagged fish released below Milford Dam (22) were captured by angling (also approximately one kilometer downstream of the Milford Dam). Fish were captured using conventional or fly-fishing gear, using a single hook lure. Fish were brought to shore as rapidly as possible, and netted without being removed from the water before and processing.

Milford Dam fish lift.--To study the behavior of shad that successfully passed Milford Dam, shad were collected for telemetry in 2018-2019 and 2021at the Milford Dam fishlift. Shad attempting to ascend the dam were intercepted by the Maine Department of Marine Resources (ME DMR) staff and lifted via a mechanical hopper to a rooftop sorting facility. Fish were held in a large circular metal tank filled with ambient river water while awaiting tagging. The tagging process was identical to that described for the fish captured via electrofishing and angling. After tagging, the shad were allowed to recover in a smaller tank of flowing water. They were released into the Milford headpond by removing a sluice gate at the end of the recovery tank and being flushed down a steep chute into the river. This is the standard method for releasing fish from the Milford sorting facility, including Atlantic salmon.

Mortality Collection at Milford Dam.--To assess the demography of shad at the Milford Dam, shad that did not survive dam passage at the Milford (mortalities) from 2014 to 2021were collected by the ME DMR (n=445). We sampled the mortalities using the same methods used for the fish being tagged (described below) except that both sagittal otoliths were removed (for subsequent aging) and sex was confirmed by internal inspection. For our dam passage motivation models (described below) mortalities were considered to have passed the dam.

Fish processing for telemetry

Prior to tagging, each fish was measured (total length) without removal from the water. sex was visually assessed, and a scale sample was taken. Scale samples were taken from the left side of the fish with a pair of locking hemostats and usually consisted of at least four scales per fish. Fish that had become lethargic while in the live well were rehabilitated and released without being sampled or tagged. Shad were gastrically double-tagged with either a radio or acoustic tag and a passive integrated transponder (PIT) tag that was attached to the radio or acoustic tag using medical-grade adhesive. Radio tags (MST-820, Lotek Wireless Inc., Newmarket, Ontario Canada) weighed up to 2.1 grams in the air. Acoustic tags (V9-6x,Vemco, Bedford, Nova Scotia, Canada) were of a similar size. All tags weighed less than 1% of the body weight of the sampled shad. Both radio and acoustic tags were applied using flexible plastic or rubber tubing that was inserted into the fish's esophagus while its head was being held out of the water. Sampling and tagging took less than 60s. Shad were released after tagging by being held in the water alongside the boat until they were able to swim away on their own volition. Fish that were not able to swim away under their own power were removed from the study and the tag was retrieved and placed in another fish, when possible (this occurred rarely).

In 2020, 30 shad captured via angling downstream of Milford Dam were surgically implanted with acoustic tags using the methods of Gahagan and Bailey (2020). Briefly, fish were placed on a V shaped surgical board, and the gills were irrigated with an MS-222 solution (100mg/L, 0.2 mM Na_2CO_3, pH=7.0). A small incision was made in the peritoneal cavity, the tag inserted, and then the incision was closed with two sutures (Ethicon 4-0 RB-1). Shad immediately recovered in river water before being allowed to swim away. These acoustic tags were programmed to have the battery last over a year, permitting the detection of returning shad in 2021.

Radio telemetry

An array of stationary, shore-based radio receivers (SRX800-D, SRX-DL, SRX1200-D, Lotek Wireless Inc., Newmarket, Ontario, Canada) at and downstream of the Milford Dam was deployed in all years of the study. Beginning in 2018, shad released into the Milford Dam headpond were also tracked on a radio array on the main-stem Penobscot and its major tributaries. Up to two 4-element Yagi antennas (Lotek Wireless Inc., Newmarket, Ontario, Canada) were attached to each receiver. Receivers at both Veazie and Milford included stripped cable antennas that were weighted and placed underwater at the entrance to or within the fishway to pick up near-field detections. Receiver units were capable of storing and scanning up to five unique radio frequencies.

A mobile tracking route was driven at least once a week in conjunction with data downloads from the stationary array. An omni-directional antenna with a magnetic base was placed on the top of a vehicle and attached to a handheld radio receiver (SRX-400, Lotek Wireless Inc., Newmarket, Ontario, Canada), which was programmed to scan through the same frequencies as the stationary receivers. Fish were tracked by driving down roads that led as close to the water as possible, and all detections and locations were manually recorded. Mobile tracking was also conducted from both motorized and non-motorized boats and by foot opportunistically throughout all seasons. Whenever a detection was made, the frequency and unique tag identification number were written down, along with the location, date, time, and signal strength of the detection.

Acoustic telemetry

Acoustic receivers (VR2 and VR2W, Vemco, Bedford, Nova Scotia, Canada) were located throughout the system from Penobscot Bay to upstream of Milford Dam (as described by Stich et al., 2015). Receivers were attached to submerged moorings made of cement and rebar. Moorings included buoy lines that were used to locate and retrieve the moorings and receivers. Maintaining the acoustic array in addition to the radio array was advantageous because acoustic transmitters can be detected in saltwater, whereas the attenuation of radio transmitters decreases with increasing salinity (Grote et al. 2014a).

PIT telemetry

Shad were only tracked via a PIT array from 2018-2021 as a supplementary tag (to either a radio or acoustic transmitter). In 2018 there was a PIT antenna located near the fishway entrance at Milford Dam, as well as antennas in the upper part of the fishway near the exit. The lower antenna was removed ahead of the 2019 tagging season and was not replaced for the duration of the study. At least two PIT antennas were located in the fishway of the dams upstream of Milford Dam (West Enfield Dam [Penobscot River, rkm 100], Weldon [Mattaceunk] Dam [Penobscot River, rkm 150], Pumpkin Hill [Lowell Tannery] Dam [Passadumkeag River, rkm 112], Brownsmill Dam [Piscataquis River, rkm 163]) to monitor entrance and exit of the fishway. The Howland Dam (Piscataquis River, rkm 99) was also included in the study but because it had been decommissioned and bypassed, there was no PIT array there (Figure 1). Design details for the PIT antennas can be found in Kazyak and Zydlewski (2012).

Telemetry analysis

Approach and passage.-- “Approach” to the Milford Dam was defined as a fish drawing near enough to the dam from downstream and coming within range of the stationary radio receivers and being detected. An approach was also recorded if fish were detected passing through a PIT antenna located at the downstream end of the fishway. “Dam passage” at Milford Dam was assigned to a tagged individual if that fish was detected on a stationary radio receiver, an acoustic receiver, or via mobile tracking upstream of the dam. Detection on a PIT antenna in the upstream part of the fishway also caused that fish to be considered a passer.

Movements upstream of Milford Dam.--For all tagged fish released upstream of Milford Dam (or for any tagged fish released downstream of Milford Dam that eventually passed), we recorded the maximum upstream extent (rkm) reached by that fish. We also recorded approach and passage events at the five upstream dams included in the study. Approach and passage at these dams was determined using the same criteria as at Milford Dam.

Scale and otolith analysis

The scales collected in this study were intended to be used for both estimating age of telemetered fish and for assessing history of spawning of all fish. However, we found poor correspondence between scale and otolith ages for samples where both were available (Appendix A), leading to only report otolith derived ages. Our observations are consistent with previous assessments that reading scales produces biased age estimates in American shad, by overestimating the ages of young fish and underestimating the ages of older fish (Elzey et al. 2014). Our process decision is congruent with the protocol of the Atlantic Stated Marine Fisheries Commission Bench Mark Stock Assessment (ASMFC 2020). Scales were used exclusively to assess previous spawning history and otoliths were used for estimating age.

The methods we used for preparing shad scales were similar to those used by Marcy (1969) for alewife (*A. pseudoharengus*) and blueback herring (*A. aestivalis*). All scales collected from the shad were rinsed in DI water, cleaned, and mounted between two glass microscope slides (25mm x 75mm x 1mm, Globe Scientific Inc., Mahwah, NJ). The slides were placed in a microfiche reader and ages determined from the projected image. Two to three readers looked at each scale and agreed on whether or not that fish had spawned previously. Previous spawns were determined by the presence of spawning checks, an annulus with a jagged appearance caused by scale erosion during the spawning migration (Marcy 1969).

Sagittal otoliths were rinsed in DI water and patted dry on a paper towel. They were then placed on a microscope slide using clear nail polish and viewed under a dissecting scope without being sectioned, as described in Elzey et al. (2014). Age was estimated by counting annuli visible on the otolith (Elzey et al. 2014). When both the left and right otoliths were present, the readers examined both otoliths before assigning an age to the fish. Complete agreement between readers was necessary for an age estimation to be included in the final dataset.

Demographics

Only those fish for which repeat spawning status (via scale reading), age (via otolith), total length, and sex were all known were used to evaluate demographics and dam passage motivation (see below). Mean otolith age, individual iteroparity (indicated with a value of one for fish that had spawned previously, hereafter "iteroparity"), and mean total length were compared among individuals for all years of available data. First time spawners—those fish that did not have any spawning checks observable on their scales--were given an iteroparity value of zero. Otolith age, mean iteroparity rate, and total length were plotted through time for all fish, and for males and females separately. We also compared two parameters (iteroparity rate and mean total length) between passers and non-passers for each year using Welch's two-sample t-test in Program R (R Core Team 2021). The same comparisons were done separately for males and females. However, comparison by sex was only possible for 2018-2021, because the sex of tagged fish was not recorded prior to 2018. Evaluating the influence of age between passers and non-passers was not possible because all fish from which otoliths were collected were passers. For all statistical tests, $\alpha=0.05$.

Dam passage motivation

We separated fish into two groups based on whether they had passed Milford Dam, which we used as an indicator of migratory motivation. We evaluated overall trends and used generalized additive linear models (gams) to determine which factors predicted passage success. The factors we evaluated for each individual were: iteroparity (a binary variable indicating whether or not spawning checks were detected on the scale), and total length (assumed to be a surrogate for age).

We used Program R (R Core Team 2021) to generate gams that used *iteroparity*, *total length*, *iteroparity + total length*, and *iteroparity * total length* to predict passage of tagged shad (0=did not pass Milford Dam, 1=passed Milford Dam). The year that the individual fish were tagged was included as a factor in all models. The models were compared using the Akaike Information Criterion (AICc) in which the model receiving the highest weight was considered the best predictor of dam passage motivation. The full dataset used to generate the models can be found in Appendix B.

RESULTS

From 2014-2021, 755 adult shad were captured and tagged for use in the movement portion of this study. Of these, we obtained usable detection datasets from 582 individuals (77% of all fish tagged [Table 1.1]). The remaining fish were either never detected after tagging, or the detections were determined to be false (resulting from radio noise). The dataset used for evaluating demographics and migratory motivation included 951 shad. All 951 shad were used to examine migratory motivation, and annual trends in iteroparity and total length. Annual demographics associated with age were evaluated using a smaller dataset of 445 fish with otolith ages. Among all years, 531 fish were identified as males and 420 fish were identified as females.

Milford Dam approach and passage.--Six hundred ten shad were tagged and released downstream of Milford Dam. The majority of these fish were captured in the vicinity of the old Veazie Dam and released in place. Only 62 (10.1%) were detected approaching Milford Dam from downstream, and none of these fish passed upstream of Milford. The fish angled from the Milford Dam tailrace only accounted for nine of the 62 approaches.

Movements upstream of Milford Dam.-- From 2018-2021, 131 shad were captured and tagged at the Milford Dam sorting facility and then released into the Milford Dam headpond, and of these 88 fish were detected moving upstream after release. The maximum upstream distance achieved by any tagged shad was a fish that was detected at river kilometer 105, on the Piscataquis River. The average maximum upstream distance, measured in river kilometers, was 64.6 km, only 3.3 km upstream from Milford Dam.

The only upstream dams where any tagged shad were detected were Howland and West Enfield Dams. Eleven tagged shad were detected approaching West Enfield Dam, but none of them were detected passing the dam. Three of seven tagged shad that approached Howland Dam were detected upstream of the dam. The one shad that passed Howland Dam in 2018 was the first shad documented using the nature-like bypass that was built at Howland Dam in 2016.

Return of acoustic-tagged shad.--Thirteen of the 30 shad (43%) that were surgically tagged with acoustic tags in 2020 were detected returning to the Penobscot River in 2021. One of these fish, a male who was a first-time spawner in 2020, was detected upstream of Milford Dam in 2021 even though it did not pass in 2020.

Demographics.--Mean otolith age and mean total length varied slightly across the years of the study but remained relatively constant, with means of 4.4 and 5.5 years, dominated by 4, 5, and 6 year old fish (Figures 1.2, 1.3 and 1.4, Table 1.2). Across all years, males had an average age of 4.4 years and females had an average age of 4.8 years. In 2020-21, total length was higher for non-passers than passers. Mean iteroparity rate increased from 2014-17 (~ 30%) and then in the remaining years of the study remained fairly constant (~50%). Iteroparity rates were higher for non-passers than for passers in 2018-19 (approximately 60% v 40%). These overall trends were similar for both males and females, with passers tending to have less spawning experience (iteroparity = 37% v. 57%) than non-passers, but there were very few statistically significant differences in parameters when compared by sex (Figures 1.3 and 1.4).

Table 1.2. Sample size, mean otolith age, mean iteroparity, and mean total length (mm) observed in American shad (*Alosa sapidissima*) in all years of our study. Data are presented as pooled (All) and by sex. Passers are fish that successfully passed upstream of Milford Dam and non-passers are those that did not pass Milford Dam. ND=no data.

Year			All	Passers	Non-passers
2014	Sample size	All	10	10	0
		Male	ND	ND	ND
		Female	10	10	ND
	Mean otolith age N=10	All	5.5	5.5	ND
		Male	ND	ND	ND
		Female	5.5	5.5	ND
	Mean iteroparity	All	30%	30%	ND
		Male	ND	ND	ND
		Female	30%	30%	ND
	Mean total length	All	520	520	ND
		Male	ND	ND	ND
		Female	520	520	ND
2015	Sample size	All	72	72	0
		Male	45	45	ND
		Female	27	27	ND
	Mean otolith age N=71	All	4.46	4.46	ND
		Male	4.39	4.39	ND
		Female	4.59	4.59	ND
	Mean iteroparity	All	22%	22%	ND
		Male	20%	20%	ND
		Female	26%	26%	ND
	Mean total length	All	466	466	ND
		Male	444	444	ND
		Female	501	501	ND

Table 1.2 (cont'd).

Year			All	Passers	Non-passers
2016	Sample size	All	258	258	0
		Male	161	161	ND
		Female	97	97	ND
	Mean otolith age N=256	All	4.84	4.84	ND
		Male	4.7	4.7	ND
		Female	5.1	5.1	ND
	Mean iteroparity	All	36%	36%	ND
		Male	32%	32%	ND
		Female	43%	43%	ND
	Mean total length	All	468	468	ND
		Male	452	452	ND
		Female	494	494	ND
2017	Sample size	All	68	68	0
		Male	39	39	ND
		Female	29	29	ND
	Mean otolith age N=52	All	5.5	5.5	ND
		Male	5.38	5.38	ND
		Female	5.7	5.7	ND
	Mean iteroparity	All	51%	51%	ND
		Male	51%	51%	ND
		Female	52%	52%	ND
	Mean total length	All	484	484	ND
		Male	465	465	ND
		Female	508	508	ND

Table 1.2 (cont'd).

Year			All	Passers	Non-passers
2018	Sample size	All	261	169	92
		Male	135	90	45
		Female	126	79	47
	Mean otolith age N=0	All	ND	ND	ND
		Male	ND	ND	ND
		Female	ND	ND	ND
	Mean iteroparity	All	46%	37%	63%
		Male	41%	38%	47%
		Female	52%	37%	79%
	Mean total length	All	469	469	468
		Male	451	451	451
		Female	487	489	484
2019	Sample size	All	98	30	68
		Male	59	20	39
		Female	39	10	29
	Mean otolith age N=0	All	ND	ND	ND
		Male	ND	ND	ND
		Female	ND	ND	ND
	Mean iteroparity	All	58%	37%	63%
		Male	56%	35%	67%
		Female	62%	50%	66%
	Mean total length	All	459	460	458
		Male	452	455	451
		Female	468	469	467

Table 1.2 (cont'd).

Year			All	Passers	Non-passers
2020	Sample size	All	75	8	67
		Male	41	5	36
		Female	34	3	31
	Mean otolith age	All	5.33	5.33	ND
	N=6	Male	5.4	5.4	ND
		Female	5	5	ND
	Mean iteroparity	All	43%	38%	43%
		Male	41%	40%	42%
		Female	44%	33%	45%
	Mean total length	All	455	403	461
		Male	451	396	458
		Female	459	494	499
2021	Sample size	All	109	72	37
		Male	51	40	11
		Female	58	32	26
	Mean otolith age	All	4.88	4.88	ND
	N=50	Male	4.71	4.71	ND
		Female	5.1	5.1	ND
	Mean iteroparity	All	50%	46%	57%
		Male	57%	55%	64%
		Female	43%	34%	54%
	Mean total length	All	475	468	490
		Male	452	447	468
		Female	496	494	499

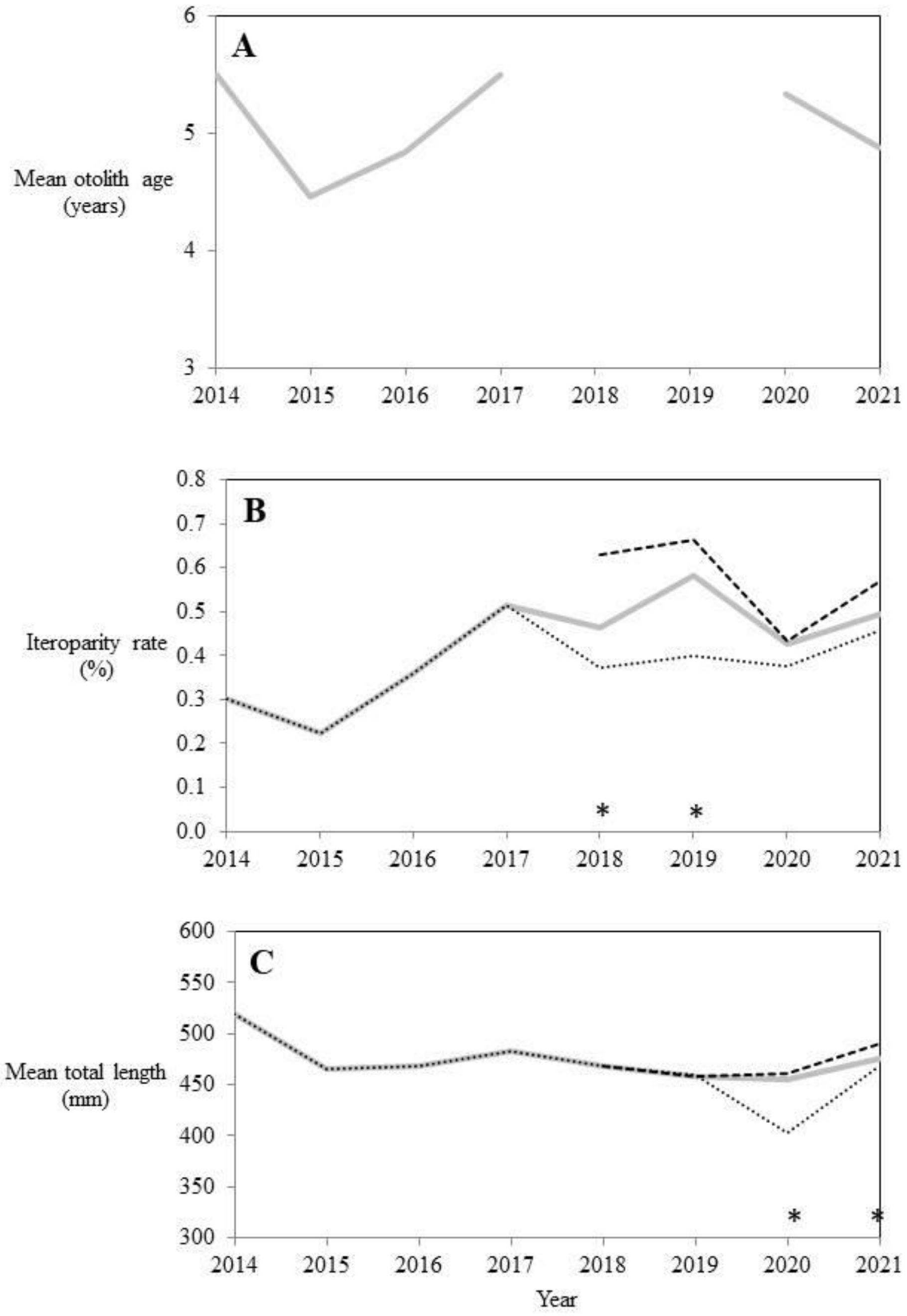


Figure 1.2. Mean otolith age (A), iteroparity rate (B), and mean total length (C) for all adult shad (*Alosa sapidissima*) in our study. The solid gray line represents the pooled data; the dotted line is the data for fish that passed Milford Dam (passers); the dashed line is the data for non-passers. Stars indicate significant differences between passers and non-passers when means were compared using a Welch's two-sample t-test with α=0.05. Passers and non-passers could only be differentiated beginning in 2014, when the Milford Dam fish lift provided upstream access to shad.

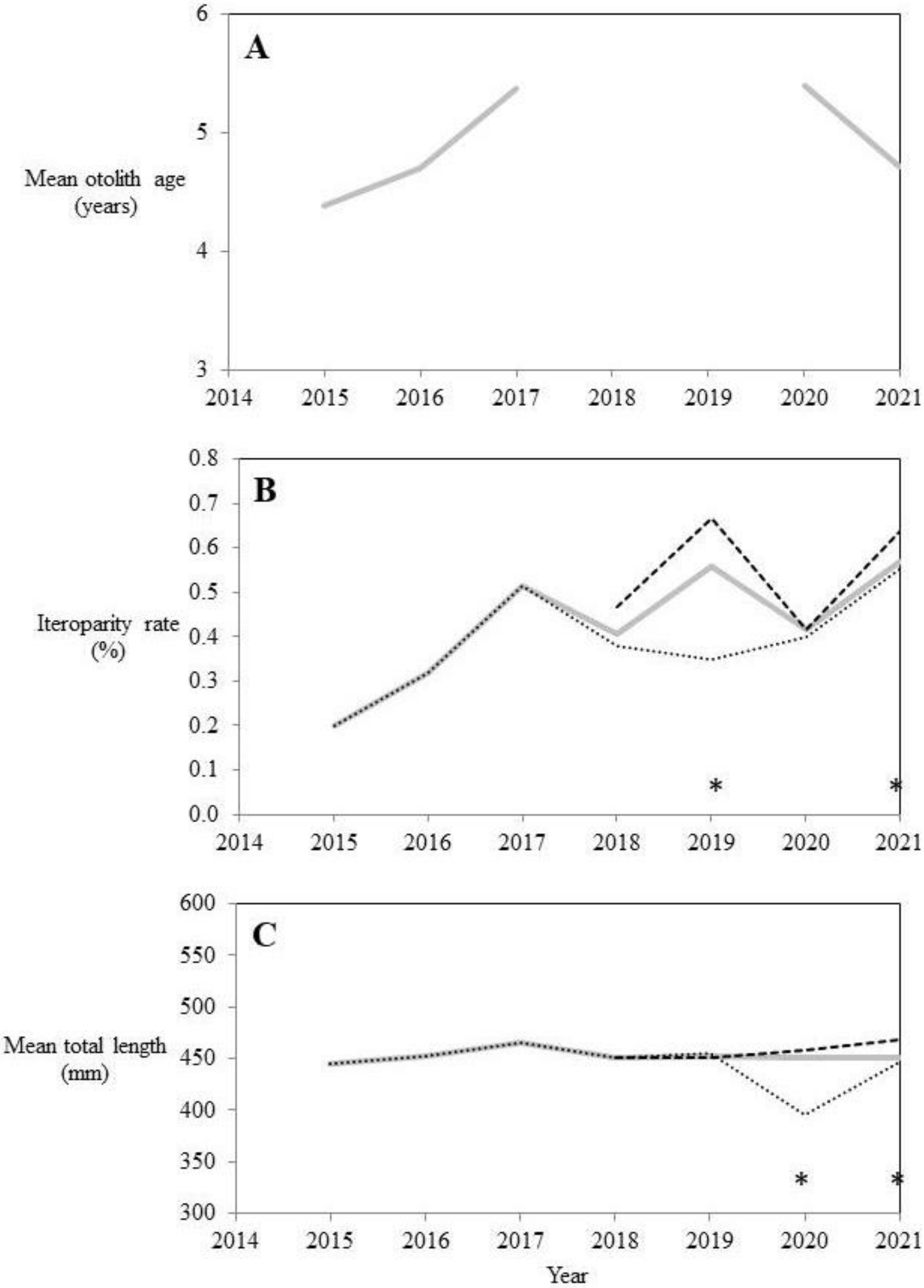


Figure 1.3. Mean otolith age (A), iteroparity rate (B), and mean total length (C) for all adult male shad (*Alosa sapidissima*) in our study from 2018-2021. The solid gray line represents the pooled data; the dotted line is the data for fish that passed Milford Dam (passers); the dashed line is the data for non-passers. Stars indicate significant differences between passers and non-passers when means were compared using a Welch's two-sample t-test with α=0.05. Sex was not recorded for live tagged shad prior to 2018.

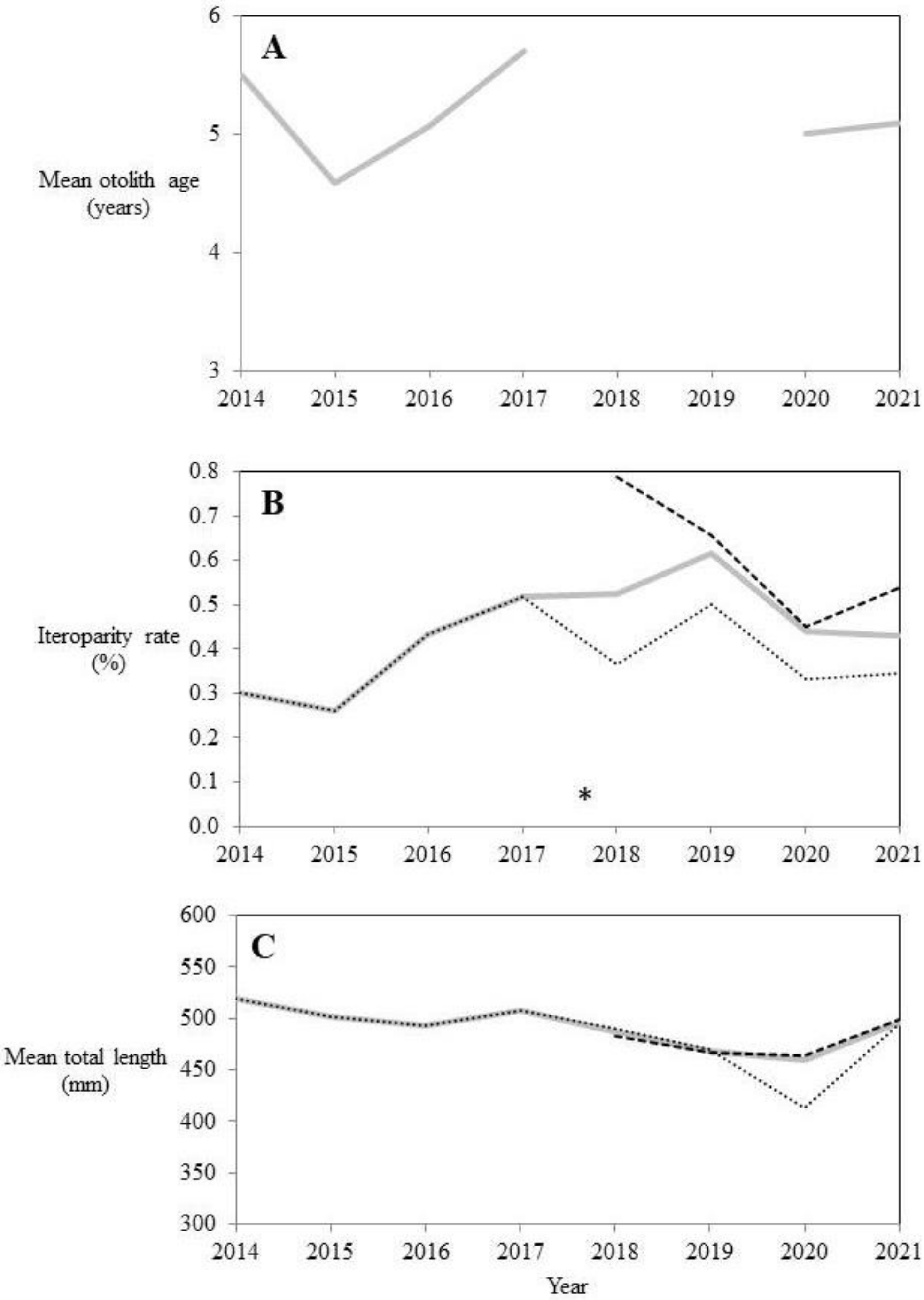


Figure 1.4. Mean otolith age (A), iteroparity rate (B), and mean total length (C) for all adult female shad (*Alosa sapidissima*) in our study from 2018-2021. The solid gray line represents the pooled data; the dotted line is the data for fish that passed Milford Dam (passers); the dashed line is the data for non-passers. Stars indicate significant differences between passers and non-passers when means were compared using a Welch's two-sample t-test with α=0.05. Sex was not recorded for live tagged shad prior to 2018.

Migratory motivation.--Iteroparity was the strongest predictor of dam passage and had a negative relationship with the probability of dam passage (Table 1.3), meaning that first-time spawners were more likely to pass Milford Dam than fish with prior spawning experience. The model containing only iteroparity was the top model, but the other two models that used iteroparity as a parameter (*iteroparity + total length* and *iteroparity*total length*) were competing models (within 5 ΔAIC of the top model). The model containing total length had the least support, but total length also had a negative relationship with the probability of dam passage.

Table 1.3. Models of factors predicting migratory motivation, based on ΔAIC. Intercepts and β values are reported for each model. Models with a ΔAIC of less than 5 are considered competing models with the top model. The top model and all competing models contained iteroparity (itero), which had a negative relationship to the probability of passage.

Model	**Intercept**	**Factor (Year)**	**Iteroparity**	**TL**	**Itero*TL**	**df**	**logLiklihood**	**AICc**	**ΔAIC**	**Weight**
Iteroparity	19.89	+	-0.8737			9	-314.698	647.6	0	0.549
*Itero*TL*	18.8	+	3.142	0.002768	-0.0085	11	-313.494	649.3	1.68	0.237
Itero+TL	20.49	+	-0.8398	-0.00118		10	-314.614	649.5	1.88	0.215
TL	22.51	+		-0.00563		9	-322.697	663.6	16	0

DISCUSSION

Restoration efforts on the Penobscot River have connected American shad to approximately two-thirds of the habitat accessible prior to damming. This raises the possibility that population demographics could change due to from increased energy expenditure associated with a longer spawning migration (Glebe and Leggett 1981) and mortality at dams during passage up and downstream (Stich et al., 2019). Specifically, this would mean that adults may be less likely to return to the ocean after spawning, shifting the population to be less iteroparous.

We did not detect any tagged shad passing upstream of Milford Dam in the same year of tagging after being released downstream of the dam. The majority of fish never came close enough to the dam to be detected on the downstream-facing radio antennas located there. Grote et al. (2014a) also witnessed low numbers of tagged shad approaching Veazie Dam despite overall high numbers of shad being detected in the vicinity of the dam (Grote et al. 2014b). American shad are generally considered to be very susceptible to handling stress (Aunins and Olney 2009, Grote et al. 2014a) and this may negatively influence the likelihood of dam passage post-tagging (Gahagan and Bailey 2020). However, we captured several shad via angling, particularly on 2020-21, and these fish exhibited similar behavior to those captured using electrofishing. Additionally, our methods for gastrically tagging American shad are commonly used and considered to be less stressful than surgical tagging (Gahagan and Bailey 2020) and our tags were within acceptable size limits for this species (Maynard 2019). This makes it unlikely that handling stress was the only factor responsible for the patterns of approach and passage observed at Milford Dam.

We note that thirteen of the 30 shad (43%) that were surgically tagged with acoustic tags in 2020 were detected returning to the Penobscot River in 2021. It is likely that these fish participated in spawning in 2020, successfully moved back downstream, and returned again to spawn. Though the number of fish is low, the ratio is consistent with our overall estimates of 40-50% repeat spawning in this study. One of these fish, a male who was a first-time spawner in 2020, was detected upstream of Milford Dam in 2021 even though it did not pass in 2020. These observations suggest that this technique may be appropriate for assessing fish over multiple years.

Given that Veazie Dam was the uppermost limit to shad migration for almost 180 years, and that this gave shad only approximately 15 km of usable spawning habitat before salinity became too high for egg survival (Grote et al. 2014a, Lipsky et al. 2016), there was considerable uncertainty as to the origin of adult shad observed at the Veazie Dam (Lipsky et al. 2016). However, Lipsky et al. (2016) demonstrated that successful reproduction was occurring below Veazie Dam by capturing pre-metamorphic individuals during a series of surveys in the summer of 2012. It is possible that our tagged shad were not motivated to explore or pass Milford Dam because they had located adequate spawning habitat downstream of the dam. Such a pattern is consistent with the hypothesis that expansion into newly available habitat in a watershed occurs as habitat is filled, rather than fish migrating as far upstream as possible.

We found dam passage motivation to be heavily influenced by individual spawning experience, with first-time spawners being more likely to pass Milford than fish that had spawned previously. This is in contrast with the trend described by Hightower et al. (2003), in which older shad and repeat spawners were more likely to continue upstream migration after tagging than younger fish and those that had not spawned previously. However, their conclusions were based only on 13 fish for which age and spawning history information was available, and so may not have been representative of the entire population. This may also reflect a differential response of handling to fish size.

Some of the shad we tagged passing Milford Dam could be strays from other rivers, as there has been a relatively high straying rate reported for American shad (Waters et al. 2000), but it is unlikely that enough strays would be included in our tagged sample to influence the results. It is possible that we were observing shad being forced to move upstream due to overcrowding on the spawning grounds below Milford, or, in the most recent years of our study, that we sampled adults that had been spawned upstream of Milford Dam shortly after the installation of the fish lift. This is a distinct possibility given that there is some evidence that shad may home to their natal tributaries to spawn (Carscadden and Leggett 1975). These two hypotheses are not mutually exclusive.

Although river connectivity has increased in the Penobscot River, there is little evidence that shad passing Milford Dam exploited all or even the majority of the habitat now available to them. Most of the shad released into the Milford headpond were only detected traveling approximately 3 km upstream. Shad that did approach upstream dams had low passage rates, and in the case of the West Enfield Dam, passage rates were 0% for 11 fish that approached. These data suggest that passage facilities at existing dams on the Penobscot River may be inadequate for shad, especially because the only upstream dam that had confirmed passage of shad was the Howland Dam, which is bypassed by a nature-like fishway.

Shad are well-known for being difficult to pass through fishways of nearly any design (Haro and Castro-Santos 2012). Shad are wary of changes in light (Larinier and Travade 2002, Haro and Castro-Santos 2012) and prefer to travel in schools (Haro and Kynard 1997, Larinier and Travade 2002, Haro and Castro-Santos 2012), making them especially unwilling to pass through any narrow openings in fishway structures. They also do not jump, despite being good sprint swimmers (Larinier and Travade 2002). All of these factors probably contribute to low passage rates seen at Howland and West Enfield Dams. Alternately, as suggested previously, a small number of fish passing Milford Dam may provide little motivation to leave suitable productive habitat and thereby abandoning the small number of conspecifics that are of obvious importance during spawning activities.

If shad spawned since the removal of Veazie Dam are indeed more likely to travel upstream of Milford Dam, there would seem to be a great potential for population growth in the coming years as shad access currently-underutilized habitat. As mentioned above, this may have implications for the population-level iteroparity rate observed as a downstream return migration if suitable downstream passage not be provided. Overall, we found that age and total length have changed very little since 2014, and that iteroparity rate has nominally increased since the installation of the Milford fish lift. This finding contrasts with Grote et al.’s (2014a) hypothesis that iteroparity rates may decline as the effects of river restoration took hold, however the population can hardly be considered to be re-established. Returns to Milford Dam in 2021 were fewer than 15,000 fish, indicating that population recovery is in its early stages relative to projected capacity (Stich et al., 2019, Zydlewski et al., 2021). Since 2017, iteroparity rates for Penobscot River shad have fluctuated between 42-58%, which is similar to rates observed by Leggett and Carscadden (1978) on the Connecticut River (38%).It may be too early to know if demographic shifts are occurring: assuming that most shad return to spawn for the first time as five year-olds, at the time of this writing it has not yet been two generations since Veazie Dam was removed. Besides just the energetic aspect of migration, the maintenance of high iteroparity rates in dammed systems hinges on successful downstream passage for both adults and juveniles

(Castro-Santos and Letcher 2010), and rates of downstream passage are currently unknown for Penobscot River American shad.

At this time of writing, shad are beginning to exploit habitat upstream of Milford Dam, but they have not realized the full migratory extent available to them and may be hindered by fish passage facilities at other dams throughout the system, or else the availability of spawning habitat compared to the relatively low numbers of fish above the dam makes further upstream travel unnecessary. These dynamics may change as shad spawned upstream of Milford Dam begin to return to the river as adults and seek upstream habitat for spawning. Continued monitoring of habitat use upstream of Milford Dam as well as dam passage efficiencies and population demographics may inform managers as to the effects of increasing connectivity on this population.

CHAPTER 2

EFFICIENCY OF ADULT SEA LAMPREY APPROACH AND PASSAGE AT THE MILFORD DAM FISHWAY, PENOBSCOT RIVER, MAINE, UNITED STATES

ABSTRACT

Sea lampreys provide important ecological services within their native range, such as nutrient cycling and habitat conditioning, which can benefit other fish species. Adult sea lampreys must access freshwater rivers in order to spawn, and because of this are susceptible to changes in river connectivity. Human-made structures, such as dams, can exclude them from usable habitat. Despite being within their native range, sea lamprey passage has not been extensively studied at dams in Maine. In 2020-21 we captured and tagged 150 sea lampreys at the Milford Dam, the lowest dam in the Penobscot River, Maine, and displaced them downstream to assess passage efficiency. In 2020, 50 lampreys were released on the east shore of the river downstream of Milford Dam; in 2021, the east shore release was repeated with an additional 50 fish, and another 50 fish were released on the west shore. Between 70-82% of lampreys passed Milford Dam again after mean delay times of 9-11 days. The location of release did affect dam passage or efficiency, however environmental factors may have resulted in higher attraction to the fishway in 2020. Passage success at dams upstream of Milford was highly variable. West Enfield Dam was not a barrier to sea lampreys (100% passage), while Brownsmill Dam apparently acted as a barrier to further migration. All years and release groups together had a median upstream migration distance of 38.8 kilometers after fish had passed Milford Dam, and a maximum upstream travel distance of approximately 100 kilometers. The insights into dam passage

efficiency provided by this study are an important first step towards ensuring that sea lampreys will continue to contribute to the ecosystems within their native range.

INTRODUCTION

Diadromous fishes migrate between marine and freshwater habitats to spawn and grow. Because their life cycle requires that they navigate between these two ecosystems, diadromous fishes are particularly vulnerable to river alterations that impede passage (Moring 2005). An analysis by Limburg and Waldman (2009) of diadromous fish abundances in the North Atlantic indicated that most of the populations in their study declined by over 90% between early surveys (late 19th-early 20th centuries) and those conducted more recently (late 20th-early 21st centuries). The authors attributed these declines largely to dams preventing migratory fishes from accessing all potential spawning reaches (Limburg and Waldman 2009).

Sea lamprey (*Petromyzon marinus*), which are native to the East Coast of North America and northern Europe and the Mediterranean (Beamish 1980, Hansen et al. 2016), have declined in parts of their North American range, likely because of damming (Moring 2005). The sea lamprey is perhaps best known for its role as an invasive species in the Great Lakes, where it feeds primarily on lake trout (*Salvelinus namaycush*) (Madenjian et al. 2008, Hansen et al. 2016). Sea lamprey control in the Great Lakes cost an average of over $5 million USD per year from 1998-2004 (Irwin et al. 2012). Therefore, most studies involving sea lamprey barriers to migration are focused on precluding sea lampreys from their spawning habitat. An internet search for scientific papers the term *"sea lamprey barriers to migration"* showed that among the first 50 results, over 70% concerned methods of sea lamprey control and other studies of sea lamprey in the Great Lakes. Until recently, sea lampreys returning to rivers in Maine, which is within their native range, were culled when they attempted dam passage (J. Zydlewski, personal observation). This practice was discontinued, but it reflects that sea lampreys were unwanted and that their ecological role was little understood.

The sea lamprey is ecologically important within its native range. Lamprey act as a conduit for marine derived nutrients into upstream river reaches and favorably condition substrate for other valuable species, such as federally endangered Atlantic salmon (*Salmo salar*) (Saunders et al. 2006; Nislow and Kynard 2009; Sousa et al. 2012). Studies in spawning streams in Maine indicate that the nutrient subsidies provided by adult sea lamprey carcasses benefit both larval sea lamprey and macroinvertebrates (Weaver et al. 2016, Weaver et al. 2018). Sea lamprey in a small tributary of the Connecticut River contributed up to 20% of the stream's total annual phosphorus budget through the decomposition of their carcasses after spawning (Nislow and Kynard 2009). This contribution was contingent upon the successful passage of lampreys at a downstream main-stem dam (Nislow and Kynard 2009).

Dams can cause significant delays for upstream migrating sea lamprey and these may even cause sea lamprey to abandon migration altogether (Castro-Santos et al. 2017). If poor passage prevents lamprey from reaching upstream river reaches, potential nutrient subsidies and habitat conditioning will be eliminated. Understanding passage efficiency for sea lamprey at dams is critical to ensuring the important ecosystem services provided by sea lamprey in dammed systems.

Little is known about sea lamprey movements and interactions with dams in the Penobscot River, Maine. The mainstem Penobscot River has an extensive history of damming (Walburg and Nichols 1967), but in the past decade restoration projects included dam removals and fish passage improvements (Opperman et al. 2011, Trinko Lake et al. 2012). Trinko-Lake et al. (2012) estimated that even after the restoration project, sea lampreys would still only have access to approximately 53% of their historic range. However, the effectiveness of dam passage for this species throughout the system is not known.

The overarching goal of this study was to describe the effectiveness of sea lamprey approach to and passage at Milford Dam. We did this by releasing sea lampreys double-tagged (radio and PIT) lampreys over two years. We also evaluated the effect of release site (east or west bank) on approach and passage at the fishway on the east side of the river. We recorded where lampreys approached the dam, and how much time they spent in the vicinity of the dam before successfully passing or abandoning upstream migration. We also tracked movements of sea lamprey above Milford Dam to gain an understanding of their migratory extent within the system and possible interactions with upstream dams.

METHODS

Study site

In 2020 and 2021 we collected adult sea lamprey at the Milford Dam as they ascended the dam on their upstream spawning migration. In 2020, 50 lampreys were captured, tagged, and released 1 km downstream of the dam on the eastern shore of the river. Tagging was repeated in 2021, with an additional 50 lampreys released at the 2020 release site (hereafter, east release), along with 50 lampreys released on the western side of the channel (west release) directly across from the east release site (Figure 2.1).

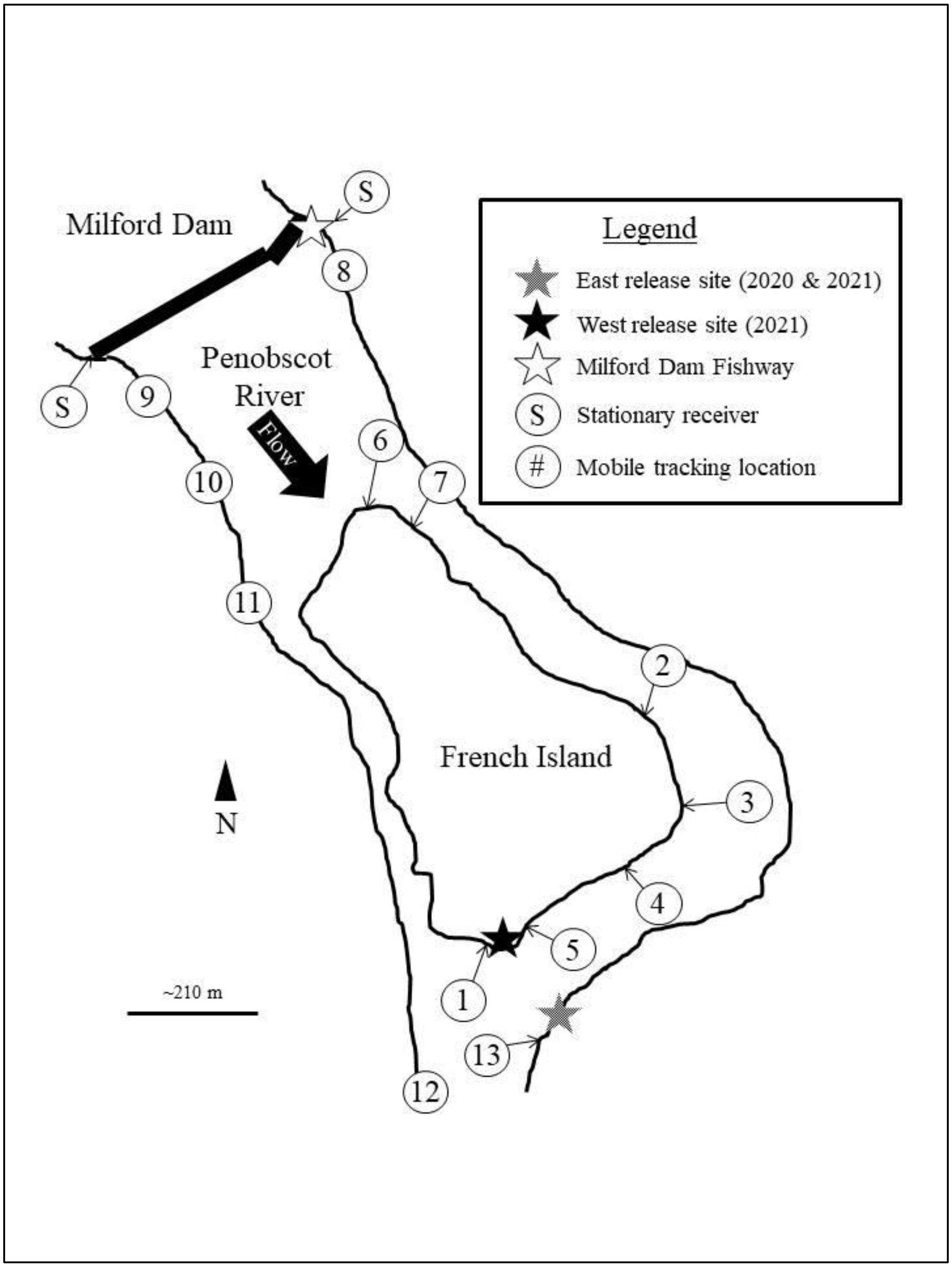


Figure 2.1. The Penobscot River immediately below the Milford Dam. Release sites are indicated by stars: Release Site 1 (shaded) was used in both 2020 and 2021, Release Site 2 (black) was used in 2021. The white star indicates the location of the Milford fish way. Radio receiver locations are shown in circles. Numbered circles indicate locations where daily mobile tracking took place in 2021, and circles marked S are the locations of the stationary receivers that were in place in 2020-21.

Milford Dam is the first dam that anadromous adult fishes encounter on their upstream spawning migration. Milford Dam has a single fishway located on the eastern shore of the Penobscot River equipped with an automated fish lift. This lift was installed in 2014 at the same time the Denil fishway that previously provided passage at Milford was decommissioned (PRRT 2018). The Denil fishway is reopened when maintenance at the dam requires that the fish lift be shut down for extended periods.

Sea lamprey capture and tagging

Capture, tagging, and release took place on 1 June and 3 June in 2020, and 25-26 May in 2021. Adult sea lampreys used in this study were intercepted at the Milford Dam by staff from the Maine Department of Marine Resources (ME DMR) after ascending the dam on their upstream migration. Sea lampreys that were judged to be in good condition (i.e., did not have any visible wounds) were placed in MS-222 solution (buffered 20 MM Na_2CO_3, pH=7.0) until they lost the ability to orient and became unresponsive to touch stimuli. Lampreys were then measured (mm) and tagged using internal radio tags. Radio tags (MST 820, Lotek Wireless, Inc. Newmarket, Ontario, Canada) measured 8 x 20 mm and weighed 2.1 g. A passive integrated transponder (PIT) tag (12 mm, APT12, Biomark, Boise, Idaho) was attached to each radio tag using a cyanoacrylate adhesive. This added approximately 2 mm to the diameter of the tag and allowed the fish to be detected on a PIT antenna array located near the exit of the Milford Dam fishway. Lampreys were wrapped in a wet towel during the surgeries, which took approximately 90s. First, a small incision just large enough to accommodate the radio tag was made in the peritoneal cavity. The radio tag antenna was threaded through a 14-gauge septum needle, passed through the incision, and pushed through the skin a few centimeters behind the incision. The tag was then guided into the incision manually while gently drawing on the antenna. The incisions were closed using two or three Vicryl sutures (Ethicon 4-0 RB-1 [Molina-Moctezuma et al. 2021]) and the lampreys were then allowed to recover in freshwater before release.

Lampreys were transported by truck to their respective release sites in a tank of aerated river water. Both release sites were less than 2.5 km from Milford Dam by road, and once the truck left the dam site, transport time to the release site was approximately 5 minutes. Fish were transferred into nets or buckets and carried to the edge of the water, where they were released near to the shore. They were monitored after release to ensure that they swam into deeper water.

Post-release tracking

Lamprey arrival to Milford Dam and passage through the fish lift was monitored by stationary radio receivers positioned at either end of the dam (Figure 2.1), and two PIT antennas in the upper part of the fishway near the exit to the headpond. Radio receiver stations consisted of a four-element Yagi antenna associated with a scanning receiver (Lotek SRX-800D, SRX-DL, and SRX-1200D, Newmarket, Ontario, Canada). The receiver station on the eastern side of Milford Dam, (located directly above the approach to the fishway), was also equipped dropper antennas placed: 1) inside the fishway near the entrance, and 2) behind the fish lift hopper (Figure 2.2). Droppers were made from coaxial cable with a single connector pin at the end and submerged using weights attached to the cable. The PIT antennas were built following the methods described in Kazyak and Zydlewski (2012). Both antennas were pass-through antennas mounted to plastic barriers on the walls and floor of the fishway. The plastic barriers prevented the antennas from touching the concrete because the rebar within the concrete can cause interference when the antennas are directly in contact with the concrete.

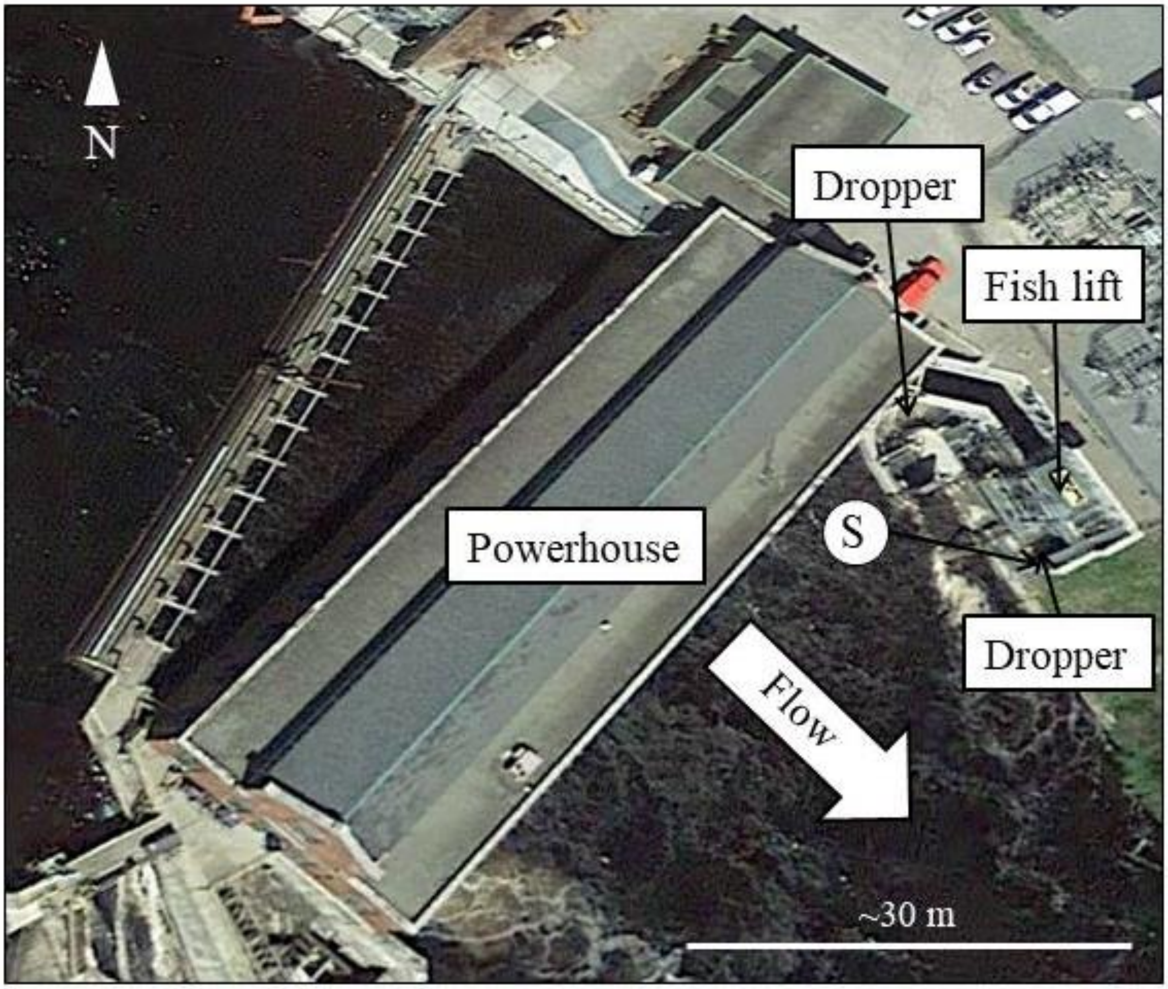


Figure 2.2. Aerial view of the Milford Dam powerhouse on the east side of the river showing the locations of the two dropper antennas relative to the fish lift. The S indicates the position of the stationary radio receiver and associated Yagi antenna.

Daily mobile tracking was carried out in the vicinity of Milford Dam during the time that stationary receivers were operational in 2021 (27 May-16 July). Personnel equipped with a portable radio receiver (Lotek SRX-400, Newmarket, Ontario, Canada) and a handheld Yagi antenna visited 13 locations from the southern tip of French Island to Milford Dam (Figure 2.1). At each location, tag codes and the signal strength of detections were recorded at a consistent gain setting. Mobile tracking above and below Milford Dam from canoes or motorized boats took place opportunistically throughout the summer during 2020 and 2021.

Approach to Milford (2021)

The relationship between detection signal strength and distance from a given antenna was established using a test tag (Lotek MCFT3-L) and a handheld GPS unit (Garmin eTrex 20x). The test tag and GPS were either carried or placed on a remote-controlled (R/C) boat within the reach extending approximately 450 m downstream of Milford Dam and spanning the width of the river (approx. 300-350 m). Transects were either walked or floated with the R/C boat while the GPS was set to actively track and record its location. After the transects were completed, the GPS tracks were downloaded and the data from the stationary radio receivers at Milford were collected.

Using the timestamps associated with the points on the GPS track and those associated with the detection of the test tag on the Milford receivers, it was possible to estimate the location of the test tag when detections occurred. The signal strength of the test tag could then be related to the tag's distance from the receiver at the time of the detection. Because the timestamp on the GPS was only accurate to the minute (it did not include a reading of seconds within each minute), the GPS coordinates and the detection signal strengths were averaged for each minute. Visual analysis in ArcGIS® Pro showed that averaging the coordinates on this timescale did not meaningfully change the location associated with the detection. Data from all minutes with both a GPS location and an estimated signal strength were retained for further analysis.

The dataset consisting of timestamp, coordinates (in decimal degrees), and average signal strength were processed and analyzed using Program R (R Core Team 2021). Coordinates were converted to UTM, and then the Pythagorean Theorem was used to calculate the distance in meters between the stationary receiver, which had a fixed location, and the location of the GPS unit. Using signal strength as a predictor variable and distance as the response variable, we fit the data to linear, exponential, and quadratic models. The adjusted R^2 for all models was between 0.72-0.73. The linear model was fit to the data and used in further analysis:

$$y = 301.97 - 0.367x \qquad \text{Eq.1}$$

Where y is the distance in meters from a given receiver set to a gain of 50, and x is the signal strength of the detected tag.

For each detection of a radio tag from a live lamprey, Equation 1 was used to compute the distance in meters between the tag (and therefore, the lamprey) and the stationary or mobile receiver on which it was recorded. Circular buffers were then created around the location of the receiver on which the detection was recorded using the computed distance from the receiver as the radius of the circle. Lamprey location was estimated on a daily basis as the intersection point of two or more buffers. Google Earth was used to create buffers and assign daily locations.

The estimated location where each lamprey first approached Milford Dam was taken to be the first assigned location after release that was upstream of French Island (i.e., within approx. 450 meters downstream of the dam). This area coincided with the area where signal strength mapping took place. If lamprey were initially located downstream of the powerhouse, they were considered to be approaching the “east side” of the dam. Lamprey that initially approached the dam structure itself were approaching the “west side” of the dam. The dam structure is approximately 630 meters wide, and the powerhouse approximately 145 meters wide. It was clear from aerial imagery and on-the-ground observations that the influence of the attraction flow coming out of the fishway is restricted to the eastern side of the channel, and likely does not extend beyond the width of the powerhouse.

For lamprey that approached Milford Dam, we obtained the time of entry (night vs. day) to the fishway and the time of dam passage. Time of fishway entrance was assigned to the timestamp of the first detection of a lamprey on either of the dropper antennas. Passage time—the time at which the fish successfully passed upstream of the dam--was assigned using either the timestamps from detection on the Milford PIT array or from detections on the stationary radio receiver immediately upstream of Milford Dam. Passage time could also be inferred as the time when lampreys that were known to pass the dam disappeared from the Milford radio antennas. Night was defined as the period between the beginning of civil twilight on the evening a given day and the end of civil twilight on the morning of the following day. The beginning and end times of civil twilight in Orono, ME were recorded from the internet (Time and Date AS 2021) for each day on which lampreys approached or passed the Milford Dam.

Upstream movements (2020 & 2021)

Movements upstream of Milford Dam were described based on radio and PIT detections above the dam in both years. Stationary, shore-based radio receivers were located throughout the Penobscot River mainstem and the Piscataquis and Passadumkeag Rivers, which are major tributaries to the Penobscot River entering the mainstem at RKM 99 and 92.3, respectively (Figure 2.3). PIT arrays similar to the one at Milford dam were also deployed in the fishways at four dams upstream of Milford: West Enfield Dam (Penobscot River, RKM 100), Weldon Dam (also known as Mattaceunk Dam, Penobscot River, RKM 150.2), Brownsmill Dam (Piscataquis

River, RKM 163), and Pumpkin Hill Dam (also known as Lowell Tannery Dam, Passadumkeag River, RKM 112.7). Howland Dam, which is located on the Piscataquis River at its confluence with the Penobscot (RKM 99) is circumvented by a nature-like fish bypass that became operational in 2016 (Opperman et al. 2011). Although the dam structure is still present, the fishway is not in use and so this site was monitored by two stationary radio receivers during our study.

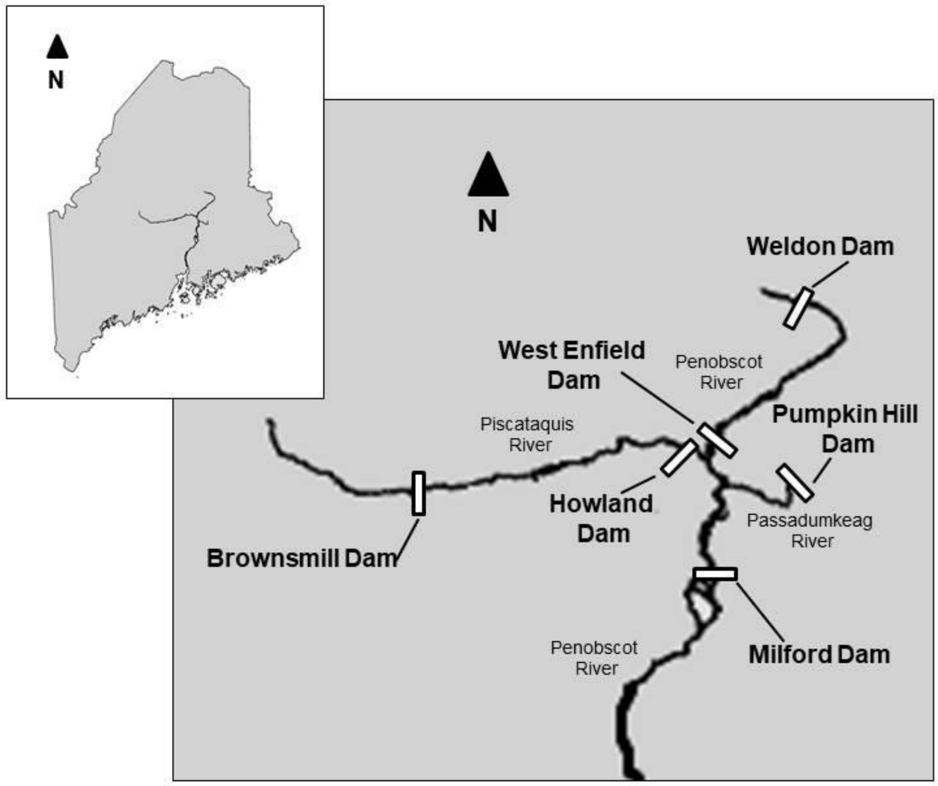


Figure 2.3. Location of six dams where the passage rates of radio-tagged sea lampreys (*Petromyzon marinus*) were recorded on the mainstem Penobscot River and its major tributaries. The location of the Penobscot River within the state of Maine is shown in the inset. Map adapted from Peterson et al. *in progress*.

Because the fish were sampled within only a few days in each year, and because they are assumed to represent a random sample of all the sea lamprey that passed Milford on those days, there was no reason to believe that their behaviors after successfully passing the dam would differ. Therefore, 2021 release site was not considered in the analysis of upstream movements. We recorded the maximum distance that tagged lampreys travelled upstream of their release sites, and whether they approached and/or successfully passed any of the dams upstream of Milford. There were no dropper antennas in any fishways upstream of Milford, so approach was determined by a detection on a downstream-facing radio antenna, or detection in a fishway via the PIT array. Successful passage was recorded when lampreys were detected on a radio antenna facing upstream of a given dam, or when they were detected on a PIT antenna located near the exit of a fishway.

River discharge

Discharge records that covered the week that tagged lamprey were released in each year (1 June to 8 June 2020 and 25 May to 1 June 2021) were taken from the U.S. Geological Survey gage at West Enfield, Maine (USGS 01034500 [USGS WaterWatch, https://waterwatch.usgs.gov/]). The gage records discharge (cubic feet per second [CFS]) every fifteen minutes. The post-release discharge records were visually compared between the two years to describe differences in river flow that might have affected sea lamprey approach or passage.

Data analysis

Lampreys from the two release groups in 2021 were categorized as either approaching the Milford fishway after release, or not approaching the fishway after release. Approach was defined as detection by one or both of the stationary receivers, or detection within approximately 450 m downstream of the dam during mobile tracking. Lamprey that did not approach the fishway after release included individuals that approached the western half of the dam (the side without passage facilities) and those that reversed direction downstream after being returned to the river. Reversal was assigned when a detection was received greater than 1 km downstream of the release site immediately following release.

We hypothesized that there may be a difference in the location of approach to Milford Dam between the east and west release groups in 2021. We therefore tested the null hypothesis that fish from both release groups were equally likely to approach the eastern half of the dam (thus the Milford fishway) as they were to approach the western half of the dam or to reverse direction after release. Counts of tagged individuals from each group that initially approached the eastern/fishway half of the dam after release were compared using a χ^2 test. A threshold of $\alpha=0.05$ was used for evaluating the results of all statistical tests.

For those fish that approached the Milford Dam at any location, the time to approach and the delay time below the dam (the time elapsed from approach to passage or abandonment of upstream movements) were recorded, as well as whether or not that fish successfully passed the dam. Fish that initially reversed direction were also included in these calculations. Approach time, delay time, and passage success were also compared between the two groups with a Welch's *t*-test, which does not require the assumption that variance between sample populations is equal (Nicholas School of the Environment 2022). All statistical analyses were performed in Program R (R Core Team 2021) with $\alpha=0.05$.

RESULTS

The mean sizes of the lamprey tagged in each year were similar among years and release sites (Table 2.1). The transmitter from one lamprey in the west release was never detected after release and was not included in any analyses. Assigning sex based on morphology was possible for 22 lampreys and was confirmed by the observation of gonads during tagging. Therefore, we know that 6 of our lamprey in 2020 were females; during 2021, 6 females and 4 males were in the east release, and 6 females were in the west release. These sample sizes were too small to be able to include sex in any of our analyses.

Table 2.1. Numbers of tagged sea lampreys released at each site throughout the study. Mean length of lampreys (mm) and length range (parentheses) are reported. Delay time is the time spent between approach to the Milford Dam and either successful passage or migratory abandonment. Maximum delay times are displayed in parentheses.

	2020	East release	West release
Number	50	50	50
Mean length (mm)	743 (650-810)	737 (650-820)	743 (630-850)
Mean delay before successful passage (Max.)	2 days (~15)	3.4 days (12)	4.2 days (13)
Mean delay before abandoning migration (Max.)	8 days (15)	11 days (44)	9 days (27)
Passage success	82%	70%	73%

Milford Dam passage and delays (2020)

In 2020, the return rate to Milford was 100%. Every tagged lamprey was detected in the Milford fishway at some point after release, with no reversal behavior documented between release and approach to the fish way. Overall passage success rate was 82% (41/50, Table 2.1). Forty-eight lamprey (96% of all fish tagged), were detected on a dropper antenna in the Milford fishway, on the Milford PIT array, or on a stationary receiver just upstream of Milford within 24 hours of release. Of the remaining two fish, one was detected entering the fish way within 36-48 hours of release (the exact time of entry was unknown), and the other was not detected at Milford but was detected in the vicinity of Howland Dam (RKM 99) approximately 48 hours after release. This observation raises the possibility that sea lampreys could be using alternate passage routes to pass Milford Dam, such as climbing up the dam face.

The average time spent below Milford Dam between approach and successful passage was 2 days (n=40, Table 2.1). One lamprey spent approximately 15 days (the exact date of passage was unknown) searching for passage. Among the nine lamprey that eventually abandoned migration, the mean time spent searching for passage was eight days and the maximum was 15 days (Table 2.1, Figure 2.4).

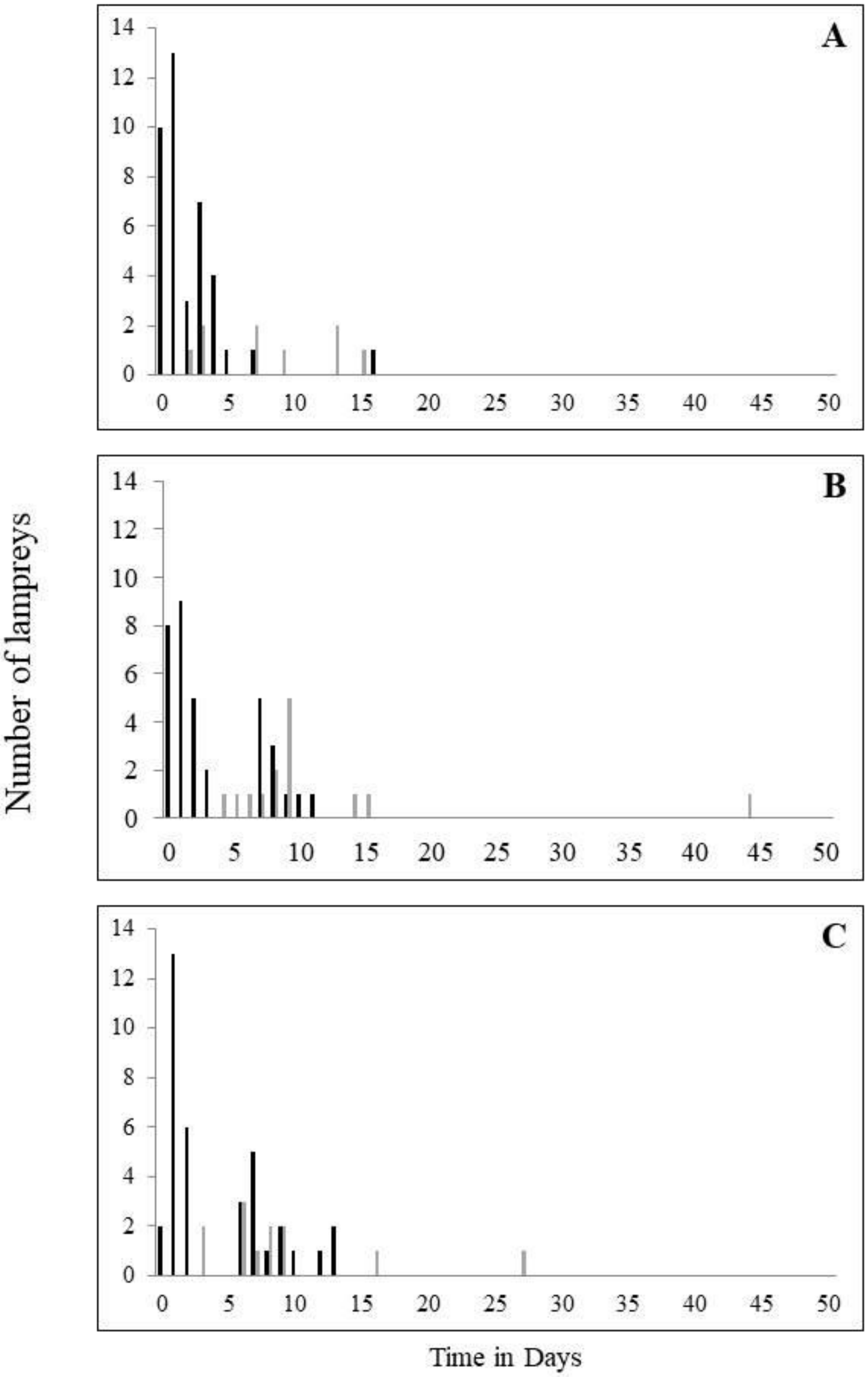


Figure 2.4. Days until successful passage (black bars) or migratory abandonment (gray bars) for tagged sea lampreys (*Petromyzon marinus*) after they had approached Milford Dam. A) sea lampreys released in 2020; B) sea lampreys from the east release in 2021; and C) sea lampreys from the west release in 2021.

The timing of fishway entrance in 2020 was skewed towards the hours between sunset and sunrise, with 31/45 (68.8%) of fish for which entry times could be determined first detected in the fishway during dark. Exact time of successful passage of Milford Dam was only known for 26 individuals, and 16 (61.5%) passed the dam during dark (Figure 2.5).

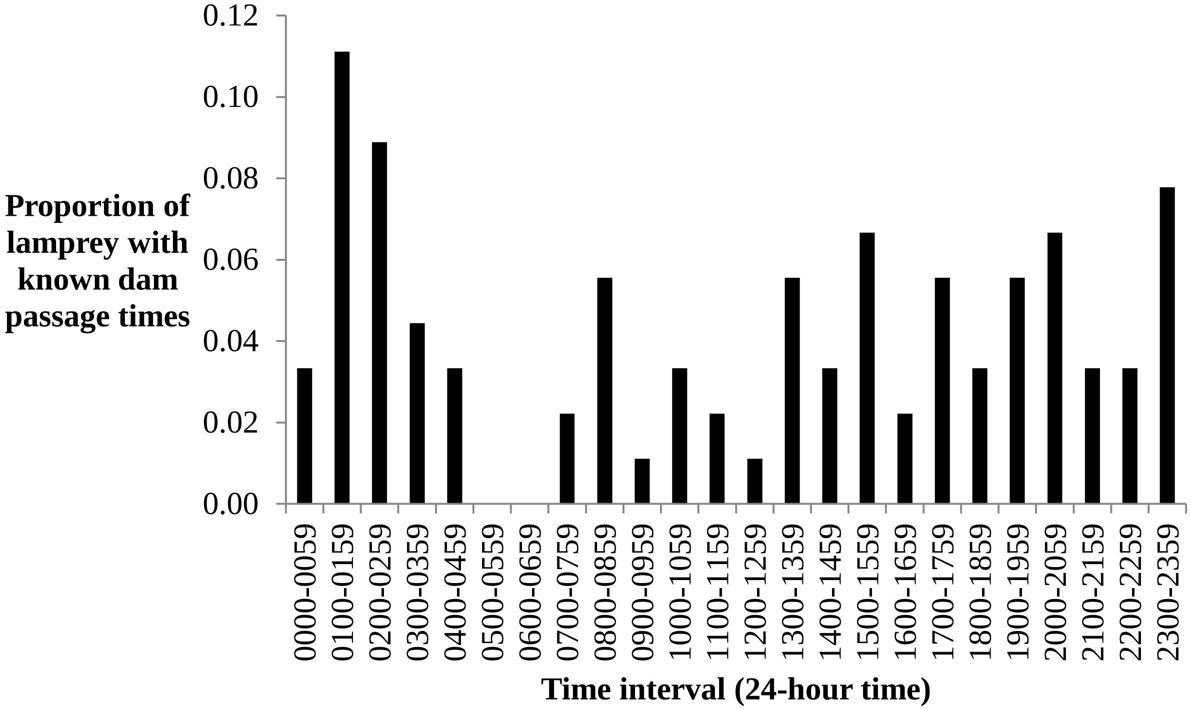


Figure 2.5. Time of dam passage for 90 sea lampreys (*Petromyzon marinus*) at the Milford Dam. Passage time is binned by hour using 24-hour time.

Milford Dam passage and delays (2021)

The majority of lampreys for which approach time was known approached Milford Dam on the day of release. This was consistent between both release groups, with 40/49 fish from the east release approaching on the same day, and 47/48 from the west release approaching on the same day. The remaining 10 lampreys approached the dam the day after release (overall return rate of 98%). Passage success rates between the two release groups were similar to but less than the overall passage success observed in 2020 (70% for the east release vs. 73% for the west release [Table 2.1]).

Time to pass after approach was not different between fish from the two release groups. On average, lampreys from the east release required 3.4 days to pass Milford after approach, and lampreys from the west release required 4.2 days (Welch two sample *t*-test, t=-0.96357, P=0.339 [Table 2.1]). The maximum number of days that any lamprey was delayed below Milford before passing the dam was 12 for the east release, and 13 for the west release. Overall, 35 lampreys from the east release and 36 lampreys from the west release were successful in reascending Milford Dam. Of the lampreys that abandoned migration, delays averaged 10 days (11 days for the east release and 9 days for the west release, Table 2.1). Maximum delay time was 44 days experienced by one lamprey from the east release. The longest delay for any fish from the west release was 27 days (Table 2.1, Figure 2.4).

In 2021, entry times to the fishway were recorded as the timing of the final fishway entry prior to successful passage. This was because the intensive mobile tracking that took place in that year made it possible to determine if lampreys had entered and exited the fishway multiple times prior to passage. Only 25 lampreys from the east release and 26 lampreys from the west release had known entry times to the fishway, and of these 12 (48%) and 8 (30.8%) entered the fishway between sunset and sunrise, respectively. Among lampreys for which individual passage times could be determined, 17/ 33 lampreys (51.5%) from the east release and 12/31 (38.7%) lampreys from the west release successfully passed Milford Dam at night (Figure 2.5).

Approach to Milford (2021)

Sixty-nine lampreys were detected from multiple locations on the day or days following release, and so were able to be included in the determination of approach location to Milford Dam. However, two lampreys from the east release were initially located adjacent to the release site and so were excluded from further analysis of approach location. The initial locations of 31 fish from the east release and 36 fish from west release are shown in Figure 2.6. Only four lampreys from each release group approached the fishway side of the dam. The proportion of lampreys from the east release that did approach the fishway (12.9%) was higher than the proportion approaching from the west release (11.0%), but the difference was not significant (Two-proportion *z*-test, χ^2=2.2e-31, P=1.0). The remaining lampreys for which an approach location could be determined approached the dam away from the fishway.

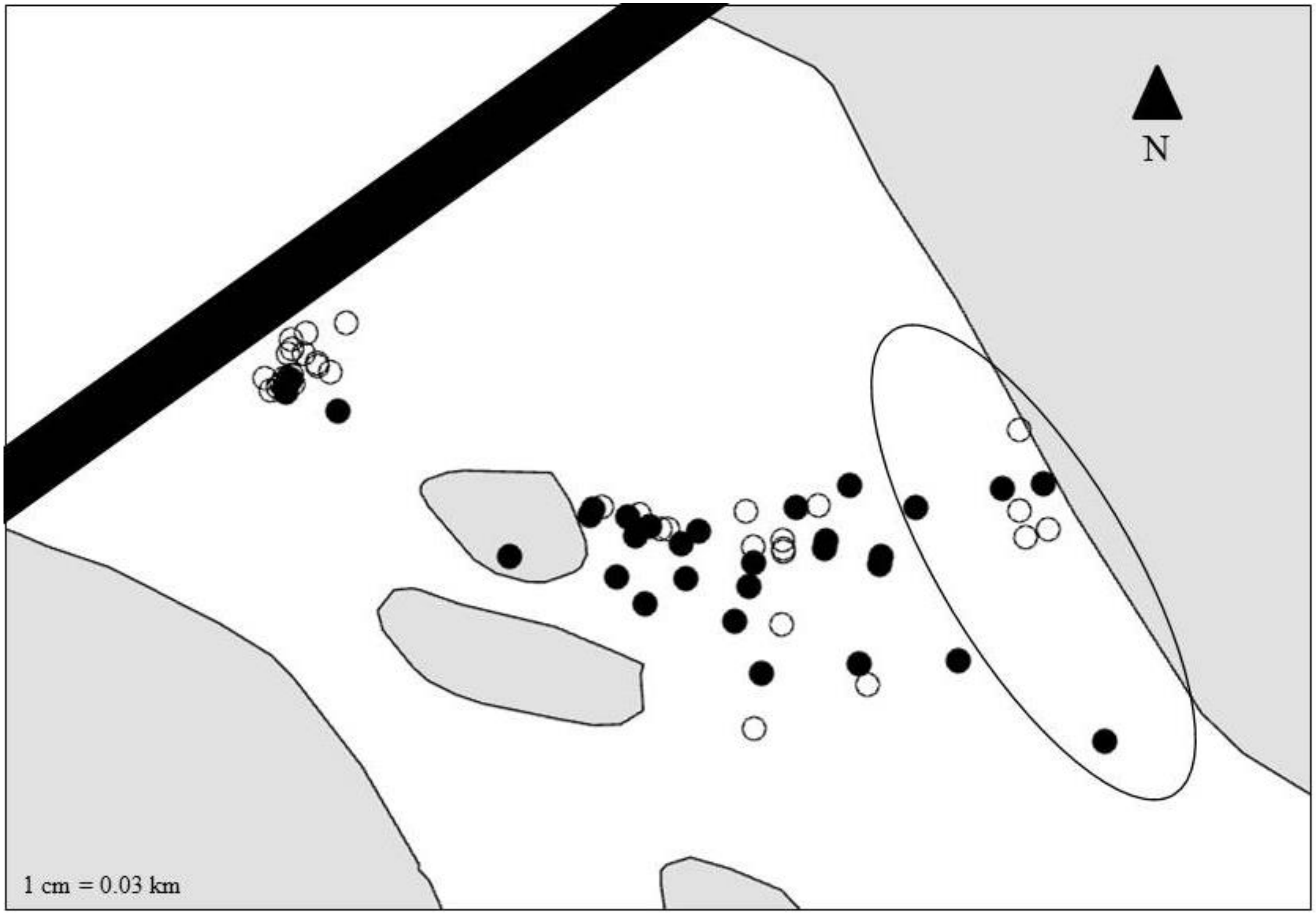


Figure 2.6. Initial location of 31 sea lampreys (*Petromyzon marinus*) released from the east release (filled circles) and 36 lampreys released from the west release (open circles) in 2021, upon approach to the Milford Dam. The lampreys within the oval approached on the "east side" of the dam, near the fishway.

Upstream movements (2020 & 2021)

The majority of lampreys that passed Milford Dam in 2020 also approached and passed West Enfield Dam (29/41, 70.7%) at RKM 100 (Table 2.2, Figure 2.7). Of those 29 fish that passed West Enfield, three traveled an additional 50 km upstream to Weldon Dam, two of which passed Weldon Dam. A small number of lampreys approached the Howland Dam at RKM 99 (7/41, 17.1%) but all seven were successful in passing, and one fish was recorded approaching the Brownsmill Dam but did not pass. The median distance traveled from the release site was 39.8 km upstream, with the greatest upstream travel distance (100.5 km upstream of the release site) being recorded by the single lamprey that approached the Brownsmill Dam (Table 2.2, Figure 2.7).

Table 2.2. Numbers of tagged sea lampreys (*Petromyzon marinus*) approaching (App.) and passing (Pass) dams throughout the Penobscot River watershed. Maximum and median distances (med. dist.) are the distances in kilometers travelled upstream of Milford Dam (RKM 61.3). MIL=Milford Dam; HOW=Howland Dam; WEN=West Enfield Dam; WEL=Weldon Dam; BRO=Brownsmill Dam; PHI=Pumpkin Hill Dam.

Year	**App. MIL**	**Pass MIL**	**App. HOW**	**Pass HOW**	**App. WEN**	**Pass WEN**	**App. WEL**	**Pass WEL**	**App. BRO**	**Pass BRO**	**App. PHI**	**Pass PHI**	**Max dist.**	**Med. dist.**
2020	50	41	7	7	29	29	3	2	1	0	0	0	100.5	39.8
2021	97	71	25	18	34	34	6	0	6	0	0	0	102.8	38.8

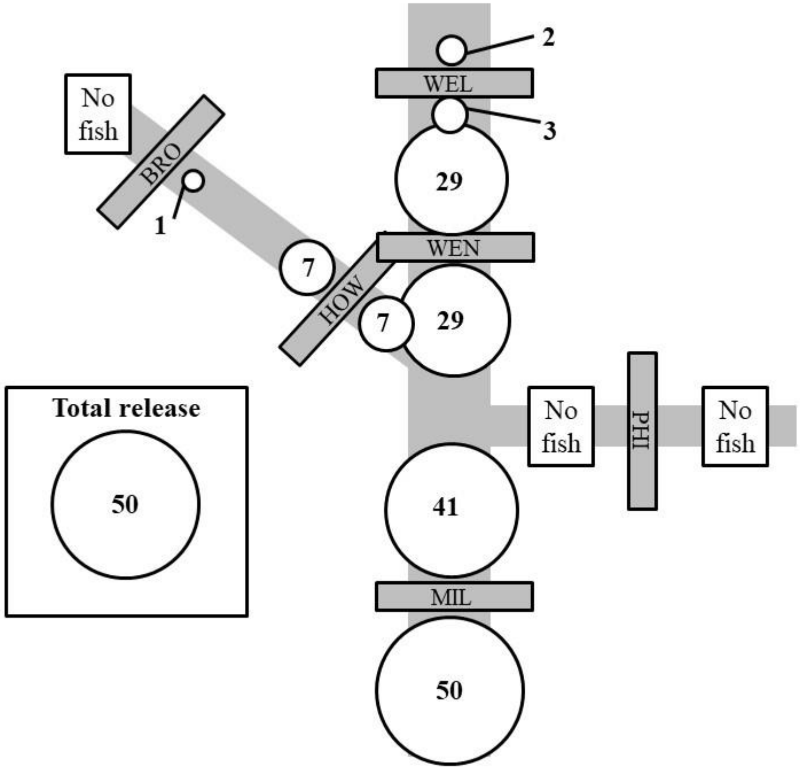


Figure 2.7. Number of tagged sea lampreys (*Petromyzon marinus*) that approached and passed each dam in the Penobscot River watershed which was being monitored by PIT and/or radio arrays in 2020. The number within each circle is the total number of sea lampreys, and the sizes of the circles are relative to the size of the release, shown in the inset. Circles immediately downstream of a given dam represent approach and the circles immediately upstream represent passage. MIL=Milford Dam; HOW=Howland Dam; WEN=West Enfield Dam; WEL=Weldon Dam; BRO=Brownsmill Dam; PHI=Pumpkin Hill Dam.

In 2021, passage rates at the West Enfield Dam were 100% among the 34 lampreys that approached from downstream (Table 2.2, Figure 2.8). Although six lampreys approached Weldon Dam in 2021, none successfully passed that dam. Eighteen out of 25 lampreys that approached Howland Dam passed successfully, and six lampreys approached Brownsmill Dam but did not pass it. Median travel distance upstream of Milford for 2021 lampreys was 38.8 km. Similar to 2020, the fish exhibiting the greatest upstream travel distances were those that approached the Brownsmill Dam.

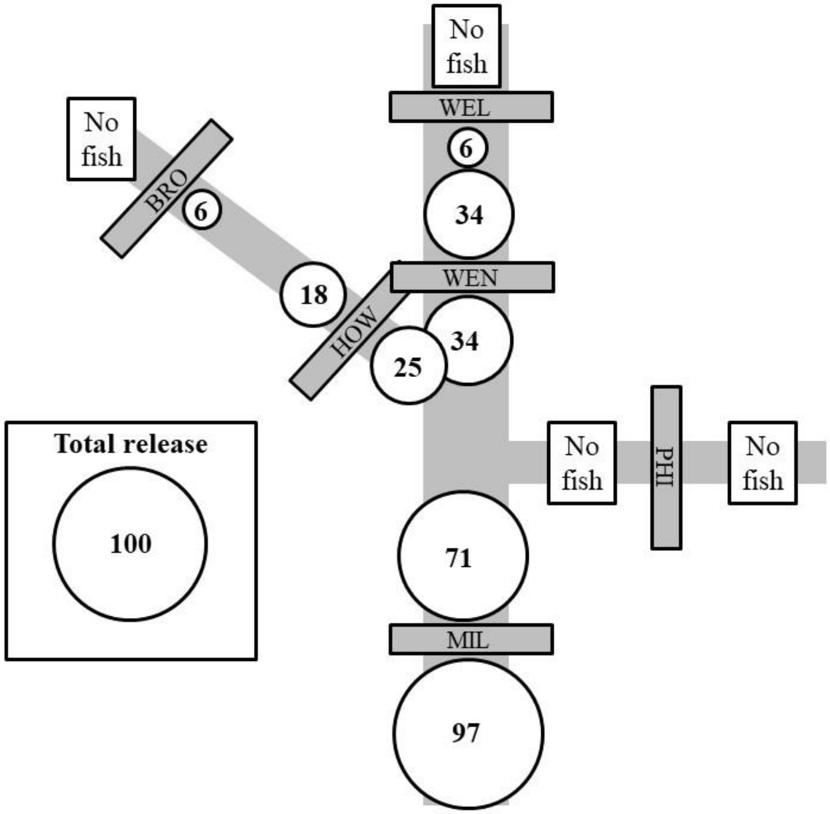


Figure 2.8. Number of tagged sea lampreys (*Petromyzon marinus*) that approached and passed each dam in the Penobscot River watershed which was being monitored by PIT and/or radio arrays in 2021 (release groups combined). The number within each circle is the total number of sea lampreys, and the sizes of the circles are relative to the size of the release, shown in the inset. Circles immediately downstream of a given dam represent approach and the circles immediately upstream represent passage. MIL=Milford Dam; HOW=Howland Dam; WEN=West Enfield Dam; WEL=Weldon Dam; BRO=Brownsmill Dam; PHI=Pumpkin Hill Dam.

River discharge

River discharge on the first release date in 2020 was approximately 3,000 CFS higher than the discharge on the first release date in 2021 (Figure 2.9). However, the 2020 discharge dropped steadily until three days post-release (27 May 2020), at which time it eclipsed the 2021 flow record (three days post-release in 2021 was 3 June 2021). For the remaining five days that flow records were compared, discharge was higher in 2021.

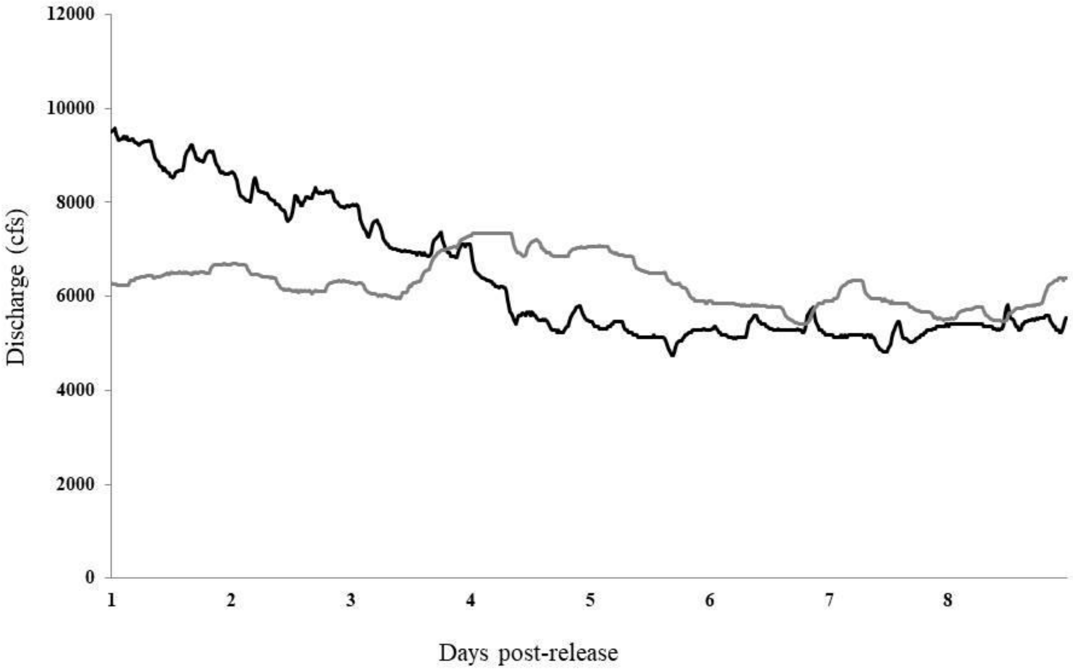


Figure 2.9. Discharge measured in cubic feet per second (cfs) at the U.S. Geological Survey gage in West Enfield, Maine (USGS 01034500) beginning on the day of release and continuing for one week. The record for 2020 (black line) spans from 1 Jun-8 Jun, and the record for 2021 (gray line) spans from 25 May to 1 Jun.

DISCUSSION

Overall, passage success of tagged sea lampreys at the Milford Dam seems to be much higher and more efficient (i.e., shorter delays) than in other major systems on the East Coast. Passage rates through four fishways on the Connecticut River were only as high as 55%, with passage success dropping below 30% at one fish way (Castro-Santos et al. 2017). In contrast, 98% of tagged sea lampreys returned to Milford Dam after release, and passage success rates were 70% or greater for all three groups (Table 2.2). The high passage success rates for our fish may be attributed to the fact that our lampreys were not naive to the Milford Dam. Fish tagged by Castro-Santos et al. (2017) were released immediately upstream of the dam where they were captured, and their movements were tracked thereafter, whereas our fish were released within 2 km downstream of the Milford Dam, which they had all already successfully passed. However, high rates of passage success were also observed elsewhere in the Penobscot, notably at West Enfield Dam, where passage was 100% for all groups, suggesting that the sea lampreys used in our study were highly motivated to move upstream at all dams, not just Milford.

Despite these relatively high passage success rates, tagged sea lampreys ultimately successfully passing Milford Dam experienced passage delay times ranging from one day to nearly two weeks (13 days). Lengthy upstream passage delays experienced by sea lampreys in the Connecticut River (median delay time of approximately two weeks) caused some fish to abandon migration (Castro-Santos et al. 2017). Likewise, delay time may have been associated with migration abandonment in the Penobscot. Mean delay time for ultimately-successful passers was 3.2 across both years of the study (Table 2.2). However, lampreys from those releases that abandoned migration experienced mean delays of 9.3 days (Table 2.2). The Milford Dam fish lift was operational until approximately November 15 each year, so even tagged lampreys experiencing the longest observed pre-abandonment delay (44 days) had the opportunity to pass upstream of the dam.

Compared to other migratory species in the Penobscot River, such as Atlantic salmon, passage rates for our tagged sea lampreys were low and migratory abandonment was triggered by relatively short delays. Atlantic salmon that were tagged at Milford Dam and transported ~20 km downstream had a passage success rate of 92% among fish that approached the dam after release, even with delays lasting as long as 155 days (Peterson et al., *in progress*). Both phenomena may be at least partially explained by the differences in sea lamprey life history compared with other anadromous species on the East Coast. Most important is that sea lampreys are semelparous. Unlike Atlantic salmon and many other diadromous fishes in their native range, all sea lampreys die after spawning (Beamish 1980). Therefore, lifetime fitness for sea lampreys is contingent upon migratory motivation in a single season, and this may help explain why our tagged lampreys abandoned upstream migration relatively quickly, and presumably sought other spawning habitat after delays at the Milford Dam. McConnachie et al. correctly predicted that pink salmon (*Oncorhynchus gorbuscha*) reproduction would not be affected by acute stressors because of the necessity for these fish to spawn before dying at the end of their freshwater migration period (McConnachie et al. 2012). Likewise, semelparous sockeye salmon (*O. nerka*) did not alter their migratory speeds after being subjected to handling and tagging (Cook et al. 2014). It makes logical sense that semelparous species would resist a certain amount of stress in favor of completing their life cycle (Wingfield and Sapolsky 2003), and this may also be why our tagged lampreys sought other spawning opportunities when they were not able to pass Milford Dam in a relatively short amount of time.

Sea lampreys also do not return to their natal steams to spawn, but instead migrate up any suitable river when they are ready to spawn (Waldman et al. 2008). This behavioral divergence from other diadromous fishes may be a result of parasitism—lampreys are dispersed throughout the ocean by their host species, in no particular pattern—and is evidenced by high rates of genetic diversity within populations collected in the same freshwater locations (Waldman et al. 2008). Because they are not returning to a specific natal stream, some sea lampreys may have less motivation for dam passage and may seek downstream spawning habitat instead of continuing to search for upstream passage.

Delays of any magnitude, including the delays that we observed for our tagged individuals, could be biologically meaningful for sea lampreys. Like most anadromous fishes, sea lampreys do not feed after entering freshwater (Beamish 1979). Energy concentration decreases significantly in adult sea lampreys as they reach maturation during their spawning migration, and a considerable amount of the total energy of both males and females is required for spawning activities (Beamish 1979). Rubenstein (2021) found that delays below a single dam could result in losses of fat reserves approaching 20% for Atlantic salmon due to the energy expenditure of search behavior and exposure to increased water temperature, and that on heavily dammed rivers where salmon experienced multiple delays these losses could lead to death before spawning. We did not investigate the energy expenditures incurred by our tagged lamprey, or quantify delays at dams upstream of Milford, but it is likely that delays did occur and that the time spent engaged in search behavior throughout the system could result in higher-than-normal energy losses compared to a situation where sea lampreys were allowed to migrate upstream unimpeded.

We know that sea lampreys use olfactory cues, particularly pheromones excreted by larvae, to locate suitable spawning reaches (Bjerselius et al. 2000), and we thought that olfaction may also direct lamprey to the Milford Dam, and specifically, attraction flows from the fishway. However, there was no evidence that release site during the 2021 season affected the ability of lamprey to find or use fish passage at Milford Dam. Intensive mobile tracking from that year indicated that sea lampreys from both release groups did not directly approach the entrance to the fishway when first approaching Milford Dam (Figure 2.6). This may be due to spill coming over the dam, causing lampreys to be attracted to areas other than the fish way entrance. For Atlantic salmon, prior experience with the Milford Dam fishway did not guarantee that subsequent search and passage would be more efficient (Peterson et al., *in progress*), and this may be the case with sea lampreys as well, although we do not know anything about their first passage attempts prior to tagging.

We hypothesize that river discharge may have contributed to the marked differences observed in approach time and location between 2020 and 2021. In 2020, 96% of tagged fish returned to the Milford Dam fishway or passed the dam within 24 hours of release, whereas we did not see any lampreys entering the fish way so soon after release in 2021. High flows in the days following the 2020 releases may have enhanced attraction flow into the Milford fishway. Conversely, because there was no intensive mobile tracking below Milford Dam in 2020, it is possible that we missed the fine-scale movements of sea lamprey in that vicinity, and that return to the fishway was not actually as efficient as it seemed.

The maximum upstream extent that we recorded for any of our tagged sea lampreys was approximately 160 km upstream from the ocean (they reached Milford Dam at RKM 61.3 and then proceeded ~100 km upstream to Brownsmill Dam), which is a similar distance travelled by lampreys in other studies where dams inhibited upstream migration (e.g., 140 km, reported by Beamish 1979). However, sea lampreys are capable of travelling even greater distances before spawning (e.g., Castro-Santos et al. 2017, Kynard and Horgan 2019), suggesting that our lampreys could have migrated further upstream if not impeded by dams.

Even short passage delays may still be biologically meaningful for Penobscot River lampreys, especially because lampreys that are motivated to move upstream encounter multiple dams throughout the system, and may even have their upstream migration denied by inadequate passage elsewhere in the system. Without adequate passage, sea lampreys cannot provide nutrient cycling or habitat conditioning services (Saunders et al. 2006, Sousa et al. 2012). The loss of sea lampreys therefore has ecological ramifications, especially for other fish that share parts of their native range, such as the Atlantic salmon. This makes understanding patterns of dam approach and passage in sea lampreys important not just for that species but for the preservation of a functioning ecosystem.

CHAPTER 3

SYSTEM-WIDE MIGRATORY DELAYS OF ATLANTIC SALMON *SALMO SALAR* IN THE PENOBSCOT RIVER, MAINE

ABSTRACT

Migratory delays caused by dams adversely affect both smolt and adult Atlantic salmon (*Salmo salar*) as they move between the ocean and freshwater habitat. We used a six-year dataset (2014-2020) of the movements of 309 (83% smolt-origin, 17% wild-origin) radio-tagged adult Atlantic salmon from the Penobscot River, Maine, to investigate delays and passage efficiency at six dams. Although most (92%) salmon did successfully pass Milford Dam, the lowermost dam at river kilometer 61, most (89%) were also delayed for over 48 hours. Salmon had low passage efficiencies and displayed extensive searching behavior when approaching dams at the confluence of the Piscataquis and the adjacent mainstem Penobscot. The vast majority of spawning adults in the Penobscot River are hatchery-origin fish stocked into the river as smolts, and current stocking practices release smolts downstream of Milford Dam and near suitable spawning habitat. While lower river stocking may achieve the goal of minimizing out-migration mortality by reducing or eliminating dam-related deaths, it may also prevent smolts from imprinting on upstream waters. Increasing migratory efficiency is first required before changing current smolt-stocking practices has any chance of allowing wild reproduction necessary to preserve the Penobscot River run of Atlantic salmon.

INTRODUCTION

Habitat loss because of dams is one of the greatest threats facing anadromous fish species on the Atlantic Coast (Limburg and Waldman 2009). The Atlantic salmon (*Salmo salar*) has experienced significant declines across its North American range due to damming, pollution, and overharvest (Parrish et al. 1998). Damming can cause this iconic species to experience significant migratory delays as they try to reach their spawning grounds, or prevent them from spawning completely.

In Maine, the Penobscot River has the largest run of returning Atlantic salmon in the state, but as in 2020 less than 1,500 adult salmon returned to the river with , the vast majority of hatchery origin (ME DMR 2021). This is far less than past estimates of 100,000 fish in historic runs (Foster and Atkins 1869 *in* Saunders et al. 2006). Both recreational and commercial harvests of the species have been closed due to population declines (Saunders et al. 2006). In addition, the Gulf of Maine Distinct Population Segment, to which the Penobscot River salmon belong, was listed as Endangered (Endangered and Threatened Species 2009), further accelerating focused efforts to restore the population. Dam passage and the restoration of river connectivity have been primary targets for conserving Atlantic salmon in the Penobscot River.

The history of damming on the Penobscot River began in the 1800's. The Bangor Dam was constructed at river kilometer (RKM) 42 in 1830, followed by the Veazie, Great Works, and Milford Dams (RKMs 48, 58, and 61, respectively) in that decade and into the early twentieth century (Walburg and Nichols 1967). The Bangor Dam was naturally breached in the 1970s (Bangor Historical Society 2016), after which the Veazie Dam was the lowermost dam on the river. After that breach Atlantic salmon had restricted access to only about 25% of their pre-damming range (Opperman et al. 2011).

In 2004 the Penobscot Indian Nation and several other conservation organizations, along with state and federal entities, began discussions with hydropower companies on the Penobscot River that eventually led to the formation of the Penobscot River Restoration Trust (PRRT, “the Trust”), which had the goal of restoring migratory fish passage to the river (Opperman et al. 2011). The Trust obtained funds to purchase and remove dams on the river beginning with the Great Works Dam in 2012 and followed by the Veazie Dam in 2013. Howland Dam (RKM 99) was not removed but was instead bypassed by a nature-like fish bypass completed in 2016. Milford Dam, which as of 2013 was the lowermost dam on the river, received a new fish lift to aid in passage, as well as two new turbines to offset the loss of production from Great Works and Veazie (PRRT 2018, Richard Dill pers. comm.). Trinko Lake et al. (2012) estimated that Atlantic salmon had access to approximately 53% of their historic habitat both pre- and post-restoration, but that accessibility was anticipated to be greatly improved. However, this assumed safe and efficient fish passage at remaining fish ways, and the authors also called for more research in this area (Trinko Lake et al. 2012).

Evaluating the efficacy of fish passage at the Milford Dam has been a priority for researchers working with Atlantic salmon and other species on the Penobscot River. Previous studies have found that passage rates at the fish lift are very high, ranging from 95.5-100% (Izzo et al. 2016). Nevertheless, success is influenced by river flows and water temperature (Holbrook et al. 2009). Even fish that eventually pass the dam may be subject to lengthy delays while searching for passage (Holbrook et al. 2009, Izzo et al. 2016). Atlantic salmon delays below Milford Dam have been found to be highly variable, ranging from a matter of hours to several months (Izzo et al. 2016). Passage criteria for Milford Dam states that 95% of individual salmon must successfully pass the dam within 48 hours of arrival, but these standards are clearly not being met (NMFS 2012).

One factor potentially influencing passage and spawning success is the origin of the fish. The vast majority of Penobscot River Atlantic salmon are hatchery origin, and studies have found that fish reared in captivity are less efficient at finding and settling on their spawning grounds as adults than are their wild counterparts (Jonsson et al. 1991a, Jokikokko 2002). Moreover, wild salmon tend to survive better in the ocean and are more likely to actually spawn after upstream migration (Jonsson et al. 1991a). Therefore, a high proportion of hatchery-reared individuals could threaten the stability of the population.

Hatchery products stocked into the Penobscot River include smolts, parr, and unfed fry (Gorsky et al. 2009). Smolts are reared at Green Lake National Fish Hatchery on the Union River, Maine. A model developed by Stevens et al. (2018) using a forty-year time series of out-migrating smolt survival on the Penobscot River suggested that shorter migration distance, and particularly migrations that involve traversing fewer dams, are more likely to result in higher survival. Beginning in 2013, hatchery-reared smolts in the Penobscot River, which make up most of the adult returns (Gorsky et al. 2009), were stocked into the river downstream of Milford Dam (J. Stevens, pers. comm.). Therefore, virtually all returning adults from smolt stocking have no chance of imprinting to upriver reaches of the Penobscot River, where the majority of spawning habitat exists, and this likely has implications for the spawning migration.

Adult Atlantic salmon return to specific sites within their natal streams to spawn (Heggberget et al. 1988), and these homing instincts seem strong in salmon smolts stocked into the Penobscot River (Gorsky et al. 2009). However, there is little viable spawning habitat below Milford Dam, and of all the spawning habitat available above Milford Dam, only 8.8% is located between Milford and any upstream dam (Table 3.1). The majority (43.5%) of the spawning habitat available above Milford Dam is located above at least three dams (Milford-West Enfield-Weldon [Figure 3.1]). Due to the current mismatch between smolt stocking location and suitable rearing habitat, returning adults may be ill-equipped to locate suitable spawning habitat in the Penobscot watershed.

Table 3.1. Amount (100 m^2) and percentage of Atlantic salmon (*Salmo salar*) rearing habitat available between study dams. These figures consider only the six study dams and not any dams that might be located upstream of them.

Dam	Rearing habitat located between dam and any upstream study dam (100m2)	Percent of above-Milford rearing habitat located between dam and any other study dam
Milford	30,048	8.8%
Howland	59,806	17.5%
West Enfield	78,337	22.9%
Weldon	149,099	43.5%
Pumpkin Hill	5,709	1.7%
Brownsmill	19,229	5.6%

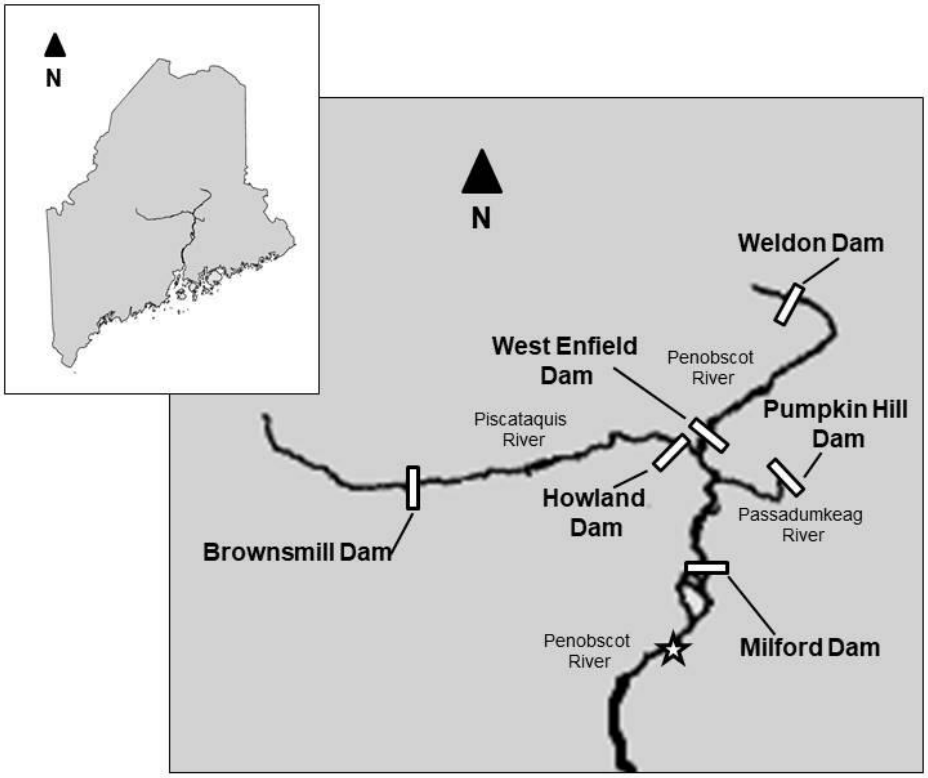


Figure 3.1. Map of the Penobscot River basin and its position within the state of Maine. White bars represent dams equipped with PIT arrays. The downstream release location of tagged Atlantic salmon (*Salmo salar*) is represented by the star.

The goal of this study was to describe Atlantic salmon movements and dam passage efficiencies throughout the Penobscot River, with a specific emphasis on Milford Dam. We sought to (1) describe post-release approach and behavior at Milford Dam, (2) quantify passage delays at Milford Dam, and (3) assess approach and passage of five other dams upstream of Milford to characterize the influence of other migratory barriers in the basin. For each of these objectives we also compared the results from hatchery-origin versus wild-origin adults in an attempt to describe the influence of current smolt stocking practices on the ability of adults to locate spawning habitat.

METHODS

Study Area

The Penobscot River watershed is the largest watershed in the state of Maine, covering over 22,000 km^2 (Figure 3.1). The river is tidal up to the town of Veazie, Maine at RKM 48. The Penobscot River and its major tributaries are heavily dammed. Three dams on the mainstem Penobscot were the focus for our study: Milford Dam, West Enfield Dam, and Weldon Dam (also known as the Mattaceunk Dam). In addition, three dams located on the major tributaries of the Penobscot River were also assessed: Pumpkin Hill Dam (also known as the Lowell Tannery Dam [Passadumkeag River]), Howland Dam, and Brownsmill Dam (both on the Piscataquis River). The Howland Dam is located at the mouth of the Piscataquis River where it flows into the Penobscot River mainstem. On both the mainstem Penobscot and its tributaries, there remain other upstream dams not included in our study that further impact access to habitat. For the duration of this study, Milford Dam was the first dam that upstream migrants encountered (Figure 3.1, Table 3.2).

Table 3.2 Six dams where Atlantic salmon (*Salmo salar*) passage was assessed from 2014-2020. **RKM** = river kilometer; **Completed** = the year the dam structure was completed.

Dam	System	RKM	Completed1	Hydropower capacity (mW)2,3,4,5	Dam height (m)1,3	Upstream fish passage
Milford	Penobscot	61.3	1906	6.4	10.41	Denil (until 2014); Fish lift (2014-present)
Howland	Penobscot	99	1916	1.9	5.21	Denil (until 2016); Nature-like bypass (2016-present)
West Enfield	Penobscot	100		13	7	Vertical slot
Weldon	Penobscot	150.2	1939	19.2	13.7	Pool and weir
Pumpkin Hill	Passadumkeag	112.7	1987	1	8.2	Denil
Brownsmill	Piscataquis	163	1856	0.6	7.3	Denil

1 National Inventory of Dams

2 Richard Dill, pers. comm.

3 Opperman et al. 2011

4 FERC 2018

5 Kruger Inc. 2018

Fish Tagging and Telemetry

Tagging.--Adult migratory Atlantic salmon were captured at the Milford Dam sorting facility operated by the Maine Department of Marine Resources (ME DMR). Each fish was identified as either smolt-stocked or wild-reared using scales (Bruchs et al. 2018). The ME DMR staff recorded fork length and sex for each individual, collected genetic samples using a fin punch, and inserted a passive integrated transponder (PIT) tag (23 mm, HPT23, Biomark, Boise, Idaho) beneath the skin below the dorsal fin (Bruchs et al. 2018). Two sea-winter salmon were processed by ME DMR staff prior to radio-tagging, and were kept in the same tank of ambient river water from capture to radio-tagging.

Fish were equipped with a coded radio transmitter (MCFT-3L, Lotek Wireless, Inc. Newmarket, Ontario) that measured 16 x 73 mm and weighed 25.0 g in the air (11.0 g in the water). A livestock castration band (Ideal Instruments, Lexington, KY) was placed around the middle of each tag to prevent regurgitation (Izzo et al. 2016). Tags were dipped in glycerin (HUMCO, Texarkana, Texas) for lubrication and inserted using a flexible plastic tube to push the tag down the fish's esophagus while it was being held against the side of the tank with its head out of the water. Tags were inserted within 30 s of the salmon's head being brought out of the water, and a gentle tug on the antenna ensured that the tag was seated properly in the fish's stomach. Fish were placed head-first into a black rubber sock and moved into an aerated tank of river water located in the bed of a truck and transported downstream to a boat launch in Brewer, ME (RKM 43.4) and released. No more than six salmon were placed in the transport tank at any one time and the water was drained in between truckloads. Total driving time between the two locations was approximately 20 minutes.

Radio telemetry.--Both stationary and active radio telemetry were used to track the movements of radio-tagged salmon above and below Milford Dam. Each stationary receiver was equipped with as many as two four-element Yagi antennas mounted to stationary objects such as trees or fence posts. One of the receivers at Milford Dam also included two dropper antennas placed at the entrance of, and just behind, the trap in the lower fishway to detect fish entering the lift. Radio receivers (Lotek SRX-800 and SRX-DL, Newmarket, Ontario, Canada) scanned continually through the connected antennas. Data were downloaded once per week from April-December, at which time the buffer in the unit was erased and the batteries were replaced.

Each week, on the same day that data were downloaded from the stationary units, a mobile-tracking route was driven to attempt to locate fish in between stationary receivers. A dipole antenna attached to a handheld unit (Lotek SRX-400, Newmarket, Ontario, Canada) was mounted to the top of a vehicle and the vehicle driven as close to the river as possible, with riverside stops where feasible. Whenever a tag was detected, the tag code, the time of detection, and a location were recorded. Mobile tracking was also conducted from a boat opportunistically using the same equipment and following the same protocols as the vehicle mobile tracking.

PIT Telemetry.--All PIT arrays were active beginning when the fishway at the respective dam opened (April or May) and ran through mid-November, or until the upstream fishway was closed. Antennas were wired to multiplexers (Destron Fearing FS 1001M, Dallas-Fort Worth, Texas, USA) that scanned continuously through the antennas and recorded data, which were downloaded periodically throughout the season. The PIT tags applied by ME DMR were detected by these antennas and provided additional information about fish passage.

System-wide Movements

Six different fish movement patterns were defined: approach, fall back, reversal, passage, delay, and searching. Approach and passage were used to describe upstream movements, while fall back and reversal described downstream movements. Delay (in this case, passage delay) was specifically described for Milford Dam. Searching behavior was an observed pattern unique to the Howland and West Enfield Dams.

Approach.--A fish was considered to have approached a dam if it was detected on the downstream radio receiver located at that dam, if it was detected below a given dam via mobile tracking, or if it was detected at the lowermost PIT antenna. Because the downstream stationary radio receiver at Howland Dam is located at a confluence, fish had to be detected on this receiver for over one hour, or be simultaneously detected on the upstream Howland receiver, to be considered as having approached the dam instead of passing by the dam as they migrated up the mainstem Penobscot River. Detection on the upstream Howland receiver indicated not only proximity to the dam, but also confirmed that detections on the downstream receiver were most likely true detections and not the result of noise.

For all dams except Milford, approach was a binary variable regardless of the number of times a salmon was detected advancing upstream towards a given dam. At Milford Dam, the number of approaches was counted as the number of times a fish drew near to the dam in between confirmed passage events. Reversal behavior (see below) followed by a return to the dam did not count as a separate approach, but was instead treated as a behavior displayed during migratory delay—in other words, if a fish approached the dam, moved downstream, and then approached the dam again, only one approach event was recorded. For the small subset of fish that passed Milford Dam, fell back below the dam (see below), and approached the dam for a second time (therefore triggering a second approach event), the approach date was assigned as the day the fish was detected at the downstream Milford receivers after having been detected further downstream of Milford Dam either on stationary arrays or via mobile tracking. This method yielded the most conservative second approach and delay times for those fish.

Fall back.--Fall back is a behavior that is typically defined by downstream movements of fishes during the period of upstream migration, and is often associated with the after-effects of handling and tagging, especially in alosines (e.g., Frank et al. 2009). Studies involving salmonids on the West Coast of North America often differentiate between fall back events caused by disorientation, and those caused when adults overshoot their natal streams and must return downstream in order to enter those streams to spawn (Boggs et al. 2004, Naughton et al. 2006). These studies often define fall back events as events in which fish that have passed upstream of a fishway are subsequently detected downstream of the dam they had successfully passed (Boggs et al. 2004, Naughton et al. 2006). Describing fall back can be important because of the behavioral implications as a result of the tagging process that may affect the interpretation of telemetry data (Frank et al. 2009), and the risk of overestimating dam passage when fish that have previously fallen back are double-counted (Boggs et al. 2004, Naughton et al. 2006).

We used the definition of fall back found in Boggs et al. (2004) and Naughton et al. (2006) to describe behavior of Atlantic salmon after passing upstream of a dam. For our purposes, downstream movements that occurred after the month of September did not coincide with the typical adult immigration period (Saunders et al. 2006) and were not considered fall back events. Overestimating passage success at Milford Dam because of fall back was not a concern for our study because the majority of adult Atlantic salmon passing through the Milford Dam are handled by ME DMR staff and PIT-tagged. PIT-tagged fish could be uniquely identified by ME DMR or by PIT antennas located in the Milford Dam fishway, and passage counts adjusted accordingly.

Reversal.—For our purposes, reversal was only recorded at the Milford Dam because of the high number of radio and PIT receivers located at and immediately upstream and downstream of the dam. A reversal event is defined as a tagged fish approaching the tailrace of a dam (see below), and subsequently being detected at a receiver further downstream, or via mobile tracking at least one kilometer downstream of the dam. The occurrence of at least one reversal event between approach and passage of Milford Dam was noted and the occurrence of a reversal did not reset the fish's approach date to the dam. The occurrence of reversal events was a binary variable that was not recorded separately for each approach event. If a fish that had previously approached Milford Dam was located downstream but was not seen returning to the dam (e.g., it abandoned migration), this movement was not considered a reversal event. As with fall backs, downstream movements that occurred after the month of September were not considered reversal events unless the fish then approached Milford Dam again.

Passage.--Passage events were recorded at each of the six dams throughout the system. A fish was considered to have successfully passed the dam when it was recaptured by ME DMR staff (Milford Dam only), detected at the PIT antenna located in the upper part of the fishway, or detected on a stationary radio antenna or via mobile tracking upstream of the dam. At the Howland Dam, where there were no PIT antennas for the majority of the study (after the installation of the nature-like bypass) and the next stationary radio array was often very far upstream (~60 km). Fish could be considered successful passers if they were detected by the radio receiver at the upstream end of the Howland bypass for a substantial amount of time (usually at least one hour), and were not then detected on any other radio receivers or via mobile tracking below the dam.

The timing of passage events (i.e., the day on which passage occurred) was recorded only for the Milford Dam because of the presence of ME DMR staff who could often confirm the exact date of passage for tagged fish. The behaviors displayed by salmon after passage at Milford, such as the approach or passage of other dams, were recorded in total but were not enumerated or separated by passage event for fish that passed Milford Dam more than once.

Delays.—Passage delays were calculated as the number of days between initial downstream approach to the Milford dam and successful passage.

Searching.—Searching was described specifically for salmon in the vicinity of Howland and West Enfield Dams in 2018-20, as this is an area of path choice. This behavior was defined by movements between both dams before fish passed either dam. The transit times for all fish that reached the confluence of the Penobscot and the Piscataquis were calculated as both ground speed (m/s) and body lengths per second (BL/s) using the elapsed time between their last detection at or near Milford Dam and their first detection at or near either of the confluence dams. Search time was then calculated as the time between detection at the confluence and passage of one of the dams.

Ground speed was calculated as the distance in meters between the Milford Dam and the confluence of the Penobscot and Piscataquis Rivers, derived from the RKM of the respective dams, divided by the number of seconds the fish required to travel that distance (taken from the timestamps of detections at both dams). Body lengths per second was calculated similarly to ground speed except that the distance between the dams was first divided by the individual fish's fork length (in meters) before being divided by time.

At the confluence, similar to Gorsky et al. (2009), we also recorded which of the two dams each salmon initially approached, which dam it passed first, and the number of attempts required to pass that dam. An individual passage attempt was considered as a set of detections below a given dam that was separated by at least 30 minutes from any other set of detections below that dam (Gorsky et al. 2009). Because our data were aggregated in 1-hour time intervals, the estimate for the number of attempts was conservative. The raw dataset was used to determine the validity of detections whenever there was only one detection in an hour, or when detections did not make sense in time or space, and suspect detections were removed from further analyses. Fall back from both dams followed the same definition found in **System-wide Movements:** *Fall back*. Additional search time after fall back was not quantified.

Ultimate disposition

At the end of the upstream migration period (approximately the end of September [Saunders et al. 2006]), the location of each radio-tagged salmon was noted. Dispositions were based on the individual movement records for each fish using the last available locations within the immigration period. Final location was assigned based on dam intervals: downstream of Milford, upstream of Milford but downstream of the next dam in the system (Howland/West Enfield/Pumpkin Hill), between West Enfield and Weldon, between Howland and Brownsmill, or upstream of Weldon, Brownsmill, or Pumpkin Hill.

Environmental factors

Flow records (cubic feet per second [CFS]) for each study year were downloaded from the U.S. Geological Survey (USGS, [USGS WaterWatch, https://waterwatch.usgs.gov/]) from the gage at West Enfield, ME (USGS 01034500), the nearest gage on the mainstem Penobscot upstream of Milford Dam. Records were taken from 15 April to 15 November in each year, which is the length of time that the upstream fishway is typically open at the Milford Dam.

Statistical analysis

Welch's two-sample *t*-test, which does not assume equal variance between groups, was most often used to compare between two groups, such as hatchery-origin and wild-origin fish. Two-proportion *z*-tests were used to compare passage rates between groups, and paired *t*-tests were used whenever behaviors were being compared for an individual, such as when comparing the length of delays for fish that experienced more than one delay. Flow records were compared visually and then separated by month and compared among years using boxplots. All statistical tests were performed in R (R Core Team 2021) with $\alpha=0.05$.

RESULTS

From 2014-2020 a total of 309 adult two sea-winter salmon were captured and radio-tagged while passing the Milford Dam (Table 3.3). The majority of captured fish (n=258, 84%) were transported and released downstream after radio-tagging, while 51 (17%) were released directly into the Milford headpond after tagging (1 in 2014, 50 in 2020). Ninety-five fish initially released below the dam were taken to the hatchery to be used as broodstock when they returned. One hundred forty-seven (49%) radio-tagged salmon were female, and 154 (51%) were males, for all known-sex fish (n=301). Of all fish for which the rearing origin was known (n=301), 250 (83%) were hatchery-origin, and the remaining 51 (17%) were of wild-reared origin. Fish ranged from 58-92 cm fork length.

Table 3.3. The number of radio-tagged Atlantic salmon (*Salmo salar*) released above and below Milford Dam in each year of the study. **Number tagged** refers to the total number of salmon tagged in that year.

		Release	
Year	**Number tagged**	**Below Milford**	**Above Milford**
2014	23	22	1
2015	50	50	0
2016	47	47	0
2017	0	0	0
2018	49	49	0
2019	50	50	0
2020	90	40	50
Total	**309**	**258**	**51**

System-wide movements

Milford Dam.—Nearly all (n=251, 97%) of radio-tagged salmon released below Milford Dam approached the dam again. This ranged from 91%-98% across years (20/22 in 2014 to 49/50 in 2019 [Table 4]). Approach times after release could be calculated for 265 fish across both upstream and downstream releases and ranged from 0 days (fish detected at Milford later on the same day it was released) to 28 days, with a median of 3 days. Twenty-five (9%) of the fish that approached Milford Dam after release could be confirmed to have passed the dam, fallen back downstream, and approached the dam a second time. There was no evidence of salmon approaching the dam more than twice over the duration of the study. Only 2/25 salmon with two recorded approach events (i.e., fish that experienced one fallback) were wild-reared, whereas the remaining 23 were of hatchery origin.

Rates of reversal were much different between fish that only approached Milford Dam once, and those that fell back and approached a second time. Among fish that could only be confirmed to have approached the dam once, 25% (62/245) experienced at least one reversal event prior to passage, but that rate increased to 64% (16/25) among salmon that had previously experienced fall back (Two-proportion *z*-test, χ^2=14.703, *P*<0.001). Only one of the fish with two fall backs was initially released upstream of Milford Dam. Sixteen fish released above the dam fell back downstream of the dam and approached once.

Ultimately, most (231/251, 92%) of tagged salmon that approached Milford after being released below the dam were successful in passing the dam again. Passage success after approach ranged from 82% in 2020 to 100% in 2014 (Table 3.4). However, 208 (90%) fish experienced a delay of at least one day between their first approach and successful passage of the dam. These first delays ranged from 1-155 days with a median of 7 days. Most first delays (185/208, 89%) lasted two days or longer. Median delays were lowest in 2014 (4 days) and highest in 2019 (11.5 days), but exceeded 2 days in all years. For fish that experienced multiple delays, the length of the first delay tended to be slightly longer than the length of the second delay (Paired *t*-test, *t*=-2.09, *P*=0.05).

Table 3.4. Approach, passage, and overall passage success (%) for radio-tagged adult Atlantic salmon (*Salmo salar*) at six dams in the Penobscot River basin. Note that no salmon were radio-tagged in 2017. Median delay time at Milford Dam refers to the first delays experienced by salmon released below the dam.

	2014	2015	2016	2018	2019	2020
Number released downstream of Milford	22	50	47	50	50	40
Number released upstream of Milford	1	0	0	0	0	50
Milford						
Approached	20	49	46	48	49	39
Passed	20	45	45	43	46	32
Success	100%	92%	98%	90%	94%	82%
Median delay (days)	4	5	7	14	11.5	7
Howland						
Approached	0	0	39	16	23	35
Passed	0	0	32	9	8	15
Success	0%	0%	82%	56%	35%	43%
West Enfield						
Approached	2	1	36	25	11	71
Passed	2	1	36	21	7	67
Success	100%	100%	100%	84%	64%	94%
Weldon						
Approached	0	0	8	4	4	57
Passed	0	0	2	0	2	37
Success	0%	0%	25%	0%	50%	65%
Pumpkin Hill						
Approached	0	0	1	1	0	5
Passed	0	0	0	0	0	0
Success	0%	0%	0%	0%	0%	0%
Brownsmill						
Approached	0	0	2	0	4	3
Passed	0	0	1	0	1	3
Success	0%	0%	50%	0%	25%	100%

The length of the first delay experienced at Milford for fish that had been released below the dam was compared by sex and by origin (hatchery vs. wild). There was no difference in delay length between males and females (Welch two sample *t*-test, t=0.046, P=0.96) or between hatchery and wild origin fish (Welch two sample *t*-test, t=-0.66, P=0.51

Howland Dam and West Enfield dams.-- There were 187 fish available to be detected in this area (136 from the downstream release, and 51 from the upstream release). Overall passage success was much higher for fish approaching West Enfield Dam (135/146, 93%) than for fish approaching Howland Dam (64/113, 57%). Out of the 92 fish that approached both dams during the study, 52 (57%) passed Howland at least once, and 84 (91%) passed West Enfield at least once. Twelve fish approached but did not pass either dam. Seventy-six (83%) were hatchery-origin fish and the remaining 16 (17%) were wild-origin. Forty-eight (52%) of the fish that approached both dams also passed both dams at least once, and 42 of those were hatchery origin.

From 2018-2020, rates of travel between Milford and the confluence could be calculated for 96 fish. Ground speeds ranged from 0.04-2.9 m/s, with a median ground speed of 0.4 m/s. These ground speeds translated into a rate of 0.06-3.8 BL/s, with a median of 0.52 BL/s. From the time they were first detected at the confluence, fish that passed at least one dam spent anywhere from 0 hours (i.e., the first detection at the confluence was in the fishway of a dam) to 120 days searching at the confluence before passing a dam (median time of 3 hours). There was one searching fish for which the origin was unknown, but for the remainder, 85% were hatchery origin. The proportion of searching hatchery fish was not different from the proportion of hatchery fish in the entire sample (Two-proportion *z*-test, χ^2=0.12, P=0.73).

Fourteen fish failed to pass either dam after approaching at least one of them. Of the remaining 82 fish, 56 initially approached and passed West Enfield and 13 initially approached and passed Howland. An additional four fish that approached West Enfield ended up passing Howland first, and nine fish that approached Howland passed West Enfield first. The median number of attempts required for fish to pass West Enfield was 1, and for Howland was 2.5.

Notably, fall back rates after first passage were high at both dams (Howland = 47%, West Enfield = 69%). Howland was the last dam passed for 12/17 (71%) of the salmon that passed that dam first, and West Enfield was the final dam passed for 58/65 (89%) of fish that initially passed it. This means that 3/8 fish that fell back after passing Howland ultimately passed it again, and that 37/45 fish that fell back from West Enfield ended up passing that dam again at least once.

Weldon Dam.--Passage success at Weldon Dam ranged from 0% (2018) to 65% (2020). Overall, 73 radio-tagged salmon approached the dam during the study period and 41 (56%) passed successfully (Table 3.4).

Pumpkin Hill Dam.--No radio-tagged salmon could be demonstrated to have passed the Pumpkin Hill Dam during the study period (Table 3.4), although seven were detected approaching the dam on either a radio antenna or the lowest PIT antenna.

Brownsmill Dam.--Five out of nine (56%) radio-tagged salmon that approached Brownsmill during the study were detected passing the dam. These approach and passage events were only recorded in 2016, 2019, and 2020. In 2016, one out of two (50%) radio-tagged salmon passed the dam and in 2019 one out of four (25%) passed the dam. Three radio-tagged salmon approached Brownsmill in 2020, and all three (100%) were detected above the dam on stationary or mobile receivers. However, a fourth radio-tagged salmon was detected a short distance downstream of Brownsmill Dam (outside the range of the stationary radio receivers) via mobile tracking consistently from July through October 2020 and was later detected moving downstream. It is likely that this fish was searching for passage unsuccessfully during that time. One of the three fish that passed Brownsmill in 2020 was captured by a bald eagle while in the Brownsmill headpond (R. Saunders, pers. comm.). Complete approach and passage information for all dams in all years can be found in Table 3.4.

Ultimate disposition

The percentage of fish located in each river segment at the end of the immigration period tended to be disproportionate to the amount of suitable rearing habitat available in that river segment (Table 3.5, Figure 3.2). In all years, a portion of radio-tagged fish was located below Milford Dam, where there is no surveyed spawning habitat in the mainstem. The proportions of fish ultimately located above Weldon and Brownsmill were lower than the proportion of available habitat in all years. However, the proportions of hatchery and wild fish located in any segment were generally consistent with the proportion of hatchery versus wild fish tagged that year (Table 3.6, Figure 3.3). No fish were located above Pumpkin Hill in any year.

Table 3.5. Proportion of radio-tagged adult Atlantic salmon (*Salmo salar*) ultimately located in a given river segment by year, compared to the amount of suitable rearing habitat surveyed in that segment.

	Percent of suitable surveyed rearing habitat located between and above study dams upstream of Milford	Ultimate disposition						
		2014 (n=5)	2015 (n=6)	2016 (n=47)	2018 (n=34)	2019 (n=31)	2020 (n=87)	All years (n=210)
Below Milford		40%	83%	13%	26%	23%	25%	24%
Milford-Howland/West Enfield/Pumpkin Hill	8.8%	20%	0%	6%	26%	35%	9%	15%
West Enfield-Weldon	22.9%	40%	17%	55%	35%	10%	23%	30%
Howland-Brownsmill	17.5%	0%	0%	19%	12%	23%	6%	12%
Above Weldon	43.5%	0%	0%	4%	0%	6%	36%	17%
Above Brownsmill	5.6%	0%	0%	2%	0%	3%	1%	1%
Above Pumpkin Hill	1.7%	0%	0%	0%	0%	0%	0%	0%

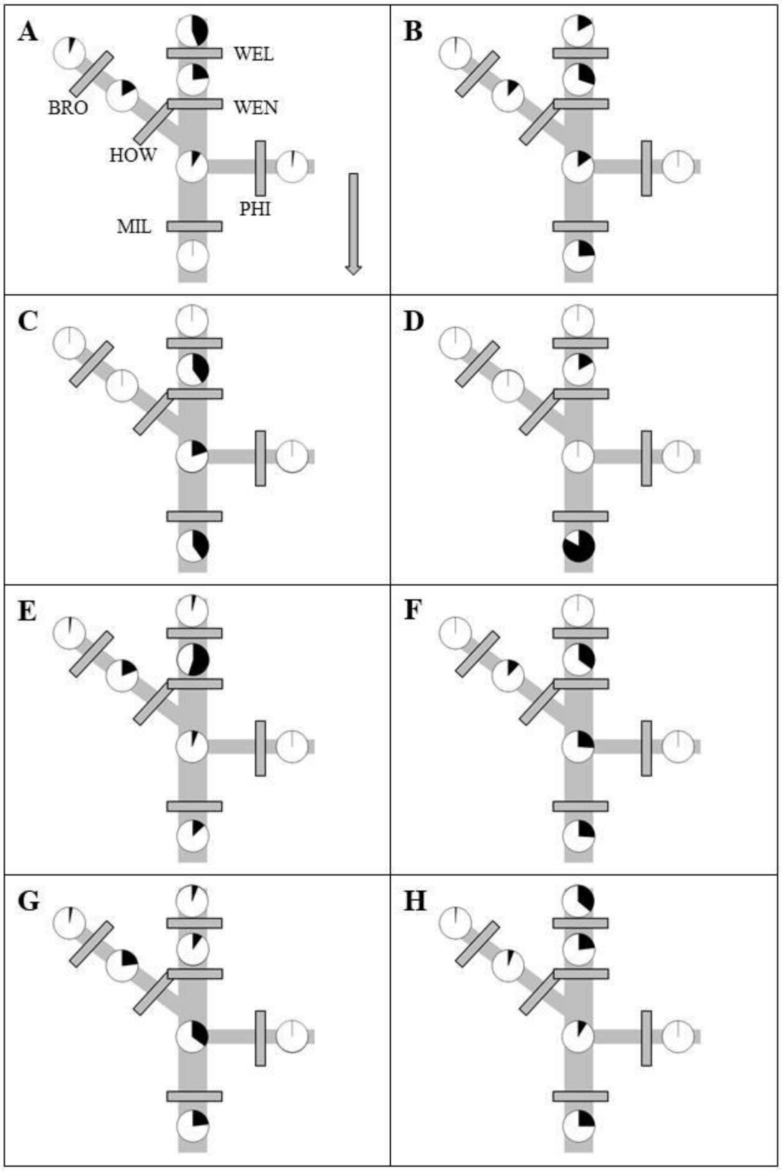


Figure 3.2. Proportion of radio-tagged adult Atlantic salmon (*Salmo salar*) ultimately located within each river segment, relative to rearing habitat availability. MIL= Milford Dam; WEN=West Enfield Dam; HOW= Howland Dam; PHI = Pumpkin Hill Dam; WEL=Weldon Dam; BRO=Brownsmill Dam. Arrow indicates direction of flow. Panels represent: A) Proportion of available habitat, B) ultimate disposition across all years, C) 2014, D) 2015, E) 2016, F) 2018, G) 2019, H) 2020.

Table 3.6. Number and proportion of radio-tagged Atlantic salmon (*Salmo salar*) of hatchery and wild origin in each study year, and the ultimate disposition of those fish at the end of the upstream migration period. MIL=Milford Dam; WEN=West Enfield Dam; HOW=Howland Dam; PHI=Pumpkin Hill Dam; WEL=Weldon Dam; and BRO=Brownsmill Dam.

	Total	Below MIL	Between MIL and WEN/HOW/PHI	Between WEN and WEL	Between HOW and BRO	Above WEL	Above BRO
2014 (n=5)							
NO. HATCH.	4	2	1	1	0	0	0
NO. WILD	1	0	0	1	0	0	0
% HATCH.	80%	100%	100%	50%	0%	0%	0%
% WILD	20%	0%	0%	50%	0%	0%	0%
2015 (n=2)							
NO. HATCH.	2	1	0	1	0	0	0
NO. WILD	0	0	0	0	0	0	0
% HATCH.	100%	100%	0%	100%	0%	0%	0%
% WILD	0%	0%	0%	0%	0%	0%	0%
2016 (n=46)							
NO. HATCH.	35	4	3	20	6	2	0
NO. WILD	11	1	0	6	3	0	1
% HATCH.	76%	80%	100%	77%	67%	100%	0%
% WILD	24%	20%	0%	23%	33%	0%	100%

Table 3.6 (cont'd).

	Total	Below MIL	Between MIL and WEN/HOW/PHI	Between WEN and WEL	Between HOW and BRO	Above WEL	Above BRO
2018 (n=33)							
NO. HATCH.	26	5	8	10	3	0	0
NO. WILD	7	3	1	2	1	0	0
% HATCH.	79%	63%	89%	83%	75%	0%	0%
% WILD	21%	38%	11%	17%	25%	0%	0%
2019 (n=31)							
NO. HATCH.	26	6	10	2	6	2	0
NO. WILD	5	1	1	1	1	0	1
% HATCH.	84%	86%	91%	67%	86%	100%	0%
% WILD	16%	14%	9%	33%	14%	0%	100%
2020 (n=85)							
NO. HATCH.	70	16	7	17	4	26	0
NO. WILD	15	6	1	3	1	3	1
% HATCH.	82%	73%	88%	85%	80%	90%	0%
% WILD	18%	27%	13%	15%	20%	10%	100%

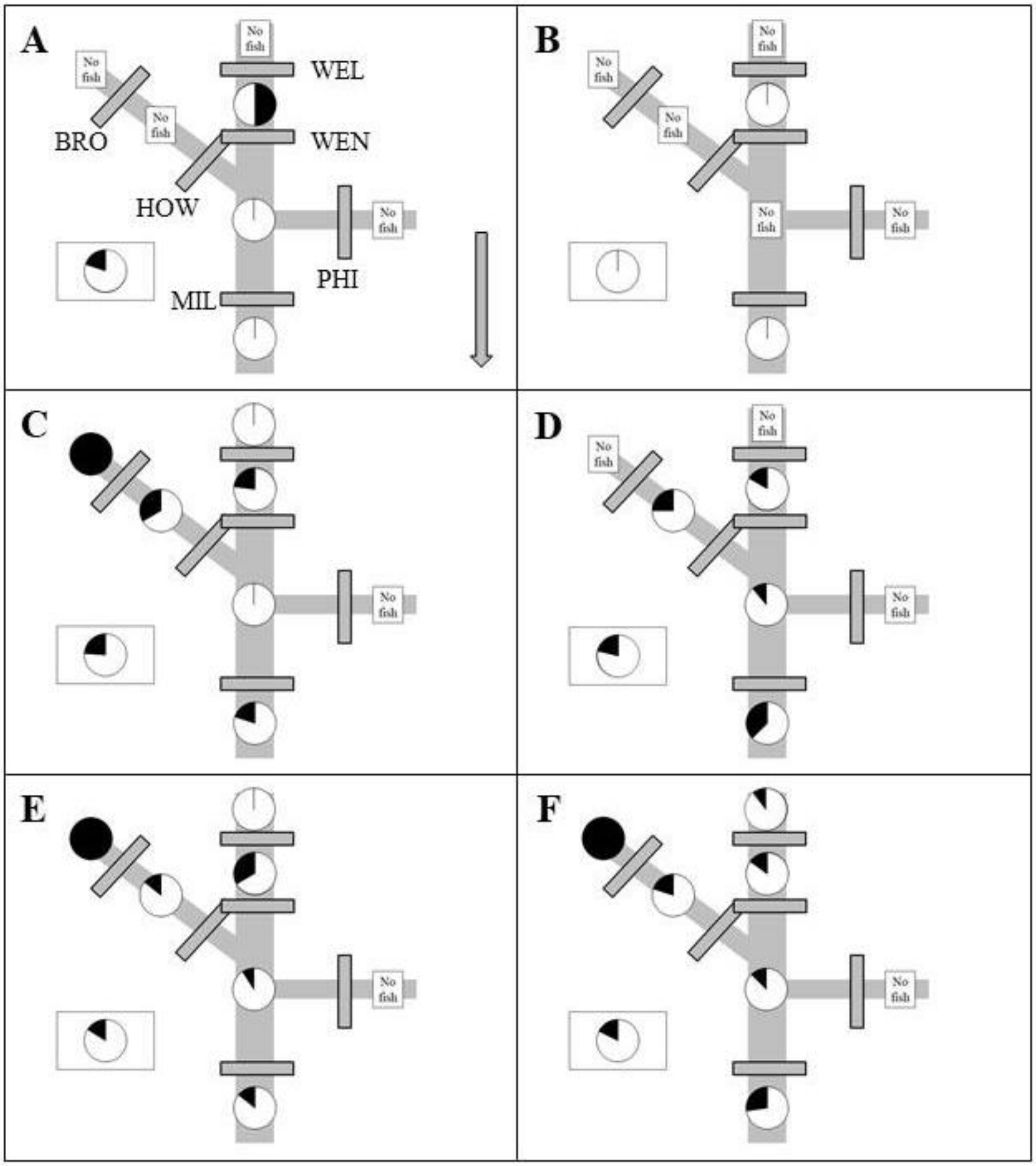


Figure 3.3. Ultimate disposition of hatchery-reared (white) versus wild-reared (black) radio-tagged Atlantic salmon (*Salmo salar*) by year. MIL= Milford Dam; WEN=West Enfield Dam; HOW= Howland Dam; PHI = Pumpkin Hill Dam; WEL=Weldon Dam; BRO=Brownsmill Dam. Segments that did not contain tagged fish at the end of the immigration period are indicated by text. The inset represents the relative proportions of hatchery- and wild-reared fish tagged in that year. Arrow indicates direction of flow. Panels represent years: A) 2014, B) 2015, C) 2016, D) 2018, E) 2019, F) 2020.

Environmental factors

For most months there was considerable variation in flow among years (Figure 3.4). The year 2020, which had the lowest passage success rate at Milford Dam out of all of our study years (Table 3.4), consistently had the lowest flows during the peak months of Atlantic salmon upstream migration (May-July [Saunders et al. 2006]) (Figure 3.5). Conversely, 2014, which had a 100% passage success rate for all salmon that approached Milford Dam, tended to have among the highest flows during the same months (Figure 3.5).

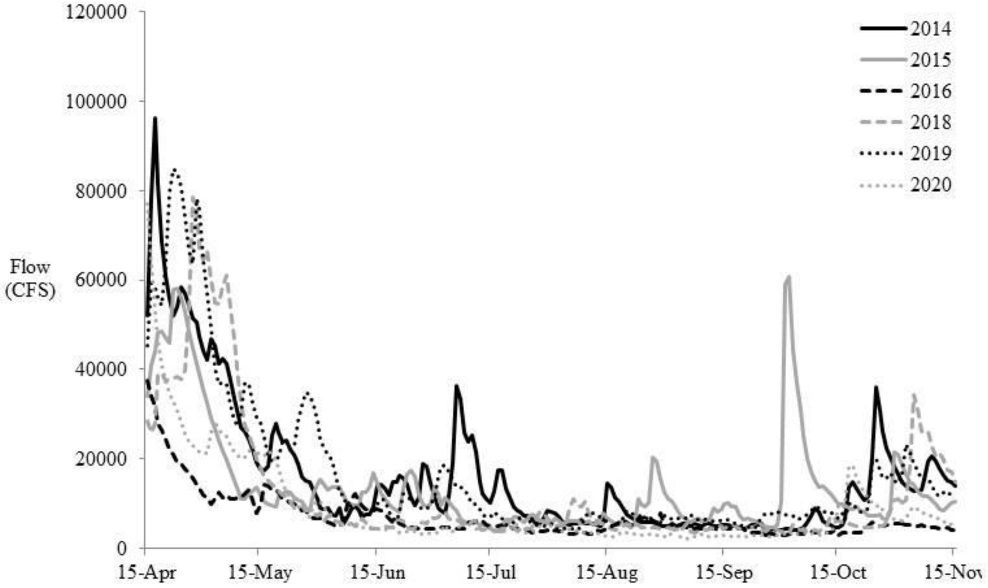


Figure 3.4. Annual flow record for all study years during the period when upstream passage structures were operational at the Milford Dam (15 April-15 November). Data were taken from the USGS gage at West Enfield, Maine (USGS 01034500).

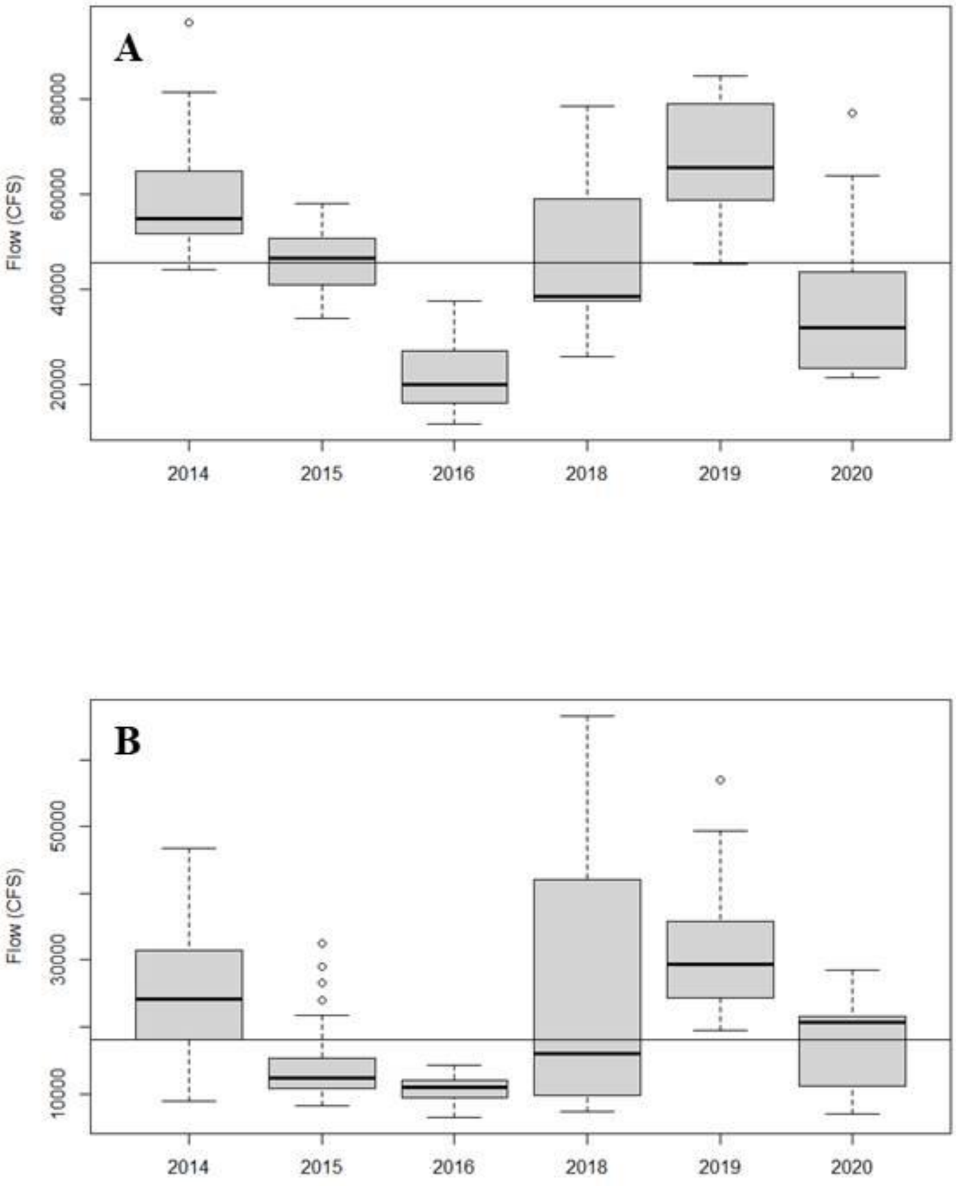


Figure 3.5. Mean flow (CFS) for each month of operation of the upstream fishway at Milford Dam across study years. A) April; B) May; C) June; D) July; E) August; F) September; G) October; H) November.

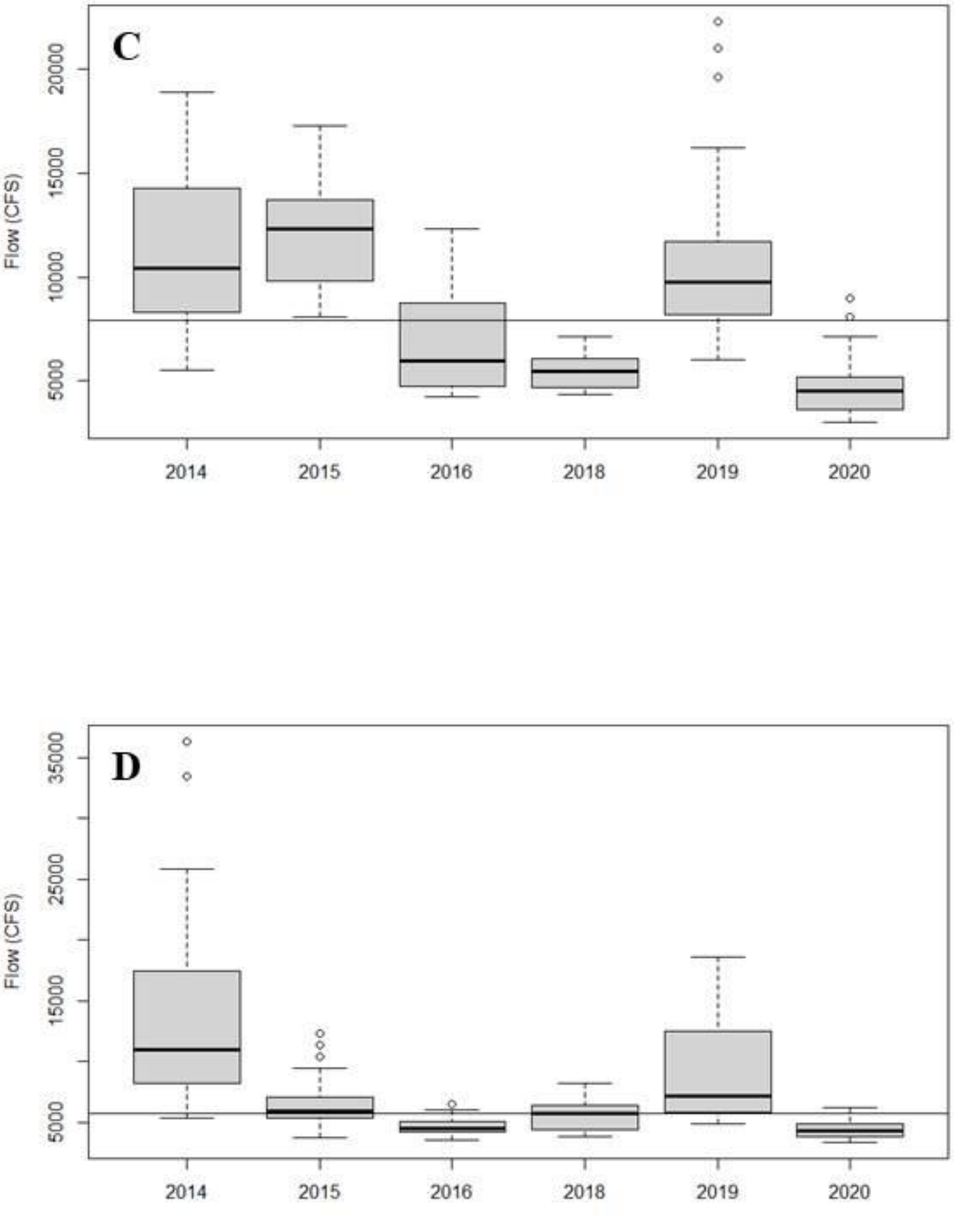
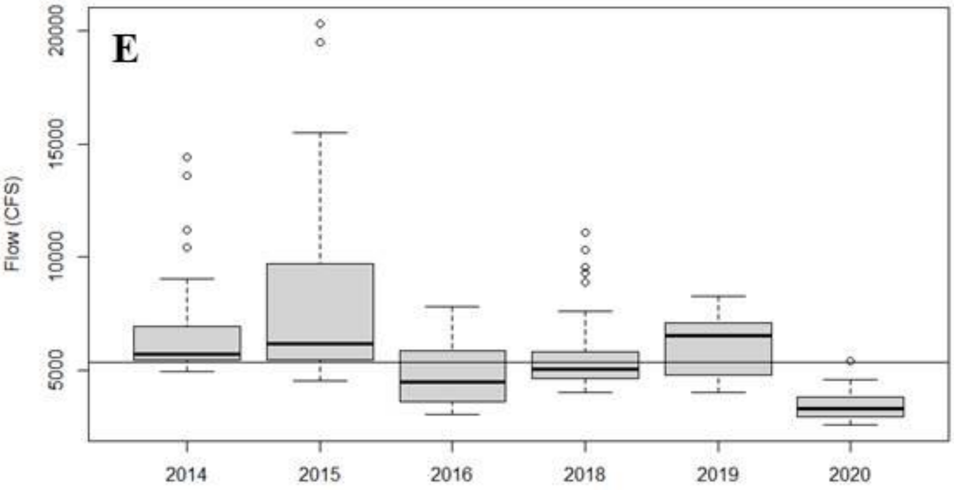


Figure 3.5 (cont'd).



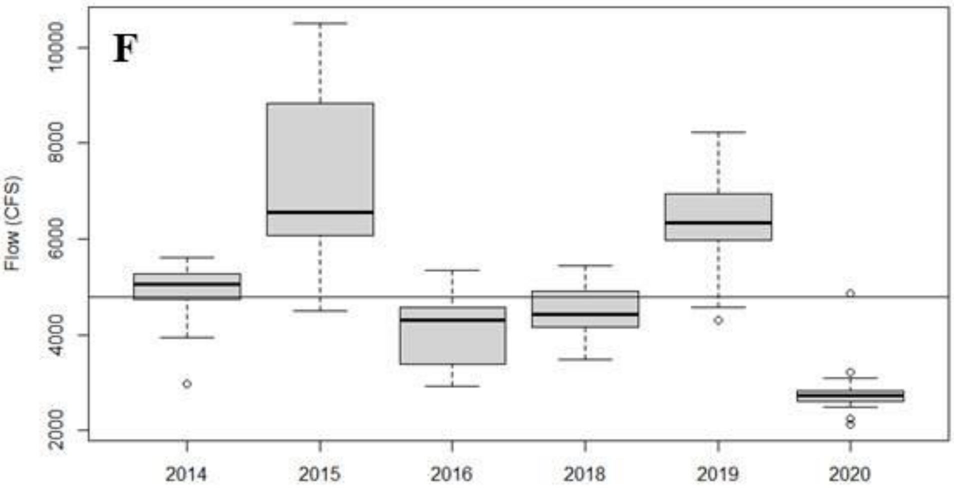


Figure 3.5 (cont'd).

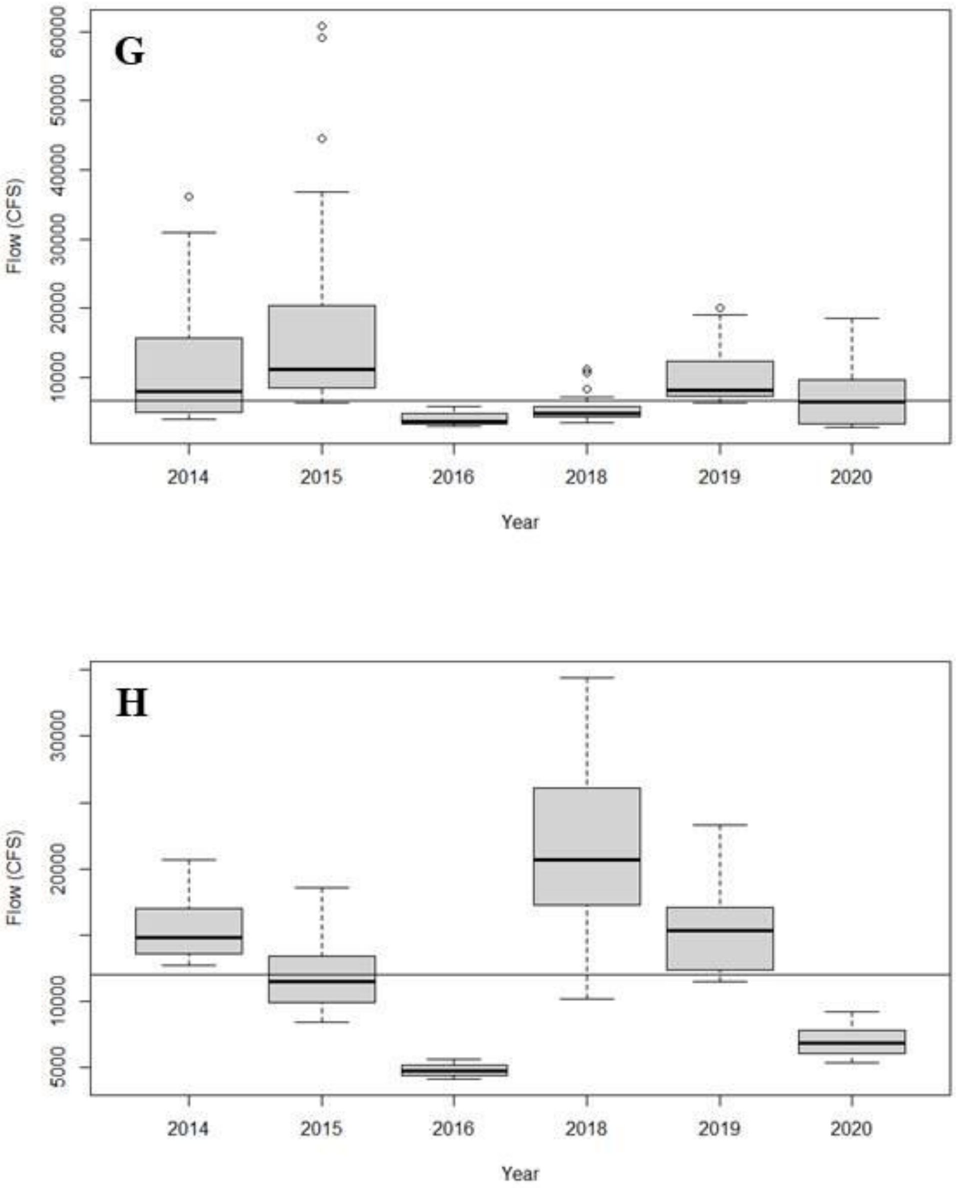


Figure 3.5 (cont'd).

DISCUSSION

We found evidence of low passage efficiencies and long delays throughout the system, with most radio-tagged fish experiencing delays in excess of the 48-hour passage criteria at Milford. Approximately 25% or more of the radio-tagged fish in every year were below Milford at the end of immigration, an area where there is little suitable rearing habitat. The proportion of hatchery versus wild fish in any segment at the end of immigration tended to be similar to the proportions tagged in that year, suggesting that the ability of fish to effectively pass dams and not just their origin affected their ultimate disposition. The most abundant rearing habitat (43.5% of the rearing habitat available above Milford), located above the Weldon Dam, typically contained less than 10% of the radio-tagged population at the end of the upstream migration period in all years except 2020, when 36% of radio-tagged fish were above Weldon at the end of September. Even if the number of fish passing Weldon was greater than these data suggest, passage inefficiencies elsewhere limit the number of fish available to occupy this habitat.

Handling stress was unlikely to influence delays because our fish were allowed to pass Milford of their own volition instead of being captured by an invasive gear-type such as gill nets, fyke nets, or angling (Bernard et al. 1999, Mäkinen et al. 2000, Hagelin et al. 2021). They also did not experience anesthesia or surgery during tagging. Once fish had moved upstream of Milford they were not captured or handled again, so their movements were not a result of these stressors. We also did not observe any fish abandoning migration after tagging and release, as can be the case when invasive gear-types are used (Mäkinen et al. 2000).

One reason for the delay and searching behavior we saw may be interactions with the dam structures themselves. Rivers that have been altered by damming are more complex and environmentally variable that un-altered rivers and this may lead to reversal behaviors that exacerbate delays for migratory adult salmonids (Keefer et al. 2006). Salmon moved rapidly in the un-impounded stretch between Milford and West Enfield, exhibiting a median ground speed of 0.394 m/s. This ground speed translates into a transit time of roughly 26.5 hours between Milford Dam and the confluence of the Penobscot and Piscataquis Rivers, or a speed of about 1.4 km/hr. However, fish searching in the 1 km stretch between Howland and West Enfield required a median of 3 hours to make a path choice, with some of them taking substantially longer (days or months).

Hatchery versus wild origin did not affect the length of delays at Milford Dam, or influence the likelihood of search behaviors at West Enfield and Howland, where the proportion of searching hatchery fish was found to be equivalent to the proportion of hatchery fish in the entire population. However, hatchery origin is a likely explanation for migratory inefficiencies observed throughout the system in that most (83.1%) of our radio-tagged adults, which are assumed to be representative of the entire population, were smolt-stocked below the Milford Dam. Evidence strongly suggests that Atlantic salmon adults return to the rivers they exited as juveniles due to imprinting taking place during their outmigration (Hansen and Jonsson 1994). Because Milford Dam is far downstream of suitable spawning habitat, these smolt-stocked fish cannot use olfactory cues to guide them back to suitable spawning habitat. Gorsky et al. (2009) confirmed that adults released into the river above Howland and West Enfield dams as smolts were more efficient at locating and passing the fish ways that led to the rivers into which they had been stocked, compared with adults that had been smolt-stocked just below the confluence. Power and McCleave (1980) also observed multiple upstream and downstream movements in adult Atlantic salmon that had been stocked below the head of tide as smolts in the Penobscot River.

Both Gorsky et al. (2009) and Power and McCleave (1980) attributed the movement patterns they observed to the influence, or lack thereof, of imprinting. The absence of any definitive movement patterns is indicative of fish that are experiencing a stretch of river for the first time (Power and McCleave 1980), as would be the case for any smolt-stocked adults above Milford Dam. It is notable that the breakdown of hatchery versus wild origin fish was reflected in the rates of fall back at Milford Dam (92% of fall backs were hatchery-origin fish), and may be attributable to the lack of experience that these fish have with upstream reaches of the river. Even though over 90% of tagged salmon released downstream successfully passed Milford again, across all years almost one quarter of the tagged population was last detected below Milford instead of on near suitable upstream spawning grounds. These fish may have travelled upstream but, being unable to navigate to a natal stream due to lack of imprinting, abandoned migration instead.

Environmental conditions, primarily flow, likely play a role in annual patterns of passage success. For sockeye salmon (*Oncorhynchus nerka*) high discharge during upstream migration may make dam passage more difficult (Roscoe et al. 2011) and cause fish to expend more energy while swimming, which could reduce their ability to successfully complete their migration (Rand and Hinch 1998, Rand et al. 2011). Conversely, increasing discharge can act as a cue to Atlantic salmon (Smith et al. 1994, Thorstad et al. 2008) to move upstream. The year 2020, which had consistently among the lowest flows during the months when Atlantic salmon are typically migrating upstream, also had the lowest overall passage success rate of all years (82%). However, all but one fish from the downstream release approached the dam in 2020, and median delay times (7 days) in that year were similar to those of other study years. It is possible that low flows in 2020 exacerbated the problem of finding adequate passage for fish that were already naïve to the river above Milford Dam.

Inability to efficiently choose a migratory pathway has important implications for spawning success and, ultimately, the recovery of Atlantic salmon in the Penobscot River. Salmon must pass at least two dams to access substantial rearing habitat, and much of the best rearing habitat lies above at least three dams, if not more (Milford-Howland-Brownsmill, or Milford-West Enfield-Weldon). If salmon display hesitancy in the presence of dams, and do so several times throughout their journey, they risk experiencing increased water temperatures and using valuable energy reserves long before reaching their spawning grounds (Rubenstein et al. submitted). Chinook salmon (*O. tshawytscha*) that spend the summer in-river prior to spawning can decrease their metabolic rate by up to 20% through the strategic use of thermal refugia (Berman and Quinn 1991). Atlantic salmon that are weeks or months behind schedule due to one or more delays at dams not only may not find adequate thermal refugia during their migration (Izzo et al. 2016), but they may also not be able to take full advantage of optimal conditions in their spawning habitat because they have a reduced time between arrival and reproduction.

The results of this long-term study suggest that migratory delays are common for adult Atlantic salmon in the Penobscot River, and that different types of fish passage structures as well as smolt-stocking practices may pose barriers to effective migration. Of particular interest and concern is the length of delays that the tagged salmon experienced below Milford Dam. The next step in this research is to use the detailed fish histories from delayed individuals to reconstruct a map of when and where salmon were located while searching for passage. This exercise may help answer questions about specific aspects of the dam or dam approach that hinder efficient passage. In-depth study of delays and behavior below other dams in the system could also be valuable for increasing passage success.

CHAPTER 4

FINE-SCALE MOVEMENTS OF MIGRATORY ADULT ATLANTIC SALMON SEARCHING FOR DAM PASSAGE

ABSTRACT

Atlantic salmon (*Salmo salar*), like many anadromous fish species, have experienced population declines and extirpations due to damming. Although fish passage facilities are commonly found at dams, Atlantic salmon populations may still be depressed as a result of poor passage efficiency. We radio-tagged adult Atlantic salmon (n=88) in the Penobscot River in 2019-2020 and investigated dam passage delays and patterns of movement while fish searched for passage. Fish that concentrated their searching in the vicinity of the fishway entrance experienced shorter delays (median 5 days) compared to fish that searched the opposite shore of the river or moved extensively throughout the river seeking passage (median 13-14 days). Fish that approached the dam near the entrance of the fishway were able to rapidly enter and use the fishway, whereas other fish required over a week to locate the fishway entrance. However, a substantial portion of the study fish passed the dam on the same day as entering the fishway, suggesting that attraction to the fishway itself is a major factor leading to extended delays. Understanding the relationship between attraction flows and fish movements could be important for minimizing migratory delays and avoiding the physiological consequences of delays.

INTRODUCTION

The large-scale migratory movements of adult Atlantic salmon (*Salmo salar*) returning to their natal rivers to spawn are both impressive and intensively studied. Atlantic salmon may travel thousands of kilometers through the ocean (Rikardsen et al. 2021) before returning to the coastal waters of either North America or Europe and locating the exact river from which they emigrated as smolts up to several years previous (Hansen and Jonsson 1994). From the time they enter freshwater, they may travel hundreds of kilometers (Økland et al. 2001) to the cold headwater streams where they were hatched (Hansen and Jonsson 1994), a journey undertaken entirely on energy reserves brought from the marine environment, as they do not feed after they have left the ocean (Kadri et al. 1995, Lennox et al. 2018). Those salmon that survive spawning can return to the ocean to recondition and prepare to make additional spawning migrations (Halttunen 2011, Lennox et al. 2018). Individual Atlantic salmon have been recorded making as many as six spawning migrations in a lifetime (Ducharme 1967).

As energetically demanding as their migration is, the scope of the distances traveled is not the only challenge facing Atlantic salmon. Their life cycle brings fish from the high seas of the Atlantic Ocean all the way to streams fed by the snowmelt of inland mountains and back again, and often requires salmon to navigate altered river systems. Damming is one of the most pervasive issues for the persistence of Atlantic salmon and migratory fish in general (Parrish et al. 1998, Limburg and Waldman 2009). Most Atlantic salmon populations in North America are declining or extirpated (Parrish et al. 1998) due to dams blocking their upstream and downstream migrations (Limburg and Waldman 2009).

Even at dams where fish passage exists, salmon may not be able to use passage structures efficiently enough to maintain a healthy population size, and may experience complete passage failure (Lundqvist et al. 2008, Peterson et al. *in progress*). This is the case in the Penobscot

River, the largest river in Maine and the second largest river in New England (Trinko-Lake et al. 2012 [Figure 4.1]), which drains an area greater than 22,000 km^2. Extensive damming on both Penobscot River and its major tributaries began in the mid-nineteenth century (Taylor 1951, Walburg and Nichols 1967) and created a highly fragmented river system.

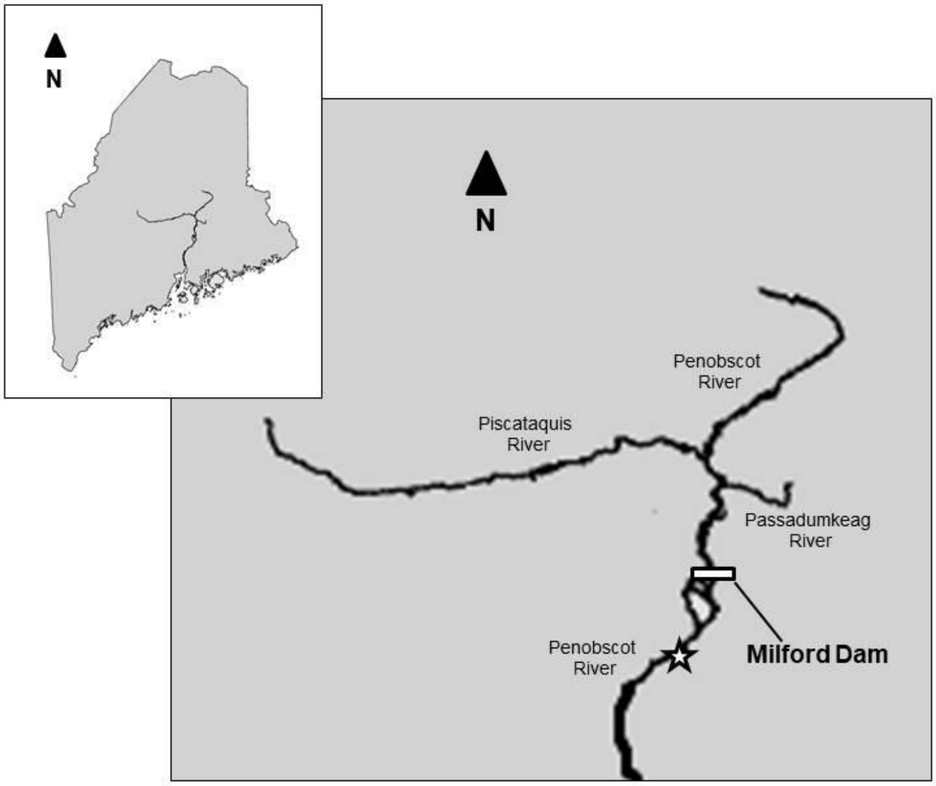


Figure 4.1. The location of the Penobscot River and its major tributaries within the state of Maine, USA. Milford Dam (rkm 61) is the most seaward dam in the system, indicated by the white rectangle. The release location of radio-tagged adult Atlantic salmon (*Salmo salar*) was at rkm 43, denoted by the star. Other main-stem and tributary dams are not shown for sake of clarity.

Penobscot River Atlantic salmon belong to the Gulf of Maine Distinct Population Segment (DPS), which was listed as Endangered in 2000 (USFWS 2000). This DPS is the only one in the United States that still contains native, wild fish (NOAA 2020). Prior to damming, over 100,000 salmon were estimated to return to the Penobscot River annually, and upper estimates for the salmon run in the Kennebec River, another major salmon river in Maine, exceeded 200,000 (Atkins 1867, Foster and Atkins 1869). At the time of this writing, estimated returns of wild adults belonging to the Penobscot Bay Salmon Habitat Recovery Unit (SHRU) are far less than 500 individuals, a target necessary for reclassifying the population (NOAA 2020). Within the Penobscot River, the majority of the most suitable spawning and rearing habitat for Atlantic salmon is located in the upper reaches of the watershed (NOAA 2020), and situated upstream of at least three main-stem dams (Peterson et al. *in progress*).

Restoration efforts on the Penobscot River have included the removal of two main-stem dams (Great Works and Veazie Dams) and fish passage improvements at other dams remaining in the system (Opperman, 2011). The Milford Dam (hereafter referred to just as Milford) is currently the most seaward dam on the Penobscot River main-stem at river kilometer (rkm) 61. Milford, completed in 1906, is a 10.4 m-high concrete dam with 6.4 mW generating capacity (Opperman et al. 2011, US ACE 2018). Until 2014, fish passage at Milford was provided by a Denil-style fishway (Opperman et al. 2011). Estimates of seasonal passage rates for Atlantic salmon at Milford Dam was higher than the two removed dams (83-87 %), but still less than contemporary passage targets for the dam (Holbrook et al. 2009, NMFS 2012). Beginning in 2014, an automated fish lift provided passage to a greater range of species, and at that time use of the Denil fishway on a regular basis was discontinued (PRRT 2018).

Effective fishways require two main functions: attraction and passage. Attraction efficiency characterizes the fraction of fish in a group that are able to locate a fishway entrance (e.g., move within 3 m *sensu* Bunt et al. 1999) or to be near enough detect and respond to the attraction flow (Aarestrup et al. 2003). Passage efficiency may be quantified as the proportion of fish that approach the fishway and successfully exit the structure (Bunt et al. 1999; Aarestrup et al. 2003). After the installation of the fishway at Milford Dam, overall passage efficiency has been relatively high (between 95% and 100%) during a two year study, but significant delays were observed (Izzo et al. 2016).

Because the current requirement for passage at Milford Dam is 95% passage within 48 h (NMFS 2012), observed delays are of interest and concern. Delays at dams may lead to depleted energy reserves, reducing both reproductive success and survival (Geist et al. 2000). Atlantic salmon delayed downstream of Milford Dam are subject unfavorable thermal conditions and rapidly lose somatic energy stores that likely reduce investments into reproduction as well as their probability of post-spawn survival (Rubenstein et al., *submitted*). It is unclear whether the ability to find the fishway or the efficacy of entrainment into the fishway, (or both), are causing the delays. It is clear, however, that some adults may be attracted to the west side of the dam where there is no upstream passage. Deep pools located against the dam face on the western side of the river may become cut off from the main channel when river levels drop during the summer, or when dam operations change the amount of water flowing over the top of the dam (Figure 4.2). These factors cause stranding events to occur on an almost annual basis, requiring salmon capture and transport over the dam by hand to avoid injury or stress (Holyoke 2019).

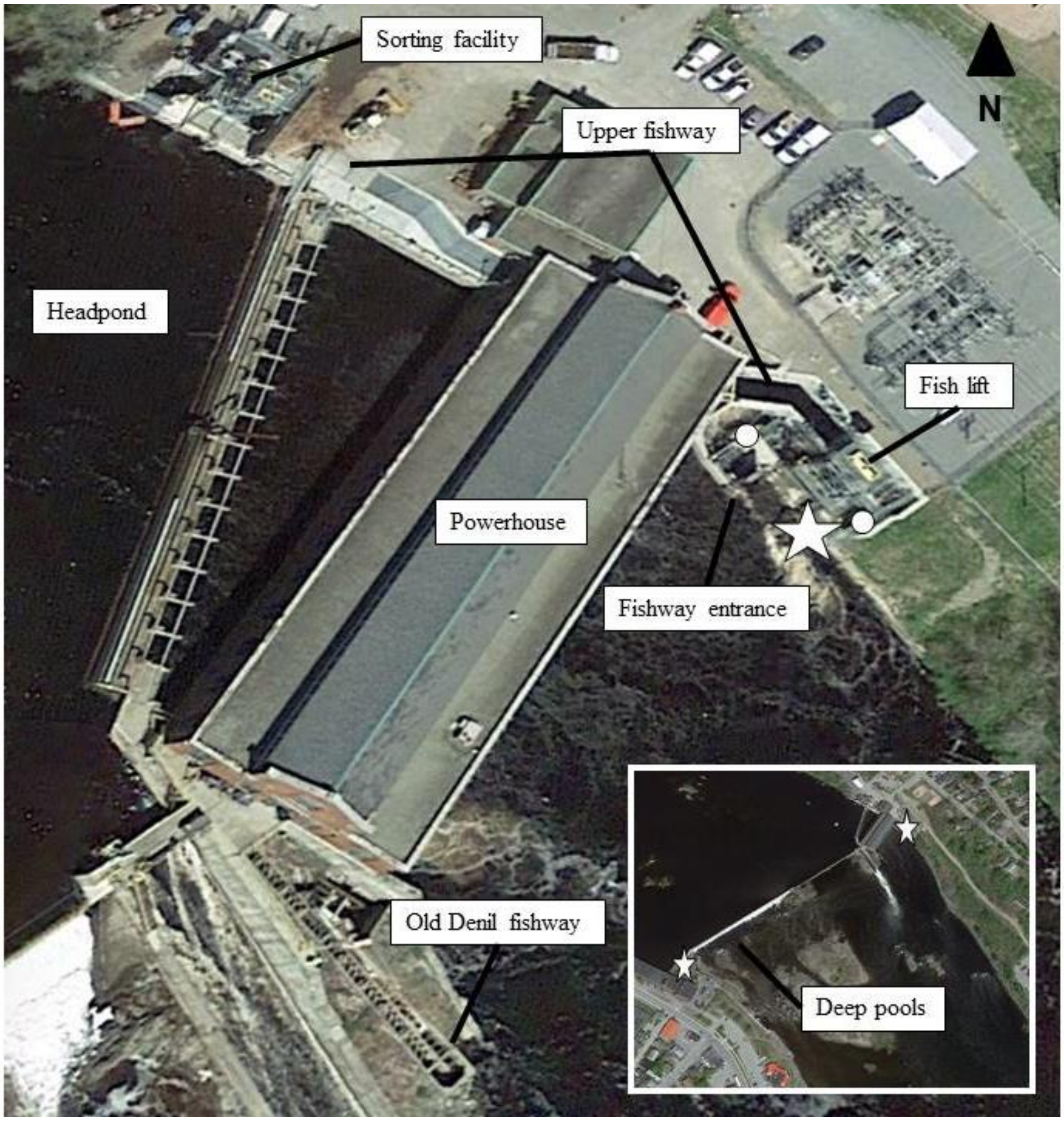


Figure 4.2. Aerial view of the Milford Dam powerhouse, fishway, and sorting facility. The inset shows the location of the deep pools on the west side of the river where salmon (*Salmo salar*) have become stranded. The stars indicate the location of radio receivers with attached Yagi antennas, and the white dots are the location of the dropper antennas in the fishway. (Google Earth Pro V 7.3.4.8248. (May 14, 2015). Milford, Maine, USA. 44.942007°, -68.644853°, Eye alt 260 meters. Digital Globe 2012. http://www.earth.google.com [March 19, 2022]).

In this study we examine the movement behaviors of adult Atlantic salmon during migratory delays experienced at the Milford Dam on the Penobscot River, Maine. The behaviors of adult Atlantic salmon while searching for dam passage are important because they may inform managers about the reasons for unsatisfactory passage performance. With this information, issues of attraction or fishway performance may be resolved and addressed. We describe the fine-scale movements of delayed salmon searching for passage using radio tagged adult salmon in 2019 and 2020. We developed an index of relative location using tag signal strength to describe patterns of movement exhibited by salmon while they searched for passage. Such knowledge may also help to quantify the risks that salmon face under a range of passage conditions, such as exposure to increased water temperatures or an increased risk of stranding.

METHODS

Milford Dam

The entrance to the Milford fishway is located on the eastern bank of the Penobscot River (Figure 4.2). After locating the entrance, fish must navigate an 180^{o} turn in the channel before arriving at the main hopper associated with the fish lift (Figure 4.2). Mechanical gates open or close to allow or restrict access to the hopper. After fish have been lifted and dumped out of the main hopper, they continue through a channel that passes beneath the Milford powerhouse and passes by a sorting facility operated by staff from the Maine Department of Marine Resources (ME DMR). The sorting facility has a secondary lift and hopper associated with it that can be used to bring fish to sorting and handling tanks on the roof of the facility.

Fish capture and tagging

All adult Atlantic salmon that return to the Penobscot River are handled by the ME DMR when they pass through the Milford sorting facility. ME DMR staff use the secondary hopper at the sorting facility and a series of crowders to direct salmon into 3-m diameter holding tanks filled with ambient river water. Each two sea-winter fish is measured (mm, fork length), sex externally judged, assessed for injuries (including fin damage), and tagged with a passive integrated transponder (PIT) tag (23 mm, HPT23, Biomark, Boise, Idaho) inserted beneath the skin (Bruchs et al. 2018). Salmon that are to be used as hatchery broodstock are retained at the sorting facility until they can be transported to the Craig Brook National Fish Hatchery in East Orland, Maine. The remaining salmon are passed upstream into the Milford head pond.

We tagged Atlantic salmon for our study when they arrived at the sorting facility. After they had been handled by ME DMR, we implanted each study fish with a uniquely-coded radio transmitter (MCFT-3L, Lotek Wireless, Inc. Newmarket, Ontario). Radio transmitters were inserted gastrically using a flexible plastic tube (as described in Izzo et al., 2016). Fish were held against the side of the tank with their heads out of the water while the tag was inserted, a process which typically took less than 30s. After tagging fish were allowed to recover in a separate section of the holding tank. No anesthesia was used during the tagging process. Radio-tagged salmon were moved into an aerated tank of ambient river water for transport. They were trucked downstream and released at a boat launch in Brewer, Maine approximately 20 rkms downstream of Milford. Transmitters emitted a signal every 2.5s that could then be used to track the movements of individual fish.

Telemetry

Stationary, shore-based radio receivers were located at each side of Milford Dam in both years of the study (Figure 4.2). The receiver station on the east side of the dam (referred to as the “east receiver”) was equipped with a four-element Yagi antenna mounted above the entrance to the fishway and pointing west across the river. Two dropper (stripped cable antennas) were also associated with the east receiver. One dropper antenna was located at the 180^o bend in the fishway and the other was located behind the main hopper (Figure 4.2). Dropper antennas provided near-field detections of radio-tagged salmon. The receiver station on the west side of the dam (“west receiver”) consisted of a single four-element Yagi antenna that was mounted on a railing above the deep pools and pointed east across the river. Radio receivers were either SRX-800 or SRX DL models (Lotek Wireless, Newmarket, Ontario, Canada). We considered a fish to have arrived at Milford from downstream when it was detected by either of these receivers following release.

An array of two pass-through PIT antennas was located just downstream of the sorting facility in the upper portion of the Milford fishway. In general, dam passage was confirmed when ME DMR staff handled a tagged fish that returned to the sorting facility, but the PIT array was used to corroborate the timing of passage and also monitor passage after water temperatures became too high to safely handle salmon (24^{o}C, Bruchs et al. 2018). PIT antenna design and function are detailed in Kazyak and Zydlewski (2012).

Fine-scale movements

Approach and passage.--“*Approach*” to the Milford Dam was defined as a fish drawing near enough to the dam from downstream and coming within range of the stationary radio receivers and being detected. An approach was also recorded if fish were detected passing through a PIT antenna located at the downstream end of the fishway. "*Dam passage*" at Milford Dam was assigned to a tagged individual if that fish was detected on a stationary radio receiver or via mobile tracking upstream of the dam. Detection on a PIT antenna in the upstream part of the fishway also confirmed passing. We refer to the period of time that salmon spend downstream of Milford, between approach and passage, as "*delay"*. Fish that fell back (i.e., successfully passed upstream then moved downstream past the dam far to no longer be detectable at the Milford Dam receivers) and approached the dam again were considered to be a new event for our analysis (two events were recorded for eight fish).

Location index.--We developed an index of relative location (IRL) using detections of Atlantic salmon on the Milford radio receivers from 2019-20. The IRL used the signal strength associated with a detection of an individual to create a visual representation of that individual's relative distance from each receiver (east and west receivers) during the time it was being detected by either one or both of those receivers.

The IRL was developed by amassing detections of an individual from both the east and west receivers and compiling these detections into a single fish history, in which each detection was associated with a time and date stamp and a signal strength (also known as power) that ranged from 0 (low power) to 255 (maximum power). The strength of the signal emitted by radio transmitters attenuates with distance (Winter et al. 1978, Heim et al. 2018). Patterns of signal strength from a radio receiver can vary depending on the location of that receiver and the ambient noise (i.e., traffic noise, overhead power lines) in the area. Therefore, signal strength is not a definitive measure of distance from a receiver, but it can be used to describe location relative to a receiver (closer vs. farther away).

We calculated a median power value for every hour that an individual was detected on each of the two Milford receivers, beginning with the hour of that individual's arrival at Milford and continuing until that individual either passed the dam or ceased to be detected on either radio receiver. For time intervals after arrival when the individual was not being detected on the Milford receivers (i.e., it had traveled back downstream out of detection range), there was no median calculated and that hour was not included in the IRL. The IRL was calculated as:

(1)

$$x_{i,j} = \frac{W_{i,j} - E_{i,j}}{W_{i,j} + E_{i,j}}$$

Where $x_{i,j}$ is the IRL value generated for *i* hour on *j* day, *W* is the median power of the west receiver, and *E* is the median power of the east receiver. If a fish was only detected on a single receiver for a given hour, that receiver which failed to detect the fish was assigned an index value of 0 for that time period. Index results ranged from $-1 \leq x_{i,j} \leq 1$, with negative results indicating that a fish was located nearer to the east receiver and positive results indicating that it was nearer to the west receiver during a given period. A result of $x_{i,j}$=-1 occurred whenever a fish was detected only on the east receiver for a given hour, and a result of $x_{i,j}$=1 occurred whenever a fish was detected only on the west receiver.

Index values were plotted against time for all individuals that were detected on at least one of the Milford receivers. These plots were used to assess movement along the dam face while individuals searched for passage. Index values and plots were all generated using Program R (R Core Team 2021).

Data analysis.--We tallied the length of delays in days for each individual, the total number of hours that each individual was detected on at least one Milford receiver, and the number of hours for which the IRL differed from 0. The IRL graphs were examined qualitatively and assigned to one of five general movement patterns (Figure 4.3):

Extensive Searching. This pattern was assigned to IRL graphs that showed extensive movements between the east and west side of the river, and the fish did not appear to spend more time on one side of the river over the other.

Eastern Exclusive. These fish were detected only on the east side of the river (IRL<0 for all detections).

Western Exclusive. These fish were detected only on the west side of the river (IRL>0 for all detections).

Eastern Focus. The majority of the detections of these fish were clearly located on the east side of the river (IRL<0 for most detections).

Western Focus. The majority of the detections of these fish were clearly located on the west side of the river (IRL>0 for most detections).

Movement patterns for salmon that experienced more than one delay (n=8) were tallied separately for each delay (up to 2 delays per fish). We also recorded delay times, approach times, and the amount of time required for fish to locate the entrance to the fishway (indicated by detections on the dropper antennas) relative to when they passed the dam to determine if fish enter the fishway, exited and continued searching for passage elsewhere. Delay, approach, and passages times were compared for fish that successfully passed and fish that were unsuccessful using Welch’s t-test in Program R (R Core Team 2021) with a threshold of $\alpha=0.05$.

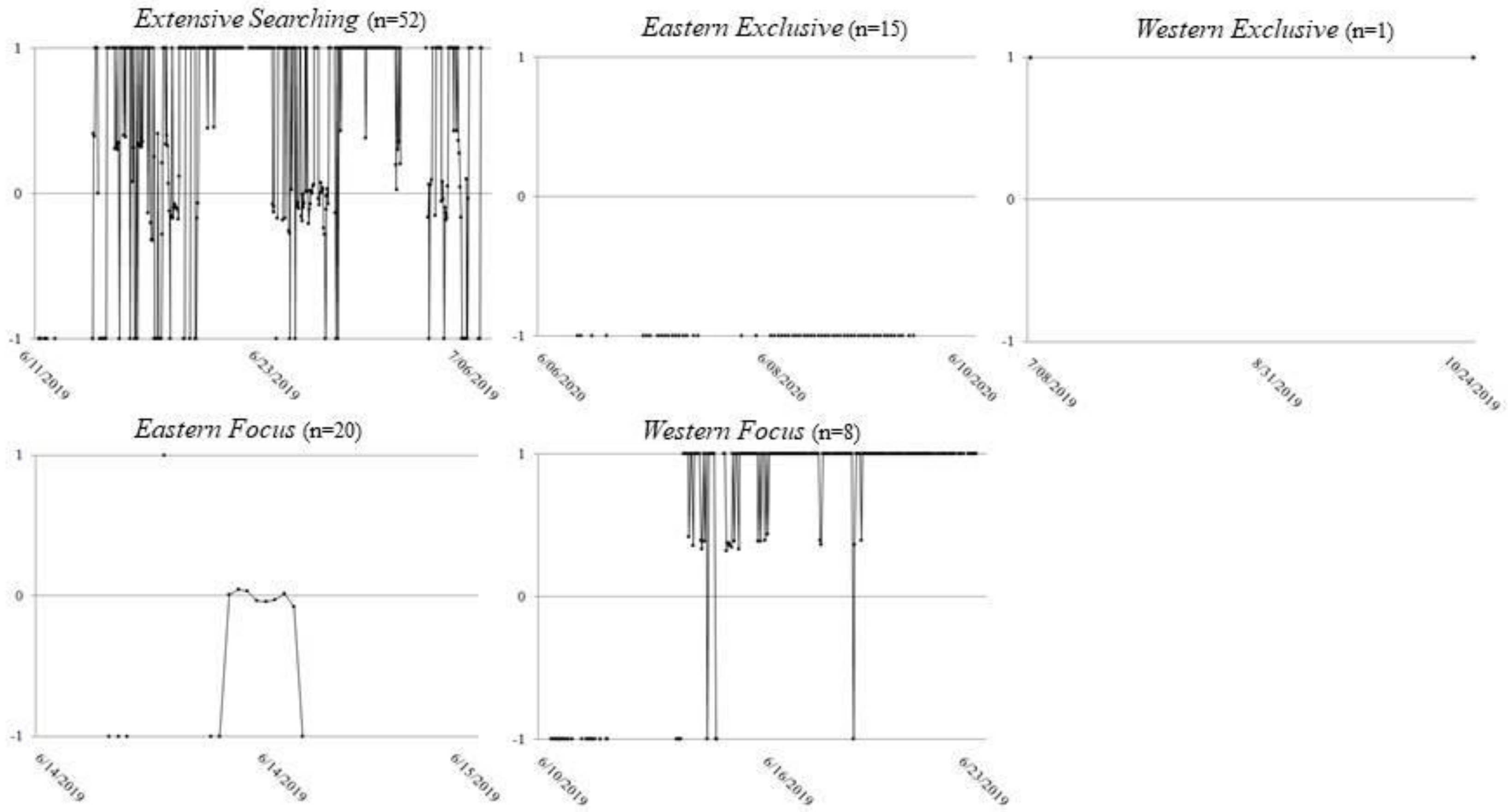


Figure 4.3. Examples of the five movement patterns identified in the graphs of the index of relative location: Eastern Exclusive, Eastern Focus, Extensive searching, Western Focus, Western Exclusive See text for definitions. On the y axis, -1 corresponds to a fish detected only on the east receiver within a one hour interval, and a value of 1 indicates detection only on the west receiver.

RESULTS

We radio-tagged a total of 88 adult 2-seawinter Atlantic salmon between 7 June-8 June 2019 (n=50) and 1 June-8 June 2020 (n=38). One fish from 2020 was of unknown sex and origin (hatchery or wild), but of the remainder, 78% were hatchery origin and 48% were female. Fork lengths ranged from 650-820 mm (Table 4.1). A total of 96 delays were recorded (includes two delays for eight fish). Eighty-two of these delays resulted in successful passage; the eight fish that experienced a second delay all successfully passed the dam after their second delay.

Table 4.1. Numbers of adult Atlantic salmon (*Salmo salar*) radio-tagged for our study in 2019 and 2020. Sample sizes are broken down by year, sex, and origin (hatchery or wild). Wild fish were identified by the presence of an adipose fin.

	2019	2020
Total	50	38
Male	27	18
Female	23	19
Hatchery	40	28
Male	24	14
Female	16	14
Wild	10	9
Male	3	4
Female	7	5

The time required for salmon to approach Milford Dam after release (for the first approach only) was a median of 3 days (range 0-12 days; Figure 4.4). This corresponds to a median travel rate of 6.7 km/d (0.6-20< km/d). Passage times ranged from 0-100 days, with a median delay of 7 days. Unsuccessful fish (n= 14) were delayed up to 180 days (range 6-180 days, median 14.5 days). Two unsuccessful fish were delayed for 139 days each. Mean delays were significantly longer for unsuccessful fish (53 days vs. 12 days, *P*=0.02).

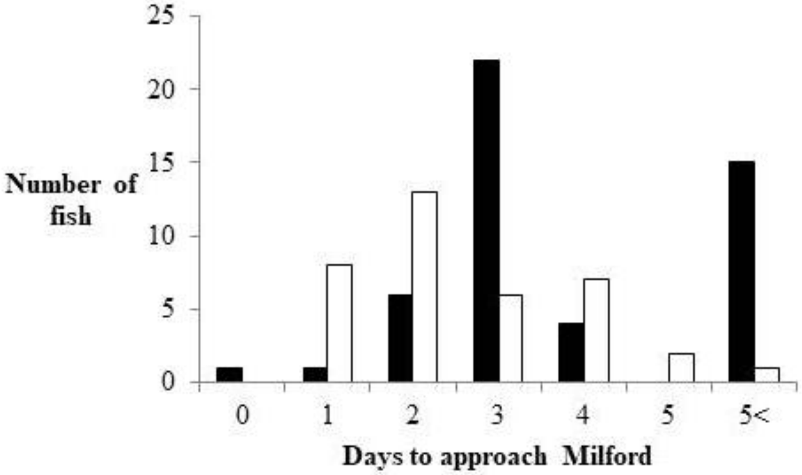


Figure 4.4. Approach time to Milford Dam for salmon tagged in 2019 (black bars) and 2020 (white bars).

We detected tagged fish on the Milford receivers for a total of 17,163 hours. Over half (56.7%) of all hours received an IRL>0, indicating that the fish was most likely located nearer to the west side of the river at some time in their approach and search. Tagged fish in our study recorded an average of 218 hours with IRL>0, and 166 hours with IRL<0. Overall, most fish experiencing delay (52/96; 54%) demonstrated a pattern of Extensive Searching, whereby time was divided evenly between the east shore (with the fishway) and the west shore. Fish exhibiting this behavior experienced median delays of 14 days (range 1-139, [Figure 4.4]). Many of the remaining fish had either an Eastern Focus (20/96; 21%) or an Eastern Exclusive (15/96; 16%) approach pattern. These fish ascended the dam more rapidly with a median delay of 5 days (range 0-13 [Figure 4.5]). In contrast, those fish with a Western Focus (8/96; 8%) or a

Western Exclusive (1/96; 1%) behavior were either delayed longer (median of 13; range 2-180) or did not pass (Appendix C). Seven of the 14 fish that did not successfully pass exhibited the Extensive searching pattern; four unsuccessful passers had either Western Focus or Western Exclusive patterns, and the behavior of the remaining three fit the Eastern Focus pattern. All of the Eastern Exclusive fish passed the dam.

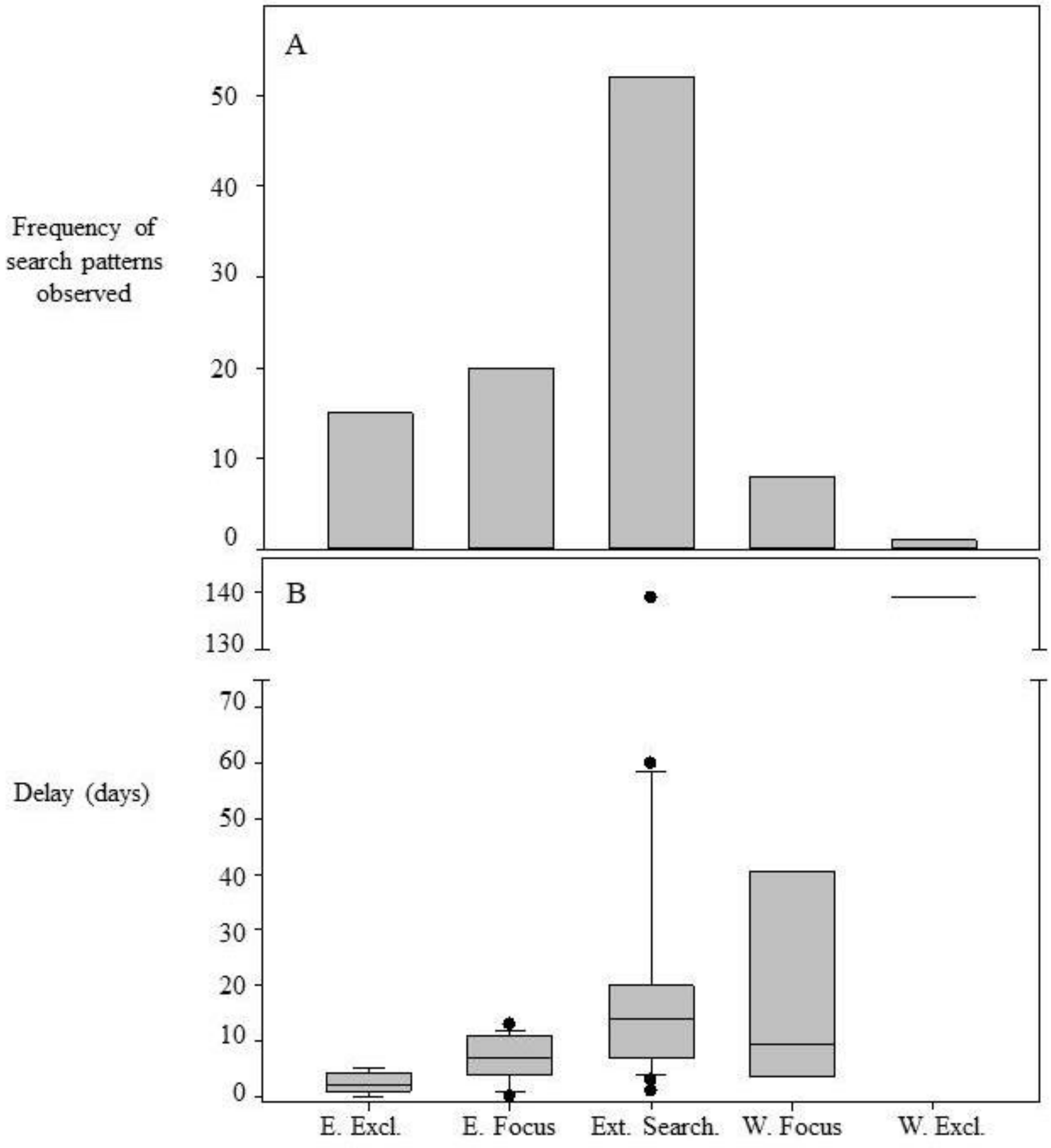


Figure 4.5. Proportion of fish returning to Milford Dam exhibiting each of the five movement patterns (identified in text and shown in Figure 4.3) based on a calculated index of relative location (A) and the length of delay in days among fish exhibiting each movement pattern (B). Eastern Exclusive (E Excl), Eastern Focus (E Focus) m, Extensive searching (Ext search), Western Focus (W Focus), Western Exclusive (W Excl).

Fish with either Eastern Focus or Eastern Exclusive movement patterns also located the fishway entrance (as evidenced by detection on the dropper antennas) much more quickly than Extensive Searching fish or fish that were associated with the western side of the river. Eastern Focus and Eastern Exclusive fish required a median of 0 days (range 0-6 days) to locate the fishway entrance, and a median of 3.5 days (range 0-13 days) to pass the dam after locating the fishway. This is in contrast with Extensive Searching fish that took a median time of 7 days (range 0-139 days) to be detected in the fishway after approaching Milford Dam, and then a median of 1 day (range 0-87 days) to pass the dam after locating the fishway. Western Focus and Western Exclusive (together western-associated) fish located the fishway slightly quicker than the Extensive Searching fish (median 6 days vs. 7 days), but one fish took 180 days to be detected on the droppers in the fishway (overall range for western-associated fish 0-180 days). After locating the fishway, western-associated fish passed within 0-46 days (median of zero days). This indicates that most western-associated fish passed the dam once they located the entrance to the fishway. Overall, 7/9 western-associated fish, 10/35 eastern-associated fish, and 29/51 Extensive Searching fish did not locate the fishway entrance until the day they passed the dam.

DISCUSSION

Only a third of tagged adult Atlantic salmon (35%) spent the majority of time of their approach on the eastern shore, where passage facilities at the Milford Dam are located. Most fish tagged in our study (54%) spent the majority of their time searching on both sides of the river when approaching Milford Dam. A small but biologically significant fraction (10%) of tagged fish had search patterns focused on the on the west side of Milford Dam. Extensive Searching and searching for passage on the western side of the river were both associated with extended delays. The median delays observed in our study exceeded those observed by Izzo et al. (2016) for tagged Atlantic salmon delayed below Milford in 2014 and 2015. The median delays in their study ranged from 3-4.3 days (Izzo et al. 2016). Holbrook et al. (2009) also reported tagged salmon ascended Milford Dam within four days of passing the old Great Works Dam (rkm 58). However it must be noted that the Denil fishway was still in use when Holbrook et al. (2009) completed their study.

Gowans et al. (1999) suggested that salmon delayed downstream of a dam may be in a natural holding period during their upstream migration. Salmon have been observed making stepwise upstream movements during their spawning migration (Økland et al. 2001), but this pattern of progression is unlikely to be the reason we observed salmon pausing downstream of Milford Dam. The majority of suitable salmon spawning habitat in the Penobscot River is located past rkm 100, and over 40% of the spawning habitat is past rkm 150 (Peterson et al. *in progress*). We observed rapid movements of fish approaching the dam, with some fish returning to Milford Dam on the same day they were released (a movement rate of >20 km/d). These movements patterns—rapid return to Milford Dam followed by a prolonged pause downstream of the Dam—were consistent with patterns observed by Izzo et al. (2016) after releasing tagged salmon in the same location. These data are consistent with the inability for these fish to either locate the fishway entrance or failure to enter the fishway.

We believe that the tagged salmon involved in our study struggled to locate the fishway entrance, but were fairly adept at using the fishway after entering it. Most Extensive Searching and western-associated fish took more than a week to locate the fishway, but then a significant portion passed the dam on the same day they were first detected by the dropper antennas within the fishway. Eastern-associated fish were both quicker to discover the fishway entrance and quicker to pass the dam after first being detected in the fishway. Izzo et al. (2016) reported that most (78%) of Atlantic salmon tagged in 2015 entered the fishway within five hours of arriving at Milford, but also visited the fishway entrance 1-47 times before passing the dam. This, taken together with our data, implies that salmon are very responsive to attraction flow cues coming from the fishway, but that this may not be the strongest cue salmon are experiencing while searching for passage.

Attraction flow on the western side of the river could be drawing fish away from the fishway entrance upon their initial approach. Gowans et al. (1999) noted that tagged salmon in the River Tummel, Scotland, were entering the turbine draught tubes at a hydroelectric dam (observations made by Webb 1990), and that this behavior ceased after screens were placed in front of the tubes. They hypothesized that flow coming out of the draught tubes had attracted salmon to those locations instead of the fishway entrance (Gowans et al. 1999). Hagelin et al. (2021) also reported low passage efficiencies during periods of high spill. A similar phenomenon may be occurring at Milford Dam when flashboards can draw salmon towards the deep pools on the west side (E. Peterson *personal observation*).

Temperature and discharge may play a role in passage success (Holbrook et al. 2009), but Gowans et al. (1999) found that delays were not correlated with flow or temperature, and our data would seem to follow this same pattern. Our fish were tagged within a relatively short time period each year, and most of our fish approached Milford Dam within a few days of tagging and release (Figure 3). These fish would have all experienced similar environmental conditions on the day of capture and between capture and approach to Milford Dam. Environmental conditions, while they may still be a very important influence on migratory behavior, are clearly not the only factors affecting salmon movements at the dam. It is possible that the location where the salmon happens to first approach the dam (whether it is closer to the east side or the west side) could influence its ability to detect the fishway entrance and therefore the length of its migratory delay.

Regardless of the reasons behind the movement patterns seen downstream of Milford Dam, these extensive delays and lack of attraction to the fishway are likely to reduce the spawning success and survival for Atlantic salmon released into the river. Atlantic salmon can use up to 60-70% of their energy reserves during the spawning migration (Jonsson et al. 1997). Glebe and Leggett (1981) maintain that this level of energy use forms the threshold between iteroparity and semelparity in anadromous species: individuals of species or populations that expend less than this amount of energy may survive the spawning migration, whereas individuals that expend more than this will not. Penobscot River Atlantic salmon can lose as much as 19% of their fat reserves just between release and recapture at Milford Dam (Rubenstein et al., *submitted*). Fat loss was directly and positively correlated with accumulated thermal units (ATUs) using many of the same fish used in our present study (Rubenstein et al. *submitted*), and downstream habitats such as stretches of river below dams were consistently warmer throughout the spawning migration than the upstream habitats where the salmon were ultimately headed. Temperatures in both upstream and downstream habitats increase throughout the summer. Thus, delays in downstream portions of the river will expose salmon to warmer conditions upstream as well by setting back the timeline of their migration (Izzo et al. 2016). The loss of critical energy store may reduce the possibility of post-spawn survival and thereby forcing the population into semelparity (Rubenstein et al. *submitted;* Zydlewski et al., 2021).

This study is among several (e.g., Holbrook et al. 2009, Izzo et al. 2016, Rubenstein et al. *submitted*, Peterson et al. *submitted*) that document Atlantic salmon approaching Milford Dam commonly experience migratory delays. We also show that extended delays may be caused by an inability to locate the fishway entrance upon first arriving at the dam. This phenomenon may be caused by attraction flow elsewhere along the dam. The subsequent movement patterns that salmon display searching for passage could put them at increased risk of stranding. Investigating attraction flow patterns along the dam, including from the fishway, is needed to identify actions to reduce delays.

CHAPTER 5

SCALE GROWTH RATES AND SCALE CIRCULUS DEPOSITION RATES OF MARINE-STAGE ATLANTIC SALMON *SALMO SALAR* RAISED UNDER SEMI-NATURAL CONDITIONS

ABSTRACT

Scale circuli yield valuable information about the life history, age, and growth of a fish. However, because circuli formation is influenced by somatic growth, the rate at which circuli are formed and the factors influencing these rates must be taken into account for the given life stage of the study species. Scales were collected from Atlantic salmon raised in marine net pens off of the coast of Maine in order to characterize the formation of scale circuli and the growth of scales during the ocean phase, and to relate circulus deposition and scale growth rate to water temperature. Fish were sampled 13 times over a period of 25 months. Neither circulus deposition rate nor growth rate were constant through time and the same trend held when circulus deposition and growth were related to thermal experience. Both rates decreased over the course of the study, presumably related to the fish reaching sexual maturity. The results of this study indicate that the pattern of circulus deposition and scale growth of Atlantic salmon vary greatly during the early marine phase, and this dynamic should be taken into account when assessing growth, especially over short time periods.

INTRODUCTION

In 1910, Lea, who was studying herring at the time, showed that scale growth is proportional to body length (Lea 1910). He found that the relative spacing of annuli was so consistent for single scales that this spacing could be used to back-calculate growth that took place in previous years of the fish's life. His detailed observations on scale structure and ages were not the first of their kind (Dahl 1907), and nor were they the last. Havey (1959) reported that scales represent a reliable method for aging Atlantic salmon (*Salmo salar)*. Similar observations have been made for a range of species, juvenile steelhead *Oncorhynchus mykiss* (Beakes et al. 2014) and northern pike *Esox lucius* (Laine et al. 1991) among them. Although other hard structures, such as otoliths, may be more reliable especially in older age classes of fish (Robillard et al. 1996, Braaten et al. 1999), many state and provincial agencies in the United States and Canada prefer to use scales over these other hard structures for aging common game species (Maceina et al. 2007). Scales require relatively little time and expense to age (Beakes et al. 2014) and, importantly, can be collected non-lethally. This is especially critical when researchers are working with threatened or endangered species.

Atlantic salmon have experienced marked declines across their range, particularly in southern North America, necessitating non-lethal methods of population assessment (Parrish et al. 1998). A recent experimental study by Thomas et al. (2019) found that scale growth and circulus deposition in Atlantic salmon post-smolts was variable and increased with increasing temperatures when food was held constant. They concluded that, while there was a strong relationship between scale and somatic growth, circulus deposition rates must be interpreted in light of the fish's thermal history in order to be more accurately used as a proxy for growth (Thomas et al. 2019).

The objective of the current study was to describe the scale growth rates and scale circulus deposition rates of marine-stage, net-pen raised Atlantic salmon. Growth and circulus deposition rates were tracked for two sea-winters, and related to time and water temperature, as well as somatic growth. The scale samples used here were collected originally by Sheehan et al.

(2005) as part of a larger study to assess phenotypic variation among stocks. We hypothesized that circulus deposition rates would not be constant through time but that they may be related to the thermal experience (water temperature) to which the fish were exposed.

MATERIALS AND METHODS

Field sampling

The field portion of this project was initiated in May 1998 when 6000 1+ Atlantic salmon smolts representing three rivers of origin were stocked into two marine net pen rearing facilities off the coast of Maine. Smolts originated from broodstock that were taken from the Dennys, East Machias, and Machias Rivers. The stocks from these rivers are all part of the Gulf of Maine Distinct Population Segment (GOM DPS), which was listed as Endangered under the Endangered Species Act (Endangered and Threatened Species, 2009) due to continued declines (National Research Council, 2004). The original broodstock were brought into captivity as parr, raised to maturity, and spawned at Craig Brook National Fish Hatchery in East Orland, ME during November 1996. Two thousand smolts from each stock were randomly chosen to be placed in net pens at either Site 1 or 2 (Cross Island or Deep Cove, see Sheehan et al. 2005 for more details [Figure 5.1]) on 5 May 1998. The selected smolts were randomly divided between the two Sites, for a total of 3,000 smolts in each net pen (Sheehan et al. 2005). While they were in the net pen the fish were fed to satiation, per industry standards (Sheehan et al. 2005).

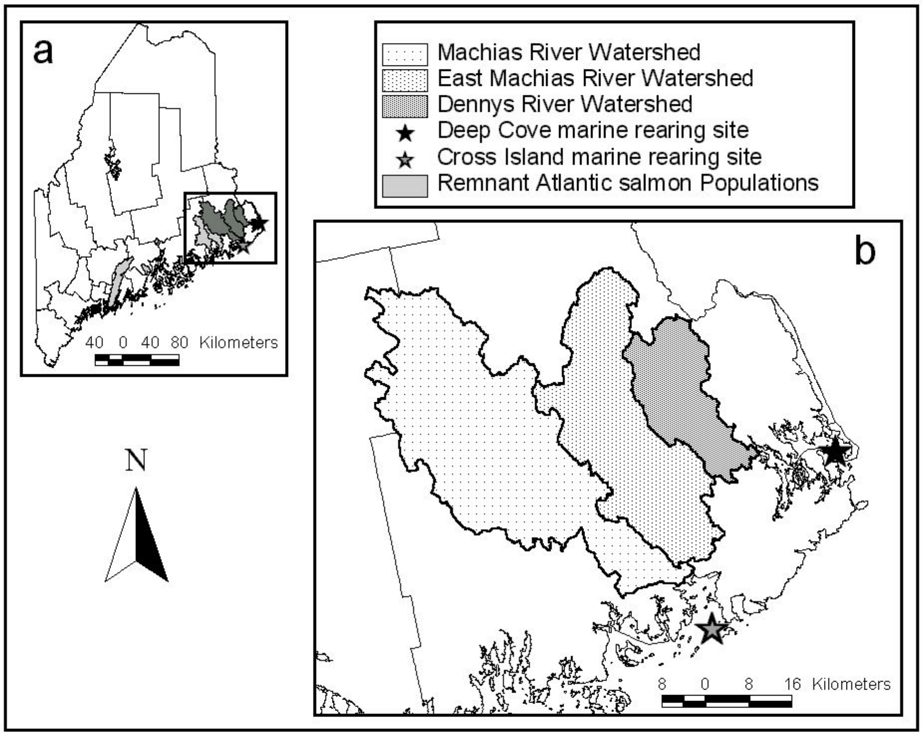


Figure 5.1. Map from Sheehan et al. (2005) showing A) the locations of remnant salmon populations as well as the rivers of origin for the stocked smolts and the stocking sites and B) the relative locations of the rivers of origin and Site 1 (gray star) and Site 2 (black star).

The salmon were sampled a total of 13 times between May 1998 and June 2000 (Table 5.1), with the first sampling event (hereafter "Event") taking place in freshwater rearing facilities prior to release into the net pens and Events 2-13 taking place in seawater. At every Event a seine was pulled through the net pen at each site. At least 30 fish from each stock at each site were measured (mass [grams] and total length [millimeters]) and a sample consisting of 1-16 scales was taken. A sample size of 30 was chosen based on prior experiences that suggested that data from 30 fish would be enough to detect differences in scale growth (T. Sheehan, pers.

comm.). Fish were sampled only at a single Event and recaptured individuals were released back into the net pen without having a second scale sample taken to avoid collecting regenerated scales from standardized scale sampling areas below the dorsal fin. However, recaptured individuals were weighed and measured each time they were recaptured. Previously sampled fish were identified with a uniquely-coded colored Visual Implant Elastomer tag (VIE, Northwest Marine Technology, Inc.). The colors of these VIE tags were specific to each stock and therefore also useful for stock identification. Sheehan et al. (2005) also obtained hourly water temperatures across the duration of the study at each of the two rearing sites using remote temperature loggers. At the end of the initial study the adults at Site 1 were released into the wild. However, disease concerns at Site 2 necessitated that the fish be sacrificed rather than stocked. The disease in question, infectious salmon anemia (ISA), was detected in the same bay as these fish, and all fish used in the samples reported by this paper were asymptomatic. It is highly unlikely that these disease concerns influenced growth rates or scale circulus deposition patterns (T. Sheehan, pers. comm.).

Table 5.1. Sampling dates for all Events that took place in the marine environment. Days in net pen is the total number of days between stocking fish in the net pen (5 May 1998) and the sampling Event. Accumulated thermal units (ATUs) are the averaged cumulative water temperatures for the two sites as of the day of the Event. Because the date of the first Event coincided with the day the fish were stocked into the net pens, those data have been omitted to include only marine growth. Weight records were incomplete for Events 4, 5, 7, 8, and 12.

Event	Sample date	Number of fish sampled	Median total length (mm) [standard dev.]	Median weight (g) [standard dev.]	Days in net pen	ATU (°C)
2	6/17/1998	167	235 [19.6]	109.1 [27.5]	43	285.5
3	7/14/1998	178	258 [17.7]	146.6 [31.4]	70	526.7
4	10/16/1998	52	379 [29.3]	NA	164	1488.6
5	11/13/1998	137	383 [39.0]	NA	192	1712.4
6	4/16/1999	162	438 [62.1]	790.0 [305.7]	346	2141.7
7	5/14/1999	143	450 [56.4]	NA	374	2296.4
8	6/14/1999	159	491 [65.4]	NA	405	2544.0
9	7/19/1999	132	521 [73.8]	1310.0 [585.5]	440	2902.6
10	8/17/1999	117	567 [72.5]	1770.0 [784.8]	469	3246.4
11	10/15/1999	68	539 [72.0]	1955.0 [737.0]	528	3994.1
12	11/19/1999	54	561 [79.8]	NA	563	4350.3
13	6/14/2000	156	695 [86.4]	3760.0 [1808.7]	771	5461.1

Laboratory methods

Scales were air-dried after collection, and cleaned by gently rubbing them between the fingertips in a dish of soapy water. Before and after mounting, the scales were placed in paper scale envelopes and stored in cardboard boxes that were kept indoors (T. Sheehan, pers.comm.).

Beginning in the fall of 2017, the slides were photographed under either 2.5x or 10x magnification on a ZEISS Axioplan 2 microscope (ZEISS International, Oberkochen, Germany) with a microscope-mounted digital camera (SPOT Insight 2 MP Color Mosaic; Diagnostic Instruments, Sterling Heights, Michigan). Previous to recording any data from the scales, a photograph of a stage micrometer at both 2.5x and 10x magnification was used to produce an appropriate calibration for the images. Each scale was uniquely coded based on the fish identifier coupled with a sequential numbering on each slide. All scales were photographed regardless of condition or regeneration status, but scales with regenerated centers or cracked edges were not processed further because they may not be useful for accurately determining age or growth (Blair 1942; McNicol and MacLellan 2010).

One reader processed each photograph of usable scales, which resulted in 1-11 replicates per fish. The number of replicates equaled the number of usable (whole, non-regenerated) scales available for each fish. We did not use the same number of replicates for each fish because this would have required using only one scale per fish, as some fish only had one usable scale available. Instead, we averaged the scale size and circulus number of all available scales for fish which had multiple usable scales. To obtain these measurements, the reader obtained circuli counts and spacing for each usable scale using ImagePro Premier software (Media Cybernetics 2012), in which a calibrated line, placed by the reader, was applied to the scale image that measured the total length from the center of the nucleus along the longest axis of the scale. ImagePro automatically placed markers on the line at the outside edge of every circulus based on the light/dark transition in the pixels. These markers could be examined and manually shifted or removed by the reader to make sure they had been placed on actual circuli. For each image, ImagePro also generated a data table that contained the number of markers (circuli) attributed to the scale and the distance from the nucleus to each circulus, as well as the total distance from the nucleus to the outside edge of the scale. The distances from the nucleus to each circulus were retained but are not reported here. The scale length and number of circuli on each scale were averaged among individual fish.

Data analysis

Reading multiple scales from the same individual can reduce sampling error, especially when sample sizes are low (Haraldstad et al. 2016). We measured all of the usable scale available for each fish, which ranged from 1-11 scales with a median of 2 scales per fish. Circulus counts and scale radius measurements among scales collected from the same individual fish were averaged.

Scale radius and fish total length were compared using simple linear regression (SLR). Differences in scale growth rate and circulus deposition rate between net pen sites were compared using a Welch two-sample t-test (W-2s t-test) with $\alpha=0.05$ because the variances in growth rates and circulus deposition rates were found to be unequal, and the W-2s t-test should be robust to non-normality. Rates were compared as both daily rates, and relative to water temperature. Accumulated thermal units (ATUs) were used to describe the thermal experience of the fish throughout the study. Accumulated thermal units were obtained by summing the mean daily water temperatures (°C) between Events. All water temperatures above 0°C were included in the calculation of ATU and negative temperatures were treated as 0°C (Boyd et al. 2010, Chezik et al. 2014). Scale growth rates and circulus deposition rates relative to time and ATUs were also compared among stocks of origin using ANOVA with $\alpha=0.05$.

Scale growth rates and circulus deposition rates were averaged among sampling Events across the duration of the study and among stocks and sites to ascertain the presence of any relationships between these rates and either time or water temperature. Growth and circulus deposition were calculated between Events, so there are a total of 12 growth/ circulus deposition intervals among the 13 sampling Events. However, data from Event 1 were omitted because Event 1 took place in the freshwater rearing facilities, leaving a total of 11 growth/ circulus deposition intervals for the analysis. Using these results we also calculated the number of days required for a single scale circulus to form.

RESULTS

A total of 1,525 fish among all stocks and net pen sites was sampled over the duration of the project. The difference in mean water temperature between Site 1 and Site 2 was only 0.15 °C (Site 1=7.45°C, Site 2=7.6°C). Therefore, the temperatures from the two sites were averaged, and the resulting temperature time series was used for all further analyses (Figure 5.2). Additionally, two large gaps in temperature data from Site 2 made it impossible to calculate reliable scale growth rates or circulus deposition rates on a pen-specific basis

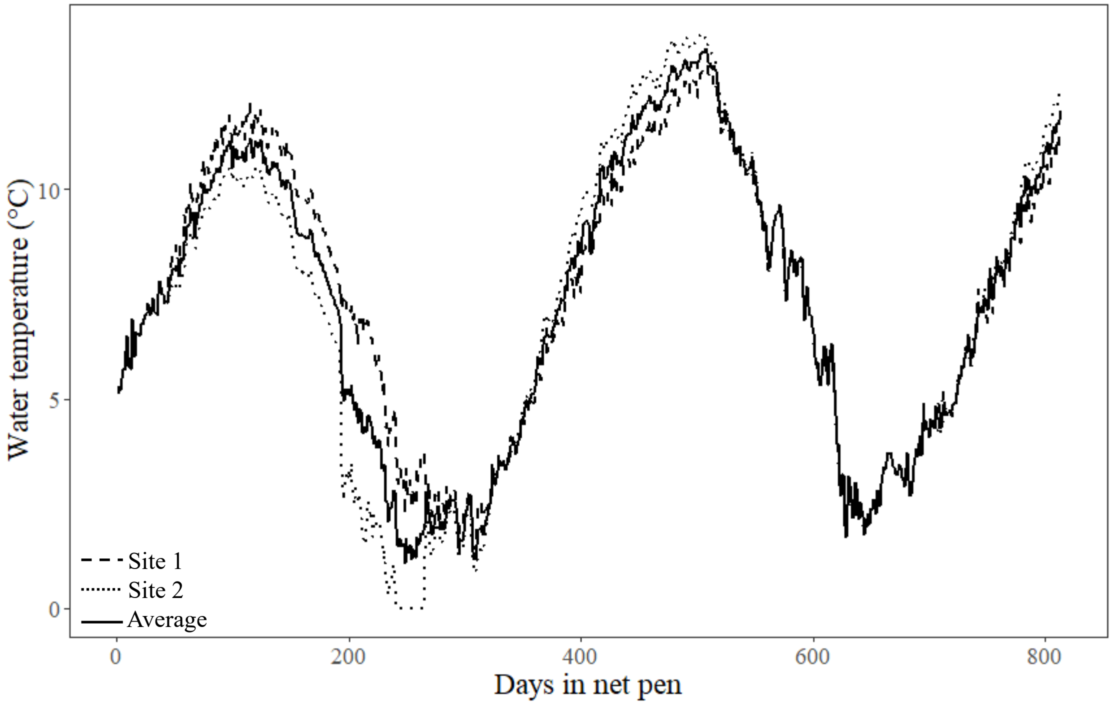


Figure 5.2. Time series of water temperature of the two net pen sites throughout the study period, and their average. Site 1= dashed line; Site 2= dotted line; Average of Site 1 and Site 2= solid line.

Daily scale growth rate and daily scale circulus deposition rate were higher at Site 1 than at Site 2 (daily scale growth: W-2s t-test, t=3.6, P<0.05; daily circulus deposition: W-2s t-test, t=2.8, P<0.05). As expected, when scale growth and circulus deposition rate were related to ATUs both rates were higher at Site 1 than at Site 2 (daily scale growth: W-2s t-test, t=3.5, P<0.05; daily circulus deposition: W-2s t-test, t=2.7, P<0.05). There were no differences in scale growth rates or circulus deposition rates among stocks for either daily rates or rates compared to ATUs (daily scale growth: ANOVA $F_{2,1522}$=0.42, P>0.05; daily circulus deposition: ANOVA

$F_{2,1522}$=0.31, P>0.05; scale growth per ATU: ANOVA $F_{2,1522}$=0.31, P>0.05; circulus deposition per ATU: ANOVA $F_{2,1522}$=0.28, P>0.05). Therefore, the data for scale growth rate and circulus deposition rate, respectively, were combined for all stocks within a site but the sites were treated separately for the remainder of the analysis.

Relationship of scale growth rate to days spent in net pen and water temperature

Scale radius and fish total length showed a strong relationship at both sites when the data was considered as a whole (Site 1: SLR, adjusted R^2=0.95, P<0.001; Site 2: SLR, adjusted R^2=0.93, P<0.001 [Figure 5.3]). However, daily growth rates showed a non-linear, negative trend through time (Figure 5.4A-B). Among Events, the daily scale growth rate was not consistent (Site 1: ANOVA, $F_{1,692}$=1207, P<0.05; Site 2: ANOVA, $F_{1,829}$=1272, P<0.05). The same trend was evident in the relationship between scale growth and water temperature through time (Site 1: ANOVA, $F_{1,692}$=864.8, P<0.001; Site 2: ANOVA, $F_{1,829}$=1229, P<0.001 [Figure 5.4c-d]).

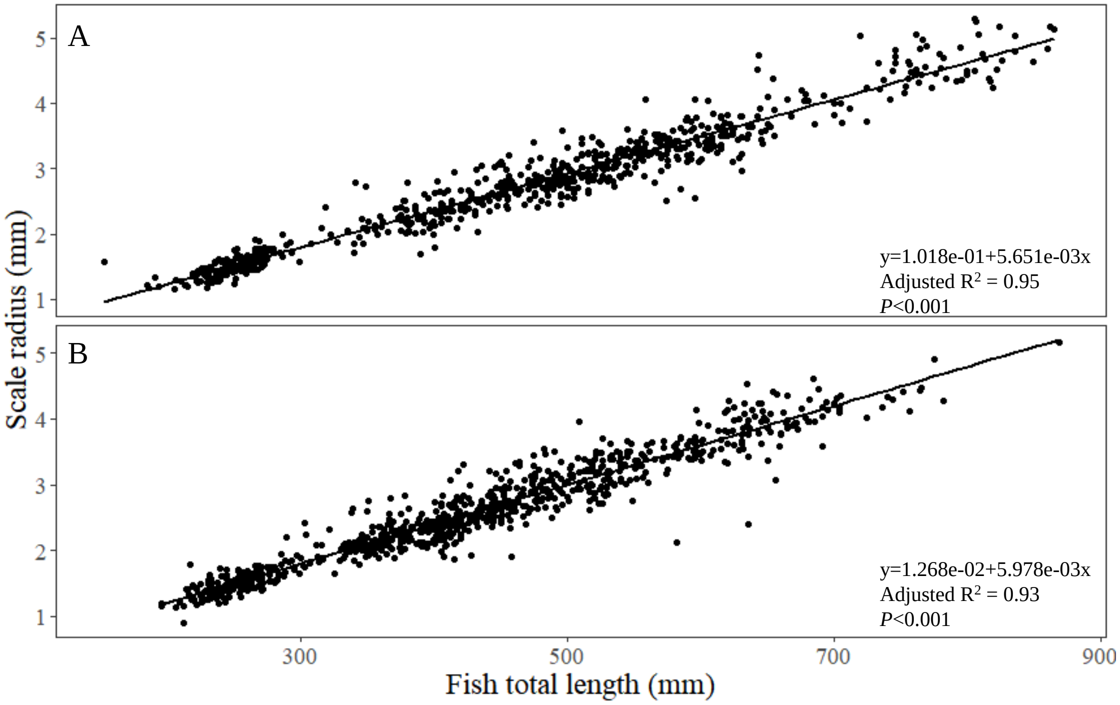


Figure 5.3. Relationship of scale radius to fish total length at Site 1 (A) and Site 2 (B).

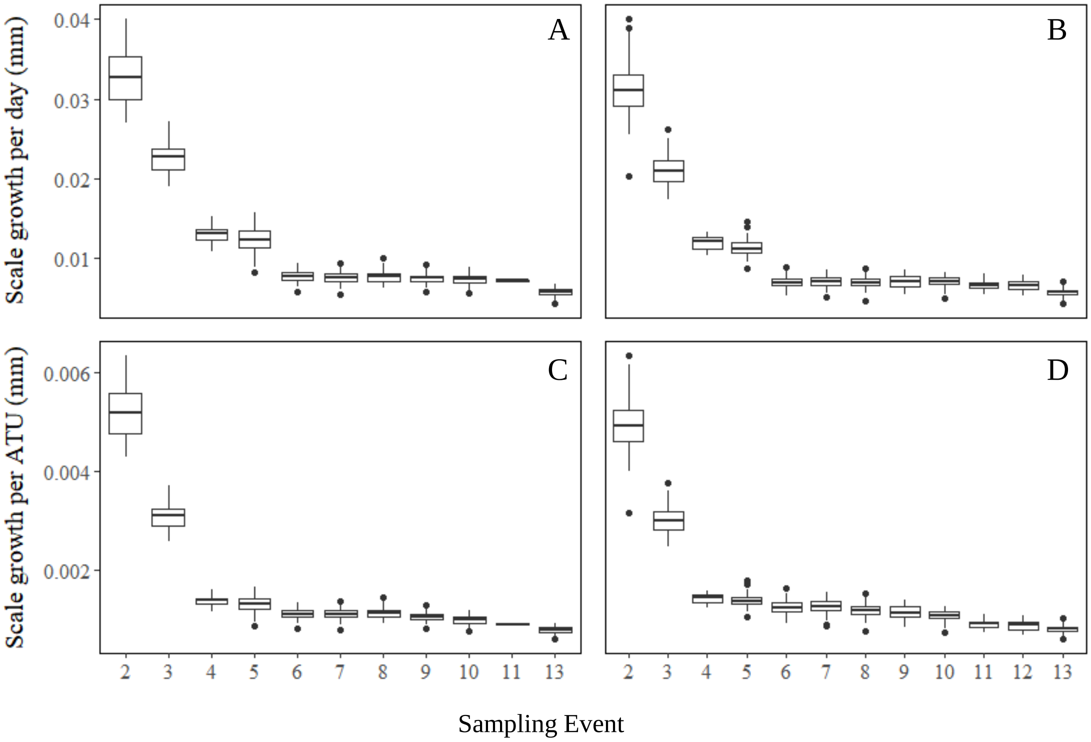


Figure 5.4. Daily scale growth rate at Site 1 (A) and Site 2 (B), and the relationship between scale growth rate and accumulated thermal units (ATU) at Site 1 (C) and Site 2 (D) over the duration of the study.

Relationship of circulus deposition rate to days spent in net pen and water temperature

Circulus deposition rate showed similar patterns to scale growth rate through time. Circulus deposition rate was not constant through time (Site 1: ANOVA, $F_{1,692}$=1183, P<0.001; Site 2: ANOVA, $F_{1,829}$=1030, P<0.001) and showed a sharp decrease throughout the first five sampling Events (192 days post-stocking, [Figure 5.5a-b]). The relationship between circulus deposition rate and water temperature was also not constant among Events, with the steepest decrease in circulus deposition rates occurring among the first three sampling Events (Site 1: ANOVA, $F_{1,692}$=898.9, P<0.001; Site 2: ANOVA, $F_{1,829}$=1036, P<0.001 [Figure 5.5c-d]).

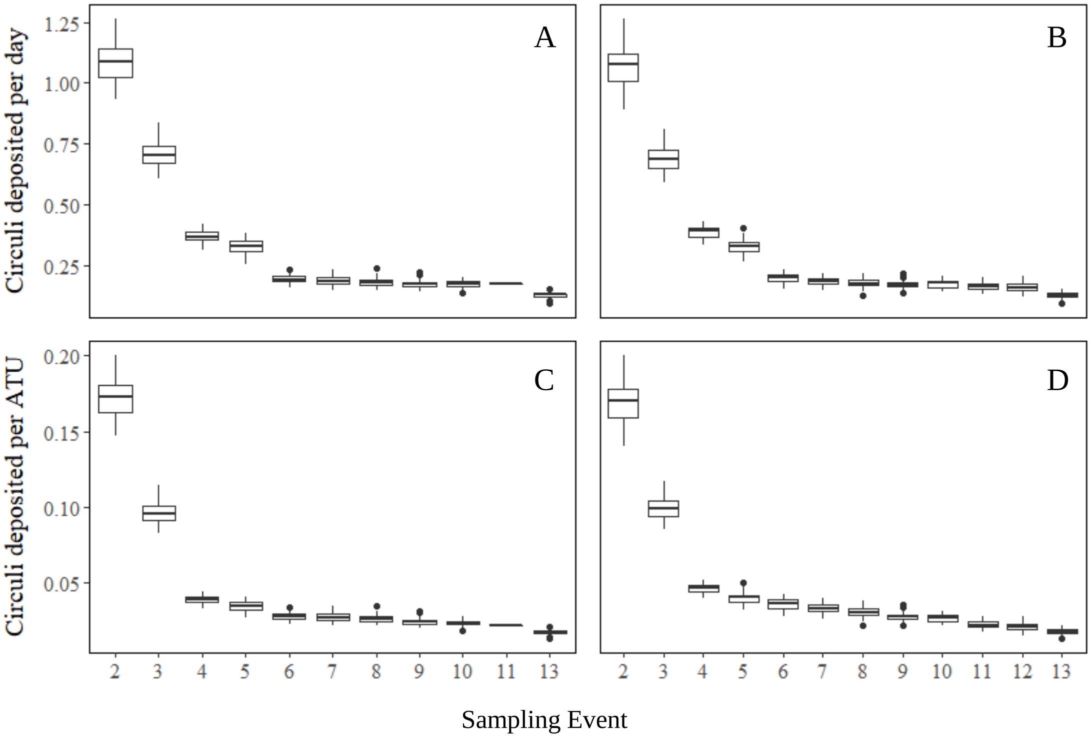


Figure 5.5. Daily circulus deposition rate at Site 1 (A) and Site 2 (B), and the relationship between circulus deposition rate and accumulated thermal units (ATU) at Site 1 (C) and Site 2 (D) over the duration of the study.

When scale circulus deposition rate was measured on a daily interval, each circulus required an average of 2.7 days to form at Site 1, with a range of 0.79-10.4 days. At Site 2, a single circulus formed on average every 3 days, with a range of 0.79-12 days. When considered relative to water temperature, a single circulus was deposited when a fish had experienced 5-75.5

ATU, with a mean of 19 ATU per circulus at Site 1. The temperature experience required for a single circulus to form on fish at Site 2 was similar, with an average of 20.5 ATU and a range of 5.3-82 ATU. The highest circulus deposition rates relative to both time and ATUs occurred between entrance to the marine environment and Event 2, the first marine sampling Event, while the lowest rates occurred among the final Events of the study

DISCUSSION

Our study demonstrated that scale growth rates and circulus deposition rates in marine-stage Atlantic salmon are not constant through time. Daily growth and circulus deposition rates decreased over the course of our study, with the highest rates occurring during the first year of marine habitation and the lowest rates occurring when the study was terminated at the end of two and a half growing seasons. The same trends were seen when scale growth rate and circulus deposition rate were plotted relative to thermal experience.

Decreasing somatic growth as fish approach sexual maturity could explain the trends seen in scale growth and circulus deposition rate. At the end of the original study, the salmon were 3+ years old and had spent two winters (1998-1999, 1999-2000) in the sea. This is a typical age for US Atlantic salmon to make their first spawning migration (Gardner 1976). However, the maturity status of the fish used in this study was not recorded, so it is not known how sexual maturity may have affected scale growth and circulus deposition rates for these particular fish.

Studies of Pacific salmonids have also found that marine growth, as evidenced by scale circulus spacing and circulus deposition rate, decreases through time, and may be at least partially attributable to a reduction in somatic growth as the fish ages. Barber and Walker (1988) found that scale circulus spacing decreased between the first and second year at sea in adult

Sockeye salmon *O. nerka*. Fisher and Pearcy (2005) compared circulus deposition rates in juvenile and maturing Coho salmon *O. kisutch*. On average, juvenile coho salmon deposited a new scale circulus every 5.3 days, whereas maturing fish deposited a new circulus every 7.6 days. Thomas et al. (2019) reported a rate that ranged between 16.2 days per circulus for Atlantic salmon held at low water temperatures (6° C) to 5.1 days per circulus for fish held at higher temperatures (15° C). They found that circulus deposition rate was also affected by the consistency of food availability. These circulus deposition rates are similar to those seen in our study fish when the first five sampling Events, which cover the first year at sea, are compared with later sampling Events.

Barber and Walker (1988) also found strong correlations between increasing photoperiod and increasing fish growth. They attributed some of the patterns in circuli spacing that they saw to changes in food availability (Barber and Walker 1988). Neither the photoperiod nor the food availability experienced by our fish represented natural conditions. Because Atlantic salmon in the wild are transient and spend a majority of their time at high latitudes, they experience a greater seasonal fluctuation in photoperiod than salmon that are confined to the Maine coast. In addition, our fish were fed to satiation, a condition which undoubtedly does not occur in the wild. However, net pen studies such as this one can be useful for conducting long term sampling of fish held under semi-natural conditions.

Fish in the current study were only sampled during a single sampling Event; any fish that were recaptured at subsequent Events were put back in the net pen and a new fish obtained in their place. Future studies aimed at gaining a detailed understanding of Atlantic salmon post-smolt scale growth rates and circulus deposition rates would benefit from frequent, repeated sampling of known individuals. Sampling events outside of the growing season would also yield beneficial information about seasonal changes in growth and circulus deposition rates. Such a sampling scheme would retain important information about individual variability in growth and circulus deposition rates and also allow for a more detailed understanding of scale formation and growth relative to different aspects of the fish's life history.

The present study expands upon previous work on Atlantic salmon marine-stage growth (i.e., Thomas et al. 2019) by tracking growth and circulus deposition rates in the marine environment through two sea-winters, under a semi-natural temperature and photoperiod regime. Under these conditions, which more closely mimic those experienced by fish in the wild than previous laboratory studies, both scale growth and circulus deposition rates were non-constant and decreased through time. Acknowledgement of these fluctuating growth and circulus deposition rates in further studies of Atlantic salmon could help researchers obtain more detailed information about growth patterns in this species.

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APPENDIX A: SCALE VS. OTOLITH AGE

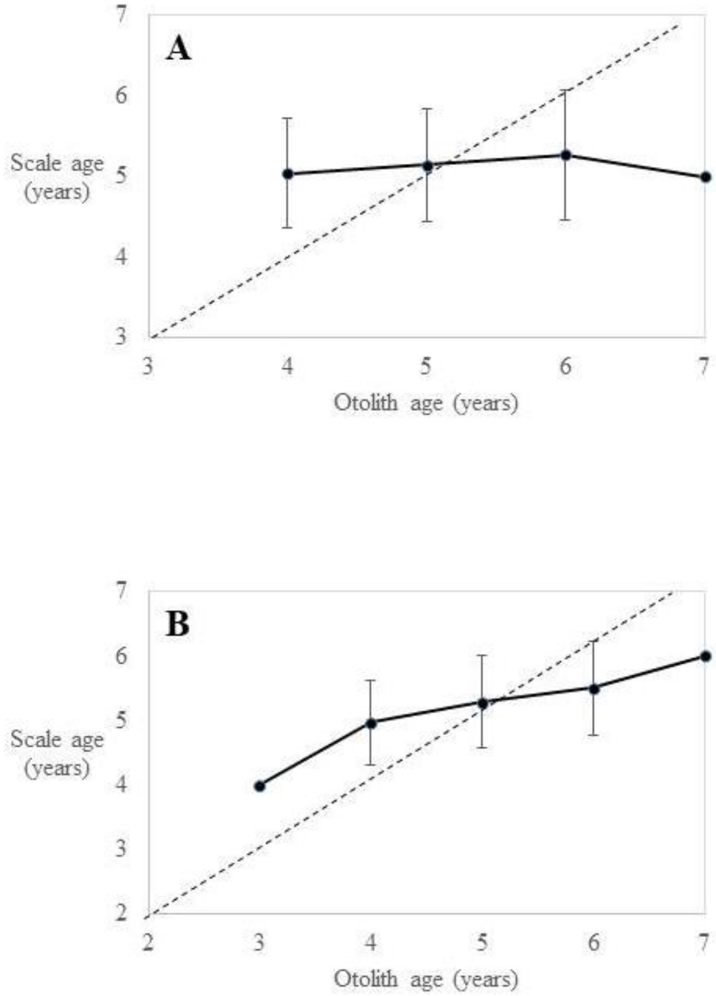


Figure A.1. Comparison of age estimates for American shad when two readers (A and B) aged both scales and otoliths from shad collected from the Milford Dam. Both readers showed a consistent pattern of overestimating the age of younger fish and underestimating the age of older fish.

APPENDIX B: DATASET FOR DAM PASSAGE MODELS

Table B.1. Full dataset used for developing dam passage motivation models. **Pass** refers to dam passage (0=did not pass Milford Dam, 1=passed Milford Dam). **Repeat** refers to iteroparity (0=no previous spawns, 1=at least one previous spawn). **Oto_Age** is the otolith age in years and **TL** is the total length in millimeters. **Scale_Age** (scale age in years) and **Spawns** (the number of previous spawns) were not used in the analysis.

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2014	1	1	7	6	1	F	585
2014	1	1	5	4	1	F	560
2014	1	0	4	5	0	F	481
2014	1	1	7	7	1	F	546
2014	1	0	4	5	0	F	530
2014	1	0	4	6	0	F	501
2014	1	0	5	5	0	F	517
2014	1	0	4	4	0	F	475
2014	1	0	5	5	0	F	475
2014	1	0	4	8	0	F	530
2015	1	0	3	3	0	F	531
2015	1	0	4	5	0	F	526
2015	1	1	5	5	1	F	502
2015	1	0	4	4	0	F	522
2015	1	0	6	5	0	F	553
2015	1	0	5	5	0	F	536
2015	1	0	4	5	0	F	501
2015	1	0	6	4	0	F	529
2015	1	0	4	4	0	F	540
2015	1	0	6	6	0	F	504
2015	1	0	5	5	0	F	490
2015	1	0	4	3	0	F	482
2015	1	1	5	3	1	F	507
2015	1	0	4	5	0	F	476
2015	1	1	6	8	2	F	563
2015	1	0	4	4	0	F	489
2015	1	0	4	5	0	F	515

Table B.1 (cont’d).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2015	1	0	5	3	0	F	517
2015	1	0	4	5	0	F	454
2015	1	0	4	4	0	F	455
2015	1	0	3	6	0	F	467
2015	1	1	7	7	1	F	524
2015	1	0	4	4	0	F	497
2015	1	1	5	3	1	F	469
2015	1	0	4	5	0	F	482
2015	1	1	4	4	1	F	416
2015	1	1	5	4	1	F	487
2015	1	1	4	4	1	M	438
2015	1	0	4	4	0	M	439
2015	1	1	5	5	1	M	446
2015	1	0	4	4	0	M	481
2015	1	0	3	4	0	M	472
2015	1	1	5	5	1	M	453
2015	1	0	4	3	0	M	402
2015	1	0	3	5	0	M	461
2015	1	1	6	7	1	M	509
2015	1	1	5	4	1	M	463
2015	1	1	4	3	1	M	436
2015	1	0	3	4	0	M	439
2015	1	0	4	5	0	M	455
2015	1	0	4	4	0	M	466
2015	1	0	3	3	0	M	437
2015	1	1	4	7	1	M	410
2015	1	0	4	5	0	M	474
2015	1	0	3	4	0	M	421
2015	1	0	5	5	0	M	444
2015	1	0	3	4	0	M	401
2015	1	0	5	5	0	M	451
2015	1	0	4	4	0	M	441
2015	1	0	3	3	0	M	435
2015	1	0	4	6	0	M	461
2015	1	0	3	3	0	M	421
2015	1	0	4	4	0	M	463
2015	1	0	4	4	0	M	457
2015	1	0	4	5	0	M	490

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2015	1	0	4	5	0	M	467
2015	1	0	5	5	0	M	452
2015	1	0	4	5	0	M	451
2015	1	0	4	4	0	M	421
2015	1	0	4	4	0	M	436
2015	1	0	4	5	0	M	423
2015	1	0	3	4	0	M	426
2015	1	0	4	5	0	M	441
2015	1	0	3	4	0	M	417
2015	1	1	4	4	1	M	429
2015	1	0	4	5	0	M	470
2015	1	0	3	3	0	M	392
2015	1	0	4		0	M	421
2015	1	0	4	4	0	M	419
2015	1	0	4	5	0	M	461
2015	1	1	4	5	1	M	466
2015	1	0	3	3	0	M	440
2016	1	1	5	6	2	F	510
2016	1	1	5	5	1	F	485
2016	1	0	4	5	0	F	480
2016	1	0	4	3	0	F	458
2016	1	0	4	5	0	F	465
2016	1	0	4	6	0	F	494
2016	1	0	4	5	0	F	500
2016	1	1	4	4	1	F	487
2016	1	1	5	5	1	F	514
2016	1	0	5	4	0	F	496
2016	1	0	4	5	0	F	476
2016	1	1	5	3	1	F	485
2016	1	0	5	5	0	F	486
2016	1	0	5	5	0	F	495
2016	1	0	5	5	0	F	501
2016	1	1	5	5	1	F	511
2016	1	0	6	7	0	F	487
2016	1	0	4	3	0	F	495
2016	1	0	4	4	0	F	515
2016	1	0	5	5	0	F	430
2016	1	1	5	6	2	F	515

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2016	1	1	5	5	1	F	524
2016	1	0	4	6	0	F	515
2016	1	0	4	4	0	F	485
2016	1	0	4	4	0	F	502
2016	1	0	4	4	0	F	495
2016	1	0	3	5	0	F	475
2016	1	0	5	5	0	F	525
2016	1	1	5	5	1	F	509
2016	1	1	5	6	1	F	468
2016	1	0	5	5	0	F	499
2016	1	1	5	5	1	F	483
2016	1	1	5	5	1	F	507
2016	1	0	4	4	0	F	509
2016	1	1	5	3	1	F	505
2016	1	0	5	6	0	F	489
2016	1	0	5	5	0	F	500
2016	1	1	5	6	1	F	530
2016	1	1	5	4	1	F	520
2016	1	0	4	5	0	F	472
2016	1	1	4	4	1	F	484
2016	1	1	5	5	1	F	460
2016	1	0	5	6	0	F	500
2016	1	1	3	6	2	F	500
2016	1	1	5	6	1	F	513
2016	1	1	4	4	1	F	461
2016	1	1	5	3	1	F	526
2016	1	0	5	5	0	F	462
2016	1	1	5	6	1	F	517
2016	1	1	4	5	1	F	464
2016	1	1	5	6	1	F	500
2016	1	0	4	5	0	F	467
2016	1	1	5	6	1	F	525
2016	1	0	5	7	0	F	507
2016	1	0	4	5	0	F	485
2016	1	1	6	9	1	F	533
2016	1	0	4	6	0	F	472
2016	1	1	5	5	1	F	520
2016	1	0	4		0	F	515

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2016	1	1	5	5	1	F	522
2016	1	0	5	6	0	F	497
2016	1	1	5	4	1	F	499
2016	1	0	5	5	0	F	433
2016	1	0	4	4	0	F	489
2016	1	1	5	6	1	F	522
2016	1	0	5	5	0	F	495
2016	1	1	5	6	1	F	475
2016	1	0	5	5	0	F	477
2016	1	0	4	4	0	F	475
2016	1	1	5	6	1	F	473
2016	1	1	5	5	1	F	494
2016	1	0	4	4	0	F	486
2016	1	0	4	4	0	F	483
2016	1	0	5	6	0	F	493
2016	1	0	4	5	0	F	461
2016	1	1	5	5	1	F	477
2016	1	0	5	5	0	F	483
2016	1	0	5	6	0	F	502
2016	1	0	3	5	0	F	445
2016	1	0	5	4	0	F	495
2016	1	1	4	4	1	F	510
2016	1	1	6	5	1	F	512
2016	1	0	3	5	0	F	480
2016	1	0	5	6	0	F	496
2016	1	0	4	5	0	F	475
2016	1	1	5	6	1	F	505
2016	1	0	5	4	0	F	477
2016	1	0	4	6	0	F	489
2016	1	1	4	4	1	F	489
2016	1	1	5	4	1	F	497
2016	1	0	6	6	0	F	501
2016	1	1	5	7	2	F	595
2016	1	0	5	6	0	F	465
2016	1	1	5	6	1	F	520
2016	1	0	4	6	0	F	480
2016	1	1	5	5	1	F	541
2016	1	0	5	4	0	F	461

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2016	1	1	4	4	1	M	426
2016	1	0	4	4	0	M	485
2016	1	0	4	6	0	M	456
2016	1	0	4	4	0	M	514
2016	1	0	5	4	0	M	471
2016	1	1	4	5	1	M	451
2016	1	1	4	5	1	M	451
2016	1	0	4	6	0	M	496
2016	1	0	3	5	0	M	398
2016	1	0	4	5	0	M	481
2016	1	0	4	5	0	M	445
2016	1	1	4	5	1	M	445
2016	1	0	4	4	0	M	446
2016	1	0	8	5	0	M	425
2016	1	0	3	3	0	M	446
2016	1	0	4	4	0	M	426
2016	1	1	6	4	1	M	382
2016	1	1	4	6	1	M	469
2016	1	0	4	5	0	M	462
2016	1	0	3	4	0	M	449
2016	1	1	5	3	1	M	460
2016	1	0	3	5	0	M	449
2016	1	0	4	5	0	M	450
2016	1	0	3	3	0	M	410
2016	1	1	4	5	1	M	455
2016	1	0	4	4	0	M	419
2016	1	0	4	4	0	M	429
2016	1	1	5	6	1	M	480
2016	1	1	4	5	1	M	465
2016	1	1	6	6	1	M	464
2016	1	0	5	4	0	M	453
2016	1	0	4	4	0	M	422
2016	1	1	5	5	2	M	441
2016	1	0	5	5	0	M	455
2016	1	1	4	4	1	M	477
2016	1	0	5	4	0	M	434
2016	1	1	5	4	1	M	446
2016	1	0	5	4	0	M	471

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2016	1	1	5	5	2	M	441
2016	1	0	4	4	0	M	501
2016	1	0	4	4	0	M	445
2016	1	0	5	5	0	M	430
2016	1	0	5	5	0	M	484
2016	1	0	3	4	0	M	501
2016	1	1	4	6	1	M	467
2016	1	0	3	3	0	M	420
2016	1	0	5	4	0	M	456
2016	1	0	4	5	0	M	446
2016	1	0	4	6	0	M	440
2016	1	0	4	5	0	M	468
2016	1	1	4	5	1	M	463
2016	1	0	4	4	0	M	451
2016	1	0	4	5	0	M	459
2016	1	0	3	4	0	M	404
2016	1	0	4	5	0	M	471
2016	1	0	3	5	0	M	444
2016	1	0	4	6	0	M	459
2016	1	1	4	7	1	M	486
2016	1	0	5	5	0	M	472
2016	1	1	4	5	1	M	460
2016	1	0	5	5	0	M	411
2016	1	0	5	5	0	M	420
2016	1	0	6	6	0	M	471
2016	1	0	6	6	0	M	431
2016	1	1	5	6	1	M	468
2016	1	0	4	4	0	M	442
2016	1	1	4	6	1	M	458
2016	1	1	5	6	1	M	462
2016	1	1	5		1	M	491
2016	1	1	5	6	1	M	449
2016	1	1	4	5	1	M	460
2016	1	0	4	4	0	M	464
2016	1	0	4	3	0	M	471
2016	1	0	5	3	0	M	415
2016	1	1	4	6	1	M	426
2016	1	0	4	6	0	M	461

Table B.1 (cont’d).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2016	1	1	5	6	2	M	467
2016	1	1	4	5	1	M	447
2016	1	0	4	6	0	M	420
2016	1	1	5	5	1	M	449
2016	1	1	4	3	1	M	436
2016	1	0	4	4	0	M	443
2016	1	1	5	3	1	M	463
2016	1	1	5	6	2	M	460
2016	1	0	4	4	0	M	430
2016	1	0	5	5	0	M	442
2016	1	1	4	5	1	M	479
2016	1	0	5	4	0	M	475
2016	1	0	4	5	0	M	471
2016	1	0	4	4	0	M	433
2016	1	0	5	5	0	M	462
2016	1	0	5	5	0	M	423
2016	1	1	4	5	1	M	481
2016	1	0	3	3	0	M	415
2016	1	1	4	5	1	M	483
2016	1	0	3	5	0	M	462
2016	1	1	4	5	1	M	485
2016	1	1	5	4	1	M	445
2016	1	0	4	5	0	M	468
2016	1	0	4	4	0	M	433
2016	1	0	4	4	0	M	443
2016	1	0	4	4	0	M	445
2016	1	1	4	4	1	M	452
2016	1	0	4	5	0	M	454
2016	1	1	5	3	2	M	487
2016	1	1	5	5	1	M	472
2016	1	0	5	5	0	M	456
2016	1	1	5	5	1	M	486
2016	1	0	4	3	0	M	436
2016	1	0	4	3	0	M	465
2016	1	1	6	7	2	M	472
2016	1	0	4	6	0	M	444
2016	1	0	5	5	0	M	471
2016	1	0	4	4	0	M	460

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2016	1	1	4	4	1	M	434
2016	1	0	4	7	0	M	486
2016	1	0	5	4	0	M	449
2016	1	0	4	6	0	M	455
2016	1	0	5	6	0	M	456
2016	1	0	4	5	0	M	462
2016	1	0	5	5	0	M	461
2016	1	0	4	4	0	M	427
2016	1	0	4	5	0	M	454
2016	1	0	5	5	0	M	460
2016	1	1	5	5	1	M	469
2016	1	0	4	6	0	M	467
2016	1	0	4	4	0	M	426
2016	1	0	5	6	0	M	495
2016	1	1	4	6	1	M	476
2016	1	0	5	5	0	M	450
2016	1	0	3	4	0	M	432
2016	1	0	4	5	0	M	450
2016	1	0	5	6	0	M	450
2016	1	0	3	3	0	M	433
2016	1	0	3	3	0	M	440
2016	1	0	4	5	0	M	469
2016	1	0	4	5	0	M	434
2016	1	0	3	4	0	M	456
2016	1	1	4	4	1	M	472
2016	1	0	3	4	0	M	445
2016	1	0	5	6	0	M	444
2016	1	1	4	4	1	M	453
2016	1	0	3	4	0	M	410
2016	1	1	5	5	1	M	511
2016	1	0	4	3	0	M	442
2016	1	0	3	3	0	M	420
2016	1	1	6	4	2	M	505
2016	1	0	3	3	0	M	361
2016	1	0	4	4	0	M	445
2016	1	1	5	5	2	M	431
2016	1	0	5	5	0	M	436
2016	1	0	5	4	0	M	470

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2016	1	0	4	3	0	M	445
2016	1	0	4	6	0	M	445
2016	1	0	3	4	0	M	421
2016	1	0	5	6	0	M	483
2016	1	1	4	5	1	M	443
2016	1	0	4	5	0	M	418
2016	1	0	4	5	0	M	468
2016	1	0	4	6	0	M	481
2016	1	0	3	5	0	M	410
2017	1	1	5	6	1	F	535
2017	1	1	6	7	1	F	519
2017	1	1	5	7	1	F	520
2017	1	0	4	5	0	F	498
2017	1	0	6	6	0	F	494
2017	1	1	5	6	1	F	520
2017	1	1	5	4	2	F	510
2017	1	0	4	5	0	F	500
2017	1	0	3	4	0	F	508
2017	1	1	5	7	1	F	547
2017	1	1	5	6	2	F	502
2017	1	1	5	5	1	F	497
2017	1	0	4	6	0	F	485
2017	1	0	6	6	0	F	516
2017	1	1	5	7	1	F	516
2017	1	0	5	6	0	F	495
2017	1	0	5	5	0	F	511
2017	1	1	5	5	2	F	542
2017	1	0	4	6	0	F	507
2017	1	0	4	5	0	F	479
2017	1	1	4		1	F	517
2017	1	0	4		0	F	475
2017	1	1	4		1	F	486
2017	1	0	4		0	F	540
2017	1	1	5		1	F	505
2017	1	0	5		0	F	491
2017	1	1	3		1	F	510
2017	1	0	5		0	F	515
2017	1	1	4		1	F	501

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2017	1	1	6	7	1	M	449
2017	1	0	4	5	0	M	479
2017	1	1	5	6	1	M	468
2017	1	0	3	5	0	M	460
2017	1	1	5	4	1	M	455
2017	1	1	6	5	1	M	458
2017	1	0	5	5	0	M	448
2017	1	1	5	7	1	M	489
2017	1	1	6	6	1	M	482
2017	1	1	5	4	1	M	479
2017	1	0	3	5	0	M	400
2017	1	1	5	6	1	M	465
2017	1	1	5	5	2	M	485
2017	1	1	5	6	1	M	465
2017	1	1	6	6	1	M	476
2017	1	1	5	6	1	M	478
2017	1	1	5	7	1	M	540
2017	1	0	5	4	0	M	481
2017	1	1	4	6	1	M	488
2017	1	0	3	6	0	M	497
2017	1	1	6	7	1	M	540
2017	1	0	6	6	0	M	496
2017	1	0	3	5	0	M	391
2017	1	0	4	4	0	M	445
2017	1	1	5	6	1	M	466
2017	1	0	5	5	0	M	467
2017	1	0	4	6	0	M	467
2017	1	0	4	5	0	M	405
2017	1	0	4	5	0	M	454
2017	1	0	4	4	0	M	430
2017	1	1	5	5	1	M	466
2017	1	0	3	3	0	M	406
2017	1	0	4		0	M	415
2017	1	0	4		0	M	522
2017	1	1	4		1	M	480
2017	1	0	3		0	M	491
2017	1	1	3		1	M	442
2017	1	1	4		1	M	457

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2017	1	0	3		0	M	456
2018	0	1	6		1	F	555
2018	0	1	4		1	F	540
2018	0	1	4		1	F	520
2018	0	1	6		2	F	560
2018	0	1	5		2	F	476
2018	0	1	5		1	F	475
2018	0	1	5		2	F	525
2018	0	1	4		1	F	445
2018	0	1	5		1	F	525
2018	0	1	5		1	F	460
2018	0	0	5		0	F	494
2018	0	1	4		1	F	479
2018	0	0	4		0	F	415
2018	0	1	4		1	F	435
2018	0	1	5		1	F	474
2018	0	1	5		1	F	517
2018	0	1	4		1	F	508
2018	0	0	4		0	F	410
2018	0	1	5		2	F	469
2018	0	0	4		0	F	437
2018	0	0	4		0	F	439
2018	0	0	4		0	F	475
2018	0	1	5		1	F	471
2018	0	1	5		2	F	484
2018	0	1	5		1	F	479
2018	0	1	5		1	F	479
2018	0	1	5		1	F	499
2018	0	1	6		1	F	505
2018	0	1	5		1	F	520
2018	0	1	5		2	F	522
2018	0	0	5		0	F	521
2018	0	1	4		1	F	506
2018	0	0	4		0	F	515
2018	0	1	5		1	F	545
2018	0	0	4		0	F	420
2018	0	1	4		1	F	425
2018	0	1	4		1	F	458

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2018	0	1	4		1	F	462
2018	0	1	4		1	F	470
2018	0	1	4		1	F	475
2018	0	1	4		1	F	490
2018	0	1	5		1	F	485
2018	0	1	4		1	F	500
2018	0	1	5		1	F	500
2018	0	0	4		0	F	418
2018	0	1	5		1	F	451
2018	0	1	5		1	F	495
2018	0	0	4		0	M	450
2018	0	1	5		1	M	495
2018	0	1	4		1	M	480
2018	0	0	5		0	M	455
2018	0	1	4		1	M	431
2018	0	0	3		0	M	412
2018	0	1	4		1	M	418
2018	0	0	4		0	M	402
2018	0	0	4		0	M	400
2018	0	0	4		0	M	412
2018	0	0	4		0	M	458
2018	0	0	4		0	M	462
2018	0	1	5		1	M	463
2018	0	1	5		1	M	490
2018	0	0	3		0	M	471
2018	0	0	4		0	M	385
2018	0	0	5		0	M	410
2018	0	1	4		1	M	395
2018	0	0	4		0	M	421
2018	0	0	4		0	M	464
2018	0	0	4		0	M	455
2018	0	1	4		1	M	455
2018	0	0	4		0	M	455
2018	0	1	5		1	M	490
2018	0	1	5		1	M	504
2018	0	0	3		0	M	437
2018	0	1	4		1	M	483
2018	0	0	4		0	M	408

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2018	0	1	4		1	M	440
2018	0	1	4		1	M	450
2018	0	1	4		1	M	482
2018	0	1	5		1	M	509
2018	0	0	4		0	M	399
2018	0	0	3		0	M	405
2018	0	0	5		0	M	405
2018	0	1	5		1	M	465
2018	0	0	4		0	M	481
2018	0	1	4		1	M	482
2018	0	1	4		1	M	493
2018	0	1	5		1	M	510
2018	0	1	5		1	M	504
2018	0	0	3		0	M	431
2018	0	0	4		0	M	441
2018	0	0	4		0	M	455
2018	0	1	5		1	M	500
2018	1	0	4		0	F	441
2018	1	0	4		0	F	486
2018	1	0	4		0	F	468
2018	1	1	4		1	F	481
2018	1	1	5		1	F	500
2018	1	0	6		0	F	500
2018	1	0	4		0	F	506
2018	1	0	4		0	F	495
2018	1	0	4		0	F	520
2018	1	0	3		0	F	446
2018	1	0	4		0	F	464
2018	1	0	4		0	F	456
2018	1	0	4		0	F	466
2018	1	1	5		1	F	495
2018	1	0	4		0	F	498
2018	1	0	6		0	F	504
2018	1	0	4		0	F	502
2018	1	0	4		0	F	510
2018	1	1	4		1	F	515
2018	1	0	4		0	F	515
2018	1	0	4		0	F	515

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2018	1	1	5		2	F	522
2018	1	1	5		1	F	539
2018	1	1	4		1	F	550
2018	1	1	5		1	F	549
2018	1	0	3		0	F	415
2018	1	0	4		0	F	440
2018	1	1	5		1	F	500
2018	1	1	5		1	F	510
2018	1	1	5		1	F	525
2018	1	1	6		1	F	525
2018	1	0	4		0	F	520
2018	1	1	4		1	F	545
2018	1	1	4		1	F	515
2018	1	0	3		0	F	495
2018	1	0	4		0	F	435
2018	1	0	4		0	F	485
2018	1	0	3		0	F	495
2018	1	0	4		0	F	469
2018	1	0	5		0	F	480
2018	1	0	5		0	F	495
2018	1	0	4		0	F	515
2018	1	0	4		0	F	430
2018	1	0	4		0	F	505
2018	1	0	4		0	F	525
2018	1	1	5		1	F	475
2018	1	0	4		0	F	505
2018	1	0	3		0	F	390
2018	1	1	4		1	F	460
2018	1	0	5		0	F	480
2018	1	0	4		0	F	440
2018	1	0	3		0	F	447
2018	1	1	4		1	F	470
2018	1	1	4		1	F	485
2018	1	0	5		0	F	450
2018	1	0	5		0	F	495
2018	1	1	5		1	F	505
2018	1	1	4		2	F	530
2018	1	0	4		0	F	535

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2018	1	0	4		0	F	465
2018	1	1	5		1	F	470
2018	1	1	4		1	F	470
2018	1	1	5		1	F	495
2018	1	0	5		0	F	485
2018	1	0	4		0	F	495
2018	1	1	4		1	F	470
2018	1	1	5		1	F	470
2018	1	0	4		0	F	470
2018	1	1	6		1	F	545
2018	1	0	4		0	F	465
2018	1	0	4		0	F	485
2018	1	0	5		0	F	490
2018	1	0	5		0	F	465
2018	1	1	5		2	F	480
2018	1	0	4		0	F	485
2018	1	1	4		1	F	500
2018	1	0	4		0	F	500
2018	1	1	5		1	F	515
2018	1	0	5		0	F	515
2018	1	0	4		0	M	430
2018	1	0	4		0	M	449
2018	1	1	4		1	M	499
2018	1	0	4		0	M	455
2018	1	1	4		1	M	442
2018	1	0	4		0	M	445
2018	1	0	5		0	M	455
2018	1	0	5		0	M	456
2018	1	1	4		1	M	482
2018	1	1	4		1	M	496
2018	1	1	5		2	M	492
2018	1	1	4		1	M	525
2018	1	1	4		1	M	530
2018	1	1	4		1	M	431
2018	1	0	4		0	M	443
2018	1	0	4		0	M	449
2018	1	0	4		0	M	444
2018	1	1	5		1	M	454

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2018	1	0	3		0	M	450
2018	1	0	4		0	M	449
2018	1	1	4		1	M	451
2018	1	1	4		1	M	470
2018	1	0	4		0	M	460
2018	1	1	5		1	M	471
2018	1	0	5		0	M	465
2018	1	0	4		0	M	474
2018	1	1	4		1	M	490
2018	1	0	4		0	M	486
2018	1	0	5		0	M	460
2018	1	1	4		1	M	501
2018	1	1	4		1	M	507
2018	1	1	5		1	M	511
2018	1	0	3		0	M	385
2018	1	0	3		0	M	380
2018	1	0	4		0	M	415
2018	1	0	4		0	M	420
2018	1	0	4		0	M	430
2018	1	0	4		0	M	440
2018	1	0	5		0	M	430
2018	1	0	3		0	M	440
2018	1	0	4		0	M	445
2018	1	0	5		0	M	455
2018	1	1	4		1	M	455
2018	1	1	4		1	M	455
2018	1	0	4		0	M	475
2018	1	1	4		1	M	485
2018	1	1	4		1	M	475
2018	1	0	3		0	M	425
2018	1	0	3		0	M	430
2018	1	0	3		0	M	440
2018	1	0	4		0	M	465
2018	1	0	4		0	M	425
2018	1	0	4		0	M	395
2018	1	1	5		1	M	470
2018	1	1	5		1	M	495
2018	1	1	6		1	M	510

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2018	1	0	3		0	M	405
2018	1	1	5		1	M	430
2018	1	0	4		0	M	430
2018	1	1	5		1	M	465
2018	1	1	5		1	M	470
2018	1	1	4		1	M	465
2018	1	0	5		0	M	425
2018	1	0	5		0	M	455
2018	1	0	3		0	M	405
2018	1	1	4		1	M	435
2018	1	0	4		0	M	460
2018	1	0	4		0	M	405
2018	1	0	4		0	M	455
2018	1	0	4		0	M	405
2018	1	0	4		0	M	460
2018	1	1	5		1	M	490
2018	1	0	3		0	M	425
2018	1	0	3		0	M	440
2018	1	0	5		0	M	485
2018	1	1	4		1	M	435
2018	1	0	3		0	M	446
2018	1	0	2		0	M	360
2018	1	0	3		0	M	425
2018	1	0	3		0	M	460
2018	1	0	4		0	M	450
2018	1	0	4		0	M	410
2018	1	0	3		0	M	430
2018	1	1	4		1	M	455
2018	1	1	5		2	M	445
2018	1	1	4		1	M	480
2018	1	0	3		0	M	410
2018	1	0	4		0	M	405
2018	1	1	4		1	M	490
2018	1	0	4		0	M	431
2019	0	1	5		1	M	473
2019	0	0	6		0	F	435
2019	0	1	6		2	F	460
2019	0	1	6		1	F	474

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2019	0	1	5		1	F	482
2019	0	1	5		1	M	440
2019	1	1	5		1	F	445
2019	1	0	5		0	M	375
2019	0	0	6		0	M	394
2019	0	1	7		1	F	464
2019	0	1	6		1	M	510
2019	0	1	5		1	M	465
2019	0	1	5		1	M	475
2019	0	1	6		1	F	490
2019	0	0	5		0	F	422
2019	0	1	6		1	F	517
2019	0	0	5		0	F	422
2019	0	0	5		0	F	477
2019	0	0	3		0	M	431
2019	0	0	5		0	M	418
2019	0	0	5		0	M	392
2019	0	1	6		1	M	443
2019	0	1	5		1	F	457
2019	0	1	7		2	F	502
2019	0	0	4		0	M	442
2019	0	1	6		1	F	505
2019	0	0	5		0	F	420
2019	0	0	6		0	F	501
2019	0	0	4		0	M	440
2019	0	0	5		0	F	505
2019	0	1	5		1	M	442
2019	0	1	6		2	M	474
2019	0	1	5		1	M	446
2019	0	1	6		1	M	526
2019	0	1	5		1	F	458
2019	0	1	5		1	M	461
2019	0	1	6		2	M	460
2019	0	1	6		1	F	511
2019	0	1	6		2	M	456
2019	0	1	5		1	M	411
2019	0	0	5		0	F	425
2019	0	1	5		2	F	492

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2019	0	1	6		2	M	532
2019	0	0	5		0	M	435
2019	0	1	6		1	F	519
2019	0	1	6		1	F	494
2019	0	1	5		1	M	455
2019	0	0	6		0	M	412
2019	0	1	5		1	F	435
2019	0	1	5		1	F	432
2019	0	0	5		0	M	422
2019	0	0	6		0	M	423
2019	0	1	6		1	F	495
2019	0	1	5		1	M	458
2019	0	1	6		1	M	442
2019	0	1	5		1	F	445
2019	1	0	4		0	M	440
2019	1	0	6		0	F	449
2019	1	1	5		2	M	461
2019	1	1	8		3	F	494
2019	1	0	7		0	F	501
2019	1	1	8		2	F	481
2019	1	1	6		2	F	502
2019	1	1	6		1	M	454
2019	1	0	5		0	M	425
2019	1	0	5		0	F	424
2019	1	0	5		0	F	440
2019	1	0	5		0	M	452
2019	1	0	5		0	M	434
2019	0	1	6		2	M	473
2019	1	0	4		0	M	430
2019	1	0	6		0	M	420
2019	0	1	5		1	F	446
2019	0	1	6		1	M	489
2019	0	1	6		1	M	457
2019	0	1	6		1	M	452
2019	0	1	5		1	M	470
2019	0	1	5		1	M	445
2019	0	1	6		2	M	472
2019	0	1	7		1	M	487

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2019	0	0	6		0	M	446
2019	0	0	7		0	F	415
2019	0	0	6		0	M	398
2019	0	0	6		0	M	418
2019	0	0	5		0	F	452
2019	1	0	5		0	M	457
2019	1	1	5		1	M	455
2019	1	0	6		0	M	484
2019	1	1	6		1	F	434
2019	1	1	7		1	M	492
2019	1	0	5		0	M	435
2019	1	1	6		1	M	469
2019	1	0	6		0	M	415
2019	1	0	7		0	F	523
2019	1	1	4		1	M	510
2019	1	0	6		0	M	532
2019	1	1	6		2	M	490
2019	1	0	6		0	M	479
2020	0	0	4		0	M	420
2020	0	0	5		0	F	450
2020	0	1	5		1	F	450
2020	0	0	4		0	F	420
2020	0	0	5		0	M	500
2020	0	0	4		0	M	420
2020	0	1	5		1	M	420
2020	0	1	6		3	M	450
2020	0	0	6		0	F	490
2020	0	1	5		1	F	510
2020	0	0	4		0	M	410
2020	0	0	5		0	F	500
2020	0	0	4		0	M	400
2020	0	0	5		0	F	420
2020	0	1	5		1	M	430
2020	0	0	4		0	F	455
2020	0	0	4		0	F	420
2020	0	1	5		1	M	450
2020	0	1	5		1	M	450
2020	0	0	5		0	M	420

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2020	0	0	5		0	M	430
2020	0	1	5		1	M	450
2020	0	0	5		0	M	430
2020	0	1	5		1	F	460
2020	0	0	5		0	F	410
2020	0	0	4		0	M	440
2020	0	1	6		2	F	540
2020	0	0	4		0	F	440
2020	0	1	5		1	M	410
2020	0	0	5		0	M	470
2020	0	0	4		0	M	450
2020	0	1	4		1	F	435
2020	0	1	5		1	M	520
2020	0	0	4		0	M	425
2020	0	1	6		1	F	470
2020	0	0	5		0	M	470
2020	0	1	5		1	M	480
2020	0	0	4		0	M	420
2020	0	0	5		0	F	450
2020	0	0	5		0	F	400
2020	0	0	4		0	M	430
2020	0	1	5		1	F	520
2020	0	1	5		1	F	460
2020	0	0	4		0	F	445
2020	0	0	4		0	F	450
2020	0	0	6		0	M	510
2020	0	1	6		1	F	500
2020	0	0	4		0	F	470
2020	0	1	6		2	M	490
2020	0	0	5		0	F	430
2020	0	0	4		0	M	440
2020	0	1	5		1	F	470
2020	0	1	5		1	F	490
2020	0	0	6		0	M	520
2020	0	0	5		0	F	440
2020	0	0	4		0	M	450
2020	0	1	5		1	M	550
2020	0	1	6		1	F	550

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2020	0	0	5		0	F	460
2020	0	1	6		2	M	490
2020	0	1	4		1	F	480
2020	0	1	5		1	M	500
2020	0	1	5		1	M	495
2020	0	1	6		2	M	510
2020	0	1	5		1	F	490
2020	0	0	4		0	M	500
2020	0	0	4		0	M	455
2020	1	0	4			F	430
2020	1	0		6		M	390
2020	1	1		5		M	380
2020	1	0				F	375
2020	1	1	5	5		F	435
2020	1	0	5	5		M	405
2020	1	0		5		M	380
2020	1	1	7	6		M	425
2021	1	1	7	6	1	F	520
2021	1	1	5	4	1	M	450
2021	1	1	6	6	1	M	470
2021	1	1	5	4	1	M	450
2021	1	1	5	5	1	M	440
2021	1	1	6	4	1	F	520
2021	1	1	6		1	M	450
2021	1	1	5	5	1	F	520
2021	1	1	5	5	1	M	470
2021	1	0	5	6	0	F	500
2021	1	0	5	4	0	F	498
2021	1	0	5	4	0	M	447
2021	1	0	5	5	0	F	490
2021	1	0	5	4	0	M	420
2021	1	0	5	5	0	F	451
2021	1	1	5		1	M	458
2021	1	1	5	5	1	M	447
2021	1	1	5	5	1	M	450
2021	1	1	6	5	1	M	474
2021	1	1	6		2	F	493
2021	1	1	4	5	1	M	470

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2021	1	1	5	5	1	M	435
2021	1	1	5	5	1	M	446
2021	1	0	5	5	0	M	467
2021	1	1	5		1	M	445
2021	1	0	5	5	0	F	477
2021	1	1	5	5	1	M	483
2021	1	0	4		0	F	430
2021	1	0	5	5	0	F	473
2021	1	1	6	5	1	F	509
2021	1	0	5		0	F	465
2021	1	1	5		1	M	430
2021	1	0	5		0	F	501
2021	1	0	6		0	F	515
2021	1	1	5		1	F	520
2021	1	0	6		0	F	513
2021	1	0	4	4	0	M	430
2021	1	0	4		0	M	451
2021	1	1	5	4	1	M	425
2021	1	0	4	5	0	M	447
2021	1	0	5	5	0	F	520
2021	1	0	5		0	F	517
2021	1	1	5	4	1	M	491
2021	1	0	4		0	M	417
2021	1	1	6	6	1	F	487
2021	1	1	5	5	1	F	491
2021	1	0	6	6	0	F	502
2021	1	0	5	6	0	F	487
2021	1	0	6	5	0	M	455
2021	1	1	5		1	F	501
2021	1	1	5		1	M	496
2021	1	1	5		1	M	432
2021	1	0	4		0	M	425
2021	1	1	6		2	M	467
2021	1	0	5	4	0	F	480
2021	1	1	6	5	1	F	500
2021	1	0	5	5	0	M	425
2021	1	0	5	4	0	M	430
2021	1	0	6	5	0	M	445

Table B.1 (cont'd).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2021	1	0	4		0	F	440
2021	1	1	7	5	1	F	585
2021	1	1	5		1	M	440
2021	1	0	5	5	0	F	490
2021	1	0	4	5	0	M	465
2021	1	0	5	5	0	F	455
2021	1	0	5	5	0	M	455
2021	1	0	4	5	0	F	485
2021	1	0	5	5	0	M	395
2021	1	0	5	5	0	F	475
2021	1	0	4		0	M	390
2021	1	0	5	4	0	M	450
2021	1	0	5	5	0	M	450
2021	0	1	5		1	M	480
2021	0	1	5		1	F	520
2021	0	0	4		0	M	465
2021	0	1	6		1	F	545
2021	0	1	5		1	F	520
2021	0	1	6		1	F	510
2021	0	0	5		0	M	445
2021	0	0	5		0	F	465
2021	0	0	5		0	F	420
2021	0	0	4		0	F	490
2021	0	0	5		0	F	500
2021	0	1	5		1	F	530
2021	0	0	4		0	M	455
2021	0	0	5		0	F	510
2021	0	1	5		1	M	455
2021	0	1	5		1	F	525
2021	0	1	5		1	M	485
2021	0	1	5		1	F	435
2021	0	0	5		0	F	520
2021	0	1	6		2	M	480
2021	0	1	6		2	F	490
2021	0	1	5		1	F	500
2021	0	1	5		1	M	460
2021	0	1	5		1	F	480
2021	0	1	6		1	F	470

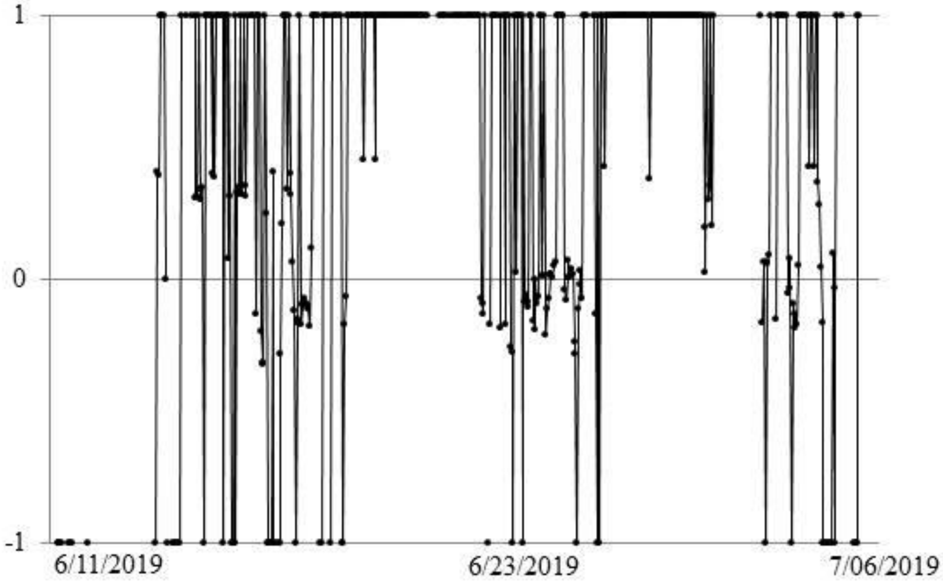
Table B.1 (cont’d).

Year	Pass	Repeat	Scale_Age	Oto_Age	Spawns	Sex	TL
2021	0	1	6		1	M	490
2021	0	1	5		1	F	535
2021	0	0	5		0	F	525
2021	0	0	5		0	F	495
2021	0	0	5		0	M	470
2021	0	0	5		0	F	470
2021	0	0	4		0	F	500
2021	0	0	5		0	F	480
2021	0	1	5		1	M	460
2021	0	1	5		1	F	510
2021	0	1	6		2	F	540
2021	0	0	5		0	F	500

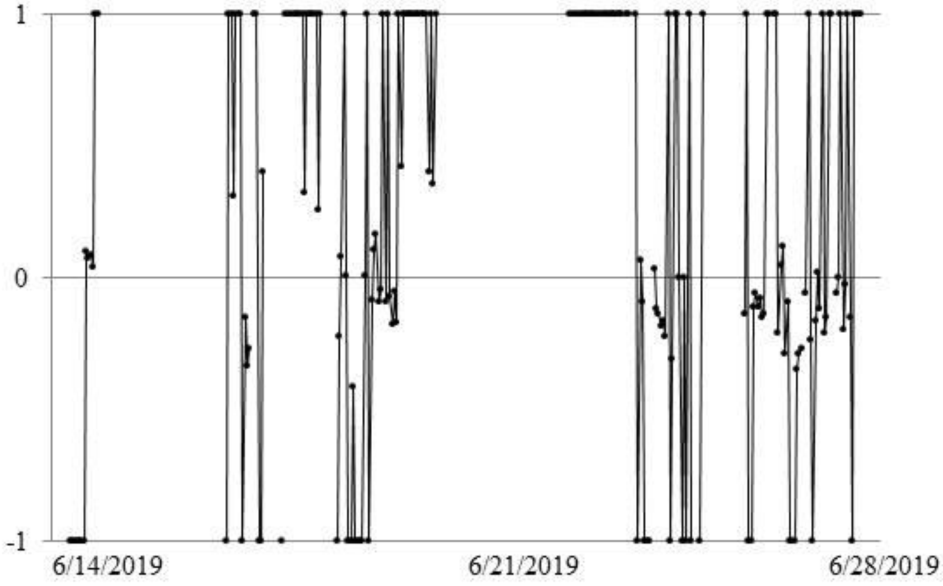
APPENDIX C: INDEX OF RELATIVE LOCATION

Graphs of the index of relative location (IRL) showing the probability of occupancy for every adult salmon (*Salmo salar*) radio-tagged in 2019-2020. The IRL graph indicates the probable located of tagged salmon based on the signal strength of detections made on the radio receivers at Milford Dam. On the IRL graphs, negative numbers indicate that fish were located closer to the east side of the river, and positive values are indicative of fish being located closer to the west side of the river. The dates indicate the date of arrival, the midpoint of the delay, and the last day that fish were located at Milford. Other information includes origin (hatchery or wild), sex, and fork length (mm). The length of the delay in days is followed by the number of hours that the individual was detected on at least one of the Milford radio receivers (in parentheses) and whether or not it passed the dam following the delay. The movement pattern displayed in the IRL graph is also listed.

Atlantic salmon 2019-92
Hatchery male, 740mm FL
Delayed 25 days (439 hours); Passed
Extensive Searching



Atlantic salmon 2019-93
Hatchery female, 820mm FL
Delayed 14 days (186 hours); Passed
Extensive Searching

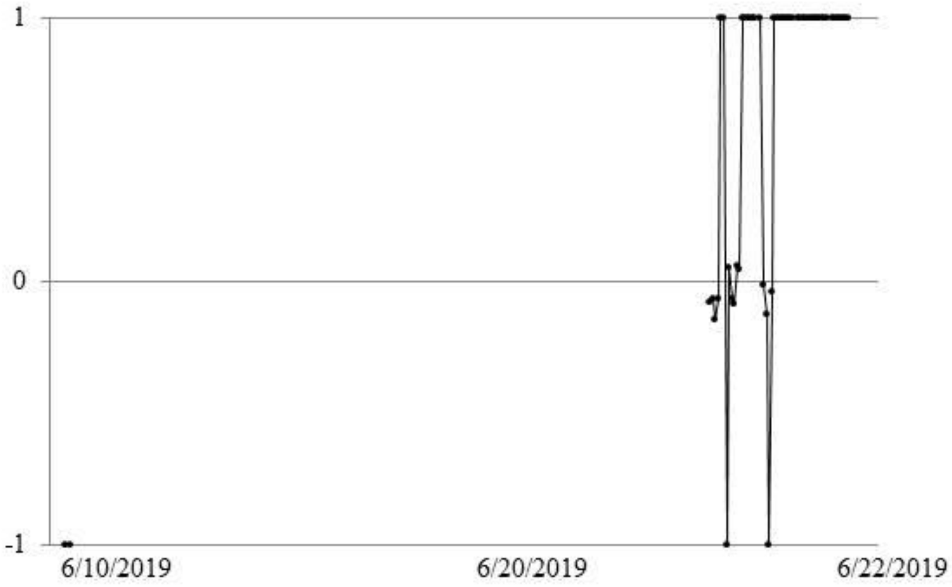


Atlantic salmon 2019-94

Hatchery female, 740mm FL

Delayed 0 days, 2 days (52 hours total); Passed both times

Eastern Exclusive, Western Focus

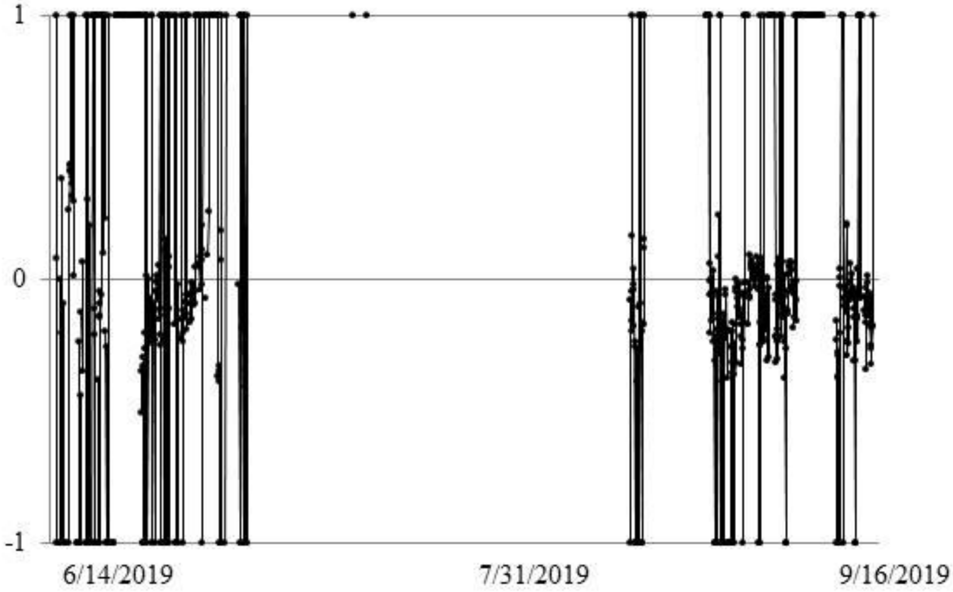


Atlantic salmon 2019-95

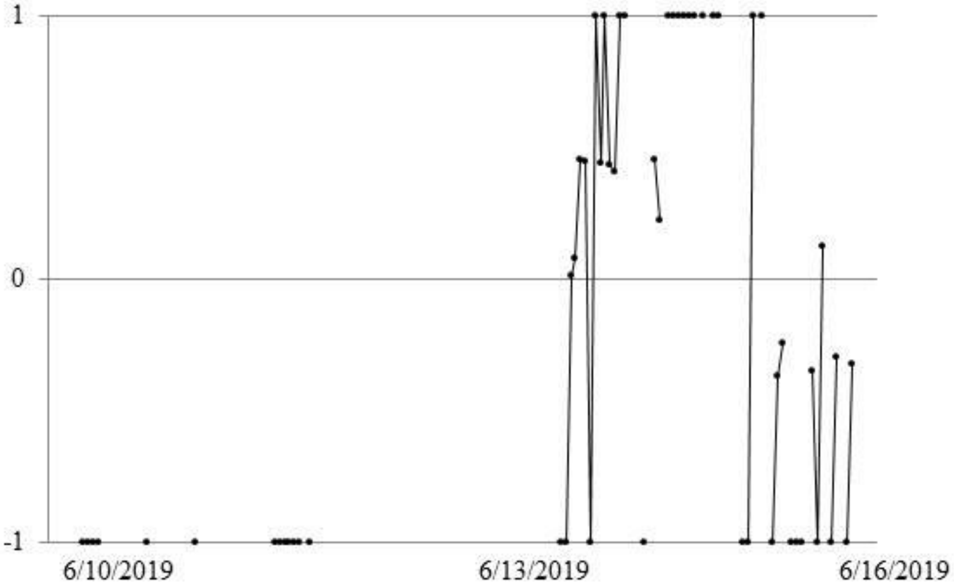
Hatchery male, 750mm FL

Delayed 94 days (756 hours); Did not pass

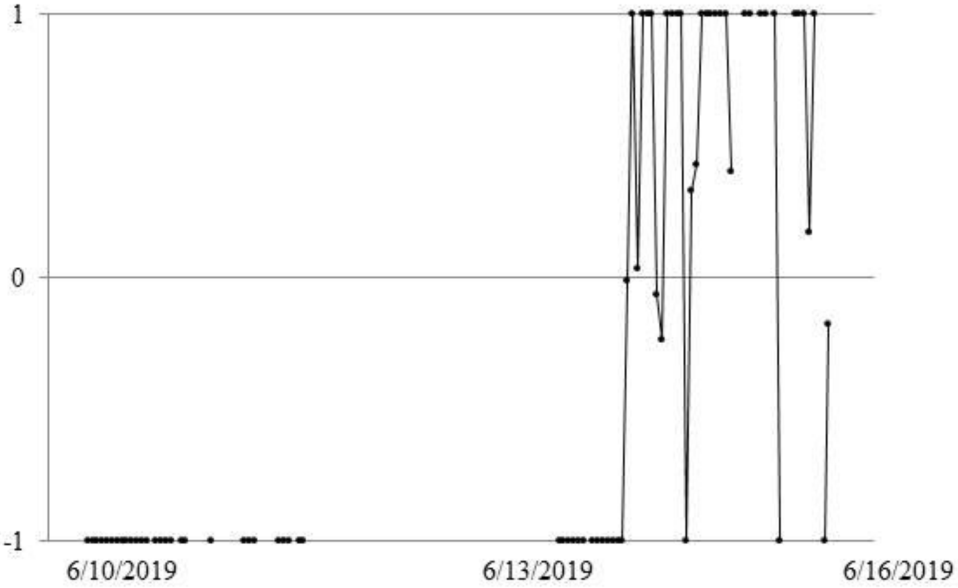
Extensive Searching



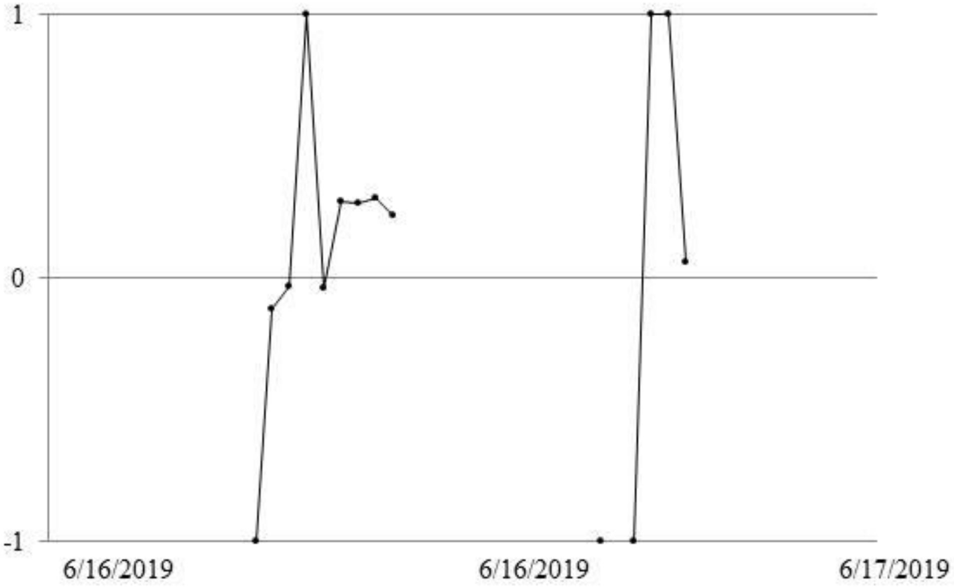
Atlantic salmon 2019-96
Hatchery male, 690mm FL
Delayed 7 days (56 hours); Passed
Extensive Searching



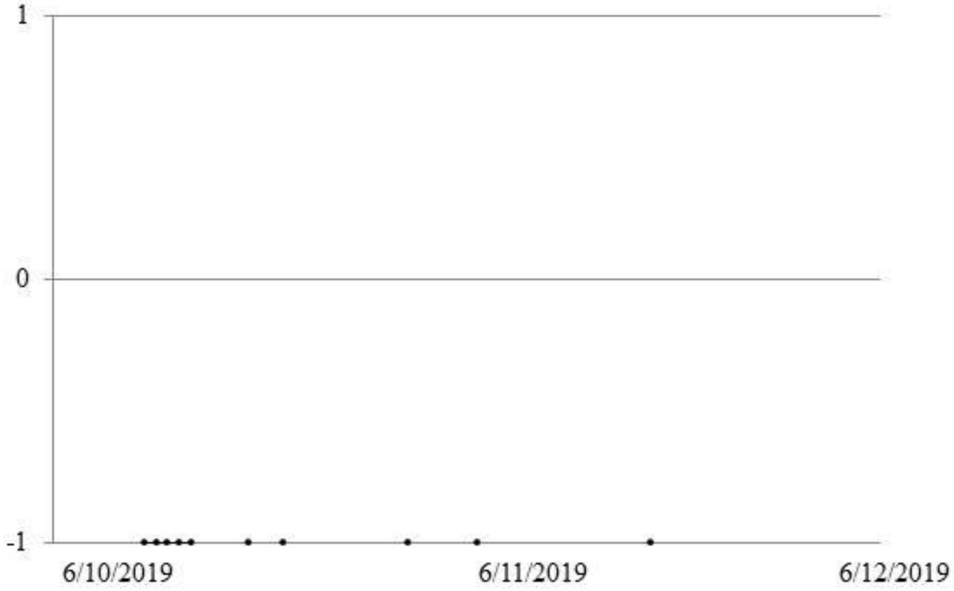
Atlantic salmon 2019-97
Hatchery male, 710mm FL
Delayed 7 days (76 hours); Passed
Extensive Searching



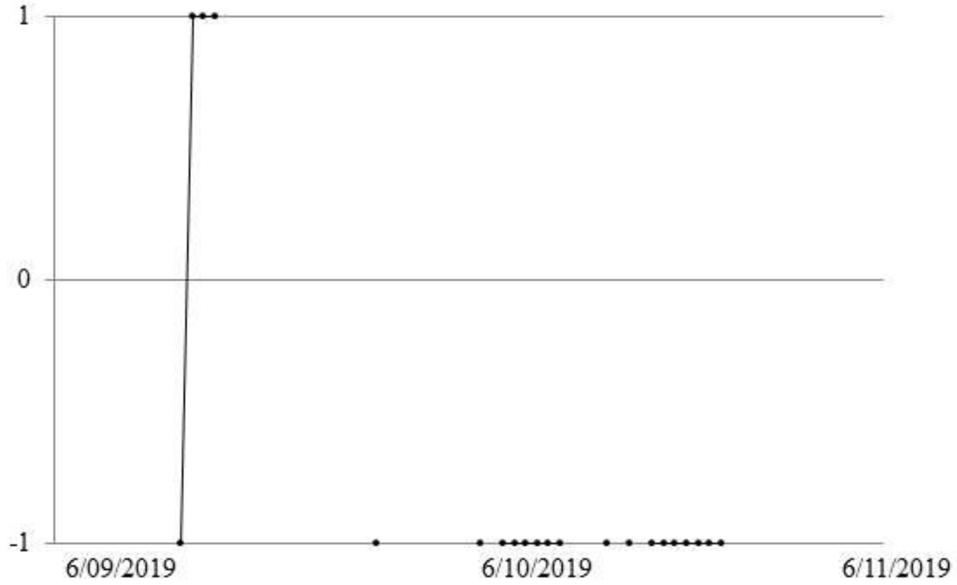
Atlantic salmon 2019-98
Hatchery female, 680mm FL
Delayed 1 day (14 hours); Passed
Pattern 1—Extensive searching



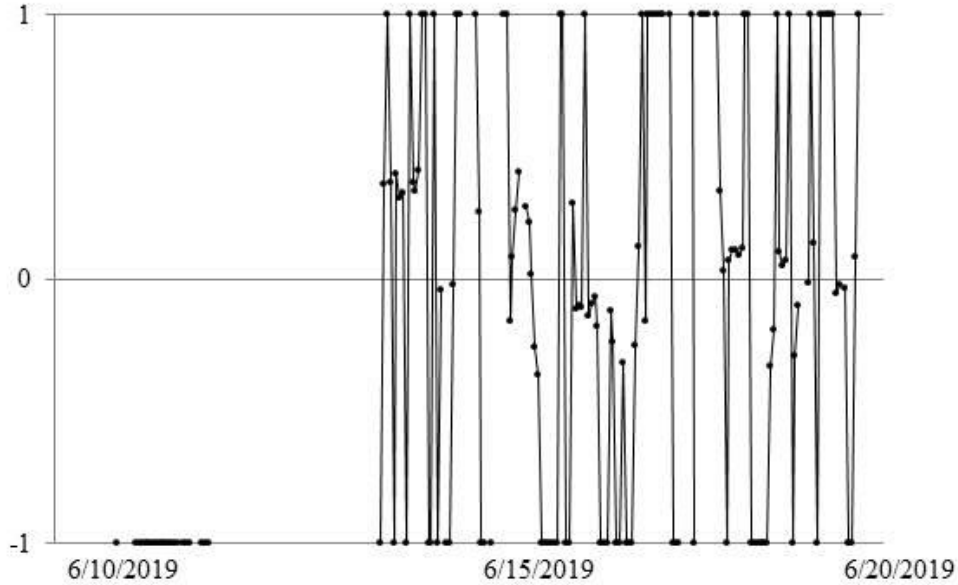
Atlantic salmon 2019-99
Hatchery male, 720mm FL
Delayed 2 days (10 hours); Passed
Eastern Exclusive



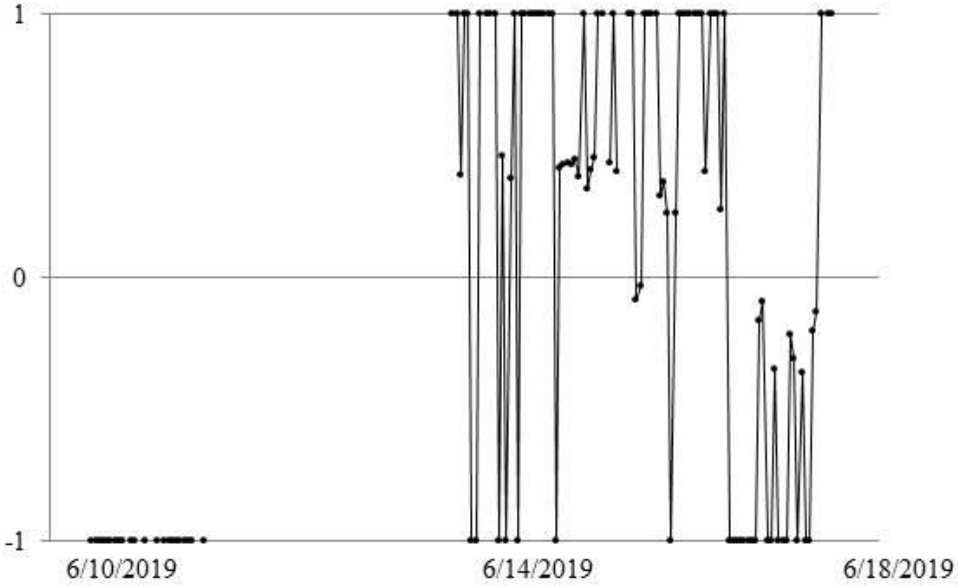
Atlantic salmon 2019-100
Hatchery male, 820mm FL
Delayed 2 days (21 hours); Passed
Eastern Focus



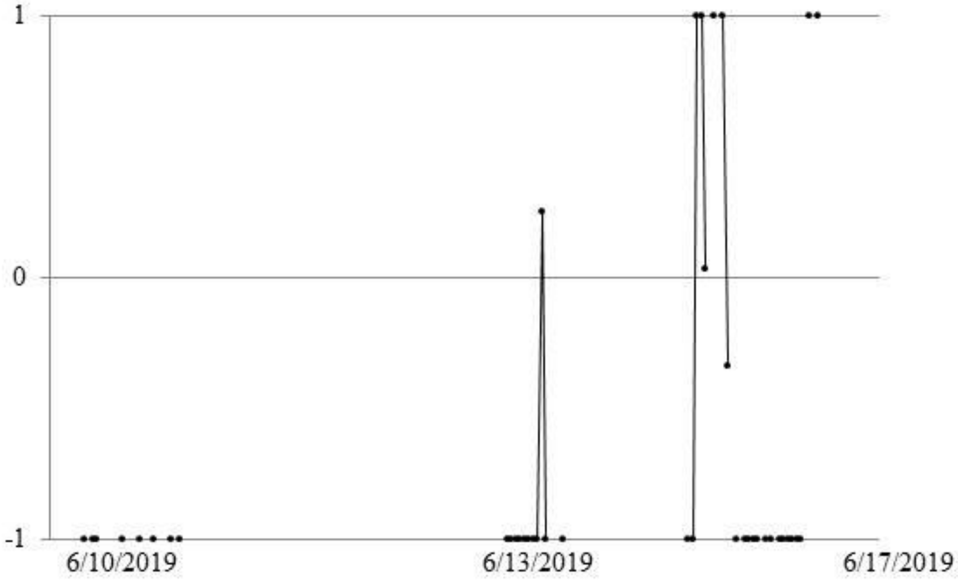
Atlantic salmon 2019-101
Hatchery male, 770mm FL
Delayed 10 days (154 hours); Passed
Extensive Searching



Atlantic salmon 2019-102
Hatchery male, 760mm FL
Delayed 8 days (117 hours); Passed
Extensive Searching



Atlantic salmon 2019-103
Hatchery male, 800mm FL
Delay uncertain (42 hours); Passed
Eastern Focus

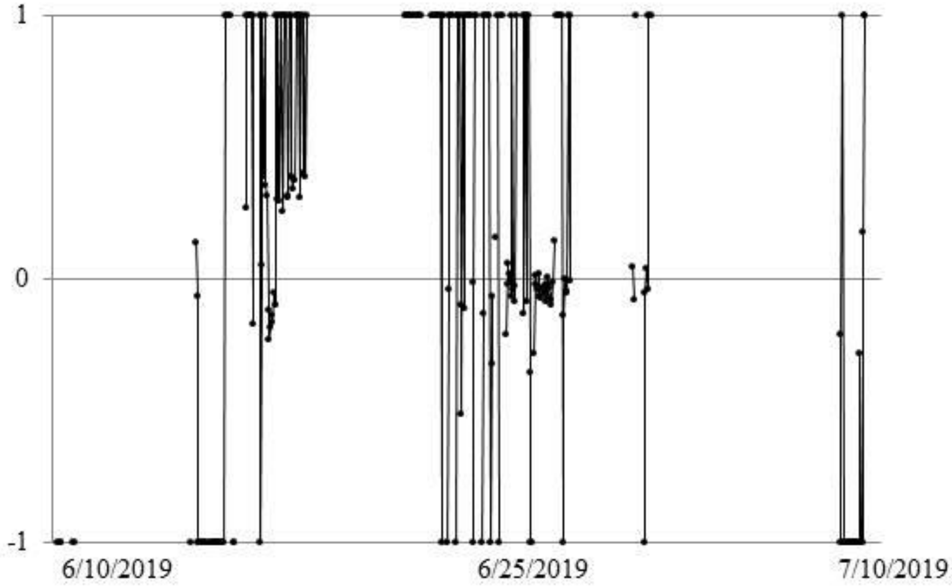


Atlantic salmon 2019-104

Wild female, 730mm FL

Delayed 30 days (233 hours); Passed

Extensive Searching

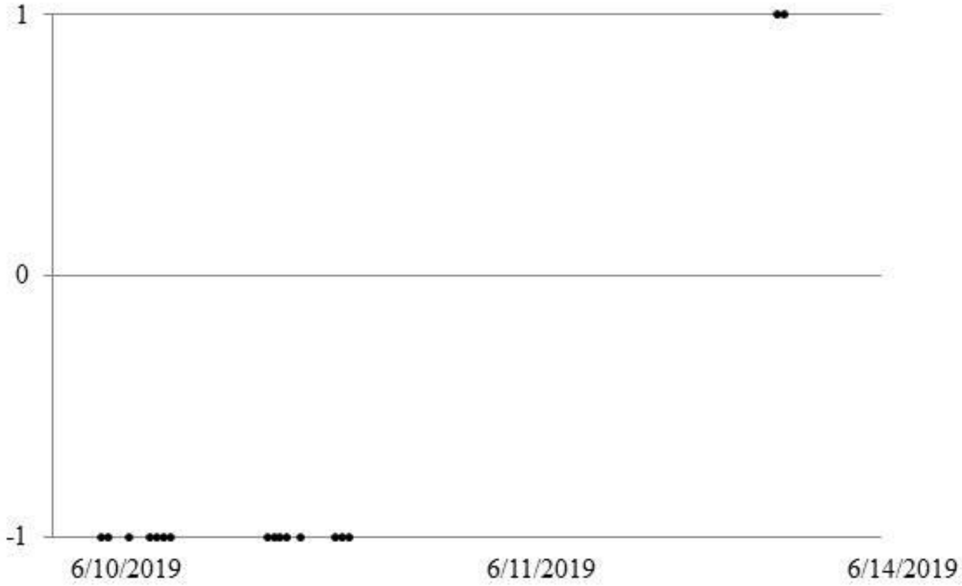


Atlantic salmon 2019-105

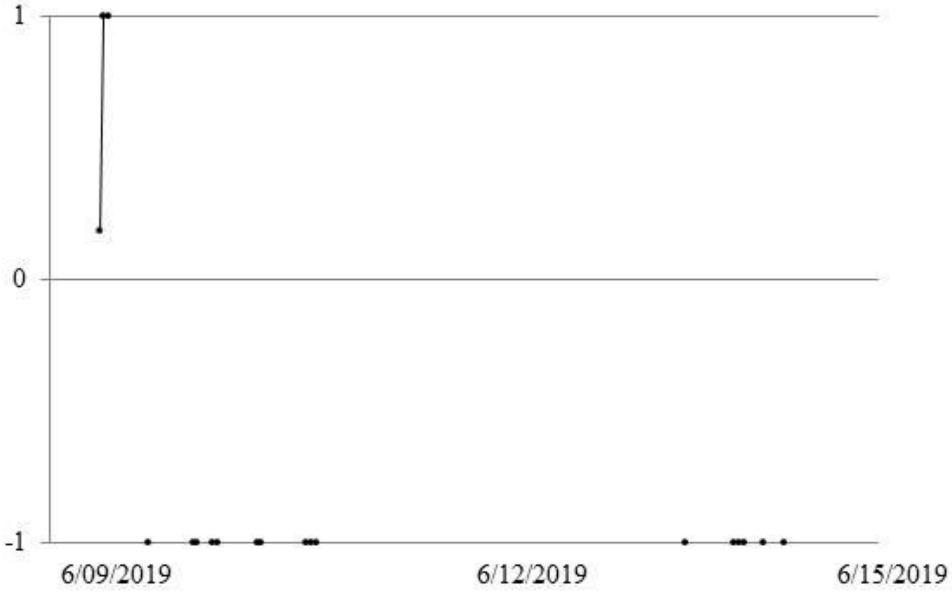
Hatchery male, 650mm FL

Delayed 4 days (17 hours); Passed

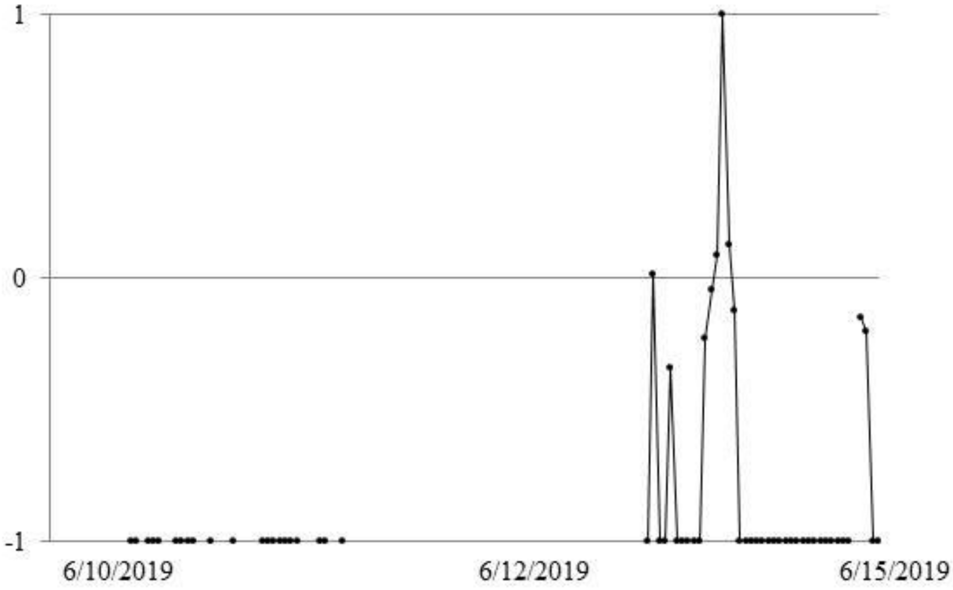
Eastern Focus



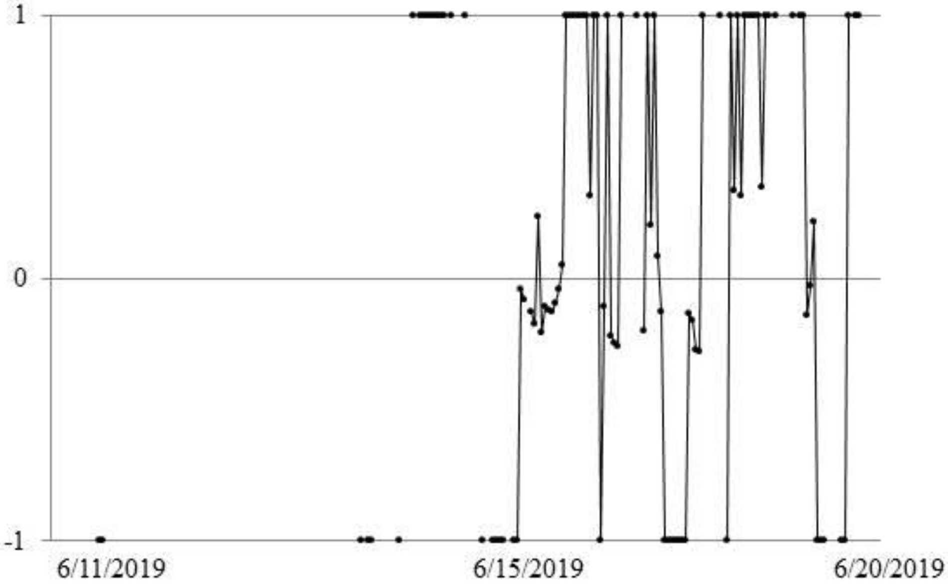
Atlantic salmon 2019-106
Wild female, 720mm FL
Delayed 6 days (19 hours); Passed
Eastern Focus



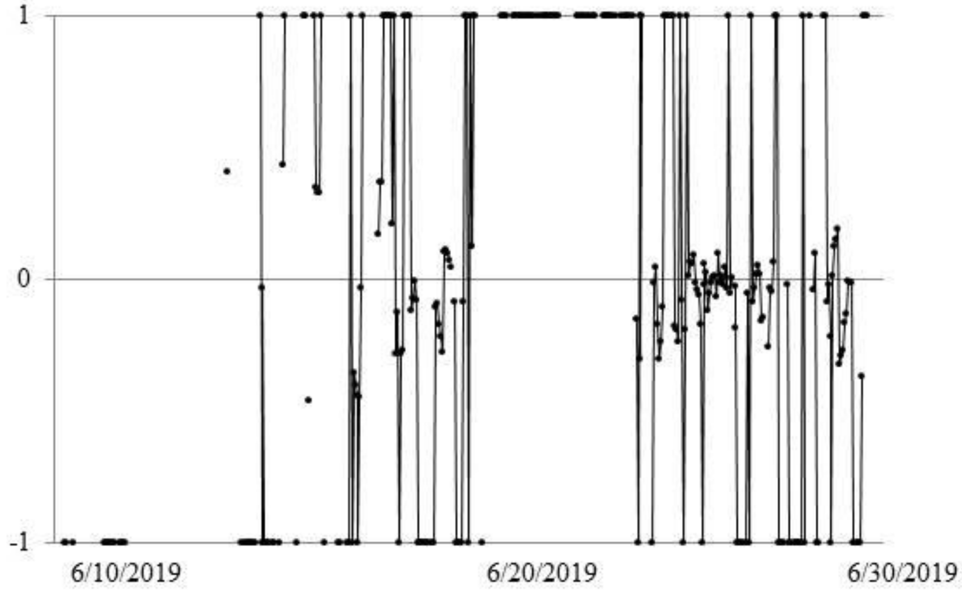
Atlantic salmon 2019-107
Hatchery male, 700mm FL
Delayed 5 days (61 hours); Passed
Eastern Focus



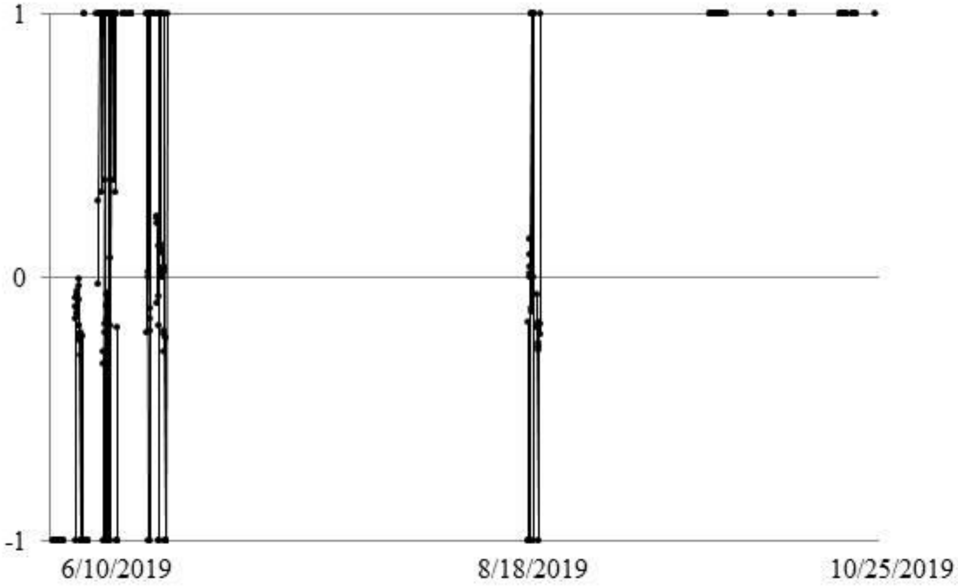
Atlantic salmon 2019-110
Wild male, 820mm FL
Delayed 9 days (102 hours); Passed
Extensive Searching



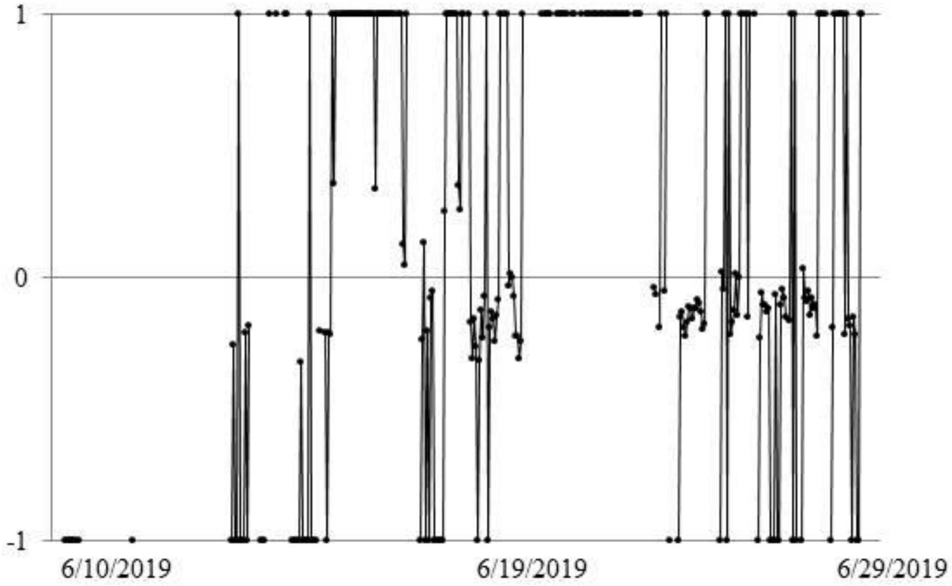
Atlantic salmon 2019-111
Hatchery female, 710mm FL
Delayed 20 days (290 hours); Passed
Extensive Searching



Atlantic salmon 2019-112
Hatchery female, 760mm FL
Delayed 18 days, 60 days (334 hours total); Passed both times
Extensive Searching (both delays)

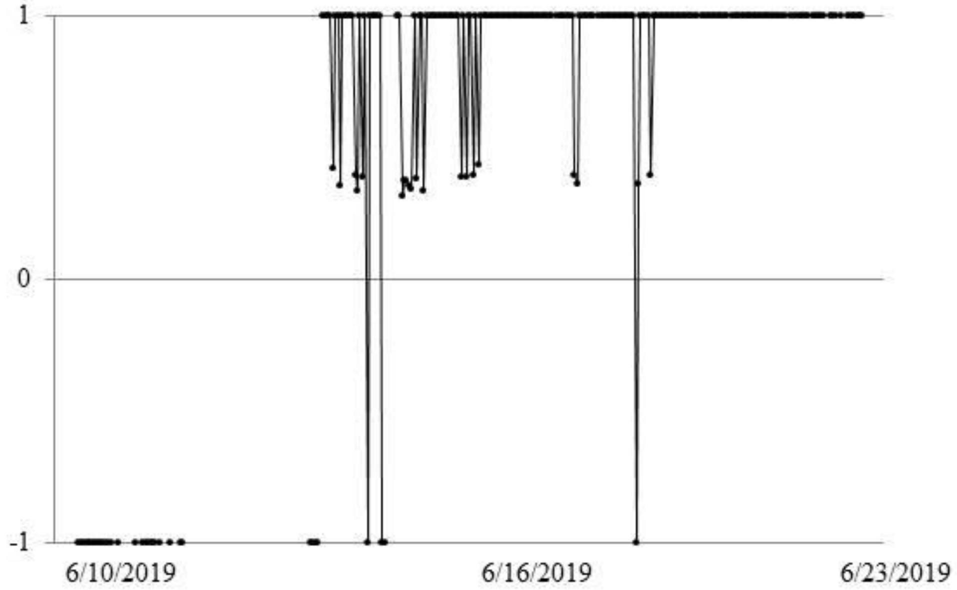


Atlantic salmon 2019-113
Hatchery female, 720mm FL
Delayed 19 days (281 hours); Passed
Extensive Searching

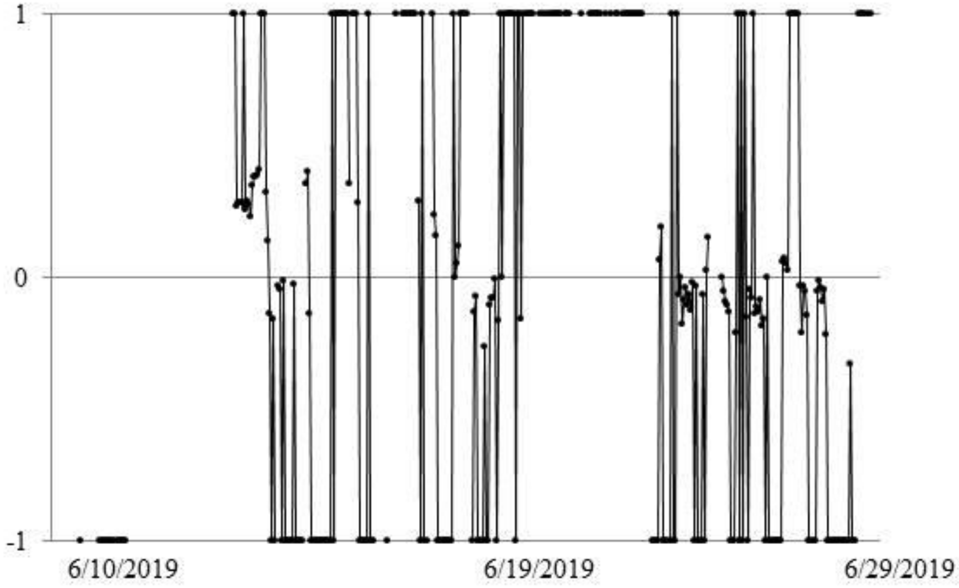


Atlantic salmon 2019-115
Hatchery male, 730mm FL
Delayed 139 days (4 hours); Did not pass
Western Exclusive

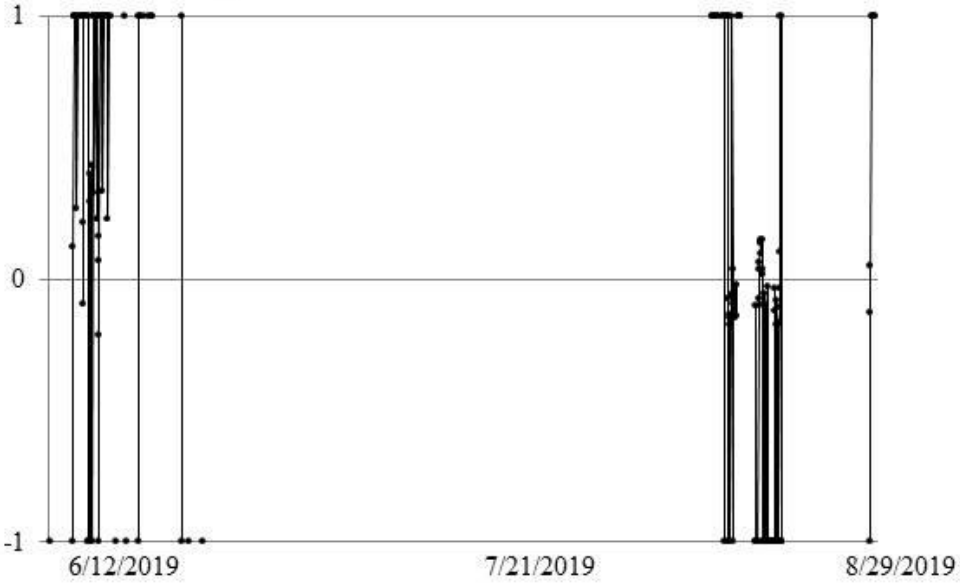
Atlantic salmon 2019-116
Hatchery female, 720mm FL
Delayed 13 days (232 hours); Passed
Western Focus



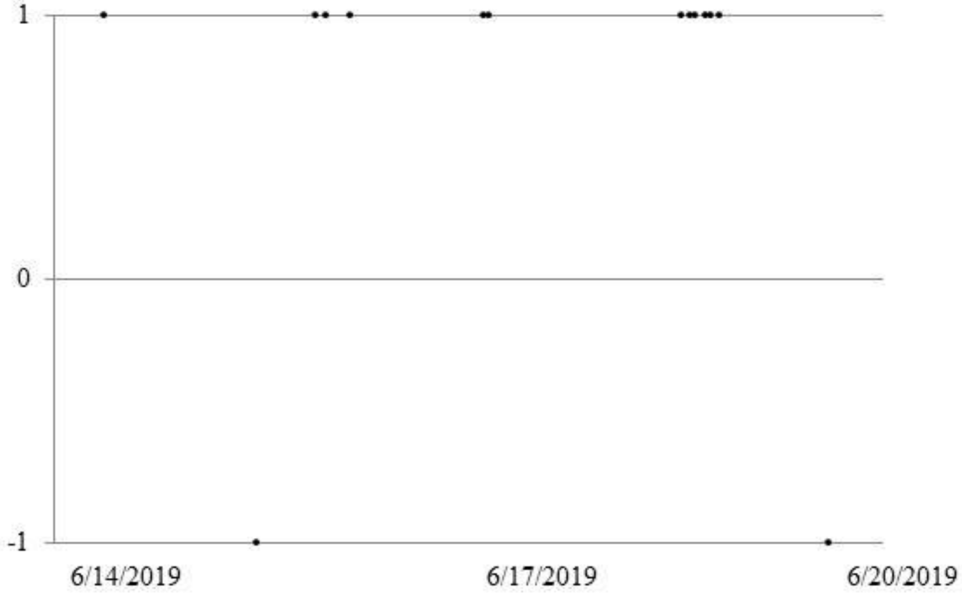
Atlantic salmon 2019-117
Hatchery male, 780mm FL
Delayed 19 days (319 hours); Passed
Extensive Searching



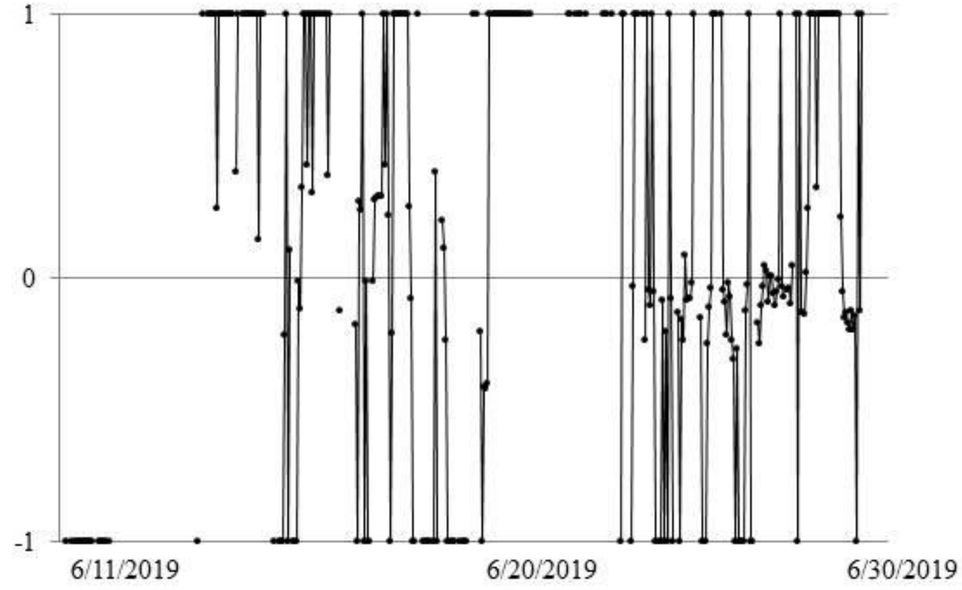
Atlantic salmon 2019-118
Hatchery male, 750mm FL
Delay uncertain (204 hours); Passed
Extensive Searching



Atlantic salmon 2019-119
Hatchery female, 670mm FL
Delayed 6 days (14 hours); Passed
Western Focus



Atlantic salmon 2019-120
Wild female, 730mm FL
Delayed 19 days (296 hours); Passed
Extensive Searching

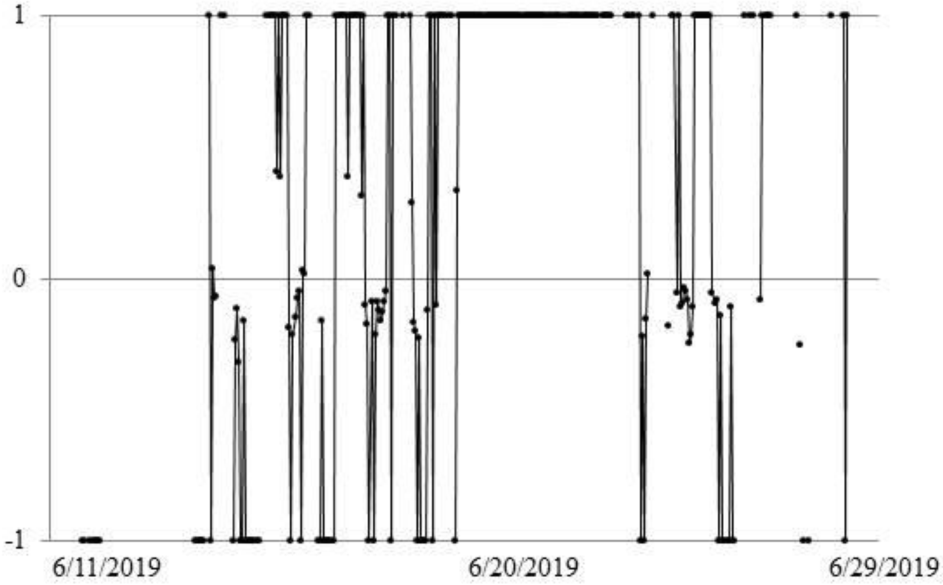


Atlantic salmon 2019-121

Hatchery female, 680mm FL

Delayed 16 days (269 hours); Passed

Extensive Searching

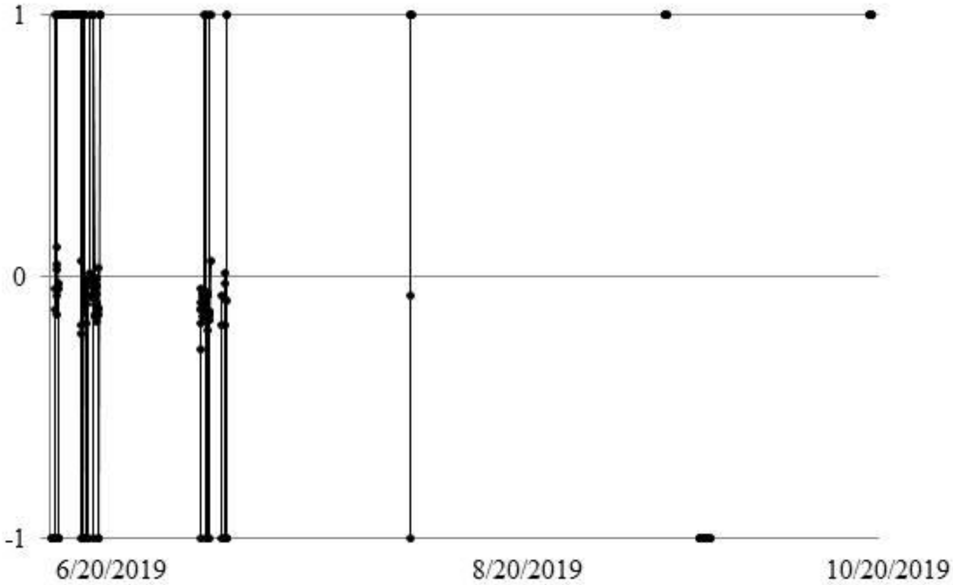


Atlantic salmon 2019-122

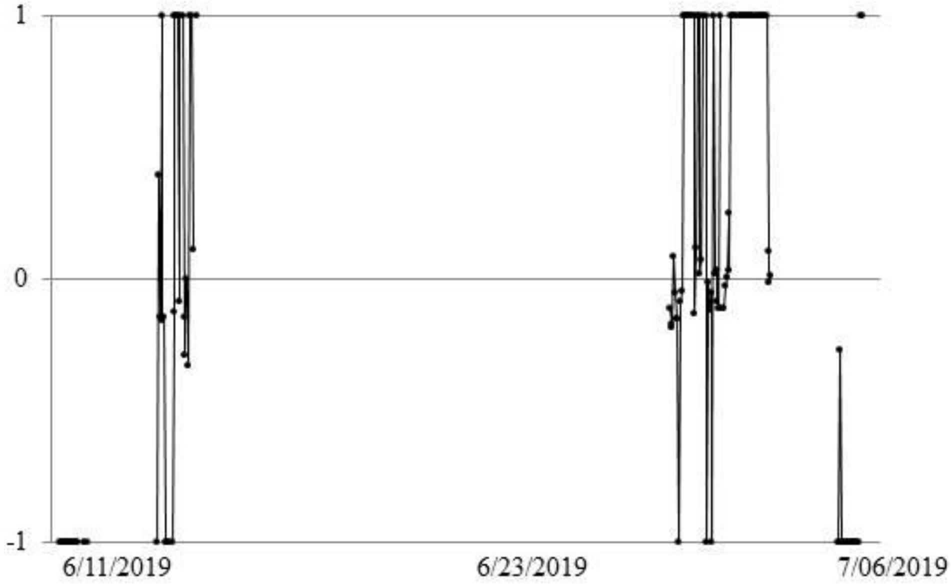
Hatchery male, 780mm FL

Delayed 13 days, 100 days (234 hours total); Passed both times

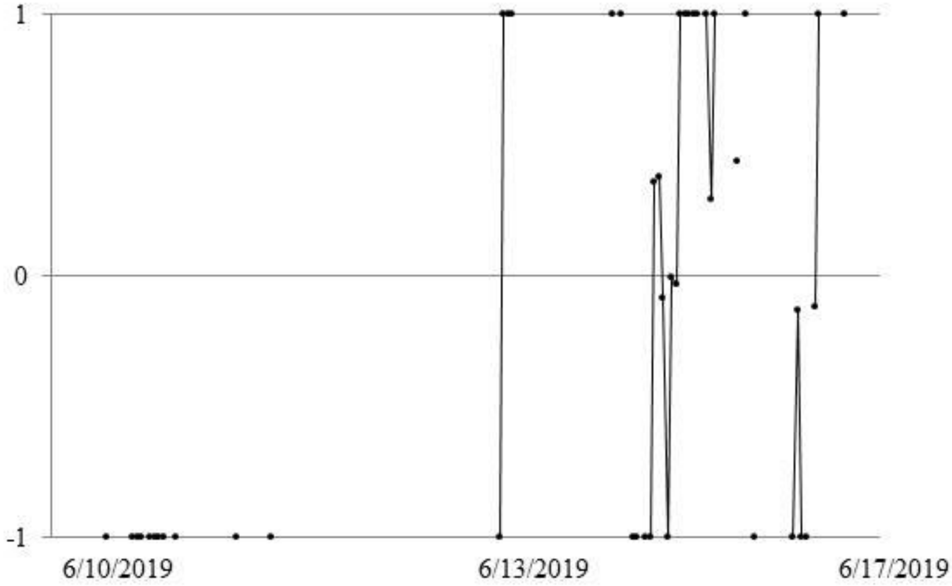
Extensive Searching (both delays)



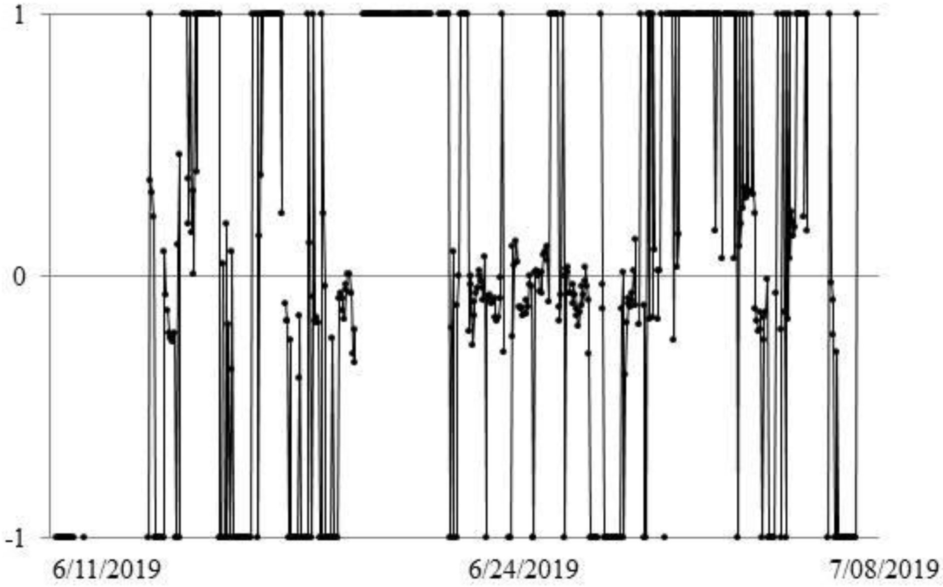
Atlantic salmon 2019-123
Hatchery female, 700mm FL
Delayed 4 days, 6 days (129 hours total); Passed both times
Extensive Searching (both delays)



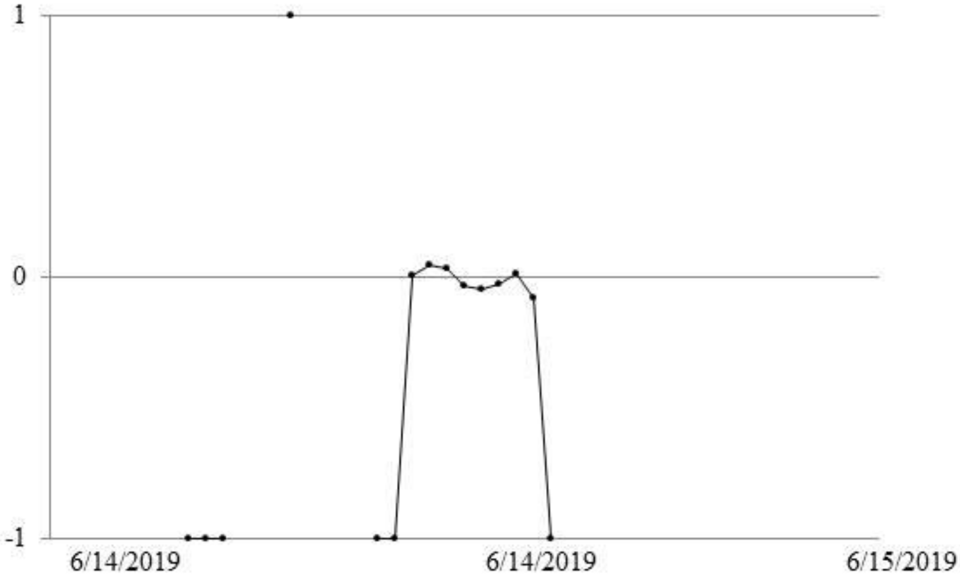
Atlantic salmon 2019-125
Wild female, 750mm FL
Delayed 7 days (45 hours); Passed
Extensive Searching



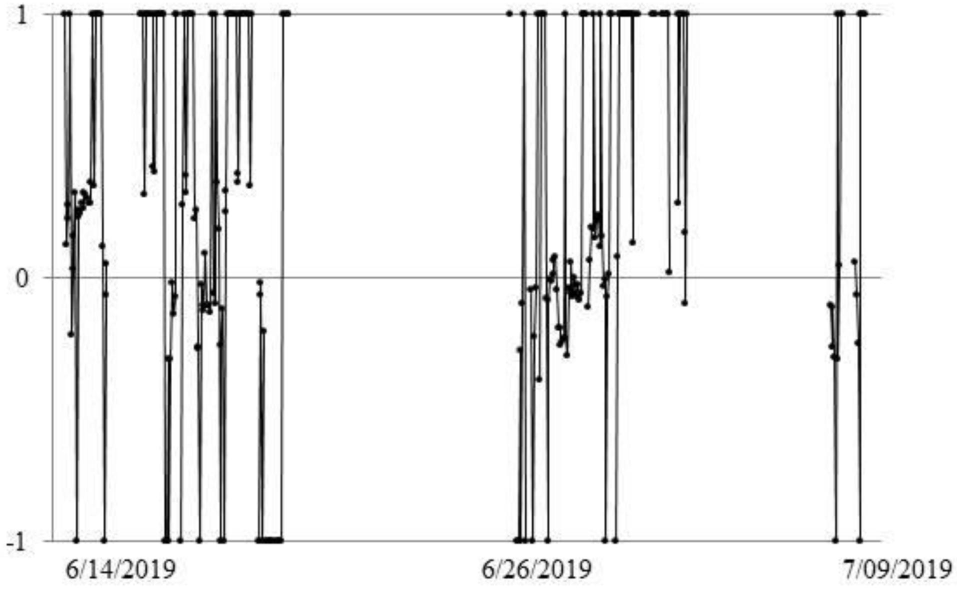
Atlantic salmon 2019-126
Hatchery female, 720mm FL
Delayed 27 days (520 hours); Passed
Extensive Searching



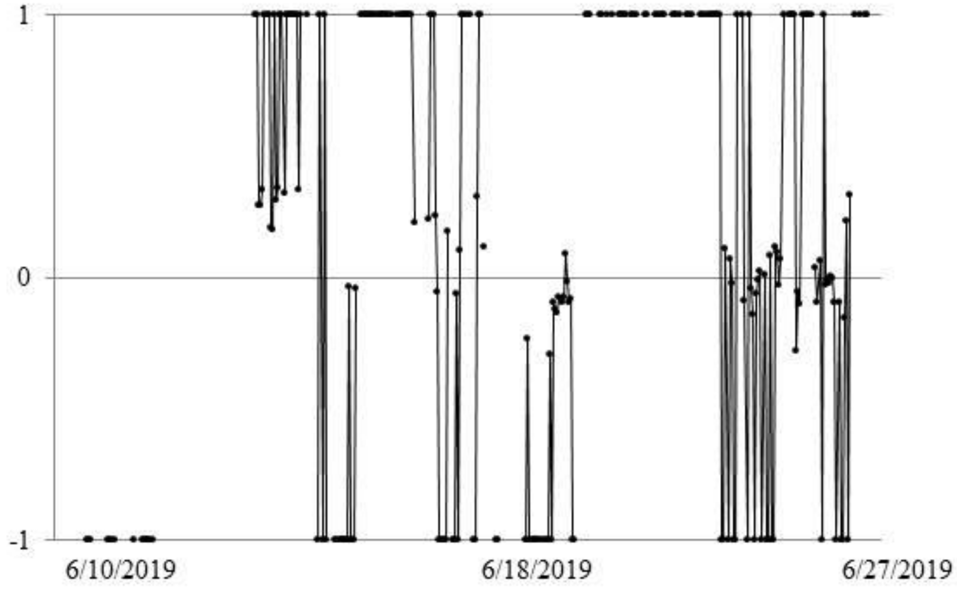
Atlantic salmon 2019-129
Hatchery male, 710mm FL
Delayed 1 day (15 hours); Passed
Eastern Focus



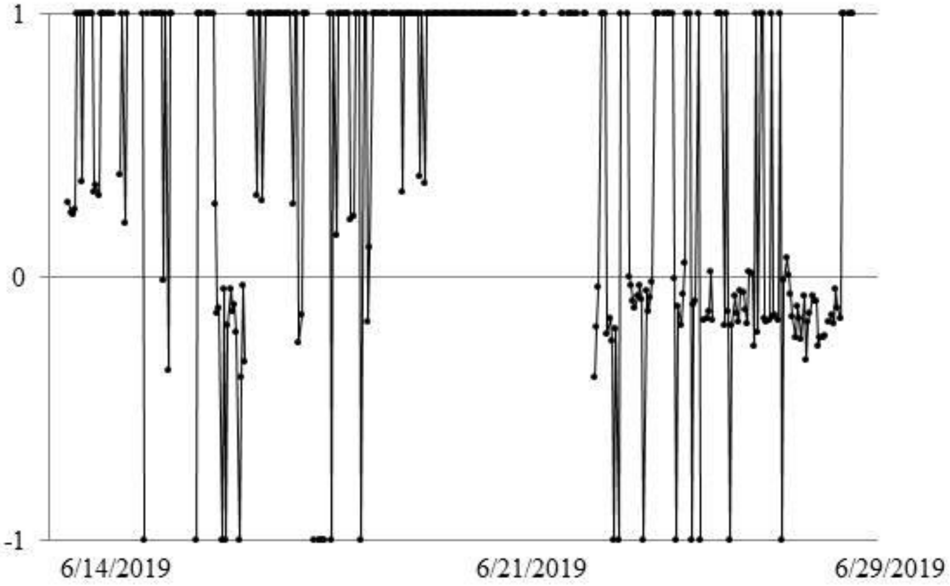
Atlantic salmon 2019-130
Hatchery female, 700mm FL
Delayed 6 days, 11 days (253 hours); Passed both times
Extensive Searching (both delays)



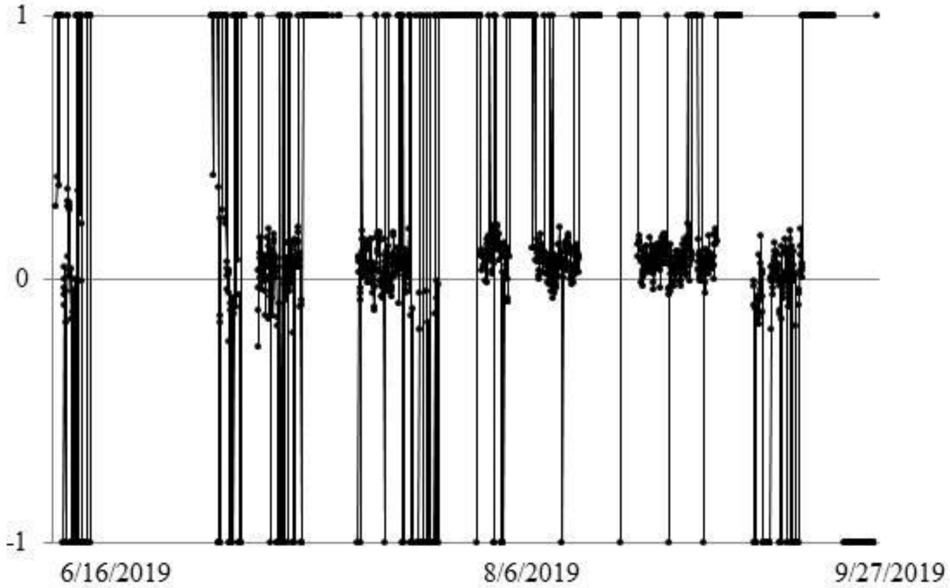
Atlantic salmon 2019-131
Hatchery male, 760mm FL
Delayed 17 days (240 hours); Passed
Extensive Searching



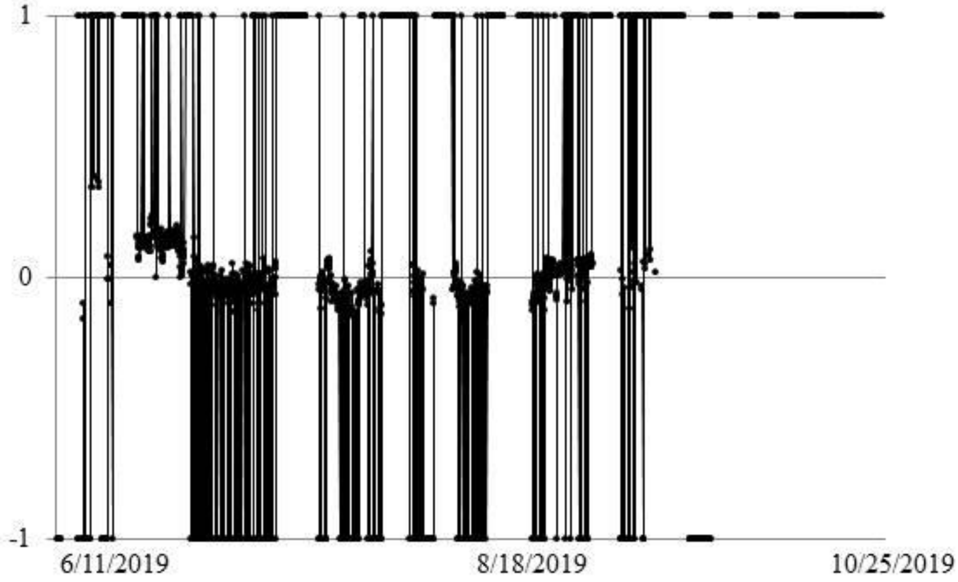
Atlantic salmon 2019-132
Hatchery female, 770mm FL
Delayed 15 days (305 hours); Passed
Extensive Searching



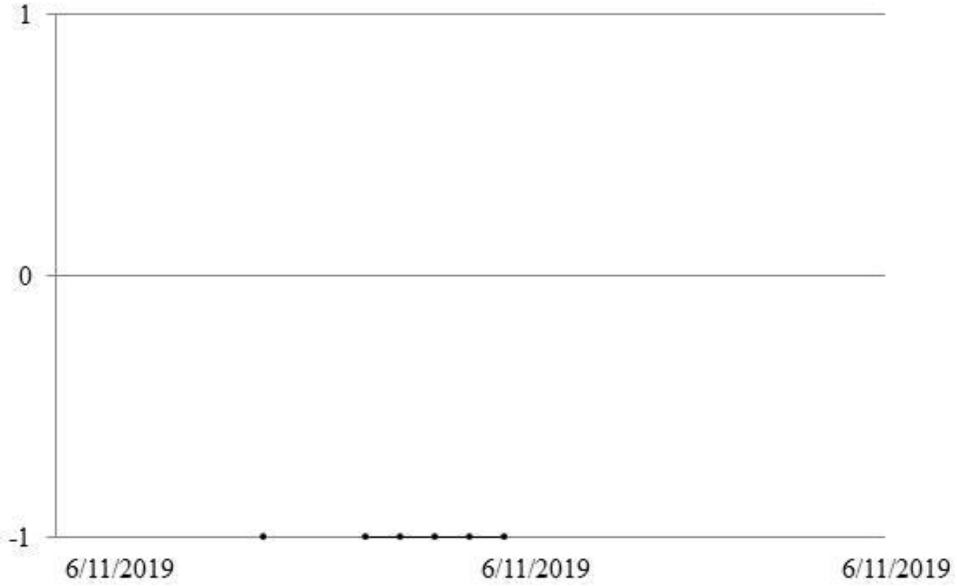
Atlantic salmon 2019-133
Hatchery male, 750mm FL
Delayed 4 days, 84 days (1,711 hours total); Passed both times
Extensive Searching (both delays)



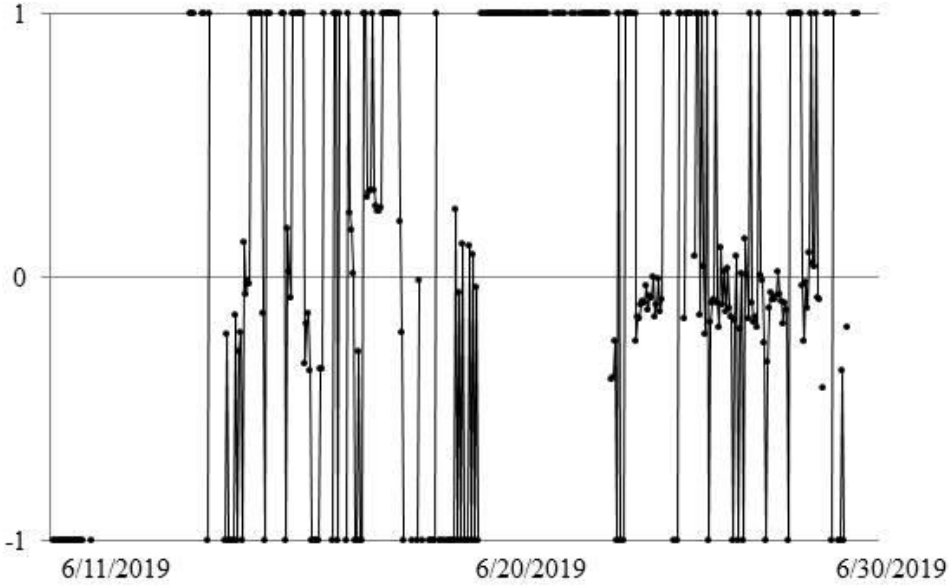
Atlantic salmon 2019-135
Hatchery male, 730mm FL
Delayed 139 days (2,154 hours); Did not pass
Extensive Searching



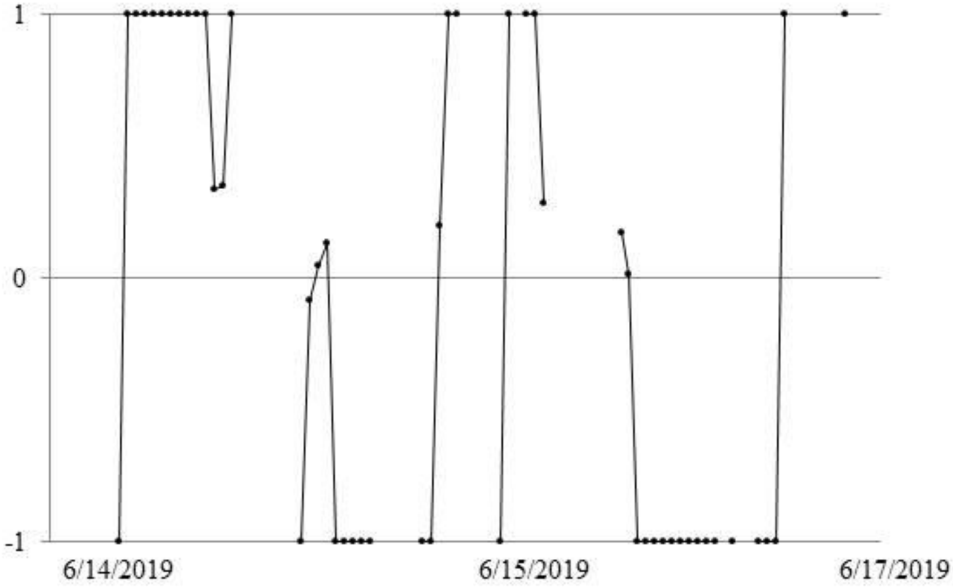
Atlantic salmon 2019-136
Wild female, 720mm FL
Delayed 0 days (6 hours); Passed
Eastern Exclusive



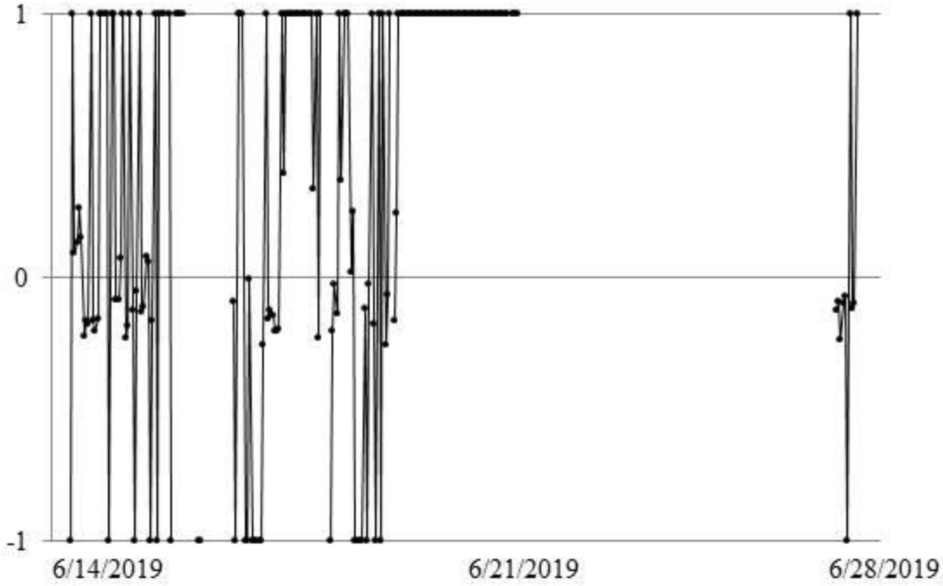
Atlantic salmon 2019-137
Wild female, 730mm FL
Delayed 19 days (325 hours); Passed
Extensive Searching



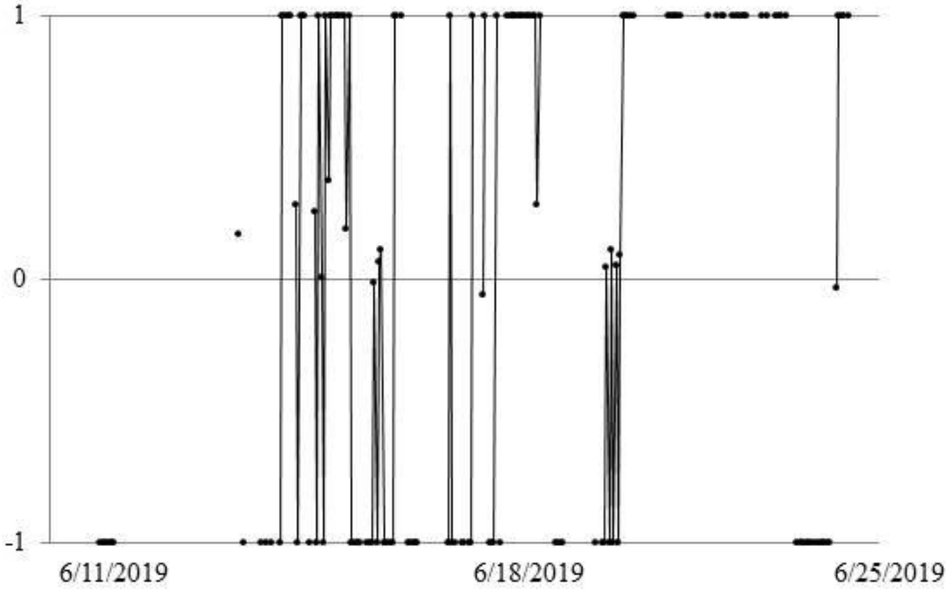
Atlantic salmon 2019-138
Hatchery female, 720mm FL
Delayed 3 days (51 hours); Passed
Extensive Searching



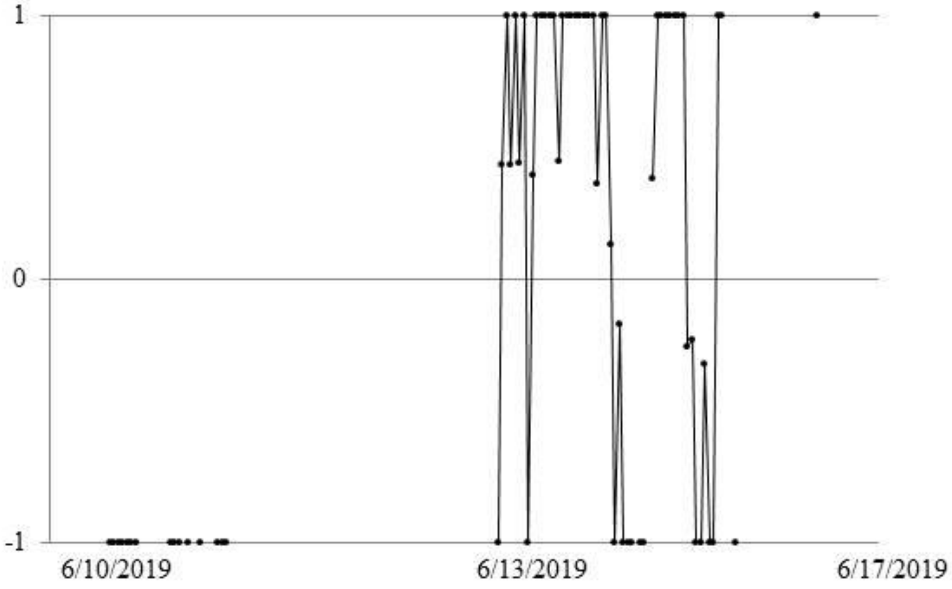
Atlantic salmon 2019-139
Hatchery male, 740mm FL
Delayed 14 days (180 hours); Passed
Extensive Searching



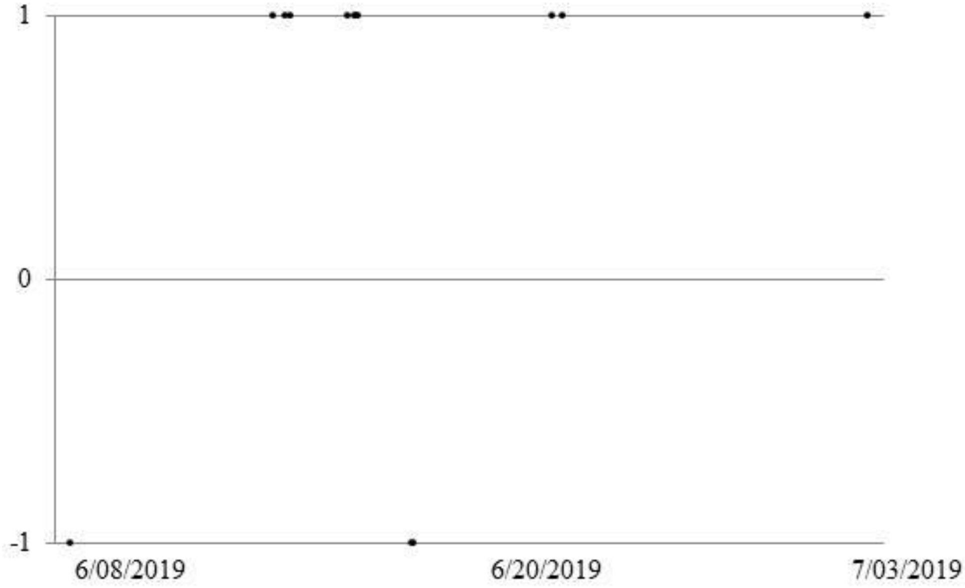
Atlantic salmon 2019-140
Hatchery female, 700mm FL
Delayed 14 days (156 hours); Passed
Extensive Searching



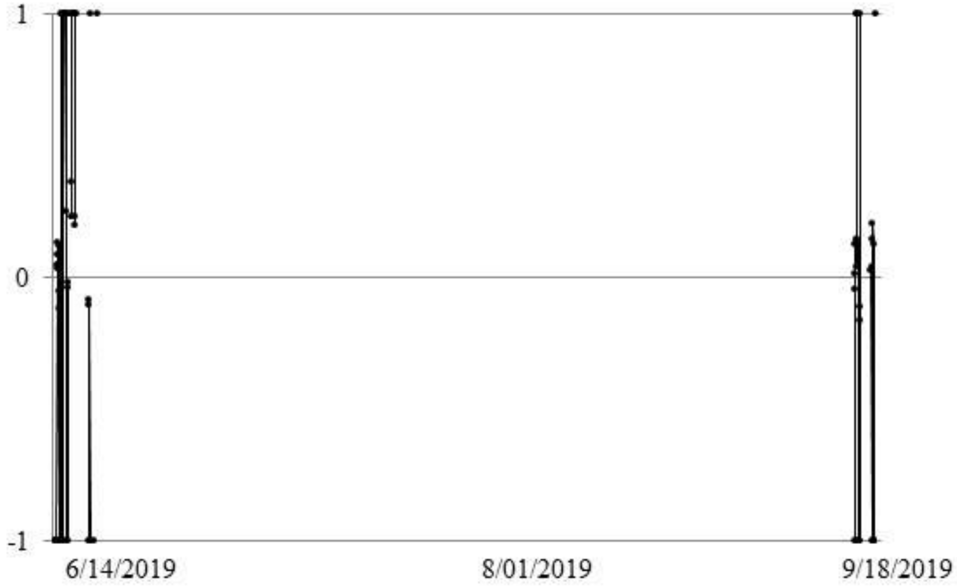
Atlantic salmon 2019-141
Hatchery male, 750mm FL
Delayed 6 days (68 hours); Passed
Extensive Searching



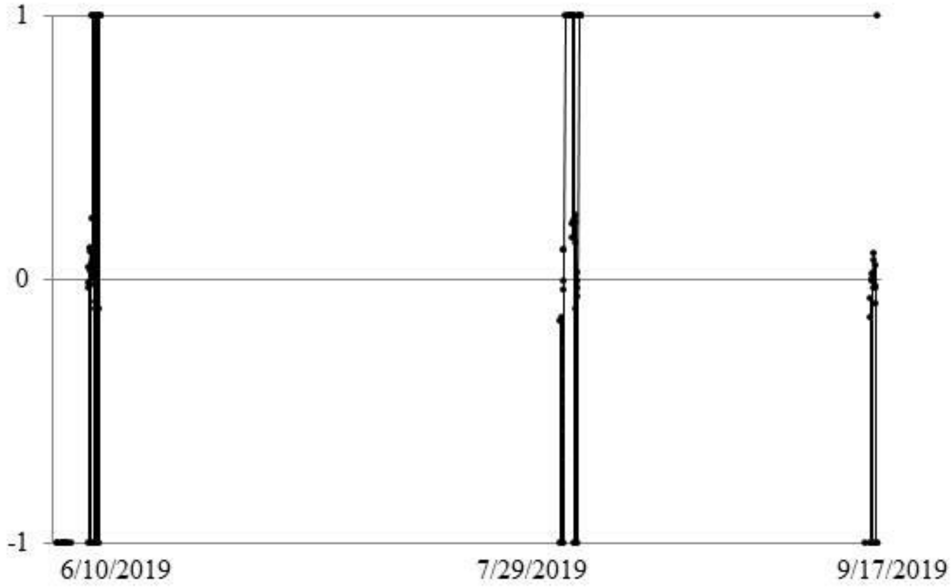
Atlantic salmon 2019-142
Hatchery male, 710mm FL
Delayed 24 days (13 hours); Passed
Western Focus



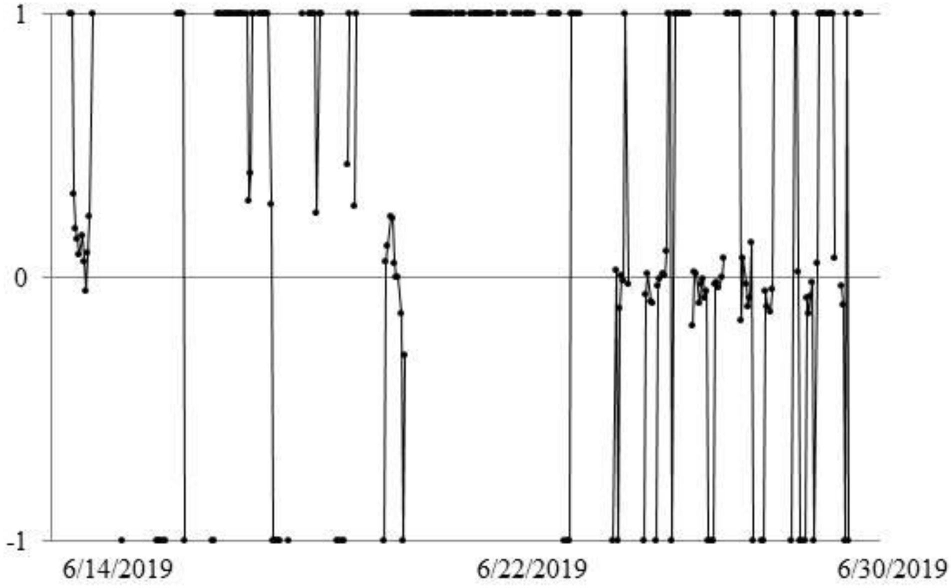
Atlantic salmon 2019-143
Hatchery female, 670mm FL
Delayed 4 days, 3 days (83 hours total); Passed both times
Extensive Searching (both delays)



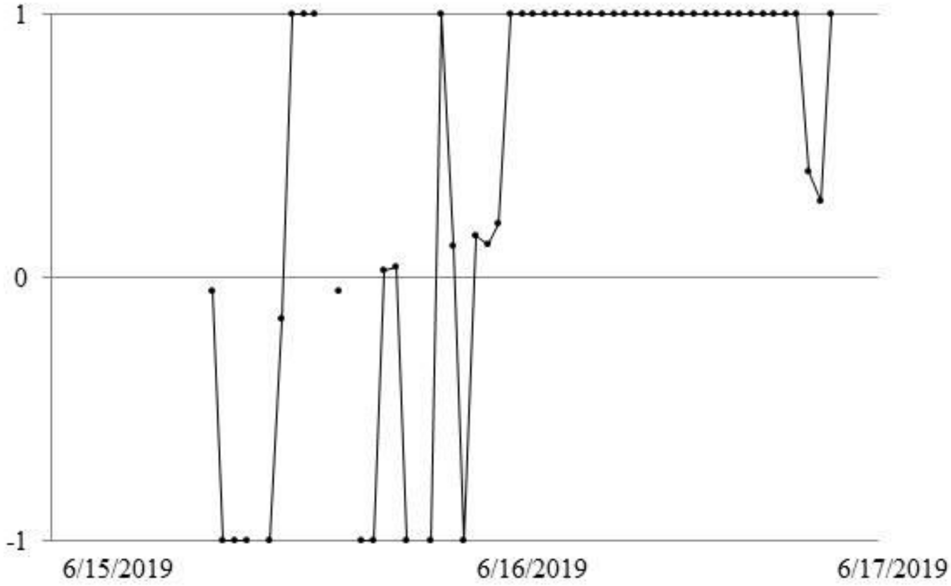
Atlantic salmon 2019-144
Hatchery male, 730mm FL
Delayed 5 days, 38 days (120 hours total); Passed both times
Extensive Searching (both delays)



Atlantic salmon 2019-145
Wild female, 670mm FL
Delayed 16 days (236 hours); Passed
Extensive Searching



Atlantic salmon 2019-180
Hatchery male, 720mm FL
Delayed 3 days (51 hours); Passed
Western Focus



Atlantic salmon 2020-234

Wild female, 710mm FL

Delayed 0 days (6 hours); Passed

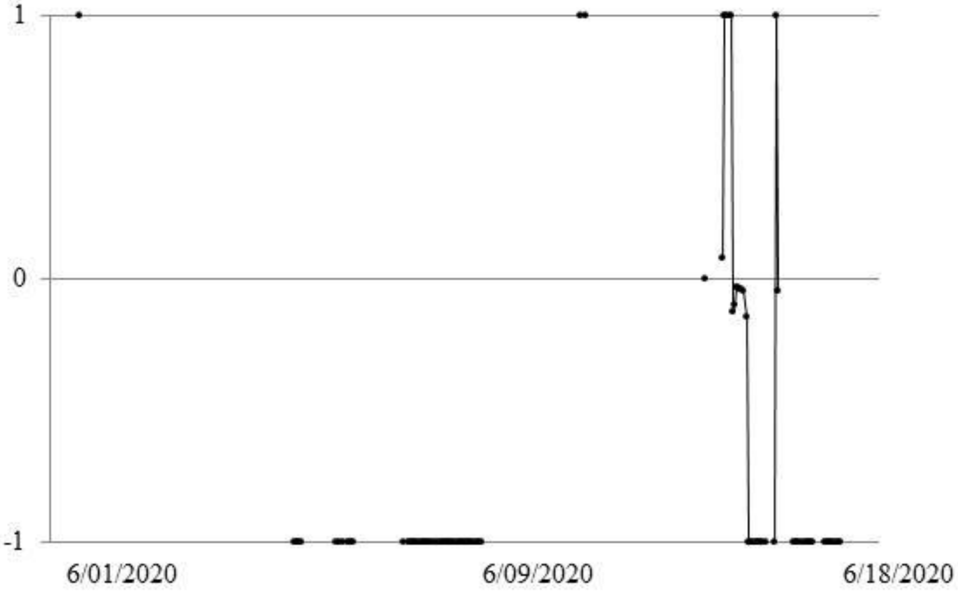
Eastern Focus

Atlantic salmon 2020-235

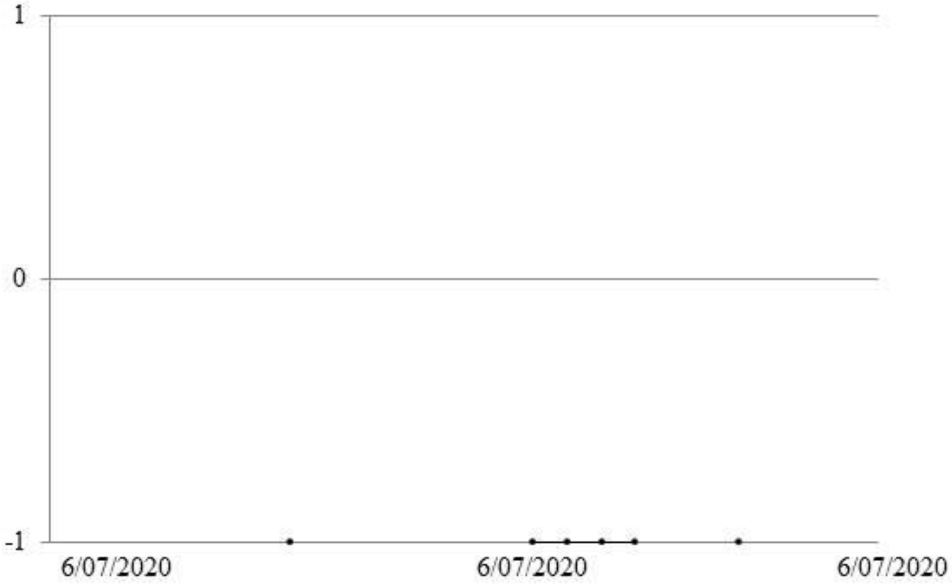
Hatchery male, 780mm FL

Delayed 12 days (99 hours); Passed

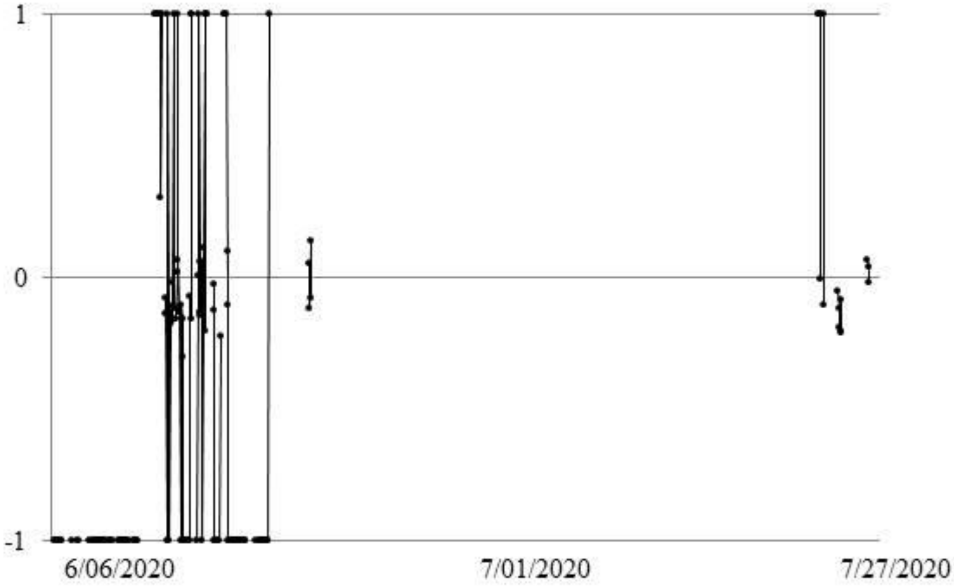
Eastern Focus



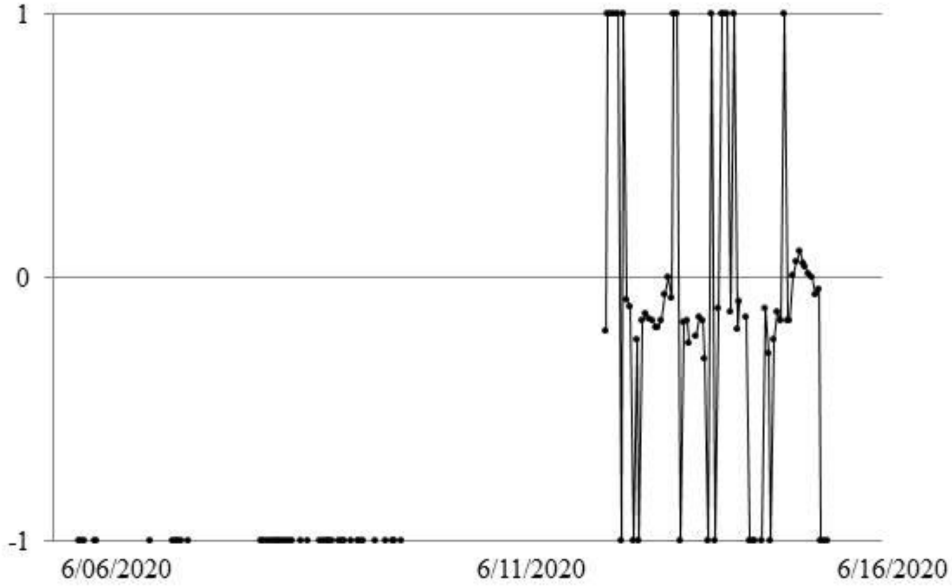
Atlantic salmon 2020-262
Hatchery male, 770mm FL
Delayed 1 day (6 hours); Passed
Eastern Exclusive



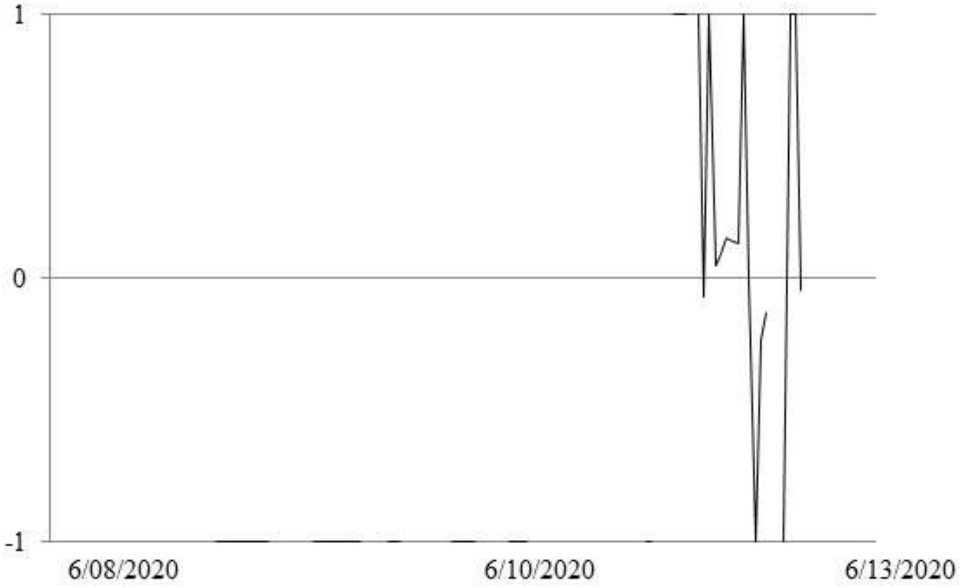
Atlantic salmon 2020-265
Hatchery female, 780mm FL
Delayed 52 days (196 hours); Did not pass
Extensive Searching



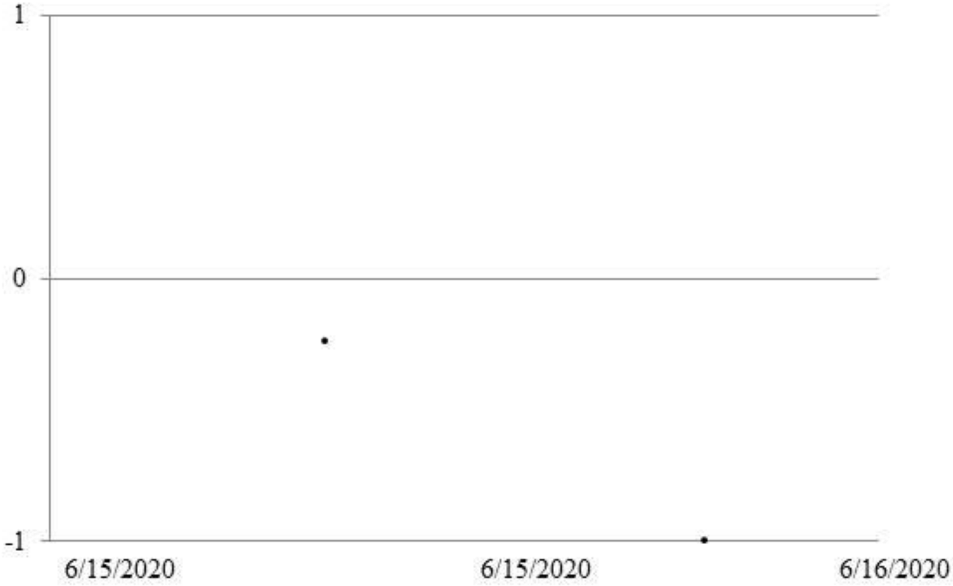
Atlantic salmon 2020-266
Hatchery male, 770mm FL
Delayed 10 days (110 hours); Passed
Eastern Focus



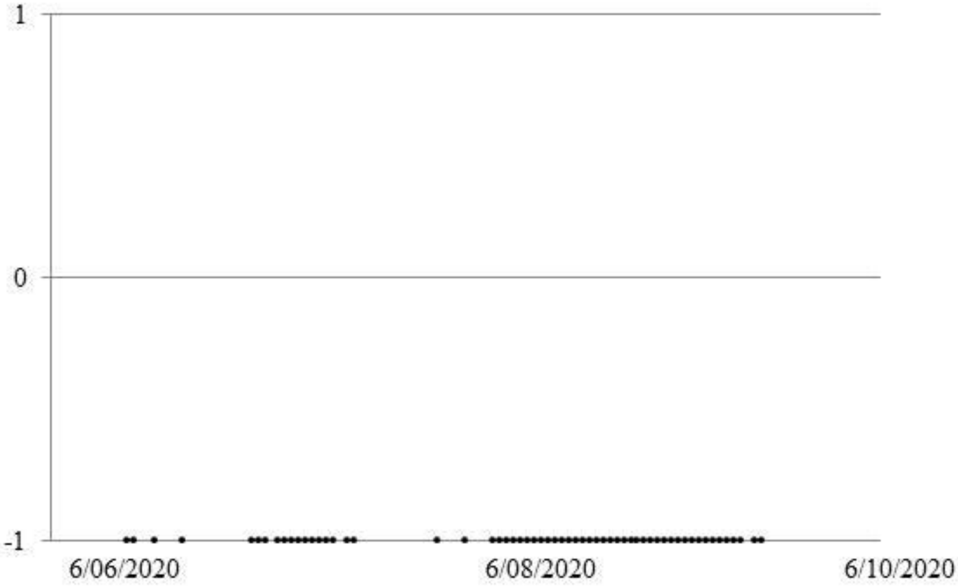
Atlantic salmon 2020-267
Hatchery male, 750mm FL
Delayed 5 days (64 hours); Passed
Western Focus



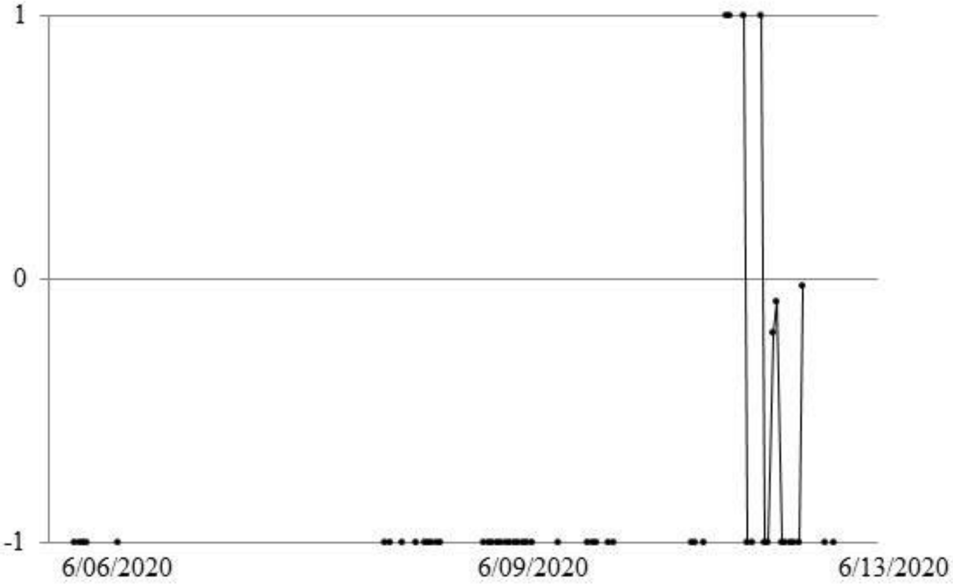
Atlantic salmon 2020-268
Hatchery male, 780mm FL
Delay uncertain (2 hours); Passed
Eastern Exclusive



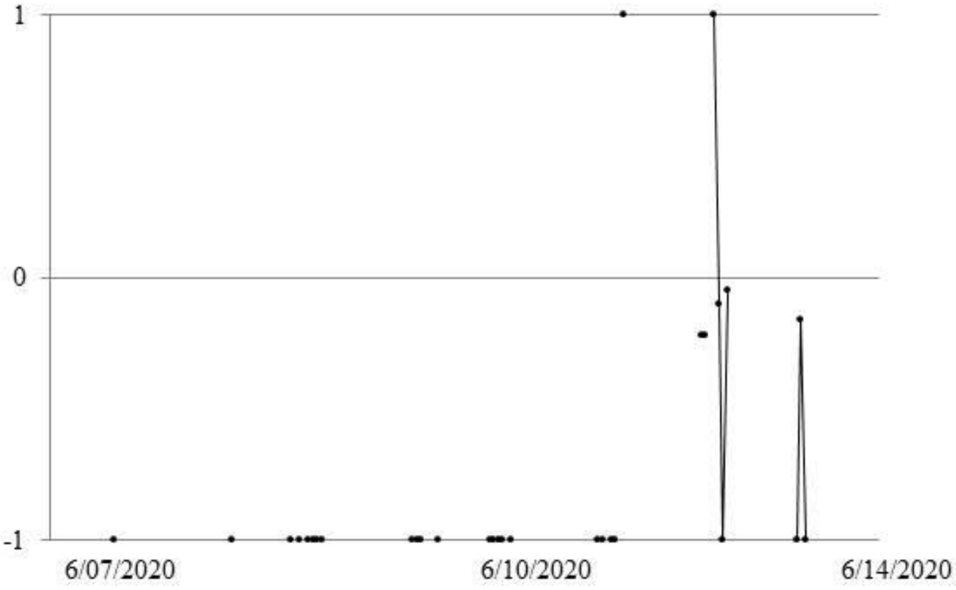
Atlantic salmon 2020-269
Hatchery male, 780mm FL
Delayed 4 days (59 hours); Passed
Eastern Exclusive



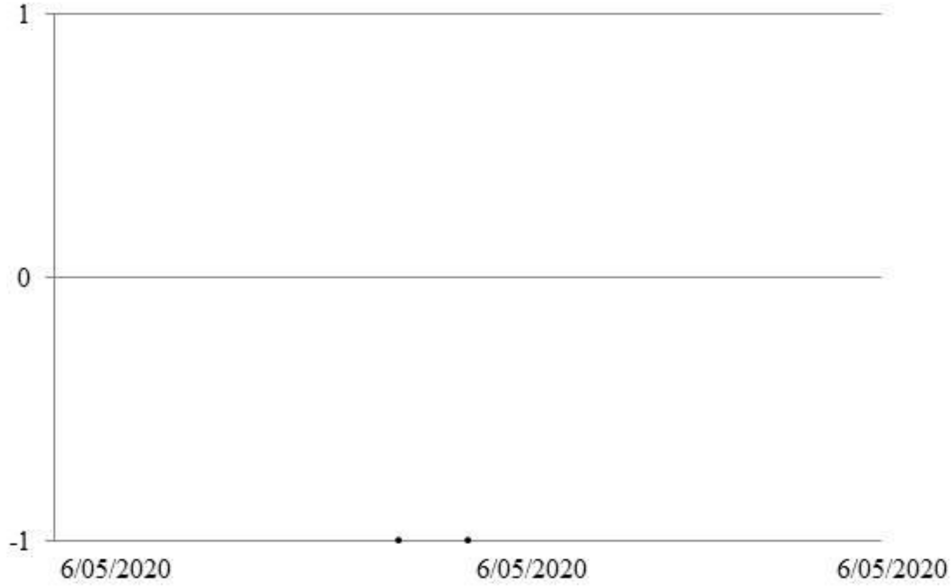
Atlantic salmon 2020-270
Hatchery male, 780mm FL
Delayed 7 days (53 hours); Passed
Eastern Focus



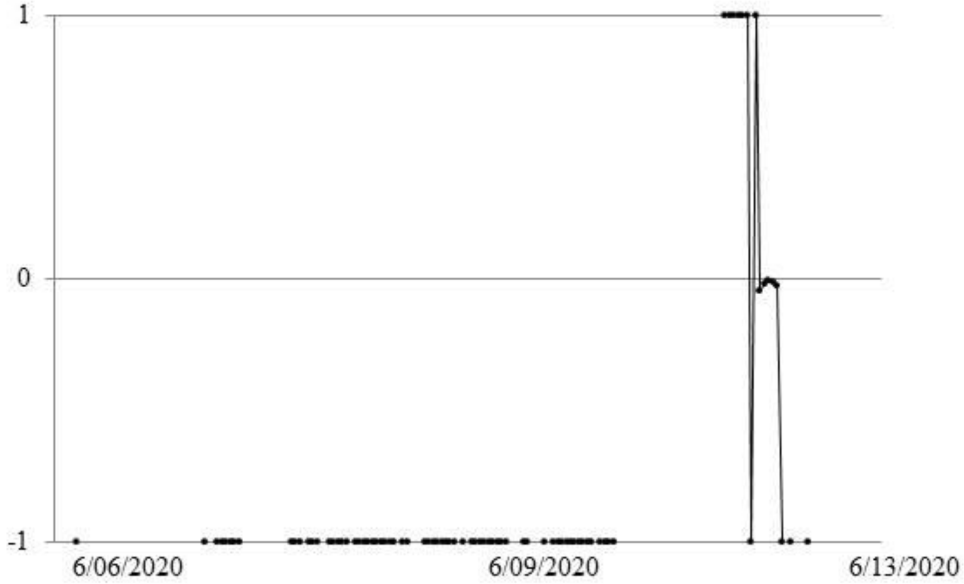
Atlantic salmon 2020-271
Hatchery female, 750mm FL
Delayed 7 days (31 hours); Passed
Eastern Focus



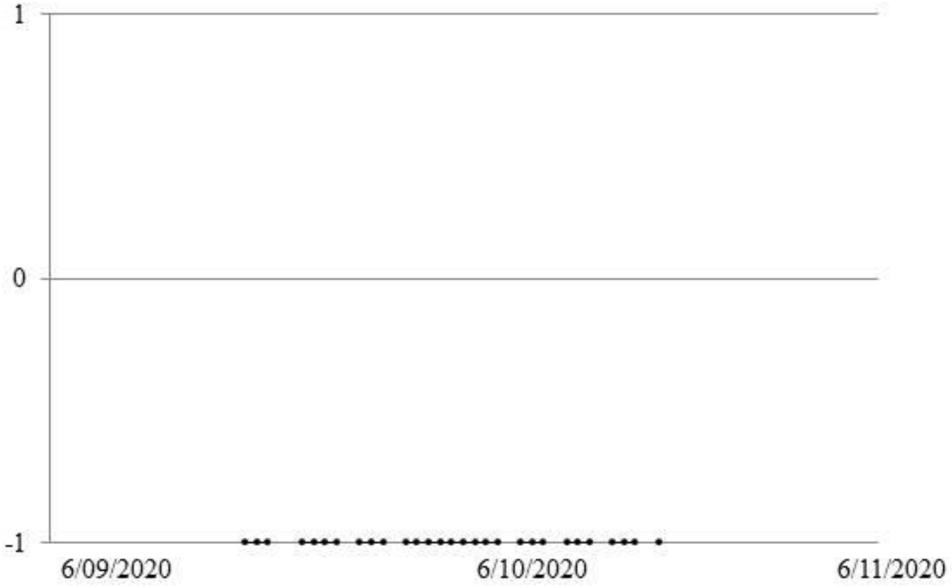
Atlantic salmon 2020-272
Hatchery male, 780mm FL
Delayed 1 day (2 hours); Passed
Eastern Exclusive



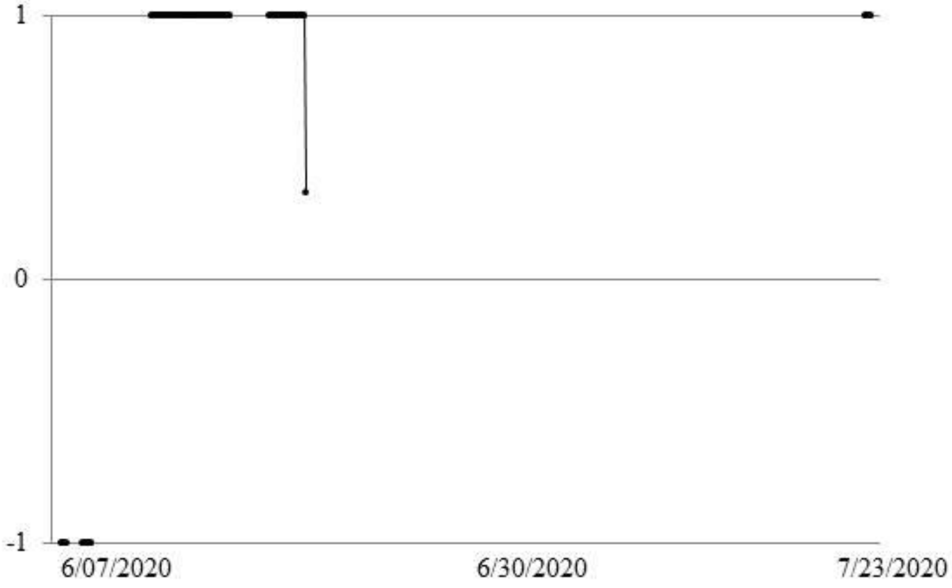
Atlantic salmon 2020-273
Hatchery female, 800mm FL
Delayed 7 days (82 hours); Passed
Eastern Focus



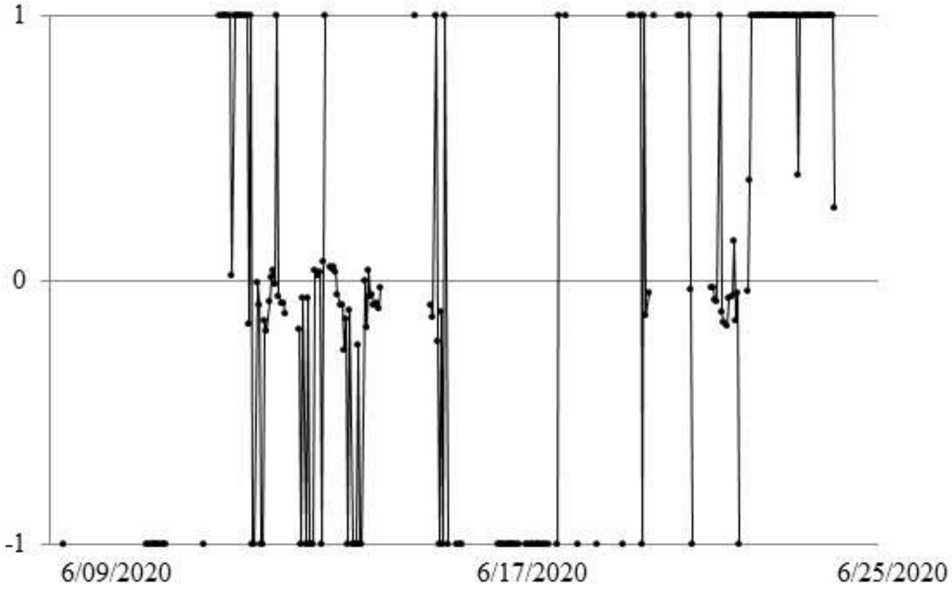
Atlantic salmon 2020-281
Hatchery female, 810mm FL
Delayed 2 days (29 hours); Passed
Eastern Exclusive



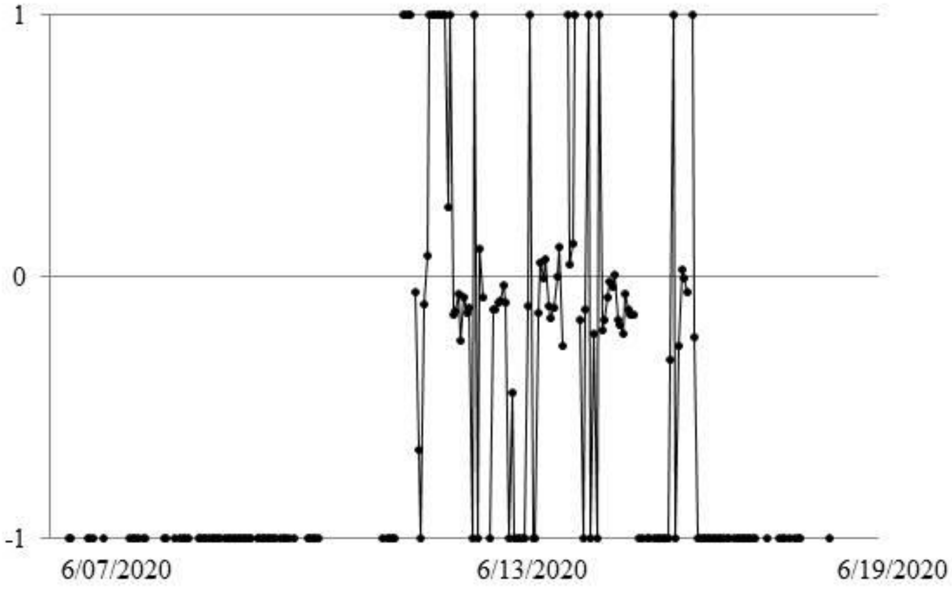
Atlantic salmon 2020-284
Wild male, 750mm FL
Delayed 46 days (178 hours); Did not pass
Western Focus



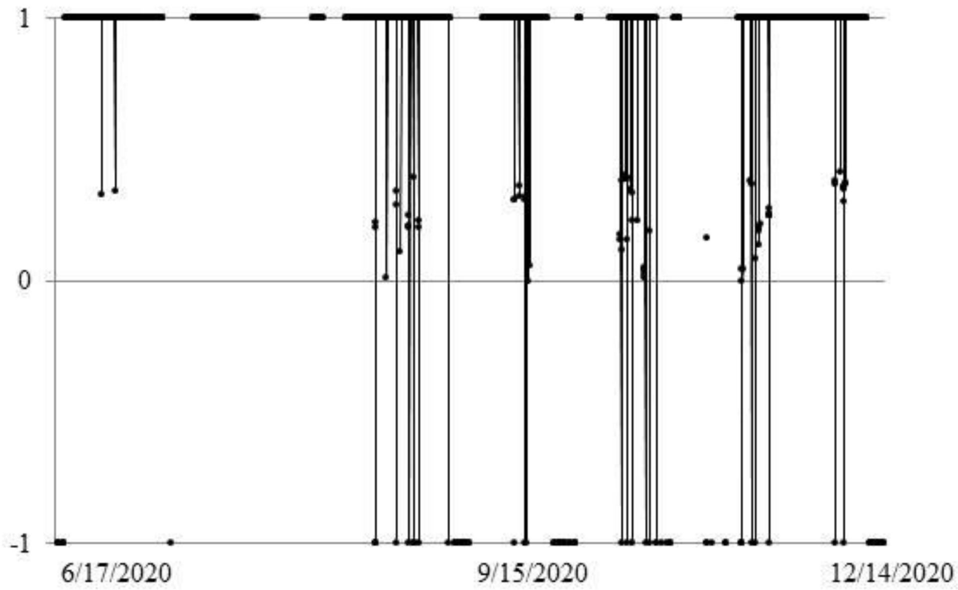
Atlantic salmon 2020-286
Wild male, 730mm FL
Delayed 16 days (195 hours); Did not pass
Extensive Searching



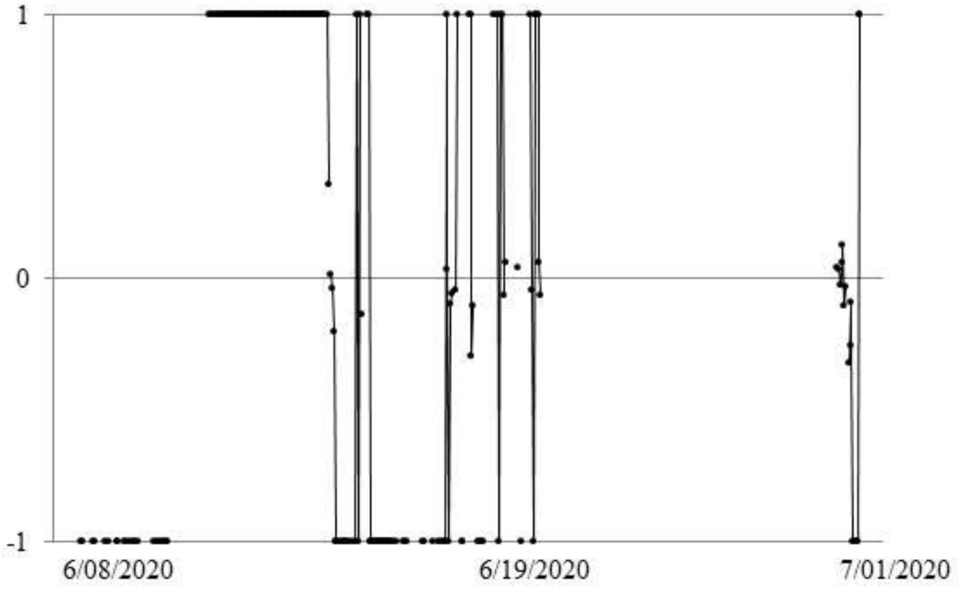
Atlantic salmon 2020-289
Wild female, 710mm FL
Delayed 13 days (195 hours); Did not pass
Eastern Focus



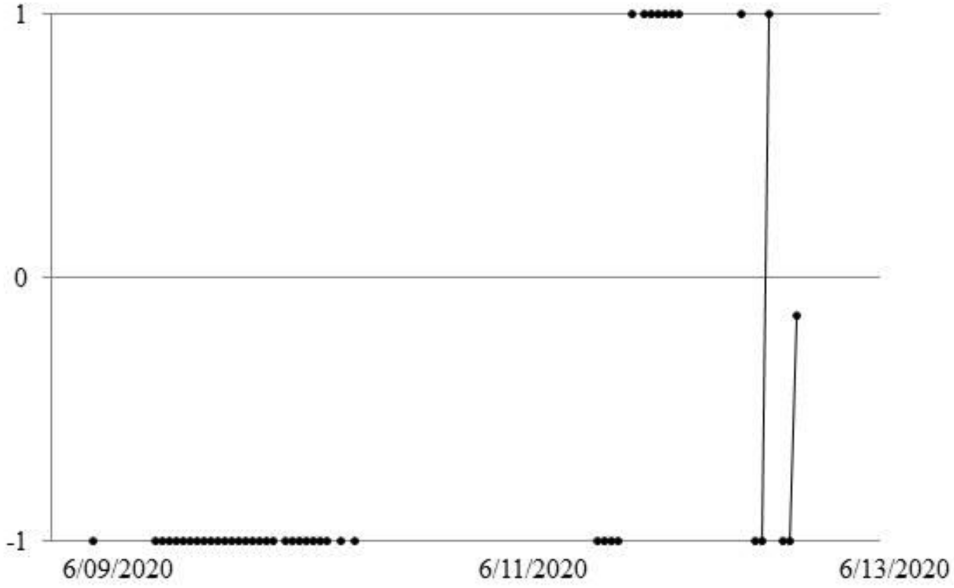
Atlantic salmon 2020-294
Wild male, 780mm FL
Delayed 180 days (2,153 hours); Did not pass
Western Focus



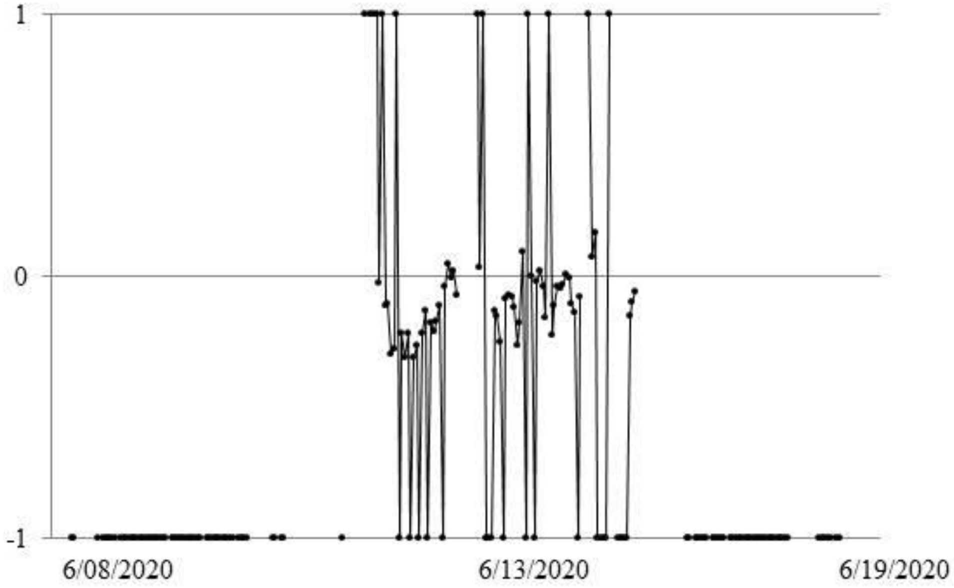
Atlantic salmon 2020-296
Hatchery female, 690mm FL
Delayed 24 days (201 hours); Passed
Extensive Searching



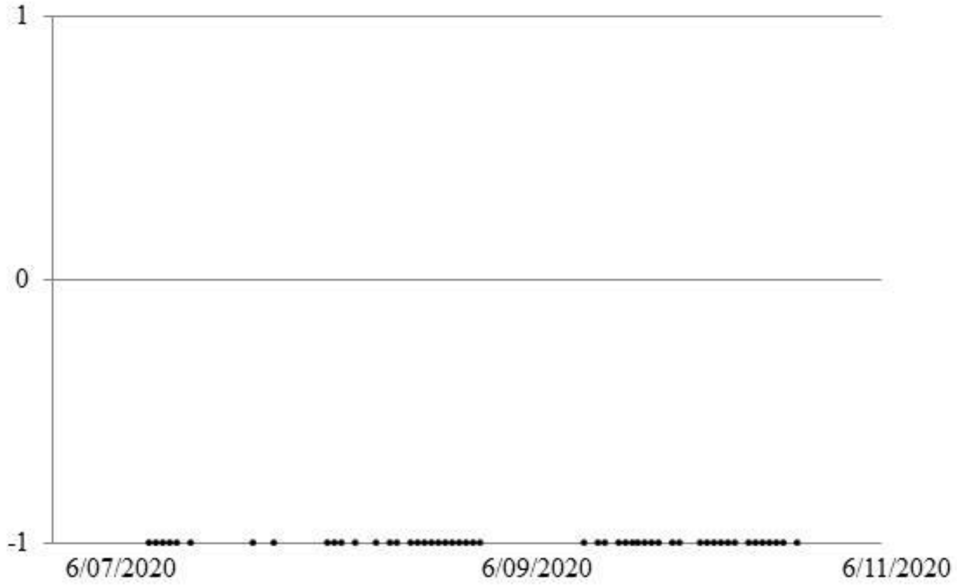
Atlantic salmon 2020-297
Hatchery male, 720mm FL
Delayed 4 days (46 hours); Passed
Eastern Focus



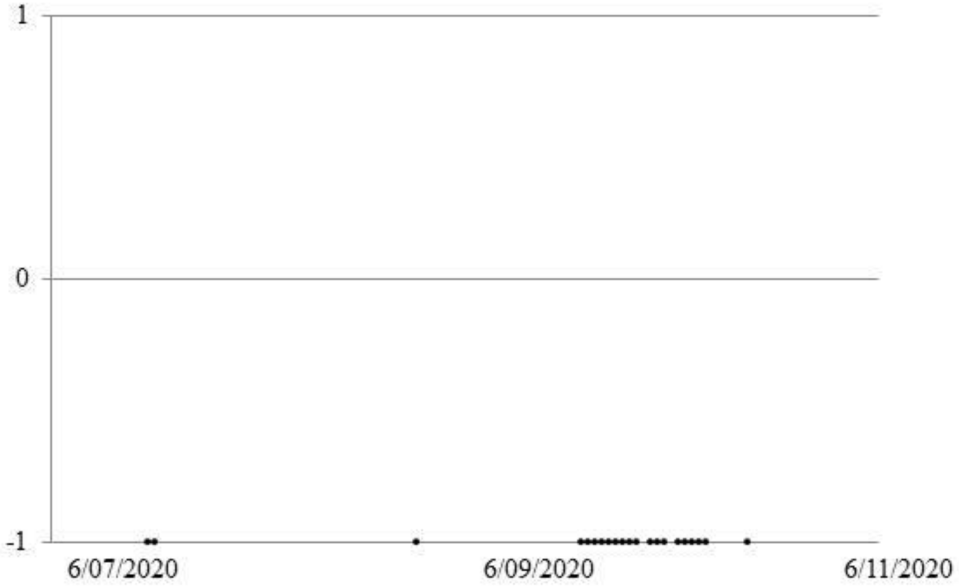
Atlantic salmon 2020-299
Hatchery male, 780mm FL
Delayed 11 days (179 hours); Did not pass
Eastern Focus



Atlantic salmon 2020-301
Hatchery female, 730mm FL
Delayed 5 days (51 hours); Passed
Eastern Exclusive



Atlantic salmon 2020-302
Wild male, 760mm FL
Delayed 5 days (21 hours); Passed
Eastern Exclusive

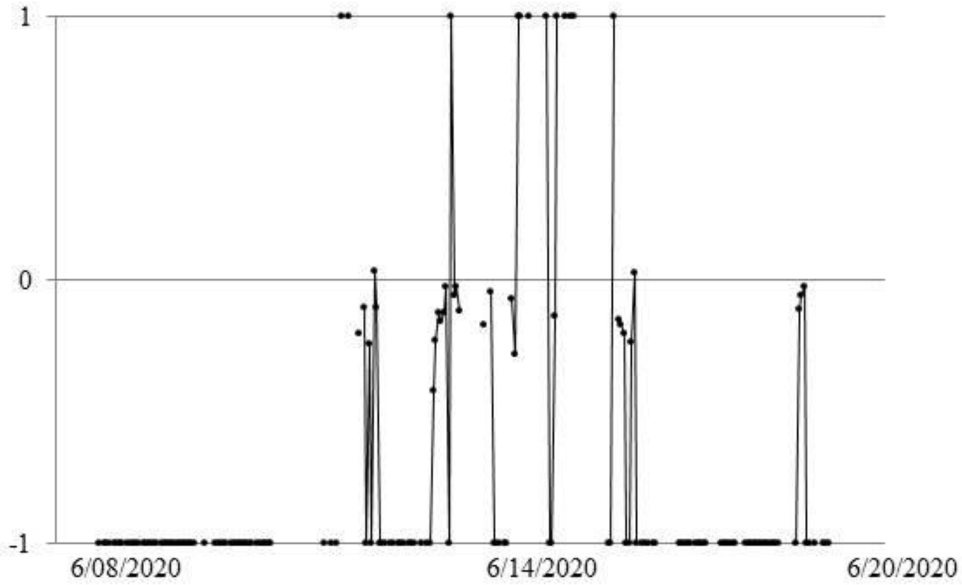


Atlantic salmon 2020-303

Wild female, 730mm FL

Delayed 12 days (165 hours); Did not pass

Eastern Focus

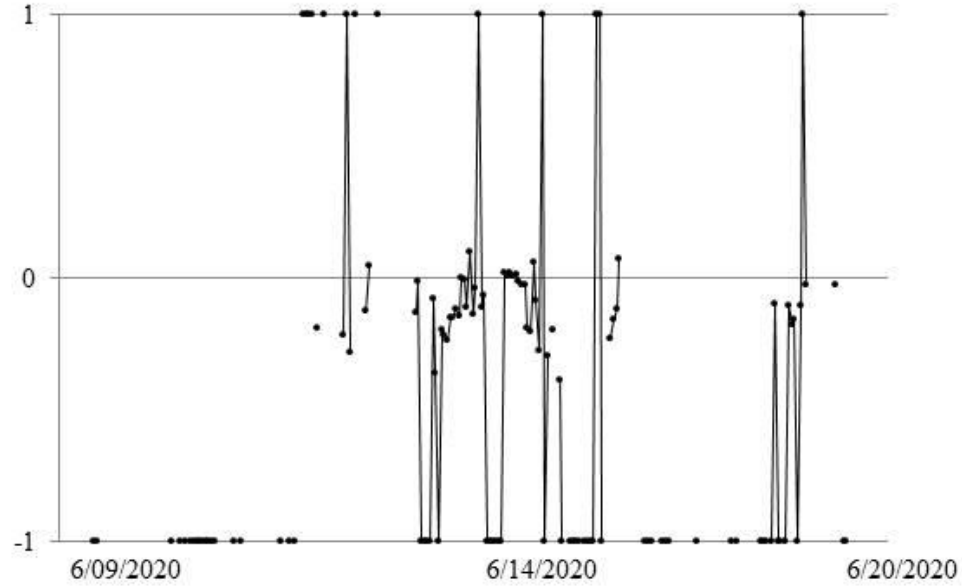


Atlantic salmon 2020-304

Hatchery female, 770mm FL

Delayed 11 days (124 hours); Did not pass

Extensive Searching

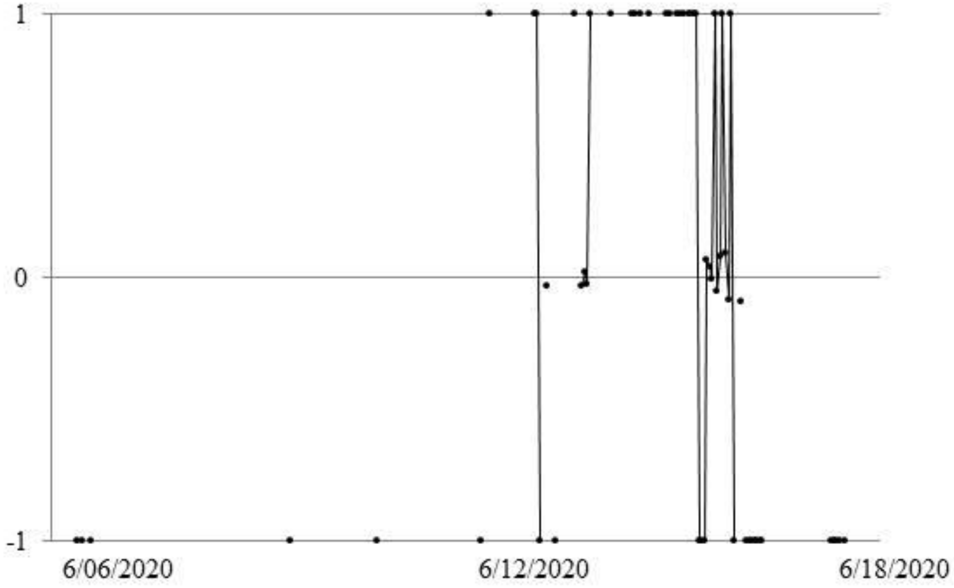


Atlantic salmon 2020-305

Hatchery male, 780mm FL

Delayed 12 days (58 hours); Passed

Extensive Searching

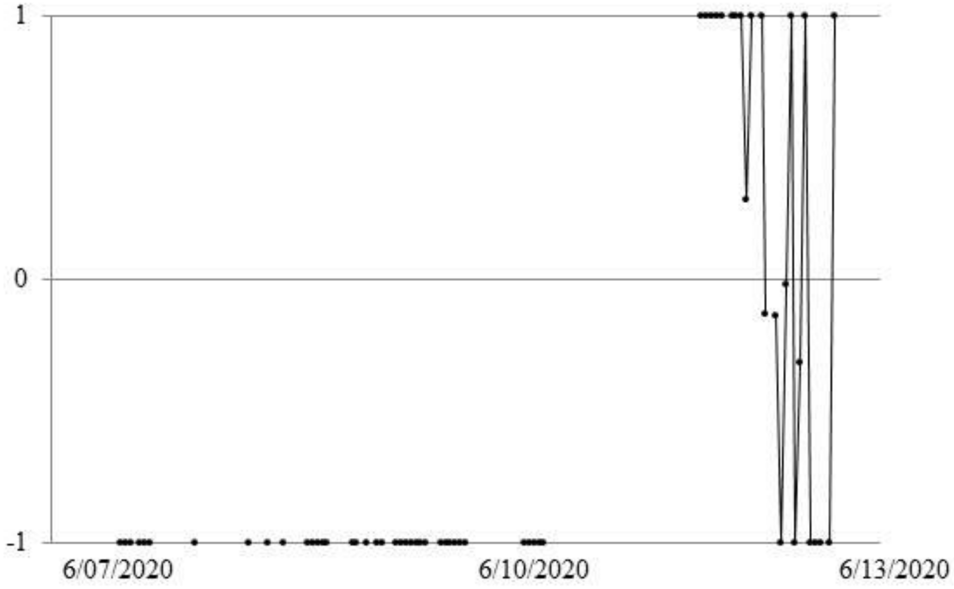


Atlantic salmon 2020-306

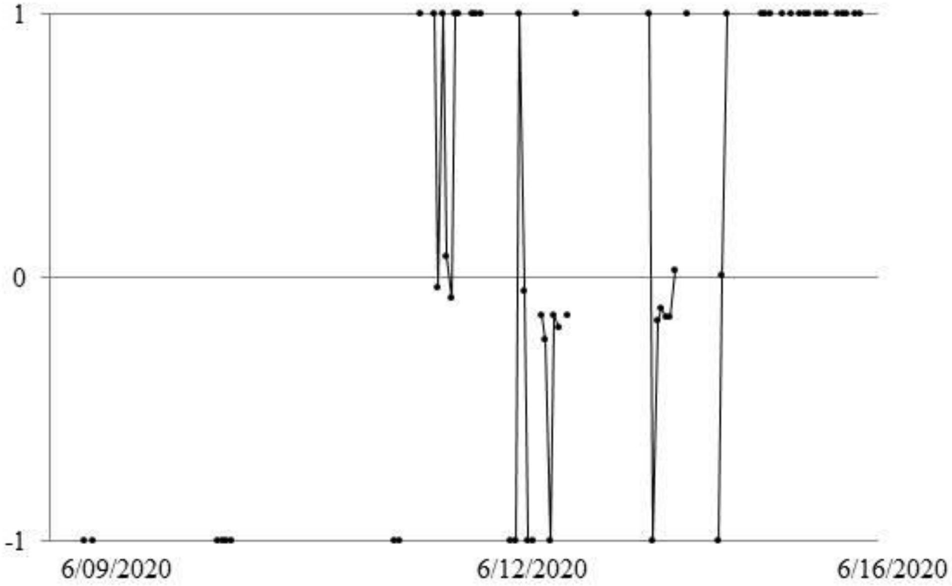
Wild female, 720mm FL

Delayed 6 days (62 hours); Passed

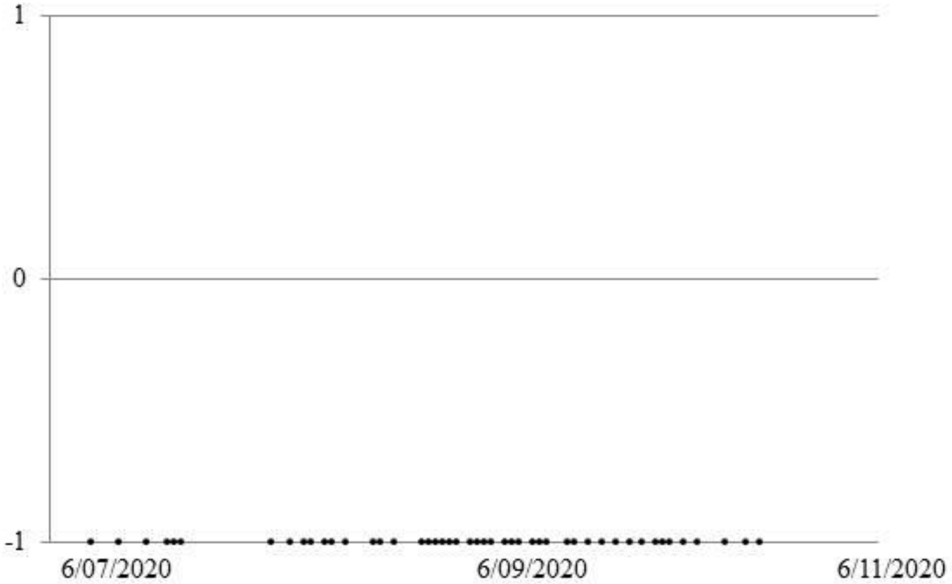
Eastern Focus



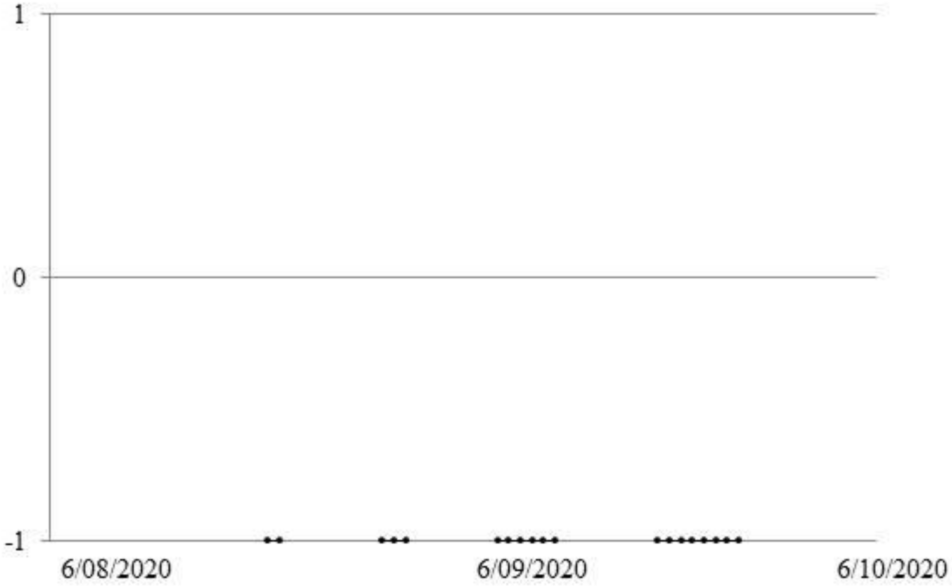
Atlantic salmon 2020-307
Hatchery male, 820mm FL
Delayed 9 days (59 hours); Did not pass
Extensive Searching



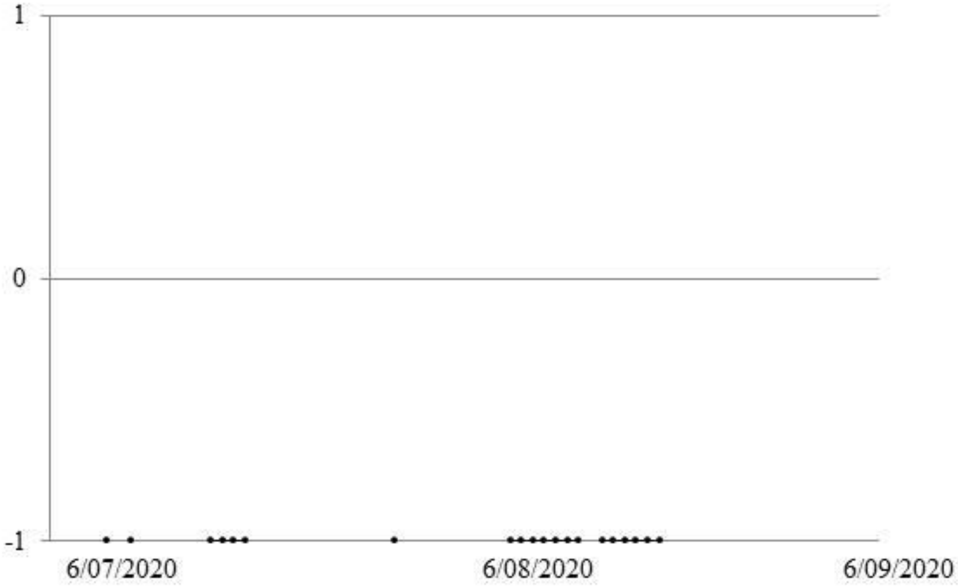
Atlantic salmon 2020-309
Wild female, 740mm FL
Delayed 4 days (47 hours); Passed
Eastern Exclusive



Atlantic salmon 2020-313
Hatchery female, 770mm FL
Delayed 3 days (19 hours); Passed
Eastern Exclusive



Atlantic salmon 2020-316
Hatchery female, 710mm FL
Delayed 2 days (20 hours); Passed
Eastern Exclusive

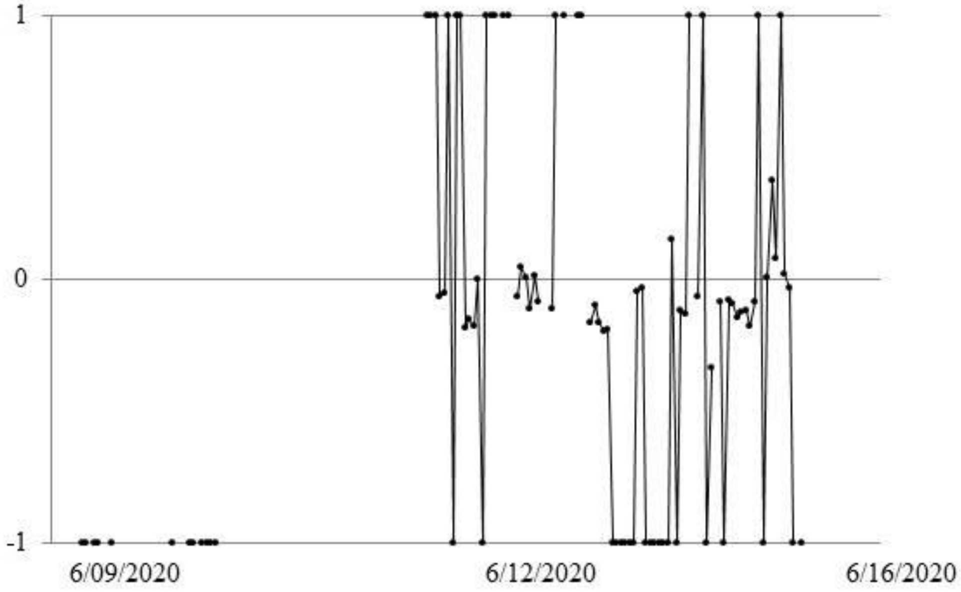


Atlantic salmon 2020-317

Hatchery female, 730mm FL

Delayed 7 days (89 hours); Passed

Extensive Searching

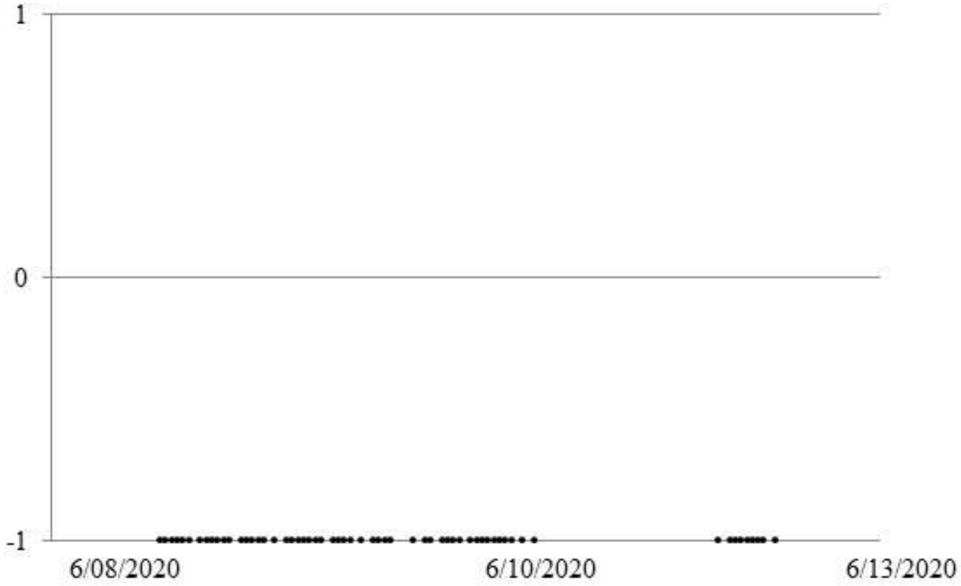


Atlantic salmon 2020-318

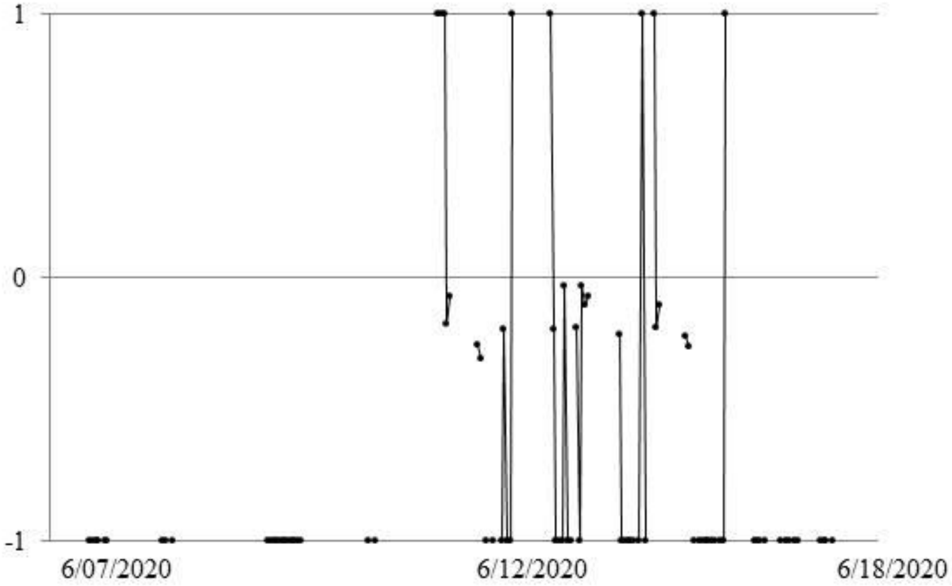
Hatchery female, 760mm FL

Delayed 5 days (60 hours); Passed

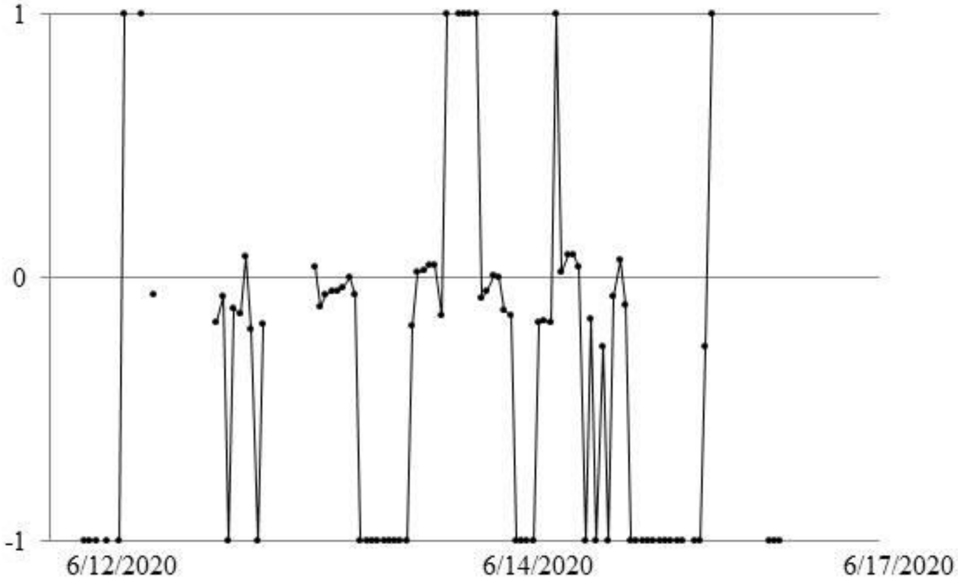
Eastern Exclusive



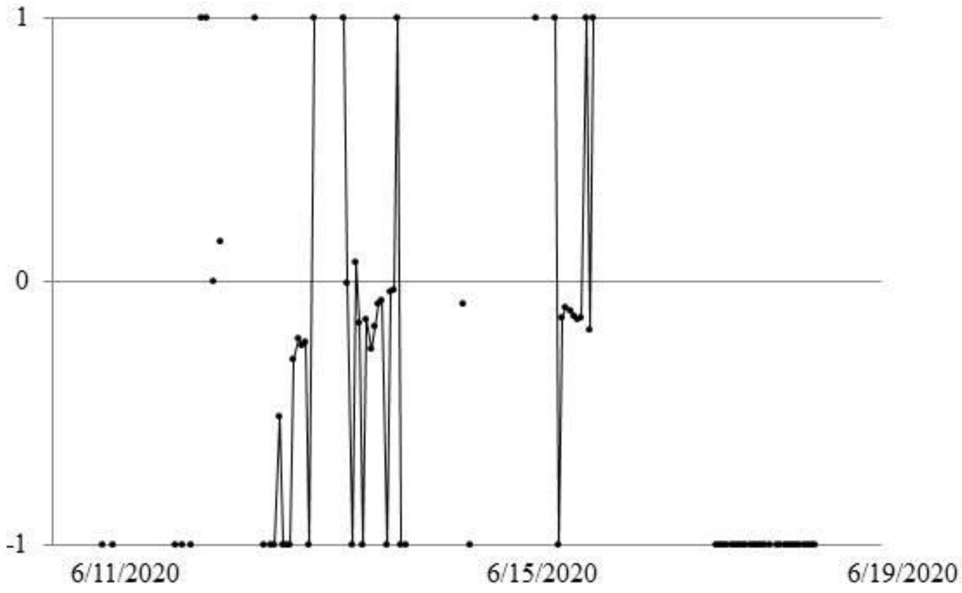
Atlantic salmon 2020-325
Hatchery female, 800mm FL
Delayed 11 days (87 hours); Passed
Eastern Focus



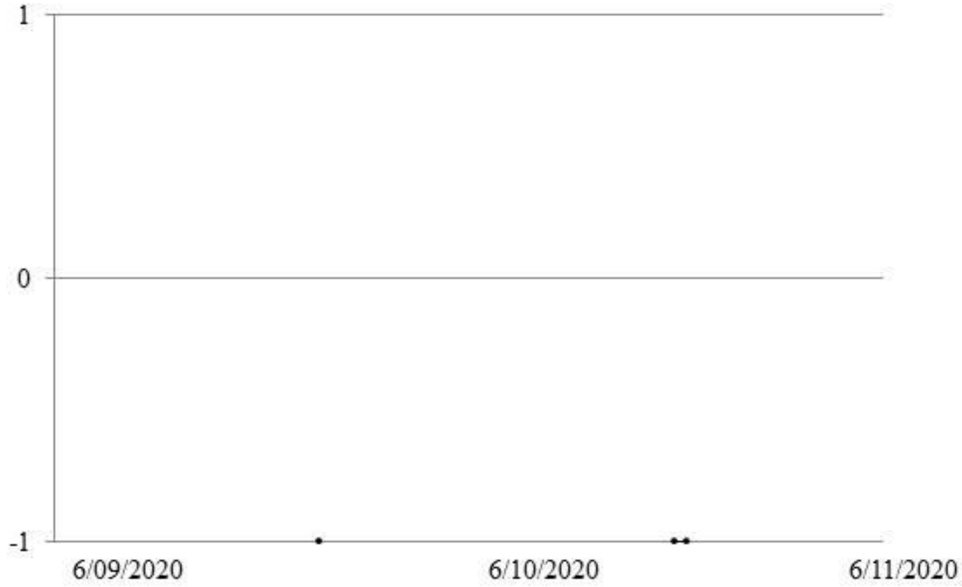
Atlantic salmon 2020-486
Hatchery male, 780mm FL
Delayed 5 days (88 hours); Passed
Extensive Searching



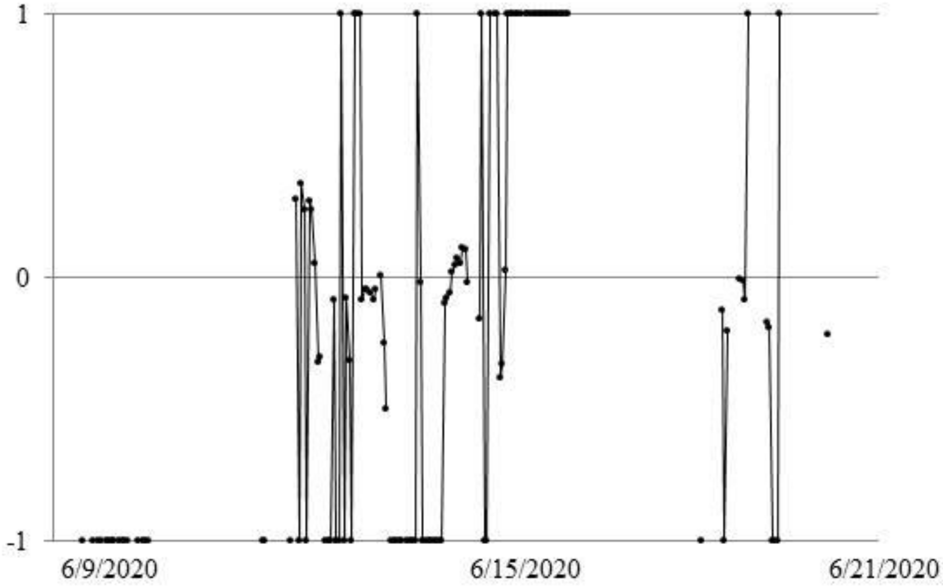
Atlantic salmon 2020-487
Hatchery female, 760mm FL
Delayed 8 days (80 hours); Passed
Eastern Focus



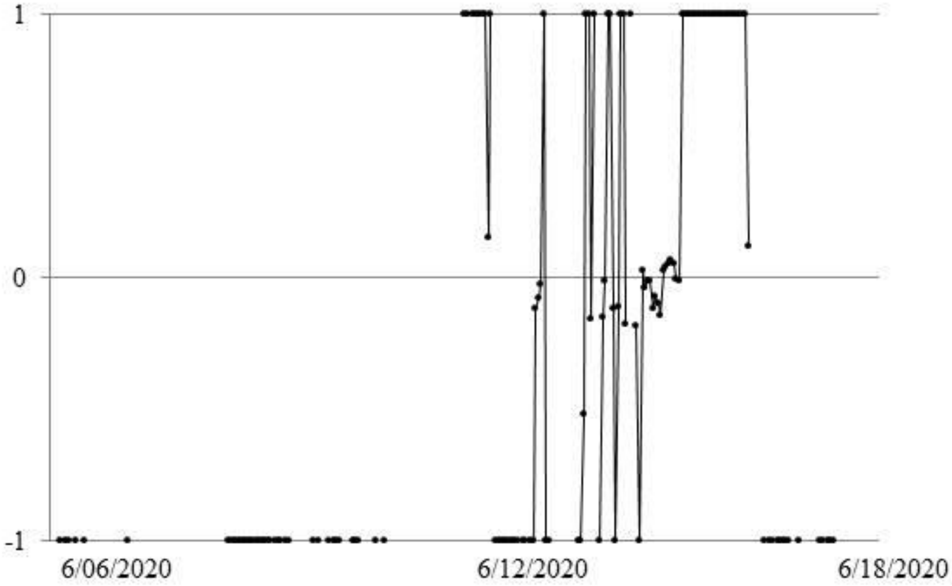
Atlantic salmon 2020-488
Hatchery female, 750mm FL
Delayed 2 days (3 hours); Passed
Eastern Exclusive



Atlantic salmon 2020-489
Hatchery male, 770mm FL
Delayed 12 days (129 hours); Did not pass
Extensive Searching



Atlantic salmon 2020-RECAP2
Unknown, 780mm FL
Delayed 12 days (144 hours); Passed
Extensive Searching



BIOGRAPHY OF THE AUTHOR

Erin Peterson was born in Bellevue, Washington on February 21, 1992. She was raised in the Seattle area and graduated high school in 2010. She attended Oregon State University and graduated in 2014 with a Bachelor’s degree in Fisheries and Wildlife. She then entered the Wildlife and Fisheries graduate program at South Dakota State University and graduated with a Master’s degree in 2017. She began a Ph.D. program at the University of Maine in the fall of 2017. Erin works as a Fish Biologist for the Washington Department of Fish and Wildlife in Ridgefield, Washington. Erin is a candidate for the Doctor of Philosophy degree in Wildlife Ecology from the University of Maine in May 2022.