Use of a Picket Weir and Passive Integrated Transponder Tags to Assess the Landlocked Atlantic Salmon Spawning Run in the Crooked River, Maine

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Abstract

Landlocked Atlantic Salmon (*Salmo salar*) in Sebago Lake comprise one of the most renowned and historically important fisheries in Maine. To improve sampling of this key population, a portable picket weir was utilized in 2018. Count, age, and growth parameters were collected from 1,845 fish, with an additional subset of 488 fish fitted with Passive Integrated Transponder (PIT) tags to assess behavioral movement and timing. Total run size was comparable to low estimates in other recent studies and higher than comparable counts from the 1970s and 1980s. Salmon quality was fair overall but a concerning number of fish were in poor condition. It is likely that predation, competition, and forage conditions in Sebago Lake have had an adverse impact on salmon quality and survival in recent years. Salmon movement was highly variable. Fish were capable of traveling great distances in short periods of time, particularly later in the season, and most movement happened at night. Numbers of salmon passing various antenna locations were comparable to known spawning habitat use observed during an earlier redd survey. The majority of salmon departed the Crooked River around mid-November, though some younger and less-fit males remained later into the season. Very few repeat spawners were seen in 2019 and 2020, suggesting skipped spawning and stress on Sebago Lake salmon. Efforts to improve conditions in the lake and to conserve spawning habitat in the Crooked River will be critical to long-term restoration of salmon quality and the continued strong contribution from wild fish to the overall fishery.

Introduction

Landlocked Atlantic Salmon (*Salmo salar*) have a rich biological, cultural, and economic history in Maine. They have long been regarded as a high-quality gamefish and are currently one of the most sought-after species by both resident and non-resident anglers (Responsive Management 2016, Southwick Assoc. 2012). Numerous towns, sporting camps, and guiding services were founded due to strong Landlocked Salmon fisheries, and Maine's recreational economy is still supported by anglers in pursuit of this species. In 1969, Landlocked Salmon were designated the State Fish by the Maine Legislature, further cementing their legacy as a key symbol of the region.

Arising as a distinct life history form of the sea-run Atlantic Salmon, Landlocked Salmon (hereafter "salmon") spend their entire lives in freshwater. Salmon naturally occur in four river basins in Maine (Kendall 1935; Boucher and Warner 2006) but have since been introduced in numerous others, including over 300 lakes and 50 rivers and streams. One of the original four salmon drainages is that of the Presumpscot River, with Sebago Lake (30,513 acres; Cumberland County) serving as the primary source of adult habitat for many of these native fish. Sebago Lake has historically produced a high-quality salmon fishery, though some notable periods of declines in quality have occurred. Heavy DDT use in the 1960s and the introduction of Lake Trout (*Salvelinus namaycush*) in the 1970s both impacted populations of a key prey fish for salmon, Rainbow Smelt (*Osmerus mordax*). Declines in smelt availability and interspecific competition with Lake Trout have periodically led to decreases in salmon numbers, though the salmon population has been able to rebound once a strong forage base of smelt was re-established.

Along with food availability, spawning and nursery habitat represent other key limiting factors for a healthy salmon population. For Sebago Lake salmon, nearly all spawning and nursery habitat is found in the largest tributary to the lake, the Crooked River. The Crooked River flows over 60 miles south from Songo Pond in Albany to its confluence with the Songo River, just north of Sebago Lake, and represents nearly 40% of total surface inflow to the lake (Holme 2019). For most of its length, the river flows over glacial outwash sand and gravel, and provides some reaches of ideal substrate for spawning salmonids and redd excavation. Water quality is also suitable for salmon and provides year-round nursery habitat for juvenile salmon. Numerous aquifers feed the river, with between ten to fifty gallons per minute of water added to surficial flows from seeps and upwellings (Williams et al. 1987; Pellerin and Pierce 2015). These aquifers contribute to recharge and base flows and, along with relatively cooler tributaries, create areas of cold water refugia for species such as salmon and Brook Trout (*Salvelinus fontinalis*) during warmer months. Though not always the case historically, today the Crooked River is a highly connected system, with limited impediments to movement for spawning fish. Virtually the whole river is accessible to salmon, and flows are unregulated in the main stem (with drawdowns from some tributary lakes being the only exception). During the fall spawning season, salmon utilize nearly the entire length of the Crooked River for spawning. A 2014 spawning survey found over 2000 redds, with more than 30% occurring over 40 miles from the mouth of the river (Pellerin and Pierce 2015). In the early spring when salmon eggs hatch, the cool, clean water of the Crooked River provides nursery habitat for juvenile fish. These juveniles typically remain in the river for two years before dropping down into Sebago Lake.

Due to the high quantity and quality of habitat in the Crooked River and resulting production capacity, the salmon population in Sebago Lake now consists of around 80% wild fish (James Pellerin, Fisheries Resource Supervisor, personal communication). Limited supplemental stocking still occurs annually, partially to maintain the availability of eggs for hatchery production. However, it is likely that the Crooked River has the potential to nearly, if not completely, sustain the salmon population in the lake. In addition to supporting one of the most popular lacustrine fisheries in the region, the Crooked River also represents an important riverine fishery for recreational anglers. Again, this fishery consists primarily of wild fish, and is dependent on the habitat that the river provides. It is also worth noting that while the Crooked River today contains extensive habitat for salmonids, it has taken decades of efforts in conservation and connectivity to restore the river to its current quality. While a full history of these efforts by the Department and partners, as well as past management challenges, is beyond the scope of this report, they are detailed in Pellerin and Pierce (2015).

Given the importance of the Crooked River to sustaining one of the most renowned salmon fisheries in Maine, it is imperative to periodically assess the population of spawning salmon in the river. Historical data is limited but includes a fish trap at the former Bolsters Mills Dam, just over 22 miles upstream from the river mouth. This fish trap was operated by biologists from the Maine Department of Inland Fisheries and Wildlife (MDIFW or the Department) for a 13-year period, from 1974-1986. At the start of operations, volitional upstream passage had only recently been established just downstream of the fish trap in 1972, at Scribners Mills, and the salmon run was still establishing homing tendencies to further upstream areas. Nevertheless, the run increased to a high of 443 salmon (of which 433 were wild) from May-November 1984. Since the last year of fish trap operations, logistical and budgetary concerns have made large-scale sampling of the Crooked River salmon run difficult. Indirect run assessment via the redd survey in 2014 and detections of wild salmon in creel surveys and redd counts indicates that the spawning salmon population had substantially increased since the 1980s, with estimates of between 2,300-4,600 adult fish in the river. These estimates did not involve any assessment of the individual fish that comprised the spawning run and resulted in limited data on salmon quality and behavior. Direct contact angler surveys are similarly challenging. The recreational fishery is predominantly a seasonal (spring and fall) fishery, spread out over a large geographical area, and only limited data can be gained through creel census. However, the fabrication of a portable picket weir in 2008 by fisheries staff from the Moosehead Lake Region greatly increased the ability of the Department to assess salmonid spawning runs. As a result, fisheries staff in the Sebago Lake Region invested in a weir specifically to assess the Crooked River salmon population.

Using this picket weir, the spawning run of wild salmon was sampled in the Crooked River in 2018. Overall goals were to assess the current status of the salmon run, including abundance, contributions from wild/hatchery fish, and age and growth parameters of spawning adults dwelling in Sebago Lake. Additionally, movement of salmon within the Crooked River was assessed, to expand knowledge of salmon behavior and timing of key events during the spawning season. To achieve these goals, salmon were trapped moving upstream to spawn in the Crooked River. Primary objectives were threefold: first, data were collected on all salmon including origin (wild or hatchery) to assess the growth, condition, and status of wild salmon in the Sebago Lake fishery. Second, adult spawners were counted to assess both current run size and, through comparisons with other recent data, the validity of using redd counts to estimate run size. Finally, Passive Integrated Transponder (PIT) tags were implanted in a subset of spawning salmon to track movement of adults throughout the system and gain insight into salmon behavior. By collecting these data on count, size, condition, age, and behavior, the status of the salmon spawning run in the Crooked River was assessed, and by extension the health of the overall salmon population in Sebago Lake. Furthermore, we aimed to make comparisons to historical data collected at both the Bolsters Mills fish trap as well as the spawning run in the Jordan River, another tributary to Sebago Lake.

Methods

Study Location

The location for the picket weir was chosen based on its position low in the Crooked River drainage, its ease of access, and its hydrological characteristics. The weir was installed approximately 5.3 river miles upstream from the mouth of the river, at a natural riffle between two deep bend pools (Figure 1).

Figure 1. Map of the Crooked River drainage within Maine (inset) and locations of the picket weir (red arrow) and PIT tag antenna arrays (red arrow, green arrows).

The relatively shallow water over the riffle and narrower river width provided for easier installation, maintenance, monitoring, and removal of project structures. The primarily sand, gravel, and cobble substrate allowed for the weir to be embedded securely in the river bottom, while simultaneously providing a relatively level area devoid of large boulders. Additionally, previous surveys indicated that over 97% of observed redds were located upstream of the chosen weir location (Pellerin and Pierce 2015), suggesting that nearly the complete fall spawning run would pass this point in the river.

Portable Picket Weir

The picket weir (Figure 2) used for this project was fabricated in 2014, principally based on designs from Department biologists. Primary weir components are made of steel, and consist of five main parts: tripods, blocking panels, entrance panels, collection box, and funnel. For a detailed summary of weir fabrication, components, and setup, see Obrey and Bagley (2018). Blocking panels, supported by tripods (6’ x 2 1/2” square tubing), prevent upstream passage of spawning fish. These blocking panels consist of channeled steel (6’ x 3” x 3/4”), with 1/2” round steel pipes (outside diameter 0.84”) of varying lengths (5’, 6’, or 7’) fed through to form the vertical “picket” structure of the weir. Pipe lengths are variable to allow for consistent weir height over changing river depth and substrate type. Pipes are also installed in an angled fashion, so the lower end of each pipe meets the river substrate further upstream than the upper end. Entrance panels placed centrally in the weir structure allow fish to progress upstream toward the funnel. This component has a large entrance but small exit, which allows fish to pass in only one direction. Once through the funnel, fish stage in the collection box (16’ long x 4’ wide) until Department biologists remove them for data collection. Similar to blocking panels, the collection box consists of panels of angled steel (8’ x 2” x 2”) with ½” pipes (5’, 6’, or 7’) placed vertically to form the sides of the box. In this study, the box was placed as near to the river thalweg as possible. Two overlapping plywood boards were also locked into place over the collection box, preventing access by predators or unauthorized individuals. The entrance was later encased in ½” plywood after some salmon were found on top of these collection box top panels. It is unknown how the salmon ended up on top of the weir collection box, as this had never occurred previously at this site nor was it associated with any high flow events. The plywood encasement was added as a precaution in case salmon were jumping the front face of the weir instead of utilizing the funnel under certain flow conditions. Surveillance cameras were also added. However, no additional salmon were ever found on top of the collection box.

Figure 2. Upstream view of the operational picket weir. Collection box is central and floating panels are visible in the foreground.

A variety of modifications were made to the weir to account for some aspects of fall stream flows in the Crooked River. At two locations, one on each side of the collection box, steel pipes were used and topped with a hinged, floating panel structure (Figure 2). Following designs from Obrey and Bagley (2018), panels consisted of 1” diameter PVC tubing, spaced similarly to steel pipes in blocking panels and within a wood frame (4’ x 3’), backed by foam blocks. These panels floated on the river’s surface downstream of the weir, preventing upstream access by salmon but acting as a safety valve for the passage of water during extreme flow events. Additionally, rigid mesh (1/2” x 1/2” stainless steel hardware cloth) was placed between the edges and top of the floating panel, to prevent salmon from jumping upstream through openings in the weir. At high flows salmon may have been capable of jumping through these openings back downstream, but any fish that did so would have had to first be captured moving upstream through the weir. Regardless, without panels to relieve pressure, leaves, sticks, and other detritus can build up on the weir, essentially forming a dam and increasing the likelihood of weir failure or bank erosion. The weir was also secured against high water pressure using multiple 5/16” galvanized steel cables wrapped around stout trees on the banks.

High seasonal flows and steep, sandy banks also necessitated further additions. Rocks and sandbags were used as armoring to prevent scour below and around the edges of the weir, and to prevent fish passage through potential scour openings. A walkway and work platform were also constructed, from which Department biologists could access the collection box and gather data (Figure 3). A prefabricated aluminum walkway descended from the riverbank to a ¾” plywood platform built between 4” x 4” x 12’ posts, supported by cross braces and covered with a similar plywood roof. From this work platform, biologists could enter the collection box via portable ladder to access trapped fish. Due to the height of the work platform, an 8” PVC pipe was employed to pass analyzed fish safely down to the river below, upstream of the weir. The tube emptied into a temporary holding pen, where anesthetized fish could recover without being swept downstream against the weir structure (Figure 4). The holding pen was built with an open upstream end, allowing fish to volitionally leave when recovered. Additionally, monitoring of the substrate of the recovery box provided notification of any expelled PIT tags.

Figure 3. Work platform and access walkway descending from the riverbank to the weir collection box.

Figure 4. Upstream view of PVC pipe and recovery pen for processed salmon.

Data Collection

The weir was installed on August 29, 2018, during low summer flows and before the fall salmon run typically begins. Department staff from the Warden Service and nearby hatcheries, as well as local volunteers from Trout Unlimited, were instrumental in efficient setup and maintenance of the weir. Following installation and for the duration of the project, the weir and collection box were checked at least three times a week, beginning August 31. At least two individuals tended the weir each visit. All debris was cleared from the weir structure at each tending, with more thorough cleaning necessitated during leaf drop. Water temperature and gauge height were also recorded with each visit. Any fish in the collection box were removed using a dipnet and passed to a 10-gallon tub of water and anaesthetic on the work platform. For the majority of salmon collected, sex, fin clips, and injuries were noted and fish were immediately passed upstream. A random subset of salmon (37.5%) were more thoroughly analyzed, with total length and weight measurements and scale samples for aging taken as well. These fish also received an upper caudal mark. Due to risk of thermal stress and one early mortality, more intensive data collection efforts did not begin until water temperatures fell below 62.6°F (17°C).

The weir was operated for two months, with removal occurring on October 29. High flows and some collapsing banks around one end of the weir necessitated immediate removal to prevent severe bank erosion. Despite the emergency removal, Bolsters Mills fish trap data and data from this sampling indicate the fall salmon run typically peaks in the second week of October (Pellerin and Pierce 2015), suggesting that most of the fall run was likely captured by weir operations.

PIT Tags

To evaluate movement of spawning salmon in the Crooked River, an additional subset of the 37.5% of salmon identified above were fitted with PIT tags for tracking of spawning movements. Tagging did not begin until water temperatures dropped below 62.6°F (17°C) to avoid unnecessary thermal stress on fish, with the first salmon PIT tagged on September 12. Following a brief hiatus due to warmer water temperatures, tagging resumed on September 21 and continued for the duration of weir operations. After tagging began, a subset of all salmon caught in the weir collection box were tagged at each visit, proceeding until a minimum of 100 salmon or all fish, whichever was less, were tagged in a given week. The intent was to tag a representative sample of salmon for the entire duration of the run and to assess if there was any correlation between run timing and distance traveled. Tagging continued until the removal of the weir structure, with the last salmon PIT tagged on October 29.

Tagged salmon were implanted with 23 mm HDX+ PIT tags from Oregon RFID. Prior to tagging salmon, a brief retention test was conducted using fall yearling Brown Trout (*Salmo* trutta) at the New Gloucester State Fish Hatchery using 3 tag locations: body cavity, dorsal sinus, and musculature of the pelvic girdle. Tag retention and surgical wounds were checked after both one and two weeks for 20 tagged fish. Tag retention was excellent for the same 23 mm size PIT tags (unpublished data), with only a single tag loss at the pelvic girdle site after two weeks, providing confidence that salmon would similarly retain tags. For male salmon, a small (about 5-10 mm) incision was made in the lateral abdominal cavity and the tags were placed internally. Surgical glue was used to seal the incision. For females, risk of tag loss with egg expulsion at spawning meant that tags could not be placed in the body cavity. Tags were instead positioned in the retractor ischii muscle, between the pelvic fins. This tag location was chosen over the dorsal sinus to minimize risk of accidental consumption by Sebago Lake anglers harvesting tagged salmon. Use of a PIT tag injector and needle were necessary to achieve the correct shallow angle of entry, and to minimize the incision. Needles were disinfected between fish with isopropyl alcohol and thrown away after a maximum of ten females were tagged to ensure sharpness. Surgical glue was also used to close incisions on females. While no strict minimum length was employed for tagging males, no females under 18.5” were implanted with PIT tags. At smaller sizes, the pelvic musculature (particularly in salmon) was too thin to properly secure a PIT tag without a high risk of tag loss. Aside from this minimum length restriction in females, all efforts were made to tag a representative sample of salmon.

Concurrent with the onset of salmon tagging, we placed four ORSR Single Antenna Readers (Oregon RFID) upstream of the weir. One additional reader was placed at the weir location following removal of the weir structure to determine directional movement of exiting fish and verify tag detection effectiveness. Readers were powered using Oregon RFID linear power supply DC converters. These readers were connected to antennas via Oregon RFID ATC auto tuners and constructed as a single, river-spanning loop of 8-gauge, oxygen-free, copper welding cable (Figure 5).

Figure 5. Upper Weir antenna, showing typical river-spanning loop of cable.

Antenna locations were chosen to sample most of the length of the Crooked River, as well as to document salmon movement at some historical barriers to fish passage, known spawning grounds, and previous sampling sites. Antenna locations were as follows, from lowest to highest in the drainage (see Table 1):

Table 1. Locations and installation dates for Crooked River tag readers and antennas.

Site	Approx. River Mile	Installation Date	Removal Date
Lower Weir	5.3	Oct. 30, 2018	Dec. 14, 2018
Upper Weir	5.4	Sept. 6, 2018	Dec. 14, 2018
Edes Falls	9.6	Sept. 12, 2018	Dec. 19, 2018
Bolsters Mills	22.3	Sept. 13, 2018	Dec. 19, 2018
Waterford	38.2	Oct. 2, 2018	Dec. 12, 2018

The first upstream antenna (Upper Weir; Naples, ME) was located roughly 0.1 miles upstream of the weir, just above a deep bend pool. Along with tracking later downstream salmon movement, this antenna's proximity to the weir allowed it to serve as an estimator of initial tagging success and tag retention. The following two upstream antennas, at Edes Falls (Naples, ME) and Bolsters Mills (Otisfield, ME), were both located below remnant dam structures. Both dams are passable to salmon today at moderate to high flows, but historically prevented upstream movement. The uppermost antenna in Waterford, ME was located much higher in the drainage than other antennas and served as an estimator of the proportion of spawning salmon that entered the upper third of the Crooked River. Some hardware and software problems prevented the Waterford antenna from successful operation until early October. Once the weir was removed the lowest antenna (Lower Weir; Naples, ME) was installed; though equipment malfunctions and winter conditions precluded much success, pairing two antennas at the same study site was intended to assess tag detection effectiveness. However, the proximity of the Lower Weir and Upper Weir antennas also allowed for determination of movement direction among salmon detected at both antennas in a short time frame, which was particularly important for subsequent spawning runs in 2019 and 2020. Readers and antennas were operated into mid-December at all sites, to determine timing of outmigration back to Sebago Lake at the end of the spawning season.

Each antenna reader stored data on PIT tag detections at study locations. PIT tags have unique numbers associated with them, allowing for individual fish to be tracked throughout the river system. When a tagged fish swims through the antenna loop, the antenna reader stores a line of code, recording the detection event. Once readers were operational, we visited each antenna location roughly once each week to download data on detection events and check antenna functionality.

In 2019 and 2020, antenna arrays were set up at the former location of the picket weir to gather information on any previously tagged salmon returning to spawn. Two antennas were placed close together (roughly twenty yards apart to avoid interference), with consecutive detections of any individual fish allowing for determination of movement direction. Antennas were operated from early September to mid/late November each year.

Results

Count Data

Over the course of two months of operation, 1,845 salmon passed through the weir. 1,036 were males while 809 were females. There were 9 mortalities associated with weir and tagging operations, for a total mortality rate of 0.5%. An additional 12 mortalities were discovered on the plywood covering over the weir collection box, though these were somewhat suspicious in origin as it seemed unlikely that salmon would possess the desire or need to jump over the fyke entrance, and this behavior had never been observed in salmon on the Crooked or other weir operations in Maine. When these additional mortalities are included, total known mortality was 21 salmon, or 1.1% of all salmon observed. Total catch of salmon peaked in late September with 385 salmon on September 28 (Figure 6).

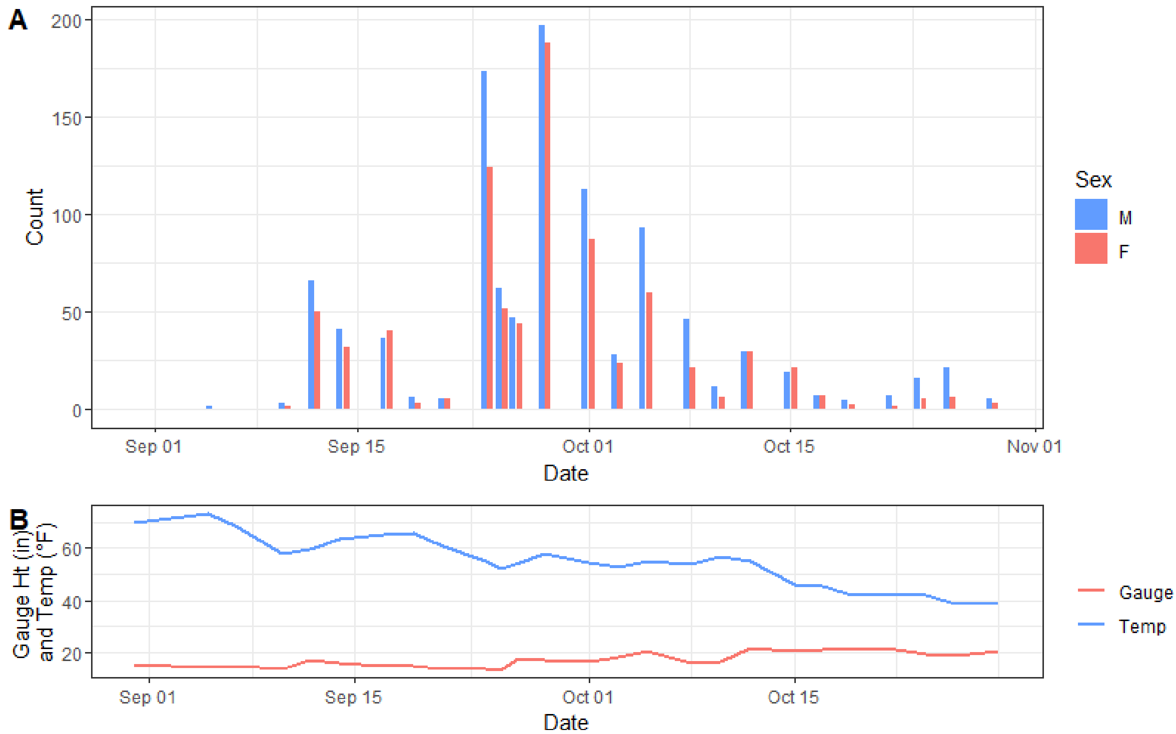

Figure 6. A) Counts of salmon in weir collection box by date and sex (M=male, F=female). B) Gauge height (inches) and temperature of the Crooked River (°F) at the weir location.

Gauge height and temperature of the river is also shown in Figure 6. The gauge showed three periods of increasing flows, one each in mid-September, late September/early October, and mid-October. Sharp increases in salmon counts at the weir also appeared to follow. Similarly, largest increases in salmon counts were associated with falling water temperatures. By the date of weir removal, catch rates had declined strongly from peak values and very few female salmon were being captured, indicating that most of the fall run was sampled. Salmon made up the vast majority of fish captured in the collection box, with other species captured including White Sucker (*Catostomus commersonii*; n=12), Fallfish (*Semotilus corporalis*; n=6), Creek Chub (*Semotilus atromaculatus*; n=2), Smallmouth Bass (*Micropterus dolomieu*; n=2), White Perch (*Morone americana*; n=1), American Eel (*Anguilla rostrata*; n=1), and Brown Bullhead (*Ameiurus nebulosus*; n=1). All non-salmon were released alive immediately. No species other than salmon were captured after September.

Age and Growth Data

Age and growth data were collected from 691 (37.5%) of all salmon captured, all of which were mature fish. Mean length, weight, and condition factors for each age class are summarized in Table 2. Eight age classes were captured, from II+ to IX+. Ages III+ and IV+ made up 70% of the catch, with age III+ alone representing a large proportion (43.8%) of all fish. With the exception of age II+ fish, which rarely exhibit spawning activity as wild fish (versus age II+ hatchery fish which commonly spawn), counts of salmon declined with each successive age class. Salmon length varied from 11.34” to 25.75”, while weight ranged from 0.52 to 6.39 pounds. Condition factor was also variable, from 0.61 to 1.07 across all fish. Using age classes III+ to IX+, overall discrete survival rate was calculated as 50.4% using catch curve regression.

Table 2. Mean length, weight, and condition factor by age class for salmon captured in the weir, plus/minus standard errors of the means. Note: n=688 for mean weight and condition factor.

Age	n	Mean Length (in)	Std. Error		Mean Weight (lb)	Std. Error		Mean K Factor	Std. Error
II+	2	11.77	0.43		0.53	0.01		0.90	0.08
III+	303	16.12	0.05		1.22	0.01		0.80	0.00
IV+	182	18.32	0.07		1.78	0.02		0.80	0.00
V+	76	19.32	0.16		2.11	0.06		0.80	0.01
VI+	57	20.74	0.19		2.48	0.08		0.76	0.02
VII+	34	22.09	0.26		3.13	0.11		0.80	0.02
VIII+	19	22.95	0.32		3.41	0.15		0.78	0.02
IX+	3	24.07	0.27		4.57	0.91		0.90	0.15
Unknown	15	19.25	0.78		2.10	0.33		0.76	0.06
All Fish	**691**	**18.00**	**0.09**		**1.76**	**0.03**		**0.80**	**0.00**

Some differences were noted between sexes, with females longer, heavier, and with higher condition factors on average across all fish (Table 3). Females also had a higher median age than males. Males dominated younger age classes by numbers, with age III+ males representing just over one third (231 fish; 33.5%) of all fish from which age and growth data were collected. The higher median age for females, combined with the preponderance of younger males, may help explain the fact that females were overall larger. Table A1 (Appendix I) shows additional comparisons between male and female salmon for the most numerous age III+ and age IV+ classes. Within these age classes, females were not significantly larger in size but were in significantly better condition. Physiological changes due to egg production in preparation for spawning likely account for better female conditions both within the most numerous age classes and overall.

Table 3. Differences in mean length, weight, condition factor, and median age between sexes of salmon captured at weir, plus/minus standard errors of the means.

Sex	Mean Length (in)	Std. Error		Mean Weight (lb)	Std. Error		Mean K Factor	Std. Error		Median Age
M (n=416)	17.70	0.12		1.66	0.04		0.78	0.00		III+
F (n=275)	18.45	0.13		1.91	0.04		0.82	0.01		IV+

Over the course of the two-month sampling period, mean length ($F_{1,686}$=0.54, p=0.462), weight ($F_{1,689}$=0.06, p=0.802), and age ($F_{1,674}$=0.037, p=0.848) did not vary significantly for salmon with date observed at the weir (significance was noted at α=0.05). However, condition factor significantly decreased over the sampling period ($F_{1,680}$=8.12, p=0.005). When analyzed separately by sex, this trend of decreasing condition factor with sampling date was observed in males ($F_{1,408}$=7.89, p=0.005) but not females ($F_{1,270}$=1.25, p=0.265). Figure 7 displays differences in condition factor over time for both sexes.

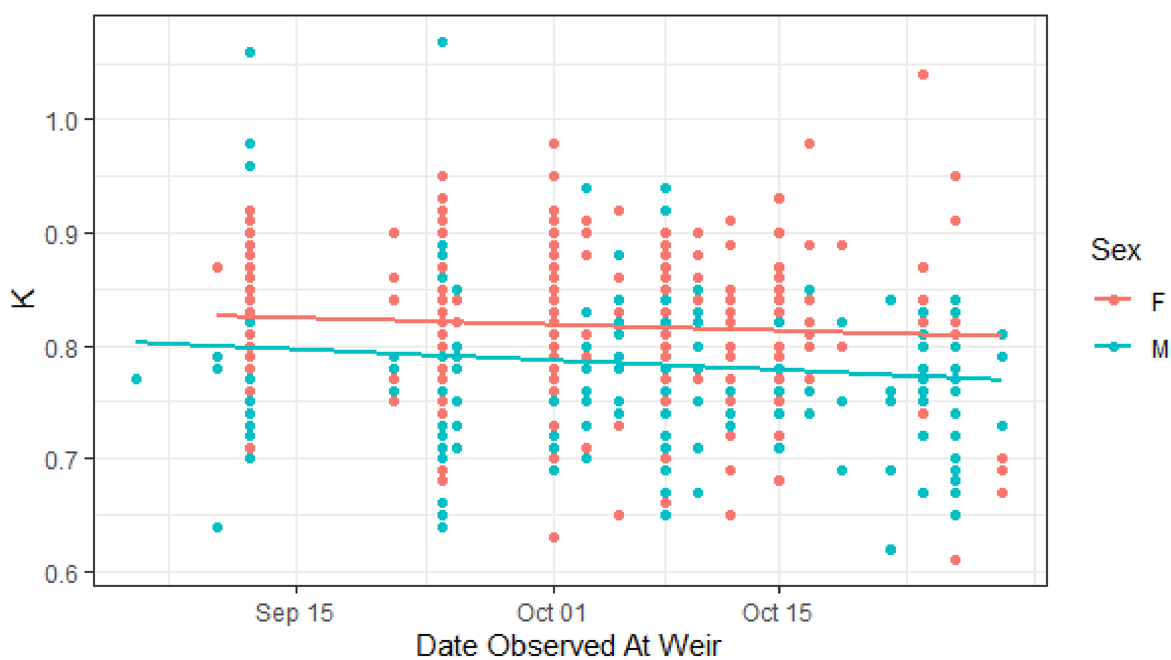

Figure 7. Condition factor (K) over time for female (red) and male (blue) salmon observed at the weir.

Of all fish captured, only ten (0.5%) were of hatchery origin. Age and growth data were collected on eight of these fish. Hatchery salmon captured at the weir ranged from ages III+ to VII+, with a median age of IV+. It should be noted that hatchery fish are rarely seen beyond age V+ in the nearby Jordan River spawning run, so it is possible that the age VI+ and VII+ fish were mismarked. Fish ranged in size as well, with length from 17.8" to 25.3", weight from 1.6 to 5.3 pounds, and condition factor from 0.62 to 0.90. Similar data is also recorded annually from the Jordan River Fish Trap, which is used for collection of eggs and milt from spawning salmon in order to supply Department hatchery operations. This larger sample of hatchery-origin salmon allowed for better comparisons of hatchery-reared salmon with the natural run in the Crooked River. Table A2 (Appendix II) shows detailed comparisons of size-at-age for wild salmon in the Crooked River and hatchery salmon in the Jordan River run. Jordan River females were stripped of eggs prior to measurements and so were not used in calculations of mean weight or condition factor. Jordan River fish were on average both longer ($F_{1,808}=45.53$, $p<0.001$) and heavier ($F_{1,448}=32.6$, $p<0.001$) than wild fish captured at the weir, but mean condition factor was not different ($F_{1,448}=1.43$, $p=0.232$). Though sample size was much smaller for Jordan River salmon (n=119), overall discrete survival rate for ages III+ to IV+ was calculated as 25.6%. This estimated survival rate was about half of that seen for fish captured at the weir (50.4%).

PIT Tagging Data

Of the subset of salmon with age and growth data collected, 488 (71% of fish with age and growth data, 26% of all salmon observed) were fitted with PIT tags. Ninety-seven (20%) of the tagged fish were females and 391 (80%) were males. Due to differences in tagging methodology as outlined earlier, tagging of males was easier, faster, could be performed on smaller individuals, and provided better confidence in tag retention. These discrepancies account for the fact that four times as many males were tagged versus females. Table 4 shows distribution of PIT tags implanted throughout the sampling period and shows that PIT tagging effort was well-distributed throughout the season.

Table 4. Distribution of PIT tagging efforts by sex of salmon.

Week	Males Tagged	Females Tagged
Aug. 26 - Sept. 1	0	0
Sept. 2 - Sept. 8	0	0
Sept. 9 - Sept. 15	63	14
Sept. 16 - Sept. 22	5	1
Sept. 23 - Sept. 29	81	20
Sept. 30 - Oct. 6	93	27
Oct. 7 - Oct. 13	80	21
Oct. 14 - Oct. 20	25	9
Oct. 21 - Oct. 27	39	3
Oct. 28 - Nov. 3	5	2
Total n=488	**391**	**97**

Post-tagging, PIT tag antenna arrays detected movements of fish throughout the Crooked River during their fall spawning run. However, it must be noted that these antennas and readers presented numerous technical difficulties over the study period. Particularly in the first few weeks of operation, the readers had a high rate of “phantom tag” readings, meaning that a detection event was recorded for tags not actually present in the system. It is possible that these phantom readings, if concurrent with actual PIT tag presence, could have reduced detection efficiency via “tag collision”. Readers also had a variety of software, hardware, and electrical issues, some of which led to periods of shutdown when no tags could be detected. Some of these major shutdown periods are summarized in Table 5, but this list is highly conservative and does not include other malfunctions where failure was likely but unconfirmed. Finally, particularly later in the season when rising water levels and ice formation affected antenna function, periods of reduced read range may have also impacted the detection rate of readers. Despite these issues, over 140,000 individual detection events were recorded by the stationary tag readers, and detailed movement patterns for many fish were able to be determined.

Table 5. Confirmed periods of reader failure by site and duration.

Site	Time Period	Comments
Lower Weir	Nov. 14 – Nov. 19	Failed restart, read range very limited
Upper Weir	Sept. 14 – Sept. 28	Database failure (unknown start of error)
Bolsters Mills	Nov. 5 – Nov. 15	Voltage shutdown error
Bolsters Mills	Nov. 19 – Nov. 21	Voltage shutdown error
Waterford	Oct. 3 – Oct. 10	Database failure

420 (86.1%) tagged fish were detected at least once post-tagging, versus only 68 (13.9%) of PIT tags that were never seen. Despite alternative tagging procedures for females, only 7 (10.3%) of undetected tags were from female salmon. This proportion of tag loss for female salmon is actually less than the overall proportion of females tagged (20%). Of the 420 detected fish, detection rates at each of the four upstream antennas are shown in Table 6. The proportions of redds found in a 2014 survey (in Pellerin and Pierce 2015) above these same sites are also shown, allowing for comparisons with another recent spawning run. Proportions of tagged fish detected were slightly higher than proportions of 2014 redds above Upper Weir, Edes Falls, and Bolsters Mills, and lower than above Waterford. However, a comparatively later installation date at Waterford, coupled with disruptions in antenna operations, may have contributed to a reduction in tagged fish detected. Additionally, past observations have suggested that many salmon that enter the Crooked River during the spring run may remain far upstream into the fall; these fish would have been untagged and may have contributed to the disparity between fish detected and redds observed in the past.

Table 6. Proportions of tagged fish detected and 2014 redds found above four antenna sites.

Site	Fish Detected of 420 Total	Percentage of Tagged Fish Detected	Percentage of 2014 Redds Above
Upper Weir	418	99.5%	98.5%
Edes Falls	368	87.6%	86.1%
Bolsters Mills	217	51.7%	48.3%
Waterford	70	16.7%	26.9%

Along with the proportion of fish that reached each antenna site, the rate and distance that fish traveled also informed movement patterns. Table 7 shows minimum and median travel times from the weir to each of the upstream antennas. Due to periods of reader shutdown, maximum upstream travel time from the weir was not able to be reliably calculated, which also precluded use of mean upstream travel times. Travel time was highly variable among fish, particularly as distances from the weir increased. Some fish took days or weeks to travel even a few miles, while others appeared to quickly head to specific destinations. For example, the fastest trip time from the weir to Edes Falls took less than half a day, which equates to a maximum travel rate of nearly 11 miles per day. In contrast, the median time to travel only a tenth of a mile upstream of the weir was nearly a third of a day, as many fish appeared to rest or stage in the deep pool upstream of the weir but below the Upper Weir antenna. Though rate of travel was variable, there was no correlation between date of tagging at the weir and maximum distance traveled upstream ($F_{1,419}$=1.12, p=0.290). However, fish tagged later in the season took less time to travel to the three uppermost antennas (Edes Falls: $F_{1,232}$=281.8, p<0.001; Bolsters Mills: $F_{1,204}$=186.3, p<0.001; Waterford: $F_{1,68}$=101.1, p<0.001)[Figure 8]. The Upper Weir site was not included in this analysis of travel time as its distance from the weir was so small.

Table 7. Minimum and median travel time in days from the weir to all upstream antennas.

From Weir To:	Approx. Distance From Weir (mi)	Min. Travel Time (days)	Median Travel Time (days)
Upper Weir	0.1	0.09	0.31
Edes Falls	4.3	0.40	1.47
Bolsters Mills	17.0	1.83	10.67
Waterford	32.9	5.55	21.12

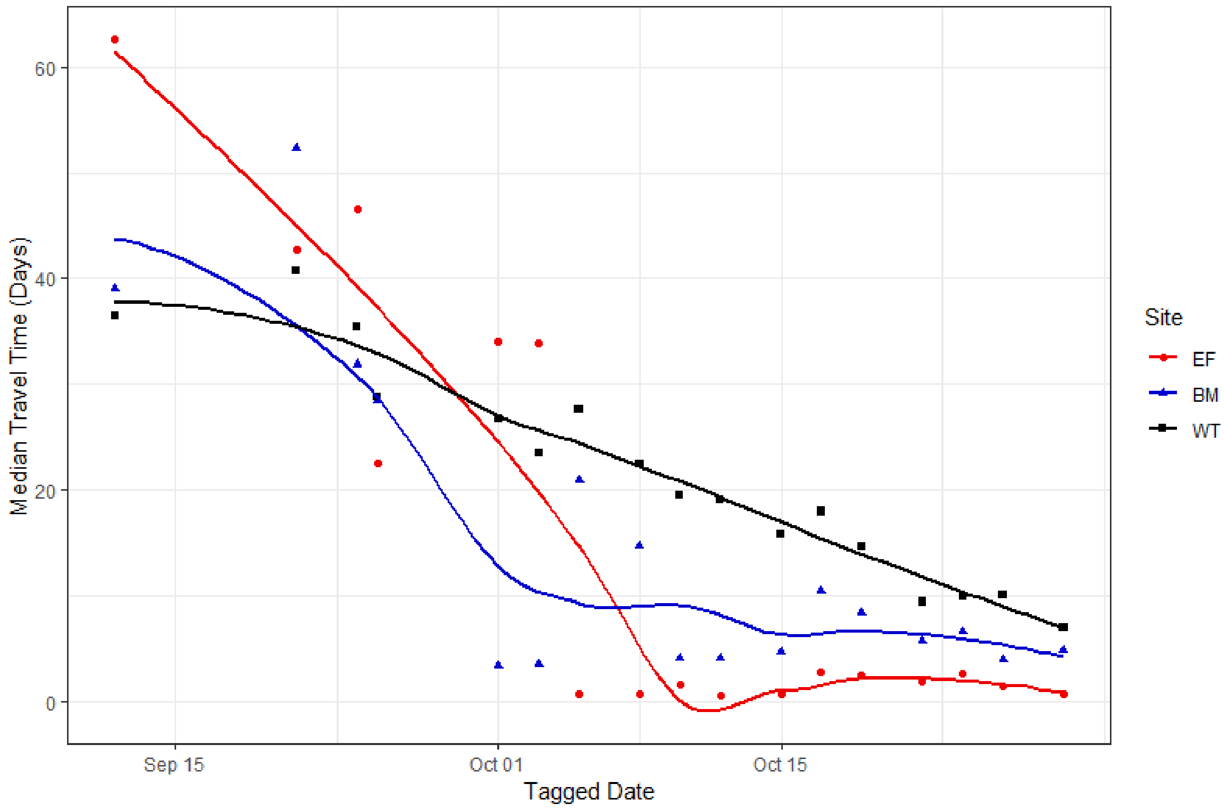

Figure 8. Median upstream travel time (days) for fish to the three uppermost antennas (Edes Falls, Bolsters Mills, and Waterford) based on tagging date at the weir.

We also examined travel times between adjacent pairs of antennas, for both upstream and downstream movement direction (Table 8). Rates of travel upstream were slower than downstream rates between Upper Weir-Edes Falls and Edes Falls-Bolsters Mills, while the opposite was seen between Bolsters Mills-Waterford.

Table 8. Mean upstream and downstream travel rates between adjacent antennas, plus/minus standard errors of the means.

Adjacent Antennas	**Distance (miles)**	**Mean Upstream Travel Rate (miles/day)**	**Std. Error**		**Mean Downstream Travel Rate (miles/day)**	**Std. Error**
Upper Weir-Edes Falls	4.2	7.14	0.68		11.29	0.97
Edes Falls-Bolsters Mills	12.7	3.37	0.26		5.15	0.74
Bolsters Mills-Waterford	15.9	4.12	0.40		2.28	0.61

Beyond individual fish, temporal trends were seen in overall salmon movement across the sampling period (Table 9). First, nearly three times as many overall detections happened at night (sunset-sunrise) than during daylight hours (sunrise-sunset), which resulted in a significant difference, X^2 (1, N=140,400) =71.24, $p<0.001$. This overall predilection for movement at night held true for individual months with the bulk of detections as well (October and November). Limited detections were seen at the tails of the run (September and December) due to lower overall salmon presence (Figure 6), and a higher incidence of technical issues with readers at the start and end of the study.

Table 9. Distribution of PIT tag detections by month and time of day; percentages indicate proportion of total detections seen at day or night.

Month	Day (sunrise-sunset)	Night (sunset-sunrise)	All Detections
September	0 (0%)	39 (100%)	39
October	8,722 (23.7%)	28,137 (76.3%)	36,859
November	26,537 (25.7%)	76,886 (74.3%)	103,423
December	13 (16.5%)	66 (83.5%)	79
Total	**35,272 (25.1%)**	**105,128 (74.9%)**	**140,400**

November had by far the most PIT tag detections of all months. By the start of this month, the maximum number of salmon were tagged, and it is likely that most fish had not yet departed the river back to Sebago Lake. To analyze this further, a subset of tagged fish was identified that had useful downstream movement data. Of these, 121 salmon were detected at multiple consecutive antennas, moving downstream, and were therefore reasonably likely to be exiting the river system. Taking the final detection at the Lower Weir antenna as the "departure date," the mean departure date for tagged salmon was November 18 (±0.65 standard error of the mean [SEM]). The earliest that any of these fish crossed the Lower Weir antenna on the way to the lake was November 7. When these departing salmon were analyzed separately by sex (31 females, 90 males), some temporal differences were found. On average, females departed a week earlier (November 12, ±0.94 SEM) than males (November 19, ±0.73 SEM), which was a significant difference in timing ($F_{1,119}$=26.39, p<0.001).

The last date that departing salmon were detected in the Crooked River was also correlated with some age and growth metrics. While condition of salmon did not affect the last detection date ($F_{1,117}$=1.77, p=0.186), fish with lower lengths ($F_{1,119}$=14.03, p<0.001), lower weights ($F_{1,119}$=15.6, p<0.001), and younger ages ($F_{1,117}$=16.0, p<0.001) had significantly later departure dates. These significant effects were only seen when both sexes were analyzed separately, suggesting that overall negative trends are largely driven by smaller, younger males remaining in the river until late in the spawning season in contrast to typical female behavior (Figure 9). For example, nearly half (58 of 121) of analyzed fish were age III+ males, which had the latest mean departure date of all age classes (Nov. 20 ±0.93 days SEM).

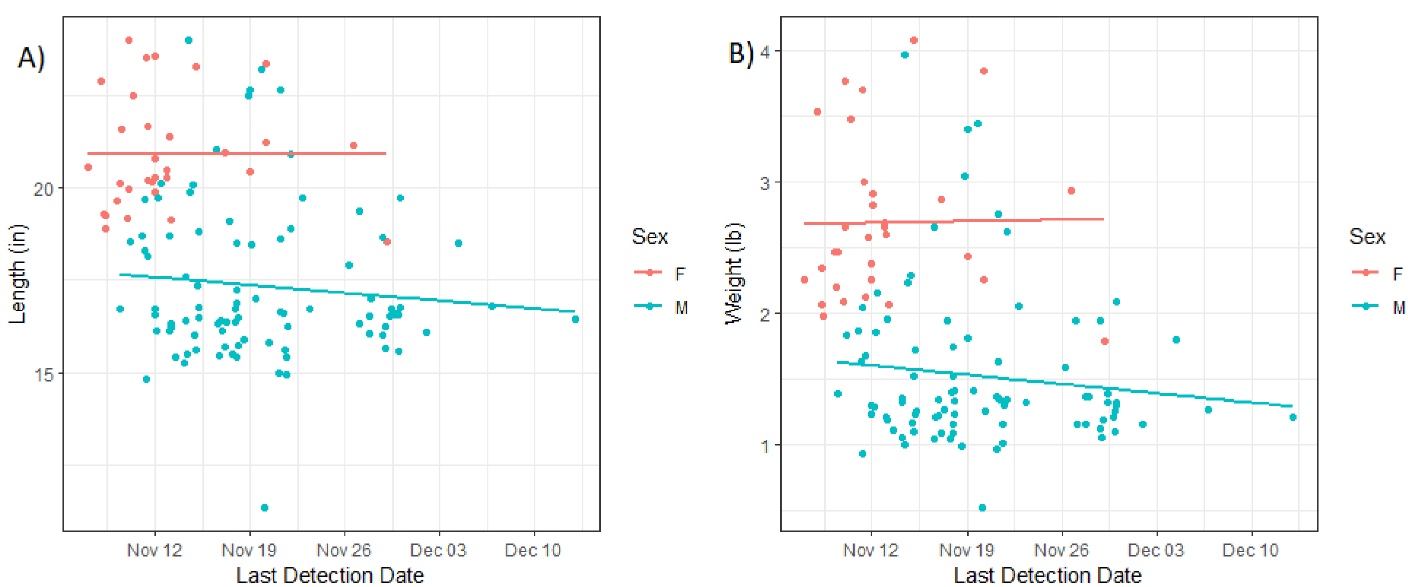

Figure 9. Distribution of A) length (in) and B) weight (lb) of salmon by last detected date in the Crooked River (n=31 females, n=90 males).

Using this same subset of 121 departing fish, approximate residency time was also calculated. On average, fish stayed in the Crooked River for 45.9 days (±1.41 SEM) with a range of 16.6-82.7 days. There was also a strong negative correlation between tagging date and residency time for this subset of fish. Salmon that arrived in the system later stayed for a shorter time before departing ($F_{1,119}$=438.2, p<0.001; Figure 10). On average, residency time for males (47.3 days ±1.66 SEM) was higher than for females (41.8 days ±2.53 SEM); however, this difference was not statistically significant ($F_{1,119}$=2.97, p=0.087). Limited numbers of females in the 121 fish subset may have affected these results.

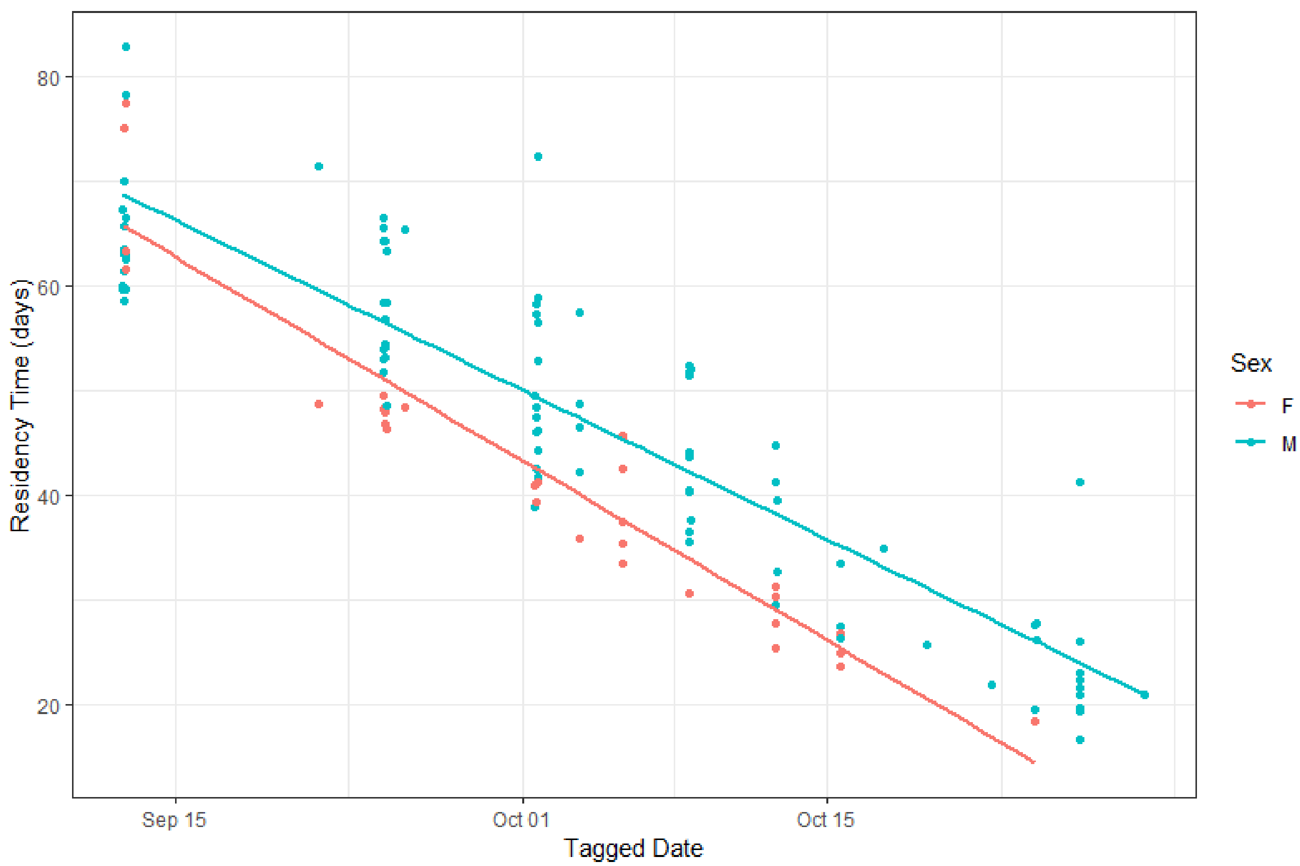

Figure 10. Variation in residency time vs tagging date for those salmon with confirmed departure dates, by sex (female n=31, male n=90).

In addition to overall upstream and downstream migration, some fish moved more variably within the Crooked River. For example, six fish were recaptured in the collection box during weir operations, suggesting successive upstream-downstream-upstream movements while in the river system. Table 10 below summarizes movement and tagging information for these recaptures. As all recaptures occurred prior to November, it is unlikely that these fish were exiting the system. Notably, the single fish recaptured multiple times was of hatchery origin. Though sample size was small, the sex ratio of recaptured fish was skewed strongly towards males. However, analyses did not suggest that males were more likely to move variably over large distances, or “roam,” more than females. By taking the total number of times that fish were detected at different sites and dividing by the maximum observed site (to account for differences in total upstream movement) an index of roaming was calculated for all tagged fish observed at upstream antennas. Males and females did not differ in mean values on this roaming index ($t_{1,347}$=-0.51, p=0.613), suggesting no measurable difference in large-scale roaming movements between sexes. Regardless of sex, fish were detected a relatively similar amount of times within the system, though males were detected slightly more overall. When moving upstream, females were detected a median of four times, while males were detected a median of eight times. Downstream median detections were five and four times for females and males, respectively. Females and males were detected a median of nine and eleven times, respectively, throughout their entire upstream and downstream spawning run.

Table 10. Initial capture date (only applicable for fish retaining previously implanted PIT tags), recapture date, sex, and number of recaptures for fish seen multiple times during operations of the weir.

Initial Capture Date	Recapture Date(s)	Sex	Number of Recaptures
Unknown[1]	Oct. 12	F	1
Unknown[1]	Oct. 12	M	1
Sept. 24	Oct. 17	M	1
Sept. 25	Oct. 17	M	1
Oct. 5	Oct. 17, Oct. 22	M	2
Sept. 24	Oct. 22	M	1

[1] Recaptures identified via tagging scar and upper caudal fin clip

One final subset of movement data was that of tagged hatchery-origin salmon. Six of the eight hatchery salmon with age and growth data collected were implanted with PIT tags. Five of the six were detected as far upstream as Edes Falls, while the sixth was never detected above the Upper Weir site. Though it is a very limited sample, it appears that hatchery salmon did not travel beyond the reach between Edes Falls and Bolsters Mills at a maximum.

Repeat Spawning 2019/2020

PIT tag detections of repeat spawners in 2019 and 2020 represented less than 1% of all fish tagged in 2018 (Table 11). In 2019, only three fish were detected, all of which were age III+ males when initially tagged in 2018. Similarly, only three fish were detected in 2020. Two were relatively young (ages III+ and IV+ males when tagged in 2018). The third 2020 detection belonged to one of only three age IX+ fish detected in 2018, making this female age XI+ in 2020 and on the oldest end for a spawning salmon. However, it must also be noted that in 2019 and 2020 there were again numerous hardware, software, and electrical problems with the continuous operation of the PIT tag readers. It is possible these errors may have led to missed detections for other repeat spawners, though it is unlikely that many fish were missed due to the operation of two paired antennas. While each single antenna experienced multiple instances of failure, there were no documented periods in which both antennas were simultaneously incapable of detecting tags.

Table 11. Summary information for all detections in 2019 and 2020, including period of detection, number of detection events, sex, age, length (as of 2018), weight (2018), and condition factor (2018). Note that ages have been advanced to reflect time passed since weir operations in 2018.

Detection Period	Detection Events	Sex	Age	2018 Length (in)	2018 Weight (lbs)	2018 K
Sept. 19, 2019	1	M	IV+	17.05	1.32	0.74
Oct. 2, 2019	1	M	IV+	14.84	0.88	0.75
Oct. 3, 2019	1	M	IV+	17.17	1.50	0.82
Sept. 24, 2020	1	M	VI+	18.50	1.74	0.76
*Sept. 25-29, 2020	2	M	V+	15.98	1.10	0.75
Oct. 1, 2020	1	F	XI+	24.02	3.77	0.75

*This fish was also detected once sometime between 11/12 and 11/24/2020. Tag reader errors prevented determination of exact date.

Discussion

Count Data

Overall, weir operations were highly successful at capturing salmon, and the majority of the fall spawning run passed through the weir. Despite the emergency removal of the weir, total catches of salmon in the collection box had dropped far below peak levels by the end of October. Additionally, very few females were moving upstream at that time regardless of high stream flows, which is usually indicative of the end stages of the spawning run. Number of salmon captured can also be compared to past estimates of the total spawning run. 1,845 salmon processed in the Fall 2018 run far exceeds counts of adults in the Bolsters Mills fish trap in the 1970s and 1980s, which ranged from 87-433 fish (inclusive of a sometimes sizeable portion of salmon that ascended the river in the spring; spring run ranged from 9-72% of total run in historical fish trap data). Even adjusted for the fact that about 48% of redds found in 2014 were above Bolsters Mills (adjusted fall 2018 run to Bolsters Mills: 891 fish), historical fish trap operations yielded far less salmon than the 2018 spawning run (Figure A1, Appendix II). Consistent with past observations in Pellerin and Pierce (2015), this project confirms substantial gains in adult returns since fish trap operations ceased decades ago. When compared to data from a recent redd survey in the Crooked River, the 2018 spawning run fell just below the estimated range of 2,300-4,600 adult salmon in the 2014 run. However, given a lack of data on the spring run in 2018, plus high predation and intraspecific competition related to a booming Lake Trout population and decreased Rainbow Smelt numbers in Sebago Lake, it is not surprising that salmon survival and abundance may appear to be reduced from a few years ago. Furthermore, open water creel surveys on Sebago Lake show a decline in salmon catch rates from a high of 0.19 salmon per hour in 2013 to 0.11 salmon per hour in 2019, which was likely reflective of changes in adult salmon numbers during the time frame between the redd and weir projects. An updated redd survey was planned as part of the weir project to compare adult spawning numbers for both methods; unfortunately, weather and river conditions have precluded it from occurring at the time of this report's writing. A redd survey is still worth pursuing to bookend what is believed to be high (2013) and low population levels (current) for the Sebago Lake salmon population.

Age and Growth Data

Current conditions in Sebago Lake are likely playing a role in the suppression of salmon size quality as well. Mean condition factor for all fish was 0.8, which is at the low end of the range typically seen for salmon. The average wild age III+ salmon, an age class that comprised nearly half of the overall run, did not weigh much more than one pound. This weight is lower than ideal for a salmon fishery, and is not sufficient to produce consistent, quality-sized catches for anglers. Additionally, mean weight and condition factor for age III+ wild fish (and age II+ hatchery fish, typically comparable in size) are below target goals in the Sebago Lake Management Plan (Brautigam and Pellerin 2008). Target goals for an age

II+ hatchery male are between 2.2-2.7 lbs with a condition factor greater than 0.90; the typical Sebago Lake salmon is currently well below these management standards, even when age III+ or IV+ wild salmon are used for comparisons with hatchery size goals to account for increased growth at a given age for hatchery fish. For most Sebago Lake salmon, wild fish growth may be most comparable to hatchery fish that are one to two years younger, indicating an early life advantage in growth for hatchery salmon (see Appendix II for additional comparisons of size-at-age). Along with being undesirable to anglers, poor size quality and condition could lead to increased natural mortality and less wild production. Efforts are currently underway to combat such a possibility. Regulations on Lake Trout have been liberalized to allow more harvest while protecting fewer trophy individuals than the previous slot regulation, to reduce both predation on salmon and reproduction potential of Lake Trout. Though harvest data is limited, 2019 winter and open water creel censuses on Sebago Lake indicate that these regulation changes have led to high levels of angler harvest. Harvest estimates for winter 2019 were 4,641 (±1,220) Lake Trout, with an additional 5,812 (±1,547) Lake Trout estimated to have been harvested in the 2019 open water season. Through continued harvest, primarily of small, voracious Lake Trout from the most abundant age classes, salmon could be released from strong interspecific competition and size quality may be able to rebound.

While mean length, weight, and age of salmon did not change throughout the run, there was a significant drop in condition later in the spawning season. This decline was primarily driven by a lack of males with high condition factors in later months. After the first week of October, no males were seen with condition factors of 0.9 or greater. Furthermore, the majority of males captured in the final two weeks of weir operations had condition factors below the overall mean of 0.8 for all fish. Spawning is an inherently stressful and energetically expensive event for fish, and some decline in condition over a prolonged spawning period is not surprising; however, the fact that only male salmon showed this significant decrease in condition over time may suggest some sex-based behavioral differences. For example, the tendency for some male salmonids to be more mobile than females (Tentelier et al. 2016) may have bioenergetic consequences. While there was no statistical difference in mean residency time between male and female salmon, males did have a higher mean by nearly six days. Additionally, fish with the longest residency times were predominantly male, as seen in the last two weeks of weir operations. Thus, it is possible that late-running males had actually been in the lower Crooked River for some time before reaching the weir, which may account for some loss in condition factor towards the end of the sampling period.

Throughout the run, distribution of age classes was typical for most populations of spawning salmon in Maine (Boucher and Warner 2006). Age III+ (age of maturity for most wild males/some females) was by far the largest age class of fish, with age IV+ representing a large proportion as well. Spawning fish in the age II+ class are typically uncommon for wild salmon but occasionally reported by Department staff statewide, represented here by two fish captured at the weir. It is also notable that weir operations captured some quite old fish, with twenty-two age VIII+ and three age IX+, one of which was detected in 2020 as an age XI+. It is relatively rare to come across salmon of those advanced ages, particularly in wild populations of fish.

__Hatchery Comparisons__

While the vast majority of age and growth parameters in this study were derived from wild fish, data were collected on some hatchery-origin fish as well, both at the weir and during the annual Jordan River egg take. Slightly higher mean length and weight for hatchery fish likely derived from advantages of the controlled hatchery environment during early life. Hatchery salmon are typically larger and older when entering the Sebago Lake system, thus providing a “head start” in terms of growth in the lake environment. However, estimated survival rate beginning with age III+ fish was nearly half for Jordan River fish versus fish captured at the weir. Though small sample size must be acknowledged, a survival rate of 25% for Jordan River fish is likely comparable to past observations and does not represent an immediate threat to hatchery operations, including the annual collection of eggs and milt from Jordan River salmon.

The impact of this survival rate on Jordan River salmon can also be seen when distribution of age classes is compared with wild fish. The oldest Jordan River salmon was age VI+, while wild salmon were captured up to age IX+. Underlying reasons for these disparities in survival and population age structure, however, are less clear. It is possible that wild fish, which almost exclusively spawn in the relatively large and dark Crooked River, are better able to avoid predation than hatchery salmon that return to the Jordan River, which is smaller and concentrates fish below a dam. Wild fish may also face less fishing pressure if a significant portion of the spawning run ascends into the Crooked River in the early summer season rather than remaining in Sebago Lake; this movement pattern has been documented in the past at the Bolster’s Mills fish trap (Pellerin and Pierce 2015). Here, adult salmon movements showed a bimodal distribution, with peaks in both June and October. For a given age class, wild salmon may also face less fishing pressure versus hatchery salmon as wild fish typically need an extra year of growth before becoming recruited to most angling gear. Thus, wild salmon may be exposed to less lake mortality within age classes. Finally, differential survival may be related to documented disparities in performance between wild and hatchery salmonids. Numerous studies have shown that wild salmonids often outcompete their hatchery-reared counterparts and contribute disproportionately to future recruitment (Leider et al. 1990; Fleming et al. 1996, 2000; Fleming and Petersson 2001).

Differences in behavior between wild fish and hatchery stock can also be seen. Only ten hatchery fish were captured at the weir, while no wild fish were captured at the Jordan River Fish Trap in 2018, thus representing a strong spatial division between these groups. All hatchery salmon are currently stocked in Sebago Lake near the mouth of the Jordan River, providing strong homing instincts to that area for stocked fish. DeRoche (1982) reported similar homing instincts for lake-stocked fish, with only 2% of fish stocked in Sebago Lake captured at the Bolsters Mills Fish Trap between 1974-1981. Similarly, of all salmon captured during a 2007 trapnetting event in the Crooked River, only 11.5% were hatchery in origin. Small sample size (61 salmon) may account for the slight increase in proportion of hatchery fish in this case, along with past stocking practices. In 2007, salmon were stocked at four locations around Sebago Lake (versus one today), perhaps allowing for increased rates of straying into the Crooked River at that time. It may also be worth considering that if stocking locations do impact straying, these geographical considerations may play a role in limiting any potential introgression of hatchery salmon genetics into wild populations. Regardless, the fact remains that wild salmon currently make up the vast majority of the Crooked River run. As nearly all wild salmon production comes from the Crooked River, wild fish are much more likely to return to their natal stream. It is also notable that of the six hatchery-origin fish implanted with PIT tags, none were detected further upstream than Edes Falls. Edes Falls is about two river miles upstream of the mouth of Mill Brook, the outlet to the Casco State Fish Hatchery where salmon stocked in Sebago Lake are raised. However, it is not clear if these fish were homing specifically to their natal hatchery, as five of six continued at least another two miles upstream. In some salmonids, including hatchery-origin fish, spawners may pass by ultimate spawning areas and drop back down later, a phenomenon termed "overshoot fallback" (Boggs et al. 2004; Richins and Skalski 2018). Alternatively, these hatchery fish may represent strays not following homing tendencies. In sea-run Atlantic salmon, straying rate for hatchery fish has been reported up to 15%, higher than rates seen in wild-origin salmon (Jonsson et al. 2003). This slightly increased tendency to stray and colonize new habitat has been documented predominately in hatchery and non-native strains in other salmonids as well (Schroeder et al. 2001; Quinn 2003), further emphasizing the importance of ancestral spawning habitat to the sustenance of native, wild runs. In the Crooked River, closer monitoring of the confluence with Mill Brook would likely be necessary for a quantitative assessment of the rate of salmon straying. Nevertheless, contribution of hatchery salmon to the Crooked River run remains low.

PIT Tagging Data

Along with the aforementioned tagged hatchery fish, general movement patterns for most tagged fish were able to be at least partially determined. Though technical issues with tag readers and antennas undoubtedly led to some undetected fish movement, most fish were detected at one or more sites during the study period. Nearly 87% of tags were detected at some point, which is relatively comparable to studies of PIT tag detection efficiency in salmonids. For example, minimum detection efficiencies were 83-97% (Zydlewski et al. 2006) and 96-100% (Connolly et al. 2008) across multiple PIT tag arrays in two field studies of Pacific salmonids. In these studies, stream size was either small (Zydlewski et al. 2006) or multiple redundant antennas were in place (Connolly et al. 2008), neither of which applied to this study on the Crooked River. Nevertheless, only 66 PIT tags went undetected in this study, and tagging successfully allowed for insight into spawning salmon behavior.

Existing data on movement of spawning fish in the Crooked River was limited, but some comparisons could be made to 2014 redd counts and Bolsters Mills Fish Trap data. Antennas at Edes Falls and Bolsters Mills, which recorded the bulk of upstream detections, could be compared with 2014 redd survey sites at similar locations. It is not surprising that many of the heavily utilized spawning areas remained the same between 2014 and 2018, as these areas likely represent key habitat during each spawning run and may represent specific natal sites to which salmon are homing (Boucher and Warner 2006). However, the uppermost antenna site, Waterford, had a lower proportion of tagged fish versus 2014 redds. It is likely that technical problems with tag readers were even more impactful higher in the drainage; numbers of fish in that upper area of the river represented only a small sample of the overall population and missed detections could more easily skew estimates of fish presence.

Beyond spatial patterns, there were also some notable temporal differences in salmon movement as well. Movement speed was highly variable, with some fish capable of covering large distances very quickly. Minimum movement times from the weir to each upstream antenna were also very impressive, with some fish capable of moving nearly four times faster than the median for a given distance (see Appendix III for specific case studies). In contrast, some fish appeared to rest in deep pools for days at a time before moving further upstream. Fish expend quite a bit of energy on a spawning run, and some individuals may need extra time to rest between upstream movements. Some limited handling stress, especially for tagged fish, may have also influenced longer recovery times between upstream movement. Post-spawn, downstream movement rates were similarly variable but did increase versus upstream rates for two of three antenna pairs examined. Once again, fish were capable of moving quickly when conditions allowed and individuals were motivated.

Environmental variables such as water level, water temperature, and daylight (among others) may further impact the rate and timing at which spawning salmon travel (Boucher and Warner 2006; Thorstad et al. 2008). DeRoche (1982) found that upstream salmon movement in the Crooked River was highly influenced by increasing river flows, but that this influence disappeared once water temperatures dropped below 50°F (10°C). This study showed similar results, with increases in catch of salmon at the weir typically following increasing gauge heights, but dropping off as the river cooled. Additionally, salmon were much more likely to move during the night, with nearly three times the total number of detections versus daylight hours. This preference for movement in the dark has been documented in sea-run Atlantic salmon as well (Smith and Smith 2005) and may be a mechanism for predator avoidance in some salmonids (Bentley et al. 2014). For Crooked River salmon, discrepancies in diel movement patterns were seen throughout the spawning run. Furthermore, the month with the greatest discrepancy between day and night detections was October, which features longer days than later months sampled but during which salmon still showed a strong preference for movement in the dark. While rate and timing of movement may have varied for individual fish, there was no correlation between initial date of the spawning run and maximum distance traveled. Notably, salmon did appear to compensate for later spawning start dates by traveling more quickly to upstream antennas. This may suggest that fish aimed to reach specific destinations regardless of date of entry into the Crooked River; this site-specific homing has been documented in both landlocked and sea-run Atlantic salmon (Boucher and Warner 2006; Thorstad et al. 2008). It is also possible that higher flows, changing water temperatures, and longer periods of darkness may have contributed to faster rates of travel later in the season. Despite these variables, the data show that many salmon may be dependent on unobstructed passage upstream to reach preferred spawning grounds at optimum times. Within a given spawning run, significant delays may compromise fish fitness to the point that spawning is unsuccessful (Geist et al. 2000). Extended over multiple years, repeated delays and migration failures may reduce reproductive potential in salmonid populations, greatly impacting long-term population growth (Lundqvist et al. 2008). Managers must therefore be sensitive to any disruptions (construction projects, beaver dams, etc.) that could hinder salmon movement upstream, as fish may arrive very quickly during ideal spawning run conditions.

Though data was more limited for downstream movement, some patterns did emerge. Most salmon stayed in the Crooked River into November, with average departure date not occurring until past the middle of the month. As has been previously documented for salmon in Maine rivers, males tended to remain around spawning habitat longer, with some males likely staying post-spawn (Boucher and Warner 2006). Males were further contrasted with females by the larger decreases in average length, weight, and age seen in males that stayed later in the river. Pooling data from smaller males that stayed in the river longer and the larger females that departed earlier led to significant decreases in length, weight, and age the later that salmon remained in the system. It is possible that these smaller, younger males were less competitively fit during the height of spawning. However, given that only limited differences in variability of movement, or roaming, were seen between sexes, it is unclear to what extent less competitively fit males may have needed to search for mates. It is also possible that roaming behaviors may have occurred at spatial scales too small to be detected by our widely-spaced antennas. Past studies have suggested increased mobility during and post-spawn for male sea-run Atlantic salmon versus females (White 1936; Tentelier et al. 2016); potential movements over a small home range may not have been detected in our study. However, additional analyses of movement patterns in spawning sea-run Atlantic salmon have shown that while males with better habitat in their home ranges were more likely to visit more redds, mate frequently, and produce offspring, male size was not related to home range habitat quality or roaming (Tentelier et al. 2016). Thus, the availability of high-quality spawning habitat may be even more important to movement patterns than characteristics of individual fish. If older and larger males ascend the river first, they may have an advantage through earliest access to the best quality habitat; the extent that this could allow for increased mating success in the Crooked River is unclear.

By combining data on tagging and exit times, an approximation of total residency time could be examined. Note that this is likely underestimated, as PIT tag readers did not account for time spent in the lower 5.3 miles of the Crooked River. Overall, fish that entered the system later had a shorter residency time, which has been documented in similar analyses of residency time for salmonids (Neilson and Geen 1981; Jonsson et al. 1990). Data show that total duration of the spawning run was highly variable for individual salmon, and highly dependent on when fish entered the system. Some stayed in the river for barely more than two weeks, while others remained for nearly twelve. Still others may have initially ascended the river in the spring and remained through the fall run. As the initial date of spawning seems to be variable for individual salmon, the start of the spawning run may have a large physiological component. In contrast, the end of the run may be strongly environmentally driven and happen more absolutely than the start. Boucher and Warner (2006) suggested that some movements in spawning salmon may begin due to physiological changes but may be completed when habitat conditions shift. DeRoche (1982) similarly noted that salmon migration at the Bolsters Mills fish trap slowed and eventually ceased as water temperatures fell below 50°F (10°C) and 40°F (4.4°C), respectively. Whether due to water temperature, day length, reduced stream flow, a lack of remaining suitable spawning partners, or some combination of the above, when the run is over, it is over. It may then be advantageous to spawn earlier in the season, which may help further explain why older, more experienced fish had significantly earlier departure dates than younger fish. Though this study did not find any differences in date of initiation of spawning run by age class, there is evidence that sea-run Atlantic salmon spawn earlier at older ages (Niemela et al. 2006a; Niemela et al. 2006b), and that this timing is hereditary (Stewart et al. 2002). For landlocked salmon in the Crooked River, it appears age does affect some elements of the spawning run, including exit timing. The extent to which this timing may be hereditary was beyond the scope of this study and is unclear.

Repeat Spawning 2019/2020

Some insights were gained from analysis of repeat spawners, though sample size was very low. Returning spawners in 2019 and 2020 represented less than 1% of total fish tagged in 2018, which was even lower than poor return rates seen in Obrey and Bagley (2018) on the Roach River. Nevertheless, it seems unlikely that mortality rates of tagged fish were commensurate with return rates seen in this study. Survival estimates based on sizes of 2018 age classes predicted about a 50% mortality rate year-to-year for mature salmon, which would be nowhere near high enough to account for lack of returning tagged fish in 2019. While it has been documented that salmon may skip a year between spawning runs (Boucher and Warner 2006) and thus forgo spawning in 2019, 2020 returns were also far too low to be explained by mortality alone two years post-tagging. Additionally, nearly 17% of fish aged in 2018 were age VI+ or greater; after age V+, most wild Maine salmon will have spawned at least once (Boucher and Warner 2006). This suggests that repeat spawning rates are higher than observed via PIT tags and that the oldest salmon seen in this study may have been veterans of one or more spawning runs. Although most spawning salmon captured at the weir were younger fish likely spawning for the first time, this older component of the run is still important. As numerous studies have found differences in run timing, egg size, and fecundity of salmonids based on age class (Thorpe et al. 1984; Stewart et al. 2002; Quinn et al. 2011), these older spawners may provide a measure of spawning diversity for the Sebago Lake salmon population. It seems likely, then, that other factors along with mortality may have contributed to very low detections of PIT tags in years following weir operations. Tags lost through spawning or through normal activity over time likely contributed to reduced detection rates. However, it is also possible that the current lack of quality forage for salmon in Sebago Lake could have led to an increase in skipped spawning. Deficiencies in diet and nutrition are commonly linked to skipped spawning (Boucher and Warner 2006; Rideout and Tomkiewicz 2011), which may be an adaptive trait in some fishes (Rideout et al. 2005). For fish that spawn multiple times over the course of their lives, energy saved by skipping spawning when nutrition is poor may lead to increased survival, better future spawning success, and higher overall reproductive output (Rideout et al. 2005). Although it is unclear to what extent skipped spawning may be occurring among Sebago Lake salmon, current poor forage conditions and strong competition in the lake may play a role.

Conclusions and Recommendations

This study, along with previous efforts in the Moosehead Lake region (Obrey and Bagley 2018), demonstrates that a picket weir can be highly effective at gathering information on salmonid spawning runs. Paired with PIT tags or other types of telemetry studies, a wealth of useful and enlightening data can be collected on run timing and numbers, age and growth parameters, and salmon behavior. Additionally, proper operation results in very low mortality to spawning fish. In the Crooked River, the 2018 salmon run remained within recent estimates numerically but indicated signs of stress on salmon in Sebago Lake. Low returns of tagged fish across the following years may have also been impacted by current poor forage conditions in the lake, though more data is necessary to determine. Recent efforts to curb the expanding Lake Trout population in Sebago Lake, including liberalizing regulations and encouraging harvest, should continue. It will take time to reduce strong interspecific competition and rebuild the forage base, but salmon quality can rebound. Continued protection of salmon during the fall spawning period is also imperative, particularly as the run can be long and variable. Similarly, the importance of the Crooked River to the existence of a self-sustaining, wild population of salmon in Sebago Lake cannot be overstated. As the human population of Southern Maine continues to grow and additional pressure is placed on aquatic resources, strong protections should be in place to ensure continued quality of spawning habitat. Any improvements to high-use spawning reaches around Edes

Falls and Bolsters Mills, including removal of defunct dam structures to enhance connectivity, have the potential to further boost self-sustaining spawning runs. In a changing climate with increasing potential for extreme weather conditions, including droughts and low water, remnants of historical dam structures may present more problems than ever before.

For future monitoring, periodic redd surveys of the Crooked River and major tributaries conducted roughly every five years provide an excellent way to indirectly measure the spawning run, while simultaneously assessing any changes to spawning habitat. Thermal profile surveys of the Crooked River may also be a useful tool to monitor salmonid habitat as climate conditions in Maine continue to change. Additionally, use of a smolt trap in the Crooked River to assess the ultimate contribution of smolts to the lake fishery would provide further information on natural rates of recruitment. Finally, long-term sampling plans could consider repeating this weir study if special concerns about the wild salmon population may arise. Though weir operation is a labor-intensive endeavor, it has proven to be the best available method to safely and effectively sample a large proportion of the wild, adult salmon population of Sebago Lake.

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Appendices

Appendix I: Additional Comparisons, Ages III+ and IV+

Table A1. Comparisons between male and female salmon for age III+ and age IV+ classes captured at the weir. Blue shaded cells indicate a significantly higher mean value for males; red shaded cells indicate a significantly higher mean value for females; unshaded cells indicate no difference between sexes.

	Length	Weight	K Factor
Age III+	$F_{1,301}=5.085$, $p=0.025$	$F_{1,300}=0.2884$, $p=0.592$	$F_{1,297}=15.97$, $p<0.005$
Age IV+	$F_{1,180}=0.6584$, $p=0.418$	$F_{1,180}=1.973$, $p=0.162$	$F_{1,180}=38.81$, $p<0.005$

Appendix II: Additional Comparisons with Historical and Hatchery Data

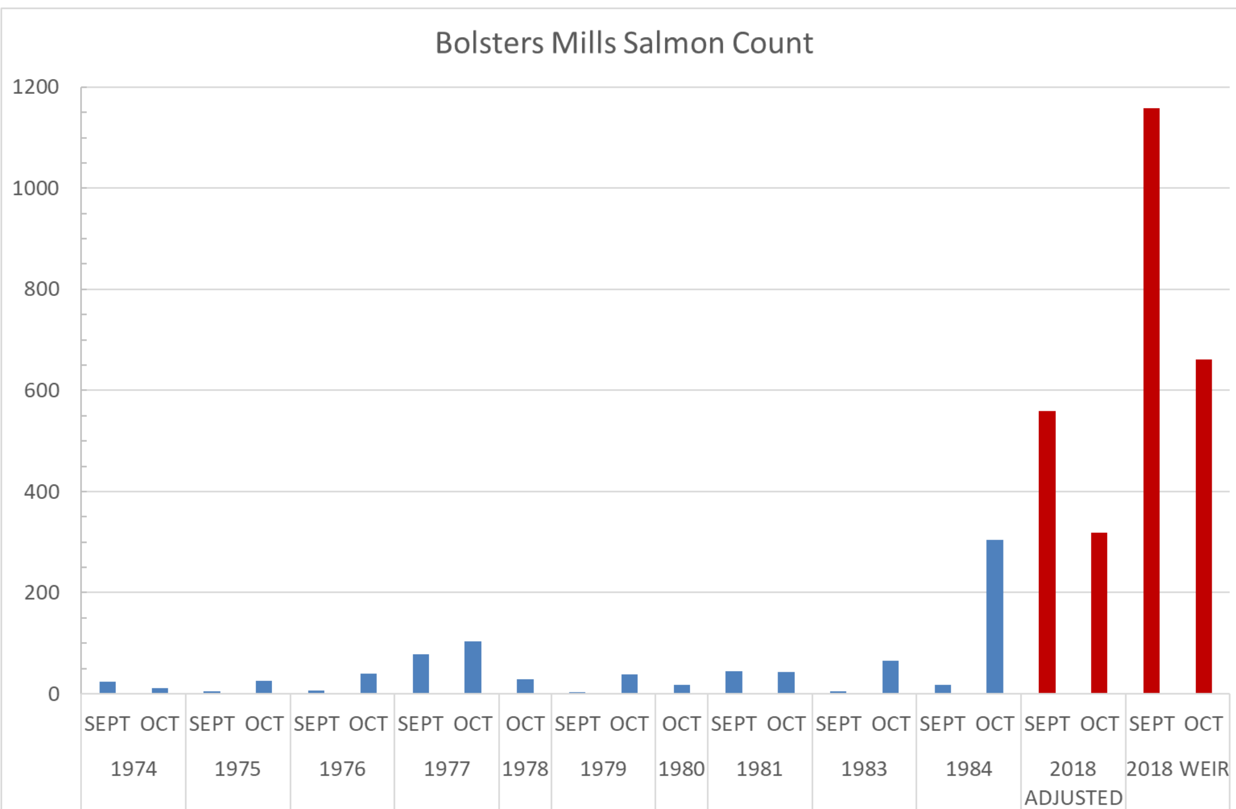

Figure A1. Comparison of September-October salmon counts at the historical Bolsters Mills fish trap and 2018 weir operations. Adjusted weir counts represent 48.3% of 2018 totals to account for the fact that only 48.3% of spawning redds were located above Bolsters Mills in previous counts.

Table A2. Mean length, weight, and condition factor by age class for salmon captured both at the weir (wild fish only; top) and at the Jordan River Fish Trap in 2018 (bottom), plus/minus standard errors of the means. Weight and condition factor were only calculated from males.

Age	n	Mean Length (in)	Std. Error		n	Mean Weight (lb)	Std. Error		n	Mean K Factor	Std. Error
II+	2	11.77	0.43		2	0.53	0.01		2	0.90	0.08
III+	303	16.12	0.52		228	1.21	0.13		228	0.80	0.05
IV+	182	18.32	0.71		86	1.74	0.25		86	0.77	0.04
V+	76	19.32	0.85		34	2.07	0.33		34	0.77	0.03
VI+	57	20.74	1.01		26	2.61	0.38		26	0.75	0.03
VII+	34	22.09	1.04		14	3.49	0.35		14	0.79	0.03
VIII+	19	22.95	1.00		9	3.76	0.49		9	0.75	0.04
IX+	3	24.07	0.34		1	6.39	n/a		1	1.19	n/a
Unknown	15	19.25	2.14		9	1.70	0.79		9	0.81	0.03
Wild Fish	**683**	**17.97**	**0.09**		**409**	**1.64**	0.54		**409**	**0.79**	0.05
II+	16	16.09	0.11		7	1.23	0.07		7	0.80	0.04
III+	89	19.71	0.10		25	2.41	0.10		25	0.79	0.01
IV+	7	22.06	0.53		2	4.25	0.64		2	0.88	0.02
V+	6	23.01	1.32		2	5.95	0.22		2	0.83	0.01
VI+	1	21.06	N/A		--	--	--		--	--	--
JR Fish	**119**	**19.54**	**0.18**		**36**	**2.48**	**0.20**		**36**	**0.80**	**0.01**

Table A2 displays detailed age and growth parameters for salmon collected at the Jordan River Fish Trap, all of which were hatchery origin in 2018, along with wild fish captured at the weir. Jordan River females were stripped of eggs prior to measurements and so were not used in calculations of mean weight or condition factor. Jordan River fish were on average both longer ($F_{1,808}$=45.53, p<0.001) and heavier ($F_{1,448}$=32.6, p<0.001) than wild fish captured at the weir, but mean condition factor was not different ($F_{1,448}$=1.43, p=0.232). Though sample size was much smaller for Jordan River salmon (n=119 vs. 683), overall discrete survival rate for ages III+ to IV+ was calculated as 25.6%. This estimated survival rate was about half of that seen for fish captured at the weir (50.4%).

Appendix III: Individual Case Studies

This study, by necessity, looked primarily at population-wide trends in salmon movement and behavior. However, it can be instructive to also look at specific movements by a few individuals as well. Examining movement on an individual basis drives home how far and fast some of these fish were capable of moving.

One of the first fish tagged was implanted with tag number 006 on Sept. 12. This fish was an age IV+ male, and in many ways was representative of movement in the lower reaches of the river. It was detected as far as Edes Falls, and likely spent time in the reach of spawning habitat between Edes Falls and Bolsters Mills that is commonly utilized by salmon. It remained in the river for about two months and was last detected heading downstream at the Lower Weir site on Nov. 11. During its residency, it was detected once at each antenna heading upstream to Edes Falls, and once at all antennas heading downstream as well.

In contrast to fish 006, it is useful to look at a salmon that was tagged later and traveled much further in the Crooked River. An age VI+ female was implanted with tag number 307 on Oct. 5 and was detected as far as the maximum upstream antenna in Waterford. Additionally, fish 307 was detected once at all antennas moving upstream and once at all antennas moving downstream, a complete picture rare for fish that traveled as far as Waterford. This salmon stayed in the Crooked River for about a month and a half, not surprisingly spending less time in the river than fish 006 due to its later arrival date.

One of the last fish tagged shows yet another pattern of movement. An age IV+ male was tagged on Oct. 29, the last date of weir operations, with tag number 493. This fish eventually made it as far upstream as Edes Falls, but primarily moved back and forth between the Lower and Upper Weir sites over the course of about a month. The proximity of these two sites shows many small movements that would not be detected around single antenna locations further upstream and suggests further caution when interpreting the lack of roaming documented in this study. For example, both fish 006 and 307 went long stretches between detections once they reached their maximum distances upstream. This may be indicative of a pattern of shorter movements that might be seen in fish that have chosen a preferred spawning location, suggestive of the pre-spawn “holding” phase seen in sea-run Atlantic salmon

(Øklamd et al. 2005). In the case of fish 493, this location was somewhere around or between the two weir antennas. It is likely that fish 493 attempted to spawn in the riffle habitat where the weir was located, as this is the only stretch of cobble and gravel nearby. Fish 493 also remained in the river until well in December and was one of the final detections recorded before antennas were removed.

When movement patterns for these three fish are plotted next to each other (Figure A2), some differences become easier to perceive. For example, a later-arriving fish like number 307 moved very quickly to its preferred spawning reach, in contrast to the more leisurely pace of fish 006. Fish 493 arrived latest of all, but barely traveled upstream and so quickly reached its preferred spawning reach as well. It is also evident that fish 006 arrived earliest and stayed longest, despite never traveling beyond ten river miles from the mouth of the river. Overall, these three fish represent just a few of the possible movement patterns that spawning salmon display and point to the high variability that can be seen between individual fish.

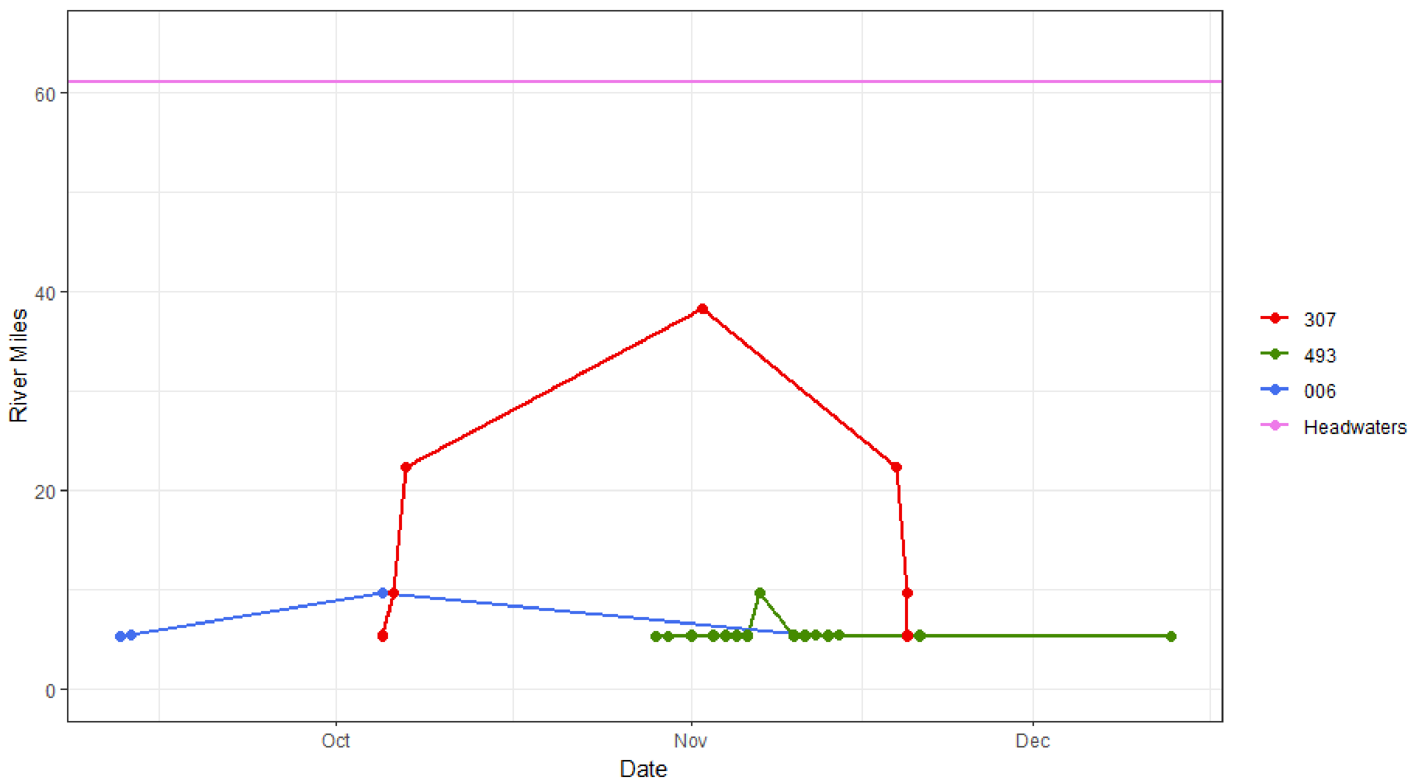

Figure A2. Variation in movement patterns among three tagged salmon, numbers 006, 307, and 493. Purple "headwaters" line represents the source of the Crooked River and shows relative areas in the drainage utilized by each fish.

Appendix IV: Angler Reported Tag

In April 2020, fisheries staff were contacted by an angler who had recently caught a Burbot (*Lota lota*; often referred to as "cusk" in Maine) in Sebago Lake. In the stomach of the fish was a PIT tag (Figure A3), implanted into a spawning salmon in the Crooked River over a year and a half earlier. After the angler returned the tag to biologists, the tag was scanned with a handheld PIT tag reader. The tag was still fully operational despite its tumultuous journey, proving a testament to the durability of PIT tags over long-term studies. Scanning showed that the tag belonged to a male salmon tagged on Sept. 24, 2018. The salmon was 20" and 2.1 lbs. at time of capture at the weir. The salmon retained its PIT tag throughout the spawning season, as it was detected at Edes Falls on Nov. 18 and the Upper Weir antenna on Nov. 19, moving downstream on its way back to Sebago Lake. After that, it is unclear what may have happened. Perhaps the salmon died, fell to the lake bottom, and was then consumed by the burbot. Alternatively, the salmon may have dropped its tag, which was then consumed by either the burbot or by another fish which was then itself consumed. Regardless, it is remarkable that this tag was ever found again and demonstrates the strong interconnectedness between the Crooked River and all depths of Sebago Lake.

Figure A3. Tag recovered by a Sebago Lake angler from the stomach of a burbot (photo credit: Kyle Pepin).

COOPERATIVE

STATE **FEDERAL**

PROJECT

This report has been funded in part by the Federal Aid in Sport Fish Restoration Program. This is a cooperative effort involving federal and state government agencies. The program is designed to increase sport fishing and boating opportunities through the wise investment of angler's and boater's tax dollars in state sport fishery projects. This program which was founded in 1950 was named the Dingell-Johnson Act in recognition of the congressmen who spearheaded this effort. In 1984 this act was amended through the Wallop Breaux Amendment (also named for the congressional sponsors) and provided a threefold increase in Federal monies for sportfish restoration, aquatic education and motorboat access.

The program is an outstanding example of a "user pays-user benefits" or "user fee" program. In this case, anglers and boaters are the users. Briefly, anglers and boaters are responsible for payment of fishing tackle, excise taxes, motorboat fuel taxes, and import duties on tackle and boats. These monies are collected by the sport fishing industry, deposited in the Department of Treasury, and are allocated the year following collection to state fishery agencies for sport fisheries and boating access projects. Generally, each project must be evaluated and approved by the U.S. Fish and Wildlife Service (USFWS). The benefits provided by these projects to users complete the cycle between "user pays – user benefits."

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