North American Journal of Fisheries Management 29:495–505, 2009

DOI: 10.1577/M08-042.1

[Article]

Movements of Prespawn Adult Atlantic Salmon Near Hydroelectric Dams in the Lower Penobscot River, Maine

CHRISTOPHER M. HOLBROOK[1]
School of Biology and Ecology, University of Maine, Orono, Maine 04469, USA

JOSEPH ZYDLEWSKI*
Maine Cooperative Fish and Wildlife Research Unit, U. S. Geological Survey,
University of Maine, Orono, Maine 04469, USA

DIMITRY GORSKY
Department of Wildlife Ecology, University of Maine, Orono, Maine 04469, USA

STEVEN L. SHEPARD
Aquatic Science Associates, Inc., Brewer, Maine 04412, USA

MICHAEL T. KINNISON
School of Biology and Ecology, University of Maine, Orono, Maine 04469, USA

Abstract.—Acoustic telemetry was used to assess riverine behavior and passage success for prespawn male adult Atlantic salmon *Salmo salar* in the lower Penobscot River, Maine, in 2005 ($n = 10$) and 2006 ($n = 25$). Only 3 of 10 (30%) and 2 of 25 (8%) tagged Atlantic salmon successfully passed all three dams between the head of tide and presumed spawning habitat in 2005 and 2006, respectively. Migrants that failed to pass the second upstream dam frequently fell back into the estuary (3 of 4 in 2005; 17 of 23 in 2006), and few successfully reascended Veazie Dam at the head of tide. Fallback behavior was associated with temperatures exceeding 22°C and may reflect a strategy for coping with thermal stress and migratory delays. Atlantic salmon were also observed to actively seek out thermal refuge near one of the dams. Passage data were compared with results from previous telemetry studies that used Carlin tags and radio telemetry from 1987–1990 and 1992, and passive integrated transponder tags from 2002–2004. For all 10 years of study combined, median passage success was 64, 72, and 93% for the three dams. While 2006 may represent an uncommonly poor year for upstream passage at these dams, median cumulative passage past two of these dams was only 71% and ranged from 8% to 87% among years. Study results indicate that poor upstream passage severely limits migratory success in this system, particularly during periods of high discharge. Planned removal of two of these lower river dams is expected to improve migratory success for adult Atlantic salmon in the Penobscot River system.

Populations of Atlantic salmon *Salmo salar* in Maine have declined and remain low, despite extensive supplementation efforts dating back to the late 1800s (Baum 1997). Dams have been identified as being one of the most acute impediments to restoration of Atlantic salmon in the United States (NRC 2004). In the Penobscot River, which hosts the largest remaining run of adult Atlantic salmon in the United States (USASAC 2005), all high-quality spawning and rearing habitats that are currently available are located upstream of at least four hydroelectric dams (Fay et al. 2006). Three of these dams (Veazie, Great Works, and Milford) are located within 15 km from the head of tide (Figure 1). Plans are currently underway to remove the two downstream-most dams (Veazie and Great Works) as part of the Penobscot River Restoration Project. Ultimately, the benefits of dam removal for Atlantic salmon restoration will depend in large part on the degree and fashion by which these dams currently affect salmon passage success and behavior.

Økland et al. (2001) suggested that in the absence of barriers, Atlantic salmon migration consists of three behavioral phases: directed upstream movement toward spawning grounds, slow searching behavior in the vicinity of spawning grounds, and long periods of station-holding near spawning grounds. As complete or partial barriers to migration, however, dams cause

---

*Corresponding author: jzydlewski@usgs.gov
[1] Current address: United States Geological Survey, Columbia River Research Laboratory, Cook, Washington 98605, USA.

Received February 26, 2008; accepted July 30, 2008

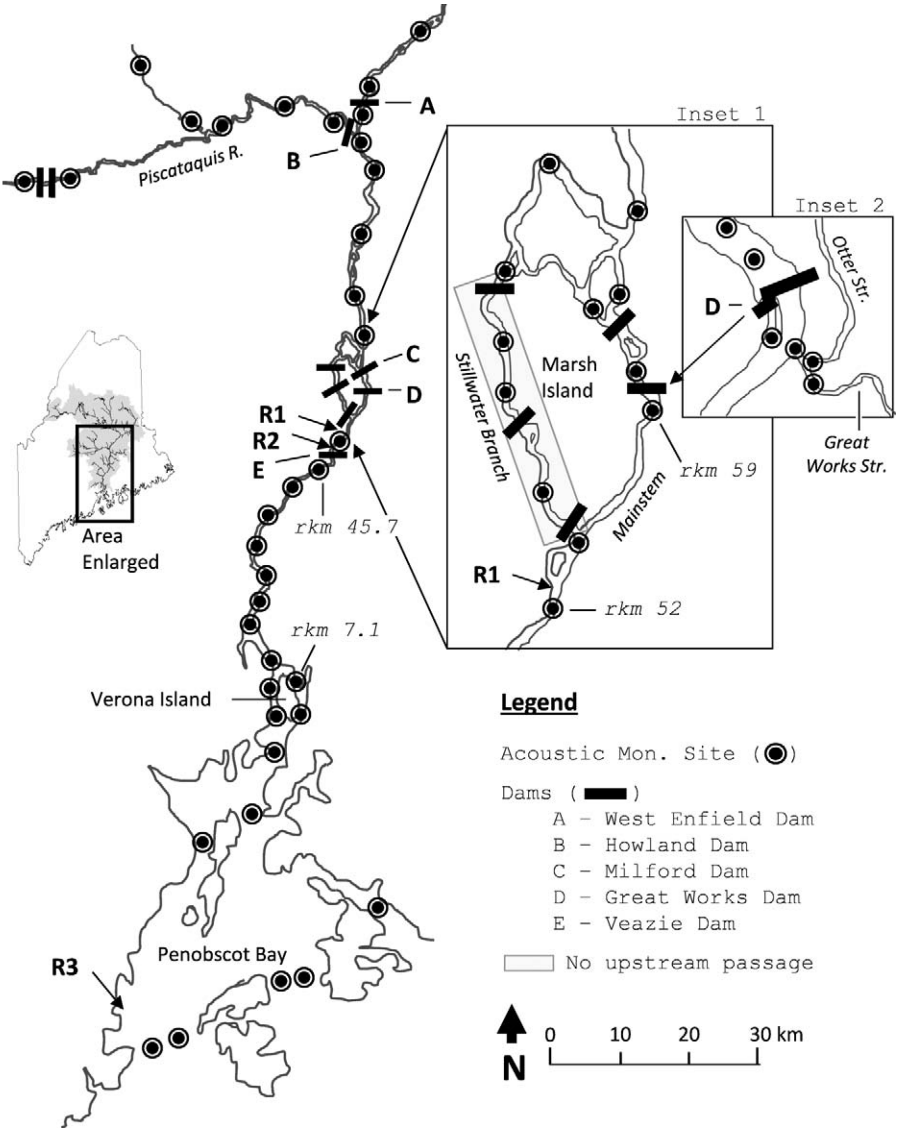

FIGURE 1.—Map of the Penobscot River showing dams, acoustic monitoring sites, and release sites in the Veazie Dam Reservoir in 2005 (R1) and 2006 (R2) and in Penobscot Bay (R3). Inset 1 shows monitoring sites in the vicinity of Marsh Island. Inset 2 provides further detail of receiver locations in the vicinity of Great Works Stream.

delays that may reduce the probability of survival or the energetic reserves needed for spawning success (Dauble and Mueller 1993; Gowans et al. 2003). Moreover, increased expenditures of energy during migrations can rob from resources otherwise allocated to egg production (Kinnison et al. 2001), secondary sexual traits (Kinnison et al. 2003), and adult survival following reproduction.

In particular, migratory delays that occur in lower river habitats may increase exposure to predators or to sub-optimal water quality. High summer temperatures can be a significant stressor and result in increased metabolic demand. This may be particularly problematic for Atlantic salmon delayed in the lower reaches of systems like the Penobscot River. In other systems, migrating salmonids are known to seek refuge in cooler tributaries or springs during periods of high temperatures (Keefer et al. 2004; Goniea et al. 2006). However, the availability of coolwater tributaries is limited between dams in the lower Penobscot River.

The primary goal of this study was to evaluate passage success and behavior of upstream migrating

Atlantic salmon in the vicinity of the lower three dams in the Penobscot River. Movement and body temperature data were used to illustrate the combined effects of migratory delays and high temperatures on passage success, thermal refuge use, and migratory abandonment in the current hydrological state. Passage data were compared with historic passage studies to provide a synthesized assessment of the impact of the lower three dams on passage success of Atlantic salmon in the Penobscot River. Results provide an important baseline to both predict and assess the outcomes of future hydro-system modifications.

Methods

Study site.—The Penobscot River watershed drains about 22,000 km^2 within the state of Maine and is tidal up to the Veazie Dam (Fay et al. 2006). Migrating adult Atlantic salmon enter freshwater from May through October, with peak migration occurring in June and early July. The three lowermost dams in the main stem are the Veazie, Great Works, and Milford dams at river kilometers (rkm, measured from the mouth of the Penobscot River) 48, 60, and 62, respectively (Figure 1). Three additional dams are located in the west channel around Marsh Island (i.e., Stillwater Branch), but these are not equipped with upstream passage structures. Further upstream, dams are located just upstream of the two major branches at rkm 99. These dams are located at rkm 100 on the western branch (Howland Dam on the Piscataquis River) and rkm 101 on the eastern branch (West Enfield Dam on the Penobscot River).

With the exception of dams in the Stillwater Branch, upstream fish passage is provided through Denil-type or vertical slot fishways. Integrated downstream bypass facilities are only installed at one of these dams (West Enfield Dam). Downstream passage at other dams has been retrofitted at waste gates, log sluices, spillways, and vacant turbine bays. All of these dams use temporary flashboards that increase electric generating head during periods of low to moderate discharge but are designed to fail during high discharge to prevent flooding. Flashboards are typically reinstalled when seasonal high discharge subsides to levels that permit safe installation (usually during spring or early summer). Flashboard installation is generally considered to improve upstream fish passage by minimizing spill and focusing attraction water near upstream fishways (as flashboards have little effect on net river flow past the dam). However, because water levels at Great Works Dam must be lowered to the spillway crest to safely reinstall the flashboards, there is typically a period when the two Great Works fishways are nonfunctional due to low water levels that reduce flow into the fishways (Scott Hall, PPL Maine, personal communication). Flashboards were installed at the Great Works Dam on June 13, 2005 and August 14, 2006.

Great Works and Otter streams are two small tributaries that combine as they enter the Penobscot River about 200 m below Great Works Dam. We refer to these streams collectively as Great Works Stream. The Otter Stream channel was stagnant during most of the study period, whereas the Great Works Stream channel maintained noticeable flow.

Passive acoustic telemetry array.—An array of up to 117 stationary acoustic receivers (VR2; Vemco, Halifax, Nova Scotia) was deployed in the Penobscot River, estuary, and bay and maintained from April through December in both 2005 and 2006 (Figure 1). Receivers were deployed to cover the entire width of the system at 40 sites and monitored continuously at 69 kHz. In some instances (e.g., wide river sections or islands) several acoustic receivers were necessary for complete "bank-to-bank" coverage. Detections on these receivers were pooled and treated as a single site. Receivers were moored on the bottom of the river at freshwater and estuarine sites, and placed approximately 10 m below the water surface in Penobscot Bay. Reservoir receivers were strategically placed to detect tagged Atlantic salmon within 500 m of each dam following successful upstream passage.

Receivers were omni-directional and had a detection range that likely exceeded the width of the river. Thus, we were unable to determine specific upstream or downstream passage routes at dams. Mobile tracking and testing indicated that the detection range exceeded 500 m in the typical riverine environment. True detection ranges were unknown, but probably varied among locations and times due to differences in entrained air, ambient acoustic noise, and bathymetry. Regardless, upstream detection data indicated that detection probabilities at monitoring sites immediately upstream of each dam were 1.0 (i.e., no tagged salmon passed any dam undetected during the study).

Tagging and release of Atlantic salmon.—Returning male adult Atlantic salmon (2005: $n = 10$, 2006: $n = 25$; Table 1) of smolt-stocked hatchery origin (first generation offspring from river-run adults) were collected at an upstream fishway trap at the Veazie Dam that is operated by the Maine Atlantic Salmon Commission. Gender was determined by morphological assessment and rearing origin was identified by scale evaluation or appearance of external tags at time of capture. Length was recorded at time of capture and fish were anesthetized in a tricaine methanesulfonate solution (100 mg/L, 0.20 mM $NaCO_3$, pH = 7.0). Anesthetic was continually poured over the gills during

TABLE 1.—Age, number (*N*), median fork length (FL), release dates, and release sites for tagged male Atlantic salmon in 2005 and 2006. 2SW indicates return after two winters at sea; 1SW indicates return after one winter at sea.

Year	Age	*N*	FL (cm, range)	Release dates	Release site
2005	2SW	5	75.0 (71.0–77.0)	6/20–6/21	Penobscot Bay
	2SW	5	74.0 (71.0–77.0)	6/21	Veazie Dam Reservoir
2006	2SW	19	77.0 (72.0–79.0)	6/2–6/7	Veazie Dam Reservoir
	1SW	6	55.5 (50.0–58.0)	6/3–6/5	Veazie Dam Reservoir

surgery to provide ventilation. Acoustic transmitters (V9P-2 L or V13TP-1H, Vemco) were surgically implanted into the abdominal cavity through a ventral incision. The incision was closed in three places with coated Vicryl 3–0 absorbable sutures (Ethicon, Inc., Somerville, New Jersey). The V9 transmitters (used in 2005) were cylindrical (9 × 46 mm), weighed 2.6 g in water, and had an estimated transmission life of 253 d. These tags also provided data on depth at detection. The V13 transmitters (used in 2006) were also cylindrical (13 × 45 mm), weighed 6.0 g in water, and had an estimated transmission life of 184 d. These tags provided data on both depth and tag temperature at detection. Each transmitter emitted a unique code on random intervals ranging from 30 to 90 s. Proper operation of tags was verified prior to implantation and during postsurgery holding. Each fish received an external T-bar anchor tag and adipose punch for future identification by trap personnel. All salmon were held in river water for a minimum of 30 min postsurgery before release.

In 2005, a total of five implanted Atlantic salmon were transported (via truck) in an 800-L tank with aeration about 95 km downstream and released in Penobscot Bay on June 20 and 21. On June 21, an additional five Atlantic salmon were transported approximately 5 km upstream and released in the Veazie Dam Reservoir. In 2006, all 25 implanted salmon were released 200 m upstream of the Veazie Dam, between June 2 and 7. For all releases, ice was added periodically to holding and transport tanks to maintain constant water temperature or to match the temperature of ambient water in the river and bay.

Passage analyses.—Because of the lack of suitable rearing habitat in the lower river, we considered passage at Milford Dam a requisite for successful migration. Thus, we considered an "unsuccessful migrant" to be any tagged Atlantic salmon that failed to pass or remain upstream of the Milford Dam. The study region was further divided into four river segments: the estuary (between rkm 7.1 and Veazie Dam; Figure 1), the Veazie Dam Reservoir (between the Veazie and Great Works dams), the Great Works Dam Reservoir (between the Great Works and Milford dams), and the Milford Dam Reservoir (between the Milford and West Enfield or Howland dams). It was assumed that all tags were retained and functioned properly throughout the study period. Passage success through each segment was defined as the proportion of all fish known to have entered a segment that in turn were detected in the next upstream segment. When no fish were released below a dam in a given study year, these estimates were based on fish that descended back (i.e., "fell back") past a dam and subsequently reapproached the facility. Fallback behavior was defined as a detected downstream movement greater than 5 km or any descent past a dam.

The initial approach time to Veazie Dam was calculated for each tagged Atlantic salmon as elapsed time between last detection at rkm 7.1 and first detection at rkm 45.7. The approach time to Great Works Dam was calculated as elapsed time between last detection at rkm 52 and first detection at rkm 59. Approach rates were calculated by dividing the approach time for each tagged salmon by the distance (rkm) between monitoring sites. Approach time and rate were not calculable for Milford Dam because no receivers were positioned in the upstream half of the Great Works Dam Reservoir. Dam passage times at individual dams represent the number of days between initial approach (first detection at immediate downstream receiver) and successful passage (first detection at immediate upstream receiver). The closest receivers were located about 2300, 250, and 1600 m downstream and about 550, 400, and 900 m upstream of each of the Veazie, Great Works, and Milford dams, respectively. We were not able to position receivers closer to the Veazie and Milford dams on the downstream side because high water velocities, excessive air entrainment, and complex bathymetries prevented adequate detection ranges at those sites.

Environmental data collection and analyses.—River discharge was measured for the Penobscot River at West Enfield (rkm 100) by the U.S. Geological Survey (USGS) and obtained for this study through the USGS National Water Information System <http://waterdata.usgs.gov>. Water temperatures were recorded at 30–60 min intervals by temperature loggers (WaterTemp

Pro; Onset Computer Corporation, Bourne, Massachusetts) located on the bottom of the river in the Great Works Dam Reservoir (main stem) and in Great Works Stream. Relative temperature differences between Great Works Stream and the main stem of the Penobscot River were calculated from hourly mean values from July 1 to July 15, 2006. We used simple linear regression to determine if a significant relation existed between mean daily discharge and temperature during the period June 1 to July 31 of each year. All statistical analyses were performed in the "R commander" package of the software program R (Fox 2005). The significance level (α) was set at 0.05 for all tests.

The hourly mean temperature for each fish was calculated between July 1 and 15, 2006. To determine if tagged Atlantic salmon were using Great Works Stream for behavioral thermoregulation, and the thermal costs or benefits of this behavior, the temperatures obtained from salmon tags were compared to temperatures recorded by the loggers in the main stem and Great Works Stream. The abundance of tagged salmon in Great Works Stream was also compared with that of the main stem by comparing the number of individual fish detected at each receiver within hourly intervals. Because of the perceived bathymetry, receiver positions, and extensive mobile tracking within this location, it was assumed that the receiver in the main stem could detect fish in Great Works or Otter streams, but the receiver in Great Works Stream could not detect fish in the main stem. Thus, for each hourly interval, we determined the number of tagged salmon in the main stem by subtracting the number of fish at Great Works Stream from that of both main stem and stream receivers combined.

Assessment of historical passage data.—Upstream passage success was assessed through the lower Penobscot River between 1987–1990 and in 1992 by means of Carlin tagging and radio telemetry, and between 2002–2004 by means of passive integrated transponder (PIT) telemetry. Data from these studies were reassessed using the criteria described above for passage success and fallback. We used simple linear regression to relate mean daily discharge to passage success estimates at each dam. Annual cumulative passage success over multiple dams was calculated as the product of passage success estimates through contiguous reaches.

As with acoustic telemetry studies, all historic passage studies used river-run adult Atlantic salmon that were captured at the upstream fishway trap at Veazie Dam. Carlin-tagged salmon were released below Veazie Dam and enumerated upon recapture at Veazie Dam (Shepard 1995). Radio tagged salmon were released at several locations throughout the migratory season and were detected by stationary antennae at each dam and by mobile tracking throughout the study area. All PIT-tagged salmon were released immediately above the Veazie Dam and detections were provided by PIT antennae at the entrance and exit of each fishway on each dam (Gorsky 2005). Since PIT-tagged fish were only detected within upstream fishways, fall-back frequencies derived from PIT data represent only fish that fell back over Veazie Dam and subsequently reentered the upstream fishway.

Results

2005 Passage Success

The acoustic array provided detailed tracks for 8 of the 10 Atlantic salmon that were tagged and released; four that were released in Penobscot Bay and four that were released in the Veazie Dam Reservoir. Of the five tagged salmon released in Penobscot Bay, one was never detected after release and four were detected entering the estuary at rkm 7.1. All four tagged salmon that entered the estuary were known to approach Veazie Dam, and two successfully passed the dam. Initial approach rates to Veazie Dam were 20, 42, 56, and 66 km/d, with approach times ranging from 0.6 to 2.0 d. Additionally, two fish released in the Veazie Dam Reservoir fell back and eventually re-ascended Veazie Dam. Individual dam passage times were 2.0 and 3.3 d for fish released in Penobscot Bay and 58.0 and 88.7 d for fish that were released upstream and fell back over Veazie Dam.

A total of seven tagged Atlantic salmon were present between the Veazie and Great Works dams. Of these, three (43%) passed the Great Works Dam, three (43%) approached the Great Works Dam but did not pass, and one (14%) was never detected. Initial approach rates to Great Works Dam were 4.3 and 7.8 km/d for fish released in Penobscot Bay and ranged from 0.9 to 1.6 km/d for fish released in the Veazie Dam Reservoir, with approach times ranging from 0.9 to 1.9 d and 4.1 to 7.0 d, respectively. Successful passage at Great Works Dam occurred when discharge ranged from 166 to 261 m^3/s, and individual dam passage times were 1.9, 13.1, and 25.4 d. All three tagged fish subsequently passed the Milford Dam 0.1, 2.9, and 3.7 d after passing the Great Works Dam. Of the seven fish that remained downstream of Great Works Dam at the end of the study period, one was last detected immediately below the Great Works Dam, two were last detected immediately upstream of the Veazie Dam, two were last detected in the estuary, and two were never detected after release.

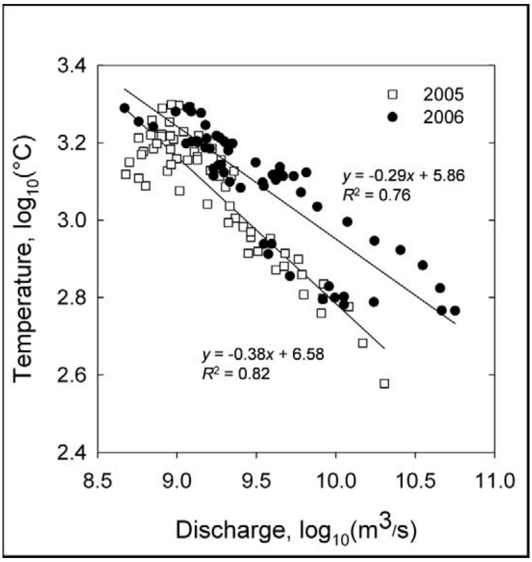

FIGURE 2.—Mean daily temperature of the Penobscot River as a function of mean daily discharge during the period June 1–July 31, 2005 (open squares) and 2006 (closed circles).

2006 Passage Success

The acoustic array provided detailed tracks for all 25 Atlantic salmon tagged and released in the Veazie Dam Reservoir in 2006. Eleven fish released in the Veazie Dam Reservoir fell back over the dam prior to October 1. Of these fish, seven reapproached Veazie Dam but only three (43%) successfully reascended. Individual dam passage times were 2.1, 6.8, and 58.4 d.

All 25 tagged Atlantic salmon released into the Veazie Dam Reservoir were known to move upstream following release and approach the Great Works Dam. However, only 3 of 25 (12%) passed the dam, and one of these three fish fell back into the Veazie Dam Reservoir within 3 d of ascent. Initial approach rates to Great Works Dam ranged from 0.3 to 7.6 km/d (median = 2.4 km/d). Approach times ranged from 0.9 to 27.7 d (median = 2.9 d) but exceeded 11.0 d for only one fish. All three successful passages at Great Works Dam occurred from June 15 to 16, prior to flashboard installation and when discharge was 795–938 m^3/s. Individual dam passage times for these three fish were 8.6, 8.7, and 12.5 d. Of the three fish that passed the Great Works Dam, two subsequently passed the Milford Dam 2.2 and 2.3 d later. Of the 23 fish that remained downstream of Great Works Dam at the end of the study period, 5 were last detected in Great Works Stream, 3 were last detected in the main stem immediately below Great Works Dam, 4 were last detected immediately upstream of Veazie Dam, and 11 were last detected in the estuary or bay.

River Temperature, Discharge, and Fallback Behavior

Mean daily temperature in the Great Works Dam Reservoir reached a maximum of 27°C in both 2005 and 2006 and fluctuated as much as 2°C daily. Mean daily temperature was inversely related to discharge during the months of June and July in both years (Figures 2 and 3a; 2005: $R^2 = 0.82$, $p < 0.001$; 2006: $R^2 = 0.76$, $p < 0.001$). In 2005, 75% (three of four) of tagged salmon that failed to pass Great Works Dam fell back to Veazie Dam (two fell back over Veazie Dam; one passed downstream toward Veazie Dam and was never again detected) during the months of June and July. Fallbacks occurred 2.8, 21.8, and 28.3 d after initial approach to Great Works Dam. In 2006, 74% (17 of 23) of unsuccessful migrants exhibited at least one fallback during the months of June, July, and August (Figure 3b). Initial fallbacks during this period occurred 3.6–40.0 d (median = 17.2 d) after initial approach to Great Works Dam. Fourteen fish fell back to Veazie Dam (11 passed downstream over Veazie Dam; 3 passed downstream toward Veazie Dam and were never again detected) as a result of fallbacks prior to October 1. We were unable to confirm the disposition of the four fish that were never detected after falling back toward Veazie Dam because these fish were never again contacted. These fish may have died just prior to or during downstream passage and remained close to the dam (i.e., out of range of the downstream receiver) or survived downstream passage and remained close to the dam for the duration of the study without passing. All fallbacks (except one in late September) occurred when mean daily main stem river temperature exceeded 22°C.

Great Works Stream reached a maximum temperature of 30°C during the summer months, and fluctuated as much as 7°C daily. Between July 1 and 15, the stream was cooler than the main stem during morning hours and warmer than the main stem during afternoon hours (Figure 4a). Mean fish body temperatures in the vicinity of the confluence of Great Works Stream and the main stem reached a minimum at 0600–0800 hours. Fish body temperatures were more similar to stream temperatures during morning hours and to main stem temperatures during afternoon hours. More tagged fish were detected in the stream than in the main stem between 0500 and 1400 hours (Figure 4b).

Historic Passage Success and Fallback

Passage success (as determined by radio/Carlin and PIT telemetry) through reaches downstream of the Veazie, Great Works and Milford dams ranged from 44% to 100%, 38% to 95%, and 86% to 100%, respectively, among 8 years of study (1987–1990,

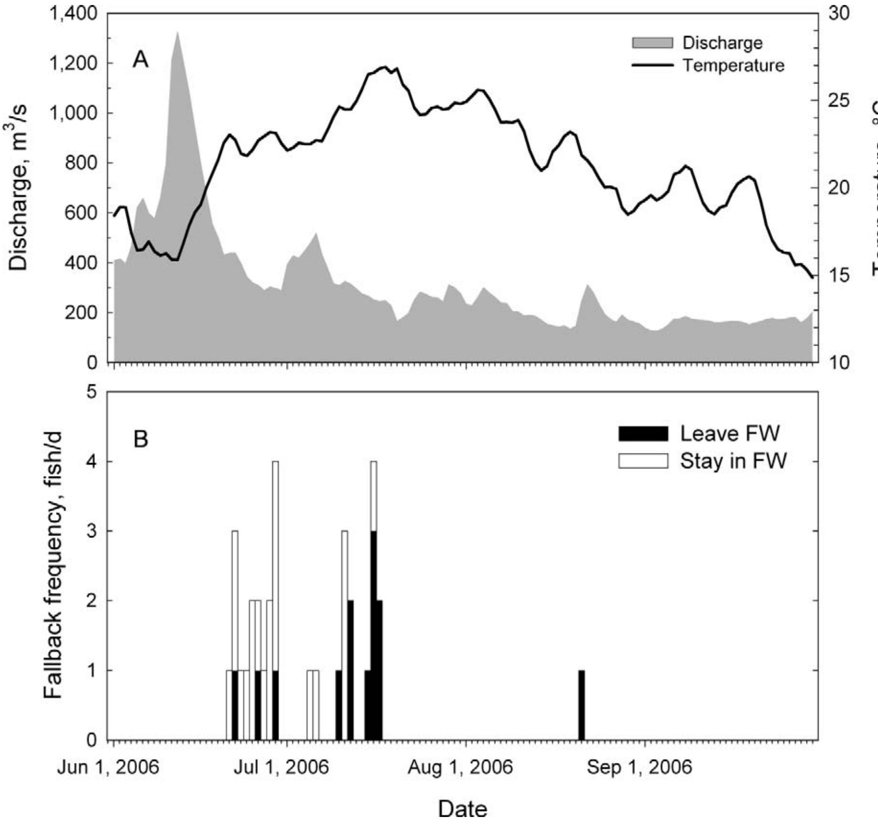

FIGURE 3.—**(A)** Temperature and discharge for the Penobscot River in 2006, with **(B)** daily fallback frequencies (stacked bars) for tagged Atlantic salmon located between the Great Works and Veazie dams (June–September 2006). Empty bars denote fallbacks that occurred entirely within freshwater (stay in FW); shaded bars denote fallbacks that resulted in estuarine entry (leave FW; i.e., passage over Veazie Dam).

1992, 2002–2004; Figure 5). When acoustic telemetry data from 2005 and 2006 are included, annual passage success at the Great Works Dam is negatively correlated ($R^2 = 0.75$, $p = 0.001$) with cumulative mean daily discharge at West Enfield (Figure 6). This relationship is weaker for the Veazie Dam ($p = 0.06$) and not significant for the Milford Dam ($p = 0.26$). Median passage success among all 10 years of radio/Carlin, PIT, and acoustic telemetry studies for the Veazie, Great Works, and Milford dams were 64% (range = 43–100%), 72% (range = 12–95%), and 93% (range = 67–100%), respectively. Within each study year, cumulative passage success through the Veazie and Great Works reservoirs ranged from 8% to 87% (median = 71%).

The proportion of total tagged Atlantic salmon that fell back and subsequently reapproached Veazie Dam was 0.8% (3 of 379), 9.4% (43 of 457), and 4.5% (32 of 713) in 2002, 2003, and 2004, respectively.

Discussion

Passage Success and Behavior, 2005–2006

Nearly all of the tagged Atlantic salmon in this study showed long delays in the lower river that were not consistent with typical migratory behavior in an unimpounded river (see Økland et al. 2001). Long delays and frequent fallbacks in the lower river have been observed in other studies of Penobscot River salmon (Power and McCleave 1980; Shepard 1995; D. Gorsky's unpublished data). Prior authors have attributed such behaviors to a number of factors, including homing to lower river stocking sites, lack of homing motivation due to hatchery rearing, high water temperatures, and the presence of hydroelectric dams. It is unlikely that adult salmon tagged in 2005 and 2006 homed to lower river reaches, because a negligible proportion of hatchery smolts were released downstream of Milford Dam from 2003 to 2005, when the adults tagged in this study would have left the river as smolts. The detailed movement and temperature data

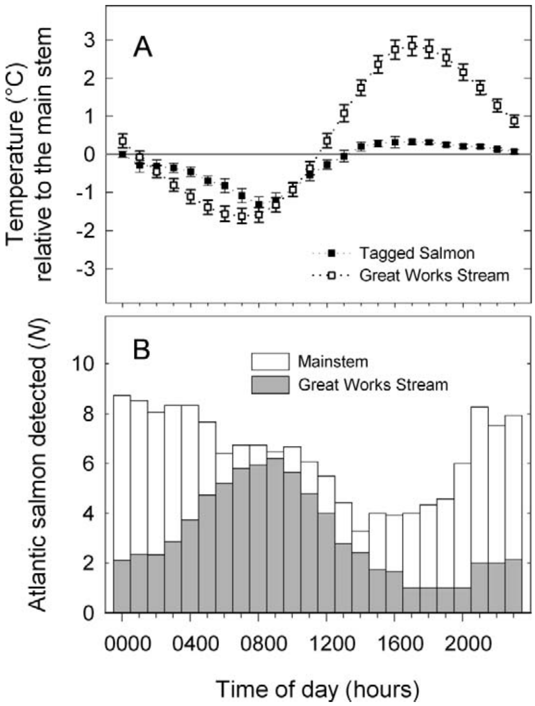

FIGURE 4.—**(A)** Mean temperatures of tagged Atlantic salmon and Great Works Stream (both expressed relative to main stem temperatures), and **(B)** mean number of fish detected during hourly intervals (stacked bars) at the Great Works Stream confluence and in the Great Works Stream for the period July 1–15, 2006. Error bars represent standard errors and reflect variation among days.

obtained in this study suggest that upstream movement was initially impeded by the presence of dams, and those delays were further compounded by high water temperatures.

Passage success was particularly low at the Great Works (12–43%) and Veazie (43–50%) dams during both 2005 and 2006. Passage at Milford Dam was substantially higher (67–100%). However, sample sizes for Milford Dam were extremely small ($n = 3$) in both years due to poor passage through downstream reaches. It is likely that overall migratory success in 2006 was severely limited by operating conditions at Great Works Dam. Although upstream fishways at this dam are believed to only function when flashboards are installed, these boards were not installed until August 14, 2006 (compared with June 13 in 2005). Timely flashboard installation is critical because peak migration of Atlantic salmon into freshwater typically occurs in June and early July in the Penobscot River. Given that all three successful ascents at Great Works Dam in 2006 occurred within a two-day window during high flows, we do not know if these few successful migrants passed over the spillway or through the upstream fishway.

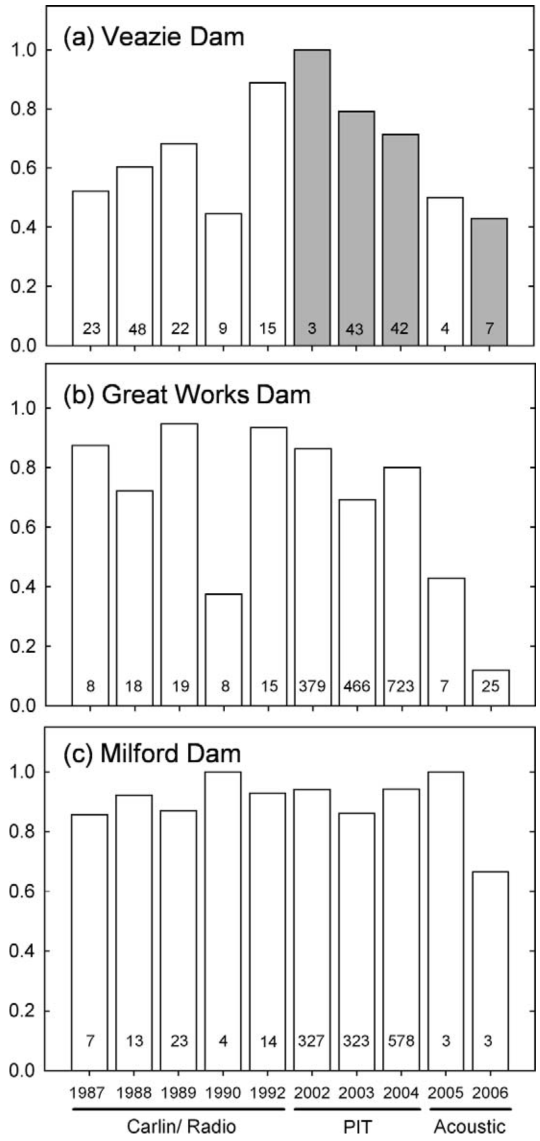

FIGURE 5.—Historic passage success for the **(a)** Veazie, **(b)** Great Works, and **(c)** Milford dams, as determined by Carlin/radio, PIT, and acoustic telemetry studies between 1987 and 2006. Numbers on bars denote initial sample sizes. Gray bars indicate passage success based on tagged Atlantic salmon that fell back over Veazie Dam and subsequently reapproached.

The inverse relationship between river temperature and discharge in the summer (Figure 2) is particularly problematic in the face of current dam management practices. The flow conditions that are conducive to flashboard installation (which themselves aid in the operation of associated passage facilities) can occur at a

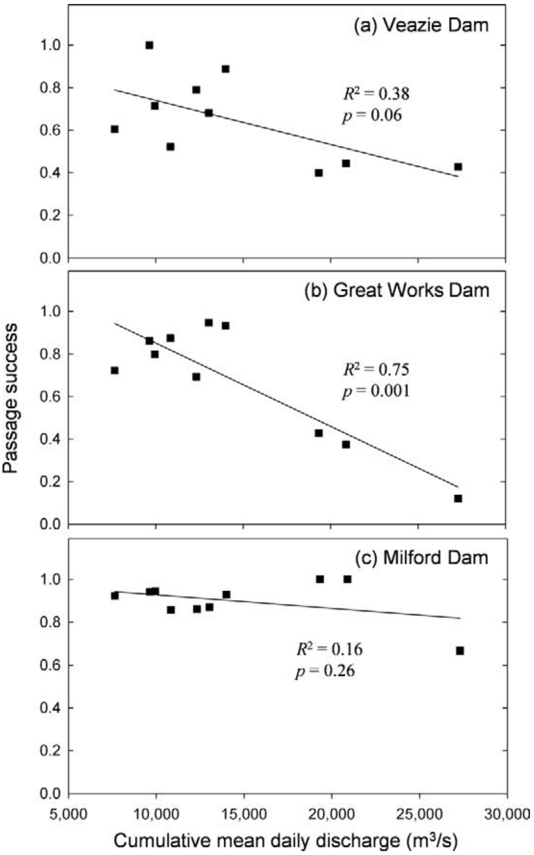

FIGURE 6.—Passage success at **(a)** Veazie, **(b)** Great Works, and **(c)** Milford dams as a function of cumulative mean daily discharge (measured at West Enfield; rkm 100) during June 1–July 31 for each year of Carlin/radio, PIT, and acoustic telemetry studies.

time of year when temperatures approach physiological tolerances for Atlantic salmon. Thermal refugia are probably found in tributaries upstream, but fish that are delayed at dams may not reach those sites given that migration can slow or cease when temperatures exceed 23°C in the Penobscot River (Shepard 1995; Gorsky 2005).

In 2006, Great Works Stream provided thermal refuge below the Great Works Dam, but only during the morning hours (Figure 4). During the evening hours, main stem temperatures at times exceeded 27°C in both study years. When temperatures rise, upstream passage is limited, and thermal refugia are not readily accessible, then fallback behavior may be an important mechanism for seeking thermal refugia downstream or in the estuary. It is not possible to infer from our data whether fish that fall back to the estuary and leave the system are able to recover and spawn in subsequent years. However, based on the frequency of this behavior and the very low occurrence of three-sea-winter fish in the Penobscot River (USASAC 2005), it is unlikely that these fish contribute to future spawning runs.

Historic Passage Success, 1987–1990, 1992, 2002–2006

Despite the presence of upstream fishways at all main stem dams, passage success at individual dams has been highly variable (12–100%) over 10 years of study between 1987 and 2006 (Figure 5). We defined passage success by “dam passage”, because dams were the only recapture and detection sites that were shared among all 10 years of study. Although we used dams to delineate reaches, we acknowledge that other factors (e.g., predation, angling mortality, temperature, tag loss, disease, etc.) probably contributed to passage failures. Nonetheless, of all tagged fish present in the Veazie Dam Reservoir over 2 years of acoustic telemetry studies, all but one (6 of 7 in 2005; 25 of 25 in 2006) approached the Great Works Dam. Although mortality or migratory and reproductive failure may have been inflicted by other factors, these results strongly suggest that the rate of upstream passage through the lower river may have been improved if passage success at all of the dams, but particularly at the Great Works Dam, were higher upon initial approach.

Sample sizes for these acoustic telemetry studies were limited by the number of Atlantic salmon available for research. Although sample sizes are small in some years, the integration of data from Carlin, radio, PIT, and acoustic telemetry studies presents a more comprehensive description of passage over 10 years than any single study could. For example, expulsion of gastrically-inserted radio tags has been documented in other systems and may have negatively biased passage success in those years of study. However, expulsion was less likely in PIT and acoustic studies, where tags were surgically implanted. Furthermore, sample size limitations of radio and acoustic telemetry studies ($3 \leq n \leq 48$) are balanced by the robust samples of PIT studies ($323 \leq n \leq 578$). The handling and tagging procedures for PIT studies were also minimally invasive compared with gastric and surgically-implanted radio and acoustic tags, and required no anesthesia. Thus, results from PIT studies are less likely to be confounded by behavioral changes (e.g., migratory delay) induced by increased handling. Finally, these 10 years of passage data encompass a broad range of environmental conditions (e.g., extreme high and low discharges) and management strategies (e.g., substantial recreational fishing for Atlantic salmon was permitted in the study area during 1987–1992 but not during 2002–2006).

These data reveal that lower river dams can be a severe impediment to upstream migration of Atlantic salmon, particularly when fishway operation is compromised by flow conditions and delayed beyond the peak of upstream salmon migration. We acknowledge that the negative relationship between discharge and passage success at Great Works Dam (Figure 6) is heavily influenced by 3 years with both the lowest passage success and low sample sizes ($n = 6$, 7, and 25). However, these data suggest a strong qualitative influence of flow on passage success at Great Works Dam. This relationship highlights the need to provide and assess upstream passage through the full range of expected flows at dams.

Although the high water conditions observed in June and July of 2006 (Figure 3a) may be extreme relative to other years of data collection, such variation should be expected in the future. A single year of poor passage at dams can have dramatic effects on natural reproduction and future recruitment and may even represent a lost opportunity for recovery given that prolonged higher flow conditions may actually be favorable to upstream migration in the absence of dams. If managers wish to minimize the potential for such losses, efforts should be taken to ensure adequate passage at a wide range of flows.

Substantial interannual variation in upstream passage at the Veazie Dam (Figure 5) should be of particular concern to fisheries managers, because the upstream fishway trap at the Veazie Dam currently serves as the sole facility for collection and enumeration of Penobscot River Atlantic salmon. If observed low upstream passage rates (40–100%) at Veazie Dam are representative of passage rates for naïve fish, a substantial proportion of the population may be denied access to the system and never encountered by researchers.

Relatively low passage success at the Veazie Dam may be confounded by the fact that experimental fish had all previously passed through the upstream fishway when they were initially collected. Studies in the Columbia River have shown that fish generally take longer to pass a dam on a second attempt after fallback compared with their first attempt (Bjornn et al. 1999). At a minimum, however, the low passage success observed in these studies is likely indicative of passage success upon reapproach to Veazie Dam after fallback, which we show to be a common occurrence in some years. Furthermore, the high incidence of fallback reported in the Penobscot (USASAC 2005) and other systems (Gowans et al. 1999; Dauble and Mueller 2000; Naughton et al. 2006) may significantly bias estimates of spawning escapement if estimates do not account for this process.

To avoid abandonment of spawning for the year, a successful fallback strategy requires both downstream passage and subsequent reascent of lower river dams. Downstream passage, however, exposes Atlantic salmon to additional risks of turbine entrainment, impingement during spill, and downstream delays at dams that are each heightened under the low flows that often correspond to fallback temperatures. Pacific salmon *Oncorhynchus* spp. exhibiting fallback behavior at dams in the Columbia River (reviewed by Dauble and Mueller 2000) are known to experience direct injury, mortality, or fatigue (Reischel and Bjornn 2003). Such behavior may also deplete the energy available for successful migration and spawning in salmon given that these fish are largely anorexic during this period. Compounding the problem, Lee et al. (2003) have shown that metabolic activity increases exponentially with increasing temperature in Pacific salmon. Thus, energy needed for continued upstream migration and spawning activity may be rapidly depleted at higher temperatures. Removal of the Veazie Dam, or head of tide dams in other salmon systems, may not only foster more efficient upstream migration, but also increase the efficiency and reduce the costs of fallback behaviors.

When passage at several dams is required for successful migration, the cumulative effects of even slightly reduced passage at these dams can be substantial. Results from our recent acoustic telemetry studies and our previous studies with other technologies (Figure 5) indicate that (1) successful upstream passage at lower Penobscot River dams is very dependent upon hydrological conditions and shows substantial interannual variation,, and (2) that migrants often exhibit long delays and fallback behavior at high temperatures that probably further limit reproductive potential in this system. Through removal of the Veazie and Great Works dams, the Penobscot River Restoration Project is expected to substantially enhance accessibility to upstream spawning habitats and thermal refugia, and reduce the prevalence and risks of migrants exhibiting fallback behavior during high summer temperatures.

Acknowledgments

We thank John Kocik (NOAA Fisheries), James McCleave (University of Maine), and three anonymous reviewers for providing valuable feedback on the manuscript. Financial support was generously provided by the University of Maine, the West Enfield Fund, the Maine Agricultural and Forest Experiment Station, and the Maine Cooperative Fisheries and Wildlife Research Unit. We thank the Maine Atlantic Salmon Commission for providing Atlantic salmon and technical expertise and the Penobscot Nation for land use permission. We also thank S. Hall (Pennsylvania Power and Light, Maine); R. Saunders, G. Goulette, P. Music, and E. Hastings (NOAA Fisheries); C. Fay (Penobscot Nation); J. Trial, R. Dill, and M. Simpson (Maine Atlantic Salmon Commission); C. Gardner, S. Fernandes, and many students from the University of Maine. Mention of trade names or commercial products does not imply endorsement by the U.S. Government.

References

Baum, E. 1997. Maine atlantic salmon: a national treasure. Atlantic Salmon Unlimited, Hermon, Maine.

Bjornn, T. C., M. L. Keefer, C. A. Peery, K. R. Tolotti, R. R. Ringe, and L. C. Stuehrenberg. 1999. Migration of adult Chinook salmon past Columbia and Snake River dams, through reservoirs and distribution into tributaries, 1996. Bonneville Power Administration and U.S. Army Corps of Engineers, Portland, Oregon, and Walla Walla, Washington.

Dauble, D. D., and R. P. Mueller. 1993. Factors affecting the survival of upstream migrant adult salmonids in the Columbia River basin. Recovery issues for threatened and endangered Snake River salmon. Technical Report 9 of 11. Report to the U.S. Department of Energy, Bonneville Power Administration, Division of Fish and Wildlife, Project 98–026, Portland, Oregon.

Dauble, D. D., and R. P. Mueller. 2000. Difficulties in estimating survival for adult Chinook salmon in the Columbia and Snake rivers. Fisheries 25(8):24–34.

Fay, C., M. Bartron, S. Craig, A. Hecht, J. Pruden, R. Saunders, T. Sheehan, and J. Trial. 2006. Status review for anadromous Atlantic salmon (*Salmo salar*) in the United States. >Report to the National Marine Fisheries Service and U.S. Fish and Wildlife Service, Washington, D.C.

Fox, J. 2005. The *R* commander: A basic-statistics graphical user interface to *R*. Journal of Statistical Software 14(9):1–42.

Goniea, T. M., M. L. Keefer, T. C. Bjornn, C. A. Peery, D. H. Bennett, and L. C. Stuehrenberg. 2006. Behavioral thermoregulation and slowed migration by adult fall Chinook salmon in response to high Columbia River water temperatures. Transactions of the American Fisheries Society 135:408–419.

Gorsky, D. 2005. Site fidelity and the influence of environmental variables on migratory movements of adult Atlantic salmon (*Salmo salar*) in the Penobscot River basin, Maine. Master's thesis. University of Maine, Orono.

Gowans, A. R. D., J. D. Armstrong, I. G. Priedie, and S. Mckelvey. 2003. Movements of Atlantic salmon migrating upstream through a fish-pass complex in Scotland. Ecology of Freshwater Fish 12(3):177–189.

Gowans, A. R. D., J. D. Armstrong, and I. G. Priede. 1999. Movements of adult Atlantic salmon through a reservoir above a hydroelectric dam: Loch Faskally. Journal of Fish Biology 54:727–740.

Keefer, M. L., C. A. Peery, T. C. Bjornn, M. A. Jepson, and L. C. Stuehrenberg. 2004. Hydrosystem, dam, and reservoir passage rates of adult Chinook salmon and steelhead in the Columbia and Snake rivers. Transactions of the American Fisheries Society 133:1413–1439.

Kinnison, M. T., M. J. Unwin, A. P. Hendry, and T. P. Quinn. 2001. Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. Evolution 55:1656–1667.

Kinnison, M. T., M. J. Unwin, and T. P. Quinn. 2003. Migratory costs and contemporary evolution of reproductive allocation in male Chinook salmon. Journal of Evolutionary Biology 16:1257–1269.

Lee, C. G., A. P. Farrell, A. Lotto, M. J. MacNutt, S. G. Hinch, and M. C. Healey. 2003. The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. Journal of Experimental Biology 206:3239–3251.

Naughton, G. P., C. C. Caudill, M. L. Keefer, T. C. Bjornn, C. A. Peery, and L. C. Stuehrenberg. 2006. Fallback by adult sockeye salmon at Columbia River dams. North American Journal of Fisheries Management 26:380–390.

NRC (National Research Council). 2004. Atlantic salmon in Maine. National Academies Press, Washington, D.C.

Økland, F., J. Erkinaro, K. Moen, E. Niemela, P. Fiske, R. S. McKinley, and E. B. Thorstad. 2001. Return migration of Atlantic salmon in the River Tana: phases of migratory behavior. Journal of Fish Biology 59:862–874.

Power, J. H., and J. D. McCleave. 1980. Riverine movements of hatchery-reared Atlantic salmon (*Salmo salar*) upon return as adults. Environmental Biology of Fishes 5:3–13.

Reischel, T. S., and T. C. Bjornn. 2003. Influence of fishway placement on fallback of adult salmon at the Bonneville Dam on the Columbia River. North American Journal of Fisheries Management 23:1215–1224.

Shepard, S. L. 1995. Atlantic salmon spawning migrations in the Penobscot River, Maine: fishways, flows and high temperatures. Master's thesis. University of Maine. Orono.

USASAC (United States Atlantic Salmon Assessment Committee). 2005. Annual report of the U.S. Atlantic Salmon Assessment Committee. USASAC, Report 17-2004 Activities, Woods Hole, Massachusetts.