


Transactions of the American Fisheries Society

ISSN: 0002-8487 (Print) 1548-8659 (Online) Journal homepage: http://www.tandfonline.com/loi/utaf20

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**To cite this article:** James P. Hawkes, Timothy F. Sheehan & Daniel S. Stich (2017) Assessment of Early Migration Dynamics of River-Specific Hatchery Atlantic Salmon Smolts, Transactions of the American Fisheries Society, 146:6, 1279-1290, DOI: 10.1080/00028487.2017.1370017

**To link to this article:** http://dx.doi.org/10.1080/00028487.2017.1370017

*Transactions of the American Fisheries Society* 146:1279–1290, 2017

ISSN: 0002-8487 print / 1548-8659 online
DOI: https://doi.org/10.1080/00028487.2017.1370017



**ARTICLE**

# Assessment of Early Migration Dynamics of River-Specific Hatchery Atlantic Salmon Smolts

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***Abstract***
**Many Atlantic Salmon *Salmo salar* populations within the southern extent of the species' range are at critically low abundances, while others have been extirpated. The focus of many ongoing recovery efforts is on maximizing the number of smolts that reach the ocean, where marine survival is low, primarily through hatchery supplementation and improvement of in-river hydropower system management. However, estuaries also are known to be sites of high mortality, although in many cases the correlates of this mortality are poorly characterized. We acoustically tagged hatchery smolts ($n$ = 666) during 2001–2005 to evaluate migration performance through freshwater, estuarine, and bay reaches of the small but tidally dynamic Dennys River, Maine, USA, to investigate potential drivers contributing to low returns within the system. Migration behaviors (e.g., migration timing and tidal use) were typical for Atlantic Salmon smolts, but reversals during migration were observed upon entry into the estuary environment more frequently in this system than in regional rivers. We used Cormack–Jolly–Seber mark–recapture models to estimate apparent survival within the study environment during this period. We found two distinct periods of survival, with much lower survival in 2003–2005 than in 2001 and 2002 (more than a 40% decrease). Among the variables considered, temperature and migratory behavior had the largest effects on survival. We found that survival increased by about 28% across the range of temperatures observed during these years; additionally, survival increased by about 15% for fish that reversed direction during migration compared to fish that did not. These results indicate that extreme environmental changes during the transition through this coastal system constitute a significant obstacle to Atlantic Salmon restoration stocking efforts.**

Atlantic Salmon *Salmo salar* in the North Atlantic have experienced significant declines in abundance across their range (ICES 2016). Although there are many anthropogenic and natural causes for these declines, poor marine survival has been identified as a primary cause throughout the North Atlantic and specifically for U.S. populations (ICES 2016; USASAC 2017). These declines are most severe in the western and southern portions of the species' range, and many populations in North America are at critically low abundance or have been extirpated (ICES 2016; USASAC 2017). Remnant stocks of Atlantic Salmon in the USA were afforded protection under the U.S. Endangered Species Act in 2000 (USFWS and NOAA 2009), and ongoing restoration efforts are being employed to recover these populations.

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Received March 30, 2017; accepted August 7, 2017

Hatchery supplementation efforts have prevented remnant populations of Atlantic Salmon from going extinct, but their recovery has not been realized, and many populations remain dependent on hatchery intervention (NRC 2004; Fay et al. 2006). Atlantic Salmon were first reared for supplementation of wild stocks in Maine during the late 1800s (Maynard and Trial 2014). Since that time, hatchery practices have evolved, with the development of a river-specific broodstock program in the early 1990s (Bartron et al. 2006). More recently, all life stages of Atlantic Salmon are stocked (Fay et al. 2006; Maynard and Trial 2014), and these hatchery products have been successful in occupying freshwater habitat. However, marine survival of U.S. stocks remains low, and populations remain at critically low abundances (USASAC 2017).

The Dennys River, Maine, is a small, coastal river that historically was home to large runs of diadromous fish, including Alewife *Alosa pseudoharengus*, Blueback Herring *Alosa aestivalis*, American Shad *Alosa sapidissima*, and Atlantic Salmon (Saunders et al. 2006). Dam construction starting in the late 1700s resulted in only 30% of river habitat being accessible by the mid-1800s. Dams remained in the watershed until the 1930s, when the last main-stem dam was removed, allowing diadromous fish to access historical habitats (Hall et al. 2011). After the removal of the last main-stem dam, restoration efforts continued but remained largely unsuccessful. Estimates of returning adult Atlantic Salmon in the late 1960s to early 1980s were between 50 and 500 adults (Beland 1996), while returns in 1986–2000 averaged fewer than 10 fish (USASAC 2001). Since the removal of dams, exploitation from fisheries, point source pollution (e.g., hazardous waste dump sites), non-point-source pollution (fertilizers, pesticides, toxic chemicals, sediment, etc.; Beland et al. 1982; Bartlett and Robinson 1988; Arter 2005), impacts from weather-induced acidification (Liebich et al. 2011), predation (Baum 1997), poor marine survival (ICES 2016; USASAC 2017), and climate change (Jonsson and Jonsson 2009) have been considered factors contributing to the observed declines of Atlantic Salmon within this system.

In response to persistently low spawner abundance, managers initiated a 5-year program in which age-1 smolts were stocked to jumpstart the Atlantic Salmon population restoration program for the Dennys River. Based on contemporary return rates for other Maine smolt stocking programs, it was estimated that annual stocking of approximately 50,000 age-1 smolts would result in 60–120 two-sea-winter adult returns annually (USASAC 2001). An acoustic telemetry study was designed to monitor the migration of these smolts through the river, estuary, and bay reaches. The objective of this study was to describe migration dynamics and survival and to identify bottlenecks in the migration of this newly employed river-specific hatchery product within the Dennys River system. Results could be used to identify stressors in the system and to provide insights into the efficacy of using hatchery-reared smolts to restore Atlantic Salmon runs to the Dennys River.

## METHODS

### Study Site

The Dennys River is a small, coastal watershed (342 $km^2$) located in eastern Maine (Figure 1). During the spring migration, Dennys River Atlantic Salmon smolts migrate through freshwater reaches including the narrow, high-gradient lower river prior to entry into the Dennys River estuary, which exhibits high rates and volumes of flushing, resulting in abrupt changes to physical and chemical characteristics during each tidal cycle. Upon exiting the estuary, these postsmolts enter the marine environment of Dennys Bay until reaching the constricted Leighton Neck corridor, which leads into Cobscook Bay. In contrast to Dennys and Cobscook bays, Leighton Neck is a dynamic, high-velocity environment of ledge outcrops, islands, and constrictions. During each tidal cycle, approximately 0.5 $km^3$ of seawater is exchanged between Dennys and Cobscook bays via the Leighton Neck corridor (Brooks et al. 1999). Cobscook Bay and the adjacent Passamaquoddy Bay are the two possible egress points for Atlantic Salmon postsmolts into the Bay of Fundy (BoF), and from there they enter the Atlantic Ocean via the Gulf of Maine (Beland 1996).

### Receiver Deployment

During April–June 2001–2005, we deployed a linear series of passive Vemco VR receivers (VR-20 and VR-2; Vemco, Halifax, Nova Scotia) throughout river, estuary, and bay reaches, covering a distance of approximately 35 km (Figure 1). Methods were similar to those of Kocik et al. (2009), with receivers deployed as a “node” (single receiver) or an “array” (linear series of multiple receivers with overlapping detection radii forming a curtain). During 2001, we deployed Vemco VR-20 receivers bolted to custom, 23-kg, concrete moorings for freshwater deployments and 36-kg moorings for tidal and marine deployments. From 2002 to 2005, we deployed Vemco VR-2 receivers on 23-kg, custom moorings in the river, estuary, and shallow bay reaches. At deeper, high-current sites, we used 11-kg Danforth anchors affixed to 2.5 m of 0.95-cm steel chain, connected to 1 cm of three-strand, braided nylon line with a scope of 2:1. Receivers were secured at 10-m depth with hydrophones positioned upward. Deployment locations were predetermined to maximize spatial coverage and take advantage of natural constriction points.

The study area was partitioned into five reaches, and receivers were deployed to monitor the movement of Atlantic Salmon between study reaches. The freshwater reach extended 3.9 km downstream from the release site to the head of tide, with an average receiver spacing of 0.7 km between nodes or arrays. The estuary reach extended 2.3 km downstream from the head of tide, with an average receiver spacing of 0.4 km. Beyond the estuary, the study area was partitioned into three locally named reaches before entering the BoF: Dennys Bay (6.5 km), Leighton Neck (4.1 km), and Cobscook Bay (14.0–19.0 km, depending on the

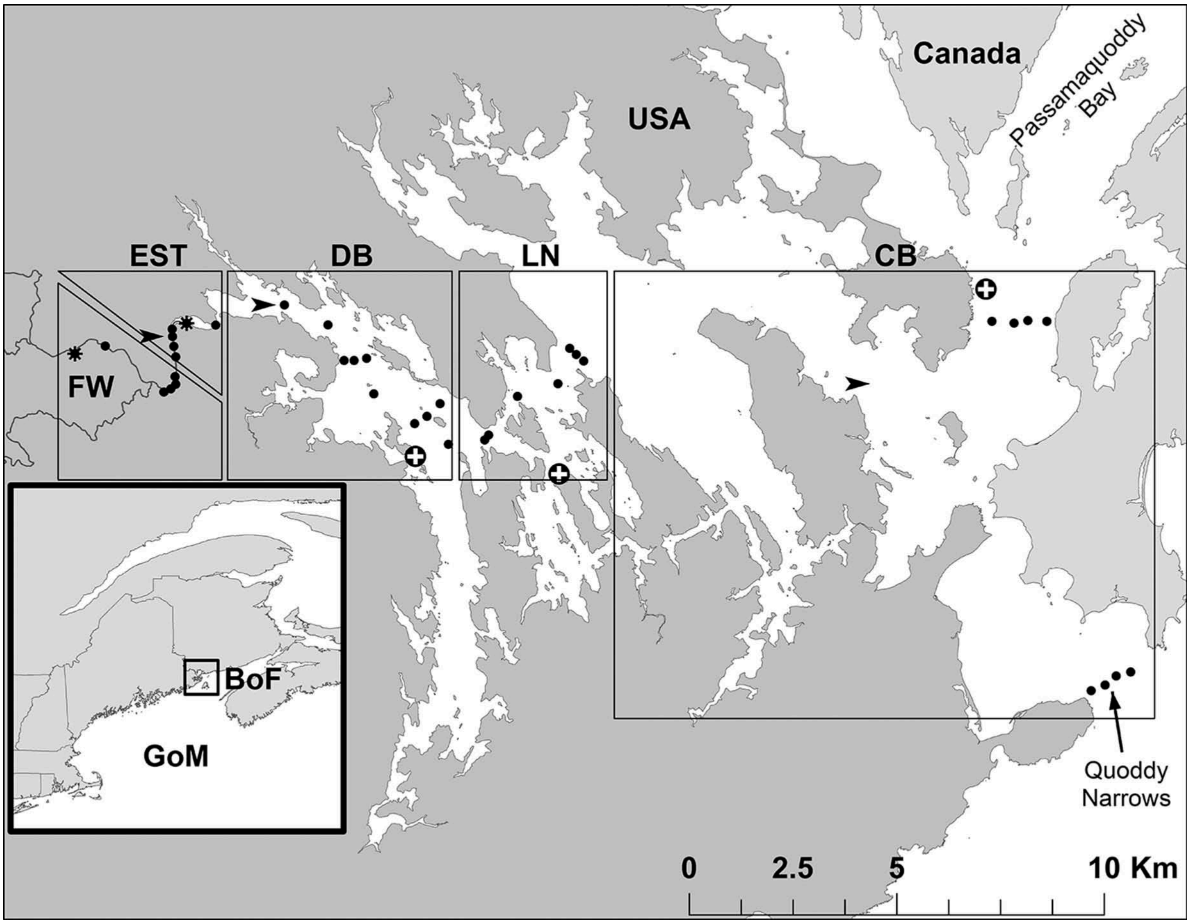


FIGURE 1. Study area in the Dennys River, Maine, where telemetry of Atlantic Salmon was conducted in 2001–2005 (BoF = Bay of Fundy; GoM = Gulf of Maine). The plotted telemetry array represents the 2005 coverage, which was the most complete array during the study, as the number of deployed units increased each year of the study period. Details on previous years' coverage are provided in the text. The study area was delineated into five reaches: freshwater (FW), estuary (EST), Dennys Bay (DB), Leighton Neck (LN), and Cobscook Bay (CB). Black dots represent receiver locations, asterisks represent stocking locations, arrows represent water quality data logging units, and circles containing a plus symbol represent tidal gauge stations.



exit point). Postsmolts could exit the Cobscook Bay reach via a northern route (Passamaquoddy Bay; 14.0 km) or a southern route (Lubec Narrows; 19.0 km) into the BoF. Receiver spacing within the Dennys Bay and Leighton Neck reaches averaged 4.5 km during 2001, 2.3 km in 2002, and 0.91 km during 2003–2005. We downloaded and replaced receivers as needed 2–4 weeks after the release of smolts.

We maintained receiver coverage consistently within the river through Leighton Neck corridor but not in Cobscook Bay. We lost up to 50% of receivers within the bay, with most losses occurring in the northern route (Figure 1).

## Smolt Origin, Surgery, and Release

We surgically implanted acoustic tags into age-1 Atlantic Salmon smolts reared from Dennys River-specific broodstock at the U.S. Fish and Wildlife Service Green Lake National Fish Hatchery in Ellsworth, Maine. Smolts were reared outdoors in 6- or 9-m, circular cement pools under a canopy allowing for ambient light conditions. Water was supplied to the hatchery from nearby Green Lake.

Surgical transmitter implantation procedures were as described by Kocik et al. (2009) except that all surgeries were performed in the hatchery (instead of streamside) and only buffered tricaine methanesulfonate (MS-222) was used as an anesthetic. We used Vemco V8-6L transmitters during 2001–2004 and both V8-6L and V7-2L transmitters in 2005. The V8-6L transmitters were 20 or 22 mm in length and weighed 2.0 g (in water), with an expected battery life of 68 d; the V7-2L transmitters were 18.5 mm and 0.75 g, with an expected battery life of 74 d. Surgeries were conducted 2 weeks prior to release. We measured the FL (mm) and mass (g) of each tagged smolt.

Immediately prior to release, tagged smolts were integrated with untagged smolts, except in 2004 and 2005, when half of the tagged fish were integrated. During 2001, 2002, and 2004, only a single stocking event occurred. In 2003 and 2005, two stocking events occurred and were characterized as either "early" (last week of April) or "late" (first week of May). During 2001–2003, all smolts were stocked 3.9 km upstream of the head of tide. During 2004 and 2005, half of the fish were stocked 3.9 km upstream of the head of tide, and half were stocked into the estuary (independent of restoration fish) 1.3 km downstream of the head of tide.

### Environmental Data Collection and Source

Tidal stage data were obtained from the University of South Carolina's Tide and Current Predictor website (tbone.biol.sc.edu/tide) for three locations within Dennys and Cobscook bays (Figure 1). Onset Optic StowAways (Onset Computer Corp., Bourne, Massachusetts) were deployed within Dennys Bay (2002–2005) to collect temperature (°C) at a depth of 1 m. A YSI 600 XLM (YSI, Inc., Yellow Springs, Ohio) was deployed (2003–2005) within the estuary (Figure 1) to collect temperature (°C), conductivity (μS/cm; i.e., salinity), and depth (m; i.e., tide stage) data. Surface temperature and salinity data for Cobscook Bay (2002–2005) were obtained from Gulf of Maine Ocean Observing System (GoMOOS) buoy J (located within the bay; www.neracoos.org/gomoos) at a depth of 1 m. Point temperatures (°C) for stocking trucks were taken prior to the release of fish into the river.

### Data Analysis

*Biological characteristics and migration dynamics.—*We compared smolt FLs between release groups (early versus late for 2003 and 2005 only) and between stocking locations (freshwater versus estuary for 2004 and 2005 only). We used one-way ANOVA to test for differences in FL between groups in 2003 and between stocking locations in 2004, whereas multivariate ANOVA was needed to compare differences in FL between the four group × stocking location combinations in 2005. We also used a one-way ANOVA to test for differences in FL between years.

Preliminary detection data indicated a high prevalence of reversals during migration, which required special consideration during data analysis. Reversals were identified by singular or multiple landward and subsequent seaward movements of at least 1,200 m, as this was beyond the listening range of the receivers (~400 m as determined through range tests); this eliminated the mischaracterization of dual detections at consecutive receivers as a reversal. We defined the duration of a reversal as the last detection of a given transmitter at a seaward receiver to the first detection of the transmitter at a landward receiver. To compare differences in reversals within the region, we summarized the data reported by Kocik et al. (2009) and Stich et al. (2015b) and our present data in an identical manner. Mean number of reversals, receiver spacing, and tidal range were used to make comparisons.

Uninterrupted receiver coverage through the Leighton Neck corridor allowed discrete migration summaries (e.g., reversals, tidal use, and duration) through this array. Because Cobscook Bay experienced moderate receiver losses within each year (up to 50%), survival estimates used a combination of Leighton Neck and Cobscook Bay arrays for the terminal receiver array within the receiver network and accounted for changes.

We estimated migration duration (d) from the point at which a smolt entered the estuary until its last detection. Fish were classified as successful and unsuccessful migrants through the study array based on detection histories. Successful fish were known to have reached a terminal receiver within the Leighton Neck array. Unsuccessful fish were those that failed to reach the terminal array and were confirmed through manual tracking, continuous transmission, or passing a subterminal receiver and not being heard from again. Durations are reported as medians with 75% confidence intervals (CIs). We provide last known location data for unsuccessful fish as a rounded distance from the head of tide (km).

*Survival of Atlantic Salmon smolts.—*Sequential detections of tagged smolts were used to estimate apparent survival (hereafter, survival) from Cormack–Jolly–Seber mark–recapture models implemented in program MARK (White and Burnham 1999) with the RMark package (Laake et al. 2012) from R (R Core Team 2017). We estimated survival through seven reaches from release through Cobscook Bay. Estimates of survival during the final interval (Leighton Neck to Cobscook Bay) were confounded with detection probability; therefore, a joint probability of detection and survival ($\lambda$) was estimated but is not reported.

We used a multiphase approach to model specification and inference. First, we constructed candidate models that constrained survival ($\Phi$) to be constant and allowed detection probability ($p$) to be constant or to vary between locations and/or years with either additive or multiplicative (interaction) effects of location and year (Supplementary Table S.1 available in the online version of this article). Using the best model from the first phase of model selection, we built a second candidate model set using a priori additive combinations of survival covariates to determine which factors were most strongly correlated with survival (Table S.2). All models in the second phase of model selection included either additive or multiplicative effects of year and reach. Other covariates included FL, the timing of release (early or late), release site (freshwater or estuary), the number of times a fish performed a reversal, and tag burden (tag weight as a percentage of body weight). Our rationale for using additive relationships during this round of model selection was twofold. First, we were more interested in determining whether relationships between covariates (e.g., FL or tag burden) and survival could be detected across the entire time series used, such that these results would be transferable to other systems and across years. Second, when we attempted to fit post hoc interactions between year and continuous covariates of interest (e.g., number of reversals or FL) in response to concerns that interannual variability was not accounted for, the survival models failed to converge, likely as a result of overparameterization.

We estimated an overdispersion parameter ($\hat{c}$) using the program U-CARE (Choquet et al. 2009). Model selection was not adjusted because $\hat{c}$ was less than or equal to 1. We used an information-theoretic approach to model selection based on Akaike's information criterion corrected for sample size ($AIC_c$). We calculated the $AIC_c$ difference for each model $i$ ($\Delta AIC_i = AIC_{c,i} - AIC_{c,minimum}$) to determine the relative support for each model, and we calculated the relative probability that each model was the best in the candidate set (Akaike weight $w_i$; Burnham and Anderson 2002). Models with $\Delta AIC_i$ values less than 2.0 were considered to have similar support relative to the best model. Using the best model from the second phase of model selection, we estimated per-kilometer rates of survival in each reach of the study area during each year. Reach-specific, per-kilometer survival rates ($\Phi_{km,i}$) were calculated as $\Phi_i \cdot d_i^{-1}$, where $\Phi_i$ is the reach-specific survival rate and $d_i$ is the corresponding reach length.

Finally, we used 2002–2005 data to assess the potential influences of temperature on smolt survival during years for which environmental data were available (Table S.3). To do this, we re-ran the best model from the post hoc analysis above by using only 2002–2005 capture histories, and compared it to a model that included temperature on the date of arrival in the estuary as an individual covariate. We replaced the variable "year" to avoid redundancy in parameters that explained annual variability in survival; for the sake of comparison, we re-ran the best model from phase 2 of model selection but without a year effect. We did not analyze models that included terms for temperature in freshwater reaches or in the bay sites because the resolution of the data was not fine enough and because those monitoring stations were not added until 2004.

*Environmental data.*—Year-specific environmental data were summed across the entire smolt migration period (April–June). Daily median temperature was compared between the estuary, Dennys Bay, and Cobscook Bay by using a nonparametric Wilcoxon's signed rank test (test statistic $W$). Tidal data were summed in 15-min bins starting at slack low tide for each tidal cycle. Not all tidal cycles are equal; therefore, the number of bins differed, with some cycles consisting of as many as 52 bins. The time of arrival for each postsmolt at each node or array was matched with the corresponding tide bins to characterize use of tides during migration. Salinity data (‰) collected from GoMOOS buoy J are presented as a range in mean values, while data collected in the estuary by using the YSI sonde are presented as the range in maximum salinities observed during the smolt migration period (April–June).

## RESULTS

### Biological Characteristics

No mortalities were observed between surgery and release during the 5 years of this study. The mean FL (±SD) for tagged hatchery smolts was 183.2 ± 12.9 mm ($n$ = 666), and mean mass was 68.8 ± 15.1 g ($n$ = 665). Differences in FL were not detected between release groups (early versus late [2003 and 2005], $P \geq 0.09$) or between locations (freshwater versus estuary [2004 and 2005], $P \geq 0.78$). We detected statistical differences in FL ($F_{4,\ 666} = 36.9$, $P < 0.01$) and mass ($F_{4,\ 665} = 39.4$, $P < 0.01$) between years and incorporated this variability into survival models by including FL as a potential survival correlate. The proportion of fish mass that was represented by V8-6L tags ($n$ = 551) and V7-2L tags ($n$ = 115; 2005 only) represented a mean of 3.0 ± 0.7% and 1.2 ± 0.2% of tagged smolt weight, respectively.

### Environmental Data

Salinities within the inner estuary ranged from 0‰ to 20‰, with values above zero found only during a brief period (~2 h) corresponding to high tide. Salinity values recorded within Cobscook Bay ranged from 18‰ to 32‰ (Figure 1).

Median daily temperatures within the study area increased during the April 20–June 1 period across years (Figure 2), and differences were observed across reaches. Stocking truck temperatures ranged from 3.9°C to 8.7°C annually, while stocking location temperatures ranged from 6.5°C to 12.6°C (median = 10.9°C) and were 3.9°C warmer on average than the stocking truck. Estuarine temperatures ranged from 6.5°C to 12.7°C (median = 10.7°C), Dennys Bay temperatures ranged from 6.4°C to 6.9°C (median = 7.0°C; 2004 and 2005 only), and Cobscook Bay temperatures ranged from 3.3°C to 6.3°C (median = 5.1°C). Progressive cooling offshore resulted in Atlantic Salmon experiencing significantly cooler temperatures as they migrated through freshwater, estuarine, and bay reaches: the Dennys River was 0.07°C warmer than the estuary ($W$ = 378,854, $P$ = 0.71), the estuary was 3.4°C warmer than Dennys Bay ($W$ = 374,531, $P < 0.01$), and Dennys Bay was 1.9°C warmer than Cobscook Bay ($W$ = 305,250, $P < 0.01$).

### Migration Dynamics

*Reversals.*—Migration through the study area was characterized by two migration behaviors: (1) unidirectional downstream or seaward movement and (2) reversals (alternating seaward and landward movements). Of the smolts that entered the estuary, 51% (321/629) reversed direction at least once, with the annual percentage of reversals ranging between 18% and 80%. Most reversals occurred within the estuary (63%), followed by Dennys Bay (31%) and Leighton Neck (6%). The mean number of reversals per individual ranged between 2.0 and 10.6 (overall mean = 8.2), with a mean distance of 3.0–6.2 km (overall mean = 3.2 km) annually. The maximum number of reversals for a single individual was 37, and the maximum cumulative migration distance was 166 km within the 35-km study area (Table 1). We compared our results to the recent work of Kocik et al. (2009) and Stich et al. (2015b), who quantified reversals and had receiver spacing similar to that used in our

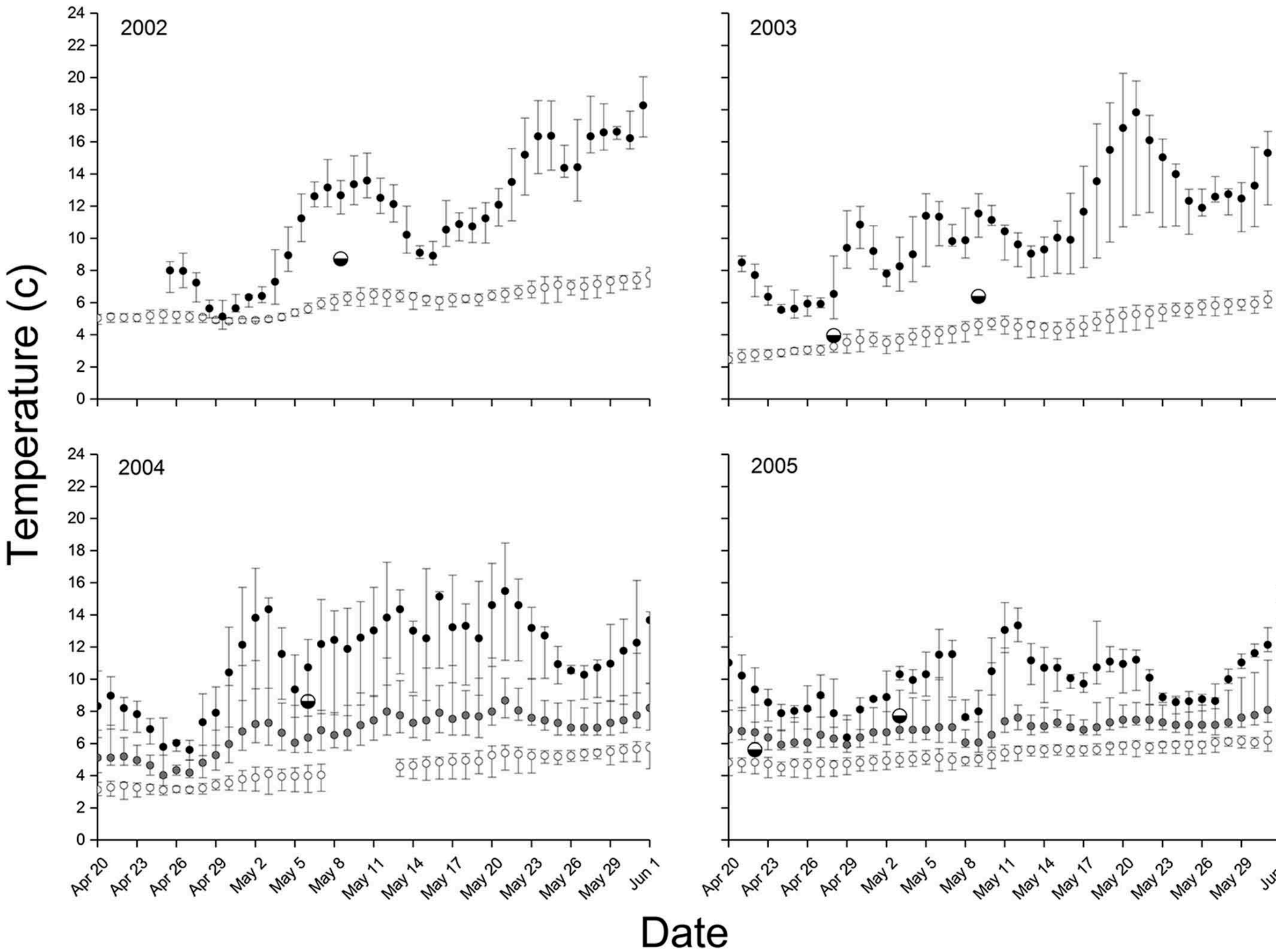


FIGURE 2. Daily median water temperatures (°C; whiskers = minimum and maximum daily values) in the study area. Solid black circles represent temperatures in the Dennys River estuary, solid gray circles represent temperatures in Dennys Bay, and open circles represent temperatures in Cobscook Bay. Half-shaded circles denote the Atlantic Salmon release date and the temperature of the stocking truck at the time of release.

TABLE 1. Summary of reversals exhibited by Dennys River Atlantic Salmon postsmolts during 2001–2005. Means are shown with SDs in parentheses.

| Year | Reverse (*n*) | Reverse (%) | Mean number of reversals | Maximum number of reversals per individual | Mean distance (km) of reversals |
|---|---|---|---|---|---|
| 2001 | 10 | 18.2 | 2.6 (2.7) | 10 | 4.2 (2.7) |
| 2002 | 33 | 23.1 | 2.0 (2.2) | 13 | 6.2 (2.7) |
| 2003 | 111 | 80.0 | 10.6 (7.5) | 33 | 3.1 (1.7) |
| 2004 | 83 | 58.9 | 10.0 (9.2) | 37 | 3.3 (2.4) |
| 2005 | 84 | 59.3 | 6.4 (5.9) | 24 | 3.0 (1.6) |
| Total | 321 | 51.0 | 8.2 (7.7) | 37 | 3.2 (2.0) |

array. Dennys River postsmolts reversed at least twice as many times as postsmolts in those studies despite the similar array spacing (Figure 3).

*Duration.*—Smolts that were stocked in the freshwater portion of the study array ($n$ = 455) quickly exited the 3.9-km stretch of freshwater from release to the estuary in a median time of less than 1 d (0.8 d; 75% CI = 0.4–1.6 d). Of the 629 smolts that entered the estuary (by migration or stocking), 123 (19.6%) successfully exited the Leighton Neck array (~13 km), with a median duration of 3.4 d (75% CI = 2.1–7.1 d). Five-hundred-six (80.4%) postsmolts did not exit the Leighton Neck array and were classified as unsuccessful. Successful postsmolts that did not reverse migration direction ($n$ = 72) had a median duration of 2.3 d (75% CI = 1.3–3.7 d), whereas postsmolts that reversed ($n$ = 51) had a median duration of 7.5 d (75% CI = 3.67–14.4 d).

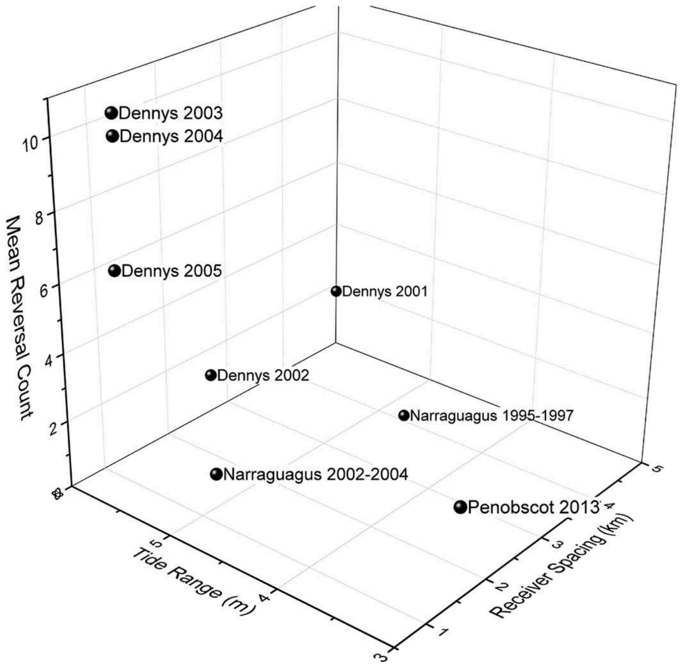


FIGURE 3. Mean counts of postsmolt Atlantic Salmon reversals with corresponding receiver spacing and tidal ranges (Narraguagus River data are from Kocik et al. 2009; Penobscot River data are from Stich et al. 2015b).

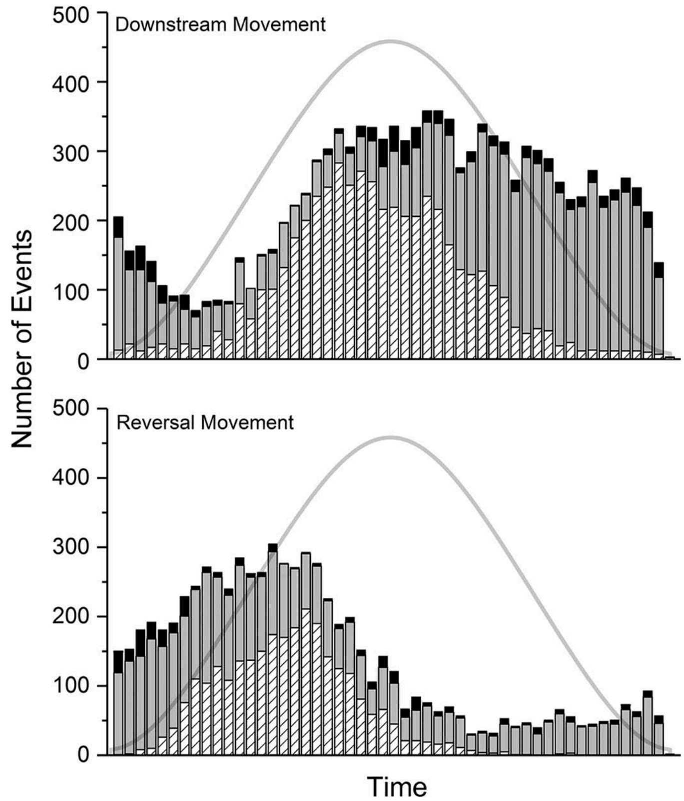


FIGURE 4. Postsmolt Atlantic Salmon arrival (downstream movement, top panel; reversal movement, bottom panel) at individual receivers according to tidal stage. Movement data are delineated for each of three environments: the Dennys River estuary (white hatched bars), Dennys Bay (gray bars), and Leighton Neck/Cobscook Bay (black bars). Histogram bars represent 15-min binned periods within a tidal cycle. The gray curve overlay represents one tidal cycle starting with slack low and progressing to the flood, slack high, and ebb stages and is not scaled to the $y$-axis value.

*Tidal movements.*—Overall, postsmolts migrated with ebb tides (ebb, 45%; flood, 18%; slack high, 22%; and slack low, 14%), but this was not consistent through all study reaches. Movement within the estuary occurred across most tidal conditions: ebb (32%), flood (26%), slack high (39%), and slack low (3%). In Dennys and Cobscook bays, egress occurred most commonly during ebb tide: ebb (55%), flood (12%), slack high (11%), and slack low (22%; Figure 4, top panel). Reversals occurred predominantly during flood tides (ebb, 7%; flood, 62%; slack high, 20%; and slack low, 11%) across all study reaches. Within the estuary, nearly 70% of reversal movements occurred during flood tides (ebb, 2%; flood, 69%; slack high, 23%; and slack low, 6%), and 50% of reversals within the bay reaches occurred during flood tides (ebb, 16%; flood, 50%; slack high, 16%; and slack low, 18%; Figure 4, bottom panel).

*Survival of Atlantic Salmon postsmolts.*—The best detection model structure for estimating detection of Atlantic Salmon postsmolts allowed detection probability to vary between locations and between years ($p_{[t\ +\ \text{year}]}$; Table S.1). Therefore, we used this model to test the relative effects of survival covariates. The two best-supported covariates of postsmolt survival were FL and the number of times a fish reversed direction. All supported models included the number of reversals (Table S.2), and the number of reversals was positively related to postsmolt survival (Table 2). Survival was predicted to increase by about 15% over the range of reversals recorded (Figure 5A). Fork length also was positively related to survival, but survival increased only slightly over the range of FLs included in this study (Figure 5B). Likewise, a model that included tag burden in addition to reversals had equivocal support, but the 95% CI for the effect of tag burden on survival overlapped zero considerably on the logit scale (95% CI = –28.94 to 6.87).

We found that estuary temperature at individual arrival in the estuary was a significant predictor of survival (Table 3). The model that included temperature effects was not supported as well as the best model from phase 2 of model selection (which included a categorical variable for year), but it was better supported than the model that excluded both annual variability and temperature effects (Table S.3). The effect of temperature on survival was much greater than that of reversals or FL (Figure 5). Survival was predicted to increase by about 28% over the range of estuary temperatures experienced by individual postsmolts in this study (Figure 5C).

Survival varied widely between 2001–2002 and 2003–2005, with cumulative survival from freshwater to

TABLE 2. Logit-scale parameter estimates, SEs, and confidence limits (CLs) for the best model of Atlantic Salmon smolt survival in the Dennys River, Maine, 2001–2005.

| Parameter | Estimate | SE | Lower 95% CL | Upper 95% CL |
|---|---|---|---|---|
| Intercept (reach 1; year 2001) | 1.871 | 0.926 | 0.056 | 3.687 |
| Reach 2 | 2.751 | 1.991 | –1.151 | 6.653 |
| Reach 3 | –0.013 | 0.286 | –0.573 | 0.548 |
| Reach 4 | –1.820 | 0.229 | –2.268 | –1.372 |
| Reach 5 | –2.536 | 0.240 | –3.005 | –2.066 |
| Reach 6 | –1.942 | 0.290 | –2.509 | –1.374 |
| Reach 7 | –2.202 | 0.339 | –2.867 | –1.537 |
| Reach 8 | 20.011 | 0.000 | 20.011 | 20.011 |
| Year 2002 | 0.645 | 0.256 | 0.144 | 1.146 |
| Year 2003 | –1.140 | 0.221 | –1.572 | –0.707 |
| Year 2004 | –1.357 | 0.216 | –1.781 | –0.933 |
| Year 2005 | –0.846 | 0.212 | –1.262 | –0.430 |
| FL | 0.009 | 0.005 | –0.001 | 0.019 |
| Reversals | 0.034 | 0.009 | 0.016 | 0.051 |

Cobscook Bay being highest in 2001 and 2002—more than twice as high as in the subsequent years (Figure 6, top panel). Per-kilometer survival generally decreased as Atlantic Salmon migrated from freshwater through to Cobscook Bay. Survival through freshwater and into the estuary was high (>90%). The transition from the estuary to the Dennys Bay reach was where significant losses occurred (10–48%), and losses continued through the remainder of the array (Dennys Bay, 3–14%; Dennys Bay to Leighton Neck, 9–44%; Leighton Neck to Cobscook Bay, 17–44%; Figure 6, bottom panel). The greatest differences between years were also observed during transition through the estuary and bay.

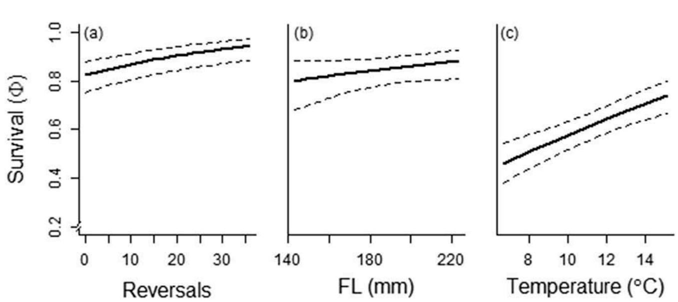


FIGURE 5. Effects of **(a)** reversals and **(b)** FL on survival of Dennys River Atlantic Salmon postsmolts, as estimated from the best model of survival in phase 2 of model selection; and **(c)** effects of temperature experienced by individual postsmolts upon arrival in the Dennys River estuary. Solid lines represent mean predictions; dashed lines represent 95% confidence intervals.

TABLE 3. Coefficient estimates for the survival submodel incorporating the effects of temperature experienced by individual Atlantic Salmon smolts at first detection in the estuary on survival. All other parameters are as defined in Table 2.

| Parameter | Estimate | SE | Lower 95% CL | Upper 95% CL |
|---|---|---|---|---|
| Reach 1 | –1.991 | 0.910 | –3.773 | –0.208 |
| Reach 2 | 2.993 | 2.639 | –2.179 | 8.165 |
| Reach 3 | –0.050 | 0.290 | –0.618 | 0.519 |
| Reach 4 | –1.808 | 0.234 | –2.266 | –1.350 |
| Reach 5 | –2.437 | 0.242 | –2.912 | –1.963 |
| Reach 6 | –1.854 | 0.281 | –2.404 | –1.304 |
| Reach 7 | –2.190 | 0.359 | –2.894 | –1.486 |
| Reach 8 | 32.682 | 0.000 | 32.682 | 32.682 |
| Reversals | 0.010 | 0.008 | –0.006 | 0.025 |
| FL | 0.018 | 0.005 | 0.009 | 0.027 |
| Temperature | 0.141 | 0.030 | 0.084 | 0.199 |

## DISCUSSION

The transition from freshwater to the marine environment for Atlantic Salmon smolts is a time of high mortality (Hvidsten and Lund 1988; Jepsen et al. 2006). Osmoregulatory stress during this transition has been identified as impactful to the response of smolts to predation threats (Handeland et al. 1996), which increase within marine environments (Hvidsten and Lund 1988; Dieperink et al. 2002). Our results demonstrate that Dennys River hatchery postsmolt migration dynamics (duration, tidal use, behavior, and survival) are similar to those of other Atlantic Salmon within the southern extent of the species' North American range (Lacroix et al. 2004, 2005; Lacroix 2008; Kocik et al. 2009; Halfyard et al. 2012; Renkawitz et al. 2012; Stich et al. 2015a). Survival during the present study was variable between years (Figure 6), with the greatest losses consistently found at the transition from the estuary to Dennys Bay reach and continuing through the Leighton Neck reach. During the first 2 years, survival estimates were similar to those reported in other regional studies (Lacroix et al. 2004, 2005; Kocik et al. 2009; Halfyard et al. 2012; Renkawitz et al. 2012; Stich et al. 2015a). However, during later years, survival was much lower and was only similar to estimates from other studies of inner BoF smolts (Lacroix 2008). The cause of this low survival is unclear, but the greatest reductions in survival between years occurred in reaches with abrupt changes in salinity and temperature.

The Dennys River estuary transition zone is short and heavily influenced by the large volume of marine water with each tidal cycle. As a result, fluctuations in temperature and salinity gradients are extreme and occur over a short distance. During flood tide conditions up to 6 m, nearly 0.5 $km^3$ of seawater inundates the tidal environments and negates the minor (1%) contribution of freshwater by the river (Brooks

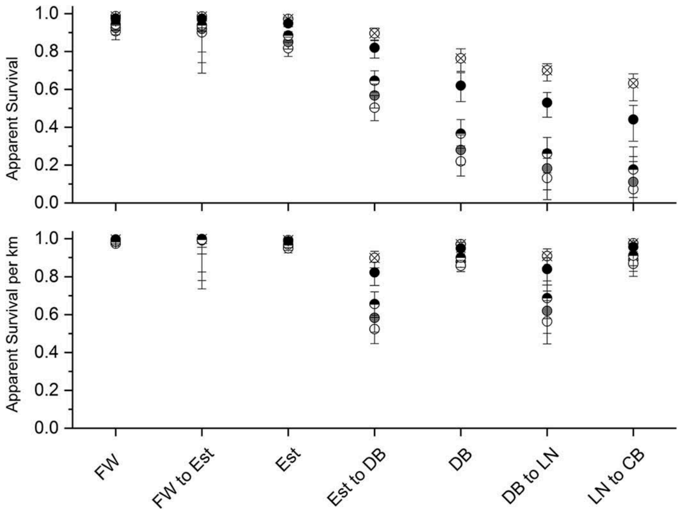


FIGURE 6. Estimated reach-specific cumulative survival (±95% confidence interval; top panel) and survival per kilometer (bottom panel) for Dennys River Atlantic Salmon smolts and postsmolts migrating through ecological reaches (FW = freshwater [Dennys River]; Est = Dennys River estuary; DB = Dennys Bay; LN = Leighton Neck; CB = Cobscook Bay) during 2001–2005 (solid circles = 2001; open circles with × = 2002; gray circles = 2003; open circles = 2004; half-shaded circles = 2005).



et al. 1999). During ebb tide or high tide conditions, fish that entered the estuary were exposed to as much as 20‰ salinity just 1 km beyond the head of tide. These conditions limit the possibility of postsmolts locating the warm, low-salinity water that is thought to be preferred during migration (Plantalech Manel-la et al. 2009) and that might otherwise aid their transition through these environments. Due to relationships between osmoregulatory ability and temperature (Sigholt and Finstad 1990; Staurnes et al. 2001), it is possible that without thermal refuge, the osmoregulatory performance of postsmolts was challenged and may have influenced migratory behavior and observed losses (Magee et al. 2001; Zydlewski et al. 2005).

Abrupt changes in estuarine conditions such as temperature may be responsible for the below-average survival of Dennys River postsmolts compared to neighboring populations. We found support for temperature effects on survival when we investigated the effects of estuary temperatures experienced by individual fish (Figure 5) despite the fact that we did not design environmental data collection specifically for this purpose. In the approximately 20 km between the estuary and bay temperature loggers, we observed a median difference of more than 5.0°C, concurrent with the greatest reductions in per-kilometer survival. Across the range of temperatures observed, we saw a 28% increase in survival. This effect was approximately double that of the next strongest factor influencing postsmolt survival (Figure 5). Staurnes et al. (2001) advised against transferring fish from freshwater to seawater at temperature differentials greater than 4–6°C, as dramatic and abrupt changes in temperature may result in poor seawater tolerance. In addition, Sigholt and Finstad (1990) observed high mortality of smolts exposed to high salinity (33‰) at temperatures of 6°C and lower. During the years with the lowest cumulative survival rates (2003–2005), temperatures in Cobscook Bay ranged from 3°C to 5°C, with salinities as high as 32‰ observed at the time of smolt release. For some European populations of Atlantic Salmon, optimal temperatures have been identified for ocean entry, and many were at or near 10°C (Hvidsten et al. 1998; Antonsson and Gudjonsson 2002; Jutila et al. 2005). Identification and alignment of stocking with environmental and physiological targets constitute a major challenge facing restoration efforts, especially with shifting run times as a result of climate change (Otero et al. 2014).

Postsmolts commonly reversed direction during our study, a behavior that has been well documented in other Atlantic Salmon stocks (McCleave 1978; Kocik et al. 2009; Halfyard et al. 2013; Stich et al. 2015a, 2015b). Dennys River postsmolts took one tidal cycle to several tidal cycles to exit the system. The proportion of fish that reversed during our study was within the range reported in previous studies, but the frequency of reversals was greater for individual fish. The reason for this increase is unclear, but the geography of the study area, the increased tidal range, the abrupt changes in temperature and salinity, and/or the origin of the fish (hatchery versus wild) may all contribute to this behavior. Within our study, it was apparent that the array structure (2001–2002 versus 2003–2005) influenced the prevalence of reversals, but the mean reversal distance was still more than twice our minimum criterion in all years. Therefore, we believe that we have provided an accurate description and an unbiased characterization of this behavior throughout all years of this study. However, the data are not available to evaluate the interactions between environmental conditions (e.g., river temperature, river discharge, estuarine temperature, and salinity), migration behavior (e.g., reversals), and survival. Given the propensity for reversal behavior throughout the North American range of the species (Lacroix et al. 2005; Kocik et al. 2009; Martin et al. 2009; Dempson et al. 2011; Halfyard et al. 2012, 2013; Stich et al. 2015b), it is a potential area of study that should be pursued and could result in management options to increase the early marine survival of hatchery stocks (Friedland 1998; Friedland et al. 2003).

We found that survival increased with an increasing number of reversals during this study (Figure 5B), as has been reported for other Maine rivers (Kocik et al. 2009). Importantly, this relationship is potentially confounded by the fact that fish surviving for a longer period may make more reversals than those that die sooner during migration simply because they have a prolonged opportunity to do so. However, reversal behavior may be (1) an adaptive strategy to aid in successfully exiting this reach, (2) a stress response, or (3) a missed opportunity to pass through constricted passages during optimal tidal conditions, as suggested by others (Lacroix et al. 2005; Kocik et al. 2009; Martin et al. 2009;

Dempson et al. 2011; Halfyard et al. 2012, 2013; Stich et al. 2015b). By contrast, it is expected that increased exposure to predators (Blackwell et al. 1997; Blackwell and Juanes 1998; Beland et al. 2001; Hawkes et al. 2013) will increase predation rates and mortality (Hvidsten and Lund 1988; Jepsen et al. 2006). Therefore, if the positive relationship between reversals and survival was solely an artifact of prolonged time at large, then we would expect a priori a neutral or even inverse relationship between the number of reversals and survival.

Reversals of Atlantic Salmon postsmolts have been suggested as conditioning, acclimation, and/or a stress signature associated with the transition to novel environments (Magee et al. 2001; Dempson et al. 2011; Halfyard et al. 2013). Reversals within estuaries and in near-coastal waters may also be an energy-saving strategy during migration. During our study, tidal use by postsmolts suggests that our fish used both passive (Fried et al. 1978; LaBar et al. 1978; Lacroix et al. 2004, 2005) and active (Moore et al. 1995, 1998; Lacroix and McCurdy 1996; Martin et al. 2009; Dempson et al. 2011) transport during migration. Reversals within this environment are likely independent or cumulative responses to current, temperature, and/or salinity gradients. Whatever the reason, further investigation into the drivers and consequences of reversals may be warranted given the potential implications for conservation stocking practices.

Regardless of lineage, it has been established that wild smolts make an easier transition to seawater (Handeland et al. 2003) and survive at higher rates than hatchery-origin fish (Jonsson et al. 1991; Maynard and Trial 2014). This may be in response to husbandry (McCormick et al. 1998), the timing of release (Karppinen et al. 2014), or a variety of other factors (as summarized by NRC 2004). Contemporary rearing and stocking efforts have likely challenged the resilience of the Dennys River population. Due to the low number of adult returns, the Dennys River broodstock is solely dependent upon parr collection to support the river-specific captive rearing program (USASAC 2017). Given the low level of wild spawning in the river over the past several decades, the Dennys River broodstock has likely originated from fish that were stocked as fry and therefore spent their entire life in freshwater, with no marine exposure. Saltwater performance of these fish has not been investigated comprehensively, although Spencer et al. (2010) determined that there was little difference in migratory urge and osmoregulatory preparedness (i.e., $Na^+$,$K^+$-ATPase activity) in freshwater when comparing the performance of hatchery smolts that originated from the Dennys River broodstock versus sea-run broodstock from the Penobscot River.

Similarly, no record of natural smolt run timing exists for the Dennys River. As such, we are uncertain whether the timing of releases during this study was representative of the historical run timing. Given the relationships between timing and survival of other stocks in the Gulf of Maine and in Europe (Thorstad et al. 2012; Stich et al. 2015a), we suspect that fish in this study entered the estuary outside of optimal physiological or ecological smolt windows (McCormick et al. 1998), which has been observed to impact survival of Atlantic Salmon (Kallio-Nyberg et al. 2004; Hvidsten et al. 2009; Karppinen et al. 2014) and other salmonids (Satterthwaite et al. 2014; Kilduff et al. 2015). In fact, smolts from the present study were released between April 22 and May 9, which is up to 3 weeks earlier than the median capture date of migrating smolts in neighboring U.S. populations (USASAC 2017).

Stocking of Atlantic Salmon smolts in the Dennys River failed to achieve the predicted numbers of adult spawners. Our telemetry study demonstrated that although early migration dynamics were similar to the wild and hatchery migration dynamics for neighboring stocks, nearshore survival was low. Furthermore, smolt-to-adult survival of these stocked fish was poor and resulted in adult returns of zero to single digits (USASAC 2008). We suggest that some of the nearshore drivers that could be responsible for this low nearshore survival are extreme conditions of the environment, the legacy of anthropogenic impacts, and challenges associated with artificial rearing. Poor marine survival is a threat across the range of the species. However, developing hatchery programs around the challenges faced by smolts and postsmolts in transition zones within the Dennys River may help to mitigate against the high nearshore losses documented in this study. This would allow more Atlantic Salmon to reach the ocean and may modestly increase the number of returning adults and the subsequent production of wild progeny.

## ACKNOWLEDGMENTS

We thank everyone who participated in the field components of this study. Special thanks are extended to the U.S. Fish and Wildlife Service Green Lake National Fish Hatchery for use of facilities, monitoring of smolts, and providing several data sets. We are grateful to reviewers M. Rankawitz, G. Goulette, and R. Haas-Castro, whose insight, suggestions, and comments helped to shape the final product. Reference to trade names does not imply endorsement by the U.S. Government.

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