

# Emigration dynamics of natural and hatchery Atlantic Salmon smolts in an impounded river system

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## ABSTRACT

**Objective:** The Gulf of Maine Distinct Population Segment of Atlantic Salmon *Salmo salar* is federally listed as endangered and is the last remaining population of Atlantic Salmon in the United States. The Penobscot River recovery program remains heavily reliant on hatchery-reared smolts to prevent extinction. The objectives of this study were to determine the proportion of emigrating natural and hatchery smolts, compare smolt size and run timing by origin, and assess whether location and timing of stocking affected recapture rates and emigration timing of hatchery smolts.

**Methods:** We analyzed a smolt sampling data set that was collected using rotary screw traps in the Penobscot River from 2001 to 2005. We identified smolts to origin (natural, hatchery, or unknown) based on scale pattern analysis and the presence of marks (adipose fin clip and/or visual implant elastomer). We calculated the proportion of emigrating natural and hatchery smolts, compared smolt size among origins, and compared capture timing with predicted emigration timing for natural smolts. We also calculated recapture rate and days at large for each group of marked smolts to assess the effects of timing and location of stocking on emigration.

**Results:** Over the 5 years of sampling, 57% of the captured smolts were hatchery origin, 40% were unknown origin, and 3% were natural smolts. Natural smolts were older and smaller than hatchery smolts. The measured 25% capture day of year was similar to the predicted 25% capture day of year for natural smolts. Hatchery smolt stocking and emigration timing was out of sync with the predicted out-migration timing for natural smolts. Recapture rates of hatchery smolts varied with stocking location and year, but days at large were not influenced by stocking location. Smolts that were stocked before April 30 took longer to reach rotary screw traps than did smolts that were stocked later.

**Conclusions:** Our finding that the timing of stocking influenced emigration of hatchery smolts provides useful information to guide management of the smolt stocking program. Aligning timing of hatchery stocking efforts with natural migration timing may improve marine survival rates of hatchery smolts and confer survival advantages to smolts of both origins.

**KEYWORDS:** Atlantic Salmon, early life history, fisheries management, rotary screw trap, stocking methods, *Salmo salar*, tags and marking, threatened and endangered species

## LAY SUMMARY

Understanding smolt emigration dynamics is essential for managers who are charged with recovery of federally endangered Atlantic Salmon. We compared smolt size and emigration dynamics between hatchery and natural smolts in the Penobscot River, home to the largest remnant population of Atlantic Salmon, using a 5-year smolt sampling data set. These data provide a historical baseline for evaluating smolt size, age, and emigration phenology, as Atlantic Salmon continue to face constantly evolving marine and freshwater ecosystems.

## INTRODUCTION

Atlantic Salmon *Salmo salar* in North America historically ranged from the Housatonic River (Connecticut, USA) to the Leaf River (Quebec, Canada), and adult returns numbered in the hundreds of thousands. However, many Atlantic Salmon populations near the southern extent of their North American range were locally extirpated by the end of the 19th century (Fay et al., 2006; Hendry et al., 2003; Spidle et al., 2003). By the end of the 20th century, Atlantic Salmon returns throughout

the remainder of the range had decreased to all-time lows, largely due to the environmental disruptions that are associated with dams, pollution, hatcheries, overfishing, and low marine survival (National Research Council, 2004). At the start of the 21st century, most of the Atlantic Salmon remaining in the United States occupied Maine rivers but at greatly depleted abundance (Fay et al., 2006; National Research Council, 2004).

In light of continued population declines in the latter half of the 20th century, the Gulf of Maine Distinct Population

Segment (GOM DPS) was listed as endangered under the U.S. Endangered Species Act (U.S. ESA; [U.S. Fish and Wildlife Service \[USFWS\] & National Marine Fisheries Service \[NMFS\], 2018](#); [U.S. Office of the Federal Register, 2009](#)). The persistence of the GOM DPS is highly dependent on hatchery supplementation, a measure first initiated in Maine during the late 1800s to preserve salmon populations ([Maynard & Trial, 2014](#)). In fact, since 1992, more than 80% of adult returns to Maine rivers have resulted from salmon that have been stocked as smolts in the Penobscot River ([U.S. Atlantic Salmon Assessment Committee \[USASAC\], 2024](#)).

Although hatchery smolt stocking produces most adult returns to the Penobscot River, hatchery smolts exhibit substantially lower marine survival than natural smolts do. There is no direct comparison between marine survival rates for natural and hatchery smolts in the Penobscot River. Therefore, estimates of marine survival rates for natural smolts in the Narraguagus River (Maine) have been used as a proxy. The smolt-to-adult return rate (a common metric used for describing marine survival) of natural smolts returning as 2-sea-winter adults in the Narraguagus River averaged 1.2% over the 10-year period from 2014 to 2023 ([USASAC, 2024](#)). The postsmolt-to-adult return rate (a variant on smolt-to-adult return rate that accounts for in-river mortality; [Stevens et al., 2019](#)) in the Narraguagus River would be greater than 1.2% over that 10-year period. During the same 10-year period, postsmolt-to-adult return rate for Penobscot River hatchery smolts was 0.15% ([USASAC, 2024](#)).

Consequently, the final recovery plan for the GOM DPS emphasizes the need to increase the number of natural smolts successfully entering the ocean to counter low marine survival rates. The main approaches are implementing habitat restoration to allow for increased production of natural smolts and expanding early life history stocking strategies, including egg planting and stocking gravid adults ([USFWS & NMFS, 2018](#)). But the focus of the conservation hatchery program for the Penobscot River has been and at present continues to rely on smolt stocking ([USASAC, 2024](#)), with returning adults either collected for use as hatchery program broodstock or allowed to migrate to spawning areas ([USASAC, 2024](#)). Therefore, if managers can implement approaches that improve the survival rate of hatchery smolts from release in-river to return as adults, then it may be possible to increase the natural spawning required for recovery of the GOM DPS.

Because of the importance of the Penobscot River to the GOM DPS, substantial research has been conducted in the watershed to characterize hatchery smolt migration patterns and survival using telemetry and modeling (e.g., [Holbrook et al., 2011](#); [Molina-Moctezuma et al., 2022](#); [Renkawitz et al., 2012](#); [Stevens et al., 2019](#); [Stich, Kinnison, et al., 2015](#)). Although less work to date has focused on natural smolts in the Penobscot River, differences in migration timing between natural and hatchery smolts have been identified there and elsewhere. For example, using acoustic telemetry [Stich, Zydlewski, et al. \(2015\)](#) found that hatchery smolts arrived in the Penobscot estuary earlier than natural smolts. [Vollset et al. \(2017\)](#) found that wild smolts migrated more slowly than hatchery smolts in the river Vosso (Norway). Using a modeling approach, [Frechette et al. \(2023\)](#) demonstrated that stocking of hatchery smolts in the Penobscot River was out of sync with the onset of emigration of natural smolts originating in upriver tributaries.

Such asynchrony in migration timing may affect estuarine and marine survival of hatchery smolts ([Hvidsten & Johnsen, 1993](#)). Ocean entry timing is thought to reflect adaptation that confers a survival advantage to smolts, ensuring that their arrival in the marine environment aligns with both physiological capability for saltwater transition and prey availability ([Hawkes et al., 2017](#); [Hvidsten et al., 1998](#); [McCormick et al., 1998](#); [Otero et al., 2014](#)). If hatchery smolt stocking is synchronized with natural smolt emigration, then hatchery smolts would be expected to enter the marine environment within the optimal window for survival. In fact, hatchery Atlantic Salmon smolts exhibited greater survival when they were stocked at the same time that natural origin smolts were emigrating in the river Oulujoki, Finland ([Karppinen et al., 2013](#)). Furthermore, estuaries are areas of elevated predation risk ([Collis et al., 2002](#); [Mensinger et al., 2023](#)). The longer estuary residence exhibited by earlier arriving hatchery smolts may result in greater mortality from predation, whereas synchrony between emigrating natural and hatchery smolts may buffer individuals from predation through predator swamping ([Furey et al., 2016](#)). If smolt stocking remains the focus of the conservation hatchery program in the Penobscot River, improving the synchronicity of migration and estuary entry timing between natural and hatchery smolts is a potential action that managers could use to advance the recovery of the GOM DPS.

Despite the breadth of research on Atlantic Salmon that has been conducted within the Penobscot River watershed, an overall characterization of the smolt run in terms of smolt size, age, and emigration timing has not been published to date. In this article, we analyze a data set comprised of smolts that were collected using rotary screw traps (RSTs; EG Solutions, Corvallis, Oregon) from the main-stem Penobscot River between 2001 and 2005. The work reported herein represents the only smolt sampling effort conducted in the lower main-stem Penobscot River. This data set was collected before both the removal of the two lowermost dams on the river as part of the Penobscot River Restoration Program and before Atlantic Salmon in the Penobscot River was listed as endangered ([Opperman et al., 2011](#); [Sheehan et al., 2021](#); [USFWS & NMFS, 2018](#)). These data provide a historical baseline for evaluating smolt size, age, and emigration phenology, as Atlantic Salmon continue to face constantly evolving marine and freshwater ecosystems.

Our objectives were to (1) determine the proportion of emigrating natural and hatchery smolts, (2) compare smolt size and run timing by origin, and (3) assess whether location and timing of stocking affected recapture rates and emigration timing of hatchery smolts. Addressing these objectives was facilitated, in part, by a marking program for hatchery smolts using the visual implant elastomer (VIE) marking (Northwest Marine Technologies, Shaw Island, Washington) that was implemented in the Penobscot River during these years. Beyond the period of this study, marking has not been a focus of the conservation hatchery program for the Penobscot River; thus, these data provide useful insight into emigration dynamics of hatchery smolts and how they compare to those of natural smolts.

## METHODS

### Stocking and marking

The Penobscot River is the largest river in Maine, with a catchment comprising approximately 22,000 km<sup>2</sup>. Historically, the

**Table 1.** Number of hatchery fish stocked by life stage in each year that could have contributed to the smolts captured in rotary screw traps during this study (2001 to 2005). Hatchery fry contributed to the production of natural smolts, whereas the other stocked life stages contributed to hatchery smolt production. Fry would be expected to contribute to the smolt cohort primarily in years  $t + 2$  and  $t + 3$ ; age-0 parr would contribute to the smolt cohorts in years  $t + 1$  and  $t + 2$ ; and age-1 parr would primarily contribute to the smolt cohort in years  $t + 1$ , where  $t$  is the year of stocking. The numbers are rounded to the nearest hundred.

| Life stage  | 1999      | 2000      | 2001      | 2002      | 2003      | 2004      | 2005      |
|-------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| Fry         | 1,498,000 | 513,000   | 364,000   | 746,000   | 741,000   | 1,811,700 | 1,898,700 |
| Age-0 parr  | 229,600   | 288,800   | 235,800   | 396,700   | 320,700   | 369,200   | 295,400   |
| Age-1 parr  | 1,500     | 700       | 2,100     | 1,800     | 2,100     | —         | —         |
| Age-1 smolt | 567,300   | 564,200   | 544,800   | 547,000   | 547,100   | 551,700   | 555,500   |
| Total       | 2,296,400 | 1,366,700 | 1,146,700 | 1,691,500 | 1,610,900 | 2,732,600 | 2,749,600 |

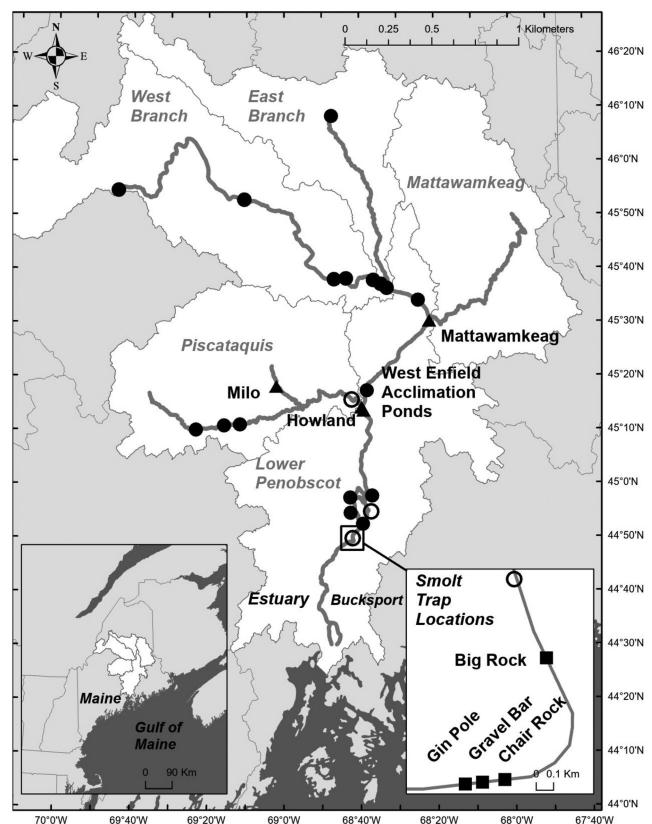
Penobscot supported one of the largest wild Atlantic Salmon runs in New England; estimated annual returns were on the order of 100,000 (Fay et al., 2006; Trinko Lake et al., 2012). Since the 2009 U.S. ESA listing, returns of Atlantic Salmon to the Penobscot River have ranged from a high of 3,125 (of which 2,878 were hatchery origin) in 2011 to a low of 261 (239 hatchery origin) in 2014 (USASAC, 2021, 2024).

All the Atlantic Salmon life stages that are stocked into the Penobscot watershed are the product of adult sea-run salmon (hatchery and natural). These adults are captured in the river at dam bypass facilities and transferred to the USFWS Craig Brook National Fish Hatchery in East Orland, Maine, where they are spawned (USASAC, 2024). Eyed eggs are then transferred to the USFWS Green Lake National Fish Hatchery, where they are reared until stocking. The smolts that were available for capture during the 5 years of sampling (2001 to 2005) would have resulted from fry, parr, and smolt stocking efforts from 1999 to 2005 (Table 1). During this period, more than 500,000 age-1 smolts were stocked annually. There was considerably more variability around the numbers of fry and age-0 parr that were stocked (Table 1). During the years of this study, a subset of stocked hatchery smolts was marked for assessment purposes.

From 2001 to 2005, we marked 30% to 62% of the smolts that were produced by Green Lake National Fish Hatchery with VIE tags, using batch marking (FitzGerald et al., 2004; Lipsky et al., 2012; Mamer & Meyer, 2016; Mortensen et al., 2016). We used unique combinations of colors, locations, and adipose fin clips to identify individual release groups; for detailed methods, see Lipsky et al. (2012). We released the marked smolts at three in-river stocking locations, identified here by river kilometer (rkm), as measured from the mouth of the Penobscot River (Mattawamkeag [rkm 142.19], Milo [134.28], and Howland [98.85]; Table 2; Figure 1). A fourth stocking location comprised a set of smolt acclimation ponds (hereafter, “acclimation ponds”), located in West Enfield, Maine (rkm 101.11), which were managed by the Penobscot Nation. The smolts that were stocked into these ponds could volitionally emigrate to the river, essentially self-releasing, although many of the smolts remained until they were actively forced out of the acclimation ponds by using crowders after the river temperatures reached 10°C. The number of stocked smolts at each location on a given date ranged from approximately 24,000 to 74,000 fish (Table 2). From 2001 to 2004, all four stocking sites were used, but only the Milo and Howland sites were used in 2005 because of a programmatic change.

## Capture methods

We used RSTs to collect data on emigrating Atlantic Salmon smolts (Music et al., 2010). We deployed 2.44-m RSTs in three locations: at rkm 45.7 (Gin Pole), rkm 45.8 (Gravel Bar), and rkm 45.9 (Chair Rock) during 2001 (Figure 1). When the water depth at Gravel Bar became too shallow to operate the RST, the trap was relocated to rkm 46.9 (Big Rock) on May 12, 2001. From 2002 to 2005, we deployed a RST at each of the Gin Pole, Chair Rock, and Big Rock sites (Table 3). The



**Figure 1.** Penobscot River with smolt stocking locations (closed triangles), existing dams (closed circles), and dams that were removed or bypassed between when the study was conducted and the present day. The left-hand insert indicates the position of the Penobscot watershed within northeastern North America, and the right-hand inset provides detail of the river reach where rotary screw traps (closed squares) were deployed.

**Table 2.** Number (*N*) of Atlantic Salmon smolts marked with visual implant elastomer tags that were stocked in the Penobscot River (2001 to 2005) by stocking location and day of year (DOY).

| Stocking location | 2001 |          | 2002 |          | 2003 |          | 2004 |          | 2005 |          |
|-------------------|------|----------|------|----------|------|----------|------|----------|------|----------|
|                   | DOY  | <i>N</i> | DOY  | <i>N</i> | DOY  | <i>N</i> | DOY  | <i>N</i> | DOY  | <i>N</i> |
| Mattawamkeag      | 116  | 24,564   | 105  | 24,615   | 108  | 24,619   | 103  | 24,638   | —    | —        |
| Mattawamkeag      | 134  | 24,679   | 126  | 24,716   | 122  | 24,685   | 121  | 24,511   | —    | —        |
| Milo              | 117  | 24,430   | 106  | 24,673   | 107  | 24,681   | 104  | 24,569   | 110  | 73,853   |
| Milo              | 131  | 26,638   | 127  | 24,698   | 121  | 24,620   | 125  | 49,270   | 117  | 73,696   |
| Milo              | —    | —        | —    | —        | 126  | 24,678   | —    | —        | —    | —        |
| Howland           | 115  | 24,401   | 107  | 24,581   | 106  | 24,692   | 105  | 24,663   | 108  | 73,968   |
| Howland           | 130  | 24,422   | 128  | 24,670   | 120  | 24,610   | 120  | 24,576   | 115  | 74,462   |
| Acclimation ponds | 120  | 24,348   | 95   | 24,636   | 112  | 25,467   | 107  | 24,663   | —    | —        |
| Total             |      | 173,482  |      | 172,589  |      | 198,052  |      | 196,890  |      | 295,979  |

wide river channel necessitated that multiple traps be deployed simultaneously, but due to a lack of available points for anchoring and the need to maintain human safety, the traps could not be strung together in a line. Consequently, we deployed traps using the best available anchorages within 1 km of each other and combined the data from all RSTs for data analysis—that is, we treated the RSTs as one single sampling unit.

The RSTs were secured with a minimum of three points of attachment to large boulders or bedrock in the river using a system of steel plates, eye bolts, chains, and cables. The RSTs were adjusted (sometimes daily) to maintain their positions in the primary flow and improve catch rates because the flow conditions and water depths varied over time. The RSTs were tended each morning following the initial start date, and sampling continued until there were 5 d or more with no smolts captured, which typically occurred in mid-June (Table 3). For human safety and fish welfare, the cones of the RSTs were occasionally lifted for one or more days during high-flow events. Because the RSTs were not operational on these days, these periods were not counted toward the total number of sampling days (Table 3). We calculated the number of sampling days for each RST by counting the number of days that the trap cone was in the water and turning (e.g., not jammed with debris) for 20–24 h.

We removed the smolts from the RST live car using fine mesh nets. Prior to handling, the smolts were anesthetized

with buffered MS-222 (100-g/1 L stock solution, 1-mL stock solution/L water). The captured fish were weighed (0.1 g) and measured (1 mm fork length [FL]). We collected scale samples from every third unmarked smolt to determine its age and origin. The scales were analyzed at the National Oceanic and Atmospheric Administration's Northeast Fisheries Science Center (Woods Hole, Massachusetts) using standard scale analysis methods to determine the origin and age of the emigrating smolts (Haas-Castro et al., 2006; Shearer, 1992). Because the scales of hatchery-stocked fry are indistinguishable from those of individuals that resulted from in-river spawning by adult salmon, we collectively referred to these two groups as “natural,” whereas the individuals that were stocked as parr or smolts were classified as being of “hatchery” origin. The smolts that were stocked as parr in the fall could be identified based on scale pattern as having been released 8 months before capture as an age-1 smolt or released 20 months before capture as an age-2 smolt. The unmarked smolts that were handled but not scale sampled were assigned the origin “unknown,” which comprised an unidentifiable number of hatchery and natural smolts.

### Smolt run composition

Once the sampled smolts were identified to origin (hatchery, natural, or unknown), we calculated the proportions of smolts

**Table 3.** Deployment dates (in day of year) for each Penobscot River rotary screw trap, with sampling days expressed as a number (*N*) and as a percentage of the total deployment period (in parentheses). Days when the traps were not operated (cones were raised out of the water) during high-flow events were not counted toward the total number of sampling days. The number of captured Atlantic Salmon smolts is presented by trap and as the annual total. The abbreviations are as follows: rkm = river kilometer; RST = rotary screw trap.

| Trap site  | rkm   |                           | 2001     | 2002      | 2003     | 2004     | 2005     |
|------------|-------|---------------------------|----------|-----------|----------|----------|----------|
| Big Rock   | 46.93 | RST deployment dates      | 132–159  | 113–165   | 111–171  | 110–166  | 110–160  |
|            |       | <i>N</i> (%) days sampled | 26 (96%) | 52 (100%) | 57 (95%) | 46 (82%) | 40 (80%) |
|            |       | Smolts captured           | 112      | 395       | 155      | 186      | 24       |
| Chair Rock | 45.95 | RST deployment dates      | 116–159  | 113–151   | 111–171  | 114–161  | 109–160  |
|            |       | <i>N</i> (%) days sampled | 39 (91%) | 38 (100%) | 51 (83%) | 44 (94%) | 32 (63%) |
|            |       | Smolts captured           | 729      | 2,274     | 166      | 830      | 134      |
| Gravel Bar | 45.82 | RST deployment dates      | 116–131  | —         | —        | —        | —        |
|            |       | <i>N</i> (%) days sampled | 14 (93%) | —         | —        | —        | —        |
|            |       | Smolts captured           | 26       | —         | —        | —        | —        |
| Gin Pole   | 45.72 | RST deployment dates      | 116–159  | 113–165   | 111–171  | 110–166  | 109–160  |
|            |       | <i>N</i> (%) days sampled | 37 (86%) | 51 (98%)  | 52 (87%) | 55 (98%) | 39 (76%) |
|            |       | Smolts captured           | 309      | 496       | 127      | 584      | 93       |
|            |       | Total                     | 1,176    | 3,165     | 448      | 1,600    | 251      |

of each origin and compared FL, mass, age, and run timing among hatchery-, natural-, and unknown-origin smolts. We computed summary statistics and visualized the composition of the smolt run using `plyr` (Wickham, 2011), `dplyr` (Wickham et al., 2023), and `ggplot` (Wickham, 2016). We conducted all the statistical tests using R version 4.4.1 (R Core Team, 2024) in R Studio version 2024.12.1.563 (Posit Team, 2025).

To place the observed emigration timing of the smolts that were captured in this study into the context of the natural smolt migration phenology in Maine rivers, we computed the day of year (DOY) that we captured 25% of the run in the RSTs, indicating that 25% of the run has emigrated (DOY25). This metric has previously been used to describe smolt run timing in North America and Europe (Otero et al., 2014; Vollset et al., 2021). We predicted the expected DOY25 for natural smolts in the RSTs using a linear regression model between measured air temperature and DOY25 that was developed by Frechette et al. (2023). We obtained the mean daily air temperature that was measured within each of the major tributaries of the Penobscot River from the same monitoring stations that were used by Frechette et al. (2023): the Millinocket Municipal Airport (East Branch Penobscot River), Houlton International Airport (Mattawamkeag River), and Dover-Foxcroft Wastewater Treatment Plant (Piscataquis River). We then computed the mean air temperature for the first 90 d of the year ( $T_{\text{mean}}$ ) for input into Equation 1 ( $\text{DOY25} = 123.72 - 1.96[T_{\text{mean}}]$ ) from Frechette et al., 2023). All the air temperature data were obtained from the Maine Climate Office ([https://mco.umaine.edu/data\\_daily/](https://mco.umaine.edu/data_daily/); accessed April 4, 2025). We generated plots of  $T_{\text{mean}}$  and the predicted DOY25 for all years between 2000 and 2025 to visually examine the trends over time and compared the DOY25 that was observed in the RSTs during the years 2001 to 2005 with the predicted DOY25.

### Recapture rates and days at large

We used the VIE marks to assign the captured smolts back to their stocking group, from which we calculated recapture rates and days at large. We computed days at large for each uniquely marked release group by subtracting the release date from the capture date in the RST. However, in 2004 and 2005, smolts with the same mark were released on two consecutive days. To compute days at large for the smolts for which the batch mark could not be assigned to a single calendar date, we set the day of release as the date when the greater number of smolts was released. The smolts that were stocked into the acclimation ponds were excluded from the analysis of days at large because no single exit date could be assigned to this group.

We assessed the effect of stocking location and stocking date on the number of days at large. The within-year recaptures of smolts from the individual stocking groups were not sufficient to assess the effect of stocking year on days at large. We tested the hypothesis that days at large did not differ among the three stocking locations (Howland, Mattawamkeag, and Milo). We assessed the assumption of normality with a Shapiro–Wilk test, graphically examined plots of the residuals, and used a Kruskal–Wallis  $H$ -test because the assumption of normality was not met (Shapiro–Wilk  $W = 0.92665$ ,  $P < 2.2 \times 10^{-16}$ ). We used a Pearson’s

product moment correlation to assess the relationship between days at large and date of stocking.

The visual examination of the plot of days at large by stock day suggested that the smolts that were stocked before April 30 (DOY 120) and those that were stocked after April 30 comprised two different stocking periods, hereafter referred to as “early” (stocked before April 30) and “late” (stocked after April 30). We plotted the frequency distributions of days at large for the early- and late-stocked smolts and tested the null hypothesis of a continuous distribution using a Kolmogorov–Smirnov test.

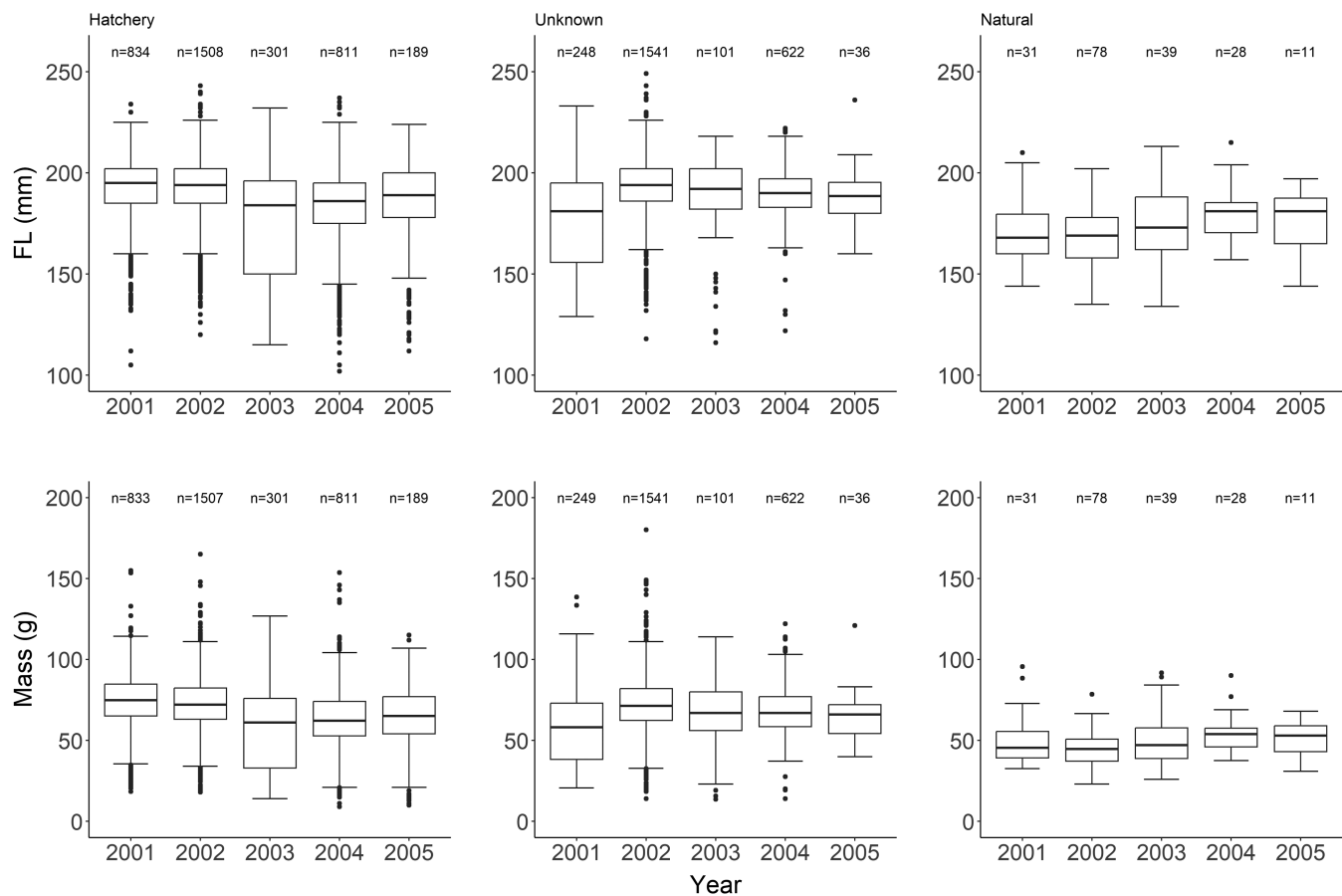
## RESULTS

### Smolt run composition

Deployment duration for each RST varied within and among years, with deployment dates generally occurring between April 19 and April 26 (Table 3). Smolt trapping operations ceased for the year between May 31 and June 20. The total number of sampled days ranged from 26 to 57 among traps and years. Smolts were captured at every site (Table 3). During 2002, one smolt was captured on the first day that the RSTs were operational, whereas the first smolt was captured 2 to 7 d after the RSTs were installed during all other years. The percentage of sampled days was greatest in 2002, when the traps were actively sampling for 100% of the operational period, and lowest in 2005, when high river discharge resulted in individual RSTs traps sampling between 63% and 80% of the operational period (Table 3; see online Supplementary Material, Figure S1).

Over the 5 years, the total number of smolts captured in the RSTs was 6,640 individuals (all origins combined). The number of captured smolts each year ranged from 251 in 2005 to 3,165 in 2002. We could determine origin for 3,961 smolts (60% of the total catch) because they either had a VIE mark or scales had been collected and analyzed; the remaining 2,679 captured smolts were assigned as unknown rearing origin because they were not VIE-marked and scales were not collected (40% of the total catch). Of the known-origin smolts, 95.3% were hatchery origin (3,774 of 3,961); only 4.7% were natural smolts (187 of 3,961). Mass (g) and fork length (mm) were recorded for all the natural smolts that were captured from 2001 to 2005 ( $N = 187$ ). Fork length was recorded for 3,643 hatchery-origin and 2,548 unknown-origin smolts, and mass was recorded for 3,641 hatchery-origin and 2,549 unknown-origin smolts.

Although there was interannual variability in smolt size, in general, hatchery- and unknown-origin smolts were longer and heavier than natural-origin smolts (Figure 2). Most of the hatchery smolts were age-1 fish (i.e., individuals that were stocked as smolts in the year of capture), although we also caught a small number of age-1 smolts that were stocked as parr 8 months before capture and age-2 smolts that were stocked as parr 20 months before capture (see online Supplementary Material, Table S1). The captures of natural smolts were dominated by age-2 individuals, followed by age-3 smolts. Natural age-1 smolts ( $n = 5$ ) were captured only during 2002, and only one age-4 smolt was captured (in 2003). Despite being older, the natural smolts were smaller than the age-1 hatchery smolts (Table 4).



**Figure 2.** Size composition (fork length, top panel) and mass (bottom panel) of hatchery (left), unknown (center) and natural (right) Atlantic Salmon smolts captured by rotary screw traps in the Penobscot River from 2001 to 2005. The horizontal lines within the boxes indicate the medians, the box dimensions show the 25th and 75th percentiles (first and third quartiles), the whiskers extend to the most extreme point within 1.5 times the interquartile range, and the closed circles denote outliers. The sample sizes are shown above the boxes. Note the different y-axes and intercepts.

There was also interannual variability in emigration timing for all three smolt origins. However, hatchery- and unknown-origin smolts had a median DOY that was more than a week earlier than the median capture DOY of natural smolts in all years except 2001, when the median capture DOY for unknown smolts was only 1 d earlier than the median DOY for natural smolts (see Table S2). From 2001 to 2005, the observed DOY25 for natural-origin smolts was similar to the expected DOY25 for naturally emigrating smolts originating in the three main production areas of the Penobscot drainage (Figure 3) that was

**Table 4.** Number of individuals and fork length (mean, standard deviation [SD], and median) by age at out-migration for hatchery and natural smolts as determined by scale pattern analysis.

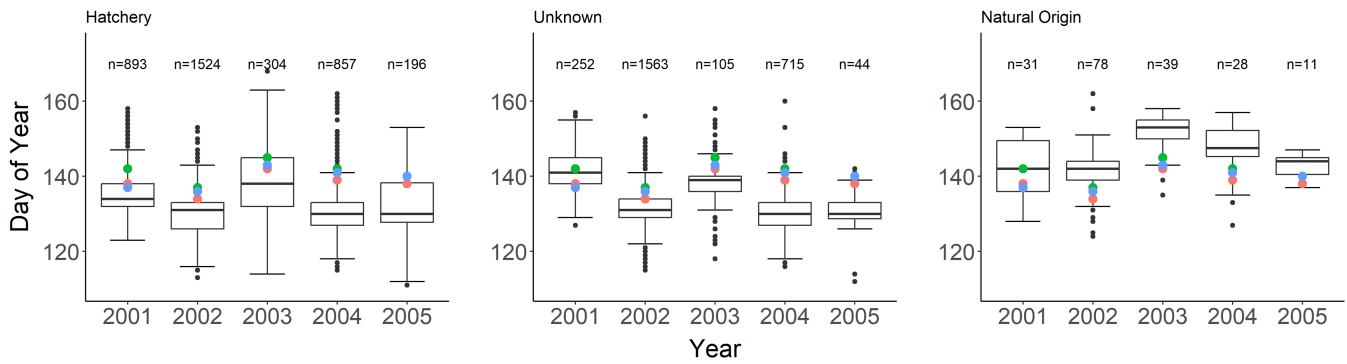
| Origin   | Age | N     | Mean fork length (mm) | SD | Median fork length (mm) |
|----------|-----|-------|-----------------------|----|-------------------------|
| Hatchery | 1   | 3,252 | 188                   | 20 | 191                     |
|          | 2   | 7     | 177                   | 13 | 175                     |
| Natural  | 1   | 5     | 149                   | 13 | 149                     |
|          | 2   | 145   | 170                   | 15 | 169                     |
|          | 3   | 34    | 182                   | 15 | 183                     |
|          | 4   | 1     | 206                   | —  | —                       |

predicted using the methods of Frechette et al. (2023). Across the 5 years and three production areas, the mean DOY25 was only 2.5 d later than the predicted DOY25. Hatchery- and unknown-origin smolts emigrated earlier than the predicted timing for naturally emigrating smolts. Across the years and production areas, the observed DOY25 of hatchery smolts was on average 10.7 d earlier than the predicted DOY25; for unknown origin smolts, observed DOY25 was 7.9 d earlier than the predicted DOY25 (Figure 3).

From 2000 to 2025, there was substantial variation in  $T_{\text{mean}}$  (Figure 4A), resulting in substantial variation in the predicted DOY25 (Figure 4B) for naturally emigrating smolts originating in the three main production areas of the Penobscot drainage. The earliest predicted DOY25 occurred during 2010 (day 128), and the latest occurred in 2015 (day 146). The mean predicted DOY25 for the 26-year time series was day 135 for the East Branch Penobscot (SD = 3.8 d), day 138 for the Mattawamkeag (SD = 4.0 d), and day 137 for the Piscataquis (SD = 3.9).

#### Recapture rates and days at large

We captured 1,865 VIE-marked smolts stocked at Milo ( $n = 677$ ), Howland ( $n = 598$ ), and Mattawamkeag ( $n = 590$ ) across the 5 years of the study (2001 to 2005). Catches across

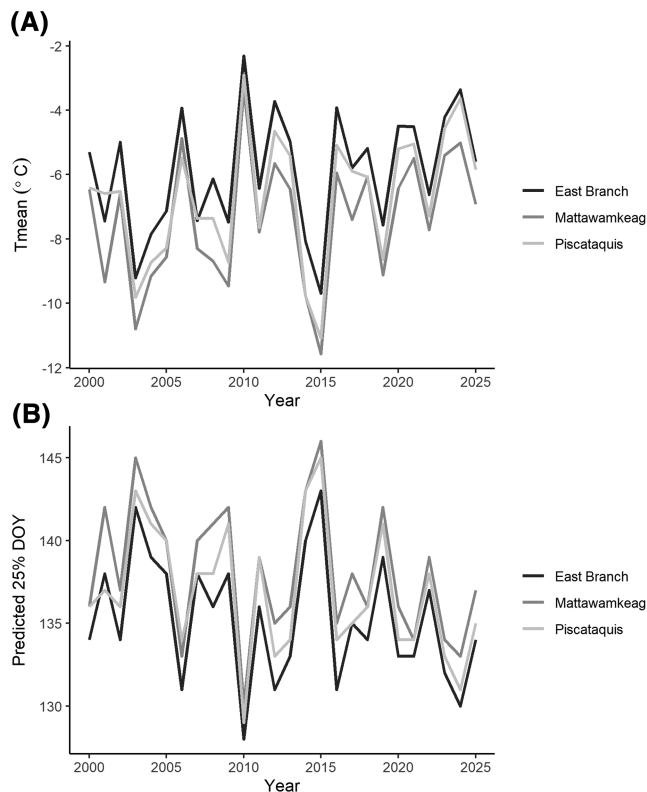


**Figure 3.** Run timing by year for hatchery (left panel), unknown (center panel), and natural Atlantic Salmon smolts (right panel). The horizontal lines within the boxes indicate the medians, the box dimensions show the 25th and 75th percentiles (first and third quartiles), the whiskers extend to the most extreme point within 1.5 times the interquartile range, and the closed black circles denote outliers. The 25th percentile (lower box) equates to the measured day of year that 25% of the run has emigrated. The colored points represent the predicted day of year that 25% of the run has emigrated for the three main smolt production areas in the Penobscot drainage (pink = East Branch Penobscot River; green = Mattawamkeag River; blue = Piscataquis River), derived from Frechette et al. (2023).

the three stocking locations were evenly distributed; however, the capture rates varied by group and by year (Table 5). Catches of the VIE-marked smolts from each stocking location are presented relative to the RST deployment dates in Figure 5A. The number of recaptures for each group of marked

fish ranged from 5 (Milo, 2005) to 320 (Howland, 2002), and the recapture rate (number of smolts captured per 1,000 smolts stocked) for each group of marked fish ranged from 0.1 to 6.5 (Table 5). In total, 224 VIE-marked smolts that were stocked into the acclimation ponds were recaptured in the RSTs across the 5 years. Total recaptures of individuals that were stocked in the acclimation ponds in the RSTs were lowest in 2001 (only one smolt captured) and were <1% of the individuals that had been stocked in each year. The greatest number of recaptures from the acclimation ponds occurred in 2003, when 120 smolts (out of 24,636 stocked; 0.5%) were captured. Although total recaptures were low, when represented in terms of captures per 1,000 smolts released, the smolts that were stocked into the acclimation ponds had a recapture rate in the RSTs that ranged between 0.0 and 4.9 per 1,000 smolts stocked, which was comparable to recaptures from the in-river stocked groups (Table 5; Sheehan et al., 2011).

Days at large did not differ among the three stocking locations (Howland, Milo, and Mattawamkeag; Kruskal–Wallis

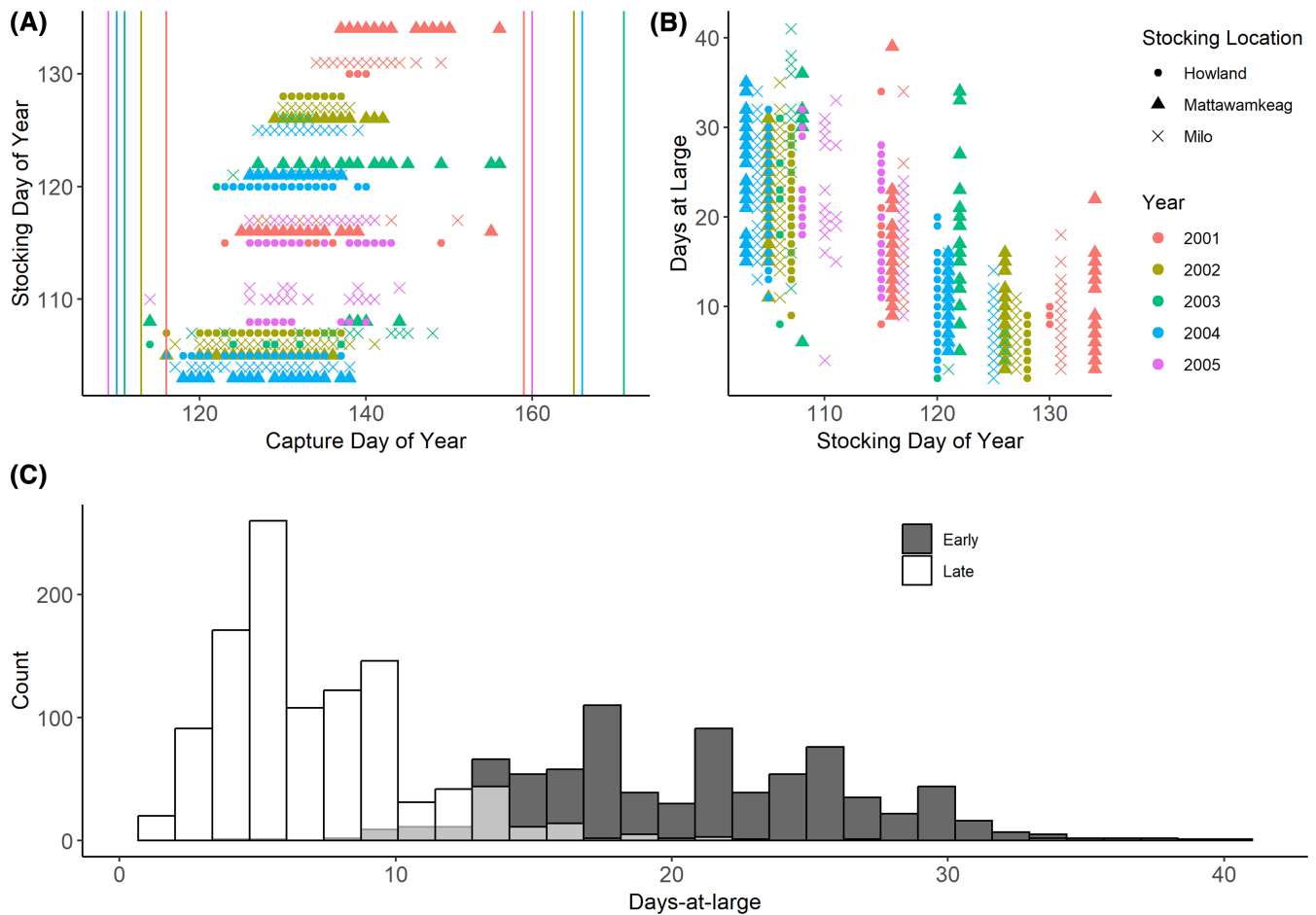


**Figure 4.** (A) Mean air temperature for the first 90 d of the year ( $T_{mean}$ ) as measured at the Millinocket Municipal Airport (East Branch Penobscot River), Houlton International Airport (Mattawamkeag River), and Dover-Foxcroft Wastewater Treatment Plant (Piscataquis River) for the years 2000 to 2025. (B) Predicted 25% capture day of year (DOY) generated using  $T_{mean}$  from panel A and Equation 1 from Frechette et al. (2023):  $DOY = 123.72 - 1.96(T_{mean})$ .

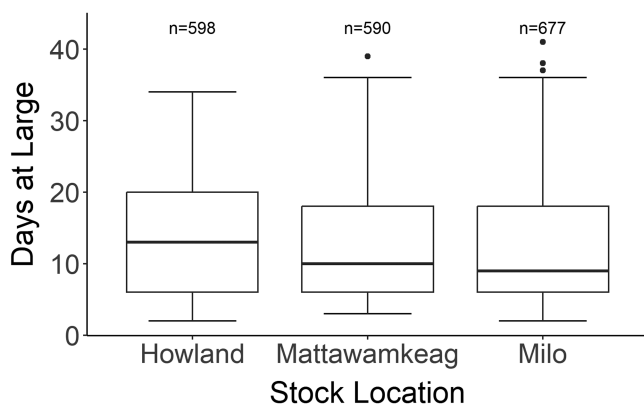
**Table 5.** Recapture rates by release group, standardized to the number recaptured per thousand released, captured by rotary screw trap (RST) and by postsmolt trawl survey (PST; reproduced from Sheehan et al., 2011) for the years 2001–2005. The bold numbers indicate the collection method that had the greater recapture rate for each combination of stocking location and year.

| Stocking group (Collection method) | 2001             | 2002       | 2003       | 2004       | 2005       |
|------------------------------------|------------------|------------|------------|------------|------------|
| Mattawamkeag (RST)                 | <b>3.5</b>       | <b>5.5</b> | 0.5        | <b>2.4</b> |            |
| Mattawamkeag (PST)                 | 1.6              | 1.6        | <b>0.6</b> | 0.9        |            |
| Milo (RST)                         | 2.9              | <b>4.9</b> | 0.4        | <b>2.8</b> | 0.3        |
| Milo (PST)                         | <b>3.4</b>       | 1.5        | <b>2</b>   | 2.3        | <b>2.5</b> |
| Howland (RST)                      | 0.8              | 6.5        | 0.5        | <b>3</b>   | 0.5        |
| Howland (PST)                      | <b>2.3</b>       | 1.8        | <b>0.9</b> | 1.1        | <b>1.2</b> |
| West Enfield acc. ponds (RST)      | 0.0 <sup>a</sup> | <b>4.9</b> | 0.7        | <b>3.4</b> |            |
| West Enfield acc. ponds (PST)      | <b>0.7</b>       | 0.5        | <b>1.5</b> | 1.1        |            |

<sup>a</sup>Only one smolt from the acclimation ponds (acc. ponds) was caught, effectively making the recapture rate zero.



**Figure 5.** Capture timing of visual implant elastomer-marked smolts: (A) Days of year smolts were captured relative to the day stocked. The symbols represent the stocking locations (closed circle = Howland, closed triangle = Mattawamkeag, cross = Milo); the colors indicate years, and the vertical, colored lines indicate the range of dates over which the rotary screw traps were operational within each year. (B) Days at large (*y*-axis) relative to stocking day of year (*x*-axis). The symbols and colors correspond to panel A. (C) Frequency histogram of days at large for visual implant elastomer-marked smolts stocked early (before April 30; white bars) or late (after April 30; dark gray bars). The light gray bars indicate the area of overlap between the two stocking periods.



**Figure 6.** Comparison of days at large among the three sites where Atlantic Salmon smolts were stocked into the Penobscot River watershed, for all years (2001 to 2005) combined. The horizontal lines within the boxes indicate the medians, the box dimensions show the 25th and 75th percentiles (first and third quartiles), the whiskers extend to the most extreme point within 1.5 times the interquartile range, and the closed circles denote outliers.

$H=2.87$ ,  $df=2$ ,  $P=0.2383$ ; Figure 6). Days at large were significantly negatively correlated with the date that the smolts were stocked,  $r(1863) = -0.852$ ,  $df=1863$ ,  $P < 2.2 \times 10^{-16}$  (Figure 5B). The smolts that were stocked before April 30 spent more time at large (it took them longer to reach traps) than those that were stocked on or after April 30 (Kolmogorov-Smirnov  $D=0.879$ ,  $P < 2.2 \times 10^{-16}$ ; Figure 5C).

## DISCUSSION

We analyzed data from a 5-year smolt sampling effort using RSTs to assess the run composition and emigration dynamics of Atlantic Salmon smolts in Maine's largest watershed, the Penobscot River. These data were collected before the listing of the stock as endangered under the U.S. ESA and the restoration efforts encompassed by the Penobscot River Restoration Program (Opperman et al., 2011; USFWS & NMFS, 2018). We used recaptures of VIE-marked smolts to assess the timing and location of smolt stocking on emigration timing and recapture rates. Although these VIE-marking data had been previously used to assess smolt survival through the Penobscot

Bay estuary (Sheehan et al., 2011), they had not been used to analyze in-river smolt run composition, run timing, or capture rates. Of the smolts that could be identified to origin based on scale pattern analysis, most (3,774) were hatchery origin; only 187 natural smolts were captured across the 5 years of the study. Although there was interannual variability, natural and hatchery smolts differed in size, age structure, and run timing. As expected, the natural smolts were older than the accelerated age-1 hatchery smolts that were produced for the Penobscot River, but they were also smaller and emigrated later in the spring than hatchery smolts. Stocking location did not affect the timing of arrival at the smolt traps, but stocking date did affect the number of days that smolts spent at large between stocking and recapture. Specifically, the hatchery smolts that were stocked before April 30 took longer to reach the RSTs than those that were released later. The recapture rates varied among stocking locations, and the smolts that were stocked into acclimation ponds were recaptured at rates that were similar to those for the smolts that were stocked in-river.

The recapture rates of the VIE-marked smolts that were stocked at Mattawamkeag, Milo, and Howland were on the order of 0.5 to 6.5 smolts per 1,000 stocked across the stocking locations and years and provide our only indication of the sampling efficiency of the RSTs. Deployment timing, duration of trap operations, and trap placement all greatly influence the quality of the data that can be collected from an RST. During 2002, a single hatchery smolt was captured on the first day of RST sampling; however, there were 2–7 d between trap deployment and the first smolt capture during the other years of the study. The sampling protocol required that sampling continued until no smolts were captured for 5 d. Therefore, the trap deployment period encompassed the start and end of the smolt run in all years except 2002, when installation may have missed the start of the run by no more than a few days. Although there was a percentage of time during the period of trap operations in most years when the traps were not sampling due to high flows (Table 3), they were operational for the majority of the smolt out-migration period.

In an ideal scenario, RSTs are placed so that they can be maintained within the thalweg even as river discharge increases or decreases to optimize trap efficiency. River reaches with wide, flat bottom profiles can make it challenging to situate an RST so that it efficiently samples the smolt run (Music et al., 2010; Volkhardt et al., 2007). The lower main-stem Penobscot River, where sampling was conducted, is 150 to 250 m wide. Each of the three RSTs was deployed at a point location; thus, the area of the river that was sampled by each trap cone (2.44 m in diameter) was a very small proportion of the total river volume passing each point. Harnessing the RSTs together to increase the stream width that was covered at any one location was not possible for this study due to human safety concerns and anchoring constraints. The recapture rates of the VIE-marked smolts in the RSTs were low across all stocking groups, highlighting the challenges of operating RSTs in the main-stem Penobscot River, with trap placement rather than sampling duration limiting the smolt captures.

Natural smolts represented only 3% of the individuals that were captured across the 5 years of the study. Although there was interannual variability in smolt size, the hatchery smolts were consistently younger (age 1), longer, and heavier than the

natural smolts. This difference is expected given the accelerated growth program employed by the USFWS to specifically rear age-1 smolts for the Atlantic Salmon conservation hatchery program in Maine (Zydlewski et al., 2014). Over the 5 years of this study, natural smolts were predominantly age 2 (78.6%) and age 3 (18.2%), with a few individuals emigrating at age 1 (2.7%) and age 4 (0.5%), which fall within the ranges that have been observed in other Maine rivers. Cohorts of emigrating smolts in other Maine rivers generally comprise 65–85% age-2 and 10–30% age-3 fish, with a handful of age-1 and age-4 fish in mixed proportions (USASAC, 2024). During the period of this study, the natural age-2 smolts in the Penobscot River were within the size ranges (FL and mass) that have been observed in other Maine rivers (USASAC, 2006).

Despite the annual stocking of  $\geq 250,000$  age-0 hatchery-reared fall parr into the Penobscot drainage (Table 1), very few ( $\leq 25$  in any given year) were recaptured as smolts in the RSTs. Of the age-0 fall parr that were captured as smolts, most emigrated at age 1; only seven smolts that were captured across the 5 years of the study were age-2 smolts that had been stocked as age-0 fall parr. The stocking of fall parr in the Penobscot drainage has largely been a by-product of the production of age-1 smolts through the accelerated rearing program (Zydlewski et al., 2014). Atlantic Salmon exhibit bimodal growth, with individuals in the upper mode having a greater probability of smolting at age 1 (Thorpe, 1977; Utrilla & Lobon-Cervia, 1999; Zydlewski et al., 2014). To rear an adequate number of accelerated age-1 smolts for the Penobscot River smolt program, USFWS Green Lake National Fish Hatchery produces an excess of parr, which are graded in the fall. The smaller (lower mode) age-0 parr are stocked into the river in the fall, whereas the larger, upper mode individuals are retained for release as smolts the following spring. These age-0 accelerated parr have historically been released into suboptimal habitats, reducing survival to the smolt stage (Zydlewski et al., 2014). Our findings are consistent with those of previous smolt sampling studies, in which survival of stocked, age-0 hatchery parr to the smolt stage was low, on the order of 5% to 10% or less (Jokikokko & Jutila, 2004; Orciari et al., 1994; Zydlewski et al., 2014). In addition to being stocked in low-quality habitat, the age-0 hatchery parr were stocked at high densities, resulting in individuals that likely lacked sufficient resources (e.g., stored energy, availability of shelter) to survive the harsh, northern latitude winters (Cunjak & Power, 1987a, 1987b; Jokikokko & Jutila, 2004), with subsequent low survival to smolt at age 2 resulting from exposure to an additional year of in-river mortality (Zydlewski et al., 2014).

As expected from previous telemetry studies in the Penobscot River, the emigration timing was earlier for the hatchery- and unknown-origin smolts than for the natural smolts. During all years, the median capture date of the hatchery smolts was similar to that of the unknown-origin smolts but was earlier than that of the natural smolts. In fact, the median capture DOY for the hatchery-origin smolts was between 8 and 17 d earlier than it was for the natural smolts. The hatchery smolts were stocked earlier than the emigration timing of natural smolts during all years of the present study (Figure 3). As a result, the hatchery smolts arrived at the RSTs in the lower Penobscot River out of sync with the natural smolts.

The difference in run timing between hatchery and natural smolts has been attributed to some combination of physiological development, photoperiod, accumulated thermal units, river discharge, release timing, and fish size (Jokikokko et al., 2006; Stich, Kinnison, et al., 2015; USASAC, 2006; Vollset et al., 2021; Zydlewski et al., 2005). However, measurements of such variables are not always readily available to managers who are charged with making decisions in real time (Frechette et al., 2023). We found that the emigration timing of natural smolts, as expressed as the DOY25, closely matched the estimated DOY25 that was generated by applying the air-temperature-based regression that was developed by Frechette et al. (2023). Therefore, our findings support the conclusions of Frechette et al. (2023) that measured air temperature in smolt production areas is a useful metric for predicting the emigration timing of natural smolts.

Given that not all the hatchery smolts were marked and not all the smolts were sampled for scales at the RSTs, it is possible that we missed some natural smolts among the unknown component of the RST catch. Had there been a comprehensive marking program whereby all the hatchery smolts were marked before release, we would have been able to attribute all the smolts to rearing origin, thus reducing the “unknown” category. However, given the similarity in run timing and size (mass and FL) between the hatchery- and unknown-origin smolts, the very low numbers of known natural smolts that were captured, and the large numbers of unmarked hatchery smolts that were stocked into the Penobscot River, the majority of unknown smolts were most likely of hatchery origin.

Over the 5 years of the study, recaptures of VIE-marked hatchery smolts were fairly evenly distributed across the three stocking locations (Figure 6); however, the recapture rates for each stocking group varied considerably within and among years (Table 5). Overall, the recapture rates were greatest in 2002, which was the year with the greatest total smolt captures. Recapture rates were the lowest during the years with the fewest total smolts captured (2003 and 2005). Stocking location did not influence the number of days that the smolts were at large between stocking and recapture, but the date that the smolts were stocked did influence days at large. That is, the smolts that were stocked before April 30 took longer to reach the RSTs than those that were released later. In the Connecticut River, McCormick et al. (2014) found no difference in the downstream detection date between groups of smolts that were released 3 weeks apart, indicating that the smolts that were released earlier had a slower migration speed. Karppinen et al. (2013) also found that smolts in early release groups migrated more slowly than those in late release groups. The slower movements of earlier released smolts may be related to the colder water temperatures that they experience or their degree of physiological preparedness. Alternatively, slower movements could stem from a conserved evolutionary strategy of synchronizing ocean entry to optimize physiological and ecological windows (e.g., adequate prey, temperature, river discharge, salinity, and presence of con- and conspecifics to buffer them from predators (Finstad & Jonsson, 2001; Furey et al., 2016; Harvey et al., 2020; McCormick et al., 1998; Saunders et al., 2006; Stewart et al., 2006). Substantial uncertainty remains concerning the effects of domestication on

emigration timing of hatchery smolts and could be the focus of future research.

Operating the RSTs allowed us to assess the smolt acclimation ponds as a release strategy in the Penobscot drainage. The acclimation ponds were thought to increase the survival and imprinting of smolts (Bosch et al., 2023). The VIE-marked smolts that were stocked into the acclimation ponds were captured in the RSTs (this study) and postsmolt trawl surveys (Sheehan et al., 2011) at rates that were comparable to those for smolts that were released at the three primary stocking locations. However, not all the smolts volitionally emigrated from the acclimation ponds into the Penobscot River, a dynamic that has been similarly reported for acclimation ponds that have been used elsewhere for Atlantic Salmon and steelhead *Oncorhynchus mykiss* (Rottiers & Redell, 1993; Tipping, 2007). Bosch et al. (2023) reported a decrease in smolt-to-adult returns for later emigrating volitionally released Chinook Salmon smolts from acclimation ponds in Washington State. Conversely, Clarke et al. (2011) found significantly higher survival for volitionally released steelhead smolts than for those that were actively forced from acclimation ponds. Although smolts from the West Enfield acclimation ponds emigrated and survived (Lipsky et al., 2012; Sheehan et al., 2011; this study), there was no observed increase in imprinting (Gorsky et al., 2009). Given the need to forcibly evict smolts, the use of the West Enfield smolt acclimation ponds was abandoned as a release method.

Globally, Atlantic Salmon smolt migrations are occurring 2.5 d earlier per decade (Otero et al., 2014). During the 20 years since our data were collected, telemetry and modeling efforts have shed additional light on smolt emigration timing and duration (e.g., Holbrook et al., 2011; Molina-Moctezuma et al., 2022; Stich, Kinnison, et al., 2015). However, our data remain the most recent and best available information on size and age composition of natural smolts that reach the Penobscot River estuary. These data also represent the conditions that were experienced by Atlantic Salmon smolts in the Penobscot River before both the U.S. ESA listing and the restoration actions that were accomplished under the Penobscot River Restoration Program, thus serving as an important baseline against which future management actions can be assessed.

## Conclusions

Our finding that timing of stocking rather than stocking location influenced the migration timing of hatchery smolts provides useful information, which when coupled with the air temperature model developed by Frechette et al. (2023) could help further optimize the timing of upstream hatchery stocking operations to align the emigration timing of hatchery and natural smolts. Allowing hatchery smolts to migrate with more natural timing could be one method to increase survival and fitness. However, any experimental changes to hatchery stocking and rearing practices need to be evaluated using a monitoring program. Implementing a new monitoring program should include an evaluation of alternatives to RSTs and would benefit from a comprehensive hatchery marking program such that natural and hatchery smolts can be reliably and easily distinguished.

## SUPPLEMENTARY MATERIAL

Supplementary Material is available at *North American Journal of Fisheries Management* online.

## DATA AVAILABILITY

Data that support the findings of this study are available from the [Northeast Fisheries Science Center, 2025](https://www.fisheries.noaa.gov/inport/item/27495): Atlantic Salmon Smolt Monitoring, <https://www.fisheries.noaa.gov/inport/item/27495>.

## ETHICS STATEMENT

Atlantic Salmon (Gulf of Maine Distinct Population Segment) are captured & handled by Northeast Fisheries Science Center under USFWS Endangered Species Permit ESPER0046838 and previous versions thereof.

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## CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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