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ARTICLE

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Abstract
Restoration of Atlantic Salmon *Salmo salar* in Maine has relied on hatchery-produced fry and smolts for critical stocking strategies. Stocking fry minimizes domestication selection, but these fish have poor survival. Conversely, stocked smolts have little freshwater experience but provide higher adult returns. Lower-mode (LM) fish, those not growing fast enough to ensure smolting by the time of stocking, are a by-product of the smolt program and are an intermediate hatchery product. From 2002 to 2009, between 70,000 and 170,000 marked LM Atlantic Salmon were stocked into the Pleasant River (a tributary in the Penobscot River drainage, Maine) in late September to early October. These fish were recaptured as actively migrating smolts (screw trapping), as nonmigrants (electrofishing), and as returning adults to the Penobscot River (Veazie Dam trap). Fork length (FL) was measured and a scale sample was taken to retrospectively estimate FL at winter annulus one (FW1) using the intercept-corrected direct proportion model. The LM fish were observed to migrate as age-1, age-2, and infrequently as age-3 smolts. Those migrating as age-1 smolts had a distinctly larger estimated FL at FW1 (>112 mm) than those that remained in the river for at least one additional year. At the time of migration, age-2 and age-3 smolts were substantially larger than age-1 smolts. Returning adult Atlantic Salmon of LM origin had estimated FLs at FW1 that corresponded to smolt age (greater FL for age 1 than age 2). The LM product produces both age-1 and age-2 smolts that have greater freshwater experience than hatchery smolts and may have growth and fitness advantages. The data from this study will allow managers to better assess the probability of smolting age and manipulate hatchery growth rates to produce a targeted-size LM product.

Populations of Atlantic Salmon *Salmo salar* throughout New England have experienced precipitous declines due to a number of factors including habitat degradation and reduced connectivity (Parrish et al. 1998; NRC 2004). Runs in the state of Maine remain the last vestiges of viable populations, though these runs are likewise at risk and have been listed as federally endangered through the Endangered Species Act in 2000 (NMFS and USFWS 2000; NMFS and USFWS 2009). Within the USA and the listed Distinct Population Segment (NMFS and USFWS 2009), the Penobscot River population has the highest numbers of adult returns, ranging between 900 and 3,000 in the last decade (USASAC 2012; Department of Marine Resources, State of Maine, unpublished data).

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Persistence of the Penobscot River population is unquestionably linked to sustained supplementation with hatchery fry and smolts (Moring et al. 1995; NMFS and USFWS 2009). This dual approach is intended to "spread the risk." Stocked fry are subjected to natural selective forces during both the freshwater (FW; as juvenile "parr") and seawater (SW) phases of their life history. Conversely, hatchery smolts by-pass the mortality (and selection) associated with FW residence. Presumptive smolts are released into river habitat a few weeks prior to the natural smolt migration. These fish generally leave the system after a few weeks in FW (Holbrook et al. 2011). All the life stages stocked are represented in smolt cohorts emigrating into Penobscot Bay (Sheehan et al. 2011).

Fry stocking, however, has been largely unsuccessful in producing adult returns and fry-origin adults represent a small fraction of the fish taken for broodstock in the Penobscot River. Although smolt stocking accounts for the majority of adult returns (USASAC 2012), smolt-to-adult survival has steadily declined since 1970 (Moring et al. 1995; USASAC 2012) implicating increased mortality in both the river and at sea. There is concern that both genetic and phenotypic effects of hatchery rearing on the smolting process may continue to influence performance (Spencer et al. 2010; McCormick et al. 2013). Fish raised in captivity may have difficulty acclimating to natural conditions and exhibit poor postrelease survival (Price 1999).

During the parr–smolt transformation, Atlantic Salmon undergo extensive physiological, behavioral, and morphological changes, which are preparatory adaptations for seaward migration (McCormick 1987; Hoar 1988). In nature, Atlantic Salmon transition from a FW parr to a migratory smolt after 1–3 years, with most naturally reared smolts emigrating from the Penobscot River after 2–3 years (NMFS and USFWS 2009). The physiological decision to smolt depends strongly on growth (Thorpe et al. 1998). Hatchery production of Atlantic Salmon smolts for the Penobscot River occurs at the U.S. Fish and Wildlife Service Green Lake National Fish Hatchery (GLNFH; Ellsworth, Maine). This program relies upon accelerated growth relative to the natural environment, targeting production of a smolt in 18 months (age-1 smolt).

While a uniform smolt product is intended, Atlantic Salmon cohorts exhibit bimodal growth (Thorpe 1977; Utrilla and Lobon-Cervia 1999). Larger juveniles (upper mode; UM) have a higher probability of smolting at age 1, whereas the lower-mode (LM) fish delay their migration for at least one additional year (Thorpe 1977; Heggenes and Metcalfe 1991; Nicieza et al. 1994; Utrilla and Lobon-Cervia 1999). To compensate for LM fish in the hatchery, a surplus of juveniles is reared. In autumn, the fish are graded and the presumptive LM fish are removed and stocked into the Penobscot River while the presumptive UM fish are retained and held until spring for stocking as age-1 smolts. The proportion of hatchery product in the LM varies annually, and stocking has historically been into habitat of uncertain suitability. Total production of LM fish has been as high as one third of the total production for the Penobscot River at GLNFH in recent years.

The stocking of LM Atlantic Salmon has transitioned to a targeted hatchery strategy rather than a by-product for several reasons. The LM fish experience increased time in FW and this is expected to result in improved synchrony with the environment compared with age-1 hatchery smolts (Virtanen and Soivio 1985). Increased FW rearing may also result in a more natural diet. Within the Penobscot River estuary, postsmolts with 8–32 months of FW experience (naturally spawned, fry-stocked, and LM-stocked) consumed more fish than hatchery-stocked age-1 smolts (Renkawitz and Sheehan 2011). Once reaching the ocean, Atlantic Salmon stocked as LM may also have survival rates more similar to wild-reared fish (Kallio-Nyberg et al. 2011).

While the LM product contributes to smolt recruitment (Sheehan et al. 2011) and to adult returns (USASAC 2012) in the Penobscot River, the performance of this hatchery product is largely uncharacterized. In order to maximize the contribution of LM production to Atlantic Salmon recovery, we studied LM juveniles released into the Penobscot River watershed from 2002 to 2009. The life history choices of these fish were assessed through recaptures as actively migrating smolts, nonmigrants, and returning adults. Scales were used to determine the age at migration and to retrospectively estimate size at the winter annulus following stocking (and any subsequent winter in FW). The objectives of our study were to (1) document the age-class and size distributions of smolts that had been released as parr in autumn, (2) characterize the growth and size thresholds of the resulting smolts, and (3) assess the importance of FW growth and smolt age to adult returns.

METHODS

Rearing at GLNFH.—Progeny of Penobscot River Atlantic Salmon were reared under natural light and in lake water at GLNFH as part of the ongoing 18-month (age-1) smolt stocking program. Sea-run broodstock for this production includes both hatchery smolt and naturally reared origin adults. As part of standard rearing, a surplus production of fish is maintained until September when the production pools are graded to reduce the rearing density to targets expected to meet production goals. Because initial egg numbers and survival can vary from year to year, the number of fish graded and the size of the graders (from 0.95 to 1.11 cm) varies among years and among pools within years.

At least half of the LM fish were given a fin clip in all years as a distinguishing mark prior to release (Table 1). Such marks have been demonstrated to have no detectable impact on growth (Dietrich and Cunjak, 2006). While long-term regeneration of fins may occur, fish used in this study were restricted to those with confirmed marks. In 2002–2004 and 2008–2009, LM fish were measured (sample sizes of 98–314) prior to release. Fish were nonselectively netted from pools and anesthetized (using

TABLE 1. Number of age-0 Atlantic Salmon parr stocked into the Pleasant River, Maine, from cohorts stocked in 2002 through 2009. A proportion was marked by fin clip and the marks were on the left ventral (LV), right ventral (RV), or adipose (AD) fins. The FLs (mm) of samples of stocked parr are indicated (with sample size in parentheses) and shared letters indicate no significant difference between groups.

Cohort year and total	Number stocked	Proportion marked	Mark	FL ± SD (*n*)
2002	91,336	0.55	LV	105.7 ± 14.0 (118) z
2003	82,941	0.88	RV	99.2 ± 8.3 (147) w
2004	89,549	0.78	LV	101.6 ± 11.5 (148) x
2005	96,320	1.00	LV	
2006	100,541	1.00	AD/LV	
2007	105,577	1.00	LV	
2008	130,561	1.00	AD/LV	107.9 ± 14.1 (98) z, y
2009	170,500	1.00	LV	102.9 ± 12.0 (314) y
Total				103.0 ± 12 (825)

100 mg/L MS-222 [tricaine methanesulfonate]) and fork length (FL) was measured. Beginning in 2002, marked LM fish (age-0 parr) were point stocked into the Pleasant River, a third-order tributary (with approximately 42 km of linear habitat) that flows into the Piscataquis River (19T 506936E 5009751N), a branch of the Penobscot River, Maine (Figure 1). From 2002 to 2009, between 70,000 and 170,000 LM fish were stocked annually (Table 1). In 2002–2005, the three sites furthest downstream were used. Beginning in 2006, the stocking site furthest downstream was dropped; three to six up-river stocking sites were used between 2006 and 2009 (Figure 1).

Smolt age and size.—To collect fish for documenting smolt age and size distributions, rotary screw traps were fished in the Pleasant River between mid-April and early June from 2004 to 2010. Traps were deployed approximately 13 km upstream from the confluence with the Piscataquis River (19T 498449E 5016242N) and downstream of all stocking sites beginning in 2006. Annual trapping effort spanned the smolt run and included a minimum of 36 d fished (Table 2). It was assumed that any fish captured in the screw trap was a smolt. Marked smolts were sampled throughout the run in all years. From 2004 to 2006, when both marked and unmarked hatchery parr contributed to the smolt cohorts, all marked migrating smolts were sampled. From 2007 to 2010 a daily maximum of five fish were sampled from each mark class but all marked fish were tallied. Upon capture, sampled fish were anesthetized using MS-222 (100 mg/L) and marks were noted. Fork length was measured and a scale sample was taken from the left side of the fish just posterior to the distal insertion of the dorsal fin and dorsal to the lateral line.

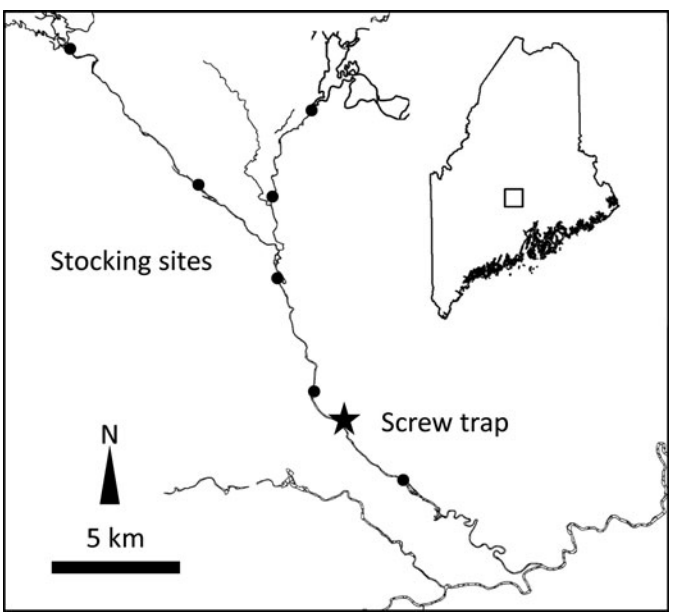

FIGURE 1. Map of the Pleasant River, a third-order tributary of the Piscataquis River, which in turn debouches into the Penobscot River, Maine. The site of the screw trap operation in 2004–2010 is indicated by a star. The filled circles indicate points at which parr were stocked from 2002 to 2010.

Electrofishing for nonmigrant LM fish.—In 2008 (August 24–September 10) and 2009 (August 25 and September 15), backpack electrofishing was used to capture LM parr that had not migrated the spring following stocking as age-1 smolts. Electrofishing occurred throughout reaches containing stocking sites (Figure 1). Fork length was measured, marks were noted, and scale samples were taken from all parr captured.

Adult returns.—Returning adult Atlantic Salmon of LM-stocking origin (as determined by marks) were collected at an upstream fishway trap operated by the Department of Marine Resources at the Veazie Dam on the Penobscot River (river kilometer 47). Annual sampling reflects a census of all fish using the fishway (generally from May 1 to October 31), except that fish were not sampled during summer conditions when water temperature was above 23°C. Fork lengths were recorded at the time of capture without anesthetizing the fish. Scale samples were taken as described above.

Scale aging and measurement.—Scales were mounted between two glass slides and observed using 25 × magnification on a Zeiss Axioplan microscope (Zeiss, Thornwood, New York). All of the scales were examined by two trained observers, each assigning an age to the fish. Ages were generally very distinct

TABLE 2. Date range, number of days, and temperature range during which screw traps were fished in the Pleasant River, Maine, from 2004 through 2010 (not cohort year). Marked migrating Atlantic Salmon originally stocked as parr were captured as age-1, age-2, and age-3 smolts. The FL (mm) at capture is indicated for each age. Shared letters indicate no significant difference between FL groups (among pooled smolt ages only).

Year	Dates fished	Days fished	Temperature (°C)	FL ± SD (*n*) at capture of smolts		
				Age 1	Age 2	Age 3
2004	May 1–May 18	36	9.0–16.0	138.5 ± 8.9 (24)	169.8 ± 18.0 (64)	170.0 ± 4.2 (4)
2005	May 5–May 25	42	6.0–10.5	129.2 ± 8.0 (17)	179.7 ± 14.6 (29)	194.7 ± 26.0 (3)
2006	Apr 13–May 27	74	6.0–13.0	144.8 ± 12.2 (61)	179.7 ± 17.4 (36)	193.0 ± 12.0 (4)
2007	May 2–Jun 1	78	3.0–15.5	135.4 ± 11.5 (99)	170.4 ± 12.8 (80)	165.0 (1)
2008	May 6–Jun 6	60	7.5–17.0	133.8 ± 11.6 (78)	167.3 ± 17.9 (32)	(0)
2009	May 4–May 22	38	9.0–15.0	135.6 ± 12.2 (96)	164.9 ± 17.8 (28)	(0)
2010	Apr 26–May 14	38	7.0–15.0	130.4 ± 8.4 (103)	179.9 ± 12.0 (58)	(0)
All years				135.2 ± 11.7 (478) z	173.1 ± 16.3 (327) y	183.4 ± 18.2 (12) y

and readers agreed on designations 98% of the time. For disagreements, the sample was eliminated unless differences were corrected by consensus of the readers. This process was validated by the recorded marks to identify cohort year (year of stocking) and age at migration. Once ages were assigned, up to three scales were selected from each fish to measure. Scales that were broken or regenerated were not used for measurements. Acceptable scales were photographed with a microscope-mounted digital camera (SPOT Insight 2 MP Color Mosaic; Sterling Heights, Michigan).

Scale images were measured using Image J software (Rasband, ImageJ: http://rsb.info.nih.gov/ij/), with distances calibrated to an external micrometer slide. For each scale, between two and four measurements were taken depending on the assigned age. Total radius was measured from the focus of the scale along the anterior axis to the margin of the scale. Measurements were taken from that same focus point, along the same line, to points at each of the annuli present. Measurements included between one and three annuli for FW residency, and one and two annuli of SW residency for sea-run adult scales.

Size thresholds, growth, and smolt age.—To estimate size thresholds and evaluate the influence of growth on the physiological decision to smolt, we used scales to provide back-calculated size estimates. While the decision to smolt is thought to occur as early as autumn in the previous year (Thorpe 1977), individual sizes at stocking could not be precisely estimated. However, it was possible to identify the transition from winter to spring. For fish captured as parr or smolt, FL at the first winter annulus in FW ("FW1" hereafter) was estimated using the intercept-corrected direct proportion model (Everhart 1975; Guy and Brown 2007). The correction factor was calculated by regressing scale radius length against measured FL for all juvenile Atlantic Salmon used in this study ($n = 860$; $R^2 = 0.644$, $P < 0.0001$) and extrapolating to the x-axis such that estimated FL at FW1(mm) was calculated as follows:

$$\mathrm{FL}_{\mathrm{FW1}} = 19.61 + (S_{\mathrm{FW1}}/S_{\mathrm{CAPTURE}}) \times (FL_{\mathrm{CAPTURE}} - 19.61),$$

where S_{FW1} is the distance from the center of the scale to end of the first FW winter annulus, S_{CAPTURE} is the distance from the center of the scale to the end of the scale margin, and FL_{CAPTURE} is FL at capture. Where reported, spring growth of smolts was calculated as the difference between the size at capture and the estimated FL at the previous winter annulus (FW1 or FW2 [second winter annulus in FW]).

Growth, smolt age, and adult returns.—For fish captured as adults, a modified size-at-age estimation method was used because of the imprecise FL measurements. Additionally, somatic growth rate and scale growth rate are closely related in FW (Dietrich and Cunjak 2007), but the relationship is more variable in SW (Heidarsson et al. 2006). Therefore, estimates of FL at FW1 were calculated based on a regression of scale radius length against measured FL for juveniles described above. Estimates using this approach were similar to those using the intercept-corrected direct proportion model based on adult FL measures ($n = 109$, R^2 of 0.809, $P < 0.0001$); therefore, only results for this modified-scale regression method are reported. For adult returns that were from age-2 smolts, the second annulus (FW2) was also used to estimate FL the winter before parr–smolt transformation. For all fish, if multiple scales were measured, these data were averaged.

Statistical analysis.—For all analyses, an α of 0.05 was adopted. The FLs and estimated FLs were not normally distributed (Kolmogorov–Smirnov, Lilliefors, $P < 0.05$); therefore, nonparametric analysis was used for all testing. For multiple comparisons, a Kruskal–Wallis analysis of variance (ANOVA) was used. Significance in this test was followed by pairwise comparisons using Kolmogorov–Smirnov two-sample tests. Unless specifically incorporated as "nonmigrants," age-3 smolts were omitted from analyses due to small sample sizes. Where relationships are reported, least-squares linear regressions were used.

In order to report size thresholds for the "decision" to smolt or postpone migration, estimated FLs at FW1 were used from age-1 smolts and nonmigrants using cumulative distributions to identify the size at which a fish had the same probability of migrating as a age-1 smolt as not. Determination of this "equivalence FL" allowed the calculation of the proportion of observed age-1 smolts that were larger than this FL at FW1 and, similarly, the proportion of observed nonmigrants that were smaller than the equivalence FL.

RESULTS

Smolt Age and Size

Fork length data were available for five of the eight stocking years reported. Annual mean FL measured at the time of stocking ranged from a low of 99 mm in 2003 to a high of 108 mm in 2008 (Table 1), a range of 9 mm. Over the 7 years of rotary screw trapping a total of 3,830 smolts stocked as autumn parr were captured. For the subset of years for which all smolt age-classes were sampled, 80% of captured fish migrated as age-1 smolts, 19% as age-2 smolts, and less than 1% as age-3 smolts (Table 3). By the spring following stocking, the measured FL of age-1 smolts differed by as much as 16 mm (12%) among years, ranging from 129 mm in 2005 to 145 mm in 2006 (Table 2). Similarly for age-2 smolts, FL at capture differed among years by as much as 15 mm (10%), from a low of 165 mm in 2009 and a high of 180 mm in 2006 (Table 2).

The average size of electrofished age-1 parr ($n = 43$) sampled in 2008 and 2009 was 12–24 mm larger than members of their cohort that migrated as age-1 smolts at least 3 months previous (Tables 2, 4). At the time of capture, the measured FL of age-2 smolts (173 mm) was 28% larger than that of age-1 smolts (135 mm). The measured FL of age-2 and age-3 smolts did not differ (Table 2). Similarly, age-2 smolts (173 mm) were 14% longer than stream-resident age-1 parr (151 mm).

TABLE 3. Number (proportion in parentheses) of parr-stocked smolts within a year cohort captured by screw trap in the Pleasant River, Maine, from 2004 through 2010. Note that sampling allowed for capture of all age-classes (ages 1, 2, and 3) only for 2003–2007. The total number and total proportion include only these years.

Cohort year and total	Number of captured smolts: Age 1	Age 2	Age 3	Total number
2001			5	5
2002		124	0	124
2003	269 (0.63)	147 (0.34)	13 (0.03)	429
2004	150 (0.50)	145 (0.49)	3 (0.01)	298
2005	685 (0.85)	122 (0.15)	0 (0.00)	807
2006	1,000 (0.89)	122 (0.11)	3 (0.00)	1,125
2007	299 (0.86)	47 (0.14)	0 (0.00)	346
2008	529	167		696
2009	903			
Total (2003–2007)	2,403 (0.80)	583 (0.19)	19 (0.01)	3,005

TABLE 4. Date range and number of days nonmigrant Atlantic Salmon were fished in the Pleasant River, Maine, by backpack electrofishing in 2008 and 2009 (exclusively from the previous year's cohort of stocked parr).

Year	Dates fished	Days fished	FL ± SD (n) at capture of nonmigrant parr
2008	Aug 24–Sep 10	3	158.6 ± 14.1 (20)
2009	Aug 22–Sep 15	5	144.5 ± 10.0 (23)
All years			151.0 ± 13.8 (43)

Size Thresholds, Growth, and Smolt Age

A total of 860 juvenile Atlantic Salmon had their FL at FW1 estimated. Readable scales were obtained from 817 presumed smolts of LM origin. For the 817 scale-sampled fish, 72.4% had three scales read per individual, 16.2% had two scales read, and 11.4% had only one readable scale. As smolts, the majority of fish were age-1 or age-2, with only eight being age-3. From electrofishing, an additional 43 nonmigrant age-1 parr had scales of sufficient quality for analysis.

Estimated FL at FW1 was predictive of the size at capture, indicating the relationship of growth the previous year with smolt size. Size at capture for age-1 smolts was positively correlated with estimated FL at FW1 ($n = 478$, $R^2 = 0.48$, $P < 0.0001$). This relationship between estimated FL at FW1 and size at capture was observed in age-2 smolts, though it was less strong ($n = 327$, $R^2 = 0.14$, $P < 0.0001$). Yearly variation in size among stocked cohorts was not linked to smolt size. Average FL of age-1 smolts was not predictive of the size of captured at age-2 smolts ($P = 0.719$) within a cohort (i.e., cohorts with larger age-1 smolts did not have larger age-2 smolts), though sample size was small ($n = 6$).

Within cohort years 2003–2008 there was a clear difference in size at FW1 between fish that migrated as age-1 smolts and nonmigrants (observed as age-1 parr and age-2 and age-3 smolts), with age-1 smolts being bigger within each cohort year (Kolmogorov–Smirnov: $P < 0.0001$ for each year; Figure 2). There were no differences in estimated FL at FW1 between age-2 and age-3 smolts. Among all captured smolts, age-1 smolts had a greater mean FW1-estimated FL (125 mm) than nonmigrants (99 mm). Most fish >112 mm at FW1 migrated as age-1 smolts, and most fish <112 mm delayed migration at least 1 year (the equivalence point). This threshold was fairly abrupt; 87% of age-1 smolts had an FW1-estimated FL greater than 112 mm while 87% of nonmigrants had a smaller estimated FL at FW1.

There were differences among years for estimated FL at FW1 for age-1 smolts. Mean FW1-estimated FLs of age-1 smolts in 2009 were smaller than all other years except 2004 (119 and 120 mm). Conversely, 2005 age-1 smolts had a greater FW1-estimated FL than all other years (133 mm). For age-2 smolts, there was no difference in estimated FL at FW1 among cohorts (Kruskal–Wallis: $P = 0.069$). There were too few 3-year smolts to compare cohorts.

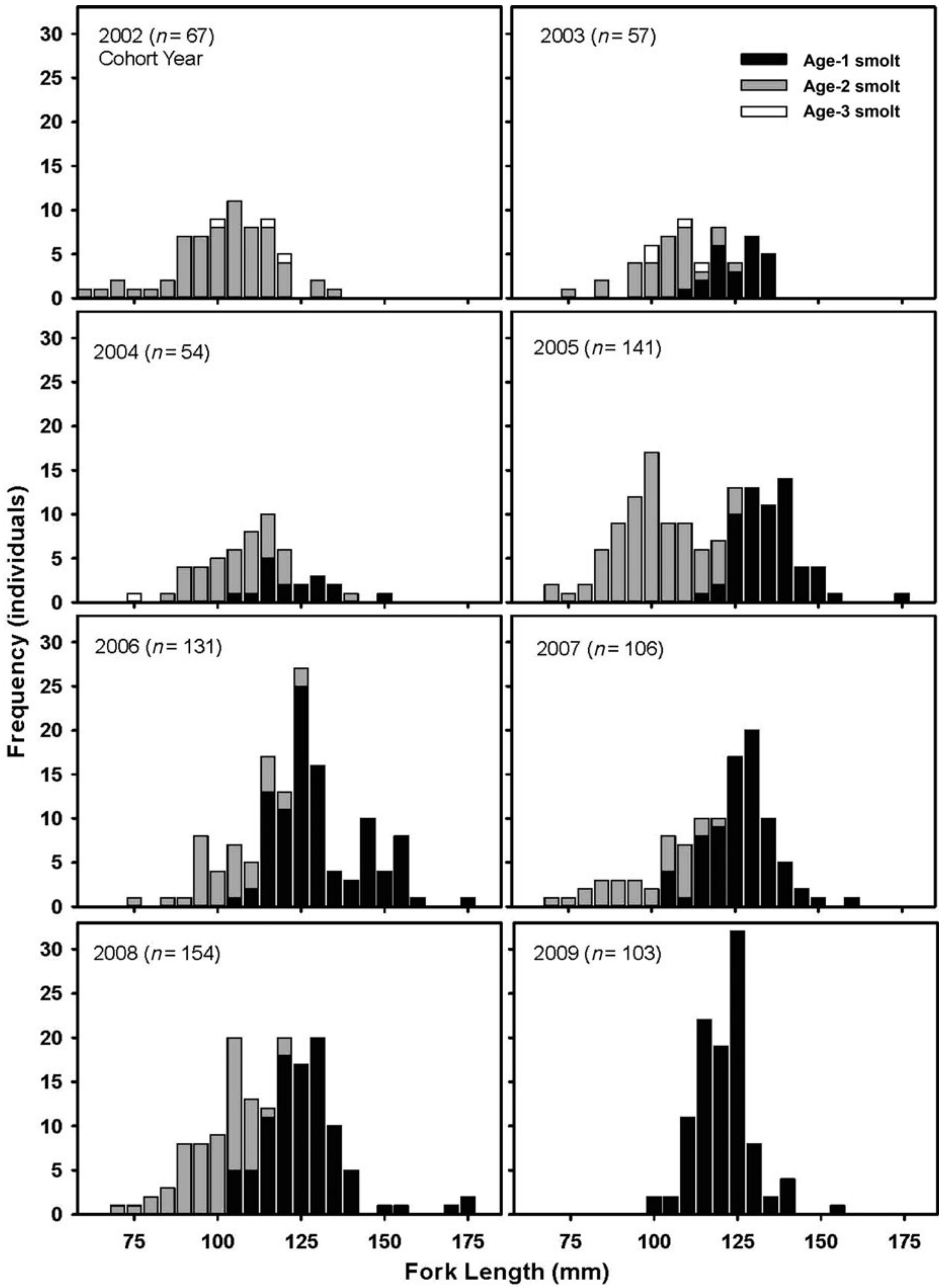

FIGURE 2. Histograms of calculated FL at winter annulus following stocking for Atlantic Salmon planted as age-0 parr and recaptured as migrating age-1, age-2, or age-3 smolts. Note that trapping was carried out between 2004 and 2010. Therefore, age-1 smolts could not be sampled for cohort 2002 nor could smolts greater than 1 year be sampled for cohort 2009.

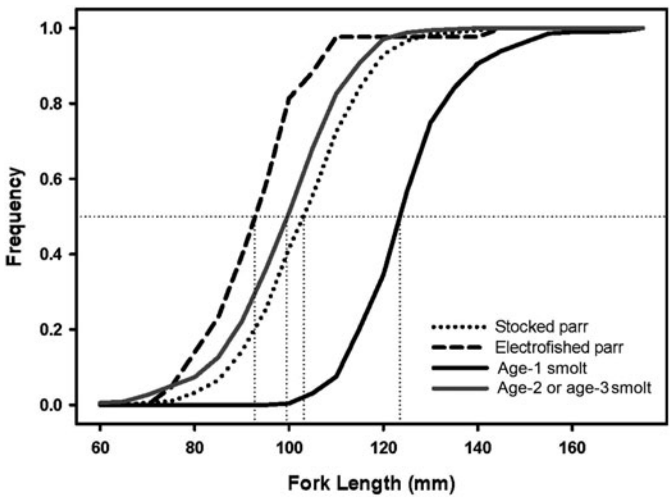

FIGURE 3. Cumulative frequency of the measured FLs of Atlantic Salmon parr stocked into the Pleasant River (cohorts 2002–2004, 2008–2009; $n = 825$), and the cumulative frequency of calculated FLs at stocking for age-1 parr recaptured by electrofishing in summer (cohorts 2008–2009; $n = 43$), age-1 smolts (cohorts 2003–2009; $n = 478$), and smolts migrating at age-2 and age-3 (cohorts 2002–2008; $n = 339$). Dotted lines indicate the 50th percentile. All groups were statistically different from one another.

Atlantic Salmon collected via electrofishing in the fall approximately a year after stocking were estimated to be smaller at FW1 than those observed migrating in subsequent years (estimated FL of 93 mm versus 99 mm). A fish that reached an estimated FL of 96 mm at FW1 was equally likely to migrate as not (60% of nonmigrants had an estimated FW1 FL less than 96 mm while 60% of age-1 smolt migrants had an estimated FL greater than 96 mm). Similar equivalence FLs were observed for electrofished nonmigrants versus age-1 smolts within 2007 and 2008 cohorts (93 and 96 mm for delineated equivalences of observation of 57% and 59%, respectively).

The FLs of directly measured Atlantic Salmon being stocked as LM were different from FW1-estimated FLs of age-1, age-2, and age-3 smolts and electrofished age-1 parr (Figure 3). The FLs measured at the hatchery (median FL of 105 mm) were smaller than the FLs of age-1 smolts at FW1 (median estimated FL of 124 mm) and fish that delayed migration and were captured as age-1 parr (median estimated FL of 83 mm) or age-2 and age-3 smolts (median, 99 mm).

The LM parr exhibited notable growth from the time the winter annulus was formed to capture as age-1 smolts. The FL at migration was 8% greater than at the time of annulus formation, representing an estimated 3–16 mm (25th–75th percentiles) increase in FL during this 4–5-month period. The spring growth increment was lower in fish migrating as age-2 smolts, with estimated increases of 1–9 mm (25th–75th percentiles) in length gained after FW2. Those fish remaining in FW through the summer had high variability in growth among individuals. While the measured FL of electrofished age-1 parr at capture was correlated with estimated FL at FW1, the relationship was weak ($R^2 = 0.23$, $P < 0.001$). Electrofished cohorts averaged 46–58 mm of growth from January to late August and early September in the river. Annual growth increments for year two averaged 62 mm for age-2 smolts ($n = 327$) and 32 mm for age-3 smolts ($n = 12$).

Growth, Smolt Age, and Adult Returns

From 2007 through 2009, 109 adult returns of known LM-stocking origin were captured in the Penobscot River (Table 5). Capture size as an adult was not predicted by juvenile size. The FL at adult capture was not correlated with either the estimated size at FW1 nor with the estimated size at smolt emigration ($P = 0.12$ and 0.21, respectively). Consistent with observations of juveniles captured as smolts, estimated FL at FW1 for adults from age-2 smolts was smaller than that of adults from age-1 smolts. Estimated size at FW1 was generally similar to the estimated size of fish captured as smolts, but differences were observed. On average (and by cohort), the estimated FL at FW1 of adults from age-1 smolts (117 mm) was slightly smaller than that of age-1 smolts captured during smolt migration (125 mm; $P < 0.001$). There was no difference between estimated FL at FW1 of adults from age-2 smolts (101 mm) and the estimated

TABLE 5. Estimated FL at FW1 of Atlantic Salmon parr stocked (2003–2007) into the Pleasant River, Maine, returning as adults to the Penobscot River. Returns include individuals that migrated as age-1 and age-2 smolts and returned as adults after one or two winters in salt water (1SW and 2SW, respectively). An “na” indicates years from which data were not yet available. There was a significant difference between groups (total) in FL (among pooled smolt ages only), as indicated by different letters.

	Age-1 smolt				Age-2 smolt			
Cohort year and total	*n*	1SW	2SW	FL ± SD	*n*	1SW	2SW	FL ± SD
2003	4	0	4	109.7 ± 9.2	1	0	1	80.6
2004	17	0	17	114.2 ± 14.6	7	0	7	107.5 ± 17.5
2005	32	3	29	114.7 ± 10.6	5	0	5	98.9 ± 17.9
2006	40	5	35	120.2 ± 19.8	1	1	0	88.5
2007	2	2	na	125.0 ± 2.3	na	na	na	
Total	95	10	85	116.9 ± 15.8 z	14	1	13	101.2 ± 17.6 y

FL at FW1 of age-2 smolts captured during smolt migration ($P = 0.38$).

DISCUSSION

Atlantic Salmon LM hatchery juveniles were observed to migrate as age-1 (82%), age-2 (17%), and rarely as age-3 smolts (<1%). The decision to smolt relies heavily on previous growth (Metcalfe et al. 1990; Berglund et al. 1992) and energy stores (Rowe and Thorpe 1990; Rowe et al. 1991; Berrill et al. 2006). Those that migrated as age-1 smolts were the largest (and presumably fastest growing) among those observed. Parr reaching more than 112 mm at FW1 were more likely to migrate in the spring following stocking (Figures 2, 3). These data are consistent with the view that the parr–smolt transformation is a physiological threshold of development (Thorpe et al. 1998). Similar size thresholds (115–125 mm) have been reported from PIT telemetry studies in Maine (Horton et al. 2009). The same study reported a smaller threshold in a stream in Massachusetts (95–100 mm), indicating variation among populations.

Differences in growth rates generate the bimodal size-frequencies observed in Atlantic Salmon. Faster-growing juveniles have a greater probability of smolting the next year while slower-growing fish postpone smolting for at least one additional year (Thorpe 1977). The growth of Atlantic Salmon in FW is seasonal and is affected primarily by temperature, food availability (McCormick et al. 1998; Amundsen et al. 2001; Bacon et al. 2005), and density (Elliott and Hurley 1997; Grant et al. 1998; Imre et al. 2005). While those fish in a hatchery setting undoubtedly benefit from controlled (higher) temperature with respect to river conditions, our data suggest that stocking in the fall allowed some individuals to recruit into the next year's migrants. Growth occurs at autumn and winter river temperatures (Koskela et al. 1997; Finstad et al. 2004) and may allow underperformers in a hatchery environment to reach threshold smolt size through release from social status influence that favors higher-ranked individuals (Chapman 1962; Fausch 1984; O'Connor et al. 2000). In this study, fish migrating as age-1 smolts had an estimated 8% increase in length over the period between annulus formation and migration. This growth was greater than that of age-2 migrants, indicating either greater feeding opportunity or growth scope for these younger fish. It is unclear how such a shift may influence the "choice" to smolt, as this physiological decision is thought to take place in the late summer and autumn preceding migration (Thorpe 1989). Therefore characterizing the influence of the natural system on growth and the "decision" to smolt remains an important direction for continued study.

In the context of this study, "LM" has been used as a convenient misnomer since both age-1 and age-2 smolts were produced from the graded hatchery product. Clearly some stocked fish were presumptive smolts (the "upper mode"). Differing sizes of grading racks between years resulted in a different mean size of LM fish being stocked and is likely responsible for the observed differences in size at capture of age-1 smolts (Table 2) and therefore the probability of smolting. Forty-nine percent of the variability observed in the FL of age-1 smolts was explained by the estimated FL at FW1. Similarly for age-2 smolts, FL differed among years. While smolt size was correlated with estimated FL at FW1, this relationship explained only 14% of the variation. It is likely that there is great annual variation in growth conditions among cohorts both in the hatchery and in river.

Both age-1 and age-2 smolts were commonly caught, and these two groups represented the majority of emigrants from LM-stocked fish. On average, LM stocking produced fourfold more age-1 than age-2 smolts (Table 3). The relative contribution was variable among years, with age-2 smolts making up half of the captured migrants in one cohort. Such comparisons need to be considered qualitatively, however, as the assumption of equal probability of capture across years is likely to have been violated (and is not characterized). Such cautions withstanding, these data demonstrate that the contributions of smolt age-classes are variable. Because stocked LM fish have a low probability of being an age-1 smolt based on FL distribution (Table 1), the relatively high proportion of age-1 smolts observed underscores the variable and significant mortality incurred by fish remaining in FW for an additional year. This observation is consistent with reports of high natural mortality of juvenile Atlantic Salmon (Orciari et al. 1994; Antonsson et al. 2005) and estimates of overall (age-0 parr to age-2 smolt) mortalities of 40–50% (Horton et al. 2009).

It is unlikely that precocious parr account for a significant proportion of stocked LM fish. There is an inherent developmental conflict between the physiological decisions to mature as a parr or to smolt (Thorpe 1986; Thorpe et al. 1987; Hansen et al. 1989; Berglund et al. 1991). Faster-growing individuals have better chances to surpass either of the thresholds that trigger early maturation or smolting (Økland et al. 1993; Metcalfe 1998; Strothotte et al. 2005). In this study, no precocious parr were captured during electrofishing, indicating that precocious maturation was infrequent or rare. Furthermore, if fish matured in autumn of the next year as age-1 parr, it is unlikely that they would successfully smolt at age 2, and fewer still would survive to migrate in subsequent years.

The LM fish that remained in the river and migrated as age-2 smolts left the river at a larger size than those that emigrated as age-1 smolts (Table 2). This growth may be important as body size can influence smolt survival in FW (Quinn and Peterson 1996) and at sea (Friedland et al. 1998; Antonsson et al. 2005; Jokikokko et al. 2006). Smolt body size is often (Eriksson et al. 1987; Lundqvist et al. 1994; Kallio-Nyberg et al. 2006), though not always, positively correlated with adult returns (Hogan and Friedland 2010). Increased length likely benefits smolts by reducing size-selective predation risk (Dieperink et al. 2002; Hyvärinen and Vehanen 2004) and advancing the diet shift of postsmolts from an invertebrate to a fish diet (Salminen 1997). Increased size during smolting may also confer an osmoregulatory advantage for SW entry (Beckman and Dickhoff 1998; Beckman et al. 2000). The greater size of age-2 smolts in this study is, however, relative. These smolts migrated at a size comparable to (or even smaller than) the standard hatchery smolt product but certainly similar in size to wild-reared fish.

Rearing in a natural FW system may confer an additional survival advantage during migration. The timing of smolting is influenced by environmental conditions, particularly photoperiod and temperature (Duston and Saunders 1997; McCormick et al. 1998; Strothotte et al. 2005). Hatchery conditions may impair the physiological development of smolting (McCormick and Björnsson 1994; Munakata et al. 2000; McCormick et al. 2003) and result in greater mortality during migration than is observed in wild-reared fish (Collis et al. 2001; Dieperink et al. 2002; Fresh et al. 2003; Johnsson et al. 2003). Conversely, rearing in a lower-density and more complex environment can result in morphological and physiological changes reflecting the natural environment (Zydlewski et al. 2003; Brockmark et al. 2007). Such changes and synchrony with the "smolt window" optimize homing ability (Hansen and Jonsson 1991) and the probability of survival (McCormick et al. 1998; Riley et al. 2002). Direct evidence from parr stocking, however, is equivocal. Parr-stocked smolts exhibit more wild-like behaviors (Larsson et al. 2011; Renkawitz and Sheehan 2011), while migration route (Kallio-Nyberg et al. 2011) and marine survival (Jokikokko et al. 2006) may be similar to hatchery-reared smolts. While the data in this study are insufficient to compare the at-sea performance of the resulting age-1 and age-2 smolts, we do note that both smolt age-classes are represented in adult returns. Though age-1 smolts produced the majority of the returns (Table 5), relative performance at sea cannot be directly compared without smolt emigration estimates. The assessment of smolt-to-adult survival is an important future direction of assessment.

Accelerated growth is highly selected for in hatcheries (McGinnity et al. 1997; Gjedrem 2000; Fleming et al. 2002). The use of the LM as a targeted product may help maintain both phenotypic and genetic diversity by reducing domestication selection, as the LM does contribute to adult returns from both juveniles that smolt the following year and those that remain at least one additional year in FW. Recruitment into the LM is variable among populations (Bailey et al. 1980), and both growth rate and age at maturity are heritable traits (Jonsson et al. 1991; Gjerde et al. 1994; Gjedrem 2000; Jonsson and Jonsson 2007). Nonetheless, relationships between FW growth and life history traits remain unclear (Otero et al. 2012). Growth rate in FW has been correlated with growth in the ocean (Einum et al. 2002), maturation age (Kallio-Nyberg and Koljonen 1997), iteroparity (Erkinaro 1997), and egg size (Jonsson et al. 1996; Fleming et al. 2003). Other studies, however, fail to demonstrate these correlations. For example, the work of Friedland et al. (2006) indicated that marine growth of postsmolts was not influenced by FW growth history.

The data provided in this study will allow managers to better assess the smolting probability of hatchery-produced parr resulting from grading or to target age-1 and age-2 smolts as specific naturally reared products. Such information would also be useful in selecting fall stocking sites based upon the proportion of age-1 and age-2 smolts for different groups. For example, some habitat may be suitable for overwintering of presumptive smolts but less desirable for Atlantic Salmon during the summer.

Currently, stocking of the LM in the Penobscot River has been a revenue neutral undertaking as these fish have been a by-product of hatchery smolt production. Regardless, parr-stocked fish have contributed to adult migration in the Penobscot River at a rate that is intermediate to fry and smolt stocking in both performance and in hatchery influence. Efforts to optimize this strategy may include stocking ungraded parr to produce a greater number of age-1 smolts, with the potential benefits of increased natural rearing. This targeted approach may be more successful than fry stocking as most size-selective mortality occurs in the first days after emergence (Einum and Fleming 2000; Bailey and Kinnison 2010) and size-selective mortality on parr is generally weak (Letcher and Horton 2008). Though parr-stocked fish may have more natural behaviors and physiology, other important traits such as sea migration may remain similar to hatchery smolts. Thus, the natural experience of a hatchery product does not obviate the need for natural selection within a population.

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