

Atlantic salmon (*Salmo salar*) smolt production: the relative importance of survival and body growth

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Abstract: The complex life history of Atlantic salmon (*Salmo salar*) coupled with interacting abiotic and biotic factors leads to extreme demographic variability across the species' range. Our goal was to evaluate the relative importance of survival and body growth in determining smolt production across space and time. We used passive integrated transponder tags and capture–mark–recapture analyses to estimate survival, emigration, and growth for six cohorts of presmolt Atlantic salmon in two streams (three cohorts per stream) in New England, USA. We observed remarkable among-cohort consistency in mean monthly survival during a 17-month period from age-0+ autumn to age-2+ spring yet high variability in monthly survival over shorter time intervals (seasons). Despite this latter variability, survival did not translate into among-cohort differences in proportions of age-2+ versus age-3+ smolts. Alternatively, the high variability across seasons and cohorts in mean individual growth rate did lead to differences in within-cohort proportions of age-2+ versus age-3+ smolts (regardless of stream). We conclude that in our two small study streams, variability in growth and size impacted smolt age and, ultimately, smolt production. Density-dependent effects on growth at the scale of the entire study site represent a possible mechanism underlying our observations.

Résumé : La complexité du cycle biologique du saumon atlantique (*Salmo salar*) combinée à l'interaction des facteurs abiotiques et biotiques explique l'extrême variabilité démographique observée sur l'ensemble de l'aire de répartition de l'espèce. Notre objectif est d'évaluer l'importance relative de la survie et de la croissance corporelle dans la détermination de la production de saumoneaux dans le temps et l'espace. Nous avons estimé la survie, l'émigration et la croissance à l'aide d'étiquettes transpondeurs intégrés passifs et d'analyses de capture–marquage–recapture chez six cohortes de saumons atlantiques au stade pré-saumoneau dans deux cours d'eau (trois cohortes par cours d'eau) de la Nouvelle-Angleterre, É.-U. Nous observons une cohérence remarquable entre les cohortes en ce qui a trait à la survie mensuelle moyenne durant une période de 17 mois, allant de l'automne de l'âge 0+ au printemps de l'âge 2+, malgré la forte variabilité de la survie mensuelle sur des intervalles de temps plus courts (saisons). Malgré cette variabilité, la survie n'entraîne pas de différences entre les cohortes en ce qui concerne les proportions de saumoneaux d'âge 2+ contre ceux d'âge 3+. Ou alors, la forte variabilité du taux moyen de croissance individuelle n'entraîne pas de différences des proportions de saumoneaux d'âge 2+ contre ceux d'âge 3+ au sein des cohortes, quel que soit le cours d'eau. Nous concluons que, dans les deux petits cours d'eau étudiés, la variabilité de la croissance et de la taille affecte l'âge des saumoneaux et, en fin de compte, la production des saumoneaux. Il est possible que les effets dépendants de la densité sur la croissance à l'échelle de l'ensemble du site d'étude soient un mécanisme explicatif de nos observations.

[Traduit par la Rédaction]

Introduction

Sorting out which factors are responsible for demographic patterns is critical for conserving Atlantic salmon (*Salmo salar*) populations, which are currently imperiled throughout much of their range in the United States (Colligan et al.

2002). Making these links is challenging, however, because of variability within and among populations and related interactions with both biotic and abiotic factors. Collectively, this variability and complexity suggests that the environmental and population contexts in which salmon carry out their life history may have a strong impact on freshwater production.

The relationship between growth and life history is a widely studied aspect of salmon biology. Importantly, studies have pointed out the conflict between parr maturity and smolting (Thorpe 1986, 1987) and its link with the timing of the “decision” to smolt. The smolting decision depends on previous growth (Metcalf et al. 1990; Berglund et al. 1992; Thorpe et al. 1998) or, more precisely, the accumulation of energy stores (Rowe and Thorpe 1990; Rowe et al. 1991). These experimental findings suggest that factors affecting growth opportunity can also affect life history outcomes. Observational data on intercohort variability in average smolt size from a given stream (e.g., Jutila et al. 2006) also

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supports the hypothesis that variation in growth opportunity influences smolt age in wild populations. Variability in both average size and smolt age also exists across the geographic range of Atlantic salmon (Klemetsen et al. 2003). Although there is evidence that latitudinal variation in smolt age is related to variation in growth opportunity (Metcalf and Thorpe 1990), it is clear that populations have also evolved different genetic threshold responses to local environmental factors (Nicieza et al. 1994; Thorpe et al. 1998). Highly seasonal growth rates within a cohort (e.g., Letcher and Gries 2003) that may be from a combination of abiotic (e.g., water temperature) and biotic factors (e.g., density-dependence) add a further level of complexity to life history variation and stage-specific demographics.

Poff and Ward (1990) conceptualized habitat as a template that influences which combinations of behavioral, physiological, and life history characteristics constitute appropriate strategies for persistence. This is a useful context for considering the relationships underlying demographic patterns observed in stream fish populations. A large body of work has focused on how various aspects of the abiotic habitat template affect Atlantic salmon demographics (e.g., Gibson 1993; Elliott et al. 1998 and references therein) and several environmental factors have been advanced as mechanistic drivers of growth and demography (e.g., water temperature: Nislow et al. 2004; stream flow: Cunjak and Therrien 1998; substrate: Finstad et al. 2007; ice cover: Cunjak et al. 1998; Whalen et al. 1999). Biotic factors can also contribute to the habitat template and thus function as population regulators in stream salmonids. The positive relationship between population density and mortality has been interpreted as evidence for intracohort competition (Cunjak and Therrien 1998), intercohort competition (Nordwall et al. 2001), and interspecific competition (Kennedy and Strange 1986). Because inadequate space can lead to competition, Grant and Kramer (1990) pointed out the importance of understanding the dynamics of territory size, which is, in turn, a function of body size (Keeley and Grant 1995), and therefore growth opportunity.

Despite the overall complexity in survival and growth patterns and lack of an obvious overriding mechanism to explain these patterns, it is clear that survival and growth interact to produce the number of individuals of salmon at a given life stage (e.g., smolts). Unfortunately, the relative importance of each on smolt production remains elusive. Because of evidence that the underlying mechanisms of survival and growth commonly vary in both space and time, we suggest that studies that assess spatiotemporal variability in these parameters will be most beneficial for partitioning the relative contribution of each to Atlantic salmon population size.

Juanes et al. (2000) made several good arguments for employing individual-based approaches to unravel the complexity described above. One example is the increasing use of capture-mark-recapture methodologies. The advent and increasing use of passive integrated transponder (PIT) tags and related technology has recently become an integral part of many studies to tackle some of the complexity related to survival and growth. However, for the study of mobile animals such as Atlantic salmon, problems related to study design still exist (Letcher et al. 2005; Horton and Letcher

2008). The problems are related to separating true survival from the availability for capture (i.e., study site fidelity), particularly when availability may be a reflection of both biology and artifacts of study design (Horton and Letcher 2008). Recently, an increased understanding of how existing capture-mark-recapture models and new approaches perform in these settings has made it possible to confidently obtain estimates of survival that are closer to true survival than to apparent survival (Horton and Letcher 2008). Our objective in the present study was to apply individual-based approaches to evaluate the relative importance of survival and growth as determinants of geographic and cohort (temporal) variation in Atlantic salmon smolt production.

Materials and methods

We analyzed data collected from six cohorts of Atlantic salmon in two streams (three cohorts per stream). Shorey Brook is a tributary to the Narraguagus River in Maine, USA (44°49'N, 68°03'W), and West Brook is a tributary to the Connecticut River in Massachusetts, USA (42°25'N, 72°39'W) (Fig. 1). Mean annual stream discharge was 0.16 m³·s⁻¹ (Shorey) and 0.34 m³·s⁻¹ (West). Study sections in both streams can be characterized as narrow (average width: Shorey, 4.4 m; West, 4.7 m), low gradient (range 0.5%–2.0%), and predominantly composed of riffles dominated by cobble-gravel substrate.

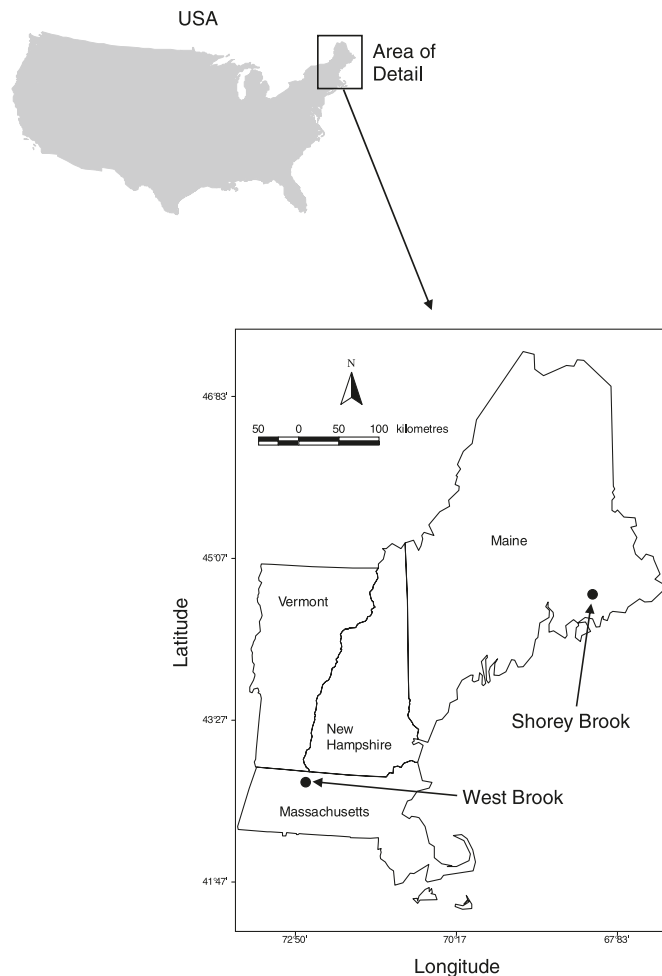
During the period of the present study, populations in both streams were supported by stocking unfed Atlantic salmon fry during April or May each year. For all cohorts, the entire length of both streams was stocked at densities of 0.5 fry·m⁻². Narraguagus River origin fry were stocked in Shorey Brook and Connecticut River origin fry were stocked in West Brook. Sampling and PIT tagging of populations in both streams followed the same protocols. In both streams, fish smolt at either age 2+ or age 3+. We highlight the salient features of the study design below (also see Letcher et al. 2002; Letcher and Gries 2003).

For evaluation of hypotheses based on normal distributions (i.e., analysis of variance (ANOVA), beta parameters from logistic models), we support our conclusions with *P* values (the probability of a type I error). For models of probability estimates (i.e., probability of survival or emigrating), we evaluated the strength of evidence for various hypotheses based on competing models using Akaike's information criterion (AIC). When AIC is corrected for sample size and overdispersion, the result is referred to as quasi-likelihood (QAIC) and is denoted with the subscript *c* (QAIC_c). For model selection, we followed the advice of Burnham and Anderson (1998) and concluded a single-most parsimonious model among competing models when delta QAIC_c values (the difference in QAIC_c between the model with the minimum QAIC_c and any other model in the set) were ≥10.

Sampling description

The length of each study reach was 720 m (Shorey) and 940 m (West). With the exception of 2002 and 2003 when winter sampling was precluded because of subfreezing temperatures on West Brook, each study reach was sampled four times per year, which approximated once per season

Fig. 1. Location of study streams in Maine and Massachusetts, USA (inset shows the location in the northeastern United States).



(Table 1). The results presented here are from cohort-specific seasonal sampling for the nearly 3 years up to and including the age-3+ summer season (9–11 sampling occasions per cohort).

Study reaches were divided into either 37 (Shorey Brook) or 47 (West Brook) contiguous sections approximately 20 m long. Sampling consisted of blocking the upstream and downstream extent of each section with block nets before making two passes with a backpack electrofishing unit (300–400 V unpulsed DC). Each sampling occasion began at section 1 (the downstream-most section). Upon completion of a given section, the next upstream section was sampled until the upstream-most section was sampled completing the sampling occasion. Usually, 5–10 sections were sampled each day resulting in 1–2 weeks to complete each sampling occasion.

Individual salmon were identified using PIT tags. For survival modeling based on live recaptures, fish that smolted at age 2+ could be observed a maximum of seven times: twice in the age-0+ year, four times during the age-1+ year, and one more time during the age-2+ year. The maximum number of observations for age-3+ smolts was 11. Upon capture, fish were placed in a bucket of water for processing. Workup consisted of anesthetizing fish, measuring fork length (FL) (± 1 mm) and wet mass (± 0.1 g), and PIT tag-

ging previously untagged fish (≥ 60 mm FL, ≥ 2.0 g) with a 12 mm, 0.1 g, 134.2 kHz radio-frequency PIT tag (manufactured by Digital Angel Corp.). Tags were implanted interperitoneally using the methods of Gries and Letcher (2002) who reported very low tag loss and mortality using these methods ($< 1\%$). Typically, some (although not all) fish were large enough to tag using this method in the autumn when they were age 0+. Upon recovery, fish were released in the same location from which they were captured (± 5 m).

Abundance

Cohort-specific estimates of abundance on each sampling occasion were necessary for some of the analyses that follow. These estimates were generated using a closed removal estimator (model M_b ; Otis et al. 1978; White et al. 1982). If there was depletion in the numbers captured between the two electrofishing passes within a section, the removal estimator was used to estimate population size for each cohort in each section sampled on each sampling occasion. If depletion between passes did not occur for a given cohort in a section, the sum of all fish of that cohort captured in the section (i.e., the minimum number in the section) was used in place of the M_b estimate. We felt justified in this approach because of (i) our high estimated probability of recapture from the Cormack–Jolly–Seber (CJS) analyses (mean = 0.72, SE = 0.003) suggesting that in most cases, few untagged fish remained at large following sampling, (ii) the high correlation between the number of fish captured and the population estimate from model M_b on a section-specific basis ($r^2 = 0.95$, $P < 0.001$, $n = 491$), and (iii) our observation that nondepletion only occurred when low numbers of fish (usually less than three) were captured in a section. Estimates of N were then summed over all sections to give us a single abundance estimate for each cohort on each sampling occasion ($\hat{N}_{\text{cohort}, k}$).

Classifying age-2+ and age-3+ smolts

We were able to detect smolts as they emigrated from the study site with a combination of periodic sampling conducted outside each study reach and continuous-recording stationary PIT tag antennas and downstream migrant traps operated during the smolt emigration season (see Adjusted apparent survival section). Because our focus was on the relative effects of survival and growth on smolt production, we attempted to differentiate eventual age-2+ smolts from age-2+ nonsmolts. We considered four sets of individuals for each cohort: set 1 comprised age-2+ individuals that were detected emigrating from the study site between the age-2+ spring and age-2+ summer sampling occasions, set 2 comprised age-2+ individuals that were detected in freshwater any time subsequent to (and including) the age-2+ summer sampling occasions (these fish were assumed to be on an age-3+ smolt trajectory), set 3 comprised age-1+ and age-2+ individuals that were detected as emigrants from the study site between the age-1+ autumn and age-2+ spring sampling occasions, and set 4 comprised age-2+ individuals that were never again detected following the age-1+ autumn sampling occasion because of death, failure to capture, or unavailability on the study site.

Set 1 fish were classified as age-2+ smolts and set 2 fish were classified as age-2+ nonsmolts. We included set 3 fish

Table 1. Timing, estimated abundance, observed emigration, status, and estimated efficiency of stationary PIT tag antennas for studies of six cohorts of presmolt Atlantic salmon (*Salmo salar*) in New England, USA.

Cohort	Age	Median sample date (season)	Shorey Brook				West Brook			
			<i>n</i>	\hat{N} (SE)	% observed emigration (<i>n</i>)	Stationary antennas operating? (% efficiency)	<i>n</i>	\hat{N} (SE)	% observed emigration (<i>n</i>)	Stationary antennas operating? (% efficiency)
2000	0+	September 2000 (autumn)	98	104 (4)	0 (0)	No	526	562 (10)	1 (7)	No
		November 2000 (winter)	95	98 (2)	3 (3)	No	304	333 (10)	2 (6)	No
	1+	April 2001 (spring)	98	122 (14)	0 (0)	No	251	318 (25)	5 (15)	Yes (no)
		June 2001 (summer)	106	113 (4)	2 (2)	No	264	307 (16)	10 (32)	Yes (no)
	2+	September 2001 (autumn)	61	62 (2)	13 (8)	Yes (no)	266	273 (4)	5 (13)	Yes (no)
		November 2001 (winter)	30	32 (2)	28 (9)	Yes (no)	149	160 (6)	53 (84)	Yes (95)
		April 2002 (spring)	27	41 (18)	32 (13)	Yes (55)	70	83 (9)	35 (29)	Yes (95)
		June 2002 (summer)	18	20 (2)	10 (2)	Yes (100)	48	50 (2)	2 (1)	Yes (92)
	3+	September 2002 (autumn)	8	8 (0)	0 (0)	Yes (94)	41	42 (2)	38 (16)	Yes (86)
		April 2003 (spring)	0	0 (0)	0 (0)	Yes (no)	2	0 (0)	0 (0)	Yes (50)
June 2003 (summer)		0	0 (0)	0 (0)	Yes (no)	3	0 (0)	0 (0)	Yes (90)	
2001	0+	September 2001 (autumn)	125	139 (8)	1 (2)	Yes (no)	408	433 (8)	0 (1)	Yes (no)
		November 2001 (winter)	145	155 (5)	7 (11)	Yes (no)	361	389 (9)	25 (99)	Yes (95)
	1+	April 2002 (spring)	166	213 (21)	3 (6)	Yes (55)	353	386 (11)	7 (28)	Yes (95)
		June 2002 (summer)	246	258 (6)	5 (12)	Yes (100)	418	456 (12)	2 (11)	Yes (92)
	2+	September 2002 (autumn)	173	175 (2)	2 (4)	Yes (94)	364	385 (8)	11 (43)	Yes (86)
		October 2002 (winter)	156	159 (2)	40 (64)	Yes (94)	—	—	—	—
		April 2003 (spring)	102	114 (7)	11 (13)	Yes (no)	152	170 (9)	15 (26)	Yes (50)
	3+	June 2003 (summer)	63	88 (20)	1 (1)	Yes (no)	120	127 (4)	1 (1)	Yes (90)
		September 2003 (autumn)	58	65 (5)	40 (26)	Yes (no)	105	113 (5)	57 (64)	Yes (12)
		April 2004 (spring)	24	26 (4)	100 (26)	Yes (no)	36	2 (0)	100 (2)	Yes (98)
2002	0+	June 2004 (summer)	4	5 (2)	20 (1)	Yes (no)	20	3 (0)	33 (1)	Yes (no)
		September 2002 (autumn)	74	76 (2)	0 (0)	Yes (94)	296	324 (10)	8 (25)	Yes (86)
	1+	October 2002 (winter)	153	157 (3)	9 (14)	Yes (94)	—	—	—	—
		April 2003 (spring)	224	279 (22)	2 (6)	Yes (no)	262	291 (11)	1 (3)	Yes (50)
		June 2003 (summer)	293	345 (18)	3 (9)	Yes (no)	334	362 (10)	1 (4)	Yes (90)
	2+	September 2003 (autumn)	249	258 (4)	34 (89)	Yes (no)	298	329 (11)	33 (107)	Yes (12)
		November 2003 (winter)	155	171 (8)	15 (26)	Yes (no)	—	—	—	—
	3+	April 2004 (spring)	120	120 (0)	13 (16)	Yes (no)	111	163 (31)	20 (32)	Yes (98)
		June 2004 (summer)	109	109 (0)	40 (44)	Yes (no)	80	83 (2)	6 (5)	Yes (no)
		October 2004 (autumn)	84	93 (6)	1 (1)	Yes (no)	63	65 (2)	71 (46)	Yes (no)
3+	April 2005 (spring)	11	12 (1)	0 (0)	Yes (no)	9	54 (10)	85 (47)	Yes (no)	
	June 2005 (summer)	10	11 (1)	0 (0)	Yes (no)	3	25 (5)	0 (0)	Yes (no)	

Note: "No" is indicated in parentheses for intervals where efficiency was not estimable. Dashes indicate no sample.

with the age-2+ smolts (set 1) based on the relationship between age-1+ autumn body size and observed eventual smolt life history for each cohort (i.e., known age-2+ smolts versus known age-2+ nonsmolts). We defined a known age-2+ smolt as any individual observed to exhibit smolt characteristics (i.e., color and shape) during the typical spring smolt migration season at seasonally operated downstream migrant traps (these fish were part of set 1). We defined a known age-2+ nonsmolt as any individual detected on the study site any time subsequent to and including the age-2+ summer sampling occasion (equivalent to set 2). Using this classification, we concluded a positive relationship between age-1+ autumn size and age-2+ smoltification (G.E. Horton and B.H. Letcher, unpublished data). This result agrees with Huntingford et al. (1992) who showed that downstream-migrating Atlantic salmon during a similar time period tended to be larger than nonmigrants and exhibit the physiological characteristics of smolts the following spring. Nevertheless, it is possible that some of the emigration relative to the age-1+ autumn sampling occasion was associated with seasonal shifts in habitat preference that are not associated with fish smolting or preparing to smolt. Furthermore, because we did not observe set 4 fish following the age-1+ autumn season, there was no way to assign these fish to an eventual smolt life history. Therefore, in the analyses that follow, we define group 1 as the sum of the number of individuals in set 1 and set 3 plus some unknown portion of the set 4 fish. Thus, group 1 actually represents a mixture of fish that were on age-2+ smolt as well as age-3+ (and possibly older) smolt trajectories. We cannot definitively conclude the effect on study results of grouping older-aged smolts with age-2+ smolts. However, because the proportion of fish in set 4 was <5% for all cohorts, the effect of this grouping was probably negligible at most. Therefore, we refer to group 1 fish as age-2+ smolts for the remainder of this paper. Group 2 fish only consisted of age-2+ nonsmolts. We cannot say with certainty that all survivors to the age-3+ spring season actually became smolts (some could have become smolts at a later age), although based on data from these systems, smolts >age 3+ are extremely rare. Therefore, we refer to those fish as age-3+ smolts for the remainder of this paper.

Survival

Apparent survival

To estimate apparent survival, we used the CJS model (Lebreton et al. 1992) in program MARK (White and Burnham 1999). For age-2+ smolts, sampling occasions from the age-0+ autumn sample to age-2+ spring sample (inclusive) were used (Table 1). For age-3+ smolts, sampling occasions from the age-2+ spring sample to age-3+ spring sample (inclusive) were considered. Each set of sampling occasions was analyzed separately. Encounter histories were coded with a “1” to represent capture or “0” to represent failure to capture. A “0” on sampling occasion k could have arisen because of either death, failure to capture despite survival, or unavailability on the study site (e.g., due to permanent or temporary emigration). Standard CJS models yield estimates of recapture probability (p) that are separate from estimates of apparent survival probability (ϕ). Unless the probability of being available for capture given survival is 1 (e.g., the

probability of emigration from the study site = 0), the survival parameter estimates from CJS models must be interpreted as the confounded probabilities of study site fidelity ($F = 1 - \text{emigration}$) and true survival (S) so that $\phi = SF$. We raised each estimate of ϕ from MARK to the inverse of the number of months during the respective interval to represent monthly apparent survival:

$$\phi_{\text{cohort}, i, \text{monthly}} = (\phi_{\text{cohort}, i})^{\frac{1}{\text{months}}}$$

Our first step in modeling ϕ was to obtain the most parsimonious structure on p for each cohort. Our hypothesis for each cohort was that p would depend on body size, environmental conditions (e.g., stream discharge, temperature), or a combination of both. To estimate the best structure for p , we developed and analyzed six separate encounter history files (one for each cohort) and evaluated various combinations of body size/time trends on p within each. For this analysis, we did not place any constraints on ϕ . We used the resultant structure on p for all subsequent capture–mark–recapture analyses.

After obtaining the most parsimonious structure on p for each cohort, we developed and analyzed a single encounter history file with the six cohorts (three cohorts on two streams) as groups. Our primary objective in this step was to select the most parsimonious model from our model set to estimate ϕ . Secondly, we were interested in evaluating hypotheses regarding similarities in ϕ over time, between streams, and among cohorts within streams. By constructing models to represent each of these hypotheses and evaluating their relative support, we concluded model(s) (and therefore hypotheses) that were most likely given the data.

Adjusted apparent survival

To account for emigration from each study site and obtain estimates of survival that approached true survival, we performed three additional types of sampling outside the study site. The observed numbers of emigrants from these additional sampling types were combined for the analyses that follow. For cohorts and sampling intervals when data were available to estimate emigration detection efficiency (Table 1), the numbers of emigrants were adjusted (see Appendix A). To estimate an interval-specific emigration probability, the number of emigrants (either observed or adjusted) was expressed as a proportion of the estimated number of individuals available to emigrate at the beginning of each interval. This proportion was then used to adjust $\hat{\phi}_{\text{cohort}, i, \text{monthly}}$ to more closely represent $\hat{S}_{\text{cohort}, i, \text{monthly}}$.

First, to account for short-distance movement, we conducted single-pass electrofishing immediately upstream and downstream of the study site for a distance of 140 m from each study reach boundary (termed “outside” sampling) following each sampling occasion. Based on our repeated sampling design, we generally observed very high fidelity of individuals to their section of initial capture (e.g., movement <20 m). Therefore, 140 m was suitable to detect emigration resulting from short-distance movements. Any tagged fish that we captured outside were classified as emigrants relative to some previous sampling occasion as follows: (i) tagged fish that were captured during outside sampling but were captured “inside” during the sampling

occasion just completed (k) were classified as emigrants with respect to k and (ii) tagged fish that were captured during outside sampling but were not captured inside during k were classified as emigrants with respect to $k - 1$.

The second method of outside sampling to account for emigrants consisted of continuously monitoring a cross section of stream near the downstream boundary of each study site for emigration during the majority of the study period. This continuous monitoring was from PIT tag antenna arrays that we placed on each study stream to detect PIT-tagged fish as they passed a point (see Horton et al. (2007) for details of antenna construction and operation). Each detection system was capable of decoding an individual tag in the antenna field and recording the time and date of each detection event. Because the antennas were located just downstream of the downstream boundary of each study site, we interpreted tag detections as emigration events. Tagged fish that were detected on the antenna array between sampling occasion $k - 1$ and k were classified as emigrants with respect to $k - 1$. Tagged fish that were detected on the antenna array during electrofishing on sampling occasion k were classified either as emigrants with respect to k (if they were also captured inside on k) or as emigrants with respect to $k - 1$ (if they were not captured inside on k).

The third method of outside sampling to account for emigrants and to assign smolt age was through the operation of a downstream migrant trap incorporated into a fixed weir (Anderson and McDonald 1978). Very few nonsmolt (<age-2+) emigrants were detected at the smolt trap.

By dividing the number of emigrants detected from both methods by $\hat{N}_{\text{cohort}, k}$, we obtained a minimum proportion of tagged fish emigrating during each interval for each cohort. We interpreted the result as the minimum probability of emigration ($\hat{E}_{\text{obs, cohort}, i}$). We are aware that the probability of detecting emigration events with the antenna system on both streams (D) was less than 1; therefore, during intervals when we could estimate antenna efficiency, we adjusted $\hat{E}_{\text{obs, cohort}, i}$ by $1 - D_{\text{obs, cohort}, i}$ and then applied either $\hat{E}_{\text{adj, cohort}, i}$ (if available) or $\hat{E}_{\text{obs, cohort}, i}$ to adjust $\hat{\phi}_{\text{cohort}, i, \text{monthly}}$ (Appendix A) to more closely represent $\hat{S}_{\text{cohort}, i, \text{monthly}}$ ($\hat{\phi}_{\text{adj, cohort}, i, \text{monthly}}$).

Mean and overall survival

A final step in analyzing survival patterns for the three cohorts was to examine how interval-specific survival patterns were reflected in mean monthly survival. The survival analyses described thus far resulted in two sets of interval-specific survival estimates for each cohort and stream combination: apparent survival and apparent survival adjusted for emigration. To estimate mean monthly survival (e.g., averaged over all intervals) for each cohort ($\hat{\phi}_{\text{cohort, mean}}$), we first modeled apparent survival by manipulating the design matrix as described by Cooch and White (2007, section 16.14) from the most parsimonious model. This method takes into account the effects of population (sample) size on mean apparent survival. Similar to the approach used for obtaining $\hat{\phi}_{\text{adj, cohort}, i}$ by adjusting for interval-specific emigration (either $\hat{E}_{\text{adj, cohort}, i}$ or $\hat{E}_{\text{obs, cohort}, i}$), we also adjusted $\hat{\phi}_{\text{cohort, mean}}$ for mean emigration probability by cohort

($\hat{E}_{\text{cohort, mean}}$). The average emigration probability was then applied to obtain $\hat{\phi}_{\text{adj, cohort, monthly}}$ as above.

Overall survival was obtained by calculating the product of all $\hat{\phi}_{\text{cohort}, i, \text{monthly}}$ for each cohort. Thus, $\hat{\phi}_{\text{cohort, overall}}$ represents an estimate of the probability of apparent survival over the entire period of interest for a given group of fish (e.g., age-2+ smolts, age-0+ autumn to age-2+ spring). We obtained an adjusted overall survival estimate ($\hat{\phi}_{\text{adj, cohort, overall}}$) by calculating the product of all $\hat{\phi}_{\text{adj, cohort}, i, \text{monthly}}$ for each cohort.

Growth

We hypothesized that if ontogenetic differences in growth among cohorts existed, such differences could lead to differences in the average age of smolting. Because size is a reflection of growth and because of the observed positive relationship between FL during the age-1+ autumn season and subsequent emigration prior to the age-2+ summer sampling occasion (i.e., becoming an age-2+ smolt) (see Results), we conducted an initial two-way ANOVA with stream, year, and the interaction as independent factors to explain variability in age-1+ autumn FL. We used the Scheffe post hoc comparison to evaluate which (if any) cohort differed and to rank \overline{FL} .

Based on the results of the initial two-way ANOVA, we conducted a three-way general linear mixed model ANOVA with individual as a random effect and stream, year, interval between sampling occasions (i), and all interactions as fixed effects. Because median sampling dates differed among cohorts, the use of FL as the response variable may have resulted in bias. Therefore, instead of FL, we calculated the mean of the individual absolute growth rates in FL over each i to reduce the potential bias related to sampling date:

$$G_{ij} = \sum_j^n \frac{FL_{k+1} - FL_k}{t_{k+1} - t_k}$$

where t_k and t_{k+1} are the beginning and ending dates for the sampling occasion, j refers to individual, and n refers to the total number of individuals captured at the beginning and end of each i . Because we were focused on size during the age-1+ autumn sampling occasion and not all cohorts were sampled immediately prior to the age-0+ winter season (Table 1), \overline{G} was calculated for only three intervals for use in the ANOVA: age-0+ autumn to age-1+ spring, age-1+ spring to age-1+ summer, and age-1+ summer to age-1+ autumn. We ranked each \overline{G} for intervals and cohorts (stream and year combination) by pairwise evaluations of the overlap in 95% confidence interval (CI) for point estimates of \overline{G} .

Effects on smolt life history

Survival

Based on our results for the cohorts that we evaluated, we did not conduct additional evaluations of the effects of survival on smolt life history.

Growth

Because of evidence that age-1+ autumn body size was positively related to smolting at age 2+ (G.E. Horton and

Table 2. Model selection results for Cormack–Jolly–Seber (CJS) models to estimate interval-specific apparent survival.

Model	Description of structure (effect) on ϕ	QAIC _c	Delta QAIC _c	QAIC _c weights	No. of parameters
$\phi_{\text{stream} \times \text{year} \times t}$	Stream, year, interval	15 718.6	0.0	0.93	55
$\phi_{\text{stream} \times t}$	Stream, no year, interval	15 800.02	81.4	0.00	20
ϕ_t	No stream, no year, interval	15 928.0	209.3	0.00	23
$\phi_{\text{stream} \times \text{year}}$	Stream, year, no interval	15 980.6	261.9	0.00	22

Note: Each stream and year combination (i.e., cohort) was coded as a group; thus, models with the presence of a stream \times year effect represent an overall cohort effect. The most parsimonious structure on p (recapture probability) was obtained from separate analyses of individual cohorts.

B.H. Letcher, unpublished data), we interpreted emigrants with respect to the age-1+ autumn season as eventual age-2+ smolts. This interpretation is not precisely correct (see Classifying age-2+ and age-3+ smolts section), but we have no evidence that this affected our conclusions. However, if we assume that emigration for reasons unrelated to eventual smolting at age 2+ was similar among cohorts (an untestable assumption given our study design), we can make a relative comparison among cohorts to gain understanding of whether previous growth can operate to regulate smolt life history expression.

To evaluate whether differences among cohorts in \overline{FL} during the age-1+ autumn season (and therefore previous growth) influenced the probability of smolting at age 2+, we used the size and growth ranks from the ANOVAs to rank \overline{FL} and \overline{G}_t . In addition, we used logistic regression to evaluate the effects of age-1+ autumn FL on the probability of emigrating prior to the age-2+ summer season (i.e., size-dependent emigration). We also calculated the simple proportion of fish that were captured on the study site during the age-1+ autumn sampling occasion and later detected off the study site prior to the age-2+ summer sampling occasion.

For the logistic regression, we calculated relative (standardized) FLs for each fish by subtracting the FL of individuals captured during the age-1+ autumn season from the respective \overline{FL} for the stream (combined for all cohorts) and then dividing by the estimated standard deviation of FL for the stream. The logistic regression analysis followed a hierarchical approach and relied on a combination of both QAIC_c in a model selection framework and whether the 95% CI for various parameter estimates overlapped zero. We first evaluated support for a stream effect on size-dependent emigration by comparing models with and without a stream effect. Based on the results of this analysis, we then evaluated support for a cohort effect within each stream.

Results

Survival

Age-2+ smolts

Both interval (time) and cohort had strong influences on estimated monthly apparent survival (Table 2). Point estimates ranged from 0.75 to 0.99 (Fig. 2) and variability in monthly survival was only slightly reduced by adjusting estimates for emigration (0.79–0.99). Seasonal variability in emigration was also evident and variable among cohorts, with the highest emigration occurring between the age-1+ autumn and age-2+ spring and between the age-2+ autumn and age-3+ spring seasons for all cohorts on both streams (Table 1). Notably lower emigration was observed for the

2001 West Brook cohort. Contrary to the high variability in survival observed within cohorts, the range of mean monthly survival for the entire period between age-0+ autumn and age-2+ spring was low among cohorts (Fig. 3) ($\hat{\phi}_{\text{cohort, monthly}}$ range 0.89–0.93, coefficient of variation (CV) = 1.3%; $\hat{\phi}_{\text{adj, cohort, monthly}}$ range 0.91–0.94, CV = 0.9%).

Age-3+ smolts

A rigorous CJS analysis of eventual age-3+ smolts was not possible owing to the low numbers of fish captured for some cohorts on some sampling occasions (Table 1). Therefore, we were unable to confidently conclude cohort or time effects; however, mean survival based on a CJS model with a time effect but no cohort effect suggested a moderately high $\hat{\phi}_{\text{cohort, monthly}}$ (approximately 0.84 ± 0.04). There were small proportions of fish observed emigrating from the study site prior to the age-3+ spring season for some cohorts, so true monthly survival was slightly higher than apparent monthly survival.

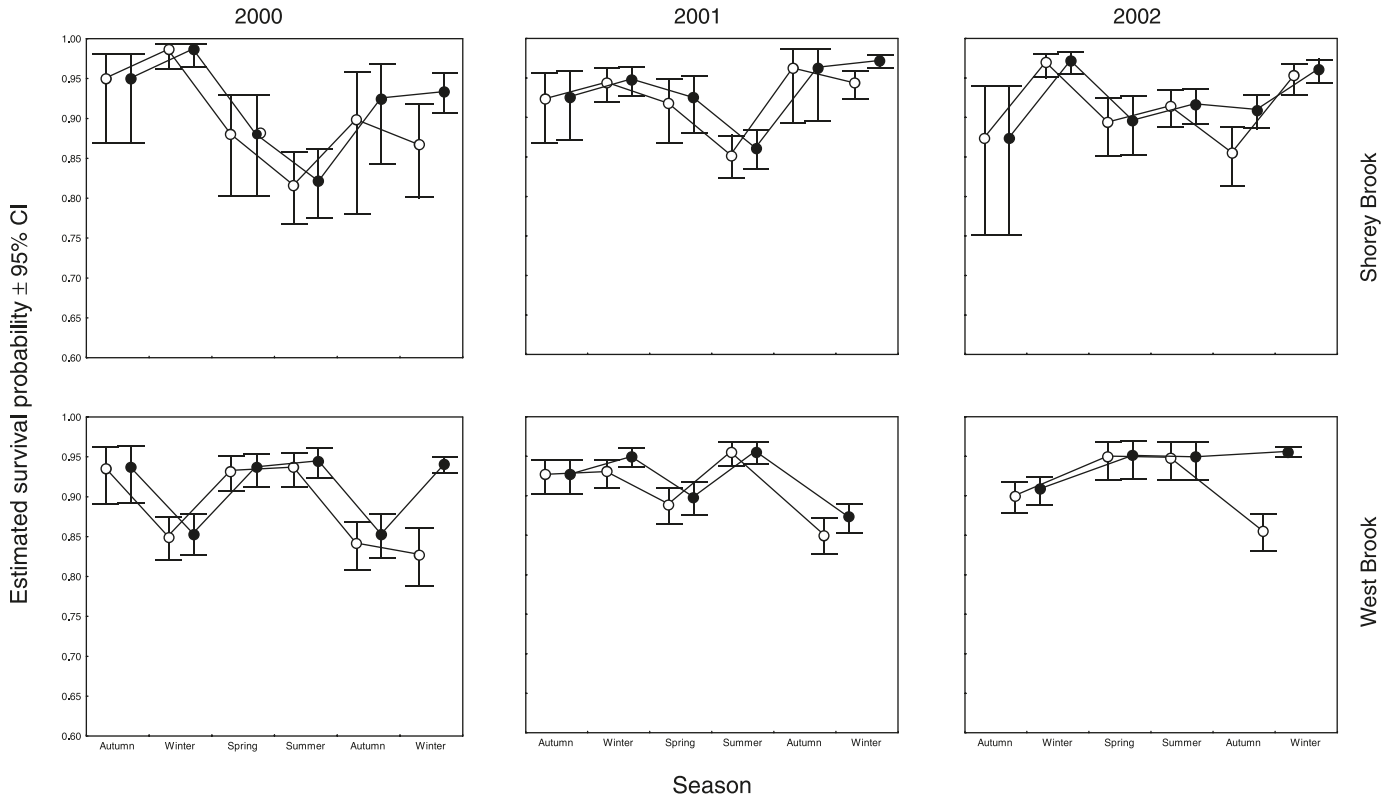
Growth

Mean individual growth rate was highly seasonal for all cohorts, with the highest growth occurring in the spring when fish were age 1+ and again when they were age 2+ (Fig. 4). For example, an average of 62% (range 55%–74%) of the growth in FL between the 12 months from the age-0+ autumn and age-1+ autumn sampling occasions occurred during 2 months during the spring (approximately 17% of the period). Unlike the low variability exhibited among cohorts in mean survival for the entire age-0+ autumn to age-2+ spring period, variability in growth rate among cohorts over the same period was high (CV = 17.6%) (Fig. 5).

The results of the two-way ANOVA to evaluate stream and year effects on age-1+ autumn \overline{FL} support an effect of both single factors and their interaction ($P < 0.0001$ for each). Based on the Scheffé post hoc comparison, \overline{FL} on Shorey Brook was similar for all three cohorts (2000 \geq 2001 \geq 2002). On West Brook, \overline{FL} for the 2001 cohort was smallest (2000 \geq 2002 \geq 2001).

The results of the three-way general linear mixed model ANOVA to evaluate stream, year, and interval effects on growth rate supported an effect of all single factors and all interactions ($P < 0.0001$ for each). Based on an evaluation of the overlap of 95% CIs for point estimates of \overline{G} , age-1+ spring growth rate was much higher than all other intervals regardless of stream or year (mean difference of 0.38 mm·day⁻¹). For the age-1+ spring season, \overline{G} was highest for the West Brook 2002 cohort (West 2002 > Shorey 2000), intermediate for the West Brook 2000 and 2001 and

Fig. 2. Point estimates of monthly apparent survival (open circles) and adjusted monthly apparent survival (solid circles) for three cohorts of Atlantic salmon (*Salmo salar*) psmolts on Shorey Brook and West Brook.

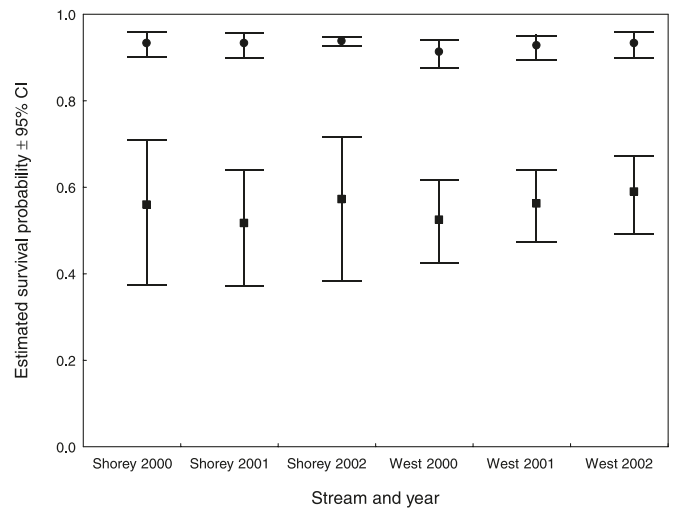


Shorey Brook 2002 cohorts (West 2001 ≥ West 2000 ≥ Shorey 2002), and lowest for the Shorey Brook 2001 cohort. Age-1+ spring growth did not fully account for differences in \overline{FL} during the age-1+ autumn sampling occasion (e.g., West Brook 2000 age-1+ autumn \overline{FL} was greatest, yet \overline{G} for West Brook during age-1+ spring was only intermediate). This suggests that either growth differences in other intervals or size-dependent processes (i.e., mortality and (or) emigration) may be affecting size distributions.

Effects on smolt life history

The proportion of fish captured on the study site during the age-1+ autumn sampling occasion that were later detected as emigrants prior to the age-2+ summer sampling occasion exceeded 0.75 for the cohorts with the largest mean size on both streams (2000) and was lower for the cohorts with the smallest average FLs (Shorey Brook 2001 and 2002: 0.52, West Brook 2001: 0.24). The probability of emigrating prior to the age-2+ summer sampling occasion as a function of relative FL in the previous autumn differed by stream (Table 3) with the size (as estimated from the model achieving the lowest QAIC_c) necessary to meet or exceed a 0.5 probability of emigrating less on Shorey Brook (98 mm) than on West Brook (119 mm). The probability of emigrating as a function of FL differed among cohorts in West Brook (Table 4) but not in Shorey Brook (cohort effect delta QAIC_c > 10, model selection results not shown). The FL necessary to meet or exceed a 0.5 probability of emigrating on West Brook was almost 9% larger for the cohort with the smallest average FL (125 mm, 2001 cohort) as compared with the cohort with the largest average FL (115 mm, 2000

Fig. 3. Point estimates of adjusted mean monthly apparent survival (circles) and adjusted overall (age-0+ autumn to age-2+ spring) apparent survival (squares) for three cohorts of Atlantic salmon (*Salmo salar*) psmolts on Shorey Brook and West Brook.



cohort). A consequence of differences in FL necessary to meet or exceed a 0.5 probability of emigrating among cohorts within a stream resulted in what we interpreted as differences in the age-2+ smolt production even when the size threshold was the same among cohorts within a stream (i.e., Shorey Brook). However, the effect was especially pronounced for West Brook where that size threshold was inversely related to mean size (Fig. 6).

Fig. 4. Mean interval-specific, individual absolute growth rate in FL for each interval between the age-0+ autumn season and age-3+ spring season for three cohorts of Atlantic salmon (*Salmo salar*) psmolts on Shorey Brook and West Brook.

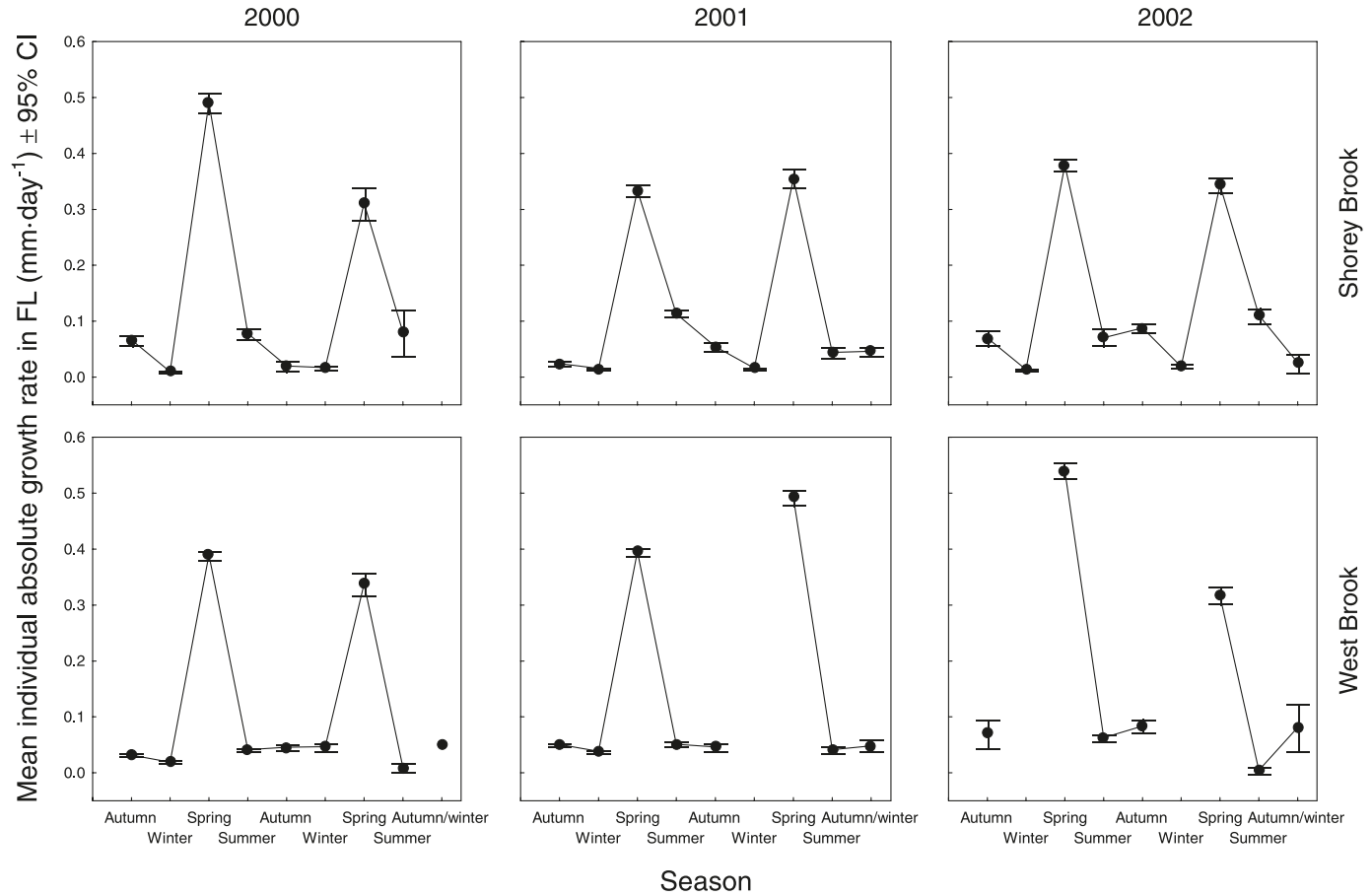
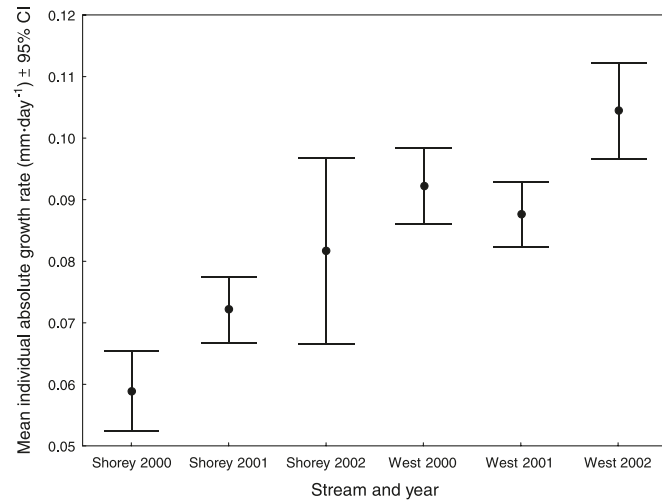


Fig. 5. Mean interval-specific, individual absolute growth rate in FL for the single interval between the age-0+ autumn season and age-2+ spring season for three cohorts of Atlantic salmon (*Salmo salar*) psmolts on Shorey Brook and West Brook.



Discussion

The high degree of within-cohort seasonal variability in monthly survival and lack of a consistent pattern in survival among cohorts even from the same stream support the no-

tion that stream environments present variable and challenging conditions to psmolt Atlantic salmon. Surprisingly, however, we found very little variability in overall survival over the course of stream residence. In contrast, overall size and growth varied by environment (Shorey Brook versus West Brook) and cohort, which had consequences for age-2+ smolt production. The consistent strength of size-dependent emigration among cohorts, yet large differences in average size of psmolts (age-1+ autumn season) and size-dependent probability of emigration, implies a difference in growth opportunity between streams (Metcalf and Thorpe 1990) as well as a difference in how fish respond to growth opportunity (Thorpe et al. 1998). Overall, our results suggest that variation in smolt production is more dependent on growth opportunity than on variation in survival following age-0+ autumn.

Population density may partially explain the observed effect on size and growth and, in turn, smolt life history. Although our study was not designed to evaluate the effects of population density on survival or growth, we noted a strong correlation during the age-1+ autumn between age-1+ population density and cohort-specific FL (Shorey: $r = -0.99$, $n = 3$ cohorts; West: $r = -0.99$, $n = 3$ cohorts). There was also evidence for a relationship between autumn age-1+ FL and the eventual proportion of age-2+ smolts (Shorey: $r = 0.85$, $n = 3$; West: $r = 0.74$, $n = 3$). However, a CJS model with population density on each sampling occasion

Table 3. Model selection results for logistic regression models to estimate the probability of emigrating between the age-1+ autumn and age-2+ summer sampling occasions (i.e., smolting at age-2+).

Model	QAIC _c	Delta QAIC _c	QAIC _c weights	No. of parameters
Stream + Zlength + stream × Zlength	1244.3	0.00	1.00	4
Stream + Zlength	1258.1	13.7	0.00	3
Zlength	1258.3	13.9	0.00	2
Stream	1411.6	167.2	0.00	2

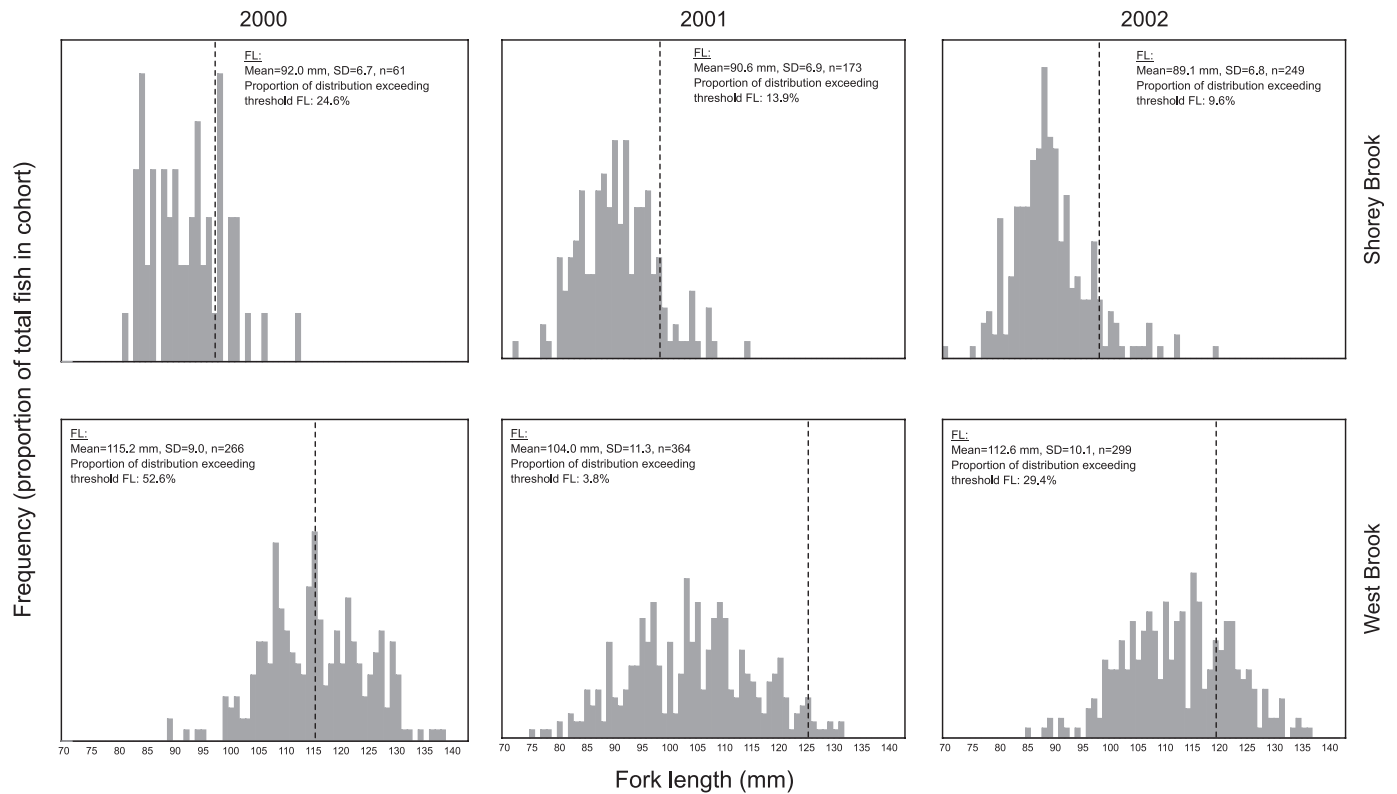
Note: Estimated overdispersion (Pearson χ^2 -df⁻¹) was 0.98. “Zlength” refers to standardized (relative) FL collapsed over the three cohorts within each stream.

Table 4. Model selection results for logistic regression models to estimate the probability of emigrating between the age-1+ autumn and age-2+ summer sampling occasions (i.e., smolting at age-2+) on West Brook.

Model	QAIC _c	Delta QAIC _c	QAIC _c weights	No. of parameters
Cohort + Zlength	705.6	0.00	0.93	3
Cohort + Zlength + cohort × Zlength	711.9	6.3	0.04	5
Zlength	713.6	7.9	0.02	1
Cohort	800.8	95.2	0.00	2

Note: Estimated overdispersion (Pearson χ^2 -df⁻¹) was 0.97. “Zlength” refers to standardized (relative) FL collapsed over the three cohorts within West Brook.

Fig. 6. FL frequency distributions for three cohorts of Atlantic salmon (*Salmo salar*) psmolts on Shorey Brook and West Brook. Vertical lines represent the estimated FL during the age-1+ autumn season necessary to have a ≥0.5 probability of emigrating from the study site prior to the age-2+ spring season (i.e., becoming an age-2+ smolt). Threshold FLs are from the most parsimonious logistic regression models.



(in place of a group effect) did not explain variability in survival as well as the more general group effect model (delta QAIC_c = 5.0). Our findings are in agreement with those of others (e.g., Crisp 1993; Jenkins et al. 1999; Imre et al. 2005) who found no effect of population density on mortality yet negative effects on somatic growth.

We do not discount the potentially important impact of population density on survival and (or) emigration (e.g., dispersal) during earlier life stages or over smaller spatial scales than those encompassed by our study. Such density effects have been documented in other studies (Cunjak and Therrien 1998; Einum and Nislow 2005; Einum et al. 2006)

and our analysis here was not designed to address those stages or scales. Another caveat of our study results in this regard is the very narrow range of population densities in comparison with other studies that have shown density-dependent effects on demographics (e.g., Elliott 1994). Populations in our study streams were maintained by fry stocking, which may partly account for our more narrow range of densities. However, that inference depends on a more detailed understanding of the role of density dependence for younger life stages than we studied as well as its relationship to initial stocking densities. Manipulation of stocking densities may offer a useful way of further evaluating the role of density dependence on smolt life history outcomes.

Our findings may also not apply for earlier life stages or over the range of environmental conditions possible in a given stream system. For example, survival of younger life stages (i.e., the first few weeks following emergence from redds) has been shown to strongly depend on environmental conditions that may differ much among years (e.g., stream discharge: Lobon-Cervia 2007). Even for older life stages (e.g., those encompassed by our study), particularly harsh conditions during a specific period (e.g., drought) that lead to high mortality could override growth as a primary determinant of smolt production.

Other than the possible effect of density on growth, we cannot definitively conclude which of the many possible mechanisms advanced to explain patterns in demographics or growth may be responsible for our observations. Some plausible explanations that cannot be addressed with our data include the following. Harwood et al. (2003) hypothesized that spatial differences within a stream can account for variability in body size because of the often patchy distribution of resources. Einum and Nislow (2005) considered the consequence of this uneven distribution of resources when evaluating density-dependent effects on growth and (or) dispersal. Einum et al. (2006) showed predation risk to be a function of size and therefore a form of size-dependent mortality. The risk of predation has also been shown to influence growth (Huntingford et al. 1988). Still others have noted abiotic factors in streams that can affect growth and (or) favor individual salmon of certain sizes (e.g., substrate size: Finstad et al. 2007; flow: Good et al. 2001; flow \times temperature interactions: Nislow et al. 2004). The consequence of avoiding additional mortality from these sources may be a decrease in energy stores, resultant energy-dependent survival (Finstad et al. 2004), and effects on life history outcomes. Collectively, these studies represent just a small sample of the breadth and complexity of possible mechanisms underlying demographics and growth patterns in pre-smolt Atlantic salmon. This sample also led us to hypothesize that rather than any single mechanism driving patterns in demographics and growth, it is likely that there is an interaction among individual, abiotic, and biotic factors. Additional research is certainly warranted to more fully understand which mechanisms may be most important, how those mechanisms operate, and whether there are certain conditions under which certain mechanisms are more dominant.

Implications for Atlantic salmon population restoration

Our results suggest that, at least in natural systems, the primary factor of concern in smolt production after age 1+

is spatiotemporal variation in growth opportunity, given that survival rates vary much less across cohorts. In addition, local populations can differ in their size-dependent smolting relationships. With this in mind, management options to influence smolt production would have greatest effect where they can influence growth conditions to optimize smolting probabilities and smolt quality relative to a given population's smolting threshold(s). At present, the options available to managers to increase stream growth conditions are limited to enhancing stream habitat, manipulating stocking densities, or manipulating resources, with the latter being more experimental (e.g., nutrient additions).

Current restoration efforts for many Atlantic salmon populations include fry stocking to augment natural smolt production. The effect of stocking fish at too high a density could lead to negative density-dependent growth and, in turn, increase smolt age. Managers should therefore consider reduced stocking densities as an important strategy for achieving a larger size at smolting (Okland et al. 1993) or increasing smolt size and numbers at younger ages. The fitness consequences of smolting at a later versus earlier age would partially depend on the size-dependent probability of marine survival. Smolt body size is often positively correlated with adult return rates (Eriksson et al. 1987; Lundqvist et al. 1994; Kallio-Nyberg et al. 2006). Therefore, lower densities may result in better age-specific growth and thus more fish smolting at a younger age, but with lower marine survival, whereas higher densities may result in fish delaying smolting a year to become significantly larger but also incur a further year of stream mortality. Optimizing the number and quality of smolts that emigrate from a system may prove difficult given the very crude tool of fry stocking alone. Moreover, the challenge in optimizing growth conditions and net fitness outcomes becomes even greater when one considers the three-way interaction of growth, smolting, and presmolting reproductive opportunities for males, which can reproduce as parr (females do not mature as parr).

Additional work to evaluate the relationships that we describe here on other systems is necessary to evaluate the generality of our results. For example, our result showing very similar mean monthly and overall survival, even between streams, may be coincidental or it may underlie a phenomenon that could be more broadly applied. Approaches employing methods similar to those presented here should inform managers of how density-dependent mechanisms operate across space and time while simultaneously contributing to more basic questions of the ultimate consequences of complex and interacting proximal factors that are a function of individual, abiotic, and biotic considerations.

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Appendix A

To account for detection inefficiencies, we developed a model to estimate interval-specific detection probabilities (Horton et al. 2007). Based on this model, we adjusted emigration:

$$\hat{E}_{\text{adj, cohort}, i} = \hat{E}_{\text{obs, cohort}, i} + \hat{E}_{\text{obs, cohort}, i}(1 - \hat{D}_i)$$

where $\hat{E}_{\text{adj, cohort}, i}$ is the cohort- and occasion-specific emigration probability adjusted based on the estimated PIT tag antenna detection efficiency over the interval \hat{D}_i . Unfortunately, during some of the sampling period, the data necessary to estimate antenna efficiencies were not available and, during other sampling occasions, antenna arrays were not in place (Table 1). Therefore, $\hat{\phi}_{\text{cohort}, i}$ was adjusted by either $\hat{E}_{\text{adj, cohort}, i}$ (if available) or $\hat{E}_{\text{cohort}, i}$.

The estimates of apparent survival from the most parsimonious model (based on the apparent survival analysis) were adjusted by applying the appropriate emigration estimated emigration coefficient to each corresponding unscaled estimate of apparent survival from program MARK ($\hat{\phi}_{\text{cohort}, i}$). The result was then scaled by time to represent monthly adjusted interval- and cohort-specific apparent survival:

$$\hat{\phi}_{\text{adj, cohort}, i, \text{monthly}} = [\hat{\phi}_{\text{cohort}, i} + (1 - \hat{\phi}_{\text{cohort}, i})\hat{E}_{\text{cohort}, i}]^{\frac{1}{\text{months}}}$$

where $\hat{\phi}_{\text{cohort}, i}$ are the interval- and cohort-specific estimates of apparent survival unscaled by time and $\hat{E}_{\text{cohort}, i}$ are either $\hat{E}_{\text{adj, cohort}, i}$ or $\hat{E}_{\text{obs, cohort}, i}$ depending on the cohort or interval (Table 1).

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