

Survival of Stream-Dwelling Atlantic Salmon: Effects of Life History Variation, Season, and Age

BENJAMIN H. LETCHER* AND GABE GRIES¹

*U.S. Geological Survey, Biological Resources Division,
S. O. Conte Anadromous Fish Research Center,
Post Office Box 796, One Migratory Way,
Turners Falls, Massachusetts 01376, USA*

FRANCIS JUANES

*Department of Natural Resources Conservation,
University of Massachusetts,
Amherst, Massachusetts 01003-4210, USA*

Abstract.—To determine seasonal and age-class variation in the abundance and survival of Atlantic salmon *Salmo salar*, we conducted multiple samplings of individually tagged juveniles in a small stream (West Brook, Massachusetts). We also estimated the differences in survival and probability of smolting for mature and immature parr. Survival was approximately twofold lower during winter as compared with summer and was higher for fish in their first winter than for fish in their second winter. Parr maturation rates were high (50% of all fish) and peaked in September. The estimated numbers of mature and immature fish were equal for the March samples preceding the smolt run, indicating no overall differences in survival between mature and immature fish during stream residence. Age-2 mature fish were one-third as likely to smolt as immature fish, however, resulting in survival probabilities (from March to smoltification) of 0.22 for mature fish and 0.61 for immature fish. Approximately one-third of the fish captured in the smolt trap were estimated as mature during previous sampling, and virtually all of the age-2 fish remaining in the stream following the smolt run were previously mature. We found no differences in gill Na⁺, K⁺ ATPase activity between previously mature smolts and immature smolts, but activity was significantly higher in March for fish that later smolted than for those that did not.

The factors shaping variation in survival are difficult to summarize and evaluate for animal populations due to seasonal variation in biotic and abiotic variables, age and size differences, life history effects, movements, and logistic constraints on censusing. A variety of techniques exists for population estimation (Lebreton et al. 1992), with varying numbers of necessary assumptions depending on the extent of movement into and out of the study area, whether individuals are tagged or not, and whether the probability of capture is constant. Closed populations with tagged individuals and a constant probability of capture tend to give the most reliable estimates, but these assumptions are rarely met in nature.

Because they tend to be territorial and are confined within the physical limits of the aquatic habitat, stream salmonids can give higher recapture rates when tagged than animals that are not con-

finned to a narrow spatial range. Although salmonids are restricted in their three-dimensional range, upstream and downstream movement can still complicate survival estimates. Long study sites that encompass the short-distance (<1 km) movements of fish should reduce the effects of short movements on survival estimates and also increase the number of recaptures. In an attempt to generate abundance and survival estimates for cohorts of Atlantic salmon *Salmo salar* L., we tagged and recaptured individual fish from a 1-km-long study site approximately monthly. The 1-km study site was much longer than the typical territory size of Atlantic salmon (0.5 m²) (Keeley and Grant 1995) and should encompass movements on short temporal and spatial scales. We were unable to measure longer-scale movements that would take fish out of our study area, but we were able to estimate numbers of fish moving into the site.

Many studies have determined the survival of stream-dwelling Atlantic salmon on yearly or greater time scales (Chadwick 1982; Crozier and Kennedy 1995; Cunjak and Therrien 1998; Jonsen et al. 1998), but less is known about fine-scale seasonal variation in survival (but see Egglishaw

* Corresponding author: bletcher@forwild.umass.edu

¹ Present address: New Hampshire Fish and Game, 25 State Route 9, Keene, New Hampshire 03431, USA.

Received July 24, 2001; accepted February 5, 2002

and Shackley [1977] for a notable exception with untagged fish). Studies operating on a short time scale (months) have estimated survival over winter (Cunjak et al. 1998). Winter survival is typically low and variable for all parr age-classes (20–45% of individuals; Cunjak et al. 1998). Though this low survival suggests that winter may be the primary freshwater bottleneck, detailed estimates of survival during other seasons are rare. In a detailed study of untagged Atlantic salmon, Egglshaw and Shackley (1977) identified four stages of decline in freshwater abundance, with alternating periods of rapid and slow decline. The fairly frequent population estimates in the Egglshaw and Shackley (1977) study allowed identification of seasonal variation in abundance and correlation between density and future abundance. Identification of patterns of abundance over time aids in relating point estimates of juvenile abundance to smolt production and can provide a basis for comparison of seasonal variation in biotic and abiotic factors with seasonal variation in survival. Detailed data on variation in seasonal abundance across systems may also allow identification of mechanisms responsible for differences among systems.

Survival estimates for Atlantic salmon in freshwater are complicated by the various life history forms possible in juveniles. A variable proportion of male parr matures in freshwater before migration to the sea (Mitans 1973; Saunders et al. 1982; Lundqvist et al. 1988). Mature parr often delay smolting for a year (Thorpe 1987) and migrate in lower frequencies than do immature parr (Hansen et al. 1989; Berglund et al. 1992; Whalen et al. 2000). In some systems, mature parr have lower estimated survival than immature fish (Lundqvist et al. 1988). The demographic effects of parr maturation are difficult to determine directly in the wild without individually tagged fish because parr maturation is a fairly short-term event with delayed consequences. Tagging and recapturing individual fish in the wild appears to offer great promise for unraveling the complex interactions between parr maturation and smolting. For example, in a study involving the resampling of individually tagged fish, Whalen et al. (2000) estimated that age-1 parr-to-smolt survival was similar for mature and immature parr, but that the probability of smolting for mature fish was one-third that of immature fish.

We initiated a long-term study with the aim of describing life history, seasonal, and age-class variation in fine-scale (~monthly) abundance, survival, and growth estimates for individually tagged

salmonids in a small stream. In this paper, we present data on Atlantic salmon collected from spring 1997 to summer 1999. The samples encompassed two spring smolt runs, age-0 to age-2 data for the 1997 age-class, and portions of the 1995 and 1996 year-classes. Our objectives were to (1) determine the seasonal variation in juvenile Atlantic salmon survival, (2) compare the variation in survival among age-classes within a given season, (3) compare the variation in survival between mature and immature parr over time, (4) determine the proportion of smolts and age-2 residents (fish that did not smolt at age 2) that were previously mature, and (5) examine the possibility of an interaction between parr maturation and the probability of smolting.

Methods

Study site.—Our study was conducted on the West Brook, Massachusetts (42°25'N, 72°39'W), a 6.3-km, second-order stream located within the Connecticut River basin. The surrounding forests are composed of mixed hardwood species, which form a dense canopy during summer. The brook originates from a reservoir that provides drinking water to the surrounding communities.

The approximately 1-km-long study site was divided into 47 contiguous sections. Sections averaged 20.3 m in length (total length = 955 m) and 96.6 m² in area (total area = 4,542 m²) and had an average gradient of 2%. On 30–31 July 1997, we quantified available habitat in our study site by placing transects across the brook every 5 m and measuring water depth and substrate size at 0.5-m intervals. Average (\pm SE) stream width was 4.7 \pm 0.1 m ($N = 187$), average water depth was 8.8 \pm 0.2 cm ($N = 1,096$) and average substrate size was 21.5 \pm 1.1 cm ($N = 1,096$). The study area consisted predominantly of riffle runs (water depth \leq 45 cm and surface water velocity \geq 20 cm/s), interspersed with 12 small pools (water depth $>$ 45 cm and surface water velocity $<$ 20 cm/s; riffle run habitat definitions from Rimmer et al. 1983). Brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, and Atlantic salmon were the only fish species present in the study reach. Fish moved freely within the study section and were not obstructed from entering or leaving the site. The study site was located approximately 1 km below the reservoir. We placed a temperature recorder (recording every 2 h) in the study site and estimated discharge for each sampling day or night from a stage–discharge curve at a permanent location.

Atlantic salmon restoration efforts in the Connecticut River basin use unfed, stocked fry as the primary source of fish. A large waterfall obstructs the potential for natural reproduction in our study stream. Atlantic salmon fry were derived from age-4 domestic broodstock (White River National Fish Hatchery, U.S. Fish and Wildlife Service, Bethel, Vermont). The broodstock were first-generation descendents of sea-run returns to the Connecticut River. During each year of our study, the West Brook was stocked on a single day within the last two weeks of April. The 26–28-mm (fork length) fry were stocked at a density of 50 fish/100 m².

Our study site lacked anadromous Atlantic salmon spawners. The absence of adult spawners may have influenced the comparison between mature and immature parr because the mature parr were unable to interact with any salmon adults, although mating with brown trout was possible (Gephard et al. 2000). This limitation may have influenced the survival estimates of mature parr in several ways. Mature parr often leave their territories in the fall and follow adults to spawning areas (Buck and Youngson 1982). As a result, local densities of mature parr may be depleted. Also, mature parr compete directly with adult males for access to spawning females (Fleming 1998), an activity that occasionally results in death of the parr (Hutchings and Myers 1987). If the mature parr survive, indirect effects on survival related to the energy expended during mate competition are also possible. Thus, our estimates of mature parr survival include only the effects of parr maturation itself, not the direct and indirect effects of interaction with anadromous spawners.

We sampled fish from stocking years (SY) 1995–1997. Sample dates ranged from May 1997 to July 1999 (Table 1). Because the majority of smolts were age-2 fish, we report complete data (age-0 to age-2) for the freshwater phase of SY 1997 fish, data on age-1 through age-3 fish from SY 1996, and data on age-3 fish from SY 1995.

Sampling

Electrofishing and night seining.—We sampled all 47 sections of the study site during 19 different samples (Table 1). To balance sampling efficiency with potential sampling impact on fish growth and survival, we conducted a combination of electrofishing and night seining samples (Table 1; also see below).

Our sampling strategy was to obtain multiple recaptures for a large percentage of the fish in the study section, without excessively influencing

TABLE 1.—Sample number, sampling technique, and dates of first and last sampling of juvenile Atlantic salmon in the West Brook, Massachusetts, in 1997, 1998, and 1999.

Sample number	Sampling technique	First sampling date	Last sampling date
1	Electrofishing	14 May 1997	27 May 1997
2	Day seining	2 Jun 1997	11 Jun 1997
3	Night seining	17 Jun 1997	25 Jun 1997
4	Night seining	10 Jul 1997	18 Jul 1997
5	Night seining	3 Aug 1997	12 Aug 1997
6	Night seining	24 Aug 1997	2 Sep 1997
7	Electrofishing	22 Sep 1997	9 Oct 1997
8	Electrofishing	10 Dec 1997	22 Dec 1997
9	Electrofishing	17 Mar 1998	1 Apr 1998
10	Smolt trap	11 Apr 1998	7 May 1998
11	Electrofishing	20 May 1998	2 Jun 1998
12	Night seining	22 Jun 1998	6 Jul 1998
13	Night seining	13 Jul 1998	22 Jul 1998
14	Night seining	10 Aug 1998	18 Aug 1998
15	Electrofishing	9 Sep 1998	28 Sep 1998
16	Night seining	21 Oct 1998	2 Nov 1998
17	Electrofishing	1 Dec 1998	11 Dec 1998
18	Electrofishing	16 Mar 1999	9 Apr 1999
19	Smolt trap	13 Apr 1999	19 May 1999
20	Electrofishing	24 May 1999	7 Jun 1999
21	Night seining	11 Jul 1999	20 Jul 1999

growth or survival. By combining electrofishing and night seining sampling methods, we may have reduced the impact of multiple samples. We used electrofishing when the majority of age-0 fish were large enough to tag (e.g., samples 7 and 15; Table 1), in the winter samples (e.g., samples 8 and 17), and in the spring samples (e.g., samples 9, 11, 18, and 20); otherwise, we used night seining, with the exception of sample 2, for which daytime seining was conducted (Table 1).

During electrofishing samples, we conducted two passes (500-V unpulsed DC) with block nets at the upstream and downstream ends of each study section. Each pass was made in an upstream direction, and sections were sampled sequentially from the lower end to the upper end of the study area. We also sampled 140 m above and below our study area at the end of each set of electrofishing samples without tagging fish to determine which fish had moved out of the study site and to estimate directional movement on the scale of the study site.

We conducted night seining (Gries and Letcher 2002) by walking downstream and startling fish into handheld block seines. We conducted two passes through each study section sequentially in an upstream direction, and each section was isolated with block nets during sampling. When water discharge was low, it was often more efficient for the sampling team to search sampled areas for fish

and then guide the fish into the seines by hand. This approach was effective, as juvenile Atlantic salmon are fairly lethargic in response to gentle prodding at night (Gries et al. 1997). Seining during the daytime (sample 2) was ineffective and was replaced with night seining thereafter.

After capture, each fish was placed quickly into one compartment of a black plastic bucket divided into four sections. Each section was numbered and contained correspondingly numbered flags that were placed at the approximate stream bank locations where the individual fish were captured. Flags facilitated returning the fish to their capture location following handling.

Smolt trap.—In addition to the sampling of each study section, a smolt trap (picket weir) was placed approximately 3 km downstream of our study site in April 1998 and 1999 (Table 1). The trap was installed as soon as water temperatures reached 5°C. In both years, no smolts were found in the trap until 2 weeks after installation. Our study reach encompassed approximately one-fourth of the habitat length (4 km) upstream of the smolt trap. The smolt trap followed the design of Anderson and McDonald (1978), and a similar design has been used effectively to trap smolts in nearby streams (Whalen and Parrish 1999). The trap was cleaned and checked for fish twice a day.

During 1998, two high-water events compromised our ability to continuously sample fish with the smolt trap; thus the smolts caught during those events only partially represented the smolt run. During 1999, low water conditions resulted in the trap acting more as a barrier to fish migration than as a sampling device. To compensate for this problem, we electrofished the 200 m of stream located above the smolt trap in a downstream direction every 2–3 d during low water periods. Gill Na⁺, K⁺ ATPase activity (see below) allowed us to determine the smoltification status of fish captured in or upstream of the trap.

We attempted to conduct efficiency tests of the smolt trap by tagging captured smolts and releasing them upstream of the trap (Dempson and Stansbury 1991; Whalen et al. 2000). The percentage of tagged fish recaptured in the trap indicates the trap efficiency. Unfortunately, we lost most of the tagged fish during the high-flow event in 1998 and therefore could not effectively estimate efficiency. Because of the lost smolts, we could only provide an estimate of survival between March 1998 and the smolt trap samples in April–May 1998. We attempted a similar efficiency test in 1999, but possibly due to the very low flows throughout the

smolt run, we recaptured only one of the fish tagged for the efficiency test, despite capturing many other migrating fish. We do not believe the low recapture rate reflected the efficiency of the trap but rather the altered behavior of the released fish. Because of the low flows, our use of electrofishing to capture fish above the trap, and the capture of relatively large numbers of migrating fish, we assumed 100% capture efficiency for the 1999 smolt run. We assumed no difference in smolt trap capture probability for immature and mature fish, so comparisons of survival between mature and immature fish were not influenced by incomplete efficiency estimates.

Fish handling.—After capture, fish were anesthetized in buffered tricaine methanesulfonate (MS-222; 100 mg/L), and scales were taken from first-time captures (except for fish that were obviously age-0 with fork lengths <75 mm). Scales allowed us to categorize fish by age and year of stocking. Fish were also checked for tags (11-mm passive integrated transponder [PIT] tags) with a handheld reader. If a tag was present, the number was recorded; otherwise, fish longer than 60 mm and heavier than 2 g were tagged (except for those captured in the smolt trap). Tags were placed intraperitoneally through a small incision between the pectoral fins. All fish were squeezed gently to test for milt expression (evidence of male parr maturation). Each fish captured within the study site was returned to the brook at the location of its numbered flag within 30 min of capture. Smolts were released into the brook downstream of the smolt trap.

To examine gill Na⁺, K⁺ ATPase activity, an index of smolt osmoregulatory ability, we took a small, nonlethal gill biopsy (McCormick 1993) from all smolts captured at the smolt trap and from all age-2 or older fish captured in the sample immediately preceding (samples 9 and 18; fish >110 mm) and following (samples 11 and 20; fish >140 mm) the smolt trap samples. Biopsy samples were placed immediately on dry ice and then held at –80°C until analysis. Gill biopsies were analyzed according to the methods of McCormick (1993).

Data Analysis

Numbers of fish caught.—For each sample, we report the numbers of captured fish from SY 1995–1997 and the proportion of fish that had been tagged previously (number tagged/[number tagged + number untagged]).

Population estimates.—We used capture histories of individual fish to derive population esti-

mates for the 1995–1997 year-classes and for mature and immature fish within each year-class. The mark–recapture model was an open population version of a Jolly–Seber model (Pollock et al. 1990). We used the software package POPAN-4 (Arnason and Schwarz 1995) to generate population estimates and confidence intervals. The capture history of each fish (captured live, captured dead, or not captured in each sample) was entered into the model. Fish that were captured for the last time outside the study section were scored as lost to the population.

Survival.—The Jolly–Seber mark–recapture model generated survival estimates for each sampling interval, but interpretation of the survival estimates was complicated by our inability to separate emigrants from mortalities. Although we use the term “survival” here for simplicity, we actually estimated a retention rate ($1 - \text{proportion of fish lost}$). Except for samples before and after the smolt trap samples, we report survival estimates and confidence intervals derived from mark–recapture analyses for fish from each of the year-classes. For the samples influenced by smolt emigration (samples 10 and 19), we calculated survival for each age-class as the number of smolts plus the estimated number of residents divided by the population estimate from the sample preceding the smolt trap samples. Residents were defined as age-2 or older fish that did not smolt and that were collected after the smolt trap samples.

Combining data across samples, we calculated cumulative survivals for a season based on multiplied sample-specific survival estimates ($\prod_i s_i$, where i is the sample number and s_i is the survival estimate from i to $i + 1$).

Maturity

To classify males as mature or immature, we used a longitudinal description that assigned a mature status to any fish that was previously observed as mature. With this approach, the default status was immature; thus, we may have misclassified some truly mature fish as immature because the fish were not expressing milt when captured. To avoid this problem, we calculated the certainty of correct classification based on the number of times fish were captured and on the proportion of mature fish captured during each sample. Specifically, for a given fish, we summed the proportions of mature fish for all samples in which that fish was present. For example, if a fish was captured in samples x , y , and z , and the proportion of mature fish was 0.0,

0.2, and 0.3 for the three samples, the summed maturity classification value would be 0.5. Based on variation in population estimates resulting from different maturity classification cutoff values (see below), we only included fish with a minimum maturity classification value of 0.4 in our comparisons of mature and immature fish.

Gill Na^+ , K^+ ATPase Activity

To test for differences in gill Na^+ , K^+ ATPase activity ($\mu\text{mole ADP/mg protein/h}$) among fish with different life history strategies, we ran one- and two-way analyses of variance, with life history strategy as the independent variable, gill Na^+ , K^+ ATPase activity as the dependent variable and sample date as the covariate. Specifically, we compared values for mature versus immature fish and smolts versus resident fish for the sample preceding the smolt trap samples and compared values for mature versus immature fish caught in the smolt trap.

Results

Environmental Conditions

Average daily summer water temperatures ranged from 15°C to 19°C, and winter water temperatures ranged from 0°C to 3°C (Figure 1). Excluding winter, the typical diel temperature range was 5°C. The stage–discharge relationship ($\text{discharge} = 16.63 - [0.35 \times \text{stage}] + [0.0019 \times \text{stage}^2]$; $r^2 = 0.95$, $N = 25$) estimated typical low summer discharge values of 0.1 m³/s, with higher spring rates and occasional very high values in spring and early summer (5–10 m³/s; Figure 1).

Numbers of Fish Caught

Study sections.—Numbers of fish captured within the study area during each sample varied with sampling technique, year-class, and age (Figure 2). For SY 1996, we caught 282 age-1 fish during sample 1. Sample 2 involved daytime seining, during which we only caught 87 fish. We caught approximately 210 fish during each of the next four night seining samples and 312 fish during electrofishing in sample 7. During the winter, numbers of SY 1996 fish captured declined from 193 in December (sample 8) to 103 in March (sample 9). We caught fewer than 50 age-2 resident (nonsmolted) fish during the remainder of 1998 and fewer than 10 age-3 residents in 1999. Numbers of age-2 residents were similar for SY 1995 and SY 1996.

For SY 1996, the proportion of previously tagged fish captured during each sample increased

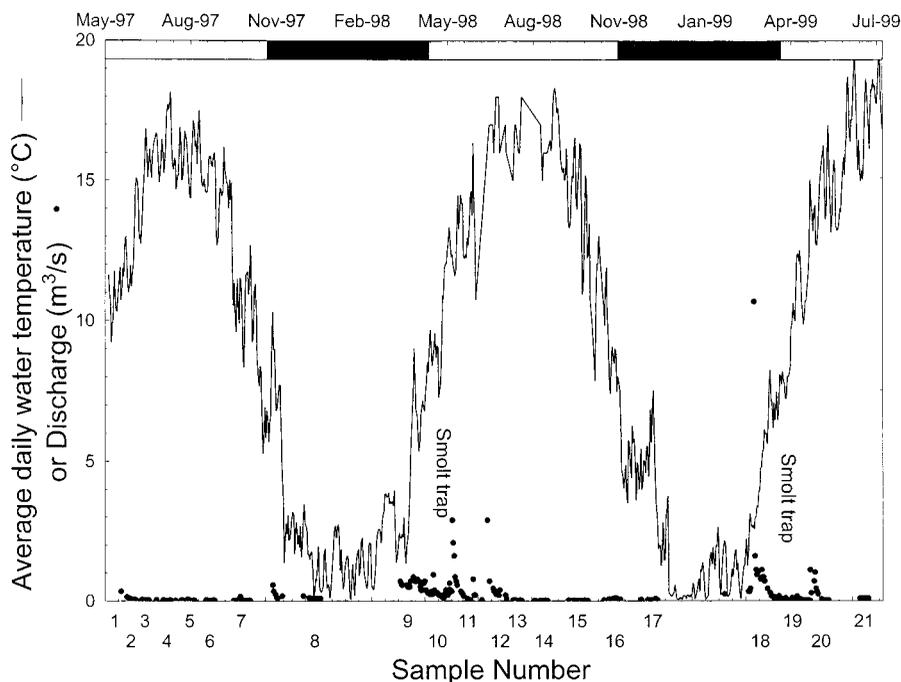


FIGURE 1.—Average daily water temperatures and discharge values for the West Brook, Massachusetts, during 1997–1999. Shaded horizontal bars represent temperatures lower than 8°C and open bars temperatures higher than 8°C.

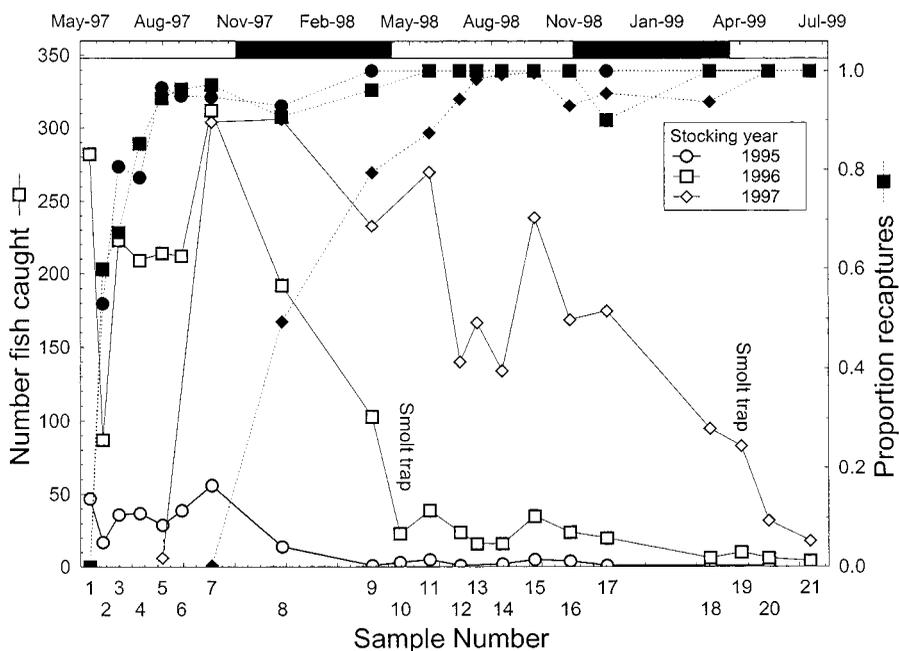


FIGURE 2.—Numbers of Atlantic salmon juveniles from stocking years 1995–1997 caught during each sample (open symbols; left scale) and the proportion of previously tagged fish caught in each sample (filled symbols; right scale) in the West Brook, Massachusetts, 1997–1999.

TABLE 2.—Numbers, ages, recapture status, and maturity status of Atlantic salmon juveniles captured in a smolt trap in the West Brook, Massachusetts, in 1998 and 1999.

Tagged	Previously mature	1998		1999	
		Age-3	Age-2	Age-3	Age-2
Yes	Yes	1	8	6	21
Yes	No	0	14	0	56
No	Unknown	2	27	4	70
Total		3	49	10	147

from 0.5 during sample 2 to 0.95 by sample 5 (Figure 2). The proportion of recaptures remained high following sample 5, with a slight dip to 0.9 in the winter samples (8 and 17). Patterns for both the numbers of fish caught and the proportion of recaptures for SY 1997 were similar to patterns for SY 1996 (Figure 2).

Smolt trap.—The numbers of fish caught in the smolt trap were lower in 1998 than in 1999 (Table 2), likely due to the differences in discharge during smolt trap operation (Figure 1). In 1998, the trap was inoperable for 24 h during a high-flow event (total of 52 fish captured during the smolt run). In 1999, discharge was low throughout the duration of the smolt run, resulting in relatively high capture rates (total of 157 fish captured). The per-

centages of previously tagged smolts captured in the smolt trap in 1998 (44%) and 1999 (53%) were similar. Smolts in both years were predominantly age 2 (94% in both years; Table 2).

Population Estimates

Study sections.—Patterns of population estimates were similar between SY 1996 and SY 1997 fish, but varied significantly across seasons and ages (Figure 3). Age-1 population numbers declined gradually over the summer but rapidly during the second winter. For both stocking years, about 180 age-2 fish were collected in the March sample prior to the smolt emigration (Figure 3). After smolts left the study area, approximately 50 age-2 residents were collected during most of the summer, and the catch of age-2 fish declined gradually over the course of the season. In contrast to the rapid decline in numbers in the second winter, SY 1997 fish numbers decreased only slightly in the first winter (Figure 3).

Known Mortalities

During the 19 samples, we recovered 59 dead fish. Of the known mortality, 36% was due to electroshocking, 27% was due to anesthetic overdose or tagging, 17% was due to being stepped on dur-

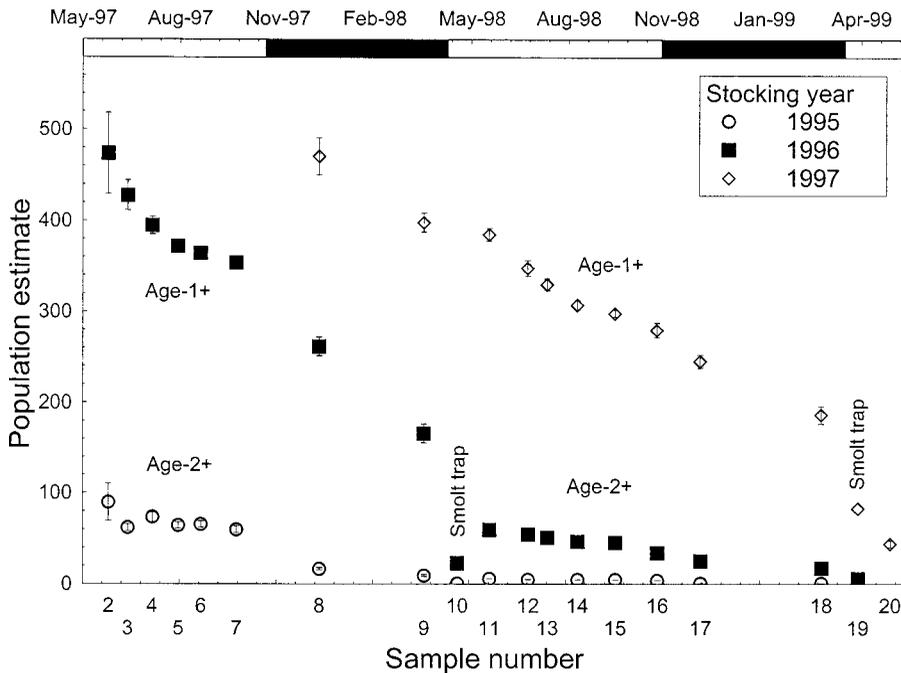


FIGURE 3.—Population estimates and standard deviations for Atlantic salmon juveniles from stocking years 1995–1997 in the West Brook, Massachusetts, during 1997–1999. The estimates are based on individual capture histories in a Jolly–Seber open-population mark–recapture model.

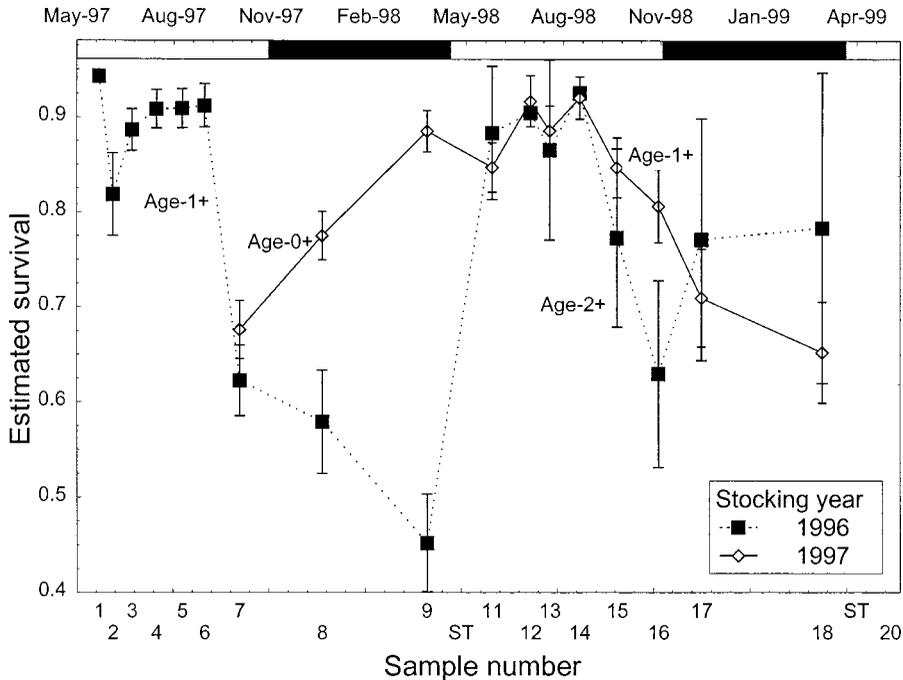


FIGURE 4.—Estimated survival from sample x to $x + 1$ for Atlantic salmon juveniles from stocking years 1996 and 1997 in the West Brook, Massachusetts (ST = smolt trap samples).

ing night seining, 10% was unknown, 7% was natural (found dead of unknown causes), and 3% was due to predation (tags or tagged fish found in the guts of piscivores). We did not search the stream bed for tags.

Survival

Age-1 summer (May to October) survival was 0.71 for both SY 1996 and SY 1997 (Figure 4; Table 3). Winter survival (0.56 in the first winter; 0.46 in the second winter) was lower than summer survival (0.71) for SY 1997. The very low second-winter survival (0.21) for SY 1996 was biased

TABLE 3.—Seasonal survival of juvenile Atlantic salmon stocked in the West Brook, Massachusetts, calculated based on the cumulative, multiplied sample-specific survivals from Figure 4.

Stocking year	Sampling series numbers	Age	Season	Cumulative survival
1996	1–7	1	Summer	0.71
	7–11	1–2	Winter	0.21
	11–16	2	Summer	0.65
	16–21	2–3	Winter	0.46
1997	7–11	0–1	Winter	0.56
	11–16	1	Summer	0.71
	16–21	1–2	Winter	0.46

downward by smolts missed by the trap during high flows. We obtained a rough estimate of over-winter survival of 0.49 for SY 1996 fish, assuming twofold as many smolts as residents (the pattern observed for SY 1997 fish). For SY 1997, the survival estimate from the March sample to the April–May smolt trap samples was 0.65 after accounting for residents. A reliable estimate of survival from March to the smolt trap samples for SY 1996 is not possible due to the missed smolts.

Differences between Mature and Immature Fish

Maximum maturation rates for age-1 fish equaled 44% for SY 1996 and 53% for SY 1997 (Figure 5). When equal sex ratios are assumed, application of the maximum rates to one-half the population produces maturation estimates of between 88% and 100% for age-1 males. Most (SY 1997) to all (SY 1998) of the age-2 and age-3 resident fish were observed to be mature (Figure 5).

Population estimates.—Population estimates varied dramatically with the variation in the maturity classification cutoff value for fish classified as immature and substantially for mature fish. Population estimates for immature fish were misleadingly high when a maturity classification cutoff value of zero

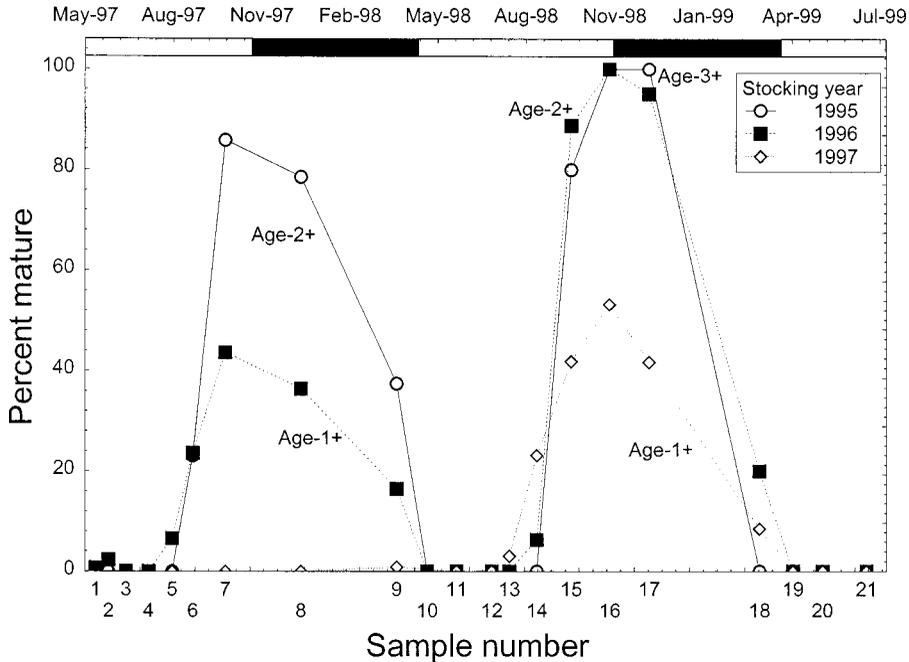


FIGURE 5.—Percentages of mature juvenile Atlantic salmon (those that expressed milt) collected during each sample in 1997–1999 in the West Brook, Massachusetts, for fish from stocking years 1995–1997.

was used because all fish that failed to express milt during sampling were classified as immature. In this case, the immature classification includes many fish sampled only once or twice but that later matured as parr, resulting in artificially high population estimates for immature fish. A balance between correct classification and inclusion of a large proportion of the fish was achieved with a maturity classification cutoff value of 0.4 (higher values resulted in at least twofold reduction in population estimates). The cutoff value was used for all subsequent population and survival estimate comparisons between mature and immature fish. We caution that population estimates based on the maturity classification cutoff value should only be used to compare relative abundances of mature and immature fish because the estimates exclude some fish that were caught but not confidently classified and because they also only include mature and immature fish that survived to the time of milt expression (Figure 5).

The relative abundances of mature and immature fish differed between SY 1996 and SY 1997 (Figure 6). Immature SY 1996 fish were slightly more abundant than mature fish (1.25 times higher abundance) during the age-1 summer, whereas immature and mature SY 1997 fish were equally abundant during their age-1 summer. In the age-1

fall, the relative abundance of immature fish increased markedly (1997) or slightly (1998) compared with previous abundances (Figure 6). In the spring before smolting, numbers of previously mature and immature fish were equal (samples 9 and 18; Figure 6). Numbers of immature age-2 fish in the smolt trap were 1.7 (1998) or 2.7 (1999) times higher than numbers of previously mature fish in the smolt trap. All recaptured age-3 smolts were previously mature (Table 2).

Survival.—Survival rates of mature and immature fish were similar during late spring and summer but differed during fall and winter for both stocking years (Table 4). For SY 1996, the survival of mature fish was 72% of the survival for immature fish from September to December (samples 7–8) but 77% higher than the survival of immature fish from December to March (samples 8–9). A similar pattern of lower fall and higher winter survival for mature fish existed also for SY 1997 fish (Table 4). The disparity in fall survival rates may be partially explained by differences in movement of mature fish in the fall. The percentage of previously tagged mature fish captured during each sample dropped from about 100% to 93% (SY 1996) or 87% (SY 1997) during the fall only, whereas immature fish displayed no corresponding decrease (Table 4). The decrease in survival and

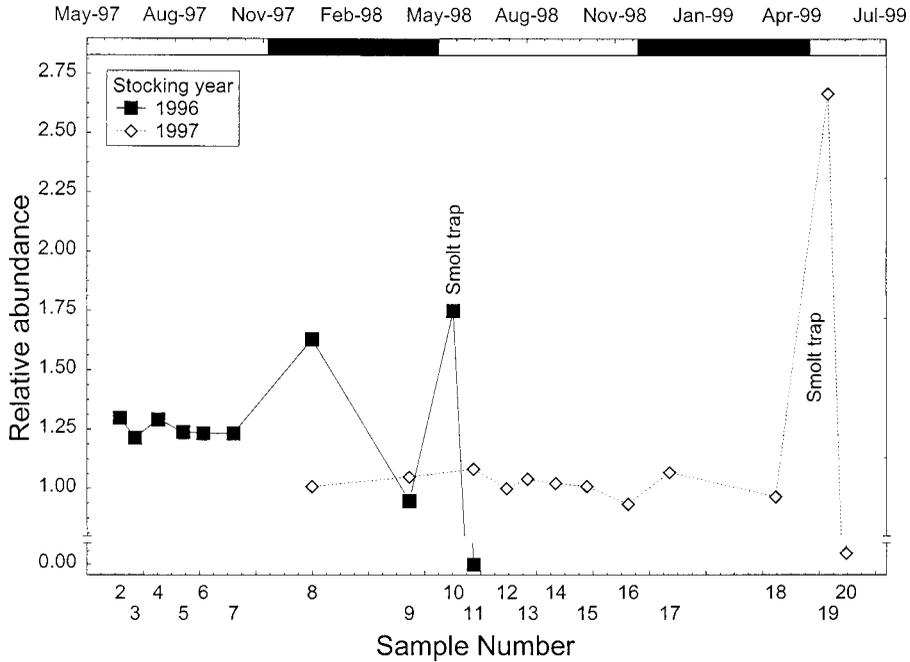


FIGURE 6.—Relative abundances of mature and immature juvenile Atlantic salmon (number immature/number mature) for the 1996 and 1997 stocking years in the West Brook, Massachusetts. Population estimates were calculated on the basis of individuals with maturity classification values of 0.4 or greater.

proportion of recaptures (fall movement) of mature fish was also observed for age-2 fish (SY 1996) in sample 17 (Table 4).

Smolt trap.—For SY 1997, based on the maturity classification cutoff value of 0.4 (which reduced absolute population estimates by about 20%), we estimated 76 previously mature fish and 73 immature fish in the March sample (18) preceding the smolt trap sample (19). Scaling these

values to the total estimate of 187 fish in sample 18 (Figure 3) yields 95 previously mature and 92 immature fish. We recaptured 59 previously mature and 58 immature fish in samples 19 and 20, which translates to survival rates of 62% for mature fish and 63% for immature fish between sample 18 in March and samples 19–20. Of the fish that survived, 36% of the previously mature fish and 97% of the immature fish smolted. Two-thirds of the

TABLE 4.—Comparison of the proportions of previously tagged fish and survival estimates (s to $s + 1$; SEs in parentheses) between immature and mature Atlantic salmon (juveniles) from stocking years 1996 and 1997 in West Brook, Massachusetts. Descriptions of sample numbers are given in Table 1.

Stocking year	Sample number	Age	Proportion tagged previously		Survival	
			Immature	Mature	Immature	Mature
1996	6	1	0.96	0.94	1.00 (0.02)	1.00 (0.03)
	7	1	0.97	0.98	0.73 (0.05)	0.52 (0.05)
	8	1	1.00	0.93	0.52 (0.09)	0.92 (0.06)
	9	2	1.00	1.00		
	15	2		1.00		0.81 (0.09)
	16	2		1.00		0.68 (0.10)
	17	2		0.92		0.82 (0.13)
	18	2		1.00		0.83 (0.16)
1997	15	1	0.99	1.00	0.90 (0.04)	0.84 (0.05)
	16	1	1.00	0.87	0.91 (0.04)	0.75 (0.05)
	17	1	0.99	0.89	0.68 (0.07)	0.79 (0.06)
	18	2	1.00	1.00	0.64 (0.07)	0.81 (0.08)

TABLE 5.—Gill Na⁺, K⁺ ATPase activity ($\mu\text{mol ADP/mg protein/h}$) for mature and immature Atlantic salmon juveniles from stocking years 1996 and 1997 in the West Brook, Massachusetts. Sample dates are given in Table 1.

Stocking year	Sample number	Maturity			
		Immature		Mature	
		Mean (SD)	<i>n</i>	Mean (SD)	<i>n</i>
1996	9	3.83 (0.99)	44	2.27 (0.74)	42
	10 (smolt trap)	8.00 (1.72)	13	8.22 (1.88)	8
	11			1.05 (0.20)	6
	18			1.99 (1.02)	10
	19 (smolt trap)			7.60 (2.01)	6
	20			1.23 (0.48)	6
1997	18	3.38 (2.08)	44	1.53 (0.81)	43
	19 (smolt trap)	9.21 (1.58)	43	8.39 (1.12)	20
	20	1.26 (0.04)	2	1.40 (0.32)	23

previously mature survivors did not smolt and were captured as residents. Thus, survival did not differ between previously mature and immature fish, but the probability of smolting of mature fish was one-third that of immature fish. Overall, the probability of smolting and surviving from March to the smolt trap samples was 22% for previously mature fish and 61% for immature fish.

Gill Na⁺, K⁺ ATPase Activity

Average gill Na⁺, K⁺ ATPase activity was highest (~8 units) for fish captured in the smolt trap, low (1 unit) with a narrow range for fish captured as residents, and higher (1–4 units) with a wide range for fish captured in the samples preceding the smolt trap samples (Table 5; Figure 7). For both stocking years, average gill Na⁺, K⁺ ATPase activity values were significantly lower ($P = 0.015$ for SY 1996; $P < 0.0001$ for SY 1997) in the sample preceding the smolt trap samples for fish that were not later captured in the smolt trap (2.94 ± 1.15 units, $N = 68$ for SY 1996; 1.72 ± 1.03 units, $N = 54$ for SY 1997) than for fish that were (3.82 ± 1.04 units, $N = 15$ for SY 1996; 3.68 ± 2.19 units, $N = 33$ for SY 1997).

Some of the variation in gill Na⁺, K⁺ ATPase activity values between smolts and nonsmolts in the samples preceding the smolt trap samples could be explained further by differences between previously mature and immature fish (Table 6). In both stocking years, gill Na⁺, K⁺ ATPase activity values were significantly higher ($P < 0.00001$ for SY 1996; $P = 0.0012$ for SY 1997) for immature fish than for previously mature fish, but were also significantly higher ($P = 0.0094$ for SY 1996; $P = 0.0006$ for SY 1997) for smolts than for nonsmolts (Table 6). Overall, we found the lowest gill Na⁺, K⁺ ATPase activity values for mature nonsmolts, the highest values for immature smolts, and

intermediate values for immature nonsmolts and previously mature smolts. The interaction between maturity and smolt status was nonsignificant for SY 1997 ($P = 0.43$; $df = 1, 82$), and it was marginally significant for SY 1996 ($P = 0.048$; $df = 1, 78$). In contrast to the differences among life history strategies in the samples preceding the smolt trap samples, gill Na⁺, K⁺ ATPase activity did not differ between previously mature and immature fish captured in the smolt trap for either stocking year ($P = 0.39$ for SY 1996; $P = 0.059$ for SY 1997; Table 5).

Discussion

Individual tagging, combined with multiple recaptures, allowed us to address the five issues listed in the introduction. We found that (1) estimated survival was lower in the winter than in the summer, (2) age-0 winter survival was greater than age-1 winter survival, (3) estimated survival was lower in fall and higher in winter for mature fish than for immature fish, although differences in fall may have been partially due to higher movement frequency of mature fish, (4) two-thirds (1998) or three-fourths (1999) of the fish in the smolt trap were immature, and virtually all of the age-2 residents were previously mature, and (5) survival did not differ between mature and immature fish, but previously mature fish were one-third as likely to smolt as immature fish.

Seasonal Survival

As in other analyses of winter survival (Cunjak et al. 1998), our results indicated that losses were important during winter, but we also found significant losses during summer. As a percentage of population estimates taken early in the fish's second summer (sample 11 for SY 1997), losses were 27% over the summer (samples 11–16) and 42%

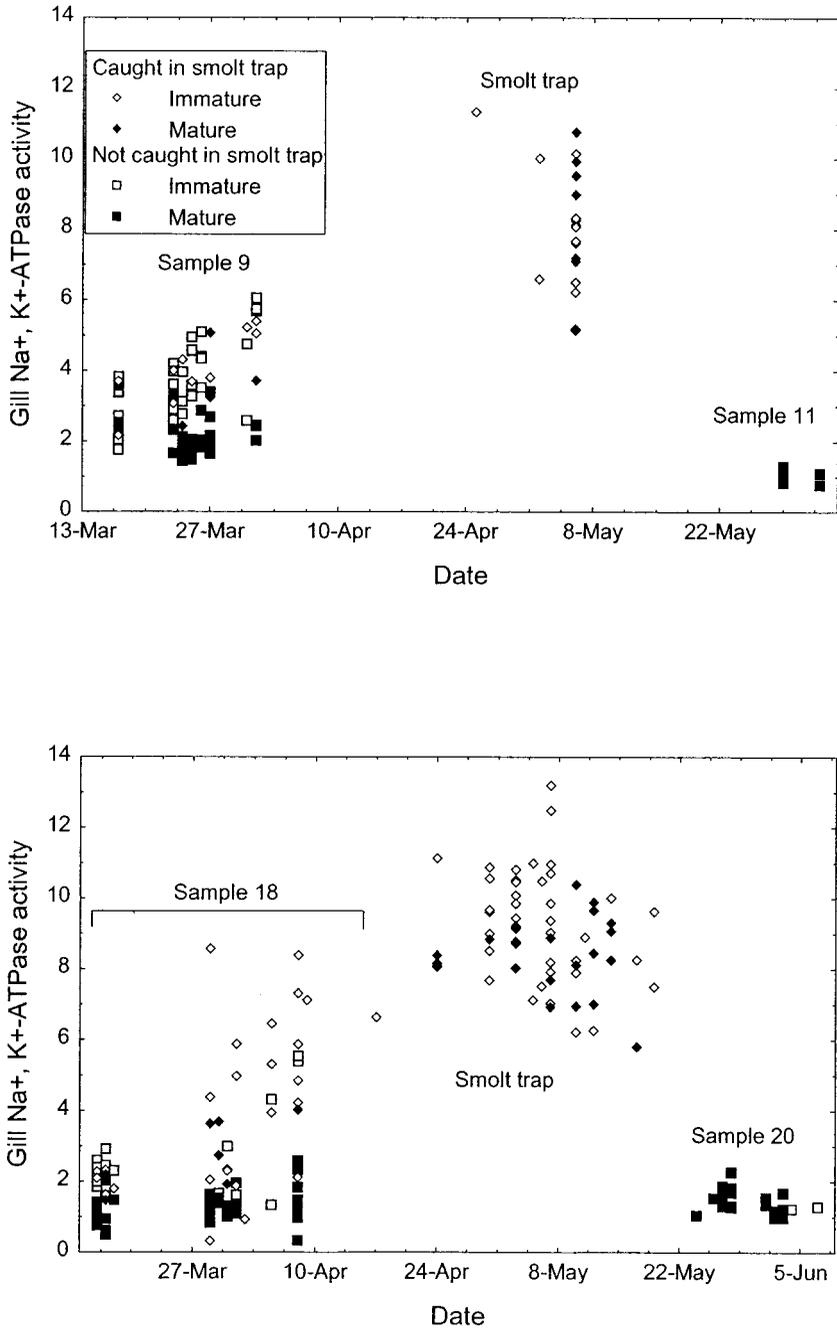


FIGURE 7.—Gill Na⁺, K⁺ ATPase activity ($\mu\text{mol ADP}/\text{mg protein}/\text{h}$) for juvenile Atlantic salmon collected in the smolt trap samples and the samples preceding and following the smolt trap samples (stocking year 1996, top; stocking year 1997, bottom). For all three sets of samples, fish are categorized as smolt trap captures or residents and as immature or mature (maturity classification value ≥ 0.4).

TABLE 6.—Gill Na⁺, K⁺ ATPase activity ($\mu\text{mol ADP/mg protein/h}$) of West Brook, Massachusetts, Atlantic salmon juveniles captured in the samples preceding the smolt trap samples. Data for mature and immature smolts and nonsmolts are provided.

Stocking year	Smolts				Nonsmolts			
	Immature		Mature		Immature		Mature	
	Mean (SD)	<i>n</i>						
1996	4.04 (1.00)	10	3.38 (1.10)	5	3.77 (0.99)	34	2.12 (0.57)	34
1997	3.91 (2.37)	26	2.81 (0.99)	7	2.61 (1.27)	18	1.28 (0.47)	36

over the second winter (samples 16–20, including smolts). Summer results were similar for SY 1996 (25%; samples 2–7), but were difficult to estimate with certainty for the winter due to incomplete smolt trapping. Egglisshaw and Shackley (1977) also found continuous declines in salmon abundance throughout freshwater residence. Highest loss rates were detected during the age-0 summer and age-1 spring. Second-winter estimates in Egglisshaw and Shackley (1977) were not considered reliable due to the small numbers of the older fish captured in the short study sections (~30 m). Seasonal survival differences in our study stream may be difficult to compare with many other streams, because the West Brook is near the southern edge of the range of Atlantic salmon. Winters are shorter than in more northerly streams, with only short periods of average daily water temperatures at 0°C and many days of 2–3°C temperatures (see Figure 1). Though occasionally covered with ice, the stream rarely develops the anchor ice responsible for limiting habitat availability (Cunjak et al. 1998; Whalen et al. 1999). In addition, although summer water temperatures were generally 16–18°C, similar to summer temperatures in more northerly streams (Elliott et al. 1998), summer water flows were very low in the West Brook. Low flows could have resulted in habitat reductions and increased fish stress, possibly leading to higher mortality or emigration rates. Our estimates of less than twofold higher loss rates in the winter than in the summer should be viewed in the context of the study system, which may pose different seasonal stressors than other systems.

Age-Class Differences in Survival

Winter survival was somewhat higher for age-0 fish (0.56) than for age-1 fish (0.46) from SY 1997. Yearly average survival (July to July) for age-0 to age-1 Atlantic salmon was identical to that for age-1 to age-2 fish (0.33) in a multi-year study in Catamaran Brook (Cunjak and Therrien 1998). In a Vermont river stocked at a low density,

McMenemy (1995) also found similar survival estimates for parr in their first (0.42) and second (0.43) years. The lower or equal survival of older, larger parr is intriguing, because larger fish within an age-class tend to survive better than smaller ones (Pickering and Pottinger 1988). The size-selective effect of the larger differences in size between age-classes appears to operate in the opposite direction from the more subtle size differences within an age-class. Older, larger fish may be habitat limited over the winter, and parr tend to seek shelter under stones during the day in winter (Cunjak et al. 1998). If larger fish have trouble finding suitable winter sheltering locations, they could be exposed to a greater risk of predation (Cunjak 1996) or higher levels of competition for space (Cunjak and Randall 1993).

Aside from high mortality, lower winter survival of large parr can also be explained by higher movement rates out of study areas. To influence population estimates of unmarked fish, a net movement of fish out of study areas would be necessary. Movement tends to increase in winter (Cunjak and Randall 1993), but random, unbiased movement into and out of study areas alone would not affect population estimates. Based on the percentage of captured fish that were tagged, we also found evidence of increased movement of fish in the late fall and winter. For SY 1997, virtually all of the fish captured in the summer of 1998 (sample 15) had been previously tagged, but the percentage dropped to about 94% for the next three samples (16–18; Figure 2), indicating movement of untagged fish into our study site. Almost all of the movements were made by mature fish (Table 4; Figure 6; most untagged fish in the study site were mature) and movement continued throughout the winter. Movement of fish was also biased downstream: for samples 15, 17, 18, and 20, 55% of the fish captured within 140 m downstream of our study site had been tagged in previous samples, but only 4% of the fish captured upstream of the site had been tagged. While the percentage of

tagged fish below our study site was fairly high, indicating a downstream bias to fish movement, the actual loss of fish, expressed as a percentage of fish captured in the study site at each sample, was quite low (average was 4%). Thus, movement appeared nonrandom, but its actual impact on population estimates on a small scale (<1 km) was probably limited.

Survival Differences between Mature and Immature Fish

Abundances of previously mature versus immature fish were equal in the March samples preceding the smolt trap samples in both years. Assuming equal sex ratios and male parr maturation rates of about 100%, the lack of difference in numbers between mature and immature fish indicates that mortality did not differ between the two groups before March of the fishes' second year. We also found no difference in the probability of survival between previously mature and immature fish from March to the April–May smolt trap samples, but only one-third of the mature survivors smolted, whereas virtually all of the immature survivors smolted. Whalen et al. (2000) also found that mature fish in Vermont rivers were equally as likely to survive as immature fish but were only one-third as likely to smolt. These results are in contrast to results of a model (Myers 1984), which estimated that lower numbers of mature smolts were due to a combination of reduced survival and smolting rates of mature fish. Whalen et al. (2000) suggested that the differences in overwinter survival of mature parr might be due to regional differences in the severity of winter or to the absence of adult sea-run males, which can harm or kill smaller mature parr during spawning (Hutchings and Myers 1987). While regional differences in winter severity could clearly affect winter mortality of mature parr, our estimates of the probability of smolting for mature parr do not include the spawning period, so it is unlikely that the lack of adult-induced mortality would influence our mortality estimates. If we extend our analysis to include the late fall, our interpretation of the relative probabilities of survival and maturation between mature and immature fish would not change, because numbers of mature and immature fish were similar throughout the summer and fall.

Numbers of Mature and Immature Smolts and Residents

Although male parr maturation did not influence survival in our study system, it notably affected

age at smoltification. Almost two-thirds of the surviving age-2 fish did not smolt and remained in the stream. In 1997 and 1998, about 70 age-2 fish resided in the study site; virtually all were previously mature. The numbers of age-2 residents declined gradually over the summer and were low in the March samples (8 and 18) preceding the smolt trap samples. We only captured 10 age-3 smolts in 1999 (6% of total, 6 were tagged). If only 6 of the 70 age-2 fish smolted at age 3, this could indicate a high survival cost of parr maturation. However, because we cannot separate emigration from mortality, we do not know which factor is responsible for the slow decline in numbers of age-2 fish. A total of 55 age-2 fish was caught in the summer and fall of 1998, of which 3 fish were untagged, suggesting low immigration into our study area and potentially low emigration as well. Age-2 salmon in other systems can migrate in the fall (Youngson et al. 1994), but the extent of an age-2 fall migration in the West Brook is unknown, as we did not monitor migration during fall.

Sampling Effects

Use of multiple sets of samples per year allowed us to discern fine-scale patterns of abundance and survival, but the relatively large number of samples could have negatively affected the study population. Though we were unable to directly determine the effects of multiple samples, we did calculate whether the number of times a fish was sampled influenced its probability of survival to later samples. The December samples (8 and 17) potentially included fish that were collected many times in prior sampling. After December, significant mortality was observed. However, we found no difference in sampling frequency between fish that survived and those that did not (*t*-tests: $P = 0.31$ for SY 1996; $P = 0.98$ for SY 1997). The average number of times fish were sampled was slightly lower (5.0) for SY 1996 fish than for SY 1997 fish (6.5). In addition, laboratory studies (Grader 2000) indicated that Atlantic salmon juveniles, electroshocked multiple times at 400-V DC, suffered no increases in mortality and were not different in size compared to controls. Although our study may have affected behavior and survival of West Brook Atlantic salmon, it appears that the impacts were minimal.

Other negative factors associated with multiple sets of samples include the effort required and the potential impacts on habitat and movement of fish. Each sample required a field crew of four and en-

compassed 7–14 d, depending on the sampling technique and the number of fish caught. By stepping in the stream, especially during night seining, we may have moved rocks and dislodged invertebrates. The extent of impacts on habitat and fish caused by personnel walking in the stream is unknown. Fish sampling also can elicit fish movement. Many of the recaptured fish were caught in the same location repeatedly, indicating minimal movement between samples (Juanes et al. 2000; B. H. Letcher and others, unpublished data), but we occasionally (<2% of all fish data, in a count of multiple captures within samples) did recapture fish more than once during a sample. Fish captured multiple times were captured further upstream in sections that were sampled later in the sample. Thus, although we could have caused extensive movement of fish, the percentage of fish that moved within a month was apparently small.

Given the trade-offs between the high resolution of seasonal data collected and the potential impacts of multiple samples over time, it is useful to consider whether the large number of samples is necessary to adequately characterize the dynamics of the system. We could either reduce the number of samples or the number of sections in the study area. Reducing the number of samples could erode the fineness of scale of seasonal abundance and survival estimates, and it could also influence the mean and variance of the subset of population estimates. When we reanalyzed the population estimates for SY 1996 and SY 1997 including only the even-numbered samples or odd-numbered samples, the abundance estimates were, on average, 91.7% of original estimates. In some cases (e.g., SY 1996 odd-numbered samples), estimates yielded by the reduced number of samples were very similar (99%) to estimates produced by the original sets of samples, and in others (SY 1997 even-numbered samples) they were substantially lower (84%). In all cases, the general abundance patterns were similar in the reduced and original data sets, though some critical samples (December or March) were excluded. Also, variance estimates for each sample were higher (roughly twofold in both stocking years) for the reduced number of samples as compared with original estimates. Therefore, reductions in the number of samples would result in lower abundance estimates with higher variance but, when necessary, would still provide reasonable estimates of abundance and survival patterns. Although not addressed here, the data lost due to reduction in the number of samples would be greater for seasonal growth rate esti-

mates from individuals caught in consecutive samples than for abundance estimates.

Reduction in the number of sections may also limit the sampling impact on the population of fish in a stream because fish outside the smaller study area would not be sampled. We explored the effect of a smaller study area on the mean and variance of abundance estimates by calculating these values for the central half of the study area. We doubled the abundance estimates for each set of samples to compare estimates between the full-sized and reduced study areas. On average, the abundance estimates for the reduced study area were 29% (SY 1996) and 21% (SY 1997) higher than the original estimates, although the overall abundance patterns were similar. Average standard error estimates were similar between the original and reduced study areas. To explore the effects of a reduced number of sections in a way that was more sensitive to small-scale movements, we calculated overall population estimates based on alternating sections. Incorporating only the odd-numbered sections into the data set resulted in population estimates that were 37% (SY 1996) or 39% (SY 1997) higher than the original estimates. In this case, variances were over twofold higher in the reduced scenario. Fragmentation of the study area into alternating sections appears to overestimate abundance and carries the additional drawback of higher variance, whereas limiting the study area to the central portion also overestimates abundance but without the increased variance.

In conducting this study on fine spatial and temporal scales, we found that survival was lower in the winter than in the summer, was higher for younger fish, and was similar between mature and immature fish. Fewer previously mature fish than immature fish smolted at age-2; this was due to the delay in smolting of previously mature fish rather than a lower probability of survival. Also, almost all age-2 non-smolts were previously mature, but very few of these fish were captured as age-3 smolts. The adaptive value of maturing as a parr (Myers 1986) depends on parr mating success and on the probability of also returning and mating as a sea-run adult. The unknown fate of previously mature age-2 non-smolts, whose numbers decreased in our system from 50–100 in early summer after the smolt run to less than 20 in the winter, prompts the question: are these fish emigrating from the system in the fall (Buck and Youngson 1982; Youngson et al. 1983), or are they dying? Future applications of PIT tag antennas (Armstrong et al. 1996; Castro-Santos et al. 1996) to

detect movement of fish past fixed locations may help resolve this important question.

Acknowledgments

We thank the many people who helped sample the study area, including Chris DeMarco, Ryan Webb, Chad Seewagen, Fernando Bairos, Nathan Henderson, Marco Nicoli, Matt O'Donnell, Melissa Grader, Chris Baxter, and particularly Todd Dubreuil and Tim Terrick. The U.S. Forest Service, Northeast Forest Experimental Research Station provided partial funding. We also thank the U.S. Fish and Wildlife Service, White River National Fish Hatchery, for fry used in stocking, the State of Massachusetts for help coordinating the stocking, and Steve McCormick and members of his laboratory for help analyzing the gill Na⁺, K⁺ ATPase activity samples. We thank Andrew Hendry, Stephanie Carlson, Gregg Horton, and Keith Nislow for reading earlier versions of the manuscript. Bob Duda, Ed Mason, and Joe Zasky graciously provided access to their land.

References

- Anderson, T. C., and B. P. McDonald. 1978. A portable weir for counting migrating fishes in rivers. Fisheries and Marine Service Technical Report 733:1–13.
- Armstrong, J. D., V. A. Braithwaite, and P. Rycroft. 1996. A flatbed passive integrated transponder antenna array for monitoring behaviour of Atlantic salmon parr and other fish. *Journal of Fish Biology* 48:539–541.
- Arnason, A. N., and C. J. Schwarz. 1995. POPAN-4: enhancements to a system for the analysis of mark-recapture data from open populations. *Journal of Applied Statistics* 22:785–800.
- Berglund, I., M. Schmitz, and H. Lundqvist. 1992. Seawater adaptability in Baltic salmon (*Salmo salar*): a bimodal smoltification pattern in previously mature males. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1097–1106.
- Buck, R. J. G., and A. F. Youngson. 1982. The downstream migration of precociously mature Atlantic salmon, *Salmo salar* L. parr in autumn, and its relation to the spawning migration of mature adult fish. *Journal of Fish Biology* 20:279–288.
- Castro-Santos, T., A. Haro, and S. Walk. 1996. A passive integrated transponder (PIT) tag system for monitoring fishways. *Fisheries Research* 28:253–261.
- Chadwick, E. M. P. 1982. Stock-recruitment relationship for Atlantic salmon (*Salmo salar*) in Newfoundland rivers. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1496–1501.
- Crozier, W. W., and G. J. A. Kennedy. 1995. Application of a fry (0+) abundance index, based on semi-quantitative electrofishing, to predict Atlantic salmon smolt runs in the River Bush, Northern Ireland. *Journal of Fish Biology* 47:107–114.
- Cunjak, R. A. 1996. Winter habitat of selected stream fishes, and potential impacts from land-use activity. *Canadian Journal of Fisheries and Aquatic Sciences* 53:267–282.
- Cunjak, R. A., T. D. Prowse, and D. L. Parrish. 1998. Atlantic salmon (*Salmo salar*) in winter: “the season of parr discontent”? *Canadian Journal of Fisheries and Aquatic Sciences* 55(Supplement 1):161–180.
- Cunjak, R. A., and R. G. Randall. 1993. In-stream movements of young Atlantic salmon (*Salmo salar*) during winter and early spring. *Canadian Special Publication of Fisheries and Aquatic Sciences* 118:43–51.
- Cunjak, R. A., and J. Therrien. 1998. Inter-stage survival of wild juvenile Atlantic salmon, *Salmo salar* L. *Fisheries Management and Ecology* 5:209–223.
- Dempson, J. B., and D. E. Stansbury. 1991. Using partial counting fences and a two-sample stratified design for mark-recapture estimation of an Atlantic salmon smolt population. *North American Journal of Fisheries Management* 11:27–37.
- Egglishaw, H. J., and P. E. Shackley. 1977. Growth, survival, and production of juvenile salmon and trout in a Scottish stream, 1966–75. *Journal of Fish Biology* 11:647–672.
- Elliott, S. R., T. A. Coe, J. M. Helfield, and R. J. Naiman. 1998. Spatial variation in environmental characteristics of Atlantic salmon (*Salmo salar*) rivers. *Canadian Journal of Fisheries and Aquatic Sciences* 55(Supplement 1):267–280.
- Fleming, I. A. 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with consequences for other salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 55(Supplement 1):59–76.
- Gephard, S., P. Moran, and E. Garcia-Vazquez. 2000. Evidence of successful natural reproduction between brown trout and mature male Atlantic salmon. *Transactions of the American Fisheries Society* 129:301–306.
- Grader, M. S. 2000. Studies investigating the factors influencing the diet and growth of juvenile Atlantic salmon. Master's thesis. University of Massachusetts, Amherst.
- Gries, G., and B. H. Letcher. 2002. A night seining technique for sampling juvenile Atlantic salmon in streams. *North American Journal of Fisheries Management* 22:595–601.
- Gries, G., K. G. Whalen, F. Juanes, and D. L. Parrish. 1997. Nocturnal activity of juvenile Atlantic salmon (*Salmo salar*) in late summer: evidence of diel activity partitioning. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1408–1413.
- Hansen, L. P., B. Jonsson, R. I. G. Morgan, and J. E. Thorpe. 1989. Influence of parr maturity on emigration of smolting Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 46:410–415.
- Hutchings, J. A., and R. A. Myers. 1987. Escalation of an asymmetric contest: mortality resulting from mate competition in Atlantic salmon, *Salmo salar*. *Canadian Journal of Zoology* 65:766–768.

- Jonsson, N., B. Jonsson, and L. P. Hansen. 1998. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* 67:751–762.
- Juanes, F., B. H. Letcher, and G. Gries. 2000. Ecology of stream fish: insights gained from an individual-based approach to juvenile Atlantic salmon. *Ecology of Freshwater Fish* 9:65–73.
- Keeley, E. R., and J. W. Grant. A. 1995. Allometric and environmental correlates of territory size in juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 52:186–196.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lundqvist, H., W. C. Clarke, and H. Johansson. 1988. The influence of precocious sexual maturation on survival to adulthood of river stocked Baltic salmon, *Salmo salar*, smolts. *Holarctic Ecology* 11:60–69.
- McCormick, S. D. 1993. Methods for nonlethal gill biopsy and measurement of Na⁺, K⁺ ATPase activity. *Canadian Journal of Fisheries and Aquatic Sciences* 50:656–658.
- McMenemy, J. R. 1995. Survival of Atlantic salmon fry stocked at low density in West River, Vermont. *North American Journal of Fisheries Management* 15:366–374.
- Mitans, A. R. 1973. Dwarf males and the sex structure of a Baltic salmon (*Salmo salar*) population. *Journal of Ichthyology* 13:192–197.
- Myers, R. A. 1984. Demographic consequences of precocious maturation of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 41:1349–1353.
- Myers, R. A. 1986. Game theory and the evolution of Atlantic salmon (*Salmo salar*) age at maturation. *Canadian Special Publication of Fisheries and Aquatic Sciences* 89:53–61.
- Pickering, A. D., and T. G. Pottinger. 1988. Lymphocytopenia and the overwinter survival of Atlantic salmon parr, *Salmo salar* L. *Journal of Fish Biology* 32:689–697.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture–recapture experiments. *Wildlife Monographs* 107:1–97.
- Rimmer, D. M., U. Paim, and R. L. Saunders. 1983. Autumnal habitat shift of juvenile Atlantic salmon (*Salmo salar*) in a small river. *Canadian Journal of Fisheries and Aquatic Sciences* 40:671–680.
- Saunders, R. L., E. B. Henderson, and B. D. Glebe. 1982. Precocious sexual maturation and smoltification in male Atlantic salmon (*Salmo salar*). *Aquaculture* 28:211–229.
- Thorpe, J. E. 1987. Smolting versus residency: developmental conflict in salmonids. Pages 244–252 in M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson, and J. E. Cooper, editors. *Common strategies of anadromous and catadromous fishes*. American Fisheries Society, Symposium 1, Bethesda, Maryland.
- Whalen, K. G., and D. L. Parrish. 1999. Effect of maturation on parr growth and smolt recruitment of Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 56:79–86.
- Whalen, K. G., D. L. Parrish, and M. E. Mather. 1999. Effect of ice formation on selection of habitats and winter distribution of post-young-of-the-year Atlantic salmon parr. *Canadian Journal of Fisheries and Aquatic Sciences* 56:87–96.
- Whalen, K. G., D. L. Parrish, M. E. Mather, and J. R. McMenemy. 2000. Cross-tributary analysis of parr-to-smolt recruitment of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 57:1607–1616.
- Youngson, A. F., R. J. G. Buck, T. H. Simpson, and D. W. Hay. 1983. The autumn and spring emigrations of juvenile Atlantic salmon, *Salmo salar* L., from the Girnock Burn, Aberdeenshire, Scotland: environmental release of migration. *Journal of Fish Biology* 23:625–639.
- Youngson, A. F., W. C. Jordan, and D. W. Hay. 1994. Homing of Atlantic salmon (*Salmo salar* L.) to a tributary spawning stream in a major river catchment. *Aquaculture* 121:259–267.