FINAL REPORT

Assessment of watershed scale habitat features on the survival of juvenile Atlantic salmon

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Summary

Atlantic salmon (*Salmo salar*) populations in the Gulf of Maine Distinct Population segment remain at critically low levels despite ongoing recovery efforts. Hatchery supplementation, of primarily unfed fry, is one of the major recovery tools. Survival of stocked fry varies greatly not only among rivers, but also within rivers as biotic and abiotic factors change along a river gradient. In order for population recovery to be successful, improved understanding of these factors, their interactions, and how they vary spatially is needed.

This study on the Sheepscot River was designed to provide managers with information to adaptively manage fry stocking in the watershed. The objectives were to use genetically marked fry to assess the effects of macro-scale habitat features and non-salmonid fish species abundance upon inter-stage survival and smolt production from various regions of the Sheepscot River.

The Sheepscot River was divided into five regions and groups of fry from known hatchery matings were stocked into a single region in 2005. Survival from fry to age 0+ parr, and survival from age 1+ parr were assessed in August and September of 2005 and 2006, respectively, through backpack electrofishing multiple sites in each region. Macro-scale habitat variables (cumulative drainage area, gradient, land use, etc.) and abundance of non-salmonid fishes were used to model survival. Rotary screw traps below Head Tide Dam were used to capture outmigrating smolts in the spring of 2007. Genetic samples were taken from all juvenile Atlantic salmon at all life stages captured, and genetic parentage analysis was used to identify the river region where individuals were originally stocked as fry.

This study identified important habitat features influencing juvenile salmon survival, and locations within the watershed which are most important to overall smolt production. Parentage analysis assigned 60% of age 0+ and age 1+ parr, and 50% of smolts to known hatchery matings. Parentage analysis also showed some movement of parr between regions in the river. Sites occurring further upstream in the watershed, with smaller cumulative drainage areas, had the highest survival of fry and age 1+ parr. This relationship with cumulative drainage is likely related to temperature as areas with smaller cumulative drainage areas tended to have lower summertime temperatures. Parentage analysis indicated the majority of outmigrating smolts were originally stocked as fry in the West Branch Sheepscot River and there was a strong correlation between total population estimates of age 1+ parr within regions of the river and relative abundance of smolts coming from those regions.

These findings suggest the greatest constraint to smolt production in the Sheepscot River is survival from fry to age 0+ parr and illustrate the importance of regions of small cumulative drainage area to smolt production. Focusing management efforts on increasing survival from fry to age 0+ parr and concentrating these efforts in regions of small drainage area will likely maximize smolt production.

Introduction

Atlantic salmon *(Salmo salar*) populations are currently at all time low levels throughout New England, with some Atlantic salmon populations in Maine were listed as an endangered distinct population segment in November 2000 (65 FR 69459). The listed entity was the Gulf of Maine Distinct Population Segment (GOM DPS). The estimated total return of adult Atlantic salmon to core rivers within the geographic range of the GOM DPS dropped to 33 individuals in 2002. On one of these rivers, the Sheepscot River, returns were estimated at only eight individuals (USASAC 2003). In addition to commercial over fishing, habitat degradation from the construction of dams, agriculture, forestry, and overall human exploitation of natural resources have added to the decline in salmon abundance.

Current recovery efforts rely heavily on stocking juvenile Atlantic salmon, with the majority being stocked as fry. The Sheepscot River, the focus of this study, has received an average of 215,000 fry (range: 64,000 – 323,000) annually since 1996. Fry are stocked throughout the watershed in suitable rearing habitat at a targeted density of 100 fry /m^2 (Fay et al. 2006). However, annual fall population estimates indicate highly variable survival for fry to the parr stage spatially (Paul Chrisman, Department of Marine Resources, personal communication). Because there had been virtually no survival of fry in the lower region of the Sheepscot River (downstream of river km 18), the region has received supplemental stocking of an average of 16,000 age 0+ parr in the fall of 2004 to 2006. The addition of age 0+ parr to the stocking of fry throughout the river is intended to compensate for low fry survival and increase smolt production in the lower river.

Survival of Atlantic salmon fry depends on both physical habitat and inter- and intra-specific biological interactions. Habitat requirements of juvenile Atlantic salmon have been well studied, and models predicting habitat suitability have been developed to describe the spatial distribution of juveniles within a watershed (Guay et al. 2000). Habitat data has also been combined with bioenergetics models to predict growth rate potential in available salmon habitat (Nislow et al. 2000). Predictions from habitat suitability and spatially explicit bioenergetic models have shown strong correlations to observed parr densities and growth, but these models have been validated in relatively short reaches on small streams. Also, an underlying assumption of habitat suitability models is that habitat selection does not change with fish density, but Bult et al. (1999) found that Atlantic salmon parr shifted habitat usage with changes in fish density and temperature.

Although microhabitat features can govern fish habitat use and distribution, it is the interaction of factors at a coarser spatial scale with factors at finer scales that influence on salmonid abundance (Deschenes and Rodriguez. 2007, Poff and Huryn 1998). Biological communities in lotic systems change along stream gradients as energy inputs, primary production, and stream temperatures change (Vannote et al. 1980). Drainage area may be a useful variable indexing these changes. Temperature is one of the most important variables governing the distribution and growth potential of salmonids (VanWinkle et al. 1997; Dunham et al. 2003). Land use within the drainage can influence temperature, water chemistry, nutrient loading, and ultimately salmonid productivity (Wilson et al. 2003; Weng et al. 2001). Stream gradient within a reach will interact with drainage area and discharge to influence current velocity and it's suitability for juvenile salmon (Trial 1989; Amiro 1993). Thus, physical, chemical, thermal, and biological components, and their interactions at multiple spatial scales will govern fish abundance.

Considering the presence of other fish species and potential predators when evaluating the potential productivity of a stream reach will better reflect stream ecology. Interactions between Atlantic salmon juveniles and other species confound habitat suitability and predictive models that do not include biotic variables. Significant positive relationships between habitat suitability and parr abundance may break down due to either inter-specific competition or direct predation on Atlantic salmon parr as the abundance of other species changes through a watershed. For example, potential productivity of stream habitat with optimal substrate, depth, and current velocity according to habitat suitability models may be negated if potential predators are high in abundance. In Connecticut River tributaries, Henderson and Letcher (2003) estimated 4.3 - 48% of stocked fry were consumed by other salmonid species.

The ultimate measure of the success of recovery efforts for Atlantic salmon is the number of returning adult fish to the river. The number of returning adults is positively correlated to the number of outmigrating smolts produced (Jonsson et al. 1998). The abundance of outmigrating smolts is a combination of the number of parr surviving to the smolt stage and their survival during emigration from the various portions of the watershed. For example, if survival to the parr stage is high for a particular area of the river, this area may not contribute a significant portion of the total smolt population if high mortality occurs during migration.

For recovery efforts on the Sheepscot River to be adaptive and successful, it is important to identify areas of the watershed that have the greatest fry to parr survival and contribute most to the outmigrating smolt population. Identifying these areas will allow managers to refine fry stocking practices to increase survival to the parr stage, optimize the number of outmigrating smolts per the number of fry stocked, and guide salmon habitat enhancement and restoration efforts.

This study on the Sheepscot River was designed to provide managers with information to adaptively manage fry stocking in the watershed. The objectives were to: (1) use genetically marked fry to identify rearing locations and assess gross movement upon capture at later life stages; (2) examine spatial patterns of juvenile Atlantic salmon growth; (3) determine quantitative relationships between juvenile Atlantic salmon survival and macrohabitat variables such as watershed area, temperature, pH, stream gradient, and abundance of non-salmon species; (4) assess relative survival to the smolt stage from various stocking locations; and (5) make recommendations to optimize smolt production from fry stocking. The Sheepscot River was chosen for a variety of reasons: there are no barriers to fish migration to most of the habitat, it contains a variety of habitat types of varying quality, and annual sampling efforts include juvenile salmon populations throughout the watershed and smolt emigration.

Methods

Study Site – Sheepscot River

The Sheepscot River is in the southern portion of the geographic range of the GOM DPS. The entire watershed has an area of 64,980 ha and drains a mosaic of forest, wetland, and agricultural lands. The major tributary of the Sheepscot River, the West Branch, enters the mainstem at river km 29.3. Two natural lakes (Long Pond and Sheepscot Pond) are located on the mainstem upstream of the West Branch confluence and one natural lake (Branch Pond) is located on the headwaters of the West Branch (Figure 1).

Some natural spawning was observed in the Sheepscot River that may have contributed offspring during the course of this study (MDMR redds database). A total of eight redds were observed in 2004. Of these, six were observed in the upper mainstem region, one in the lower mainstem region, and one in the lower West Branch. Only one redd was observed in 2003. It was located in the mainstem above the West Branch region.

Spawning and batching of family groups

Offspring from the 2004 spawn of the Sheepscot River broodstock maintained at Craig Brook National Fish Hatchery were used for this study. Adults were generally spawned only once, and single paired matings were used (one male and one female). Families (fertilized eggs) were kept separate in the hatchery until grouped into stocking batches. All spawning (family), batching, and stocking data were tracked to facilitate transfer of unique family groups to specific river reaches and identification by parentage analysis during sampling. The majority of the spawners were uniquely marked (PIT tags) and genotyped. However, there were a total of six families that did not have complete genotypes for both parents: four families where the females were not uniquely marked and two males that were spawned twice were not uniquely marked or genotyped. Five of these families were part of this study: four families were part of the group stocked into the mainstem above the West Branch as fry, and one stocked into the lower West Branch as fry.

Stocking information

In total, 77 unique families were spawned within the Sheepscot River broodstock in 2004, and were used to create 13 unique stocking batches. Ten of these batches representing 64 families were part of the study, either as instream or streamside incubation, fry stocking, or fall parr stocking. Six batches were stocked as fry into specific reaches of the Sheepscot River (Table 1, Figure 1) in the spring of 2005. Two additional unique batches were used for a streamside incubation study, two batches were used for an instream incubation study, and one for the fall parr stocking, all conducted by Maine Department of Marine Resources (MDMR, Table 1).

Fry stocking occurred between May 6 and May 13, 2005. A total of 120,400 fry were stocked in the river upstream of Head Tide Dam with an average stocking density of 72 fry per 100 m^2 of suitable habitat (range 45 – 130 fry per 100 m^2, Table 1). The stocking density in the upper mainstem reach was 45 fry per 100 m^2 (Table 1) to accommodate additional fry from 14,000 fertilized hatchery eggs were artificially planted in this reach. The intent was that the resulting density of fry (emerging + stocking) in the upper mainstem would be closer to that of other regions. Fry were not stocked in the lower mainstem. Because poor fry survival in the lower mainstem (river km < 17.33) had been observed in recent years, approximately 15,900 0+ parr were stocked in the lower mainstem in September 2005. The 0+ parr stocked had adipose fins clipped to identify their stocking stage/origin in the field when recaptured as later parr stages or as smolts. These fish were not considered as part of this study.

Fry stocked in the West Branch Sheepscot River were part of a concurrent experiment being conducted by MDMR to compare the survival of hatchery versus streamside incubated fry. Both groups were part of the 2004 spawn year at CBNFH, but the streamside group was moved from the hatchery and incubated in refrigerators located along the river and supplied with water from the river. The streamside incubated fry were different family groups than the hatchery reared fry to account for any differences in survival using parentage analysis following collections at later life stages. The lower West Branch was stocked with 15,900 hatchery and 13,700 streamside incubated fry and the upper West Branch was stocked with 17,000 hatchery and 15,700 streamside incubated fry.

Juvenile sampling

The juveniles from the 2004 spawn year and 2005 fry stocking were captured during electrofishing (0+ and 1+ parr) to assess density and growth and in rotary screw traps as emigrating smolts. Electrofishing occurred between August and September in 2005 and 2006 at 19 sites distributed throughout the watershed (Figure 1). Age 0+ parr were targeted in 2005 and age 1+ parr in 2006. The size of each site ranged from 149 to 482 m^2 depending on stream width and the location of the site within the river basin. Block nets were placed at the upstream and downstream end of a site and multiple electrofishing passes (typically 2 – 3 passes) were made to calculate a removal population estimate (Carle and Strub 1978). If no parr were collected on the first electrofishing pass, subsequent passes were not conducted at that site. Population estimates were divided by the area of the site to estimate density. Genetic samples were obtained from the first 30 juveniles sampled per site, and then from every 5th individual. We also estimated populations, and densities of non-salmon fishes grouped into major taxonomic classes (e.g. centrarcids, cyprinids, eel, lamprey, esocids, sucker, and other trout).

Smolt sampling occurred from April 22 to May 16, 2006 and May 2 to May 22, 2007 by NOAA Fisheries. The majority of smolts were expected to emigrate as 2 year olds (in the spring of 2007), but early emigrants (age 1+ smolts) were also expected in 2006. To capture emigrating smolts, two rotary screw traps were placed immediately below Head Tide Dam and were checked twice daily for smolt captures during the sampling period in each year. Scale samples for aging by NOAA, and caudal fin clips for genetic analysis were obtained from each smolt that did not have an adipose fin clip. Adipose clipped fish corresponded to the age 0+ parr stocked in the lower mainstem and therefore their age and stocking location were known.

Genetic analysis

Genetic samples (fin clips) from Sheepscot River juvenile Atlantic salmon were stored in 95% ethanol and taken to the Northeast Fishery Center Conservation Genetics Lab, Lamar, PA. DNA was extracted using Purgene (Qiagen Inc., Valencia, California) protocols. Genotypes were obtained at 11 microsatellte loci: Ssa197, Ssa171, Ssa202, Ssa85 (O'Reilly et al. 1996), Ssa14, Ssa289 (McConnell et al. 1995), SSOSL25, SSOSL85, SSOSL311, SSOSL438 (Slettan et al. 1995, 1996), and SSLEEN82 (GenBank accession number U86706). PCR protocols followed those described in King et al.

(2001). Genotypes were visualized using an ABI 3100 (Applied Biosystems Inc., Foster City, California), and the software GeneScan and Genotyper (Applied Biosystems Inc., Foster City, California). Size standards were used to standardize allele designations (Applied Biosystems Inc., Foster City, California).

Genetic parentage analysis was conducted using Cervus ver. 3.0 (Kalinowski et al. 2007). Genotypes from the 2004 spawn year of the Sheepscot River broodstock represented the potential know parents for comparison for the four sets of juvenile collections (0+ parr, 1+ parr, 1+ smolts, and 2+ smolts). Parentage was also assessed for the 2003 and 2005 Sheepscot River broodstock spawn years to account for contributions these cohorts. Assignment criteria for parentage analysis included complete genotypes at all 11 loci for both parents and offspring, and no genotype mismatches between offspring and both parents. Results of parental spawning pairs which complied with the assignment criteria were also compared to documented spawning pairs.

Biotic and Abiotic Macrohabitat

Water quality parameters including dissolved oxygen, specific conductance, salinity, pH, and temperature were measured at each electrofishing site when the fry were stocked, and collected as age 0+ and age 1+ parr. Temperature loggers (HOBO Stowaway® TidbiT^{TM}) were also deployed in the vicinity of electrofishing sites and recorded hourly temperatures from May 2005 to September 2006. Temperature data were summarized as the total number of hours the temperature exceeded 20ºC between May and September of each year. During electrofishing trips, the number and family/species of all other fish species encountered were recorded to document community composition and estimate density by taxonomic group.

Physical macrohabitat features were determined using GIS. The drainage area (ha) above each electrofishing site was determined from digital raster graphics (DRGs). Landsat data and wetland cover data obtained for the Gulf of Maine watershed (USFWS 2002) was used to estimate the proportion of the drainage area upstream of an electrofishing site falling into land cover categories of forest, open/agriculture, and wetland. Stream gradient of an electrofishing site was determined by dividing the change in elevation between two contour intervals on the DRG (located upstream and downstream of the site) by the distance between those contour intervals.

Statistical Analysis

Only those individuals that were genetically assigned parentage to the Sheepscot River hatchery broodstock were used to relate parr and smolts to a specific fry stocking location. All individuals were used in analyses of density, survival and growth.

A chi-square test was used to examine differences among regions of the river in the percentage of genetic sampled age 0+ and age 1+ parr that could be assigned to known matings in the hatchery. The number of samples assigned and the number not assigned to known matings were combined over 2005 and 2006 field samplings.

Relative survival of hatchery stocked fry was compared to streamside incubated fry in the West Branch Sheepscot River using a replicated G-test. The replicates considered were the upper and lower West Branch regions. A G-test was used to compare the ratio of hatchery to streamside incubated fry for fish assigned to these genetic groups from age 0+ parr through smolt stages to determine if the ratio remained the same after the age 0+ parr stage.

Possible density dependent survival and growth was examined graphically and with linear regression (Jonson et al. 1998). Density and survival at each site were plotted on density at the previous life stage. Length of age 0+ and age 1+ parr were also plotted on the density at the previous life stage and density within the life stage. A negative slope to the regression line or an increase followed by an asymptote in the above cases would indicate a density dependent relationship.

Differences in parr size between regions were determined by ANOVA. This analysis was conducted on the mean fork length (mm) and mean weight (g) of individuals within an electrofishing site.

Fry and age 0+ parr survival was modeled using multiple least-squares regression (SAS version 9.1) for sites that were stocked with fry. Apparent survival of fry to the age 0+ parr stage (S_f) was calculated as the density of age 0+ parr at an electrofishing site divided by the fry stocking density for that region of the river in 2005. The term "apparent" survival is used to indicate that the sample may include parr resulting from hatchery stocked fry as well as any from natural reproduction. Apparent survival of age 0+ parr to age 1+ parr stage (S_0) was calculated as the density of age 1+ parr at an electrofishing site in 2006 divided by the density of age 0+ parr at that site in 2005. Apparent survival data was arsine-square root transformed prior to statistical analysis. Overall comparisons of survival among river regions were also evaluated with a Kruskal-Wallace test.

Because streamside incubated fry were only stocked in the West Branch Sheepscot River, this confounded the experiment when examining the influence of other variables on apparent survival from fry to age 0+ parr for over the entire watershed. To account for this potential effect, the proportion of age 0+ parr coming from hatchery incubated fry based on parentage analysis at each site in the upper and lower West Branch was multiplied by the observed density of age 0+ parr, and then divided by the stocking density of hatchery fry to yield an adjusted apparent survival, S^{*}_{f}, specific to hatchery incubated fry.

To avoid multicolinearity, all habitat variables were screened for significant correlations, and one variable of the pair was eliminated if the correlation was significant (Pearson correlation coefficient, $p \leq 0.05$). This resulted in many possible competing models and best subsets regression was used to identify a subset of five potentially optimal models based on Akaike's Information Criteria (AIC). After a reduced set of potential models were identified with low AIC values, models were evaluated based upon significance of model parameters and overall coefficients of determination (r^2). Separate models were determined for both S_f and S_0.

Total age 1+ parr production was estimated for the five river reaches stocked with fry according to methods described in Sweka et al. (2006). The total population within a reach was

$\hat{Y}_r = \frac{N_r}{n_r}\sum^{n}\hat{Y}_i$ and the associated variance was

$$\hat{V}\left(\hat{Y}_r\right) = \frac{N_r\left(N_r - n_r\right)\sum^{n}\left(\hat{Y}_i - \hat{\bar{Y}}_r\right)^{2}}{n_r\left(n_r - 1\right)} + \frac{N_r\sum^{n}\hat{\sigma}_i^{2}}{n_r}$$

where $\hat{Y}_r =$ total population in reach *r*, $\hat{Y}_i =$ population estimate at site *i*, N_r = the number of potential sites in reach *r*, n_r = the number of sites sampled in reach *r*, $\hat{V}\left(\hat{Y}_r\right) =$ variance of reach *r* total population estimate, $\hat{\bar{Y}}_r = \frac{\sum \hat{Y}_i}{n_r} =$ mean population estimate in reach *r*, and $\hat{\sigma}_i^2 =$ the variance of the Carle and Strub (1978) population estimate at site *i*. We estimated the number of potential sites in a reach (N_r) as the total area of the reach divided by the average area of the sites sampled in the reach.

The study provided an opportunity to test the hypothesis that reaches producing the most parr also produce the most smolts. Relative smolt production from each region was regressed on the point estimates of parr production from each region. Relative smolt production from a region was equal to the number of smolts assigned to a region based on parentage analysis. If reaches that produced the most parr also produced the most smolts, then the regression line was expected to have a significant positive slope.

Results

Genetic analysis

For this study, a total of 62 Sheepscot River female broodstock were spawned in 2004. Most female broodstock spawned in 2004 contributed to only one family, with the exception of four families where the females were not uniquely marked. Therefore it is unknown if these represent unique or re-used females. A total of 61 male broodstock were spawned, four males were spawned twice, and one male was not uniquely marked or genotyped. Genotypic data was not available for the unmarked female(s) or male.

These families were stocked out in the genetics groups 3 and 8 which were stocked in the mainstem above the West Branch and in the lower West Brach, respectively (Figure 1).

A total of 873 juvenile Atlantic salmon were sampled for genetic analysis from the Sheepscot River (Table 2). Parentage was assigned to a total of 491 individuals from the three potentially contributing spawn years (2003, 2004, and 2005; Table 3), and 459 from the 2004 spawn year (Table 3). Tissue sampling during electrofishing in 2005 targeted age 0+ parr, as a result genetic analysis identified only age 0+ parr (from the 2004 spawn year; Table 3). In 2006 larger parr and smolts were targeted for tissue sampling. This resulted in juveniles being identified from the 2003, and 2004 spawn years (Table 3). Of the eight potential 1+ smolts captured in 2006, only one was from the 2004 spawn year. In 2007, only emigrating smolts were collected, with individuals identified from the 2003, 2004, and 2005 spawn years (Table 3). These results indicate that juvenile Atlantic salmon in the Sheepscot River can reside in the river up to age 3+ parr, and can smolt at age 1+ parr.

With the exception of the instream incubation group, juvenile Atlantic salmon were recovered from each of the stocked genetic groups, and most groups were recovered at each targeted sampling age (Table 4). Of the 48 families stocked as hatchery fry in this study, 25 families were recovered. Five of the seven families from the streamside incubation studies were recovered, and three of the seven families stocked as fall parr were recovered. Neither of the two families used for the instream egg incubation study were recovered.

Overall, the percentage of samples assigned to known hatchery matings was 60% for age 0+ and age 1+ parr, combined, and 50% for smolts. Percent assignment for parr differed among regions of the river (Table 5; $X^2 = 11.85$, d.f. = 4, $p = 0.02$) with the lowest percent assignment occurring in the mainstem above the West Branch (24%). The other regions showed similar percent assignment (56 – 65%).

Parr movement

Relatively little movement of parr was observed from their original stocking region. Among age 0+ parr who were assigned to known matings, only 14 out of 194 individuals (7%) were collected outside their original region of stocking. Among age 1+ parr, 10 out of 111 individuals (9%) were collected outside their original region of stocking. In both life stages, all individuals moved downstream (Table 6), with the lower mainstem (0+ parr) and lower West Branch (1+ parr) having the greatest immigration at different life stages.

Density and Survival of fry and age 0 + parr

Both parr density and survival varied greatly among sites (Table 7). Age 0+ parr density ranged from 0 to 46.7 fish / 100 m^2 and tended to be greater in the upper and lower West Branch compared to the mainstem. Likewise, the highest age 1+ parr densities (> 20 fish / 100 m^2) were found in the upper and lower West Branch. Apparent survival from fry to age 0+ parr, S_f, ranged from 0 to 45% and differed among regions (Kruskal-Wallis Test: $X^2 = 15.61$, d.f. = 4, $p < 0.01$). It tended to be highest in the upper and lower West Branch. At some sites, survival of age 0+ parr to age 1+ parr, S_0, exceeded 100% indicating immigration of parr between 2005 and 2006 samplings.

There was no evidence of density dependent survival of fry or age 0+ parr in the Sheepsoct River over the course of this study. Age 0+ parr density increased significantly as stocking density increased and age 1+ parr density increased significantly as age 0+ parr density increased (Figure 2). Also, survival of fry increased significantly with increasing stocking density, but age 0+ survival showed not relationship with age 0+ density. If survival were density dependent, regression lines of the plots in Figure 2 would have had negative, rather than positive, slopes.

Although there was no evidence of density dependent survival, there was some indication of density dependent growth. Mean fork length of age 0+ parr decreased as stocking density increased, but showed no relationship with age 0+ density. Mean fork length of age 1+ parr in 2006 decreased with increasing age 0+ parr density in 2005. Also, mean fork length of age 1+ parr showed a negative relationship with the density of age 1+ parr in 2006 (Figure 3).

Streamside incubated fry survived to age 0+ parr at a greater rate than did hatchery incubated fry (Table 8) in both the upper ($G = 46.38$, $df = 1$, $p < 0.01$) and lower ($G = 8.99$, $df = 1$, $p < 0.01$) West Branch. Also, the relative contribution of streamside incubated fry in the lower West Branch was higher than that in the upper West Brach (Heterogeneous $G = 5.07$, $df = 1$, $p = 0.02$). However, the ratio of streamside to hatchery incubated fry contributing to subsequent lifestages (age 1+ parr and smolts) did not change beyond the age 0+ parr stage (Table 9) for either the lower ($G = 0.10362$, $df = 2$, $p = 0.95$) or upper West Branch ($G = 0.16$, $df = 2$, $p = 0.92$).

Parr Growth

Size of parr was also significantly different among regions of the Sheepscot River. There were significant differences in the size of age 0+ parr between regions (fork length: $F_{4,16} = 3.72$, $p = 0.03$; weight: $F_{4,16} = 4.57$, $p = 0.02$), but not age 1+ parr (fork length: $F_{2,12} = 2.67$, $p = 0.11$; weight: $F_{2,12} = 3.14$, $p = 0.90$). Both length and weight of age 0+ parr were greater in the upper mainstem region compared to all other regions (Table 10). Age 1+ parr were only collected from 1 site in both the middle mainstem and mainstem above the West Branch regions, therefore these data were not included in the statistical analysis of age 1+ parr size.

Biotic and Abiotic Habitat Factors and Effects on Juvenile salmon

Water quality and land use varied throughout the Sheepscot watershed. Mean pH and specific conductance tended to be highest in the West Branch regions compared to the upper mainstem and the mainstem above the West Branch (Table 11). On the mainstem Sheepscot river, mean pH and specific conductance tended to increase downstream of confluence of the West Branch. The number of hours that temperature exceeded 20ºC tended to increase moving from upstream to downstream reaches. Landuse differed between the West Branch and mainstem regions. The proportion of the watershed that was forested was greater in the mainstem regions, while the proportion of the watershed that was open/agricultural was greater in the West Branch (Table 12).

Fish communities also varied throughout the watershed (Table 13). Centrarcids (smallmouth and largemouth bass), cyprinids (fallfish, blacknose dace, shiners spp.) and American eels were found in each region of the river in both years. However, cyprinids tended to have greater densities in more upstream sites compared to sites lower in the watershed. Trout species (brook and brown trout) were only found in upstream sites of the upper mainstem and West Branch. Sea lamprey, chain pickerel (the only esocid), and white suckers were found in low abundance in sites scattered throughout the watershed (Table 13).

Many of the macrohabitat variables and non-slamon densities were significantly correlated (Table 14). For example, mean pH was significantly correlated with mean specific conductance, drainage area, percent of the water that was forested, open, and wetland, and centrarcid density. Drainage area was significantly correlated with the number of hours that summer temperatures exceeded 20ºC and cyprinid density. Potential models for multiple regression analysis were developed by dropping one variable of a correlated pair, until the model consisted of only non-correlated predictor variables.

Multiple regression models relating habitat and S_f and S_0 (Table 8) were similar between age 0+ and age 1+ parr. Even after reducing the number of potential habitat variables to account for correlated predictor variables, there were many possible competing models (Table 15). Of these, we retained the best models for S_f and S_0 based on the lowest AIC values and significance ($p \leq 0.05$) of slope parameters for predictor variables (Table 16). Significant variables describing the variation in S_f, included: drainage area upstream of a site, percent of watershed forested, percent of watershed open/agriculture, specific conductance, and cyprinid density. Multiple regression analysis of the adjusted S^*_f again showed drainage area upstream of an electrofishing site had a significantly negative slope and cyprinid density had a positive slope. If models with drainage area are excluded, those with the numbers of hours temperature exceeded 20ºC had the lowest AIC values and the slope of this variable was significantly different from 0 for both S_f and S^*_f.

We omitted from the analysis of S_0 those sites where S_0 exceeded 100% and where no age 0+ parr were caught in 2005 (density of age 0+ parr = 0). Two optimal models emerged describing the variability in S_0. One had mean pH, the number of hours temperature exceeded 20ºC, and cyprinid density as significant predictor variables while the other had only drainage area upstream of a site as a significant predictor.

Total parr and smolt production

Extrapolating site level population estimates to an entire region illustrated the differences in total parr production among regions where Atlantic salmon fry were stocked (Table 17). The upper West Branch produced the greatest number of age 1+ parr (5,406 ± 2,278) and the upper and lower West Branch, combined, produced approximately 88% of age 1+ parr that originated from fry stocking, but these areas only comprised 44% of the total habitat in which fry were stocked.

Fry stocked in the upper and lower West Branch contributed most to the total number of smolts that were assigned to known matings (Table 17). Further, there was a significant relationship between point estimates of age 1+ parr production for each region and the number of smolts assigned parentage specific to those regions (Figure 4). Thus, the regions of the river that produced the most parr also produced the most smolts.

Discussion

Genetic parentage analysis was successfully used to assign individuals to specific locations where they were stocked as fry. However, parentage was not assigned for all sampled juvenile Atlantic salmon. Genetic marking through parentage analysis requires complete genotypes for all potentially contributing parents and the sampled offspring, multiple and variable bi-parentally inherited genetic markers, and mating information if available to resolve assignments to multiple potential mating combinations if alleleic variability isn't sufficient to provide unique genotypes. When one or more of these components are insufficiently met, then the ability to identify parents may be confounded. We had fry stocked from 5 matings where one or both of the parents were not characterized. Additional sources of errors include laboratory or computational errors, or genetic mutations which would result in non-assignment of parentage.

In this study, missing genotypes for some of the parental broodstock accounted for some of the lack of assignment. The lowest percent assignment for parr came from the mainstem above the West Branch, where of the nine families stocked, four were from parents with missing genotypes. However, this missing data could not necessarily account for all non-assignments observed. Natural reproduction of returning adult Atlantic salmon occurs within the Sheepscot River. Combining the 2003 and 2004 surveys, redds were observed in all the regions except the upper West Branch. Six of these were in the upper Mainstem region (Table 5). It is also possible that additional redds were missed by survey crews. Juveniles from natural reproduction were likely captured in the sampling process, particularly in and downstream of regions where redds were documented. Their relative proportion of non-assigned juveniles observed is difficult to assess because regions with the most redds had similar assignment rates to those with few redds.

Although, this study was not designed to gain quantitative estimates of fry and parr movement, it showed through parentage analysis that movement between regions of the Sheepscot River occurred. Dispersal and movement rates of juvenile Atlantic salmon varies depending on the age of the juveniles. Crisp (1995) found dispersal of fry from original stocking locations was predominantly in a downstream direction with distances from 50 m upstream to 500 m downstream of the stocking site. However, Armstrong et al. (1994) and Erkinaro & Niemelä (1995) showed movement of age 1+ parr could be substantial with individuals moving from mainstem reaches to tributaries. Movement in this study was consistently in a downstream direction and may be a likely reason why estimates of survival from age 0+ to age 1+ parr exceeded 100% at some sites.

Density dependent effects were observed on growth, but not survival of Atlantic salmon parr in this study. Others have also observed density dependent growth in Atlantic salmon (Egglishaw and Shackley 1980, Imre et al.2005). Lack of any density dependent survival in this study may be due to fry stocking densities below those which would illicit a density dependent response. Density dependent survival is commonly observed in other Atlantic salmon populations (Gee et al. 1978; Egglishaw and Shackley 1980; Cunjak and Therrien 1998; Jonsson et al. 1998). Egglishaw and Shackey (1980) found mortality of fry increased as stocking density of fry increased, but they stocked at densities ranging from 360 to 2,930 fry per 100 m^2. Gee et al. (1978) found parr densities declined after fry densities reached 100 fry per 100 m^2. In an analysis of fry stocking densities and resulting parr densities, Gibson (1992) suggested 111 fry per 100 m^2 was the optimum stocking density for New England rivers. The greatest stocking density in this study was 103 fry per 100 m^2.

Density and survival of Atlantic salmon parr within the Sheepscot River watershed was most influenced by the drainage area upstream of a given site. Sites in smaller drainage areas had higher parr survival and densities. This relationship seems to be a general feature across salmon rivers in Maine. In an analysis of parr density data from nine salmon drainages between 1991 and 2005, Sweka and Mackey (*in review*) also found parr densities decrease with increasing cumulative drainage areas. Others have also shown relative abundance of other salmonids decreases as cumulative drainage area increases (Roper et al. 1994; Petty et al. 2005; Creque et al. 2005; Deschenes and Rodriguez 2007). The observation of higher survival and densities of Atlantic salmon parr in stream reaches of smaller drainage areas is similar to ongoing displacement of brook trout (*Salvelinus fontinalis*) in the eastern United States to small headwater streams (Larsen and Moore 1985; Strange and Habera 1998).

A likely mechanism for higher survival in stream reaches of smaller drainage area is that these areas provide more favorable temperatures. Drainage area and the number of hours temperature exceeded 20ºC were positively correlated in each year and could not be included in the same model. In the two best models predicting age 0+ survival, one had the number of hours temperature exceeded 20ºC while the other had drainage area. Thus, when questions exist about the suitability of stream temperature for juvenile Atlantic salmon, and empirical temperature data does not exist, drainage area may be used a likely surrogate to index temperature effects.

In addition to density dependent effects, temperature may have also played a role in the differences observed in the size of age 0+ parr in the upper mainstem compared to other regions. Although the temperature in the upper mainstem often exceeded 20ºC as in other regions, actual temperatures were still lower than other regions. The specific growth rate grams (growth/gram of body weight/ day) begins to decline as temperatures exceed 16 – 18ºC and become negative when temperatures exceed 25ºC (Murphy 2003). The upper mainstem region never reached this 25ºC threshold unlike other regions of the river during the summer of 2005.

Other significant variables in multiple regression models predicting fry survival included the proportion of the drainage area above a site that was forested and open, and mean specific conductance. The relationships with proportion forested and proportion open were counterintuitive to the expected result that sites with a greater proportion forested would have higher survival. Sites with a greater proportion forested would represent areas with lower overall anthropogenic disturbance and lower stream temperatures due to shading by the overhead canopy. The reason the negative slope was associated with the proportion forested, and positive slope for the proportion open, was due to the West Branch having proportionately more open/agricultural land use compared to the mainstem, and the West Branch had greater age 0+ parr densities and fry survival compared to the mainstem. The positive slope parameter associated with mean specific conductance was also likely associated with a greater degree of agricultural land use in the West Branch compared to the mainstem. Specific conductance is an indicator of stream fertility and productivity, and salmonid production increases with increasing specific conductance (O'Connor and Power 1976; Scarnecchia and Bergersen 1987;

Deegan and Peterson 1992). Although agricultural runoff is considered a source of pollution and water quality degradation, the increased nutrient loading in the West Branch may have increased the productivity of this region compared to the mainstem. Hesthagen et al. (1986) also noted higher salmon production in agricultural areas compared to forested areas in a Norwegion river. This is not to suggest that agricultural runoff benefits Atlantic salmon parr, but it does speak to the general natural low productivity of contemporary Maine Atlantic salmon rivers.

A few factors may have potentially complicated data interpretation. First, stocking streamside incubated fry in addition to hatchery incubated fry in the West Branch may have confounded the observed higher age 0+ parr densities and higher fry survival as a function of better habitat in the West Brach, the stocking of streamside incubated fry, or both. By adjusting the survival of fry to age 0+ parr stages, this factor may be accounted for, and drainage area was still determined to be the most influential habitat variable on fry survival. The ratio of fish originating from hatchery or streamside incubated fry did not change at life stages beyond age 0+ parr, thus any benefit to survival from streamside incubation was realized prior to sampling of age 0+ parr and did not confound the study at later life stages.

Another confounding factor was the stocking of eggs in the upper mainstem. No parr or smolts corresponding to egg stocking were identified through parentage analysis; therefore egg plants most likely did not have an effect on the results. Finally, fry stocking densities varied considerably among regions with the West Branch receiving greater densities than mainstem regions. This discrepancy was accounted for by using fry to age 0+ parr survival in the multiple regression analysis rather than age 0+ parr density.

Nevertheless, the concurrent management activities made interpretation of the results more difficult.

Management implications

The greatest constraint to smolt production in the Sheepscot River is survival from fry to age 0+ parr. Regions in the river with smaller drainage areas had the greatest fry to age 0+ survival and these also corresponded to regions where total population estimates of age 1+ parr and contribution to the smolt population were greatest. Focusing management efforts on increasing 0+ parr densities would result in a subsequent increase in smolts. This could be accomplished through modifying stocking practices. For example, if a limited numbers of fry are available for stocking, then stocking at relatively high density in small tributaries would result in a greater production of smolts compared to low density stocking throughout all available habitat. No density dependence was observed between age 0+ parr and fry stocking density, therefore an increase in stocking density, focused in small watersheds, may also increase the total production of parr and ultimately smolts. Additionally, the use of alternate rearing mechanisms such as streamside and instream incubation should be continued to be explored as an important recovery and restoration tool.

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Literature Cited

Amiro, P. G. 1993. Habitat measurement and population estimation of juvenile Atlantic salmon (*Salmo salar*). p81 – 97. *In* R.J. Gibson and R.E. Cutting (editors) Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Canadian Special Publication of Fisheries and Aquatic Sciences 118.

Armstrong, J. D., P. E. Shackley, and W. R. Gardiner. 1994. Redistribution of juvenile salmonid fishes after localized catastrophic depletion. Journal of Fish Biology 45: 1027-1039

Bult, T.P., S.C. Riley, R.L. Haedrich, R.J. Gibson, and J. Heggenes. 1999. Density-dependent habitat selection by juvenile Atlantic salmon (*Salmo salar*) in experimental riverine habitats. Canadian Journal of Fisheries and Aquatic Sciences 56: 1298-1306.

Carle, F.L. and M.R. Strub. 1978. A new method for estimating population size from removal data. Biometrics 34: 621-630.

Cornuet, J-M., S. Piry, G. Luikart, A. Estoup, and M. Solignac. 1999. New methods employing multilocus genotypes to select or exclude populations as origins of individuals. Genetics 153: 1989-2000.

Creque S. M., E. S. Rutherford, and T. G. Zorn. 2005. Use of GIS-derived landscape-scale habitat features to explain spatial patterns of fish density in Michigan rivers. North American Journal of Fisheries Management 25: 1411-1425.

Crisp, D. T. (1995). Dispersal and growth rate of 0-group salmon (*Salmo salar* L.) from point stocking together with some information from scatter stocking. Ecology of Freshwater Fish 4: 1-8.

Cunjak, R. A. and J. Therrien. 1998. Inter-stage survival of wild Atlantic salmon, *Salmo salar* L. Fisheries Management and Ecology 5: 209-223.

Deegan, L. A. and B. J. Peterson. 1992. Whole-river fertilization stimulates fish production in an Arctic tundra river. Canadian Journal of Fisheries and Aquatic Sciences 49: 1890-1901.

Deschênes J. and M. A. Rodríguez. 2007. Hierarchical analysis of relationships between brook trout (*Salvelinus fontinalis*) density and stream habitat features. Canadian Journal of Fisheries and Aquatic Sciences 64: 777-785.

Dunham, J., B. Rieman, and G. Chandler. 2003. Influences of temperature and environmental variables on the distribution of bull trout within streams at the southern margin of its range. North American Journal of Fisheries Management 23: 894-904.

Egglishaw, H. J. and P. E. Shackley. 1980. Survival and growth of salmon, *Salmo salar* (L.), planted in a Scottish stream. Journal of Fish Biology 16: 565-584.

Erkinaro, J. and E. Niemelä. 1995. Growth differences between Atlantic salmon parr, *Salmo salar*, of nursery brooks and natal rivers in the River Tano watercourse in northern Finland. Environmental Biology of Fishes 42: 277-287.

Fay, C., M. Bartron, S. Craig, A. Hecht, J. Pruden, R. Saunders, T. Sheehan, and J. Trial. 2006. Status review for anadromous Atlantic salmon (*Salmo salar*) in the United States. Report to the National Marine Fisheries Service and U.S. Fish and Wildlife Service. 294 pages.

Gibson, M. R. 1992. Analysis of fry stocking results in New England salmon restoration: Effect of stocking density and environment on survival. Working Paper of the U.S. Atlantic Salmon Assessment Committee.

Henderson, J.N., and B.H. Letcher. 2003. Predation on stocked Atlantic Salmon (*Salmo salar*) fry. Canadian Journal of Fisheries and Aquatic Sciences 60: 32-42.

Hesthagen, T., J-O Ousdal, and A. aBergheim. 1986. Smolt production of Atlantic salmon (*Salmo salar*) L. and brown trout (*Salmon trutta*) L. in a small Norwegian river influenced by agricultural activity. Polish Archives of Hydrobiology. 33: 423-432.

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.

Guay, J.C., D. Boisclair, D. Rioux, M. Leclerc, M. Lapoint, and P. Legendre. 2000. Development and validation of numerical habitat models for juveniles of Atlantic Salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 57: 2065-2075.

Kalinowski, S.T., M.L. Taper, and T.C. Marshall. 2006. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Molecular Ecology 16:1099-1106.

King, T.L., S. T. Kalinowski, W. B Schill, A.P. Spidle, and B. A. Lubinski. 2001. Population structure of Atlantic salmon (Salmo salar L.): a range-wide perspective from microsatellite DNA variation. Molecular Ecology 10:807-821.

Larsen G. L. and S. E. Moore. 1985. Encroachment of exotic rainbow trout into stream populations of native brook trout in the southern Appalachian mountains. Transactions of the American Fisheries Society 114: 195-203.

McConnell, S., L. Hamilton, D. Morris, D. Cook, D. Paquet, P. Bentzen, and J. Wright. 1995. Isolation of salmonid microsatellite loci and their application to the population genetics of Canadian east coast stocks of Atlantic salmon. Aquaculture 137:19-30.

Murphy, M. H. 2003. Ecology of young-of-the-year Atlantic salmon: Evaluation of strain differences and over-winter survival. Doctoral Dissertation. State University of New York, Syracuse, New York.

Nislow, K.H., C.L. Folt, and D.L. Parrish. 2000. Spatially explicit bioenergetic analysis of habitat quality for age-0 Atlantic salmon. Transactions of the American Fisheries Society 129: 1067-1081.

O'Connor, J. F. and G. Power. 1976. Production by brook trout (*Salvelinus fontinalis*) in four streams in the Matameck watershed, Quebec. Journal of the Fisheries Research Board of Canada 33: 6-18.

O'Reilly, P.T., L.C. Hamilton, S.K. McConnell, and J. M. Wright. 1996. Rapid detection of genetic variation in Atlantic salmon (*Salmo salar*) by PCR multiplexing of dinucleotide and tetranucleotide microsatellites. Canadian Journal of Fisheries and Aquatic Science 53:2292-2298.

Petty J. T., P. J. Lamothe, P. M. Mazik. 2005. Spatial and seasonal dynamics of brook trout population inhabiting a central Appalachian watershed. Transactions of the American Fisheries Society 134: 572-587.

Roper B. B., D. L. Scarnecchia, and T. J. La Marr. 1994. Summer distribution of and habitat use by Chinook salmon and steelhead within a major basin of the South Umpqua River, Oregon. Transactions of the American Fisheries Society 123: 298-308.

Scarnecchia, D. L. and E. P. Bergersen. 1987. Trout production and standing crop in Colorado's small streams, as related to environmental features. North American Journal of Fisheries Management 7: 315-330.

Slettan, A. I. Olsaker, and O. Lie. 1995. Atlantic salmon, *Salmo salar*, microsatellites at the *SSOSL25, SSOSL85, SSOSL311, SSOSL417* loci. Animal Genetics 26:281-282.

Slettan, A. I. Olsaker, and O. Lie. 1996. Polymorphic Atlantic salmon *Salmo salar* L., microsatellites at the *SSOSL438, SSOSL429, and SSOSL444* loci. Animal Genetics 27:57-58.

Strange R. J. and J. W. Habera. 1998. No net loss of brook trout distribution in areas of sympatry with rainbow trout in Tennessee streams. Transactions of the American Fisheries Society 127: 434-440.

Sweka, J. A., C. M. Legault, K. F. Beland, J. Trial, M. J. Millard. 2006. Evaluation of removal sampling for basinwide assessment of Atlantic salmon. North American Journal of Fisheries Management 26: 995-1002.

Sweka, J. A. and G. Mackey. In Review. A functional relationship between watershed size and Atlantic salmon parr density. Fisheries Management and Ecology 00: 00-00.

Trial, J. G. 1989. Test habitat models for blacknose dace and Atlantic salmon. Dorcrotal Thesis, University of Maine, Orono, ME.

USASAC. 2003. Annual report of the U.S. Atlantic salmon assessment committee. Report No. 15 – 2002 Activities.

USASAC. 2005. Annual report of the U.S. Atlantic salmon assessment committee. Report No. 17 – 2004 Activities.

Van Winkle, W., K. A. Rose, B. J. Shuter, H. I. Jager, and B. D. Halcomb. 1997. Effects of climatic temperature change on growth, survival, and reproduction of rainbow trout: predictions from a simulation model. Canadian Journal of Fisheries and Aquatic Sciences 54: 2526-2542.

Table 1. Sheepscot River study regions, 2005 stockings, number of families, available habitat, and stocking densities.

Region	River Km	Number Stocked	Life stage stocked	Total number of families	Total rearing habitat (100 m^2)	Stocking Density
Middle Mainstem	17.33 - 29.34	32,300	Hatchery fry	21	509.59	63
Mainstem Above West Branch	29.34 - 32.68	12,400	Hatchery fry	9	211.69	59
Upper Mainstem[1]	40.44 - 46.88	13,400	Hatchery fry, eggs	9, 2	300.39	45
Lower West Branch	0.00 - 11.31	32,700	Hatchery & streamside incubated fry	2, 2	368.65	89
Upper West Branch	20.59 - 33.04	29,600	Hatchery & streamside incubated fry	7, 5	287.21	103

[1] An additonal 14,000 fertilized hatchery eggs from X families were planted in this section of river. Parentage analysis of parr and smolts did not assign any offspring to these families.

Table 2. Summary of sampling efforts for juvenile Atlantic salmon in the Sheepscot River.

Sample Year	Life stage targeted	Number juveniles sampled	Number sampled for genetic analysis
2005	0+ parr	428	311
2006	1+ parr	276	213
2006	1+ smolts	27[1]	8[1]
2007	2+ smolts	520	341

[1] 19 samples were identified as 1+ smolts by adipose fin clips and therefore not part of this study and 8 by scale analysis.

Table 3. The number of juvenile Atlantic salmon genetically assigned parents by spawn year and by the life stage sampled.

Sample Year	Parent spawn year	Number offspring assigned
2005	2004	194
2006	2003	11
	2004	112
2007	2003	19
	2004	153
	2005	2
Total		491

Table 4. Number of assigned offspring per genetics group, by age sampled (for the 2004 spawn year only).

Genetic Group	Stocking Region	Stage Stocked	Stage Sampled*	Year sampled	Number assigned
1	Upper Mainstem	Fry	0+ parr	2005	22
			1+ parr	2006	8
			2+ smolts	2007	9
2	Middle Mainstem	Fry	1+ parr	2006	1
			2+ smolts	2007	2
3	Mainstem above WB	Fry	1+ parr	2006	3
			2+ smolts	2007	4
4	Middle Mainstem	Fry	0+ parr	2005	20
			1+ parr	2006	2
			2+ smolts	2007	10
5	Lower Mainstem	fall parr	0+ parr	2005	1
			1+ parr	2006	7
			2+ smolts	2007	4
6	Upper West Branch	Fry	0+ parr	2005	22
			1+ parr	2006	17
			2+ smolts	2007	27
7	Upper West Branch	SI [1]	0+ parr	2005	41
			1+ parr	2006	37
			2+ smolts	2007	54
8	Lower West Branch	Fry	0+ parr	2005	15
			1+ parr	2006	8
			2+ smolts	2007	7
9	Lower West Branch	SI	0+ parr	2005	73
			1+ parr	2006	29
			2+ smolts	2007	36
Total					459

[1] Streamside incubation of eggs and volitional release

Table 5. Distribution of observed redds (2003 and 2004), number of families stocked per region, and number of families without available genotypes for both parents, as reference for the percentage of age 0+ and age 1+ parr genetic samples (combined for 2005 & 2006) collected from the Sheepscot River that could be assigned to known hatchery matings. The distribution of assigned/not assigned parr was significantly different among regions with a lower percentage assigned from the mainstem above the West Branch region ($X^2 = 11.85$, d.f. = 4, p = 0.02).

Region	Observed redds	Families stocked (without both parents genotyped)	Juveniles assigned parentage	Juveniles not assigned	Juveniles collected	Percent assignment
Middle Mainstem	1	21 (0)	9	7	16	56%
Mainstem Above West Branch	1	9 (4)	4	13	17	24%
Upper Mainstem	6	11 (0)	30	16	46	65%
Lower West Branch	1	4 (1)	135	76	211	64%
Upper West Branch	0	12 (0)	115	64	179	64%

Table 6. Movement of Atlantic salmon parr from regions where they were stocked as fry in the Sheepscot River, 2005 - 2006. "Number moved" refers to the number of individuals assigned to known matings, but were collected outside of their original stocking region as fry. "Total samples" refers to the total number of individuals assigned to known matings. All movement was in a downstream direction.

Life Stage	Direction of Movement	Number moved	Total samples	% Moved
0+ Parr	Middle Mainstem to Lower Mainstem	14	194	7.22%
1+ Parr	Middle Mainstem to Lower Mainstem	1	111	9.01%
	Lower West Branch to Middle Mainstem	1		
	Upper West Branch to Lower West Branch	8		

Table 7. Parr density and survival in the Sheepsoct River, 2005 - 2006. Site values represent the river Km of the site. Densities are number per 100 m^2. S_f represents survival from fry to age 0+ parr; S^*_f represents fry to age 0+ parr adjusted to account for streamside incubated fry; and S_0 represents survival from age 0+ parr to age 1+ parr.

Region	Site	Site area (100 m^2)	Fry stocking density	2005 age 0+ density	2006 age 1+ density	S_f	S^*_f	S_0
Middle Mainstem	19.47	3.61	63	2.8	0.0	4%		0%
	25.58	4.22	63	0.0	0.0	0%		
	26.21	2.82	63	0.7	0.0	1%		0%
	26.53	2.52	63	0.4	1.6	1%		400%
	26.70	3.14	63	0.0	0.0	0%		
Upper Mainstem	40.51	2.79	45	4.3	2.9	10%		67%
	40.68	1.87	45	2.1	1.6	5%		75%
	45.65	2.69	45	2.6	0.4	6%		14%
	46.22	1.67	45	2.4	3.6	5%		150%
Mainstem Above West Branch	32.32	3.33	59	0.6	0.0	1%		0%
	32.48	3.72	59	1.6	2.7	3%		167%
Lower West Branch	0.54	4.82	89	8.9	2.7	10%	4%	30%
	7.99	1.49	89	32.2	2.7	36%	9%	8%
	8.19	1.98	89	8.1	6.0	9%	4%	75%
	11.13	3.32	89	15.1	5.7	17%	2%	38%
	11.25	1.63	89	13.5	20.9	15%	12%	155%
Upper West Branch	20.78	2.46	103	46.7	22.7	45%	28%	49%
	25.07	2.08	103	25.9	23.4	25%	14%	90%
	32.72	1.97	103	11.7	5.6	11%	12%	48%

Table 8. Parentage analysis results for age 0+ parr from the West Branch Sheepcot River, 2005. The number of 0+parr assigned to streamside incubated genetic groups of fry was significantly higher than those assiged to hatchery incubated genetic groups (Upper West Brach: $G = 46.38$, $df = 1$, $p < 0.01$; Lower West Brach: $G = 8.99$, $df = 1$, $p < 0.01$). Also, streamside incubated fry made a greater relative contribution to 0+parr in the Lower West Branch compared to the Upper West Brach (Heterogeneous $G = 5.07$, $df = 1$, $p = 0.02$).

Region	Incubation Method	Number of 0+ parr	Number Stocked
Lower West Branch	Hatchery	15	17,000
	Streamside Inc. Fry	73	15,700
Upper West Branch	Hatchery Fry	22	15,900
	Streamside Inc. Fry	41	13,700

Table 9. Numbers of idividuals assigned to hatchery and streamside fry incubation genetic groups. The ratio of hatchery:streamside incubated fry contributing to subsequent life stages did not change through time in either the Lower ($G = 0.10362$, $df = 2$, $p = 0.95$) or Upper West Branch ($G = 0.16$, $df = 2$, $p = 0.92$).

Region	Life Stage	Hatchery Incubation	Streamside Incubation	Ratio
Lower West Branch	0+ parr	15	73	0.21
	1+ parr	7	29	0.24
	smolt	8	36	0.22
Upper West Branch	0+ parr	22	41	0.54
	1+ parr	17	37	0.46
	smolt	27	54	0.50

Table 10. Mean (standard deviation) size of Sheepscot River Atlantic salmon parr by region. Sample size, n, refers to the number of sites where parr were found in each region. The Upper Mainstem region had significantly larger age 0+ parr than other regions. There was no difference in size bweteen regions for age 1+parr. Only data with n < 1 were included in statistical analyses.

	Age 0+ parr (2005)			Age 1+ parr (2006)		
Region	n	Fork length (mm)	Weight (g)	n	Fork length (mm)	Weight (g)
Middle Mainstem	2	66 (5)	3.6 (0.9)	1	162.5	52.4
Mainstem Above West Branch	2	61 (3)	2.9 (0.3)	1	174.6	73.7
Upper Mainstem	5	76 (11)	5.8 (2.2)	5	152 (10)	47.1 (9.1)
Lower West Branch	5	63 (2)	2.9 (0.3)	5	145 (7)	37.9 (8.2)
Upper West Branch	3	59 (4)	2.2 (0.5)	3	136 (13)	31.6 (9.2)

Table 11. Summary of water quality data collected at sites on the Sheepcot River during 2005 and 2006.

Year	RegionCode	Site	Mean pH	Mean Specific Conductance (μs/cm)	Hours > 20ºC
2005	Middle Mainstem	19.47	7.44	76	2,099
		25.58	7.40	73	2,071
		26.21	7.41	72	2,069
		26.53	7.49	69	2,069
		26.70	6.93	59	2,069
	Mainstem Above West Branch	32.32	6.66	44	2,284
		32.48	6.13	40	2,284
	Upper Mainstem	40.51	6.07	38	1,470
		40.68	6.21	40	1,470
		45.65	6.34	37	2,046
		46.22	6.27	37	2,046
	Lower West Branch	0.54	7.13	93	1,900
		7.99	7.10	111	1,939
		8.19	6.89	90	1,939
		11.13	6.90	90	1,657
		11.23	7.16	114	1,657
	Upper West Branch	20.78	7.11	74	1,328
		25.07	6.86	67	1,664
		32.72	7.07	67	2,266
2006	Middle Mainstem	19.47	7.44	68	1,889
		25.58	7.30	73	1,839
		26.21	7.23	68	1,877
		26.53	7.00	67	1,877
		26.70	7.40	65	1,877
	Mainstem Above West Branch	32.32	6.96	38	2,144
		32.48	6.96	38	2,144
	Upper Mainstem	40.51	6.46	38	1,557
		40.68	6.65	38	1,557
		45.65	6.77	38	2,062
		46.22	6.50	38	2,062
	Lower West Branch	0.54	7.62	103	1,597
		7.99	7.39	97	1,486
		8.19	7.39	97	1,486
		11.13	7.24	95	1,325
		11.25	7.24	95	1,325
	Upper West Branch	20.78	7.55	76	1,244
		25.07	7.53	69	1,611
		32.72	7.20	68	2,182

Table 12. Drainage area and gradient for each site and proportion in forest, open, and wetlands for regions within the Sheepscot River watershed.

Year	RegionCode	Site	Drainage Area (ha)	Gradient	Forest	Open	Swamp
2005	Middle Mainstem	19.47	38,607.31	0.11	0.61	0.16	0.10
		25.58	37,687.05	0.03	0.61	0.15	0.10
		26.21	37,622.68	0.03	0.61	0.15	0.10
		26.53	37,604.21	0.03	0.61	0.15	0.10
		26.70	37,049.27	0.03	0.61	0.15	0.10
	Mainstem Above West Branch	32.32	20,785.53	0.47	0.65	0.10	0.12
		32.48	20,781.30	0.58	0.65	0.10	0.12
	Upper Mainstem	40.51	12,849.35	0.07	0.67	0.10	0.11
		40.68	12,844.11	0.07	0.67	0.10	0.11
		45.65	12,142.47	0.49	0.67	0.10	0.10
		46.22	12,100.90	0.41	0.67	0.10	0.10
	Lower West Branch	0.54	13,181.01	0.31	0.56	0.22	0.08
		7.99	11,258.78	0.24	0.56	0.22	0.09
		8.19	11,116.28	0.24	0.56	0.22	0.09
		11.13	9,118.96	0.12	0.56	0.22	0.09
		11.23	9,117.38	0.12	0.56	0.22	0.09
	Upper West Branch	20.78	5,278.86	0.33	0.58	0.18	0.10
		25.07	3,563.43	0.20	0.58	0.16	0.12
		32.72	2,426.05	0.11	0.59	0.17	0.09

Table 13. Density estimates (number per 100 m^2) of non-Atlantic salmon fishes at sites throughout the Sheepscot River, 2005 - 2006.

Year	RegionCode	Site	Centrarcids	Cyprinids	American eel	Sea lamprey	Esocid	Sucker	Trout
2005	Middle Mainstem	19.47	2.21	14.40	6.92	0.00	0.00	0.00	0.00
		25.58	1.89	4.03	1.42	0.47	0.00	0.00	0.00
		26.21	1.06	25.14	2.12	0.00	0.00	0.00	0.00
		26.53	3.57	14.67	3.97	0.00	0.00	0.40	0.00
		26.70	1.28	4.78	1.59	0.00	0.00	0.00	0.00
	Mainstem Above West Branch	32.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		32.48	0.54	1.88	3.23	0.00	0.00	0.00	0.00
	Upper Mainstem	40.51	0.72	24.76	10.05	0.36	0.00	0.00	0.00
		40.68	0.00	7.49	6.42	0.00	0.00	0.00	0.00
		45.65	0.00	12.27	0.00	0.00	0.00	0.74	2.23
		46.22	0.00	17.94	2.99	0.00	0.00	4.78	1.20
	Lower West Branch	0.54	3.73	56.38	0.62	0.00	0.00	0.00	0.00
		7.99	4.69	85.84	12.07	0.00	0.00	0.00	0.00
		8.19	10.57	81.52	9.56	0.50	0.00	1.51	0.00
		11.13	0.90	54.82	1.81	0.00	0.00	0.30	0.00
		11.23	1.23	132.15	1.84	0.00	0.00	3.69	0.00
	Upper West Branch	20.78	0.00	77.56	1.22	0.00	0.00	0.41	0.41
		25.07	0.00	75.93	0.96	0.00	0.00	0.96	0.00
		32.72	1.52	15.72	1.01	0.00	0.00	2.03	0.00
2006	Middle Mainstem	19.47	0.28	0.00	2.21	0.00	0.00	0.00	0.00
		25.58	0.82	3.29	4.94	0.00	0.82	0.82	0.00
		26.21	0.00	0.82	0.27	0.27	0.00	0.00	0.00
		26.53	0.79	11.50	2.38	0.00	0.40	0.00	0.00
		26.70	0.64	4.78	1.91	0.00	0.00	0.00	0.00
	Mainstem Above West Branch	32.32	0.00	1.20	0.60	0.00	0.00	0.00	0.00
		32.48	0.00	2.69	4.84	0.00	0.00	0.00	0.00
	Upper Mainstem	40.51	0.00	13.63	3.23	0.00	0.00	0.36	0.00
		40.68	0.00	2.14	0.00	0.00	0.00	0.00	0.00
		45.65	0.00	5.95	0.00	0.00	0.00	0.00	0.37
		46.22	0.00	7.18	2.99	0.00	0.00	0.00	0.00

Table 13. Continued.

Year	RegionCode	Site	Centrarcids	Cyprinids	American eel	Sea lamprey	Esocid	Sucker	Trout
2006	Lower West Branch	0.54	1.04	14.92	0.62	0.00	0.00	0.00	0.00
		7.99	0.45	17.81	1.34	0.00	0.00	0.00	0.00
		8.19	1.01	25.66	7.55	0.00	0.00	0.00	0.00
		11.13	0.30	9.64	0.90	0.00	0.00	0.30	0.00
		11.25	0.61	86.66	3.07	0.00	0.00	5.53	0.00
	Upper West Branch	20.78	0.00	57.66	1.62	0.00	0.00	0.41	0.41
		25.07	0.00	59.53	2.45	0.00	0.00	0.00	0.00
		32.72	0.51	69.45	3.55	0.00	0.00	0.00	0.00

Table 14. Pearson correlation coefficients of macrohabitat variables and density of non-salmon fish species in the Sheepscot River, 2005 - 2006. Numbers in bold indicate significant correlations ($p < 0.05$).

Year		Mean sp. cond.	Drainage area	Gradient	Forest	Open	Wetland	Hours > 20ºC	Centrarcid	Cyprinid	Eel	Lamprey	Esocid	Sucker	Trout
2005	Mean pH	**0.65**	**0.41**	-0.42	**-0.60**	**0.57**	**-0.39**	0.20	**0.52**	0.17	-0.14	0.08	.	-0.17	-0.36
	Mean sp. cond.		-0.07	0.14	**-0.93**	**0.95**	**-0.70**	-0.15	**0.48**	**0.73**	0.13	0.03	.	0.06	-0.40
	Drainage area			-0.10	0.15	-0.10	0.00	**0.54**	0.15	**-0.57**	-0.02	0.31	.	-0.47	-0.27
	Gradient				-0.16	0.25	-0.29	0.06	0.06	0.09	-0.23	-0.03	.	-0.10	0.04
	Forest					**-0.97**	**0.64**	0.17	**-0.42**	**-0.71**	-0.03	-0.01	.	-0.04	**0.43**
	Open						**-0.77**	-0.17	**0.48**	**0.70**	0.09	0.05	.	0.04	-0.38
	Wetland							0.07	-0.39	**-0.40**	-0.11	-0.12	.	-0.16	0.12
	Hours > 20ºC								0.17	**-0.56**	-0.17	0.09	.	-0.08	0.01
	Centrarcid									0.23	0.32	0.37	.	-0.07	-0.24
	Cyprinid										0.11	-0.03	.	**0.39**	-0.09
	Eel											0.01	.	-0.11	-0.22
	Lamprey												.	-0.15	-0.15
	Esocid													.	.
	Sucker														0.36

Table 14. Continued.

Year		Mean sp. cond.	Drainage area	Gradient	Forest	Open	Wetland	Hours > 20ºC	Centrarcid	Cyprinid	Eel	Lamprey	Esocid	Sucker	Trout
2006	Mean pH	**0.77**	0.31	0.26	**-0.79**	**0.75**	**-0.40**	-0.12	0.23	0.23	0.09	0.09	0.00	0.00	-0.02
	Mean sp. cond.		0.00	0.28	**-0.97**	**0.99**	-0.74	**-0.40**	0.21	**0.36**	0.12	0.03	0.06	0.27	-0.12
	Drainage area			-0.10	0.15	-0.10	0.00	**0.44**	0.31	-0.51	0.12	0.28	0.25	-0.22	-0.29
	Gradient				-0.16	0.25	-0.29	0.01	0.10	-0.07	-0.13	-0.02	-0.01	-0.28	0.08
	Forest					**-0.97**	**0.64**	0.37	-0.14	**-0.51**	-0.13	-0.02	-0.01	-0.28	0.08
	Open						**-0.77**	**-0.42**	0.19	**0.41**	0.11	0.02	-0.01	0.30	0.10
	Wetland							0.32	-0.30	-0.22	-0.03	-0.01	0.08	-0.27	0.08
	Hours > 20ºC								-0.07	-0.28	0.13	0.14	0.09	**-0.38**	-0.13
	Centrarcid									0.15	**0.72**	**0.66**	0.07	0.01	-0.22
	Cyprinid										0.37	0.17	-0.12	**0.56**	0.19
	Eel											**0.73**	0.12	0.03	0.14
	Lamprey												-0.07	-0.07	-0.08
	Esocid													0.07	-0.08
	Sucker														-0.02

Table 15. Potential models to describe the variability in Atlantic salmon apparent fry (S_f) and age 0+ parr (S_0) survival in the Sheepscot River, 2005 - 2006. Each model is comprised of non-correlated predictor variables. The variables Forest, Open, and Wetland represent the proportion of the drainage area upstream of an electrofishing site with that type of land cover. Fish species groups represent the density (number per 100 m^2) of that group. The variable Hours > 20ºC represents the total number of hours that temperature exceeded 20ºC betwen May and September of each year. Akaike's Information Criteria (AIC) was used to select the best five models for each apparent survival for further analysis. Models represent arcsine-square root transformed survivals.

	Model	R^2	AIC
$S_f =$	Drainage area + Gradient + Forest + Eel + Lamprey + Sucker	0.81	-79.73
	Mean Specific Conductance + Drainage area + Gradient + Eel + Lamprey + Sucker + Trout	0.83	-79.05
	Drainage area + Gradient + Open + Eel + Lamprey + Sucker + Trout	0.81	-77.82
	Centrarcid + Gradient + Cyprinid + Eel + Lamprey + Trout	0.68	-69.71
	Mean pH + Gradient + Cyprinid + Eel + Lamprey + Sucker + Trout	0.69	-67.85
	Forest + Gradient + Hours > 20ºC + Eel + Lamprey + Sucker	0.65	-67.78
	Drainage area + Gradient + Wetland + Centrarcid + Eel + Lamprey + Sucker + Trout	0.71	-67.38
	Mean Specific Conductance + Hours > 20ºC + Eel + Lamprey + Sucker + Trout	0.61	-65.97
	Open + Gradient + Hours > 20ºC + Eel + Lamprey + Sucker + Trout	0.64	-65.20
	Hours > 20ºC + Gradient + Centrarcid + Eel + Lamprey + Sucker + Trout	0.54	-60.79
	Mean pH + Gradient + Hours > 20ºC + Eel + Lamprey + Sucker + Trout	0.53	-60.40
	Wetland + Gradient + Hours > 20ºC + Centrarcid + Eel + Lamprey + Sucker + Trout	0.54	-58.83
	Centrarcid + Gradient + Eel + Lamprey + Sucker + Trout	0.18	-51.55
$S_0 =$	Mean pH + Hours > 20ºC + Gradient + Centrarcid + Cyprinid + Trout	0.79	-29.12
	Drainage area + Gradient + Open + Eel + Sucker + Trout	0.71	-24.90
	Drainage area + Gradient + Wetland + Eel + Sucker + Trout	0.71	-24.88
	Drainage area + Gradient + Forest + Eel + Sucker + Trout	0.70	-24.69
	Drainage area + Gradient + Wetland + Cyprinid + Eel + Trout	0.69	-24.20
	Mean pH + Drainage area + Gradient + Eel + Sucker + Trout	0.69	-23.94
	Mean pH + Drainage area + Gradient + Cyprinid + Eel + Trout	0.68	-23.74
	Drainage area + Gradient + Wetland + Centrarcid + Sucker + Trout	0.68	-23.54
	Mean specific conductance + Drainage area + Gradient + Wetland + Eel + Sucker + Trout	0.71	-23.03
	Drainage area + Gradient + Open + Centrarcid + Sucker + Trout	0.65	-22.69
	Drainage area + Gradient + Wetland + Lamprey + Sucker + Trout	0.64	-22.34
	Drainage area + Gradient + Forest + Centrarcid + Sucker + Trout	0.64	-22.31
	Drainage area + Gradient + Open + Lamprey + Sucker + Trout	0.64	-22.13
	Drainage area + Gradient + Forest + Lamprey + Sucker + Trout	0.64	-22.09
	Mean pH + Drainage area + Gradient + Centrarcid + Cyprinid + Trout	0.63	-21.92
	Drainage area + Gradient + Wetland + Cyprinid + Lamprey + Trout	0.63	-21.84
	Mean pH + Drainage area + Gradient + Cyprinid + Lamprey + Trout	0.63	-21.84
	Mean pH + Drainage area + Gradient + Lamprey + Sucker + Trout	0.63	-21.83
	Mean specific conductance + Drainage area + Gradient + Wetland + Centrarcid + Sucker + Trout	0.68	-21.75
	Wetland + Gradient + Hours > 20ºC + Cyprinid + Lamprey + Trout	0.61	-21.05
	Wetland + Gradient + Hours > 20ºC + Cyprinid + Eel + Trout	0.59	-20.58
	Mean specific conductance + Drainage area + Gradient + Wetland + Lamprey + Sucker + Trout	0.64	-20.34
	Wetland + Gradient + Hours > 20ºC + Centrarcid + Cyprinid + Trout	0.57	-19.79
	Forest + Gradient + Hours > 20ºC + Eel + Trout	0.47	-19.69
	Forest + Gradient + Hours > 20ºC + Lamprey + Trout	0.39	-17.32
	Forest + Gradient + Hours > 20ºC + Centrarcid + Trout	0.31	-15.81

Table 16. Regression models for predicting juvenile Atlantic salmon survival. Abbreviations area as follows: S_f = survival from fry to age 0+ parr, S_0 = survival from age 0+ to age 1+ parr, S_f^* = survival from fry to age 0+ parr adjusted to account for streamside incubated fry in the West Branch Sheepscot River, N = number of sites used in model, and AIC = Akaike's information criteria. All slope parameters were significantly different from 0 ($p < 0.05$). Models represent arcsine-square root transformed survivals.

Model	N	R^2	AIC
S_f = 1.53 - 0.000011·Drainage area - 1.73·Proportion forested	19	0.70	-79.06
S_f= 0.28 - 0.000011·Drainage area+ 0.0031·Mean specific conductance	19	0.72	-79.78
S_f = 0.24 - 0.000011·Drainage area + 1.54·Proportion open	19	0.69	-78.16
S_f = 0.14 - 0.0039·Cyprinid density	19	0.54	-72.76
S_0 = 5.86 - 0.059·Mean pH - 0.00077·Hours > 20ºC + 0.012·Cypinid density	13	0.70	-30.42
S_0 = 1.01 - 0.000029·Drainage area	13	0.56	-29.73
S^*_f = 0.37 - 0.0000083·Drainage area	19	0.59	-89.30
S^*_f = 0.14 + 0.0022·Cyprinid density	19	0.35	-80.36

Table 17. Estimated total age 1+ parr populations by river region and the number of smolts assigned to known matings whose offspring were stocked in that region.

Region	Age 1+ parr population	Number of assigned smolts
Middle Mainstem	144 (142)	12
Mainstem Above West Branch	300 (295)	4
Upper Mainstem	509 (183)	9
Lower West Branch	2,218 (618)	44
Upper West Branch	5,406 (2,278)	81

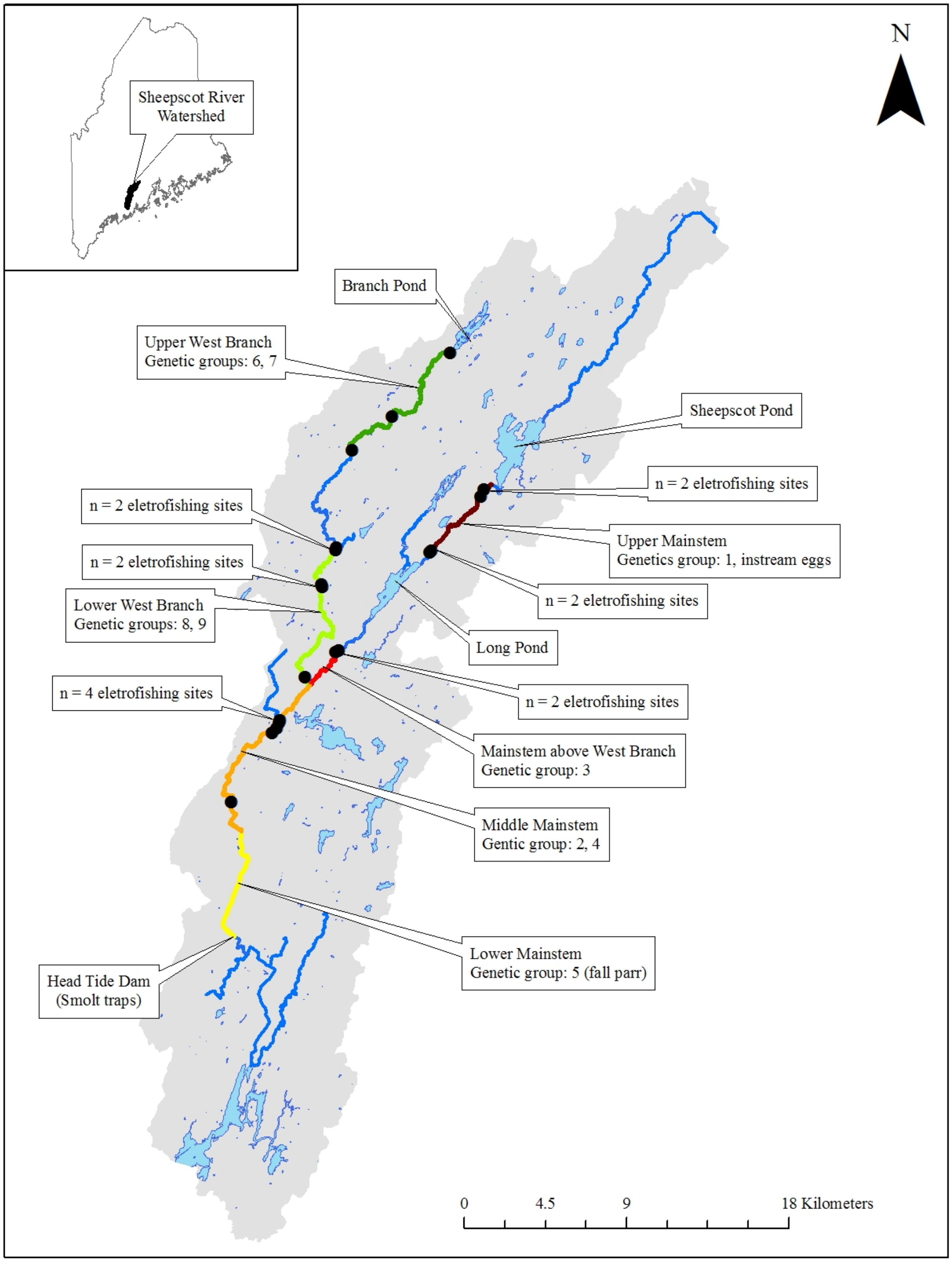

Figure 1: Map of the Sheepscot River watershed showing study regions and genetic groups stocked. Black dots represent electrofishing sites for parr (n = 19).

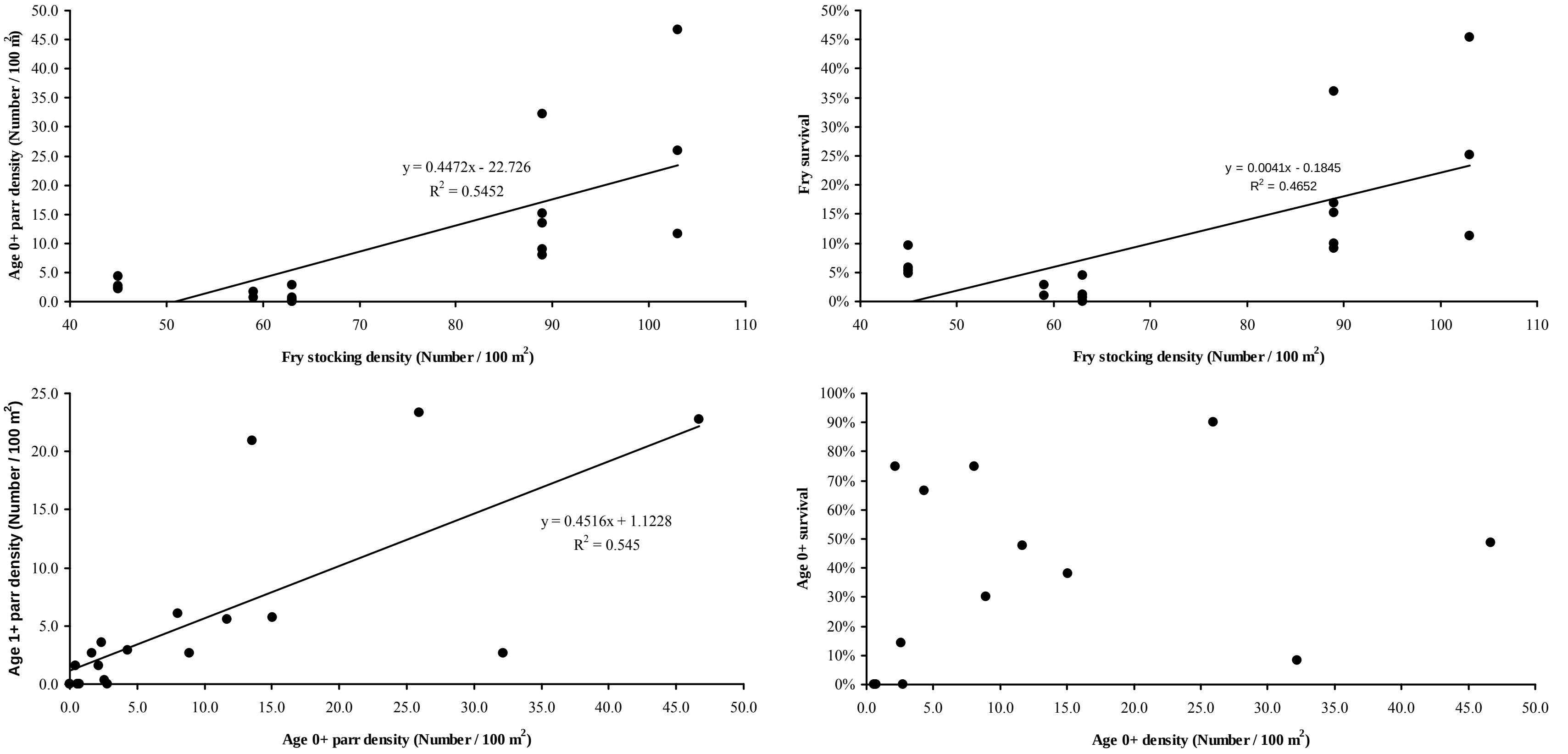

Figure 2: Examination of density dependence in fry and parr survival in the Sheepcot River. There was no evidence of density dependent survival. As fry stocking density increased, so did age 0+ parr density at an electrofishing site. Likewise, as age 0+ parr density increased, so did age 1+ parr density. Neither fry or age 0+ survival showed a decline or an asymptote as density increased. Regression lines shown on the graphs had significant slopes (*p* < 0.05 in all cases).

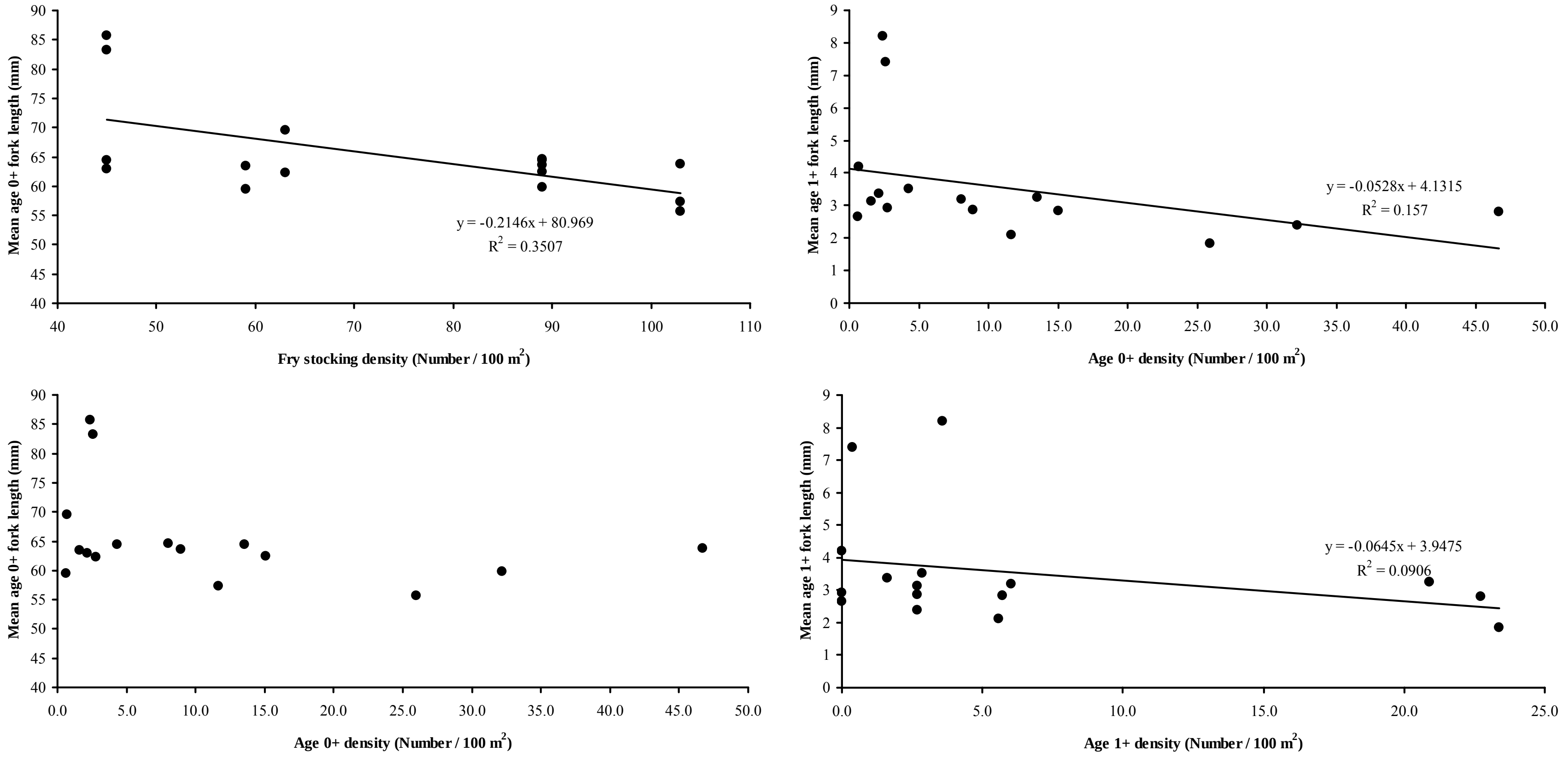

Figure 3: Examination of density dependent growth of parr in the Sheepcot River. Density dependent growth was evident at both the age 0+ and age 1+ stages. For age 0+ parr, mean fork lengths decreased as stocking density at a site increased. For age 1+ parr, mean for lengths decreased as age 0+ parr densities from 2005 year increased, and age 1+ parr densities in 2006 increased. Regression lines shown on the graphs had significant slopes ($p < 0.05$ in all cases).

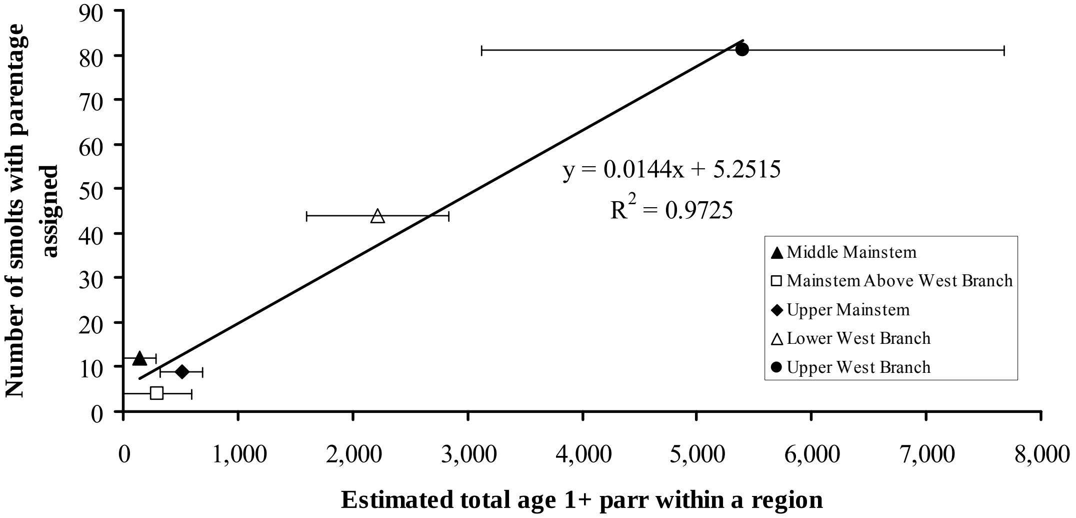

Figure 4: Plot of the number of smolts assigned to known matings whose offspring was stocked in a given river region versus the estimated total parr within that region. Error bars represent standard deviations of the total parr estimates.