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The effects of environmental and biological factors on the length of Atlantic Salmon *Salmo salar* age 1+ parr in three Maine drainages

Running Head: Effects on *Salmo salar* parr length in Maine

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For submission to Transactions of the American Fisheries Society

Abstract

Atlantic salmon *Salmo salar* in the United States have been the focus of recovery efforts for >150 years, but long-term analyses of juvenile demographics are limited. We examined how parr size (fork length; FL) varied across three Maine drainages (East Machias, Narraguagus, and Sheepscot) 1980-2014 and was affected by habitat and biological variables using a long-term electrofishing dataset. We fit generalized additive mixed models (GAMMs) to determine how parr FL varied with explanatory variables, including mean summer air temperature, elevation, mean channel width, juvenile salmon density, age-0 parr stocked, a metric for number of effective fry stocked, and year. When examining model-averaged GAMM results, we found parr size varied throughout the 34-year time-period across the three drainages. Between 1980 – 2014, parr FL in the Sheepscot drainage (mean 143.9 mm) steadily increased (~5-mm increase) while parr FL in the Narraguagus drainage (mean 124.4 mm) declined from 1980 - ~2005, then increased from 2006 - 2014, and parr FL in the East Machias drainage (mean 127.7 mm) experienced a ~10-mm decrease. Density dependence was evident across drainages, suggesting that habitats were at capacity or parr were experiencing competition. Given that the production of parr in Maine is highly reliant on stock enhancement, localized high stocking densities may limit parr growth without further restoration or habitat improvements. Stocking intensities generally decreased in all three drainages post-2000, possibly relaxing density dependence and partially explaining FL plateauing or increasing in recent years in Sheepscot and Narraguagus. Relationships between FL and summer air temperatures were drainage-specific, while wide channels and lower elevations were consistently associated with larger parr. Given our results,

management should continue to prioritize habitat improvements to improve local carrying capacity and potentially reduce density-dependent growth to increase stock enhancement efficacy within an adaptive management framework at Atlantic salmon's southern range edge.

Introduction

Atlantic salmon *Salmo salar* in the United States have been a focus of conservation concern for over 150 years (Parrish et al. 1998). Even after the Gulf of Maine distinct population segment (GOM DPS) was listed on the Endangered Species Act in 2000, recovery has been elusive (USFWS and NMFS 2000). Stock enhancement continues to add juvenile Atlantic salmon in Maine streams and rivers to maintain local populations (Wagner and Sweka 2011), with most fish present being of presumed hatchery origin due to continued low natural production. Even with these consistent stock enhancement efforts, there is little evidence of increased juvenile production thus far, with densities of juveniles holding steady or decreasing over the past three decades (Wagner and Sweka 2011; USASAC 2021). However, fish density is only one measure of productivity for juvenile fishes, as size and physical condition of individuals can also affect survival at later life history stages (Good et al. 2001; Armstrong 2018). Reduced growth of parr has also been suggested to reduce population productivity (Swansburg et al. 2002; Arnekleiv et al. 2006). Parr growth influences smolt size at age and the survival and condition of smolts are suggested to in turn influence the rate of adult returns (Baglinière et al. 2005; Armstrong et al. 2018). Thus, identifying trends in parr size over the past decades can further inform recovery efforts and help identify factors that affect parr productivity to determine actions that could maximize the efficacy of stock enhancement and aid population recovery.

Beyond characterizing how parr sizes have varied in recent decades, identifying biological and environmental correlates of parr size can further inform stock enhancement locations and procedures. Parr can experience density-dependent growth, when increased juvenile densities result in decreased growth (Jonsson et al. 1991; Marschall et al. 1998; Ward et al. 2009). Within Maine streams, densities of juvenile Atlantic salmon populations have largely declined over the past ~30 years (Wagner and Sweka 2011) and thus it is possible that density dependent limitations of growth have decreased, which would allow parr sizes to increase. growth rates and thus parr size. But it is not known whether these declines in densities have allowed parr size to increase over the same time-period or not. In addition, if densities of parr are declining due to habitat-based limitations in freshwater, we might not expect to see increased parr sizes broadly, particularly in the Gulf of Maine at the southern edge of Atlantic Salmon's distribution.

Density dependence is generally a response to habitat-specific limitations, and environmental conditions can further influence the growth and therefore the size of juvenile Atlantic salmon parr during their freshwater phase (Power 1958; Wagner and Sweka 2011). For example, stream temperature (Gibson 2015), air temperature (Swansburg et al. 2002), and habitat type (Oakland et al. 2004; Davidson et al. 2018) have all correlated with parr size. Atlantic Salmon in Maine streams are at the southern edge of their range, and thus presumed to be among the most likely to exhibit negative relationships between parr size and summer temperatures as observed in Maritime Canada (e.g., Swansburg 2002). However, upstream, higher elevation habitats tend to be smaller habitats (i.e., narrower), which may provide less habitat or growth opportunities for juvenile salmonids (Johnston 2013; Gibson 2015; Hedger et al. 2015), making size-habitat predictions difficult across a drainage.

Within the GOM DPS of Atlantic salmon, the Sheepscot, Narraguagus, and East Machias drainages represent three of the six coastal drainages that have retained remnant populations (USFWS and NMFS 2018). As elsewhere throughout the state, these drainages have experienced intensive stock enhancement efforts with the aim of facilitating recovery. Collectively, these drainages represent a gradient in longitude and latitude, with the East Machias drainage as one of the farthest east among United States populations followed by the Narraguagus drainage and Sheepscot drainage, which is at the current southwestern extreme for North America. In addition, the East Machias drainage is unique in that recent stock enhancement efforts are based on a cooperative program with a non-government agency that stock parr in the fall instead of spring. These drainages represent three of the eight remnant populations within Maine. Collectively these three drainages contain a large portion of the remaining naturally reared parr extant in Maine; natural production remains low, however.

In this study, we assessed long-term variability in lengths of Atlantic salmon parr within these three Maine drainages and identified biological, environmental, and temporal correlates. Specifically, our objectives were 1) determine how juvenile Atlantic salmon length varied among drainages, 2) determine how length varied through time, between the years 1980 and 2014, 3) assess the variations in age through time, and 4) determine if density dependence (i.e., conspecific densities and stocking intensity) or environmental (i.e. summer air temperature, elevation, and channel width) are predictive of juvenile Atlantic salmon length among and within drainages.

Methods

Study Area

For this study, we focused on three drainages (Figure 1) within the Gulf of Maine DPS: the East Machias (~650 km^2), Narraguagus (~600 km^2), and the Sheepscot drainage (~590 km^2)

drainages (Table 1; Table 2). East Machias and Narraguagus salmon are within the Downeast Coastal Salmon Habitat Recovery Unit (SHRU), and Sheepscot, the furthest south, is within the Merrymeeting Bay SHRU (USFWS and NMFS 2018). The Downeast area is mostly commercial forest land and wild blueberry agriculture and rural in nature with ~5 people per square km. East Machias headwaters are 40 m above sea level and the river runs about 60 km through coastally influenced sediments; lakes and low-lying peat bogs are common (Fletcher et al. 1982). Stream habitats occur over a greater range of elevations, including higher altitudes, in the Narraguagus drainage relative to the other two drainages (Figure 1). The Narraguagus headwaters are 122 m above sea level and the mainstem flows about 70 km through steep hills and ridges resulting in deep-cut channels (Baum and Jordan 1982). Intensive restoration efforts have occurred on smaller streams in the upper Narraguagus watershed, with nearly complete stream connectivity restored (USASAC Report 2019). The Sheepscot River is largely surrounded by forested riparian areas, but a higher human population of ~30 people per square km and a higher density of year-round roads relative to the other two drainages yields higher sediment loads. In some areas of the Sheepscot drainage, agricultural lands border streams, resulting in variations in water quality including dissolved oxygen, nutrients, and non-point source pollution (McLean et al. 2007). There are numerous dams within the Sheepscot drainage and there are a few dams and water control structures in the Narraguagus, while the East Machias drainage is nearly barrier-free (Baum and Jordan 1982; Fletcher et al. 1982; Meister 1982).

Electrofishing Data

We used the Electrofishing Archive collected and maintained by the Maine Department of Marine Resources (DMR). This dataset contains information from electrofishing sampling surveys focused on juvenile Atlantic salmon over a 61-year time-period (1956-2017) throughout the entire state of Maine. We focused our efforts on 1980 - 2014 to mirror the availability of temperature data (see details below) and more consistent monitoring effort. These surveys represent the efforts of many different management and research goals, resulting in variable sampling locations across time but all focused on reaches under active management. Sampling followed a standardized protocols for electrofishing and biological sampling of Atlantic salmon (see below; Temple and Pearsons 2007). DMR electrofishing sampling was generally conducted in August and September with common protocols. At each site, samplers with electrofishing units moved upstream in a standardized pass-and-sweep pattern for multiple runs and collected as many stunned salmonids as possible. Additional runs were conducted when more than two individuals were caught. Although samplers attempted to collect all species, Atlantic salmon fry and parr were prioritized. At the end of sampling, the number of fry (age-0) and parr (age-1 and older) collected was recorded. After an anesthetic of either buffered tricaine methanesulfonate (MS-222) or clove oil was given, the fork length (FL; mm) of all captured individuals was recorded. A subset of all Atlantic salmon caught had scales removed for aging (see methods in Haas-Castro et al. 2006). Within our time-period of interest (1980–2014), electrofishing within the East Machias drainage consisted of a total of 36 sites sampled during 131 sampling events that measured 2,469 Atlantic salmon juveniles (Table 1). Within the Narraguagus drainage there were a total of 91 sites sampled during 549 sampling events over 34 years (1980 - 2014) that measured 8,753 Atlantic salmon juveniles. Within the Sheepscot drainage there were a total of 28 sites sampled during 207 sampling events over 31 years (1983-2014) that measured 2,409 Atlantic salmon juveniles. These three drainages account for ~45% (n = 13,631) of the juvenile Atlantic salmon sampled from all Maine salmon rivers from 1980 – 2014. Within the sites sampled, streams were narrowest and at lowest elevations in the East Machias, while elevations in the Narraguagus were both the most variable and the highest (Table 2).

Drainage-Specific Stock Enhancement Procedures

In general, conservation hatcheries in these systems stock fry or plant eggs to supplement wild populations (Baum 1997; USASAC 2021). Managers plant Atlantic salmon eggs in January that hatch in February or March of the same year. Wild fish follow a similar life history, with spawning occurring in October-November the year prior with hatching occurring at similar times as stocked eggs (February or March). Fry from planted and wild spawned eggs emerge from the streambeds in April or May. Fry stocking occurs in May and June in these systems but in different reaches than both wild production and egg planting. Wild, egg-planted, or fry-stocked groups form a single annual cohort of naturally reared fish. This cohort would be captured as age-0 fish during electrofishing in August and September (which we removed via mixture models; see *Data Preparation* below). Typically, a cohort stays within the system where they could be caught as age-1 parr in the following fall's electrofishing surveys before about 85% of the cohort emigrates to sea at age-2 (prior to the following year's sampling). The remaining 15% of parr continue to stay in these systems and may be sampled a second time as age-2 parr before smoltifying at age-3 (< 15%) or a third time for those that smoltify at age-4+ (< 0.5%).

In the East Machias drainage, fry were stocked in most years since 1985 (through 2014 for our analyses). Hatchery age-0 parr were stocked from (2012 – 2014) and were generally the same size as wild fish of the same age. These parr were from the Peter Gray Hatchery (PGH) with egg sources identical to fry sourced from the Craig Brook National Fish Hatchery (CBNFH). Eggs were not stocked in the East Machias drainage during our study. Within the

Narraguagus drainage, efforts were focused on stocking fry annually from 1985 – 2014. Small numbers of age-0 parr (<20,000) were stocked per year in the 1990s and early 2000s. These parr are generally larger than wild fish of the same age. In the Sheepscot drainage, fry were stocked every year 1985 – 2014. Eggs were stocked 2005 – 2014. Age-0 parr were stocked in most years following 1985 by the CBNFH and are also larger than wild fish of the same age.

Data preparation prior to modeling

Within the Electrofishing Archive data for these three drainages, we focused on large age-1 and older parr (hereafter referred to as 1+ parr) to ensure maximal duration in time between stocking and electrofishing to maximize river growth and best ensure size variability reflected local conditions prior to initial smolt emigration. Salmon fry (age-0) were also encountered and captured during electrofishing. To identify and remove fry based on FL, we used mixture models (Figure S1). Mixture models identify likely cutoffs between groupings within multimodal data. We used the "mixtools" package (Benaglia et al. 2009) in R (R Core Team 2019). The drainage-specific size cutoff chosen was the smallest FL that resulted in a <5% probability of being identified an age-0 fish. These FL cutoffs were: 81 mm for East Machias and Narraguagus, and 99 mm for Sheepscot. Thus, all fish at these lengths or larger were assumed to be parr and used in our analyses. We also only included fish < 200 mm FL in analyses to further reduce potential measurement error; very few fish (129; ~0.5% of all measured fish) exceeded this length. There were some obvious recording errors within the data when assessing FL-mass relationships. To remove likely erroneous data in a systematic way, FL values were binned within 10 mm windows and the interquartile range (IQR) of masses within each 10 mm FL bin was calculated. Likely erroneous measurements were defined as when the corresponding mass values were extreme outliers within the FL bin (smaller than the 1st quartile within the window minus two-times the IQR or greater than the 3rd quartile plus two-times the IQR). Bins of 10 mm FL resulted in more consistent auditing of the data than larger size bins (which tended to remove values likely to be valid). Two-times the IQR was used instead of the traditional 1.5-times for the same reason (e.g., 1.5-times resulted in removal of values that did not appear obviously incorrect). A total of 47 fish (approximately ~0.2% of all measured fish) were removed by this process.

Explanatory variables used in modeling

To understand variability in parr lengths, we gathered a series of environmental and biological variables. From the Electrofishing Archive data, we used information on both the sites fished and the individual Atlantic salmon parr captured. Specifically, we used the FL of each captured parr, its age (when available; see details below), and the following variables describing electrofishing sites: mean channel width, year of sampling event, and juvenile salmon density (catch per 100 m^2). A maximum likelihood estimator was used to determine density by conducting multiple runs over the sample area (Temple and Pearsons 2007). Supplemental data sources were used to link further biological and environmental factors to electrofished sites. Each site's elevation was calculated within ArcMAP (ESRI, Redlands CA) by joining site location to a full earth terrain model (GEBCO Compilation Group 2020), that estimated elevations at a spatial resolution of 15 arc seconds (450 m). For each site and each year, we also calculated a mean summer air temperature (MSAT) using Daymet data (Thornton et al. 1997; 2020; 2021), which provides gridded (1 km x 1 km) estimates of daily weather parameters and accessed via the "daymetr" package (Hufkins et al. 2018) in R (R Core Team 2019). Daily air temperatures (available beginning in 1980) were collected for each electrofishing site. For each site and year, MSAT was estimated by calculating the average of daily air temperatures from days 152-243 of each year, which corresponds to June 1st through August 30th (except leap years).

Information on stock enhancement efforts was collected within each drainage each year. Yearly counts of the total number of parr, eggs, and fry stocked within each drainage were recorded (USASAC 2021). Stocking data were not linked to specific sites over all years - thus values only varied by year for all sites within each drainage. Because stocking strategies within drainages varied through time, we also calculated a variable to represent the total potential fry production from stock enhancement efforts. This variable of "estimated fry stocked" was calculated for each year and each drainage by multiplying the number of eggs stocked by a 15% survival rate, and then summing this number with the total of fry stocked (Figure 2). We used 15% as an estimate of egg-to-fry survival, within a range of published estimates (~2% to 35%; Fletcher et al. 1982; Pauwvels and Haines 1994; Legault 2017). In response, we used two explanatory variables describing stock enhancement efforts: our calculated number of the estimated fry stocked and the total number of age-0 parr stocked. Both variables were used because age-0 parr remained within the hatchery until their stocking in October, after August and September electrofishing surveys, and therefore would not be caught until the following year.

Modeling effects on Fork Length

To determine how FL of Atlantic salmon age-1+ parr varied with biological and environmental conditions in the three drainages, we used generalized additive mixed models (GAMMs). GAMMs are semiparametric versions of generalized linear mixed models (Wood 2008; 2017), and allow for flexible, nonlinear relationships between the response and explanatory variables. Generally, the GAMMs used took on the form of:

$$E[y] = \beta_0 + \sum_k S_k(X_k) + S_Q(R_q)$$

where E[y] represents the predicted response on FL, β_0 equals the intercept, k equals the number of explanatory variables, S_k represents the smoothing function for each explanatory variable (X_k), and S_q represents the smoothing function on the random effect variable (R_q). We constructed GAMMs for each drainage; separate models were constructed because data availability among explanatory variables varied among drainages (Table 2). As the GAMMs did not allow for missing values, we only used data for each drainage that contained values for each variable assessed: FL, elevation, mean width, MSAT, year, juvenile salmon density, age-0 parr stocked, estimated fry stocked, and site ID (Table 2). Site ID was used as a random effect within each model. Each explanatory variable was centered by taking the variable and subtracting the mean and divided by two of its standard deviations (Gelman 2008).

Before modelling, potential multicollinearity between and among explanatory variables was assessed. First, Pearson correlation coefficients were calculated between each pair of explanatory variables within each drainage; whenever the absolute value exceeded 0.5, one of the two variables was removed. To determine which variable within each pair to remove, two simple GAMMs were constructed, with FL as the response and one of the two variables as the explanatory variable (with Site ID as a random effect). The variable resulting in the GAMM with the lowest Akaike Information Criterion (AIC) was retained; the other variable was discarded (Zuur et al. 2009). The only exception to this process was when year was correlated with another variable. In these instances, year was retained and the other variable was discarded because one of our main objectives was to characterize changes through time. These effects of discarded variables are visualized in the Supplemental Material (Figure S2; Figure S3; Figure S4). After pairwise correlation issues were resolved, Variance Inflation Factors (VIF) were used to detect any further multicollinearity in the updated global models, with VIFs ≥ 5 of explanatory variables indicating collinearity (Zuur et al. 2009). When a VIF ≥ 5 occurred, the variable with the highest VIF was removed and VIFs recalculated. We identified collinearity for at least one pair of variables for each of the three drainages. Due to Spearman $\rho > |0.5|$ with other variables, age-0 parr stocked and elevation were removed from the Sheepscot global model, estimated fry stocked was removed from the Narraguagus global model, and elevation and estimated fry stocked were removed from the East Machias global model. After removing collinear variables, the three global drainage models prior to variable selection contained either five or six explanatory variables and Site ID as a random effect.

After collinear variables were removed, global GAMMs for each drainage were constructed using the *mgcv* package (Wood 2004; 2011; 2017) in R (v3.6.2; R Development Core Team 2019). Each explanatory variable was entered as a spline, with a maximum degrees of freedom (df) of three allowed per variable to help prevent overfitting. To determine which variables were most important in explaining variability of parr FL, all-subsets regression and model averaging approaches were used. All-subsets regression was completed using the *dredge* function within the *MuMIn* package (Barton 2019) in R (R Development Core Team 2019) to compare models containing every combination of explanatory variables (only the random effect of site ID was kept constant in all models) and rank them based on the AIC. For each model, the AIC weight (w_i) was calculated, which provided the probability that the model was the best model at representing the raw data (Symonds and Moussalli, 2011). We averaged across the top-ranked models to include up to, but not exceeding, 95% by w_i to generate a final model for interpretation. To further assess model fit, deviance explained was assessed. We used each population's final, averaged model to predict and visualize FL of parr across the observed values of explanatory variables.

Temporal changes in age composition

As fish's length was related to its age, we assessed how age composition of parr varied among the three drainages, through time, and with FL to provide further context from our GAMM results. Age was not included as an explanatory variable in the previous GAMMs because only a subset of the fish captured electrofishing were aged via reading scales (~87% in East Machias, ~52% in Narraguagus, and ~84% in Sheepscot). As noted above, we attempted to remove all age-0 fish during the previous mixture model methods; remaining juveniles were parr (ages 1 through 4). Percent contributions of each age class were calculated for cohorts for each drainage. Cohorts were created by subtracting the age of the fish from the sampling year to find the birth year of the fish. We used correlations for the yearly age-1 percentages to investigate how the proportion of age-1 fish (the age class that dominated the data) varied among years. Also, we developed simple GAMMs, one for each drainage, with FL as the response variable and age as the explanatory variable using this subset of data. As with broader GAMMs, these GAMMs included Site ID as a random variable and the explanatory variable (age) was given a maximum df of three.

Results

The East Machias averaged model retained the explanatory variables of mean channel width, MSAT, year, juvenile salmon density, and age-0 parr stocked. Among candidate models, the three best-ranked models that were averaged each had a w_i of ~0.25 – 0.28 (Table 3). All three of these models contained the variables of juvenile salmon density, MSAT, and year (Table 3). The variable of mean channel width was retained in only the third-best model and age-0 parr stocked was retained in the first- and third-ranked models for East Machias (Table 3). The averaged model for East Machias explained 24.7% of the total deviance.

The Narraguagus averaged model retained the explanatory variables of elevation, mean channel width, MSAT, year, juvenile salmon density, and age-0 parr stocked. Ranking candidate models resulted in two models for averaging, with the top-ranked two models having w_i of 0.51 and 0.41 (Table 3). The variables of juvenile salmon density, MSAT, elevation, age-0 parr stocked, and year were all within both top-ranked models for Narraguagus (Table 3). Mean channel width was only found in the top-ranked model for Narraguagus (Table 3). The averaged model for the Narraguagus population explained 40.8% of the total deviance, best among the three populations.

For the Sheepscot population, the best model contained the majority of the model weight (0.535) and was used as the final model (no further averaging needed; Table 3). This model retained the explanatory variables of mean channel width, MSAT, year, juvenile salmon density, and estimated fry stocked. This model explained 32.8% of the total deviance in parr FL. Among the populations, each of the three final averaged models retained at least these four explanatory variables: mean channel width, MSAT, juvenile salmon density, and year (Table 3). The variables of year, juvenile salmon density, and MSAT were all also contained in the top-ranked model for each drainage.

Interannual Effects

Relationships between year and FL varied among the three drainages (Figure 3; Figure 4; Figure 5). The East Machias averaged model represented the strongest negative relationship between FL and year among the three drainages, with FL decreasing by ~10 mm through the mid-2000s (~155 mm to ~145 mm), after which FL remained relatively constant (Figure 3). The

Narraguagus averaged model initially exhibited a similar relationship between year and FL, with decreasing FL until the mid-2000s, but then followed by a ~10-mm increase afterwards (~125 mm to ~135 mm; Figure 4). For the Sheepscot population, a ~10-mm increase was first observed (~145 mm to ~155 mm) between 1980 and 2000, followed by a ~5-mm decrease to ~150 mm until 2013 (Figure 5).

Density Dependent Effects

Evidence of density dependence was observed in all three populations, with the juvenile salmon density variable retained in every top-ranked model that was averaged. In all three drainages, increases in juvenile salmon density resulted in decreases in FL (Figure 3; Figure 4; Figure 5). The East Machias averaged model resulted in the strongest FL-juvenile salmon density relationship with the predicted FL decreasing ~25 mm from ~160 mm to ~135 mm as densities increased (Figure 3). The other two populations also demonstrated a negative FL-juvenile salmon density relationship with predicted FL decreasing ~15 mm from ~165 mm to ~150 mm in the Narraguagus averaged model, and ~125 mm to ~110 mm in the Sheepscot averaged model (Figure 4; Figure 5).

In addition, each drainage retained a stocking variable among its top-ranked models. The East Machias and Narraguagus averaged models both retained the age-0 parr stocked variable (in all three top-ranked models for Narraguagus and in two of the four top-ranked models for East Machias), while the Sheepscot averaged model retained the estimated fry stocked variable (Table 3). Within both the East Machias and Narraguagus averaged models, FL had a positive relationship with the number of age-0 parr stocked. Overall, however, a negative relationship between the number of estimated fry stocked and FL were observed in both the East Machias and Narraguagus populations when examined individually (due to collinearity between year and estimated fry stocked; Figure S2; Figure S3). Within the Sheepscot averaged model, estimated fry stocked showed a similar negative relationship with FL (Figure 5). Age-0 parr stocked was removed from the Sheepscot averaged model due to its collinearity with year, but the when modeled individually a slightly negative age-0 parr stocked-FL trend was observed with FL decreasing ~5 mm from ~145 mm to ~140 mm (Figure S4).

Habitat Effects

Two stream habitat variables were assessed in models: mean channel width and elevation. In all the averaged models, wider channels yielded larger FLs (Figure 3; Figure 4; Figure 5). The East Machias averaged model demonstrated the smallest range of mean channel width (~2 m to ~20 m), which yielded a small increase in FL (~140 mm to ~145 mm; Figure 3). The Narraguagus averaged model demonstrated the largest range in mean channel width (~2 m to ~42 m) and exhibited a slightly larger increase in FL (~120 mm to ~130 mm). The Sheepscot averaged model demonstrated an intermediate range in mean channel width (~4 m to ~32 m), with a ~5-mm predicted increase in FL as well (~150 mm to ~155 mm; Figure 5). Elevation was only retained within the Narraguagus averaged model, with smaller FL occurring at higher elevations in the averaged model (FL dropping from ~130 mm to ~115 mm with increasing elevation from ~10 m to ~130 m; Figure 4). Elevation was correlated to mean channel width and removed for both East Machias and Sheepscot. Therefore, the elevation ~ FL relationship was visually assessed within individual models. Within the individual models for East Machias and Sheepscot there was an overall negative elevation-FL relationship (Figure S2; Figure S4).

Temperature Effects

All models for all drainages that were retained and used in averaging included MSAT. Both the East Machias and Narraguagus models showed an increase of FL between the temperatures of 16°C and 17°C; the minimum MSAT estimated for the Sheepscot drainage was ~ 17°C (Figure 3; Figure 4; Figure 5). From 17.5°C - 19°C, both the East Machias and Sheepscot averaged models demonstrated a ~5-mm decrease in FL (~140 mm to ~135 mm and ~160 mm to ~155 mm; respectively; Figure 3; Figure 5). However, the Narraguagus averaged model demonstrated a different relationship at these higher temperatures; temperatures exceeding 18°C were associated with an increase in FL (~120 mm to ~130 mm; Figure 4).

Age Composition

In all populations, GAMMs demonstrated that increasing age yielded larger FLs (Figure 5). Within the East Machias and Narraguagus drainages, the greater the proportion of age-1 observed in a year, the smaller the mean FL observed (Figure 7). With the proportion of age 1 fish decreasing from ~80% to ~70%, the mean FL increased ~100 mm in both the East Machias and Narraguagus drainages (Figure 7). However, within the Sheepscot model, the opposite was shown, with higher age 1 proportions yielding larger fish (Figure 7). With the proportion of age-1 fish increasing from ~75% to ~85%, the FL increased ~100 mm (Figure 7). The Narraguagus drainage contained parr ranging from age 1 to 4, followed by the East Machias drainage with ages 1 to 3, and then the Sheepscot drainage contained only ages 1 and 2 (Figure 8). Ages were not monitored consistently throughout the years with larger effort post-1990 and 2005 for the Narraguagus and East Machias populations, respectively (Figure 8). Scales from the Sheepscot population were most often aged between 2000 and 2005 (Figure 8). Age-1 fish were the dominant age class among all three drainages and years (85% of all aged fish); any exceptions were characterized by low sample sizes (Figure 8).

Discussion

Atlantic salmon populations in all three drainages showed evidence of variable change in FL of parr throughout the 34-year time-period (1980 – 2014). Parr in both the Sheepscot and Narraguagus drainages experienced increases in FL of ~5 mm, which represents an increase of ~4% of the average fish size (among the drainages) and could indicate modest improvement in parr quality. However, the observed increase in Narraguagus parr occurred in the last ~10 years of the data and only returned FLs to those observed in the 1980s. In addition, East Machias experienced an overall reduction in FL by 5-10 mm from 1980 – 2014. Furthermore, the lengths of parr we observed in these three drainages were similar or smaller than those observed broadly 1950 – 1992 (Baum 1997), further suggesting interannual variability and little historical change in FL. This general lack of increase in length suggests little-to-no improvement in parr growth and is concurrent with documented reductions in density and abundance in the Gulf of Maine populations (Wagner and Sweka 2011; USFWS and NMFS 2018; USASAC 2021). Although we only examined three populations in this study, these trends could be broadly applicable given that these drainages represent two of the three salmon habitat recovery units (SHRUs) found within the Gulf of Maine DPS, cover 34 years of data, and represent wide ranges of environmental conditions within the state.

The bigger-is-better paradigm is a frequently accepted assumption that has been supported for fishes broadly (Pauly 1980; Gislason et al. 2010), stream salmonids (Hume and Parkinson 1988; Connor and Tiffan 2012), and specifically juvenile Atlantic salmon (Saloniemi et al. 2004; Armstrong et al. 2018). However, some populations can lack this size-survival relationship (Newton et al. 2016; Gregory et al. 2018) or exhibit decreased survival at larger sizes in habitats with little food availablility (Griswold et al. 2011). For Pacific salmon species, a growth or size threshold (rather than a monotonic relationship) may be needed for juvenile salmon to survive their early marine experience (Beamish and Mahnken 2001). In addition, the bigger-is-better paradigm focuses on the perspective of an individual fish; but larger mean body size in the population might not be a positive sign of recovery if it is the result of very low population sizes (and thus very little density dependence experienced). Thus, the importance of Atlantic salmon parr size may be context-specific and habitat-quality dependent. Studies investigating variability in body condition (modified mass:weight ratio), further biomarkers indicative of health, and survival would complement this study on length and previous work on densities (Wagner and Sweka 2011) to further inform the current state of Atlantic salmon in populations across Maine and identify important predictive variables.

Evidence of density dependence was observed in all three drainages, as both juvenile salmon density (in all three averaged models) and estimated fry stocked (in the Sheepscot averaged model) exhibited negative relationships with FL (Figure 3; Figure 4; Figure 5). Density-dependent growth can occur due to intraspecific competition over food and space (Marschall et al. 1998; Ward et al. 2009; Jonsson et al. 2020) and can lead to dispersal (Einum et al. 2006; Brunsdon et al. 2017). However, density dependent growth in juvenile Atlantic salmon consistently occurs at low salmon densities (Grant and Imre 2005), which may be the result of either exploitative competition (Imre et al. 2005) or interference competition (Ward et al. 2007). Further efforts to directly incorporate the densities of competitors (other salmonids) into analyses would be valuable to further elucidate the mechanisms of the density dependence we observed. Regardless, density dependence and potential limitations of stream habitats may have implications for Atlantic salmon in Maine, where stocking efforts are needed currently to maintain Atlantic salmon populations (Wagner and Sweka 2011).

Stock enhancement is often a dominant and necessary choice for population recovery (Baum and Jordan 1982; Fletcher et al. 1982; Meister 1982; Maynard and Trial 2014). However, this process needs to focus on determining the ideal amount of stocking among habitats that will benefit the population the most, rather than stocking the maximum possible quantity of fish. Parr densities and estimated fry stocking densities maintained negative relationships with parr length, providing further evidence of density dependent limitations to lengths. In fact, recent reductions in stocking densities ~post-2010 (Figure 2) are approximately concurrent with predicted increases or stabilization in salmon lengths in most recent years, potentially demonstrating that density-dependent limitations to size can be relaxed. However, the number of age-0 parr stocked yielded variable and even positive relationships with FL in both the East Machias and Narraguagus drainages. However, these responses were either more complex (Narraguagus) or characterized by low sample sizes and wide confidence intervals at higher parr stocking densities (East Machias). Furthermore, we included stocking data coarsely (single value per drainage per year, and thus not spatially explicit) within our models. Thus, we caution against over-interpretation of these results and focus on the clear and consistent density dependent signal observed with local juvenile salmonid densities at the habitat-scale. Atlantic salmon hatcheries are acting to mitigate for reductions in habitat availability and quality (Maynard and Trial 2014), and the observed density-dependence of parr size can help inform future stock enhancement efforts to identify both understocked habitats but also qualitatively identify optimal stocking intensity. In fact, stocking densities in these systems have already been declining since ~2010 (Figure 2), potentially releasing some density-dependence. Regardless, site-specific stocking information within populations would allow for a better understanding of how stocking effort and habitat variables interact to influence parr growth and size. More broadly, we suggest that our understanding of these relationships would be improved if stocking and monitoring efforts and methods were more used consistently among drainages in an adaptive management framework.

Beyond density dependence, summer air temperatures were an important predictor of parr FL, with MSAT retained within every top-ranked model for each of the three drainages, providing informative drainage-specific differences. Sheepscot, the most southern drainage we examined, contained the warmest sites (all MSAT > 18°C) and was the only drainage to show a consistently negative FL-temperature relationship across the range of experienced temperatures. Thus, parr growth may already be temperature-limited in this drainage that is near the current southern limit of this species' range (USFWS and NMFS 2018). Narraguagus was the only drainage to show increased FL at the highest temperatures. Sites within the Narraguagus drainage are also characterized by other factors found to promote large parr, namely lower salmon densities and wider stream channels (discussed below). Thus, it is possible that other optimal habitat characteristics facilitate parr growth even at higher temperatures in this drainage. In addition, parr are mobile and can move between habitats (Dugdale et al. 2016) to exploit variability in food and temperature, including between mainstem and tributary habitats (Cunjak et al. 2005). Parr may be able to find seasonal refuge habitats (or move from mainstem habitat to tributaries) at local scales that are not reflected in our MSAT variable. Thus, potential fine-scale heterogeneity in thermal habitats and parr mobility may help explain why MSAT had variable influences on lengths among populations, but further research is needed. Regardless, among all three drainages, parr lengths generally increased between mean summer air temperatures 15°C and 17.5°C, consistent with findings in laboratory (Elliott and Hurley 1997; Gibson 2015) and field (Foldvik et al. 2017) studies. These studies found parr to grow at a wider range of temperatures, up to 22.5°C (Elliott and Hurley 1997; Gibson 2015). However, we used air temperatures in our models rather than stream temperatures which require care in interpretation. Direct measures of stream temperature may therefore show different, or potentially even stronger, relationships with parr FL, or when not available, modeled products (e.g., Ecosheds; Letcher et al. 2016).

Beyond temperature, habitat-based variables of mean channel width and elevation both were found to correlate with Atlantic salmon parr FL among the drainages. Within this study, wider channels resulted in larger FLs for parr in all three drainages, which is suggested to be metabolically profitable and selected for by parr (Gibson 2015). Wider channels can provide more potential habitat that is deeper and has larger complex substrate which is selected for by parr (Hedger et al. 2005; Johnson 2013). Wider channels allow for salmon to drift feed agnostically while mitigating the impacts of territoriality (Gibson 2015). Larger mean channel widths are most often observed at lower elevations (consistent with expectations regarding stream order), which gives a potential explanation of why both trend with larger fish due to increased feeding opportunities from the larger habitat availability (Gibson 2015). Narrower channel width was correlated with higher elevations in both the East Machias and Sheepscot models, which implies that the FL-elevation relationships would resemble the trends between FL and channel width. This suggests that areas of low elevation could be metabolically profitable for parr as well, provided they are within ideal temperatures. However, fish do not stay in one location nor within a single stream order and parr can move among habitats to optimize foraging or find thermal refugia (Cunjak et al. 2005; Dugdale et al. 2016); although generally parr exhibit little movement (Stickler et al. 2008; Boavida et al. 2017), dispersal of hundreds of meters or even kilometers can occur (Ovidio et al. 2007; Boavida et al. 2017).

Age composition of Atlantic salmon parr likely further reflects growth conditions across the drainages. We consistently observed age-1 parr as the dominant age class among all three drainages and through time. Juveniles are known to leave their stream habitats and smoltify between 1 – 4 years of life (Power 1958; Kocik and Friedland 2002), but the Sheepscot drainage only contained age-1 and age-2 parr, with fish then smoltifying at ages 2 and 3. The Sheepscot population is within the most southerly drainage in this study and contained the largest fish on average, consistent with fewer age classes found at more southern latitudes (Power 1958). Even in the Narraguagus population, where parr ages 1-4 were observed, the contribution of age-2+ parr decreased through ~2005 to < 10% (later years beyond 2005 had much lower sample sizes and variability in age composition). Although few scales from Narraguagus parr were aged prior to the 1980s, a sample of nearly 4,000 scales from Narraguagus smolts were aged 1960-1966, revealing 20% of the emigrating fish were age-3 (Baum 1997); these fish could be encountered as both age-1 then age-2 parr during electrofishing surveys. However, it appears the contributions of age-2+ parr have been reduced, simplifying age composition in the population. Larger age-1 parr (pre-smolts) are more likely to emigrate in the spring as age-2 smolts (Nicieza et al. 1991; Metcalfe and Thorpe 1992; Thorpe et al. 1992; Elliott and Hurley 1997) and warming waters due to climate change could further simplify age structuring in populations provided habitats provide enough productivity to support increased parr growth and therefore increased smoltification and emigration.

There are numerous variables that could further describe variability in parr size. Although the levels of deviance explained by GAMMs for each of the drainages were all reasonable (between 24.7% and 40.8%), most of the variation remained unexplained. Other variables that have been found to influence parr size or growth include, physical habitat characteristics such and stream depth (Oakland et al. 2004; Johnson 2013) and stream discharge (Davidson et al. 2018). Optimal habitats are likely complex, requiring heterogeneous mosaics of these physical characteristics (Waldman et al. 2016) among others such as large woody debris, sediment size, and cover types (Whalen and Parrish 1999; Heggenes et al. 2009; Venter et al. 2008). These physical habitat characteristics likely affect prey availability and may drive parr growth and size (Ward et al. 2009; Jonsson et al. 2020), which is underscored by the consistent influences of salmon density (e.g., density dependence) and summer temperatures on length we observed. Fine-scale variation in microhabitat conditions can yield substantial differences in juvenile salmon growth even within a drainage (Gibson 2002). Thus, future assessments should balance the increasing complexity of models as more habitat variables are measured and included with the ability to scale among streams and among drainages. In addition, use and performance in various habitats may be linked to genetic differentiation, both between wild and hatchery fish (Jonsson et al. 1991; Saloniemi et al. 2004; Araki et al. 2008; Sheehan et al. 2010) but also among wild strains in Maine (King et al. 2000; Spidle et al. 2003), requiring investigation in local adaptation (Obedzinski and Letcher 2004; Sheehan et al. 2005; Wilke and Kinnison 2011). The importance of complex physical habitat characteristics need to be considered in watersheds such as these where active habitat improvements are ongoing with reconnection of cold-water tributaries, instream habitat work, and modified stocking projects.

In conclusion, as recovery efforts in Maine, USA focus on restoring access to habitats by removing dams and other barriers (USFWS and NMFS 2018), it is important to prioritize future stocking and restoration efforts into high-quality locations, taking into account the potential impacts of density dependence, water temperatures, and habitat quality to promote parr growth. Current estimates suggest that much of the region’s suitable rearing habitat may be vacant

(USASAC 2021), and thus if stocking were more evenly distributed between areas where stocking efforts are currently high (minimizing the impacts of density-dependent growth) and underutilized habitats, density-dependent effects could be minimized while via spatially expanding stocking efforts. River and stream temperatures across the U.S. are predicted to increase by 0.01°C – 0.05°C per year, with Maine being on the higher end of this range at an increase of ~0.05°C per year (Kaushal et al. 2010; Fernandez et al. 2020). Atlantic salmon are highly exposed and vulnerable to climate change throughout their lifespan (Borggaard et al. 2019; Hare et al. 2016), which further hinders parr along with suboptimal habitats due to anthropogenic modifications and loss of connectivity (Gibson 2017). Thus, we recommend that effort be put into 1) enhancing habitat quality, 2) decreasing stocking densities in discrete habitat reaches likely to be experiencing density-dependent limitations, and 3) further optimizing stocking site selection to spread stocking efforts into vacant high-quality habitats. Our results suggest some currently stocked habitats may not support optimal growth at current densities. Due to reach-specific factors, we also recommend more rigorous evaluations of ongoing actions in a quantitative adaptive management framework that examines both average size and densities of pre-smolts. Use of an adaptive management framework could also leverage the intensive stock enhancement efforts to conduct further natural experiments to identify conditions that may be successful in rearing high-quality parr or smolts. Creative solutions will be needed for effective conservation of Atlantic salmon at the southern edge of their range (Kocik et al. 2022).

Acknowledgements

We recognize the efforts taken by dozens of field crews over the past several decades to collect these data across the state of Maine. We also thank the numerous database technicians and specialists that modernized these datasets and moved them from paper file cabinets to a relational database. We especially thank Justin Stevens for assistance with the electrofishing database. Furey was supported by UNH School of Marine Science and Ocean Engineering’s Class of 1937 Professorship in Marine Biology. We thank multiple reviewers who provided valuable feedback on earlier versions of the submitted manuscript.

Tables

Table 1 Summary of electrofishing surveys conducted, and the range of sampling years used to sample the Atlantic salmon parr used within the generalized additive mixed models.

	East Machias	Narraguagus	Sheepscot
Sampling years	1980 – 2014	1980 – 2014	1983 – 2014
Number of sites	36	91	28
Number of sampling events	131	549	207
Number of juvenile Atlantic salmon	2469	8753	2409
Mean Fork Length (mm)	127.7	124.4	143.9

Table 2 Summary of explanatory variables evaluated within generalized additive mixed models, including range and mean in parentheses.

	East Machias	Narraguagus	Sheepscot
Mean Summer Air Temperature (°C)	15.74 – 19.00 (17.82)	16.53 – 19.45 (18.15)	17.62 – 19.72 (18.91)
Elevation (m)	19.78 – 84.75 (42.33)	12.15 – 130.18 (86.06)	33.16 – 106.30 (62.30)
Mean Channel Width (m)	2.40 – 20.67 (8.56)	2.87 – 42.47 (13.68)	4.57 – 31.09 (12.04)
Juvenile Salmon Density (catch per 100 m^2)	0.00 – 40.36 (10.22)	0.00 – 24.78 (5.47)	0.09 – 50.27 (10.91)
Age-0 Parr Stocked	0 – 149,815 (3239)	0 – 209,90 (3474)	0 -17,925 (10,708)
Estimated Fry Stocked	0 – 319,138 (174,326)	0 – 698,200 (258,264)	0 – 323,000 (153,384)
Year	1980 – 2014	1980 – 2014	1983 – 2014

Table 3 Rankings for models investigating variability in Atlantic salmon parr FL after all-subsets modelling, with a single model per row and ranked by Akaike Information Criterion (AIC). These models were selected for model averaging for each drainage (containing up to, but not exceeding, 95% of model weights, w_i). Abbreviations are as follows: df = number of parameters, LL = log likelihood, Δ_I = the difference between the AIC value for the i^{th} model and the minimum AIC value for all models for that drainage, - = a variable that was removed during the collinearity process, and a blank represents a variable not included in the given model.

Model Ranking for Population	Juvenile Salmon Density	Estimated Fry Stocked	Elevation	Mean Channel Width	Mean Summer Air Temperature	Age-0 Parr Stocked	Year	df	LL	AIC	Δ_i	w_i
	East Machias											
1	X	-	-		X	X	X	39	-10952.8	21983.8	0.00	0.278
2	X	-	-		X		X	38	-10953.0	21984.0	0.19	0.253
3	X	-	-	X	X	X	X	39	-10952.4	21984.0	0.23	0.248
	Narraguagus											
1	X	-	X	X	X	X	X	84	-37214.8	74597.8	0.00	0.510
2	X	-	X		X	X	X	84	-37214.3	74598.2	0.43	0.410
	Sheepscot											
1	X	X	-	X	X	-	X	36	-9844.0	19760.4	0.00	0.535

Figures

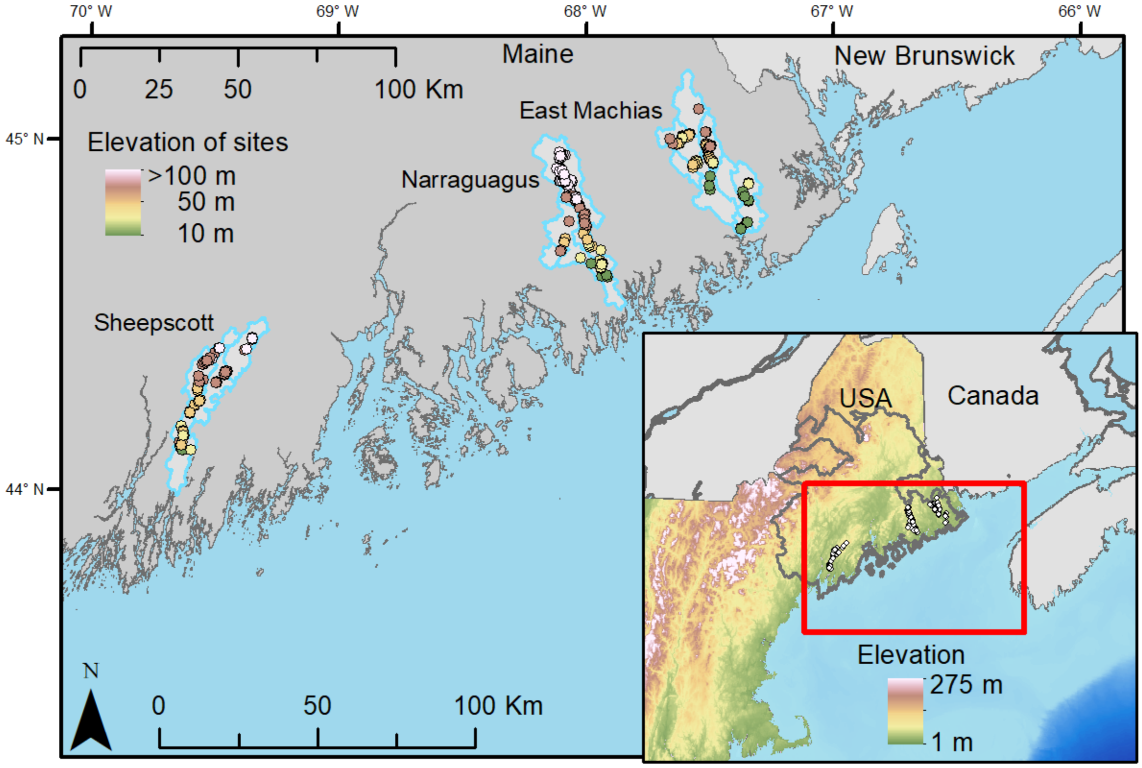

Figure 1 Map of the electrofishing sites within the three Maine drainages used for assessed trends in juvenile Atlantic salmon parr fork length. The HUC-12 drainages containing used data are outlined in light blue in the main panel. Points represent electrofishing sites used in analyses and are colored relative to each site's elevation. In the inset (bottom right), the grey outline represents the boundary of the Gulf of Maine distinct population segment (DPS; https://www.fisheries.noaa.gov/resource/map/atlantic-salmon-gulf-maine-dps-boundaries). Please note that the scaling of colors between the main panel and the inset vary to increase visibility of variability in elevations at each scale.

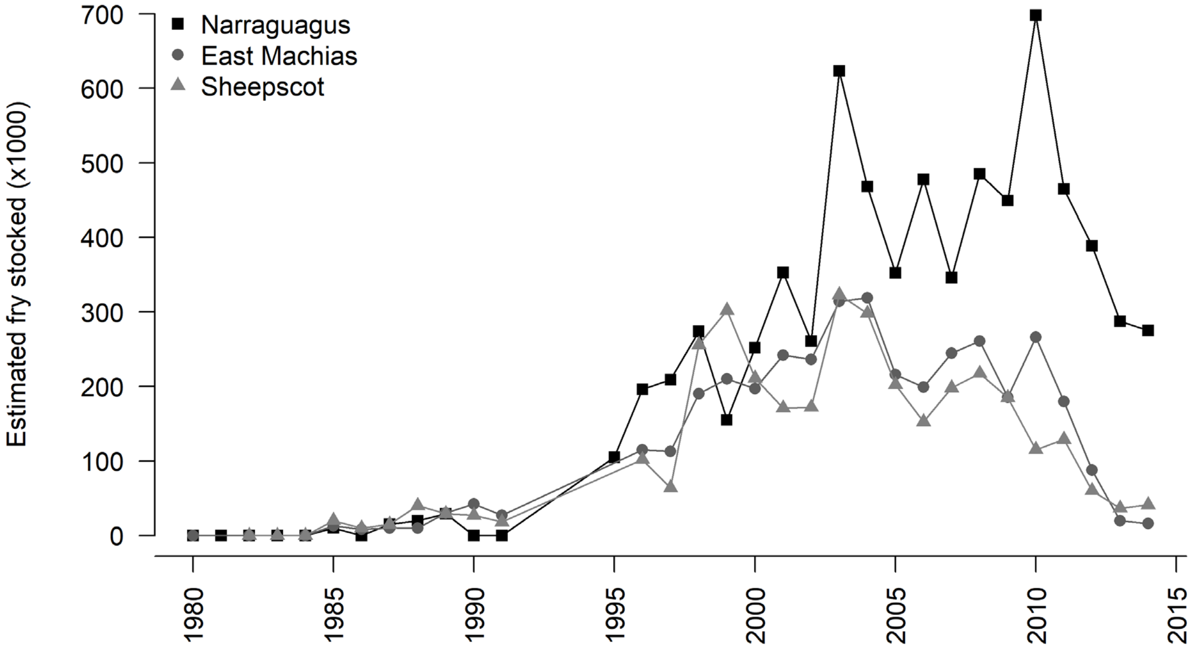

Figure 2 Summary of stock enhancement efforts in the three Maine drainages of interest through time, using calculated metric of equivalent or estimated amount of fry stocked (see Methods for details of calculation) during the years of interest (1980 – 2014).

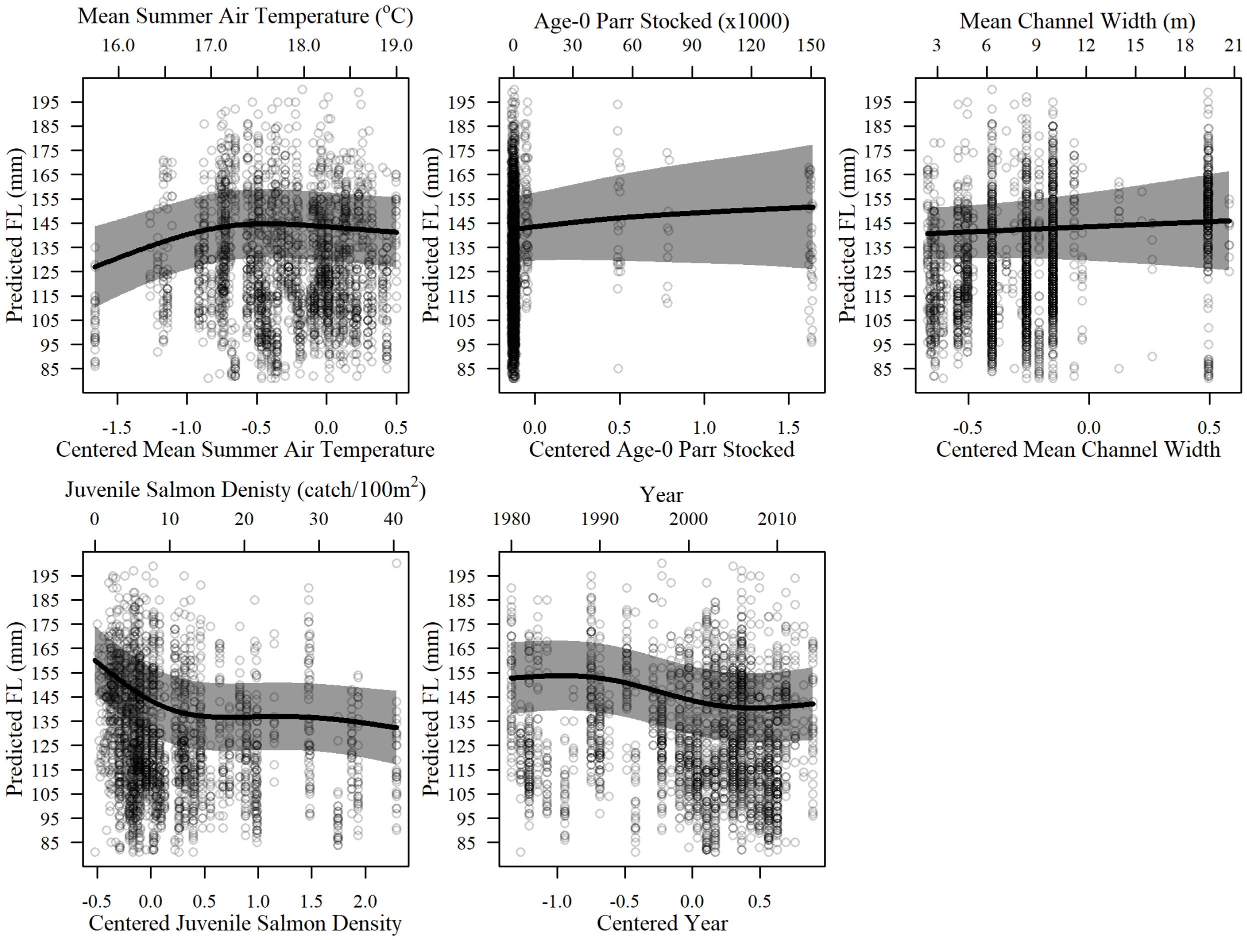

Figure 3 Predicted response curves of the relationships among explanatory variables and Atlantic salmon parr fork length as generated through generalized additive mixed models for the East Machias population. The dots represent an individual fish. The grey polygon represents the 95% confidence interval of the predicted response curve.

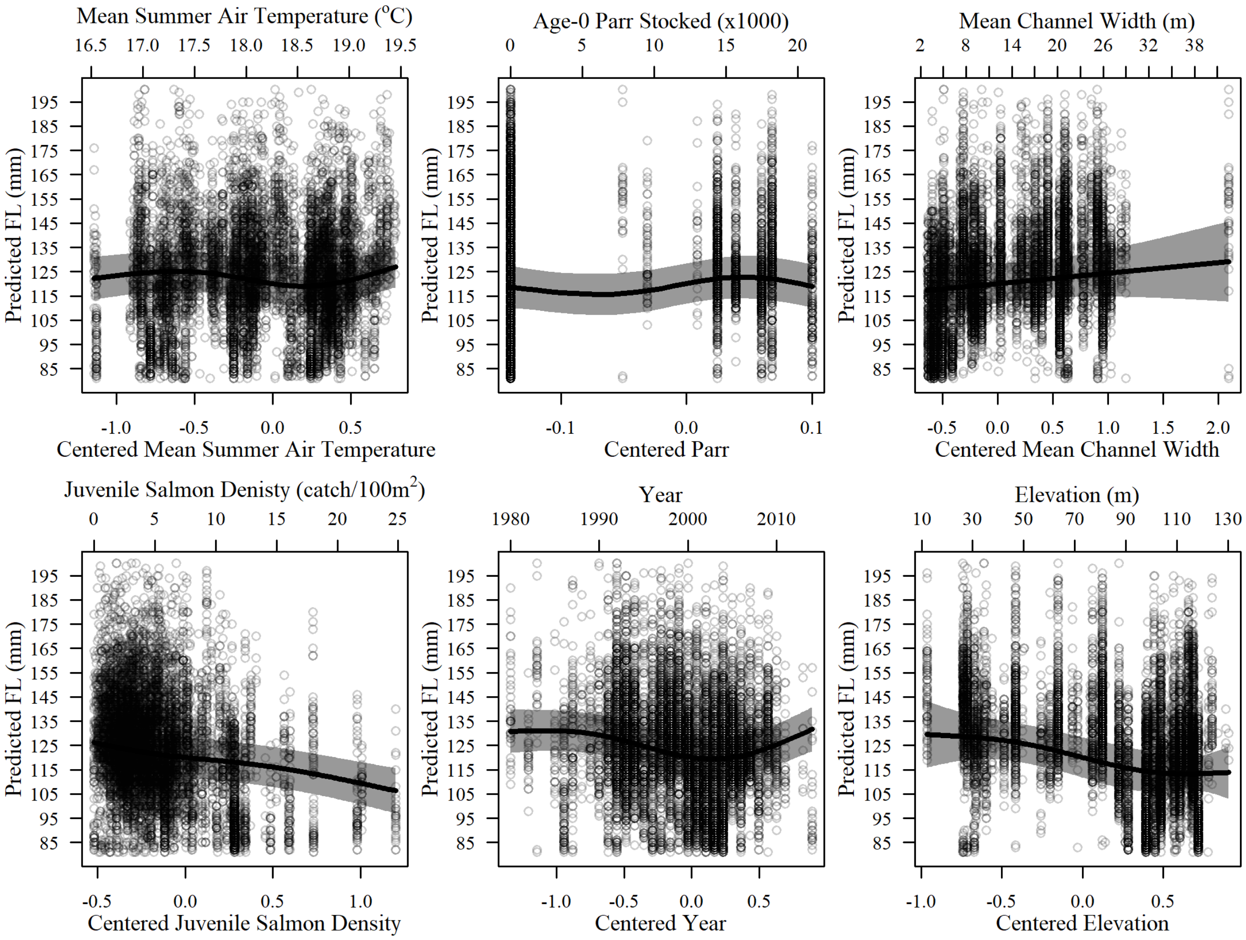

Figure 4 Predicted response curves of the relationships among explanatory variables and Atlantic salmon parr fork length as generated through generalized additive mixed models for the Narraguagus population. The dots represent an individual fish. The grey polygon represents the 95% confidence interval of the predicted response curve.

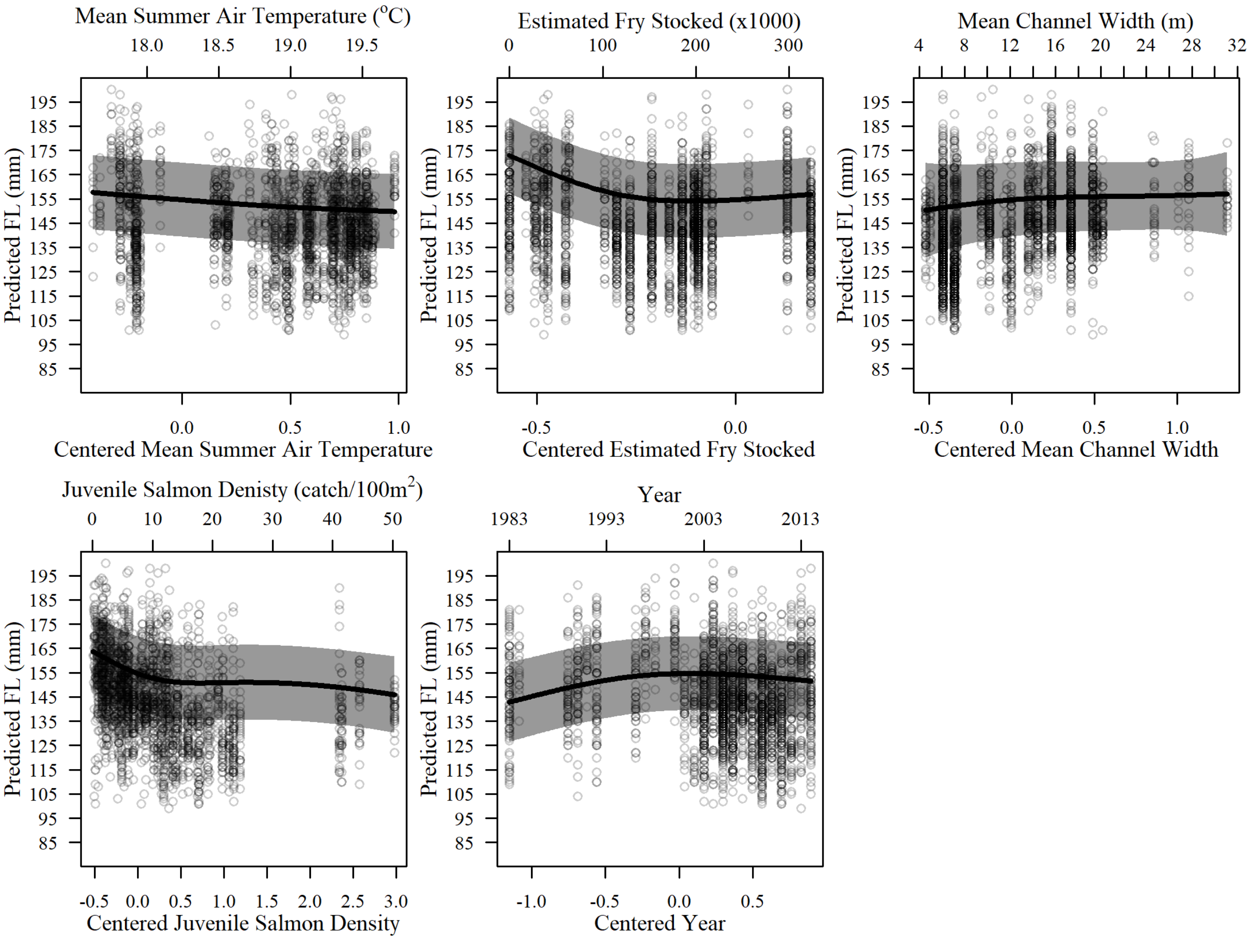

Figure 5 Predicted response curves of the relationships among explanatory variables and Atlantic salmon parr fork length as generated through generalized additive mixed models for the Sheepscot population. The dots represent an individual fish. The grey polygon represents the 95% confidence interval of the predicted response curve.

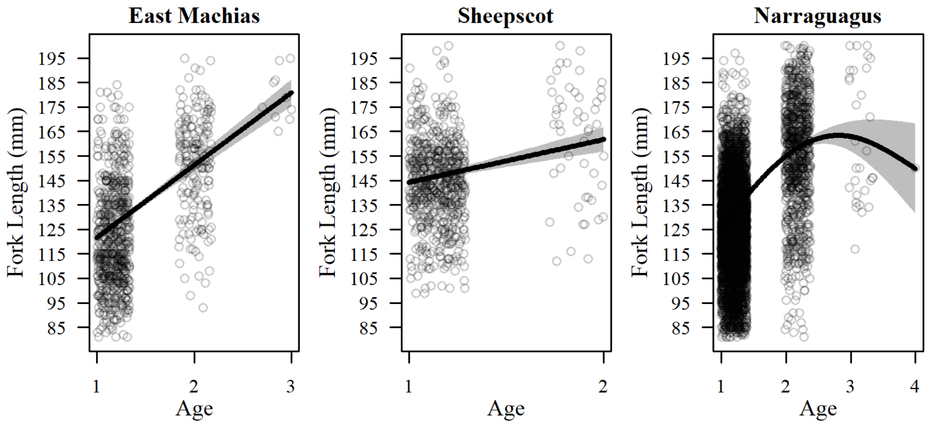

Figure 6 Response curves of the relationship of Atlantic salmon parr age and their fork length as generated through generalized additive models for each population. The dots represent an individual fish with darker shading in higher concentrations of fish. The grey polygon represents the 95% confidence interval of the predicted response curve.

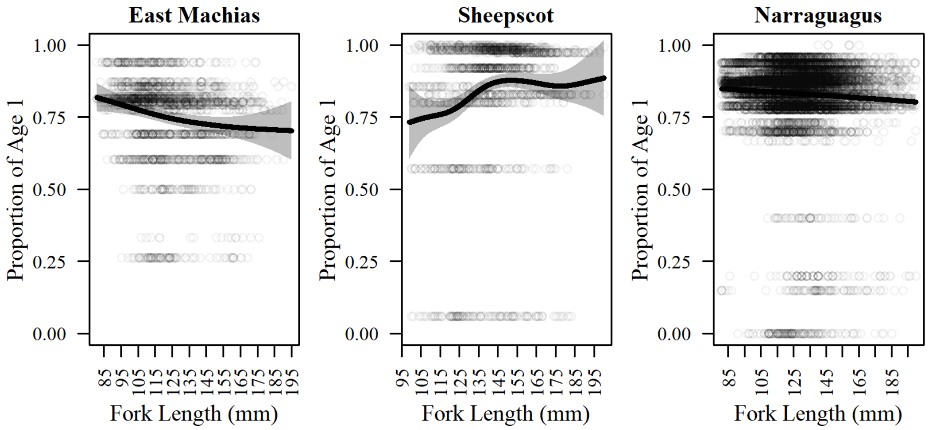

Figure 7 Response curves of the relationship of Atlantic salmon parr fork length and proportion of age-1 Atlantic salmon as generated through generalized additive models for each population. The dots represent an individual fish with darker shading indicating higher concentrations of fish. The grey polygon represents the 95% confidence interval of the predicted response curve.

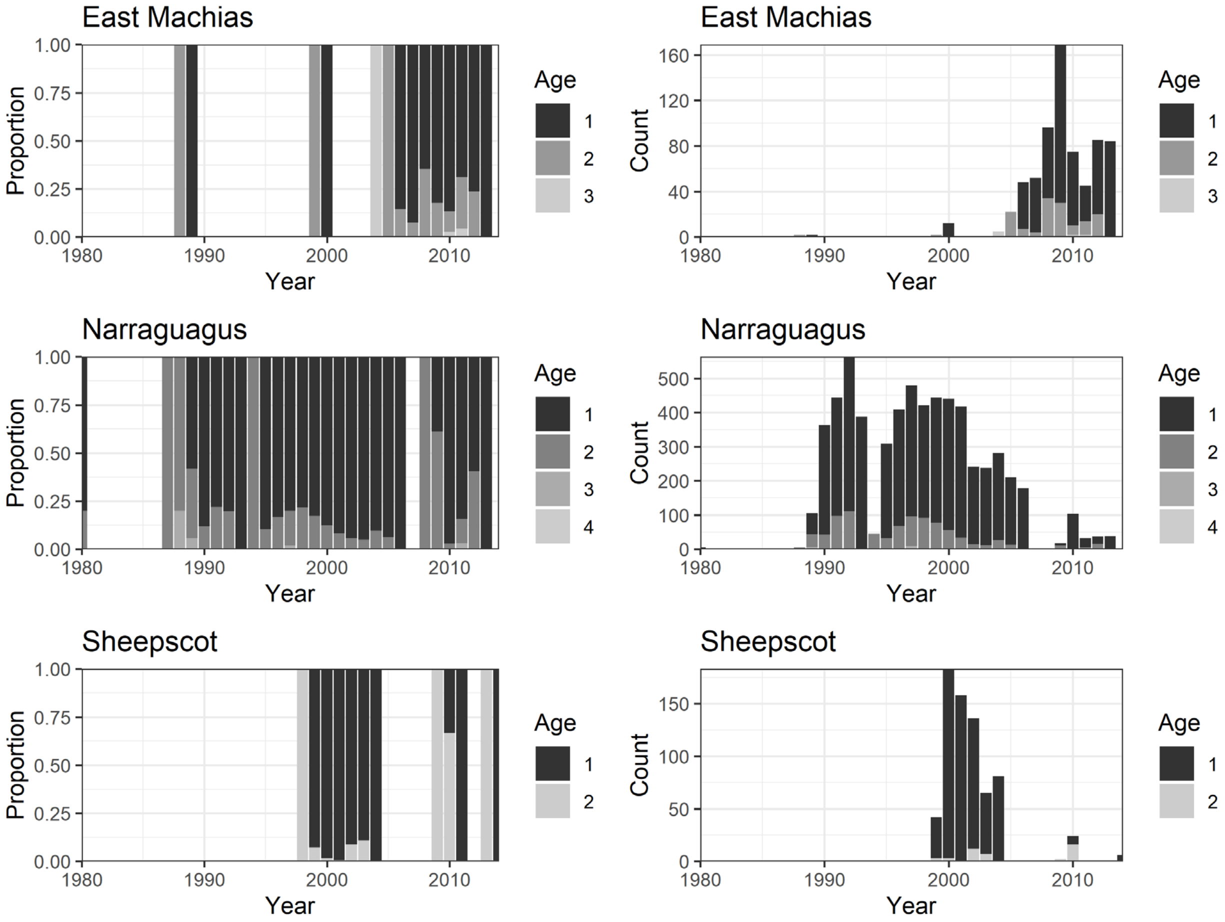

Figure 8 The proportion and count of Atlantic salmon parr ages 1980-2014 (per birth year cohort) for each population (East Machias, Narraguagus, and Sheepscot). Differing colors represent the differing ages.

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