Assessing the Variability in Length of Juvenile Atlantic Salmon in Maine Streams Through a Long-term Electrofishing Dataset

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ASSESSING THE VARIABILITY IN LENGTH OF JUVENILE ATLANTIC SALMON IN MAINE STREAMS THROUGH A LONG-TERM ELECTROFISHING DATASET

BY

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BS Marine, Freshwater, Estuarine Biology, University of New Hampshire, 2018

THESIS

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ABSTRACT

ASSESSING THE VARIABILITY IN LENGTH OF JUVENILE ATLANTIC SALMON IN MAINE STREAMS THROUGH A LONG-TERM ELECTROFISHING DATASET

by

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University of New Hampshire, May 2021

Atlantic salmon *Salmo salar* are an endangered migratory fish with recovery projects in their last remaining habitats in Maine focused on juvenile stocking and habitat restoration efforts. Population productivity of Atlantic salmon has been linked to size of juveniles, suggesting that conditions that facilitate growth in stream habitats are important to recovery. Broadly, the objectives of my thesis were to examine how different habitat and biological variables affect the size of juvenile parr throughout Maine and to assess long-term trends (1969 – 2017) among four drainages (East Machias, Narraguagus, Sheepscot, and Penobscot). Extensive electrofishing surveys captured ~250,000 individual Atlantic salmon across the four drainages within 61 years (1956 – 2017). I fit generalized additive mixed models to determine relationships between parr size (fork length) and environmental and biological variables as well as through time. Site- and drainage-specific variables evaluated included temperature (mean summer air temperature in Chapter 2, and mean summer stream temperature in Chapter 3), elevation, mean channel width, juvenile salmon density, age-0 parr stocked, estimated fry stocked (a metric to combine egg and fry stocking efforts into one metric), and year. The averaged models for each of the drainages allowed for comparisons within and across drainages. The largest increase in parr size throughout the time period was ~5mm, with smolting occurring early at between 1 and 4 years of
age. Consistently among the drainages, sites with low-elevation, wide channels, and warmer temperatures were associated with longer parr. The Sheepscot drainage demonstrated the most positive trend of size over time with a ~5mm increase in FL in both Chapters. Density dependence was evident in every model that included a density related variable. Stronger FL relationships were found with air temperature rather than stream temperature, which implied that temporal variations in temperature were more important to parr size than the difference between stream and air. Although my models found important linkages between parr size and environmental and biological factors, the percent deviance explained was only moderate (12% - 40% among all) and the inclusion of further variables (such as habitat complexity, distance from dams, and stream discharge) would improve further work. These studies conclude that rather than increasing stocking intensities, managers should prioritize stream restoration to improve habitat quality and access to better benefit parr growth.
CHAPTER 1: INTRODUCTION

Introduction

Diadromous fish, those that migrate between fresh and saltwater to complete their lifecycle, impact terrestrial, estuarine, and marine ecosystems (Saunders et al. 2006; Nieland et al. 2015). While diadromous species make up less than 1% of the world’s fishes, they are also economically important to fisheries (Limburg and Waldman 2009). However, diadromous fish populations have declined in many regions due to factors such as overfishing, pollution, and climate change (Musick et al. 2000; Limburg and Waldman, 2009; Nieland et al. 2015). Specifically, diadromous fishes of the North Atlantic continue to decline, some to less than 98% of their historic levels (Christensen et al. 2003; Limburg and Waldman 2009). North Atlantic diadromous fish face multiple challenges such as habitat loss due to dams, overfishing, and pollution, all of which contribute to their declines (Limburg and Waldman 2009).

Atlantic salmon (*Salmon salar*) are a diadromous fish that range across the entire North Atlantic (historically from New England, United States through Atlantic Canada and Europe) (Pinfold 2011). This species sustained one of the largest fisheries in New England before its closure in 1948 (Chase 2003). In other countries, such as Canada, large profits are still made from the recreational fishing community (Pinfold 2011). Atlantic salmon are anadromous, spawning in freshwater and then migrating to the marine environment to feed and growth before returning to spawn (Aldvén et al. 2015). The conservation status of Atlantic salmon varies among countries, but within the United States this species was listed as an endangered species in 2000 (USFWS and NMFS 2000). There are many factors that negatively affect Atlantic salmon such as loss of habitat by dams and destruction (Fay et al. 2006; NRC 2004), historical overexploitation by the fishing industry (Chase 2003), and stress from increasing temperatures
(Good et al. 2001; Swansburg et al. 2002). In this chapter, I review the Atlantic salmon life cycle, the importance of freshwater habitats to juvenile Atlantic salmon parr, and the current status of Atlantic salmon in the northeast United States and recovery efforts, before defining the goals of this thesis.

Life Cycle

Adult Atlantic salmon spend two to three years at sea in the North Atlantic Ocean before initiating coastward spawning migrations that can exceed 4,000 km through marine and freshwater habitats (Saunders et al. 2006). Adult salmon begin their migration from the ocean to their natal streams in April, and spawn in late October and November (Kocik and Friedland 2002). Technically, Atlantic salmon are iteroparous, meaning they can spawn in multiple years before dying. However, iteroparity is energetically expensive due to energy expenditure and lack of eating during these spawning migrations. But iteroparity in Maine is rare with less than 1% partaking in multiple spawns due to the energy expenditure and the lack of eating during this time (Saunders et al. 2006; Kocik and Friedland 2002). The prevalence of iteroparity is likely affected by both natural and anthropogenic causes which leads to a higher percent of repeat spawners in northern locations (Bordeleau et al. 2020). Eggs hatch in January and live in the gravel substrate and are referred to as alevin (Kocik and Friedland 2002).

Juvenile Atlantic salmon reside within freshwater riverine environments. Alevin emerge from the gravel in late April or May and develop into fry, prior to developing vertical bars on their sides and becoming known as 0+ parr when caught in that year’s fall electrofishing survey (Saunders et al. 2006). The juveniles reside in these streams for ~1-4 years before migrating out to sea as smolts where they then travel to the North Atlantic Ocean and mix with European populations (Power 1958; Kocik and Friedland 2002). Latitudinal gradient has been linked to the
range of age classes of parr with less age classes more prevalent in more southern locations (Power 1958). The success of the juvenile life stage is influential on the survival and condition of the smolts and the overall population productivity (Vauclin and Baglinie 2005; Armstrong et al. 2018).

The smolt life stage is an important and challenging time for Atlantic salmon as it requires physiological changes to adapt to salt water and a large-scale migration. It has been suggested that smolts learn navigational cues during their outward migration to use for their return spawning migrations (Hansen et al. 1993). However, Atlantic salmon may also use magnetic fields to sense their location (Moriarty et al. 2016; Putman 2018). In a riverine movement study of smolts, full expression of migratory behavior (with no extended periods of stopping) occurred when water temperatures reached above 9°C during the Spring (Fried et al. 1978). However, it was found that the main factor influencing rates and routes of migration was water current (Fried et al. 1978). Similar data analyzed on the open-water movements of this species and suggested that water current was the only affecting factor on routes and rates of travel for the fish. Although the smolt life stage itself is challenging, smolt production, which requires success of parr, can affect the overall population productivity (Vauclin and Baglinie 2005). Increasing the population of juveniles has contributed to successful smolt migration out of streams which links both these life stages to the preservation of the Atlantic salmon population (Sweka et al. 2007).

Environmental and biological variables affecting juvenile Atlantic salmon parr

Density dependence has been found to affect the size and health of Atlantic salmon parr. Survival and growth of the parr has been found to be density-dependent within stream environments (Marschall et al. 1998). Density-limiting growth has been observed in parr which
therefore affects the survival of the juvenile cohorts (Jonsson et al. 1991; Marschall et al. 1998; Ward, Nilson and Folt, 2009). At high densities, smaller fish experience increased growth due to the disproportionate effect on large fish (Armstrong et al. 1999). However, it was also found that temperature and stream discharge demonstrated a greater influence on growth than did density or habitat availability (Davidson et al. 2018).

Juvenile Atlantic salmon thrive in specific habitats during their ~1-4 years within streams. Parr are found to be most productive in deeper pool and riffle type habitats in lower-order streams (Oakland et al. 2004; Johnson 2013; Gibson 2017). The substrate in these productive areas include boulders, rubble, cobble, and gravel (Gibson 2017). Deeper and faster habitats with more cover and larger substrate are most often selected by the juveniles (Johnson 2013). Positive stream discharge-growth relationships are also evident in parr, which is likely associated with increased fish size, likely due to increased feeding opportunities (Davidson et al. 2018). Many areas where Atlantic salmon once thrived are now inaccessible due to habitat destruction or dam construction and therefore, they inhabit much less of their historical habitat (Fay et al. 2006; USFWS and NMFS 2000).

Temperature is another potential indicator of suitable parr habitat. Increasing air and water temperatures have been observed to reduce growth and increase mortality (Good et al. 2001; Swansburg et al. 2002). Growth occurs at temperatures between 6°C and 20°C, with optimal growth facilitated between 16°-20°C (Gibson 2015). Temperatures above 20°C induce decreased growth in juveniles (Gibson 2015). Temperature plays an important role for juvenile Atlantic salmon due to its effect on the growth and survival of the individuals (Gibson 2002; Davidson et al. 2018).
Atlantic Salmon in the North Atlantic

Historically, Atlantic salmon thrived in more than 2,000 rivers that drain into the North Atlantic (Chaput 2012). For more than 300 years the commercial fishery for Atlantic salmon was important to the development of coastal communities across the North Atlantic (Chase 2003). The Atlantic salmon fishery in New England grew in the late 1800s, with the catch peaking in 1889 with over 17,000 individual salmon (Kocik and Friedland 2002). After this peak, the fishery quickly dropped with only 40 fish caught in 1947, which then led to the closure of the American fishery in 1948 (Kocik and Friedland 2002). One of the hardest-hitting factors for the decline of the fishery was overexploitation (Chase 2003). The Maine population has maintained low numbers of Atlantic salmon since the early 1800s with less than half of historical habitat occupied (~19,000 km²) of their 34 historic rivers (~46,000 km²) (Saunders et al. 2006; Wagner and Sweka 2011; USFWS and NMFS 2018). The Gulf of Maine (GOM) population is within the GOM distinct population segment (DPS) that was listed on the Endangered Species Act in (USFWS and NMFS 2000). This DPS is further split into three salmon habitat recovery units (SHRU) to facilitate region-specific management efforts (USFWS and NMFS 2018).

Atlantic salmon can be found across the state of Maine. However, in this thesis I focused on four different drainages (East Machias, Narraguagus, Sheepscot, and Penobscot). The East Machias drainage has an area of ~650 km² and is within the Downeast Coastal SHRU (Fletcher et al. 1982; USFWS and NMFS 2018). The Narraguagus drainage has an area of ~600 km² and is also within the Downeast Coastal SHRU (Baum and Jordan 1982; USFWS and NMFS 2018). The Sheepscot is the farthest south out of all four drainages covering an area of ~590 km² and is the only one within the Merrymeeting Bay SHRU (Meister 1982; USFWS and NMFS 2018). The Penobscot drainage was assessed in only Chapter 3 of this study. It is the largest of the four
drainages at ~13,800 km² and is within the Penobscot SHRU (Baum 1983; USFWS and NMFS 2018). The Penobscot drainage’s recovery focus is intensive with the Penobscot River being the first large river system in Maine to receive concentrated effort (Baum 1983; Watson et al. 2018; Izzo and Maynard 2020). Overfishing along with the multiple dams and habitat destruction lead to declines of Atlantic salmon in these drainages (Baum et al. 1982; Fletcher et al. 1982; Meister 1982). To combat these declines, hatcheries are used to try and rebuild the Maine Atlantic salmon population (Baum et al. 1982).

Throughout New England, there are hatcheries that raise young Atlantic salmon and release them in rivers to assist in rebuilding stocks. The general process for Atlantic salmon hatchery production starts with egg planting in January or the stream release of fry in spring. However, some programs rear fish to parr before releasing in October to try an ensure a higher survival rate with larger individuals. Stocking programs and their strategies in terms of life stages and quantities stocked have varied greatly among Maine drainages, including those I focus on this thesis, and through time. However, densities of Atlantic salmon parr have continued to decrease, even with stocking efforts (Wagner and Sweka, 2011). In some circumstances stocking can lead to no recovery and have undesired effects wild-born fish (Glover et al. 2018). It is recommended that before creating stocking management practices, the local population dynamics should be understood (Glover et al. 2018). The work of Wagner and Sweka (2011) quantified changes in parr densities across New England, but further assessments would help understand how individual salmon have responded to regional recovery actions.

Electrofishing is the main method used for collection of Atlantic salmon juvenile data in freshwater habitats. Electrofishing uses electronic pulses to shock and immobilize fish without substantial harm. In small streams, such as those where juvenile Atlantic salmon rear,
electrofishing units are worn as “backpacks” by scientists wading in sampled habitats. Shocked fish rise to the surface, allowing for easy enumeration and collection for further assessment (e.g. taking body measurements or biological samples). Such sampling allows for habitat-specific estimates of productivity, including fish density, size, and condition. Specialized training is needed for this method of sampling, but it is common method for stream sampling. The Maine Department of Marine Resources has used electrofishing for several decades as a tool to monitor juvenile salmon populations in the state. Electrofishing data can be used to monitor trends in juvenile salmon densities (Wagner and Sweka 2011).

*Overview of Thesis Aims*

The decline of the United States Atlantic salmon population’s ability to produce smolts, despite intense stocking efforts, points towards the lack of fully understanding what limits parr productivity in stream habitats. The goal of this study is to identify biological and environmental variables affecting parr size in Maine populations, specifically the East Machias, Narraguagus, Sheepscot, and Penobscot drainages. In Chapter 2, I focus on the East Machias, Narraguagus and Sheepscot drainages, identifying variables linked to parr size between the years of 1980 – 2014, including spatially explicit estimates of summer air temperature, via generalized additive mixed effects models (GAMMs). In Chapter 3, a longer-time series (1969 – 2017) was analyzed in a similar GAMM framework. Spatially explicit air temperature data were not available for this entire time series, so instead modeled stream temperature data were used (and compared to Chapter 2’s findings). In addition, expanding the time series and using modeled stream temperature data also allowed for the inclusion of the fourth watershed: Penobscot (see Chapter 3 for more details and justification). More specifically, my goals in both chapters are to use the long-term electrofishing data from the drainages to 1) determine how juvenile Atlantic salmon
length varies among drainages, 2) determine how length varies through time, 3) assess the variations in age composition through time, and determine if it has an effect on Atlantic salmon length, and 4) determine what factors (i.e. water temperature, air temperature, elevation, channel width, conspecific densities, and stocking intensity) are predictive of juvenile Atlantic salmon length among and within drainage. My research provides an in-depth look at the relationships different populations have with their environment that contributes to the overall conservation and management of this endangered species.
CHAPTER 2: THE EFFECTS OF ENVIRONMENTAL AND BIOLOGICAL FACTORS ON THE LENGTH OF SALMO SALAR PARR IN THREE MAINE DRAINAGES

INTRODUCTION

Atlantic salmon *Salmo salar* in the United States continue to be of conservation concern, even after the Gulf of Maine (GOM) population was listed as an endangered species in 2000 (USFWS and NMFS 2000). Stock enhancement continues to place juvenile Atlantic salmon in Maine streams and rivers to help maintain local populations (Wagner and Sweka 2011). Even with these consistent efforts, there is little evidence of recovery thus far, with densities of juveniles holding steady or decreasing over the past three decades (Wagner and Sweka 2011). However, fish density is not the only measure of productivity for juvenile fishes, as individual fish size and physical condition can also positively affect survival (Good et al. 2001; Armstrong 2018), and reduced growth of parr has been suggested to reduce population productivity (Swansburg et al. 2002; Arnekleiv et al. 2006). Also, the success of the parr life stage is influential on the survival and condition of smolts which are suggested to in turn have influence on marine survival and returning adults (Vauclin and Baglinie 2005; Armstrong et al. 2018). Thus, characterizing trends in fish size can further inform current recovery efforts, and identify factors that affect parr size can be helpful in identifying actions that could maximize the efficacy of stock enhancement and aid population recovery.

A variety of environmental and biological conditions influence the growth and therefore the size of juvenile Atlantic salmon parr during their freshwater phase (Power 1958). 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 been observed to correlate with parr size. Parr have also exhibited density dependence where decreased growth has been suggested to
result from an increase in juvenile densities (Jonsson et al. 1991; Marschall et al. 1998; Ward et al. 2009). Within Maine, USA streams, densities of juvenile Atlantic salmon populations have largely declined over the past ~30 years (Wagner and Sweka 2011), but it is not known how sizes of these same fish have changed over time.

My objective was to assess long-term variability in lengths of Atlantic salmon parr within Maine streams and to identify biological, environmental, and temporal correlates. I used a generalized additive mixed model (GAMM) framework to examine the trends of Atlantic salmon size through time and the effects of environmental and density-related variables in three different Maine drainages (East Machias, Narraguagus, and Sheepscot). These three drainages are within the Gulf of Maine distinct population segment (DPS) of Atlantic salmon and, encompass a geographic range across the three salmon habitat recovery units (SHRU) (USFWS and NMFS 2018). These three drainages were of focus for electrofishing surveys over the past several decades, providing information on habitat, juvenile salmon densities (Wagner and Sweka 2011), and individual body size. 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, with the East Machias Drainage as one of the furthest East populations in followed by the Narraguagus and Sheepscot drainages. In addition, the East Machias drainage is unique in that its stock enhancement efforts are based on a cooperative program with a NGO that stock parr in the fall instead of spring. These drainages represent three of the eight remnant populations within Maine, however, collectively these three drainages contain a large portion of naturally-reared parr extant in Maine. My goals were to use long-term electrofishing data from these three drainages to 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-at-age through time, and 4) determine what factors (i.e. air temperature, elevation, channel width, conspecific densities, and stocking intensity) are predictive of juvenile Atlantic salmon length among and within drainages.
METHODOLOGY

Electrofishing Data and Study Area

For this study, I 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. My work focused on 1980-2014 due to the availability of temperature data (see details below). These surveys represent the efforts of many different management and research goals over time, resulting in variable sampling efforts among locales and time periods. However, all sampling followed a standardized electrofishing protocol and a standard measure for catching and measuring of Atlantic salmon (see below). From this statewide dataset, I focus on three drainages (Figure 1) within the Gulf of Maine DPS. The East Machias (~650 km²) and Narraguagus (~600 km²) drainages are within the Downeast Coastal SHRU (Baum and Jordan 1982; Fletcher et al. 1982; USFWS and NMFS 2018) The Sheepscot drainage (~590 km²) is within the Merrymeeting Bay SHRU (Meister 1982; USFWS and NMFS 2018). These three drainages account for ~45% of the juvenile fish sampled from all Maine salmon rivers from 1980-2014.

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 retain all species, fry and parr salmon 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 tricaine methanesulfonate or clove oil was given (5% Clove oil in
70% ethanol), the length (mm) and mass (g) of salmon were recorded. A subset of all Atlantic salmon caught had scales removed for aging (Haas-Castro et al. 2006). Within my 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 (Table 1). 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 (Table 1). Because I focused my analyses on recent decades, these numbers are a subset of the total sampling that is within the Electrofishing Database that contains 61 years of data.

To focus my study on large, age-1+ parr (hereafter referred to as parr), the data were first audited based on fish fork length (FL) (Figure S1). First, there were some obvious recording errors within the data when assessing FL-mass relationships. To remove erroneous data in a systematic way, FL values were binned within 10-mm windows. 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; Figure 3). 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 the outlier removal process. Salmon fry (age 0) were also encountered and captured during electrofishing. As such, my second audit step was to
remove these younger fish from my analyses. I identified parr (age 1+) from fry based on FL using mixture models (Figure S1). Mixture models identify likely cutoffs between groupings within multimodal data. 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: East Machias - 81 mm, Narraguagus - 81 mm, and Sheepscot - 99 mm. Thus, all fish at these sizes or larger were assumed to be parr. I also only included fish less than 200 mm FL in my analyses in case of measuring errors due to a low sample size of fish this large; very few fish (129; ~0.5% of all measured fish) exceeded this length.

**Drainage-Specific Stock Enhancement Procedures**

In general, conservation hatcheries in these systems stock fry or plant eggs to supplement the wild population. Managers plant Atlantic salmon eggs in January that hatch in February or March of the same year. Fry emerge from the streambeds in April or May; this cohort would be captured as age-0 fish during electrofishing in August and September. Fry stocking occurs in May and June in these systems but in different reaches. Egg planting has become more common in the past 10 years. Wild, egg-planted, or fry-stocked groups form a single annual cohort of fish. Typically, about 85% of cohort stays within the system where they could be caught as age-1 parr in the following fall’s electrofishing surveys before heading to sea at age-2+. Similarly, the remaining 15% of parr continue to stay in these systems before smoltifying at age-3 (< 15 %) or age-4+ (<0.5 %). Wild born fish follow a similar life history, with spawning occurring in October and hatching alongside stocked eggs in February or March. However, hatchery practices varied through time among the three drainages, described briefly below.

*East Machias.* — The Peter Gray Hatchery (PGH) stocked the Atlantic salmon in the East Machias, which were provided for as eggs by the Craig Brook National Fish Hatchery
(CBNFH). Fry were stocked in most years since 1985 (through 2014 for the analyses) and were stocked in May which then could be captured as age-0 parr the same year. Hatchery age-0 parr were stocked in October and were generally the same size as wild fish of the same age. The hatchery parr were generally stocked after electrofishing surveys and likely were detected in the following year’s fall electrofishing as age-1 parr. Eggs were never stocked in the East Machias drainage.

**Narraguagus.** — The Narraguagus drainage focused most of their efforts on fry stocking nearly every year since 1985, which would be captured as age-0 parr during the same year’s electrofishing surveys. The CBNFH stocked small numbers of age-0 parr (<15,000) parr in the 1990s and early 2000s that would be captured as age-1 parr during subsequent fall surveys. There were also parr from the Green Lake National Fish Hatchery (GLNFH) that were stocked variably since 1988, but they would mostly smolt and out-migrate prior to that year’s surveys.

**Sheepscot.** — Fry were stocked every year following 1985 in the Sheepscot drainage. Age-0 parr were stocked in most years following 1985 by the CBNFH non-accelerated smolt program, where ~80% would be detected as age-1 parr the following year. During the fall release, stocked parr (95-100mm FL) were larger than wild parr at the same age and all were marked. Eggs were also stocked following 2005 and would be captured as age-0 parr during the same year’s fall electrofishing surveys. An individual year’s wild born fish, hatchery egg stock, and age-0 parr stock would all be the same age during the fall e-fishing. However, the age-parr stock would not be accessible until next year due to their stocking taking place after fall e-fishing.


Explanatory variables used in modeling

From the Electrofishing Archive, I used information on both the sites fished and the individual captured Atlantic salmon parr. Specifically, I used the FL of each captured salmon, its age (when available; see details below), and the following variables regarding 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 (Stevens et al. 2010). Supplemental data sources were used to link further biological and environmental factors to electro-fished 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 calculated sea and land elevations at a special resolution of 15 arc seconds. For each site and each year, I also calculated a mean summer air temperature (MSAT) using Daymet data, which provides gridded (1 km x 1 km) estimates of daily weather parameters. 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 1$^{st}$ through August 30$^{th}$ (except on leap years). Since the Daymet temperatures are only available beginning in 1980, my analyses were restricted to FLs of parr captured during these years as mentioned previously.

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 Report 2019). Stocking data were not linked to specific sites over all years, and thus values only varied by year for all sites within each drainage. Because stocking strategies within drainages varied through time (e.g. strategies shifted between the most common method}
of fry stocking to then egg planting), I 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. I used 15% as an estimate of egg-to-fry survival due to it falling within the range of published estimates (~2% to 35% (Fletcher et al. 1982; Pauwels and Haines 1985; Legault 2017). Therefore, only two stock enhancement explanatory variables were used: estimated fry stocked and the total number of age-0 parr stocked. Age-0 parr stocked and estimated fry stocked were separated 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. In summary, I used the following explanatory variables to investigate variations in parr FL: sampling year, mean channel width, juvenile salmon density, site elevation, yearly average site summer air temperature, yearly estimated fry stocked, and total age-0 parr stocked.

Modeling effects on Fork Length

To determine how FL of Atlantic salmon parr were linked to biological and environmental factors in the three drainages, I used generalized additive mixed models (GAMMs). GAMMs are semiparametric versions of generalized linear mixed models (Wood 2006; 2008), 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, \( \beta_0 \) 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 \( (R_q) \). I constructed GAMMs for each drainage. Separate models were conducted because data availability among explanatory variables varied among drainages (Table 2). The GAMMs I used do not allow for missing values. Thus, only data for each drainage that contained values for every parameter assessed (FL, elevation, mean width, MSAT, year, juvenile salmon density, age-0 parr stocked, estimated fry stocked, and site ID) were used (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 by two of its standard deviations (Gelman 2008). Centering the variables allowed for easier characterization of distributions of explanatory variables.

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 (still using 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 those instances, I always included year in global models and discarded the other variable because one of my main objectives was to characterize changes through time. In these instances, I still visualize the effect of discarded variables 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 \( \geq 5 \) of explanatory variables indicating collinearity (Zuur et al. 2009).
After collinear variables were removed, global GAMMs for each drainage were constructed using the “mgcv” package (Wood 2004; 2011; 2017) in R 3.6.2 (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). I averaged across the top-ranked 95% of models by \(w_i\) to generate a final model for interpretation. To assess the averaged models’ quality, I looked at each of their deviance explained. Finally, I used each drainage’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 size was related to age, I assessed how age composition of parr varied among the three drainages, through time, and with FL to further inform GAMM results. I did not include age in my models described above 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, all age-0 fish were removed 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. I further investigated how the proportion of age-1 fish (the age class that dominated the data) varied among years. Correlations were calculated for the yearly age-1 percentages to determine which years were statistically significant to one another. Also, I used a GAM to assess how FL (response variable) varies with age (explanatory variable) for each drainage using this subset of data (fish with ages). As with my broader GAMMs, these GAMs included Site ID as a random variable and the explanatory variable (age) was given a maximum df of three.
RESULTS

I 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 between five and six explanatory variables. Site ID was included as a random variable in all models. After ranking candidate models and model averaging, each of the 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. Among the three drainages, the averaged model for East Machias explained 24.7% of the deviance, the Narraguagus averaged model explained 40.8% and the Sheepscot averaged model explained 32.8% of the deviance.

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 four best-ranked models that were averaged each had a $w_i$ of ~0.22 – 0.28 (Table 3). All four of these models contained the variables of juvenile salmon density, MSAT, and year (Table 3). The variables of mean channel width and age-0 parr stocked were only contained in two of the top-ranked four models for East Machias (Table 3).

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 three models contributing to the top-ranked 95% of $w_i$, with the top-ranked
two models having \( w_i \) of 0.51 and 0.41, and the third with \( \sim 0.06 \) (Table 3). The variables of juvenile salmon density, MSAT, age-0 parr stocked, and year were all within the three top-ranked models for Narraguagus (Table 3). The variables of elevation and mean channel width were only found in two of the three top-ranked models for Narraguagus (Table 3). However, those top-ranked two models for Narraguagus accounted for \( >90\% \) of the \( w_i \) (Table 3).

The Sheepscot averaged model retained the explanatory variables of mean channel width, MSAT, year, juvenile salmon density, and estimated fry stocked. Ranking candidate models resulted in one model contributing to the top-ranked 95\% of \( w_i \), with the model having a \( w_i \) of 0.54 (Table 3).

**Interannual Effects**

Relationships between year and FL varied among the three drainages (Figure 2; Figure 3; Figure 4). The East Machias averaged model represented the strongest negative relationship between FL and year among the three drainages, with FL decreasing through the mid-2000s (~155 mm to ~145 mm), after which FL remained relatively constant (Figure 2). The Narraguagus averaged model showed a similar relationship between year and FL, with decreasing FL until the mid-2000s, but then increased from then on (~125 mm to ~135 mm) (Figure 3). Year demonstrated the weakest effect in the Sheepscot averaged model with a slight increase in FL (~145 mm to ~155 mm) between 1980 and 2000, followed by a slight decline to ~150 mm until 2013 (Figure 4).

**Density Dependent Effects**

Evidence of density dependence was observed in all three drainages, with the juvenile salmon density variable demonstrated in each averaged model. In all three, increases in juvenile
salmon density resulted in decreases in FL (Figure 2; Figure 3; Figure 4). The East Machias averaged model resulted in the strongest FL-juvenile salmon density relationship with the predicted FL dropping from ~160 mm to ~135 mm as densities increased (Figure 2). The other two averaged models also demonstrated a negative FL-juvenile salmon density relationship with predicted FL dropping from ~165 mm to ~150 mm in the Narraguagus averaged model, and ~125 mm to ~110 mm in the Sheepscot averaged model (Figure 3 and Figure 4).

In addition, each averaged model utilized a stocking variable. 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). In addition, within the Sheepscot averaged model, estimated fry stocked showed a similar negative relationship with FL (Figure 4). An overall negative estimated fry stocked-FL relationship was observed in both the individual East Machias and Narraguagus models (Figure S2 and Figure S3). However, within both the East Machias and Narraguagus averaged models, FL had a positive relationship with the number of age-0 parr stocked. Age-0 parr stocked was removed from the Sheepscot averaged model due to its collinearity with year (Figure 2 and Figure 3), but the individual model of Sheepscot yielded a slightly negative age-0 parr stocked-FL trend with FL decreasing from ~145 mm to ~140 mm (Figure S4).

Habitat Effects

I examined two stream habitat variables: mean channel width and elevation. Mean channel width was within all the averaged models, with wider channels yielding larger FLs in all the averaged models (Figure 2; Figure 3; Figure 4). 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 2). 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 increase in FL as well (~150 mm to ~155 mm; Figure 4). Elevation was only kept 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 3). Elevation was correlated to mean channel width and removed for both East Machias and Sheepscot, therefore the elevation ~ FL relationship was looked at within individual models. Within the individual models for East Machias and Sheepscot there was an overall negative elevation ~ FL trend (Figure S2 and Figure S4).

**Temperature Effects**

Final averaged models for all three drainages utilized 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 2; Figure 3; Figure 4). From 17.5°C - 19°C, both the East Machias and Sheepscot averaged models demonstrated a decrease in FL (~140 mm to ~135 mm and ~160 mm to ~155 mm; respectively; Figure 2; Figure 4). 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 3).
Age Composition

In all drainages, GAMs demonstrated that increasing age yielded larger FLs (Figure 5). The only exception was the Narraguagus drainage that showed a decrease at age four, but there was only a single fish in this age class (FL = 150 mm; Figure 5). Within the Narraguagus age GAM the confidence bands around age 4 fish were very wide therefore I caution interpretation using this age class (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 6). With the proportion of age 1 decreasing from ~80% to ~70% the FL increased ~100mm in both the East Machias and Narraguagus drainages (Figure 6). However, within the Sheepscot model, the opposite was shown with higher age one proportions yielding larger fish (Figure 6). With the proportion of age 1 increasing from ~75% to ~85% the FL increased ~100mm (Figure 6). 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 7). Ages were not sampled consistently throughout the years with larger effort after the 1990s and 2005 for the Narraguagus and East Machias drainages, respectively, and between 2000 and 2005 for the Sheepscot drainage (Figure 7). Age-1 fish were the dominant age class (give %) among all three drainages and years; any exceptions were characterized by low sample sizes (Figure 7).
DISCUSSION

Atlantic salmon populations in all three drainages showed evidence of little to modest increase in FL throughout the 34-year time period (1980 - 2014). The largest gain in FL was 5-mm in the Sheepscot and Narraguagus drainages, which represents an increase of ~4% of the averages fish size (among the drainages) and may be indicating some improvement in parr quality. However, the documented reductions in density and abundance in the Gulf of Maine populations (Saunders et al. 2006; Wagner and Sweka 2011; USFWS and NMFS 2018), paired with the small increase in size demonstrated in this study suggests that any improvement in parr productivity is minimal. Although I only examined three populations in this study, these trends could be broadly applicable given that they are within two of the three SHRUs, cover 34 years of data, and represent wide ranges of environmental conditions within the state. The recent positive trend in the Narraguagus population may be indicating that the increased management practices conducted may be benefiting parr growth. These management practices include removal of barriers to habitat connectivity and improving damaged habitat such as increasing complexity (Snyder et al. 2008; USFWS and NMFS 2018; Wilkins and Snyder 2011). The overall trends found in this study demonstrate very little recovery in Atlantic salmon parr size implying that these management efforts were unable to overcome the growth-limiting factors. The bigger-is-better paradigm is a frequently accepted assumption that has been supported through many studies (Saloniemi et al. 2004; Armstrong et al. 2018). However, it has also been demonstrated that some specific populations lack this size-mortality relationship (Newton et al. 2016; Gregory et al. 2018). Therefore, this assumption should be used with caution and should be tested on these populations in the future before concluding that larger parr are better suited for survival.
Summer air temperatures were found to be an important variable to understand parr FL trends, with the variable of MSAT within every top-ranked model for each of the three drainages, implying that summer air temperatures are potentially a consistent driver of parr length among Maine drainages. All three models showed reduced FLs above 17.5°C, apart from Narraguagus which showed an increase at the highest temperatures experienced (~19°C – 19.5°C). Parr lengths generally increased between 15°C and 17.5°C among all three drainages, 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, I used air temperatures in my models rather than stream temperatures which require more care in interpretation. I used MSAT due to the greater availability of air temperature data for the electrofishing sites. The air-stream temperature relationship resembles an S-shaped curve that is affected by multiple factors such as storms and flow (Mohseni and Stefan 1999). However, within the range of 0°C – 20°C, which is the primary air temperature range in this study, the relationship can be more linear and therefore more easily related to each other (Mohseni and Stefan 1999). Similarly, Morrill et al. 2005 found a general increase of 0.6°C – 0.8°C of stream temperature for a 1°C increase in air temperature, which highlights the different magnitude of effects these variables may have (Morrill et al. 2005). Direct measures of stream temperature may therefore show different, or potentially even stronger, relationships with parr FL. Therefore, there is value in assessing the results within this study in relation to stream temperatures models that are available in this region. I suggest using the Ecosheds stream temperature model that estimates daily stream temperature, while it accounts for many of the challenges of stream temperature estimation (Letcher et al. 2016). Letcher et al 2016 found that
as stream flow increased the effect of air temperature decreased, which further highlights the importance of assessing stream temperature to benefit this study as well as the importance of adding more variables such as stream flow (Letcher et al. 2016).

Regardless, temperature was consistently an important predictor of parr length, with informative drainage-specific differences. Sheepscot sites were the warmest (all MSAT > 18°C) and was the only drainage to show a consistently negative FL-MSAT 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. Narraguagus was the only drainage to show increased FL at temperatures above 19°C. Sites within the Narraguagus drainage are at higher average elevations, wider mean channel widths, and lower juvenile salmon density than the other two drainages, which all had trend with larger parr (discussed below). Thus, it is possible that other optimal habitat characteristics facilitate parr growth even at higher temperatures in this drainage.

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 all three models, 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, which gives a potential explanation of why both trend with larger fish due to increased feeding opportunities from the larger habitat availability (Gibson 2015). Mean channel width was correlated with elevation in both the East Machias and Sheepscot
models (with narrower channels at higher elevations), which implies that the FL-elevation relationships would be like 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. This relationship is supported by the Narraguagus model which exhibited a negative FL-elevation relationship. This relationship leads to the assumption that lower elevation and higher mean channel width both are producing larger fish both separately and collectively due to these areas being metabolically profitable with more food availability for parr. Prey biomass would also be potentially beneficial to assess because it has been found to have a greater impact juvenile body size than density (Ward et al. 2009). Prey biomass was not assessed in this study, but future work on assessing the most ideal Atlantic salmon habitat should make use of this variable due to its effect on the carrying capacity of the salmon habitat (Jonsson et al. 2020).

This study demonstrates that the low-elevation habitats are the best suited to facilitate parr growth, which is a function of productivity along with abundance. However, likely these relationships will become more complex as climate change accelerates (Elliott and Hurley 1997; Gibson 2015; Fernandez et al. 2020). However, it is predicted that these low-elevation habitats will be less affected by climate change accelerates (Fernandez et al. 2020) and therefore should be prioritized during management efforts.

In addition to habitat-related variables, the densities of juvenile salmon present or stocked within habitats also determined parr size. Density dependence was evident in all three drainages, which supports other studies findings of density-limited growth due to competition over food and space (Marschall et al. 1998; Ward et al. 2009; Jonsson et al. 2020). Stocking related mortality was evident in some cases where the density passed the carrying capacity of the habitats (Whalen and LaBar 1994). All three of the density variables (juvenile salmon density, age-0 parr stocked,
and estimated fry stocked), were found within the top-ranked model for all three drainages, which indicates the important role density variables have on explaining the trends in parr growth. Both juvenile salmon density (found in all three averaged models) and estimated fry stocked (found in only the Sheepscot averaged model) had a negative relationship with FL further demonstrating the density dependence found among the drainages (Figures 2, 3, and 4). Stocking data indicate that in more recent years (i.e. more recently than included in my analyses), age-0 parr in the East Machias drainage have been stocked at some of the highest levels which may lead to increased growth as demonstrated from the positive age-0 parr stocked-FL relationship (Figure 2). The growth-limiting age-0 parr and juvenile density relationships in the Narraguagus model indicate that the high stocking levels of age-0 parr in recent years likely is continuing to hinder parr growth (Figure 3). Estimated fry stocking in the Sheepscot drainage has declined in recent years but still was within the negative estimated fry stock-FL trends and therefore is suggested to further limit parr growth (Figure 4). Although stocking efforts in Maine are needed currently to maintain Atlantic salmon populations (Wagner and Sweka 2011), there are limits to effectiveness as demonstrated through the density dependence evident in all three drainages.

Stock enhancement is often a dominant choice for population recovery (Baum and Jordan 1982; Fletcher et al. 1982; Meister 1982). However, this process needs to focus on determining the ideal amount of stocking that will benefit the population the most, rather than stocking the maximum possible quantity of fish. Although parr densities and fry stocking densities maintained negative relationships with parr length, 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). Thus, I caution over-interpretation of these results but believe that further study of this relationship is warranted to improve efficacy of supplemental stocking. Stocking intensity for combined estimated fry and age-0 parr varied among the drainages with Sheepscot at ~3 million fish, East Machias at ~4.0 million fish, and Narraguagus at ~7.3 million fish over the study’s time period (with yearly averages following this same order) (USASAC 2019). The differing stocking intensity is also affected by the lengths of the rivers (Narraguagus ~70km, East Machias ~60km, and Sheepscot ~55km) (Baum and Jordan 1982; Fletcher et al. 1982; Meister 1982). Sheepscot demonstrated the most positive trend of FL through the years even with the lowest amount of stocking overall, which further implies that the increase in the amount of stocking may not have increased the benefit to the parr population. However, a limitation to this study is that I focus on course-scale stocking intensity at the drainage level. Site-specific stocking information would allow for a better understanding of how stocking effort and habitat variables interact to influence parr growth and size. More broadly, I suggest that our understanding of these relationships would be improved if effort and methods were used consistently among drainages across.

Age composition of Atlantic salmon parr likely further reflects growth conditions across the drainages. I 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. The Sheepscot drainage is the most southerly drainage in this study and contained the largest fish on average which may explain why fewer age classes of parr are observed here due to fewer age classes found at more southern latitudes (Power 1958). However, all the drainages are at very similar latitudes compared to the full Atlantic salmon
habitat range. Larger age-1 parr (pre-smolts) characterized in the fall electrofishing surveys are more likely to emigrate in the spring as 2+ smolts (Nicieza et al. 1991; Metcalfe and Thorpe 1992; Thorpe et al. 1992; Elliott and Hurley 1997), and therefore would create fewer age classes for that system which was evident in the Sheepscot drainage. Also, the positive temperature-FL relationship found within this study may suggest that warming waters due to climate change likely will further reduce size classes due to increased parr growth and therefore increased emigration. However, with the small proportion of aged fish in this study it difficult to accurately interpret the age results. Therefore, managers should prioritize consistent age analysis to more accurately understand the age dynamics of these populations.

There are likely numerous variables that would further describe parr size within the drainages examined. 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. In particular, the East Machias model explained the lowest amount of deviance (24.7%) and each of the three top-ranked models had low $w_i$ (~0.2). Therefore, the models are likely missing important explanatory variables that would have better described the FL relationships. Other variables that have been found to influence parr size or growth include, physical habitat characteristics such as potential territories and stream depth (Oakland et al. 2004; Johnson 2013) as well as stream discharge (Davidson et al. 2018). I recommend that data collection of these variables would be beneficial for scientists to further explain variations in parr size. Additional variables are especially important in watersheds such as these where active habitat improvements are ongoing with reconnection of cold-water tributaries, instream habitat work, and modified stocking projects. Furthermore, although FL is a measure of individual condition to complement previous work on densities (Wagner and Sweka, 2011), investigating
variations in individual body condition indices (mass relative to size) would further inform the current state of Atlantic salmon in populations across Maine and identify important predictive variables. Also, the addition of genetic testing would further inform management efforts by providing information on the composition and status of the wild and hatchery-reared juveniles (Sheehan et al. 2010). There have been differences found in the fitness and survival rate for the wild and hatchery-reared fish (Jonsson et al. 1991; Saloniemi et al. 2004; Araki et al. 2008; Sheehan et al. 2010) that I could not account for in analyses.

In conclusion, as recovery efforts in New England focus on restoring access to habitats by removing dams and other barriers for multiple decades (USFWS and NMFS 2018), it is important to prioritize future stocking and restoration efforts into high-quality locations. Among the three drainages, Sheepscot contained the largest fish and shortest parr residency, but also exhibited the strongest negative relationship with summer temperatures. Thus, this population towards the southern extent of Atlantic salmon’s range is likely to experience deleterious temperatures as climate continues to warm (Fernandez et al. 2020). River and stream temperatures across the U.S. are predicted to increase by 0.009°C – 0.077°C per year, with Maine being on the higher end of this range at an increase of 0.047°C per year (Kaushal et al. 2010; Fernandez et al. 2020). Northern inland regions of the state are predicted to be more affected by climate change, which indicates that more coastal sites, particularly in the East Machias and Narraguagus drainage, will be the least affected (Fernandez et al. 2020). Climate change velocity can help understand and predict where and when thermal stress will occur (Daigle et al. 2015; Detenbeck et al. 2016; Letcher et al. 2016) and should be integrated into recovery and restoration actions. Atlantic salmon are highly exposed and vulnerable to climate change throughout their lifespan (Borggaard et al. 2019; Hare et al. 2016), which further hinders
the parr along with inopportune habitats due to factors such as loss of connectivity (Gibson 2017). From my results, wide habitats that are resilient to climate change-induced temperature are valuable, and likely can be found in more northern and coastal drainages within the state. Furthermore, I recommend that effort be put into recovering habitat quality rather than increasing the number of stocked individuals. As demonstrated through this study, an increase of stocked fish can result in smaller individuals, suggesting the habitats cannot support optimal growth at current experienced densities.
### 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.

<table>
<thead>
<tr>
<th></th>
<th>East Machias</th>
<th>Narraguagus</th>
<th>Sheepscot</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Sites</td>
<td>36</td>
<td>91</td>
<td>28</td>
</tr>
<tr>
<td>Number of Events</td>
<td>131</td>
<td>549</td>
<td>207</td>
</tr>
<tr>
<td>Number of Fish</td>
<td>2469</td>
<td>8753</td>
<td>2409</td>
</tr>
<tr>
<td>Mean Fish Fork Length (mm)</td>
<td>127.7</td>
<td>124.4</td>
<td>143.9</td>
</tr>
</tbody>
</table>
Table 2:

Summary of explanatory variables evaluated within generalized additive mixed models, including range and mean in parentheses. (For the number of sites and sampling events within each drainage see Table 1).

<table>
<thead>
<tr>
<th></th>
<th>East Machias</th>
<th>Narraguagus</th>
<th>Sheepscot</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Summer Air Temperature</td>
<td>15.74 - 19.00 (17.82)</td>
<td>16.53 - 19.45 (18.15)</td>
<td>17.62 - 19.72 (18.91)</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>19.78 - 84.75 (42.33)</td>
<td>12.15 - 130.18 (86.06)</td>
<td>33.16 - 106.30 (62.30)</td>
</tr>
<tr>
<td>Mean Channel Width (m)</td>
<td>2.40 - 20.67 (8.56)</td>
<td>2.87 - 42.47 (13.68)</td>
<td>4.57 - 31.09 (12.04)</td>
</tr>
<tr>
<td>Juvenile Salmon Density (catch per 100 m²)</td>
<td>0.00 - 40.36 (10.22)</td>
<td>0.00 - 24.78 (5.47)</td>
<td>0.09 - 50.27 (10.91)</td>
</tr>
<tr>
<td>Age-0 Parr Stocked</td>
<td>0 - 149,815 (3239)</td>
<td>0 – 209,90 (3474)</td>
<td>0 - 17,925 (10,708)</td>
</tr>
<tr>
<td>Estimated Fry Stocked</td>
<td>0 - 319,138 (174,326)</td>
<td>0 - 698,200 (258,264)</td>
<td>0 - 323,000 (153,384)</td>
</tr>
</tbody>
</table>
Table 3: Model rankings after all-subsets modelling, with the top-ranked models each represented by a row; ranked by Akaike Information Criterion (AIC). The top-ranked 95% of models by AIC weight ($w_i$) from each drainage were selected for model averaging. Abbreviations are as follows: $df$ = number of parameters, $LL$ = log likelihood, $\Delta_i$ = the difference between the AIC value for the $i^{th}$ model and the minimum AIC value for all models for that drainage, and - = a variable that was removed during the collinearity process.

<table>
<thead>
<tr>
<th>Juvenile Salmon Density</th>
<th>Estimated Fry Stocked</th>
<th>Elevation</th>
<th>Mean Channel Width</th>
<th>Mean Summer Air Temperature</th>
<th>Age-0 Parr Stocked</th>
<th>Year</th>
<th>$df$</th>
<th>$LL$</th>
<th>AIC</th>
<th>$\Delta_i$</th>
<th>$w_i$</th>
</tr>
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<tr>
<td>East Machias</td>
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<tr>
<td>X</td>
<td>-</td>
<td>-</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>39</td>
<td>-</td>
<td>10952.80</td>
<td>21983.8</td>
<td>0.00</td>
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<td>X</td>
<td>X</td>
<td>X</td>
<td>38</td>
<td>-</td>
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<td>21984.0</td>
<td>0.19</td>
<td>0.253</td>
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<td>-</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>39</td>
<td>-</td>
<td>10952.35</td>
<td>21984.0</td>
<td>0.23</td>
<td>0.248</td>
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<tr>
<td>Narraguagus</td>
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<tr>
<td>X</td>
<td>-</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>84</td>
<td>-</td>
<td>37214.79</td>
<td>74597.8</td>
<td>0.00</td>
<td>0.510</td>
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<td>37214.30</td>
<td>74598.2</td>
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<td>0.410</td>
</tr>
<tr>
<td>Sheepscot</td>
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<td>X</td>
<td>-</td>
<td>X</td>
<td>X</td>
<td>36</td>
<td>-</td>
<td>-9843.97</td>
<td>19760.4</td>
<td>0.00</td>
<td>0.535</td>
</tr>
</tbody>
</table>
Figure 1:

Map of the electrofishing sites within the three Maine drainages used for assessed trends in juvenile Atlantic salmon parr fork length. Each drainage is outlined and the sites within them are represented by dots with darker dots representing more sites in that area.
Figure 2:

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 drainage. 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 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 Narraguagus drainage. 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 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 Sheepscot drainage. 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 5

Response curves of the relationship of Atlantic salmon parr age and their fork length as generated through generalized additive models for each drainage. 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 6

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 drainage. 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 7

Summary of the percent and count of Atlantic salmon parr age through time (per birth year cohort) for each drainage (East Machias, Narraguagus, and Sheepscot). Differing colors represent the differing ages.
**Figure S1**
Mixture model of the two curves representing the size distributions of two age classes of fry (red) and parr (blue) for all three drainages.
Figure S2

Predicted response curves of the relationships among explanatory variables removed from the averaged model due to collinearity and Atlantic salmon parr fork length as generated through generalized additive mixed models for the East Machias drainage.
Figure S3

Predicted response curves of the relationships among explanatory variables removed from the averaged model due to collinearity and Atlantic salmon parr fork length as generated through generalized additive mixed models for the Narraguagus drainage.
Figure S4

Predicted response curves of the relationships among explanatory variables removed from the averaged model due to collinearity and Atlantic salmon parr fork length as generated through generalized additive mixed models for the Sheepscot drainage.
CHAPTER 3: EXAMINING LENGTH-HABITAT EFFECTS FOR PARR OVER BROAD TIME SCALES WITH THE USE OF MODELED STREAM TEMPERATURE WITH FOCUS ON THE PENOBSCOT DRAINAGE

INTRODUCTION

The population of United States Atlantic salmon *Salmo salar* has remained a cause for concern even after being listed as an endangered species in 2000 (USFWS and NMFS 2000). In New England various management practices and stock enhancement programs have been utilized, however there is little sign of recovery, with density and abundance of Atlantic salmon continuing to decline in recent decades (Saunders et al. 2006; Wagner and Sweka 2011; USFWS and NMFS 2018). Management practices focus primarily on freshwater habitat where juveniles reside and aim to either directly increase abundance of juveniles (stock enhancement) or increase access to or quality of habitat (restoration). In addition to abundance, growth, and condition of juvenile salmon parr is suggested to affect population productivity (Good et al. 2001; Swansburg et al. 2002; Arnekleiv et al. 2006; Armstrong 2018). Chapter 2 found several variables to affect parr size (length) within three Maine drainages, including mean summer air temperature (MSAT), mean channel width, stream elevation, stocking densities, and site-specific density of juvenile salmon. In addition, parr lengths were found to demonstrate no consistent improvement among drainages over the past several decades, further indicating a lack of recovery (Chapter 2). Although Chapter 2 demonstrated important linkages between parr length and environmental, biological, and temporal variables, its use of air temperatures instead of stream temperatures may be limiting the strength in interpretation of the results.

Temperature controls the metabolism and growth of salmonids and is often an important indicator of habitat for juvenile salmon mortality (Good et al. 2001; Swansburg et al. 2002). I utilized mean summer air temperature in Chapter 2 because it was readily available among the
three study drainages from 1980 – 2014, allowing me to investigate how changing temperatures through time might affect parr FL. However, although air and stream temperatures can be correlated (Mohseni and Stefan 1999), and salmonids directly experience the temperature of the water rather than the air. Thus, it would be useful to incorporate stream temperatures within a similar modeling framework as Chapter 2, to further understand how experienced summer temperatures affect parr size. In particular, increased growth of parr generally occurs in waters 6°C-20°C with their optimum growth between 16°C-20°C, followed by decreasing (>20°C) to no growth at 25°C (Gibson 2015).

Furthermore, Chapter 2’s focus on air temperatures, derived from remote sensing products, restricted analyses to more recent years (1980 – 2014), limiting not only the temporal extent of the investigation but also precluding drainages for which data were limited to earlier years (such as the Penobscot drainage). Although sites within the Penobscot drainage have been assessed with electrofishing in recent years, a large proportion of such sampling occurred between 1970-1980, preventing its inclusion in Chapter 2. The Penobscot drainage was not included in Chapter 2’s analyses even though is the watershed covers an area of ~13,700 km², which is about 22 times the size of the other three drainages, and has been a location of management focus for many years (Baum 1983). However, the active recovery zones are not much bigger than the Downeast composite. In this chapter, I use estimates of site-specific stream temperatures (i.e. single estimate per site that does not vary through time), allowing me to not only compare the effects of two different summer temperature metrics, but also assess changes in FL of Atlantic salmon parr in the Penobscot drainage.

The purpose of this study is to extend Chapter 2’s investigation of long-term variability in lengths of Atlantic salmon parr within Maine streams and to identify biological, environmental,
and temporal correlates, focusing on a fourth drainage (Penobscot) and use of modeled stream temperatures. As in Chapter 2, a generalized additive mixed model (GAMM) framework was used to examine the Atlantic salmon size trends through time and among different environmental variables. My goals were to use the long-term electrofishing data from these four drainages to 1) determine how juvenile Atlantic salmon length varies among drainages, 2) determine how length varies through time, between the years 1969 and 2017, 3) assess the variations in age composition through time, and determine if it has an effect on Atlantic salmon length, and 4) determine what factors (i.e. water temperature, elevation, channel width, conspecific densities, and stocking intensity) are predictive of juvenile Atlantic salmon length among and within drainages.
METHODOLOGY

Electrofishing Data and Study Area

For this study, the drainage of Penobscot was added to the analysis along with the three others assessed in Chapter 2. The description of the East Machias, Sheepscot, and Narraguagus drainages are found within the Methods section of Chapter 2 (see ‘Electrofishing Data and Study Area’). The Electrofishing Archive provided data for all four of the drainages. At each site the same standardized e-fishing protocol and fish measuring protocol was conducted (detailed explanation in Chapter 2). However, the exact sample size of data used, in terms of number of sites, electrofishing events, and numbers of parr measured, vary from Chapter 2 due to variances in data availability (more details below). Within the Penobscot drainage there were a total of 34 sites sampled during 88 sampling events over 45 years (1972-2017) that measured 2,231 Atlantic salmon juveniles (Table 4). Within the East Machias drainage there were a total of 32 sites sampled during 122 sampling events over 40 years (1974-2014) that measured 2,581 Atlantic salmon juveniles (Table 4). Within the Narraguagus drainage there were a total of 60 sites sampled during 356 sampling events over 44 years (1970-2014) that measured 7,281 Atlantic salmon juveniles (Table 4). Within the Sheepscot drainage there were a total of 15 sites sampled during 143 sampling events over 45 years (1969-2014) that measured 1,904 Atlantic salmon juveniles (Table 4). These numbers are a subset of the total sampling that has been done in the 61-year time period of the full dataset.

As in Chapter 2, the data were audited further based on FL to assure that Atlantic salmon parr was the life stage assessed in this study. Within the Electrofishing Archive, erroneous FL-mass relationship data were removed by binning the data in 10-mm windows and removing fish that fell outside of the two-times IQR (detailed further in Chapter 2). I also used mixture models
to determine the FL cutoff between Atlantic salmon fry and parr (Figure S5). These FL cutoffs were as follows: Narraguagus = 81 mm, Sheepscot = 99 mm, Penobscot 80 mm, and East Machias = 81 mm (Figure S5). A max size cutoff of 200 mm was also implemented due to the low sample size of fish above this length (<1% of the assessed fish). With these analyses I was able to confidently find the most likely size range of Atlantic salmon that were in the parr life stage.

**Drainage-Specific Stock Enhancement Procedures**

The general stocking of Atlantic salmon in Maine follows a similar calendar pattern. Eggs are planted in January then hatch by February or March. These fry then emerge in April or May and live within the stream, being caught as age-0 fish during the fall electrofishing in August or September. The juveniles are then able to smoltify and leave their stream locations, or they overwinter and are caught as age-1 fish the following fall. Wild fish in these streams follow a similar pattern, the difference being that eggs are laid in October during the fall natural spawning. Within each drainage there are variations to this general pattern. The East Machias, Sheepscot, and Narraguagus procedures are outlined in Chapter 2. Below, I focus on stocking practices in the Penobscot drainage.

Non-wild egg, fry, and parr population were stocked within the Penobscot drainage by the Green Lake National Fish Hatchery (GLNFH). Both fry and parr were stocked almost every year since 1980. The parr were a byproduct of their accelerated smolt program and were usually sorted out by size, with the smallest of the group stocked as age 0 parr. Each year around 300,000 of these byproduct parr were stocked, which were often >100 mm larger than wild parr of the same age. These parr were stocked in the fall after the electrofishing surveys and were also released in sites that are usually not surveyed by electrofishing. The difference of location of the
stocking and electrofishing sites was because the locations the stocked parr were released were best for larger parr while electrofishing sites included sites best suited for smaller parr. Therefore, the stocked parr were very unlikely to be sampled due to their high probability of emigrating out of the system as well as their stocked locations differing from electrofishing sampling sites. These parr were not all marked as hatchery fish. Penobscot eggs were planted in January, and fry were stocked in May. Therefore, they both would have been counted as age 1 parr the following year. These fry and eggs were also not marked.

*Explanatory variables used in modeling*

From the Electrofishing Archive, I used the sampling site data and the Atlantic salmon size data for the individuals captured. Fork length (FL) for each of the individuals was utilized as the response variable in the models. The site data included the variables of mean channel width, year of sampling event, and juvenile salmon density (catch per 100m²). 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 calculated sea and land elevations at a special resolution of 15 arc seconds. Stocking data for each drainage added the variables of estimated fry stocked and age-0 parr stocked (USASAC Report 2019). Age-0 parr stocked was utilized in all the drainages except Penobscot, due to the age-0 parr being stocked in non-electrofishing locations in this drainage.

The only variable that differs between Chapter 2 and this chapter is the use of Mean Summer Stream Temperature (MSST) rather than MSAT. The Spatial Hydro-Ecological Decision System provided the SHEDS stream temperature model estimated daily stream temperature and accounted for many of the challenges of stream temperature estimation. This dataset allowed me to extract the MSST for 141 of the electrofishing sites (Letcher et al. 2016,
Walker et al. 2020). The model utilizes stream gauge observations, climate estimate data, and geospatial characteristics to predict mean daily stream temperature values across much of the northeast U.S by utilizing Bayesian structure to link near-by locations by temperature (Letcher et al. 2016, Walker et al. 2020). These models generate a variety of stream-temperature-related variables, but I extracted MSST for use in this chapter, which is a site-specific mean stream temperature value that does not vary with time due to the model aggregating daily predicted temperature over all years (Walker et al. 2020). In summary, I used the following explanatory variables to explain variations in parr FL: sampling year, mean channel width, juvenile salmon density, site elevation, yearly average site summer stream temperature, yearly estimated fry stocked, and total age-0 parr stocked.

**Modeling effects on Fork Length**

As in Chapter 2, generalized additive mixed models (GAMMs) were used to determine relationships between FL of Atlantic salmon and biological and environmental factors among the three drainages. GAMMs are semiparametric versions of generalized linear mixed models (Wood 2006, 2008), 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, $\beta_0$ 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 ($R_q$). I constructed GAMMs for each of the individual drainages. Separate models were conducted because data availability among explanatory variables varied among drainages (Table 5). The
GAMMs I used do not allow for missing values, thus only data for each drainage that contained values for every parameter assessed (FL, elevation, mean width, MSST, year, juvenile salmon density, age-0 parr stocked, estimated fry stocked, and site ID) was kept (~14,000 fish; ~80% of fish measured) (Table 5). Site ID was used as a random effect within each model. Each explanatory variable was centered by taking the variable and subtracting the mean by two of its standard deviations (Gelman 2008). Centering the variables allows for easier comparisons of effect size among variables and characterized distributions of explanatory variables.

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 (still retaining Site ID as a random). The variable resulting in the GAMM with the lowest AIC was retained; the other variable was discarded. The only exception to this process was when year was correlated with another variable, I always kept year in global models and discarded the other variable because one of my main objectives was to characterize how parr FL changes through time in each of the drainages. In these instances, I still visualize the effect of discarded variables in the Supplemental Material (Figure S6; Figure S7; Figure S8; Figure S9). 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. No VIF values were found to exceed 5 in my analyses.

After collinear variables were removed, global GAMMs for each drainage were constructed using the “mgcv” package (Wood 2004, Wood 2011, Wood 2017) in R 3.6.2 (R
Development Core Team 2019). Each explanatory variable was entered as a spline, with a maximum degrees of freedom (df) allowed per variable limited to three 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), 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 Akaike Information Criterion (AIC). For each model, the AIC weight ($w_i$) was calculated, which provides the probability that the model is the best model at representing the raw data (Symonds and Moussalli 2011). I averaged across the top-ranked 95% of models by $w_i$ to generate a final model for interpretation. To assess the averaged models’ quality, I looked at each of their deviance explained. Finally, I used each drainage’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 size was directly related to age, I assessed how age composition of parr varied among the three drainages, through time, and with FL to further inform GAMM results. A subset of the fish captured through electrofishing were aged via reading scales (~86% in Penobscot, ~87% in East Machias, ~52% in Narraguagus, and ~84% in Sheepscot). All age-0 fish were removed during the previous mixture model methods; remaining juveniles were found to be ages 1 through 4 (Figure S1). 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. Fish with the same birth year were then grouped together to create cohorts. I further investigated how the proportion of age 1 fish (the age class that dominated my
data) varied among years. The yearly age 1 percentages were correlated to determine which years were statistically significant to one another (>0.5) (Appendix). Also, I used a GAM to assess how FL (response variable) varies with age (explanatory variable) for each drainage using this subset of data (fish with ages). As with my broader GAMMs, these GAMs included Site ID as a random variable and the explanatory variable (age) was given a maximum df of three.
RESULTS

The four global models for each drainage entered into the model selection and averaging contained between three and five explanatory variables. Due to Spearman $\rho > 0.5$ with other variables, estimated fry stocked, mean channel width, and juvenile salmon density were removed from the Penobscot global model; juvenile salmon density, estimated fry stocked, and elevation were removed from the East Machias global model; estimated fry stocked and mean channel width were removed from the Narraguagus global model; and age-0 parr stocked and mean channel width were removed from the Sheepscot global model. Age-0 parr stocked was also removed from the Penobscot global model because the age-0 parr stocked within this drainage, that were a byproduct of an accelerated growth program for stocking smolts and thus are generally larger and more variable in size than wild and other stocked parr, were placed in different locations than most sample sites (John Kocik, NOAA pers. comm.). Site ID was included as a random variable in all models. After ranking candidate models and model averaging, only the variables of MSST and year were retained in all four of the final averaged models (Table 6). Year was also contained in the top-ranked model for each drainage.

The Penobscot averaged model retained the explanatory variables of elevation, MSST, and year. Two models contributed to the top-ranked 95% of $w_i$, having $w_i$ of $\sim0.70$ and $\sim0.21$, respectively (Table 6). The variables of MSST and year were found within both the top-ranked models (Table 6). The variable of elevation was only found within the second top-ranked model (Table 6). Among the three drainages, the averaged model for Penobscot explained 36.8% of the deviance, followed by the Narraguagus averaged model at 32.7%, the Sheepscot averaged model at 23.7%, and lastly the East Machias model at 12.4% deviance explained.
The East Machias averaged model retained the explanatory variables of mean channel width, MSST, year, and age-0 parr stocked. Three models contributed to the top-ranked 95% of $w_i$, each having $w_i$ of $\sim0.24–0.28$ (Table 6). The variables of age-0 parr stocked and year were found in all three of these models (Table 6). The variable of MSST was only found in the second-ranked model, while mean channel width was then found only in the third-ranked model (Table 6).

The Narraguagus averaged model retained the explanatory variables of juvenile salmon density, elevation, MSST, age-0 parr stocked, and year. Three models contributed to the top-ranked 95% of $w_i$, each having $w_i$ of $\sim0.41$, $\sim0.26$, and $\sim0.16$ (Table 6). The variables of juvenile salmon density, age-0 parr stocked, and year were all found within the three top-ranked models for Narraguagus (Table 6). The variable of MSST was found only within the top-ranked model (Table 6). The variable of elevation was found in each of the two top-ranked models (Table 6).

The Sheepscot averaged model retained the explanatory variable of juvenile salmon density, estimated fry stocked, elevation, MSST, and year. Two models contributed to the top-ranked 95% of $w_i$, each having $w_i$ of between $\sim0.24–0.26$ (Table 6). The variable of juvenile salmon density, estimated fry stocked, and year were all found within the three top-ranked models (Table 6). The variable of elevation was only found within the two top-ranked models, and the variable of MSST was only found within the first and third top-ranked model (Table 6).

**Temperature Effects**

All four averaged models utilized MSST. The Sheepscot and Narraguagus averaged models all yielded a slight positive trend of FL and MSST with an increase of $\sim5$mm of FL between MSST of $18^\circ$C and $22^\circ$C (Figure 11 and Figure 12). The East Machias averaged model
also showed a positive trend; however, it was a very small increase in FL representing a very weak temperature-length relationship (Figure 10). The Penobscot averaged model exhibited a more complex, non-linear relationship between MSST and FL (Figure 9). This model showed a ~40 mm increase in FL from 16°C to 20°C, followed by a ~20-mm decrease between 20°C and 22°C (Figure 9).

*Habitat Effects*

The variables of mean channel width and elevation were the two stream habitat variables assessed in this study. Elevation was demonstrated in all the averaged models except the East Machias averaged model, with the averaged trend being a negative relationship between FL and elevation in both the Sheepscot and Narraguagus averaged models (Figure 11 and Figure 12). At low elevations (<70 m) and at very high elevations (>110 m) the Narraguagus averaged model showed a small positive relationship with FL and elevation (Figure 11). The Penobscot elevation-FL relationship is unique in that intermediate elevations resulted in smaller FL values; however, this relationship is very weak (Figure 9). The East Machias averaged model was the only model that utilized the mean channel width variable. There was a slight positive trend with FL and mean channel width with FL increasing ~5 mm with a ~12 m increase of mean channel width (Figure 10).

*Interannual Effects*

The relationships between year and FL greatly varied among the four drainages (Figure 9: Figure 10: Figure 11: Figure 12). The Penobscot averaged model demonstrated FL increasing until the early 2000s, but then decreasing from then on (~145 mm to 130 mm) (Figure 9). The East Machias averaged model demonstrated a ~20 mm FL increase from 1974 to ~1990 (~135
mm to 155 mm), followed by a ~15 mm FL decrease from ~1990 to 2014 (~155 mm to 140 mm) (Figure 10). The Narraguagus averaged model represented the strongest negative relationship between FL and year among the four drainages, with FL decreasing from ~145 mm to ~135 mm through 1970 to 2014 (Figure 11). The Sheepscot averaged model demonstrated a ~5 mm decrease in FL from the 1960s to the 1970s, followed by a ~20 mm increase until the mid-2000s, where then the FL dropped ~10 mm until 2014 (Figure 12).

Density Dependent Effects

Evidence of density dependence was observed in three of the four drainages, with only the Penobscot averaged model removing all the density variables due to its collinearity issues with both year and mean channel width. However, in the supplemental Penobscot GAMMs, density dependence was observed (Figure S6). These supplemental GAMMs indicate a complex relationship showing that larger parr are found at lower juvenile salmon densities and higher estimated fry stocked numbers (Figure S6). However, these two variables were removed from the Penobscot averaged models and therefore must be considered during interpretation of these results. The East Machias averaged model only demonstrated the density variable of age-0 parr stocked which showed the greatest FL at ~30,000 parr stocked, with a slight decrease in FL at higher stocking densities (Figure 10). The model prediction hinted at a complex relationship, but there were very few unique values with only five years stocking parr, thus there is less confidence in this relationship to not risk over-interpretation. The Sheepscot averaged model demonstrated a negative relationship between FL and both estimated fry stocked (with predicted FL falling from ~155 mm to ~135 mm between zero stocking and ~300,000 fry stocked) and juvenile salmon density (with FL decreasing from ~140 mm to ~125 mm with increasing
densities) (Figure 12). The Narraguagus averaged model predicted a very weak positive relationship with both age-0 parr stocked and juvenile salmon density (Figure 11).

Age Composition

The Penobscot and Sheepscot drainages contained parr ranging from age 1 to 2, followed by the East Machias drainage with ages 1 through 3, and then the Narraguagus drainage with ages 1 through 4 (Figure 15). Ages were inconsistently sampled through the time series with larger efforts post-2000 for the East Machias and Penobscot drainages, post 1990 for the Narraguagus drainage, and pre-2005 for the Sheepscot drainage (Figure 15). Age-1 fish were predominantly found throughout all the sampling years among all four drainages, with exceptions observed in years with low sample size (Figure 15). The GAMs for each of the drainages showed an increase of FL with age, except for a decrease at age 4 in Narraguagus but this was only a single fish (Figure 13). Greater proportions of age-1 fish yielded smaller FL values for both the East Machias and Narraguagus drainages (Figure 14). The Penobscot GAM resulted in a slight increase in proportion of age 1 until 105 mm FL where then it followed the decrease in FL like the East Machias and Narraguagus GAMs (Figure 14). However, the Sheepscot GAM showed a positive relationship with proportion of age-1 fish and FL throughout the entire trend (Figure 14).
DISCUSSION

This study extends the work of Chapter 2 by assessing correlates of juvenile Atlantic salmon parr size in the Penobscot drainage, accounting for all three of the SHRUss within Maine and 48 years of data (1969 - 2017). Parr size in the Penobscot drainage did not increase through time, but rather experienced an overall ~5-mm decrease in FL (~4% the length of the average fish), between 1972 and 2017. The Penobscot averaged model demonstrated the second largest FL decrease through time following the 10-mm decrease (~8% the length of the average fish), observed in the Narraguagus model. This decline in FL indicates that the Penobscot and Narraguagus drainages may be less suited for parr growth than the East Machias and Sheepscot drainages. However, the East Machias averaged model resulted in a net decrease of ~10-mm in Chapter 2, which further highlights the need for more robust modeling that will allow for stronger conclusions. These decreases (or lack of increases) in size are concurrent with decreases in parr density and abundance for the Gulf of Maine populations (Saunders et al. 2006; Wagner and Sweka 2011; USFWS and NMFS 2018, Chapter 2). The paired decline of size and density may indicate a lack of quality habitat suitable for parr growth within the state of Maine.

It is important to note that I used stream temperature in my models rather than air temperature as observed in Chapter 2. Stream temperature was used due to the greater availability of long-term stream temperature data which did not require this study to subset by year, as air temperature did (which only accounted for data post 1979). However, by utilizing stream temperatures, the parr required a subset by sites due to the lack of temperature data in certain areas across Maine. Stream and air temperatures do not always reflect each other as observed through their S-Shaped curve relationship (Mohseni and Stefan 1999). The stream-air temperature relationship is more linear within the range of 0°C –20°C, which was seen in
Chapter 2 and therefore both chapters are more easily related (Mohseni and Stefan 1999). The MSST variable was an average over time and was not calculated for all the sites in this study therefore causing a limitation to interpretation. The utilization of both temperatures in this study required too large of a subset and would make for extremely weak results. In future studies more consistent stream temperatures and more long-term air temperatures should be used and could potentially account for some of the missing deviance. The results from this chapter and Chapter 2 demonstrated the differing effects from these variables on Atlantic salmon size. These results representing the importance in assessing both variables to determine any strong relationships they may have with the parr.

Summer stream temperatures only demonstrated a strong relationship within the Penobscot averaged model; however, this variable was found within every top-ranked model for three of the four drainages. Therefore, this finding implies that even though there is not a strong relationship with MSST, it still may be a consistent driver of parr length among the Maine drainages. All the averaged models represented a slight positive relationship with MSST and FL, with the Penobscot averaged model predicting the strongest positive and most unique relationship. In the Penobscot averaged model, parr lengths increased from 16°C to 20°C, followed by a decrease in size until the highest observed temperature (22°C; Figure 9). This relationship implies that parr in the Penobscot drainage may already be experiencing temperatures beyond their optimum, which is not yet evident in the other three drainages. In fact, this relationship between temperature and size, with sizes decrease at temperatures exceeding 20°C, closely matches other work (Elliott and Hurley 1997; Gibson 2015). Northern-inland Penobscot sites are predicted to be more heavily affected by increasing temperatures due to climate change than the coastal sites within the other drainages (Fernandez et al. 2020). The lack of a strong relationship in the other
drainages implies that those parr are currently less temperature-limited and therefore other environmental and/or biological variables may be greater size limiting. The MSAT-FL trends in Chapter 2 are unexpectedly stronger than the MSST-FL trends as observed in this Chapter. Likely, MSAT has a stronger relationship with parr due to the large difference in spatial and temporal resolutions of the datasets. The MSST had one averaged temperature value per site, while the MSAT dataset accounted for temperature changes through time which better represented the rapidly changing parr environment. Furthermore, this result signifies the importance of utilizing datasets that account for temporal changes to more accurately describe parr growth.

Beyond temperature, habitat-based variables of mean channel width and elevation resulted in relationships with Atlantic salmon parr FL among the drainages. However, these variables do not have a great impact on parr size and did not have strong trends with parr FL. As in Chapter 2, the overall trends demonstrated larger-lower elevation streams supported growth, which likely due to these habitats being metabolically profitable and selected by parr (Gibson 2015; Gibson 2017). The positive channel width-FL relationship is likely due to the increased feeding opportunities and habitat availability wider channels allow (Hedger et al. 2013; Johnson 2013; Gibson 2015). However, increased growth at wider-lower elevation streams appears to be maintained within drainages rather than among drainages. For example, the Penobscot drainage contained the narrowest habitats among the four drainages but contained the highest densities which is potentially due to the lower amount of available habitat forcing the juveniles to group together. The high densities may also be due to the Penobscot drainage having the highest max estimated fry stocking value (Table 5). The Penobscot averaged model only demonstrated the habitat variable of elevation which supported growth at the lowest and highest elevations, but also
represented one of the weakest elevation relationships. The sites sampled within the Penobscot drainage only reached ~75 m, so I am unable to speak to higher the trends the higher elevations across the drainage would produce. The mean channel width variable was correlated with elevation in three of the four drainages (and Chapter 2) and allows for the assumption that the trends of elevation and mean channel width can be related, showing that higher elevations and narrower channels trend with smaller fish. These habitat relationships while consistent among drainages, are still relatively weak which suggests that there may be other variables that facilitate FL changes through time. It is likely that these habitat relationships will become more complicated as climate change continues to warm these habitats past levels that facilitate growth (Elliott and Hurley 1997; Gibson 2015; Fernandez et al. 2020). However, these low-elevation habitats are predicted to be the best suited for the accelerating climate change accelerates (Fernandez et al. 2020) and therefore should be prioritized for future habitat restoration projects and stock enhancement.

Density dependence was observed at some level within all the drainages, except Penobscot where none of the density-dependent variables were kept for modeling due to collinearity issues. However, I suggest that there is density dependence in Penobscot due to this drainage having the highest mean juvenile salmon density (Table 5) with the smallest mean fork length which coincides with other studies findings of decreased growth at high densities (Marschall et al. 1998; Ward et al. 2009; Jonsson et al. 2020). However, fry stocking intensity was lowest within the Penobscot drainage among the drainages, which may have alternatively reduced density-dependence on newly stocked fish. It should also be noted that the age-0 parr stocking variable was not added to the Penobscot model due to these parr being stocked in non-electrofishing areas, further reducing our ability to strongly identify density dependence. The
other three drainage averaged models resulted in similar trends to Chapter 2, with weak Narraguagus trends and slightly stronger Sheepscot trends in Chapter 3. The East Machias averaged model density relationships were more complex in Chapter 3, however, the trend contained large confidence bands and relatively few values of high stocking intensity, and thus I caution interpretation. Overall, parr growth was determined to be density limited which is likely due increased competition over food and space (Jonsson et al. 2020) that is further amplified by overstocking in inopportune habitats (Whalen and LaBar 1994).

Age composition of Atlantic salmon parr likely further reflects growth conditions among the four drainages. As in Chapter 2, age-1 parr was consistently the dominant age class found among all the drainages throughout the study period, including Penobscot parr. Both the Sheepscot and Penobscot drainages only contained age-1 and age-2 parr which is an earlier smolt age for these two drainages compared to the other two drainages (age 1-4) and other Atlantic salmon populations in North America (age 1-7) (Power 1958). The Penobscot and Sheepscot drainages are the lowest latitude drainages in this study which may explain why fewer age classes of parr are observed here (Power 1958). However, all the drainages are within similar latitudes compared to the entire range of Atlantic salmon habitat. It is well documented that larger parr are more likely to emigrate from the system as smolts therefore creating fewer age classes (Nicieza et al. 1991; Metcalfe and Thorpe 1992; Thorpe et al. 1992; Elliott and Hurley 1997). The simplification of age classes could be due to the high density seen in the Penobscot drainage (Table 4). The presence of smaller age classes as well as the high average densities, may indicate that the Penobscot drainage can produce a larger number of parr that can grow and smolt more quickly. However, only ~14% of the Penobscot parr were aged and efforts to assess ages were inconsistent among years, which needs to be considered when interpreting these results (similar
to the other three drainages in Chapter 2). The limited sample sizes among the drainages makes it difficult to identify shifts in age composition, but it does give an insight to the overall composition of these drainages and how they all primarily support smaller age classes.

There are likely multiple other variables that would help describe parr size and its change over time within the drainages examined. The levels of deviance explained by the GAMMS were reasonable (between 12% and 36.8%), however, most of the deviance is unexplained. Variability in parr FL was best explained within the Penobscot drainage at 36.8%. The Penobscot averaged model also only demonstrated three variables (MSST, elevation, and year), which with the higher amount of deviance explained further implies that these three variables are important predictors of parr length. Also, the Penobscot averaged model demonstrated the strongest relationship with MSAT which may be resulting in the larger amount of deviance explained and highlights the importance of a temperature variable that accounts for the constantly changing environment. The East Machias averaged model was the lowest at 12% deviance explained, compared to 24% explained in Chapter 2. The loss of MSAT variable in this population’s model resulted in less of the FL variability to be explained and therefore it is harder to have strong results for this specific drainage compared to the others. The Sheepscot and Narraguagus models also lost deviance explained but not to the extent of the East Machias model. The four populations’ range in deviance explained points to the need for more variables to be integrated in the models to describe parr size which in turn will allow for more sites to be included in the analysis potentially leading to stronger results. Some of the unexplained variation may be found through the addition of other growth limiting variables such as density of predators/competitors (Gibson 2017), proximity from lakes and dams (Gibson 2015; Gibson 2017), number of potential
territories and stream depth (Oakland et al. 2004; Johnson 2013), and stream discharge (Davidson et al. 2018).

In conclusion, this chapter further demonstrates that the Maine Atlantic salmon population has been declining in both size (as observed in Chapter 2) and density (Wagner and Sweka 2011) and has not shown signs of recovery. The Penobscot population is demonstrating temperature limited growth that is not yet evident in the other drainages but closely matches other works (Elliott and Hurley 1997; Gibson 2015) and may be more accurately representing parr size (as well as its high percentage of deviance explained). The Penobscot drainage demonstrated the highest deviance explained; however, I do recognize that there is likely more unaccounted variability in the trends due to the limitation of spatial data that does not cover the entire drainage. Furthermore, I recommend focusing management practices on more downstream northern habitats within each drainage, but deeper drainage-specific assessments should be conducted with the use of these results to determine the areas of best habitat quality.
Table 4:
Summary of electrofishing surveys conducted, and the range of sampling years used to sample the Atlantic salmon parr utilized within the generalized additive mixed models.

<table>
<thead>
<tr>
<th></th>
<th>Penobscot</th>
<th>East Machias</th>
<th>Narraguagus</th>
<th>Sheepscot</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Sites</td>
<td>34</td>
<td>32</td>
<td>60</td>
<td>15</td>
</tr>
<tr>
<td>Number of Sampling Events</td>
<td>88</td>
<td>122</td>
<td>356</td>
<td>143</td>
</tr>
<tr>
<td>Number of Fish</td>
<td>2231</td>
<td>2581</td>
<td>7236</td>
<td>1904</td>
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<tr>
<td>Mean Fish Fork Length (mm)</td>
<td>118.1</td>
<td>124.0</td>
<td>120.7</td>
<td>141.0</td>
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</table>
Table 5:
Summary of explanatory variables evaluated within generalized additive mixed models, including range and mean in parentheses. (For the number of sites and sampling events within each drainage see Table 4).

<table>
<thead>
<tr>
<th></th>
<th>Penobscot</th>
<th>East Machias</th>
<th>Narraguagus</th>
<th>Sheepscot</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Summer Stream Temperature</td>
<td>15.93 – 21.84 (17.35)</td>
<td>16.53 – 21.92 (19.09)</td>
<td>15.99 – 21.77 (19.08)</td>
<td>18.05 – 21.98 (20.01)</td>
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<td>Elevation</td>
<td>9.65 – 75.72 (40.33)</td>
<td>19.78 – 84.75 (41.84)</td>
<td>26.36 – 130.18 (99.76)</td>
<td>48.34 – 106.30 (68.73)</td>
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<tr>
<td>Mean Channel Width</td>
<td>1.52 – 9.45 (4.73)</td>
<td>2.40 – 16.00 (7.62)</td>
<td>2.87 – 27.03 (12.06)</td>
<td>4.57 – 19.30 (8.98)</td>
</tr>
<tr>
<td>Juvenile Salmon Density (catch per 100 m²)</td>
<td>0.00 – 86.78 (30.37)</td>
<td>0.00 – 45.62 (13.78)</td>
<td>0.00 – 27.75 (6.60)</td>
<td>0.21 – 44.45 (13.26)</td>
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<td>Age-0 Parr Stocked</td>
<td>N/A</td>
<td>0 – 149,815 (3,035)</td>
<td>0 – 20,990 (2,938)</td>
<td>0 - 17925 (10,272)</td>
</tr>
<tr>
<td>Estimated Fry Stocked</td>
<td>0 – 1,898,747 (238,735)</td>
<td>0 - 319,138 (174,326)</td>
<td>0 - 698,200 (258,264)</td>
<td>0 - 323,000 (153,384)</td>
</tr>
</tbody>
</table>
Table 6: Model rankings after all-subsets modelling, with the top-ranked models each represented by a row; ranked by Akaike Information Criterion (AIC). The top-ranked 95% by AIC weight \( (w_i) \) from each drainage model were selected for model averaging. Abbreviations are as follows: df = number of parameters, LL = log likelihood, \( \Delta_i \) = the difference between the AIC value for the \( i^{th} \) model and the minimum AIC value for all models, and = a variable that was removed during the collinearity process. Age-0 parr stocked was not used within the Penobscot modeling and therefore is marked with N/A.

<table>
<thead>
<tr>
<th>Juvenile Salmon Density</th>
<th>Estimated Fry Stocked</th>
<th>Elevation</th>
<th>Mean Channel Width</th>
<th>Mean Summer Stream Temperature</th>
<th>Age-0 Parr Stocked</th>
<th>Year</th>
<th>df</th>
<th>LL</th>
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Figure 8:
Map of the electrofishing sites within the four Maine drainages used for assessed trends in juvenile Atlantic salmon parr fork length. Each drainage is outlined and the sites within them are represented by dots with darker dots representing more sites in that area.
Figure 9:
Predicted response curves of the relationships among explanatory variables and Atlantic salmon parr fork length as generated through generalized additive mixed models for the Penobscot drainage. 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 10:

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 drainage. 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 11:

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 drainage. 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 12:
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 drainage. 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 13:
Response curves of the relationship of Atlantic salmon parr age and their fork length as generated through generalized additive models for each drainage. 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 14:**

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 drainage. 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 15:

Summary of the percent and count of Atlantic salmon parr age through time (as seen in birth year) for each drainage (Penobscot, East Machias, Narraguagus, and Sheepscot). Differing colors represent the differing ages.
Figure S5:
Mixture model of the two curves representing the two age classes of fry (red) and parr (blue) for all four drainages.
Figure S6:

Predicted response curves of the relationships among explanatory variables removed from the averaged model due to collinearity and Atlantic salmon parr fork length as generated through generalized additive mixed models for the Penobscot drainage.
Figure S7

Predicted response curves of the relationships among explanatory variables removed from the averaged model due to collinearity and Atlantic salmon parr fork length as generated through generalized additive mixed models for the East Machias drainage.
Figure S8

Predicted response curves of the relationships among explanatory variables removed from the averaged model due to collinearity and Atlantic salmon parr fork length as generated through generalized additive mixed models for the Narraguagus drainage.
Figure S9

Predicted response curves of the relationships among explanatory variables removed from the averaged model due to collinearity and Atlantic salmon parr fork length as generated through generalized additive mixed models for the Sheepscot drainage.
CHAPTER 4: CONCLUSION

Parr density, growth, and condition all are suggested to affect overall Atlantic salmon population productivity in freshwater (Good et al. 2001; Swansburg et al. 2002; Arnekleiv et al. 2006; Armstrong and Armstrong 2018), and therefore the success of this life stage is likely vital for species recovery. Identifying the variables that affect these parr is key in improving the management of this juvenile life stage. My thesis examined the relationships between parr size and multiple biological and environmental variables in Maine, providing valuable new insight into the juvenile ecology of this endangered species. In Chapter 2, I assessed variations in size among three drainages (East Machias, Sheepscot, and Narraguagus). In Chapter 3, an additional drainage (Penobscot) was included, along with the investigation of the modeled summer stream temperature-parr size relationship. In the following sections, I discuss how my results have expanded the understanding of the Maine juvenile Atlantic salmon and how they can be used to improve management and conservation of this species.

My thesis explored if an individual-level metric (length) followed similar patterns to previous work that described a lack of recovery based on a population-level metric (parr density) (Wagner and Sweka 2011). Between both chapters, the greatest gain in FL through time was 5-mm (~4% of the average length among the drainages), which may indicate some improvement of parr quality. This ~5mm FL gain was demonstrated within the Sheepscot averaged models in both chapters. Wagner and Sweka (2011) concluded that rivers across New England, including the Sheepscot River, were decreasing in density, which they suggest is a sign that these populations were not improving. However, this loss of density may have facilitated growth due to the density dependence found within the Sheepscot drainage within these studies. The other three drainages demonstrated reductions in FL through time in at least one of the chapters, with
the largest loss over time of 10-mm (~8% of the average fish among the drainages). Therefore, signs of improvements in parr size are limited, which is concerning when paired with the decline in densities found in previous work in this region (Wagner and Sweka 2011), further indicating a lack of recovery.

Temperature was found to be an important predictor of Atlantic salmon parr length in both studies, with the MSST and MSAT variables remaining within most of the top-ranked models for their respective studies. In general, I found a stronger relationship between parr FL and air temperature (Chapter 2) than with stream temperature (Chapter 3). This unexpected difference in strengths of FL-temperature relationships is likely due to the difference in the spatial and temporal resolution between the two temperature datasets. There was much less variability for MSST, with only one value for each site throughout time, while MSAT was estimated for each year at each site (but only starting in 1980). Thus, although stream temperature better represents the actual temperatures experienced by parr, the air temperature dataset likely better represents and accounts for the temporal fluctuations in temperature that parr experience. Therefore, my results suggest that temporal variability in temperatures is likely important for Atlantic salmon parr.

The temperature ranges observed within my research generally fall within the optimum growth temperatures found in other studies (Elliott and Hurley 1997; Gibson 2015), which helps explain the positive relationships observed with FL. However, Atlantic salmon are vulnerable to climate change which is putting strain on some populations (Borggaard et al. 2019; Hare et al. 2016). Future increases in temperature due to climate change are predicted to exceed optimum ranges (Fernandez et al. 2020), which could result in detrimental impacts on the parr. In particular, the Penobscot drainage demonstrated the greatest temperature-dependent growth and
is predicted to be the greatest affected by climate change due to its inland northern location (Fernandez et al. 2020). In addition, among the drainages, Sheepscot is the warmest, and demonstrated a clear negative relationship between mean summer air temperature and parr length (Chapter 2, but see Chapter 3 where a very weak but positive relationship was observed). Thus, parr in the Sheepscot drainage may already be experiencing size-limiting temperatures, sooner than the coastal northern sites (East Machias and Sheepscot) (Fernandez et al. 2020).

Other than temperature, habitat elevation and mean channel width also resulted in variable responses on parr FL which also differed between the chapters. My results indicate that low-elevation, wide, and warm habitats support increased growth which is suggested to be selected by parr and metabolically profitable (Gibson 2015; Gibson 2017). These relationships may become more complicated as climate change continues to warm these habitats, potentially to temperatures exceeding those that can facilitate growth (Elliott and Hurley 1997; Gibson 2015; Fernandez et al. 2020) However, the coastal locations are predicted to be less impacted by climate change (Fernandez et al. 2020), and therefore the low elevation habitats (more coastal) may continue to be best suited for parr growth. Therefore, these locations could be of focus for future habitat restoration projects and the improved stocking efforts.

In addition to the habitat effects, parr size appeared to be density dependent. I consistently observed a negative relationship between density and FL across drainages and between chapters, which supports other findings of competition for food and space (Marschall et al. 1998; Ward et al. 2009; Jonsson et al. 2020). Therefore, this relationship shows that although stocking efforts in Maine are currently needed to maintain Atlantic salmon populations, there are limits to its effectiveness. Given the density dependence demonstrated in the Narraguagus and Sheepscot drainages (Figure 3, Figure 4, Figure 11, and Figure 12), I expect that the high volume
of current stocking densities are further limiting parr growth. Increases in stocking has been linked to increased mortality when passing the habitat’s carrying capacity (Whalen and LaBar 1994), which likely is lower than optimum due to the lower habitat quality (Snyder et al. 2008; Wilkins and Snyder 2011). Furthermore, the density dependence found within these two drainages implies that the continuation of high stocking volumes may have undesired effects by further limiting parr growth. However, this needs to be balanced against population level production with it being suggested that parr size is density limited (Marschall et al. 1998; Ward et al. 2009; Jonsson et al. 2020).

However, there are exceptions to the overall trends of density dependence seen throughout both chapters. Although the supplemental Penobscot GAM as well as the East Machias averaged model demonstrated negative relationships with increased juvenile salmon density (Figure 2 and Figure S6), there were also positive relationships between FL and with the number of estimated fry stocked (Figure S6) and age-0 parr stocked (Figure 2 and Figure 10). These positive relationships can be interpreted as increased density benefiting growth, however the East Machias age-0 parr trends have wide confidence bands with low sample sizes and therefore should be interpreted with caution (Figure 2 and Figure 10). Stocked fish can also exhibit relatively rapid dispersal post-stocking, allowing for self-thinning (Brunsdon et al. 2017) before stocking and capture via electrofishing. For the Penobscot drainage, density variables were not retained in averaged models, indicating density dependence may be less important in this drainage. I was also limited to a single stocking value per year within each drainage due to the lack of within-year resolution in the stocking data which requires further caution when interpreting the data. To ensure stronger conclusions, a more detailed stocking dataset with
location specific data should be created during future stocking events so that density dependence can be linked to more specific locations rather than entire drainage areas.

There are some limitations to my modeling process that should be considered while interpreting these results. Some variables within both studies that did not have as strong of a relationship with parr size as found in other work. These weak relationships may have been due to the choice of limiting the maximum degrees of freedom to three within the GAMM models, which serves to limit overfitting of the relationships but may have oversimplified the response curves in instances where the relationships are complex. A potential example of underfitting was the weaker MSST-FL relationships that were stronger in other literature (Swansburg et al. 2002; Gibson 2015; Foldvik et al. 2017). Further examination of these relationships with increased flexibility may help uncover more complex relationships that better represent the data. Investigating the impacts of varying the flexibility of individual response curves (e.g. Furey and Rooker 2013), would help determine how my imposed limits on curve “wiggliness” affected my results. Similarly, the use of other types of models that assess habitat suitability may yield a higher deviance explained and account for parr growth more accurately. Wagner and Sweka (2011) directly compared the performance of various types of models to determine which one to focus on for interpreting results. Manipulating the models used in my studies as well as an analysis on how they compete with others would likely produce a modeling process that is better suited to explaining the trends of parr in this region.

Furthermore, better understanding and quantification of potential genetic differences and influences within and among drainages is another potential avenue for strengthening my modeling. First, hatchery-reared fish may respond differently than wild fish to these stressors and therefore they both should be utilized in future modeling. Wild and hatchery fish can differ in
fitness and survival (Jonsson et al. 1991; Saloniemi et al. 2004; Araki et al. 2008; Sheehan et al. 2010). Second, aside from hatchery vs wild influences, distinct genetic differences exist among wild populations of Atlantic salmon, even within Maine (King et al. 2000; Spidle et al. 2003). Thus, quantifying any potential local adaptation (Sheehan et al. 2005) to specific habitat variables (those I investigated and those not examined here) would help understand drainage-specific relationships between size and explanatory variables.

Furthermore, the datasets I utilized also limited my research due to variable sampling effort of parr (different approaches over time) as well as lack of habitat variables across the parr sampling timeframe. Among the drainages the sampling effort varied among sites with many of the sites being sampled inconsistently through the years which yielded less detailed analysis. An increase of consistent sampling at the same locations would permit site specific modeling to be conducted which would provide a more detailed analysis on individual drainages. In addition, the limitation of sample size for many of the variables, such as the lack of consistent yearly sampling for many of the sites, may also be resulting in the inability for the models to truly represent the entire watershed through the entire time series. For example, the MSST variable was only recorded as one value for each site throughout time, which likely does not accurately account for the constantly changing parr habitat. A potential improvement would be to assess temperature within critical time periods (summer and winter months) which may better serve to capture seasonal and interannual variability. Alternatively, more localized analysis could be conducted instead, focused on streams with more complete and regular water temperature morning.

The addition other explanatory variables may also increase the deviance explained. Other habitat-related variables that have been shown to impact parr include distance from lakes and dams (Gibson 2015; Gibson 2017), number of potential territories and stream depth (Oakland et
al. 2004; Johnson 2013), and stream discharge (Davidson et al. 2018). Another improvement for this study would be to create a more comprehensive dataset for the stocking variables that allowed for more detailed analysis such as a study of the relationship of parr size relative to their distance from stocking locations. Having exact stocking locations would allow for the stocking variables to be better linked to sites rather than applied to the entire drainage. Creation of a more detailed dataset with the addition of more biological and habitat variables likely would increase the percent deviance my models explained, which were 12.4% - 40.8% between both chapters.

From my findings, management practices utilized throughout the region, such as dam removal and habitat connectivity projects, have not yet been able to overcome the challenges that have been harming the Maine population as observed through lack of an increase in size (Chapter 2, Chapter 3) or density in the parr (Wagner and Sweka 2011). However, dam removal has been observed to enhance fish assemblage locally, although the timeframe of improvements varied among species and locations which may explain why the benefits of past recovery efforts have not been observed yet (Poulos et al. 2014; Hogg and Zydlewski 2015; Watson et al. 2018). Fish size has also been found to increase post-restoration efforts such as dam removals, dam passage improvements, and stocking (Stevens 2019), however many of the historical habitats are not artificially stocked or accessible to wild fish and therefore are still unoccupied by Atlantic salmon. My study suggests that further management steps need to be taken to further these size increases. Stevens (2019) also found that these positive responses to restoration can occur many years after efforts (Stevens 2019), which further indicates that the benefits of the past restoration efforts may have not been observed yet and a continuation of this study would find them in future years. However, Stevens (2019) assessed the Penobscot River, and therefore an additional study focusing on the other three drainages would allow for these results to better connected to
my findings. Further restoration should still be prioritized and assessed to more confidently predict benefits to these populations. More immediately, priority should be given to habitat restoration projects such as increasing habitat complexity by the addition of physical structures such as wood and boulders (USFWS and NMFS 2018) and increasing habitat connectivity by dam removal and remediation (Gibson 2017). Atlantic salmon habitat has been damaged at differing levels across watersheds (Snyder et al. 2008; Wilkins and Snyder 2011), and therefore habitat restoration efforts as well as increasing connectivity should be conducted to have a greater chance at benefiting parr. Restoration efforts would increase the amount of accessible habitat that could help alleviate the density dependence observed in these studies, therefore promoting parr growth.

Overall, my thesis determined the influence of multiple biological and environmental variables on the size of juvenile Atlantic salmon. My research confirms that this region’s population is not showing strong signs of recovery related to size changes. Through GAMMs I confirmed that multiple variables, including metrics of density dependence, temperature, and channel width, are linked with parr lengths. Collectively, this thesis enhances our understanding of the factors potentially influencing population productivity and increases the current knowledge of the ecology of the juvenile life stage of the United States Atlantic salmon.
REFERENCES


