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ARTICLE

# Retrospective Analysis of Seasonal Ocean Growth Rates of Two Sea Winter Atlantic Salmon in Eastern Maine Using Historic Scales

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## Abstract

Substantial declines of anadromous Atlantic Salmon *Salmo salar* have occurred throughout its range, with many populations at the southern extent of the distribution currently extirpated or endangered. While both one sea winter (1SW) and two sea winter (2SW) spawner numbers for the North American stocks have declined since the 1950s, the decline has been most severe in 2SW spawners. The first months at sea are considered a period of high mortality. However, early ocean mortality alone cannot explain the more pronounced decline of 2SW spawners, suggesting that the second year at sea may be more critical than previously thought. Atlantic Salmon scales collected by anglers and the state agency from 1946 to 2013 from five rivers in eastern Maine were used to estimate smolt age and ocean age of returning adults. Additionally, seasonal growth rates of maiden 2SW spawners were estimated using intercirculi measurements and linear back-calculation methods. Generalized linear mixed models (Gaussian family, log link function) were used to investigate the influence of average sea surface temperature, accumulated thermal units, the Atlantic Multidecadal Oscillation (AMO) and North Atlantic Oscillation indices, smolt age, smolt length, postsmolt growth, and river of origin on growth rate during the oceanic migration of North American Atlantic Salmon. Results suggest that different factors influence salmon growth throughout their oceanic migration, and previous growth can be a strong predictor of future size. Growth was negatively impacted by the phase of the AMO, which has been linked to salmon abundance trends, in early spring following the postsmolt period. This is likely when the 1SW and 2SW stock components separate, and our results suggest that this period may be of interest in future work examining the disproportionate decline in 2SW spawners.

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Anadromous Atlantic Salmon *Salmo salar* are native to multiple countries in both Europe and North America, but substantial declines have occurred throughout the range of this once abundant species. On both sides of the Atlantic

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Ocean, southern runs have declined more extensively, and many populations are currently extirpated (Parrish et al. 1998). By the mid-1990s, runs of the species had declined to 500–2,000 fish in all Maine rivers combined, leading to the listing of the Gulf of Maine distinct population segment (GOM DPS) as federally endangered in 2000 (Fay et al. 2006).

The complex life history of this species, which involves a juvenile freshwater phase followed by a marine phase that can last 1 to 5 years before adults return to freshwater to spawn (Webb et al. 2007), has exposed Atlantic Salmon to a series of threats, such as pollution, dams, ocean conditions, and overfishing, that have contributed to their continued decline (Parrish et al. 1998; NRC 2004). The continued declines of Atlantic Salmon across populations from multiple rivers supports the hypothesis that common events operating in the marine environment are at least partially responsible for population declines (Hutchinson and Mills 2000; Mills et al. 2013). Atlantic Salmon juveniles complete an extensive migration from their natal rivers to reach ocean feeding grounds. For North American stocks, juveniles enter the ocean environment as smolts and travel to the southern coasts of Nova Scotia and Newfoundland to feed during the summer as “postsmolts” (Friedland et al. 2014) and spend their first winter in the Labrador Sea (Reddin and Short 1991). These juveniles are considered postsmolts until their first winter at sea. Following this first winter, some will mature as one sea winter (1SW) fish and return to their natal rivers to spawn. The majority of salmon from rivers in the United States will remain in the ocean for at least one more year. These fish migrate to the west coast of Greenland to feed from June to September of their second year (Hansen and Jacobsen 2000) and then return to the southern Labrador Sea to overwinter (Figure 1). Most adults, then known as two sea winter (2SW) fish, will return to rivers to spawn after their second winter at sea (Mills et al. 2013).

The initial time in seawater is a period of high mortality and therefore has a large influence on the success of a year-class (Hansen and Quinn 1998). In Europe, return rates in multiple rivers have been linked to postsmolt growth, which has been shown to correlate with sea surface temperature (SST) (Friedland et al. 1993, 2000, 2005; McCarthy et al. 2008; Todd et al. 2008). While data suggest that growth-mediated mortality during the postsmolt period has been important for recruitment of European Atlantic Salmon stocks, this trend has not been observed in North American stocks. Climatic factors experienced in the early postsmolt period (the first few months at sea) have been linked to stock abundance (Friedland et al. 2003, 2014); however, postsmolt growth of both hatchery- and wild-origin fish from North American rivers has not been clearly linked to stock abundance (Friedland et al. 2005, 2009b; Hogan and Friedland 2010). These results suggest that growth during the postsmolt period

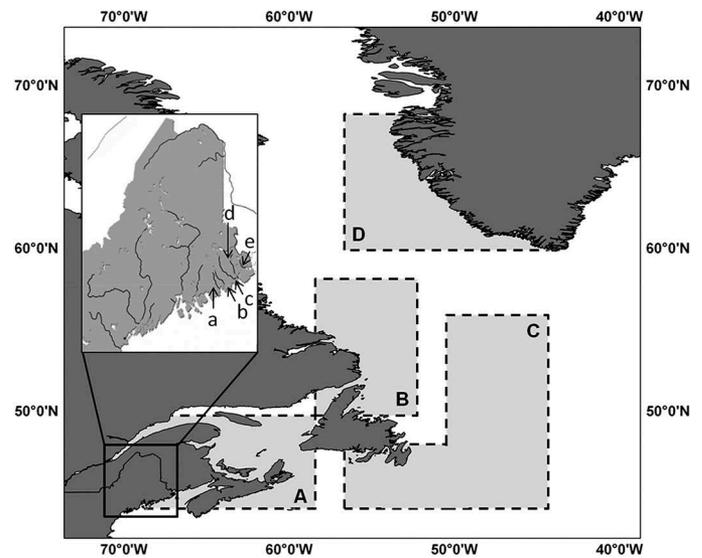


FIGURE 1. Areas used during the oceanic migration of Atlantic Salmon from rivers in eastern Maine. Rivers (inset) used for analysis were the Narraguagus River (a), Pleasant River (b), Machias River (c), East Machias River (d), and Dennys River (e). Light gray boxed areas represent areas used for temperature analysis during the early postsmolt migration period (A), the postsmolt fall nursery (B), the overwintering area (C), and the 2SW summer feeding grounds (D).

may not be a primary driver of marine survival in North American stocks.

While mortality experienced during the second year at sea is lower than during the early marine migratory period, estimates of mortality in the second year at sea can also be high and variable (Potter et al. 2003). Both 1SW and 2SW spawner numbers for the North American stock have declined since the 1950s, but the decline has been most severe in 2SW fish, especially since the 1980s (Chaput et al. 2005; Mills et al. 2013; Friedland et al. 2014). It has been difficult to study Atlantic Salmon throughout their entire marine migration, and it is likely that many mechanisms are affecting the survival of this species at sea. It is unclear whether the more pronounced decline in 2SW spawners is due to climate and ecosystem conditions that influence salmon throughout their entire period at sea, having a greater cumulative impact on 2SW fish, or conditions that influence mortality following the first winter at sea when the maturing and nonmaturing portions of the stock separate (Mills et al. 2013). Multiple biological and physical factors have been linked to Atlantic Salmon abundance and productivity trends, including SST, the Atlantic Multidecadal Oscillation (AMO), the North Atlantic Oscillation (NAO), and the size and energy content of Capelin *Mallotus villosus*, an important prey species (Mills et al. 2013; Renkawitz et al. 2015). Decreased energy density of prey could have important implications for growth, condition, survival, and overall recruitment of 2SW spawners. The question remains whether changes in growth during the second year at

sea are noticeable since the 1950s, as this could support the hypothesis that an energy deficit is contributing to the decline of 2SW spawners. Furthermore, which factors influence the ocean growth of Atlantic Salmon during different phases of their oceanic migration could elucidate factors that are playing a role in the continued decline of the species in North American rivers.

Multiple Atlantic Salmon runs have been monitored during the latter half of the 20th century as conservation efforts have attempted to mitigate declines. Included in these efforts was the collection of scales from returning adults that have been used to estimate age and determine the rearing origin (hatchery or wild) of these fish. Scales can also be used to estimate size at age and ocean growth of individuals, and have often been used in the past to examine growth during the postsmolt period (Friedland et al. 2000, 2005, 2006). However, little emphasis has been placed on growth of Atlantic Salmon during their second year at sea, a period that may play at least some role in recruitment. During their oceanic migration, 2SW spawners span a large area of the ocean, making it possible that different factors are influencing the overall growth of salmon during different times of the year. The objective of this study was to use scales collected from Atlantic Salmon from five eastern Maine rivers (Narraguagus, Pleasant, Machias, East Machias, and Dennys rivers) to evaluate changes in seasonal growth rates of maiden (first-time) 2SW spawners from the 1950s to the 2000s in order to evaluate factors influencing growth during the oceanic phase of these individuals.

## METHODS

*Capture, fish length, and scale collection.*—Adult Atlantic Salmon scales were obtained from the Maine Department of Marine Resources (MDMR). Scales were collected from returning adults captured in the Narraguagus, Pleasant, Machias, East Machias, and Dennys rivers in eastern Maine (Figure 1) from 1946 to 2013. These rivers were included in the initial listing of the GOM DPS in 2000, and while they once supported robust recreational fisheries for Atlantic Salmon, recent returns in all five rivers combined have been typically fewer than 100 individuals (NRC 2004). Samples were from both angler-collected scales as well as scales collected during state monitoring efforts. Both FL (mm) and TL (mm) data at capture were obtained from MDMR. Prior to the 1980s, most lengths for returning adults were reported as TL, and lengths from later years were reported as FL. A subset of our samples ( $n = 94$ ) contained both TL and FL for each individual. The relationship of TL to FL for these fish was linear ( $r^2 = 0.97$ ), so any TL data were converted to FL using the equation:

$$FL = 0.9302 \cdot TL + 15.77.$$

*Scale processing and age estimation.*—Scales were cleaned with water and then mounted between two glass microscope slides. Each scale was viewed using 25 $\times$  magnification on a Zeiss Axioplan microscope and imaged with a microscope-mounted digital camera (SPOT Insight 2 MP Color Mosaic; Diagnostic Instruments, Sterling Heights, Michigan). Each sample was viewed by at least two trained scale readers to estimate both smolt age and ocean age (ICES 2011). If ages from the two initial readers were not in agreement, a third reader aged the sample to resolve conflicting readings by majority rule.

*Scale measurements for growth analysis.*—During aging, we identified “high quality” scales from maiden 2SW spawners for measuring. Scales that were eroded, cracked, or had broken circuli or regenerated centers were excluded from measurement analysis. One scale was measured from each fish. For each smolt year (year at emigration), we attempted to find 50 quality samples for measurement (Table 1). This goal was met in many years in the 1960s and 1970s when salmon were more abundant; however, in later years sample numbers were limited due to the low numbers of returning adults.

Scale images were measured using ImagePro Premier software (Media Cybernetics, [www.mediacy.com](http://www.mediacy.com)). Total radius was measured from the focus of the scale along the anterior axis to the margin of the scale (ICES 2011). The end of the freshwater growth zone was marked along this axis, indicated by the end of closely spaced circuli pairs. Circuli in the ocean growth zone (starting at the first circuli following the freshwater zone) were counted on each scale, and the distance between circuli pairs was measured (Friedland et al. 1993). For each fish, we calculated a mean circuli spacing index for each pair by taking the average intercirculi distance of the indicated pair, the two pairs before the indicated pair, and the two pairs following the indicated pair. This index was used to avoid misidentification of important growth points on the scale due to the high variability in intercirculi spacing (Friedland et al. 2009b). The first winter annulus was estimated by identifying the minimum of the mean circuli spacing index that was within the first three-quarters of the total marine circuli on the scale and after pair 15. We focused on pairs greater than 15 to avoid misidentification of the winter minimum due to growth checks observed on some scales during the first year at sea.

*Growth sections.*—Marine circuli pairs prior to the first winter annulus were used to measure the postsmolt growth increment. Using methods similar to Friedland et al. (2009b) and Hogan and Friedland (2010), we divided the postsmolt growth increment into seven equal sections by circuli count to approximate growth during the months of June to December in the smolt year. Growth in the second year at sea was investigated by extracting circuli pairs laid down after the first winter annulus for analysis. The minimum value of the mean circuli spacing index for the last five circuli pairs was used to designate the second winter minimum, as some scales were used from fish that exhibited “plus growth” after their

TABLE 1. Sample sizes, by river, of scales used for growth analysis of Atlantic Salmon in Maine.

Smolt Year	Dennys River	East		Narraguagus River	Total
		Machias River	Machias River		
1950	0	0	0	2	2
1951	0	0	0	26	26
1952	0	1	1	8	10
1953	2	0	2	5	9
1954	4	0	0	14	18
1955			Data missing		
1956	1	0	4	2	7
1957	12	3	0	35	50
1958	6	2	5	6	19
1959	4	3	23	0	30
1960	10	1	24	0	35
1961	5	0	2	43	50
1962	0	0	1	49	50
1963	0	1	25	1	27
1964	0	0	12	38	50
1965	0	0	50	0	50
1966	0	0	50	0	50
1967	0	0	50	0	50
1968	0	0	21	29	50
1969	0	0	50	0	50
1970	0	0	50	0	50
1971	0	0	0	50	50
1972	0	0	2	48	50
1973	0	3	1	46	50
1974	0	9	6	15	30
1975	0	10	2	38	50
1976	0	9	10	31	50
1977	0	1	9	17	27
1978	9	5	8	28	50
1979	2	11	5	31	49
1980	1	4	13	32	50
1981	0	1	1	26	28
1982	2	10	4	23	39
1983	0	8	4	26	38
1984	2	0	1	21	24
1985	0	2	1	15	18
1986	0	2	2	7	11
1987	2	5	1	13	24
1988	7	5	2	22	36
1989	4	0	0	42	46
1990	0	0	0	18	18
1991	1	0	0	49	50
1992			Data missing		
1993	5	0	0	25	30
1994	2	0	0	32	34
1995	0	0	0	4	4
1996	0	0	0	13	13

TABLE 1. Continued.

Smolt Year	Dennys River	East		Narraguagus River	Total
		Machias River	Machias River		
1997–1999			Data missing		
2000	0	0	0	1	1
2001	0	0	0	13	13
2002	0	0	0	8	8
2003	0	0	0	2	2
2004	1	0	0	2	3
2005	0	0	0	4	4
2006	0	0	0	10	10
2007	4	0	0	3	7
2008	1	0	0	26	27
2009	1	0	0	1	2
2010	0	0	0	12	12
Total	88	99	442	1,012	1,641

second winter as sea, indicated by an increase in circuli spacing near the edge of the scale. We additionally divided the second sea-year growth increment into 12 equal sections by circuli count to estimate monthly growth during the second year at sea.

To avoid a mismatch of monthly growth zones with environmental conditions, we combined monthly increments into seven sections that represented different periods of adult growth during the first and second years at sea. These sections were chosen based on circuli spacing patterns (Figure 2) and general known locations of Atlantic Salmon during their time at sea, and are indicated by year (Y1 or Y2, based on a calendar year system) and season (Winter, Spring, Summer, Fall). During the first year at sea, the estimated months of June and July were combined to represent the initial summer growth during the postsmolt period (Y1-Summer). The Y1-Fall period consisted of August, September, and October during the postsmolt period, when postsmolts have been located in the “fall nursery” in the Labrador Sea north of Newfoundland (Reddin and Short 1991). The period Y1-Winter consisted of November and December before the first winter annulus, when fish have moved into the overwintering area in the Labrador Sea (Figure 1). The months of January, February, and March were combined to represent the first growth period following the winter annulus in the Labrador Sea (Y2-Winter). The months of April and May were combined to represent spring growth, indicated by increasing intercirculi spacing (Y2-Spring). The months of June, July, August, and September were combined to represent summer growth when fish are feeding in western Greenland (Y2-Summer). The last months of October, November, and December were combined to represent the final growth section

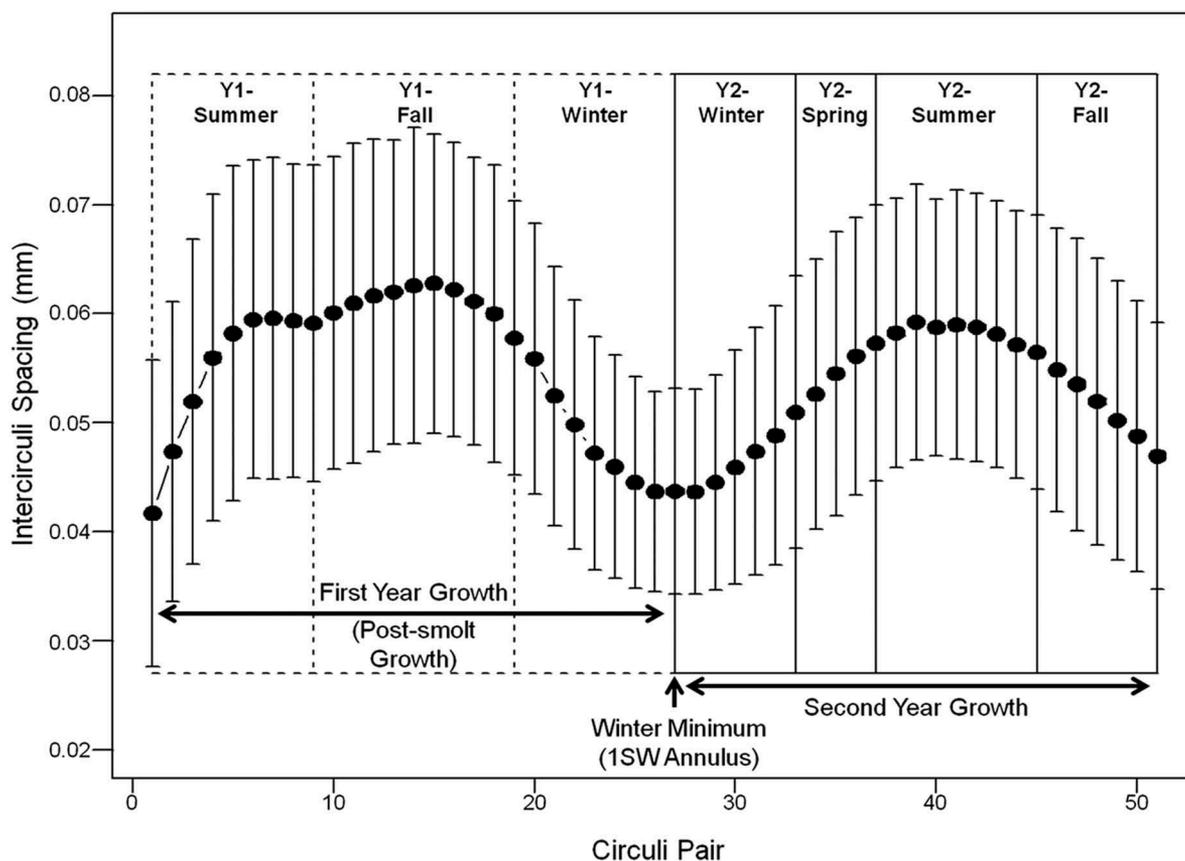


FIGURE 2. Example of growth sections used in regression analysis based on mean intercirculi spacing ( $\pm$ SD) patterns from Atlantic Salmon scales collected from adults returning to Maine's eastern rivers. Closely spaced circuli represent decreased growth during winter periods, while increased spacing represents increased growth during summer and fall seasons.

of the second year, when adults move back to the Labrador Sea to overwinter (Y2-Fall). An example of these growth zones is indicated by Figure 2.

**Back-calculated lengths.**—Dahl-Lea proportional back-calculation (Lea 1910), the recommended method for Atlantic Salmon scales (Friedland et al. 2000; Heidarsson et al. 2006; Kuparinen et al. 2009), was used to estimate smolt length (FL) and length after the first winter at sea (FL) for each individual. Smolt length was calculated based on the end of the freshwater growth zone, and a Welch's *t*-test was used to test for differences in estimated smolt lengths between hatchery- and wild-origin smolts. Length after the first winter at sea was calculated based on the identified winter annulus. The postsmolt growth increment was calculated by subtracting estimated smolt length from estimated length after the first winter at sea. Additionally, we calculated estimates of monthly growth rates for each growth section for use in regression analysis. Back-calculation methods, as described above, were used to calculate the growth of the fish (mm) during each growth section. We then divided the calculated growth increment by the number of months corresponding to that growth section (see above) to obtain growth rates in

millimeters per month. While it is unlikely that growth during each section is entirely linear, the assumption of linear growth allows us to investigate growth during the same interval for different individual fish.

**Growth rate correlations.**—Spearman's rank correlation coefficients ( $\rho$ ) were calculated between each growth increment and the previous growth increment in the year for individual fish. This analysis was used to investigate whether faster-growing fish sustained rapid growth throughout their entire time at sea, and if not, to identify time periods where the reverse relationship (a negative correlation) occurred, as this could indicate a shift in resource allocation or utilization. Significance was assessed at a level of  $\alpha = 0.05$ .

**Environmental variables.**—The data for SST were obtained from the Extended Reconstructed SST (ERSST) version 4. The ERSST is a global monthly SST data set derived from the International Comprehensive Ocean Atmosphere Data Set (ICOADS) and is produced on a  $2^\circ$  latitude  $\times$   $2^\circ$  longitude grid. (Huang et al. 2015). A series of these grids (Figure 1) was chosen for the presumed postsmolt migration area, fall nursery in the Labrador Sea (Reddin and Short 1991; Friedland and Todd 2012), the overwintering area in the southern Labrador Sea,

and the west coast of Greenland, the presumed summer feeding grounds for 2SW spawners (Mills et al. 2013). Values from each grid in an area were averaged based on the months corresponding to each growth section (see above) to obtain a single average temperature value for each growth section in each year. Accumulated thermal units (ATUs) were calculated by summing the monthly accumulated thermal units (number of days in the month  $\times$  average temperature for that month) for the months corresponding to each growth section.

The smoothed AMO Index (detrended to remove the influence of anthropogenic climate change) and the North Atlantic Oscillation (NAO) Index (Rogers Index, normalized using the monthly means and standard deviations for the 1981–2010 base period) were used to examine the influence of large-scale climatic factors on growth (NOAA 2016a, 2016b). The AMO operates on 60–80-year time scales and is a measure of the SST variability across the entire North Atlantic Ocean, which is believed to be driven by the strength of global thermohaline circulation (Drinkwater et al. 2014). While the AMO Index describes temperature variability, and regional effects can vary throughout the Atlantic Ocean, this multi-decadal forcing also influences currents and sea ice, phytoplankton and zooplankton abundance, and recruitment dynamics and growth of fishes (Mills et al. 2013; Drinkwater et al. 2014; Nye et al. 2014). The NAO index describes the pressure difference between the subtropical atmospheric high-pressure zone (the Azores) and the low-pressure zone (Iceland) in the North Atlantic and often occurs at shorter than decadal time scales (Ottersen et al. 2001). This climate forcing is strongest in the winter, and can influence the distribution of major water masses and currents in the Atlantic Ocean, climate variability in the Labrador Sea, sea ice extent, phytoplankton biomass, and recruitment, growth, and distribution of organisms at higher trophic levels (Ottersen et al. 2001; Mills et al. 2013). For the purposes of this study, we used the AMO and the NAO indices to attempt to capture more broad-scale ecosystem effects that could influence Atlantic Salmon growth. Both of these data sets contained monthly values for these indices. The average value was taken for the months corresponding to each growth section.

**Regression analysis.**—We used generalized linear mixed models (Gaussian family, log link function) to investigate the influence of average SST, ATUs, the AMO and NAO indices, smolt age, smolt length, the postsmolt growth increment, and river of origin on monthly growth rate of Atlantic Salmon during each growth section. The postsmolt growth increment was only used in models pertaining to the second year at sea, as this increment was calculated based on length after the first year at sea, and all other predictors were used for both years. We developed a set of 21 a priori models for each growth section during the postsmolt period (Y1 sections) and a set of 24 a priori models for each of the four growth sections in the second year at sea (Y2 sections). These models are reported in Table 2, and the basis for the included predictors is explained below.

For models for Y1-Summer we used temperatures calculated from the postsmolt migration area, and for models for Y1-Fall we used temperatures from the fall nursery area in the Labrador Sea. We used southern Labrador Sea temperatures for models regarding Y1-Winter, Y2-Winter, Y2-Spring, and Y2-Fall. Lastly, we used temperatures from the west coast of Greenland for models regarding Y2-Summer. Continuous predictors were z-standardized prior to use in regression models. Average SST was included as a quadratic term when used, as we expected there to be an optimal relationship between average temperature and growth (Handeland et al. 2003). We included smolt length and the postsmolt growth increment to investigate the hypothesis that previous size would influence future growth. Smolt age was included as a factor with three levels (wild-origin 2-year smolts, wild-origin 3-year smolts, and smolts determined to be of hatchery origin) to investigate whether differences in freshwater rearing had an influence on growth throughout the oceanic period. To attempt to capture more broad-scale ecosystem changes that could influence salmon ocean growth, we included climate indices (NAO and AMO) in our models. Sample year was included as a random effect in all models.

Samples from four rivers (Narraguagus, Machias, East Machias, and Dennys rivers) were used in models for ocean growth analysis. The Pleasant River was not included in this analysis because our samples from this river consisted primarily of kelts, which show considerable scale erosion after overwintering in rivers and were therefore not suitable for measurement. Previous work has documented synchronization in ocean growth from rivers that are in close proximity to one another (Jensen et al. 2011). Additionally, Hogan and Friedland (2010) found that postsmolt growth of salmon from the Machias and Narraguagus rivers was not different. Based on these results, we decided to pool samples from the four rivers for use in regression models. Each a priori model (Table 2) was run both with and without river as a factor to test for any differences due to river of origin.

For each growth section, competing models were compared using Akaike's information criterion (AIC) corrected for small sample size ( $AIC_c$ ). Models that had a  $\Delta AIC \leq 2$  were considered to be competitive. All analysis was completed in Program R version 3.3.2 (R Core Team 2016). Regression models were constructed using R package lme4 (Bates et al. 2015) and  $AIC_c$  tables were computed using R package MuMIn (Barton 2015). Additionally, likelihood ratio based pseudo- $R^2$  values for the top models for each growth section were calculated using R package MuMIn (Barton 2015).

## RESULTS

### Age Composition

Our samples from the Narraguagus, Pleasant, Machias, East Machias, and Dennys rivers consisted primarily of wild-origin, age-2 Atlantic Salmon smolts (80% of all samples aged; Figure 3). The proportion of hatchery-origin smolts increased

TABLE 2. A priori models developed for growth rates of Atlantic Salmon during the first and second years at sea. Each model was run both with and without river ( $\pm R$ ) as a factor. Predictors, selected based on literature for North American Atlantic Salmon (discussed in text), include average temperature (AVT), accumulated thermal units (ATU), smolt age (SMA), smolt length (SML), the postsmolt growth increment (PSI), the Atlantic Multidecadal Oscillation Index (AMO), and the North Atlantic Oscillation Index (NAO). Sample year was included as a random effect in all models.

A priori models (response = estimated growth rate [mm/month])	
First year at sea	Second year at sea
AVT + AVT <sup>2</sup> ( $\pm R$ )	AVT + AVT <sup>2</sup> ( $\pm R$ )
AVT + AVT <sup>2</sup> + SMA ( $\pm R$ )	AVT + AVT <sup>2</sup> + SMA ( $\pm R$ )
ATU ( $\pm R$ )	ATU ( $\pm R$ )
ATU + SMA ( $\pm R$ )	ATU + SMA ( $\pm R$ )
SML ( $\pm R$ )	PSI ( $\pm R$ )
SML + SMA ( $\pm R$ )	PSI + SMA ( $\pm R$ )
SML + SMA + (SML $\times$ SMA) ( $\pm R$ )	PSI + SMA + (PSI $\times$ SMA) ( $\pm R$ )
AVT + AVT <sup>2</sup> + SML ( $\pm R$ )	SML ( $\pm R$ )
ATU + SML ( $\pm R$ )	SML + SMA ( $\pm R$ )
AVT + AVT <sup>2</sup> + SML + SMA ( $\pm R$ )	SML + SMA + (SML $\times$ SMA) ( $\pm R$ )
ATU + SML + SMA ( $\pm R$ )	AVT + AVT <sup>2</sup> + PSI ( $\pm R$ )
AMO ( $\pm R$ )	ATU + PSI ( $\pm R$ )
AMO + SML ( $\pm R$ )	AVT + AVT <sup>2</sup> + PSI + SMA ( $\pm R$ )
AMO + AVT + (AMO $\times$ AVT) ( $\pm R$ )	ATU + PSI + SMA ( $\pm R$ )
AMO + ATU + (AMO $\times$ ATU) ( $\pm R$ )	AMO ( $\pm R$ )
AMO + SML + (AMO $\times$ SML) ( $\pm R$ )	AMO + PSI ( $\pm R$ )
NAO ( $\pm R$ )	AMO + AVT + (AMO $\times$ AVT) ( $\pm R$ )
NAO + SML ( $\pm R$ )	AMO + ATU + (AMO $\times$ ATU) ( $\pm R$ )
NAO + AVT + (NAO $\times$ AVT) ( $\pm R$ )	AMO + PSI + (AMO $\times$ PSI) ( $\pm R$ )
NAO + ATU + (NAO $\times$ ATU) ( $\pm R$ )	NAO ( $\pm R$ )
NAO + SML + (NAO $\times$ SML) ( $\pm R$ )	NAO + PSI ( $\pm R$ )
	NAO + AVT + (NAO $\times$ AVT) ( $\pm R$ )
	NAO + ATU + (NAO $\times$ ATU) ( $\pm R$ )
	NAO + PSI + (NAO $\times$ PSI) ( $\pm R$ )

from the 1970s until the end of the time series, and the majority of returning adults in the late 2000s were of hatchery origin. Returning adults consisted primarily of maiden 2SW spawners (90% of all samples aged). The proportion of maiden 1SW spawners remained low and relatively consistent throughout the majority of the time series (<10% per year); however, this proportion increased from the early 1990s (generally >20% per year). The proportion of repeat spawners showed a slight decrease beginning in the 1970s. The apparent increase in repeat spawner proportion after the 1990s may be due to the comparatively low sample sizes for those years. The proportion of maiden 3SW spawners was low (only 2% of all samples aged), and these adults were often absent in many of the years in our series, particularly in the last 19 years.

### Back-Calculated Lengths

The mean back-calculated smolt FL from all samples across years was 152 mm (SD, 27), and the mean back-calculated value for the postsmolt growth increment was 274 mm (SD, 41). The mean smolt FL of hatchery-origin

fish was 165 mm (SD, 31) and was significantly different from both wild-origin, age-2 smolts ( $150 \pm 25$  mm,  $t = -5.14$ ,  $df = 116.55$ ,  $P < 0.001$ ) and wild-origin, age-3 smolts ( $178 \pm 26$  mm,  $t = 3.40$ ,  $df = 208.29$ ,  $P < 0.001$ ). Both smolt length and the postsmolt growth increment fluctuated throughout the time series with no obvious trends. Throughout the time series, growth trends in the second year at sea were similar in the four growth sections that we investigated. A peak in growth in all three sections appears in 1973 (which corresponds to smolt year 1972), but overall growth in the second year at sea oscillated over time with no obvious trends (Figure 4).

### Growth Rate Correlations

Observed growth rates followed the expected pattern of high summer growth followed by minimal winter growth during both years at sea (Figure 2). During the first year at sea, correlation coefficients were moderately positive and significant (Spearman's rho:  $\rho = 0.49$ – $0.45$ ). The correlation between monthly growth rate during the Y1-Winter and Y2-

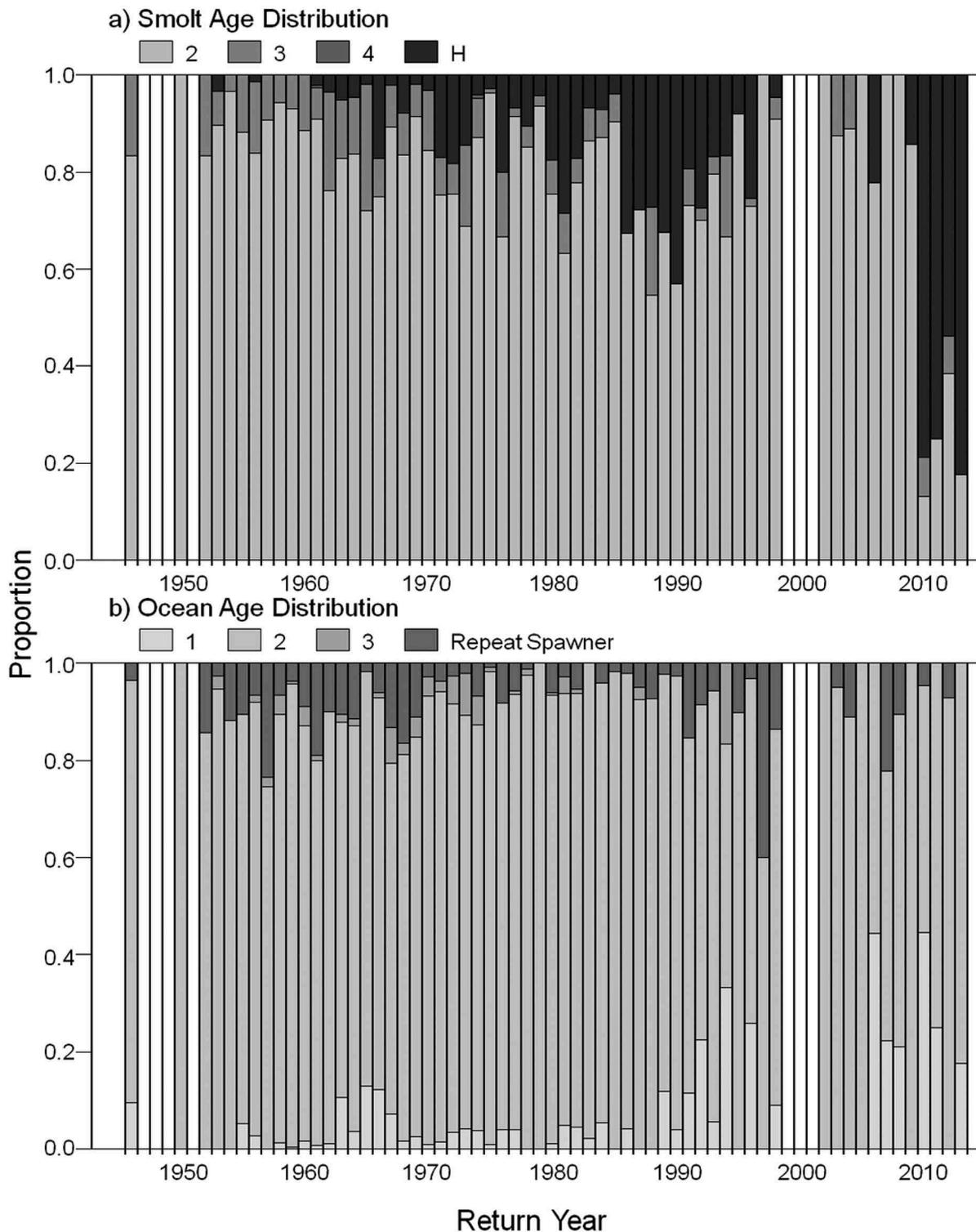


FIGURE 3. (a) Smolt age and (b) ocean age distribution by return year of Atlantic Salmon from the Narraguagus, Pleasant, Machias, East Machias, and Dennys rivers from 1946 to 2013. H = smolts of hatchery origin.

Winter is also significant ( $P < 0.01$ ), yet was negative and weak ( $\rho = -0.09$ ). Correlations between growth sections in the second year at sea were also positive and significant,

and were slightly stronger ( $\rho = 0.56-0.60$ ) than those during the first year at sea. These relationships are illustrated in Figure 5.

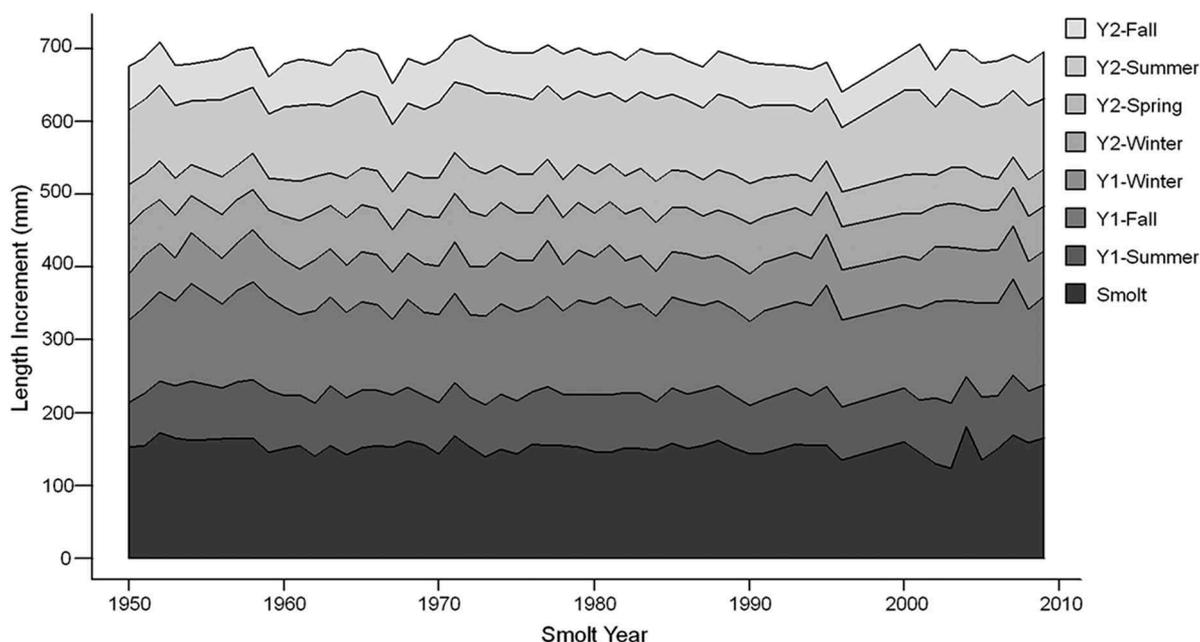


FIGURE 4. Mean back-calculated smolt FL and mean back-calculated growth increments for Atlantic Salmon during each growth section over the time series. Note: growth data were not available for 1955, 1992, and 1997–1999. Smolt represents smolt FL at emigration.

### Regression Analysis

The  $AIC_c$  tables for each growth section are reported in Table 3, and a summary of the top models for each growth section is reported in Figure 6. Growth during the summer in the first year at sea was high, and the AIC analysis identified three competitive models (with a  $\Delta AIC \leq 2.0$ ). All three had a very poor fit (pseudo- $R^2 = 0.06$ ) and included a significant, negative relationship with the back-calculated smolt length. The highest-ranked model additionally included smolt age (Figure 6a), with the following competitive models including the additive model of smolt length, smolt age, and accumulated thermal units (ATUs were not significant); and the interactive model of smolt age and smolt length.

During fall and winter of the first year at sea, growth began to slow. Four competitive models were identified for the Y1-Fall section. As with the previous growth section, the top model included smolt age and a significant, negative relationship with smolt length (Figure 6b). The three models that followed also contained smolt length and smolt age, but additionally incorporated average temperature (as a quadratic term), the interaction between smolt length and smolt age, or ATUs; these additional terms were not significant. Model fit was slightly better than in the initial growth section, with pseudo- $R^2$  values of 0.13. Five competitive models were identified for the Y1-Winter section, and all included a significant, negative relationship with smolt length. The top model additionally included ATUs and river as a factor (Figure 6c). The model was closely followed ( $\Delta AIC = 0.17$ ) by the same model with average temperature instead of ATUs, but the quadratic

term was not significant ( $P = 0.17$ ). The next two competitive models mirrored the first two but did not include river as a factor. The last model was the interactive model of the NAO index and smolt length. While smolt length and the interaction term were significant ( $P < 0.001$  and  $P < 0.05$ , respectively), the NAO index on its own was not ( $P = 0.61$ ). The pseudo- $R^2$  values for these models were 0.12.

Growth remained low during the months following the first winter annulus (Y2-Winter), and increased in the spring months (Y2-Spring). The models produced for growth during the second year at sea had a better fit than those during the first year at sea. Two models were considered competitive for the Y2-Winter growth section. The top model included smolt age as a factor, a negative relationship with the postsmolt growth increment, and a negative relationship with ATUs (pseudo- $R^2 = 0.25$ ; Figure 6d). The other competitive model ( $\Delta AIC = 1.81$ ) included average temperature ( $\beta = -0.022$ ,  $P < 0.05$ ) instead of ATUs, although the quadratic term was not significant ( $P = 0.76$ ). The Y2-Spring growth section also had two competitive models. The interactive model of the AMO index and the postsmolt growth increment was ranked as the top model (pseudo- $R^2 = 0.25$ ; Figure 6e). This model included a negative relationship with the postsmolt growth increment, a weak negative relationship with the AMO index, and a significant interaction term. The other competitive model ( $\Delta AIC = 1.71$ ) included a negative relationship with the post-smolt growth increment and smolt age as factor.

Growth rates were high during the Y2-Summer period. The two top models for Y2-Summer also contained a significant, negative relationship with the postsmolt growth

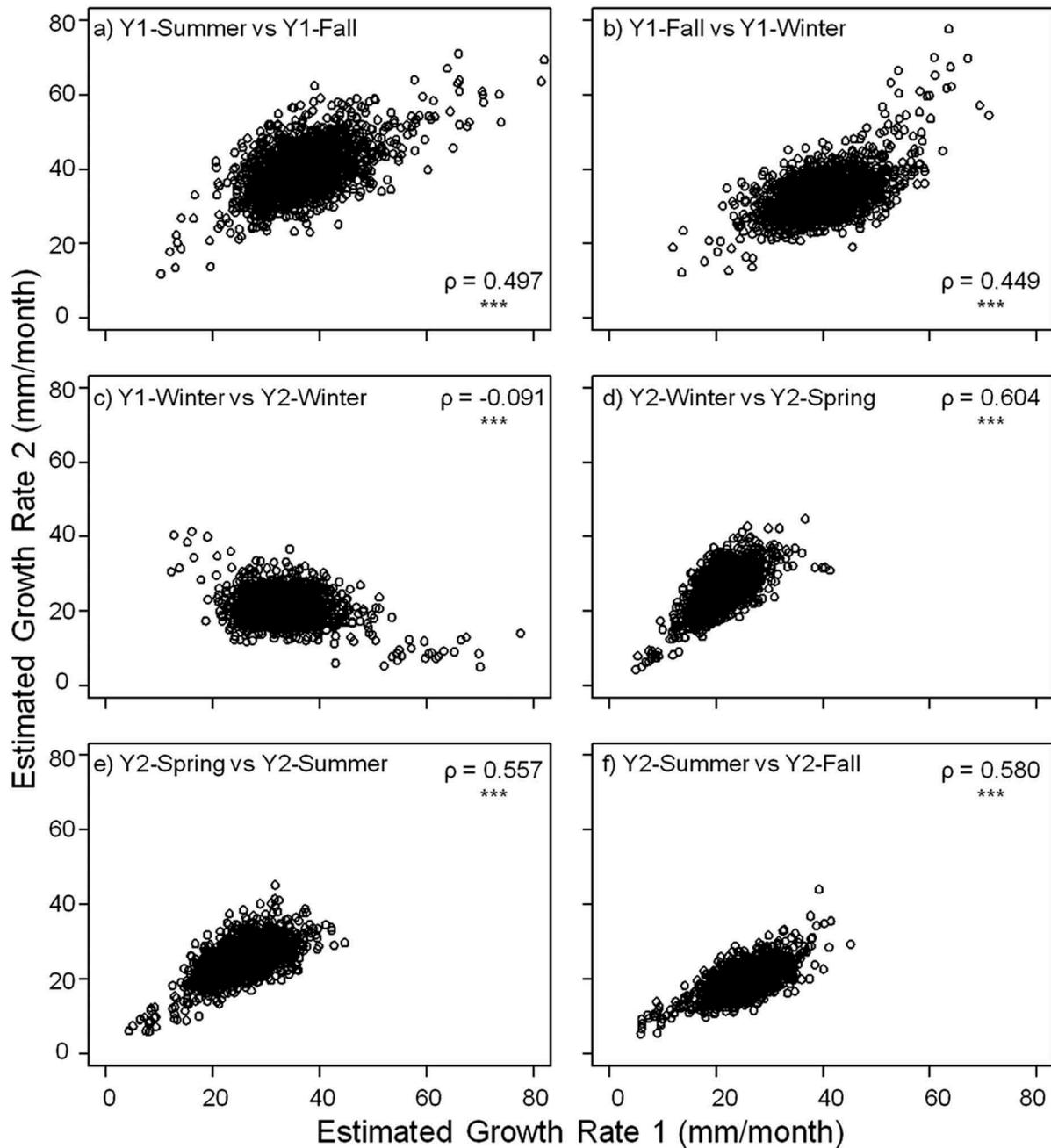


FIGURE 5. Scatter plots representing the correlations between successive estimated monthly growth rates over the time that Atlantic Salmon spend at sea. Spearman's rho ( $\rho$ ) is reported for each correlation (\*\*\*) denotes  $P < 0.001$ ).

increment ( $\beta = -0.108$ ,  $P < 0.001$ ; Figure 6f). These models additionally included smolt age as a significant factor. The highest ranked model included only smolt length and smolt age. The next competitive model ( $\Delta\text{AIC} = 1.71$ ) additionally included ATUs, although this predictor was not significant ( $P = 0.58$ ). The pseudo- $R^2$  for both of the top models was 0.38.

During the final growth section (Y2-Fall), growth began to slow as fish approached the second winter minimum. Two top models were identified for Y2-Fall (pseudo- $R^2 = 0.31$ ). Once again the highest ranking model included a significant, negative relationship with the postsmolt growth increment ( $\beta = -0.102$ ,  $P < 0.001$ ), as well as smolt age as a factor (Figure 6g). The next competitive model additionally included accumulated thermal units ( $\Delta\text{AIC} =$

TABLE 3. AIC<sub>c</sub> tables for competitive models of each growth section for Atlantic Salmon ( $\Delta AIC_c < 2$ ), with the next highest ranked model also reported. Predictor abbreviations are defined in Table 2. (Note: all models included sample year as a random effect, and  $k$  indicates number of model parameters).

Model	Log-likelihood	$k$	AIC <sub>c</sub>	$\Delta AIC_c$	Akaike weight	Pseudo- $R^2$
<b>Y1-Summer</b>						
SML + SMA	-1,825.5	6	3,663.1	0.00	0.343	0.062
ATU + SML + SMA	-1,825.0	7	3,664.1	1.00	0.208	0.062
SML + SMA + (SML $\times$ SMA)	-1,824.1	8	3,664.4	1.27	0.182	0.063
AVT + AVT <sup>2</sup> + SML + SMA	-1,825.0	8	3,666.1	3.00	0.077	0.032
<b>Y1-Fall</b>						
SML + SMA	-1,564.0	6	3,180.0	0.00	0.249	0.129
AVT + AVT <sup>2</sup> + SML + SMA	-1,582.3	8	3,180.7	0.63	0.181	0.131
SML + SMA + (SML $\times$ SMA)	-1,582.6	8	3,181.2	1.19	0.137	0.131
ATU + SML + SMA	-1,583.8	7	3,181.7	1.64	0.110	0.129
AMO + SML + (AMO $\times$ SML)	-1,585.3	6	3,182.7	2.63	0.067	0.128
<b>Y1-Winter</b>						
ATU + SML + R	-1,392.9	8	2,801.9	0.00	0.166	0.124
AVT + AVT <sup>2</sup> + SML + R	-1,392.0	9	2,802.1	0.17	0.153	0.125
ATU + SML	-1,396.2	5	2,802.5	0.62	0.122	0.121
AVT + AVT <sup>2</sup> + SML	-1,395.8	6	2,803.0	1.09	0.096	0.122
NAO + SML + (NAO $\times$ SML)	-1,395.8	6	2,803.7	1.76	0.069	0.121
NAO + SML + (NAO $\times$ SML) + R	-1,393.0	9	2,804.1	2.17	0.056	0.124
<b>Y2-Winter</b>						
ATU + PSI + SMA	-603.4	7	1,220.8	0.00	0.381	0.252
AVT + AVT <sup>2</sup> + PSI + SMA	-603.3	8	1,222.6	1.81	0.154	0.252
ATU + PSI + SMA + R	-601.4	10	1,223.0	2.20	0.126	0.253
<b>Y2-Spring</b>						
AMO + PSI + (AMO $\times$ PSI)	-982.7	6	1,977.4	0.00	0.335	0.254
PSI + SMA	-983.5	6	1,979.1	1.71	0.143	0.253
AMO + PSI	-984.7	5	1,979.4	2.06	0.119	0.252
<b>Y2-Summer</b>						
PSI + SMA	-692.8	6	1,397.7	0.00	0.440	0.376
ATU + PSI + SMA	-692.7	7	1,399.4	1.71	0.187	0.376
PSI + SMA + (PSI $\times$ SMA)	-691.8	8	1,399.7	2.03	0.159	0.377
<b>Y2-Fall</b>						
PSI + SMA	-474.9	6	961.9	0.00	0.521	0.307
ATU + PSI + SMA	-474.9	7	963.9	1.99	0.192	0.307
PSI + SMA + (PSI $\times$ SMA)	-474.2	8	964.6	2.69	0.135	0.308

1.99), but this predictor was not significant as in the previous growth section ( $P = 0.87$ ).

## DISCUSSION

The majority of samples aged for the Narraguagus, Pleasant, Machias, East Machias, and Dennys rivers over our time series were composed of 2SW spawners, which is the most common life history strategy for Maine's Atlantic Salmon (NRC 2004). Unlike the Penobscot River, Maine's largest river, which has salmon that are primarily of hatchery origin (Friedland et al. 1996), the eastern rivers over the past six decades have contained primarily wild-origin, age-2

smolts. It is possible that some of the fish that we classified as wild origin were, in fact, stocked as fry. Managers used fry stocking as a primary recovery tool in these rivers especially after 1990 (Hogan and Friedland 2010; Maynard and Trial 2014). Hatchery-origin stocked fry would be indistinguishable from wild-spawned fish based on scale readings, so it is unclear what percentage of fish in our sample were entirely wild. An increase in the proportion of hatchery-origin fish, which would have been stocked as smolts, is seen beginning in 2010. The number of samples from these last 4 years in our time series is limited (only 100 individuals), and most were from the Narraguagus River. While stocking practices in this river prior to 2007 consisted of primarily stocking fry, an

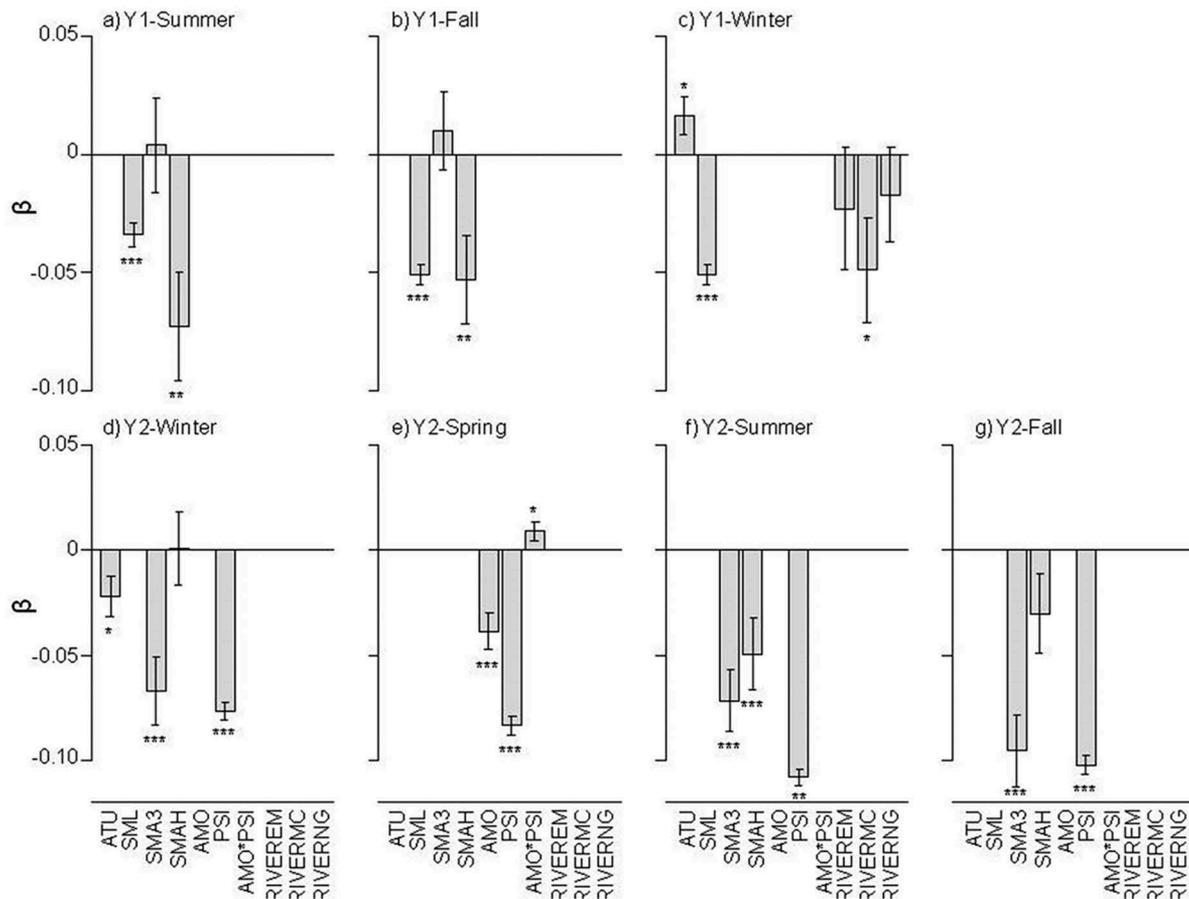


FIGURE 6. Summary of standardized coefficients for the top model in each Atlantic Salmon growth section ( $\pm$ SE). Significance of coefficients is denoted as:  $P < 0.001$ \*\*\*,  $P < 0.01$ \*\* ,  $P < 0.05$ \*. Beta-values ( $\beta$ ) are included for accumulated thermal units (ATU), smolt length (SML), wild-origin, age-3 smolts (SMA3), hatchery-origin smolts (SMAH), the Atlantic Multidecadal Oscillation Index (AMO), the postsmolt growth increment (PSI), the interaction of the AMO and the postsmolt growth increment (AMO  $\times$  PSI), and river of origin (EM = East Machias, MC = Machias, NG = Narraguagus).

increased number of hatchery smolts were stocked beginning in 2008 (USASAC 2012), which explains the increase in hatchery-origin fish observed at the end of our time series.

Examination of seasonal growth in this study did not reveal any obvious trends in smolt size, postsmolt growth, or growth during the second year at sea. This is in agreement with other work examining both wild- and hatchery-origin stocks from North America (Friedland et al. 1996, 2009b; Hogan and Friedland 2010), which have not shown clear trends in the growth of Atlantic Salmon in the second half of the 20th century despite declines in abundance across the range of the species. Individually, estimated seasonal growth followed the expected pattern of a rapid increase in growth in the first few months at sea, followed by decreasing growth prior to the winter minimum. High growth once again occurs during the second summer at sea, when 2SW spawners are presumably on the feeding grounds off of West Greenland for up to 4 months. Finally, growth slows during the second winter at sea prior to fish migrating back to their natal rivers to spawn.

The pattern of intercirculi spacing has been used in previous studies to investigate postsmolt monthly growth increments in both European and North American Atlantic Salmon (Friedland et al. 2009a, 2009b; Hogan and Friedland 2010) and is a useful way to estimate seasonal growth patterns and evaluate those patterns during different times of year and locations throughout the oceanic migration of the species. We note that these studies, as well as our own, are fundamentally linked to the assumption of equal rates of circuli formation, and deviation from this assumption is a potential source of error. There may, in fact, be individual variability in the timing of circuli deposition, and this process may not be perfectly linear (Todd et al. 2014). However, in the absence of a clear pattern that could be invoked, we worked to limit this source of error by reducing the presumptive intervals from monthly estimates to seasonal intervals. This approach likely provided a more robust interpretation of growth for our analysis.

Due to the large geographic range of migrating postsmolts and adult Atlantic Salmon in the ocean, our analysis shows that different factors influence growth at different time periods throughout the 2 years the salmon spent at sea. Based on a review of previous work, Hayes and Kocik (2014) hypothesized that Atlantic Salmon are being influenced by both top-down and bottom-up factors at different points in their oceanic migration. Our results support this hypothesis; both biological and physical factors appeared in top models for salmon growth during different seasons at sea, and these predictors shifted depending on season and presumed location. While this study focused on growth and did not investigate top-down processes over spatial and temporal scales, it appears that the factors regulating bottom-up drivers in Atlantic Salmon populations change as these fish migrate through the oceanic environment.

Our results related to growth also are similar to recent studies that found the combination of smolt traits (such as length, age, and origin) and environmental variables (such as SST and climate indices) ultimately influence survival of Atlantic Salmon from the Penobscot River (Miller et al. 2012), the Simojoki River in the Baltic Sea (Kallio-Nyberg et al. 2004), and multiple populations from rivers in Ireland (Peyronnet et al. 2008). Additionally, Miller et al. (2014) found that smolt age, release date, and SST influenced the marine growth of North American Atlantic Salmon when examined in terms of the von Bertalanffy growth and allometric growth parameters. These studies, in combination with the results of this work, highlight the importance of investigating a series of factors in combination when describing the marine migration of Atlantic Salmon.

Multiple factors, expressed in various competitive models, had an influence on growth during the initial months that Atlantic Salmon postsmolts spent at sea. Despite multiple competitive models that attempted to describe early ocean growth, the fit of these models was extremely poor. The growth of postsmolts in their first months at sea is likely influenced by many factors such as migration corridors and timing, availability of prey, and optimal temperatures. The poor fit of these models suggests that the available environmental data sets were not able to fully capture the ecosystem variables that affect early marine growth. This may be due to the broad area selected to represent temperatures during the postsmolt migration, which could have masked smaller-scale variations in coastal habitats that could have a greater influence on postsmolt growth. Atlantic Salmon are believed to migrate along narrow coastal bands during their journey to the summer feeding grounds (Hayes and Kocik 2014). Additionally, smolts typically migrate over approximately a 4–5-week period from Maine's rivers (Kocik et al. 2009), causing individual fish to potentially experience different conditions that could influence their growth during this period.

Following the early ocean growth period, temperature does appear to be an important predictor for growth during the first winter at sea. This result is to be expected as growth in

salmonids is temperature dependent (Handeland et al. 2008). However, starting in the spring of the second year at sea, temperature on its own disappears from the best models in favor of biological factors such as smolt age and previous size, as well as the AMO, one of the climate indices investigated to examine the effects of broad-scale ecosystem changes on adult salmon growth (Condrón et al. 2005; Mills et al. 2013; Friedland et al. 2014).

The large and complex migration of Atlantic Salmon at sea makes it difficult at times to isolate specific factors influencing their growth. However, investigating the influence of broad-scale climate forcing can give an indication of potential ecosystem effects as drivers. While other authors have noted that the NAO index correlates with Atlantic Salmon abundance trends (Friedland et al. 2003; Mills et al. 2013), this predictor was not included in the majority of our top models and was not significant when it did appear, suggesting that the factors influencing recruitment and survival related to the NAO are likely not growth related. The AMO, on the other hand, did appear as a predictor in the spring after the postsmolt period. In this case, the results indicated a weak, negative relationship between salmon growth rate and the AMO during this time period. Interestingly, the AMO has also been noted as a dominant climate force affecting Atlantic Salmon abundance on both sides of the Atlantic Ocean, and it has been hypothesized that the influence of the AMO operates through both thermal stress and ecosystem changes (Condrón et al. 2005; Mills et al. 2013; Friedland et al. 2014). As the AMO replaced temperature in our best-supported models during the early spring, our results support the conclusion that ecosystem changes that are a response to climate-related variations are more important than the direct influence of temperature during this time period.

Mature 1SW Atlantic Salmon adults from U.S. rivers migrate south at some point after their first winter at sea to reach natal rivers in the spring. At the same time, immature adults that will return as maiden 2SW spawners move northward from the overwintering area, following the receding ice cover and associated isotherms to eventually reach the west coast of Greenland to feed in the summer and early autumn (Friedland and Todd 2012). Friedland et al. (2014) reported that the AMO was strongly correlated with pre-fishery abundance of the immature (2SW) portion of the North American stock but was weakly correlated with the maturing (1SW) portion of the North American stocks, and that the North American stocks appear to be in opposite phase to the AMO. While the effect of the AMO detected in our study is very slight, growth in maiden 2SW spawners in the early spring is also in opposite phase with the AMO. This time period likely coincides with the time when the mature and immature portions of the stock are beginning to separate. Based on these results, it is possible that ecosystem variables and ongoing climate-related changes that are affecting adult growth and condition during this time period

are playing a role in the disproportionate decline of 2SW fish of North American origin, and it may be advantageous for future work to investigate survival during this time period.

Our results suggest that climate and physical factors play a very little role in the overall growth of 2SW salmon by the time they have reached the west coast of Greenland to feed. The absence of the AMO in the top models for the second summer at sea is consistent with the effects of this climate regime on regional SST anomalies. While the phase of the AMO correlates with SST anomalies near Newfoundland and the Grand Banks in the winter, it does not correlate significantly with the waters off Greenland in the summer (Condrón et al. 2005). It is possible that the abundance and accessibility of prey are stronger drivers of growth during the second summer at sea than are physical factors. Mills et al. (2013) recently showed that the size of Capelin, the primary prey for Atlantic Salmon, in the northwestern Atlantic Ocean is highly correlated with salmon abundance trends. In addition to an overall decrease in size, the energy density of Capelin has decreased by over 30% since 1990, and currently adult salmon feeding off western Greenland are consuming fewer Capelin and seeking alternate prey sources (Renkawitz et al. 2015). Our analysis did not reveal a specific decrease in second-year growth after 1990 during summers off the west coast of Greenland. However, using salmon scales only gave us access to estimated lengths and not condition factor, which may provide more evidence to support an energy deficit in 2SW spawners. During the final winter at sea, climate and physical factors did not play a role in the top models. By this time, 2SW adult salmon have achieved a large size and are likely preparing to return to natal rivers to spawn, so external factors have little influence on overall growth rates.

While different factors can influence Atlantic Salmon growth at different periods at sea, overall previous size seems to play a significant role in the growth of an individual. Our data are generally consistent with previous work examining postsmolt growth on the Narraguagus and Machias rivers, which observed an increase in the postsmolt growth increment in the early 1990s despite a continued decline in stock abundance (Hogan and Friedland 2010). With the addition of the East Machias and Dennys rivers, we also observed a slightly increasing trend in the 1990s in the postsmolt growth increment. The postsmolt growth increment began to decline again after 2000 in our time series. Hogan and Friedland (2010) also found that maximum growth during the postsmolt period was positively correlated with growth in the first month at sea. Similarly, we observed that fish that experience initially high growth rates continue to experience high growth rates throughout their first year at sea.

In contrast to previous work on Atlantic Salmon from eastern Maine, which found that there was no relationship

between first- and second-year growth (Hogan and Friedland 2010), our results suggested a negative relationship between smolt length and the postsmolt growth increment, as well as the postsmolt growth increment and growth during the second year at sea. Similar relationships were reported for Atlantic Salmon from the River Narcea in northern Spain, where the first marine growth period and the second marine growth period (following the first winter at sea) were negatively correlated (Nicieza and Brana 1993). Further investigation of estimated growth rates in our study revealed that this change in pattern occurs sometime during the first winter at sea. The observed relationship could point to compensatory growth in smaller individuals after the first winter at sea, while larger individuals do not need to sustain high growth rates. Compensatory growth has been suggested for Atlantic Salmon at multiple points in their life cycle (Nicieza and Brana 1993; Hogan and Friedland 2010) indicating that years of poor postsmolt growth have the potential to be mitigated by high growth in the second year at sea.

It is important to note that, based on the nature of the scale sample collection, the conclusions in this study are drawn from only 2SW fish that survived the marine migration. Additionally, we acknowledge that the use of angler-collected samples has the potential to bias these results due to inconsistent collection methods over time. While it is advantageous to be able to examine long-term data sets such as this one, they are inherently not able to capture the growth responses of fish that experience mortality at sea. Expanding more studies on growth and condition to include Atlantic Salmon caught during their marine migration could result in a clearer picture of the environmental factors that influence population declines. However, this study expands on the methods previously used to examine growth during the postsmolt period (Friedland et al. 2009a, 2009b; Hogan and Friedland 2010) to include the second year at sea, offering new insight into changes that Atlantic Salmon are experiencing during their time at sea.

The decline of North American Atlantic Salmon has involved multiple factors that span both the freshwater and marine environments. Despite steps that have been taken to reduce the human-induced causes of salmon declines, the continued low abundance of these populations points to the influence of large-scale effects acting throughout the range of the species. Previous work has suggested that the first winter at sea is a critical period for North American Atlantic Salmon (Friedland et al. 1993; Condrón et al. 2005). While the postsmolt period is often considered the primary source of Atlantic Salmon mortality, mortality during the postsmolt period cannot fully explain the decline of North American salmon, as the decline of 2SW fish has been more severe than that of 1SW fish. These portions of the stock separate after the first winter at sea, suggesting that factors acting throughout the entire marine period are cumulatively affecting 2SW spawners, increasing their decline, or that factors operating on salmon after their first winter at sea are responsible for the

disproportionately low numbers of maiden 2SW spawners. Our models have shown that slightly different factors are acting on the growth of 2SW Atlantic Salmon throughout their time at sea. During the early spring of the second year at sea, salmon growth is negatively impacted by the phase of the AMO, which has also been linked to salmon abundance. The factors influencing the decline of this highly migratory species are complex; however, more emphasis on the study of migration patterns, growth, and condition during the second year at sea could be advantageous for future management of the North American Atlantic Salmon stocks.

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