Growth models and growing degree-days: assessment of young-of-year Alewife and Blueback Herring in Potomac River tributaries

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Abstract Geography and nursery-specific dynamics guide environmental drivers of growth for young-of-year (YOY; larval and juvenile) Alewife (*Alosa pseudoharengus*) and Blueback Herring (*Alosa aestivalis*), two species collectively termed river herring; of these factors, temperature is considered one of the most influential. To better understand future YOY growth relative to climate change, this study was designed to determine the site-specific growth rates of YOY river herring in Potomac River tributaries, and determine if temperature was a driving factor of growth. Daily ages were ascertained from YOY otoliths and used to calculate growth rates using nine growth models. Weighted Akaike information criterion (AIC_w) determined the best-fit model for both species was the von Bertalanffy growth model. Von Bertalanffy growth parameters differed between species ($p < 0.0001$), between years for both species ($p < 0.0001$), and between locations for Blueback Herring ($p = 0.0002$), emphasizing the need for species-specific assessments. Standard length and cumulative growing degree-days were highly correlated within each year for both species, but significantly different between species and years for each species (Pearson's $r = 0.740$–0.913, $p < 0.0001$). Esti-

mating site-specific growth rates and drivers of growth can help managers determine the potential of Potomac River tributaries as viable nurseries in future climates.

Keywords Growing degree-days · Growth models · von Bertalanffy · River herring · Temperature · Climate change

Introduction

A history of overexploitation and habitat degradation in Potomac River tributaries led to a need for the management of two anadromous alosine species: Alewife (*Alosa pseudoharengus*) and Blueback Herring (*Alosa aestivalis*). Shared habitat and similar physical appearance resulted in co-management of the two species under the collective term river herring (ASMFC 2009, 2012, 2017; NMFS 2009; NRDC 2011). This consolidation prompted a gap in species-specific life history data, most notably growth rates. Generally, growth and success of larval and juvenile river herring is dependent on site-specific environmental variables, such as temperature, dissolved oxygen (DO), prey availability, and predation (Edsall 1970; Heinrich 1981; Houde and Zastrow 1993; Kosa and Mather 2001; Tommasi et al. 2015). Studies assessing the interaction between the surrounding environment and fish growth prior to maturation are important, as year class success of a species depends on the growth rates of young-of-year (YOY) (Houde 1987, 1997). Tommasi et al. (2015) found that year class success of YOY was not related to the number of river

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herring spawners, but rather was related to water flow and temperature. Since the distribution of river herring extends from New Brunswick, Canada to Florida, USA, the timing of spawning and thermal exposure (i.e., water temperatures) experienced by river herring within the population varies with regional climates (Edsall 1970; Fay et al. 1983; Klauda et al. 1991; Tuckey 2009). Therefore, growth within each population should be examined on a local scale to account for this variability.

Many studies have found evidence to suggest that fish growth is strongly tied to variations in surrounding abiotic and biotic factors. Mallet et al. (1999) found that accurate growth predictions could be made by assessing variations in water temperature over the lifespan of European Grayling (*Thymallus thymallus*) cohorts, and that growth increased following exposure to temperatures between the minimum and optimum temperature values. A subsequent study by Dion and Hughes (2004), confirmed the assertion that temperature was an accurate predictor of growth in European Grayling (*T. thymallus*) populations, as long as an adequate food supply was available. Additional efforts to quantify the interaction between water temperature and fish growth were conducted by Neuheimer and Taggart (2007) and Chezik et al. (2014) each applied the growing degree-day metric (GDD; °C·day), routinely used in agricultural and entomological settings, to the assessment of fish growth prior to maturation. The results found by Neuheimer and Taggart (2007) supported the application of the GDD metric in a fisheries setting, as over 92% of fish length-at-day data from various studies exhibited a strong linear correlation with the GDD metric. Additionally, Shackell et al. (2019) found that the GDD metric positively correlated with growth rates and maturity status in the southern stock domain (i.e., 7 divisions and subdivisions) of Northwest Atlantic Halibut (*Hippoglossus hippoglossus L.*) encompassing an area of 20° longitude by 6° latitude. In larval Alewife, Edsall (1970) found that growth rates increased with temperature until the maximum tolerance was reached. Data surrounding the influence of temperature on larval Blueback Herring growth is lacking. Given the anticipated change in surface water temperatures throughout the river herring range (Shearman and Lentz 2010), determination of the growth rates of larval and juvenile river herring as it pertains to temperature should be a high priority for management of these species.

Rountrey et al. (2014) determined that the anticipated warming of ocean water over the next century may only increase the body length of the Western Blue Groper (*Achoerodus gouldii*) by 5%. However, this change in length could have compounding effects on the population growth and ecology of the species by decreasing predation in early life stages, and therefore increasing feeding pressure on prey species as more Groper survive into adulthood. Long-term increases in feeding pressure by larger Gropers could result in overgrazed prey species, and loss of resources for the surrounding fish community. Many stock management strategies are based on known growth rates of the target species, and therefore changes in growth have the potential to impact the effectiveness of management. For example, increased growth rates could influence the size at maturation of future generations of Groper, a metric commonly used to set catch size limits, which would also require adjustments to current fisheries management plans. A study on Atlantic Halibut in the northwest Atlantic demonstrated that stocks with higher average GDDs reached maturity at significantly smaller sizes than stocks with significantly lower average GDDs (Shackell et al. 2019). Collectively, these studies support the notion that limiting the geographic scope of fish growth assessments may contribute valuable insight towards accounting for environmental variability throughout the range of a species.

In addition to narrowing assessments by region, to account for the unique set of abiotic and biotic factors experienced, the best-fit growth model should be determined independently for each species to account for biologic variability. Traditionally, the von Bertalanffy growth model was the most used model for fisheries; however, Katsanevakis and Maravelias (2008) reported that the von Bertalanffy growth model was not the best-fit model for 65.4% species tested. Furthermore, Lester et al. (2004) documented that YOY grow at more linear rates than adults, making more linear growth models a better fit and suggesting that different models may be needed to assess growth across life stages. In order to determine the best-fit growth model for river herring in Potomac River tributaries, this study focused on YOY, as later life stages are known to allocate energy to auxiliary life processes beyond growth, such as transition to salt water and reproduction (Lester et al. 2004; Neuheimer and Taggart 2007). Identifying the best-fit model specific to species and life stage within Potomac River tributaries will allow for a better determination of site-specific growth rates for these populations. Establishing site-specific growth rates for river herring in this

region will ultimately lead to a more complete understanding of the health of Potomac River tributaries as nursery habitats for YOY river herring.

Latitudinal orientation and composition of the surrounding landscape contribute to variations in environmental pressures throughout the river herring range. This combination of factors drives the need to assess the growth of individuals within the population on smaller, regional scales, such as within tributaries of the Potomac River. The goal of this study was to assess the growth of YOY Alewife and Blueback Herring in two Potomac River tributaries, Gunston Cove and Hunting Creek. In order to address this goal, six primary objectives were identified: 1) determine the best-fit growth model for YOY river herring, 2) determine if YOY growth differed between each species, 3) determine if YOY growth differed between sampling years for each species, 4) determine if YOY growth differed between sampling locations for each species, 5) determine if the cumulative GDD metric (i.e., accumulated positive GDDs, $\sum$GDD; °C·day) correlated to the standard length (SL; mm) of YOY between species, and 6) determine if the cumulative GDDs-SL correlation differed between years. Overall, developing a system for quantifying individual growth within a region is critical in order to effectively manage future cohorts and determine the success of a habitat as a nursery area, in this case the Potomac River.

Materials and methods

Study sites

Gunston Cove and Hunting Creek are shallow, tidal embayment systems fed by third-order tributaries that drain into the Virginia portion of the Potomac River (Fig. 1; Jones et al. 2008; Jones and de Mutsert 2014; Lippson et al. 1981). After migrating through Gunston Cove, adult river herring continue to move upstream into Pohick Creek and Accotink Creek to spawn. Following spawning, the river herring eggs and larvae are then transported downstream to nursery grounds in Gunston Cove (De Mutsert 2013; Schlick 2016; Schlick and de Mutsert 2019). Similarly, adult river herring migrate through Hunting Creek into the upstream tributary of Cameron Run to spawn, so that the eggs and larvae will eventually settle in Hunting Creek to develop (De Mutsert 2014). The environmental

conditions of each system directly impact YOY survival, until fall when the individuals leave these nursery habitats. Both systems are classified as eutrophic, with excess nutrients added by runoff from the surrounding watershed and through wastewater treatment plants, such as the Noman M. Cole, Jr. Pollution Control Plant (located on Pohick Creek) and the Alexandria Renew Management Facility (located on Cameron Run). Both treatment facilities have reduced nutrient loading since the 1970's, but urbanization has continued to increase in both watersheds throughout the same period (Jones and de Mutsert 2013, 2014). YOY river herring have been collected in Gunston Cove since 1984 and Hunting Creek since 2013 (Jones and de Mutsert 2013, 2014), but growth rates have not been studied in either system.

Field methods

Ichthyoplankton were sampled in Pohick Creek, Accotink Creek, and Cameron Run from March to May in 2013, 2014, and 2015 (Fig. 1). Larvae drifting downstream from spawning sites were sampled once a week for 20 min using 0.25 meter (m) diameter conical plankton net with a square mesh size of 0.333 mm. A flow meter was attached to the mouth of each net to determine the water volume sampled. Depth and flow profiles were conducted to determine total discharge of the stream concurrently with plankton tows. Additionally, ichthyoplankton were collected in Gunston Cove (STA7 and STA9) and Hunting Creek (AR2 and AR4) with 0.5 millimeter (mm) diameter conical plankton net with 0.333 mm square mesh (Fig. 1). The ichthyoplankton net was towed behind the boat for 2 min at each of three depths: near bottom, mid-depth, and near surface. Ichthyoplankton nets were fitted with flow meters to determine the water volume sampled during the tow. Collected ichthyoplankton were preserved with 70% ethanol and identified to lowest possible taxa in the laboratory.

Juveniles were sampled in Gunston Cove and Hunting Creek from April to September in 2013, 2014, and 2015 (Fig. 1). Collection occurred using otter trawls, seine nets, and fyke nets at predetermined sites every other week for 10 weeks. In Gunston Cove, three otter trawls were pulled for 5 min at 2 knots (STA10, STA7, and STA9), four seine nets were pulled along the shore for 50 to 100 m (STA4, STA4A, STA6, and STA11), and two fyke nets were soaked for 5 hours (STA4 and STA10; Fig. 1). In Hunting Creek, two otter trawls were towed for 5 min at 2 knots (AR3 and AR4) and two
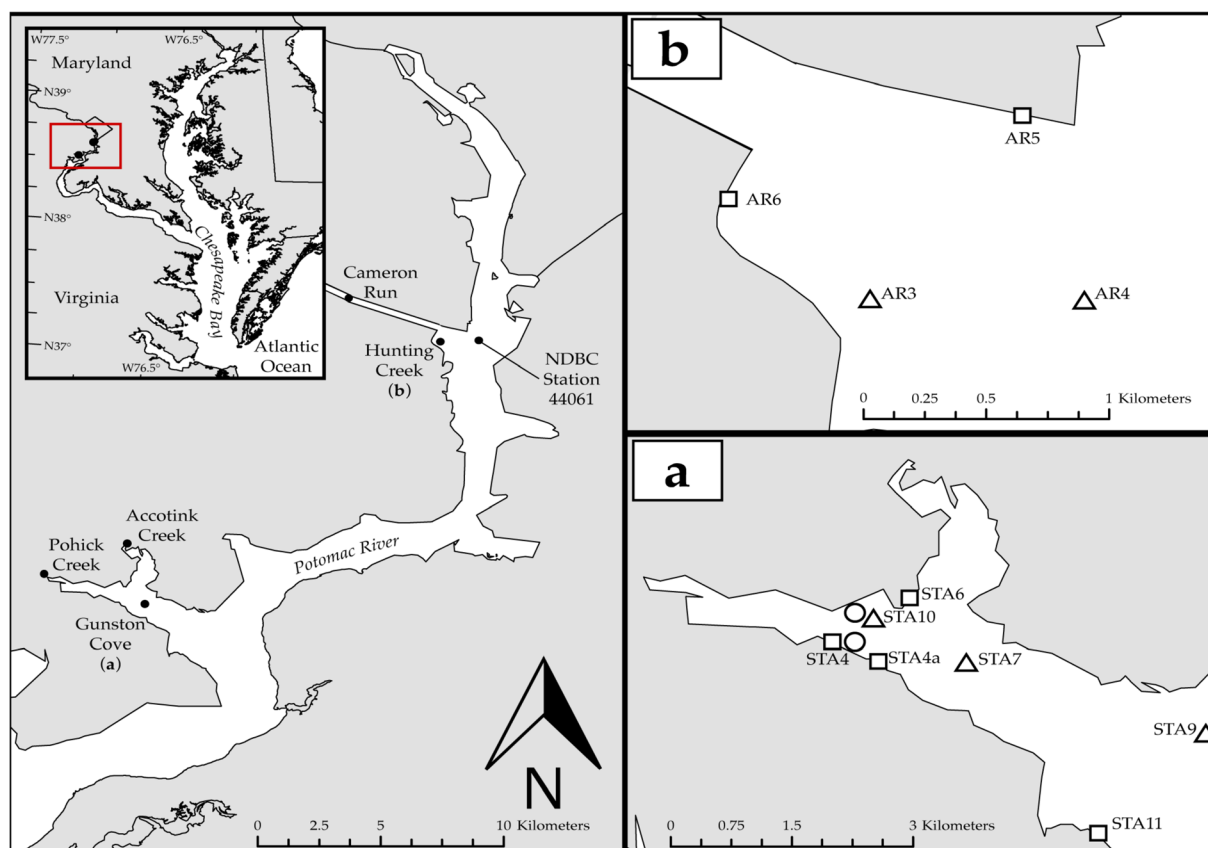
Fig. 1 Locations of the Potomac River tributaries (**a**) Gunston Cove and (**b**) Hunting Creek, and the smaller tributaries, Pohick Creek, Accotink Creek, and Cameron Run, that lead into them, respectively; Seines (square) were conducted at STA4, STA4A, STA6, STA11, AR5, and AR6; Trawls (triangle) were conducted at STA10, STA7, STA9, AR3, and AR4; and Fyke nets (circle) were only set in Gunston Cove and were conducted at STA4 and STA10

seine nets were pulled along the shore for 50 to 100 m (AR5 and AR6; Fig. 1).

Laboratory methods

The standard length (SL) of young-of-year Alewife (larvae $n = 2566$ and juveniles $n = 1468$) and Blueback Herring (larvae $n = 3386$ and juveniles $n = 714$) was measured for all fish evaluated in this study. Larvae were immediately stored in 70% ethanol in the field, then identified using a dissecting microscope and measured for SL or notochord length (NL), depending on the stage of development. The influence of ethanol preservation on larval fish length was assumed negligible for this analysis, as the change in size was minimal relative to the range of lengths incorporated into the growth models. Identification of larval *Alosa sp.* was conducted following methods developed by Walsh et al. (2005). Juveniles that did not survive capture were frozen until dissection could occur in the lab, wherein SL was measured prior to dissection. Treatment of fish were in accordance with approved American Association of Laboratory Animal Science Institutional Animal Care and Use Committee permits (under protocol #0194 and #0279). Sagittal otoliths were removed from a random subsample (Alewife $n = 319$ and Blueback Herring $n = 391$) of YOY specimens and mounted on slides using thermoplastic glue. Subsamples were weighted based on the weekly catch, so that smaller catches would have more individuals sampled at a higher frequency than larger catches (i.e., landings of five fish would have a higher percentage sampled than a landing of 200). Larval otoliths were aged whole, and juvenile otoliths were ground using 600-grit sandpaper until rings were clear under transmitted light.

Thirty otoliths of known age from juveniles of a similar species, the American Shad (*Alosa sapidissima*), were provided by the Virginia Institute of Marine

Science to aid in the validation of the aging technique. Aging otoliths consisted of two separate readers counting the daily growth increments (rings) in blind readings. Prior to determining the age of unknown, field-collected samples, each reader interpreted the samples of known age. This step encouraged consistency in age assessments between reading periods. The ages were averaged for each individual if the difference between the two readings was less than 10%, but samples with readings differing more than 10% were discarded.

Growth models

Nine growth models (von Bertalanffy [von Bertalanffy 1938], logistic [Ricker 1975], linear [Haddon 2011], Gompertz [Gompertz 1825], Laird-Gompertz [Laird 1964, Zweifel and Lasker 1976], Richards [Richards 1959], Ratkowsky [Ratkowsky 1986], Cerrato [Cerrato 1990], and Francis [Francis 1988]) were fitted to age-at-length data for immature individuals of each species using Microsoft Excel © Solver. Within each species, only YOY were utilized in the models as river herring grow at different rates once they have left the nursery - growth of YOY predominantly occurs at a linear rate, while growth of adults is assumed to occur at an asymptotic rate (Lester et al. 2004). The best-fit model for Alewife and Blueback Herring was determined using weighted Akaike information criterion (AIC_w, Akaike 1974). Juveniles of each species were binned into yearly cohorts, then the von Bertalanffy growth model (due to its popular use in fisheries throughout history) was fitted to each cohort and an analysis of residual sum of squares (ARSS) was used to determine if the fitted growth models differed between cohorts (Haddon 2011). Additionally, juveniles of each species were further separated by collection location (Gunston Cove versus Hunting Creek) to test if there was a difference in growth within each species between each embayment. The von Bertalanffy growth model for each species-specific location was compared using an ARSS.

The largest fish captured each year varied, which caused the asymptotic length (i.e., the hypothetical maximum at which growth is zero; L_∞) in the von Bertalanffy growth model to be different each year as well. Since L_∞ varied between years, the Brody growth coefficient (i.e., the rate at which L_∞ is reached; K) was not a good indication of growth rate within the tributaries. Therefore, instantaneous growth

rates were needed. Instantaneous growth rates (G_t) were calculated based on a derivative of the von Bertalanffy growth curve. Instantaneous growth rates were estimated for larvae at age 2 and 20 days (G_2 and G_{20}), as well as for juveniles at age 60 and 120 days (G_{60} and G_{120}).

Growing degree-day analysis

Daily maximum and minimum water temperatures were downloaded from the National Data Buoy Center, Station 44061, located where Hunting Creek meets the Potomac River as an estimate of daily thermal exposure to the fish. To ensure the daily temperatures were comparable to the study locations, a chi-square test was used to compare temperatures collected with a YSI multiparameter sonde when fish were captured (once every two weeks) to the temperatures recorded by the buoy. The two temperature collection methods were a comparable fit statistically ($p = 0.32$). The GDD metric was determined using:

$$GDD = \left(\frac{(T_{max} + T_{min})}{2} \right) - T_0 \qquad (1)$$

where, T_{max} = maximum daily ambient temperature, T_{min} = minimum daily ambient temperature, T_0 = the minimum temperature required for growth for each species (Chezik et al. 2014). The T_0 used was 10 °C for Alewife (Pardue 1983) and 14 °C for Blueback Herring (Loesch and Lund 1977). A linear regression was used to determine the correlation between the accumulated positive GDDs ($\sum GDD$; °C·day) and the SL (mm) of the fish. An ANCOVA was performed to determine if there was a difference in the relationship of the standard length (mm) of individuals and the amount of thermal energy experienced (i.e., cumulative GDDs, $\sum GDD$; °C·day), as they pertained to three factors: species, yearly cohorts of each species, and collection location of each species.

Results

Otoliths were collected from 319 YOY Alewife (i.e., 60 larvae and 259 juveniles) and 391 YOY Blueback Herring (i.e., 51 larvae and 340 juveniles). Readers were

within 10% agreement for the daily age of 315 YOY Alewife otoliths and 387 YOY Blueback Herring otoliths. Young-of-year Alewife ranged from 2.5 mm to 69.8 mm, and YOY Blueback Herring ranged from 3.8 mm to 54.8 mm (Fig. 2). Larval Alewife and Blueback Herring (i.e., up to 20 mm) ranged from 1 to 22 days (d), while juvenile Alewife ranged from 25 to 161 d and juvenile Blueback Herring 26 to 132 d.

Growth rates

The von Bertalanffy, Francis, Cerrato, and Ratkowsky growth models were the best fitting models of the nine tested models for YOY Alewife ($AIC_w = 22.15\%$) and YOY Blueback Herring ($AIC_w = 22.06\%$) (Table 1). Since the von Bertalanffy model has been the most commonly used model in previous studies, it was selected for further analysis over the comparable Francis, Cerrato, and Ratkowsky growth models. The linear and logistic models were the worst-fit models for both species with an AIC_w of 0.0% (Table 1).

The von Bertalanffy growth curves differed between YOY Alewife and YOY Blueback Herring ($p < 0.001$) based on an ARSS comparison. Alewife grew to larger sizes than Blueback Herring and had faster growth rates in the juvenile stages (i.e., G_{60} and G_{120}; Table 2). However, larval Blueback Herring had faster initial growth rates (i.e., G_2). Blueback Herring growing faster as yolk-sac larvae was expected since this species hatches later in the season in warmer temperatures.

The von Bertalanffy growth curves for YOY Alewife differed between years ($p < 0.001$) but not between sampling locations ($p = 0.111$) based on ARSS comparisons. The asymptotic length (L_∞) decreased from 2013 to 2015, while the rate at which L_∞ was reached (K) increased (Table 2; Fig. 3a). The standardized residuals for the Alewife growth curves were randomly distributed (Fig. 3b), verifying that the von Bertalanffy growth model appropriately accounted for the increasing
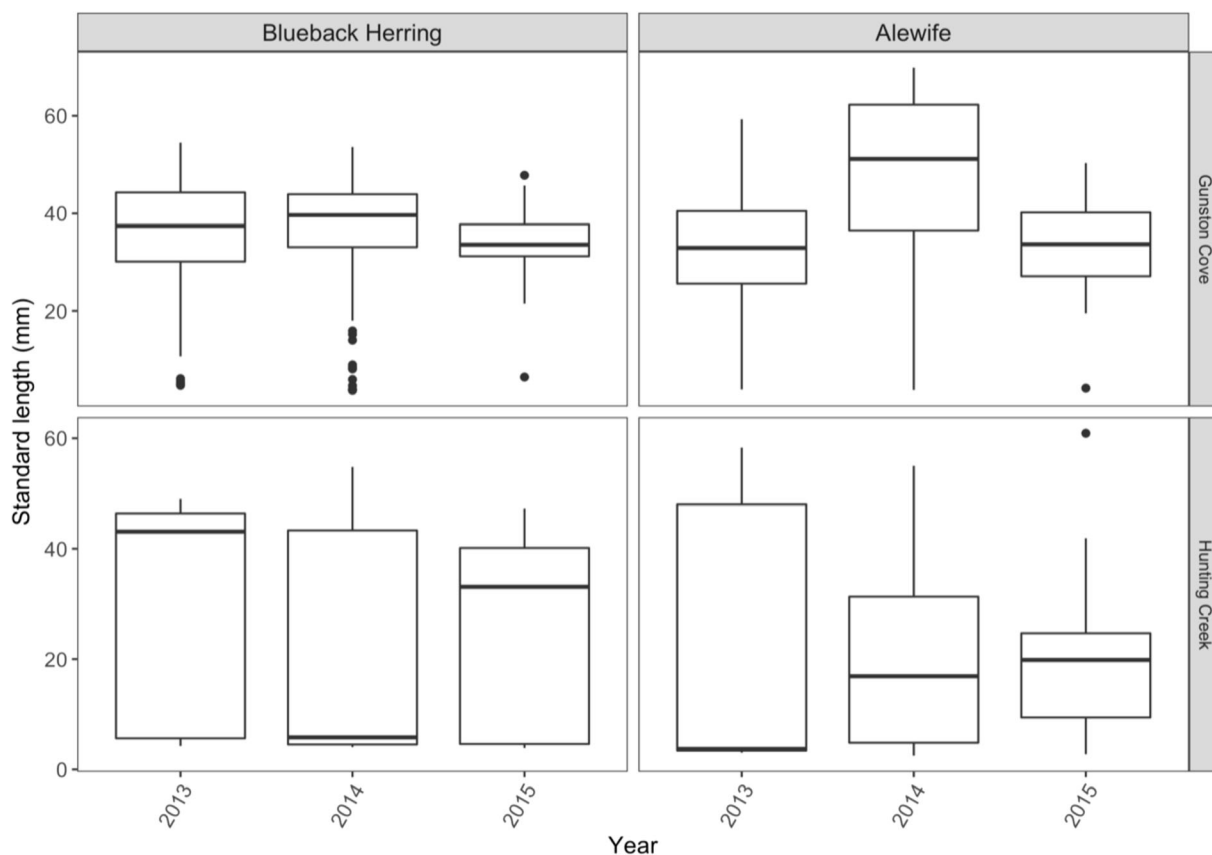

Fig. 2 Boxplot of the standard lengths (SL; mm) of juvenile Alewife (*Alosa pseudoharengus*) and Blueback Herring (*A. aestivalis*) captured in Potomac River tributaries, Virginia

Table 1 Rank of Akaike information criterion weights (AIC$_w$) calculated for young-of-year Alewife and Blueback Herring based on sample size (*n*), number of parameters, sums of squares (SSQ), and Akaike information criterion (AIC) from each growth model

Species	Model	*n*	Parameters	SSQ	AIC	w (%)	Rank
Alewife	Cerrato	311	3	7526	684.59	22.15	1
	Francis	311	3	7526	684.59	22.15	1
	Gompertz	311	3	8361	698.81	0.018	6
	Laird-Gompertz	311	3	8361	698.81	0.018	6
	Linear	311	2	10,278	724.69	0.000	9
	Logistic	311	3	9479	715.75	0.000	8
	Ratkowsky	311	3	7526	684.59	22.15	1
	Richard	311	4	7489	685.93	11.36	5
	von Bertalanffy	311	3	7526	684.59	22.15	1
Blueback Herring	Cerrato	387	3	7370	810.16	22.06	1
	Francis	387	3	7370	810.16	22.06	1
	Gompertz	387	3	7830	820.35	0.135	6
	Laird-Gompertz	387	3	7830	820.35	0.135	6
	Linear	387	2	1023	476.22	0.000	9
	Logistic	387	3	8519	834.51	0.000	8
	Ratkowsky	387	3	7370	810.16	22.06	1
	Richards	387	4	7339	811.46	11.49	5
	von Bertalanffy	387	3	7370	810.16	22.06	1

lengths with age. Instantaneous growth rates were variable between years at 2 d and 20 d of age (i.e., prior to transitioning to juveniles), with growth the fastest in 2014 and the slowest in 2013 (Table 2). However, after transitioning to juveniles, growth rates slowed at 60 d and slowed again at 120 d. Additionally, growth rates were less variable between years at 60 d and 120 d (Table 2).

Table 2 Asymptotic length (L$_\infty$), Brody growth coefficient (K), and minimum temperature required for growth of each species (t$_0$) (i.e., von Bertalanffy growth model parameters) of young-of-year Alewife and Blueback Herring for each year of collection (2013, 2014, and 2015) and all years pooled together with subsequent sums of squares (SSQ) from model fitting, sample size (*n*), and instantaneous growth rates in mm d^{-1} for larvae (G$_2$ and G$_{20}$) and juveniles (G$_{60}$ and G$_{120}$)

Species	Year	L$_\infty$ (cm SL)	K (year^{-1})	t$_0$ (year^{-1})	SSQ	*n*	G$_2$	G$_{20}$	G$_{60}$	G$_{120}$
Alewife	Pooled	88.3	0.009	−3.76	7526	311	0.7	0.6	0.4	0.3
	2013	112.1	0.006	−4.44	2691	105	0.7	0.6	0.5	0.3
	2014	79.2	0.012	−1.13	1271	86	0.9	0.7	0.5	0.2
	2015	57.7	0.015	−2.84	2014	120	0.8	0.6	0.3	0.1
Blueback Herring	Pooled	54.8	0.016	−2.39	6644	382	0.8	0.6	0.3	0.1
both locations	2013	63.3	0.014	−1.87	1782	112	0.8	0.6	0.4	0.2
	2014	52.4	0.018	−1.54	1774	132	0.9	0.7	0.3	0.1
	2015	46.1	0.020	−2.60	1641	138	0.8	0.6	0.3	0.1
Gunston Cove	Pooled	51.6	0.017	−3.28	6403	331	0.8	0.6	0.3	0.1
	2013	53.9	0.018	−2.14	1983	95	0.9	0.7	0.3	0.1
	2014	50.6	0.020	−0.70	1485	116	1.0	0.7	0.3	0.1
	2015	46.7	0.016	−13.45	1564	120	0.6	0.4	0.2	0.1
Hunting Creek	Pooled	71.9	0.011	−2.625	603	56	0.7	0.6	0.4	0.2

Fig. 3 (a) Observed length-at-age for young-of-year Alewife collected in 2013 (black triangles), 2014 (gray dots), and 2015 (gray asterisks) with predicted length-at-age based on von Bertalanffy growth model (corresponding lines); (b) standardized residuals vs. fitted values for the von Bertalanffy growth curves for young-of-year Alewife
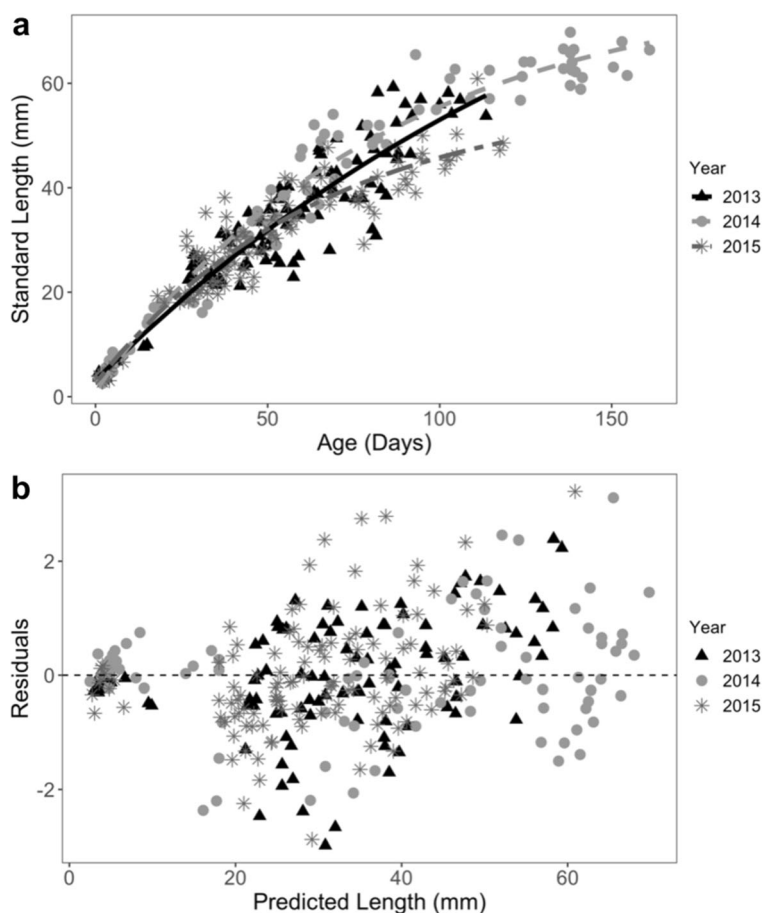
The von Bertalanffy growth curves for YOY Blueback Herring differed between years ($p < 0.0001$) as well as sampling locations ($p = 0.004$) based on the ARSS comparison. Similar to Alewife, the L_∞ decreased and K increased between 2013 and 2015 (Table 2, Fig. 4a). The standardized residuals for Blueback Herring growth curves were randomly distributed (Fig. 4b), indicating that the von Bertalanffy growth model was a good fit to the data. Instantaneous growth rates for larvae (i.e., 2 and 20 d) were highest in 2014 but were lowest for yolk-sac larvae (i.e., 2 d) in 2013 and lowest for post yolk-sac larvae (i.e., 20 d; Table 2) in 2015. However, instantaneous growth rates for juveniles (i.e., 60 and 120 d) were highest in 2013 and lowest in 2015.

The von Bertalanffy growth curves for YOY Blueback Herring differed between individuals captured in Hunting Creek and individuals captured in Gunston Cove ($p = 0.0002$) across all years based on an ARSS comparison. The L_∞ was higher for individuals captured in Hunting Creek than individuals in Gunston Cove but K was less for individuals in Hunting Creek than in Gunston Cove. Instantaneous growth rates were higher in Hunting Creek than in Gunston Cove for all ages except 2 d (Table 2). When the von Bertalanffy growth model was run with only Blueback Herring from Gunston Cove, a difference between years was still present ($p < 0.0001$). Instantaneous growth rates were highest in 2014 for larval Blueback Herring (2 d and 20 d) but highest for juveniles in 2013 (60 d and 120 d). The lowest instantaneous growth rates for Blueback Herring collected in Gunston Cove were observed in 2015 for all life stages. The von Bertalanffy growth model could not be run with individuals from Hunting Creek by year due to a lack of Blueback Herring captured in Hunting Creek each year (2013 $n = 21$, 2014 $n = 16$, and 2015 $n = 19$).
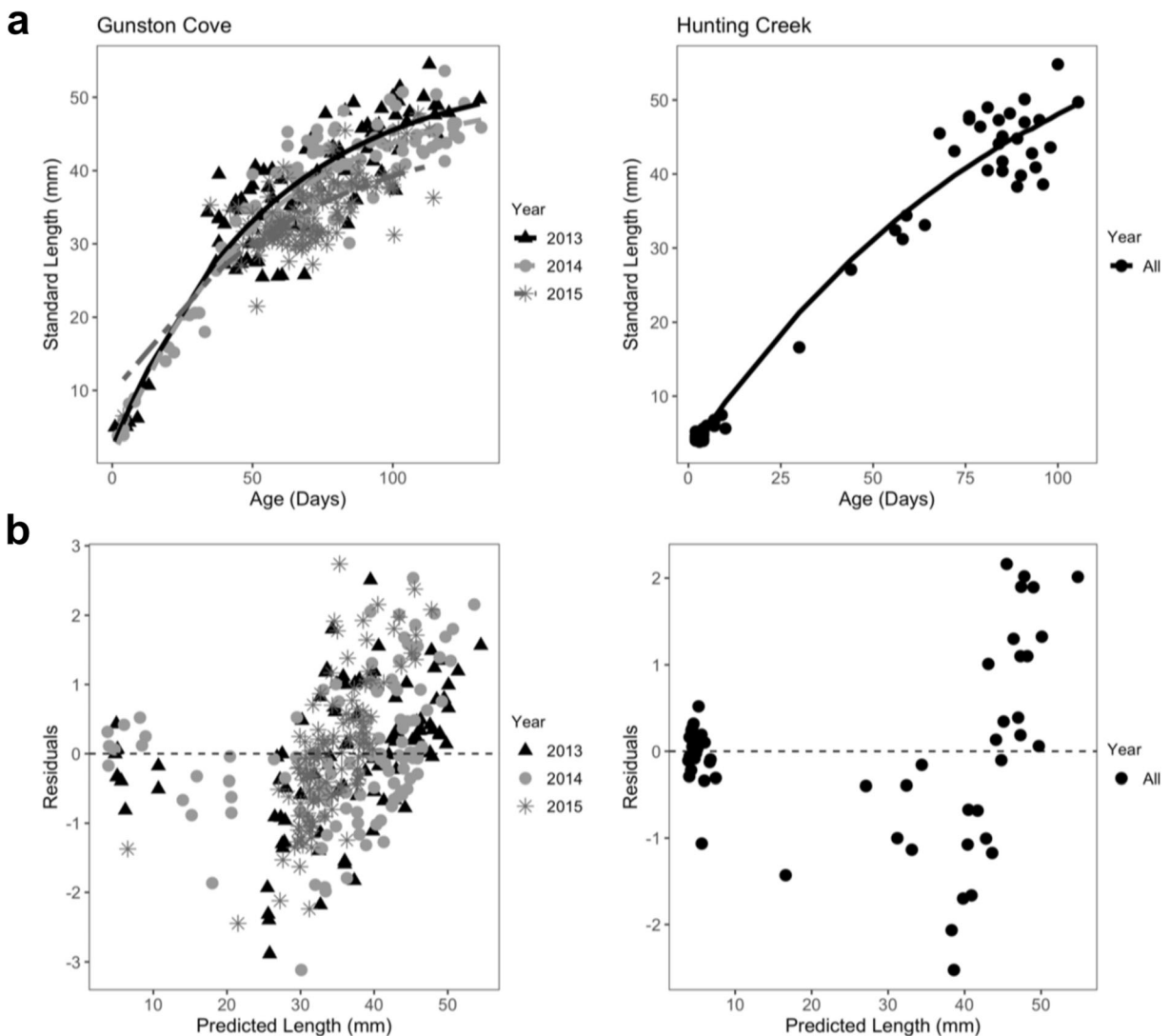
Fig. 4 (a) Observed length-at-age for young-of-year Blueback Herring collected from Gunston Cove (left) in 2013 (black triangles), 2014 (gray dots), and 2015 (gray asterisks), as well as Blueback Herring collected from Hunting Creek with all years combined (right), with predicted length-at-age based on von Bertalanffy growth model (corresponding lines); (b) standardized residuals vs. fitted values for the von Bertalanffy growth curves for young-of-year Blueback Herring in Gunston Cove (left) and Hunting Creek (right)

Growing degree-day

Linear regression analysis yielded a strong correlation between the accumulated positive GDDs ($\sum$GDD; °C·day) and SL (mm) of all YOY Alewife across years (Table 3, Fig. 5), and all YOY Blueback Herring across years (Table 3, Fig. 5). A single linear function of cumulative GDDs across years explains 79.0% of the variation in SL for Alewife and 57.5% of the variation in SL for Blueback Herring (Table 3); however, this relationship significantly differs between the two species

($p < 0.001$). The variation in SL based on the linear function of GDDs also significantly changed between years for both species ($p < 0.001$), indicating that other environmental variables play strong roles in the development of YOY river herring. However, the linear functions still account 64.9% to 83.1% of variation in SL for Alewife each year, and 54.5% to 63.9% of variation in SL for Blueback Herring each year.

The relationship between SL and cumulative GDDs did not differ for Alewife that were captured in Gunston Cove versus Alewife captured in Hunting Creek ($p =$

Table 3 Simple linear relationship between cumulative growing degree-days ($\sum$GDD, °C·day) and the standard length (SL, mm) for young-of-year Alewife and Blueback Herring in Potomac River tributaries from 2013 to 2015

Species	Year	Linear Model	R^2	F	Pearson r	p
Alewife	Pooled	16.18 + 0.0197X	0.79	894	0.898	<0.001
	2013	14.42 + 0.0214X	0.65	164	0.808	<0.001
	2014	21.69 + 0.0178X	0.83	320	0.913	<0.001
	2015	15.74 + 0.0175X	0.78	278	0.881	<0.001
Blueback Herring	Pooled	21.84 + 0.0183X	0.58	463	0.759	<0.001
both locations	2013	22.99 + 0.197X	0.64	168	0.797	<0.001
	2014	22.23 + 0.019X	0.63	196	0.796	<0.001
	2015	22.06 + 0.015X	0.55	155	0.740	<0.001
Gunston Cove	Pooled	22.31 + 0.0175X	0.56	399	0.750	<0.001
	2013	23.12 + 0.0190X	0.63	147	0.797	<0.001
	2014	23.07 + 0.0175X	0.61	165	0.781	<0.001
	2015	22.49 + 0.-146X	0.50	120	0.713	<0.001
Hunting Creek	Pooled	16.98 + 0.0258	0.70	71	0.843	<0.001

0.115) but did differ between Blueback Herring captured in Gunston Cove versus Blueback Herring captured in Hunting Creek ($p = 0.035$). A single linear function of cumulative GDDs explains 70.0% of the variation in SL for Blueback Herring in Hunting Creek and a linear function that accounts for 56.1% of the variation for Blueback Herring in Gunston Cove (Table 3). Within Gunston Cove, the linear relationships between SL and cumulative degree-days differed between years ($p < 0.0001$) with the functions accounting for a range of 50.4% to 63.1% of the variation of each year (Table 3). Linear functions could not be run between SL and cumulative degree-days for Blueback Herring captured in Hunting Creek between years due to the low sample size within each given year.

Discussion

Growth rates were significantly different between YOY Alewife and Blueback Herring, suggesting species-specific growth rates should be accounted for in the management of these two species typically managed as river herring. Additionally, the significant differences in YOY growth between years within each species and between locations for Blueback Herring indicate that annual variations in environmental patterns, as well as site-specific conditions, likely contribute to differences in individual growth. However, the larval growth rates determined by this study for Alewife (0.13–0.91 mm d^{-1}) were comparable to daily growth rates reported in 1984 for two separate populations of Alewife in the northern portion of the river herring range, a New Jersey population (0.625 mm d^{-1}) and a Massachusetts population (0.820–0.996 mm d^{-1}) (Richkus 1975). Relative to the current study in Potomac River tributaries, Tuckey (2009) reported instantaneous growth rates at day 60 that were more variable for juvenile Blueback Herring in four other Virginia rivers located further south; James (0.06–0.61 mm d^{-1}), Pamunkey (0.44–0.71 mm d^{-1}), Mattaponi (0.42–0.70 mm d^{-1}), and Rappahannock (0.15–0.5 mm d^{-1}). Tuckey (2009) found that growth rates were significantly different between rivers, suggesting that river-specific processes dictated patterns in growth. Similar to the present study, Tuckey (2009) found that growth between spawning seasons within individual rivers varied significantly, which suggests that additional factors beyond those specific to each river influence patterns in growth.

Our results indicated a significant difference in growth rates between species. Instantaneous growth rates were on average 5.3% higher for larval Blueback Herring than larval Alewife (i.e., G_2 and G_{20}) in 2013 and 2015; however, later in life juvenile Alewife had growth rates that were on average 39.0% higher than juvenile Blueback Herring in all three years (i.e., G_{60} and G_{120}). A previous report documented young Blueback Herring growing faster
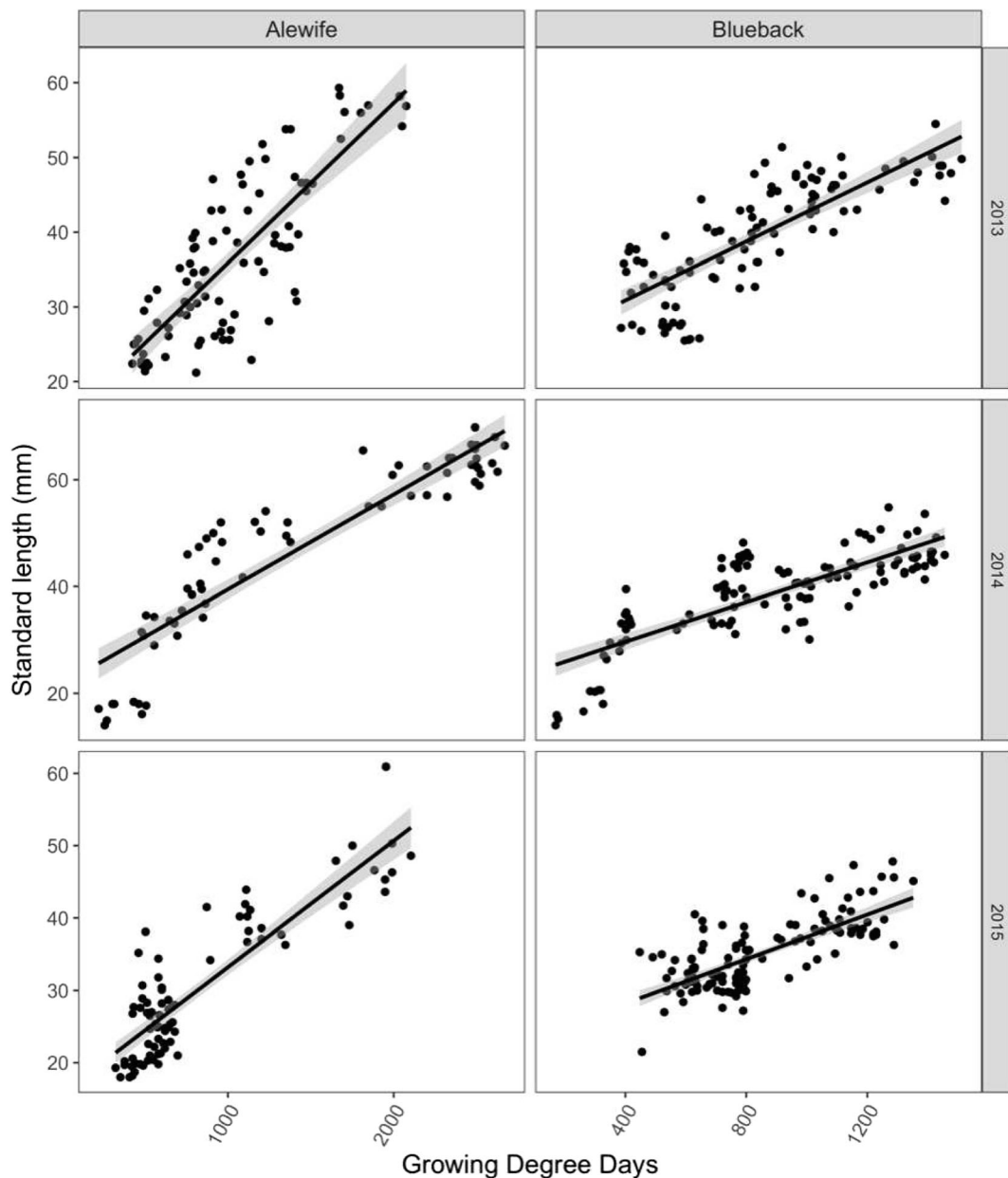
Fig. 5 Observed length (mm) of young-of-year Alewife and Blueback Herring collected during the spawning seasons of 2013, 2014, and 2015 with associated cumulative growing degree-day ($\sum$GDD, °C·day) values calculated using Formula 1, note that the scale for growing degree-days differs between the two species and the scale for standard length differs between years

than young Alewife (Hildebrand and Schroeder 1928), but did not specify whether the study referred to larvae, juveniles, or both life stages. Klauda et al. (1991) partially attributed higher Blueback Herring growth rates to hatching later in the growing season than Alewife, when temperatures are warmer. Characterizing drivers of differences in growth between

these species is important for improving management strategies.

Traditionally, the two species have been paired together in management strategies and population modeling (ASMFC 2009; NRDC 2011). However, if growth between the two species is different, then utilizing general growth equations developed for the combination of

the two species will result in inaccurate estimates of population recruitment. For example, overestimating growth rates could lead to assumptions that fish will be recruited to the spawning population before they actually become reproductively capable. Additionally, overestimating growth could also lead to an underestimation of mortality if mortality is calculated from growth parameters such as the method described by Pauly (1980). Alternatively, if growth rates were estimated to be lower than reality, management would not be as effective at tracking potential positive changes in a recovering population (Tyszko and Pritt 2017). Contrary to approaches currently utilized by fisheries managers, this result suggests that a single set of stock von Bertalanffy growth parameters are not sufficient for serially assessing YOY Alewife and YOY Blueback Herring growth in Potomac River tributaries.

While growth for Alewife and Blueback Herring differed, strong correlations between thermal exposure and size occurred for both species throughout the study. Overall, the GDD metric strongly correlated with SL across all sampling seasons (2013–2015) for each species, Alewife (Pearson's $r = 0.889$, $p < 0.0001$) and Blueback Herring (Pearson's $r = 0.759$, $p < 0.0001$). This correlation remained strong within each year for each species, Alewife (Pearson's $r = 0.808$–0.913, $p < 0.0001$) and Blueback Herring at both locations (Pearson's $r = 0.740$–0.797, $p < 0.0001$), as well as for Blueback Herring at Gunston Cove only (Pearson's $r = 0.712$–0.797, $p < 0.0001$). These correlations support our hypothesis that temperature is a driving factor for growth in the two species. Additionally, there was a significant difference in the GDD metric when compared between species, which was expected as Blueback Herring are known to spawn later in the season when water temperatures are higher (i.e., 13–27 °C instead of 10–22 °C, Cianci 1969; Jones et al. 1978; Pardue 1983; Schlick 2016). This offset in spawning period results in YOY Alewife spending more time in the Potomac River tributaries on average than YOY Blueback Herring since both species emigrate out of the system at the same relative time (Loesch 1987).

Changes in climate, including altered patterns of annual temperatures and precipitation, are anticipated to modify global ocean temperatures (Abraham et al. 2013). Interestingly, managers could argue that earlier warming of surface water temperatures, as a product of climate change, could benefit river herring by enabling a longer optimal growing season for YOY. However,

there is no evidence to suggest how the rest of the ecosystem would respond to this change, or how the growth of Alewife and Blueback Herring would be impacted by any of the other changes associated with a shifting climate. Moreover, if seasonal temperatures increase or begin warming earlier in the spawning season, then YOY river herring growth will also increase to reflect this change in magnitude or timing of increased thermal exposure. Houde (1997) connected slowed rates of growth to increased rates of mortality as a result of slower growing individuals having higher mortality rates through predation because they are small for a longer period of time. Therefore, this increase in growth rates early on may result in a decrease in mortality by predation, as individuals are physiologically better equipped to avoid predation (i.e., transition from plankton to nekton quicker). However, increased rates of growth would also result in a higher consumption rate, thus a larger prey source would need to be available faster (Jobling 2002). If prey availability is a limiting factor in a nursery system, then an increase in temperature could result in a lower carrying capacity of that ecosystem and ultimately reduce the amount of river herring juveniles surviving to adulthood.

Increased spawning and growth early on in the spawning season due to elevated water temperatures may result in a timing mismatch between food availability and increased YOY abundances (i.e., match/mismatch hypothesis, Cushing 1990). Young-of-year river herring primarily consume zooplankton and macroinvertebrates (Davis and Cheek 1966; Gannon 1976; Nigro and Ney 1982; Stone and Daborn 1987; Schlick unpublished), which are typically abundant in Potomac River tributaries in the late spring to early summer (Jones and de Mutsert 2013, 2014). The abundance of these prey items is usually linked with peaks in phytoplankton production, which is correlated to sunlight availability rather than temperature (Cushing 1990). On average, adult copepod abundances in Hunting Creek peak in April, and are followed by June and July peaks in cladoceran abundances (Jones et al. 2017b). While variations in future climate are anticipated to alter global temperature regimes, regional light availability is anticipated to remain consistent with historic levels. As seasonal temperatures fluctuate stochastically, so will the growth of ectothermic species like Alewife and Blueback Herring. Alternatively, photosynthetic species such as phytoplankton will continue to respond to cyclic changes in light availability, which will in turn reinforce

the temporally stable boom and bust cycle of organisms that directly rely on these populations, such as zooplankton on which YOY river herring rely. Ultimately, early warming trends expected with climate change could result in YOY river herring not matching with prey availability.

Additionally, Lane et al. (2015) concluded that if the current climate change trajectory is maintained, then the range of recreationally valuable coldwater fishes as they exist today in the United States will not exist. Even under two separate climate mitigation climate mitigation scenarios, coldwater ranges are anticipated to decrease, resulting in a concurrent increase in newly-available habitat for warm water-species to immigrate. This scenario is not ideal for coldwater-limited fish species, like brown trout (Salmo trutta), but could present an opportunity for warm water species, like Alewife and Blueback Herring, to expand their range. Unfortunately, river herring spawning ranges typically intersect urban centers, as they require inland tributaries to spawn. These species are therefore limited to the tributaries that host passable infrastructure with sufficient water flow and optimal water temperatures (Dynesius and Nilsson 1995; Hall et al. 2011). This limitation is especially true within the northern Virginia portions of the Potomac River nursery, as the streams are surrounded by a densely populated region. Limited knowledge is available surrounding the efficiency of current fish passage infrastructure and in turn the accessibility of inland waterways to migratory fish, sufficiently minimizing the potential positive impact of elevated temperatures beyond the current river herring range. A difference between sampling locations for Blueback Herring suggests that growth rates are highly variable on small spatial scales due to environmental conditions. How temperature will further impact this species will vary based on other environmental conditions, and not enough data are currently available to examine how these species will respond in each water system.

Correlations between SL and GDD also differed between years for each species and between locations for Blueback Herring, which indicate that while temperature is a driving factor, it is not the only driver. The results of this study support the hypothesis developed by Tommasi et al. (2015) wherein YOY river herring development was greatly impacted by thermal exposure alongside other environmental variables. If thermal exposure was the only dominant environmental variable for YOY, then the instantaneous growth rates

would be highest in the years with the highest average GDD. However, the average GDD was highest in 2014 for Alewife and in 2015 for Blueback Herring. The highest instantaneous growth rates were in 2014 for larval Alewife and Blueback Herring, but were highest in 2013 for juvenile Alewife and Blueback herring. The growth rates for Blueback Herring were lowest in 2015, even though the average GDD was highest that year. Tommasi et al. (2015) concluded that YOY recruitment for Alewife and Blueback Herring varied based on the timing of the peak flow and/or the average flow rates within each river. Lane et al. (2015) found that current climate change expectations would result in an increase in annual stream flow of up to 50–100% greater than current annual flows. These elevated stream flows have the potential to alter the suitability of Potomac River tributaries as nurseries for YOY river herring by increasing the chance of washout-events, wherein elevated stream flow rapidly moves larval ichthyoplankton downstream to less suitable habitat. The results of the current study and that of Tommasi et al. (2015) emphasize the importance of accounting for local and time specific conditions when estimating the development and recruitment of YOY river herring, as multiple site-specific abiotic factors likely contributed to the growth and survival of each species. Therefore, the persistence of the observed high level of variation in growth between years, even when thermal exposure was accounted for, suggests that the growth of these fishes in these early life stages (i.e., larval and juvenile) has the greatest potential to be altered by future environmental change.

During this study period (i.e., 2013 to 2015), Jones et al. (2017a) observed a slight decrease in the annual abundances per area of adult copepods and cladocerans (i.e., two common river herring prey items) in Gunston Cove, as indicated by local polynomial regressions applied to each species. Alternatively, Jones et al. (2017b) observed a peak in the abundances of cladocerans in 2014 and a sharp decline of adult copepods in 2015 within Hunting Creek. Although the abundance of these organisms within Gunston Cove experienced slight declines over the study period, the overall abundances per area for each year of the study were at least three-fold more for adult copepods and nine-fold more for cladocerans relative to that of Hunting Creek (Jones et al. 2017a, b). These results suggest that the growth rates in Gunston Cove should have been higher than the rates in Hunting Creek, as there was a much greater

abundance of prey available (e.g. adult copepods and cladocerans). However, the growth rates for Blueback Herring were higher in Hunting Creek, not Gunston Cove, which suggests that prey availability in the nursery habitats did not play a major role in the variations in growth rates observed between years and between locations in this study. Both Gunston Cove and Hunting Creek are well documented as productive habitats for many of the species river herring feed on during YOY development, so prey is likely not a limiting factor in these environments.

Few studies are currently available on the von Bertalanffy growth parameters of juvenile Alewife and Blueback Herring, particularly in the Potomac River. Estimations of growth are essential to many stock assessment strategies (Beverton and Holt 1957; Haddon 2011; Hilborn and Walters 1992; Quinn II and Deriso 1999). More specifically, many population modeling strategies, such as ecosystem models developed with Ecopath with Ecosim, utilize the von Bertalanffy K parameter to simulate growth of a species within the model (Christensen and Walters 2004). The current study provides the von Bertalanffy parameters for juvenile river herring species in the Potomac River. Furthermore, this study illustrates the importance of future studies to account for abiotic conditions when estimating the growth (e.g., growth rates) and development (e.g., recruitment potential) of YOY fishes.

Frequently, studies find that recruitment success is weakly correlated with the number of spawning adults in a population, but that success is more strongly related to a combination of environmental or ecological factors in tandem with spawner abundances (Parkos and Wahl 2010; Post et al. 1998; Siepker and Michaletz 2013). Post et al. (1998) found that ultimately the number of spawning adults was the most limiting factor for recruitment, as a scenario with fewer reproductively viable individuals produces less offspring to contribute to a year-class. However, in instances where the number of adults were not considered low, environmental factors were then considered to have the greatest influence over recruitment. While an increased number of spawners may increase offspring production, additional post-hatch pressures may also influence the success of each year-class prior to recruitment. These conclusions suggest that management actions focused solely on promoting the numbers of spawners in populations are likely insufficient in maintaining continued growth in the size of a population. Alternatively, management should focus on maintaining suitable nursery environments from which YOY are reared so that a higher number of spawning individuals will more directly yield an increased number of recruits. In order to achieve this goal, future studies should focus on identifying the most influential environmental factors impacting YOY success in each geographically and temporally unique population of interest, and then develop management strategies guided by these limiting factors. We have demonstrated that temperature is closely linked to YOY growth in Alewife and Blueback Herring residing in tributaries of the Potomac River. The next step for wildlife managers in this region is to begin assessing how the timing and magnitude of changing temperatures will impact growth, and ultimately recruitment of YOY Alewife and Blueback Herring - a once valuable living resource.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants performed by any of the authors. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the American Association of Laboratory Animal Science Institutional Animal Care and Use Committee (under protocol #0194 and #0279).

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