Growth of juvenile Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) in response to dual-season spawning and latitudinal thermal regimes

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Abstract—Populations of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) occur over a broad latitudinal range, such that size-dependent winter mortality of juveniles could select for latitudinal countergradient variation in growth rate of juveniles. To investigate latitudinal countergradient variation in growth between populations, growth of strains of the Saint John River (New Brunswick, Canada) and the Altamaha River (Georgia) was compared in a common-garden experiment by exposing juveniles (Altamaha River strain: mean length of 178 mm [standard deviation (SD) 8.1]; Saint John River strain: mean length of 180 mm [SD 9.2]) to simulated temperature regimes representing the latitudinal range of this subspecies (in the Saint John, Choptank, and Edisto Rivers). No strain effect was detected. To evaluate thermal phenology, a growth-degree-day (GDD) model was developed from responses of fish in a laboratory. Growth degree days were predicted for juveniles that spawned in the fall and for systems south of Chesapeake Bay, where supraoptimal summertime temperatures occur. Predicted lengths of age-1 Atlantic sturgeon generally fell within the range of values reported in literature. Results of analyses with the GDD model support evidence that spawning occurs in the fall only in systems south of the New York Bight, and the model could be applied in evaluation of scenarios of warming and dual-season spawning throughout the range of this subspecies.

Conservation success of threatened and endangered sturgeon species is most sensitive to factors that influence first-year survival; therefore, juvenile sturgeon should receive the highest conservation priority (Gross et al., 2002; Secor et al., 2002). Age-0 and older juveniles (<100 cm total length [TL]) of the Atlantic sturgeon subspecies *Acipenser oxyrinchus oxyrinchus*, distinct population segments of which are protected as threatened or endangered under the U.S. Endangered Species Act (Federal Register, 2012a, 2012b), are encountered in over a dozen tributaries used for spawning (Hilton et al., 2016). Their growth and survival conditions may vary widely across the broad latitudinal range (of about 15° or 2200 km) in which these nursery systems occur (from the Satilla River in Florida [31° N] to the Saint Lawrence River in Canada [44°30′ N]). Assessment and conservation of juvenile

production is confounded further by the recent discovery that, in some portions of their range, Atlantic sturgeon spawn in both spring and fall (Balazik et al., 2012; Hager et al., 2014; Balazik and Musick, 2015; Smith et al., 2015). Such dual-season spawning would result in 2 size modes associated with age-0 and age-1 juveniles in any given season. Therefore, to assess recruitment, lengths of sampled juveniles need to be discriminated between subannual spawning cohorts.

In some species that occur over broad latitudinal ranges, juvenile growth rates are faster at higher latitudes (Conover, 1992). Regions in higher latitudes support shorter growing seasons, earlier onsets of winter, and greater severity of winter (Yamahira and Conover, 2002) as well as scarcity of prey in winter (Shuter et al., 2012). In North America, the latitudinal gradient of shorter summers and longer winters in

the north, compared with winters in the south, can result in systematic changes in population traits, such as spawning time, somatic growth, size and age at reproduction, and lifespan (Shuter et al., 2012), but juvenile growth may be particularly responsive to countergradient selection.

Atlantic silverside (*Menidia menidia*) occur over a latitudinal range similar to that of Atlantic sturgeon, and juveniles grow faster at higher latitudes, a difference in growth that has reproductive implications for this short-lived species (Conover and Present, 1990). For populations sampled from a representative range of latitudes, length of growing season varied by a factor of 2.5, but sizes of Atlantic silverside at the end of the season were similar across latitudes (Conover and Present, 1990). Northern strains of mummichog (*Fundulus heteroclitus*) had a higher capacity for growth when reared in a common-garden experiment with fish from southern latitudes (Schultz et al., 1996). Similarly, larval (Conover et al., 1997) and juvenile (Secor et al., 2000) striped bass (*Morone saxatilis*) obtained from higher latitudes grew faster than those from lower latitudes in common-garden experiments. Northern populations of lake sturgeon (*Acipenser fulvescens*) were smaller at a given age than southern populations, but they grew at a higher rate when growth was adjusted for expected thermal conditions (Power and McKinley, 1997). Therefore, countergradient variation in growth is expected for species that occur across wide temperate latitudinal ranges.

In temperate systems, cessation of growth and lethal temperatures during winter months are thought to drive latitudinal countergradient trends in juvenile growth (Conover, 1992; Schultz et al., 1996; Power and McKinley, 1997). Winter mortality may occur because of thermal stress, starvation, predation, disease, winter hypoxia, and physical disturbance (e.g., ice flows). However, it is thermal stress (e.g., inability to maintain homeostasis) and starvation (e.g., insufficient energy stores) that likely account for a significant proportion of winter mortality (Hurst, 2007). At higher latitudes, smaller body size and lower energy stores may increase winter mortality (Yamahira and Conover, 2002; Garvey and Marschall, 2003; Crossman et al., 2009; Pörtner and Peck, 2010; Shuter et al., 2012). Striped bass in the Hudson River in New York shifted from increasing length early in the growing season to increasing energy reserves toward the end of the growing season, presumably to reduce risk of winter mortality (Hurst and Conover, 2003). Atlantic silverside in northern latitudes accumulated energy stores faster than their southern counterparts, providing evidence that risk of winter starvation resulted in selection to accumulate energy during the first growing season (Schultz and Conover, 1997). There has been little research on winter mortality of sturgeon species. Crossman et al. (2009) observed that only 40% of stocked juvenile lake sturgeon survived their first winter, indicating that winter mortality could be an important agent of natural selection. Still, they observed no relationship between size and winter survival.

Seasonal changes in temperature that juveniles encounter during their first year of life, referenced here as *thermal phenology*, play an integral role in determining their growth and survival (Neuheimer and Taggart, 2007; Puckett et al., 2008; Humphrey et al., 2014). To evaluate thermal phenology, a valuable tool is the growth-degree-day (GDD) model, which integrates temperatures that a fish experiences together with thermal tolerance thresholds. The GDD method allows individual growth calendars to be tracked for differing hatch dates and regions, supporting simulation of thermal phenologies for growth of Atlantic sturgeon across latitudes. Although fish weight can be used as the principal growth variable explained by GDD, length of fish is preferred because it either does not change or changes positively on a seasonal basis (i.e., fish will not shrink in length) (Neuheimer and Taggart, 2007; Humphrey et al., 2014). In addition, length is the most commonly monitored measure of size, allowing us to compare model predictions with published length-at-age data.

To test if northern and southern populations of Atlantic sturgeon express countergradient variation in growth, we reared juveniles in common-garden experiments in 3 thermal regimes representative of the latitudinal range of this subspecies. In addition to this laboratory experiment, we applied a GDD model over the latitudinal range of Atlantic sturgeon to determine: 1) the number of GDD accumulated during the first year of life and 2) the predicted size of Atlantic sturgeon at the end of the first year of life (age: 1.0 year). Specific hypotheses included 1) juvenile growth rate will be positively associated with the latitude of their source strain, 2) strain growth rates will differ among thermal regimes, 3) accumulated GDD (juvenile growth performance) and size at age of 1.0 year will be less for northern strains than southern strains, and 4) the accumulated GDD and size at winter onset will be higher for Atlantic sturgeon that spawned in spring than for those that spawned in fall.

Materials and methods

Laboratory experiment

A comparison of juvenile growth between the strains of Atlantic sturgeon from the Saint John River in New Brunswick, Canada, and the Altamaha River in Georgia was conducted under controlled laboratory conditions. Atlantic sturgeon from the population in the Saint John River were provided by C. Ceapa (Acadian Sturgeon and Caviar Inc.[1], Saint John, Canada) in July 2013 (hatch date: 21 July 2013; water temperature: ~15°C) from a spawning by 1 female and 3–4 males. Atlantic sturgeon from the population in the Altamaha River were acquired from the U.S. Fish and Wildlife Bears Bluff National Fish Hatchery in Wadmalaw Island, South Carolina, in August 2013 (hatch date: 9 August 2013; water temperature: ~22°C) from a spawning by 1 female and 1 male. Upon arrival, larvae (~10 mm TL) were reared in freshwater

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[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

(~17.8°C) and fed nauplii of brine shrimp (*Artemia* spp.) before being weaned to a commercial diet at ~35 mm TL and acclimated to water from the Choptank River (a tributary of Chesapeake Bay, Maryland) (salinity: ~10) until the start of the experiment.

Fish from the populations in the Altamaha and Saint John Rivers were exposed to 3 thermal regimes. Ambient seasonal temperatures at the Choptank River (intermediate latitude: data from in situ measurements; senior author, unpubl. data) were used for one thermal regime, and other regimes simulated the mean monthly temperatures recorded in the winter and spring of 2013 at the Edisto River, South Carolina (low latitude: data available from the National Estuarine Research Reserve System [NERRS] at website), and at the Saint John River (high latitude; Ceapa[2]). The treatment in which fish from the Saint John River strain were exposed to the thermal regime of the Edisto River received 6 replicates. The treatment in which fish from the Altamaha River strain were exposed to the thermal regime of the Saint John River received 6 replicates. The treatment in which both strains were exposed to the thermal regime of the Choptank River received 3 replicates.

Smaller tanks (148 L) were used for the Edisto and Saint John River thermal regimes, but owing to tank availability, larger tanks (1600 L) were used for the Choptank River thermal regime treatments. Seven fish were stocked into each tank and acclimated to the target temperature at a rate of 1°C/d. The experiment was conducted during December 2013–June 2014 for the thermal regime treatments that simulated temperatures in the Choptank River and Edisto River. Owing to a mechanical failure, the Saint John River thermal regime treatment was terminated in March 2014. The Saint John River and Edisto River thermal regimes were controlled by using heat exchangers in a partially recirculating aquaculture system with filtered (2 μm) water from the Choptank River. Salinity ranged from 8 to 12. Fish were fed an amount equal to 5% of their body weight per day (sturgeon booster diet, Zeigler Bros Inc., Gardners, PA) during the course of the experiment. The amount of food consumed or discarded was not quantified.

Weights in grams and TLs in millimeters were measured for all experimental fish and recorded at intervals of approximately 4 weeks. Because of the small initial size of the fish from the Altamaha River strain (mean: 178 mm TL [standard deviation (SD) 8.1] and 22 g [SD 3.0]) and the Saint John River strain (mean: 180 mm TL [SD 9.2] and 24 g [SD 3.1]), individual fish were not marked; therefore, lengths and weights for each tank were summed for statistical comparisons. Among treatments, there was no statistical difference in the initial lengths (analysis of variance [ANOVA]: between strains, sample size [*n*]=30, *P*=0.48; between thermal regimes, *n*=30, *P*=0.76) or in weights (ANOVA: between strains, *n*=30, *P*=0.06; between thermal regimes, *n*=30, *P*=0.84).

Growth-degree-day model and analysis

The GDDs were calculated for each temperature profile as follows:

$$GDD = \Sigma \, (T_{\mathrm{i}} - T_{\mathrm{th\text{-}min}}) \times \Delta d \text{ or} \qquad (1)$$

$$GDD = \Sigma \, (T_{\mathrm{th\text{-}max}} - T_{\mathrm{i}}) \times \Delta d, \qquad (2)$$

where T_{i} = the mean daily water temperature;
  $T_{\mathrm{th\text{-}min}}$ = the minimum threshold (4°C);
  $T_{\mathrm{th\text{-}max}}$ = the maximum threshold (28°C); and
    Δd = the number of days between sampling.

Note that we assumed that fish cannot lose length; therefore, GDD was assigned a value of 0 if temperatures were outside the tolerance limits of the Atlantic sturgeon. The minimum and maximum thermal growth thresholds were selected at 4°C and 28°C on the basis of laboratory experiments and observations of thermal limits in Atlantic sturgeon (Dovel and Berggren, 1983; Mohler[3]; Niklitschek and Secor, 2005, 2009).

Repeated measures ANOVA, conducted in statistical software R, vers. 3.3.2 (R Core Team, 2016), was used to compare the effects of thermal regime and strain on the tank means for repeated measurements of length, weight, and specific growth rate. Four models were compared to determine the best covariance structure among repeated measures: 1) a baseline model assuming independence (model 1), 2) a model with dependence between tanks but no correlation between days (model 2), 3) a model with dependence between tanks and first-order autoregressive correlation (an autoregressive lag-1 covariance structure) between days (model 3), and 4) a model with dependence between tanks and autoregressive–moving average (1,1) correlation (autoregressive–moving average model) between days (model 4). The best model was determined by using the lowest Akaike information criterion (AIC), after which the final model structure was determined by using restricted maximum likelihood. Post-hoc comparisons were made by using Tukey's honestly significant difference to determine which comparisons were significant.

Growth degree days along a latitudinal gradient

Water temperature data for estuarine systems during the period 2008–2013 were obtained from 7 NERRS sites, representing the latitudinal distribution of Atlantic sturgeon: (1) Wells, Maine, (2) Great Bay, New Hampshire, (3) Hudson River, New York, (4) Chesapeake Bay, Maryland, (5) North Carolina, (6) the area from North Inlet to Winyah Bay, South Carolina (hereafter, referred to as *South Carolina*), and (7) Ashepoo–Combahee–Edisto Basin in South Carolina. For consistency and under the assumption that tidal freshwater areas represent a substantial fraction of habitats where growth of age-0 fish occurs,

[2] Ceapa, C. 2013. Personal commun. Acadian Sturgeon and Caviar Inc., 214 King St. E., Saint John, New Brunswick E2L 1H3, Canada.

[3] Mohler, J. W. 2004. Culture manual for the Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus*, 70 p. [Available from Region 5, U.S. Fish Wildl. Serv., 300 Westgate Center Dr., Hadley, MA.]

Table 1

Mean total length and weight of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) during each sampling period for each thermal regime from December 2013 to March 2014. Thermal regimes included ambient seasonal temperatures at the Choptank River in Maryland (intermediate latitude) and mean monthly temperatures recorded in the winter and spring of 2013 at the Edisto River in South Carolina (low latitude) and at the Saint John River in Canada (high latitude). Standard deviations are given in parentheses.

Sampling period	Total length (mm)			Weight (g)		
	Saint John River	Choptank River	Edisto River	Saint John River	Choptank River	Edisto River
0	179 (11)	181 (6)	178 (7)	23 (4)	24 (3)	23 (2)
1	181 (10)	196 (5)	208 (11)	24 (4)	30 (5)	37 (4)
2	181 (10)	196 (5)	246 (17)	23 (3)	33 (4)	61 (10)
3	182 (11)	199 (5)	298 (13)	24 (4)	36 (4)	107 (10)

temperature records for a single station within each NERRS site corresponding with tidal freshwater or the lowest salinity station were used to estimate GDDs from daily average means for each station and then summed by month. For stations where winter water temperatures were not recorded, we assumed zero growth occurred during this season because water temperatures recorded before or after the missing period were at or below the thermal tolerance threshold for Atlantic sturgeon.

Using ANOVA, we compared GDD between NERRS sites and years. Additionally, cumulative GDD was calculated for the first year of life (age: 1.0 year) for each NERRS site, for Atlantic sturgeon that spawned in spring and for those that spawned in fall. Assumed spawning dates for sturgeon that spawned in spring were 1 July (Maine), 1 June (New Hampshire), 1 May (New York and Maryland), and 1 April (North Carolina and South Carolina), and assumed spawning dates for sturgeon that spawned in fall were 1 September (Maryland) and 1 October (North Carolina and South Carolina) (Dovel[4]; Smith et al., 1984; Gilbert[5]; Collins et al., 2000; Balazik et al., 2012). Tukey's honestly significant difference was used for post-hoc comparisons between sites and years.

Length at age 1 was predicted from combined experimental data by using a von Bertalanffy growth function with nonlinear regression:

$$L_{\text{GDD}} = L_\infty \left(1 - e^{-K(GDD - GDD_0)}\right), \qquad (3)$$

where L_∞ = asymptotic length;
K = growth coefficient;
GDD = GDD at age 1; and
GDD_0 = GDD at hatch.

[4] Dovel, W. L. 1979. The biology and management of shortnose and Atlantic sturgeon of the Hudson River, 54 p. NY Dep. Environ. Conserv. final rep. Proj. no. AFS9-R. [Available from NY Dep. Environ. Conserv., 625 Broadway, Albany, NY 12233-0001.]
[5] Gilbert, C. R. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic Bight)—Atlantic and shortnose sturgeons. U.S. Fish Wildl. Serv. Biol. Rep. 82 (11.122), 28 p. [Available from website.]

The model was fitted by using an iterative fitting procedure (Solver, Frontline Systems Inc., Incline Village, NV) within Microsoft Excel 2003 (Microsoft Corp., Redmond, WA). Adjustments to GDDs used in this model were needed for the growth period prior to the experiment, which was estimated as 1708 GDD=122 d×18°C. Predicted length at the onset of winter (1 January), from the assumed date of fall spawning was also calculated by using the von Bertalanffy growth function. Predicted length at the onset of summer (1 July) from the assumed date of spring spawning was also calculated by using the von Bertalanffy growth model for systems south of the Hudson River, New York.

Results

Laboratory experiment

The effect of thermal regime and strain on specific growth rate has been evaluated (Markin, 2017); therefore, the results reported here focus on effects on length and weight. Owing to the early termination of the experiment that used the Saint John River thermal regime, we did initial comparisons of thermal regimes for the abbreviated period December 2013–March 2014 (Table 1). Based on AIC criteria, ANOVA tests of average sturgeon length and weight responses used a within-tank autoregressive–moving average model between days (Table 2). There was no effect of strain on average fish length (P=0.82) or weight (P=0.88). Nor was there a significant interaction between thermal regime and strain on length (P=0.80) or weight (P=0.78). Therefore, these factors were dropped in the development of the final model. Both sturgeon length and weight were significantly influenced by thermal regime treatment (Table 3). As a result, regardless of strain, juveniles exposed to the Edisto River thermal regime were significantly larger (mean: 232.0 mm TL and 57.0 g) than those that experienced the Saint John River thermal regime (mean: 180.6 mm TL and 23.6 g; P<0.001) and the Choptank River thermal regime (mean: 192.8 mm TL and 30.7 g; P<0.03). Although higher growth

Table 2

Comparison of models used for repeated measures analysis of variance of total length and weight of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) between thermal regimes. Three thermal regimes were used to represent the latitudinal range of this subspecies, with ambient seasonal temperatures at the Choptank River in Maryland and simulated temperatures of the Edisto River in South Carolina and the Saint John River in Canada. Total lengths were measured between December 2013 and March 2014. The models were designed with no covariance (model 1), with dependence between tanks only (model 2), with an autoregressive lag-1 covariance structure (model 3), and with autoregressive–moving average correlation (model 4). Values for Akaike information criterion (AIC) and the change in AIC (ΔAIC) are provided.

Model structure	Model	AIC	ΔAIC	Random
Length~thermal regime	1	1136.90	59.10	~1|Tank
	2	1128.20	50.40	~1|Tank
	3	1109.40	31.60	~1|Tank
	4	1077.80	0.00	~1|Tank
Weight~thermal regime	1	1051.80	34.90	~1|Tank
	2	1022.30	5.40	~1|Tank
	3	1035.40	18.50	~1|Tank
	4	1016.90	0.00	~1|Tank

Table 3

Summary of results from analysis of variance and Tukey's honestly significant difference pairwise comparisons between total length of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) and the thermal regime to which fish were exposed in experiments conducted between December 2013 and March 2014. Thermal regimes included ambient seasonal temperatures at the Choptank River in Maryland and temperatures recorded at the Edisto River in South Carolina and the Saint John River in Canada. lsmean=least-square mean; SE=standard error of the mean.

| Model structure	Treatment	lsmean	SE	df	Contrasts	*P*-value
Length~thermal regime	Saint John	180.3	10.2	27	Choptank–Saint John	0.86
	Choptank	189.6	10.2	27	Choptank–Edisto	0.02
	Edisto	239.0	14.4	27	Edisto–Saint John	<0.00
Weight~thermal regime	Saint John	23.7	6.0	27	Choptank–Saint John	0.82
	Choptank	30.1	8.6	27	Choptank–Edisto	0.01
	Edisto	63.9	6.0	27	Edisto–Saint John	<0.00

was observed for fish exposed to the Choptank River thermal regime, no significant difference was detected in the lengths of fish between the Saint John River (mean: 180.6 mm TL and 23.6 g) and the Choptank River (mean: 192.8 mm TL and 30.7 g) thermal regimes (*P*>0.8).

Because strain did not influence growth performance or interact with thermal regime, growth data were combined across all treatments to develop a predictive length-versus-GDD model for juveniles. A von Bertalanffy growth model best fit the nonlinear relationship (Fig. 1). The resulting equation was used to estimate growth of age-1 sturgeon along a latitudinal gradient, as discussed in subsequent sections:

$$length = 803.93\left(1 - e^{(-0.000167(GDD-110.3))}\right), \qquad (4)$$

Growth degree days along a latitudinal gradient

For Atlantic sturgeon that spawned in spring, the accumulation of GDDs increased along a latitudinal gradient from Maine to Chesapeake Bay (n=35, P<0.01) (Fig. 2). Age-1 sturgeon in the 3 most northern systems (Maine, New Hampshire, and New York) accumulated significantly less GDD over the first year of life than more southerly sites. Age-1 sturgeon in the Chesapeake Bay region accumulated the most GDDs (mean: 4295 [SD 149]) compared with those in all other systems, particularly those in systems north of Chesapeake Bay. Between Chesapeake Bay and systems to its south, GDDs of fish were fairly similar. Latitudinal trends in GDDs were the result of days in each system experiencing suboptimal and supraoptimal temperatures (Table 4). Chesapeake Bay had the fewest number of days during which no growth occurred. Northern systems had
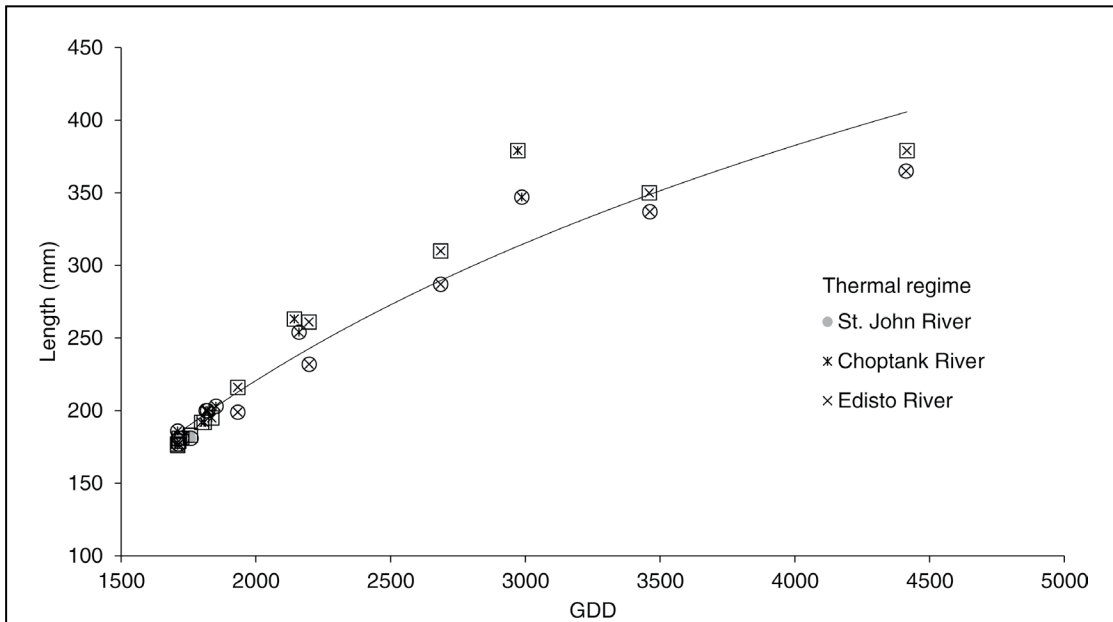
Figure 1

Relationship of total lengths and growth degree days (GDDs) of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) for 3 thermal regimes that represent temperatures experienced by fish in the Edisto River in South Carolina, the Choptank River in Maryland, and the Saint John River in Canada and for 2 strains of Atlantic sturgeon from the Saint John River and the Altamaha River in Georgia, modeled by using a von Bertalanffy growth function. Total lengths were measured between December 2013 and March 2014. Open circles represent the strain from the Saint John River. Open squares represent the strain from the Altamaha River. Other symbols represent the thermal regimes, as indicated in the figure key.
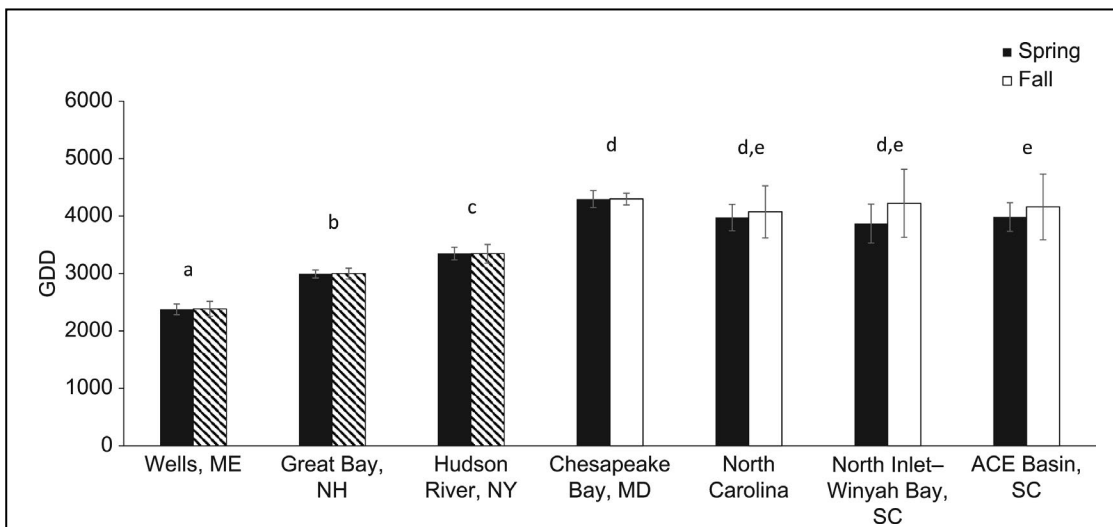
Figure 2

Accumulated growth degree days (GDD) of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) in relation to their spawning cohort (fall and spring) and the thermal regimes to which they were exposed across a latitudinal range. Water temperature data used for thermal regimes were collected from National Estuarine Research Reserve System sites from Maine to South Carolina during 2008–2013. Different letters denote significant difference ($P<0.05$) according to results from analysis of variance and comparisons with Tukey's honestly significant difference. The bars with diagonal lines indicate a hypothetical scenario in which spawning occurs in fall in those locations. The southernmost site is the Ashepoo–Combahee–Edisto Basin (ACE Basin) in South Carolina. Error bars indicate standard deviations.

Table 4

Average annual growth degree days (GDDs) and the number of days of suboptimal and supraoptimal temperatures collected from the National Estuarine Research Reserve System (NERRS) sites across the latitudinal range of the Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) in the United States for the years 2008–2013. Standard deviations are given in parentheses.

NERRS site	Average annual GDD (d)	Average no. of days with suboptimal temperatures	Average no. of days with supraoptimal temperatures
Well, ME	197.3 (9.8)	123.8 (10.9)	0.0 (0.0)
Great Bay, NH	249.2 (9.7)	123.7 (9.6)	0.0 (0.0)
Hudson River, NY	277.7 (14.8)	119.2 (13.8)	0.7 (1.1)
Chesapeake Bay, MD	358.4 (14.5)	4.2 (6.0)	0.0 (0.0)
North Carolina	340.3 (28.2)	3.5 (4.8)	58.7 (20.0)
North Inlet–Winyah Bay, SC	348.5 (49.9)	2.0 (4.0)	62.0 (21.8)
Ashepoo–Combahee–Edisto Basin, SC	333.4 (50.2)	1.2 (2.6)	78.0 (22.5)

119–124 d with suboptimal temperatures, and southern systems had 59–79 d of supraoptimal temperatures. Sturgeon in systems where spawning is believed to occur in both spring and fall accumulated more GDDs during their first year of life than those in systems where spawning occurs only in spring (Fig. 2). In these systems, similar size at the age of 1.0 year was observed between fall and spring spawning cohorts for each system, but this result was largely an outcome of the simulation exercise in which each cohort experienced 365 d of GDDs for the same thermal regime. Slight deviations between cohorts are likely due to the difference in start times for the 2 cohorts.

Lengths along a latitudinal gradient

We estimated the TL of age-1 fish along a latitudinal gradient by using the accumulated GDD for each system during 2008–2012 (Table 5, Fig. 3). Age-1 Atlantic sturgeon that spawned in spring attained the smallest size in Maine (mean: 253.2 mm TL [SD 8.6]; range: 241.8–267.6 mm TL), whereas Chesapeake Bay produced the largest-sized Atlantic sturgeon (404.2 mm TL [SD 10.0]; range: 386.9–416.0 mm TL). Age-1 Atlantic sturgeon in New Hampshire had an estimated mean length of 307.0 mm TL (SD 5.7), in a range of 300.8–315.4 mm TL, and the mean length of age-1 sturgeon in New York was estimated to be 335.7 mm TL (SD 8.7), with a range of 321.5–346.0 mm TL. South of Chesapeake Bay, sizes of age-1 sturgeon were similar. Monthly lengths were estimated along a latitudinal gradient for Atlantic sturgeon that spawned in spring (Fig. 4, A–G) and fall (Fig. 5, A–D). For Atlantic sturgeon spawned in spring, the mean length after the first month of growth was estimated to be 45.6 mm TL (SD 6.0), in a range of 29.1–53.8 mm TL. For Atlantic sturgeon that spawned in fall, lengths after the first month of growth were estimated to have a mean of 53.4 mm TL (SD 4.0) and a range of 42.0–59.4 mm TL. Size at the onset of winter varied considerably for the fall cohort when exposed to a thermal regime that simulated temperatures in northern systems where the fall cohort is not observed, ranging from 22 to 102 mm TL from Maine to New York. In comparison, the size of fish in systems where the fall cohort

is observed varied less: 119–174 mm TL for Chesapeake Bay and the systems south of it (Fig. 6). Juveniles that spawned in spring were considerably larger, with latitudinal trends mirroring trends in size at age of 1.0 year. Size at the onset of summer ranged from 108 to 157 mm TL for Chesapeake Bay and the systems south of it.

Discussion

In the laboratory experiment, we failed to detect an effect of strain on juvenile growth in a common-garden environment; therefore, the results of this study of Atlantic sturgeon do not support the existence of latitudinal countergradient growth variation. Although countergradient growth variation has been highlighted in other ectotherms that have wide latitudinal ranges (Conover et al., 2009), there are species for which countergradient growth variation has not been observed. Countergradient growth has not been reported for the California grunion (*Leuresthes tenuis*), possibly because of its oceanic life history (Brown et al., 2012). Populations of Atlantic cod (*Gadus morhua*) have responded similarly to a warm thermal regime, indicating that observed higher growth rates of southern populations were not a result of higher genetic capacities for growth (Purchase and Brown, 2001). For Atlantic salmon (*Salmo salar*) from 5 rivers in Norway that were reared in common thermal conditions in a previous study, no association between their river of origin and maximal or threshold growth rates was observed (Jonsson et al., 2001). In our study, Atlantic sturgeon had higher growth in warmer temperatures, a relationship that is expected for ectotherms, but the population of the Saint John River did not compensate for a shorter growing season with a greater capacity for growth. If strain does not influence growth, it should be possible to generalize thermal growth performance across latitudes and spawning periods and to predict sizes of juveniles across the range of this subspecies.

Seasonal observations of adult and early life stages in tributaries where Atlantic sturgeon spawn provide direct or circumstantial evidence for dual-season spawning for

Table 5

Reported and predicted total lengths of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) at ages of 0–1 year along a latitudinal gradient from Canada to Georgia. Observed sizes are total lengths measured between December 2013 and March 2014; for some observed sizes, a mean is given instead of a range. Predicted sizes are estimates from nonlinear regression in this study. Modeled sampling months are hypothetical for this study.

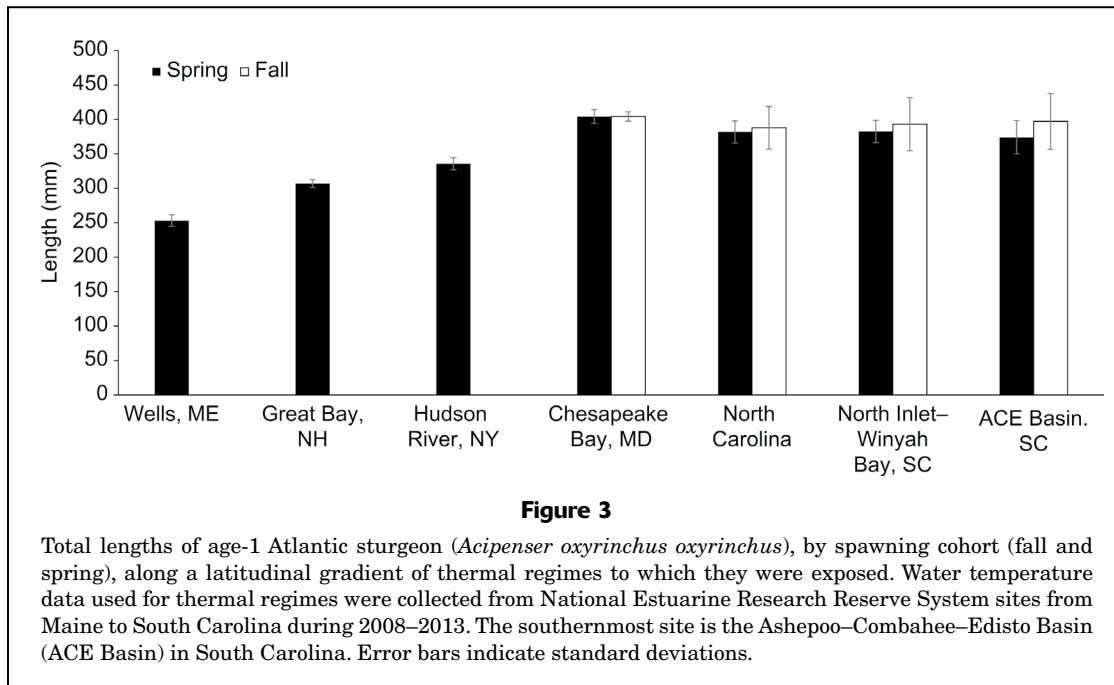| Location	Observed size (mm)	Age (years)	Predicted size (mm)	Age (years)	Reported sampling period	Modeled sampling month	Source
Saint John River, Canada	217	1			May–October		Stewart et al. (2015)
Maine			241.8-267.6	1.0		June	This study
New Hampshire			300.8-315.4	1.0		May	This study
Connecticut River	225–640	1			May–October 2014		Savoy et al. (2017)
New York			321.5–346.0	1.0		April	This study
Hudson River, NY	323	0[+]			October–May 1975, 1976, 1978		Dovel[a]
Hudson River, NY	502	1			October–May 1975–1978		Dovel[a]; Dovel and Berggren (1983)
Hudson River, NY	425–525	1			March–July		Peterson et al. (2000)
Hudson River, NY	450–550	1			August		Peterson et al. (2000)
Hudson River, NY	525–600	1			September		Peterson et al. (2000)
Hudson River, NY	575–625	1			October–December		Peterson et al. (2000)
Chesapeake Bay			386.9–416.0	1.0		April	This study
James River, VA	406–431[+]	Unknown			November		Balazik[b]
North Carolina			367.1–406.8	1.0		March	This study
South Carolina coastal rivers	550	1			Unknown		McCord et al. (2007); Schueller and Peterson (2010)
South Carolina			340.9–409.2	1.0		March	This study
Savannah River, SC/GA	410	0–1			Various		Peterson et al. (2008)
Ogeechee River, GA	310	0–1			May–December		Peterson et al. (2008)
Ogeechee River, GA	242–361	1			June–August 2007		Farrae et al. (2009)
Altamaha River, GA	379	0–1			June–August 2005		Peterson et al. (2008)
Altamaha River, GA	350–550	1			various		Schueller and Peterson (2010)
Satilla River, GA	340–540	1			September–July		Fritts et al. (2016)

[+] Total lengths were reported as 16–17 in.

[a] Dovel, W. L. 1979. The biology and management of shortnose and Atlantic sturgeon of the Hudson River, 54 p. Final report. Proj. no. AFS9-R. [Available from NY Dep. Environ. Conserv., 625 Broadway, Albany, NY 12233-0001.]

[b] Balazik, M. 2016. Personal commun. Virginia Commonwealth Univ., P.O. Box 842030, Richmond, VA 23284-2030.

populations in Maryland, Virginia, North Carolina, and South Carolina (Smith et al., 1984; Balazik et al., 2012; Hager et al., 2014; Balazik and Musick, 2015; Smith et al., 2015) and evidence that, in the Altamaha River, spawning of Atlantic sturgeon may occur only in the fall (Ingram and Peterson, 2016). Results from the GDD model indicate that thermal conditions experienced by northern populations (from Maine to New York), particularly in advance of their first winter, may be inadequate to support spawning in fall (Fig. 6). Smaller sizes at the onset of winter would

Figure 3

Total lengths of age-1 Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*), by spawning cohort (fall and spring), along a latitudinal gradient of thermal regimes to which they were exposed. Water temperature data used for thermal regimes were collected from National Estuarine Research Reserve System sites from Maine to South Carolina during 2008–2013. The southernmost site is the Ashepoo–Combahee–Edisto Basin (ACE Basin) in South Carolina. Error bars indicate standard deviations.

be expected to result in increased mortality (Hurst, 2007), and future research should focus on factors that may drive winter mortality in sturgeon (e.g., starvation, predation, and thermal stress). Juveniles from northern populations that spawned in spring, albeit at smaller sizes than their counterparts from the southern population, must be sufficiently large at winter onset to weather the longer and more intense winters encountered at higher latitudes.
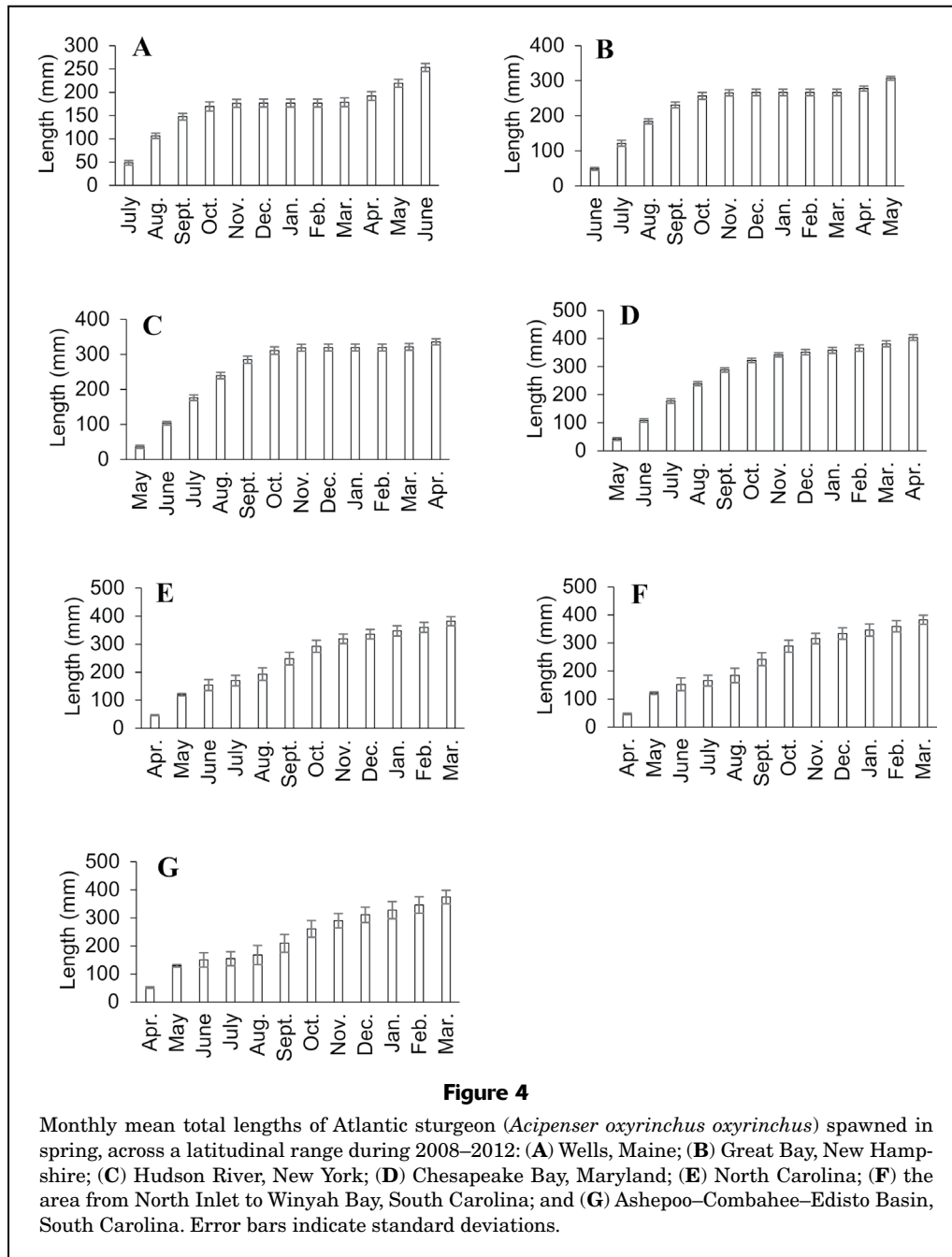
Interestingly, a strong difference in days with temperatures below the minimum threshold ($<4°C$) between the Hudson River (119.2 d [SD 13.8]) and Chesapeake Bay (4.2 d [SD 6.0]) is associated with the apparent shift from spawning in spring in the north to spawning in both spring and fall in the south. A supraoptimal thermal threshold may also curtail the incidence of dual-season spawning. In areas where spawning may occur exclusively in fall, as has been proposed for the Altamaha River (Ingram and Peterson, 2016), supraoptimal temperatures ($>28°C$) may curtail successful spawning events in spring or at least reduce growth and possibly survival of juveniles. Atlantic sturgeon experienced a sharp increase in the number of supraoptimal days between Chesapeake Bay (0.0 d) and North Carolina (mean: 58.7 d [SD 20]). With regional warming in coastal waters of Maryland and the southeastern United States (Kennedy et al.[6]; Najjar et al., 2010), increased supraoptimal days experienced could negatively affect Atlantic sturgeon that spawn in spring. If this results in a reduction of recruitment of individuals

that spawn in spring, population persistence and recovery would increasingly depend on successful fall cohorts.

There is some evidence that, in systems where Atlantic sturgeon spawn in spring and fall, cohorts are genetically distinct (Balazik and Musick, 2015; Hilton et al., 2016; Farrae et al., 2017) and may use separate spawning grounds (Balazik and Musick, 2015). Further investigations are needed to determine if dual-season spawning is related to genetic differentiation and if larval and juvenile sturgeon are able to imprint on specific seasonal signals in tributaries where they spawn. If genetic differences exist, additional studies are needed to determine if there are growth differences between strains that spawn in spring and those that spawn in fall.

The laboratory design assumed that 1) the 2 sampled populations were representative of latitudinal differences in growth responses, 2) batch growth rates were representative of growth performance, 3) growth is linear between the upper and lower thresholds, and 4) hatchery-sourced cohorts were representative of naturally spawned juveniles. Although the 2 strains of Atlantic sturgeon used in this study—strains of fish from the Altamaha River and the Saint John River—represented the northern and southern parts of the latitudinal range, the addition of other strains would have strengthened inferences by providing a continuum of expected growth rates. The small size of the Atlantic sturgeon at the start of the experiment was not conducive to marking individual fish; hence, length and weight data were pooled by tank. Because individual growth rates can vary substantially within populations, investigation into the variability of growth among different population is warranted. Finally, using progeny from 1 spawning event in a hatchery may not well represent the genetic variability in wild populations. However, hatchery-reared Atlantic
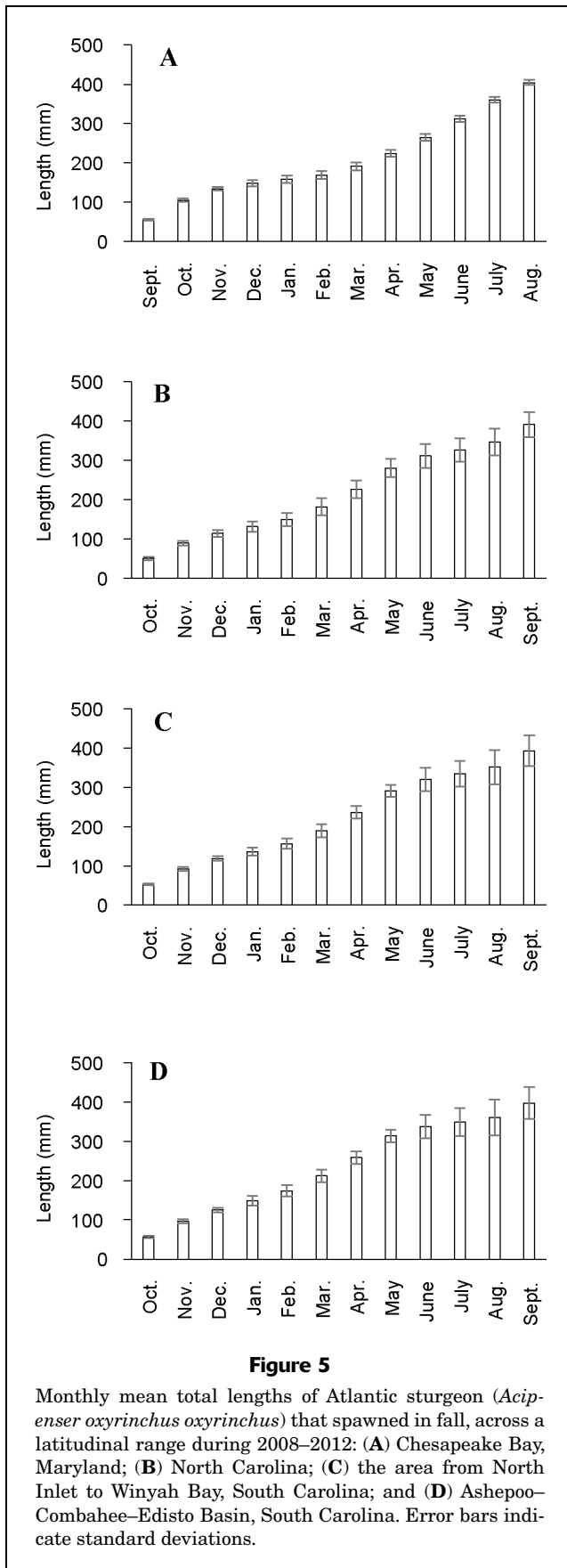
[6] Kennedy, V. S., R. R. Twilley, J. A. Kleypas, J. H. Cowan Jr., and S. R. Hare. 2002. Coastal and marine ecosystems and global climate change: potential effects on U.S. resources, 52 p. Pew Center on Global Climate Change, Arlington, VA. [Available from website.]

Figure 4

Monthly mean total lengths of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) spawned in spring, across a latitudinal range during 2008–2012: (**A**) Wells, Maine; (**B**) Great Bay, New Hampshire; (**C**) Hudson River, New York; (**D**) Chesapeake Bay, Maryland; (**E**) North Carolina; (**F**) the area from North Inlet to Winyah Bay, South Carolina; and (**G**) Ashepoo–Combahee–Edisto Basin, South Carolina. Error bars indicate standard deviations.

sturgeon provide a reliable source for experimental research with known genetic parentage, and use of hatchery-reared sturgeon does not affect wild populations.

Important assumptions of the GDD model included 1) specification of lower and upper threshold temperatures of 4°C and 28°C and 2) specification of time of spawning associated with spring and fall periods (GDD along a latitudinal gradient; see the "Materials and methods" section), which likely vary with latitude. Investigations of thermal tolerances of Atlantic sturgeon have been primarily

focused on the population in the Hudson River (Mohler[3]; Niklitschek and Secor, 2009). It is conceivable that these thresholds could vary among populations, and such differences would influence inferences made related to predictions of juvenile sizes. Still, the results of our laboratory experiments indicate that both strains experienced no growth for the thermal regime treatment that simulated the temperatures of the Saint John River at <4°C. In the Edisto River thermal regime experiment, fish were exposed briefly to 28°C, and this period coincided with a marked
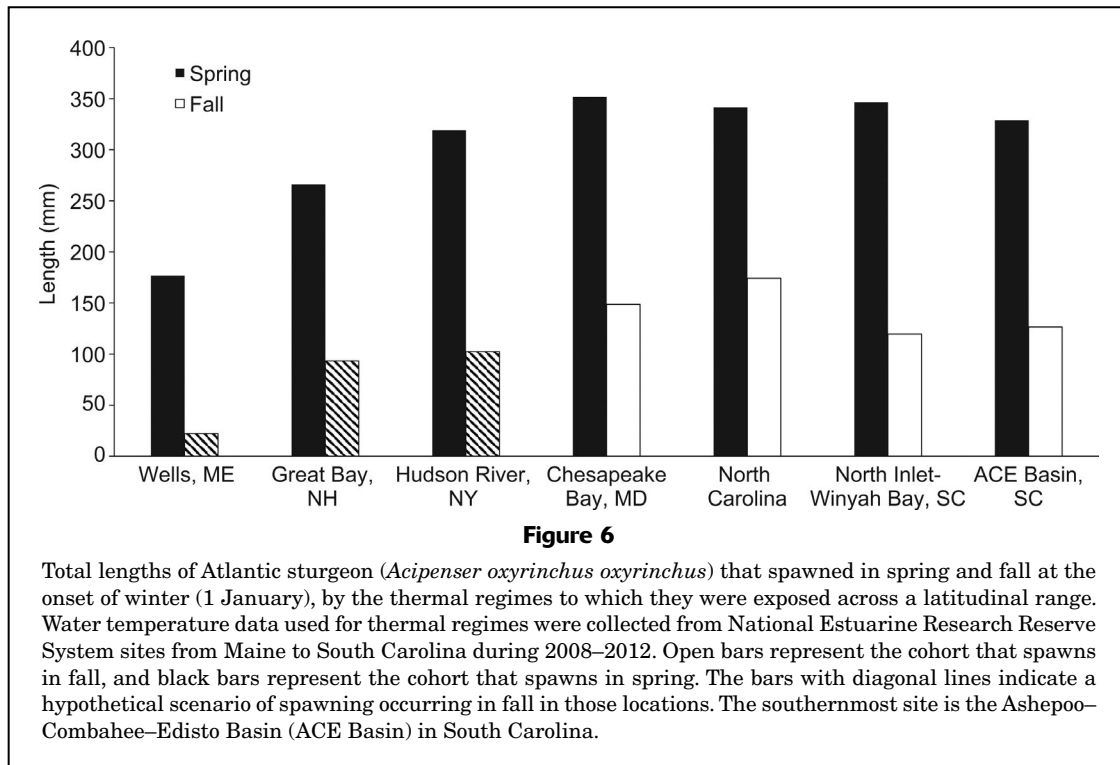
Figure 5

Monthly mean total lengths of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) that spawned in fall, across a latitudinal range during 2008–2012: (**A**) Chesapeake Bay, Maryland; (**B**) North Carolina; (**C**) the area from North Inlet to Winyah Bay, South Carolina; and (**D**) Ashepoo–Combahee–Edisto Basin, South Carolina. Error bars indicate standard deviations.

decline in growth. Early termination of the Saint John River treatment constrained analysis on growth under this temperature regime, although results support the notion that the Saint John River strain performed similarly to the Altamaha River strain. Still, having measurements of growth over an entire year's thermal regime, starting at hatch, would improve the model used in determining size at the age of 1.0 year.

Reported ranges of juvenile sizes are highly variable across systems without a strong latitudinal trend. In part, this high variation relates to not knowing the exact age of juveniles, which is typically assigned according to size alone. Because collections occur in different seasons (spring, summer, and fall), sometimes without knowledge of spawning (spring or fall) cohort, ages may vary between 0.5 and 1.9 years. Indeed, discerning length thresholds for age-0 juveniles is a priority in surveys of Atlantic sturgeon (ASMFC, 2017), and for this priority, GDD growth predictions have application. The predicted lengths of age-1 sturgeon generally fell within the range reported in literature for age-1 Atlantic sturgeon, supporting the approach used in our study (Table 5). As expected, the predicted sizes at the age of 1.0 year indicate a strong latitudinal pattern across systems, whereas observed lengths do not. Further, the GDD model—if credible—can be used to predict juvenile age and hatch date period.

In conclusion, populations of Atlantic sturgeon in the Saint John River and the Altamaha River did not differ in their capacity for growth in thermal regimes that represented the latitudinal range of this subspecies. The results of comparisons of GDDs, as a measure of growth performance, among systems corroborate the observation of dual-season spawning in systems from Chesapeake Bay to South Carolina and provide a rationale for why this behavior may not occur in the more northern and extreme southern systems of the range. Accumulated GDDs can be used to predict lengths at date to improve assessments of juvenile occurrence and production. Further, juvenile growth performance associated with dual-season spawning can be forecast under different climate change scenarios by using the GDD model.

Acknowledgments

Figure 6

Total lengths of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) that spawned in spring and fall at the onset of winter (1 January), by the thermal regimes to which they were exposed across a latitudinal range. Water temperature data used for thermal regimes were collected from National Estuarine Research Reserve System sites from Maine to South Carolina during 2008–2012. Open bars represent the cohort that spawns in fall, and black bars represent the cohort that spawns in spring. The bars with diagonal lines indicate a hypothetical scenario of spawning occurring in fall in those locations. The southernmost site is the Ashepoo–Combahee–Edisto Basin (ACE Basin) in South Carolina.

Literature cited

ASMFC (Atlantic States Marine Fisheries Commission).
    2017. 2017 Atlantic sturgeon benchmark stock assessment and peer review report, 368 p. Atlantic States Mar. Fish. Comm., Arlington, VA. [Available from website.]

Balazik, M. T., and J. A. Musick.
    2015. Dual annual spawning races in Atlantic sturgeon. PLoS ONE 10(5):e0128234. Crossref

Balazik, M. T., G. C. Garman, J. P. Van Eenennaam, J. Mohler, and L. C. Woods III.
    2012. Empirical evidence of fall spawning by Atlantic sturgeon in the James River, Virginia. Trans. Am. Fish. Soc. 141:1465–1471. Crossref

Brown, E. E., H. Baumann, and D. O. Conover.
    2012. Absence of countergradient and cogradient variation in an oceanic silverside, the California grunion *Leuresthes tenuis*. Mar. Ecol. Prog. Ser. 461:175–186. Crossref

Collins, M. R., T. I. J. Smith, W. C. Post, and O. Pashuk.
    2000. Habitat utilization and biological characteristics of adult Atlantic sturgeon in two South Carolina rivers. Trans. Am. Fish. Soc. 129:982–988. Crossref

Conover, D. O.
    1992. Seasonality and the scheduling of life history at different latitudes. J. Fish Biol. 41(sB):161–178. Crossref

Conover, D. O., and T. M. C. Present.
    1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. Oecologia 83: 316–324. Crossref

Conover, D. O., J. J. Brown, and A. Ehtisham.
    1997. Countergradient variation in growth of young striped bass (*Morone saxatilis*) from difference latitudes 1. Can. J. Fish. Aquat. Sci. 54:2401–2409. Crossref

Conover, D. O., T. A. Duffy, and L. A. Hice.
    2009. The covariance between genetic and environmental influences across ecological gradients: reassessing the evolutionary significance of countergradient and cogradient variation. Ann. N.Y. Acad. Sci. 1168:100–129. Crossref

Crossman, J. A., P. S. Forsythe, E. A. Baker, and K. T. Scribner.
    2009. Overwinter survival of stocked age-0 lake sturgeon. J. Appl. Ichthyol. 25:516–521. Crossref

Dovel, W. L., and T. J. Berggren.
    1983. Atlantic sturgeon of the Hudson estuary, New York. New York Fish Game J. 30(2):140–172.

Farrae, D., P. M. Schueller, and D. L. Peterson.
    2009. Abundance of juvenile Atlantic sturgeon in the Ogeechee River, Georgia. Proc. Annu. Conf. SEAFWA 63:172–176.

Farrae, D. J., W. C. Post, and T. L. Darden.
    2017. Genetic characterization of Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus*, in the Edisto River, South Carolina and identification of genetically discrete fall and spring spawning. Conserv. Genet. 18:813–823. Crossref

Federal Register.
    2012a. Endangered and threatened wildlife and plants; threatened and endangered status for distinct population segments of Atlantic sturgeon in the Northeast Region. Fed. Regist. 77:5880–5912. [Available from website.]
    2012b. Endangered and threatened wildlife and plants; final listing. Determinations for two distinct population segments of Atlantic sturgeon (Acipenser oxyrinchus oxyrinchus) in the Southeast. Fed. Regist. 77:5914–5982. [Available from website.]

Fritts, M. W., C. Grunwald, I. Wirgin, T. L. King, and D. L. Peterson.
    2016. Status and genetic character of Atlantic sturgeon in the Satilla River, Georgia. Trans. Am. Fish. Soc. 145: 69–82. Crossref

Garvey, J. E., and E. A. Marschall.
   2003. Understanding latitudinal trends in fish body size through models of optimal seasonal energy allocation. Can. J. Fish. Aquat. Sci. 60:938–948. Crossref

Gross, M. R., J. Repka, C. T. Robertson, D. H. Secor, and W. Van Winkle.
   2002. Sturgeon conservation: insights from elasticity analysis. Am. Fish. Soc. Symp. 28:13–30.

Hager, C., J. Kahn, C. Watterson, J. Russo, and K. Hartman.
   2014. Evidence of Atlantic sturgeon spawning in the York River system. Trans. Am. Fish. Soc. 143:1217–1219. Crossref

Hilton, E. J., B. Kynard, M. T. Balazik, A. Z. Horodysky, and C. B. Dillman.
   2016. Review of the biology, fisheries, and conservation status of the Atlantic sturgeon, (*Acipenser oxyrinchus oxyrinchus* Mitchill, 1815). J. Appl. Ichthyol. 32(S1):30–66. Crossref

Humphrey, J., M. J. Wilberg, E. D. Houde, and M. C. Fabrizio.
   2014. Effects of temperature on age-0 Atlantic menhaden growth in Chesapeake Bay. Trans. Am. Fish. Soc. 143: 1255–1265. Crossref

Hurst, T. P.
   2007. Causes and consequences of winter mortality in fishes. J. Fish Biol. 71:315–345. Crossref

Hurst, T. P., and D. O. Conover.
   2003. Seasonal and interannual variation in the allometry of energy allocation in juvenile striped bass. Ecology 84:3360–3369. Crossref

Ingram, E. C., and D. L. Peterson.
   2016. Annual spawning migrations of adult Atlantic sturgeon in the Altamaha River, Georgia. Mar. Coast. Fish. 8: 595–606. Crossref

Jonsson, B., T. Forseth, A. J. Jensen, and R. F. Næsje.
   2001. Thermal performance in juvenile Atlantic salmon, *Salmo salar* L. Funct. Ecol. 15:701–711. Crossref

Markin, E.
   2017. Atlantic sturgeon growth responses to dual seasonal spawning, latitudinal thermal regimes, and Chesapeake Bay environmental stressors. Ph.D. diss., 223 p. Univ. Maryland, College Park, MD. [Available from website.]

McCord, J. W., M. R. Collins, W. C. Post, and T. I. J. Smith.
   2007. Attempts to develop an index of abundance for age-1 Atlantic sturgeon in South Carolina, USA. Am. Fish. Soc. Symp. 56:397–403.

Najjar, R. G., C. R. Pyke, M. B. Adams, D. Breitburg, C. Hershner, M. Kemp, R. Howarth, M. R. Mulholland, M. Paolisso, D. Secor, et al.
   2010. Potential climate-change impacts on the Chesapeake Bay. Est. Coast. Shelf Sci. 86:1–20. Crossref

Neuheimer, A. B., and C. T. Taggart.
   2007. The growing degree-day and fish size-at-age: the overlooked metric. Can. J. Fish. Aquat. Sci. 64:375–385. Crossref

Niklitschek, E. J., and D. H. Secor.
   2005. Modeling spatial and temporal variation of suitable nursery habitats for Atlantic sturgeon in the Chesapeake Bay. Est. Coast. Shelf Sci. 64:135–148. Crossref
   2009. Dissolved oxygen, temperature and salinity effects on the ecophysiology and survival of juvenile Atlantic sturgeon in estuarine waters: I. laboratory results. J. Mar. Biol. Ecol. 381(Suppl.):150–160. Crossref

Peterson, D. L., M. B. Bain, and N. Haley.
   2000. Evidence of declining recruitment of Atlantic sturgeon in the Hudson River. North Am. J. Fish. Manage. 20: 231–238. Crossref

Peterson, D. L., P. Schueller, R. DeVries, J. Fleming, C. Grunwald, and I. Wirgin.
   2008. Annual run size and genetic characteristics of Atlantic sturgeon in the Altamaha River, Georgia. Trans. Am. Fish. Soc. 137:393–401. Crossref

Pörtner, H. O., and M. A. Peck.
   2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. J. Fish Biol. 77: 1745–1779. Crossref

Power, M., and R. S. McKinley.
   1997. Latitudinal variation in lake sturgeon size as related to the thermal opportunity for growth. Trans. Am. Fish. Soc. 126:549–558. Crossref

Puckett, B. J., D. H. Secor, and S-J. Ju.
   2008. Validation and application of lipofuscin-based age determination for Chesapeake Bay blue crabs. Trans. Am. Fish. Soc. 137:1637–1649. Crossref

Purchase, C. F., and J. A. Brown.
   2001. Stock-specific changes in growth rates, food conversion efficiencies, and energy allocation in response to temperature change in juvenile Atlantic cod. J. Fish Biol. 58: 36–52. Crossref

R Core Team.
   2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available from website, accessed October 2016.]

Savoy, T., L. Maceda, N. K. Roy, D. Peterson, and I. Wirgin.
   2017. Evidence of natural reproduction of Atlantic sturgeon in the Connecticut River from unlikely sources. PLoS ONE 12(4):e0175085. Crossref

Schueller, P., and D. L. Peterson.
   2010. Abundance and recruitment of juvenile Atlantic sturgeon in the Altamaha River, Georgia. Trans. Am. Fish. Soc. 139:1526–1535. Crossref

Schultz, E. T., and D. O. Conover.
   1997. Latitudinal differences in somatic energy storage: adaptive responses to seasonality in an estuarine fish (Atherinidae: *Menidia mendia*). Oecologia 109:516–529. Crossref

Schultz, E. T., K. E. Reynolds, and D. O. Conover.
   1996. Countergradient variation in growth among newly hatched *Fundulus heteroclitus*: geographic differences revealed by common-environment experiments. Funct. Ecol. 10:366–374.

Secor, D. H., T. E. Gunderson, and K. Karlsson.
   2000. Effect of temperature and salinity on growth performance in anadromous (Chesapeake Bay) and nonanadromous (Santee-Cooper) strains of striped bass *Morone saxatilis*. Copeia 2000:291–296.

Secor, D. H., P. J. Anders, W. Van Winkle, and D. A. Dixon.
   2002. Can we study sturgeons to extinction? What we do and don't know about the conservation of North American sturgeons. Am. Fish. Soc. Symp. 28:3–10.

Shuter, B. J., A. G. Finstad, I. P. Helland, I. Zweimüller, and F. Hölker.
   2012. The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. Aquat. Sci. 74:637–657. Crossref

Smith, J. A., H. J. Flowers, and J. E. Hightower.
   2015. Fall spawning of Atlantic sturgeon in the Roanoke River, North Carolina. Trans. Am. Fish. Soc. 144:48–54. Crossref

Smith, T. I. J., D. E. Marchette, and G. D. Ulrich.
   1984. The Atlantic sturgeon fishery in South Carolina. North Am. J. Fish. Manage. 4:164–176. Crossref

Stewart, N. D., M. J. Dadswell, P. Leblanc, R. G. Bradford, C. Ceapa, and M. J. W. Stokesbury.
   2015. Age and growth of Atlantic sturgeon from the Saint John River, New Brunswick, Canada. North Am. J. Fish. Manage. 35:364–371. Crossref

Yamahira, K., and D. O. Conover.
   2002. Intra- vs. interspecific latitudinal variation in growth: adaptation to temperature of seasonality? Ecology 83: 1252–1262. Crossref