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Temperature affects transition timing and phenotype between key developmental stages in white sturgeon *Acipenser transmontanus* yolk-sac larvae

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Abstract Temperature differentially influences developmental trajectories of traits during early life stages that can affect survival and recruitment. Experiments were conducted to quantify temperature-induced developmental responses of White Sturgeon (*Acipenser transmontanus*) yolk-sac larvae (YSL) reared at temperatures encountered across the species' range (12.5, 14.0, 15.5, and 17.0 °C). We quantified effects of temperature on timing of transitions between sequential developmental stages from hatch to initiation of exogenous feeding. Rate of development significantly increased at warmer compared to cooler temperatures; no significant difference was observed between 15.5 and 17.0 °C or 12.5 and 14.0 °C. When standardized by relative timing of development (RT_i), developmental rate was not significantly different among treatments. Morphological traits (total length; body area; yolk-sac area; head area; gill filament area; mouth area; pectoral fin area) were measured daily, though only data for YSL reared at 12.5 and 17.0 °C was used to quantify phenotypic variation. Morphological traits (excluding yolk-sac area) were generally larger 48+ hours post hatch for YSL reared at 17. 0 °C compared to 12.5 °C. In contrast, these same traits, with the exception of gill filament area, were larger in 12.5 °C reared YSL when considered as a function of developmental stage. These opposing results suggest trade-offs associated with allocating resources to a particular trait depended on rearing temperature. Our results provide the ability to estimate timing of critical early life stages (i.e., hatch, emergence) as a function of temperature which is an important management tool to understand how early life development contributes to recruitment processes and adaptability in thermally altered systems.

Keywords Temperature · Developmental stage · Yolk-sac larvae · White sturgeon · Phenotype · Transition

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Introduction

Temperature induced developmental responses have a significant influence on traits associated with timing of life-stage transitions, and survival of fishes during early ontogeny (Morbey and Ydenberg 2003). High rates of mortality during early life stages can result from limited capacity to effectively swim, avoid predators, and respond to variation in the surrounding environment (Killgore et al. 1987; Rice et al. 1987; Miller et al. 1988; Shepherd et al. 2000). During this critical period, temperature is an important environmental factor, with effects on traits (e.g., body length and timing of

emergence) particularly pronounced under extreme thermally deviant conditions (Dammerman et al. 2016).

Most aquatic ectotherms experience changes in temperature regimes relative to historical or associated with changing climate or other human-related activities (Ficke et al. 2007). Altered thermal regimes are known to significantly affect growth and reproduction (Hill and Magnuson 1990; Angilletta et al. 2008; Donelson et al. 2010; Pankhurst and Munday 2011). For example, during early ontogenetic stages in fish, warmer temperatures can lead to more rapid absorption of yolk-sac reserves (Hardy and Litvak 2004), earlier onset of first feeding (Wang et al. 1987; Pepin et al. 1997; Hardy and Litvak 2004), increased growth and developmental rates (Wang et al. 1985; Pelosi et al. 1993; Atkinson 1994; Hansen and Falk-Peterson 2002), decreased size at hatch (Laurel and Blood 2011; Ojanguren and Brana 2003), and a higher incidence of deformities (Lahnsteiner et al. 2012). Understanding the effects of temperature during early ontogenetic stages is important when characterizing and interpreting data regarding rates of embryo and larval development, recruitment patterns, and projecting species' capacity to adapt to variable environmental conditions.

White Sturgeon *Acipenser transmontanus* is a species of conservation concern, with many populations experiencing recruitment failure (Jager et al. 2001; Anders et al. 2002; McAdam et al. 2005; Hildebrand et al. 2016). Many sturgeon populations reside in aquatic systems that are highly altered due to river regulation, where impacts to physcial habitat attributes like temperature regimes have occured (Hildebrand et al. 2016). Altered temperature regimes have been shown to influence sturgeon populations by increasing variance in phenotypic traits (e.g., body length; Dammerman et al. 2016), delaying initiation of spawning behaviour (Paragamian and Wakkinen 2002), impeding development and growth (Parsley et al. 2011; Kappenman et al. 2013), bioenergetic alterations (Mayfield and Cech 2004), and increasing rates of mortality (Chapman and Carr 1995; Van Eenennaam et al. 2005). Studies on White Sturgeon development during early life stages have largely focused on descriptions of embryonic and larval development associated with aquacultural settings (Beer 1981; Dettlaff et al. 1993; Conte et al. 1988). While rates of development and phenotypic trait variation associated with sequential developmental stages have been described for many sturgeon species (e.g., Dettlaff et al. 1993), no work has been conducted beyond the embryonic stage comparing rates of development and phenotypic trait variation across temperatures.

We hypothesized that development of yolk-sac larvae (YSL) is delayed in cooler water temperatures, and this delay is further pronounced at the period of transition between key stages and in the change in morphological traits over time. We tested this hypothesis by 1) quantifying and comparing the developmental rates of White Sturgeon YSL exposed to different temperatures during incubation and post-hatch rearing prior to initiation of exogenous feeding, and 2) quantifying variance in seven larval morphological traits associated with different incubation and rearing temperatures to determine the effects of temperature on growth. Describing thermally induced responses in the development of White Sturgeon is important to understanding factors limiting recruitment processes and adaptability in anthropogenically altered systems.

Methods

Gamete collection and fertilization

Adult White Sturgeon were captured in June 2012, from the upper Columbia River in Canada between Hugh Keenleyside Dam and the Canada/USA border (BC Hydro 2015). Fish in spawning condition were transported to the Kootenay Trout Hatchery, Forte Steele, British Columbia. Two females (fork length and weight; F1: 202 cm, 69 kg; F2: 209 cm, 77 kg) and two males (M1: 191 cm, 60 kg; M2: 197 cm, 62 kg) were artificially induced for gamete collection. Approximately 12,000 eggs (estimated by subsampling a known volume of eggs) were collected from each female and fertilized following methods described by Conte et al. (1988) using 15 °C water. Each female was crossed with one different male to produce two full-sibling families. Fertilized eggs were transferred to family-specific hatching jars (MacDonald Type; J30, Dynamic Aqua-Supply Ltd., Surrey, BC) for incubation with the entire process taking approximately 90 min.

Experimental treatments

Experimental treatments included rearing White Sturgeon embryos and YSL at constant water temperatures (± 0.2 °C) of 12.5 °C, 14.0 °C, 15.5 °C and

17.0 °C. Embryos are referred to the period of incubation from fertilization through to hatch and YSL refers to the period following hatch to the onset of exogenous feeding. Temperature treatments were developed based on conditions measured at White Sturgeon spawning, incubation and early rearing sites in the upper Columbia River (Golder Associates Ltd. 2009; Terraquatic 2011; AMEC 2014), other White Sturgeon inhabited rivers (Fraser River; Perrin et al. 2003; Kootenai River; Paragamian et al. 2001), and previous studies investigating the effects of temperature on embryotic development (Wang et al. 1985; Parsley et al. 2011). Both ambient (10.0 °C) and heated (17.0 °C) groundwater were supplied to each treatment with adjustable valves to maintain experimental temperatures throughout the experiment. Temperatures were manually measured four times per day using a thermometer and necessary adjustments were made. VEMCO Minilog-II T temperature loggers (Bedford, Nova Scotia) recorded hourly temperatures within each treatment tank throughout the experiment.

Immediately following fertilization, approximately 3000 embryos per family were incubated for each of the four temperature treatments in family specific hatching jars. When placed in the hatching jars, embryos were acclimated from 15 °C to the temperature treatments at a rate of 1C degree/h. To ensure adequate embryo separation and oxygenation, water flow was maintained at 8 L min^{-1} and raised to 12 L min^{-1} following neurulation (transformation of the neural plate into the neural tube) (FFSBC 2013). To allow for natural rates of development, we limited handling of individuals throughout the experiment. At the embryo stage, survival to neurulation was estimated by randomly sampling 100 embryos once in each hatching jar and survival was then assumed to be constant until hatch (Dettlaff et al. 1993). Time to hatch was recorded for each treatment when approximately 50% of embryos were observed to have hatched. Changes in development during the incubation period were not measured as they have been reported previously for these thermal regimes (Wang et al. 1985; Parsley et al. 2011).

Upon hatching, YSL were passed on their own volition from the hatching jars into treatment and family specific rearing troughs (152.4 × 76.2 × 20.3 cm; L x W X H) with water levels of 10 cm depth (water volume of 116,128 cm^3). Given volitional transfer and the intent to limit handling to only specific collection intervals, the number of hatched YSL was not counted, and therefore survival to hatch and during larval development could not be evaluated across treatments. However, each rearing trough contained a maximum larval density of 0.02 individuals/cm^3 of water based on starting numbers of embryos and survival to neurulation. Density was controlled to allow for adequate sample size but remain sufficiently low to reduce potential confounding effects of density on growth or size-at-age. Following hatch, water flows were reduced (10 L min^{-1}) to exchange rearing trough water at least twice per hour. YSL exhibit negative phototaxis (Conte et al. 1988), therefore all rearing troughs were covered with dark plastic sheets to eliminate effects of overhead light. Additionally, troughs were supplied with artificial substrate (2.5 cm diameter sinking Bio-Spheres; Dynamic Aqua-Supply Ltd. Surrey, BC) allowing YSL to utilize interstitial spaces to reduce energy consumption instead of searching for cover, which has been shown to reduce growth (McAdam 2011; Boucher et al. 2014). Since the experiment was terminated prior to the release of the yolk plug and onset of exogenous feeding (Stage 45), YSL were not provided a food source during the experiment.

Sampling and developmental staging

Ten YSL per treatment were sampled when observations of approximately 50% of embryos had hatched within a hatching jar (time zero) and every 12 h thereafter until complete yolk-sac absorption. Based on previous studies (Beer 1981; Wang et al. 1985; Dettlaff et al. 1993), 12 h was assumed to be a sufficient sampling interval to record all developmental stages. For each sampling interval, accumulated thermal units (ATU; °C•d; Rombough 1985) was also recorded; where one thermal unit is accumulated by a specimen held in water of 1 °C for 24 h and is additive for every additional 24 h period (hatch was assigned 0 ATU). Due to the effects of temperature on developmental rate, number of sampling intervals varied between treatments (e.g., 28 vs. 14 sampling intervals for 12.5 and 17.0 °C, respectively). Specimens were euthanized by anaesthetic overdose (tricaine methanesulfonate [MS-222], 1 g/l) and preserved in Prefer buffer (solution of glyoxcal,

buffer and ethanol; Anatech Ltd. Battle Creek MI, USA). Preserved samples were examined using a digital compound microscope (Nikon SMZ-745 t Stereo Microscope with 10X eyepiece) and assigned a developmental stage. Stage designation corresponded to the classification by Dettlaff et al. (1993), with the following traits easily observed: stage 36 – hatch; 37 – pectoral fin rudiment, opening of mouth; 38 – gill filament rudiments; 39 – digestive system rudiment divides into stomach and intestine; 40 – ventral fin rudiment; 41 – liver subdivided; 42 – complete liver division, pyloric appendage rudiment; 43 – ventral fin extends to preanal fin fold margin; 44 – complete yolk-sac absorption.

The proportional time (HPH) to transition to a given stage relative to the total required time to develop to stage 44 (hatch to end of study) was estimated following the formula (Klimogianni et al. 2004):

$$RT_i = \left(\frac{t_i}{TSD}\right)$$

where RT_i is the relative time of total development (as a proportion), t_i was the time interval (HPH) from t_0 (hatch) to initial occurrence of developmental stage i, and TSD was total duration of the YSL period (stage 36, hatch, to 44, prior to initiation of exogenous feeding). A table including the initial occurrence of each developmental stage for all temperature treatments and both units of measure (HPH and ATU) was constructed to provide a tool for estimating time of development for YSL of unknown age (Table 2).

Morphological traits

Photographs of preserved YSL were taken from the time of hatch to the end of the experiment at 24-h intervals (starting at t_0) for analysis of seven morphological traits. Photographs were taken using a camera adaptor (DS-2Mv colour non-cooled digital camera head) on a digital compound microscope. YSL were placed in a petri dish with a ruler (mm) and morphological traits were measured to the nearest 0.01 mm using the program ImageJ (Schneider et al. 2012; version 1.43r, Bethesda). We only analyzed traits of individuals of both families reared at temperatures of 12.5 °C and 17.0 °C due to the number of photographs required ($N = 2922$).

Traits examined included total length (TL; mm), body area (BA; mm^2), yolk sac area (YSA; mm^2), head area (HA; mm^2), mouth area (MA; mm^2), pectoral fin area (PFA; mm^2), and gill filament area (GFA; mm^2). HA was measured as the lateral area of the head from tip of snout to posterior margin of operculum (Fig. 1a). MA was measured following the inner margin of the mouth opening; the mouth was not forced open prior to measurement (Fig. 1b). PFA measured the ventral surface area of the right pectoral fin (Fig. 1c). GFA measured the lateral area of all developed gill filaments (Fig. 1d). GFA was not measured after stage 41 due to operculum growth over gill filaments. Morphological traits of TL, BA, HA, PA, GFA and YSA were measured parallel to the sagittal (longitudinal) axis of the body, and MA was measured perpendicular to this axis. Each trait was measured twice for each specimen by a single technician and the mean was used. If the examined morphological trait was damaged, the photograph was discarded.

Statistical analysis

All analyses were performed using the statistical software "R" (version 3.0.3, R Development Core Team 2011; http://www.r-project.org). Given the experiment only included two maternal families, family was included as a replicate and family effects on developmental rate and growth of morphological traits were not investigated. Developmental rate of YSL was quantified as a function of temperature by fitting a least squares regression. This relationship between developmental stage i and measured transition to developmental stage i was calculated individually for each HPH, ATU and RT_i measuring unit. Temperature was applied as a fixed, categorical variable as it remained constant under each treatment. Analysis of variance (ANOVA) was used to test for differences in rate of stage transition among all temperature treatments measured in HPH, ATU and RT_i. All pairwise comparisons were made using a post hoc Tukey's HSD test.

To quantify variance in size of each morphological trait associated with different temperature treatments, a Student's t test was applied to determine the effects of temperature on growth. Comparisons were made between the two temperatures treatments of 12.5 °C and 17.0 °C at each 24-h period, and each developmental stage. Again, temperature was treated as a categorical variable. Morphological traits could not be compared as a function of ATU since trait measurements were not recorded based on specific ATU values.

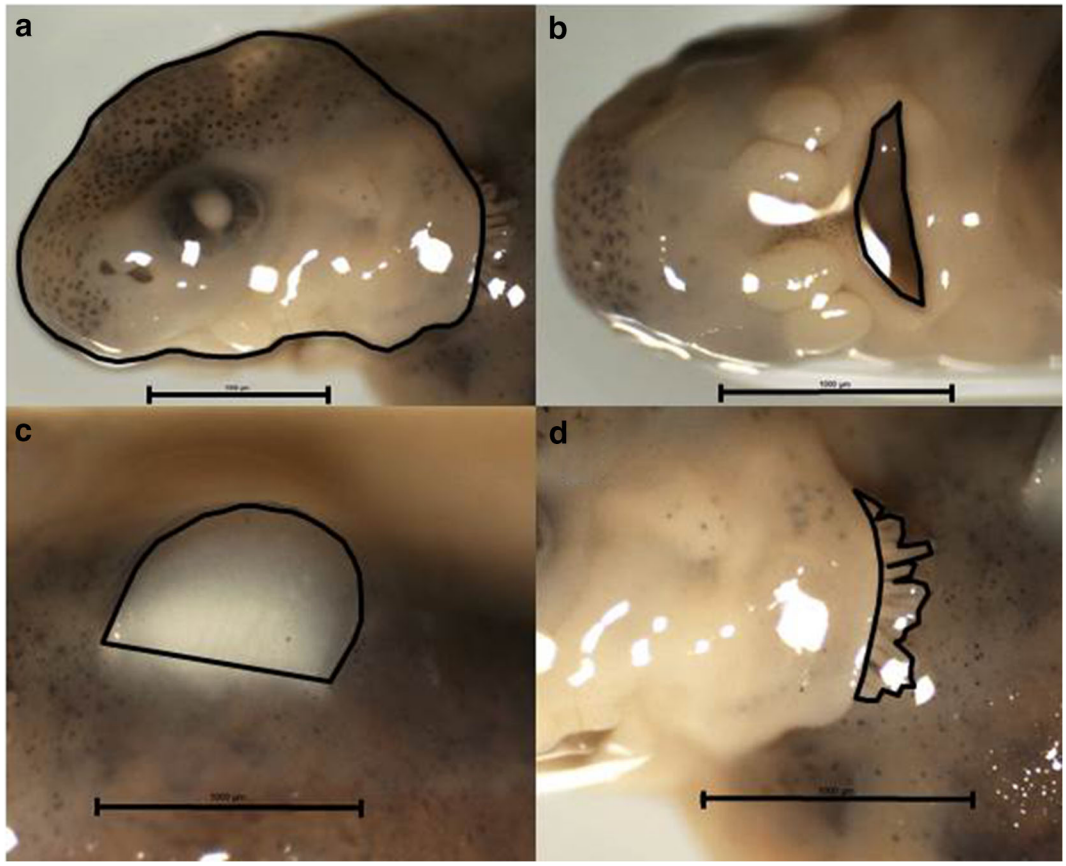


Fig. 1 Yolk sac larval White Sturgeon morphological trait measurements including: **a** - head area (HA; mm^2); **b** - mouth area (MA; mm^2); **c** - pectoral fin area (PFA; mm^2); and **d** - gill filament area (GFA; mm^2). HA was measured as the lateral area of the head from tip of snout to posterior margin of operculum. MA was measured following the inner margin of the mouth opening. PFA was measured the ventral surface area of the right pectoral fin. GFA was measured the lateral area of all developed gill filaments. All scales represent 1 mm

Results

Developmental staging

Embryonic survival to neurulation and time to hatch (hours and ATU) varied among temperature treatments and between families (Table 1). Temperature affected the rate of stage transition in YSL as a function of both time (HPH) and ATU (Table 2 and Fig. 2) For example, time to attain stage 44 was 324–336 HPH (168.8–175.0 ATU) at 12.5 °C, 264 HPH (154.0 ATU) at 14.0 °C, 192 HPH (124.0 ATU) at 15.5 °C, and 156–168 HPH (110.5–119.0 ATU) at 17.0 °C. In terms of RT_i, rate of stage transition appeared independent of temperature treatments (Table 3). The regression analyses showed a good fit for developmental rate for each temperature treatment (12.5 °C, $R^2 = 0.916$; 14.0 °C, $R^2 = 0.940$; 15.5 °C, $R^2 = 0.938$; 17.0 °C, $R^2 = 0.960$; Table 4).

The rate of stage transition increased significantly with increased temperatures as a function of time (Table 4), with the exception of the 14.0 °C and 12.5 °C comparison (Tukey's HSD, $P = 0.08$). As a function of ATU, the rate of stage transition was significantly greater at higher temperatures (Table 4), however no difference was found between 17.0 °C and 15.5 °C (Tukey's HSD, $P = 0.322$), or between 14.0 °C and 12.5 °C (Tukey's HSD, $P = 0.228$). In terms of RT_i, rate of stage transition was not significantly different between the temperature rearing conditions (Table 4).

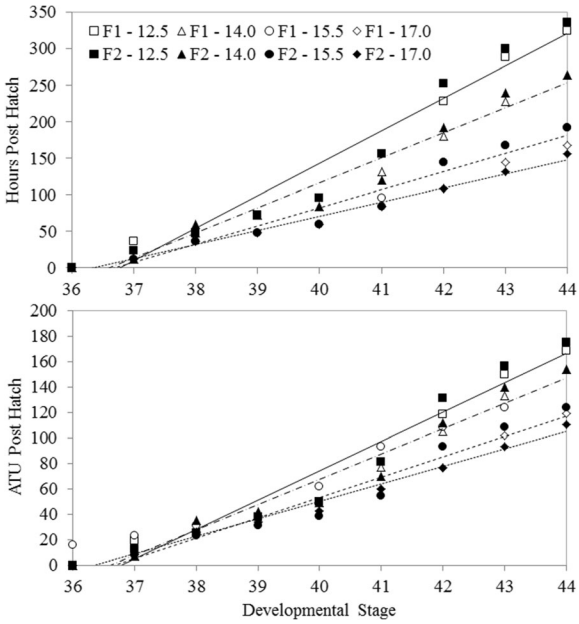


Fig. 2 White Sturgeon yolk-sac larvae (YSL) developmental stage transitions in time series (hours post hatch) and accumulated thermal units (ATU) for each family (F1 and F2) and experimental temperature treatment: of 12.5 °C (solid line; $R^2 = 0.916$), 14.0 °C (broken line; $R^2 = 0.940$), 15.5 °C (dashed line; $R^2 = 0.938$), and 17.0 °C (dotted line; $R^2 = 0.960$)

Morphological traits

At hatch, fish reared in 12.5 °C were larger, but not significantly, when compared to fish reared in 17.0 °C across all morphological traits measured as a function of days post hatch (DPH; Student's *t* test; BA, $P = 0.5254$; GFA, $P = 0.350$; HA, $P = 0.875$; TL, $P = 0.343$; MA, $P = 0.666$; PFA, $P = 0.078$; YSA, $P = 0.716$; left panels of Fig. 3). Student's *t*-tests found significant differences in size at hatch as a function of developmental stage for BA ($P = 0.0087$), HA ($P = 0.039$), TL (P = 0.008), and PFA ($P = 0.001$) but not in GFA ($P = 0.658$), MA ($P = 0.951$), and YSA ($P = 0.830$) (right panels of Fig. 3).

Morphological traits, excluding YSA, were generally larger across developmental stages (DPH) in fish reared at 17.0 °C than at rearing temperature of 12.5 °C after 1 DPH (significant difference found at: BA, 3 to 9 DPH, $P = 0.006$; GFA, 2 to 4 DPH, $P < 0.0001$; HA, 1 to 9 DPH, $P = 0.036$; TL, 1 to 9 DPH, $P = 0.016$; MA, 2 to 9 DPH, $P < 0.0001$; PFA, 2 to 9 DPH, $P < 0.0001$; Fig. 3). In contrast, as a function of developmental stage, morphological traits of BA, HA, TL, MA, and PFA were generally larger for fish reared at 12.5 °C compared to 17.0 °C reared fish beyond stage of 38 (significant difference found at: BA, stage 41 to 44, $P < 0.010$; HA, stage 41 to 44, $P < 0.005$; TL, stage 42 to 44, $P < 0.0001$; MA, stage 41 to 44, $P < 0.002$; PFA, stage 41 to 44, $P < 0.002$; Fig. 3). Gill filament areas of YSL were larger across developmental stages when reared at 17.0 °C compared to 12.5 °C (e.g., stage 39 to 40, $P < 0.010$; Fig. 3). YSA was smaller over time for individuals reared at 17.0 °C (significant difference at 2 to 9 DPH, $P < 0.0001$), however, YSA was smaller for fish reared at 12.5 °C as a function of developmental stage (significant difference at stages 39 and 43, $P < 0.040$).

Discussion

This is the first study to show temperature-mediated effects on trait development in White Sturgeon YSL. Further, we compared three methods that characterize developmental trajectories of White Sturgeon during early ontogenic stages and allowed for the evaluation

Table 1 Embryo survival to neurulation, hours to hatch and accumulative thermal units (ATU) to hatch for each family (1 and 2) and temperature treatment. Survival to neurulation was estimated by randomly sampling 100 embryos in each hatching jar; experimental design excluded survival to hatch. Time to hatch was estimated by observation of approximately 50% of embryos hatched within a hatching jar

Incubation temperature	Survival to neurulation		Hours to hatch		ATU to hatch	
	1	2	1	2	1	2
12.5 °C	0.61	0.96	240	240	125	125
14.0 °C	0.79	0.96	192	200	112	117
15.5 °C	0.79	0.94	168	171	109	110
17.0 °C	0.66	0.97	144	152	102	108

Table 2 White Sturgeon yolk-sac larvae (YSL) developmental stage transitions in time series (hours post hatch) and accumulated thermal units (ATU) at experimental temperature treatments for two family groups reared at 12.5 °C, 14.0 °C, 15.5 °C, and 17.0 °C. This table is intended as a management field tool for estimating time of development for YSL of unknown age; therefore, only means are reported

Developmental stage										
		36	37	38	39	40	41	42	43	44
Rearing Temperature	Family	Hours Post Hatch								
12.5 °C	1	0	36	48	72	96	156	228	288	324
	2	0	24	48	72	96	156	252	300	336
14.0 °C	1	0	12	48	72	84	132	180	228	264
	2	0	12	60	72	84	120	192	240	264
15.5 °C	1	0	24	36	48	60	96	144	168	192
	2	0	12	36	48	60	84	144	168	192
17.0 °C	1	0	12	36	48	60	84	108	144	168
	2	0	12	36	48	60	84	108	132	156
Rearing Temperature	Family	ATU Post Hatch								
12.5 °C	1	0	18.8	25.0	37.5	50.0	81.3	118.8	150.0	168.8
	2	0	12.5	25.0	37.5	50.0	81.3	131.3	156.3	175.0
14.0 °C	1	0	7.0	28.0	42.0	49.0	77.0	105.0	133.0	154.0
	2	0	7.0	35.0	42.0	49.0	70.0	112.0	140.0	154.0
15.5 °C	1	0	15.5	23.3	31.0	38.8	62.0	93.0	108.5	124.0
	2	0	7.8	23.3	31.0	38.8	54.3	93.0	108.5	124.0
17.0 °C	1	0	8.5	25.5	34.0	42.5	59.5	76.5	102.0	119.0
	2	0	8.5	25.5	34.0	42.5	59.5	76.5	93.5	110.5

of sources of variation in development across different temperatures. While trends in the rate of development were similar when developmental stage was used to standardize between temperature treatments, differences

Table 3 Mean (standard deviation; SD) proportional time to transition to a given developmental stage from hatch (RT_i;) and between consecutive stages (CS) relative to the total required time to develop to stage 44 (hatch to end of study) across two families of White Sturgeon yolk-sac larvae reared at 12.5 °C, 14.0 °C, 15.5 °C, and 17.0 °C

Rearing temperature												
	12.5 °C			14.0 °C			15.5 °C			17.0 °C		
Stage	RT_i	SD	CS	RT_i	SD	CS	RT_i	SD	CS	RT_i	SD	CS
36	0.00	(0.00)	–	0.00	(0.00)	–	0.00	(0.00)	–	0.00	(0.00)	–
37	0.09	(0.00)	0.09	0.05	(0.00)	0.05	0.09	(0.00)	0.09	0.07	(0.00)	0.07
38	0.15	(0.01)	0.06	0.20	(0.01)	0.15	0.19	(0.01)	0.10	0.22	(0.01)	0.15
39	0.22	(0.02)	0.07	0.27	(0.02)	0.07	0.25	(0.02)	0.06	0.30	(0.02)	0.08
40	0.29	(0.02)	0.07	0.32	(0.02)	0.05	0.31	(0.02)	0.06	0.37	(0.02)	0.07
41	0.47	(0.03)	0.18	0.48	(0.03)	0.16	0.47	(0.03)	0.16	0.52	(0.03)	0.15
42	0.73	(0.03)	0.26	0.70	(0.03)	0.22	0.75	(0.03)	0.28	0.67	(0.03)	0.15
43	0.89	(0.01)	0.16	0.89	(0.01)	0.19	0.88	(0.01)	0.13	0.85	(0.01)	0.18
44	1.00	(0.00)	0.11	1.00	(0.00)	0.11	1.00	(0.00)	0.12	1.00	(0.00)	0.15

Table 4 Slope (m), intercept (b) and proportion of variation explained (R^2) from linear regressions describing relationships between developmental stage and inter-stage transition measured in hours (post hatch), accumulative thermal units (ATU) and RT_i (proportional time to transition to a given developmental stage relative to the total required time to develop to stage 44) as a function of rearing temperature. Different superscripts for each slope parameter indicate significant differences ($P < 0.05$; Tukey's HSD)

Rearing temperature	m_{hours}	m_{ATU}	m_{RTi}	b	R^2
12.5 °C	0.021^a	0.040^a	6.790^a	36.882	0.916
14.0 °C	0.027^a	0.047^a	7.184^a	36.663	0.940
15.5 °C	0.038^b	0.059^b	7.337^a	36.590	0.938
17.0 °C	0.046^c	0.065^b	7.471^a	36.558	0.960

existed at key stages (liver development; following stage 40) and underline the importance of developmental staging YSL when comparing individuals across treatments within experiments and across different environmental conditions in the wild. Accordingly, we discuss our results as they relate to the two major aspects of our work; time to reach specific developmental stages and how morphological traits changed over time. We end with specific management implications and conclusions from our work.

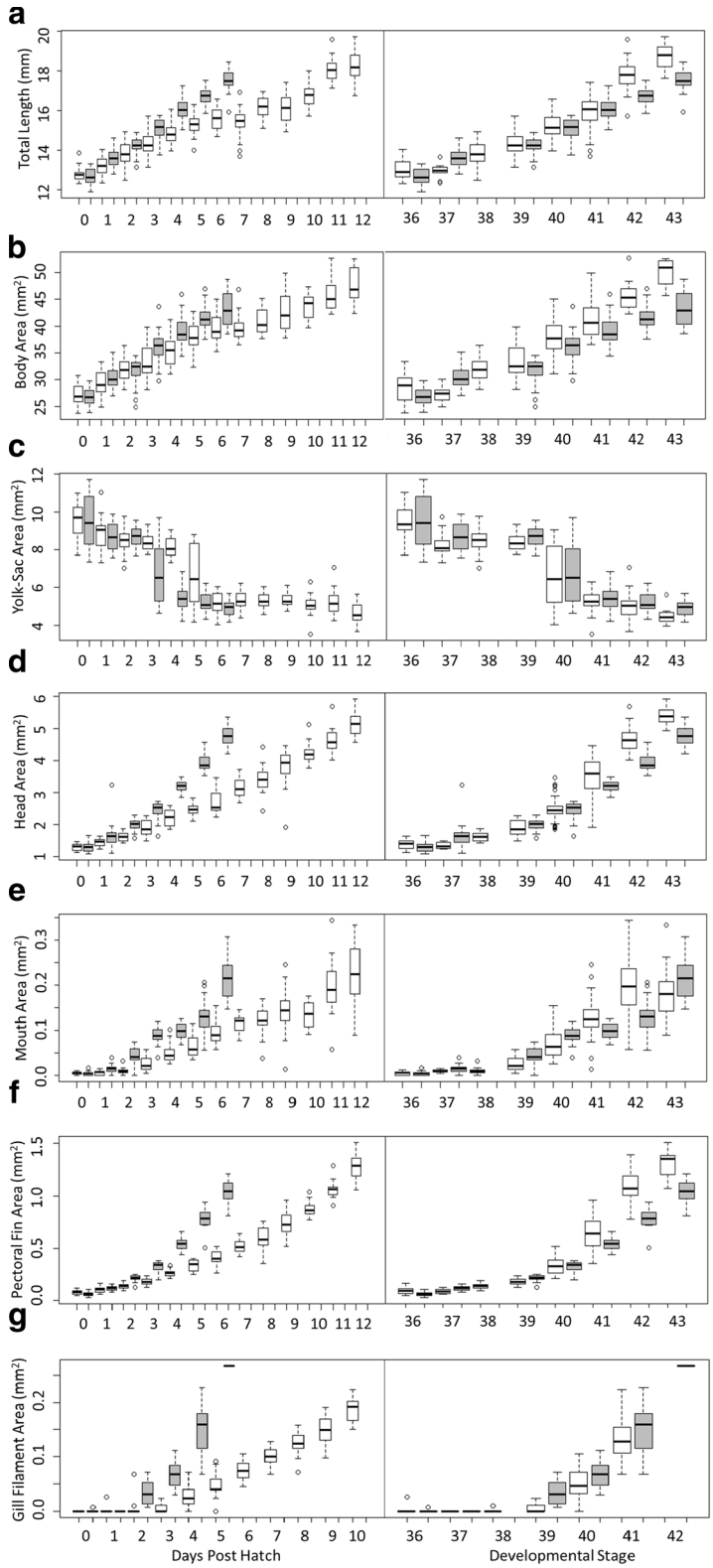
Time to reach developmental stages

The amount of time between developmental stages relative to total time of the YSL period was independent of temperature. While considerable variation between temperature rearing treatments was explained using RT_i in our study (Table 3), we found that transitions between consecutive developmental stages 40 through 43 identified by the appearance of liver subdivision and pyloric appendage rudiment were more rapid in the warmest treatment compared to all other treatments (Table 3).

Accumulated degree-days, or ATU, during rearing, is a common measure of fish development and is widely used in aquaculture to predict timing of hatching, emergence, and initiation of exogenous feeding. ATU is used to standardize development across varying rearing temperatures (Boucher et al. 2014). However, we observed differences in developmental rate as a function of ATU between the upper (15.5 °C and 17.0 °C) and lower (12.5 °C and 14.0 °C) temperature treatments. Variation between treatments increased in later stages, starting at stage 40, where a delay in developmental rate was observed, particularly in the colder treatments (Table 2). Similar trends have also been recorded during the embryo stage (Parsley et al. 2011). Importantly, evidence of developmental rate deceleration was particularly apparent in colder temperatures when development was expressed by ATU (Table 2). Delays were associated with the development of major structures in both embryo (neural tube; following stage 19; Parsley et al. 2011) and YSL (liver development; following stage 40; this study) stages. It is uncertain how this cumulative delay in embryo and YSL development will affect later life stages, though observations of ontogenetic contingency (phenotypes at the current time are conditional on environmental conditions during previous life stages; Diggle 1994) have been documented in prior studies on sturgeon (Dammerman et al. 2015, 2016).

Developmental rate was temperature dependent, decreasing significantly with colder rearing temperatures. This translates into additional time at the YSL stage for individuals reared in colder environments, extending time spent near spawning grounds or undergoing drift behaviour while underdeveloped, potentially exposing fish to additional risks. For example, spawning activity of White Sturgeon in the most upstream portions of the upper Columbia River typically begins in late July at the coldest known temperatures (9–11 °C; Amec Foster Wheeler 2018) for the species. Embryo incubation has been documented to last for 20 days at this temperature regime (Parsley et al. 2011) followed by an extended YSL development period of up to 30 days (Crossman and Hildebrand 2012) resulting in larval dispersal occurring into the early fall. This prolonged period of early development directly affects the developmental stage

Fig. 3 Measurements of morphological traits between families of White Sturgeon yolk-sac larvae reared at 12.5 °C (white) and 17.0 °C (grey) calculated as box (25%–75% quartiles) and whisker plots (95% CI). Data is shown as a function of days post hatch (left) and developmental stage (right) including: **a** total length (mm); **b** body area (mm^2); **c** yolk-sac area (mm^2); **d** head area (mm^2); **e** mouth area (mm^2); **f** pectoral fin area (mm^2); and **g** gill filament area (mm^2). Morphological traits were measured to developmental stage 43 (up to twelve days post hatch) for yolk-sac larvae reared at 17.0 °C. C. Sample size ranged for each temperature treatment as a function of developmental stage: stage 36 (n = 20–30), stage 37 (n = 10–20), stage 38 (n = 0–20), stage 39 (n = 19–20), stage 40 (n = 19–60), stage 41 (n = 19–69), stage 42 (n = 14–37), stage 43 (n = 9–20)


a
Total Length (mm)
b
Body Area (mm²)
c
Yolk-Sac Area (mm²)
d
Head Area (mm²)
e
Mouth Area (mm²)
f
Pectoral Fin Area (mm²)
g
Gill Filament Area (mm²)
Days Post Hatch
Developmental Stage

and size of individuals potentially reducing survival probabilities for individuals entering periods of slower growth (e.g., fall and winter). In this study we tested temperatures similar to the thermal maximums experienced in this population and it is uncertain how development may be influenced at higher temperatures as mortality is known to increase as temperatures approach 20 °C (Wang et al. 1985). We controlled temperature as a constant in order to partition variation in development but sturgeon have evolved to be adaptable to annual variations in spawning and incubation temperatures within and among years. Variability in temperatures experienced during incubation has been shown to have considerable effects on larval body size and aspects of development (Dammerman et al. 2016). Accordingly, the potential effects of climate change on stream temperatures and variability in patterns among years, especially in regulated rivers, represents an important area of further early life history research for sturgeons.

Our study extends previous research examining YSL development in sturgeon species (Lake Sturgeon *A. fulvescens* Wang et al. 1985; Shortnose Sturgeon *A. brevirostrum,* Atlantic Sturgeon *A oxyrhynchus*, Hardy and Litvak 2004; Green Sturgeon *A. medirostris,* Van Eenennaam et al. 2005; Pallid Sturgeon *Scaphirhynchus albus,* Miller et al. 2016*;* Shovelnose Sturgeon *S. platorynchus*, Kappenman et al. 2013) where data pertaining to developmental rates and morphological trait growth for the YSL stage was lacking. In particular, results indicate that experimental studies that pool YSL from multiple DPH at the start of the experiment (e.g. Pallid Sturgeon, 0–4 DPH, Miller et al. 2016) could suffer from confounding effects within treatments based on differences in developmental rate and morphological trait development between stages (e.g., RTi between stage 40–41 and 41–42 relative to earlier and later stage transitions; Table 3). Additionally, inferences from studies where results are strictly based on DPH should be interpreted with caution, especially when information is summarized across temperature regimes, as results can't be compared using DPH alone, particularly after 3–4 DPH (Fig. 3). Therefore, we recommend experimental designs and analytical approaches be developed as a function of developmental stage rather than time. In addition to the importance of developmental stage, confounding effects of embryo incubation temperatures on subsequent YSL development should also be considered in study experimental designs. Embryo incubation temperature has been shown to significantly influence development (Wang et al. 1987; Parsley et al. 2011) and size at hatch (Wang et al. 1987) with unknown effects on later life stages reared at different temperatures than those experienced during incubation. To remove confounding effects, and better represent natural conditions, temperature treatments should be initiated at time of fertilization and applied through embryo and YSL stages.

Morphological traits

We examined morphological trait growth as a function of developmental stage between cold (12.5 °C) and warm (17.5 °C) temperature treatments to quantify differences described above in the time to reach any given stage. We compared common traits (TL, BA, and YSA) measured for sturgeon during early life stages (*Acipenser transmontanus*, Boucher et al. 2014; *A. fulvescens*, Hastings et al. 2013; *A. brevirostrum*, *A. oxyrhynchus,* Hardy and Litvak 2004) and other fish species (*Danio rerio*, Jardine and Litvak 2003; *Pomacentrus amboinensis*, McCormick 1999; *Morone saxatillis,* Brown et al. 1988).

Morphological traits BA, HA, TL, MA, PFA, and GFA (Fig. 3) exhibited similar trends of larger size as a function of time (DPH) in the warm temperature treatment compared to individuals reared in the cold temperature treatment. In contrast, the opposite relationship was observed for YSA in relation to time, with smaller YSA recorded in the warm temperature treatment (Fig. 3). This has also been observed in other sturgeon species (Atlantic and Shortnose Sturgeon, Hardy and Litvak 2004; Lake Sturgeon, Wang et al. 1985) and in teleosts generally (Kamler 2008).

Temperature effects on morphological trait growth were generally the opposite when evaluated as a function of developmental stage compared to DPH (e.g., Fig. 3b). Depletion of yolk reserves was higher across all stages and morphological traits BA, HA, TL, MA, and PFA tended to be larger starting at stage 39 with significant differences observed at stage 41 for YSL reared in the cold temperature treatment compared to warm. This coincides with the observed delayed stage transition occurring at stage 40 that is particularly pronounced in individuals reared in colder temperatures (Table 3). The apparent connection between delayed stage transition and appearance of major structures (i.e., liver development) appears to be further coupled with increased growth of most morphological traits (excluding GFA)

measured in this study. When standardized by developmental stage, GFA was larger in warm temperature treatments; a trend also observed as a function of time. This allocation of resources could be an adaptive mechanism for individuals reared in warmer temperatures where levels of dissolved oxygen are lower compared to colder water and a larger GFA is a higher developmental priority for resource allocation and survival.

The thermal induced responses observed either as a function of time or developmental stage could have either beneficial or detrimental effects on survival of individuals at the YSL stage and later in life. Increased yolk utilization and growth rates documented in individuals reared in warmer temperatures initiate the transition to exogenous feeding (Wang et al. 1987), ability to escape predators (Hardy and Litvak 2004), and initiation of drift behaviour earlier (Duong et al. 2011), thereby avoiding additional risks of predation at the vulnerable YSL stage. Individuals developing at a slower rate due to colder rearing temperatures later in the season may also experience mismatches between onset of exogenous feeding and environmental conditions (Edwards and Richardson 2004; Laurel et al. 2011), thereby missing periods of optimal food resources available to warmer reared YSL earlier in the season. However, larger morphological traits observed in cold reared YSL could enhance swimming ability and predator avoidance (Miller et al. 1988). Large YSL body size may also reduce predation risk after transitioning to the drifting larval stage (Schael et al. 1991). For seasonally early YSL (e.g., spring), slower development may be beneficial by prolonging endogenous resource availability when river productivity is relatively poor. Further studies to examine effects of the rate of temperature induced trait development on fitness and survival of YSL and later life stages would be beneficial.

Management implications

Our results identify early life stage developmental physiology and trait variability that can enhance recovery planning and conservation aquaculture programs. Morphologic traits and growth (development rate and stage transitions) can be measured with high precision and those data have direct application for estimation of egg fertilization and hatch dates of wild caught YSL. This allows more reliable estimates of the duration of spawning activity, number of spawning days, and spawning related responses to environmental cues such as water temperatures and flow regimes (Jay et al. 2014).

Many conservation aquaculture programs for sturgeon have been shifting to repatriation of wild caught progeny to meet program objectives (e.g. Crossman et al. 2011; Thorstensen et al. 2019). These individuals are collected from spawning locations experiencing natural stream temperature profiles and then reared in hatchery environments under temperatures directed at promoting growth. Understanding trade-offs in how development is altered following transition to the hatchery environment would be important to consider as repatriation goals primarily focus on maximizing genetic diversity. Further, aquaculture programs with captive broodstock typically have spawning involving multiple adults occurring over multiple days, resulting in offspring from different families being reared at different ontogenic stages. Incubation temperatures could be altered to synchronize the onset of first feeding between family groups to simplify hatchery procedures and reduce probabilities that slower developing individuals are less successful in the hatchery setting. If fish are being raised for release at the larval stage, adjusted incubation temperatures could maximize larval size or synchronize release date with optimal environmental conditions (i.e., temperature, flow, natural larval drift, prey availability, etc.).

Conclusions

Developmental rates during early ontogeny are associated with year-class strength (Myers 1997), survival, and recruitment in fishes (Cushing 1972). Standardization of developmental rate as demonstrated here allows for improved predictions on timing of important life stage transitions that better characterize aspects of YSL ecology that can restrict recruitment. Variability attributed to different measurements of development is an important consideration for studies focusing on describing the timing, frequency, and duration of spawning in the wild. Further research is required to determine the effect of thermal regimes on developmental rates, behaviour, physiology, and morphology, not only within the embryo and YSL stages but also extending observations into juvenile stages (e.g. Atlantic and Shortnose

Sturgeon, Spear and Kieffer 2016; Sterlet Sturgeon *A. ruthenus*, Mandal et al. 2016).

Results we report have ecological and evolutionary implications for fish species in terms of long-term adaptability to rapidly changing thermal conditions and anthropogenically altered aquatic systems. Life history strategies have evolved as a function of trade-offs among traits that have consequences for fitness in different environments (Winemiller and Rose 1992). Trade-offs typically involve resource allocation decisions that limit the possible set(s) of trait combinations, potentially affecting age-specific survival. Phenotypic plasticity can mitigate fitness declines in stochastic environments (Schlaepfer et al. 2002). However, comprehensive studies are lacking that quantify causal factors underlying complex patterns of covariation among functionally related traits (Schlichting and Pigliucci 1998; Pigliucci and Preston 2004). This information is particularly important for threatened or endangered populations where recovery actions are necessary. Generally, there is a paucity of information for mobile vertebrate species due in part to difficulties of disentangling temporal and spatial dependencies of environmental variable states and the tendencies of related individuals to co-occur in similar environments during sequential early ontogenetic stages.

Based on our results, we recommend future studies to focus on developmental stages when comparing experimental treatments or YSL groups, as developmental rate can differ greatly between temperature regimes depending on how it is measured. Researchers should consider incorporating multiple measures of development timing into study designs to improve understanding of environmental effects.

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