Growth of Larval to Juvenile Green Sturgeon in Elevated Temperature Regimes

PETER J. ALLEN, MARY NICHOLL, STEPHANIE COLE, AMY VLAZNY, AND
JOSEPH J. CECH, JR.

*Department of Wildlife, Fish, and Conservation Biology
and the Center for Aquatic Biology and Aquaculture, University of California,
1 Shields Avenue, Davis, California 95616, USA*

Abstract.—To determine the effect of high river temperatures on post-yolk-sac larval to early juvenile green sturgeon *Acipenser medirostris*, growth rates at elevated and cycling temperature regimes were measured. Water temperatures were chosen based on temperature regimes in their highly altered natal rivers. Post-yolk-sac fish (15 d after hatching) were placed into twenty-four 60-L tanks. Fish were kept on a natural photoperiod, receiving continuous well water and aeration and ad libitum commercial rations. Significant differences were found between final wet weights, total lengths, and specific growth rates (at 24°C and at cycling 19–24°C > 19°C) because of increases in food consumption, despite increases in activity (both significantly greater at 24°C than at 19–24°C or 19°C). Elevated and cycling temperatures in the 19–24°C range do not adversely affect juveniles (body size range, ~0.1–10 g), when abundant food and oxygen are available.

Many species have adapted to take advantage of certain temperature ranges and exhibit maximum growth rates within an optimal range (Jobling 1981, 1994). Increases in temperature affect the rates of biochemical and physiological processes (Hochachka and Somero 2002), typically requiring more substrates for faster energy turnover rates and potentially damaging metabolically associated proteins (Somero and Hoffman 1997). In response, ''chaperone'' or ''repair'' proteins (e.g., heat-shock proteins) may be synthesized to repair the damage, thereby increasing total energy requirements (Kregel 2002). Chronically elevated temperatures can force fish to seek thermal refugia (Snucins and Gunn 1994; Diaz and Bückle 1999; Sauter et al. 2001; Baird and Krueger 2003). If fish are unable to locate more optimal temperature ranges, the results may be reduced growth rates, poor physical condition, or mortality (Meffe 1992; Clapp et al. 1997; Wendelaar Bonga 1997).

Sturgeons are distributed in large-river temperate ecosystems throughout the northern hemisphere. Most sturgeon populations are declining, and most species are threatened or endangered (Birstein 1993) because of overfishing (Boreman 1997), pollution (Kruse and Scarnecchia 2002), and habitat alterations (Secor et al. 2002). Little is known about the response of sturgeons to increased temperatures, particularly during early life history stages, when their exposure and vulnerability to environmental disturbances may be increased (Kamler 1992; Parsley et al. 2002; Schiemer et al. 2002). Growth is a physiological measure of well being, an integrated sum of the internal and external processes that result in a net increase in length or body mass. Growth can be defined simply as an increase in the energy content of the body (Jobling 1994). Because of this, growth can be used to assess how an organism is functioning under certain imposed conditions. Few studies have been conducted on the effects of elevated temperatures on sturgeon growth.

The green sturgeon *Acipenser medirostris* is distributed along the Pacific coast of North America, ranging from the Bering Sea to Ensenada, Mexico (Moyle 2002). However, spawning is known from only three rivers: the Sacramento and Klamath rivers in northern California, and the Rogue River in southern Oregon (Moyle 2002). The green sturgeon is considered to be one of the few truly anadromous sturgeons (Doroshov 1985), although very little is known about its early life history stages. Recently, there has been concern that the numbers of these fish have been significantly declining (Moyle 1994, 2002; EPIC et al. 2001). Currently in the United States, the green sturgeon is not federally protected, principally because of a lack of information (Adams et al. 2002). In Canada it is a rare species in the province of British Columbia (Houston 1988) and has been classified as a ''special concern'' species (COSEWIC 2004).

Along the Pacific coast of North America, many rivers have been modified with dams and diversions for agricultural and urban uses, altering their

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* Corresponding author: pjallen@ucdavis.edu

natural flow and seasonal temperature regimes. Summertime river temperatures are often elevated (up to 24°C) or undergo rapid diel fluctuations as a result of the timing of water releases and ambient air temperatures (Erickson et al. 2002; USGS 2004). In the Klamath River, historical river temperature data are limited, but evidence for the post–Iron Gate Dam period (1962–present) indicates that river temperatures and the duration of summer high river temperatures are increasing (Bartholow 2005). Van Eenennaam et al. (2005) found that 17–18°C was the probable upper limit of the thermal optima for green sturgeon embryos, their developmental abnormality rates increasing significantly above these temperatures. J. Linares-Casenave and coworkers (University of California Davis, unpublished data) found that yolk sac larval fish at temperatures of 22°C or more had significantly more deformities, and I. Werner and coworkers (University of California Davis, unpublished data) found that these fish also had elevated concentrations of heat shock proteins. Mayfield and Cech (2004) found that 15–19°C appeared to be the optimal growth range for larger juvenile fish (144 d posthatch [dph], mean wet weight: 150 g), although higher temperatures were not studied. As a part of a swimming study, they also found that these larger juveniles were less resilient to transport stress at 24°C versus 19°C, the higher temperature resulting in high mortality (60%). In addition, they found that aerobic metabolic rates of younger juveniles (mean wet weight: 30 g) increased significantly between 19°C and 24°C. However, none of these studies examined growth in post-yolk-sac larval fish to early juvenile stages, which are the stages of this species most likely to be exposed to the highest river temperatures and the greatest diel temperature fluctuations. These fish are present during summer water impoundment releases but have not yet developed the capability to osmoregulate in seawater (Allen 2005).

We conducted a growth experiment to determine the effects of elevated and daily cycling river temperatures on post-yolk-sac larval to early juvenile green sturgeon. Growth was analyzed with groups of fish in large tanks at constant temperatures of 19°C and 24°C and also at cycling temperatures of 19–24°C to simulate river conditions. We hypothesized that fish at 24°C would grow slowest, followed by those at the cycling 19–24°C regime, and finally those at 19°C.

Methods

Preexperiment conditions for fish rearing.— Green sturgeon were hatched according to the methods described by Van Eenennaam et al. (2001). Yolk sac larval fish were held in 1-m diameter, circular fiberglass tanks, with continuous flows of nonchlorinated well water at 18.6 ± 0.3°C (mean ± SD). Inflowing water was oriented with a spray bar to provide a very slight current in the tank. Small amounts of commercial diet (Nelson & Sons, Inc., Murray, Utah, USA; Silver Cup Soft-Moist Trout Diet) were added starting at 10 d posthatch (dph; prior to exogenous feeding) to train larval fish onto commercial diet at the onset of exogenous feeding. Deng et al. (2002) found that at 18.5°C the larvae started exogenous feeding at 10–15 dph and that at 45 dph they were fully metamorphosed into juveniles. Ad libitum rations of commercial diet were added once the fish started exogenous feeding. Currents in holding tanks were gradually increased as the fish grew and were better able to hold position.

Growth.—Post-yolk-sac fish (19°C) were randomly assigned to 24 fiberglass tanks (60-L circular tanks, 8 tanks/treatment, 40 fish/tank) immediately after the onset of exogenous feeding (15 dph). Before their distribution into tanks, sturgeon were measured for total length (TL; nearest mm) with a flat metric ruler affixed to an acrylic board and were weighed (nearest 0.01 g) by using a tared beaker of water on a recently calibrated, electronic balance after the net containing the fish was dabbed onto absorbent paper towels to remove any excess water. For each treatment group, 80 fish were individually weighed (mean, 0.10 g) and measured (mean, 28 mm) at the start of the experiment. These fish were also weighed in groups of 10. Because there was very little variance in wet weights and TLs, the sum of the weights of the individually weighed fish corresponded closely to the weights of fish in groups of 10. Therefore, groups of 10 fish (as in Deng et al. 2003) were used thereafter for wet weights because of similar accuracy and concerns over handling stress to the yolk sac larval fish. Temperature was increased 1°C/d to 24°C in elevated and cycling temperature tanks, after which 19–24°C cycling tanks were started on a diel cycle (warming to 24°C at 1700 hours and cooling to 19°C at 0500 hours). The mean ± SD for each treatment was as follows: for the 19°C treatment, 18.6 ± 0.3°C; for 19–24°C, 21.4 ± 1.8°C; and for 24°C, 24.2 ± 0.4°C. These results are based on temperature loggers that recorded temperature every 15 min in two tanks in each treatment group. Fish were kept on a natural photoperiod via lights and overhead skylights (May–July period; approximately 14.6 h : 9.4h light

: dark) and receiving flow-through well water (~3 L/min) and constant aeration via air stones. Ad libitum rations (Silver Cup Soft-Moist Trout Diet) were supplied by 24-h feeders, and wastes and uneaten food were siphoned away in the morning and evening daily. Algal growth was also scrubbed from all tanks at least once every 2 d. Dissolved oxygen (always >80% of air saturation; Yellow Springs Instruments, Ohio, USA, Model YSI 85) and unionized ammonia (always <15 μg/L CHEMetrics, Virginia, USA, Model DCI3001) were measured daily and weekly respectively, in all tanks. At least one fish from each tank (n = 8 per treatment for each age) was removed at ages 35, 50, and 65 dph (on d 20, 35, and 50 in the experiment) and measured for wet weight and TL. All fish were food deprived for 24 h before these measurements. Specific growth rates (SGR; percent change in weight per day) were calculated from the equation (Houde and Schekter 1981), namely,

$$SGR = 100(e^G - 1), \tag{1}$$

where $G = (\log_e W_F - \log_e W_I)/t$, W_I = wet weight (g) at the start of the growth experiment, W_F = wet weight (g) at the end of the growth experiment, and t = the length (d) of the growth experiment.

Percent body moisture.—Fish were randomly selected and weighed from the same cohort (n = 15) at the initiation of the experiment and from each temperature treatment (n = 16–17) at the termination of the experiment. Fish were euthanized with an overdose of MS-222 (tricaine methanesulfonate; 500 mg/L). Percent body moisture was determined by drying whole fish (n = 15–17 per treatment) at 60°C and weighing periodically until no further weight loss occurred (14 d). Fish were then placed into a sealed glass desiccator, cooled, and weighed for dry weights. Percent body moisture was determined as

$$\% \text{ body moisture}$$
$$= \frac{\text{wet weight} - \text{dry weight}}{\text{wet weight}} \times 100. \tag{2}$$

Food consumption.—A qualitative measurement of food consumption was made by estimating the amount of food remaining each morning in relation to the amount of food fed the previous day, because juvenile green sturgeon forage most actively at night (Kynard et al. 2005). The food remaining was assigned a value on an ordinal scale: 1 = low, 2 = medium, 3 = high amount. We made a total of 37 measurements per tank to calculate tank

means (8 per treatment) for the duration of the experiment. This measurement was used because the size and consistency of food (powder-small pellets, crumble) did not lend itself to removal, drying, and quantification. All fish were fed ad libitum rations and always had some food remaining. There were known amounts of food fed per tank and equal amounts between treatments. The amount of food from early in the experiment was increased as fish size and food consumption increased. After observers' measurements were standardized for making qualitative assessments, all three observers separately evaluated and jointly agreed on the amount of food left over for one previous day's feeding.

Activity.—To quantify fish activity, a clear acrylic sheet with a 9-cm × 9-cm grid was placed over randomly chosen tanks for each treatment. A remote, overhanging video camera was placed above the tanks and was connected to a nearby monitor. After the grid was placed on top of the tank and fish were given a 5-min acclimation period, the fish closest to a previously selected, randomly chosen grid-square was tracked for a 5-min period. The total number of gridlines the fish crossed was observed on the monitor. Fish in each tank were measured two to three times during the duration of the experiment, and an equivalent number of replicates from all treatments were randomly selected each measurement day. Measurements were conducted within a 2-h period for all treatment groups on each measurement day, and similar numbers of runs were conducted among treatment groups for morning (0530–0930 hours), midday (0930–1530 hours), and evening (1530–1730 hours) time periods. Two extra runs were done in the 19–24°C temperature group, because activity was assessed an equivalent number of times at approximately 19, 21.5, and 24°C to capture the full range of temperatures encountered.

Statistical analyses.—One-way analysis of variance (ANOVA) procedures (Sall et al. 2001) were run for each date separately (35, 50, and 65 dph) to compare the wet weights, TLs, and SGRs of the three treatment groups. We also used a one-way ANOVA to compare activity rates between temperatures with a posthoc Tukey's multiple comparison test. A natural log transformation was used for comparisons of wet weight at 35 dph to meet the assumptions of normality and homogeneity of variance. Multiple comparison tests (Tukey's honestly significant difference test or least significant difference test) were used only if the overall one-way ANOVA was found to be significant. A Krus-

kal–Wallis rank test was used to compare percent body moisture and food remaining between temperatures, and a Bonferroni multiple comparison test correlate was used to compare treatment means for both tests separately. In all cases, differences were considered significant at $P < 0.05$. All statistical values for measurements are reported as means $\pm$ SE.

Results

Growth

Juvenile green sturgeon grew faster at warmer temperatures. At 35 dph, wet weight, TL, and SGR were significantly greater at the warmer and cycling temperatures than at 19°C (24°C and 19–24°C > 19°C; Figure 1). At 50 dph, wet weight, TL, and SGR were significantly higher in the 24°C fish than either the 19–24°C or the 19°C fish. At 65 dph, significant differences were found among final wet weights, final TLs, and final SGRs (24°C and 19–24°C > 19°C).

Early in the experiment, some fish escaped through screens on the top of tank standpipes. The number of fish that escaped was proportional to temperature treatment (24°C > 19–24°C > 19°C), possibly indicating higher activity rates. The numbers of fish were adjusted at d 20 (35 dph; 30 d remaining in experiment), the numbers of fish per tank being equalized by removal of randomly selected, appropriate numbers of individuals from each tank. Also, because one of the 24°C tanks had a sudden, unexplained (based on gill histological analyses) die-off of fish ($n = 6$ fish remaining), we excluded that tank from analyses. Histological analyses did not reveal any obvious signs of toxicological effects in the gills, but the remaining fish in this tank also displayed behavioral differences (e.g., swimming in the water column) and therefore were not included in analyses.

Percent Body Moisture

Fish at the start of the experiment had significantly higher percent body moisture (89.9 ± 0.53%, $n = 15$, 19°C) than those in any of the temperature treatments at the end of the experiment. Also, there were no differences among the treatments at the end of the experiment: Final percent body moisture ($n = 16–17$) was 70.9 ± 2.20% at 19°C, 68.0 ± 1.02% at 19–24°C, and 73.6 ± 0.82% at 24°C.

Food Consumption

The 24°C group consumed significantly more food than those in either the 19–24°C or the 19°C
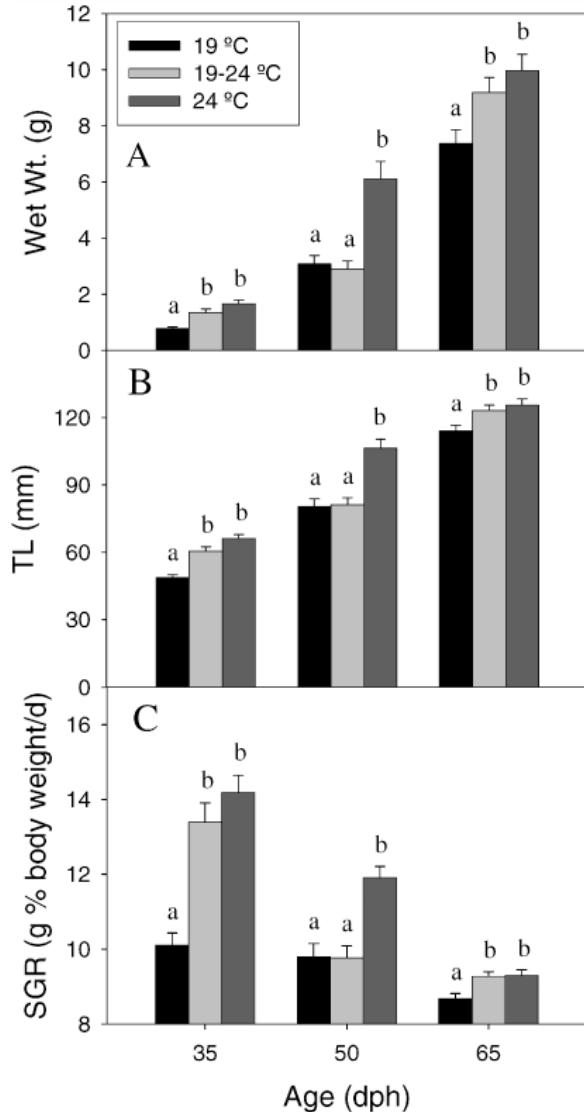

FIGURE 1.—Growth data ([A] wet weight, [B] total length [TL], and [C] specific growth rate [SGR]) for juvenile green sturgeon with regard to temperature and age. Data represent means + SEs at specific ages (days posthatch [dph]; $n = 7–8$). Different lowercase letters indicate significant differences ($P < 0.05$) among temperature groups within an age-group.

groups. Food consumption, which was based on an ordinal index of food remaining (see Methods), was 1.25 ± 0.06 in the 24°C group, 1.57 ± 0.07 in the 19–24°C group, and 1.70 ± 0.06 in the 19°C group.

Activity

Activity, the number of gridlines crossed during a 5-min period, was significantly greater for fish in the 24°C group (260 ± 39) than for those in either the 19–24°C (130 ± 37) or 19°C (129 ± 37) groups.

Discussion

High water temperatures are stressful to early life history stages of green sturgeon (Van Eenennaam et al. 2005). Regulated water releases and high summer temperatures may adversely affect young-of-the-year fish that have not out-migrated to seawater. However, for the simulated river temperatures and regimes used here, exogenously feeding larval fish actually grew faster at warmer temperatures.

Juvenile green sturgeon had greater wet weights, TLs, and SGRs at 24°C and 19–24°C than at 19°C and greater food consumption and activity rates at 24°C than at either 19–24°C or 19°C at 65 dph, which caused us to reject our hypothesis. Different explanations seem apparent for the similar final growth measurements in the 24°C and 19–24°C treatment groups. In the 24°C group, increased food consumption apparently overcompensates for higher maintenance metabolic costs and activity costs. For the 19–24°C group, however, lower activity levels and the increasing trend in food conversion efficiency (grams of weight gained per gram of feed) with warmer water temperatures (Mayfield and Cech 2004) overcompensate for lower food consumption. The 19°C group had the lowest growth; its food consumption was lower than that of the 24°C group and food conversion efficiency was lower than in the 19–24°C group. Finally, the lack of difference in percent body moisture among temperatures indicates that water weight was not affecting the final differences in body weights.

The differences between wet weights, TLs, and SGRs among treatments at different ages appear to be temperature mediated. This is evidenced by early increases in the 24°C group (35–50 dph) compared with later changes (50–65 dph) in the 19–24°C and 19°C groups.

The observed results could reflect differential escape rates between treatment groups, because a greater number of fish escaped at warmer temperatures early in the experiment. Results could have been biased if a representative group of fish had not been left in these tanks. However, the standard errors of growth-related measurements (wet weight and TL) were largest in the warmest temperatures, indicating that a representative group remained, leading us to reject this hypothesis.

Growth studies in other juvenile sturgeon species determined temperature optima within the 19–24°C range used in our experiments. Hung et al. (1993) found that 30-g juvenile white sturgeon *A.*

transmontanus had an optimum growth temperature closer to 23°C than 26°C. Amerio et al. (1999) found that larger juvenile Siberian sturgeon *A. baeri* (average wet weight, 1,350 g) did not have significantly different growth rates between 18 and 24°C. Vaccaro et al. (2004) found that growth slowed at 25°C in 45-g hybrids of Adriatic sturgeon *A. naccarii* × Siberian sturgeon, although growth was tracked seasonally rather than concurrently at different temperatures. Gershanovich (1983) studied growth in thorn sturgeon *A. nudiventris* and beluga *Huso huso* from the onset of exogenous feeding (0.07 and 0.02 g, respectively) to a wet weight of 7–10 g (50–80 d and 30–50 d, respectively). Using a temperature range of 12–24°C, he found that sheap sturgeon had the most efficient growth at 24°C and beluga grew best at 20°C.

Diel temperature cycles have been associated with fast growth rates in sturgeon. Konstantinov et al. (1999) found that oscillating temperature regimes accelerated growth and increased the food conversion efficiency in juveniles of three sturgeon species as compared with those found in static temperature regimes. Using stellate sturgeon *A. stellatus* (15–45 dph, 0.2–3 g weight), Konstantinov and Sholokhov (1993) found that fish at a temperature regime of 25 ± 2°C with a 12-h oscillation had the highest growth rate, compared with that of fish at 23 ± 2°C or of fish at static temperature regimes of 21, 23, 25, or 27°C.

Our results revealed similar final wet weights, TLs, and SGRs in the cycling 19–24°C and static 24°C temperatures. Because the cycling temperature treatments more closely resemble natural temperature regimes of warming during diurnal hours and cooling during nocturnal hours, the fish may be adapted to some temperature fluctuations. Jobling (1994) reported that when growth at fluctuating temperature means is compared with that at the same constant temperatures, growth is generally faster for fluctuating temperatures when temperatures are low, and slower when temperatures are above the optimum. Therefore, the similar growth rates of the green sturgeon at the cycle's mean (21.5°C) and at the static 24°C (Figure 1) indicate that both temperatures are within their optimal growth range.

In the spawning rivers of green sturgeon, dam releases and rising air temperatures have resulted in an increasing trend in river temperatures and a longer duration of high river temperatures (Bartholow 2005). The size range of green sturgeon used in our experiments (ca. 0.1–10 g) character-

izes fish immediately after the absorption of the yolk sac, with the onset of exogenous feeding. This age range has been called the ''critical age'' in fishes because of its relevance to successful recruitment classes into the adult population (Hardy and Litvak 2004). Because, unlike teleosts, sturgeons have a holoblastic development style, they are practically unable to feed before yolk sac absorption and differentiation of the stomach from the anterior yolk sac (Gisbert and Doroshov 2003) rather than the gut utilizing the yolk sac. Thus, there is little overlap between the time the yolk sac is absorbed and the fish begin exogenous feeding. This developmental pattern increases the sensitivity of larval sturgeons at this developmental stage, especially to temperature (Nilo et al. 1997), which influences metabolic rate, and to the availability of metabolic fuels and substrates for somatic growth. This age range may very well be adapted to grow fastest at the warm river temperatures that would have occurred in mid- to late summer, historically. The increased growth and corresponding developmental rates would have minimized predation vulnerability (Werner and Hall 1988) and maximized developmental readiness for seawater entry with the first winter storms (Allen 2005). However, if the onset of warm temperatures occurs before yolk absorption, these fish are likely to be thermally challenged. For example, 17–18°C appears to be the upper temperature tolerance limit of the thermal optima for green sturgeon embryos (Van Eenennaam et al. 2005), and 22°C appears to be the upper limit for newly hatched yolk sac larvae (J. Linares-Casenave and coworkers, University of California Davis, unpublished data).

With unlimited food and high water quality, juvenile green sturgeon grew faster at 24°C and at a simulated river temperature daily cycle of 19–24°C than at 19°C. However, if other potential stress factors (e.g., low food or oxygen resources) are present, results could vary. Thus, green sturgeon in the ages and sizes studied (~0.1–10 g) appear more temperature-tolerant than the egg, embryonic, larval, or larger juvenile stages. These fish may be able to take advantage, metabolically, of these temperatures during this age and developmental period, which, at least for the later portion of the age ranges studied, most probably coincided with warm river temperatures, historically.

Acknowledgments

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