

Temperature Effects on Green Sturgeon Bioenergetics

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Abstract.—The green sturgeon *Acipenser medirostris* is relatively rare, and little is known about the effects of important habitat-related influences on its life history. Temperature directly or indirectly impacts the distribution of fish as well as their physiological and behavioral processes. Because the Klamath and Rogue rivers may reach 24–25°C and egg and embryo incubation temperatures above 22°C are associated with deformities in juvenile green sturgeon, data on the temperature-related bioenergetic responses of these juveniles would be especially useful in designing effective conservation and management strategies. We measured the food consumption, growth, food conversion efficiency, oxygen consumption, volitional activity, ventilatory frequency, thermal preference, and swimming performance of juveniles at several temperatures spanning their warm-season temperature range (11–24°C). Food consumption, growth, and food conversion efficiency generally increased with temperature between 11°C and 15°C but stayed constant between 15°C and 19°C. Growth increased and food conversion efficiency decreased with ration size. Oxygen consumption, volitional activity rate, and ventilatory frequency generally increased with temperature, while preferred temperature increased and swimming performance decreased with temperature from 19°C to 24°C. Relative to other sturgeon species, the green sturgeon has high growth and oxygen consumption rates. Overall, we found that bioenergetic performance was optimal between 15°C and 19°C under either full or reduced rations, thus providing a temperature-related habitat target for conservation of this rare species.

The North American green sturgeon *Acipenser medirostris* is an anadromous chondrosteian with a distribution ranging from the Bering Sea to Ensenada, Mexico (Moyle et al. 1995). Despite this wide range, less is known about the green sturgeon than the other 24 living sturgeon species worldwide (Erickson et al. 2002). Green sturgeon are known to spawn in three Pacific river systems: the Rogue River in Oregon and the Sacramento and Klamath rivers in California (Moyle 2002). The temperature in the Klamath River varies from 4°C to 25°C (C. Chamberlain, Yurok Tribal Fisheries Program, personal communication) due to natural (e.g., seasonal and precipitation-related cycles) as well as human-induced (e.g., impoundments) effects. The Rogue River is the most northern of the three, with temperature ranging from 4°C to 24°C during 2000–2001 (Erickson et al. 2002). Because egg and embryo incubation temperatures above 22°C are associated with deformities in juvenile green sturgeon and temperature directly or indirectly affects the distribution of fish as well as their physiological and behavioral processes (Cech et

al. 1990; Schmidt-Nielsen 1999), it is important to determine the temperature-related effects on green sturgeon. The use of environmental temperatures in defining optimal fish habitat or restricting the distribution of species is well documented (McCauley and Fry 1986; Armour 1991; Hurst and Conover 2002).

Green sturgeon are considered an “at risk” species by the California Bay-Delta Authority and a species of special concern by the California Department of Fish and Game. Habitat changes (e.g., due to dams, loss of riparian cover, and thermal pollution) leading to temperature increases are known to have serious consequences for resident fish populations (Chart and Bergesen 1992). Data on this species’ temperature-related responses, particularly regarding their patterns of resource use and survival (Wainwright 1994; Cech and Crocker 2002) would be particularly useful in designing effective conservation and management strategies. Temperatures in regulated rivers such as the Rogue, Sacramento, and Klamath can be altered with releases of reservoir water from various depths. Warm temperatures associated with low, drought-induced flows in a major Sacramento tributary, the Feather River, produced major changes in its fish community (Moyle et al. 1983).

The energetic (metabolic) demands of fish typically increase with temperature (reviewed by Fry

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1971). As a result, food consumption (energy ingested) often increases with increasing water temperature to satisfy increasing body maintenance demands and, often, increasing growth and reproduction demands. Our objectives were to assess the effects of temperature on important bioenergetic variables in juvenile green sturgeon and to compare these effects with those documented for other sturgeons. These variables can be modeled as

$$I = G + A + M + R + E + \text{SDA}, \quad (1)$$

where the energy ingested (I) is balanced by energy allocated to growth (G), activity (A), maintenance (M), reproduction (R), excretion (E), and specific dynamic action (SDA, i.e., the energy associated with digestive and anabolic processes following feeding; Jobling 1994).

Methods

The age-0 and age-1 green sturgeon (mean body weight range, 150–851 g) used in this 2-year study were progeny of wild-caught Klamath River sturgeon that had been artificially spawned during late May 1999 (Van Eenennaam et al. 2001). Eggs were incubated at the University of California-Davis and juveniles reared in aerated water at temperatures similar to those in the Klamath River (11–15°C) during late spring. The age-0 fish were fed commercial Silvercup trout pellets at 3–5% of body weight per day based on a feeding table for white sturgeon *A. transmontanus*. Fish (age, 31-d posthatch) were acclimated (1°C/d) to 19°C (ambient well water temperature) and held in round 284-L fiberglass holding tanks. Because tanks received continuous flows of the air-equilibrated, 19°C well water, high water quality conditions were ensured until fish were needed for experiments. Within the temperature control limitations of the growth laboratory facility, the experimental temperatures that were chosen spanned the warm-season temperature ranges of the Klamath and Rogue rivers. Dissolved ammonia concentrations were measured twice weekly and were always below detection limits (<0.01/L).

Experiment 1: Food Consumption, Growth, and Food Efficiency

At 144 d posthatch, fish (body weight, 149.8 ± 41.0 g [mean \pm SD]; $n = 144$) from a holding tank were randomly distributed into 24 round 110-L tanks (six fish/tank) and either held at 19°C or acclimated to 11°C or 15°C (at 1°C/d). There were four replicate tanks for each of the six treatments

(three temperatures \times two ration levels) for the 33-d experiment, which was sufficient to measure substantial growth. Tanks were indoors and were maintained on a natural photoperiod for 38°55'N in October–December using both natural (translucent roof panels) and artificial (fluorescent lights) sources. Incoming water flow (4 L/min) was adjusted by means of angled spray bars to provide a current of 10 cm/s, and current direction was reversed every 5 d to uniformly exercise the fish.

Food consumption.—Half of the age-0 fish (tanks selected randomly) at each temperature were fed to satiation (range, 8.0–13.1 g Silvercup pellets per tank of 6 fish per feeding), and the rest were fed at 50% of satiation (as measured from the observed feeding levels of sated fish at each temperature). Fish were fed twice daily, and the amount of food consumed was quantified by collecting (after 20 min) and counting the uneaten pellets and subtracting their predetermined weight from that of the total fed at each feeding. Due to observable erosion of the pellets in the water, feeding was limited to 20 min so that uneaten pellets could still be counted. This erosion may have resulted in an overestimate of food consumption rates and an underestimate of food conversion efficiency. The mean daily food consumption rate (CR; grams of feed per gram of fish per day) for each tank of fish was calculated from the equation

$$\text{CR} = \frac{\sum C \log_e(W_2/W_1)}{t(W_2 + W_1)}, \quad (2)$$

where C = total food consumed (dry weight [g]) for the duration of the experiment; W_1 and W_2 = individual fish wet weights (g) at the beginning and end of the experiment, respectively; and t = experiment duration (i.e., 33 d).

Growth.—The age-0 fish were individually weighed and measured at 11-d intervals and were fasted 24 h prior to being weighed and measured to minimize food weight contributions. Just prior to weighing, the fish were blot-dried. Fork and total lengths were measured (mm), and weight (nearest 0.1 g) was determined with an electronic balance. Mean live weights were used to calculate the instantaneous specific growth rate (SGR; percent change in weight per day) with the equation

$$\text{SGR} = \frac{\log_e(W_2/W_1)}{t}(100). \quad (3)$$

Food conversion efficiency.—After the experiment, six age-0 fish from each treatment were dried

to a constant weight at 60°C in a drying oven to derive the following relationship between dry weight (DW) and wet weight:

$$DW = 0.203W - 3.435, \quad (R^2 = 0.92),$$

where W = wet weight. We calculated gross food conversion efficiencies (CE; weight gained per gram of feed) for each tank from the equation

$$CE = \frac{DW_2 - DW_1}{\sum C}, \quad (4)$$

where DW_1 = the mean dry weight (g) of fish sampled from the holding tank at the start of the experiments and DW_2 = the mean dry weight of the experimental fish in each tank at the end of the experiment.

Experiment 2: Metabolic Rate and Activity

Metabolic (oxygen consumption) rates were measured for both age-0 (routine rates) and age-1 fish (resting routine rates). Routine metabolic rates were determined by measuring oxygen consumption rates via closed respirometry (Cech 1990). Fish (age-0; body weight, 30.3 ± 17.5 g, $n = 39$, 33, and 33 for 11, 19, and 24°C, respectively) were randomly taken from their holding tanks and transferred to three indoor experimental tanks also receiving air-equilibrated well water at 19°C. Two randomly chosen tanks were cooled or warmed at 1°C/d to reach the acclimation temperatures of 11°C and 24°C, respectively. This temperature range spanned the warm-season range of the Klamath and Rogue rivers (Chamberlain, personal communication; Erickson et al. 2002). Respirometers were of clear polyvinyl chloride (PVC) pipe construction with an opaque PVC end cap and neoprene stopper and were equipped with water flushing and sampling tubes on the ends. Individual postabsorptive fish were acclimated for at least 6 h in the respirometers before the start of the experiments. A blank respirometer (i.e., one without fish) was used to account for microbial respiration. As a pilot study showed that age-0 fish continued to exhibit activity (tail beats) even after 8 h of acclimation, we quantified the tail beats using videotapes from an overhead video camera. Metabolic rates (MO_2 ; mg O₂/h) were calculated from the equation

$$MO_2 = \frac{(CO_{2i} - CO_{2f})}{t}(V_R), \quad (5)$$

where CO_{2i} and CO_{2f} = the respirometer O₂ con-

centrations (mg/L) at the beginning and end of the experiment; V_R = the respirometer volume (L); and t = the experiment time (h). The O₂ partial pressures (PO_2) were measured with a Radiometer PHM71/E5046/D616 O₂ analyzer system and converted to O₂ concentrations using an O₂ solubility nomogram (Green and Carritt 1967).

The resting routine metabolic rates of juvenile green sturgeon (age-1; $n = 19$, 21, and 20 for 11, 19, and 24°C, respectively) were determined by measuring oxygen consumption rates via open respirometry (Cech 1990). Age-1 fish were transferred and acclimated as described above. Fish (body weight, 851.2 ± 240.2 g) were completely quiescent in their triangular (cross-sectional) 11-L respirometers after 8 h of respirometer acclimation. Respirometer water flow rates were measured by means of the timed collection of water in a calibrated, graduated cylinder, and oxygen contents were calculated from inflow and outflow PO_{2s} , as above. Measurements from a blank respirometer accounted for microbial respiration. Age-1 fish MO_{2s} were calculated from the equation

$$MO_2 = (CO_{2in} - CO_{2out})(Vw), \quad (6)$$

where CO_{2in} and CO_{2out} = the O₂ contents (mg O₂/L) of water flowing into and out of the respirometer and Vw = the water flow rate through the respirometer (L/h). The effects of temperature on metabolic rates were determined from Q_{10} values (Schmidt-Nielsen 1999), which express the rate of change in a process with temperature as follows:

$$Q_{10} = (R_2/R_1)^{10/(T_2-T_1)}, \quad (7)$$

where R_2 is the rate at T_2 (the higher temperature) and R_1 is the rate at T_1 (the lower temperature).

Experiment 3: Thermal Preference

Thermal preference experiments on age-0 green sturgeon (weight, 38.4 ± 17.2 g; $n = 20$, 20, and 9 for 11, 19, and 24°C, respectively) were conducted in an annular, 1-m-diameter, flow-through thermal gradient tank constructed of clear acrylic plastic and designed to avoid vertical stratification (Myrick et al. 2004). Age-1 fish were too large for this apparatus. A light-colored shade cloth cover shielded the apparatus and fish from investigators, minimizing tank position effects. Observations of the individual fish positions were made via a CRT monitor wired to an overhead video camera. Water flows throughout the thermal gradient tank were isothermal at the acclimation temperature for the first hour after each fish was placed in the appa-

ratus. Then the thermal gradient (11.5–31.0°C) was established. During each 1-h experiment, the location of the fish and the corresponding water temperature data (YSI 44TD telethermometer with 10 calibrated YSI 401 thermistor probes placed at regular intervals around the gradient tank) were recorded at 10-min intervals. Fish could easily swim around the entire annulus in 30 s, minimizing any possible space and time autocorrelation.

Experiment 4: Swimming Performance

The critical swimming velocities (U_{crit}) of age-1 sturgeon (weight, $1,132.5 \pm 424.2$ g; $n = 19$, 11, and 8 for 11, 19, and 24°C, respectively) were determined during year 2 of the study with a 200-L recirculating-water flume (Brett 1964) incorporating a variable-speed motor. The flume was partly immersed in a temperature-controlled water bath, and the velocities were calibrated with a digital Marsh-McBirney (Model 201D) water current meter. Individual fish were placed in the swimming chamber, and after 1 h of acclimation at 10 cm/s, the U_{crit} was measured by 10-cm/s increases in water velocity every 20 min until the fish became fatigued (Beamish 1978). A fish was considered fatigued when it impinged three times at the downstream end of the chamber. Absolute U_{crit} (U_{crit_a}) was calculated (Brett 1964) from the equation

$$U_{crit_a} = U_i + (10 \text{ cm/s}) \cdot (T_i \cdot 20/\text{min}), \quad (8)$$

where U_i = the highest velocity maintained for 20 min and T_i = the time elapsed at fatigue velocity. Tail beat frequencies were measured for each fish by counting the number of tail beats over a 1-min period at each swimming velocity.

Statistical Analyses

A one-way analysis of variance (ANOVA; parametric data) was conducted (SIGMASTAT software; SPSS 2003) to test for significant effects of experimental factors (e.g., temperature; $n > 2$), Tukey's tests being used for post hoc pairwise comparisons. A two-way ANOVA was also conducted to test for significant interactions between experimental factors (temperature and ration), Tukey's tests being used for post hoc pairwise comparisons. A Kruskal–Wallis test was conducted to test for significant effects and Dunn's test for post hoc pairwise comparisons. Student's t -tests were used to compare the two food ration levels. Analysis of covariance (ANCOVA) was used to determine significant interacting effects of body weight and activity on metabolic rate (SAS software;

SPSS 2003). Differences were considered significant at $P < 0.05$.

Results

Food Consumption

Mean food consumption rates increased significantly with temperature (Table 1) for both ration levels between 11°C and 15°C ($Q_{10} = 3.33$), but no significant difference was found for either ration level between 15°C and 19°C ($Q_{10} = 1.16$).

Growth

Both temperature and ration level influenced green sturgeon growth rates. Specific growth rates were higher among fish held at 15°C than among those held at 11°C ($Q_{10} = 4.65$) for both rations, whereas no significant differences were detected between the 15°C and 19°C ($Q_{10} = 1.47$) groups at either ration level (Table 1). Specific growth rates were also higher at 100% rations than at 50% rations at all temperatures (Table 1). No significant ($P = 0.25$) interaction occurred between temperature and ration level.

Food Conversion Efficiency

Temperature did not affect green sturgeon food conversion efficiency at 100% rations ($P = 0.38$ – 1.0), whereas efficiency was significantly higher at 15°C than at 11°C ($Q_{10} = 1.42$) at 50% rations (Table 1). Increases in ration level significantly decreased food conversion efficiencies only in the 15°C and 19°C treatments. There was a significant ($P = 0.02$) interaction between temperature and ration level.

Metabolism and Activity

The temperature increase from 11°C to 19°C did not affect the MO_2 s of age-0 green sturgeon ($Q_{10} = 1.50$), but the increase from 19°C to 24°C resulted in a significant increase in MO_2 ($Q_{10} = 4.12$; Table 1). Significant increases in volitional activity (tail beat frequencies) occurred with all temperature increases (Table 1).

In age-1 fish, significant increases in mean resting routine metabolic rate were associated with increases in temperature in all treatments (Table 1); there was greater similarity in the Q_{10} values of the 11–19°C (1.36) and 19–24°C rates (1.72) than there was for the age-0 fish. Ventilatory frequency increased with temperature (Table 1).

As would be expected, the larger, age-1 fish consumed more oxygen than the smaller, age-0 fish (Figure 1). The slopes of these relationships at the

TABLE 1.—Summary (mean \pm SD) of temperature and ration (where applicable) effects on juvenile green sturgeon. Within rows, different letters indicate significant differences (ANOVA; $P < 0.05$).

| Response variable | Ration | Acclimation temperature ($^{\circ}\text{C}$) | | | | <i>P</i> |
|--|--------|--|----------------------|---------------------|---------------------|----------|
| | | 11 | 15 | 19 | 24 | |
| Food consumption (g feed·g fish ⁻¹ ·d ⁻¹) | 50% | 0.0057 \pm 0.0007 z | 0.009 \pm 0.0008 y | 0.01 \pm 0.0008 y | | <0.008 |
| | 100% | 0.01 \pm 0.01 z | 0.02 \pm 0.002 y | 0.02 \pm 0.001 y | | <0.001 |
| Specific growth rate (% weight gain/d) | 50% | 0.65 \pm 0.06 z | 1.39 \pm 0.13 y | 1.59 \pm 0.16 y | | <0.001 |
| | 100% | 1.06 \pm 0.15 z | 1.96 \pm 0.10 y | 2.29 \pm 0.31 y | | <0.001 |
| Food conversion efficiency (g weight gained/g feed) | 50% | 0.23 \pm 0.02 z | 0.32 \pm 0.01 y | 0.32 \pm 0.02 y | | <0.001 |
| | 100% | 0.2 \pm 0.02 z | 0.23 \pm 0.01 z | 0.23 \pm 0.02 z | | 1.000 |
| Age-0 metabolic rate (mg O ₂ ·h ⁻¹ ·g fish ⁻¹) | | 0.1 \pm 0.05 z | | 0.13 \pm 0.07 z | 0.27 \pm 0.08 y | <0.001 |
| Activity (tail beats) | | 537 \pm 567 z | | 1,108 \pm 1,074 y | 1,802 \pm 1,013 x | <0.001 |
| Age-1 metabolic rate (mg O ₂ ·h ⁻¹ ·g fish ⁻¹) | | 0.16 \pm 0.08 z | | 0.20 \pm 0.08 y | 0.27 \pm 0.06 x | <0.02 |
| Ventilatory frequency (strokes/min) | | 67.7 \pm 9.0 z | | 104.8 \pm 13.2 y | 117.6 \pm 17.2 x | <0.01 |
| Preferred temperature ($^{\circ}\text{C}$) | | 15.9 \pm 1.7 z | | 15.7 \pm 2.9 z | 20.4 \pm 3.1 y | |
| Swimming performance (Ucrit. [cm/s]) | | 68.3 \pm 11.9 z | | 80.4 \pm 16.1 z | 56.4 \pm 20.8 y | <0.005 |

three temperatures were similar (weighted mean = 1.07).

Thermal Preference

Fish acclimated to 11 $^{\circ}\text{C}$ and 19 $^{\circ}\text{C}$ did not differ significantly ($P = 0.95$) in their thermal preferences ($15.9 \pm 1.7^{\circ}\text{C}$ and $15.7 \pm 2.9^{\circ}\text{C}$, respec-

tively); however, fish acclimated to 24 $^{\circ}\text{C}$ exhibited a significantly higher ($P < 0.001$) preferred temperature ($20.4 \pm 3.1^{\circ}\text{C}$; Table 1).

Swimming Performance

There was no difference ($P = 0.10$) between the Ucrit values for the 11 $^{\circ}\text{C}$ and 19 $^{\circ}\text{C}$ treatments (Table 1). However, the Ucrit for the 24 $^{\circ}\text{C}$ group was significantly lower than that of the 19 $^{\circ}\text{C}$ group. Approximately 60% of the 24 $^{\circ}\text{C}$ fish died after transport but before being tested for swimming performance.

Discussion

Temperature affected several bioenergetic variables of juvenile green sturgeon. Given the large temperature ranges measured for the Klamath and Rogue rivers (Chamberlain, personal communication; Erickson et al. 2002) when juvenile green sturgeon are likely to be present, effective conservation and management strategies should include water temperature criteria.

Food Consumption

Temperature changes are a major factor influencing oxygen and food demand in fish (Lovell 1989; Nikinmaa 2002). The average food con-

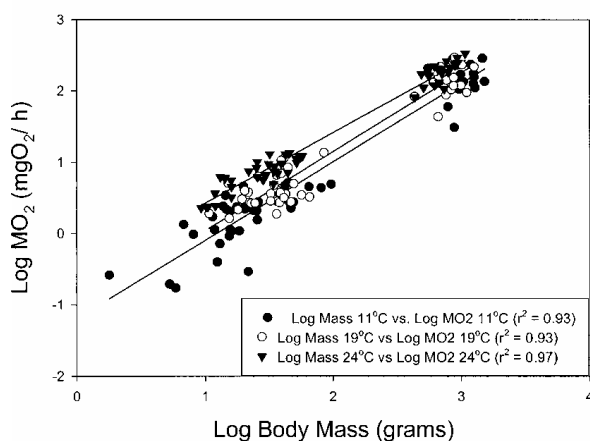


FIGURE 1.—Relationships between \log_{10} metabolic rate (MO_2) and \log_{10} body mass of age-0 and age-1 green sturgeon acclimated to water temperatures of 11, 19, and 24 $^{\circ}\text{C}$. The intercepts and slopes of the equations for the three temperature groups are as follows: $-1.20, 1.10$ (11 $^{\circ}\text{C}$); $-1.06, 1.11$ (19 $^{\circ}\text{C}$); and $-0.56, 0.99$ (24 $^{\circ}\text{C}$).

TABLE 2.—Summary of studies on sturgeon growth rates.

| Species | Weight (g) | Temperature (°C) | Growth rate (% body weight/d) | Feed rate (% body weight/d) | Reference |
|---|------------|------------------|-------------------------------|-----------------------------|------------------------------|
| White sturgeon | 0.5–5 | 15, 20, 25 | 1.6, 2.6, 2.9 | Ad libitum | Cech et al. (1984) |
| Chinese sturgeon <i>Acipenser sinensis</i> | 3.8 | 16 | 4.5 | 6.0 | Xiao et al. (1999) |
| Sterlet <i>A. ruthenus</i> | 20 | 23 | 1.1 | 3.5 | Jahnichen and Rennert (1999) |
| White sturgeon | 26.2 | 20 | 2.1 | 2.0 | Hung and Lutes (1987) |
| White sturgeon | 30.3 | 23, 26 | 2.2, 1.9 | 2.0 | Hung et al. (1993) |
| Atlantic sturgeon <i>A. oxyrinchus</i> | 10.0–70.0 | 19, 26 | 5.0, 3.6 | 2.5 | Secor and Gunderson (1998) |
| Siberian sturgeon | 181 | 11 to 19 | 1.4 | 1.5–2.1 | Prokes et al. (1997) |
| Green sturgeon | 184 | 11, 15, 19 | 1.1, 2.0, 2.3 | 1.3, 1.8, 2.1 | This study |
| White sturgeon | 250 | 18 | 1.5 | 2.0 | Hung et al. (1989) |
| Lake sturgeon | 10–1,322 | 18 | –1.5, 0.0, 1.8, 2.6 | 0.0, 2.2, 9.4, 13.2 | Diana et al. (2000) |

sumption rate increase for green sturgeon associated with the increase from 11°C to 15°C can be at least partly attributed to the increased energetic demands of the fish at the higher temperature. Increased food consumption fueled the increased growth, activity, and maintenance demands. Increased food consumption at higher water temperatures is not unique to sturgeon species. Given adequate access to food, fish increase their consumption as temperature rises; peak consumption occurs before the temperature reaches the upper thermal tolerance limit for the species (Jobling 1994). Larsson and Berglund (1998) found this pattern for age-0 Arctic char *Salvelinus alpinus*, for which food consumption peaked at 16°C over a 5–20°C range. In contrast, the food consumption of the green sturgeon in this study never declined at temperatures up to 19°C, although this result suggests the need for more data at higher temperatures and at temperatures between 15°C and 19°C to determine a peak temperature for food consumption.

Growth

When food is available, fish growth increases with temperature, followed by a decline when lethal temperatures are approached (Jobling 1994). In this study, the diminishing growth effect at temperatures above 15°C was linked to increased energy demands for maintenance and activity associated with higher temperatures. The maximum growth rates of our fish may have been limited by the twice-daily (rather than continuous) feeding schedule.

Despite the potentially suboptimal feeding regime in our study, the fish had high growth rates (given their acclimation temperature and ration levels) compared with other sturgeon species of similar

body size. For example, Siberian sturgeon *A. baeri*, lake sturgeon *A. fulvescens* of a large size range, and sympatric white sturgeon all grew more slowly at temperatures similar to those in our study (Table 2) despite having equal or higher ration levels (Hung and Lutes 1987; Hung et al. 1989; Prokes et al. 1997; Diana et al. 2000). Furthermore, despite a higher temperature and ration level, sterlet (20 g) grew more slowly than our green sturgeon (Jahnichen and Rennert 1999). At comparable or higher temperatures, Chinese sturgeon (Xiao et al. 1999) and Atlantic sturgeon (Secor and Gunderson 1998) did grow faster than our green sturgeon, but they were fed higher ration levels (Table 2). These latter comparisons can be deceiving, however, because the smaller body size of sterlet and Chinese and Atlantic sturgeon contributes to higher specific growth rates (Ricker 1979).

Food Conversion Efficiency

Food conversion efficiency in fish typically increases with temperature to some maximum, followed by a decline (Jobling 1981). Common carp *Cyprinus carpio* increased their food conversion efficiency from 0.28 to 0.55 with temperature increases over the 12–30°C range (Goolish and Adelman 1984). Furthermore, peak food conversion efficiency may typify intermediate rations rather than maintenance (no growth) and maximal rations (Davis and Warren 1971). At all temperatures, Goolish and Adelman's (1984) carp showed peak food conversion efficiency at intermediate rations. Because our green sturgeon grew moderately well at the 50% ration level, this level could be considered a moderate one, with a food conversion efficiency pattern comparable to that of the carp.

Despite a possible underestimate of food conversion efficiency owing to the partial erosion of

TABLE 3.—Summary of studies on sturgeon feeding efficiencies. Feeding efficiency = wet weight gained by fish/total amount of feed fed to the fish.

| Species | Weight (g) | Temperature (°C) | Feeding efficiency (g weight gain/g feed) | Feed rate (% body weight/d) | Reference |
|-------------------|------------|------------------|---|-----------------------------|------------------------------|
| Sterlet | 20.0 | 23 | 2.0 | 3.5 | Jahnichen and Rennert (1999) |
| White sturgeon | 30.0 | 23, 26 | 1.3, 1.1 | 2.0 | Hung et al. (1993) |
| Green sturgeon | 184.0 | 11, 15, 19 | 1.0, 1.1, 1.1 | 1.3, 1.8, 2.1 | This study |
| Siberian sturgeon | 190.7 | 11.0–18.0 | 1.4 | 1.5–2.1 | Prokes et al. (1997) |
| White sturgeon | 250.0 | 18.0 | 0.9 | 2.0 | Hung et al. (1989) |

the pellets, green sturgeon appear to have food conversion efficiencies similar to those of other *Acipenser* species. Using feeding efficiency (wet weight gained per amount of feed consumed during the experiment) for comparative purposes (Table 3), the feeding efficiencies of our juvenile green sturgeon approximate those of juvenile white sturgeon at similar temperatures (Hung et al. 1989, 1993). Hung et al. (1993) and Hung and Lutes (1987) found that the highest feeding efficiency for juvenile white sturgeon occurred between 20 and 23°C, which was beyond the range used in our studies.

Metabolism and Activity

The metabolic and activity patterns of the age-0 and age-1 green sturgeon reflect different temperature sensitivities. While the high Q_{10} value (4.12) for age-0 green sturgeon between the 19°C and 24°C treatments shows a high metabolic temperature sensitivity, the lower Q_{10} value (1.50) and the lack of a significant difference between the MO_2 s for the 11°C and 19°C treatments demonstrates a relative insensitivity. Assuming that this relative insensitivity does not stem from increased relative error at lower MO_2 s, it would be advantageous to allow age-0 green sturgeon to forage in thermally diverse habitats. The larger Q_{10} value and the significant difference in MO_2 s between the two higher temperature treatments suggests that age-0 green sturgeon inhabiting water warmer than 19°C would be at an energetic disadvantage in having to expend significantly more energy on maintenance and activity and comparatively less on growth.

Increases in volitional swimming and activity with temperature typify poikilothermic animal behavior (e.g., Wurtsbaugh and Cech 1993), including that of our age-0 sturgeon ($r^2 = 0.98$). White sturgeon also significantly increase their activity with temperature over a 10–25°C range (Cech et al. 1984; Crocker and Cech 1997). Such increases presumably facilitate more widespread foraging to meet temperature-associated increases in energy

requirements for growth (Cech et al. 1984) and metabolism (Crocker and Cech 1997). Concurrent measurements showed that volitional activity (tail beats) increased with temperature over the 11–19°C range, whereas routine metabolism remained unchanged over the same range. Without being penalized energetically for increased activity (e.g., for foraging) over the above temperature range, a fish would be able to devote more energy to growth. Faster growth can decrease predation risk by minimizing the time spent as small, relatively vulnerable prey (Werner and Hall 1988). Although the age-1 green sturgeon significantly increased their MO_2 s with each temperature increase, they were quiescent in flow-through respirometers and their Q_{10} s were more consistent across the temperatures than those of age-0 fish. The quiescence of the age-1 fish may reflect either an age-related difference in volitional activity or the more confining dimensions of the flow-through respirometers. All metabolic measurements were conducted during daylight hours. Lankford et al. (2003) noted that green sturgeon in the size range of our age-1 fish were more nocturnally active.

Green sturgeon exhibited high metabolic rates relative to other sturgeon species (Table 4). For example, McKenzie et al. (1997) reported an MO_2 in Adriatic sturgeon (mean weight, 198 g) at 23°C that was less than one-half the value for our green sturgeon at 24°C. The higher MO_2 s of our fish may be due to proportionally larger red muscle masses. Moyle (2002) describes the extensive red muscle in green sturgeon. Red muscle, with its higher mitochondrial density than white muscle, exhibits higher tissue MO_2 s (Gordon 1968).

In terms of the bioenergetic model (equation 1), temperature-related increases in I were allocated proportionately more to G at temperatures up to 15°C and proportionately more to M at temperatures above 15°C. Volitional activity (A) increased throughout the temperature range. While E and SDA were not measured, they have been shown

TABLE 4.—Summary of routine metabolism studies for sturgeons.

| Species | Weight (g) | Temperature (°C) | Routine metabolism (mg O ₂ ·h ⁻¹ ·g fish ⁻¹) | Reference |
|-------------------|------------|------------------|--|-----------------------------|
| White sturgeon | 02–63 | 10, 16, 20 | 0.26, 0.20, 0.18 | Crocker and Cech (1997) |
| Green sturgeon | 22.3 | 11, 19, 24 | 0.10, 0.13, 0.27 | This study |
| Atlantic sturgeon | 12.0–69 | 19, 26 | 0.20, 0.30 | Secor and Gunderson (1998) |
| Adriatic sturgeon | 198 | 23 | 0.11 | McKenzie et al. (1997) |
| Green sturgeon | 851 | 11, 19, 24 | 0.16, 0.20, 0.27 | This study |
| White sturgeon | 950 | 15 | 0.08 | Burggren and Randall (1978) |
| Siberian sturgeon | 1,800 | 15 | 0.06 | Nonnette et al. (1993) |
| White sturgeon | 2,000 | 18 | 0.10 | Ruer et al. (1987) |

to increase with I (Kitchell et al. 1977), and R is irrelevant in these juvenile fish.

Thermal Preference

Conservation efforts will also require knowledge of sturgeon behavior (thermal preference) and locomotory (swimming) performance to develop the best management plans. Although both the 11°C and 19°C acclimation temperatures fall within the thermal regimes of the Rogue and Klamath rivers (Erickson et al. 2002; Chamberlain, personal communication), the similar thermal preference values (15.9°C and 15.7°C, respectively) suggest that 15–16°C is the temperature range preferred by age-0 green sturgeon in their natural habitats. Interestingly, the 11–15°C range was the one in which the fish showed the sharpest increase in growth rates and in food conversion efficiency (followed by slight increases beyond 15°C). Fish commonly select temperatures that promote optimal growth (Jobling 1981) and those at which physiological functions operate at maximum efficiency (Crawshaw 1977). The less pronounced temperature effect beyond 15°C suggests a lesser benefit with respect to growth for age-0 green sturgeon at higher temperatures. Conversely, regimes cooler than 15°C would decrease the growth rate regardless of food availability and can decrease muscle twitch time (Rome 1990), increasing vulnerability to predators via slower escape initiation or swimming performance. Marbled rockfish *Sebastes marmoratus* (weight, 10.7 ± 1.4 g) preferred 21°C within the 15–25°C range (Kita et al. 1996). Further, they found that the observed preferred temperature coincided with the temperature range at which MO_2 increases were less pronounced. This pattern was similar to that seen in our study, in which the preferred temperatures (although based on short laboratory observations) were between 11°C and 19°C and the corresponding MO_2 s were not significantly different.

Thermal tolerance was originally planned to be

part of this study; however, the anatomy (large pectoral fins) and demersal nature of green sturgeon made it difficult to define a loss of equilibrium for some of the fish, which was our endpoint for measuring this variable. Jobling (1981) reported the following linear relationship between preferred (X) and lethal (Y) temperatures in fish:

$$Y = 0.66X + 16.45 \quad (r = 0.880). \quad (8)$$

Applying this equation to the juvenile green sturgeon's preferred temperature (15.8°C) results in a 27°C lethal temperature. Whereas many of the age-1 fish acclimated to 25°C died after being transported to a holding tank for high-temperature (24°C) swimming performance measurements, identical transportation of age-1 fish acclimated and swum at cooler temperatures never resulted in mortality, suggesting that 25°C approximates the maximum temperature for transporting age-1 green sturgeon. The lethal temperature would thus be near the value calculated from the regression equation. The continuous flow of water (with non-detectable ammonia levels) in these experiments ensured that the calculated lethal temperature was not influenced by dissolved substances.

Conclusions

The presence of significant differences in swimming performance associated with temperature may have been confounded by the thermal sensitivity of the fish to handling (see above). Peake et al. (1997) recommended 14°C for adult lake sturgeon migrating up their spawning rivers. Swimming ability could be relevant to the successful instream rearing (foraging and predator avoidance) and downstream migration of juvenile sturgeon. Reduced swimming performance at temperatures above 19°C could jeopardize those essential life history activities.

Overall, management plans for watersheds containing juvenile green sturgeon should include water

temperature criteria that prevent prolonged exposure to regimes beyond 19°C, which represent the species' growth and locomotory optima. Using temperature as a management tool to provide optimal environmental conditions for protecting fish is well documented. Magnuson et al. (1979) described the temperature-related habitat partitioning of several freshwater fishes using laboratory preference and field distribution data sets. Armour (1991) related individual temperature tolerance data to predicted population-level responses to protect fish in natural habitats. Future studies on green sturgeon should examine the effects of other relevant factors (e.g., dissolved oxygen) to foster better understanding of this species' environmental requirements and better protection of its populations.

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