

## Comparison of Early Life Stages and Growth of Green and White Sturgeon

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**Abstract.**—Gametes of green sturgeon *Acipenser medirostris* (caught in the Klamath River, California) and farm-reared white sturgeon *A. transmontanus* were obtained using hormonal induction of ovulation and spermiation. The offspring of one female in each species were reared in the laboratory, to compare their development and growth. Green and white sturgeon embryos had similar rates of development and hatched after 169 h and 176 h, respectively, at incubation temperature  $15.7 \pm 0.2^\circ\text{C}$ . Embryos of both species exhibited similar holoblastic development and passed through 36 stages characteristic of acipenserids. Green sturgeon fertilization and hatching rates were 41.2% and 28.0%, compared with 95.4% and 82.1% for the white sturgeon. Larval survival to 45 d (metamorphosis) was 93.3% in green and 92.1% in white sturgeon. Newly hatched green sturgeon (length  $13.7 \pm 0.4$  mm, mean  $\pm$  SD) were larger and less pigmented, compared with white sturgeon. They had large ovoid yolk sacs and did not exhibit pelagic behavior that was observed in white sturgeon. The onset of exogenous feeding in green sturgeon occurred at age 10–15 d and length  $24.0 \pm 0.5$  mm, and metamorphosis was completed at age 45 d and length  $74.4 \pm 5.9$  mm (rearing temperature  $18.5 \pm 0.2^\circ\text{C}$ ). Weight and length of green sturgeon larvae and juveniles were considerably greater than in white sturgeon at each sampling time, but the relative growth rate and weight-length relationship were similar in both species. This suggests an effect of larger egg size and maternal yolk supply on the growth of green sturgeon. We conclude that green sturgeon differs from the white sturgeon in their reproductive strategy and, potentially, reproductive habitat.

Green sturgeon *Acipenser medirostris* are widely distributed in the coastal waters along the north Pacific Ocean, having been recorded from at least six countries: the United States, Canada, Mexico, Russia, Japan, and Korea. However, because of low abundance, the green sturgeon are considered a threatened or vulnerable species in Canada and the United States and an endangered species in Russia (Houston 1988; Artyukhin and Andronov 1990; Moyle et al. 1994). Spawning populations of the anadromous green sturgeon have been identified in only a few rivers. In Asia, spawning has been found in the Tumnin River, and a successful artificial spawning of two females was reported (Artyukhin and Andronov 1990). In North America, green sturgeon spawning occurs in the Sacramento and Klamath Rivers, California, and in the Rogue River, Oregon (Moyle et al. 1994). Despite the green sturgeon's wide geographic distribution, there is no information on spawning migrations, spawning and nursery habitats, or the early life stages of this species.

We recently initiated studies on hatchery spawning and reproduction of green sturgeon and conducted the first artificial spawning in 1999 on the Klamath River (Van Eenennaam et al. 2001). As part of a larger project to study the biology of green sturgeon, the objective of this study was to examine the development and growth of green sturgeon in comparison with the sympatric white sturgeon *A. transmontanus*. Although the fertilized eggs of only one green and white sturgeon female were used in this study, we describe the important characteristics of the embryonic development and early life stages, as well as the larval growth in two species.

### Methods

The artificial spawning of green sturgeon was conducted on the lower Klamath River at Weitchpec, during 18–20 May 1999. One female (weight 48 kg) and five males, captured by gill net, were induced to ovulate and spermiate by administration of GnRH $\alpha$  and domperidone (Van Eenennaam et al. 2001). Fertilized with pooled milt, eggs

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were transported (6 h) to facilities of the Center for Aquatic Biology and Aquaculture (CABA) at the University of California, Davis. Fertilized eggs from one female white sturgeon (weight 63 kg) were obtained from Stolt Sea Farm California, LLC (Wilton, California), in July 1999, and transported (1 h) to CABA. Gametes were obtained using the same spawning induction protocol as for the green sturgeon but without domperidone. All husbandry procedures and sampling methods were identical for both species, as described below.

Upon arrival to CABA, fertilized eggs were acclimated to the incubation temperature for 1 h and placed in McDonald jars at a density of 1–1.5 L of eggs per jar (Conte et al. 1988). A 14 L:10 D photoperiod was maintained by artificial illumination throughout the incubation period. The water flow in the incubators was carefully adjusted, to allow the eggs to roll gently during the early stages (cleavage and gastrulation), and was increased at the later stages of development, to reduce the incidence of fungal infection. Dead eggs were periodically removed by siphon and counted as mortality. Incubation was conducted in a semirecirculation system, where the water was filtered and chilled and temperature was maintained at  $15.7 \pm 0.2^\circ\text{C}$  (range  $15.5$ – $15.8^\circ\text{C}$ ).

Hatched larvae were transferred into the circular larval receiving tank (1.2 m-diameter) connected to the semirecirculation system, and during the next 5 d the water temperature, was increased to  $18.5^\circ\text{C}$ , at a rate of  $1^\circ\text{C}$  per day. One-thousand five-hundred 5 d old larvae were stocked into a circular flow-through tank of 1.2 m-diameter and 355 L-volume, in a separate building with skylight windows. Water was supplied by a spray bar, at a rate of 9–10 L/min, creating a circular current in the tank. Fish were fed a commercial semimoist fry feed (Silver Cup, Nelson & Sons, Inc., Murray, Utah), provided continuously over 24 h by 3 automatic feeders placed at equal distances around the wall of the tank. The fish were also hand fed 5 g of chopped *Tubifex* worms twice a day. The tank was exposed to natural photoperiod, but the light intensity was partially reduced by black plastic shade cloth extending over 2/3 of the tank. The tank was cleaned daily, and mortalities were removed and recorded. Larval behavior was observed during the day and at night, with a white dim flashlight with which no obvious disturbance occurred. Water temperature was recorded daily and averaged  $18.5 \pm 0.2^\circ\text{C}$  (range  $18.2$ – $18.7^\circ\text{C}$ ). The dissolved oxygen exceeded 8.6 mg/L during the entire 45 d rearing period.

Staging of embryonic development followed the classification of Dettlaff et al. (1993) that includes 36 stages to hatching. More than 300 eggs were randomly sampled at cleavage (stages 5–6) to determine the rates of fertilization. The embryonic development was closely monitored in McDonald jars, and the published developmental rates of white (Wang et al. 1985) and Russian (Dettlaff et al. 1993) sturgeon *A. gueldenstaedti*, at similar temperatures, were used to estimate sampling time for specific stages of the green sturgeon. To estimate the rate of development, the post fertilization time was recorded when more than 50% of the eggs reached a defined stage. All embryos were fixed in 10% phosphate-buffered formaldehyde solution for further observations and measurements. Thirty preserved ova and stage 5 (second cleavage, fully formed perivitelline space) eggs were weighed ( $\pm 0.1$  mg) and measured ( $\pm 0.01$  mm) for maximum diameters under a dissecting microscope with a digital image-analyzing tablet. The chorions of the additional five eggs at each stage were removed under a dissecting microscope before fixation, to facilitate photomicrography.

Samples of 30 larvae and juveniles were collected at days 0 (hatching), 1, 3, 6, 10, 15, 21, 28, 36, and 45 post hatch. Animals were euthanatized by overdose of MS-222 and preserved in buffered formalin for further observations and measurements. All larvae were individually weighed and measured for length under a dissecting microscope or by using a micrometer caliper. Measurements reflect minor shrinkage due to fixation in formalin.

Mean weight and length of green and white sturgeon were compared by Student's *t*-test. A few larvae (with bent bodies or other defects) were deleted from the samples before calculation of means and standard deviations. The specific growth rates were calculated as  $100 \times (\ln W_t - \ln W_0) / t$ , where  $W_t$  and  $W_0$  are mean body weight at each of the two samplings, and *t* is the number of days between the two samplings. Weight-length relationships were evaluated by linear regression analysis using  $\log_{10}$ -transformed data. The regressions were tested for the lack of fit and their slopes compared using a *t*-test. The JMP Statistical Software (Version 3, SAS Institute, Cary, NC) was used for data analysis. The accepted significance level was  $P < 0.05$ .

Photomicrographs of embryos and larvae were scanned by SprintScan 35 plus (Polaroid Cooperation, Cambridge, Massachusetts) and

edited using Adobe Photoshop Software (Version 5.0) to remove the dark background and to adjust contrast for clearer pictures.

## Results

### Survival Rate

Fertilization (Stage 5) and hatching (Stage 36) rates for eggs from the wild green sturgeon were 41.2% and 28.0%, respectively (Van Eenennaam et al. 2001), whereas the domestically reared white sturgeon exhibited higher fertilization (95.4%) and hatching (82.1%) rates. Larval survival from hatching to metamorphosis (age 45 d) was high in both species, 93.3% in green and 92.1% in white sturgeon. No mortalities occurred after 32 d posthatch in green sturgeon, while cumulative mortality of white sturgeon exhibited small but steady increases throughout the 45 d experiment.

### Embryonic Development

Early development of green sturgeon followed the holoblastic style of Acipenseriformes described in detail by Dettlaff et al. (1993). We refer to their descriptions and briefly characterize selected stages with the distinguishing characteristics of green sturgeon (Figure 1 and 2). For comparative purposes, similar stages of white sturgeon are given (for more detailed illustrations see Beer, 1981). Enumeration of stages corresponds to the classification of Dettlaff et al. (1993).

*Stage 5* (second cleavage, Figure 1).—The eggs of green sturgeon, although varying slightly in pigmentation, had a flattened white animal region with a small dark pigmented spot in the center, which was unevenly divided by the two cleavage furrows. Their vegetal hemisphere was brown-olive green. A narrow pigmented ring (with lighter pigmentation on the other side), which was not apparent at this stage in white sturgeon eggs, appeared along the boundary between animal and vegetal regions. The weight of green sturgeon eggs that completed hydration and hardening increased from  $35.6 \pm 0.9$  mg (ova) to  $38.6 \pm 1.2$  mg (stage 5) and their maximum diameter from  $4.17 \pm 0.12$  to  $4.44 \pm 0.15$  mm, respectively ( $N = 30$ ). Smaller white sturgeon eggs were more darkly pigmented and exhibited similar relative increases in weight (from  $17.9 \pm 1.1$  to  $21.6 \pm 0.8$  mg) and diameter (from  $3.40 \pm 0.09$  to  $3.57 \pm 0.11$  mm) at stage 5 ( $N = 30$ ).

*Stage 14* (early gastrula, Figure 1).—The horizontal blastopore in green sturgeon embryos ap-

peared as a short shallow groove and was darkly pigmented. Blastomeres positioned along the border between animal and vegetal regions (marginal zone) were intermediate in size and darker than those at either pole, forming a wide speckled zone that appeared at the late cleavage stage. A ratio of the distance from blastopore to animal pole to that from blastopore to vegetal pole varied within a range of 0.60–0.95, indicating the variable location of the blastopore above the egg equator. The horizontal blastopore of white sturgeon embryos appeared on the equator (Beer 1981; Bolker 1993b).

*Stage 22* (late neurula, Figure 1).—The neural plate (in a process of folding) slightly protruded above the surface of the green sturgeon egg with a diamond-shaped opening in the anterior part and incomplete closure of neural fold in the trunk region. The region of the neural plate was grayish, and the rest of the embryo was yellowish. White sturgeon eggs had a similar neurulation pattern with a darker pigmented neural plate. Epiboly was completed in both species before the onset of neurulation.

*Stage 35* (embryo before hatch, Figure 1).—The egg chorion was softened and became fragile after secretion of a hatching enzyme (Dettlaff et al. 1993). The hatching gland was evident in front of the mouth cleft. With an actively twisting tail and trunk, the tail of an embryo was able to break through the chorion and stretch out. The chorion surrounding the head and ovoid shaped "yolk sac" (endoderm in sturgeon) was discarded by further movement of the trunk.

*Rates of embryo development.*—The chronology of embryonic development of the green and white sturgeon was similar (Table 1). Despite the great difference in egg size, the green and white sturgeon embryos exhibited an overall similar rate of development at 15.7°C. Cleavage and morphogenetic movement appeared to proceed at slower rates in green sturgeon. However, the developmental pace was accelerated before hatching, resulting in an 8 h earlier mass hatching than in the white sturgeon. Hatching occurred over two days in both species, from 144 to 192 h after fertilization in green sturgeon and from 152 to 200 h in white sturgeon. The earlier hatching of the green sturgeon could also be associated with its thin and fragile chorion.

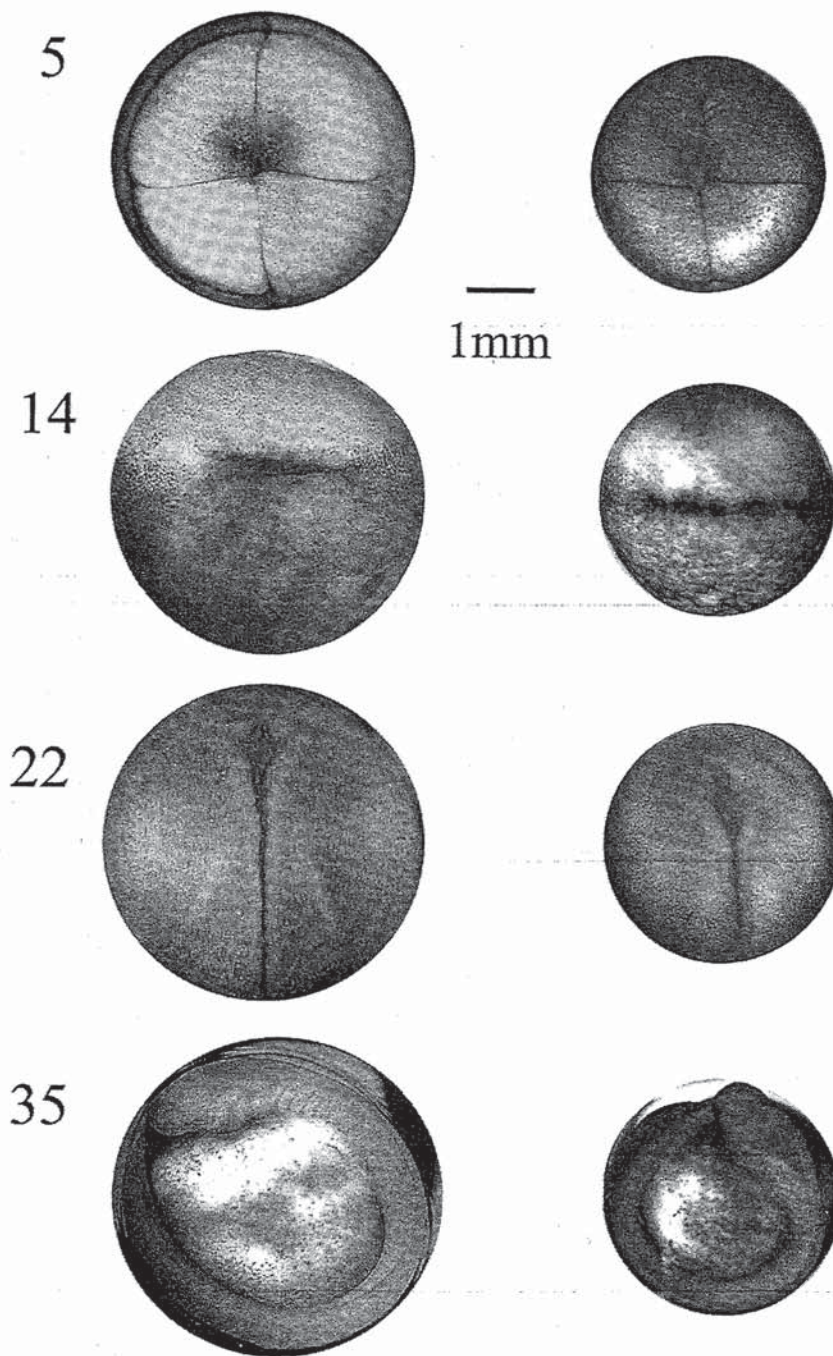


Figure 1. Stages of embryonic development of green sturgeon (left) and white sturgeon (right). Stage 5—second cleavage; Stage 14—early gastrula; Stage 22—late neurula; Stage 35—prehatch embryo (stages by Dettlaff et al. 1993).

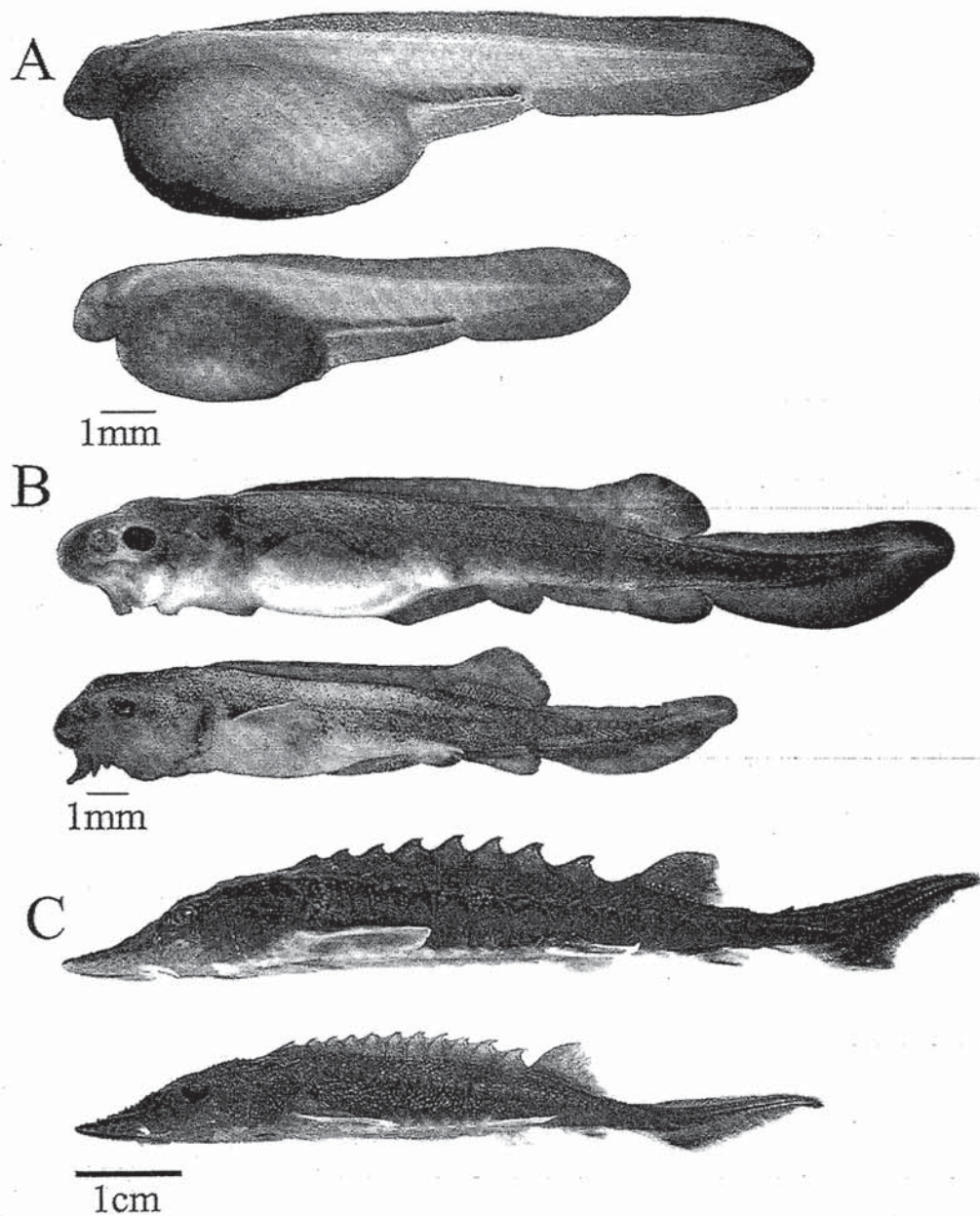


Figure 2. Larvae and juveniles of green and white sturgeon at the same age. Green sturgeon on the top and white sturgeon at the bottom in A, B, and C, respectively. A—posthatch larvae (stage 36); B—larvae at the onset of feeding (10 d posthatch); C—juveniles (45 d posthatch).

Table 1. Chronology of embryonic development of green and white sturgeon at 15.7°C. Time of respective stages (Dettlaff et al. 1993) is in h:min after fertilization.

Stages	Green sturgeon	White sturgeon
1	0	0
4	6:10	4:10
5	7:40	4:55
6	9:40	5:50
7	10:30	7:00
8	10:57	7:30
9	-	9:10
10	-	10:10
11	17:55	13:00
12	23:58	-
13	27:15	23:40
14	31:35	-
15	-	31:20
16	41:45	35:00
17	45:25	39:50
18	47:45	-
19	48:30	-
20	49:25	46:10
21	52:50	49:00
22	55:00	52:50
23	57:30	-
24	65:40	-
25	68:52	70:00
26	-	-
27	80:40	77:20
28	89:50	83:00
29	97:35	-
30	-	95:00
31	-	104:00
32	145:35	120:00
33	154:05	128:30
34	161:50	144:00
35	-	159:40
36	169:00	176:40

### Larval Development

*Larvae at hatch* (Figure 2A). —Newly hatched green sturgeon (L = 12.6 - 14.5 mm, range) were grayish in the trunk and had a large ovoid yolk sac with yellowish coloration. They were considerably less pigmented than the white sturgeon larvae. The larval body had 63-71 myotomes, of which 36-41 are anterior to the cloaca and 27-31 were posterior to the cloaca. The eyes were well developed, with differentiated lenses and a dark pigmented spots. Olfactory and auditory vesicles were present. Mouth and gill cover differentiation began as a shallow cleft. The posterior intestine contained a dark pigment in the spiral valve. The paired Cuvier's ducts and yolk veins with red

blood were highly developed. The continuous fin fold was interrupted at the cloaca and had a slightly wrinkled area in the preanal region posterior to the yolk sac. The rudiments of pectoral fins appeared as small buds on the dorsal part of the yolk sac behind the pronephros. White sturgeon hatchlings (L = 10.0 - 11.0 mm) were darker, with dense melanin pigmentation of the trunk and yolk sac. White sturgeon larvae appeared to be less developed at hatching, lacking eye lenses and pectoral fin buds. Their fin folds were smooth and not wrinkled at the preanal regions as it was in green sturgeon.

*Larvae at the onset of feeding* (Figure 2B). —At 10 d of age, pigmentation of green sturgeon (L = 23.0 - 25.2 mm) greatly increased on the head and along the trunk, except the ventral region. The larvae became dark gray. Myotomes extended to the ventral side of the yolk sac, which was greatly diminished in size, resulting in a streamlined body shape. The barbels had been elongated. Rays started to form in all fin rudiments, including the lower lobe of the caudal fin. The pectoral fins moved down to the ventral region and acquired a horizontal position. The fin fold discontinued posterior to both the dorsal and anal fins. The lateral lines extended over the mid-body. The third pair of branchial arches had formed. Larval teeth were visible on the upper and lower jaws. The spleen was present as a bright red spot. In white sturgeon of the same age (L = 17.3 - 19 mm), larvae were darkly pigmented in the tail region. Their yolk was practically absorbed, and the lateral lines were completely developed. Some of the larvae started releasing their melanin plugs. White sturgeon larvae started exogenous feeding at this stage.

*Juveniles at metamorphosis* (Figure 2C). —At 45 d of age, the green sturgeon (L = 62.5 - 94.4 mm) had completed metamorphosis, which was characterized by development of dorsal, lateral, and ventral scutes, elongation of barbels, rostrum, and caudal peduncle, full resorption of caudal and ventral fin folds, and development of fin rays. Juveniles were similar to adults in body shape and olive-green coloration, with a dark midventral stripe. Development of lateral scutes started at the anterior portion of the trunk immediately posterior to the gill cover, progressing toward the caudal region, while dorsal and ventral scutes started differentiation in the mid-body region anterior to

the dorsal and ventral fins. The ventral scutes appeared at 28 d after the dorsal and lateral scutes had been differentiated. At age 45 d, green sturgeon juveniles had 25.7 (24–28) lateral scutes, compared with 37.8 (34–40) in the white sturgeon (mean and range,  $N = 5$ ). A few small bony grains and platelets started to develop at age 28 d between the dorsal and lateral scutes, but they were not abundant at metamorphosis and gave the green sturgeon skin a smooth appearance, compared with the white sturgeon. In white sturgeon ( $L = 31.0 - 78.2$  mm at 45 d), the bony grains and platelets began to appear on the dorsal portion of the head as early as 15 d post hatch. They continued to develop and became abundant on the head, operculum and the whole trunk (except the ventral portion), giving the skin of white sturgeon juveniles a rugged appearance. White sturgeon juveniles had the uniform gray coloration of their bodies.

#### Growth and Weight-Length Relationship

Changes in length and weight of green and white sturgeon larvae and juveniles are shown in Figure 3. Mean ( $\pm$ SD) weight and length of newly hatched larvae were  $36.3 \pm 2.4$  mg and  $13.7 \pm 0.4$  mm ( $N = 29$ ), for green sturgeon, and  $15.8 \pm 0.9$  mg and  $10.6 \pm 0.3$  mm ( $N = 28$ ), for white sturgeon. Based on the biochemical study with white sturgeon larvae (Wang et al. 1987), the increase in wet weight during the endogenous feeding (days 0–10) was caused by an increase of moisture content, since the dry matter decreases during the endogenous feeding phase. At the feeding stage (age 10 d), mean weight and length were  $88.3 \pm 4.3$  mg and  $24.0 \pm 0.5$  mm ( $N = 27$ ), for green sturgeon, and  $41.9 \pm 2.4$  mg and  $18.4 \pm 0.5$  mm ( $N = 27$ ), for white sturgeon. Mean weights increased rapidly in both species during exogenous feeding (days 15–45), and green sturgeon were larger at each sampling time (Figure 3). At age 45 d, the weight and length of green sturgeon juveniles were  $2500 \pm 525$  mg and  $74.4 \pm 5.9$  mm ( $N = 27$ ), while the weight and length of the white sturgeon were  $1471 \pm 864$  mg and  $60.9 \pm 15.3$  mm ( $N = 29$ ). However, the specific growth rates during the exogenous feeding phase (15–45 d) were similar in both species,  $10.4\% d^{-1}$  and  $10.2\% d^{-1}$  for green and white sturgeon, respectively.

The analysis of weight-length relationship revealed two developmental periods of allometric growth: the yolk absorption phase, with low regression slopes, and the exogenous feeding phase, with higher slopes (Figure 4). The linear

equations for log-transformed variables are given below ( $W$ ,  $L$ , and  $R^2$  are body weight, total length and coefficient of determination):

Green sturgeon: age 0–6 d  $\log W = 0.118 + 1.267 \log L$ ,  $R^2 = 0.93$  ( $N = 115$ )

21–45 d  $\log W = -1.764 + 2.764 \log L$ ,  $R^2 = 0.99$  ( $N = 111$ )

White sturgeon: age 0–6 d  $\log W = -0.207 + 1.384 \log L$ ,  $R^2 = 0.93$  ( $N = 117$ )

15–45 d  $\log W = -1.869 + 2.795 \log L$ ,  $R^2 = 0.99$  ( $N = 146$ )

There was no significant difference in the regression line slopes for each developmental period between the two species, indicating similar patterns of allometric growth. Fish sampled at the onset of exogenous feeding (10 d in white and 10–15 d in green sturgeon) had a large variation in weight and length and did not fit either regression line (Figure 4, shown by larger symbols).

#### Larval Behavior

Green sturgeon larvae did not exhibit the pelagic swim-up behavior seen in other acipenserids. During the first 5 d post hatch, the green sturgeon larvae exhibited a strong tendency to clump together in large numbers at the bottom, around the edges of stones, polyvinyl chloride (PVC) pipes, the central drain pipe, or along the wall of the tank. They remained in clumps with limited movement during the night. Larvae began to display a nocturnal swim-up behavior at 6 d post hatch, when the rudiments of the pectoral and ventral fins were developed, dorsal and anal fin rays became apparent, yolk of the mid-intestine was depleted, and the mandible started rhythmic movement. Larvae clumped under the shade cloth during the day but swam actively during the night. These nocturnal behavior patterns persisted in green sturgeon from the onset of exogenous feeding to metamorphosis.

Unlike the green sturgeon, white sturgeon exhibited pelagic behavior during the first 5 d after hatching. The white sturgeon larvae swam up and out of the incubation jars upon hatching, dispersed throughout the water column in the rearing tank, and swam constantly during the day and night. They began to display nocturnal behavior, similar to green sturgeon, at 6 d post hatch, with the transition from the pelagic to a demersal swimming during the day and dispersal into the water column during the night. The white sturgeon swam at the bottom of the tank, aggregating in small groups, but never clumped as strongly as the green sturgeon. At the onset of exogenous

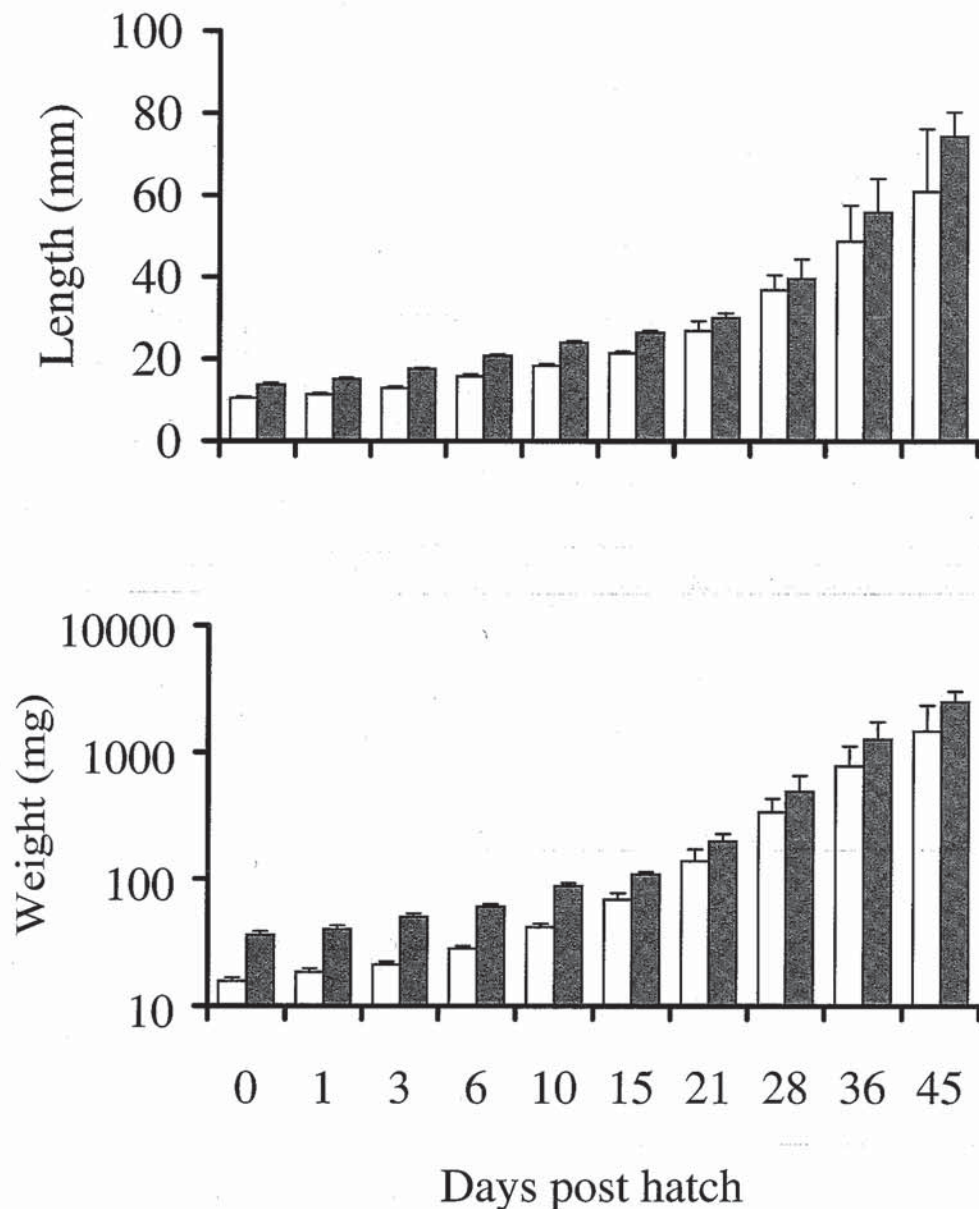


Figure 3. Length and weight (mean  $\pm$  SD) of white (open bars) and green (shaded bars) sturgeon from hatching to metamorphosis. Weight is shown in log-scale.

feeding, the clumping behavior disappeared, and larvae dispersed along the tank bottom.

#### Discussion

Embryos of green sturgeon exhibit the holoblastic pattern of development, similar to white stur-

geon (Beer 1981; Bolker 1993a, 1993b) and other acipenserids (Dettlaff et al. 1993). The rates of embryonic development and hatching time, at temperature 15.7°C, are similar in green and white sturgeon. Newly hatched larvae of green sturgeon are longer and heavier than larvae of white sturgeon, and they possess large reserves of endoder-



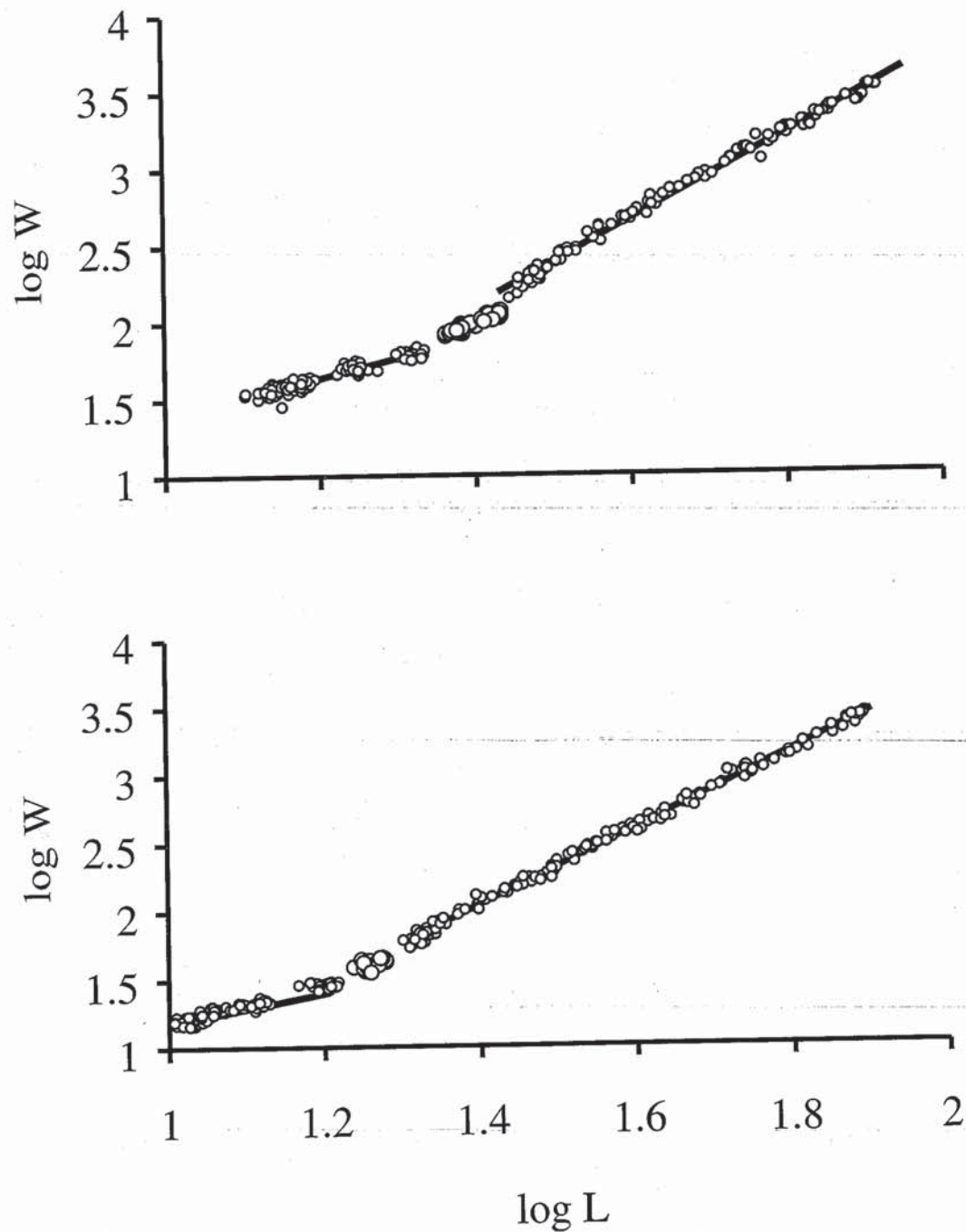


Figure 4. Weight-length relationships of green (top) and white (bottom) sturgeon (scatters and regression lines). The enlarged symbols (circle) show samples taken at the onset of exogenous feeding (not included in regression).

mal yolk. They can be distinguished from white sturgeon by their light pigmentation and the shape and size of the yolk sac. Juveniles of the two species are clearly distinguished by the number of lateral scutes, coloration, and the smooth skin in green sturgeon (versus rugged skin of white sturgeon).

While the fertilization and hatching rates were lower in green sturgeon (likely due to stress from capture and handling or delayed removal of eggs), the survival of larvae to metamorphosis was very high (93.3%). The large size and robustness of green sturgeon larvae contributed to their high survival rate in our previously reported hatchery trials (Van Eenennaam et al. 2001). Since the specific growth rates of green and white sturgeon, from the onset of exogenous feeding to metamorphosis, were similar, it appears that green sturgeon juveniles are larger due to the greater reserve of maternal yolk and, consequently, larger size at the onset of exogenous feeding.

Based on one progeny of each species, we present the first information on green sturgeon development and growth, which are comparable to those of white sturgeon under our specific culture conditions. While our study does not account for individual variation of egg size in the two species, the literature currently available does support significantly larger egg size in green sturgeon (Van Eenennaam et al. 2001), compared with white sturgeon (Lutes et al. 1987). However, egg size and color are known to vary greatly in sturgeon (Dettlaff et al. 1993); therefore, the egg pigmentation pattern needs to be verified, and the effects of egg size and maternal yolk reserves on growth of juveniles should also be further investigated.

Egg adhesiveness in sturgeon is another characteristic considered to be species-specific and associated with reproductive behavior, including selection of spawning substrate and hydrological environment. Based on studies of seven sturgeon species with different structure and adhesiveness of egg chorions, Vorobyeva and Markov (1999) concluded that the anadromous species, spawning under conditions of variable and generally slower river currents, had less adhesive eggs than the resident species spawning in strong water current. This appears to contradict our first (Van Eenennaam et al. 2001) and more recent (unpublished) observations on the poor adhesion of eggs in green sturgeon spawning in the fast flowing Klamath River. Our experience with the artificial spawning of wild green sturgeon indicates a con-

sistent weak adhesiveness of the fertilized eggs, and preliminary histological observations of the egg membranes revealed that the outer layer of chorion was approximately half the thickness of that in the white sturgeon. Vorobyeva and Markov (1999) also noted that the thickness of the chorion varied among the species with strongly or weakly adhesive eggs. The adhesiveness of eggs in sturgeon probably depends on the adhesive material secreted upon activation, the specific molecular structure of the outer chorion membrane, and the mode of egg attachment to a substrate. It is possible that green sturgeon eggs may not be attaching at all to the open substrate in the fast flowing Klamath River; instead, they may be trapped in the crevices of river bedrock or under gravel where the early development occurs. The pale coloration, limited mobility, and photophobic behavior of newly emerged green sturgeon larvae support this explanation.

We observed substantial differences in larval behavior between the two species. Unlike white sturgeon larvae, green sturgeon larvae do not swim up after hatching, similar to the observations of Artyukhin and Andronov (1990) on the Asian green sturgeon. It appears that green sturgeon larvae do not have an early pelagic phase, which facilitates larval dispersal and downstream migration to nursery grounds, as in white sturgeon of the Sacramento and Columbia rivers.

In conclusion, our study provides the first comparative information on the early development of North American green and white sturgeon. Sharing a holoblastic style of development, green sturgeon differ from white sturgeon by having larger eggs and larvae, weaker adhesiveness of fertilized eggs, and demersal larval behavior, suggesting a reproductive strategy different from that of white sturgeon, with regards to conditions of spawning rivers and larval nursery habitat. Unfortunately, neither spawning nor rearing habitats of green sturgeon are known at present time, and our laboratory results are not verified by field observations. Characterization of the reproductive habitat of green sturgeon is a priority for stock management and preservation of this species.

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