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Effects of Pulsed, High-Velocity Water Flow on Larval Robust Redhorse and V-Lip Redhorse

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Abstract.—The pulsed, high-velocity water flow characteristic of water-flow patterns downstream from hydropower-generating dams has been implicated in the declining abundance of both aquatic insects and fishes in dam-regulated rivers. This study examined the effects of 0, 4, and 12 h per day of pulsed, high-velocity water flow on the egg mortality, hatch length, final length, and survival of larval robust redhorse *Moxostoma robustum,* a presumedly extinct species that was rediscovered in the 1990s, and V-lip redhorse *M. collapsum* (previously synonomized with the silver redhorse *M. anisurum*) over a 3–5 week period in three separate experiments. Twelve 38.0-L aquaria (four per treatment) were modified to simulate pulsed, high-velocity water flow (>35 cm/s) and stable, low-velocity water flow (<10 cm/s). Temperature, dissolved oxygen, zooplankton density, and water quality variables were kept the same across treatments. Fertilized eggs were placed in gravel nests in each aquarium. Hatch success was estimated visually at greater than 90%, and the mean larval length at 24 h posthatch was similar in each experiment. After emergence from the gravel nest, larvae exposed to 4 and 12 h of pulsed, high-velocity water flow grew significantly more slowly and had lower survival than those in the 0-h treatment. These results demonstrate that the altered water-flow patterns that typically occur when water is released during hydropower generation can have negative effects on the growth and survival of larval catostomid suckers.

Human activities encroach upon freshwater stream and riverine habitats, often resulting in altered species assemblages and reduced species diversity (Benke 1990; Hughes and Noss 1992; Lydeard and Mayden 1995). Construction of hydroelectric dams has been among the human activities that cause the most damage to aquatic ecosystems. Hydroelectric dams impound many large streams and rivers worldwide (McCully 1996). In the United States, very few free-flowing, high-quality rivers greater than 200 km in length remain in the contiguous 48 states (Benke 1990). Pulsed, high-velocity water flows (i.e., rapid hourly or daily fluctuations of instream flow) caused by water release during hydropower generation are unnatural disturbances that decrease habitat stability in a riverine environment. Hydropower generation often increases the frequency of both high-velocity and low-velocity flow pulses while decreasing their duration. As a result, the extended, stable-velocity flow periods characteristic of natural water-flow patterns are substantially reduced (Richter et al. 1996; Bowen et al. 1998; Freeman et al. 2001). Pulsed, high-velocity water flow creates an unstable environment that adversely affects habitat variables such as water velocity, depth, temperature, dissolved oxygen, sediment transport, and channel morphology (Cushman 1985; Bain et al. 1988; Allan and Flecker 1993). Consequently, pulsed, high-velocity water flow has been implicated in declining aquatic insect and fish abundance in dam-regulated rivers (Travnichek and Maceina 1994;

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Kubecka et al. 1997; Cereghino and Lavandier 1998).

Hydroelectric dams strongly affect native fishes in the southeastern United States (Pringle et al. 2000), a global center of temperate freshwater diversity (Lydeard and Mayden 1995). Comparisons of fish assemblages in similar habitat types in regulated (strongly influenced by dam operations) and unregulated (minimal or no dam operation influences) flow regimes in Alabama rivers demonstrate that shallow-water fish assemblages are significantly different between regimes (Kinsolving and Bain 1993; Travnichek and Maceina 1994; Bowen et al. 1998). Species diversity and density are higher in unregulated sites, corresponding to a greater persistence of shallow, low-velocity habitat (Bowen et al. 1998; Freeman et al. 2001). In addition, the abundance of juveniles at some regulated sites is dominated by species with spawning seasons that extend into late summer, when lower, more stable flows occur (Freeman et al. 2001).

Catostomid suckers are a major component of riverine fish assemblages in the southeastern United States and usually are associated with highly diverse communities and productive ecosystems (Jenkins and Burkhead 1994). An estimated 31% of catostomids are considered extinct, endangered, threatened, or of special concern in the United States (Warren and Burr 1994). Life history studies on catostomids indicate that the larvae and juveniles of some taxa are highly susceptible to hydrologic variability in their environment (Modde 1996; Kennedy and Vinyard 1997; Gadomski and Barefoot 1998; Jennings 1998). Young-of-year suckers are more abundant in shallow, low-velocity (<20 cm/s) pool and margin habitat than in high-velocity (>35 cm/s) riffle and channel habitat (Lobb and Orth 1991; Aadland 1993). Some studies have shown lower abundance of redhorse suckers (*Moxostoma* spp.) in dam-regulated rivers where low-velocity habitat is not available for extended periods of time (Travnichek and Maceina 1994; Bowen et al. 1998).

In this study, we investigated the effects of pulsed, high-velocity water flow on the eggs and larvae of robust redhorse *M. robustum*[3] and V-lip redhorse *M. collapsum*[4] in three separate experiments that lasted from 21 to 38 d after egg fertilization. Hatch success and length at 24 h posthatch were quantified for eggs and larvae to discern any effects before larvae emerged from nests. Final length (of surviving larvae) and larval survival were quantified at the end of experimental periods to discern any effects after larvae emerged from nests.

Methods

Study species.—The robust redhorse is an imperiled riverine sucker endemic to Atlantic slope drainages from the Pee Dee River in North Carolina to the Ocmulgee River in Georgia. The robust redhorse is considered endangered (Warren et al. 2000), as few adult fish have been collected in recent years. The largest known population, estimated at 600 fish, inhabits a 30-km reach of the Oconee River in Georgia directly downstream from Sinclair Dam, a hydropower-generating facility. An extensive stocking program by the U.S. Fish and Wildlife Service, the Georgia Department of Natural Resources, and the Robust Redhorse Conservation Committee has been implemented in recent years because of low larval abundance and juvenile recruitment (Jennings 1998; Ruetz and Jennings 2000).

The V-lip redhorse occurs in medium to large rivers in Atlantic slope drainages from the Roanoke River in Virginia to the Altamaha River in Georgia. Until recently, V-lip redhorse was considered the same species as the silver redhorse *M. anisurum* (Jenkins and Burkhead 1994). In contrast to the robust redhorse, the V-lip redhorse is considered stable with respect to conservation status (Warren et al. 2000).

Experimental chambers.—Twelve 38.0-L glass aquaria were modified with Plexiglas inserts and water pumps to generate pulsed, high-velocity and stable, low-velocity water flow in a simulated stream habitat (Figure 1). The 12 aquaria were placed on a wooden stand that was partially submerged in a large, rectangular, fiberglass tank. The large tank was filled with water to a level equal

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[3] The robust redhorse *M. robustum* was described by Cope in 1870, and subsequently lost to science until its rediscovery in the early 1990s. The name *M. robustum* had been erroneously assigned to the smallfin jumprock *Scartomyzon robustus* (Jenkins and Burkhead 1994).

[4] The V-lip redhorse *M. collapsum* was synonomized with the silver redhorse *M. anisurum* by R. E. Jenkins in his unpublished dissertation (1970). The common name V-lip redhorse was subsequently assigned to *M. pappillosum* (Jenkins and Burkhead 1994). Jenkins (personal communication) and others (Warren et. al. 2000) now recognize *M. collapsum* as the V-lip redhorse, a separate species of Atlantic slope sucker closely related to silver redhorse.

FIGURE 1.—Top view of aquarium modified to simulate pulsed, high-velocity water (>35 cm/s) and stable, low-velocity water (<10 cm/s). Water pumps were placed in squared pockets to prevent the eggs and larvae from being sucked into the water intakes.

to the water level in the aquaria, and a 1-hp water chiller was used to maintain a constant temperature. Three 100-W fluorescent grow lights were hung overhead to ensure equal light intensity, and timers were used to maintain a natural photoperiod. Gravel substrate similar in size, shape, and composition to that at spawning sites was collected from nearby rivers and placed in the aquaria to a depth of 2–5 cm. Additional spawning substrate was used to create nests 5–10 cm deep on one side of the channel divider in each aquarium.

Experimental design.—Experiments consisted of three treatments with four replicates per treatment. Treatment 1 assessed the effects of 12 h of high-velocity water flow on larval growth and survival. One MagDrive MD 350 (1,325 L/h) submersible water pump and one Mini Jet PU 14 variable-flow (300–580 L/h) submersible water pump were used to generate and maintain high water velocities (>35 cm/s) for a 12-h period each day. The Mini Jet pump also was used to maintain stable, low-velocity flows (<10 cm/s) during the 12-h ‘‘nongeneration’’ period. The setup for treatment 2 was identical to that of treatment 1 except that the pumps in treatment 2 generated a 4-h high-velocity period and a 20-h low-velocity period. Treatment 3 (the control group) consisted of stable, low-velocity flows (<10 cm/s) maintained for 24-h each day with two Mini Jet PU 14 pumps.

Egg collection.—Robust redhorse broodfish were collected in early May 1999 and 2000 by means of boat electroshocking in the Oconee River. Male and female broodfish were transported to a portable hatchery at Beaverdam Wildlife Management Area and injected with Ovaprim (Barrett 1997) to induce spawning. Eggs from a single female were fertilized with milt from two males, placed in a small cooler with a portable aerator, and transported to the Whitehall Fisheries Research Laboratory at the University of Georgia.

V-lip redhorse eggs were collected on April 1, 2000, from the North Fork Broad River downstream from the Royston, Georgia, water intake structure. Naturally spawned, fertilized eggs were obtained by locating nesting sites and removing the eggs from several nests. Eggs were collected by shoveling the gravel substrate into the water column and allowing the eggs to drift into a Surber sampler (1-mm mesh) placed directly downstream from the disturbed substrate. Eggs were removed from the Surber sampler, placed in a small cooler with an aerator, and transported to the laboratory.

Experiments.—Three experiments were conducted, two with robust redhorses (RR1 and RR2) and one with V-lip redhorses (VR1). Experiment 1 (RR1) was conducted from May 6 to May 31, 1999, with 300 robust redhorse eggs buried in nests in each aquarium. Experiment 2 (VR1) was conducted from April 1 to April 22, 2000, with 105 V-lip redhorse eggs in each aquarium. Experiment 3 (RR2) was conducted from May 4 to June 11, 2000, with 105 robust redhorse eggs in each aquarium. The eggs were stocked in the aquaria by siphoning them into a vinyl tube and then holding the tube up to a light to count the number of live eggs (i.e., visible development on yolk globule). The tube was then placed into the gravel nest and the eggs allowed to fall into the interstitial spaces between rocks. This method was repeated until each aquarium had an equal number of eggs.

Twenty-four hours after hatching was first observed in the aquaria, all pumps were shut off and larvae were collected to determine the hatch lengths. Gravel from nests was removed carefully to expose newly hatched larvae. About 5 larvae were siphoned from each replicate (~20 larvae per treatment) and preserved in a 5% solution of formalin. Gravel nests were rebuilt, and pumps were restarted for the duration of the experiment. Preserved larvae were measured with a microscope (6.6× magnification) fitted with a 100-μm ocular micrometer.

After larval mouthparts had formed (4–6 d posthatch), the aquaria were inoculated with live zooplankton (e.g., protozoans, rotifers, cladocerans, ostracods, and copepods) collected from ponds near the laboratory. Larger (>500-μm) organisms incapable of being ingested by fish larvae were removed by rinsing the collected zooplankton through a 500-μm-mesh plankton sieve into a 15-L bucket. The bucket contents were thoroughly mixed before removing 200 mL at a time and pouring equal portions of this volume into different areas of the aquarium. This method was repeated for each aquarium until all the zooplankton had been added. Additional concentrations were added every 1–2 d when sufficient quantities had been collected.

At the end of each experiment, all pumps were shut off and the gravel substrate was removed by hand. Larvae were captured, counted, and preserved in 12% buffered formalin. Final length, measured at 6.6× magnification to the nearest micrometer, was calculated from the preserved larvae.

Behavioral observations.—Observations on eggs and larvae were conducted for about 2 h every 1–2 d. Each aquarium was observed in 5-min periods during each flow regime. The number of larvae in different areas (i.e., gravel substrate, water column, high flow, and low flow) was recorded for each treatment. The movements of individual larvae in each area were observed, and any migration or displacement to other areas was recorded. For any larva displaced by flows, the number of ‘‘trips’’ around the aquarium needed to escape the displacing flow was recorded.

Water velocity.—Water velocity was measured 2–4 times per week with either a Marsh-McBirney model 201D or model 2000 current meter. Water velocity was taken at 60% water depth in four fixed positions spaced about equally around the path of water flow. Velocity data were classified under three flow regimes: pulsed, high-velocity water flow; nongenerating, low-velocity water flow; and stable, low-velocity water flow. In the 4- and 12-h treatments, pulsed, high-velocity water flow occurred when the MagDrive MD 350 pump was running; nongenerating, low-velocity water flow occurred when that pump was off. Mean velocity ranged from 23.6 to 52.7 cm/s during the high-velocity periods and from 4.8 to 9.5 cm/s during nongenerating, low-velocity periods. The nongenerating, low-velocity water flow was set to mimic the stable, low-velocity water flow in the 0-h treatment (Table 1). Additional velocity measurements were recorded in areas where groups of larvae were seen during observation periods.

Water quality.—Temperature (°C) and dissolved oxygen concentration (DO; mg/L) were measured once every 2 d with a YSI model 55 temperature–DO meter. The water temperature in the aquaria (21.0–23.5°C) was kept similar to the temperatures measured at spawning sites. Temperature differences greater than 0.5°C were not measured at any point during an experiment in any aquarium. Dissolved oxygen concentrations were maintained well above the biological requirements of larval fishes in all aquaria (Boyd 1982). All dissolved oxygen concentrations were greater than 7.3 mg/L, and variations greater than 0.5 mg/L did not occur at any point during an experiment in any aquarium (Weyers 2000).

Ammonia (NH_3) and nitrite (NO_2) concentrations (mg/L) were checked every 2–5 d with a Lamotte water quality test kit. Concentrations for these variables were below detectable limits (ammonia, <0.2 mg/L; nitrite, <0.05 mg/L) for all but a few measurements (Weyers 2000). Conductivity (μS/cm), pH, and turbidity (nephelometric turbidity units [NTU]) were measured with a YSI 600 XLM MiniSonde and had the following target values: conductivity, <150 μS/cm; pH, 7.0–8.2; and turbidity, <5.0 NTU (Boyd 1982). Any variation from the target values in any tank resulted in a two-thirds water exchange for all 12 aquaria.

Data analysis.—All statistical analysis was performed with JMP software (SAS Institute 1996). The hatch length, final length, and survival data sets were tested for normality with a Shapiro–Wilk test. Homogeneity of variances was evaluated with a Bartlett's test (SAS Institute 1996). Although the variances were equal, these data were not distributed normally. Data transformations did not achieve normal distributions.

Mean lengths were calculated for each replicate ($n = 4$), then replicate means were used to calculate treatment means ($n = 3$) and variances. Treatment means for the hatch length, final length, and survival data sets were evaluated with a Kruskal–Wallis nonparametric one-way analysis of variance at a significance level of 0.05. When treatment means were shown to be different, a Tukey–Kramer mean separation test was used to identify where the differences occurred.

Results

Egg Mortality, Hatch Length, Final Length, and Survival

In all three experiments, eggs were not observed outside of the nests or in the water column of any aquarium. Hatch success was estimated visually at greater than 90% in all treatments. After hatching, all larvae in the three experiments remained in the gravel substrate for 5–10 d. Larvae of both species seemed to move freely within the interstitial spaces and were observed in all areas of the substrate, usually in groups of 3–4 individuals.

After emergence from the gravel, robust and V-lip redhorse larvae that attempted to move to the surface during high-velocity periods were caught in the high flows and carried around the channel. The number of trips around the aquarium ranged from 5 to 62 for robust redhorses and from 0 to 28 for V-lip redhorses. The larvae displaced by the high flows had to swim vigorously to extricate themselves from the high-velocity areas and usually needed 10–20 trips around the aquarium to reach a low-velocity area. No larvae were observed caught in low flows and carried around an aquarium.

In experiment 1, robust redhorse eggs hatched 5–6 d after fertilization and had similar mean hatch lengths ($P = 0.64$) among the three treatments (Figure 2). The mean final lengths for the 0-h and 4-h treatments (13.7 and 13.5 mm, respectively) were significantly ($P = 0.04$) greater than that in the 12-h treatment (13.2 mm; Figure 2). Mean survival in the 0-h treatment (37.0 larvae) was significantly ($P = 0.02$) greater than that in the 4-h (9.0 larvae) and 12-h (6.8 larvae) treatments. Mean survival in the 4-h and 12-h treatments was similar (Figure 3).

In experiment 2, V-lip redhorse eggs hatched about 10–12 d after collection from the river and had similar ($P = 0.33$) mean hatch lengths (Figure 2). Mean final lengths at the end of the 21-d experiment were significantly different ($P = 0.02$), with the larvae in the 0-h treatment being longer (14.3 mm) than those in the 4-h and 12-h treatments (14.0 mm in both). Mean final lengths were similar for the 4- and 12-h treatments (Figure 2). Mean survival was not significantly different ($P = 0.06$) across treatments but decreased from 40.5

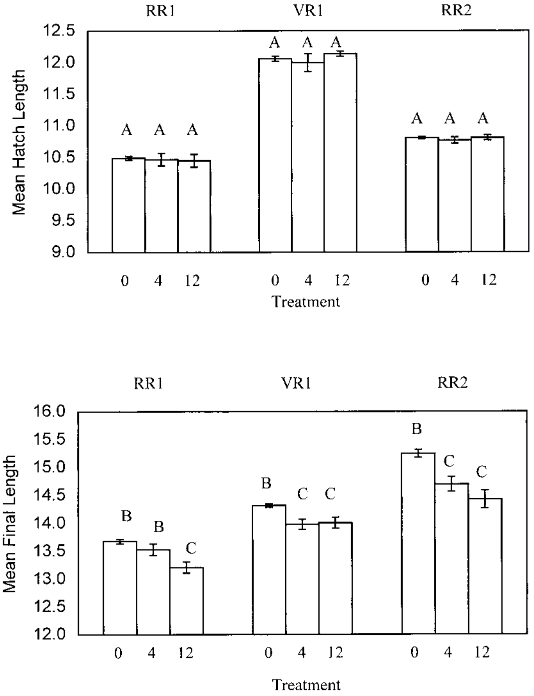

FIGURE 2.—Mean hatch and final lengths (mm; ±SE) for robust redhorse and V-lip redhorse larvae exposed to 0, 4, and 12 h of pulsed, high-velocity water flow. There were two experiments with robust redhorse larvae (RR1 and RR2) and one with V-lip redhorse larvae (VR1). Different letters denote treatments with significantly different mean lengths within an experiment.

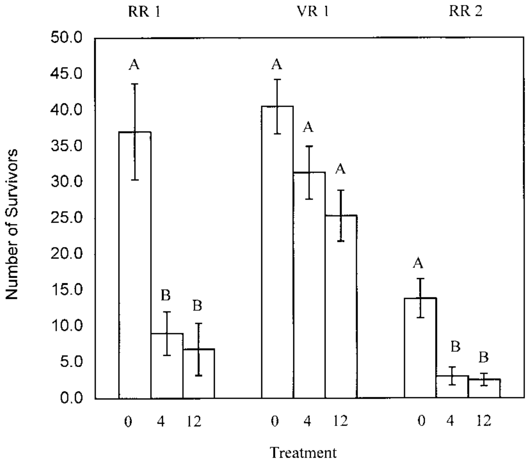

FIGURE 3.—Mean survival (±SE) of robust redhorse (RR 1 and RR 2) and V-lip redhorse (VR 1) larvae in the 0-, 4-, and 12-h treatments. Different letters denote significantly different mean survival within an experiment

larvae to 31.3 and 25.3 larvae as the high-flow period increased from 0 to 12 h (Figure 3).

In experiment 3, robust redhorses hatched 4–5 d after fertilization, and mean hatch lengths at 24 h posthatch were similar among treatments (P = 0.87; Figure 2). Mean final lengths, calculated at the end of the 38-d experiment, were significantly different (P = 0.03) among treatments. The mean final length in the 0-h treatment (15.3 mm) was greater than those in the 4-h (14.7 mm) and 12-h (14.4 mm) treatments. Mean final lengths were similar for the 4- and 12-h treatments (Figure 2). Mean survival in the 0-h treatment (13.8 larvae) was significantly greater (P = 0.02) than that in the 4-h (3.0 larvae) and 12-h (2.5 larvae) treatments. Mean survival in the 4- and 12-h treatments was similar (Figure 3).

Discussion

Effects of Pulsed, High-Velocity Water Flow on Eggs and Newly Hatched Larvae

Pulsed, high-velocity water flow had little effect on robust and V-lip redhorse survival and growth for the first 10–14 d after fertilization. Areas of low shear stress (i.e., reduced velocity), such as the hyporheic zone, can act as flow refugia for benthic organisms (Lancaster and Hildrew 1993; Winterbottom et al. 1997; Angradi and Hood 1998; Rempel et al. 1999). The interstitial spaces in the gravel nests probably provided protection to the slightly adhesive sucker eggs by reducing water velocity, which helped prevent their dislodgment. The adhesiveness allowed them to attach to each other and to the gravel, which further reduced the possibility of being dislodged by high-velocity water flow. During the yolk sac stage of development, the larvae remained exclusively in the protective gravel, which reduced their likelihood of being displaced.

Effects of Pulsed, High-Velocity Water Flow on Emergence, Growth, and Survival

Under the pulsed, high-velocity flow regime, few larval redhorses were able to swim up and inflate their gas bladders when water velocity was high. The larvae that attempted to do so usually were caught in the high flows and carried around the aquarium. These individuals were unable to reach the surface until the high-velocity period ended. Initial inflation of the gas bladder is a high-energy process (Marty et al. 1995) that requires larvae to move to the surface, break the surface tension, and gulp air (Pelster 1997). Delay or failure in gas bladder inflation has been shown to decrease the survival of larval fishes (Bailey and Doroshov 1995; Egloff 1996; Martin-Robichaud and Peterson 1998). Specific counts of swim-up success could not be made without compromising the experiments, but visual observations suggested that more larvae survived past this developmental stage in the stable, low-velocity treatment than in the pulsed, high-velocity treatment in each experiment.

The struggle by both robust and V-lip redhorse larvae to escape the high velocities during gas bladder inflation and the course of the experiments probably required substantial energy consumption that would otherwise have been available for growth (Jobling 1994). Some larval fishes have shown a higher net energy gain (i.e., faster growth) at lower water velocities (Flore and Keckeis 1998). When expressed in terms of relative growth (Jennings 1996), the length differences observed in the RR1 experiment amounted to a 2% (4-h) and 5% (12-h) reduction compared with the 0-h treatment. In the RR2 experiment, which ran 14 d longer, the decrease in relative growth was more evident, specifically, 6% in the 4-h treatment and 9% in the 12-h treatment compared with that in the 0-h treatment. V-lip redhorse larvae showed a somewhat similar response to pulsed, high velocities after 22 d, with 1% and 2% reductions in relative growth compared with the 0-h treatment. These results suggest that hydropower-generating patterns that expose larval suckers to daily pulses of high-velocity water flow can reduce growth rates and that the daily duration (number of hours) of high-flow pulse affects the magnitude of this reduction.

In these experiments, the survival patterns were similar to the growth patterns, with higher survival in the 0-h treatment and significant decreases as the duration of the high flows increased. The reduction in larval growth most likely resulted in the lower larval survival. Length can affect the swimming ability of a larval sucker (Ruetz and Jennings 2000) and thus the ability to capture prey (Osse and van den Boogaart 1995). Because a longer fish has a lower tailbeat frequency, less head drag, and greater gliding distance and can attain a higher swimming velocity than a shorter fish, larger larvae are more successful at capturing prey (Osse and van den Boogaart 1995). Longer robust and V-lip redhorse larvae would be expected to swim better and capture zooplankton more efficiently than their smaller counterparts, which should increase their survival (Chick and Van Den Avyle 2000). The survival rates of V-lip redhorses were higher than those of robust redhorses, possibly because the former were about 1.5 mm longer at hatch (12.0–12.1 mm versus 10.5–10.8 mm).

Conclusions

This research supports the hypothesis that pulsed, high-velocity water flow can affect some aspects of catostomid early life development. Catostomid suckers are a diverse group of fishes endemic to most streams and rivers in the southeastern United States. Reproduction occurs during late spring when water temperatures begin to rise. Water releases from hydropower-generating dams often occur in the spring as energy demand for cooling increases. These water releases increase the frequency of both high-velocity and low-velocity flow pulses while reducing their duration. Because of the low abundance of robust redhorses and other species of catostomids across their historic ranges, special attention should be given to understanding the biological and physical conditions necessary for successful reproduction. Extended low-velocity flow periods are natural occurrences in low-rainfall years, and at least two species of catostomids (i.e., robust and V-lip redhorse) might benefit from longer periods of stable, low-velocity water flow during the spring spawning season. A return to natural flow patterns in dam-regulated rivers could help increase early larval survival and restore populations downstream from dams to their predam densities.

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