RIVER RESEARCH AND APPLICATIONS

River Res. Applic. 29: 574-581 (2013)

Published online 31 January 2012 in Wiley Online Library (wileyonlinelibrary.com) DOI: 10.1002/rra.2561

REDD DEWATERING EFFECTS ON HATCHING AND LARVAL SURVIVAL OF THE ROBUST REDHORSE †

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ABSTRACT

Riverine habitats have been altered and fragmented from hydroelectric dams and change spatially and temporally with hydropower flow releases. Hydropeaking flow regimes for electrical power production inundate areas that create temporary suitable habitat for fish that may be rapidly drained. Robust redhorse *Moxostoma robustum*, an imperiled, rare fish species, uses such temporary habitats to spawn, but when power generation ceases, these areas are dewatered until the next pulse of water is released. We experimentally simulated the effects of dewatering periods on the survival of robust redhorse eggs and larvae in the laboratory. Robust redhorse eggs were placed in gravel in eyeing-hatching jars (three jars per treatment) and subjected to one of four dewatering periods (6, 12, 24 and 48 h), followed by 12 h of inundation for each treatment, and a control treatment was never dewatered. Egg desiccation was observed in some eggs in the 24- and 48-h treatments after one dewatering period. For all treatments except the control, the subsequent dewatering period after eggs hatched was lethal. Larval emergence for the control treatment was observed on day 5 post-hatching and continued until the end of the experiment (day 21). Larval survival was significantly different between the control and all dewatering treatments for individuals in the gravel. These findings support the need for hydropower facilities to set minimum flows to maintain inundation of spawning areas for robust redhorse and other species to reduce dewatering mortality. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS: hydropeaking; larval emergence; Moxostoma robustum; redd dewatering

Received 8 July 2011; Revised 6 December 2011; Accepted 6 January 2012

INTRODUCTION

The construction and operation of dams fragment and alter the natural flow of over half of the world's major rivers (Dynesius and Nilsson 1994; Nilsson *et al.*, 2005). In the contiguous USA, the Yellowstone River is the only river over 1000 km that has not been severely altered for hydropower, flood control and navigation (Benke 1990). Dams cut migratory routes for fishes including access to spawning habitats (Baxter 1977; Lucas and Baras 2001), and available habitats downstream are dependent on either dam spillage or hydropower discharge (Poff *et al.*, 1997; Bowen *et al.*, 1998). These downstream habitats can be altered spatially and temporally (Freeman *et al.*, 2001) and have led to changes in fish communities (Pringle *et al.*, 2000; Bunn and Arthington 2002; Quinn and Kwak 2003). Hydropeaking power generation is a method used to meet short-term electricity demands that

requires a large pulse of water released in a short period that creates great fluctuations in available habitats (Freeman *et al.*, 2001). The regularity and duration of hydropeaking is dependent on available water and electrical power demands and typically ranges from multiple peaks of flow per day to peaks once every other day.

Fluctuations from hydropeaking can inundate areas with water and create temporary suitable habitats that can be exploited by aquatic biota for foraging, cover or reproduction. The biological consequences of occupying and exploiting these temporary habitats can be risky. Juvenile Atlantic salmon *Salmo salar*, Chinook salmon *Oncorhynchus tshawytscha* and brown trout *Salmo trutta* that use these habitats are vulnerable to becoming stranded and isolated from the main river channel in pools, leading to high mortality (Hvidsten 1985; Bradford 1997; Saltveit *et al.*, 2001). Lithophilic spawning fish that utilize these habitats to deposit demersal eggs in the substrate are subjected to periodic dewatering. These fish include catostomids, cyprinids, salmonids and others (Breder and Rosen 1966).

Redd dewatering has been documented in Kokanee salmon *Oncorhynchus nerka*, (Stober and Tyler 1982),

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[†]The contribution of T. J. Kwak was prepared as part of his official duty as a US Government employee.

Chinook salmon (McMichael *et al.*, 2005), quinnant salmon *Oncorhynchus tshawytscha* (Hawke 1978), brown trout and steelhead trout *Oncorhynchus mykiss* (Becker and Neitzel 1985), rainbow trout *Oncorhynchus mykiss* (Becker *et al.*, 1985; Pender and Kwak 2002), and recently in the Savannah River, Georgia and South Carolina, for the robust redhorse *Moxostoma robustum* (Grabowski and Isely 2007b).

The robust redhorse is a rare and imperiled, large catostomid fish found in only three regulated river drainages in the southeastern USA. After being described by Edward Cope in 1870 (Cope 1870), it was 'lost to science' for 120 years until being rediscovered in Georgia in 1991 and later found in South Carolina and North Carolina rivers (Bryant et al., 1996). Populations exist in the Pee Dee (North Carolina, South Carolina), Savannah (Georgia and South Carolina), Ocmulgee and Oconee rivers (Georgia), as well as stocked populations in Georgia and South Carolina within its historical range. The robust redhorse is a large, deep bodied fish with large pharyngeal teeth used for crushing mollusks and other invertebrates. Like other Moxostoma species, they are potamodromous, in that they inhabit freshwater river systems and make seasonal migrations within these systems (Breder and Rosen 1966; Grabowski and Isely 2006; Fisk 2010). The robust redhorse has been negatively affected by habitat modification and fragmentation from hydroelectric dams, introduced species, degraded water quality and sedimentation (Warren et al., 1997, 2000; Ricciardi and Rasmussen, 1999; Cooke et al., 2005; Jennings et al., 2010).

The effects of redd dewatering have primarily been studied in salmonids in western US rivers, with no research on nongame or imperiled species. Salmon eggs appear resilient to dewatering for periods up to 5 weeks as long as they are kept moist and do not freeze or temperatures do not exceed incubation tolerances (Reiser and White 1981, 1983; Becker *et al.*, 1985; McMichael *et al.*, 2005). Salmon eggs are tolerant of dewatering under experimental and natural conditions, but mortality increases significantly when eggs hatch and larvae are dependent on gills for respiration (Becker *et al.*, 1982; Stober and Tyler 1982; Becker *et al.*, 1983; Reiser and White 1983). However, little is known of the effects of redd dewatering on non-salmonid fishes, and this is especially true for imperiled species.

Thus, we initiated a laboratory experiment to simulate the effects of dewatering on robust redhorse fertilized eggs and larvae. Dewatered robust redhorse redds have been found in the Savannah River, Georgia and South Carolina (Grabowski and Isely 2007b) and were observed anecdotally in the Pee Dee River, North Carolina (authors' personal observations). Knowledge of the dynamics and ecological consequences of redd dewatering is vital to the conservation and long-term survival of this species. Furthermore, the hydro-regulated flow regimes of all drainages where robust redhorse currently exist warrant such a study. This research also will enhance understanding of the dynamics and effects of redd dewatering on fish eggs and larvae in southeastern warm water systems, which contain the most diverse and vulnerable fish fauna in the USA (Jelks *et al.*, 2008).

METHODS

Laboratory apparatus

The experiment was conducted indoors at the McKinney Lake State Fish Hatchery near Hoffman, North Carolina. Fifteen 14.2-L eveing-hatching jars (Eagar, Inc., North Salt Lake, UT) were used for experimental replicates. Each cylindrical jar was 30.5 cm in diameter with a height of 66 cm. These hatching jars have been used by the South Carolina Department of Natural Resources to hatch and rear fertilized robust redhorse as a component of a state stocking program. The hatching jars have a hemispherical bottom to facilitate hatching by creating upwelling that diffuses through the 20-mm thick random nylon mesh mat filter. This ensures adequate water movement over the eggs for aeration and to remove waste with minimal flow. Robust redhorse eggs can successfully hatch in an aquarium environment with minimal flow ($< 3.8 \, \text{L} \cdot \text{min}^{-1}$), as long as water flows around them. These jars were assembled with water supplied through the bottom and flowing out the top from the pour spout that drains into a common reservoir. Water was then forced through a Hayward S310S sand filter with a Hayward 0.75-horsepower Super Pump (Hayward Pool Products, Elizabeth, NJ). The filter was used to prevent the introduction of Savannah River genetic strain robust redhorse into the Pee Dee River drainage because the hatchery effluent ultimately drained into a tributary of the Pee Dee River.

Groups of three hatching jars were designated to one of four dewatering treatments (6, 12, 24 and 48 h) that mimicked hydropeaking conditions in the Pee Dee River and other drainages and a control treatment that was never dewatered. When the treatment jars were not dewatered, water flowed through them for 12 h until the cycle was repeated. All treatments were initiated with 12 h of inundation followed by their prescribed treatment. Gravel similar to spawning substrate used by robust redhorse (12–50 mm diameter; Freeman and Freeman 2001) was placed in each jar 5 cm deep on a nylon mesh diffusing mat that was supported by an aluminum cone perforated screen that allowed for uniform upwelling and served as a medium upon which eggs were placed.

Eggs were obtained on 6 May 2009 from wild Savannah River, Georgia and South Carolina, brood stock at river km 283, (16 rkm downstream of the New Savannah Bluff Lock and Dam). One female was stripped, and eggs were divided into three equal groups. Three males were stripped to fertilize one group of eggs, and then, all three groups were combined again and taken to Bayless Striped Bass Hatchery, Saint Stephen, South Carolina. Fertilized eggs were transported to McKinney Lake State Fish Hatchery the same day. Each treatment jar was stocked with 100 eggs, and each control treatment jar contained 250 eggs. More eggs were placed in the controls to determine overall hatch success to understand if differences in each treatment were related to experimental design instead of egg viability. Eggs were not treated with formalin or any other prophylactic treatment solution throughout the experiment. Eggs were distributed with a glass siphon throughout the gravel and settled into interstitial spaces between the gravel with some eggs resting on top of the gravel. We used hatchery well water that was pumped through an aeration system that oxygenates and denitrogenates it before being stored in a water tower for later use.

Four Claber (Aquauno Video 6, Claber Inc. Elk Grove Village, IL) automatic water timers controlled each treatment water flow and were programmed with water flowing for 12 h and then turned off for the specified time of each treatment automatically. Each treatment hatching jar had an outflow of at least 3.8 L·min⁻¹. Each treatment was piped together using 3.8-cm polyvinyl chloride main pipe. After flowing out of the water timer, each treatment pipe split off the main pipe to the appropriate hatching jar. After branching off to the appropriate hatching jar, the main pipe for each treatment continued underneath the last hatching jar and was oriented into the common reservoir and controlled with a ball valve on the terminal end. The main pipe and terminal ball valve were at a lower elevation than all three jars for each treatment to facilitate draining when water timers shut off at the beginning of a dewatering cycle. The terminal ball valve for each treatment was adjusted to constantly drain so that when a water timer shuts off, all three hatching jars for that treatment drain and become dewatered for the specified time. The jars for each treatment drained completely in 20-25 min. The outflow volume from the terminal ball valve was less than the inflow from the water timer to allow the hatching jars to fill and overflow automatically.

After the initial dewatering period for each treatment, and following reinundation, some of the eggs lost their adhesiveness and were elevated by water surface tension. To prevent eggs from flowing up and out of each jar, a fiberglass screen was placed 5 cm below the pour spout of each hatching jar. As eggs came into contact with the screen, water continued to fill the jar, and any eggs present fell back into the gravel substrate. The screen was removed to allow larvae access to the water surface after observations indicated that hatching was complete.

The experiment was initiated at 2400 h on 7 May 2009 and was monitored twice daily, approximately every 12 h. Any larval physical development or behavior was recorded.

Dissolved oxygen $(mg \cdot L^{-1})$ and temperature (°C) were measured throughout the experiment (Yellow Springs Instrument model 550A meter). Once distributed into the substrate, egg number and fate could not be precisely quantified at any given time, but larvae observed swimming out of the gravel were considered emerged and were captured with an aquarium net and preserved in a 5% buffered formalin solution. To compensate for restricted time to observe and collect emerging larvae, as well as their tendency to emerge at night (Clifford 1972; Muth and Schmulbach 1984; D'Amours et al., 2001), a net was placed onto the pour spout of each jar to collect any emerging larvae that may be caught in the outflow current. Total length (mm) was recorded for all robust redhorse larvae captured. At the termination of the experiment, all gravel was carefully removed, and any larvae remaining in each hatching jar were preserved.

Statistical analyses

Differences in larval survival among experimental control and dewatering treatments were analysed for larvae remaining in the gravel at the end of the experiment. Larvae that emerged throughout the experiment (in control replicates only) were excluded from this analysis because they were removed and subsequently not subjected to additional dewatering periods. Larval survival data did not conform to a normal distribution, and the condition was not improved with an arcsin transformation (Zar 1996). Thus, a Kruskal–Wallis test was used to detect significant differences among experimental groups (SAS Institute Inc. 2010). To test if robust redhorse larvae emerge at a specific length, simple regression was used to analyse the relationship between larval emergence day and total length. Larvae that appeared deformed (N=12) or were not well preserved (N=16) were excluded.

RESULTS

Mean water temperature during the experiment was 18.65 °C (SE 0.21 °C, range 16.97–20.22 °C, N=21) with mean dissolved oxygen of 10.28 mg·L⁻¹ (SE 0.24 mg·L⁻¹, range 8.95–10.99 mg·L⁻¹, N=10). After the initial 12 h of inundation, the dewatering treatment cycles were initiated. Eggs were observed on the substrate surface and interstitial spaces in all control and dewatered treatments. When dewatered in those treatments, eggs in the gravel were difficult to observe, but some on the gravel surface were dried out by the end of the first cycle of the 24- and 48-h treatments. By day 7 post-fertilization, all observed eggs in the control and movement was observed inside the control treatment, all signs of normal development. One egg of seven (14.3%) observed in the 12-h treatment had eye spots. At the same

Table I. Numbers of emerged larval robust redhorse collected
according to day post-hatching. Table headings Night and Day
refer to periods when larvae emerged. All emerged larvae were
collected from control replicate jars; no larvae emerged from any
dewatering treatment

5	Number of larvae			
Day (post-hatching)	Night	Day	Total	
5	1	0	1	
6	13	7	20	
7	14	4	18	
8	9	1	10	
9	11	3	14	
10	11	1	12	
11	15	0	15	
12	1	0	1	
13	1	0	1	
14	1	0	1	
Total	77	16	93	

time (day 7), hatched larvae were observed in the 24-h (N=5) and 48-h (N=1) treatments on the substrate surface, with no other eggs observed in the 24-h treatment and some dried eggs on the substrate surface in the 48-h treatment. By eight days after fertilization, most observable eggs in the control treatment hatched (17 observed not hatched), and all visible eggs in the 6-h treatment had hatched and were down in the substrate. No eggs or larvae were observed in any other treatment. All visible eggs were hatched and in the substrate by 9 days after fertilization for the control and 6-h treatment. Once hatched, many of the larvae observed were oriented in a vertical position with their heads toward the mesh filter. By 10 days after fertilization, only the larvae in the control treatment jars were visible, and no eggs or larvae were observed in any treatment throughout the remainder of the experiment.

Emergent larvae were collected beginning 12 days after fertilization (5 days post-hatching) to the end of the experiment only in the control treatment replicates (Table I). All larvae were caught in the collection nets attached to pour spouts, suggesting they were suspended or swam out of the jars, except for five caught by hand. Typically, when an observer approached the jars, larvae that were suspended in the water column retreated into the substrate. This fleeing behavior also was observed for larvae in the substrate that were observed on the perimeter of jars; those larvae moved to the center of the jar through interstitial spaces. Larval emergence peaked over two days (6–7 days posthatching) and decreased significantly by day 11 post-hatching. A total of 93 larvae were collected, 77 (83%) in the morning (night emergence) and 16 (17%) in the evening (day emergence) (Table I).

Upon conclusion of the experiment on 28 May 2009 (after day 21), a total of 108 live larvae were found, all in the control treatment. No larvae were collected from the gravel above the nylon mesh filter in any of the dewatered treatments. After removing the gravel, the nylon mesh and perforated aluminum screen were removed, and unexpectedly, additional live larvae were found in the residual water that remained in the bottom of the eyeing-hatching jars, primarily in the control treatment with a few from the 12-, 24-, and 48-h treatments (Table II). This finding of additional larvae below the screen and filter also indicated that larvae had direct access through the terminal ball valve into the common reservoir, and seven additional larvae were collected there.

Larval survival in the control was significantly different (p < 0.01) from all treatments, based on collections from the gravel substrate (Table II). Larvae collected below the mesh filter were not included in any analysis because once escaped, they were not subjected to additional dewatering periods.

There was a positive relationship between day of emergence and larvae total length (Figure 1), indicating that larvae did not emerge at a specific length but continued to grow and emerge throughout the experiment. Yolk sacs were present on 29 (31%) of the emerged larvae, and six (4%) contained some amount of yolk sac at the end of the experiment. The mean total length for all larvae recovered was 12.75 mm (SE=0.079 mm).

Table II. Larval survival according to treatment at experiment termination (day 21). Larvae from below the filter (N=43) and the common reservoir (N=7) were omitted from analysis. Means followed by the same letter are not significantly different (p < 0.05)

Treatment	Number of larvae collected from gravel	Number of larvae collected below filter	Mean percentage of larvae collected in gravel among replicates	SE
Control	108	34	16.44(a)	0.05
6 h	0	0	0(b)	0
12 h	0	4	0(b)	0
24 h	0	3	0(b)	0
48 h	0	2	0(b)	0
Total	108	43		

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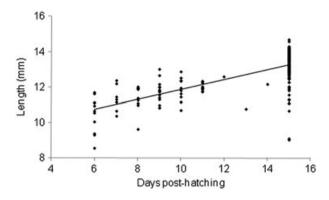


Figure 1. Total length of emerged larval robust redhorse by day (post-hatching, N = 223). Larvae collected that appeared deformed (N = 12) or were not well preserved (N = 16) were excluded

DISCUSSION

Robust redhorse eggs can withstand some degree of dewatering, but once hatched, dewatering for 6 h or longer was lethal. This finding is similar to those in salmonid studies where salmon eggs have the ability to survive dewatered conditions, but when larvae become dependent on gills for respiration, mortality increases significantly (Becker *et al.*, 1982; Stober and Tyler 1982; Becker *et al.*, 1983; Reiser and White 1983). Ambient moisture and humidity may play an important role in egg survival. The few eggs that were on the substrate surface became desiccated in dewatering periods of 12 h or more. Under natural conditions, these eggs would likely be pushed down into the substrate by flow or be preyed upon if they remained on the gravel surface, and such egg desiccation may be rare.

Water temperature was not controlled in our experiment and fluctuated several degrees according to ambient daily air temperatures. Water was pumped from a well but was stored in an elevated water tank until used, which buffered the range of temperature fluctuation. Water temperatures in our experiment (17-20°C) were slightly cooler than temperatures normally used (20-22 °C) to hatch robust redhorse in hatchery conditions. Robust redhorse usually hatch in 4-6 days in the hatchery environment but hatched in our control jars on days 8 and 9. The 24- and 48-h treatments hatched on day 7, and the 6-h treatment hatched on day 8. The dewatering period appeared to accelerate development, likely from exposure to warmer ambient air temperatures, and the treatments with the longest dewatering period hatched earlier. Reiser and White (1983) also found that steelhead and Chinook salmon eggs subjected to dewatering hatched earlier than those continually immersed. Faster development could benefit larvae if density dependent factors, such as the availability of interstitial gravel space or food, are limited. However, if redd temperatures exceed thermal tolerance limits for developing eggs, then mortality could increase substantially. In natural conditions, redd temperature fluctuations could vary much greater than what occurred $(17-20 \,^{\circ}\text{C})$ in our experiment.

After initial dewatering cycles, some eggs lost their adhesiveness and were suspended by the surface tension of rising water in hatching jars. Robust redhorse eggs are demersal, only slightly adhesive and probably rely on being deposited down in the substrate where they adhere or are held there by flowing water. If a redd is dewatered, then inundated again, eggs could potentially be removed from the substrate and swept downstream into less suitable habitat or preyed upon while in the water column. Eggs can tolerate some amount of dewatering, but this could ultimately increase mortality. This observation (i.e. suspended eggs) has not been noted in other such laboratory studies and may be unique to the robust redhorse or *Moxostoma* in general.

Larval escapement was an unforeseen occurrence in our experiment. Larvae were able to penetrate below the mesh filter and aluminum screen and survive for at least 48 h in the small amount of residual water after treatment jars were drained. This may have implications on the fate of larvae in the substrate that becomes dewatered. Once dependent on gill respiration, larvae in dewatered jars suffered 100% mortality. Our observations and those of Weyers et al. (2003) found that robust redhorse larvae can stay in the substrate 5-10 days before emerging, leaving them vulnerable to multiple dewatering events. These two studies also found that larvae can move freely through the interstitial space of gravel, provided adequate space. Garcia de Leaniz et al. (1993) revealed that larval salmon migrate laterally through the gravel before emerging. This behavioral strategy also may apply to robust redhorse larvae to allow migration without vertical movement into the water column, which would reduce predation risk but is dependent on the availability of interstitial space in the gravel. If the interstitial space in the gravel is filled with sediment, movement would be impeded, and this behavior would not be possible.

In a hydro-regulated river setting, larvae that locate residual water in the substrate and survive during a dewatering event may be trapped until the next release of water. Factors affecting the presence of residual water in redds within and among spawning sites include timing and duration of dewatering events, evaporation rate within the redd, substrate composition, and water table level and groundwater dynamics. Dewatered robust redhorse redds have been observed in two different river systems (Savannah and Pee Dee rivers; Grabowski and Isely 2007b; personal observation), but microhabitat conditions within redds have not been measured or described, and that remains an area for future investigation.

Larval robust redhorse do not emerge at a specific length but continually grow and emerge in response to other physical or chemical cues. A similar pattern is known for salmon (McMichael *et al.*, 2005) and sturgeon (Braaten *et al.*, 2008). Emergence is probably related to energetic needs as yolk sacs are absorbed. Yolk sacs were absent in 69% of emerged larvae. Although emergence was not related to length, it displayed a diel pattern with most larval robust redhorse emerging at night (77%). This behavior has been found in other catostomids (Clifford 1972; Muth and Schmulbach 1984) and is likely a mechanism to avoid visual predators (Iguchi and Mizuno 1990; Flecker *et al.*, 1991).

Differences in survival were clearly evident between the control and all other treatments. No larvae in any dewatering treatment survived in the gravel, and none emerged throughout the duration of the experiment. After hatching, no larvae were observed in any treatment after the following dewatering period, and thus, it is uncertain when some larvae escaped through the mesh filter. When eggs hatched, almost all larvae observed were oriented vertically with their head facing the mesh filter; this is most likely the time they escaped through the filter. The percentages of larvae of each group found below the mesh and screen were low [control (3%), 6-h (0%), 12-h (1%), 24-h (3%), and 48-h (1%)]. As larvae grew throughout the experiment, it would be increasingly difficult to pass through the mesh filter and screen. Thus, we suggest that the larvae escaped through the mesh screen at a similarly low rate among groups. Under natural conditions, migration from the original hatching location would be expected at least from a small proportion of larvae (Garcia de Leaniz et al., 1993).

Our findings contribute to a better understanding of the basic ecology of robust redhorse early life stages and their tolerance to fluctuating environmental conditions. To our knowledge, the only other published studies of the effects of redd dewatering heretofore were on salmon and trout. Salmon redd dewatering usually occurs in fall spawning fish, where eggs must overwinter in the substrate. Salmon eggs appear more resilient, as they endure colder temperatures and significantly longer incubation and larval intragravel periods (up to 7 months for Chinook salmon; McMichael et al., 2005). In contrast, robust redhorse eggs incubate for only 4-6 days, hatch, and emerge in 5-10 days. The temporal opportunity for dewatering is small when compared with species that incubate over winter but is no less critical, as our results show that even relatively brief periods (6h) of dewatering are lethal to larvae.

Our results suggest that survival of robust redhorse eggs and larvae can be enhanced with the proper management of minimum flows to keep spawning gravel bars inundated. Fish communities have responded to augmented flows, with increased species diversity and abundance (Travnichek *et al.*, 1995; Lamouroux *et al.*, 2006). This is likely related to access to newly available habitats but also may be a result of successful recruitment from areas that previously were dewatered. Blewett Falls Hydro-facility on the Pee Dee River, North Carolina, has undergone the Federal Energy Regulatory Commission relicensing process and will implement a new minimum flow regime. Our personal observations throughout the primary spawning reach downstream of Blewett Falls Dam during periods of experimental minimum flows, as well as modeled estimates, demonstrate that the primary main-channel and side-channel gravel bars will be inundated under the new minimum flow (Progress Energy 2006; Fisk 2010). Our experimental results suggest that this would benefit robust redhorse eggs, but most importantly, larval survival would be enhanced with continuous inundation. Other species would benefit from higher water surface elevations during the spawning period as well. Grabowski and Isely (2007a) observed notchlip redhorse Moxostoma collapsum, spotted sucker Minytrema melanops, and a carpsucker species Carpiodes sp., utilizing the same gravel bars for spawning as those by robust redhorse in the Savannah River, Georgia and South Carolina. In the Pee Dee River, North Carolina and South Carolina, other Moxostoma species occur sympatrically with robust redhorse including the rare, undescribed Carolina redhorse Moxostoma sp. Other less conspicuous species such as cyprinids also may use these same habitats for spawning or other functions and could benefit as well. Future monitoring under augmented flows and additional research on the mechanisms associated with the ecological effects of the flow regime will further enhance our understanding and guide management of the fish community in regulated warm water rivers.

ACKNOWLEDGEMENTS

This research was funded by a State Wildlife Grant through the North Carolina Wildlife Resources Commission and by Progress Energy, Carolinas. We thank Rick Bradford and Doug Hinshaw of the North Carolina Wildlife Resources Commission for use of the McKinney Lake State Fish Hatchery and their critical assistance throughout the experiment. Andrew Rominger and Martha Fisk assisted with construction and experimental observations. We thank Jason Brown and Progress Energy, Carolinas, for laboratory access and assistance. Jessica Baumann and Julie Harris provided constructive reviews of an earlier draft of this manuscript. The North Carolina Cooperative Fish and Wildlife Research Unit is jointly supported by North Carolina State University, North Carolina Wildlife Resources Commission, US Geological Survey, US Fish and Wildlife Service and Wildlife Management Institute. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

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