

This article was downloaded by: [North Carolina State University]

On: 21 November 2011, At: 11:19

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/utaf20>

Swimming Performance of Larval Robust Redhorse *Moxostoma robustum* and Low-Velocity Habitat Modeling in the Oconee River, Georgia

Carl R. Ruetz III^a & Cecil A. Jennings^b

^a Georgia Cooperative Fish and Wildlife Research Unit, Daniel B. Warnell School of Forest Resources, University of Georgia, Athens, Georgia, 30602-2152, USA

^b U.S. Geological Survey, Biological Resources Division, Georgia Cooperative Fish and Wildlife Research Unit, Daniel B. Warnell School of Forest Resources, University of Georgia, Athens, Georgia, 30602-2152, USA

Available online: 09 Jan 2011

To cite this article: Carl R. Ruetz III & Cecil A. Jennings (2000): Swimming Performance of Larval Robust Redhorse *Moxostoma robustum* and Low-Velocity Habitat Modeling in the Oconee River, Georgia, *Transactions of the American Fisheries Society*, 129:2, 398-407

To link to this article: [http://dx.doi.org/10.1577/1548-8659\(2000\)129<0398:SPOLRR>2.0.CO;2](http://dx.doi.org/10.1577/1548-8659(2000)129<0398:SPOLRR>2.0.CO;2)

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Swimming Performance of Larval Robust Redhorse *Moxostoma robustum* and Low-Velocity Habitat Modeling in the Oconee River, Georgia

CARL R. RUETZ III¹

Georgia Cooperative Fish and Wildlife Research Unit,²
Daniel B. Warnell School of Forest Resources, University of Georgia,
Athens, Georgia 30602-2152, USA

CECIL A. JENNINGS*

U.S. Geological Survey, Biological Resources Division,
Georgia Cooperative Fish and Wildlife Research Unit,
Daniel B. Warnell School of Forest Resources, University of Georgia,
Athens, Georgia 30602-2152, USA

Abstract.—The robust redhorse *Moxostoma robustum* occurs in an 85-km stretch of the Oconee River, Georgia, downstream of a hydropower dam. The population consists primarily of older individuals and recruitment in recent years has been minimal. Operation of the hydropower dam may have affected recruitment negatively by displacing newly hatched larvae downstream and away from nursery habitats. Our null hypothesis was that larval robust redhorse can tolerate water velocities that occur in the Oconee River during peak river discharge related to hydropower generation. We measured swimming speeds for three size-classes of larvae (means: 13.1, 16.2, and 20.4 mm total length) and modeled low-velocity habitat (i.e., as defined by larval swimming speeds) in the Oconee River. We used logistic regression to calculate prolonged swimming speeds (i.e., water velocity at which 50% of fish failed to swim for 1 h) for each size-class and to predict the proportion of larvae in the water column that could maintain their position in the river. Prolonged swimming speeds were 6.9, 10.6, and 11.7 cm/s for 13.1-, 16.2-, and 20.4-mm fish, respectively. Habitat modeling suggested that low-velocity areas were present in the river and that there was not a strong relationship between low-velocity habitat and discharge. However, low-velocity habitats were dynamic during fluctuating discharge, and the ability of larval robust redhorse to access these dynamic areas is unknown.

The robust redhorse *Moxostoma robustum*³ is a large, riverine catostomid first described by Edward Drinker Cope in 1870 (Jenkins and Burkhead

1994). Cope's original specimens were lost, and the species went unnoticed until the 1980s when two robust redhorse were collected in the Savannah and Pee Dee rivers (Jenkins and Burkhead 1994). In 1991, an extant population of robust redhorse was discovered in the Oconee River, Georgia. Archeological and limited species distribution records suggest that robust redhorse probably inhabited Piedmont and Upper Coastal Plain rivers along the Atlantic slope drainage, ranging from the Altamaha River system in Georgia north to the Pee Dee River in the Carolinas (Evans 1994). Attempts to locate other populations have been largely unsuccessful. Age-0 robust redhorse have been collected rarely in the Oconee River since their discovery, suggesting that recent recruitment has been minimal even though spawning adults have been collected in the same areas (Evans 1994; Jennings et al. 1996). Although the species is long-lived (20+ years) compared to other *Moxostoma* spp. (8–15 years; Evans 1994; Jenkins and Burkhead 1994), whether the current level of recruit-

* Corresponding author:

jennings@smokey.forestry.uga.edu

¹ Present address: Minnesota Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, University of Minnesota, 200 Hodson Hall, 1980 Folwell Avenue, St. Paul, Minnesota 55108-6124, USA.

² The Unit is sponsored jointly by the U.S. Geological Survey, Biological Resources Division, the Georgia Department of Natural Resources, the University of Georgia, and the Wildlife Management Institute.

³ Once thought to be a rare Atlantic slope population of river redhorse *Moxostoma carinatum*, this species has been rediscovered and renamed the robust redhorse; its scientific name, *M. robustum*, was transferred by Jenkins and Burkhead (1994). The species previously recognized as *M. robustum*, the smallfin redhorse, represents an undescribed species of jumprock sucker (R. E. Jenkins, Roanoke College, personal communication).

Received August 26, 1998; accepted May 19, 1999

ment is sufficient to maintain the robust redhorse population or not is unknown.

Water velocity is an important factor influencing larval fish habitat selection because velocities of many habitats are greater than the maximum sustained swimming speed of larvae (Scheidegger and Bain 1995). As fins and musculature of larvae develop, young fish become sufficiently mobile to actively avoid displacement by high water velocity (Carter et al. 1986; Harvey 1987). Scheidegger and Bain (1995) defined larval fish nursery habitat in two Alabama rivers as shallow water areas (<1.3 m) with water velocities less than the estimated sustained swimming speed of 12-mm larvae (8.4 cm/s). The Oconee River lacks extensive backwaters and off-channel areas; thus, gradually sloping shoreline areas with low velocities and with vegetation and other structures should be important for providing nursery habitats for larval fishes (Scheidegger and Bain 1995).

The direct effects of naturally occurring floods on fishes generally are greater for early life history stages than for adults (John 1964; Elwood and Waters 1969; Seegrist and Gard 1972; Schlosser 1985), and downstream displacement of larval fish during flood conditions is greater than during non-flood conditions in some small streams (Harvey 1987). Downstream displacement of larvae may decrease survival (John 1964; Schlosser 1982; Harvey 1987, 1991). However, susceptibility of larvae to flood-related downstream displacement may be taxon- and size-specific (Harvey 1987) and may vary among streams (Stehr and Branson 1938). Variability among streams occurs because the topography of the surrounding landscape determines the degree to which populations in various parts of the stream are affected (Stehr and Branson 1938).

Peak river discharge related to hydropower generation (hereafter called hydropower peaking) has reduced stream fish community structure in some regulated rivers (Bain et al. 1988; Kinsolving and Bain 1993; Travnichek and Maceina 1994). The immediate effects of hydropower peaking are probably similar to the effects of naturally occurring floods; however, hydropower peaking is more frequent and may result in more rapid changes in stream hydraulics than naturally occurring floods. Sinclair Dam, a hydropower facility on the Oconee River, is located 8.4 km upstream from the robust redhorse population. Nongeneration release from Sinclair Dam is about 9 m³/s and powerhouse capacity is about 193 m³/s (EA Engineering 1994). Hydropower peaking alters daily flow patterns in

the Oconee River (see Figure 1) because releases are determined by daily electricity demands rather than local precipitation. This variability in river discharge may affect other physical and chemical conditions such as velocity, depth, channel width, temperature, sediment transport, and water quality (Cushman 1985). Flow manipulation in the Oconee River results in a highly variable, unpredictable flow regime downstream that may affect the survival of larval robust redhorse by a variety of factors, including reduced availability of suitable flow-dependent nursery habitats.

We investigated the swimming performance of larval robust redhorse under varying flow conditions. Our goals were to test the hypothesis that larval robust redhorse can tolerate typical low-velocity areas in the Oconee River that occur during hydropower peaking and to determine whether the availability of these habitats was limited by hydropower generation. Specific objectives were to measure prolonged swimming speeds of larval robust redhorse, and to model the presence and availability of low-velocity habitats (i.e., as defined by larval swimming speeds) in the Oconee River during the hydropower peaking cycle when larval robust redhorse would be most vulnerable.

Methods

Prolonged swimming experiments.—Fertilized robust redhorse eggs from 14 different male × female crosses were obtained from adult fish collected from the Oconee River during 15–23 May 1996. The eggs were taken to laboratory facilities at the University of Georgia, and hatching jars were used to incubate fertilized eggs. About 1,000 newly hatched larvae were collected from hatching jars and reared in a 114-L tank equipped with a recirculating biofiltration system. Larvae were reared at water temperatures that matched those at which swimming performance was tested. Larvae were fed naupli of *Artemia* sp. 2–4 times per day ad libitum and switched to a combination of *Artemia* nauplii and starter trout chow once fish were able to ingest larger particles.

Fixed velocity tests were conducted to determine larval robust redhorse swimming performance. These tests have been used extensively to determine prolonged swimming speeds of larval fishes (see Houde 1969; Meng 1993; Childs and Clarkson 1996). Swimming tests were initiated once larvae reached the swim-up stage, indicated by their dispersal throughout the water column in the rearing tank. Larvae hatched at about 7 mm total length (TL), but swim-up did not occur until

larvae were about 11 mm TL. If the length of a larva was not within the predetermined length interval for the size-class (12.5–14.5, 15.5–17.5, or 19.5–21.5 mm TL), then the larva was excluded from the analysis (TL of each fish was measured to the nearest 0.1 mm with dial calipers). Mean total lengths of the three size-classes of larval robust redhorse tested were 13.1 (SE = 0.05), 16.2 (SE = 0.06), and 20.4 mm (SE = 0.08). Larvae in the 13.1- and 16.2-mm size-classes were in the yolk sac and larval phases, respectively. The 20.4-mm size-class was in transition between larval and prejuvenile phases because the finfold was absent or a only small remnant was present, and fin development was complete or nearly so. The range of water velocities tested was 3.6–16.7 cm/s, with mean increment between test velocities of 1.1 cm/s (SE = 0.07). The 13.1-mm larvae were tested at eight velocities, ranging from 3.6 to 10.1 cm/s; 16.2-mm larvae were tested at nine velocities (6.6–14.4 cm/s); and 20.4-mm fish were tested at seven velocities (8.5–16.7 cm/s). Nine to 14 fish were tested individually at each fixed velocity (larvae were used only once).

Water temperature in the swim chamber was kept constant for each size-class of fish tested but was increased for each successive size-class tested. Robust redhorse spawn at water temperatures from 20°C to 24°C in the spring when water temperatures were warming in the Oconee River. Therefore, larval robust redhorse were expected to encounter warmer temperatures as the season progressed and fish grew. Accordingly, 13.1-, 16.2-, and 20.4-mm fish were tested at 22.5 (SE = 0.07), 24.2 (SE = 0.07), and 25.5°C (SE = 0.05) to mimic water temperatures in the Oconee River.

A gravity-flow swim chamber was used to test larvae (see Bishai 1960; Houde 1969; Meng 1993). Fish were tested in a 5.1 cm diameter, 70-cm long horizontal section of the swim chamber (termed swim tube) that was constructed of clear polyvinyl chloride (PVC) pipe and blocked on each end with fine mesh screening to enclose fish. Water velocity and direction in the swim tube were controlled by ball valves located in the four corners of the swim chamber.

Water velocity in the swim tube was determined by measuring the water volume delivered from the swim chamber in an observed time period (Bishai 1960; Houde 1969). Velocity was calculated with the equation

$$V = (v/t)/a, \quad (1)$$

where V was velocity (cm/s) in the swim tube, v was volume (mL) of water delivered from the swim chamber, t was elapsed time (s), and a was the cross-sectional area of the PVC pipe ($a = 20.3 \text{ cm}^2$). Water velocity in the swim tube was calculated as the mean of 15 consecutive volume-time measurements taken from the outlet of the swim chamber.

The experimental protocol for swim tests was based on methods described by Meng (1993). A larva, chosen randomly from the rearing tank, was introduced into the swim tube through a water-filled funnel and allowed at least 5 min to acclimate at zero velocity. Velocity was increased gradually to each test velocity. Tests were terminated and omitted from analyses when fish would not swim as the velocity was increased gradually to the test velocity, or when the larva was damaged during handling. A light source was used to help orient fish into the flow. Once the test velocity was reached, each larva that swam for 1 h was scored as “passed.” Those larvae that became impinged on the fabric screen during the test were scored as “failed.” To reduce the amount of handling experienced by fish used in swimming tests, larval length was measured at the conclusion of a test.

Swimming performance tests were treated as a bioassay (Brett 1967; Houde 1969) in which water velocity and fish score (pass or fail) were synonymous with toxin dosage and animal survival in a toxicity experiment (Meng 1993). Prolonged swimming speeds of larval robust redhorse were determined by calculating the velocity at which 50% of fish tested failed to maintain their position in the swim tube for 1 h, a procedure similar to that used to calculate median lethal dose for animal survival in response to a toxin (Meng 1993). The relationship between fish score and imposed water velocity was sigmoidal, with asymptotes at zero and one.

Logistic regression was used to model the relationship between fish score and imposed water velocity. Logistic regression is similar to probit analysis, a method used to estimate fish swimming speeds by Meng (1993) and Childs and Clarkson (1996) and was easier to fit mathematically than probit analysis (Montgomery and Peck 1992). Therefore, prolonged swimming speeds and confidence intervals were calculated with logistic regression for each of the three size-classes. The SAS logistic and probit procedures were used to conduct logistic regression calculations (SAS Institute 1987).

Low-velocity habitat modeling.—Four sites in

the Oconee River were used to assess the downstream effects of hydropower peaking by Sinclair Dam on low-velocity habitat. Sites were chosen based on three criteria: (1) site must be near a suspected robust redhorse spawning site, (2) site must be near a U.S. Geological Survey (USGS) water-gauge recorder, and (3) site must be representative of the downstream gradient from Sinclair Dam within the reach of river inhabited by robust redhorse. Sites were located near Avant Kaolin Mine (32°56'N, 83°05'W), downstream from the Central of Georgia Railroad bridge (32°49'N, 82°58'W), downstream from Georgia Highway 57 (32°43'N, 82°57'W), and upstream from Dublin (32°38'N, 82°56'W). Under most circumstances, minimum river discharge in the Oconee River during May and June 1993–1996 at the four sites was greater than 14 m³/s at the four USGS water-gauge recorders, and maximum river discharge that resulted from hydropower generation was less than 170 m³/s (Figure 1; R. D. McFarlane, USGS, Water Resources Division, unpublished data).

A hydraulic simulation developed by EA Engineering (1994) for the Oconee River was used to describe stream depth and velocity as a function of discharge. Hydraulic data were collected to meet the requirements of the physical habitat simulation (PHABSIM) system single-velocity IGF-4 hydraulic simulation submodel (Milhous et al. 1989). Fifty-four transects were established in the Oconee River between Milledgeville and Dublin, Georgia. To describe the cross-sectional profile of the channel, 34–81 sampling stations were established along each transect. Depth and mean water column velocity were measured at these sampling stations during low (mean = 23 m³/s, SE = 0.88) and intermediate (mean = 110 m³/s, SE = 1.3) flow. Water surface elevations were measured along each transect at a minimum of three streamflows. In the present application, the mid-flow calibrated IGF-4 model for steady flow conditions was used to predict point estimates of mean water column velocity (predicted as 0.6 × depth from surface) at transects located near the four sites to assess the presence and availability of low-velocity habitats. The number of transects used at each site ranged from 5 to 13.

Logistic regression models developed from robust redhorse swimming performance experiments were used to predict the proportion of larvae that could maintain their position in the water column for 1 h at each velocity point estimate along the transect and was estimated for the 13.1-mm size-class with the equation

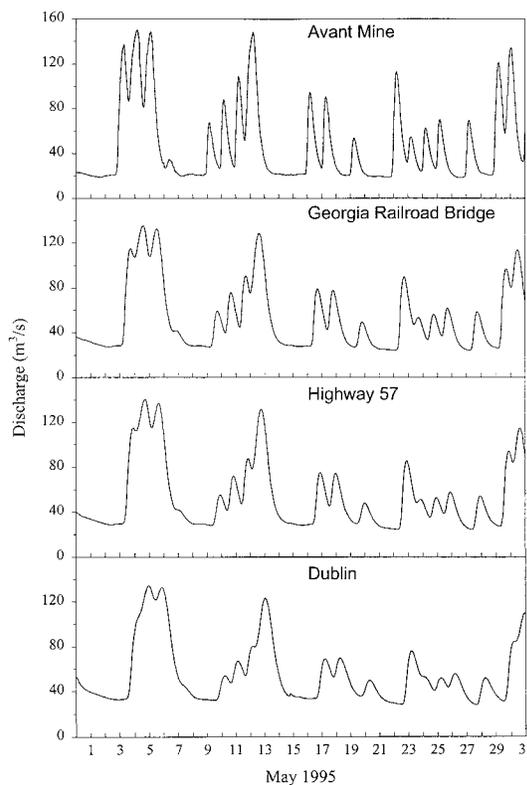


FIGURE 1.—Hydrographs of the Oconee River, Georgia, during hydropower peaking (R. D. McFarlane, USGS, Water Resources Division, unpublished data). Avant Mine, Georgia Railroad bridge, Highway 57, and Dublin were 40, 60, 68, and 103 km downstream from Sinclair Dam, respectively.

$$P_i = \frac{e^{\beta_0 + \beta_1 \cdot x_i}}{1 + e^{\beta_0 + \beta_1 \cdot x_i}}, \quad (2)$$

where P_i was the predicted proportion of larvae that could maintain their position in the water column for 1 h, β_0 was the estimated intercept for the logistic model, β_1 was the estimated slope for the logistic model, and x_i was mean water column velocity estimated with IGF-4. Subscript i was used to describe each point along a transect where water velocity was estimated. This approach allowed all points along the transect where water velocity was estimated to be given a probability related to whether a larva could maintain position for at least 1 h and was similar to a habitat suitability index developed from direct field observations (Bovee 1986; Nestler et al. 1989).

Weighted linear habitat (WLH) was an index of low-velocity habitat along a transect (m) and was estimated for each transect with the equation

$$\text{WLH} = \sum_{i=1}^n P_i \cdot w_i, \quad (3)$$

where $i = 1, 2, \dots, n$; P_i and w_i were as defined for equation (2), w_i was one-half the distance between points $i - 1$ and $i + 1$ on the transect (this accounted for asymmetry in horizontal distances between point estimates), and n was the total number of points along the transect. For each transect, WLH was calculated at 14, 28, 57, 85, 113, 142, and 170 m^3/s . The underlying assumptions of the WLH model were that mean water column velocity estimates along a transect approximately represented velocities that larval robust redhorse would experience in the river and that logistic regression models estimated from laboratory experiments provided reasonable approximations of larval fish swimming performance in the Oconee River.

The relationship between river discharge and low-velocity habitat at each site was investigated with regression analysis. Transect estimates of WLH at each site were considered replicates and to approximately represent the actual low-velocity habitat at a site. Plots of residual versus predicted response variable (WLH) and residual versus explanatory variable (river discharge) were used to check the assumption that variance of the error term was constant (Montgomery and Peck 1992). A natural logarithm transformation of WLH was used to meet the constant variance assumption for the Avant Mine, Georgia Railroad bridge, and Highway 57 sites, whereas a reciprocal transformation was used for the Dublin site.

Effective habitat analysis was conducted to determine the dynamic nature of low-velocity areas during hydropower peaking (Nestler et al. 1989). Effective WLH (EWLH) was calculated for each transect with the equation

$$\text{EWLH} = \sum_{i=1}^n [\min(\text{WLH}_i)]_{q_p}^{q_b} \quad (4)$$

where $i = 1, 2, \dots, n$; i and n were as defined for equations (2) and (3), $\text{WLH}_i = P_i \cdot w_i$ (from equation 3), q_p was the peak discharge evaluated (170 m^3/s), and q_b was the base discharge evaluated (14 m^3/s). Nestler et al. (1989) acknowledged that while a range of intermediate flows is associated with hydropower peaking, minimum habitat in a specific river cell usually occurs at base or peak flow (making evaluation at all possible flows unnecessary).

Results

Prolonged Swimming Experiments

The proportion of fish that continued swimming for 1 h during swim trials at imposed water velocities decreased as velocity increased for each size-class tested (Figure 2). Goodness-of-fit tests (Pearson chi-square) suggested that logistic regression models were appropriate ($P = 0.25, 0.33,$ and 0.14) for the three size-classes tested. Parameter estimates were significant ($P < 0.001$) for all three logistic regression models. The estimated slopes and intercepts of logistic regression models for the three size-classes are given as follows: 13.1-mm larvae: $\beta_1 = -0.91$ (SE = 0.19) and $\beta_0 = 6.3$ (SE = 1.3); 16.2-mm larvae: $\beta_1 = -0.75$ (SE = 0.14) and $\beta_0 = 8.0$ (SE = 1.5); and 20.4-mm larvae: $\beta_1 = -0.70$ (SE = 0.17) and $\beta_0 = 8.3$ (SE = 2.0). Prolonged swimming speeds of the 13.1-, 16.2-, and 20.4-mm size-classes were 6.9 cm/s (95% confidence interval [CI] = 6.2–7.7), 10.6 cm/s (95% CI = 9.9–11.4), and 11.7 cm/s (95% CI = 10.7–12.6), respectively.

Low-Velocity Habitat Modeling

The estimated WLH along transects at the Avant Mine, Georgia Railroad bridge, and Highway 57 sites were between 1 and 5 m at the seven river discharges investigated (Figure 3). The greatest amount of low-velocity habitat (9.5–20.9 m) along a transect was calculated for the Dublin site at river discharges between 113 and 170 m^3/s (Figure 3). There was a negative linear relationship between WLH and discharge at the Avant Mine (slope [b] = -0.0001 , SE = 0.00004; $P = 0.0098$, $R^2 = 0.07$) and Georgia Railroad bridge ($b = -0.0002$, SE = 0.00005; $P = 0.0016$, $R^2 = 0.19$) sites; WLH and discharge were not related at the Highway 57 or Dublin sites ($P > 0.20$). The EWLH calculated along a transect was substantially less than WLH computed for constant river discharges. Mean EWLH along transects within each site approached zero (EWLH < 0.001 m). The Highway 57 site had the greatest mean EWLH (0.0009 m, SE = 0.0009) of the four sites.

Discussion

Prolonged swimming speed of robust redhorse increased with increases in fish size. This increase in swimming performance probably resulted from among size-classes differences in larval length and from increases in water temperature. Larger fish tend to swim faster than smaller fish in absolute terms (Beamish 1978), which is particularly evi-

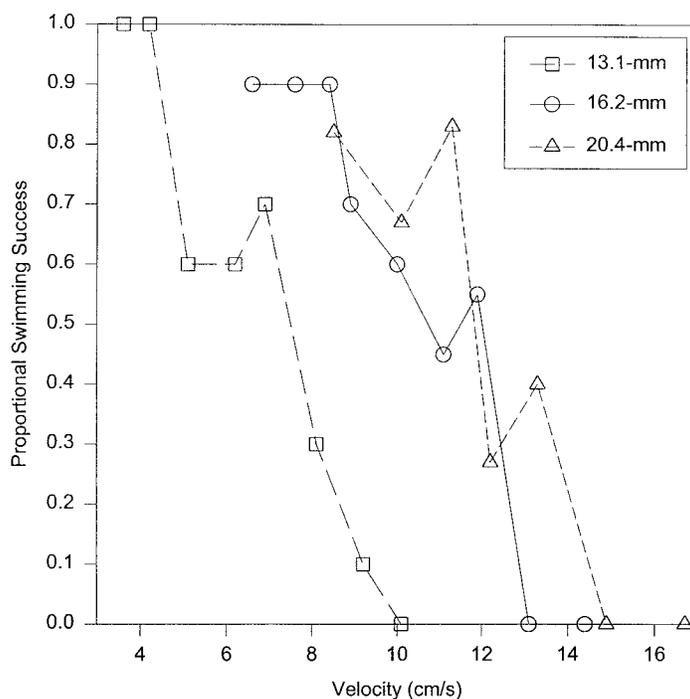


FIGURE 2.—Proportion of larval robust redhorse in the 13.1-, 16.2-, and 20.4-mm size-classes that successfully completed a 1 h swim trial at various water velocities.

dent for early life history stages because the development of the musculature and fins increases rapidly with growth. Further, swimming performance may be positively correlated with water temperature (e.g., Larimore and Duever 1968; Berry and Pimentel 1985; Childs and Clarkson 1996). Therefore, of the three size-classes tested, the 13.1-mm size-class of robust redhorse should be the most vulnerable to downstream displacement in the Oconee River.

Swimming performance of fish should vary between individuals and among species because swimming performance is restricted by bodyform and regulated by metabolic capacity (Beamish 1981). For example, the variation in swimming performance of juvenile largemouth bass *Micropterus salmoides* was substantial and repeatable (Kolak 1992). We found that larval robust redhorse exhibited individual variation in swimming performance, and some larvae swam better at higher current velocities than at lower current velocities. For example, proportional swimming success of 13.1-mm larvae was greater at 6.9 m/s than at 6.2 m/s (Figure 2). The scarcity of swimming speed estimates for larval catostomids and cyprinids make interspecific comparisons difficult. Never-

theless, we suspect that robust redhorse swimming speeds may be greater than many other fish in the Oconee River because larval robust redhorse emerge from spawning sites and enter the water column at larger sizes than many other fishes.

Low-velocity habitat was present in the Oconee River during variable river discharge. We based our assessment of low-velocity habitat on the swimming performance of the 13.1-mm size-class, which had the slowest prolonged swimming speed of the three size-classes tested. We conclude that larval fish nursery habitats were present in the Oconee River during fluctuating flow conditions because water velocity was one of the most important features that defines nursery habitats (Simonson and Swenson 1990; Scheidegger and Bain 1995). Although low-velocity habitats are present in the Oconee River during hydropower peaking, we are unsure of the accessibility or quality of these habitats to larval robust redhorse.

The relationship between WLH and discharge at the sites we investigated was not strong. Although there was a significant negative relationship between WLH and discharge at two (Avant Mine and Georgia Railroad bridge) of the four sites, the regression models only explained a small

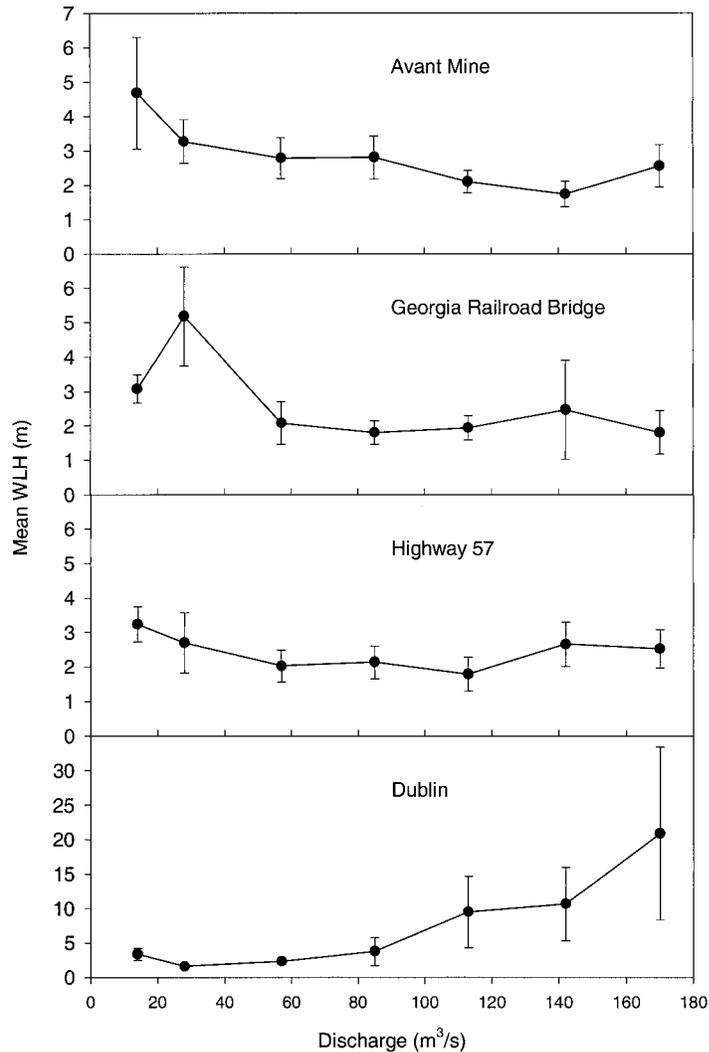


FIGURE 3.—Mean weighted linear habitat (WLH; estimated for the 13.1-mm size-class of robust redhorse) at river discharges that occurred commonly in the Oconee River, Georgia, as a result of hydropower generation during May–June 1993–1996. Error bars represent \pm SE.

percentage of the variation in the data (both $R^2 < 0.20$) and the estimated regression slopes were small (Avant Mine: $b = -0.0001$, Georgia Railroad bridge: $b = -0.0002$). In this case, we did not believe that statistical significance of the estimated regression slopes indicated a strong biologically relevant difference. Similarly, Leonard and Orth (1988) showed that some life stages of fishes (e.g., larvae) preferred narrow ranges of habitat variables (e.g., velocity) that decline only moderately with increasing river discharge.

Low-velocity habitat in the Oconee River was dynamic during fluctuating river discharge be-

cause our estimate of EWLH approached zero even though low-velocity areas were present at the seven discharges we investigated. The ability of larval robust redhorse to move laterally with low-velocity habitats, seek refuge from increasing water velocity, or relocate downstream to different low-velocity habitats during fluctuating flow conditions is unknown. However, we observed some larval robust redhorse lying on the bottom of the swim tube in response to increasing velocity during laboratory swimming tests, suggesting that at least some larvae may use the boundary layer as refuge from increasing velocities in the water column.

Larval Warner suckers *Catostomus warnerensis* exposed to mid-channel water velocities resisted downstream displacement by swimming to areas behind rocks, vegetation, and woody debris that provided shelter (Kennedy and Vinyard 1997). Larvae unable to seek refuge (i.e., velocity breaks or low-velocity areas associated with the bottom) from high water velocities during fluctuating river discharge will be displaced downstream. Downstream displacement of larval fish during natural flood conditions often increases mortality (John 1964; Schlosser 1982; Harvey 1987, 1991). However, if larval robust redhorse are able to use dynamic low-velocity habitats with minimal negative effects (e.g., high energy expenditure or reduced time spent foraging), then nursery habitats should be available to larvae during variable flow conditions.

Quality of larval fish nursery habitat may be an important factor in determining the distribution, abundance, and recruitment of age-0 robust redhorse. Hydropower peaking causes high-frequency disturbances in rivers that affect fishes according to their habitat use (Bain et al. 1988) and seem capable of degrading larval fish nursery habitats (Scheidegger and Bain 1995). Water velocity may not decrease the abundance of larval fish nursery habitat in the Oconee River, but may limit the accessibility of these habitats to larvae. However, factors other than mean water column velocity, such as vegetation, substrate, woody debris, or near-substrate hydraulic conditions, may be important in providing high-quality nursery habitats for larval robust redhorse. Pearsons et al. (1992) reported that the effects of naturally occurring floods on fish communities declined with increasing habitat complexity in some stream reaches. Vegetated and channel edge areas served as nursery habitats in a warmwater West Virginia stream (Lobb and Orth 1991), and larval catostomids in an Alabama river were associated with shallow, near-shore habitats with vegetation (Scheidegger and Bain 1995). Hydropower peaking causes changes in near-substrate hydraulic conditions, which could be important to larval robust redhorse, to form a mosaic of patches with varying risk to benthic organisms because the associated stresses are not uniform in distribution, intensity, and duration along a river channel (Gore et al. 1994).

Mean water column velocity was used to estimate low-velocity habitat for larval robust redhorse. The relationship between mean water column velocity and the hydraulic conditions experienced by larval robust redhorse in the river is

unclear. This could be problematic because larvae are relatively small compared to the size of a river cell, suggesting that larvae could be distributed anywhere within a river cell. Although our low-velocity habitat model may be simplistic with regard to the complex nature of the hydraulic conditions experienced by larvae, we believe our model is a good first approximation because the distribution of larval robust redhorse within the water column is unknown.

We used logistic regression models based on laboratory swimming tests to approximate larval robust redhorse swimming performance in the Oconee River. We recognized three potential problems (listed below) with extrapolating laboratory results to the river and concluded that they would cause consistently biased habitat estimates that would not affect the relationship between WLH and river discharge, which we considered most important. First, swimming performance of larvae reared in the laboratory may have been greater than that of wild fish because laboratory-reared fish were in predator-free and food-rich environments. If this were the case, then our estimates of WLH would be biased high. Second, the WLH model was appropriate for the water temperature at which prolonged swimming speeds were estimated in the laboratory. Differences in water temperature between the test system and the river may have resulted in over- or underestimates of WLH. Finally, physical factors other than water temperature could influence larval swimming speeds. Larimore (1975) concluded that fry of smallmouth bass *Micropterus dolomieu* were displaced more frequently by velocity in turbid water than in clear water because visual cues were used for orientation. Larval robust redhorse displayed positive phototaxis in swimming tests; thus, turbidity may affect swimming performance of larvae in the river.

We suspect that less-variable flow conditions in the Oconee River than those that result from hydropower peaking may increase larval robust redhorse access to nursery habitats when larval swimming speeds are lowest (i.e., May–June). Increased access to nursery habitats may increase survival of age-0 fish, although strong evidence to evaluate this is lacking. A better understanding of larval robust redhorse behavioral responses to increasing water velocity and larval distribution in the water column is needed to determine whether water velocities resulting from hydropower peaking are limiting access to nursery habitats. Similarly, further research on biotic and abiotic factors that af-

fect robust redhorse is needed to explain their poor recruitment in the Oconee River and their extirpation from many southeastern Atlantic slope rivers.

Acknowledgments

Discussions with M. Freeman and J. Reeves improved habitat modeling; J. Reeves provided statistical advice; M. Childs, T. Miller, J. Nestler, R. Newman, D. Orth, B. Vondracek, and one anonymous reviewer provided critical comments on an earlier draft of this paper; D. Higginbotham, S. Love, and T. Waldrop assisted with the laboratory experiment; J. Evans and other personnel from the Georgia Department of Natural Resources collected adult robust redhorse from the Oconee River for artificial spawning; T. Barrett, B. Hess, G. Looney, and J. Shelton provided fertilized robust redhorse eggs; R. McFarlane provided hourly river discharge data from USGS water-gauge recorders in the Oconee River; and P. Leonard performed the hydraulic modeling. The Georgia Power company provided funding for this research.

References

- Bain, M. B., J. T. Finn, and H. E. Booke. 1988. Stream-flow regulation and fish community structure. *Ecology* 69:382–392.
- Beamish, F. W. H. 1978. Swimming capacity. Pages 101–189 in W. S. Hoar and D. J. Randall, editors. *Fish physiology*, volume 7. Academic Press, New York.
- Beamish, F. W. H. 1981. Swimming performance and metabolic rate of three tropical fishes in relation to temperature. *Hydrobiologia* 83:245–254.
- Berry, B. R., Jr., and R. Pimentel. 1985. Swimming performance of three rare Colorado River fishes. *Transactions of the American Fisheries Society* 114:397–402.
- Bishai, H. M. 1960. The effects of water currents on the survival and distribution of fish larvae. *Journal du Conseil Permanent International pour l'Exploration de la Mer* 25:135–146.
- Bovee, K. D. 1986. Development and evaluation of habitat suitability criteria for use in the instream flow incremental methodology. U.S. Fish and Wildlife Service Biological Report 86(7). (Instream Flow Paper 21.)
- Brett, J. R. 1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue time and temperature. *Journal of the Fisheries Research Board of Canada* 24:1731–1741.
- Carter, J. G., V. A. Lamarra, and R. J. Ryel. 1986. Drift of larval fish in the upper Colorado River. *Journal of Freshwater Ecology* 3:567–577.
- Childs, M. R., and R. W. Clarkson. 1996. Temperature effects on swimming performance of larval and juvenile Colorado squawfish: implications for survival and species recovery. *Transactions of the American Fisheries Society* 125:940–947.
- Cushman, R. M. 1985. Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. *North American Journal of Fisheries Management* 5:330–339.
- EA Engineering, Science, and Technology. 1994. Sinclair hydroelectric project relicensing technical studies: (FERC No. 1951) Oconee River instream flow study. Report to Georgia Power Company, Atlanta.
- Elwood, J. W., and T. F. Waters. 1969. Effects of floods on food consumption and production rates of a stream brook trout population. *Transactions of the American Fisheries Society* 98:253–262.
- Evans, J. W. 1994. A fisheries survey of Oconee River between Sinclair Dam and Dublin, Georgia. Georgia Department of Natural Resources, Wildlife Resources Division, Federal Aid in Sport Fish Restoration, Project F-33, Final Report, Social Circle, Georgia.
- Gore, J. A., S. Niemela, V. H. Resh, and B. Stutzner. 1994. Near-substrate hydraulic conditions under artificial floods from peaking hydropower operation: a preliminary analysis of disturbance intensity and duration. *Regulated Rivers: Research and Management* 9:15–34.
- Harvey, B. C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. *Transactions of the American Fisheries Society* 116:851–855.
- Harvey, B. C. 1991. Interactions of abiotic and biotic factors influencing larval fish survival in an Oklahoma stream. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1476–1480.
- Houde, E. D. 1969. Sustained swimming ability of larvae of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*). *Journal of the Fisheries Research Board of Canada* 26:1647–1659.
- Jenkins, R. E., and N. M. Burkhead. 1994. *Freshwater fishes of Virginia*. American Fisheries Society, Bethesda, Maryland.
- Jennings, C. A., J. L. Shelton, B. F. Freeman, and G. L. Looney. 1996. Culture techniques and ecological studies of the robust redhorse *Moxostoma robustum*. Annual Report to Georgia Power Company, Atlanta.
- John, K. R. 1964. Survival of fish in intermittent streams of the Chiricahua Mountains, Arizona. *Ecology* 45:112–119.
- Kennedy, T. B., and G. L. Vinyard. 1997. Drift ecology of western catostomid larvae with emphasis on Warner suckers, *Catostomus warnerensis* (Teleostei). *Environmental Biology of Fishes* 49:187–195.
- Kinsolving, A. D., and M. B. Bain. 1993. Fish assemblage recovery along a riverine disturbance gradient. *Ecological Applications* 3:531–544.
- Kolok, A. S. 1992. The swimming performances of individual largemouth bass (*Micropterus salmoides*) are repeatable. *Journal of Experimental Biology* 170:265–270.
- Larimore, R. W. 1975. Visual and tactile orientation of smallmouth bass fry under floodwater conditions.

- Pages 323–332 in H. Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D.C.
- Larimore, R. W., and M. J. Duever. 1968. Effects of temperature acclimation on the swimming ability of smallmouth bass fry. *Transactions of the American Fisheries Society* 97:175–184.
- Leonard, P. M., and D. J. Orth. 1988. Use of habitat guilds of fishes to determine instream flow requirements. *North American Journal of Fisheries Management* 8:399–409.
- Lobb, M. D., III, and D. J. Orth. 1991. Habitat use by an assemblage of fish in a large warmwater stream. *Transactions of the American Fisheries Society* 120: 65–78.
- Meng, L. 1993. Sustainable swimming speeds of striped bass larvae. *Transactions of the American Fisheries Society* 112:702–708.
- Milhous, R. T., M. A. Updike, and D. M. Schneider. 1989. Physical habitat simulation system reference manual, version 2. U.S. Fish and Wildlife Service Biological Report 89(16). (Instream Flow Information Paper 26.)
- Montgomery, D. C., and E. A. Peck. 1992. Introduction to linear regression analysis, 2nd edition. Wiley, New York.
- Nestler, J. M., R. T. Milhous, and J. B. Layzer. 1989. Instream habitat modeling techniques. Pages 295–315 in J. A. Gore and G. E. Petts, editors. Alternatives in regulated river management. CRC Press, Boca Raton, Florida.
- Pearsons, T. N., H. W. Li, and G. A. Lamberti. 1992. Influences of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Transactions of the American Fisheries Society* 121: 427–436.
- SAS Institute. 1987. SAS/STAT users guide for personal computers, version 6. SAS Institute, Cary, North Carolina.
- Scheidegger, K. J., and M. B. Bain. 1995. Larval fish distribution and microhabitat use in free-flowing and regulated rivers. *Copeia* 1995:125–135.
- Schlösser, I. J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. *Ecological Monographs* 52:395–414.
- Schlösser, I. J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. *Ecology* 66:1484–1490.
- Seegrist, D. W., and R. Gard. 1972. Effects of floods on trout in Sagehen Creek, California. *Transactions of the American Fisheries Society* 101:478–482.
- Simonson, T. D., and W. A. Swenson. 1990. Critical stream velocities for young-of-the-year smallmouth bass in relation to habitat use. *Transactions of the American Fisheries Society* 119:902–909.
- Stehr, W. C., and J. W. Branson. 1938. An ecological study of an intermittent stream. *Ecology* 19:294–310.
- Travnicek, V. H., and M. J. Maccina. 1994. Comparison of flow regulation effects on fish assemblages in shallow and deep water habitats in the Tallapoosa River, Alabama. *Journal of Freshwater Ecology* 9: 207–216.