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Factors Affecting Nesting Success of Smallmouth Bass in a Regulated Virginia Stream

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Abstract.—We examined the influences of habitat, temperature, stream discharge, and the timing of spawning on the nesting success of smallmouth bass *Micropterus dolomieu.* Smallmouth bass began spawning when temperatures reached 15°C, and high flow disrupted spawning five times. Larger males spawned earlier than smaller males; a log-linear relation between male length and degree-days accumulated was significant ($r = -0.63$, $P < 0.01$). In all, 45 of 105 nests (43%) and 42 of 81 males (52%) produced free-swimming larvae. Production of free-swimming larvae was variable and lower than previously reported, ranging from 98 to 1,802 (mean, 608). Large males (>305 mm total length) accounted for the highest production of free-swimming larvae and also made the most renesting attempts, which suggests that large males can have a strong influence on year-class strength. Stepwise discriminant analysis distinguished successful nests from unsuccessful nests by higher flow at time of nest construction, higher mean temperatures, lower mean stream discharge during nest incubation, and shorter distance to shore. High flow (>10 m^3/s) was responsible for most nest failures (85%). Increased water velocity at nest sites with increased stream discharge was the most likely cause of nest failures. The increase of mean velocity with increased stream discharge was significantly lower for successful nests than for unsuccessful nests, which showed that nest location determines the degree of exposure to high flows. The temporal pattern of streamflow fluctuation appears to be the most important abiotic factor determining nesting success or failure for smallmouth bass in this perennial stream.

In temperate warmwater streams, especially perennial streams for which flood predictability is low (Poff and Ward 1989), stochastic abiotic factors may be more important than biotic factors in regulating fish populations (Grossman et al. 1982, 1990). Although biotic factors still play a role, their importance is probably contingent on past stochastic events. This contingency of biotic regulation means that we should develop a better understanding of the physical disturbance thresholds that result in catastrophic mortality to fish populations. Stream-dwelling centrarchids are particularly sensitive to variable streamflow during spawning and early life stages (Jennings and Philipp 1994). In this study we measured nesting success of individual male smallmouth bass *Micropterus dolomieu* as the number of larvae successfully reared to the free-swimming stage. Although abiotic factors such as temperature, streamflow, and physical habitat are important determinants of nesting success (Pflieger 1966, 1975; Winemiller and Taylor 1982; Reynolds and O'Bara 1991), we suspected that biotic factors, particularly male size and experience (Ridgway et al. 1991), and habitat selection might mitigate somewhat for the effects of variable streamflow.

In order to gain a more mechanistic understanding of the nesting success of smallmouth bass for development and testing of individual-based models (Jager et al. 1993), we examined individual male smallmouth bass nesting chronology and larval production to discover important biotic and abiotic determinants of (1) the timing of nesting, (2) nesting success, and (3) production of free-swimming larvae.

Study Area

The study area was a 4.8-km reach of the North Anna River in eastern Virginia 22 km below Lake Anna Dam. In 1972, the Virginia Electric and Power Co. (Virginia Power) impounded the river to form 5,000-ha Lake Anna, which provides cooling water for a nuclear power plant. Virginia Power also operates two small hydropower turbines at the dam. Normal operations consist of epilimnial releases of a minimum of 1.13 m^3 through one turbine. When Lake Anna exceeds a level of 76.2 m above mean sea level, both turbines are used. Lake Anna has very limited storage capacity and runoff in excess of 5.10 m^3/s is spilled. This creates pseudonatural flows during periods of high runoff. Flooding is not uncommon in the North Anna River, and hydrographs for 1972–1985 showed that

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mean daily discharge ranged from 1.13 to 445 m^3/s. Discharge during most years fluctuates widely in April and May, the months when smallmouth bass typically spawn.

The North Anna River averages 35 m in width and has an average gradient of 1.6 m/km (King et al. 1991). Pools are frequently greater than 100 m long and their depths range from 0.5 to 2.0 m. Most pools contain ample cover and have a mixture of sand and bedrock or boulder substrates. Streamside vegetation is well developed and consists of a variety of deciduous trees, which shade a considerable portion of the river. We chose the 4.8-km study site below the dam because smallmouth bass are known to nest in low densities in streams (5–9 nests/km; Pflieger 1966, 1975).

Methods

We located nests by floating the study reach from April through June of 1992. We thoroughly searched all pools, using polarized glasses to locate fish and nest depressions. Once we located a nest, a numbered rock was placed immediately downstream of the nest. After the nest was marked, we angled the male smallmouth bass from the nest and then measured (total length, TL, to nearest millimeter), weighed (to nearest gram), and released it.

Data necessary to determine the influence of male size on the timing of spawning included male size, spawning day, and water temperature. Subsequent visits to marked nests allowed us to estimate the day that the nest received eggs (margin of error, about 1 d). We distinguished renesting males from first-time nesters by (1) recapturing the male and measuring its length while examining it for hook scars (dark, bruised area of scar was noted at first time of capture) and (2) comparing the length of the suspected renester to previously recorded lengths of males from failed nests in that area. Temperatures were measured with digital thermographs installed near the upper and lower ends of the study reach. Thermographs were placed at a depth of about 1 m and set to record temperatures hourly.

We analyzed the influence of male size on the timing of first spawning by regressing $\log_{10}$ (male TL) against $\log_{10}$ (degree-days, the sum of daily average temperatures above 10°C) accumulated by the male after temperatures reached 10°C (degree-days > 10°C) and before the estimated day of egg deposition. Only the first nesting date was used for males that renested. We compared the relation for smallmouth bass from the North Anna River to $\log_e$ male TL $= 5.61 - 0.355 \log_e$ (degree-days $> 10°C$), which is the relation of Ridgway et al. (1991).

We determined the fates of individual nests by snorkeling at each nest 4–8 times during the incubation period. At each visit, we noted the developmental stage of progeny in the nest (eggs, yolk sac, near swim-up, swim-up) as well as any disturbance or obvious mortalities (i.e., due to fungus). At each marked nest, we measured 28 variables as potential predictor variables for explaining success or failure of individual nests (Table 1). We used a pebble count technique (Wolman 1954) to determine median size of nest substrate. Cover was described by counting the number of submerged object surfaces (Kinsolving and Bain 1990) within a 1- and 2-m radius of each nest and measuring the distance to nearest cover. We obtained flow data from the U.S. Geological Survey for their gauge located at the Route 601 Louisa bridge. Temperature data were recovered from the digital thermographs in mid-June when nesting activity ended. A sample of about 10 eggs from each nest was measured to the nearest 0.1 mm to obtain median egg diameter.

We used two-sample *t*-tests, multivariate analysis of variance (MANOVA), and stepwise discriminant analysis (SAS Institute 1988) to assess multivariate separation between successful and unsuccessful nests for the 28 predictor variables. We then used the best model from a stepwise discriminant analysis to produce linear discriminant functions and cross-validations for successful and unsuccessful nests (SAS Institute 1988).

To determine the number of free-swimming larvae produced by individual nests, we counted larvae within 24 h of the time they transformed from free embryos to free-swimming larvae. This transition is characterized by absorption of the yolk sac, an increase in dark pigmentation, and a rise from the substrate to swim in the water column (Goff 1986). At each nest, we counted the total number of larvae produced (Noltie 1986).

We analyzed these data by testing for significant simple correlations between variables measured (Table 1) and the number of free-swimming larvae produced at each nest. We divided successful nests into groups of low, medium, and high production of free-swimming larvae (numeric categories were assigned to balance the sample size at 15 per group) and used stepwise discriminant analysis and discriminant function analysis to determine which variables provided significant separation among the groups.

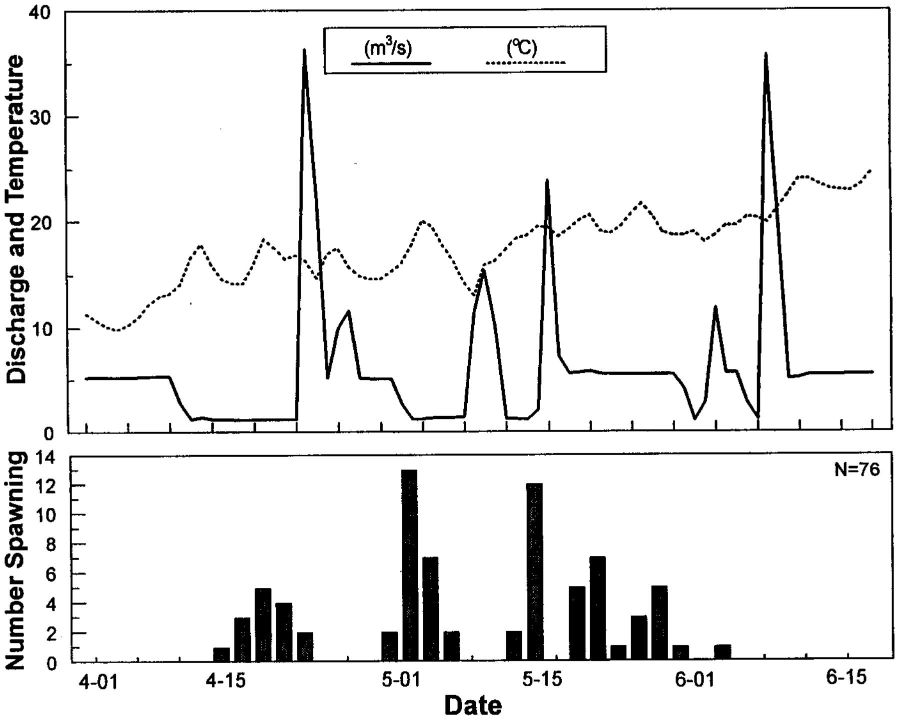

FIGURE 1.—Temperature and discharge during spawning by smallmouth bass and (below) the distribution of first-time spawners in 1992.

lection methods. Stepwise discriminant analysis of 22 variables showed that discharge, temperature, and nest location variables provided the best separation between successful and unsuccessful nests (Table 3). Successful nests had higher flows at nest construction, lower mean flow during incubation, and higher temperatures and they were located closer to the streambank than failed nests. Flow at nest construction and mean flow during incubation were both selected in the model, but were not strongly correlated ($r = -0.29$) and provide different information. Mean and minimum temperature were both selected, so we dropped minimum temperature because these variables were highly correlated ($r = 0.93$) and provide similar information. Cross-validation with linear discriminant functions correctly classified 79% (83 of 105) of nests with correct classification for 80% of failed nests and 77% of successful nests.

Production of free-swimming larvae from the 45 successful nests was highly variable, ranging from 98 to 1,802 (mean, 608). Early nests were unsuccessful; most successful nests produced free-swimming larvae the last 2 weeks of May, during a period of stable flow (Figure 1). Direct observations on sources of this variation were limited to egg mortality resulting from fungus. Fifteen of the 100 nests with eggs had fungus, although we observed no fungus after 16 May, when mean daily temperatures exceeded 20°C.

Single variables explained a small proportion of the variation in production of free-swimming larvae. Simple correlations with male TL ($r = 0.42$, $P = 0.005$; Figure 3) and weight ($r = 0.43$, $P = 0.003$) were significant, as were correlations with distance to cover ($r = 0.42$, $P = 0.004$) and nest diameter ($r = 0.38$, $P = 0.01$). However, male TL and weight were highly correlated and provide similar information. Stepwise discriminant analysis selected 4 of 27 variables that provided separation between low, medium, and high levels of free-swimming larvae (Table 4). Higher values for nest substrate size, nest diameter, male TL, and degree-days were associated with higher production of free-swimming larvae. Cross-validation with linear discriminant functions correctly classified 60% (27 of 45) of nests for low, medium, and high levels of free-swimming larvae.

Males selected areas for nest sites that had smaller increases in mean velocity with increased discharge than random locations in pool habitat. The individual slope of the mean velocity-versus-

TABLE 2.—Summary statistics and two-sample *t*-tests for variables measured to compare successful and unsuccessful nests (*t*-test, $P < 0.05$). Entries are listed in order of decreasing significance of differences between successful ("yes") and unsuccessful ("no") nests. Variables are described in Table 1.

Variable	Successful nest?	N	Mean	95% confidence interval	SD	Median	P
Free-swimming larvae	Yes	45	608	491–726	390.4	470	
Day nest located	Yes	45	137.1	133.9–140.3	10.65	140	
	No	60	124.2	120.9–127.4	12.71	125	0.0001
Degree-days	Yes	45	735	682–789	178.4	766	
	No	60	542	488–595	207.3	542	0.0001
Nest Q (m^3/s)	Yes	45	4.93	4.33–5.53	1.99	5.50	
	No	60	2.25	1.85–2.66	1.58	1.33	0.0001
Change Q (m^3/s)	Yes	45	7.06	5.16–8.97	6.34	4.62	
	No	60	20.74	17.83–23.64	11.24	21.56	0.0001
Maximum Q (m^3/s)	Yes	45	10.19	8.84–11.54	4.5	7.20	
	No	60	22.36	19.58–25.14	10.77	23.71	0.0001
Mean temperature (°C)	Yes	45	19.2	18.7–19.6	1.38	19.5	
	No	60	17.6	17.2–18.1	1.72	16.8	0.0001
Mean Q (m^3/s)	Yes	45	5.03	4.81–5.26	0.75	5.32	
	No	60	7.67	6.76–8.57	3.51	6.97	0.0001
Maximum temperature (°C)	Yes	45	23.0	22.8–23.2	0.66	22.8	
	No	60	21.0	20.6–21.4	1.49	20.9	0.0001
Minimum Q (m^3/s)	Yes	45	3.13	2.49–3.77	2.14	1.19	
	No	60	1.62	1.34–1.9	1.09	1.22	0.0001
Minimum temperature (°C)	Yes	45	16.1	15.4–16.8	2.41	17.1	
	No	60	14.8	14.2–15.4	2.32	13.9	0.007
Male weight (g)	Yes	45	355	253–456	337	194	
	No	41	536	393–679	453	440	0.04
Water depth (m)	Yes	45	1.09	1–1.17	0.28	1.07	
	No	60	0.99	0.92–1.05	0.26	0.96	0.06
Distance to cover (m)	Yes	45	0.92	0.62–1.22	1.0	0.6	
	No	60	0.61	0.47–0.75	0.54	0.5	0.06
Upstream adjacent velocity (m/s)	Yes	45	0.09	0.06–0.11	0.08	0.07	
	No	60	0.06	0.05–0.08	0.06	0.04	0.09
Male TL (mm)	Yes	45	286	263–310	77.8	252	
	No	56	315	291–339	89.4	310	0.09
Egg diameter (mm)	Yes	30	2.26	2.19–2.34	0.2	2.3	
	No	33	2.18	2.11–2.26	0.21	2.2	0.12
Distance to shore (m)	Yes	45	11.7	9.9–13.6	6.03	13	
	No	60	13.2	12.1–14.4	4.62	14	0.17
Change in temperature (°C)	Yes	45	6.8	6.2–7.5	2.2	6.1	
	No	60	6.2	5.7–6.8	2.2	6.0	0.18
Nest depth (cm)	Yes	45	5.4	4.6–6.2	2.82	3	
	No	60	6.2	5.2–7.2	3.87	5	0.22
Upstream adjacent bottom velocity (m/s)	Yes	45	0.04	0.02–0.06	0.06	0.02	
	No	60	0.03	0.02–0.04	0.04	0.02	0.35
Mean velocity (m/s)	Yes	45	0.06	0.04–0.07	0.04	0.04	
	No	60	0.05	0.04–0.06	0.05	0.04	0.36
Cover (2 m)	Yes	45	6.1	4.9–7.3	3.87	6	
	No	60	6.6	5.8–7.5	3.28	6	0.44
W_r	Yes	45	0.97	0.97–0.97	0.01	0.97	
	No	41	0.97	0.97–0.98	0.01	0.97	0.55
Next nest (m)	Yes	45	50	27–74	77	24	
	No	60	58	38–79	80	18	0.60
Bottom velocity (m/s)	Yes	45	0.01	0.00–0.01	0.01	0	
	No	60	0.01	0.01–0.01	0.01	0	0.77
Cover (1 m)	Yes	45	3	2.4–3.7	2.15	3	
	No	60	3.1	2.6–3.7	2.12	3	0.82
Substrate size (mm)	Yes	45	24	21–28	11	23	
	No	60	24	21–27	10	23	0.83
Nest diameter (cm)	Yes	45	50	44–55	18	46	
	No	60	49	45–53	16	45	0.86

TABLE 5.—Two-sample *t*-tests comparing slopes of the mean velocity versus discharge relation for individual nests and individual points along pool transects. Coefficient of variation (CV) = 100·SD/mean. Probabilities (*P*) are for comparisons of pools with all nests or of failed with successful nests.

Comparison	Mean slope	CV	*N*	*P*
Pools	0.024	66.93	136	
All nests	0.010	117.81	104	0.0001
Failed nests	0.013	99.10	59	
Successful nests	0.007	151.88	45	0.02

by larger males. Larger males nested earlier when temperatures were lower, which resulted in longer nest incubation times and more failures due to the increased probability of high flow during incubation. After early nesting attempts failed, 21 large males renested (mean TL of renesters, 339 mm; mean TL of first-time nesters, 288 mm) and were more successful than first-time spawners (renesters, 59% success; first-time nesters, 32% success). This provides support for Pflieger's (1966, 1975) hypothesis that renesting by stream-dwelling smallmouth bass assures reproductive success in years of high and unstable flow.

Smallmouth bass in the North Anna River were only moderately successful in producing free-swimming larvae. The success rate for nests (42%) was within the range of success reported from other studies on reproduction by smallmouth bass. In Lakes Erie and Opeongo, cold, windy conditions in 1982 resulted in 33 and 34% nesting success, whereas warm, calm conditions in 1983 resulted in 88 and 92% nesting success (Goff 1986; Ridgway and Friesen 1992). This-annual variation in reproductive success has accounted for variation in year-class strength in northern lakes (Ridgway and Friesen 1992). Cold, windy conditions in lakes may be viewed as analogous to the high-flow and variable temperature conditions that influenced nesting success in the North Anna River. Similarly, in a year of low, stable flow in a Tennessee stream, nesting success was 73%, whereas in a year with heavy precipitation, nesting success fell to 35% (Reynolds and O'Bara 1991).

High flows create increased water velocities at nest sites, which were the primary cause of failure for smallmouth bass nests in the North Anna River. Two basic mechanisms accounted for the failure of nests during periods of high flow. Some nests were physically destroyed by being filled with sand during flow events. Many nests remained undisturbed following high flows, so it was likely that males abandoned nests following substantial increases in velocity and turbidity. Eggs and larvae were absent from abandoned nests probably because they were washed from the nest by high water velocity or consumed by predators after the male abandoned the nest (Pflieger 1966, 1975; Winemiller and Taylor 1982; Reynolds and O'Bara 1991).

Mean water column velocities must be relatively low to prevent the nest from being scoured and eggs and larvae washed from the nest. In this study, velocities were less than 0.20 m/s at the time of nest construction, which is consistent with observations from other studies (Pflieger 1966, 1975; Winemiller and Taylor 1982; Reynolds and O'Bara 1991; Aadland 1993). However, some nest site velocities in this study appeared to be higher than those reported by others. Winemiller and Taylor (1982) reported that nests were exposed to velocities of 0.15 m/s during moderate flooding, which is less than the highest figure in this study. Aadland (1993) reported lower velocities at nest sites. Flow during nest construction may explain the higher nest site velocities in the North Anna River. Many nests in this study were constructed at flows considerably greater than minimum flow, which may account for the higher mean velocities. Bottom velocities at these nests remained at 0.03 m/s or lower because males selected nest sites that offered protection from increased flow (Table 5).

Most nest failures in this study could be directly attributed to high flows, whereas flow at nest construction influenced selection for protected sites. A mean column velocity of approximately 0.20 m/s may be the maximum at which a nest will remain occupied, at least for the depths and vertical velocity profiles in the North Anna River. Nests constructed during moderately high flows were more successful than nests constructed at or near minimum flow. At increased flows, males probably selected nest sites that would remain protected with further increases in flow. Similarly, Reynolds and O'Bara (1991) suggested that in high flows, males located nests near complex upstream cover and in coarser substrate. Mean flows during incubation of successful nests were close to the flow at nest construction, whereas failed nests were constructed at flows much lower than the mean flow during incubation.

Production of free-swimming larvae from smallmouth bass nests in the North Anna River was lower than production reported from other studies and seems to be influenced by disturbance, fish size, substrate size, and development times. Mean

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