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ARTICLE

Spawning Habitat Selection of Hickory Shad

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Abstract

We examined the spawning habitat selectivity of hickory shad *Alosa mediocris*, an anadromous species on the Atlantic coast of North America. Using plankton tows and artificial substrates (spawning pads), we collected hickory shad eggs in the Roanoke River, North Carolina, to identify spawning timing, temperature, and microhabitat use. Hickory shad eggs were collected by both sampling gears in March and April. The results from this and three other studies in North Carolina indicate that spawning peaks at water temperatures between 12.0°C and 14.9°C and that approximately 90% occurs between 11.0°C and 18.9°C. Hickory shad eggs were collected in run and riffle habitats. Water velocity and substrate were significantly different at spawning pads with eggs than at those without eggs, suggesting that these are important microhabitat factors for spawning. Hickory shad eggs were usually collected in velocities of at least 0.1 m/s and on all substrates except those dominated by silt. Eggs were most abundant on gravel, cobble, and boulder substrates. Hickory shad spawned further upstream in years when water discharge rates at Roanoke Rapids were approximately average during March and April (2005 and 2007), as compared with a severe drought year (2006), suggesting that water flows may affect not only spawning site selection but also the quantity and quality of spawning habitat available at a macrohabitat scale. Using our field data and a Bayesian approach to resource selection analysis, we developed a preliminary habitat suitability model for hickory shad. This Bayesian approach provides an objective framework for updating the model as future studies of hickory shad spawning habitat are conducted.

Hickory shad *Alosa mediocris* is an anadromous alosine that spawns in coastal rivers from Maryland to Florida, USA (Richkus and DiNardo 1984). Within river systems, hickory shad spawn in both tributary and main-channel habitats (Sparks 1998; Burdick and Hightower 2006; Smith 2006). Like other anadromous alosines, water temperature appears to regulate the annual timing of the spawning run for hickory shad (Leggett and Whitney 1972; Loesch 1987; Aprahamian et al. 2003; Bagliniere et al. 2003; Harris et al. 2007). Hatching occurs approximately 48–76 h after fertilization, depending on temperature (Mansueti 1962). Hickory shad eggs are initially semiadhesive and semidemersal but become less adhesive with age and can be buoyant in fast-moving water (Mansueti 1962). Although hickory shad eggs have been collected from multiple rivers (Godwin and Adams 1969; Sholar 1977; Burdick and Hightower 2006; Smith 2006), and egg development has been studied (Mansueti 1962), little on the specific macro- and microhabitats required for spawning is known. Because hickory shad are ecologically important and support commercial and recreational fisheries, information about spawning habitat in rivers is important to facilitate conservation and management.

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One approach to characterizing spawning habitat is the development of a habitat suitability model. The U.S. Fish and Wildlife Service (USFWS) began using habitat suitability models in the early 1980s to facilitate habitat management, impact assessment, and project planning (USFWS 1981). These models can be developed using a variety of methods and can include information gathered from field data and surveys of knowledgeable scientists. These models produce an estimate of relative habitat suitability between 0 (unsuitable) and 1 (optimally suitable), based on criteria considered important to the species at a particular life stage (USFWS 1981; Stier and Crance 1985). Habitat suitability models focused mainly on riverine habitat requirements have been developed for American shad *A. sapidissima*, as well as blueback herring *A. aestivalis* and alewife *A. pseudoharengus* (often referred to collectively as river herring) (Pardue 1983; Stier and Crance 1985), but not for hickory shad. Limited information on the life history and habitat requirements of hickory shad may have prevented development of a habitat suitability model for this species.

Our objectives for this study were to characterize the spawning habitat of hickory shad and to develop a preliminary habitat suitability model. We used data on the dates and water temperatures when hickory shad eggs were collected in oblique plankton tows from this and three other studies in North Carolina to identify the seasonal period and temperature range at spawning. We also collected hickory shad eggs on spawning pads placed in a variety of habitats within presumed spawning areas to identify spawning microhabitat use.

Our preliminary habitat suitability model is based on resource selection functions (RSFs), which are widely used to characterize habitat selectivity (Boyce et al. 2002). These RSFs evaluate habitat selectivity on the basis of an animal's use of particular habitats as compared with the availability of those habitats in the landscape (Boyce et al. 2002). Resource selection functions are data-driven (i.e., they do not include expert opinion to assign values), which makes them statistically rigorous for evaluating habitat suitability (Boyce et al. 2002). An assumption of this approach is that detection is similar in all habitat types and that the proportionate use of a particular habitat is equal to the suitability of that habitat. We followed the approach of Thomas et al. (2004) in using Bayesian statistical methods to construct RSFs. One strength of the Bayesian approach is that information from previous work can be combined with new data to obtain refined estimates of model parameters (McCarthy 2007). Also, this approach provides a measure of uncertainty for the suitability of each habitat category (Bayesian credible intervals), based on the actual sample sizes rather than large sample theory (Thomas et al. 2004). Our preliminary habitat suitability model can inform present management but can also guide future research and serve as prior information in future Bayesian analyses.

METHODS

Study area.—The Roanoke River runs over 600 river kilometers (rkm) from western Virginia to Albemarle Sound, North Carolina. The Roanoke River's fall line occurs within a 16.1-km reach between rkm 209 (Weldon; Figure 1) and rkm 225 in North Carolina (Smith 1907; Coe 1964). In this reach, the river's average gradient change steepens to over 1.5 m/rkm and numerous islands and larger substrates are present (Smith 1907). Anadromous fish migration is presently limited by a large hydroelectric dam at Roanoke Rapids (rkm 221) that provides no fish passage (Rulifson and Manooch 1990; Walsh et al. 2005; Figure 1). The tailrace of the Roanoke Rapids Dam was constructed adjacent to the original river channel; the original river channel there is now referred to as the bypass. Regular flows were reintroduced into the bypass in 2004 as part of the Federal Energy Regulatory Commission license for the Roanoke Rapids Dam. To assess use of this restored habitat by anadromous fish, we sampled in 2005 and 2006 at the lower end of the bypass (Figure 1), which

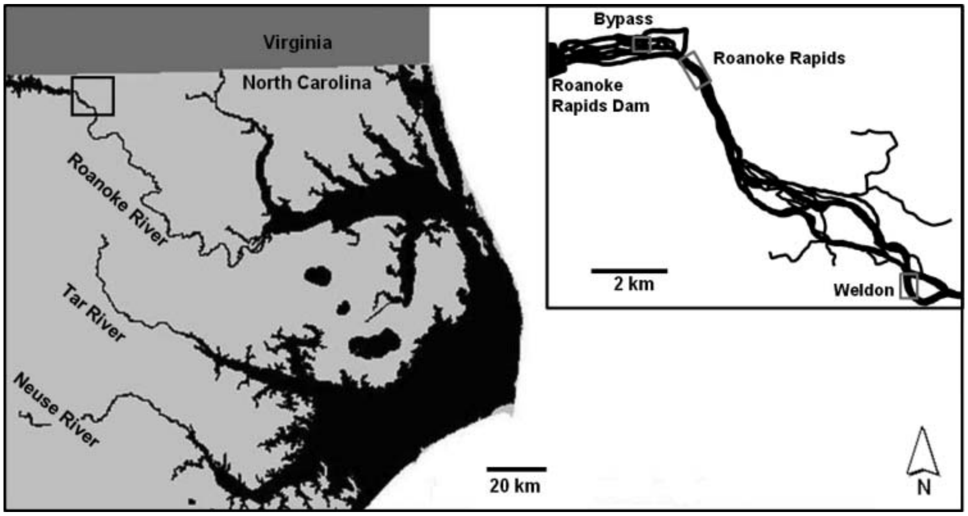

FIGURE 1. Map showing the general sampling sites on the Roanoke River and other rivers cited in the study.

is shallow (usually <2 m in depth) and mainly characterized by riffle and pool habitats. Sampling for this project was also completed in 2006 and 2007 in the main channel of the river near Weldon (Figure 1). Weldon is considered the main spawning site for hickory shad in the Roanoke River (Marshall 1977; Sparks 1998). At Weldon, the river is characterized mostly by run habitat with some eddies and riffles during low water. A sharp gradient change occurs at Weldon; boulders are visible and water is swift during periods of drought or low water releases from the Roanoke Rapids Dam, as was the case in the spring of 2006.

Field sampling.—To identify the seasonal timing, temperature, and microhabitat use during spawning, we collected hickory shad eggs with plankton tows and spawning pads. Sampling was conducted from the start of March to the end of May between 1000 and 1800 hours Eastern Standard Time (EST). Hickory shad eggs water-harden less than 1 h after fertilization and are semiadhesive and demersal, especially in early stages, but can be retained in the water column by currents (Mansueti 1961; Jones et al. 1978). As a result of these characteristics, hickory shad eggs are successfully collected with plankton sampling and spawning pads (Sparks 1998; Burdick and Hightower 2006; Smith 2006; Harris and Hightower 2010). Sampling (plankton tows and spawning pads) was completed every 3 d in 2005 and once per week in 2006 and 2007 (Figure 1). For inclusion in another study (Harris and Hightower 2010), plankton tows were also completed at least weekly in 2005–2007 at Roanoke Rapids. Roanoke Rapids is considered the main spawning area for American shad in the Roanoke River (Hightower and Sparks 2003) and is located 1–3 km below the Roanoke Rapids Dam (Figure 1). Although these plankton tow samples were not collected specifically for this study, we incorporated information on hickory shad egg densities and average daily water discharge (m^3/s) from the U.S. Geological Survey (USGS) gauging station at that location (Roanoke Rapids: 02080500) to examine the effects of water level on the annual upstream extent of spawning by hickory shad. All samples from plankton tows and spawning pads were fixed in 5–10% solution of buffered formalin in the field. In the laboratory, hickory shad eggs were identified, counted, and staged for approximate age (Mansueti 1962; Jones et al. 1978). Dead eggs were removed because they often cannot be identified reliably. Plankton tow and spawning pad samples had highly skewed distributions of eggs, with most samples containing no hickory shad eggs. For this reason and because eggs were collected using two methods (plankton tows and spawning pads) and the data were from four studies, most analyses of habitat selectivity were completed in terms of presence or absence of hickory shad eggs, rather than abundance or density.

We used collections of hickory shad eggs from oblique plankton tows to evaluate the seasonal spawning period and temperature range during spawning. Fifteen-minute oblique plankton tows were conducted from a stationary boat using a bongo frame with two 0.3-m-diameter plankton nets with 6:1 tail to mouth ratios, 500-μm mesh, and solid sampling cups. Plankton samples were collected in water depths between 0.5 and 5.2 m. Water temperature was measured at 60% of the water depth at each plankton tow with a YSI meter (Yellow Springs Instrument, Yellow Springs, Ohio). A standard General Oceanics Environmental flowmeter (General Oceanics, Miami, Florida) was deployed adjacent to the net to estimate the volume of water filtered during each tow. At the bypass site, the plankton tow was completed immediately downstream of a gradient change where flows were high enough to maintain the plankton tow in the water column. At Weldon, the plankton tow was completed just downstream of the sharp gradient change, which was the most upstream area passable by boat during 2006. To evaluate habitat suitability with respect to temperature, we combined results from this and three other studies in North Carolina that similarly sampled hickory shad eggs and temperature: Hightower and Sparks (2003) from the Roanoke River (data in Sparks 1998), Burdick and Hightower (2006) from the Neuse River (data in Burdick 2005), and Smith (2006) from the Tar River (Figure 1). For all studies, only sites where eggs were collected on at least one date during the sampled year were used; other areas might have had appropriate temperature, but were not used for spawning as a result of other environmental or physical factors.

Hickory shad eggs were collected on spawning pads to identify the microhabitat variables that were important for spawning. Spawning pads usually collect young (≤1 h in age) hickory shad eggs in clumped distributions, so the eggs are probably collected close to where they were spawned (Harris and Hightower 2010) and can therefore be used to estimate spawning microhabitat preferences. Spawning pads were red polyester floor buffing pads, 0.5 m in diameter (model PAD 4020 Red), and weighted with plate weights to lie flat on the river bottom. In the bypass, we deployed 10 spawning pads during 2005 and eight during 2006. At Weldon, we deployed nine spawning pads in 2006 and seven in 2007. The specific locations where spawning pads were deployed were selected to represent the range of available substrates, velocities, and depths in the area. In 2007, we specifically selected locations for placement of spawning pads to fill gaps in combinations of substrate type, water velocity, and depth. On each sampling date, at each spawning pad, we recorded depth, dissolved oxygen using a YSI meter and velocity using a Swoffer 2100 current meter (Swoffer Instruments, Inc., Seattle, Washington) from the water column at 60% of the depth. The primary substrate at each spawning pad was recorded as an ordered categorical variable (silt, sand, gravel, cobble, boulder, or bedrock) and a secondary type was also recorded, if it represented at least 30% of the overall substrate at the site. After recording these environmental variables, on each sampling date, the spawning pad was retrieved from the river bottom and all eggs were removed; thus, each spawning pad was considered an independent sample on each date. After eggs were removed, each spawning pad was placed back into the river until the next sampling date. Therefore, spawning pads were in the river for 3 to 7 days between sampling events. Hickory shad eggs more than 24 h old were removed from analysis. Water velocity and depth sometimes changed dramatically in the lower Roanoke River as a result of flow releases from the Roanoke Rapids Dam. By examining releases, we determined that water levels did not change much within 24 h of our sampling dates; thus, water velocity and depth measurements at sampling would have been similar to those experienced at the time of spawning. Occasionally, a spawning pad was removed from the water by a person or moved downstream by water currents and could not be sampled on a given date.

Data analysis.—Statistical tests were used to examine the importance of environmental variables (dissolved oxygen, depth, velocity, and substrate) on spawning microhabitat selection. To examine for differences in the distributions of these variables between spawning pads with and without eggs, we completed a Kolmogorov–Smirnov test for each continuous variable (dissolved oxygen, depth, and velocity) and used a Fisher exact test for substrate (Hollander and Wolfe 1999). To test for any inherent correlations between microhabitat variables that differed significantly in the Kolmogorov–Smirnov or Fisher exact tests, we calculated Spearman rank correlations on data from all spawning pads (Hollander and Wolfe 1999). We also examined Spearman rank correlations on just data from spawning pads with eggs, for comparison with correlations detected for all spawning pads. If significant correlations between microhabitat variables are represented on both all spawning pads and only spawning pads with eggs, identifying the specific habitat variable of importance can be difficult. For analysis, we included only spawning pad samples completed within the seasonal spawning period for that year (i.e., samples during the interval between dates when the first and last hickory shad eggs were collected in the Roanoke River for that year). Samples completed before or after the seasonal spawning period did not collect any hickory shad eggs and could not indicate information about selection of the specific microhabitat variables examined for this analysis.

Habitat suitability model.—We used temperature and significant microhabitat variables to develop the preliminary habitat suitability model for spawning hickory shad. The Bayesian analysis was based on the RSF developed by Thomas et al. (2004). Their model assumes that the n observations are drawn from a multinomial distribution in which p_j represents the probability of using habitat j. The RSF accounts for differences among categories in available habitat (a_j) through the following expression:

$$p_j = \frac{w_j a_j}{\sum_{i=1}^{h} (w_i a_i)},$$

in which w_j is the unscaled relative probability of using habitat j if all habitats were equally available (Thomas et al. 2004). If habitats are used in proportion to their availability, then estimates of the w_j will be similar in magnitude (indicating no selection). Because we have no previous information on hickory shad spawning habitat selection, we followed the recommendations of Thomas et al. (2004) in estimating $a_j = \log_e w_j$ and using uninformative prior distributions for the a_j. We used all of our samples (plankton tows for temperature and spawning pads for other environmental variables) to identify habitat availability and the samples with hickory shad eggs to identify habitat use. Binning is required when using continuous data in a multinomial model, and bin sizes were selected on the basis of data availability. We grouped values considered unsuitably high (i.e., values over which eggs were not collected) or unsuitably low (i.e., values under which eggs were not collected) to improve sample size and reduce the number of bins. Unscaled w_j values were scaled in the model between 0 and 1, 1 indicating the bin with the highest suitability, for use as suitability scores. Bayesian P-values for the probability of no selection were estimated by comparing a statistic for our observed use data with that obtained from simulated use data under the null hypothesis (Gelman et al. 2004; Thomas et al. 2004). Bayesian models were analyzed using open-source OpenBUGS software (http://www.openbugs.info/w/; Spiegelhalter et al. 2010). OpenBUGS code used in the analyses is available from the authors.

RESULTS

Field Sampling

Hickory shad eggs were collected by plankton sampling in the Roanoke River from mid-March to mid-April in 2005–2007 (Figure 2). The extent of spawning at sites upstream from Weldon varied annually, probably in response to water discharge rates (Figure 2). Hickory shad eggs were collected from the main channel at Roanoke Rapids in 2005 and 2007, when March–April discharge rates (302 and 291 m^3/s, respectively) were similar to the 1964–2010 March–April average (290 m^3/s) at the USGS gauging station in Roanoke Rapids. In contrast, hickory shad eggs were not collected upstream of Weldon in 2006, when the March–April average discharge rate was only 79 m^3/s. Similarly, eggs were collected in the bypass in 2005 during our study and in 2007 in a continuation study by Gunter (2009), but not in 2006.

Hickory shad eggs were collected from plankton tows in the Roanoke River at temperatures ranging from 10.7°C to 17.8°C. The temperature range for the four studies combined (Hightower and Sparks 2003; Burdick and Hightower 2006; Smith 2006; present study) was 10.2–22.5°C (Figure 3A). Over 50% of the plankton tows with eggs were completed when temperatures ranged from 12.0°C to 14.9°C and over 90% were completed when temperatures ranged from 11.0°C to 18.9°C. The peak spawning temperature for all systems combined was 14.0–14.9°C, when 52.6% of the tows contained hickory shad eggs. While the temperature ranges when eggs were collected overlapped, higher proportions of eggs were collected at colder temperatures in the Neuse River than in the Roanoke and the Tar rivers (Figure 3B). Peak spawning in the Roanoke and Tar rivers was 14.0–14.9°C, whereas peak spawning in the Neuse River was 11.0–11.9°C (Figure 3B).

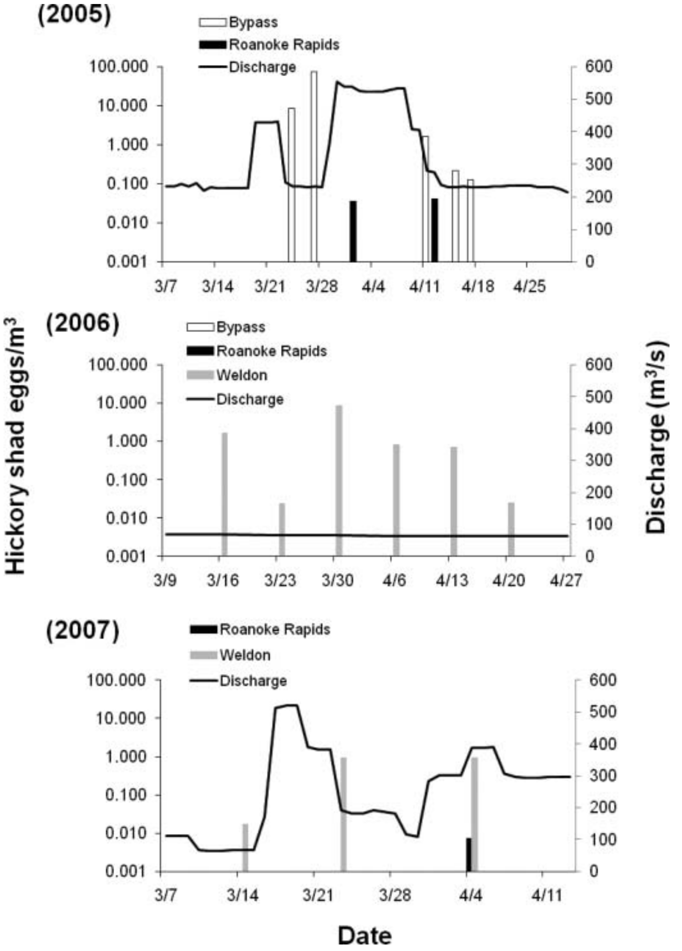

FIGURE 2. Hickory shad eggs collected by plankton tows ($\log_{10}$ scale) and average daily discharge at the U.S. Geological Survey gauging station at Roanoke Rapids for 2005, 2006, and 2007. The legends include all sites where plankton tows were completed during each year.

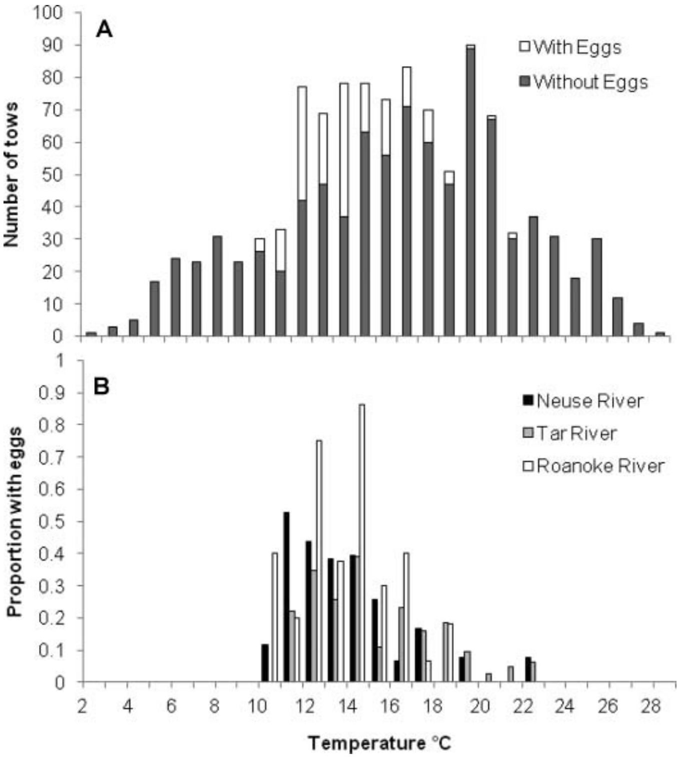

FIGURE 3. Panel **(A)** shows the number of plankton tows with and without hickory shad eggs in relation to water temperature from four studies in three North Carolina rivers: the present study in the Roanoke River, Sparks (1998) in the Roanoke River, Burdick (2005) in the Neuse River, and Smith (2006) in the Tar River. Panel **(B)** shows the proportions of plankton tows with hickory shad eggs in relation to water temperature, by river system.

Behavior suggestive of spawning by hickory shad was opportunistically observed on two occasions: once in the bypass during 2005 and once at Weldon in 2006. Similar to spawning American shad (Walburg and Nichols 1967), these hickory shad grouped close together and moved rapidly near the water surface, producing splashes. Eggs were collected by plankton tows on the trips when spawning behavior was observed. On both occasions, fish engaged in these behaviors were observed in shallow ($\leq$1 m) water with at least moderate water velocity ($\geq$0.2 m/s), and were highly visible and identifiable. Both observations were made from 1400 to 1800 hours EST in rocky riffle or run habitats.

There was high temporal and spatial variability in the number of hickory shad eggs collected by the spawning pads in the bypass and at Weldon. The number of eggs not more than 24 h old per spawning pad ranged from 1 to 2,450. The highest densities of eggs were often collected from spawning pads at or just below sharp changes in gradient within an area (i.e., bypass or Weldon); however, spawning pads in close proximity to each other often collected very different numbers of eggs (Figure 4). Kolmogorov–Smirnov tests indicated that water velocity over spawning pads with eggs was significantly higher than over those without eggs, but tests for differences in other environmental variables were not significant (Table 1). Hickory shad eggs were collected in velocities ranging from 0.02 to 1.26 m/s, with a median of 0.29 m/s (Table 1). Most spawning pads that collected a large number of hickory shad eggs during the season were in areas with water velocity of at least 0.1 m/s (Figure 4). Although frequently sampled ($N = 76$), only 3% of the spawning pad samples in velocities less than 0.1 m/s contained eggs (Figure 5A). A Fisher exact test showed a significant difference in substrate type where eggs were collected in comparison with that where eggs were not collected (Table 1). Eggs were found on all substrates except silt but were more frequently collected on spawning pads as substrate size increased (Table 1; Figure 5B). When both velocity and substrate were examined in relation to the abundance of hickory shad eggs per spawning pad, high numbers of eggs were collected in velocities from 0.10 to 1.26 m/s and on substrates dominated by gravel, cobble, and boulder, but especially cobble (Figures 4, 5C).

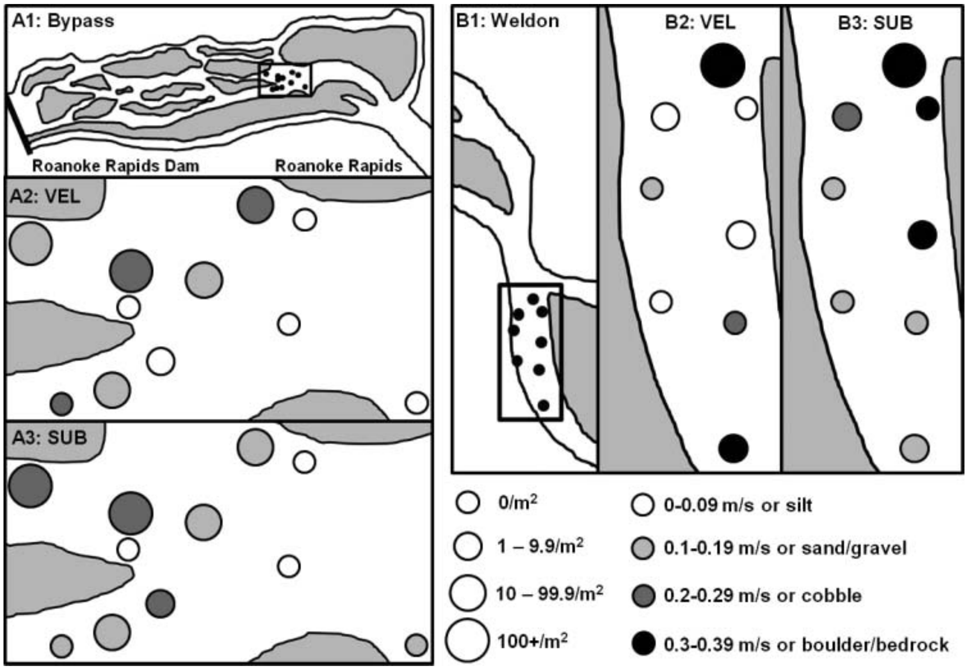

FIGURE 4. Average density of hickory shad eggs, average water velocity (VEL), and substrate type (SUB) at each spawning pad in **(A1–A3)** the bypass in 2005 and **(B1–B3)** Weldon in 2006 (see Figure 1) during a spawning period. Each spawning pad comprised an area of 0.196 m^2; densities were calculated based on the total number of eggs collected and the number of times the spawning pad was examined during the spawning period.

Velocity and substrate were significantly correlated with each other in both the complete data set ($N = 124$) and in the data set including only spawning pads with eggs ($N = 23$). In the complete data set, velocity was positively correlated with substrate ($R = 0.305$, $P < 0.001$), but in the data set including only spawning pads with at least one hickory shad egg, velocity was negatively correlated with substrate ($R = –0.467$, $P = 0.025$). When substrate sizes were smaller (sand and gravel), eggs were less frequently collected overall and were found only when velocities were at least 0.19 m/s, whereas when substrates were larger, eggs were collected on spawning pads over a wider range of velocity (Figure 5C).

Habitat Suitability Model

Hickory shad spawning occurred at water temperatures ranging from 10°C to 22°C, with highest spawning activity from 11.0°C to 14.9°C (Figures 3, 6A). The probability of observing this pattern of spawning under the null hypothesis of no selection with respect to water temperature was estimated to be 0. For water velocity, spawning was not detected at velocities below 0.02 m/s, despite high availability (Figure 5A). Bayesian estimates of scaled resource selection parameters generally increased with increasing velocity, but 95%-credible intervals were wide and overlapping as a result of low sample sizes (Figure 6B). The probability of the observed pattern of spawning under the null hypothesis of no selection with respect to velocity was estimated to be 0.00025. For substrate, spawning was not detected on silt, and relative use (and Bayesian estimates of scaled resource selection parameters) increased with increasing substrate size (Figures 5B, 6C). The probability of the observed pattern of spawning under the null hypothesis of no selection with respect to substrate was estimated to be 0.00625. Estimates of the log-scale parameters (a_j) for the three resource selection

TABLE 1. Range and median values of examined habitat variables for spawning pads with hickory shad eggs ($N = 23$) and those without eggs ($N = 101$). Kolmogorov–Smirnov (K–S) tests were performed for the continuous variables (dissolved oxygen, depth, and water velocity) and Fisher's exact test for the categorical variable (substrate type).

Variable	Range with eggs	Median with eggs	Range without eggs	Median without eggs	K–S test value (*D*)	*P*-value
Dissolved oxygen (mg/L)	6.76–11.27	9.33	6.99–16.27	9.69	0.508	0.959
Depth (m)	0.20–3.96	1.00	0.20–3.38	1.05	0.897	0.397
Water velocity (m/s)	0.02–1.26	0.29	0.00–0.72	0.01	2.824	<0.001
Substrate	Sand–bedrock	Cobble	Silt–bedrock	Gravel		0.003

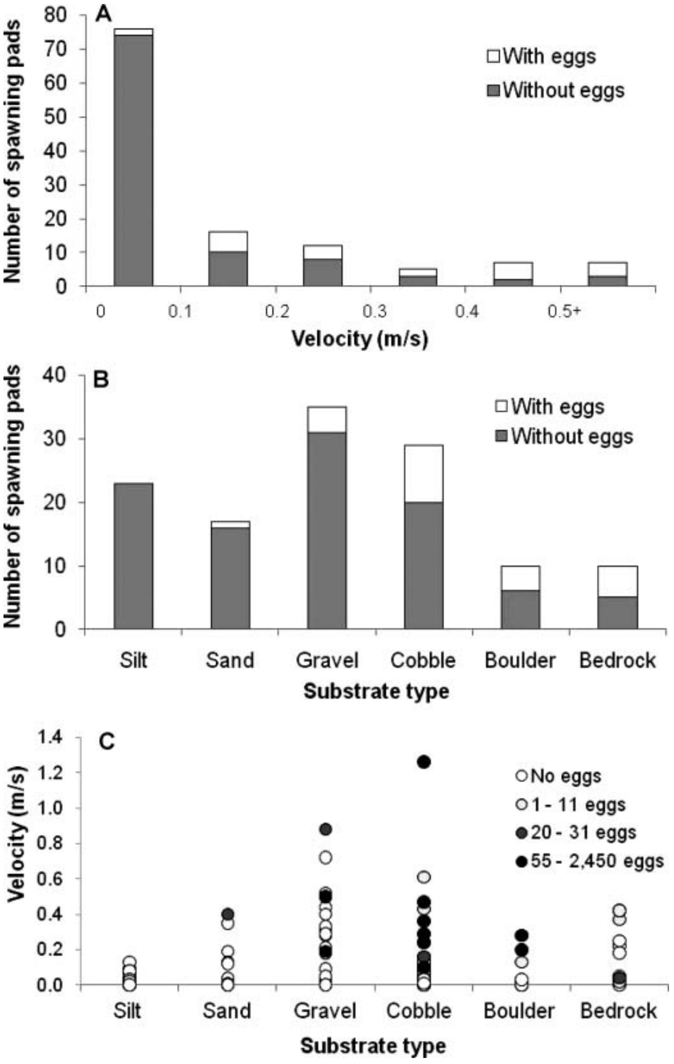

FIGURE 5. Number of spawning pads with and without hickory shad eggs by **(A)** water velocity and **(B)** substrate type, and **(C)** velocity and substrate type at spawning pads where different numbers of hickory shad eggs were collected.

functions (Table A.1 in the appendix) can be used to establish the prior distributions for Bayesian analyses in future studies.

DISCUSSION

Our results indicate that hickory shad spawning occurs mostly at water temperatures between 12.0°C and 14.9°C and at sites characterized by water velocities of at least 0.1 m/s and larger substrates. Our Bayesian analysis of habitat selectivity demonstrates that spawning habitat use is not random with respect to these environmental variables. This Bayesian analysis provides resource selection functions that can be components of a preliminary habitat suitability model for spawning hickory shad. For example, suitability of a particular site could be estimated as a product of the scaled probabilities of selection (w_j) for temperature, velocity, and substrate.

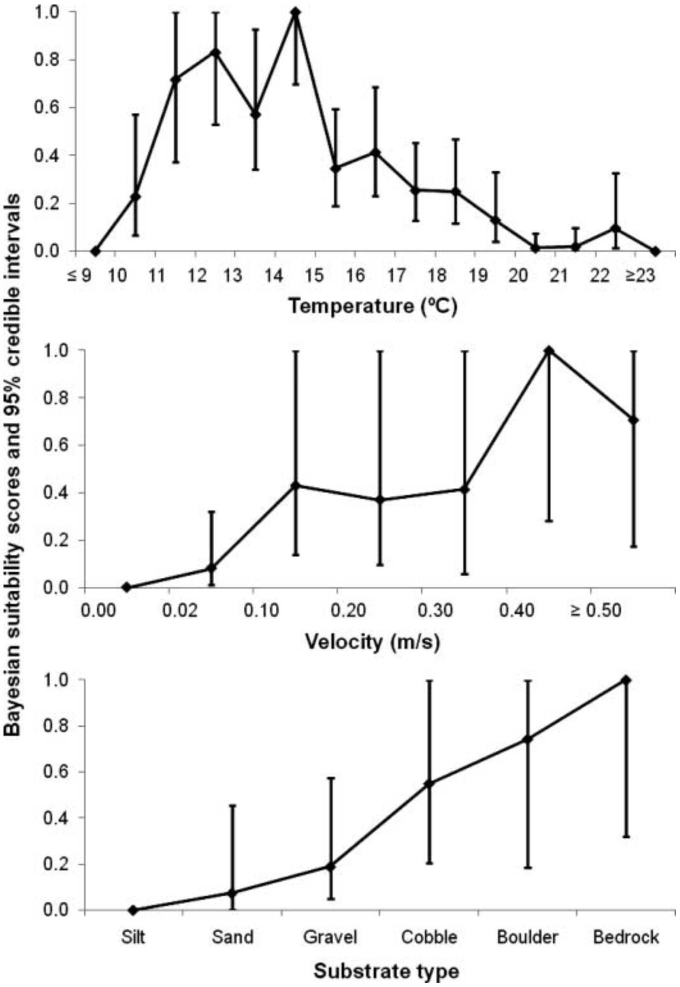

FIGURE 6. Bayesian suitability scores and 95%-credible intervals for hickory shad spawning at various **(A)** temperatures, **(B)** velocities, and **(C)** substrate types.

Credible intervals, which show the precision of current suitability estimates, should improve as new studies are conducted and analyzed within this Bayesian framework. Updating will be particularly valuable for assessing effects of water velocity and substrate type because sample sizes are small and all samples are from a single river system. Results for water temperature are based on studies from three North Carolina rivers and the larger sample size results in more precise estimates of suitability. It will nevertheless be useful to update the water temperature results with new data from other systems in order to determine whether the suitability estimates for North Carolina apply over a broader latitudinal range.

Temperature is an important factor in determining the timing of hickory shad spawning (Harris et al. 2007). In this study, spawning was observed in waters ranging from 10°C to 23°C. Even at the southern limit of their range (Georgia–Florida), where hickory shad spawning may peak at slightly higher temperatures, spawning ends when temperatures reach approximately 23°C (Street and Adams 1969; Street 1970; Harris et al. 2007). The cessation of spawning at approximately 23°C could potentially benefit young and adults. Laboratory studies for American shad resulted in higher rates of mortality and developmental abnormalities when eggs were maintained at 22°C and 26°C instead of at 12°C or 17°C (Leim 1924). High water temperatures also increase metabolic demands for adult American shad (Leonard et al. 1999). Hickory shad are thought to be iteroparous throughout their range (Street and Adams 1969; Sholar 1977; Batsavage and Rullifson 1998; Harris et al. 2007), and spawning earlier when temperatures are lower may reduce energetic expenditures during the spawning run and possibly increase survival to spawn during another year.

In North Carolina, hickory shad spawn earlier and at colder water temperatures than do other alosines (Burdick and Hightower 2006; Smith 2006). In addition, juvenile hickory shad are generally larger and less prevalent in juvenile surveys in the lower Roanoke River than are juvenile American shad (Kevin Dockendorf, North Carolina Wildlife Resources Commission, personal communication). Similarly, juvenile hickory shad collected in the St. Johns River, Florida, were generally larger during out-migration than were American shad and blueback herring juveniles collected from that system during the same time period (Trippel et al. 2007). In the Altamaha River, Georgia, hickory shad young were not prevalent in riverine nursery habitats and authors suggested that out-migration to the ocean may be rapid (Godwin and Adams 1969). Despite the longer development times associated with cooler temperatures (Mansueti 1962), growing and out-migrating earlier may improve survival of young hickory shad and reduce competition with other alosines.

Hickory shad generally avoided spawning in areas with very low (<0.1 m/s) or no water velocity, especially when substrates were small. When water velocities were low (<0.1 m/s), spawning occurred only on bedrock substrates. In contrast, when water velocities were higher (≥ 0.1 m/s), spawning occurred on a variety of substrate types, including gravel and occasionally sand. Hickory shad eggs are only somewhat negatively buoyant and some probably remain in the water column longer during periods of high velocity (Mansueti 1962). Perhaps eggs are distributed over a wider variety of substrates during high-flow events, when water velocities are generally higher throughout the river channel, and are more concentrated in riffle areas with larger substrates during periods of low flow. Regardless of water releases, spawning pads in areas with no water velocity or silt substrates did not collect eggs at any time during the spawning season. Areas with no water velocity or silt substrates probably do not represent suitable spawning habitat for hickory shad.

Hickory shad eggs were most often collected in areas dominated by larger substrates, often near changes in gradient. Hickory shad avoided spawning in locations dominated by silt or any mix of silt and sand. Possibly hickory shad eggs have poor growth or survival in areas with small substrates. Adhesive eggs of white sturgeon *Acipenser transmontanus* had lower survival and slower growth rates in the laboratory when covered by fine sediments (Kock et al. 2006). Kock et al. suggested that eggs covered by fine sediments had higher mortality as a result of reduced exchange rates of oxygen and carbon dioxide. Similarly, decreased survival has been observed for salmonid eggs when silt is mixed with the gravel selected for spawning, even when silt represents only a very small fraction of the total substrate (Julien and Bergeron 2006). Larger substrates free of silt are important for a variety of anadromous species that spawn demersal eggs. Larger substrates may allow for increased exchange of oxygen and carbon dioxide and are often found in areas of high gradient.

No pattern was observed for the distribution of eggs in relation to dissolved oxygen or water depth, but this does not confirm a lack of relationship. American shad are suggested to spawn in areas with dissolved oxygen content of at least 5 mg/L, whereas egg and larval mortality may increase below 3 mg/L (Stier and Crance 1985). Chittenden (1976) suggested that pollution leading to low dissolved oxygen levels affected the distribution and spawning activity of American shad in the Delaware River. During our study, dissolved oxygen concentrations were within the range considered suitable for and often used by American shad (Stier and Crance 1985; Ross et al. 1993); therefore, we suspect that no relationship was observed because dissolved oxygen was always adequate or optimal and did not limit spawning activity at any location sampled. Thus, while dissolved oxygen likely is an important component for spawning habitat, the areas of the Roanoke River that we studied appeared to have optimal levels of dissolved oxygen, which did not allow us to evaluate suitability as related to dissolved oxygen. In this study, hickory shad eggs were collected in depths ranging from 0.2 to 4.0 m. Depths greater than 4.0 m are common further downstream in the Roanoke River, and in other river systems with spawning populations of hickory shad. Whether depths over 4.0 m would be used if other environmental variables were suitable (e.g., velocity and substrate) could not be determined.

The range of riverine microhabitat used for spawning by hickory shad in this study was similar to the spawning habitat characterized as suitable for American shad. Hickory shad and American shad generally spawn in areas with overlapping ranges of depth, substrate, and velocity (Stier and Crance 1985; Ross et al. 1993; Beasley and Hightower 2000; Hightower and Sparks 2003). However, eggs of the two species are morphologically different—American shad eggs are larger and nonadhesive—and while their spawning ranges within a river system generally overlap, the specific sites selected for spawning are often different (Williams et al. 1975; Jones et al. 1978; Sparks 1998; Burdick and Hightower 2006). In the Roanoke River, American shad appear to spawn primarily in the main channel at Roanoke Rapids, whereas hickory shad spawn little at Roanoke Rapids, despite apparently adequate habitat. In the St. Johns River, Florida, adult hickory shad have been collected along with American shad, but spawning sites have not been identified from main-channel surveys of either gravid females or eggs, suggesting that hickory shad in that system may spawn primarily in tributaries (Williams et al. 1975; Harris et al. 2007). The main channel of the St. Johns River is slow flowing and mainly composed of sandy substrates, so hickory shad may use shallower riffle habitats in tributaries for spawning. While sampling for river herring in the Cashie River, North Carolina, biologists sometimes observed hickory shad in high abundance in small tributaries (Kevin Dockendorf, North Carolina Wildlife Resources Commission, personal communication). Burdick and Hightower (2006) also suggested that hickory shad may use tributaries for spawning in the Neuse River, North Carolina, with greater frequency than do other anadromous species. Different spawning locations may be selected to reduce competition, although generally hickory shad spawn earlier than American shad, which limits temporal overlap to some degree. We did not sample riverwide, but macrohabitat variables probably affect the distribution of spawning for both species.

Water discharge rates during the spawning season and the presence of dams appear to affect the upstream extent of the hickory shad migration and the total amount of available spawning habitat in the Roanoke River. Hickory shad migrate as far upstream as Roanoke Rapids and, in some years, spawn just below the lowermost dam in the system at rkm 221. When water discharge rates were average (i.e., in 2005 and 2007), hickory shad migrated and spawned further upstream than they did in a lower flow year (2006). A further upstream migration during higher flow years has been observed for this species in the Neuse River, North Carolina (Burdick and Hightower 2006). Water releases from dams in regulated rivers affect the total amount of spawning habitat available to anadromous fishes, and years with low releases could make potential spawning habitat below the dam inaccessible. However, even during years with average water discharge rates during the spawning period, some hickory shad in the Roanoke River spawned just below a rocky area at Weldon, suggesting that they chose this type of habitat even during years when other upstream areas were accessible.

Although hickory shad eggs were successfully collected on spawning pads, we do not know whether spawning pads have different levels of effectiveness in different habitat types. Spawning pads have mainly been used to study spawning habitat selection for sturgeons *Acipenser* spp. (Marchant and Shutters 1996; Sulak and Cluston 1998; Perrin et al. 2003; Duncan et al. 2004). Like sturgeon eggs, hickory shad eggs are initially adhesive and likely to adhere to spawning pads soon after spawning in close proximity to the location of the spawning fish. Exactly how far eggs traveled before settling out is not known, but since eggs were often collected in high abundances and in significantly clumped distributions (Harris and Hightower 2010), especially within a given sampling area (i.e., bypass or Weldon), the collection sites appear to give a reasonable assessment of spawning habitat use. Spawning pads with large abundances of eggs, such as those at sites with substrates dominated by cobble, were probably very close to a spawning fish.

Although our models greatly improve our understanding of hickory shad spawning habitat selectivity, they were parameterized mostly from 3 years of data on one river in North Carolina and must be viewed as preliminary. Additional data from other river systems along the species' range would help verify the environmental variables included and the specific relationships between those environmental variables and spawning by hickory shad. We think a better understanding of habitat suitability could be achieved through a Bayesian analysis, using our results as a starting point. If results of new studies are consistent with our estimates, then those results build support for the model and increase the precision of suitability estimates. If new results conflict with our estimates, it may indicate an important difference among river systems or a latitudinal gradient that should be incorporated into a refined model.

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Appendix: *a* Parameters

TABLE A.1. Mean, SD, lower 2.5% value, median, and upper 97.5% value for the *a* parameters used in Bayesian suitability models of temperature, water velocity, and substrate type. The *a* parameter of one (arbitrary) level is fixed at zero for identifiability.

	a parameter				
Bin	Mean	SD	2.5%	Median	97.5%
Temperature (°C)					
≤9	−257.3	190.5	−716.5	−218.8	−16.7
10	−1.5	0.6	−2.7	−1.4	−0.5
11	−0.3	0.3	−1.0	−0.3	0.3
12	−0.2	0.2	−0.6	−0.2	0.3
13	−0.5	0.3	−1.0	−0.5	0.0
14	0.0				
15	−1.0	0.3	−1.6	−1.0	−0.4
16	−0.8	0.3	−1.4	−0.8	−0.3
17	−1.3	0.3	−2.0	−1.3	−0.7
18	−1.3	0.4	−2.1	−1.3	−0.7
19	−2.0	0.6	−3.2	−2.0	−1.0
20	−4.4	1.3	−7.5	−4.2	−2.5
21	−4.1	1.3	−7.3	−3.9	−2.3
22	−2.4	0.8	−4.3	−2.3	−1.0
≥23	−254.4	190.4	−721.5	−213.9	−14.0
Water velocity (m/s)					
0.00	−254.8	191.6	−716.7	−215.8	−13.3
0.02	−2.1	1.0	−4.2	−2.1	−0.3
0.1	−0.4	0.7	−1.7	−0.4	1.0
0.2	−0.5	0.8	−2.0	−0.5	0.9
0.3	−0.5	1.0	−2.5	−0.5	1.3
0.4	0.2	0.7	−1.1	0.2	1.7
≥0.5	0				
Substrate					
Silt	−255.5	190.7	−712.1	−216.4	−12.6
Sand	−2.6	1.4	−5.8	−2.4	−0.4
Gravel	−1.5	0.7	−2.9	−1.5	−0.1
Cobble	−0.4	0.6	−1.5	−0.4	0.8
Boulder	−0.2	0.7	−1.7	−0.2	1.1
Bedrock	0.0				