Distribution of Spawning Activity by Anadromous Fishes in an Atlantic Slope Drainage after Removal of a Low-Head Dam

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Abstract.—In 1998, the Quaker Neck Dam was removed from the Neuse River near Goldsboro, North Carolina, restoring access to more than 120 km of potential main-stem spawning habitat and 1,488 km of potential tributary spawning habitat to anadromous fishes. We used plankton sampling and standardized electrofishing to examine the extent to which anadromous fishes utilized this restored spawning habitat in 2003 and 2004. Evidence of spawning activity was detected upstream of the former dam site for three anadromous species: American shad *Alosa sapidissima*, hickory shad *A. mediocris*, and striped bass *Morone saxatilis*. The percentages of eggs and larvae collected in the restored upstream habitat were greater in 2003, when spring flows were high, than in 2004. River reaches where spawning occurred were estimated from egg stage and water velocity data. Spawning of American shad and striped bass occurred primarily in main-stem river reaches that were further upstream during the year of higher spring flows. Hickory shad generally spawned in downstream reaches and in tributaries above and below the former dam site. These results demonstrate that anadromous fishes will take advantage of upper basin spawning habitat restored through dam removal as long as instream flows are adequate to facilitate upstream migration.

Dams provide a number of benefits to society, including electric power production and flood control, but there are also negative impacts on lotic ecosystems. Dams fragment habitat, convert free-flowing rivers into lentic systems, reorganize trophic cascades, alter thermal regimes, disrupt natural flows, simplify downstream channels, and prevent access to flood plains and suitable spawning habitat (Fontaine and Bartell 1983; Zincone and Rulifson 1991; Ligon et al. 1995; Auer 1996; Collier et al. 1996; Beasley and Hightower 2000; Pringle et al. 2000; Mérona et al. 2001; Poff and Hart 2002; Freeman et al. 2003). Dams that prevent migration and disrupt natural flows have contributed to the decline of several Atlantic Slope anadromous species, (including sturgeons *Acipenser* spp., American shad *Alosa sapidissima*, hickory shad *Alosa mediocris*, and striped bass *Morone saxatilis*), by limiting spawning success (Walburg and Nichols 1967; Zincone and Rulifson 1991; Rulifson 1994; Pringle et al. 2000).

There are more than 76,500 dams taller than 14 m

and 2,000,000 more dams less than 14 m tall in the United States (Collier et al. 1996; Poff and Hart 2002). These estimates may be low, especially when dams less than 2 m high are considered (Poff and Hart 2002). Several factors nationwide have led to a recent increase in dam removals. The average age of dams in the United States is over 40 years, and many are in need of costly rehabilitation (Shuman 1995). Removals have also been based on environmental impacts, particularly those affecting anadromous fish migration (Shuman 1995). An estimated 497 dams have been removed nationwide since 1900, all of which were less than 14 m high (Poff and Hart 2002). Fewer than 5% of these dam removals were accompanied by an ecological study, and none of these studies examined long-term effects (Hart et al. 2002).

Cost-benefit analysis of dam removal is a critical part of deciding whether or not to remove a dam. The cost of dam removal depends largely on the size of the dam and can be quite expensive. However, as dams age and deteriorate, removal can cost less than repair (Born et al. 1998). The cost of removing a small dam (<14 m) can range from US\$35,000 to \$1.2 million (Born et al. 1998; Smith et al. 2000). Given that the cost of dam removal may be substantial, it is important to understand as much as possible about the potential ecological effects of removal.

In 1952, Quaker Neck Dam was constructed on the

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Neuse River at river kilometer (rkm) 225 near Goldsboro, North Carolina (rkm 0 = mouth of the river at Pamlico Sound). This low-head dam rose approximately 1 m above the water's surface and was built with the purpose of impounding cooling water for a steam-electric plant. Despite the presence of a fish ladder, it was concluded in several studies that the dam restricted American shad and striped bass migration by only allowing passage over the dam during periods of high flow, when the dam was submerged (Baker 1968; Hawkins 1980; Beasley and Hightower 2000). Prior to construction of Quaker Neck Dam, American shad in the Neuse River basin traveled as far as 483 km upstream to spawn (McDonald 1884; Walburg and Nichols 1967). Quaker Neck Dam was removed in May 1998 after the water intake was modified to eliminate the need for the dam. This made available 120 km of main-stem river habitat and an estimated 1,488 km of tributary habitat for anadromous fish.

Several studies have been conducted to determine the distribution of spawning activity by anadromous fishes in the Neuse River and its tributaries. Hawkins (1980) collected eggs and larvae of striped bass, American shad, hickory shad, and river herring (blueback herring *Alosa aestivalis* and alewife *Alosa pseudoharengus*) prior to the removal of Quaker Neck Dam. He sampled 104 sites on tributaries and the main stem both above and below the dam. Hawkins (1980) showed the majority of anadromous spawning activity occurred below Quaker Neck Dam (spawning was detected for American shad and hickory shad at a few sites upstream of the dam). Prior to the removal of the dam, Beasley and Hightower (2000) implanted sonic transmitters in American shad and striped bass. Of 13 striped bass and 8 American shad that were tracked to the base of the dam, only 3 striped bass passed over the dam while it was submerged. After the dam was removed, Bowman and Hightower (2001) found that 12 of 22 American shad and 15 of 23 striped bass with transmitters migrated upstream of the former dam site. The goal of this follow-up study was to use plankton sampling methods to examine spawning activity throughout the upper basin. Our results can be contrasted with those obtained by Hawkins (1980) prior to removal of the dam.

In this paper, we refer to the habitat upstream of the dam, reconnected by its removal, as restored habitat. It is important to note that the removal of dam did not change the characteristics of the habitat; rather, it made the upstream reaches accessible to upstream migrants.

Study Area

The Neuse River flows through two physiographic provinces—the Piedmont and coastal plain—before

discharging into Pamlico Sound 399 rkm from its origin. The river crosses the fall line, a region of high gradient separating the Piedmont and coastal plain, about 297 rkm from the mouth. Downstream of the fall line, the Neuse River is a slow-moving, sinuous river with silt and sand substrate. Upstream of the fall line, there are small riffles and rapids characterized by the presence of exposed bedrock, boulders, and gravel (Bayless and Smith 1962).

The lowermost dam on the Neuse River is Milburnie Dam at rkm 352 (Figure 1). This run-of-river dam is a complete barrier to fish migration. The other remaining dam on the Neuse River is Falls Dam, a large U.S. Army Corps of Engineers dam that regulates flows in the upper river to address objectives for municipal water supply and flood control. We sampled nine main-stem sites (M1–M9; Figure 1) below Milburnie Dam that were approximately evenly spaced throughout the upper river except for a grouping of sites (M3–M5) near a known American shad spawning location (Bowman and Hightower 2001). We also selected five tributary sites, three upstream and two downstream of the former Quaker Neck Dam site (T1–T5; Figure 1) that varied in size and were downstream of any impediments to migration. Preference was given to tributary locations at which Hawkins (1980) caught eggs or larvae and where water quality was relatively good, based on macroinvertebrate surveys (NCDWQ 2002). The Crabtree and Swift Creek subbasins are dominated by urban development, whereas land use surrounding the other tributaries is primarily agricultural or forested (NCDWQ 2002). Crabtree Creek, Swift Creek, and the Little River have riffles, rock outcroppings, and variations in channel gradient, creating a diversity of instream habitats. Mill and Contentnea creeks are slow-moving, tannic streams lined with bottomland hardwoods. There are dams on all five tributaries in this study.

Methods

Standardized electrofishing was conducted at two main-stem sites to provide information about run timing, sex ratios, and species composition. The lower site, Ferry Rapids (Figure 1), was chosen because of its known importance as a spawning reach for American shad and striped bass (Beasley and Hightower 2000; Bowman and Hightower 2001). The area around Ferry Rapids includes gravel sections, swift-moving water, and small rapids. The upstream site, Rogers Lane, was chosen due to its proximity to Milburnie Dam and the availability of rudimentary boat access (Figure 1). We sampled each site for 30 min weekly between March 4 and May 27, 2003. In 2004, we sampled biweekly between March 9 and May 7 at Ferry Rapids and

FIGURE 1.—Map of Neuse River sample sites and distribution of American shad spawning activity, as determined by egg and larval sampling before and after the removal of Quaker Neck Dam, North Carolina. Egg and larval distribution data collected prior to dam removal are from Hawkins (1980).

between April 8 and May 15 at Rogers Lane. Fewer samples were taken at Rogers Lane in 2004 because low water prohibited access in March.

At each location, we delineated a 500-m section of river and electrofished for 15 min along each bank, starting at the upstream end and moving downstream. We standardized our effort by using 680 V and a DC waveform set at 120 pulses/s. The pulse width was adjusted to obtain a current of about 4 A. All fish

species were collected and total length was measured to the nearest millimeter; sex was determined, when possible, for all migratory fish.

Plankton sampling was done to investigate the spatial distribution of spawning activity. As in some prior studies (Gadomski and Barfoot 1998; Rulifson and Tull 1999; Hightower and Sparks 2003), we used 0.3-m-diameter nets with a 6:1 tail-to-mouth ratio, solid cod ends, and 500- μ m mesh. Two nets were mounted

together with a General Oceanics standard flowmeter between them to estimate water velocity and volume of water filtered. Nets were fished from bridges at 12 of our sites and from a boat at the other two sites.

Sampling was conducted between 0715 and 1915 hours at each site for 15 min twice per week during the springs of 2003 and 2004. An oblique tow was used to sample all portions of the water column evenly. After sampling, nets were rinsed thoroughly and all samples were field preserved in a 5–10% buffered solution of formalin (Murphy and Willis 1996). Dissolved oxygen concentration (mg/L), pH, maximum sample depth (m), and water temperature (°C) also were recorded during each sample.

Occasionally, the flowmeter became entangled with the nets, resulting in an inaccurate flow measurement. To correct for this problem, velocity data were plotted against river stage from the nearest U.S. Geological Survey (USGS) gauge. A linear regression was used to identify and correct outliers. Flow measurements that had an error greater than 400% were considered outliers and were corrected.

Eggs and larvae from preserved samples were categorized as originating from either a target or nontarget species. Target species were striped bass, American shad, hickory shad, alewives, and blueback herring. Eggs from the latter three species cannot be easily distinguished and were grouped together. These eggs were assumed to be from hickory shad, the most common of the three species collected by electrofishing ($N = 43$ hickory shad, 1 blueback herring, and 0 alewives).

Lippon and Moran (1974) differentiated hickory shad larvae from alewife and blueback herring larvae based on myomere counts. However, it is more commonly assumed that alewife, blueback herring, and hickory shad larvae cannot be distinguished from each other based on myomere counts (Jones et al. 1978; Wang and Kernehan 1979). Walsh et al. (2005) describe a method of differentiating larval hickory shad, alewives, and blueback herring that depends on precise length measurement and pigmentation patterns for larvae preserved in a 70% solution of ethanol. Larval fish shrink when preserved, and the degree of shrinkage depends upon the type of preservative, concentration of preservative, specimen size and age, and the time for which the specimen remains in preservative (Takizawa et al. 1994; Fey 1999). Because our specimens were preserved in formalin, had a wide length distribution, and were sorted several hours to several months after collection, we were unable to use the Walsh et al. (2005) key. Therefore, we grouped larval blueback herring, alewives, and hickory shad into the single category “hickory shad” because of this

species’ relative abundance in our electrofishing survey.

All American shad, hickory shad, and striped bass eggs collected in our study were staged. American shad eggs were classified into five stages of variable duration (4–12 h in length) according to developmental characteristics described by Jones et al. (1978) for eggs maturing at 16–17°C. Hickory shad eggs were classified into five stages of variable duration (1–14 h in length) based on descriptions by Mansueti (1962) for eggs developing at 17.8°C. Striped bass eggs were classified into four 12-h stages based on developmental characteristics at 17.9°C as described by Pearson (1938). Eggs that were opaque, cloudy, or had grainy-scattered yolks were considered to have died prior to preservation.

The plankton sampling data were analyzed using several approaches. We estimated egg and larval density by site and compared locations where eggs or larvae were present with results from the study Hawkins (1980) conducted prior to dam removal.

We estimated the distance each sampled block of water could have traveled using the minimum age for each stage category and the average water velocity as measured during sampling. This distance was added to the station location in order to estimate origin (spawning location) within a 15-km reach. Reaches started at the most downstream plankton sampling site on each stream and were consecutively extended upstream 15 km at a time until a barrier was reached. The density estimates (including zeros) for newly spawned eggs were averaged by river reach across all samples taken during the 3-month field season. Density estimates were not adjusted for mortality occurring between time of spawning and collection. Samples that were predicted to originate upstream of a dam were excluded from averages.

Results

Electrofishing samples documented that American shad and striped bass migrated as far as the first mainstem dam. Hickory shad and the single blueback herring were encountered only at the lower (coastal plain) site, and no alewives or sturgeons were collected. The peaks of the anadromous fish runs occurred in a series: first hickory shad, then American shad, and finally striped bass.

Our egg and larval sampling showed a substantial upstream expansion for American shad spawning activity relative to the spawning area identified in the late 1970s when the Quaker Neck Dam was still in place (Figure 1). Limited spawning in the 1970s was detected above the Quaker Neck Dam, indicating that the low-head dam was not a complete blockage to

TABLE 1.—Percentage of eggs and larvae collected upstream of rkm 225, the former site of the Quaker Neck Dam, North Carolina, and within tributaries. The remaining percentage for each category (e.g., $100\% - [91.8\% + 2.1\%] = 6.1\%$ for American shad eggs in 2003) was collected in the main stem below the former dam site. Based on the volume of water filtered, the percentage of sampling effort in the Neuse River above the former dam site was 63.7% in 2003 and 70.8% in 2004. The percentage of sampling effort in tributaries was 27.4% in 2003 and 19.7% in 2004.

Species	Above dam site				In tributaries			
	Eggs		Larvae		Eggs		Larvae	
	2003	2004	2003	2004	2003	2004	2003	2004
American shad	91.8	65.0	89.1	20.0	2.1	5.4	9.1	32.0
Hickory shad	28.2	1.9	13.2	16.0	3.5	11.4	73.6	68.0
Striped bass	76.8	18.8	77.8	0.0	0.3	0.1	7.4	40.0

migration. In 2003, sites upstream of the former dam site accounted for high percentages of American shad eggs and larvae (Table 1). The percentages of both eggs and larvae above the dam site decreased in 2004, when spring flows were lower. The percentages of eggs and larvae collected in tributaries were relatively low in both years. American shad spawning was detected between February 21 and May 28 in 2003 and between March 16 and May 17 in 2004. American shad eggs and larvae were collected at water temperatures ranging from 6°C to 26°C; peak collections occurred at 18–20°C.

Hickory shad eggs and larvae occurred at only a few sites in the late 1970s but were found throughout the upper basin in 2003–2004 (Figure 2). Based on the percentages of eggs and larvae collected above the former dam site, hickory shad utilized upper basin spawning habitat to a lesser degree than did American shad and striped bass (Table 1). Hickory shad utilized tributaries for spawning to a greater degree than did the other anadromous species (Table 1). Hickory shad spawning was detected between March 12 and the end of sampling (May 28) in 2003 and between March 5 and May 6 in 2004. Eggs and larvae were collected at water temperatures between 10°C and 23°C, and peak hickory shad egg collections occurred at 12–16°C.

The upper extent of striped bass spawning activity after dam removal was located 120 km upstream of the late-1970s limit (Figure 3). Striped bass eggs or larvae in 2003–2004 were observed at every main-stem site up to the lowermost dam. The percentages of eggs and larvae collected upstream of the former dam site in 2003 were slightly greater than the percentage of sampling effort above the dam site (Table 1). The percentages of eggs and larvae collected above the dam site decreased dramatically in 2004 when spring flows were lower. Relative to egg catches at main-stem sites, few eggs or larvae were collected at tributary stations. Striped bass eggs or larvae were collected between April 8 and the last day of sampling (May 28) in 2003

and between April 19 and May 12 in 2004. Striped bass eggs, which were much more common than larvae in our samples, were present at water temperatures ranging between 14°C and 28°C, and their occurrence peaked at 16–18°C in 2003 and at 20–22°C in 2004.

Mean $\pm$ SE water velocity in the main stem of the Neuse River was 0.56 ± 0.07 m/s in 2003 and 0.51 ± 0.06 m/s in 2004. In the tributaries, water velocity was 0.37 ± 0.03 m/s in 2003 and 0.36 ± 0.05 m/s in 2004. In both years, most American shad eggs were in stage 1 (Table 2). American shad spawning activity, as estimated by back-calculating the transport of live eggs, was concentrated in main-stem sites; a minor amount of spawning took place in tributaries (Table 3). River reaches with highest densities were further upstream in 2003 than in 2004 (Table 3). The upstream limit to estimated American shad spawning grounds coincided with a dam location on Crabtree Creek and the Neuse River in 2003 and on Mill Creek, Little River, and the Neuse River in 2004. Back-calculated spawning locations appeared to have an acceptable level of error; only 1.2% of American shad eggs collected in 2003 and 2.6% in 2004 were estimated (erroneously) to have originated upstream of a dam.

Hickory shad spawning activity was estimated to have occurred in patches throughout the study area (Table 4). In both years, collected eggs were primarily in stage 3 (Table 2). Both main-stem and tributary sites were used for spawning. Average main-stem densities of newly spawned eggs per $1,000 \text{ m}^3$ were substantially lower for hickory shad than for American shad (Table 4). One dam (Mill Creek in 2004) coincided with the upstream limit to hickory shad spawning. Only 0.5% of hickory shad eggs in 2004 and 0.0% in 2003 were estimated to have originated upstream of a dam.

Striped bass spawning activity in the main stem extended to the lowermost dam (Table 5). Striped bass eggs were nearly evenly distributed between stages 1–3 (Table 2). The percentage of striped bass eggs

FIGURE 2.—Distribution of hickory shad spawning activity, as determined by egg and larval sampling before and after the removal of Quaker Neck Dam, North Carolina. Egg and larval distribution data collected prior to dam removal are from Hawkins (1980).

estimated to have originated upstream of a dam was 13.5% in 2003 and 7.5% in 2004.

Discussion

Telemetry studies before and after removal of the Quaker Neck Dam showed that this low-head dam was an important obstruction to migration for striped bass and American shad (Beasley and Hightower 2000;

Bowman and Hightower 2001). After the dam was removed, both species migrated into the restored habitat and American shad spawning appeared to be concentrated in an area about 26 km upstream of the former dam site. Conclusions from these telemetry studies are limited, however, by the small sample sizes and the focus on only two species. Another concern is that the migration of fish with transmitters might not be

FIGURE 3.—Distribution of striped bass spawning activity, as determined by egg and larval sampling before and after the removal of Quaker Neck Dam, North Carolina. Egg and larval distribution data collected prior to dam removal are from Hawkins (1980).

representative of the migration of untagged fish (Bowman and Hightower 2001).

The current study, based on plankton sampling at multiple main-stem and tributary sites, provides a more complete picture of how the restored habitat is being utilized. Eggs and larvae of American shad, striped bass, and hickory shad were collected at every main-stem site from below the former dam site to our uppermost site, just below the first dam. Compared

with data collected prior to dam removal, this appears to represent a considerable expansion of spawning habitat. When the dam was in place, striped bass spawning was detected only downstream of the dam (Hawkins 1980). American shad and hickory shad spawning was detected at a few sites above the dam, indicating that some fish were able to move over the dam during periods of high water (Hawkins 1980).

A few prior studies have documented an extended

TABLE 2.—Percentages of American shad, hickory shad, and striped bass eggs in each developmental stage (see Methods) collected in the Neuse River, North Carolina, and its tributaries in 2003 and 2004.

Stage	American shad (%)		Hickory shad (%)		Striped bass (%)	
	2003	2004	2003	2004	2003	2004
1	47	66	38	6	33	35
2	43	29	6	0	44	30
3	5	1	48	74	22	33
4	4	2	9	13	1	3
5	0	1	0	7		

spawning migration of anadromous fishes after a dam was removed (Hart et al. 2002). Walburg and Nichols (1967) reported an increase in migration distance for American shad in the Delaware River after removal of Burrows Dam. Extended migration for Pacific salmon *Oncorhynchus* spp. was documented after the breaching of Jackson Street Dam in Oregon and the removal of Washington Power Dam in Idaho (Shuman 1995; Smith et al. 2000). O'Donnell et al. (2000) documented large numbers of alewives, Atlantic sturgeon *Acipenser*

TABLE 3.—Average initial density (catch per unit effort [CPUE]) of American shad eggs per 1,000 m³ of water for estimated spawning reaches in the Neuse River system, North Carolina, 2003–2004. Distance from the mouth of the river to the downstream end of each reach is given in river kilometers; N is the number of times a given reach was sampled.

Location	Rkm	2003 CPUE			2004 CPUE		
		Estimate	SE	N	Estimate	SE	N
Neuse River	204	7	7.0	43	3	1.8	50
	219	0	0.0	16	4	3.8	11
	234	4	2.2	37	6	3.0	47
	249	0	0.0	19	9	4.0	33
	264	0	0.0	15	0	0.0	20
	279	9	2.9	58	40	22.4	111
	294	1	0.4	46	31	9.2	53
	309	2	1.7	26	1	1.3	22
	324	736	626.2	44	89	59.1	92
	339	35	11.6	57	7	2.2	74
	354	13	4.4	67	9	2.6	84
	369	7	5.1	50	5	1.8	70
384	6	1.9	51	2	0.8	58	
Crabtree Creek	11	639	638.7	35	0	0.0	49
Swift Creek	8	1	0.7	45	4	1.7	51
	23	0	0.0	13	12	10.4	6
	38	0	0.0	10	0	0.0	19
Mill Creek	2	0	0.0	40	3	1.4	70
Little River	11	3	2.2	40	5	2.9	51
	26	0	0.0	10	0	0.0	25
	41	0	0.0	6	1	0.6	24
Contentnea Creek	7	0	0.0	42	3	1.3	62
	22	0	0.0	14	0	0.0	27
	37	0	0.0	8	0	0.0	16
	52	0	0.0	4	0	0.0	12
	67	0	0.0	4	0	0.0	3
	82	0	0.0	4	0	0.0	1

TABLE 4.—Average initial density (catch per unit effort [CPUE]) of hickory shad eggs per 1,000 m³ of water for estimated spawning reaches in the Neuse River system, North Carolina, 2003–2004. Distance from the mouth of the river to the downstream end of each reach is given in river kilometers; N is the number of times a given reach was sampled.

Location	Rkm	2003 CPUE			2004 CPUE			
		Estimate	SE	N	Estimate	SE	N	
Neuse River	204	1	1.2	64	2	1.0	79	
	219	0	0.0	16	2	2.0	19	
	234	1	0.4	51	6	4.0	93	
	249	0	0.0	9	0	0.0	8	
	264	0	0.0	13	0	0.0	20	
	279	7	3.4	145	2	0.6	195	
	294	5	5.0	12	1	0.9	26	
	309	1	1.1	23	2	1.3	35	
	324	0	0.3	49	0	0.0	69	
	339	1	0.7	98	0	0.0	146	
	354	1	0.6	54	1	1.4	50	
	369	0	0.3	42	0	0.0	63	
	384	0	0.1	54	0	0.0	69	
	Crabtree Creek	11	0	0.1	50	0	0.0	76
	Swift Creek	8	0	0.0	63	1	0.8	78
23		0	0.0	10	0	0.0	15	
38		0	0.0	3	0	0.0	23	
Mill Creek	2	0	0.0	54	11	3.6	99	
Little River	11	0	0.3	59	60	31.7	83	
	26	0	0.0	6	34	26.3	31	
	41	0	0.0	7	0	0.0	5	
	Contentnea Creek	7	0	0.0	60	2	0.8	93
	22	0	0.0	11	0	0.0	22	
	37	0	0.0	5	0	0.0	7	
	52	0	0.0	2	0	0.0	1	
	67	0	0.0	2	0	0.0	1	
	82	0	0.0	0	0	0.0	1	

oxyrinchus, shortnose sturgeon *A. brevirostrum*, and striped bass in habitats made available by the removal of Edwards Dam on the Kennebec River, Maine. In 2000 (2 years after dam removal), 1,000 larval and juvenile American shad from natural reproduction (lacking a hatchery oxytetracycline mark) were collected in reaches upstream of the former dam site (Hart et al. 2002).

Our plankton sampling approach showed differences in habitat utilization among species. American shad and striped bass spawning was concentrated in the main stem, whereas hickory shad made greater use of tributary streams. Our results showed that primary spawning areas for American shad and striped bass overlapped. Bilkovic et al. (2002) found that primary spawning grounds did not overlap in the York River, Virginia. We also found that hickory shad spawning tended to occur further downstream relative to the other two species. This pattern was consistent with our electrofishing results in that we collected American shad and striped bass at both sites but only collected hickory shad at our lower (coastal plain) site. Pate (1971) documented hickory shad spawning within

TABLE 5.—Average initial density (catch per unit effort [CPUE]) of striped bass eggs per 1,000 m³ of water for estimated spawning reaches in the Neuse River system, North Carolina, 2003–2004. Distance from the mouth of the river to the downstream end of each reach is given in river kilometers; *N* is the number of times a given reach was sampled.

Location	Rkm	2003 CPUE			2004 CPUE		
		Estimate	SE	<i>N</i>	Estimate	SE	<i>N</i>
Neuse River	204	14	10.7	39	0	0	31
	219	0	0.0	14	0	0	27
	234	0	0.0	26	0	0.4	40
	249	0	0.0	17	0	0	16
	264	0	0.0	14	8	3.5	32
	279	7	5.3	58	2	1.8	79
	294	13	12.1	17	85	63.7	38
	309	8	6.8	38	60	31.8	59
	324	13	10.3	40	15	9.7	64
	339	7	5.3	54	21	8.8	58
	354	14	8.3	49	0	0.4	66
	369	22	22.5	34	10	6.2	50
	384	10	6.8	39	1	0.9	57
	11	0	0.0	24	0	0	29
Crabtree Creek	8	0	0.0	35	0	0	29
Swift Creek	23	0	0.0	13	0	0	23
	38	0	0.0	6	0	0	16
Mill Creek	2	0	0.0	24	0	0	58
Little River	11	0	0.0	30	0	0	45
	26	0	0.0	10	0	0	24
	41	0	0.0	9	0	0	20
Contentnea Creek	7	0	0.0	33	0	0	50
	22	0	0.0	14	0	0	24
	37	0	0.0	8	0	0	16
	52	0	0.0	2	0	0	5
	67	0	0.0	5	0	0	2
	82	0	0.0	0	0	0	1

three coastal plain tributaries in the lower Neuse basin. Hawkins (1980) detected hickory shad spawning activity at only a few sites, about evenly divided between the main stem and tributaries.

The degree to which anadromous fishes utilize habitat restored though dam removal may depend on flows, which can vary due to weather or regulated releases by dams. We observed a downstream shift in spawning locations for all three anadromous species in 2004 relative to spawning areas in 2003, when spring flows were higher. For March–May 2003, average discharge at the USGS Goldsboro gauging station (approximately in the middle of our study area) was above the 90th percentile of historical discharge. For the same period in 2004, discharge was slightly greater than the historic 25th percentile (USGS 2005).

Spawning sites for American shad and striped bass were estimated to extend to the lowermost main-stem dam. Habitat characteristics in the restored reaches (shallow, high-velocity reaches with large substrates) on the upper Neuse River may help explain the use of this area for spawning. Previous studies have shown that American shad in the Neuse River preferentially

spawn at sites with coarser substrates, such as cobble and gravel (Beasley and Hightower 2000; Bowman and Hightower 2001). These coarser substrates are more common in the upper river, as are the shallow areas that are also preferred for American shad spawning (Mansueti and Kolb 1953; Walburg 1957; Marcy 1972; Beasley and Hightower 2000; Bowman and Hightower 2001). American shad eggs are negatively buoyant and may lodge into crevices created by coarser substrates (Chittenden 1969). A prior Neuse River study indicated that striped bass spawn at sites with higher water velocities and coarser substrates (Beasley and Hightower 2000). However, the two variables were significantly correlated; therefore, striped bass may be selecting sites strictly on the basis of water velocity, which makes sense given the requirement that eggs be suspended during development (Mansueti and Hollis 1963; Bayless 1967). The dependence on water velocity may explain why striped bass shifted their spawning location between the high- and low-flow years. Variation in striped bass spawning locations among years has also been reported for the Tar and Roanoke rivers in North Carolina (Humphries 1966; Hassler 1984).

Our approach of back-calculating distances that eggs traveled provided additional information about spawning locations and dates that egg and larval collections alone could not provide. It allowed us to locate spawning reaches on a basinwide scale, evaluate the use of habitat upstream and downstream of the former dam site, and compare spatial distributions under the influence of two flow conditions. One potential bias in our estimates is that because spawning for American shad and striped bass typically occurs in the evening, our daytime sampling may have missed eggs spawned in some sections of the river or may have underrepresented the number of newly spawned eggs. Also, variation in channel morphology may have caused egg and larval densities to be greater upstream (where the channel has a smaller cross-sectional area) than downstream (where the channel is shallow and wide).

Egg aging errors could arise because the time it takes for an egg to reach a particular stage of development and the time spent in that stage depend on the temperature profile to which the egg has been exposed. Depending on whether the temperature profile was warmer or colder than that of the staging key, we may have over- or underestimated egg ages. For example, American shad eggs were staged according to a key for eggs developing between 16°C and 17°C. However, we collected the majority of American shad eggs at water temperatures between 18°C and 20°C. Egg staging is useful for estimating an approximate age with an upper and lower age limit but does not provide the exact age

of an egg collected from the river. We used the lower age limit for each stage (instead of upper or median) to estimate the location of spawning; therefore, we may have underestimated the distance an egg traveled, biasing results in a downstream direction.

Spatial and temporal variation in water velocity may have also caused error in the estimation of spawning site locations. We used the velocity measured at the time of egg collection to estimate egg transport distances; however, the water velocity was not consistent among sites or through the season. Distances to upstream spawning locations could be underestimated if water velocities decreased as eggs drifted downstream.

The approach used in our study was effective in characterizing the large-scale spatial distribution of spawning activity. The projected spawning sites, based on egg stage and current velocity, established which river reaches are most important for spawning. They also identified dams that are limiting spawning habitat and that may be candidates for fish passage or removal. Further research should be conducted to identify the smaller-scale factors in spawning site selection (e.g., current velocity versus substrate). Long-term research is needed to better understand how anadromous fishes respond to different levels of spring flow and to determine if dam releases could be manipulated to improve or increase spawning habitat and survival of eggs and larvae.

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