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Effects of a Low-Head Dam on the Distribution and Characteristics of Spawning Habitat Used by Striped Bass and American Shad

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Abstract.—Striped bass *Morone saxatilis* and American shad *Alosa sapidissima* in the Neuse River, North Carolina, historically migrated up to 435 km upriver to spawn. However, migration was impeded in 1952 by the construction of Quaker Neck Dam at river kilometer 225 (measured from the point where the Neuse River enters Pamlico Sound). To determine the fraction of tagged fish that migrated upstream of this low-head dam and the characteristics of selected spawning habitat, we implanted sonic transmitters in 25 striped bass and 25 American shad during 1996 and 1997. We determined preferred depth, water velocity, and substrate composition by measuring those characteristics at both randomly selected sites and sites where spawning was observed. Of 13 striped bass and 8 American shad with transmitters that migrated to the base of Quaker Neck Dam, only 3 striped bass passed the structure, indicating that the dam was an impediment to migration. Striped bass spawning was observed only in the area directly below (within 1.5 km of) Quaker Neck Dam. Although none of the telemetered American shad passed Quaker Neck Dam, American shad spawning was observed from the base of the dam to 1.5 km downstream as well as 3 km above the dam. Striped bass spawned at sites with significantly higher water velocity and significantly larger substrate than on average was found at randomly sampled locations. American shad spawned at sites that were significantly shallower and had significantly larger substrate than was found in random samples. The type of spawning habitat selected by both species is more abundant above than below Quaker Neck Dam, indicating that improved access to upstream reaches would benefit both species.

Striped bass *Morone saxatilis* and American shad *Alosa sapidissima* historically supported important commercial and recreational fisheries within the Neuse River system in North Carolina (Cobb 1906; Smith 1907; Walburg and Nichols 1967; Hawkins 1980). However, landings of anadromous fish within the Neuse River declined substantially during the 1960s and 1970s (Hawkins 1980). One factor contributing to this decline may have been the loss of habitat due to dam construction. American shad historically migrated to the headwaters, about 435 river kilometers (rkm) upstream from Pamlico Sound, and profitable commercial fisheries for American shad operated in the Raleigh area (Figure 1) (Stevenson 1899; Cobb 1906; Walburg 1957; Walburg and Nichols 1967).

Access to upstream habitat decreased after 1952, when Quaker Neck Dam was constructed at rkm 225 near Goldsboro (Walburg 1957; Hawkins 1980; Collier and Odom 1989). This low-head dam rose approximately 1 m above the surface at average discharge (82 m^3/s). It was constructed to divert water to a cooling reservoir operated by Carolina Power and Light Company. Until its removal in 1998 (after completion of this study), Quaker Neck Dam and an impassable dam at rkm 352 near Raleigh resulted in the loss of up to 48% of the striped bass and American shad's historical migratory range.

Throughout the existence of Quaker Neck Dam, its impact on the migration of anadromous fishes, including the effectiveness of a pool-type fishway constructed adjacent to the dam (Walburg 1957; Walburg and Nichols 1967), was the subject of debate. Tarplee and Partin (1979, 1981) performed

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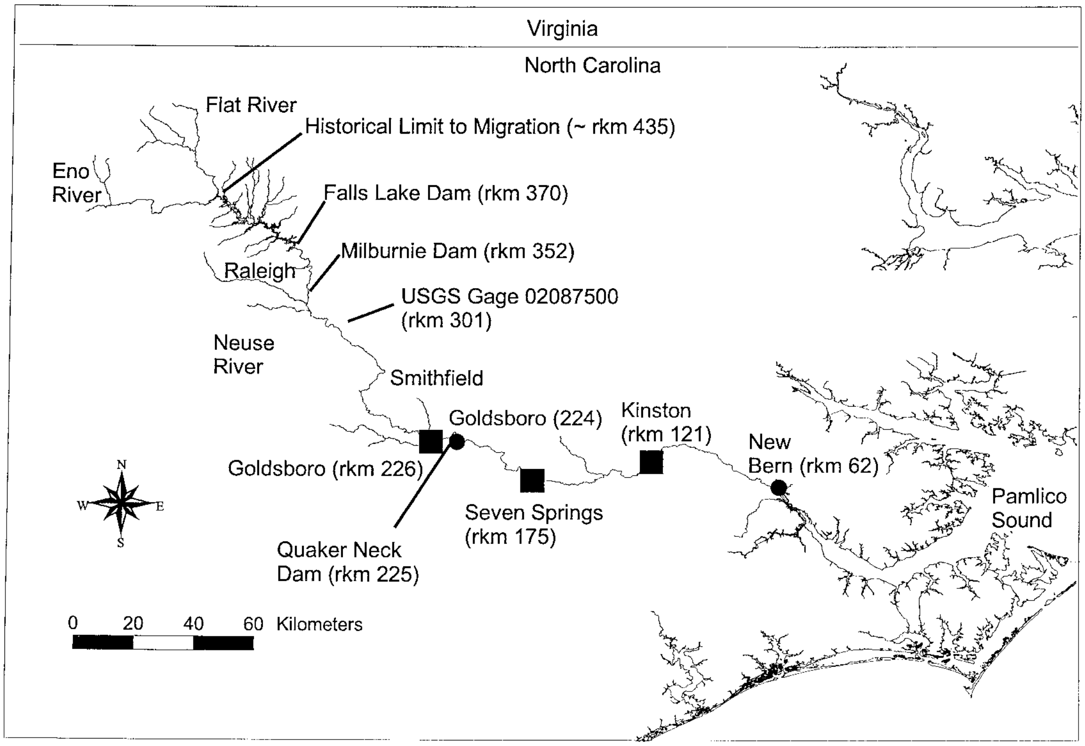

FIGURE 1.—Historical limit of striped bass and American shad migration, impediments to migration, and locations of stationary receivers (squares) and stationary receivers with temperature recorders (circles).

surveys using electrofishing, seines, trawls, and gill, fyke, and plankton nets to determine if the dam impeded fish movement. They concluded that the dam had a minimal effect on fish migration because fish navigated the structure either by swimming directly over it during periods of high discharge or by using the fish ladder. However, several investigators have disputed that conclusion. Walburg (1957) reported that relatively few American shad used the fish ladder to move above the dam and suggested that gates (removable sections) on Quaker Neck Dam should be removed from 15 March to 15 July to allow anadromous species improved access to upstream reaches. Baker (1968) reported that the dam effectively blocked the migration of striped bass and decreased the number of American shad spawning above the dam. Hawkins (1980) found evidence of American shad and striped bass spawning activity above the dam, but concluded that the migration of anadromous fishes was greatly hindered by the dam. It was suggested by A. Little (North Carolina Wildlife Resources Commission, retired, personal communication) that striped bass pass the dam only in high water years when it is possible to swim directly over the structure. In spring electrofishing surveys conducted above and below Quaker Neck Dam by the North Carolina Wildlife Resources Commission in 1994 and 1995, only 3 of 221 striped bass were collected in areas above the dam (Hammers et al. 1995). During low-discharge years, when the dam is impassable, Hammers et al. (1995) suggested that year-class strength might be decreased.

The objectives of this study were (1) to characterize the spawning habitat used by striped bass and American shad in the Neuse River, (2) to determine whether the two species exhibit spawning habitat preferences, (3) to determine whether Quaker Neck Dam was an obstruction to migration, and (4) to determine whether removal of the dam would benefit the two species by increasing access to higher-quality or more abundant spawning habitat.

Study Site

The Neuse River is formed by the confluence of the Eno and Flat rivers from which it flows southeast 435 rkm to Pamlico Sound (Figure 1). The Neuse River drains 14,499 km^2 and has an average discharge of 82 m^3/s near Kinston (Hawkins 1980; USGS 1995). The upper third of the river lies within the Piedmont region of North Carolina. The fall line is located near Smithfield, although the first considerable falls historically occurred at the location of Milburnie Dam (Smith 1907). Below the fall line, the river slows and broadens as it flows eastward across the coastal plain (USGS 1995).

Methods

Striped bass.—We collected striped bass by electrofishing in the Neuse River near New Bern (rkm 61) from December 1995 to February 1996 and from December 1996 to February 1997, several months before upstream migration typically occurs (April to May). We selected these collection dates to minimize the changes in migratory behavior that are known to result from the capture and handling of striped bass during migration (Carmichael et al. 1998).

Captured fish were weighed to the nearest gram and measured to the nearest millimeter total length (TL). Sex was determined by direct observation of the gonads through a surgical incision. Striped bass scales used for age determinations were collected from either side of the fish in the area above the midline and below the dorsal fin. Scales were analyzed by at least one experienced individual using a microfiche reader.

Following the methods described by Haeseker et al. (1996), striped bass were surgically implanted with V16–6L sonic transmitters (VEMCO, Ltd., Nova Scotia, Canada) that measured 96 mm by 16 mm and weighed approximately 36 g (in air). The transmitters normally have a guaranteed battery life of 476 d; however, their life expectancy was increased to about 754 d by using a 7-month-on, 5-month-off duty cycle. Thus, any striped bass that were tagged in 1995–1996 and returned to spawn in 1997 would still have a functional transmitter. To ensure that only mature fish were tagged, we selected females greater than 550 mm fork length (age 4–5) and males greater than 500 mm fork length (age 2–3; Merriman 1941; Olsen and Rulifson 1992). Transmitters were placed in fish weighing more than 1.8 kg to avoid behavioral changes associated with the implantation of transmitters weighing more than 2% of wet body weight (Winter 1983). We divided transmitters equally between sexes. In addition, each fish was fitted with an internal anchor tag identifying it as a study animal and offering a reward for its return.

American shad.—American shad were collected at night by using drifted gill nets near New Bern (rkm 62) in March and April of 1996 and 1997. Captured fish were weighed to the nearest gram and measured to the nearest millimeter total length (TL). Ages of telemetered individuals were estimated by examining scales. To minimize handling stress, which may alter migratory behavior (Moser and Ross 1993; B. Kynard, U.S. Geological Survey, personal communication), American shad scales used for age analysis were those shed during measuring, weighing, and transmitter implantation. Scales were examined by at least one experienced individual using a microfiche reader. Spawning marks were identified based on the criteria provided by Cating (1953).

We fitted American shad with V16–4L ultrasonic transmitters (VEMCO). The transmitters measured 74 mm by 16 mm, weighed approximately 10 g (in air), and had a guaranteed battery life of 111 d. Transmitters were gently forced into the stomach after being dipped in glycerin to minimize abrasion of the esophagus. We selected fish weighing in excess of 0.5 kg in order to minimize behavioral changes resulting from implantation of transmitters weighing in excess of 2% of wet body weight (Winter 1983). We assumed that American shad collected during the spawning migration were sexually mature, so minimum length requirements were not established. Sex was determined, when possible, by gently expressing eggs or milt from running-ripe fish, and we attempted to distribute transmitters equally between sexes. Because of reported changes in behavior elicited by external tag attachment (Sutherland 1998), no external markings were used to identify the fish as study animals.

Sampling.—Relocations of telemetered fish were used to characterize the spawning migration, to estimate the fraction of striped bass and American shad migrating upstream of Quaker Neck Dam, and to locate primary spawning grounds. Stationary data-logging receivers (VEMCO VR-20) located at five sites along the river were used to determine the general location of migrating fish and rates of upstream migration (Figure 1). Two receivers were located near Goldsboro, 0.5 km above and 0.25 km below Quaker Neck Dam. For fish passing the stationary receivers, tag number, date, and time were recorded automatically. Shoreline surface temperature was recorded hourly at the monitoring stations immediately below Quaker Neck Dam and near New Bern by means of automatic temperature-logging devices (HOBO TEMP, Onset, Inc., Pocasset, Massachusetts). Additional relocations of telemetered fish (within about 10 m) during migration and residency on spawning grounds were obtained by manual searching using a handheld receiver (Sonotronics, Inc., Tucson, Arizona).

We measured salinity, temperature, dissolved oxygen, pH, water velocity, depth, and substrate composition at sites where we observed striped bass or American shad spawning behavior, as well as at randomly selected locations. River reaches in which spawning occurred were located by tracking telemetered individuals and by manually searching by boat for nighttime spawning activity. Thus, spawning observations may have included, but were not limited to, fish with transmitters. We used a spotlight to determine the species spawning and characterized habitat at the precise location at which spawning behavior was observed. Site selection for random habitat samples was accomplished by dividing the river into 4,000 sections of equal length (roughly 100 m) from its mouth to the base of Milburnie Dam in Raleigh. Habitat was characterized at the midpoint of one of five randomly selected regions; the characterization was from bank to bank, the width varying as a function of stream width.

Data Analysis

Discharge

Discharge information was obtained from the U.S. Geological Survey (USGS) gauging station near Clayton, North Carolina (USGS gauge 02087500, rkm 301), 76 rkm upstream from Quaker Neck Dam (Figure 1). Mean daily discharge values from 1973 to 1995 and 95% confidence intervals were used to determine if daily discharge during the 1996 and 1997 field seasons (1 March to 30 May) were within historical ranges. Similarly, for both years we determined if telemetered individuals encountered typical discharge values while residing on the spawning grounds (28 March to 26 May). Daily discharge values were considered to be similar to historical ranges if they were within the 95% confidence intervals about the 1973–1995 daily mean. The 1996 and 1997 mean daily discharge values were obtained from the USGS provisional database and are subject to change upon review.

Habitat Preference

Habitat preference was determined by comparing the distribution of water velocity, depth, and substrate composition at sites where spawning occurred to the distributions at randomly selected sites throughout the Neuse River by means of a Wilcoxon rank-sum nonparametric test for two unpaired samples (Hollander and Wolfe 1973; Zar 1984). For water velocity and depth, the measured values were used in the Wilcoxon test. For substrate composition, we followed the approach taken by Schaffter (1997) of converting the percentage of clay, silt, sand, gravel, cobble, and bedrock at a site to a numerical value. Clay was assigned a rank value of 1, silt a value of 2, sand a value of 3, gravel a value of 4, cobble a value of 5, and bedrock a value of 6. For each sample, the percentage of substrate in each category was multiplied by the rank value; the resulting measures were then summed across samples and divided by 100 to yield a number equivalent to the average substrate category per sample. For comparisons of habitat characteristics in spawning locations with those at randomly selected sites, we used only random samples from river reaches to which spawning individuals had access. For example, American shad spawning habitat samples from below Quaker Neck Dam were compared with random habitat samples from below Quaker Neck Dam. For American shad spawning habitat samples from above Quaker Neck Dam, we used random habitat samples from the entire river below Milburnie Dam. Because mean discharge differed on the days during which random habitat samples and spawning habitat samples were collected, it would have been possible to misinterpret differences in depth and current velocity between random and spawning habitat samples as habitat preference. To avoid this confounding effect, we excluded spawning habitat samples that were collected when the mean daily discharge exceeded the 95% confidence interval about the mean discharge for dates when the corresponding random habitat samples were collected. Because substrate should remain consistent throughout a range of discharge values, comparisons of substrate composition among samples included all samples regardless of discharge. Significant differences ($P < 0.05$) between the distribution of habitat variables at sites used for spawning and the distribution at the randomly selected sites were used to establish whether certain spawning habitats are preferred.

Because water quality variables, such as pH, temperature, salinity, and dissolved oxygen, change on an hourly or diel basis and the spawning and random habitat samples were not collected simultaneously, we were unable to test for differences in the distribution of these variables between the spawning and random habitat samples. Instead, we compared the observed range of these variables at the spawning sites to published information about the ranges that are acceptable to egg and larval stages (Klauda et al. 1991).

Characterization of Spawning Migration

When possible, we determined the start and end of the spawning migration and length of residency within the Neuse River for individual striped bass and American shad. For striped bass, the start of migration was defined as the date and time when a fish moved upstream past the most seaward receiver (New Bern; Figure 1). For American shad, the capture location was immediately upstream of the New Bern receiver site; consequently, we used the capture date as the date of river entry for fish that immediately continued upstream migration subsequent to capture. For telemetered American shad that moved downstream subsequent to release but later resumed migration, we assigned the date on which the individual moved upstream past the New Bern receiver as the date of river entry. For both species, the end of migration was defined as the date and time when a telemetered individual moved downstream past the New Bern receiver after spawning. Length of residency in the river was calculated as the difference between the two dates. Individual rates of migration were calculated as the distance in kilometers between the Kinston and Seven Springs receivers (Figure 1) divided by the number of hours between an individual's detection at those receiver sites.

Results

Striped Bass

Ultrasonic transmitters were implanted in seven female and eight male striped bass (503–722 mm TL, 1.90–4.25 kg in weight, and 4–7 years of age) in 1996 and in seven female and six male striped bass (512–758 mm TL, 1.82–5.03 kg in weight, and 3–7 years of age) in 1997. Instrumented individuals typically moved several kilometers downstream after surgery but regained upstream positions in the following days. Using the handheld receiver, we relocated 15 telemetered striped bass 76 times from 7 February to 24 May 1996 and 19 individuals 111 times from 5 February to 26 May 1997.

During February and April 1996 (i.e., before migration), we conducted searches to determine the location and characteristics of overwintering habitat. Prior to migration, all telemetered individuals were located in freshwater tributaries of the Neuse River. Overwintering sites were typically narrow, deep (mean = 3.9 m) channels with abundant structure. Individuals did not enter the main stem of the Neuse River until beginning migration or when moving between tributaries.

Of 15 telemetered striped bass released in 1996, 9 migrated upriver (4 males and 5 females) at dates of entry ranging from 14 April to 12 May. The water temperature recorded at the New Bern receiver at the time of entrance ranged from 15.9°C to 23.2°C (mean = 20.1°C). Rates of upstream migration varied between 0.29 km/h and 1.5 km/h. The duration of residency within the river ranged from 6.8 to 22.6 d. In 1997, 19 telemetered individuals entered the river, including 7 individuals implanted in 1996. Dates of entry ranged from 3 March to 22 May. The water temperature recorded at New Bern between these dates ranged from 15.0°C to 23.6°C (mean = 18.1°C). Rates of upstream migration ranged from 0.23 km/h to 2.26 km/h. The duration of residency within the river ranged from 22.2 to 57.8 d.

Our telemetry results and observations of spawning activity indicate that the primary spawning grounds for striped bass extended from the base of Quaker Neck Dam to a point 1 km downstream. In 1996, 7 of the 9 telemetered individuals that were detected passing the New Bern receiver site were subsequently located between Seven Springs and the base of Quaker Neck Dam, compared with 10 of 19 individuals in 1997. In 1996, water temperature on the primary spawning grounds (taken at the receiving station 0.25 km below the dam) ranged from 19.1°C to 22.9°C (mean = 20.1°C) while telemetered individuals were present (29 April to 15 May); in 1997, it ranged from 13.9°C to 23.2°C (mean = 17.7°C) while such individuals were present (28 March to 22 May). In 1996, none of the telemetered individuals navigated the dam, even during periods of high discharge when the dam was completely submerged. In 1997, three telemetered striped bass moved upstream of Quaker Neck Dam when it was completely submerged. Two were relocated about 3 km upstream, and the third was relocated at the base of the Milburnie Dam (127 rkm upstream from Quaker Neck Dam, Figure 1). We did not observe striped bass spawning above Quaker Neck Dam in either year.

Six of the nine telemetered striped bass that migrated upriver in 1996 successfully migrated back downstream, presumably after spawning. We were unable to locate two of the remaining three individuals, but because the transmitters were not detected, we assume that they were harvested. The remaining fish was found dead near New Bern. This fish and another telemetered striped bass

TABLE 1.—Depth (m), current velocity (m/s), and substrate (weighted size) at striped bass and American shad spawning sites and randomly selected sites. The *P*-values are based on Wilcoxon tests.

		Spawning sites		Random sites		
Species and year	Variable	*N*	Mean (SE)	*N*	Mean (SE)	*P*
Striped bass, 1996	Depth	44	2.26 (0.12)	49	2.22 (0.22)	0.05
	Current velocity	44	0.49 (0.01)	49	0.34 (0.04)	<0.01
	Substrate	55	3.60 (0.07)	49	2.97 (0.12)	<0.01
Striped bass, 1997	Depth	79	1.91 (0.05)	62	1.88 (0.10)	0.32
	Current velocity	79	0.55 (0.01)	62	0.37 (0.03)	<0.01
	Substrate	79	3.91 (0.15)	62	2.90 (0.04)	<0.01
American shad, 1996	Depth	31	1.23 (0.06)	49	2.22 (0.22)	<0.01
	Current velocity	31	0.21 (0.08)	49	0.34 (0.04)	0.15
	Substrate	31	3.95 (0.14)	49	2.97 (0.12)	<0.01
American shad below dam, 1997	Depth	60	1.39 (0.05)	62	1.88 (0.10)	<0.01
	Current velocity	60	0.41 (0.01)	62	0.37 (0.03)	0.86
	Substrate	60	4.28 (0.17)	62	2.90 (0.04)	<0.01
American shad above dam, 1997	Depth	21	1.63 (0.03)	78	1.69 (0.09)	<0.01
	Current velocity	21	1.01 (0.03)	78	0.40 (0.28)	<0.001
	Substrate	50	5.99 (0.00)	103	3.08 (0.06)	<0.01

(which did not migrate past New Bern) were caught by anglers near New Bern (rkm 62) and returned for rewards. Necropsies performed on both individuals indicated that the surgical incisions had completely healed. There were no signs of infection or abrasion around the transmitter, and in each case the transmitters were encysted and surrounded by fat bodies (A. Stamper, North Carolina State University College of Veterinary Medicine, personal communication).

Sixteen of the 19 striped bass that migrated upriver in 1997 successfully migrated out of the river after the spawning season. Two of the remaining three individuals that undertook the spawning migration were not relocated, but because the transmitters were not detected, we assume that they were harvested. The remaining individual was caught 3 rkm downstream from Quaker Neck Dam by an angler who returned the transmitter for a reward. Because this fish had been at large only 76 d since surgery, the wound had not completely healed, but the sutures were intact and there was no sign of infection.

Striped bass in both years spawned at sites with significantly higher water velocity and larger substrate than those observed at random sites (Table 1; Figures 2, 3). There were no significant differences in depth between random and spawning habitat samples (Table 1; Figure 4). We found a low positive correlation ($r = 0.25$, $P = 0.0023$) between water velocity and substrate size in random samples; thus, striped bass may not be selecting for both water velocity and substrate. The observed ranges for salinity, water temperature, dissolved oxygen, and pH were generally within acceptable ranges for the egg and larval stages of striped bass (Table 2).

American Shad

From 4 to 16 April 1996, we implanted transmitters in 12 American shad, of which 6 were females, 3 males, and 3 of unknown sex. Fish ranged from 466 to 547 mm TL, from 1.1 to 1.9 kg, and from 5 to 8 years of age. From 3 to 17 March 1997, we implanted transmitters in 13 American shad, 7 females and 6 males ranging from 433 to 552 mm TL, from 0.9 to 1.8 kg, and from 4 to 7 years of age. In 1997, an angler harvested one telemetered female on 9 April, and the returned transmitter was subsequently redeployed in a captured female on 11 April. Scale marks characteristic of repeat spawners were observed in 5 of 12 fish in 1996 and in 5 of 14 fish in 1997. In the area from New Bern to Quaker Neck Dam, we relocated 12 telemetered individuals 65 times from 9 April to 24 May 1996 and 13 individuals 60 times from 13 March to 19 May 1997.

Several instrumented American shad exhibited a ''fallback response'' (Moser and Ross 1993) after insertion of the transmitter. Newly telemetered individuals moved varying distances downstream for a period of hours to days. Individuals that resumed the spawning migration either did not fall back or regained upstream position quickly (< 10 h).

From 17 to 21 April 1996, three female, one male, and one telemetered American shad of unknown sex passed the New Bern receiver site. The water temperature at the New Bern receiving station ranged from 18.6°C to 19.0°C (mean = 18.7°C) during this period. Repeated relocations

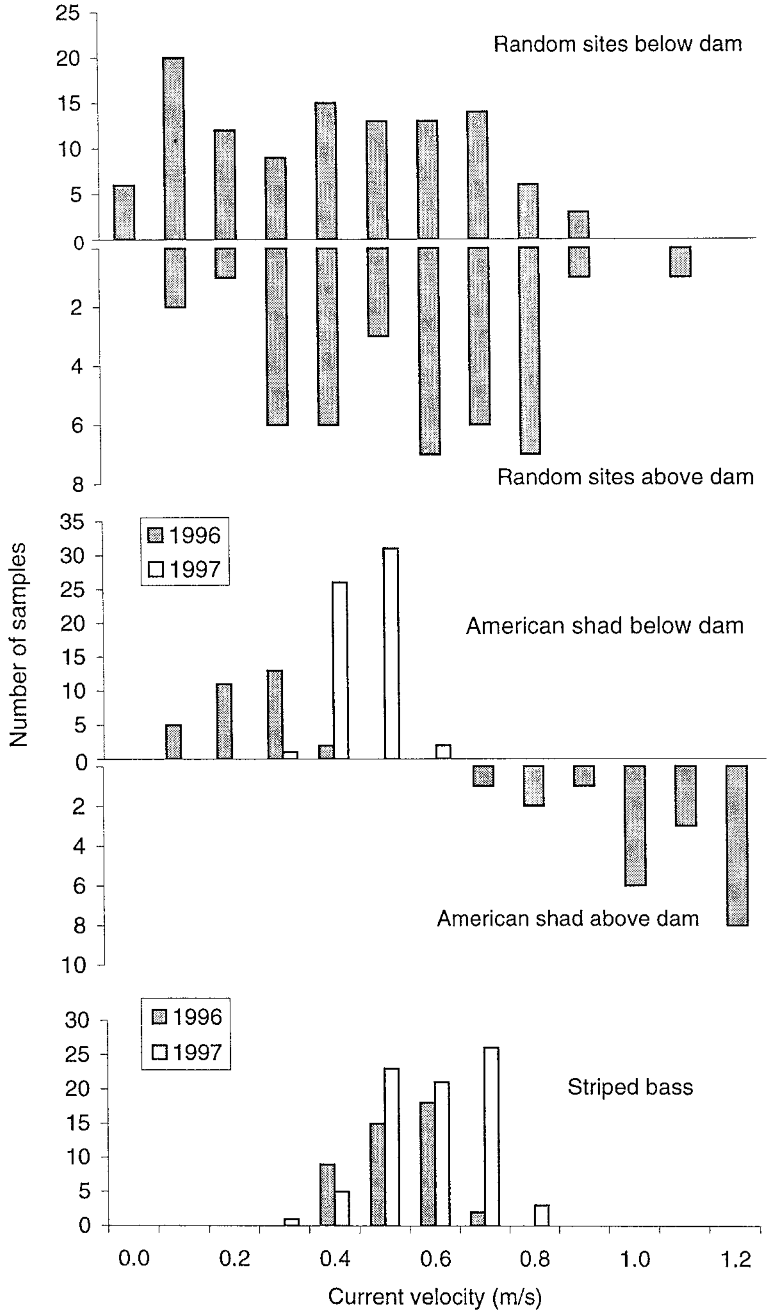

FIGURE 2.—Distribution of water velocity at striped bass and American shad spawning sites versus water velocity at random sites above and below Quaker Neck Dam. Random values are based on pooled 1996 and 1997 samples.

at the same sites indicate that all telemetered individuals that migrated upriver died either on the spawning grounds or during emigration. For this reason, we could not calculate the period of residency.

From 16 March to 15 April 1997, 6 male and 8 female telemetered American shad passed the New Bern receiver site. Of the 14 American shad that entered the river, 4 males and 3 females reached the primary spawning grounds, while the remain-

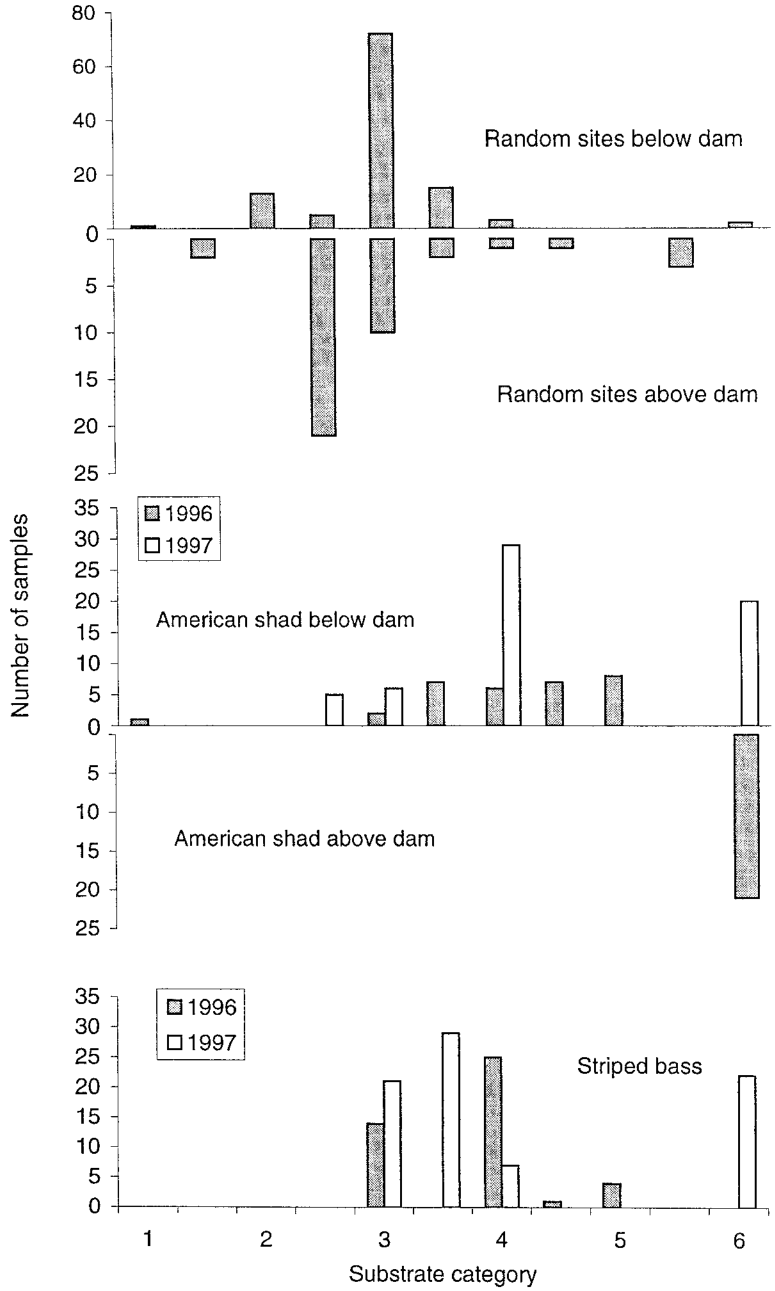

FIGURE 3.—Distribution of substrate at striped bass and American shad spawning sites versus substrate at random sites above and below Quaker Neck Dam. Random values are based on pooled 1996 and 1997 samples.

ing 7 individuals did not migrate past the Kinston receiver (Figure 1). The rate of migration varied between 0.33 km/h and 1.28 km/h. Some migrating fish were not detected at the Kinston receiving station, so rates of migration could be calculated for only one female and three males. Period of residency ranged from 13.8 to 69.7 d. Repeated relocations at the same sites indicate that four of the seven migrating individuals died either on the spawning grounds or during emigration.

In 1996, American shad spawning was observed solely from the base of Quaker Neck Dam to a

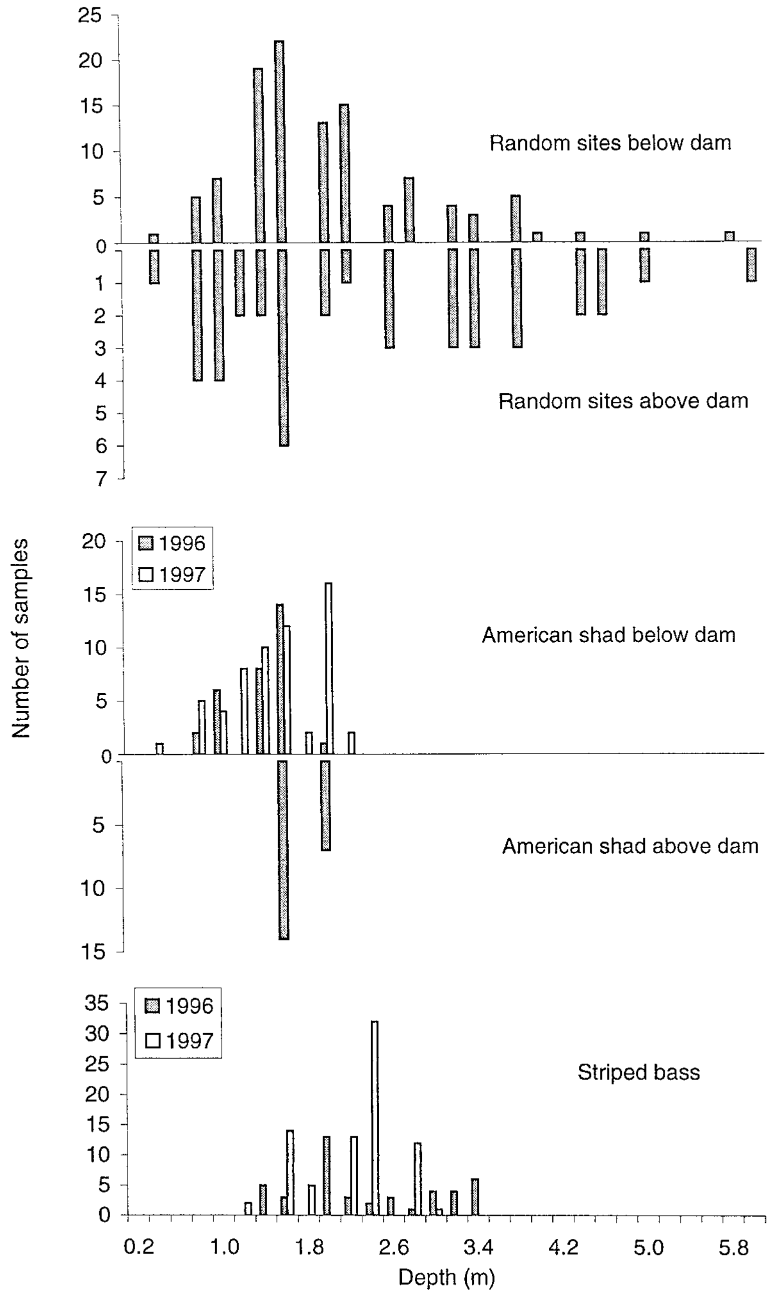

FIGURE 4.—Distribution of depth at striped bass and American shad spawning sites versus depth at random sites above and below Quaker Neck Dam. Random values are based on pooled 1996 and 1997 samples.

point 1 km downstream. Because four telemetered individuals migrated to within 1 km of Quaker Neck Dam and spawning was observed only in this location, we refer to this area as the primary spawning grounds for American shad, though spawning may have occurred elsewhere. Temperature on the spawning grounds (measured at the receiving station immediately downstream from Quaker Neck Dam) ranged from 18.0°C to 23.6°C (mean = 20.0°C) while telemetered individuals were present (21 April to 15 May 1996). In 1997, we observed American shad spawning behavior

TABLE 2.—Means and ranges of pH, temperature, salinity, and dissolved oxygen at spawning sites and randomly selected sites, compared with published estimates of required levels for egg and larval stages of striped bass and American shad (Klauda et al. 1991). NA indicates value not available.

	pH		Temperature (°C)		Salinity (mg/L)		Dissolved oxygen (mg/L)	
Sites and requirements	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Sites								
Striped bass spawning sites, 1996	7.3	6.9–9.2	21.5	18.9–25.0	0	0–0	7.3	6.6–8.4
Striped bass spawning sites, 1997	8.8	8.3–9.5	20.4	19.2–22.9	0.1	0.1–0.1	8.0	7.1–9.9
American shad spawning sites, 1996	6.9	6.8–6.9	25.9	25.2–26.0	0	0–0	6.5	6.2–7.2
American shad spawning sites below dam, 1997	8.9	5.9–9.5	21.3	20.5–22.9	0.1	0.1–0.1	8.7	8.0–9.9
American shad spawning sites above dam, 1997	7.7	7.5–8.2	16.4	14.9–19.2	0	0–0	7.8	7.7–7.8
Combined randomly selected sites	8.4	6.8–10.3	22.9	18.3–26.9	0.2	0–6.2	7.9	5.2–12.5
Published requirements:								
Striped bass eggs		7.0–9.5		12.0–23.0		0–10.0		>5.0
Striped bass larvae		7.0–8.5		12.0–23.0		0–15.0		>5.0
American shad eggs		>6.0		13.0–26.0		0–15.0		>5.0
American shad larvae		>6.7		15.5–26.5[a]		0–15.0		>5.0

[a] Optimal values.

from the base of Quaker Neck Dam to a point 1.5 km downstream as well as in an area 3 rkm above the dam. During the period when American shad were on the spawning grounds (28 March to 15 May 1997), water temperature ranged from 18.0°C to 23.7°C (mean = 21.3°C). None of the 11 telemetered American shad (4 in 1996 and 7 in 1997) that migrated upriver passed Quaker Neck Dam, although individuals were on the spawning grounds during periods when the dam was submerged.

For both years, current velocity did not differ significantly between American shad spawning sites below the dam and random sites. For American shad spawning sites located above the dam (1997 only), current velocity was significantly greater than at the random sites (Table 1; Figure 2). Regardless of location (above or below the dam), in both years, American shad spawned in areas that were significantly shallower and with significantly ($P < 0.01$) larger substrate than were observed at random sites (Table 1; Figures 3, 4). In both years, the observed ranges for salinity, temperature, dissolved oxygen, and pH were within acceptable ranges for the egg and larval stages of American shad, regardless of location (Table 2).

Habitat Availability

In order to determine the distribution of preferred spawning habitat, we tested whether the habitat variables consistently selected by each species (water velocity and substrate for striped bass, depth and substrate for American shad) had different distributions above and below Quaker Neck Dam. Based on 1997 random habitat samples, we found that river reaches above Quaker Neck Dam were shallower ($P = 0.0001$), with higher water velocities ($P = 0.04$) and larger substrates ($P = 0.0005$) than reaches below Quaker Neck Dam.

Discharge

During periods when telemetered fish were on the spawning grounds, discharge was above the 95% confidence interval about the historical daily mean on 21–32% of days for striped bass and 16–41% of days for American shad (Figure 5). Discharge was substantially higher in 1997 than in 1996, and it exceeded the 95% confidence interval for 15 consecutive days when telemetered striped bass were on the spawning grounds.

Discussion

Quaker Neck Dam, which was removed in 1998, did constitute a barrier to migration for both striped bass and American shad. Of 13 striped bass and 8 American shad that migrated to the base of the dam, only 3 striped bass passed the structure, even though the dam was often completely submerged during periods when telemetered fish were on the spawning grounds. Although these telemetry results are based on small sample sizes, they are supported by our observations of spawning activity. Discharge during both years was above the historical mean from late April to mid-May. This suggests that telemetered individuals were at least as likely to pass Quaker Neck Dam during the 1996

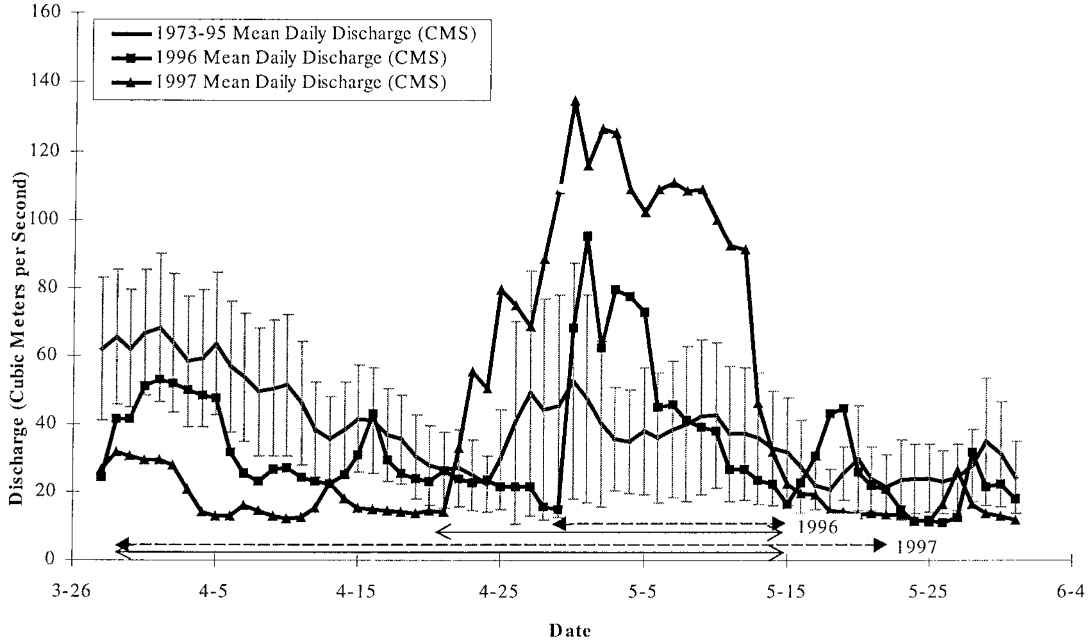

FIGURE 5.—Mean daily discharges on given dates for the period 1973–1995 and during the 1996 and 1997 field seasons. For the longer period, 95% confidence intervals are also shown. The horizontal lines beneath the discharge curves indicate the periods during which telemetered striped bass (dotted line) and American shad (solid line) were on the primary spawning grounds.

and 1997 field seasons as they were at any time during the 45 years since its construction.

Water velocity measurements taken immediately over the dam ranged from 1.20 to 1.66 m/s. Although these values are higher than those typically encountered in the Neuse River, they do not exceed the burst swimming velocity of striped bass or American shad (Mudre et al. 1985), suggesting that high water velocity was not a limiting factor for fish passage. However, turbulence created by water flowing over the submerged dam may have impeded fish passage (Mudre et al. 1985; Barry and Kynard 1986). In addition, the preference of migrating American shad for deep water (Witherell and Kynard 1990) may have reduced the likelihood of passing over the dam.

We found no evidence that striped bass or American shad used the fish ladder. Both species were present at the base of the dam during periods of low to average mean daily discharge. However, none of the telemetered individuals passed the dam until it was completely submerged. Our conclusion that the fish ladder was ineffective is consistent with the observations of Walburg (1957), who recommended removing the gates from the dam during the spring migration, and Baker (1968) who reported that the dam effectively blocked the migration of striped bass and substantially reduced the number of American shad spawning above the dam. Unfortunately, the gates were never removed during the lifetime of the dam.

Neuse River striped bass selected spawning sites with significantly higher water velocities than those found at randomly selected sites. Current velocity is an important limiting factor for striped bass egg survival and hatching. Eggs may tolerate current velocities from 0.31 m/s to 5.00 m/s; however, below 0.31 m/s egg settling occurs and survival decreases drastically (Mansueti 1958; Albrecht 1964; Regan et al. 1968). Current velocities of 0.00–0.84 m/s were available to striped bass, but we observed spawning behavior only at water velocities of 0.22–0.73 m/s (mean = 0.53 m/s). Similar velocities have been observed in other systems. Rulifson (1992) collected striped bass eggs in the Roanoke River, North Carolina, at current velocities of 0.4–1.2 m/s, with 66% of eggs collected at velocities of 0.6–0.8 m/s. Dickson (1958) recorded current velocity near the primary striped bass spawning grounds in the Roanoke River to be about 0.49 m/s. Velocities in areas where striped bass eggs have been collected range from 0.12 to

0.88 m/s in Virginia, from 0.18 to 0.99 m/s in California, and from 0.50 to 0.84 m/s in Oklahoma (see Crance 1984 and references therein). The riverine component of the inland striped bass habitat suitability index model assumes suitability to be optimal for any current velocity greater than 0.31 m/s (Bain and Bain 1982). Regan et al. (1968) suggested that current velocities of 0.30–1.00 m/s were optimal for larval striped bass. The only observation that conflicts with our results is that of Mansueti (1958), who reported current velocities of 1–2 m/s to be optimal for striped bass eggs. Current velocities greater than 1 m/s were not observed during our 1996 and 1997 field seasons; therefore, we were unable to test whether Neuse River striped bass would spawn preferentially at these velocities. However, Rulifson (1992) reported that eggs of Roanoke River striped bass were primarily collected when surface velocities were less than 1 m/s, even though velocities up to 1.26 m/s occurred during the spawning season.

Neuse River striped bass spawned at sites with significantly ($P < 0.01$) larger substrate than that observed at randomly selected sites. However, this apparent selection of larger substrates may stem from the correlation between water velocity and substrate. The relative importance of these variables may become clearer from more localized studies of habitat use and availability, for example, by comparing the use of sites within the spawning grounds that have similar current velocities but different substrates. Spawning habitat studies conducted after removal of the dam will also establish whether our characterization of spawning habitat was biased by the inaccessibility of historical spawning habitat, as the striped bass spawning behavior that we observed occurred directly below the dam.

Both above and below Quaker Neck Dam, American shad selected spawning sites that were significantly shallower and had significantly larger substrate ($P < 0.01$ in all cases) than randomly selected sites. Spawning occurred at a wide range of current velocities; thus, the selection of spawning sites with larger substrates does not appear to reflect the correlation between current velocity and substrate size. We observed American shad spawning below Quaker Neck Dam at depths between 0.30 and 1.83 m (mean = 1.35 m) with primarily gravel substrate. Above Quaker Neck Dam, we observed American shad spawning at sites with bedrock substrate and depths of 1.52–1.83 m (mean = 1.63 m). These results are similar to the criteria established for suitable American shad spawning habitat in the Susquehanna River restoration program. Carlson (1968) characterized suitable habitat for survival of eggs and larvae as moving, well-oxygenated waters passing over shallow sections of sand and gravel bottom with sufficient velocity to eliminate silt deposits.

Other studies have indicated that American shad use a wide range of depths and substrate types for spawning. Walburg and Nichols (1967) reported that spawning occurred on flats, adjacent river channels, and occasionally below barriers in areas with sand or gravel substrates at depths between 0.91 and 12.19 m. MacKenzie et al. (1985) reported that American shad in North Carolina spawn over sand shoals at depths between 1.5 and 6.1 m. Depth and substrate were not included in the current habitat suitability model (Stier and Crance 1985) because published reports indicated that spawning occurred at a wide variety of substrates and depths. Ross et al. (1993a) did not find a significant relationship between spawning site selection and depth or substrate size, but noted that spawning activity was greatest at depths of 1 m or less. Further observations taken at exact spawning locations are needed to evaluate the substrate and depth preferences that we observed.

It is not known whether American shad would gain a selective advantage by spawning at sites with larger substrates. American shad eggs are slightly heavier than water and sink gradually as they are carried downstream (Massman 1952; Walburg and Nichols 1967). Massman (1952) suggested that currents may transport American shad eggs downstream along the bottom. Most of the American shad eggs collected by Marcy (1972) were estimated from age data to have traveled 2–6 km downstream. The fertilized eggs are nonadhesive (Mackenzie et al. 1985), but they can reportedly lodge a short distance downstream of the spawning site (Marcy 1972; Moser et al. 1998). Moser et al. (1998) collected American shad eggs on floor buffing pads anchored at the base of dams in the Cape Fear River, North Carolina. The buffing pads have a rough texture and are used to sample for the eggs of sturgeons *Acipenser* spp. (Marchant and Shutters 1996). Eggs that lodge in larger substrates such as gravel might be at reduced risk of suffocation or predation, which can result in high mortality of American shad eggs (Mackenzie et al. 1985).

The American shad spawning activity that we observed below Quaker Neck Dam occurred at water velocities of 0.06–0.51 m/s (mean = 0.34 m/s). We observed much higher water velocities at spawning sites located above the dam (0.69–1.28 m/s, mean 1.01 m/s), but those observations were also made when discharge was much higher. Stier and Crance (1985) proposed an upper limit of 0.9 m/s for optimal current velocity, whereas Ross et al. (1993a) suggested an upper limit of 0.7 m/s. Walburg and Nichols (1967) indicated that spawning occurs at current velocities of 0.34–1.00 m/s. Mackenzie et al. (1985) reported that in North Carolina, American shad spawn in areas with water velocity ranging from 0.30 to 0.91 m/s.

We observed American shad spawning at temperatures between 18.0°C and 23.7°C. Walburg and Nichols (1967) reported that spawning occurs between 8°C and 26°C, with most spawning occurring between 14°C and 21°C. Ross et al. (1993b) observed relatively high spawning activity between 14°C and 24.5°C. For the Neuse River during 1977–1979, Hawkins (1980) reported temperatures of 11–26°C during the spawning period. In the Roanoke River, Sparks and Hightower (1998) collected American shad eggs in bongo net samples when water temperatures were between 20°C and 23°C.

A substantial fraction (five of five in 1996, four of seven in 1997) of our telemetered American shad died either on the spawning grounds or while emigrating. This result is consistent with the low percentage of repeat spawners in scale samples from the Neuse River population of American shad (Walburg 1957; Walburg and Nichols 1967; Hawkins 1980). Direct evidence from telemetry is useful, because indirect inferences about postspawning mortality from scale samples can be biased. The fraction of spawning fish that return in subsequent years depends on both natural and fishing mortality during the spawning migration. For example, Walburg (1957) estimated the rate of exploitation in the Neuse River during 1953 to be 65%, which would greatly limit the number of repeat spawners.

The removal of Quaker Neck Dam in 1998 has reopened an additional 127 rkm of historical mainstem spawning habitat. The section of the Neuse River upstream from the Quaker Neck Dam site is shallower and has higher current velocities and larger substrate than the downstream section. Because striped bass spawned at sites with higher current velocities and larger substrate and American shad spawned at shallower sites with larger substrate, this newly available habitat should be beneficial for both species. We conclude that where suitable habitat prevails upstream, the removal of low-head dams from rivers with historical anadromous runs can be a substantial restoration tool for depleted anadromous populations.

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