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ARTICLE

Effect of Low-Head Lock-and-Dam Structures on Migration and Spawning of American Shad and Striped Bass in the Cape Fear River, North Carolina

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Abstract

Anadromous fish populations within the Cape Fear River, North Carolina, have declined substantially since the late 1800s. Three low-head lock-and-dam (LD) structures on the river (LD-1–3) contributed to this decline by limiting access to upstream spawning habitat. We used egg sampling and sonic telemetry to examine the effects of the LD structures on migration and spawning activity of American shad *Alosa sapidissima* and striped bass *Morone saxatilis*. Egg distribution and stage of development suggested that most of the American shad spawning took place downstream from the lowermost structure, LD-1. The predicted mean density of stage-1 American shad eggs at a water temperature of 21°C was 895 eggs/1,000 m³ (95% credible interval [CI] = 800–994) below LD-1; 147 eggs/1,000 m³ (95% CI = 103–197) below LD-2; and 32 eggs/1,000 m³ (95% CI = 17–49) below the uppermost structure, LD-3. The probability of capturing a stage-1 American shad egg was strongly dependent on water temperature and hour of egg collection. Transmitter detections for 20 sonic-tagged American shad and 20 striped bass in 2008 showed that for both species, the majority of fish moved upstream of LD-1; 35% of American shad and 25% of striped bass migrated upstream of LD-3. Based on passage rates at the three LD structures, American shad would be expected to be most abundant downstream of LD-1 and upstream of LD-3. For striped bass, the river section between LD-2 and LD-3 had the highest egg collections and highest predicted proportion of the run. In combination, these results demonstrate that the locking program provides some access to historical spawning habitat, although further improvements in fish passage could benefit both species.

The Cape Fear River in North Carolina historically supported large runs of anadromous fish species, but population levels have declined substantially over the last two centuries (Rulifson 1994; Winslow 1994). Sturgeons *Acipenser* spp. dominated the fishery in the late 1800s (McDonald 1887), but only a small population of Atlantic sturgeon *Acipenser oxyrinchus* and very few shortnose sturgeon *Acipenser brevirostrum* persist today

(Winslow et al. 1983; Moser and Ross 1995). The Cape Fear River was one of the most productive rivers for American shad *Alosa sapidissima* in North Carolina at the beginning of the 20th century, but current commercial landings are 87% lower than historic estimates (Stevenson 1899; Nichols and Louder 1970; ASMFC 2007). The fishery for striped bass *Morone saxatilis* in the Cape Fear River has traditionally been smaller than those

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in other North Carolina coastal river systems, and the current striped bass population is considered to be among the lowest of the state's coastal river populations (McDonald 1887; Patrick and Moser 2001; Ashley and Rachels 2007).

Declines in landings of anadromous species in the Cape Fear River have been attributed to the same variety of anthropogenic stressors (e.g., overfishing, pollution, habitat degradation, and dam construction) that have affected many other Atlantic coastal rivers (Winslow et al. 1983; Winslow 1994). The most apparent of these stressors in the Cape Fear River is the presence of three low-head lock-and-dam (LD) structures (LD-1–3; each approximately 4 m tall) that were constructed between 1915 and 1934 by the U.S. Army Corps of Engineers (USACOE) for commercial navigation. These structures are downstream from North Carolina's geologic and topographic transition zone, referred to as the "fall line" (Hack 1982); this zone includes the Smiley Falls area, which is considered to be the historical spawning grounds for American shad (Nichols and Louder 1970). Upstream passage was limited except during boat lockage and possibly during extended periods of high flow (Nichols and Louder 1970). Fish ladders were constructed at each of the three LD facilities, but anadromous fishes were unsuccessful in using them (Davis and Cheek 1967; Nichols and Louder 1970).

In 1962, through an agreement among the North Carolina Wildlife Resources Commission (NCWRC), USACOE, and the U.S. Fish and Wildlife Service, a program was implemented in which the lock at each dam was used for moving fish upstream to continue their spawning run (Fischer 1980; Moser et al. 2000). Nichols and Louder (1970) evaluated the use of the locks for anadromous fish passage from 1962 to 1966. They estimated that 9,770 American shad passed through LD-1 (the lowermost structure), 1,110 passed at LD-2, and 50 passed at LD-3 (the uppermost structure). Subsequent studies estimated passage efficiency rates of 18–61% for American shad and striped bass at LD-1 (Moser et al. 2000; CZR Incorporated 2004). Currently, the USACOE conducts fish lockages (detailed by Smith 2009) at each dam three times per day from March to June and once each day throughout the remainder of the year under normal flow conditions (R. Hall, USACOE, personal communication).

Although the findings of previous research on the Cape Fear River indicate some upstream passage of American shad via the lock chambers, these studies also illustrate that there remains a substantial proportion of fish that do not access the upstream spawning areas. This problem has prompted new discussion about ways to improve anadromous fish passage in the Cape Fear River. The goal of this research was to characterize the current patterns of migration and spawning activity for American shad and striped bass in the Cape Fear River and to examine the potential effect of the LD structures on fish passage and spawning distribution. Results of this study should contribute to effective management of American shad and striped bass stocks throughout their range, particularly in systems where LD facilities affect migration.

METHODS

Study area.—The Cape Fear River basin is the largest watershed that is situated completely within North Carolina; the basin has a total drainage area of 23,310 km² and contains 27% of the state's population (Mallin et al. 2008). The Cape Fear River flows south–southeast approximately 320 km from the confluence of the Deep and Haw rivers in Chatham County to the Atlantic Ocean, 40 km downstream from Wilmington (Walburg and Nichols 1967). The three USACOE LD structures are located within the first 200 river kilometers (rkm; as measured from the mouth at the Atlantic Ocean; Figure 1): LD-1 was constructed at rkm 97 in 1915, LD-2 was constructed at rkm 149 in 1917, and LD-3 was constructed at rkm 186 in 1934 (Nichols and Louder 1970). Because of the open connection with the Atlantic Ocean, tidal effects are detectable 97 rkm upstream at LD-1 (Mallin et al. 2008). Channel morphology and substrate types are distinct between the upper and lower portions of the river. Above the fall line, substrates are dominated by coarse rocky material, and exposed shoals are common. In contrast, the lower river has relatively monotypic depth and substrates are dominated by sand and fine material. The transition in substrate composition begins about 45 rkm upstream of LD-3.

Egg sampling.—We conducted egg surveys at five locations twice per week during March 9–May 31, 2007, and March 5–June 4, 2008 (Figure 1). One sampling location was established within 0.5 km downstream of each LD structure (rkm 97, 149, and 186). All LD sites were sampled after sunset, with the exception of two samples in 2007. We selected two additional upstream sites at rkm 226 and 273. However, low water levels resulted in poor sampling conditions at rkm 273, so in 2008 the location was moved 3 km upstream.

Oblique plankton samples (15 min/sample) were collected with a bongo-style net consisting of two 0.3-m hoops with 500- μ m mesh, a 6:1 tail-to-mouth ratio, and solid-cup cod ends. A General Oceanics model 2030R flowmeter was used to estimate current velocity (m/s) and the volume of water sampled during each collection effort. Readings of depth, temperature, and dissolved oxygen concentration were taken with an onboard sonar and a hand-held, multiparameter water quality monitoring unit. Plankton sample contents were fixed with a 5–10% solution of formalin.

Processed American shad eggs were categorized by developmental stage based on criteria defined by Jones et al. (1978). American shad larvae were collected during the study, but numbers were insufficient for useful analyses. Relatively small numbers of eggs and larvae from nontarget species were also collected but were likewise not used in analysis.

Egg data analysis.—In order to focus on dam effects, we limited our analyses to stage-1 (newly spawned) American shad eggs collected below the LD structures. No analyses were performed for striped bass egg densities because of the low numbers collected.

FIGURE 1. Locations (rkm = river kilometer) of egg sampling stations and stationary acoustic receivers relative to the three lock-and-dam (LD) facilities on the Cape Fear River, North Carolina, 2007–2009. Acoustic monitoring for returning striped bass was conducted at the same locations in 2009 as in 2008, except that the receivers at rkm 212 and 231 were moved inside the lock chambers at LD-2 and LD-3 for 2009. Lock chamber receivers for 2008 (LD-1) and 2009 (LD-1–3) are not depicted by symbols due to the proximity of upstream LD receivers.

By using logistic regression, the probability of one or more American shad eggs being present (Ψ_i) was modeled as a function of water temperature and time of day in which the sample was collected (hour bins). Logistic regression is commonly used to model a categorical or binary response variable in relation to one or more predictor variables (Rahel and Jackson 2007). In this case, we used regression analysis to determine the environmental conditions under which spawning was most likely to occur. Parameter estimates were obtained with a logit (log odds ratio) transformation for Ψ (McCarthy 2007); LD number (categorical variable), water temperature ($^{\circ}\text{C}$), hour of sample collection, mean daily flow (m^3/s), and current velocity (m/s) were used as potential covariates. The LD number (i.e., 1–3) was related to position along the river, with LD-1 being the lowermost structure in the system. River discharge values were obtained from the U.S. Geological Survey (waterdata.usgs.gov/nwis/sw). Dissolved oxygen readings were excluded from analysis owing to consistently high values. Depth readings were also excluded because sample sites were fixed and differences in depth were due to river flow, which was already included.

Counts of American shad eggs were analyzed with generalized linear models. This modeling framework includes tradi-

tional linear regression as a special case but can also handle dependent variables with nonnormal distributions, such as egg counts (Gelman and Hill 2007; McCarthy 2007; Kéry 2010). We used a Poisson distribution to model egg count as a function of environmental variables, such as temperature and flow. For the i th sample, the single parameter for the Poisson distribution (mean λ_i) was modeled as a $\log_e$ -scale function of covariates (LD number as a categorical variable, water temperature, hour of sample collection, flow, and current velocity). Volume of water sampled was included in the model as an offset to account for differences among samples (Kéry 2010). Covariates were added sequentially after choosing the best model at each stage (e.g., we selected the best model with a single continuous covariate and then included an additional continuous covariate).

Reduced models were compared to each full model by using the deviance information criterion (DIC; McCarthy 2007):

$$\text{DIC} = \hat{D} + 2p_D,$$

where $\hat{D}$ is the deviance ($-2 \times$ the log likelihood) based on the mean of the posterior distributions for the parameters; and p_D is the effective number of estimated parameters (McCarthy 2007).

Similar to Akaike's information criterion, the DIC is a relative measure of fit for different models. The first term describes how well the model fits the data, and the second term is a penalty for increased model complexity; lower DIC values are better. The regression models were fitted by using Bayesian methods and OpenBUGS software (Lunn et al. 2000; McCarthy 2007). Code used for the analyses is available upon request from the authors.

Fish collection and tagging.—The protocol for telemetry work differed between 2007 and 2008. In 2007, we collected 20 American shad (eight males: mean total length [TL] = 440 mm; 12 females: mean TL = 503 mm) during April 24–May 14, and we collected 20 striped bass (16 males: mean TL = 626 mm; 4 females: mean TL = 749 mm) during April 13–May 7. Both species were collected by boat electrofishing in areas below the LD structures. Fish were held in a round, 378-L, onboard live well, which included a 100% oxygen-fed circulating system. Fish were then transported upstream of the LD facilities (i.e., to rkm 219) to be tagged and released.

At the release site, live fish were measured (mm TL), examined to determine sex, tagged, and placed into an instream holding pen. For American shad, Model V9-1 L-R04K coded transmitters (24 mm long, 2.2 g in water; VEMCO) were inserted into the gut through the esophagus by using a small length of clear tubing. For striped bass, a similar but larger coded transmitter (VEMCO Model V13-1 L-R64k; 36 mm long, 6 g in water) was surgically implanted into each fish by following the methods of Haeseker et al. (1996).

The poor performance of telemetered fish in 2007 led us to abandon the trap-and-transport method in favor of tagging and release at the point of capture. In 2008, we collected 20 American shad (19 males: mean TL = 427 mm; 1 female: TL = 505 mm) during March 13–25, and we collected 20 striped bass (16 males: mean TL = 630 mm; 4 females: mean TL = 756 mm) during February 26–April 21. Two striped bass were caught and released downstream of LD-2; all others were captured, tagged, and released from locations downstream of LD-1. Nineteen of 20 striped bass and 8 of 20 American shad were collected by electrofishing. The remaining fish were captured with hook and line. The same tag types and implantation procedures used for both species in 2007 were used again in 2008.

Adverse reaction of fish to trap-and-transport activities in 2007 confounded between-year comparisons of migratory behavior. Therefore, with the exception of some observations on the extent of migration, analyses of movement data are restricted to the 2008 sample population. As a result, evaluation of differences in migratory characteristics between sexes was impossible due to the insufficient sample sizes obtained in 2008.

Tracking.—All transmitters emitted a unique sequence at random time intervals that allowed for individual identification. Time intervals between coded tag bursts were set at 15–45 s (84-d life span) for American shad and 30–90 s (616-d life span) for striped bass. Transmitters were detected with an array of stationary VR2W receivers (VEMCO) and through manual searches.

Six VR2W receivers were used in 2007, and 10 receivers were used in 2008–2009 (Figure 1). The four new receiver locations in 2008 were inside the lock chamber of LD-1 and at rkm 246, 261, and 276. In 2009, the receiver array was further modified to provide additional information on upstream passage at the LD structures. Two receivers that were upriver from LD-3 in 2008 (rkm 212 and 231) were repositioned inside the lock chambers at LD-2 and LD-3, respectively.

Manual tracking in 2007 and 2008 was conducted by boat with a portable VR100 receiver (VEMCO) equipped with either a VH165 omnidirectional hydrophone or a VH110 directional hydrophone. Relocation coordinates were logged by using the receiver's internal Global Positioning System unit. Date, time, depth, temperature, dissolved oxygen, and flow rate measurements were also taken. Associated streamflow and precipitation data were obtained from the U.S. Geological Survey (water-data.usgs.gov/nwis/sw).

Receiver detections and relocations.—We determined the minimum extent of upstream migration for each fish based on the upstream-most stationary receiver detection or manual relocation. Upstream passage efficiency through the LD structures was calculated for both species in 2008 and for returning striped bass in 2009. Efficiency was calculated as the number of fish detected by the receiver upstream of a given LD facility divided by the number of fish that could potentially be present downstream from that structure (i.e., fish that were known to be available for passage). For striped bass, the potential number of fish that were present downstream of LD-1 was established by confirmed detections on the receiver located inside the lock chamber of LD-1. This estimate may slightly overestimate passage because some fish may have moved up to the area around the dam without being detected by the chamber receiver. Because American shad were tagged and released before the deployment of the chamber receiver at LD-1, the potential number of American shad present downstream of LD-1 was the total number of fish that were tagged and released during 2008. Therefore, the passage estimate obtained by using this number may be more conservative than that for striped bass; furthermore, it does not account for any handling stress bias that may have influenced American shad migratory behavior.

RESULTS

Egg Data

American shad.—Total numbers of American shad eggs collected were 586 in 2007 and 728 in 2008 (Table 1). For both years combined, the LD-1 site yielded 1,083 eggs, or approximately 82% of the total number collected during the study, compared with 154 eggs (12%) at the LD-2 site, 72 eggs (6%) at the LD-3 site, and 6 eggs (0.003%) at the rkm-226 site. We collected no eggs from the uppermost site in either year. Stage-1 eggs (age = 0–2 h) made up 95% of the total number of American shad eggs collected, whereas 4% of the eggs were found to be in stage 2 (Table 1). The Ψ_i was strongly dependent

TABLE 1. Number of American shad eggs (by stage of development) collected from five locations (rkm = river kilometer) sampled near or at lock-and-dam (LD) facilities on the Cape Fear River, North Carolina (March 9–June 1, 2007; March 5–June 4, 2008). Egg development criteria are from Jones et al. (1978).

Distance upriver (rkm) and site	Stage 1		Stage 2		Stage 3		Stage 4		Stage 5		Total number of eggs	
	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008
97 (LD-1)	466	600	6	4	0	3	2	2	1	1	474	609
149 (LD-2)	70	57	8	14	1	0	2	2	1	1	81	73
186 (LD-3)	21	33	8	4	0	6	0	0	0	0	29	43
226	2	3	0	0	0	0	0	0	0	1	2	4
273	0	0	0	0	0	0	0	0	0	0	0	0
Total (all sites)											586	728

on water temperature and the time of day when sampling occurred (Figures 2, 3). The DIC scores supported models that contained quadratic terms for temperature and hour of sample collection (Table 2), although the 95% credible interval (CI) for hour of collection (linear term only) included zero. The DIC

scores (and quadratic functions for temperature and hour of collection) were similar for models 5–7 listed in Table 2. Results for model 5 are presented for parsimony and because the 95% CIs for flow (model 6) and current velocity (model 7) included zero.

FIGURE 2. Predicted probability of American shad egg presence (upper panel) as a function of water temperature (°C) based on a logistic regression model that included an intercept, water temperature (linear and quadratic), and hour of sample collection (linear and quadratic). Solid lines indicate median responses; dashed lines represent the 95% credible interval. The number of plankton tows (by 1° temperature intervals) in which American shad eggs were present or absent is shown in the lower panel.

FIGURE 3. Predicted probability of American shad egg presence (upper panel) as a function of the hour of sample collection based on a logistic regression model that included an intercept, water temperature (linear and quadratic), and hour of collection (linear and quadratic). Solid lines indicate median responses; dashed lines represent the 95% credible interval. The number of plankton tows (by hour of collection) in which American shad eggs were present or absent is shown in the lower panel.

TABLE 2. Comparison of deviance information criterion (DIC) scores among logistic regression models of the presence of stage-1 American shad eggs below the three lock-and-dam facilities on the Cape Fear River (p_D = estimated number of effective parameters [McCarthy 2007]; Temp = temperature, °C; Hr = hour of sample collection; Flow = mean daily flow, m³/s; Vel = current velocity, m/s).

Model	DIC	p_D
1. Intercept	196.1	1.1
2. Intercept, Temp	185.5	2.0
3. Intercept, Temp, Temp ²	163.3	2.9
4. Intercept, Temp, Temp ² , Hr	165.3	4.1
5. Intercept, Temp, Temp ² , Hr, Hr ²	153.6	5.0
6. Intercept, Temp, Temp ² , Hr, Hr ² , Flow	154.4	6.3
7. Intercept, Temp, Temp ² , Hr, Hr ² , Vel	155.6	5.9

The best model for counts of stage-1 American shad eggs used volume sampled as an offset, an LD-specific intercept, and LD-specific slopes for water temperature (linear and quadratic terms), hour of sample collection, and current velocity (Table 3). We were unable to get convergence on more-complex models (e.g., adding a squared term for hour of sample collection). Predicted and observed counts showed reasonable agreement as a function of water temperature (Figure 4). At a water temperature of 21°C (close to the peak for all three LD

TABLE 3. Comparison of deviance information criterion (DIC) scores among generalized linear regression models of American shad stage-1 egg counts below the three lock-and-dam (LD) facilities on the Cape Fear River (p_D = estimated number of effective parameters [McCarthy 2007]). All models included $\log_e(\text{volume})$ with a slope of 1.0 as an offset to account for the volume of water filtered in each sample (Kéry 2010). The model term "LD" refers to the LD number (1–3), which was a categorical variable that provided a separate intercept for each LD facility. Slopes that were specific to each LD were used for all continuous covariates (Temp = temperature, °C; Hr = hour of sample collection; Flow = mean daily flow, m³/s; Vel = current velocity, m/s).

Model	DIC	p_D
1. Intercept	6,266	1.047
2. LD	5,210	2.983
3. LD, Temp	3,237	5.88
4. LD, Flow	4,567	5.898
5. LD, Vel	3,539	5.923
6. LD, Hr	5,093	6.022
7. LD, Temp, Hr	3,064	8.792
8. LD, Temp, Flow	3,214	8.916
9. LD, Temp, Vel	3,095	9.01
10. LD, Temp, Temp ²	2,755	9.044
11. LD, Temp, Temp ² , Hr	2,443	11.8
12. LD, Temp, Temp ² , Flow	2,701	11.77
13. LD, Temp, Temp ² , Vel	2,518	11.98
14. LD, Temp, Temp ² , Hr, Hr ²	2,310	15.14
15. LD, Temp, Temp ² , Hr, Flow	2,371	15.2
16. LD, Temp, Temp ² , Hr, Vel	2,254	14.75

structures), the predicted mean density was 895 eggs/1,000 m³ (95% CI = 800–994) below LD-1; 147 eggs/1,000 m³ (95% CI = 103–197) below LD-2; and 32 eggs/1,000 m³ (95% CI = 17–49) below LD-3.

FIGURE 4. Observed (obs) and predicted number of American shad eggs collected per sample (λ of Poisson distribution) as a function of water temperature (°C) for the three lock-and-dam (LD) facilities on the Cape Fear River: LD-1 (upper panel), LD-2 (middle panel), and LD-3 (lower panel). Predicted values were based on means for sampling volume, hour of sample collection, and flow. Solid lines indicate median responses; dashed lines represent the 95% credible interval (0.025 = lower limit of interval; 0.975 = upper limit).

FIGURE 5. Minimum extent of upstream migration by American shad (2008) and striped bass (2008 and 2009) based on stationary receiver detections in the Cape Fear River. The x-axis shows the location (rkm = river kilometer) of the receiver; the y-axis indicates the number of fish that were detected by the given receiver but not by receivers located farther upstream. Dashed lines represent the dams at each lock-and-dam (LD) facility. The first receiver (rkm 97) was located inside of the lock chamber at LD-1, and fish that were only detected at this site (3 striped bass in 2008; 1 striped bass in 2009) were not successful in migrating upstream of the dam. Receivers that were moved inside a lock chamber in 2009 are denoted by double asterisks (**) on the x-axis. The receiver at rkm 261 was missing at the end of the 2009 field season.

Striped bass.—No striped bass eggs were collected during the 2007 season; however, similar efforts yielded 41 eggs in 2008 (Smith 2009). All sites except the uppermost site (rkm 276) produced at least one striped bass egg, but most (29 eggs, or 71% of the total) were collected at LD-3. Mean density (eggs/1,000 m³ ± SE) of eggs collected in 2008 was 2.6 ± 2.1 (LD-1), 6.2 ± 5.5 (LD-2), 22.0 ± 16.8 (LD-3), and 0.28 ± 0.28 (upriver sites). Sample sizes were small, but a majority of striped bass eggs (56%) were in the first stage of development and all but two of the remaining eggs (39%) were in the third stage.

Migratory Characteristics

In 2007, 18 of 20 (90%) tagged American shad were relocated at some point in the study based on combined data from manual tracking and stationary receivers. Twelve (60%) of the fish moved upstream from the release site (rkm 219) and six (30%) moved downstream. Three of the six fish that moved downstream went below LD-3, and none of those individuals made secondary upstream movements. Three American shad were manually located upstream of the uppermost receiver at rkm 231; one of these fish was located at rkm 252.

Nineteen tagged striped bass were relocated in 2007, and all fish immediately moved downstream of the release site. Two striped bass that initially moved downstream and within range of the receiver at LD-1 made secondary movements upstream by using the fish locking procedure.

In 2008, 15 American shad and 16 striped bass (including two striped bass that were tagged in 2007) were relocated by stationary receivers or by manual tracking efforts. Thirteen American

shad and 12 striped bass made movements upstream through at least one LD structure (Figure 5). Seven American shad and four striped bass migrated upstream of LD-3, and all but two of these fish moved upstream to or beyond rkm 231, where shoal habitat first occurs in the river. The maximum documented upstream migration occurred in 2008 and was exhibited by a 761-mm male striped bass from the group of fish tagged in 2007. On May 7, 2008, the fish was relocated 1 rkm downstream from Buckhorn Dam (rkm 300), which represents the endpoint for upstream migration. The longest migration for American shad was made by a 442-mm male; this individual was released at rkm 97 on March 25, 2008, and was relocated at rkm 280 on May 7, 2008.

Based on tag life and 2008 detection histories, 14 striped bass were considered viable for relocation in 2009. Stationary receiver data indicated that nine striped bass made upstream migrations to at least the LD-1 lock chamber in 2009 (Figure 5). Overall, the extent of migration in 2009 was somewhat similar to that seen in 2008. Four striped bass migrated upstream of LD-3, and two of those fish moved upstream of the habitat shift (rkm 231) to at least rkm 246. The receiver at rkm 261 was missing at the time of retrieval in 2009, and no data were recovered. No fish were detected by the uppermost receiver at rkm 276.

Two of the striped bass detected in 2009 either resided in the river year-round or migrated upriver before receiver deployment at the beginning of April. Year-round residence seems most likely given that (1) both fish were last detected in late-summer 2008 in the vicinity of LD-3 and (2) both were first detected in 2009 by the lock chamber receiver at LD-3. The other seven

TABLE 4. Passage rates of American shad and striped bass at the three lock-and-dam (LD) facilities on the Cape Fear River. Passage rates (% passed) were estimated as the number of fish detected by the receiver upstream of an LD structure (number passed) divided by the number of fish that were known to be available for passage (i.e., fish downstream of that LD; number available). Striped bass that were tagged below LD-2 (in 2008) or present below LD-3 (in 2009) account for the differences between the number of fish available for passage (indicated by asterisks; 12 in 2008, 8 in 2009) and the number that passed the preceding LD.

Species and year	LD-1			LD-2			LD-3		
	Number available	Number passed	Passage rate (%)	Number available	Number passed	Passage rate (%)	Number available	Number passed	Passage rate (%)
American shad, 2008	20	13	65	13	11	85	11	7	64
Striped bass, 2008	13	10	77	12*	9	75	9	4	44
Striped bass, 2009	7	6	86	6	6	100	8*	4	50

striped bass from the 2008 tagging group were first detected at LD-1 between April 1 and April 24, 2009.

In addition to migratory information, 2009 relocation data provided a point estimate of mortality for tagged striped bass. We assumed that the tagged fish that were detected and alive at the end of 2008 were available for return migration in 2009. We further assumed that there was a negligible risk that fish would not undertake a spawning run, would migrate into a different river, or would migrate to a point downstream of the lowermost receiver. Any of those occurrences would lead to an overestimate of mortality. The estimated survival (S) was 64%, and therefore total mortality (Z) was calculated as 0.45 (i.e., $Z = -\log_e[S]$). Subtracting an assumed natural mortality rate of 0.15 (NEFSC 2008) from this Z yields an estimated fishing mortality (F) of 0.30.

Passage Efficiency

Passage rates for American shad and striped bass in 2008 were relatively similar (Table 4). The higher number of striped bass available for passage at LD-2 (12 fish) relative to the number of fish that passed LD-1 (10 fish) was due to the collection and release of two additional striped bass downstream of LD-2. Passage rates for striped bass in 2009 showed a pattern similar to that in 2008 (Table 4). In 2009, the number of striped bass available for passage at LD-3 (8 fish) was greater than the number known to have passed LD-2 (6 fish). This difference occurred because the two fish were present in the area between LD-2 and LD-3 before the receivers were deployed and they were first detected by the lock chamber receiver at LD-3.

Results for 2009 showed that there was substantial variation in the amount of time spent by fish inside the lock chambers during migration (Figure 6). For example, fish 6 quickly passed all three LD structures, whereas fish 3 spent 6 d moving into and out of the lock chamber at LD-1, spent 5 d at LD-2, and was detected for over 8 d at the LD-3 chamber without passing upstream.

Passage estimates for American shad indicated that 35% ($[1 - 0.65] \times 100$) of spawning adults remained below LD-1; 10% ($0.65 \times [1 - 0.85] \times 100$) were between LD-1 and LD-2; 20% ($0.65 \times 0.85 \times [1 - 0.64] \times 100$) were between

LD-2 and LD-3; and the remainder (35%) were above LD-3. For striped bass in 2008, the predicted distribution of spawning adults was 23% below LD-1, 19% between LD-1 and LD-2, 32% between LD-2 and LD-3, and the remainder (25%) above LD-3. These predicted distributions share some characteristics with the distributions of collected eggs, although both distributions overestimated the proportion of eggs that would be collected above LD-3 (Figure 7).

DISCUSSION

Spawning Distribution

The number of American shad eggs in plankton samples declined substantially in relation to the number of LD structures encountered. This pattern, which remained consistent between the 2 years, suggests that access to habitat above the three structures is substantially limited. We collected only six American shad eggs upstream of the LD facilities, all from one location (rkm 226). A similar result was obtained in a previous study (Dial Cordy and Associates 2006). This may be another indication that American shad have limited access to upriver sites, but it may also be due to the inherent differences between upriver sites and sites downstream from the LD structures. Lock-and-dam sites tend to concentrate fish in one location, so samples taken below these obstructions are more likely to contain newly spawned eggs if spawning occurs. Evidence for this lies in the fact that the vast majority (95%) of American shad eggs collected downstream of the LD facilities were in stage 1 of development. Samples at upriver sites were not taken downstream of any barriers that might have concentrated fish; these samples were therefore more likely to capture eggs drifting from random upstream spawning locations. Such was the case on the Neuse River, North Carolina, where American shad eggs were collected at multiple sites after the removal of a low-head dam (Burdick and Hightower 2006). Many of those sites were not immediately downstream of obstructions or known aggregates of fish, and collections contained eggs at various stages of development. Similarly, Marcy (1972) collected American shad eggs up to 6.4 km from where the fish were assumed to have spawned.

FIGURE 6. Detections of migrating striped bass by lock chamber and upper pool receivers at each lock-and-dam facility (LD-1–3) in the Cape Fear River, 2009. Each fish was assigned an arbitrary y-axis value for display; each symbol represents the date and time of a single detection. Gray symbols represent lock chamber receivers (e.g., “LD3C” = the lock chamber at LD-3), and black symbols represent upper pool receivers (numbers in parentheses are the receiver locations in river kilometers).

It is also possible (depending on streamflow and channel morphology) that American shad eggs drifting downstream from upriver spawning events may have settled out before reaching the upper-basin sampling locations. Massmann (1952) suggested that the distance traveled by newly spawned American shad eggs is positively correlated with water current and turbulence. The run–riffle–pool complex present in the upper portion of the Cape Fear River produces breaks in current velocity that may allow drifting eggs an opportunity to settle out. The upper-basin sites also have more-diverse substrates, including gravel and cobble. This could have substantially limited the downstream transport of eggs; for example, Chittenden (1969) observed that stripped American shad eggs lodged in large substrates 1.5–1.8 m downstream from their release point.

Conducting daytime sampling as opposed to nighttime sampling at upriver sites should not have negatively affected egg collections since we were not sampling downstream from known aggregates of fish. Previous studies have resulted in successful collection of American shad eggs in daytime plankton samples (Massmann 1952; Marcy 1972; Hawkins 1980; Burdick and Hightower 2006). However, if nighttime spawning had occurred in close proximity upstream from these sites, then newly spawned eggs may have drifted by the sites before the samples were taken.

Egg Sampling

American shad eggs were present in our samples over a range of water temperatures (18–23.7°C), which is consistent with the results of previous studies (Walburg and Nichols 1967; Leggett and Whitney 1972; Ross et al. 1993). The Ψ_i was strongly affected by temperature: a peak occurred at 20°C, and a decrease to near zero occurred at about 11°C. The timing of sampling also affected Ψ_i ; the highest probability occurred at 2100 hours. In a survey of the Roanoke River, North Carolina, Hightower and Sparks (2003) reported that the number of eggs in samples was highest at around 2100 hours. In addition, Ross et al. (1993) found that American shad eggs were most numerous in samples taken between 2000 and 2400 hours on the Delaware River.

The plankton sampling strategy used to collect newly spawned American shad eggs during this study proved to be more effective than the approach used during a similar study on the Cape Fear River in 2006 (Dial Cordy and Associates 2006). In both cases, samples were taken downstream of the LD structures, but we conducted sampling during dusk and evening hours, whereas samples in the Dial Cordy and Associates (2006) study were taken during the day. The increased success rate is consistent with published findings that the timing of spawning for American shad is concentrated around the early evening hours (Massmann 1952; Walburg and Nichols 1967; Chittenden

FIGURE 7. Estimated distribution of spawning adults (Migration%) and observed distribution of collected eggs (Egg%) for American shad (upper panel) and striped bass (lower panel) relative to the three lock-and-dam (LD) facilities on the Cape Fear River (on the x-axis, "upper" = the reach upstream of LD-3).

1976; Ross et al. 1993). The timing of sampling is particularly critical for a site below an obstruction because spawning fish are likely to be immediately upstream of the sampling site.

Telemetry

To reduce handling stress experienced by the fish in 2008, fish were collected as early in the year as possible and were tagged and released at the same location. Earlier collection provided more time for recovery before the spawning run and cooler water temperatures during the stress of capture and tagging. Our decision to change protocol appeared to be correct based on the number of fish that moved upstream after release and the number of fish that moved above all three LD structures.

On a similar note, the use of hook and line to collect fish for tagging appeared to lead to greater postrelease movement upriver for American shad. Of the 12 American shad that were collected by hook and line and released within a lock chamber, 11 made movements upstream of LD-1. Ely et al. (2008) used hook and line to collect Alabama shad *Alosa alabamae* for a tagging study on the Apalachicola River, Florida. This method was also incorporated by the Maryland Department of Natural Resources as a low-cost, nonlethal way to collect broodfish for an American shad aquaculture program (S. P. Minkinen and B. M. Richardson, paper read at the World Aquaculture Society meeting, 1998).

Migration

Based on our receiver array and manual tracking, we documented upriver movements of at least 280 rkm for American shad and 299 rkm for striped bass. This section of the Cape Fear River has a complex structure of shoals and pools, unlike the monotypic depth, flow, and channel shape of the lower river. Similar results were reported in a previous Cape Fear River study (CZR Incorporated 2004), with maximum upstream movements of 257 rkm for American shad and 300 rkm for striped bass. These distances are similar to those traveled by anadromous species in other systems to reach spawning grounds or before reaching artificial obstructions (Chittenden 1976; Carmichael et al. 1998; Beasley and Hightower 2000; Bowman 2001; Bailey et al. 2004).

Our estimated passage rates of American shad (65% at LD-1, 85% at LD-2, and 64% at LD-3) and striped bass (77, 75, and 44%, respectively) through LD facilities on the Cape Fear River were higher than previous estimates. Moser et al. (2000) reported American shad passage rates of 18–61% at LD-1 and 33% at LD-2 on the Cape Fear River. As in our study, these rates of passage were based on fish that remained or returned to the dam after being tagged and had the potential for passage. Our higher estimates may be due to changes in locking procedures aimed at improving fish passage; these changes were initiated during the study by Moser et al. (2000). However, estimates from a recent Cape Fear River study (CZR Incorporated 2004) were also lower than our estimates and ranged from 25% to 50% for American shad and from 0% to 61% for striped bass. Bailey et al. (2004) estimated that the passage rates for American shad returning to the New Savannah Bluff LD in Georgia ranged from 9% to 50%.

Passage rates at LD-1 and LD-2 were relatively similar between American shad and striped bass. For passage at LD-3, American shad showed higher passage rates than did striped bass (although sample sizes were small). This could indicate a problem with striped bass passage at LD-3 but might also be linked to the fact that the majority of striped bass eggs were collected from the LD-3 site. Some striped bass may forego migration beyond LD-3 if this section of the river is suitable for spawning. Further investigations are required to better understand this potential link.

The amount of time spent below an LD structure (and within a lock chamber) varied considerably among individual fish. Some fish passed very quickly from the lock chamber to the upper pool, while others took several hours to days before passing upstream. In 2008 and 2009, some striped bass were detected by chamber receivers but failed to use the locks to move upstream, despite the fact that they were detected during times of day when locking procedures were conducted. Similarly, Moser et al. (2000) observed that American shad entered the lock chamber at LD-1 but failed to pass upstream. These delays in migration are further supported by migration rate analyses showing that both American shad and striped bass exhibited slower speeds through the lower section of the river where the LD structures are present (Smith 2009).

Our estimate of F for telemetered striped bass is very similar to a catch-at-age model F -estimate of 0.31 for age-8–11 coastal migratory Atlantic striped bass in 2006 (NEFSC 2008) and matches the Atlantic States Marine Fisheries Commission target F of 0.30 (NEFSC 2008). This approach illustrates that telemetry conducted with an array of stationary receivers can provide mortality estimates for migratory fish with relatively little effort. This approach requires transmitters with a battery life of 1 year or more, but it avoids issues such as gear selectivity and errors due to age determination. Lindley et al. (2008) used telemetry data from marine receiver arrays to estimate annual survival of green sturgeon *Acipenser medirostris*. For striped bass in the Cape Fear River, a larger sample size of telemetered fish would provide a precise estimate of Z and would enable managers to monitor the effectiveness of management actions.

Future Directions

The numbers of eggs collected from the upper river were lower than expected, probably because LD sites aggregate fish during peak spawning times and upriver sites do not. A possible direction for future research could be more-intensive diel tracking of tagged fish to locate potential upriver spawning areas. These locations could then be sampled during the evening hours, when spawning activity is more likely to take place. However, such an approach would be logistically challenging due to limited access at the upper sections of the Cape Fear River.

It would also be valuable to estimate the size of the American shad spawning population present in the Cape Fear River. Such estimates have been obtained in other systems through mark-recapture methods (Bailey et al. 2004). An estimate for the Cape Fear River population, coupled with information about egg densities and passage rates, could provide a much clearer picture of the effects of the three LD structures on anadromous fish migrations.

Limburg et al. (2003) showed that American shad spawning runs in major Atlantic coastal drainages are substantially reduced from their historical extent. Much effort has been placed into addressing this systemwide issue, and restoration activities have improved access to upriver habitats in many systems (Cooke and Leach 2003; Olney et al. 2003; St. Pierre 2003; Burdick and Hightower 2006). However, the current study reveals that mechanisms for promoting upstream passage of anadromous species do not ensure the use of historical upriver spawning grounds. Future researchers evaluating passage of anadromous species should examine passage efficiency and delays as well as the distribution of spawning activity within the system.

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