



Abstract—In recent years, the Alabama shad (*Alosa alabamae*) has experienced dramatic declines and extirpations from portions of its native range. Habitat degradation and barriers to migration are considered contributing factors to contraction in the distributional range this species. To identify conditions during successful spawning, river temperatures and discharges in 2 drainages of the northern Gulf of Mexico (the Apalachicola and Pascagoula rivers) were characterized during successful hatching “windows.” Sampling during 2005–2009 yielded 400 juvenile Alabama shad of which 261 were aged from counts of rings on sagittal otoliths. Results from logistic regression revealed that successful spawning coincided with increases in temperature within a specific range (9.4–21.5°C) and with an average drainage-dependent discharge volume (625.6 m³/s in the Apalachicola River and >400.7 m³/s in the Pascagoula River). Timing of successful hatching windows differed between drainages but not between years within each drainage. Documenting and identifying the river conditions during successful reproduction provide important information on how to manage rivers to aid in the recovery of this species of conservation concern.

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Environmental conditions of 2 river drainages into the northern Gulf of Mexico during successful hatching of Alabama shad (*Alosa alabamae*)

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Migratory species invest significant resources in moving through a variety of disparate habitats to reach spawning sites (Gross, 1987; Roff, 1988). For fish species, these costs can be substantial (i.e., osmoregulation in diadromous fishes, or movement through suboptimal habitat that increases exposure to predators, disease, or anthropogenic disturbances), and spawning migrations require energetic demands associated with gonad maturation (Leggett and Whitney, 1972; Hodgson and Quinn, 2002). These costs also are linked inextricably to a number of species life history traits (e.g., body size, fecundity, and age of maturation) that have co-evolved with migration to maximize individual fitness (Gross, 1987; Kinnison et al., 2001). Despite the evolution of complex behaviors, physiology, and morphology, many migratory species show substantial

flexibility in the timing of migration and the routes taken (Berthold, 2001; Alerstam et al., 2003).

River conditions that are possible cues for migration in fish species include discharge, flow velocity, temperature, suspended sediment, pH, conductivity, and dissolved oxygen (McLean et al., 1982; Quinn and Adams, 1996; Hewitt, 2003). These parameters are susceptible to rapid changes during spring rains when river discharge increases dramatically, possibly ultimately influencing the potential for successful recruitment (Maurice et al., 1987). Flow and temperature are correlated with oxygen levels and egg development time and ultimately with hatching success (Mann, 1996). After hatching, temperatures, nutrient levels, and turbidity are expected also to influence growth and survivorship. Therefore, individuals spawned at different

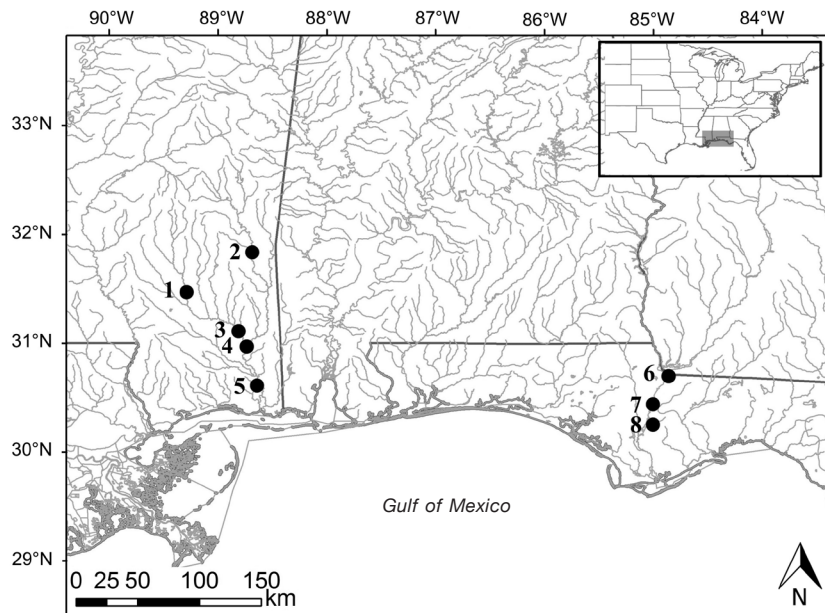


Figure 1

Map of the 2 river drainages sampled for Alabama shad (*Alosa alabamae*) during 2005–2009. Five sites were sampled in the Pascagoula River basin in Mississippi: 1) Eastabuchie; 2) Shubuta; 3) McLain; 4) Merrill; and 5) Wade. Three sites were sampled in the Apalachicola River basin in Florida: 6) Woodruff; 7) Wewahitchka; and 8) Blountstown.

times (early versus late) in a season may have different growth and mortality rates (Limburg, 1996).

Fish otoliths provide a detailed history of the daily and annual growth of an individual and can provide a useful tool for retrospective assessment of the growth rates of early juveniles (Parsons and Peters, 1989; Geffen, 1992). Daily growth rings on otoliths consist of alternating calcium- and protein-rich layers (Geffen, 1992; Armstrong et al., 2004). Diel feeding cycles lead to variable growth, resulting in alternating opaque and translucent rings in each 24-h period. Unlike other skeletal elements, otoliths do not undergo bone remodeling that would potentially resorb layers (Simkiss, 1974). Therefore, the daily deposition of otolith rings provides a method for determining age (in days) in species of bony fish.

Alabama shad (*Alosa alabamae*) is an anadromous fish that ascends rivers in the Mississippi River basin and northern Gulf of Mexico to spawn during spring months (February–May) of each year (Mettee and O’Neil, 2003). A special conservation status has been conferred on Alabama shad by several states, including Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, and Missouri (Meadows et al., 2006). Population-level genetic data indicate a high degree of site fidelity within some populations of Alabama shad (Bowen, 2005). As a result, differences in spawning timing and recruitment due to genetic drift or local adaptation are possible.

Until recently, much of the basic biology for Alabama

shad had been inferred from research on the American shad (*A. sapidissima*) in northern Atlantic basins. The American shad is fairly well studied; published works address fecundity, spawning, feeding behavior, and even restoration (Olney and McBride, 2003; Walter and Olney, 2003). Much less is known about the ecology of Alabama shad (Mickle et al., 2010). The goals of this study were to improve our understanding of river conditions during successful hatching of Alabama shad and compare these conditions among river drainages. Our objectives were 1) to assess differences in successful hatching timing of Alabama shad between 2 basins, 2) to evaluate and compare river conditions during successful hatching between the basins, and 3) to assess interannual variability in both hatch timing and river conditions during successful hatching. For this study, we defined successful hatching as hatching that resulted in larval survival to the juvenile stage. Once the timing of successful hatching was determined (from daily age data), we were able to compare river condition and hatch timing for the 2 rivers and sampling years—findings that would help to identify the necessary conditions for recruitment of Alabama shad.

Materials and methods

Hatch timing and river conditions during hatching were compared between 2 rivers in the central Gulf of Mexico (Fig. 1). The Apalachicola River is a large river

in the Florida panhandle and contains the largest extant population of Alabama shad (Mettee and O'Neil, 2003). This river has a dam on the mainstem (Jim Woodruff Lock and Dam, at river kilometer 171), and Alabama shad spawn below the dam, although some pass through a lock system that is opened twice a day (Laurence and Yerger, 1967; Ely et al., 2008). The Pascagoula River, located in Mississippi, is the last large, free-flowing river in the contiguous United States (Dynesius and Nilsson, 1994). No spawning grounds of Alabama shad have been documented for the Pascagoula River, although juveniles are consistently present within this river system (Mickle et al., 2010).

To investigate drainage-level differences in successful hatch timing, juveniles were collected from the Pascagoula River basin in Mississippi during 2005–2009 and from the Apalachicola River basin in Florida during 2007–2008 and then aged by counting daily otolith rings. Samples were taken during June and October in the Apalachicola River basin and in June through October in the Pascagoula River basin, excluding September and October 2005 after Hurricane Katrina. The year 2007 was the only year during the sampling period that was categorized as a severe drought year by the Palmer Drought Severity Index for the region (U.S. Drought Monitor, website). The other years (2005, 2006, 2008, and 2009) were characterized as low water, but not drought, years.

Fish were collected with a SR-14EB¹ electrofishing boat (Smith-Root Inc., Vancouver, WA) operated at 5000 W and 16 A with pulses-per-second ranging from 7.5 to 120. Electrofishing effort typically occurred for 1200 s at each site and was focused on the habitat types of sand bar, open channel, and bank. Alabama shad were tagged individually and placed in 95% ethanol. During low-water periods, some sites (typically shallow sand bars) were not accessible by the electrofishing boat. Because Alabama shad undergo ontogenetic shifts in habitat use (Mickle et al., 2010), these sites were seined and occasionally a cast net was used to ensure individuals of all ages were sampled throughout the sampling period. Cast nets had diameters of 1.52–2.43 m and a bar mesh of 1.59 cm. Seines were 3.0–3.7 m wide by 1.8–2.4 m deep and had a 0.3-cm-wide mesh.

Age was estimated in days by counting daily rings on the sagittal otoliths (Secor et al., 1992). One otolith per individual fish was removed and mounted on a slide with Crystalbond mounting adhesive (Ted Pella, Inc., Redding, CA). Otoliths were mounted with the primordia facing down and sanded by hand with sequentially finer grit-size paper, as necessary, to expose the rings. Daily rings were counted with a Wild Heerbrugg compound microscope (Leica Microsystems Inc., Buffalo Grove, IL). Magnification ranged from 290× to 1080× depending on the diameter (0.25–0.50 mm) of the otolith. Otolith images were taken with a SPOT Insight

Color digital camera (Diagnostic Instruments Inc., Sterling Heights, MI) and by using SPOT Advanced software, vers. 3.3 (Diagnostic Instruments Inc.), and were enhanced by using Image-Pro Express, vers. 4.0.1 (Media Cybernetics Inc., Rockville, MD).

Age rings on each otolith were counted 3 times by the same person during separate sessions, and counts were averaged over the 3 observations. Of the otoliths read, 5% were randomly selected for independent validation by another reader and compared with the range of original readings. The otoliths of older fish (>250 days, all from individuals >100 mm in total length [TL] captured later in the year) were thick and brittle, making sanding and accurate reading of daily rings difficult. These older fish were removed from our analysis. As suggested by Geffen (1992), fish age was determined by adding 10 days to each daily ring count to compensate for the posthatching yolk stage that precedes daily ring formation in certain species. The hatch date for each individual was determined by counting back the age of the fish from its collection date. The successful hatching period (average time from the start of hatching to the end of hatching [hereafter “hatch window”]) for each drainage and year was defined as the period between the earliest and latest hatching date for all Alabama shad younger than 250 days captured within a given drainage in a given year.

To evaluate river conditions during the successful hatching time, mean daily river discharge and temperatures were analyzed for the period January–July of each year. For the Pascagoula River basin, river data were collected from the U.S. Geological Survey flow-gauging station (02479000) at Merrill (at river kilometer 137; Fig. 1). For the Apalachicola River basin, the data were collected from a U.S. Geological Survey gauging station (02358000) and a Florida Department of Environmental Protection station at Jim Woodruff Dam (at river kilometer 171; Fig. 1). All missing data (usually 1 or 2 daily mean values per data lapse) were compensated with mean datum from before and after the lapse period (<2% of all data).

Overall difference in the timing of successful hatching between rivers was assessed as the modal difference between rivers and with years pooled. To test for significance of this value, we used a randomization procedure to build a null distribution of expected modal differences given the observed hatching times. For 10,000 permutations, 50 observations were randomly drawn (without replacement) for 2 groups (representing the 2 rivers) and a modal difference calculated (by using the sample function in R statistical software, vers. 3.2.3 [R Core Team, 2015]). The significance of the observed modal difference between rivers was assessed by comparison with the distribution of permuted values.

We used logistic regression to assess our ability to predict hatching periods from river conditions. In each of the 7 river-year combinations, we divided the first 182 d into 26 7-d periods. For each period, we calculated standardized (z-score) mean temperature and

¹ Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Summary table of successful hatch windows for Alabama shad (*Alosa alabamae*) and river conditions during those windows in 2005–2009 in the Pascagoula River basin, Mississippi, and in 2007–2008 in the Apalachicola River basin, Florida (only data from within hatch windows are summarized). Minimums and maximums are for daily means during hatch windows.

Year	Number of Alabama shad collected	Julian days of hatching	Hatch window duration (d)	Mean temperature (°C)	Mean discharge rate (m ³ /s)	Minimum temperature (°C)	Maximum temperature (°C)	Minimum discharge rate (m ³ /s)	Maximum discharge rate (m ³ /s)
Pascagoula River									
2005	85	32–58	27	13.1	747.8	12.8	15.8	255.1	1322.4
2006	79	38–73	36	14.9	436.5	10.2	16.5	187.7	914.6
2007	49	38–65	28	14.2	187.9	10.8	21.5	130.5	294.5
2008	57	32–79	48	15.2	422.2	10.7	21.0	166.2	852.3
2009	34	27–54	28	13.9	209.2	11.0	16.1	115.2	535.2
Grand Mean	60.8	33.4–65.8	33.4	14.3	400.7	11.1	18.18	170.9	783.8
Apalachicola River									
2007	52	6–64	58	13.3	592.3	9.8	18.4	385.1	974.1
2008	44	10–67	58	14.5	658.4	9.4	18.8	285.9	1602.7
Grand Mean	48.0	8.0–65.5	58.0	13.9	625.6	9.6	18.60	335.5	1288.4

discharge (m³/s) and the change in temperature and discharge (difference in standardized temperature and flow from the previous period). Each period was scored as if it were part of the hatch window if it overlapped by ≥ 1 d with the established hatch window for that river and year. The logistic regression model (developed by using the glm function in R) predicted hatching from the mean and change in temperature and flow conditions and with year nested within river as factors.

Results

Over the 5 years of this study, 400 juvenile Alabama shad were collected: 304 from the Pascagoula River basin (85, 79, 49, 57, 34 individuals in each year during the period 2005–2009, respectively) and 96 individuals from the Apalachicola River basin (52 and 44 in 2007 and 2008, respectively). Although it was sometimes difficult to find otoliths clear enough to reveal a continuous sequence of rings, daily ring counts were completed successfully on otoliths from 208 Alabama shad from the Pascagoula River basin and from 53 Alabama shad from the Apalachicola River basin. Variability between the repeated counts of rings for individuals was low. Repeated counts typically differed by less than 5 rings; maximum disparity of 18 occurred in 1 otolith and the individual with maximum disparity was removed from analyses. Validation of the ring count was confirmed by the second reader whose counts fell within the range of the original 3 readings for each otolith. In all readable otoliths, the interior rings (around the primordium) remained clear; however, some fish collected later in the year had otoliths that were too thick to be aged accurately.

Daily age validation was conducted by comparing natural, date-specific markers with specific river conditions (MacLellan and Saunders, 1995). We compared the number of rings during low growth periods (high-water events) with the number of days of high water events. This identification of events also allowed date-specific markers to be used for a comparison of ages by year and river. A 1:1 ratio of incremental count versus age was observed—a relationship that is consistent with results from other clupeid species for which daily otolith rings have been validated (Geffen, 1982; Campana et al., 1987; Moksness and Wespestad, 1989).

In the Pascagoula River basin, successful hatch windows began from late January to early February (Julian days 32, 38, 35, 32, and 27 in each year in the period 2005–2009, respectively) and ended from late February to late March (Julian days 58, 73, 65, 79, and 55) (Table 1, Figs. 2–5). For the Apalachicola River basin, the successful hatch windows began in early January (Julian days 6 and 9 in 2007 and 2008, respectively) and ended in early February (Julian days 64 and 67) (Table 1). Median hatching days (midway within each window) in the Pascagoula River basin occurred from early to late February (Julian days 45, 55.5, 50, 55.5, and 41 for the years in the period 2005–2009, respectively) compared with early to mid-February in the Apalachicola River basin (Julian days 35 and 38 for 2007 and 2008). Length of time of a successful hatch window was shorter in the Pascagoula River basin; an average window length was 30.8 d (SD 10.8), compared with 58 d (SD 0.0) in the Apalachicola River basin (Table 1, Figs. 2 and 3). All successful hatches occurred in the first 12 weeks of each year in both river basins. When all years were pooled, the modal hatching time

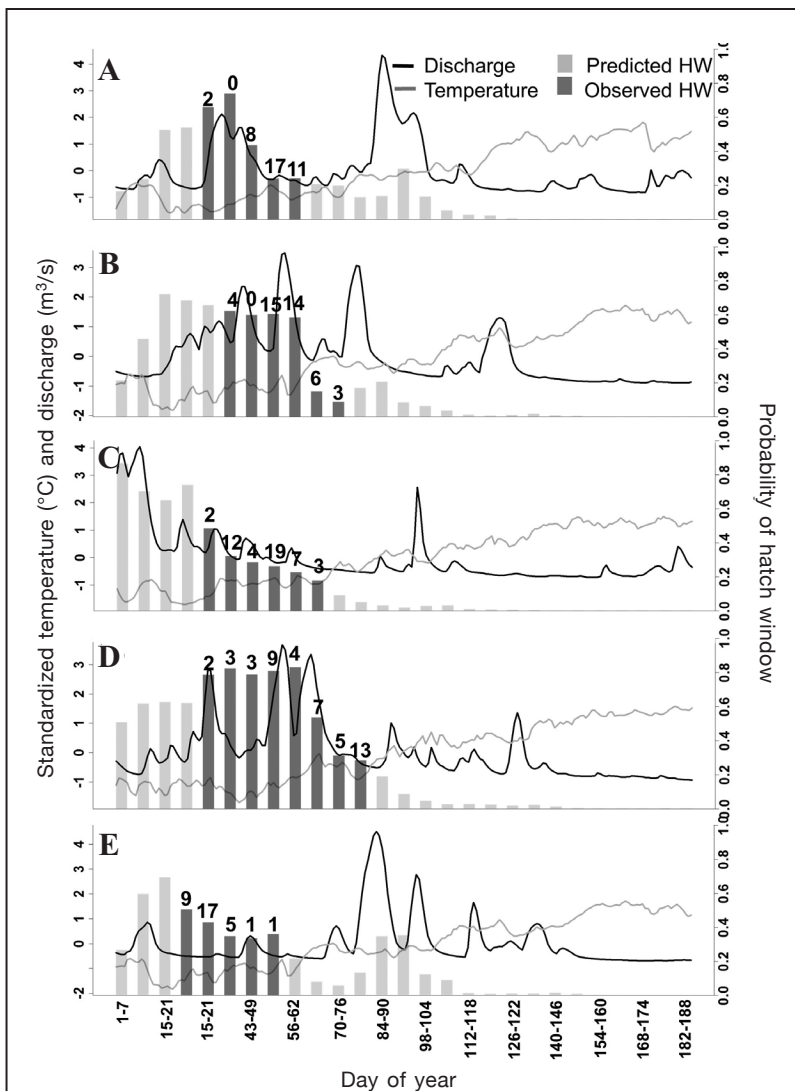


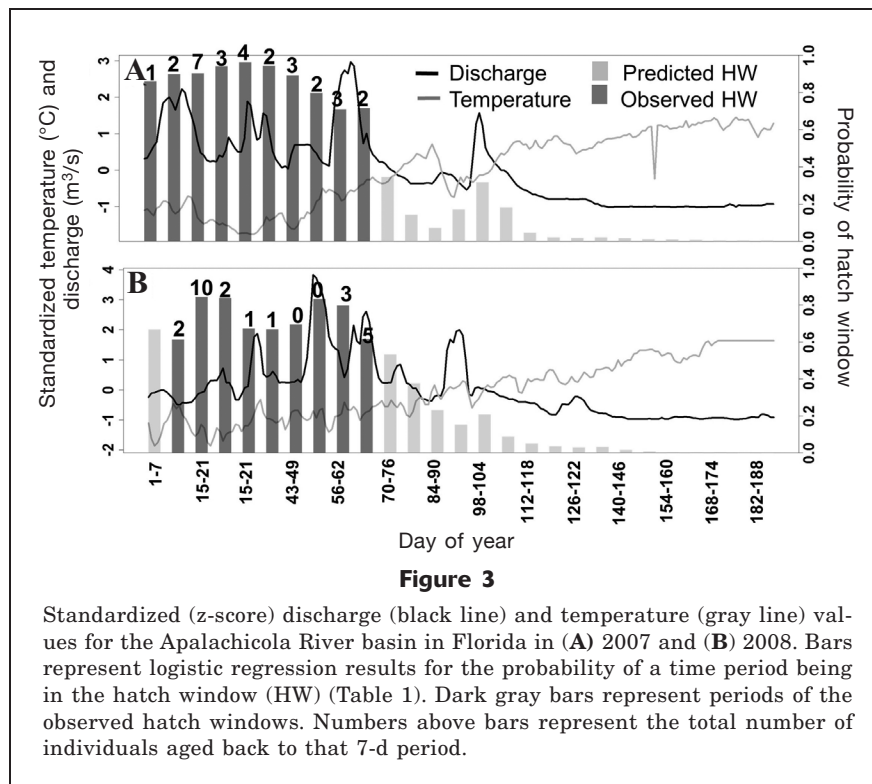
Figure 2

Standardized (z-score) discharge (black line) and temperature (gray line) values for the Pascagoula River basin in Mississippi during (A) 2005; (B) 2006; (C) 2007; (D) 2008; and (E) 2009. Bars represent logistic regression results for the probability of a time period being in the hatch window (HW) (Table 1). Dark gray bars represent periods of the observed hatch windows. Numbers above bars represent the total number of individuals aged back to that 7-d period.

was 33 days later in the Pascagoula River basin (day 52) than in the Apalachicola River basin (day 19). This difference was greater than 99.3% of the permuted values ($P < 0.003$).

The logistic regression allowed us to correctly classify 86% of 7-d periods (with the use of a 50% probability cutoff) as within or outside hatch windows. Mean temperature and discharge were significant contributors to the model and hatch windows occurred during periods of lower temperatures and higher discharges (Table 2). Neither change in temperature, nor

change in discharge, were significant factors, but river as a factor was marginally significant. Averaging across years, grand mean temperature during hatching was 14.3°C in the Pascagoula River and 13.9°C in the Apalachicola River, with average rates of discharge during hatching of 400.7 m³/s and 625.4 m³/s, respectively (Table 1). In general, predicted and observed hatch windows were similar in the Apalachicola River, whereas observed hatching in the Pascagoula tended to be 2–3 weeks later than that predicted by the logistic regression.



Discussion

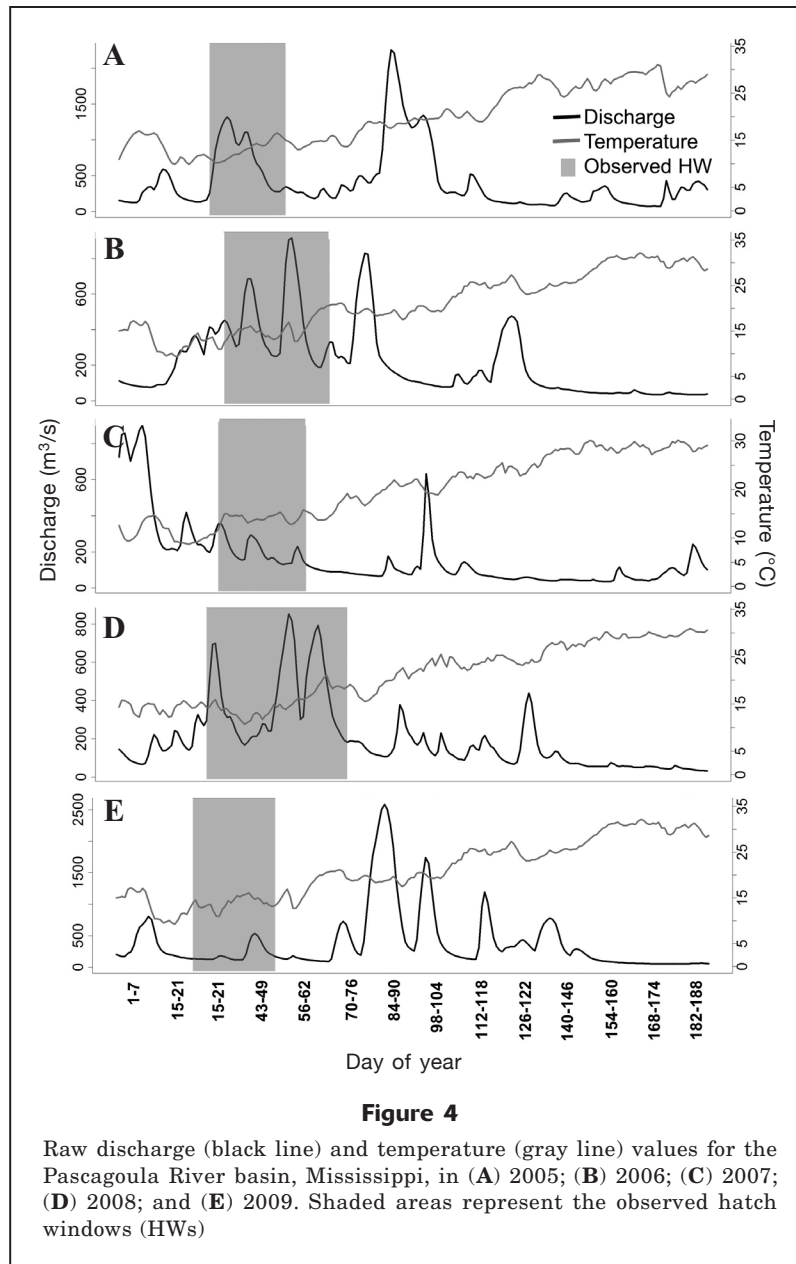
Hatch windows for Alabama shad were consistently longer and earlier in the Apalachicola River basin than in the Pascagoula River basin. There are 3 possible explanations for these observed differences: 1) the cues, or timing of cues, that trigger spawning runs or acts of spawning differ between these river basins; 2) spawning runs and hatching take place at the same time, but in the years sampled, differences in recruit survival gave the appearance of significantly different hatch windows; or 3) the fish populations are different in the river basins, and they respond differently to cues. Previous work on population genetics of Alabama shad has indicated some drainage-level fidelity that would allow for interpopulation variability in the timing of spawning runs (Bowen, 2005; Bowen et al., 2008). Other, unmeasured variables may also play key roles as migration or spawning cues. It should be noted that a lower sample size in the Apalachicola River basin (2 versus 5 years sampled) could have contributed to differences. However, annual variation in timing of hatch windows within the drainages was clearly less than the variation in timing of hatch windows across drainages.

The distribution of successful hatching dates from each drainage and year indicates that prolonged or multiple spawning events occurred (Figs. 2 and 3). The overall lengths of the windows for successful hatching from the Apalachicola River basin were comparable with lengths of hatch window documented for Ameri-

can shad on the St. Lawrence River, between Canada and the United States (Maltais et al., 2010). In general, in our study, hatch windows of Alabama shad coincided with spring floods that had above-average flows and low, but increasing water temperatures. Spawning migrations of American shad are also linked to river temperature (Leggett and Whitney, 1972; Quinn and Adams, 1996). The Apalachicola River is impounded, and the effects of that control have the potential to artificially influence temperature and flow. The buffering of these parameters by the impoundment would be expected to prolong spawning windows—an outcome that would be consistent with our logistic regression results, which indicated that longer periods of lower temperatures were associated with successful spawning.

In contrast to our findings, previous studies by Laurence and Yerger (1967) and Mills (1972) have reported that spawning temperatures fall in a range of 19–22°C. However, Ely et al. (2008) found adult Alabama shad present on the spawning grounds when temperatures were similar (13.1–15.2°C) to temperatures found in other studies (Laurence and Yerger, 1967; Mills, 1972) during the hatch windows that we detected. We found that mean daily water temperatures of 19–22°C did not occur until late March and April, after 96% of all documented successful hatching was complete.

Mean temperature and discharge were the most important variables for predicting hatch windows. With these variables, hatch windows were found to be similar in the 2 basins, but, in general, observed hatch windows were later than predicted in the Pascagoula River



basin. This result indicates that temperature and discharge conditions in the Pascagoula River basin may be suitable when there is either limited spawning or recruitment earlier in the year. It should be noted that we cannot rule out the possibility that spawning in one or both rivers occurs over longer periods and that the differences in successful hatch timing among drainages reflect differences only in the time of successful recruitment. It is also possible that other cohorts of Alabama shad were present but not collected, or represented in the analysis; we deem this possibility unlikely given the extensive sampling in the drainages and the absence of outliers to the observed hatch windows. Size data (Mickle et al., 2010) also are consistent with size

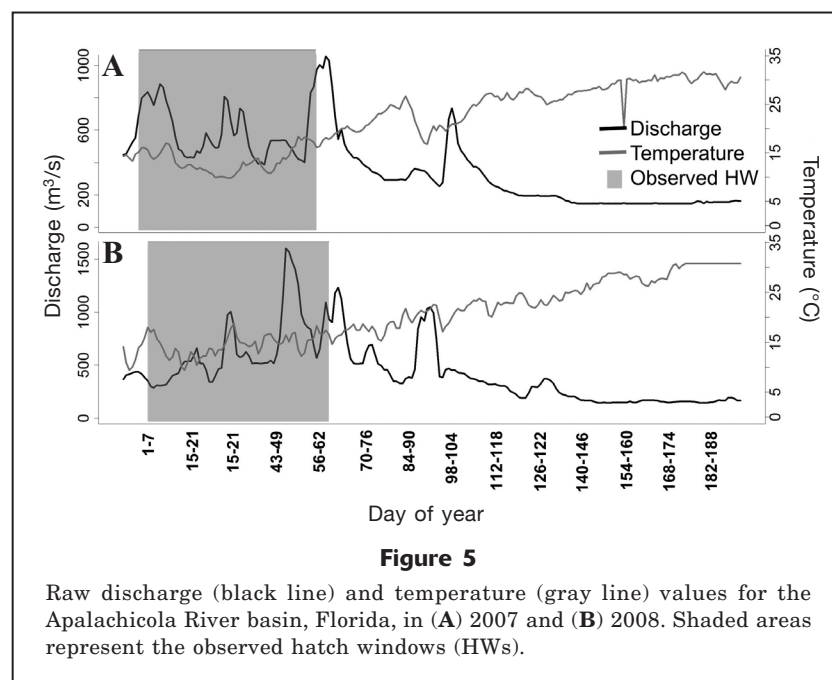
of fish when hatching occurs in early spring (no smaller individuals [<55 mm TL] were sampled later in the year than July) and growth occurs through the summer and early fall. Therefore, drainage differences were more likely due to other unmeasured variables that might have contributed to the reduced hatch window or successful recruitment in the Pascagoula River basin.

The data regarding differences in successful hatch windows provide valuable information but do not allow for definitive conclusions on the mechanisms at work. Additional spatial and temporal data are needed to elucidate these mechanisms. Unfortunately, the Alabama shad is a species in decline and sample sizes are likely to be too small, or populations judged too imper-

Table 2

Results from the logistic regression in predicting hatch windows from mean and change (Δ) in standardized temperature and discharge. Significant predictors (chi-squared statistic) are shown in bold font. df=degrees of freedom.

	df	Estimate	Standard error	χ^2	P
Discharge	1	0.576	0.260	4.91	0.027
Δ Discharge	1	0.121	0.261	0.64	0.645
Temperature	1	-2.490	0.463	51.89	<0.001
Δ Temperature	1	-1.207	0.734	2.76	0.097
River	1	-1.109	0.815	0.972	0.061
River*Year	5			1.53	0.909



iled, to allow for intensive adult sampling for migration analyses. The initial experimental design of this study included a comparison of samples from inland drainages in Arkansas and Missouri, where spring increases in water temperature would lag behind those in Gulf of Mexico drainages. However, 3 years of sampling during August within these systems, at sites where fish had been collected in earlier years, yielded no juvenile fish.

Within impounded water systems, flow regimes may be managed through water releases to mimic natural cues and allow populations to complete their spawning runs. Castro-Santos and Letcher (2010) found that flow-regulated systems altered spawning success and migration timing of American shad both upstream and downstream. Other riverine species have also been affected adversely by altered flow regimes. Manipulated flows physically altered habitats, resulting in decreased

diversity of fish species (Freeman et al., 2001). Altering systems in which Alabama shad reproduce may add stressors to migrating juveniles and adults. Unfortunately, the drainages along the coast of the northern Gulf of Mexico are also areas that have been rapidly developed over the past 75 years and that development may ultimately lead to further extirpations of this species (Turner, 1990).

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