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Habitat use of age 0 Alabama shad in the Pascagoula River drainage, USA

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Abstract –Alabama shad (*Alosa alabamae*) is an anadromous species that spawns in Gulf of Mexico drainages and is a NOAA Fisheries Species of Concern. Habitat degradation and barriers to migration are considered contributing factors to range contraction that has left just the Pascagoula River drainage population in Mississippi. We studied juvenile life history and autecology in three rivers within the drainage. We collected fish, habitat and physicochemical data in three habitat types (sandbar, open channel and bank) from June to October 2004–2006. Sandbar habitat was favoured by smaller individuals early in the year. Catch per unit effort (CPUE) decreased through the summer as larger fish began occupying bank and open channel habitat. The most parsimonious model of abundance included year and river variables, while patterns of presence and absence were best explained by river, habitat type and physiochemical variables. While all three rivers in the drainage contained Alabama shad, fish were less abundant and had lower condition values in the Chickasawhay River. Earlier work suggested the Alabama shad may gradually move downstream towards the Gulf of Mexico in their first year. However, we found no evidence of this and captured large fish high in the drainage late in the year.

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Key words: Alabama shad; Alosa; anadromous; habitat use

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Introduction

Anadromous life cycles feature obligate movement through various ecosystems, making anadromous species vulnerable to anthropogenic habitat fragmentation or degradation in any of the required ecosystems. Habitat degradation, fragmentation, channelization, flow regulation and declining water quality all contribute to the imperilment of fish species in North America and elsewhere (Dynesius & Nilsson 1994; Warren et al. 2000). Due to their life cycle requirements, many anadromous fishes are particularly susceptible to several of these disturbances. To effectively manage declining anadromous fish populations, information is needed about all life history stages, including habitat use by age 0 fish.

The shad sub-family (Alosinae) contains seven genera and 31 species that are among the world's most commercially important fishes (Waldman 2003). Shad occur on all continents except Australia and Antarctica and are mostly anadromous (Berra 2001; Waldman 2003). In rivers draining the Atlantic Slope of North America, American shad (*Alosa sapidissima*) have supported important commercial and recreational fisheries for over 100 years (McPhee 2002). American shad have been extensively studied, with successful stock enhancements in many northern rivers (Hendricks 2003). In contrast, relatively little is known about the American shad's sister species (Bowen et al. 2008), the Alabama shad (*Alosa alabamae*). Alabama shad are not as commercially important as American shad and have received little research attention despite substantial range contractions. The freshwater life stages have not been studied in depth, and there is virtually no published data on marine life stages. Conservation of this species will require the

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identification and preservation of essential fish habitat necessary to sustain early life stages (Benaka 1999).

Range and autecology

Alabama shad are a NOAA Fisheries Species of Concern (Cain 2004) and are considered endangered by the IUCN (Meadows et al. 2008). Huntsman (1994) described Alabama shad populations as ‘reduced’ and ‘vulnerable to extinction’. The species experienced substantial range contraction over the last six decades, resulting in its extirpation from the northern and eastern reaches of its historical distribution (Fig. 1) (Coker 1930, Douglas 1974, Etnier & Starnes 1993; Boschung & Mayden 2004). The species disappeared from the Pearl River, Mississippi (MS), in 1980s, leaving only the Pascagoula River population in the state (Gunning & Suttkus 1990). The major factor contributing to the decline is large numbers of impoundments blocking upstream migration to spawning grounds and loss of putative spawning habitat. Other potential contributing factors include habitat degradation, such as declining water quality and increased siltation (Mettee & O’Neil 2003).

The spawning ecology of Alabama shad has been documented in several river drainages. Spawning is thought to occur in swift water over sandy substrate, gravel shoals, or limestone outcrops, when water temperatures range from 10 to 22 °C (Laurence & Yerger 1967; Mills 1972; Fox et al. 2000). Spawning individuals range in age from 1 to 5 years for males and 2 to 6 years for females in the Choctawhatchee River, Alabama and Florida (Mettee & O’Neil 2003). Mills (1972) found that 25–38% of the adult Alabama shad in the Apalachicola River, FL, were repeat spawners. Alabama shad spawn from January to April in southern drainages (Laurence & Yerger 1967; Mills 1972) and from May to June in northern drainages (Coker 1930; Burr et al. 1996).

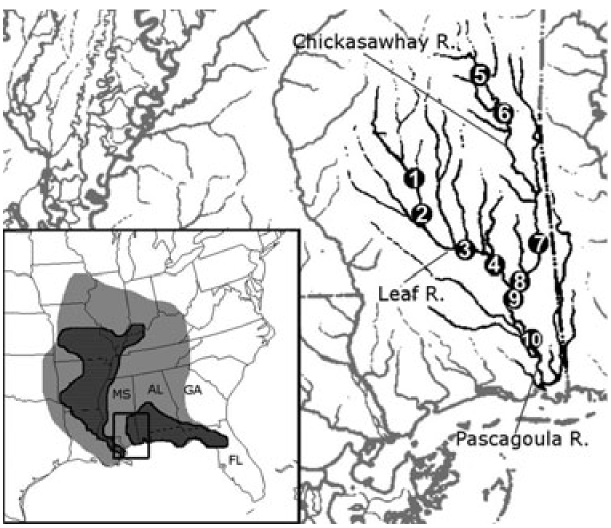

Fig. 1. Sampling sites in the Leaf (#1–4), Chickasawhay (#5–8) and Pascagoula (#9–10) rivers in southeastern Mississippi (MS), USA. The inset map indicates historical (light shaded area) and current (dark shaded area) distributions of Alabama shad as well as a box around the Pascagoula River drainage.

Juvenile Alabama shad spend the summer and fall in their natal drainage before returning to the Gulf of Mexico in late fall or winter (Barkuloo et al. 1995). Mills (1972) identified three putative spawning cohorts originating from different locations in the Apalachicola River drainage. Based on length-frequencies of age 0 fish, Mills (1972) suggested that fish begin leaving the river in August and continue to emigrate through November. This timeline has fish leaving natal rivers at sizes ranging from roughly 105 to 125 mm fork length. However, collection of age 0 fish in the lower Apalachicola River as late as December, led Laurence & Yerger (1967) to propose that age 0 fish slowly descend rivers throughout the summer, leaving spawning grounds in spring and arriving in the Gulf of Mexico in late fall and winter. Several studies have examined juvenile Alabama shad use of shallow (i.e., wadeable) habitats, but no studies have explored their use of deeper habitats.

The purpose of this study was to document freshwater habitat use by age 0 Alabama shad in an unimpounded river system, the Pascagoula River drainage, MS. Our objectives were to characterise patterns in abundance, presence/absence, length and condition of Alabama shad by spatial (rivers and habitat type), temporal (years and months) and physicochemical variables.

Based on characteristics of Alabama shad spawning habitats in the Apalachicola River (Laurence & Yerger 1967; Mills 1972) and spawning habitat requirements for American shad (Emmett et al. 1991; Hightower & Sparks 2003), we predicted that Alabama shad in the study system would spawn in the upper reaches of the Leaf and Chickasawhay rivers. The Pascagoula River is generally deeper, with lower current velocities and, thus, was not predicted to contain suitable spawning habitat for the species.

Study system

The Pascagoula River drainage is the largest unimpounded river system in the contiguous United States (Dynesius & Nilsson 1994). Two large tributaries, the Leaf and Chickasawhay rivers, join to form the Pascagoula River approximately 105 km from the coast (Fig. 1). The drainage lies entirely within the Gulf Coastal Plain province, and its large rivers are characterised by sinuous channels dominated by large sandbar, open channel and steep bank habitats, the latter typically containing large woody debris. Land use within the drainage consists of forestry and agriculture, with limited industrial and urban development.

The Leaf and Chickasawhay rivers differ from one another in a number of ways. The Leaf River is more sinuous and has a larger floodplain, whereas the Chickasawhay River has a more confined channel along the upper segments. Discharge is typically lower in the Chickasawhay River than in the Leaf River. Mean annual discharge is 99.3 $m^3 \cdot s^{-1}$ [1.24 coefficient of variation (CV)] in the Chickasawhay River, 125.5 $m^3 \cdot s^{-1}$ (1.47 CV) in the Leaf River and 306.0 $m^3 \cdot s^{-1}$ (1.2 CV) in the Pascagoula River (data from USGS gauging stations 02478500, 02475000 and 2479310, respectively). Of the three rivers studied, the Leaf River is shallowest and tends to have lower, current velocities and higher, water clarity and conductivity (Appendix S1).

Methods

We sampled fish monthly at 10 sites (Fig. 1) within the Pascagoula drainage from June to October of 2004, 2005 and 2006. Sites were chosen based on boat access and the presence of three dominant habitat types within the drainage: gradually sloping sandbars, open channels and steep banks with large woody debris (hereafter referred to as sandbar, channel and bank habitats). September and October samples were pooled because unusual drought and hurricane conditions limited electrofishing boat access late in the summers of 2005 and 2006. Sites were spaced longitudinally throughout the basin to allow detection of any gradual, downstream migration by juvenile Alabama shad as the season progressed. During each site visit, we sampled fish and measured physicochemical variables separately in all three habitat types. Physicochemical measurements included water temperature, dissolved oxygen ($mg \cdot l^{-1}$, DO), conductivity, pH, water clarity (Secchi depth), depth and current velocity at the surface and subsurface (see Mickle 2006 for details). Current velocity and depth were measured multiple times along transects at the upstream and downstream portions of each habitat. All current velocity and depth values are represented as means for both upstream and downstream transects. We reduced the dimensionality of the physicochemical data (DO, pH, temperature, depth, Secchi depth, current velocity at upstream and downstream edge of the habitat, and conductivity) with a principle components analysis (PCA).

Fish were sampled with a Smith-Root™ SR-14EB electrofishing boat at 5000 watts and 16 A. Pulses-per-second varied from 7.5 to 120, depending on water conditions, but were 120 for most electrofishing runs. Electrofishing effort was typically 400 s for each habitat type in each site. Sand bars and banks averaged 550 m in length and could be sampled effectively in 400 s. Some of the larger sand bars were electrofished an additional 50–75 s. Boat electrofishing was the only means of standardising effort across all three habitat types because some were typically deep and fast flowing (e.g., July bank samples averaged

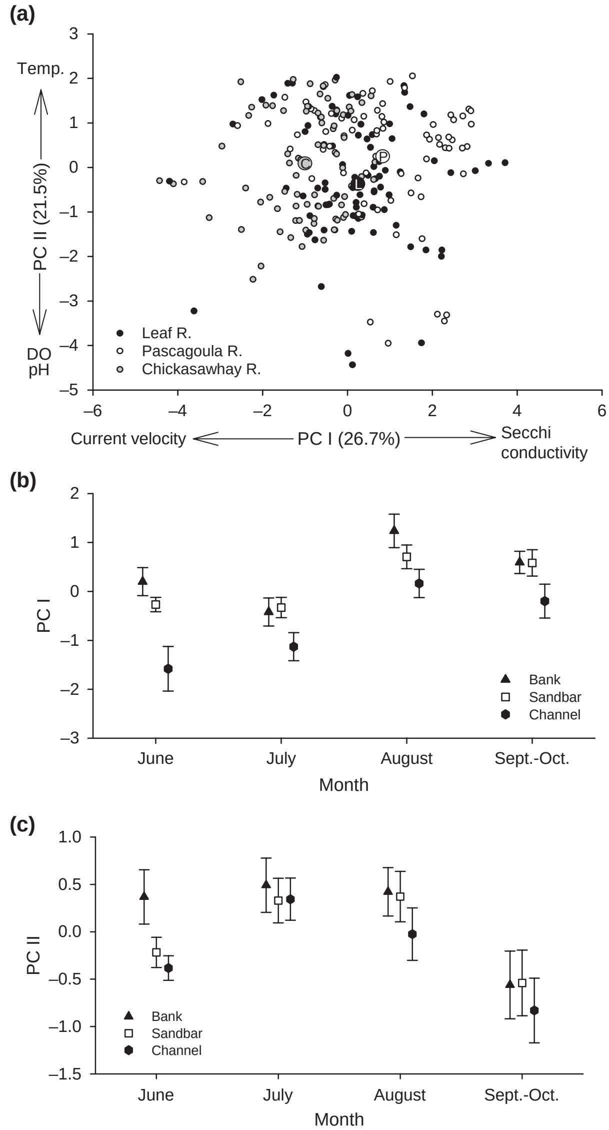

Fig. 2. Principal components analysis (PCA) of eight physicochemical variables measured in each sample. (a) Samples represented by individual points. Points are shaded by river, and the centroid for each river is represented by a large circle labelled as L (Leaf), C (Chickasawhay) or P (Pascagoula). Variables with loadings >0.40 are listed on the appropriate axis with arrows indicating the direction of increased value for that variable. (b) Mean (±1 SE) score on PCA axis 1 by month and habitat (pooling data among rivers and years). (c) Mean (±1 SE) score on PCA axis 2 by month and habitat (pooling data among rivers and years).

3.17 m deep with a water velocity of 0.52 $m \cdot s^{-1}$, Appendix S1). This sampling approach was effective for a number of species, yielding reliable community data (Schaefer et al. 2006).

Abundance was quantified as catch per unit effort [(CPUE) fish caught per 400 s of electrofishing effort]. Alabama shad were weighed (wet weight, to the nearest 0.01 g) and measured [standard length (SL), to the nearest mm] in the field before being individually tagged and placed in 95% ethanol. All Alabama shad were deposited in The University of Southern Mississippi Museum of Ichthyology. We used Fulton's index (wet weight per SL^3) as a measure of fish condition. For analyses, fish length and condition index were averaged across individuals within each sample (site, habitat type and date). Standard deviations (SD) within a sample were low, with a maximum SD of 6.93 and 0.068 for length and condition, respectively. We used Akaike's Information Criterion adjusted for small sample size (AIC_c) to assess the quality of competing candidate models for predicting CPUE, shad presence or absence, mean length and mean condition of juvenile Alabama shad in samples (Burnham & Anderson 2002). Models with low ΔAIC_c and high Akaike weights (w_i) have the best combination of parsimony (fewer parameters) and fit (accuracy) for the data. Candidate models were constructed based on expected spatial and temporal patterns seen in other similar systems and earlier work on Alabama shad. Variables were categorised as spatial (river and habitat), temporal (year and month) and physicochemical (PCA axis scores, PC1 and PC2). Within each of these categories of variables, we created three candidate models [e.g., spatial models included river only, habitat only, and river, habitat, and their interaction term (latter model noted as river*habitat in tables), Table 1]. Sixteen additional candidate models combined one or more variables from two categories (spatial + temporal, spatial + physicochemical, temporal + physicochemical). The last two models were a null model (no variables) and a global model (all variables). Three way and higher interaction terms were excluded from all models because they would be problematic to interpret. Candidate models were applied to each response variable (CPUE, presence/absence, mean length and mean condition). For each set of models, we only interpreted those with a w_i >10% of the highest w_i (Burnham & Anderson 2006, Grossman et al. 2006).

Results

From a total of 235 samples (77, 82 and 76 samples in the Chickasawhay, Leaf and Pascagoula rivers, respec-

Table 1. Candidate models used in AIC_c model selection for all four response variables (presence/absence, CPUE, mean length and mean condition). Third order and higher interaction terms were excluded from all models. *K* indicates the number of model parameters.

Model	Number	Variables	*K*	Hypotheses – presence/absence, abundance, size and condition of Alabama shad are best explained by
Null	1	None	2	None of the measured variables.
Temporal	2	Month	5	Differences at the fine temporal scale (monthly), large temporal
	3	Year	4	scale (yearly), or a combination of both.
	4	Month*Year	11	
Spatial	5	Habitat	4	Differences at the fine spatial scale (channel, bank and sandbar habitat),
	6	River	4	large spatial scale (Chickasawhay, Pascagoula and Leaf rivers) or a
	7	Habitat*River	9	combination of both.
Physicochemical	8	PC1	3	Sample differences in physicochemical variables. PC1 is primarily current
	9	PC2	3	velocity, Secchi depth and conductivity. PC2 is primarily temperature,
	10	PC1*PC2	5	DO and pH.
Temporal + spatial	11	Month*Habitat	10	Fine scale temporal (monthly) and habitat variability.
	12	Year*River	9	Large scale temporal (yearly) and river variability.
	13	Year + Month*Habitat	12	Fine spatial scale and large temporal scale variability.
	14	Month + River*Year	12	Large spatial scale and fine temporal scale variability.
Temporal + physicochemical	15	Month*PCl	9	Fine scale temporal and one physicochemical axis variables.
	16	Month*PC2	9	
	17	Year*PC1	7	Large scale temporal and one physicochemical axis variables.
	18	Year*PC2	7	
	19	Month*PCl*PC2	14	Large or fine scale temporal and both physicochemical axis variables.
	20	Year*PCl*PC2	11	
Spatial + physicochemical	21	Habitat*PCl	7	Fine spatial scale and one physicochemical axis variables.
	22	Habitat*PC2	7	
	23	River*PCl	7	Large spatial scale and one physicochemical axis variables.
	24	River*PC2	7	
	25	Habitat*PCl*PC2	11	Large or fine scale spatial and both physicochemical axis variables.
	26	River*PCl*PC2	11	
Global	27	All	28	Combination of all temporal, spatial and physicochemical variables.

tively), we collected 133 juvenile Alabama shad. Alabama shad were collected in all three habitat types, in all months (June–September/October), and at 8 of 10 sampling sites. The majority of shad were captured in the Leaf (66) followed by the Pascagoula (55) and Chickasawhay (12) rivers (Appendix S1).

The first two axes of the PCA accounted for 48% of the variability in the eight physicochemical parameters measured for each sample (Fig. 2a). Current velocity, Secchi depth and conductivity had the highest loadings (>0.4) on the first axis (26.7% of variance), and pH, temperature and DO loaded on the second axis (21.5% of variance). Physicochemical differences among the three habitat types were subtle, with most of the variability among samples explained by differences among rivers and months (Fig. 2b,c). The three rivers clustered along the first axis (mean PC 1 scores of −1.01, 0.22 and 0.78 for the Chickasawhay, Leaf and Pascagoula rivers, respectively), largely reflecting different hydrologic properties. Samples from the Chickasawhay and Leaf rivers generally had greater current velocities (Appendix S1). August bank samples were typically low flow with higher conductivity (Fig 2b), while September–October channel samples were cooler with higher DO (Fig. 2c). Descriptive statistics for all physicochemical variables are summarised by river, month and habitat type in Appendix S1.

Alabama shad were captured in 43 of the 235 samples, and five of the models predicting presence/absence were interpretable (Table 2). While none of the models were particularly strong (w_i ranged from 0.034 to 0.28), the three strongest contained the habitat variable, and four contained PC2. Alabama shad were most often captured in sandbar habitats and in bank habitat in the Leaf River (Fig. 3). Pooling rivers and months, Alabama shad were captured in 9.8% of bank samples, 16.3% of channel samples and 26.1% of sandbar samples (Appendix S1). Overall, samples with Alabama shad had significantly lower PC2 scores (lower temperature and higher DO and pH; ANOVA $F = 9.21$, $P < 0.003$) than sites without (mean PC2 scores: present = −0.54 ± 0.24 SE, absent = 0.12 ± 0.09 SE). Abundance (CPUE) was best explained by the model containing river and year variables. Twelve Alabama shad were captured in 77 Chickasawhay samples (CPUE 0.15), 55 captured in 76 Pascagoula samples (CPUE 0.71) and 66 captured in 82 Leaf River samples (CPUE 0.73). CPUE ranged from 0.38 in 2004 to 0.50 in 2005 and 1.07 in 2006.

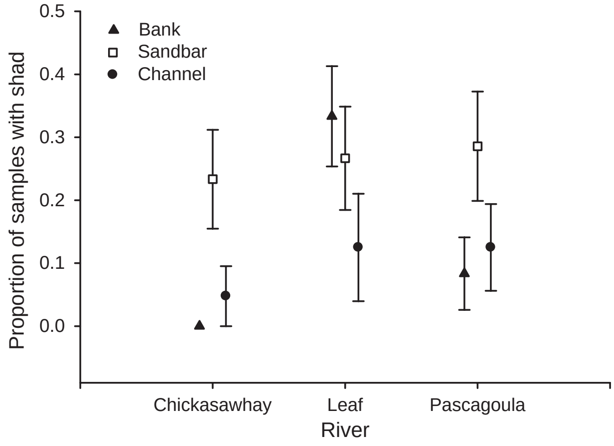

Fig. 3. Proportion of samples (±1 SE), by river and habitat type, in which juvenile Alabama shad were collected.

Alabama shad increased in size over the summer from a mean of 47.0 mm (±2.94 SE) in June to 101 mm (±4.44 SE) in October. All three interpretable models of mean size included both temporal variables (year and month, Table 2). The two strongest models (w_i = 0.392 and 0.310) also included either habitat or river variables. Fish in sandbar samples were significantly (ANOVA $F = 11.89$, $P < 0.001$) smaller (65.0 mm SL ± 4.18 SE) than those in channel and bank habitats (90.8 mm ± 4.62 SE and 95.1 mm ± 4.42 SE, respectively; Fig. 4). There was no significant difference in Alabama shad length among rivers.

Mean condition was best described by a single interpretable model (w_i = 0.93) containing month,

Table 2. Interpretable models, AIC_c statistics and weights (w_i) for all four response variables. Only models with a weight >10% of the best model were interpreted and listed. Model numbers match list in Table 1.

Response variable	#	Variables	AIC_c	ΔAIC_c	w_i
Presence/absence	7	Habitat*River	217.50	0.00	0.282
	25	Habitat*PCl*PC2	218.50	1.00	0.173
	22	Habitat*PC2	218.80	1.40	0.143
	9	PC2	219.20	1.80	0.116
	24	River*PC2	221.70	4.30	0.034
Abundance (CPUE)	12	Year*River	865.80	0.00	0.602
	7	Habitat*River	868.80	3.00	0.132
Mean length	13	Year + Month*Habitat	348.70	0.00	0.392
	14	Month + River*Year	349.20	0.50	0.310
	27	All	350.40	1.70	0.169
Condition	14	Month + River*Year	−23.30	0.00	0.934

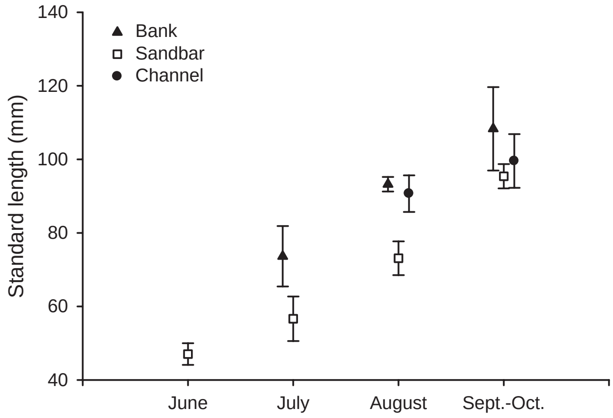

Fig. 4. Mean standard length (±1 SE), by month and habitat type, of juvenile Alabama shad collected.

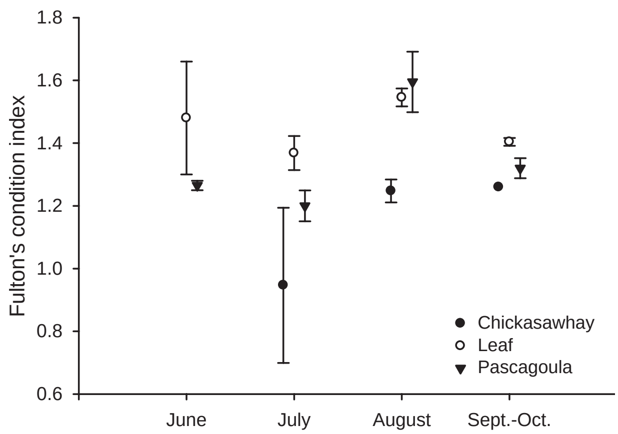

Fig. 5. Mean Fulton's condition index (±1 SE), by month and river, of juvenile Alabama shad collected.

year and river variables (Table 2, Fig. 5). Fish from the Chickasawhay River had significantly (ANOVA $F = 8.77$, $P < 0.001$) lower condition indices than those from the Pascagoula and Leaf rivers (1.13 ± 0.099 in the Chickasawhay vs. 1.36 ± 0.056 and 1.46 ± 0.027 in the Pascagoula and Leaf rivers, respectively). While fish condition did not differ significantly among years (ANOVA $F = 0.10$, $P <$ 0.903), there were differences among months ($F = 4.64$, $P < 0.007$) as fish had higher mean condition indices in August (1.49 ± 0.043 SE) compared to June (1.37 ± 0.096), July (1.22 ± 0.073) or September/October (1.36 ± 0.022).

Discussion

Habitat type and physicochemical variables were the best predictors of Alabama shad presence, while river and year variables were the best predictors of abundance (CPUE). Overall, fish were most often found on sandbar habitat and in bank habitat in the Leaf River (Fig. 3, Appendix S1). Sandbar habitat was also favoured by smaller individuals early in the year. CPUE on sandbars was highest in June (no captures in June bank or channel samples, Fig. 4) and declined over the summer. In contrast, CPUE in channel and bank habitat increased over the summer (Appendix S1). These data indicate there is an ontogenetic shift towards bank and channel habitat as fish grow through the summer. Capturing more shad on sandbar habitat could be due to greater abundance of smaller juveniles early in the spring. However, smaller fish avoided channel and bank habitat entirely, and in months where shad were sampled in all habitats, fish from channel and bank habitats tended to be larger (Table 2, Fig. 4).

The Leaf and Pascagoula rivers provided more productive habitat for Alabama shad than did the Chickasawhay River. We collected fewer fish in the Chickasawhay River, and they had lower condition indices than those from the other rivers (Fig. 4, Appendix S1). There is likely some spawning in the Chickasawhay River, as most of the juveniles sampled were small and probably did not move upstream to the sampled locations. However, CPUE was very low later in the summer indicating that these fish either did not survive the early summer or moved downstream, possibly into the Pascagoula River. The Leaf and Pascagoula rivers are shallower with more abundant sandbar habitat compared with the Chickasawhay River that has a more confined channel, higher current velocities and less sandbar habitat (Fig. 2a).

The reasons for the observed ontogenetic habitat shift from sandbars to deeper waters are unknown, but could include release from predation pressure, changes in food availability, foraging needs, or thermal ecology. Shifts in habitat use by prey species, once they exceed predator gape limitations, are well-documented (Byström et al. 2003). Potential predators in our system (e.g., *Micropterus* spp., caught as bycatch, Schaefer et al. 2006) were most abundant in the open channel and bank habitats avoided by the smaller fish. We cannot fully assess the role of diet in the habitat shifts until we learn more about the feeding ecology of juvenile Alabama shad. Buchanan et al. (1999) found benthic invertebrates in stomachs of 10 juvenile Alabama shad, and Ross (2001) stated that age 0 fish are opportunistic feeders, eating fish, dipterans, and copepods. We observed age 0 fish feeding at the surface, indicating they feed in part on terrestrial or emerging aquatic insects. A shift away from sand bars might be expected once fish are large enough to hold position and surface-feed in faster flowing habitats. Finally, the shift in habitat was not absolute, as some of the largest fish sampled late in the year were caught on sandbar habitats in the Pascagoula River.

Small juvenile Alabama shad were collected at the downstream-most sites in the drainage in early spring, indicating that spawning may also occur in the Pascagoula River. Given what is known of spawning habitat; however, this seems unlikely. We think it more likely that some larvae from the Chickasawhay and Leaf Rivers drifted downstream during high spring flows and remained in the Pascagoula River for the summer.

We found no evidence of a gradual downstream migration of juvenile Alabama shad throughout the summer. We collected small fish (45 mm mean SL) in June at downstream sites (Fig. 1, sites 3, 4, and 10) in the Leaf and Pascagoula rivers and large fish (141 mm mean SL) in September/October at some upstream sites in the Leaf River (Fig. 1, sites 1 and 2). Juvenile Alabama shad were present in the upper Leaf River as late as December 5, 2005, but early spring and early summer sampling yielded no Alabama shad >20 mm, indicating that the fish did not overwinter in fresh water. Most studies indicate Alabama shad migrate to the marine environment from September to December (Laurence & Yerger 1967; Mills 1972; Pfleiger 1975; Etnier & Starnes 1993; Buchanan et al. 1999). Mills (1972) suggested emigration from the Apalachicola River was triggered by size (>125 mm fork length) for early cohorts and by low water temperatures for later cohorts. However, he sampled age 0 fish only by seining, and, thus, could have misinterpreted a shift to deeper habitats by large age 0 fish as emigration from the system. We found that within the Pascagoula drainage, fish began to emigrate between 140 and 160 mm and as late as December. A better understanding of when the transition between ecosystems occurs and what factors influence it would be useful for the conservation of this species, especially in drainages with controlled discharge (e.g., Buchanan et al. 1999).

No studies have examined Alabama shad thermal preferences or tolerances, but other members of the Alosinae sub-family are sensitive to high temperatures (e.g., lethal temperature for the alewife *Alosa pseudoharaengus* is 25 °C; Beitinger et al. 2000; McCauley & Binkowski 1982). Summer conditions in the Pascagoula River drainage typically feature decreasing discharge and increasing temperatures through August. The maximum water temperature measured during this study was 32.6 °C. In the drainage, both Gulf sturgeon (*Acipenser oxyrinchus desotoi*) and striped bass (*Morone saxatalis*) seek out coolwater refugia during the warmest periods (Jackson et al. 2000; Heise et al. 2005). Alabama shad movement off of shallow sand bars to deeper water in the summer may be a means of minimising thermal stress. Juvenile Alabama shad have been sampled in water as warm as 32 °C (Buchanan et al. 1999; P. Mickle, unpublished data). With one exception (Pascagoula River in July), in all river-habitat and month-habitat combinations the mean temperature in samples with shad was lower than those without shad (Appendix S1). These differences were usually small except in August, when temperatures were highest. In August, samples with shad were typically ~2 °C cooler than similar samples without shad. For example, Pascagoula River samples in August with shad averaged 29.08 °C (±1.66 SE) while those without were 31.09 °C (±0.22 SE).

In early summer, the mean length of Alabama shad varies across the range (Arkansas to Florida), but length differences disappear by mid-summer (Mills 1972; Buchanan 1999; Buchanan et al. 1999; this study). Mean length was highly variable among years (year was a component of all interpretable models of SL, Table 2) within both the Pascagoula and Ouachita (Arkansas) river systems (Buchanan 1999; Buchanan et al. 1999). High variability in early summer lengths among rivers could be due to small sample sizes, variations in spawn timing and growth rates, size-selective mortality, differences in thermal regimes or a variety of other stochastic variables. Additional research is needed to assess factors influencing summer growth.

Management and conservation plans for Alabama shad should ensure that the dynamic processes responsible for creating and maintaining large sand bar habitats and woody debris accumulations along steep banks are preserved and that connectivity and fish passage are maintained throughout drainages. We recommend further study in the Pascagoula River and other drainage systems to identify spawning locations and habitat use by age 0 fish and to discern the potential importance of thermal refugia to Alabama shad.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Number of samples, total Alabama shad catch, CPUE (# fish per 400 s), Fulton's condition index and mean ± 1 SE for all physicochemical variables in samples with and without shad. Top portion of table presents data by river and month, bottom portion by habitat type and month.

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