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Population Characteristics of Paddlefish in Two Tennessee-Tombigbee Waterway Habitats

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Abstract.—Paddlefish *Polyodon spathula* vanished from areas of the upper Tombigbee River basin in Mississippi and Alabama during the 1950s, long before channelization and damming associated with construction of the Tennessee-Tombigbee Waterway (TTW) were completed in 1984. This study was undertaken to assess distribution and population dynamics of any remaining stock. Paddlefish were not captured in upstream impoundments, but an unexploited remnant population was located in the downstream impoundment: Demopolis Lake, Alabama. Paddlefish in Demopolis Lake were characterized by a population density of 2.6 fish/ha, high growth rate relative to more northern populations, and natural annual mortality rate (A = 0.406) similar to other southern populations. Two wintering habitats (cutoff bendways) were heavily utilized by paddlefish. Large males primarily inhabited the more lotic bendway while females and small males were more common in the more lentic bendway, indicating differential importance of habitats among demographic groups. The restricted distribution of TTW paddlefish and demographic differences between habitats suggest that areas heavily utilized by paddlefish should be protected from further degradation. Sedimentation has resulted in reductions of bendway depth and reduced connectivity of backwaters, reducing availability of suitable paddlefish habitat. Restoring connectivity of bendways through dredging could reverse this trend and provide other benefits to fisheries.

Introduction

The paddlefish *Polyodon spathula* inhabits a variety of large floodplain river environments through the course of its life cycle. Paddlefish often utilize food-rich, lacustrine, off-channel habitats for feeding (Hoxmeier and DeVries 1997) but require lotic environments with high current velocity for spawning (Purkett 1961; Pasch et al. 1980). The paddlefish's range consists of major Gulf of Mexico tributaries west of Florida and east of the Colorado River in Texas (Carlson and Bonislawsky 1981). Widespread impoundment and development of these systems for purposes of navigation, flood control, and production of hydroelectricity have negatively impacted paddlefish abundance in many areas (Jennings and Zigler 2000).

Sedimentation, inundation of spawning habitat, habitat fragmentation, and alteration of natural current regime associated with damming and waterway development have the potential to negatively impact paddlefish recruitment and cause eventual declines in abundance (Sparrowe 1986; Unkenholz 1986). However, impoundments created by dams often

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provide low current velocities (Hubert et al. 1984) and high zooplankton densities (Sparrowe 1986) that are ideal for feeding paddlefish. As a result, paddlefish length at age is typically high in impoundments, which is attributed primarily to increased growth of juveniles (Paukert and Fisher 2001). Impoundment populations often support fisheries in areas where dams have not eliminated or severely reduced natural reproduction (Paukert and Fisher 2001; Scholten and Bettoli 2005) or where stocking is used to augment paddlefish abundance (Graham 1986).

Impoundments of the Tennessee-Tombigbee Waterway (TTW; Figure 1) in Mississippi and Alabama do not currently support paddlefish fisheries. Anecdotal reports and photographic evidence suggest that paddlefish were locally abundant in Mississippi waters of the upper Tombigbee River basin prior to 1955, long before TTW construction began in 1971. Prior to the current study, extensive sampling by the Mississippi Department of Wildlife, Fisheries and Parks (MDWFP) in Mississippi waters of the TTW and its tributaries during and following waterway construction

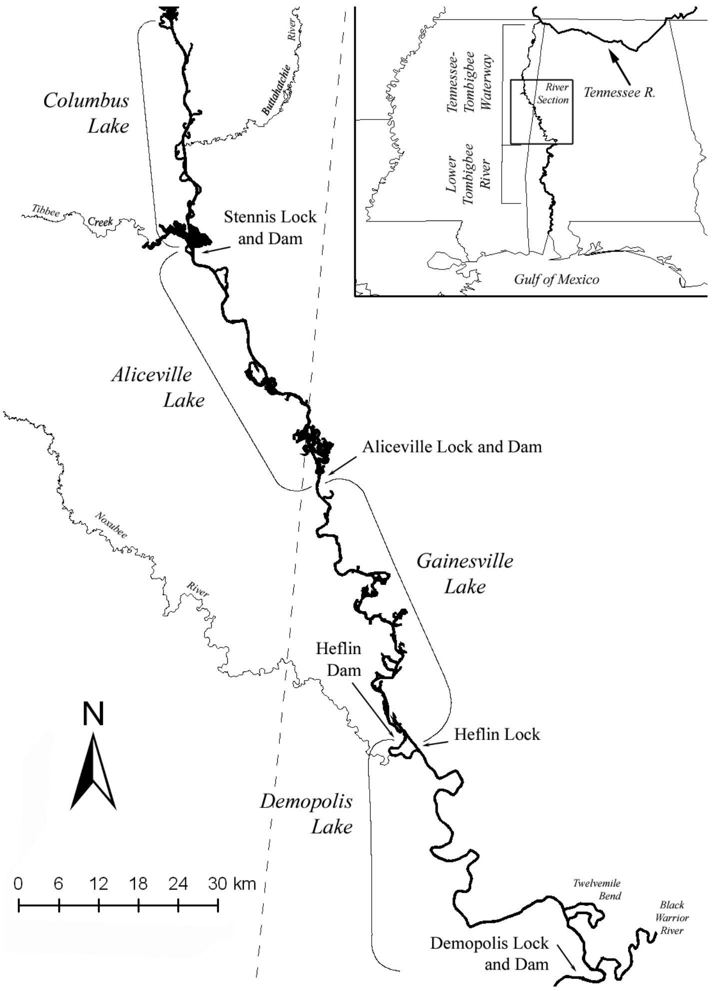


Figure 1. River section of the Tennessee-Tombigbee Waterway in Mississippi and Alabama, with selected tributaries.

did not result in the capture of any paddlefish (O'Keefe 2006). However, previous sampling efforts did not target paddlefish populations and may have underestimated paddlefish relative abundance. During 2003, MDWFP funded the current study to assess the status of paddlefish populations in the TTW system and develop management recommendations. Toward that end, the objectives of this study were to (1) examine current distribution and relative abundance of paddlefish in the TTW, and (2) characterize any remnant TTW paddlefish population.

Study Area

The TTW consists of a series of impoundments, canals, and modified channels of the upper Tombigbee River (Figure 1). The TTW was constructed by the U.S. Army Corps of Engineers to provide an alternate route for commercial barge traffic traveling between the Tennessee River and the Gulf of Mexico; construction was completed in December 1984 (Green 1985). The upper Tombigbee River and the TTW extend downstream to the confluence of the Black Warrior River. Below this confluence, the lower Tombigbee River and the Tombigbee-Black Warrior Waterway begin.

The TTW is divided into three sections that vary with respect to habitat types available: Divide section, Canal section, and River section. The Divide and Canal sections provide little suitable habitat, consisting primarily of a 3.7-m-deep maintained navigation channel and small (<1,100 ha), shallow (mean depth <4 m) impoundments. Paddlefish sampling was therefore confined to the River section in Mississippi and Alabama (Figure 1). Impoundments of the River section include Columbus (3,606 ha; 37 km of navigation channel), Aliceville (3,359 ha; 45 km), Gainesville (2,590 ha; 64 km), and Demopolis (1,356 ha; 85 km, excluding Black Warrior River Arm) lakes.

Main-stem habitats of the River section include sections of the upper Tombigbee River maintained for navigation, cutoff canals constructed to shorten overall navigation channel distance, meanders of the upper Tombigbee River that are not used by navigational traffic due to cutoffs (hereafter referred to as bendways), tailraces, and impounded areas. Most bendways are subject to sedimentation, resulting in annual decreases in depth (Pennington et al. 1981) and eventual loss of connectivity. The lotic bendway below Howell Heflin Dam at the upstream end of Demopolis Lake is an exception due to spatial decoupling of the dam and its respective lock (O'Keefe et al. 2007). Although relatively undisturbed lotic habitats such as this are rare in main-stem environments of the River section, several free-flowing and unchannelized tributaries provide such habitat. These include the Buttahatchie River, Tibbee Creek, and Noxubee River (Figure 1).

Methods

Distribution and Relative Abundance

Assessment of distribution and relative abundance in the TTW was limited to four impoundments of the River section (Figure 1). Our sampling program was devised to allow for comparison of paddlefish catch per unit effort (CPUE) among fixed bendway and tailrace sampling sites in each of the four lakes (Columbus, Aliceville, Gainesville, and Demopolis). Fixed bendway sites were chosen primarily on the basis of the availability of deep (>9 m) water because paddlefish often prefer the deepest water available (Zigler et al. 2003). Three groups of tandem nets were fished at each bendway site. One was set in deep (>9 m) water, one was set in middepth water (3–6 m) adjacent to deep water, and one was set at a creek mouth. Although actual net placement within locations was not always consistent across months due to changes in current and suspended debris, locations were considered fixed as opposed to random. Tailrace net placement was nearly always identical from one sampling period to the next due to the limited area available at tailrace locations. All tailrace nets were set between 240 and 800 m downstream from a dam. At each site, one pair of nets was fished parallel to the current flow approximately 240 m from the dam in moderate current, another was fished parallel to current flow on the edge of an eddy, and a third was set perpendicular to the current flow down a steep drop-off ending in approximately 6 m of water. Under relatively high-flow conditions, perpendicular net sets were replaced with parallel sets to avoid accumulation of debris and drifting of nets.

Sampling at fixed sites began in May 2003 and ended in December 2003. Sampling gear consisted of gill nets, which were 30.5 m long, 3.7 m deep, and hobbled to 2.4 m. Nets were hung with 101.6-, 127.0-, or 152.4-mm bar-mesh multifilament webbing and fished in tandem. Each of the eight fixed sampling locations (four tailraces and four bendways) was sampled once per 2-month period with six nets (two of each mesh size) set for a target of 5 h per net. When gear failure or lack of personnel prevented sampling on a randomly determined date, an alternate date was chosen. From March 2003 through December 2003, supplemental nets were set in a wide variety of habitats to provide greater spatial coverage than possible using fixed sites and to validate the assumption that fixed sites represented the most productive sampling sites available.

Demopolis Lake Population Characteristics

Sampling for stock assessment in Demopolis Lake was conducted on 12 dates during the 2004 sample season (December 2003 through April 2004) and on 23 dates during the 2005 sample season (December 2004 through May 2005). Sampling was limited to winter and spring to facilitate sexing of paddlefish using external characteristics (Rosen et al. 1982) and minimize mortality in nets, which can be high when water temperature is warm (Paukert and Fisher 2001). During the 2004 season, the lotic bendway between Howell Heflin Dam and Howell Heflin Lock (Figure 1) was the only area of paddlefish capture in Demopolis Lake. Sampling during the 2004 season included eight nets set in Twelvemile Bend (Figure 1), which did not result in the capture of any paddlefish. Unpublished telemetry data from 2004 revealed more productive areas of Twelvemile Bend. Consequentially, 108 net-days were recorded in Twelvemile Bend during the 2005 season. Attempts also were made to sample the navigation channel of Demopolis Lake during 2005. Only two net-days were recorded in the navigation channel due to gear damage and dangerous sampling conditions.

In addition to multifilament gill nets described above, monofilament nets of two types were used for Demopolis Lake stock assessment. Monofilament nets 47.7 m long and 3.7 m deep (hobbled to 3.0 m) and hung with 127.0-mm bar-mesh were fished singly with lead lines resting on the substrate. Experimental mesh (101.6-, 127.0-, and 152.4-mm bar) monofilament gill nets 61 m long and 5.5 m deep were used during 2005. The experimental nets were used to reach fish suspended in water deeper than 9 m. The light (20 lb) lead line and buoyant foamcore float line enabled us to fish these nets stationary with the float line on the surface, drifting with the float line on the surface, or oblique with one end of the float line tied to shore and the opposite end of the lead line anchored such the deepest portion of the net fished 3 m above the substrate.

Nets were checked regularly to minimize netting mortality. Depending on water temperature and work load, nets were checked at 20- to 180-min intervals. Captured fish were measured to the nearest millimeter and weighed to the nearest 0.1 kg. Eye-to-fork length (EFL) was chosen as the standard measurement for paddlefish length due to frequent rostrum abnormalities (Russell 1986).

During 2003 and 2004, paddlefish were marked with lock-on and T-bar anchor tags at the base of the dorsal fin and with opercular flap notches. The opercular flap notch was not visible in one paddlefish recaptured 404 d after marking, but seven other paddlefish retained the mark for up to 326 d. Two paddlefish shed lock-on tags prior to recapture, and five retained the lock-on tag for up to 326 d. Lock-on tag loss occurred in as little as 89 d after marking. Beginning in January 2005 fish were double-marked with T-bar tags, and use of lock-on tags was suspended due to their poor retention. Thirteen paddlefish marked with at least one T-bar tag were recaptured in Demopolis Lake, and all tags were retained. One paddlefish recaptured for broodstock during 2007 had retained two T-bar tags for 776 d.

Mature paddlefish were sexed using secondary sex characteristics (e.g., tubercles on males) when possible (Rosen et al. 1982). Sex of moribund fish was confirmed through necropsy and examination of gonads. Sex was confirmed in paddlefish used as broodstock for a concurrent experimental stocking program. Paddlefish captured in Demopolis Lake 2004–2007 were sexed using external characteristics in the field and subsequently transported to Private John Allen National Fish Hatchery in Tupelo, Mississippi. At the hatchery, injection with luteinizing hormone-releasing hormone stimulated the release of sperm in males and the ripening of eggs in females. This allowed for verification of sex determination using external characteristics.

Stock structure.—The chi-squared test for independence was used to test for differences in length–frequency distribution of paddlefish according to sample site (lotic bendway versus Twelvemile Bend) and year (Heath 1995). Only paddlefish captured during 2005 were included in the sample site comparison because the Twelvemile Bend habitat was not sampled extensively during 2004. In comparing 2004 and 2005 sample seasons, only males caught in the lotic bendway were used because of small female sample size and lack of paddlefish capture at Twelvemile Bend during 2004.

Sex ratio.—The null hypothesis that paddlefish exhibited a 50:50 sex ratio during 2005 was tested using chi-squared goodness-of-fit (Heath 1995). Sex ratios were examined separately for paddlefish caught in the lotic bendway and in Twelvemile Bend. The null hypothesis that sex ratio was independent of location was tested using the chi-squared test of independence (Heath 1995). For all chi-squared tests, groups were combined such that expected values less than 1 did not occur and fewer than 20% of expected values for any test were greater than 5 (Heath 1995).

Condition.—-Relative weight (W_r) was calculated for each paddlefish captured during 2004 and 2005 using the sex-specific W_s equations (Brown and Murphy 1993). Years were divided into two seasons: prespawn (December–March) and postspawn (April 16–May 10). For 2004, the effect of season on W_r was tested separately for males and females using two sample *t*-tests (Heath 1995). A two factor analysis of variance (ANOVA) was used to test for effects of season, habitat, and interaction of season and habitat on condition of paddlefish caught during 2005 (Petersen 1985). Separate analyses were performed for male and female paddlefish.

Age and growth.—Four to seven latlateral (leading) pectoral fin rays (Mabee and Noordsy 2004), including the longest (primary) ray, were removed from 80 male paddlefish for aging during 2005. Fin rays were not removed from females because data collected prior to 2005 suggested that few females would be captured during the 2005 sample season. Dentaries have been used by other researchers to age paddlefish (Adams 1942; Reed et al. 1992; Hoxmeier and DeVries 1997; Scarnecchia et al. 2006), but dentaries were not used in this study because doing so would have required the sacrifice of a large number of fish from a population of unknown size. Pectoral fin rays have been used to age other acipenseriforms and removal of pectoral fin rays from shortnose sturgeon *Acipenser brevirostrum* and Atlantic sturgeon *A. oxyrinchus oxyrinchus* does not affect growth or survival (Collins and Smith 1996). Fin rays were removed approximately 2 mm distal from the body using wire cutters. Cutting fin rays closer to the body resulted in heavy bleeding. Fin rays were dried overnight at room temperature in scale envelopes before storing in a freezer. Epoxy was used to coat the pectoral fin rays before sectioning to prevent the rays from slipping during sectioning. The epoxy-covered fin rays were sectioned to approximately 500 μm width using an Isomet low-speed saw and diamond wafering blade manufactured by Buehler, Inc. (Evanston, Illinois).

One to three sections per sample were mounted between two 1.1-mm-wide glass microscope slides. A single reader blindly selected and read each of the slides three times under a stereoscope at 80× magnification. Each section contained multiple fin rays, but only the primary rays were used for aging (Figure 2). Distance between the focus and each annulus was measured to 0.01 mm during the second and third reading using an ocular micrometer. If the reader assigned the same age to a given section in at least two of the three readings, that age was considered correct. A similar system was used by Hoxmeier and DeVries (1997) when aging paddlefish from the Alabama River system, Alabama, using dentaries.

The Fraser-Lee method of back-calculation was used to generate mean lengths at age for male paddlefish after determining the intercept parameter (DeVries and Frie 1996). The intercept parameter (*a*) was calculated through linear regression of 110 measurements of primary pectoral fin ray

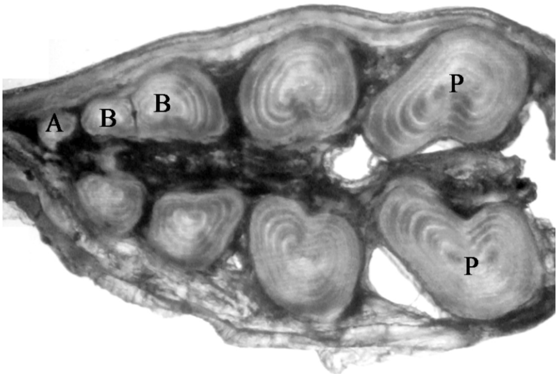


Figure 2. Cross section of lateral pectoral fin rays taken from a paddlefish on January 24, 2005 in the lotic bendway of Demopolis Lake. Primary rays (P) exhibit a different cross-sectional shape and more consistent annuli patterns than more lateral rays. The lack of clear annuli on the leading ray (A) suggests that it formed late in life. Two other rays (B) are in the process of fusing together. Fusing was often noted in rays lateral to primary rays but never in primary rays or those immediately medial to primary rays.

radius and EFL. To ensure adequate representation of all paddlefish size-classes, pectoral fin rays measured for intercept calculation included those from adult and juvenile paddlefish caught in Demopolis Lake, juvenile paddlefish spawned from Demopolis Lake broodstock and reared in ponds, and postlarval paddlefish reared in the laboratory from wild-spawned Demopolis Lake and Noxubee River eggs (see O'Keefe et al. [2007] for details). Of 80 pectoral fin samples taken from male paddlefish, 57 were used for back-calculation. Fin rays were not used if (1) ages did not agree in two of three aging attempts, (2) fin regrowth or damage was evident, or (3) a lumen formed at the focus of the rays.

Mean lengths at age were calculated separately for male paddlefish in the lotic bendway and Twelvemile Bend. These were used to generate von Bertalanffy growth curves for each habitat (Busacker et al. 1990). Von Bertalanffy parameters (L_∞, K, and t_0) and 95% confidence intervals were calculated using all age-groups present in both habitats. Confidence intervals overlapped, so male paddlefish in the two habitats were considered components of the same population. Mean lengths at age were subsequently calculated using length and age data from both habitats. These were used to produce a von Bertalanffy curve applicable to all of Demopolis Lake.

Mortality.—A catch curve was generated by using the Demopolis Lake von Bertalanffy curve to assign ages to male paddlefish that were inconsistently aged or not aged during 2005 and including these values with ages at capture for fish consistently aged using methods described above (Hoxmeier and DeVries 1997). Mortality was determined using the slope of the log-transformed descending limb of the catch curve (Ricker 1975).

Population abundance and density.—A population abundance estimate was calculated using Chapman's modification of the Lincoln-Petersen mark–recapture estimator (Chapman 1951). A 95% CI was calculated using the Poisson distribution due to low number of recaptures (Ricker 1975). The marking period included 12 dates from December 31, 2004 until March 21, 2005, and fish were recaptured on nine dates between March 30 and May 10, 2005. The choice of a closed population estimator was supported by concurrently collected radio telemetry data, which indicated a lack of paddlefish emigration from Demopolis Lake (O'Keefe 2006). Immigration of paddlefish into Demopolis Lake from downstream impoundments and the Black Warrior River was not assessed. Closed population estimators can be used when immigration occurs between the marking and recapture periods, although the resulting estimate is only unbiased for the recapture period (Kendall 1999).

Paddlefish were captured during the marking phase using targeted gill net effort to maximize catch in the lotic bendway and Twelvemile Bend. During the recapture period, gill nets were set in two randomly chosen river kilometers on two dates in both the lotic bendway and Twelvemile Bend. Random kilometers also were chosen for sampling in the navigation channel, but adverse conditions only allowed one net set. Due to the low catch rate of randomly placed nets in the lotic bendway, additional nets were set in productive areas to augment the catch during the recapture period.

Results

Distribution and Relative Abundance

During 2003, 367 gill nets were set in the river section of the TTW and its tributaries. This includes net sets at fixed locations (N = 190) and net sets at supplemental locations (N = 177). Mean soak time at fixed locations was 258 min (SD = 103 min). At fixed sites, 29 paddlefish were captured from Demopolis Lake and 2 from Gainesville Lake. Both fish captured in Gainesville Lake were juveniles (470 and 594 mm EFL). No paddlefish were captured in the Mississippi portion of the TTW. During sampling at fixed locations, CPUE was zero at all sites other than the Demopolis Lake tailrace and bendway sites and the Gainesville Lake bendway site (Table 1). Three paddlefish were captured during supplemental netting. One of these fish was taken from a gravel pit at the mouth of an unnamed tributary to Gainesville Lake and the other two were captured in Oktoc Creek, a tributary of the Noxubee River (Figure 1).

Demopolis Lake Population Characteristics

Net sets recorded during the 2004 and 2005 sample seasons totaled 72 and 108, respectively. Soak time averaged 194 min across years (SD = 130 min). Sixty-three paddlefish were captured from Demopolis Lake during the 2004 season, and 267 were captured during the 2005 season.

Stock structure.—Male paddlefish in Twelvemile Bend exhibited a different length distribution than males in the lotic bendway (χ^2 test for independence P = 0.046; Figure 3), with smaller size-classes being more common and larger size-classes being comparatively rare in Twelvemile Bend. Females did not exhibit a significant difference in length distribution between habitats (χ^2 test for independence P = 0.126; Figure 3). Year of capture did not affect length distribution of males in the lotic bendway (χ^2 test for independence P = 0.746).

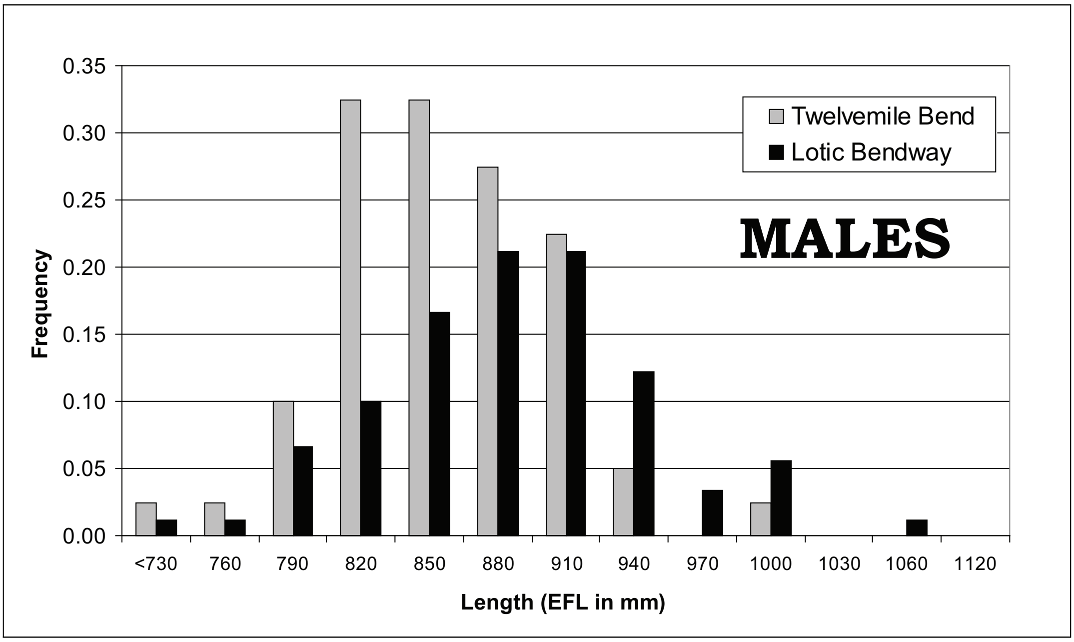
Sex ratio.—Males were more than twice as abundant as females during 2004 (male:female sex ratio 2.8:1) and 2005 (sex ratio 2.1:1) in the lotic bendway (χ^2 test for goodness-of-fit $P < 0.001$ in each year). In Twelvemile Bend, the sex ratio did not differ from 1:1 during 2005 (0.9:1 sex ratio; χ^2 test for goodness-of-fit $P = 0.461$). Twelvemile Bend and lotic bendway sex ratios differed significantly (χ^2 test for independence $P < 0.001$).

Sex ratios were determined using 302 paddlefish captured during 2004 and 2005 sample seasons. Most of these fish were sexed using only external characteristics in the field. Sex was verified in 61 paddlefish taken from Demopolis Lake for use as broodstock during 2004–2007. Of these, 49 were captured in the flowing bendway and sexed correctly in the field using external characteristics. Twelve paddlefish were captured in Twelvemile Bend and used as broodstock, and one of these fish was incorrectly identified as a female in the field.

Condition.—Mean sex-specific relative weight was 82 for males and females during winter 2004 and 78 during 2005. Neither female nor male (two sample t-tests $P > 0.05$) relative weight was affected by season in 2004. During 2005, habitat and the interaction between habitat and season did not affect female or male W_r (two factor ANOVAs $P > 0.05$). However, the main

Table 1. Paddlefish catch per unit effort (mean number caught per 5-h net-day ± SE) in gill nets at fixed bendway and tailrace sampling locations in four impoundments of the River Section of the Tennessee-Tombigbee Waterway May to December of 2003.

	Columbus Lake	Aliceville Lake	Gainesville Lake	Demopolis Lake	Mean
Tailrace	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.09 ± 0.66	0.27 ± 0.26
Bendway	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.05	0.25 ± 0.15	0.08 ± 0.05
Mean	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.03	0.67 ± 0.35	–



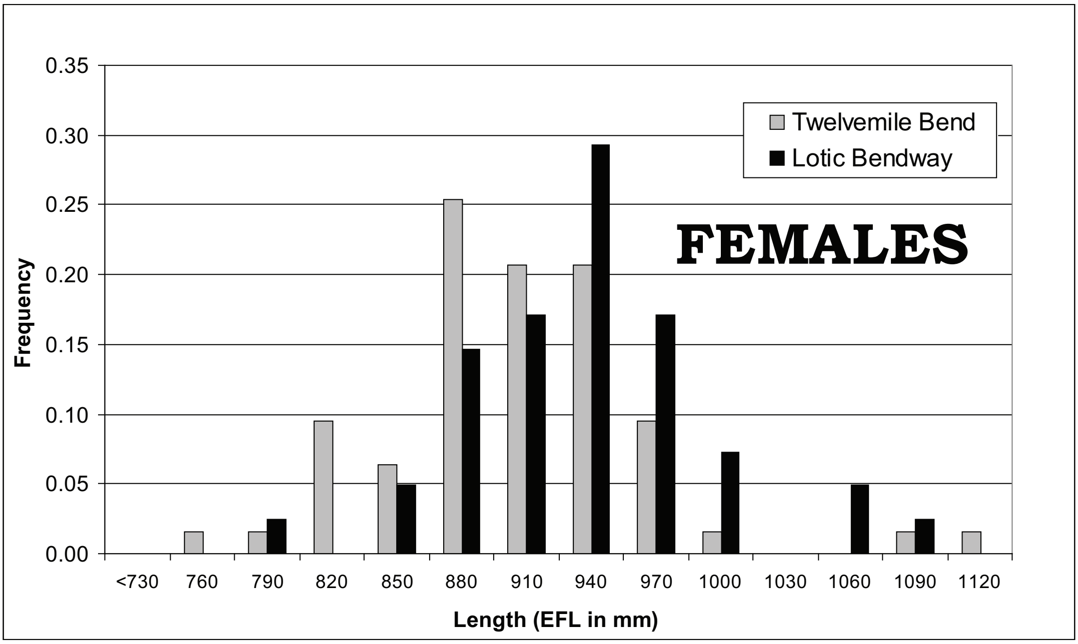


Figure 3. Lengths of paddlefish caught in gill nets set in Demopolis Lake during the 2005 sample season in Twelvemile Bend (N = 55 males, 63 females) and the lotic bendway between Heflin Dam and Heflin Lock (N = 90 males, 41 females).

effect of season was significant during 2005 for males ($P = 0.007$) and females ($P < 0.001$). During 2005, male relative weight dropped to 75 and female relative weight dropped to 72 during the postspawn summer period.

Age and growth.—The relationship between primary pectoral fin ray radius (r, in mm) and paddlefish length (EFL, in mm) was best described by

$$\mathrm{EFL} = 724.36\ (r) + 52$$

($r^2 = 0.963$; $P < 0.001$; Figure 4). The y-axis intercept (52 mm EFL at age 0) was used in Fraser-Lee back-calculation (DeVries and Frie 1996). Back-calculated lengths at age were used to determine growth, which was best described by the von Bertalanffy equation

$$\mathrm{EFL}_t = 971.8\ [1 - e^{-0.2844(t\ +\ 0.6962)}],$$

where t is age. This model predicted lengths at age (in mm) of 372(1), 520(2), 632(3), 716(4), 779(5), 827(6), 863(7), 890(8), 910(9), 925(10), 937(11), and 946(12).

Mortality.—Male paddlefish of ages 7–10 were used in calculation of mortality rate from the catch curve. Fish recruited to the gear at age 7 (Figure 5), and fish of age 11 and over were not used for mortality rate calculation because of small sample size (<5; Ricker 1975) at given ages and questionable validity of extrapolating beyond the age of the oldest aged fish (age 12). The descending limb of the catch curve yielded an annual mortality rate (A) of 0.406. All mortality was assumed to be natural due to Alabama regulations that prohibit paddlefish harvest.

Population abundance and density.—During the marking period, 176 paddlefish were marked in the lotic bendway and Twelvemile Bend. Of 99 fish checked for marks at these sites during the recapture period, 4 were marked. The estimated population size during spring 2005 was 3,541 (95% CI = 1,581–8,851) paddlefish in Demopolis Lake (excluding the Black Warrior Arm). This represents a density of 2.6 paddlefish/ha (95% CI 1.2–6.5) in Demopolis Lake during 2005.

Discussion

Distribution in the Tennessee-Tombigbee Waterway

Precise explanations for the cause of paddlefish decline in upstream (Mississippi)

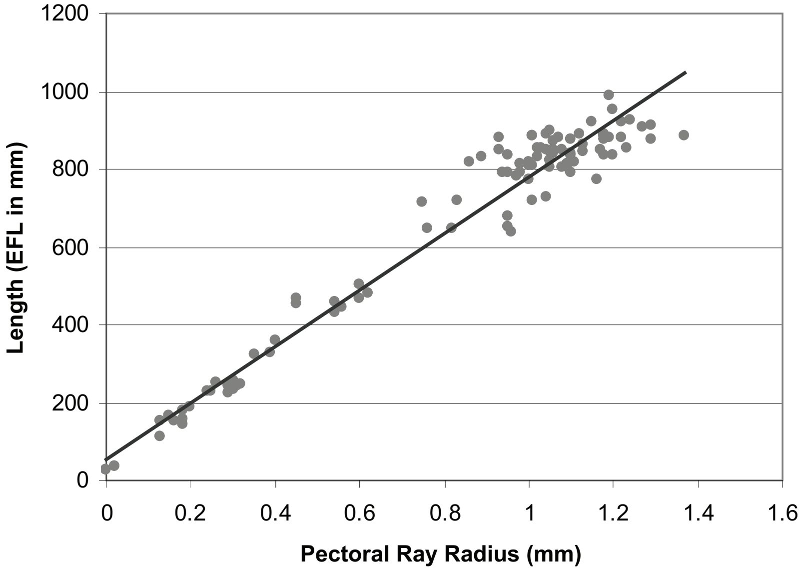


Figure 4. Relationship between pectoral fin ray and length measurements for male paddlefish in Demopolis Lake.

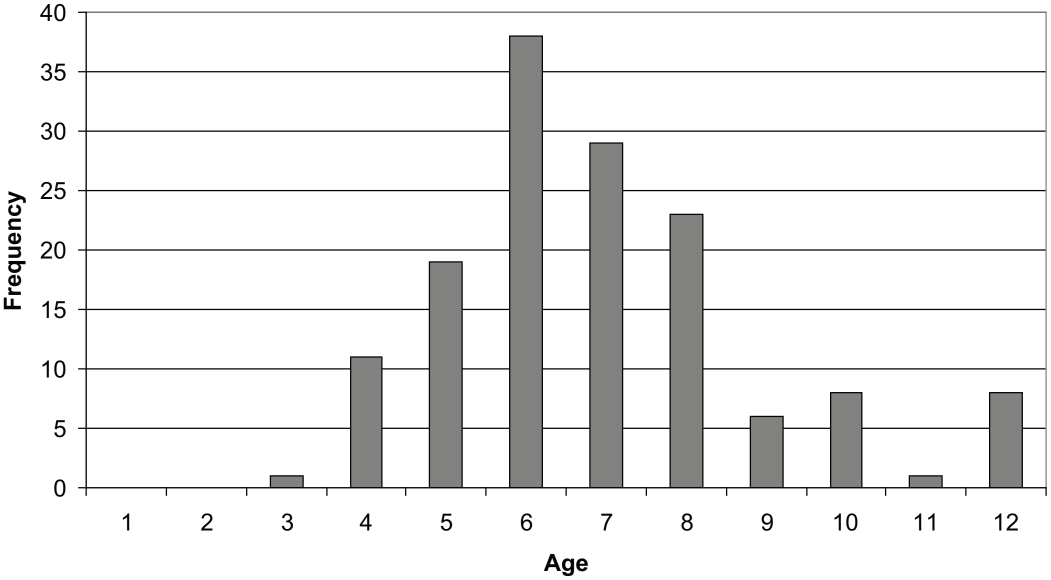


Figure 5. Age frequency of male paddlefish (*N* = 145) caught during the 2005 sample season in Demopolis Lake.

waters of the upper Tombigbee River basin are speculative in nature, but the best evidence available suggests that TTW construction was not the only factor. Anecdotal reports supported by photographic evidence (O'Keefe 2006) suggest that upper Tombigbee River basin paddlefish declined drastically in abundance during the mid-1950s, perhaps due to downstream fragmentation or industrial and agricultural pollution. Anecdotal reports (O'Keefe 2006) and museum specimens (Boschung 1989) predating the TTW include paddlefish records from tributaries and backwaters adjacent to tributaries, as opposed to the main stem of the upper Tombigbee River. This suggests that paddlefish may have historically used small streams, such as the Buttahatchie River (Boschung 1989) and Tibbee Creek (O'Keefe 2006), for spawning (Figure 1).

It is possible that the upper Tombigbee River and its tributaries functioned primarily as spawning habitat for paddlefish prior to TTW construction while backwaters of the lower Tombigbee River served as nurseries and main-stem environments provided adults with winter and feeding habitat. An ontogenetic shift in habitat use was noted in the Alabama River (Hoxmeier and DeVries 1997). Completion of the Demopolis Dam in 1955 may have restricted access of adult paddlefish to upstream spawning areas. A historic lack of overwintering adults in the relatively shallow upper Tombigbee River would explain the paucity of historical records for this area. Historic scarcity of adults would not be surprising given that the shallow stream habitat available in the upper Tombigbee River and its tributaries was probably not ideal for paddlefish, except when spawning.

Demopolis Lake Population Characteristics

Density of gear-vulnerable paddlefish in Demopolis Lake (2.6 paddlefish/ha) compared favorably with other published estimates. After severe overfishing in Watts Bar Reservoir, Tennessee, density of harvestable (>700 mm EFL) adult paddlefish was estimated at a much lower 0.14–0.42 paddlefish/ha (Alexander et al. 1987). The heavily, but not excessively, exploited paddlefish population of Neosho River/Grand Lake, Oklahoma was estimated at 0.92–1.55 paddlefish/ha (Combs 1982). In Keystone Reservoir, Oklahoma annual density estimates for a self-sustaining and lightly exploited paddlefish population ranged from 0.62 to 0.97 paddlefish/ha (Paukert and Fisher 2001). Higher density estimates have been reported for the unfished populations of South Cross Creek Reservoir, Tennessee (8.8 paddlefish/ha; Boone and Timmons 1995) and an oxbow of the Alabama River, which was dominated by young paddlefish (13.1 paddlefish/ha; Hoxmeier and DeVries 1997).

A study of Mobile River drainage paddlefish in the Tallapoosa and Cahaba rivers, Alabama revealed a short life span (maximum age 11 years) and an age structure that suggested high mortality (Lein and DeVries 1998). Similar observations were made in Demopolis Lake. The oldest paddlefish accurately aged from Demopolis Lake was 12 years old, and natural annual mortality based on the catch curve was 41%. In the lower Alabama River, annual mortality was 34% (Hoxmeier and DeVries 1997). Mortality estimates for Demopolis Lake and Alabama River populations represent approximations of natural mortality rate due to the harvest moratorium instituted in 1988.

Natural mortality in Mobile River basin populations is high relative to more northern Mississippi River basin populations. Natural annual mortality was 9% for the unfished population of South Cross Creek Reservoir (Boone and Timmons 1995), 9% in an exploited population of the Missouri River, Nebraska/South Dakota (Rosen et al. 1982), and 27% in the unexploited population of Wisconsin River, Minnesota/Wisconsin (Runstrom et al. 2001). Differences noted between these Mississippi River drainage natural mortality rates and those of the Mobile River drainage are likely due, in part, to latitudinal effects. Three unexploited populations in Louisiana exhibited natural annual mortality rates between 26% and 48% (Reed et al. 1992), which are comparable to observations in the Mobile River drainage.

Growth rates of male TTW paddlefish were lower than those of Louisiana populations but greater than those of more northern populations (Figure 6). Parameters of the Demopolis Lake von Bertalanffy curve are consistent with values expected based on published studies that relied on dentaries. The unvalidated and nonlethal pectoral fin aging technique therefore appears useful for situations in which paddlefish cannot be sacrificed for aging. Dentary aging was recently validated for the Yellowstone-Sakakawea, Montata/South Dakota, paddlefish stock (Scarnecchia et al. 2006) but has not been validated in more southern populations for which aging can be more problematic due to frequent formation of halo bands (Lein and DeVries 1998; Scarnecchia et al. 2006).

Predicted lengths at age for the TTW were very similar to those reported for the Tallapoosa River, aside from lower values recorded early in life for TTW paddlefish (Figure 6). These may be an artifact of aging methodology shortcomings. Precise determination of the position of the first two annuli was difficult when using pectoral fin ray sections because these annuli were often less distinct than those produced later in life (Figure 7). False annuli (halo bands) often were visible between the origin and second annulus of pectoral ray sections but were not often readily apparent between later annuli.

Linton (1961) reported that ages determined using paddlefish pectoral fin rays from Fort Gibson Reservoir, Arkansas River, and Cimmaron River in Oklahoma were similar to those obtained from oto-

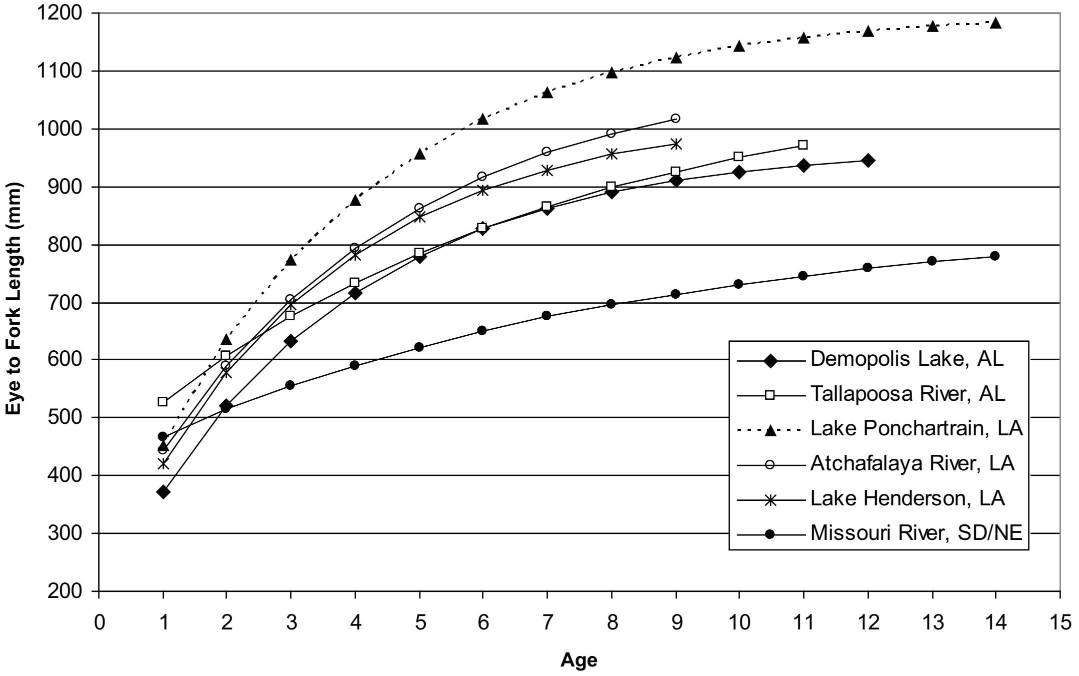


Figure 6. Comparison of von Bertalanffy growth curves for paddlefish in Demopolis Lake, the Tallapoosa River (Lein and DeVries 1998), Lake Ponchartrain, Atchafalaya River, Lake Henderson (Reed et al. 1992), and the Missouri River (Rosen et al. 1982). Curves shown are for males only with the exception of the three Louisiana populations, which did not show sexual dichotomy in growth rates.

liths from the same fish and did not note difficulty in determining early annuli. Dentaries are more commonly used than fin rays for aging paddlefish, in part due to the findings of Meyer (1960), who recommended the use of dentaries as opposed to fin rays because multiple rays from a given fish yielded differing age estimates. We noted that one to three lateral pectoral rays (Mabee and Noordsy 2004) of a given fin often did not exhibit as many annuli as rays immediately medial to these leading rays (Figure 2). Lateral rays often exhibited fewer annuli than primary rays, especially in older fish. Accordingly, we used only the longest, or primary, rays for age determination. The close agreement of Tallapoosa River growth rate calculated using dentaries (Lein and DeVries 1998) and our growth curve, calculated using ages from pectoral rays, suggests that this method of age-determination from pectoral fin rays provides reasonably accurate age estimates. However, future validation of pectoral fin aging using known-age paddlefish would provide better evidence for the reliability of this nonlethal technique.

The relative weight of Demopolis Lake paddlefish (78 during winter 2005) was low compared to the national average of 90 (Brown and Murphy 1993), but this is not necessarily reflective of inadequate conditions for paddlefish growth and survival. As early as 1907, researchers noted the difference between deep-bodied lacustrine paddlefish and slender riverine paddlefish (Stockard 1907; Paukert and Fisher 2001). The national average computed by Brown and Murphy (1993), includes lacustrine and riverine populations. The lotic bendway

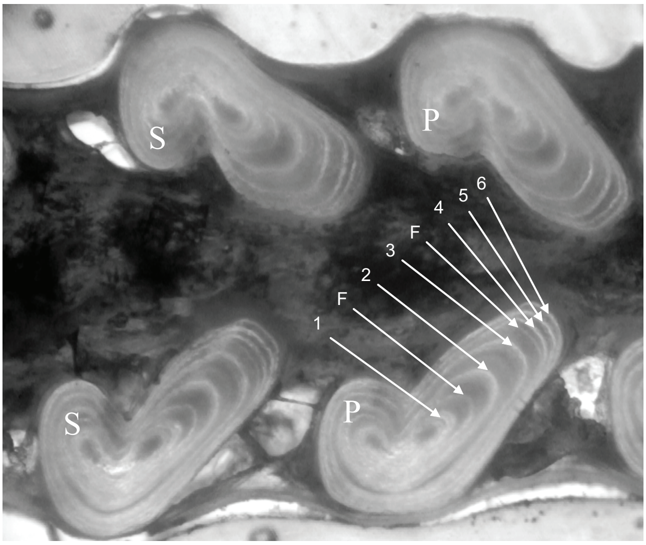


Figure 7. Cross section of dorsal and ventral primary fin rays (P), and secondary rays (S). Although leading rays often differed substantially in annulus count from primary rays, secondary and subsequent rays often showed growth patterns very similar to the primary rays. This fish shows six distinct annuli (numbered), in addition to two false annuli (F). The first annulus is not clearly delineated by the sharp, white edge present at later annuli, making exact determination of its position difficult. These rays were removed from a tuberculate, postspawn male paddlefish captured on April 25, 2005 in the lotic bendway of Demopolis Lake. The position of the sixth annulus at the edge of each ray indicates its recent formation and suggests that male paddlefish grow little while staging in wintering habitats, engaging in prespawn movements, and spawning.

provided a riverine environment, whereas current velocity in Twelvemile Bend varied considerably according to water level. Thus, it would be expected that Demopolis Lake paddlefish would exhibit lower relative weight than strictly lacustrine paddlefish.

The remnant paddlefish of Demopolis Lake used two distinct wintering habitats (the lotic bendway and Twelvemile Bend), which are isolated from one another by 67 km of TTW navigation channel. Although gill-net effort was extremely low in the navigation channel, radio telemetry data indicated that use of navigation channel habitat was limited to high water periods during spring, at which time paddlefish were moving between wintering and spawning habitats (O'Keefe 2006).

The lotic bendway and Twelvemile Bend differed in terms of paddlefish sex ratio and male length frequency, suggesting that Twelvemile Bend serves as wintering habitat for juveniles and females, whereas the flowing bendway provides wintering habitat primarily for adult males. Growth of males did not differ among habitats, further indicating that they were components of the same population, segregated by age during winter months, and not two distinct populations. Smaller and younger males were present in the more lentic Twelvemile Bend habitat, which would be expected to produce higher growth rates than the lotic bendway if the two habitats represented separate populations (Hubert et al. 1984; Paukert and Fisher 2001). Verification of spawning in the lotic bendway during 2005 (O'Keefe et al. 2007) further suggests that adult males stage near spawning grounds throughout the winter months prior to spawning. In Lake Francis Case, South Dakota, Stancill et al. (2002) found that prespawn male paddlefish were more likely to be found in staging locations than were females. Hoxmeier and DeVries (1997) found smaller paddlefish in oxbows of the Alabama River than in main-stem environments. In the highly modified TTW, Twelvemile Bend serves a nursery function similar to oxbow lakes in the Alabama River, whereas the lotic bendway and Noxubee River provide spawning habitat (O'Keefe et al. 2007) that is not available in Twelvemile Bend.

Use of External Characteristics for Sex Determination

Sex determination using external characteristics is an imperfect method, although it has been used by other investigators (Rosen et al. 1982) and has the advantage of being noninvasive. It is likely that a small percentage of paddlefish in Twelvemile Bend were incorrectly sexed in the field during the course of this study. Analyses that depended on sexing included age and growth, relative weight, and sex ratio. Results from Twelvemile Bend may have been impacted slightly by imprecise sexing, but we believe that these analyses were preferable to the alternatives: not using sex-based information or using an invasive technique that may have been detrimental to paddlefish survival.

In addition to the 302 captured paddlefish that were sexed during 2004 and 2005 sample seasons, 26 captured paddlefish were not sexed due to ambiguity of external characteristics. The majority (N = 18) of unsexed fish were less than 770 mm in length. These were thought to be juveniles not yet displaying sexual dimorphism. Male paddlefish as small as 648 mm exhibited tubercles, but the smallest male to produce milt was 780 mm. Any fish that displayed heavy tuberculation was considered a male, but lack of heavy tuberculation was not considered indicative of females less than 750 mm in length. Some females exhibited sparse, barely visible tubercles. These fish were typically taken near the peak of spawning condition and exhibited swollen abdomens that readily identified them as female. Eight fish more than 770 mm in length could not be identified using external characteristics due to ambiguous external characteristics. These fish, in addition to the juveniles, were excluded from sex ratio analysis. During 2005, unsexed fish comprised 8% of fish captured in Twelvemile Bend and 4% of fish captured in the lotic bendway. During 2004, 21% of paddlefish were not sexed in the lotic bendway. The high number of ambiguous paddlefish during 2004 may have been due to lack of discharge-related spawning cues resulting from low flow (O'Keefe 2006).

Exclusion of unsexed fish does not cast doubt on our conclusion that males were more abundant than females in the lotic bendway. Sex ratios differed so markedly from 1:1 that inclusion of all unsexed fish in either sex category would still have produced a result significantly different from 1:1 ($P < 0.001$). Likewise, comparison of sex ratios in the lotic bendway and Twelvemile Bend would still yield a significant result ($P < 0.05$) if unsexed fish were all females in the lotic bendway and all males in Twelvemile Bend.

Implications for Restoration and Management

Given that the upper Tombigbee River may never have supported a self-sustaining population year-round, attempts to restore self-sustaining paddlefish populations in TTW impoundments of Mississippi are not necessarily doomed to failure based on degradation or fragmentation of habitat. Although spawning habitat is now extremely rare in the TTW main stem (Boschung 1989), upstream impoundments may provide ideal nursery and adult feeding habitat (Paukert and Fisher 2001) and tributaries may continue to provide suitable spawning habitat.

Concurrent with this study, an experimental stocking program was initiated in Columbus Lake, Mississippi during 2004. Broodstock from Demopolis Lake were used; most males were captured in the lotic bendway while the majority of females were taken from Twelvemile Bend. Management recommendations were drafted suggesting continuation of the stocking program through 2009, at which time stock structure and density will be reassessed to determine if stocking results in establishment of a paddlefish population in Columbus Lake (O'Keefe and Jackson 2006).

In the TTW, the lotic bendway and Twelvemile Bend serve distinctly different functions, both of which are critical for sustaining the paddlefish population of Demopolis Lake. This highlights the need for protection of what little suitable habitat remains in the TTW. Paddlefish utilize a variety of habitat types throughout their life history (Russell 1986), rendering them especially vulnerable to habitat fragmentation. Persistence of paddlefish in Demopolis Lake in the fragmented TTW is likely contingent upon maintenance of habitats used by all life stages.

Sedimentation of Twelvemile Bend (Pennington et al. 1981) is reducing the area of preferred secondary-channel, deep water (>6 m; Zigler et al. 2003) habitat and might eventually reduce connectivity (O'Keefe 2006). Sedimentation of Demopolis Lake has reduced connectivity of many backwaters, restricting angler access (Jackson and Dillard 1993) and reducing species richness (Splike and Maceina 2006). Restoring connectivity and increasing depth of TTW bendways through dredging could increase the availability of suitable paddlefish wintering and feeding habitat. Paddlefish were not found in closed-access backwaters of Demopolis Lake by Splike and Maceina (2006), although one paddlefish was taken in riverine habitat and one in an open-access backwater.

The limited distribution of paddlefish in the TTW reflects a history of human-induced habitat alteration. However, population dynamics of the remnant Demopolis Lake stock indicate a healthy population. Limited movements and site fidelity of Demopolis Lake paddlefish observed by O'Keefe (2006) are likely the result of behavioral response to small, isolated patches of suitable wintering and feeding habitat, resulting in a virtual lack of emigration. Reproduction in the Noxubee River and flowing bendway (O'Keefe et al. 2007) further suggest that Demopolis Lake supports a self-sustaining paddlefish population and is not simply a sink maintained by immigration from downstream habitats and the Black Warrior River. The apparent success of the remnant Demopolis Lake population gives some cause for cautious optimism regarding the success of paddlefish reintroduction efforts in fragmented systems with limited availability of suitable main-stem habitat. Through the use of small tributaries for spawning and fidelity to suitable wintering and feeding habitats, paddlefish reintroduced to highly fragmented systems may be able to maintain self-sustaining populations as Demopolis Lake paddlefish have.

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