Am. Midl. Nat. 152:336–346

Status of the Mussel Fauna of the Poteau River and Implications for Commercial Harvest

CARYN C. VAUGHN AND DANIEL E. SPOONER
Oklahoma Biological Survey and Department of Zoology, University of Oklahoma, Norman 73019

ABSTRACT.—The Poteau River, a major tributary of the Arkansas River, flows through the Ouachita Uplands of eastern Oklahoma and western Arkansas. The river has been harvested for mussels, historically by the Caddo Indians and recently for the pearl industry. We documented the current distribution and abundance of mussels in the river, compared this with historical distributions and examined whether the river can sustain current levels of commercial harvest. The Poteau River retains a rich mussel fauna of 35 species. However, mussel abundance is much lower than in surrounding rivers. Mean total mussel densities in the largest beds in the river are 3.8 individuals/m^2. Densities of the two commercially harvested species, *Megalonaias nervosa* (washboard) and *Amblema plicata* (threeridge), are only 0.15 and 1.25 individuals/m^2, respectively. Mussel size distributions indicate very low recent recruitment of both *M. nervosa* and *A. plicata*. The majority of *M. nervosa* exceed the shell height limit of 4 inches established by the state of Oklahoma and, thus, are not protected by this regulation. Our data indicate that the Poteau River cannot sustain commercial mussel harvest. A recently established mussel sanctuary should be retained and further commercial harvest of mussels should be avoided.

INTRODUCTION

The Ouachita Mountains physiographic subprovince covers 8.6 million acres in central and western Arkansas and southeastern Oklahoma. The area consists of rugged, long, parallel east-west trending mountain ridges, broad valleys and the headwaters of several large river systems (Shimer, 1972). The area is bordered on the north and south by two of the large tributaries of the Mississippi River, the Arkansas and Red rivers. The Ouachitas are unglaciated and have been isolated from other mountain systems for 225 million years. They are a center of speciation for both terrestrial and aquatic organisms, with a high number of endemic species (Gordon, 1980; Mayden, 1985; Allen, 1990; Moulton and Stewart, 1996) and a rich unionid fauna (Gordon, 1980; Vaughn and Pyron, 1995; Vaughn *et al.*, 1996).

The Poteau River is one of three major tributaries of the Arkansas River originating in the Ouachita Uplands. The Poteau River is 4^{th} order, 228 km long, drains 4840 km^2 and is impounded by Lake Wister 116 km upstream from the mouth. Above Lake Wister the river is high gradient as it flows through the Ouachita Mountains. Below Lake Wister the river makes an abrupt transition to low-gradient turbid conditions as it flows across the Arkansas River floodplain (Matthews *et al.*, 2005).

The Poteau River has been harvested for mussels, both historically and continuing to the present. In 1947–48 several thousand unionid shells and shell fragments were excavated from a Caddo Indian midden (ca. 3500–1000 B.P.) along Fourche Maline Creek, a major tributary to the Poteau (Bell, 1953; Wyckoff, 1976; White, 1977). Of the excavated shells, 927 were identifiable to species. In recent years, the Poteau has been heavily harvested for *Megalonaias nervosa* (washboard mussel) and *Amblema plicta* (threeridge mussel) for use in the cultured pearl industry. In 1999 over 150,000 pounds of *M. nervosa* were harvested from the Poteau and the nearby Clear and Muddy Boggy Rivers (Oklahoma Department of Wildlife Conservation). Concern over this recent increase in harvest pressure prompted the

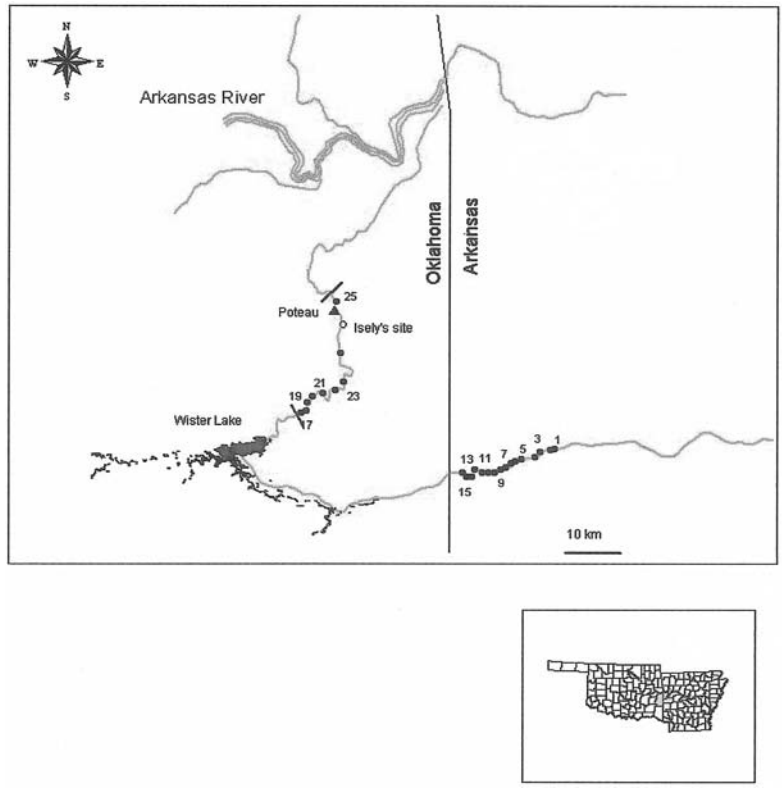


FIG. 1.—Map of Poteau River showing the location of the 25 sampling sites, Isely's historical site, and the Oklahoma Department of Wildlife Conservation mussel sanctuary (delineated as the area within the lines below site 17 and above site 25)

Oklahoma Department of Wildlife Conservation to establish a mussel sanctuary in the lower Poteau River in 2000 (Fig. 1).

In addition to the archeological find, there is more recent historical information on the Poteau River fauna. In 1912 (Isely, 1924) semi-quantitatively surveyed a site near the city of Poteau, now directly above Lake Wister. In 1976 (White, 1977) surveyed a site on a tributary to the Poteau, 100 m upstream from the Caddoan midden. In 1994 (Harris, 1994) surveyed 23 sites in the Upper Poteau River in Arkansas.

The objectives of this study were to document the current distribution of mussels in the river, compare current and historical distribution information and assess whether the river can sustain current levels of commercial harvest.

METHODS

The Poteau River was surveyed for mussels from June–August 2000. We explored the river from where it became large enough to travel via canoe to where it became too deep for us to sample with our methodology (*see* below), a distance of approximately 100 km (Fig. 1). Reconnaissance snorkel searches were conducted in areas where shells were observed and in

areas where habitat was judged to be appropriate for mussels. When live mussels were observed, the site was sampled using a timed search (described below), resulting in 25 sampling locations. We had 16 sampling sites above and 9 below Lake Wister (Fig. 1). From site 16 downstream to Wister Lake, the river was lake-like and too deep to sample with our methodology. Likewise, below site 25 the river is a deep, navigable channel that also was too deep for us to sample. Sites 17–25 were within the area of the river that has been commercially harvested. This reach of river was established as a mussel sanctuary by the Oklahoma Department of Wildlife Conservation in 2000 (Fig. 1).

A timed search is the most common technique for collecting information on mussel abundance, and is the only technique which can reliably be used to obtain estimates of total species richness and locate rare species (Strayer *et al.*, 1997; Vaughn *et al.*, 1997). Timed surveys were conducted by searching the entire site for a minimum of 1 h by experienced surveyors. Surveyors systematically swam over the area wearing a mask and snorkel and picked up mussels by hand. Mussels with either part of the shell or their siphon exposed at the surface were located by both sight and feel; when a patch of mussels was located, the surveyor also dug in the substrate for buried mussels. SCUBA was used in deeper areas (>1 m). Mussels were placed in a canvas bag underwater and removed to shore. Individual mussels were identified (Table 1) and their shell dimensions measured. Mussels were returned to the stream alive after all sampling was completed. Using this technique, mussel abundance was standardized as mussels encountered per person-hour of searching. Limited voucher specimens of each species were taken and were deposited in the mollusk collection of the Oklahoma Biological Survey (www.biosurvey.ou.edu).

At six sites with relatively high mussel abundance (sites 8, 14, 15, 16, 19 and 25) we also sampled mussels using 0.25 m^2 quadrats to estimate density (expressed as mussels per square meter). Quadrat sampling was conducted prior to timed searches. Fifteen randomly placed quadrats were excavated to a depth of 15 cm and all mussels were removed, identified, measured and returned to the stream as described above.

RESULTS AND DISCUSSION

We found 25 species of mussels in our survey of the Poteau River, and 35 species of mussels are known to occur in the river and its tributaries (Table 1). The mussel fauna of the river is dominated by *Amblema plicata* (threeridge), followed by *Tritogonia verrucosa* (pistolgrip), *Megalonaias nervosa* (washboard) and *Quadrula pustulosa* (pimpleback) (Fig. 2). These species also are common in other streams in the Ouachita Highlands (Vaughn *et al.*, 1996; Vaughn and Taylor, 1999) and throughout the Mississippi drainage (Parmalee and Bogan, 1998).

We found three species that were not found by Harris (1994) or historically and, thus, are new records for the river, *Arcidens confragosus* (rock pocketbook), *Ptychobranchus occidentalis* (Ouachita kidneyshell) and *Quadrula nobilus* (Gulf mapleleaf) (Table 1). The occurrences of *Arcidens confragosus* and *Quadrula nobilis* represent westward range expansions for these species. These are the first records of these species from the Poteau River and also in the state of Oklahoma (Branson, 1983; Howells *et al.*, 1996; Parmalee and Bogan, 1998). *Ptychobranchus occidentalis* is an Interior Highlands endemic (Oesch, 1984) that is common in other rivers in the region (Vaughn and Taylor, 1999; Vaughn, 2003), however, this is the first record of its occurrence in the Poteau River.

In addition, we found three species that were historically documented from the river but not found by Harris, *Ellipsaria lineolata* (butterfly), *Megalonaias nervosa* (washboard) and *Quadrula nodulata* (wartyback) (Table 1). *Ellipsaria lineolata*, *Megalonaias nervosa* and

TABLE 1.—Mussels known from the Poteau River and tributaries

Species	Common name	Caddoan midden (1 site)	Isely, 1910 (1 site)	White, 1976 (1 site)	Harris, 1994 (23 sites)	This study, 2000 (25 sites)
Actinonais ligamentina	mucket	X	X		X	X
Amblema plicata	threeridge	X	X	X	X	X
Arcidens confragosus	rock pocketbook					X
Elliptio dilatata	spike	X	X		X	
Ellipsaria lineolata	butterfly	X	X			X
Fusconaia flava	Wabash pigtoe		X	X	X	X
Lampsilis cardium	plain pocketbook	X	X		X	X
Lampsilis hydiana	Louisiana fatmucket				X	
Lampsilis siliquoidea	fatmucket	X			X	X
Lampsilis teres	yellow sandshell	X	X	X	X	X
Lasmigona complanata	white heelsplitter		X	X	X	X
Lasmigona costata	flutedshell				X	X
Leptodea fragilis	fragile papershell				X	X
Ligumia subrostrata	pondmussel				X	X
Megalonaias nervosa	washboard	X	X	X		X
Oliquaria reflexa	threehorn wartyback	X	X		X	X
Obovaria jacksoniana	southern hickorynut				X	
Pleurobema sintoxia	round pigtoe	X	X	X	X	X
Potamilus purpuratus	bleufer	X	X	X	X	X
Pyganodon grandis	giant floater				X	
Ptychobranchus occidentalis	Ouachita kidneyshell					X
Quadrula nobilus	Gulf mapleleaf					X
Quadrula nodulata	wartyback	X				X
Quadrula pustulosa	pimpleback	X	X	X	X	X
Quadrula quadrula	mapleleaf	X			X	X
Strophitus undulates	creeper				X	X
Toxolasma lividus	purple lilliput				X	
Toxolasma parvus	lilliput		X		X	X
Tritogonia verrucosa	pistolgrip	X	X	X	X	X
Truncilla donaciformis	fawnsfoot				X	
Truncilla truncata	deertoe	X	X	X	X	X
Utterbackia imbecillis	paper pondshell				X	
Villosa arkansasensis	Ouachita creekshell				X	
Villosa iris	rainbow				X	
Villosa lienosa	little spectaclecase				X	

Quadrula nodulata occur throughout the Mississippi drainage, but are most common in larger rivers (Parmalee and Bogan, 1998), which is why Harris (1994) likely did not find them in the upper reaches of the Poteau.

Harris (1994) found nine species that were not documented historically nor found in our study, *Lampsilis hydiana* (Louisiana fatmucket), *Obovaria jacksoniana* (southern hickorynut), *Pyganodon grandis* (fat floater), *Toxolasma lividus* (purple lilliput), *Truncilla donaciformis* (fawnsfoot), *Utterbackia imbecillis* (paper pondshell), *Villosa arkansasensis* (Ouachita creekshell), *Villosa iris* (rainbow) and *Villosa lienosa* (little spectaclecase). These species were found in the upper most reaches of the river where we did not have any sampling sites.

All of the species documented historically from the archeological site, the single site surveyed at the turn of the century, and the site surveyed in 1976 also were found recently

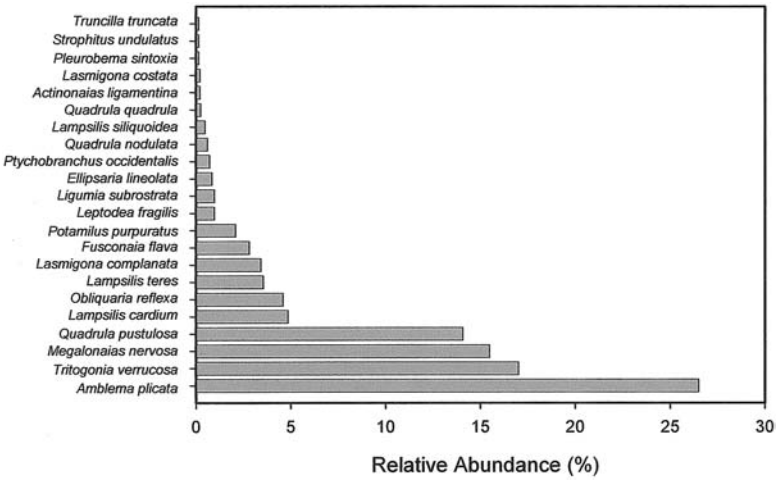


FIG. 2.—Relative abundance of mussel species in the Poteau River

either in our survey or by Harris (1994) (Table 1). Many more species were located in this survey and that of Harris (1994) than were documented historically; however, the historical data are for only a few sites in the lower river and tributary, whereas the recent data are for multiple sites along the entire river course. In addition, caution should be used when comparing mussel populations based on presence-absence data from a limited number of sites (Strayer, 1999). Within these constraints, it appears that no mussel species have been extirpated from the Poteau River.

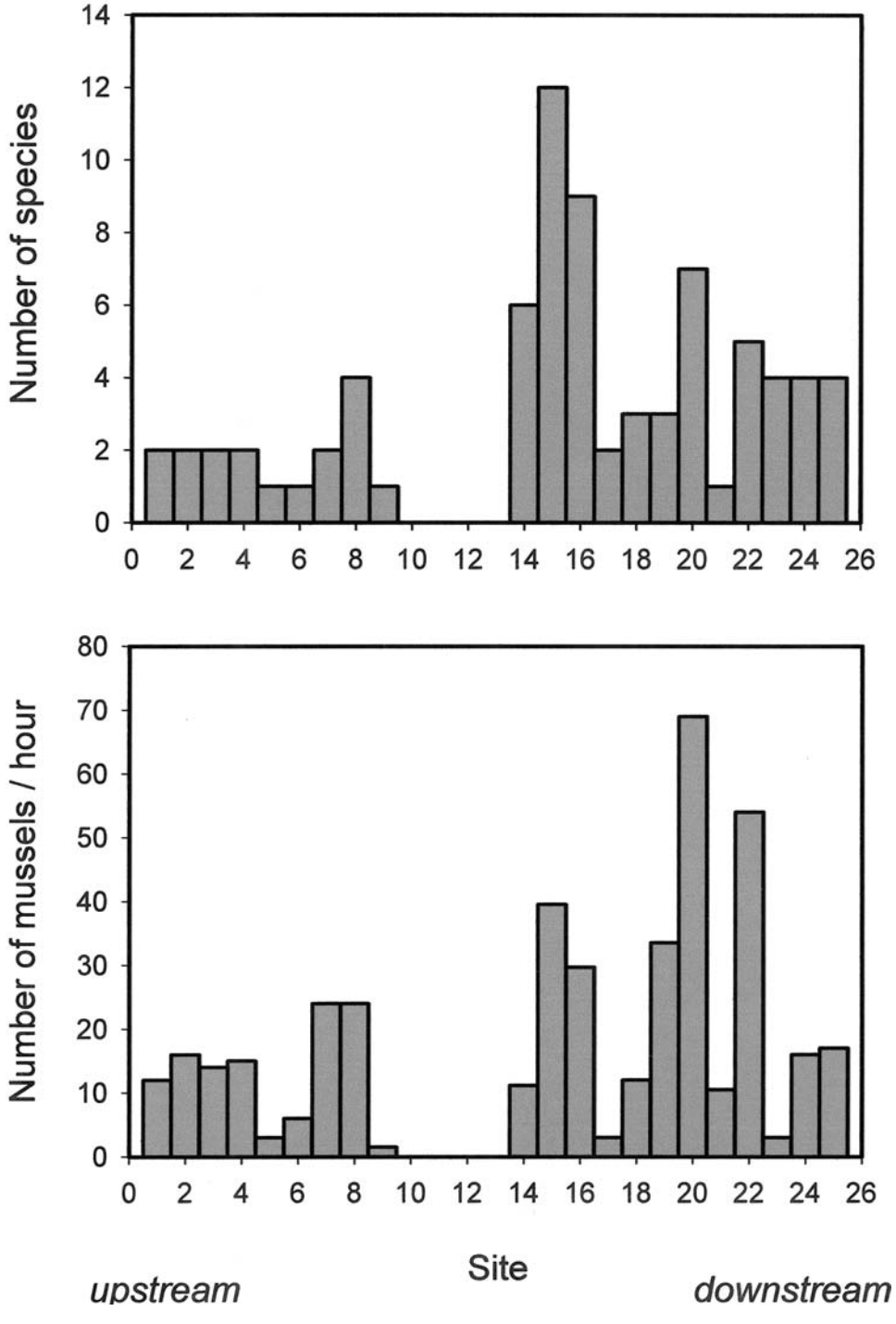
Mussel species richness increases in a downstream direction, peaks at mid-reaches above Lake Wister, and then decreases below Lake Wister (Fig. 3A). In undisturbed, intermediate-sized rivers, mussel species richness typically increases as a function of both increasing drainage area and increasing fish species richness and peaks in downstream reaches (Watters, 1992; Vaughn and Taylor, 2000). Thus, we expected the highest species richness at our most downstream sites. In the Poteau River, decreased richness at downstream sites is probably a reflection of large-scale disturbance from the upstream impoundment, urban land-use impacts from the city of Poteau (Fig. 1) and more localized disturbance from mussel harvesting, which has occurred primarily at downstream sites.

River reaches below impoundments are often substantially different than free-flowing rivers with altered seasonality of flow and temperature regimes, changed patterns of sediment scour and deposition and altered transport of particulate organic matter, the food base for mussels (Ligon *et al.*, 1995; Poff *et al.*, 1997). Several studies have documented mussel declines below impoundments (Suloway *et al.*, 1981; Miller *et al.*, 1984; Williams *et al.*, 1992; Layzer *et al.*, 1993; Vaughn and Taylor, 1999).

Harvesting of commercial species has been shown to lead to declines in biodiversity of non-commercial species (Anthony and Downing, 2001), and commercial harvest may have

→

FIG. 3.—(A) Species richness and (B) abundance of mussels at the 25 sample sites. Mussel abundance is standardized as mussels found per person-hour of searching


Number of species
0
2
4
6
8
10
12
14
0 2 4 6 8 10 12 14 16 18 20 22 24 26
Number of mussels / hour
0
10
20
30
40
50
60
70
80
0 2 4 6 8 10 12 14 16 18 20 22 24 26
Site
upstream
downstream

contributed to declines in mussel species richness in the lower Poteau. Although responsible musselers return unwanted shells to the bed, others do not. We have observed piles of discarded mussels left to die in very shallow water or streamside in the Poteau. In addition, when culled mussels are returned to the stream, they are often placed in suboptimal habitats where their chances of survival and reproduction are decreased (Cochran and Layzer, 1993). Finally, because large, commercially-valuable species such as *Megalonaias nervosa* stabilize the streambed and perform ecosystem processes that provide habitat for and may facilitate other species (Vaughn and Hakenkamp, 2001; Spooner, 2002), their removal may jeopardize the success of non-commercial mussel species.

Mussel abundance was lowest in the upper-most reaches and increased in a downstream direction (Fig. 3B) as the river decreases in gradient and more extensive areas of sand and gravel become available for mussels to colonize, a pattern typical of other small rivers in the region (Vaughn and Taylor, 1999; Vaughn, 2003). However, overall densities of mussels in the river were quite low. Overall mean mussel density (all species combined) within beds for the five sites that were quantitatively sampled was $3.8/m^2$. In comparison, mean densities of mussels in beds in three nearby, similarly-sized rivers are much higher (Clear Boggy River, $21/m^2$; Little River, $17/m^2$; Kiamichi River, $20/m^2$; Vaughn and Pyron, 1995; Vaughn *et al.*, 1997. Because we do not have historical mussel density data for the Poteau River, we don't know if densities have always been low or if this is a recent phenomenon.

In the Poteau River, *Megalonaias nervosa* is restricted to reaches below Lake Wister and *Amblema plicata* is most abundant below Lake Wister (Fig. 4). Mean densities of *M. nervosa* and *A. plicata* at these sites were 0.15 and 1.25 m^2, respectively. The restricted range and overall low densities of *M. nervosa* and *A. plicata* would seem to contraindicate commercial harvesting of these species in the Poteau. However, the river below Lake Wister also is where extensive mussel harvesting has occurred in recent years. For example, in 1999 and 2000, 306,004 and 108,871 pounds of mussels were harvested from Oklahoma rivers (Oklahoma Department of Wildlife Conservation). Although by-river statistics are not available, most harvesting is believed to have been *M. nervosa* taken from the Poteau River (Oklahoma Department of Wildlife Conservation).

In the Poteau, as in many small rivers, most harvesting occurs in late summer when water levels are low. Under these conditions it is relatively easy for even inexperienced musselers to "clean out" large mussel beds by simply wading and picking up all visible mussels (Anthony and Downing, 2001). Mussels that are found undesirable are simply thrown back regardless of whether or not they are being returned to appropriate habitat. Mussels which are not collected remain at such low densities that successful reproduction is unlikely (Downing *et al.*, 1993). Although it has been suggested that *Megalonaias nervosa* occurring at lower densities may be facultative hermaphrodites (Heinricher and Layzer, 1999), which would allow reproduction at lower densities (Bauer, 1987), Holland-Bartels and Kammer (1989) found no hermaphrodites in 255 *M. nervosa* collected from Upper Mississippi where summer water temperatures exceeded 25 C.

In Oklahoma waters, *Megalonaias nervosa* and *Amblema plicata* must have a shell height of 4 inches or greater to be legally harvested. The purpose of minimum size limit regulations is to protect species from harvest until they reach sexual maturity and have had the opportunity to spawn at least once (Todd, 1993). An assumption underlying size regulations is that the majority of mussels reproduce when they reach a certain minimum size. The four-inch size limit for *M. nervosa* in Oklahoma is based on information on the reproductive habits of the species in the Upper Mississippi River (Woody and Holland-Bartels, 1993) and Kentucky Reservoir (Todd, 1993) where the species can begin reproduction at age eight (correlated with a four-inch shell height). We do not have any information on the

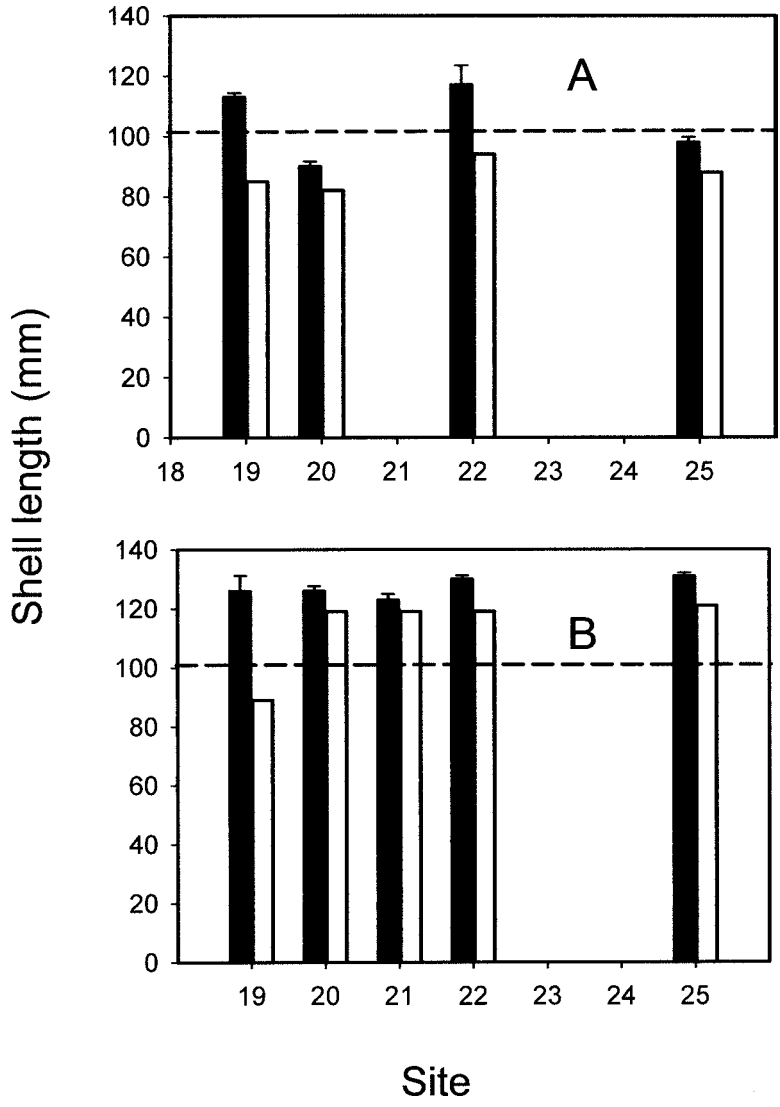


FIG. 4.—Size distribution of (A) *Amblema plicata* and (B) *Megalonaias nervosa* by site. The black bar represents mean shell height, the white bar is minimum shell height, and the dashed line represents the Oklahoma 4 inch size limit

reproductive biology *M. nervosa* in the Poteau River and we do not know if they follow this pattern. However, examination of the size distributions of both *M. nervosa* and *A. plicata* indicate that recruitment of these species in the Poteau River has been poor in recent years (Fig. 4). Most *M. nervosa* exceed the four inch limit, indicating that this size restriction offers little protection from overharvest (Fig. 4). In fact, *M. nervosa* individuals under the size limit only occurred at one site (Fig. 4). *Amblema plicata* has more individuals that fall under the size limit and, thus, may be better protected (Fig. 4).

Additional assumptions underlying size-limit regulations are that mussels reproduce every year and that older individuals are post-reproductive. However, many mussel species have episodic reproduction with years in which no recruitment occurs (Payne and Miller, 1989), and we suspect that this is the case in the Poteau River. Mussels are iteroparous and can continue reproducing throughout their life (Kat, 1984). *Megalonaias nervosa* in particular is a very long-lived species that has been documented to live greater than 80 y in nearby rivers in Kansas (B. Obermeyer, pers. comm.) and to be reproductively active at this age. In 2000 we extracted glochidia from an *M. nervosa* individual within the mussel sanctuary that had a shell height of over 5 inches. Thus, it appears that reproduction occurs in older *M. nervosa* individuals in the Poteau River.

In summary, the Poteau River retains a rich mussel fauna whose species composition appears to have changed little in the last several thousand years. However, abundance of mussels is much lower than in surrounding rivers. Density and demographic data both contraindicate commercial harvesting of mussels in the Poteau River. To protect the Poteau River mussel fauna into the future, the recently established mussel sanctuary should be retained and further commercial harvest of mussels halted.

Acknowledgments.—We thank Jennifer Johnson, Melissa Moore and Adam Richardson for field assistance. John Harris provided unpublished reports and information on Arkansas populations and Art Bogan verified identifications. We thank the Oklahoma Department of Wildlife Conservation for commercial harvest information. Funding was provided by the National Science Foundation, Biotic Surveys and Inventories Program (DEB9870092). This publication is a contribution to the program of the Oklahoma Biological Survey.

LITERATURE CITED

ALLEN, R. T. 1990. Insect endemism in the Interior Highlands of North America. *Florida Entomol.,* **73**:539–569.

ANTHONY, J. L. AND J. A. DOWNING. 2001. Exploitation trajectory of a declining fauna: a century of freshwater mussel fisheries in North America. *Can. J. Fish. Aquat. Sci.,* **58**:2071–2090.

BAUER, G. 1987. Reproductive strategy of the freshwater pearl mussel *Margaritifera margaritifera. J. Anim. Ecol.,* **56**:691–704.

BELL, R. E. 1953. The Scott Site, Leflore County, Oklahoma. *Am. Antiquity,* **18**:314–331.

BRANSON, B. A. 1983. The mussels (Unionacea: Bivalvia) of Oklahoma—part 2: the Unioninae, Pleurobemini and Anodontini. *Proc. Oklahoma Acad. Sci.,* **63**:49–59.

COCHRAN, T. G. AND J. B. LAYZER. 1993. Effects of commercial harvest on unionid habitat use in the Green and Barren rivers, Kentucky, p. 61–68. *In:* K. S. Cummings, A. C. Buchanan and L. M. Koch (eds.). Conservation and management of freshwater mussels. Preceedings of a UMRCC Symposium. Upper Mississippi River Conservation Committee, Rock Island, Ill.

DOWNING, J. A., Y. ROCHON, M. PERUSSE, AND H. HARVEY. 1993. Spatial aggregation, body size, and reproductive success in the freshwater mussel *Elliptio complanta. J. N. Am. Benthol. Soc.,* **12**: 148–156.

GORDON, M. E. 1980. Recent mollusca of Arkansas with annotations to systematics and zoogeography. *Proc. Arkansas Acad. Sci.,* **34**:58–62.

HARRIS, J. L. 1994. Survey of the freshwater mussels (Mollusca: Unionidae) of the Poteau River drainage in Arkansas. USDA Forest Service, Hot Springs.

HEINRICHER, J. R. AND J. B. LAYZER. 1999. Reproduction by individuals of a nonreproducing population of *Megalonaias nervosa* (Mollusca: Unionidae) following translocation. *Am. Midl. Nat.,* **141**: 140–148.

HOLLAND-BARTELS, L. E. AND T. W. KAMMER. 1989. Seasonal reproductive development of *Lampsilis cardium, Amblema plicata,* and *Potamilus alatus* (Pelecypoda: Unionidae) in the Upper Mississippi River. *J. Freshw. Ecol.,* **5**:87–92.

HOWELLS, R. G., R. W. NECK AND H. D. MURRAY. 1996. Freshwater mussels of Texas. Texas Parks and Wildlife, Austin, Tex.

ISELY, F. B. 1924. The freshwater mussel fauna of eastern Oklahoma. *Proc. Oklahoma Acad. Sci.,* **4**:43–118.

KAT, P. W. 1984. Parasitism and the Unionacea (Bivalvia). *Biol. Rev.,* **59**:189–207.

LAYZER, J. B., M. E. GORDON, AND R. M. ANDERSON. 1993. Mussels: the forgotten fauna of regulated rivers. A case study of the Caney Fork River. *Regul. River,* **8**:63–71.

LIGON, F. K., W. E. DIETRICH AND W. J. TRASH. 1995. Downstream ecological effects of dams. *BioScience,* **45**:183–192.

MATTHEWS, W. J., C. C. VAUGHN, K. B. GIDO AND E. MARSH-MATTHEWS. 2005. Chapter 7: Southern Plains Rivers. *In:* A. C. Benke and C. E. Cushing (eds.). Rivers of North America. Academic Press.

MAYDEN, R. L. 1985. Biogeography of Ouachita Highland fishes. *Southwest. Nat.,* **30**:195–211.

MILLER, A. C., L. RHODES, AND R. TIPPIT. 1984. Changes in the naiad fauna of the Cumberland River below Lake Cumberland in Central Kentucky. *Nautilus,* **98**:107–110.

MOULTON, S. R. AND K. W. STEWART. 1996. Caddisflies (Trichoptera) of the Interior Highlands of North America. *Mem. Am. Entomol. Inst.,* **56**:313.

OESCH, R. D. 1984. Missouri Naiades: a guide to the mussels of Missouri. Missouri Department of Conservation.

PARMALEE, P. W. AND A. E. BOGAN. 1998. The freshwater mussels of Tennessee. University of Tennessee, Knoxville.

PAYNE, B. S. AND A. C. MILLER. 1989. Growth and survival of recent recruits to a population of *Fusconaia ebena* (Bivalvia: Mollusca) in the lower Ohio River. *Am. Midl. Nat.,* **121**:99–104.

POFF, N. L., J. D. ALLAN, M. B. BAIN, J. R. KARR, K. L. PRESTEGAARD, B. D. RICHTER, R. E. SPARKS, AND J. C. STROMBERG. 1997. The natural flow regime. *BioScience,* **47**:769–784.

SHIMER, J. A. 1972. Field guide to the landforms of the United States. MacMillan, N. Y.

SPOONER, D. E. 2002. A field experiment examining the effect of freshwater mussels (Unionidae) on sediment ecosystem function. M.S. Thesis, University of Okla.

STRAYER, D. L. 1999. Statistical power of presence-absence data to detect population declines. *Conserv. Biol.,* **13**:1034–1038.

——— S. CLAYPOOL AND S. J. SPRAGUE. 1997. Assessing unionid populations with quadrats and timed searches. p. 163–169. *In:* L. M. Koch (ed.). Conservation and management of freshwater mussels II: initiatives for the future. Upper Mississippi River Conservation Committee, Rock Island, Ill.

SULOWAY, L., J. J. SULOWAY AND E. E. HERRICKS. 1981. Changes in the freshwater mussel (Pelecypoda: Unionidae) fauna of the Kaskaskia River, Illinois, with emphasis on the effects of impoundment. *Trans. Illinois Acad. Sci.,* **74**:79–90.

TODD, R. M. 1993. Tennessee's commercial musseling regulations, p. 32–37. *In:* K. S. Cummings, A. C. Buchanan and L. M. Koch (eds.). Conservation and management of freshwater mussels. Upper Mississippi Conservation Committee, St. Louis, Mo.

VAUGHN, C. C. 2003. The mussel fauna of the Glover River, Oklahoma. *Proc. Oklahoma Acad. Sci.,* **83**:1–6.

——— AND C. C. HAKENKAMP. 2001. The functional role of burrowing bivalves in freshwater ecosystems. *Freshw. Biol.,* **46**:1431–1446.

——— C. M. MATHER, M. PYRON, P. MEHLHOP AND E. K. MILLER. 1996. The current and historical mussel fauna of the Kiamichi River, Oklahoma. *Southwest. Nat.,* **41**:325–328.

——— AND M. PYRON. 1995. Population ecology of the endangered Ouachita Rock Pocketbook mussel, *Arkansia wheeleri* (Bivalvia: Unionidae), in the Kiamichi River, Oklahoma. *Am. Malacol. Bull.,* **11**:145–151.

——— AND C. M. TAYLOR. 1999. Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. *Conserv. Biol.,* **13**:912–920.

——— AND ———. 2000. Macroecology of a host-parasite relationship. *Ecography,* **23**:11–20.

———., ——— AND K. J. EBERHARD. 1997. A comparison of the effectiveness of timed searches vs. quadrat sampling in mussel surveys, p. 157–162. *In:* L. M. Koch (ed.). Conservation and management of freshwater mussels II: initiatives for the future.

WATTERS, G. T. 1992. Unionids, fishes, and the species-area curve. *J. Biogeogr.,* **19**:481–490.

WHITE, D. S. 1977. Changes in the freshwater mussel populations of the Poteau River system, Le Flore County, Oklahoma. *Proc. Oklahoma Acad. Sci.,* **57**:103–105.

WILLIAMS, J. D., S. L. H. FULLER AND R. GRACE. 1992. Effects of impoundments on freshwater mussels (Mollusca: Bivalvia: Unionidae) in the main channel of the Black Warrior and Tombigbee Rivers in western Alabama. *Bull. Alabama Mus. Nat. Hist.,* **13**:1–10.

WOODY, C. A. AND L. HOLLAND-BARTELS. 1993. Reproductive characteristics of a population of the washboard mussel *Megalonaias nervosa* (Rafinesque 1820) in the upper Mississippi River. *J. Freshw. Ecol.,* **8**:57–66.

WYCKOFF, D. G. 1976. Faunal materials from four early Caddoan tradition sites, Arkansas Basin, eastern Oklahoma. University of Oklahoma Department of Archaeology, Norman.

SUBMITTED 30 MAY 2003 ACCEPTED 23 FEBRUARY 2004