Population ecology of the endangered Ouachita rock-pocketbook mussel, *Arkansia wheeleri* (Bivalvia: Unionidae), in the Kiamichi River, Oklahoma

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Abstract. The only known remaining viable population of Arkansia wheeleri Ortmann and Walker, 1912, in the world occurs within a 128-km stretch of the Kiamichi River in Pushmataha County, Oklahoma. Within this river, A. wheeleri occurs only within the most species-rich mussel beds. In its optimal habitat, this species is always rare; mean relative abundance varies from 0.2-0.7% and the mean density is 0.27 individuals/m². The youngest individual A. wheeleri encountered was approximately 12 years of age. Forty-three percent of the historically known subpopulations of A. wheeleri below where inflow from an impounded tributary enters the Kiamichi River have apparently been extirpated, and no new subpopulations have been located. A. wheeleri survives at 75% of the historically known locations above the impounded tributary and five new subpopulations have been located.

Arkansia (syn. Arcidens) wheeleri Ortmann and Walker, 1912 (Bivalvia: Unionoidea), the Ouachita rock-pocketbook mussel, is a federal endangered species (Federal Register, 1991). Originally named Arkansia wheeleri by Ortmann and Walker (1912), Clarke (1981, 1985) recognized Arkansia as a subgenus of Arcidens. The species was considered by Clarke to be distinct. However, Turgeon et al. (1988) have continued to use the binomial Arkansia wheeleri.

The historical distribution of Arkansia wheeleri was in the Ouachita and Little Rivers in Arkansas and the Kiamichi River in Oklahoma, all south-flowing rivers out of the Ouachita Mountains (Fig. 1). A survey by Clarke (1987) indicated that the species was probably extirpated from the Ouachita River and severely depleted in the Little River in Arkansas. In 1992 and 1993, relict shells of A. wheeleri were found in the Little River in Oklahoma below Pine Creek Reservoir (Vaughn, 1993).

Arkansia wheeleri was first reported from the Kiamichi River by Isely (1924) who conducted a survey of the river in 1911. Clarke (1987) and Mehlhop and Miller (1989) both conducted recent status surveys for this species in the Kiamichi River. They found that A. wheeleri was patchily distributed and rare in the Kiamichi River from above Hugo Reservoir to Whitesboro (Fig. 2). Since the construction of a dam and reservoir in the lower reaches of the Kiamichi in the 1970s, some of the backwater areas

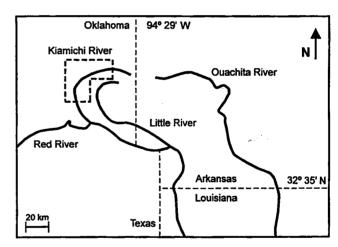


Fig. 1. Rivers in which *Arkansia wheeleri* historically occurred. Dashed box indicates area depicted in Fig. 2.

where it was known to occur have been destroyed (Valentine and Stansbery, 1971), and connection with potential habitats on the Red River and other tributaries to it has been blocked. Based on the above information A. wheeleri was listed as endangered in October 1991 (Federal Register, 1991).

The objectives of this study were to determine the distribution and abundance of *Arkansia wheeleri* in the Kiamichi River, characterize the species' microhabitat, and determine movement, growth, and survivorship of individuals. We also examined the impact of a reservoir on the population.

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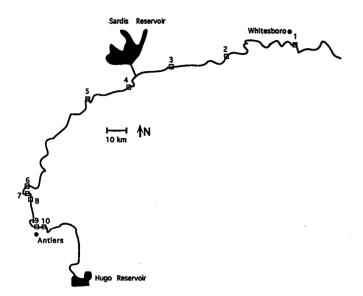


Fig. 2. Population monitoring sites for Arkansia wheeleri on the Kiamichi River.

STUDY SITE

The Kiamichi River is a major tributary of the Red River. It flows for a total of 180 km through a 4,800 km² drainage area across the Ridge and Valley Belt of the Ouachita Mountain geologic province and the Dissected Coastal Plain province (Curtis and Ham, 1972). The average gradient of the river is 0.47 m/km. Two reservoirs influence the river: Sardis Reservoir is an impoundment of Jackfork Creek, a tributary of the Kiamichi River. Hugo Reservoir is an impoundment of the lower Kiamichi River. The vegetation cover in the watershed can be described as a patchwork of forest made up of short-leaf and loblolly pine, mesic oak forests, and diverse bottomland habitats in various stages of maturity. Another large component of the watershed coverage is made up of pasture and other agricultural lands (Vaughn et al., 1993).

The Kiamichi River is located near the western edge of mussel species richness in the United States (Williams et al., 1992; Warren and Burr, 1994). Therefore, because of historical biogeographic factors, one would not expect diversity in the Kiamichi River to be as high as that in rivers in more eastern states. Nevertheless, the Kiamichi River has high mussel diversity for its size and geographic location. Fifty-five species of mussels are known from Oklahoma (Williams et al., 1992), and 29 of these currently occur in the Kiamichi River (Vaughn et al., 1993). Only two species that were known historically from the Kiamichi River (Isley, 1924) no longer occur there. Several species of mussels from the Kiamichi River are endemic to rivers in the Ouachita Mountains, including Arkansia wheeleri,

Ptychobranchus occidentalis (Conrad, 1836) and Villosa arkansasensis (Lea, 1862) (Pyron and Vaughn, 1994). P. occidentalis, the Ouachita kidneyshell, is a candidate for federal listing.

METHODS

Our quantitative survey efforts were restricted to areas that contained concentrations of mussels and thus could be defined as "beds." Mussel relative abundance and habitat data for 22 sites in the Kiamichi River were collected during July-August 1990. These sites included 11 areas defined as "pools," six areas defined as "backwaters," and five areas defined as "runs" (see Discussion). Mussel survevs (timed to standardize sampling effort) (Green et al., 1985: Kovalak et al., 1986) were conducted by handsearching with the aid of SCUBA in deeper areas and by hand searches in shallow areas in the following manner: (1) a shoal was identified for surveying; (2) the entire area was searched by at least two people for one hr; (3) all mussels encountered were removed to shore; (4) all mussels were immediately identified; (5) mussels were put back into the water as close to where they were removed as possible.

At each of the 22 sites, we measured water depth, water temperature, current velocity, conductivity, dissolved oxygen, and pH. Five measures of water depth and current velocity were taken across the mussel bed and averaged. Current velocity was measured 10 cm above the stream bottom with a Marsh-McBirney model 201 portable flow meter. Conductivity and dissolved oxygen were measured with Yellow Springs Instruments conductivity and dissolved oxygen meters, respectively. pH was measured with a Fisher Accumet portable pH meter.

At each site, we recorded the proximity of the site to entering tributaries, islands, and macrophyte cover. Three replicate substratum samples were collected at each site. These were brought back to the laboratory and allowed to dry. Samples were dry sieved, weighed, and individual proportions of samples were assigned to the appropriate substratum size class (in mm) following Hynes (1970:24). Standard sieving techniques do not segregate particles greater than about 2 mm in diameter (i.e. gravel from pebble from cobble). To determine the proportion of fine gravel, coarse gravel, pebble, and cobble in samples we randomly measured the diameter of 100 particles in the subsample greater than 2 mm in particle diameter (Dunne and Leopold, 1978).

In 1991, we selected ten of the 22 sites as long-term population monitoring sites for Arkansia wheeleri (Fig. 2). The ten sites were chosen to be as evenly distributed as possible along the Kiamichi River above Hugo Reservoir, but still be reasonably accessible, and included sites where A. wheeleri had been located by us in 1990, sites where it

had been found historically (Mehlhop and Miller, 1989; Clarke, 1987), and sites above and below the Sardis Reservoir and Jackfork Creek. Density and relative abundance data for mussel species at the ten monitoring sites were collected during July-August 1991. Densities were calculated from quadrat samples and relative abundances were estimated from timed searches, as described above. Ouadrat sampling was done with quarter-meter-square PVC pipe quadrats. Fifteen random quadrats were sampled for each site. Quadrats were searched by hand, with the aid of SCUBA in deeper areas, until all mussels had been recovered to a depth of 15 cm. Individual mussels were returned to the mussel bed as in timed searches. All A. wheeleri were measured using digital calipers (height, width, and length), and individually marked using numbered, laminated plastic fish tags. All specimens were returned to the same location from which they were captured.

To obtain additional information on Arkansia wheeleri size and age distribution, we measured relict shells of A. wheeleri deposited in the Oklahoma Museum of Natural History (OMNH, University of Oklahoma, Norman) or that we found on the Kiamichi River between 1990 and 1992. We counted external annuli on shells we had collected and those in OMNH (Neves and Moyer, 1988; McMahon, 1991). From the above data, we calculated shell length, width, and height vs. number of annuli regression lines. Shell height vs. number of annuli produced the best fit, and the resulting equation was used to predict the number of annuli for live mussels that had been measured in the field. We used Replicated Goodness of Fit tests (G_H) (Sokal and Rohlf, 1981) to compare size distributions of relict shells and live mussels, and to compare predicted age distributions of mussels.

We used several statistical techniques to explore relationships between Arkansia wheeleri distribution and abundance and measured habitat parameters. For all of these analyses, we used the data collected from the 22 sites in 1990. Associations between A. wheeleri and other species of mussels were calculated using Spearman Rank correlations on relative abundance data (Ludwig and Reynolds, 1988). We used discriminant function analysis (Sokal and Rohlf, 1981) to predict the presence or absence of A. wheeleri at a site based on the habitat characteristics of that site. We used an independent-sample t-test (one-tailed) (Sokal and Rohlf, 1981) to compare species richness at sites with and without A. wheeleri.

RESULTS

Arkansia wheeleri was found in ten of the 22 mussel beds that were sampled. Six of these ten sites were classified as pools and four were classified as backwaters. No

Table 1. Results of univariate F-tests of the presence or absence of Arkansia wheeleri at a site using four habitat variables. The multivariate model is significant ($F_{(1,20)} = 0.54$, P = 0.03).

Variable	F _(4,17)	P	
Depth	6.87	0.016	
Habitat type (pool, backwater, or run)	0.95	0.342	
Emergent vegetation (presence/absence)	5.45	0.030	
Mussel species richness	10.72	0.004	

specimens were found in any of the run areas sampled. A multivariate analysis of variance using all of the habitat variables to predict the presence or absence of A. wheeleri at a site was not significant ($F_{(12,9)} = 1.22$, P = 0.39). A significant discriminant model was produced using four habitat variables: depth, habitat type (pool, backwater, or run), presence or absence of emergent vegetation at the site, and mussel species richness (Table 1). This model successfully predicted the presence or absence of A. wheeleri 17 out of 22 times ($G_{(1)} = 7.72$, P = 0.005). Mussel species richness at a site was the best individual predictor of A. wheeleri occurrence (Table 1). Mussel sites where A. wheeleri occurred were more species-rich than other mussel sites that we sampled in the Kiamichi River ($t_{(15)} = 3.18$, P = 0.006).

Spearman rank correlations of relative abundance data revealed three significant associations between Arkansia wheeleri and other mussel species. A. wheeleri was positively correlated with the relative abundance of Quadrula cf. apiculata (Say, 1829) ($r_s = 0.437$, P < 0.05) and Megalonaias nervosa (Rafinesque, 1820) ($r_s = 0.423$, P < 0.05), and negatively correlated with Lampsilis teres (Rafinesque, 1820) ($r_s = -0.368$, P < 0.05).

In most cases Arkansia wheeleri was located only through timed searches and did not occur in quadrat samples. Mean relative abundance of A. wheeleri at monitoring sites in 1990-1992 is shown in Fig. 3 and varied from 0.2-0.7%. In 1991, A. wheeleri was found in quadrat samples at sites 6 and 7. This allowed us to estimate the density of A. wheeleri at 0.27 individuals m², at each of these sites.

In 1990 and 1991, we marked and released nine Arkansia wheeleri at the point of capture. In 1991, we recaptured only two marked individuals, although we found nine live individuals. Both recaptured specimens were found at site 3 (Fig. 2). Both of these individuals were found within one meter of where they were released in 1990. No other live A. wheeleri were found at site 3. In 1992, we recaptured the same two A. wheeleri at site 3 that we had recaptured in 1991. The individuals were within a few meters of where they had been released in 1991. The recaptured individuals had not grown discernably (i.e. not more than 1 mm, within the margin of error of our calipers). No other marked specimens were recaptured in 1992. The

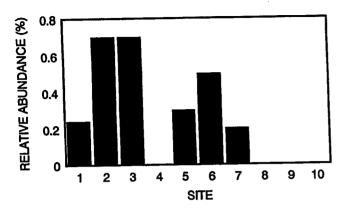


Fig. 3. Mean relative abundance of Arkansia wheeleri at the 10 monitoring sites in 1990-1992.

size distribution (means for 1990-1992) for A. wheeleri in the Kiamichi River is shown in Fig. 4.

The overall size distribution of relict shells in OMNH (N = 50) was significantly different than the size distribution of live Arkansia wheeleri in the Kiamichi River (N = 43) (Fig. 4, $G_{H(5)} = 23.1$, P < 0.001). The resulting regression equation for number of annuli on shell height was Y = (-0.483)X + 49.62 (N = 24, R² = 0.467, P < 0.05). We used the above equation to predict the age of A. wheeleri specimens from shell height. Predicted age distributions of spent shells vs. live A. wheeleri were also significantly different ($G_{H(12)} = 57.43$, P < 0.001). Using this technique, the youngest predicted age for a live specimen was 12 years. If this estimate is accurate, none of the A. wheeleri we encountered on the Kiamichi River during our study were produced after Sardis Reservoir was filled in 1983.

Arkansia wheeleri occurs both above and below the inflow to the Kiamichi River from Sardis Reservoir via Jackfork Creek. Of our ten monitoring sites, three were located above Sardis Reservoir and seven below (Fig. 2). All of these sites historically harbored A. wheeleri. A. wheeleri was found during this study at all three sites (100%) above Sardis Reservoir. A. wheeleri was found at three of seven sites (43%) below the reservoir inflow. The relative abundance of A. wheeleri at sites above Sardis Reservoir was generally greater than the relative abundance of A. wheeleri at sites below the reservoir (Fig. 3), although these differences were not statistically significant.

DISCUSSION

Prior to this study, the habitat of Arkansia wheeleri was reported to be backwater reaches of rivers where current is slow and where there are relatively non-shifting deposits of silt/mud and sand (Wheeler, 1918; Isely, 1924;

Clarke, 1987). We found that this species occured in both pools and backwaters in the Kiamichi River, not just in backwaters as was previously believed. The distribution of A. wheeleri may have been underestimated in past surveys because backwaters are relatively easy to survey, whereas pools often require SCUBA.

Although pools and backwaters were considered different habitat types in this study, in reality they are tightly interconnected and share many characteristics in common. Backwater areas tend to be shallower and have finer substrata. As backwaters merge into the main river channel they turn into deeper pools with coarser substrata and slightly higher current velocities. In the Kiamichi River, Arkansia wheeleri occurs in both of these habitats. In addition, we believe A. wheeleri moves back and forth between these habitats either voluntarily or through physical displacement of shifting sediments. Locomotory tendencies differ among different mussel species. For example, individuals of Anodonta grandis Say, 1829, migrate up and down with changes in water level (White, 1979) and in this way avoid stranding at low water. Other species such as Uniomerus tetralasmus (Say, 1831) and the introduced Corbicula fluminea (Müller, 1774) remain in position and suffer prolonged exposure to air (McMahon, 1991). Marked individual A. wheeleri in a backwater area (site 3) did not move significantly from July 1990 to July 1992. However at another site (site 5), unmarked individuals moved from a backwater area into the adjacent pool area. This movement was probably the result of physical displacement of these individuals through sediment scour and redeposition.

Unlike previous surveys (Wheeler, 1918; Isely, 1924; Clarke, 1987), we did not find Arkansia wheeleri to be restricted to areas where the substratum was predominantly mud or fine sand. In the Kiamichi River, A. wheeleri is just as prevalent in gravel/cobble/coarse sand substrata (which predominates in pools) as in finer substrata. Recent studies

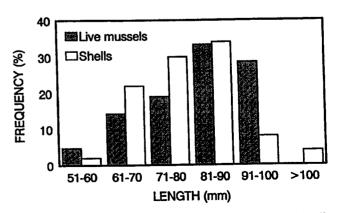


Fig. 4. Total lengths of live Arkansia wheeleri (N = 43) compared to relict shells (N = 50) from the Kiamichi River.

addressing the substratum preferences of unionids have reached different conclusions, and substratum preferences among unionids remain poorly understood. However, mussels are generally believed to be most successful in stable, sand/gravel mixtures and are generally absent from substrata with heavy silt loads (Salmon and Green, 1983; Stern, 1983; Cooper, 1984; Way et al., 1990). Most unionid species can be found on a number of different substrata, but growth rates of individuals in each microhabitat can be quite different (Kat, 1982; Hinch et al., 1989). Furthermore, many mussel species can occupy a wide range of habitats as a result of extensive larval dispersal over a heterogenous stream environment (Strayer, 1981), but growth and reproduction can be optimized only under the habitat conditions described above.

Arkansia wheeleri only occurred at the most speciesrich sites in the Kiamichi River. These shoals represent optimal habitat for most mussel species, as evidenced by the large number of species and their high abundance. These shoals usually contain both pool and backwater areas, have significant gravel-bar development with accompanying vegetation [dominated by Justicia americana (Linné) Vahl], and are close to a tributary (usually within 0.4 km). Shoals are usually adjacent to a major riffle area, although they can be either up- or downstream of the riffle. Other studies have shown that these mainstream river shoals in shallower areas with slow, steady current and vegetation and coarse substrate are optimal habitat for lotic unionids because of minimal turbulence, low silt and steady food supply (Salmon and Green, 1983).

In the majority of mussel species, the greatest amount of growth occurs in the first few years of life. Shell growth rate then declines exponentially with age, although the rate of tissue biomass accumulation usually remains constant (McMahon, 1991). Our examination of live Arkansia wheeleri in the Kiamichi River and of relict A. wheeleri shells in museum collections indicates that this growth pattern is also followed by A. wheeleri. Early annuli (those near the umbo) are much wider than later annuli near the edge of the shell. Therefore, our finding of no discernable growth in the two marked individuals that we recaptured is not surprising because they were older, adult specimens.

Recruitment, growth and survival of mussels can be assessed by monitoring changes in density and size demography of natural populations (Payne and Miller, 1989). We have no quantitative historical data on densities of Arkansia wheeleri in the Kiamichi River or anywhere else. Past size distribution, however, can be assessed by examining the size distribution of relict shells. The size distribution of live A. wheeleri in the Kiamichi River is skewed to the left (Sokal and Rohlf, 1981) (Fig. 4) with more large individuals and fewer small individuals than one would expect from

a statistically normal distribution. The size distribution of relict shells (Fig. 4) follows a more normal distribution, with a greater proportion of smaller individuals than in the live population. Looking at these shell length data alone, one would conclude that the size distribution of A. wheeleri in the Kiamichi River has changed over time and recruitment has decreased.

There may be problems with comparing the size distributions of relict shells with live shells. Relict shells from museum collections may have been collected in a size-biased manner because the rate at which dead shells are moved by currents, disintegrate through time, and are collected, could all be functions of shell size. Nevertheless, we would predict that these forces would make it more likely for collectors to find large relict shells rather than small relict shells. Because we found that our "population" of relict shells was generally smaller than our population of live mussels, such a size bias would actually make our demographic estimates conservative.

External annular rings have long been used to determine mussel age and growth rates. Recently this technique has been criticized as being replete with problems (Neves and Moyer, 1988; Downing et al., 1992). Natural erosion and corrosion of shells makes it difficult to distinguish true from false annuli. For example, false annuli can be formed by the incorporation of small substrate particles into mussel shells. It is difficult to count closely deposited growth lines near the margins of old shells. This produces an underestimate of shell age that becomes more erroneous with shell age. Downing et al. (1992) studied populations of Lampsilis radiata (Gmelin, 1791) and Anondonta grandis in an oligotrophic lake. In these populations, many mussels showed no new external annuli at all, even several years after individual animals had been marked. They concluded that estimates of growth based on shell annuli consistently overestimated real shell growth. In addition, shell size and growth rates are linked to environmental conditions. For example, some species form narrower shells in coarser substrates (Hinch et al., 1989) or grow faster in sand than in mud (Hinch et al., 1986). However, taking into account the large margin of error in using this method, most Arkansia wheeleri encountered in the Kiamichi River were old. Using this method, the youngest live A. wheeleri specimen we encountered was approximately 12 years of age. No juveniles were encountered. Both types of data, shell-size distributions and ages predicted from external annuli, demonstrated that most A. wheeleri encountered in the Kiamichi River were old.

Because of its rarity, the reproductive biology of Arkansia wheeleri remains unknown. Like other anodontines, it is probably bradytictic. The closest relative of A. wheeleri, Arcidens confragosus (Say, 1829), becomes gravid in the fall and releases glochidia in the spring

(Clarke, 1981). We were unable to obtain any gravid A. wheeleri and thus obtained no glochidia. A. wheeleri glochidia are probably similar to other alasmidontine glochidia. Alasmidontine glochidia are asymmetrical and have a stylet covered with microstylets which facilitate attachment to the fish host. Glochidial releases are probably tied to natural water temperature changes in the spring and fall (Jirka and Neves, 1992).

It appears that historically, Arkansia wheeleri survived equally well above and below the impounded tributary to the Kiamichi River (Clarke, 1987). Historically, A. wheeleri occurred in at least seven sites below the tributary. However, in five years of combined sampling effort by Mehlhop and Miller (1989), 1988-1989, and ourselves, 1990-1992, only three subpopulations of A. wheeleri have been found below Jackfork Creek. Therefore, only three out of seven (43%) of the known subpopulations of A. wheeleri survive below Jackfork Creek. In contrast, three out of four (75%) of the historical locations of A. wheeleri above Jackfork Creek have been confirmed and five new locations have been discovered. No new locations have been discovered below Jackfork Creek despite intensive survey efforts. In addition, the relative abundance of A. wheeleri is slightly higher above Jackfork Creek than below, although these differences are not statistically significant. Unfortunately, we have no historical abundance data for A. wheeleri in the Kiamichi River.

The greatest threats to the continued existence of Arkansia wheeleri in the Kiamichi River are land use changes, including further impoundment of the river, water transfers, timber harvesting, and pollution from agricultural and industrial development (Neves, 1993; Mehlhop and Vaughn, 1994). This species is also threatened by the invasion of exotic bivalve species, particularly the zebra mussel, Dreissena polymorpha (Pallas, 1771). D. polymorpha is now found in the Arkansas River system in Oklahoma. The high dispersal capabilities of this species make it highly probable that it will invade the Red River system, including the Kiamichi River, in the near future (French, 1990).

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