Freshwater Mussel Populations in Southeastern Oklahoma:
Population Trends and Ecosystem Services

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Abstract

Both overall abundance and species richness of freshwater mussels have declined over the past century. Mussels are natural 'biofilters' that provide important ecosystem services in the rivers. Thus, the decline of this fauna may have long-term, negative consequences for the functioning of river ecosystems. The major cause of mussel decline is from the alteration of the natural flow regime of rivers, primarily by impoundments and channelization. Hydrologic alterations impact mussels both directly through physical stress, such as temperature changes, siltation and scour, and indirectly through changes in habitat, food and fish-host availability. There are approximately 52 mussel species that presently occur in Oklahoma waters, with the highest biodiversity and healthiest populations in the southeast. For example, 41/55 species (80%) occur in the Kiamichi and Little River watersheds. Within these watersheds, the number of sites at which species occur and species abundances are declining, and the biological integrity of numerous subpopulations have been greatly decreased by the loss of individuals. Three federally endangered mussel species occur in these rivers, the Ouachita rock pocketbook (*Arkansia wheeleri*), the winged mapleleaf (*Quadrula fragosa*), and the scaleshell (*Leptodea leptodon)*, while a fourth species, *Quadrula cylindrica*, the rabbitsfoot mussel, is being considered for listing.

Introduction

General impacts of hydrologic alterations on unionid mussels

The freshwater mussel (Unionidae) fauna of North America is the most diverse in the world, but is highly threatened (Bogan 1993), with major declines of mussel populations and species diversity occurring over the past century (Neves 1992; Neves *et al.* 1997; Ricciardi *et al.* 1998; Vaughn & Taylor 1999; McMahon & Bogan 2001). Currently, the U.S. Fish and Wildlife Service recognizes 12% of the native mussel fauna as extinct and 23% as threatened or endangered, and The Nature Conservancy considers 68% of the U.S. unionid species at risk, compared to only 17% for mammals and 15% for birds (Biggins & Butler 2000). Recent work has demonstrated that unionid mussels provide important ecosystem services in the rivers where they are abundant (Kasprzak 1986; Welker & Walz 1998; Vaughn *et al.* 2004a). Mussels are natural 'biofilters' that remove algae, bacteria and particulate organic matter from the water

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column. They influence nutrient dynamics in freshwaters through excretion as well as biodeposition of feces and pseudofeces (rejected food particles). By burrowing in the sediment they increase sediment water and oxygen content, and release nutrients from the sediment to the water column. Finally, the physical presence of both living mussels and their spent shells stabilizes sediment and creates habitat for other benthic organisms (Vaughn & Hakenkamp 2001; Spooner 2002; Strayer *et al.* 2004). Thus, the overall decline of this fauna may have long-term, negative consequences for the functioning of river ecosystems (Strayer *et al.* 1999; Vaughn & Hakenkamp 2001; Vaughn *et al.* 2004a).

Table 1. Life history traits of unionid mussels. Modified from McMahon & Bogan (2001) and Mehlhop & Vaughn (1994).

Life span	6 to 100 yr
Age at maturity	6 – 12 yr
Strategy	Iteroparous
Fecundity	200,000 – 17,000,000
Reproductive efforts per year	Typically 1
Juvenile size	50 – 400 um
Relative juvenile survivorship	Very low
Relative adult survivorship	High in undisturbed habitats
Larval habitat	Obligate parasite on fish

Unionid mussels possess a suite of traits that make them highly vulnerable to habitat disturbance (Table 1). Although fecundity is high, the odds of an egg successfully becoming an adult mussel are quite low. Unionids have a complex life history in which the larvae (glochidia) are obligate ectoparasites on the gills and fins of fish. The glochidia of many mussel species can only survive on a narrow range of fish-host species (Kat 1984; Watters 1993; McMahon & Bogan 2001). Once they have metamorphosed from the glochidial stage, juveniles must be deposited in favorable habitat in order to survive. Successful settlement of juveniles appears to be particularly affected by disturbance (Layzer & Madison 1995), and the demography of many mussel populations in disturbed areas is marked by periods when entire year classes are not recruited (Payne & Miller 1989). Because only larvae, attached to fish, can move between mussel beds, and juvenile survival is low (Yeager *et al.* 1994; Sparks & Strayer 1998), potential mussel colonization rates are low (Vaughn 1993). Reproductive maturity of unionid mussels is not reached until at least age 6 and most species live greater than 10 years, with some living as long as 100 years (Imlay 1982; McMahon & Bogan 2001). Once mature, adults in undisturbed habitat exhibit high survivorship (McMahon & Bogan 2001). However, adult mussels are sedentary; movements are seasonal and on a scale of a few to an estimated maximum 100 meters (Green *et al.* 1985; Waller *et al.* 1999). Therefore, unlike many stream organisms such as fish and aquatic insects (Townsend 1989; Matthews 1998), adult mussels have limited refugia from disturbance events in streams. In addition, the filter-feeding habits of mussels make them especially vulnerable to sedimentation and chemical pollution events (Havlik & Marking 1987).

The majority of mussel species are most successful where water velocities are low enough to allow substrate stability but high enough to prevent excessive siltation (Vannote & Minshall 1982; Hartfield & Ebert 1986; Strayer 1993; Strayer 1999). Because of this dependence on appropriate substrate and flow conditions, mussels are naturally patchily distributed in many rivers, often occurring in densely aggregated multi-species "beds" separated by areas where mussels occur sporadically or not at all (Strayer *et al.* 1994; Strayer *et al.* 2004). These habitat characteristics have been difficult to quantify, and mussels are often absent from areas that visually appear to be good habitat (Strayer 1993; Strayer & Ralley 1993; Vaughn *et al.* 1995; Strayer *et al.* 2004). Conventional methods for estimating instream flow preferences for mussels have been largely unsuccessful (Gore et al. 2001). Layzer & Madison

(1995) investigated the use of instream flow incremental methodology (IFIM) for determining microhabitat preferences of mussels in Horse Lick Creek, Kentucky. They found that results were flow conditional; i.e. because mussels are non-mobile and have highly clumped distributions, they appeared to prefer different hydraulic conditions at different stream discharges. However, unlike simple hydraulic variables such a depth and velocity, complex hydraulic characteristics such as shear stress were significantly correlated with mussel abundance (Layzer & Madison 1995). Strayer (1999) found that mussel beds were located in areas protected from high flows and subsequent shear stress and Hardison & Layzer (2001) found that shear velocity varies on a small spatial scale within mussel beds and is negatively correlated with mussel density.

The major cause of mussel decline in the U.S. is from the alteration of the natural flow regime of rivers, primarily by impoundments and channelization (Neves 1992; Allan & Flecker 1993; Bogan 1993; Watters 1996; Neves *et al.* 1997; Master *et al.* 1998; Vaughn & Taylor 1999; Watters 1999). The ways in which impoundments alter existing stream habitat and processes have been extensively described (Baxter 1977; Petts 1984; Yeager 1993; Ligon *et al.* 1995; Sparks 1995). Many mussels do poorly in the altered conditions within impoundments, which include general lack of flow, sedimentation, and frequent anoxic conditions in deeper areas (Haag & Thorp 1991; Watters 1999). Several dozen mussel species have been driven to extinction wholly or in large part by the construction of dams (Layzer *et al.* 1993; Lydeard & Mayden 1995; Watters 1999); nearly without exception impounded rivers have lost or changed their mussel faunas (Blalock & Sickel 1996; Watters 1999). For example, the mussel fauna of the Chickamauga Reservoir portion of the Tennessee River remained essentially unchanged for 2000 years prior to impoundment. After impoundment, over 30 species were extirpated and several are now extinct (Parmalee *et al.* 1982; Watters 1999).

Mussel populations also are impacted up and downstream of impoundments. River sections below impoundments are substantially different than free-flowing rivers (Yeager 1993; Poff *et al.* 1997). Effects include altered seasonality of flow and temperature regimes, changed patterns of sediment scour and deposition (Anderson et al. 1991), and altered transport of particulate organic matter, the food base for mussels (Petts 1984; Frissell *et al.* 1986; Ward & Stanford 1987; Ligon *et al.* 1995). Numerous studies have documented mussel declines below impoundments (Suloway *et al.* 1981; Miller *et al.* 1984; Williams *et al.* 1992a; Layzer *et al.* 1993; Vaughn & Taylor 1999; Garner & McGregor 2001). For example, the Kaskaskia River supported 40 mussel species prior to impoundment; eight years after impoundment the species count was down to 24 species, some sites no longer supported any mussels, and abundance had declined (Suloway *et al.* 1981; Watters 1999).

Hydrologic alterations impact mussels both directly through physical stress, such as temperature, siltation, and scour, and indirectly through changes in habitat, food, and fish-host availability. Fluctuating discharge alters the transport of the particulate material in the water column that is the primary food source for mussels. Depending on season and normal seston loads, this can impact mussels. Releases from impoundments often result in both abnormally high and low flows, sometimes on a daily basis, and these often occur at the "wrong" time of year (Yeager 1993; Poff *et al.* 1997; Richter & Richter 2000). Discharge that is either high during the wrong season or high too frequently can have devastating impacts on mussels. High discharge can displace settling juveniles before they have burrowed into the streambed or attached their byssal threads to sediment (Neves & Widlak 1987; Holland-Bartels 1990; Layzer & Madison 1995; Hardison & Layzer 2001). Increased discharge alters the distribution of sediment through scour, flushing, and deposition of newly eroded material from the banks. Mussels are often killed by sediment scour directly below dams (Layzer et al. 1993) and scour is a major reason for the failure of mussel re-introductions (Layzer & Gordon 1993). Sediment deposition clogs mussel siphons and gills (i.e. smothers them) and interferes with feeding and reproduction (Young & Williams 1983; Dennis 1984; Aldridge *et al.* 1987). Erosion caused by increased discharge at one location in a stream results in deposition of the eroded material further downstream, increasing the width-depth ratio of that portion of the channel and the potential for further bedload transport (Frissell et al. 1986). Therefore, increased discharge can cause habitat loss through both sediment deposition and increased bed mobility. Over time, higher base discharge levels and reduced periods between peak flood events decrease habitat complexity

by preventing the formation of areas of stabilized sediments (Frissell et al. 1986). As stated above, sediment stability is a critical habitat requirement for most mussels (Di Maio & Corkum 1995; Strayer 1999; Hardison & Layzer 2001).

Discharge that is either low during the wrong season or abnormally low for extended periods of time also negatively impacts mussels. Extended periods of low flow below impoundments results in the stranding of mussels (Fisher & Lavoy 1972; Spooner & Vaughn 2000); mortality in such cases is usually a result of desiccation and/or thermal stress as the temperature buffering capacity of the water is decreased with reduced water volumes (Watters 1999; Spooner & Vaughn 2000). Numerous mussel dieoffs related to the dewatering of tailwaters below dams and subsequent high water temperatures in the remaining shallow water have been documented (Riggs & Webb 1956; Watters 1999) If stranding does not result in mortality, the associated physiological stress reduces mussel condition and ultimately reproductive potential (McMahon & Bogan 2001). Long periods of excessively reduced discharge often result in the fragmentation of rivers into shallow pools isolated by long reaches of dry riverbed. Within these shallow pools mussel can be exposed to water temperatures exceeding 40ºC. In dry stretches stranded mussels are exposed to air and to solar insolation. Given that mussels are thermo-conformers without the ability to regulate body temperature, these conditions often result in high mortality rates (Spooner & Vaughn 2000). Mussels in shallow, isolated pools are also exposed to hypoxia from algal production. Unionids are typically tolerant of moderate bouts of hypoxia (as low as 2 mg/l) (Chen 1998); however, other bivalves, such as invasive *Corbicula* have reduced anaerobic capacity resulting in massive die-offs (White & White 1977; Milton & McMahon 1999). Ammonia pulses from decaying bivalves kill juvenile unionids and potentially reduce the condition of adult mussels.

Water temperature is especially critical to mussels and they deal with thermal stress in a variety of ways. In the event of dewatering, some species can move either vertically into the sediment or horizontally to deeper areas; this strategy can be energetically costly depending on substrate texture and the distance to cooler water (McMahon & Bogan 2001). A second strategy to contend with emersion is direct transfer of oxygen across the mantle edge exposed to the air, which mussels control by gaping. This approach is limited to environments with high humidity and moderate temperature (Dietz 1974). A third strategy is to close the valves and anaerobically catabalyze stored energy reserves. The success of this strategy depends on the amount of energy reserves available and the duration of dewatering (McMahon & Bogan 2001). The main anaerobic storage pathway for mussels is glycogen catabolism. Glycogen is easily transferred to glucose through glucogenesis and its metabolites are non-toxic (Chen et al. 2001) (unlike catabolism of protein which produces toxic ammonia by products); however, shifts in hemolymph pH due to metabolites produced by glycogen catabolism must be buffered by the sequestration of carbonated from the shell (Byrne et al. 1991). Given that anaerobic catabolism is an underlying mechanism for emersion survival, factors that control glycogen storage capacity should directly influence the ability of mussels to survive drought events.

Reductions in water temperature below hypolimnetic release dams have been shown to reduce and even eliminate mussel populations for long distances (Ahlstedt 1983; Miller *et al.* 1984; Yeager 1993; Lydeard & Mayden 1995; Vaughn & Taylor 1999). Release of cold water during the summer when water temperatures should be warm suppresses mussel metabolic rates during a time of year when growth should be high (McMahon & Bogan 2001) and inhibits reproduction (Layzer et al. 1993). Coldwater releases also may eliminate or inhibit reproduction of some species of warmwater fishes (Layzer *et al.* 1993; Yeager 1993) and increase the success of introduced coldwater species such as trout. Therefore, abnormally cold discharge, particularly in summer, may act as a permanent colonization barrier to mussels (Vaughn & Taylor 1999).

Because mussels are dependent on fish hosts, any effects of hydrologic alterations on fish hosts also impacts mussel populations. Distribution, abundance, and movement patterns of fish hosts have been shown to be critical to the distribution and abundance of mussels (Watters 1993; Vaughn 1997; Haag & Warren 1998; Vaughn & Taylor 2000). The disappearance of mussel species from several rivers has been linked to the disappearance of the appropriate fish host (Kat & Davis 1984), and mussels have re-colonized rivers after their fish hosts were re-introduced (Smith 1985). Lowhead dams have been shown

to block fish-host migration and lead to the extirpation of mussels in reaches above the dams (Watters 1996). Altered flow regimes can decrease both the species richness and abundance of fish communities (Gore & Bryant 1986; Kinsolving & Bain 1993; Scheidegger & Bain 1995), potentially eliminating mussel hosts. Impacts likely vary both seasonally and with river microhabitat. For example, a high proportion of nest-building fish species, such a centrarchids, are common mussel hosts (Kat 1984; Watters 1994). Thus, altered hydrology that impacts or prevents nesting could result in mussel glochidia failing to attach to hosts, and reduced mussel recruitment.

Mussels evolved in rivers that typically experienced seasonal periods of low and high flow. Recent studies indicate that instream flow needs are not the same for all mussel species (Hardison & Layzer 2001) and that natural, temporal variability in flows is important to maintaining diverse mussel assemblages. For example, recruitment of some species seems to be greatest at below average discharges, while other species require a more normal flow rate for successful recruitment (Gore et al. 2001). To maintain diverse mussel communities, annual hydrographs may need to vary seasonally and annually to provide optimal flows for different groups of species (Gore et al. 2001).

Mussels of southeastern Oklahoma Rivers

Historical information
Based on archeological evidence, the overall mussel species composition of southeastern Oklahoma rivers has changed little over the last several thousand years. For example, all mussel species identified from a Caddo Indian midden (ca. 3500-1000 B.P.) near the Poteau River, were found in the Poteau River in the last decade (Bell 1953; Wyckoff 1976; White 1977; Vaughn & Spooner 2004). No mussel species are known to be entirely extirpated from either the Kiamichi (Vaughn et al. 1996) or Little Rivers (Vaughn & Taylor 1999), the two rivers in the region that have been studied the most extensively.

While few rivers in the region have lost species outright, within rivers both the number of sites at which species occur and species abundances have declined. The recent fauna was first surveyed by Isely in the early 1900s (Isely 1911, 1914; Isely 1924; Isely 1931). He conducted a comprehensive distributional survey of the mussel fauna of the Red River drainage, focusing on the eastern half of Oklahoma, as part of a nation-wide effort by the U.S. Bureau of Fisheries to find mussel populations to harvest for the pearl-button industry. Isely sampled 20 sites in the Red River drainage from 1910-1912 (Isely 1924); six of these sites are now under impoundments. From 1990-1995 Vaughn (2000) re-sampled 19 sites in the Red River drainage, the majority in southeastern Oklahoma, that had been sampled historically by Isely and Valentine and Stansbery. She found that species richness decreased at 89% of the sites and that 86% of species occurred at fewer sites than in the past. Vaughn used these data to calculate local extinction rates (extinction rate from a local patch or site, not the river as a whole). Local extinction rates were significantly greater than colonization rates, indicating that mortality of mussels is exceeding recruitment in the region (Vaughn 2000).

In the early 1990s Vaughn & Taylor (1999) examined the distribution and abundance of mussels along a 240 km length of the Little River in Oklahoma, from above Pine Creek reservoir to the state line. They observed a mussel extinction gradient downstream from impoundments in the watershed. With increasing distance from Pine Creek Reservoir, an impoundment of the mainstem Little River, there was a gradual, linear increase in mussel species richness and abundance. Rare species only occurred at sites furthest from the reservoir. These same trends were apparent below the inflow from the Mountain Fork River, which is impounded upstream as Lake Broken Bow, and mussel abundance was greatly reduced. In both situations, below reservoir inflows abundance of even common, widespread mussel species was greatly reduced. Thus, even though no species extirpations are known from the Little River, the biological integrity of numerous subpopulations has been greatly decreased by the loss of individuals (Vaughn & Taylor 1999).

The lower Kiamichi River is impounded by Hugo Reservoir. Jackfork Creek, a tributary of the Kiamichi, flows into the river approximately half way down its 180 km length. Jackfork Creek is impounded by Sardis Reservoir. This creek is the largest tributary of the Kiamichi, contributing nearly

30% of the average river flows at the confluence of the two streams. During recent drought years, water that would normally drain into the Kiamichi has been held in Sardis Reservoir, exacerbating drought conditions and causing sections of the Kiamichi to stop flowing and in some cases go completely dry. The summer of 2000 was particularly harsh because of higher than average air temperatures and no rain. During the summer of 2000 Spooner and Vaughn (2000) monitored the effect of these extremely low water levels on a mussel assemblage in the lower Kiamichi near Moyers for which we had two previous years of population data; at this particular site, there was no flow and water temperature during our sampling exceeded 40°C. Mussel mortality was significantly correlated with water depth, with the highest survival in the deepest, coolest water. Mortality was species-specific, with smaller mussels appearing to be hardest hit. Mortalities of federally endangered species were observed (*A. wheeleri* (1 individual) and *L. leptodon* (1 individual)); both individuals were found freshly dead, with tissue still attached, suggesting that the recent mortality was due to the drought and high water temperature. In an effort to minimize mortality, The Army Corps of Engineering released a series of 12 cfs (cubic feet per second) surges of water from Sardis Reservoir resulting in a 4.4 cfs spike in discharge at Clayton and a 1.2 cfs spike at Antlers. Unfortunately, because to the riverbed was already very dry, most of the flow was lost to the water table, and the release was insufficient to reduce water temperature for mussels.

Current mussel fauna
Despite the declines discussed above, the four rivers of far southeastern Oklahoma (Kiamichi, Little, Glover and Mountain Fork) continue to harbor a rich and overall healthy mussel fauna. There are approximately 52 extant unionid mussel species known to presently occur in Oklahoma waters (Williams et al. 1992b), and 41 of these (80%) occur in these rivers. In 1998, The Nature Conservancy identified the Interior Highlands (which includes the four rivers in question) as one of the most critical regions in the U.S. for protecting freshwater biodiversity, based on its rich fish and mussel fauna. Based on a comprehensive national assessment of available data, The Nature Conservancy determined that all of the at-risk freshwater fish and mussel species in the U.S. could be conserved by protecting and restoring 327 watersheds (15% of total US watersheds) across the country; the Kiamichi and Little River watersheds were included in this highly select group (Master et al. 1998).

Three federally endangered species occur in these rivers, the Ouachita rock pocketbook, the winged mapleleaf, and the scaleshell. *Arkansia wheeleri*, the Ouachita rock pocketbook mussel, occurs in only three rivers in the world, the Kiamichi and Little rivers in Oklahoma, and in the Ouachita River in Arkansas (Vaughn *et al.* 1993; Vaughn 1994; Vaughn & Pyron 1995; Vaughn *et al.* 1995; Vaughn *et al.* 2004b). The Kiamichi population is considered the most viable; subpopulations are patchily located over a 128 km stretch of the river from near Whitesboro to directly above Lake Hugo. Within these subpopulations, the species is quite rare. Vaughn & Pyron (1995) found that in the Kiamichi River, *A. wheeleri* occurs only in the largest, most species-rich mussel beds. Even its optimal habitat the species was always rare; mean relative abundance varied from 0.2 to 0.7% and the mean density within large mussel beds was 0.27 individuals / m^2. The youngest individual *A. wheeleri* encountered was approximately 12 years of age, indicating that recruitment is low (Vaughn & Pyron 1995). One of the *A. wheeleri* subpopulations in the Kiamichi is located near the proposed water outtake at Moyers (Vaughn *et al.* 2004b). Two subpopulations of *A. wheeleri* have been identified in the Little River; both of these are located on the U.S. Fish and Wildlife Service Little River Wildlife Refuge (Vaughn *et al.* 1995).

Leptodea leptodon, the scaleshell mussel, was historically distributed throughout much of the Interior Basin but has been extirpated from much of its range. The species is now restricted to 13 streams in the Interior Highlands, including the Kiamichi River, where it is known from several sites (Vaughn *et al.* 2004b).

Quadrula fragosa, the winged mapleleaf, historically occurred in the Interior Basin from Minnesota to Alabama. Currently, the best population is in the St. Croix River in Wisconsin. A viable population is thought to exist in the Ouachita River in Arkansas (Hove *et al.* 2003). *Q. fragosa* have been observed in

the Kiamichi River, and in August, 2005, a population of what is believed to be *Q. fragosa* was discovered in the Little River. Genetic studies need to be conducted to determine if these are indeed *Q. fragosa*.

Several of the mussel species occurring in the four rivers are endemic to the Ouachita Highlands or Interior Highlands. These include *Arkansia wheeleri*, discussed above, *Ptychobranchus occidentalis* and *Villosa arkansasensis*. *Ptychobranchus occidentalis*, the Ouachita kidneyshell, occurs sporadically throughout the Kiamichi and Little rivers (Vaughn *et al.* 1996; Vaughn & Taylor 1999), and is a dominant species in the Mountain Fork (Vaughn & Spooner 2000) and Glover rivers (Vaughn 2003b). *Villosa arkansasensis*, the Ouachita creekshell, occurs in the Little, Glover and Mountain Fork rivers (Vaughn & Taylor 1999; Vaughn & Spooner 2000; Vaughn 2003b).

Quadrula cylindrica, the rabbitsfoot mussel, is being considered for listing as an endangered species by the U.S. Fish and Wildlife Service. The range of this species has declined significantly. One of the most viable remaining populations is in the Little River in Oklahoma (USFWS 2005) where at least 5 subpopulations exist from just above Idabel through upper portions of Little River Wildlife Refuge (Vaughn et al., unpublished data). A small population occurs in the Glover River above the Highway 3 crossing (Vaughn 2003b).

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