Impoundments and the Decline of Freshwater Mussels: a Case Study of an Extinction Gradient

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Abstract: *One major factor leading to the imperilment of freshwater mussels (Bivalvia, Unionidae) has been the large-scale impoundment of rivers. We examined the distribution and abundance of mussels at 37 sites along a 240-km length of the Little River in southeastern Oklahoma, U.S.A., which is affected by both main-stem and tributary reservoirs. We observed a mussel extinction gradient downstream from impoundments in this river: with increasing distance from the mainstem reservoir there was a gradual, linear increase in mussel species richness and abundance. Mussel species distributions were significantly nested, with only sites furthest from the impoundment containing relatively rare species. Below the confluence with the inflow from the second reservoir these same trends were apparent but much weaker, and overall mussel abundance was greatly reduced. Our results suggest that considerable stream lengths are necessary to overcome the effects of impoundment on mussel populations, and such information should be considered in conservation and management plans.*

Represamiento y Declive de Mejillones de Agua Dulce: El caso de Estudio de un Gradiente de Extinción

Resumen: *Uno de los factores que conduce mayormente al riesgo de los mejillones de agua dulce (Bivalvia, Unionidae) ha sido el represamiento de rios a gran escala. Examinamos la distribución y abundancia de mejillones en 37 sitios a lo largo de 240 km de longitud de el río Little en el Sureste de Oklahoma, U.S., el cual ha sido afectado por la construcción de reservorios tanto en sus tributarios, como en el cauce principal. Observamos un gradiente de extinción rio abajo a partir de los reservorios: al incrementarse la distancia a partir del reservorio en el cauce principal, se presenta un incremento gradual en la riqueza y abundancia de especies de mejillones. La distribución de especies de mejillones fue significativamente anidada, con únicamente los sitios más alejados del reservorio conteniendo especies relativamnete raras. Este mismo patrón fue aparente hacia abajo de la confluencia con el segundo reservorio, aunque de manera más débil y con una abundancia total de mejillones grandemente reducida. Nuestros resultados sugieren que se necesita una longitud considerable de arroyo para contrarrestar los efectos del represamiento sobre las poblaciones de mejillones y esta información deberá ser considerada en planes de conservación y manejo.*

Introduction

Freshwater ecosystems and the species that inhabit them are imperiled disproportionately compared to other groups (Master 1990). The most highly threatened and rapidly declining group of freshwater organisms are the unionid mussels (Mollusca, Bivalvia, Unionidae). Of the 297 species and subspecies of native North American mussels, 19 are extinct, 62 are listed as federally endangered or threatened, and 130 are in need of conservation status (Neves 1993; Williams et al. 1993; U.S. Fish and Wildlife Service 1995, 1996). The U.S. Fish and Wildlife Service estimates that as many as 45 species of mussels may become extinct in the United States within

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the next 10 years (Shannon et al. 1993). The consequences of this catastrophic decline of an entire fauna go beyond the loss of species per se. Mussels serve critical trophic and nontrophic roles in the functioning of river ecosystems (Negus 1966; Kasprzak 1986; Layzer et al. 1993; Strayer et al. 1994); their extirpation likely will alter ecosystem functioning in many North American rivers.

Freshwater mussels possess a suite of traits that render them especially vulnerable to habitat disturbance. Mussels have extended life spans that range to over 100 years depending on the species (Bauer 1983; Heller 1990). Maturity is delayed, with many species not reproducing until 6–12 years of age (Bauer 1983; McMahon 1991). They have reduced powers of dispersal (Kat 1984), poor juvenile survival (Yeager et al. 1994; Sparks & Strayer 1998), and long turnover times (Negus 1966). Adult mussels are sedentary filter-feeders that may remain in approximately the same location for their entire long life span, so mussels have limited refugia from habitat alteration (Sibly & Calow 1986; Townsend 1989). The larvae (glochidia) of freshwater mussels are obligate parasites on the gills or fins of fishes (Kat 1984), and many glochidia can survive only on a narrow range of host fish species (Watters 1994). 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).

A major factor in the demise of freshwater mussels has been the large-scale impoundment of rivers over the past 75 years (Benke 1990; Bogan 1993; Yeager 1993). Many mussel species do poorly in the altered conditions within impoundments, a phenomenon that is well documented (Williams et al. 1992; Blalock & Sickel 1996). Often, however, river sections below impoundments are also substantially different from 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, and altered transport of particulate organic matter, the food base for mussels (Baxter 1977; Petts 1980; Frissell 1986; Ward & Stanford 1987; Ligon et al. 1995). Several studies have documented mussel declines below impoundments (Suloway et al. 1981; A. C. Miller et al. 1984; Williams et al. 1992; Layzer et al. 1993), but these studies have not examined the spatial pattern of mussel distributions for long distances below impoundments. Because streams are basically linear systems, the altered flow, temperature, and other physicochemical parameters directly downstream from impoundments should display a gradual change toward background conditions with increasing distance from the source of disturbance. Rates of local extinction of species should be highly correlated with this linear gradient in habitat "recovery." As the habitat recovers or becomes less affected with distance

from the disturbance source, extinction rates should decline and faunal assemblages should become more similar to conditions above the impoundment or prior to the impoundment. This phenomenon has been documented for fish (Bain et al. 1988; Kinsolving & Bain 1993) and benthic macroinvertebrate (Voelz & Ward 1991) communities. We document a spatial extinction gradient in mussel assemblages in response to the influence of multiple impoundments along a river.

Methods

Study Area

The Little River, a major tributary of the Red River, drains 5700 km^2 in southeastern Oklahoma and southwestern Arkansas, U.S.A., and is known for its high diversity of mussels (31 species) and fish (>100 species; R. J. Miller & Robison 1973). Comparisons of historical mussel distributions (Isely 1924; Valentine & Stansbery 1971) with current distributions (Vaughn 1997 & unpublished data) reveal no known mussel extirpations from the river. The upper reaches of the river are in the Ouachita Mountains, an area of rugged, long, parallel, east-west-trending mountain ridges. The upper watershed is heavily forested and used primarily for silviculture. Lower reaches of the river flow through the fertile bottomlands of the Gulf Coastal Plain (Rutherford et al. 1992).

The Little River is influenced by two impoundments. The mainstem of the river is impounded by 1644-km^2 Pine Creek Reservoir (Fig. 1). This reservoir began operation in 1969 and is used for flood control, water supply, and recreation (Oklahoma Water Resources Board 1990). A major tributary to the Little River, the Mountain Fork River, is impounded by 1952-km^2 Broken Bow Reservoir, which was formed in 1968 for generation of hydroelectric power, flood control, water supply, and recreation. Outflow from Broken Bow Reservoir enters the Little River via the Mountain Fork River, 64 km downstream of Pine Creek dam (Fig. 1).

Sampling

Riverine mussels 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; McMahon 1991; but see Strayer & Ralley 1993). Because of this dependence on appropriate substrate and flow conditions, mussels are naturally patchily distributed in many rivers, sometimes occurring in densely aggregated multi-species "beds" separated by areas where mussels occur sporadically or not at all (Dennis 1984; Neves & Widlak 1987; Strayer et al. 1994; Vaughn & Pyron 1995). We traversed
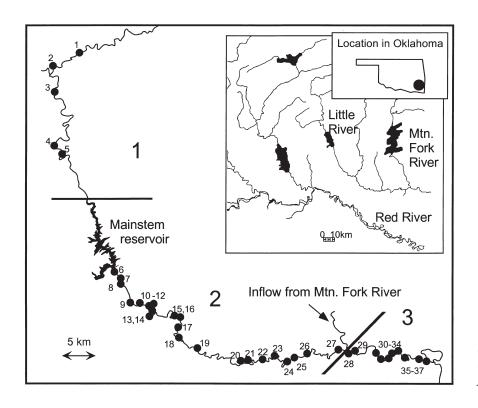
Figure 1. Map of the Little River showing sections (1–3) and sampling locations (circles).

the Little River (Fig. 1) by small boat and conducted reconnaissance snorkel searches for live mussels in areas where dead shells were observed and in areas where substrate and flow conditions were deemed appropriate for mussels (Vaughn et al. 1997). When live mussels were observed, we used snorkeling or scuba to determine the up- and downstream boundaries of mussels in that stream reach. We then conducted a timed search of that area. A timed search is the most common technique for collecting information on mussel abundance and is the only technique that can reliably be used to obtain estimates of total species richness and to locate rare species (Kovalak et al. 1986; Cawley 1993; Strayer et al. 1997; Vaughn et al. 1997). Timed surveys were conducted by two experienced surveyors systematically swimming over the area of mussel concentration wearing a mask and snorkel and picking up mussels by hand. Scuba was used in deeper areas (>75 cm). 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, surveyors also dug in the substrate for buried mussels. Mussels were returned to the mussel bed alive after all sampling was completed. Total search time varied with mussel abundance; each site was searched for at least 1 hour. More time was spent in large beds that contained more individuals.

Data Analyses

For data analysis we divided the Little River into three sections (Fig. 1): section one upstream of the mainstem reservoir, section two between the mainstem reservoir and the confluence with the Mountain Fork River, and section three downstream of the confluence with the Mountain Fork River. We limited our analysis of the hypothesized extinction gradient to the areas below impoundments, sections two and three. Section one was a high-gradient, upland reach of the river that differed from the coastal plain sections (two and three) in many important habitat characteristics such as substrate and stream size (Taylor & Lienesch 1996).

We used linear regression to determine if mussel species richness and abundance increased with distance downstream from the impact source. The significance of each regression was determined with a randomization procedure (Manly 1991). The dependent variable was shuffled 5000 times, and the observed regression coefficient was compared to the distribution of those obtained from the randomization procedure.

Nestedness of species assemblages occurs when the species found at sites with lower numbers of species are subsets of the species found at richer sites (Patterson 1987; Wright & Reeves 1992). Strong nestedness patterns are common in island and anthropogenically fragmented systems and are often the result of highly ordered extinction processes. Atmar and Patterson (1993) developed a metric, *T*, that quantifies the degree of nestedness among a series of sites by measuring unexpected presences and absences on sites that have been "packed" into a state of maximum nestedness. The *T* is derived from entropy and information theory and describes the "biogeographic temperature" of a species by

site matrix. When $T = 0°$, a matrix is completely ordered or maximally nested. When $T = 100°$, locations of species in the site matrix are completely random. We used this metric to determine the degree of nestedness of mussel species assemblages in sections two and three of the river. A Monte Carlo procedure (Atmar & Patterson 1995) was used to assess the probability that the resulting distribution patterns could occur by chance. Observed T values were compared to those from 5000 randomly generated matrices.

Results

There was a strong, gradual, linear increase in mussel species richness and abundance in river section two at sites further away from the mainstem impoundment (Fig. 2). Mussel species richness ($R = 0.72$, $p < 0.0002$; Fig. 3) and total abundance ($R = 0.76$, $p < 0.0002$; Fig. 4) were significantly associated with distance downstream from the impoundment. Mussel species richness and abundance within section two did not begin to "recover" until 20 km downstream of the impoundment (Fig. 2, site 14) and did not peak until 53 km downstream of the impoundment (Fig. 2, sites 23–26). Abundant dead shell material, representing a diverse array of species, was found throughout section two, including directly below the dam where no live mussels were found (sites 6–8), indicating that mussels once thrived throughout the area. Mussel abundance never recovered within the 15 km of section three that we surveyed (Fig. 2).

Mussel species distributions within section two were significantly nested ($T = 14.71°$, $p < 0.001$), with only sites at the furthest distances downstream from the impoundments containing relatively rare species. For example, common species such as *Amblema plicata*, *Fusconaia flava*, and *Quadrula pustulosa* occurred throughout section two (Appendix). *Pleurobema rubrum* and *Quadrula cylindrica* occurred only at the more species-rich downstream sites (Appendix). The federally endangered species *Arkansia wheeleri* (Vaughn & Pyron 1995) occurred only at one downstream site (Appendix). Mussel species distributions within section three were not significantly nested ($T = 27.72°$, $p = 0.58$).

Discussion

Mussel assemblages in section two of the river were highly nested. This reach of river flows across the coastal plain through bottomland hardwood forest. There is no reason to expect that sites near the upper end of this river reach were, before impoundment by Pine Creek reservoir, measurably different with respect to habitat structure or flow regime. Dead shell is abun-
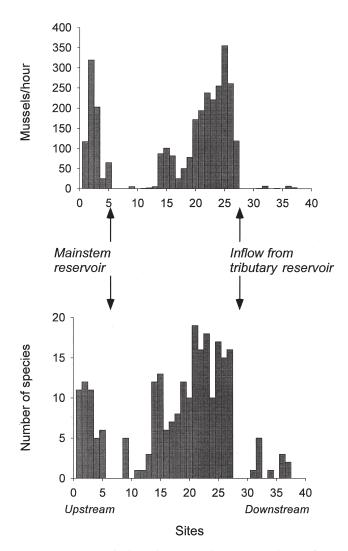

Figure 2. Mussel abundance and species richness for 37 sites in the Little River. Sites are shown in longitudinal sequence from upstream to downstream. Blank spaces indicate sites that were sampled and contained no live mussels. Actual site locations and distances between sites are shown in Fig. 1.

dant in the upper reaches and indicates that mussels once thrived there. Sites in the upper reaches are comparable to lower sites in terms of substrate size composition and vegetation (C.C.V., unpublished data). The most obvious difference since reservoir construction has been the alteration of the flow and temperature regimes, which gradually "recover" with downstream distance from the dam (U.S. Army Corps of Engineers, personal communication). These alterations appear to have produced an extinction gradient that is most severe near the source of the alteration.

The net result of this extinction gradient is a strong nested subset pattern of species composition. This nonrandom pattern of species' incidences is common in nature (Wright & Reeves 1992; Cook & Quinn 1995) but
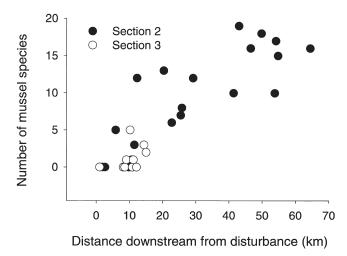
Figure 3. Mussel species richness versus distance downstream from Pine Creek Reservoir (section 2) and the inflow from the Mountain Fork River (section 3).

by itself reveals little about the underlying causes of nestedness. Previous studies have emphasized the importance of extinction in producing nested community patterns (Wright et al. 1998). Systems thought to be influenced largely by colonization (e.g., oceanic archipelagoes) were often poorly nested. Long-lived and slowly reproducing mussels would be unlikely to recolonize affected sites in the 25 years since dam operation began. In our study, the most likely cause of the nested pattern is selective extinction (rather than a gradient of recolonization) of mussel species. These selective extinctions are likely due to two factors. First, mussel assemblages typically consist of a few dominant, common species and many more less-abundant or rare species (Vaughn 1997). In our study, total mussel abundance increased with distance from the impoundment. Reservoir releases have likely caused a linear impact gradient, with more mussels killed or affected closer to the disturbance source. Although all mussel species are affected, the lower abundances of the rarer species would cause them to have higher local extinction rates (Lawton & May 1995). In addition, mussel species may vary in their tolerance to modified flow and temperature regimes; more sensitive species should have higher local extinction rates. Both of these processes should result in a gradient in species richness that forms a nested subset pattern, with the least abundant and/or most sensitive species only appearing in samples furthest downstream from the dam. Such a pattern is consistent with what we found.

Below the inflow from the second reservoir (section three), mussel species richness and abundance generally followed the same pattern as in section two, but mussel abundance was greatly reduced overall. We surveyed only the first 15 km of section three; there may be an ex-

tinction pattern within section three that was not observable within the limited spatial extent of our survey.

Mussels downstream of impoundments are likely affected both directly through physical stress (e.g., scour, temperature) and indirectly through changes in habitat, food, and fish-host availability. Stream organisms, including mussels, evolved in rivers that typically experienced seasonal low-flow and high-flow periods. 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 the year (Yeager 1993; Poff et al. 1997). High water velocities can displace settling juveniles before they can burrow in or attach their byssal threads to the substrate (Holland-Bartels 1990; Layzer & Madison 1995). Increased flows alter the distribution of sediment through scour, flushing, and deposition of newly eroded materials from the banks. Directly below dams, mussels are often killed by sediment scour (Layzer et al. 1993), and scour is a major cause of failure of mussel reintroductions (Layzer & Gordon 1993). Increased flows may result in bedload movement that is deleterious to mussels, particularly juveniles (Young & Williams 1983). Erosion caused by increased flows at one location results in deposition of this material further downstream, increasing the width-depth ratio of that portion of the channel and the potential for bedload transport (Frissell 1986). Thus, increased flows cause habitat loss through both sediment deposition and increased bed mobility. Over time, higher base flow levels and shorter periods between peak flood periods decrease habitat complexity by preventing the formation of areas of stabilized sediments (Frissell 1986). Sediment stability may be the most critical habitat requirement for mussels (Williams et al. 1993; Di Maio & Corkum 1995).
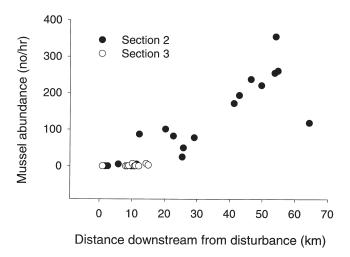

Figure 4. Mussel abundance (number/hour) versus distance downstream from Pine Creek Reservoir (section 2) and the inflow from the Mountain Fork River (section 3).

Unusually extended periods of low flow below impoundments have been shown to result in the stranding of mussels (Fisher & LaVoy 1972). Unlike highly mobile species such as fishes, which can move rapidly in and out of microhabitats with changes in water levels, mussels move slowly and are unable to respond to sudden drawdowns. Even if stranding does not actually kill a mussel, desiccation and thermal extremes will cause physiological stress and may reduce its reproductive potential (McMahon 1991). Fluctuating flows also mean that transport of particulates will vary. Depending on the flow schedule and the materials normally transported in the water column, there is the potential for loss of the organic materials that are the food base for mussels (Mehlhop & Vaughn 1994).

Habitat alteration downstream of impoundments also affects fishes, and dams block their upstream migration. Distribution and movement patterns of fish hosts have been shown to play an important role in the distribution of mussels (Watters 1992; Vaughn 1997; Haag & Warren 1998; C.C.V. & C.M.T., unpublished data). Extirpation of mussel species from several rivers has been linked to the disappearance of the appropriate fish host (Kat & Davis 1984), and mussel species have also recolonized rivers when their fish host was reintroduced (Smith 1985). Watters (1996) found that the distributions of two unionid species in five midwestern rivers were restricted to areas downstream of lowhead dams and attributed this to the dams blocking upstream migration of fish hosts.

Flow regulation decreases both the density and species richness of fish assemblages (Gore & Bryant 1986; Bain et al. 1988; Kinsolving & Bain 1993; Scheidegger & Bain 1995). Mussels prefer shallow water, so fishes that use shallow water—at least when mussels are expelling their larvae—are more likely to be the hosts of mussel species. For example, a high proportion of nest-building fish species, such as centrarchids, are common mussel hosts (Kat 1984; Watters 1994). Yet shallow-water fish assemblages are affected to a greater magnitude by altered hydrologic regimes than are deepwater fishes (Travnichek & Maceina 1994).

In our study, water releases during the summer months from both reservoirs are colder than the receiving waters. This change in temperature regimen also undoubtedly is affecting mussel populations. Downstream reductions in water temperature have been shown to reduce and even eliminate mussel populations for long distances in many rivers throughout the southeastern United States (Ahlstedt 1983; Miller et al. 1984; Yeager 1993; Lydeard & Mayden 1995). Coldwater releases during summer suppress mussel metabolic rates during the time of year when growth should be high (McMahon 1991) and directly inhibit 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) while increasing the success of tolerant species and introduced coldwater species such as rainbow (*Oncorhynchus mykiss*) and brown (*Salmo trutta*) trout (Burr 1991). Thus, coldwater releases may act as a permanent colonization barrier to mussels.

Other anthropogenic factors undoubtedly are influencing the Little River mussel fauna. For example, a paper mill discharges effluent into the river 9 km below Pine Creek Reservoir, directly above site 10 (Fig. 1). At this site dead mussels were recently found with holes dissolved in their shells. Within 2 km of the paper mill, mussel abundance and species richness recovered. Thus, although effluent from the paper mill affected mussels, it had only small-scale effects in comparison to those from the impoundment. Another possible anthropogenic disturbance in the watershed is siltation. A heavy layer of silt can cause suffocation of an entire mussel bed, and siltation has contributed to massive extirpations of mussels in other rivers (Anderson et al. 1991). Sources of increased siltation in rivers, including the Little River, include head cutting, gravel mining, runoff from poor agricultural practices, cattle grazing, and clearing of riparian vegetation (Bogan 1993). Siltation within the Little River is patchy and occurs in all of the sections of the river we sampled. There is no correspondence between siltation and the linear recovery of mussel abundance and species richness that we observed.

Environmental assessments are often based on patterns of species presence and absence at large spatial scales (Niemi et al. 1990). In the Little River, the biological integrity of the mussel populations obviously has been affected severely, even though we are not aware of any actual species extirpations from the river as a whole. Multiple factors often interact in a species' demise (Allan & Flecker 1993), and there are likely multiple impoundment-induced factors, as well as other anthropogenic factors, linked to the decline of the Little River mussel fauna. Nevertheless, our results demonstrate that, whatever the proximate factors effecting the mussels, considerable stream lengths below impoundments are necessary for mussel assemblages to recover pre-impoundment abundance and species richness values, and such information must be considered in conservation and management plans.

Acknowledgments

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Appendix

Abundance* of mussel species at the 37 sites sampled on the Little River.

Site number

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
All species combined	117	319	203	25	65	0	0	0	5	0	1	2	5	87	101	82	24	50	78	172	193	235	242	253	335	261	119	0	0	0	1	5	0	1	0	7	2.5
Actinonaias ligamentina														6.3	22	7	7	5	6		21	57	40	27	40	3	24										
Amblema plicata plicata	37	117	61	11	8				1		1		2	26	47	23	10	15	24	78	103	17	121	74	115	51	30					1				2	
Arkansia wheeleri																							0.7														
Ellipsaria lineolata																						1.3	2														
Elliptio dilatata																1		1.4			1.6																
Fusconaia flava	4	97	11	3	45				1					2.5	6.7	24	0.7	8	3.4			4.8	4	37	77	26	2					1				3	
Lampsilis cardium	4	3	7		2										2.7						1.1		1.3		1	2	2					1		1			
Lampsilis radiata	2	11	39													2	0.7																				
Lampsilis teres	1												1	0.5						14							0.5										1
Lasmigona complanata									1					0.3							0.6					0.5											
Lasmigona costata															0.7										3												
Leptodea fragilis														0.5					0.7			0.7	0.7				1										
Ligumia subrostrata			13																																		
Megalonaias nervosa															2.7	3			17		3.8	19	16	35	8	34	13										
Obliquaria reflexa															0.7	1		1			2.7	1.3	1.3	3	2	17	6									2	
Plectomerus dombeyanus									1					33	4	12	2	3	8	54	30	33	37	30	24	70	25										
Pleurobema rubrum																			5.4	2	2.7	4.7	1.3	5.5	15												
Potamilus purpuratus														0.2						4	0.6		0.7			1	1.5				0.7						
Ptychobranchus occidentalis		2		1														1							2												
Quadrula cylindrica												2	2	2	0.7	2					0.6	3.4	0.7	3	4												
Quadrula pustulosa	7	6	12	3	4									12	4.7	4		15	8	12	15	8	6	33	34	39	3.5					1					
Quadrula quadrula												2		2.7	6	2		1			2.2	76	4.7	3.5	3	4	3.5					1					
Strophitus undulatus																			1.3				0.7		1	2	1										
Toxolasma parva		1	2																	2																	
Tritogonia verrucosa	11	30	25	7	5									1.9	2					2	2.7	3.4	1.3	2	2	1	4										
Truncilla donaciformis																				2	0.6	3.4															
Truncilla truncata									1					1.4							1.6		0.7		1	1	2.5										1.5
Utterbackia imbecillis																							0.7														
Villosa arkansasensis	15	33	16															1				0.7				6											
Villosa iris	30	14	14																																		
Villosa lienosa	5	3	14												1.3				2		3.3	2															

*Abundance is standardized as the number of mussels found per hour spent searching.