AN ABSTRACT OF THE THESIS OF

Matthew D. Combes for the degree of Master of Science in Biological Sciences presented on 16 October 2003. Title: Mussel assemblages upstream from three Kansas reservoirs. Abstract approved: ______________________

Reservoir construction by damming of rivers has contributed to dramatic declines in species richness and abundance of freshwater mussel assemblages throughout North America. The effects of reservoirs on mussel assemblages within and downstream from the reservoir pool are relatively well known, but few studies have examined effects on upstream mussel assemblages. During summers 1999 and 2000, I surveyed 40 sites in the Marais des Cygnes (n=15), Fall (n=13), and Elk (n=12) rivers in eastern Kansas, upstream from three reservoirs, to examine effects of reservoir inundation on upstream mussel assemblages. I predicted that the present mussel assemblage would be composed of fewer species than the historic assemblage, that the percent of species missing from the historic assemblage would increase nearer the reservoirs, that mussel species richness and abundance would decrease nearer the reservoirs, and that substrate embeddedness and silt in the substrate would increase downstream. I recorded present and historically-occurring species plus 10 habitat variables at each site, then used Student's t-test, linear regression, and canonical correspondence analysis to examine decline in species richness in each river, to elucidate trends in species richness, mussel abundance, and habitat values in relation to frequency of reservoir inundation, and to model environmental correlates of assemblage structure. I collected 1367 live mussels of 18 species, and 29 species as weathered valves. In all three rivers, significantly fewer species were present alive than were present as weathered valves. Live species richness and abundance decreased nearer the reservior in the three rivers, whereas historic species richness was not significantly related to flood frequency in any river. Percent of species missing from the historic assemblage increased nearer the reservoirs, but this trend was significant only in the Marais des Cygnes. Substrate embeddedness and percent of silt in the substrate were not related to flood frequency in any river. Canonical correspondence indicated that Marais des Cygnes sites had a higher percentage of fine substrates than Fall and Elk river sites, and that this river's mussel assemblage was different from those of the Fall and Elk. Siltation caused by reservoir inundation might be an episodic event that does impact species richness and abundance nearer the reservoir, but that is difficult to detect except during inundation events.

MUSSEL ASSEMBLAGES UPSTREAM FROM THREE KANSAS RESERVOIRS

A Thesis

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by

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PREFACE

My thesis is composed of one chapter and is written in the style of the Journal of Freshwater Ecology. Style and formatting instructions can be found on the internet at http://www.jfreshwaterecol.com.

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INTRODUCTION

North America has the greatest diversity of freshwater mussels in the world, with approximately 300 species and subspecies (Williams et al., 1993; Turgeon et al., 1998). However, freshwater mussel populations have declined dramatically since Euro-American settlement (Neves, 1993; Strayer and Ralley, 1993; Williams et al., 1993; Brim Box and Mossa, 1999). Nearly half the species of freshwater mussels in North America are either federally listed, species of concern, or already extinct (Neves, 1993). Over-harvesting of mussels, chemical pollution, channel dredging, sedimentation from land use practices, competition from exotic species, and damming of rivers are proposed causes of the precipitous decline of North America's mussel fauna (Williams et al., 1993; Neves, 1993, 1997; Brim Box and Mossa, 1999).

Freshwater mussels also have declined in Kansas (Obermeyer et al., 1997). Historically, Kansas had at least 46 species of mussels (Obermeyer, 2000). However, 7 of these are now listed by the state as endangered, 4 as threatened, 12 as species in need of conservation, and 4 are believed to be extirpated from the state (Obermeyer et al., 1997; Obermeyer, 2000). The decline of freshwater mussels in Kansas is largely attributed to pollution, increased siltation from agricultural practices, channelization, and reservoir dam construction (Obermeyer et al., 1997; Obermeyer, 2000).

Reservoir dams affect mussel populations by changing rivers to lakes (Bates, 1962; Negus, 1966; Williams et al., 1993; Blalock and Sickel, 1996; Brim Box and Mossa, 1999). This change from lotic to lentic habitat can result in anoxic conditions that can suffocate mussels (Bates, 1962; Williams et al., 1993; Brim Box and Mossa, 1999). Siltation caused by decreased current velocities can bury mussels in the substrate, dilute food resources, lower productivity of food organisms, foul gills, reduce habitat for juveniles in the interstices of the substrate, and obscure glochidial dispersal mechanisms from potential sight-feeding host species (Bates, 1962; Harmon, 1972; Williams et al., 1993; Brim Box and Mossa, 1999). The change in habitat can alter composition of the ichthyofauna associated with a mussel assemblage, eliminating or reducing fish populations that serve as hosts for glochidial mussel larvae (Ruhr, 1956; Bates, 1962; Erman, 1973; Neves and Angermeier, 1990; Williams et al., 1993; Morgan et al., 1997; Brim Box and Mossa, 1999; Bonner and Wilde, 2000). Reservoir dams hinder mussel recolonization of suitable upstream habitat because host fish species infected with glochidia cannot pass upstream through a dam or through the lentic environment of a reservoir (Smith, 1985; Watters, 1996; Morgan et al., 1997; Wilde and Ostrand, 1999; Kelner and Sietman, 2000). Dams also have been shown to decimate mussel assemblages in their tailwaters by increasing water level fluctuations, destabilizing substrates, maintaining low water temperatures not conducive to mussel reproduction, and changing the ichthyofauna of the river (Neves and Angermeier, 1990; Poff et al., 1997; Tippit et al., 1997; Vaughn and Taylor, 1999). Little has been published on the effects of reservoirs on upstream mussel assemblages. Vaughn and Taylor (1999) reported reductions in species richness of mussel assemblages upstream from reservoirs. Watters (1996) and Kelner and Sietman (2000) reported extirpations of mussel species upstream from reservoirs, and suggested inhibition of host fish species' movements as a cause.

Reservoirs in Kansas can have more than 10 m difference in elevation between conservation pool and maximum flood pool. This difference in elevation leads to a reach of river upstream being inundated periodically with still reservoir water. Areas closer to conservation pool elevation are inundated more frequently than areas closer to maximum flood pool elevation, and thus are likely more prone to the combined negative effects of reservoirs. Mussel assemblages at lower elevations, with reservoir effects, would be expected to have fewer species and lower abundances (Bates, 1962; Parmalee and Hughes, 1993). A decrease in species richness would be opposite that expected for low to medium stream order reaches of natural streams, in which aquatic communities generally show greater diversity downstream (Vannote et al., 1980).

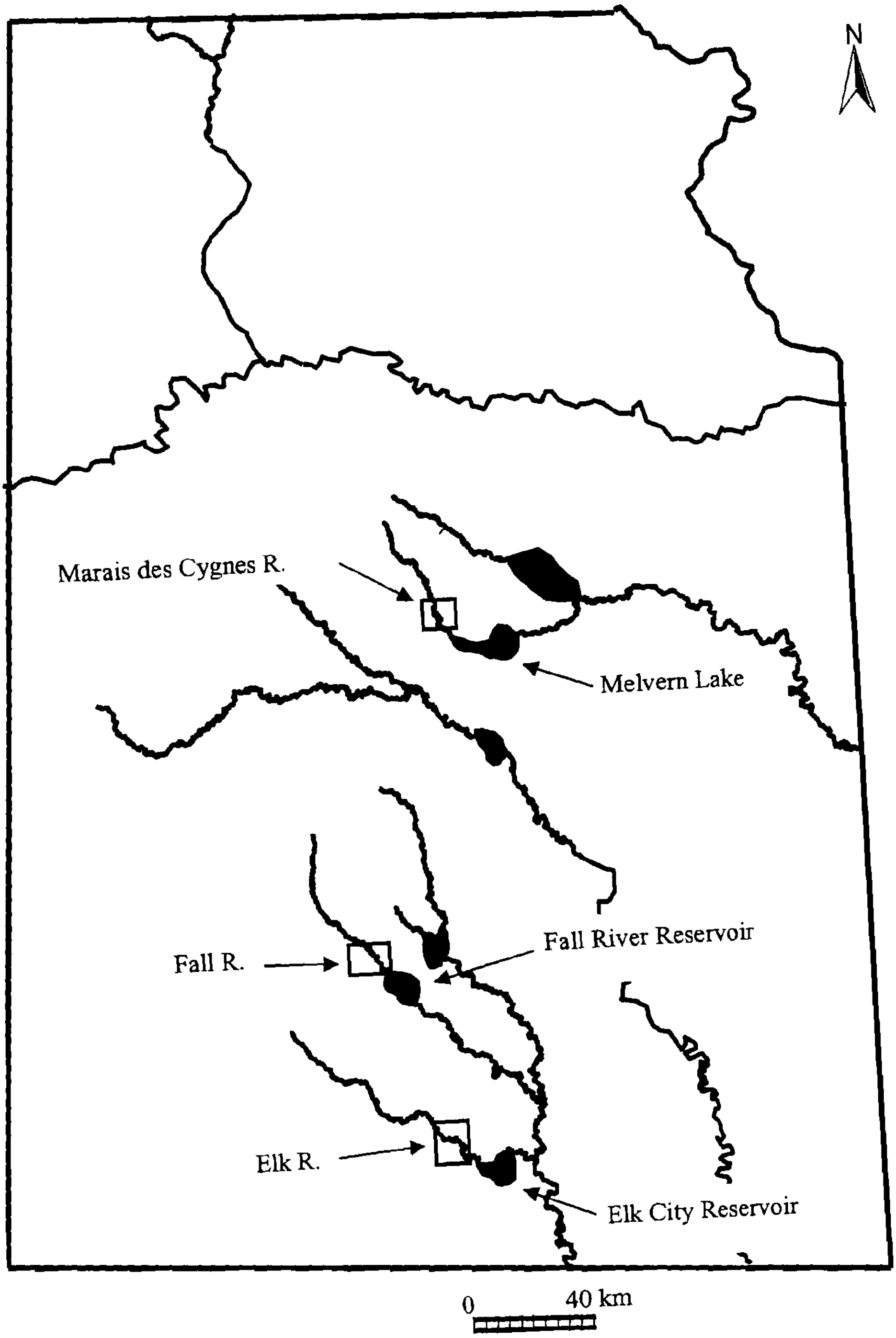
The goals of my study were to assess the influence of reservoirs on mussel assemblages and habitat characteristics upstream from three Kansas reservoirs. I predicted that the present mussel assemblage would be composed of fewer species than the historic assemblage, that the percent of species missing from the historic assemblage would increase nearer conservation pool of the reservoirs, that mussel species richness and abundance would decrease nearer the reservoirs, and that substrate embeddedness and percent of silt in the substrate would increase nearer the reservoirs.

MATERIALS AND METHODS

Study Areas

Melvern Lake, completed in 1970, impounds the 5^{th}-order Marais des Cygnes River in Osage County, Kansas (Figure 1), receives runoff from 907 km^2, and has a 6 m difference in elevation between flood and conservation pool. Fall River Lake, completed in 1949, impounds the 5^{th}-order Fall River in Greenwood County (Figure 1), receives runoff from 1521 km^2, and has an 11 m difference in elevation between flood and

Figure 1. Location of study areas in eastern Kansas.


N
Marais des Cygnes R.
Melvern Lake
Fall River Reservoir
Fall R.
Elk R.
Elk City Reservoir
0
40 km

conservation pool. Elk City Lake, completed in 1966, impounds the 5^{th}-order Elk River in Montgomery County (Figure 1), receives runoff from 1648 km^2, and has a 9 m difference in elevation between flood and conservation pool.

Methods

I obtained historic data on daily pool elevations for Melvern, Fall River, and Elk City reservoirs from the U.S. Army Corps of Engineers. From these data, I determined the duration of flooding (in days) at any given elevation (Appendix 1) of each river upstream from its respective reservoir. To examine the effect of reservoirs on the mussels of its respective river, I divided each river into three habitat reaches based on the total number of days the reservoir had inundated that section of the river (from the date the reservoir first reached conservation pool to 28 January 2000). The three habitat reaches were: (1) an upstream reach (areas inundated ≤1% of the total days above conservation pool elevation), (2) a middle reach (areas inundated > 1% and < 10% of the total days above conservation pool elevation), and (3) a downstream reach (areas inundated ≥10% of the total days above conservation pool elevation). I located boundaries for the habitat reaches with a microsurveying altimeter (Model M-1, American Paulin Systems, Cottonwood, Arizona).

I located four to six sites in each habitat reach, for a total of 15 sites on the Marais des Cygnes River (Figure 2), 13 on the Fall River (Figure 3), and 12 on the Elk River (Figure 4). I chose site locations based on hydrological similarities (e.g., gravel bars and riffles with shallow water), and by selecting locations spaced as evenly as

Figure 2. Location of 15 mussel survey sites in the Marais des Cygnes River, eastern Kansas.

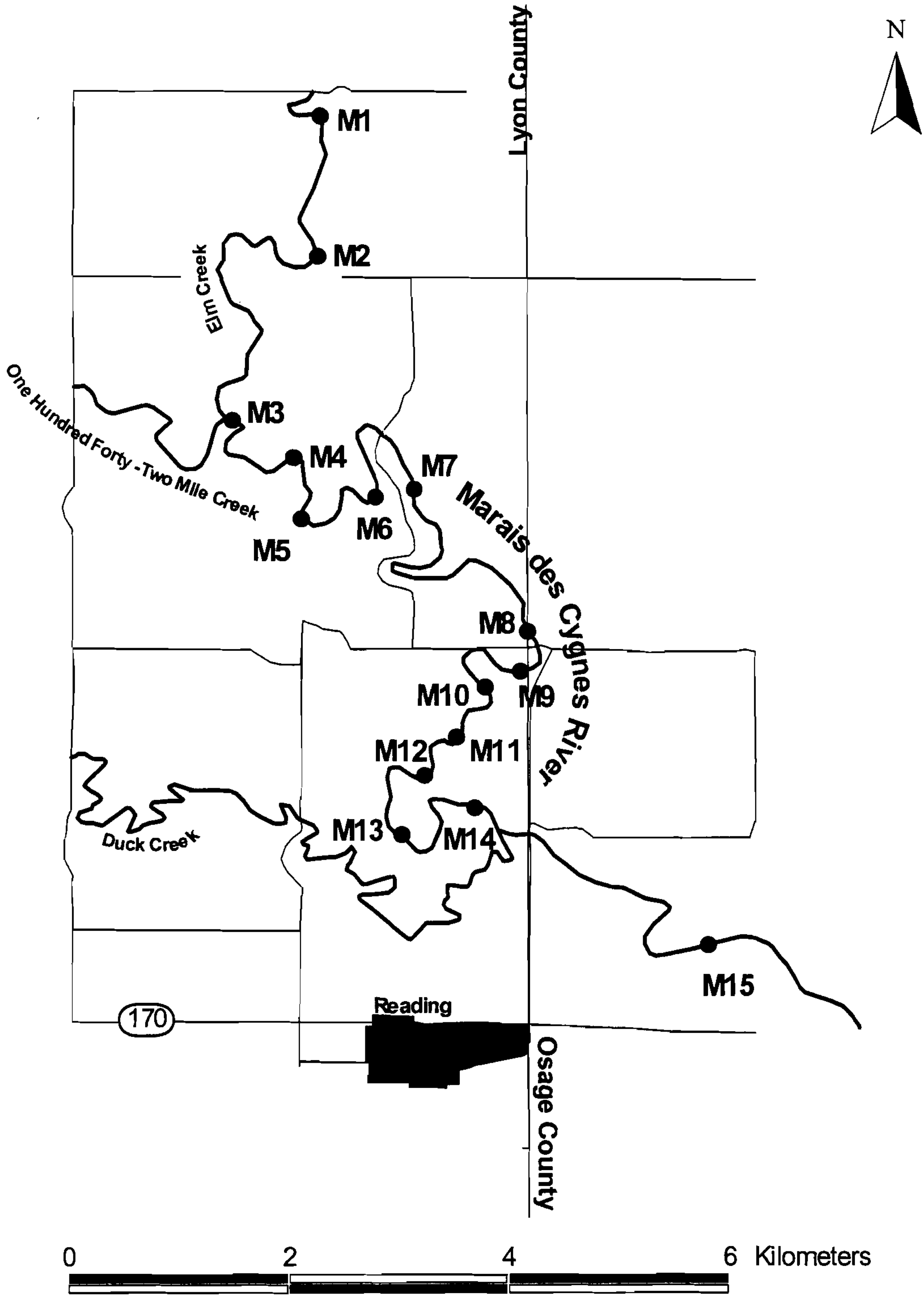

N
Lyon County
M1
M2
Elm Creek
One Hundred Forty - Two Mile Creek
M3
M4
M5
M6
M7
Marais des Cygnes River
M8
M9
M10
M11
M12
M13
M14
Duck Creek
M15
170
Reading
Osage County
0
2
4
6 Kilometers

Figure 3. Location of 13 mussel survey sites in the Fall River, eastern Kansas.

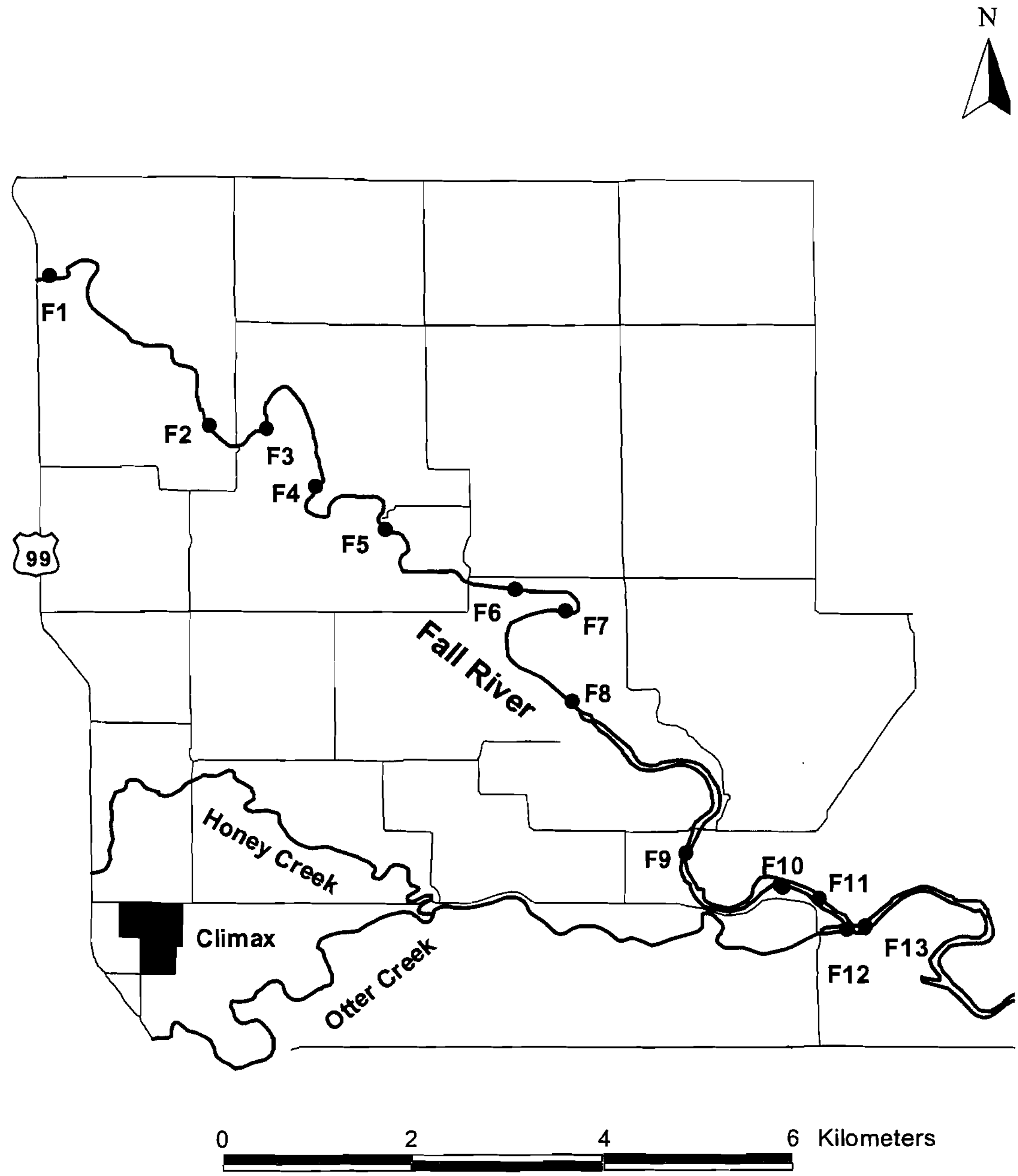
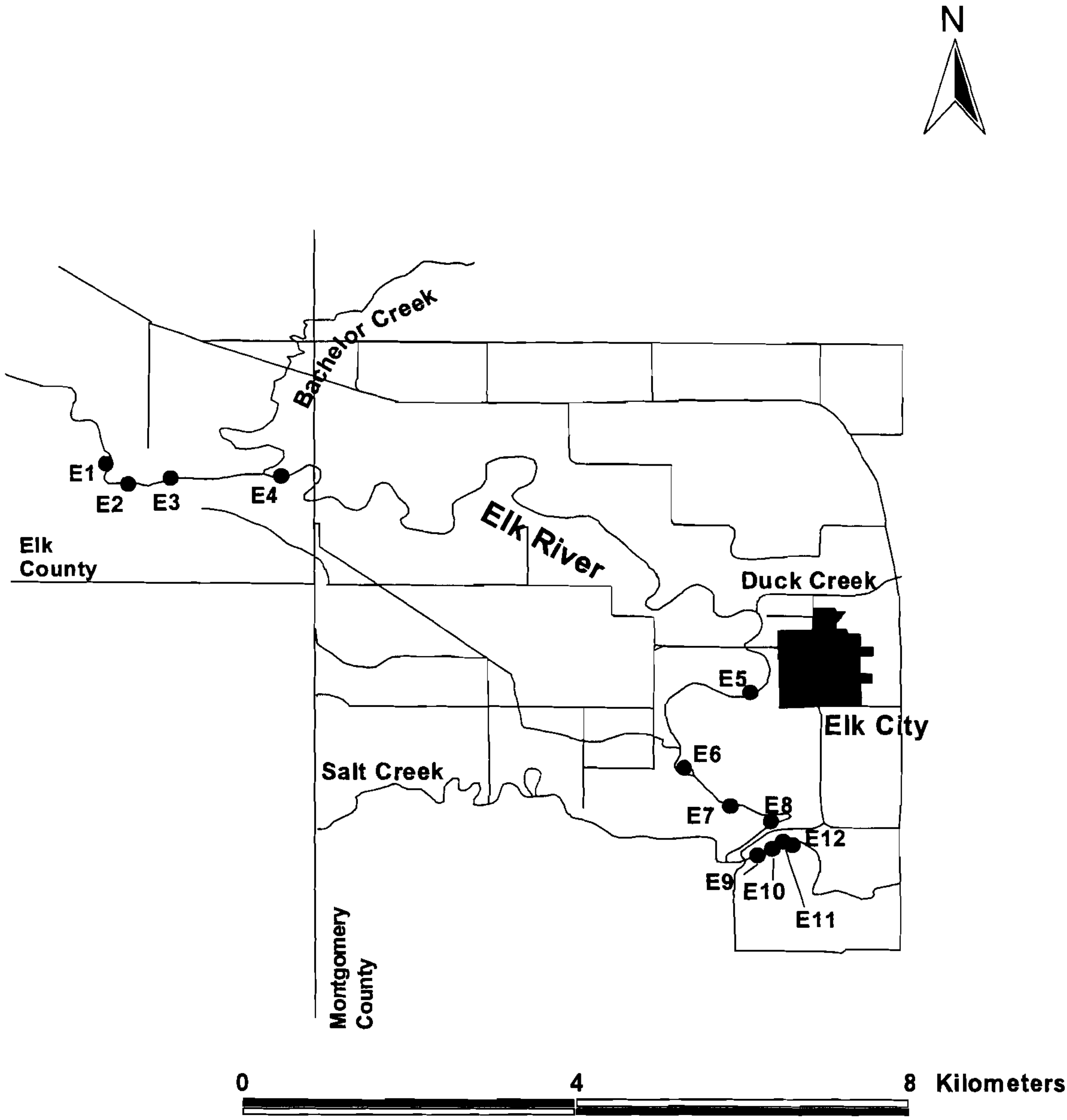

N
99
F1
F2
F3
F4
F5
F6
F7
F8
F9
F10
F11
F12
F13
Fall River
Honey Creek
Otter Creek
Climax
0
2
4
6
Kilometers

Figure 4. Location of 12 mussel survey sites in the Elk River, eastern Kansas.


N
Bachelor Creek
E1
E2
E3
E4
Elk County
Elk River
Duck Creek
E5
Elk City
E6
Salt Creek
E7
E8
E12
E9
E10
E11
Montgomery County
0
4
8 Kilometers

possible within each reach, and landowner permission to trespass. See site summaries in Combes et al. (2001) for descriptions of all sites.

I surveyed sites from 8 July to 6 September 1999 and 20 May to 26 July 2000. I sampled mussels with timed groping surveys, which have been demonstrated to be an effective and efficient means of estimating the abundance and species richness of freshwater mussel assemblages (Miller and Payne, 1993; Strayer et al., 1997; Vaughn et al., 1997; Obermeyer, 1998). I began surveying each site at the downstream end of a marked reach, and proceeded upstream in a zigzag pattern from bank to bank. I attempted to search approximately 750 m^2 along a 50 m reach at each site; actual searches varied from 410 to 1277 m^2 area ($\bar{x}$ = 839.0 m^2, SD = 239.4) and 30 to 70 m long ($\bar{x}$ = 52.1 m, SD = 10.3 m). Area, length, and time (60 to 186 min, $\bar{x}$ = 113.0 min, SD = 31.9) spent searching varied with width of channel, type of substrate, and abundance of mussels. I located mussels by tactile and visual cues, kept them in mesh bags until the end of each survey, then identified, counted, and redistributed them throughout the site.

To estimate the number of species that historically occurred at each site, I searched for weathered shell material along a 300 m reach of shore centered on the live mussel search area for ca. 40 min ($\bar{x}$= 38.0, range = 20 to 60, SD = 9.4). Time spent searching for weathered valves varied by extent of exposed gravel bar. At seven sites (M4, M10, M15, F11, F12, F13, E3) with little or no exposed gravel bar, I collected weathered valves along with live mussels during the timed groping surveys as well as from any exposed gravel bar present. I identified weathered valves from each site to generate a list of historically occurring species.

I characterized habitat at each site by assessing 10 variables along transects spaced every 10 m (perpendicular to flow) along the site: width, percent substrate composition (seven categories), substrate embeddedness, and substrate compaction. I measured width of each transect, and assessed the other variables at 2 m intervals along each transect. I estimated substrate composition by hand (Bain, 1999), visually estimating percent clay, silt, sand, gravel, cobble, boulder, and bedrock (size categories modified from Platts et al., 1983). I estimated and coded substrate embeddedness (defined as the layer of silt atop the substrate) as free of silt (1), a detectable layer of silt (2), moderately covered with silt (3), or heavily silted (4). I estimated substrate compaction by touch and categorized it as loose (1), medium compact (2), very compact (3), or bedrock or claypan (4).

Analysis

I used Student's t-test to compare number of live and historically occurring species at each site and linear regression to examine the effect of reservoir presence on mussel assemblages and habitat variables (SAS, ver. 8e; SAS Institute, Cary, North Carolina). I regressed species richness (number of species found alive), historic species richness (number of species represented by weathered valves), mussel abundance (number of live individuals of all species), percent of species missing from the historic mussel assemblage, and the 10 habitat variables against elevation of each site. I used elevation as the independent variable because it includes components of both inundation frequency and distance from reservoir. I arcsine square root transformed all species abundances and proportions of substrate to improve normality. I accepted the premise that linear regression is a robust method that can tolerate some departure from normality (Zar, 1996). Where experiment-wise errors were of concern, I adjusted alpha levels for rejecting null hypotheses with Bonferroni correction (Rice, 1989); otherwise, my alpha level was 0.05. I used canonical correspondence analysis (CCA; PC-Ord version 4; MjM Software Design, Gleneden Beach, Oregon) to model species-environment relationships of mussel assemblages in the three rivers. Species occurring at only one site were excluded from CCA following Gauch (1982) who recommended eliminating rare species that can have undue influence on the ordination. Only environmental correlates with jointplot scores greater than 0.20 are plotted in the ordination diagrams.

RESULTS

Overall

At 40 sites in the Marais des Cygnes, Fall, and Elk rivers, I collected 1367 live mussels. I collected 29 species as weathered valves, but only 18 as live individuals (Table 1). Significantly fewer species were present alive than present as weathered valves ($n = 40$, $t = -19.8$, $P < 0.0001$). All species collected alive also were collected as weathered valves.

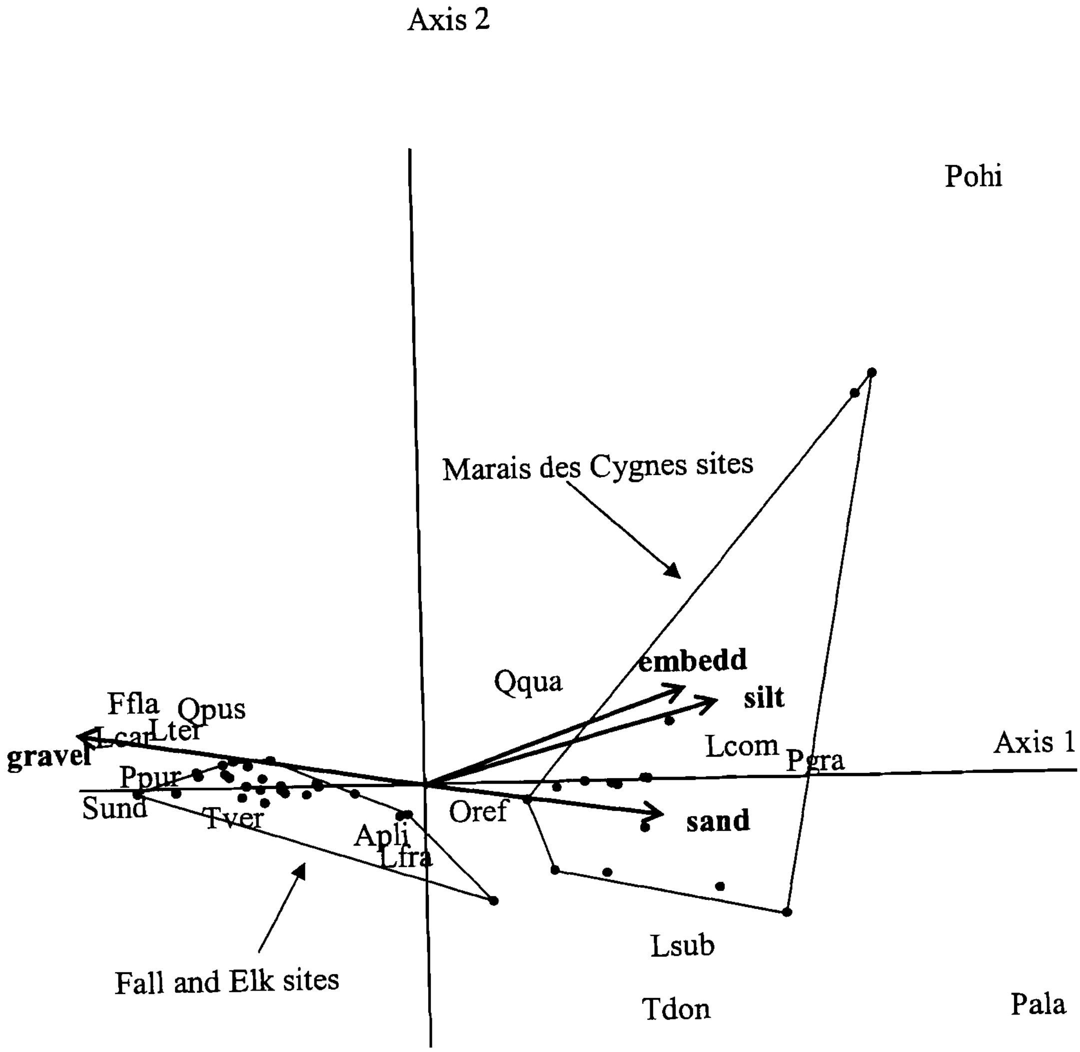
Ordination of 40 sites, 16 live species, and 10 habitat variables by CCA illustrated species-environment relationships for the three rivers (Figure 5). I excluded *Utterbackia imbecillis* from the ordination because it was found at only one site. Axis 1 (eigenvalue = 0.437; 3.2 SD) accounted for 16% of the variance in the species data, and Axis 2 (eigenvalue = 0.249; 3.8 SD) accounted for 9%. Both Axis 1 ($P = 0.01$) and Axis 2 ($P = 0.04$) were significant based on a 9999 iteration Monte Carlo test. Axis 1 indicated

Table 1. Key to common names, scientific names, jointplot abbreviations, and Kansas conservation status for mussel species collected live and as weathered valves in the Marais des Cygnes, Fall, and Elk rivers, 1999 and 2000. Abbreviations are given only for those species included in CCA jointplots. (*) indicates species present only as weathered valves. SINC = species in need of conservation.

Common name	Scientific name	Abbreviation	Status
threeridge	*Amblema plicata*	Apli	
western fanshell*	*Cyprogenia aberti*		Endangered
spike*	*Elliptio dilatata*		SINC
Wabash pigtoe	*Fusconaia flava*	Ffla	SINC
plain pocketbook	*Lampsilis cardium*	Lcar	
Neosho mucket*	*Lampsilis rafinesqueana*		Endangered
fatmucket*	*Lampsilis siliquoidea*		SINC
yellow sandshell	*Lampsilis teres*	Lter	SINC
white heelsplitter	*Lasmigona complanata*	Lcom	
flutedshell*	*Lasmigona costata*		Threatened
fragile papershell	*Leptodea fragilis*	Lfra	
black sandshell*	*Ligumia recta*		Extirpated[a]
pondmussel	*Ligumia subrostrata*	Lsub	
threehorn wartyback	*Obliquaria reflexa*	Oref	
round pigtoe*	*Pleurobema sintoxia*		SINC
pink heelsplitter	*Potamilus alatus*	Pala	
pink papershell	*Potamilus ohiensis*	Pohi	
bleufer	*Potamilus purpuratus*	Ppur	
Ouachita kidneyshell*	*Ptychobranchus occidentalis*		Threatened
giant floater	*Pyganodon grandis*	Pgra	
monkeyface*	*Quadrula metanevra*		
pimpleback	*Quadrula pustulosa*	Qpus	
mapleleaf	*Quadrula quadrula*	Qqua	
creeper	*Strophitus undulatus*	Sund	SINC
lilliput*	*Toxolasma parvus*		
pistolgrip	*Tritogonia verrucosa*	Tver	
fawnsfoot	*Truncilla donaciformis*	Tdon	SINC
deertoe*	*Truncilla truncata*		SINC
paper pondshell	*Utterbackia imbecillis*		

[a] Considered extirpated from Kansas until a single live individual was captured in the Marais des Cygnes River in 2002. Angelo, R.T. and M.S. Cringan. 2003. Rediscovery of the black sandshell, *Ligumia recta* (Lamarck, 1919), in Kansas. Transactions of the Kansas Academy of Science 106:111-113.

Figure 5. CCA axes 1 and 2 jointplot of sites, mussel species, and habitat variables from the Marais des Cygnes, Fall, and Elk rivers, Kansas, 1999 and 2000. Species abbreviations are given in Table 1. Environmental variables are substrate embeddedness and percent of substrate composed of silt, sand, and gravel. • indicate sites.



Axis 2
Pohi
Marais des Cygnes sites
Qqua
embedd
silt
Ffla
Qpus
Lcar
Lter
gravel
Lcom
Pgra
Axis 1
Ppur
Sund
Tver
Oref
sand
Apli
Lfra
Fall and Elk sites
Lsub
Tdon
Pala

an environmental gradient of embeddedness and percent substrate composed of silt and sand, versus gravel (Figure 5). All sites from the Marais des Cygnes River scored highest on this axis, and Fall and Elk river sites scored lowest. Mussel species scoring high on Axis 1 occurred only at Marais des Cygnes sites (*Potamilus alatus*, *Potamilus ohiensis,* and *Pyganodon grandis*) or were found in far greater abundance there than in the other two rivers (*Lasmigona complanata*, *Ligumia subrostrata*, and *Truncilla donaciformis*). Species scoring low on Axis 1 occurred only in the Fall and Elk rivers (*Strophitus undulatus*, *Lampsilis cardium*, *Fusconaia flava*, *Potamilus purpuratus*, *Lampsilis teres*, and *Quadrula pustulosa*).

Axis 2 suggested a gradient of embeddedness, and percent of substrate composed of silt and gravel versus sand (Figure 5). Two Marais des Cygnes River sites scored high on this axis, but other sites from all three rivers were near the centroid. *Potamilus ohiensis* scored high on this axis, and *P. alatus, T. donaciformis,* and *L. subrostrata* scored low.

The 15 Marais des Cygnes sites formed a discrete polygon in the jointplot separate from Fall and Elk river sites (Figure 5), indicating that Marais des Cygnes River sites were composed of a higher percentage of fine substrates than the Fall and Elk river sites. This separation is not surprising, as the rivers occur in two different river systems (Marais des Cygnes = Osage/Missouri system, Fall and Elk rivers = Verdigris/Arkansas system) that have had separate geological histories. Because ordination of the data set was dominated by differences between river systems, I conducted separate analyses for each river that more directly examined environmental correlates of their mussel assemblages.

Marais des Cygnes River

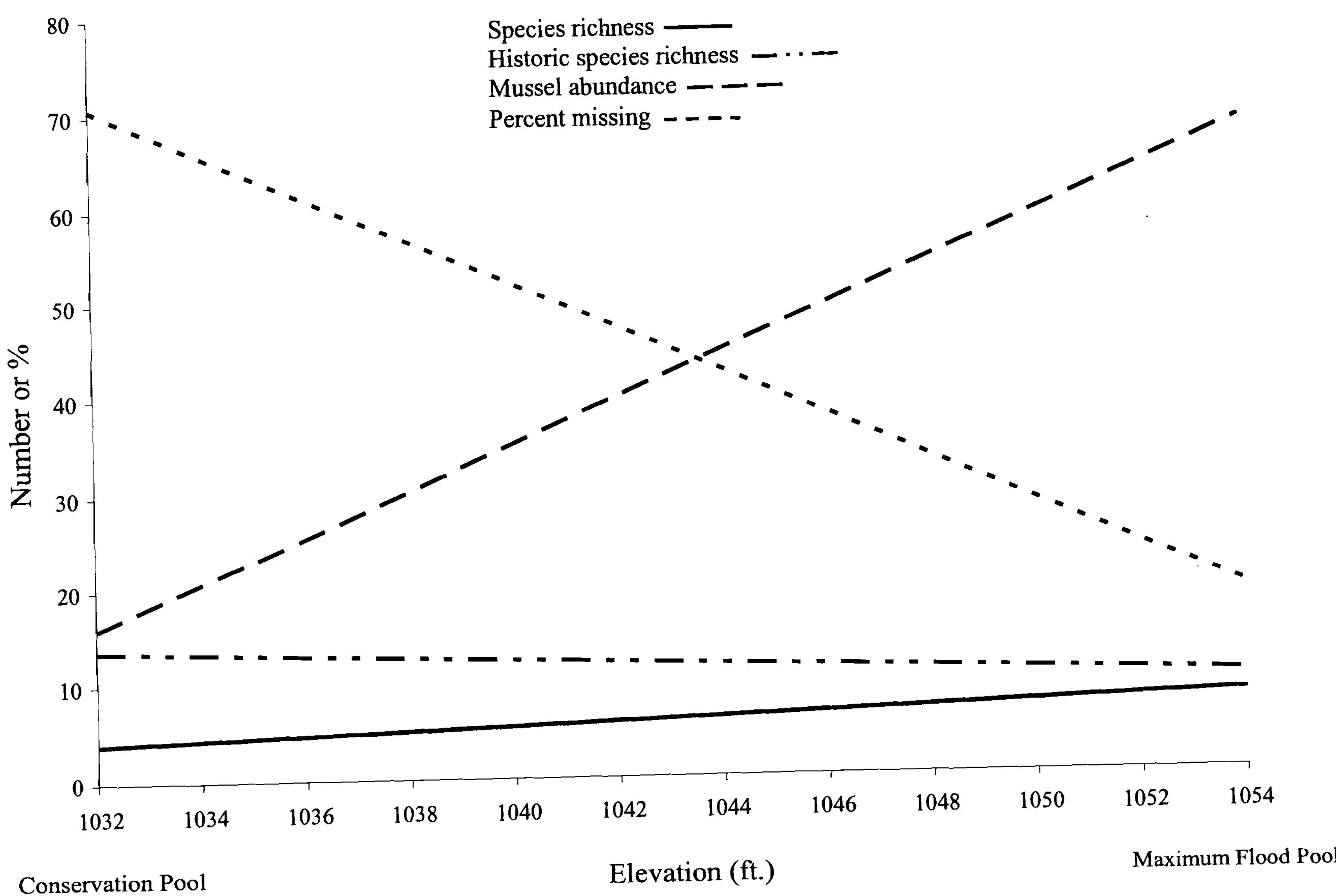
In 15 samples from the Marais des Cygnes River, I collected 515 ($\bar{x}$ = 34.3, SD = 26.8) live mussels of 12 species ($\bar{x}$ = 5.3, SD = 2.0) and 24 species ($\bar{x}$ = 12.3, SD = 3.6) represented by weathered valves (Table 2). Significantly fewer species were present alive than were present as weathered valves ($t = -6.49$, $P < 0.0001$). Species richness ($P = 0.03$, $R^2 = 0.33$) and mussel abundance ($P = 0.05$, $R^2 = 0.27$) were significantly related to site elevation, and each decreased nearer the reservoir (Figure 6). Percent of species missing from the historic mussel assemblage also was significantly related to site elevation ($P = 0.02$, $R^2 = 0.34$), and increased closer to the reservoir (Figure 6). Historic species richness increased downstream (Figure 6), but was not significantly related to site elevation ($P = 0.33$, $R^2 = 0.07$). No habitat variables were significantly related to site elevation (Table 3).

Ordination of 15 sites, 11 species, and 10 habitat variables from the Marais des Cygnes illustrated the species-environment relationship for this river (Figure 7). I did not include *Utterbackia imbecillis* in the ordination because it occurred at only one site. Axis 1 (eigenvalue = 0.473; 4.6 SD) accounted for 32% of the total variation in the species data, and Axis 2 (eigenvalue = 0.306; 2.1 SD) accounted for 21%. Axis 1 ($P = 0.09$) was not statistically significant, but Axis 2 ($P = 0.01$) was. Axis 2 indicated a gradient of percent substrate composed of bedrock, embeddedness, and mean site width (Figure 7). *Truncilla donaciformis* and *T. verrucosa* were associated with wider, embedded bedrock sites. *Ligumia subrostrata*, *P. alatus*, and *P. grandis* were associated with narrower, unembedded sites having little or no bedrock (Figure 7).

Table 2. Distribution of 12 mussel species collected alive and 24 represented by weathered valves at 15 sites in Marais des Cygnes River, Kansas, 1999 and 2000. Sites are arranged from upstream (M1) to downstream (M15). Numerals indicate number of live individuals found at site. (+) = Present as weathered valve, (-) = Not present as weathered valves.

Site	*Amblema plicata*	*Eliptio dilatata*	*Fusconaia flava*	*Lampsilis cardium*	*Lampsilis siliquoidea*	*Lampsilis teres*	*Lasmigona complanata*	*Lasmigona costata*	*Leptodea fragilis*	*Ligumia recta*	*Ligumia subrostrata*	*Obliqueria reflexa*	*Pleurobema sintoxia*	*Potamilus alatus*	*Potamilus ohiensis*	*Pyganodon grandis*	*Quadrula pustulosa*	*Quadrula quadrula*	*Strophitus undulatus*	*Toxolasma parvus*	*Tritogonia verrucosa*	*Truncilla donaciformis*	*Truncilla truncata*	*Utterbackia imbecillis*	Number of weathered species	Number of live species	Number of live individuals
M1	2+	-	+	-	-	-	41+	-	4+	-	1+	1-	-	-	1-	20+	-	16+	-	-	2-	-	-	+	8	9	88
M2	+	+	+	+	+	+	13+	-	1+	-	1+	1+	-	-	-	7+	-	15+	-	+	-	-	-	1+	14	7	39
M3	+	+	+	-	+	-	5+	-	+	-	+	-	-	-	3+	1+	+	2+	-	-	-	-	-	-	11	4	11
M4	3+	+	+	+	+	+	5+	-	1-	-	-	-	-	4+	+	-	-	7-	-	-	-	-	-	-	9	5	20
M5	6+	+	+	+	+	+	32+	-	3+	-	2+	-	-	5+	-	3+	-	33+	-	+	-	+	-	-	14	7	84
M6	1-	-	-	-	+	-	24+	-	+	-	-	1-	-	-	-	3+	-	8+	-	-	-	-	-	-	5	5	37
M7	3+	+	+	+	+	-	2+	-	+	+	+	-	-	-	+	1+	+	13+	+	+	2+	+	-	-	17	5	21
M8	2-	+	+	+	+	+	27+	-	+	-	+	-	-	+	-	-	-	12+	-	-	1-	-	-	-	10	4	42
M9	14-	+	+	+	+	+	7+	-	1+	+	+	1-	+	+	-	+	+	39+	+	+	1+	2+	+	-	19	7	65
M10	19+	+	+	+	+	-	6+	-	5+	-	+	3-	-	2+	-	1+	+	16+	-	-	3-	1+	-	-	13	9	56
M11	+	+	+	+	+	+	1+	-	1+	-	+	-	-	+	-	1+	+	+	-	-	-	+	-	-	14	3	3
M12	2+	+	+	+	+	+	6+	+	+	-	+	-	-	-	-	1+	+	2+	+	-	+	+	+	-	17	4	11
M13	2-	+	+	-	+	-	5+	-	1+	+	+	2-	-	+	+	+	-	5+	-	-	-	-	-	-	11	5	15
M14	1+	+	+	+	+	-	6+	-	+	-	+	-	-	-	+	+	+	8+	-	-	-	+	-	-	13	3	15
M15	+	+	+	-	+	+	5+	-	+	+	-	-	-	+	1-	-	+	2-	-	-	-	-	-	-	10	3	8
Total live	55	0	0	0	0	0	185	0	17	0	4	9	0	11	5	38	0	178	0	0	9	3	0	1	24	12	515

Figure 6. Regressions for species richness, historic species richness, mussel abundance, and percent of species missing from the historic mussel assemblage in the Marais des Cygnes River, Kansas, 1999 and 2000. Species richness, mussel abundance, and percent of species missing regressions were significant ($P < 0.05$).

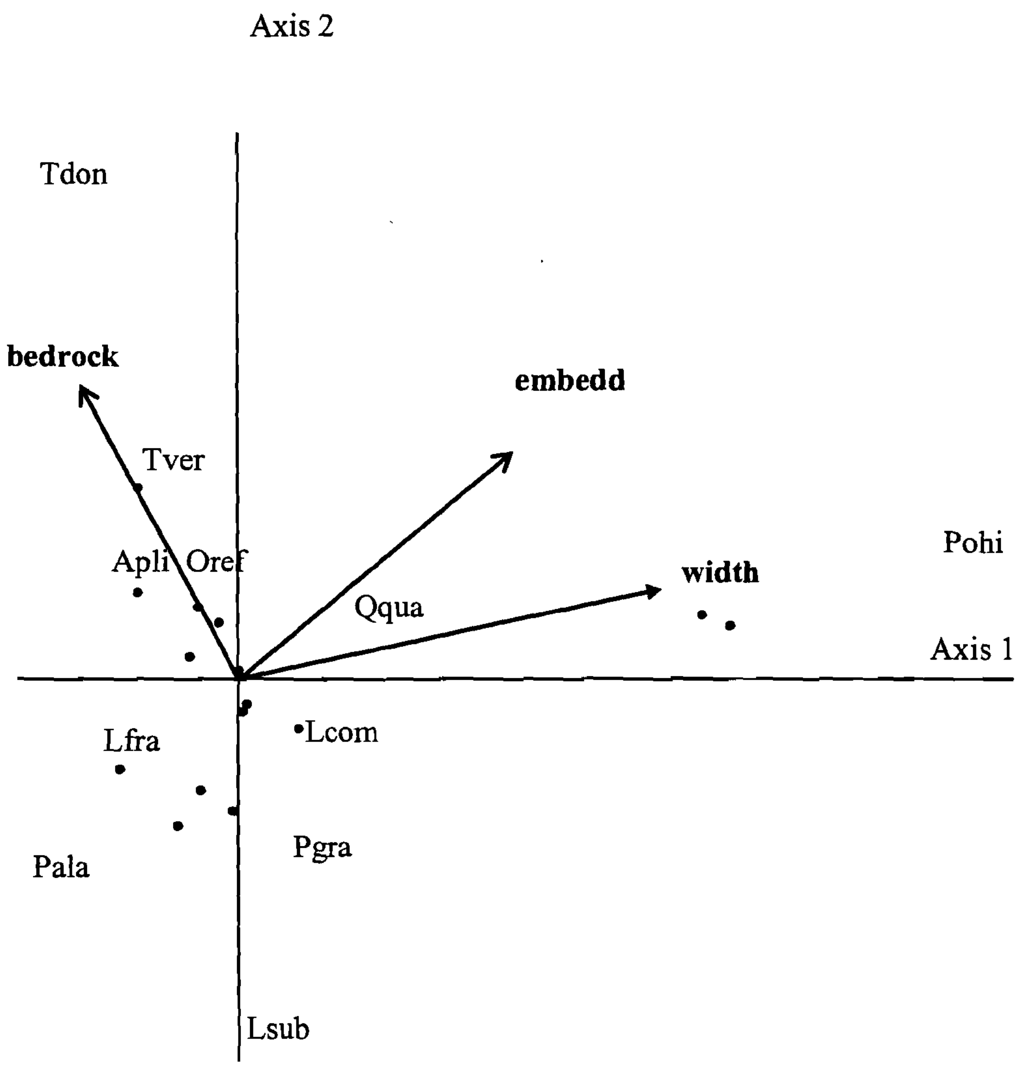


Species richness
Historic species richness
Mussel abundance
Percent missing
Number or %
0
10
20
30
40
50
60
70
80
1032
1034
1036
1038
1040
1042
1044
1046
1048
1050
1052
1054
Elevation (ft.)
Conservation Pool
Maximum Flood Pool

Table 3. Sign of regression coefficient, R^2, and P–values for regression analysis of habitat variables in three eastern Kansas rivers, 1999 and 2000. Alpha levels Bonferroni-adjusted to P = 0.005. MDC = Marais des Cygnes. *indicates significance.

	MDC River			Fall River			Elk River		
	Sign	R^2	P	Sign	R^2	P	Sign	R^2	P
width	+	0.01	0.68	-	0.28	0.06	+	0.43	0.02
%clay	-	0.09	0.27	-	0.02	0.62	+	0.09	0.33
%silt	-	0.01	0.76	+	0.01	0.71	+	0.05	0.50
%sand	+	0.01	0.75	+	0.05	0.49	-	0.03	0.09
%gravel	+	0.25	0.06	+	0.36	0.03	+	0.36	0.04
%cobble	-	0.01	0.73	-	0.31	0.05	-	0.52	0.008
%boulder	-	0.01	0.76	-	0.25	0.08	+	0.02	0.63
%bedrock	-	0.02	0.66	-	0.21	0.11	-	0.05	0.51
compaction	+	0.00	0.98	-	0.22	0.11	-	0.07	0.40
embeddedness	-	0.05	0.40	+	0.01	0.83	-	0.07	0.40

Figure 7. CCA axes 1 and 2 jointplot of sites, mussel species, and habitat variables from the Marais des Cygnes River, Kansas, 1999 and 2000. Species abbreviations are given in Table 1. Environmental variables are percent of substrate composed of bedrock, substrate embeddedness, and mean site width. • indicate sites.


Axis 2
Tdon
bedrock
embedd
Tver
Pohi
Apli
Oref
width
Qqua
Axis 1
Lfra
Lcom
Pgra
Pala
Lsub

Fall River

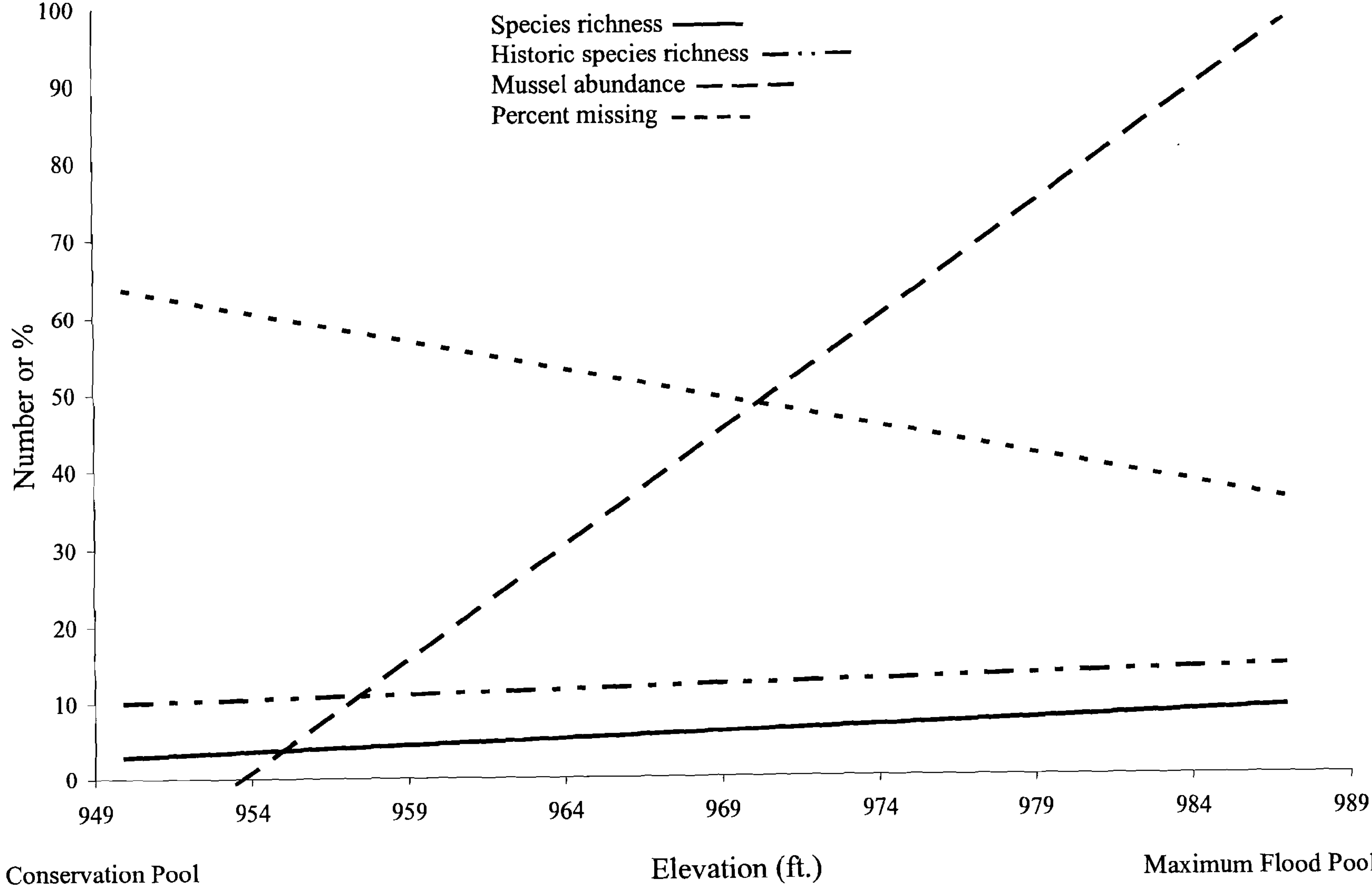
In 13 samples from Fall River, I collected 468 live individuals ($\bar{x}$ = 36.0, SD = 62.0) of 11 mussel species ($\bar{x}$ = 5.5, SD = 3.0) and 22 species ($\bar{x}$ = 11.8, SD = 3.3) represented by weathered valves (Table 4). Significantly fewer species were present alive than were present as weathered valves (t = -4.92, P < 0.0004). Both species richness (P = 0.02, R^2 = 0.43) and mussel abundance (P = 0.02, R^2 = 0.40) were significantly related to site elevation, each decreasing nearer the reservoir (Figure 8). Historic richness decreased downstream and percent of species missing increased nearer the reservoir (Figure 8), but neither was significant (historic richness P = 0.16, R^2 = 0.17; percent missing P = 0.21, R^2 = 0.14). No habitat variables were significantly related to site elevation (Table 3).

Ordination of 13 sites, 10 species, and 10 habitat variables from Fall River produced Axis 1 (eigenvalue = 0.204; 2.3 SD), accounting for 33% of the variation in the species data, and Axis 2 (eigenvalue = 0.118; 2.1 SD), accounting for 19%. I excluded *Lampsilis teres* from the ordination as it occurred at only one site. Axis 1 (P = 0.02) was statistically significant, but Axis 2 (P = 0.22) was not. Axis 1 indicated a gradient of percent of substrate composed of boulder and mean site width (Figure 9). *Strophitus undulatus*, *Quadrula quadrula,* and *Q. pustulosa* were associated with narrower sites upstream that had little or no boulder. *Leptodea fragilis* and *L. complanata* were associated with wider sites downstream that had a higher percent of substrate with boulder (Figure 9).

Table 4. Distribution of 11 mussel species collected alive and 22 represented by weathered valves at 13 sites in Fall River, Kansas, 1999 and 2000. Sites are arranged from upstream (F1) to downstream (F13). Numerals indicate number of live individuals found at site. (+) = Present as weathered valve, (-) = Not present as weathered valves.

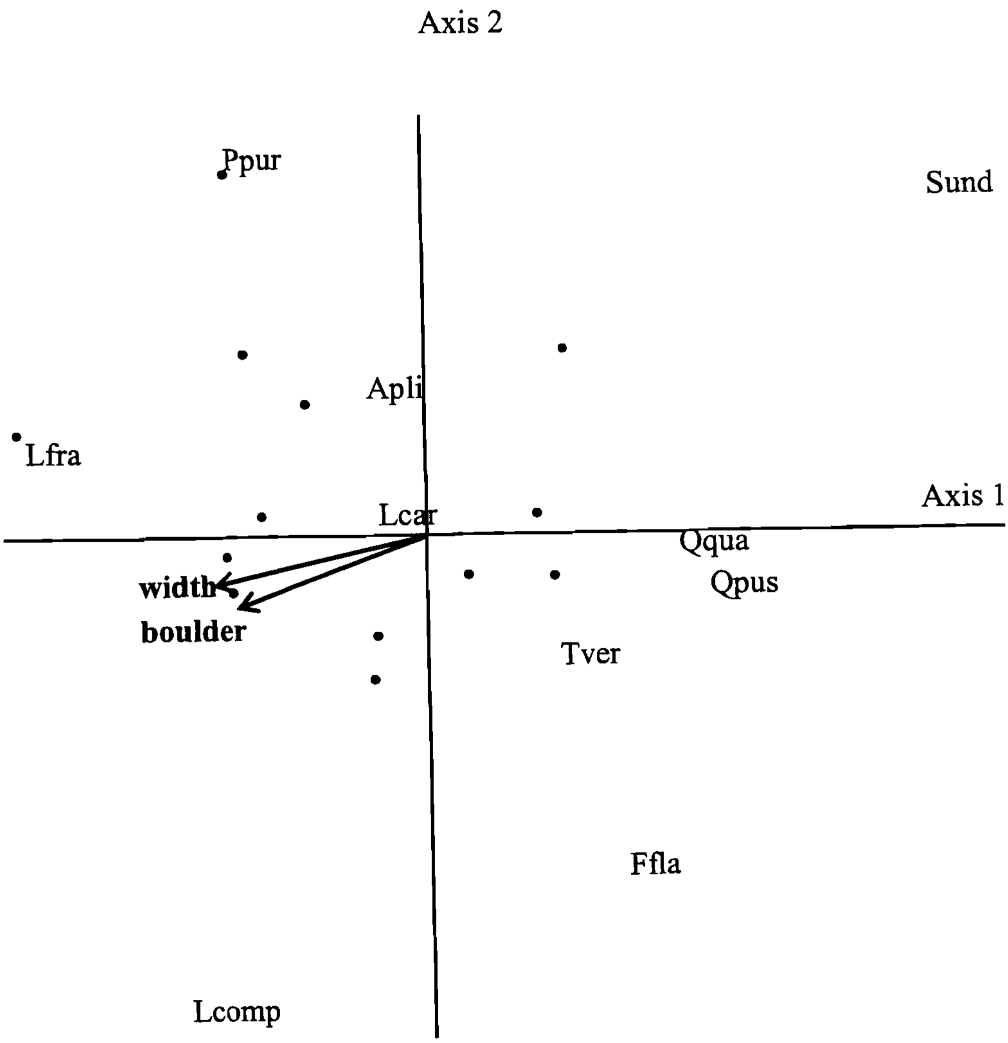
Site	*Amblema plicata*	*Cyprogenia aberti*	*Fusconaia flava*	*Lampsilis cardium*	*Lampsilis siliquoidea*	*Lampsilis teres*	*Lasmigona complanata*	*Leptodea fragilis*	*Ligumia recta*	*Ligumia subrostrata*	*Obliquaria reflexa*	*Pleurobema sintoxia*	*Potamilus purpuratus*	*Ptychobranchus occidentalis*	*Pyganodon grandis*	*Quadrula metanevra*	*Quadrula pustulosa*	*Quadrula quadrula*	*Strophitus undulatus*	*Tritogonia verrucosa*	*Truncilla donaciformis*	*Truncilla truncata*	Number of weathered species	Number of live species	Number of live individuals
F1	43+	-	7+	15+	+	2+	2+	5+	-	+	-	-	15+	-	-	-	60+	36+	6+	31+	-	-	13	11	222
F2	11+	-	1+	1-	+	+	6+	3-	-	+	-	+	3+	-	-	-	5+	5+	-	14+	-	-	11	9	49
F3	+	-	+	3+	-	+	-	+	-	+	-	-	+	+	+	-	1+	1+	+	1+	+	-	14	4	6
F4	2+	-	+	4+	+	+	1+	1+	-	+	-	+	1+	+	-	-	+	+	+	+	-	+	16	5	9
F5	4+	+	+	1+	-	+	-	2+	-	+	-	-	3+	-	-	+	1+	1+	+	+	-	-	13	6	12
F6	24+	-	9+	36+	-	+	2+	4-	-	+	-	-	4+	+	-	-	16+	6+	1+	18+	-	+	13	10	120
F7	+	-	1+	5+	+	+	2-	+	-	+	-	+	2+	-	-	-	+	1-	+	+	+	-	13	5	11
F8	7+	-	+	2+	-	+	-	1+	-	+	-	-	4+	-	-	-	+	+	+	+	-	-	11	4	14
F9	+	-	+	2+	-	+	+	1+	-	+	-	-	+	+	-	-	+	+	-	1+	-	-	12	3	4
F10	1+	-	-	1+	+	+	2+	2+	-	+	-	-	2+	-	-	-	-	+	-	2+	-	-	10	6	10
F11	1+	-	-	2-	-	-	+	+	-	-	-	-	3+	-	-	-	-	1-	1-	1-	-	-	4	6	9
F12	+	+	+	+	+	+	+	+	+	+	+	+	1+	+	-	-	+	+	-	+	-	-	17	1	1
F13	+	-	-	+	+	-	+	1-	-	-	-	-	+	-	-	-	+	-	-	+	-	-	7	1	1
Total live	93	0	18	72	0	2	15	20	0	0	0	0	38	0	0	0	83	51	8	68	0	0	22	11	468

Figure 8. Regressions for species richness, historic species richness, mussel abundance, and percent of species missing from the historic mussel assemblage in the Fall River, Kansas, 1999 and 2000. Species richness and mussel abundance regressions were significant ($P < 0.05$).



Species richness
Historic species richness
Mussel abundance
Percent missing
Number or %
100
90
80
70
60
50
40
30
20
10
0
949
954
959
964
969
974
979
984
989
Conservation Pool
Elevation (ft.)
Maximum Flood Pool

Figure 9. CCA axes 1 and 2 jointplot of sites, mussel species, and habitat variables from Fall River, Kansas, 1999 and 2000. Species abbreviations are given in Table 1. Environmental variables are percent of substrate composed of boulder and mean site width. ● indicate sites.



Axis 2
Ppur
Sund
Apli
Lfra
Axis 1
Lcar
Qqua
width
Qpus
boulder
Tver
Ffla
Lcomp

<u>Elk River</u>

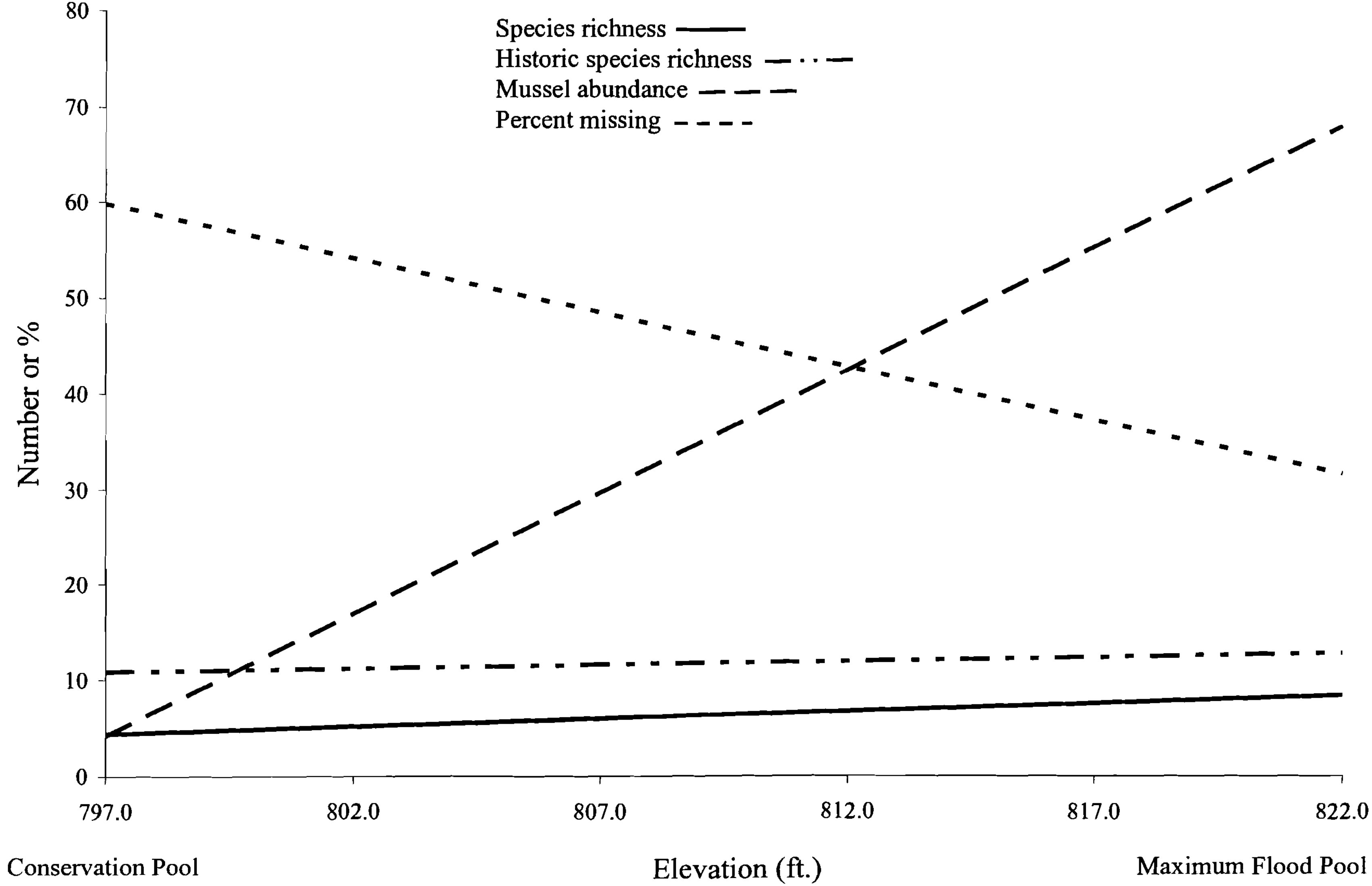
In 12 samples from the Elk River, I collected 384 live individuals ($\bar{x}$ = 32.0, SD = 48.0) of 14 mussel species ($\bar{x}$ = 6.1, SD = 2.5) and 23 species ($\bar{x}$ = 11.7, SD = 3.1) represented by weathered valves (Table 5). Significantly fewer species were present alive than were present as weathered valves (t = -6.62, P < 0.0001). Species richness (P = 0.03, R^2=0.41) and mussel abundance (P = 0.05, R^2 = 0.34) were significantly related to site elevation, each decreasing nearer the reservoir (Figure 10). Historic richness decreased downstream and percent of species missing increased nearer the reservoir (Figure 10), but neither was significant (historic richness P = 0.47, R^2 = 0.06; percent missing P = 0.47, R^2 = 0.05). No habitat variables were significantly related to site elevation (Table 3).

Ordination of 12 sites, 12 species, and 10 habitat variables from the Elk River produced Axis 1 (eigenvalue = 0.316; 2.7 SD), accounting for 27% of the variation in the species data, and Axis 2 (eigenvalue = 0.176; 1.5 SD), accounting for 15% (Figure 11). I excluded *Ligumia subrostrata* and *T. donaciformis* from the ordination as they occurred at only one site. Axis 1 (P = 0.04) was statistically significant, but Axis 2 (P = 0.97) was not. Axis 1 indicated a gradient of mean site width and percent of substrate composed of cobble versus percent of substrate composed of gravel, clay, and silt. *Potamilus purpuratus* and *L. fragilis* were associated with wider sites downstream having high percent cobble and low percent gravel, clay, and silt. *Strophitus undulatus*, *Q. pustulosa*, and *L. teres* were associated with upstream narrower sites having substrates composed of high proportions of gravel, clay, and silt, but low cobble (Figure 11).

Table 5. Distribution of 14 mussel species collected alive and 23 represented by weathered valves at 12 sites in Elk River, Kansas, 1999 and 2000. Sites are arranged from upstream (E1) to downstream (E12). Numerals indicate number of live individuals found at site. (+) = Present as weathered valve, (-) = Not present as weathered valves.

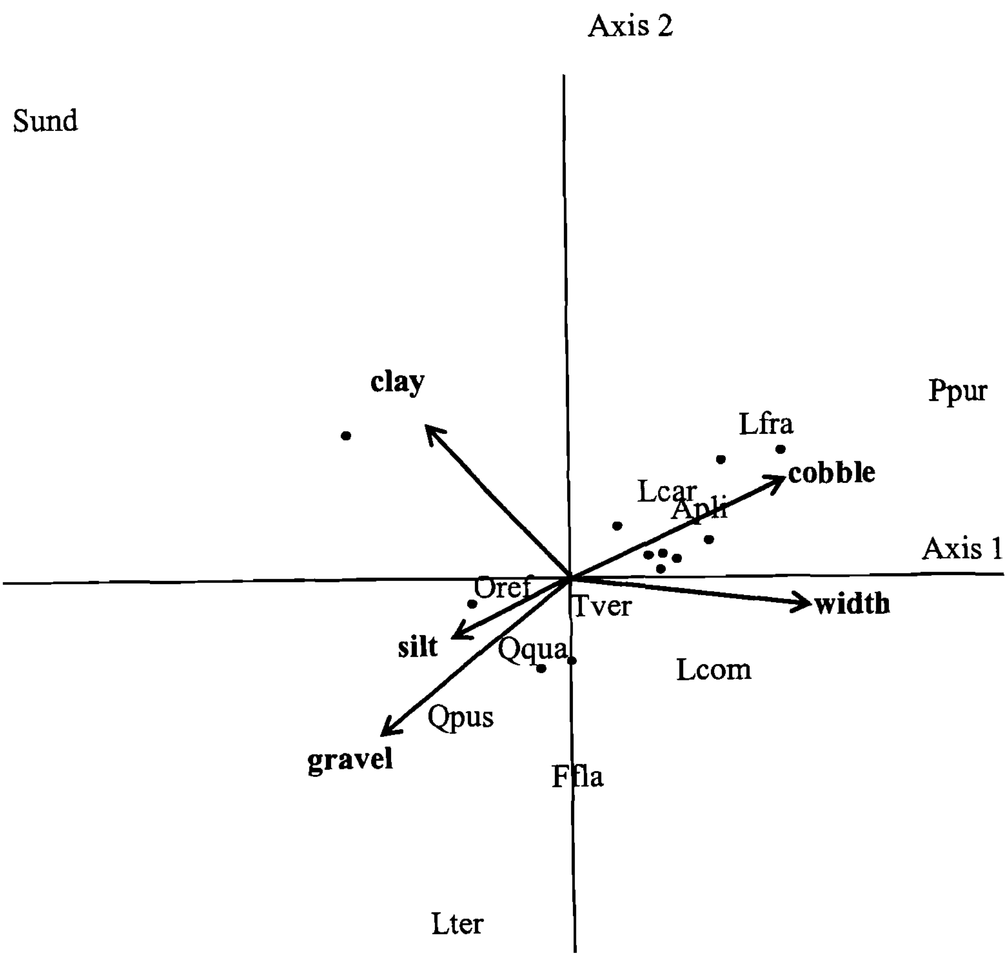
Site	*Amblema plicata*	*Cyprogenia aberti*	*Fusconaia flava*	*Lampsilis cardium*	*Lampsilis rafinesqueana*	*Lampsilis siliquoidea*	*Lampsilis teres*	*Lasmigonia complanata*	*Leptodea fragilis*	*Ligumia subrostata*	*Obliquaria reflexa*	*Pleurobema sintoxia*	*Potamilus purpuratus*	*Ptychobranchus occidentalis*	*Pyganodon grandis*	*Quadrula metanevra*	*Quadrula pustulosa*	*Quadrula quadrula*	*Strophitus undulatus*	*Toxolasma parvus*	*Tritogonia verrucosa*	*Truncilla donaciformis*	*Truncilla truncata*	Number of weathered species	Number of live species	Number of live individuals
E1	7+	-	2-	1+	-	+	+	+	+	-	-	-	1+	-	+	-	+	+	+	-	4+	-	-	12	5	15
E2	10+	-	14+	5+	+	+	3+	5+	1+	+	6+	-	+	-	+	-	115+	9+	+	-	17+	+	+	18	10	185
E3	7+	-	6+	1+	-	-	3+	1-	1-	-	3+	+	+	-	-	-	29+	2+	1+	-	2+	-	-	11	11	56
E4	2+	-	-	1+	-	-	+	+	+	-	2-	-	+	-	-	-	9+	2+	2+	-	6-	-	+	10	7	24
E5	4-	-	+	1+	-	-	-	3-	+	-	2+	-	6+	-	-	-	+	1+	+	-	+	-	-	9	6	17
E6	1+	-	-	+	-	-	2+	+	+	-	1+	-	1+	-	-	-	+	1-	+	+	6+	-	+	12	6	12
E7	3+	-	+	2+	+	-	+	2+	+	-	+	+	1+	-	+	+	+	2+	+	-	3+	-	-	16	6	13
E8	6+	-	1+	-	+	-	+	+	1-	+	-	-	+	-	-	-	+	+	-	-	4+	-	+	11	4	12
E9	+	-	-	+	-	-	-	+	1+	-	-	-	1+	-	-	-	+	-	-	-	1-	-	-	6	3	3
E10	1+	-	-	+	-	+	+	-	1+	-	-	-	+	-	-	+	+	-	-	-	-	-	+	9	2	2
E11	9+	+	1+	3+	+	-	+	-	-	-	+	-	1+	+	-	+	3+	+	-	-	2+	-	-	13	6	19
E12	6+	-	+	6+	-	+	+	-	2+	1-	2+	=	+	-	-	+	6-	+	+	-	+	3+	-	13	7	26
Total live	56	0	24	20	0	0	8	11	7	1	16	0	11	0	0	0	162	17	3	0	45	3	0	23	14	384

Figure 10. Regressions for species richness, historic species richness, mussel abundance, and percent of species missing from the historic mussel assemblage in the Elk River, Kansas, 1999 and 2000. Species richness and mussel abundance regressions were significant ($P < 0.05$).



Species richness
Historic species richness
Mussel abundance
Percent missing
Number or %
0
10
20
30
40
50
60
70
80
797.0
802.0
807.0
812.0
817.0
822.0
Conservation Pool
Elevation (ft.)
Maximum Flood Pool

Figure 11. CCA axes 1 and 2 jointplot of sites, mussel species, and habitat variables from Elk River, Kansas, 1999 and 2000. Species abbreviations are given in Table 1. Environmental variables are mean site width and percent of substrate composed of clay, silt, gravel, and cobble. • indicate sites.



Axis 2
Sund
clay
Ppur
Lfra
cobble
Lcar
Apli
Axis 1
Oref
Tver
width
silt
Qqua
Lcom
Qpus
gravel
Ffla
Lter

DISCUSSION

My data demonstrate a downstream decrease in species richness and abundance of mussels in rivers upstream from three Kansas reservoirs. Percent of species missing from the historic assemblage increased nearer the reservoir in all three rivers, although this trend was statistically significant only in the Marais des Cygnes River. In all three rivers, the current mussel assemblage was composed of significantly fewer species than the historic assemblage, a situation seen throughout eastern Kansas (Obermeyer et al., 1997) and nationwide (Neves, 1993).

I found that 50% (12/24) of historically occurring mussel species were missing from the Marais des Cygnes River, 50% (11/22) from the Fall River, and 39% (9/23) from the Elk River. Obermeyer (1996) sampled mussels throughout the Fall (n = 12 sites), Elk (n = 4), Verdigris (n = 14), Neosho (n = 23), Cottonwood (n = 6), and Spring (n = 7) rivers in eastern Kansas in 1993 to 1995. Although the number of historically occurring species missing at his sites was similar in the Elk (54%; 14/26) and Cottonwood (80%; 20/25)rivers, fewer species were missing from most rivers sampled, including the Fall (23%; 7/23), Verdigris (24%; 8/25), Neosho (17%; 5/29), and Spring (8%; 2/25), suggesting that the river reaches I sampled upstream from reservoirs might have lost more species than is generally occurring throughout eastern Kansas.

Similar trends of decreased species richness in mussel assemblages have been documented in other rivers affected by reservoirs. In general, many of the original riverine mussel species become extirpated within reservoirs, but a few species tolerant of lentic conditions might colonize or become more abundant (Bates, 1962; Parmalee and Hughes, 1993; Blalock and Sickel, 1996; Howells et al., 1997). This causes an assemblage shift, but the net result is still usually much reduced species richness. Some depauperate mussel assemblages might experience no change in species richness from reservoir construction if all are lentic species (Neck, 1989).

Studies of mussel assemblages downstream from reservoirs typically have indicated reduced species richness due to extirpation, with no increase in abundance of formerly rare species (Bates, 1962; Parmalee and Hughes, 1993; Blalock and Sickel, 1996). Vaughn and Taylor (1999) reported that species richness and mussel abundance were least near Pine Creek Reservoir, Oklahoma, dam and increased downstream, and the proportion of species missing from the historic community was highest near the dam and decreased downstream. However, some species might increase in abundance immediately downstream from reservoirs (Miller and Obermeyer, 1997), and species richness might be greatest immediately downstream from dams in rivers that have a string of impoundments in close proximity (Blalock and Sickel, 1996; Watters, 1996).

Upstream from reservoirs, mussel species are usually lost and not replaced with lentic species. Watters (1996) and Kelner and Sietman (2000) presented evidence of mussel species' current distributions ending abruptly at dams upstream from which they had historically occurred, possibly due to the inability of their host fish species to move upstream past the dam. Vaughn and Taylor (1999) sampled Little River, Oklahoma, from its headwaters downstream past Pine Creek Reservoir, and found that species richness and abundance decreased from the headwaters to just upstream of the reservoir's flood pool, indicating that reservoirs also might affect mussel assemblages upstream from reaches they can inundate.

Siltation variables were important in distinguishing between the mussel communities at a broad geographic scale, but in general did not explain mussel assemblage structure within each river. Substrate embeddedness was significantly related to canonical axes in the Marais des Cygnes River, but site width and larger substrate particle size categories explained structure of the mussel assemblages in the Fall and Elk rivers. Width could be a surrogate for some unmeasured variable (Gauch, 1982). Additionally, siltation variables were not significantly related to site elevation in any river. The effects of artificial flooding on substrate siltation in impounded rivers might be short-term episodic events (Waters, 1995) and therefore only detectable when a reservoir is pooling water over a normally flowing stream section. During inundation events, the substrate of these three rivers was covered with a layer of silt up to 46 cm deep in areas where pooled waters arrested the normal flow (personal observation). Flow was restored as the pooled waters retreated, and the substrate surface was swept clear of silt. However, the layer of silt can persist up to several months in areas closest to the reservoir (personal observation). This extended smothering might cause the extirpation of sensitive species, but would not be detected at normal flows. I observed two such inundation events during two summers of sampling. In 1999, silt was deposited in a thick (up to 30 cm deep) layer over the substrate of the downstream reach of Fall River as backwater from the reservoir temporarily inundated the river channel. When the backwater receded four days later, the normal flow of the river swept the layer of silt from the substrate. In the Elk River, the downstream reach was inundated for 12 days in 2000. I visited three inundated sites and found that all were heavily silted (30 cm deep).

However, most of the silt had been swept from the substrate by the following day when the backwater receded and flows returned to normal.

Although siltation variables were not significantly related to site elevation in any river studied, the trend of downstream decrease in species richness and abundance suggested that some facet of proximity to reservoirs caused extirpation of mussel species sensitive to the altered habitat. Biotic and abiotic environmental parameters other than siltation might also become unfavorable to mussels during inundation events. Food organism populations might decline due to lack of light from deepening of silt laden water (Williams et al., 1993). Host fish species that some mussel species rely on for reproduction may be driven from a mussel bed during inundation events and likely could not see glochidial dispersal mechanisms if they remained, suggesting that protracted inundation when mussels spawn could diminish or extirpate species (Brim Box and Mossa, 1999). Mussels can smother as oxygen levels become low in the stilled and deepened water over inundated mussel beds. Some combination of these effects of reservoir inundation could cause the observed decline in richness and abundance, but might remain undetectable except during inundation events. Future studies of the effects of reservoirs on upstream mussel assemblages and habitats should consider the episodic nature of reservoir inundation.

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Appendix 1. Latitude, longitude, site elevation, and number of days each site has been inundated (from dam closure to 28 January 2000) for 40 sites in the Marais des Cygnes, Fall, and Elk rivers, eastern Kansas.

site	Latitude	Longitude	elevation (ft.)	days inundated
M1	N38E39.19	W95E56.76	1054.0	0
M2	N38E38.22	W95E56.79	1049.0	46
M3	N38E34.08	W95E58.48	1045.0	210
M4	N38E33.90	W95E58.12	1044.0	261
M5	N38E33.58	W95E58.05	1043.0	312
M6	N38E33.86	W95E57.70	1039.5	761
M7	N38E35.79	W95E57.62	1039.0	877
M8	N38E33.19	W95E57.01	1037.3	1975
M9	N38E34.91	W95E56.99	1036.9	2500
M10	N38E34.73	W95E56.45	1036.3	3550
M11	N38E32.54	W95E57.39	1035.9	4237
M12	N38E32.39	W95E57.51	1035.2	5160
M13	N38E32.18	W95E57.70	1034.7	5942
M14	N38E32.29	W95E57.70	1034.0	7524
M15	N38E32.68	W95E53.45	1032.0	7687
F1	N37E48.51	W96E13.26	987.0	2
F2	N37E46.16	W96E13.07	981.0	46
F3	N37E46.20	W96E12.77	980.5	80
F4	N37E45.84	W96E12.49	975.0	115
F5	N37E45.67	W96E12.14	970.0	179
F6	N37E45.20	W96E11.28	968.0	232
F7	N37E45.08	W96E11.09	967.0	264
F8	N37E44.48	W96E11.03	964.0	409
F9	N37E43.75	W96E10.36	959.0	824
F10	N37E43.44	W96E09.86	954.0	1425
F11	N37E43.36	W96E09.70	952.0	1911
F12	N37E43.16	W96E09.41	950.0	3010
F13	N37E43.21	W96E09.36	949.9	5650
E1	N37E18.69	W95E59.23	822.0	24
E2	N37E18.69	W95E58.88	820.0	41
E3	N37E18.70	W95E58.77	819.7	46
E4	N37E18.44	W95E58.10	819.0	48
E5	N37E17.31	W95E54.93	811.0	208
E6	N37E16.63	W95E55.52	805.5	490
E7	N37E16.39	W95E55.24	804.0	596
E8	N37E16.30	W95E54.78	802.0	756
E9	N37E16.05	W95E54.98	799.0	1181
E10	N37E16.07	W95E54.95	798.0	1460
E11	N37E16.09	W95E54.88	797.5	1600
E12	N37E16.12	W95E54.82	797.0	1802

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