Ecological Responses to Hydrogeomorphic Fluctuations in a Sand Bed Prairie River: River Complexity, Habitat Availability, and Benthic Invertebrates

By

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River: River Complexity, Habitat Availability, and Benthic Invertebrates**

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Abstract

Rivers with stochastic precipitation have fauna that overcome unique challenges. Organisms surmount these challenges by using refugia. Research was conducted on the sand bed Kansas River (Kaw). I (a) quantified how the hydrology affects the Kaw's shallow habitat complexity, (b) compared the amounts of hard vs. sand substrates, and (c) related abiotic variables to the community composition of benthic macroinvertebrates. I developed the riverscape complexity ratio, a metric that measures all types of river structures, found there was little hard substrate for zoobenthos to colonize, and that the zoobenthos had different communities at different river complexity levels. Zoobenthos in the Kaw use the river structures as refuges from flow spikes that eliminate species in the main channel. Unfortunately, flood control structures have eliminated much of the complexity in the Kaw. These habitats must be preserved since much of the food web uses these structures as vital nursery and feeding habitats.

Introduction

As an ecosystem driver, the hydrologic cycle has received much attention in lotic ecology (Marks *et al.,* 2000, Poff *et al.*, 1997, Power *et al.*, 1995, Resh *et al.*, 1988). River ecosystems with predictable hydrologic cycles in humid regions and with unpredictable cycles in arid regions have garnered the most study (Moore and Thorp, 2008). However, systems with consistent flow but unpredictable flood events, such as rivers of the U.S. Great Plains, have been largely ignored. Great Plains rivers are temporally dynamic because of the stochasticity of their precipitation events (Dodds *et al*., 2004); therefore, fauna living within these rivers have unique challenges to overcome, especially during flood events.

One way organisms surmount these challenges is by using refugia, defined as habitats or environmental factors that convey spatial or temporal resistance and/or resilience to biotic communities impacted by biophysical disturbances (derived from Sedell *et al*., 1990). Common refugia for riverine organisms include slow-flowing areas of inundated floodplains, hyporheic zones, and within-channel, low-shear stress areas. However, many rivers have little hyporheic habitat and rarely, if ever, experience overbank flooding (gorges, naturally incised channels, and leveed systems), leaving organisms no option other than within-channel refugia (Robson, 1996).

Physically complex rivers have more refuges, and these play a large role in the ecological processes that govern lotic systems, thereby making the structural variety

of habitats vital to the existence of well-balanced aquatic communities (Jungwirth *et al.*, 1993). River complexity can be considered a measure of the number and variety of geomorphic features within and along the river channel such as sandbars, multiple channels, periodically connected water bodies, semi-isolated water bodies (bays), and shoreline sinuosity. All such areas experience relatively low or zero current velocities for extended periods. Rivers usually considered structurally complex are classified as highly braided or anabranched. River complexity is distinguished here from the more spatially constrained measures of habitat complexity/heterogeneity in that the former involves geomorphic structures while the latter, a measure of the number and variety of habitats, is embedded within river complexity. However, a river that is structurally or physically complex will likely have higher habitat complexity or heterogeneity (Graf, 2006).

The Flood Pulse Concept (Junk *et al.*, 1989) articulated that the main ecosystem driver in a large floodplain river is the hydrological cycle which opens the highly productive and complex floodplain to the river biota. In non-arid regions, the floodplain normally consists of highly-vegetated, slow-moving productive waters where integral processes of the river take place, including feeding, and reproduction. In the sandbed prairie rivers common to the Great Plains of the United States, flood timing and duration are so unpredictable, that organisms cannot depend on floods for integral parts of their life cycle. Additionally, complex river structures, for example slackwaters and bays, usually arise from within the river channel, not the floodplain,

making the Flood Pulse Concept inappropriate for explaining the ecology of many Great Plains rivers.

Conversely, the Inshore Retention Concept (Schiemer *et al.,* 2001) advocates that diverse shoreline morphology creates refuges allowing for higher community persistence, production, diversity, and reach retentivity (hydrologic storage). Inshore retentive areas or other regions of low-flow can play a substantial role in affecting biodiversity and ecological function. Sandbars, the only available low-flow habitat in plains rivers, are integral to the ecology of these rivers because they produce flow refuges for invertebrate and fish production. Shallow littoral areas can be an especially important site for food webs in turbid systems, such as some Australian rivers (Bunn *et al.*, 2003), because of highly restricted depths for primary production. Thus, rivers with channel structures like sandbars create more substrate in contact with the photic zone (Figure 1), thereby allowing greater benthic production and shorter nutrient spiraling length.

Figure 1. (a) Cross section of single-thread river with limited area available for benthic colonization and production. (b) cross section of multi-thread river where sandbars create multiple areas for increased benthic production and colonization.
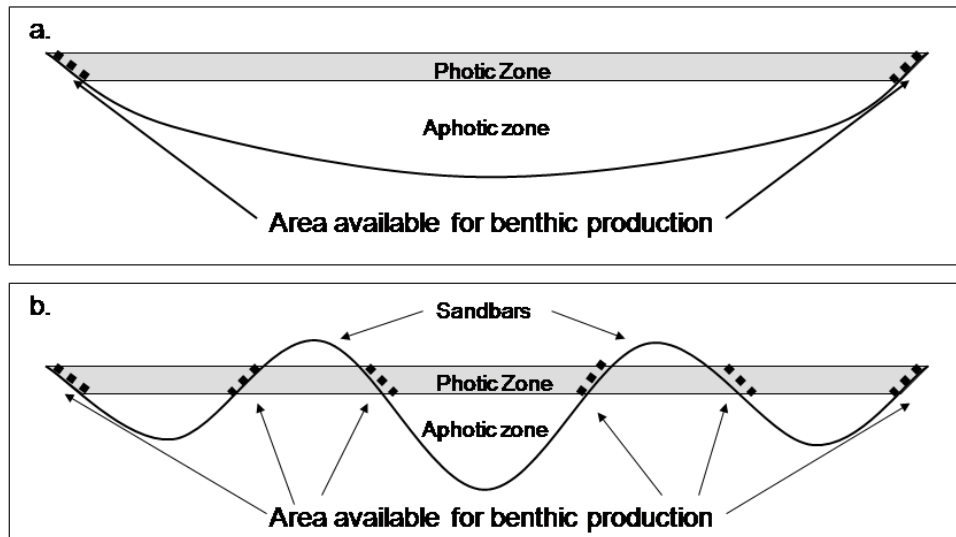
Moreover, a sandbar's capillary fringe area (the wet substrate next to the water/land interface) can be the most intense site of invertebrate production in large rivers with shifting sand bottoms (Ferrington and Goldhammer, 1992). More complex rivers, consequently, have more capillary fringe habitat available for colonization. Overall, in rivers where the natural flow regime creates in-channel structures and refuges, the biota are adapted to and depend on that complexity to survive (Bunn and Arthington, 2002).

The principal goal of my study in the Kansas River, a typical Great Plains river, was to understand how the benthic community ecology was affected by hydrogeomorphic fluctuations and resultant changes in the structure and abundance of

in-channel refuges. This knowledge could help river managers predict effects of climate change in an ecoregion where the variability of precipitation events is expected to increase as a result of climate change (Gleick, 1989, Groisman *et al.*, 1999, Easterling *et al.*, 2000). Without knowledge of how the river reacts to current fluctuations in the river, it will be extremely difficult to predict future responses.

To gain insights on relationships among hydrogeomorphic fluctuations, in-channel refuges, and river ecology, I: (a) quantified how the hydrologic cycle affects the amount of shallow, low flow habitat in the Kansas River (or Kaw); (b) compared the relative amounts of sand habitats vs. hard substrates (wood snags); and (c) related these abiotic variables to the density, diversity, and community composition of benthic macroinvertebrates inhabiting the sandbars. This benthic community in sand habitats is integral to the entire food web of the Kansas River because the vast majority of habitat for invertebrates in most plains rivers is open sand. These organisms probably serve as the food base for most of the remaining metazoan food web in the Kaw. This study demonstrates the influence of river flow fluctuations on the benthic community and to the likely impact on the entire food web.

Methods

Study Site

Research was conducted on the Kansas River, a 7th order tributary of the Missouri River, with a watershed encompassing 159,000 km^2 of Kansas, Colorado, and Nebraska (Galat *et al.*, 2005). The Kaw is characterized as temporally dynamic in that its flow is highly unpredictable at small temporal scales (one to two months); however, at larger yearly scales, a general trend of high discharge and flooding is tied to the thunderstorm season common to the Great Plains region in May and June (Figure 2).

Figure 2. Hydrograph showing average monthly discharge. Insert - hydrograph of May 2007 when the discharge peak was 3500 m^{3}s^{-1}.
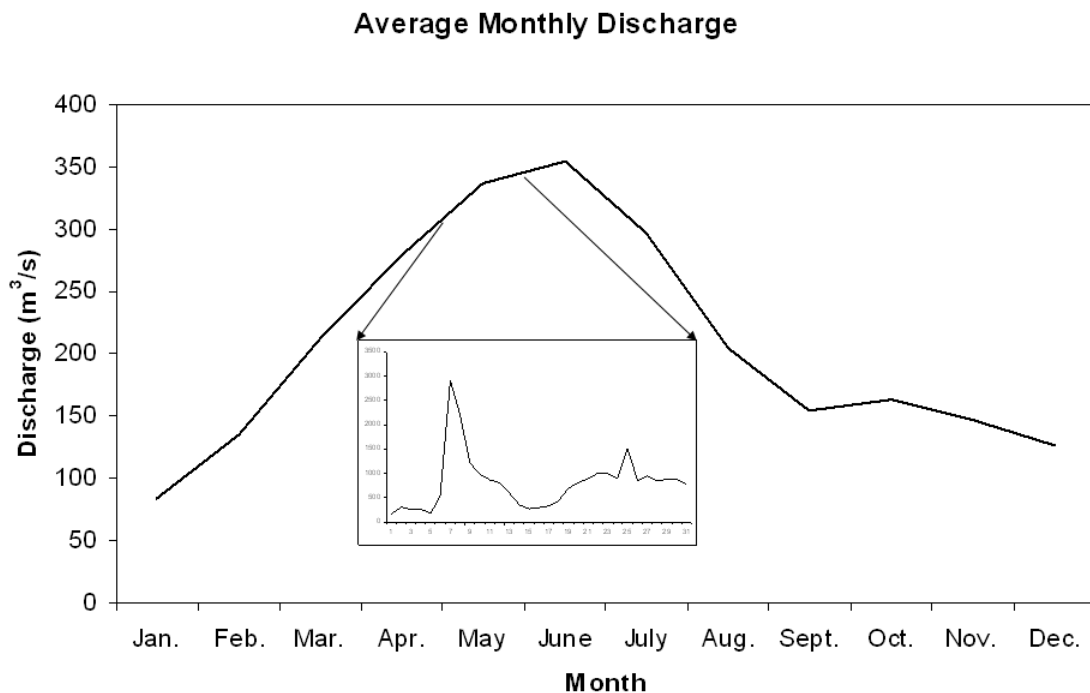
Many of the Kaw's major tributaries have reservoirs near their confluence with the main stem. The river is generally free of flood control structures; however, levees and bank stabilization structures are common near cities. During high flow, the Kaw is characterized by a single channel with a few large relatively permanent islands (those with persistent rooted vegetation) spaced approximately every 8-10 km. As the river stage decreases, mid-channel and alternating sandbars appear as the river braids. Sandbars are mostly bare sand, yet the larger bars support small annual plants and young willows (Salicaceae). The river bed consists mostly of sand, gravel at the leading edges of sandbars in the main channel, and silt in the slow flowing slackwaters. The Kaw fluctuates between single and multi-thread sections depending on position along the river. Sandbars are moderately consistent year-to-year in that they are found in the same section of river; however, the bars completely reorganize themselves into different configurations with flow pulses and gradual erosion.

This study took place on two sandbars between river kilometer 102 and 108, just above the Kaw's confluence with the local Delaware River in a relatively heavily braided section of the river. Two larger mid-channel sandbars were chosen that were considered persistent (sufficient height above average river level and rooted willows showing evidence of recent persistence) so that they would endure flow pulses and river rearrangement throughout the duration of the study (Figure 3). While these bars remained throughout the study, they were substantially restructured with flow pulses and small flow spikes.

Figure 3. Aerial photograph of field sites on the Kansas River. Flow travels left to right.
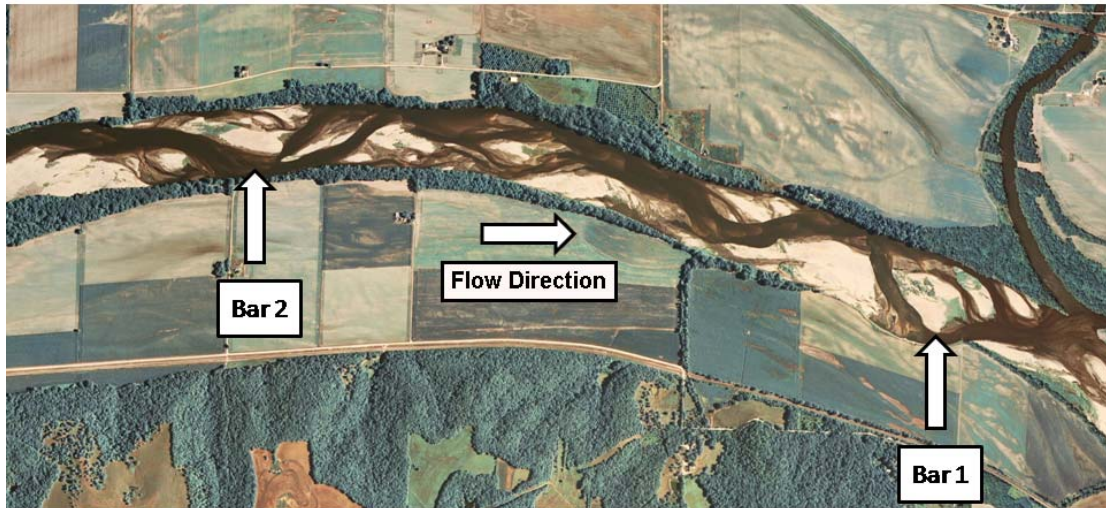

As a consequence of the river's dynamic hydrology and sand substrate, true midges (Diptera, Chironomidae) and biting midges (Ceratopogonidae) dominate the benthic invertebrate community. Other insects occur sporadically on the extremely rare wood snags, such as mayflies, stoneflies, and caddisflies (Ephemeroptera, Plecoptera, and Trichoptera, respectively). The most abundant fishes are in the families Cyprinidae (e.g. red shiners, emerald shiners, and common carp) and Poeciliidae (mosquitofish). Some of the larger fish in the community are gar (Lepisosteidae), catfish (Ictaluridae), and freshwater drum (*Aplodinotus grunniens*) (Cross and DeNoyelles, 1982)

Riverscape Complexity and the Hydrologic Cycle

The dynamic nature of river complexity was a principal independent variable in this study; however, all current metrics failed to identify and explain the type of complexity found in the Kansas River. River complexity metrics in common use are employed to classify and study the geomorphology of rivers. They are used to improve our understanding of factors that produce the varying patterns in the river rather than to quantify those patterns (Friend and Sinha, 1993). Present metrics also fail to detect alternating or point bars, thereby overlooking geomorphic structures potentially essential to the ecosystem structure and function in rivers. Brice's (1964) Braiding Index (Figure 4a) compared twice the length of the bars (Li) divided by the length of the downstream channel (Lr). By doubling the length of the mid-channel bars, it simplifies the calculation because most bars are assumed to be oriented longitudinally. However, by measuring only the downstream length of the bar, the metric ignores potential effects of bar shape, thereby overlooking small scale structures, slackwaters, or differences in habitat heterogeneity that result from differently shaped sandbars. These unnecessary shortcuts, which were developed prior to more sophisticated computer techniques, have become obsolete with current Geographical Information Systems (GIS) methods. Rust's (1978) Braiding Parameter (Figure 4b) introduced the idea that channel thalweg divergence and convergence could be used to eliminate metric instability caused by water level fluctuations. A stable metric would be advantageous when classifying rivers into a certain category. However, a robust metric that removes the fluctuations caused by stage height

variations eliminates the ability of the metric to detect river changes caused by the

hydrologic cycle, the main ecosystem driver in lotic ecosystems (Graf, 2001, Marks

et al., 2000, Poff *et al.*, 1997, Power *et al.*, 1995, Resh *et al.*, 1988) This neglect of

hydrologic variation is understandable since fluvial geomorphologists are more likely

concerned with river classification, whereas ecologists are more likely to focus on

how organisms react to changes in the river's stages over space and time. The

complexity metric (Figure 4c) of Friend and Sinha (1993) uses the sum of the thalweg

lengths (Lctot) divided by the length of the widest thalweg length (lcmax).

**Figure 4** (a) Brice's Braiding Index as calculated by doubling the sum of bank lengths and dividing by the line midway between river banks.   (b) Rust's Braiding Parameter as calculated by dividing the sum of the lengths of the thalweg divergences to convergences (Lb) by the mean meander wavelength (Lm); (c) Friend and Sinha as calculated by dividing the lengths of the primary channels by the length of the widest channel.
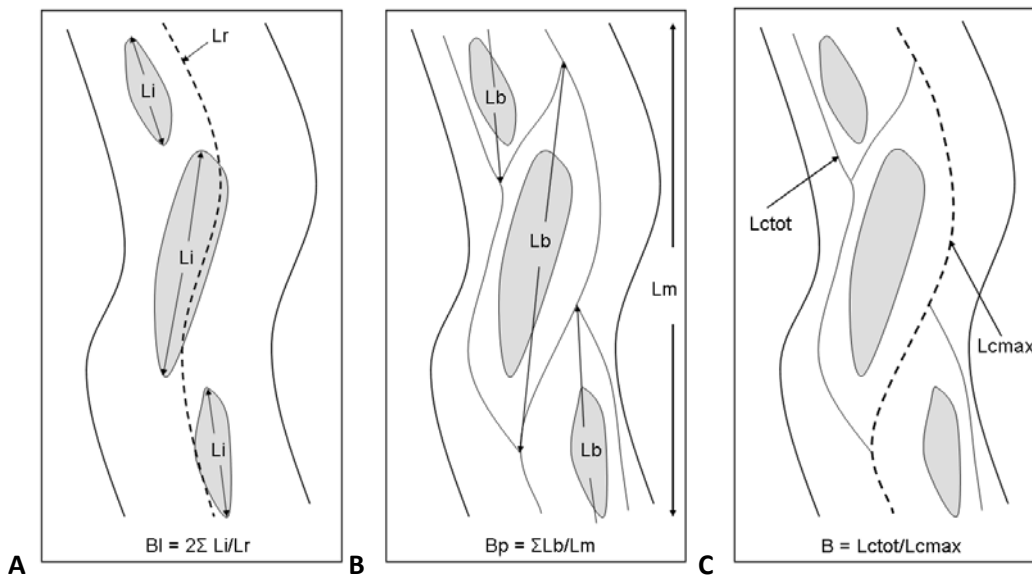
By using the thalweg lengths, this and the above metrics all miss the ability to detect the influence of the actual shape of the ecotones and the inshore sinuosity, a major determinant of biological processes and biodiversity, especially in large rivers (Schiemer *et al.,* 2001).

These deficiencies in older metrics then led me to develop the Riverscape Complexity Ratio (RCR). The RCR is similar to the Lakeshore Development Ratio (Wetzel, 2001) in that it compares a length to a standard shape; but instead of dividing the shoreline length by the perimeter of a circle with equal area, it divides the total perimeter of the land/water interface at bars, islands, and banks by the length of the two opposing 'permanent' (bankfull) banks. Therefore, it compares the total observed edge of a structurally complex river to an equal sized, single channel river (Figure 5).

Figure 5. (a) Rivescape Complexity Ratio (RCR) as calculated by dividing the length of the total edge (Lb + Lp) by the length of the permanent banks (Lp); (b) example of how to calculate RCR with point or alternating bars.

A   B

RCR = (Lp + Lb) / Lp   RCR = (Lb + Lp + La) / (Lp + La)
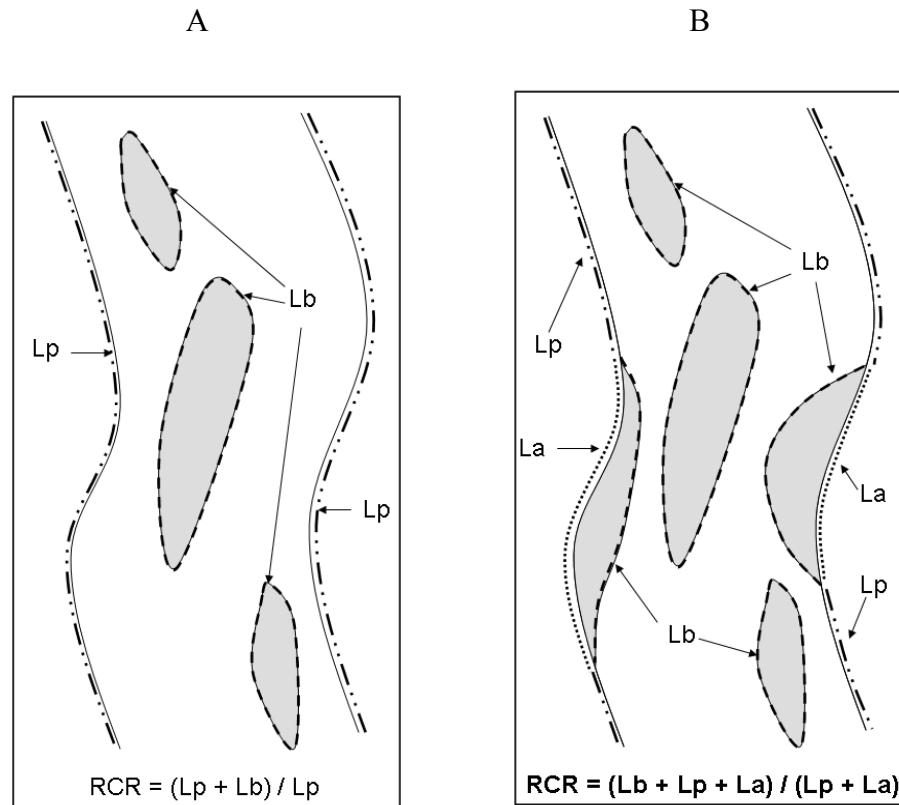
The final ratio is similar to sinuosity ratios in that: (a) a single channel river has a value of unity; and (b) as a river gets more complex, the value increases to infinity.

The Riverscape Complexity Ratio was calculated for the Kansas River using 20 Landsat images spanning the period from 1983 to 2005 for the Topeka to Lecompton reach of the Kansas River. Images were taken from various spring, summer, and fall dates. Landsat images were chosen for their regular intervals, period of record, and ease of procurement. Higher resolution images, where

available, should be used when measuring the RCR to increase the power to detect smaller spatio-temporal fluctuations in the river's complexity. Some caution, however, should be taken when comparing values of vastly different resolutions since higher resolution images could result in higher RCR values through the increased ability to detect smaller and more complex shoreline morphologies. RCR was calculated in ArcMap 9.2 and regressed over discharge values taken from the USGS National Water Information System. The discharge range encompassed by the study included some of the wettest (1993) and driest (2005) years on record for the Kansas River.

Woody Habitat Analysis

To determine whether the sandbar habitats in the river were relatively important to the river's ecology in comparison to other habitat types, the amount of wood snag habitat was estimated on the 20 km section of river from Topeka to Lecompton. The study was completed at minimum flow (about 1 m water depth) so that the maximum amount of wood would be visible throughout the river. Any wood found that was currently submerged or would have been underwater at bankfull height was included in this study. Researchers floated down the river and each piece of woody debris was visually identified, its location marked on a river map, and its diameter and length visually estimated by two researchers independently. Any conflicting estimates were discussed until a consensus was reached. Each piece was assumed to be of cylindrical shape to allow for a rough estimate of surface area. The

amount of wood habitat or surface area was then compared to the total area of sand

habitat available along the entire 20 km sample section. Sand habitat area was

calculated as the total wetted area at bankfull height using Landsat imagery in

ArcGIS 9.3.

Field Sampling

Benthic invertebrates were collected along with physicochemical

measurements from 12 sample sites in each of the two sandbars, consisting of three

habitats (capillary fringe, edge, and main channel) at four positions on the sandbar

(head, left, right, and tail). Three samples were taken within each habitat for a total of

36 samples per sandbar per sampling period. The head and tail of a bar were defined

as the most upstream and downstream sections, respectively, while the left and right

sides corresponded to the left and right banks of the river, respectively, when looking

downstream. The capillary fringe habitat follows the definition of Bear (1979) and

Ferrington and Goldhammer (1992) as the semi-aquatic areas of sand along the

margin of the river that are moist due to capillary movement of both river and ground

water extending to the sand surface (Figure 6).

Figure 6. Photograph of capillary fringe habitat on a sanbar in the Kansas River.
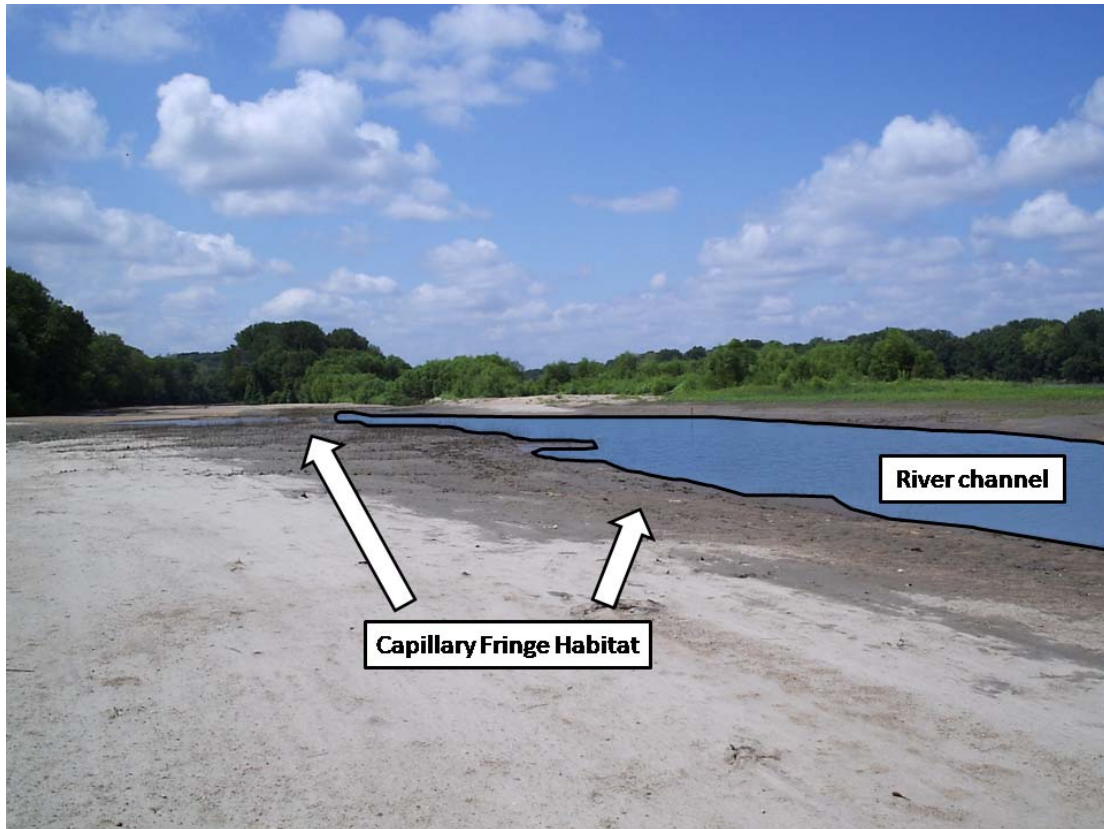
The edge habitat was defined as the submerged benthic substrate within approximately 30 cm from the water's edge, usually 5-10 cm deep. The main channel habitat was at a variable distance into the river channel (where significant flow was found, similar to main channel flow rate) straight out from the capillary fringe habitat. Unpredictable flow events precluded a set sampling regime, but six samples were taken approximately every two weeks from early June to late August (June 4, July7, July 20, August 3, August 18, August 31, and September 29). In addition, a seventh sample was taken in late September to cover late season conditions.

Physicochemical measurements were made for water temperature (°C),

conductivity (μS· cm^{-1}), pH, and salinity (%) using a HydroLab Quanta™. Flow

velocity was measured using a Swoffer™ 2100 Current Velocity Meter. Sand surface

temperature and sand temperature at a depth of 5 cm in the capillary fringe were

measured using an infrared thermometer. Depth was measured by a meter stick and

substrate type was noted. Sand substrate samples were collected using a device

similar to a Wildco Swamp Sucker™ (Figure 7).

Figure 7. Swamp Sucker sampling device – When the plunger is extended
completely downward, the plexiglass tube is forced into the substrate. The sediment
is then sucked into the plexiglass tube when the plunger is lifted. After sealing the
bottom of the device and removing it from the water, the plunger is pushed down to
eliminate all but the desired depth of sample.
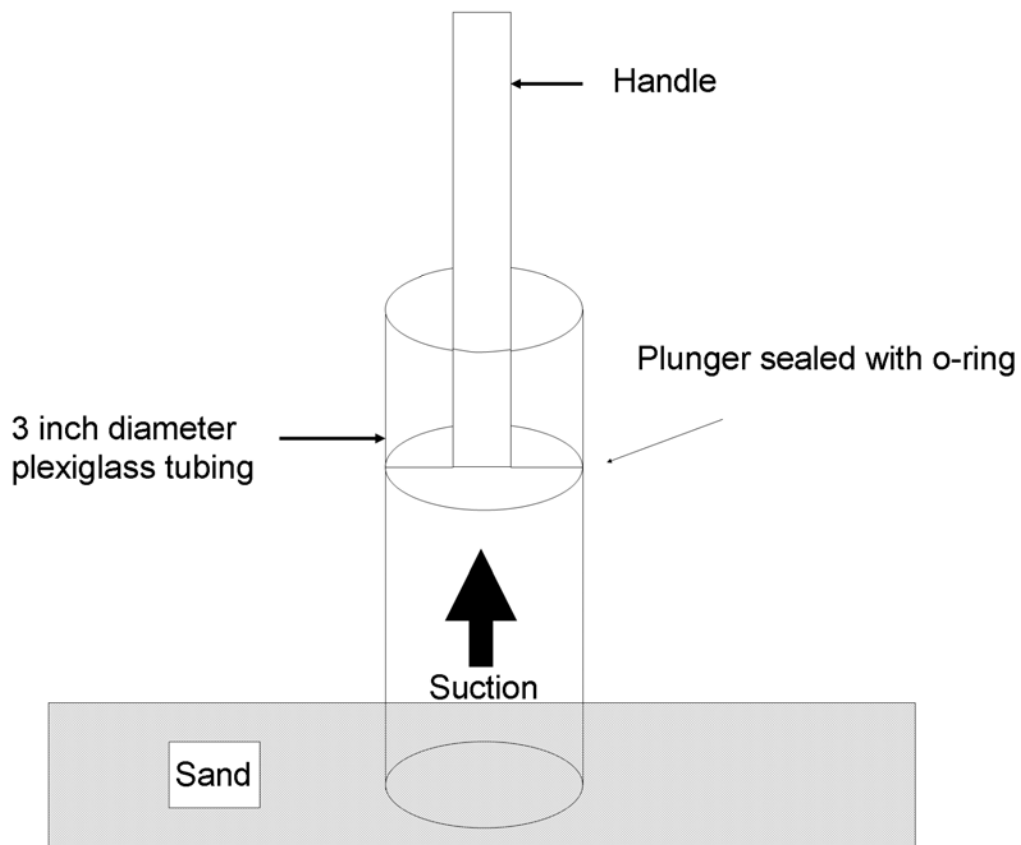
To characterize each sample site for organic content and substrate size, the top 20 cm of sand was collected and dried for 72 h in an incubator at 75°C to eliminate water. The samples were then homogenized and portions were burned at 500°C to calculate ash free dry mass (AFDM) for analyzing organic content. The remaining sample was used for substrate characterization by passing the homogenized sand sample through a series of 1, 0.5, and 0.25 mm mesh sieves. Sand subsections were then massed and percent of each size category was calculated (>1 mm, 0.5-1 mm, 0.25 mm-0.5 mm, <0.25 mm).

Benthic invertebrates were collected from cores (7.62 cm in diameter, 10 cm deep) using the Swamp Sucker. The invertebrates were later separated in the lab from the sediment by an elutriation device (Figure 8) modified after Whitman *et al.* (1983) and preserved in 75% EtOH.

Figure 8. Elutriator device modified after Whitman et al. (1983). Water and air bubbles through a 20 μm cloth filter and lifts invertebrates out through tubing into a 100 μm sieve. Sand and gravel remain at bottom of cone.
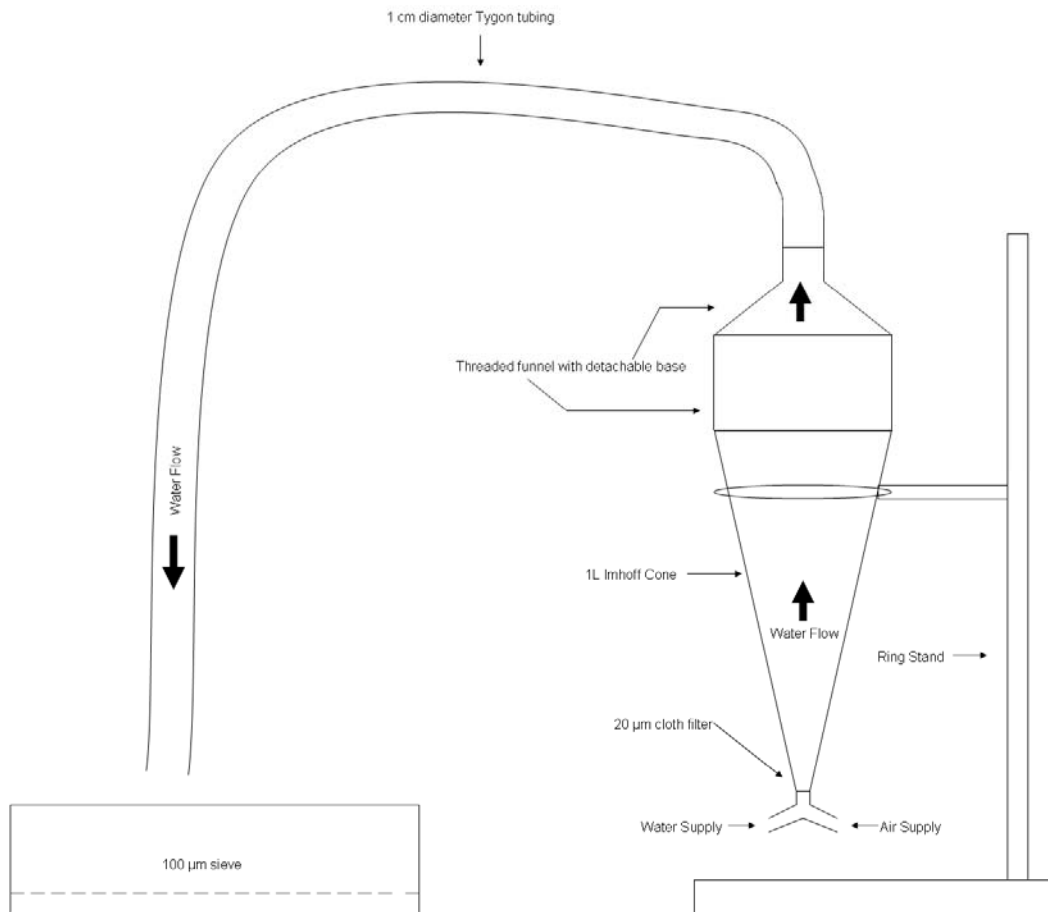
The remaining sediment was saved and inspected for invertebrates to ensure that all specimens were collected in the sieve. However, this step was discontinued after the third sampling date because an insignificant number of invertebrates were missed with this device (only 5 total organisms were found to have been missed by the elutriator in 216 samples). The non-chironomid taxa were then identified to the

lowest practical taxa (genus level for most insects, higher taxonomic levels for

oligochaetes, Collembola, etc.). Chironomids were mounted and subsequently

identified to genus on glass slides using CMC-9 and CMC-10 mounting media.

Several large samples (~300 invertebrates) were subsampled by homogenizing the

sample in a radially divided Petri dish and collecting a quarter of the sample for

identification. Keys used for invertebrate identification included McCafferty (1981),

Wiederholm (1983), Merritt and Cummins (1996), Wiggins (1996), Epler (2001), and

Thorp and Covich (2001).

Statistical Analyses

The polynomial regressions used to determine riverscape complexity ratios

(RCR) were calculated using SigmaPlot version 9.0. All nonmetric multidimensional

scaling ordinations were completed with the program PC-ORD version 5. General

procedure and starting configurations followed guidelines in McCune and Grace

(2002). Each ordination used the Sorensen (Bray-Curtis) distance measure, started

with six dimensions stepping down to one, 50 runs with real data, and 15 iterations to

evaluate stability with a stability criterion of 0.00001. A supplied seed integer of

4483 was used for the starting configuration. The possibility of a better-than-random

solution was evaluated using a Monte Carlo test with 10,000 iterations. A scree plot

and final stress was used to determine the number of dimensions to use in the final

test. Stability of each ordination was evaluated by using the plot of stress vs. iteration

number and by the final instability.

Multi-response Permutation Procedures (MRPP) were conducted to test for differences between communities in PC-ORD version 5, following the recommendations of McCune and Grace (2002). Sorenesen (Bray-Curtis) distance measures were used. Pairwise comparisons were done on *a priori* groups and were Bonferroni corrected.

All tests used a significance level of 0.05.

Results

Riverscape Complexity and the Hydrologic Cycle

Riverscape complexity ratio (RCR) was calculated for every Landsat photograph and graphed over discharge. The graph of RCR to discharge (Figure 9) closely fits a 3-parameter, exponential decay equation (Y=0.9943 + 0.7967 $e^{(-0.0056x)}$, where Y= RCR and X = discharge, R^2=0.909, p<0.0001).

Figure 9. Rivescape Complexity Ratio (RCR) regressed over discharge in the Kansas River. Best fit equation is a 3-parameter exponential decay.
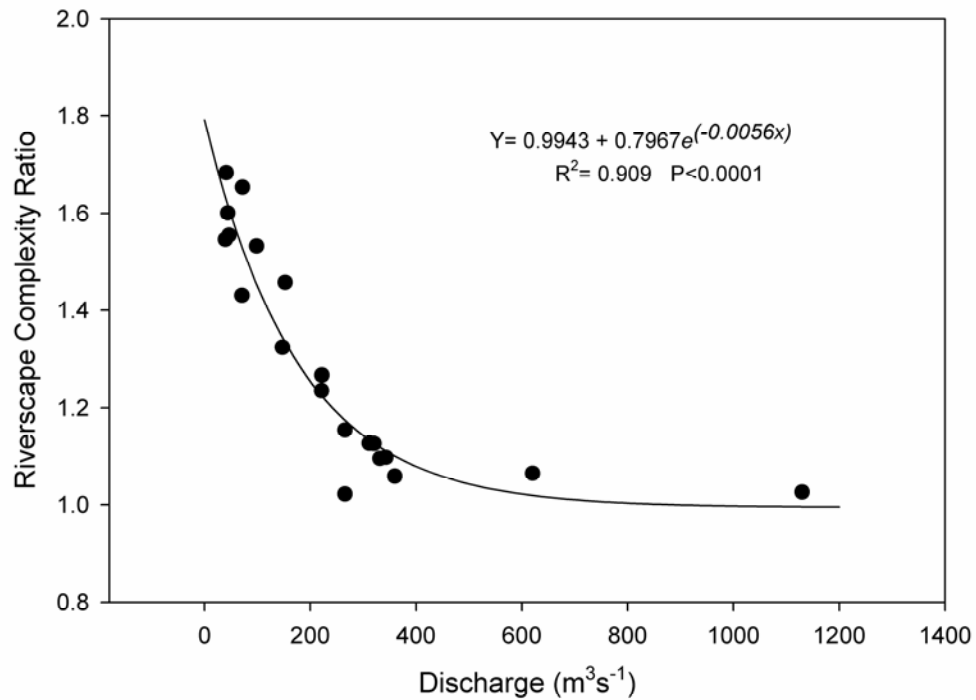
At high discharge, RCR approaches one because the river is mostly a single channel, with few large semi-permanent islands. As the river stage decreases, mid-channel and alternating bars appear and the river braids, increasing the RCR value. At extremely low discharge, however, RCR values may eventually decrease to an intermediate value since the Kansas River becomes a meandering single channel that follows the previous thalweg. The RCR value would be intermediate instead of low because the tortuous path inside the wider bed of the river would have more edge than the river at high single channel stage and less than the river at intermediate discharge where many islands and sandbars are present. Landsat images of these extremely low discharges were not available, so analysis of this behavior could not be carried out.

The RCR is sensitive to ecological variables such as amount of edge available for colonization, and the resulting slackwater habitats created. It can be used for all types of bars, islands, and river structures including previously neglected alternating and point bars. The RCR is also sensitive to changes in discharge, so it can be used to show changes in a river's structure over time and throughout the hydrologic cycle.

For these reasons, I propose the RCR as a new metric for use when river complexity is an issue in studies of lotic ecology involving hydrologic changes. The RCR is useful in these contexts because it integrates and responds to the effects of various dynamic hydrologic and geomorphic parameters essential for ecological questions, for example, hydrologic and geomorphic fluctuations. The RCR can also account for all types of bars, islands, and slackwaters within the river channel and

along the shoreline. One of the main benefits of the RCR is its responsiveness to

changes in river discharge. Thus, if a river is not drastically changing its behavior

from some anthropogenic or natural event, the fitted RCR equation can predict the

complexity of a river at any time as long as the discharge is known (Figure 10).

Figure 10. River Complexity Ratio (RCR) shown for the Kansas River in summer 2007.

The fitted equation could then be useful when trying to find a time where a river has

the most flow refuges created by features within the river, for example, mid-channel

sandbars and slackwaters. In addition, the shape of the RCR curve is telling of the

behavior of each unique river and when comparing similar rivers. The shape of the

curve found in the Kansas River should not be taken as a model for all types of rivers.

Large floodplain rivers would most likely have different RCR curves (Figure 11) and

have a low RCR at low discharge until a threshold where the RCR would drastically

increase when the river overflowed its banks onto a structurally complex floodplain.

Figure 11. Hypothetical riverscape complexity ratio curve for a floodplain river.
RCR stays steady at some level of low complexity and then is dramatically increased
once overbank flooding occurs into the geomorphically complex floodplain.
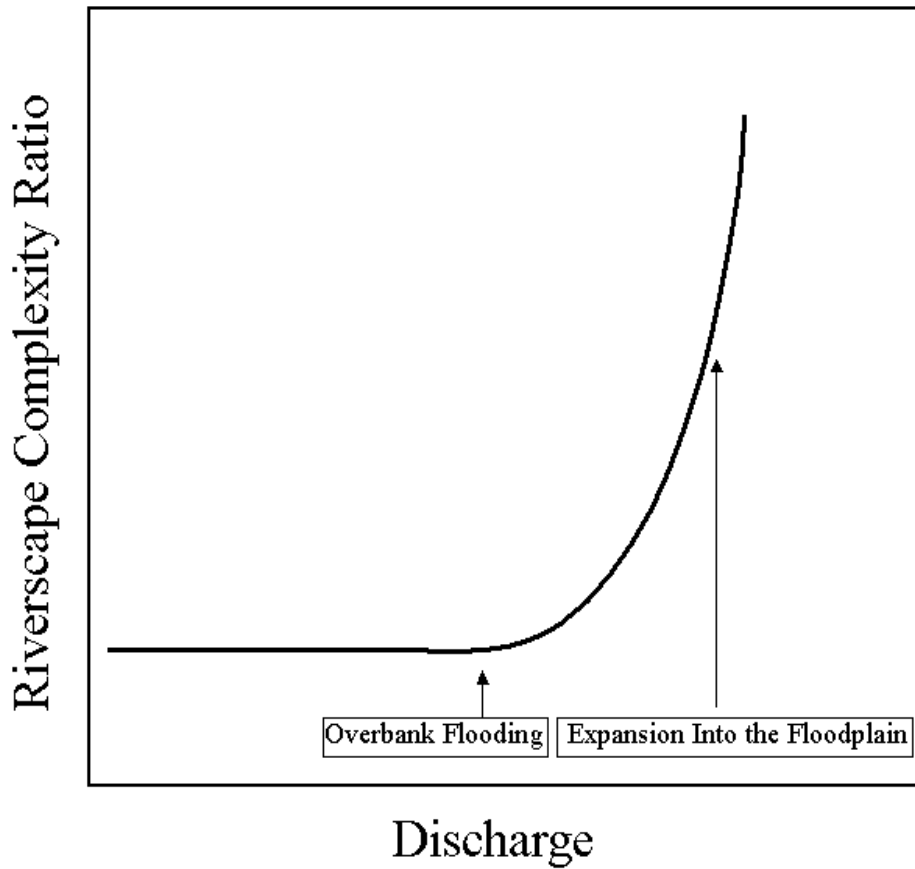
Conversely, naturally or artificially constricted rivers would have a very stable RCR

curve (Figure 12).

Figure 12. Hypothetical River Complexity (RCR) for a constricted channel river. RCR stays steady throughout discharge range since river banks constrain river to a single channel.
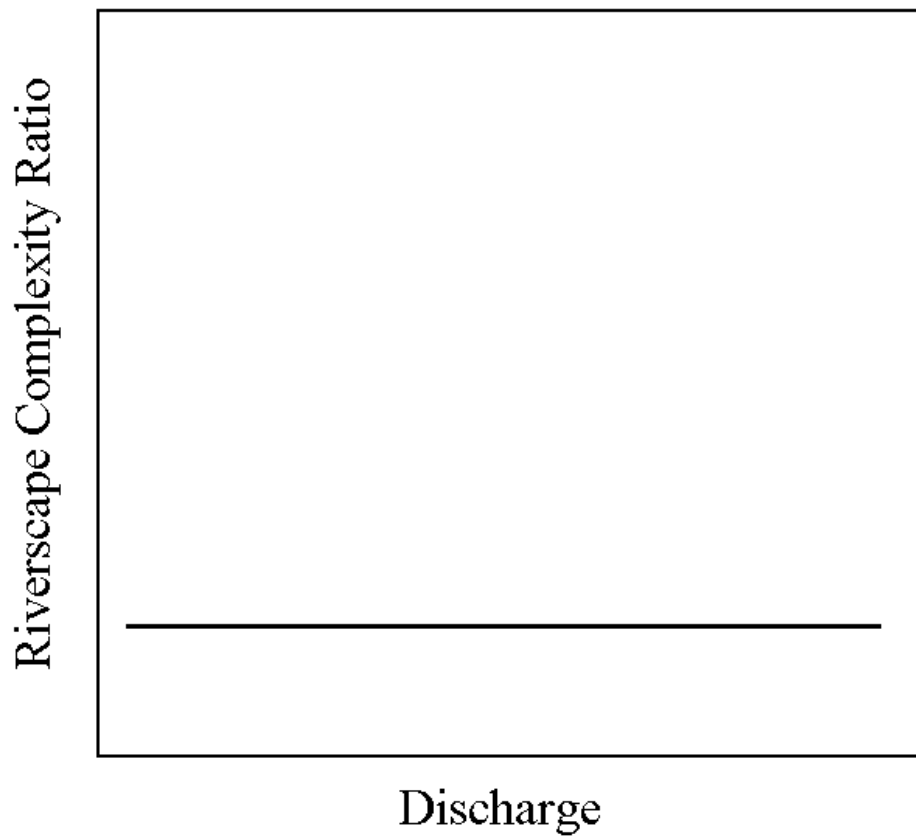
These rivers rarely overflow their banks and are almost always a single channel;

therefore, the RCR value would be low throughout their discharge range. Using this

knowledge, one could compare the RCR curves of different types of rivers as a new

tool for river comparison and research.

As with any riverscape complexity metric, attention should be paid to hydrogeomorphic changes within the river. River reaches with differing channel shape, depth, or width could cause the river to have different RCR values at the same discharge. However, only changes at the reach scale should be considered since smaller scale changes would be irrelevant when analyzing RCR, which is a reach level metric. The RCR should not be measured across these patches since doing so would lump two very different river behaviors into the same calculation and the distinct behavior of the RCR within each patch would be lost in the average. However, it would be useful when contrasting the behavior of distinct physical hydrogeomorphic patches within the river, for example, studying braided and single channel reaches of the same river. One could then create individual RCR curves for each individual patch within the river. Comparing the curves of the different patches over the entire discharge would then eliminate the problem of having different RCR values at the same discharge.

Woody Habitat Analysis

Using the method described earlier, I estimated that woody habitat represented 0.067% (3688 m^2 of wood in a total of 5,497,829 m^2 of sand) of the available river bottom for this 20 km section of the Kaw. This corresponds to 6.7 cm^2 of wood habitat per square meter of sand habitat. This process may actually have overestimated the amount of wood available in the system to aquatic organisms at lower discharges, since all wood that would be inundated at bankfull height was

included in this study. Furthermore, the wetted area of the river remains relatively

constant throughout the sub-bankfull discharge range, due to the relatively flat river

bed, steep river banks, and the fact that the capillary fringe acts as an aquatic habitat

even though it is above the water level. This would then overestimate the 6.7cm^2 of

wood/m^2 of sand, because much of the wood surveyed would be inaccessible to

aquatic organisms compared to a relatively constant area of aquatic habitat

throughout most of the year.

Diversity trend in the overall benthic community

Benthic invertebrates found throughout the study consisted mainly of insects

from the order Diptera, especially the families Chironomidae and Ceratopogonidae.

Oligochaetes and members of several other invertebrate and insect groups were found

sporadically throughout the study for a total of 60 taxa (Table 1).

Table 1. Table of Invertebrates found throughout the study. Left columns identify sampling date and habitat. Dates: 1=June 4, 2=July 7, 3=July 20, 4=August 3, 5=August 18, 6=August 31, 7=September 19. Habitat: C=Capillary Fringe, E=Edge, M=Mid Channel.   Taxa were identified to genus for Chironomidae and Ceratopogonidae; other groups were identified to lowest practical taxonomic level. The abbreviation "Unk" denotes where taxa were not identified past the taxonomic level given.

Date	Habitat	Polypedilum B	Polypedilum	Paratendipes B	Paratendipes	Paralauterborniella	Paracladopelma	Harnischia	Dicrotendipes	Crytochironomus	Chironomus	Chernovskiia	Chironominae	Rheosmittia	Parametriocnemus	Nanocladius	Lopescladius	Krenosmittia	Cric/Orth	Corynoneura	Procladius	Nilotanypus	Djalmabatista	Tanypodinae	Chironomid pupa
1	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
1	E	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
1	M	0	3	1	21	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1
2	C	0	1	0	6	0	0	0	1	0	1	0	0	0	0	0	3	4	0	1	3	0	1	0	0
2	E	0	4	1	8	0	0	0	0	0	0	0	0	0	0	0	4	15	0	1	1	0	0	1	1
2	M	0	1	0	24	0	0	0	0	0	0	0	0	1	0	0	10	14	0	0	2	0	0	0	0
3	C	0	85	0	31	0	0	0	2	3	8	1	0	3	0	2	12	16	1	0	0	0	0	1	17
3	E	0	145	0	21	2	2	2	6	19	36	2	4	10	0	2	21	41	7	0	0	0	0	2	17
3	M	0	20	0	24	2	0	0	1	11	23	5	0	137	0	27	33	10	0	22	0	0	0	1	1
4	C	1	20	1	21	0	0	0	1	0	8	0	0	1	1	0	0	27	1	0	0	0	0	0	1
4	E	0	37	0	9	0	0	0	2	1	13	0	2	0	0	4	0	26	1	0	0	1	0	1	7
4	M	0	33	0	7	0	0	0	2	9	0	3	0	2	0	6	25	35	1	0	0	0	0	0	5
5	C	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
5	E	0	17	0	0	2	0	0	0	9	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	M	0	29	0	7	0	0	0	0	2	0	1	4	10	0	2	38	3	0	0	0	0	0	0	1
6	C	0	57	0	16	0	0	0	2	0	3	0	3	0	0	0	1	0	0	0	0	0	0	0	4
6	E	0	76	0	5	2	0	0	1	8	8	1	0	0	0	1	21	5	0	0	0	0	0	0	9
6	M	0	23	0	5	0	0	0	1	1	3	2	4	4	0	0	21	12	0	0	0	0	0	0	1
7	C	0	10	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
7	E	0	7	0	1	1	0	0	0	0	1	0	0	0	0	0	0	9	0	5	0	0	0	0	0
7	M	0	5	0	2	0	0	0	0	0	0	1	0	7	0	0	2	5	0	0	0	0	0	0	0
	Total	1	576	4	208	9	2	2	19	63	105	16	17	175	1	45	194	223	13	31	6	1	1	6	65

Taxon	1C	1E	1M	2C	2E	2M	3C	3E	3M	4C	4E	4M	5C	5E	5M	6C	6E	6M	7C	7E	7M	Total
Hydrachnida Unk.	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Hirudinea Unk.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Branchiura sowerbyi	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Oligochaete Unk.	21	30	23	3	0	13	1	0	4	2	1	1	2	0	1	0	1	0	0	2	2	107
Nematoda	2	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	4
Tipulidae Unk.	0	0	0	0	0	0	0	0	8	1	1	0	0	0	0	0	0	1	0	0	0	11
Simulium	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Ephydridae Unk.	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	2	1	0	0	0	0	6
Discocerina	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3
Dolichopodidae Unk.	1	1	0	0	0	0	0	0	0	11	3	0	1	0	0	0	0	0	0	1	0	18
Stilobezzia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sphaeromias	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	3
Probezzia	0	1	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	5
Monohelea	0	0	0	0	0	0	0	0	0	24	4	1	0	0	0	0	0	0	0	0	0	29
Mallochohelea	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Dasyhelea	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Culicoides	3	1	0	0	0	0	0	0	0	246	34	10	1	0	0	0	0	0	3	0	0	298
Bezzia	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
pupa	0	0	0	0	0	0	0	0	0	24	0	1	0	1	0	0	0	1	0	0	0	27
Tanytarsus	0	0	0	0	2	0	234	392	25	13	45	20	1	5	0	15	18	4	2	3	0	779
Saetheria	0	0	0	0	5	2	17	18	1	2	1	16	8	0	50	14	39	2	0	2	0	177
Robackia	0	0	0	0	1	14	4	14	23	0	21	9	0	2	3	0	32	22	1	3	5	154
Rheotanytarsus	0	0	0	0	0	0	125	389	19	0	4	21	0	1	0	0	2	4	0	0	0	565
Pseudochironomus	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2
Habitat	C	E	M	C	E	M	C	E	M	C	E	M	C	E	M	C	E	M	C	E	M	
Date	1	1	1	2	2	2	3	3	3	4	4	4	5	5	5	6	6	6	7	7	7	

3

Date	Habitat	Collembola Unk.	Americanis	Ephemeroptera Unk.	Stylurus	Nigronia	Hydropsychidae	Hydroptilidae	Trichoptera Unk.	Dubiraphia	Elmidae Unk.	Ostracoda	Unidentified	Richness	Total numbers
1	C	1	0	0	0	0	0	0	0	0	0	0	0	8	31
1	E	1	0	0	0	0	0	0	0	0	0	1	0	15	47
1	M	0	0	0	0	0	0	0	0	0	0	0	0	9	54
2	C	0	0	0	0	1	0	0	0	0	0	0	0	11	25
2	E	0	0	0	0	0	1	0	1	0	0	0	0	14	46
2	M	0	0	0	0	0	0	0	0	0	0	0	0	9	81
3	C	6	0	0	0	0	0	0	0	1	0	0	0	22	572
3	E	1	12	2	0	0	7	0	0	10	0	0	0	23	1178
3	M	0	3	0	0	0	1	0	0	0	0	0	0	26	402
4	C	0	0	0	0	0	1	0	0	0	0	0	0	23	417
4	E	0	0	0	1	0	0	0	0	0	0	0	0	25	224
4	M	0	0	0	0	0	7	0	0	0	0	0	0	23	217
5	C	0	0	0	0	0	0	0	0	0	0	0	0	6	16
5	E	0	0	0	0	0	0	0	0	0	0	0	1	9	40
5	M	0	0	0	0	0	0	0	0	0	1	0	0	15	153
6	C	0	0	0	0	0	0	0	0	0	0	0	0	10	116
6	E	0	0	0	0	0	0	0	0	0	0	0	0	17	231
6	M	0	0	0	0	0	1	2	0	0	0	0	0	17	112
7	C	0	0	0	0	0	0	0	0	0	0	0	0	9	21
7	E	0	0	0	0	0	0	0	0	0	0	0	0	11	35
7	M	0	0	0	0	0	0	0	0	0	0	0	0	8	29
		9	15	2	1	1	18	2	1	11	1	1	1		4047

An overwhelming majority of taxa found in this study were considered either sand
habitat specialists or are normally found in depositional habitats (Merritt and
Cummins, 1996; Epler, 2001) The dominant chironomid taxa throughout the study
were mainly of the subfamily Chironominae (*Tanytarsus, Polypedilum,*
Rheotanytarsus, and *Paratendipes*) with smaller numbers of the subfamily
Orthocladinae (*Krenosmittia, Lopescladius,* and *Rheosmittia*). Ceratopogonidae were
found only on one sampling date in considerable numbers and were dominated by the
genus *Culicoides.*

The proportions of functional feeding groups varied through time; however
the collector/gatherer guild dominated the community and varied little (Table 2).

Table 2. Proportion of functional feeding groups across sampling dates

Date	Unknown	Predator	Herbivore	Collector/Gatherer
1	0.16	0.06	0.02	0.76
2	0.03	0.15	0.04	0.78
3	0.11	0.03	0.12	0.74
4	0.09	0.43	0.11	0.38
5	0.09	0.08	0.24	0.59
6	0.07	0.14	0.34	0.45
7	0.19	0.14	0.26	0.47

Collector/gatherers generally consume detritus which is carried by the current

(Merritt and Cummins, 1996), and this food source should not vary as much with

flow fluctuations compared to the abundance of other types of food, such as algae

which are easily disturbed by flow spates (Uehlinger *et al*., 2002). However,

herbivores generally increased through time as stability of the river concurrently

increased. As the river stabilized and algae flourished, the invertebrate herbivore

guild expanded. This trend, however, was not as pronounced in the mid-channel

habitat (Figure 13).

Figure 13. Graph showing percentage of invertebrates that are herbivores through time and by habitat. C, E, and M, represent capillary fringe, edge, and mid-channel respectively.
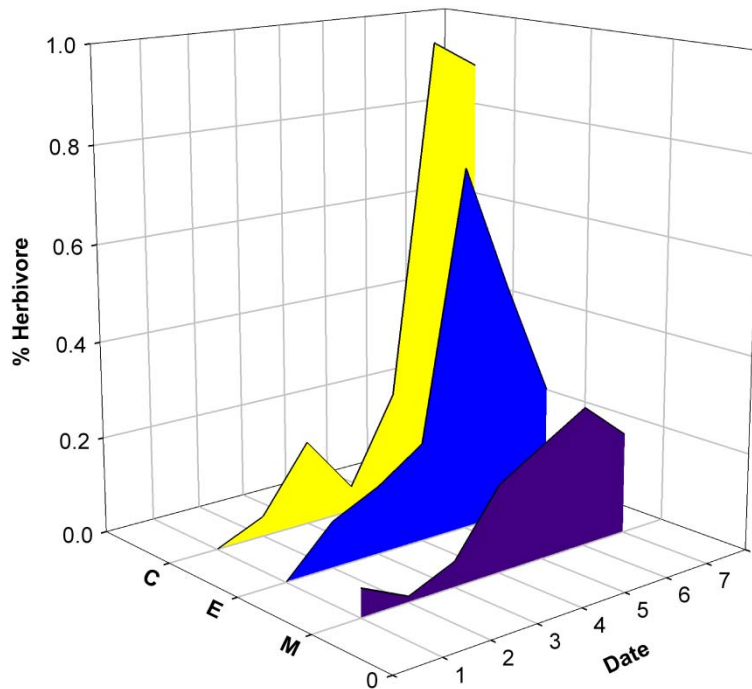
This was expected because fewer plants and algae generally occur in the main channel of a swiftly flowing sand bed river and are limited because of two different reasons: (a) the benthic habitat in the main channel is generally in the aphotic zone due to the high turbidity; and (b) in the flow velocities commonly found within the main channel, the sand bed is fluidized and continuously moving, creating an unstable and abrasive environment.

Benthic community structure analyzed by habitat

RCR values for the 7 sampling dates were placed into low, medium, and high

groups. An extremely low RCR value occurred on June 4 and was delineated as the

single representative of the low group. The remaining dates were relatively

continuous and were consequently grouped into categories of medium (July 7, August

18, and September 19) and high (July 20, August 3, and 31) (Figure 14).

Figure 14. Graph of RCR and discharge. RCR indicated in background gray.
Discharge indicated by solid black line. Each sample date is noted at top of graph.
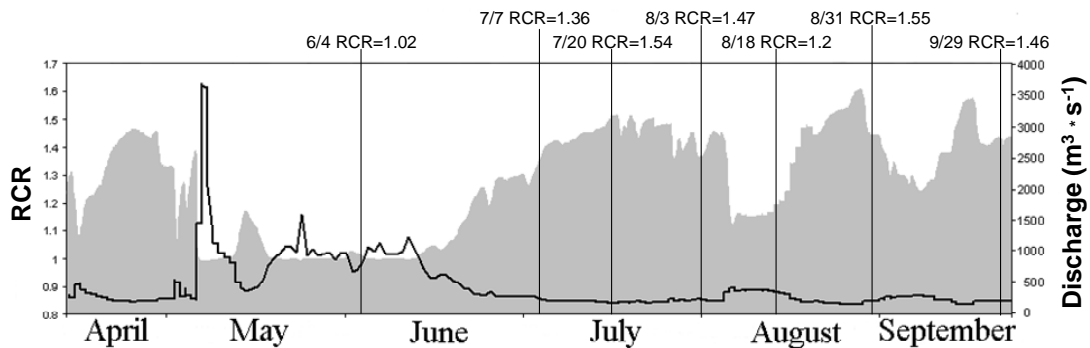
Rather than analyzing my entire large and complex hierarchical data set of 7

dates, 2 sandbars, 4 sandbar areas, 3 habitats, and 3 repetitions (504 data points), I

condensed the sandbar, area, and repetition level to maximize data manageability (21

data points). This left the data organized by habitat nested within sample date. This

allowed me to focus on the question of how the benthic community changed with

habitat by date while temporarily eliminating the effects of bar, area, and repetition.

To reduce the data even further into a manageable and interpretable format, nonmetric multidimensional scaling (nms) was performed to reveal how the benthic community reacted to changes in hydrogeomorphology as measured by change in RCR. After stepping down from a 6-dimensional solution, an analysis of the stress and instability led to the conclusion that a 3-dimensional solution would best explain the data (Figure 15).

Figure 15. NMS scree plot of data by date and habitat.
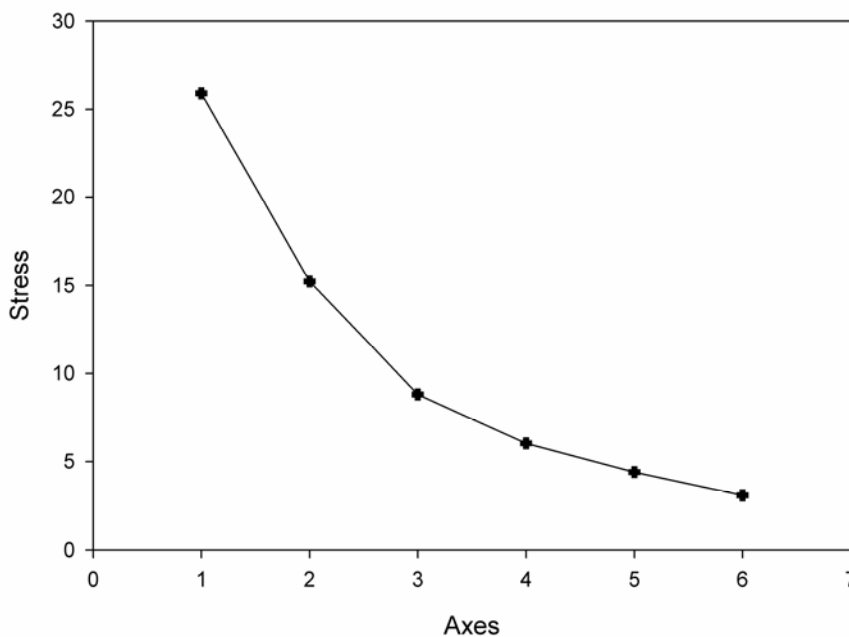
Final stress was 8.806 with instability of 0.00048 after 31 iterations. Following this, a multi-response permutation procedure (MRPP) was used to check for differences between the *a priori* RCR groups.

The MRPP showed that there were significant differences in the community structure between RCR groups. The chance-corrected within-group agreement, "A",

was found to be 0.201, with a p value of <0.001. Pairwise comparisons between the

groups showed that all community structures were significantly different (all p values

<0.001). Even though a 3-dimensional solution was found for the nms solution, a 2-

dimensional biplot of axis 2 and 3 of the original 3-dimensional solution was

adequate for explanatory purposes (Figure 16).

Figure 16. NMS jointplot of axis 2 and axis 3 showing differences in community structure between RCR groups. Δ = low RCR, += medium RCR, □= high RCR. Sediment proportions: avg25=sediment <25μm, av15=sediments between 250 and 500 μm, avg1=sediments larger than 1 mm, avgsize=average sediment size. Make avg easier to see
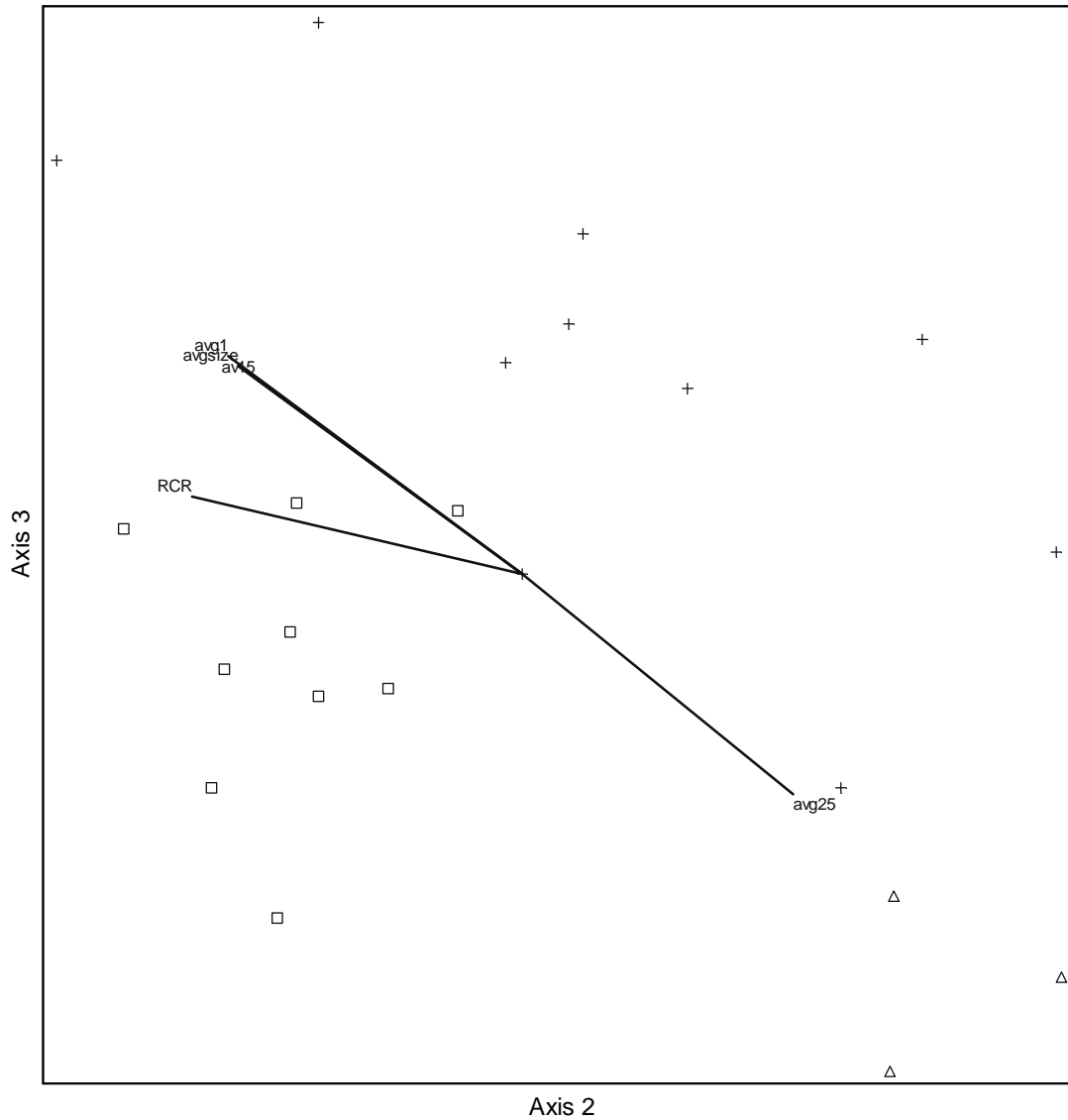
Figure 16 clearly shows three separate groups of points. The low RCR group is positively correlated with axis 2 and negatively with axis 3, corresponding to higher abundances of oligochaetes, nematodes, and the chironomid *Paratendipes*. Vector analysis (Figure 16) showed that the low RCR date had a higher proportion of smaller sediments (avg25) when compared to the high RCR group which was correlated with larger sediments (avg1, and avgsize). The high RCR group is negatively correlated with axis 2 corresponding to higher abundances of *Polypedilum, Tanytarsus, Cryptochironomus, Robackia, Lopescladius*, and *Krenosmittia.* The medium RCR group, however, is only correlated with the chironomid *Procladius*; all other taxa seem to be present, but at much lower densities when compared to the high RCR group.

The jointplot showing correlations with sediment size corresponds well with the observation that high amounts of runoff from agricultural fields along the tributaries and main channel of the river following thunderstorms results in large amounts of smaller sediments to be washed into the main channel. This causes the substrate characteristics of the channel to vary greatly throughout the year. During the early summer thunderstorm season, the channel tends to be very silty, but as the flow stabilizes at lower flow levels, less small sediments are brought into the stream and the channel gradually washes them downstream leaving larger sediments behind. These fluctuations make for varying benthic habitats, and the organisms respond in predictable ways. For example, oligochaetes were common during the low complexity, silty-sediment sampling date (June 4), with an average density of 150

individuals per m^2 and maximum densities of over 2900 individuals per m^2. All other sampling dates had average densities of only 11 oligochaetes per m^2. As the small sediments were washed downstream, a higher diversity of interstitial habitats was made available, which should lead to increases in taxa richness. This can be seen by the infiltration of more insect species, especially in the order Diptera.

Benthic community analyzed by sandbar area

Benthic community richness grouped by area was significantly correlated with RCR in all areas (H= 0.523, p<0.001; L=0.218, p=.014; R=0.445 p<0.001, T=0.315 p<0.001). Interestingly, the correlation coefficient was higher in the head and right side of the sandbar. This was not unexpected since the head and right side of the sandbars were the areas most exposed to currents. The sandbar tails had lower flow velocities because the sandbar itself blocked the flow, and the left sides of both study bars were protected in different ways. Even though the left side of the downstream bar (Bar 1; Figure 3) was adjacent to the main channel flow, it was sheltered by a sandbar projection upstream of the sampling point, effectively creating a slackwater area. The left side of the upstream bar (Bar 2) was adjacent to a small side channel with a slower flow rate. Overall, the richness was lower in the head and right side at low RCR, whereas the richness in the tail and protected sides were not higher, but more stable throughout the year regardless of RCR.

Fortunately for my study, the left side of sandbar 2 changed from a small side channel to a cut-off slackwater several times throughout the study. During sample

dates 3 (July 20) and 6 (August 31), the area was completely cut off into a backwater and an area of zero flow was created that caused the water to have a stratified temperature profile (difference of 1.33°C between surface and bottom). Similarly, during sample date 7 (September 29), the area turned into a weakly flowing slackwater with a shallow 2-3 m wide connection to the main channel. To evaluate how the community structure responded to these changes, a separate nonmetric multidimensional scaling analysis was done on the left side of sandbar 2. After stepping down from a 6-dimensional solution, an analysis of the stress and instability led to the conclusion that a 3-dimensional solution would best explain the data. Final stress was 11.02 with an instability of 0.0001 after 54 iterations. The sample dates were formed into 3 *a priori* groups: side channel (dates 1, 2, 4, and 5), weakly flowing slackwater (date 7), and backwater (dates 3 and 6). A multi-response permutation procedure was used to compare the community structure of the groups. The chance-corrected within-group agreement, "A", was found to be 0.105, with a p value of 0.002. Pairwise comparisons were made, and the community structure of the backwater group proved different from both the side channel (p=0.005) and slackwater groups (p=0.011) (Figure 17).

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Figure 17. NMS configuration of communities from left side of sandbar 2.
Centroids are used instead of the full cluster of points for ease of readability.
* denotes backwater dates, + denotes weakly flowing slackwater.
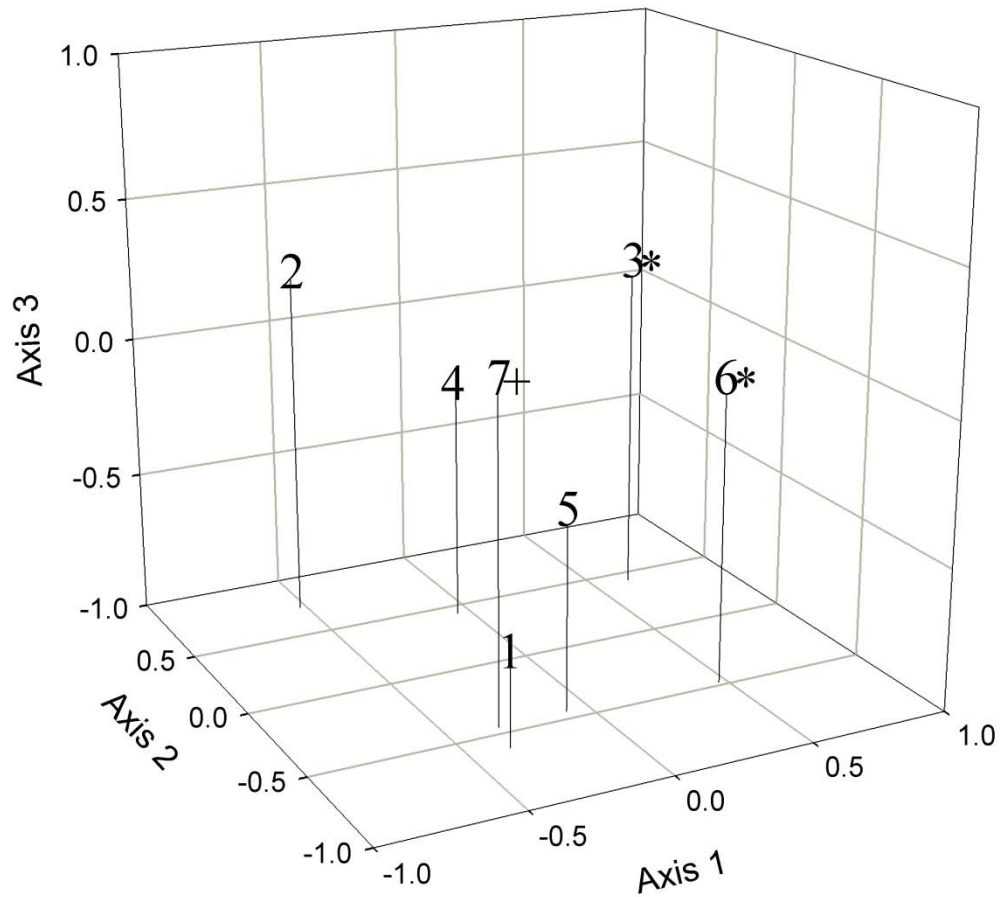
The slackwater community, however, was not significantly different from the side

channel (p=0.117). A vector analysis of the nms configuration showed that

Krenosmittia and oligochaetes were associated with the side channel groups, whereas

Chironomus, Tanytarsus, Polypedilum, and *Cryptochironomus* were associated with

the backwater groups. *Culicoides, Robackia,* and *Saetheria* were found only during the side channel dates, while *Chironomus* and *Dicrotendipes* were found only during the backwater dates. *Polypedilum* was found during both the side channel and backwater dates throughout the study, but it was found in higher numbers when the habitat was cut off into a backwater.

Discussion

Historically, most ecological studies dealing with flow disturbances focus on the importance of refugia before and after discrete flow or flood events, but prairie streams repeatedly experience flow disturbances throughout the year, especially during the spring and summer thunderstorm seasons. Few studies have examined systems with continuous flow disturbances, especially in prairie rivers, although one could question whether such frequent events constitute true disturbances. The observed flow events greatly changed the habitat complexity and structure in the Kansas River, with varying responses from the invertebrate community.

Considering that prairie river habitats are potentially so harsh, it is intriguing that so many benthic invertebrates occur in the Kansas River. Invertebrates in the Kaw and prairie rivers in general must have many strategies and adaptations for surviving in such a variable and potentially stressful environment. These strategies could include, but are not limited to, resisting disturbances, fleeing the system entirely, finding temporary refuges, and recolonizing following population depletion.

In the Kansas River, the larger flow events generally eliminated most of the benthic community; consequently simply resisting the disturbance does not seem to be a viable strategy in the Kaw for benthic insects. However, several species of chironomids were collected from the main channel throughout much of the study. These included three genera of small size from the Orthocladiinae (*Krenosmittia, Lopescladius,* and *Rheosmittia*) and four larger sized genera from the Chironominae

(*Paratendipes, Polypedilum, Robackia,* and *Saetheria*). Whether these seven taxa

actually withstood the flow disturbances in the main channel remains unclear. They

may have just as easily burrowed deep into the substrate to escape the higher currents

and fluidized bed load in the main channel. This latter strategy is probably true of the

smaller orthoclads, but whether the larger genera of Chironominae sought shelter in

the substrate is unclear.

Invertebrates seemed completely absent from some substrate areas following

high flow events, but it was not feasible to determine whether these invertebrates

sought shelter in a different areas of the river, departed the river entirely, or were

unwillingly flushed downstream. Some insects in desert streams are known to

evacuate stream channels to escape flash floods (Lytle *et al.,* 2008). However, this

strategy would not work for most invertebrates found in the Kansas River for various

reasons. First, the mobility of the invertebrates commonly found in the Kaw is

inadequate compared to invertebrates that are known to commonly leave their aquatic

habitats, for example predaceous diving beetles and the giant water bugs considered

in the 2008 Lytle *et al.* study. Second, it would be very difficult for a larval dipteran

of only several millimeters in length to emigrate from the 250 m wide stream channel.

Finally, most of the invertebrates found in the Kaw are physiologically incapable of

tolerating terrestrial conditions. They could not extract oxygen from the air, avoid

desiccation, or support their own bodies outside of the water column due to the lack

of robust support structures found in some larger aquatic invertebrates. From these

reasons, I believe that most invertebrates in the Kaw do not evacuate the stream channel to avoid being flushed downstream.

A more viable strategy for the invertebrates in the Kansas River could be for them to seek a refuge within the stream channel. A highly productive habitat and possible refuge for invertebrates in some sand bed rivers is woody debris, with the abundance of this substrate seemingly enhancing benthic production. Wood snags contributed up to one third of the total habitat, or 0.5 m^2 of wood/m^2 of sand habitat in some sand bed rivers of the southeastern coastal plain of the USA (Wallace and Benke, 1984). Although only 4-6% of the available habitat in the Satilla River was wood snags, this amount contributed a disproportionate amount (between 14.5-16.2%) of the river's total invertebrate production (Benke *et al.* 1984). Woody debris is relatively rare in the Kansas River, however, with only 0.00067 m^2 of wood habitat per m^2 of sand habitat. This is two orders of magnitude less than in the Satilla River and three orders of magnitude lower than in coastal plain rivers. The Kansas River has apparently never had large amounts of wood, at least in historical times as evidenced by Lieutenant Joseph Tidball's written description in the first official survey of the Kansas River in 1853 (Langsdorf, 1950). Moreover, snagging operations to enhance boat traffic have never been undertaken on the Kansas River.

This leads to the conclusion that while woody habitats may have high densities of aquatic invertebrates and have very high production of invertebrates, the exceedingly small amount of wood present in the Kansas River probably makes it

insignificant to food web dynamics and secondary production for the river as a whole. Great Plains rivers like the Kaw seem, therefore, to be examples of rivers where the geomorphic structure of the river itself is primarily responsible for enhancing diversity and production, which is consistent with theories like the inshore retention concept (Schiemer, 2001). Such models emphasize the ecological importance of structurally complex shallow areas at the land-water interface, not just stable substrates within the main channel. In the Kansas River, these shallow and complex areas take the form of slackwaters created from the dynamic geomorphic structure of the river channel, located behind and around sandbars and along the river bank.

The Kansas River provides an example of how a potentially mobile substrate in a sheltered area can serve as a refuge during flow pulses. In my study the species richness values were not higher in protected areas behind sandbars, but were significantly more stable or consistent than in areas exposed to higher and more variable flow within the main channel. It is not surprising that the more exposed areas respond more strongly to changes in river complexity because there is more hydraulic forcing on these areas. Moreover, the protected areas would be sheltered from the small flow spikes that do not overtop the sandbars, while organisms in the exposed areas would be more easily swept downstream during the high flow-low complexity spates throughout the year.

The Kaw also had significantly different benthic communities at different complexity levels (Figure 16), which lends more support to the idea that within-

channel structures are important. During periods of low complexity, the river was mainly inhabited by oligochaetes, nematodes, and the dipteran *Paratendipes*; however, at higher complexity, the river became much more diverse and had many more insect species, especially dipterans. This is most likely explained by the fact that when the river is more complex it has a higher number and diversity of habitats and refuges. The appearance of sandbars within the river creates small side channels, areas of low to zero flow, and much more edge habitat. In addition to influencing benthic habitat at larger scales by increasing the number and diversity of those habitats mentioned above, sandbars also affect benthic habitat at small scales. Silt laden habitats are formed in low flow areas behind sandbars, and more gravel type habitats are created at the head of sandbars where the continual hydraulic forcing of water washes away smaller sediments. Increases in interstitial habitat diversity are known to affect and sometimes drive benthic invertebrate diversity and abundance (e.g., Cummings and Lauf, 1969, Minshall and Minshall, 1977, Tolkamp, 1982). Overall, the appearance of sandbars increases the complexity of the river at several scales, thereby increasing habitat diversity and creating refuges. Changes in river complexity can then drastically change the benthic community and act as a driving force in the community dynamics of the river.

While seeking a refuge is an adequate strategy for many levels of disturbance, some flood events in the Kansas River may be so drastic that the benthic fauna is completely eliminated and must recolonize from other areas. This likely happens continually throughout the year and involves species dispersing from nearby

tributaries and other aquatic habitats (via either aerial or aquatic means). After a large flood pulse, however, this source of immigrants may contribute the greatest to rebuilding the benthic community. Fortunately, through the course of my study, I witnessed how the benthic community changed in one area that was repeatedly eliminated and recolonized after large flow fluctuations. The left side of sandbar 2 often changed from a side channel to a zero-flow backwater, and the community within this area was significantly different during these different times. An interesting aspect of this analysis is that the communities from the two dates in the backwater group are similar even though the two dates were separated by 6 wk. By following communities in nms space through time (Figure 17) as the secondary channel is cut off and then reopened, one can see that the community shifts back and forth between a "side channel community" and a "backwater community". Even the weakly flowing slackwater group is on the edge of the cluster of points, which could be on a trajectory towards the nms space occupied by the backwater groups. Distinct and relatively consistent communities can be seen forming and reacting to the changing conditions of this environment. These changes throughout the river then create a mosaic of different habitat patches, increasing species diversity and richness throughout the river.

Zoobenthos of prairie are well adapted to exploit newly created or exposed structures within their environment by using a variety of strategies for resistance, escape to in-stream refuges, and/or recolonization from outside the river proper. The dominant zoobenthos in the Kansas River are generally small, short lived, and

multivoltine. Laboratory experiments have found that chironomids can hatch and emerge within nine days at the temperatures regularly found in the Kaw, making it possible to produce many generations per year (Gray, 1981). The presence in the Kaw throughout the year of larvae in a wide range of size classes ensures that enough mature larvae are present to rapidly replenish depleted populations (Scrimgeour *et al.,* 1988). These attributes of resilience (Reice, 1990) allow species to exploit rapidly any resources made available by frequent and unpredictable disturbances (c.f. Winemiller and Rose, 1992).

In general, the benthic community of the Kansas River seems composed of very hardy and resilient species. They are adapted to the types of disturbance that are common in prairie rivers and thrive in this environment. Many seem to rely on the geomorphic complexity of the river to provide refuges and create opportunities for recolonization. These complex geomorphic structures and slackwaters then become integral to the entire food web, not just the zoobenthos, because ecotone complexity, which is a large part of physical habitat structure, is also a key factor for fish communities (Schiemer and Zalewski, 1992). This is not only because of the relief from physical forces that the slackwaters provide to the fish, but also because the benthos are the main source of animal food for the entire ecosystem. Moreover, the only place in the river with high densities of food items is the slackwaters and structures within the river. These sandbars and slackwaters in the braided sections of the river create a network that is important for the critical life stages of fish and is tied to recruitment, especially during times of strong water level fluxes and floods

(Schiemer and Zalewski, 1992). Even attributes of the slackwaters, for example their size, distribution, availability and seasonality may be crucial for the biota whose life history strategies are adapted to an environment with natural complexity (Richardson, 2004).

Unfortunately, the Kansas River has seen dramatic changes in complexity from anthropogenic disturbances. The addition of levees in the urbanized areas and dams on the tributaries close to the main stem Kaw have dramatically reduced the complexity of the river (Figure 18), essentially simplifying the river to a single channel, and eliminating many benthic invertebrate hotspots and nursery habitats for fish.

Figure 18. Riverscape Complexity Ratio (RCR) calculated along the Kansas River, from river kilometer 130 to its mouth at the Missouri river.
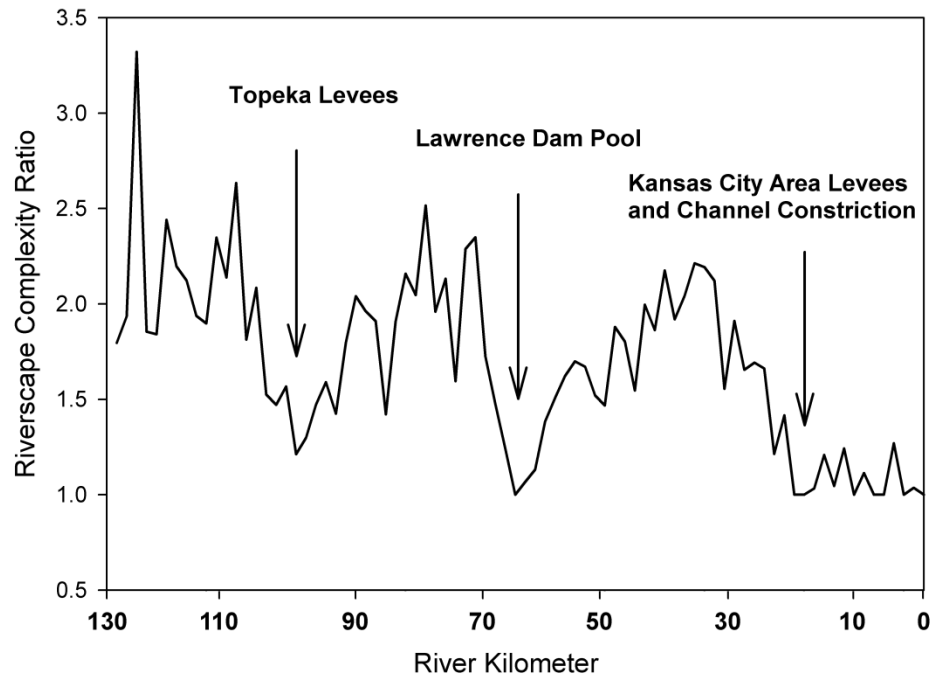
Another type of major anthropogenic impact on the Kansas River was the construction of dams along the major tributaries after the Great Flood of 1951. These dams have decreased the chance for a catastrophic flood. In the process, however, the resulting large reservoirs eliminate much of the normal bed load and suspended sediment (Graf, 1999), especially gravel and coarse sand that normally would have been passed through to the main channel. This filtering of sediments can change a river's sediment regime and starve it of sediment, causing it to degrade the river bed, erode its banks, and simplify its channel.

Conserving the natural complexity of a river is paramount to preserving the biodiversity and ecosystem processes within a river. The continual degradation of rivers through straightening projects and the construction of dams and levees has

caused harm and probably the extirpation of species. Changes to the natural flow

regime alter the underlying fluvial processes of a river, causing modification to its

ecology (Lotspeich, 1980). Regulation in rivers causes side channels and backwaters

to become disconnected and abandoned by the main channel as they fill in (Hill and

Platts, 1991) until they become shrunken, simplified versions of their predecessors

(Graf, 2006). Complexity reduction has been shown to reduce natural fish stock

density and biomass by 90% in some rivers (Jungwirth *et al.,* 1993). Another effect

of changes in river complexity is that biotic diversity and the ability of the riparian

forest to retain sediments and nutrients are severely diminished; resulting in

deteriorating water quality and an increased probability of economic losses from

floods (Naiman *et al.,* 1988). Overall, the natural complexity of a river must be

preserved if the organisms within the river are to be conserved. Future managers

should incorporate river complexity issues into their strategies.

Acknowledgements

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