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Harshness: characterisation of intermittent stream habitat over space and time

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Abstract. Frequently disturbed environments, such as intermittent streams, are ecologically useful for studying how disturbance characteristics (e.g. frequency, magnitude) affect community structure and succession. We developed a harshness index that quantifies ecologically pertinent spatial and temporal characteristics of prairie intermittent streams that may limit or reduce diversity and abundance to predict benthic macroinvertebrate assemblage characteristics. The index incorporates 11 variables that describe the hydrological regime (e.g. average flow, flow variability, drying and flooding) and distance to perennial surface water. We started with 27 variables, but removed 16 that did not increase the predictive value of the index. The relationships among index values and annual mean macroinvertebrate assemblage characteristics (taxonomic richness, diversity, evenness and abundance) were tested over two years using seven sites that represent a range of flow permanence (recent and historical), flood magnitude (recent and historical) and surface-water connectivity. Mean annual taxonomic richness was significantly related to the harshness index. Evenness and abundance were not related to harshness. Further analyses indicated that distance to the nearest permanent habitat was less important than annual or historical hydrological parameters, even though prior research had documented higher rates of colonisation at sites that were closer to nearest permanent habitat. Both annual factors that can alter abundance and colonisation immediately (e.g. floods, drought in each year) and historical factors (e.g. probability of drying, average length of dry period over decades) may influence assemblage characteristics. Historical factors may influence evolutionary adaptations of invertebrates and may predominate when relative disturbance rates are lower such as in years with less flooding.

Introduction

Intermittent streams are widespread globally and a significant proportion of runoff occurs through these streams (Dodds 1997). Understanding factors constraining the biological communities in such systems will be useful in basic ecological studies (Dodds *et al*. 2004) and in attempts to create indices of biotic integrity. The biological classification of streams has been useful for comparing differences in ecological processes and assemblage characteristics among different systems (Illies and Botosaneanu 1963; Hynes 1970; Pennak 1971; Puckridge *et al*. 1998).

Early classification of intermittent streams separated ephemeral from intermittent and vernal from autumnal waters (e.g. Usinger 1956; Clifford 1966; Abell 1984). More recently, Uys and O'Keefe (1997) identified terminology to describe the hydrology of South African rivers, including six types that incorporate drying as a regular hydrological phase. Among the six types identified by Uys and O'Keefe (1997), the spatial extent of drying and predictability of floods and drying were important in the definitions.

Recently, more detailed characterisation schemes of intermittent streams use point measurements of abiotic parameters (Boulton and Lake 1990, 1992; Feminella 1996). These measures have been related to differences in macroinvertebrate assemblage characteristics across a gradient of intermittence or permanence and have been useful in identifying similarities across intermittent stream types (Boulton 2003). This approach uses ecological time to predict assemblage characteristics while ignoring selective pressure by environmental constraints over greater time scales. Traits selected over longer time scales (e.g. physiological tolerance, life history and behaviour) can be important to the maintenance of populations in temporary waters (e.g. Hinton 1953; Williams 1985; Williams 1996, 1998) and in other disturbance-prone environments (Scrimgeour *et al*. 1988).

We consider prairie streams harsh habitats for stream organisms because they regularly flood and dry; this hydrological regime dramatically lowers abundance and diversity of stream organisms (Dodds *et al*. 2004). In this paper, the term 'harshness' is used to describe natural physicochemical

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conditions that limit or reduce the diversity and abundance of stream macroinvertebrates (*sensu* Peckarsky 1983). An index that includes variables representing the historical and immediate hydrological regime should characterise the physical template that constrains assemblage characteristics of intermittent streams.

Indices that summarise long-term hydrological variability and extremes have proven successful for classifying streams (Poff and Ward 1989; Poff 1996; Puckridge *et al*. 1998; Olden and Poff 2003). Such indices are rarely used for predicting community metrics (except see Clausen and Biggs 1997) and describing taxonomic and functional attributes (Poff and Allan 1995) in perennial streams. Rather, such indices assume that historical features of hydrological conditions represent a range of conditions under which organisms evolved and can be used to describe a range of abiotic templates that should correspond to assemblage characteristics. We are not aware of any studies that have used indices to directly predict assemblage characteristics among intermittent streams.

Our objective is to explore values that may be useful in creating an 'index of harshness'. This index should quantify spatial and temporal characteristics of intermittent streams that could predict the assemblage characteristics and evaluate the importance of recent and historical flow regime (temporal) and surface-water connectivity (spatial) to the benthic macroinvertebrate assemblage characteristics. We predicted that streams with higher harshness values (e.g. greater frequency of floods, longer duration of dry periods, lower predictability of flow and further distances to perennial surface water) would have assemblages with lower diversity and abundance than streams with lower harshness values. These attributes were chosen based on prior research on invertebrates (Fritz and Dodds 2004) and other organisms (Dodds *et al*. 2004) in prairie streams. We developed and tested this concept of an index that encompasses temporal and spatial aspects using intermittent prairie streams in Kansas, USA.

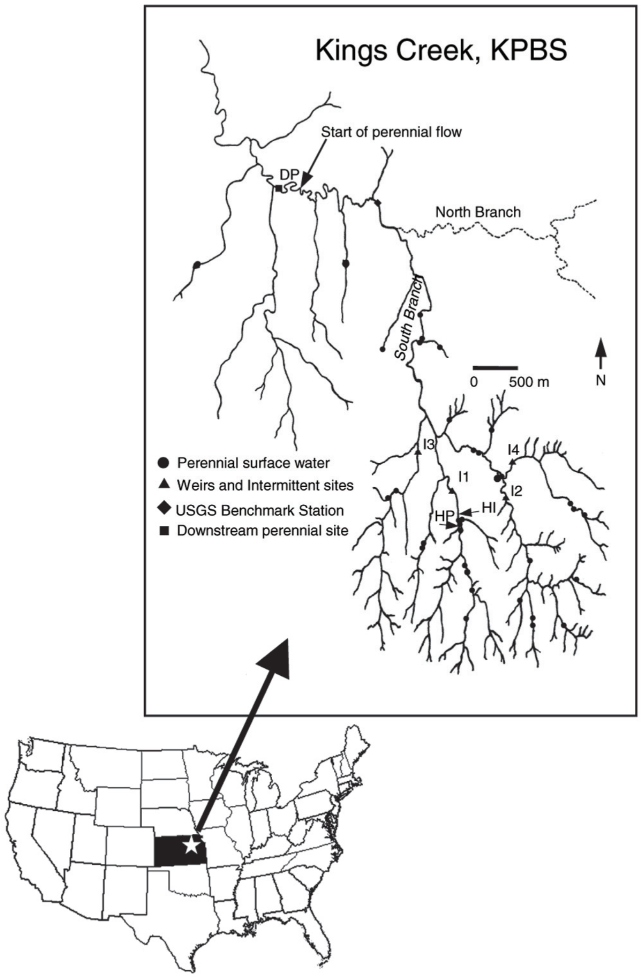

Fig. 1. Maps indicating the location of Konza Prairie Biological Station (KPBS) within Kansas (shaded) and study sites on Kings Creek within KPBS.

Materials and methods

Study sites

Kings Creek is located in the 3497 ha Konza Prairie Biological Station (KPBS), a tract of native tallgrass prairie within the Flint Hills Uplands of eastern Kansas, USA. Basic hydrology (Gray *et al*. 1998) and ecology (Gray and Dodds 1998; Dodds *et al*. 2004) of the stream has been described. During a year with average precipitation, the majority (83–90%) of the channel length is completely dry for 6–9 months of the year. Macroinvertebrates were sampled from seven sites within the Kings Creek drainage in 1995 and 1996 (Fig. 1) during wet periods. These sites included five intermittent sites (I1, I2, I3, I4 and HI), a perennially flowing headwater site (HP) and a downstream perennially flowing site (DP). Site HP is a spring-fed section located *c*. 20 m and 333 m upstream from HI and I1 respectively. Site DP is located *c*. 4 km downstream from the nearest intermittent site (I3). All sites except DP had grass and shrub riparian vegetation; DP had riparian oak deciduous forest.

Hydrological measurement

Discharge was measured continuously at all intermittent study sites except HI. Short periods of missing discharge data were estimated based on manual point measurements and linear interpolation (Gordon *et al*. 1992: 64). Discharge has been recorded since 1986 at I1 (11-year record) and since 1987 for the other intermittent tributaries (I2 10-year, I3 10-year and I4 8-year records).

The United States Geological Survey (USGS) maintains a Benchmark Station (no. 06879650) on Kings Creek. Although discharge at the USGS gauging station is intermittent, it represented relative discharge for DP because of the close proximity and the lack of major tributaries entering the channel below the gauging station. Over the last 11 years, personnel have visited the DP site at least three times per week and there never has been a time when the channel was dry even though the USGS discharge was zero (discharge at DP is typically 1–10 L s^{-1} when the channel is dry at the USGS station). There also has never been a flood at DP that was not also recorded at the USGS station. More details about methods used to measure hydrological variables are given elsewhere (Fritz 1997; Fritz *et al*. 1999; Fritz and Dodds 2004).

Macroinvertebrate sampling

Sampling details have been described previously (Fritz 1997; Fritz *et al*. 1999; Fritz and Dodds 2004). Briefly, three randomly selected samples

Table 1. Descriptors of annual hydrological conditions, historical hydrological regime and spatial characteristics of potential colonisation refugia

Detailed explanation of these descriptors has been published previously (Colwell 1974; Poff and Ward 1989; Jowett and Duncan 1990; Poff and Allan 1995; Poff 1996; Olden and Poff 2003)

Variable category	Variable	Description
Annual hydrology	AQ_{day}	Daily mean discharge during each study year.
	AR_{ann}	Mean annual runoff during each study year.
	AN_{BF}	Number of bankfull floods (1.67 ARI) during each study year.
	AQ_{max}	Maximum peak discharge during each study year.
	ANQ_{zero}	Number of days with zero discharge during each study year.
	AN_{int}	Number of intermittent periods during each study year.
	AT_{int}	Mean duration of intermittent periods during each study year.
Historical hydrology	HQ_{day}	Daily mean discharge during entire period of record.
	HR_{ann}	Mean annual runoff during entire period of record.
	ANNCV	Coefficient of variation of annual mean discharge over entire period of record, %.
	DAYCV	Mean annual coefficient of variation of discharge over the years of record, %.
	PQ	Predictability of discharge.
	C/P	Proportion of PQ associated with constancy of discharge.
	Q_{BF}	Magnitude of bankfull flood (1.67 annual return interval).
	HN_{BF}	Mean number of bankfull floods per year over entire period of record.
	HPQ_{BF}	Predictability of bankfull floods or the maximum percentage of all floods over period of record that occurred in one of six 60-days periods.
	$HNoQ_{BF}$	Percentage of year when no bankfull floods have occurred during entire period of record.
	HNQ_{zero}	Mean number of days per year with zero discharge over entire period of record.
	LOWFLOW	Mean of the annual lowest daily mean discharge over entire period of record.
	HT_{int}	Mean duration of intermittent periods over entire period of record.
	HN_{int}	Mean number of intermittent periods per year over entire period of record.
	BFI	Baseflow index or average ratio of the annual lowest daily mean discharge to the mean daily discharge over entire period of record multiplied by 100.
	HPQ	Highest proportion in which minimum daily discharge was above zero for a given day over the entire period of record.
Refugia	D_{up}	Channel distance to nearest upstream perennial surface water.
	D_{down}	Channel distance to nearest downstream perennial surface water.
	A_{up}	Total surface area of upstream perennial surface water within watershed.
	A_{down}	Total surface area of downstream perennial surface water within 1 km of site.

were taken with a 20-cm-diameter ($0.0314\,m^2$) stovepipe sampler to a depth of 10 cm into gravel-dominated riffle habitats at each site. Samples were collected weekly during the first four weeks of flow and then once every two weeks until the intermittent streams completely dried in 1995 and 1996. Site HI was not sampled in 1996. Samples were sieved (250 μm) and preserved (80% alcohol) in the field. Most invertebrates were identified to genus and species. Chironomids and annelids were identified to subfamily and class levels respectively. A complete taxonomic list and further sampling details are given elsewhere (Fritz and Dodds 2002).

Harshness index

Annual hydrological conditions, historical hydrological regime and spatial characteristics of potential colonisation refugia were used to characterise each study site along a gradient of harshness. An initial set of seven annual and 17 historical hydrological variables was calculated (Table 1). Only those indices requiring special explanation will be described here. Mean duration of intermittent periods (AT_{int}, HT_{int}) did not include any periods of flow that were <10 days (i.e. short flow events were counted as part of the intermittent period) since 10 days would not allow complete development (egg to adult) for most fauna studied (Gray 1989).

Predictability of flow (PQ) is an index based on information theory developed by Colwell (1974) and takes into account the temporal sequence of variation in flow. Colwell's predictability index values can vary depending on the assigned categories of flow magnitude and the number of years on record (Gan *et al*. 1991; Gordon *et al*. 1992). The estimates of predictability and contingency may be overestimated because the hydrological record for some KPBS sites used in this study are ≤10 years (Gan *et al*. 1991). This potential problem, and the redundancy of PQ with other indices, ultimately led us not to use PQ in our harshness index.

Annual return interval (ARI) of 1.67 years has been used in previous studies to represent 'bankfull' floods (e.g. Poff 1996) and is the magnitude that maintains average channel morphology (Gordon *et al*. 1992; Leopold 1994) and moves cobble in floods in Kings Creek (Dodds *et al*. 1996). A partial series of the daily maximum flow records was used to identify high-flow events (Q_{BF}). This was chosen rather than the annual peak series because it more accurately predicts floods with short recurrence intervals (ARI <10 years, Gordon *et al*. 1992). We designated partial series values for the intermittent sites, whereas the USGS partial series was used for the downstream perennial site. Care was taken to choose single daily peak values that represented distinct flood events and not daily peak values associated with the rising and falling limbs of floods. Twenty values were chosen for I2, I3 and I4, and 22 were chosen for I1. The number of years on record was considered in determining the number of values within each partial series. The USGS partial series contained 64 values.

Six low-flow descriptors were used. Over the entire period of record, only one year had an annual daily minimum discharge > 0, so rather than using low-flow values of designated return intervals (e.g. Poff 1996), number of days with no discharge was used to characterise low flow periods.

Spatial characteristics of potential colonisation refugia (i.e. pools, seeps and runs) were determined by mapping locations with perennial surface water and measuring wetted surface area during Autumn 1995. Unpublished data (M. Gurtz, United States Geological Survey) from the mid-1980s were used to confirm the stability of these refugia. Perennial surface waters in this system are most often spring-fed reaches that include both riffle and pool habitats. The channel distance between the nearest upstream and downstream perennial surface water and each intermittent site (D_{up} and D_{down} respectively) was used as a measure of immigration potential. Although colonists from these refugia to intermittent sites could travel shorter distances (straight-line distances by aerial colonisers) than the channel distance, colonisation in this system is predominated by drift (Fritz and Dodds 2004), therefore channel distance is the more conservative and logical measure. Total wetted area of the upstream and downstream perennial surface water (A_{up} and A_{down}) was used as a measure of the size of the immigration pool.

Relationships among hydrological variables were evaluated using Pearson correlation coefficients to reduce the number of interrelated hydrological characteristics and devise a simple model that could be tested. We selected variables that would represent average flow conditions, variability of flow and magnitude and frequency of disturbances in addition to spatial characteristics. To reduce duplication or overweighing hydrological factors, we selected variables that would (*i*) best represent a group of correlated measures and (*ii*) be most likely available to investigators or resource managers to test in other systems. Selection of variables was determined by *a priori* predictions that measures of magnitude and frequency of disturbance would be important in determining community structure.

A final group of eleven variables (three annual, four historical and four refugia) were used to calculate the harshness index. Ranks were assigned to sites for each variable with the harshest site assigned the highest rank, while ties were assigned with all ranks set to the lowest ranking of the ties. Because the headwater sites (HP and HI) were not gauged, ranks for hydrological variables were assigned relative to the known values obtained from the downstream I1 site, point measurements and personal observations.

The degree to which harshness influenced annual assemblage characteristics was tested after normality (Shapiro–Wilks test) and homogeneity of variance (residual plots) were confirmed. Total annual richness, Shannon diversity (H'), total annual abundance and evenness (J') for each site were regressed against their respective harshness scores. Since 1995 was wet and had several floods, and 1996 was drier and had extensive dry conditions, each year was considered to have an independent harshness. Analysis of covariance indicated a non-significant effect of year ($P > 0.05$), so both years were combined. Relationships among assemblage variables and sum of the three variable groups (annual hydrological conditions, historical hydrological conditions and spatial characteristics of potential colonisation refugia) were examined using regression analyses (SAS 2001). Best subsets regressions, using Mallow's Cp as an information criterion, were used to establish the influence of the three individual variable groups (Helsel and Hirsch 2002).

Results

Hydrological conditions over the entire period of record for each of the five sites that we gauged (Fig. 2, Table 2) were used to construct the harshness index. Hydrological conditions varied in 1995 and 1996. AQ_{day} 1995 was at least 1.5 times greater than the HQ_{day} at four of the five gauged sites, whereas AQ_{day} in 1996 was less than or equal to HQ_{day} at three of the five gauged sites (Table 2). Floods were more frequent and had higher magnitudes for most sites in 1995 than in 1996 (Table 2).

As expected, there were several significant correlations among both annual (Table 3) and historical hydrological variables (Table 4). The low correlation coefficients between hydrological variables between years, particularly static basin and flood descriptors, further indicate that hydrological conditions varied greatly between 1995 and 1996. The subset of variables chosen for the harshness index incorporate mean discharge, discharge variability, flooding and drying over ecological and evolutionary time scales as well as spatial position and area of refugia while avoiding variables that are cross-correlated (Table 5). For example, AQ_{day} and AR_{ann} indicate mean discharge and annual runoff respectively so they are related. However AR_{ann} was correlated with the number of bankfull floods in 1995 ($AN_{BF,95}$), but AQ_{day} was not (Table 3), so AQ_{day} was used to estimate stream discharge and AR_{ann} was not used in the index. Likewise the number of days with 0 discharge in each year (ANQ_{zero}) was significantly and positively correlated with the two other estimates of intermittency (AN_{int} and AT_{int}, Table 3) so only ANQ_{zero} was used to construct the harshness index.

The intermittent sites had high harshness indices. The permanent sites had lower harshness indices. The upstream permanent site had the lowest harshness index because it did not dry and the floods were not as severe at this site. Variations in flow among sites and among years, including the fact that floods were common one year and drought another, meant that the same sites did not receive the same rankings between years (Table 5).

A total of 84 943 individuals of 104 taxa were collected from benthic samples. The greatest total annual richness and abundance occurred at perennially flowing sites (Table 6), but at times richness was relatively high at intermittent sites (e.g. site I2 had unexpectedly high richness in 1995). Total annual macroinvertebrate abundance was greatest at the downstream perennial site. When the four biotic indices were analysed against the harshness with analysis of covariance, in no case was year a significant covariate, so further statistical analyses combined both years. Linear regression revealed a significant negative relationship between both Shannon diversity (H') and the mean number of taxa per sample and harshness (Fig. 3, Table 7). There was no significant relationship between harshness and evenness or number of individuals collected per sample.

Best subsets regression (Mallow's Cp) explicitly recognises that r^2 can be increased simply by adding variables and tests all models to find the subset that provides the most explanatory power (Helsel and Hirsch 2002). Best subsets regression analyses indicated that annual and historical hydrological components of the harshness index both

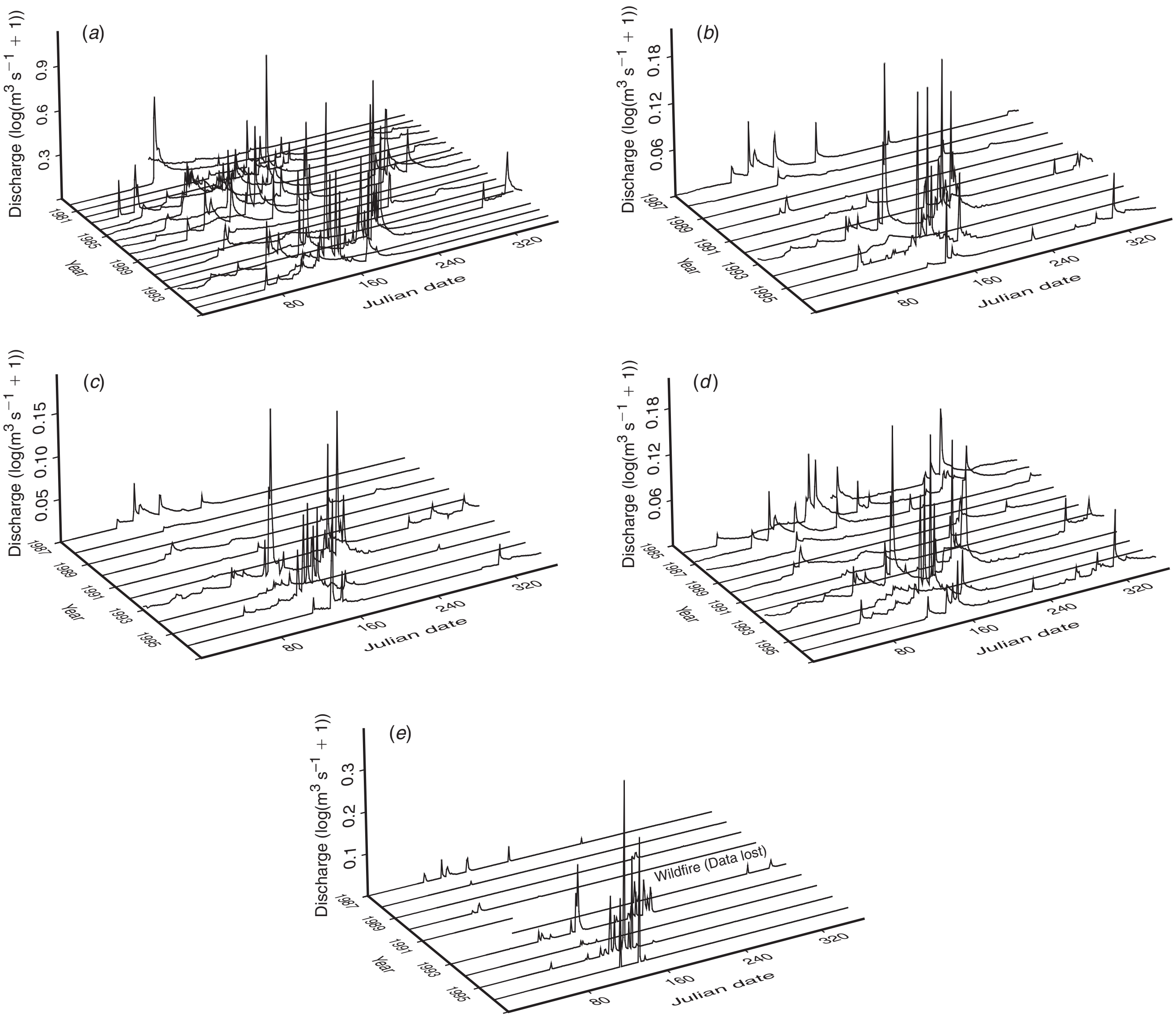

Fig. 2. Long-term hydrographs of study sites: (*a*) DP 1979–96; (*b*) I2 1987–96; (*c*) I3 1987–96; (*d*) I1 1985–96; and (*e*) I4 1987–96. Shown as log transformed (daily mean discharge + 1) to facilitate plotting of zero discharge days.

explained most of the variance in the biological indices (Table 7) and that colonisation distance did not add substantial predictive power. No component had explanatory power for evenness.

Discussion

According to the stream classification described by Poff (1996), the four intermittent streams studied at KPBS belong to the harsh intermittent stream type, whereas the downstream perennial site (DP) has characteristics of the perennial flashy type. Although we did not have quantitative hydrological data for the upstream perennial site (HP), it would most likely fit Poff's stable groundwater category because it was a spring-fed site that is high in the watershed, so only moderately impacted by floods. These characterisations are reflected in our harshness rankings.

Our data support Poff and Ward's (1989) predictions that biological attributes of populations (e.g. diapause/aestivation) and assemblages (e.g. low richness) will be controlled by abiotic factors among intermittent streams. However, our data indicate differences in assemblage characteristics and recovery from disturbances among intermittent streams (Fritz and Dodds 2002). Although not strongly reflected by the harshness index, the flow regime for I4 was especially extreme (frequent drying and floods) and is the likely explanation for low numbers and taxonomic richness at that site. Given our experience we would rank those attributes more heavily if revising the index to use in

Table 2. Physical characteristics of study sites in the Kings Creek drainage on Konza Prairie Biological Station (KPBS), Kansas

Acronyms are defined in materials and methods. Asterisks indicate highest peak discharge on record for a given stream

Characteristic		I2	I3	I1	I4	DP
Years in record		10 (87–96)	10 (87–96)	11 (86–96)	8 (87–90, 93–96)	17 (80–96)
Strahler order		3	3	3	3	5
Elevation drop (m)		74.0	97.0	83.0	77.0	92.0
Mean watershed slope (%)		11.0	9.9	11.6	9.5	8
AREA (km^{-2})		1.18	1.24	1.34	0.86	10.60
AQ_{day} ($L\,s^{-1}$)	1995	14.2	9.25	17.0	11.1	143
	1996	4.12	7.25	8.62	7.93	25.2
AN_{BF} (no. year $^{-1}$)	1995	2	1	2	2	2
	1996	1	0	0	2	1
AQ_{max} ($m^3\,s^{-1}$)	1995	15.64	5.30	6.45	15.85	303
	1996	15.41	2.34	1.34	83.78*	24.55
ANQ_{zero} (days year^{-1})	1995	232	242	228	309	0
	1996	224	250	199	360	0
AN_{int} (no. year^{-1})	1995	2	2	2	2	2
	1996	2	2	2	1	2
AT_{int} (days year^{-1})	1995	116.0	120.5	114.0	161.5	104.0
	1996	152.0	124.5	101.0	366.0	120.0
HQ_{day} ($L\,s^{-1}$)		5.90	4.87	10.1	3.71	70.6
ANNCV ($m^3\,s^{-1}$)		89.18	88.27	119.05	83.43	113.58
DAYCV (%)		378.79	332.82	247.43	803.80	343.62
PQ		0.67	0.71	0.49	0.92	0.47
C/P		0.75	0.78	0.61	0.93	0.62
Q_{BF} 1.67 ($m^3\,s^{-1}$)		6.20	3.12	3.61	6.54	14.54
HN_{BF} (no. year^{-1})		0.50	0.40	0.36	0.50	0.41
HPQ_{BF}		0.60	0.50	0.50	1.00	0.70
$HNoQ_{BF}$		0.986	0.984	0.984	0.989	0.975
HNQ_{zero} (days year^{-1})		254.80	269.20	189.27	340.12	168.35
LOWFLOW ($L\,s^{-1}$)		0.00	0.00	2.56	0.00	1.39
HT_{int} (days year^{-1})		204.46	179.00	159.69	348.56	175.06
HN_{int} (no. year^{-1})		1.90	2.20	1.64	1.75	1.35
BFI (%)		0.00	0.00	0.49	0.00	4.86
HPQ[a]		0.70 (14)	0.70 (13)	0.82 (51)	0.32 (2)	0.94 (5)
D_{up} (m)		619.0	503.0	303.0	1045.0	0
D_{down} (m)		254.0	1096.0	1034.0	93.0	0
A_{up} (m^2)[b]		96.5	102.3	493.8	183.5	–
A_{down} (m^2)[c]		771.7	21.6	50.7	771.7	–

[a] Parentheses enclose number of days a year that have the maximum proportion. [b] Within watershed. [c] Within watershed and 1 km of stream length from intermittent site.

other streams. However, our aim was to test the general concept and weighting the index to fit the existing data better would not be statistically defensible. One recent classification scheme would categorise I4 as temporary-episodic, whereas the other intermittent sites would be temporary-ephemeral (Uys and O'Keefe 1997) and our data support the validity of this classification scheme.

The ranking method used in the harshness index better separated the hydrological conditions of the perennial and intermittent sites than it did among the intermittent sites. The factors used in the harshness index were equally weighted. Therefore, any hydrological differences among the intermittent sites were overwhelmed by similarities in some hydrological aspects and the greater differences between the intermittent and perennial sites. It is likely that assemblages are not equally influenced by each hydrological factor and we must have missed some factors that may have been critical in determining the assemblage differences among some of the intermittent sites (I2 and I3). Perhaps future research will elucidate those factors.

Our results (Table 6) suggest that in years of unusually extreme hydrological disturbance (1995), immediate hydrological conditions are the dominant structuring force, but in typical years, such as 1996, hydrological conditions over historical time scales and spatial positioning of refugia may be equally important. Thus, with extreme flooding, adaptations to drying are not important. We did not have an extreme drought during this study, but would expect the immediate

Table 3. Pearson correlation coefficients among annual hydrological variables for I1, I2, I3, I4 and DP ($n = 5$)
Acronyms are defined in materials and methods. Bold typeface indicates significant relationship ($P \leq 0.10$). Dash mark indicates variable is constant and correlation not calculated

	$AQ_{day,95}$	$AQ_{day,96}$	$AR_{ann,95}$	$AR_{ann,96}$	$AN_{BF,95}$	$AN_{BF,96}$	$AQ_{max,95}$	$AQ_{max,96}$	$ANQ_{zero,95}$	$ANQ_{zero,96}$	$AN_{int,95}$	$AN_{int,96}$	$AT_{int,95}$	$AT_{int,96}$
$AQ_{day,95}$	1.00													
$AQ_{day,96}$	0.01	1.00												
$AR_{ann,95}$	0.43	0.05	1.00											
$AR_{ann,96}$	−0.78	0.48	−0.15	1.00										
$AN_{BF,95}$	0.28	−0.09	**0.98**	−0.12	1.00									
$AN_{BF,96}$	−0.39	−0.16	0.56	0.20	0.53	1.00								
$AQ_{max,95}$	**1.00**	−0.01	0.43	−0.77	0.27	0.17	1.00							
$AQ_{max,96}$	−0.03	0.17	0.44	0.49	0.38	**0.93**	0.01	1.00						
$ANQ_{zero,95}$	−0.54	0.26	0.02	**0.86**	0.03	0.64	−0.50	**0.84**	1.00					
$ANQ_{zero,96}$	−0.07	0.22	0.15	0.53	0.06	**0.82**	−0.02	**0.95**	**0.86**	1.00				
$AN_{int,95}$	–	–	–	–	–	–	–	–	–	–				
$AN_{int,96}$	0.27	−0.31	−0.29	−0.71	0.25	**−0.80**	0.23	**−0.96**	**−0.95**	**−0.93**	–	1.00		
$AT_{int,95}$	−0.50	0.26	0.07	**0.84**	0.07	0.67	−0.46	**0.86**	**1.00**	**0.88**	–	**−0.96**	1.00	
$AT_{int,96}$	−0.29	0.14	0.27	0.66	0.24	**0.85**	−0.24	**0.96**	**0.94**	**0.94**	–	**−0.99**	**0.96**	1.00

Table 4. Pearson correlation coefficients among historical hydrological variables of I1, I2, I3, I4 and DP ($n = 5$)
Acronyms are defined in materials and methods. Bold typeface indicates significant relationship ($P \leq 0.10$)

	HQ_{day}	HR_{ann}	ANNCV	DAYCV	PQ	C/P	Q_{BF}	HN_{BF}	HPQ_{BF}	$HNoQ_{BF}$	HNQ_{zero}	LOWFLOW	HT_{int}	HN_{int}	BFI	HPQ
HQ_{day}	1.00															
HR_{ann}	0.50	1.00														
ANNCV	−0.60	**−0.96**	1.00													
DAYCV	−0.26	−0.54	0.67	1.00												
PQ	−0.62	**−0.84**	**0.93**	**0.86**	1.00											
C/P	−0.56	**−0.85**	**0.93**	**0.87**	**1.00**	1.00										
Q_{BF}	**0.96**	0.35	−0.40	−0.01	−0.41	−0.35	1.00									
HN_{BF}	−0.28	−0.59	0.76	0.73	0.71	0.73	0.01	1.00								
HPQ_{BF}	0.06	−0.30	0.44	**0.94**	0.65	0.68	0.30	0.66	1.00							
$HNoQ_{BF}$	**−0.92**	−0.55	0.72	0.58	0.80	0.76	−0.77	0.58	0.32	1.00						
HNQ_{zero}	−0.68	**−0.83**	**0.93**	**0.83**	**1.00**	**0.99**	−0.48	0.71	0.61	**0.84**	1.00					
LOWFLOW	0.36	**0.96**	**−0.94**	−0.54	−0.78	**−0.81**	0.16	−0.75	−0.37	−0.48	−0.77	1.00				
HT_{int}	−0.03	−0.53	0.68	**1.00**	**0.87**	**0.88**	−0.09	0.74	**0.92**	0.65	**0.85**	−0.53	1.00			
HN_{int}	−0.77	−0.76	0.69	0.02	0.52	0.50	−0.77	0.15	−0.30	0.57	0.56	−0.62	0.05	1.00		
BFI	1.00	0.52	−0.61	−0.25	−0.62	−0.56	**0.95**	−0.29	0.07	**−0.92**	−0.68	0.38	−0.32	−0.78	1.00	
HPQ	0.64	0.67	**−0.81**	**−0.91**	**−0.96**	**−0.95**	0.43	−0.68	−0.72	**−0.85**	**−0.97**	0.60	**−0.93**	−0.37	0.63	1.00

Table 5. Variables, corresponding ranks and harshness scores for study sites combining 1995 and 1996 data and subsequently used to test relationships with annual richness, diversity, abundance and evenness
See Table 1 for acronyms and Table 2 for values

Category	Variable	1995							1996					
		I2	I3	I1	I4	DP	HP	HI	I2	I3	I1	I4	DP	HP
Annual	AQ_{day}	7	9	5	8	1	4	6	13	12	10	11	2	3
	ANQ_{zero}	9	10	7	12	1	7	1	6	11	5	13	1	1
	AN_{BF}	8	5	8	8	8	8	8	5	1	1	8	5	1
Historical	HQ_{day}	8	10	6	12	1	3	5	8	10	6	12	1	3
	ANNCV	7	5	12	3	9	1	11	7	5	12	3	9	1
	$HNoQ_{BF}$	3	5	5	1	12	5	5	3	5	5	1	12	5
	HPQ_{BF}	8	1	1	12	10	1	1	8	1	1	12	10	1
Refugia	D_{up}	10	8	6	12	1	1	5	10	8	6	12	1	1
	D_{down}	7	11	9	5	1	1	13	7	11	9	5	1	1
	A_{up}	12	10	5	8	1	1	5	12	10	5	8	1	1
	A_{down}	5	12	9	5	1	1	9	5	12	9	5	1	1
	SUM	84	86	73	86	46	33	69	84	86	69	90	44	19

Table 6. Biotic parameters (total taxa sampled and mean Shannon diversity (H′), evenness (J′), number of taxa and abundance per sample) by site and by year
See Table 1 for acronyms

Site	Year	Taxa	H′	J′	Taxa per sample	No. per sample
DP	1995	55	0.471	0.457	1.41	356
HI	1995	39	0.702	0.693	2.17	230
HP	1995	43	0.658	0.593	2.39	286
I1	1995	33	0.468	0.575	0.92	186
I2	1995	48	0.445	0.480	1.33	253
I3	1995	34	0.469	0.560	1.03	246
I4	1995	13	0.364	0.696	0.62	14
DP	1996	45	0.637	0.547	2.14	901
HP	1996	50	0.845	0.734	2.38	125
I1	1996	39	0.455	0.469	1.62	337
I2	1996	33	0.440	0.503	1.52	280
I3	1996	27	0.407	0.495	1.50	220
I4	1996	12	0.520	0.854	2.00	15

differences in the extent of drying (i.e. duration, substrate moisture) among sites to be more important in such a year than the historical aspects of hydrology.

The intermediate disturbance hypothesis predicts maximum diversity at intermediate disturbance (Connell 1978). Using rock movement as their measure of disturbance intensity and frequency among 27 New Zealand streams, Townsend *et al*. (1997) reported results supporting the bell-shaped curve predicted by the intermediate disturbance hypothesis. When considering the harshness index as a measure for disturbance intensity and frequency we did not see evidence supporting the intermediate disturbance hypothesis. However, our sites may represent only half of the disturbance gradient, where DP and HP represent sites with intermediate levels of disturbance (intense flooding only) and the intermittent sites experience more frequent and intense disturbances (flooding and seasonal drying). Because disturbance is frequent and often intense in these streams, biotic interactions are likely to contribute little to the assemblage characteristics, whereas density-independent factors controlling recolonisation rates and the regional species pool are more important (Hildrew and Giller 1992). This points out a weakness in the intermediate disturbance hypotheses: it is impossible to predict *a priori* what disturbance intensity should be considered ‘intermediate’.

Many hydrological indices describe temporal variability, but do not provide spatial information on the intermittent stream habitat template. A spatial characteristic that differed among the intermittent sites at KPBS was distance and area of upstream and downstream refugia (see Table 2). Recovery from floods and seasonal drying is faster at intermittent sites with close upstream perennial surface water (Delucchi 1988; Paltridge *et al*. 1997; Fritz and Dodds 2004). Sites with shorter distances or with higher connectivity to perennial water will tend to recover from seasonal drying more rapidly and therefore a community similar to perennial sources will be more likely to develop before the next drying event than at intermittent sites with distant refugia. Colonisation of these sites is primarily through downstream drift (Fritz and Dodds 2004). Sites with longer flow duration are more likely to be colonised by species from upstream perennial surface waters. Sites closer to perennial water also may hold water longer and therefore allow more time for species replacement. However, spatial aspects were not an important predictor of mean annual biological characteristics in our study. This is probably because given average water velocity during periods of flow, water can move several km per day (i.e. down the entire stream network in a few days). Thus, increases in diversity over weeks may be influenced by proximity to sources of colonists (Fritz and Dodds 2004), but annual means of diversity are not.

The harshness index that has been proposed in this study takes into account aspects of abiotic control (recent hydrology, historical hydrology and surface-water connectivity)

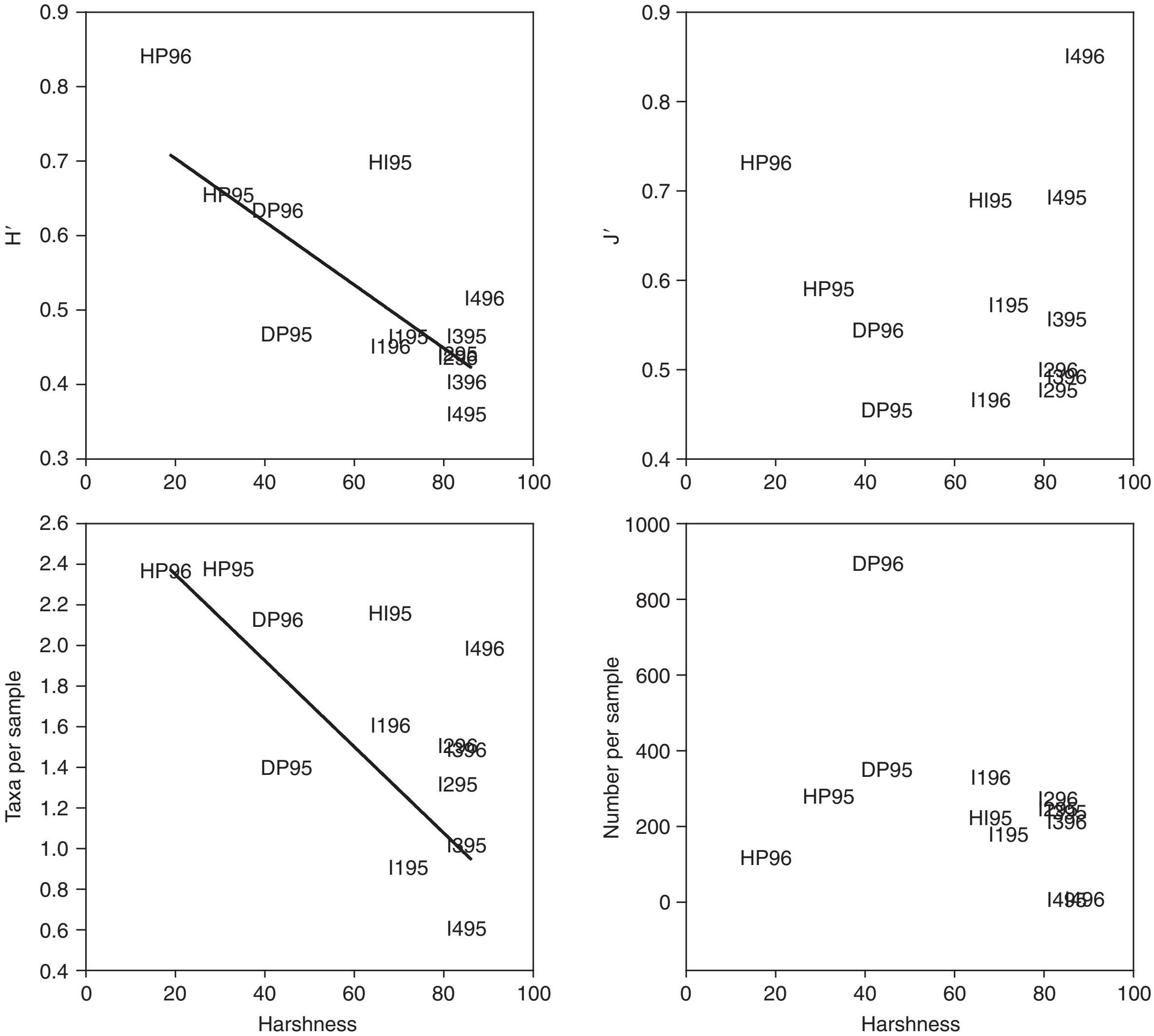

Fig. 3. Relationships between harshness scores and Shannon diversity (H′), evenness (J′), taxon richness and abundance for 1995 and 1996 data. Lines are drawn where the relationship was significant (Table 7).

Table 7. Results of regression analysis of total harshness index as a predictor of average H′, J′, taxa and abundance per sample

The adjusted R^2 and significance of the slope are both reported. Multiple regression models were constructed using annual, historical and spatial components of the harshness index and all models were assessed using Mallow's Cp for the components that provided the most information. The components that added the most information are listed in the 'Best subsets' column

Factor	Adjusted R^2	P slope	Best subsets model (Mallow's Cp)
H′	0.636	0.001	Annual and historical
J′	0.007	0.778	Intercept (no model)
Taxa	0.457	0.011	Annual and historical
Abundance	0.119	0.248	Annual and historical

on intermittent assemblages. It also may be applied using individual dates, rather than annual values, to test for significant relationships between harshness and assemblage variables. Application of similar indices to other intermittent systems may require consideration of other factors such as bed stability (in sand bottom streams), hyporheic refugia (in streams with relatively greater subsurface habitat), infiltration and evapotranspiration rates of surrounding watershed (forested *v.* grassland) and climate (in aseasonal and strongly seasonal climates). However, this study verifies that a moderately diverse invertebrate assemblage can be maintained even in stream habitats that appear quite harsh. We also demonstrate that temporal hydrological variation can predict roughly half of assemblage diversity.

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