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PRIMARY RESEARCH PAPER

The influence of habitat structure and flow permanence on macroinvertebrate assemblages in temporary rivers in northwestern Zimbabwe

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Abstract Temporary rivers within the Nyaodza-Gachegache subcatchment in northwestern Zimbabwe were investigated to examine the role of flow permanence and habitat structure on macroinvertebrate community composition. Macroinvertebrate communities of intermittent and ephemeral rivers displayed significant differences in the number of taxa, macroinvertebrate abundance, Shannon and Simpson diversity indices and in size class structure. Intermittent sites were characterised by higher numbers of taxa, diversity and Ephemeroptera and Trichoptera richness compared to ephemeral sites. The fauna of ephemeral sites was dominated by a single taxon (*Afrobaetodes*) (Ephemeroptera, Baetidae) whilst larger sized taxa (e.g. *Elassoneuria* (Ephemeroptera, Oligoneuriidae), *Dicentroptilum* (Ephemeroptera, Baetidae), *Aethaloptera* (Trichoptera, Hydropsychidae), *Pseudagrion* (Odonata, Coenagrionidae) and *Tholymis* (Odonata, Libellulidae) were exclusively restricted to intermittent sites. Clear differences were observed between sand, gravel, cobble and vegetation habitats. Vegetation and cobbles supported distinct communities, with some taxa exclusively restricted either to vegetation (e.g. *Pseudagrion*, *Leptocerina* (Trichoptera, Leptoceridae), *Cloeon* (Ephemeroptera, Baetidae), *Afronurus* (Ephemeroptera, Heptageniidae) and *Povilla* (Ephemeroptera, Polymitarcidae) or cobble (e.g. *Aethaloptera* and *Dicentroptilum*) habitats. In terms of ensuring optimum diversity within the subcatchment, we consider conservation of critical habitats (cobbles and vegetation) and maintenance of natural flows as the appropriate management actions.

Keywords Dry-land rivers · Flow regime · Macroinvertebrates · Management

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Introduction

Temporary rivers are the dominant river types in the largely arid to semi-arid southern African subregion (Davies et al., 1994). Although the study of temporary rivers in Southern Africa has been largely ignored (Uys & O'Keeffe, 1997a, b), results from other regions indicate that arid-zone rivers are highly productive environments (Puckridge et al., 2000; Bunn et al., 2006). Floods ('the boom') result in intense reproduction and high productivity by opportunistic plants and animals which play a critical role in nutrient cycling and food webs (Kingsford, 2000; Bunn et al., 2006). Invertebrates comprise a significant proportion of the biomass and are vital to the successful recruitment of fish which depend on them for their first feed after hatching (King, 2005). Pulses of fish after flooding in arid-zone rivers has been linked to invertebrates as a key dietary resource (Puckridge et al., 1998; Balcombe et al., 2005).

Despite being highly productive habitats, many dryland rivers in the southern African subregion suffer severe degradation through transformation of the natural flow regimes (Uys & O'Keeffe, 1997a) and loss of critical habitats resulting in significant declines in their biodiversity. In most rivers, flood frequency has been reduced as a result of inter-basin transfers, over abstraction and land use changes, and the length of time that the rivers remain dry is increasing (Uys & O'Keeffe, 1997a). For example, in Zimbabwe, the Save, the Mazoe and the Sanyati Rivers which used to have perennial flow have been significantly reduced to seasonal sand rivers mainly due to high amounts of agricultural developments within their catchments.

Given the apparent relationship between species richness and the duration of the dry phase in extant temporary streams (Poff & Ward, 1989), any extension of the dry phase may have enormous implications on the biota and thus productivity of temporary rivers. This may significantly disrupt ecosystem processes such as nutrient cycling in the aquatic environment (Boulton et al., 2006) and transfer of energy and matter to higher trophic levels (Bunn et al., 2006). The negative implications of altered hydrological regimes on aquatic biota are likely to be accentuated by the loss of critical habitats (Samways, 2005) because of increasing anthropogenic pressures within the catchments of most dryland rivers. However, fundamental studies on the influence of flow permanence and habitat structure on invertebrate community composition in temporary rivers are few (Boulton & Lake, 1992; Bonada et al., 2007; Jenkins & Boulton, 2007).

Much of the research effort in temporary rivers has been directed at long-term descriptive studies and the consideration of theoretical issues such as disturbance and recovery (Boulton, 2003; Lake, 2003; Boulton et al., 2006) while neglecting the influence of the hydrological regime and habitat structure. Consequently, the ecological effects of flow and other modifications to temporary rivers are poorly understood and difficult to define because of lack of contemporary and historical ecological data. Studies from the karst spring systems report that habitat and flow permanence have a strong influence on macroinvertebrate community structure (Smith & Wood, 2002; Smith et al., 2003; Wood et al., 2005). Such an understanding of the factors that control ecosystem structure and function is necessary to underpin conservation and management practices.

This study was carried out to: (a) explore the influence of flow permanence on benthic macroinvertebrate assemblages by comparing communities of intermittent and ephemeral rivers within a single undisturbed catchment in northwestern Zimbabwe, and (b) determine the influence of habitat structure on macroinvertebrate assemblages by comparing differences between the communities of cobbles, gravel, sand and vegetation biotopes. We hypothesise that (a) community structure and diversity in temporary rivers are largely a function of the degree of flow impermanence, and (b) different habitats support distinctive communities composed of taxa adapted to either the stability or complexity of the habitat. This forms part of a wider study to investigate the ecology of aquatic fauna of dry-land rivers in northwestern Zimbabwe.

Study area

The study was carried out in the Nyaodza-Gachegache subcatchment in northwestern Zimbabwe and all the rivers from this subcatchment drain into Lake Kariba. The subcatchment has a typical semi-arid to arid climate with a mean annual rainfall of about 600 mm (range 350–1,000 mm) falling between November and April and the rest of the months are mostly very dry. There is high inter-annual variability in the volume and timing of rainfall and hence streamflow. Rainfall data was collected from the Zambezi River Authority (ZRA). All the streams and rivers within the area are either intermittent (recede into isolated pools during the dry season) or ephemeral (only flow during and for a short period after the rains). The subcatchment has a dominant granitic geology, with highly permeable substrates and, therefore, surface flow in most smaller streams may cease in hours or days after rainfall (episodic/

ephemeral streams). Vegetation is dominated by typical xerophytic trees: *Colophospermum mopane*, *Sterculia* spp., *Combretum* spp., *Acacia* spp., *Adansonia digitata* but some areas have patches that are dominated by generas of *Brachystegia* and *Julbernardia* (miombo woodland).

Methods

The study sites comprised of two ephemeral rivers (sites 1 and 2) and four intermittent rivers (sites 3–6) (Table 1). Sites (1, 2, 3, 4 and 6) were located within the protected Kariba wildlife area (Fig. 1). Although site 5 was located outside the wildlife area, it had a protected riparian buffer strip of about 200 m on either side of the bank (Fig. 1). All the sampling sites can, therefore, be referred to as reference sites due to the minimal human activities.

The two ephemeral rivers Ruia (site 1) and Moto (site 2) were generally similar, with channel widths ranging between 7 and 10 m and a similar substratum dominated by cobbles. Under base flow conditions, there is no surface flow in the streams. The rivers only flow in response to rainfall events and the flow duration ranges between 15 and 30 days. From each site four stations (approximately 30–40 m apart within a 200 m stream reach; Table 1) were established for sampling. Samples from these stations will hereafter be referred to as 1c1–1c4 and 2c1–2c4 indicating a station with cobble substratum taken from either site 1 or site 2.

Flow in the intermittent Murereshi, Nyaodza, Sunde and Gachegache Rivers may last up to 6 months (from November to May) after which the rivers recede into as series of pools connected by subterranean discharge during the dry season.

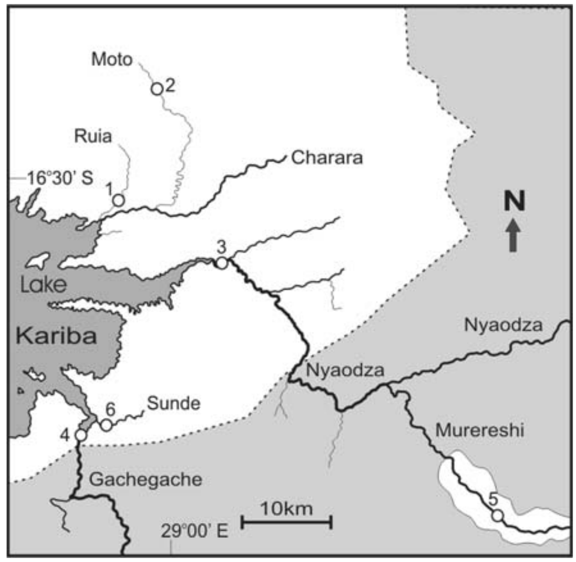

Fig. 1 Map of the study area showing: part of the Sanyati Basin (the eastern most basin of Lake Kariba), the six sampling sites within protected areas (unshaded) and communal areas (light gray)

Baseflow may persist to the next rain season depending on the length and severity of the dry season. From the Nyaodza River (site 3), six stations (two with cobble, two with gravel and two with sand substratum were established for sampling of macroinvertebrates within a 300 m stream reach (Table 1). The distance between the stations within each site ranged between 20 and 60 m. These samples will hereafter be referred to as 3c1 and 3c2 (for cobble), 3g1 and 3g2 (for gravel), 3s1 and 3s2 (for sand). Similarly six stations were established from the Gachegache River (site 4; Table 1) and these will be referred to as 4c1 and 4c2 (for cobble), 4g1 and 4g2 (for gravel) and 4s1 and 4s2 (for sand). Two stations with cobble substratum (5c1 and 5c2) and

Table 1 Physical characteristics of the temporary river sample sites in the Nyaodza-Gachegachesubcatchment

Site code	River name	Altitude	Mean width (m)	Reach length (m)	Land use	Habitats sampled	Impermanence
1	Ruia	483	8	200	Dense woodland	Cobbles	E
2	Moto	689	7	200	Dense woodland	Cobbles	E
3	Nyaodza	488	36	300	Dense woodland	Cobbles, sand & gravel	I
4	Gachegache	482	32	300	Dense woodland	Cobbles, sand & gravel	I
5	Murereshi	1134	12	200	Sparse woodland	Cobbles & vegetation	I
6	Sunde	515	9	200	Dense woodland	Vegetation	I

The degree of impermanence is denoted by E (ephemeral) and I (intermittent) three stations with vegetation habitat (5v1–5v3) were sampled from the Murereshi River (site 5; Table 1). The macrophytes at this site were dominated by *Phragmites*. Two stations with vegetation habitat (6v1 and 6v2) were established for sampling from the Sunde River (site 6; Table 1). The dominant macrophytes at this site were *Ludwigia stolonifera* and *Nymphea* spp.

Macroinvertebrate sampling and water chemistry measurements were undertaken at the sites on 07 February and 20 March 2007 when all the rivers were flowing. For both sampling occasions, samples were collected at least 2 weeks after rainfall, high enough to produce surface flows in the ephemeral rivers had fallen. Water temperature (°C), pH, turbidity (NTU), conductivity (μS cm^{-1}), and dissolved oxygen concentration (mg l^{-1}) of the water were measured using a Horiba UU 23 multiparameter probe (Horiba Ltd., Japan).

Samples of zoobenthos in cobbles, gravel and sand were collected by disturbing the substratum within a 1 m^{-2} quadrant for 2 min (for cobbles) and for 1 min (for gravel and sand). The dislodged animals were collected using a hand net (mesh size 250 μm). At sites with vegetation, the macroinvertebrate fauna were collected by sweeping a hand net (mesh size 250 μm) for five times over a patch of vegetation and the area swept was calculated in-order to express the animals as numbers per square metre. Three replicate samples of macroinvertebrates were collected from each station at each site on each occasion. The replicates were pooled into a composite sample for each station for each occasion and preserved in 70% ethanol before being transported to the laboratory for sorting and identification. Identification was undertaken to generic level where possible, although some early instar larvae of Gomphidae and some taxonomically demanding groups such as Chironomidae and Coleoptera were not identified to generic level. Results presented in this article are only for the insects because they were the dominant group, comprising more than 98% for both taxa richness and abundance of the assemblages collected during the study period.

Data analysis

Spatial patterns in the macroinvertebrate assemblage data were explored using multivariate statistical analyses in the PRIMER version 5 (Clarke & Gorley, 2001) software package. In order to reduce the contribution of taxa represented by many individuals to patterns, averaged macroinvertebrate abundance data, with all taxa included, were $\log_{10}(x + 1)$ transformed before all analyses. The data was analysed using the Bray–Curtis similarity coefficient followed by hierarchical clustering with group average linking. Assemblage patterns were visualised in reduced dimensional space using nonmetric multidimensional scaling (nMDS). Analysis of similarities (ANOSIM) was used to test for differences between a priori defined sites (ephemeral vs. intermittent) and habitats (cobble, gravel, sand and vegetation). Similarity percentages (SIMPER) was used to determine the taxa that contributed most to the differences in the macroinvertebrate assemblages between the river types and habitats.

To examine the differences between the invertebrate communities of the rivers and habitats, the Shannon-Wiener, Simpson, and Margalef diversity indices were calculated using the PRIMER version 5 statistical software. In addition, species richness (number of taxa), Ephemeroptera and Trichoptera richness (ET) and invertebrate abundance (individuals m^2) were calculated. Univariate data (e.g. Simpson diversity) were compared using one-way analysis of variance (ANOVA) (Zar, 1984).

To determine the influence of flow permanence on macroinvertebrate body size, insect body lengths were measured using a dissecting microscope fitted with a graticule. The Kolmogorov–Smirnov test (Zar, 1984) was used to test for the significance of differences in the proportions of the 1 mm size-classes of animals between ephemeral and intermittent sites. Data were arcsine-square root transformed a priori (Zar, 1984). These calculations were done using STATISTICA ver 7 software package (StatSoft, 2004).

Results

Environmental conditions

The hydrochemistry (Table 2) of the rivers generally displayed little variability during the study period, reflecting the similar geology and soil cover within the subcatchments. The only exception was conductivity

Table 2 Summary of the physicochemical variables (mean ± standard deviation) measured during this study

Site	Temp (°C)	pH	Cond (μS cm^{-1})	Turb (NTU)	DO (mg l^{-1})
1 ($n = 8$)	27.3 ± 3.1	7.4 ± 0.1	191 ± 11	34 ± 8	6.8 ± 1.2
2 ($n = 8$)	28.1 ± 2.8	7.6 ± 0.4	202 ± 23	45 ± 20	7.2 ± 1.7
3 ($n = 12$)	28.6 ± 4.4	7.2 ± 0.3	189 ± 17	39 ± 9	6.6 ± 1.9
4 ($n = 12$)	29.9 ± 2.2	7.5 ± 0.3	242 ± 49	26 ± 13	7.1 ± 0.9
5 ($n = 10$)	28.1 ± 3.5	7.6 ± 0.2	90 ± 12	19 ± 9	7.4 ± 3.4
6 ($n = 4$)	27.6 ± 3.3	7.4 ± 0.1	2160.0 ± 234	21 ± 8	6.9 ± 0.9

which was significantly higher in the Sunde River. Due to the general similarity in the hydrochemistry of the water, the physical and chemical data measured during this study were not included in subsequent analyses so that the influence of flow permanence and habitat could be examined in isolation of the other variables.

Assemblage structure analysis

Overall, 54 taxa were recorded across all the sites and habitats. The macroinvertebrate community composition was typical of temporary streams, comprising predominantly of larval insects. Ephemeroptera and Diptera were the most ubiquitous orders, occurring at all the sites and all habitats, followed by Trichoptera which occurred at (75%) of the habitats.

Spatial patterns in assemblage composition

Influence of flow permanence

Hierarchical clustering and MDS ordination showed strong differences in the macroinvertebrate assemblages of intermittent and ephemeral rivers (Fig. 2a and b). There was a complete separation of the intermittent and ephemeral communities, being separated on the Bray–Curtis similarity axis at a similarity level of 24% (Fig. 2a). Differences between these a priori defined river types were significant (Global $R = 0.536$; $P < 0.001$; Table 3). SIMPER analyses identified eleven taxa as major contributors to pairwise differences between ephemeral and intermittent rivers (sites) (Table 3). Mean abundances of these taxa displayed considerable differences between the two river categories (Table 4). *Afrobaetodes* was more abundant at the ephemeral sites compared to the intermittent sites while *Elassoneuria*, *Dicentroptilum*, *Pseudocloeon*, *Cheumatopsyche*, *Aethaloptera*, *Leptocerina*, *Syncordulia* and *Tholymis* were abundant and restricted to the intermittent sites (Table 4). None of the taxa recorded were restricted or unique to the ephemeral sites.

One-way ANOVA indicated that there were significant differences between intermittent and ephemeral rivers for: the number of taxa (F-ratio 15.2, $P < 0.001$), the number of Ephemeroptera and Trichoptera (ET) taxa (F-ratio 9.7, $P < 0.005$), the Shannon (F-ratio 5.2, $P < 0.01$) and Simpson diversity indices (F-ratio 17.3, $P < 0.001$), and log-abundance (F-ratio 11.1, $P < 0.005$) (Table 4). All these community indices (with the exception of log-abundance) were significantly lower at ephemeral sites than at intermittent sites (Table 4).

Examination of the macroinvertebrate size structure demonstrated that there were significant differences in the proportion of macroinvertebrate size classes between intermittent and ephemeral sites (Kolmogorov–Smirnov test, $P < 0.01$; Fig. 3). The larger taxa were more abundant and exclusively restricted to the intermittent sites whilst ephemeral sites were dominated by the smaller taxa (Fig. 3).

Comparisons between different habitats

Classification of composite samples for the stations from the six sites showed strong differences between habitats, based on the $\log_{10}(x + 1)$ transformed relative abundances of taxa (Fig. 2a). Similarly, ordination of the composite samples revealed differences in the faunas among sites (Fig. 2c). ANOSIM revealed that all paired differences between habitats were significant (Table 3). Sixteen taxa were repeatedly identified by SIMPER as significantly contributing to pairwise differences between habitats (Table 3). Mean abundances of these taxa displayed considerable

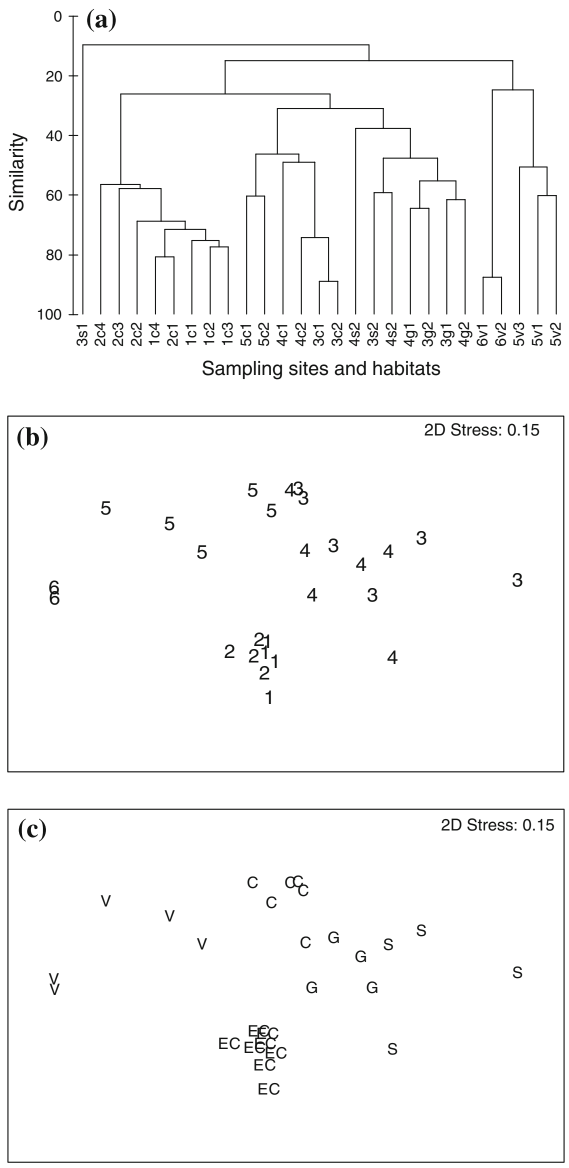

Fig. 2 Hierarchical clustering (**a**) and multidimensional scaling plots of the macroinvertebrate communities during the study period. The MDS plots are overlayed by codes for the sampling sites (**b**) and habitats (**c**). Abbreviations for habitats: V = vegetation; C = cobble; g = gravel, S = sand; EC = cobbles from the ephemeral sites

variations between habitats (Fig. 4). The Ephemeropterans (*Elassoneuria*, *Dicentroptilum*, *Pseudocloeon*, *Euthraulus* and *Baetis*), Trichopterans (*Aethaloptera* and *Cheumatopsyche*) and Odonata (*Tholymis*) were major indicator species of the cobble habitat while *Leptocerina* (Trichoptera), *Syncordulia* (Odonata), *Pseudagrion* (Odonata), *Plea* (Hemiptera), *Afronurus* (Ephemeroptera) and *Cloeon* (Ephemeroptera) were major indicators of the vegetation biotope. Sand was the habitat biotope least preferred by all the species of insects recorded in this study (Fig. 4). Eight of the taxa recorded from this study were restricted to the vegetation biotope while three were restricted to the cobble biotope but none of the taxa were unique to either the gravel or sand biotopes (Table 5). Consequently, the total number of taxa and the Shannon and Margalef diversity indices were significantly higher for the vegetation and cobble than the gravel and sand biotopes (Table 5).

Discussion

Macroinvertebrate assemblages

The benthic composition determined in this study was consistent with other studies of temporary river systems that have recorded dominance of insects in the benthic samples (Feminella, 1996; Marshall et al., 2006). It has been argued that the ability of insect taxa to survive in environments which experience regular drying may be related to their terrestrial origin (Williams, 1987), hence they are already adapted to water loss. A number of these taxa display life cycle adaptations, such as an extended flight period from spring to autumn, egg diapause or aestivation as adults in the summer months, which allow them to survive periods of flow cessation (Sommerhäuser et al., 1996). As a result they have a competitive advantage over noninsect groups, which are unable to withstand extended periods of flow cessation (Covich et al., 2003; Marshall, 2006).

The influence of flow permanence on assemblage composition

The hypothesis that the macroinvertebrate structure and community composition would be affected by the duration of flow of the temporary rivers is supported by the complete separation of ephemeral and intermittent sites (Fig. 2a and b), the low apparent diversity (Table 4) and shift in size-class distribution in the ephemeral rivers (Fig. 3). Patterns in the macroinvertebrate community composition and diversity determined in this study correlates with findings from other temporary aquatic habitats where macroinvertebrates were found to be sensitive to the

Table 3 Results of ANOSIM pairwise spatial comparisons between a priori defined river types (intermittent vs. ephemeral) and habitats, plus the taxa identified by SIMPER as making significant contributions to pairwise differences

	Pairwise comparisons	ANOSIM result (*R*)	Average dissimilarity	Significant taxa (SIMPER)
Permanence	Intermittent vs. ephemeral	0.536**	95.1	*Afrobaetodes*, *Elassoneuria*, *Pseudocloeon*, *Cheumatopsyche*, Syncordulia, Gomphidae, *Simulium*, *Aethaloptera*, *Leptocerina*, *Tholymis*, *Dicentroptilum*
Habitat	Gravel vs. sand	0.375*	74.8	*Euthraulus*, *Pseudocloeon*, *Elassoneuria*, Gomphidae
	Gravel vs. cobble	0.563**	80.6	*Elassoneuria*, *Pseudocloeon*, *Euthraulus*, *Afrobaetodes*, *Cheumatopsyche*, *Dicentroptilum*, *Tholymis*, *Aethaloptera*, *Simulium*
	Gravel vs. vegetation	0.875**	92.7	*Leptocerina*, *Pseudocloeon*, *Syncordulia*, *Euthraulus*, *Pseudagrion*, *Cloeon*, Gomphidae, *Elassoneuria*, *Afronurus*, Plea
	Sand vs. vegetation	0.881**	94.7	*Leptocerina*, *Syncordulia*, *Pseudagrion*, *Cloeon*, Gomphidae, *Pseudocloeon*, *Afronurus*, *Plea*, *Euthraulus*
	Cobble vs. vegetation	0.952**	94.8	*Elassoneuria*, *Pseudocloeon*, *Euthraulus*, *Cheumatopsyche*, *Dicentroptilum*, *Afrobaetodes*, *Syncordulia*, *Tholymis*, *Leptocerina*, *Pseudagrion*, *Aethaloptera*, *Cloeon*
	Sand vs. cobble	0.975**	94.8	*Elassoneuria*, *Afrobaetodes*, *Pseudocloeon*, *Euthraulus*, *Cheumatopsyche*, *Dicentroptilum*, *Tholymis*, *Aethaloptera*, *Baetis*

*$P < 0.05$; **$P < 0.001$

Table 4 Values (mean ± SE) of the eleven taxa identified by SIMPER as making significant contributions to overall faunal differences between intermittent (I) and ephemeral (E) rivers

Order	Family	Genus	Permanence	
			I	E
Ephemeroptera	Baetidae	*Afrobaetodes*	4 ± 3	675 ± 197
		Dicentroptilum	10 ± 7	
		Pseudocloeon	32 ± 18	
	Oligoneuriidae	*Elassoneuria*	48 ± 30	
Odonata	Corduliidae	*Syncordulia*	26 ± 23	1 ± 0
	Gomphidae		8 ± 6	3 ± 1
	Libellulidae	*Tholymis*	11 ± 5	
Trichoptera	Hydropsychidae	*Aethaloptera*	24 ± 13	
		Cheumatopsyche	23 ± 13	
	Leptoceridae	*Leptocerina*	7 ± 7	
Diptera	Simuliidae	*Simulium*	7 ± 6	5 ± 1
		Total number of taxa	27 ± 5	15 ± 1
		Number of ET taxa	8 ± 3	2 ± 0
		Log abundance	2.48 ± 0.02	2.94 ± 0.19
		Shanon diversity	1.02 ± 0.10	0.21 ± 0.11
		Simpson diversity	0.85 ± 0.03	0.20 ± 0.13

Also given are the community indices that were significantly different between the river types

degree of flow impermanence (Pires et al., 2000; Smith & Wood, 2002). The low taxon richness recorded from the Ruia and Moto Rivers may reflect the inability of most benthic macroinvertebrate taxa to colonise and sustain populations at sites with regularly occurring and longer desiccation periods. The dominant taxon of ephemeral rivers (Ephemeroptera; *Afrobaetodes*) exhibited typical

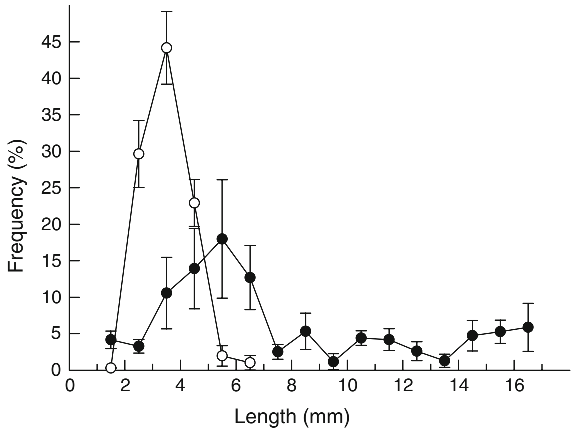

Fig. 3 The length–frequency distribution of macroinvertebrates from the intermittent (●) and ephemeral rivers (○). The data was pooled across all sampling dates and biotope types

r-selected strategies (Colinvaux, 1986): high abundances (which could be used as a proxy for fecundity) (Fig. 2) and smaller body size compared to taxa from intermittent rivers (Table 4; Fig. 3). It appears from this study, therefore, that ephemeral sites were composed of taxa whose life-histories are brief enough to be completed while flow persists in the rivers. In contrast, larger sized Ephemeropteran taxa (e.g. *Elassoneuria* and *Dicentroptilum*), Trichoptera (e.g. *Aethaloptera*) and several Odonata taxa were exclusively restricted to intermittent sites. These results suggest that regular desiccation in the Ruia and Moto Rivers and the shorter duration of flow may act as a filter that may lead to exclusion of bi- or multivoltine macroinvertebrates and those with longer life cycles.

The causes of low apparent diversity in the Ruia and Moto Rivers may be related to the relatively harsh environmental conditions (i.e. high flow variability and unpredictability) in these ephemeral rivers. Lake (2003) suggested that taxa from systems that experience predictable disturbances could be expected to have evolved adaptations for survival, such as high resistance and resilience. It is possible that the intermittent Nyaodza, Gachegache, Murereshi and Sunde Rivers experience more predictable disturbances. Conversely, disturbances in the ephemeral Moto and Ruia Rivers are likely to be unpredictable in both timing and duration. The exposure of ephemeral rivers to longer periods of drying (press disturbance) and sometimes dramatic disturbances such as flash floods (pulse disturbances) is unlikely to allow organisms to adapt (Lake, 2003). As a result, the Ruia and Moto Rivers were found to support only fugitive or opportunist taxa.

The low levels of habitat heterogeneity and diversity at ephemeral sites are other likely contributors to the low invertebrate diversity recorded at these sites. The unpredictable nature of the ephemeral Ruia and Moto Rivers possibly affected the establishment of aquatic vegetation whilst the rapid drawdown of water from the river banks isolates the marginal vegetation, removing an important habitat for many aquatic macroinvertebrates that feed, shelter or emerge among plants. Furthermore, the absence of refugia for invertebrates during the dry season is another possible contributor to the reduced diversity in ephemeral rivers. Although surface flow ceases in the intermittent Nyaodza, Gachegache, Murereshi and Sunde Rivers, subterranean flow persists throughout the dry season. Studies have shown that ground water recharge in intermittent rivers buffers aquatic environments from droughts while the hyporheos provides refuge for macroinvertebrates during the dry season (Boulton, 2000; Hose et al., 2005). However, this interstitial refuge may be unavailable in the ephemeral Moto and Ruia Rivers because the longer dry periods in these rivers may disrupt vertical linkages between surface and ground water as well as lateral linkages with the riparian zones.

From a management perspective, these results have important implications for the conservation of arid-zone rivers. Many dry-land rivers in Zimbabwe suffer severe degradation due to increased water demand, abstraction and siltation, resulting in alteration of natural flows for most rivers. These problems are compounded by the predicted increase in global air temperatures, implying that more extreme and drier conditions may become prevalent. Higher temperatures and consequent reduction in the permanence of rivers may result in the community balance tilting permanently towards the ephemeral river assemblages, with possible dominance by a few hardy species. Since macroinvertebrates are an important component of both the aquatic and terrestrial food webs, reductions in macroinvertebrate production and biodiversity have ramifications for the management of native fisheries and insectivorous birds. Indeed, there is evidence that changes in invertebrate production can affect successful

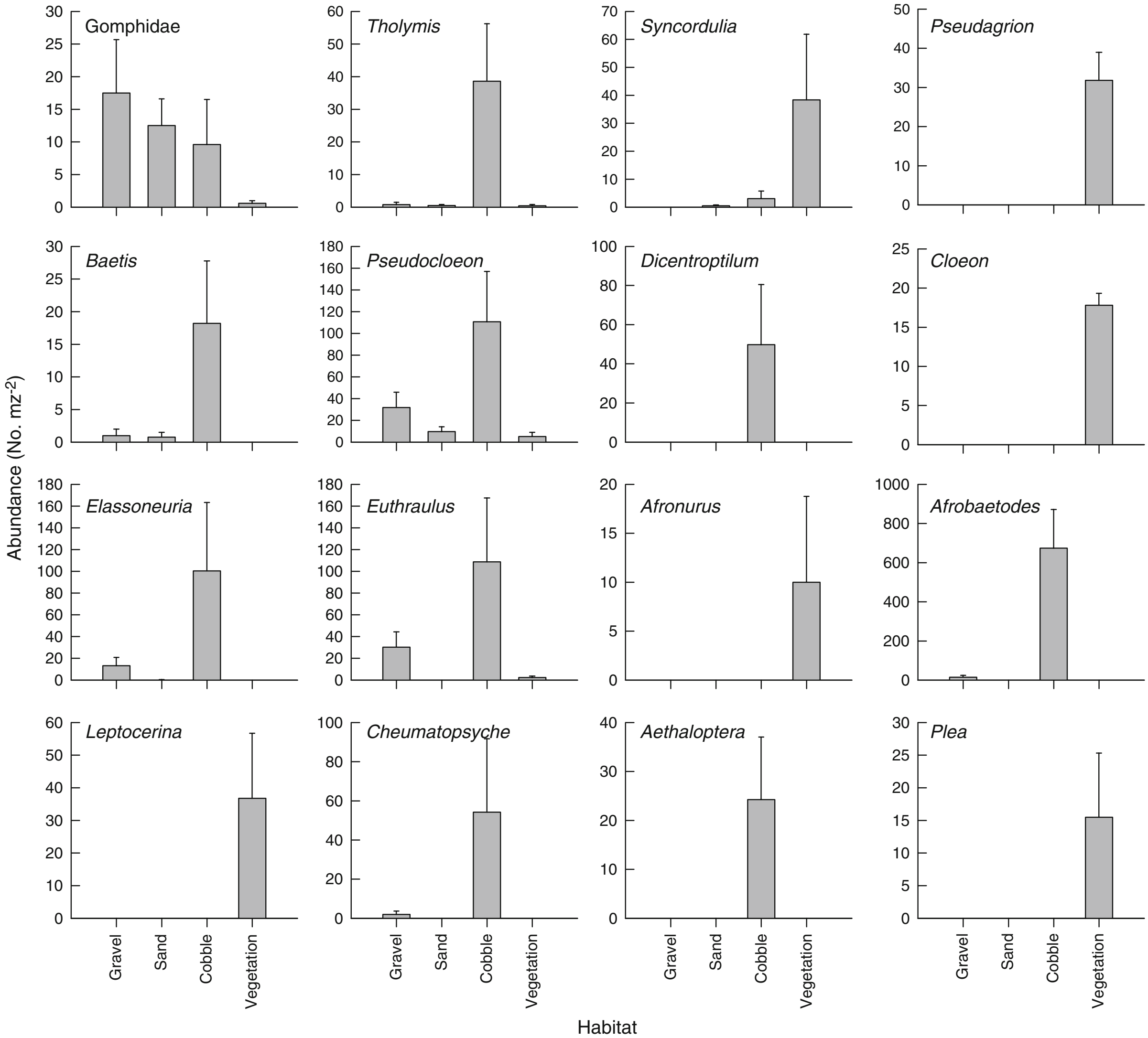

Fig. 4 The mean abundance for each habitat for the 16 taxa that were identified by SIMPER as making large contributions to overall faunal differences between habitats. Bars represent standard errors of the means

recruitment of fish and waterbirds (Jenkins & Boulton, 2007).

The influence of habitat on assemblage composition

The occurrence of aquatic invertebrate taxa within many riverine systems has been shown to be strongly influenced by in stream habitat structure and substratum composition (Dallas, 2007). Results from the Nyaodza-Gachegache catchment similarly suggest that habitat had a strong influence on in-stream community composition (Fig. 2a and c). The cobble and vegetation habitats supported a greater abundance, richness and diversity of taxa than the gravel and sand habitats (Table 5). Macroinvertebrates showed stronger preference for the vegetation and cobbles possibly because they are complex habitats that provide refuge from current and fish predation, food for a variety of herbivores and detritivores, attachment for filter-feeding taxa and exit points for emerging insects with aerial adult stages (Harrison, 2000; Harrison & Harris, 2002). On the contrary, sand and gravel were the least preferred habitats

Table 5 Taxa restricted to either cobble or vegetation biotopes and the overall community indices for the habitats

Order	Family		Cobble	Vegetation	Gravel	Sand
Ephemeroptera	Baetidae	*Dicentroptilum*	+			
		Cloeon		+		
		Ophelmatostoma		+		
	Heptageniidae	*Afronurus*		+		
	Polymitarcidae	*Povilla*		+		
Odonata	Coenagrionidae	*Pseudagrion*		+		
	Libellulidae	*Macrodiplax*		+		
Trichoptera	Hydropsychidae	*Aethaloptera*	+			
		Macrostermum	+			
	Leptoceridae	*Leptocerina*		+		
Hemiptera	Pleidae	*Plea*		+		
		Total number of taxa	21 ± 2	19 ± 1	10 ± 1	5 ± 4
		Shannon diversity	1.03 ± 0.05	0.96 ± 0.03	0.66 ± 0.03	0.48 ± 0.07
		Margalef diversity	2.84 ± 0.42	3.35 ± 0.14	1.82 ± 0.24	1.55 ± 0.31

(Fig. 4), suggesting that habitat simplification through siltation may significantly reduce macroinvertebrate diversity possibly through reduction of available refugia and reduction of habitat stability.

It was evident from this study that distinct faunal assemblages were associated with specific habitats, in keeping with results reported by Pardo & Armitage (1997) and Wood & Armitage (1999). The vegetation habitat was preferred by some rare and endangered taxa particularly *Pseudagrion* and *Syncordulia* (Samways, 2005), *Leptocerina* and *Povilla* while rheophilus taxa: *Elassoneuria*, *Aethaloptera*, *Cheumatopsyche* and *Dicentroptilum* were unique to the cobble substratum (Fig. 4). Thus, in terms of ensuring optimum diversity and protection of macroinvertebrate communities within these rivers, we consider the cobble and vegetation habitats to be the critical habitats for conservation. The greatest threat to macroinvertebrate species within the Nyaodza-Gachegache subcatchment is habitat loss. Landscape changes such as removal of riparian vegetation, stream bank cultivation, siltation, trampling of banks by livestock and overabstraction are the most serious disturbances which have led to the degradation and loss of the critical habitats within the subcatchment.

Overall, our results suggest that the macroinvertebrate fauna from the Nyaodza-Gachegache subcatchment is sufficiently sensitive to habitat and hydrologic variations to be used as rapid and effective indicators of habitat loss, alteration of flow regime and to measure the success of river restoration projects. Management actions for conservation of dry-land rivers should target protection of critical habitats and maintenance of the natural flow regimes.

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