RESEARCH PAPER

Longitudinal distribution of the functional feeding groups (FFGs) of aquatic macroinvertebrates and ecosystem integrity of Tokwe River, Zimbabwe

Caston Makaka*[1], Tinashe Muteveri[1], Paul Makoni[2], Crispen Phiri[3], Trevor Dube[1]

[1]*Department of Applied Biosciences and Biotechnology, Midlands State University, Gweru, Zimbabwe*

[2]*Department of Research, National University of Science and Technology, Ascot Bulawayo, Zimbabwe*

[3]*School of Wildlife, Ecology and Conservation, Chinhoyi University of Technology, Chinhoyi Zimbabwe*

Abstract
Knowledge of functional feeding groups (FFGs) is key in understanding energy flow and matter transfer in lotic systems. The River Continuum Concept (RCC) model attempts to capture this flow by looking at the distribution of FFGs. The FFGs approach is informative because it allows assessment of the degree to which invertebrates in streams are dependent upon particular nutritional resource/s. We assessed the ecosystem integrity of Tokwe River, Zimbabwe, and whether it conforms to the RCC by analyzing macroinvertebrates from three zones along the river. A total of 2 172 specimens belonging to five feeding groups (FFGs) were collected. Filters were the dominant group in all zones with proportions of 37.7%, 53.1%, and 53.2% in the upstream, inundated and downstream zones, respectively. Predators (33.9% upstream) and collector-gatherers (25.9% inundated, 32.9% downstream) were second in frequency. Shredders were the least represented in all zones (< 3.1%). The highest proportion of filters (53.1%) and shredders (3.1%) occurred in inundated zones. Predator population was generally but insignificantly correlated to prey (p > 0.05). Scraper's contribution was significantly lower in the inundated than in other environments (p < 0.05). All zones were strongly heterotrophic, non-performing and overburdened with predators although channel stability was high, hence high proportion of filters. The study showed that the distribution of FFG was not in conformity to the RCC but had tenants of Hierarchical Patch Distribution model which was modified by elements of the Flood Pulse model, and that ecosystem integrity and health are highly compromised by anthropogenic activities.

*****Corresponding Author:** Caston Makaka ✉ crispenphiri@gmail.com

Introduction

The flow of matter and energy transformation determine to a large extend the dynamic processes in invertebrate community structure in lotic ecosystems among different habitats (Allan & Castillo 2007). The River Continuum Concept is one of the many synthetic models that has been used to describe lotic environments from river source to mouths The RCC relates the pattern of energy flow with species variations both longitudinally and laterally in lotic systems (Vannote *et al.,* 1980).

The RCC model predicts longitudinal changes in the functional and taxonomic composition of invertebrate communities from the headwater to the mouth (Brasil *et al.*, 2014). In addition to variable energy flow, the environmental heterogeneity (e.g. depth, width, flow regime and temperature) along the course of the river constrains the invertebrate communities (Vannote *et al.,* 1980).

The RCC hypothesize that there is a longitudinal zonation of macro invertebratefunctional feeding groups (FFG) down the long profile of a river because of the differential distribution of energy inputs and matter transfers (Brasil *et al.*, 2014). RCC predict that headwaters are dominated by shredders that can utilize the allochthonous course particulate organic matter (CPOM) broken-down into fine particulate organic matter (FPOM) and ultrafine particulate organic matter (UPOM) which is utilized further downstream by other invertebrate groups such as collectors, gatherers and filters (Cummins *et al.,* 2005). Given the close relationship between the feeding behavior of aquatic animals and the availability of their feeding resources, FFG approach has been used as a tool for evaluating environmental conditions and variables (Cummins *et al.*, 2005).Knowledge of the functional composition of invertebrates in tropical streams is important to understand organic matter processing, energy flow, and trophic relationship and management activities needed to minimize the impairment of ecosystem functioning (Fereira *et al.*, 2012).

Information of functional feeding groups in the Afrotropical region is increasing (e.g. Palmer *et al.,* 1993; Arimoro, 2007; Uwadiae, 2010; Masese *et al.,* 2014). However, in Zimbabwe, the paucity of literature on macroinvertebrate functional feeding composition points to very limited research and understanding of the functional composition of aquatic invertebrates and their consequence on ecosystem structure and function.

In the present study, the longitudinal distribution of macro invertebrates FFGs was assessed in Tokwe River, Masvingo Province, Zimbabwe. The first aim was to determine if the distribution of macroinvertebrate FFGs in Tokwe River, which transverse through three Zimbabwe's ecological land use regions (Regions III, IV and V) conform to the RCC. We hypothesized a change in macro invertebrate FFGs from headwaters to mouth in relation to change in energy flow as predicted by the RCC. The second was to assess the ecological integrity of Tokwe River using ratios of numerical abundance of the different functional feeding groups as surrogates for ecosystem attributes (Vannote *et al.*, 1980; Merritt *et al.*, 1996). We hypothesized a change from heterotrophy (upstream) to autotrophy (downstream) due to changes in the physical nature of the river channel as predicted by the RCC.

Material and methods

Study area

We sampled nine sitealong Tokwe River from Chenge gomo ($30^o16'$ 09", $19^o25'$ 09")in the Midlands Province to Yahombe ($31^o02'$ 45", $20^o55'$ 15")in Masvingo Province, close to the confluence between Tokwe River and Runde River (Figure 1).

The nine sites are Chenge gomo (Site 1), Chitora (Site 2), Mashava Bridge (Site 3), Chibi Turnoff Bridge (Site 4), Sese (Site 5), Maringire (Site 6), Zunga (Site 7), Matandamaviri (Site 8) and Nyahombe (Site 9). Sites 1 -5 are upstream of Tokwe Dam site, sites 5 -8 were within Tokwe Dam (inundated area) and sites 8 and 9 were downstream of the dam wall.
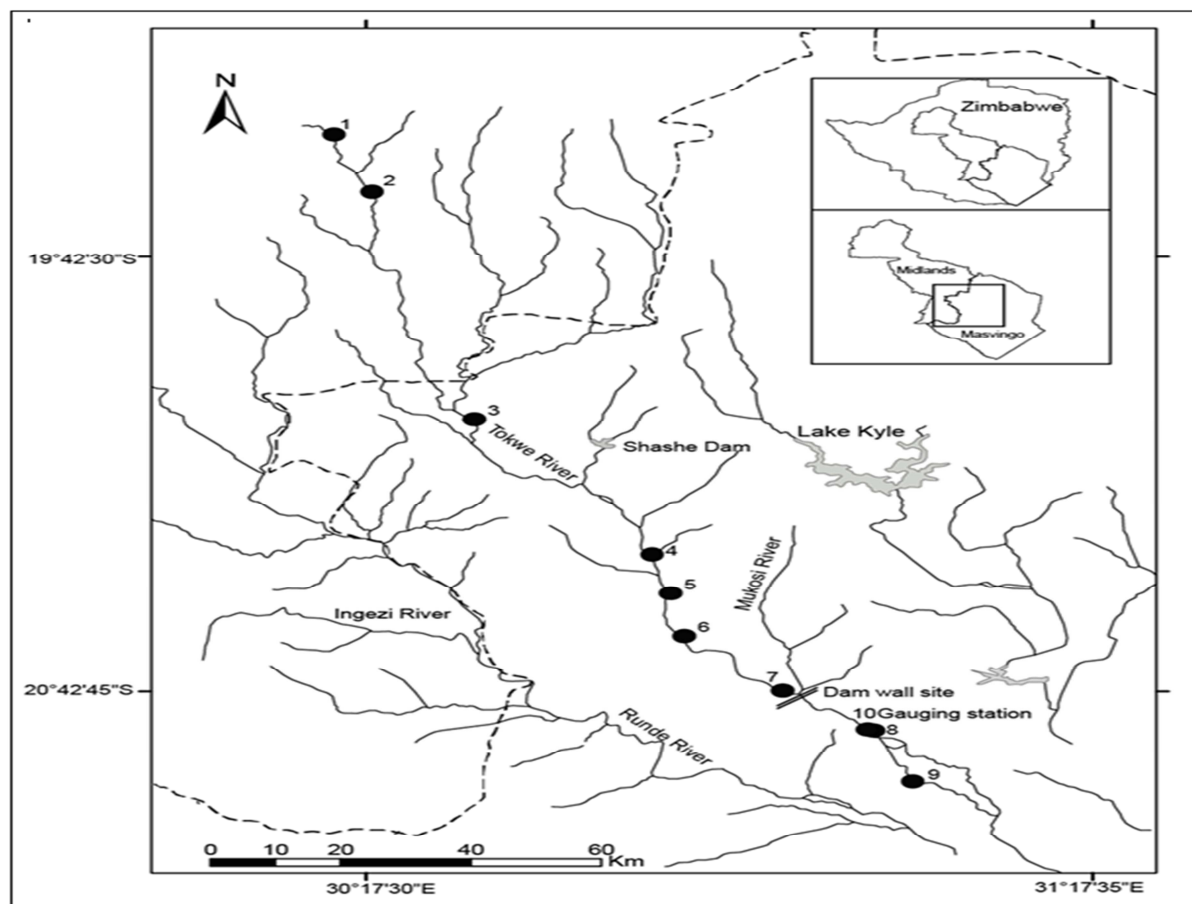
Fig. 1. Location of sampling site along Tokwe River, Zimbabwe.

The region's climate is tropical continental savanna alternately humid and dry with mean annual temperatures varying from 16°C to 24°C (Mugandani *et al.,* 2012), and mean annual rainfall is about 684 mm and is plagued by frequent droughts(ZINWA, 1995). The sampled river reach marks a drop in altitude of 840m 1 352 to 512 m.a.s.l. The area traverses through Zimbabwe's three Natural Ecological Regions III, V, and IV (www.google.co.zw/search?q=ecological+land+use).

Region III is characterized by rainfall ranging from 500 to 800mm yr^{-1}. Temperatures are relatively high. Rainfall is infrequent and often comes in heavy falls, hence the region is subject to seasonal droughts and severe mid-season dry spells. In Region IV rainfall ranges from 450 to 650mm yr^{-1} and the region is subject to frequent seasonal droughts and severe dry spells during the rainy season.

On the other hand Region V receives less than 450mm yr^{-1} and the rainfall is very erratic.

The headwaters of Tokwe are located in Lalapanz i(30°16' 09", 19°25' 09") in the Midlands Province in Region III. The moderate rainfalls (500 – 800mm per annum) that come as infrequent heavy showers, together with the generally high temperatures, reduce the effectiveness of the rain. The region is therefore dominated by grasslands, with occasional stands of acacia and miombo woodlands.

Atlower altitudes, after Mashava Bridge (sites 4 to 9) the river courses its way through Ecological Region IV then further downstream into Region V. The riparian vegetation in these two ecological zones is mainly acacia and food crop cultivation predominates. These sites are also highly exposed to sunlight for much of the year because of the more open nature of the river channel.

Data collection

We sampled aquatic macro invertebrates at nine sites (upstream, midstream and downstream of Tokwe Dam site) along Tokwe River from July 2014 to July 2015 using the all habitat sampling strategy. Our sampling protocol included the three major sites that captures the full range of FFG, which include course and fine sediments and plant litter of in-channel and riparian origin (Merritt *et al.*, 2017). A 250µm D-frame scoop net was used to collect macroinvertebrates in deep waters for three minutes. At each station, substrate from a one metre by one metre quadrat was collected into a white tray before macroinvertebrates were searched and collected into sampling bottles. Stones submerged in water were also collected and washed into white trays and macroinvertebrates picked using blunt forceps. Large woody debris (LWD) and rooted vascular plants were shaken upstream in front of net and macroinvetebrates collected.

Collected macroinvertebrates were taken to the Midlands State University Department of Applied Biosciences and Biotechnology for identification under X100 dissecting microscope using keys by Martens *et al.*(2001), Stals*et al.*(2001), Day *et al.* 2001, Day *et al.*(2002a), Day *et al.*(2002b), Day *et al.*(2002c), Barber-Tames *et al*(2003), de Moor *et al*(2003a), de Moor *et al.*(2003b), Mansell *et al.*(2003), Barber-Tames *et al.* (2003),Suhling and Martens (2007) and Kippings (2010). Functional feeding groups of aquatic insects were identified based on Merritt and Cummins (1996), Baptista *et al.*(2006) and Merritt *et al.* (2008).We complimented the classification of the families into FFGs with other published data (Campbell, 1985; *Palmeret al., 1993;* Benk and Wallace 1997; Gooderham & Tsyrlin 2002;Arimoro, 2007; Dominguez and Fernandes, 2009; Nesemann,2011;Masese *at al.,* 2014*;* Mishra *et al.,* 2013; Barman *et al.,* 2015; *www.mdfrc.org.au/bugguide/)*. These sources were augmented by specimen observation of the mouthparts under a binocular dissecting microscope.

Stream ecological health status

Stream ecological health was assessed following the method of Masese *et al* (2014). Balance between autotrophy and heterotrophy (Production/respiration) index was calculated as the ratio of scrappers to (shredders +total collectors [filters +collector-gatherers]); Linkage between riparian inputs and stream food webs (CPOM/FPOM) was calculated as the ratio of shredders total collectors (filters +collector-gatherers).

The FFG surrogate for the availability of stream FPOM in transport (suspended load) relative to that in the benthos (bed load) was calculated as the ratio of filters to collector-gatherers. Channel stability was calculated as the ratio between scrappers plus filters to shredders plus collector-gatherers (Merritt *et al.*, 2017) Top-down predator control was calculated as the ratio of predators to prey (total of all other groups). Interpretations were based on Merritt *et al.* (2017) general criteria thresholds for ratios: $P/R > 1$ indicates autotrophy, CPOM/FPOM > 0.25 indicates shredder association linked to functioning riparian zone; FPOM (suspended)/FPOM (sediment) > 0.50 indicates enriched, unusual particulate loading of fine particulate food for filters; scrappers + filters/shredders+ collector-gatherer > 0.50 indicates plentiful stable substrates; and predator/prey between 0.1 and 0.2 indicates a normal predator to prey balance whereas a value > 0.2 indicates an overabundance of predators.

Data analysis

Chi-squared goodness of fit test was used to assess the percentage of occurrence of FFGs in the three ecological environments (upstream, inundated and downstream) basedon the assumptions that no expected frequency could be lessthan one, and only 25% could be less than five (Zar, 2010). We determined the percentage contribution of each FFG to the different communities as well as the percentage of each family to the respective FFG to find out the relative contribution of each group.

Pearson's correlation coefficient was used to assess the relationship between abundance of predator and their prey (filters, collectors, shredders, and scrapers)

(Zar, 2010) and to evaluate the relationship between the different FFGs with altitude.

Results

Proportions and distribution of functional feeding groups

A total of 2 172 specimens were collected in 56 families of the following orders and phyla: Coleoptera (9), Ephemeroptera (7), Plecoptera (1), Trichoptera (3), Odonata (8), Hemiptera (11), Diptera (7), Neuroptera (1), Areaneae (2), Mollusca (10) and Crustaceans (one). Representatives of the phyla Annelida and Nematomorpha were also collected (Table 1).

Table 1. The functional feeding groups (FFG)—predators (P), collector–gatherers (CG), collector–filterers (CF), shredders (SH), and scrapers (SC)—assigned to the genera of aquatic macroinvertebrates analyzed in the present study The FFGs were defined based on the literature cited. L – Larvae, A – Adult.

Order/family	FFG	References
Coleoptera		
Chrysomelidae	Generally Sh (L and A)	Merritt *et al.*, 2008
Curculionidae	Sh (L and A)	Merritt *et al.*, 2008
Dytiscidae	Generally Pr	Merritt *et al.*, 2008
Dryopidae	Generally Sh, (L) Generally Sc, Sh (A)	Merritt *et al.*, 2008
Elmidae	Generally CG, Sc, Sh (L and A)	Merrit*et al.*, 2008
Gyrinidae	Generally Pr (L and A)	Merritt *et al.*, 2008
Hydrochidae	Shredder (A), larvae unknown	Gooderham & Tsyrlin 2002; www.mdfrc.org.au/bugguide/display.asp?type=5&class=17&subclass
Hydrophilidae	Generally Pr (L), generally CG (A)	Merrit*et al.*, 2008
Psephenidae	Sc (L), (A) non-feeding	Merritt *et al.*, 2008
Ephemeroptera		
Beatidae	Cf; CG	Palmer *et al.*,1993; Baptista *et al.*, 2006, Merritt *et al.*, 2008
Caenidae	CF , CG	Palmer *et al.*, 1993, Merritt *et al.*, 2008
Ephemerythidae	Sc	Masese *et al.,* 2013
Heptageniidae	Sc	Merritt *et al.*,2008; Palmer *et al.*, 1993
Leptophlebidae	CG	Merritt *et al.*, 2008
Oligoneuridae	Ft	Palmer *et al.,*1993; Campbell I.C., 1985; Baptista *et al.,* 2006; Merritt *et al.*, 2008
Polymitarcidae	CG	Merritt *et al.*, 2008
Plecoptera		
Perlidae	Pr, early stage Dt	Merritt *et al.,* 2008
Tricoptera		
Ecnomidae	Ft	Merritt *et al.,* 2008
Glossosomadidae	Generally obligate SC	Merritt *et al.,* 2008
Hydropsychidae	Generally Ft, some Prans seasonal Sc	Palmer *et al.,* 1993; Benk and Wallace 1997; Merritt *et al.*, 2008
Hemiptera		
Aphelocheiridae	Pr	Barman and Gupta, 2015
Belostomatidae	Pr	Dominguez and Fernandes, 2009
Corixidae	Generally Pc-Hb some Pr or SC	Merritt *et al.*,2008
Gelastocoridae	Pr	Dominguez and Fernandes, 2009
Gerridae	Pr	Dominguez and Fernandes, 2009
Leptopodidae	Pr	Dominguez and Fernandes, 2009
Mesoveliidae	Pr	Dominguez and Fernandes, 2009
Naucoridae	Pr	Dominguez and Fernandes, 2009
Notonectidae	Pr	Dominguez and Fernandes, 2009
Ochteridae	Pr	Domínguez & Fernández, 2009
Pleidae	Pr	Dominguez and Fernandes, 2009
Odonata		
Aeshnidae	Pr	Merritt *et al.*, 2008
Coenagrionoidae	*Pr*	Merritt *et al.*, 2008
Chlorocyphidae	Pr	Francis and Arimono, 2007
Corduliidae	*Pr*	Merritt *et al.*, 2008
Gomphidae	Pr	Merritt *et al.*, 2008
Libellulidae	Pr	Merritt *et al.*, 2008

Lestidae	Pr		Merritt *et al.*, 2008
Platycnemidae	Pr		Arimono *et al*,2007
Diptera			
Athericidae	Pr		Merritt *et al.*, 2008
Ceratopogonidae	Generally Pr, some facultative CG and Sc		Merritt *et al* 2008
Chironomidae	CG and Ft , Pr		Merritt *et al.*, 2008
S/FChironominae	Generally CG, Ft		Merritt *et al.*, 2008
Tabanidae	Generally Pr		Merritt *et al.*, 2008
Choaboridae	Pr		Merritt *et al.*, 2008
Culicidae	Generally Ft and CG		Merritt *et al.*, 2008
Tanypodidae	Pr		Merritt *et al.*, 2008
S/F Tanypodinae	Pr		Merritt *et al.,* 2008
Areneae			
Pisauridae	Pr		
Lycosidae	Pr		
Neuroptera	Pr		Dominguez and Fernandes, 2009
Nematomorpha	Pr		Mishra *et al.*, 2013
Crustacea/Decapoda			
Potamonautidae	Sh		Orimoro, 2007
Oligocheata	CG		Orimoro, 2007
Polycheata	CF		Orimoro, 2007
Hirudinea	Pr		Orimoro, 2007
Molusca			
Bivalvia			
Uionidae	*FC*		http://dep.wv.gov/WWE/getinvolved/sos/Documents/Benthic/AquaticInvertGuide.pdf
Gastropoda			
Ancylidae	Sc		http://dep.wv.gov/WWE/getinvolved/sos/Documents/Benthic/AquaticInvertGuide.pdf
Assimineidae	unknown		www.mdfrc.org.au/bugguide/display.asp?type=5&class=21&subclass=&Order=45&family=208&couplet=0 (Retrived: 3:37pm, 20/02/18)
Corbiculidae	FC		Mishra *et al.*,2013
Littorinidae	Sc		https://books.google.co.zw
Lymnaedae	Sc		Nesemann *et al.*, 2011
Planorbidae	Sc		Orimoro, 2007
Succineidae	Sc		
Thiaridae	*Sc*		Mishra *et al.*, 2013

Table 1 also shows the designation of the different taxa into functional feeding groups (FFGs). The Mollusca constituted the largest proportion (50.5%) followed by the Odonata (15.7%), Diptera (9.3%), Ephemeroptera (9.0%), Coleoptera (5.3%), Hemiptera (4.9%), Trichoptera (3.5%), Plecoptera (1.2%), Oligocheata (0.3%), Areneae (0.2%), Potamautidae (0.1%) and Nueroptera (0.02%).

The most common of the functional feeding groups in the entire river were the filterers (41.3%). This was followed by predators (25%), collector-gatherers (17.7%), scrappers (14.8%) and shredders (1.2%) (Figure 2).

There were significant differences in the proportions of the different functional feeding groups (Chi-square= 42.8, $p < 0.05$).

The frequencies of filterers and shredders were significantly higher and lower respectively, than those of predators, collector-gatherers and scrappers (Chi-square, $p < 0.05$). Whilst there were no significant differences between the proportions of predators, collector-gatherers and scrappers (Chi-square, $p > 0.05$).

Table 2. Abundance of functional feeding groups (FFGs) of macro invertebrates in upstream, inundated and downstream environments along Tokwe River. The functional feeding groups (FFG)—Filterers (Ft), collector–gatherers (CG), predators (Pr), scrappers and shredders (SH) —assigned to the families of aquatic macro invertebrates analyzed in the present study.

Site	Ft	CG	Pr	Sc	Sh	Total	RA (%)
Upstream	435	92	394	234	8	1163	53.5
inundated	287	140	74	22	17	540	24.9
Downstream	176	152	74	66	1	469	21.6
Total	898	384	542	322	26	2172	100

The relative contributions of the three environments is given in Table 2. The upstream zone had the highest proportion (53.5%), followed by the inundated (24.9%) and the least proportion was recorded from downstream sites (21.6%).

The proportions of the various FFG varied markedly among habitats. In all three environments (upstream, inundated area, and downstream) filters feeders were the dominant group and shredders were the least dominant (Figure 3, 4, and 5).

Table 3. Correlations between numbers of different functional feeding groups with altitude

Functional feeding group (FFG)	Pearson's correlation	p-value
Filterers	-0.011	0.979
Collector gatherers	-0.047	0.197
Predators	0.733	0.025
Scrappers	0.472	0.199
Shredders	-0.090	0.818

The second predominant group in the upstream sites were predators (33.9%), followed by scrappers (20.1%), collector-gatherers (7.9%) and the least were shredders (0.7%) (Fig 3).

In the inundated and downstream sites the order of dominance was filterers> collector-gatherers > predators > scrappers > shredders (Figures 4 and 5).

The predominant family of filterers in the three sites were corbiculids that constituted 34.2% (upstream), 46.0% (inundated area) and 21.7% (downstream) of all individuals. The numerically dominant families of collector-gatherers in upstream environment were Caenidae (3.8%), whereas Elmidae(8.1%) and Chironomidae (19.1%) dominated the inundated and downstream environments respectively.

Table 4. Chi-square analysis of variations in the distribution of the FFGs among the different environments (upstream, inundated area, and downstream).

	Percentage of FFG by environments					
FFG	Upstream	Inundated area	Downstream	X^2	d.f	p
Filterers	37.4a	53.1a	37.6a	3.766	2	0.152
Collector-gatherers	7.9a	25.9b	32.3b	14.182	2	0.001
Predators	33.9a	13.7b	15.8b	11.375	2	0.003
Scrappers	20.1a	4.1b	14.1a	10.316	2	0.006
Shredders	0.7a	3.1a	0.2a	1.0	1	0.317

Proportions in the same row with different letters are significantly different (Chi-square, p < 0.05)

In all sites, the Gomphidae were the predominant predators, comprising 12.6%, 9.6% and 3.6%relative abundances in the upstream, inundated and downstream sites, respectively. The Moluscawere the major scrapers with planorbids dominating the upstream (15.5%) and inundated (2.2%) environments whilst the Thiaridae dominated the downstream area (9.4%).

Table 5. Calculated ratios of the FFGs used as surrogates of ecosystem function - P/R = Production/ Respiration ratio, CPOM/FPOM = Course particulate organic matter/Fine particulate organic matter ratio, CPOM(suspended)/CPOM(sediment) = Course particulate organic matter in suspended load/Course particulate organic matter in sediment, Channel stability = (Scrapper +filter)/Shredders + collector-gatherers, and P/P = Predator/Prey ratio.

Zone	P/R	CPOM/FPOM	CPOM(suspended)/CPOM(sediment)	Channel stability	P/P
Entire river	0.25	0.02	2.3	2.9	0.33
Upstream	0.44	0.015	4.7	6.7	0.51
Inundated area	0.05	0.052	2.1	1.9	0.16
Downstream	0.20	0.003	1.2	1.6	0.19

There were also variations in the relative frequencies of each of the five feeding guilds in each of the studied zones (Figure 6). The proportion of filter feeders was highest in the inundated environment but they constituted less and about the same proportions in the upstream and downstream zones. The proportion of collector-gatherers increased downstream having their highest proportion in the downstream environment. Predators were most represented in the upstream river reach with less and almost equal proportions in the inundated and downstream river reaches. Pearson's correlation analysis showed that there was a significant positive correlation between predator numbers and altitude (r = 0.733, p =0.025) (Table 3). There was also a general increase in predator population with prey population although insignificant (r = 0.97, p = 0.15).
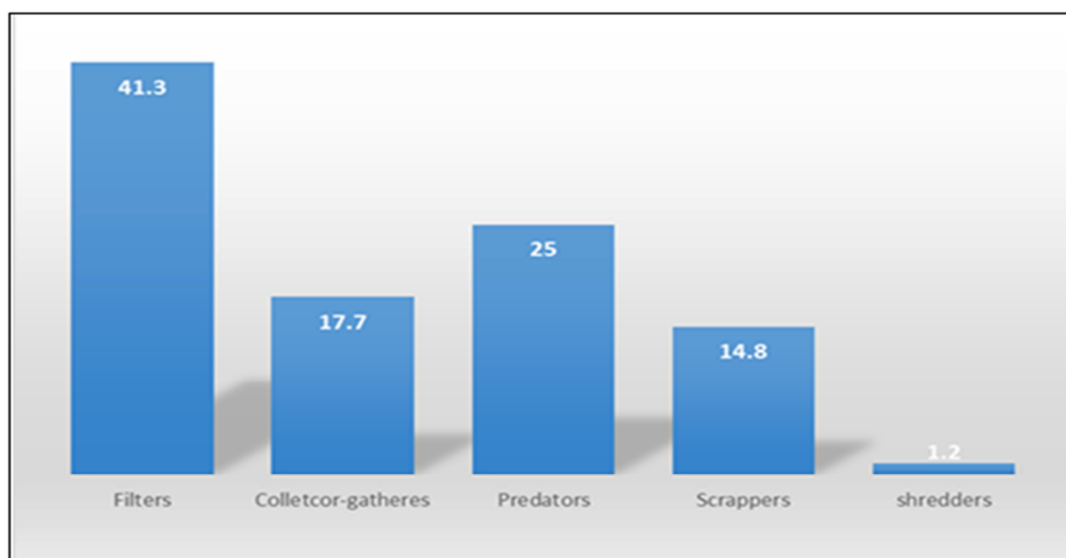

Fig. 2. Proportions (%) of different functional feeding groups in Tokwe River.

The contribution of scrappers was highest in the upstream fauna followed by the downstream zones and lowest in the inundated area. Shredders on the other hand had their largest contribution in the inundated area with very low frequencies in both upstream and downstream environments.
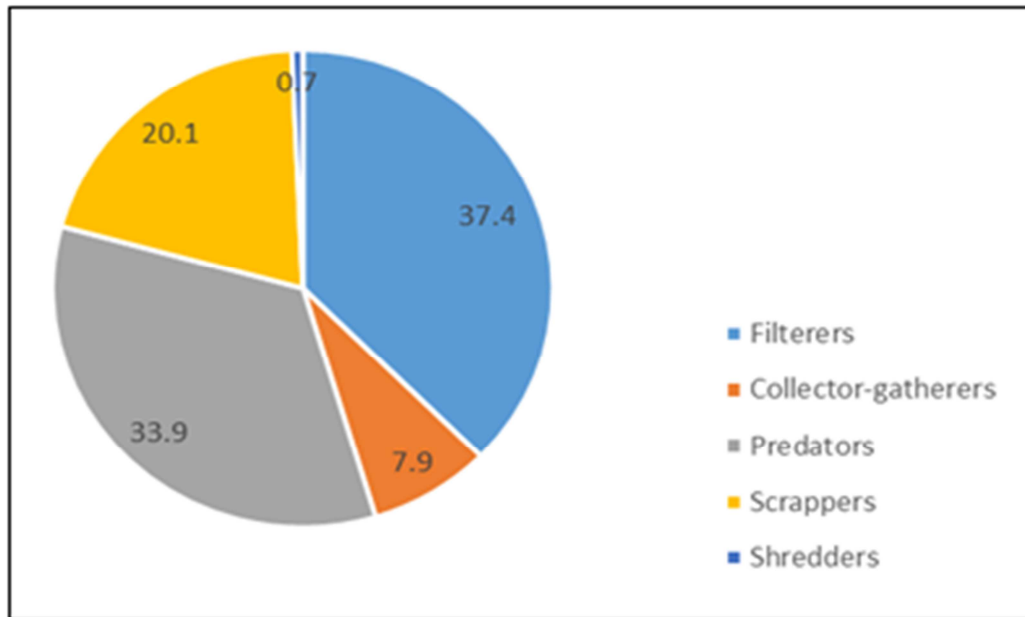
Fig. 3. Proportions (%) of different functional feeding groups upstream of inundated area.

Chi-square goodness of fit comparisons of the frequencies of the different functional feeding groups in each of the three zone sare shown in Table 4. The percentage of predators was significantly higher in upstream reaches than in the inundated and downstream zones whilst the frequency of collector – gatherers were significantly lower in the upstream

than in the inundated and downstream river reaches (Table 4).

There were no significant differences in the frequencies of filters and shredders among the three zones but the percentage of scrappers was significantly higher in upstream and downstream sites as compared to the inundated area (Table 4).
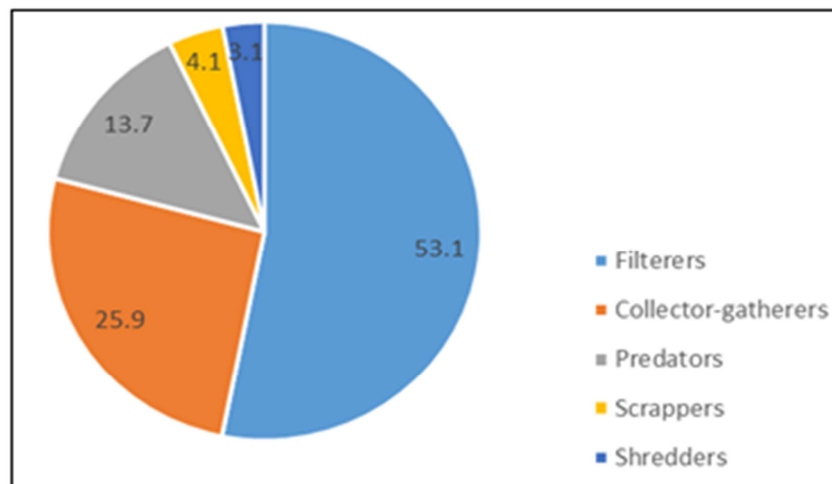

Fig. 4. Proportions (%) of different functional feeding groups in inundated area.

Ecosystem attributes
P/R ratios based on abundance indicated that all zones were heterotrophic (P/R < 0.75) (Table 5). All environments had CPOM/FPOM < 0.25 indicating a non-functioning riparian area.

All zones had plentiful loading of fine particulate organic matter for filters [CPOM (suspended)/CPOM (sediment) > 0.5] and stable substrates for scrappers and filters (Channel stability > 0.5).
The downstream and inundated areas had normal predator-prey balances (P/P of 0.1 -0.2) whereas the

upstream was overburdened with predators (P/P > 0.2) and this contributed to the overall overburden of predators for the entire river (P/P > 0.2).

Discussion

Proportions and distribution of functional feeding groups

The results of this study showed that there is high diversity of FFGs in Tokwe River.

It was also noted that their distribution is not wholly in tandem with the RCC model as envisioned by Vannote *et al* (1980).

The high diversity and non-compliance of many tropical rivers to the Vannote's RCC model have also been observed by other workers (e.g. Masese *et al.,* 2014; Brasil *et al.,* 2014).
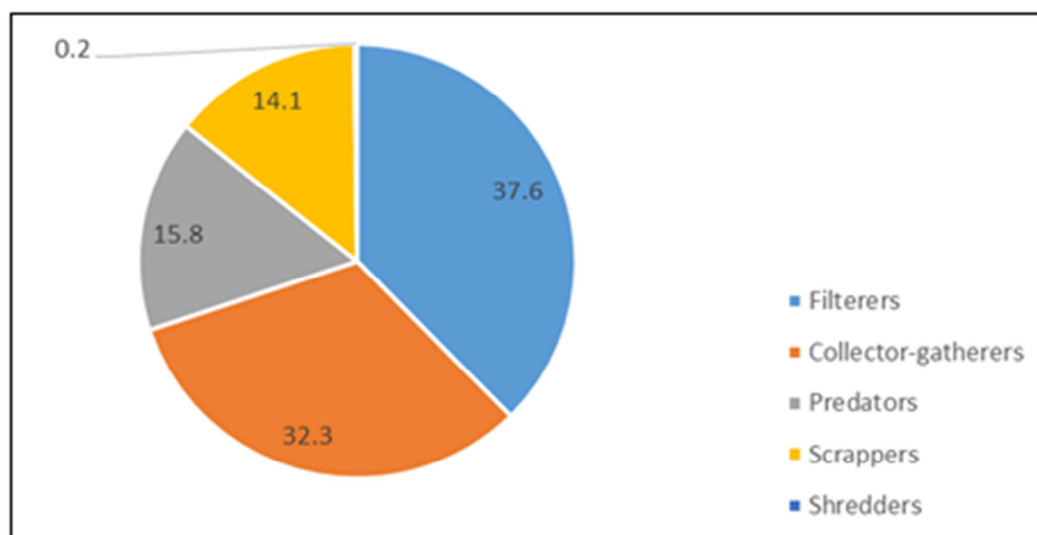

Fig. 5. Proportions (%) of different functional feeding groups downstream of dam wall.

Tokwe River traverse Zimbabwe's Ecological Region III, IV, and V and this may explain the high diversity of FFGs (five) observed in this study. Overall, filter feeders predominated the whole river and each of the three environments (Upstream, Inundated area, and Downstream). Filters feeders play a vital role in clarifying water, and therefore considered ecosystem engineers (Bullivant, 1968). The high proportions of filters (41.5%) can be attributed to the relatively high velocities of water in Tokwe River (unpublished data of this study) which facilitate filtration (Parker *et al.,* 2013). Wildish and Kristmanson (1997) cited in Pratt (2008) attributed high feeding rates and hence abundance of filter feeders to the increased encounter of food particles with increased water velocities. The Mollusca, which were collected in large proportions in this study, are efficient filter feeders. The predominant family of filterers in the three sites was Corbiculidae that contributed 34.2% (upstream), 46.0% (inundated area) and 21.7% (downstream) of all samples.

The abundance of corbiculids may be attributed to high dissolved salts in the water as indicated by high conductivity levels (unpublished data of this study). High concentrations of salts especially calcium carbonate has been linked to high populations of molluscs as it contributes to the building of their calcareous shells (Parker*et al.,* 2013).

Predators were the second most abundant FFG in the entire long profile of Tokwe River. They were also the second most abundant in the upstream reaches and the third most abundant in the inundated and downstream reaches. Abundance of predators is largely determined by the availability of their prey (Vannote *et al.,* 1980).This is further corroborated by the general positive linear relationship between predators and their prey obtained in this study. Odonata families (Libellulidae and Gomphidae) were the most common predators.In all sites, the Gomphidae were the predominant predators, comprising 12.6%, 9.6% and 3.6% relative

abundances in the upstream, inundated and downstream sites respectively. The odonata are known to prey on Ephemeroptera larvae like beatids (Gamboe*et al.*, 2009) and molluscan larvae. Themolluscs constituted the largest proportion of individuals (50.5%) collected in the study.

Collector-gatherers were the third most abundant overall, second most important guild in the inundated and downstream reaches and the least represented in the upstream reaches. However, collector-gatherers were expected to be highly represented in the upstream and middle reaches of the river because of their direct response to fine particulate organic matter generated by shredders upstream (Vannote *et al.*, 1980), but, contrary to this, they were overridden by filters in either environments. According to Vannote *et al.*(1980) collector-gatherers should be co-dominant with shredders in the headwaters (upstream environment) because of the availability of allochthonous resources (leaf litter from overhanging vegetation) with the collector-gatherers directly utilizing the fine particulate organic matter (FPOM) generated by shredders.
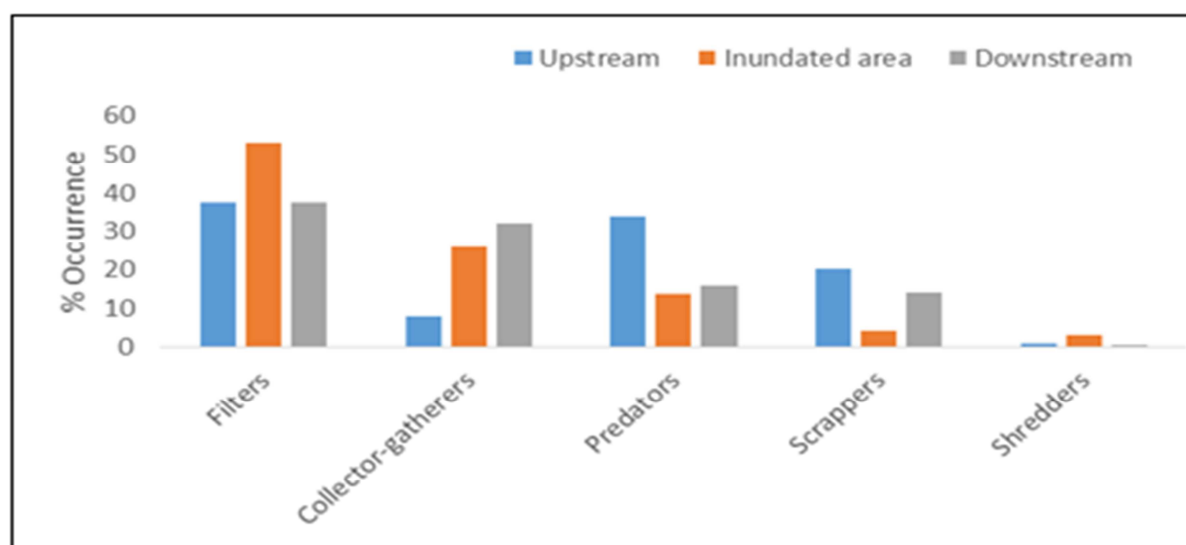

Fig. 6. Relative frequency(%) of each functional feeding group (FFG) of aquatic macro invertebrates in each zne.

However the general increase in collector-gatherers proportion downstream observed in this study is in consonance with Vannote *et al.*(1980) concept although they did not attain predominant status in the lower reaches. According to the RCC, the general increase in FPOM downstream should also increase the collector-gatherer contribution so that they become the dominant FFG in downstream river reaches given the diminished contribution of scrappers because of the reduced autochthonous resource production by algae owing to increased depth and increased turbididty.

The scrappers were the fourth most abundant feeding guild in the entire river, third in abundance in the upper stretch, but fourth in the inundated and downstream river reaches.

Scrapers feed off of the periphyton that accumulates on larger structures such as stones, wood or large aquatic plants (Vannote *et al.*, 1980). The scrappers collected in this study include snails (Mollusca .eg. planorbids) and caddisflies (Glossosomatidae). One would expect the scrappers to become more abundant in the middle reaches (inundated area) given the more abundant periphyton owing to more light that reaches the water surface because of the more open nature of the river channel (www.en.wikipedia.org/wiki/River_Continuum_Co ncept). Further downstream, scrapper activity may be limited by low periphyton productivity because greater depth and increased turbidity associated with these river reaches limit light penetration (Vannote *et al.,* 1980).

The shredders were the least FFG along the entire river stretch and constituted the least proportion in each of the three environments. However, Vannote *et al.* (1980)in their RCC model hypothesize that shredders are the predominant functional feeding group in the headwaters owing to their reliance on allochthonous resources falling from overhanging vegetation in the riparian zones of a river. The low occurrence of shredder guild is consistent with many studies in the tropics (e.g. Irons *et al.*, 1994: Arimoro, 2007; Brasil *et al.*, 2014) and in some cases their total absence. Chakona and Marshal (2007) reported the total absence of shredders in their studies of two rivers (Nyahode and Haruni) in the eastern highlands of Zimbabwe. Shredders are intimately related with the riparian vegetation, because of their reliance on allochthonous feeding resources and hence contribute much in the degradation of leaf materials dropping into aquatic systems from overhanging vegetation (Allan and Castillo, 2007; Brasil *et al.*, 2014). However, this degradation function is very important, especially in temperate regions where temperatures tend to limit the role of other decomposers like aquatic bacteria and fungi. In temperate regions shredders are therefore the dominant FFG in headwaters, but as (Brasil *et al.*, 2014) observed, in tropical regions their degradation function is taken over by bacteria and fungi. Arimoro (2007)also noted that the high temperatures in the tropics promote active bacterial and fungal activity which reduces the food available to shredders, henceforth their reduced frequencies in these environments. However, other authors have attributed the low shredder guild in tropics to the use of temperate keys to assign FFGs to tropical taxa, thereby overlooking many tropical shredders (Dobson *et al.*, 2002; Camacho, 2009).Others have attributed this to the limited scale and sampling effort put in such studies (Masese *et al.*, 2014). In addition riparian deforestation also has a negative effect on shredder as this reduces or eliminate their main source of food. It has also been pointed out that many shredder species are adapted to cold water and may be closer to their thermal maxima in the tropics or rivers rendered bear of vegetation by deforestation (Masese *et al.,* 2014). Thus they may be especially susceptible to increases in temperatures (Irons *et al.*, 1994; Boyero *et al.*, 2011).

On the overall, the distribution of FFGs was discontinuous among the three environments. This is not in consonance with Vannote *et al.*(1980) River Continuum Concept (RCC) which insists that feeding guilds are distributed in a continuum from headwaters to river mouths with one group predominating in one zone and giving way to domination by another in the proceeding river reach down the long profile of the river. Downstream guilds depend on the leaks or inefficiencies of upstream guilds and such succession holds because of the nature of resources utilization (Vannote *et al.*, 1980). Throughout the continuum of the river, the proportion of the functional feeding guilds; shredders, collectors, scrapers (grazers), filters and predatorschange (Vannote *et al.*, 1980). With the exception of the predators, all these organisms feed directly from plant material (saprobes) (https://en.wikipedia.org/wiki/River_Continuum_C oncept). According to the RCC, headwaters should be dominated by shredders given the abundant allochthnous resources from the riparian overhanging vegetation (Brassil *et al.*, 2014). Shredders feed on course organic matter (CPOM) from leaves and grasses breaking them down so that they are used by collector-gatherers that feed on fine particulate organic matter (FPOM).Shredders and collector-gatherers should thus co-dominate the headwaters with the former giving way to the latter in midstream and downstream stream reaches as FPOM dominates the food resource (Vannote *et al.*, 1980). Filter feeders also filter from transported FPOM and UPOM and should thus increase downstream in the midsection of the river. Scrappers on the other hand are adapted primarily for shearing attached algae from surfaces. The dominance of scrapers thus follows direct shifts in primary production, being maximized in midsized rivers (mid-reaches) where production exceeds respiration (Vannote *et al.*, 1980). Further downstream the proportion of scrapers may be compromised by reduced productivity as depth and turbidity decreases light penetration and hence periphyton growth (Brasil *et al.,* 2014).

The discontinuous distribution of feeding guilds observed in this study tends to be in tandem with the Hierarchical Patch distribution (HPD) model which was developed to address some oversights in the RCC. The HPD model hypothesize that different functional feeding groups are distributed longitudinally and laterally in a river channel mainly on the basis of preferred microhabitat and mesohabitat conditions. This is because of the vertical aspect which is brought about by the depth of the water in the channel (Petts *et al.*, 2000) an aspect not considered in the RCC. This aspect is important given the dynamic geomorphological and hydrological processes which are part of river systems. These complex changes in aquatic systems brought about by stream dynamics have become more evident in light of increased fluctuations brought about by climate change (Petts *et al.*, 2000), and as Ta Fang (2000) noted, there is always potential for change in river morphology over time. Such variations in channel characteristics include channel structure (presence of rapids, riffles, plant cover and water flow (Brasil *et al.,* 2014) which give rise to a diversity of substrates and microhabitats, which in turn determine the arrangement of FFGs in lotic environments. This could explain the deviations noted in this study from precincts of the RCC model as different communities were affected by the differential suitability of the various patches along the river. This heterogeneity in terms of hydrogeomorphical attributes, the HPD hypothesize, shapes the distribution of FFGs longitudinally and laterally in the river channel. Statzner(1981) and Minshall *et al.*(1982) cited in Statzner and Higler (1985), in their critique of the RCC, also insist that the sequence of change in species and hence FFGs downstream occurs irrespective of stream reach or order. Schlosser (1982) also argues that the environmental variability of a particular physical structure may influence the diversity of one group in a different way than that of other groups. Quite deviant from the RCC also in this study, was the increase of shredders in mid-stream zone (inundated area). The increase in the shredder guild in the inundated area would be attributed to the transient blocking of Tokwe River at Tokwe-Mukosi Dam wall

prior to completion which mimicked flooding. The temporary blocking of the water was a strategy to wade off local villagers who were resisting evacuation from the riparian area to give way for dam construction (Paradzai, pers com.). This resulted in water submerging the riparian area of the temporary holding weir. This was analogous to temporary flooding. The transient change in the abundance of shredders in this area brings in elements of the Flood Pulse Model (FPM) of Junk *et al.* (1989). The FPM hypothesize that productivity and biotic interactions in lotic systems are driven by lateral energy transfer in floodplain systems. According to this model, primary productivity in the riparian areas is increased during flooding activity when floods flash out nutrients from the river channel. When floods subside the opposite occurs as water flows back into the channel fluvial system bringing with it nutrients and particulate organic matter which results inspecies richness and abundance as shredders and collectors are favored.

These episodes of high and low water levels, the FPM insists, shape the distribution of feeding guildsin lotic systems frequently subjected to flooding. During flooding, flushing of water over the banks carries nutrients out of the channel and when flooding recedes the nutrients are taken back into the river channel thereby promoting a boom in favored feeding guilds. Shredders are one such guild which would proliferate as allochthonous resources like tree leaves and grasses are also washed back into the river channel. This may explain the slight increase in shredders in the inundated area as compared to upstream and downstream zones. This lateral and vertical connectivity between the river channel and margins thus explains the boom in shredders (Tokner *et al.*, 2000; Junk and Wantzen, 2006).

Ecological attributes
The use of ratios of scrapers to (shredders and total collectors) as a surrogate for P/R showed that the whole of Tokwe River is heterotrophic, indicating the importance of allochthonous resources in the ecology of the whole river system.

This observation is however contrary to field observations that showed that much of the inundated and downstream zones had very little riparian vegetation and that the channels are wide open, allowing sunlight to reach the water surface thereby activating autotrophy by promoting periphyton growth.

The predominance of heterotrophy over autotrophic production could be attributed to extensive pollution by livestock waste that tend to promote high abundance of collectors over scrappers (Masese *et al.*, 2014). The riparian area of Tokwe River is grazing area and cattle wastes are a common sight (pers. Field observ). Masese *et al.*(2014) also observe more heterotrophy in a potentially autotrophic river system in the Kenyan highland streams and attributes it to cattle and human waste in the riparian areas of the rivers.

The low riparian integrity observed in this study as depicted by the low CPOM/FPOM ratio indicates a non-functioning riparian zone as the shredder population was largely depleted. Human interference with the riparian zone has been cited by some authors as the major contributing factor to a non-functional riparian zone (Masese *et al.*, 2014).

Removal of indigenous vegetation for agricultural purposes depletes the allochthonous resources to a river and hence reduces shredder abundances (Minaya *et al.,* 2013).Agricultural activities like gardening and field crop farming are common along Tokwe River and could be a cause of the non-functional riparian zone. However the high channel stability points to availability of suitable substrates like bedrocks, boulders, cobbles, large woody debris that could provide stable substrates for filter feeding and scrapping hence the high filter FFG frequency obtained in this study.

The high predator/prey ratio (P/P > 0.2) obtained in this study shows a strong top-down control along the entire long profile of Tokwe River. This indicates an overburden of the ecosystem by predators (Cummins *et al.*, 2005). The predator overburden was more pronounced in the upstream environment.

The most abundant predators collected in this study were the odonates (Gomphidae and Libellulidae) and there was a general increase of odonates with altitude (unpublished data of this research). The increase in Odonata with altitude is attributed to more vegetation in the headwaters of Tokwe River (unpublished data of this research). Adult Odonata use vegetation as hunting ground for food (prey) (Koneri *et al.,* 2017), for perching and resting positions especially for the less mobile species (Acquah-Lamptey *et al.,* 2013) and for provision of shade (Hofmann and Mason, 2005).

Overall, the FFG ratios provided evidence of widespread human influences in Tokwe River in the form of removal of vegetation, livestock grazing, gardening and crop farming. This also indicates the extent to which Tokwe River ecosystem function is impaired.

Conclusion

In the present study, has shown that whilst the distribution of feeding guilds do not conform to the RCC, much of the distribution can be explained by the HPM which is also slightly modified by aspects of the Flood Pulse model. The FFG ratios obtained in the study offered some insights into the overall functioning of Tokwe river system and reflected a shift from autotrophy to heterotrophy which can be attributed to changing land use and clearing of riparian vegetation. The study thus shows the effect of riparian disturbances on macro invertebrate community and ecosystem function and how functional ecosystems can be impaired by anthropogenic activities. It is thus important that feature watershed management practices limit or reduce the ecosystem damage on Tokwe River.

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