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To cite this article: Trevor Dube, Lizan DeNecker, Johan H.J. van Vuren, Victor Wepener, Nico J. Smit & Luc Brendonck (2017) Spatial and temporal variation of invertebrate community structure in flood-controlled tropical floodplain wetlands, *Journal of Freshwater Ecology*, 32:1, 1-15, DOI: [10.1080/02705060.2016.1230562](https://doi.org/10.1080/02705060.2016.1230562)

To link to this article: <https://doi.org/10.1080/02705060.2016.1230562>



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Published online: 20 Sep 2016.



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Spatial and temporal variation of invertebrate community structure in flood-controlled tropical floodplain wetlands

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ABSTRACT

The Phongolo floodplain in South Africa is a unique system because of its biodiversity and socio-economic value. The spatial and temporal changes of invertebrate communities of the downstream floodplain influenced by controlled flooding from an upstream dam are poorly understood. The study investigated the spatial and temporal changes in community assemblage of macroinvertebrates and zooplankton in the permanent wetlands (pans) of the Phongolo floodplain in relation to controlled flooding. This was achieved by sampling during the dry period (September) and after controlled release of water (December). Although controlled flooding did not coincide with significant changes in the taxon diversity of macroinvertebrates and zooplankton, macroinvertebrate regional taxa richness (γ -diversity) was relatively higher in the period coinciding with controlled flood (December) compared to the dry period. For zooplankton, regional taxa diversity was similar in both periods. The average local taxa richness (α -diversity) was higher after the controlled flooding period for both macroinvertebrates and zooplankton. Spatial species turnover (β -diversity) was lower after the controlled flooding period suggesting the homogenization of aquatic communities through flooding. The community pattern of macroinvertebrates, but not of zooplankton, significantly changed after the controlled flooding period. The most important local environmental variables determining the distribution of both macroinvertebrates and zooplankton were macrophyte cover and dissolved oxygen. As the invertebrate diversity in this unique floodplain is at least partly dependent on release of water from the dam, future management schemes aimed to meet irrigation demands for agriculture should always consider flooding of the precious floodplain wetlands to maintain ecosystem integrity.

ARTICLE HISTORY

Received 4 April 2016
Accepted 12 July 2016

KEYWORDS



Regulated flow; diversity; pans; Phongolo floodplain

Introduction

Floodplain wetlands are among the most diverse and productive freshwater ecosystems on the planet (Kingsford 2000; Rosenberg et al. 2000). Despite their invaluable ecosystem functions, a decline in wetland aquatic biodiversity has been observed that is mainly driven by changes in land

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use and climate (Verhoeven et al. 2006; Palmer et al. 2008). In addition to these, river floodplain ecosystems are also threatened by the alteration of flow regimes through construction of dams (Dynesius & Nilsson 1994; Tockner et al. 2010).

The construction of dams across rivers is important to supply water for agriculture, industrial and domestic needs. However, such construction tends to alter the natural hydrologic regimes of rivers (Dynesius & Nilsson 1994; Wouter et al. 2006). The regulation of river flow through dam construction often reduces rivers to single thread channels (Ward & Stanford 1995; Ward 1998; Amoros & Bornette 2002). A result is loss of lateral hydrological connectivity between the river and associated floodplain (Ward & Stanford 1995; Ward et al. 2002). The lateral hydrological connectivity of the floodplain to the river is important in maintaining the ecological functioning and integrity of the floodplain habitat (Junk et al. 1989).

The Phongolo floodplain is the most important floodplain system in South Africa with high ecological and socio-economic importance of which part is protected by the Ndumo Game Reserve (NGR), known as a hotspot of biodiversity (Dube et al. 2015). The NGR was declared a RAMSAR site in 1997 due to its unique wetlands that are locally known as pans. The connectivity of these floodplain wetlands to the Phongolo River is dependent on flow volumes in the river which are regulated by the Pongolapoort Dam (Figure 1) that was constructed 52 years ago. There has been a shift of seasonal flow in the Phongolo River from one annual peak (December–March), coinciding with the rain period, to one with a second peak due to controlled flooding in October (Dube et al. 2015). During the dry period, the Phongolo floodplain wetlands are disconnected from the river due to low base flow. This change in flooding pattern has a possible impact on the structure and functioning of the floodplain wetlands by influencing both volume and timing of flow, but so far no detailed information is known on the structure and temporal patterns of invertebrate floodplain wetland communities in relation to river flooding.

The aim of this study was to assess the spatial and temporal changes in biodiversity patterns of macroinvertebrates and zooplankton in the permanent wetlands of the Phongolo floodplain in relation to controlled flooding. To achieve this objective, we compared species richness and composition during the dry period (September) and after controlled flooding (December). We expected changes in invertebrate community patterns from the dry to the period after controlled flooding due to changes in the life cycle patterns of insects. We predicted an increase in local (wetland) and regional (Phongolo floodplain) diversity in the period after controlled flow release from Pongolapoort Dam due to increased productivity through the enrichment of wetlands with nutrients and organic matter from river water. We also hypothesized that controlled flooding acts as a homogenizing force, thereby decreasing β -diversity among floodplain wetlands after the flooding period (Tockner et al. 1999). We also predicted to what extent temporal changes in macroinvertebrate and zooplankton community structures could be explained by local environmental factors.

Methods

Study area

This study was conducted in the Phongolo floodplain located between latitudes 26° 90' and 27° 25' E and longitudes 32° 00' 32° 20' S (Figure 1). The floodplain has an estimated area of about 13,000 ha at full inundation (Heeg & Breen 1982; Rossouw 1985). The floodplain extends to the confluence of the Phongolo and Usuthu Rivers in the NGR up to the border with Mozambique.

The flow of the Phongolo River is gauged below and above the dam. The gauging station below the dam was installed in 2000, well after the dam was constructed. The monthly flow records at the closest upstream gauging station upstream of the dam indicate that the Phongolo River flow is naturally seasonal (Figure 2). The major portion of flow (70% of total) occurs during the wet period from December to March, with greatest discharge (17.5%) in February. Lowest flow occurs from June to September accounting for almost 10% of the flow. The

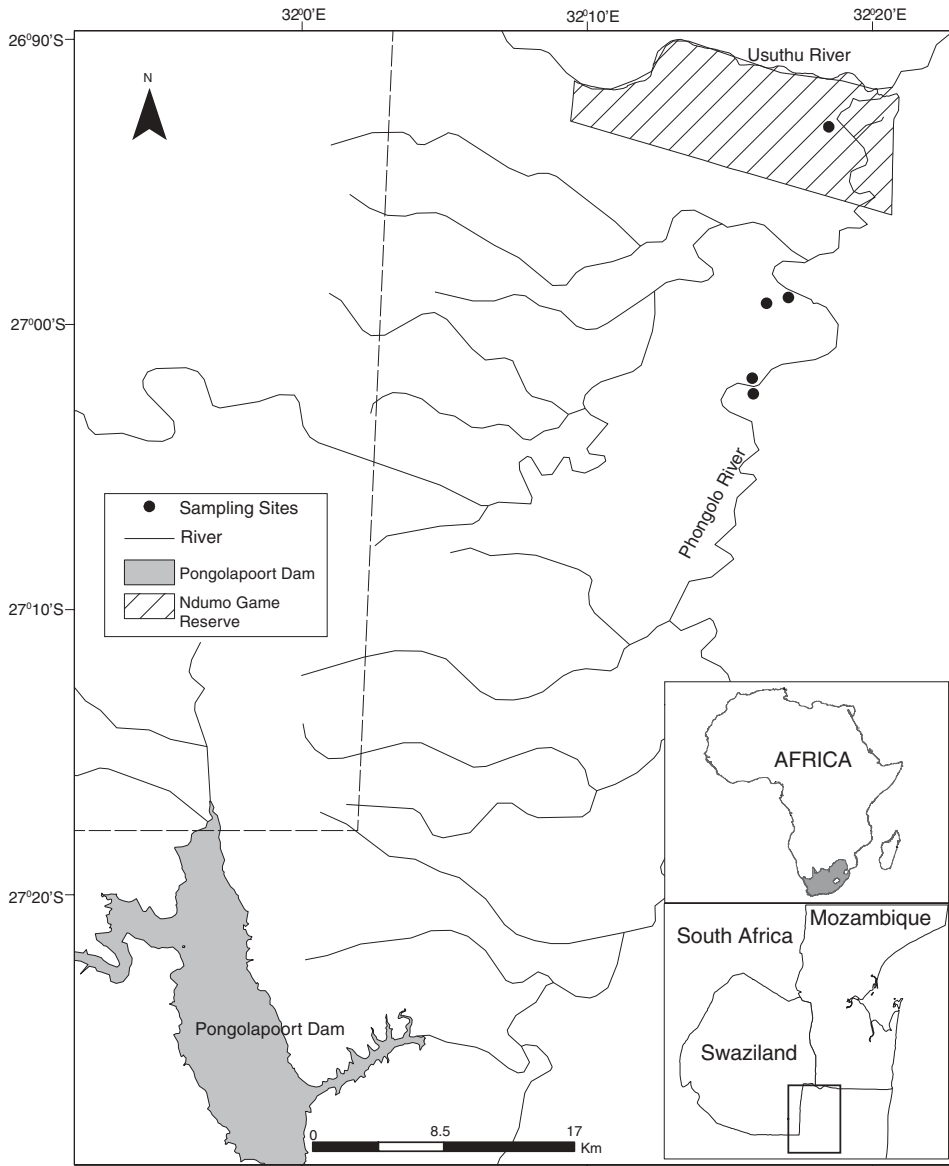


Figure 1. Study area showing the location of the Pongolapoort Dam and sampling locations in the Phongolo floodplain.

construction of the Pongolapoort Dam has altered the natural seasonal flow, which is reflected by differences in discharge at the height of the peak wet period downstream (modified flows) and upstream (historical flows) of the dam.

Sampling design

The spatial and temporal changes in macroinvertebrate and zooplankton communities were assessed by sampling five floodplain wetlands during the dry period (September 2014) and after controlled flooding (December 2014). Both sampling campaigns took place before the start of the rain period. The five selected permanent wetland pans are connected with the Phongolo River when flooding

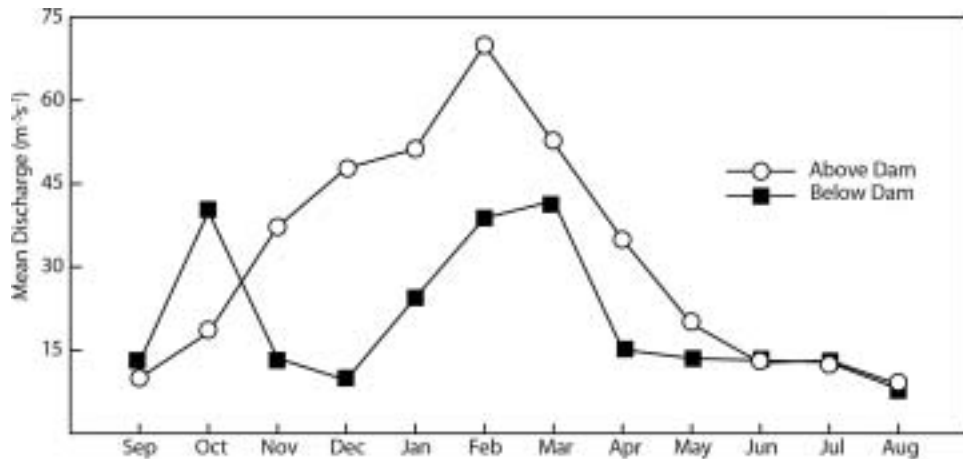


Figure 2. Mean monthly flow of the Phongolo River for the period 1929–1976 above the dam (open circles) and for the period 1983–2013 below the dam (closed squares) (Dube et al. 2015).

occurs. These sites were selected on the basis of their accessibility and permission to sample by local authorities. The wetlands in this study are generally shallow with an average depth of less than 2 m.

Morphometric and water quality measurements

The location of each wetland was geo-referenced using a handheld GPS (eTrex 30) and its surface area delineated using ArcGis version 10.2.2. Dissolved oxygen and temperature were measured directly in the wetlands while conductivity and pH were measured in a depth integrated sample with a handheld combo meter (8602 IP67). Nutrient concentrations were assessed in the laboratory using the standard spectrophotometric methods (with a Spectroquant Pharo 100) for each nutrient (with reference to standard method shown in parentheses): ammonia (14,752), nitrate (14,773), nitrite (14,776), orthophosphate (14,848), total phosphate (14,543) and total nitrogen (14,763). The total percentage cover of macrophytes was assessed by visual estimates for four categories (emergent, submerged, floating and marginal) on a scale: 0, 1%–25%, 26%–50%, 51%–75%, 76%–95% and 96%–100%.

Macroinvertebrates were collected by sweeping a 500 μm D-frame net 20 times across different habitats (i.e. open water, submerged vegetation and emergent vegetation). This semi-quantitative method allowed direct comparisons across sites and sampling surveys (September and December). The collected samples were preserved in 5% buffered formalin stained with Bengal Rose Dye. All macroinvertebrates were sorted from detritus under a stereo microscope (Olympus SZX12) at 90 \times magnification and stored in 70% ethanol.

Zooplankton was collected by filtering at least 80 L of water collected from different habitats in the wetlands through a 64 μm mesh. The filtrate was concentrated to 30 mL and preserved in 70% ethanol stained with Bengal Rose Dye. In the laboratory, subsamples of 5 mL were examined for species presence. Counting was done under a stereo microscope (Olympus SZX12) at 90 \times up to at least 300 individuals were encountered in a sample (Ohman & Lavaniegos 2002). An additional subsample was examined where necessary.

Data analyses

We computed three macroinvertebrates and zooplankton diversity indices for each wetland during the dry period and after controlled flooding. The first index is regional or gamma diversity (γ) which

measures the total number of species encountered at each sampling moment. The second diversity index is the local or alpha diversity (α), which determines the average number of taxa per wetland. The third diversity index is the taxon turnover or beta diversity calculated by $\beta = [(\gamma/\alpha_{av}) - 1]/[(N - 1)] \times 100$, where α_{av} = mean α -diversity and N = number of sampled habitats each time (Harrison et al. 1992). The β index is a modification of Whittakers' β_w (Whittaker 1960) and reflects the extent by which regional diversity (here during each survey) exceeds the mean diversity of its constituent samples (Harrison et al. 1992). It varies between 0 (complete similarity; all regional species occur in all habitats) and 100 (complete dissimilarity, each species occurring in a single habitat). The β index is less dependent on the number of sampling sites than other common turnover measures (Harrison et al. 1992; Blackburn & Gaston 1996). We then tested the local diversity in the wetlands before and after controlled flooding using a parametric paired t -test. Diversity data were normally distributed ($p > 0.05$) as tested using Shapiro–Wilk test.

Similarities in macroinvertebrate and zooplankton assemblages during the dry period and after controlled flooding were examined using non-metric dimensional scaling (nMDS) ordination based on Bray–Curtis dissimilarity matrices of Hellinger transformed presence/absence data. Significant differences between the two sampling occasions were identified using one-way analysis of similarity (ANOSIM) with up to 999 permutations.

To determine the possible relations between environmental variables, a centred and standardized principal component analysis (PCA) was performed (Legendre & Legendre 1998). All local environmental variables were log transformed before analysis except for pH. Nitrites were excluded from the analysis since readings after controlled flooding were below detection limits ($<0.01 \text{ mg L}^{-1}$). Most water quality variables were not normally distributed (Shapiro–Wilk test; $p < 0.05$), and therefore the water quality variables in the dry period and after controlled flooding were compared using a non-parametric Wilcoxon rank sum test. To relate community structure with local environmental variables, we used multivariate statistics. The macroinvertebrate and zooplankton presence–absence data were first Hellinger transformed (Legendre & Gallagher 2001). Redundancy analysis (RDA) was performed to isolate the important local variables that explain the macroinvertebrate and zooplankton community structure at each moment. This was done through a stepwise forward selection procedure based on Akaike Information Criteria (AIC) and p values from 999 Monte Carlo permutation test. A PCA based on sites and predictor variables was used to visualize the effects of the explanatory variables on the zooplankton and macroinvertebrate community structure. Species were added as supplementary variables. The analysis was conducted in R free software (R Core Team 2015) version 3.1.0, using the packages: ade4, vegan and packfor.

Results

Macroinvertebrate diversity patterns

Regional diversity in floodplain wetlands was higher after the period coinciding with controlled flood release from the dam (77 taxa) compared to the dry period (62 taxa; Figure 3). Similarly, there was a non-significant trend of a higher alpha diversity after controlled flooding (35.2 ± 3.70) compared to the dry period (26.2 ± 7.05 ; paired t -test, $p = 0.11$). Taxon turnover in space (β -diversity) was slightly higher during the dry period ($\beta = 34.16$) compared to the period coinciding with controlled flooding ($\beta = 29.69$). The list of encountered taxa during the dry period and after controlled flooding is presented in Table S1 as supplementary material.

Macroinvertebrate taxon composition

There was a significant difference in taxonomic composition of macroinvertebrates during the dry period and after the period coinciding with controlled flooding (ANOSIM, Global $R = 0.34$, $p =$

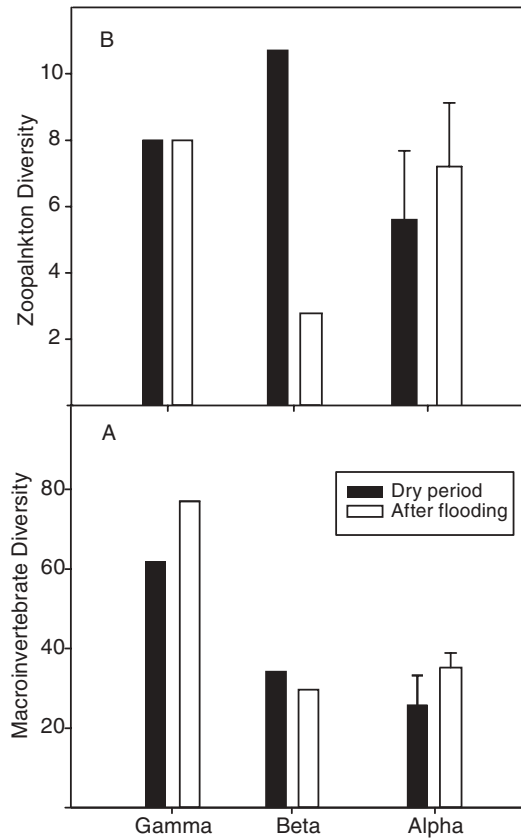


Figure 3. The taxa diversity of (A) macroinvertebrates and (B) zooplankton in floodplain wetlands collected in the dry period (September) and after controlled flooding (December).

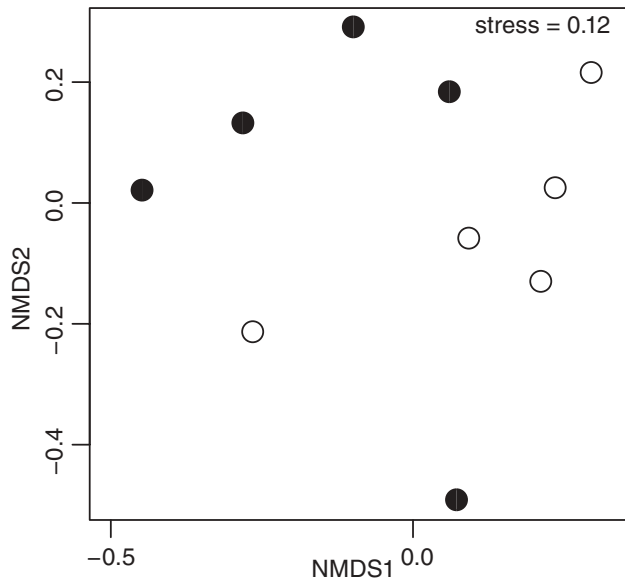


Figure 4. nMDS ordination on the Bray–Curtis matrix of Hellinger transformed presence–absence data of macroinvertebrate samples collected in the floodplain wetlands in the dry period (closed circle) and after controlled flooding (open circle).

0.04), as clearly reflected in the nMDS ordination which separated the assemblages during the dry period (September) and after controlled flooding (December; Figure 4). The taxa (e.g. *Caridina nilotica*, *Tarebia granifera*, *Agraptocorixa* sp., *Cloeon* sp., *Procloeon* sp. and Tanipodinae) contributed more than 50% of the difference between the two inundations. The abundances of Hemiptera (e.g. *Anisops* sp., *Agraptocorixa* sp., *Appasus* sp.) and Odonata (*Enallagma* sp.) were important in separating the dry period and after controlled flooding assemblages. The most abundant taxa after controlled flooding period were *C. nilotica* (22.06%), while *Cloeon* sp., *Procloeon* sp. and Tanipodinae were equally abundant (18%). Other insects that were abundant after the controlled flooding period are Coleoptera (e.g. *Pseudobagous* sp., *Derovatellus* sp., *Hyphydrus* sp., *Laccobius* sp., *Stenolophus* sp., *Hydrochus* sp., *Regimbartia* sp., *Spercheus* sp., *Hydrocanthus* sp.), Ephemeroptera (*Caenis* sp.), Hemiptera (e.g. *Limnogeton fiebrii*, *Limnogonus* sp., *Naboandelus africanus*, *Neogerris severini*, *Marcocoris* sp., *Nychia limpida*), Odonata (e.g. *Agriocnemis* sp., *Ictinogomphus ferox*, *Diplacodes lefebrii*), Diptera (*Culex* sp., Tabanidae, Taniponidae), Mollusca (e.g. *Lanistes ovum*, *Bulinus forskalii*, *Neritina pulligera*, *Burnupia* sp.) and Decapoda (*Malaya*). During the dry period, the taxa with high abundance were *T. granifera* (20.78%) and *C. nilotica* (18%).

Zooplankton diversity patterns and taxon composition

Regional taxa diversity was the same (eight taxa) during the dry period and after controlled flooding period. Species were represented by Cladocera (e.g. *Diaphanosozoma peramatum*, *Ceriodaphnia rigaudi*, *Macrothrix propinqua*, *Moina micrura*, *Alona* sp., *Chydorus sphaericus*, *Simocephalus vetulus*, *Bosmina longirostris*, calanoids and cyclopoids). Alpha diversity was generally higher after controlled flooding period (7.2 ± 1.93) compared to the dry period (5.6 ± 0.93) but the difference was not significant (paired *t*-test, $p = 0.404$). Zooplankton taxon turnover in space (β -diversity) was very low during the dry period ($\beta = 10.70$) and after ($\beta = 2.78$) controlled flooding (Figure 3). The zooplankton composition during the dry period and after flooding was also very similar (Global

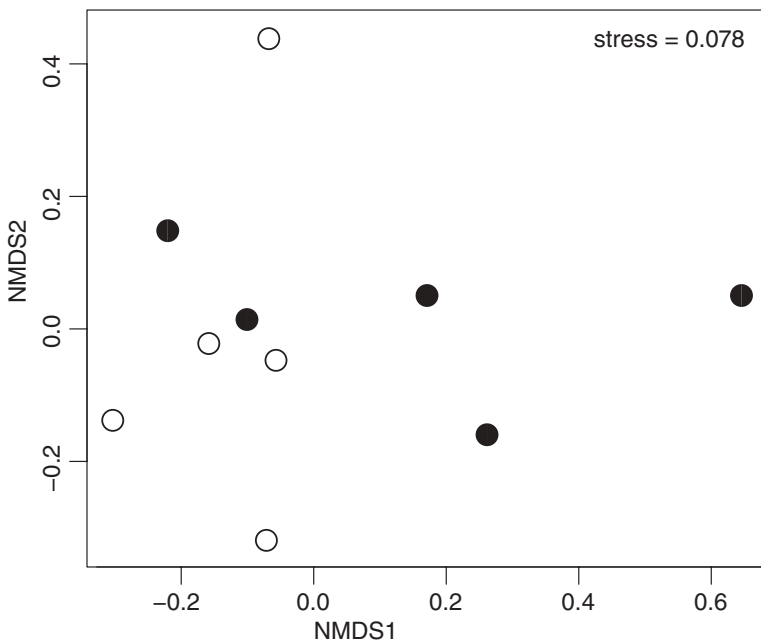


Figure 5. nMDS ordination on the Bray–Curtis matrix of Hellinger transformed presence–absence data of zooplankton samples collected in the floodplain wetlands in the dry period (closed circle) and after controlled flooding (open circle).

Table 1. Mean (\pm SD) of environmental variables in floodplain wetlands in the dry period and after controlled inundation.

Water quality variable	Before	After	<i>p</i> value
Dissolved oxygen (mg L^{-1})	4.6 (1.23)	7.6 (1.18)	0.0625
Conductivity ($\mu\text{S cm}^{-1}$)	2765 (2873)	1049 (1383)	0.0625
Temperature ($^{\circ}\text{C}$)	25.94 (2.08)	28.29 (2.16)	0.312
pH	7.8 (0.6)	7.4 (0.36)	0.312
Orthophosphate (mg L^{-1})	0.7 (1.34)	0.24 (0.05)	0.587
Total nitrogen (mg L^{-1})	6.72 (3.33)	2.9 (1.33)	0.0625
Ammonia (mg L^{-1})	0.192 (0.13)	0.17 (0.13)	0.813
Macrophytes (%)	38 (17.67)	43 (20.91)	0.345

$R = 0.04$, $p = 0.29$), as also reflected in the nMDS ordination, which did not separate the zooplankton assemblages into dry period (September) and after controlled flooding period (December) groupings (Figure 5).

Environmental variables

The comparison of environmental variables during the dry period and after controlled flooding is summarized in Table 1 and Figure 6. The first two PCA axes explained 59.7% of total variation of the environmental characteristics. The second PCA axis separated the environmental variables in

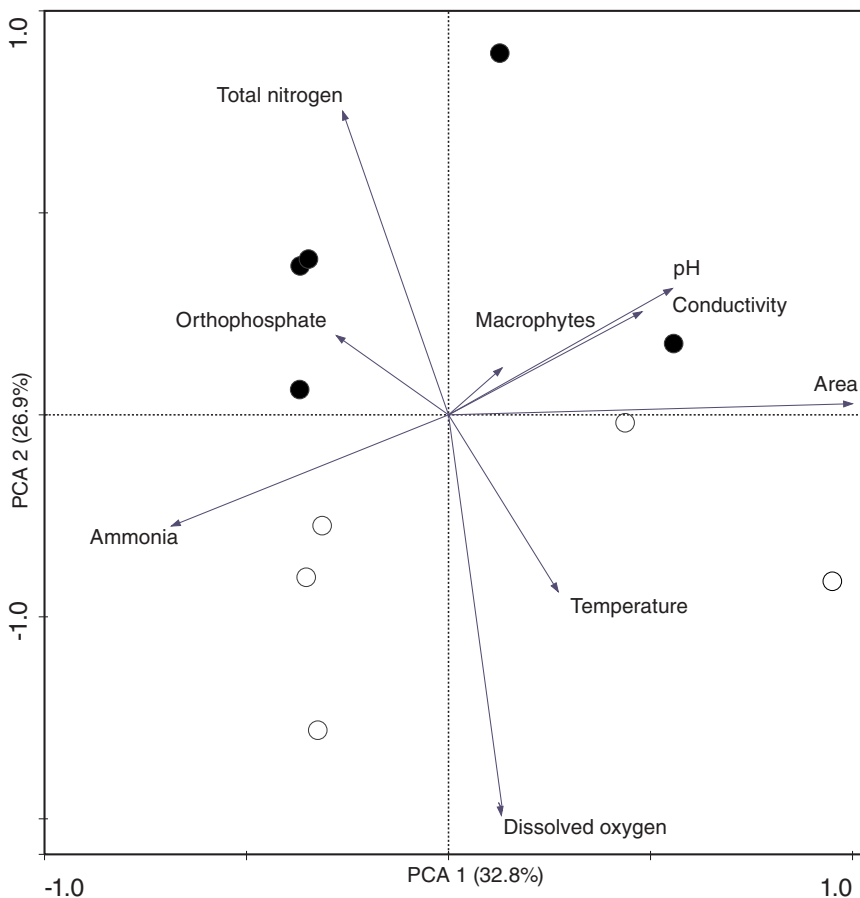


Figure 6. PCA ordination biplot of environmental variables in floodplain wetlands in the dry period (closed circles) and after (open circles) controlled flooding.

Table 2. Results of RDA analyses with forward selection of environmental variables explaining the assemblage of macroinvertebrates and zooplankton in Phongolo floodplain.

Macroinvertebrates	df	AIC	F	p value
Macrophyte cover	2	-4.4671	1.3173	0.025*
Dissolved oxygen	1	-3.8564	1.6443	0.005**
Zooplankton				
Ammonia	1	-16.084	8.7919	0.02*
Conductivity	1	-16.169	8.7094	0.015*
Surface area	1	-15.66	9.2158	0.015*
Macrophyte cover	2	-14.259	6.6774	0.015*
pH	1	-15.517	9.3634	0.01**
Total nitrogen	1	-15.261	9.6322	0.01**
Dissolved oxygen	1	-13.72	11.4031	0.005**

** $p < 0.01$; * $p < 0.05$.

the dry period (open circles) and after controlled flooding (closed circle; Figure 6). There were no significant differences in the environmental variables during the dry period and after controlled flooding (Table 1). The water quality variables (conductivity and pH) and surface area were positively correlated ($r > 0.5$) on the first axis while the nutrients (total nitrogen, orthophosphate and ammonium) were negatively correlated. Dissolved oxygen levels in the wetlands were generally higher after controlled flooding (7.6 ± 1.18) mg L⁻¹ but not significantly different from the dry period (4.6 ± 1.23) mg L⁻¹ (Wilcoxon test, $p = 0.06$). The temperature was higher after the flooding period (28.29 ± 2.16 °C) but not significantly different (25.94 ± 2.08 °C) from pre-flooded conditions in the dry period. The nutrient levels were relatively higher in the dry period though the difference was not significant Wilcoxon test, $p > 0.05$ (Table 1). The same pattern was observed with conductivity levels which were generally higher in the dry period. Conductivity values were very high specifically in the site inside NGR on both sampling occasions.

There was a significant effect of local environmental variables on the macroinvertebrate community assemblages ($F = 1.39$, $p = 0.03$) and they explained 25.9% of the variation in the composition of macroinvertebrates. Macrophyte cover and dissolved oxygen emerged as the most important local explanatory variables (Table 2). Some genera (e.g. *Naucoris* sp., *Agraptocorixia* sp., *Sigara* sp. and *Anisops* sp.) preferred open water as indicated by their dominance in the site with less vegetation cover on both sampling occasions (Figure 7). Similarly, there was a significant effect of local factors on zooplankton community assemblage ($F = 7.94$ and $p = 0.003$) that explained 86% of the variation in zooplankton community composition. Dissolved oxygen, total nitrogen and pH were highly significant explanatory variables (Table 2). *S. vetulus*, *B. longirostris*, *M. propinqua*, *C. rigaudi*, *C. sphaericus* and *D. peramatum* occurred in wetlands with high vegetation cover and far less in the site which had less macrophytes (Figure 8); on both sampling occasions, *M. micrura* and *Alona* sp. were more abundant specifically in the site inside NGR with high conductivity.

Discussion

To determine the spatial and temporal variation in water quality, invertebrate diversity and community structure in a socio-economically valuable South African floodplain system, we monitored floodplain wetlands (pans) in the dry period (September) and after a period of controlled flooding (December). There was a significant change in the macroinvertebrate but not the zooplankton community composition after the flooding period. After controlled flooding, macroinvertebrate taxa richness increased in the floodplain pans which could not be explained by concurrent changes in water quality.

The Phongolo floodplain wetlands were organically enriched by large herds of wildlife grazing in the fertile vegetation of the dry pans in NGR or by livestock grazing outside the NGR. Flooding of the wetlands by incoming river water (i.e. after the controlled flood period) had a diluting effect as reflected by relatively lower nutrient levels and conductivity values. The dilution effect of river water

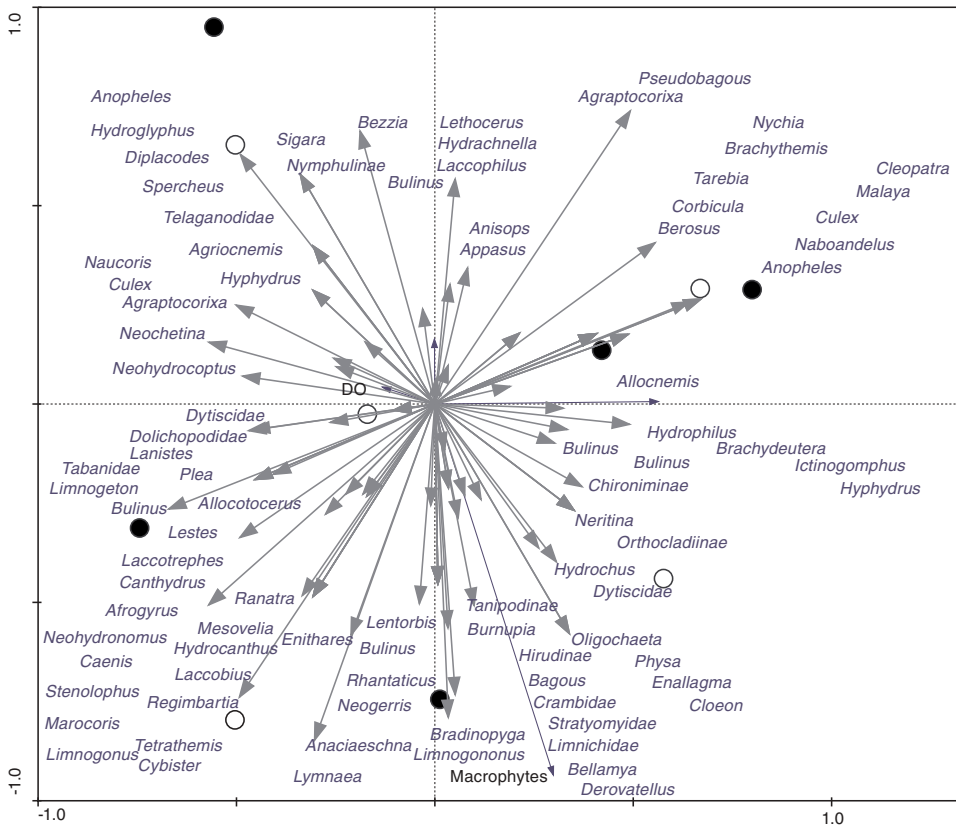


Figure 7. PCA ordination diagram visualizing the relation between the important explanatory variables and the zooplankton community structure in the floodplain wetlands in the dry period (closed circles) and after (open circles) controlled flooding.

on floodplain water is to a large extent dependent on the timing, duration and magnitude of flooding (Weilhoefer et al. 2008; Agostinho et al. 2009).

The release of water from the Pongolapoort Dam introduced an additional flood into all studied permanent wetlands in the floodplain. The period of controlled flooding coincided with a significant change in the macroinvertebrate assemblages having higher average taxon richness (α -diversity) compared to the dry period before flooding. This increase in wetland taxon richness was to a large extent due to additions of mainly insect species. Some riverine species (e.g. *C. nilotica*) probably entered the floodplain wetlands with inflowing river water. Winged insects (e.g. *Derovatellus* sp., *Hyphydrus* sp., *Hydrochus* sp., *Regimbartia* sp., *Spercheus* sp., *Hydrocanthus* sp., *Caenis* sp. and *Culex* sp.) may have survived higher velocity of the flooding river by finding shelter in the floodplain (Gray 1981; Lytle 1999).

There was a tendency of increased temperature and oxygen values after the flooding period. Values, however, were not significantly different from the dry period and hence could not entirely explain the observed changes in macroinvertebrate communities. The observed changes in insect communities from the dry period to the period coinciding with the controlled flooding could also be explained by temporal variation in the life history strategies of some of the species. For example, *C. nilotica* release their larvae early before the wet period peak flows as a life history adaptation to increase survival of their young (Hancock & Bunn 1997), which could explain their higher abundance in this study after controlled flooding. In order to get more insights on the temporal taxon changes associated with controlled flooding, there is a need to verify our results with data collected during the natural rainfall period.

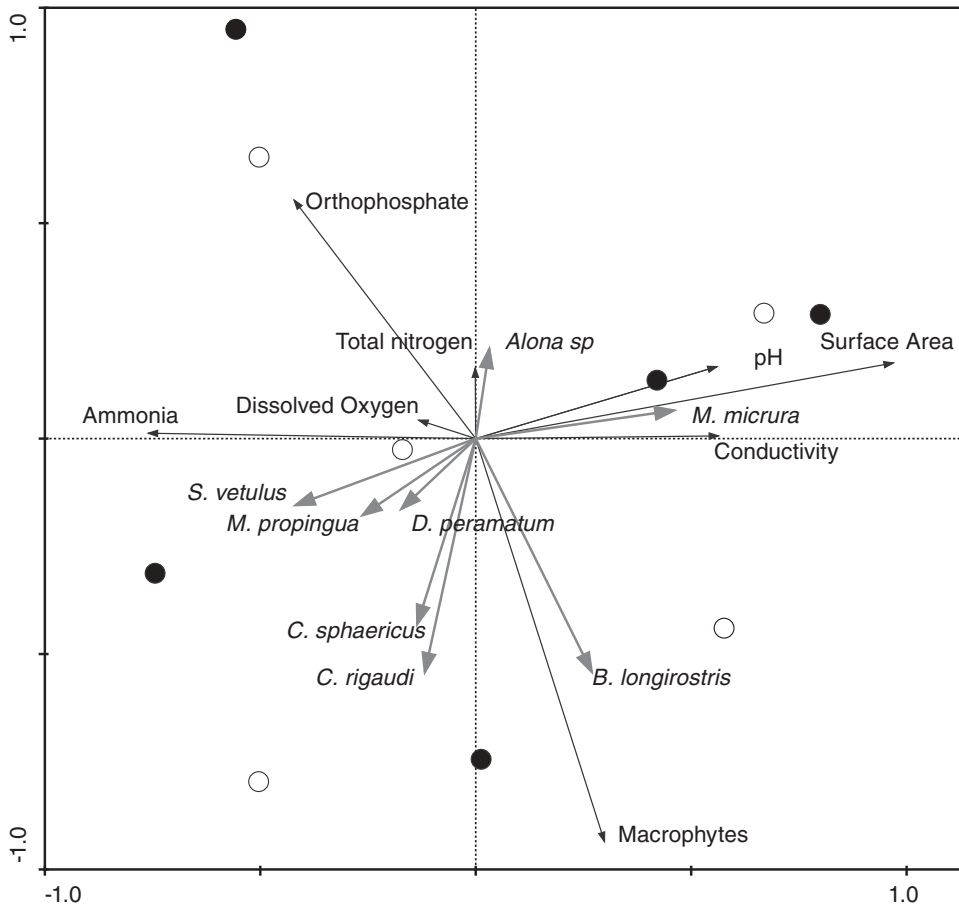


Figure 8. PCA ordination diagram visualizing the relation between the explanatory variables and the macroinvertebrate community structure in the floodplain wetlands in the dry period (closed circles) and after (open circles) controlled flooding.

In contrast to macroinvertebrates, the zooplankton community structure did not significantly change from the dry period to the period after controlled flooding. Zooplankton are generally efficient passive overland dispersers especially over small scales (Havel & Shurin 2004; Padial et al. 2014). They produce dormant resting eggs that are accumulated in a persistent egg bank (Brendonck & De Meester 2003) which increases their likelihood of dispersal by wind and animal vectors (Waterkeyn et al. 2010; Vanschoenwinkel et al. 2011). The Phongolo floodplain wetlands provide ecosystem goods (e.g. fish, water for domestic purposes and livestock) to the local community. In the process, there is a high possibility of unintentional transport of resting eggs from one wetland to another, thereby homogenizing the zooplankton community (Waterkeyn et al. 2010). As dispersal of zooplankton among lakes separated by short spatial scales (<10 km) has been shown to be rapid (Havel & Shurin 2004), we also expect it to be an important process in our study region, with studied wetlands usually less than 10 km apart (except for the wetland inside NGR; Figure 1).

Macrophyte cover in this study was not related to flooding of wetlands as there were no significant differences between sampling events. Macrophytes cover, however, significantly explained macroinvertebrate and zooplankton community patterns on both sampling occasions. As we only monitored percentage plant cover, it is however still possible that biomass was different between both sampling moments and at least partly explained the higher macroinvertebrate richness after the flooding period. After flooding, we noticed a dominance of marginal aquatic plant communities

(e.g. *Cyperus fastigiatus*, *Echinochloa pyramidalis*, *Phragmites* sp.) that are common in the Phongolo floodplain (Furness & Breen 1980). During the dry period, there was a dominance of submerged vegetation such as *Potamogeton crispus* and *Najas* sp. Such structural differences add to habitat heterogeneity that is important in the structuring of macroinvertebrate and zooplankton communities. Macrophytes not only provide shelter, but also influence invertebrate community composition by generating better habitat conditions through the production of dissolved oxygen, and by providing attachment and oviposition sites (Ságová-Marecková & Kvet 2002; Declerck et al. 2007; Maia-Barbosa et al. 2008). Macrophytes also promote aquatic invertebrates by reducing predation pressure from visual predators such as fish and other invertebrates (Diehl 1995). Other insect groups such as the Hemiptera (e.g. *Naucoris*, *Agraptocorixia*, *Sigara* and *Anisops*) prefer open water (Bloechl et al. 2010; Mereta et al. 2012). In our study, these taxa were also more abundant in less vegetated wetlands.

In our study, the assessment of temporal changes in macroinvertebrate and zooplankton community assemblages was limited to the permanent floodplain pans that are flooded by riverine connection. Unfortunately, there are no permanently isolated floodplain pans that are inundated by surface run-off only in our study area, as they could have acted as a control and allowed to correct for temporal variation in species composition uncoupled from flooding.

Management and conservation implications

There was a change in water quality (mainly diluting effects of the river) and the macroinvertebrate diversity and community structure of the permanent wetlands after a period of controlled flooding of the Phongolo floodplain. Flooding of the wetlands coincided with an increase in macroinvertebrate taxon richness. The taxa encountered in this study are furthermore of least concern according to the IUCN Red List of Threatened Species (www.iucnredlist.org).

The function of zooplankton and macroinvertebrates as a food source in the food web structure (Medeiros & Arthington 2008) is crucial to higher trophic feeders especially birds that are unique to this floodplain (Whittington et al. 2013) and fish that are a source of protein to the local communities (Coetzee et al. 2015). Therefore, effective fisheries management and biodiversity conservation in the Phongolo floodplain should account for fish-invertebrate and resource-invertebrate linkages. The current controlled flooding pattern of Phongolo floodplain is mainly meant to satisfy the community water needs who are dependent on the goods and services from the floodplain. The prioritization of flow should be flexible to allow for biodiversity conservation of invertebrates, fish, birds and reptiles (Merron et al. 1993; Whittington et al. 2013; Calverley & Downs 2014) in the Phongolo floodplain. Long-term monitoring of biodiversity in the floodplain wetlands is needed to properly evaluate and formulate recommendations on the effects of controlled flow on the temporal changes in biodiversity and ecosystem characteristics in the Phongolo floodplain.

Acknowledgments

This work was supported by funding from Flemish Interuniversity Council (VLIR-OUS) (TEAM project ZEIN21013PR396), Water Research Commission (WRC) of South Africa (Project K5-2185, N.J. Smit, PI) and KU Leuven Interfaculty Council for Development Cooperation (IRO). Special thanks to the Zoology Department, University of Johannesburg, for the laboratory facilities for nutrient analysis, sorting and identification of macroinvertebrates. Ezemvelo KZN Wildlife is thanked for research permit number OP 1787/2013 and staff at Ndumo Game Reserve for fieldwork logistic support.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

Flemish Interuniversity Council (VLIR-OUS TEAM) [project number ZEIN21013PR396]; Water Research Commission (WRC) of South Africa [project number K5-2185]; KU Leuven Interfaculty Council for Development Cooperation (IRO) (Contract 000000030548).

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