Article

Aquatic invertebrate community structure of selected endorheic wetlands (pans) in South Africa

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Received 22 August 2014; accepted 8 February 2016; published 1 June 2016

Abstract

Shallow wetlands, such as pans, are not well studied in South Africa, even though they perform many important functions, such as providing an important food source for migratory birds and habitat to highly specialized fauna. Aquatic invertebrate diversity, abundance, and water quality in pans were analysed seasonally from 3 provinces in South Africa with contrasting climates. Univariate and multivariate statistics were used to assess similarities in aquatic invertebrate communities and water chemistry among pans. Pans inundated for extended periods had greater aquatic invertebrate diversity, and several of these taxa were not adapted to the temporary environment common to pans. The subtropical region had greater aquatic macroinvertebrate diversity than semiarid regions due to more rainfall per annum in the subtropical region. Water temperature was a major driving factor for diversity, with greater diversity occurring in warmer seasons. High water hardness and salinity were found to drive decreased diversity and encourage the presence of hardy and more tolerant species. Understanding the importance of these aforementioned factors (i.e., pan longevity, temperature, water hardness, and salinity) influencing aquatic invertebrate biodiversity in pans provides a baseline for future studies and impact assessments on these important and understudied systems.

Key words: aquatic invertebrates, diversity, pans, seasonal variation, South Africa, spatial variation, wetlands

Introduction

Endorheic pans are defined as natural shallow depressions that receive water during the rainy season, have no outlets, and usually dry up seasonally due to evaporation (Geldenhuys 1982). These systems have characteristics not found in palustrine and lacustrine systems. For a system to be classified as endorheic it must be circular, oval, kidney-shaped, or lobed, have a flat basin floor, be <3 m deep when fully inundated, and have a closed drainage (Duthie 1999). Endorheic pans play an integral role in the hydrologic cycle and in biodiversity as important habitats for waterfowl, especially migratory birds (Allan 1987). With each inundation, considerable changes occur in the physical and chemical properties of pans (Allan et al. 1995). High evaporation rates and air temperatures during the dry season contribute to high salinity and extreme changes in water quality of pans during each inundation; a site may start as a freshwater system during the wet season and progress toward a saline system during the drier season (Meintjies et al. 1994, Duthie 1999). Pans act as sinks, accumulating and storing any natural or anthropogenic substances flowing into them and are therefore threatened by agricultural and mining drainage, anthropogenic pollution, eutrophication, exotic species, cultivation, road construction, mineral extraction, and groundwater pumping (Rodriguez-Rodriguez 2007). The longevity of endorheic pans depends on the amount of water entering at inundation, soil permeability, and other meteorological conditions (e.g., temperature and humidity). These factors make it difficult to create a baseline ecological integrity study on pans. Recent interest

DOI: 10.5268/IW-6.3.783

in opencast coal mining in the Mpumalanga Lake District has raised concerns about serious negative impacts on pans because acid mine drainage is a major hazard associated with mining that severely impacts water sources and associated fauna (McCarthy et al. 2007).

Although studies have been conducted on a variety of wetlands worldwide (Whiles and Goldowitz 2005, Dallas 2008, Bird 2010), few have focused on endorheic pans and even fewer on pans in South Africa. Most information on South African pans arises from studies by Hutchinson et al. (1932) on 2 pans in the Transvaal (Mpumalanga) region. Although the macroinvertebrate fauna associated with temporary systems has been studied (Jocque et al. 2006, Studinski and Grubbs 2007, De Klerk and Wepener 2013), information about their biogeographic distribution is lacking. Distribution of aquatic invertebrates is, however, known globally for better-studied systems such as rivers (Buschke et al. 2010, Eady et al. 2013, Watson and Dallas 2013). Macroinvertebrate diversity in pans is high (Studinski and Grubbs 2007), with most organisms being opportunistic and having specialized adaptations to survive periods of drying that may occur numerous times throughout the year (Day et al. 2009). These invertebrates play an integral role in the food chain of pans and are especially important as the primary food source for many waterfowl (Allan 1987). A variety of crustaceans and insects are also well represented in temporary wetlands, and not all insects permanently reside in these habitats but migrate from more permanent nearby waterbodies (Day et al. 2009). In contrast to the freshwater pans, salt pans in South Africa have low macroinvertebrate species diversity, and no fauna are exclusively confined to saline pans (Seaman et al. 1991).

The aim of this study was to investigate the diversity and community structure of invertebrates living within endorheic pans in 3 provinces in South Africa. An additional aim was to investigate the environmental variables responsible for the specific diversity in endorheic pans. The hypothesis was that spatial variation occurs in water quality and aquatic invertebrate biodiversity in pans across provinces and among seasons within each province.

Materials and methods

Study area

Three surveys of 19 pans were conducted across 3 provinces in South Africa; Mpumalanga, North West, and Free State were sampled during winter (survey 1: May 2012), summer (survey 2: Dec 2012–Jan 2013), and autumn (survey 3: Mar–Apr 2013; Fig. 1). Sites were sampled during each season when possible, but because pans are so reliant on rainfall, it was not possible to sample each site during every season, particularly in drier regions of the Free State and North West provinces. Only one site was selected for sampling in the Free State (FS N), sampled once during summer and once during autumn (FS N-2 and FS N-3, respectively). Six sites were selected in the North West (NW) for sampling (A, B, E, F, I, and J), 4 sampled only once during summer (NW A-2, NW B-2, NW E-2, NW J-2); one sampled twice, once during winter (NW F-1) and once during summer (NW F-2); and only one site sampled during all 3 surveys (NW I-1, NW I-2, and NW I-3). In Mpumalanga (MP), 12 sites were selected for sampling (MP A, B, C, D, E, F, G, H, I, J, Q, and R), 3 sampled only once. One of these sites was sampled during summer (MP F-1) and the other 2 (MP Q-3 and MP R-3) during autumn; the remaining 9 pans were sampled in all seasons.

Water quality

One water sample was collected at each site in a prewashed 2 L polypropylene bottle during each survey. Samples were stored at −4 °C in a mobile freezer, transported to the laboratory at the University of Johannesburg, and kept frozen until analysed with a Merck Spectroquant Pharo 100 Spectrophotometer (Merck KGaA 2007). The unfiltered samples were analysed for the following chemical variables: NO_3^- (NO_3-N), NO_2^- (NO_2-N), SO_4^{2-}, NH_4^+ (NH_4-N), Cl^-, total hardness, and orthophosphates (PO_4-P) using standard protocols of the test kits. In addition, samples were analysed for calcium (Ca), potassium (K), sodium (Na), magnesium (Mg), and total alkalinity by a South African National Accreditation System accredited laboratory using inductively coupled plasma-atomic emission spectrometry (ICP-AES) and following EPA Method 200.7 for the determination of metals and trace elements in water and wastes.

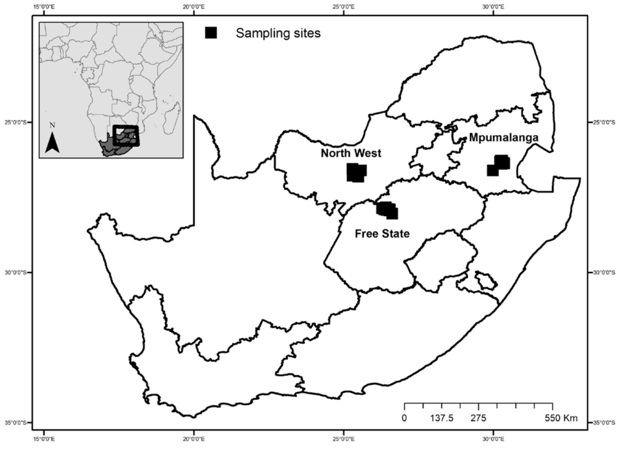

Fig. 1. Republic of South Africa showing the provinces and locations of sampling sites.

DOI: 10.5268/IW-6.3.783

Table 1. Number of taxa, number of individuals, means, and standard deviations for macroinvertebrate data collected from selected pans across 3 South African provinces.

Province	Number of taxa (min–max)	Mean	SD	Number of individuals (min–max)	Mean	SD
Free State	10–15	12	±3.5	830–1348	1089	±366.3
North West	4–19	9.3	±4.5	407–14 681	2957.1	±4553.8
Mpumalanga	6–26	15	±5.3	781–34 786	7159.5	±8505.8

Aquatic invertebrate analysis

Zooplankton samples were collected from pans on each sampling date using a 63 µm mesh plankton net (60 × 60 cm). Samples were collected by submerging the net or placing it as deep as possible and towing for a distance of 10–12 m. Light traps were also placed underwater in pans at dusk and removed early the next morning. Benthic invertebrates were collected from each site for each survey using the "kick-stir-sweep" method adapted from the South African Scoring System (SASS) 5 protocol (Dickens and Graham 2002) with a standard 500 µm mesh sweep net (30 × 30 cm). The net was swept through the water and vegetation (if present) for a distance of ~2 m. Benthic invertebrates and zooplankton samples were fixed with 5% neutral buffered formalin and stained with Rose Bengal vital dye. In the laboratory, samples were placed in a 63 µm mesh sieve, washed under flowing tap water, preserved in 70% ethanol, and counted and identified to the lowest possible taxonomic level (Appendix A). Aquatic invertebrates and zooplankton were identified using Guides to Freshwater Aquatic Invertebrates of Southern Africa (Day et al. 1999, 2001a, 2001b, 2003, Day and de Moor 2002a, 2002b, de Moor et al. 2003a, 2003b, Stals and de Moor 2008).

Statistical analysis

Statistical analyses were used to examine spatial or temporal variation in invertebrate communities among the various sites. Primer v6 (Clarke and Gorley 2006) was used to conduct univariate diversity indices and nonmetric multidimensional scaling (nMDS). Margalef's index, which accounts for sample size and effort, was used to calculate species richness; Pielou's evenness index was used to determine overall evenness; and Shannon-Wiener diversity index was used to integrate both species richness and equitability components (Clarke and Warwick 1994). These various univariate indices were used to describe species abundance relationships, diversity, and evenness among invertebrate communities across sampling sites.

A Bray-Curtis similarity matrix composed of aquatic invertebrate data for each site was used in a 2-dimensional nMDS, which grouped sites based on invertebrate communities (Clarke and Warwick 1994). These groupings were then tested for significance using the analysis of similarities (ANOSIM) procedure with *a priori* groupings by province that provides a Global R value (range 0 to 1; Clarke and Gorley 2006). Values close to 1 (≥ 0.5) indicate substantial differences whereas values close to 0 (<0.5) indicate substantial similarity. Macroinvertebrate data were log transformed prior to analysis to eliminate the effect of dominant taxa (Malherbe et al. 2010).

Canoco 5 (Ter Braak and Šmilauer 2012) was used for the ordination analysis to determine differences between sampling sites as well as the environmental variables responsible for the differences between site groupings (Van den Brink et al. 2003, Šmilauer and Lepš 2014). Redundancy analysis (RDA) was based on invertebrate community composition for each sampling occasion, and water quality data obtained from the various sites for each sampling occasion were used as explanatory variables (Van den Brink et al. 2003, Malherbe et al 2010). A Monte Carlo permutation test was used to determine if the site groupings of the RDA were significant ($P < 0.05$; Van den Brink et al. 2003). Macroinvertebrate data were log transformed before the analysis to eliminate the effect of dominant taxa skewing the results.

Results

Both number of taxa and number of individuals (Table 1) in the Free State pan were lower during the summer (10 and 830, respectively) than during the autumn (15 and 1348, respectively). The same trend was seen in the other 2 provinces. The number of taxa in North West pans ranged from 4 (summer) to 19 (autumn) taxa per pan, and number of individuals per pan ranged from 407 (summer) to 14 681 (autumn). The number of taxa in Mpumalanga pans ranged from 6 (summer) to 26 (autumn), and the number of individuals per pan ranged from 781 (summer) to 34 786 (autumn; Table 1).

Species richness in the Free State was greater in autumn (1.94) than summer (1.34). Species richness in the North West ranged from 0.36 to 2.93, with the most (NW I-3) and least (NW J-2) species rich sites occurring in this province (Fig. 2a). Mpumalanga was the most species-rich province across all seasons with a range of 0.75 (MP J-2) to 2.89 (MP I-3). The site with the highest species

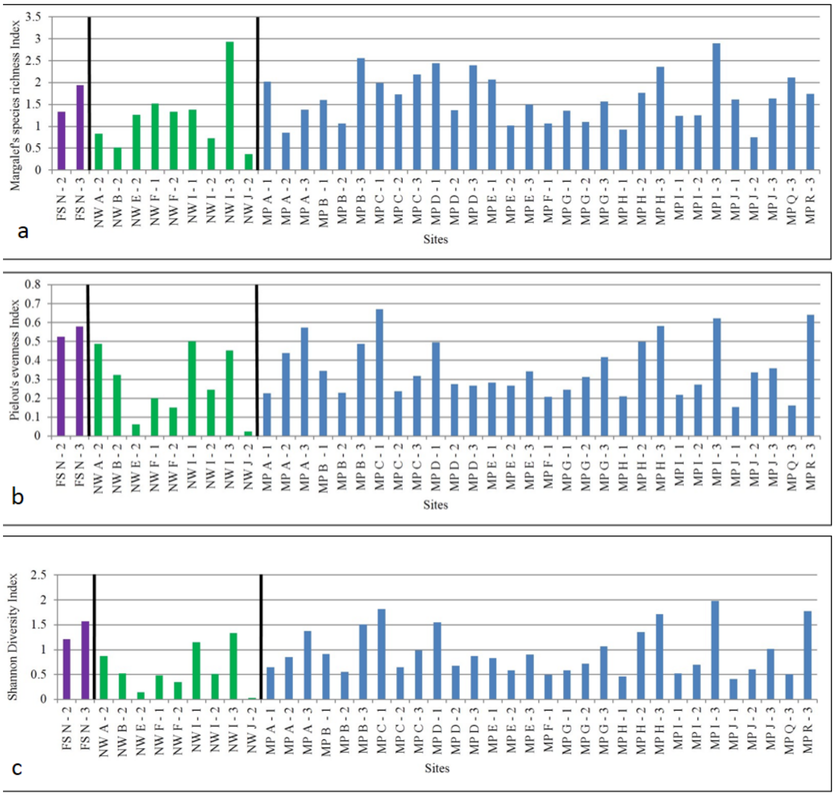

Fig. 2. Univariate indices for aquatic invertebrates sampled from each site, Republic of South Africa, during surveys over 3 seasons (1-winter, 2-summer, and 3-autumn). (a) Margalef's species richness index; (b) Pielou's evenness index; (c) Shannon's diversity index. Province abbreviations: FS = Free State, NW = North West, MP = Mpumalanga. Letters following provinces denote sample sites (pans).

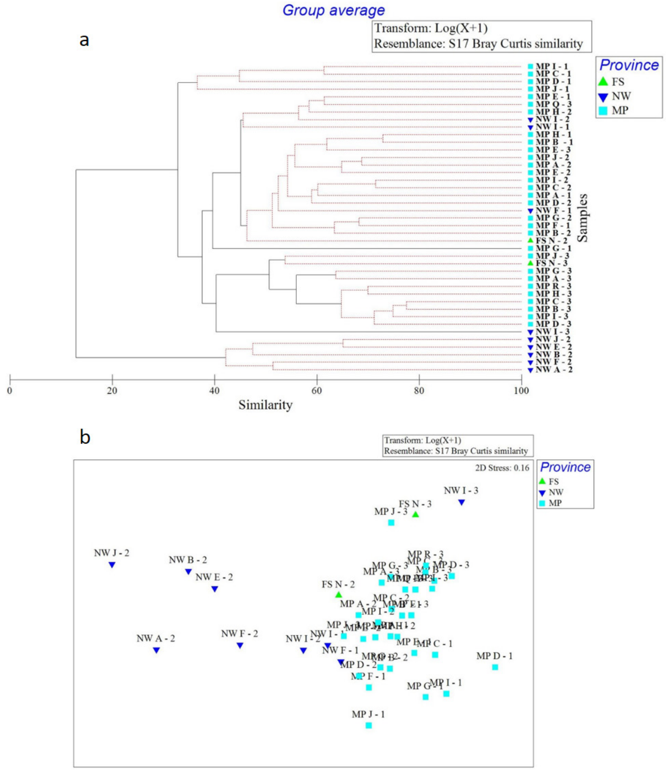

Fig. 3. (a) Hierarchical cluster and (b) nMDS plots were drawn based on the Bray Curtis similarity matrix of the aquatic invertebrates sampled from Free State (FS), North West (NW), and Mpumalanga (MP) provinces, Republic of South Africa. Site and season abbreviations as in Figure 2.

richness, NW I during autumn, was an outlier for the North West Province and was more typical of Mpumalanga Province pans.

The single study site in the Free State had similar evenness scores in summer (0.53) and autumn (0.58; Fig. 2b). Evenness in the North West ranged from 0.02 (NW J-2) to 0.50 (NW I-1). Evenness in Mpumalanga pans ranged from 0.15 to 0.67, with both the highest (MP C-1) and lowest (MP J-1) evenness found during winter. Mpumalanga was also the province with the most even distribution compared to the other provinces throughout the study.

The Shannon index showed that diversity in the Free State was similar between summer (1.21) and winter (1.57), whereas the highest and lowest diversity in the North West occurred in the same pan and ranged from 0.03 (NW I-2) to 1.33 (NW I-3; Fig. 2c). Diversity in Mpumalanga ranged from 0.40 (MP J-1) to 1.98 (MP I-3). Invertebrate diversity among all provinces was highest in Mpumalanga pans and lowest in North West pans across all seasons and sites. Throughout the study, diversity followed a seasonal trend at the majority of sampling sites, decreasing toward the hot, dry summer and increasing toward the cooler, wet autumn.

Three groups of aquatic invertebrates were differentiated at 40% similarity in the hierarchical cluster plots according to province (Fig. 3a), and the nMDS plots confirmed these groupings at a stress level of 0.16 (Fig. 3b). The 2 largest groupings were formed by sites from North West and Mpumalanga, but these groupings were formed at a low similarity (20–30%). All sites begin to group separately at higher similarity percentages, indicating differences in aquatic invertebrate community structure between sites. The ANOSIM analysis for significance indicated these groupings were significant (Global $R = 0.585$).

A clear pattern also emerged when samples were ordinated by sampling season (Fig. 4a). Three clusters formed that represent the 3 sampling seasons; ANOSIM, however, indicated that sampling season was not significantly different (Global $R = 0.339$). At a similarity of 40%, autumn samples in Mpumalanga grouped separately, whereas the majority of North West summer survey sites grouped separately from the other pans (Fig. 4b). Pans from all 3 provinces grouped together in winter. This grouping at 40% similarity was also highly significant (Global $R = 0.775$) according to the ANOSIM analysis.

The RDA tri-plot (explaining 28.18% of total variation) for similarities and dissimilarities of invertebrate communities and water quality parameters among sites in all 3 provinces and seasons indicated both spatial and temporal variation (Fig. 5). Separation along the first axis (explaining 18.67% of total variation) occurred as the 3 sampling seasons separated from one another. Temperature was a major influence in the separation because most of the Mpumalanga sites from the autumn sampling period grouped together on the right, whereas most of the North West sites sampled during the summer period clustered on the left. This grouping was also due to 3 invertebrate species sampled only in the North West: brine shrimp (*Artemiidae*), fairy shrimp (*Streptocephalus*), and *Branchiopodopsis* sp. Sites higher in invertebrate diversity and abundance separated from those with lower diversity and abundance, which was driven by differences in pH and salinity. Separation along the second axis (explaining 9.51% of total variation) was associated with invertebrate community structure and water chemistry. Sites located lower on axis 2 had different invertebrate community structures than sites located higher on axis 2 because of differences in water chemistry, notably salt content. The Mpumalanga sites separated into 2 groups based on seasonal differences. Most sites clustered in the lower right section of the tri-plot were sampled during autumn, whereas sites clustered in the upper left section of the tri-plot were sampled during winter and summer. The North West sites mostly clustered in the lower left section of the tri-plot due to similar invertebrate communities as well as temperature and water chemistry.

The RDA tri-plot (Fig. 6) for Free State and North West pans based on macroinvertebrate communities and water quality parameters explained 56.53% of total data variation. Free State and North West sites did not separate much from one another due to similarities in water chemistry and invertebrate community structures. Slight separation on the first axis (explaining 32.56% of data variation) was largely due to differences in invertebrate community structure and, to a lesser extent, water chemistry. Mg, Ca, and total hardness were major drivers on the first axis indicating that sites farther to the right of the first axis consisted of harder water than those on the left of the axis. On the second axis (explaining 23.97% of data variation), separation occurred based mostly on season as well as water quality parameters, with temperature and phosphates acting as major driving factors. North West sites separated into 2 groups, the summer sampling period and the winter period. Differences in temperature resulted separation of invertebrate community structures along the second axis.

Seasonal relationships among pans with respect to aquatic invertebrate community structure and water chemistry in Mpumalanga are shown in an RDA tri-plot explaining 36.43 of all data variation (Fig. 7). Separation between sites in Mpumalanga occurred according to invertebrate community structure shown on the first axis

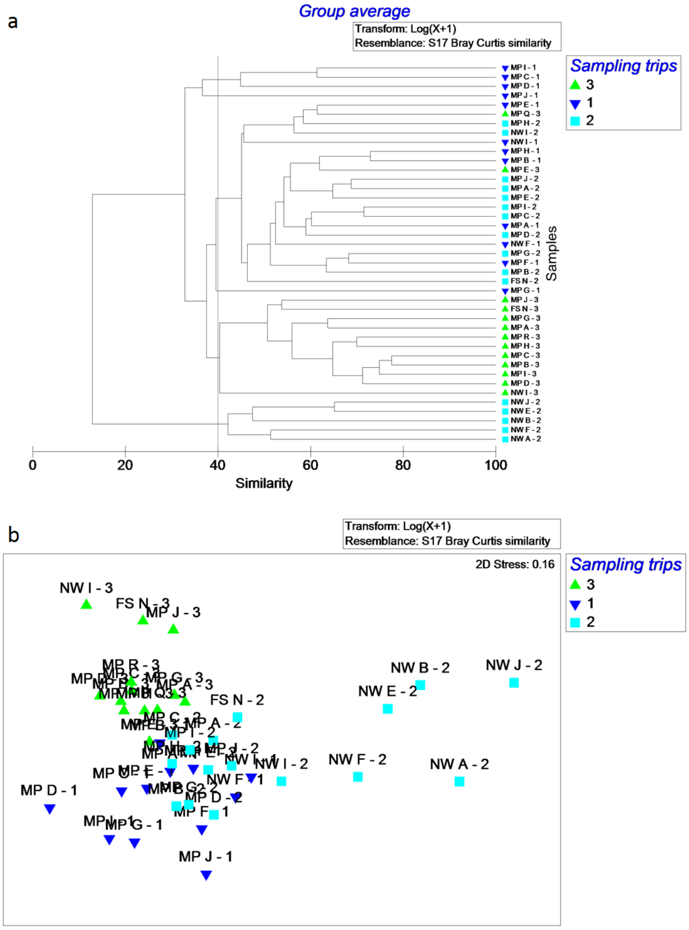

Fig. 4. (a) Hierarchical cluster and (b) nMDS plots based on Bray Curtis similarity matrix of aquatic invertebrates sampled from pans, Republic of South Africa, during (1) winter, (2) summer, (3) and autumn. Province and site abbreviations as in Figure 2.

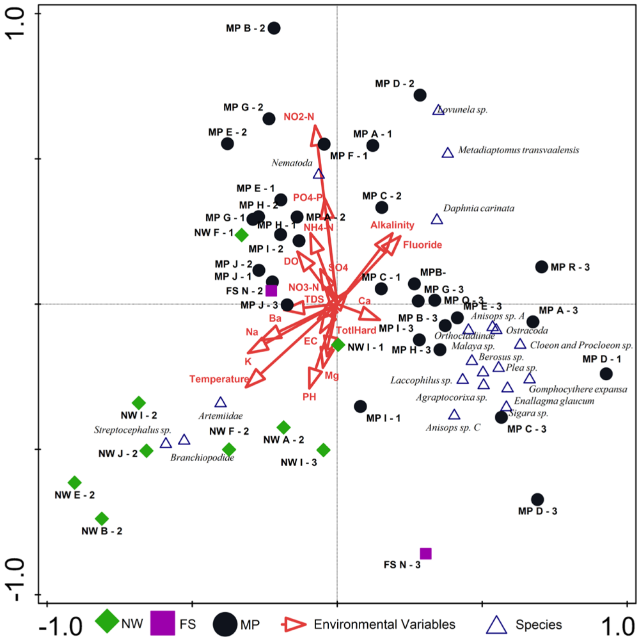

Fig. 5. Redundancy analysis (RDA) tri-plot of the relationship among seasons, aquatic invertebrates and physicochemical variables. The tri-plot explains 28.18% of all variation, with 18.67% explained on the first axis and 9.51% on the second axis. Site and season abbreviations as in Figure 2.

DOI: 10.5268/IW-6.3.783

(explaining 23.52% of data variation) and water quality parameters on the second axis (explaining 12.91% of data variation). Seasonal separation in invertebrate communities is evidenced by most of the sites sampled during autumn clustered together on the right, with different invertebrate assemblages than sites sampled in summer and winter on the left. Separation along the second axis is primarily associated with physicochemical parameters with water temperature acting as a key driving factor. Most of the sites located high on the second axis were sampled during winter (MP C-1, MP D-1, MP E-1, MP H-1, MP I-1, and MP J-1), whereas the remaining sites were sampled in either autumn or summer when water temperatures were much higher.

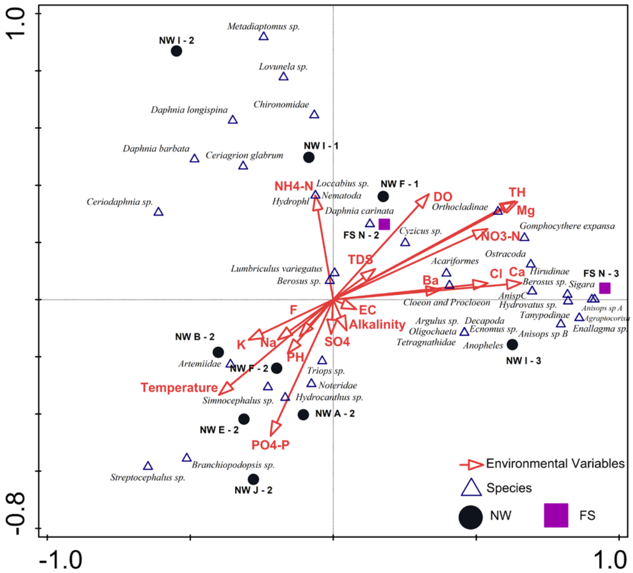

Fig. 6. RDA tri-plot of similarities between Free State and North West provinces based on aquatic invertebrates and physicochemical variables. The tri-plot explains 56.53% of all variation with 32.56% explained on the first axis and 23.97% on the second axis. Province, site and season abbreviations as in Figure 2.

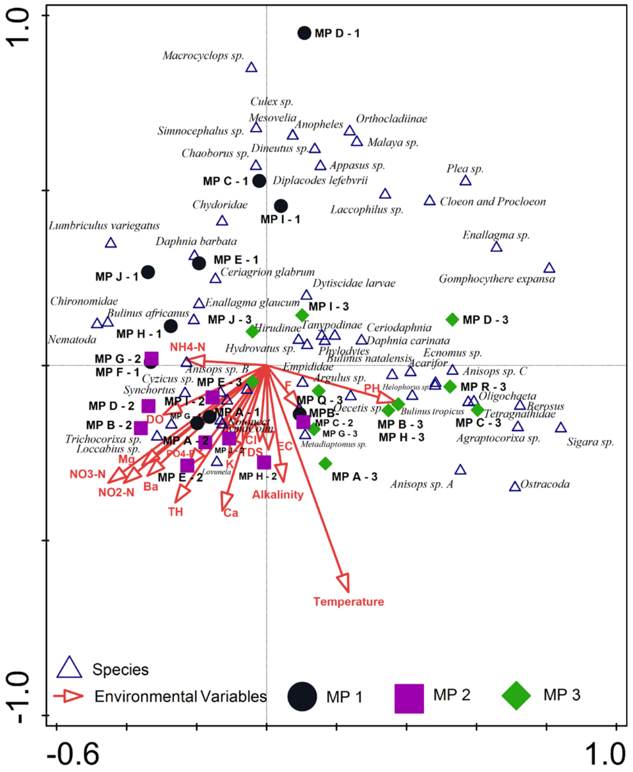

Fig. 7. RDA tri-plot of similarities among seasons, aquatic invertebrates, and physicochemical variables from Mpumalanga sites. The tri-plot explains 36.43% of all variation with 23.52% explained on the first axis and 12.91% on the second axis.

Discussion

Aquatic organisms in South Africa have adapted to high daily and seasonal fluctuations in rainfall due to the country's semiarid climate with uneven rainfall distribution both unpredictable and variable (Minshall et al. 1985, DWAF 1994). Many environmental factors naturally affect aquatic invertebrate distributions including geography, habitat size, depth, permanence, food availability, and water chemistry (Hutchinson et al. 1932, Ferreira 2010). Change in water temperature is considered one of the more important driving factors for seasonal variation in aquatic invertebrate community structure and function (Eady et al. 2013). Salinity has a less significant effect on invertebrate community structure because of substantial similarities in biota of fresh and inland saline waters (Williams 1998); however, salinity does negatively impact taxa diversity and abundance (Hammer 1986). Studies conducted by Hammer (1986), Seaman et al. (1991), and Ferreira (2010) indicated no distinct separation between invertebrate communities found in saline and freshwater environments. Examples include highly tolerant freshwater taxa such as *Lovunela* sp., *Metadiaptomus* sp., several taxa of corixids (Corixidae) and notonectids (Notonectidae) found in saline aquatic environments, whereas ostracods (Ostracoda), usually regarded as "typical" saline taxa, have been known to occur in freshwater systems (Seaman et al. 1991). Only when salinity is substantially higher (i.e., >3 g/L) are there considerable differences in biota between fresh and saline systems (Hammer 1986, Williams 1998). Pans are considered the least diverse wetlands and temporary waterbodies when compared to other similar-sized systems worldwide (Lake et al. 1989, Timms and Boulton 2001). Regardless, pans can be unexpectedly diverse when considering their harsh physicochemical environments, short inundation periods, and small size (Hutchinson et al. 1932).

Univariate statistical analyses indicated seasonal variation in number of taxa, abundance, species richness, evenness distribution, and diversity, which all occur as a consequence of seasonal changes in temperature and rainfall (Water and Rivers Commission 2001). Alterations to invertebrate communities as a result of these seasonal fluctuations have been well studied in many rivers in Mpumalanga (Dallas 2004, Ferreira et al. 2009). The greatest taxa richness and number of aquatic invertebrates in all provinces occurred during colder seasons, specifically autumn, which was not unexpected because rainfall, particularly in Mpumalanga, occurs during summer, and by autumn pans are fully inundated (Ferreira 2010). With the onset of winter, rainfall decreases, evaporation increases, and pans lose water until many dry up by the end of spring. Loss of water also concentrates salts, which when high enough are known to negatively impact aquatic species diversity and biomass (Hammer 1986); therefore, as water levels decrease, the abundance and number of aquatic invertebrate taxa in pans also declines.

The 3 provinces examined in this study differed from one another on a spatial scale, with the Mpumalanga pans having the highest abundance, species richness, and diversity. This finding was expected because Mpumalanga is a subtropical region with more rainfall and less evaporation than the other provinces. Pans in Mpumalanga are thus inundated for longer periods, and studies have shown that longer inundation not only has an additive effect on taxa and number of aquatic invertebrates (Studinski and Grubbs 2007) but also leads to colonisation by species not adapted to temporary conditions (Schneider and Frost 1996). Because of the longer inundation period, however, more pans and seasonal surveys were completed in Mpumalanga, possibly influencing the observation of higher species richness. Overall, the North West sites had the least taxa and abundance, although some sites had high abundance of certain species. The North West is an extremely dry region with little rainfall and high evaporation, meaning the period of inundation is much shorter than in the other provinces. This lack of water prevents colonisation by a greater diversity of taxa, and only species with developed mechanisms to survive in the harsh and extremely temporary conditions would be successful in pans of the North West (Meintjies et al. 1994). Comparing the Free State to the other 2 provinces is difficult because only one site was sampled; however, our limited data suggest that Free State pans may have lower invertebrate abundance and diversity than Mpumalanga pans but not as low as the North West. The low number of taxa and abundance in the Free State may be attributed to higher salinity because pans with greater salinity have more specialised invertebrate species tolerant of high salt concentrations (Wolfram et al. 1999).

North West pans ordinated distinctly from Mpumalanga pans based on water temperature, salinity, and aquatic invertebrates. Temperature effects were due to seasonal variations because the North West sites that grouped together were mostly sampled during summer when water temperatures are high. Salinity also accounts for the groupings of more ephemeral pans in arid areas such as the North West, whereas pans in subtropical areas, such as Mpumalanga, are more permanent and therefore less saline (Ferreira 2010). Finally, the 3 invertebrate species found only in North West pans also contributed to the distinct ordination. Among these taxa, brine shrimp, which prefer saline conditions (Day et al. 1999), are characteristic of pans in the North West

Invertebrate assemblages in pans were expected to differ seasonally because of differences in water quality parameters. The majority of sites sampled during the same season clustered together in ordinations irrespective of province because of similar seasonal variations in water temperature and water availability. Seasonal separation of invertebrate communities occurred within each province and across the 3 provinces because of water availability and pan volume. Pans have more water during autumn whereas in summer and winter have less water or are dry. Water temperature was a driving factor for the seasonal separation of invertebrate communities. Eady et al. (2013) found that total taxon richness of invertebrates increased from winter to autumn in streams in the Western and Eastern Cape (South Africa), and Dallas (2004) found that taxa richness of invertebrates varied spatially because of temperature differences associated with latitude and climate such as between the Western Cape (temperate climate) and Mpumalanga (subtropical climate). Seasonal variations in invertebrate communities within the 3 provinces examined in this study were similar to results found by Ferreira (2010) in a study of Mpumalanga pans.

In hardwater habitats, such as in the North West and Free State, there was a reduction in taxa richness. More sensitive species were absent and more tolerant taxa increased, leading to decreased invertebrate diversity (Buss et al. 2002), evidenced by the presence of tolerant and hardy taxa such as tanypod midges (Chironomidae: Tanypodinae) and oligochaetes (Oligochaeta) commonly reported in polluted and degraded systems (Buss et al. 2002, Gerber and Gabriel 2002). Other tolerant species found in these sites in high abundance were *Gomphocythere expansa* (Ostracoda) and *Anisops* sp. (Hemiptera: Notonectidae; Gerber and Gabriel 2002, Day et al. 2009).

Important drivers of invertebrate community structure were orthophosphates and salinity. Increased orthophosphates are attributed to surface runoff because they are not present in high concentrations in groundwater (a major source of water for pans), and increased salinity indicates

DOI: 10.5268/IW-6.3.783

that these particular pans were in the process of drying, resulting in an increase in solute concentration (Dallas and Day 2004, Russell 2008). Increased salinity in these pans may also explain the presence of brine shrimp in NW B-2 and NW E-2 but not in any other sites.

Mpumalanga pans were seasonally distinct because of differences in water quality, quantity, temperature, and invertebrate community assemblages. Greater diversity of invertebrate species in autumn included species less adapted to dry conditions such as oligochaetes. These aquatic invertebrates, although hardy and cosmopolitan, cannot tolerate dry conditions and will only occur in pans inundated for an extended period of time (Day and de Moor 2002a), as would occur from summer to autumn. Salinity and nutrient concentrations are high during summer when water is scarce, whereas in autumn nutrients and salts are more dilute because of rainfall. Exhaustion of food and nutrients during winter may explain lower nutrient concentrations, resulting in lower diversity and abundance of aquatic invertebrates. Williams (1996) noted that many physicochemical factors, such as nutrient availability, in water are known to affect insect fauna. Water temperature was a major driving factor for separation of Mpumalanga pans in ordinations of physicochemical parameters because temperatures are warmer in summer and autumn than in winter. Water temperature most likely also caused differences in invertebrate community structure between warmer and colder seasons.

In this study we found that differences in water chemistry and invertebrate community structure among pans in different provinces and seasons were due to natural factors such as climate, rainfall, temperature, and inundation period. Pans inundated for extended periods of time tended to have greater diversity and abundance of invertebrates, some of which are not necessarily permanent residents of pans or specifically adapted to living in temporary or saline environments. These spatial differences between provinces were present irrespective of the sampling season. Spatial variation between sites within a specific province was most prominent in invertebrate communities and was affected by climate. Seasonal variation between sites was most apparent in water quality parameters, which also affected invertebrate community structure.

The study of temporary aquatic systems such as pans is challenging because they differ substantially in size, depth, and hydroperiod. Providing baseline information on pan fauna is therefore particularly difficult but extremely important because they are distinctive, understudied, and severely threatened systems. Many pans are influenced by local anthropogenic activities ranging from high impact opencast mining to low impact livestock agriculture. Research from this study provides vital, seriously lacking baseline information on aquatic invertebrate biodiversity and water chemistry of endorheic pans of South Africa. This information will be particularly useful in future studies and impact assessments. Results from this study also provide a better understanding of temporal and spatial variation of endorheic pan systems and will help inform decision-makers and stakeholders on the importance of these systems in terms of biodiversity. A more thorough understanding of pans in South Africa will help protect the structure and function of these threatened habitats from future impacts.

Acknowledgements

We thank and acknowledge the Water Research Commission (WRC) for funding the project (K5/2190) and the University of Johannesburg (UJ) for support and facilities that made this project possible. Further, we thank Dr. Ruan Gerber for proofreading the document and Ms. Lee-Ann Foster for her input as well as 2 anonymous reviewers for their valuable contribution.

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Supplementary information

Appendix A is available for download via the Inland Waters website, https://www.fba.org.uk/journals/index.php/IW/issue/current/showToc

DOI: 10.5268/IW-6.3.783