A comparison of mollusc diversity between the relatively pristine Marico River and the impacted Crocodile River, two major tributaries of the Limpopo River, South Africa

Mathilde Kemp[1]*, Kenné N de Kock[1], Jazelle L Zaayman[1] and Cornelius T Wolmarans[1]

[1]*Unit for Environmental Sciences and Management, Potchefstroom Campus of the North-West University, Private Bag X6001, Potchefstroom 2520, South Africa.*

ABSTRACT

A study of the freshwater mollusc diversity was conducted at selected sites in the relatively pristine Marico River and the impacted Crocodile River, the major tributaries of the Limpopo River. Four surveys were conducted, two in an early (May 2013 and 2014) and two in a late (November 2013 and 2014) low-flow period. Semi-quantitative surveys were done by sampling the vegetation, as well as the substratum, with a standard SASS net for approximately 15 min each. Environmental parameters including water temperature, electrical conductivity (EC) and pH were measured at each site. Molluscs were identified up to species level, sorted, counted, and the presence of juvenile specimens recorded. Historical data for the 1/16th degree square grids (loci), in which each of the sampling sites of the current study was located, were extracted from the National Freshwater Snail Collection at the Unit for Environmental Sciences and Management, Potchefstroom Campus of the North-West University. During this study, 20 and 9 species were recovered from the Marico and Crocodile Rivers, respectively, as compared to 13 and 12 species on record for these loci, respectively. Juvenile specimens were present during the four surveys at most of the sites. Canonical correspondence analyses were applied which revealed that biotopes, water temperature and EC played the most significant role in the distribution and abundance of species. The relatively high mollusc diversity and the fact that juveniles were present throughout the study, demonstrated that current habitat and environmental conditions were suitable to promote recruitment and the sustainability of diverse mollusc populations in the Marico River and its tributaries. However, in contrast to this, the exploitation of and habitat transformation in the Crocodile River has resulted in the decrease of biotopes which eventually could have led to the decrease in diversity and the establishment of *P. acuta*, an exotic invader species.

Keywords: freshwater molluscs, biodiversity, Marico River, Crocodile River, environmental variables

INTRODUCTION

Freshwater molluscs are the second most diverse animal phylum on earth (Lydeard et al., 2004). However, they are poorly documented, extremely threatened and have the highest number of recorded extinctions of any major taxonomic group (Lydeard et al., 2004; Vaughn and Taylor, 1999). The decline in freshwater molluscs goes unnoticed due to poor documentation and monitoring, as only a fragment of molluscan species (<2%) have had their conservation status accurately assessed (Lydeard et al., 2004; Reckendorfer et al., 2006).

Four hundred species of freshwater molluscs have been previously identified in Africa (Brown, 1994) and, according to De Kock and Wolmarans (1998), the distribution of these molluscs is primarily influenced by the availability of suitable aquatic biotopes. The association of different freshwater molluscs with specific biotopes, such as marginal and aquatic vegetation and sediment present at different water velocities and depths, is well known and documented (Brown, 1978; Brown, 1994; Dallas, 2007; Odume et al., 2015). These biotopes are under constant threat worldwide as a consequence of various anthropogenic impacts, geomorphological alterations and the changing availability of water (Wittmann, 1975; Vaughn and Taylor, 1999; Reckendorfer et al., 2006; Taylor et al. 2007; De Klerk et al., 2012; DWA, 2012).

With regard to South Africa, nearly 71% of the main rivers are considered as either endangered or critically endangered as the result of exploitation (Nel et al., 2004). The Crocodile River, which is characterised by sprawling urbanization and industrialization in the region of northern Johannesburg and Pretoria, is also under severe threat of pollution due to extensive agricultural activities, the sporadic release of water from impoundments such as the Hartbeespoort Dam, and large mining developments north of the Magaliesberg (Wittmann, 1975; Taylor et al., 2007; De Klerk et al., 2012; DWA, 2012). All of these stressors could have a detrimental effect on the aquatic ecosystems and biotope availability. In contrast, the general state of the Marico River is considered to be 'natural' to 'good', free of significant organic pollution, with a pronounced biodiversity and overall good water quality (RHP, 2005). However, the water quality of two of its major tributaries, namely, the Klein Marico River and the Sterkstroom, is defined as 'fair' to 'poor' (RHP, 2005).

Although mollusc surveys have previously been done in the Marico and Crocodile River catchment areas, (National Freshwater Snail Collection Database, North-West University, Potchefstroom Campus), limited information regarding diversity has previously been published. Furthermore, in view of the fact that the Marico River is still considered to be relatively pristine, while the Crocodile River has been subjected to ongoing exploitation and habitat transformation, it is of great importance to survey these areas in order to establish the current status of the mollusc diversity for conservation purposes.

* To whom all correspondence should be addressed.
e-mail: Hilde.kemp@nwu.ac.za
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Study area

The Marico River stretches from its source, the Marico Eye near Swartruggens, for 250 km until its confluence with the Crocodile River to form the Limpopo River. The Crocodile River, originating at Roodepoort, meanders via Hartbeespoort Dam past Thabazimbi to the Botswana border where it joins the Marico River. Nine sites in the Marico River and seven sites in the Crocodile River catchments were selected for sampling. Site selection was influenced by logistical accessibility to the rivers, availability of water and suitable biotopes (Dickens and Graham, 2002; Gerber and Gabriel, 2002; Dallas, 2007). Locations of these sites are depicted in Fig. 1 while site descriptions and aquatic biotopes are displayed in Table 1.

Sampling equipment and techniques

Four surveys were conducted, two in an early (May 2013 and 2014) and two in a late (November 2013 and 2014) low-flow period. The coordinates of each sampling site were determined with a Garmin Nuvi 500 GPS.

Semi-quantitative surveys were done by sampling the vegetation, as well as the substratum, with a standard SASS net (Dickens and Graham, 2002) for approximately 15 min each. Molluscs were collected along the margins of the rivers up to a depth of 70 cm. Aquatic vegetation and marginal vegetation were sampled by pushing the net vigorously into the vegetation and moving it backwards and forwards through the same area. Substrata of biotopes consisting mainly of mud, sand, gravel or stones were sampled by shuffling the feet whilst continuously sweeping the net

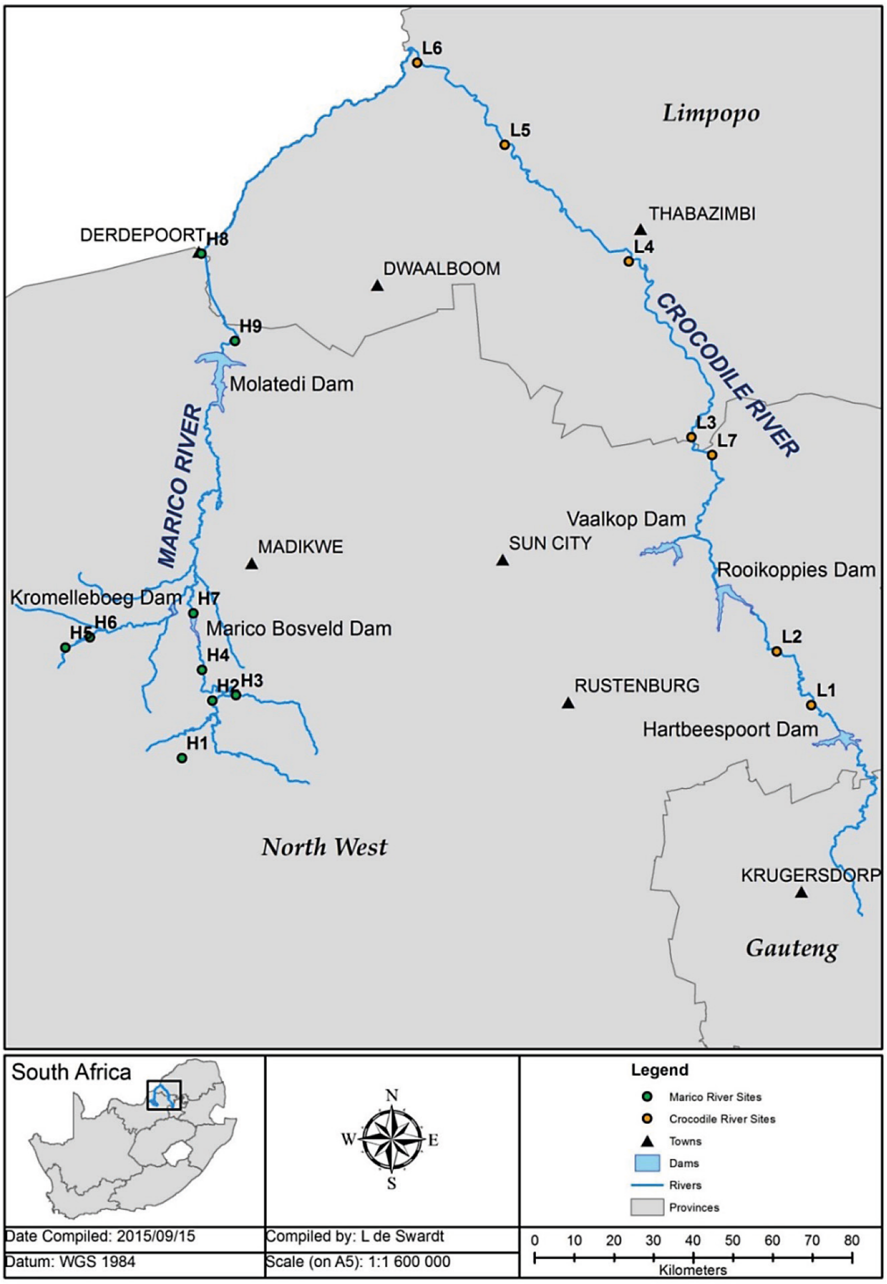

Figure 1
Map of the study area

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TABLE 1
Site location, river name and aquatic biotopes present at each site

Site, coordinates and altitude	River	Aquatic biotopes (according to Gerber and Gabriel, 2002)
Marico River		
Site H1 S 25°47′32.1 E 26°21′54.1 1 480 m	Marico Eye, source of Marico River	Abundant marginal and aquatic vegetation, pool and backwaters with stones
Site H2 S 25°39′45.1 E 26°26′01.9 1 197 m	Marico River before its confluence with Sterkstroom, 20 km downstream of the Eye	Little to no marginal vegetation, stones in current, stones out of current, riffle, run and pool.
Site H3 S 25°39′00.6 E 26°29′16.3 1 170 m	Sterkstroom 5 km before its confluence with Marico River	Little to no vegetation, bedrock, stones in current, riffle, run and pool
Site H4 S 25°35′33.4 E 26°24′39.4 1 077 m	Marico River 10 km above Marico-Bosveld Dam, after its confluence with Sterkstroom	Muddy and sandy substratum, filamentous algae, abundant marginal and aquatic vegetation, stones in current, stones out of current, riffle, run and pool
Site H5 S 25°32′31.4 E 26°06′17.3 1 150 m	Klein Marico River 5 km above Klein-Maricopoort (Bospoort) Dam	Little to no marginal and aquatic vegetation, filamentous algae, muddy substratum, riffle and run
Site H6 S 25°31′09.2 E26°09′25.1 1 135 m	Klein Marico River 1 km below Klein-Maricopoort (Bospoort) Dam	Little to no marginal and aquatic vegetation, pool with muddy substratum stones in current, riffle and run
Site H7 S 25°27′52.6 E 26°23′26.9 1 037 m	Marico River directly below Marico-Bosveld Dam	Marginal and aquatic vegetation, filamentous algae and bedrock
Site H8 S 24°39′15.9 E 26°24′28.7 914 m	Marico River at Derdepoort	Abundant marginal and aquatic vegetation, backwater with muddy and sandy substratum, filamentous algae
Site H9 S 24°50′54.2 E 26°29′07.1 926 m	Marico River 2 km below Molatedi Dam	Run with muddy substratum, bedrock, stones in current, stones out of current, riffle and pool
Crocodile River		
Site L1 S 25°40′22.1 E 27°47′25 1 104 m	Crocodile River at Brits	Marginal and aquatic vegetation, filamentous algae, riffle and run with sand and bedrock substratum, stones in current
Site L2 S 25°33′02.9 E 27°42′40.9 1 055 m	Crocodile River downstream of Brits	Run and pool with sand substratum and filamentous algae
Site L3 S 25°03′59.6 E 27°31′06.2 936 m	Crocodile River at Koedoeskop Bridge	Run and pool with muddy substratum and filamentous algae
Site L4 S 24°40′05.8 E 27°22′35.2 904 m	Crocodile River at Thabazimbi	Run and pool with sand substratum and filamentous algae
Site L5 S 24°24′16.8 E 27°05′46.7 905 m	Crocodile River downstream of Thabazimbi	Run and pool, sand substratum and filamentous algae
Site L6 S 24°13′07 E 26°53′51.6 836 m	Crocodile River at Rooibokkraal	Run and pool with sand substratum, sparse marginal and aquatic vegetation, filamentous algae
Site L S 25°06′24.7 E 27°33′55.2 956 m	Pienaars River	Run and pool with mud and clay substratum, stones in current

over the disturbed area. Contents of the net were then transferred to a rectangular plastic container (360 × 470 × 80 mm) which was filled with water from the habitat to a level of approximately 40 mm. Most of the debris was then carefully removed by hand and scrutinised for specimens that might still be attached. Thereafter the contents of the container were decanted into a cone-shaped Perlon gauze net (0.25 mm mesh) suspended on a stand. The content of the net was transferred to a plastic container with a tight-fitting lid and 90% ethanol was added to preserve the samples. The container was then labelled with relevant site information. The samples were transported to the laboratory where each sample was decanted into a rectangular Perspex sorting tray (300 × 200 × 25 mm) with a transparent bottom provided with a 10 mm square grid. All molluscs were subsequently removed under a stereomicroscope mounted on a sliding stand and identified up to species level (Walker, 1923; Connolly, 1939; Brown, 1994; Appleton, 2002). To obtain an indication of recruitment, the presence of juvenile specimens was also recorded.

Historical data

Historical data (1958 to 1984), for the 1/16th degree square grids (loci) in which each of the sampling sites of the current study was located, were extracted from the National Freshwater Snail Collection (NFSC). These data represent species collected in both lotic and lentic waterbodies.

Environmental parameters

Electrical conductivity, pH and water temperature were measured in situ at all sites during each survey using a portable digital thermometer (Checktemp, Hanna Instruments), portable digital conductivity meter (DIST 3, HI 98303, Hanna Instruments) and portable digital pH probe (HI 98128, Hanna Instruments).

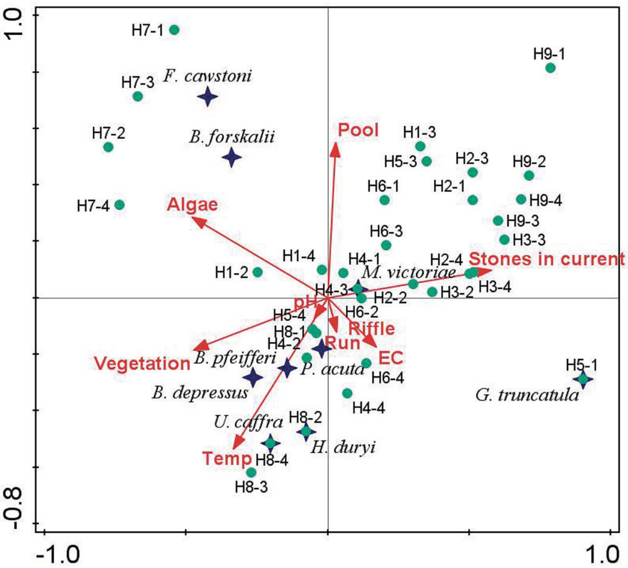

Figure 2

CCA tri-plot illustrating associations between species (blue stars), sampling sites in the Marico River during 4 surveys (green dots), environmental variables (red arrows; electrical conductivity (EC), water temperature and pH) and biotope availability (pool, riffle, run, stones in current, vegetation and the presence of algae). Only taxa for which more than 10% of the variation is explained by the model are depicted. The tri-plot describes 57.26% of the total variation, with 38.52% being described on the first axis and 18.74% on the second axis.

Statistical analyses

Canonical correspondence analyses (CCAs) were conducted using CANOCO 5 software, to investigate the distribution and abundance of mollusc species between sites and surveys in relation to the influence of selected environmental variables (water temperature, pH, electrical conductivity (EC) and biotope availability).

RESULTS

The location of each site is depicted in Fig. 1 and site coordinates, river names and biotopes present at each site are given in Table 1. Mollusc diversity, abundance and species richness (SR), and selected environmental parameters for each of the four surveys, are displayed in Tables 2 and 3. The molluscs on record in the NFSC database which were previously collected from the same loci (not necessarily from the same sites), as well as those species recovered during the present study, are presented in Table 4. Canonical correspondence analyses (CCAs), illustrating associations between species, sampling sites during four surveys, environmental variables and biotope availability, are depicted in Figs 2 and 3.

A total number of 20 species were recovered from the Marico River and tributaries (Table 2). The highest species diversity in the Marico River (SR=12) was recorded for both Sites H4 and H8, while the highest total number of species per survey (9) was also found at these two sites (Table 2). The most common and abundant species were *Burnupia trapezoidea, Lymnaea natalensis* and *Pisidium langleyanum* (Table 2). The lowest species richness was found at Sites H5 and H9, with a total number of 4 and 2 species, respectively. Only one specimen of *Galba truncatula, Helisoma duryi* and *Unio caffra* was found during the study. Seven species not previously on record for this area were recorded during the present study. However, *Bulinus tropicus*, which was previously recorded in the area (Table 4), was not found. Water temperature and pH did not vary considerably between sites, but seasonal fluctuation in temperature between surveys was observed (Table 2). Electrical

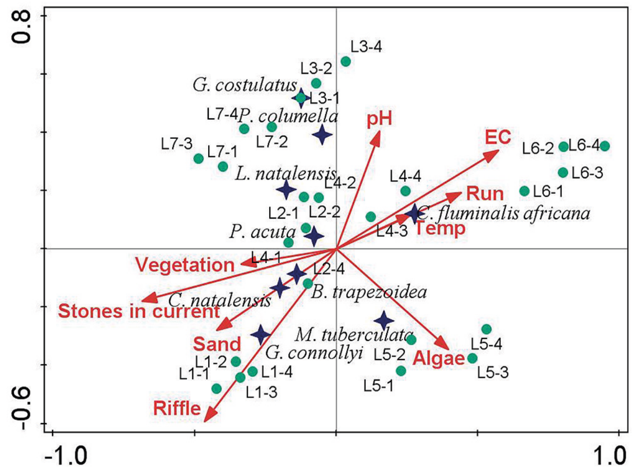

Figure 3

CCA tri-plot illustrating associations between species (blue stars), sampling sites in the Crocodile River during 4 surveys (green dots), environmental variables (red arrows; electrical conductivity (EC), water temperature and pH) and biotope availability (riffle, run, stones in current, sand, vegetation and the presence of algae). The tri-plot describes 66.92% of the total variation, with 40.75% being described on the first axis and 26.17% on the second axis.

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TABLE 2
Mollusc species collected, species richness and abundances during Surveys 1 to 4 in the Marico River, as well as environmental parameters determined at the time of collection

Site	H1				H2				H3				H4			
Mollusc species	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
B. pfeifferi		1														
B. africanus					1									1		
B. forskalii																
B. trapezoidea		1	1	1		2	14	26		2	7	23	6	2		4
C. fluminalis africana													17	4	3	
G. truncatula																
G. connollyi		4	1	1	6					1		3	84	58		
G. costulatus													73	14		
L. natalensis		5	1	1	5	2				1			172	36	1	1
M. tuberculata													7	65	4	1
M. victoriae															1	
**P. acuta*													1	9		1
P. costulosum					7	4				14	1		2	4		
P. langleyanum		2	1		25	15	1			12	1	1	8	7	5	
P. viridarium										7	1	1				
**P. columella*																1
Total per site/survey	0	5	4	3	5	4	2	1	0	6	4	4	9	9	4	5
Species richness	5				6				6				12			
Temp (°C)	22	21	18	18	16	23	13	19	12	22	15	19	17	24	15	21
pH	7.2	7.9	6.8	6.7	7.4	8	7.5	6.8	6	7.8	6.6	7.1	8.1	8.2	7.3	6.8
EC (µS/cm)	282	253	630	309	295	282	263	290	120	97	96	108	302	308	241	260

Site	H5				H6				H7				H8				H9			
Mollusc species	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
B. pfeifferi													4			4				
B. africanus												5	6	16	4	35				
B. forskalii			1									1	1	1	1	1				
B. trapezoidea			1	1							7		1							
C. fluminalis africana					12	42	8	1			2		8	5	4	21				
G. truncatula	2																	3	1	1
G. connollyi					1				4	1										
G. costulatus					9						22	39	3	2	5					
L. natalensis									2			5	4	6		33				
M. tuberculata														1						
M. victoriae					2				3	5	3	26	22	29	7	77	2	2		
**P. acuta*													5	52	3	233				
P. costulosum					64	86	6	4				1		1						
P. langleyanum	5						1	3												
P. viridarium											2	18								
**P. columella*																1				
Total per site/survey	2	0	2	1	5	2	3	3	3	2	5	7	9	9	6	8	1	2	1	1
Species richness	4				6				10				12				2			
Temp (°C)	11	22.7	13	19	18.6	21.5	20	22.2	19.4	25.6	17.3	23.2	13.5	23.7	16.1	24.1	18.3	30.6	15.9	24.4
pH	7.9	8.2	7.7	7.8	514	501	574	622	613	529	608	732	651	760	621	781	601	652	786	904
EC (µS/cm)	773	1103	918	667	8.3	7.12	8.04	8.24	8.64	7.59	7.91	8.41	8.46	9.77	7.91	8.55	9.33	8.95	7.86	8.23

*Alien species

TABLE 3
Mollusc species collected, species richness and abundances during Surveys 1 to 4 in the Crocodile River, as well as environmental parameters determined at the time of collection

Site	L1				L2				L3				L4			
Mollusc species	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
B. trapezoidea	40	8	79	127	15	9		5					10	6	10	2
C. fluminalis africana			6											6		
C. natalensis					3			1				52	39	28	25	32
G. connollyi		1	2	3	2											
G. costulatus									1							
L. natalensis	1								20				4	30		
M. tuberculata	2		14	15	1			3		1				8	1	1
**P. acuta*	3	112	9	862	23	131		145	35	410		3	83	403	12	24
**P. columella*										1						1
Total spp. per site/survey	4	3	5	4	5	2	0	4	3	3	0	2	4	6	4	5
Species richness	6				5				5				7			
Temp (°C)	18.6	21.5	20	22.2	19.4	25.6	17.3	23.2	13.5	23.7	16.1	24.1	18.3	30.6	15.9	24.4
EC (µS/cm)	514	501	574	622	613	529	608	732	651	760	621	781	601	652	786	904
pH	8.3	7.12	8.04	8.24	8.64	7.59	7.91	8.41	8.46	9.77	7.91	8.55	9.33	8.95	7.86	8.23

Site	L5				L6				L7			
Mollusc species	1	2	3	4	1	2	3	4	1	2	3	4
B. trapezoidea	1	1	14	3		1			10	7	9	8
C. fluminalis africana												
C. natalensis	4	28	9	25	1	48	25	20			3	5
G. connollyi												
G. costulatus												
L. natalensis		9							32	21	4	
M. tuberculata	280	336	138	15	7							
**P. acuta*	42	42	13		1	3			131	144		6
**P. columella*												1
Total spp. per site/survey	4	5	4	3	3	3	1	1	3	3	3	4
Species richness	5				4							
Temp (°C)	18	28.6	18	28.7	15.6	32.5	20.4	27.2	15.9	26.7	15.7	26.7
EC (µS/cm)	612	630	843	888	628	773	753	877	682	819	544	714
pH	8.54	8.62	8.5	8.81	8.36	9.16	8.48	8.48	8.97	8.94	8.01	8.71

*Alien Species

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Table 4 Mollusc species on record in the National Freshwater Snail Collection (NFSC) from 1958 to 1984 and species collected during the 2013 and 2014 study				
Mollusc species	**Marico River and Catchment**		**Crocodile River and Catchment**	
	1958–1984	**2013–2014**	**1958–1984**	**2013–2014**
B. pfeifferi	✗	✗	✗	
B. africanus	✗	✗	✗	
B. depressus	✗	✗	✗	
B. forskalii	✗	✗	✗	
B. tropicus	✗		✗	
B. trapezoidea	✗	✗	✗	✗
C. natalensis				✗
C. fluminalis africana	✗	✗	✗	✗
F. cawstoni		✗		
G. truncatula		✗		
G. costulatus	✗	✗	✗	✗
G. connollyi	✗	✗		✗
**H. duryi*		✗		
L. natalensis	✗	✗	✗	✗
M. tuberculata	✗	✗	✗	✗
M. victoriae		✗		
**P. acuta*		✗	✗	✗
P. costulosum		✗		
P. langleyanum		✗		
P. viridarium		✗		
**P. columella*	✗	✗	✗	✗
U. caffra	✗	✗		

**Alien species*

conductivity, however, was markedly higher during the third survey at Site H1 and during all the surveys at Site H5.

The length of the arrows in the CCA tri-plot (Fig. 2) indicates that algae, pools, stones in current and vegetation biotopes, as well as water temperature, played a significant role in the occurrence and distribution of species, while pH, EC and riffle-and-run biotopes had a minor influence. An association can be seen between *Ferrissia cawstoni, Bulinus forskalii*, Site H7 and algae. *G. truncatula* associated with Site H5, Survey 1, while *H. duryi* and *U. caffra* associated with Site H8, Survey 2 and Site H8, Survey 3, respectively (Fig. 2).

Regarding the Crocodile River, a total number of 9 species was recovered during the study (Table 2). The highest species diversity (SR = 7) was recorded for Site L4, while the highest total number of species per survey (6), was also found at this site. The most common and abundant species were *B. trapezoidea, Corbicula fluminalis africana, Melanoides tuberculata* and *Physa acuta*, while the lowest species richness was found at Site L6 (SR=4) (Table 2). Only one specimen of *Gyraulus costulatus* was found during the study. Five species previously on record for this area were not found (Table 4); however, *Ceratophallus natalensis* and *Gyraulus connollyi*, which were not yet on record for this area, were recovered during the present study. Water temperature, pH and EC did not vary considerably between sites, but seasonal temperature fluctuation between surveys was observed (Table 3).

The length of the arrows in the CCA tri-plot (Fig. 3) indicates that EC, algae, riffle and stones in current biotopes played a significant role on the occurrence and distribution of species, while pH, run and sand biotopes had a lesser, and temperature and vegetation an even smaller, influence. An association can be seen between *C. fluminalis africana*, Site L6 and EC. *Melanoides tuberculata* associated with Site L5 and the presence of algae, while *G. connollyi* associated with Site L1 and a riffle biotope.

DISCUSSION

From historical data in the database of the NFSC it is clear that the Marico and Crocodile River areas had a similar molluscan diversity, with only one more species recorded from the Marico River than the Crocodile (Table 4). The results of the current study, however, show a dramatic change in this similarity. The number of species found in the Marico River area increased from 13 to 20 species, while the number of species in the Crocodile River area decreased from 12 to 9 species.

Of the 13 species on record for the Marico River area, only *B. tropicus* was not recovered during the present study, probably due to the fact that this snail is primarily found in lentic waterbodies such as dams and lakes and various ephemeral habitats, which were included in the previous surveys (De Kock et al., 2002). Of the 12 species on record for the Crocodile River area, only 7 were collected during this study, while 2 species, *C. natalensis* and *G. connollyi* were recorded for the first time. Of the 21 species recovered during this study, only 7 were found in both the Marico and Crocodile Rivers. Of these 7 species 6 can be considered as generalists which are able to utilise both sediment and vegetation biotopes, while the 7th species, *C. fluminalis africana*, is a bottom dweller and not dependent on vegetation biotopes (De Kock and Wolmarans, 2007a).

The importance of the effect of biotope availability on biodiversity (Dallas, 2007) is supported by the high species richness (SR = 12) found at Sites H4 and H8 in the Marico River, where a large selection of biotopes was present (Table 1). The low species richness (SR = 2) found at Site H9 was possibly due to the fact that this site was situated directly downstream from the Molatedi Dam where the constant release of large volumes of water every 4 to 6 weeks (RHP, 2005) possibly resulted in gross disturbance and transformation of the aquatic biotopes, as reflected in the absence of marginal and aquatic vegetation (Table 1). Furthermore, this site was also negatively impacted by the clearing of riparian vegetation and grazing by cattle from a nearby informal settlement, as observed during the surveys. With regard to Site H5, located close to Zeerust, the low mollusc diversity (SR = 4) could be ascribed to the lack of suitable biotopes and possible negative impacts from the nearby industrial and urban activities (RHP, 2005), as obvious signs of littering and eutrophication were observed. The fact that *B. trapezoidea, L. natalensis and P. langleyanum* were the most commonly occurring species in the Marico River and tributaries, could be attributed to their wide distribution in the area, as previously recorded (NFSC database; De Kock et al., 2001; De Kock and Wolmarans, 2008). The single specimen of *M. victoriae* collected at Site H4 was unexpected, as this locality is well beyond the distribution range previously reported by De Kock and Wolmarans (2009).

The ordination in the CCA tri-plot (Fig. 2) shows that, regarding the environmental variables, pH and EC did not play a significant role in species occurrence and distribution, but water temperature and the presence or absence of different biotopes did play a significant role. The fact that water temperature played such a significant role in the distribution of mollusc species, is in accordance with the results of similar studies in Africa (Tchakonte et al., 2014; Abd El-Wakeil et al., 2015). Water temperature is further considered as one of the major factors influencing reproduction of molluscs (De Kock and Van Eeden, 1982). However, the lower temperature during the May surveys and the higher temperature during the November surveys did not prevent recruitment, as juvenile specimens of different generations of the majority of species were present at most of the sampling sites.

The association of *G. truncatula* with Site H5 and *H. duryi* and *U. caffra* with Site H8, is most probably due to the fact that these species were found only once and in single numbers at these sites.

A comparison between the historical data and the results of the current study is not really feasible as the historic data have been collected by many different people over several decades. However, it is still clear that a higher diversity is currently found in the Marico River, possibly due to the fact that previous surveys did not concentrate on the Marico River *per se*, as well as the fact that this river has not been seriously impacted by anthropogenic activities over the past three decades (RHP, 2005).

Of the 9 species found in the Crocodile River, the occurrence of several of these, namely *C. fluminalis africana, B. trapezoidea, G. costulatus*, *G. connollyi* and *C. natalensis,* could be expected, as they are widely distributed in South Africa (Database of the NFSC; De Kock and Wolmarans, 2004; 2006; 2007a; b) and predominantly associate with sediment biotopes that were available at almost all of the sites. However, the limited availability of marginal and aquatic vegetation at most of the sites did not prevent the occurrence of *P. acuta*, *L. natalensis* and *P. columella*, which are generalists in respect of their biotope preferences (De Kock et al., 1989; Brown, 1994; De Kock et al., 2001). As in the case of the Marico River, the ordination in the CCA tri-plot (Fig. 3) shows that biotope availability played a significant role in species occurrence and distribution. In the Crocodile River, however, EC was also an important factor in this respect and these results are in agreement with the conclusions of Tchakonte et al. (2014) and Abd El-Wakeil et al. (2015). The presence of filamentous algae, an indication of organic enrichment, and the considerably higher recorded EC values at most of the sites throughout the study, could be attributed to the anthropogenic stressors mentioned above.

Three alien species, namely *H. duryi, P. acuta*, and *P. columella*, were found during this study. Of these, *P. columella* is on record as the third most widespread freshwater snail species in South Africa (De Kock and Wolmarans, 2008). However, during this study it was found only in a few sites and also in limited numbers in both the Marico River (Sites H4 and H7) and the Crocodile River (Sites L3, L4 and L7). The fact that *P. acuta* was found at all the sites in the Crocodile River, often in high numbers, is not surprising as it has attributes such as a superior fecundity rate, as reported by Appleton and Brackenbury (1998), and the ability to migrate upstream (Appleton and Branch, 1989). Furthermore, this species can serve as an indicator of organic-enriched water, commonly occurs in areas where sewage pollution is obvious and, according to Brown (1994), seems to be closely associated with human activities. *Helisoma duryi*, of which only one specimen was found at Site H8, is widespread in artificial waterbodies but not invasive (Appleton, 2003). Of the 41 records of this species in the NFSC database reported by De Kock and Joubert (1991), only 15 were from natural habitats.

The relatively high mollusc diversity, and the fact that juveniles were present throughout the study, demonstrated that current habitat and environmental conditions were suitable to promote recruitment and the sustainability of diverse mollusc populations in the Marico River and its tributaries. However, in contrast to this, the exploitation of and habitat transformation in the Crocodile River resulted in the decrease of biotopes which eventually could have led to the decrease in diversity and the establishment of *P. acuta*, an exotic invader species.

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