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1 **Deeper knowledge of shallow waters: reviewing the invertebrate fauna of**  
2 **southern African temporary wetlands**

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## 20 **Abstract**

21 Temporary lentic wetlands are becoming increasingly recognised for their collective role in  
22 contributing to biodiversity at the landscape scale. In southern Africa, a region with a high  
23 density of such wetlands, information characterising the fauna of these systems is disparate  
24 and often obscurely published. Here we provide a collation and synthesis of published  
25 research on the aquatic invertebrate fauna inhabiting temporary lentic wetlands of the region.  
26 We expose the poor taxonomic knowledge of most groups, which makes it difficult to  
27 comment on patterns of richness and endemism. Only a few groups (e.g. large branchiopods,  
28 ostracods, copepods and cladocerans) appear to reach higher richness and/or endemism in  
29 temporary wetlands compared to their permanent wetland counterparts. IUCN Red List  
30 information is lacking for most taxa, thus making it difficult to comment on the conservation  
31 status of much of the invertebrate fauna. However, except for a few specialist groups, many  
32 of the taxa inhabiting these environments appear to be habitat generalists that  
33 opportunistically exploit these waterbodies and this is hypothesized as one of the reasons why  
34 endemism appears to be low for most taxa. Given that taxonomy underpins ecology, the  
35 urgent need for more foundational taxonomic work on these systems becomes glaringly  
36 apparent.

## 37 **Keywords**

38 aquatic invertebrates; wetland invertebrates; ephemeral wetlands; temporary ponds;  
39 ephemeral ponds; pans; southern Africa; African wetlands

## 41 **Introduction**

42 Invertebrates dominate the faunas of temporary wetlands worldwide, in terms of species  
43 diversity, abundance and animal biomass (Williams, 2006). Insects and crustaceans, in  
44 particular, are ubiquitous in such systems. Temporary wetlands house a suite of uniquely  
45 specialized invertebrates (Wiggins et al., 1980; Collinson et al., 1995; Brucet et al., 2005;  
46 Escalera-Vázquez & Zambrano, 2010; Strachan et al., 2015) which are particularly  
47 vulnerable to habitat and hydrological modifications (Calhoun et al., 2017; Dalu et al.,  
48 2017a). The southern African region, with its distinct climatic and geomorphic features, has  
49 one of the highest densities of temporary depression wetlands (known locally as ‘pans’)  
50 worldwide (Goudie & Wells, 1995). Reviews of the invertebrate fauna of temporary wetlands

51 have been conducted for a number of regions globally (e.g. Batzer et al., 1999; Batzer &  
52 Boix, 2016), but not for southern Africa; as such, this study aims to fill the knowledge gap.  
53 Southern Africa is generally defined as the area south of the Kunene River in the west and the  
54 Zambezi River in the east (including the countries of Botswana, Lesotho, Namibia, South  
55 Africa, Swaziland, Zimbabwe, and southern parts of Angola and Mozambique). These  
56 boundaries are referred to as ‘the region’ or ‘the southern African region’ throughout this  
57 review.

58 Providing a checklist of all the species within each invertebrate group known from  
59 temporary wetlands in the region is beyond the scope of this review and in many cases  
60 insufficient information is available. For certain groups, we summarise reported checklists  
61 and highlight gaps in taxonomic and ecological understanding. We review taxonomic and  
62 biodiversity studies pertaining to freshwater invertebrates in temporary lentic wetlands in the  
63 region, group-by-group. Our primary aim is to provide an overview of available information  
64 (taxonomic, faunistic and ecological) for each of the major invertebrate taxa found in  
65 temporary lentic wetlands in the region, highlighting major gaps in knowledge. The key  
66 adaptations that each invertebrate taxon has evolved to cope with desiccation are also briefly  
67 covered where such information exists. For general information on wetland invertebrate  
68 adaptations to drought, see Wiggins et al. (1980), Brendonck & De Meester (2003), Williams  
69 (2006), Strachan et al. (2015) and Batzer & Boix (2016).

70

## 71 **Methods**

72 A comprehensive review of all published material in peer-reviewed journals for the period  
73 1960 to 2016 was conducted using a combination of the following terms: ‘temporary’,  
74 ‘seasonal’, ‘ephemeral’, ‘vernal’, ‘endorheic’, ‘rock’, ‘rain’, ‘pond’, ‘pool’, ‘pan’, ‘tarn’,  
75 ‘depression’, ‘southern Africa’, plus all the individual countries within it, and ‘invertebrates’,  
76 plus all the major taxa within. References to other important studies cited in the published  
77 material above were also referred to and in turn these were also searched thoroughly for  
78 further important cited work. In this way, the relevant literature has been comprehensively  
79 surveyed. Only those papers that tackled invertebrate populations or communities from  
80 wetland systems that temporarily dry up were included in the final list used for this review.  
81 However, in certain cases, there was no mention of whether the wetland was temporarily  
82 inundated or not. In such cases it was necessary to pay careful attention to the mention of or

83 inference to flagship taxa (sensu De Roeck et al., 2007) or the adaptive traits to drying  
84 conditions (Lahr, 1997) as this would confirm the temporary nature of the wetland. The  
85 review aims to focus on lentic isolated depressional wetlands that are not connected to  
86 longitudinal watercourses (i.e. non-riverine systems). However, such specific habitat  
87 information is often not available for a given taxon, and thus we include taxa that have  
88 simply been recorded as occurring in temporary wetland environments, even if information  
89 on the specific nature of these environments is not available for the taxon in question.

90 The material from peer-reviewed journals was further complemented by consulting key  
91 texts in the ‘grey literature’ that contain comprehensive species lists, including the Water  
92 Research Commission’s ‘Guides to the Freshwater Invertebrates of Southern Africa’  
93 (relevant chapters are referenced separately throughout the text). For the molluscs, for  
94 example, Brown’s (1994) comprehensive account of African freshwater gastropods was used  
95 to systematically search each species’ information to establish whether or not it is known to  
96 inhabit temporary wetland environments. Similarly, for odonates, which have several species  
97 checklist publications covering the various sub-regions of southern Africa (Martens et al.,  
98 2003; Kipping, 2010; Samways & Simaika, 2016), it was assessed whether the habitat  
99 preferences for the various species have been noted or not, and this information was used to  
100 construct a list of temporary wetland-dependent species.

101

## 102 **Major invertebrate groups**

### 103 *Porifera*

104 Sponges occur in permanent and temporary freshwater systems worldwide, both lotic and  
105 lentic (Manconi & Pronzato, 2008). In southern Africa there are two known families,  
106 Spongillidae (five genera, seven species) and Potamolepidae (two genera, species information  
107 unavailable, Heeg, 2002a). There appears to be a low richness of sponge taxa in southern  
108 African freshwater environments compared to other regions (Manconi & Pronzato, 2008) but,  
109 as with many of the lesser-known phyla, additional collecting effort is likely to reveal more  
110 species (Heeg, 2002a). *Ephydatia fluviatilis* (Linneaus, 1758) of the Spongillidae is the only  
111 known species that has often been recorded from temporary wetlands in the region, usually  
112 found on the stems of emergent macrophytes. This species appears to be distributed  
113 throughout South Africa (SA) and Namibia (Heeg, 2002a). Sponges generally survive

114 drought periods through formation of gemmules, which are internal buds composed of  
115 amoebocytes surrounded by an external protective coat comprising collagen layers embedded  
116 with spicules (for review, see Frost, 1991).

### 117 *Cnidaria*

118 *Hydra* (class Hydrozoa) is the best-known cnidarian taxon in freshwater wetlands, and is  
119 particularly abundant in temporary lentic ponds, where it is represented by solitary polyps  
120 (Williams, 2006). In the region, out of the five species of Hydrozoa recorded, only  
121 *Limnognathia tanzanica* (Günther, 1893) is recognised as indigenous to Africa, the rest being  
122 cosmopolitan species (Rayner et al., 2002). An invasive freshwater jellyfish, *Craspedacusta*  
123 *sowerbyi* (Lankester, 1880), has been recorded in large numbers of man-made reservoirs  
124 (Rayner et al., 2002). Hydras are capable of both asexual and sexual reproduction and are  
125 known to survive in desiccated wetlands via the latter technique, whereby fertilized eggs are  
126 surrounded by a thecal coat that is resistant to external desiccation and extreme changes in  
127 environmental conditions in general (Williams, 2006).

### 128 *Platyhelminthes (flatworms)*

129 ‘Turbellarians’ are common and widespread in southern African temporary wetlands, yet no  
130 taxonomic key exists for species or even genera in the region (Appleton, 2002a). Young  
131 (1976) recorded 80 valid species of freshwater turbellarians across Africa, but little work has  
132 been done since to describe African taxa. Artois et al. (2004) described one new genus and  
133 four new species of flatworm from ephemeral rock pools in Botswana. Intensive ecological  
134 studies of temporary rock pool invertebrate communities in south-eastern Botswana  
135 (Brendonck et al., 2002) found that turbellarians (particularly *Mesostoma* spp.) are key  
136 predators of anostracan (fairy shrimp) egg banks in these systems, seriously affecting  
137 anostracan population sizes (De Roeck et al., 2005). *Mesostoma* species have even been  
138 recorded preying on adult *Branchipodopsis* shrimp in these pools (Brendonck et al., 2000b).

139 Curtis (1991) reported that only one species of freshwater turbellarian, *Mesostoma brincki*  
140 Marcus 1970, had been positively identified from Namibia. In a comprehensive global  
141 collation of turbellarian species with Gondwanan affinities, Noreña et al. (2003) listed six  
142 freshwater turbellarians (*Xenostenostomum microstomoides* Reisinger, 1976; *Prorhynchus*  
143 *brincki* Marcus, 1955; *Bothrioplana semperi* Braun, 1881; *Mesostoma brincki*; *M. ewerum*  
144 Du Bois-Reymond Marcus 1951; *Phaenocora foliacea* (Böhmgig, 1914)) from the region, but

145 did not indicate how many of these occur in temporary wetlands. Houben et al. (2014)  
146 reported *P. foliacea* from a temporary pond in Hluhluwe Game Reserve, SA. Tubellarians  
147 can cope with the periodic drying up of temporary wetlands by producing cysts, and these can  
148 come out of dormancy after 5-7 minutes of inundation (Van Steenkiste et al., 2010).

149 The other major platyhelminth groups with notable freshwater representatives are the  
150 trematodes and cestodes, both of which are parasitic. There is no existing taxonomic key for  
151 African trematodes and they are poorly known. Appleton (2002a) treats them according to  
152 groups (types) based on morphology of the cercariae. The obvious exception to an otherwise  
153 poorly-known fauna is the genus *Schistosoma*, which has seven species implicated in human  
154 or bovine bilharzia infection and that uses *Biomphalaria* or *Bulinus* gastropod snails as  
155 intermediate hosts (see 'Molluscs' below for further review of this topic). False tapeworms  
156 (subclass Cotyloda) constitute the group of cestodes that can be found in freshwater  
157 environments, and in the region are a common parasite of the platanna frog *Xenopus laevis*  
158 (Daudin, 1802), but their free-living larval stages are microscopic and are never seen unless  
159 specifically sought (Appleton, 2002a).

#### 160 *Gastrotricha*

161 Gastrotrichs have been recorded from temporary wetlands worldwide, but very little  
162 ecological or taxonomic information is available on these organisms in freshwater  
163 environments of southern Africa (Williams, 2006). In the review of Heeg (2002b), not a  
164 single species description existed for the region. The genera that have been recorded so far in  
165 the region are cosmopolitan, being found particularly in Europe but also elsewhere (Heeg,  
166 2002b). One recent exception is the new planktonic gastrotrich species, *Kijanebalola*  
167 *devestiva* Todaro, Perissinotto and Bownes, 2013, described from a shallow pond on the  
168 shores of iSimangaliso Wetland Park (KwaZulu-Natal, SA). However, despite the pond being  
169 small, it appears to be permanently inundated (Todaro et al., 2013). Nevertheless, gastrotrichs  
170 are well adapted to life in temporary wetlands through their production of dormant eggs  
171 (Ricci & Balsamo, 2000).

#### 172 *Bryozoa*

173 Bryozoans have been noted as relatively common in freshwater environments in southern  
174 Africa (Heeg, 2002c; de Moor & Day, 2013), but remain largely uncollected and unstudied in  
175 the region. Heeg (2002c) comments that the bryozoan fauna of Africa appears to contain

176 mostly cosmopolitan species, but lists only four species as recorded from the region  
177 (*Plumatella emarginata* (Allman, 1844), *P. repens* (Linnaeus, 1758), *Lophopodella capensis*  
178 (Sollas, 1908) and *Hyalinella punctata* (Hancock, 1850)). It is highly likely that bryozoans  
179 inhabit temporary wetlands across large areas of the southern African region, given that they  
180 are well adapted to survive desiccation. Bryozoans germinate by producing desiccation-  
181 resistant statoblasts that have hooks for clinging to large mobile animals such as waterfowl  
182 and are thus able to disperse passively over wide geographical areas (Bilton et al., 2001).

### 183 *Nematoda*

184 Nematodes are a highly diverse group worldwide (conservatively estimated at one million  
185 species, Abebe et al., 2008) and there are approximately 150 known species of freshwater  
186 nematodes in southern Africa, of which most are likely to be capable of surviving dry periods  
187 in moist soil (Heyns, 2002). Thirty-four of the 150 species listed by Heyns (2002) have been  
188 recorded in semi-aquatic environments and are capable of surviving near-terrestrial  
189 conditions, for example in moist soil during the dry phase of a temporary wetland.  
190 Nematodes have commonly been recorded elsewhere as able to enter a quiescent phase  
191 without water loss in response to drying in temporary ponds (Womersley & Ching, 1989;  
192 Wharton, 2004; Abebe et al., 2006) and thus are not expected to be limited by extreme  
193 environments in southern African temporary wetlands.

### 194 *Nematomorpha*

195 Information on the genera and species of the parasite phylum Nematomorpha (horsehair  
196 worms) in southern African water bodies is extremely sparse, but the few records that do  
197 exist suggest a wide distribution (Rayner & Appleton, 2002). Corrêa (1951) reported two  
198 species of *Prostoma* as widespread in SA. In a review of known African species, Schmidt-  
199 Rhaesa & Perissinotto (2016) reported a further six species from SA belonging to the genera  
200 *Chordodes*, *Paragordius* and *Beatogordius*. They also described a previously unconfirmed  
201 species (*Chordodes ferox* Camerano, 1897) collected from a live praying mantid floating in a  
202 river in the Eastern Cape province, SA. Nine species recorded by Corrêa (1951) and Schmidt-  
203 Rhaesa & Perissinotto (2016) appear to be all that is known taxonomically of the fauna from  
204 the southern African region to date. Nematomorph larvae are dependent on an aquatic  
205 medium, where they generally penetrate the bodies of arthropods (particularly orthopterans)  
206 and spend the vast majority of their lives growing into large adult worms inside the host



207 body. Thus, nematomorphs possess traits that pre-adapt them to life in temporary wetlands  
208 (Williams, 2006) and it is likely that they inhabit such environments in southern Africa.

### 209 *Rotifera*

210 Microscopic animals belonging to the phylum Rotifera (commonly called ‘wheel animals’)  
211 are found in a wide variety of freshwater habitats from large lakes to damp moss and are well  
212 adapted to life in temporary wetlands. Rotifers have two major means of dealing with  
213 desiccation. Bdelloid rotifers are able to slowly dry out and then return to activity when they  
214 are rehydrated, a process known as cryptobiosis (Brain, 2002). Monogonant rotifers instead  
215 survive as desiccation-tolerant resting eggs (Ricci & Balsamo, 2000). Both desiccated  
216 bdelloids and monogonant eggs are carried by wind and for this reason freshwater rotifers are  
217 mostly cosmopolitan, being able to flourish wherever suitable conditions are encountered  
218 (Brain, 2002). According to Dumont (1983), African rotifers are particularly cosmopolitan,  
219 although no comprehensive species list exists. Brain (2002) provided a list and an  
220 identification key for the 47 genera of freshwater rotifers known from southern Africa (8  
221 digonants and 39 monogonants), but it is not known how many of these taxa are found in  
222 temporary wetland environments. Anusa et al. (2012) reported eight rotifer species  
223 (belonging to the genera *Asplanchna*, *Brachionus*, *Conochilus*, *Epiphanes*, *Lepadella*,  
224 *Rotaria* and *Synchaeta*) as common inhabitants across a range of hydroperiods in temporary  
225 rock pools in northern Zimbabwe. They found that rotifers were more abundant in pools with  
226 longer hydroperiods, but were able to withstand the ephemerality of the shallow short-lived  
227 pools. Dalu et al. (2016) recorded five rotifer species belonging to four genera (*Brachionus*,  
228 *Euchlanis*, *Filinia*, *Pompholyx*) in an ephemeral pond in the Eastern Cape. However, more  
229 species are expected to be found with more studies currently underway. Riato et al. (2014)  
230 compared the zooplankton communities of temporary and permanent depression wetlands in  
231 the Mpumalanga Highveld, SA, and found that *Platyias quadricornis* (Ehrenberg, 1832) only  
232 occurred in the temporary wetlands. All nine species reported from the studies of Anusa et al.  
233 (2012) and Riato et al. (2014) are widespread and all occur on other continents, thus  
234 providing some preliminary indication that the temporary wetland rotifers in the region  
235 comprise largely cosmopolitan species.

236 *Tardigrada*

237 Phylum Tardigrada ('waterbears') are tiny coelomate animals (50 µm to 1.2 mm in length)  
238 represented by approximately 900 species worldwide, of which only 62 species (representing  
239 13 genera) are truly aquatic (Garey et al., 2008). Very little is known about the aquatic  
240 tardigrades in the region and there has been no definitive study on the group. They are not  
241 commonly encountered by freshwater ecologists and are easily overlooked due to their small  
242 size (Rayner, 2002). No taxonomic or ecological information on the aquatic tardigrades of  
243 southern Africa is available. There are however a number of studies on the terrestrial and  
244 semi-terrestrial tardigrade fauna of mosses, lichens and leaf litter habitats in the region (for  
245 reviews see Meyer & Hinton, 2009; Zawierucha et al., 2012). Despite the lack of studies, it is  
246 strongly suspected that tardigrades inhabit southern African temporary wetlands, given their  
247 exceptional adaptations to desiccation and physico-chemical extremes (reviewed by  
248 Williams, 2006; Møbjerg et al., 2011).

249 Tardigrades are able to spend long periods in a desiccated cryptobiotic state, during which  
250 time they are unique among metazoans in their ability to withstand extreme physico-chemical  
251 fluctuations, tolerating laboratory immersion in liquid helium at -272°C and temperatures as  
252 high as 340°C (Williams, 2006). During cryptobiosis, tardigrades are also easily dispersed by  
253 wind, as are their eggs. Once their environment is re-flooded with water they rehydrate and  
254 become active (Williams, 2006). Incredibly, tardigrades can survive for up to 70 years in the  
255 cryptobiotic state (Rayner, 2002). Life spans are more commonly less than one year however  
256 (Rayner, 2002).

257 *Annelida*

258 Annelid worms found in temporary wetlands in the region include earthworms (subclass  
259 Oligochaeta) and leeches (subclass Hirudinea). Although sabellid polychaetes (class  
260 Polychaeta) have been recorded elsewhere in temporary wetlands (Yozzo & Diaz, 1999), they  
261 have not been reported in southern African. *Ceratonereis keiskama* Day, 1953 appears to be  
262 the only polychaete worm recorded in entirely freshwater environments in SA, where it has  
263 been recorded from permanent freshwater lakes that are estuarine relicts, being particularly  
264 abundant in Lake Sibaya in KwaZulu-Natal (Day & Day, 2002).

265 Approximately one-third of the almost 5 000 valid species of oligochaetes worldwide are  
266 aquatic, of which approximately 1 100 are found in freshwater environments (Martin et al.,

267 2008). About 50 microdrile and 20 megadrile taxa have been recorded from southern Africa  
268 (van Hoven & Day, 2002). Whilst most of the microdrile species are cosmopolitan, the  
269 megadriles are mostly African endemics (van Hoven & Day, 2002). None of the taxonomic  
270 works specifically report on which oligochaete taxa are found in southern African temporary  
271 wetlands, but the megadrile earthworm *Lumbriculus variegatus* (Müller, 1774) (cosmopolitan  
272 species) and microdriles belonging to *Nais* (Naididae) have been reported in faunal lists from  
273 ecological studies of temporary wetlands in the region (e.g. Bird & Day, 2016). Oligochaete  
274 specimens from southern African wetland studies are most commonly reported at the ordinal  
275 level as ‘Oligochaeta’ (e.g. Anusa et al., 2012; Ferreira et al., 2012). Oligochaetes can survive  
276 desiccation in temporary wetland environments by forming dehydration-resistant cysts,  
277 empirically documented for lumbriculids (Anlauf, 1990) and naidids (Montalto & Marchese,  
278 2005).

279       Leeches are found in most freshwater habitats, although they are sparse in fast-flowing  
280 water or wetlands that are highly ephemeral (Oosthuizen & Siddall, 2002). Leeches are,  
281 however, well adapted to live in temporary waterbodies, mostly due to their ability to  
282 disperse via mobile vertebrates such as waterfowl (Davies et al., 1982; Williams, 2006) or  
283 attached to large invertebrates (Oosthuizen & Siddall, 2002). Some leeches are capable of  
284 surviving droughts as adults in mucus-lined cysts (Williams, 2006). The excellent dispersal  
285 ability of leeches results in their distributions in temporary wetlands in other regions of the  
286 world being well known (Williams, 2006). There are approximately 50 species of leeches in  
287 southern Africa (Oosthuizen & Siddall, 2002), but it is unknown how many can tolerate  
288 living in temporary wetlands. Bird & Day (2016) reported two species, the African leech  
289 *Helobdella conifera* (Moore, 1933) and the globally widespread *H. stagnalis* (Linnaeus,  
290 1758) from temporary depression wetlands in Cape Town, SA. Oosthuizen & Siddall (2002)  
291 have recorded *Placobdelloides multistriata* (Jahansson, 1909) from temporary wetlands  
292 throughout southern Africa (the species is distributed across Africa), although they remark  
293 that the leeches usually enter small temporary pools inadvertently while attached to water  
294 scorpions and other hemipterans as transport hosts. All three of the above-mentioned species  
295 occurring in temporary wetlands thus have wide geographic distributions.

## 296 *Mollusca*

297 Approximately 111 species of gastropod and 26 bivalves have been reported from southern  
298 Africa, which includes 10 alien gastropod species (Appleton, 2002b). The region has very

299 low freshwater molluscan endemicity at about 12.3% (Appleton, 2002b). According to  
300 Brown's (1994) habitat records, the following species are frequently found in temporary  
301 wetlands: *Pila occidentalis* (Mousson, 1887); *Lanistes ovum* Troschel, 1845; *Tomichia*  
302 *ventricosa* (Reeve, 1842); *Ceratophallus natalensis* (Krauss, 1848); *Lymnaea natalensis*  
303 Krauss, 1848; *L. columella* (introduced from North America, now widespread in Africa);  
304 *Physa acuta* Draparnaud, 1805 (introduced from Europe, now widespread in Africa);  
305 *Biomphalaria pfeifferi* (Krauss, 1848); *Bulinus globosus* (Morelet, 1866) *B. forskalii*  
306 (Ehrenberg, 1831); *B. reticulatus* (Mandahl-Barth, 1954); *B. tropicus* (Krauss, 1848); *B.*  
307 *scalaris* (Dunker, 1845); and *Aplexa marmorata* (Guilding, 1828). *Aplexa marmorata* is an  
308 invasive species from South America, which has recently been recorded from temporary  
309 wetlands as far south as Cape Town by Mlambo et al. (2011).

310 The genus *Ferrissia* are freshwater limpets that are found in varied habitats including  
311 seasonal pools throughout Africa (Brown, 1994). Although several studies have recorded  
312 *Ferrissia* at the generic level in South African temporary wetlands (Mlambo et al., 2011; Bird  
313 et al., 2013; Bird & Day, 2016), species level information is unavailable. Members of this  
314 genus are able to partly close the shell using a septum, which facilitates aestivation during the  
315 dry phase of a temporary wetland (Brown, 1994).

316 Of the African gastropods, the genus *Bulinus* excels in temporary wetland environments  
317 (Vera et al., 1995). For example, *B. depressus* and *B. scalaris* were the species most  
318 commonly found in isolated seasonal pools in Moremi Game Reserve, Botswana (Appleton  
319 et al., 2003). Similarly, *B. forskalii* was the only mollusc collected together with  
320 branchiopods in rain pools on the Makathini Flats (Hamer, 1989). The success of *Bulinus*  
321 snails can, at least in part, be put down to their ability to aestivate for up to six months and  
322 then exploit nutrient-rich temporary water bodies upon re-inundation by breeding rapidly (r-  
323 selected growth) during the short breeding season (Brown, 1994).

324 *Bulinus* and *Biomphalaria* are the two best-studied gastropod genera in southern Africa  
325 because they are the aquatic intermediate hosts of human and bovine schistosomiasis (Rubaba  
326 et al., 2016). Although species of *Biomphalaria* commonly occur in temporary habitats in the  
327 Neotropical region (Paraense, 1996), this is rare for the African counterparts. *Biomphalaria*  
328 species in the Neotropics often have lamellae in their shells' apertures that are thought to play  
329 a role in tolerating desiccation. In a southern African context, only one specimen of *B.*  
330 *pfeifferi* is known to have apertural lamellae (Appleton CC, *personal communication*).

331 Of the freshwater bivalves, members belonging to the family Sphaeriidae commonly  
332 inhabit temporary wetlands (Williams, 2006). The three genera of Sphaeriidae (*Sphaerium*,  
333 *Pisidium* and *Eupera*) present in southern Africa are in need of revision (Appleton, 2002b)  
334 and information on which sphaeriid species are known to inhabit temporary wetlands in the  
335 region appears to be lacking. Sphaeriids have been shown elsewhere to deal with desiccation  
336 by burrowing into the substrates of drying wetlands (McKee & Mackie, 1980). Most species  
337 require some residual moisture in the substrate to survive the dry season (at least 15%  
338 moisture for two Canadian sphaeriid species, McKee & Mackie, 1980) and thus are not likely  
339 to be encountered in highly ephemeral wetlands. Sphaeriids have effective dispersal  
340 mechanisms (e.g. clipping onto the limbs of mobile invertebrates and waterfowl) and are self-  
341 fertilizing hermaphrodites, adaptations that further allow them to exploit temporary  
342 environments (Williams, 2006).

#### 343 *Crustaceans: Malacostraca*

344 Most freshwater-dwelling members of the class Malacostraca (i.e. Amphipoda, Isopoda and  
345 Decapoda) lack physical adaptations for diapause or dispersal. Thus, they are not commonly  
346 associated with temporary wetlands but, due mostly to behavioural adaptations, certain  
347 species are able to persist in temporary waters (Williams, 2006). Amphipods appear to be  
348 very scarce in southern African temporary wetlands and virtually no records exist of their  
349 occurrence in these systems. Mlambo et al. (2011) and Bird & Day (2016) both recorded  
350 populations of the Gondwanan relictual species *Paramelita capensis* (Barnard 1916) and *P.*  
351 *pinnicornis* Stewart and Griffiths 1992 in small temporary wetlands of the Kenilworth  
352 Racecourse Conservation Area in Cape Town. However, studies of how these amphipods  
353 survive the summer dry phase have not been undertaken. A study of the North American  
354 amphipod *Crangonyx pseudogracilis* Bousfield, 1958 provides evidence that this epigean  
355 species is able to inhabit parts of the water table during the dry phase of a temporary wetland  
356 and this mechanism explains both its ability to persist and its ubiquity across a network of  
357 nearby wetlands (Harris et al., 2002). The authors suggest that such subterranean explorations  
358 by epigean amphipods may be a key mechanism for amphipod survival in temporary  
359 wetlands in other parts of the world. Another interesting behavioural adaptation in amphipods  
360 is reported from a congeneric North American amphipod, *C. antennatus* Packard, 1881,  
361 which survives the desiccated phase of mud-bottom pools by digging a burrow into the mud

362 that is then blocked off from the outside with an air bubble (Holsinger & Dickson, 1977). The  
363 burrow itself remains hydrated and provides a temporary aquatic refuge until the pool refills.

364 True crabs (Brachyura) also deal with desiccation by burrowing into the substrate. At least  
365 four southern African species (namely *Potamonautes lividus* Gouws, Stewart and Reavell,  
366 2001, *P. flavusjo* Daniels, Phiri and Bayliss, 2014, *P. isimangaliso* Peer & Gouws, 2015, and  
367 *P. calcaratus* (Gordon, 1929)) exhibit a vaulted carapace, which is an adaptation to a semi-  
368 terrestrial lifestyle away from permanent waters (Daniels et al., 2014). All of these species  
369 may appear superficially similar morphologically, but phylogenetically they are very distinct  
370 (Daniels et al., 2014; Peer et al., 2015). From north-eastern KwaZulu-Natal, *Potamonautes*  
371 *lividus* and *P. isimangaliso* are documented to live in close association with highly ephemeral  
372 depression wetlands (Peer et al., 2015). These crabs occupy 0.3-0.5 m deep burrows within  
373 the wetland substrate that remain moist throughout the dry season. Brachyurans associated  
374 with temporary waterbodies worldwide have often also evolved physiological air-breathing  
375 adaptations such as the ability to efficiently draw oxygen from moist air within burrows  
376 (Cumberlidge, 2009), and this appears to be the case for *P. isimangaliso* (Peer et al., 2015).  
377 Similarly, *P. calcaratus* displays the same ecological habits as *P. isimangaliso*, surviving in  
378 burrows around ephemeral pools in the KNP (Daniels et al., 2014). Another congeneric, *P.*  
379 *flavusjo*, burrows into peat soils in Highveld wetlands in Mpumalanga province where it  
380 remains submerged in water by following the vertical movement of the water table (Daniels  
381 et al., 2014).

382 The only freshwater isopods known to inhabit temporary wetlands in the region belong to  
383 the genus *Mesamphisopus* (Gouws et al., 2005). Barnard (1926) observed that  
384 *Mesamphisopus abbreviatus* (Barnard, 1927) burrows into muddy substrata in small  
385 mountain streams that seasonally run dry. It aestivates in these burrows by lowering its  
386 metabolism and breathing the moist air in the burrows, in a similar fashion to *P. isimangaliso*.  
387 *Mesamphisopus* has been reported from temporary depression wetlands in the Western Cape  
388 province (Mlambo et al., 2011; Bird et al., 2013).

389 To our knowledge, and based on extensive literature searching, there are no records of  
390 prawns or shrimps in the freshwater temporary wetlands of southern Africa (indigenous  
391 freshwater crayfish do not occur in Africa).

392 *Crustaceans: Large branchiopods*

393 The class Branchiopoda, as a matter of convenience rather than taxonomic distinction, are  
394 usually treated as two groups: the large branchiopods (fairy shrimps, tadpole shrimps and  
395 clam shrimps) and the cladocerans (water fleas). Following suit, we address the cladocerans  
396 in a separate section together with their microcrustacean counterparts, the ostracods and  
397 copepods.

398 The large branchiopods are the enigmatic flagship invertebrates of temporary wetlands  
399 worldwide (Brendonck et al., 2008). They are specialists of lentic environments that  
400 incorporate a dry phase, although in some cases they do occur in fishless semi-permanent  
401 waterbodies (Ferreira et al., 2011). Their adaptations to ephemeral waterbodies have led to  
402 their prevalence in arid and semi-arid regions, where such waterbodies predominate. This is  
403 no exception in the largely semi-arid subcontinent of southern Africa, where they are  
404 widespread and diverse. The large branchiopod fauna is well studied in the region compared  
405 to most of the aquatic invertebrate groups so far covered in this review and to date  
406 approximately 66 species have been recorded (Tuytens et al., 2015).

407 Large branchiopods generally exhibit a lifestyle of rapid growth and maturation, followed  
408 by the production of drought-resistant eggs that can lie dormant in dry sediment under harsh  
409 conditions for decades and perhaps even centuries (Brendonck et al., 2008). Generally  
410 speaking, populations adopt a ‘bet-hedging’ strategy in that not all eggs hatch with the first  
411 onset of inundation, but rather some eggs remain dormant and only hatch after subsequent  
412 inundations so as to ensure survival of the population in a wetland that dries before a cohort  
413 reaches maturity (Simovich & Hathaway, 1997; Brendonck et al., 1998; Brendonck et al.,  
414 2008). Eggs are generally dispersed passively to other waterbodies via wind (Brendonck &  
415 Riddoch, 1999; Vanschoenwinkel et al., 2009), ingestion by predators, which transport the  
416 eggs in their gut (Rogers, 2014, 2015), or by attachment to mobile fauna (Vanschoenwinkel  
417 et al., 2011). More specific aspects of the adaptations of large branchiopods to temporary  
418 wetlands environments, including their biology and reproduction, are covered elsewhere (for  
419 reviews see Belk et al., 1991; Brendonck, 1996; Brendonck et al., 1998; Dumont & Negrea,  
420 2002; Rogers, 2009).

421 Various aspects of the ecology of southern African large branchiopods (including  
422 metacommunity dynamics, competition and predation, adaptations to drying and local abiotic

423 conditions, human impacts, management and conservation) have received considerable  
424 research attention due largely to a series of studies of rock pools in the eastern Free State  
425 province (Vanschoenwinkel et al., 2007; Vanschoenwinkel et al., 2009; Vanschoenwinkel et  
426 al., 2010a; Vanschoenwinkel et al., 2010b; Pinceel et al., 2013; Vanschoenwinkel et al.,  
427 2013; Tuytens et al., 2014) and south-eastern Botswana (Brendonck et al., 1998; Brendonck  
428 et al., 2000a; Brendonck et al., 2000b; De Roeck et al., 2005; Jocqué et al., 2006; Jocqué et  
429 al., 2010). Recently, the large branchiopod fauna of soft-bottomed wetlands and rock pools  
430 have received ecological attention in Zimbabwe (Nhiwatiwa et al., 2011; Anusa et al., 2012;  
431 Nhiwatiwa et al., 2014; Tuytens et al., 2015; Nhiwatiwa et al., 2017a; Nhiwatiwa & Dalu,  
432 2017; Nhiwatiwa et al., 2017b) and the Western Cape province (De Roeck et al., 2007; De  
433 Roeck et al., 2010; Mlambo et al., 2011). A scattering of studies exists from various other  
434 localities, including Namibia (Day, 1990; Curtis, 1991), Botswana (Brendonck & Riddoch,  
435 1997), the Drakensberg (Hamer & Martens, 1998), and soft-bottomed wetlands in the Free  
436 State (Seaman et al., 1991; Meintjes, 1996), Mpumalanga (Ferreira et al., 2011, 2012), North-  
437 West (de Necker et al., 2016), Northern Cape (Hamer & Rayner, 1996) and KwaZulu-Natal  
438 (Hamer & Appleton, 1991) provinces of SA. As far as we are aware, no ecological studies on  
439 large branchiopods have been recorded from Mozambique.

440 The best-known of the large branchiopods is the order Anostraca (fairy shrimps). Early  
441 taxonomic descriptions in the southern African region were pioneered by G.O. Sars and E.  
442 Daday, but largest contribution to anostracans systematics was made by K.H. Barnard of the  
443 South African Museum during the 1930s-1940s. During the 1990s, various workers updated  
444 diversity and distribution data for the anostraca of the region. Hamer et al. (1994) and  
445 Brendonck & Coomans (1994) reviewed the Streptocephalidae south of the Zambezi and  
446 Kunene rivers and reported a total of 16 species. Brendonck (1995) added a new genus and  
447 species *Rhinobrachipus martensi* Brendonck, 1995 (Branchipodidae) to the southern  
448 African list of anostraca, which was collected from a shallow depression wetland in the  
449 Thomas Baines Nature Reserve in the Eastern Cape province. Hamer (1999) provided a  
450 taxonomic key for identification of the 46 southern African species of anostracans (six genera  
451 and four families) known at the time, all of which are known to occur in temporary  
452 freshwater wetlands with the exception of members of the genera *Artemia* and *Parartemia*,  
453 which are adapted to hypersaline salt lakes and salt pans. Nhiwatiwa et al. (2017b) recently  
454 described a new species, *Streptocephalus sangoensis* Nhiwatiwa, Dalu & Brendonck, 2017 in  
455 the south-eastern Lowveld of Zimbabwe, which was formerly published as *Streptocephalus*



456 cf. *bidentatus*, indicating that more research is still required to prove valid species status and  
457 identify more taxa.

458 Brendonck et al. (2000b) provided a focussed review on the genus *Branchipodopsis*, the  
459 members of which are shown to be specialists of transparent, very fresh (<50  $\mu\text{S cm}^{-1}$ ) and  
460 often highly ephemeral rock pools in the region. They described *Branchipodopsis* species as  
461 the ‘record holders’ of an ephemeral lifestyle in these rock pools, where populations are able  
462 to grow to maturity within the first week after inundation. Their long-distance dispersal  
463 ability by wind appears to be rare and rather they disperse to other nearby pools via  
464 overflows. This is suggested as a potential factor behind the high levels of endemism of  
465 *Branchipodopsis* species within the region. Since 2000, two new anostracan species have  
466 been described from KwaZulu-Natal province belonging to the genus *Metabranchipus* (*M.*  
467 *rubra* Rogers and Hamer, 2012 and *M. prodigiosus* Rogers and Hamer, 2012) of the family  
468 Branchipodidae.

469 Otherwise, the only recent notable taxonomic work in southern Africa concerning the  
470 anostracans is for the genus *Artemia* (Artemiidae, commonly known as brine shrimp).  
471 *Artemia* has been in a state of taxonomic confusion for quite some time (Hamer, 1999). The  
472 genus is cosmopolitan and restricted to salt lakes and salt pans with salinity levels above  
473 approximately 40 g L<sup>-1</sup>, where fish and many predatory invertebrates are absent (Kaiser et al.,  
474 2006). In southern Africa, populations seem to be a mix of bisexual and parthenogenetic  
475 forms (Kaiser et al., 2006). The sexually reproducing species cannot be distinguished by  
476 gross morphological characters and require genetic analyses to separate species. Since such  
477 work had not been conducted in the region until recently, members of the genus have been  
478 referred to at generic level. However, Baxevanis et al. (2014) attempted the genetic  
479 identification of *Artemia* species in SA. Phylogenetic and network analyses revealed that  
480 three out of the seven studied populations belong to the invasive *A. franciscana* Kellog, 1906,  
481 while four belong to *A. salina* (Linnaeus, 1758). This is the first confirmed report of the  
482 invasive *A. franciscana* in the region and highlights concern regarding its invasive ability, as  
483 demonstrated by its complete replacement of the native *A. salina* population at the Veldrift  
484 Saltworks on the west coast of SA. Given that Baxevanis et al. (2014) only investigated seven  
485 populations, the taxonomic status of *Artemia* populations in the broader southern African  
486 region stills requires investigation.

487       Brendonck & Riddoch (1997) conducted a comprehensive survey of the anostracan fauna  
488 of Botswana, sampling from approximately 200 localities around the country, collecting both  
489 live specimens and mud samples containing eggs. They reported 14 anostracan species, with  
490 only one (*Branchipodopsis kalaharensis* Daday, 1910) being endemic to Botswana. They  
491 attribute the higher species richness (33) and endemism (64%) in SA to greater habitable  
492 surface area, topographic and environmental heterogeneity, and research effort. Hamer &  
493 Brendonck (1997) expanded on the work of Brendonck & Riddoch (1997) by establishing a  
494 species-level checklist of the anostracan fauna for the whole region, providing a detailed  
495 distribution of each species. They divided the anostracan fauna into ten biogeographic  
496 categories, shaped largely by climatic factors: (i) widespread species occurring across  
497 southern Africa; (ii) eastern escarpment species occurring at high altitude within the  
498 Drakensberg; (iii) arid south-west species occurring in the arid and semi-arid regions of  
499 Namibia and the Karoo; (iv) tropical/subtropical species occurring on the low-lying eastern  
500 margin of southern Africa; (v) southern savannah species; (vi) Highveld species occurring in  
501 summer rainfall areas on the plateau at altitudes of 1000 – 1500 m; (vii) Cape east coast  
502 species occurring in winter-rainfall areas of the southern and south-eastern Cape margins;  
503 (viii) Cape west coast species occurring from Cape Town northwards along the west coast;  
504 (ix) Eastern Cape inland species (two species), of which *Streptocephalus dregei* Sars, 1899  
505 occurs in the more arid lowland areas towards the south, whilst *S. spinicaudatus* Hamer and  
506 Appleton, 1993 occurs more northwards at higher altitude and with higher annual rainfall;  
507 and (x) Zimbabwean species that have been collected mainly from Zimbabwe and also  
508 Zambia, but not further south.

509       The order Notostraca (tadpole shrimps) are branchiopod crustaceans that are known from  
510 as far back as the Triassic Period, earning them the status of ‘living fossils’ (Fryer, 1988;  
511 Vanschoenwinkel et al., 2012), although recently this concept for the group has been  
512 challenged (Mathers et al., 2013). Rayner (1999) provides an overview of the morphology,  
513 habitat preferences, feeding, reproduction and identification of southern African notostracans.  
514 Two species of *Triops* have been recorded from southern Africa, *T. granarius* (Lucas, 1864)  
515 and *T. cancriformis* (Bosc, 1801), although the latter is rare and has only been recorded from  
516 Ovamboland (northern Namibia) and the Kalahari (Hamer & Rayner, 1995). *T. granarius* is  
517 common and widespread in the drier areas of southern Africa (<500 mm mean annual  
518 rainfall), preferring muddy temporary pools seldom exceeding one hectare in size (for more  
519 detailed distribution records see Hamer & Rayner, 1995). *Triops* taxonomy in southern Africa

520 (and worldwide for that matter) is not without controversy. For instance, Korn &  
521 Hundsdoerfer (2006) used ribosomal DNA markers to investigate genetic distinctiveness of  
522 *T. granarius* populations from Tunisia, Namibia and Japan, and their results strongly suggest  
523 that the three populations belong to different, possibly cryptic species. Thus, further  
524 molecular phylogenetic work on African *Triops* populations is required to more clearly  
525 resolve cryptic species complexes.

526 The third major group of large branchiopods frequenting temporary wetlands are the clam  
527 shrimps, although the colloquial term is used here solely for descriptive convenience. The  
528 clam shrimps consist of the order Laevicaudata (smooth clam shrimp, one family with three  
529 genera and 39 species) and, in the order Diplostraca, two suborders: Spinicaudata and  
530 Cyclestherida, with approximately 116 known species (four families and 16 genera)  
531 worldwide (Brendonck et al., 2008; Rogers et al., 2012). All three groups are primitive and  
532 known as far back as the Devonian (Gueriau et al., 2016). Despite being abundant and  
533 widespread in arid-zone temporary wetlands of the region (and worldwide), the taxonomy of  
534 the clam shrimps has been poorly studied. The systematics has been problematic and  
535 complicated by morphological plasticity in the fine details, despite generally uniform gross  
536 morphology (Rogers et al., 2012). The difficulty in finding diagnostic morphological  
537 characters appears to be a prime reason why virtually no taxonomists have tackled the  
538 systematics of southern African clam shrimps since the studies of G.O. Sars, R. Gurney, G.S.  
539 Brady, E. Daday, K.H. Barnard and V. Brehm.

540 Brendonck (1999) provides a taxonomic key to distinguish the southern African species of  
541 clam shrimps, although only genus-level distinction is provided in some cases (e.g. *Cyzicus*  
542 Audouin, 1837), due to difficult taxonomy. Brendonck (1999) also provides distribution  
543 records for the 18 species known at the time of his assessment. The only notable taxonomic  
544 work that includes southern African clam shrimps in recent times is a revision of the  
545 worldwide genera of the Limnadiidae (Spinicaudata) by Rogers et al. (2012), who combined  
546 morphological and molecular information to show the presence of eight well-defined genera,  
547 including two new genera (*Afrolimnadia* Rogers, Rabet & Weeks, 2012 and *Calalimnadia*  
548 Rogers, Rabet & Weeks, 2012). South African material was used for the description of  
549 *Afrolimnadia alluaudi* (Daday, 1926). *Afrolimnadia* was subsequently renamed  
550 *Gondwanalimnadia* Rogers, Rabet & Weeks, 2016 because it is a junior homonym of

551 *Afrolimnadia* Tasch, 1987, an fossil genus of spinicaudatan clam shrimps (Rogers et al.  
552 2016).

553 *Crustaceans: Ostracoda*

554 Southern Africa has a diverse ostracod fauna. Martens (2001) reported about 155 species (ca.  
555 55 genera) belonging to the class Ostracoda from the region, but remarked that dozens of new  
556 species await description. Since this publication, several new species and genera have also  
557 been added to the regional list (Martens, 2003, 2007; Jocqué et al., 2010), including the re-  
558 discovery of two species of giant ostracod (*Liocypris grandis* Sars, 1924 and *Afrocypris*  
559 *barnardi* Sars, 1924) that were thought to be extinct (Martens, 2003; Matzke-Karasz &  
560 Martens, 2007), both from temporary wetland habitats. The most striking feature of the  
561 ostracod fauna of the region is the high endemism of the Western and Eastern Cape  
562 provinces, which although possessing few endemic genera, harbour many endemic species  
563 (de Moor & Day, 2013). The northern and central parts of Namibia and Botswana and the  
564 southern part of Zimbabwe form another belt of high endemism, with generic endemism in  
565 these areas being comparable to the exceptionally rich and endemic ostracod fauna of Lake  
566 Tanganyika (Jocqué et al., 2010). The ostracod fauna of southern Africa exhibits its highest  
567 endemism and diversity in temporary wetland environments where few cosmopolitan species  
568 occur (Martens, 2001). Ostracods are mostly benthic scavengers (although some forms are  
569 pelagic) and play an important role in temporary wetland ecosystems as detritivores  
570 (Martens, 2001). The success of ostracods in temporary wetlands is largely attributed to their  
571 production of highly desiccation-resistant eggs, but also their ability to reproduce  
572 parthenogenetically and the ease with which their eggs are passively dispersed to other  
573 waterbodies via wind dispersal or attached to other animals (for review see Horne & Martens,  
574 1998).

575 Martens (2001) provides a taxonomic key for the genera (and species for some recently-  
576 revised genera) of southern African freshwater ostracods, many of which are found in  
577 temporary wetland environments. Following this reference, the genera that have been  
578 unequivocally recorded from temporary wetlands are: *Cypricercus*, *Eundacypris*,  
579 *Gomphocythere*, *Globocypris*, *Korannacythere*, *Leucocythere*, *Megalocypris*,  
580 *Ovambocythere*, *Physocypris*, *Pseudocypris*, *Ramotha*, *Sarscypridopsis*, *Sclerocypris*,  
581 *Zonocypris*. Jocqué et al. (2006) reported *Potamocypris* and *Strandesia* from temporary rock  
582 pools in Botswana, while *Amphibolocypris* (*A. arida* and *A. exigua*) were recorded from

583 temporary rock pools in Botswana and a temporary soft-bottomed wetland in KNP,  
584 respectively (Jocqué et al., 2010).

585 In the Western Cape province, Martens (2007) recorded the genus *Mnementh* from  
586 temporary wetlands; and Martens et al. (1996) reported *Zonocypris cordata* Sars, 1924 and  
587 *Physocypris capensis* Sars, 1896, which are both found in temporary and permanent  
588 wetlands. Additionally, Bird & Day (2016) recorded the following genera *Chrissia*;  
589 *Sarscypridopsis*; and *Gomphocythere* from temporary depression wetlands within the  
590 Kenilworth Racecourse Conservation Area, Cape Town. This also included the following  
591 species: *Cypretta turgida* Sars, 1896, *Cypricercus episphaena* (Müller, 1908), *Cypridopsis*  
592 *vidua* (Müller, 1908), *Paracyprretta acanthifera* Sars, 1924, *P. capensis*, *Ramotha capensis*  
593 (Müller, 1908), and *Zonocypris cordata* Sars, 1924.

594 Reviewing the ostracod fauna of KwaZulu-Natal, Martens et al. (1998) report that most of  
595 the diversity in lowland temporary wetlands of the province is in the genera *Heterocypris* and  
596 *Cypricercus*, but diversity and endemism in these habitats is generally low. The higher  
597 altitude temporary rock pools of the Drakensberg have high diversity and endemism in the  
598 genera *Sarscypridopsis* and *Heterocypris*. However, most notable of the Drakensberg pools is  
599 the diversity within the family Limnocytheridae that is unmatched anywhere else in the  
600 world.

#### 601 *Crustaceans: Copepoda*

602 Copepods are one of the most diverse crustacean groups, including over 14,000 known  
603 species of both free-living and symbiotic forms. Most free-living copepods are marine, but  
604 approximately 2,800 species have colonized a wide variety of freshwater habitats (Boxshall  
605 & Defaye, 2008). Copepods in freshwaters represent a pivotal component of the food webs as  
606 part of the zooplankton and benthic/littoral communities worldwide. Up to 20 genera and 51  
607 species of freshwater copepods have been recorded from the region (Rayner, 2001). Most of  
608 the information available for the region concerns the calanoid copepods (order Calanoida)  
609 and there has been virtually no recent taxonomic research on the cyclopoids or harpacticoids.  
610 Among the calanoids, only members of the exclusively freshwater family Diaptomidae have  
611 been recorded in the region (Rayner & Heeg, 1994). The subfamily Diaptominae, containing  
612 about 410 species, is represented in the region by the genera *Tropodiptomus* and  
613 *Thermodiptomus*, both of which occur in more permanent waters and are not considered

614 further here. The diaptomid subfamily Paradiaptominae currently consists of 25 species  
615 (Suárez-Morales et al., 2015), most of which are endemic to Africa and adapted to life in  
616 temporary wetlands (Rayner, 2001). This largely endemic group includes a genus, *Lovenula*,  
617 that comprises extremely large individuals (de Moor & Day, 2013). Rayner (2001) provides a  
618 taxonomic key to the species of Diaptomidae in the region, along with cursory notes on the  
619 cyclopoid and harpacticoid taxa that have been described or recorded from the region. The  
620 following species in the subfamily Paradiaptominae have thus far been recorded from  
621 temporary wetlands in the region (for distributional information, see Day, 1990; Rayner,  
622 1998; Rayner, 2000, 2001; Suárez-Morales & Rayner, 2004; Suárez-Morales et al., 2015):  
623 *Lovenula falcifera* (Lovén 1845), *L. africana* (Daday, 1908), *L. simplex* Kiefer, 1929, *L.*  
624 *raynerae* Suárez-Morales, Wasserman & Dalu 2015, *Paradiaptomus lamellatus* Sars, 1895,  
625 *P. schultzei* van Douwe, 1912, *P. similis* van Douwe, 1912, *P. peninsularis* Rayner, 1999, *P.*  
626 *hameri* Rayner, 1999, *Metadiaptomus capensis* (Sars, 1907), *M. purcelli* (Sars, 1907), and *M.*  
627 *meridianus* (van Douwe, 1912).

628 The cyclopoids (order Cyclopoida), on the other hand, are represented in freshwaters by  
629 the widespread family Cyclopidae; in Africa this group is represented by 167 species, a figure  
630 that resembles that of the Neotropical region (174 species), but is about half the number  
631 found in the Palaearctic region (337 species) (Boxshall & Defaye, 2008). In southern Africa,  
632 records of cyclopids are scarce and mostly consist of cosmopolitan species. This is probably  
633 the result of the 19<sup>th</sup> Century species concepts and delimitations that were extensively used  
634 and applied by European researchers who named species from different geographic regions  
635 on the basis of their resemblance with European species. Revisionary studies have proved  
636 that records of some of these “cosmopolitan” nominal species (i.e. *Acanthocyclops vernalis*  
637 (Fischer, 1853) and *A. robustus* (Sars, 1863)) represent species complexes containing  
638 undescribed taxa. The South African cyclopoid copepod fauna certainly deserves further  
639 examination with recent taxonomic standards. The following cyclopoids have been recorded  
640 in temporary wetlands in the region (for distributional information, see Day, 1990; Rayner,  
641 2001): *A. vernalis*, *Mesocyclops major* Sars, 1927, *Thermocyclops oblongatus* Sars, 1927, *T.*  
642 *macracanthus* Kiefer, 1929, *T. schuurmanae* Kiefer, 1928, *Microcyclops crassipes* (Sars  
643 1927), *M. inopinatus* (Sars, 1927), *Eucyclops (Afrocyclops) gibsoni* (Brady, 1904), *E.*  
644 *sublaevis* (Sars, 1927), *E. serrulatus* (Fischer, 1851), *Tropocyclops prasinus* (Fischer, 1860),  
645 *Ectocyclops phaleratus* (Koch, 1838), *Paracyclops poppei* (Rehberg, 1880), and *P.*  
646 *fimbriatus* (Fischer, 1853).

647 Information on the African freshwater harpacticoids (order Harpacticoida) reveals a  
648 moderate diversity (108 species), which is comparable to that of India and Thailand. The  
649 most diverse harpacticoid family, the Canthocamptidae is represented by only 46 species in  
650 Africa, whereas more than 320 occur in the Palaearctic region (Boxshall & Defaye, 2008).  
651 Records of Harpacticoida in southern Africa are extremely scarce, let alone which taxa are  
652 known from temporary waters. *Nitokra dubia* Sars, 1927 and *Elaphoidella bidens coronata*  
653 Kiefer, 1934 have both been recorded from temporary wetlands of the Cape Flats near Cape  
654 Town, SA (Rayner, 2001). Vanschoenwinkel et al. (2008) recorded *Bryocamptus* sp. from  
655 temporary rock pools of the eastern Free State province. Rayner (2001) lists *Attheyella*  
656 *natalis* Brady, 1904, *A. warreni* Brady, 1913, *Harpacticus meridionalis* Sars, 1927,  
657 *Cletocamptus confluens meridionalis* Kiefer, 1934 and *C. trichotus* Kiefer, 1934 as other  
658 harpacticoid species that occur in southern Africa, but information could not be sourced on  
659 whether these species occur in temporary wetlands.

660 Of the ecological work directed specifically at copepods, most has focussed on aspects  
661 related to diapause. Diapause is a stop in the ontogenetic development induced by the need of  
662 physiological adjustments in the individual; in copepods this process affects one stage only,  
663 occurs regularly and is only partially related to environmental factors. Dormancy is a  
664 reversible cessation of development clearly related to environmental changes and involves  
665 different stages (depending on the species and environmental scenario) including eggs,  
666 nauplii, copepodites and adults (Dahms, 1995). Eggs are the most common dormant stage  
667 among diaptomids, and in cyclopoids dormancy is frequently related to copepodites C4 or C5  
668 (Suárez-Morales et al., 2015). Diapause occurs under drying or unfavourable environmental  
669 conditions and is a dominant feature of the life cycle of many copepod species and a major  
670 factor in their successful colonisation of temporary wetland habitats worldwide (Dahms,  
671 1995; Williams, 2006). In temporary ponds, cyclopine cyclopoids can emerge from diapause  
672 within a single day of the appearance of water (Reid & Williamson, 2010). Unlike ostracods,  
673 copepods generally reproduce sexually, but often have very fast development times, as little  
674 as one week to reach the adult stage, depending on prevailing environmental conditions  
675 (Williams, 2006). Similarly to ostracods, however, eggs are passively dispersed via wind or  
676 attached to mobile fauna (Dahms, 1995). Very little other ecological work has been directed  
677 specifically at copepods, with the exception of Wasserman et al. (2016a), Dalu et al. (2017b),  
678 Dalu et al. (2017c) and Wasserman et al. (2018), who all investigated aspects of the trophic

679 ecology of the paradiaptominids *L. raynerae* and *P. lamellatus* in the Eastern Cape province  
680 of SA.

681 *Crustaceans: Cladocera*

682 In contrast to copepods, most of the world's over 600 species (Forró et al., 2008) of  
683 Cladocera ('water fleas') occur in freshwater environments, where they often dominate the  
684 lentic fauna in terms of abundance. Southern Africa harbours a mixture of Afrotropical,  
685 Palaearctic, circumtropical and local endemic elements in its cladoceran fauna (Smirnov,  
686 2008; Van Damme et al., 2013). The taxonomy of cladocerans in the region requires an  
687 urgent overhaul, particularly the Chydoridae and the Daphniidae (Seaman et al., 1999; Van  
688 Damme et al., 2013), thus an estimate of the number of species in the region is not presently  
689 available. Smirnov (2008) reported 112 cladoceran species from SA, with a wide  
690 representation of Palearctic species. Traditionally, the region was considered to possess low  
691 levels of cladoceran endemism (Frey, 1993; Korovchinsky, 2006; Smirnov, 2008), but more  
692 recently this has been attributed to the limited state of knowledge of the fauna rather than  
693 genuinely low endemism (Van Damme et al., 2013). As is the pattern for Ostracoda and  
694 Copepoda, the greatest cladoceran species richness and endemism in the region occurs in  
695 temporary wetland environments, particularly montane rock pools in the east (e.g.  
696 Drakensberg) and endemics of Western Cape lowland pools (Van Damme et al., 2013). The  
697 families Chydoridae and Macrothricidae, the sub-genus *Daphnia* (*Ctenodaphnia*) and the  
698 genera *Ceriodaphnia* and *Moina* are common inhabitants of temporary wetlands in the region  
699 (Seaman et al., 1999). A literature search of taxonomic and ecological records of cladocerans  
700 from temporary wetlands in the region was attempted, but given the urgent need of  
701 taxonomic revision of species in this region (Van Damme et al., 2013), it was later  
702 abandoned.

703 Survival strategies of cladocerans in temporary wetlands are broadly similar to those of the  
704 other microcrustaceans, with highly desiccation-resistant eggs being produced as water levels  
705 draw down (Vandekerckhove et al., 2005). Cladocerans favour parthenogenetic (asexual)  
706 cloning during favourable times when the wetland is inundated and males are rare for much  
707 of the hydroperiod (Williams, 2006). Males appear more frequently towards the end of the  
708 hydroperiod and sexual reproduction prevails as water disappears from the wetland. Whilst  
709 parthenogenetic cloning produces soft eggs for rapid development, sexually produced eggs  
710 are encased in a hardened ephippium and can withstand drying, freezing and passive dispersal



711 to other waterbodies (Bilton et al., 2001; Vandekerkhove et al., 2005; Williams, 2006). As  
712 has been found in many aquatic environments globally, cladocerans have also been identified  
713 as important trophic components in systems of the region (Dalu et al., 2016; Wasserman et  
714 al., 2016b; Dalu et al., 2017b; Dalu et al., 2017c).

#### 715 *Hydrachnidia: Water mites*

716 Water mites (suborder Hydrachnidia) are abundant and ubiquitous in temporary wetlands and  
717 over 6 000 species have been described worldwide from freshwater environments, including  
718 160 species from southern Africa (Di Sabatino et al., 2008). Since then, more species have  
719 been added to the southern African records for Torrenticolidae (Goldschmidt & Smit, 2009),  
720 Hygrobatidae (Pešić et al., 2013), Mideopsidae (Pešić et al., 2013), Arrenuridae (Smit, 2012)  
721 and Hydryphantidae (Gerecke, 2004). Jansen van Rensburg (1976) provided a taxonomic key  
722 to identify the 22 water mite families from the region (updated by Jansen van Rensburg &  
723 Day, 2002). Throughout the key, and indeed also for more recent species-level accounts (see  
724 above), no mention is made in the habitat descriptions for each taxon as to the preference for  
725 temporary versus permanent water bodies. Hence, we are unable to provide further  
726 information from the taxonomic literature regarding those taxa specifically known to inhabit  
727 temporary wetlands in the region. The following taxa have been recorded from temporary  
728 wetlands in the south-western Cape Mediterranean-climate region of SA (records from  
729 Mlambo et al., 2011 unless otherwise specified), with the help of Dr R. Gerecke, Tübingen,  
730 Germany, and Dr E. Ueckerman, ARC, Pretoria: *Arrenurus* spp. (Arrenuridae), *Eylais* spp.  
731 (Eylaidae), *Hydrachna fissigera* Koenike, 1898, *Hydryphantes parmulatus* Koenike, 1912,  
732 *Diplodontus schaubi* (Koenike, 1893), *Mamersa testudinata* Koenike, 1898, *Limnochares*  
733 *crinita* Koenicke, 1898, *Piona* sp. (Pionidae), and *Neumania* spp. (Unionicolidae). In  
734 addition, hygrophilous representatives of several terrestrial mite taxa were reported by Bird et  
735 al. (2013) from the cohorts Gamasina (*Macrocheles* sp., Macrochelidae), Astigmatina  
736 (Oribatida), and Parasitengona (Trombidiidae).

737 The great diversity of water mites in temporary habitats is remarkable, given that most do  
738 not possess the typical adaptations of temporary wetland invertebrates (either diapause of  
739 eggs/adults or active dispersal as adults) (Bohonak et al., 2004). Instead, the radiation of  
740 water mites in temporary wetlands has been facilitated by parasitic larvae that, once hatched  
741 from eggs laid within a waterbody, parasitize adult insects and are thus dispersed to other  
742 waterbodies (Bilton et al., 2001; Bohonak et al., 2004). Parasitism is obligate in all species

743 studied so far that colonize astatic water bodies, and mite larvae die if they fail to penetrate an  
744 insect host (Bohonak et al., 2004). However, not all water mites survive the dry phase via  
745 parasitism, and certain taxa (e.g. some members of the Hydryphantidae) are capable of  
746 surviving dry phases as deutonymphs or adults that enter an inactive state in microhabitats  
747 with persistent moisture, such as moist mud or damp crevices in logs (Wiggins et al., 1980;  
748 Bohonak et al., 2004).

749 *Insecta: Ephemeroptera (mayflies)*

750 The order Ephemeroptera have the distinction of being the most ancient lineage of extant  
751 winged insects, dating back to the late Carboniferous or early Permian periods (Brittain &  
752 Sartori, 2003; Barber-James et al., 2008). Despite over 3 500 species worldwide and 435  
753 species from the Afrotropical region (Sartori & Barber-James, 2018), most mayfly diversity  
754 is represented in running waters and this ancient group is relatively depauperate in lentic  
755 environments (Newell & Hossack, 2009). A baetid species, *Cloeodes hydatation* McCafferty &  
756 Lugo-Ortiz, 1995, from temporary wetlands (rock pools, ephemeral pools and springs) of the  
757 Pantanal wetland system was the first mayfly species to be experimentally shown to  
758 withstand repeated drying conditions of up to nine hours at a time (Nolte et al., 1996). On the  
759 contrary, a known inhabitant of intermittent waters, *Daleatidium* spp. (Leptophlebiidae), from  
760 New Zealand dies only after three hours of drying exposure (Robinson & Buser, 2007).  
761 However, Nolte et al. (1996) made a distinction between *C. hydatation* and the chironomid  
762 *Polypedilum vanderplanki* Hinton, 1951, calling it drying-tolerant as opposed to drying-  
763 resistant, which the latter is. Although the genus *Cloeodes* occurs in the region, a similar  
764 characteristic of drying-tolerance has not been demonstrated, and it has also not been reported  
765 from temporary wetlands. In southern Africa, only members of the genera *Cloeon* Leach,  
766 1815 and *Procloeon* Bengtsson, 1915 (Baetidae) are known from truly lentic waterbodies  
767 such as dams and wetlands and appear to be capable of reaching high abundance in  
768 temporary waterbodies (Barber-James & Lugo-Ortiz, 2003). Similar results have been  
769 reported in Irish turloughs (Reynolds, 2000).

770 Although the aquatic nymphal phase of these baetid mayflies is rather delicate and  
771 desiccation-intolerant, populations persist in temporary wetlands due to the nymphs being  
772 extremely fast-growing (reaching maturity in 2-3 weeks) and the adults apparently producing  
773 desiccation-resistant eggs (Williams, 2006). Dispersal is via short-lived winged adults or via  
774 passive dispersal of eggs (Bilton et al., 2001; Williams, 2006). Barber-James & Lugo-Ortiz

775 (2003) list 22 Afrotropical species of *Cloeon* (nine from SA) and three species of *Procloeon*  
776 (one from SA). It is not yet known which of these species inhabit temporary wetland  
777 environments, which reflects the desperate need for more species-level studies of mayflies in  
778 Africa (Barber-James & Gattolliat, 2012). *Cloeon* is widespread in the region and has been  
779 recorded from temporary wetlands throughout the region, including the Western Cape  
780 (Mlambo et al., 2011; Bird et al., 2013) and Mpumalanga (Foster et al., 2015) provinces of  
781 SA, Namibia (Day, 1990), Zimbabwe (Chakona et al., 2008) and Botswana (Jocqué et al.,  
782 2006).

783 Gillies (1990) reported the unusual habitat of the baetid *Acanthiops erepens* (Gillies,  
784 1990), which occurs in Tanzania on rock in semi-permanent vertical trickles and in the splash  
785 zone next to small cascades. The nymphs cling to moss growing on the rock face that is kept  
786 moist by spray from the adjacent waterfall, and if disturbed they plummet into the waterfall  
787 pool below.

#### 788 *Insecta: Odonata*

789 The order Odonata, comprising some 5,680 species worldwide (Kalkman et al., 2008), is  
790 divided into the suborders Zygoptera (damselflies) and Epiprocta, which is further divided  
791 into the infraorders Anisoptera (dragonflies) and Aniszygoptera (Asian species only) (Rehn,  
792 2003). As with the Ephemeroptera, the odonates are an ancient order, dating back well into  
793 the Permian (Kalkman et al., 2008). The Odonata are relatively well studied, especially in the  
794 Afrotropical region where their diversity is depauperate compared to other tropical regions  
795 (Dijkstra, 2003) and thus their taxonomy is relatively well known in comparison to other  
796 freshwater invertebrate groups (but still not without some confusion, see Dijkstra, 2003).  
797 That said, Dijkstra et al. (2015) recently described a further 60 new African species as adults,  
798 from regions north of the area under review in this paper. Therefore, if brightly coloured,  
799 charismatic creatures such as adult Odonata are still incompletely known, how much less do  
800 we yet know about the more obscure freshwater invertebrates, especially those inhabiting  
801 temporary waterbodies in Africa.

802 Unlike many of the African freshwater invertebrates, IUCN Red List information has been  
803 compiled for many of the southern African odonate species, with most of the threatened  
804 species being habitat specialists occurring in highland areas of the Western and Eastern Cape  
805 provinces (Samways, 2004), many frequenting temporary water bodies, but most as

806 opportunistic visitors rather than being dependent upon these habitats. Odonate species  
807 exploiting temporary habitats depend on dispersal for survival and tend to have large home  
808 ranges and are habitat generalists, being tolerant of ecological change (Clausnitzer et al.,  
809 2012). Thus, temporary wetland species are generally not threatened. In southern African arid  
810 regions, no desert endemics are known and most of the widespread desert-inhabiting species  
811 are powerful fliers belonging to the Anisoptera that are not restricted to deserts, being more  
812 common in savannah wetlands (Suhling et al., 2003). The 889 known odonate species of the  
813 Afrotropical region (Kalkman et al., 2008) all have aquatic larvae, which are not capable of  
814 withstanding desiccation themselves (for a rare exception from Brazil, see Van Damme &  
815 Dumont, 1999). Odonate populations are however, able to persist in temporary habitats  
816 through production of drought-resistant eggs combined with fast-growing larvae, multivoltine  
817 life cycles and strong active dispersal of adults (for more detailed reviews of odonate  
818 adaptations to temporary habitats, see Johansson & Suhling, 2004; Suhling et al., 2005; De  
819 Block et al., 2008; Hassall & Thompson, 2008). Timing of hatching may also be important.  
820 Schiel & Buchwald (2015) showed that for 15 species of odonates across three genera (*Lestes*  
821 – *Lestidae*, *Aeshna* – *Aeshnidae* and *Sympetrum* – *Libellulidae*), species inhabiting only  
822 temporary ponds hatched significantly earlier in the year than congeners inhabiting a  
823 combination of permanent and temporary ponds. Despite the harsh environmental conditions  
824 often presented in temporary waterbodies, a major reward for exploiting such habitats is often  
825 the reduced predation pressure on larvae (lack of fish for instance) allowing them to forage  
826 actively for food, whereas in permanent waters larvae generally need to remain concealed and  
827 rely on ambush predation (Hassall & Thompson, 2008).

828 Several checklists are available covering various sub-regions of southern Africa, from  
829 which habitat preferences of the various species can be discerned (if such information is  
830 available at all). Martens et al. (2003) listed 102 odonate species from Namibia. They listed  
831 the following taxa as facultative inhabitants of temporary wetlands: *Lestes pallidus* Rambur,  
832 1842, *Ischnura senegalensis* (Rambur, 1842), *Anax ephippiger* (Burmeister, 1839), *Pantala*  
833 *flavescens* (Fabricius, 1798), and *Sympetrum fonscolombii* (Selys, 1840). Suhling et al.  
834 (2003), in their investigation of desert-adapted odonates, listed the following species from  
835 ephemeral pools in the Namib desert of Namibia: *Africallagma glaucum* (Burmeister, 1839),  
836 *Ischnura senegalensis* (Rambur, 1842), *Anax ephippiger*, *A. imperator* Leach, 1815,  
837 *Paragomphus genei* (Selys, 1841), *Crocothemis erythraea* (Brullé, 1832), *Orthetrum*  
838 *chryso stigma* (Burmeister, 1839), *Palpopleura lucia* (Drury, 1773), *P. flavescens*, *S.*

839 *fonscolombii*, *Trithemis annulata* (Palisot de Beauvois, 1807) and *T. kirbyi ardens*  
840 (Gerstäcker, 1891). Mlambo et al. (2011) recorded the anisopteran genera *Anax* (Aeshnidae)  
841 and *Trithemis* (Libellulidae) and the zygopteran genera *Africallagma*, *Ischnura* and  
842 *Pseudagrion* (all Coenagrionidae) from temporary wetlands of the Western Cape. Jocqué et  
843 al. (2006) reported the larvae of *P. flavescens* as top predators in temporary rock pools of  
844 south-eastern Botswana. Simaika et al. (2016) investigated the benefits of artificial ponds as  
845 biodiversity refugia for Western Cape dragonflies and listed the following taxa from a  
846 temporary pond: *A. imperator*, *C. erythraea*, *I. senegalensis*, *Orthetrum chrysostigma*  
847 (Burmeister, 1839), *O. trinacria* (Selys, 1841) and *Trithemis arteriosa* (Burmeister, 1839).  
848 Samways (1999) noted *L. pallidus* as a frequent inhabitant of temporary wetlands in SA,  
849 while Clark & Samways (1996) recorded *Palpopleura deceptor* (Calvert, 1899), *P. jucunda*  
850 Rambur, 1842, *P. lucia*, *Bradinopyga cornuta* Ris, 1911, *T. kirbyi ardens* and *P. flavescens*  
851 from ephemeral rock pools in KNP. Interestingly, larvae of the libellulid *Hemistigma*  
852 *albipunctum* (Rambur, 1842), which inhabits marshes and swamps, can remain alive in the  
853 mud as these habitats dry out, surviving with minimal water and emerging as an adult before  
854 the local area completely dries out (Samways, 2008).

855 Kipping (2010) provided a checklist of the odonates of Botswana and noted that most of  
856 the country's odonates are widespread African savannah species that, although having a  
857 preference for more stable habitats, are able to disperse over wide distances and breed in  
858 temporary waterbodies in arid areas such as the Kalahari Desert. Suhling et al. (2009)  
859 reported that true obligate migrant species of the arid Kalahari region include *P. flavescens*,  
860 *S. fonscolombii* and *A. ephippiger*. Kipping (2010) recorded the following species as  
861 facultative inhabitants of temporary wetlands of Botswana: *Lestes dissimulans* Fraser, 1955,  
862 *L. pallidus*, *L. pinheyi* Fraser, 1955, *A. glaucum*, *Azuragrion nigradorsum* (Selys, 1876),  
863 *Ceriagrion suave* Ris, 1921, *I. senegalensis*, *A. ephippiger*, *A. tristis* Hagen, 1867,  
864 *Brachythemis leucosticta* (Burmeister, 1839), *B. cornuta*, *Diplacodes luminans* (Karsch,  
865 1893), *Orthetrum brachiale* (Palisot de Beauvois, 1817), *O. caffrum caffrum* (Burmeister,  
866 1839), *O. chrysostigma chrysostigma* (Burmeister, 1839), *O. trinacria*, *P. deceptor*, *P.*  
867 *flavescens*, *Rhyothemis semihyalina* (Desjardins, 1832), *S. fonscolombii*, *Tramea basilaris*  
868 (Palisot de Beauvois, 1807), *T. kirbyi ardens* and *Urothemis assignata* (Selys, 1872). For  
869 more detailed information on the distribution, habitat and Red List status of these species, the  
870 reader is referred to Kipping (2010) and Samways & Simaika (2016).

871 In some odonate species there are temporal changes in geographic range in accordance  
872 with the wet and dry cycles of the El Niño Southern Oscillation. An extreme case was for  
873 *Aciagrion dondoense* Dijkstra, 2007, which was not known in SA prior to the year 2000  
874 when it appeared in great numbers on the KwaZulu-Natal coast, having come down the coast  
875 with flooding farther north. A few years later it was gone from the country with the dry phase  
876 appearing (Samways, 2010). Several South African species are adapted to these cycles, with  
877 species like *Orthetrum robustum* Balinsky, 1965 retreating from temporary pools in the dry  
878 phase to permanent lakes, to return later to the temporary pools in the wet cycle (Samways,  
879 2008). One last factor to consider is that rivers that stop flowing and have only pools ('kuile')  
880 in the dry season. Such pools in these rivers may attract species temporarily until the river  
881 flows again. There may even be a succession of species as the pools gradually dry out, with  
882 *Pseudagrion commoniae* (Förster, 1902) and *P. salisburyense* Ris, 1921 being the last to  
883 survive before the pools finally dry out (Samways, 2008).

#### 884 *Insecta: Hemiptera*

885 The hemimetabolous insect order Hemiptera is usually considered to contain four suborders:  
886 Sternorrhyncha (aphids, whiteflies, and scale insects); Auchenorrhyncha (cicadas and  
887 hoppers); Coleorrhyncha (moss bugs); and Heteroptera (true bugs) (Capinera, 2008; Forero,  
888 2008). It comprises some 82,000 described species, and possibly almost 200,000 species in  
889 total worldwide. The bugs associated with water all belong to the Heteroptera, particularly  
890 the semi-aquatic Gerromorpha and the predominantly aquatic Nepomorpha. Gerromorphs  
891 have hydrophobic tarsi and gracile bodies that allow them to stand on the water surface  
892 supported by the surface tension of the meniscus, while nepomorphs generally crawl or swim  
893 underwater and typically have reduced antennae and ocelli. The Nepomorpha have a fossil  
894 record dating back about 250 million years (Grimaldi & Engel, 2005).

895 Most species have winged adults that disperse well and can therefore colonise temporary  
896 wetlands quickly. The nepomorph families all breathe air through plastrons or respiratory  
897 tubes, and the gerromorph families are epipleustonic, living just above the water surface  
898 rather than in the water, so dissolved oxygen does not limit the potential of a water body for  
899 colonisation by water bugs. The species in most families are generalist predators, and can  
900 therefore inhabit a wide variety of waters with flow rates that are slow or absent. Many  
901 gerromorphs associate with floating or emergent vegetation that helps them to avoid  
902 predators and being washed away in flowing waters (Reavell, 2003). Immature nymphs have

903 biologies similar to their adults, but cannot fly, so they complete their development only in  
904 temporary wetlands that take more than (generally) four to ten weeks to dry up. Adults of  
905 some species of gerromorph may be winged or apterous (regulated by temperature and  
906 photoperiod); when apterous adults inhabit a temporary wetland, they indicate that at least  
907 one generation has completed its life cycle in the wetland. The high mobility and broader  
908 habitat preferences of most aquatic bugs means that populations of temporary wetland species  
909 are generally not threatened (Collinson et al., 1995).

910 The morphology, taxonomy and general ecology of the southern African water bug fauna  
911 was summarised by Reavell (2003), who stated that little work had been done on the fauna of  
912 the region, and that it needed urgent taxonomic revision. Reavell (2003) provided a key to the  
913 families of aquatic Hemiptera in the region, and a list of the known genera, but keys to the  
914 genera and species are still lacking. Ecological and life history studies of temporary wetland  
915 water bugs in the region include Hutchinson (1933), Hynes (1955), Weir (1966), Tawfik  
916 (1969), Boettger (1974), Mlambo et al. (2011), Ferreira et al. (2012), Bird et al. (2013) and  
917 Nhiwatiwa et al. (2017a). Hemiptera from six families constituted an average of 14% of the  
918 individual invertebrates surveyed in a large number of temporary waters in the Western Cape  
919 (Mlambo et al., 2011), and Hemiptera were co-dominant with Coleoptera (beetles) in nine  
920 temporary pans in Mpumalanga (Ferreira et al., 2012). The dominant families are usually  
921 Corixidae and Notonectidae. The water bugs tend to be associated with warmer, alkaline  
922 water in temporary pans (Ferreira et al., 2012), and larger-bodied species are more common  
923 in the absence of fishes in ephemeral pans (Nhiwatiwa et al., 2017a; Nhiwatiwa et al.,  
924 2017b). However, because of their high vagility and relatively broad habitat tolerances, water  
925 bugs may be poor indicators of anthropogenic effects on temporary wetlands in SA (cf. Bird  
926 et al., 2013), an effect that can be compounded by artefacts of the sampling method (de Klerk  
927 & Wepener, 2013). Their instantaneous diversity may also be related to the stage of the  
928 wetland's hydroperiod (Lahr et al., 1999; Dalu et al., 2017b; Dalu et al., 2017c), since older  
929 wetlands have had more time to become colonised and develop prey populations, thus  
930 obscuring the effects of human activities.

### 931 *Insecta: Trichoptera*

932 Trichoptera are holometabolous insects, mostly with an aquatic larval and a terrestrial adult  
933 phase. They have been recorded worldwide with the exception of some oceanic islands and  
934 the polar regions (de Moor & Scott, 2003). The Trichoptera World Checklist (Morse, 2011)

935 lists 14 548 species of 616 genera in 49 families recorded globally thus far. Of these, 1 193  
936 species (8.2%) in 83 genera from 21 families are known to occur in southern Africa (Tobias  
937 & Tobias, 2008). Recently, some species were collected in temporary wetlands, despite the  
938 earlier assertion of Scott (1970) that Trichoptera do not inhabit temporary lentic waters of the  
939 region: *Oxyethria velocipes* (Barnard, 1934) (Jones, 2002; Day et al., 2010) and *Athripsodes*  
940 sp. (Bird, 2012), both from the Western Cape province; and *Ecnomus thomasseti* Mosely,  
941 1932, *Oecetis* sp. and *Oxyethira* sp. from Mpumalanga province (Ferreira et al., 2012).  
942 Trichoptera found in temporary waters show several adaptations to this habitat in different  
943 life stages, but little is known about this in southern Africa as research has mainly been  
944 conducted on species from other regions, discussed below. Larvae use silk to construct  
945 transportable or fixed cases from material readily available, such as sand, small stones, sticks,  
946 leaves and algae. The ability to build cases has allowed trichopteran larvae to adapt to a wide  
947 range of environmental conditions: spring sources, mountain streams, splash zones of  
948 waterfalls, large rivers, lakes and temporary wetlands (de Moor & Scott, 2003). Many species  
949 are represented in cooler and faster-moving waters as dissolved oxygen is a limiting factor for  
950 habitat colonisation (de Moor & Scott, 2003).

951 Trichopteran larvae are apneustic, which means that they lack spiracles; they take up  
952 dissolved oxygen through the thin abdominal membrane by direct diffusion. Their abdominal  
953 surfaces are often expanded with tubular or branched gills that increase the surface area of the  
954 abdominal membrane. To ensure sufficient uptake of dissolved oxygen, larvae can create a  
955 current through their cases by abdominal undulation. This aids gas exchange when oxygen  
956 concentrations are low, as is the case in temporary wetlands (Williams, 1987; de Moor &  
957 Scott, 2003).

958 As water levels decrease during drying, faunal density increases and cases offer a  
959 protective body covering and camouflage to protect larvae from predation. A combination of  
960 case material (mineral rather than organic), shape (short, wide case with “hedgehog” structure  
961 rather than long tubular cases or flat purses) and defensive behaviour (retreating deep into the  
962 case and remaining motionless) are adaptive strategies employed by *Limnephilus externus*  
963 Hagen, 1861 against predation by diving beetle larvae (*Dytiscus* sp.) (Wissinger et al., 2006).  
964 Another species, *L. picturatus* McLachlan, 1875, evades predation of pupae by burrowing  
965 into soft substrates to pupate, whereas larvae of *Asynarchus nigriculus* (Limnephilidae)  
966 (Banks, 1908) build stronger mineral cases prior to pupation. Furthermore, both species have



967 faster developmental times, which reduce temporal overlap with predators (Wissinger et al.,  
968 2003). Pupae can develop while the water column has dried up and the soil is still moist  
969 (Wiggins, 1973). The case material is important with regard to pond-drying. Larvae of *L.*  
970 *coenosus* Curtis, 1834 construct cases using organic material whereas *L. vittatus* (Fabricius,  
971 1798) larvae use mineral material. Organic material has been shown to retain moisture better  
972 than mineral material, preventing drying of larvae (Zamora-Muñoz & Svensson, 1996).

973 Cases also protect caddisfly larvae from inter- and intraspecific aggression as water levels  
974 decrease (Wissinger et al., 2004b). Aggressive behaviour includes fighting (foreleg wrestling,  
975 biting, case shaking) and mobbing of individuals (involving 5-10 larvae) which often results  
976 in death and cannibalism of conspecifics (Lund et al., 2016). Wissinger et al. (2004b) have  
977 shown that cases reduced or prevented cannibalism significantly among larvae of *A.*  
978 *nigriculus*. Cases also reduced vulnerability of three *Limnephilus* species (*L. externus*, *L.*  
979 *picturatus*, *L. secludens* Banks, 1914) to intraguild predation by *A. nigriculus* (Banks, 1908).  
980 Aggression among *A. nigriculus* in mesocosm experiments was higher in high-density  
981 treatment and even higher in the absence of dietary protein supplement (Lund et al., 2016).  
982 Although aggressive behaviour has trade-offs, such as injury and subsequently becoming a  
983 secondary victim, cannibalism provides an important protein- or lipid-rich dietary supplement  
984 that offers advantages later in the life-cycle.

985 Dietary experiments on *L. coenotus* and *L. vittatus* supplementing detritus diet with  
986 protein have shown that larger larvae survive drying better as they contain more water  
987 compared to smaller ones (Zamora-Muñoz & Svensson, 1996). Furthermore, body mass of  
988 adult *L. externus* significantly increased when ambient food treatment was supplemented with  
989 a protein-rich supplement (Jannot et al., 2008). Larval diet can have a significant long-term  
990 effect on adult fitness (Jannot, 2009) as female body size is correlated with fecundity and  
991 male body size with mating success (Wissinger et al., 2004a).

992 Adults of *L. externus*, *L. picturatus* and *A. nigriculus* emerge prior to pond-drying and  
993 females enter an ovarian diapause after mating (Wissinger et al., 2003). Summer diapause is  
994 an important adaptation to survive dry periods (Wiggins, 1973; Wiggins et al., 1980), which  
995 also protects eggs from predation, drying and freezing (Wissinger et al., 2003). Oviposition in  
996 temporary pools usually occurs above or near water, not directly in water as is normal for  
997 most trichopteran species (Wiggins, 1973). Eggs are deposited in a gelatinous egg-matrix,  
998 which is highly resistant to extremes like desiccation and freezing (Wiggins, 1973). Eggs are

999 deposited under rocks and logs, where larvae hatch and develop further within a gelatinous  
1000 mass until re-wetting occurs (Wissinger et al., 2003). *Lectrides varians* Mosely, 1953 show a  
1001 bimodal response – some larvae become active with the first onset of re-wetting or re-  
1002 immersion whereas others remain aestivating and only become active when surface water  
1003 levels are more stable. Although this adaptation ensures population survival, it is at the cost  
1004 of larval survivorship (Wickson et al., 2012). Larvae enter the temporary ponds with, for  
1005 example, melt water, develop further and pupate prior to pond-drying (Wissinger et al.,  
1006 2003).

#### 1007 *Insecta: Diptera*

1008 Virtually all African temporary waters support the larvae of at least one species of fly, and  
1009 flies boast of a large array of adaptive mechanisms for this variable environment (McLachlan  
1010 & Ladle, 2001). In the region, the families Chironomidae, Ceratopogonidae and Culicidae  
1011 commonly occur even in the Kalahari and Namib deserts, where rain may fall only at  
1012 intervals of several years. Although dipterans are ubiquitous in these systems, very few  
1013 species are able to survive desiccation (Williams, 2006). Unlike many branchiopod  
1014 crustaceans, which withstand dry periods as desiccation-resistant cysts, most flies that occur  
1015 in temporary waters survive the dry period as adults or, in the case of some culicids, as larvae  
1016 in perennial water bodies. Hinton (1953) indicated that some African Stratiomyidae can  
1017 withstand desiccation, though this is not recorded in southern Africa.

1018 Chironomids mostly survive dry periods as adults. Frouz et al. (2003) reviewed the  
1019 strategies employed by chironomids to survive the variable environment of temporary  
1020 wetlands. Given that larvae of several species are found in hyper-arid conditions in the  
1021 Namib Desert, where pools may not form for 5 to 10 years at a stretch, the question yet to be  
1022 answered is, “How are the *adults* able to survive the dry years in these environments?” A few  
1023 other species survive for some time in stout pupal cocoons during dry periods (Armitage,  
1024 1995), but presumably these periods are relatively short. When it comes to survival under  
1025 harsh conditions, larvae of the ‘sleeping chironomid’, *Polypedilum vanderplanki* Hinton,  
1026 1951, hold the record. The species breeds in small unshaded rock pools in Central and West  
1027 Africa. Larvae can undergo up to 17 years of desiccation and, when wetted, will ‘wake up’  
1028 and behave normally, feeding and growing until the next time they are desiccated. Hinton  
1029 (1960) performed various experiments on these remarkable organisms, showing that they can  
1030 withstand temperatures between -270°C and +102°C and can survive through a

1031 wetting/drying cycle at least ten times. An additional species of ‘sleeping chironomid’, *P.*  
1032 *ovahimba* Cranston, 2014, has been recently described from rock pools of the Waterberg  
1033 Plateau, Namibia (Cranston, 2014).

1034 Other chironomids, such as *Chironomus pulcher* Wiedemann, 1830, also breed in rain  
1035 pools on rocks throughout much of Africa and have rapid life cycles. Larvae of the  
1036 chironomid subfamily Podonominae (*Archaeochlus* sp. and *Afrochlus harrisoni* Freeman,  
1037 1964) are found in temporary trickles over rocks and boulders in the Drakensberg, on granite  
1038 inselbergs near Harare, and in Namibia (Harrison, 2002). Similarly, *Harrisonina petricola*  
1039 Freeman, 1956 was originally found breeding in the thin film of water running over stones in  
1040 an ephemeral stream in the Olifants River Valley. It is not known how these survive dry  
1041 periods. Rock pools in Africa are dominated by dipteran larvae (up to 300 000 per pool),  
1042 which are often the only macroinvertebrate inhabitants. If the pools are very short-lived (1-2  
1043 days), the only inhabitants are larvae of *P. vanderplanki*. Pools lasting several weeks often  
1044 support *Chironomus imicola* Kieffer, 1913, which has little tolerance of desiccation, but is  
1045 able to complete its life cycle in 10-12 days (McLachlan & Cantrell, 1980).

1046 Larvae of a few ceratopogonid species are found in extremely arid regions (de Meillon &  
1047 Wirth, 2002) and yet they seem not to be particularly adapted to withstanding desiccation.  
1048 There are no African examples. Larvae of *Culicoides sonorensis* Wirth & Jones, 1957 from  
1049 the Sonoran Desert in North America, for instance, are able to survive drying, but only for a  
1050 day or two (McDermott & Mullens, 2014). Pools lasting several days often contain larvae of  
1051 the ceratopogonid *Dasyhelea thompsoni* de Meillon, 1936 that burrow into mud at the bottom  
1052 of the pond when water evaporates (McLachlan & Cantrell, 1980). Similarly, Dodson (1987)  
1053 found that *Dasyhelea subletti* Wirth, 1987 was the most common taxon in short-lived  
1054 ephemeral rock pools in the Moab desert, USA.

1055 Numerous species of culicid are associated with temporary waters in Africa (Coetzee,  
1056 2002), and many of them are vectors of parasites causing disease in humans and other  
1057 vertebrates. Several of the vectors prefer to breed in very small containers such as old tyres,  
1058 pots, and in footprints, or in phytotelmata: pools of water held by plants, for instance in the  
1059 axils of leaves. *Aedes aegypti* (Linnaeus, 1762) is the vector of yellow fever. While the  
1060 disease does not occur in southern Africa, *Ae. aegypti* does. It breeds in tiny containers, and  
1061 the eggs can withstand desiccation for years (Coetzee, 2002). Farnesi et al. (2015), comparing  
1062 the degree of resistance to desiccation of eggs of three species of mosquito, have shown that

1063 eggs of *Ae. Aegypti* can survive in a dry form for months, those of *Anopheles aquasalis*  
1064 Curry, 1932 for a day, and of *Culex quinquefasciatus* Say, 1823 for a few hours, these times  
1065 relating to the thickness of the egg shell. The members of ‘floodwater Aedes’, which can be  
1066 vectors of Rift Valley Fever, such as *Ae. (Neomelanicion) mcintoshi* Huang, 1985, *Ae.*  
1067 *(Neo.) circumluteolus* (Theobald, 1908), *Aedes (Neo.) luridus* Mcintosh, 1971, *Aedes (Neo.)*  
1068 *lineatopennis* (Ludlow, 1905), *Aedes (Ochlerotatus) caballus* (Theobald, 1912) and *Aedes*  
1069 *(Och.) juppi* Mcintosh, 1973, aestivate as eggs for up to 20 months (Jupp et al., 1980).

1070 Several members of the genus *Anopheles* are vectors of malarial parasites. Although some  
1071 anophelines prefer to oviposit in temporary waters, neither the eggs nor the larvae are  
1072 resistant to desiccation. First-instar larvae of *An. gambiae* s.l. are said to be amphibious  
1073 (Miller et al., 2007), in that they can survive in the film of water on the surface of mud. Both  
1074 *An. gambiae* s.s. and *An. arabiensis* Patton, 1905 (two South African vectors of malaria)  
1075 prefer sunny temporary pools and puddles, the major adaptation to this biotope being very  
1076 rapid larval development. Mosquitoes appear to overwinter as larvae in permanent waters  
1077 (Appleton et al., 1995).

1078 A few species of other dipteran families are known to occur in temporary waters in  
1079 southern Africa, but very little is known about their systematics or their biology. We  
1080 hypothesise that those occurring in the very arid western areas, such as the Namib Desert,  
1081 have some specific adaptations that allow them to persist in areas where rain pools are the  
1082 only surface freshwaters and these may fill only every few years.

### 1083 *Insecta: Coleoptera*

1084 Worldwide, beetles are one of the most abundant and speciose macroinvertebrate groups in  
1085 inland waters, occurring across the entire hydrological spectrum, from the smallest puddles  
1086 and phytotelmata, to large lakes and rivers. Water beetles are not a single taxonomic group,  
1087 and instead result from around 15-20 transitions between land and water during the  
1088 evolutionary history of the Coleoptera (Jäch & Balke, 2008; Mckenna et al., 2015; Short,  
1089 2018). Beetles are diverse and frequent inhabitants of temporary waterbodies, where  
1090 carnivorous taxa such as diving beetles (Dytiscidae) are often the top predators. Temporary  
1091 pool inhabitants are typically a mix of specialist and more generalist species, some of which  
1092 may only occur there temporarily as adults. In many cases, specialising in temporary pools  
1093 may have arisen as a life-history strategy to evade fish predation, and in the northern

1094 hemisphere some taxa characteristic of temporary ponds (e.g. *Agabus labiatus* (Brahm,  
1095 1790)) are also found in permanent, acidic, fish-free sites (Foster et al., 2016). Unlike most  
1096 freshwater insect groups, the majority of water beetles are aquatic as both larvae and adults,  
1097 but in many cases, the precise ecology of these life-history stages differs to some extent.  
1098 Some beetles utilise temporary waters primarily for reproduction, with adults occupying  
1099 different habitats. In the Mediterranean, *Acilius duvergeri* Gobert, 1874 for example,  
1100 breeding occurs in temporary lagoons, where larvae feed on microcrustacea in open water (a  
1101 strategy which would make them vulnerable to fish predation in permanent waters), whilst  
1102 adults occupy permanent ponds during summer drought (Dettner, 1982).

1103 Temporary pond water beetles have a variety of strategies to survive during the dry phase,  
1104 reflecting the diverse origins of aquatic beetles themselves, and the repeated evolution of  
1105 temporary water specialists from within these aquatic lineages. Temporary water species may  
1106 have shorter larval duration compared to their permanent water relatives, allowing  
1107 development to be completed during relatively short hydroperiods (e.g. Peters, 1972), and a  
1108 range of approaches exists to surviving dry phases, including migration to permanent waters  
1109 or adult/egg diapause *in situ* (e.g. Nilsson, 1986a, b, c). The most temporary of water bodies  
1110 appear to be devoid of breeding water beetles, suggesting that the extent to which larval  
1111 duration can be truncated may be limited. In addition, beetle larvae do not seem to have the  
1112 same resistance to desiccation as many temporary-water Crustacea (see above), but do have  
1113 the advantage that adults of most species can fly between habitats (e.g. Bilton et al., 2001).

1114 In southern Africa, members of a number of beetle families can be found in temporary  
1115 water bodies, although there are no formal publications dealing with their biology and  
1116 ecology. As a consequence, the following information is based on Bilton (pers. obs.), unless  
1117 otherwise stated. The faunas of vegetated temporary pools and rock pools appear to be quite  
1118 distinct, and in addition brackish water bodies have their own specialised beetle fauna.  
1119 Haliplidae are relatively rare in southern Africa, and members of *Haliphus* and *Peltodytes* are  
1120 mostly found in larger, more permanent waters. The rare Cape endemic, *Algophilus*  
1121 *lathridioides* Zimmermann, 1924 is poorly known ecologically, but appears to be a specialist  
1122 of slightly mineralised waters. The only recent record of this beetle is from the Berg River  
1123 floodplain close to Hopefield, where it occurs abundantly in slightly brackish temporary  
1124 flood pools in grassland. *Algophilus* is wingless, and is likely to be dispersed during floods,  
1125 having been found in floodwater along the Berg River in spring.

1126 Whereas the Noteridae are largely permanent water inhabitants, a number of Dytiscidae  
1127 are temporary pond specialists, and others are found there occasionally or temporarily as  
1128 adults. *Canthyporus* species occur across a spectrum of freshwater habitats, including  
1129 seepages, streams and ponds, both permanent and temporary (Biström & Nilsson, 2006;  
1130 Bilton et al., 2015). This genus is particularly diverse in the Cape, where most of its species  
1131 are endemic. Many of the species in this genus, including *C. aenigmaticus* Biström & Nilsson  
1132 2006 and *C. lateralis* (Boheman, 1848), are characteristic inhabitants of small mountain rock  
1133 pools, where both adults and presumed larvae can be found. Some inhabited pools form parts  
1134 of temporary stream/seepage systems during periods of high rainfall, whereas others  
1135 constitute completely isolated basins. Cape vernal pools are also inhabited by *Canthyporus*,  
1136 including the relatively generalist *C. hottentottus* (Gemminger & Harold, 1868) and *C.*  
1137 *petulans* Guignot, 1951, as well as *C. exilis* (Boheman, 1848), a species otherwise found in  
1138 temporary seeps and marshes. Besides the widespread genus *Hyphydrus*, the South African  
1139 Hyphydrini includes five endemic genera (see Ribera & Balke, 2007), three of which occur in  
1140 temporary ponds. *Darwinhydrus solidus* Sharp is found from the Cederberg to Port Elizabeth,  
1141 in both permanent and temporary waters, but is most frequent in densely vegetated Cape  
1142 vernal pools. *Primospes suturalis* Sharp, 1882 is largely restricted to the far southwest of the  
1143 Western Cape, and occurs in temporary pools and rivers, and two *Hydropeplus* species are  
1144 inhabitants of both stream pools and temporary lentic pools, both vegetated and rock pools.  
1145 Species of the genus *Rhantus* can also be found in vegetated temporary ponds, as both adults  
1146 and presumed larvae, as can the phylogenetically isolated Cape endemic *Caperhantus*  
1147 *cicurius* (Fabricius, 1787) (Bilton, 2017). The Critically Endangered Cape endemic  
1148 *Capelatus prykei* Turner & Bilton 2015 has been found in vernal pools on the Cape Flats  
1149 (Bilton et al., 2015).

1150 To date, only a single species of the largely Holarctic genus *Helophorus* has been reported  
1151 from southern Africa. *Helophorus aethiops* Balfour-Browne, 1954 is found throughout much  
1152 of the winter rainfall zone, and is common in a variety of temporary pools, particularly  
1153 shallow sites with exposed silt or sand substrates. The species-level taxonomy of southern  
1154 African *Hydrochus* remains incompletely resolved, but a number of species are found in  
1155 vegetated temporary ponds, as can many members of the Hydrophilidae, including *Enochrus*  
1156 *hartmanni* Hebauer, 1998; *Enochrus (Methydrus)* spp.; *Helochares* spp; *Paracymus* spp;  
1157 *Berosus* spp. and *Limnoxenus sjoestedti* Knisch, 1924, the latter being restricted to the South  
1158 African Cape (Short & Liebherr, 2007).

1159 The regional hydraenid beetle fauna is one of the most diverse on earth, most species in  
1160 the region being Cape endemics. Here the family also attains its maximum ecological and  
1161 morphological diversity, with both aquatic and (semi)terrestrial representatives (e.g. Perkins  
1162 & Balfour-Browne, 1994). Species of the genus *Prosthetops*, which includes some of the  
1163 largest hydraenids on earth, are characteristic inhabitants of temporary rock pools, where  
1164 larvae and adults can be abundant, grazing biofilms. Bilton (2013) noted that large larvae of  
1165 *P. wolfbergensis* Bilton, 2013 became active underwater in previously dry rock pools one day  
1166 after rains, suggesting some desiccation resistance mechanism in these insects. During dry  
1167 periods, *Prosthetops* adults can be found in rocky streams, although this does not appear to be  
1168 their breeding habitat. Temporary vegetated freshwater ponds are inhabited by a number of  
1169 species of *Hydraena* (*Hydraenopsis*), *Ochthebius* and *Parhydraena*, whilst temporary saline  
1170 pools are home to species of *Ochthebius*, including *O. capicola* (Péringuey, 1892), a  
1171 specialist of supralittoral coastal rock pools (Sabatelli et al., 2013), a habitat independently  
1172 colonised by members of this genus on a number of occasions worldwide (Sabatelli et al.,  
1173 2016).

## 1174 **Discussion**

1175 Much of southern Africa is characterised by a semi-arid or arid climate (Davis, 2011) and  
1176 small temporary wetlands, though not widely acknowledged, are one of the most abundant  
1177 and ubiquitous aquatic features of such landscapes (Silberbauer & King, 1991; Brendonck &  
1178 Williams, 2000; Williams, 2006). The invertebrates found in these wetlands, whilst not  
1179 widely acknowledged, constitute a significant proportion of the total aquatic biodiversity of  
1180 the region. Whilst some recent research has highlighted the ecological and biodiversity  
1181 importance of temporary wetland invertebrates (e.g. Spencer et al., 2002; Nicolet et al., 2004;  
1182 Urban, 2004; Jeffries, 2005; Williams, 2006; Vanschoenwinkel et al., 2007; Ruhí et al., 2013;  
1183 Batzer & Boix, 2016; Kneitel, 2016; Dalu et al., 2017a), baseline biodiversity data on these  
1184 faunas are often lacking. Here we present such a synthesis for southern Africa, in the hope  
1185 that this will aid further ecological investigations of temporary wetlands in the region.

1186 A clear finding of this work is that, with the exception of a few groups (e.g. gastropod  
1187 molluscs, odonates and certain dipteran families that act as disease vectors), we are often  
1188 unable to reliably name many of the invertebrate organisms inhabiting these waterbodies.  
1189 This becomes most obvious for the ‘lower’ invertebrate groups covered in this review, which  
1190 is perhaps not surprising given their small size and the practical difficulties which may be

1191 associated with collection and identification. For some of these groups, notably gastrotrichs,  
1192 bryozoans and tardigrades, there is very little information about the freshwater species that  
1193 occur throughout the region, including temporary wetlands. Although there is better  
1194 information in this regard for the Northern Hemisphere, the ‘lower’ invertebrate phyla of  
1195 freshwater environments have been relatively neglected worldwide (see Balian et al., 2008).  
1196 Perhaps more surprisingly, the status quo reveals that in some cases we cannot put reliable  
1197 names on species for groups represented by larger and more ‘charismatic’ organisms such as  
1198 the ‘clam shrimps’ (Laevicaudata, Cyclestherida and Spinicaudata, but see Rogers et al., 2012  
1199 for revision of the family Limnadiidae), ephemeropterans and many of the hemipterans from  
1200 temporary freshwater wetlands of the region. Harpacticoid copepods are another example of a  
1201 taxon completely unstudied in the region, even from permanent freshwater systems.

1202 To get a better hold on patterns of richness and endemism, one first needs to know what  
1203 species are present in these wetland systems. A case in point is the Cladocera, which have  
1204 traditionally been considered to contain few endemics in the region (Frey, 1993;  
1205 Korovchinsky, 2006; Smirnov, 2008). More recent work suggests that the apparent low  
1206 endemism is most likely an artefact of the limited state of knowledge of the fauna, rather than  
1207 genuinely low endemism (Van Damme et al., 2013). Thus, statements on patterns of richness  
1208 and endemism are of a preliminary nature at present for many of the invertebrate groups. A  
1209 few such patterns are worthy of comment here. First, only for a few of the groups is evidence  
1210 presented that they reach higher richness and/or endemism in temporary wetlands than for  
1211 their permanent wetland counterparts. These taxa include large branchiopods, ostracods,  
1212 copepods, cladocerans, certain dipterans (notably culicids) and coleopterans (some dytiscids).  
1213 Thus, for the vast majority of freshwater invertebrate taxa in the region, permanent  
1214 waterbodies would appear to hold a greater richness and/or endemism than temporary ones.  
1215 Despite this, temporary wetlands support unique and specialised taxa. For instance, the  
1216 temporary wetland ostracod fauna of northern and central Namibia and Botswana has a  
1217 generic endemism rivalled worldwide only by East African paleolakes (Martens, 2001).  
1218 Another feature of the ostracod fauna is the specific diversity in the family Lymnocytheridae  
1219 for rock pools of the Drakensberg (SA), which is unmatched anywhere else in the world  
1220 (Martens et al., 1998). Southern Africa is considered one of the world’s hotspots of large  
1221 branchiopod diversity (Tuytens et al., 2015), almost all of which is housed in temporary  
1222 wetlands. When considering the region’s area, the anostracan fauna is one of the richest  
1223 worldwide and also has a very high endemism (~80% at the time of the review of Hamer &



1224 Brendonck, 1997). Other than for the anostracans and ostracods, further commentary on  
1225 which of the major invertebrate groups covered in this review stand out globally for their  
1226 richness/endemism is limited due to the taxonomic uncertainty associated with most of the  
1227 groups in the region, as highlighted above.

1228 Identifications to genus and species level of specimens mentioned in this review are  
1229 mostly based on morphological characteristics (unless specifically mentioned otherwise) and  
1230 accuracy greatly depends on reliable identification keys and taxonomic expertise, which is  
1231 considered a scarce skill in southern Africa (Hamer, 2013). The few region-specific keys that  
1232 exist are in need of updating (Barber-James & Gattolliat, 2012). Species identification using  
1233 molecular systematics has only become prominent in the region recently (da Silva &  
1234 Willows-Munro, 2016) and will greatly contribute to more accurate identification of species  
1235 recorded in temporary wetlands in future.

1236 Another general trend picked up from this review is that virtually all of the major  
1237 invertebrate groups possess some sort of adaptation for survival in temporary wetlands.  
1238 Although only certain taxa can truly withstand desiccation (e.g. branchiopods, ostracods and  
1239 copepods), many taxa have dispersal mechanisms which allow them to leave the waterbody  
1240 before it dries up (e.g. leeches, water mites and odonates), or are able to survive the drought  
1241 phase as adults (e.g. dipterans). Many of the taxa inhabiting these environments are habitat  
1242 generalists that may opportunistically exploit temporary waterbodies for the advantages  
1243 afforded by these environments, such as reduced levels of predation and competition  
1244 (although this notion is in itself controversial, see Brendonck et al., 2002). A case in point is  
1245 the Odonata and Hemiptera, which are common and widespread in temporary wetlands of the  
1246 region, but tend to be opportunistic colonisers of these environments, depending on dispersal  
1247 for survival and having large home ranges, and thus are generally not threatened. This  
1248 generalistic nature of many of the inhabitants of temporary wetlands in the region is  
1249 hypothesized as one of the reasons why many of the taxa do not display high levels of  
1250 endemism. There are certain exceptions, such as for rock pools of the Drakensberg in the east  
1251 of the region, and the lowland pools of the Western Cape province, both of which are  
1252 hotspots of ostracod and cladoceran endemism and richness (Martens et al., 1998; Martens,  
1253 2001; de Moor & Day, 2013; Van Damme et al., 2013).

1254 In terms of the best known of the temporary wetland specialists, ‘fairy shrimp’  
1255 (anostracan) species richness is depicted as an array of hotspots throughout the region, not

1256 being centered on any particular area and does not appear to be governed by any particular  
1257 climatic factor (Hamer & Brendonck, 1997). The large branchiopod crustaceans show the  
1258 greatest potential as ‘flagships’ for conservation of temporary wetlands in the region, given  
1259 their relatively large size and uniqueness in terms of adaptations to life in the temporary  
1260 aquatic realm. The odonates, molluscs and anostracans are the only groups covered in this  
1261 review to have an appreciable amount of IUCN Red List information in the region. The  
1262 freshwater molluscs appear to have few threatened species in the region (10 species, 8.6%  
1263 of the fauna, Kristensen et al., 2009). Anostracan Red List information is still far from  
1264 comprehensive. For instance, De Roeck et al. (2007) reported that only two of the 14  
1265 anostracan species known to occur in the Western Cape province of SA were listed by IUCN  
1266 and that insufficient data were available to determine the IUCN Red Data Category of six of  
1267 these species. Of the 46 anostracan species reported for southern Africa by Hamer &  
1268 Brendonck (1997), two were considered by IUCN (1994) as ‘Critically Endangered’, four  
1269 were ‘Endangered’, three were ‘Vulnerable’ and 24 were ‘Least Concern’, whilst data were  
1270 deficient for the categorisation of 13 species. As is the trend worldwide, the anostracans of  
1271 the region are threatened by agriculture and urbanization, due to both indirect (pollution and  
1272 pesticides) and direct (physical) habitat alteration arising from these activities (Brendonck et  
1273 al., 2008). These factors are thought to have driven the extinction of *Streptocephalus gracilis*  
1274 Sars, 1898 and *Branchipodopsis karroensis* Barnard, 1929 (De Roeck et al., 2007).

1275 We hypothesize that temporary wetland specialists such as the branchiopods (including  
1276 cladocerans), ostracods and copepods, which tend to be more habitat-restricted and less  
1277 capable of escaping degradation, are more likely to be affected by human impacts than for  
1278 taxa that are able to easily disperse to other more favourable areas (e.g. dipterans,  
1279 hemipterans, odonates and coleopterans). The sensitivity of the region’s temporary wetland  
1280 invertebrates to human impacts such as pollution and habitat alteration is a topic still under  
1281 investigation, with some evidence indicating a resilient fauna (Bird et al., 2013), whilst other  
1282 evidence is in favour of a more sensitive fauna (Bird & Day, 2016), especially when effects  
1283 are combined with climate change impacts (Dalu et al., 2017a). Whatever the case may be,  
1284 what is certain is that temporary wetland habitats worldwide have been degraded and  
1285 destroyed at an alarming rate (Semlitsch & Bodie, 1998), and various studies indicate that the  
1286 situation is no different in southern Africa (De Roeck et al., 2007; Bird & Day, 2014; Dalu et  
1287 al., 2017a).

1288 In terms of the way forward, we cannot expect to properly understand and conserve  
1289 temporary wetlands if we don't know what lives in them. As things stand, this is certainly the  
1290 case in southern Africa in that we lack updated taxonomic information for many groups that  
1291 inhabit these systems. This review shows that we have a base of knowledge on which to  
1292 work, but the now famous stagnation of taxonomic expertise both locally and abroad (see  
1293 Godfray, 2002; Wheeler et al., 2004; Agnarsson & Kuntner, 2007; Bebber et al., 2014) is a  
1294 major threat hindering the further progression of this knowledge. In addition to providing a  
1295 synthesis for southern Africa, this work highlights the dearth of fundamental taxonomic  
1296 information on the invertebrate fauna of temporary wetlands in the region, and constitutes a  
1297 plea for more foundational taxonomic work to be initiated.

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1304

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