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

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Abstract

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

Keywords

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

Introduction

Invertebrates dominate the faunas of temporary wetlands worldwide, in terms of species diversity, abundance and animal biomass (Williams, 2006). Insects and crustaceans, in particular, are ubiquitous in such systems. Temporary wetlands house a suite of uniquely specialized invertebrates (Wiggins et al., 1980; Collinson et al., 1995; Brucet et al., 2005; Escalera-Vázquez & Zambrano, 2010; Strachan et al., 2015) which are particularly vulnerable to habitat and hydrological modifications (Calhoun et al., 2017; Dalu et al., 2017a). The southern African region, with its distinct climatic and geomorphic features, has one of the highest densities of temporary depression wetlands (known locally as ‘pans’) worldwide (Goudie & Wells, 1995). Reviews of the invertebrate fauna of temporary wetlands have been conducted for a number of regions globally (e.g. Batzer et al., 1999; Batzer & Boix, 2016), but not for southern Africa; as such, this study aims to fill the knowledge gap. Southern Africa is generally defined as the area south of the Kunene River in the west and the Zambezi River in the east (including the countries of Botswana, Lesotho, Namibia, South Africa, Swaziland, Zimbabwe, and southern parts of Angola and Mozambique). These boundaries are referred to as ‘the region’ or ‘the southern African region’ throughout this review.

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

Methods

A comprehensive review of all published material in peer-reviewed journals for the period 1960 to 2016 was conducted using a combination of the following terms: ‘temporary’, ‘seasonal’, ‘ephemeral’, ‘vernal’, ‘endorheic’, ‘rock’, ‘rain’, ‘pond’, ‘pool’, ‘pan’, ‘tarn’, ‘depression’, ‘southern Africa’, plus all the individual countries within it, and ‘invertebrates’, plus all the major taxa within. References to other important studies cited in the published material above were also referred to and in turn these were also searched thoroughly for further important cited work. In this way, the relevant literature has been comprehensively surveyed. Only those papers that tackled invertebrate populations or communities from wetland systems that temporarily dry up were included in the final list used for this review. However, in certain cases, there was no mention of whether the wetland was temporarily inundated or not. In such cases it was necessary to pay careful attention to the mention of or inference to flagship taxa (sensu De Roeck et al., 2007) or the adaptive traits to drying conditions (Lahr, 1997) as this would confirm the temporary nature of the wetland. The review aims to focus on lentic isolated depressional wetlands that are not connected to longitudinal watercourses (i.e. non-riverine systems). However, such specific habitat information is often not available for a given taxon, and thus we include taxa that have simply been recorded as occurring in temporary wetland environments, even if information on the specific nature of these environments is not available for the taxon in question.

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

Major invertebrate groups

Porifera

Sponges occur in permanent and temporary freshwater systems worldwide, both lotic and lentic (Manconi & Pronzato, 2008). In southern Africa there are two known families, Spongillidae (five genera, seven species) and Potamolepidae (two genera, species information unavailable, Heeg, 2002a). There appears to be a low richness of sponge taxa in southern African freshwater environments compared to other regions (Manconi & Pronzato, 2008) but, as with many of the lesser-known phyla, additional collecting effort is likely to reveal more species (Heeg, 2002a). *Ephydatia fluviatilis* (Linneaus, 1758) of the Spongillidae is the only known species that has often been recorded from temporary wetlands in the region, usually found on the stems of emergent macrophytes. This species appears to be distributed throughout South Africa (SA) and Namibia (Heeg, 2002a). Sponges generally survive drought periods through formation of gemmules, which are internal buds composed of amoebocytes surrounded by an external protective coat comprising collagen layers embedded with spicules (for review, see Frost, 1991).

Cnidaria

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

Platyhelminthes (flatworms)

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

Curtis (1991) reported that only one species of freshwater turbellarian, *Mesostoma brincki* Marcus 1970, had been positively identified from Namibia. In a comprehensive global collation of turbellarian species with Gondwanan affinities, Noreña et al. (2003) listed six freshwater turbellarians (*Xenostenostomum microstomoides* Reisinger, 1976; *Prorhynchus brincki* Marcus, 1955; *Bothrioplana semperi* Braun, 1881; *Mesostoma brincki*; *M. ewerum* Du Bois-Reymond Marcus 1951; *Phaenocora foliacea* (Böhmig, 1914)) from the region, but did not indicate how many of these occur in temporary wetlands. Houben et al. (2014) reported *P. foliacea* from a temporary pond in Hluhluwe Game Reserve, SA. Tubellarians can cope with the periodic drying up of temporary wetlands by producing cysts, and these can come out of dormancy after 5-7 minutes of inundation (Van Steenkiste et al., 2010).

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

Gastrotricha

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

Bryozoa

Bryozoans have been noted as relatively common in freshwater environments in southern Africa (Heeg, 2002c; de Moor & Day, 2013), but remain largely uncollected and unstudied in the region. Heeg (2002c) comments that the bryozoan fauna of Africa appears to contain mostly cosmopolitan species, but lists only four species as recorded from the region (*Plumatella emarginata* (Allman, 1844), *P. repens* (Linnaeus, 1758), *Lophopodella capensis* (Sollas, 1908) and *Hyalinella punctata* (Hancook, 1850)). It is highly likely that bryozoans inhabit temporary wetlands across large areas of the southern African region, given that they are well adapted to survive desiccation. Bryozoans germinate by producing desiccation-resistant statoblasts that have hooks for clinging to large mobile animals such as waterfowl and are thus able to disperse passively over wide geographical areas (Bilton et al., 2001).

Nematoda

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

Nematomorpha

Information on the genera and species of the parasite phylum Nematomorpha (horsehair worms) in southern African water bodies is extremely sparse, but the few records that do exist suggest a wide distribution (Rayner & Appleton, 2002). Corrêa (1951) reported two species of *Prostoma* as widespread in SA. In a review of known African species, Schmidt-Rhaesa & Perissinotto (2016) reported a further six species from SA belonging to the genera *Chordodes, Paragordius* and *Beatogordius*. They also described a previously unconfirmed species (*Chordodes ferox* Camerano, 1897) collected from a live praying mantid floating in a river in the Eastern Cape province, SA. Nine species recorded by Corrêa (1951) and Schmidt-Rhaesa & Perissinotto (2016) appear to be all that is known taxonomically of the fauna from the southern African region to date. Nematomorph larvae are dependent on an aquatic medium, where they generally penetrate the bodies of arthropods (particularly orthopterans) and spend the vast majority of their lives growing into large adult worms inside the host body. Thus, nematomorphs possess traits that pre-adapt them to life in temporary wetlands (Williams, 2006) and it is likely that they inhabit such environments in southern Africa.

Rotifera

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

Tardigrada

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

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

Annelida

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

Approximately one-third of the almost 5 000 valid species of oligochaetes worldwide are aquatic, of which approximately 1 100 are found in freshwater environments (Martin et al., 2008). About 50 microdrile and 20 megadrile taxa have been recorded from southern Africa (van Hoven & Day, 2002). Whilst most of the microdrile species are cosmopolitan, the megadriles are mostly African endemics (van Hoven & Day, 2002). None of the taxonomic works specifically report on which oligochaete taxa are found in southern African temporary wetlands, but the megadrile earthworm *Lumbriculus variegatus* (Müller, 1774) (cosmopolitan species) and microdriles belonging to *Nais* (Naididae) have been reported in faunal lists from ecological studies of temporary wetlands in the region (e.g. Bird & Day, 2016). Oligochaete specimens from southern African wetland studies are most commonly reported at the ordinal level as ‘Oligochaeta’ (e.g. Anusa et al., 2012; Ferreira et al., 2012). Oligochaetes can survive desiccation in temporary wetland environments by forming dehydration-resistant cysts, empirically documented for lumbriculids (Anlauf, 1990) and naidids (Montalto & Marchese, 2005).

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

Mollusca

Approximately 111 species of gastropod and 26 bivalves have been reported from southern Africa, which includes 10 alien gastropod species (Appleton, 2002b). The region has very low freshwater molluscan endemicity at about 12.3% (Appleton, 2002b). According to Brown's (1994) habitat records, the following species are frequently found in temporary wetlands: *Pila occidentalis* (Mousson, 1887); *Lanistes ovum* Troschel, 1845; *Tomichia ventricosa* (Reeve, 1842); *Ceratophallus natalensis* (Krauss, 1848); *Lymnaea natalensis* Krauss, 1848; *L. columella* (introduced from North America, now widespread in Africa); *Physa acuta* Draparnaud, 1805 (introduced from Europe, now widespread in Africa); *Biomphalaria pfeifferi* (Krauss, 1848); *Bulinus globosus* (Morelet, 1866) *B. forskalii* (Ehrenberg, 1831); *B. reticulatus* (Mandahl-Barth, 1954); *B. tropicus* (Krauss, 1848); *B. scalaris* (Dunker, 1845); and *Aplexa marmorata* (Guilding, 1828). *Aplexa marmorata* is an invasive species from South America, which has recently been recorded from temporary wetlands as far south as Cape Town by Mlambo et al. (2011).

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

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

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

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

Crustaceans: Malacostraca

Most freshwater-dwelling members of the class Malacostraca (i.e. Amphipoda, Isopoda and Decapoda) lack physical adaptations for diapause or dispersal. Thus, they are not commonly associated with temporary wetlands but, due mostly to behavioural adaptations, certain species are able to persist in temporary waters (Williams, 2006). Amphipods appear to be very scarce in southern African temporary wetlands and virtually no records exist of their occurrence in these systems. Mlambo et al. (2011) and Bird & Day (2016) both recorded populations of the Gondwanan relictual species *Paramelita capensis* (Barnard 1916) and *P. pinnicornis* Stewart and Griffiths 1992 in small temporary wetlands of the Kenilworth Racecourse Conservation Area in Cape Town. However, studies of how these amphipods survive the summer dry phase have not been undertaken. A study of the North American amphipod *Crangonyx pseudogracilis* Bousfield, 1958 provides evidence that this epigean species is able to inhabit parts of the water table during the dry phase of a temporary wetland and this mechanism explains both its ability to persist and its ubiquity across a network of nearby wetlands (Harris et al., 2002). The authors suggest that such subterranean explorations by epigean amphipods may be a key mechanism for amphipod survival in temporary wetlands in other parts of the world. Another interesting behavioural adaptation in amphipods is reported from a congeneric North American amphipod, *C. antennatus* Packard, 1881, which survives the desiccated phase of mud-bottom pools by digging a burrow into the mud that is then blocked off from the outside with an air bubble (Holsinger & Dickson, 1977). The burrow itself remains hydrated and provides a temporary aquatic refuge until the pool refills.

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

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

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

Crustaceans: Large branchiopods

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

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

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

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

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

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

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

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

The order Notostraca (tadpole shrimps) are branchiopod crustaceans that are known from as far back as the Triassic Period, earning them the status of ‘living fossils’ (Fryer, 1988; Vanschoenwinkel et al., 2012), although recently this concept for the group has been challenged (Mathers et al., 2013). Rayner (1999) provides an overview of the morphology, habitat preferences, feeding, reproduction and identification of southern African notostracans. Two species of *Triops* have been recorded from southern Africa, *T. granarius* (Lucas, 1864) and *T. cancriformis* (Bosc, 1801), although the latter is rare and has only been recorded from Ovamboland (northern Namibia) and the Kalahari (Hamer & Rayner, 1995). *T. granarius* is common and widespread in the drier areas of southern Africa (<500 mm mean annual rainfall), preferring muddy temporary pools seldom exceeding one hectare in size (for more detailed distribution records see Hamer & Rayner, 1995). *Triops* taxonomy in southern Africa (and worldwide for that matter) is not without controversy. For instance, Korn & Hundsdoerfer (2006) used ribosomal DNA markers to investigate genetic distinctiveness of *T. granarius* populations from Tunisia, Namibia and Japan, and their results strongly suggest that the three populations belong to different, possibly cryptic species. Thus, further molecular phylogenetic work on African *Triops* populations is required to more clearly resolve cryptic species complexes.

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

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

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

Crustaceans: Ostracoda

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

Martens (2001) provides a taxonomic key for the genera (and species for some recently-revised genera) of southern African freshwater ostracods, many of which are found in temporary wetland environments. Following this reference, the genera that have been unequivocally recorded from temporary wetlands are: *Cypricercus, Eundacypris, Gomphocythere, Globocypris, Korannacythere, Leucocythere, Megalocypris, Ovambocythere, Physocypria, Pseudocypris, Ramotha, Sarscypridopsis, Sclerocypris, Zonocypris*. Jocqué et al. (2006) reported *Potamocypris* and *Strandesia* from temporary rock pools in Botswana, while *Amphibolocypris* (*A. arida* and *A. exigua*) were recorded from temporay rock pools in Botswana and a temporary soft-bottomed wetland in KNP, respectively (Jocqué et al., 2010).

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

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

Crustaceans: Copepoda

Copepods are one of the most diverse crustacean groups, including over 14,000 known species of both free-living and symbiotic forms. Most free-living copepods are marine, but approximately 2,800 species have colonized a wide variety of freshwater habitats (Boxshall & Defaye, 2008). Copepods in freshwaters represent a pivotal component of the food webs as part of the zooplankton and benthic/littoral communities worldwide. Up to 20 genera and 51 species of freshwater copepods have been recorded from the region (Rayner, 2001). Most of the information available for the region concerns the calanoid copepods (order Calanoida) and there has been virtually no recent taxonomic research on the cyclopoids or harpacticoids. Among the calanoids, only members of the exclusively freshwater family Diaptomidae have been recorded in the region (Rayner & Heeg, 1994). The subfamily Diaptominae, containing about 410 species, is represented in the region by the genera *Tropodiaptomus* and *Thermodiaptomus*, both of which occur in more permanent waters and are not considered further here. The diaptomid subfamily Paradiaptominae currently consists of 25 species (Suárez-Morales et al., 2015), most of which are endemic to Africa and adapted to life in temporary wetlands (Rayner, 2001). This largely endemic group includes a genus, *Lovenula*, that comprises extremely large individuals (de Moor & Day, 2013). Rayner (2001) provides a taxonomic key to the species of Diaptomidae in the region, along with cursory notes on the cyclopoid and harpacticoid taxa that have been described or recorded from the region. The following species in the subfamily Paradiaptominae have thus far been recorded from temporary wetlands in the region (for distributional information, see Day, 1990; Rayner, 1998; Rayner, 2000, 2001; Suárez-Morales & Rayner, 2004; Suárez-Morales et al., 2015): *Lovenula falcifera* (Lovén 1845), *L. africana* (Daday, 1908), *L. simplex* Kiefer, 1929, *L. raynerae* Suárez-Morales, Wasserman & Dalu 2015, *Paradiaptomus lamellatus* Sars, 1895, *P. schultzei* van Douwe, 1912, *P. similis* van Douwe, 1912, *P. peninsularis* Rayner, 1999, *P. hameri* Rayner, 1999, *Metadiaptomus capensis* (Sars, 1907), *M. purcelli* (Sars, 1907), and *M. meridianus* (van Douwe, 1912).

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

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

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

Crustaceans: Cladocera

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

Survival strategies of cladocerans in temporary wetlands are broadly similar to those of the other microcrustaceans, with highly desiccation-resistant eggs being produced as water levels draw down (Vandekerkhove et al., 2005). Cladocerans favour parthenogenetic (asexual) cloning during favourable times when the wetland is inundated and males are rare for much of the hydroperiod (Williams, 2006). Males appear more frequently towards the end of the hydroperiod and sexual reproduction prevails as water disappears from the wetland. Whilst parthenogenetic cloning produces soft eggs for rapid development, sexually produced eggs are encased in a hardened ephippium and can withstand drying, freezing and passive dispersal to other waterbodies (Bilton et al., 2001; Vandekerkhove et al., 2005; Williams, 2006). As has been found in many aquatic environments globally, cladocerans have also been identified as important trophic components in systems of the region (Dalu et al., 2016; Wasserman et al., 2016b; Dalu et al., 2017b; Dalu et al., 2017c).

Hydrachnidia: Water mites

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

The great diversity of water mites in temporary habitats is remarkable, given that most do not possess the typical adaptations of temporary wetland invertebrates (either diapause of eggs/adults or active dispersal as adults) (Bohonak et al., 2004). Instead, the radiation of water mites in temporary wetlands has been facilitated by parasitic larvae that, once hatched from eggs laid within a waterbody, parasitize adult insects and are thus dispersed to other waterbodies (Bilton et al., 2001; Bohonak et al., 2004). Parasitism is obligate in all species studied so far that colonize astatic water bodies, and mite larvae die if they fail to penetrate an insect host (Bohonak et al., 2004). However, not all water mites survive the dry phase via parasitism, and certain taxa (e.g. some members of the Hydryphantidae) are capable of surviving dry phases as deutonymphs or adults that enter an inactive state in microhabitats with persistent moisture, such as moist mud or damp crevices in logs (Wiggins et al., 1980; Bohonak et al., 2004).

Insecta: Ephemeroptera (mayflies)

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

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

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

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

Insecta: Odonata

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

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

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

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

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

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

Insecta: Hemiptera

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

Most species have winged adults that disperse well and can therefore colonise temporary wetlands quickly. The nepomorph families all breathe air through plastrons or respiratory tubes, and the gerromorph families are epipleustonic, living just above the water surface rather than in the water, so dissolved oxygen does not limit the potential of a water body for colonisation by water bugs. The species in most families are generalist predators, and can therefore inhabit a wide variety of waters with flow rates that are slow or absent. Many gerromorphs associate with floating or emergent vegetation that helps them to avoid predators and being washed away in flowing waters (Reavell, 2003). Immature nymphs have biologies similar to their adults, but cannot fly, so they complete their development only in temporary wetlands that take more than (generally) four to ten weeks to dry up. Adults of some species of gerromorph may be winged or apterous (regulated by temperature and photoperiod); when apterous adults inhabit a temporary wetland, they indicate that at least one generation has completed its life cycle in the wetland. The high mobility and broader habitat preferences of most aquatic bugs means that populations of temporary wetland species are generally not threatened (Collinson et al., 1995).

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

Insecta: Trichoptera

Trichoptera are holometabolous insects, mostly with an aquatic larval and a terrestrial adult phase. They have been recorded worldwide with the exception of some oceanic islands and the polar regions (de Moor & Scott, 2003). The Trichoptera World Checklist (Morse, 2011) lists 14 548 species of 616 genera in 49 families recorded globally thus far. Of these, 1 193 species (8.2%) in 83 genera from 21 families are known to occur in southern Africa (Tobias & Tobias, 2008). Recently, some species were collected in temporary wetlands, despite the earlier assertion of Scott (1970) that Trichoptera do not inhabit temporary lentic waters of the region: *Oxyethria velocipes* (Barnard, 1934) (Jones, 2002; Day et al., 2010) and *Athripsodes* sp. (Bird, 2012), both from the Western Cape province; and *Ecnomus thomasseti* Mosely, 1932, *Oecetis* sp. and *Oxyethira* sp. from Mpumalanga province (Ferreira et al., 2012). Trichoptera found in temporary waters show several adaptations to this habitat in different life stages, but little is known about this in southern Africa as research has mainly been conducted on species from other regions, discussed below. Larvae use silk to construct transportable or fixed cases from material readily available, such as sand, small stones, sticks, leaves and algae. The ability to build cases has allowed trichopteran larvae to adapt to a wide range of environmental conditions: spring sources, mountain streams, splash zones of waterfalls, large rivers, lakes and temporary wetlands (de Moor & Scott, 2003). Many species are represented in cooler and faster-moving waters as dissolved oxygen is a limiting factor for habitat colonisation (de Moor & Scott, 2003).

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

As water levels decrease during drying, faunal density increases and cases offer a protective body covering and camouflage to protect larvae from predation. A combination of case material (mineral rather than organic), shape (short, wide case with “hedgehog” structure rather than long tubular cases or flat purses) and defensive behaviour (retreating deep into the case and remaining motionless) are adaptive strategies employed by *Limnephilus externus* Hagen, 1861 against predation by diving beetle larvae (*Dytiscus* sp.) (Wissinger et al., 2006). Another species, *L. picturatus* McLachlan, 1875, evades predation of pupae by burrowing into soft substrates to pupate, whereas larvae of *Asynarchus nigriculus* (Limnephilidae) (Banks, 1908) build stronger mineral cases prior to pupation. Furthermore, both species have faster developmental times, which reduce temporal overlap with predators (Wissinger et al., 2003). Pupae can develop while the water column has dried up and the soil is still moist (Wiggins, 1973). The case material is important with regard to pond-drying. Larvae of *L. coenosus* Curtis, 1834 construct cases using organic material whereas *L. vittatus* (Fabricius, 1798) larvae use mineral material. Organic material has been shown to retain moisture better than mineral material, preventing drying of larvae (Zamora-Muñoz & Svensson, 1996).

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

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

Adults of *L. externus*, *L. picturatus* and *A. nigriculus* emerge prior to pond-drying and females enter an ovarian diapause after mating (Wissinger et al., 2003). Summer diapause is an important adaptation to survive dry periods (Wiggins, 1973; Wiggins et al., 1980), which also protects eggs from predation, drying and freezing (Wissinger et al., 2003). Oviposition in temporary pools usually occurs above or near water, not directly in water as is normal for most trichopteran species (Wiggins, 1973). Eggs are deposited in a gelatinous egg-matrix, which is highly resistant to extremes like desiccation and freezing (Wiggins, 1973). Eggs are deposited under rocks and logs, where larvae hatch and develop further within a gelatinous mass until re-wetting occurs (Wissinger et al., 2003). *Lectrides varians* Mosely, 1953 show a bimodal response – some larvae become active with the first onset of re-wetting or re-immersion whereas others remain aestivating and only become active when surface water levels are more stable. Although this adaptation ensures population survival, it is at the cost of larval survivorship (Wickson et al., 2012). Larvae enter the temporary ponds with, for example, melt water, develop further and pupate prior to pond-drying (Wissinger et al., 2003).

Insecta: Diptera

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

Chironomids mostly survive dry periods as adults. Frouz et al. (2003) reviewed the strategies employed by chironomids to survive the variable environment of temporary wetlands. Given that larvae of several species are found in hyper-arid conditions in the Namib Desert, where pools may not form for 5 to10 years at a stretch, the question yet to be answered is, “How are the *adults* able to survive the dry years in these environments?” A few other species survive for some time in stout pupal cocoons during dry periods (Armitage, 1995), but presumably these periods are relatively short. When it comes to survival under harsh conditions, larvae of the ‘sleeping chironomid’, *Polypedilum vanderplanki* Hinton, 1951, hold the record. The species breeds in small unshaded rock pools in Central and West Africa. Larvae can undergo up to 17 years of desiccation and, when wetted, will ‘wake up’ and behave normally, feeding and growing until the next time they are desiccated. Hinton (1960) performed various experiments on these remarkable organisms, showing that they can withstand temperatures between -270°C and +102°C and can survive through a wetting/drying cycle at least ten times. An additional species of ‘sleeping chironomid’, *P. ovahimba* Cranston, 2014, has been recently described from rock pools of the Waterberg Plateau, Namibia (Cranston, 2014).

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

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

Numerous species of culicid are associated with temporary waters in Africa (Coetzee, 2002), and many of them are vectors of parasites causing disease in humans and other vertebrates. Several of the vectors prefer to breed in very small containers such as old tyres, pots, and in footprints, or in phytotelmata: pools of water held by plants, for instance in the axils of leaves. *Aedes aegypti* (Linnaeus, 1762) is the vector of yellow fever. While the disease does not occur in southern Africa, *Ae. aegypti* does. It breeds in tiny containers, and the eggs can withstand desiccation for years (Coetzee, 2002). Farnesi et al. (2015), comparing the degree of resistance to desiccation of eggs of three species of mosquito, have shown that eggs of *Ae. Aegypti* can survive in a dry form for months, those of *Anopheles aquasalis* Curry, 1932 for a day, and of *Culex quinquefasciatus* Say, 1823 for a few hours, these times relating to the thickness of the egg shell. The members of 'floodwater Aedes', which can be vectors of Rift Valley Fever, such as *Ae.* (*Neomelaniconion*) *mcintoshi* Huang, 1985, *Ae.* (*Neo.*) *circumluteolus* (Theobald, 1908), *Aedes* (*Neo.*) *luridus* Mcintosh, 1971, *Aedes* (*Neo.*) *lineatopennis* (Ludlow, 1905), *Aedes* (*Ochlerotatus*) *caballus* (Theobald, 1912) and *Aedes* (*Och.*) *juppi* Mcintosh, 1973, aestivate as eggs for up to 20 months (Jupp et al., 1980).

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

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

Insecta: Coleoptera

Worldwide, beetles are one of the most abundant and speciose macroinvertebrate groups in inland waters, occurring across the entire hydrological spectrum, from the smallest puddles and phytotelmata, to large lakes and rivers. Water beetles are not a single taxonomic group, and instead result from around 15-20 transitions between land and water during the evolutionary history of the Coleoptera (Jäch & Balke, 2008; Mckenna et al., 2015; Short, 2018). Beetles are diverse and frequent inhabitants of temporary waterbodies, where carnivorous taxa such as diving beetles (Dytiscidae) are often the top predators. Temporary pool inhabitants are typically a mix of specialist and more generalist species, some of which may only occur there temporarily as adults. In many cases, specialising in temporary pools may have arisen as a life-history strategy to evade fish predation, and in the northern hemisphere some taxa characteristic of temporary ponds (e.g. *Agabus labiatus* (Brahm, 1790)) are also found in permanent, acidic, fish-free sites (Foster et al., 2016). Unlike most freshwater insect groups, the majority of water beetles are aquatic as both larvae and adults, but in many cases, the precise ecology of these life-history stages differs to some extent. Some beetles utilise temporary waters primarily for reproduction, with adults occupying different habitats. In the Mediterranean, *Acilius duvergeri* Gobert, 1874 for example, breeding occurs in temporary lagoons, where larvae feed on microcrustacea in open water (a strategy which would make them vulnerable to fish predation in permanent waters), whilst adults occupy permanent ponds during summer drought (Dettner, 1982).

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

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

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

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

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

Discussion

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

A clear finding of this work is that, with the exception of a few groups (e.g. gastropod molluscs, odonates and certain dipteran families that act as disease vectors), we are often unable to reliably name many of the invertebrate organisms inhabiting these waterbodies. This becomes most obvious for the ‘lower’ invertebrate groups covered in this review, which is perhaps not surprising given their small size and the practical difficulties which may be associated with collection and identification. For some of these groups, notably gastrotrichs, bryozoans and tardigrades, there is very little information about the freshwater species that occur throughout the region, including temporary wetlands. Although there is better information in this regard for the Northern Hemisphere, the 'lower' invertebrate phyla of freshwater environments have been relatively neglected worldwide (see Balian et al., 2008). Perhaps more surprisingly, the status quo reveals that in some cases we cannot put reliable names on species for groups represented by larger and more 'charismastic' organisms such as the 'clam shrimps' (Laevicaudata, Cyclestherida and Spinicaudata, but see Rogers et al., 2012 for revision of the family Limnadiidae), ephemeropterans and many of the hemipterans from temporary freshwater wetlands of the region. Harpacticoid copepods are another example of a taxon completely unstudied in the region, even from permanent freshwater systems.

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

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

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

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

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

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

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

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