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Freshwater rock pools: a review of habitat characteristics, faunal diversity and conservation value

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SUMMARY

1. In the light of the recent surge of interest in small and often temporary wetlands as model systems for ecological and evolutionary research, this article reviews current knowledge on freshwater rock pools and their fauna.
2. Freshwater rock pools occur all over the globe in all major biomes and depend mainly on precipitation for filling. Rock pool clusters are some of the more persistent and oldest freshwater habitats worldwide. Interactions between climate and geology (e.g. limestone, sandstone, granite) generally determine the morphology and hydrology of rock pool habitats, with hydroperiods ranging from several days up to the whole year. Pool volume is usually small, resulting in strongly fluctuating environmental conditions, low conductivity and wide variations in pH (from 4.0 to 11.0) and temperature (from freezing point to 40 °C) often with well-marked diel cycles. The highly variable environmental conditions, combined with the unpredictability of the flooding regime, require high stress tolerance of the inhabitants, with adaptations for surviving the dry phase such as the production of resistant stages and active emigration followed by recolonisation.
3. About 460 aquatic animal species have been recorded from freshwater rock pools around the world. Approximately 170 of these are passive dispersers, which mainly disperse as resting stages via wind and overflow of water between pools. Successful long distance dispersal seems limited. This group is composed mainly of rock pool specialists with a high degree of endemicity. The remaining taxa can be considered active dispersers, with migration usually restricted to the adult stage. Often these taxa are broadly distributed and occur in a wide range of temporary habitats in addition to rock pools.
4. The inherent characteristics of freshwater rock pools, such as their simple structure and occurrence on similar substrata all over the world, facilitate comparison of research results and promote rock pools as model systems for ecological and evolutionary research. Nevertheless, despite their potential as model systems, the unique fauna and their importance as sources of freshwater in dry countries, the ecology of freshwater rock pools remain virtually unexplored in large parts of the world.

Keywords: diversity, freshwater, model system, rock pool, temporary

Introduction

Compared to permanent waters, small and temporary waterbodies have been the subject of rather little ecological research (McKay, 1996; Williams, 2006). Their importance as a natural resource was thought to be limited and they were often overlooked (Dudgeon *et al*., 2006). One type of temporary water body that has so far received only sparse and scattered attention, are freshwater rock pools. Of late, interest in the

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ecology of rocky outcrops has increased, as illustrated by recent key publications (Withers & Edward, 1997; Porembski & Barthlott, 2000; Withers & Hopper, 2000). Emphasis, however, has mainly focussed on the terrestrial part of the ecosystem and only two papers discuss the fauna of freshwater rock pool habitats (Bayly, 1997; Pinder *et al*., 2000), both in Western Australia. In addition to these works, there have been several individual small-scale studies on rock pools in different parts of the world. However, there is no overview of published research conducted on these peculiar systems and their unique biota.

The aim of this article is to assemble all current information on freshwater rock pools and their component fauna on a global scale; highlight the most important habitat characteristics and the consequences for their fauna; assess overall diversity patterns from the different studies; summarise current knowledge on the biotic interactions in rock pools and discuss the conservational, cultural and scientific value of this poorly known aquatic habitat. We reviewed more than 150 papers on animal freshwater rock pool communities, spanning more than 100 years of research, starting from 1900 (Levander, 1900). A complete list of the literature considered is presented as supporting information (Appendix S1).

The rock pool habitat

Definition and distribution

The name 'freshwater rock pool' groups all types of depressions that occur on rocky substrata and (periodically) hold fresh water. A distinction should be made, however, between pools filled by precipitation and those fed by rivers and ground water. Groundwater-fed rock pools (e.g. quarry ponds) and potholes scoured out in bedrock in river floodplains have biological communities largely composed of organisms brought in with the water. Animals in these communities are not particularly adapted to temporary pool conditions, whereas these in precipitation-dependent rock pools contain communities of organisms able to survive dynamic and unpredictable flooding cycles. Rain-fed rock pools are the more typical freshwater rock pool habitats and, unless stated otherwise, this paper deals with the latter. We included some studies on rock pools occurring on coastal rock flats in Jamaica and in the Tvärmine archipelago (Finland). These are not tidal pools but are fed by precipitation, though they may receive spray from the sea.

Freshwater rock pools are found worldwide in all major biomes and are known under different names: 'oricangas' in South America, 'rock pools' in South Africa, 'gnammas' in Australia, 'lithothelms' in Bulgaria, 'potholes' in USA, 'tinajas' in the Western USA and Mexico and 'Opferkessel' in Germany (after Bremer & Sander, 2000). 'Pans' are terms often used for flat-floored, mostly shallow rock pools (Twidale, 1982; Campbell, 1997; Bremer & Sander, 2000) and 'pit gnammas' are deep rock pools in Australia that may contain water throughout the year, even in very dry regions (Timms B., pers. comm.).

Geological formation

Pools form in eroded depressions on outcropping rock layers and depend on precipitation for filling. The shape and dimensions of rock pools depend on weathering rates and patterns, dictated by local climate and the composition and resistance to erosion of the rock (Campbell, 1997). The pan is probably the most common rock pool type characterised by almost vertical edges and a horizontal floor. An overview of other pool types and development of rock pools on granite outcrops in (Western) Australia is given by Twidale & Corbin (1963), Campbell (1997) and Withers (2000).

The archetypal topology of freshwater rock pool habitats consists of clusters of close-set pools on top of granite outcrops or 'inselbergs' (Campbell, 1997; Twidale & Bourne, 2003). The term inselberg is German for 'island mountain' and refers to the remarkable differences in fauna and flora on these outcrops compared with the surrounding environment (Bremer & Sander, 2000). The differential erosion rate between solid masses of resistant granite and the softer surrounding geology results in remnant rock layers lying scattered in the landscape as humps in a flat matrix. Based on the conservative estimate that 2–6 million years of weathering are needed to lower a plain by 100 m, an inselberg 300–400 m high would be at least 20–30 million years old (Bremer & Sander, 2000), with the rock pools on top presumably of a similar age.

Rock pools also occur on sandstone (Chan *et al*., 2005) and limestone formations (Disney, 1974). Rock pools on sandstone are typically shallow and pan-shaped and occur in large numbers on relatively young exposed flats (Jocque, Riddoch & Brendonck, 2007). Occasionally, however, pool basins may be several metres deep and wide, particularly on older sandstone ridges (Dodson, 1987). Sandstone is more readily erodible than granite, and sandstone slabs are often younger than granite layers. The Navajo sandstone in Utah, for instance, dates back from the early Jurassic (roughly 180 Ma years ago) (Chan *et al.*, 2005). The age of the rock pools will be much younger still, as they are formed only when the sandstone becomes exposed. Limestone is even more erodible than sandstone, and rock pool basins rapidly lose their water holding capacity.

Once formed, most rock pool basins will persist for a long time but may lose their water holding capacity by filling up with sediment and the overgrowth of terrestrial plants. A potential succession sequence would start with the generation of a sediment layer by erosion and aeolian activity. This thin layer of sediment can then be colonised by (water) plants (for instance *Isoetes* sp.). The (aquatic) vegetation adds dead vegetative material to the sediment layer, and via a 'windscreen' effect, this may further facilitate the accumulation of aeolian transported material. Eventually, the sediment layer will allow terrestrial plants to establish and over time the pool may be completely filled with sediment and vegetation. The pool basically becomes a botanical island community with its own catchment area (Burbanck & Platt, 1964; Burbanck & Phillips, 1983; Houle & Phillips, 1989). Large mammals (Vanschoenwinkel B., pers. obs.) or wind (Vanschoenwinkel *et al.*, 2008b) can disturb these little gardens enough to remove soil, sometimes allowing pools to be restored.

Hydrology

Frequency and duration of inundations depend on basin morphometry, catchment area, presence of vegetation and local climate. Maximum depth of the basin often gives a reasonable indication of the maximum length of the inundation period (Vanschoenwinkel *et al.*, 2009). A more exact filling pattern for individual pools can be modelled with information on rainfall, evapotranspiration and basin geometry (De Vries, 1996; Hulsmans *et al.*, 2008). Rock pools occurring in semi-arid regions with low rainfall and high evaporation rates, such as in southeastern Botswana, are highly unpredictable in both timing and length of the inundation period (Brendonck *et al.*, 1998, 2000a). The length of the inundation period (hydroperiod) averages from several days to little more than a month (Brendonck *et al.*, 2000a). Rock pools in more temperate regions may remain inundated for several seasons.

Chemical and physical characteristics

Water quality characteristics of freshwater rock pools assessed from different studies are presented in Table 1. The physical conditions of the brackish water rock pools in the Baltic region are not included (Ganning & Wulff, 1969, 1970; Ganning, 1971). The generally small volume of sandstone and granite rock pools results in a low buffering capacity, with marked changes of physical and chemical variables over short time scales often in a diel cycle (Scholnick, 1994).

Rock pools are characterised by low conductivity immediately after filling, typically fluctuating between 10 and 30 μS cm^{-1}. As the water evaporates, conductivity increases mainly because of the con-

Table 1 Minimum and maximum values of conductivity (μS cm^{-1}), temperature (°C) and pH measured in rock pools worldwide. All measurements were carried out in pools on granite outcrops, except for Scholnick (1994) and Chan *et al.* (2005) on sandstone. The table also lists the number of pools and sites incorporated in the study

Study	Cond	Temp	pH	Locality	Pools	Sites
Scholnick (1994)	–	15.9–34.7	6.7–9.6	Utah, USA	4	1
De Vries (1996)	20–535	11.0–31.0	5.0–11.3	South Africa	36	1
Bayly (1997)	34–1490	–	4.6–7.9	Western Australia	36	17
Baron *et al.* (1998)	52–114	4.0–35.0	7.0–7.6	Utah, USA	20	5
Hamer & Martens (1998)	2.3–142.6	13.4–29.7	5.0–9.2	South Africa	39	6
Brendonck *et al.* (2000a)	12–140	28.0–31.4	4.3–7.7	Botswana	30	2
Pinder *et al.* (2000)	–	–	5.8–8.8	Western Australia	9	9
Chan *et al.* (2005)	35–266	2.2–24.2	7.4–10.1	Utah, USA	28	4
Jocque *et al.* (2007)	4.2–27.1	9.2–28.8	8.9–10.3	Utah, USA	27	3

centration of metabolites and can reach values up to 1400 μS cm^{-1} in pools with the longest hydroperiod (Table 1). Water temperature in rock pools depends on climate and maxima have been shown to vary from 32 °C in Finland (Ganning, 1971), 35 °C in Utah (Scholnick, 1994) to over 40 °C in Botswana (Brendonck *et al.*, 2000a). Water temperature seldom exceeds 40 °C because of the balance between cooling through evaporation and heating by insolation. Dissolved oxygen also follows a strong diel and seasonal cycle, with concentrations in one study fluctuating between 5.8 and 7.9 mg L^{-1} (De Vries, 1996) averaged over eight pools measured during 8 days in South Africa. Variation between pools in oxygen concentration over a complete inundation cycle seems to be small, however, ranging in one study from 3.5 to 9.6 mg L^{-1} (De Vries, 1996). It is likely that variability is greater in other systems. Where measurements have been made, water in rock pools ranges from acid (pH = 4.3) to basic (pH = 11.3) (Table 1). At night, respiration from the phytoplankton and macrophytes produces carbon dioxide, thus decreasing pH early in the morning (Chan *et al.*, 2005); pH values can vary by 1.5 units in a diurnal cycle (Scholnick, 1994, mean of four pools).

Rock pools in general are oligotrophic systems open to nutrient inputs and outputs. Enrichment happens mainly through bacterial degradation of dead aquatic organisms, faeces from large (terrestrial) vertebrates and organic material blown in (McLachlan, 1981; Osborne & McLachlan, 1985). Immediately after filling, dissolved nitrogen and phosphorus concentrations may be quite high, but decline quickly because of nutrient uptake by organisms and a reduced rate of nutrient supply from the sediment (Osborne & McLachlan, 1985). Nutrients in the sediment get into the water via bioturbation by tadpoles and some crustaceans (e.g. Notostraca and Spinicaudata) (Osborne & McLachlan, 1985). Removal of nutrients from the system is largely by flushing by intense rain, sediment erosion by wind and, to a lesser extent, by terrestrial predators and scavengers removing organisms from the pool basins (Osborne & McLachlan, 1985), and possibly also by the emergence of adult insects. Concentrations of nutrients and dissolved metal ions in freshwater rock pools have only occasionally been measured. Two studies by Baron, La Francois & Kondrateiff (1998) and Chan *et al.* (2005) give measurements of metal concentrations and chemical components in sandstone rock pools in Utah. Values reported were 27 μg L^{-1} (Mn), 52 μg L^{-1} (Fe), 23.4 mg L^{-1} (Ca), 0.6 mg L^{-1} (Si), 2.0 mg L^{-1} (Mg), 1.5 mg L^{-1} (Na), 1.5 mg L^{-1} (K), 134 μg L^{-1} (F), 2.5 mg L^{-1} (Cl), 29 μg L^{-1} NO_2-N, 527 μg L^{-1} NO_3-N, 15.1 mg L^{-1} Br and 7.1 mg L^{-1} SO_4^{2-}. Most of these values are normal to low for freshwater habitats, but the NO_3-N reached remarkably high concentrations (up to 3184 μg L^{-1}) (Chan *et al.*, 2005), possibly related to variation in N-fixation by cyanobacterial mats, which lined the potholes in that particular study.

Rock pool inhabitants and comments on selected taxa

General

Rock pool inhabitants can be divided in two groups based on life cycle and dispersal strategy: active and passive dispersers (based on Wiggins, Mackay & Smith, 1980). Passive dispersers survive the dry periods *in situ* via drought resistant resting stages such as resting eggs (Crustacea, Turbellaria, monogonont Rotifera), encapsulation with water (Oribatidae) or 'tun' formation (Tardigrada). Encapsulation is the formation of a vesicle surrounding the animal that contains water from the pool (Williams, 2006). Tun formation is the contraction of limbs and the body after which a waxy extrusion covers the surface and protects the organism against desiccation (Wright, 1989). Passive dispersers need vectors such as water, wind or other animals to disperse between pools. Active dispersers, such as insects, are usually only present in the rock pools during the wet phase and the adults can migrate before pools dry up (Williams, 2006). A few exceptions to this rule have been documented, with larvae of active dispersers able to survive droughts. *Polypedilum vanderplanki* Hinton (Chironomidae) has the ability to survive in a diapause state (Hinton, 1951). *Dasyhelea sublettei* Wirth (Ceratopogonidae) burrows into the sediment and encysts in capsules filled with fluid and fixed to the rock surface (McLachlan & Cantrell, 1980). *Cloeodes hydation* Nolte, Tietbohl & McCafferty (Ephemeroptera) can survive brief (up to 9 h) droughts in the larval phase (Nolte & Tietbohl, 1996). In addition, some active dispersers have desiccation-resistant eggs, such as *Aedes vittatus* Bigot (Roberts, 2004).

The most important variable explaining distributional patterns and community structure in rock pools, and in temporary pools in general, is the length of inundations (hydroperiod) (Lanfranco, 1995; Wellborn, Skelly & Werner, 1996). Community stability (composition over several inundation cycles) in rock pools is known to decrease with increasing frequency of pool desiccation (Therriault & Kolasa, 1999, 2000a,b, 2001) and short-lived pools contain fewer species (Therriault & Kolasa, 2001). Changes in community structure along the permanence gradient are the direct result of a shift in environmental stress from abiotic (mainly the risk of drying) to biotic factors. As the hydroperiod increases, biotic interactions such as predation and competition gain importance and will gradually become the dominant community structuring agents, particularly later in the inundations (Wellborn *et al*., 1996). Ecological specialization usually limits species to certain sections of the permanence gradient. Anostraca, for instance, are virtually absent from permanent pools because of their sensitivity to (fish) predation (Brendonck *et al*., 2000a) and most larger aquatic insects, such as dragon flies, are usually not found in the most ephemeral pools because of the limited time available to grow and emerge as an adult (Williams, 2006).

The highly variable rock pool environment, with continuously changing abiotic and biotic conditions, therefore continuously tests the tolerance limits of the inhabitants (Brendonck *et al*., 2000a). Average values of environmental variables may therefore be of little use in explaining the community structure in specific pools, and extremes of temperatures, conductivity and pH may sometimes be more important than mean values (Vanschoenwinkel *et al*., 2007). Species-specific requirements may also account for community structure. This idea is nicely illustrated by a detailed study of the comparative distribution of three larval Diptera (*Polypedilum vanderplanki, Chironomus imicola* Kieffer, and *Dasyhelea thompsoni* de Meillon), in rock pools in central Africa (McLachlan & Cantrell, 1980; McLachlan, 1981, 1983a,b; Cantrell & McLachlan, 1982). The distribution of these Diptera was primarily explained by pool permanence. As *Chironomus imicola* has the longest larval lifespan of the three, and has no physiological adaptations against desiccation, it needed pools of long duration. *Dasyhelea thompsoni* and *Polypedilum vanderplanki* both occurred in pools with a shorter hydroperiod than the pools inhabited by *C. imicola*. Further research showed that the characteristics of the substratum, which is relevant for tube construction in *P. vanderplanki*, and the presence of dung of civet and genet cats (Viverridae) for *D. thompsoni*, further explained the differential occurrence of these last two species.

As for all temporary waterbodies, appropriate timing of colonisation (for active dispersers) and hatching (for passive dispersers) is essential for inhabitants to maximise the chances of maturation before the habitat disappears. In general, the best time for colonization is immediately after the rains that fill the pool basins. Increased presence of active dispersers after additional rains was observed in a study of the colonisation sequence of freshwater rock pools in Botswana (Jocque *et al*., 2007). Passive dispersers in freshwater rock pools, on the other hand, frequently use low conductivity and temperature, which is lowest immediately after rain, as a trigger to hatch (Brendonck *et al*., 1998; Brendonck & Riddoch, 2000).

Besides timing, there is also a level of uncertainty associated with the length of the inundation that depends on additional rains and evaporation rate after filling. Passive dispersers often exhibit partial hatching of the resting bank, a specific sort of risk-spreading strategy, with a smaller fraction of the resting egg bank hatching in more ephemeral pools, hereby compensating for the uncertainty of the length of the hydroperiod (Philippi *et al*., 2001). Some active dispersers also use risk-spreading strategies to maximise their reproductive output and are often combined with different degrees of habitat selection. Different species of odonates in Namibian rock pools have different strategies (Schenk, Suhling & Martens, 2004). Some dragonflies [e.g. *Pantala flavescens* (Fabricius)] distribute their eggs stochastically over different pools, clearly spreading the risk of selecting an unfavourable pool for the offspring. Other species select a single pool [e.g. *Trithemis kirbyi* (Selys)], favouring large and deep pools with a long hydroperiod (Schenk *et al*., 2004). A similar selection for pools with a longer hydroperiod was observed in certain rock pool chironomids (McLachlan & Ladle, 2001).

Time stress, hydroperiod and associated variation in the probability of successful reproduction, is one reason why habitat selection and risk-spreading strategies can be beneficial. Another reason may be provided by the variable presence of predators. Mosquitoes from the genus *Culiseta*, for instance, avoid rock pools with *Notonecta* sp. (Blaustein *et al*., 2004) and *Anax* sp. (Stav *et al*., 1999). The presence of these predators was detected based on the presence of chemicals (Blaustein *et al*., 2004).

In addition to rapid and effective colonisation of newly inundated pools, a high development rate is essential to grow to maturity and reproduce before the pool dries out. Many Anostraca, which represent some of the largest passive dispersers inhabiting rock pools, can mature within a week (Brendonck *et al*., 2000a for *Branchipodopsis wolfi* Daday) or less (Jocque M., pers. obs. for *Branchinecta packardi* Pearse). Most active dispersers in rock pools, on the other hand, take more time to grow and mature than the passively dispersing permanent residents. There are some exceptions as illustrated by the chironomid, *Apedilum elachistus* Townes (Chironomidae) in central Brazil (Nolte, 1995), which matures from egg to imago in just 7 days. Odonata in rock pools in the Namib Desert need between 38 and 70 days to mature (Suhling *et al*., 2004). Although this is relatively long for a temporary habitat, the growth rate of these active dispersers is still high compared with conspecifics in more permanent waters (Johansson & Suhling, 2004).

As shown for certain chironomids and anurans, such as clawfooted toads of the genus *Ceratophrys* (Duellman & Trueb, 1986), populations in evaporating and shrinking pools can reach a point where the normal distribution of body sizes within the larval population becomes bimodal – a group of abnormally small individuals (‘dwarfs’) and another group of abnormally large larva (‘giants’). Differences in food quantity and quality consumed by the two groups are usually invoked to explain this pattern. The giants often eat the smaller ones or feed on the protein-rich bodies of starved and decomposing dwarfs, further promoting the accelerated growth of giants. The size separation carries over to the adults, with the giants completing their larval development sooner and emerging earlier as adults than the dwarfs (McLachlan, 1989).

Tolerance of high UV radiation in rock pools, which are usually shallow and clear, is thought to be a prerequisite to survive in these habitats. Ranta & Nuutinen (1985) showed that *Daphnia* in Scandinavian rock pools stayed close to the sediment during the day but were more evenly distributed during the night. This behaviour was not satisfactorily explained by predation and was hypothesised to be an adaptation preventing excessive exposure to UV. Similar observations are known from other habitats (Leech & Williamson, 2001; Rhode, Pawlowski & Tollrian, 2001). Pigmentation (Hebert & Emery, 1990) could be an alternative protection mechanism. Some Copepoda (for instance *Boeckella opaqua* Fairbridge*)* in Western Australia have remarkable red pigmentation, while several Cladocera such as *Daphnia jollyi* Petkovski in Western Australian rock pools, and a newly discovered chydorid (*Leberis* sp.) in southeastern Botswana, have black pigmentation in the dormant stage.

Comments on selected taxa

A list of inhabitants recorded worldwide from freshwater rock pools was compiled primarily through a search of literature. Unpublished information was included when available. The list comprises *c*. 460 taxa (see Appendix S2). In total, 213 passive dispersers have been recorded. Not included in the list are Rotifera, Hydrachnida and Protozoa.

Large branchiopods, the dominant filter feeders of temporary waters, are well represented (Fig. 1). Six genera of Anostraca have been recorded. Typical rock pool genera are *Branchinecta* in the USA, *Branchinella* in Australia, *Branchipodopsis* in Africa and *Branchipus* and *Tanymastix* in Europe. *Streptocephalus* and *Linderiella* species are the only non-obligatory rock pool

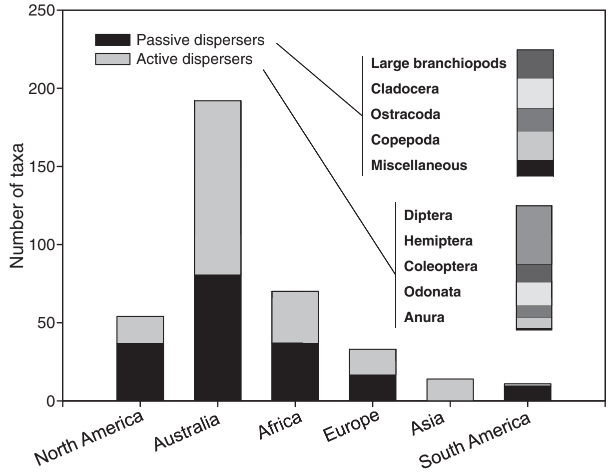

Fig. 1 The number of animal taxa recorded in freshwater rock pools on the different continents, for active and passive dispersers. The proportional richness of major taxonomic groups for the passive and active dispersers recorded in freshwater rock pools worldwide is also shown.

genera, generally preferring low-transparency mud pools. *Streptocephalus* species have a slower maturation rate than the typical rock pool species and are usually out-competed from this habitat (Belk, 1991). Nevertheless, some *Streptocephalus* species have been found in rock pools on all continents, with the exception of Europe (Appendix 1). The near global occurrence of *Streptocephalus,* in contrast to the limited distribution of genera of rock pool specialists (Belk & Brtek, 1995), together with its frequent presence in suboptimal habitats (rock pools), may suggest a trade-off between dispersal ability and ecological specialisation in the Anostraca.

Six out of the nine families of Anomopoda occur in rock pools. Bosminidae, Ophryoxidae and Acantholeberidae are usually absent. The Chydoridae are best represented in terms of species richness (34 species) followed by Macrothricidae (seven species) and Daphniidae (five species). The 35 ostracod species recorded in rock pools mostly belong to the families Cyprididae and Limnocytheridae. The poor representation of ostracod families in temporary rock pools may be linked with the lack of drought resistant resting stages in most families (Martens, 1996). Of the remaining passive dispersers, some scattered studies indicate an unexpected diversity in sparsely studied groups and areas. Turbellaria are an excellent example: only five species have been recorded from rock pools worldwide, four of which were described by Artois *et al.* (2004) from a single site in Botswana. The number is obviously an underestimate of the diversity of one of the most important predatory groups in rock pool systems (Brendonck *et al.*, 2002).

A total of 247 species of active dispersers have been recorded from rock pools (Appendix S2). The Diptera in the list are mainly Chironomidae (35 species), Culicidae of the genera *Aedes* (19 species) or *Culex* (14 species), and Ceratopogonidae (eight species). Almost all the Hemiptera are Corixidae (13 species) and Notonectidae (11 species). Beetles are represented mainly by Dytiscidae (37 species) and Hydrophilidae (16 species). Only three species of salamander have been recorded from rock pools; *Ambystoma laterale* Hallowell and *Ambystoma tigrinum* (Green), both from North America (Smith, 1983; Dodson, 1987), and *Salamandra salamandra* from Israel (Blaustein, Friedman & Fahima, 1996; Blaustein *et al.*, 2004). Fourteen species of toads and frogs belonging to several families have been found in rock pools.

Compared with other temporary waterbodies, such as phytotelmata (water held in or on plants), rock pools house a remarkably high diversity of passive dispersers. This probably results from a combination of the temporal stability and physical properties of the habitats, together with low exchange rates of individuals between clusters of habitat patches often isolated on different outcrops. The flat shape of rock pool basins, which are usually situated at the summit of rocky outcrops with little surrounding vegetation, provide ideal settings for aeolian (Brendonck & Riddoch, 1999; Vanschoenwinkel *et al.*, 2008a) and water-mediated (Hulsmans *et al.*, 2007) dispersal of propagules. Short distance dispersal is common in freshwater rock pool systems, but effective long distance seems to be a rare and random event. Based on allozyme variation in the Botswana rock pool fairy shrimp *Branchipodopsis wolfi,* Brendonck, Riddoch & De Meester (2000b) and Hulsmans *et al.* (2007) found strong indications for gene flow at a local scale (within pool clusters on a single inselberg) but not at a regional scale (among pool clusters on different inselbergs). The study by Hulsmans *et al.* (2007) revealed a distinct pattern of isolation by distance up to about 50 m, beyond which the pattern became more random, indicative of low effective dispersal.

Diversity patterns

The number of species recorded varies considerably among studies. Two studies in Utah reported 23 (Dodson, 1987) and 59 (Baron *et al.*, 1998) species, respectively. The first study looked at single samplings of 50 pools spread over three sites; while the second study was based on weekly samplings of 20 rock pools distributed evenly over five different drainage basins. Research in Western Australia revealed 66 species in a survey of 92 pools on two outcrops (Jocque *et al.*, 2007), 88 species in 36 rock pools on 17 granite outcrops (Bayly, 1997), and 230 species sampled from 90 pools equally divided over nine different rocks (Pinder *et al.*, 2000). Over four sample periods, 39 species were recorded in 36 rock pools on a single outcrop in South Africa (Vanschoenwinkel *et al.*, 2007), and 26 species were recorded in Botswana from 27 rock pools, spread equally over three rocky outcrops (Jocque *et al.*, 2006). These studies differed strongly in the number of rocks and pools sampled as well as in sampling intensity of individual pools, which probably explains part of the variation in diversity recorded. Only a few studies mention the invertebrate species richness per rock pool; it averaged 8.2 in Western Australia (Pinder *et al.*, 2000), between 9.0 and 10.3 in Botswana (Jocque *et al.*, 2006), 18.7 ± 5.0 in the rock pools on Wave Rock in WA (Jocque *et al.*, 2007), and between six and 29 (average 20.3) in South African rock pools (Vanschoenwinkel *et al.*, 2007). Different rock pool characteristics (e.g. hydroperiod, pool size, metapopulation size) as well as the taxonomic resolution and the invertebrate groups considered may further contribute to the observed differences in diversity.

The total list of animal species found (Appendix S2) confirms considerable variation in richness among continents (Fig. 1). The Australian continent exceeds all others, with roughly 200 species recorded. Australia is followed by North America, Africa and Europe, respectively. Both South America and Asia trail behind, with some isolated reports of Diptera and unpublished occurrences of Copepoda in rock pools. The considerable differences in species richness recorded on the different continents probably mainly reflects the difference in study effort and, particularly, the paucity of studies on freshwater rock pools throughout the whole of Asia and South America and large parts of Africa. Freshwater rock pools do occur on these continents as is clear from botanical studies reporting specialised aquatic vegetation from such habitats in these regions (see for instance Porembski & Barthlott, 2000 and Deil, 2005). The best studied rock pool sites are found (in no particular order) in the area around the Baltic Sea, Malta, Namibia, South Africa, Botswana, Israel (Negev desert), Western Australia, Utah and Jamaica. Based on our data some regions, particularly in arid to semi-arid regions with old rock formations (such as Western Australia, southern Africa and central USA), might qualify as diversity 'hot spots'. The presence of similar conditions in understudied areas such as South America suggests the possibility of other areas with biodiverse rock pool communities.

Biogeography

The ancient habitat (rock) and broad distribution of rock pools makes them well suited for biogeographic and phylogeographic studies. The few studies so far suggest that at least some passive dispersers were present before the break-up of Gondwana, roughly 170 Ma years ago, and that differentiation occurred when the continents drifted apart. This general idea was based on the basis of morphological characters of oribatid mites (Hammer & Wallwork, 1979; Wallwork, 1981), centropagid copepods (e.g. *Boeckella*) (Maly & Bayly, 1991) and chydorids (Fryer, 1995; Frey, 1998; Sacherova & Hebert, 2003). The presence of Gondwana ancestors has strong implications for global patterns in community structure of freshwater rock pools. With the assumed presence of ancestors for most of the passively dispersing taxa on the Gondwana continent before it split up, we expect a high chance of representation of all of these groups on the present-day continents. In the conservative expectation that these taxa kept a similar functional role, community structure in rock pool habitats on the different continents is therefore expected to be very similar.

To understand some of these biogeographic relations, we have tried to establish a more general view of regional patterns of endemicity of rock pool inhabitants and the sharing of taxa among continents. A visual representation of the number of endemic genera on each continent and the number of genera shared with other continents (Fig. 2) generally shows considerable overlap in genera for both active (a) and passive (b) dispersers. There is almost no overlap between both South America and Asia, a direct result of the current lack of data on the rock pool communities of these continents. The presence of shared genera between isolated continents such as Australia and both Europe and North America may reflect their former geographical linkages, or colonization after the break up of landmasses. The vast time span since the breakup of Pangaea and Gondwana should have resulted in considerable differentiation and speciation among spatially isolated evolutionary lines, with divergence up to the level of genus. Current sharing of genera among different continents is therefore likely to be, at least partly, because of successful long distance colonization events. Echoes of geographic isolation are still present in the biogeography of rock pool animals as is illustrated by the substantial number of endemic genera confined to different continents (e.g. Anostraca).

(a) Active dispersers

(b) Passive dispersers

Fig. 2 The number of animal genera recorded in freshwater rock pools on the different continents, for active (a) and passive (b) dispersers. The connecting lines between the continents present the number of genera in common.

Biotic interactions

Predation is one of the major community structuring forces in permanent waterbodies (Kerfoot & Sih, 1987), and ephemeral rock pools also house numerous predatory taxa (Brendonck *et al*., 2002). Some studies found that predator–prey interactions in rock pools can explain the distribution of specific species (Jones, 1974) or entire assemblages (Dodson, 1987). Notonectidae can strongly reduce *Daphnia* sp. populations (Arner *et al*., 1998), while *Culiseta* sp. (Blaustein, Kotler & Ward, 1995) and Corixidae, in turn, predate on Chironomidae (Pajunen & Salmi, 1991). Turbellaria (*Mesostoma* sp.) species actively prey on fairy shrimps (Anostraca) and other branchiopod crustaceans and probably have a significant impact on prey population dynamics (Brendonck *et al*., 2002; De Roeck, Artois & Brendonck, 2005).

Competitive interactions, both inter- and intraspecific, are common in rock pool habitats as reported, for instance, for gyrinid beetles (Svensson, 1992, 1998, 1999) and tadpoles (Laurila, 2000). Pajunen (1977, 1979a,b, 1982, 1990), Vepsalainen (1978) and Ranta (1982) reported competition between the rock pool corixids *Arctocorisa carinata* Sahlberg and *Callicorixa producta* Reuter based on the sharing of a similar habitat and reproductive phenology (Pajunen & Ukkonen, 1987). The impact of competitive interactions on local community structure and distributional patterns within a metacommunity is often less clear than the impact of strong agents such as predation. Still, competition has been shown to increase the local extinction rates and limit species richness in rock pool systems (Bengtsson, 1989, 1991, 1993; Pajunen & Pajunen, 1993). This was demonstrated in a long-term study of three species of non-rock pool specialist Cladocera (*Daphnia magna*, *D. pulex* and *D. longispina*) with common food resources (Hanski & Ranta,1983; Bengtsson, 1986, 1987, 1993). In an experimental setup of small (4 L) to large (500 L) artificial rock pools, Bengtsson (1989) found that coexistence of three cladoceran species led to depletion of food and intense interspecific competition, negatively affecting reproduction rate. Small population sizes in conjunction with interspecific competition made populations more vulnerable to extinction.

In addition to predation and competition, parasite communities are an important component of rock pool communities. For *Daphnia* species inhabiting coastal rock pools in Finland, for instance, parasites were important drivers of population dynamics and extinction (Bengtsson & Ebert, 1998; Altermatt, Hottinger & Ebert, 2007).

As the diversity of communities decreases with decreasing hydroperiod (Therriault & Kolasa, 2001), biotic interactions become less important (Wellborn *et al.*, 1996). Towards the more ephemeral side of the hydroperiod gradient, the outcome of competitive and predatory interactions seems to depend more and more on a temporal advantage obtained by early colonization (Blaustein & Margalit, 1996; De Meester *et al.*, 2002; Padeffke & Suhling, 2003). This stochastic aspect, which may also be important early during community development, was also observed in a long-term dataset on invertebrate communities in rock pools in Jamaica. Romanuk & Kolasa (2001, 2002) reported a negative correlation between variability in the abundance of all species in a community and species richness. Richness–variability relationships were significant only in rock pools with low environmental variability. More species in a community obviously complicates the food web, but also seems to stabilise variability in aggregate abundance of all the species in the community (Romanuk & Kolasa, 2001, 2002) as well as variation in their relative abundance (Kolasa & Li, 2003).

Cultural importance, human impact and conservation

Rocky outcrops have played a significant role throughout human history for many human societies and still do so today. Indications of the intimate connections between early tribal life and inselbergs are provided, for instance, by the rich rock art left by the San people in Southern Africa and the Aboriginal people of Australia. For an extensive review of the cultural aspects of inselbergs and human impact on these habitats see Seine (2000), Burke (2002, 2003) and Bayly (2002a,b), among others. The pools on rocky outcrops were and still are invaluable for the local population as water reservoirs, both for humans and their cattle (Seine, 2000). In Western Australia, for instance, fresh water is scarce and local aborigines therefore intensively used the natural water reservoirs on rocky outcrops as a source of drinking water. They sometimes even enlarged and excavated the rock pools to increase their water storage capacity (Laing & Hauck, 1997). Even today water is still collected from granite outcrops for public use (Twidale, 2000) as is the case for the village of Hyden in Western Australia (Bayly, 1999; Seine, 2000).

While inselberg vegetation is relatively tolerant of human interference and can easily withstand moderate disturbance (Seine, 2000), terrestrial habitats on many granite rocks are still often compromised by human activities (Main, 1997). Little is known about the sensitivity of rock pool communities to external disturbance, but it seems that the rock pool environment is often pristine. Even the intensive tourist visits to Wave Rock seem not to have noticeably degraded the rock pools in Western Australia (Jocque *et al.*, 2007). The pothole environment on sandstone flats in the USA, on the other hand, may be vulnerable to human impact because of the low buffering capacity of the system (Scholnick, 1994; Chan *et al.*, 2005). A recent study in Utah found that sediment in dry rock pools is more prone to (wind) erosion after the biological crust covering the sediment has been disturbed (Graham & Wirth, 2008), possibly removing large parts of the resting egg banks.

Since rock pools communities are completely dependent on length and frequency of inundations, the active community reflects the prevailing climatic conditions. Rock pool communities may therefore provide a suitable monitoring system for tracking environmental change on both short and long-time scales and studying the effect of climate change on biological communities.

Freshwater rock pools are unique habitats housing a high diversity of specialist and endemic species and therefore contribute substantially to regional diversity (Pinder *et al.*, 2000; Jocque *et al.*, 2007). Although protection of these habitats is essential, establishment of a conservation strategy may not be straightforward (Mawson, 2000). Low dispersal among inselbergs, as well as patterns of local endemicity and genetic regionalism, underline the need to implement conservation strategies at regional rather than local scales. Strong links between local hydrological and climatological conditions and diversity patterns also indicate the need to conserve pools with different hydrologies and inselbergs in different climatological regions. As rock pools with a longer hydroperiod tend to house a higher diversity of invertebrates, including specialists of early and late successional phases (nested communities; Jocque *et al.*, 2007; Vanschoenwinkel *et al.*, 2009), some priority could be given to the conservation of pools with longer hydroperiods and of inselbergs in high rainfall areas.

Rock pools as model systems for ecological and evolutionary research

To detect clear ecological patterns and elucidate underlying processes, well-known study systems and organisms are required. However, the complexity of the study system often makes it difficult to draw clear conclusions and to compare and extrapolate the results to other (similar) systems. Small waterbodies therefore provide ideal study systems for testing ecological and evolutionary theories and processes (Kitching, 2000; Blaustein & Schwartz, 2001; Srivastava *et al.*, 2004; De Meester *et al.*, 2005; Scheffer *et al.*, 2006). These habitats are small, well-defined patches, with simple food webs in a natural environment, often occurring in clusters close to each other. These habitat characteristics allow easy manipulation and experimental control. Freshwater rock pool systems, and especially rock pools on inselbergs, excel in all these characteristics and even have some additional advantages. Outcropping rocks occur in all major biomes. They have roughly the same physical structure (Porembski & Barthlott, 2000) allowing comparison of results worldwide. The physical simplicity in both phenology and biotic composition, combined with the proximity of systems of pools in well-defined places, allows the investigation of a wide range of ecological topics, especially those concerning island biogeography and metacommunity research (Kolasa & Romanuk, 2005). Studies on the community ecology of small natural waterbodies, and rock pools in particular, have contributed substantially to our current understanding of metacommunities (Kneitel & Miller, 2003; Kolasa & Romanuk, 2005; Vanschoenwinkel *et al.*, 2007). Independently, these systems have also frequently been used as model systems in population genetics (Brendonck *et al.*, 2000b; Hulsmans *et al.*, 2007) and evolutionary biology (Altermatt & Ebert, 2007; Altermatt *et al.*, 2007). Rock pools on inselbergs may well be (at least in aggregate) some of the oldest and most persistent aquatic habitats in nature and the temporal stability of these systems holds great potential for studying historical biogeography and related topics such as speciation and rates of adaptation. In addition, compared to other small aquatic habitats, they are usually undisturbed and pristine. Despite these obvious advantages of freshwater rock pools as model habitats for ecological research, surprisingly little attention has so far been devoted to their study. We hope this review might stimulate interest in this neglected freshwater habitat.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Freshwater rock pool literature.

Appendix S2. A species list of all animals recorded in freshwater rock pools, mainly based on literature.

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