

Chapter 2

Invertebrates in Rock Pools

Luc Brendonck, Sandro Lanfranco, Brian Timms,
and Bram Vanschoenwinkel

Introduction to Rock Pools: Geology, Hydrology, Environmental Conditions, Flora, and Fauna

Rock Pool Geology and Geography

Rock pools are eroded depressions that occur in a matrix of bedrock (Fig. 2.1). In intertidal zones these habitats contain seawater and house communities of marine organisms; however, further up the rock platform, rainfall input becomes a more important source of water than saltwater spray resulting first in brackish and, further inland, in freshwater supralittoral habitats (Ganning 1971; Egan and Ferrington 2015).

Rock pools are found in different types of bedrock but most often in granite, sandstone, and limestone. Granite is an intrusive igneous rock which forms at high temperatures and under great pressure below the surface. Subsurface weathering can fragment the granite, and only the sturdiest fragments, rich in the more resistant potassium feldspars and quartz, typically remain when they become exposed after erosion of the covering sediments (Campbell 1997). This type of granite outcrop is common in the inland areas of Western Australia. Pools may already be present in these rock slabs (Fig. 2.1a) upon exposure as a result of weathering below the surface (Twidale and Bourne 1975). Once exposed, corrosion by acidic water along near-surface horizontal cracks formed by cycles of hot days and cold nights and rare frosts results in a pool basin, with detritus blown away by wind (Timms and Rankin 2014).

Many sandstone rock pools in Southern Africa (Fig. 2.1c) are formed in a different way. Here, organic concretions that got locked in the sandstone during sedimentation erode faster than the surrounding quartzite. Resulting pool basins in this rock often have near vertical walls, while granite rock pools are most often pan shaped. For the rock pools in the sandstone of the Colorado plateau in

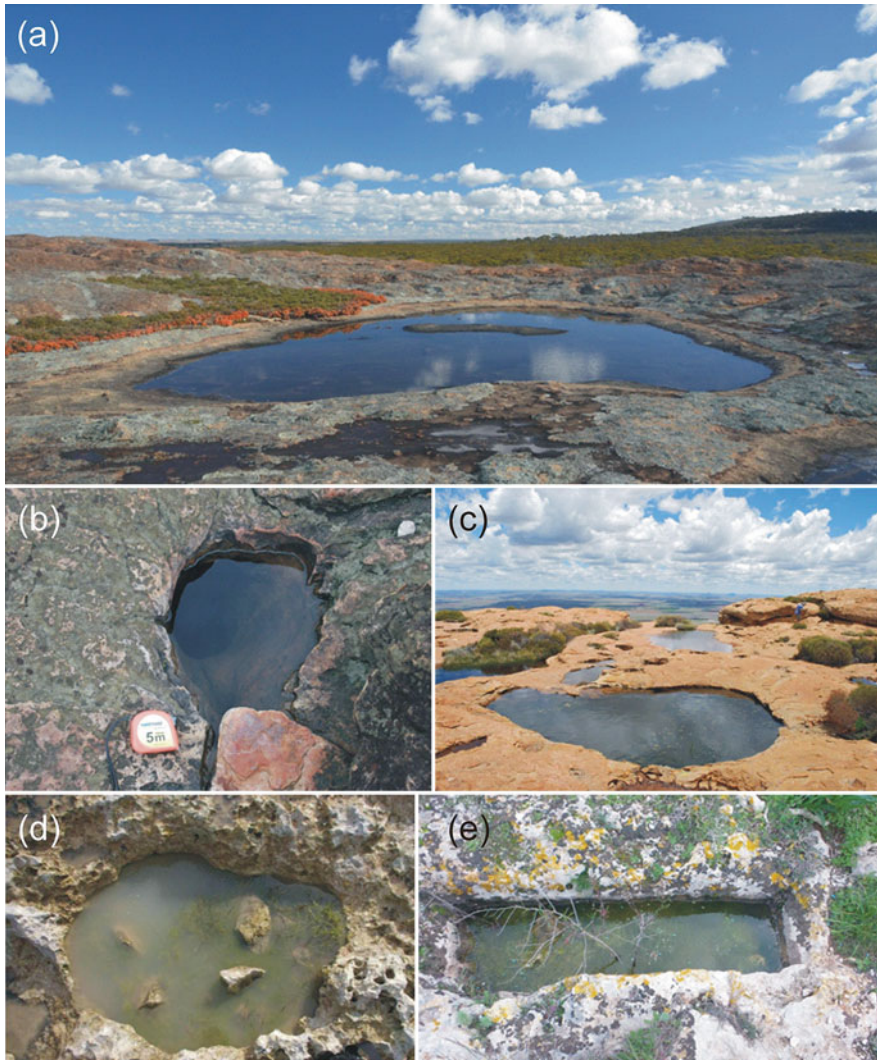


Fig 2.1 Examples of rock pool habitats around the world. **(a)** Inland rock pool on a granite outcrop near Mount Madden, Western Australia; **(b)** 1-m deep pit gnamma in a granite outcrop in Zimbabwe; **(c)** sandstone rock pools on Thaba Phatswa in the Free State, South Africa; **(d)** Rock pool in karstified limestone (Malta); **(e)** man-made rock cut structure at Mosta (Malta) functioning as a rock pool. (Photos a, b, c by B Vanschoenwinkel; d, e by S Lanfranco)

Utah in the USA, it has been suggested that biofilms of cyanobacteria play an important role as they may help dissolve the cement between the sand grains and ensure that pool basins erode faster than the surrounding matrix. Additionally, this film may also help to seal the basins when they hold water (Chan et al. 2005).

Limestone can also hold rock pools (Fig. 2.1d) but since this rock is more susceptible to weathering and erosion, rock pools in limestone presumably have a younger origin and do not persist for millions of years as granite rock pools do. Geological uplifting of ancient limestone reefs, e.g., in coastal areas of the Caribbean, can provide a matrix for rock pools to form (Romanuk and Kolasa 2002).

In the biseasonal Mediterranean climate, the initial stages of pool formation on karstic limestone involve ponding of rainwater and runoff water in small, localized sinks. This promotes solutional erosion of the bedrock gradually forming basin-like depressions. The sides of these basins are generally steep due to undercutting and often display a basal corrosion notch. The gradual enlargement of a solution basin modifies the microtopography in the vicinity and allows the interception of surface water that would otherwise accumulate elsewhere. As such, the formation process tends to develop isolated, relatively large basins surrounded by smaller pits. As the basin grows, adjacent basins may merge giving the lobed margin of several rock pools. Breaching of the walls of these basins arrests their gradual enlargement by forming an overflow channel that drains the pool and provides hydrological connectivity with other basins in the same pool landscape.

Rock pools act as traps for material transported by runoff and wind and therefore accumulate a layer of unconsolidated bottom sediment that mainly comprises clastic mineral particles and organic detritus that, depending of the age of the basin, is mainly from endogenic or exogenic origin. The sediment layer is a fundamental factor in determining the year-to-year persistence of species within these habitats, as it provides a matrix for the accumulation of propagules (seeds and spores) and resting stages (eggs, cysts) of pool species. This creates a “reserve of dormant stages” that could emerge under different conditions (storage effect, cf. Chesson 1985) and may promote long-term species coexistence. The sediment layer also provides a last reserve of moisture for pool biota toward the end of the wet season. Exploiting this reserve of moisture may lengthen the time available for reproductive cycles to be completed and may be the difference between reproductive success and reproductive failure. A study based on 39 pools from six pool landscapes showed that as sediment depth decreased, the number of faunal taxa in the pool decreased too (Briffa et al. 2014).

Freshwater rock pools are known under different names: “oricangas” in South America, “rock pools” in South Africa, “gnammas” in Australia, “lithothelms” in Bulgaria, riverine “potholes” in the USA, “tinajas” in the Western USA and Mexico, and “opferkessel” in Germany (Jocqué et al. 2010a). “Pans or pan gnammas” are terms often used for flat-floored, mostly shallow rock pools and “pit gnammas” are deep rock pools in Australia that may contain water throughout the year, even in very dry regions (White 2009; Timms 2013). Non-coastal, inland rock pool habitats occur worldwide but are most frequently found in arid and semiarid regions where the elements are more likely to expose large rock slabs. On the other end of the climate spectrum, rock pools also exist in arctic and alpine regions where glaciers can expose underlying bedrock (Ghilarov 1967; Meier and Soininen 2014). Rock

pools may hold water from several days up to several months depending on pool depth, surface area, and local climatic conditions. In some cases very large or very deep rock pools may keep water year-round. Examples of these are the pit gnammas which can, for instance, be found in Australia (Timms 2013) (Fig. 2.1b) and Zimbabwe (Anusa et al. 2012).

Not all eroded depressions in exposed bedrock evolve into rock pools. Some may fill up with soil and house terrestrial plants. A recent study in South Africa has shown that the most exposed depressions on the edge of a rocky outcrop are more likely to lose any sediment and terrestrial vegetation and become pools, while less exposed basins situated near the center of outcrops can more easily accumulate sediment and evolve into terrestrial “gardens” (Buschke et al. 2012). The balance between sediment capture and sediment loss determines whether the sediment layer is stable or unstable in the long term. If the autochthonous organic component is disregarded, then the rates of sediment capture and loss would mainly depend on wind-borne and waterborne transport of particles. For a given basin, these rates depend on the surface area to morphological volume ratio ($A:V$) of the basin concerned (Lanfranco and Briffa 2012). Pool basins with a large surface area are a larger target and intercept a larger volume of sediment than basins with smaller surface areas. Deeper basins are efficient sediment traps since captured sediment is less likely to be removed. Basins with a low $A:V$ may undergo complete infilling and would not function as an aquatic system since the aquatic phase would either be very brief or absent altogether. In these situations, the sediment is colonized by terrestrial macrophytes and further consolidated by the anchorage systems of these plants. Basins with a high surface area and shallow depth would not retain a confluent layer of sediment since they would be inadequately shielded from outward transport by wind and runoff. Such basins would not generally be functional rock pools since the high surface area to volume ratio would also promote high rates of evaporative water loss.

Inland rock pools on granite and sandstone outcrops (inselbergs) typically occur in a particular spatial hierarchical structure (Brendonck et al. 2010). Not only do pools occur in clusters with variable distances between clusters and pools, also the inselbergs are dotted in the landscape and add to the overall spatial structure of “islands (inselbergs) of islands (clusters) of islands (pools).”

A different type of freshwater rock pool can be found in or near rocky riverbeds. Water currents moving rocks can erode cylindrical river potholes within the riverbed (Springer et al. 2006). When the water level of the river drops, these habitats can be isolated from flowing water. Particularly old riverine potholes are often exposed along the edges of rivers and can rely both on riverine and on rainfall input for water. In terms of invertebrate biodiversity, these pools are often species poor, particularly when fish are abundant. Regular flushing by the river can prevent the establishment of egg banks for zooplankton. Additionally, regular colonization by fish may exclude predation-sensitive taxa. In this chapter, we will focus mainly on the endorheic rock

pool habitats, i.e., rock pools that rely solely on rainfall for filling. It is these pools that typically contain the most diverse communities including many specialized and endemic taxa.

Finally, a special type of pool that deserves mentioning is man-made rock pools. For instance, a monastery near the town of Montmajour in France has a graveyard of tombs excavated in limestone which now form a cluster of temporary rock pools (Cher 2008). In Malta, in the Mediterranean, Punic tombs excavated in rock also act as temporary pools (Fig. 2.1e).

Rock Pool Hydrology

The hydrology of rock pools is relatively simple. With limestone as a likely exception, most rock pools are not leaky. Rainfall and overflow from neighboring pools are typically the only sources of water input, while it is sensible to assume that evapotranspiration is the most important loss factor. This assumption, however, no longer holds in areas where large mammals or cattle may drink from rock pools. A family of simple models has been developed to reconstruct the long-term inundation regime of rock pools based on long-term climate data and pool morphometry (Hulsmans et al. 2008; Altermatt et al. 2009; Vanschoenwinkel et al. 2009; Lanfranco and Grillas 2010; Tuytens et al. 2014). These models, however, do require some water level time series data to calibrate and validate the models for each pool. Applications of these models include the possibility of accurately quantifying the long-term hydrological selection regime that has helped to shape rock pool communities as well as variation in the evolution of traits in the local populations. For instance, it has been shown that long-term hydrological disturbance regimes can better predict current community structure than the hydroperiod of the pools as observed during sampling (Vanschoenwinkel et al. 2009). New model extensions not only assess water levels and the length of aquatic phases, they also allow estimations of the number of times a pool overflows or receives overflow by neighbors and the volume of water transported. In addition, they generate proxies for the salinity of the water during inundations (Tuytens et al. 2014). The latter is relevant since many rock pool invertebrates use low salinities as a cue for hatching from dormant propagules. Low salinities or conductivities are indicative of heavily diluted water and presumably of a long inundation. It should be emphasized that the total annual rainfall is not necessarily a good predictor of hydroperiod characteristics. A simple hydrological model for rock pools based on 7 years of baseline data (Lanfranco and Grillas 2010) predicted that November to December is the key period for pools in Malta. Rainfall during this period will determine the hydroperiod and, consequently, reproductive success of the pool biota.

Physical and Chemical Environment of Rock Pools

An overview of the chemical and physical conditions in freshwater inland rock pools is summarized in Brendonck et al. (2000) for Southern African rock pools and at a global scale by Jocqué et al. (2010a). In general, basins are filled with rain water, resulting in a highly diluted environment at the start of the inundation with conductivities below $10 \mu\text{S cm}^{-1}$, approaching those of distilled water. At later stages of the inundation, conductivity values of up to about $200 \mu\text{S cm}^{-1}$ were measured. While most western Australian rock pools (gnammas) contain very fresh waters, some are so incised they never overflow and are hyposaline, as in a few on the western Nullarbor Plain (Timms 2012b). If so they support appropriate widespread hyposaline species and not the specialized fauna characteristic of typical gnammas. The generally shallow rock pools also have poor buffering capacity to changes in water quality variables such as pH, temperature, and oxygen. In southern African rock pools, pH values were recorded that varied between 4 and 11, depending on time of the day and phase in the hydro-cycle (Brendonck et al. 2000). Pools also closely followed air temperature with values between 10 and 40°C . Dissolved oxygen also follows a strong diel and seasonal cycle, with concentrations in South African rock pools fluctuating between 5.8 and 7.9 mg L^{-1} (De Vries 1996). Freshwater rock pools in general are rather oligotrophic (Jocqué et al. 2010a). Enrichment happens mainly through bacterial degradation of decaying organisms, fecal input from large (terrestrial) vertebrates, and allochthonous organic material (McLachlan 1981; Osborne and 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 and McLachlan 1985). Nutrients in the sediment get into the water via bioturbation (e.g., by Notostraca and Spinicaudata) (Osborne and McLachlan 1985). Nutrients are mainly removed from the system 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 and McLachlan 1985), and possibly also by the emergence of adult insects (Jocqué et al. 2010a). Concentrations of nutrients and dissolved metal ions in freshwater rock pools have only occasionally been measured. Two studies by Baron et al. (1998) and Chan et al. (2005) give measurements of metal concentrations and chemical components in sandstone rock pools in Utah. Most of the values were normal to low for freshwater habitats, but the $\text{NO}_3\text{-N}$ reached high concentrations (up to $3184 \mu\text{g L}^{-1}$) (Chan et al. 2005); this was possibly related to variation in N-fixation by cyanobacterial mats, which lined the potholes in that particular study. Levels of nitrate and phosphate were found to be relatively low in temporary rock pools in Malta, suggesting tight nutrient recycling (Lanfranco 1995).

Flora and Fauna of Rock Pools

Aquatic flora of rock pool systems is often very limited. However, particularly in deeper freshwater rock pools, several groups of submerged, floating, and emergent macrophytes including macroalgae can be found. In many short-lived rock pools in Africa and Australia, mats of the fern *Isoetes* can be found. In Western Australia, the mudwort (*Glossostigma*) is a common rock pool plant. Several rare endemic *Myriophyllum* species are known from the region. Some are known from just one type locality (Geldard 2005). In Botswana rock pools, *Limosella capensis* occurred in more than half of the basins, without clear preference for short- or longer-lived pools (Brendonck 2003, pers. obs.). Mediterranean rock pools are colonized by several species from the genera *Damasonium*, *Ranunculus*, *Elatine*, *Crassula*, and *Callitriche*. Aquatic ferns, such as *Marsilea* and *Pilularia*, are also associated with these habitats. In Australia, Victorian rock pools often support *Callitriche*, *Isoetes*, and *Crassula* (Bayly 2011).

A detailed overview of the fauna found in rock pools worldwide has been assembled by Jocqué et al. (2010a). Although there clearly are biogeographic differences in the species and genera that inhabit rock pools, there are strong similarities in the major phyla, classes, orders, and families of freshwater invertebrates that inhabit rock pools in different parts of the world. The shallowest pools typically lack any aquatic vegetation and house communities of very disturbance-resistant taxa such as oribatid mites. Short-lived pools also often provide good breeding habitats for several groups of dipterans including ceratopogonid and chironomid midges, particularly for those with larvae that can resist desiccation. Slightly deeper pools with hydroperiods typically exceeding 1 week often house specialized temporary pool crustaceans belonging to the class Branchiopoda. Fairy shrimps (Anostraca), clam shrimps (Spinicaudata, Laevicaudata), and water fleas (Anomopoda) form resistant resting eggs and all are relatively common inhabitants of rock pools worldwide. Tadpole shrimps (Notostraca) are also occasionally found in rock pools but less commonly so (Dodson 1987; Vanschoenwinkel et al. 2012). Turbellaria may also hatch shortly after inundation and often become important predators of branchiopod crustaceans (Brendonck et al. 2002). Both branchiopods and flatworms typically hatch early after inundation and quickly reach high population densities. Fairy shrimp and tadpole shrimp tend to hatch first. The more predation-resistant clam shrimp and water fleas presumably can afford to hatch and mature later. Many pools also house diverse assemblages of seed shrimps (Ostracoda). These detritivorous organisms can reach high population densities in the sediment layer of rock pools. Some ostracods have been observed to hatch within a few hours of wetting at the start of the wet season, having survived the summer in a cryptobiotic state (Lanfranco 1995).

Only three species of salamander have been recorded from rock pools: *Ambystoma laterale* and *Ambystoma tigrinum*, both from North America (Smith 1983; Dodson 1987), and *Salamandra salamandra* from Israel (Blaustein et al. 1996, 2004). Fourteen species of toads and frogs belonging to several families have been found in rock pools (Jocqué et al. 2010a).

Overview of Invertebrate Research in Rock Pools

Invertebrate Assemblages of Rock Pools

Several rock pool sites around the world have been the subject of long-term studies. Excellent examples include the coastal rock pools along the Baltic Sea in Europe such as those on the Tvärmine archipelago in Finland (Pajunen and Pajunen 2003). Comparable coastal rock pools can be found on Appledore Island in Maine, USA (Simonis 2013). In Jamaica a large set of coastal rock pools have been studied on a fossil reef in Discovery Bay (Kolasa and Romanuk 2005). Mediterranean rock pools have been studied in Malta (Lanfranco et al. 1991; Lanfranco 1995) and Israël (Blaustein et al. 2004). In arid regions, rock pools have been studied on granite outcrops in Western Australia (Bayly 1982, 1997; Pinder et al. 2000; Weeks et al. 2006; Timms 2012a, b, 2013, 2014a, b), on three granite hills in Botswana (Riddoch et al. 1994), the Korannaberg mountain in central South Africa (Vanschoenwinkel et al. 2007), the rock pools on mountains in Malawi (McLachlan and Ladle 2001), and the rock pools on the Colorado plateau in Utah, USA (Dodson 1987; Graham 1994; Jocqué et al. 2007a, b, c). Studies from tropical and equatorial regions are underrepresented. At least in part this is likely due to the fact that in moister regions, outcropping rock is often covered by vegetation as is the case in the moister SW of Australia. It is also possible that rock pools do not form as readily under tropical conditions. For instance, the rainforests in SE Cameroon house quite a few granite outcrops; however, these do not hold proper rock pools (Vanschoenwinkel pers. obs.). Space restrictions prevent us from providing a complete account of rock pool research. Instead, we highlight different aspects of rock pool ecology, conservation, and evolutionary biology that have been studied in rock pool habitats in different parts of the world.

To fill a gap in integrated knowledge on rock pool ecology, Jocqué et al. (2010a) reviewed more than 150 papers on freshwater rock pools around the world spanning more than 100 years of research. Besides compiling a list of rock pool animal species, in that paper, the authors also present an elaborated and integrated picture of global diversity patterns and the most significant abiotic and biotic processes and also summarize cultural and conservation aspects specifically related to rock pools. As it is not the intention to repeat that rather complete review, we will restrict ourselves here to a summary of the most important patterns in faunal assemblages and bring some updated views on important ecological and evolutionary processes relevant for rock pool populations. About 460 aquatic animal species were listed (Jocqué et al. 2010a), and Appendix provides a truncated list of the invertebrate genera. Approximately 213 of these species were permanent inhabitants without an active migratory stage (i.e., so-called passive dispersers). As the local environmental conditions in rock pools can be highly variable and the flooding regimes unpredictable, this resident fauna is often composed of specialist and endemic species with a high tolerance to stress. A prominent group of rock pool residents are large branchiopods that are especially well represented by anostracans. As these organisms are large and have many pairs of filter-feeding appendages, they are the dominant

filter feeders in freshwater rock pools. And although these pools are shallow, clear, and often devoid of vegetation, populations can be surprisingly dense and egg banks vast (Brendonck and Riddoch 2000). Of the six Anostraca genera recorded, *Branchinecta* (USA), *Branchinella* (Australia), *Branchipodopsis* (Africa), and *Branchipus* and *Tanymastix* (Europe) are considered rock pool specialists. *Streptocephalus* and *Linderiella* generally prefer low-transparency mud pools but were occasionally also found in rock pools (De Roeck et al. 2010). *Streptocephalus* species have a slower maturation rate than the typical rock pool species and are therefore less likely to be found in rock pools (Belk 1991; De Roeck et al. 2010). As for the small branchiopods (anomopod cladocerans), six out of the nine families were recorded from rock pools, with Bosminidae, Ophryoxidae, and Acantholeberidae usually absent (Jocqué et al. 2010a). In terms of species richness, Chydoridae, Macrothricidae, and Daphniidae were best represented. Rock pool ostracods are represented by 35 species mostly belonging to the Cyprididae and Limnocytheridae (Martens et al. 2008). The other families are poorly represented, probably due to the lack of drought-resistant resting stages (Martens 1996). Several rock pool taxa are poorly studied and current lists are still an underestimation of the real animal diversity in rock pools. Of the five known Turbellaria species from rock pools, for example, four were described from a single rock pool site in Botswana (Artois et al. 2004).

The remaining taxa listed by Jocqué et al. (2010a), and Appendix, were so-called active dispersers with migration usually restricted to the adult stage. Often these taxa were broadly distributed and also occurred in a wide range of temporary habitats besides rock pools. The Diptera were mainly represented by Chironomidae, Culicidae of the genera *Aedes* and *Culex*, and Ceratopogonidae. Almost all Hemiptera were Corixidae or Notonectidae. Beetles were represented mainly by Dytiscidae and Hydrophilidae.

Jocqué et al. (2010a) compared rock pool species richness among different regions and continents and drew some general patterns. It is no surprise that the highest species richness with a significant endemic component was revealed in southwestern West Australia, thanks to the consistent work on the fauna of freshwater rock pools by Bayly (1997), Pinder et al. (2000), and Timms (2012a,b; 2013, 2014a). At least 230 species have been recorded in the area, with rotifers, branchiopods, ostracods, dytiscids, and chironomids well represented (Pinder et al. 2000). On any rock outcrop, up to about 60–70 species are comprised within one metacommunity, though species lists for individual pools usually number fewer than 30 (Jocqué et al. 2007a, 2010a; Timms 2012a, b). Alpha and gamma diversities decrease northward and northwestward due to shorter and less reliable hydroperiods (Timms 2012a, b; Brendonck et al. 2014); cladocerans and ostracods are particularly affected. Diversity is also lower in the forests of the west coast possibly because of increased acidity due to leaf fall input (Bayly 1982, 1997; Timms 2012b) and the lack of deep pool basins in that area (Vanschoenwinkel pers. obs.). These pools are also more shallow and probably of a younger age. Eastward across the vast waterless Nullarbor Plain, there is a small area of similar inselbergs with gnammas on the upper Eyre Peninsula in South Australia. These are less species rich than the southwestern Australian gnammas, with an average of 18 species present per

pool, a diversity per rock outcrop of about 30 species, and an overall fauna of about 60 species (Timms 2014b). The pan gnammas in that region have a limited endemic list mainly of chydorid cladocerans, while pit gnammas have a similar fauna of eurytopic species as in southwestern Australia. The iconic large branchiopods are represented by just two species, *Eulimnadia* n. sp. in the pans and *Lynceus magdalenae* in the pits. When comparing the shallow Australian rock pools (pan gnammas) with the deeper pit gnammas, it is the shallower gnammas that support the most diverse and characteristic fauna (Pinder et al. 2000). The deeper pit gnammas, while largely seasonal, have longer hydroperiods and a less harsh environment overall and hence tend to have a widespread and ubiquitous fauna (Timms 2014a). Like pan gnammas, they also have iconic branchiopods, in this case two species of the laevicaudatan clam shrimp *Lynceus*.

Metacommunity Dynamics

Several studies showed that species sorting, i.e., the distribution of species based on local environmental conditions, is a dominant structuring process in rock pool communities (Vanschoenwinkel et al. 2007; Ng et al. 2009; Pandit et al. 2009). However, species sorting is imperfect, and within pool clusters there are indications for both mass effects and dispersal limitation. Pajunen (1986) wrote that *Daphnia* populations in certain favorable rock pools were much less prone to go extinct and that these pools are likely to be sources for colonization of less suitable marginal rock pool habitats from which populations regularly go extinct. Spatial community analyses performed in South African rock pools found that nearby and neighboring communities were more similar than would be expected based on similarities in environmental conditions (Vanschoenwinkel et al. 2007). The dispersal that fuels this homogenization over short distances is likely to be mediated by different vectors. First of all, dispersal via temporary overflows or rivulets has been shown to be substantial (Hulsmans et al. 2007; Vanschoenwinkel et al. 2008b; Pellowe-Wagstaff and Simonis 2014), and their homogenizing effect on communities was observed in empirical community patterns (Vanschoenwinkel et al. 2007). On Appledore Island, local differences in the abundance of sea gulls frequenting rock pool clusters were shown to have similar homogenizing effects on communities (Simonis and Ellis 2014). In an inland South African rock pool cluster that is not frequently visited by birds, dispersal fluxes via wind, overflows, and amphibian vectors were compared. Here, wind was shown to be the dominant dispersal agent (Vanschoenwinkel et al. 2008b). Despite high dispersal rates in this system, there was still dispersal limitation. But this was restricted to pools that were both isolated and highly disturbed. In these habitats dispersal can probably not compensate for extinctions mediated by frequent disturbances (Vanschoenwinkel et al. 2013).

Analyses of the genetic structure of fairy shrimp metapopulations in Botswana rock pools revealed that even at the scale of several tens of meters, there was genetic differentiation with an isolation by distance pattern (Brendonck et al. 2000;

Hulsmans et al. 2007). This supports the presence of genetic regionalism even within small pool clusters as also confirmed in other areas (Vanschoenwinkel et al. 2011). Over larger spatial scales—among pool clusters on different mountains—there does not seem to be any gene flow. Instead these fairy shrimp metapopulations seem to be linked by very rare long-distance dispersal events that occur at a timescale of at least tens of thousands of years for mountain populations in South Africa (Vanschoenwinkel et al. 2011) or even up to several millions of years for certain inselberg populations in Western Australia (Zofkova and Timms 2009).

Daphnid Rock Pool Community Ecology

Several researchers have worked on the coexistence of *Daphnia* water flea species and corixid water bugs in Finnish rock pools. Pajunen and Pajunen (2003) assembled data on the occurrence of three *Daphnia* species in 507 rock pools on 16 islands over 17 years. Hanski and Ranta (1983) explained temporal variation in distribution patterns of these species in terms of differences in dispersal and competitive ability. Bengtsson's (1986) experiments showed that competitive exclusion did not occur in the field. He argued that variable responses to biotic and abiotic gradients could be a more likely explanation for variation in species distributions and that, although competition can be intense, closely related *Daphnia* may not be able to outcompete one another in the field. In later experiments he showed that extinctions were more frequent in mesocosms in which all three species were present subscribing the importance of interspecific competition as a driver of extinction (Bengtsson 1989). Building further on the same dataset, Altermatt et al. (2008, 2009) noticed that colonization events occurred more frequently in dry years, when many pools were dry. This claim is supported by earlier observations in African rock pools. Here, it was shown that wind dispersal fluxes were highest immediately after pools dried out (Vanschoenwinkel et al. 2008a, b). Brendonck and Riddoch (2000) also illustrated egg bank erosion in Botswana rock pools that was more significant in shallow pools not protected by vegetation. Altermatt and Ebert (2010) furthermore revealed that small and ephemeral pools contributed to more than 90 % of all dormant stages (ephippia) exposed during desiccation events in the entire metapopulation. They indicated this prominent role of small water bodies as drivers of metapopulation dynamics as an "inverse mainland-island type metapopulation."

Another line of research focused on the microparasites of *Daphnia* species (Bengtsson and Ebert 1998). Among many other findings, it has been shown that gene flow of rock pool *Daphnia* would be beneficial for persistence of the metapopulations because it counteracted the negative effects of inbreeding (Ebert et al. 2002). Besides the long-term data from Finland, another time series dataset exists for the small coastal rock pools (13–200 cm diameter) at Discovery Bay in Jamaica. In this system it was shown that more specious communities exhibited less variation in total abundances over years than less specious ones, although this pattern was initially not observed for individual populations (Romanuk and Kolasa 2002) but

could only be confirmed after variation associated with species habitat specialization was taken into account (Kolasa and Li 2003). Additionally, diversity was shown to decrease if ponds dried out more frequently (Therriault and Kolasa 2001). Egan and Ferrington (2015) compared chironomid communities between two zones of freshwater coastal rock pools on Isle Royale (Michigan) in relation to distance from the shore. Pools closer to the shore had significantly higher diversity and housed a totally different community in comparison with more inland pools.

The morphometry of rock pools also has an effect on species diversity. Basin morphometrics favoring several short hydroperiods resulted in more diverse microcrustacean communities (Briffa et al. 2014), while life-form diversity of plants was positively correlated with morphometric heterogeneity and sediment-depth heterogeneity of the basins. While pioneer studies explored the predictive power of using a Levins-type metapopulation perspective with identical patches of rock pools (Hanski and Ranta 1983), more and more evidence has accumulated that even seemingly identical rock pools can be much more heterogeneous than one would expect.

Invertebrate Adaptations for Rock Pool Conditions

A large body of research has focused on life history adaptations of organisms to the temporary rock pool environment. In clusters of rock pools in Botswana, the life history and diapause ecology of the fairy shrimp *Branchipodopsis wolfi* were studied. It was shown that the species hatches at reduced electrical conductivities indicative of fresh rains and well-filled pools (Brendonck et al. 1998). Animals became mature in less than 1 week, depending on temperature and the hydroperiod of the pool (Brendonck et al. 2000). Maturation rate was faster and broods had smaller eggs in the more short-lived pools. A similar pattern was observed for anostracans in South African rock pools by Vanschoenwinkel et al. (2010a). Several parameters were determined that contribute to the egg bank budget in the freshwater rock pool system (Brendonck et al. 1998; Brendonck and Riddoch 2000; Hulsmans et al. 2007; Vanschoenwinkel et al. 2010a, b). It turns out that many populations of this species—with exceptions of those in very ephemeral pools—are remarkably stable and, because of the adaptations to this environment, do not frequently go extinct. Brendonck et al. (1998) tested the capacity of egg banks of *B. wolfi* to buffer against subsequent population crashes due to early drying of the pools. They discovered that the egg bank still served as the source of new cohorts after 16 consecutive wet/dry cycles with premature drying, spread over 2 years.

Although prominent, diapause, of course, is not exclusive to rock pool crustaceans. McLachlan and Ladle (2001) show that diapause also provides important opportunities for certain Diptera to thrive in the most ephemeral rock pools. Many aquatic insects, however, do not diapause and have developed keen senses to

actively select suitable rock pools for egg deposition. This has been investigated in detail for mosquitoes in Israeli rock pools (Spencer et al. 2002). Among other observations it was shown that the presence of predatory salamanders affects their choice (Blaustein et al. 1996). In the coastal rock pools in Maine, prey abundance was shown to be a cue for interactive habitat selection in water bugs (Simonis 2013).

As freshwater rock pools usually hold shallow and clear water, it is expected that local populations are exposed to relatively high UV radiation and may require specific adaptations for protection against UV damage (Jocqué et al. 2010a). Adaptations can be behavioral, like the escape behavior observed in *Daphnia* from Scandinavian rock pools that stay close to the sediment during the day but are more evenly distributed during the night (Ranta and Nuutinen 1985). Exposed animals can also show morphological protective adaptations, such as increased pigmentation (Hebert and Emery 1990). Some Copepoda (for instance, *Boeckella opaqua* in Western Australia) have remarkable red pigmentation, while several Cladocera such as *Daphnia jollyi* in Western Australian rock pools, and a chydorid (*Leberis* sp.) in southeastern Botswana, have black pigmentation, not only in the ephippial capsule but also as adults (Jocqué et al. 2010a).

Key Ecological Factors Controlling Invertebrates in Rock Pools

Hydroperiod

Much the same as in other types of temporary aquatic habitats, the *length of the inundation* or *hydroperiod* is an important determinant of the species composition that can be found in a rock pool at a given moment (Fig. 2.2). However, due to strong variation in the lengths of inundations of individual rock pools, the long-term inundation history, including variation in the length of inundations and the onset and the frequency of inundations (often summarized as a multivariate entity known as the hydroregime), may constitute a better predictor. This is particularly so for organisms with dormant propagules that can be considered permanent residents of rock pools, i.e., the Group 1 organisms of Wiggins et al. (1980). For organisms that do not persist in situ during the dry period, past conditions are likely to be much less important than current conditions. For instance, actively dispersing insects obviously use currently available cues to select habitats for oviposition (Spencer et al. 2002), while for organisms with banks of long-lived propagules, current abundances may reflect both successes and demographic catastrophes experienced during an entire sequence of past growing periods. Hydroperiod acts as a life history-based selective filter. For instance, in Malawi, only Diptera with drought-resistant larvae can survive in the most short-lived pools, while those that lack this adaptation require longer hydroperiods (Cantrell and McLachlan 1982).

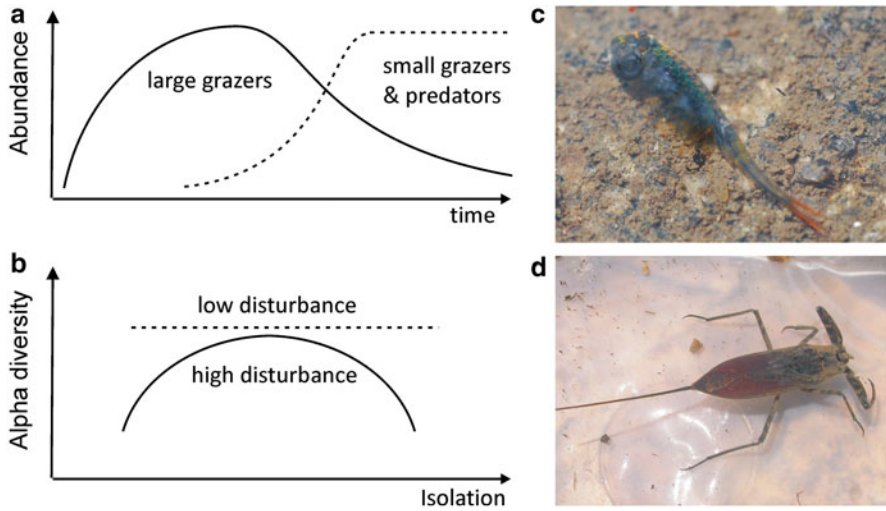


Fig. 2.2 (a) Conceptual diagram of succession in temporary rock pools based on observations in Southern Africa (Vanschoenwinkel et al. 2010b). Depending on the length of the hydroperiod, a first group of fast-growing large grazers declines as a result of increasing predation and can be replaced by smaller more predation-resistant grazers. (b) A unimodal relationship between isolation and alpha diversity was shown for passive dispersers in frequently disturbed pools in a South African pool cluster. This shows that location of pools within clusters as well as hydrological disturbance regime may determine local diversity patterns. (c) *Branchinella longirostris*, a typical early successional large grazing fairy shrimp in Australian rock pools. (d) A water scorpion, an occasional late successional actively dispersing inhabitant of rock pools in South Africa. (Photos: B Vanschoenwinkel)

Competition and Predation

There is circumstantial evidence pointing at the importance of a *trade-off between competition and predation tolerance* as an important underlying factor driving succession in these systems (Fig. 2.2). Three studies have documented succession in temporary rock pools in Botswana (30 days) (Jocqué et al. 2007b), South Africa (140 days) (Vanschoenwinkel et al. 2013), and Australia (140 days) (Timms 2012a), respectively. While species abundances do change over time, short-lived pools do not undergo major successional phases over the time period of 1 month (Jocqué et al. 2007b). These communities were dominated by fairy shrimp and clam shrimp as the dominant grazers of algae. In more long-lived pools in South Africa and Australia, a second successional phase could be observed. The arrival and population increase of many flying colonists via active dispersal including many predators (notonectids, beetles, dragonflies) represents the start of a new successional phase (Fig. 2.2b). The increase in predation ensures that populations of the predation-sensitive taxa such as fairy shrimp (Fig. 2.2c) will crash. This may be exacerbated

by high densities of predatory flatworms. The large predation-sensitive grazers are replaced by more predation-resistant grazers such as water fleas. Competition trials have shown that these smaller water fleas are competitively inferior to the larger fairy shrimp (Jocqué et al. 2010b), suggesting that a trade-off between competitive ability and predation resistance could facilitate coexistence of these groups. Population dynamics of ostracods and copepods showed variable responses but typically also benefited from longer inundations. While these observations are based on just three field studies, the conclusions might hold for a wider range of rock pools as suggested by observations from other habitats in Australia (Brendonck et al. 2014). Large branchiopods and Turbellaria are typically lacking in the less speciose coastal rock pools where different successional dynamics are expected. Nestedness analyses support that subtropical and semiarid rock pool invertebrate assemblages consist of a core of generalist species that occur in both short-lived pools and in the early successional stages of long-lived pools (Vanschoenwinkel et al. 2013). This group is complemented by a second group of taxa that require longer inundations. The latter include both taxa that are quite predictably present in rock pools but also rarer taxa with longer aquatic life cycles and vagrants that only very rarely disperse into rock pools such as water scorpions (Fig. 2.2d) and Trichoptera.

While temporary rock pools are typically fishless, with exception of pools close to rivers or to the sea (Pajunen and Pajunen 2003), the presence of *keystone predators* such as salamanders impacts habitat selection by mosquitoes. Variable presence of *Notonecta* and *Salamandra* as a top predator had important top-down effects on consumers (Blaustein et al. 1995, 1999) even cascading down to primary producers (Arnér et al. 1998). In a survey of 45 rock pools in southeast Botswana, Brendonck et al. (2002) revealed a negative association between dragonfly nymphs and notonectids on the one hand and the anostracan prey populations on the other hand. In situ predation experiments revealed the predation efficiency of these groups that were indicated as top predators. Turbellarians are also often quite abundant and effective in predating on even much larger prey like fairy shrimp. In addition, they hatch at least as fast from the egg bank as their fairy shrimp prey (Brendonck et al. 2002). De Roeck et al. (2005) showed that besides impact by direct predation, turbellarians also had an indirect impact on the anostracan population by reducing the hatching success of the egg bank. A similar suppression of hatching of zooplankton resting eggs by the presence of predatory salamander larvae was suggested by Blaustein (1997) and confirmed by Spencer and Blaustein (2001).

Spatial Location and Connectivity

Pools near the edge of outcrops are more likely to lose sediment (Buschke et al. 2012). This might increase extinction risk for organisms with dormant egg banks. In rock pools in Malawi, McLachlan (1983) showed that isolation also matters for active dispersers. He found that certain chironomids from isolated pools were larger

than their counterparts from pools with lots of proximate neighbors, presumably because of higher dispersal ability. Within a rock pool cluster in South Africa, it was shown that an interaction between pool isolation and long-term disturbance regime determined alpha diversity in these pools, as assessed using four sampling periods (Vanschoenwinkel et al. 2013). A hump-shaped relationship between pool isolation and alpha diversity was only detected in passive dispersers in the most frequently disturbed pools. This suggests that dispersal was not needed to maintain diversity in the least disturbed pools with long hydroperiods (Fig. 2.2b). In isolated disturbed pools it seems dispersal cannot always compensate for local extinctions due to frequent droughts. Lower isolation and increasing connectivity resulted in higher species richness. However richness decreased again in the most connected pools, possibly due to higher abundance of generalist predators in these habitats. Meier and Soininen (2014) report that spatial distances along water connections were more important for explaining similarities in phytoplankton communities than overland distances. Interestingly, spatial patterns in community composition, independent of measured environmental similarities, were even shown for bacteria in coastal pools at small spatial scales, suggesting that history of colonization or localized dispersal dynamics matter even for organisms with such rapid generation times. Using long-term observations of three types of ecosystems, including Jamaican rock pools, Hammond and Kolasa (2014) studied the link between spatial and temporal variation in ecosystem variables. They revealed a strong quantitative link between spatial and regional temporal variation in 136 variables and suggested this as a basis for substituting variables, when long-time series are lacking.

Local Abiotic Conditions

Local abiotic conditions can impose important filters in rock pools that affect community membership. Salinity clearly matters for rock pools in coastal areas (Ganning 1971), but even minor differences in salinity or electrical conductivity can have important consequences for inland temporary pool communities. It has been shown that electrical conductivity was an important hatching cue for temporary pool invertebrates (Brendonck 1996). In a study on the impact of salinity on *Daphnia* communities (three species) in Swedish coastal rock pools, Liao et al. (2015) found that exposure to the local stressor was more important for stress tolerance than genetic diversity or level of isolation in the metacommunity. Little work has been done on the importance of nutrient addition in inland rock pool clusters on rocky outcrops as most rock pools are very oligotrophic. However, as further discussed below, it could be of potential conservation concern. Soininen and Meier (2014) studied patterns of phytoplankton species richness in subarctic Finish rock pools in relation with abiotic conditions and pool size. They found a highly significant positive relation with total P concentrations and a marginally negative relationship with conductivity, while the size of pools was not important. Romanuk and Kolasa (2005) suggested that resource availability (determined by nutrient input and species diversity) may

be the principal mechanism determining invasibility at local scales in multi-trophic rock pool communities. Beisner et al. (2006) experimentally tested the invasibility of Jamaican rock pools by a competing ostracod in relation to local productivity and species richness. High resource availability and low species richness increased establishment success of the ostracod species.

Conservation and Management Issues of Importance to Rock Pool Invertebrates

Overall, rock pool habitats are not severely threatened worldwide and are less disturbed by man than many other ecosystems. In part this is likely due to the fact that, unlike many temporary wetlands in lowland areas, the robust nature of the rock slabs makes these habitats difficult to destroy. Additionally, people do not have many incentives to interact with these habitats that are often located away from human settlements. Their occurrence in rocky terrains also makes them largely useless as water sources for agriculture or intensive grazing. Occasionally, local people will build huts on top of the rocky outcrops and use the rock pools to wash their clothes, as is the case in the Gutu region of Zimbabwe. Even those subject to pressure from tourism like Wave Rock in Western Australia have faunas no less diverse than pools on rocks away from the public (Jocqué et al. 2006).

Direct Human Impacts

In the past, native Australian tribes used rock pools as sources of water and marked rock pools, and deeper pit gnammas in particular, on maps they painted under overhanging rocks and in caves (White 2009). For native Australian (aboriginal) people in the arid areas of South Australia, gnammas also facilitated access to a wider area and a larger range of resources. Aboriginal routes in arid areas were largely governed by the occurrence and distribution of rock pools with tracks radiating out from them. Many of the pit gnammas are currently disturbed partly from natural sedimentation due to failure of their former aboriginal custodians to clean them out occasionally and thus maintain their value as a water source. However, in some areas of the country, there is a reconnection of aboriginal communities to their land and appropriate management of their heritage (White 2009). Today, the rainwater that falls on rocky outcrops is still used by farmers in Western Australia. By building walls around an outcrop, they can guide the water, which would otherwise drain into the sediment around the outcrop, to large collector tanks. This practice does not damage rock pools per se since the water in the pools is not harvested. But the walls that are put in place might act as migration barriers for amphibians and reptiles and may prevent some pool habitats that heavily rely on outcrop runoff to fill. Farmers often cover pools to keep wandering sheep from drowning, and damage is done by

the decaying infrastructure. In earlier times aboriginals covered some pools to reduce evaporation, and these covers, plus farmer's covers, reduce diversity (Timms 2014a). Quantitative studies of the potential effects of such modifications on biota and pool hydrology are, however, lacking.

Whether rock pools or pool clusters are expendable or not depends on the regional context. In some cases landscapes may be dotted with hundreds of outcrops, each containing clusters of rock pools. However, in other cases small numbers of rocky outcrops with endemic lineages may exist on a single outcrop in a region that lacks similar habitats (Vanschoenwinkel et al. 2011). Community patterns suggest that dispersal among rock pools is often essential to maintain local diversity in rock pool patches (Vanschoenwinkel et al. 2013) and may help to counteract regular extinctions due to disturbance. Therefore it would be recommended to conserve entire clusters rather than single habitats.

Although many rock pool systems are oligotrophic, nutrient enrichment and eutrophication can be problematic in some areas. In the Australian outback, feral goats often gather in substantial numbers around granite outcrops. As a result of wind action, dried goat droppings often accumulate in the rock pools on these outcrops leading to eutrophic conditions or dead pools, without any sign of invertebrate life. During periods of drought in Australia, kangaroos, emus, and assorted reptiles find water in rock pools and can fall in and drown; as a result, their decaying bodies pollute the limited water volume in the pool. Due to the typical oligotrophic state and small volume of inland rock pools, one could argue that even small additions of nutrients could have important effects on biodiversity, but this remains to be studied quantitatively. It has also been hypothesized that nutrient enrichment as a result of mass tourism on the sandstone monolith Uluru could possibly explain the decline of an endemic rock pool crustacean (Timms pers. comm.). Coastal rock pools tend to be more eutrophic. In this case nutrients may be added by visiting sea birds.

In some cases, rock slabs with rock pools are accessible to all-terrain vehicles. Besides damaging the fragile vegetation on the escarpment, vehicles will sometimes drive through rock pools. An experiment by Graham and Wirth (2008) has shown that such physical disturbance of the sediment bank in pools loosens the eggs and seeds contained therein that can hence be blown more easily away by wind. In a South African pool cluster, it was shown that the dried remains of aquatic vegetation that remained during the dry season correlate with the abundance of resting eggs of the fairy shrimp *Branchipodopsis wolffi* that could be maintained in these pools (Vanschoenwinkel et al. 2010a). This was surprising since no link could be found with other factors such as hydroperiod that would directly be linked to reproductive success. Also Brendonck and Riddoch (2000) found egg bank sizes were more stable in pools where eggs were protected by vegetation against wind erosion. These studies indicate that wind erosion during the dry season is likely an important factor affecting long-term persistence of populations.

Climate Change

Given the direct dependence on rainfall and evaporation for filling and on the proportion of inundations that will be suitable for reproduction by different species (Hulsmans et al. 2008; Tuytens et al. 2014), it is no surprise that predicted changes in the earth's climate will ensure that certain rock pool habitats will become less suitable for certain inhabitants. Simulations of realistic changes in rainfall and evaporation for central South Africa revealed that the proportion of inundations suitable for the reproduction of fairy shrimp may decrease by up to 21 %. This is worrying, since among rock pool inhabitants, fairy shrimps are still among the most rapidly reproducing species. Therefore, effects on the reproductive success of most other species are likely to be even more detrimental. Given the strong selection for rapid reproduction in these systems, it is also questionable whether species can adapt to reproduce even faster. It seems more likely that they are already at their physiological limit. In Australia, future climate change may act to reduce hydroperiods, particularly at northern and northwest fringes of the Wheatbelt and Goldfields (Timms 2012a, b). It was sometimes stated that Arctic and subarctic rock pool and pond ecosystems are in general very sensitive to environmental changes because of their small size and high surface area to depth ratios (Smol and Douglas 2007). Tuck and Romanuk (2012), however, conducted an experiment to determine whether thermal variability of +4 °C leads to consistent changes in community structure, temporal dynamics, and ecosystem functioning in laboratory analogues of natural freshwater supralittoral rock pool communities inhabited by meiofauna and zooplankton collected from subarctic, temperate and tropical regions. Subarctic zooplankton communities proved to be more robust to thermal variability than temperate or tropical communities, and this suggests that increasing thermal variability with climate change may have the greatest effects on community structure and function in tropical and temperate regions. Studies on such rock pools give important insights into how future climate changes would affect these sensitive small aquatic ecosystems in polar regions (Soininen and Meier 2014). Altermatt et al. (2008) demonstrated the effect of weather changes on the metacommunity dynamics of three *Daphnia* species in Finnish rock pools. A fourfold increase in colonization rate was observed with warm and dry weather conditions, when egg banks were more exposed to dispersal by animals and winds.

Compared to other temporary aquatic systems, it is likely that given their small water volume, rock pools will be the first to experience the effects of climate warming and changes in the seasonal distribution of water (Hulsmans et al. 2008). As a result they could be considered “sentinel ecosystems.” Overall, species with long aquatic life cycles might especially struggle to reproduce in rock pools in the foreseeable future. As an alternative tool for long-term monitoring to track differences in rock pool plant communities, Lanfranco et al. (2015) suggested phylogenetic clustering. According to this method, following the position of pools along a continuum of phylogenetic relatedness may reveal the response of local communities to climate warming.

Although rock pools are usually small and therefore sensitive to climate change, permanent plant and animal inhabitants do show resilience against early drying, mainly through the buffering effect of the egg or seed bank in the sediment. Sediment from Botswana rock pools, for example, still functioned as a source of new hatchlings after 16 subsequent wet/dry cycles with simulated population crashes and no addition of new eggs (Brendonck et al. 1998). Cross et al. (2015) performed a similar experiment with plant seed banks from Australian rock pools and found that a viable seed bank persisted even after ten consecutive wetting events during 3 years.

Conservation Strategies

As freshwater rock pools are rather unique habitats housing a surprisingly high diversity of specialist and endemic species, protection of these habitats is essential. In Mauritania, mountain rock pools are holding a disproportional high richness (32 % of all taxa and 78 % of all Mauritanian endemics) in vertebrates in comparison with the size of the pools (total: 46 ha), while more than 60 % of these pools are currently unprotected (Vale et al. 2015). These pools could function as microrefugia under climate change and expanding dry regions.

Low dispersal among inselbergs, as well as patterns of local endemism and genetic regionalism, underscore the need to implement conservation strategies at regional rather than local scales (Jocqué 2006, 2007c, 2010a). 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 (Jocqué et al. 2010a). The intensive biological surveys on granite outcrops in Western Australia highlight the need for conservation of these freshwater refuge habitats due to freshwater wetland depletion in the wheat belt from salinization (Jocqué et al. 2007c; White 2009). However, very few gnammas occur in the nation's conservation estate, and if so, it is more by accident than design, i.e., within reserves established for other reasons. Not one gnamma on Eyre Peninsula, South Australia, lies within a National Park, and very few do in Western Australia. Many rock pools, though, lie in reserves set aside for water conservation and so enjoy a measure of protection. Public education is a key process, and already in some local council areas in Western Australia, e.g., at Trayning, tourists are encouraged by roadside signage and brochures to visit extraordinary gnammas. Another interesting rock pool site offering good opportunities to reconcile tourism with conservation of biodiversity is the pilgrimage site of Montmajour near the Camargue in France (Cher 2008). While tourists are in the first place attracted by the Medieval monastery (a world heritage site), they also show interest in the 48 tombs that were cut in the rocks and that became mature rock pools even holding *Triops*. Suggestions were made to the site manager to produce a brochure to inform visitors on the functioning of the rock pool ecosystem.

Appendix

Passive (*left columns*) and active (*right columns*) dispersing invertebrate families and genera recorded from rock pools worldwide (adapted from Jocqué et al. 2010a)

Passive dispersers		Active dispersers	
Higher taxa	Genera	Higher taxa	Genera
Turbellaria		Insecta	
Rhabdocoela		Ephemeroptera	
Dalyelliidae	<i>Caliadne</i>	Baetidae	<i>Baetis</i>
	<i>Gieysztorja</i>		<i>Callibaetis</i>
Typhloplanidae	<i>Bothromesostoma</i>		<i>Cloeodes</i>
	<i>Mesostoma</i>		<i>Cloeon</i>
	<i>Syrinx</i>	Odonata	
Nematoda		Aeshnidae	<i>Aeshna</i>
Dorylaimidae	<i>Dorylaimus</i>		<i>Anax</i>
Mollusca			<i>Hemianax</i>
Physidae	<i>Physella</i>		<i>Polycanthagyna</i>
Planorbidae	<i>Bulinus</i>	Coenagrionidae	<i>Argia</i>
	<i>Glyptophysa</i>		<i>Enallagma</i>
	<i>Isidorella</i>		<i>Ischnura</i>
Annelida			<i>Xanthagrion</i>
Aelosomatidae		Corduliidae	<i>Hemicordulia</i>
Phreodrilidae	<i>Antarctodrilus</i>	Lestidae	<i>Archilestes</i>
	<i>Astacopsidrilus</i>		<i>Austrolestes</i>
Tubificidae	.	Libellulidae	<i>Bradinopyga</i>
Tardigrada			<i>Libellula</i>
Macrobiotidae	<i>Macrobiotus</i>		<i>Diplacodes</i>
Crustacea			<i>Orthetrum</i>
Anostraca			<i>Pantala</i>
Branchinectidae	<i>Branchinecta</i>		<i>Sympetrum</i>
Branchipodidae	<i>Branchipodopsis</i>		<i>Trithemis</i>
	<i>Branchipus</i>	Hemiptera	
Chirocephalidae	<i>Linderiella</i>	Belostomatidae	<i>Lethocerus</i>
Streptocephalidae	<i>Streptocephalus</i>	Corixidae	<i>Agraptocorixa</i>
Thamnocephalidae	<i>Branchinella</i>		<i>Arctocorisa</i>
Spinicaudata			<i>Callicorixa</i>
Cyzicidae	<i>Caenestheriella</i>		<i>Diaprepocoris</i>
	<i>Cyzicus</i>		<i>Graptocorixa</i>
	<i>Eocycticus</i>		<i>Micronecta</i>
Lepthesteriidae	<i>Leptestheria</i>		<i>Sigara</i>
Limnadiidae	<i>Limnadia</i>	Gerridae	<i>Aquarius</i>
	<i>Eulimnadia</i>		<i>Gerris</i>
Laevicaudata		Naucoridae	<i>Ambrysus</i>

(continued)

(continued)

Passive dispersers		Active dispersers	
Lynceidae	<i>Lynceus</i>	Notonectidae	<i>Anisops</i>
Notostraca			<i>Buenoa</i>
Triopsidae	<i>Lepidurus</i>		<i>Notonecta</i>
	<i>Triops</i>	Pleidae	<i>Plea</i>
Anomopoda		Veliidae	<i>Microvelia</i>
Chydoridae	<i>Allonella</i>	Coleoptera	
	<i>Alona</i>	Dytiscidae	<i>Agabus</i>
	<i>Celsinotum</i>		<i>Allodessus</i>
	<i>Chydorus</i>		<i>Deronectes</i>
	<i>Dunhevedia</i>		<i>Dytiscus</i>
	<i>Ephemeroporus</i>		<i>Eretes</i>
	<i>Leberis</i>		<i>Hydroglyphus</i>
	<i>Monospilus</i>		<i>Hygrotus</i>
	<i>Planicirclus</i>		<i>Hyphydrus</i>
	<i>Pleuroxus</i>		<i>Ilybius</i>
	<i>Plurispina</i>		<i>Laccophilus</i>
	<i>Rak</i>		<i>Lancetes</i>
Daphniidae	<i>Ceriodaphnia</i>		<i>Liodessus</i>
	<i>Daphnia</i>		<i>Megaporus</i>
Ilyocryptidae	<i>Ilyocryptus</i>		<i>Necterosoma</i>
Macrothricidae	<i>Macrothrix</i>		<i>Neoclypeodytes</i>
Moinidae	<i>Moina</i>		<i>Paroster</i>
Neothricidae	<i>Neothrix</i>		<i>Platynectes</i>
Simocephalidae	<i>Simocephalus</i>		<i>Potamonectes</i>
Ostracoda			<i>Rhantus</i>
Cyprididae	<i>Alboa</i>		<i>Sternopriscus</i>
	<i>Amphibolocypis</i>		<i>Stictotarsus</i>
	<i>Bennelongia</i>		<i>Thermonectus</i>
	<i>Candonocypis</i>		<i>Uvarus</i>
	<i>Chlamydotheca</i>	Gyrinidae	<i>Gyrinus</i>
	<i>Cypretta</i>	Haliplidae	<i>Peltodytes</i>
	<i>Cypricercus</i>	Hydrophilidae	<i>Berosus</i>
	<i>Cypriconcha</i>		<i>Enochrus</i>
	<i>Cypridopsis</i>		<i>Hydrochara</i>
	<i>Cyprinotus</i>		<i>Hydrophilus</i>
	<i>Eucyprinotus</i>		<i>Laccobius</i>
	<i>Heterocypris</i>		<i>Limnoxenus</i>
	<i>Ilyodromus</i>		<i>Limnoxenus</i>
	<i>Kapcypridopsis</i>		<i>Tropisternus</i>
	<i>Potamocypis</i>	Hydraenidae	<i>Tympanogaster</i>
	<i>Strandesia</i>	Limnichidae	

Cypridopsidae	<i>Sarscypridopsis</i>	Scirtidae	
Ilyocyprididae	<i>Ilyocypris</i>	Trichoptera	
Limnocytheridae	<i>Gomphodella</i>	Limnephilidae	<i>Limnephilus</i>
	<i>Korannacythere</i>	Leptoceridae	<i>Oecetis</i>
	<i>Limnocythere</i>		<i>Triplectides</i>
Copepoda		Lepidoptera	
Cyclopoida		Pyralidae	
Harpacticoida		Diptera	
Parastenocarididae		Culicidae	<i>Aedes</i>
Canthocamptidae	<i>Attheyella</i>		<i>Anopheles</i>
	<i>Elaphoidella</i>		<i>Culex</i>
	<i>Epactophanes</i>		<i>Culiciomyia</i>
	<i>Pindamoraria</i>		<i>Culiseta</i>
Centropagidae	<i>Boeckella</i>		<i>Mimomyia</i>
	<i>Calamoecia</i>		<i>Ochlerotatus</i>
Cyclopidae	<i>Acanthocyclops</i>		<i>Opifex</i>
	<i>Cyclops</i>		<i>Theobaldia</i>
	<i>Diacyclops</i>		<i>Tripteroides</i>
	<i>Ectocyclops</i>		<i>Uranotaenia</i>
	<i>Eucyclops</i>	Ceratopogonidae	<i>Atrichopogon</i>
	<i>Macrocyclops</i>		<i>Bezzia</i>
	<i>Megacyclops</i>		<i>Culicoides</i>
	<i>Metacyclops</i>		<i>Dasyhelea</i>
	<i>Microcyclops</i>		<i>Monohelea</i>
	<i>Mixocyclops</i>	Chironomidae	<i>Ablabesmyia</i>
	<i>Paracyclops</i>		<i>Allotriisocladus</i>
	<i>Stolonicyclops</i>		<i>Alotanypus</i>
Diaptomidae	<i>Tropocyclops</i>		<i>Apedilum</i>
	<i>Diaptomus</i>		<i>Archaeochlus</i>
	<i>Hesperodiaptomus</i>		<i>Botryocladus</i>
	<i>Leptodiaptomus</i>		<i>Chironomus</i>
	<i>Lovenula</i>		<i>Cladopelma</i>
	<i>Metadiaptomus</i>		<i>Comptosmittia</i>
Amphipoda			<i>Cryptochironomus</i>
Gammaridae	<i>Gammarus</i>		<i>Dicrotendipes</i>
Acari			<i>Gymnometriocnemus</i>
Eylaidae	<i>Eylais</i>		<i>Kiefferulus</i>
Oribatidae	<i>Aquanothrus</i>		<i>Microsestra</i>
	<i>Chudalupia</i>		<i>Parabornia</i>
	<i>Scapheremaeus</i>		<i>Parakiefferiella</i>
	<i>Trimalaconothrus</i>		<i>Paramerina</i>
Trombidiidae			<i>Paratendipes</i>

(continued)

(continued)

Passive dispersers		Active dispersers	
Mesostigmata			<i>Phaenopsectra</i>
			<i>Phaenopsectra</i>
			<i>Polypedilum</i>
			<i>Procladius</i>
			<i>Tanytarsus</i>
		Dolichopodidae	
		Ephydriidae	
		Muscidae	
		Sciomyzidae	
		Tabanidae	<i>Tabanus</i>
		Tipulidae	

References

- Altermatt F, Ebert D (2010) Populations in small, ephemeral habitat patches may drive dynamics in a *Daphnia magna* metapopulation. *Ecology* 91:2975–2982
- Altermatt F, Pajunen VI, Ebert D (2008) Climate change affects colonisation dynamics in a meta-community of three *Daphnia* species. *Glob Chg Biol* 14:1209–1220
- Altermatt F, Pajunen VI, Ebert D (2009) Desiccation of rock pool habitats and its influence on population persistence in a *Daphnia* metacommunity. *PLoS One* 4
- Anusa A, Ndagurwa HGT, Magadza CHD (2012) The influence of pool size on species diversity and water chemistry in temporary rock pools on Domboshawa Mountain, northern Zimbabwe. *Afr J Aquat Sci* 37:89–99
- Arner M, Koivisto S, Norberg J, Kautsky N (1998) Trophic interactions in rockpool food webs: regulation of zooplankton and phytoplankton by *Notonecta* and *Daphnia*. *Freshw Biol* 39:79–90
- Artois T, Willems W et al (2004) Freshwater Rhabdocoela (Platyhelminthes) from ephemeral rock pools from Botswana, with the description of four new species and one new genus. *Zool Sci* 21:1063–1072
- Baron JS, La Francois T, Kondratieff BC (1998) Chemical and biological characteristics of desert rock pools in intermittent streams of Capitol Reef National Park, Utah. *Great Basin Nat* 58:250–264
- Bayly IAE (1982) Invertebrate fauna and ecology of temporary pools on granite outcrops in southern Western Australia. *Austral J Mar Freshw Res* 33:599–606
- Bayly IAE (1997) Invertebrates of temporary waters in gnammas on granite outcrops in Western Australia. *J Royal Soc W Austral* 80:167–172
- Bayly IAE (2011) Australia's granite wonderlands. Bas Publishing, Melbourne
- Beisner BE, Hovius J et al (2006) Environmental productivity and biodiversity effects on invertebrate community invasibility. *Biol Invasions* 8:655–664
- Belk D (1991) Why only one of 2 common central Texas Anostraca atop Enchanted Rock. *Hydrobiologia* 212:83–86
- Bengtsson J (1986) Life histories and interspecific competition between three *Daphnia* species in rock pools. *J Anim Ecol* 55:641–655
- Bengtsson J (1989) Interspecific competition increases local extinction rate in a metapopulation system. *Nature* 340:713–715
- Bengtsson J, Ebert D (1998) Distributions and impacts of microparasites on *Daphnia* in a rock pool metapopulation. *Oecologia* 115:213–221

- Blaustein L (1997) Non-consumptive effects of larval *Salamandra* on crustacean prey: can eggs detect predators? *Oecologia* 110:212–217
- Blaustein L, Kotler BP, Ward D (1995) Direct and indirect effects of a predatory backswimmer (*Notonecta maculata*) on community structure of desert temporary pools. *Ecol Entomol* 20:311–318
- Blaustein L, Friedman J, Fahima T (1996) Larval *Salamandra* drive temporary pool community dynamics: evidence from an artificial pool experiment. *Oikos* 76:392–402
- Blaustein L, Garb JE, Shebitz D, Nevo E (1999) Microclimate, developmental plasticity and community structure in artificial temporary pools. *Hydrobiologia* 392:187–196
- Blaustein L, Kiflawi M et al (2004) Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue. *Oecologia* 138:300–305
- Brendonck L (1996) Diapause, quiescence, hatching requirements: what we can learn from large freshwater branchiopods (Crustacea: Branchiopoda: Anostraca, Notostraca, Conchostraca). *Hydrobiologia* 320:85–97
- Brendonck L (2003) Egg banks in freshwater zooplankton: evolutionary and ecological archives in sediment. In: Vandonk E, Boersma M, Spaak P (eds), *Proc Vol Recent developments in fundamental and applied plankton research*. *Hydrobiologia* 491:65–84
- Brendonck L, Riddoch BJ (2000) Egg bank dynamics in anostracan desert rock pool populations (Crustacea: Branchiopoda). *Arch Hydrobiol* 148:71–84
- Brendonck L, Riddoch BJ, Van de Weghe V, Van Dooren T (1998) The maintenance of egg banks in very short-lived pools—a case study with anostracans (Branchiopoda). In: Brendonck L, De Meester L, Hairston NG (eds), *Evolutionary and Ecological Aspects of Crustacean Diapause*. *Arch Hydrobiol (Spec issue)* 52:141–161
- Brendonck L, Hamer ML, Riddoch BJ, Seaman MT (2000) *Branchipodopsis* species: specialists of ephemeral rock pools. *Afr J Aqua Sci* 25:98–104
- Brendonck L, Michels E, De Meester L, Riddoch B (2002) Temporary pools are not ‘enemy-free’. In: Maeda-Martinez AM, Timms BV (eds), *Studies on large branchiopod biology 4*. *Hydrobiologia* 486:147–159
- Brendonck L, Jocqué M, Hulsmans A, Vanschoenwinkel B (2010) Pools ‘on the rocks’: freshwater rock pools as model systems in ecological and evolutionary research. *Limnética* 29:25–40
- Brendonck L, Jocqué M et al (2014) Hydrological stability drives both local and regional diversity patterns in rock pool metacommunities. *Oikos*. doi:[10.1111/oik.01710](https://doi.org/10.1111/oik.01710)
- Briffa K, Sammut S, Lanfranco S (2014). Morphometric heterogeneity of temporary pools in Malta and its effect on species richness: implications for management and restoration. *Proc 6th EPCN Conference, Huesca, Spain, abstract*
- Buschke FT, Esterhuysen S et al (2012) The dynamics of mountain rock pools—are aquatic and terrestrial habitats alternative stable states? *Acta Oecol* 47:24–29
- Campbell EM (1997) Granite landforms. *J Roy Soc W Austral* 80:101
- Cantrell MA, McLachlan AJ (1982) Habitat duration and dipteran larvae in tropical rain pools. *Oikos* 38:343–348
- Chan M, Moser K et al (2005) Desert potholes: ephemeral aquatic microsystems. *Aqua Geochem* 11:279–302
- Cher O (2008) *EPCN Newsl* 2:3–4
- Chesson PL (1985) Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. *Theor Popul Biol* 28:263–287
- Cross AT, Turner SR et al (2015) Seed dormancy and persistent sediment seed banks of ephemeral freshwater rock pools in the Australian monsoon tropics. *Annal Bot* 115:847–859
- De Roeck ERM, Artois T, Brendonck L (2005) Consumptive and non-consumptive effects of turbellarian (*Mesostoma* sp.) predation on anostracans. *Hydrobiologia* 542:103–111
- De Roeck ER, Waterkeyn A, Brendonck L (2010) Life history traits of *Streptocephalus purcelli* Sars, 1898 (Branchiopoda, Anostraca) from temporary waters with different phenology. *Water SA* 36:323–328

- De Vries CP (1996) Invertebrate community structure and dynamics in Korannaberg rock pools. Univ Orange Free State, Bloemfontein South Africa, MS thesis
- Dodson SI (1987) Animal assemblages in temporary desert rock pools: aspects of the ecology of *Dasyhelea sublettei* (Diptera: Ceratopogonidae). J N Am Benthol Soc 6:65–71
- Ebert D, Haag C et al (2002) Outbreeding confers a selective advantage to immigrant genes in a metapopulation. Science 295:485–488
- Egan AT, Ferrington LC (2015) Zonal stratification and geographic clustering of a species rich chironomid community in freshwater coastal rock pools. Hydrobiologia 751:147–158
- Ganning B (1971) Studies on chemical, physical and biological conditions in Swedish rock pool ecosystems. Ophelia 9:51–105
- Geldard M (2005) Saving the ridged water-milfoil. Austral Plan Conserv 13:27
- Ghilarov AM (1967) Zooplankton of arctic rock pools. Oikos 18:82–95
- Graham TB (1994) Predation by dipteran larvae on fairy shrimp (Crustacea: Anostraca) in Utah rock-pools. SW Natural 39:206–207
- Graham TB, Wirth D (2008) Dispersal of large branchiopod cysts: potential movement by wind from potholes on the Colorado Plateau. Hydrobiologia 600:17–27
- Hammond MP, Kolasa J (2014) Spatial variation as a tool for inferring temporal variation and diagnosing types of mechanisms in ecosystems. PLoS One 9(2), e89245. doi:10.1371/journal.pone.0089245
- Hanski I, Ranta E (1983) Coexistence in a patchy environment—three species of *Daphnia* in rock pools. J Anim Ecol 52:263–279
- Hebert PDN, Emery CJ (1990) The adaptive significance of cuticular pigmentation in *Daphnia*. Func Ecol 4:703–710
- Hulsmans A, Moreau K et al (2007) Direct and indirect measures of dispersal in the fairy shrimp *Branchipodopsis wolfei* indicate a small scale isolation-by-distance pattern. Limnol Oceanogr 52:676–684
- Hulsmans A, Vanschoenwinkel B et al (2008) Quantifying the hydroregime of a temporary pool habitat: a modelling approach for ephemeral rock pools in SE Botswana. Ecosystems 11:89–100
- Jocqué M, Martens K, Riddoch B, Brendonck L (2006) Faunistics of ephemeral rock pools in southeastern Botswana. Arch Hydrobiol 165:415–431
- Jocqué M, Graham T, Brendonck L (2007a) Local structuring factors of invertebrate communities in ephemeral freshwater rock pools and the influence of more permanent water bodies in the region. Hydrobiologia 592:271–280
- Jocqué M, Riddoch B, Brendonck L (2007b) Successional phases and species replacements in freshwater rock pools: towards a biological definition of ephemeral systems. Freshw Biol 52:1734–1744
- Jocqué M, Timms B, Brendonck L (2007c) A contribution on the biodiversity and conservation of the freshwater fauna of rocky outcrops in the central Wheatbelt of Western Australia. J Royal Soc W Austral 90:137–142
- Jocqué M, Vanschoenwinkel B, Brendonck L (2010a) Freshwater rock pools: a review of habitat characteristics, faunal diversity and conservation value. Freshw Biol 55:1587–1602
- Jocqué M, Vanschoenwinkel B, Brendonck L (2010b) Anostracan monopolisation of early successional phases in temporary waters? Fund Appl Limnol 176:127–132
- Kolasa J, Li BL (2003) Removing the confounding effect of habitat specialization reveals the stabilizing contribution of diversity to species variability. Proc Royal Soc London B Suppl 270:198–201
- Kolasa J, Romanuk TN (2005) Assembly of unequals in the unequal world of a rock pool meta-community. In: Holyoak M, Leibold MA, Holt RD (eds) Metacommunities: spatial dynamics and ecological communities. Univ Chicago Press, Chicago, pp 212–232
- Lanfranco S (1995) Ecological succession in Maltese freshwater rock pools. Univ Malta, PhD Dis
- Lanfranco S, Briffa K (2012) Temporary freshwater pools of the Maltese Islands. In: Gauci R, Schembri J (eds) Landscapes and landforms of the Maltese Islands, World geomorphological landscapes. Springer, Dordrecht

- Lanfranco S, Grillas P (2010) Hydrological characteristics of temporary freshwater pools of the Maltese Islands. 4th Conf European Pond Conserv Network (EPCN) Berlin (Erkner), abstract
- Lanfranco S, De Walsche C, Schembri P, Mertens J (1991) Branchiopods (non-cladocerans) of the Maltese Islands (central Mediterranean). *Hydrobiologia* 212:241–243
- Lanfranco S, Grima C et al (2015) Phylogenetic clustering as a tool for long term monitoring of plant communities in rock pools. Mediterranean Temporary Ponds, Paulis Project. Sassari, Italy, Proc Internat Sympo
- Liao Y-F, Faulks LK, Östman Ö (2015) Stress tolerance and population stability of rock pool *Daphnia* in relation to local conditions and population isolation. *Hydrobiologia* 742: 267–278
- Martens K (1996) On *Korannacythere* nov. gen. (Crustacea, Ostracoda): a new genus of temporary pool limnocytherids from Southern Africa, with the description of three new species and a generic reassessment of the Limnocytherinae. *Bulle Koninklijk Belgisch Instit Natuurwet Biol* 66:51–72
- Martens K, Schön I, Meisch C, Horne DJ (2008) Global diversity of ostracods (Ostracoda, Crustacea) in freshwater. *Hydrobiologia* 595:185–193
- McLachlan AJ (1981) Food sources and foraging tactics in tropical rain pools. *Zool J Linnean Soc* 71:265–277
- McLachlan A (1983) Habitat distribution and body size in rain-pool dwellers. *Zool J Linnean Soc* 79:399–407
- McLachlan AJ, Ladle R (2001) Life in the puddle: behavioural and life-cycle adaptations in the Diptera of tropical rain pools. *Biol Rev* 76:377–388
- Meier S, Soininen J (2014) Phytoplankton metacommunity structure in subarctic rock pools. *Aqua Microbial Ecol* 73:81–91
- Ng ISY, Carr CM, Cottenie K (2009) Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia* 619:133–143
- Osborne PL, McLachlan AJ (1985) The effect of tadpoles on algal growth in temporary, rain-filled rock pools. *Freshw Biol* 15:77–87
- Pajunen VI (1986) Distributional dynamics of *Daphnia* species in a rock-pool environment. *Ann Zool Fenn* 23:131–140
- Pajunen VI, Pajunen I (2003) Long-term dynamics in rock pool *Daphnia* metapopulations. *Ecography* 26:731–738
- Pandit SN, Kolasa J, Cottenie K (2009) Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology* 90:2253–2262
- Pellowe-Wagstaff KE, Simonis JL (2014) The ecology and mechanisms of overflow-mediated dispersal in a rock-pool metacommunity. *Freshw Biol* 59:1161–1172
- Pinder AM, Halse SA, Shiel RJ, McRae JM (2000) Granite outcrop pools in south Western Australia: foci of diversification and refugia for aquatic invertebrates. *J Royal Soc W Austral* 83:149–161
- Ranta E, Nuutinen V (1985) *Daphnia* exhibit diurnal vertical migration in shallow rock pools. *Hydrobiologia* 127:253–256
- Riddoch BJ, Mpoloka SW, Cantrell M (1994) Genetic variation and localised gene flow in the fairy shrimp, *Branchipodopsis wolfi* in temporary rainwater pools in south-eastern Botswana. In: Beaumont AR (ed) Genetics and evolution of aquatic organisms. Chapman Hall, London, pp 96–102
- Romanuk TN, Kolasa J (2002) Environmental variability alters the relationship between richness and variability of community abundances in aquatic rock pool microcosms. *Ecoscience* 9:55–62
- Romanuk TN, Kolasa J (2005) Resource limitation, biodiversity, and competitive effects interact to determine the invisibility of rock pool microcosm. *Biol Invasions* 7:711–722
- Simonis JL (2013) Prey (*Moina macrocopa*) population density drives emigration rate of its predator (*Trichocorixa verticalis*) in a rock-pool metacommunity. *Hydrobiologia* 715:19–27
- Simonis JL, Ellis JC (2014) Bathing birds bias beta-diversity: Frequent dispersal by gulls homogenizes fauna in a rock-pool metacommunity. *Ecology* 95:1545–1555

- Smith DC (1983) Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan. *Ecology* 64:501–510
- Smol J, Douglas MSV (2007) Crossing the final ecological threshold in high Arctic ponds. *Proc Natl Acad Sci U S A* 104:12395–12397
- Soininen J, Meier S (2014) Phytoplankton richness is related to nutrient availability, not to pool size, in a subarctic rock pool system. *Hydrobiologia* 740:137–145
- Spencer M, Blaustein L (2001) Hatching responses of temporary pool invertebrates to signals of environmental quality. *Isr J Zool* 47:397–418
- Spencer M, Blaustein L, Cohen JE (2002) Oviposition habitat selection by mosquitoes (*Culiseta longiareolata*) and consequences for population size. *Ecology* 83:669–679
- Springer GS, Tooth S, Wohl EE (2006) Theoretical modeling of stream potholes based upon empirical observations from the Orange River, Republic of South Africa. *Geologija* 82:160–176
- Therriault TW, Kolasa J (2001) Desiccation frequency reduces species diversity and predictability of community structure in coastal rock pools. *Isr J Zool* 47:477–489
- Timms BV (2012a) Seasonal study of aquatic invertebrates in five sets of latitudinally separated gnammas in southern western Australian. *J Royal Soc W Austral* 95:13–28
- Timms BV (2012b) Influence of climatic gradients on metacommunities of aquatic invertebrates on granite outcrops in southern western Australia. *J Royal Soc W Austral* 95:125–135
- Timms BV (2013) Geomorphology of pit gnammas in southwestern Australia. *J Royal Soc W Austral* 96:7–16
- Timms BV (2014a) Invertebrates of pit gnammas in Southwest Australia. *J Royal Soc W Austral* 96:55–67
- Timms BV (2014b) Community ecology of aquatic invertebrates in gnammas (rock-holes) of North-Western Eyre Peninsula, South Australia. *Trans Royal Soc S Austral* 138:147–160
- Timms BV, Rankin C (2014) The geomorphology of gnammas (weathering pits) of north-western Eyre Peninsula, South Australia: typology, influence of haloclasty and origins. *Trans Royal Soc S Austral*
- Tuck C, Romanuk TN (2012) Robustness to thermal variability differs along a latitudinal gradient in zooplankton communities. *Glob Chg Biol* 118:1597–1608
- Tuytens K, Vanschoenwinkel B, Waterkeyn A, Brendonck L (2014) Predictions of climate change infer increased environmental harshness and altered connectivity in a cluster of temporary pools. *Freshw Biol* 59:955–968
- Twidale C, Bourne J (1975) Episodic exposure of inselbergs. *Geol Soc Am Bull* 86:1473–1481
- Vale CG, Pimm SL, Brito JC (2015) Overlooked mountain rock pools in deserts are critical local hotspots of biodiversity. *PLoS One* 10(2), e0118367. doi:[10.1371/journal.pone.0118367](https://doi.org/10.1371/journal.pone.0118367)
- Vanschoenwinkel B, De Vries C, Seaman MT, Brendonck L (2007) The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. *Oikos* 116:1255–1266
- Vanschoenwinkel B, Gielen S, Seaman MT, Brendonck L (2008a) Any way the wind blows—frequent wind dispersal drives species sorting in ephemeral aquatic habitats. *Oikos* 117:125–134
- Vanschoenwinkel B, Gielen S, Vandewaerde H, Brendonck L (2008b) Relative importance of different dispersal vectors for small aquatic invertebrates in a rock pool metacommunity. *Ecography* 31:567–577
- Vanschoenwinkel B, Hulsmans A et al (2009) Community structure in temporary freshwater pools: disentangling the effects of habitat size and hydroregime. *Freshw Biol* 54:1487–1500
- Vanschoenwinkel B, Seaman MT, Brendonck L (2010a) Hatching phenology, life history and egg bank size of a fairy shrimp (Branchiopoda, Crustacea) in relation to the ephemerality of its habitat. *Aqua Ecol* 44:771–780
- Vanschoenwinkel B, Waterkeyn A et al (2010b) Species sorting in space and time—the impact of disturbance regime on community assembly in a temporary pool metacommunity. *J N Am Benth Soc* 29:1267–1278

- Vanschoenwinkel B, Mergeay J et al (2011) Long distance dispersal of zooplankton endemic to isolated mountaintops—an example of an ecological process operating on an evolutionary time scale. PLoS One 6(11), e26730. doi:[10.1371/journal.pone.0026730](https://doi.org/10.1371/journal.pone.0026730)
- Vanschoenwinkel B, Pinceel T et al (2012) Toward a global phylogeny of the “Living Fossil” crustacean order of the Notostraca. PLoS One 7(4), e34998
- Vanschoenwinkel B, Buschke FT, Brendonck L (2013) Disturbance regime alters the impact of dispersal on alpha and beta diversity in a natural metacommunity. Ecology 94:2547–2557
- Weeks SC, Zofkova M, Knott B (2006) Limnadiid clam shrimp distribution in Australia (Crustacea: Branchiopoda: Spinicaudata). J Royal Soc W Austral 89:155–161
- White M (2009) Prioritising Rock-holes of Aboriginal and ecological significance in the Gawler Ranges, DWLBC Report 2009/08 Version 1. Gov South Australia, Dept Water Land Biodiver Conserv, Adelaide
- Wiggins GB, Mackay RJ, Smith IM (1980) Evolutionary and ecological strategies of animals in annual temporary pools. Arch Hydrobiol Suppl 58:97–206
- Zofkova M, Timms BV (2009) A conflict of morphological and genetic patterns in the Australian anostracan *Branchinella longirostris*. Hydrobiologia 635:67–80

Invertebrates in Freshwater Wetlands

An International Perspective on their Ecology

Batzer, D.; Boix, D. (Eds.)

2016, X, 645 p. 91 illus., 61 illus. in color., Hardcover

ISBN: 978-3-319-24976-6