Hydrobiologia (2007) 592:271–280
DOI 10.1007/s10750-007-0766-7

PRIMARY RESEARCH PAPER

Local structuring factors of invertebrate communities in ephemeral freshwater rock pools and the influence of more permanent water bodies in the region.

Merlijn Jocqué · Tim Graham · Luc Brendonck

Received: 30 November 2006 / Revised: 17 April 2007 / Accepted: 11 May 2007 / Published online: 24 July 2007

Abstract We used three isolated clusters of small ephemeral rock pools on a sandstone flat in Utah to test the importance of local structuring processes on aquatic invertebrate communities. In the three clusters we characterized all ephemeral rock pools (total: 27) for their morphometry, and monitored their water quality, hydrology and community assemblage during a full hydrocycle. In each cluster we also sampled a set of more permanent interconnected freshwater systems positioned in a wash, draining the water from each cluster of rock pools. This design allowed additional testing for the potential role of more permanent water bodies in the region as source populations for the active dispersers and the effect on the community structure in the rock pools. Species richness and community composition in the rock pools correlated with level of permanence and the ammonia concentration. The length of the rock pool inundation cycle shaped community structure, most probably by inhibiting colonization by some taxa (e.g. tadpoles and insect larvae) through developmental constraints. The gradient in ammonia concentrations probably reflects differences in primary production. The more permanent water bodies in each wash differed both environmentally and in community composition from the connected set of rock pools. A limited set of active dispersers was observed in the rock pools. Our findings indicate that aquatic invertebrate communities in the ephemeral rock pools are mainly structured through habitat permanence, possibly linked with biotic interactions and primary production.

Keywords Rock pool · Community structure · Ephemeral · Permanence · Primary production

Handling editor: S. I. Dodson

M. Jocqué (✉) · L. Brendonck
Laboratory of Aquatic Ecology, K.U. Leuven, de Bériotstraat 32, 3000 Leuven, Belgium
e-mail: Merlijn.Jocque@bio.kuleuven.ac.be

T. Graham
USGS, 2290 West Resources Blvd, Moab, UT 84532, USA

Introduction

The identification of factors and processes structuring communities is a fundamental element of community ecology. These processes are usually divided in local and regional processes (Ricklefs, 1987, 2004; Ricklefs & Schluter, 1993). Local factors and processes, mainly habitat characteristics (abiotic) and interactions between inhabitants (biotic), act as a filter and define the pool of species potentially occurring in a community through processes such as species sorting (Leibold et al., 2004) and habitat selection (Resetarits, 2001, 2005). The realized assemblage (the actual species in a community) is a subset of all the species occurring in the surrounding region (regional species pool) and often is positively related to the regional species pool (Karlson & Cornell, 1999; Shurin et al., 2000).

Regional factors and processes include all variables affecting the exchange (dispersal) between communities. These regional variables determine which species and in what quantity may arrive in a community, further affecting the community structure. Regional factors include elements affecting the connectivity between two communities such as rivulets between water bodies, providing a potentially large and continuous influx of colonizers (Cottenie et al., 2003) that can keep species present under suboptimal conditions (Leibold et al., 2004). Also species-specific dispersal behaviour and particularly the difference between active (e.g. most Insecta) and passive dispersers (e.g. most freshwater Crustacea) will influence the dispersal between communities through the effective scale of dispersal (Graham, 2002; Rundle et al., 2002).

Small water bodies have recently been brought to the foreground as model systems to test ecological and evolutionary hypotheses (Blaustein & Schwartz, 2001; Srivastava et al., 2004; De Meester et al., 2005). These habitats have many advantages, such as small food webs in a realistic setting and the ease of manipulation through their small size. The small size combined with the occurrence of these habitats in large numbers in relatively small areas makes them attractive habitat systems to use in community studies. Freshwater rock pools are additionally typified by a simple structure of the pool basin. Despite these favourable characteristics for ecological research, little information on the community structuring processes in temporary freshwater rock pools is available. Ecological rock pool research so far was mainly based on parts of the whole community; on single species such as on *Daphnia longispina* (Ranta and Tsossmem, 1987) and *Branchipodopsis wolfi* (Brendonck & Riddoch, 1999, 2000) or on multiple species (e.g. Dodson, 1987; Bengtsson, 1989; Blaustein et al., 1995; Brendonck & Riddoch, 1999; De Roeck et al., 2005). Some studies, also mostly on a limited set of species, identified the local structuring factors in rock pools. The relationship between species richness and the environment was for example studied in micro-Turbellaria (Eitam et al., 2004a) and Cladocera and Ostracoda (Eitam et al., 2004b) in rock pools in Israel. In these studies, diversity was mainly related to pool size (micro-Turbellaria) and pool permanence (Cladocera and Ostracoda). Additional variation in ostracod species richness was further explained by water and sediment depth. In another study, pool size also influenced the proportion of predatory animals in a rock pool community (Spencer et al., 1999). Community richness and diversity patterns in relation to habitat variability were studied in a set of Jamaican rock pools (Therriault & Kolasa, 1999, 2000, 2001; Romanuk & Kolasa, 2001, 2002, 2005). In these rock pools, richness of communities was negatively correlated with desiccation frequency and environmental variability.

With this study we aimed at contributing to the ecology of invertebrate communities in temporary rock pools. We therefore studied three sets of nine ephemeral rock pools on a sandstone flat, isolated from each other by rocky ridges, during an entire flooding cycle. Each set of rock pools had its own drainage system with a central wash containing more permanent and interconnected water bodies. We identified the major factors determining the richness and community composition in the rock pools. To assess the importance of the regional species pool and to test the potential value as source habitats for active dispersers to colonize the rock pools, these more permanent water bodies were also sampled and communities compared with those in the rock pools. Considering the unidirectional water flow from the rock pools to the more permanent pools, together with the predicted richer communities in the more permanent systems, we expect the rock pool communities to be a subset of those in the more permanent water bodies.

Materials and methods

Site description & pool selection

Three clusters of rock pools were studied on different exposures of the Moab Tongue of the Entrada Sandstone northwest of Moab, Utah in an area known as Hidden Canyon. Each cluster was separated from the others by rocky ridges of approximately 50 m high. The three sites; Hidden Canyon 1 (HC1), Hidden Canyon 2 (HC2) and Hidden Canyon 3 (HC3), had separated watersheds with each site containing a deeply eroded wash collecting run off water from the flat. At the start of the monitoring, all pools on the sandstone flat were dry. A set of nine rock pools close to each other was chosen at each site (total: 27 pools), aiming to include some variation along the permanence gradient. The average depth of each basin was here used as a proxy for the level of permanence. The selected rock pools were sampled quantitatively from dry to dry phase (maximum 12 days) with a two-day sampling frequency. Sampling of the whole community was initiated the second day after filling at HC1 and HC2 and the third day at HC3.

The more permanent water bodies in the region (<500 m radius) were pools in the wash, often deeply eroded rock pools and some mud pools. Most of these pools contained water during the whole survey (15 August–15 October 2003). We randomly selected five of these pools at each of the three sites (total: 15 pools) for sampling. Sampling of the more permanent wash pools was done nine (HC2) and ten (HC1) days before, and 9 days after (HC3) the precipitation. The water flow in the systems provides a one-way connection for inhabitants with a passive dispersal (for instance Crustacea) from the rock pools on the flat to the more permanent pools in the wash. As long as the more permanent pools contain water, the only possible exchange from the wash pools to the rock pools on the flat is by active dispersers (mostly Insecta).

Characterization of the pools

A thunderstorm filled hundreds of pools on the rocky surface completely and synchronously at all three rock pool sites. We characterized the 27 rock pools on the flat the day after filling and before the first sampling. The water quality variables in the 15 more permanent water bodies in the wash were measured together with the sampling of the communities. Temperature, conductivity, oxygen and pH were recorded every sampling with WTW meters. The first day after rain, maximum length, maximum width (orthogonal on the length) and the deepest point in each pool were recorded. Based on these measurements, surface area was calculated as length times width. Volume was estimated by multiplying surface area with average depth. Turbidity was measured with a Snel's tube in centimetres. Water samples taken in the field were stored and transported in a cooler with ice. Nutrient concentrations were measured with a HACH DR/700 portable colorimeter within 5 h after sampling and after acclimatization of the water to room temperature. We used method 8,155 (NH_3–N, ammonia), 8,192 (NO_3–N, nitrate), 8,408 (PO_4^{3-}, reactive phosphorus) and 8,507 (NO_2–N, nitrite) in the instrument manual (Hach, 1992). For chlorophyll a measurements, as much water as possible was filtered over GF/C Whatman filters using a manual vacuum pump at 1 bar pressure. The filter was dried for half a minute under vacuum, folded inwards, packed in foil paper and transported on top of ice in a cool box. In the laboratory, samples were stored in a –81°C freezer. Chlorophyll a was measured spectrophotometrically after extraction in 96% ethanol following the method of Bergmann & Peters (1980). Absorption was measured at 665 ± 1 nm. We corrected for turbidity by subtracting the absorption at 750 ± 1 nm. For the analyses, surface, volume, chl a, conductivity and nutrient concentrations were logarithmically transformed to make differences equally important.

Sampling design and faunistics

Sampling of pools on the sandstone flat was done by placing a plastic tube (height: 40 cm; diameter: 10 cm) with rubber edge on one side, randomly in each pool. The rubber edge fitted the tube to the sediment surface and isolated the water column. The tube sampler was consequently emptied by a PRIJON ''thirsty-mate'' Kayak pump attached to a tube (diameter: 5 cm) leading the water over a sieve (20-µm netting). Pumped water was quantified and the tubing and pump were rinsed between pools. At each occasion sampling was done three times per pool in a swift move to avoid flight of the active swimmers.

The qualitative sampling of the more permanent water bodies in the wash was done using approximately 1 m sweeps of a kick sampler (500-μm netting) and zooplankton net (64-μm netting) to collect macroinvertebrates and zooplankton, respectively.

The collected material for both series of samplings was preserved in 70% ethanol. Rock pool samples were rinsed over a net (64-μm netting) and decantation removed the smallest mud and the heavier sand particles, respectively. Samples were stained with rose Bengal solution. For each replicate sample, sub-samples of 300 animals were counted. One of the replicates was analyzed in toto, to detect any rare taxa. Samples of the more permanent water bodies were analyzed completely to compose a presence-absence matrix. With exception of the Turbellaria and Rotifera, we identified morphospecies and identified taxa to the lowest possible level using Merrit & Cummins (1996) and Thorp & Covich (2001). In the analysis of the rock pool community composition, 14 morphospecies were used. The two morphospecies of Oribatidae were grouped together in the analyses, as we were not sure whether these were different species. Estimated densities were expressed as individuals per litre.

Analyses of pool types and community structure

The physical and chemical environment and species richness were compared between the different habitat types making use of averages for the ephemeral rock pools on the flat and the single measurements for the more permanent water bodies in the wash, using independent *t*-tests (ANOVA) in STATISTICA 6.0 (Statsoft Inc., 2001).

Initial analyses of the rock pool community composition with a Detrended Canonical Correspondence Analysis (DCCA) showed a gradient length of <3 standard deviation units (SD), implying a linear response of the taxa to the inserted variables (Ter Braak & Smilauer, 1998). We therefore used a Redundancy Analysis (RDA) to analyze both the invertebrate community composition and the species richness in the 27 rock pools. In the analysis of the community composition we log transformed ($y = \text{Log}\ x + 1$) the abundance data. Samples were standardized by norm since we were interested in relative proportions of the composing species. For the multiple regression on the species richness no transformations or standardizations were performed on the data. In both analyses, the sites were inserted as covariables with permutation blocks defined by covariables and significant ($P < 0.05$) variables were chosen using random Monte Carlo permutations ($n = 999$) in the forward selection procedure. Multivariate and univariate analyses were performed in CANOCO (Ter Braak & Smilauer, 1998).

To test whether the rock pool communities were a subset of the communities in the more permanent water bodies in the region, and to specifically test whether the more permanent pool populations were sources of active dispersers for the rock pools, we evaluated the presence of a nested design using the binary matrix nestedness temperature calculator (BINMATNEST) (Rodríguez-Gironés & Santamaría, 2006). Nestedness is a property of binary matrices of ecological data, and is quantified by the matrix's "temperature", a measure for the extent of order present in the matrix (Atmar & Patterson, 1993).

Results

Characterization of the pools

The 27 rock pools on the flat were shallow (9 ± 4 cm) and varied strongly in size (10.6 ± 6.3 m^2), with low nutrient and chlorophyll a (1.8 ± 0.7 μg/l) content (Table 1). The water was clear (Snel's reading of 34 ± 5 cm) and often reached relatively high temperatures (25.6 ± 3.8°C) and oxygen saturation (156.7 ± 13.8%) levels. The 15 more permanent pools in the wash differed significantly in environmental conditions from the rock pools for all measured variables, except for ammonia concentration and temperature (Table 1). The more permanent water bodies were on average deeper (44 ± 35 cm), more turbid (Snel's reading of 20 ± 6 cm) and had

Table 1 Physical and chemical characteristics of 27 rock pools on a sandstone flat and 15 more permanent pools in the region

	Rock pools				More permanent water bodies						
	Avg	SD	Max	Min	Avg	SD	Max	Min	*t*-value	df	*P*-value
Depth (cm)	9	4	20	4	44	35	112	4	–5.17	40	0.000
Surface (m^2)	0.7	0.2	1.1	0.3	7.3	7.2	27.2	0.9	–4.82	40	0.000
Chlorophyll a (μg/l)	1.8	0.7	3.2	0.7	4.9	4.2	11.5	–1.9	–3.76	34	0.001
Turbidity (cm)	34	5	42	23	20	6	29	5	7.58	40	0.000
Ammonia (mg/l)	0.27	0.88	4.60	0.01	0.63	1.21	4.90	0.10	–1.10	40	0.280
Phosphorus (mg/l)	1.06	0.72	2.75	0.13	1.68	0.99	2.75	0.12	–2.34	40	0.024
Nitrates (mg/l)	0.10	0.07	0.25	0.01	0.24	0.18	0.55	0.00	–3.70	40	0.001
Nitrites (mg/l)	0.002	0.001	0.005	0.001	0.039	0.101	0.340	–0.003	–2.78	40	0.008
Temperature (°C)	25.6	3.8	28.8	9.2	23.8	6.8	32.9	14.0	1.12	40	0.268
Conductivity (μS/cm)	16.5	4.2	27.1	8.7	24.4	7.6	40.5	13.8	–4.38	40	0.000
Oxygen (%)	156.7	13.8	180.0	121.5	121.5	44.0	188.0	19.0	3.86	40	0.000
pH	9.7	0.3	10.3	8.9	9.2	0.6	10.1	7.7	3.37	40	0.002
Permanence (days)	5	3	12	2	–	–	–	–	–	–	–

Averages (avg), standard deviations (SD), maximum and minimum values (max. and min.) are presented. Independent *t*-tests are performed to test for significant differences between the two types of pools, *t*-values, *P*-values and degrees of freedom (df) are given

higher nutrient (except ammonia) and chlorophyll a (4.9 ± 4.2 μg/l) levels. Their temperature (23.8 ± 6.8°C) and oxygen saturation (121.5 ± 44.0%) was slightly lower.

Faunistics

A total of 15 species were collected from the 27 rock pools, with an average of 5.9 ± 1.8 species per pool (Table 2). The species occurring in most of the pools were *Cypriconcha* sp. (Ostracoda), *Branchinecta packardi* (Anostraca), *Dasyhelea* sp. (Ceratopogonidae) and *Pseudobiotus* sp. (Tardigrada).

The more permanent pools in the wash housed a total of 29 species with on average 7.6 ± 2.6 species per pool. The most common species in these pools were *Cypriconcha* sp. (Ostracoda), *Limnocythere* sp. (Ostracoda) and *Branchinecta packardi* (Anostraca). Turbellaria were well presented in both the rock pools and the more permanent water bodies.

Community structure

Forward selection in the RDA analysing the community composition isolated depth and ammonia concentration, together explaining 24.3% of the variance in the dataset ($F = 4.076$, $P = 0.001$) (Fig. 1). The unconstrained axes explained a total of 92.9% of the variance. The multiple regression (RDA) of the species richness linked the variance in species richness between rock pool communities with pool permanence and log ammonia (28.8% of the variance in the dataset, $F = 5.545$, $P = 0.004$). The unconstrained axes explained 88.5% of the variance. The pools with a short inundation period were characterized by high densities of *Pseudobiotus* sp. and Rotifera, and to a minor extent also by oribatid mites. Pools with a longer inundation period housed higher densities of *Branchinecta packardi*, *Dasyhelea* sp. and *Limnocythere* sp.

At all three study sites, the rock pool communities on the flat revealed a pattern of nestedness, indicating a non-random distribution of the inhabitants over the rock pools (Table 3). The communities remained nested at two of the three sites (HC1 and HC3) after addition of the wash pools to the dataset. The total of all sampled pools (both rock and wash pools) together, also showed a nested pattern (Table 3). All species in the ephemeral rock pools were also retrieved in the more permanent pools in the wash. A total of 16 active dispersers were present in the more permanent water bodies, with 13 insects and one ostracod species (*Potamocypris compressa*) found exclusively in the more permanent wash pools (Table 2). In the rock pools only three species of

Table 2 Collected taxa in 27 rock pools on the sandstone flat (RP) and 15 more permanent water bodies in the region (MPW)

Major group	Taxon	RP	MPW
Anostraca	*Branchinecta packardi* Pearse	19	10
Ostracoda	*Cypriconcha* sp. Dobbin	21	13
	Limnocythere sp.	5	13
	Potamocypris compressa	0	1
Spinicaudata	*Eulimnadia* cf. *texana*	3	1
Notostraca	*Triops longicaudatus* (Le Conte)	1	4
Cladocera		1	2
Copepoda	Harpacticoida	1	1
Ephemeroptera	Baetidae (L)	3	8
Hemiptera	*Notonecta* sp. (A)	1	3
	Corixidae (L)	0	3
	Microvelia sp. (A & L)	0	1
	Gerridae	0	3
Diptera	*Limnophora* sp.	0	3
	Culicidae	0	7
	Chironomidae	0	9
	Dasyhelea sp.	18	1
Coleoptera	*Coptotomus* sp. (A)	0	1
	Eretes sticticus (Linneaus) (L)	0	5
	Agabus sp. (A)	0	1
	Berosus sp. (L)	0	1
Odonata	Cordullidae (L)	0	1
	Coenagrionidae (L)	0	1
Turbellaria	1 sp.?	25	13
Tardigrada	*Pseudobiotus* sp.	25	1
Acari	Oribatidae sp. A	9	1
	Oribatidae sp. B	1	1
Rotifera		27	15
Anura	*Bufo punctatus* Baird & Girard	0	5

The number of pools housing the taxon is mentioned. A = adult, L = Larvae

active dispersers were found; *Dasyhelea* sp., a mayflie (Baetidae) and a backswimmer (Notonectidae).

Discussion

The length of the inundation period (pool permanence) and the concentration of ammonia were the most important local factors determining the invertebrate community composition and the species richness in ephemeral rock pools on a sandstone flat in Utah. The more permanent water bodies in the washes differed substantially from these rock pools, both in physical and chemical water characteristics as in the animal communities. The communities in the rock pools were a subset of the communities in the more permanent wash pools, with 14 species (mainly active dispersers) exclusively collected from the more permanent pools. The more permanent pools hence held the entire species richness of the region and may function as source habitats for actively dispersing organisms.

The most important community-structuring factor of the rock pool communities was the length of the inundation period. The short duration pools were typified by high densities of Rotifera, Tardigrada and oribatid mites, and these communities were a subset of the more diverse communities in the larger pools with a longer persistence. Communities from the pools with longer permanence were characterized by larger inhabitants, such as *Branchinecta packardi* (Anostraca), *Dasyhelea* sp. (Ceratopogonidae) and Ostracoda species. Development constraints most probably prevent some of these larger species to occur in the most ephemeral pools.

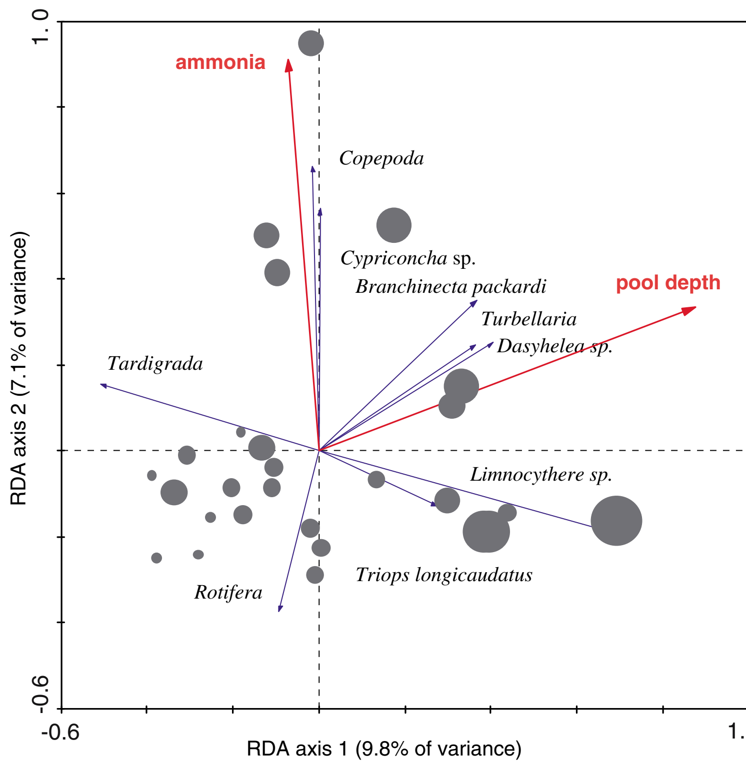

Fig. 1 Redundancy Analysis based on invertebrate abundances in freshwater rock pools constrained by pool depth and ammonia concentration. Size of the circles reflects the level of permanence of the 27 rock pools sampled. The nine taxa best fitting the analysis were included

Most of the larger species, except for *Dasyhelea* sp., which can resist desiccation in the larval phase (Dodson, 1987), die upon early pool drying.

Table 3 Results of nestedness calculations on invertebrate communities of the three studied sites: Hidden Canyon 1 (HC1), Hidden Canyon 2 (HC2), Hidden Canyon 3 (HC3) separately, and on all 27 rock pools in Hidden Canyon (HC) together

Site	Temp	*P*-value
HC1	14.916	0.046
HC1 + MPW	16.163	0.010
HC2	8.125	0.000
HC2 + MPW	25.799	0.222
HC3	8.673	0.000
HC3 + MPW	17.238	0.001
HC	12.204	0.000
HC + MPW	11.845	0.000

The same analyses were done including the more permanent water bodies in the wash (+MPW). The temperature as calculated by the program BINMATNEST, reflecting the extent of order present in the dataset, and the correlated *P*-values are presented. The *P*-value reflects the probability that a ''random'' matrix has the same level of nestedness as the inserted matrix

The species occurring in the most ephemeral pools, in contrast, are able to develop over subsequent inundation cycles, by tun formation (Rotifera and Tardigrada) (Wright, 2001), by encapsulating in the sediment (Oribatidae) (Norton et al., 1997) or by drought resistance (Chironomidae) (Cantrell & McLachlan, 1982; Frouz et al., 2003). Other studies documented that physical (developmental) constraints can prevent the occurrence of large organisms (often predators or dominant competitors) in pools with a short hydroperiod (Tevis, 1966; Jeffries, 1994). The absence of these large organisms often allows smaller and more vulnerable organisms, adapted to the ephemeral part of the permanence gradient, to reach higher densities in the ephemeral habitats. Fairy shrimp species in rock pools, which typically are well adapted to ephemeral habitats, by a high developmental rate among other adaptations (Brendonck et al., 2000), still need approximately 5 days to mature in the studied rock pools (Jocqué M. pers. obs.). This minimal development time makes it impossible to persist in the most ephemeral pools (4 days or less). The absence of Anostraca (*Branchinecta packardi*) in the most ephemeral rock pools will consequently have a strong effect on the community structure as they are competitively superior filter feeders (e.g. to Cladocera). This may explain the observed high densities of Rotifera in these pools. Starkweather (2005) confirmed that fairy shrimp in rock pools can have a strong negative influence on Rotifera (*Hexarthra* sp.) populations.

Only three active dispersers were collected from the rock pools (*Dasyhelea* sp., Notonectidae and Baetidae) (Table 2). This is a small fraction of the regional species pool, considering the diversity of active dispersers such as dragonfly larvae, tadpoles, beetles and hemipterans collected in the more permanent wash pools (Table 2). The presence of all active dispersers in the more permanent pools, together with the observation that Notonectidae (Table 2) and adult Coleoptera (pers. obs.) dispersed to the ephemeral rock pools, suggests that these wash pools act as a source for active dispersers. Deduced from the observed low densities, however, they never reside long. The small representation of the active dispersers was also here most probably the result of development constraints linked with the permanence of the rock pools. Although we do not have data of the maturation time of the active dispersers in the studied rock pools, we can learn from data derived from comparable systems. Dragonfly larvae in rock pools in Namibia, for example, needed between 38 and 70 days to mature (Suhling et al., 2004), much longer than the inundation length of the rock pools in our study. Larger temporary ponds with a longer permanence in England also contained a richer diversity of active dispersers (Coleoptera) (Rundle et al., 2002). In a study on the habitat selection by rock pool corixids in Scandinavia, pool permanence (size) and competition were suggested as the most important selection criteria (Pajunen & Pajunen, 2003). Pools with a short inundation period were avoided through the high correlated mortality of offspring through drought before maturation. Pools with fewer competitors were preferred for the abundance of food (prey). The expected strong inter- and intra-specific competition for food in the more permanent pools is probably the driving force for the exploitation of the rock pools in our study system, in search for adequate habitat patches to deposit offspring and possibly also to feed.

The species richness and community composition of the rock pool communities on the flat were also positively related with the concentration of ammonia. Especially Copepoda and *Cypriconcha* sp. occurred in higher densities in pools with high ammonia concentrations. The relatively high nitrogen (ammonia) content in the shallow rock pools is remarkable as rock pools have open nutrient cycles and large parts of the nutrients are removed by winds during the dry phase or are flushed after heavy rains (Osborne & McLachlan, 1985). The importance of external ammonia sources added during the dry period therefore seems unlikely to explain our observations. During the wet phase, ammonia is mostly derived from the organisms themselves. Although we have no direct measurements, cyanobacteria likely are responsible for the observed pattern. Chan et al. (2005), in similar systems, also found an ammonia gradient and could link this with cyanobacterial activity in similar shallow potholes on a sandstone flat in the same area as our study system.

In conclusion, communities in the ephemeral rock pool system of a sandstone flat near Utah were mainly structured by the length of the hydroperiod. Development constraints most probably set a threshold pool permanence for species to occur and in this way the presence/absence of species together with the interactions with the other community members structures the communities.

Acknowledgements We thank Koen Martens and David Horne for identification of the Ostracoda. M. Jocqué is supported by an IWT (Institute for the Promotion of Innovation by Science and Technology in Flanders) PhD scholarship. This research is financially supported by project G.0118.03 of the FWO (Fund for Scientific Research in Flanders).

References

Atmar, W. & B. D. Patterson, 1993. The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia 96: 373–382.

Bengtsson, J., 1989. Interspecific competition increases local extinction rate in a meta-population system. Letters to Nature 340: 713–715.

Bergmann, M. & R. H. Peters, 1980. Simple reflectance method for the measurement of particulate pigment in lake water and its applications to phosphorus-chlorophyll-seston relationships. Canadian Journal of Fisheries and Aquatic Sciences 37: 111–114.

Blaustein, L. & S. S. Schwartz, 2001. Why study ecology in temporary pools?. Israel Journal of Zoology 47: 303–312.

Blaustein, L., B. P. Kotler & D. Ward, 1995. Direct and indirect effects of a predatory backswimmer (*Notonecta maculata*) on community structure of desert temporary pools. Ecological Entomology 20: 311–318.

Brendonck, L. & B. J. Riddoch, 1999. Wind-borne short-range egg dispersal in anostracans (Crustacea: Branchiopoda). Biological Journal of the Linnean Society 67: 87–95.

Brendonck, L. & B. J. Riddoch, 2000. Egg bank dynamics in anostracan desert rock pool populations (Crustacea: Branchiopoda). Archiv für Hydrobiologie 148: 71–84.

Brendonck, L., M. L. Hamer, B. J. Riddoch & M. T. Seaman, 2000. *Branchipodopsis* species—specialists of ephemeral rock pools. African Journal of Aquatic Science 25: 98–104.

Cantrell, M. A. & A. J. McLachlan, 1982. Habitat duration and dipteran larvae in tropical rain pools. Oikos 38: 343–348.

Chan, M. A., K. Moser, J. M. Davis, G. Southam, K. Hughes & T. Graham, 2005. Desert potholes: ephemeral aquatic microsystems. Aquatic Geochemistry 11: 279–302.

Cottenie, K., E. Michels, N. Nuytten & L. De Meester, 2003. Zooplankton meta-community structure: regional vs. local processes in highly interconnected ponds. Ecology 84: 991–1000.

De Meester, L., S. Declerck, R. Stoks, G. Louette, F. Van de Meutter, T. De Bie, E. Michels & L. Brendonck, 2005. Ponds and pools as model systems in conservation biology, ecology and evolutionary biology. Aquatic conservation – Marine and Freshwater Ecosystems 15: 715–725.

De Roeck, E. R. M., T. Artois & L. Brendonck, 2005. Consumptive and non-consumptive effects of turbellarian (*Mesostoma* sp.) predation on anostracans. Hydrobiologia 542: 103–111.

Dodson, S. I., 1987 Animal assemblages in temporary desert rock pools: aspects of the ecology of *Dasyhelea sublettei* (Diptera: Ceratopogonidae). Journal of the North American Benthological Society 6: 65–71.

Eitam, A., C. Norena & L. Blaustein, 2004a. Microturbellarian species richness and community similarity among temporary pools: relationships with habitat properties. Biodiversity and Conservation 13: 2107–2117.

Eitam, A., L. Blaustein, K. Van Damme, H. J. Dumont & K. Martens, 2004b. Crustacean species richness in temporary pools: relationships with habitat traits. Hydrobiologia 525: 125–130.

Frouz, J., J. Matena & A. Ali, 2003. Survival strategies of chironomids (Diptera: Chironomidae) living in temporary habitats: a review. European Journal of Entomology 100: 459–465.

Graham, T. B., 2002. Survey of ephemeral pool invertebrates at Wupatki NM: an evaluation of the significance of constructed impoundments as habitat. Hydrobiologia 486: 215–224.

Hach, 1992. Hach DR/700 Colorimeter Manual. Hach. Loveland, Colorado.

Jeffries, M., 1994. Invertebrate communities and turnover in wetland ponds affected by drought. Freshwater Biology 32: 603–612.

Karlson, R. H. & H. V. Cornell, 1999. Integration of local and regional perspectives on the species richness of coral assemblages. American Zoologist 39: 104–112.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau & A. Gonzalez, 2004. The meta-community concept: a framework for multi-scale community ecology. Ecology Letters 7: 601–613.

Merrit, R. W. & K. W. Cummins, 1996. Aquatic insects of North America, 3rd edn. Kendall/Hunt Publishing Company, Iowa.

Norton, R. A., T. Graham & G. Albert, 1997. A rotifer eating ameronothroid (Acari: Ameronothroidae) mite from ephemeral pools on the Colorado plateau. In Mitchell, R., D. J. Horn, G. R. Needham & W. C. Welbourn (eds), Acarology IX, Proceedings (IXth Inter. Congr. Acarology). Ohio Biological Survey, Columbus.

Osborne, P. L. & A. J. McLachlan, 1985. The effect of tadpoles on algal growth in temporary, rain-filled rock pools. Freshwater Biology 15: 77–87.

Pajunen, V. I. & I. Pajunen, 2003. Long-term dynamics in rock pool *Daphnia* metapopulations. Ecography 26: 731–738.

Ranta, E. & S. Tjossmem, 1987. Size and shape of *Daphnia longispina* in rock pools. Hydrobiologia 145: 259–268.

Resetarits, W. J., 2001. Colonization under threat of predation: avoidance of fish by an aquatic beetle, *Tropisternus lateralis* (Coleoptera: Hydrophilidae). Oecologia 129: 155–160.

Resetarits, W. J., 2005. Habitat selection behaviour links local and regional scales in aquatic systems. Ecology Letters 8: 480–486.

Ricklefs, R. E., 1987. Community diversity—relative roles of local and regional processes. Science 235: 167–171.

Ricklefs, R. E., 2004. A comprehensive framework for global patterns in biodiversity. Ecology Letters 7: 1–15.

Ricklefs, R. E. & D. Schluter, 1993. Species Diversity in Ecological Communities. University of Chicago Press, Chicago.

Rodríguez-Gironés, M. A. & L. Santamaría, 2006. A new algorithm to calculate the nestedness temperature of presence–absence matrices. Journal of Biogeography 33: 924–935.

Romanuk, T. N. & J. Kolasa, 2001. Simplifying the complexity of temporal diversity dynamics: a differentiation approach. Ecoscience 8: 259–263.

Romanuk, T. N. & J. Kolasa, 2002. Environmental variability alters the relationship between richness and

variability of community abundances in aquatic rock pool microcosms. Ecoscience 9: 55–62.
Romanuk, T. N. & J. Kolasa, 2005. Resource limitation, biodiversity, and competitive effects interact to determine the invasibility of rock pool microcosms. Biological Invasions 7: 711–722.
Rundle, S. D., A. Foggo, V. Choiseul & D. T. Bilton, 2002. Are distribution patterns linked to dispersal mechanism? An investigation using pond invertebrate assemblages. Freshwater Biology 47: 1571–1581.
Shurin, J. B., J. E. Havel, M. A. Leibold & B. Pinel-Alloul, 2000. Local and regional zooplankton species richness: a scale-independent test for saturation. Ecology 81: 3062–3073.
Spencer, M., L. Blaustein, S. S. Schwartz & J. E. Cohen, 1999. Species richness and the proportion of predatory animal species in temporary freshwater pools: relationships with habitat size and permanence. Ecology Letters 2: 157–166.
Srivastava, D. S., J. Kolasa, J. Bengtsson, A. Gonzalez, S. P. Lawler, T. E. Miller, P. Munguia, T. Romanuk, D. C. Schneider & M. K. Trzcinski, 2004. Are natural microcosms useful model systems for ecology?. Trends in Ecology and Evolution 19: 379–384.
Stal, L., 1995. Physiological ecology of cyanobacteria in microbial mats and other communities. The New Phytolologist 131: 1–32.
Starkweather, P. L., 2005. Susceptibility of ephemeral pool *Hexarthra* to predation by the fairy shrimp *Branchinecta mackini*: can predation drive local extinction?. Hydrobiologia 546: 503–508.
Statsoft, Inc., 2001. STATISTICA (data analysis software system), version 6. www.statsoft.com.
Suhling, F., K. Schenk, T. Padeffe & A. Martens, 2004. A field study of larval development in a dragonfly assemblage in African desert ponds (Odonata). Hydrobiologia 528: 75–85.
Tevis, L., 1966. Unsuccessful breeding by desert toads (*Bufo punctatus*) at the limit of their ecological tolerance. Ecology, 47: 766–775.
Ter Braak, C. J. F. & P. Smilauer, 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (Version 4). Microcomputer Power, New York.
Therriault, T. W. & J. Kolasa, 1999. Physical determinants of richness, diversity, evenness and abundance in natural aquatic microcosms. Hydrobiologia 412: 123–130.
Therriault, T. W. & J. Kolasa, 2000. Explicit links among physical stress, habitat heterogeneity and biodiversity. Oikos 89: 387–391.
Therriault, T. W. & J. Kolasa, 2001. Desiccation frequency reduces species diversity and predictability of community structure in coastal rock pools. Israel Journal of Zoology 47: 477–489.
Thorp, J. H. & A. P. Covich, 2001. Ecology and Classification of North American Freshwater Invertebrates, 2nd edn. Academic Press, California.
Wright, J. C., 2001. Cryptobiosis 300 years on from van leuwenhoek: what have we learned about tardigrades?. Zoologischer Anzeiger 240: 563–582.