

Full Length Research Paper

Structure and cyanobacterial species composition of microbial mats in an Arabian Desert stream

Raeid M. M. Abed^{1*}, Michael J. Barry¹, Sumaiya Al Kindi¹ and Stjepko Golubic²

¹Biology Department, College of Science, Sultan Qaboos University, P.O. Box: 36, postal code 123, Al Khoud, Sultanate of Oman.

²Biological Science Center, Boston University, 5 Cummington Street, Boston, MA 02215, USA.

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Microbial mats are often the dominant benthic biotype in desert streams, however information on such mats is very scarce. We investigated the gross morphology of microbial mats and their cyanobacterial species composition in a perennially flowing wadi in Northern Oman, in relation to current flow and other biotic and abiotic variables. Physical and chemical parameters at the six sites were generally similar with low concentrations of soluble phosphorus and nitrogen; however, flow rates varied greatly with the highest velocity being 50 cm/s. The mats varied greatly in their gross morphology with the four sites with the highest current velocities forming low laminated structures attached to cobbles, and the two sites with minimal or no flow forming complex three-dimensional structures or free floating balls 1 to 3 cm in diameter. The concentration of chlorophyll *a* varied between 2.6 (± 0.02) and 1.4 (± 0.11) mg chlorophyll *a* g⁻¹ mat fresh weight, with the highest concentration detected in the free floating balls. Twenty one cyanobacterial morphotypes belonging to 14 genera (5 unicellular and 9 filamentous) were identified with *Calothrix* and *Leptolyngbya* spp. as the most abundant. Cluster analysis of the cyanobacterial species composition showed that mats could have very different morphologies despite similar species compositions suggesting a high degree of plasticity of mat form. We conclude that microbial mats are important elements in Wadi ecosystems and have great variety of structure and community composition.

Key words: Microbial mats, desert stream, cyanobacteria, nutrients, nitrogen fixation.

INTRODUCTION

Microbial mats are dense and often vertically stratified benthic communities (Stal and Caumette, 1994). They contain both autotrophic and heterotrophic bacteria and maintain tight internal cycling of nutrients, justifying their description as complete miniature ecosystems (Paerl and Pinckney, 1996). Although microbial mats are most commonly associated with extreme environments such as hot springs, hypersaline environments and hydrothermal vents (Paerl et al., 2000), they are often found in arid region streams, where they constitute an important component of ecosystem biomass and

functionality (Stanley et al., 1997). In lotic ecosystems, microbial mats commonly contain heterocystous cyanobacteria with the capability of fixing atmospheric nitrogen (Grimm and Petrone, 1997). Although the contribution of nitrogen fixation to the annual nitrogen budget in mesic regions is usually less than 5%, within arid zones that contribution is commonly much higher (Stal and Caumette, 1994).

Wadi is an Arabian term used to describe corridors for fluvial run-off that may contain perennial, intermittent, or ephemeral surface flow. They are important foci for both regional biodiversity and human activities including agriculture and recreation. They are also major exit points for nutrients and sediments entering the coastal environment. Flow is the defining feature of lotic ecosystems affecting both structure and function of

*Corresponding author. E-mail: rabad@mpi-bremen.de. Tel: +968-24141450.

benthic communities (Battin et al., 2003). During periods of low flow, spatial patchiness is common and in coarse cobble beds flow velocity may be an important determinant of periphyton biomass (Biggs et al., 1998). This patchiness can have significant effects on many important stream processes including the processing of organic carbon nutrient levels and grazer distribution (Casamatta and Vis, 2003).

Despite the central importance of wadis to the ecology of the region, very few studies have examined the diversity and spatial distribution of cyanobacterial mats in these ecosystems (Fisher et al., 1998), although they are often the spatially dominant benthic biotypes in desert streams. Indeed, arid region streams in general have been poorly studied in comparison to temperate counterparts, with most information coming from a small number of locations in south-western United States and from dryland regions of Africa (Grimm and Fisher, 1986; Bunn et al., 2006). In a previous study, we compared the bacterial communities, pigment composition and nitrogen fixation rates of six mats before and after flooding in a single desert stream in Northern Oman (Abed et al., 2011). We noted large differences in the bacterial community and nitrogen fixation rates between sites, although individual species were not identified. In this study, we describe cyanobacterial species diversity in microbial mats within the same wadi in relation to mat gross morphology as well as physical, chemical and biological parameters. In particular we asked the question, "what physical and chemical parameters are important in determining the structural morphology and species composition of cyanobacterial mats in a wadi ecosystem?". Further, as different cyanobacterial taxa have distinct growth patterns, we predicted that mat morphology would be determined by species composition. The field site contains a mosaic of microhabitats providing an opportunity to study factors which regulate these important structural and functional attributes of the mats.

MATERIALS AND METHODS

Site description and field sampling

The study site was Wadi Al Khoud, located approximately 60 km north-west of Muscat in the Sultanate of Oman. The source of the wadi water is an aquifer originating in the Northern Al Hajar Mountains. Surface flow is normally visible for approximately 10 km from the village of Fanja (23°28'22.15"N, 58°06'04.46"E) to beyond the village of Al Khoud (23°31' 54.29" N, 58°06' 41.91"E). The wadi is situated in a wide valley, between 100 and 500 m in width. It is subjected to human activity, primarily farming at the Eastern and Western ends and extraction of water for irrigation. The wadi flows perennially but varies seasonally with peak flows in spring and minimal flows in summer. Typical of most arid zone streams, it is a mosaic of habitats with a shallow main channel rarely more than 50 cm deep and 2 m wide, several braided minor channels closely connected to the hyporheic zone and isolated pools that connect with the main channel only during flooding. Average annual rainfall in the region is 86 mm but can vary widely. The recorded air

temperature range is from 10 to 50°C with an average of 28.7°C (Fischer and Membery, 1998).

Six sites with differing flow rates were selected for sampling and numbered sequentially from 1 to 6 with site 1 being the furthest downstream. With the exception of sites 3 and 4 all sites were isolated from each other with no surface flow connection. Sites 3 and 4 were situated in the same surface flow zone but separated by about 30 m. Site 5 was an isolated pool with no surface flow and no connection to the main channel at the time of sampling. The sites were sampled in November 2008 by selecting representative cobbles with attached complete microbial mats (sites 1 to 4), cutting out a segment of a large contiguous semi-floating mat (site 5), or collecting discrete non-attached balls at site 6. Samples were placed in plastic containers in wadi water and immediately returned to the laboratory. Samples for cultivation and quantification of chlorophyll *a* were used immediately. The oxygen concentration at each site was measured using a YSI oxygen meter (YSI Incorporated, Yellow Springs Ohio, USA), pH using a Hanna pH Meter (Hanna Instruments, Smithfield, Rhode Island, USA) and salinity was determined using a refractometer (ATAGO, Bellevue, USA). Triplicate 1.5 L water samples for chemical analysis were also collected from each site in plastic containers and kept on ice until they were returned to the laboratory for storage at -20 °C. Ammonia (NH₃) was determined by Foss Kjeltac 2300 (Foss, Minnesota, USA) whereas sulphate (SO₄²⁻), phosphate (PO₄³⁻), nitrate (NO₃⁻), nitrite (NO₂⁻), and chloride (Cl⁻) were measured using ion chromatography-Dionex IC 2000 (Dionex cooperation, Sunnyvale, California, USA). Flow rate was estimated by measuring the displacement of a small float with neutral buoyancy over time.

The abundance of macro-invertebrates was sampled semi-quantitatively by kicking vigorously for 60 s and collecting the disturbed sediments with a 200 µm long-handled net. Samples were also taken from macrophyte beds where present. Samples were sieved and preserved in 70% ethanol until they could be identified.

Chlorophyll *a* content, microscopy and cultivation

Chlorophyll *a* content from triplicate mat samples (5 to 8 g each fresh weight) was measured using the 95% acetone extraction method (Stal et al., 1984) and used as a proxy of the abundance of oxygenic phototrophs. Chlorophyll *a* content was detected at 662 nm wavelength using a spectrophotometer, after setting the blank with acetone alone. Samples for microscopy were mounted in water on microscopic glass slide and observed using light and phase-contrast Olympus ® .U-TVO.35XC microscope (Olympus, Centre Valley, Pennsylvania, USA). The images were recorded with an Olympus® digital camera. Three samples from each site were observed microscopically to ensure a good overall representation of resident cyanobacteria. The cyanobacterial morphotype identification was done according to standard determination manuals (Geitler, 1932; Komárek and Anagnostidis, 1998; Castenholz, 2001; Komárek and Anagnostidis, 2005). Enrichment cultivation of cyanobacteria was carried out in BG-11 media with and without NaNO₃ (Castenholz, 1981). Small mat pieces were cut and transferred into sterile culture flasks under aseptic conditions. In the case of site 5, the top layer of the floating mat was taken whereas in site 6 a small cross section of the ball was cultivated. To mimic the field condition, the bottles were placed outdoors under direct sunlight. Single filaments were obtained from raw cultures of field samples by using a binocular microscope and then placed in fresh BG-11 medium.

Statistical analysis

Differences in the chlorophyll *a* concentration of mat samples were

Table 1. Physical and chemical parameters of the six sites where the microbial mats used in this study were collected. Common alphabetic superscripts on chlorophyll a data indicate no significant difference using Tukey's test.

Parameters	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
GPS	N23 34.423 E058 07.080	N23 34.262 E058 07.017	N23 33.309 E058 06.263	N23 33.105 E058 06.265	N23 32.377 E058 05.923	N23 32.377 E058 05.921
Flow Rate (cm s ⁻¹)	3.8	25	5.5	50	Zero	< 1
Temperature (°C)	31	29	26.5	24.2	24.3	24.6
Salinity (%)	1	0.5	1	1	1	1
Depth (cm)	10	49	12	12	40	40
pH	7.1	7.2	7.6	7.2	7.5	7.7
Oxygen (mg l ⁻¹)	6.5	8.8	15.5	15.1	14.5	14.5
Chlorophyll a (µg g ⁻¹)	1.92±0.19 ^{ab}	1.65±0.39 ^{ab}	1.33±0.20 ^a	2.3±0.14 ^{ab}	1.82±0.86 ^{ab}	2.58±0.017 ^b
ARR (nmol C ₂ H ₄ cm ⁻² d ⁻¹)*	42.5 ±13	20.2 ±2	12.1 ±2.6	7.3 ±0.2	0	0
PO ₄ ⁴⁻	<0.5	<0.5	<0.5	<0.5	<0.5	NA
NO ₃ ³⁻	2.6	2.9	4.7	5.9	1.2	NA
NO ₂ ²⁻	4.44	4.37	3.56	3.55	3.8	NA
SO ₄ ²⁻	390.92	426.91	366.26	409.11	307.19	NA
Cl ⁻	457.87	506.35	381.69	463.84	369.11	NA
F ⁻	0.62	0.61	0.69	0.67	0.62	NA
NH ₃ ³	<0.5	<0.5	<0.5	<0.5	<0.5	NA
Total nitrogen	27	54	267	226	221	NA

*From Abed et al. (2011), NA: not available

tested using 1-way ANOVA. Data was first log-transformed to reduce heteroscedacity. A value of $P < 0.05$ was regarded as evidence of a significant difference. Tukey's test was used to determine significant differences within a factor level. Differences in cyanobacterial community composition of the mats and the vertebrate and invertebrate communities of the sites were visualised with cluster analysis using the PAST program (Paleontological Statistics, ver. 1.47, <http://folk.uio.no/ohammer/past>). For the analysis of the cyanobacterial community, the 20 identified taxa were assigned relative abundances based on light microscopy: 0 = absent; 1 = rare; 2 = common; 3 = abundant. Communities were clustered using a Bray-Curtis similarity coefficient. A similar approach was used to determine similarities in the macroinvertebrate community.

RESULTS

Characteristics of the studied sites and microbial mats

The six sites varied greatly in flow rates, consistency of substrates covered and in mat morphology, but physicochemical parameters were broadly similar (Table 1). Soluble PO₄ and NH₃ concentrations were low and NO₃ levels were <6 mg/l. Flow rates varied from zero to 50 cm/s. Site 1 (the most downstream) was a shallow basin with a slow flow rate of 3.8 cm s⁻¹. It was unshaded, except for an emergent stand of *Schenoplectus littoralis* at one end, which may explain why the water temperature was slightly higher than at the other sites. Site 2 was similar to site 1, but with a higher flow rate of

25 cm s⁻¹. Sites 3 and 4 were the only two sites directly interconnected by continuous surface flow and with thick riparian vegetation on one side, dominated by the invasive tree *Prosopis juliflora*.

The sediment at sites 1 to 4 was mainly small cobbles but parts of site 1 were sandy. Site 5 was a stagnant pool separated by about 5 m from the flowing channel with sediment of fine silt. Site 6 was very broad with a maximum width of ca. 8 m with very slow moving water and with silt-covered bottom. Water temperatures at the time of sampling were between 25 to 30°C and salinities around 10‰.

The mats from sites 1, 2, 3 and 4 colonized the surfaces of small cobbles (Figure 1A to H). At site 5, the pool margins were lined with a 5 cm thick mat with a dry outer crust and spongy moisture absorbent lower layer (Figure 1 I and J). The top 3 mm of the mat was green with the lower part a cream-yellow in colour. When observed under the microscope, the mat had a fabric-like texture, which probably conducted the water and nutrients by capillarity to the upper layer where cyanobacteria and other phototrophs dominated. At site 6, the microbial mat formed loose spherical to elongated balls, 1 to 3 cm in diameter varying in colour from green to brown (Figure 1K and L).

These ball-shaped mats at site 6 had a smooth leathery surface, showing in cross-section a distinct lamination with layers forming concentric rings of different colours and thicknesses. They were formed around a core of inert loose sediment.

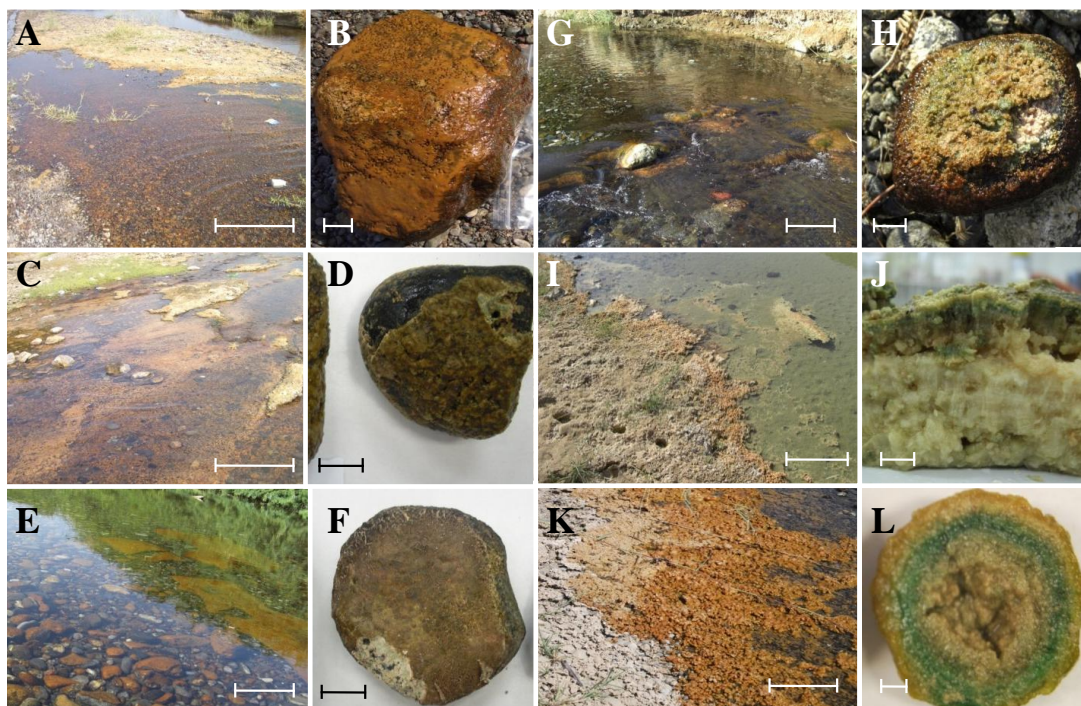


Figure 1. Field views of the six study sites and close-up photographs of the associated mats. A-B. site 1; C-D site 2; E-F site 3; G-H site 4; I-J site 5; K-L site 6. Scale Bars: A, C, E, G, I, K = 10 cm; B, D, F, H = 5 cm; J, L = 2 cm.

Because the balls were relatively light in weight, they rolled in a gentle current, so that all surfaces were exposed to light and colonized by cyanobacteria. Over time, as the organic product accumulated, the active photosynthesis was maintained in the blue-green layer close to the surface, whereas the layers deeper in the interior were exposed to decomposition and respiratory oxygen removal. The layering may have been caused by “vertical” differentiation of microbial communities along the light gradient and oxycline, or may have reflected more than one cycle of mat establishment.

Abundance of phototrophs and diversity of cyanobacteria

Chlorophyll *a*, used as a proxy for the abundance of oxygenic phototrophs in the studied microbial mats, showed a weak overall distinction among sites ($P=0.032$). The highest concentrations were found in the balls at site 6 whereas the lowest were found at site 3 with 2.6 (± 0.02) and 1.4 (± 0.11) mg chlorophyll *a* g^{-1} mat fresh weight, respectively (Table 1). The other sites did not show a great deal of difference in chlorophyll *a* concentration (Table 1).

Mats harboured a variety of cyanobacterial morphotypes (Figure 2). Populations belonging to fourteen

cyanobacterial genera were observed, five coccoidal (*Aphanocapsa*, *Aphanothece*, *Gloeocapsa*, *Gomphosphaeria* and *Chroococcus*) and nine filamentous (*Calothrix*, *Nostochopsis*, *Spirulina*, *Microcoleus*, *Schizothrix*, *Lyngbya*, *Geitlerinema*, *Oscillatoria*, and *Leptolyngbya*) (Figure 2 and Table 2). Filamentous cyanobacteria belonging to the heterocystous genus *Calothrix* and the non-heterocystous *Leptolyngbya* (formerly classified under the genus *Phormidium*) were the most abundant in all sites. The dominant heterocystous cyanobacterium, close to *Calothrix fusca* Bornet et Flahault, was characterized by basal heterocysts and swollen bases of trichomes. The sheaths in specimens exposed to direct sunlight were darkly stained by extracellular protective pigment scytonemin (Figure 2A, B), whereas the shaded filaments had colourless sheaths (Figure 2C). Among the non-heterocystous cyanobacteria are two morphotypes of the genus *Schizothrix*, one with affinity to *S. heufleri* Grunow, with blue sunscreensing pigment, gloeocapsin embedded in the sheath (Figure 2D) and the other morphotype, close to the common freshwater species *S. lacustris* A. Braun (Figure 2F, P). Some mats were comprised of densely interwoven filaments of a *Leptolyngbya* sp. similar to *L. foveolarum* (Rabenhorst) Anagnostidis et Komarek (Figure 2E). Morphotypes belonging to the genus *Spirulina* were found mainly in mats from sites 5 and 6, represented by morphotypes corresponding to *S.*

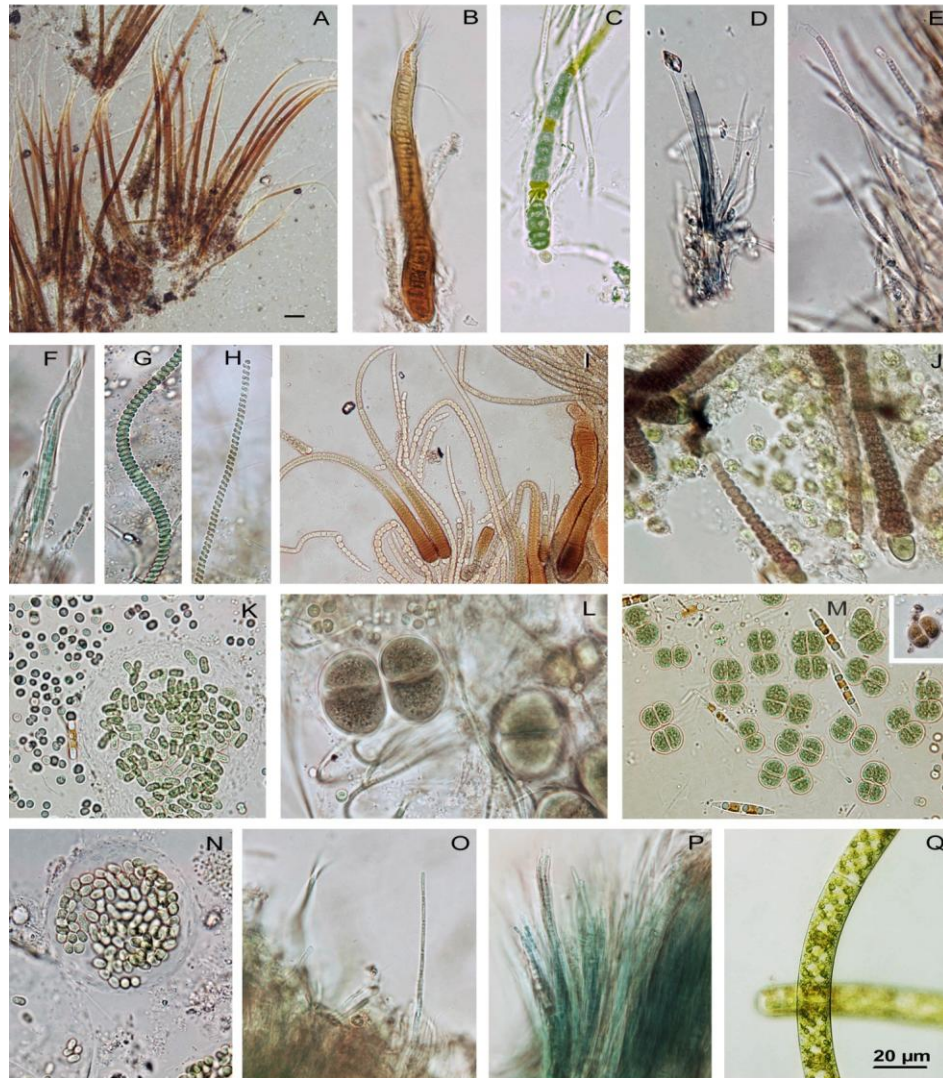


Figure 2. Filametous and coccoid cyanobacteria from the six studied microbial mats (A-H) and in subsequently established enrichment cultures (I-Q). **A.** Small fragment of the mat dominated by *Calothrix* cf. *fusca*. **B.** A single filament of *C. cf. fusca*; note that filaments exposed to sun developed a dark scytonemin-stained sheath. **C.** *Calothrix* filament from the shaded part of the mat formed colorless exopolymer sheath. **D.** *Schizothrix* cf. *heufleri* with blue gloeocapsin pigmented sheaths. **E.** *Leptolyngbya* sp.1. is a major component of the mats. **F.** *Schizothrix* cf. *lacustris*. **G.** *Spirulina* cf. *subsalsa*. **H.** *Spirulina* cf. *labyrinthiformis*. -- Two species of *Calothrix* responded and grew in culture in BG11 medium without nitrate (I, J): **I.** *C. cf. fusca*, accompanied by a *Nostochopsis* sp., an *Anabaena*-like cyanobacterium with true branching and **J.** *Calothrix* sp., a somewhat larger species, characterized by constrictions at the cross walls and phycoerythrin pigmentation of cells. -- Coccoid cyanobacteria responded to enrichment medium containing nitrate (K-Q): **K.** *Aphanocapsa* cf. *muscicola* (left) and *Aphanothece* cf. *nidulans* (right). **L.** Large *Chroococcus* cf. *westii*, containing phycoerythrin intermixed with *Leptolyngbya* sp.1 **M.** *Chroococcus* cf. *membraninus*, a much smaller species surrounded by thin simple exopolymer envelopes, also observed in the pond mats (insert) with diatom *Nitzschia* sp. **N.** *Aphanothece* cf. *elabens* with oval cell shape. **O.** *Leptolyngbya* sp. 2 is a minor component of the mats. **P.** *Schizothrix* cf. *lacustris* (same as in F). **Q.** The green alga *Spirogyra* sp. experienced short term dominance following the periodic floods of the wadi channels. Scale in A. is 20 μ m for A and 5 μ m for B – P.

subsalsa Oerstedt (Figure 2G), *S. labyrinthiformis* Gomont (Figure 2H) and *S. tenerrima* Kützing. The

unicellular cyanobacteria of the genera *Aphanocapsa* and *Aphanothece* were the second most abundant

Table 2. Relative abundance of cyanobacterial morphotypes in Wadi Al Khoud as determined by light and epifluorescence microscopy and in culture

Taxon	Cell width (μm)	Direct microscopy						Cultures					
		S1	S2	S3	S4	S5	S6	S1	S2	S3	S4	S5	S6
<i>Aphanocapsa muscicola</i>	0.5-1.0	-	-	-	+	++	++	+	+	-	-	-	+
<i>Aphanocapsa</i> sp.	1.0-2.0		++	-	+++	++	++	-	+	+	+	-	+
<i>Aphanothece</i> cf. <i>nidulans</i>	0.5-1.0	+	-	-	++	-	-	-	-	-	+	-	+
<i>Aphanothece</i> cf. <i>elabens</i>	1.0-2.0	-	-	-	+++	+++	++	-	-	+	-	-	+
<i>Gleocapsa</i> sp.	0.5-1.5	-	-	-	-	++	++	-	-	-	-	-	+
<i>Gomphosphaeria</i> sp.	1.0-1.5	-	-	-	-	-	-	-	-	-	-	-	+
<i>Calothrix</i> cf. <i>fusca</i>	3.0-6.0	+++	+++	+++	++	++	++	+	+	+	+	+	-
<i>Calothrix</i> sp.	5.0-7.0	-	+	-	-	-	+	+	+	+	+	+	+
<i>Nostochopsis</i> sp.	2.0-2.5	-	-	-	-	-	-	-	-	-	-	-	+
<i>Spirulina subsalsa</i>	2.0-2.5	-	-	-	-	-	+	-	-	-	-	+	-
<i>Spirulina labyrinthiformis</i>	1.0-2.0	-	-	-	-	++	+++	-	-	-	-	+	+
<i>Oscillatoria</i> sp.	5.0-10.0	+	-	+++	-	-	-	+	-	-	-	-	-
<i>Geitlerinema</i> sp.	1.0-2.5	-	-	-	-	+	-	-	-	-	-	-	+
<i>Lyngbya</i> sp.	5.0-10.5	+++	-	-	+	+	-	-	+	-	-	-	-
<i>Microcoleus tenerimus</i>	1.0-2.0	++	+	++	-	-	-	-	-	-	-	-	-
<i>Schizothrix</i> cf. <i>heufleri</i>	0.5-1.0	-	-	-	+	-	-	-	-	-	-	-	+
<i>Schizothrix</i> cf. <i>lacustris</i>	0.5-1.0	-	-	-	-	-	-	+	+	+	+	+	+
<i>Leptolyngbya</i> sp.1	0.7-1.2	+++	+++	+++	+++	+++	+++	-	+	+	-	-	-
<i>Leptolyngbya</i> sp.2	0.5-0.7	+	+	+	+++	-	-	-	-	-	+	-	-
<i>Leptolyngbya</i> sp.3	0.5-1.0	-	-	+++	-	-	-	-	-	-	-	+	+

- absent; + present; ++ common; +++ abundant.

morphotypes in all ponds, except for sites 1 and 3. The populations of unicellular cyanobacteria covered a wide range of sizes, the most common one here assigned as *Aphanocapsa* sp. similar to *Aphanocapsa anodontae* Hansgirg and *Aphanothece nidulans* P. Richter. The results of cluster analysis (Figure 3A) indicate that the communities of sites 1, 2 and 3 were similar while those of sites 4, 5 and 6 formed a distinct grouping despite having very disparate structures. The sponge mat from site 5 and the ball-shaped mats from site 6 shared the greatest similarity, but also shared similarity with the flat mats from site 4. Interestingly, sites 3 and 4 were the only sites directly connected by surface flow but had quite different communities.

The dominant filamentous cyanobacteria grown in the BG11 medium without nitrate were the two morphotypes of *Calothrix*, one corresponding to the taxon that dominated in the field populations of the wadi (Figure 2I), and the other characterized by reddish cell pigmentation due to high phycoerythrin content (Figure 2J). In BG11 medium with nitrate, the unicellular colonial cyanobacteria close to *Aphanocapsa muscicola* (Meneghini) Wille (Figure 2K, left) and *Aphanothece* cf. *nidulans* P. Richter (Figure 2K, right) were abundant in cultures, especially those isolated from site 6. Cyanobacteria belonging to *Aphanocapsa* were also found in site 1, whereas *Aphanothece* types appeared

mainly at sites 3 and 4. A prominent large *Chroococcus* sp. with affinity to *C. westii* (W. West) Boye-Petersen and characterized by high phycoerythrin content was grown in medium BG11 with nitrate (Figure 2L), together with a smaller species close to *C. membraninus* (Meneghini) Nägeli (Figure 2M). The latter taxon has also been encountered in the mats (Figure 2M, insert). Another coccoid representative common in nitrate-containing medium was *Aphanothece* cf. *fonticola* Hansgirg (Figure 2N). *Leptolyngbya* morphotypes were readily cultured from all mats (Figure 2O). Less common in culture was the growth of a *Schizothrix* cf. *lacustris* (Figure 2P). Among the eukaryotic algae, the most commonly observed were various diatoms, many of them responded to the applied growth medium with N, for example, *Nitzschia* sp. (Figure 2M). A periodic growth of the conjugatophyte *Spirogyra* sp. (Figure 2Q) was observed in the wadi following floods.

Vertebrate and Invertebrate diversity

Fourteen taxa were identified, with site 1 having the maximum of ten species (Table 3). The most common herbivores were mayflies of the families *Leptophlebiidae* and *Caenidae*, and the gastropod *Melanoids turburculata*. Two species of native fish (that is, *Garra barreimiae* and

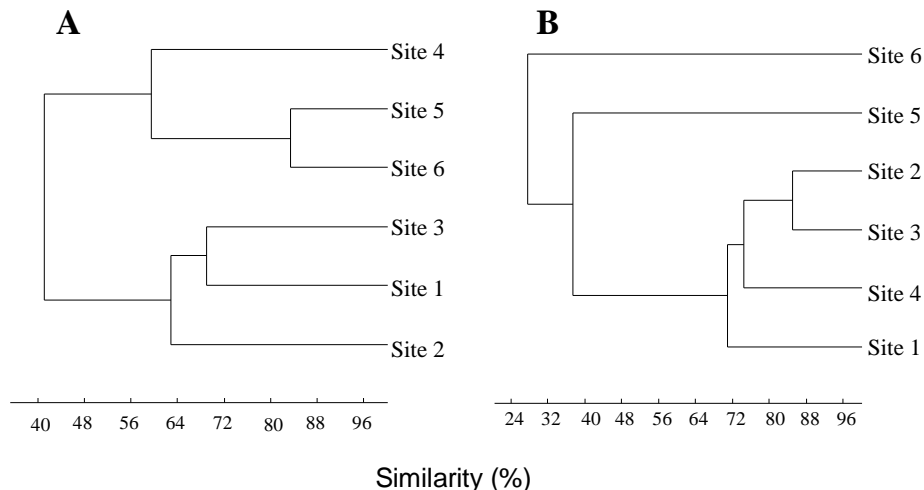


Figure 3. Cluster analysis (A) showing dissimilarities between the cyanobacterial communities of the six mats and multi-dimension scaling (B) showing dissimilarities between the vertebrate and invertebrate communities of the six sites.

Table 3. Vertebrate and invertebrate fauna of the sites in Wadi AlKhoud

Phylum/Class	Order	Taxa/common name	1	2	3	4	5	6	
Annelida/Oligochaeta		Type 1	+	-	-	-	-	-	
		Type 2	+	-	-	-	-	-	
Mollusca/Gastropoda	Neotaenioglossa	<i>Melanoides turburculata</i>	+++	+++	++	+	-	-	
Crustacea	Amphipoda	Eyeless amphipod	++	-	++	++	+	-	
Insecta	Diptera	Tipulidae	-	+	-	+	-	-	
		Ceratopogonidae	-	++	++	+	+++	+	
	Ephemeroptera	Caenidae	+++	++	++	-	-	-	
		Leptophlebiae	+++	+++	++	++	+	-	
	Coleoptera	Dytiscidae	-	++	++	+	-	-	
	Tricoptera	Hydropsychodae	+++	++	++	++	-	-	
	Odonata	Anisoptera	Type 1	+	+	+	-	-	-
			Type 2	-	-	-	-	+	-
		Zygoptera	Type 1	+	+	-	+	-	-
		Pisces	Teleostei	<i>Aphanius dispar dispar</i>	++	++	++	++	+
<i>Garra barreinei</i>	+			+	+	+	+	-	
<i>Tilapia</i> spp.	+			+	+	+	-	+	

Aphanius dispar) were observed in all sites of the wadi. Introduced *Tilapia* sp. was found throughout the wadi but was particularly common at site 6 and absent in the isolated site 5. The slow flow sites 5 and 6 had very low species diversity and separated from the remaining sites (Figure 3B). The other sites had similar communities and clustered more closely together.

DISCUSSION

The six studied microbial mats at Wadi Al Khoud showed

remarkable variations in their macrostructure as well as in their cyanobacterial species composition. Using microscopic methods, morphotypes belonging to 14 genera were detected. The most dominant cyanobacteria in these mats could be isolated in culture. A parallel study on the same mats using automated rRNA intergenic spacer analysis (ARISA) technique reported up to 140 distinctive operational taxonomic units (OTU) in a single mat sample (Abed et al., 2011), suggesting that the mats harbor a diverse bacterial community. The most abundant cyanobacterial species were *Calothrix* and *Leptolyngbya*. The co-dominance of these two species in

the studied mats is interesting, as it is often that mats are dominated by only a single phototrophic species (Stal, 1995). The heterocystous *Calothrix* is often a late succession species in desert streams (Fischer et al. 1982) and is frequently the dominant species in nitrogen-limited marine and hypersaline mats (Stal, 1995). *Calothrix* spp. has a high phosphate storage capacity and may be well suited to environments with low phosphate levels that experience episodic pulses of nutrients (Mateo et al., 2006). This description compares well with the situation in the wadi where nutrient levels are likely to be low most of the time, but increase dramatically during floods. Indeed, *Calothrix* was shown to increase markedly after flooding (Abed et al., 2011).

A key finding was that mat morphology was not closely correlated with species composition, thus the flat laminated mats from site 4, the deep spongy mat from site 5 and the ball-like mats from site 6 all sat closely in the cluster analysis. Furthermore, species composition did not correlate to geographical proximity, since the closely situated sites 3 and 4 had quite distinct cyanobacterial communities (Figure 3A). While this study has only sampled six sites from one wadi some interesting observations can be made. It was clear that flat laminated mats dominated at flowing-water sites and the deeper mats found at the static and very slow flowing sites. Flow velocity has contrasting effects of biomass accrual and as velocity increases the rate of nutrient supply and renewal increase but simultaneously the rate of cell loss through sloughing and shear stress also increases (Stevenson, 1996; Biggs et al., 1998). The mats at the free-flowing sites (1 to 4) were cobbled and this provided an ideal substrate for the low laminated mats to form. The two dimensional structure minimises drag force and maximises surface area exposed to the flowing water allowing efficient uptake of nutrients (Stevenson, 1996). At high currents, biofilms uptake a higher proportion of organic carbon from the water than at low flow speeds (Battin et al., 2003). The substrate at sites 5 and 6 lacked cobbles for mat adherence but site 6 had a low flow that may have provided nutrients and movement while site 5 was completely stagnant. This suggests that subtle differences in physical factors may inter-play to create large differences in structure and composition. The balls at site 6 had the highest concentration of chlorophyll *a*. In typical microbial mats, light is strongly attenuated from the surface inward due to their dense texture (Stal, 1995) however the balls at site 6 were unattached and could roll when exposed to very gentle current thereby exposing all sides to light. Consequently they were colonised by phototrophic cells on all surfaces. Light attenuation in this case was towards the centre of the balls and the inner layers showed clear signs of anoxic conditions.

The studied mats showed significant differences in nitrogen fixation rates as previously measured using acetylene reduction rate (Abed et al., 2011) (Table 1).

These rates were comparable to those measured in other freshwater and hypersaline mats (Grimm and Petrone, 1997). The observed differences in acetylene reduction rates among the sites could be related to the nutrient availability. While sites 1 and 2 had higher rates of nitrogen fixation compared to sites 3 and 4, they had relatively lower total nitrogen concentration. Nutrient concentrations in desert streams have been shown to be patchy both in space and time (Dent and Grimm, 1999). We found very low levels of phosphorus at all sites but moderate concentrations of N-NO₃. There was a negative correlation between N-NO₃ concentration and the acetylene reduction rate among the sites with strong surface flow. However, the stagnant water at site 5 had the lowest nitrate concentration but negligible nitrogen-fixation rates. Unfortunately, chemical data for site 6 which also had negligible nitrogen-fixation rates were not available. It is possible that nitrogen-fixation by *Calothrix* in the mat at site 5 was nutrient-limited. All diazotrophs require an iron-molybdenum protein complex (Bohme, 1998), so depletion of either metal may inhibit nitrogen-fixation. After flooding, the same mats showed a high rate of nitrogen fixation (Abed et al., 2011). Several studies have reported patchiness in the distribution of nitrogen fixation in relation to nutrient availability within a single stream where increased uptake of nitrogen in upper parts of a flow may lead to depletion down-stream and cause a shift toward dominance of N-fixing cyanobacteria (Fischer et al., 1982; Peterson and Grimm, 1992; Mulholland et al., 1995).

It has been argued that cyanobacterial mats are normally restricted to extreme environments, because grazing pressure prevents accumulation of biomass (Stal, 1995). The diversity of macroinvertebrates in Wadi Al Khoud was roughly similar to other lotic systems in the region, which typically range for around 15 to 30 common species (Burt, 2003; Victor, 2004). However, grazing mayflies and gastropods were present as was the herbivorous fish *Garra barreimiae*. Their impact on the biomass and species composition of the mats is currently unknown although the importance of grazing is well documented (Wellnitz and Poff, 2006; Hillebrand, 2008). Interestingly, *Calothrix* spp. the dominant genus in the mats is noted for being resistant to grazing (Power, 2001). However, Wadi Al Khoud shows higher diversity and degree of development of microbial mats compared to many other wadis in the region. We suggest that wadi morphology and hydrology are the main determinants of mat development. Wadi Al Khoud is situated in a wide valley, often over 500 m from side to side. High flows capable of removing the mats develop only after extremely strong rains, which occur at irregular intervals allowing long periods of growth between them. Wadis that have narrower channels are subjected to more frequent disturbance limiting the chance for extensive mat development. At the time of this study, the last major flood event in the wadi was in June 2007 when cyclone

Gonu caused intense rainfall and catastrophic flooding. The studied mats were therefore around 18 months old.

Our study shows that mats varied in structure and species composition and they are an important element in desert streams. However, this study was only a snapshot in time and further work is required to characterise changes in structure and function over time and to determine the major factors driving these ecosystems. The relative simplicity of these systems makes them useful models for testing basic questions on the forces that determine the structure and function of lotic ecosystems.

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