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Haydee Montoya

Natural History Museum, UNMSM, and Biological Sciences, Ricardo Palma University, Lima, Peru

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Algal and Cyanobacterial Saline Biofilms of the
Grande Coastal Lagoon, Lima, Peru

Haydee Montoya[1]

[1]Natural History Museum, UNMSM, and Biological Sciences Faculty, Ricardo Palma University, Av. Arenales 1256, Apartado 14-0434, Lima 14, Perú,
E-mail: haydmon@yahoo.com

ABSTRACT

Tropical coastal wetland ecosystems are widely distributed in arid regions. The Grande coastal lagoon in Peru's central plain is shallow, eutrophic and alkaline, exposed to the annual hydrological regime with flooding and desiccation periods, when a salt crust is formed. The brackish to hypersaline habitats showed salinity gradients from 2-90 ppt (NaCl) to saturation, pH values from 7.0 to 10.5, temperatures from 18 to 31°C, phosphate concentrations from 0.5 to 50 mg l^{-1} and nitrate up to 0.88 mg l^{-1}. Dominance of halophilic biofilms of benthic cyanobacteria followed by diatoms and the submerged macrophytes *Chara hornemannii* and *Ruppia maritima* during the clear water state supported the alternative stable states for this lagoon. A cohesive slimy layer formed mainly of the cyanobacteria *Chroococcus dispersus*, *C. turgidus*, *Aphanothece stagnina*, *Oscillatoria tenuis*, *Lyngbya martensiana*, *L. diguetti*, *Phormidium valderianum* associated with *C. hornemannii*, *Rhizoclonium hieroglyphicum* resting cells, *Aphanizomenon flos-aquae* akinetes, and *Tetraselmis contracta* cysts. Cyanobacterial biofilms flourished on the dried lagoon bed below the dicotyledonous halophytes *Salicornia fruticosa*, *Sesuvium portulacastrum* and *Baccopa monnieri*. The adaptive strategies included a biomass allocation (extracellular matrix formation) and complex reproductive processes for successful colonization.

INTRODUCTION

Extreme environments such as saline and hypersaline lagoons are hostile to most forms of life; however, they harbor significant populations of microorganisms. Their colonization by primary producers (algae and cyanobacteria) demonstrates that such organisms can adapt to extreme ecological niches. Both eukaryotes and prokaryotes have evolved a broad variety of adaptations, including the accumulation of osmolytes, to cope with osmotic and ionic stress (Ben-Amotz & Avron 1983; Javor 1989; Kirst 1995; Oren 2000).

In shallow water ecosystems, the dynamics of the sediments influence water quality, and the nutrient exchange rates across the sediment-water interface are regulated by chemical equilibria. Sediments can be colonized by biofilms: complex biotic systems known as microbial mats, microphytobenthos or periphytic mats. They represent unique systems in which microorganism assemblages coexist at an interface, with a distinct macromolecular matrix typically attached to a surface in which complex food webs occur (Davey & O'Toole 2000; Larson & Passy 2005; De Vicente et al. 2006). Photosynthetic activity by benthic microalgae is the primary source of fixed carbon in shallow aquatic ecosystems. Microalgae are abundant in many soft-sediment aquatic habitats (estuaries, shallow subtidal seas), and they can contribute up to 50% of the total autotrophic production in some ecosystems (Underwood & Kromkamp 1999). Microphytobenthos may represent up to 50% of the microalgae present in the water column after its resuspension during low tide in coastal ecosystems (De Jonge & van Beusekom 1992). The activity of benthic attached algae in wetlands may rival or even surpass primary productivity rates of aquatic macrophytes (Cronk & Mitsch 1994; Poulickova et al. 2008).

Coastal wetland ecosystems are widely distributed in arid regions along the Peruvian coast in western South America. These coastal saline wetlands have rarely been studied, and the few published accounts of the photosynthetic organisms are mainly descriptive. Presence of the cyanobacteria *Aphanothece halophytica*, *Pleurocapsa entophysaloides* and *Microcoleus chthonoplastes* has been reported and some data have been obtained based on enrichment culture studies, yielding isolates such as *Dunaliella viridis*, *D. salina* and *Tetraselmis contracta* (Montoya & Golubic 1991; Montoya & Olivera 1993; Aguilar 1998). The Grande coastal lagoon forms part of the biological corridor of the South American Pacific coast. Because of the important functions of this shallow lagoon ecosystem, we here examined the biofilm community structure and its species composition (algae and cyanobacteria), as well as their spatial and temporal variability related to their succession along the salinity gradient until the lagoon dries out with formation of a saline crust.

MATERIALS AND METHODS

The Grande coastal lagoon is located in the central coastal region of Peru in the department of Lima, Cañete province, in the Chilca district (12°33'14.96"–12° 33'21.70" S, 76°42'42.38"–76°42'50.49" W), approximately 69.5-70 km south of Lima, along the Pan-American highway.

Algae were collected and the physical - chemical parameters (pH, salinity, temperature, phosphate, nitrate) of the lagoon were monitored intermittently between 2001 and 2007. Biofilm collections included the sampling of patches of microphytobenthos from the mud flats. Portions of benthic mats and endolithic submerged growth were removed from the substrate with a scalpel, and microalgal cells, both bound to sediment particles and free in the sediments, were recovered. Biofilms were examined in vivo and the settled algal material was removed. In some cases cells were detached by breaking the mucopolysaccharide layers within the assemblage. Subsamples were fixed and preserved in 5% formaldehyde and in Lugol's solution.

Identification of algae and cyanobacteria was performed using the following manuals: for Cyanophyta/ Cyanobacteria, have been consulted Geitler (1932), Anagnostidis & Komárek (1988), and Komárek & Anagnostidis (1986, 1989); for diatoms, Patrick & Reimer (1975), Round et al. (1996), and Krammer & Lange-Bertalot (1997); for chlorophytes, Lerche (1937), Silva (1982), Poole & Raven (1997), and Round (1984); for the prasinophyte, Butcher (1959) and Hori et al. (1982).

Salinity (NaCl) was measured using an American Optical T/C salinometer. The pH was recorded with indicator paper (5.5-14.0). Phosphate (as orthophosphate ions in mg l^{-1}) was measured using Merck analytical strips, and nitrates were quantified (mg l^{-1}) by the La Motte nitrate test kit (model NCR). Morphospecies were identified and morphometric data, microphotography sequences of the vegetative and reproductive stages were obtained.

RESULTS

The Study Area

The tropical Peruvian desert extends as a narrow coastal band along the western edge of the Andean Cordillera and is interrupted by coastal lagoons and occasional rivers. The Grande coastal lagoon, located at the northern part of the Puerto Viejo wetlands, reaches up to 50 m above sea level. This inland eutrophic brackish - saline shallow lagoon has an area of approximately 60 km^2 and a maximum depth of 3 m. The salinity gradients were between 2-90 ppt (NaCl) up to saturation, the pH range was from 7.0 to 10.5, the water temperature ranged from 18 to 31°C, phosphate concentrations were from 0.5 to 50 mg l^{-1}, and nitrate was up to 0.88 mg l^{-1}.

The southern end of the lagoon is partially surrounded and sheltered by the La Bruja Hills, where the Andes coastal slope intercepts the winds. The wind force pushed the soil dust particles into the water column and together with the

aeolian dust (mineral and salts) contributed to the bioavailable nutrients at the lagoon surface and in the water bed. The lagoon sediment consisted of mudflats composed of particles that include silt, clay, sand, decaying vegetation, and animal and microbial particulates. Soft sediments were present on the surface as saline loam soil structure with mineral and organic colloids. The colloidal organic substance possesses valuable retentive properties to algae attachment, providing the substratum necessary for the formation of their assemblages. In some cases, water disturbance induced by wind action removed the sediment surface and caused resuspension of the benthos. This phenomenon is linked to light attenuation in the unconsolidated sediments; however, regeneration of the unique benthic algal communities was observed.

The Grande coastal lagoon with its athalassohaline waters has been exposed to unstable conditions throughout the last years. It is subjected to an annual fluctuating hydrological regime, with flooding and desiccation periods and formation of a saline crust, during which halophilic cyanobacteria and microalgae thrive. It is periodically flooded by subterranean seepage according to the water table levels (aquifers) of the Chilca river, followed by prolonged intensive evaporation with drastic reduction of the water column and with permanent and periodical formation of pools with hypersaline conditions, mainly in summer and early fall (January through April). The flooding period starts about mid-fall (early May) through 4 to 5 months up to mid-spring (late October through early November). It is followed by a desiccation period with emersion of the sediment with microphytobenthos biofilms, increase of the lacustrine fringe, and a sequence of increasingly saline brines where evaporite minerals precipitate from the brines (superficial and interstitial). Progressive efflorescence of salts (crystallization and precipitation of salts) is displayed on the exposed soft surface sediments with the development of whitish saline crusts. Deposited precipitates are mainly chlorides (halite), carbonates (calcite, aragonite, natron), sulfates (gypsum, mirabilite, anhydrite and magnesium sulfate), and potash. The hydrological input from underground is usually fresh water, causing dissolution of salt on the saline soil. This saline intrusion causes a renewed increase in salinity of the water column, leading to considerable fluctuations in salinity.

The regime shifts in the Grande lagoon due to drastic water level changes are mainly related to seepage inflow and weather conditions. The shallow lagoon provided evidence of alternating stable states with a regime shift from a clear to a turbid state according to the annual hydrological regime. Water level decreased in summer, and a salinity increase (2-90 ppt) was induced with a shift from a clear to

a turbid state. The eutrophic conditions in the lagoon during the warmer season (January through March) promoted the turbid state with phytoplanktonic water blooms of *Aphanizomenon flos-aquae*, *Chroococcus dispersus*, *Merismopedia glauca*, *Rhabdoderma minima*, *Euglena chlorophoenicea*, *Prorocentrum cassubicum* and *Tetraselmis contracta*. The sediment disturbance during the flooding period also increased the concentration of suspended particles (turbid water), attenuating the light available to macrophytes and benthic cyanobacteria and microalgae. Nevertheless, permanent pools of turbid waters within the lagoon harbor submerged macrophytes such as the stone-wort *Chara hornemannii* and the seagrass *Ruppia maritima* which remain present as perennial sciophytes, as well as microphytobenthic biofilm communities. During the clear water state, submerged macrophytes patches were observed, densely colonized by young stands of *C. hornemannii* after the flooding period and early fall (April) right after water blooms collapsed. During the desiccation period, the upper part of the dominant charophyte stands became whitish, and later they showed a seasonal collapse (die-off) in most of the dried sediment lagoon.

Algal and Cyanobacterial Biofilm Colonization

As a consequence of the regime shifts in the Grande lagoon, the submerged macrophytes were able to coexist with algae and cyanobacterial mats within the photic zone up to 5 mm thick benthic biofilms. Their presence was evident during the clear water state with salinity gradients from 2 to 41 ppt, the highest salt concentration that enabled macrophyte growth in this lagoon.

The multispecies biofilm structure composition (algae and cyanobacteria) included 38 salt-tolerant species, distributed in the following taxa: Cyanophyceae (21), Bacillariophyceae (10), Chlorophyceae (5), Prasinophyceae (1) and Dinophyceae (1). The benthic biofilm communities were mainly formed by the cyanophytes *Chroococcus turgidus*, *C. dispersus*, *C. giganteus*, *Aphanothece stagnina*, *Aphanocapsa pulchra*, *Gomphosphaeria aponina*, *Johannesbaptistia pellucida*, *Oscillatoria limnetica*, *O. tenuis*, *Spirulina subsalsa*, *Phormidium valderianum*, *Lyngbya martensiana*, *L. diguetii*, *L. aestuarii*, *Microcoleus chthonoplastes*, *Calothrix crustacea*, *Nodularia spumigena*, *N. harveyana*, *Aphanizomenon flos-aquae*, *Gloeotrichia natans*, *Pleurocapsa entophysaloides*, the diatoms *Campylodiscus americanus*, *Cyclotella meneghiniana*, *Cylindrotheca closterium*, *Synedra ulna*, *Amphora coffeaeformis*, *Pleurosigma strigosum*, *Entomoneis* sp., *Nitzschia* sp., *Navicula* sp., *Mastogloia* sp., the chlorophytes *Dunaliella viridis*, *Oocystis eremosphaeria*, *Enteromorpha intestinalis*, *Oedogonium pringsheimii*, *Rhizoclonium hieroglyphicum*, the prasinophyte *Tetraselmis contracta* and the dinophyte *Prorocentrum cassubicum*.
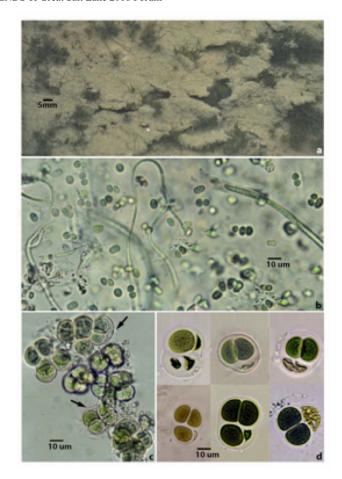

Figure 1–(a), Algae and cyanobacterial benthic cohesive biofilms forming ondulated layers, partially lifted from the bottom of the Grande lagoon and associated with macrophyte young stands of *Chara hornemannii* and *Ruppia maritima*; (b), Biofilm species composition of a mixed community with cyanobacterial cells and colonies of *Chroococcus dispersus* associated with filaments of *Lyngbya diguetii* and *Oscillatoria tenuis* within the mucilaginous matrix; (c), Aggregated capsulated colonies of *C. turgidus* with stratified sheath from a biofilm on the air-exposed sediment surface; (d), Partially reactivated capsulated colonies of *C. turgidus* after a period of drying, with some damaged cells.

A multispecies biofilm with complex and aggregated microphytobenthos communities colonized the loamy mud sediment surfaces. Cohesive laminate or flocculent patterns were also influenced by the adhesive and adsorption properties of the mucilaginous material released mainly by sheathed cyanobacteria: *Lyngbya martensiana*, *L. aestuarii*, *L. diguetii*, *Microcoleus chthonoplastes*, *Aphanothece stagnina*, *Aphanocapsa pulchra*, *Gomphosphaeria aponina*, *Pleurocapsa entophysaloides*, *Nodularia spumigena* and *Chroococcus turgidus*.

The spatial arrangement of the biofilm showed a cohesive slime layer embedding the cyanobacterial communities with variation in thickness and compactness (Figure 1a). Cyanobacterial cells and colonies (microcolony cluster size) typified the less compact biofilms, mainly composed of a mixture of *Chroococcus dispersus*, *Lyngbya diguetii* and *Oscillatoria tenuis* (Figure 1b). Compacted biofilms formed

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mainly as evaporation and gradual desiccation occurred, and they were composed of loosely or tightly packed filaments of the oscillatoriacean *Lyngbya martensiana*, *Johannesbaptistia pellucida*, and the heterocystous cyanobacteria *Nodularia spumigena*, *Calothrix crustacea*, and the green algae *Enteromorpha intestinalis* and *Rhizoclonium hieroglyphicum*.

The microphytobenthos was subjected to variability in flooding and recurrent drought effects in situ as gradually water depletion increased. Its heterogeneity and complexity was related to adaptive strategies of the algae and cyanobacteria such as the alternation of transitional life forms (planktic and benthic). The planktonic species *Chroococcus turgidus*, *C. dispersus*, *Aphanocapsa pulchra*, *Gomphosphaeria aponina*, *Tetraselmis contracta*, *Prorocentrum cassubicum*, *Aphanizomenon flos-aquae*, *Nodularia spumigena* and *Oedogonium pringsheimii* withstand greater seasonal chemical variability. Their assemblages also remained at the air-water interface, where the stress conditions increased gradually with the formation of the dried salt crusts. Most of these species with resting benthic phases can harbor resting stages (akinetes, cysts, aplanospores, oospores, resting cells or colonies). The onset of the dry period favored the formation of resting cells occurring isolated (*A. flos-aquae*, *Oocystis eremosphaeria*, *D. viridis*, *P. cassubicum*), isolated or in pairs (*T. contracta*) or in chains (*N. spumigena*, *N. harveyana*).

The biofilm succession displayed flocculent or homogeneous layers in the early stages. These occurred as a gelatinous coating on the sediment surface, dominated by cyanobacteria. In the intermediary stages, parts of the biofilm were lifted from the bottom (by wind or water turbulence or seepage inflow), forming occasional floating algal mats on the water surface of the lagoon. Benthic or floating mucilaginous biofilms including detritus, mineral and salt particles became progressively stratified. Submerged cryptoendolithic biofilms formed mainly by *O. tenuis* and *Pleurocapsa entophysaloides* were also recognized as the salinity gradient increased up to saturation levels in brines pools. In the final stages, original benthic biofilms became dry, dispersed and exposed with the formation of a saline soil crust. The dry bed lagoon allowed benthic biofilm to be exposed to air. Exposed subaerial microphytobenthic communities with spatial and temporal species distribution in the mats displayed response in extracellular pigmentation: *Lyngbya aestuarii* as well as *P. entophysaloides* displayed thick cell walls and brown sheaths pigmented by scytonemin.

The spatial arrangement within the dried biofilms showed complex stratification patterns of sheaths. Cells of *Chroococcus dispersus* developed individual sheaths which became confluent, forming macroscopic mucilaginous

biofilms. *Chroococcus turgidus* sheaths tended to be copious or diffuse at low salinities (2-10 ppt), resulting in less-defining colonies that favored the formation of a cohesive biofilm. However, colonies with firm or hard sheaths embedding groups of cells developed during the gradual desiccation period. Soil particles and detritus were trapped within capsulated colonies of *C. turgidus* with their mucopolysaccharide structures (Figure 1c). Initial sediment moisture (rewetting), due to groundwater infiltration at the onset of the flooding period, removed evaporite salts and reactivated the dried biofilms, changing the stratified sheaths into diffluent mucilage in *C. turgidus*, *C. dispersus* and *C. giganteus* as well as in the filamentous cyanobacteria. The external surface of the organic mucilage dissolved into the external medium and eventually contributed to the pool of dissolved organic material excreted by the cells. Partial photooxidative damage of exposed *C. turgidus* colonies was recognized during desiccation, with the formation of pale dead cells; however, some cells could be reactivated to resume growth (Figure 1d).

The landscape of the exposed surface sediments in the Grande lagoon with the efflorescent salts alternated with mats of halophilic higher plants. Patches of halophytes such as *Salicornia fruticosa*, *Sesuvium portulacastrum* and *Baccopa monnieri* alternated with areas of deposition of crusts of evaporite mineral overlying brines and dried thalli of *Chara hornemannii*. Benthic cyanobacterial mats dominated on the exposed surface sediments in ephemeral pools and in the desiccated littoral lagoon. Sometimes sciophyte subaerial complex communities (*Chroococcus turgidus*, *C. dispersus*, *Oscillatoria tenuis*, *Lyngbya diguetii*) developed under the halophyte plants and below the dried fragile *Chara hornemannii* thalli in the bed of the dried saline lagoon.

Along the spatiotemporal changes in the species composition of the microphytobenthos biofilm, the dominance of cyanobacteria (55%) was recognized as primary producers followed by diatoms (26%) in the developing hypersaline benthic communities as well as in the desert environments. Besides, colonization of the filamentous chlorophytes *Rhizoclonium hieroglyphicum* with resting cells with thick sheaths and *Enteromorpha intestinalis* were frequently observed in the saline crusts. They were found to be tolerant to desiccation, can could later be reactivated to successfully colonize the fluctuating and dynamic ecosystem.

DISCUSSION

Cyanobacteria, a phylogenetically coherent group of oxygenic photoautotrophic prokaryotes, grow in a wide variety of habitats, including extreme saline environments. They are the dominant constituents of wetland microphytobenthic biofilm communities in many aquatic saline ecosystems, including the soft sediments of the Grande ephemeral lagoon. Hypersaline environments in this shallow and sheltered lagoon showed temporal and spatial differences in salinity up to desiccation due to large fluctuations of temperature related to high rates of evaporation and low precipitation in the coastal desert. Most euryhaline algae and cyanobacteria found in the lagoon have been reported for other saline environments as well. The cyanobacterial species found to dominate in the present study such as *Chroococcus turgidus*, *Gomphosphaeria aponina*, *Aphanothece stagnina*, *Spirulina subsalsa*, *Pleurocapsa entophysaloides*, *Nodularia spumigena*, *Microcoleus chthonoplastes*, *Oscillatoria limnetica*, *O. tenuis*, *Phormidium hypolimneticum*, *Lyngbya aestuarii*, and *Aphanothece* spp. also occur in other saline and hypersaline ecosystems (Campbell & Golubic 1985; Erlich & Dor 1985; Javor 1989; Montoya & Golubic 1991; Garcia-Pichel et al. 2001). Hypersaline waters are usually dominated by unicellular cyanobacteria or chlorophytes (Brock 1976; Borowitzka 1981; Mackay et al. 1984; Garcia-Pichel et al. 1998). The Grande coastal lagoon was mainly typified by coccoid colonies and filamentous cyanobacteria, unicellular diatoms and unicellular or filamentous chlorophytes.

In the Grande coastal lagoon, mats of soft, flocculent, well-defined irregular colonies of *Aphanothece stagnina* on the sediment surface formed cohesive mats containing bright green unicellular cyanobacteria within copious amounts of clear mucilage. These findings are in agreement with the report of this species from the hypersaline Gavish Sabkha, Sinai (Erlich & Dor 1985). *Aphanothece* formed mucilaginous coatings in the benthos of the Yallahs saline ponds, Jamaica, and Solar Lake, Sinai Peninsula, Egypt (Cohen et al. 1977; Krumbein et al. 1977; Golubic 1980; Jørgensen & Revsbech 1983). The unicellular cyanobacteria *Synechocystis* and *Synechococcus* could be ecophenes (ecomorphs) of the colonial *Aphanothece*. They were also recognized in the top slime layer of dome-shaped laminated mats (Reed 1986; Javor 1989).

The colonial coccoid cyanobacteria species *Gomphosphaeria aponina* was also reported from the saline Hot Lake, Washington and from the hypersaline habitats (90-180 ppt) of the Gavish Sabkha where it was associated with colonies of *Chroococcus turgidus* that formed a loose mat at a salinity range between 50 and 70 ppt (Bauld 1981;

Erlich & Dor 1985; Gerdes et al. 1985). Benthic mats with crusty colonies adhering firmly to hard substrate were formed by irregular nodular communities of *Pleurocapsa enthophysaloides* at the Grande lagoon where it was also present as epiphytic thalli on *Lyngbya aestuarii*.

The benthic filamentous oscillatorian cyanobacterium *Microcoleus chthonoplastes* has a cosmopolitan distribution and its populations (field and cultures) are phenotypically and phylogenetically extremely coherent (Garcia-Pichel et al. 1996). It is a dominant constituent of microbial mats in hypersaline habitats such as the Solar Lake, Exportadora de Sal (Baja California Sur, Mexico), the Yallahs salt ponds, and shallow marine intertidal environments (Golubic 1980; Jørgensen & Revsbech 1983; Campbell & Golubic 1985; Garcia-Pichel et al. 1996; Montoya et al. 1999). *M. chthonoplastes* of the island of Mellum (southern North Sea), Germany, has accreted and fixed the sediment (Stal 2000). Cyanobacterial mats in Australia (Spencer Gulf and Shark Bay) are dominated by *M. chthonoplastes* (Bauld 1984; Javor 1989) and so is the Gavish Sabkha with a salinity range of 50-180 ppt (Erlich & Dor 1985). Coastal mature mats of *M. chthonoplastes* in the Solar Lake were intermingled with *Spirulina subsalsa* and *Aphanothece* sp. (Krumbein et al. 1977; Golubic 1980; Campbell & Golubic 1985), and it formed stratiform mats in the northern part of the saline Lake Coorong, South Australia, where it was associated with crenulate mats of *Calothrix crustacea* (Bauld 1981). *M. chthonoplastes* was associated with *Lyngbya aestuarii* forming extensive and compact layers in African saline ponds in Tunisia and Algeria as well as in the Mexican saline Laguna Mormona, where it occurred together with tufted and laminated mats of *L. aestuarii* which was also reported for the Gavish Sabkha (Hof & Fremy 1933; Bauld 1981; Erlich & Dor 1985). The hypersaline ponds of Yallahs with fluctuating salinities were colonized by *M. chthonoplastes*, *S. subsalsa*, *L. aestuarii*, and *Johannesbaptistia pellucida*. The last species has also been reported for the Gavish Sabkha (Golubic 1980; Erlich & Dor 1985). Also in the Grande coastal lagoon, *M. chthonoplastes* was mainly associated with *L. aestuarii*, *A. stagnina*, *S. subsalsa*, *C. crustacea*, and *J. pellucida*. The species have thus expanded their distribution range in extreme environments.

Although the benthic mats are composed primarily of cyanobacteria, eukaryotic algae such as diatoms are important constituents of the surface layer of complex laminated assemblages (Jørgensen & Revsbech 1983; Clavero et al. 2000). Benthic epipelic diatoms were not dominant in the microbial mats of the Grande coastal lagoon, but they were present in soft-sediment habitats at salinity values up to 90 ppt. However, diatoms have been reported from hypersaline ecosystems such as the Gavish

Sabkha and solar salterns with salinity values as high as 205-213 ppt (Davis 1978; Ehrlich & Dor 1985; Javor 1989). *Amphora coffeaeformis*, a common diatom, was reported from the South Arm of Great Salt Lake, from the Gavish Sabkha, and from Little Manitou Lake (Felix & Rushforth 1979; Erlich & Dor 1985; Hammer et al. 1983). *A. coffeaeformis* associated with *Navicula* sp. and *Nitzschia* sp. formed flat mats in the Solar Lake (Krumbein et al. 1977).

Unicellular chlorophytes such as the halophilic flagellate *Dunaliella viridis* and *D. salina* are widely distributed in hypersaline aquatic ecosystems. The benthic palmelloid stage formed mixed algal photosynthetic mats in the northern arm of Great Salt Lake (Post 1977) as well as the ones registered for the Huacho Salines, Lima (Barberena & Montoya 1990). The euryhaline prasinophyte *Tetraselmis contracta* colonized a few ponds of the Grande coastal lagoon during the initial flooding period. This species is common among the phytoplankton of British coastal and brackish waters ranging in salinity between 5 and 40 ppt (Butcher 1959).

Benthic biofilm colonization and species patch dynamics provided a laminated or flocculent colloidal texture and contributed to the sediment stabilization in the Grande coastal lagoon. The structural integrity of sediment assemblages is maintained by the cyanobacterial extracellular matrix that contains the extracellular polymeric substance (EPS). A highly hydrated EPS layer may provide protection against desiccation in some cyanobacterial species (Whitton 1987; De Philippis et al. 1998; Otero & Vincenzini 2004). The production of EPS in the aquatic environment is ecologically significant because it is related to the biogenic sediment stabilization (Cibic et al. 2007). The EPS also plays a functional role in motility within the biofilm. Motility is an important behavioral process for photoacclimation, allowing cyanobacterial cells to migrate into the photic zone of the sediment near the surface after periods of sediment mixing or deposition. *Oscillatoria tenuis*, *O. limnetica* and *Lyngbya diguetii* filaments are motile, and they were seen to migrate through the biofilm mucilage of *Chroococcus dispersus*.

Stressed microalgal communities of saline lagoons, solar salterns and harsh habitats within desert crusts display a morphological diversity of cyanobacteria with different community structures (Jørgensen & Revsbech 1983; Garcia-Pichel et al. 2001; Oren 2002). In the desert saline crust of the studied coastal lagoon, the capsulated morphotypes of *Chroococcus turgidus*, *C. dispersus*, *C. giganteus*, *Gomphosphaeria aponina*, filaments of *O. tenuis*, *Lyngbya diguetii*, *L. aestuarii* and *L. martensiana* were recognized in addition to *T. contracta*, *R. hieroglyphicum* and *E. intestinalis*. The thick mucilaginous capsule that encases *C. turgidus* cells under hypersaline conditions might be a protective adaptation that permits the organism to flourish under conditions where most other species cannot survive saline desiccation, such as was established for the brown tidal alga *Aureoumbra lagunensis* from a hypersaline coastal lagoon where hypersalinity enhanced EPS production (Liu & Buskey 2000). *C. turgidus* has a remarkable morphological plasticity under natural growth, particularly influenced by salinity and desiccation. According to Whitton (1992), sheath production depends on environmental and culture conditions. Sheath formation by *C. turgidus* could be triggered by the presence of bacteria, as has also been recognized for field populations of *M. chthonoplastes* (Garcia-Pichel et al. 1998).

Phenotypic plasticity traits have also been observed in some cyanobacterial strains that grow slowly at high salinities. The tendency to form compact mucilage that slows down cell dispersal results in the formation of large colonies (Dor & Hornoff 1985; Garcia-Pichel et al. 1998). Significant size differences with smaller cells at higher salinities, as well as changes in shape were reported for *Cyanothece* or *Aphanothece* strain from a solar evaporation pond in Eilat, Israel (Yopp et al. 1978). These findings support the idea that morphological divergence is not always reflected in genetic diversity (Palinska et al. 1996). In other cyanobacteria, however, morphological and phylogenetic traits were congruent (Casamatta et al. 2005).

The dynamic benthic biofilm ecosystem has been considered a depositional environment that entraps particles and precipitates, in which the extracellular matrix controls preservation and viability of the species. The growth and reproductive phases of phytoplankton (cyanobacteria and microalgae) during the turbid state of the lagoon showed the heterogeneity and complexity of their adaptive strategies. *Tetraselmis contracta*, *Prorocentrum cassubicum*, *Aphanizomenon flos-aquae*, *Nodularia spumigena*, *Oedogonium pringsheimii* and other species have evolved an alternation of generations, between vegetative planktic and resting benthic phases. This combination offers them a strategy for successful colonization. The resting stages are tolerant to extreme conditions such as desiccation. They can survive buried in the sediment for many years, although the level of tolerance may vary with the species and the amount of sediment disturbance. The resting stages in the microphytobenthos can serve as refuge populations (seed bank) for recolonization following harsh times of unfavorable conditions, as was reported for other algal groups (Fryxell 1983; Gao & Ye 2007). Therefore, the shallow sediments of the Grande coastal lagoon are important for the recruitment of species from sediments, to serve as inoculum enabling development of future blooms.

ACKNOWLEDGEMENTS

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