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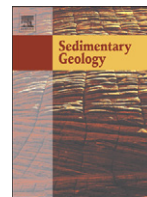
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Biostabilization of sediments by microbial mats in a temperate siliciclastic tidal flat, Bahía Blanca estuary (Argentina)

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ABSTRACT

Extensive microbial mats have been found in the siliciclastic tidal flats of the temperate Bahía Blanca estuary in the Atlantic coast of Buenos Aires province, Argentina. Several microbially induced sedimentary structures (MISS) occur especially in the upper intertidal and lower supratidal flats, among which the most conspicuous are erosional pockets, gas domes, microbial mat chips, and polygonal oscillation cracks. Biostabilization processes by epibenthic and endobenthic mats are also analyzed. Endobenthic mats occur in the upper intertidal area stabilizing ripples that despite the occurrence of severe storms persist in a fixed position for at least 2 months. Epibenthic mats occurring in the lower supratidal area also protect the substrate forming a thick microbial cover through the studied period. This thick cover was only affected by a strong storm that formed areas with erosional pockets and mat pieces. Nevertheless, the loose sediment within the erosional pockets was quickly colonized by microorganisms that developed a thin biofilm layer after a week. Changes in sediment accumulation were also recorded all over the upper tidal flat during a year, showing an important increase due to bioturbation activities of crabs. This situation also affected microbial mat growth, which evolved from a thin microbial biofilm into a thick, stratified microbial mat community in almost 2 years, mainly in the lower supratidal areas. The results of this study not only help us to better characterize the complex interactions between the microorganisms forming microbial mats, the tidal-flat sediment and the physical parameters that control this setting, but also have important implications for the understanding of analogous fossil sedimentary successions.

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1. Introduction

Geobiology is a fast evolving discipline that attempts to decipher and understand the interactions between the biosphere and the geosphere at all scales in space and time (Nealson and Ghiorse, 2001). One of the most productive areas of geobiology is represented by actualistic studies of the interactions between microorganisms and the sediment in modern shallow-marine settings. These environments are commonly colonized by epibenthic bacteria, cyanobacteria and diatoms that form biofilms or microbial mats (Noffke et al., 2002 and references therein). The influence of these bacteria on sedimentation has been mainly studied in carbonate environments, where these microbial organisms produce strong, stromatolitic build-ups (Reid et al., 2000). On the contrary, microbial signatures associated to siliciclastic settings have been much less studied (Noffke, 2007). Microbial mats occurring in siliciclastic environments produce distinctive and particular sedimentary structures, named microbially induced sedimentary structures (MISS) that happen both in modern and fossil settings (Hagadorn and

Bottjer, 1997; Schieber, 1998; Noffke et al., 2002). Particularly, the benthic microbiotas react to sediment erosion by biostabilizing the substrate, and to sediment deposition by baffling and trapping of mineral particles (Noffke, 2010).

During the last years, some studies comprising both field and laboratory analysis have already considered the biostabilization processes in sandy and silty sediments due to the presence of biofilms (e.g. de Boer, 1981; Grant, 1988; Noffke, 1998; Noffke and Krumbein, 1999; Friend et al., 2008). In this sense, the significance of the biostabilization processes is not only important to understand the biotic-physical relationships that occur in modern tidal flats, but it is also critical for the reconstruction of their fossil counterparts. The main objectives of this contribution are to characterize the occurrence of MISS and the biostabilization processes observed in the siliciclastic tidal flat of the temperate Bahía Blanca estuary. Additionally, the relationship between sediment accumulation, vegetation and bioturbation are examined in detail.

2. Study area

Puerto Rosales (38° 55.5' S; 62° 03' W) is located on the northern coast of the central zone of the mesotidal Bahía Blanca estuary in Buenos

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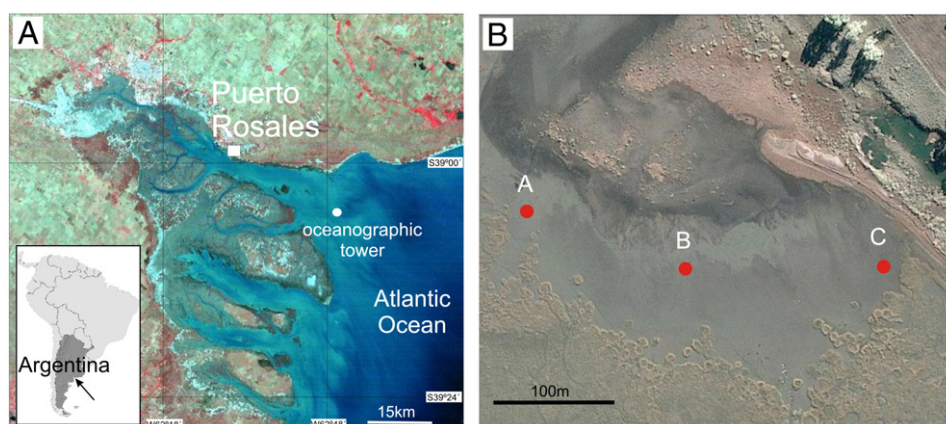


Fig. 1. (A) Satellite image showing location of the study area. (B) Studied stations along the upper intertidal and lower supratidal flats. The lower margin of the intertidal area is determined by the *Spartina* vegetated zones.

Aires province, Argentina (Fig. 1). Semi-diurnal tides predominate and therefore, large areas are covered by water only during short periods at high tide, being exposed for several days at neap tides. The average tidal amplitude ranges between 2.5 and 3.4 m during neap and spring tides, respectively. A dry temperate climate characterizes Puerto Rosales, with low precipitation and high evaporation rates. The annual mean temperature is 15.6 °C, while temperatures average 22.7 °C in Austral

summer (January) and 8.1 °C in Austral winter (July). Mean precipitation in this area is 460.5 mm, with maximum precipitations during Austral autumn (March) (Piccolo and Diez, 2004).

In Puerto Rosales, large tidal flats, 1000 m wide and with a very gentle slope, are composed of fine sediments that range in size from fine sand to mud. The substrate of the tidal flats often experiences large fluctuations in water content, salinity and temperature, resulting in

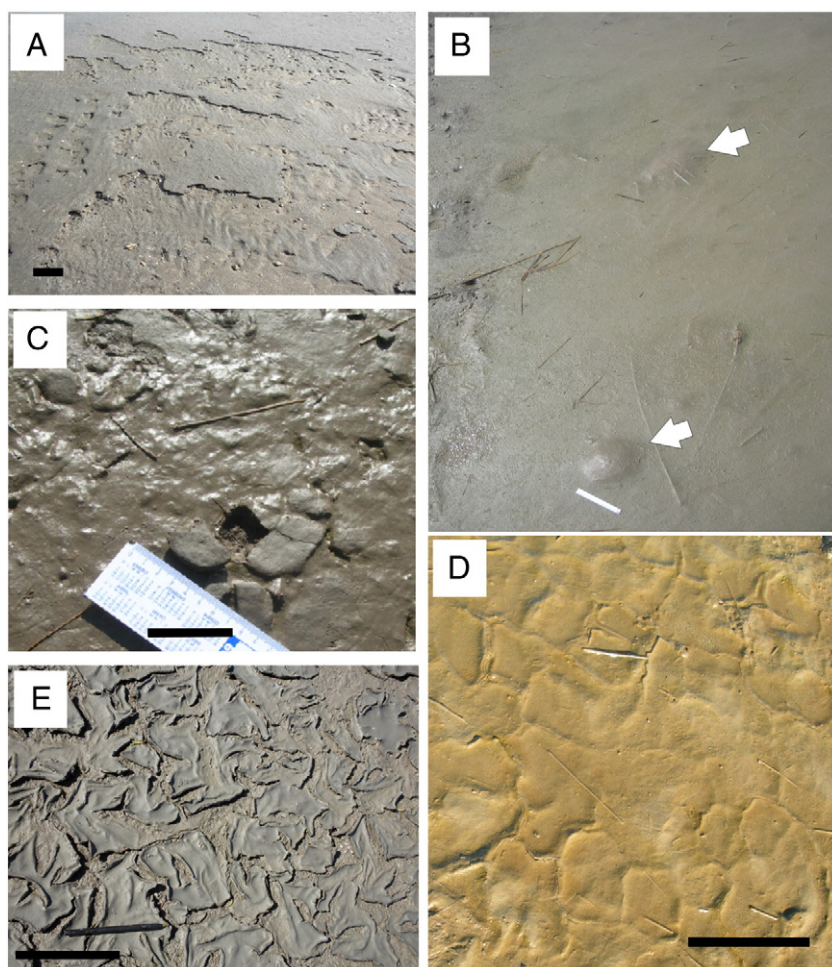


Fig. 2. Typical microbially induced sedimentary structures found on the tidal flat. (A) Erosional pockets in the lower supratidal flat. Scale bar is 30 cm. (B) Gas domes (arrows) in the upper intertidal flat. Scale bar is 10 cm. (C) Mat chips produced by erosion of the microbial mats by waves and currents in the upper intertidal and lower supratidal zones. Scale bar is 5 cm. (D) Polygonal mat cracks in the upper intertidal zone. Scale bar is 15 cm. (E) Mat cracks with upturned and locally curled margins in the upper supratidal zone. Scale bar is 15 cm.

extreme conditions that limit the range of organisms able to inhabit this environment. The upper intertidal area is flooded by seawater 30 to 50 cm depth during spring tides. Surface current velocity reaches up to 50 cm s^{-1} and waves reaches 5 cm height with periods of 2 to 7 s. Average significant wave height at Puerto Rosales locality is 0.30 m, doubling this value at the mouth of the estuary in the Oceanographic Tower (Fig. 1A), where it reaches 0.60 m (Nedeco-Arconsult, 1983).

Surface sediments (0–2 cm) of the tidal flats show a bimodal grain distribution, peaking at 0.350 mm (medium to fine sand) and at 0.020 mm (fine silt), indicating mixed sediments. The sand fraction is absent between 2 and 4 cm depth, whereas silt (0.040 mm) and clay (0.004 mm) dominate at this depth (Cuadrado and Pizani, 2007). Siliciclastic grains are predominantly composed of subangular to rounded quartz grains, associated with mica, clay, feldspar, heavy minerals, and organic matter. The biological assemblages mostly consist of pennate diatoms such as *Navicula phyllepta*, *Nitzschia palea* and *Surirella minuta*, among the most common species, and

cyanobacteria, such as *Microcoleus chthonoplastes*, *Oscillatoria* sp. and *Arthrospira* sp. (Pizani, 2009). Salt-grasses, primarily *Spartina* and *Sarcocornia*, are patchily distributed along the intertidal areas. *Sarcocornia* occurs above the highest tide-level whereas *Spartina alterniflora* grows in the lower and middle intertidal areas. The boundary of the grass-dominated zones forms an abrupt limit on the tidal flats (see Fig. 1B).

3. Materials and methods

Sediment composition as well as the development of MISS in the tidal flats was investigated through microscopic analysis and serial photographs during the studied interval. Undisturbed mats and sediment samples were collected in plastic Petri-dishes to observe the composition and structure under a Nikon SMZ 1500 optical microscope. Additionally, subsurficial sediment samples were retrieved with 10 cm long and 3 cm diameter cores.

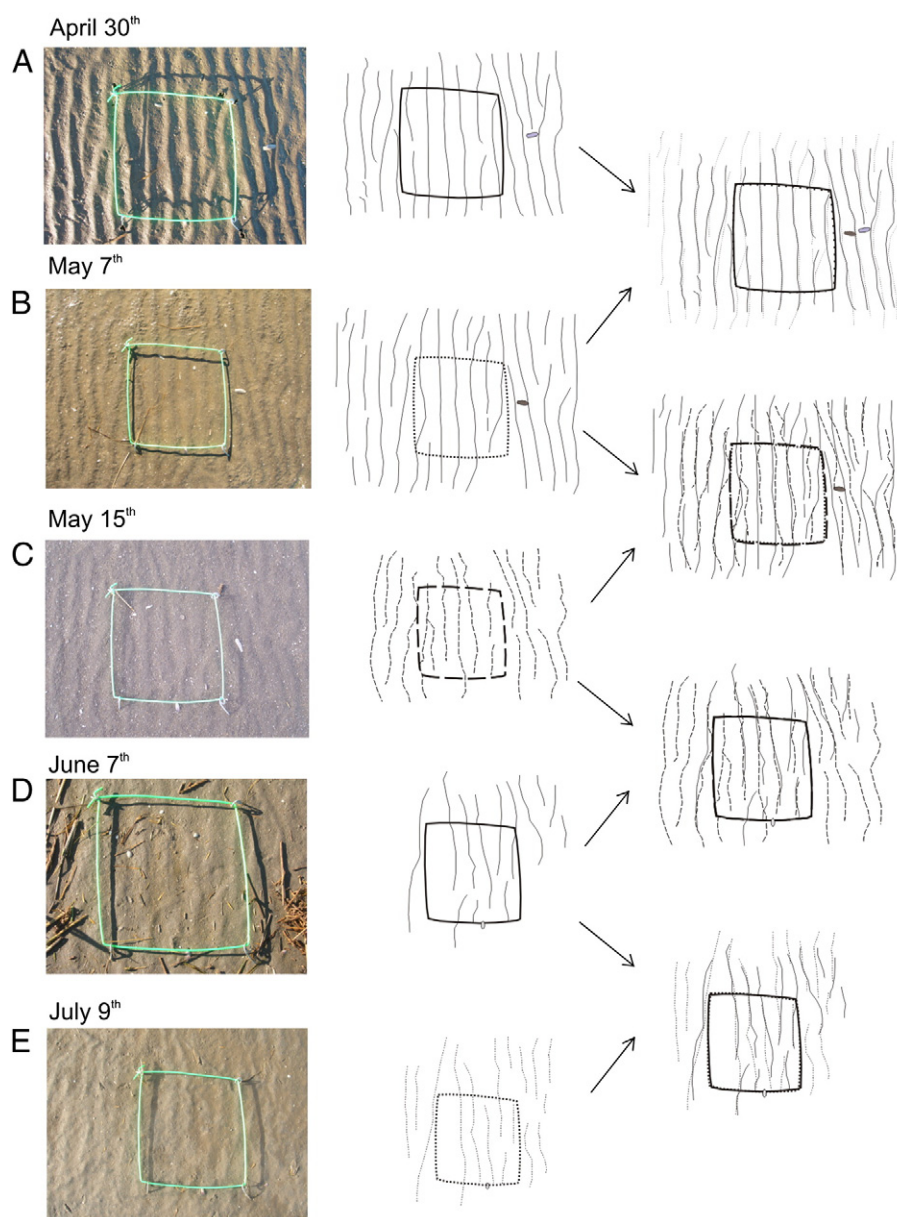


Fig. 3. Left column: Serial photographs of the same rippled-surface area in the upper intertidal flat (20 cm steel square as reference). Middle column: Sketch drawings of the photographs in the left, showing the position of the ripple crests. Right column: comparison between subsequent drawings to elucidate any ripple migration during the studied period.

In order to document the biostabilization processes related to the presence of the microbial mats, field observations focusing on ripple migration in the upper intertidal flat were conducted for more than 2 months (from April 30th to July 9th), similarly to Friend et al. (2008). During this period, photographs monitored modifications in ripple morphology and migration.

Sedimentation rates over the tidal flat were estimated using the method proposed by Pasternack and Brush (1998). A detachable 20 × 20 cm ceramic tile was flushed with the tidal surface. The bottom tile involved gluing a 10-cm-long acrylic tube of 2.5 cm inner diameter which was sunk into the substrate. This analysis was performed over a year, from June 2006 to May 2007 in three stations located on the tidal flat (Fig. 1B), and the accumulated sediment was recovered monthly. The accumulated sediments were scraped into pre-washed and pre-weighed glass jars, obtaining the accumulation rate in g cm^{-2} per month.

4. Results and discussion

4.1. Characterization of microbial mats and occurrence of MISS

The analyzed sediments are overgrown by microorganisms that form a thin, brownish to greenish film, 0.1 to 1 cm thick on the sediment surfaces. Sometimes, this film developed into a microbial mat that can be peeled off from the sediment in large coherent pieces (more than 5 cm long). The adhesive microbial extracellular polymeric substances (EPS) affect the erosion stability of the surface (de Winder et al., 1999).

Despite the extensive development of tidal flats in Puerto Rosales, microbial mats are present mainly in the upper vegetation free intertidal zone, and in the lower supratidal flat. MISS (Fig. 2) include erosional pockets, gas domes, microbial mat chips, and polygonal oscillation cracks. Erosional pockets formed when pieces of biofilm are removed by erosion. These structures have an irregular-shaped mat border surrounding a shallow depression that exposes the underlying sediment, which frequently displayed a rippled surface (Fig. 2A; Noffke, 1999; Gerdes et al., 2000). Similarly, human footprints can also produce these erosional pockets in modern environments, being commonly preserved during several months (Cuadrado and Pizani, 2007). Gas domes also occur in the studied tidal flat (Fig. 2B). These structures are formed due to gas accumulation below the mat that produces the mechanical deformation of biostabilized sediments (Noffke et al., 2001). Occasionally, gas pressure leads the doming of the mat that under extreme tension it may break or can be desiccated by subaerial exposure. The gasses can have different origins, being commonly derived from organic matter decay, from the activity of photosynthetic microbes, and/or from the gasses present within the intergranular spaces during sedimentation that are trapped below the impermeable mat layer (Bose and Chafetz, 2009). Mat chips form by the erosion of the surfaces stabilized by the microbial mats (Fig. 2C) that break into little, flat pieces under the action of high energy waves or currents (Pflüger and Gresse, 1996; Gerdes et al., 2000; Bose and Chafetz, 2009). Mat chips have a relatively wide size ranges, most commonly between 1 and 5 cm. Commonly, microbial mats in the supratidal zone are fractured as a result of desiccation and shrinkage. These processes are evidenced by polygonal-organized cracks (Fig. 2D), and in the upper areas of the supratidal zone, they present curled upward margins (Fig. 2E) in a similar way as in the cracks described by Noffke et al. (2003) and Gerdes (2007).

4.2. Biostabilization processes

A specific area over the upper intertidal-lower supertidal flat with straight crest ripples was chosen to analyze the biostabilization processes of endobenthic microbial mats and its evolution during the

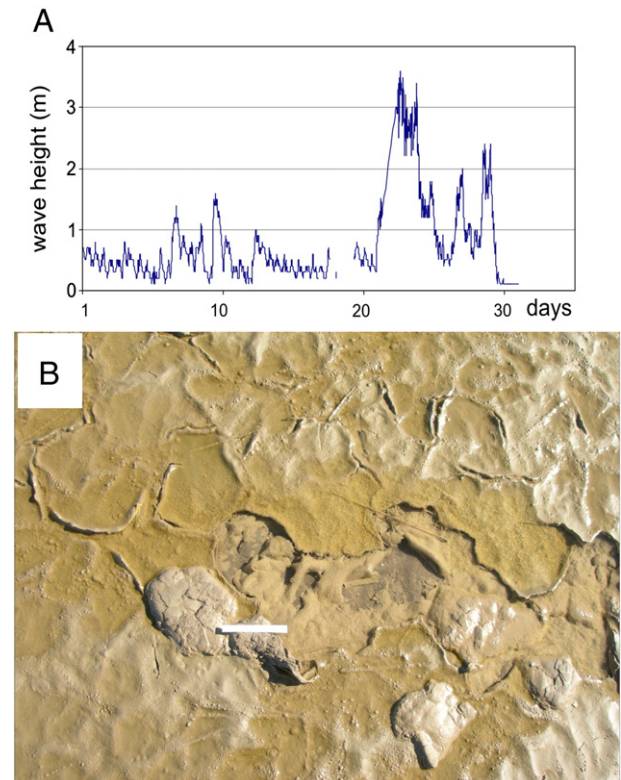


Fig. 4. (A) Wave height during July, 2009. Note the remarkable increase in wave heights at the end of July that affected the tidal flat. (B) Quick recolonization (after a week) and development of a thin biofilm over the loose sediments within the erosional pockets (August, 8th).

experimental period (Fig. 3). This type of mats develops within the sediment and not on top of the sandy substrate (Noffke, 2010). Mean ripple height and spacing were 0.65 cm and 41.3 mm ($n=10$), respectively. An initial smoothing of the ripple height was observed, although the crests and troughs remained distinctive. The comparison of a series of subsequent photographs shows a negligible displacement of the ripples through time (Fig. 3). Smoothing of the ripples could be implying the initiation of microbial “leveling” of the ripples. This process takes place during periods of low sedimentation rates and low erosion (Noffke et al., 2003). The biostabilization processes could also be evaluated during a severe storm that affected the tidal flat at the beginning of June, with wave heights of 2.2 m and period of 8.8 s measured by a wave-gage installed at the Oceanographic Tower (see Fig. 1). This substantial increment in energy does not seem to have affected on the studied ripples as documented in Fig. 3C–D.

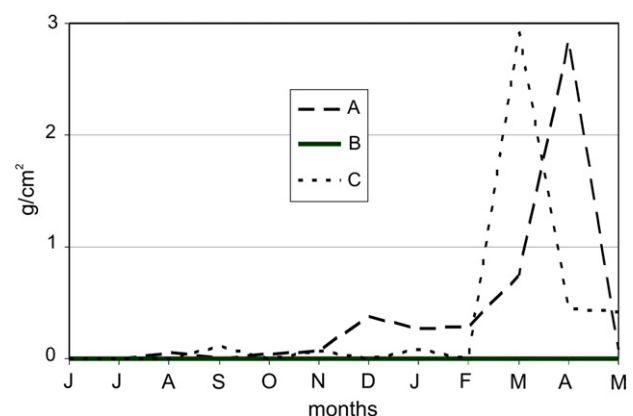


Fig. 5. Sediment accumulation on the tidal flat from June 2006 to May 2007. Location of the studied stations is shown in Fig. 1B. See text for explanation.

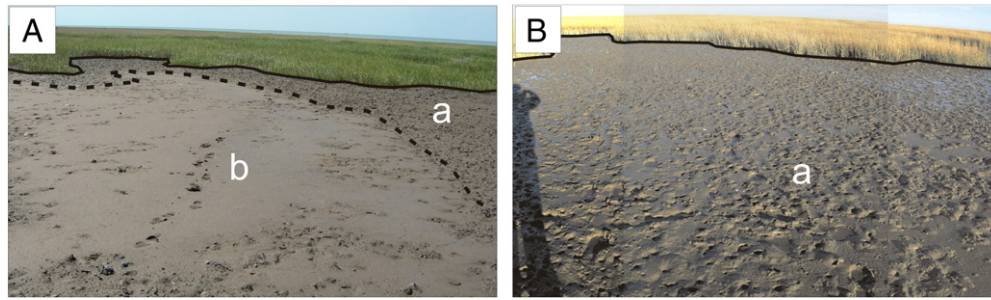


Fig. 6. Photographs of the intertidal flat showing expansion of the area affected by crab bioturbation. (A) December 2006. During this period two different areas were clearly identified, a lower area close to the vegetated zones, completely bioturbated by crab burrows (a); an upper area with less or no biogenic activity (b). (B) June 2007. The whole area was colonized by crabs, with the subsequent reworking of the substrate. Solid line delimits the vegetation zone.

Moreover, these results indicate that the position and morphology of the ripple crests and troughs remained almost identical for at least 2 months. It is worthy to mention that some studies have already shown that the erosion threshold of sediments with this type of biostabilization (defined as Type II by Noffke) can be 3 to 5 times higher than sediments without endobenthic microbial mats (Noffke, 2010).

Biostabilization by epibenthic microbial mats (mature mats developed on top of the sediment; Noffke, 2010) was observed in the same area of the tidal flat. This area is covered by thick microbial mats that display extensive polygonal oscillation cracks (Fig. 2D). Direct observations of this zone revealed that during April 2009, the supratidal zone had a flat appearance due to the leveling of the thick, epibenthic microbial mat. Numerous erosional pockets with torn and flipped-over pieces of mats developed after a severe storm that occurred at the end of July, with a twofold increased in wave height during 5 to 10 days (Fig. 4A). However, the substrate remained protected below a thick microbial coat in the areas surrounding these erosional features. Furthermore, a rapid development of a thin biofilm layer on the loose sandy grains within the erosional pockets could be observed a couple of days after the storm (Fig. 4B). This quick colonization by the microbial mat forming microorganisms initiate the biostabilization processes of the sediment within the erosional pockets.

4.3. Changes in sedimentation rates

The three stations showed variable sedimentation rates throughout the studied period (Fig. 5). In station B no sediment accumulation was recorded along the year, whereas in the other two sites (stations A and C) there was a substantial variation in sediment deposition during the same period (Fig. 5). During the first 6 months (winter and spring), there was almost no sedimentation, although there was a peak in sedimentation at the beginning of summer (December) in station A. Both stations A and C show the maximum accumulation at the end of the summer and beginning of autumn. These two stations are located near vegetated patches (see Fig. 1B) and are areas preferred by the infaunal crab *Chasmagnatus granulata* for growth and recruitment (Bortolus and Iribarne, 1999). Therefore, the peaks revealed in Fig. 5 are reflecting periods with greater crabs' activity and thus, higher bioturbation of the substrate. Moreover, during the last years the middle and lower intertidal flats of Puerto Rosales have become increasingly vegetated by patches of *S. alterniflora*, as shown when comparing present satellite images with older aerial photographs. Although the limit of the vegetation in the upper zone remained stable, the density of the vegetation in the lower most zones increased significantly. Additionally, the area reworked by the infaunal crabs also expanded over the flat (Fig. 6), producing a major reworking of the substrate. This fact results in a markedly increment in the quantity of fine sediment available to be transported all over the tidal flats.

The previously mentioned change in sediment availability has also been detected in alterations of the morphology and thickness of the microbial mat. When we started the investigations in Puerto Rosales

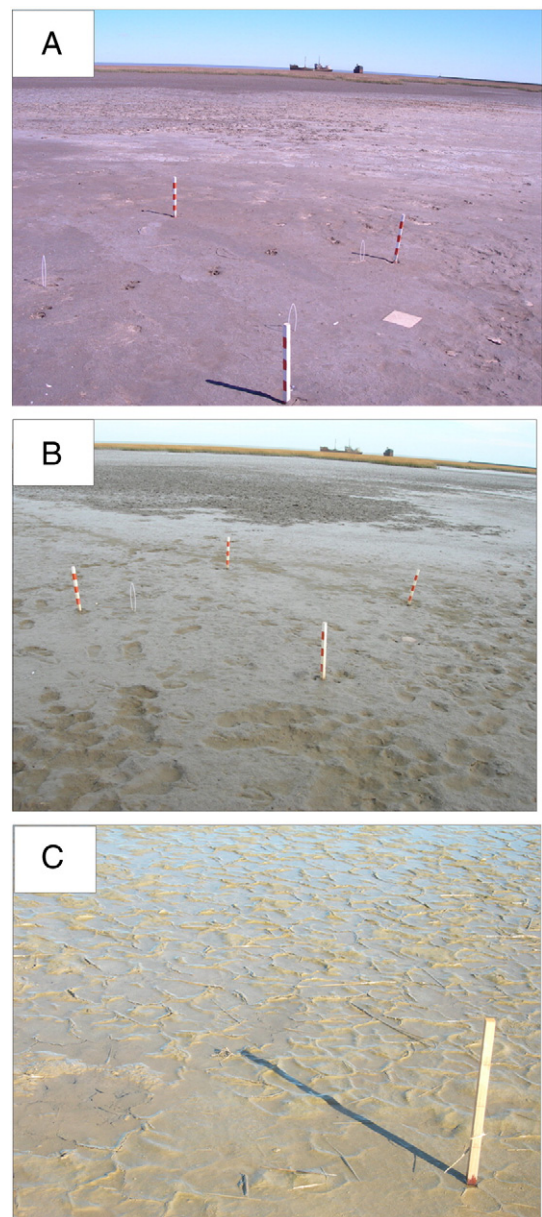


Fig. 7. Photographs showing changes in the microbial mats occurring in lower supratidal flat through the studied period. (A) September, 2007. See the clean tile indicating almost no sediment accumulation in this zone of the tidal flat. (B) June, 2008. (C) May, 2009.

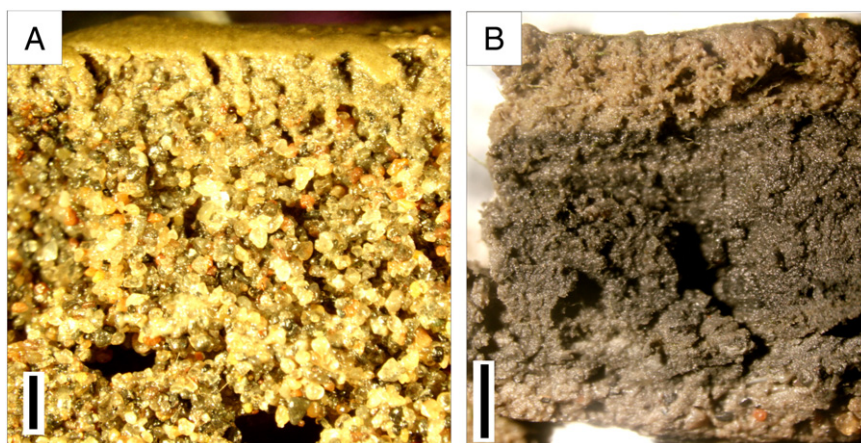


Fig. 8. Cross-section of the lower supratidal flat sediments. (A) 2007. The adhesive mucilage produced by the microorganisms forms a thin, upper biofilm. Below this layer, grains are glued together by EPS. In the lowermost part of the section, the hollow cavities produce a spongy sandy layer. (B) 2009. Two different layers can be identified in this thick microbial mat. The upper layer is light brown to yellowish in color, indicating the presence of diatoms and cyanobacteria. The underlying layer is black due to sulfate reducing bacteria. Scale bars are 1 mm.

(September 2007), most of the lower supratidal flat was mainly composed of non-cohesive sediments, except for a thin biofilm that glued the top sandy sediments (Fig. 7A). This period was characterized by no- or low-sedimentation rates, as it can be deduced from the clean tile (Fig. 7A). This situation changed after 9 months, when sedimentation rates increased as it is evidenced by the sediment covering the edges of the same tile (Fig. 7B), and a thick epibenthic microbial mat started to develop. In May 2009, polygonal cracks developed on the thick microbial mats (Fig. 7C), remaining this way until the present.

The MISS macroscopic changes documented in the tidal flat from 2007 to 2009 were also recorded microscopically in the retrieved microbial mat samples. As already mentioned, on 2007 (see Fig. 7) colonization of photosynthetic microorganisms and biofilm development were favored by the clean, translucent and fine-grained quartz sand that dominated the tidal flats. Microscopic analysis of cross sections of the upper centimeter of the substrate revealed that from base to top, medium to fine sand graded into fine sand (Fig. 8A). In the lowest part of these sections, it was common the presence of hollow cavities of about 0.8 mm length on average (Fig. 8A), defined as secondary pores by Noffke et al. (1997), producing a sponge sandy level. Towards the top layers, the sections showed an upper level enriched with microbially produced EPS. These EPS occurred as a matrix between the sedimentary grains. The layer with EPS could be identified 1 mm below the surface (Fig. 8A), whilst below this level, its presence was inferred by some grains that remained adhered. This appearance changed in the most recent samples (Fig. 8B), where two different layers can be clearly identified: an uppermost yellowish layer, with dominance of diatoms, and to a lesser extent cyanobacteria, and probably a high concentration of carotenoids (see Pierson et al., 1987); and a black layer, approximately 1 mm below the surface, indicative of the activity of sulfate reducing bacteria (Fig. 8B). The recorded changes in the studied microbial mat reflect how the initial, simple biofilm layer, evolved into a more complex, stratified community after 2 years, revealing the dynamics of these microbial communities.

5. Conclusions

Several MISS occur in the temperate, siliciclastic tidal flats of Puerto Rosales, in the South American Bahía Blanca estuary. This area is affected by moderate tidal and wave energy and is protected by vegetated patches of seagrasses. This environment, with episodic and low sedimentation rates, is optimal for the development of microbial mats constructed by benthic cyanobacteria and diatoms.

Experimental work demonstrated the biostabilization processes in ripples occurring in the upper intertidal zone, showing that these sedimentary structures remained fixed in position for at least 2 months, despite the occurrence of a severe storm during the studied period.

Biostabilization processes have been also observed in the lower supratidal area with the gradual development of thick microbial mats that protected the substrate. Increase energy during storms generated erosional pockets and flipped over mat pieces, although the rest of the substrate remained protected under the thick microbial layer. After a week, a thin biofilm developed on the loose sandy grains in the erosional pocket.

Sedimentation rates substantially increase during summer and autumn due to a concomitant increase in crab bioturbation within the studied tidal flat. The resulting amount of sediment is transported all over the tidal flats producing major changes in microbial mat growth, which evolved from a thin microbial biofilm into a thick, stratified microbial mat community in almost 2 years, especially in the lower supratidal areas.

The results of these investigations shed new light on the complex biologic and sedimentologic interactions that occur in this temperate tidal flat with development of microbial mats, and also serve to infer paleoecological conditions in analogous paleoenvironments. Future investigations will focus on a continuous monitoring of the changes in sedimentation rates all over the tidal flat in order to elucidate the relationship between sediment availability and energy with the formation and development of microbial mats and MISS.

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