

Laminated cyanobacterial mats in sediments of solar salt works: some sedimentological implications

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ABSTRACT

Formation of microlaminated sediments in solar salt works along the Mediterranean coast in southern France only occurs within a restricted salinity range of 60–150 g l⁻¹. These salinities are associated with development of a laminated cyanobacterial mat composed primarily of the filamentous cyanobacteria *Microcoleus chthonoplastes* interbedded with detrital laminae. Transplants of the cyanobacterial mat to a less saline zone (36–60 g l⁻¹) indicated that the cyanobacterial mats failed to colonize the less saline waters due to herbivorous snails and competition for light from floating algal masses of *Cladophora* and *Enteromorpha*. Neither the snails nor the *Cladophora* and *Enteromorpha* masses are tolerant of salinities above 60 g l⁻¹, and therefore the *Microcoleus* mats are restricted to those areas of the solar salt works with these higher salinities.

Analyses of salinity, conductivity, dissolved oxygen and pH in shallow salt pans (with salinities of 60–150 g l⁻¹) established a relationship between the daily development of oxygen supersaturation and cyanobacterial photosynthesis.

Sediments are unlaminated in those portions of the solar salt works where there are no cyanobacterial mats. These mats are frequently drained of their overlying water, and thus desiccation cracks divide them into polygonal plates. The development and translocation of these plates is enhanced by gas bubbles which form under the surface of the mats. No correlation between the microlaminae in sections from two cores located approximately 1 m apart was observed. This was consistent with the hypothesis that the surface of the desiccation crack polygons can be removed by currents and redeposited on the top of other cyanobacterial mat polygons. This process results in a 'patchwork quilt' of young and old cyanobacterial mat polygons with an irregular microlamination pattern. The presence of such an irregular pattern of laminae permits an important distinction to be made between sediments associated with stromatolite formation and those associated with the very fine and horizontal varved sediments of stratified (meromictic) water bodies. The sedimentological significance of these observations is reviewed in relation to the processes of stromatolite genesis.

INTRODUCTION

The Salin-de-Giraud solar salt works are situated near the mouth of the Rhone River in the southernmost part of the Camargue in southern France (Fig. 1). Each year from April to September, 80–85 million m³ of seawater enters the 10 km wide by 18 km long salt works complex (Cie des Salins du Midi, personal communication). The seawater is pumped south and eastward from the sea at the mouth of the salt works (Golfe de Beauduc). Intense evaporation takes place

over the length of a myriad of artificial ponds referred to as salt pans. Sluice gates control the flow of water through these pans. In general, when the salinity of the water in any particular pan reaches the required value, the water flows by gravity or is pumped as the case requires, into the next, more saline, pan (Fig. 1). This movement conducts the water from the sea, where salinities are around 36 g l⁻¹, to locations where salinities of more than 350 g l⁻¹ can be found.

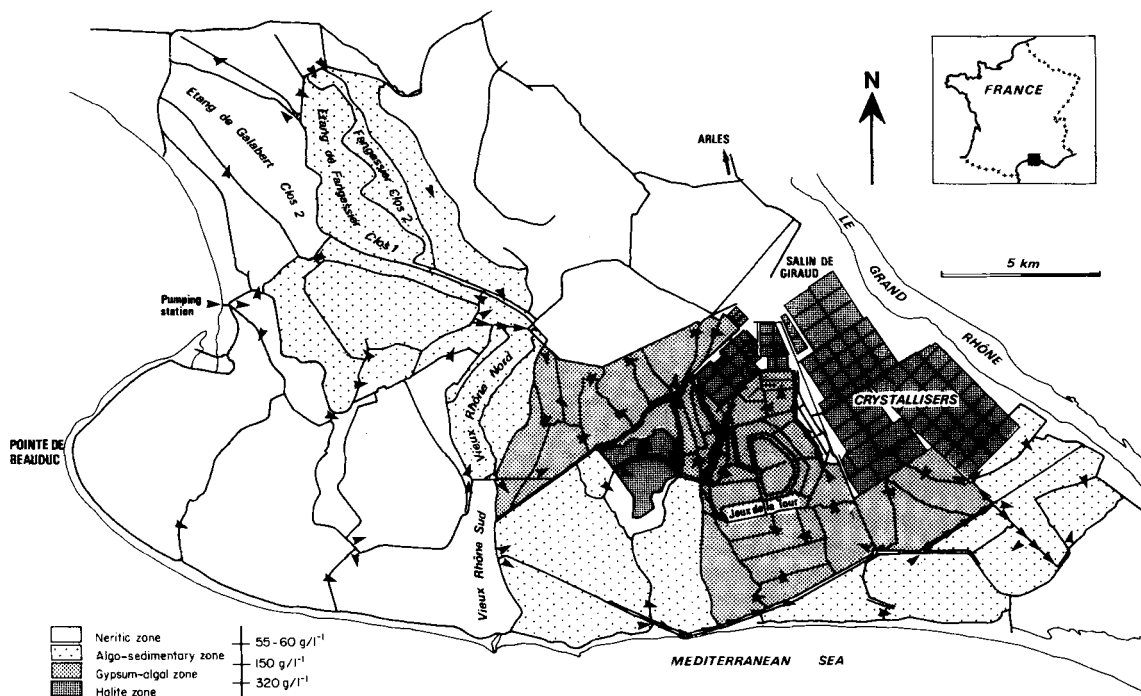


Fig. 1. Location of the Salin-de-Giraud solar salt works (Perthuisot, 1982) and spatial variation of water density. The progress of the brines in different pans is shown by arrowheads.

Four main zones have been recognized on the basis of ecosedimentology (Busson, 1982; Table 1). The naming of salinity zones is relatively subjective (Lowe, 1972; Ehrlich, 1975) and it is unfortunate that factors such as the frequency of water renewal rates in confined areas are difficult to take into account as these may be more critical than the absolute salinity levels (Perthuisot & Guelorget, 1983). The changes in salinity along the above mentioned salinity gradient have an appreciable impact on the spatial distribution of both the fauna and flora of the salt works (Perthuisot, 1982; Fig. 2).

Zone 1, referred to as the neritic or holoeuryhaline zone, has no generalized microbial mat. This zone displays the highest biotic diversity of any of the four

Table 1. The four principal zones recognized in the Salin-de-Giraud salt works.

Zone	Salinity (g l ⁻¹)
1. Holoeuryhaline/neritic zone	32-60
2. Polyhaline/algal-sedimentary zone	60-150
3. Hypersaline/gypsum-algal zone	150-320
4. Extremely hypersaline/halite zone	> 320

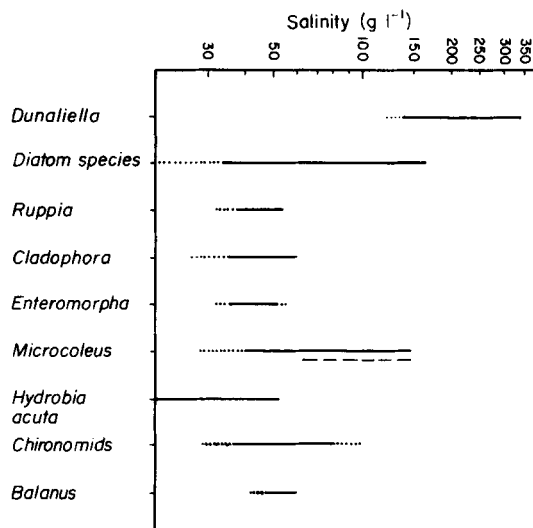


Fig. 2. Salinity tolerance ranges of six common plants and three common invertebrates in the Salin-de-Giraud solar salt works (modified from Perthuisot, 1982). The solid lines represent the tolerance ranges of these taxa (dotted where they may be present under special circumstances), and the dashed line represents our observed salinity range of *Microcoleus chthonoplastes*.

zones with its variety of bivalves, gastropods, crustaceans, foraminifera, ostracods, etc. The green algae *Cladophora* sp. and *Enteromorpha intestinalis* and the phanerogam *Ruppia maritima* are the dominant macrophytes in this zone (Perthuisot, 1982).

The algal-sedimentary or polyhaline zone (Zone 2) is characterized by a cyanobacterial mat dominated by *Microcoleus chthonoplastes*; foraminifera (60–100 g l⁻¹), ostracods, bivalves, crustacea (*Artemia*) and diatoms have all been noted in this zone (Noël, 1982; Zaninetti, 1982).

Zone 3, the gypsum-algal or hypersaline zone, is composed of deposits of gypsum intimately associated with populations of cyanobacteria and phototrophic bacteria (Cornée, 1982; Thomas & Geisler, 1982).

The extremely hypersaline, halite zone (Zone 4) is associated with the precipitation and mechanical harvesting of salt. The supersaturated brines formed in Zone 4 are favourable for the development of only a few species (mainly *Dunaliella* and *Halobacterium*; Cornée, 1982; Thomas & Geisler, 1982).

This study focuses on the laminated cyanobacterial mats in Zone 2. The carbonate-rich microlaminated sediments are frequently referred to in the geological literature as stromatolites. It is 84 years since E. Kalkowsky coined and defined the term 'stromatolith' and today the term 'stromatolite' is employed to refer to a diverse group of organosedimentary structures. Krumbein (1983) proposed a new definition for stromatolites and gave many examples of these structures. He also defined the term 'potential stromatolites' to describe modern laminated microbial structures. A frequently used modern model for stromatolite formation is that based on the sabkhas of the Persian Gulf (Kendall & Skipwith, 1968), but there are other modern environments where cyanobacterial mats are well developed and can be regarded as analogues of ancient stromatolites, especially in numerous hypersaline lagoons and lakes (Walter, 1976; Bauld, 1981a,b, 1984; Cohen *et al.*, 1984; Friedman & Krumbein, 1985; Gerdes & Krumbein, 1987). Another model may be represented by large tide-free solar salt works where cyanobacterial mats are generally quite extensive (Schneider & Herrmann, 1980; Busson *et al.*, 1982; Orti Cabo *et al.*, 1984; Giani *et al.*, 1989; Reineck *et al.*, 1990).

In the present paper, numerous environmental factors such as the specific conductivity, salinity, pH, temperature and dissolved oxygen of the water are explored in relation to the alternating organic and inorganic layers of cyanobacterial microlaminated mats at Salin-de-Giraud. In addition, direct experi-

mental evidence is used to suggest why these cyanobacterial mats are not found at salinities of 30–60 g l⁻¹ (Zone 1 of the solar salt works). Salinity is not the critical factor because these cyanobacteria can grow at salinities below 30 g l⁻¹ (Lepailleur, 1971; Gerdes *et al.*, 1985b). An explanation is given of the characteristic irregularity of the pattern of microstratification between different locations in the microbial mat as a whole, since this permits the microlaminated sediments formed in solar salt works to be distinguished from those associated with meromictic lakes.

The depth of the reducing layer in each of five subzones within Zone 2 was examined, and compared with the dissolved oxygen and pH assessments of microbial mat productivity.

METHODOLOGY

A Hydrolab Series 4000 Environmental Data Systems (Austin, Texas) and a standard Atago N1 salinometer and densimeter were used to measure changes in density, salinity, temperature, specific conductivity, dissolved oxygen and pH at hourly intervals from 9 a.m. to 1 p.m. and thereafter at 4 h intervals until 8 p.m. This protocol was carried out for each of four subzones within Zone 2 in an attempt to determine why the cyanobacterial mat was restricted to Zone 2. These analyses were made in only one pan of Zone 2, considered as typical.

Four sections of the *Microcoleus* 'mat' were removed from Zone 2 and transplanted to a site in Zone 1 that was free of competing algae. For comparative purposes, four pieces of a free floating *Cladophora* and *Enteromorpha* mass in Zone 1 were cut and the number of invertebrates on each was determined. After 24 h, the number of invertebrates on two of four transplanted *Microcoleus* mats was counted in each of four randomly selected 10 cm × 10 cm areas and the means recorded. The number of gastropods (*Hydrobia acuta* = *Peringia acuta*) on the two remaining *Microcoleus*-dominated cyanobacterial mats was estimated without removing the mats. A similar procedure was followed for the floating mass of *Cladophora* and *Enteromorpha* except that the number of invertebrates on each of the four pieces was counted directly. In addition, the mats were photographed for later reference.

To test the hypothesis that the cyanobacterial (*Microcoleus*) mat might be light limited in Zone 1, various thicknesses of a floating *Cladophora*–*Enteromorpha* mass were examined for relative transparency.

This was assessed by placing the algal mass in a Petri dish held up to the sun, with a light meter on the other side (base) to record the intensity of the sunlight passing through the algal mass. A Pentax SF1 light meter was used at F 3.5 and ASA 100 to determine the intensity of light penetrating various thicknesses of the Zone 1 floating mass in order to determine whether it was capable of reducing light intensities to such a level that an underlying cyanobacterial mat would become light limited. The light meter was calibrated in W m^{-2} using known light intensities. A similar procedure was followed to determine the amount of light penetrating various thicknesses of the Zone 2 *Microcoleus* mat to determine whether phototrophic bacteria growing under this mat might be light limited.

The depth of the reducing environment in Zones 1 and 2 was tested by placing thin (10 cm long by 1 cm wide) strips of pure silver into the surface layer of sediment for 10 min and, after removal, the depth of the reducing layer was inferred from the depth of the blackened portion of the silver strip. Upon removal, the depth of any black (AgS) deposits was recorded along with the colour and colour intensity over the length of the silver strip.

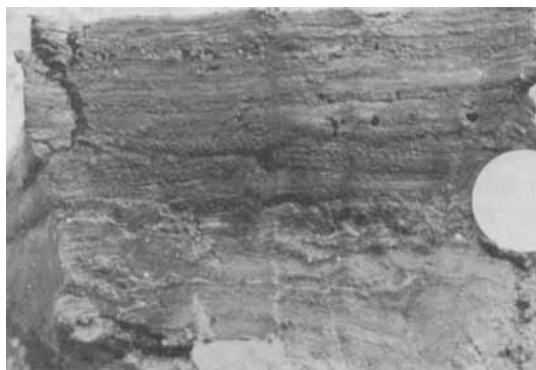
RESULTS

A brief description of Zone 1 was provided in the Introduction. The object of this research was the question of microlamina formation in hypersaline environments, and, as such, most attention was given to the cyanobacterial mats in Zone 2.

Description of the cyanobacterial mat of Zone 2

Zone 2 is characterized by dark green, laminated mats of *Microcoleus chthonoplastes* (Fig. 3) occasionally covered by a thin, orange coloured layer of *Lyngbya aestuarii*. The *Microcoleus* mats are interbedded with fine grained, light coloured, detrital layers. These layers were apparently deposited in three ways:

- (1) the filling of an empty pan is associated with the introduction of considerable quantities of inorganic material which, if of sufficient quantity, is capable of forming a light coloured lamina on top of the *Microcoleus* mat;
- (2) wind action may erode inorganic particles from the levees or dykes which surround the pans and deposit them as a fine sediment layer on top of the *Microcoleus* mat;



(a)



(b)

Fig. 3. Microlaminated algal mats with alternating layers of black organic material (*Microcoleus*) and mineral particles (grey). In (b) the mineral particle layers are mainly sand grains and are much thicker than the dark, organic-rich layers. Coin is 2.3 cm in diameter.

- (3) very strong winter storms may produce inundations of seawater which breach the sand dune and dyke system in the solar salt works, resulting in the flooding of the salt pans with sediment-laden seawater and deposition of considerable quantities of sand and detrital material on top of the cyanobacterial mat.

These three processes do not completely explain the lack of continuity of the microstrata between sediment cores, even those taken less than 1 m apart (Fig. 4). This lack of correlation has considerable significance for the interpretation of laminated patterns of sediments formed in these salt pans, and for the interpretation of ancient laminated deposits.

Zone 2 was divided into five subzones (Fig. 5) on

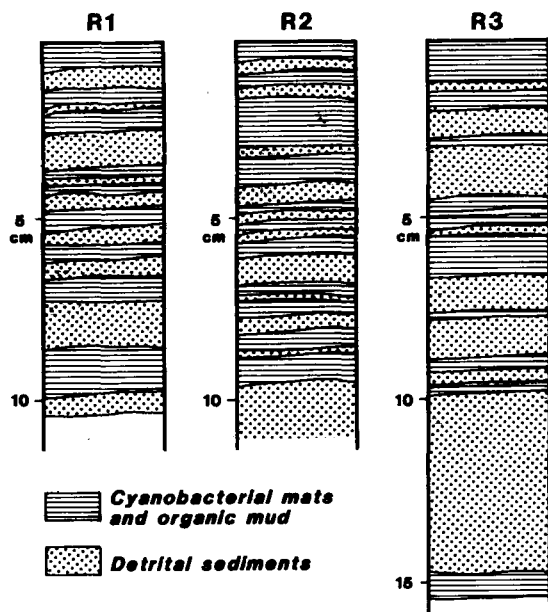


Fig. 4. Three cores taken less than 1 m apart from Salin-de-Giraud. Although the distance between these cores is very small, there is no lateral continuity between the different laminae (after Busson, 1982, fig. 3). Fangassier Clos 2 pan (see Fig. 1), water depth typically <0.5 m, salinity c. 70‰.

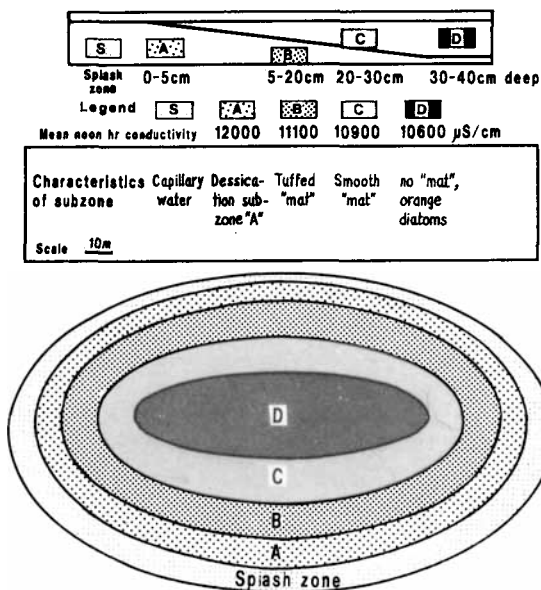


Fig. 5. A topographic and cross-sectional schematic view of the spatial variation in the subzones of the algal mat zone.

the basis of the composition and morphology of its cyanobacterial mats.

Subzone S was termed the splash subzone or capillary water subzone. The cyanobacterial mat is very thin in this subzone.

Subzone A was distinguished by the small size of its desiccation crack polygons which may be called 'petees'. This term was used by Gavish *et al.* (1985) to describe biogenic structures very similar to sharp-edged triangular desiccation crack structures designated as 'tepee' structures and well known in evaporitic deposits. Tepees are abiogenic whereas petee structures result from the interplay of biological and physical processes. *Microcoleus* and *Lyngbya* form the dominant cyanobacterial mat association in this subzone. In Subzone A, which is frequently 30 m or more in width (i.e. the distance between Subzones S and B), there is a very gradual change in water depth from 0 to 5 cm.

Subzone B was distinguished by its tufted cyanobacterial (*Microcoleus*-*Lyngbya*) mat. Desiccation cracks in this subzone are far less numerous and the cyanobacterial mat polygons are more than twice the size of those from Subzone A.

Subzone C was distinguished by the presence of a flat (untufted, *Lyngbya*-free) cyanobacterial (*Microcoleus*) mat.

At one location only, Vieux Rhône Nord (Fig. 1), a fifth subzone (Subzone D) was observed. This subzone was distinguished by its complete lack of a cyanobacterial mat. The cyanobacterial mat in Subzone C on the boundary of Subzone D contained numerous small (1-10 cm) holes (Fig. 6). It was speculated that benthic invertebrates which were intolerant of the higher



Fig. 6. Holes in the algal mat occurring at the transition area between Subzones C and D. Disruption of mat may be due to benthic grazing.

salinities in Subzones A–C (Subzone D had the lowest salinity of any of the four subzones) were feeding on the cyanobacterial mat. However, microscopic analyses of the sediments in Subzones C and D did not reveal any noticeable differences in the densities of grazers such as chironomids, nematode worms or ciliates. The base of Subzone D was covered by a thin flocculent layer primarily composed of orange coloured diatoms with a few filaments of *Lyngbya*. It is possible that the diatoms and *Lyngbya* filaments are more shade tolerant than the *Microcoleus* and that therefore a cyanobacterial mat fails to form in the deeper water.

Cyanobacterial mat transplants from Zone 2 to Zone 1

The specific gravity of the water in the Zone 1 salt pan was 1.035, equivalent to a salinity of about 50 g l⁻¹. To determine the possible reasons for the absence of cyanobacterial mats in Zone 1, four pieces (56–220 cm²) of *Microcoleus* were removed from Zone 2 (from a pan with an average salinity of 65 g l⁻¹) and transplanted into Zone 1. After 24 h numerous small gastropods (*Hydrobia acuta*) were found on, under and in the four transplanted cyanobacterial mats (Table 2). The density of these snails on the nearby sand, rocks and algal masses of *Cladophora-Enteromorpha* was significantly lower ($P < 0.05$, Student's *t*-test) than on the transplanted *Microcoleus* mat (Table 2).

The *Microcoleus* microlaminated mat with its significantly higher density of snails provided an indication that grazing by these invertebrate herbivores in Zone 1 might limit the growth of this important cyanobacterial mat to areas where these gastropods did not occur. Note that this grazer does not occur at the higher salinities encountered in Zone 2.

Competition for light

Competition for light between the cyanobacterial mat characteristic of Zone 2 and the floating green algal mass characteristic of Zone 1 was estimated by measuring the amount of light passing through a layer of the green algal mass taken from Zone 1 (Table 3). The algal mass was composed of intertwined filaments of *Cladophora* sp. and *Enteromorpha intestinalis* with an average thickness of 8 mm. In full (direct) sunlight the algal mass reduced the incident light intensity from 75 to 0.01 W m⁻². It is unlikely that a *Microcoleus* mat beneath this floating mass of *Cladophora* and

Table 2. Density of *Hydrobia acuta* on algal masses and on *Microcoleus* mats.

Mat size (cm ²)		Gastropods per 100 cm ²	
<i>Microcoleus</i>	<i>Cladophora-Enteromorpha</i>	<i>Microcoleus</i>	<i>Cladophora-Enteromorpha</i>
56	71	59	6
150	146	90	11
170	152	70	9
220	211	142	23
Means:			
149	145	90.25 ± 36.8 *	12.25 ± 7.46

* Statistically significant at $P < 0.05$.

Table 3. Reduction of light intensity under *Cladophora-Enteromorpha* masses and the growing layer of *Microcoleus* mats.

Mat	Thickness (mm)*	Estimated light intensities passing through the mat (W m ⁻²)
<i>Microcoleus</i> (growing layer)	1	0.01
<i>Microcoleus</i> (three couplets)	2	0.0007
<i>Microcoleus</i> (six couplets)	4	0.00015
<i>Cladophora-Enteromorpha</i>	8	0.01

* Mean of four readings.

Enteromorpha would receive sufficient light to permit active growth.

A reduction of light intensity to 0.01 W m⁻² would, according to published accounts cited by Guerrero *et al.* (1985), result in light becoming limiting to algae but not to photosynthetic bacteria. According to Guerrero *et al.* (1985) the lowest light intensity at which phototrophic bacteria can grow is 95 µE cm⁻² s⁻¹, approximately 0.001 W m⁻². Thus, phototrophic bacteria are commonly found below the decomposing masses of *Cladophora-Enteromorpha* that accumulate along the leeward shores of Zone 1 pans. This occurrence was correlated with the presence of H₂S at the same depth (as indicated by our silver strip experiments). H₂S is an essential requirement for the growth of phototrophic bacteria (Trüper, 1978).

The light intensity reduced from 78 to 0.01 W m⁻² on passing through the growing layer of a smooth *Microcoleus* mat (c. 1 mm thick). This was similar to the reduction in light intensity caused by an 8 mm thick *Cladophora-Enteromorpha* mass. Such a reduction of light intensity under the growing layer of *Microcoleus* does not explain why, in comparison with many other places in the world (e.g. Javor & Castenholz, 1980, 1984a,b; Potts, 1980; Giani *et al.*,

1989), no pink layer of phototrophic bacteria was observed in the cyanobacterial mat from Salin-de-Giraud.

Silver strip experiments

A dynamic cycle of oxidation and reduction occurs in the organic layers of cyanobacteria and bacteria living in the salt pans at Salin-de-Giraud. An equilibrium state is established between the reduced and oxidized sulphur in the respective interstitial and overlying 'free' waters (Pierre & Fontes, 1982).

A rapid assessment of the depth of the reducing layer in each zone was obtained using the silver strip method. The silver strip experiments were carried out in Zone 1 and all five subzones of Zone 2. These rapid and direct measures lacked precision, but were useful for establishing a relationship between the depth of the reducing layer and the morphology and composition of biological populations.

Near the margin of Zone 1, where masses of *Cladophora* and *Enteromorpha* were found along the leeward side of the pan, the sediments underneath decomposing masses of vegetation were strongly

reducing. This resulted in a rapid blackening of the silver strip immediately below the surface of the sediments. At locations free of decomposing vegetation, the silver strip turned a pale brown colour at about 1–2 mm depth and remained at this colour to its base; this indicates that very little H_2S was present at these depths in the sandy sediments as long as they were free of overlying algal masses. There is therefore an association between the amount of decomposing vegetation and the amount of H_2S in the sediments.

In the cyanobacterial mats of Zone 2, the first 3–5 mm were generally oxidizing (Fig. 7). The strips remained a silver colour. This layer corresponded to the green, living layer of cyanobacteria and diatoms at the surface. The thickness of the reducing zone was dependent on the thickness of the decomposing cyanobacterial mats: about 2 mm in Subzone S, 1.5 cm in Subzone A, more than 8 cm in Subzones B and C. The inorganic sediment of the pan substrate was not reducing. In Subzone D (which did not contain a cyanobacterial mat but had a flocculent layer mainly composed of diatoms), the top of the reducing layer was deeper (2–2.5 cm), and the intensity of reducing conditions was lower.



Fig. 7. 100 mm long silver strips exposed for 10 min to the sediments in Subzones A–D (represented by the numbers 1–4 respectively) from Zone 2 of Salin-de-Giraud solar salt works.

Temporal and horizontal variation in Zone 2 water chemistry

Variations in temperature were analysed along with the other physico-chemical parameters (Fig. 8).

The temperatures of Subzones A and B, which are very shallow, closely follow the air temperature. In contrast, in Subzones C and D, brine heating is less

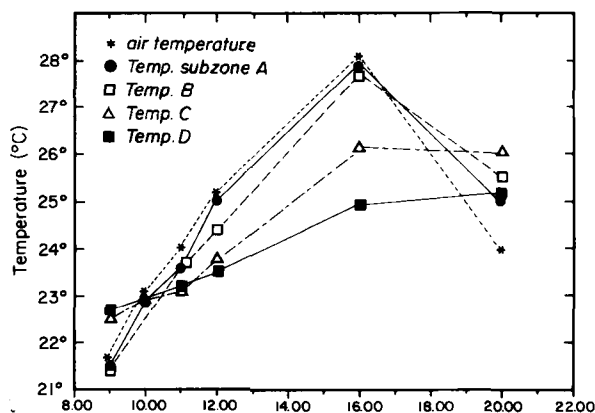


Fig. 8. Temporal changes in temperature in Subzones A–D in Zone 2 of the Salin-de-Giraud solar salt works. The abscissa gives the time of day on 1 July 1990.

important, even near the surface. In both subzones the range of temperatures is smaller during the day. Brine cooling is also slower in the pan centre than at the margins (pellicular brines). This type of temperature distribution is related to the initiation of salt crystallization (gypsum, halite) at the margins of the pan (see also next section).

Horizontal (spatial) variation in conductivity

Salinity and specific conductivity were characteristically higher near the margins of the salt pans than near the centre (Fig. 9). This fact appears to be of considerable relevance to cyanobacterial mat development. This type of salinity distribution appears to be general. In most cases, in Zone 2, the mat first appears along the upper margins of the pans where salinities are highest and where the densities of high salinity intolerant benthic invertebrates capable of eating the cyanobacterial mat are presumably lowest. This observation has been made both in the Salin-de-Giraud salt works and in the Santa Pola (Spain) salt works (cf. Cornée, 1988, fig. 3).

The data here indicate that water contained in Subzone A, and to a lesser extent in Subzone B, increases salinity as evaporation takes place. This increase in salinity occurs more rapidly than the downslope movement of saline (denser) water to deeper parts of the salt pan. Thus, even at night or in

the morning, the salinity of the shallowest subzone exceeds that of all the deeper subzones.

A similar pattern occurs in Zone 3 where the highest salinities occur around the margin of the pans as indicated by the initiation of gypsum crystal formation. At a Cl^- concentration of 2.2 mol l^{-1} , gypsum crystals were found only at the upper margins of the pan or on upper areas of the pan where the brine is shallower (Geisler, 1982; Dulau & Trauth, 1982). This was consistent with our findings that the surface layers of water near the periphery of the pans generally had higher salinities than the water at the deepest point near the centre of the pans.

Zone 2 spatial variation in dissolved oxygen (Fig. 10)

There are 5.95 mg l^{-1} of dissolved oxygen (DO) in seawater at 28°C (Herrmann *et al.*, 1973). As the specific gravity of the water from Salin-de-Giraud increased along the salinity gradient from seawater-filled pans near its entrance to the Zone 4 halite deposition pans (Fig. 1), the concentration of DO declined. In addition, as has been reported elsewhere (e.g. Herrmann *et al.*, 1973; Northcote & Hall, 1990), it was found that supersaturation of DO results in much higher DO values than those predicted from standard curves of DO saturation levels. As expected, supersaturation was greatest in Subzones A and B of Zone 2, where the greatest accumulation of gas bubbles on the surface of the cyanobacterial mat was observed.

In the neritic zone (Zone 1), where salinities are generally less than 60 g l^{-1} , the observed DO reached maximum levels of 7.8 mg l^{-1} (131% supersaturation).

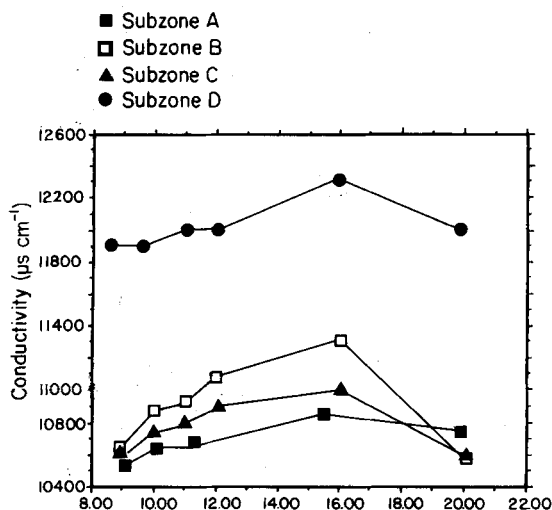


Fig. 9. Temporal changes in temperature-corrected specific conductivity in Subzones A–D in Zone 2 of the Salin-de-Giraud solar salt works. The abscissa gives the time of day on 1 July 1990.

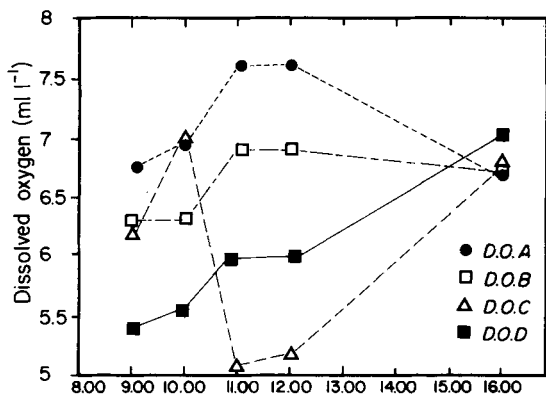


Fig. 10. Temporal changes in dissolved oxygen (DO) in Subzones A–D in Zone 2 of the Salin-de-Giraud solar salt works. The abscissa gives the time of day on 1 July 1990.

In the cyanobacterial mat zone (Zone 2), where salinity increased from 60 to 150 g l⁻¹, the DO reached levels of 7.6 mg l⁻¹ (c. 140% supersaturation). The daily changes in DO in Zone 2 were complex (Fig. 10). Generally, DO concentrations in the water column of each of the four subzones (A–D) increased from early morning until early afternoon. The only exception to this occurred in Subzone C, where DO suddenly declined between 10 and 11 a.m. and then slowly increased in the afternoon. The reasons for this different pattern in Subzone C are speculative. Below a water depth of 20 cm, both pH (Fig. 11) and DO remained low throughout the early part of the day. This was interpreted to indicate that the deeper water layers (i.e. those in contact with the cyanobacterial mat in Subzones C and D) may have developed an oxygen deficit at night associated with cyanobacterial respiration and the decomposition of organic matter deposited there. Wind mixing at 10 a.m. would mix the deeper oxygen-poor waters with the surface layer of well oxygenated waters resulting in a sudden decline in DO at 10 cm (Subzones C and D were both sampled at this depth). Some of the implications of this are discussed in the following sections.

Zone 2 spatial variation in pH

Changes in pH may mirror changes in primary production, which, in turn, are in equilibrium with decomposition processes. Just below the splash zone, where the cyanobacterial mat first appears, the water was only 0–5 cm deep and from 9 to 10 a.m., pH increased from 8.6 to 9.2 (Fig. 11). As noted above, this was associated with the appearance of small gas

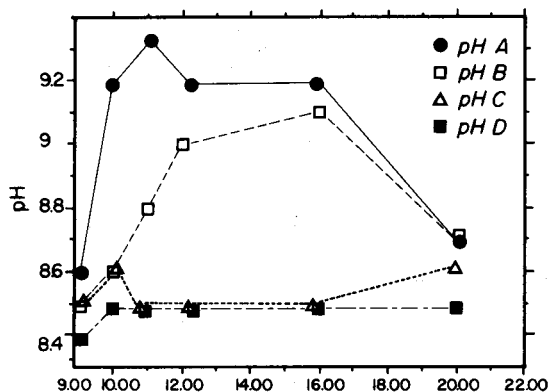


Fig. 11. Temporal changes in pH in Subzones A–D in Zone 2 of the Salin-de-Giraud solar salt works. The abscissa gives the time of day on 1 July 1990.

bubbles covering the upper surface of the cyanobacterial mat in this subzone. These bubbles, which appeared in the morning and were associated with supersaturated levels of DO, were assumed to be oxygen-filled. It is tempting to speculate that the smooth *Microcoleus* mat in Subzone C was photosynthesizing less rapidly than the cyanobacterial mats in the shallower and warmer subzones as fewer gas bubbles were detected on the surface of the *Microcoleus* mat in Subzone C. As a result, DO and pH remained lower throughout the day in the deeper subzones (Figs 10 & 11).

DISCUSSION AND SEDIMENTOLOGICAL IMPLICATIONS

Distribution of microphytobenthic laminated cyanobacterial mats

The location of cyanobacterial mats depends ultimately on the salinity of the water. At a salinity of about 60 g l⁻¹, the growth of many mat-consuming herbivores, such as *Hydrobia acuta*, is inhibited. This small gastropod has a radula which is capable of abrading cyanobacteria such as *Microcoleus* (S. Gofas, personal communication). The abundance of this herbivore in Zone 1 may, in part, explain the lack of cyanobacterial mats in this zone. Numerous other authors have evoked the role of grazers in limiting cyanobacterial mat colonization (Garrett, 1970; and Pace *et al.*, 1979, in Bauld, 1981a). However, few have offered direct experimental evidence to confirm this point, as has been attempted here. Gerdes & Krumbein (1984) verified in laboratory experiments that *Pirenella conica* inhibits the development of extended mats in the Gavish Sabkha. In Laguna Guerrero Negro (Baja California), Javor & Castenholz (1984b, p. 93) empirically demonstrated that (1) hypersalinity limits gastropod populations (*Cerithidea californica*) and (2) invertebrates 'can effectively prevent the development of stromatolitic microbial mats in an environment that is otherwise suitable for their growth.' Our study of *Hydrobia acuta* is an additional demonstration of the role of gastropods in limiting cyanobacterial mat formation.

At the high end of the salinity spectrum, where gypsum begins to crystallize out of the solution (at a salinity of c. 150 g l⁻¹), cyanobacterial mats disappear because they are incapable of growing at salinities in excess of 150 g l⁻¹ (Thomas & Geisler, 1982).

Another factor, low light intensity, may prevent the growth of cyanobacterial mats at low salinities. Below 60 g l^{-1} the growth of floating algal masses (e.g. *Cladophora-Enteromorpha* masses) substantially reduces the penetration of light so that microphytobenthos growth on the bottom may be light limited. Javor (1985, p. 202) noted that cyanobacterial mats could not develop when phytoplankton were abundant because they 'shaded the (phyto) benthos'.

A sharp decrease in stromatolite development coincided with the appearance of grazing invertebrates (Awramik, 1984) and probably the appearance of green algae. In Precambrian and early Cambrian times, cyanobacteria did not have to compete with chlorophytes and were not exposed to gastropod grazing. Thus, in the early history of the Earth, the cyanobacteria may have lived in environments which were not as hostile as those found today.

The role of desiccation as a critical factor in limiting the growth of cyanobacterial mat grazers in subtidal zones has been described by Bauld (1981a). Repeated periods of desiccation appear to be an additional favourable condition for extensive microbial mat development. The absence of desiccation could provide an explanation for the lack of cyanobacterial mats at the centre of Subzone D in the Vieux Rhône Nord pan: this depressed zone is a pan where the winter storage of brines prevents drying out. In salt works at Santa Pola, where desiccation in winter does not occur, generalized *Microcoleus* mats do not exist at otherwise favourable salinities ($80\text{--}130 \text{ g l}^{-1}$; Orti Cabo *et al.*, 1984).

Laminated mats and microstratigraphic correlations

Interpretations of microlaminated sedimentary successions sometimes diverge. For the same laminated succession, some workers may support a stromatolitic origin (a priori shallow water or even marginal conditions), whereas others favour an anaerobic origin (typically encountered in deeper environments). The palaeoenvironmental importance of the correct interpretation of laminated sediments is very high (cf. Park, 1976).

Previous observations (Busson, 1982) established the absence of possible lamina-by-lamina correlation, even for very closely spaced sections (Fig. 4). There is now a better understanding of this phenomenon. During the winter, and during periods when the pans are drained or when winds push back the waters from the windward portion of the pan, the cyanobacterial mats dry out and develop deep fissures (desiccation

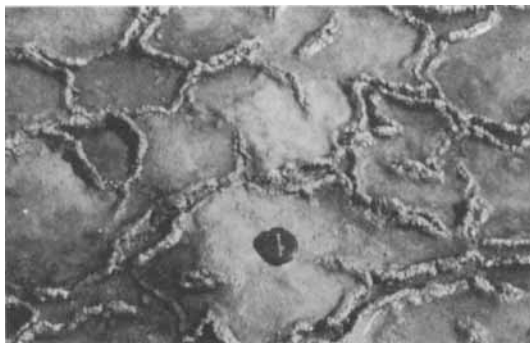


Fig. 12. Polygonal desiccation cracks in the cyanobacterial mat of Zone 2 at Salin-de-Giraud solar salt works. These structures are designated as 'petees' (see text) and are due to the interplay of biological and physical processes.

cracks) giving them the appearance of polygonal plates (Fig. 12). Thomas & Geisler (1982), among others, observed these cyanobacterial mat polygons and they classically attributed them to desiccation phenomena. Insofar as these desiccation cracks concern biological material, the resulting structures may be referred to as petees. Such structures are described in detail in Reineck *et al.* (1990). They have also been noted by Gavish *et al.* (1985), Gerdes *et al.* (1985a) and Bernier *et al.* (1991). Gas bubbles were observed to accumulate under the mats and enhance polygon formation: gas produces dome-shaped structures where tension may cause cracking. The bubbles also enhance polygon separation and movement. A similar observation was mentioned by Reineck *et al.* (1990) and Bernier *et al.* (1991), who evoked the role of subsurface gas pressure in the genesis of these petee structures. These gas bubbles are probably produced by the degradation of organic matter. The top layers of these polygons are not permanent features of the mat, and may peel away during storms. The newly exposed surface of the remaining material (i.e. that portion of the polygon which was not removed by the storm) is rapidly colonized by *Lyngbya* which can easily be recognized by its long, orange coloured filaments. Ultimately, this process leads to the development at the bottom of these pans of a heterogeneous 'patchwork quilt' made up of cyanobacterial polygons. Each polygon displays a quite different lamina succession to adjacent polygons. The displacement process results in very different downcore laminae profiles, even in closely spaced cores. This is not normally the case in meromictic systems, where adjacent cores typically show similar downcore stratigraphies.

Modern cyanobacterial mats and stromatolites

Modern cyanobacterial mats are considered to be homologous with stromatolites, and, as such, the processes of lithification of these formations need to be examined. In Salin-de-Giraud, the precipitation of aragonite or calcite cement is not generally observed, except for the occurrence of aragonite laminae in one pan (Geisler, 1982). In contrast, cyanobacterial mats from other sites, such as the salt works in Santa Pola, Spain (Ortí Cabo *et al.*, 1984), Laguna Guerrero Negro, Mexico (Javor & Castenholz, 1980), Laguna Mormona, Mexico (Horodyski *et al.*, 1977), Solar Lake, Sinai (Krumbein & Cohen, 1974), and MacLeod Lake, Australia (Logan, 1987), are commonly associated with carbonate precipitation, both as lithifying cements and uncemented grains.

Hydrology

Whatever the mean salinity of successive pans, the more saline waters are located at the pan margins. The obvious reason is that given the same rate of surface evaporation, the increase of salinity is higher in shallow water than in deeper water. This process could potentially be cancelled—or even reversed—by the sinking of marginal brines flowing towards deeper areas as is typical in some large basins (i.e. the Dead Sea; Neev & Emery, 1967). At Salin-de-Giraud this process was not observed. Our observations indicated that brine movement in these gently sloping pans was negligible.

The type of salinity distribution seen at Salin-de-Giraud is of significance for the interpretation of ancient evaporitic deposits. For example, a similar pattern exists in Messinian selenitic facies in San Miguel de Salinas (Alicante, Spain; F. Ortí Cabo, personal communication). In the absence of direct salinity measurements, Ortí Cabo used Sr content in gypsum as an indicator of palaeosalinity. Here, each selenitic unit shows high Sr contents at the basin margin and low Sr contents in the centre. 'This means that the salinity in the centre remained permanently lower than on the borders during selenite precipitation' (F. Ortí Cabo, personal communication).

In the *Microcoleus* pans, very high oxygen supersaturations (130–140%; Fig. 10) were observed due to photosynthesis. Oxygen and pH analysis correlated with the observation of gas bubbles at the surface of the mats indicates that photosynthesis is especially active in shallower parts of the pan (for example less than 20 cm). These areas are also warmer and receive

more light. By midday slightly deeper areas are less warm and have lower oxygen contents, suggesting limited mixing. This contrast between surface water and 'deeper' water results in a type of reverse brine stratification with the more saline (denser) waters at the margins of the pans.

Productivity and organic preservation

Intense oxygenation is evidence of high cyanobacterial productivity. High productivity is enhanced by several related factors: (1) continuous supply of nutrients due to permanent seawater influx; (2) the absence of grazers or predators; and (3) good light penetration in very shallow waters. High rates of production, mainly by microphytobenthos, can explain the organic-rich layers common in many ancient evaporitic environments. In ancient evaporites, however, high production is of interest as a source of organic matter only if conditions favourable to its early preservation are ensured.

At Salin-de-Giraud, it is clear that much of the organic matter is produced by the microphytobenthos and therefore it is not destroyed in the water column, even though this water is well oxygenated. Moreover, the tight and continuous cyanobacterial mat forms a barrier for both gas and solute transfer between sediments and brines and thus enhances reducing conditions in the sediments, as confirmed by the silver strip tests. Cyanobacterial mats therefore not only generate organic matter, but may also enhance its preservation at depth. Organic geochemical analyses confirm that in the Salin-de-Giraud salt works, the highest organic contents occur in sediments underlying the cyanobacterial mats (Thomas, 1982). Moreover, these analyses showed that bacterial decomposition transformed the cyanobacterial mats into sapropelic sediment with a high hydrocarbon potential.

Despite these favourable conditions, an assessment of the amount of organic matter preserved in this type of environment is difficult (Cornée, 1988). Some authors, for example Bauld (1981a) and Friedman (1982), assign a high potential for hydrocarbon formation to the organic matter produced in shallow evaporitic environments. However, Busson (1982, 1988) and Warren (1986) have emphasized the extreme fragility of these very shallow environments since weathering processes induced by prolonged desiccation may have catastrophic consequences for organic matter preservation.

CONCLUSIONS

This study has revealed some of the complex interacting factors associated with the presence and absence of cyanobacterial mats in salt pans. In the past, geologists have often associated the presence of these mats with supratidal environments, but their widespread development in basins in which there are no tidal effects, such as those at Salin-de-Giraud, must also be acknowledged.

In Zone 2 (the cyanobacterial zone) of the Salin-de-Giraud solar salt works, *Cladophora* and *Enteromorpha* and herbivorous snails such as *Hydrobia acuta* are unable to survive because of their intolerance to salinities above 60 g l^{-1} . As a result, *Microcoleus chthonoplastes* forms thick mats in this zone where both its predators and competitors are excluded. In salt pans of higher salinities ($150\text{--}320 \text{ g l}^{-1}$), this species of cyanobacteria is absent, as it is intolerant to such extreme conditions.

In Zone 2, Subzones A and B, the cyanobacterial mat is characterized by desiccation polygons. Wind-driven currents may remove the upper layers of the cyanobacterial mat which have been loosened by gas formation in the organic-rich microlaminae. These loosened cyanobacterial mat polygon sections are then free to 'float' to new locations where they are redeposited on top of other cyanobacterial mat polygons. This process explains why there is no similarity in the microlamina banding patterns in cores taken very close to one another.

Gypsum and halite deposits are common in the geological record. The former begin to precipitate after 75% of the seawater has been removed by evaporation, while halite precipitates from solution after a 90% evaporative reduction in the initial volume of seawater. A large range of geological deposits are associated with environments where the salinities are intermediate between those of seawater ($32\text{--}38 \text{ g l}^{-1}$) and gypsum deposition ($> 150 \text{ g l}^{-1}$). Such pre-saline evaporitic deposits are difficult to identify but are important for palaeogeographical reconstructions. It is hoped that by understanding more about the cyanobacterial mats of solar salt works, geologists will be aided in recognizing sediments of pre-saline and saline environments. These salt works may represent a valuable 'laboratory' for the study of both biological and mineralogical processes operating under controlled conditions. Solar salt works (e.g. Secoljve, Schneider & Herrmann, 1980; Salin-de-Giraud, Busson *et al.*, 1982; Santa Pola, Ortí Cabo & Busson, 1984) are all the more useful to the interpretation of

cyanobacterial mat growth because the biological and mineralogical distribution is much more constant than in natural settings (e.g. Gulf of Aqaba, Potts, 1980; Gavish Sabkha, Gerdes *et al.*, 1985a), which are subject to very aleatory changes.

It is also important to note that the maximum production of benthic cyanobacterial mats occurs in extremely shallow waters (2–12 cm), which often corresponds to the area where desiccation and decomposition processes are most intense. As a result, preservation is frequently poor. Given such complex and delicate conditions required for the preservation of microlaminated cyanobacterial structures, it is surprising that stromatolitic units, such as those of the Cambrian in western North America, cover such vast areas (fig. 14H in Lochman-Back, 1972). Their interpretation based on present day analogues presents a considerable challenge.

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