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Ecology and physiology of phototrophic bacteria and sulfate-reducing bacteria in marine salterns

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Abstract. Marine salterns are habitats for a large variety of halophilic bacteria. In the anoxic zones, halophilic sulfur bacteria develop mainly at the sediment surface, but only a few of them have so far been isolated from such environments. Among the phototrophic sulfur bacteria that sometimes form purple layers underneath the green cyanobacterial layers, members of the genera *Ectothiorhodospira, Chromatium (C. salexigens), Thiocapsa (T. halophila)* were isolated. They grow by using sulfide as an electron donor. In the marine salterns, sulfide originates from active sulfate reduction. Among the halophilic sulfate-reducing bacteria, only *Desulfovibrio halophilus* and *Desulfohalobium retbaense* have so far been isolated. The ecology and physiology of both kinds of bacteria are discussed in this paper.
Key words. Phototrophic bacteria; sulfate-reducing bacteria; marine salterns; halophilic sulfur bacteria.

Introduction

Marine salterns are generally man-made formations based on a succession of various shallow ponds in which sea water circulates and evaporates until the sodium chloride level reaches saturation, with resulting precipitation and crystallization. Consequently, in the successive ponds a gradient of brines forms with increasing salinity in each pond. These special aquatic systems are habitats for a large variety of halophilic or halotolerant bacteria which occur over the salinity gradient, depending on the optimum salinity for growth of each species. In the first ponds most of the bacteria isolated are slightly halophilic or marine bacteria, according to the description of halophilic bacteria and their salinity range from Trüper and Galinski[40]. In the intermediary ponds, where the sea water is concentrated to a salinity of about 10 to 20%, most of the bacteria we can isolate belong to the groups of moderately halophilic or halophilic sensu stricto bacteria. The last ponds are inhabited by extremely halophilic bacteria particularly the Halobacteriaceae, the family that contains all bacteria of the halophilic branch of the Archaea[45]. Most of the extremely halophilic eubacteria that are genetically completely separate from the Archaea have so far been isolated from anoxic hypersaline environments. Among them, two bacterial groups are well represented: the fermentative bacteria belonging to the family Haloanaerobiaceae[32] and the phototrophic sulfur oxidizing bacteria of the family Ectothiorhodospiraceae[17].

The phototrophic sulfur oxidizing bacteria grow at the anoxic sediment surface in a narrow zone containing sulfide and reached by light. They use sulfide as an electron donor for their photosynthesis. The sediment of the marine salterns is very anoxic and rich in sulfide in any pond throughout the salinity gradient, from sea-water salinity up to NaCl saturation. Consequently, various kinds of phototrophic sulfur-oxidizing bacteria are encountered in the different ponds. Most of them originate from the marine environment and tolerate salt concentrations up to 8–10%. They grow in the first ponds. Some moderately halophilic sensu stricto or extremely halophilic organisms populate the other ponds. The sulfide stored in the anoxic sediments, that serves as electron donor for anoxygenic photosynthesis, is mainly produced from sulfate reduction. Sulfate is one of the major mineral compounds of sea-water (25 mM). It is concentrated in the salterns up to saturation point and precipitated in the form of calcium sulfate (gypsum). Consequently, it is never a limiting factor for sulfate-reduction in the salterns and serves as the final electron acceptor for sulfate-reducing bacteria. These bacteria need low molecular weight organic compounds as energy sources. Such compounds originate from organic matter, produced by halophilic organisms and degraded via halophilic aerobic or fermentative bacteria. The sulfate-reducing bacteria are present in various ponds of the salterns; however, so far only a few have been isolated. Both kinds of bacteria (phototrophic and sulfate-reducing) contribute to the turnover of the sulfur cycle in the anoxic zone of the hypersaline environments. The present paper examines their physiology and ecology in marine salterns.

The phototrophic bacteria in saline environments

The anoxygenic phototrophic bacteria constitute a physiological group of microbes that have the common property of anoxygenic photosynthesis. They possess

Table 1. Different families or groups of anoxygenic phototrophic bacteria and their major characteristics[e]

Bacterial type	Family or group	Main electron donors	BChls	Sulfur globules
Purple bacteria	Purple nonsulfur bacteria	Organic compounds[a] (H_2S, $Na_2S_2O_3$, H_2)	BChl *a* or *b* and carotenoids	None
	Chromatiaceae[b]	H_2S, S^0, Na_2SO_3, $Na_2S_2O_3$, H_2 (organic compounds)[a,d]	BChl *a* or *b*[c] and carotenoids	Inside the cells
	Ectothiorhodospiraceae[b]	H_2S, S^0, Na_2SO_3, H_2 (organic compounds)[a,d]	BChl *a* or *c*[c]	Outside the cells
Green and brown bacteria	Chlorobiaceae[b]	H_2S, S^0, Na_2SO_3, (organic compounds[d] in the presence of CO_2	BChl *c*, *d* or *e*; small amount of BChl *a* and cartenoids	Outside the cells
	Chloroflexaceae	Organic compounds[d] (H_2S)	BChl *c* or *d*; small amount of BChl *a* and cartenoids	None or outside the filament
Heliobacteria		Organic compounds[d]	BChl *g*; small amount of carotenoids	None

[a]Organic compounds can serve as electron donors.
[b]The three families which form phototrophic sulfur bacteria.
[c]Only a few species.
[d]Organic compounds serve as the photosynthetic carbon source.
[e]Redrawn from Caumette (cf. ref. 4).

light harvesting pigments (bacteriochlorophylls (BChls) and carotenoids) that act in the transfer of electrons through one photosystem and a cyclic chain of electron transport. Consequently, in contrast to cyanobacteria (so-called oxygenic phototrophic bacteria) that use water as electron donor and produce oxygen during their photosynthesis, the anoxygenic phototrophic bacteria can use H_2, organic compounds or sulfur-reduced compounds; they live in anoxic environments reached by light. In the case of sulfur compounds, they produce various oxidized sulfur metabolites, the final product being sulfate.

Phototrophic bacteria are divided into purple and green bacteria according to their respective bacteriochlorophylls and carotenoids (table 1). The purple bacteria contain BChl a or b and numerous carotenoids (okenone, spirilloxanthin, rhodopinal, lycopenal, etc.) incorporated into a complex cell membrane system which is continuous with the photosynthetic membrane[35,36,38]. The varying amounts of carotenoids present produce colors ranging from yellow-brown to red purple-violet. The green and brown bacteria contain BChl c, d, or e and carotenoids of the isorenieratene series as light-harvesting pigments which are located in vesicles (chlorosomes) attached to the cell membrane at the intracytoplasmic periphery of the cells. They also contain a small amount of BChl a as a photosynthetic reaction center located in the membrane. In addition, other phototrophic bacteria contain β-carotene as their major carotenoid[2]. They are grouped in different families and genera according to their physiological and genetic characteristics[36].

The family or group of purple non-sulfur bacteria (table 2) consists of bacteria containing mainly BChl a or BChl b and using organic compounds or H_2 as electron donors.

The members of the families Chromatiaceae and Ectothiorhodospiraceae (table 2) (purple sulfur bacteria) also contain BChl a or BChl b, and use mainly sulfur compounds as electron donors. The Chromatiaceae family members store elemental sulfur globules as intermediary products of photosynthesis inside the cells. The Ectothiorhodospiraceae members excrete sulfur globules outside the cells.

The green bacteria (table 3) are divided into two groups. Members of both groups contain BChl c, d or e. The group of green sulfur bacteria comprises bacteria that use mainly reduced sulfur compounds as electron donors and excrete elemental sulfur as the intermediary product of their photosynthesis in the form of globules outside the cell.

The family Chloroflexaceae (green non-sulfur bacteria) comprises filamentous bacteria which show a pronounced tendency to use organic compounds, although photolithotrophic growth with sulfide as electron donor has been observed in *Chloroflexus* mats[16].

Recently, other genera and species of phototrophic bacteria have been described, including 'heliobacteria', which contain BChl g. For these strains, a new family (*Heliobacteriaceae*) has been suggested[1].

Anoxygenic phototrophic bacteria often develop as dense layers in a wide variety of anoxic, generally poorly illuminated, environments found in metalimnia or hypolimnia of stratified water bodies or at the sedi-

Table 2. Genera of the phototrophic purple bacteria[a]

Group and genus	Morphology	Division	Motility	Gas vacuoles
Purple nonsulfur bacteria				
Rhodopseudomonas	Rods	Budding	+	−
Rhodomicrobium	Ovoid cells	Budding	+	−
Rhodospirillum	Spirilloid cells	Binary	+	−
Rhodocyclus	Curved cells in circle	Binary	+ or −	−
Rhodopila	Spherical cells	Binary	+	−
Rhodobacter	Rods	Binary	+ or −	−
Purple sulfur bacteria				
Chromatiaceae[b]				
Chromatium	Rods to ovoid cells	Binary	+	−
Thiocystis	Spherical cells	Binary	+	−
Thiospirillum	Spirilloid cells	Binary	+	−
Thiocapsa	Spherical cells	Binary	−	−
Lamprocystis	Spherical cells	Binary	+	+
Lamprobacter	Rods	Binary	+	+
Thiodictyon	Rods	Binary	−	+
Thiopedia	Spherical cells in platelets	Binary	−	+
Amoebobacter	Spherical cells	Binary	−	+
Thiorhodovibrio	Spirilloid cells	Binary	+	−
Ectothiorhodospiraceae[c]				
Ectothiorodospira	Spirilloid to curved cells	Binary	+	+ or −

[a]Modified after Caumette[4] and Overman et al.[5]
[b]Sulfur globules inside the cells.
[c]Sulfur globules outside the cells.

Table 3. Genera and groups of green, brown and filamentous phototrophic bacteria[a]

Group and genus	Morphology	Motility	Gas vacuoles
Green sulfur bacteria[b]			
Chlorobiaceae			
Chlorobium	Straight or curved rods	−	−
Prosthecochloris	Irregular cells with appendages	−	−
Pelodictyon	Straight, curved or ovoid cells	−	+
Ancalochloris	Spherical cells with appendages	−	+
Chloroherpeton	Long flexing rods	Gliding	+
Filamentous green bacteria			
Chloroflexus	Filaments of 30 to 300 μm	Gliding	−
Chloronema	Filaments of 150 to 250 μm	Gliding	+
Oscillochloris	Filaments of a few mm	Gliding	+
Heliothrix	Filaments	Gliding	−
Brown (BChl *g*) phototrophic bacteria			
Heliobacterium	Long rods	Gliding	−
Heliobacillus	Long rods	+	−
Heliospirillum	Spirilloid rods	+	−

[a]Modified after Caumette[4].
[b]Sulfur globules outside the cells.

ment surface in the presence of sufficient light. Most of the blooms of phototrophic bacteria have been observed as colored biomasses, mainly of purple or green sulfur bacteria. In addition to requiring anoxic conditions and photosynthetically active radiation, phototrophic purple and green sulfur bacteria need a suitable electron donor such as hydrogen sulfide. Most of the hydrogen sulfide which accumulates in anoxic layers is of biogenic origin, with the exception of that in sulfur springs and hydrothermal vents. In anoxic sediments hydrogen sulfide is derived mainly from bacterial breakdown of sulfur proteins via fermentation processes or from the anaerobic respiration of sulfate or sulfur by sulfate- or sulfur-reducing bacteria[41]. The latter process can produce more than 95% of the biogenic sulfide found in anoxic layers of sulfate- or sulfur-rich habitats. Based on the turnover of the microbial sulfur cycle – so-called 'sulfureta' – most of these environments are found in shallow coastal marine environments with salinity ranging from brackish to hypersaline. In these environments, the purple and green sulfur bacteria are distributed according to vertical oxygen, sulfide and light gradients.

In coastal anoxic sediments the oxic/anoxic interface (chemocline or redoxcline) is generally found within the first millimeter or centimeter[3,21,37]. The narrow interface between the oxygen and sulfide layers often reveals a transition zone of less than 1 mm, free of both compounds[23], in contrast to stratified lakes, where both compounds can be found in a larger transition layer.

Oxygen in the overlying water column does not usually penetrate sediments deeper than 2 mm, although in sediments covered by cyanobacterial or algal mats it can be detected as deep as 10 mm[20,23]. At greater depths, oxygen is depleted as a consequence both of chemical combination with sulfide and consumption by different heterotrophic and chemotrophic organisms, particularly the colorless sulfur-oxidizing bacteria. In many sediments of shallow water bodies, adequate photosynthetically active radiation reaches depths of 2 to 8 mm[13,22,23]. The blue and green parts of the light spectrum penetrate less deeply than does red and near-infrared light, which is used by phototrophic bacteria. Light penetration into sediments depends on the depth of the overlying water; near-infrared light can only penetrate sediments under very shallow water bodies (less than 50 to 100 cm in depth). In water bodies deeper than 2 to 4 m, only wave lengths between 450 and 550 nm reach the sediment surface; they can be used by phototrophic bacteria which have BChls and some specific carotenoids as light-harvesting pigments.

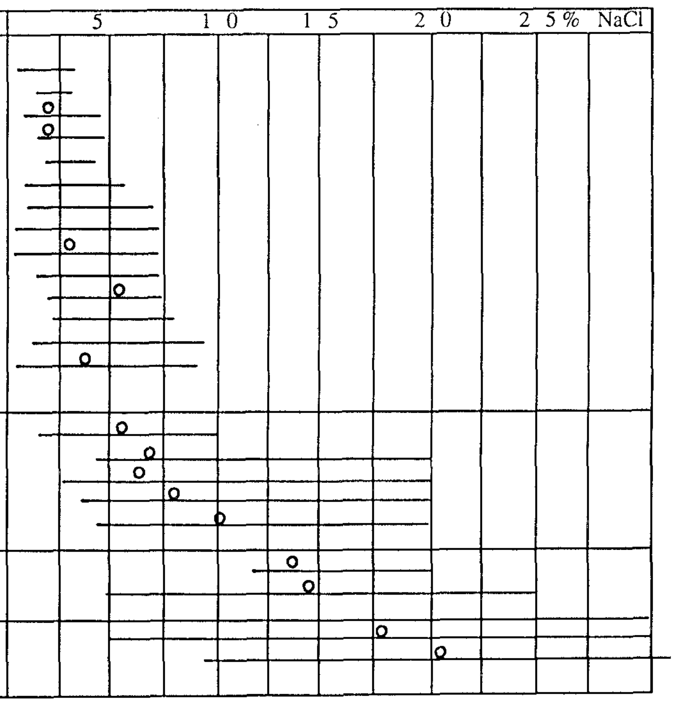
Some phototrophic bacteria found in the marine coastal environments are halotolerant up to 2–4% NaCl, but strictly halophilic purple or green bacteria have frequently been isolated. These generally exhibit optimal growth at salinities between 2 and 5% NaCl and are classed as marine or slightly halophilic bacteria (table 4). They are abundant in the first ponds of marine salterns connected to the sea where the sea water is concentrated to about 6 to 8% NaCl.

In contrast, only a few purple bacteria have so far been isolated from hypersaline habitats; some green sulfur bacteria have been observed[11,15] but not isolated. Most of the purple bacteria isolated from hypersaline ponds in marine salterns are moderately halophilic to halophilic sensu stricto bacteria with optimal growth at salinities between 6 and 11% NaCl (table 4). They belong to the genera *Rhodospirillum*, *Chromatium*, *Thiocapsa* and *Ectothiorhodospira*. The most common organisms isolated so far are *Chromatium salexigens*[6], *Thiocapsa halophila*[7] and *Rhodospirillum salinarum*[28].

Extremely halophilic purple bacteria have most commonly been isolated from alkaline brines in athalassohaline environments such as desert lakes[18,19]. They require about 20 to 25% NaCl for optimal growth. They belong to the family Ectothiorodospiraceae. In these

Table 4. Halophilic phototrophic bacteria grouped according to their salt requirements and classification of halophilic organisms[a]

Bacterial Type	Species
Marine to slightly halophilic (1.5 to 6% NaCl)	*Chromatium buderi* *Chloroherpeton thalassium* *Ectothiorhodospira mobilis* *Rhodobacter sulfidophilus* *Pelodictyon phaeum* *Rhodopseudomonas marina* *Ectothiorhodospira vacuolata* *Prosthecochloris phaeoasteroidea* *Thiorhodovibrio winogradskyi* *Chlorobium chlorovibrioides* *Chromatium purpuratum* *Rhodobacter adriaticus* *Prosthecochloris aestuarii* *Chromatium vinosum HPC* *Lamprobacter modestohalophilus*
Moderately halophilic (3 to 15% NaCl)	*Rhodospirillum mediosalinum* *Rhodospirillum salexigens* *Ectothiorhodospira marismortui* *Thiocapsa halophila* *Chromatium salexigens*
Halophilic *sensu stricto* (9 to 24% NaCl)	*Ectothiorhodospira abdelmalekii* *Rhodospirillum salinarum*
Extremely halophilic (18 to 30% NaCl)	*Ectothiorhodospira halophila* *Ectothiorhodospira halochloris*



[a]O, optimum salinity. Data from Caumette[4]; Caumette et al.[7]; Oren et al.[31] and Overmann et al.[33].

Table 5. Compatible solutes synthetized by different halophilic bacteria grown with 0.5 M or 1.5 M NaCl in the synthetic medium. The uptake of glycine betaine is also indicated (from R. Herbert, unpubl. observ.)

Organism	Salinity	Solutes synthesized	Glycine betaine uptake
Thiocapsa roseopersicina OP1	0.5 M	Sucrose	+
Thiocapsa roseopersicina 5811	0.5 M	Sucrose	+ +
Thiocapsa roseopersicina 5911	0.5 M	Sucrose	+
Thiocapsa halophila SG3202	1.5 M	Betaine Sucrose N-acetyl-glutaminylglutamine amide	+ + + +
Amoebobacter roseus 6611	0.5 M	Sucrose	+ + +
Thiocystis violacea 2311	0.5 M	Sucrose	+
Chromatium minus 1211	0.5 M	Sucrose Betaine	+ + +
Chromatium vinosum D	0.5 M	Sucrose	+
Chromatium NCIMB 8379	1.5 M	Sucrose Betaine	+ + +
Chromatium salexigens SG 3201	1.5 M	Betaine Sucrose N-acetyl-glutaminylglutamine amide	+ + + +
Chlorobium limicola kios 6230	0.5 M	Trehalose	+ + +
Chlorobium vibrioforme 6030	0.5 M	Trehalose	+ +

+ = weak uptake.
+ + = good uptake.
+ + + = very good uptake.

hypersaline environments, phototrophic bacteria control their osmoregulation by synthesis or uptake of compatible solutes that accumulate in their cytoplasm. The most common such solute is glycine-betaine. However, most of the purple and green bacteria are able to accumulate sugars (trehalose or sucrose) and some of them accumulate N-acetylated compounds such as N-acetyl-glutaminyl glutamine amide (table 5).

The extremely halophilic purple bacteria synthesize another type of compatible solute (ectoine) which is an amino acid derivative[40]. The biosynthetic pathway of ectoine in *Ectothiorhodospira halochloris* has recently been identified[34].

The sulfate-reducing bacteria in hypersaline environments

The sulfate-reducing bacteria (SRB) form an ecophysiological group of microbes that share the common property of using sulfate as the main electron acceptor during their anaerobic respiration. They are recognized as strict anaerobes although their activity in the presence of oxygen has recently been observed[12,14]. Most of them are also able to use thiosulfate, sulfite or sulfur as electron acceptors; a few can also use nitrate or fumarate. When they use a sulfur compound as electron acceptor, the final product of their respiration is hydrogen sulfide which is excreted into their environment. They are generally chemoorganotrophs. They use low molecular weight organic compounds such as lactate, pyruvate, ethanol, volatile fatty acids, or H_2 as electron donors. Some sulfate reducers can use higher fatty acids (up to C_{16} or C_{18}), degrading them to CO_2. Others can use alcohols up to C_3, sugars (glucose, fructose) and, in a few cases, particular organic compounds such as indol, phenol or catechol. Organic compounds are also used as carbon sources; only a very few sulfate reducers are autotrophs, using CO_2 as their carbon source. Some can use formate as an electron donor or carbon source in the presence of H_2 and CO_2.

Metabolically the sulfate-reducing bacteria differ by oxidizing completely or incompletely the organic electron donors. Species which perform incomplete oxidation produce low molecular weight fatty acids (mainly acetate) as the end product of their metabolism. The physiology and systematics of sulfate reducing bacteria have been well reviewed and discussed recently[41,84,43,42]. Bacterial sulfate reduction has been reported to occur as an important process in organic matter mineralization in anoxic environments ranging from marine to hypersaline[20,3,24,27,46,25,30]. In the marine environment, most of the sulfate reduction takes place in the anoxic sediment or in bottom anoxic waters of stratified lagoons, and is performed by halotolerant or slightly halophilic sulfate reducers of many different species and genera. The slightly halophilic sulfate reducers have been allotted to the genera *Desulfovibrio*, *Desulfobacter*, *Desulfococcus*, *Desulfosarcina*, *Desulfobacterium* or *Desulfonema* and show optimal growth at salinities ranging from 1 to 4% (table 6).

Only a very few moderately halophilic sulfate reducers have been isolated from different kinds of hypersaline environments including marine salterns. Trüper[39] has isolated a few strains of SRB from hot brines in the Red Sea. One of these tolerated up to 17% NaCl and seems to be similar to *Desulfovibrio halophilus*, a moderately halophilic sulfate reducer recently isolated by Caumette et al.[7] from the hypersaline Solar Lake in Sinai. Cord-Ruwisch et al.[10] isolated several strains of SRB from oil field water containing about 10% NaCl. One of them, a lactate and fatty acid oxidizing strain, has been found to grow slowly in media containing up to 27% NaCl but has not been described in more detail.

Table 6. Grouping of halophilic species of sulfate-reducing bacteria according to the classification of halophilic organisms[40]

	Salinity range (% NaCl)	Salinity optimum (% NaCl)
1. Marine or slightly halophilic species		
Desulfovibrio desulfuricans subsp. *aestuarii*	0.5–6	2.5
Desulfovibrio salexigens	0.5–12	2–4
Desulfovibrio giganteus	0.2–6	2–3
Desulfobacter postgatei	0.5–4	0.7
Desulfobacter latus		2
Desulfobacter curvatus		2
Desulfobacter hydrogenophilus		1
Desulfococcus multivorans		0.5
Desulfococcus niacini		1.5
Desulfosarcina variabilis		1.5
Desulfobacterium autotrophicum		2
Desulfobacterium vacuolatum		2
Desulfobacterium phenolicum		2
Desulfobacterium indolicum		2
Desulfonema limicola		1.5
Desulfonema magnum		2–3
2. Moderately halophilic species		
Desulfovibrio halophilus	3–18	6–7
Desulfohalobium retbaense	3–25	10

Very recently, a second moderately halophilic sulfate reducer has been fully described and characterized as a new species in a new genus *Desulfohalobium retbaense*, by Ollivier et al.[29]. It was isolated from the small hypersaline Retba Lake in Senegal and showed a tendency to thermophily. This species consists of non-sporulating motile straight rods. This species and *Desulfovibrio halophilus* represent the only two moderately halophilic species so far isolated (table 6), although many other halophilic sulfate reducers should exist in hypersaline environments. Both species have a salinity range between 3 and 20% NaCl with an optimal growth at salinities between 6 and 10%. They use a narrow range of organic compounds such as lactate, pyruvate, formate, and also H_2 as electron donors. They are able to use acetate as a carbon source in the presence of H_2 as electron donor. The osmoregulation of these bacteria is not yet well elucidated. Recent experiments suggest that *Desulfovibrio halophilus* cannot synthesize compatible solutes and is able to grow in defined mineral media by accumulating salts in the cytoplasm (Galinski, unpublished observation).

Example of mass bloom developments of phototrophic bacteria in marine salterns

In the marine salterns of Salin-de-Giraud, located on the mediterranean French coast in the Rhone Delta, microbial mats of oxygenic and anoxygenic phototrophic bacteria were observed underneath the gypsum crust in ponds at salinities ranging between 13 and 20%. These mats have been investigated over the last 5 years[6,7,9]. They were composed of cyanobacteria and phototrophic purple bacteria organized in laminated thin layers as shown in figure 1. Above the gypsum crust, there was a brown layer, 2 to 5 mm thick, of unicellular cyanobacteria of the group *Aphanothece* embedded in a mucoid substance. Below the gypsum crust, a green layer, 2 mm thick, of the filamentous cyanobacterium *Phormidium* formed an overlayer above the purple layer of phototrophic bacteria, which was 2 to 4 mm thick and composed mainly of purple sulfur bacteria of the family Chromatiaceae. These mats were very fully developed during the spring and summer seasons.

Recent investigations have shown that the purple sulfur bacteria grow by using sulfide originating from sulfate reduction in the underlying sediment[9]. In the first 5 cm of this sediment sulfate reduction occurs at very high rates; it was calculated from ^{35}S incubations to amount to about 8 $\mu mol \cdot cm^{-3} \cdot day^{-1}$ or 400 $mmol \cdot m^{-2} \cdot day^{-1}$. In the purple layer, sulfide oxidation measured with micro-electrodes[9] was calculated to be about 12 $\mu mol \cdot cm^{-3} \cdot h^{-1}$ in the 3 mm depth of this layer. This value can be estimated at 300 to 380 $mmol \cdot m^{-2} \cdot day^{-1}$ assuming a photosynthetic period of 8–10 hours. From such observations it becomes evident that the sulfide produced is not completely reoxidized by the phototrophic purple bacteria. Cyanobacteria could be involved in the reoxidation, either by producing oxygen

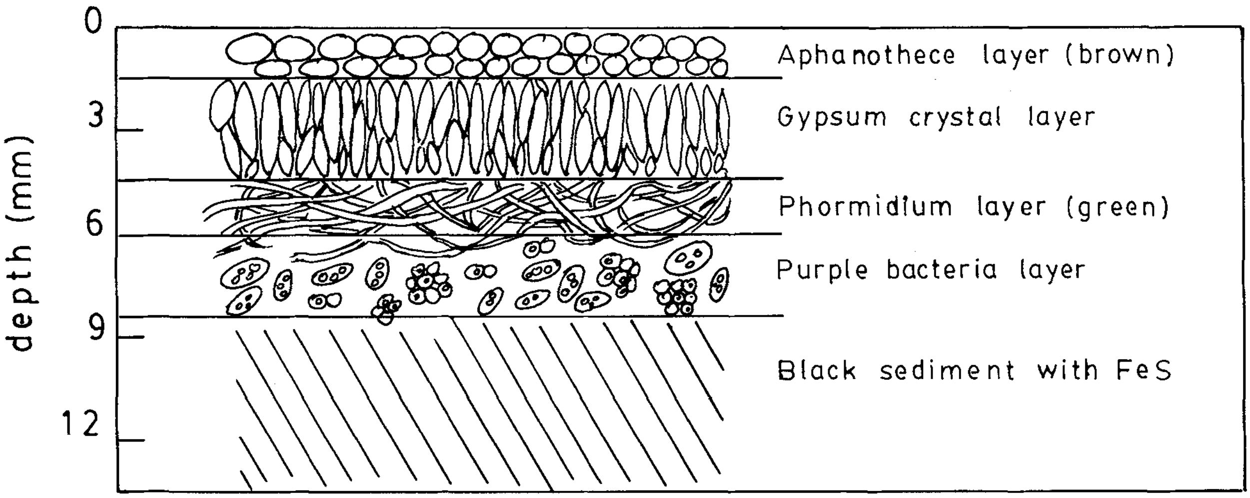


Figure 1. Typical laminated microbial mats observed in hypersaline environments of the marine salterns of Salin-de-Giraud (Rhone Delta, France). These mats occur in hypersaline ponds with salinities ranging from 13% to 20%. Redrawn from Caumette et al.[9]

which chemically reacts with sulfide or by performing an anoxygenic photosynthesis. Microprofiles of oxygen and sulfide in the mats support this observation: during daylight, sulfide was detected deeper (below the purple layer) while during the night until the early morning it was found in the whole mat up to the gypsum crust[9], thus forming an anoxic environment for cyanobacteria. From the purple layer two new species of halophilic bacteria belonging to the family Chromatiaceae were isolated (fig. 2). *Chromatium salexigens*[6] and *Thiocapsa halophila*[8] are able to grow at salinities between 4 and 20% NaCl with optimal growth at 6 to 10% NaCl in synthetic medium. Thus they are well adapted to their environments, where salinities range from 13 to 20% of total salinity. Both organisms are able to use sulfide, sulfate, sulfur or thiosulfate as electron donor and CO_2 as carbon source. They can also use some organic compounds, mainly acetate and pyruvate.

In the mats they can grow by using light wavelengths and intensity that reach the purple layer. During maximum daylight, the light intensity reaching the purple layer was about 460 lux (i.e. 0.1 to 0.5% of PAR at the sediment surface). Both bacteria can grow at such light intensity. Their growth rate at optimum light intensity (1000 lux) is $0.030\ h^{-1}$. It decreases to $0.018\ h^{-1}$ at 460 lux. The bacteria seem to be adapted to low light intensity as they are able to grow at 25 lux with a growth rate of $0.006\ h^{-1}$ [6,8]. As discussed earlier and presented in table 5, both species synthesize or take up compatible solutes for their osmoregulatory processes.

From the sediment of these hypersaline environments a few strains of halophilic *Desulfovibrio* have been isolated (fig. 2). They were very similar to *Desulfovibrio halophilus* strain SL 8903 isolated from the hypersaline solar lake in Sinai[7]. These strains (SG 3802, SG 3805), members of the species *Desulfovibrio halophilus*, have a

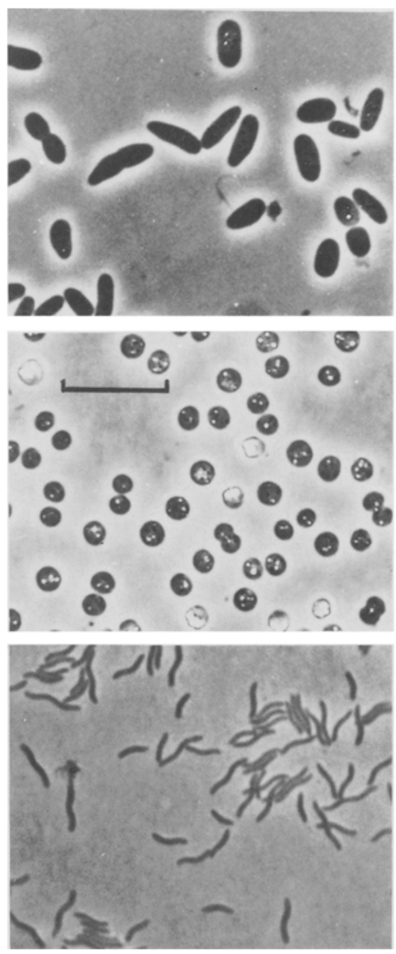


Figure 2. Phototrophic purple bacteria and sulfate reducing bacteria isolated from the laminated microbial mats that occur in the hypersaline ponds of the marine salterns of Salin-de-Giraud (Rhone Delta, France). From top to bottom: *Chromatium salexigens* strain SG 3201; *Thiocapsa halophila* strain SG 3202; *Desulfovibrio halophilus* strain SG3802. Bar indicates 10 µm; all photographs at same magnification.

salinity range from 1 to 17% NaCl and an optimal growth at salinities between 4 and 6% NaCl in synthetic media. Like the purple sulfur bacteria, they are well adapted to the salinity range of the ponds investigated in the marine salterns of Salin-de-Giraud. They use lactate, pyruvate, formate, ethanol, propanol and H_2 as energy sources. They can also use acetate as their carbon source in the presence of H_2, a major compound originating from the fermentation processes that take place in these hypersaline anoxic sediments.
Recent investigations showed that these halophilic sulfate reducers are not able to synthesize compatible solutes and accumulate salt when they are grown in mineral media with lactate as carbon and energy sources (Galinski, unpubl. observ.). Further investigations are in progress to verify if they are able to take up compatible solutes as do the heterotrophic bacteria such as *Enterobacteria*[26]. If this hypothesis is verified, various new halophilic sulfate reducers could be isolated with the help of compatible solutes in the defined culture media.

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