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BACTERIAL COMMUNITIES IN COASTAL LAGOONS. AN OVERVIEW

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COASTAL LAGOONS
MICROGRADIENTS
SULFIDE
HETEROTROPHIC BACTERIA
ANAEROBIC BACTERIA
PHOTOSYNTHETIC BACTERIA
SULFATE-REDUCING BACTERIA

LAGUNES
MICROGRADIENTS
SULFURE
BACTÉRIES HÉTÉROTROPHES
BACTÉRIES ANAÉROBES
BACTÉRIES PHOTOSYNTHÉTIQUES
BACTÉRIES SULFATO-RÉDUCTRICES

ABSTRACT – Coastal lagoons are typical environments found at the interface between continents and seas and are characterised by physical and chemical gradients that are very unstable and sensitive to fluctuating conditions. Along such gradients, diverse bacterial communities should find optimal conditions of growth. Bacteria are distributed according to their metabolic activity and their tolerance to the fluctuating conditions. In the present paper four typical gradients are discussed : gradient of salinity from fresh to marine water, gradient of oxygen and sulfide from oxic to anoxic environment, gradient of light and gradient of organic matter from continental to the marine environment. These parameters have a great impact on the selection of bacteria with diverse metabolisms which are often distributed in stratified layers. It remains to find out if the multiphenotypic potentialities observed along the different gradients in coastal lagoons are characteristic at the level of the bacterial community, the bacterial population or the individual.

RÉSUMÉ – Les lagunes côtières constituent des milieux particuliers à l'interface mer-continent, instables et sensibles aux fluctuations des conditions environnementales de part la présence de gradients physiques et chimiques. Les diverses communautés bactériennes trouvent des conditions de croissance optimales le long de ces gradients. Les bactéries se répartissent en fonction de leurs activités métaboliques et de leur tolérance vis-à-vis des fluctuations des conditions environnementales. Quatre gradients caractéristiques seront abordés ici : le gradient de salinité qui va des eaux douces aux eaux marines, les gradients d'oxygène et sulfure entre les milieux oxygènes et anoxiques, le gradient d'éclairement et, enfin, le gradient de matière organique des milieux continentaux aux milieux marins. Ces gradients influent sur la sélection des bactéries et sur les divers métabolismes bactériens qui le plus souvent se distribuent en couches stratifiées. L'important est de savoir si les potentialités multiphénotypiques observées au travers des différents gradients des lagunes côtières sont caractéristiques des communautés bactériennes, des populations ou bien des individus.

INTRODUCTION

As a consequence of their position between land and sea, coastal lagoons are mainly characterized by large fluctuations of physical and chemical parameters depending on both marine and continental influences. Therefore, bacteriological studies should take into account this variability which greatly affects bacterial community structure and bacterial activity. In coastal lagoons, bacteria are often distributed along physical and chemical gradients horizontally from the continental part to the connection with the sea, and vertically from the air-water interface to the sediment. The major gradients observed in coastal lagoons

are the gradients of salinity, of oxygen and sulfide, of light and of organic material including pollutants. The present paper examines the bacterial communities and their maintenance in coastal lagoons in relation to these gradients.

BACTERIAL COMMUNITIES IN SALINITY GRADIENTS

According to the salinity responses, two major kinds of bacteria occur in coastal lagoons : i) those originating from the marine environment, well adapted to sea water salinity. They generally need salt for growth and are considered as slightly halo-

Lagoons	Authors	A		B	
		NA	MA	NA	MA
Etang de Thau (France)	Troussellier, 1987	$5 \times 10^2 \pm 10^2$	$5 \times 10^4 \pm 10^4$	$5 \times 10^5 \pm 10^5$	$2 \times 10^5 \pm 10^5$
Ebrié lagoon	Carmouze & Caumette, 1985	$6.10^4 \pm 1.10^4$	$2.10^5 \pm 1.10^4$	$9.10^4 \pm 1.10^4$	$3.10^4 \pm 1.10^4$
Venezuela	Lizzaraga-Partida, 1984	$1.2 \times 10^3 \pm 10^3$	$3.5 \times 10^3 \pm 2.10^3$	$4.7 \times 10^3 \pm 3 \times 10^2$	$5.2 \times 10^3 \pm 1.5 \times 10^3$

Table I. – Average numbers of heterotrophic bacteria in some coastal lagoons estimated by bacterial counts of colony forming units in marine or fresh water nutrient media (Numbers of bacteria per ml of sampling water). NA = nutrient agar with fresh water; MA = marine nutrient agar with salt water A = lagoonal part submitted to marine influence; B = lagoonal part submitted to continental influence with fresh water inputs.

philic bacteria; ii) those originating from the continental environment and discharged with fresh water inputs in coastal lagoons. They are halotolerant organisms and are able to grow in a rather large salt range depending on their physiology. They generally tolerate about 5 to 7 % total salinity.

The halophilic or halotolerant bacteria that are exposed to optimal conditions along the salinity gradients grow faster and represent the dominant communities in coastal lagoons. Both kinds of bacteria are adapted to osmotic changes for their maintenance in salinity gradients. We know that for active metabolism, the intracellular environment must remain relatively constant in ionic composition, pH and metabolite levels (Csonka & Hanson, 1991); thus comparative data showed the limits to be similar among most species (Somero, 1986). When intracellular osmotic adaptation is required, most metabolites and inorganic ions can be used to fill the role of osmoregulatory solute (Yancey *et al.*, 1982). Thus, accumulation of specialized osmolytes that are non toxic (compatible solutes) at high concentrations is required. Marine bacteria and halotolerant bacteria are able to accumulate both inorganic and organic compounds as compatible solutes in their cytoplasm.

Hypothetically, the primary osmoregulatory mechanisms were considered as homeostatic control that maintains turgor within a range that can support cell growth (Booth & Higgins, 1990; Epstein, 1986). Self-regulation was postulated to result from the regulation of the intracellular K^+ concentration. It was in addition proposed that the concentration of K^+ is the signal for the other osmoregulatory responses including assimilation of organic solutes (Csonka & Hanson, 1991). K^+ can also be involved in the chemical changes of the cell wall in halophilic bacteria (Bertrand & Larsen, 1989). However, K^+ accumulation must also be regulated by growth rate (Tempest & Meers, 1968) for salinity adaptation that is depending on other physical and chemical factors.

In addition to K^+ accumulation or excretion depending on external osmolarity, bacteria stressed by salinity changes can accumulate a large variety of organic compounds such as aminoacids (glutamate, proline), disaccharides (trehalose, mannosucrose), N-methylated aminoacids (glycine-betaine, proline-betaine...), peptides or other compounds such as ectoine or sulfonium compounds (dimethylsulfoniopropionate). The regulation systems of accumulation of the compounds is very complex and not well elucidated. It depends particularly on their synthesis and/or their transport across the membranes. Only few phototrophic bacteria or chemotrophic bacteria are able to carry out the complete synthesis of such compounds, particularly glycine-betaine, by using carbonate as sole carbon source. In contrast, many heterotrophic halotolerant bacteria originating from fresh water and exposed to brackish or marine conditions can accumulate such compatible solutes if they or their precursors are present in the environment. Thus, these bacteria need permease systems involved in the transport of osmoregulator compounds or their precursors across the membranes. An example is the transport of choline or proline that accumulate in heterotrophic bacteria such as *Escherichia coli* or in photoorganotrophic bacteria. Choline is not an osmolyte itself and is immediately oxidized to glycine-betaine; thus it serves as osmolyte precursor (Abee *et al.*, 1990). Some bacteria can uptake directly osmoregulator compounds such as glycine-betaine, proline-betaine or 3-dimethylsulfoniopropionate by means of specific permease systems.

That many bacteria depend on transport for the accumulation of osmoprotectant implies that these substances should be present in the natural environment of the lagoons. Glycine-betaine, proline-betaine and 3-dimethylsulfoniopropionate are synthesized by cyanobacteria or algae and are found in fresh or salt waters as a result of excretion or leakage from the producing organisms (Oren, 1990). Glycine-betaine has been detected in marine and brackish sediments (Breitmayer & Gauthier, 1990). This compound is also found in

several marine animals living in brackish lagoons, where it plays the role of osmoprotectant and is continuously excreted with urine. Therefore when discharged into the brackish lagoons, bacteria of continental origin able to accumulate such osmoprotectants will be able to tolerate the brackish environments of the lagoons. This is also the case for enteric contaminants such as enterobacteria (*Escherichia coli*, *Salmonella*...) that are transported into the lagoons with polluted sewage. The survival of these bacteria is enhanced in marine or brackish sediments where they can use glycine-betaine or its precursor (choline) as osmoprotectant (Munro *et al.*, 1989). In the anoxic environment of lagoon sediments, they are also stimulated by high organic matter contents and well protected against predatory processes. Therefore, these bacteria occur in relatively high numbers, particularly in sediment, in many coastal lagoons that receive polluted discharges from urban sewages (Baleux *et al.*, 1988; Montfort and Baleux, 1991; Lanusse, 1987). They increase the size of the halotolerant bacterial community that lives along salinity gradients in the brackish environment of coastal lagoons.

The ratio between both marine and continental bacterial communities varies according to the salinity gradient. Often the numbers of heterotrophic aerobic bacteria that grow in culture medium with low NaCl were compared to those enumerated in marine culture media. The results showed a very strong difference between sites submitted to marine influence and those submitted to continental influence (Table I).

Many bacteria of continental or enteric origin able to survive in the brackish environment of coastal lagoons through the utilisation of osmoprotectants cannot grow again in selective media. It has been demonstrated that organisms submitted to brackish or marine conditions obtain a strong resistance and remain capable of metabolic activity after months of starvation in marine water but this can only be detected by means of fluorescence and immuno-fluorescence microscopy (Brayton *et al.*, 1986; Grimes & Colwell, 1986; Elliot & Colwell, 1985; Xu *et al.*, 1982). Survival or in some cases growth of halotolerant contaminants or pathogens in coastal lagoons is a very important problem for protection and pollution monitoring of such coastal lagoon environments often devoted to human activities (bathing, aquaculture...). Today, much scientific effort is devoted to this field of research, especially to gain insights into the molecular basis of osmoregulation processes and the resistance of halotolerant organisms (including pathogens) in the marine environment after long starvation phases (Matin, 1991; Kolter, 1992).

Some coastal lagoons without fresh water inputs have evaporitic zones with increasing salinity

(25-35 %) and salt deposition. These environments are habitats for moderate to extreme halophilic micro-organisms. Many of them are archaeobacteria belonging to the Family *Halobacteriaceae* (Tindall & Trüper, 1986); others are halophilic eubacteria either aerobic (some *Vibrio* and *Pseudomonas*) or anaerobic (*Haloanaerobiaceae*, few anoxygenic phototrophic bacteria). The *Halobacteriaceae* possess specific membranes that make them particularly well adapted to osmotic stress. The extreme halophilic eubacteria are able to synthesize organic osmoprotectants as compatible solutes (trehalose, glycine-betaine, ectoine..., Trüper & Galinski, 1986).

Another feature of some coastal lagoons is the vertical gradient of salinity that induces stratification through the water column (Caumette, 1989). A halocline is formed between an upper layer containing waters of lower salinity and a deeper layer more dense with waters of higher salinity. Exchanges between both layers are rather limited and subsequently the deeper waters are more confined and generally anoxic. In this case, the vertical distribution of bacteria depends not only on the salinity gradient but also and mainly to the chemical gradients induced by stratification (Caumette, 1987; Caumette *et al.*, 1983), particularly oxygen and sulfide gradients.

BACTERIA COMMUNITIES IN OXYGEN AND SULFIDE GRADIENTS

In lagoons of sufficient water depth to be stratified, upper oxic waters and deeper anoxic waters occur frequently. Such coastal lagoons are called meromictic or monomictic according to their periods of stratification (Caumette, 1989). In the anoxic layers large amounts of hydrogen sulfide can be found. Sulfate reduction is a major mineralization pathway in anoxic marine environments (Jorgensen, 1990) and accounts for more than 95 % of the sulfide stored in the anoxic layers as a result of the anaerobic respiration of sulfate (Jorgensen, 1983). The hydrogen sulfide produced contributes to the maintenance of anoxic and reduced conditions but has a toxic effect on strictly aerobic bacteria, plants and animals living in the lagoons.

Recently, sulfate-reducing bacteria were found to be capable not only of sulfate reduction, but also of fermentation of inorganic sulfur compounds using the so-called disproportionation process (Bak & Cypionka, 1987), and even of chemolithotrophic growth by this process or the possession of an aerobic heterotrophic metabolism (Dilling & Cypionka, 1990). Although these bacteria grow better by using anoxic sulfate respiration, their metabolic flexibility makes them very

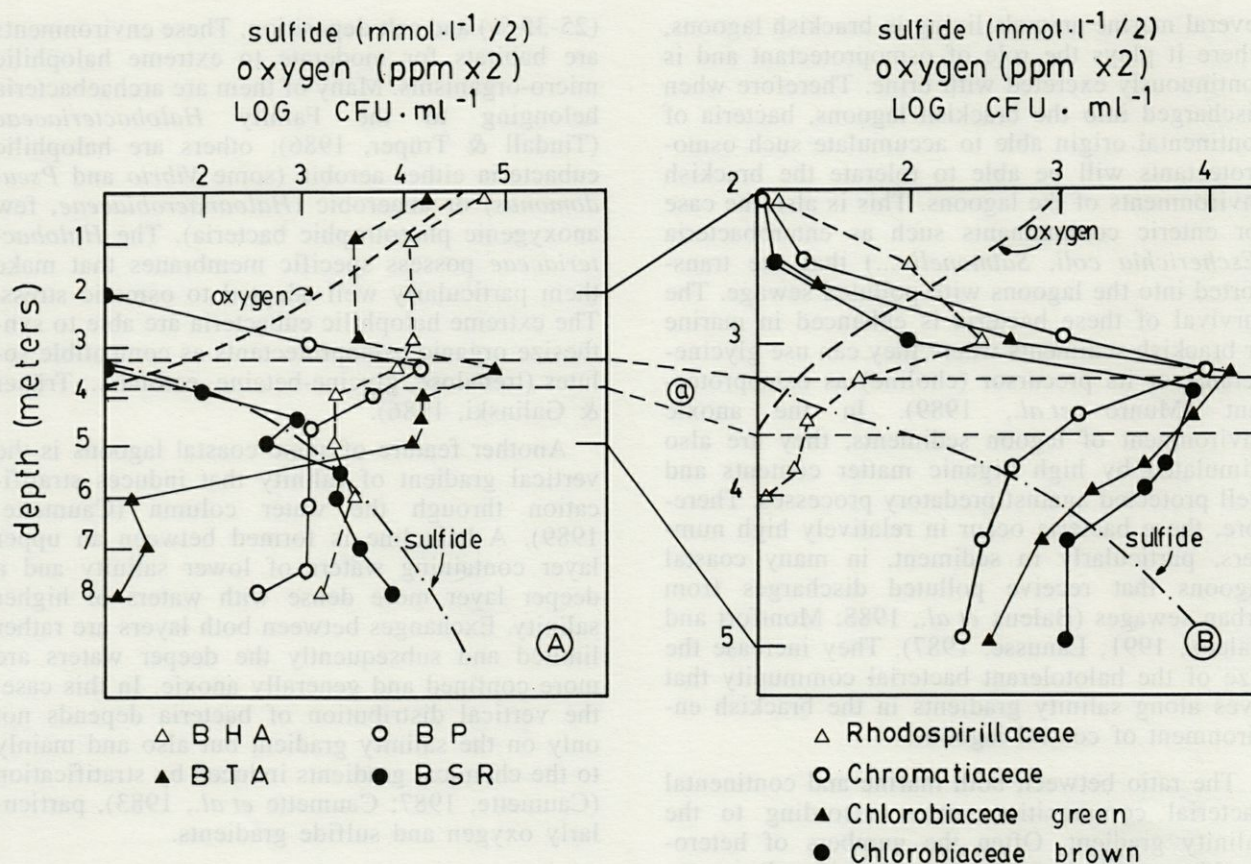


Fig. 1. - Vertical profiles of oxygen, sulfide and different bacterial populations in the water column of the stratified tropical coastal lagoon of Ebrié (Ivory Coast). Redrawn from Caumette (1987).

BHA = aerobic heterotrophic bacteria; BP = anoxygenic phototrophic bacteria; BTA = colorless sulfur oxidizing bacteria; BSR = sulfate-reducing bacteria. @ = layer between 3.2 m and 3.7 m depth where oxygen and sulfide coexist in panel B: larger magnification of stratification with distribution of the different families of purple (*Rhodospirillaceae*, *Chromatiaceae*) and green (*Chlorobiaceae*) anoxygenic phototrophic bacteria.

well adapted to the fluctuating oxygen-sulfide gradients and environmental conditions in coastal lagoons. They were found to be relatively more abundant at the interface between oxic and anoxic conditions, within microgradients of oxygen and sulfide. They play a very active role in the sulfur cycle in coexistence with sulfur-oxidizing bacteria.

In stratified waters, gradients of oxygen and sulfide co-exist in a narrow zone of generally less than 1 m. Within this layer, abundant communities of sulfur bacteria live and interact by metabolic processes based on the oxidation and the reduction of sulfur. The colorless sulfur oxidizing bacteria often form dense communities that grow by using sulfide mainly originating from sulfate reduction in the deeper anoxic layer and oxygen present in the upper layer (Fig. 1).

Most of them belong to the genus *Thiobacillus* (Caumette *et al.*, 1983). However many other morphologically remarkable sulfur oxidizing bacteria can densely populate this interface. They generally belong to the genera *Thiovolum* or *Thiomicrospira*.

The combination of high oxygen and low sulfide concentrations generally favor the growth of *Thiobacillus* spp, whereas the opposite situation, i.e. low oxygen and high sulfide, support growth of *Thiomicrospira* spp. (Kuenen *et al.*, 1985; Kuenen, 1989; Visscher, 1991). However, in the absence of oxygen some chemotrophic sulfur-oxidizing bacteria are able to use other electron acceptors such as manganese, iron oxides or nitrate (Jorgensen, 1987; Sorensen & Jorgensen, 1987) and consequently are active in the anoxic layer of stratified lagoons.

In addition to such dense communities of colorless sulphur bacteria, purple or green sulfur bacteria often show massive grow and form colored layers due to their bacteriochlorophylls and carotenoids (Caumette & Matheron, 1989). They generally occur at the upperpart of the anoxic layer and grow by using sulfide or reduced sulfur compounds as electron donors for their anoxygenic photosynthesis. Typical examples are Lake Faro at Messina, Sicily (Trüper & Genovese, 1968), Lake Mogil'noe, USSR (Gorlenko *et al.*, 1978), Ebrie Lagoon, Ivory Coast (Caumette,

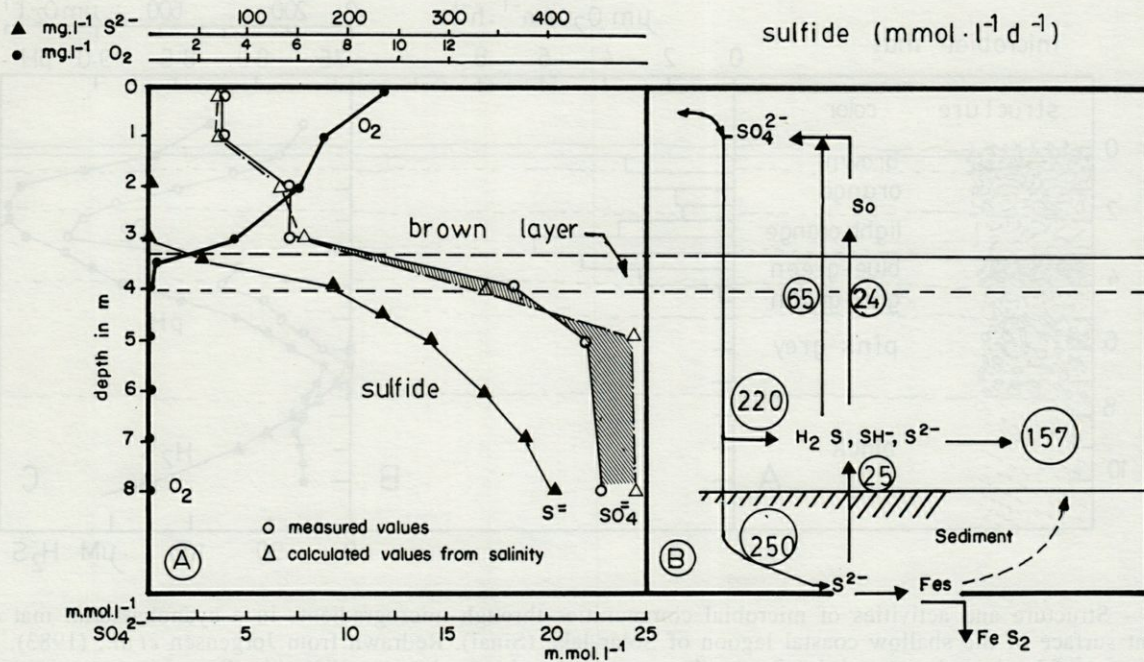


Fig. 2. - Activities of sulfur bacteria in the water column of the stratified tropical coastal lagoon of Ebrié (Ivory coast). Redrawn from Caumette (1987). Brown layer of anoxygenic phototrophic bacteria between 3.2 and 4 m depth. Numbers in open circles represent the production or the oxidation of sulfide calculated in $mmol.m^{-2}.d^{-1}$.

1984) and some other lagoons listed in Table 2. In these lagoons, the blooms of phototrophic bacteria occur almost permanently throughout the year at the interface between the stagnant anoxic and sulfide-containing sea water and the oxie less salty overlying water. The dominant species of these colored blooms mainly belong to genera *Chlorobium*, *Pelodictyon* and in smaller numbers *Chromatium* or *Thiocapsa*. They use reduced sulfur compounds originating from sulfate reduction in the deeper layer and compete at the oxic-anoxic interface with chemotrophic sulfur bacteria. They prevent the diffusion of such reduced compounds up to the overlying oxic layers by oxidizing them to sulfate (Fig. 2).

In shallow coastal lagoons with a water column no deeper than about 2 m, the water is almost completely mixed and mostly brackish. In these lagoons, the interface between oxic and anoxic layers occurs mainly at the water-sediment interface where micro-gradients of oxygen and sulfide can only be detected by use of micro-electrodes. Over the past ten years microsensors and micro-electrodes have been developed and used for benthic ecosystems in microbial ecology (Revsbech & Jorgensen, 1986; Stal *et al.*, 1985; Van Gemerden *et al.*, 1989). Many observations reported in the literature demonstrate that oxygen and sulfide microgradients occur together within the first few mm of the sediment (Jorgensen, 1982; 1983; Revsbech *et al.*, 1989; Revsbech, 1989; Revsbech & Jorgensen, 1986). Oxygen residing in the overlying water column usually does

not penetrate sediments of coastal lagoons deeper than 2 mm, although in sediment covered by cyanobacterial or algal mats it can be detected as deep as 10 mm (Jorgensen, 1982; Jorgensen & Des Marais, 1986).

Below in the anoxic sediment, sulfate-reducing bacteria are the dominant organisms and contribute greatly to the mineralization of organic compounds and to the production of hydrogen sulfide. Maximum sulfate reduction generally occurs between 5 and 10 cm in the sediment (Jorgensen, 1978; Caumette, 1986; Marty *et al.*, 1990; Hines *et al.*, 1991). Among the sulfate-reducing bacteria isolated from the sediments of coastal lagoons, the genera *Desulfovibrio* and *Desulfobacter* are dominant. The bacteria belonging to the genus *Desulfovibrio* have the possibility to grow by using different substrates such as lactate, pyruvate, ethanol... and also hydrogen as electron donors but they cannot carry out a complete oxidation of substrates. *Desulfobacter* spp. are able to completely oxidize low molecular organic compounds, especially acetate, to CO_2 (Widdel, 1988). During the mineralization of organic matter, there bacteria produce large quantities of H_2S thus contributing to increasing anoxic conditions and negative redox potential.

Sulfide is used at the oxic/anoxic interface by sulfur oxidizing bacteria, with are mainly colorless like *Thiobacillus* or gliding organisms. The latter which belong to the genera *Beggiatoa* or *Thiothrix*, are very common at the sediment surface of coastal lagoons. They move through the

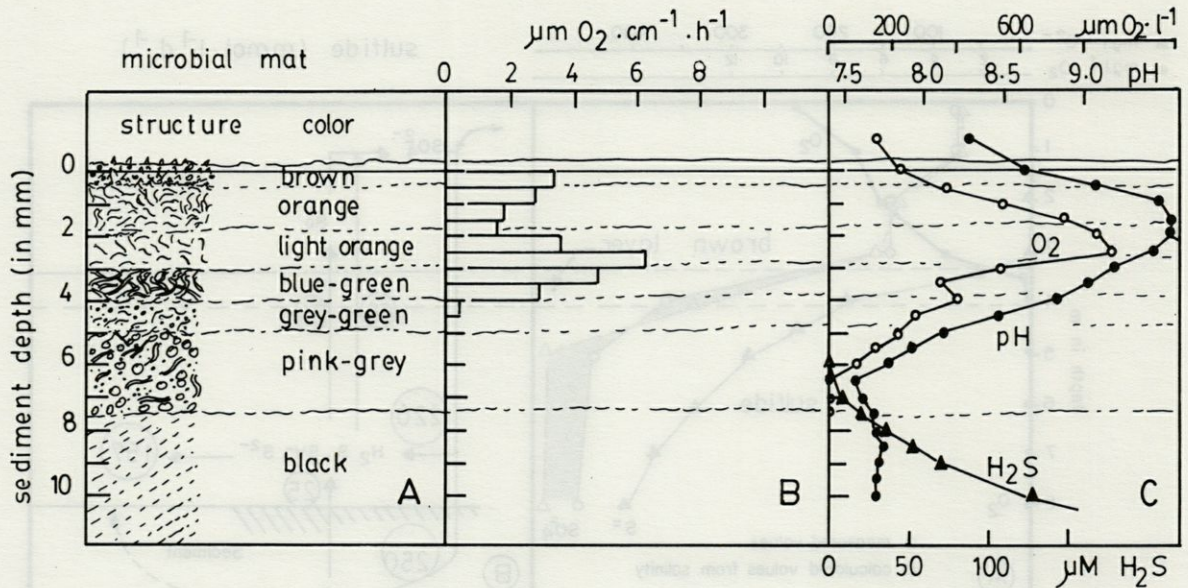


Fig. 3. - Structure and activities of microbial communities through microgradients in a cyanobacterial mat at the sediment surface of the shallow coastal lagoon of Solar lake (Sinai). Redrawn from Jorgensen *et al.*, (1983). *Panel A*: Structure of laminated mat and dominant micro-organisms: brown layer = *Nitzschia*, *Synechococcus*; orange and light orange layers: *Phormidium* and *chloroflexus*; blue-green layer = *Microcoleus*; grey-green layer = *Phormidium*; pink-grey layer = *Microcoleus* and anoxygenic purple phototrophic bacteria; black layer = sediment with iron sulfide; *Panel B*: Oxygenic photosynthesis measured by oxygen micro-probes; *Panel C*: Micro profiles of oxygen, pH and sulfide measured by micro-electrodes, directly in the mat.

sediment by gliding and consequently can find the best zone for their metabolic activity, i.e. the narrow interface where oxygen and sulfide coexist. They often proliferate and form chemotrophic microbial white mats. In many coastal lagoons these bacteria are not involved alone in the formation of mats but co-exist with dense populations of cyanobacteria, purple and green sulfur bacteria in colored laminated bacterial mats. All these organisms interact and compete to maximize their exploitation of oxygen, sulfide and light at the sediment surface. Within this so-called *sulfuretum* the micro-organisms are mostly motile. They constantly move around throughout the diurnal cycle in the few mm of the uppermost part of the sediment as evidenced in some studies of brackish sediments in the coastal zone of Denmark (Jorgensen, 1982). Generally along the micro-gradients, the oxygenic phototrophs (cyanobacteria, diatoms) are distributed in the uppermost part of the mat and produce O_2 which partly diffuses to in the underlying sediment. Below, this layer, a white layer of colorless sulfur bacteria is generally observed at the interface between oxygen and sulfide, whereas purple or green phototrophic bacteria occur in the lower part of the mat, i.e. in the upper sulfide zone (Fig. 3). Such laminated mats were observed in many shallow coastal brackish and hypersaline lagoons throughout the world (Pierson *et al.*, 1987; D'amelio *et al.*, 1989; Caumette *et al.*, 1991; Jorgensen & Des Marais, 1986). However, according to the

diurnal cycle and the light regime, oxygen and sulfide microgradients vary and the oxic/anoxic interface is found more or less deep in the sediment, as a consequence of photosynthetic activities. Consequently colorless sulfur bacteria and anoxygenic phototrophic bacteria change: during maximum daylight the organisms are stratified as described above, but during the night, the motile purple bacteria move up, above the colorless and the oxygenic phototrophs, on top of the mat and continue to grow by using their facultative chemotrophic metabolism. Thus, they, prevent the diffusion of toxic sulfide produced at deep to the overlying water column in the shallow lagoons.

However, in some eutrophic coastal lagoons, waters typically turn anoxic during warm summers after the decay of blooming algae. A very typical example is Prevost lagoon in the French mediterranean coast (Caumette, 1986). In this lagoon, during warm summer, dystrophic crises occur with anoxic waters rich in sulfide originating from sediment sulfide production. During this period, plants and animals die and a part of H_2S together with organic sulfur compounds such as D.M.S., are released to the atmosphere. If this situation occurs for a long period, the water column turns pink to purple-red due to blooms of phototrophic sulfur bacteria. They oxidize reduced sulfur compounds to sulfate thus removing toxic products from lagoon waters. During the rest of the year, the various kinds of purple bacteria thrive and survive

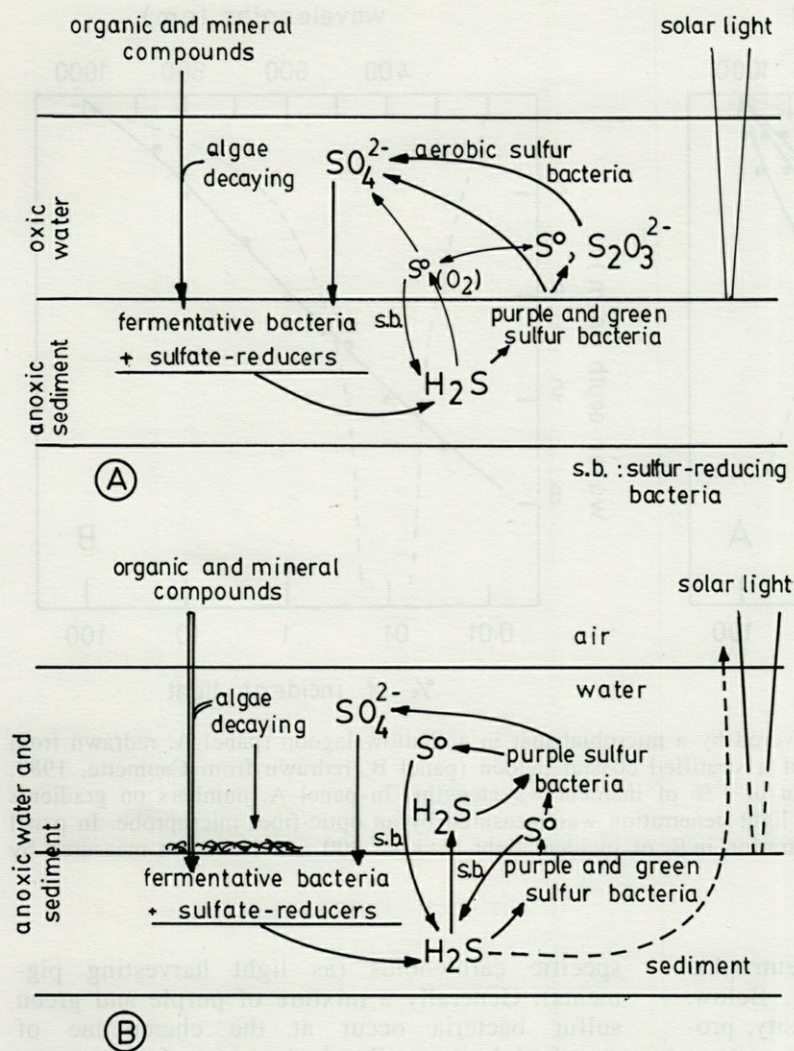


Fig. 4. - Scheme of sulfur bacteria activities through biodegradation processes of organic matter in the shallow coastal lagoon of Prevost (France). Redrawn from Caumette (1987). A, typical bacterial processes in the shallow lagoon with oxic water column and anoxic sediment. B, bacterial processes during dystrophic crises in the summertime with anoxia of the whole water column.

in the upper sediment layers (Fig. 4). The phototrophic bacteria in these shallow lagoons are represented by a number of species which are quite characteristic for this type of environment: *Thiocapsa roseopersicina*, *Thiocapsa pfennigii*, *Amoebobacter pendens*, *Chromatium vinosum*, *C. gracile*, *Thiocystis violacea* and as minor components *Chromatium buderi* and the green sulfur bacteria *Chlorobium vibrioforme* and *Prosthecochloris aestuarii* (Pfennig, 1989; Caumette, 1986; Trüper, 1970; Matheron & Baulaigue, 1972; Pierson *et al.*, 1987; Nicholson, *et al.*, 1987). In hypersaline coastal lagoons, the major representatives, isolated to date are *Chromatium salexigens* (Caumette *et al.*, 1988) and *Thiocapsa halophila* (Caumette *et al.*, 1991). *Thiocapsa*, *Thiopedia* and *Ectothiorhodospira* can also be found in microbial mats in the coastal environment (Stal *et al.*, 1985). Most of these species are facultatively chemotrophs, and tolerate wide and rapid variations of light intensity, temperature and salt concentrations which make them very well adapted to coastal lagoon environments.

BACTERIAL COMMUNITIES ALONG LIGHT GRADIENTS

Light penetrates water bodies according to their transparency which depends on the suspended particulate matter loads. Suspended particles cause scattering and a reduction in light transmission. This has been particularly observed in very productive and eutrophic lakes and coastal lagoons (Wetzel, 1975). Depending on the density of particulate suspensions and on phytoplankton production, light penetrates, to a greater or lesser extent in the water column of coastal lagoons. In many eutrophic coastal lagoons, the 1% of light intensity occurs between 2 and 4 m depth. In addition, most of the light spectrum is absorbed in the first 4 m and only wavelengths between 450 and 550 nm reach the deeper layers (Fig. 5).

Therefore phototrophic micro-organisms are distributed in the water column according to this light gradient. It is known that phytoplankton including cyanobacteria grow in the upper photic

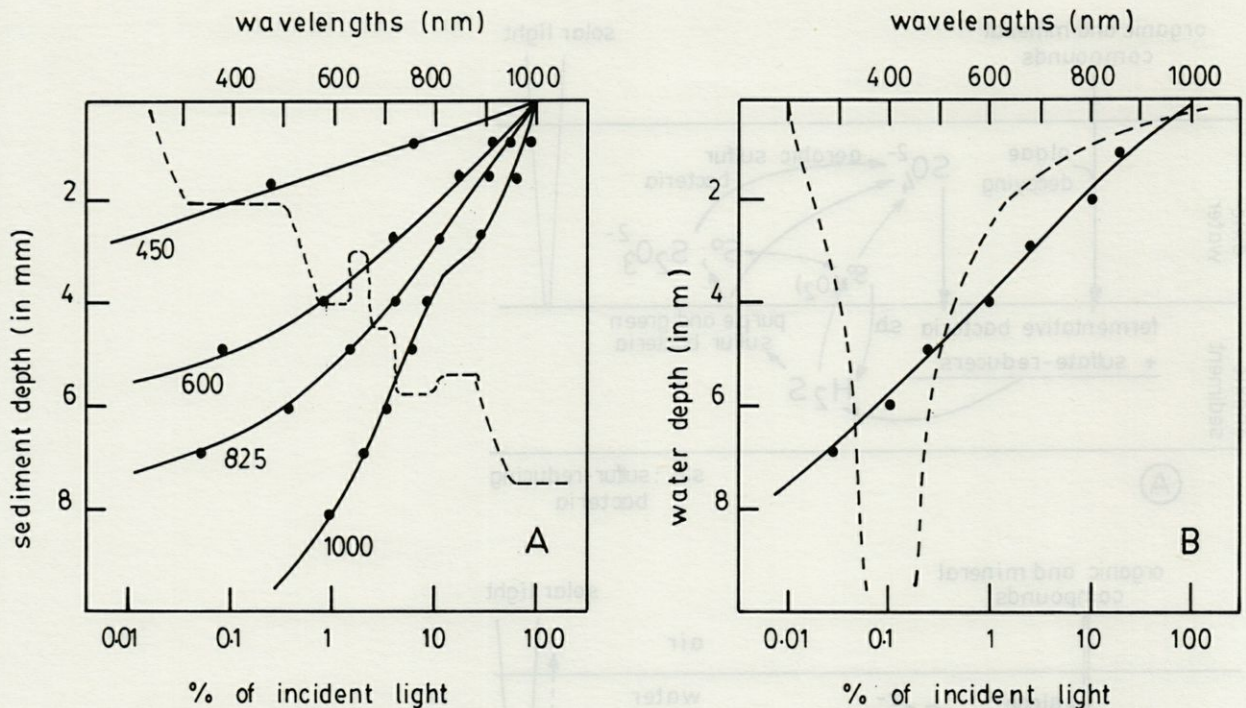


Fig. 5. — Light penetration in a sediment covered by a microbial mat in a shallow lagoon (panel A, redrawn from Jorgensen, 1989) and in the water column of a stratified coastal lagoon (panel B, redrawn from Caumette, 1987, 1989). Dashed lines represent the penetration of 1% of incident wavelengths. In panel A, numbers on gradients indicate the wavelengths in nm at which the light penetration was measured by an optic-fiber microprobe. In panel B, the gradient indicates the total light penetration in % of incident light between 300 and 1 000 nm measured by a submerged photoelectric cell.

zone, between 1 and 3 m depth in eutrophic coastal lagoons (Caumette *et al.*, 1983). Below, this zone at the level of 1% light intensity, production equals respiration and in deeper waters, respiration is the dominant process, i.e. photosynthesis and phytoplankton growth are inhibited by insufficient light intensity and inadequate wavelengths.

In deeper meromictic or holomictic coastal lagoons, light often reaches the interface between upper oxic and lower anoxic waters. Therefore various kinds of phototrophic sulfur bacteria can grow in the uppermost part of the anoxic layer according to the wavelengths and light intensity that penetrate to this level.

In the stratified lagoons that are listed in Table 2, the phototrophic bacteria that develop at the chemocline depend on the gradients of light. Purple sulfur bacteria need relatively more light intensity for growth than green or brown sulfur bacteria. However both kinds of bacteria grow at a light intensity of about 1–5% of solar light, and some green and brown sulfur bacteria are efficient at only 0.01% of incident light levels. They are usually dominant in deeper stratified waters reached by very low light intensities where they use wavelengths of 450 to 550 nm by means of

specific carotenoids (as light harvesting pigments). Generally a mixture of purple and green sulfur bacteria occur at the chemocline of stratified lagoons. Purple bacteria of the genera *Chromatium*, *Thiocapsa*, *Thiopedia* or *Lamprocystis* are most commonly isolated. They frequently grow by forming a dense layer above green and brown bacteria belonging to the genera *Chlorobium* or *Pelodictyon* (Caumette, 1989; Caumette & Matheron, 1989; Pfennig, 1988). Thus, they are stratified according not only to light but also to oxygen and sulfide gradients. Green bacteria tolerate higher sulfide concentrations and grow at lower light intensities than purple bacteria; they consequently are able to develop below purple bacteria in stratified water bodies by using the remaining available wavelengths.

Similar observations can be made at the sediment surface of shallow coastal lagoons. Since these lagoons are never much deeper than about 2 or 3 m, sufficient radiation penetrates to the bottom. They are thus characterized by a very high benthic photosynthetic production enhanced by organic and mineral enrichment. At the sediment surface, therefore, benthic cyanobacteria or eucaryotic photosynthetic organisms often form microbial mats and use adequate wavelengths that reach the sediment surface. However, a part of the

Table II. – Main typical examples of blooms of phototrophic bacteria in coastal lagoons with formation of colored waters.

Authors	Lagoon	Water color	Major phototrophic bacteria
Shallow lagoons			
Forti, 1938	Lago di Sangue (Sicily)	red	<i>Thiopedia, Thiocapsa</i>
Deveze & Fauvel, 1966	Etang de l'Ingril (France)	red	<i>Rhodospseudomonas</i>
Heldt, 1952	Lagune de Tunis (Tunisia)	red-violet	<i>Chromatium</i>
Gietsen, 1931	Lagoon of Danish coast	red	<i>Lamprocystis, Thiopedia</i>
Utermöhl, 1925	Drecker lagoon (Danmark)	red	<i>Chromatium, Thiopedia</i>
Caumette, 1986	Prevost lagoon	rose-red	<i>Thiocapsa, Chromatium</i>
Deeper stratified lagoons			
Hatzikakidis, 1952	Messolonghi lagoon (Greece)	red	not reported
Trüper and Genovese, 1968	Lago Faro (Sicily)	red	<i>Chromatium Chlorobium</i>
Gorlenko <i>et al.</i> , 1978	Mogilnoye lagoon (CEI)	brown	<i>Chlorobium Pelodictyon</i> <i>Prosthecochloris</i>
Caumette, 1984	Bietry Bay (Ivory coast)	brown	<i>Chlorobium Pelodictyon</i> <i>Chromatium</i>
Guerrero <i>et al.</i> , 1987	Cullera Remolar (Spain)	brown	<i>Chlorobium</i>

solar light spectrum penetrates deeper into the sediment. In the very shallow coastal lagoons with a water column of 0.50 to 1 m depth, near infrared light reaches depths of 2 to 8 mm in the anoxic sediment (Jorgensen & Des Marais, 1986). Consequently, anoxygenic phototrophic bacteria mainly of the genus *Chromatium* can grow underneath cyanobacterial mats by using adequate wavelengths (800 nm) that penetrate deeper (Fig. 5). In multilayered microbial mats almost all the light spectrum can be efficiently used by many kinds of phototrophic organisms. The mats consist of vertically laminated benthic phototrophic communities and do not exceed 5-10 mm in thickness. The cyanobacteria or filamentous algae on top of the mats form a filamentous layer that has a high sediment binding capacity and protects sediments against erosion. Below these layers of chlorophyll *a* containing organisms, diverse microlayers with characteristic colors of pink, purple or green and brown, are composed of phototrophic sulfur bacteria containing bacteriochlorophylls *a*, *b*, *c*, *d*, or *e*. Micro-analysis of light penetrating these layers using fiber optic microprobes (Jorgensen & Des Marais, 1986) show that under the cyanobacterial mat, the intensity of radiation below 700 nm are too low to support oxygenic photosynthesis, but radiation above 700 nm and particularly 1000 nm are still available for anoxygenic phototrophic bacteria that use different wavelengths depending on their bacteriochlorophylls: *a* (800-850 nm), *b* (above 1000 nm), *c* (750 nm), *d* (725-750 nm), *e* (710-730 nm). Consequently, light penetration in the sediment selects for various phototrophic organisms that live in microgradients of oxygen, sulfide and light. As for stratified lagoons the purple bacteria live above the green bacteria in a layer with higher light intensity and co-existence of oxygen and sulfide. These facultative anaerobic

purple phototrophs protect the strictly anaerobic sulfide dependent green bacteria against oxygen (Pfennig, 1989). In contrast to stratified waters where these bacteria densely populate a layer of about 1 m in thickness, in sediment they occur in a very narrow zone of about 5 to 10 mm.

BACTERIAL COMMUNITIES IN ORGANIC MATTER GRADIENTS

Two pools of organic matter occur in coastal lagoons: one originating from polluted continental inputs and discharged in the coastal environment; one coming from *in situ* production in the photic zone as a result of the recycling of mineral nutrients. However only a part of the organic matter is mineralized via aerobic processes. It represents generally less or about 50 % of the total organic matter. Because of the low water depth in coastal lagoons, a large part of organic matter reaches the anoxic layers.

Through organic matter gradients, the distribution of bacteria depends not only on the quantity and the quality of particulate and dissolved organic matter but also on the concentration of dissolved oxygen. In zones containing high amounts of organic matter, the respiratory processes of aerobic heterotrophic bacteria lead to oxygen depletion. Consequently organic rich layers in coastal lagoons are often anoxic. This is true not only for sediments and deeper water in stratified lagoons but also for sewage waters coming into the lagoon and for organic particles. In sewage waters, the oxygen tension is very low as a consequence of low primary production and high respiratory processes of mineralization. This oxygen tension increases again in the lagoon water when

organic matter is partly mineralized to nutrients that enhance the photosynthetic production of oxygen. Organic particles are also often anoxic. At the surface of the particle (interface particle-water), a very thin bacterial biofilm of aerobic heterotrophic bacteria produces dissolved organic compounds and nutrients from the mineralization processes but consumes oxygen and prevents its diffusion deeper into the organic particle. Consequently anoxic conditions often prevail inside and allow the growth of anaerobic heterotrophic bacteria by fermentative or anaerobic respiratory metabolism, such as sulfate reduction or methanogenesis. These bacteria contribute to the production of reduced compounds (H_2 , N_2 , H_2S , CH_4) inside the anoxic microniches restricted to organic particles of small size that transit in a fully oxic environment. In coastal lagoons most of the organic particles originate from sediment resuspension.

The organic matter that reaches the anoxic sediment or the deeper anoxic waters in stratified coastal lagoons is mineralized via successive anaerobic metabolisms. From these anoxic layers

about 90 % of the organic detritus then recycled in the overlying oxic water after mineralization (Jorgensen, 1983). For anaerobic mineralization to occur, various kinds of anaerobic bacteria coexist within the first cm of the anoxic sediment or just below the interface in stratified lagoons. Fermentative bacteria are able to degrade macromolecules and produce a series of intermediary metabolites, mainly H_2 , low molecular weight fatty acids (lactate, acetate, propionate) and alcohols. These compounds serve as substrate for various anaerobic bacteria such as nitrate-reducing bacteria, sulfate-reducing bacteria or methanogenic bacteria that carry out a complete oxidation of organic matter. They all contribute together to the total mineralization of organic matter in the anoxic zones of coastal lagoons. Jorgensen (1983) calculated that about 50 % of the organic matter in the coastal environment is mineralized via sulfate reduction processes. Among the anaerobic respiration processes occurring in coastal lagoons, denitrification is often limited by the availability of nitrate (Marty *et al.*, 1990) whereas sulfate reduction is always enhanced by the large amounts of sulfate

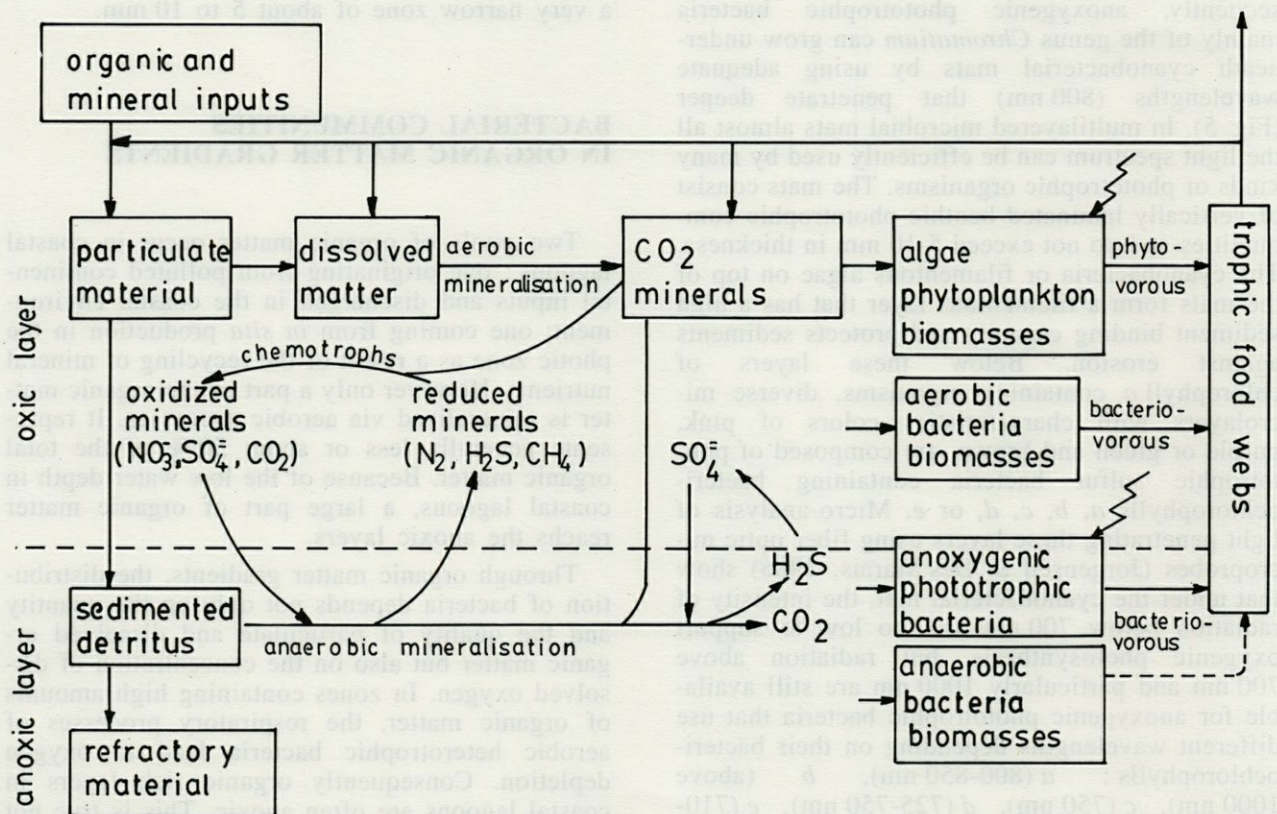


Fig. 6. - General scheme of the role of bacteria in the carbon cycle of a coastal lagoon.

In the oxic layer, aerobic mineralization is carried out by aerobic heterotrophic bacteria that produce nutrients and mineral for algae, phytoplankton and chemotrophic bacteria. In the anoxic layer, anaerobic mineralization is carried out by a series of fermentative and anaerobic oxidative bacteria that involve oxidized mineral compounds, particularly sulfate used by sulfate-reducing bacteria. Anoxygenic phototrophic bacteria grow if light reaches the anoxic layer. All bacterial biomasses contribute to the trophic food webs.

originating from sea water (20-25 mM). In contrast, methanogenesis is generally about quite negligible in the coastal environment (Marty *et al.*, 1990) and little is known about the other forms of respiration such as iron or manganese reduction. The methanogenic bacteria were found to play, however, an important role in the mineralization of some specific organic products such as osmoprotectants. In the anoxic layers of coastal lagoons, glycine-betaine is fermented to methylamines (mono, di or trimethylamines) as end products. Some marine methanogens (such as *Methanosarcina*) oxidize preferentially methylamine to methane, carbon dioxide and ammonia (Marty *et al.*, 1990).

CONCLUSION

Along the different physical and chemical gradients that occur in coastal lagoons, both halophilic and halotolerant heterotrophic bacteria play a very important role in the mineralization of organic matter. Due to the large amounts of organic matter in the lagoons, they are consequently responsible for the oxygen depletion in the sediment of shallow lagoons or in the aphotic zone of deeper stratified lagoons.

Therefore, various kinds of aerobic and anaerobic bacteria act together in the mineralization of organic matter. They produce large amounts of CO₂ but also different reduced compounds that are stored in the lagoons or diffuse up to the atmosphere such as H₂S, D.M.S., N₂, CH₄... In many coastal lagoons, excessive amounts of organic matter enhance mineralization processes and lead to drastic events with anoxia of the whole water column and sulfide production. Such events with blooms of phototrophic sulfur bacteria, so-called dystrophic crises or "malaïgue" in French mediterranean lagoons, should be considered as a reaction of excessive organic pollution in the lagoons and as purification process. They are of great importance in the re-establishment of an ecological balance in such lagoons.

It remains to find out if the multiphenotypic potentialities observed along different gradients in coastal lagoons are characteristic at the level of the bacterial community, the bacterial population or the single bacterium. Changing environmental conditions modify the phenotypic characters of the community suggesting that the observed character are optimally selected. However, Foster (1982) proposed that it is not the organism but its informational molecules that are under selection. Thus, a non-dividing cell is, potentially, multiphenotypic, a characteristic previously thought to be true of the community not the individual (Foster, 1982).

When bacteria are active in any ecosystem, not only do they transform organic or mineral compounds but they also produce new biomass available for higher organisms such as protozoa, meiofauna, that use them as a food source (Fig. 6). Over the past ten years many studies have provided information about bacterial biomass and bacterial production in the coastal environment and emphasized the great importance of bacteria as a food source for different organisms. Particular attention has been paid to coastal lagoons and fjords in which the bacterial production can equal phytoplanktonic production and can amount, to 1 to 5 g wet weight m⁻³.d⁻¹ in the most eutrophic coastal lagoons. Due to the low water depth in coastal lagoons, both pelagic and benthic bacterial production make a large contribution to the first level of the detritic food chain. This production is dependent on organic and mineral exchanges between the land and the sea, between water and sediments and on the exchanges that occur along the different gradients, an of which contribute to the perceived richness of coastal lagoons.

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