SULFATE-REDUCING BACTERIA IN MARINE SEDIMENTS[1]

By

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The occurrence of hydrogen sulfide in the waters of certain seas, fjords, and basins, as well as the presence of black or "blue" stinking sediments, can hardly escape the notice of any marine scientist. It is not surprising, therefore, that the eminent oceanographer Murray (Murray and Irvine, 1895) concerned himself with the nature of these materials and postulated their bacterial origin even before bacteriologists had described the specific organisms involved.

It is now accepted that much of the sulfide arises from the bacterial reduction of sulfate. Bacteria which reduce sulfate appear to be very widely distributed in the sea, and it is the purpose of this report to summarize our knowledge of these bacteria with particular reference to their significance in marine sediments, a subject which has been under investigation for several years by the authors and their collaborators at the Scripps Institution.

NOMENCLATURE

Virtually all bacteria and higher plants, as well as a good many animals, may reduce the sulfur in sulfate to the sulfhydryl or disulfide form in the process of synthesizing sulfur-containing proteins, but the term "sulfate reducer" is applied only to those organisms which can utilize sulfates as hydrogen acceptors in their energy-producing reactions. The sulfur in excess of that required for the synthesis of protoplasm is generally reduced to and liberated as hydrogen sulfide by such organisms. As far as is known, only a limited group of bacteria has this unique property. Most of the common bacteria, yeasts, and molds which have been reported to produce traces of hydrogen sulfide from sulfate probably do so by the synthesis of sulfur-

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containing proteins which, upon the death and autolysis of the cells, are decomposed with the liberation of hydrogen sulfide. The amount of sulfate so reduced to hydrogen sulfide by this process, called "indirect reduction" by Beyjerinck (1900), is extremely small compared to the large amounts reduced to hydrogen sulfide by the true sulfate-reducing bacteria.

Although there were earlier reports of the microbial reduction of sulfate to hydrogen sulfide, Beyjerinck (1895) is credited with the isolation of the first pure culture of a sulfate reducer originally called *Spirillum desulfuricans*, which was found in ditch water at Delft, Holland. A similar organism, designated *Microspira aestuarii*, which required three per cent salt for its growth, was isolated from mud and water along the North Sea coast by van Delden (1904). A third sulfate-reducing organism called *Vibrio thermodesulfuricans*, allegedly differing from the two named above only in having a higher optimum temperature for growth, was described by Elion (1924).

Baars (1930) regarded all three organisms as varieties of a single species, which he termed *Vibrio desulfuricans*, since he found that certain fresh-water, salt-water, and thermophilic cultures were interconvertible by laboratory acclimatization procedures. These observations were substantiated by Starkey (1938), who also showed that his cultures could be induced to form endospores. He, therefore, proposed the generic name *Sporovibrio* for the entire group of sulfate reducers.

Rittenberg (1941) was unsuccessful in repeated attempts to induce the cultures of sulfate reducers isolated from marine sediments to form spores. Neither could they be adapted to grow in fresh-water media nor at temperatures higher than 40° to 45° C. These observations suggest that at least some of the sulfate reducers found in the sea are sufficiently distinctive to be considered as separate species.

For reasons outlined by the senior author in Bergey's (1948) Manual, it seems best to apply the generic name *Desulfovibrio* to the entire group of sulfate-reducing vibrios, and *Desulfovibrio aestuarii* to the marine forms. Besides *Desulfovibrio aestuarii*, which seems to be quite widely distributed in the sea, there may be several other related species of sulfate reducers in recent or ancient marine sediments and possibly other genera with similar physiology, but information in this regard is too fragmentary for valid conclusions.

MORPHOLOGY

The characteristic form of *Desulfovibrio aestuarii* in young, actively reproducing cultures is that of a slightly twisted spirillum or curved rod ranging in size from 0.6 to 0.8 μ in width by 3 to 4 μ in length.

The young cells may occur in chains of four or more cells attached end to end by plasmodesm, giving such groupings of comma-shaped rods the appearance of long spirilla. Coccus forms and straight rods also occur under certain conditions in young cultures. Older cells may be highly pleomorphic with coccoid forms, rods with swollen ends, and other bizarre forms predominating. Metachromatic granules (probably volutin), sulfur granules, and deposits of iron sulfide have been observed in cells. Beyjerinck (1895), Issatschenko (1929), Baars (1930), and others have noted marked thickenings of older cells or dead cells due to the accumulation of iron sulfide.

While there may be species peculiarities, the morphological variations are attributable primarily to the conditions under which the bacteria have been cultured. The chemical composition, osmotic pressure, pH, and oxygen tension of the medium influence the morphology of sulfate reducers.

In the absence of free oxygen, most young cells are actively motile by means of one or more flagella. Electron microscope photographs of *Desulfovibrio aestuarii* show that these marine species have a single flagellum which generally has a polar insertion. Starkey (1938) found that his sporogenous cultures had peritrichous flagella, the number and location being quite variable.

The *Desulfovibrio* stain fairly well with the common aniline dyes. They are Gram negative.

PHYSIOLOGY

Sulfate reducers are obligate anaerobes. Though not killed rapidly by exposure to oxygen, they fail to reproduce in the presence of free oxygen. Growth is best in a reducing medium, an oxidation-reduction potential of E_h − 0.1 to − 0.3 volt at pH 7 and 30° C being most favorable for multiplication. In asparagine lactate medium, the first evidence of sulfate reduction observed by Aleshina (1938) was at E_h + 0.027 volt. As sulfate reduction proceeded, the oxidation-reduction potential of the medium dropped to E_h − 0.2 to − 0.3 volt, at which point conditions were optimal. The sulfate reducers studied by Starkey and Wight (1945) grew within the range of pH 5.5 to 8.5 and reduced the E_h from + 0.3 volt to − 0.2 or − 0.3 volt. The pH range of the marine species is 5.4 to 9.0, the optimum being pH 6 to 8.

Under favorable conditions certain cultures may produce as much as 1,500 mgm/L. of hydrogen sulfide. According to Baars (1930), halophilic strains produce considerably more hydrogen sulfide than fresh-water strains—his cultures of the former producing a maximum of 1,448 mgm/L. as compared with only 794 mgm/L. for the latter. Rittenberg (1941) found that the rate and the total amount of hydro-

gen sulfide produced by *Desulfovibrio aestuarii* varied with the concentration of salt in the medium. In general, increasing the salt content within the range of 2 to 4% diminished the rate but increased the total amount of hydrogen sulfide produced. This may be illustrated by the following results:

Period of incubation	*Hydrogen sulfide formed in media containing*		
	2% NaCl	*3% NaCl*	*4% NaCl*
119 hours	56 mgm/L.	37 mgm/L.	8 mgm/L.
143 hours	370 mgm/L.	234 mgm/L.	30 mgm/L.
167 hours	520 mgm/L.	513 mgm/L.	126 mgm/L.
191 hours	622 mgm/L.	660 mgm/L.	518 mgm/L.
239 hours	692 mgm/L.	809 mgm/L.	902 mgm/L.
287 hours	715 mgm/L.	826 mgm/L.	1013 mgm/L.

Sulfur, sulfite, thiosulfate, and tetrathionate are also reduced to hydrogen sulfide by sulfate reducing bacteria. These compounds are assumed to be intermediates in the reduction of sulfate and are assumed to be reduced more readily than sulfate, since they do not accumulate in the medium.

It is a moot question whether sulfate is ever reduced only to and deposited as sulfur in an anaerobic environment, although recently Datta (1943) described an organism as a new species which was claimed to have this ability. Sulfur is often found in cultures or cells of sulfate-reducing bacteria, but there is always some question as to whether it is formed directly from the reduction of sulfate or from the oxidation of sulfide upon coming into contact with oxygen or other oxidizing agents. It is possible, as suggested by Zil'berman (1940), that sulfite, which is believed to be an intermediate product in the reduction of sulfate, reacts with hydrogen sulfide to produce free sulfur: $H_2SO_3 + 2H_2S \rightarrow 3S + 3H_2O$

Apart from sulfate and the intermediate inorganic sulfur compounds already mentioned, no other hydrogen acceptors have been demonstrated for this group of bacteria. Several organic sulfur compounds, phosphate, selenate, tellurate, and peptone were tested in this connection (Rittenberg, 1941) with negative results. Nitrate, although assimilated as a source of nitrogen, was not utilized as a hydrogen acceptor in the energy-yielding reactions of the sulfate reducers.

There are strains of sulfate-reducing bacteria which can utilize nearly any type of organic matter as hydrogen donors. Energy can apparently be derived by sulfate reduction and the concomitant oxidation of cellulose (Rubentschik, 1928), chitin and glucosamine (Aleshina, 1938), beef and mutton tallow (Seliber, 1928, 1945), aliphatic

and aromatic hydrocarbons (Rosenfeld, 1947), and other resistant materials.

Simple compounds like lactate and asparagine are the best sources of carbon or energy for most cultures of sulfate-reducing bacteria. A large variety of mono- and disaccharides, alcohols, aldehydes, aliphatic acids, and amino acids are metabolized by some species.

The types of materials used vary somewhat from strain to strain. Baars (1930) described *Desulfovibrio rubentschikii* as a new species of sulfate reducer primarily upon a basis of its ability to attack fatty acids and sugars not used by other species.

HYDROGEN UTILIZATION

A large body of data indicate that at least certain sulfate reducers can obtain energy by the oxidation of molecular hydrogen and even live autotrophically by this mechanism. The work of Nikitinsky (1907), Kroulik (1913), and Niklewski (1914) gave presumptive evidence of hydrogen uptake by sulfate reducers, but it remained for Stephenson and Stickland (1931) to isolate, from river mud, a pure culture which reduced sulfate to hydrogen sulfide with the consumption of molecular hydrogen:

$$H_2SO_4 + 4H_2 \rightarrow H_2S + 4H_2O + 56{,}750 \text{ calories.}$$

This culture, designated Strain 182, also catalyzed the reduction of sulfite and thiosulfate with molecular hydrogen. The demonstration of hydrogen uptake was obtained with resting cells using the Warburg technique, and there was no proof of carbon dioxide uptake or cell synthesis under these conditions. Wight and Starkey (1945), however, demonstrated the ability of sulfate reducers to live autotrophically by obtaining their energy requirements from the oxidation of molecular hydrogen and their carbon from bicarbonate or carbon dioxide. Certain other cultures studied by Starkey and Wight (1945) utilized hydrogen in lactate medium but not in a purely mineral medium.

Several different pure or partially purified cultures of sulfate-reducing bacteria, isolated from marine mud, were reported by ZoBell (1947a) to consume hydrogen while producing hydrogen sulfide from sulfate in a strictly mineral medium. The ratio of the amount of hydrogen consumed to the amount of hydrogen sulfide produced exceeded the theoretical value of 4.0 which would result if hydrogen were oxidized quantitatively to hydrogen sulfide and water. This suggests that part of the hydrogen may have been used to reduce carbon dioxide in the synthesis of cell substance.

OTHER CULTURAL REQUIREMENTS

Considerable importance has been attached to the salinity requirements of sulfate-reducing bacteria, because this has been employed as the main criterion for distinguishing the marine or halophilic species, *Desulfovibrio aestuarii*, from other species. Baars (1930) was able to acclimatize a fresh-water strain to grow in a medium containing 3% salt, and therefore he concluded that the strains were identical. It should be pointed out that the fresh-water culture Baars employed produced some hydrogen sulfide in his 3% salt medium before the adaptation procedure. In this instance at least "adaptation" may have been a selection process. Rittenberg (1941), however, could not induce halophilic strains which he isolated from marine sediments to grow in nutrient fresh-water medium. They grew normally, though with decreased sulfide production, when the sea water medium, in which they were most active, was diluted 1 : 1 with fresh-water medium. A few cultures were induced to grow in a nutrient medium containing only 25 parts of sea water to 75 parts of fresh water, but only a little hydrogen sulfide was produced. The lack of adaptability was also reflected in the abnormal morphology of the sulfate reducers which were induced to grow in media containing less than 50% sea water.

The salinity picture is further complicated by the observations of other investigators. Strains apparently indistinguishable from *Desulfovibrio desulfuricans* and *Desulfovibrio aestuarii* in all other respects have been described with a salt optimum of 8% and a growth range between traces and 20% sodium chloride (Chait, 1924); with an optimum of 5% (Rubentschik, 1928); with salt ranges of traces to 1%, traces to 5%, and 1% to 3% (Gahl and Anderson, 1928); with a range of 1% to 18% (Ginsburg-Karagitscheva, 1933); and so on. It is entirely possible that there are obligate halophiles, obligate fresh-water strains, and a host of intermediate forms with varying ranges of salt tolerances. Any attempt to classify these various forms into separate species, however, should logically wait until some knowledge is obtained concerning the mechanism of salt adaptation and the factors controlling the salt ranges of growth.

Similarly, various temperature ranges and optima have been reported for different cultures of sulfate-reducing bacteria. His being able to develop cultures, from the same material, having an optimum temperature of either 30° or 55° C., led Baars (1930) to regard Beyjerinck's (1895) *desulfuricans* (optimum temperature of 30°) and Elion's (1924) *thermodesulfuricans* (optimum temperature of 55°) as adaptation forms of the same plurivalent or thermally adaptable type. How-

ever, since Baars did not start with single cell isolations, he may have been producing enrichment cultures of one type or the other of organisms of different potentialities initially present by the selective temperature of incubation. Rittenberg (1941) was unable to acclimatize pure cultures of *Desulfovibrio aestuarii* isolated from marine sediments to reduce sulfate at temperatures higher than 40° to 45° C.

OCCURRENCE IN THE SEA

Sulfate-reducing bacteria appear to be abundantly and widely distributed in the marine environment, especially in bottom deposits. Such bacteria are occasionally found in samples of sea water, where their presence may be of doubtful significance, since sulfate reducers are active only in strictly anaerobic environments. In the wake of a prolific diatom bloom or other circumstances resulting in the occurrence of enough decaying organic matter to consume all of the dissolved oxygen, or in stagnant water basins, conditions in sea water may be suitable for the activity of sulfate reducers. Such conditions prevail in the Black Sea, the water of which contains no free oxygen at depths exceeding 200 meters (Sverdrup, *et al.*, 1942). Water below the euphotic zone in the Caspian Sea, Norwegian fjords, and certain localized areas in the ocean are also sufficiently anaerobic at times to favor the growth of sulfate reducers. The activities of sulfate reducers are largely responsible for maintaining anaerobic conditions by the production of hydrogen sulfide which depletes free oxygen.

According to Daniltchenko and Tschigirine (1926), the concentration of hydrogen sulfide near the bottom of the Black Sea, where sulfate reducers are most active, is sometimes as high as 3,000 mgm/L. Copenhagen (1934) described an area approximately 25 by 200 miles in the Atlantic Ocean off Walvis Bay, South Africa, where hydrogen sulfide is produced periodically by sulfate reducers in quantities sufficient to be lethal to flora and fauna almost to the surface of the overlying water.

It was in the Black Sea where sulfate-reducing bacteria were first demonstrated by Zelinski (1893). Issatschenko (1924, 1929) and Ravich-Sherbo (1930) found vigorous sulfate reducers in virtually all Black Sea water samples examined. In the Caspian Sea, Butkevich (1938) found up to two million bacteria per ml. of water, many of which were sulfate reducers. Sulfate reducers were found in the Salton Sea by Brannon (1914), in the Mediterranean Sea by Bertel (1935), and in Russian limans by Rubentschik (1928). The freshening of certain limans in the Odessa region during the rainy season was found by Rubentschik and Goicherman (1936) to be followed by a ten- to thousand-fold increase in the abundance of sulfate reducers.

In bottom deposits, where bacteria are generally most abundant, ZoBell (1938) demonstrated from 1,000 to 10,000 sulfate reducers per gram. Large numbers of sulfate reducers were found by Bavendamm (1932) in nearly all samples of calcareous mud in the region of the Bahama Islands. A good many of the bacteria recovered from deep sea bottom deposits by Ginsburg-Karagitschewa and Rodionowa (1935) were sulfate reducers.

Rittenberg (1941) found viable sulfate reducers in about half of 450 2- to 3-gram samples (wet weight) from 160 different stations off the coast of California and Lower California. Profile series showed that the abundance decreased with the depth of the sediment, sulfate reducers being detected in only 10% of the samples from depths exceeding 60 inches, as compared with 32% positive at depths of 12 to 60 inches, and 64% positive in the topmost 12 inches of sediment. Sulfate reducers were detected in 92% of the samples of silty sand, 86% of the sandy silt samples, 65% of the silty mud samples, and in 51% of the samples of clayey mud.

The presence of these bacteria, together with the occurrence of sulfide and the decreasing concentration of sulfate with depth in the interstitial water in certain sediments, suggests that the sulfate reducers have been active *in situ.*

OCCURRENCE IN ANCIENT MARINE SEDIMENTS

Bastin (1926) demonstrated the presence of sulfate-reducing bacteria in 28 oil-field waters, believed to have a marine origin, out of 30 sampled in Illinois and in 15 out of 37 sampled in California. He attributed the generally low content of sulfate in oil-well waters to the activity of the bacteria. The samples of oil-well waters were obtained from ancient marine sediments at depths ranging from 400 to 1,866 feet. Similar observations were made by Gahl and Anderson (1928), who found sulfate reducers in 17 out of 40 oil-well waters sampled in California fields from depths as great as 3,090 feet. The isolated organisms grew at temperatures ranging from 28° to 50° C. The temperature of the oil-well waters was 44° to 47° C.

Sulfate reducers were found in the water from six producing oil wells in Illinois fields by Bastin and Greer (1930). The waters were rich in hydrogen sulfide. In oil-well waters containing no sulfide, sulfate reducers were absent. Further evidence that sulfate-reducing bacteria are present and active in waters associated with petroleum deposits has been presented by Ginter (1930, 1934). He points out that carbonate and sulfide in many brines increased as sulfate decreased, presumably due to the reduction of sulfate to hydrogen

sulfide and the simultaneous oxidation of carbon compounds to carbon dioxide which appears as carbonate or bicarbonate.

Besides demonstrating the occurrence of sulfate reducers in water from several oil wells, Ginsburg-Karagitscheva (1933) reported the presence of such bacteria in 14 out of 15 samples of oil sands from Grozny oil-field formation. The bacteria were believed to be indigenous species responsible for the abundance of hydrogen sulfide, the low concentration or lack of sulfate, and the modification of the associated crude oil. Baier (1937) reasoned that sulfate reducers could be active at the oil-water interface where petroleum constituents provide the carbon and energy necessary for the growth of the bacteria.

While the possibilities of surface contamination have not been ruled out, it is significant that sulfate reducers are generally the predominant bacteria detected in oil-well waters. They grow best or exclusively at the temperature and salinity of the water in which they were found, and it has been established that the sulfate reducers can obtain all of their food requirements from the reservoir fluids in which they are found. This circumstantial evidence, plus the fact that appreciable numbers of sulfate reducers have been recovered from oil wells long after anything has been introduced into the wells, strongly suggests that if the bacteria are not actually species indigenous to the formation, they have been multiplying in the oil wells.

ZoBell (1946) detected living sulfate-reducing bacteria in aseptically collected samples of sulfur limestone anhydrite from a depth of 1,560 feet. Cultures which reduced sulfate at temperatures ranging from 75° to 85° C have been observed. Recent observations indicate that the activity of sulfate reducing bacteria is promoted by high hydrostatic pressures such as prevail in the ocean or in petroleum deposits at depths of several thousand feet.

IMPORTANCE OF SULFATE REDUCERS IN SEDIMENTS

There are several ways in which the activities of sulfate-reducing bacteria may modify conditions in marine sediments both recent and ancient. Besides contributing to the sulfur cycle in sediments (Galliher, 1933) by converting sulfate into sulfide and possibly to free sulfur, they transform various kinds of organic matter, consume molecular hydrogen, affect the pH and E_h of their environment, and otherwise influence chemical or physico-chemical conditions.

The free sulfur quite commonly found by Buchanan (1891) in marine bottom deposits was believed to result from sulfides coming in contact with oxygen in the overlying water. He was mistaken, though, in believing that sulfate was reduced to sulfide by the digestive secretions

of animals. Hunt (1915) has attributed the origin of sulfur deposits in Sicily to the bacterial reduction of sulfate, and the Louisiana and Texas Gulf Coast sulfur deposits were believed by Ridgway (1930) to result from the bacterial reduction of gypsum. Ahlfeld (1937), Murzaiev (1937), and Sturm (1937) agree that certain sulfur deposits in Russia resulted from the oxidation of hydrogen sulfide that could have come only from the bacterial reduction of sulfate. Associated with sulfur deposits on the east coast of India, Iya and Sreenivasaya (1945 a, b) found sulfate-reducing bacteria which were thought to form sulfur.

Sulfate reducers may quite definitely contribute to the formation of metallic sulfide deposits. Murray and Irvine (1895) attributed the formation of ferrous sulfide deposits in black marine mud to the activity of sulfate-reducing bacteria, which were also believed to account for the loss of sulfate and an increase in the carbonate content, the latter resulting from the oxidation of organic matter by bacteria. The increased carbonate content in the mud examined on the CHALLENGER Expedition was equivalent to the decreased sulfate content.

Issatschenko (1929) demonstrated the formation of iron sulfide inside the cells of sulfate-reducing bacteria, which were credited with being responsible for the deposition of pyrite in the Black Sea and the Sea of Azov. Similar deposits of iron sulfide, attributable to the activities of sulfate reducers, have been reported by Doss (1912) in the Mediterranean, Caspian, and Black Sea, by Ellis (1925) in the Clyde Sea Aestuary, by Kindle (1926) in the Bay of Fundy, by Strøm (1939) in Norwegian fjords, and by Copenhagen (1934) in Walvis Bay off the South African Coast. Manganese sulfide may be precipitated in a like manner. The formation of copper sulfide in marine sediments has been attributed to the activities of sulfate-reducing bacteria by Schneiderhöhn (1923), Trask (1925), Thiel (1926), and Bastin (1933). Thiel (1927) explained the formation of bauxite and other aluminum oxides from aluminous silicates as being partly due to the activities of sulfate-reducing bacteria.

Not only is sulfate in interstitial water reduced, but sulfate rocks in consolidated sediments may be attacked by sulfate-reducing bacteria. Gypsum, anhydrite, or other sulfate rocks may be slowly dissolved under conditions which are favorable for the activity of sulfate-reducing bacteria (ZoBell, 1947b). The dissolution of sulfate rocks is favored by low pH. The conversion of the strongly acidic sulfate radicle to neutral sulfur or to the only slightly acidic sulfide radicle tends to increase the pH, but the oxidation of organic compounds required as a source of energy for the sulfate-reducing bacteria generally yields acidic products, so the over-all effect may be to lower the

pH. In one series of experiments, for example, Rittenberg (1941) found the final reaction of unbuffered media to be pH 5.8 to 5.9 as a result of the activity of sulfate reducers for 35 days in media having initial reactions of pH 6.0, 7.0, and 7.8, respectively.

The commonly reported occurrence of sulfate-reducing bacteria in the reservoir fluids in petroliferous marine sediments suggests that these bacteria may play a role in the formation or modification of petroleum. That such bacteria may modify the chemical composition of certain oil-field waters is quite generally accepted. The ability of some of them to attack petroleum hydrocarbons has been established (Tausson and Aleshina, 1932; Tausson and Vesselov, 1934; Novelli and ZoBell, 1944; Rosenfeld, 1947). The formation of liquid and waxy hydrocarbons by sulfate reducers has been reported by Jankowski and ZoBell (1944). Fatty acids ranging from acetic to stearic were also assimilated with the formation of small amounts of hydrocarbons in the cell substance of sulfate reducers.

Sulfate-reducing bacteria may have contributed greatly to the formation and migration of petroleum in ancient marine sediments by releasing oil from oil-bearing materials and promoting its flow. ZoBell (1947b) has shown that this may be done by dissolving either carbonate or sulfate rocks on which oil is adsorbed, by producing carbon dioxide which decreases the viscosity of oil, by the bacteria's displacing oil films physically, or by their producing detergents or surface active substances.

These bacteria are also of significance in the anaerobic corrosion of iron, a field actively investigated by Wight and Starkey (1945) and others.

It may also be mentioned that these organisms have been isolated from mineral waters of various spas and resorts in Europe and America (Gosling, 1904; Rank, 1907). One might speculate as to whether the sulfate reducers contribute to the "curative" properties of these waters or merely to their odors.

SUMMARY

Desulfovibrio aestuarii is described as the type species of marine bacteria which reduce sulfates as hydrogen acceptors in their energy-yielding reactions, although there may be other genera and species. Such bacteria are physiologically active only in the absence of free oxygen and they tend to maintain or create reducing conditions by producing hydrogen sulfide, particularly in stagnant water basins and in sedimentary deposits. Sulfate-reducing bacteria oxidize a large variety of organic compounds and some can utilize molecular hydrogen as an energy source.

Sulfate-reducers occur quite widely and abundantly in marine bottom deposits. They have also been found at appreciable depths in ancient marine sediments where they may play a part in petroleum formation. Besides affecting the pH, E_h, and organic content of bottom deposits, sulfate-reducers may be responsible for the formation of various metallic sulfides and the modification of other minerals in marine sediments.

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