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Invitational ONR Lecture

Feast or Famine in the Deep Sea*

RICHARD Y. MORITA

Department of Microbiology and College of Oceanography, Oregon State University, Corvallis, Oregon 97330-3804

INTRODUCTION

Although the title of this ONR Invitational Lecture is "Feast or Famine in the Deep Sea," it should be recognized the subject is related to the other disciplines in oceanography—mainly physical, chemical, geological, and biological oceanography. Therefore, I would like to present some background information for this lecture since most microbiologists are not versed in the various disciplines that make up the field of oceanography. In addition, these other areas of oceanography are important to this lecture.

BACKGROUND INFORMATION

The deep sea is considered by many to be a constant environment because there is no sunlight, the average temperature is around 2 C, the salinity is 35 ‰, and the oxygen concentration is approximately 3.0 ml/liter. In addition, the organic-matter content of the environment is low and the water mass may have a long residence time.

Geological features of the deep sea. As we move away from the shore line (intertidal), the first major feature is the edge of the continental shelf which has a depth of approximately 200 m. As we go deeper, we have the continental slope ranging from 2,000 to 4,000 m, followed by the abyssal plain which has a depth of approximately 4,000 m, and then the continental rise which has a depth of 2,000 to 4,000 m. Off some of the rivers running into the ocean, a submarine canyon may exist and its mouth ends into the continental rise. The deepest portions of the oceans are the trenches and deeps which are formed when two plates are pressed together and one slips below the other, forming a deep or trench. Generally, deeps and trenches have depths exceeding 6,000 m and the deepest trench is known as the Marianas Trench (11,035 m). On the other hand, when continental plates are pulled away from each other, rifts are formed. All deeps and trenches are near land or in an island-arc system. The Rift area may have a few hydrothermal vents which discharge hot water. There are three types of vents: black smokers, white smokers, and cracks and fissures in volcanic rock. The microbiology of these areas will be discussed later.

Physical features of the deep sea. The main environmental variable in the deep sea is the hydrostatic pressure which increases approximately 1 atm for every 10 m of

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depth. Hence, the Marianas Trench would have a pressure of more than 1,100 atm. The average depth of the oceans is 3,800 m (380 atm). In addition to the depth, one must take into consideration the residence time of any deep seawater mass since seawater is not a homogenous water mass. From a microbiological point of view, the pressure and the residence time must be addressed, as well as the cold environmental temperature. The residence time may be several years to over 1,000 yr (Broecker 1963). The average residence times of deep water are 275 and 500 yr for the Atlantic Ocean and the Pacific Ocean, respectively (Stuiver et al. 1983).

Chemical aspects of the deep sea. The main chemical aspect of the deep sea in terms of its microbiology is the availability of energy for growth of microbes. Since no photosynthetic processes occur at this depth, the only production of cellular carbon comes from the organic matter present or by chemolithotrophic organisms. The amount of particulate organic carbon (POC) and dissolved organic carbon (DOC) is 3 to 10 μg/liter and 0.35 to 70 mg/liter, respectively (Menzel and Ryther 1970). Hence, the total combined maximum organic carbon amounts to slightly over 70 mg C/liter. The total organic carbon at the bottom of the sea averages around 31 μmoles/kg of seawater in the area near 12° 53′ N and 173° 38′ E at depths around 5,700 m (L. I. Gordon, pers. commun.). Much of this material is not readily microbial degradable (Barber 1968). In addition, the nutritional quality of the organic carbon is not fully known, mainly because the state of the art in analyzing the organic matter in the deep sea still remains to be improved. In the amino acid analysis of deep water, Lee and Bada (1975) did not report the presence of methionine. Bada and Lee (1977) also pointed out that amino acids detected in seawater (including the dissolved combined amino acids) may actually be constituents of intact bacterial cells which simply pass through the glass-fiber filter. What is important is not the quantity of organic matter in the deep sea but its nutritional quality. Morita (1979a) pointed out that without any methionine, there cannot be translation for protein synthesis.

Although the organic matter content per liter of seawater may not seem to be very much, the total amount in seawater is very large due to the total volume of the oceans. Menzel (1974), employing a value of 0.5 mg C/liter and 10 μg C/liter, extrapolated these values to yield 6.65×10^9 and 14×10^9 tons of C in the oceans. Therefore, in actuality we are dealing with a large amount of carbon. However, the average age of dissolved carbon in the Northeast Pacific waters at a depth of approximately 1,800 m was determined to be 3,400 yr by Williams et al. (1969). The oxygen utilization rate in Pacific Deep Water was 0.004 ml/liter/yr (Craig 1971). The turnover time of the dissolved organic matter was estimated to be 3,300 yr (Menzel 1974).

The above, coupled with the residence time of deep seawater, provides a clue to the famine conditions of the abyssal region of the ocean.

However, where deeps and trenches are concerned, the organic matter is much higher than the rest of the abyssal portions of the sea. Shore plant remains are known to be transported into the deep regions (Wolff 1976; George and Huggins 1979). The Puerto Rico Trench sediments are rather unusual in that a low redox potential of +40 to −30 mv have been recorded, indicating sufficient organic matter as energy for microbes to lower the Eh. Abyssal sediments generally have a high redox potential simply because insufficient organic matter sediments to the bottom for the microbes to bring about reducing conditions.

Biological (nonmicrobiological) aspects of the deep sea. As the continental slope descends deeper, the average size for the Ascidians decreases from more than 1 cm in the neritic zone to 2.5 mm in the abyssal plains which is a reflection on the scarcity of suspended particles (food) in the deep sea (Monniot 1979). This decrease in size corresponds to a decrease in weight from 25 to 1. This dwarfism affects all organs equally. Growth rates are slow, the fecundity is low, and the species are miniaturized (Allen 1979). The changes that occur between the abyssal and hadal faunas occur between 6,000 and 7,000 m and are caused primarily by the increased hydrostatic pressure but also by favorable feeding conditions in the trenches due to extensive sedimentation (Wolff 1970). The latter is mainly due to the proximity of trenches to land.

The adaptive strategies that promote immigration and speciation into the deep-sea environment are the low temperature, hydrostatic pressure, and low energy available to organisms. The adaptative strategy is then the low metabolic rate due to the foregoing factors (George 1979). This is also an adaptation for survival of deep-sea organisms when the food scarcity is severe which results in reduced reproductive and growth potential (Oliver 1979). "The evolution at this level of activity could only be achieved if the ecosystem remained stable over a long period. This conclusion is in keeping with current conceptions on the stability and longevity of the abyssal ecosystem" (Oliver 1979).

The age of marine organisms is difficult to date. As a result only a few have been dated. Turekian et al. (1975), by use of ^{228}Ra chronology, found that the bivalve (*Tindaria callistiformis*) taken from 3806 m at 38° 0.7′ N, 69° 16′ W took 50 to 60 yr for gonad development and 100 yr for 8-mm size. Another bivalve (*Astarte borealis*) dredged up alive from 50 m in the Bering Sea (65° 04′ 5″ N; 168° 50′ 5″ W; 40 km southeast of Nome, Alaska) was found to be 540 ± 200 yr old (sample W-2768 of M. Rubin [written commun.], USGS Radiocarbon Lab., Reston, VA). The life span of many bivalves are much greater than previously assumed and may have life spans greater than 100 yr (Jones 1983). According to Jones (1983), "It is ironic that to find some of the oldest animals known one need travel only as far as the soup section of the local grocery store."

Bennett et al. (1982) employed $^{210}Pb/^{226}Ra$ measurements in the otoliths of a splitnose rockfish (*Sebastes diploproa*) and estimated the longevity to be nearly 80 yr. This organism lives no deeper than 500 m and growth to adult size (ca. 30 cm) takes approximately 25 yr (Boehlert, pers. commun.). Yet for certain species that are harvested by man, we take no consideration as to how long it takes to replenish the organism in the marine environment.

Because the fauna that lives in the abyssal regions has a microflora in its gut as well as on surfaces, biological systems are intimately in contact with bacteria at all times. The bacteria probably make up a great portion of the first trophic level of the food chain in the abyssal region. Furthermore, bacteria were used as a source of food during the evolutionary development of the higher forms (Morita 1980a).

Historical Background

Azoic zone. In 1846 Edward Forbes (cf. Menzies et al. 1973) presented the concept of the Azoic zone below 300 fathoms (ca. 549 m), based on the fact that with depth

fewer and fewer organisms were dredged up. Secondly, the type of dredge he employed was inadequate. Unknown to him, others had dredged up organisms from greater depths than 300 fathoms.

Talisman Expedition (1882–83). Research on pressure effects on organisms began in the 19th century when organisms were dredged from depths up to 6,000 m of the ocean (Regnard 1891). thus the Azoic concept became the Zoic concept. During this period, Certes (1884) demonstrated that marine bacteria collected from depths of 5,000 m were more resistant to pressure than terrestrial forms. Since modern biology had yet to make its debut, no explanation for this phenomenon was given.

Contemporary Deep-Sea Microbiology

Enumeration of deep-sea bacteria. The first serious attempt to investigate the microbiology of the deep sea beyond the continental shelf since the Talisman Expedition occurred during the Mid-Pacific Expedition of 1950. Bacteria were found in the sediments at all deep-sea stations between California and the Marshall Islands ranging from 1,700 to 6,000 m in depth (Morita and ZoBell 1955). The abundance of viable bacteria in the sediments (red clay and globigerina ooze) decreased with core depth. Living bacteria were found in the bottom of the longest cores examined, nearly 8 m, representing material believed to have been deposited more than a million years ago. This is the first evidence that marine bacteria can survive long periods of time and this survival state will be discussed later.

ZoBell and Johnson (1949) proposed the term "barophile" to describe bacteria that grew at pressure higher than 500 atm, while the term "barotolerant" or "baroduric" was reserved for those organisms which were not injured by prolonged incubation at, or subjection to, higher pressures. These terms were proposed before barophilic bacteria were isolated. During the Royal Danish Navy Galathea Deep Sea Expedition, barophilic and baroduric bacteria were observed from various samples taken in the various deeps and trenches of the Pacific and Indian Oceans (ZoBell 1952; ZoBell and Morita 1957, 1959). Employing sediment samples from the Weber Trench, an enrichment culture of sulfate-reducing bacteria took 10 mo of incubation before any signs of sulfate reduction appeared (ZoBell and Morita 1959). Approximately two decades later, others (Schwartz et al. 1976; Yayanos et al. 1979; Jannasch et al. 1976) reconfirmed the existence of barophilic bacteria. The first pure culture of a barophile was obtained by Yayanos et al. (1979), employing a silica gel medium formulated by Dietz and Yayanos (1978). The use of silica gel medium, unlike agar media, permits solidification at low temperature. These barophilic bacteria were isolated from various deeps or trenches. Whether or not true barophilic bacteria can be isolated from the abyssal plains has not yet been documented. Many of the barophiles isolated from the deeps and trenches are from the gut of higher forms (Deming et al. 1981; ZoBell and Morita 1957; Schwartz et al. 1976; Hessler et al. 1978; Jannasch et al. 1976). However, nonbarophilic bacteria also can be isolated which will not grow at elevated pressures isobaric to the original environment from which they were isolated (Quigley and Colwell 1968). A barophile that cannot withstand atmospheric pressure has been described by Yayanos et al. (1979). As with previous elucidation of barophiles, the incubation period is long. The generation time reported by Yayanos et al. (1982) was 5 to 35 h when nutrient medium

was employed. The question is what is the generation time for the barophiles in their natural environment when the organic carbon content of the environment is extremely low and this organic matter probably is not optimally nutritious in terms of vitamins, amino acids, etc. Carlucci and Williams (1978) calculated a doubling time of 210 h for organisms obtained at a depth of 5,500 m. In addition, incubation temperatures were low (e.g., 5 C or lower). Thus, the barophiles can be characterized as having a requirement for hydrostatic pressure, slow metabolism, and being psychrophilic in nature. The slow rate of metabolism of bacteria in the deep sea is considered a "blessing in disguise" by Morita (1979a,b, 1980b) since a good rate of metabolism would use up all the organic matter present and then the deep sea would definitely become azoic. This is further borne out by the description of obligately barophilic bacteria isolated from the Mariana Trench by Yayanos et al. (1981).

In order to detect rates of activity by microbes in the deep sea, many have resorted to the use of radioactive compounds. However, I wish to point out that when exogenous substrates are added to deep sea samples, the added increase in organic matter becomes substantial compared to the amount that exists in nature. Also, one must take into consideration the bottle effect (in which some investigators do not believe). Last, but most important, is the ability of starved cells to readily take up substrate (Novitsky and Morita 1976, 1977; Amy et al. 1983a,b; Kurath and Morita 1983). Even starved cells under pressure will demonstrate a rapid uptake of substrate (Yorgey and Morita, unpubl. data).

Pressure effects on bacteria. There are many papers dealing with this subject by various investigators, and reviews of the subject have been authored by Johnson et al. (1954); Morita (1965, 1967, 1968, 1972, 1973, 1976); Morita and Becker (1970). There are many complicating factors involved in the study of hydrostatic pressure effects on organisms such as pH changes in seawater, ionization of water, ionization of salts, viscosity changes, chemical reaction rates, etc. However, the one that enters most often in this lecture is the effect of hydrostatic pressure on molecular volume changes (molar volume changes in chemistry). Pressure decreases the molecular volume of a substance, whereas increased temperature increases the molecular volume. Basically, this is the reason why certain enzyme systems have been observed to function above 100 C. This was noted with malic dehydrogenase (Morita and Haight 1962) and with inorganic pyrophosphatase (Morita and Mathemeier 1964). In other words, denaturation of the enzymes does not take place (involves a molecular volume increase) due to the pressure applied (involves a molecular volume decrease). A good example of an enzymatic reaction rate at the cellular level is the study of pressure-temperature on aspartase activity by *Escherichia coli* (Haight and Morita 1962).

It also should be noted as surface organisms sink they are subjected to reduced temperature and increased pressure. Hence, both reduced temperature and increased pressure are added in making the molecular volume decrease. In addition to volume changes, it should be noted that pressure also reduces the ability of surface forms to transport substrates from the surrounding environment into the cell (Paul and Morita 1971).

Decompression of a barophile obtained from a depth of 10,476 m in the Pacific Ocean slowly lost its colony-forming ability during incubation at 1 atm and 0 C (Yayanos and Dietz 1983).

Psychrophilic nature of barophiles. Psychrophiles were thought not to exist before the mid-1960s. The early literature on marine psychrophilic bacteria is reviewed by Morita (1966). Morita (1975) redefined the term "psychrophile" as organisms having an optimal temperature for growth at about 15 C or lower, a maximal temperature for growth at about 20 C or lower, and a minimal temperature for growth at 0 C or below. Some psychrophilic bacteria have maximal growth temperatures of 10 C or below. Various aspects concerning psychrophiles and the ecological role in the environment were reviewed by Morita (1975) and Baross and Morita (1978).

Thermal inactivation of barophiles takes place readily. At atmospheric pressure Yayanos and Dietz (1982) demonstrated that their barophilic bacterium designated CNPT-3 was inactivated at 10 C. Based on their studies, they (Yayanos and Dietz 1982; Yayanos et al. 1979, 1981) postulated that autochthonous deep-sea bacteria are extremely psychrophilic and barophilic. Thus far, it appears that all true barophilic bacteria isolated and cultured are psychrophilic with the exception of those isolated from thermal vents. This psychrophilic nature of barophilic bacteria was probably one of the main reasons why the earlier investigators were not able to isolate the barophiles in pure culture.

Starvation survival studies. Because we recognize that deep sea is ultraoligotrophic, we initiated studies on starvation survival. Each species of bacteria has its threshold level of nutrients for growth and reproduction. The term was coined by Morita (1982) to indicate the process of survival in the absence of energy-yielding substrates. Previously in this paper I mentioned the age of various fish and bivalves, some in the deep sea. Since it is impossible to determine the age of a bacterial cell, one has to try to figure out when it last replicated from growth data. Without nutrients, what would the generation time be? How long can a species of bacterium live without an exogenous source of energy?

In order to answer the latter question above, we initiated studies on starvation survival. When cells of Ant-300 were placed in mineral salts medium without the presence of an energy source, we noted that cells would fragment into many more small cells (ultramicrocells) (Novitsky and Morita 1976) and the increase in the number of cells may be a survival strategy of marine organisms (Novitsky and Morita 1978a). Many plants and animals produce numerous offspring in hopes that one will survive. Starvation actually made cells more barotolerant and this starvation-induced barotolerance is a means by which bacteria can survive in the Antarctic Convergence until conditions become more optimal for growth (Novitsky and Morita 1978b). However, during the starvation period, the endogenous respiration rate was reduced to 0.0071%/h (Novitsky and Morita 1977). If one extrapolated this value for the residence time of a water mass, then it would be too high. Where then is the energy for maintenance? Ant-300 had remained viable for 2.5 yr without an exogenous energy source in the medium when an electrical power failure stopped the experiment.

The ultramicrocells have been seen by many investigators in samples collected near shore (MacDonell and Hood 1982; Torrella and Morita 1981) and in the deep sea (Tabor et al. 1981). On an oceanographic expedition off the coast of Africa, Watson et al. (1977) noted that approximately half of the organisms were ultramicrocells. By use of a microcultural study, Torrella and Morita (1981) demonstrated that some of the microcells would grow into normal size bacteria. This also was noted for *Aeromonas*, *Vibrio*, *Pseudomonas*, and *Alcaligenes* by MacDonell and Hood (1982) and

Tabor et al. (1981). Small starved marine bacteria were noted to colonize surfaces and later grow into normal size cells (Kjelleberg et al. 1982; Humphrey et al. 1982).

There are apparently three patterns of starvation survival thus far elucidated. These are: (1) an initial increase in numbers and followed by a decrease until a constant viability was attained; (2) a decrease in numbers until a constant viability was attained; and (3) an increase until a constant viability was attained (Amy and Morita 1983a). The physiological processes involved with starvation survival are discussed by Amy and Morita (1983b), Amy et al. (1983a,b), and Kurath and Morita (1983). However, one of the startling features during starvation survival (not initially) is that starved cells have more ATP per viable cells than nonstarved cells. Since 20% of the energy needed by cells is for transport of the substrate into the cell (Stouthamer 1973), this energy is needed when the cell encounters substrates that require active transport.

Ultramicrocells in nutrient-poor waters have certain advantages over the normal size cells that grow in environments that have sufficient energy sources. These are: (1) cell's surface/volume ratio which enhances its ability to scavenge energy-yielding substrates from its environment (Morita 1983); (2) an increase in uptake affinities as demonstrated by km values (Jones and Morita 1983a,b); and (3) in some marine bacteria chemotaxis does not take place until the organism has been starved (Torrella and Morita 1982).

Jones and Rhodes-Roberts (1981) stated that the ability of cells to survive long periods of time without an exogenous source of energy cannot be explained by the cell's ability to survive at the expense of intracellular material, low maintenance energy requirements, or the ability to scavenge substrates. If readily utilizable organic compounds in the deep sea are lacking (Morita 1979b), what then is the energy for maintenance? Since carbon monoxide, hydrogen, and methane occur in the atmosphere, hydrosphere, and geosphere in few parts per million, we have initiated studies on the utilization of these compounds as the source of energies of maintenance. Thus far, we have shown that the nitrifying bacteria can utilize methane and carbon monoxide in low concentrations. We also believe that hydrogen can be used since most organisms have a hydrogenase. Further laboratory experiments will determine if any of these gases can satisfy the requirement of marine microorganisms for energies of maintenance.

Occurrence of bacteria in the hydrothermal vents. A research expedition, instigated by Dr. Jack Corliss of Oregon State University, revealed the presence of Galapagos hydrothermal vents (Corliss et al. 1979) and later hydrothermal vents were discovered in the 20°N East Pacific Rise. The Galapagos Rift region occurs at 500 m to 2,800 m. Although the discovery of hydrothermal vents was a great geological event, Corliss et al. (1979) found various types of biological forms present. The vesicomyid clams (Turekian et al. 1979; Turekian and Cochrane 1981) and the mytilid mussels (Rhoads et al. 1981) were judged to have a growth rate of 4 cm/yr and 1 cm/yr, respectively. These growth rates are 500 and 120 times faster than that of *Tindaria* and are faster than some shallow-water bivalves (Jones 1983). This only points to the fact that these organisms have evolved to utilize the abundant organic matter present due to the ability of chemolithotrophic bacteria to utilize reduced sulfur as an energy source. Therefore, these hydrothermal environments are not energy limited. A possible chemoautotrophic bacterial symbiont was found associated with the hydrothermal vent tube worm, *Riftia pachyptila* (Cavanaugh et al 1981). This sulfur-oxidizing bacterium was in the tissue

of the tube worm but the respiration plume tissue is insensitive to sulfide (Arp and Childress 1983). The blood of the tube worm contains a sulfide-binding protein that appears to concentrate sulfide from the environment and may function to transport the sulfide to the internal endosymbiotic bacteria contained within the coelomic organ, the trophosome (Powell and Somero 1983). The sulfide protein apparently prevents sulfide poisoning and prevents sulfide from inhibiting cytochrome c oxidase.

Unfortunately, the water samples taken by Corliss for microbiological examination were not collected aseptically. A return to the same area by biologists, including microbiologists, did reveal the presence of chemolithotrophic bacteria, and these chemolithotrophic organs utilizing reduced sulfur compounds probably sustained the primary productivity (Karl et al. 1980). Three distinct physiological types of sulfur-oxidizing bacteria were isolated by Ruby et al. (1981). These were various strains of obligately chemolithotrophic *Thiomicrospira*, *Thiobacillus*-like organisms, and *Pseudomonas*-like heterotrophs. They also observed microbial mats which resembled *Beggiatoa* and *Thiothrix*. Later, Harwood et al. (1982) isolated an anaerobic marine *Spirochaeta* sp. which indicates that some of the vent areas are anoxic. From an evolutional viewpoint, bacteria as food for higher forms should be expected since the higher animal forms need a source of food during their evolutionary development (Morita 1980a). Bacterial cells contain all necessary nutrients for growth of higher forms.

However, the most significant discovery from the hydrothermal vents is the growth of bacteria within the thermal vent itself where temperatures are well above 100 C. Baross and Deming (1983) cultured organisms from samples collected from 350 C water emanating from a black smoker sulfide chimney at 21°N along the East Pacific Rise. Several organisms grew at 1 atm, producing methane, hydrogen, and carbon monoxide. Methane, hydrogen, carbon monoxide, and dinitrogen oxide occur in submarine hydrothermal vent waters (Lilley et al. 1982) and they may be of microbiological origin (Baross et al. 1982). In order to grow these organisms a titanium growth chamber was used, permitting the system to be heated to temperatures at least 250 C at 265 atm (Baross and Deming 1983). The microorganisms appeared to be two different morphological types as evidenced by transmission electron microscopy. The doubling times for the bacteria cells were 8 h at 150 C, 1.5 h at 200 C, and 40 min at 250 C. At 250 C, the protein concentration doubled at the same rate as the number of bacteria.

The key to the above result is the pressure present. This hydrostatic pressure permits the water to remain in the liquid form. Hence, Baross and Deming's (1983) results confirm Brock's (1967) hypothesis that "life is possible at any temperature at which there is liquid water." Secondly, pressure decreases the molecular volume of the cellular substances which may aid in its growth at high temperature.

However, an interesting hypothesis has arisen from the thermal vent studies. Corliss et al. (1981) has postulated that this is the site of the origin of life. It has a reducing condition, thermal energy to synthesize organic compounds, the presence of carbon monoxide, hydrogen, nitrogen, methane, appropriate catalytic surface areas (Fe-Mg clay minerals), metals, mixing gradient of temperature and composition, and a continuous flow that removes products from sites of reactions.

If this hypothesis is correct, then all life forms evolved from the ancestors of the bacteria found in the hydrothermal vent. Bacteria as food is then well illustrated by the other higher organisms present close to the hydrothermal vent area, and the interaction between bacteria and the vent worm is a good illustration of higher organisms being dependent on bacteria in their evolutionary development.

CONCLUSIONS

Both thermophilic and psychrophilic barophiles have been found in the deep sea. However, the most important governing factor in their growth is the availability of energy. For the psychrophilic bacteria the energy source is scarce unless they are "on" or "in" deep-sea organisms. Hence, for these organisms it is not a Koch's (1971) feast or famine situation but more like Poindexter's (1981) fast and famine situation. Occasionally, there will be a feast not only for the bacteria but higher forms when a large organism falls through the water column to the bottom of the deep sea. For the thermophilic barophilic bacteria, it is a feast situation in and near the thermal vent but when the water containing the thermophilic bacteria cools, they then come into a famine situation. For the chemolithotrophic bacteria their source of reduced sulfur also will disappear either by abiological oxidation, biological oxidation, and dilution due to the water currents. For the indigenous ocean-surface bacteria that sediment to the bottom of the deep sea, it is a famine situation. Whatever the type of organism that is addressed, eventually it will have to face a starvation-survival situation until conditions become sufficiently improved so that the species can express itself and take its role in the environment.

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