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Adenosine triphosphate and organic carbon in the Cariaco Trench

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Abstract—Measurements were made of the vertical distribution of adenosine triphosphate (ATP), sulfide (HS^-), and dissolved and particulate organic carbon (DOC and POC) within the water column of the Cariaco Trench. All three profiles indicate a large active microbial population (15 μg Cl^{-1}) at the depth interval corresponding to the oxic–anoxic interface (350 to 400 m). The average concentrations of POC (60 μg l^{-1}) and ATP (5 to 12 ng l^{-1}) within the lower portion of the anoxic zone (> 500 m) are between 4 and 12 times greater than values previously reported from oxygenated oceanic environments. Significant chemical and biological differences (HS^- and ATP) were observed between the eastern and western basin stations. These results are discussed relative to the processes involved in periodic renewal of the deep anoxic waters.

INTRODUCTION

THE CARIACO Trench (basin) is in the eastern portion of the continental borderland of Venezuela, and is the world's largest known tropical anoxic basin. The presence of hydrogen sulfide (HS^-) in the depths of the Cariaco Trench was first discovered by L. V. Worthington in December 1954, and a detailed chemical description was subsequently published by RICHARDS and VACCARO (1956). Although the surface waters (0 to 150 m) exchange freely with the surrounding Caribbean Sea, a strong pycnocline induced by thermal stratification restricts deep vertical circulation, thus isolating the lower portion of the basin from the oxygen-rich surface layers. As a result, the basin is anoxic below about 350 m, and the water is essentially isothermal and isohaline from 600 m to the bottom (RICHARDS, 1965, pp. 618).

During the past 20 years a great deal of information has been compiled concerning the origin, maintenance and consequences of anoxia in the Cariaco Trench (see RICHARDS, 1975). Steady-state vertical advection-diffusion models have recently been applied to the Cariaco Trench in an attempt to evaluate the relative effects of physical processes (i.e. mixing) and *in situ* biological activity on the chemical composition of the water column (FANNING and PILSON, 1972; REEBURGH, 1976). Although the distribution (both presence and absence) of many chemical species [O_2, HS^-, HPO_4^{2-}, NO_3^-, NO_2^-, NH_4^+, CH_4, and $Si(OH)_4$] is ultimately controlled by biological processes, little information is available concerning the abundance and metabolic activity of the microorganisms responsible for these biochemical transformations. During recent cruises aboard the U.S.N.S. *Mizar* (cruise 72-11-01), and the R.V. *Eastward* (cruise E-23F 72/73), water samples were analyzed for HS^-, DOC, POC, and for total microbial biomass using a quantitative assay for ATP.

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METHODS AND MATERIALS

Samples for DOC and POC analyses were collected at 10°37.4′N, 65°44.8′W between 9 and 11 March 1972, aboard the U.S.N.S. *Mizar* (Sta. M-1, Fig. 1). All samples were collected in 12-l. Niskin bottles and transferred immediately to acid-washed 2.5-l. Pyrex bottles. For each POC determination, 6 to 8 l. of seawater were filtered through a combusted (450°C, 4 hr) 47-mm glass fiber filter (Gelman, type AA), which was carefully transferred to a glass Petri dish, fumed with concentrated hydrochloric acid and stored in a vacuum desiccator. For DOC determinations, each sample bottle was rinsed twice with some of the filtrate, and then a portion of the remaining filtrate was transferred back into the glass sample bottle. To

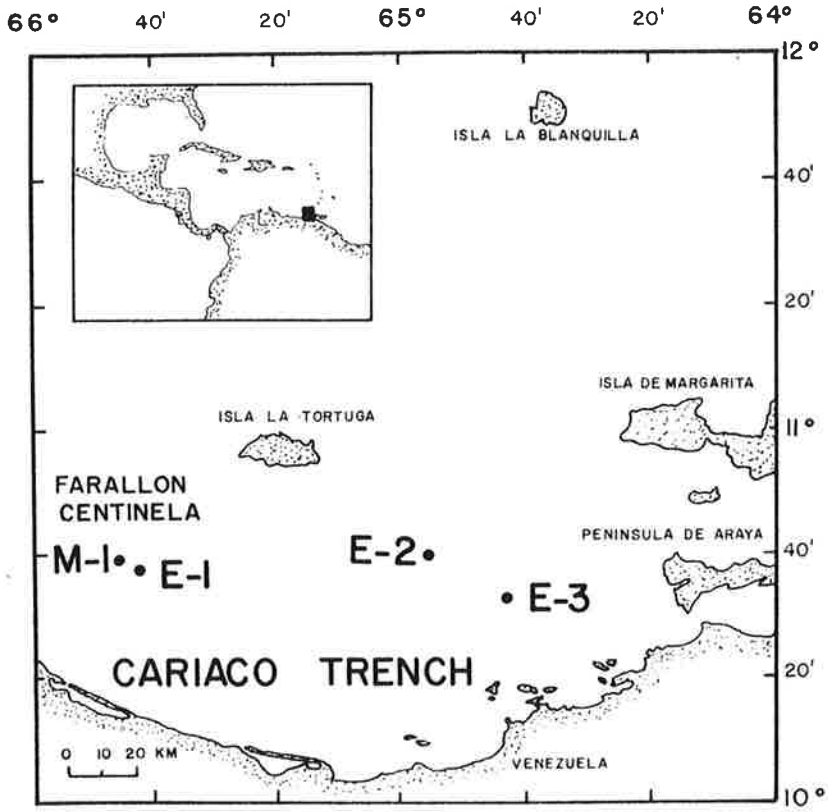


Fig. 1. Locations of the four Cariaco Trench hydrostations. Station M-1 was sampled from the U.S.N.S. *Mizar*, and Stas. E-1, E-2, and E-3 from the R.V. *Eastward*.

preserve and acidify the samples for subsequent analysis, 5 ml of a saturated solution of mercuric chloride and copper sulfate ($HgCl_2$–$CuSO_4$) and 5 ml of concentrated phosphoric acid (H_3PO_4) were added to each bottle. The samples were sparged with helium that was purified by passing it through in-line molecular sieve and Mallcosorb columns. The bottles were tightly sealed for subsequent laboratory analysis.

In the laboratory, the DOC was oxidized to carbon dioxide (CO_2) according to the method of MENZEL and VACCARO (1964). The gas was collected and measured manometrically following the procedure outlined by CALDER (1969). All DOC measurements were carried out in duplicate, and the error bars in Fig. 5 represent the actual range of these duplicate determinations. For POC analysis, the filter pads were combusted in a vacuum line similar to the one described by CRAIG (1953). The CO_2 that was evolved was collected and

measured manometrically (CALDER, 1969). Duplicate samples were not available for POC determinations, primarily because of the large volume of water required for each measurement. The error bar associated with the POC determinations in Fig. 5 represents the error associated with the analytical procedure (S.D. = 10 μg C l^{-1}), as determined from previous field measurements. The data points at 100 and 900 m are the POC concentrations for samples collected on different days, but at the same depth. In both cases, these 'replicate' determinations had overlapping error fields (± 1 S.D.), indicating that the variation between these samples was within the previously determined analytical error for the POC measurements.

Water samples for HS^- and ATP analyses were collected between 17 and 19 February 1973 aboard the R.V. *Eastward* (Fig. 1). All hydrocasts were with 8-l. Niskin bottles, and the extractions were completed on board ship. The stations were E-1 at 10°36.7′N, 65°42.4′W; E-2 at 10°39.9′N, 64°55.8′W, and E-3 at 10°32.2′N, 64°43.4′W.

Sulfide samples were drawn immediately into BOD bottles and the contents allowed to overflow to displace entirely the volume of the bottle. The HS^- concentration was determined at sea using the spectrophotometric procedure described by STRICKLAND and PARSONS (1972).

ATP was extracted using a modification of the method first described by HOLM-HANSEN and BOOTH (1966). Between 0.5 and 2.0 l. of seawater were concentrated onto a 0.45-μm membrane filter (Millipore®, type HA), and the filter was immediately plunged into 10 ml of boiling Tris buffer (0.02 M, pH 7.8) in a calibrated screw cap tube. After 10 min in an oil bath (120°C), the tubes were cooled to room temperature and the volume restored to 10 ml with additional Tris. All samples were extracted immediately after collection, and the extracts were kept frozen for subsequent laboratory analysis using the firefly bioluminescent assay procedure. The enzyme preparation and a detailed description of the instrumentation have been reported elsewhere (KARL and LAROCK, 1975).

RESULTS

The Cariaco Trench is enclosed by a submarine bank extending from Isla Margarita to Cabo Codera, and is divided into an eastern (1390 m) and a western basin (1428 m), separated by a sill rising to 900 m (MALONEY, 1966). The samples were collected at a shallow station on the edge of the eastern basin (E-2, Fig. 1), a deep station in the eastern basin (E-3, Fig. 1) and two deep stations in the western basin (E-1 and M-1, Fig. 1). The results for HS^- and ATP at Sta. E-1, E-2 and E-3 are given in Figs. 2, 3, and 4.

Sulfide was first detected at the depth interval between 350 to 400 m at all three stations. In the eastern basin (E-2 and E-3, Fig. 1), the HS^- concentration rapidly increased to a value of 20 to 21 μg-atoms S l^{-1} at a depth of 600 m. Below this depth, the HS^- continued to increase to a maximum concentration of 32 μg-atoms S l^{-1} at a depth of 1250 m (Fig. 4). In the western basin, however, the HS^- concentration was less (i.e. 18.2 μg-atoms S l^{-1} at 600 m, Fig. 2), and attained a maximum concentration of 25.7 μg-atoms S l^{-1} at 900 m. From 900 to 1200 m, there was no significant change in the HS^- concentration. These results are in excellent agreement with the data previously reported by RICHARDS and VACCARO (1956) for a similar station in the western basin.

In both the deep ATP profiles observed in the western and eastern basins (Figs. 2 and 4) there is a sub-surface peak in the ATP concentration at a depth corresponding to the oxic–anoxic interface (approximately 350 to 400 m). The maximum for this sub-surface peak was 60 ng ATP l^{-1} in both basins (Figs. 2 and 4). Below the interface region, the ATP

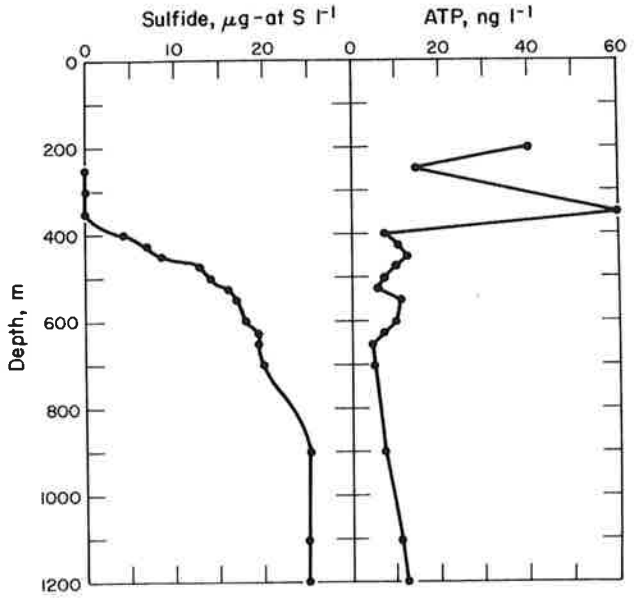


Fig. 2. The vertical distribution of sulfide and ATP at Sta. E-1 in the western basin of the Cariaco Trench.

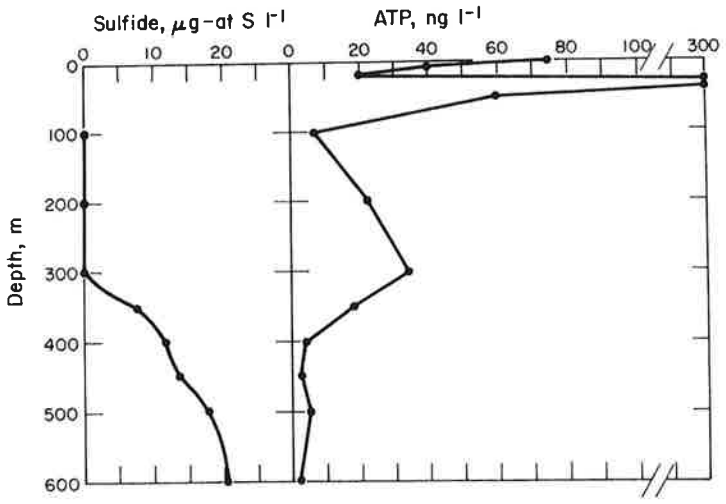


Fig. 3. The vertical distribution of sulfide and ATP at Sta. E-2 on the northern edge of the eastern basin of the Cariaco Trench.

decreased and fluctuated between 1.7 and 5.4 ng l^{-1} between 475 and 700 m in the eastern basin, and between 7.2 and 13.5 ng l^{-1} in the western basin. At greater depths, the ATP values gradually increased to levels of 8.0 ng l^{-1} in the eastern and 12.5 ng l^{-1} in the western basin (Figs. 2 and 4). The ATP concentrations within the anoxic zone at Sta. E-1 were consistently higher than those observed at Sta. E-3, although the general features of both profiles were similar. The ATP levels within the deep anoxic zone (700 to 1200 m) are from 2 to 10 times greater than concentrations reported elsewhere from comparable depths in oxygenated oceanic waters (HOBBIE, HOLM-HANSEN, PACKARD, POMEROY, SHELDON, THOMAS and WIEBE, 1972; HOLM-HANSEN and BOOTH, 1966; HOLM-HANSEN, 1969; KARL, LAROCK, MORSE and STURGES, 1976).

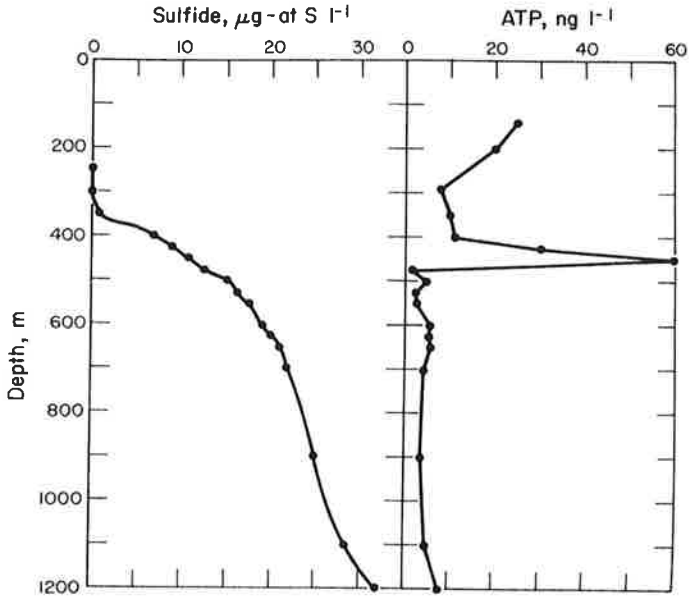


Fig. 4. The vertical distribution of sulfide and ATP at Sta. E-3 in the eastern basin of the Cariaco Trench.

In the upper 75 m at the shallow eastern basin station (E-2, Fig. 1), the ATP is relatively high, obtaining a maximum value of 300 ng l^{-1} at 40 m (Fig. 3). Deeper, it decreased to 9.1 ng l^{-1} at 100 m, increased to 33.5 ng l^{-1} at 300 m, and then decreased with depth to a minimum of 1.5 ng l^{-1} at 590 m. The sub-surface peak was centered at approximately 300 m, and corresponded to the depth interval of the oxic–anoxic interface.

At Sta. M-1, in the western basin (Fig. 5), the POC maximum concentration was 243 μg

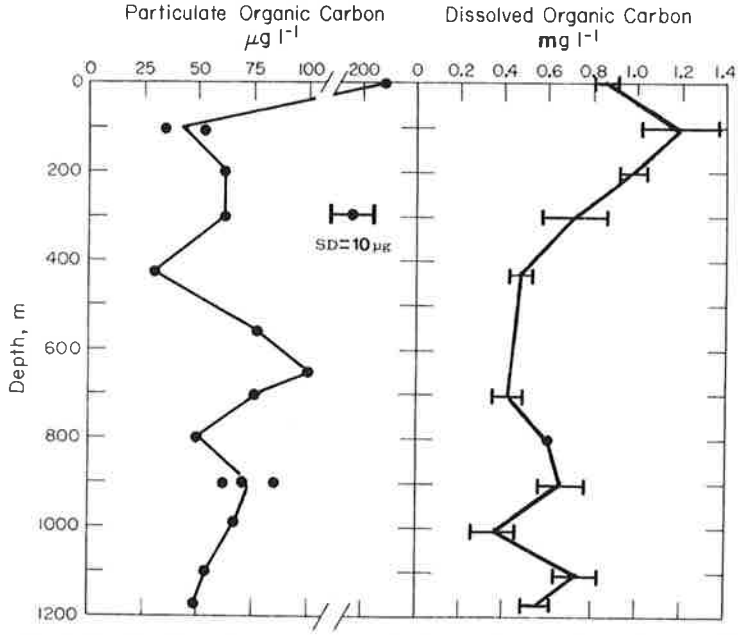


Fig. 5. The vertical distribution of particulate and dissolved organic carbon at Sta. M-1 in the western basin of the Cariaco Trench. Each individual POC data point represents a discrete water sample determination, and the multiple data points at 100 and 900 m represent samples collected on separate hydrocasts. The average standard deviation of the analytical procedure is shown in the upper portion of the graph (S.D. = 10 μg C l^{-1}). The DOC concentrations represent the actual range of duplicate samples from each water depth.

l^{-1} at the surface. The POC then decreased to a minimum of 30 $\mu g\, l^{-1}$ below the interface at 480 m; below this depth it increased to a sub-surface maximum of 101 $\mu g\, C\, l^{-1}$ at 650 m. With increasing depth, it decreased to an average of 50 to 60 $\mu g\, l^{-1}$. The DOC concentration was greatest at 100 m (1.02 to 1.38 mg $C\, l^{-1}$) and decreased to a minimum of 0.35 to 0.49 mg $C\, l^{-1}$ at 700 m. At greater depths, DOC varied between 0.26 and 0.84 mg $C\, l^{-1}$, with an average of 0.56 mg $C\, l^{-1}$.

DISCUSSION

Significant findings for the ATP data are: (1) a secondary maximum across the oxic–anoxic interface, (2) high concentrations of ATP within the anoxic zone relative to oxygenated waters of comparable depth and (3) a gradual increase in ATP with depth below 700 m.

SOROKIN (1964) found a large concentration of living cells in the Black Sea near the surface and at the oxic–anoxic interface, but from 100 m below the interface to the bottom, heterotrophic bacteria were practically absent. The ATP profiles (Figs. 2 to 4) are like the Black Sea observations in that they show increased biomass near the surface and within the interface region, but below the interface our results indicate the presence of a sizeable microbial population. The obligate aerobic heterotrophy of algae (GIBBS, 1962) enables us to use the ATP data to estimate the magnitude of the bacterial density in the anoxic zone, as bacteria should be the predominant organisms present under prolonged anoxic conditions. Assuming the average intracellular ATP content for a bacterial cell to be 1.3×10^{-15} g, with a range of 0.2 to 9.7×10^{-15} g (HAMILTON and HOLM-HANSEN, 1967; D'EUSTACHIO and JOHNSON, 1968; LEVIN, SCHROT and HESS, 1975), at 1200 m the approximate bacterial density is 6.2×10^3 (range 8.0×10^2 to 4.0×10^4) cells ml^{-1} at Sta. E-3 and 9.6×10^3 (range 1.3×10^3 to 6.3×10^4) cells ml^{-1} at Sta. E-1.

The increase in ATP across the oxic–anoxic interface could be the result of several differing microbial processes. The first factor that may contribute to an increased biomass across the interface is the development of an active sulfide and thiosulfate-oxidizing population. These bacteria were isolated from the interface region of the Cariaco Trench by TUTTLE and JANNASCH (1973). A second factor affecting the ATP interface peak might be related to the distribution of sulfate-reducing bacteria. In the Black Sea, SOROKIN (1964) and JANNASCH, TRUPER and TUTTLE (1974) detected sulfate reduction in the water column just below the interface, and again at the bottom, but no substantial activity was detected in between. Oxidizable organic matter produced in the euphotic zone could rapidly be degraded and converted into cell mass by a variety of obligate anaerobic microorganisms in the uppermost region of the anoxic zone. JANNASCH, TRUPER and TUTTLE (1974) suggested that the sulfate reduction zone at the interface might be the result of photosynthetically derived material 'leaking' through the interface into the anoxic zone. Our observed ATP peak could be the result of a natural enrichment of either sulfide-oxidizing or sulfate-reducing bacteria, or both. Although the ATP peak at Sta. E-3 (Fig. 4) appears to be well within the anoxic zone, sulfide-oxidizing bacteria might still be active if nitrate were present as a hydrogen acceptor. The possible presence of other physiologically distinct anaerobic microorganisms (i.e. methanogenic or fermentative bacteria) should not be overlooked.

Although the DOC concentration within Lake Nitinat, an anoxic fjord (ADAMS and RICHARDS, 1968), and the Black Sea (Datsko, 1951, cited by RICHARDS, 1965; DEUSER, 1971) has been reported to increase with depth within the anoxic zone, no consistent pattern was

evident for the DOC in the western basin of the Cariaco Trench (Fig. 5). The concentrations reported here are well within the range of values previously reported for oxygenated waters of the western tropical Atlantic (MENZEL, 1967).

On the other hand, the POC concentrations of the deep water (> 500 m) were consistently greater than reported for an oxygenated station in the Caribbean Sea only 350 km northwest of Sta. M-1 (MENZEL and GOERING, 1966). Other published POC concentrations for the North Atlantic range from 5 to 15 $\mu g\ C\ l^{-1}$ (MENZEL and GOERING, 1966; MENZEL and RYTHER, 1970), or a factor of $\frac{1}{4}$ to $\frac{1}{12}$ the average deep water concentrations in the Cariaco Trench (50 to 60 $\mu g\ C\ l^{-1}$, Fig. 5). The elevated POC values in the anoxic zone could be the result of conversion of DOC to POC (SUTCLIFFE, BAYLOR and MENZEL, 1963), organic material sinking out of the highly productive surface waters, or input of terrigenous material at depth. A recent report by DEUSER (1973) based on $^{13}C/^{12}C$ measurements of water samples from the Cariaco Trench, suggests that nearly one-third of the sedimentary organic carbon may be of continental origin. Another possible explanation for the elevated POC concentrations at depth may be related to the movement and activity of the deep scattering layer (DSL). Using a 25-kHz acoustic profiler in the Cariaco Trench, WILSON (1972) observed that the descending DSL split into two components at or near the oxic–anoxic interface. A minor component remained at the interface, while the major portion migrated deep within the anoxic zone to a depth of 500 to 600 m. Fecal material or dead organisms may be a substantial source of organic carbon throughout this depth interval.

Relatively high concentrations of ATP in both basins of the Cariaco Trench might be a response to the anomalously high POC levels previously discussed. As bacteria in the sea are generally considered to be carbon limited (ZOBELL and GRANT, 1943; Kriss, 1953, cited by JANNASCH and JONES, 1959), especially at the low organic carbon levels found in seawater, any increase in utilizable organic matter should be reflected by an increase in the standing stock or biomass of heterotrophic organisms. The increase in ATP with depth below about 700 m might also reflect a vertical gradient in utilizable substrates generated via fermentation reactions within the organic-rich sediments. The absence of a defined gradient in DOC within the deep waters of the Cariaco Trench (Fig. 5) does not preclude the possibility of gradients in specific utilizable substrates, accounting for only a small and therefore undetectable fraction of the total DOC.

Although our results suggest that similar microbiological processes occur in both the eastern and western basins of the Cariaco Trench, several significant chemical differences have been observed. The HS^- concentration in the western basin is consistently less than in the eastern basin, whereas the ATP concentrations are nearly twice as great as in the eastern portion. The relatively small density gradients in the Cariaco Trench may facilitate periodic renewal of the deep anoxic waters (DEUSER, 1973). If oxygen-rich Caribbean water intermittently enters the anoxic zone of the Cariaco Trench across the sill near Farallon Centinela (see Fig. 1), as suggested by RICHARDS and VACCARO (1956), then *in situ* oxidation of the HS^- could occur, resulting in reduced concentrations of HS^- at depth. In contrast to the western basin, the distribution of HS^- within the eastern portion of the Trench shows a consistent increase toward a maximum concentration at the bottom (Fig. 4), with no apparent chemical evidence for vertical downward advection of oxygenated water.

In conclusion, the distribution of microorganisms within the anoxic waters of the Cariaco Trench appears to be maintained by the following processes:

(1) relatively high rates of primary production in the surface waters as a result of coastal upwelling of nutrients (RICHARDS, 1960);

(2) oxidation of photosynthetically derived organic matter by anaerobic bacteria within the upper portions of the anoxic zone;

(3) a natural enrichment of sulfide-oxidizing bacteria, which require both oxygen (or nitrate) and reduced sulfur compounds for chemosynthetic fixation of CO_2, at or near the interface;

(4) vertical upward diffusion of utilizable dissolved organic substrates into the deepest portions of the water column, primarily as a result of fermentation reactions occurring within the organic-rich sediments.

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