Reports

Deep-Sea Primary Production at the Galápagos Hydrothermal Vents

Abstract. *Dense animal populations surrounding recently discovered hydrothermal vents at the Galápagos Rift sea-floor spreading center, 2550 meters deep, are probably sustained by microbial primary production. Energy in the form of geothermally reduced sulfur compounds emitted from the vents is liberated during oxidation and used for the reduction of carbon dioxide to organic matter by chemosynthetic bacteria.*

The Galápagos Rift, located approximately 640 km west of Ecuador and 330 km northeast of the Galápagos Islands, is part of the global mid-oceanic ridge system. In May 1976, several potential temperature anomalies identified as hydrothermal discharges were detected above the central volcanic ridge of the spreading axis with the unmanned Deep-Tow vehicle of the Scripps Institution of Oceanography (*1*). A subsequent analysis of the underwater photographs obtained during the passage of this vehicle through the hydrothermal fields revealed a correlation between the discharge centers and the occurrence of dense benthic communities dominated by bivalve mollusks (*2*). The area associated with the communities was restricted to the immediate proximity of the heated effluent as determined by positive temperature anomalies) and occurred nowhere else in the area of the photographic survey (*3*).

During February and March 1977, this oceanic site was revisited by a team of geologists, geophysicists, and geochemists using the extended research capabilities of the unmanned vehicle *Angus* and the deep-sea research submersible *Alvin* of the Woods Hole Oceanographic Institution. Most of the results, including a detailed description of the topography, bathymetry, geology, and chemistry of the individual vent fields, have been published (*4, 5*). The extraordinary biological discoveries recorded during that expedition prompted biologists at several universities and institutions to organize a joint Galápagos Rift Biology Expedition, which took place during January 1979 (*6*).

The typically sparse, slow-growing populations characteristic of most deep-sea environments are generally considered to be food-limited, ultimately deriving their nutritional needs from that small fraction of euphotic primary production which reaches greater depths by sedimentation or advective transport. In contrast, the occurrence of hydrogen sulfide in the water emitted by the Galápagos Rift vents suggests the existence of a restricted area of high chemoautotrophic-microbial productivity as the basis of the food chain supporting the animal populations (*4, 5*). A general report on the first microbial observations deals with physiological characteristics of bacterial isolates obtained from the vent waters, microbial growth on surfaces near the vents, and a discussion of bacterial sulfur oxidation as the source of energy for the reduction of CO_2 to organic carbon (chemosynthetic primary production) (*7*). Data on ^{13}C depletion in the tissue of a mussel collected near the vents suggested chemoautotrophic bacteria as the food source (*8*). Several unique adaptations in various other invertebrates appear to enable these organisms to harvest microorganisms by filtration and grazing (*6*).

In this report we describe preliminary data on the microbial biomass and activity in the vent waters in terms of microscopic cell count, adenosine 5′-triphosphate (ATP), total adenylates (A_T), ratios of guanosine 5′-triphosphate to adenosine 5′-triphosphate (GTP : ATP), and uptake of $^{14}CO_2$. Water was collected in situ and in precise locations relative to the vent discharges by two techniques adapted for use with *Alvin*: (i) sterile Niskin samplers and (ii) a newly designed pumping system (*9*). In addition to the water samples, scrapings obtained from various solid substrata (for example, rocks, shells, and animal surfaces) and gut contents of collected invertebrates were used for enrichment culture experiments and for microscopic studies.

The number of microbial cells in the

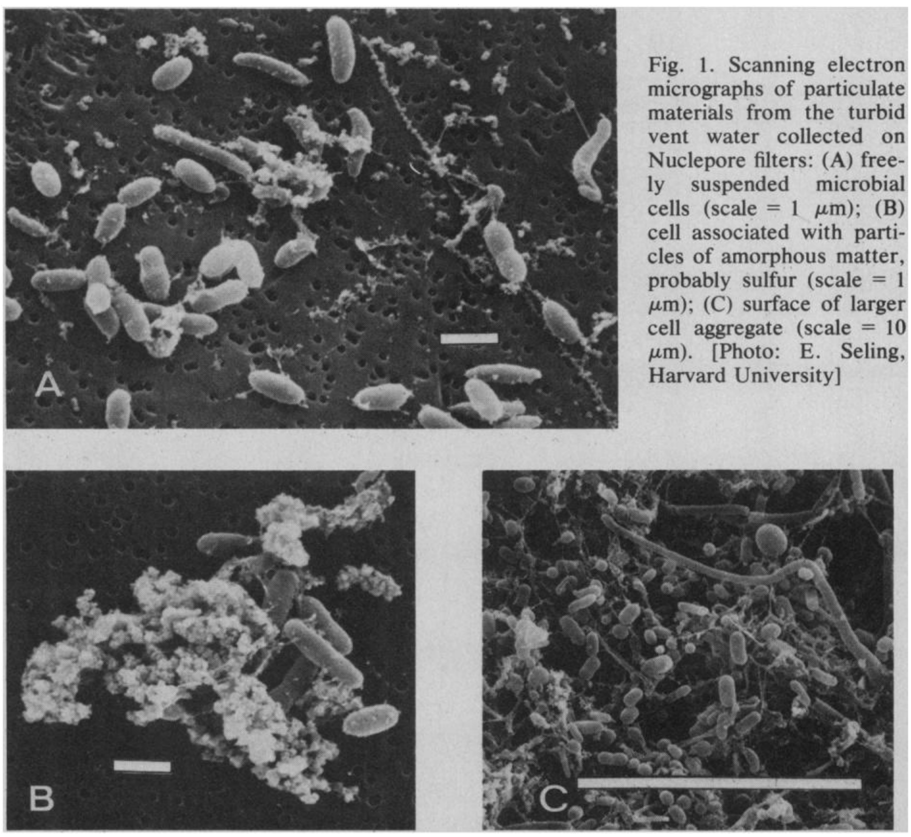

Fig. 1. Scanning electron micrographs of particulate materials from the turbid vent water collected on Nuclepore filters: (A) freely suspended microbial cells (scale = 1 μm); (B) cell associated with particles of amorphous matter, probably sulfur (scale = 1 μm); (C) surface of larger cell aggregate (scale = 10 μm). [Photo: E. Seling, Harvard University]

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Table 1. Adenosine 5′-triphosphate (ATP), total adenylates (A_T), and the ratio of guanosine 5′-triphosphate to adenosine 5′-triphosphate (GTP : ATP) in the residual material on filters and in particles which settled from the turbid water collected by two sampling systems from one of the Galápagos Rift vents (Garden of Eden, dive 883). The values in parentheses represent ± 1 standard deviation from the mean.

Sampling system	Filter or particles	*N*	ATP	A_T	GTP : ATP
Pump	12-μm Nuclepore	3	360 (± 71) ng liter^{-1}	819 (± 240) ng liter^{-1}	0.42 (± 0.03)
	984-H Reeve-Angel	6	537 (± 107) ng liter^{-1}	1373 (± 320) ng liter^{-1}	0.62 (± 0.09)
Niskin bags	984-H Reeve-Angel	7	491 (± 151) ng liter^{-1}	1494 (± 553) ng liter^{-1}	0.86 (± 0.17)
Pump and Niskin bags	Particles	8	1943 (± 1143) ng g^{-1} *	4248 (± 2031) ng g^{-1} *	0.89 (± 0.35)

*Dry-weight basis.

slightly turbid and shimmering water emitted from the vents, determined by epifluorescence microscopy on Nuclepore filters, was found to be in the range of 5×10^5 to 10^6 ml^{-1}. Because of fluctuating dilution with ambient seawater at any distance from the vents, this number can be expected to vary greatly. Also, the presence of clumps containing bacterial cells and nonliving particulate matter in varying proportions make a calculation of biomass from these numbers difficult. Very high cell numbers, up to 10^9 ml^{-1}, were reported in preserved water samples from an earlier cruise (*5*).

Scanning electron micrographs of the Nuclepore filters show suspended cells (Fig. 1A) of a rather uniform morphological appearance. Similar cells are found in small clumps (Fig. 1B), and aggregates up to 100 μm in diameter show a large variety of morphological types (Fig. 1C).

For the measurement of cellular nucleotides, we extracted and assayed the filtered particulate materials by using a minor modification of methods described in (*10*). Extremely high concentrations of ATP (and A_T) were detected in all of the vent samples ($\bar{x}_{ATP}$ = 500 ng liter^{-1}; $\bar{x}A_T$ = 1445 ng liter^{-1}), indicating a substantial population of viable microorganisms (Table 1). If an average microbial C : ATP ratio of 200 to 500 is used to convert to living biomass carbon (*11*), there would be approximately 100 to 250 μg of microbial cell carbon per liter of vent seawater. By comparison, most deep-sea environments contain less than 10 μg of total particulate organic carbon (living plus nonliving) per liter, the vast majority of which is nonliving particulate matter (≥ 95 percent of the total). Although we have not measured the ratio of biomass carbon to total carbon for the Galápagos vent waters, the high concentration of living carbon (as determined by ATP), and the characteristically low C : N ratios of most microbial cells (C : N, ~ 3 to 5) indicate that this particulate organic carbon should be an excellent food source for any organisms capable of ingesting it.

Over 60 percent of the total ATP biomass is present as particles larger than or equal to 12 μm (Table 1). In addition, larger particles (< 1 mm), which settled out of the water samples by gravity, were found to contain between 0.8 to 3.1 μg of ATP per gram (dry weight). This suggests that the majority of cells are present as clumps or are associated with nonliving particulate materials. This size distribution of organic carbon is important in an assessment of the harvesting (feeding) capabilities of the various types of filter and suspension feeders.

In order to compare the microbial biomass of the hydrothermal vent with that of the water column, a vertical profile (0 to 2400 m) of samples was obtained, extracted, and analyzed as before (*10*) (Fig. 2). The absolute ATP and A_T concentrations, as well as the characteristic depth variations are comparable to those of other published oceanic profiles. The data indicate that the microbial ATP biomass within the particular vent water is 334 times greater than that in the "control" deep-water samples collected at 2400 m (501 ng liter^{-1} for vent water versus 1.5 ng liter^{-1} for the 2400-m sample) and 3.9 times greater than that in the productive surface waters. These results demonstrate a high productivity and narrowly localized source of biomass at the vents.

Since the GTP : ATP ratio in microbial cells is positively correlated with the growth rate, this ratio has been suggested as an index of the rate of cellular biosynthesis (*12*). The GTP : ATP ratios of the Galápagos vent microbial communities (Table 1) are comparable to those reported from productive intertidal sediments of the Southern California coast and are higher, by a factor of 5 to 10, than the mean ratios measured in the water column of the Southern California Bight (*12*). By comparison, the productive surface waters (50 to 100 m) overlying the region of the Galápagos vents had GTP : ATP ratios ranging from 0.16 ± 0.08 to 0.17 ± 0.09. At all water depths greater than 500 m, GTP was undetectable (that is, GTP : ATP ≤ 0.075). These data suggest that the microbial populations at the hydrothermal vents are growing at a faster rate than the surface-collected populations mentioned

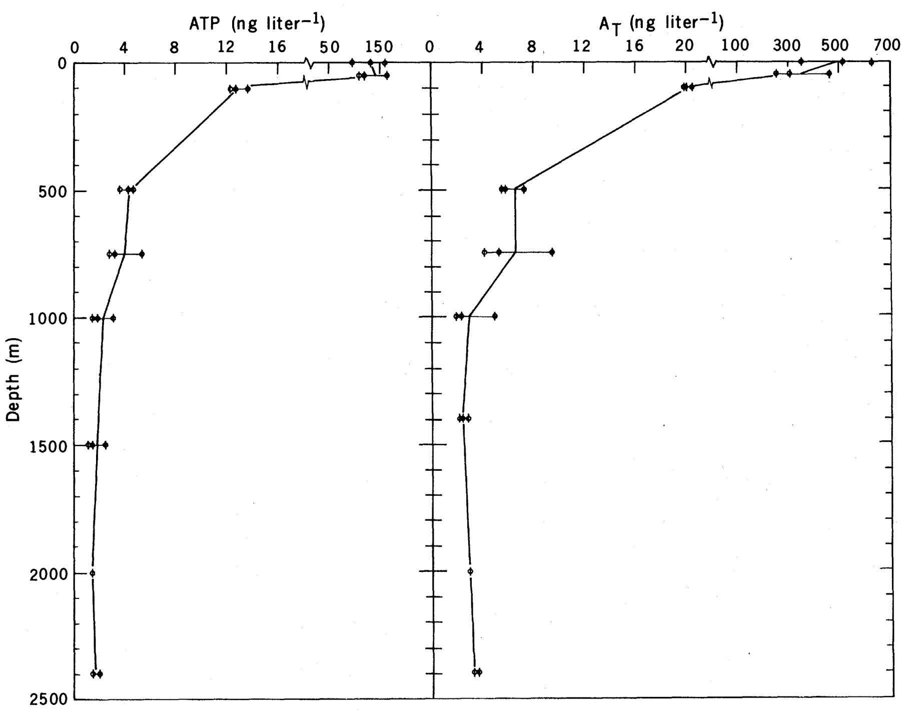

Fig. 2. Profiles of adenosine 5′-triphosphate (ATP) and total adenylates (A_T) in the water column near the Galápagos Rift vents.

above. Experiments conducted in pressurized culture vessels or in situ growth rate studies will have to be conducted to confirm this result.

The uptake of $^{14}CO_2$ as a result of the assumed chemosynthetic oxidation of H_2S was measured in situ. It was planned that an array of 200-ml syringes, precharged with the radiolabeled material and filled by *Alvin* in situ, be deposited for a 4- to 6-day incubation period approximately a meter away from the vents. Because of a mechanical problem, the scheduled recovery dive was canceled and the samples were retrieved after a 10-day delay. Since the recycling of the CO_2 in a closed system will lower the values of carbon incorporation with time, the obtained data must be considered conservative. In spite of this, they are considerably higher than in similar experiments conducted at the interfaces of H_2S to O_2 of the Black Sea and the Cariaco Trench (*13*). Of the 200 isolates obtained, those tested thus far show a considerable variability in CO_2 fixation.

Our preliminary results indicate a high production of metabolically active bacterial biomass in the water emitted from the investigated Galápagos hydrothermal vents. Although complementary data on the stoichiometric transformation of reduced sulfur, and iron and manganese as well, to a more oxidized form cannot be obtained in the presence of a substantial spontaneous (chemical) oxidation, we feel confident that the striking quantity of CO_2 fixation observed is, in fact, bacterial chemosynthesis. This form of primary production represents the basis of the food chain sustaining the dense populations of higher organisms discovered around the vents. In view of the complexity of the entire vent system and the limited amount of sampling possible, a useful quantification of deep-sea primary production is quite out of reach at this time.

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Mass Measurement at the National Bureau of Standards: A Revision

Abstract. *In 1975, the results of a series of mass measurements undertaken by the National Bureau of Standards were published in* Science. *The inconsistencies reported seemed to depend on barometric pressure. An inference to be drawn from the report is that buoyant forces on objects weighed in air are somehow incorrectly accounted for by the usual appeal to Archimedes' principle in which the density of air, ρ, is computed from an equation of state. The magnitude of the unexpected effect was estimated as approaching 1 milligram in 1 kilogram over a pressure range from 0.5 to 2.0 atmospheres for objects having a volume difference of 200 cubic centimeters. In a new experiment at the National Bureau of Standards, in which more elaborate and precise equipment was used, the calculation of air density from the atmospheric variables is confirmed to within 0.05 percent, hence within the uncertainty usually claimed for the air density and buoyancy calculations.*

Several years ago a monitory paper from the National Bureau of Standards (NBS) (*1*) reported the discovery of what was termed an "anomaly" in the weighing at various altitudes of objects nominally equal in mass but differing in density (D). The reported effect emerged as a finding of a set of measurements carried out in several laboratories. Kilograms of low density ($D \sim 2.7$ g cm^{-3}) appeared to lose mass at high-elevation sites and kilograms of high density ($D \sim 16$ g cm^{-3}) seemed to gain, when compared to standard kilograms ($D \sim 8$ g cm^{-3}). The greatest departure, an apparent loss of 1 mg kg^{-1}, was recorded at an elevation of 1600 m above mean sea level. Because the observed anomalies appeared only in weighings which required a substantial correction for buoyancy in air and because the magnitude of the anomalies was a function of air density ρ, the source of the peculiar results has been sought in some aspect of the buoyancy correction. The reported effect, if confirmed, would be of consequence in the determination of the fundamental constants and in precise force measurements.

The warning appearing in *Science* was the result of the analysis of three exploratory experiments. In these experiments the correction for the buoyancy of the air was made through the use of hydrostatically determined volumes of the artifacts and through use of an algorithm, or equation of state, for calculating ρ. The algorithm used the pressure, temperature, relative humidity, and CO_2 fraction of the air (*2*). The algorithm consists of the ideal gas law with small corrections for the nonideality of the constituents of the air. Such calculations are usually assigned an uncertainty of about 0.04 percent, or less, of ρ.

In these experiments, a failure of the algorithm to calculate ρ accurately under the various conditions would manifest itself as apparent differences in mass. The data on weighings made at the different sites and under various conditions did indeed yield an apparent variation in mass, about five times the maximum expected uncertainty arising from the calculation of ρ (*1*). The losses in mass, if interpreted as resulting from errors in the calculation of ρ, show the calculation to be in error by 1 percent per atmosphere of pressure change.

Subsequent to the publication in *Science*, a careful recalculation of the equation for the density of moist air was car-

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