Cah. Biol. Mar. (1998) 39 : 249-252

Global hydrothermal primary production rate estimated from the southern East Pacific Rise

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It had been speculated that photosynthetic primary production in the surface ocean regulates microbial production in deeper seawater layers through rapid transportation of biogenic products via dense, heavy faecal pellets excreted by zooplankton. Recent findings, however, on numerous microbial populations in deep-sea hydrothermal environments (i.e. Karl et al., 1980; Winn et al., 1986; Maruyama et al., 1993) are changing conventional concepts on the deep-sea microbial world. This is because volatile and reduced compounds derived from axial magma or the earth's mantle as dissolved in the hydrothermal system, such as methane, hydrogen, hydrogen sulphide, manganese and iron, stimulate the chemosynthetic growth of microorganisms even at deep-sea levels. To date, however, little is known about the microbial chemosynthetic primary production rate in global hydrothermal environments, in contrast to the large number of reports on photosynthetic primary production rate in the euphotic marine surface.

Huge amounts of volatile and reduced compounds discharged from worldwide hydrothermal activity appear to transfer substantial amounts of biogenic material from ocean-bottom marine environments. Higher biological production and biogeochemical processes in the area of global oceanic ridges presumably are greatly stimulated or modified by this upward flux of biogenic materials, including living microbes. Thus, top priority should be given to study on hydrothermal primary production rate in deep-sea ecology. At present, however, we face difficulties in the estimation of the global hydrothermal primary production rate by such a direct method as measuring the in situ carbon assimilation rate common in euphotic surface marine research, because of the wide variety of energy sources and habitats of microorganisms in such extreme deep-sea environments.

To date, the deep-sea hydrothermal ecosystem is thought to reach 100 to 100,000 times more in animal biomass than that of ambient deep-sea; e.g., 2 to 8.5 kg wet weight m^{-2}, as the standing stock of benthic macrofauna around hydrothermal vents on the northern East Pacific Rise (Gage & Tyler, 1991), compared to 0.01 to 100 g wet weight m^{-2} in the general deep-sea at depths between 1000 to 3000 m. (Rowe, 1983). Although a considerable number of benthic animals in hydrothermal regions, such as a tube-worm *Riftia pachyptila* Jones, 1981 and large-sized bivalves *Calyptogena magnifica* Boss & Turner, 1980 and *Bathymodiolus thermophilus* Kenk & Wilson, 1985 are known to have developed symbiotic relationships with chemoautotrophic bacteria (Gage & Tyler, 1991), free-living microorganisms must also be important as a potential food source for many suspension-feeding zooplankton and benthic animals.

The southern East Pacific Rise (S-EPR) between 13°40' and 18°40'S is a representative superfast-spreading mid-ocean ridge with a full spreading rate of ca. 15 cm yr^{-1}. In 1993 and 1994, we conducted Ridge Flux'93 cruises via the R/V *Melville,* Scripps Institution of Oceanography, and MODE'94 cruises via the R/V *Yokosuka,* with a manned submersible, *Shinkai 6500,* Japan Marine Science and Technology Center, for an extensive study of the S-EPR region. The hydrothermal flux in this superfast-spreading region has proved to be the highest among mid-ocean ridge systems (Urabe et al., 1995). Volatile and metallic components in hydrothermal plumes show a wide variety due to the evolution of the system (Feely et al., 1996; Ishibashi et al., 1997). However, little is known about microbial population and production scales in this robust hydrothermal region.

A dense microbial population was found in water columns between the seafloor (~2600 m) and about 2300 m below the sea surface along the 500-km-long survey area of the S-EPR in 1993. Microbial cells, mostly cocci less than 1 µm in length, existed up to the order of 10^4 cells ml^{-1} over the ridge axis at 15°00’, 16°30’, 17°00’, 17°30’, 18°10’, and 18°30’S (Fig. 1). Except for seafloor venting sites, the highest level of cell densities, exceeding $5x10^4$ cells ml^{-1}, was observed between 2300 and 2600 m. The cell abundance corresponded well in general to the location of maximum nephelometer intensity, while it was not usually accompanied by stronger anomalies of hydrothermal indicators in detailed vertical profiles, suggesting a “donut” distribution of microorganisms. Such a high density was found exclusively in the southern part (17°20’S-18°40’S) of the survey area such as Stations RM23, 24, and 29 (Fig. 1). Microbial populations on the across-ridge section at Stn. RM11 (14°59’ to 15°05’ S) also showed that the high cell density appeared to be limited to the deep-sea region over and around ridge segments (Fig. 1), indicating the vital contribution of hydrothermal input to microbial primary production. A similar across-ridge distribution pattern in the microbial population was found in nephelometer intensity, particulate carbon (P-C), and nitrogen (P-N) concentrations.

The strong correlation between cell density and nephelometer intensity in the whole surveyed region (Fig. 2a) suggests that a significant part of the suspended particulate matter consists of microbial cells and their debris. Cell density in the south region between 17°20’S and 18°40’S, where the significant enrichment of volatile gases in the source fluid is observed (Urabe et al., 1995), made higher correlation to both particulate sulphur (P-S) and methane concentrations than that in the north (Fig. 2 b, c). Since little correlation was found between cell density and other hydrothermal indicators observed, we assume that the microbial abundance in the plume may be primary regulated by such chemoautotrophic energy sources as reduced sulphur, methane and hydrogen which consist in volatile components discharged in the early magma explosion process. In addition, microbial growth would not be rate-limited by inorganic nitrogen and phosphate concentrations in the S-EPR (Fig. 2 d,e,f). It is highly likely that hydrothermal primary production is regulated by energy sources rather than nutrient sources, unlike in the surface euphotic zone.

Excess microbial cell number and excess amount of particulate carbon in the S- EPR were calculated based on along- and across-ridge observations. We estimated the total excess microbial number (x) in the surveyed region at 8.6×10^{22} cells by using the equation of $x = (A - B) v$, in which A is the mean cell density in the hydrothermal plume; B is the background cell density in this region; and v is the total water volume, 3086 km^3, obtained from anomalous dimension of about 10’ longitude (18.5 km) in width, 5° latitude (556 km) in length, and 0.3 km in height (Fig. 1). In the same way, the excess amount of P-C in this region could be calculated as approximately 6.5×10^7 kg. Atomic C:N ratio analysis indicated that most of the particulate material

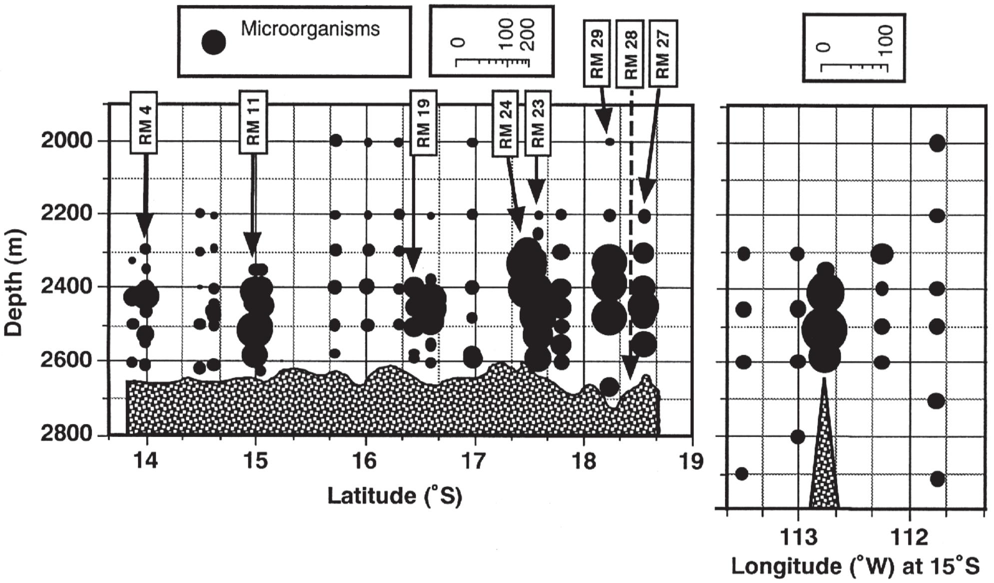

Figure 1. Along- and across-ridge distributions of microbial cell density observed during R/V *Melville* cruise of November to December 1993. The size of closed circles is proportional to the cell density, which was measured by direct cell counting under an epi-fluorescence microscope. Stations in across-ridge section locate between 14°59’ and 15°05’ S. Representative sampling stations are shown by RM number. The cross section of the ridge segment (shaded) is only schematic. New black smokers were found around Stns. RM 4, 24, 28, and 29 north in submersible *Shinkai 6500* dives of September to November 1994.

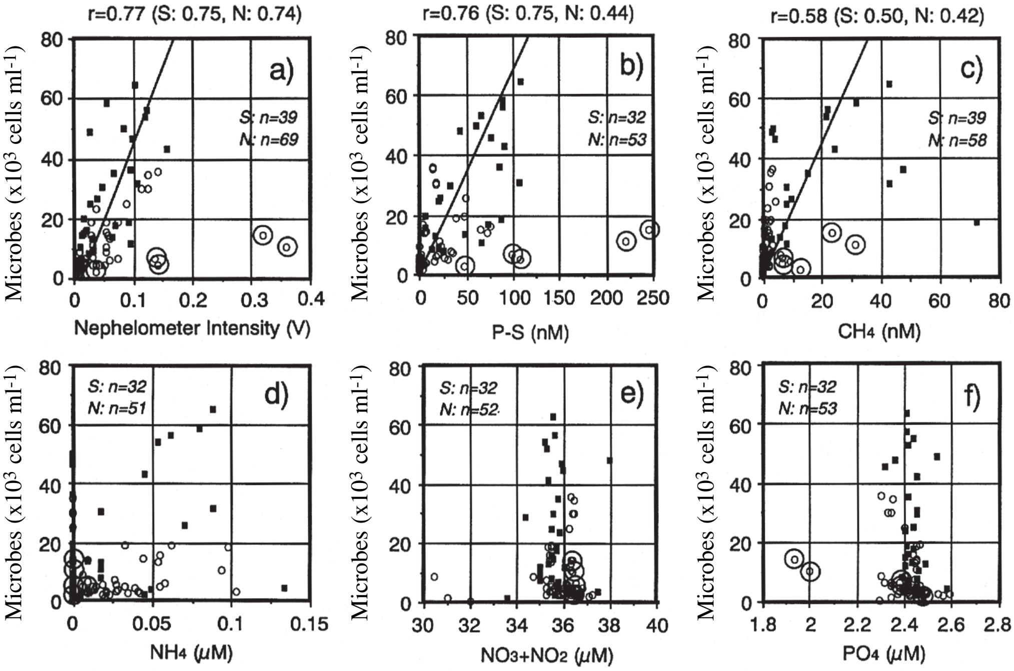

Figure 2. Microbial cell density versus hydrothermal indicators and inorganic nutrients in samples from *Melville* cruise of 1993. The correlation line was made from all samples except for five with strong hydrothermal evidence, indicated by circled dots ◎, as the appearance of many black particles and H_2S smell in sample treatment processes. Samples from the south region (17°20'-18°40'S; ○) and the north region (13°40'-17°00'S; ■) are shown separately. Correlation factors in parentheses were calculated separately by using samples from the south (S) and north (N) regions.

obtained from the hydrothermal plume region in the S-EPR consists of fresh biogenic materials, rather than those sinking and decaying from the sea surface.

Total hydrothermal net primary production (HNPP), including both chemoautotrophic and chemoorganotrophic, in the S-EPR region could be obtained from the division of the estimated excess P-C amount by a turnover rate of hydrothermal plumes. Total net production rate in the S-EPR region is then calculated as 3.3×10^8 kg yr^{-1} of particulate carbon. This HNPP rate corresponds to 0.0008 to 0.002% of the total photosynthetic net primary production (PNPP) rate in the sea, i.e., 20 to 44 x 10^{12} kg C yr^{-1} (De Vooys, 1979). To evaluate the total HNPP rate in entire aphotic oceanic ridges, the rate estimated in the S-EPR must be amplified by 144, from the total ridge length (80,000 km) and the observed ridge length (l = 556 km). Since plume frequency and intensity are proportional to the spread of oceanic ridges and a mean spreading rate is estimated at 40 mm yr^{-1} for global ridges, the rate must be corrected by a conversion factor around 0.27. Considering that the composition of chemosynthetic energy sources should vary in time and space due to the evolution of the hydrothermal system, we assume that the total HNPP rate in the ocean may vary from 5 to 24 x 10^9 kg C yr^{-1}, which corresponds to 0.01 to 0.12% of the total PNPP rate in the sea.

This calculation of excess P-C amount in the S-EPR could still be an underestimation. Although we limit the total water body of hydrothermal plumes to 3086 km^3 in this calculation, based on microbial population anomaly, P-C anomaly seemed to be wider than the microbial population anomaly. Since POC concentration in the south Pacific Ocean, 10 to 20°S at 150°W, is reported at 6 to 8 μg C l^{-1} at depths from 1000 to 3000 m., the minimum concentration of 12 μg C l^{-1} which we used as a base P-C concentration in this region should make an underestimation for the total water volume, not only the base concentration. We also have to include the chemosynthetic production rate of dissolved organic carbon (DOC) in the calculation. Considering these factors, we would conclude that the real HNPP might be in the range from 0.01 to 1%, possibly on the order of 0.1% of the PNPP in the sea.

This HNPP scale may be insignificant in the total primary production on earth, but is not negligible in deep-sea environments because the amount of particulate carbon exported from the ocean surface to the deep sea at 2000 to 5000 m could be estimated as only 4 to 8%. Percentage of the downward carbon flow for the PNPP would be less than 3% in depths below 2000 m (Suess 1980). We therefore calculate that the new production from the hydrothermal activity corresponds to 1 to 25% of the total imported carbon flow to the deep-sea region. This estimate would be comparable to the downward carbon flow from the surface to the deep-sea level in the vicinity of actively spreading regions and enough to affect biological and biogeochemical processes in the middle- to deep-sea layers even far from oceanic ridges. How do these large amount of biogenic materials act in the deep ocean? Where is a main microbial growth field in the ridges and how fast are they growing? How many different microbial communities are there in heterogenous hydrothermal environments? Our recent study shows that a significant portion of microbial production in hydrothermal waters along the S-EPR originates from subsurface extreme environments. We need to exploit different approaches and technologies from those used in surface seawater for an overall understanding of the hydrothermal primary production mechanism.

Acknowledgements

We are grateful to officers and crew of the R/V *Melville* and the R/V *Yokosuka* for their support during the cruises. We also thank the diving team staff of the *Shinkai 6500* for their technical support and Nozomi Ytow and Michinari Sunamura for their technical assistance during the *Melville* and *Yokosuka* cruises, respectively. This study was supported by a grant for "International Cooperative Research on the Energy and Mass Flux of Ridge Crests (Ridge Flux project)" from the Science and Technology Agency of Japan.

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