The Journal of the Oceanological Society of Korea
Vol. 26, No. 3, pp. 255-261, September 1991

Bacterial Biomass and Production in the Water Column Over two Central North Pacific Seamounts

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中北部 태평양 海山上 수층의 박테리아 생체량과 생산력

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Bacterial abundance and production in the water column over two seamounts (Horizon Guyot and Magellan Rise) in the central North Pacific were studied in March 1987. Bacterial abundance ($0.9-2.3\times10^8$ l^{-1}) in surface waters during the study period were in the lower limit of the values reported for oligotrophic areas. Further, bacterial abundance in mesopelagic zone (mostly$<5\times10^7$ l^{-1}) was much lower than that reported from other tropical areas. Bacterial production (20-466 ng C l^{-1} d^{-1}) in surface waters was also low compared to other oligotrophic oceanic environments. However, comparison of bacterial production with the earlier reported values of primary production from these regions suggested a significant role of bacteria in the utilization of organic matter in the surface waters. Though data on distribution of bacterial production are limited in this study, further studies on spatial distribution of bacterial production on both small and large scales in very oligotrophic aquatic environments are suggested to be necessary.

중앙 북부 태평양의 두개의 해산(Horizon guyot와 Magellan rise) 상의 수층에서 박테리아의 생체량과 생산력이 1987년 3월에 조사되었다. 이 기간에 관찰된 표층수의 박테리아 개체수는($0.9-2.3\times10^8$ l^{-1}) 빈영양 해역에서 보고된 박테리아의 개체수에 비해 낮은 값을 나타냈다. 또한 mesopelagic zone의 박테리아 개체수도(대개 $<5\times10^7$ l^{-1}) 다른 아열대 지역에서 보고된 것보다 훨씬 낮았다. 표층수에서의 박테리아 생산력(20-466 ng C l^{-1} d^{-1}) 또한 다른 빈영양 해역과 비교시 낮았다. 그러나 표층수의 박테리아 생산력을 이 지역에서 발표된 일차 생산력과 비교한 경우, 유기물의 이용에 있어서 박테리아의 역활이 중요한 것으로 추정되었다. 이 연구에서 보고된 박테리아 생산력의 공간적 분포에 대한 자료는 충분하진 않으나, 매우 빈영양인 수서 환경에서 소규모 그리고 대규모적 공간상의 박테리아 생산력 분포에 대한 연구의 필요성을 제시하고 있다.

INTRODUCTION

Bacterial biomass and production are now well recognized as important factors in marine food web dynamics (Azam *et al.*, 1983, 1990; Cole *et al.*, 1988; Sherr and Sherr, 1988). Bacterial biomass can be a significant fraction of particulate organic carbon in the marine water column (Cho and Azam, 1988; 1990) and bacterial production has been found to require a significant fraction of primary production in the euphotic zone from various aquatic environments (Fuhrman and Azam,

Table 1. Sampling stations for studies of bacterial parameters during a 1987 cruise.

Date	Stn. No.	Water column depth (m)	Coordinates	Seamount	Location
March 4	109	1454	19° 18.8'N 168° 59.3'W	Horizon	Center
March 5	112	1843	19° 26.0'N 169° 03.7'W	Horizon	North flank
March 8	121	4928	19° 48.7'N 169° 07.7'W	Horizon	Open site
March 11	126	*	19° 25.8'N 169° 04.6'W	Horizon	North flank
March 11	128	1792	19° 10.5'N 168° 56.3'W	Horizon	South flank
March 17	135	3098	07° 04.1'N 176° 52.3'W	Magellan	Center
March 22	147	**	07° 04.9'N 176° 53.0'W	Magellan	Center

*There was no measurement of water column depth, but the depth was similar to station 128.
**There was no measurement of water column depth, but the depth was similar to station 147.

1982; Larsson and Hagstrom, 1982; Cole *et al.*, 1988). Furthermore, bacteria have been reported to utilize a significant fraction of sinking flux into the ocean's interior (Cho and Azam, 1988) and into the benthic boundary layer (BBL; Smith *et al.*, 1986, 1987).

Participating a study on carbon flux in BBL of two central North Pacific seamounts, I could have limited opportunities to study distributions of bacterial abundance and production and the role of bacteria in organic matter decomposition in the water column. The studied areas have been reported to have primary production ranged from 15-60 g C m^{-2} y^{-1} (Berger *et al.*, 1987), and can be regarded to be oligotrophic. In this report, unique data of bacterial abundance and production in the areas are presented.

MATERIALS AND METHODS

During a cruise in the central North Pacific to Horizon and Magellan seamounts in Feb.-March 1987, a horizontal transect over Horizon Guyot with total of 4 profiles including an open ocean station for comparison was taken. Over Magellan Rise no transect was available, but 2 profiles were taken on two different dates over the center of the seamount. Locations of sampling stations during this study are shown in Table 1. Seawater samples were collected by using Niskin bottles mounted on a rosette-CTD (conductivity, temperature, depth) in the water column. All the bottles were acid-cleaned before use. In the benthic boundary layer (BBL), a Niskin bottle attached to the submersible "Alvin" was used to collect seawater samples.

Bacterial abundance was measured by epifluorescence microscopy after staining bacteria with acridine orange (Hobbie *et al.*, 1977). Bacteria were also enumerated in the material collected in the sediment traps, kindly provided by W.W. Wakefield (for details of trap design and deployments, see Smith *et al.*, 1989). Briefly, sediment traps were deployed 100 m above the summit station at the Horizon Guyot (1,390 m) and Magellan Rise (3,000 m and 3032 m). Samples from each collection cup were filtered through precombusted, preweighed GF/C filters, and stored frozen. In the laboratory, a section of each filter was examined for bacterial abundance (Hobbie *et al.*, 1977) after resuspending bacteria by vigorously vortexing the piece of filter in filter-sterilized seawater in vials. Bacterial production was measured by the [methyl-^{3}H]thymidine (80.9 Ci $mmol^{-1}$; New England Nuclear, Boston, Massachusetts) incorporation method (Fuhrman and Azam, 1982). Trichloroacetic acid (TCA) extraction (total macromolecular labeling) and determination of [^{3}H] labeling in the DNA fraction by acid-base treatments were essentially the same as the method of Fuhrman and Azam (1982). Bacterial production was calculated from thymidine incorporation rates into DNA by using a conservative conversion factor of 1.18×10^{18} cells per mole thymidine incorporated into DNA (Riemann *et al.*, 1987).

Shipboard measurements of bacterial production were restricted to the upper 1000 m of the water column, where pressure effects on growth were ex-

pected to be small (Jannasch and Wirsen, 1982). In the BBL, in situ incubation was done. For in situ measurements of bacterial production in the BBL, a 'syringe array sampling device' was mounted, manipulated, and deployed by Alvin at the sampling depth (Smith *et al.*, 1986); this device could simultaneously operate 8 syringes of 60 m*l* (4 syringes for thymidine incorporation, 3 for blank, and 1 for bacterial count). A 20 μ*l* aliquot of [methyl-^{3}H]thymidine was dried on a piece of acid-cleaned Teflon, and the Teflon piece was put inside syringes to achieve a final concentration of 5 mM. Fifty m*l* of seawater was reproducibly collected in each syringe. For blank controls, mercuric chloride solution (1 mM) was added to the well of the device, which the syringe needle penetrated upon activation. After an in situ incubation time of about one day, the device was retrieved and samples were processed as described above for measurements of bacterial abundance and production. Some size-fractionation studies were carried out for bacterial abundance and thymidine incorporation by bacteria for samples from the BBL. Samples were gravity-filtered through a 0.8 μm Nuclepore filter and filtrates were collected for bacterial abundance and production measurements (see above). Bacterial carbon was calculated on the basis of 20 fg C bacterium^{-1} (Lee and Fuhrman, 1987). Discussion on bacterial carbon content will not be made here, but readers can refer recent papers dealing that matter (Cho and Azam, 1990; Roland, 1990). For the calculation of carbon demand (sum of production and respiration) by bacteria, 60% of assimilation efficiency in bacteria (Calow, 1977) was assumed.

RESULTS AND DISCUSSION

Bacterial abundance in the water column, BBL, and sediment trap

A notable observation was that bacterial abundance in the ocean's interior (up to 1 km depth) over two seamounts was much lower than that reported from other tropical regions. Even in the euphotic zone bacterial abundance was in the lower limit of the values reported for oligotrophic waters (Bird and Kalff, 1984; Cho and Azam, 1990).

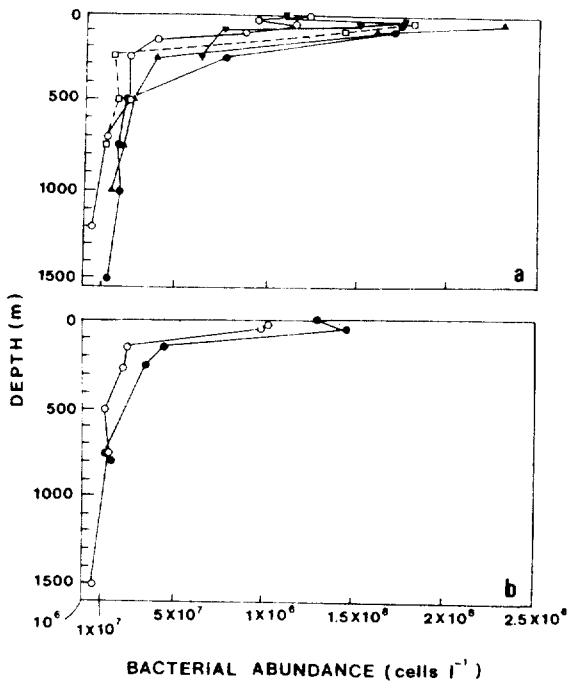

Fig. 1. Depth-distribution of bacterial abundance in the water column. (a) Over the Horizon Guyot; closed circles represent March 4, open squares March 5, closed triangles March 8, open circles evening cast on March 11, and closed inverted triangles noon cast on March 11, 1987. (b) Over the Magellan Rise; open circles represent March 17, and closed circles March 22, 1987.

Bacterial abundance was higest in the upper 0-50 m of the water column over the seamounts and steadily decreased with depth (Fig. 1). Horizon Guyot surface bacterial abundance ($1.2-2.3\times10^8$ cells l^{-1}) was higher than that for Magellan Rise ($0.9-1.5\times10^8$ cells l^{-1}). In a recent study in the central North Pacific gyre, bacterial abundance in surface waters was found to be $>5\times10^8$ cells l^{-1} (Cho, 1988). In the Atlantic ocean during a deep mixing period, bacterial abundance was ~$3-4\times10^8$ cells l^{-1} (Ducklow, 1986). Bacterial abundance in surface waters found in polar regions, like Antarctic, the Drake passage (Hanson *et al.*, 1983) and Eastern Canadian Arctic (Harrison *et al.*, 1987), were similar to or even sometimes higher

Table 2. Bacterial abundance, biomass carbon, size-fractionation, and production in the benthic boundary layer above the Horizon and Magellan seamounts.

Elevation above seamount surface (m)	Abundance ($\times 10^7$ l^{-1})	Calculated biomass carbon (μg C l^{-1})	Prodution* (ng C l^{-1} d^{-1})	Size-fractionation (% in <0.8 μm) Abundance	Production
Horizon Guyot					
1	1.42	0.3	5.8	94	NA
5	0.55	0.1	5.1/0.9	NA	NA
10	1.31	0.3	2.3	NA	NA
20	1.30	0.3	NA**	87	NA
Magellan Rise					
1	0.93	0.2	0.6	68	73
5	8.01	1.6	3.1	81	87
10	7.36	1.5	NA	96	NA
20	1.15	0.2	NA	37	NA

*Of [^{3}H-methyl]thymidine incorporation into macromolecules, an average of 52% was in DNA for seawater samples collected at the same time as in situ samples but incubated at atmosphere pressure. The same value was used for calculation of bacterial production in other samples in both seamounts.
**NA: Data are not available.

Table 3. Bacterial abundance and particulate organic carbon (POC) in sediment traps. Bacterial carbon (BOC) was calculated on the basis of 20 fg C cell $^{-1}$ (Lee and Fuhrman, 1987). Traps numbered 131 and 103 were deployed at 3032 m and 1390 m depth, respectively, over the summit cap of both seamounts, and trap 129 was deployed at a depth of 3000 m over the base of Magellan Rise.

Trap identification	Organic carbon* per trap (mg C)	Bacterial abundance per trap (x10^9 cells)	Bacterial carbon per trap (μg C)	BOC:POC flux ratio (%)
Horizon Guyot				
103	0.872	0.92	18.4	2.2
Magellan Rise				
131 #1**	2.214	0.68	13.6	0.6
131 #2	2.390	0.82	16.4	0.6
129 #1	7.550	0.56	11.0	0.2

*Values from Reimers and Wakefield (1989).
**For a more detailed description of sediment traps, see Smith *et al.* (1989).

than that found in this study areas. All these comparisons indicate possibly low biological activity in the areas (see below). Below the surface waters, bacterial abundance (>250 m to <100 m) over seamounts was similar at all sites (Fig. 1), and the bacterial abundance ($1-3\times10^7$ l^{-1}) was up to 10 fold lower than that from other tropical zone of oceanic areas (Spinrad *et al.*, 1989; Cho and Azam, 1988, Carlucci *et al.*, 1986; Alldredge and Youngbluth, 1985; Sorokin *et al.*, 1985). At a depth of 1000 m, bacterial abundance was $1-2\times10^7$ l^{-1} in both seamount areas, and is also much less than that reported from other regions, such as central North Pacific gyre (Cho and Azam, 1988) and Indian ocean waters (Sorokin *et al.*, 1985). Even in Antartic waters of Drake passage, bacterial abundance ranged $1-5\times10^7$ l^{-1}. However, bacterial abundance in the BBL increased significantly, especially over Magellan Rise ($1-8\times10^7$ cells l^{-1}, Table 2). Bacteria were in most cases in free-living state (Table 2). In the BBL, bacterial abundance was significantly higher than that in waters much above the BBL in both areas, consistent with the finding of increased bacterial abundance in the BBL (Smith *et al.*, 1986).

Bacterial carbon (BOC) captured in sediment

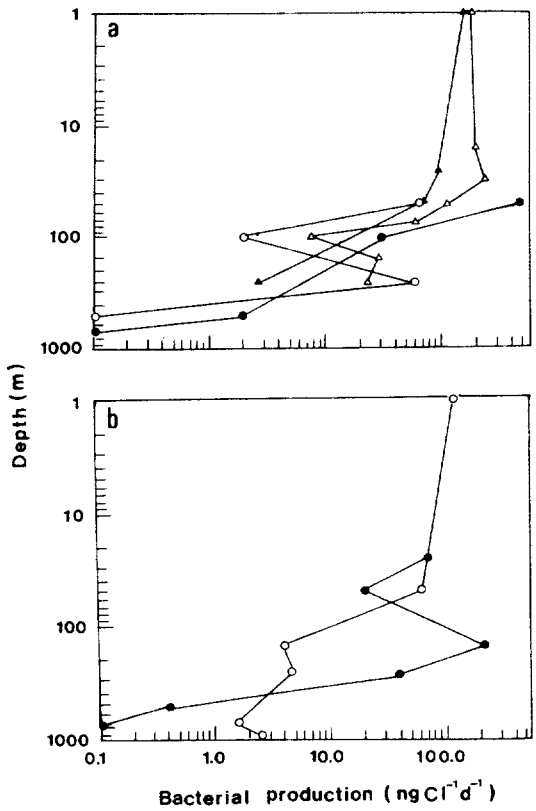

Fig. 2. Depth-distribution of bacterial production in the water column. (a) Over the Horizon Guyot; closed circles represent March 4, open circles March 8, closed triangles evening cast on March 11, and open triangles noon cast on March 11, 1987. (b) Over the Magellan Rise; closed circles represent March 17, and open circles March 22, 1987.

traps is shown in Table 3. Bacterial carbon (BOC) flux represented a very small portion of particulate organic carbon (POC) flux (0.2−2.2%). The BOC : POC flux ratio values are in agreement with those of Duclow *et al.* (1985, 0.3−3.3%; mean of 1.2%) and Taylor *et al.* (1986, <5%). The BOC : POC flux ratio calculated from sediment trap materials over Horizon Guyot was 3.7 times higher than that over Magellan Rise. This appears to be in accordance with the higher bacterial abundance in the water column over Horizon Guyot than over Magellan Rise. This apparently indicates that BOC flux might depend on bacterial abundance in the water column, and that the BOC : POC ratios might reflect scavenging of bacteria by particles sinking through water of different bacterial abundance. To test this possibility, I made a close examination of the data of Duclow *et al.* (1985), Taylor *et al.* (1986), and this study. Results show that BOC : POC flux ratios did not change systematically with depth nor with POC flux (data not shown). Thus, the BOC : POC flux raitos reflect the combined results of the following processes in the water column: scavenging of bacteria by the particles, bacterial production on sinking particles, and detachment of bacteria from the particles.

Bacterial production in the water column and BBL

Depth-profiles of bacterial production (Fig. 1) were rather complex, with subsurface maxima (to 466 ng C l^{-1} d^{-1}) between 50-200 m. Calculated turnover time of bacterial assemblages (from the data in Figs. 1 & 2) in surface waters in this study were very long, on the order of 10-200 days. Historic values of primary production range from 15-35 g C m^{-2} y^{-1} over Horizon Guyot and from 35-60 g C m^{-2} y^{-1} over Magellan Rise (Berger *et al.*, 1987). Thus, comparison of bacterial production data from this study with those primary production values indicates that in the surface waters a significant fraction (from 38-83% for Horizon Guyot and from 23-39% for Magellan Rise) primary production would be required to support measured carbon utilization by bacteria. Bacterial production was in the order of 100 ng C l^{-1} d^{-1} at the surface and decreased by 2-3 orders of magnitude at 1000 m (Fig. 2). The magnitude of bacterial production in the water column (surface and mesopelagic) over two seamounts is lower (5- to 10-fold), like bacterial abundance, than those in other oligotrophic environments such as the central North Pacific gyre (Cho and Azam, 1988). With respect to both bacterial production and abundance, the seamount water columns during the study period might be ultraoligotrophic.

Another noteworthy result from this study is that there is an indication of large-scale heterogeneity of bacterial production found among stations over Horizon Guyot (7- to 15-fold) at the 50-150

m depth interval (Fig. 2a). Such a large spatial heterogeneity in bacterial production has not been well noted in other oceanic euphotic zones, including the oligotrophic regions such as the central North Pacific gyre (Cho, 1988). So far, it is not known what causes such a large-scale heterogeneity. But, it seems that in very oligotrophic waters distribution of organic matter sources for bacteria must be highly heterogeneous. Thus, it may be important to take this high spatial variability into account in studies of the role of bacteria in organic matter utilization and food web dynamics in ultraoligotrophic waters.

Measurements of bacterial production in the BBL were often difficult because of high blank values. This may have been due to the presence of a high particle load (grey colored material was seen on filters), possibly derived from resuspension of sediments in the BBL. The bacterial production values in the BBL (Table 2) were much higher than those at 1000 m. Interestingly, 3- to 21-fold variations in bacterial production and 5- to 7-fold variations among the 4 replicate samples taken by a syringe-array sampler were found over Horizon Guyot and Magellan Rise, respectively. Since the between syringe distances range from 5-30 cm, this suggests that the sources of utilizable organic matter available to bacteria might not be randomly distributed in the BBL.

To summerize, data on the distribution of bacterial abundance and production suggest that the water column above seamounts during the period of this study might be ultraoligotrophic. A significant role of bacteria in organic matter cycling is suggested in the surface waters over the seamounts. Large- and small-scale heterogeneous spatial variations of bacterial production found in surface waters and in the BBL suggest further understanding of spatial distribution of bacterial activity in such oligotrophic waters necessary.

ACKNOWLEDGMENTS

I thank F. Azam for helpful comments on the manuscript and K.L. Smith for the invitation to join the cruise. I appreciate C. Reimers and W.W. Wakefield for use of sediment trap samples and their data. This research was supported by NSF grants OCE 84-17913 (K.L. Smith) and OCE 87-16994 (F. Azam).

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Received May 31, 1991
Accepted August 28, 1991