

26. BACTERIAL PROFILES IN DEEP SEDIMENT LAYERS FROM THE EASTERN EQUATORIAL PACIFIC OCEAN, SITE 851¹

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ABSTRACT

Bacterial depth profiles were obtained from sediment samples taken from a deep-water (3761 m) site in the eastern equatorial Pacific to a depth of 317.4 m below seafloor (mbsf) using the Acridine Orange direct count (AODC) technique. Bacterial cells were observed at all depths and dividing/divided cells were observed in 47 of 58 samples. Numbers were consistent with a low organic carbon environment. Total counts decreased from near-surface levels of 2.08×10^8 to 4.88×10^5 cells/cm³ at 12 mbsf before increasing to a local maximum of 9.33×10^6 cells/cm³ at 91 mbsf. The maximum number of dividing/divided cells (4.85×10^7 cells/cm³) were detected at the near-surface. They decreased to "not detectable" by 4.5 mbsf and did not display a sustained increase in numbers until approximately 30 mbsf, with a peak at 2.62×10^6 cells/cm³ at 91 mbsf. The increase in counts below 30 mbsf was attributed to a change in the depositional history resulting in elevated buried organic carbon concentrations between 30 and 290 mbsf. Dividing/divided cell counts may provide an index of the bioavailability of this organic carbon. Inorganic and organic chemical profiles correlated significantly with bacterial counts and indicated a zone of limited bacterial activity (sulfate reduction and methanogenesis) between 30 and 290 mbsf. The reasons for the existence of a band of low total counts and almost negligible dividing/divided cell counts between 1.5 and 25–30 mbsf is not understood, as the chemical profiles suggest that bacteria should be both present and active.

When compared with equivalent bacterial counts taken on sediment samples from the Peru Margin and Japan Sea (areas of higher oceanic productivity) and Lau Basin (lower oceanic productivity), near-surface total counts were lower than those in the Lau Basin. This is attributed to considerably lower concentrations of organic carbon (0.06% compared with 0.27%) in the near-surface sediments at this site owing to greater water depth. The rate decrease in both the total and dividing/divided cell counts over the top 80 mbsf was less than that observed in the Lau Basin (but greater than in the Peru Margin or Japan Sea); however, this observation is probably related to the depositional history of the site, rather than the overlying oceanic productivity.

INTRODUCTION

Sediment bacteria play a central role in the biogeochemical cycling of the elements (Jørgensen, 1983) and are intimately involved in both remineralization and selective preservation of organic matter in marine sediments. The importance of their presence and activity at the sediment surface has long been accepted (Sørensen, 1978; Sørensen and Jørgensen, 1987). Here, they are at the interface between the water column and the sediment, where sinking detrital microaggregates concentrate in an oxic or dysoxic environment to produce a favorable habitat for bacterial growth (Lochte and Turley, 1988; Turley and Lochte, 1990). It is only relatively recently, however, that their importance in much deeper sediments has become more widely accepted, with more thorough investigations of indirect evidence suggesting that bacteria are active to significant depths (e.g., chemical changes in pore water, production of kerogen, concretion formation, and isotopic evidence; Krumbein, 1983).

Early evidence of the existence of deep sediment bacterial populations (Rittenberg, 1940; ZoBell, 1958; Davis, 1967) was restricted by the techniques available to obtain and culture sediment samples, which resulted in an elevated potential for contamination of deep sediment layers by the more active surface sediments. Using more rigorous methods, recent workers have reported the detection and cultivation of bacteria to 200 m below seafloor (mbsf) (Oremland et al., 1982; Belyaev and Ivanov, 1983; Bianchi, 1986) and their presence has been demonstrated to more than 400 mbsf in aquifers (White

et al., 1983; Balkwill, 1989; Erlich and Ghiorse, 1989; Phelps et al., 1989; Chapelle and Lovley, 1990; Fredrickson et al., 1991).

In marine environments, positive evidence for low levels of anaerobic bacterial activity (methanogenesis and sulfate reduction) has been found in sediments to 167 mbsf in the Gulf of Mexico and the North Atlantic (Whelan et al., 1986; Tarafa et al., 1987). Cragg et al. (1990) and Parkes et al. (1990) described bacterial populations associated with significant levels of sulfate reduction and methanogenic activity in a comprehensive study of sediments from the Peru Margin to 80 mbsf. More recently, significant bacterial populations linked to low levels of activity have been reported to more than 500 mbsf in sediment samples from the Japan Sea (Cragg et al., 1992; Getliff et al., 1992).

Both the Peru Margin and the Japan Sea are relatively shallow sites (150 and 900 mbsf, respectively) in areas of comparatively high oceanic productivity. Interestingly, results obtained to more than 100 mbsf from the Lau Basin, a deep (2692 mbsf) mid-Pacific site in an area of low oceanic productivity, also revealed bacteria present at all depths sampled, albeit at greatly reduced levels, with counts decreasing at a significantly faster rate with depth when compared to more productive sites (Cragg, in press). Geochemical data provided no indirect evidence for any bacterial activity and the low levels of buried organic carbon reported in the data suggested that the bacterial populations were merely surviving in an extreme low-energy environment.

Ocean Drilling Program (ODP) Site 851 in the eastern equatorial Pacific is a deep-water area (3761 m) with an annual water column primary productivity rate between that of the Lau Basin and the Japan Sea (Berger, 1989). The bulk of the material deposited as sediments onto the seafloor over the last 11 m.y. has consisted of biogenic carbonates in the form of coccoliths and foraminifers and biogenic opal mainly as diatoms with subordinate radiolarians (Mayer, Pisias, Janecek, et al., 1992). Sediment core samples were obtained from this site on Leg 138 to determine the presence, concentration, and depth distribution of sediment bacteria in such an environment.

¹ Pisias, N.G., Mayer, L.A., Janecek, T.R., Palmer-Julson, A., and van Andel, T.H. (Eds.), 1995. *Proc. ODP, Sci. Results*, 138: College Station, TX (Ocean Drilling Program).

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MATERIALS AND METHODS

Shipboard Handling

Sediment samples were removed from 58 core sections, between 0 and 317.4 mbsf, of Holes 851A and 851B (Table 1). Hole 851A was a single mud-line core taken to capture the surficial sediments. Nevertheless, a significant amount of loose sediment will have been displaced during penetration of the corer, and so the sample from 0 mbsf is more properly defined as near-surface. Pollen analysis evidence from similar mud-line cores taken in the Japan Sea suggested that some 60 cm had been lost from the top of the first core (L. Heusser, pers. comm., 1991). Immediately after a core was cut into 1.5-m sections on the outside catwalk, a thin layer of sediment was removed from the section end using a sterile scalpel to expose an uncontaminated surface. A 2-cm³ sample was then taken with a sterile (autoclaved) 5-mL syringe from which the leuc end had been removed. The sample was divided in two with 1 cm³ ejected directly into a tared serum vial containing 9 mL of filter-sterilized (0.2 µm) 4% formaldehyde in artificial seawater and the second 1 cm³ placed in a glass sample vial for wet/dry-weight determination.

Laboratory Handling

Direct Microscopic Observations

Acridine Orange staining and microscopic observations were based on the general recommendations of Fry (1988) with minor modification. Fixed samples were vortex mixed and between 15 and 40 µL added to 10 mL of 2% filter-sterilized (0.1 µm) formaldehyde in 2.5% acetic acid (vol/vol). Acridine Orange (50 µL) was added to give a final concentration of 5 mg/dm³. After 3 min, the solution was filtered through a 25-mm Nucleopore black polycarbonate membrane (Appleton Woods, Birmingham, U.K.) of 0.2-µm pore size. The filter was rinsed with a further 10 mL of 2% filter-sterilized formaldehyde in 2.5% acetic acid and mounted in a minimum amount of paraffin oil under a cover slip. The sediment samples had a particularly high carbonate concentration (approximately 75% with some intervals of 20%–50%; Mayer, Pisias, Janecek, et al., 1992), and the large number of carbonate particles concealed bacterial cells when viewed through a microscope, which necessitated an undesirable dilution of the sample to obtain a reliable count. The use of acetic acid removed this problem by dissolving the carbonate. A check of this technique on two marine sediments from different areas of the world, counting in triplicate both with and without acetic acid, showed no significant difference in either total cell count or dividing cell count between treatments ($F = 0.366$; $d.f. = 1, 8$; $P = 0.56$, and $F = 0.204$; $d.f. = 1, 8$; $P = 0.67$, respectively).

Mounted membrane filters were viewed under incident illumination with a Zeiss Axioskop microscope fitted with a 50-W mercury-vapor lamp, a wide-band interference set for blue excitation, a 100× (numerical aperture = 1.3) Plan Neofluar objective lens, and 10× eyepieces. Bacterially shaped green and red fluorescing objects were counted. Cells on or off particles were counted separately, and the numbers of those on particles were doubled in the final calculations to account for cells hidden from view by particles (Goulder, 1977). Dividing cells (those with a clear invagination) and divided cells (pairs of cells of identical morphology) also were counted.

Porosity and Organic Matter

Sediment wet/dry-weight ratios and porosity were obtained by drying the tared 1 cm³ of sediment to constant weight at 105°C. Organic matter content was estimated by heating subsamples of dried sediment in a muffle furnace at 450°C to constant weight. After the sample had been destructively treated for this measurement, a small random error was detected in the balance, making the data unreliable, and they were discarded. Shipboard data have been used where necessary.

Table 1. List of Leg 138 Holes 851A and 851B samples provided for direct bacterial counts.

Hole	Position	Water depth (m)	Maximum sample depth (mbsf)	Number of samples
851A	2°46.218'N 110°34.308'W	3779.5	4.51	3
851B	2°46.218'N 110°34.308'W	3760.3	317.4	55

RESULTS AND DISCUSSION

A paired sample t-test performed on bacterial count data from congruent depths of the mud-line core of Hole 851A and the first core of Hole 851B showed no significant difference ($P > 0.05$) between the two cores, and the data were combined.

A significance limit was constructed from the data by selecting all counts where fewer than 20 cells in total were enumerated on a membrane and calculating the total count on the basis of a single cell encountered on that membrane. The mean and 95% confidence limits of these results was $1.49 \times 10^5 \pm 1.07 \times 10^4$ cells/cm³. The significance limit was set to the mean plus 95% confidence limit at 1.60×10^5 cells/cm³ or 5.20 log₁₀ units (Fig. 1).

Bacteria were present in all samples to 317.4 mbsf (Fig. 1). The abrupt decline in numbers between the near-surface (2.08×10^8 cells/cm³) and 12 mbsf (4.88×10^5 cells/cm³) represents a 427-fold decrease. This was a local minimum after which counts sharply increased to 2.98×10^6 cells/cm³ by 21.5 mbsf, a six-fold increase on the minimum, and then more gradually increased to 9.33×10^6 cells/cm³ at 91 mbsf, a 19-fold increase, on the minimum. This latter count was the highest obtained below the first near-surface value and was in a local group of relatively high counts between 75.5 and 97.5 mbsf (average = 5.76×10^6 cells/cm³). Thereafter, the numbers of bacteria gradually declined to 1.38×10^6 cells/cm³ at 307.7 mbsf. There was a sharp decrease (approximately 3.7-fold) in cell numbers between this depth and the deepest sample at 317.4 mbsf to 3.73×10^5 cells/cm³, which was the lowest count obtained and represented a 558-fold decrease on the near-surface count. This last sample was taken 6 m above basement (Mayer, Pisias, Janecek, et al., 1992).

Site 851 presently occupies a position near the northern margin of the equatorial high-productivity zone. The average annual primary productivity of the overlying water at this site is therefore relatively high (Berger, 1989), and despite a greater depth than at other ODP sites for which similar bacterial counts have been made (Cragg, in press), these data can be placed between a slightly more productive Japan Sea and a substantially less productive Lau Basin (Table 2). Nevertheless, the greater water depth does reduce the proportion and quality of primary production reaching the seafloor (Jørgensen, 1983). This is revealed in the depth-weighted mean organic carbon content, calculated over the upper 105 m at both sites, of approximately 0.17% for sediments from the Lau Basin Site 834 (derived from Parson, Hawkins, Allan, et al., 1992), compared with approximately 0.10% in the sediments from Site 851 (derived from Mayer, Pisias, Janecek, et al., 1992); a difference that is accentuated when calculations are performed on data from Pleistocene sediments only, with 0.27% organic carbon at Site 834 (0–32 mbsf) compared with 0.06% at Site 851 (0–26 mbsf). This is reflected in lower bacterial counts at both the near-surface and at approximately 80 mbsf compared with the Lau Basin site (Table 2). It is, therefore, perhaps more meaningful to sequence these data according to the overlying water depth from Legs 112 through 138.

Because at approximately 80 mbsf a comparatively high percentage of the near-surface count remains at Site 851 (2.0%), placing the data firmly between Legs 128 and 135, Table 2 is slightly misleading. At 80 mbsf the total count is still increasing from a minimum of 4.88×10^5 cells/cm³ at 12 mbsf to a maximum of 9.33×10^6 cells/cm³ at 91 mbsf. A possible explanation for this inconsistency is provided by evidence of significant variations in the amount of buried deposi-

Table 2. Comparison of direct bacterial count data from ODP legs for total counts and dividing cell counts.

Leg:	Cells/cm ³			
	112 Peru Margin	128 Japan Sea	138 Equatorial Pacific	135 Lau Basin
Hole:	681C	798B	851A/B	834A
Water depth (m):	150	900	3761	2692
<i>Total counts</i>				
Near-surface	(1.5 mbsf) 1.06×10^9	(0 mbsf) 7.82×10^8	(0 mbsf) 2.08×10^8	(0 mbsf) 6.12×10^8
Approximately 80 mbsf	(80.2 mbsf) 3.33×10^8	(78.9 mbsf) 1.71×10^7	(78.5 mbsf) 4.24×10^6	(81.6 mbsf) 7.50×10^5
Percentage near-surface	31	2.2	2.0	1.2
<i>Dividing cell counts</i>				
Near-surface	(1.5 mbsf) 8.84×10^7	(0 mbsf) 6.35×10^7	(0 mbsf) 4.85×10^7	(0 mbsf) 9.75×10^7
Approximately 80 mbsf	(80.2 mbsf) 1.94×10^6	(78.9 mbsf) 1.14×10^6	(78.5 mbsf) 6.60×10^5	(81.6 mbsf) 4.05×10^5
Percentage near-surface	2.2	1.8	1.4	0.4

Notes: Oceanic productivity relationship from Berger (1989). Depth data from Suess, von Huene, et al. (1988; Leg 112); Ingle, Suyehiro, von Breymann, et al. (1990; Leg 128); Parson, Hawkins, Allan, et al. (1992; Leg 135); and Mayer, Pisias, Janecek, et al. (1992; Leg 138), with 0 mbsf, defined according to ODP. Approximately 80 mbsf selected as the comparison depth, as this was the deepest sample counted at Leg 112 Hole 681C (Cragg et al., 1990; adapted from Cragg, in press). Bacterial data from Cragg et al. (1990; Leg 112), Cragg et al. (1992; Leg 128) and Cragg (in press; Leg 135).

tional organic carbon, which is linked to large changes in sedimentation rates over time (Fig. 2). The current deposition rate, estimated over the top 11.2 m of the sediment to be 16.6 m/m.y., is particularly low and is associated with a relatively low buried organic carbon concentration of approximately 0.06%. Additionally, conditions are believed to be only weakly reducing in the top 5 m relative to the nearer-equator Sites 849 and 850 (Mayer, Pisias, Janecek, et al., 1992). In such an environment the bacterial populations are most likely to be dominated by aerobic, microaerophilic, and facultatively anaerobic heterotrophs, which will rapidly metabolize any labile organic carbon leaving only the more recalcitrant carbon to be subsequently buried. This would be demonstrated by a comparatively large surficial bacterial population that abruptly declines in numbers as depth increases (Fig. 1). Clearly, this depositional environment has not always existed. For example, between 29.3 and 103.3 mbsf the deposition rate increased from 10.3 to 59.6 m/m.y. concurrent with an increase in buried organic carbon from 0.08% to 0.18% over an approximately 3.3-m.y. time period (Fig. 2). This increase in organic carbon is coincident with the increase in bacterial counts over the same depth range (Fig. 1).

Significant numbers of dividing cells were present in 47 of the 58 samples (Fig. 1). The highest value was at the near-surface at 4.85×10^7 cells/cm³ after which the count abruptly declined to "not-detectable" by 4.5 mbsf, where it was constant until 15 mbsf. The dividing cell count then increased to 7.41×10^5 cells/cm³ at 21.5 mbsf (1.5% of the near-surface count) before decreasing to not-detectable again by 28 mbsf. From 34 mbsf the count gradually increased to a local maximum of 2.62×10^6 cells/cm³ at 91 mbsf, which represents approximately 5% of the near surface count. Thereafter, cell numbers declined gradually with depth, with recorded nondetectables at 243.6 and 317.4 mbsf.

The dividing cell profile correlates well with that of the total count ($R = 0.908$, $N = 45$, $P < 0.002$), a relationship that has been observed at other sites (Cragg et al., 1990; 1992; Cragg, in press). Comparison with the numbers of dividing cells at the near-surface observed at other sites shows great similarity (Table 2), with 4.853×10^7 cells/cm³ close to the average of 7.447×10^7 cells/cm³. By approximately 80 mbsf dividing cell numbers have reduced to 1.4% of the near-surface count and both this value and the absolute number of dividing cells at 80 mbsf correspond with a descending sequence of sites based on oceanic productivity at each site (Table 2). Nevertheless, as with the total cell

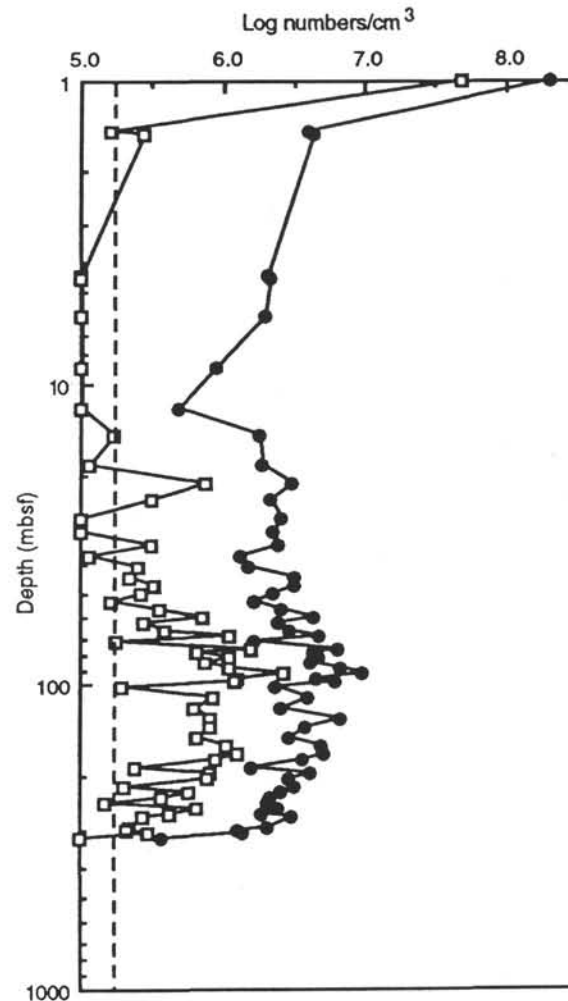


Figure 1. Depth distribution of total bacteria (dots) and dividing/divided cells (squares) to 317.4 mbsf in Holes 851A and 851B (combined data). The dashed line at 5.2 is the calculated detection limit of 1.6×10^5 cells/cm³. (Depth values given on log₁₀ scale to highlight near-surface data.)

count, this view is deceptive in that the numbers of dividing cells were actually increasing, by a factor of nearly 16, over the depth range used for the comparison (1.67×10^5 at 15 mbsf to 2.62×10^6 at 91 mbsf), concurrent with an increase in the organic carbon concentration between these depths (Fig. 2). Again, this emphasizes the importance of attempting to understand the past depositional environment to explain contemporary sediment bacterial distributions.

Numbers of dividing cells are significantly related ($R = 0.610$; $N = 34$; $P < 0.002$) to the organic carbon concentration when calculated over the entire sediment column (Fig. 3). A similar relationship ($R = 0.536$; $N = 34$; $P < 0.002$) can also be demonstrated between the total count and organic carbon levels (data not shown), although the relationship is not as strong. This is not surprising as numbers of dividing cells may well represent a more sensitive index of bioavailable organic carbon than absolute numbers of bacteria in sediment layers where the bacterial populations and the organic carbon have been in intimate contact for perhaps many millions of years.

Geochemical data (Mayer, Pisias, Janecek, et al., 1992) suggest that any bacterial activity would be low at this site. Sodium, magnesium, calcium, and potassium profiles are invariant to the basement. This is attributed to the low organic carbon burial rate, resulting in fewer diagenetic effects, and an open-pore structure in the sediment, owing to the absence of a contiguous chert zone, which resulted in the dilution

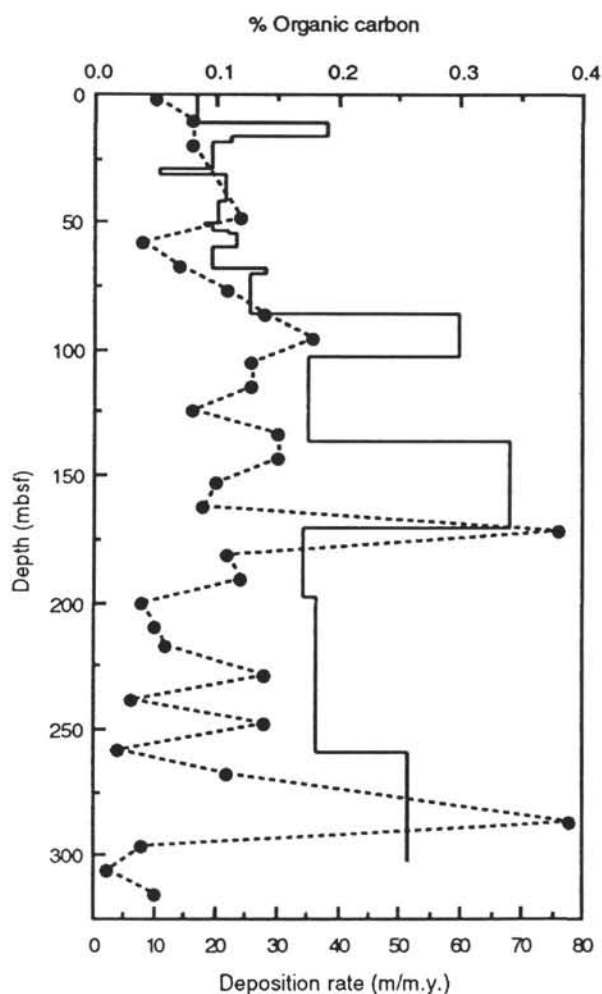


Figure 2. Depth distribution of percentage of organic carbon (dots) and sediment deposition rate (solid line) to 317.4 mbsf at Site 851. (Redrawn from Mayer, Pisias, Janecek, et al., 1992.)

of any localized changes in pore-water chemistry. In addition, no evidence of the vertical advection of pore waters can be seen.

Small, but detectable, changes were seen in concentrations of interstitial ammonia, alkalinity, and sulfate. Values of ammonia increased from 13 Mm at 1.4 mbsf to 101 Mm at 165.8 mbsf before declining to less than 10 mM by 310.7 mbsf (Fig. 4B). Alkalinity showed a similar profile, gradually increasing from 2.95 mM at 1.4 mbsf to a low maximum of 3.84 mM at 165.8 mbsf before declining to near-surface values at 310.7 mbsf (Fig. 4A). Conversely, concentrations of sulfate decreased from 27.31 mM at 1.4 mbsf to a minimum of 25.77 mM at 195.8 mbsf before rising to near-surface values at 310.7 mbsf (Fig. 4C). However, the sulfate profile was not straightforward, as after an initial decline from 27.31 to 26.76 mM between 1.4 and 5.9 mbsf, there was an increase to 28.11 mM at 26 mbsf (the highest concentration recorded) before the major decrease occurred. In addition, methane was present at low levels throughout the sediment core (Fig. 4D). After a relatively high value of 17.7 $\mu\text{L/L}$ at 4.45 mbsf it decreased abruptly to 1.3 $\mu\text{L/L}$ at 13.45 mbsf. Below this depth, a trend of increase with local maxima ($>18 \mu\text{L/L}$) at 149.4, 225.7, and 292.9 mbsf was seen before an abrupt decrease to zero at 310.6 mbsf (Mayer, Pisias, Janecek, et al., 1992). These geochemical profiles indicate a wide zone of slightly reducing pore water between about 30 and 290 mbsf. The variations in pore-water chemistry track changes in the profiles of total bacterial cells and dividing cell count with significant relationships observed between ammonia ($R = 0.949$; $N = 13$; $P < 0.002$, and R

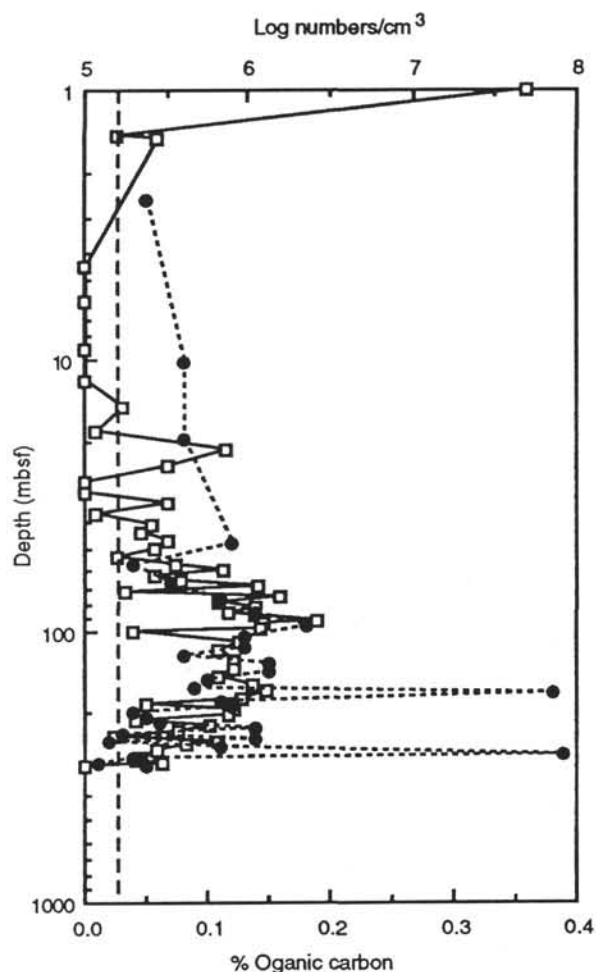


Figure 3. Depth distribution of numbers of dividing/divided bacterial cells (squares) and percentage of organic carbon (dots) to 317.4 mbsf in Holes 851A and 851B (combined data). The dashed line at 5.2 is the calculated detection limit of $1.6 \times 10^5 \text{ cells/cm}^3$. (Organic carbon data from Mayer, Pisias, Janecek, et al., 1992; depth values given on \log_{10} scale to highlight near-surface data.)

$= 0.946$; $N = 10$; $P < 0.002$), alkalinity ($R = 0.791$; $N = 15$; $P < 0.002$, and $R = 0.826$; $N = 13$; $P < 0.002$), and, to a slightly lesser extent, sulfate concentrations ($R = -0.677$; $N = 15$; $P < 0.01$, and $R = -0.628$; $N = 13$; $P < 0.05$) for the total count and numbers of dividing cells, respectively. No such relationship was found between either cell count and methane concentration ($R = < 0.2$). This was expected, as methane gas in sediments will migrate upward and pore-water concentrations at any one depth will depend more on sediment porosity than in-situ bacterial count, particularly in sediments with low bacterial activity. Together with the observed relationship between both total count and numbers of dividing cells with organic carbon concentrations, these data indicate that a limited amount of bacterial activity (sulfate reduction and methanogenesis) is occurring within these sediments. Previous work (Cragg et al., 1990, 1992; Parkes et al., 1990) has produced good correlations between microbial parameters and geochemical data, and there is no reason to think that the implied relationship between the bacterial counts and changes in pore-water chemistry is not a realistic indicator of activity in the in-situ population.

The bacterial profiles between the near-surface and approximately 30 mbsf are puzzling. Organic carbon concentrations are not particularly low (Fig. 2) and yet total counts decrease sharply and the numbers of dividing cells become not detectable by 1.48 mbsf and

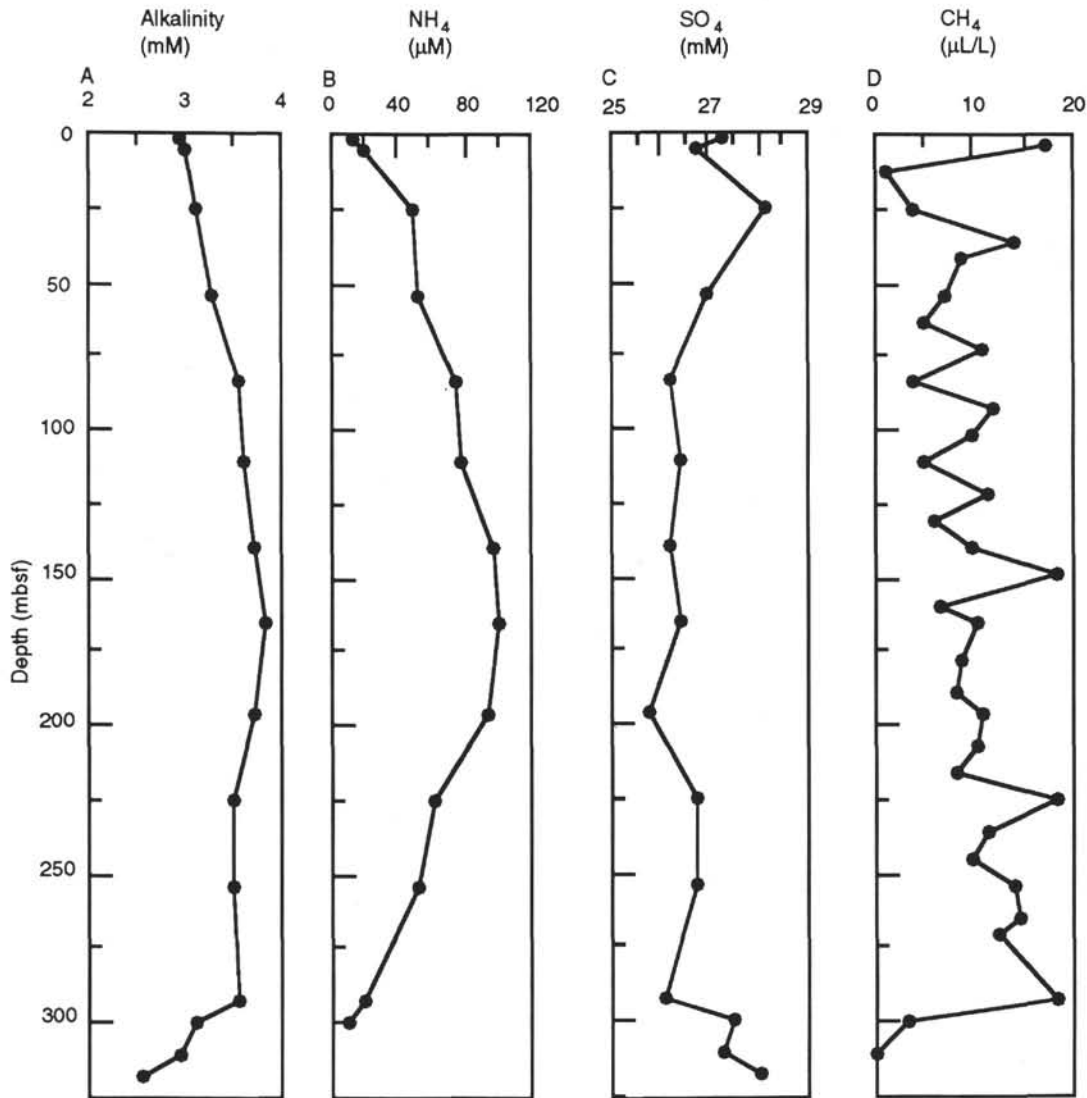


Figure 4. Depth profiles to 317.4 mbsf in Holes 851A and 851B (combined data). A. Alkalinity. B. Ammonia. C. Sulfate. D. Methane. (Redrawn from Mayer, Pisias, Janecek, et al., 1992.)

remain low or absent (Fig. 1). Of the 11 occurrences of nondetectable dividing cells, seven such occurrences are within this zone. It is within this zone, however, that bacterial biomass is usually relatively high (Novitsky and Karl, 1986) and that activity rates are maximal (Fossing, 1990; Jørgensen et al., 1990). Over this same depth range, methane decreases from 17.5 to 1.3 $\mu\text{L/L}$, alkalinity remains relatively constant (Fig. 4B), and sulfate concentrations increase (Fig. 4C), all of which is consistent with negligible bacterial activity. No changes were observed in either the organic or inorganic geochemistry of the porewaters (Mayer, Pisias, Janecek, et al., 1992), which would suggest reasons for the paucity of bacteria and bacterial activity within this zone; the lithostratigraphy recognizes no boundary at the 25- to 30-mbsf level. The only event recorded for this depth interval is the biostratigraphic definition of the Pliocene/Pleistocene boundary at approximately 26.5 mbsf (Mayer, Pisias, Janecek, et al., 1992). The middle Miocene to upper Pliocene sediments below this boundary appear to represent a band of elevated sedimentation rates encompassing most of the sediment column, which indicates a significantly different depositional history over much of the 11 m.y. represented by the sediment column compared to that over the last 1.6 m.y.

SUMMARY

Investigation of these Leg 138 sediment samples has shown low total and divided cell counts consistent with a low organic carbon environment. At the sediment near-surface, total counts, in comparison to similar counts from other ODP sites, suggest that the absolute numbers of bacteria on the sediment surface may be more strongly influenced by the depth of the overlying water rather than the annual primary productivity of that water column. The rate of decrease in bacterial numbers with depth, however, may be linked to the water column productivity. This interpretation is complicated by a rise in buried organic carbon between 30 and 290 mbsf which results in a significant increase in bacterial numbers with depth, unlike the depth profiles at other sites. The relationship between both total count and dividing cells with organic carbon indicate that a limited amount of bacterial activity is taking place in these sediments, and this is supported by the inorganic chemical data and methane levels which indirectly suggest that low levels of methanogenesis and sulfate reduction are occurring within this zone. Dividing cells were detected in all but two samples within the zone; however, both above 30 mbsf

and below 290 mbsf a total of nine samples had no detectable dividing cells. At these depths, apart from the near-surface layers from 0 to 1.5 mbsf, geochemical analyses suggested bacterial activity was probably absent. Interpretation of the bacterial depth distributions at this site requires an understanding of the depositional history of the sediment, and this emphasizes the need to avoid making assumptions relating changes in sedimentary bacterial populations to depositional conditions at the current sediment surface.

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