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3. Bacterial Abundances and Pore Water Acetate Concentrations in Sediments of the Southern Ocean (Sites 1088 and 1093)[1]

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ABSTRACT

Bacterial populations and pore water acetate concentrations were quantified at two sites in the southeast Atlantic sector of the Southern Ocean during Ocean Drilling Program (ODP) Leg 177. Bacterial abundances in the carbonate-rich, low organic carbon Sites 1088 and 1093 were lower than the general trend for bacteria in deep marine sediments. Site 1088, which is ~10° closer to the equator and only approximately half the water depth of Site 1093, had the lowest bacterial populations. Calcium carbonate was ~10 times more abundant in Site 1088 sediments (average = 88.2 wt%) compared to Site 1093 (average = 9.2 wt%). Thus, neither latitude nor water depth is as significant as organic carbon in controlling bacterial distributions. Including data for carbonate-rich sediments to a previous model, the global bacterial biomass in marine sediments extrapolates to ~10.2% of living carbon in the surface biosphere. Pore water acetate concentrations at both sites were generally low (0–15 µM). At Site 1093 many acetate peaks (to 110 µM) were present, probably because of the presence of localized diatom-rich laminae in the sediments. The low acetate concentrations are in marked contrast with data from gas hydrate sediments at Blake Ridge (ODP Leg 164), where concentrations exceeded 15,000 µM by ~700 m below seafloor, suggesting that high acetate concentrations may be a characteristic of gas hydrate sediments and not the general situation in deep marine sediments.

[1]Wellsbury, P., Mather, I.D., and Parkes, R.J., 2001. Bacterial abundances and pore water acetate concentrations in sediments of the Southern Ocean (Sites 1088 and 1093). *In* Gersonde, R., Hodell, D.A., and Blum, P. (Eds.), *Proc. ODP, Sci. Results,* 177, 1–12 [Online]. Available from World Wide Web: <http://www-odp.tamu.edu/publications/177_SR/VOLUME/CHAPTERS/SR177_03.PDF>. [Cited YYYY-MM-DD]
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INTRODUCTION

The deep bacterial populations in marine sediments have been documented in a range of different oceanographic settings around the world (Parkes et al., 2000). Bacteria have been detected in all sites studied, to a current reported maximum depth of 842 m below seafloor (mbsf) (Shipboard Scientific Party, 1999). The biomass of bacteria in deep sediments is considerable, estimated at ~10% of living carbon in the surface biosphere (Parkes et al., 1994). However, this estimate was based on data from five sites located between 18°S (Leg 135 [Cragg, 1994]) and 48°N (Leg 139 [Cragg and Parkes, 1994]), which were mainly hemipelagic mud/clays. Data from only two low-productivity, carbonate-rich sites were included. Extending the model to include data from more southerly regions and carbonate-dominated sediments could significantly alter this estimate.

The presence of active bacteria in sediments of extreme depth is surprising. Bacterial activity in near-surface sediments rapidly removes substrates for growth (Nedwell, 1984; Capone and Kiene, 1988). How can bacteria be present in sediments up to 15 m.y. old? What are they using as an energy source?

In anaerobic sediments, pore water volatile fatty acids (VFA) can reflect the pathways and intensity of organic matter degradation, as they are important metabolic intermediates in anaerobic bacterial metabolism (Capone and Kiene, 1988; Sørensen et al., 1981; Parkes et al., 1989). The most important of these intermediates is acetate, which accounts for ~100% of sulfate reduction (Parkes et al., 1989), the dominant anaerobic process in marine sediments (Jørgensen, 1982), and between 61% and 85% of methanogenesis, the dominant anaerobic process in freshwater sediments (Kuivila et al., 1989). Normally, rates of production and consumption of acetate are closely coupled, and the pore water concentration is maintained at ≤15 µM (Wellsbury and Parkes, 1995).

In the gas hydrate sediments of the Blake Ridge (Ocean Drilling Program [ODP] Leg 164), acetate and other VFA increased by three orders of magnitude with increasing depth (Wellsbury et al., 2000; Egeberg and Barth, 1997). This dramatic increase in deep acetate was associated with increased bioavailability of organic matter on heating and burial (Wellsbury et al., 1997) and may provide a mechanism for continued bacterial activity to even greater depths. However, it is crucial to determine whether elevated deep acetate concentrations are present at non-hydrate sites.

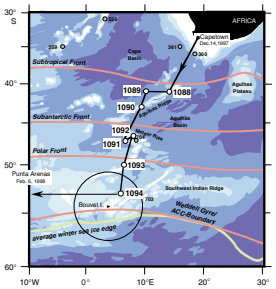
ODP Leg 177 provided an opportunity not only to extend our knowledge of bacterial abundances to new regions, but also to investigate how widespread deep acetate generation is in sediments.

MATERIALS AND METHODS

Site Description

Bacterial populations and pore water acetate concentrations were quantified at two sites in the southeast Atlantic sector of the Southern Ocean during Leg 177 (Gersonde, Hodell, Blum, et al., 1999). Site 1088 (41°8.163′S, 13°33.770′E) is located on the Agulhas Ridge at a water depth of 2082 m and had a sediment surface temperature of ~2.4°C (Fig. F1). Site 1093 (50°58.596′S, 5°51.924′E) is located ~10° farther

F1. Locations of drill sites from Leg 177, p. 9.



south of Site 1088, at a water depth of 3636 m. The sediment surface temperature was ~2.6°C (Gersonde, Hodell, Blum, et al., 1999).

Shipboard Sample Handling

Direct Bacterial Enumeration

Sediment samples (1 cm^3) were taken for direct determination of bacterial numbers. These samples were taken from the end of selected 1.5-m core sections immediately after the sections were cut on the catwalk and before sealing the section with an end cap. A thin layer of potentially contaminated sediment was removed from the core using a sterile scalpel to expose an uncontaminated surface. A 1-cm^3 sample was then removed using a sterile (autoclaved) 5-mL syringe from which the luer end had been removed. The sample was ejected directly into a sterile serum vial containing 9 mL of filter-sterilized (0.2 µm) 4% (v/v) formaldehyde in artificial seawater.

Pore Waters

Pore water samples were filter sterilized (0.1 µm) and stored, frozen, in 2.5-mL capped vials before transportation back to the laboratory for determination of acetate concentrations by high-performance liquid chromatography (HPLC).

Laboratory Sample Handling

Direct Microscopy

Total numbers of bacteria were determined using acridine orange staining and epifluorescence microscopy (Wellsbury et al., 2000). Formaldehyde-fixed samples were vortex mixed, and 5–10 µL of the fixed sample was added to 10 mL of 2% filter-sterilized (0.1-µm filter) formaldehyde containing 2.5% (v/v) acetic acid to remove any carbonate impurities that autofluoresce under illumination. Acridine orange (50 µL of filter-sterilized 1 g/L solution) was added, and after 3 min of incubation, the solution was filtered through a 25-mm Nucleopore (0.2 µm pore size) black polycarbonate membrane (Costar, United Kingdom). The membrane was rinsed further with 10 mL of filter-sterilized formaldehyde/acetic acid solution and mounted on a glass slide in a minimal amount of paraffin oil under a cover slip.

Mounted membranes were viewed under epifluorescent illumination (Zeiss Axioscop, 50-W mercury vapor lamp, blue excitation, 100× Plan Neofluor oil-immersion objective and 10× eyepiece). Fluorescent bacteria were enumerated; cells were recorded as "on" or "off" particles, doubling the number of cells on particles in the final calculations to account for bacteria beneath the sediment particle. Triplicate membranes were prepared and counted for each sample, with a minimum number of 200 fields of view examined for each membrane. Where replicate log-10 counts differed by more than 0.5, a fourth membrane was prepared. This gives a detection limit of 2.23×10^5 cells/mL (Mather and Parkes, 2000). Blank membranes were also counted periodically to monitor potential contamination.

Pore Water Acetate Determination by HPLC

Pore water acetate concentrations were determined using an enzymatic method described by King (1991). Aliquots (20 µL) of each of (1) bovine serum albumin (BSA, 200 µg/mL), (2) disodium adenosine triphosphate (ATP) (10 mM), (3) coenzyme A (sodium salt, from yeast, 10 mM), and (4) acetyl coenzyme A synthase (20 U/mL, ~4.9 U/mg protein) were added to 1 mL of thawed pore water in a screw-cap 2.5-mL vial with an integral O-ring seal (Sarstedt, Leicester, United Kingdom). The samples were mixed thoroughly and incubated at 37°C for 1 hr before termination by immersion in a boiling water bath for 2 min. Once cool, 800-µL aliquots were transferred to a cooled autosampler at 5°C before separation by HPLC (Dionex). Samples (10-µL injections) were injected onto an analytical column (Supelco LC-18-T, 25 cm × 4.6 mm) with a mobile phase of 0.1-M KH_2PO_4 (pH = 6.0) at 1.0 mL/min, with UV/vis detection at 254 nm.

RESULTS AND DISCUSSION

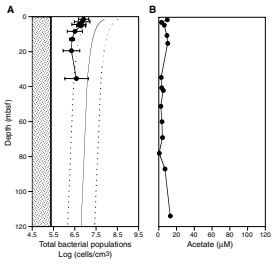
Site 1088

Bacteria were present in all samples from Sites 1088 (Fig. F2A). Total cell counts were generally lower than the trend found at other ODP sites (Parkes et al., 2000). Near-surface samples (1.5 mbsf) contained 8.22×10^6 cells/cm³ and cell numbers decreased slightly with increasing depth to 3.79×10^6 cells/cm³ by 35.5 mbsf, the deepest sample.

Geochemical evidence shows only minimal levels of bacterial activity in Site 1088 sediments (Gersonde, Hodell, Blum, et al., 1999). Sulfate was present throughout the hole with only a small decrease in concentration from the sediment surface (29 mM) to 230 mbsf (~20 mM). The sulfate decrease with depth was strongly correlated with increasing ammonia. Alkalinity was also almost constant with depth, indicating slow rates of organic matter degradation at this site. This was consistent with the low sulfate removal and the generally very low methane levels throughout the hole (4–11 ppmv).

Acetate concentrations in pore waters from Site 1088 were low, in the range 0–15 µM (Fig. F2B). These levels are consistent with a carbonate-rich low organic matter sediment and are similar to those reported in sediments of the carbonate-rich Lau Basin (ODP Leg 135; Haggerty and Fisher, 1994). Although total organic carbon (TOC) contents were not determined at Site 1088 (Gersonde, Hodell, Blum, et al., 1999), calcium carbonate compositions were extremely high (85–95 wt%; average 88.2 wt%). The sediments at Site 1088 were dominated by nannofossil ooze, foraminifer-bearing nannofossil ooze, foraminifer nannofossil ooze, and nannofossil foraminifer ooze (Gersonde, Hodell, Blum, et al., 1999).

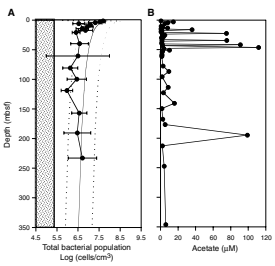
F2. Depth distributions of total bacterial populations and pore water acetate, Site 1088, p. 10



Site 1093

Bacteria were present in all samples from Site 1093 (Fig. F3A). Bacterial populations were higher than those at Site 1088, despite the site location being ~10° farther south and at a much deeper water column. Bacteria were most abundant at the surface (4.87×10^7 cells/cm³) and decreased rapidly with increasing depth, reaching 2.57×10^6 cells/cm³ by 21 mbsf. Below this, populations remained relatively constant, al-

F3. Depth distributions of total bacterial populations and pore water acetate, Site 1093, p. 11.



though numbers increased slightly to 5.14×10^6 cells/cm^3 by the deepest sample at 233 mbsf.

In contrast to Site 1088, the sediments at Site 1093 were diatom-rich pelagic deposits consisting of diatom ooze containing varying proportions of mud, foraminifers, and nannofossils. Calcium carbonate concentrations ranged from 0 to 56.9 wt% with an average of ~9.2 wt%. Geochemical data again indicated that bacterial activity was low at this site. Although TOC varied between 0.34 and 1.21 wt%, with an average value of 0.77 wt%, sulfate was present throughout the hole (Gersonde, Hodell, Blum, et al., 1999). Sulfate concentrations decreased gradually with increasing depth, from 28.4 mM at the sediment surface to 19.4 mM at ~486 mbsf. This decrease was accompanied by a steady increase in ammonia to values of nearly 1500 µM at ~300 mbsf. Methane concentrations were low throughout, ranging between 2 and 19 ppmv, generally increasing with depth.

Pore water acetate concentrations were again generally low, within the 0–15 µM range (Fig. **F3B**). However, in contrast to Site 1088 (Fig. **F2B**), there were several peaks in acetate concentrations (to 110 µM). These peaks may well be associated with the presence of localized diatom-rich laminae in the sediments at Site 1093 (Gersonde, Hodell, Blum, et al., 1999).

General Discussion

The distribution of bacteria in deep-sea sediment generally conforms to the model of Parkes et al. (1994). However, most of the model's data set derives from hemipelagic mud/clay sediments. Bacterial abundances from carbonate-rich, low organic carbon sites have previously been shown to be lower than the general trend for bacteria in deep marine sediments (Parkes et al., 2000). The data from Sites 1088 and 1093 confirm this relationship. It is interesting to note that neither latitude nor water depth seems to be a major control on bacterial distributions, as populations were higher at the deeper, southernmost site. Bacterial numbers were much lower in the carbonate-rich sediments at Site 1088, confirming that organic carbon concentrations are the key control on bacterial distributions.

In general, pore water acetate concentrations in samples from Leg 177 were low, in the range 0–15 µM (Figs. **F2B, F3B**). This is in marked contrast with the data from Leg 164, where concentrations exceeded 15,000 µM by ~700 mbsf (Egeberg and Barth, 1997; Wellsbury et al., 2000). Leg 164 sediments are biogeochemically active zones (Wellsbury et al., 2000), with extensive gas hydrate deposits (Dickens et al., 1997). The results from Leg 177 suggest that the high acetate concentrations in the pore waters of gas hydrate sediments are a special case and not the general situation in deep marine sediments.

Implications for a Deep Bacterial Biosphere

Data from Leg 177 confirm and extend previous demonstrations of a deep bacterial biosphere in marine sediments. Parkes et al. (1994) estimate the biomass of deep sediment bacteria to be ~10% of living carbon in the surface biosphere. Their estimate was based on data from only five sites, mostly hemipelagic mud/clay sediments. However, carbonate-rich sediments account for ~52% of seafloor area (Brown et al., 1989; Rothery and Wright, 1998). If bacterial numbers are lower in carbonate

sediments, then estimates of the global biomass of deep sediment bacteria may be too high based on the general model.

The distribution of bacteria in carbonate-rich and "normal" sediments is shown in Figure F4. Best-fit regression lines show that the distribution of bacteria in the low organic carbon, carbonate-rich sites is very different to "typical" hemipelagic sediments. The depth-integrated bacterial biomass in carbonate-rich sediments to an average oceanic sediment depth of 500 mbsf (Chester, 1990) is 1.0 t/ha organic carbon. This is only approximately two-thirds of the ~1.5 t/ha calculated by Parkes et al. (1994). However, once data from carbonate sites are removed from the general model, the bacterial biomass in "normal" sediments increases correspondingly to 2.2 t/ha. Thus, including data for carbonate-rich sediments, the global bacterial biomass in marine sediments extrapolates to ~10.2% of living carbon in the surface biosphere. This is almost identical to the value calculated by Parkes et al. (1994).

F4. General regression models of bacterial distributions in deep-sea sediments, p. 12.

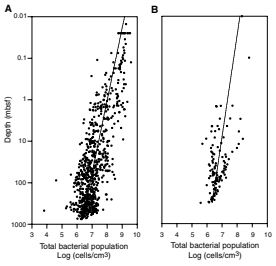


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Figure F1. Locations of drill sites during Leg 177 (Gersonde, Hodell, Blum, et al., 1999). Samples for analysis of bacterial populations and pore water acetate were obtained from Sites 1088 and 1093.

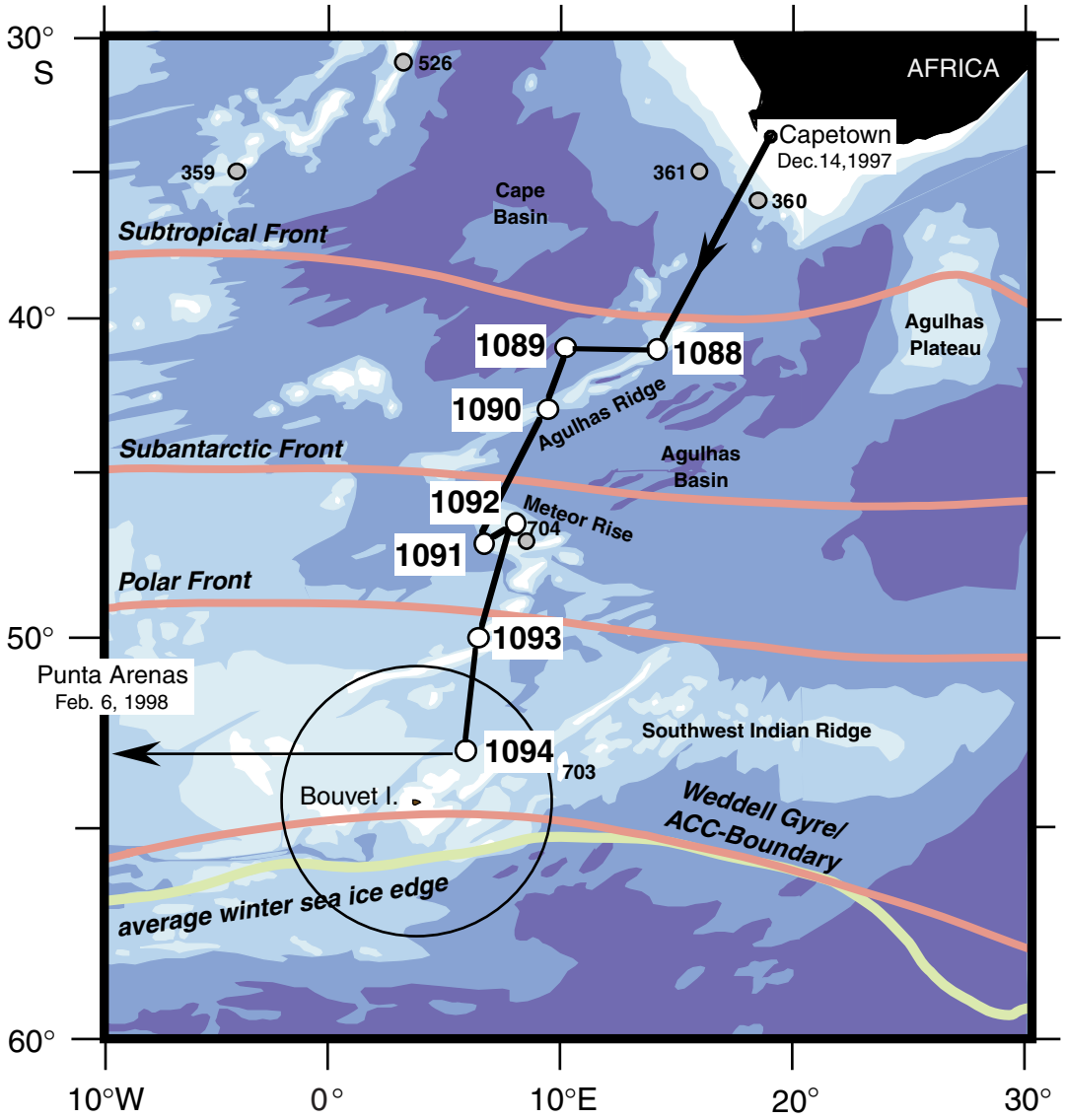

Figure F2. Depth distributions in sediments from Site 1088 of (**A**) total bacterial populations and (**B**) pore water acetate. Solid line = the general model for bacterial depth distributions of Parkes et al. (1994). Dashed lines = the 95% prediction limits of the model. Gray shaded area = data below the detection limit of the technique (2.23×10^5 cells/cm^3).

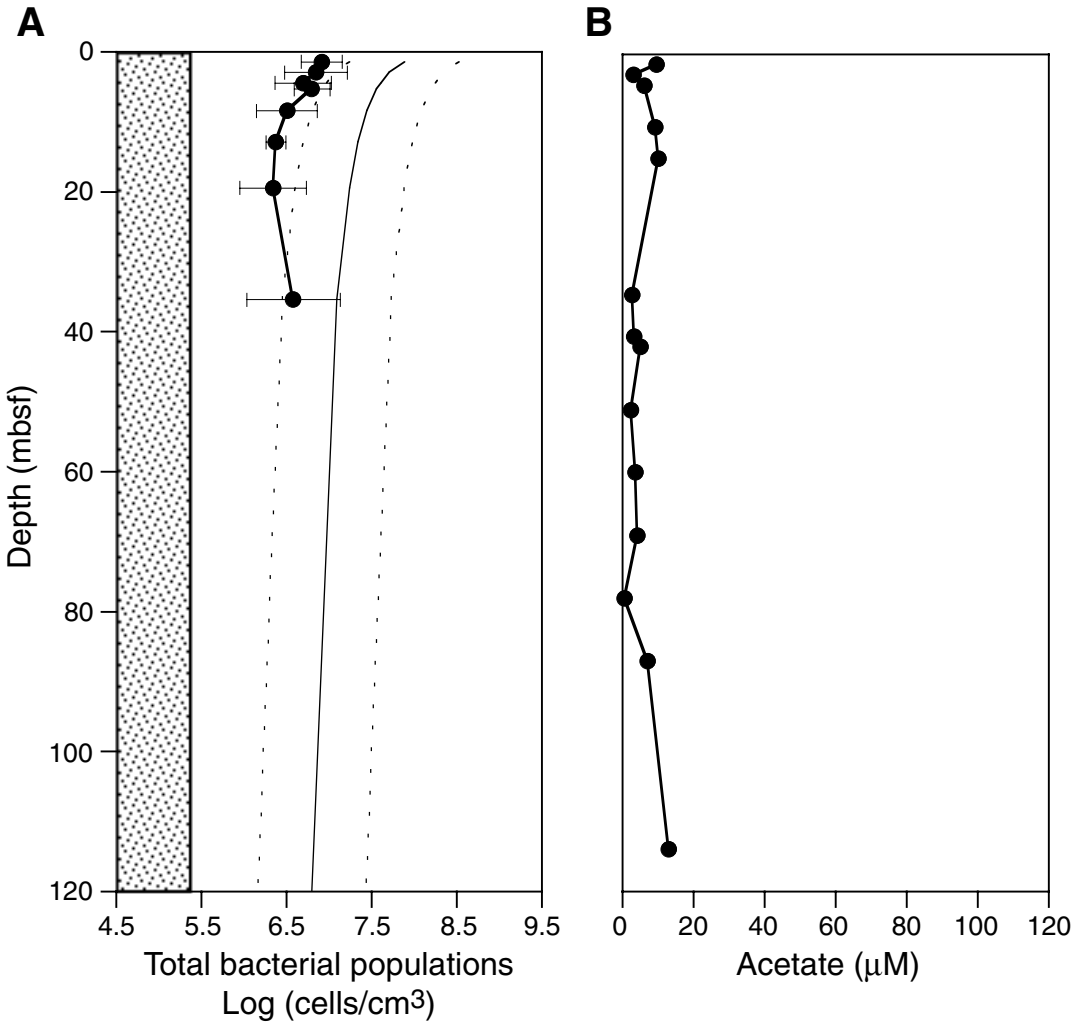

Figure F3. Depth distributions in sediments from Site 1093 of (**A**) total bacterial populations and (**B**) pore water acetate. Solid line = the general model for bacterial depth distributions of Parkes et al. (1994). Dashed lines = the 95% prediction limits of the model. Gray shaded area = data below the detection limit of the technique (2.23×10^5 cells/cm^3).

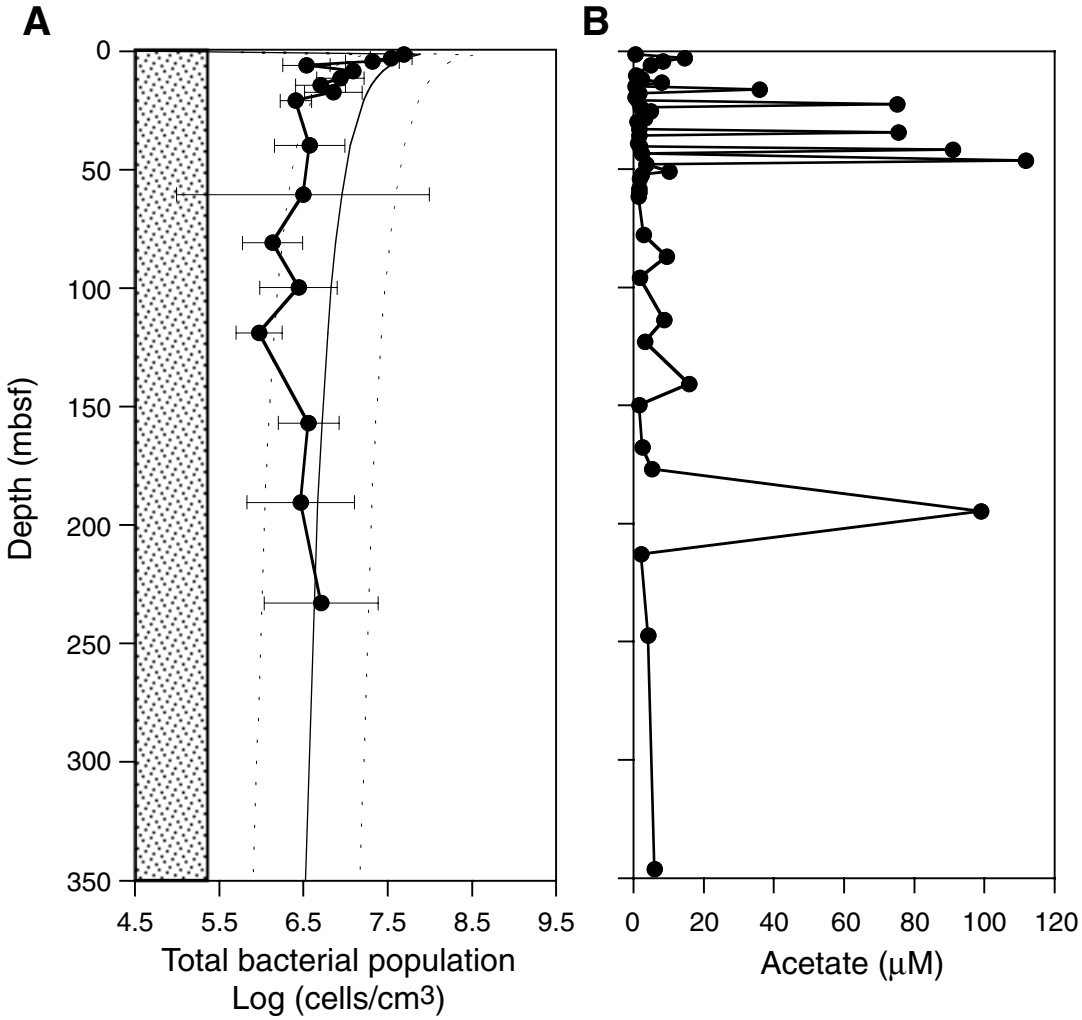

Figure F4. General regression models of bacterial distributions in deep-sea sediments. **A.** Data from hemipelagic mud/clay sites from ODP Legs 112 (Cragg et al., 1990), 128 (Cragg et al., 1992), 146 (Cragg et al., 1995a; Cragg et al., 1995b), 155 (Cragg et al., 1997), 160 (Cragg et al., 1998), 161 (Cragg et al., 1999), and 164 (Wellsbury et al., 2000). Log (cells/cm^3) = 8.02 – 0.57 log depth. Log (depth): r = 0.76, *N* = 738. **B.** Data from carbonate-rich, low organic carbon sediments from ODP Legs 135 (Cragg, 1994) and 138 (Cragg and Kemp, 1995) and Sites 1088 and 1093. Log (cells/cm^3) = 7.37 – 0.41 log depth. Log (depth): r = 0.53, *N* = 116.