

## NOTES

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### Constancy of bacterial abundance in surficial marine sediments

**Abstract**—Controls on bacterial abundance in marine sediments remain poorly understood despite the importance to biogeochemical processes, benthic ecology, and in situ bioremediation. We report an analysis of direct microscopic counts of widely distributed surficial marine sediments, using a new approach of scaling abundance to the fluid volume of pore water within the sediments (bacteria  $FV^{-1}$ ). The analysis identified a greater constancy in benthic bacterial abundance than has been appreciated previously. Whether tested as a combined dataset or separately according to geographic region, less variance was observed when abundance was scaled to fluid volume rather than the traditional dimension of dry sediment mass. The decrease in variance suggests that the primary controls on abundance, such as nutrient acquisition or predator encounter rate, may also scale with porewater fluid volume. With values centered around  $10^9$  bacteria  $ml^{-1} FV$ , regulation must differ fundamentally from the water column, where values average  $10^5$ – $10^6$  bacteria  $ml^{-1} FV$ .

Bacteria in marine and estuarine sediments worldwide influence elemental biogeochemical cycles in the oceans, foraging strategies of benthic fauna, and engineering designs for in situ bioremediation of toxic organic compounds. However, an understanding of controls on benthic bacterial abundance has eluded researchers for decades. In water-column research, a “remarkable constancy” in numbers at  $10^5$ – $10^6$  bacteria  $ml^{-1}$  over wide ranges in geographic distribution, nutrient regimes, and bacterial activities was discovered after the development of direct microscopic counting techniques (Wright 1988; Duarte and Vaque 1992). The observed constancy prompted energetic and encounter-rate arguments pointing to top-down, or grazer-regulated, control of bacterial abundance (Fenchel 1984). Benthic microbial research in this area has lagged behind its pelagic counterpart due in part to methodological and conceptual difficulties (Kemp 1990).

Two broad, complementary approaches can be used to investigate constraints on organismal abundance in nature: analyzing the causes of variance in observations or developing an explanation for the average value. Microbial work in marine sediments has predominantly taken the former approach. Given a constant temperature, sediment-grain surface area has been identified as the strongest correlate of abundance in surficial coastal sediments (DeFlaun and Mayer 1983; Dale 1974; Yamamoto and Lopez 1985). The relationship could not be due to simple space limitation, as bacteria inhabit only 0.05–5% of the available surface area (DeFlaun and Mayer 1983). The dependency has been ascribed to sorbed substrate, protective habitat, or, conversely, accumulated clay grains in bacterial exudates (DeFlaun and Mayer

1983). In the comparatively sparse deep-sea literature, the downward flux of particulate organic carbon most clearly predicts bacterial abundance (Deming and Baross 1993).

A lack of consistency in published dimensions used to scale benthic microbial parameters reflects the challenge of working with a complex, porous sedimentary matrix. Bacterial abundance has been scaled most frequently against dimensions of dry sediment mass (DSM) or wet sediment volume (WSV). Most publications do not include enough information to convert among dimensions (Deming and Baross 1993). More importantly, the dimensions contain varying information about the physical environment, such that ecological relationships can be masked or falsely quantified when inappropriate scaling is used (Craven et al. 1986; Bird and Duarte 1989). In retrospect, ecological interpretations of bacteria  $DSM^{-1}$  and bacteria  $WSV^{-1}$  are both puzzling in their incorporation of space fundamentally unavailable for occupation by the organisms. In a limited number of studies, abundance varied less when scaled to grain surface area (GSA) than when scaled to dry sediment mass, suggestive of a more informative reference frame (Dale 1974; Yamamoto and Lopez 1985). This scaling dimension has not been adopted, in part because surface-area measurements are time-consuming, require specialized equipment, and vary with the spatial resolution of the method (e.g. optical microscopy vs. chemical adsorption; DeFlaun and Mayer 1983). A larger problem is that the surface-area relationship fails for sediments of grain sizes approaching those of the bacteria themselves (DeFlaun and Mayer 1983), e.g. the fine silts and clays that characterize vast areas of the sea floor.

To address the need for an appropriate reference frame for enumerating bacteria in fine-grained sediments, we considered that the organisms utilize and respond to solute concentrations and gradients within the sediment pore water, e.g. to electron acceptors, dissolved substrates, metabolites, chemotactic stimuli, and extracellular enzymes. Departing from previous benthic approaches, we thus examined the number of bacteria scaled to the volume of pore water within the sediment. In the first use of this scaling dimension, we recalculated numerous large datasets from subtidal, shelf, and deep-sea sediments.

To avoid the uncertainties associated with heterogeneous methods of obtaining total bacterial numbers (Epstein and Rossel 1995), we restricted our primary analysis to data generated by one method in one laboratory. Sediments were collected from box cores ( $n$  in Table 1) on cruises conducted between 1989 and 1994. Many of the resulting bacterial counts have already been published in other contexts (GS, NS: Deming and Yager 1992; WAC: Relexans et al. 1996;

Table 1. Analysis of bacterial abundance data. N, number of samples counted and tested statistically; n, number of box cores sampled (see text for explanation); CV = 100(standard deviation/geometric mean).

Dataset	Location	N(n)	Descriptive: Median (CV)		Squared ranks test* P (CV <sub>DSM</sub> ≥ CV <sub>FV</sub> )	Ranked regression, on porosity			
			Bacteria (×10 <sup>9</sup> g <sup>-1</sup> DSM)	Log bacteria (×10 <sup>9</sup> ml <sup>-1</sup> FV)		Log bacteria g <sup>-1</sup> DSM		Log bacteria ml <sup>-1</sup> FV	
						ρ†	P ≤	ρ	P ≤
Subtidal									
BH93	Blakely Harbor,	8(1)	9.2(2.0)	2.5(1.6)	0.15	0.74	0.04	0.00	1.0
BH94	Puget Sound, Washington	23(3)	3.2(2.5)	1.5(1.5)	0.019	0.77	0.0001	-0.26	0.23
EH93	Eagle Harbor,	24(3)	16(2.1)	6.7(1.7)	0.14	0.55	0.006	-0.13	0.55
EH94	Puget Sound, Washington	46(6)	6.8(2.1)	3.5(1.6)	0.045	0.67	0.0001	-0.24	0.11
Shelf									
EGS92	East Greenland Shelf	82(9)	1.1(4.0)	1.2(2.5)	0.0010	0.79	0.0001	0.21	0.06
EGS93		134(18)	1.4(5.3)	1.7(4.1)	0.004	0.66	0.0001	0.02	0.78
SCB	Santa Catalina Basin, California	204(22)	1.5(5.7)	0.96(5.3)	0.14	0.43	0.0001	0.19	0.007
Deep sea									
WAC	West African Coast	76(6)	0.47(5.6)	0.64(5.0)	0.24	0.35	0.002	0.15	0.21
GS	Greenland Sea	80(4)	0.21(5.0)	0.28(4.6)	0.16	0.30	0.006	0.06	0.58
NS	Norwegian Sea	58(3)	0.52(4.2)	0.33(3.5)	0.047	0.68	0.0001	0.50	0.001
Combined		735(75)	1.3(6.7)	1.1(5.5)	<0.0001	0.63	0.0001	0.28	0.0001

\* Nonparametric analogue of *F*-test for difference between variances of two samples, where CV<sub>DSM</sub> = CV(Log bacteria g<sup>-1</sup> DSM) and CV<sub>FV</sub> = CV(log bacteria ml<sup>-1</sup> FV). Quantity ranked was [log bacterial abundance - mean log bacterial abundance/mean log bacterial abundance] (Conover 1980).

† Spearman's ρ: nonparametric analogue of Pearson's *r* and equivalent to Pearson's *r* calculated on ranked data (Conover 1980; SYSTAT for Windows, vers. 5 Ed., 1992).

EH, BH: Geiselbrecht et al. 1996; SCB: Smith et al. 1998; see Table 1 for abbreviations); other counts are presented here for the first time. In all cases, sediment cores were divided into depth horizons (typically 1 cm thick) to 10 cm, diluted (typically 1:5) with particle-free (0.2 μm-filtered) natural or artificial seawater, and fixed with formaldehyde (2% final concn) while at sea. These samples (*N* in Tables

1 and 2) were stored at 4°C in the dark until processed for counting, which was completed, on average, within 6 months of sample collection (range of 3–9 months). In the laboratory, bacterial counts were made under epifluorescence microscopy as described by Deming and Colwell (1982) and Deming et al. (1997), with the following specifications: subsamples were diluted further (typically 1:1,000) to reduce

Table 2. Measurements and statistical analysis of grain surface area. N, total number of samples tested (see text for explanation).

Dataset	N	Grain surface area		Log bacterial abundance	Partial correlation matrix			
		Mean (range) (m <sup>2</sup> g <sup>-1</sup> DSM)	Mean (range) (μm <sup>2</sup> bacterium <sup>-1</sup> )		Porosity		Grain surface area	
					ρ*	Partial ρ†	ρ	Partial ρ‡
					(P)	(P)	(P)	(P)
Shelf								
EGS92	19	18.7 (12.4–27.1)	21,100 (4,080–48,300)	g <sup>-1</sup> DSM	0.72 (0.0002)	0.79 (<0.0001)	-0.047 (0.85)	-0.49 (0.031)
				ml <sup>-1</sup> FV	0.13 (0.59)	0.37 (0.12)	-0.46 (0.040)	-0.56 (0.011)
Subtidal								
BH93/EH93	35	5.59 (1.66–11.6)	1,080 (277–2,450)	g <sup>-1</sup> DSM	0.52 (0.0010)	0.64 (<0.0001)	0.69 (<0.0001)	0.76 (<0.0001)
				ml <sup>-1</sup> FV	-0.13 (0.46)	0.29 (0.10)	0.75 (<0.0001)	0.77 (<0.0001)

\* Spearman's ρ: (see Table 1).

† Grain surface area held constant.

‡ Porosity held constant.

interference from sediment particles and to ensure an average count of 20–50 bacteria per microscopic field. Diluted subsamples were treated with Triton X-100 (0.01% wt vol<sup>-1</sup>) and sonicated (3 min) to help detach bacteria from sediment grains before staining with acridine orange (AO; Sigma) at a concentration of 0.01% (wt vol<sup>-1</sup>) for 3 min. After filtration onto 0.22- $\mu$ m Nuclepore black polycarbonate filters (Polysciences), samples were stained with 20  $\mu$ g ml<sup>-1</sup> 4',6-diamidino-2-phenylindole (DAPI; Sigma) for 5 min. Routine counts were made using optical filters for AO; periodic switching to DAPI optical filters allowed verification of questionable bacterial morphologies.

Additional subsamples were dried at 60°C for 18 h to determine the dry-weight content of the sediments. We calculated porosity from the dry-weight measurements after correcting for dilutions. We did not correct for salt content, which in high-porosity sediments can account for up to 20% of dry weight. Sensitivity calculations showed that the results presented here were not affected materially by this omission.

Scaling dimensions were converted with the total bacterial count, the water content of the sediment (porosity), and the dry sediment density (assumed to be 2.6 g cm<sup>-3</sup> in all calculations; Dyer 1986). Because abundances scaled to fluid volume and wet sediment volume converge at porosities typical of surficial marine sediments, we focus on dimensions of bacteria FV<sup>-1</sup> and bacteria DSM<sup>-1</sup> in the following discussion.

To address the potential for covariance between GSA and sediment porosity (Bernier 1980), we measured GSA (m<sup>2</sup> g<sup>-1</sup> dry wt) on archived subsets of the continental shelf and shallower subtidal samples. Sampled cores within each dataset were chosen randomly, while depth intervals were chosen by compromise between profile representation and sample availability. Fixed samples had been stored at 2°C for up to 2 years before this GSA analysis. As described by Mayer (1994), the single-point BET N<sub>2</sub> adsorption technique was used to measure the N-specific surface area of precleaned sediments. Because N<sub>2</sub> molecules adsorb within micro- and mesopores of sediments, the technique overestimates the GSA available to bacteria (DeFlaun and Mayer 1983).

Owing to nonnormal distributions of some variables in some datasets, descriptive statistics and statistics of association were nonparametric (Conover 1980; SYSTAT for Windows, vers. 5 Ed., 1992). Abundance values were log-transformed prior to parametric analysis. Results were deemed significant at  $\alpha \leq 0.05$  unless otherwise noted.

Less variance was observed when abundance was scaled to fluid volume than when scaled to dry sediment mass, whether tested as a combined dataset or separately according to geographic region (Table 1); in the combined data and in 5 of 10 datasets these differences in variance were significant. Medians among datasets ranged from 0.28 to 6.7  $\times 10^9$  bacteria ml<sup>-1</sup> FV, with an overall median of 1.1  $\times 10^9$  bacteria ml<sup>-1</sup> FV.

The ratio of porewater volume to dry sediment mass varied predictably with porosity, as did the relationship among bacterial abundance in different dimensions. For example, when the number of bacteria FV<sup>-1</sup> was assumed to be constant, bacteria DSM<sup>-1</sup> increased exponentially with porosity

due to the ever-decreasing dry sediment mass (Fig. 1a). This pattern was observed in the data repeatedly: in each dataset, bacterial abundance scaled to dry sediment mass increased significantly with porosity. With abundance scaled to fluid volume, Spearman's  $\rho$  was lower and differed significantly from zero in only 2 of 10 datasets and the combined data (Table 1). The EGS92 data showed this pattern most clearly (Fig. 1b). The relationship between bacterial abundance (DSM<sup>-1</sup>) and porosity, which held when data from all sites were combined, resembled the curve generated by assuming a constant value of bacteria FV<sup>-1</sup> (Fig. 1c,d).

Alternative explanations for the increase in bacterial abundance (bacteria DSM<sup>-1</sup>) with porosity include potential covariances with GSA and with depth in the sediment. Generally, high-porosity sediments correspond to small grain sizes (Bernier 1980), i.e. to those with high grain surface area and increased microtopography of clay minerals. In neither the shelf nor the subtidal sediments we examined could the relationship between porosity and abundance be attributed to covariance with GSA, as shown by the higher partial correlation coefficients obtained when GSA was held constant (Table 2). In the shelf sediments, there was a significant negative correlation between bacteria FV<sup>-1</sup> and GSA and a weak negative correlation between bacteria DSM<sup>-1</sup> and GSA (Table 2). Holding porosity constant enhanced the negative relationships. Bacterial abundance (bacteria DSM<sup>-1</sup> and FV<sup>-1</sup>) did correlate significantly with grain surface area, independent of porosity, in the subtidal sediments (Table 2).

Multiple regression on ranked data (grouped as in Table 1), which eliminates assumptions of linearity, showed that depth in the sediment was not responsible for the relationship between abundance (bacteria DSM<sup>-1</sup>) and porosity. The level of significance was retained for each site except NS, GS, and WAC (data not shown). As further corroboration, regression analyses were repeated for data from different depth groupings, e.g. 0–1, 1–2, 0–3, <5, and >5 cm. For the combined data, each of these depth groupings retained a significant relationship between abundance (bacteria DSM<sup>-1</sup>) and porosity (data not shown). Despite small sample sizes when grouped by depth and study site, significant results were obtained in 24 of 39 groupings (data not shown).

In summary, results showed significantly less variance in bacterial abundance when scaled to fluid volume than when scaled traditionally to dry sediment mass. The analyses also demonstrated the likelihood of ecologically questionable results when scaling to dry sediment mass, as many high levels of abundance reported previously (bacteria DSM<sup>-1</sup>) were likely due to a relatively constant number of bacteria FV<sup>-1</sup> and high porosity. It appears that neither grain surface area nor depth within the sediment was responsible for the strong and consistent relationship seen between bacterial abundance (DSM<sup>-1</sup>) and porosity.

The importance of identifying a relevant reference frame for bacteria in sediments can be recognized most clearly in the variable ecological interpretations of depth profiles plotted with alternative scaling dimensions. In shelf sediments (EGS92), abundance scaled to dry sediment mass decreased with depth in the sediment at a consistent logarithmic rate to 11 cm (Fig. 2a). Typical a posteriori explanations would point to abundance being set by factors at the sediment-water

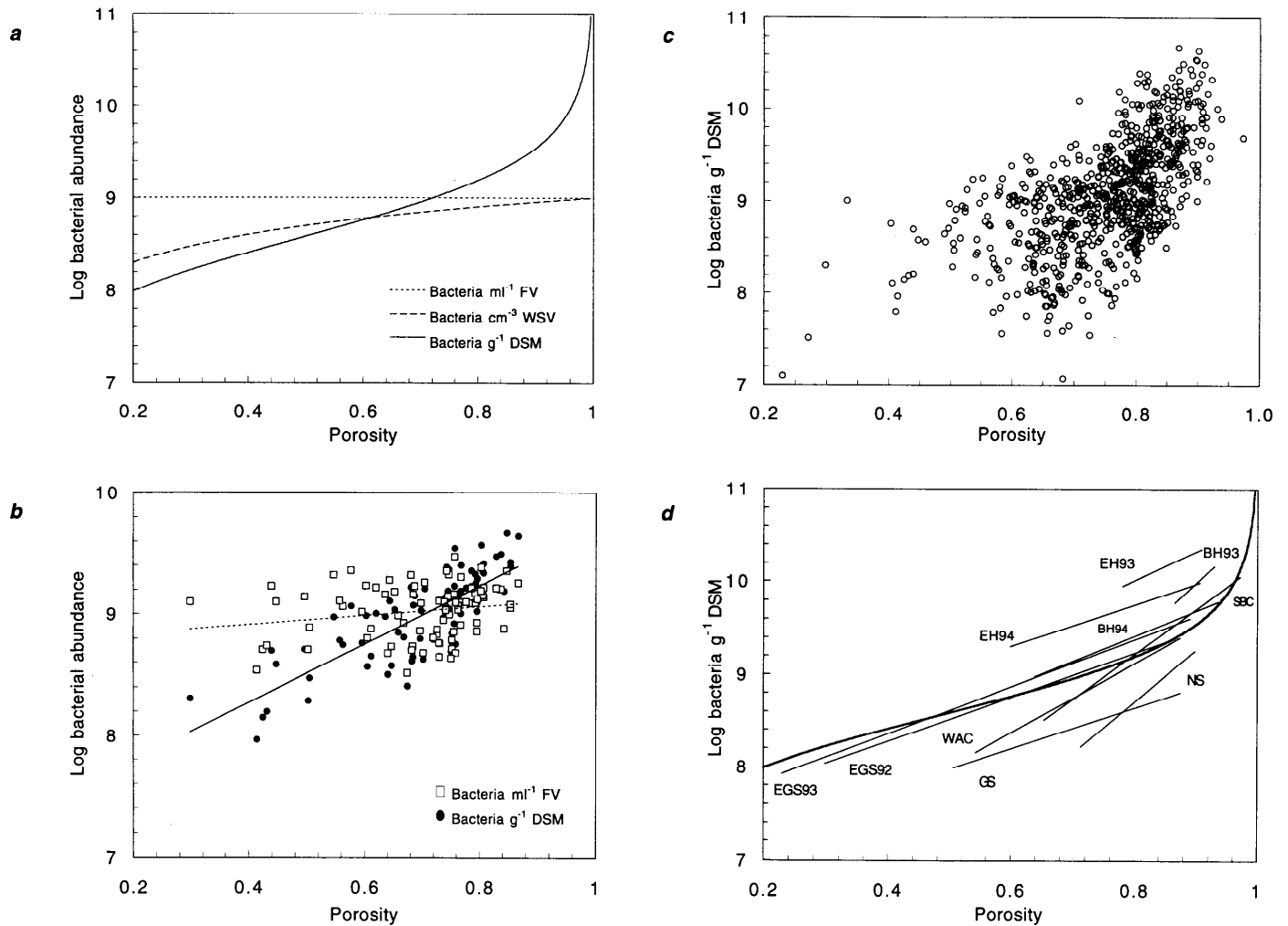


Fig. 1. Bacterial abundance as a function of porosity. (a) Theoretical results of bacterial abundance in alternative scaling dimensions, assuming a constant value of  $10^9$  bacteria  $\text{ml}^{-1}$  FV. (b) Scatterplot of EGS92 with abundance scaled to dry sediment mass (bacteria  $\text{g}^{-1}$  DSM and to fluid volume (bacteria  $\text{ml}^{-1}$  FV). Lines represent least-squares, linear regression fits. (c) Scatterplot of combined data with abundance scaled to DSM. (d) Least-squares, linear regression lines with abundance scaled to DSM for each dataset. Curve as in panel a, with a constant value of  $1.1 \times 10^9$  bacteria  $\text{ml}^{-1}$  FV (median value of combined data; Table 1). See Table 1 for labels and (nonparametric) association statistics.

interface and then decreasing with time (depth) after burial. Scaled to fluid volume, abundance remained constant to 4 cm before decreasing with depth, evoking effects of bioturbation as an explanation. Evidence from  $^{210}\text{Pb}$  profiles obtained on the same sampling expedition suggested 4 cm as the average depth of mixing (Roberts et al. 1997).

In deep-sea sediments, profiles of abundance scaled to dry sediment mass showed enriched abundance at the sediment surface (0–1 cm) compared to underlying sediments (1–3 cm), whereas profiles scaled to fluid volume remained relatively constant (0–3 cm; Fig. 2b). The observed differences are a result of increased porosity at the sediment–water interface, where a small change in porosity leads to a relatively large difference in parameters scaled to dry sediment mass (Fig. 1a). This analysis calls into question previous reports of greatly enhanced bacterial biomass and activity ( $\text{DSM}^{-1}$ ) at the sediment–water interface, based on interface samples of likely very high porosity (Novitsky 1983).

The relative constancy in bacterial numbers when scaled to fluid volume suggests to us a valid reference frame not only for abundance measurements, but also for mechanisms controlling abundance. A compelling approach, using water-column research as a guide, is to try to understand why the values take on the observed average of  $10^9$  bacteria  $\text{ml}^{-1}$  FV; that is, to identify the mechanisms that “crop” the numbers from above (loss) and “support” them from below (growth, resupply). Our shallow-water observations agree with those published in reviews of surficial estuarine sediments ( $4\text{--}17 \times 10^9$  bacteria  $\text{cm}^{-3}$  WSV; Rublee 1982) and of surficial lake sediments (average of  $6.3 \times 10^9$  bacteria  $\text{cm}^{-3}$  WSV; Schallenberg and Kalff 1993).

Interestingly, in some cases it may not be necessary a priori to invoke a loss term, for abundances can be near upper theoretical limits. For example, one of the upper values of reported bacterial abundance, found in tropical mangrove sediments, is estimated at  $3.9 \times 10^{11}$  bacteria  $\text{ml}^{-1}$  FV

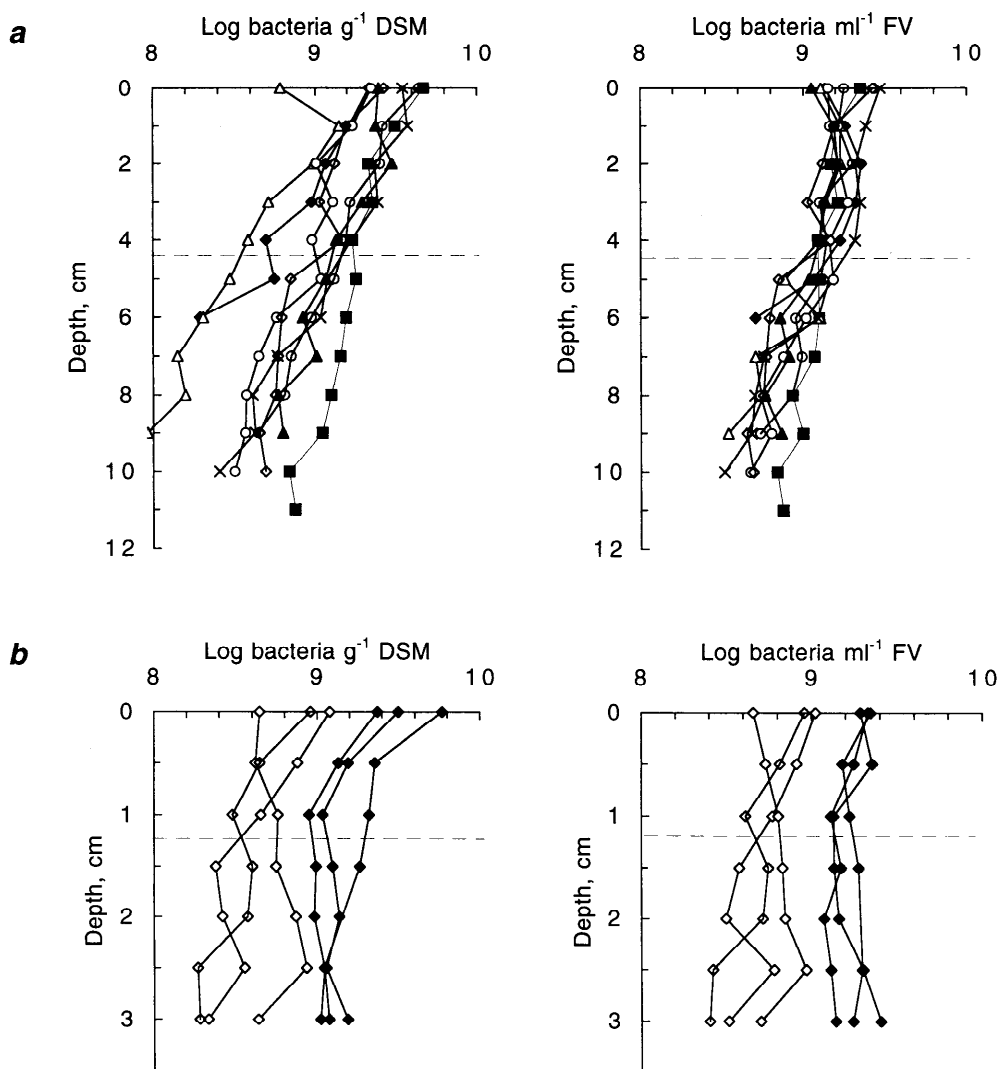


Fig. 2. Sediment depth profiles of bacterial abundance in alternative scaling dimensions. Dashed lines represent depth breaks used in statistical analyses, as described in the text. (a) Surficial shelf sediments (EGS92), with different symbols representing different stations. The sign test (Conover 1980) showed significantly greater differences ( $P = 0.04$ ) between regression coefficients on ranked data [ $b$ , bacterial abundance =  $b(\text{depth in sediment}) + \text{constant}$ ] of the upper and lower layer for bacteria  $\text{FV}^{-1}$  than for bacteria  $\text{DSM}^{-1}$ . (b) Surficial deep-sea sediments (WAC), with open symbols representing replicate box cores from an oligotrophic site and closed symbols representing replicate box cores from a mesotrophic site (Relexans et al. 1996). The sign test showed suggestively greater differences ( $P = 0.11$ ) between regression coefficients (calculated as in panel a) of the two layers for bacteria  $\text{DSM}^{-1}$  than for bacteria  $\text{FV}^{-1}$ .

(from reported bacterial abundance  $\text{DSM}^{-1}$  and water content values in Alongi 1988). If these bacteria are assumed to have cell volumes of  $0.39 \mu\text{m}^3$  (equivalent spherical diameter of  $1.0 \mu\text{m}$ ), the resulting total biovolume, not including extracellular polysaccharide matrix or space between cells, would comprise 15% of the total pore volume.

What might prevent bacterial numbers in surficial sediments from dropping far below the observed values? Unlike the ecology of most eukaryotic organisms, long survival times of dormant bacteria can maintain bacterial numbers even under famine conditions (Parkes et al. 1994). Bacterivore feeding (or viral lysis) thresholds, at which encounter

rates with prey are too infrequent to support energetic requirements, have not yet been investigated for sediments.

A proposed theoretical explanation for the numbers of bacteria found in batch cultures (Koch and Wang 1982), stagnant waters (Jumars et al. 1993), and sediments (Vetter et al. 1998) has been that "spheres of diffusional influence," or the volume in which a bacterium's uptake of a substance affects the surrounding concentration, intersect at a density of  $10^9$  bacteria  $\text{ml}^{-1} \text{FV}$  (assuming cell diameter of  $1 \mu\text{m}$ ). Clinical microbiologists have shown that bacterial entry into stationary-phase growth is driven by the expression of suites of specialized proteins (Kolter et al. 1993). Recently it has

been found that stationary-phase growth can be triggered not only by starvation, but also by autoinduction, or quorum sensing of bacterial density (Sitnikov et al. 1996). Autoinducer activity, which has been implicated in many density-dependent bacterial behaviors (Fuqua et al. 1996), has been found in natural biofilms on submerged stream rocks (McLean et al. 1997). The validity of the hypothesis that bacteria themselves may limit cell numbers when living in porous media, thus denying a consistent regulatory role for bacterivores, awaits testing. Further implicit predictions involve the importance of porewater flow, which could disrupt chemical signaling and provide solutes at greater rates than is possible by molecular diffusion alone.

In seawater, the numbers of active bacteria can vary considerably more than the numbers of total bacteria, suggesting decoupled regulation (del Giorgio and Scarborough 1995). We have found similar results, using a vital redox dye, in the first marine sediments examined in this way (Schmidt and Deming in prep.). Reducing the complex environment of the sediment matrix to simple predictors of bacterial abundance and (eventually) activity will speed progress in understanding concepts as diverse as optimal sediment-cap design for bioremediation treatments of contaminated sediments, and biological carrying capacity of subsurface terrain influenced by advecting hydrothermal fluids.

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## Ocean scalar irradiance near-surface maxima

**Abstract**—Estimates of the in-water spectral scalar irradiance,  $E_0$ , are needed to quantify the photosynthetically available radiation. When a highly scattering, optically thick medium is illuminated at its surface, it is possible under certain conditions for  $E_0$  to increase with penetration depth near the surface, even if there are no internal sources at the wavelength of interest. Analysis and numerical examples presented here help to explain and quantify the magnitude and location of potential subsurface  $E_0$  peaks in source-free ocean waters and the dependence of the phenomenon on the seawater optical properties and surface conditions. Peaking in  $E_0$  most likely occurs when the incident illumination is strongly directed at the zenith angle, and the location of the maximum is deepest when the asymmetry of the scattering phase function is large. The presence of surface waves and internal reflection greatly reduces the chance of  $E_0$  peaks being present, making a maximum in  $E_0$  below the surface possible only if the single scattering albedo,  $\omega_0$ , is  $>0.95$  in homogeneous waters or at potentially smaller values if  $\omega_0$  increases with depth.

In optical oceanography it is generally assumed that the in situ scalar irradiance  $E_0(\tau)$  decreases monotonically with optical depth  $\tau$ . Although it is well known that the radiance in a particular direction can increase with depth near the surface (Preisendorfer 1976; Mobley 1994), it is generally assumed that in the absence of internal sources the various direction-integrated irradiances decrease from the surface in an approximately exponential manner (e.g. Kirk 1994b). In contrast, researchers studying optics in biological tissue have reported  $E_0(\tau)$  profiles that increase with penetration depth near the surface and reach a peak before dropping off monotonically. Scalar irradiance peaking has been both predicted by theoretical models (e.g. Flock et al. 1989; Jacques and Prah 1987; Rastegar et al. 1989; Star et al. 1988) and observed in experimental measurements on tissue phantoms (Moes et al. 1989; Star et al. 1987). Analogously, Lassen et al. (1992) observed a peak in the infrared and near-infrared scalar irradiance in marine microbial mats, and Sanchez

(pers. comm.) has reported computing peaks in nuclear reactor neutronic fluxes.

It is important to know if and where  $E_0(\tau)$  peaking can occur in natural waters in order to accurately estimate from surface measurements the total photosynthetically available radiation (PAR) for randomly oriented phytoplankton in ocean water or for algal mats at the bottom of ice layers. We investigate both analytically and with numerical simulations the cause of  $E_0(\tau)$  peaking and predict under what conditions this phenomenon might be observed in natural waters. The location and magnitude of  $E_0(\tau)$  maximums are determined by solving the classical albedo problem of radiative transfer theory for particular seawater properties and surface illumination conditions.

**Analysis**—We are interested in the radiance  $L$  that satisfies the integrodifferential radiative transfer equation

$$\mu \partial L(\tau, \mu) / \partial \tau + L(\tau, \mu) = \omega_0(\tau) \int_{-1}^1 \tilde{\beta}(\tau, \mu' \rightarrow \mu) L(\tau, \mu') d\mu', \quad (1)$$

where  $\tau$  is the dimensionless downward optical depth measured from the surface and the single-scattering albedo,  $\omega_0$ , is the ratio of spectral volume scattering coefficient  $b$  to the spectral volume attenuation coefficient  $c$ , with  $\omega_0 \leq 1$ . Here  $L(\tau, \mu)$  is the spectral radiance, integrated over the azimuthal angle, whose direction cosine with respect to  $\tau$  is  $\mu$ , and  $\tilde{\beta}$  is the azimuthally integrated spectral scattering phase function. Internal sources, such as from fluorescence, bioluminescence, or Raman scattering, are not considered here.

The scalar irradiance  $E_0(\tau) = E_{0d}(\tau) + E_{0u}(\tau)$  is given in terms of its downward and upward components by

$$E_{0d}(\tau) = \int_0^1 L(\tau, \mu) d\mu \quad \text{and} \quad E_{0u}(\tau) = \int_{-1}^0 L(\tau, \mu) d\mu, \quad (2)$$