Limnol. Oceanogr., 45(2), 2000, 426–435
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Bacterioplankton distribution and production in deep Pacific waters: Large-scale geographic variations and possible coupling with sinking particle fluxes

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Abstract

Bacterial abundance and leucine incorporation rate were measured throughout the water column (depth, 4,000–6,000 m) at stations occupied in the equatorial, subtropical, and subarctic Pacific as well as in the Bering Sea during three cruises conducted between 1993 and 1997. In general, depth-dependent decreases of bacterial abundance and leucine incorporation in the bathypelagic layer (depth, >1,000 m) were well described by a power function with remarkably uniform exponents among distant locations: average exponents were −0.900 and −1.33 for abundance and leucine incorporation, respectively. Depth profiles of bacterial properties were complex at some subarctic stations, suggesting lateral transport of organic carbon by local eddies. Organic carbon fluxes from abyssal sediment to overlying water would explain increases in bacterial abundance and leucine incorporation in near-bottom layers. Biomass was twofold to fourfold and the production was threefold to sevenfold greater in subarctic than in subtropical regions. This latitudinal pattern was consistent with the basin-scale distribution of sinking fluxes of particulate organic carbon (POC) reported in the literature. Rates of bacterial carbon uptake accounted for 51% (range, 31–153) and 23% (14–58) of deep sinking POC fluxes in subarctic and subtropical regions, respectively. Average turnover time of deep bacterial assemblages was estimated to be 1–30 yr. These results suggest that deep bacterial biomass and production are generally coupled with sinking POC fluxes and that organic carbon is substantially transformed within bathypelagic environments via a sinking POC → dissolved organic carbon → bacteria pathway, as previously suggested in the mesopelagic zone.

The importance of heterotrophic bacteria in oceanic carbon cycling has been widely accepted. Bacteria consume on average 50% of daily primary production in the euphotic zone (reviewed by Ducklow and Carlson 1992) and 40–100% of sinking fluxes of particulate organic carbon (POC) in the mesopelagic zone (Cho and Azam 1988; Simon et al. 1992). However, data are scarce on biomass, production, and carbon consumption of bacteria in the bathypelagic zone (depth, 1,000–5,000 m) and there are very few depth profiles of these properties with sufficient vertical resolution (Turley and Mackie 1994; Dufour and Torréton 1996; Patching and Eardly 1997). Consequently, we know very little about turnover, and controls of bacterial assemblages in deep oceanic waters. Given that 74% of total seawater on earth resides at depths below 1,000 m, this paucity of data hinders our attempts to completely understand carbon and energy fluxes in the oceans.

From a biogeochemical perspective, the bathypelagic system can be viewed as a huge, dilute organic carbon reactor that operates at low temperature (2°C) and high pressure (>100 atm). Globally, the export of organic carbon via the sinking of POC below 1,000 m has been estimated to be 0.83 Gt yr^{-1}, accounting for 2% of primary production and 14% of new production in open oceans (Martin et al. 1987). In an ocean area with a depth of 5,000 m, 75% of this carbon is consumed within the water column, leaving 0.5% of primary production available for benthic consumption or burial (Martin et al. 1987). Beside the sinking POC, investigators have suggested that sediment resuspension (Druffel et al. 1996), diffusive inputs of dissolved organic carbon (DOC) from sediment pore water (Bauer et al. 1995), and large-scale advective transport of DOC (Hansell and Carlson 1998) may also introduce a large amount of organic carbon to deep waters. However, the relative magnitude, variability and controls of these organic fluxes are not well understood (Druffel et al. 1992).

Depth profiles of bacterial biomass and production in a variety of oceanic regions could help identify patterns and dominant routes of organic carbon fluxes in deep waters. Previous work has suggested that the coupling between sinking POC and free-living bacteria in aphotic environments could be tight (Cho and Azam 1988; Smith et al. 1992). These authors proposed that large sinking particles are enzymatically hydrolyzed to release DOC, which supports production of free-living bacteria in the mesopelagic zone. If this model applies to deep waters, one would expect that the depth profile and geographic variation of bacterial biomass and production in deep water largely reflect sinking flux regimes. Alternatively, complex patterns of depth profiles of bacterial properties might be observed if the sinking POC field is superimposed by sediment water or advective DOC fluxes with significant magnitudes.

We report here our measurements of depth profiles of bacterial abundance and production in the Pacific. Samples were collected at 15 stations occupied within major biogeochemical domains, including subarctic, subtropical, and equatorial regions. Our purposes were to examine vertical distribution patterns of bacterial properties throughout the water column of diverse regions and to infer the mode of regulation and timescale of bacterial dynamics and carbon consumption in

Acknowledgments

We thank D. L. Kirchman, H. W. Ducklow, and J. J. Cole for valuable comments on the manuscript. Thanks are also due to the captains, officers and crews of RV *Hakuho-Maru,* and H. Hasumoto, T. Miura, and N. Saotome for the support during field operations.

This work was supported by grants from the MESSC, Japan.

Table 1. Location, position, date of the survey, and oceanographic properties of sampling stations.

Location	Station	Date of survey	Position (° ′)	Water depth (m)	Surface temp (°C)	NO_3* (μM)	Chl *a** (μg liter^{-1})
Subarctic							
(Western)	A	18 Oct 93	45 12 N 165 23 E	5,988	10.2	11.4	0.93
	A	24 Oct 95	45 00 N 165 59 E	5,959	9.9	11.0	0.3
	2	12 Jul 97	43 05 N 155 05 E	5,381	10.4	9.3	0.52
	4	14 Jul 97	48 01 N 165 03 E	5,945	7.9	15.4	2.24
	6	21 Jul 97	48 00 N 177 04 E	4,822	8.9	16.6	0.30
(Eastern)	14	6 Aug 97	53 00 N 149 59 W	4,483	15.2	10.5	0.52
	15	8 Aug 97	49 53 N 144 54 W	4,263	14.4	8.7	0.24
	16	13 Aug 97	49 59 N 140 01 W	3,960	15.6	4.0	0.16
	17	24 Aug 97	44 59 N 139 59 W	4,392	16.8	<0.1	0.37
	19	27 Aug 97	47 01 N 159 59 W	5,273	14.4	6.1	0.21
Bering Sea	9	25 Jul 97	57 24 N 179 53 E	3,807	9.1	13.3	0.46
Subtropical	M2	17 Nov 95	34 58 N 164 59 E	5,886	21.9	<0.1	0.32
	B′	25 Oct 93	24 32 N 169 59 E	5,606	27.7	<0.1	0.073
	B	13 Nov 95	25 01 N 164 05 E	5,965	27.0	<0.1	0.06
	C	31 Oct 93	22 46 N 158 06 W	4,845	25.7	<0.1	0.11
Equatorial	D2′	16 Nov 93	0 05 N 158 60 W	4,795	27.3	3.69	0.31

* Concentrations in surface waters. Data are from the cruise report (ORI) of each cruise.

bathypelagic environments. To our knowledge, our study is the first to provide the data on large-scale geographic variations of bacterial biomass and production in deep oceanic waters. The results suggest a strong influence of sinking flux regimes on biomass, production, and carbon consumption of bacterioplankton in the bathypelagic zone.

Methods and Materials

Study area and sampling—This work was carried out aboard the RV *Hakuho-Maru* during three cruises conducted between 1993 and 1997 (KH-93–4, 14 October–3 December 1993; KH-95–3, 19 October–24 November 1995; KH-97–2, 9 July–8 September 1997). We collected seawater samples at 15 stations occupied in the subarctic, subtropical, and equatorial Pacific, as well as in the Bering Sea (Table 1). Different cruises occupied different stations, except that Sta. A was visited first in 1993 and then revisited in 1995. Water samples were collected by using 12-liter, Teflon-coated Niskin or lever-action–type Niskin bottles mounted on CTD/rosette. Before each cruise, sampling bottles were washed with detergent and HCl and then rinsed with Milli-Q water. Plastic gloves were worn and care was taken to minimize organic contamination during collection of waters from the bottles.

Bacterial abundance and production—Bacterial abundance was counted by epifluorescence microscopy after staining with DAPI (Porter and Feig 1980). One slide was prepared for each depth and at least 300 cells were counted for each slide. Blank counts from reagents and filters were regularly checked and they were always <5% of total counts. All the samples were counted by a single investigator. Bacteria attached to particles were <5% of total bacteria.

Bacterial production was estimated from the incorporation of ^{3}H-leucine (Kirchman 1992) during the 1995 and 1997 cruises. Subsamples (10–50 ml) from each depth were amended with 10 nM ^{3}H-leucine (Amersham) and incubated at in situ temperature (±2°C) in the dark. Incubation time varied depending on depth: 1–24 hr for upper (0–1,000 m) waters and 40–50 hr for deep (1,000–5,000 m) waters. The time course of the incorporation was generally linear over time. After incubation, samples were filtered through Sartorius filters (pore size, 0.2 μm) and rinsed with both ice-cold 5% trichloroacetic acid and 80% ethanol. The samples were radioassayed with a liquid scintillation counter (Wallac). Duplicate samples and one trichloroacetic acid-killed control were prepared for each depth. Radioactivity from killed controls was subtracted from the samples. For bathypelagic samples, incorporated radioactivity by live samples was usually more than twofold greater than for killed controls. Errors associated with scintillation counting were relatively minor (C.V. < 5%) compared to replication errors: the range of duplicate measurements was 26% (SD = ±26%, $n = 48$, data for bathypelagic measurements) of the mean values.

Bacterial carbon biomass was estimated assuming that one bacterial cell contains 15×10^{-15} g of carbon (Fukuda et al. 1998). Incorporation rates of leucine were converted to bacterial production by assuming a 1.55 kg C mol^{-1} conversion factor, which results from assuming no isotope dilution, 7.3% leucine in protein, and protein is 61.8% of total cellular carbon (Simon and Azam 1989). We also assumed that the turnover of bacterial protein pool was not significant during the incubation (Kirchman et al. 1986). Simon and Azam (1989) found that isotope dilution was twofold for surface bacterial assemblages, deriving a commonly used factor of 3.1 kg C mol^{-1}. However, no prior work has determined this parameter for deep bacterial assemblages. We used a conservative assumption (no isotope dilution), which probably provides minimum estimates of bacterial production.

The effects of hydrostatic pressure on bacterial activity are complex and variable (Jannasch and Wirsen 1982). In the Atlantic, Patching and Eardly (1997) measured leucine incorporation rates in a sediment contact water (depth, 4,800

m) and found that the rates were sixfold lower in the decompressed samples than in the samples incubated at in situ pressure. If these results are generally applicable, the leucine incorporation rates that we determined with decompressed samples would be too low.

Results

General features of depth profiles of bacterial abundance and leucine incorporation—The depth profiles of bacterioplankton abundance and leucine incorporation were determined during three cruises conducted between 1993 and 1997 (Table 1). The methods used for water sampling, sample handling, and measurements were strictly consistent among different cruises, allowing us to examine systematically the variability of bacterioplankton distributions over a wide variety of oceanic environments. Bacterial abundance in surface waters varied from 4×10^5 to 4×10^6 cells ml^{-1} and was generally higher in subarctic than in subtropical regions. The abundance decreased sharply (ca. 1 order of magnitude) from surface to 1,000 m (3×10^4–1×10^5 cells ml^{-1}). Below 1,000 m, the decrease over depth of bacterial abundance was not as pronounced as that in the upper (0–1,000 m) layer. The abundance at depths of 4,000–5,000 m varied in the range of 7×10^3–1×10^5 cells ml^{-1}. This approximately tenfold geographic variability in bacterial abundance within the deep waters is as great as that in the surface waters. Bacterial abundance generally decreased smoothly as a function of depth in deep water, except that the abundance exhibited somewhat noisy depth profiles at three stations in the eastern subarctic Pacific (Stas. 15, 16, 17) and at a station in the Bering Sea (*see Fig. 1 for representative profiles*). Also notable is a significant increase in bacterial abundance in the near-bottom layer (a water layer ca. <400 m above the bottom) at an equatorial station (D2′) and subarctic stations (Stas. 4, 19, 15, 17, 9) (Fig. 1).

Leucine incorporation was determined during the 1995 and 1997 cruises. The main features of leucine incorporation profiles were generally similar to those of bacterial abundance (Fig. 1). The incorporation rate decreased greatly from surface waters (80–2,900 pM d^{-1}) to 1,000 m (0.07–0.8 pM d^{-1}), and to a lesser extent to deep waters (0.009–0.7 pM d^{-1} at 3,000–5,000 m). At all the stations examined in subarctic regions, we observed significant increases in rates of leucine incorporation in the near-bottom layer (Fig. 1), a pattern that is consistent with the profile of bacterial abundance. Over the entire water column, leucine incorporation decreased by a factor of 10^3–10^4, which was much more pronounced than the decrease of bacterial abundance (10^1–10^2). Cell-specific activities of leucine incorporation rates varied in the range of 1.4×10^{-20}–1.6×10^{-18}, 2.0×10^{-21}–1.5×10^{-19}, and 9.3×10^{-22}–1.6×10^{-20} mole $cell^{-1}$ d^{-1} in surface (0–100 m), mesopelagic (100–1,000 m), and bathypelagic (1,000–5,000 m) layers, respectively.

The decrease of bacterial abundance and leucine incorporation in deep waters—The decrease over depth of bacterial abundance and leucine incorporation in deep water was statistically analyzed by fitting the data to a power function after double logarithmic transformations (Tables 2, 3). Using

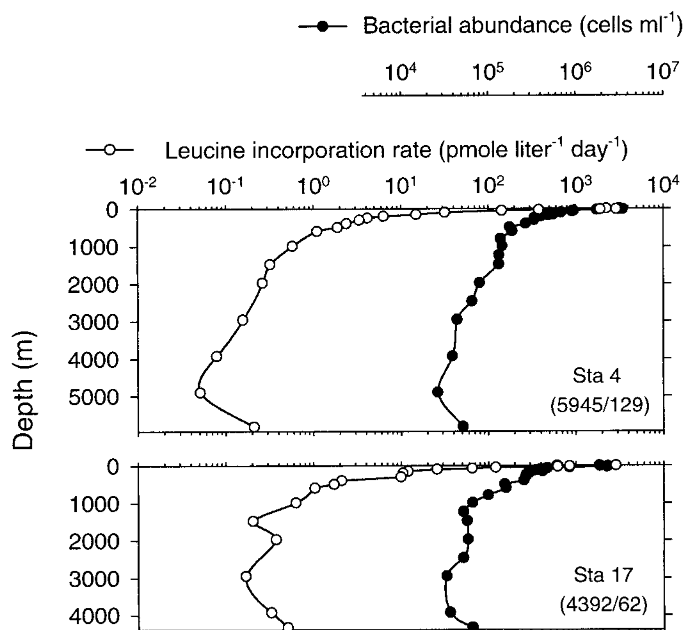

Fig. 1. Depth profiles of bacterial abundance (closed circles) and leucine incorporation rate (open circles) at two representative stations. The profiles at Sta. 4 (*see Table 1 for the location and date of sampling*) exhibit a smooth decline over depth of bacterial abundance and leucine incorporation, whereas the ones at Sta. 17 show somewhat noisy patterns typical for the eastern subarctic Pacific. In both cases, note that bacterial abundance and leucine incorporation increase in near-bottom layers. Bacterial abundance for each depth was estimated by using a single slide (>300 cells were counted for each slide). Leucine incorporation rate at each depth represents the average of duplicate measurements (for bathypelagic samples, ranges of the duplicates were ca. 26% of the mean). Values in parentheses are Z_{max}/MAB: Z_{max} is the maximum water depth (m) and MAB is the distance (m) above the bottom for the sample collected at the deepest water layer in each station.

the log–log model is purely empirical, but it facilitates comparisons between bacterial profiles and sinking fluxes of particles (*see below*), which have been typically modeled by using a negative power function (Martin et al. 1987). Our data showed that log–log model describes well the relationship between bacterial abundance and depth ($r^2 = 0.892$–0.991) except for some stations in eastern subarctic Pacific (Stas. 15, 16, 17; $r^2 = 0.674$–0.699) and the Bering Sea (Sta. 9; $r^2 = 0.252$) (Table 2). At stations where the r^2 exceeds 0.94 (most stations in equatorial, subtropical, and western subarctic regions and Stas. 14 and 19 in eastern subarctic), the log–log slopes were remarkably constant (Fig. 2a), with a mean slope of -0.900 ± 0.150 (±SD, $n = 11$). At these stations, the regression-derived bacterial abundance at a depth of 1,000 m (N_{1000}) was generally low at subtropical and equatorial stations (3×10^4–4×10^4 cells ml^{-1} except at Sta. M2), compared to the high abundance at subarctic stations (5×10^4–2×10^5 cells ml^{-1}) (Table 2).

The depth-dependent decrease of leucine incorporation in deep waters is also described well by a power function at six out of nine stations examined ($r^2 = 0.939$–1.000) (Table 3). At these stations, the log–log slopes were relatively constant with a mean slope of -1.33 ± 0.19 (±SD, $n = 6$; Fig.

Table 2. Regression results of the decline of bacterial abundance over depth (>990 m). The model used was $N = N_{1000}\cdot(Z/1000)^b$ where N and Z are bacterial abundance (cells ml^{-1}) and depth (m), respectively. N_{1000} is bacterial abundance ($\times 10^4$ cells ml^{-1}) at a depth of 1,000 m and b is the log–log slope of depth-dependent decline of N, which were estimated by the linear regression of log N on log Z. The data for samples collected in the near bottom layer (<400 m above the bottom) were not used for the regression analysis (*see text for explanation*).

Location	Station (yr)	Water layer (m)	N_{1000}	Slope (SE) b	n	r^2	P
Subarctic	A (93)	989–4,902	5.8	−0.850 (0.085)	8	0.943	<0.0001
(Western)	A (95)	998–4,954	12.5	−0.932 (0.083)	8	0.954	<0.0001
	2 (97)	995–4,915	15.0	−0.888 (0.080)	8	0.954	<0.0001
	4 (97)	992–4,913	16.5	−1.13 (0.086)	8	0.966	<0.0001
	6 (97)	991–3,939	10.0	−0.927 (0.144)	7	0.892	0.0014
(Eastern)	14 (97)	992–3,940	8.9	−0.728 (0.070)	6	0.956	0.0001
	15 (97)	992–2,962	8.1	−0.787 (0.273)	6	0.674	0.045
	16 (97)	990–2,960	10.0	−1.05 (0.344)	6	0.699	0.038
	17 (97)	992–3,939	6.5	−0.427 (0.129)	7	0.688	0.021
	19 (97)	992–3,939	4.9	−0.732 (0.078)	7	0.946	0.0002
Bering Sea	9 (97)	991–2,960	7.3	−0.369 (0.318)	6	0.252	0.3
Subtropical	M2 (95)	989–4,910	7.8	−1.19 (0.055)	8	0.987	<0.0001
	B′ (93)	992–4,909	2.5	−0.828 (0.041)	8	0.985	<0.0001
	B (95)	992–4,913	3.1	−0.841 (0.040)	8	0.987	<0.0001
	C (93)	991–3,936	3.3	−0.963 (0.041)	7	0.991	<0.0001
Equatorial	D2′ (93)	991–3,937	3.9	−0.814 (0.064)	7	0.970	<0.0001

2b). This mean slope for leucine incorporation was significantly greater than that for bacterial abundance (Student's t-test, $p = 0.0001$). The regression-derived estimates of leucine incorporation at a depth of 1,000 m (V_{1000}) were lower in the subtropical (0.05–0.18 pM d^{-1}) than in the subarctic (0.30–0.77 pM d^{-1}) regions. As observed for bacterial abundance, the coefficients of determination (r^2) for the data collected in eastern subarctic Pacific were low (Stas. 15, 17, $r^2 = 0.251$–0.834; Table 3).

Depth-integrated biomass and production of bacteria—We estimated bacterial biomass in the entire water column by using a single conversion factor, 15 fg C cell^{-1}, which has been estimated for bacterial assemblages in oceanic surface waters (Fukuda et al. 1998). This estimation should be regarded as a first-order approximation because bacterial cell size and carbon content may vary depending on environments, although previous work has found that there is no systematic difference in bacterial mean cell volumes between upper and deep Atlantic waters (Patching and Eardly 1997).

The integrated biomass of bacteria in the water column of different depths (0–100, 100–1,000, and 1,000–4,000 m) is summarized in Table 4. For comparison, estimates of phytoplankton biomass (chlorophyll *a* concentration $\times$ 50) in the upper 100 m are also shown. Bacterial biomass in deep waters (1,000–4,000 m) varied from 0.59 to 3.35 g C m^{-2}. This range is nearly equivalent to that of phytoplankton biomass in the 0–100-m layer (range, 0.52–3.80 g C m^{-2}) and that of bacterial biomass in the 0–100-m layer (0.62–2.95 g C m^{-2}) and 100–1,000-m layer (0.85–4.31 g C m^{-2}). There was a notable latitudinal gradient in bacterial biomass in deep waters, with low values in the south, especially in the

Table 3. Regression results of the decline of leucine incorporation rate over depth (>990 m). The model used was $V = V_{1000}\cdot(Z/1000)^b$, where V and Z are leucine incorporation (pmole liter^{-1} d^{-1}) and depth (m), respectively. V_{1000} is leucine incorporation rate (pmole liter^{-1} d^{-1}) at a depth of 1,000 m and b is the log–log slope of depth-dependent decline of V, which were estimated by the linear regression of log V on log Z. The data for samples collected in the near bottom layer (<400 m above the bottom) were not used for the regression analysis (*see text for explanation*).

Location	Station (yr)	Water layer (m)	V_{1000}	Slope (SE) b	n	r^2	P
Subarctic	A (95)	998–4,954	0.30	−1.53 (0.14)	3	0.992	0.06
(Western)	4 (97)	992–4,913	0.62	−1.48 (0.12)	6	0.974	0.0003
	6 (97)	991–3,939	0.77	−1.36 (0.07)	4	0.995	0.004
(Eastern)	15 (97)	992–2,962	0.38	−0.708 (0.22)	4	0.834	0.09
	17 (97)	992–3,939	0.42	−0.477 (0.48)	5	0.251	0.4
	19 (97)	992–3,939	0.62	−1.13 (0.17)	5	0.939	0.007
Bering Sea	9 (97)	991–2,960	0.59	−1.07 (0.01)	4	1.000	0.0001
Subtropical	M2 (95)	989–4,910	0.18	−1.41 (0.15)	4	0.977	0.01
	B (95)	992–4,913	0.05	−0.948 (0.32)	5	0.747	0.06

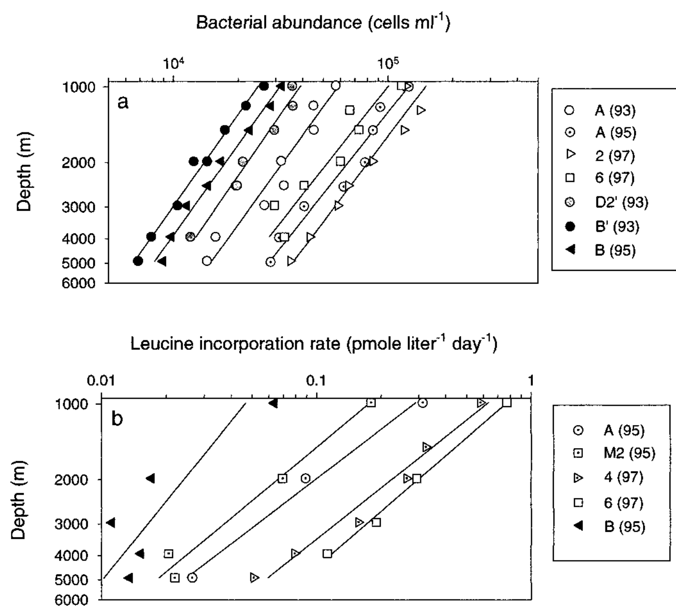

Fig. 2. Log–log plots of bacterial abundance (a) and leucine incorporation rate (b) versus depth in the bathypelagic zone. Regression results are summarized in Tables 2 and 3.

subtropical region, and high values in the north (Fig. 3b). This pattern generally follows the latitudinal distribution of phytoplankton biomass (Fig. 3a), although the Pearson correlation between deep bacterial biomass and phytoplankton biomass was marginally insignificant ($r = 0.504$, $p = 0.06$, $n = 15$). Although bathypelagic bacterial biomass varied among different oceanic regions, biomass also varied temporally within a region. At subarctic Sta. A, the only station that we visited over time, the biomass of bacteria in 1,000–4,000-m layer increased 2.3 fold between 1993 (1.4 g C m^{-2}) and 1995 (3.2 g C m^{-2}) (Table 4).

The scale of regional variability of bacterial production integrated over the deep-water layer (1,000–4,000 m) was a factor of ~10 with the lowest value at a subtropical station (Sta. B, 0.11 mg C m^{-2} d^{-1}) and the highest value at a subarctic station (Sta. 6, 1.47 mg C m^{-2} d^{-1}) (Table 4). As observed for bacterial biomass, a northward increase in the integrated bacterial production in the deep layer (1,000–4,000 m) was observed (Fig. 3c). These values accounted for 0.5–4% of bacterial production in the 0–100-m layer (7.7–115 mg C m^{-2} d^{-1}) and 4–24% of bacterial production in the 100–1,000-m layer (2.05–11.0 mg C m^{-2} d^{-1}) (Table 4).

Discussion

Our results revealed new features of the large-scale geographic pattern of bacterial biomass and production in deep Pacific waters (1,000–5,000 m). Bathypelagic biomass and production were higher in the north than the south, with twofold to fourfold greater biomass and threefold to sevenfold greater production in the subarctic than in the subtropical deep waters (Table 4, Fig. 3). This pattern is consistent with a basin-scale distribution of export production, which is characterized by low flux in the subtropical gyre (F_{100} = <5–10 g C m^{-2} y^{-1}; F_{100} represents the flux of sinking POC at a depth of 100 m) and high flux in the subarctic gyre (F_{100} = 10–50 g C m^{-2} y^{-1}) (Berger and Wefer 1991). These data agree with results of Patching and Eardly (1997), who determined depth profiles (maximum depth, 4,800 m) of bacterial abundance at two stations in the eastern North Atlantic. These authors reported that bacterial abundance in deep wa-

Table 4. Depth integrated bacterial biomass and production, and bacterial turnover time (biomass/production) in the upper (0–100 m), mesopelagic (100–1,000 m) and bathypelagic (1,000–4,000 m) water columns. Phytoplankton biomass (chl a × 50) in the upper 100 m water column is also presented. The integrated value (I) in a layer between water depths of z_1 and z_2 was calculated as $I = (q_1 + q_2) \times (z_1 - z_2)/2$, where q_1 and q_2 are the biomass or production at depths of z_1 and z_2, respectively.

			Bacterial biomass (g C m^{-2})			Bacterial production (mg C m^{-2} d^{-1})			Turnover time (yr)		
Location	Station (yr)	Phytopl. biomass (g C m^{-2})	0–100 m	100–1,000 m	1,000–4,000 m	0–100 m	100–1,000 m	1,000–4,000 m	0–100 m	100–1,000 m	1,000–4,000 m
Subarctic	A (93)	2.57	0.62	1.27	1.40						
(Western)	A (95)	0.94	0.99	3.14	3.20	14.5	5.41	0.53	0.19	1.6	16.5
	2 (97)	1.49	2.95	4.31	3.49						
	4 (97)	3.80	2.41	3.29	3.35	115	5.06	1.11	0.06	1.8	8.3
	6 (97)	1.66	2.18	2.86	2.18	78.2	6.08	1.47	0.08	1.3	4.1
(Eastern)	14 (97)	1.60	1.33	2.11	2.29						
	15 (97)	1.31	1.09	2.32	1.91	33.9	6.24	1.13	0.09	1.0	4.6
	16 (97)	1.65	1.82	2.04	2.21*						
	17 (97)	2.32	1.79	2.48	2.08	68.4	6.06	1.40	0.07	1.1	4.1
	19 (97)	1.20	1.26	1.87	1.23	65.5	11.0	1.32	0.05	0.5	2.6
Bering Sea	9 (97)	2.50	2.11	2.69	—	78.7	6.74	—	0.07	1.1	—
Subtropical	M2 (95)	1.16	0.75	1.67	1.41	7.7	2.05	0.34	0.27	2.2	11.4
	B′ (93)	0.57	0.64	0.85	0.59						
	B (95)	0.52	1.13	1.37	0.72	23.3	3.12	0.11	0.13	1.2	17.9
	C (93)	0.61	0.69	1.21	0.71						
Equatorial	D2′ (93)	1.82	0.74	1.08	0.94						

* 1,000–3,500 m.

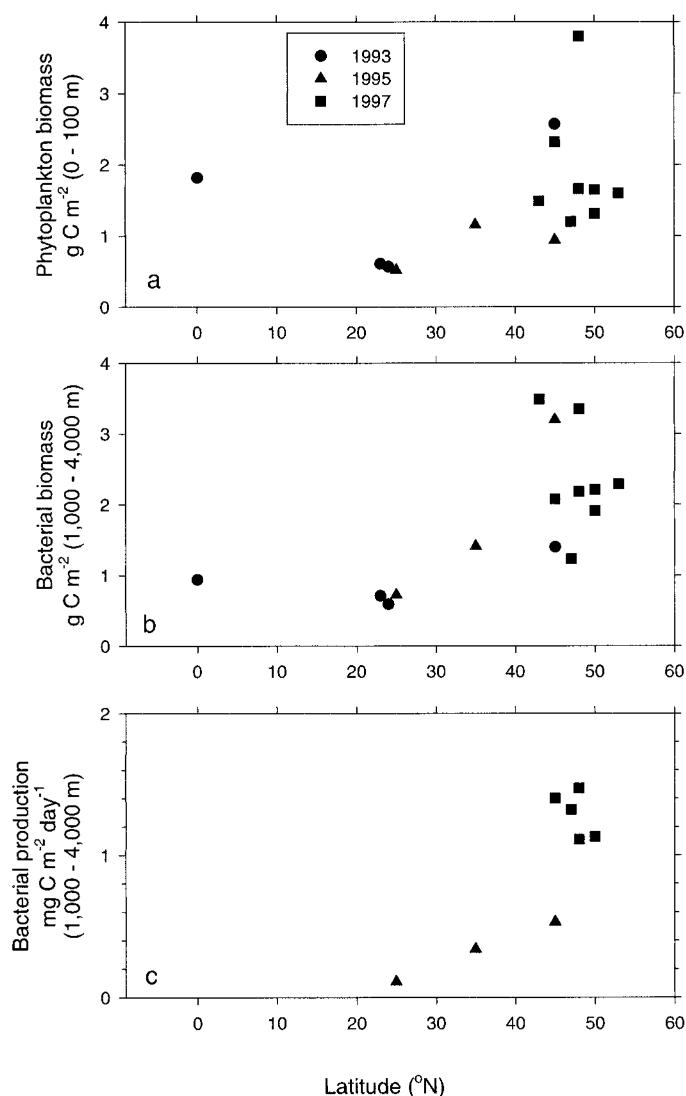

Fig. 3. Phytoplankton biomass in the upper layer (0–100 m), bacterioplankton biomass in the bathypelagic layer (1,000–4,000 m), and bacterial production in the bathypelagic layer (1,000–4,000 m) plotted against latitude. Data were collected during three cruises as indicated by different symbols: KH-93–4 (1993), KH-95–3 (1995), and KH-97–2 (1997).

ter is twofold to threefold higher in a northern (50°N) than in a southern (28°N) station. Similarly, in a limited region off the tropical northeastern Atlantic, Dufour and Torréton (1996) found that bacterial abundance in deep water tended to correlate with surface productivity.

Our data also demonstrated that the depth-dependent decrease of bacterial abundance was described well by a power function with a remarkably constant slope (Fig. 2a; Table 2). A similar trend holds for depth profiles of leucine incorporation (Fig. 2b, Table 3). This uniformity in slopes is noteworthy given that our samples were collected from quite diverse and distant geographic locations. Importantly, this vertical pattern of bacterial properties is consistent with profiles of oceanic POC fluxes in the Pacific. Martin et al. (1987) found that sinking POC fluxes decrease as a negative power function of depth with a relatively invariant slope, regardless of the location where traps were deployed. An overall implication of the above results is that bacterioplankton processes in deep waters are generally coupled to the sinking flux of POC. The following section will discuss possible modes and scales of sinking POC–bacterial couplings in deep-water environments.

The metabolic coupling between sinking POC and deep bacteria—Cho and Azam (1988) proposed that sinking particles are solubilized to release DOC, which fuels production of free-living bacteria in the aphotic zone. This model provides a basis for relating POC flux to bacterial carbon consumption in deep waters (Ducklow 1993). In this section, we analyze our data on the basis of this model. To examine bacteria–POC flux relationships, open-ocean composite carbon mineralization equation of Martin et al. (1987) is used:

$$R = R_{100}\,(Z/100)^{b-1} \qquad R_{100} = (F_{100} \cdot b)/100, \qquad (1)$$

where R is carbon mineralization rate (mg C m^{-3} d^{-1}), F_{100} (mg C m^{-2} d^{-1}) is the POC flux at 100 m, Z is the depth in m, and b is the slope of the log–log regression of sinking POC flux as a function of Z. For subarctic regions, R was estimated by using a slope (b) of −0.858 (Martin et al. 1987) and assuming that F_{100} values are in the range of 27–137 mg C m^{-2} d^{-1} (10–50 g C m^{-2} y^{-1}) with a midrange value of 82 mg C m^{-2} d^{-1} (30 g C m^{-2} y^{-1}) (Berger and Wefer 1991). Note that the model-derived estimates of deep POC fluxes are consistent with data from time-series traps deployed in the subarctic Pacific (Honjo et al. 1995; Takahashi et al. 1997) as indicated in Fig. 4. The rate of bacterial mineralization of organic carbon (bacterial respiration; BR, mg C m^{-3} d^{-1}) was estimated from the leucine-based bacterial production (BP) by assuming a bacterial growth efficiency (BGE) of 0.2 (del Giorgio and Cole 1998):

$$\mathrm{BR} = (1 - \mathrm{BGE})/\mathrm{BGE} \cdot \mathrm{BP}. \qquad (2)$$

Our comparison (Fig. 4) revealed that estimates of BR are generally within the range of R over the depth of 1,000–5,000 m except for some data obtained at Stas. A and 15. The slopes of the decrease of BR (mean slope for western subarctic, −1.46) were ca. 20% less steep than the slope of R ($b - 1 = -1.858$; *see Eq. 1*), small difference given the inherent variability of b (Martin et al. 1987). These vertical patterns suggest a close coupling between R and BR throughout the deep-water column of the subarctic Pacific.

We also calculated the depth-integrated amounts of total organic carbon entering into bacterial cells (bacterial carbon flux = BP/BGE; BGE = 0.2, del Giorgio and Cole 1998), and these amounts were compared with the amount of sinking POC entering into the same depth horizon. In the bathypelagic layer (1,000–4,000 m) of the subarctic Pacific, the bacterial carbon flux accounted for 31–153% of the POC flux (average, 51%; Table 5), suggesting that a large fraction of sinking POC is used by free-living bacteria. For subtropical regions, the corresponding values were 14–58% (average of 23%). These results agree with data reported by Turley and Mackie (1994), who found that the bacterial carbon flux represents 42–63% of POC fluxes in the bathypelagic water column within the Northeastern Atlantic. On the other

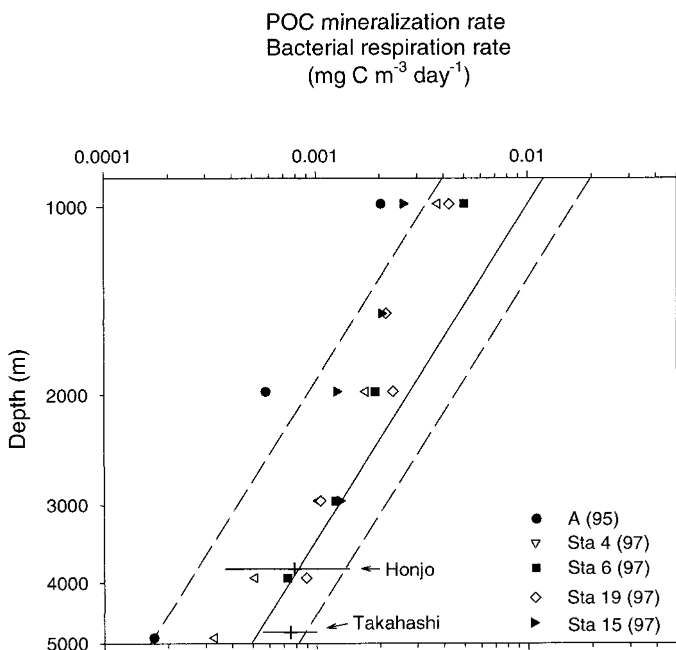

Fig. 4. Comparison of bacterial respiration rate and the mineralization rate of sinking POC (R) in the subarctic Pacific. Bacterial respiration rates are presented with different symbols for different stations as explained in the figure. The range and the midrange estimates of R are presented as negative power function of depth by using three straight lines: two broken lines are the minimum and maximum estimates, whereas a solid line is the midrange estimates (*see text for explanation*). Horizontal bars indicate ranges of R estimated from the data obtained by time series, moored sediment traps deployed in the subarctic region (Honjo et al. 1995; Takahashi et al. 1997). The trap-derived data at a depth of Z m (F_z; mg C m^{-2} d^{-1}) were used to estimate R at the corresponding depth (R_z; mg C m^{-3} d^{-1}) by using the following equation: $R_z = b \cdot F_z/Z$, where b is an exponent of power function relating sinking POC flux to depth [b is assumed to be -0.858 after Martin et al. (1987)]. The trap data of Honjo et al. (1995) were obtained in the eastern subarctic Pacific (50°N 145°W) between 1982 and 1985, whereas those of Takahashi et al. (1997) were collected in the central subarctic Pacific (49°N 174°W) between 1990 and 1995. The ranges of R_z reflect interannual variability of F_z (crosses are mean values).

hand, we estimate that the bacterial carbon flux in the mesopelagic zone was 41% of the POC flux in subarctic and 38% in subtropical regions. These values are in the lower range of previous estimates (80–99%, Cho and Azam 1988; 41–172%, Simon et al. 1992; $\gg$100%, Ducklow 1993; 118%, Turley and Mackie 1994; Table 5), but they still represent a substantial fraction of organic carbon fluxes in a water column. Note that in some oceanic regions, large amounts of surface DOC can be advectively transported to the mesopelagial, which may result in high bacterial production relative to the POC flux (Ducklow 1993). In short, our data and that of others suggest that bacterioplankton are a major consumer of organic carbon in both mesopelagic and bathypelagic oceans and that a large-scale metabolic conversion via a large sinking POC $\rightarrow$ DOC $\rightarrow$ bacteria pathway (Cho and Azam 1988) occurs throughout the water column in a variety of oceanic regions.

The above model of the POC $\rightarrow$ DOC $\rightarrow$ bacteria pathway implies that a large fraction of sinking POC must be converted to DOC before it sediments at the seafloor, but it does not exclude the possibility that a part of sinking POC is consumed directly by zooplankton. Koppelmann and Weikert (1999) have suggested that organic carbon consumption by mesozooplankton (copepods) could be high in deep Northeast Atlantic waters. These authors estimated that the metabolic carbon requirement of mesozooplankton in the bathypelagic zone (1,000–4,250 m) was 1.6–4.1 mg C m^{-2} d^{-1}, representing a significant fraction (20–60%) of sinking POC lost in the same depth horizon.

We note that our estimates of bacterial carbon flux and respiration bear uncertainties due to inherent assumptions that have yet to be tested specifically for deep bacterial assemblages. The most critical parameters include leucine conversion factor (especially isotope dilution and protein turnover; *see* Kirchman et al. 1986), BGE (*see Eq. 2*; del Giorgio and Cole 1998), and pressure effects (Patching and Eardly 1997). These assumptions should be verified by future studies to gain a deeper understanding of the organic carbon budget in the bathypelagial.

Turnover time of deep bacterial assemblages—To evaluate the timescale of bacterial dynamics in deep waters, we divided bacterial biomass by bacterial production to estimate an average turnover time. This calculation may yield the maximum turnover times of actively dividing cells because our counts of bacteria may include inactive, dormant, or even ghost cells (Zweifel and Hagström 1995). To what extent nongrowing or dead cells account for total bacterial counts of deep-water samples is unknown. The plot of turnover time against the depth was highly scattered; the estimates varied in the range of 1–30 yr depending on depth and locations (data not shown).

To compare bacterial turnover times among different regions and different water layers, depth-integrated bacterial biomass was divided by depth-integrated bacterial production for layers of 0–100, 100–1,000, and 1,000–4,000 m. The average turnover time varied in the range of 2.6 and 17.9 yr in the 1,000–4,000-m layer (Table 4). Excluding one datum collected at Sta. A, the turnover time was significantly (Student's t-test, $p = 0.008$) shorter in the subarctic (average $\pm$SD $= 4.7 \pm 2.1$ yr) than in the subtropical (14.6 yr, range 11.4–17.9) Pacific. Not surprisingly, turnover times of bacteria in 100–1,000 and 0–100-m layers were much shorter than those in deep waters. Turnover times in the upper two layers were in the range of 0.5–2.2 yr and 19–97 d, respectively (Table 4). Thus, there are up to two orders of magnitude differences in average bacterial turnover times between surface and deep waters. Dufour and Torréton (1996) reported that turnover times of bacteria were higher by a factor of 10^2 in surface than at 3,000 m in the tropical Northeastern Atlantic, a result that is consistent with our data. However, these authors' estimates of turnover times in deep (1,000–3,000 m) water columns were 100–500 d, substantially shorter than those of our estimates (2.6–17.9 yr). The difference could be due to geographic variation of bacterial turnover time or due to difference in methodology (e.g., thymidine-based measurement of Dufour and Torréton versus our leucine-based measurement).

Table 5. Comparisons of bacterial carbon flux (the total flux of organic carbon entering into bacterial cells) and sinking POC flux in mesopelagic and bathypelagic water columns.

	Mesopelagic (<1,000 m)			Bathypelagic (>1,000 m)			
Locations	POC flux F_{100} (mg C m^{-2} d^{-1})	Bacterial C flux (mg C m^{-2} d^{-1})	% Bacterial C flux/ POC flux	POC flux $F_{1,000}$ (mg C m^{-2} d^{-1})	Bacterial C flux (mg C m^{-2} d^{-1})	% Bacterial C flux/ POC flux	References
North Pacific gyre	79	78	99				Cho and Azam (1988)
Santa Monica basin	634	507	80				Cho and Azam (1988)
Subarctic Pacific	93–102	42–160	41–172				Simon et al. (1992)
Indian Ocean*	8–26	90–620	≫100				Ducklow (1993)
North east Atlantic	99	117	118	8–12	5	42–63	Turley and Mackie (1994)
Subarctic Pacific†	82 (27–137)	33.2 ± 10.9 (n = 6)	41 (24–124)	11.4 (3.8–19)	5.8 ± 1.7 (n = 6)	51 (31–153)	This study
North subtropical Pacific†	34 (14–55)	12.9 (10.2, 15.6)	38 (23–92)	4.7 (1.9–7.6)	1.1 (0.6, 1.7)	23 (14–58)	This study

* Bacterial carbon flux was calculated from the integrated (100–1,000 m) bacterial production and BGE (0.2). Since the production data listed in table 2 of Ducklow (1993) are for the full 0–1,000 m water column, rather than 100–1,000 m as claimed in the table legend (H.W. Ducklow, pers. comm.), the data were corrected for our calculation.

† POC fluxes were estimated by assuming that F_{100} (POC flux at a depth of 100 m) at subarctic and subtropical regions are 27–137 mg C m^{-2} d^{-1} (midrange, 82) and 14–55 mg C m^{-2} d^{-1} (midrange, 34), respectively (Berger and Wefer 1991), and that the flux at a depth of z meter (denoted as Fz) can be predicted by Martin et al.'s (1987) open ocean composite C flux equation: $Fz = (F_{100}/100)^{-0.858 \cdot Z}$. Bacterial carbon fluxes for the subarctic Pacific are averages (±SD) of the data from six stations [Stas. A(95), 4, 6, 15, 17, 19], whereas those values for the subtropical Pacific are averages (range) of the data from two stations [Stas. M2, B (95)]. Assumptions for estimations of these rates are explained in the text.

One important finding of our study is that the biomass of bacteria in 1,000–4,000-m layer differed substantially (2.3 fold) between 1993 (1.4 g C m^{-2}) and 1995 (3.2 g C m^{-2}) at subarctic Sta. A (Table 4). The vertical pattern of bacterial abundance was the same at both dates (Fig. 2). The observed change in bacterial biomass could be due to lateral advection, although it is difficult to envision how all parts of the water column advected similarly so that the depth profile was shifted proportionally and thus the pattern was left unchanged. Alternatively, one could hypothesize that deep bacterial assemblages responded in an integrative manner to changes in surface primary production and sinking POC flux (supply of organic carbon) over the 2 yr. This idea is consistent with a bottom-up model (Billen et al. 1990), which suggests that bacterial biomass, in steady state, should depend on rates of organic carbon supply in oligotrophic systems such as deep waters (Dufour and Torréton 1996). Future studies should test this hypothesis by examining interannual changes of bacterial properties in deep waters along with corresponding changes of surface productivity and sinking POC flux. Importantly, this change in deep-water bacterial biomass over 2 yr sets a lower limit to bacterial growth rates and suggests that our leucine-derived estimates of average bacterial turnover time (Table 4) cannot be too short. Indeed, the turnover time has to be shorter than 2 yr at Sta. A in order to explain the observed increase in deep bacterial biomass.

Vertical transport of bacteria and controls of bacterial distribution in deep waters—One potential mechanism that would explain the apparent coupling between the sinking POC flux and deep bacterial biomass would be the physical transport of bacterial cells attached to sinking particles and dissociation of these cells in the bathypelagic zone. A few studies have determined sinking bacterial fluxes in the oceans (Taylor and Karl 1991; Turley and Mackie 1995), but to what extent these fluxes could contribute to bacterioplankton turnover in deep waters has rarely been discussed (Turley and Mackie 1995). To provide some insight into this problem, we estimated the flux of bacteria attached to large particles sinking out of the depth of 1,000 m (f_{1000}) and compared this flux with bathypelagic bacterial biomass that we determined in the subarctic Pacific. Note that this calculation provides the maximum (potential) replacement rates due to sinking bacterial fluxes because all the attached cells may not dissociate during the transit in the bathypelagic water column. Assuming that the contribution of bacterial carbon to sinking POC is on the order of 1–2% (Ducklow et al. 1985; Taylor and Karl 1991; Turley and Mackie 1995), our estimates of f_{1000} in the subarctic Pacific are 110–220 μg C m^{-2} d^{-1} [sinking POC flux at a depth of 1,000 m was estimated by using Martin et al.'s (1987) open-ocean composite equation with a midrange value of F_{100} (82 mg C m^{-2} d^{-1}) reported for this region (Berger and Wefer 1991)]. The estimated f_{1000} suggests that bacterial biomass in the bathypelagial (1.2–3.5 g C m^{-2}) could be replaced on a timescale of 15–87 yr (potential replacement time = biomass/f_{1000}). Because this replacement time is longer than the timescale of bacterial turnover due to growth (3–17 yr; Table 4), we conclude that the physical transport of attached bacteria by sinking particles has little effect on bulk bacterioplankton turnover in deep subarctic waters.

Although the available evidence just discussed suggests that bacterial growth rather than transport largely controls bathypelagic bacterial distributions, the lack of knowledge on removal processes of bacterial assemblages in deep-water environments severely limits our ability to model and to understand regulation of bacterial dynamics. Previous work has found that heterotrophic nanoflagellates are present in deep Atlantic waters at a density of ~10 cells ml^{-1} (Patterson et

al. 1993). A form of barophilic, bacterivorous flagellates has been isolated from 4,500 m in the mid-Atlantic (Turley et al. 1988). These results strongly suggest that bacteria-flagellate food chains exist in deep waters, but the rate of bacterivory and its coupling with bacterial growth have yet to be determined. Also virus-like particles have been enumerated in deep Pacific waters (Hara et al. 1996), but the magnitude of bacterial mortality due to viral infection remains unknown. In addition to biological processes, bacteria could be removed from the water column by scavenging, i.e., attachment of bacteria to large sinking particles and subsequent loss due to sedimentation (Stolzenbach and Elimelech 1994). Identifying the dominant controls of bacterial dynamics and the microbial loop in deep water is an intriguing and challenging area of future studies.

Influence of sediment-water flux and lateral advection of organic carbon—An important exception to the general consistency among depth profiles of deep bacterial abundance is the variability in profiles obtained at three stations in the eastern subarctic Pacific (Stas. 15, 16, 17) and the Bering Sea (Sta. 9): these data were poorly described by the log–log model ($r^2 = 0.252$–0.699) (Table 2). It is unlikely that these variations are due to high counting errors specifically (and inexplicably) associated with these samples because depth profiles of leucine incorporation were also variable at eastern subarctic Stas. 15 and 17 (Fig. 1; Table 3). We note that these noisy profiles were observed at stations relatively close to the continental slope. This proximity to the slope might suggest that organic carbon was introduced into seawater from slope sediments and that this organic carbon was laterally advected by local eddies to the sampling sites. Bacterial depth profiles at the sites could be affected by advectively introduced organic carbon in a complex way. Our data partly support this hypothesis. We found that bacterial abundance and production were generally high in near-bottom layers (Fig. 1), which suggests that inputs of organic matter from bathyal sediment to seawater and their influence on bacterial properties in water column could be significant. Potential mechanisms that may facilitate sediment-water fluxes of organic matter include resuspension of sediments (Turley and Mackie 1994; Druffel et al. 1996), diffusional release of pore water DOC (Bauer et al. 1995), and hydrothermal activity and volcanic eruption at limited locations and times. In any case, our data demonstrating depth-trend anomalies of bacterial properties in some restricted areas of the oceans suggest that the deep bacterial profile could be used as a microbiological signature of mesoscale perturbations on the organic matter field in deep waters.

The advective transport of DOC by the large-scale ocean circulation (the conveyor belt; Broecker 1991) is another potential mechanism by which organic carbon is introduced into deep waters to support bacterial carbon consumption and production therein. It has been suggested that the bulk DOC pool in deep water is largely refractory in nature (Barber 1968) with an average age of 4,000–6,000 yr (Williams and Druffel 1987), yet bacterial mineralization must represent one of the important sinks for refractory DOC (Williams and Carlucci 1976; Cherrier et al. 1999). Recently, Hansell and Carlson (1998) have reported that deep-water DOC concentrations decrease by 29% in transit from the north Atlantic to the Pacific. The authors' estimate of the carbon budget in the deep central Atlantic suggests that DOC oxidation during transit could be equivalent to the deep sinking POC flux in the investigated region. If this model applies to the deep northern Pacific and if free bacteria are the major consumer of this DOC, we would expect to observe influences of the advective DOC field on bacterial property distributions in the Pacific.

Such expectations may include: (1) Bacterial carbon consumption could be more or less uniform over the deep-water column, because DOC concentrations in deep waters change little over the depth (Hansell and Carlson 1998). (2) Bacterial carbon consumption could be greater in the subtropical than in the subarctic regions because DOC concentrations significantly decrease northward along the deep path of conveyor in the Pacific (Hansell and Carlson 1998). Clearly, these expected patterns contradict our observations; we found that bacteria decrease sharply over the depth (Fig. 2) and increase northward over the basin (Fig. 3). Thus our data do not support the hypothesis that the DOC transported by the conveyor is a major organic carbon source for bacterioplankton in the deep Pacific. Hansell and Carlson (1998) pointed out that one potential mechanism by which the concentration of deep-water DOC is reduced during its transit in the Pacific is the adsorption of DOC onto suspended particulate materials and subsequent loss of these materials due to sedimentation (Druffel et al. 1992, 1996). If this is the case, attached bacteria, rather than free bacteria, could be a major agent in oxidizing adsorbed DOC (Williams in press).

Conclusions

Our data on bacterial biomass and production in various deep Pacific waters suggest that bacterial production and carbon consumption in the bathypelagic zone are largely coupled with sinking fluxes of POC. The data in support of this hypothesis include: (1) the basin-scale distributions of bacterial biomass and production in deep waters that are consistent with sinking flux regimes (Fig. 3), and (2) the general consistency among depth profiles of bacterial respiration and the mineralization of sinking POC (Fig. 4). Conservative estimates of bacterial carbon uptake accounted for 23–51% of sinking POC fluxes (Table 5), which suggests that a substantial transformation of organic carbon via a sinking POC $\rightarrow$ DOC $\rightarrow$ bacteria route occurs in the bathypelagic zone. A possible turnover time of deep bacterial biomass was estimated to be on the order of 1–30 yr. Anomalies in depth profiles of bacterial abundance and production were observed at some stations and they were interpreted as a possible indication of lateral transport of organic carbon by local eddies. Based on the above results, we propose that full depth profiles of bacterial biomass and production provide useful information regarding spatial and temporal variability in sinking fluxes and advective fluxes of organic carbon in deep waters. This information may supplement and help interpret the data obtained by time-series deep ocean traps. Important areas for future research include regulation of growth and mortality processes of deep bacterial assemblages and elucidation of microbial food webs in deep waters.

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Received: 15 June 1999
Accepted: 16 November 1999
Amended: 9 December 1999