

Depth-related cell-specific bacterial leucine incorporation rates on particles and its biogeochemical significance in the Northwest Mediterranean

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Abstract

A study of total and particle-associated bacteria in the Northwest Mediterranean revealed notable relationships with depth. Cell-specific leucine incorporation rates by total bacteria decreased significantly with depth (to 380 m), best fitting the power function $\log(\text{rate}) = 2.1 - 0.54 \log(\text{depth})$, $r^2 = 0.57$, $P = <0.001$. In contrast, cell-specific leucine incorporation rates by particle-associated bacteria increased with depth as described by the power function $\log(\text{rate}) = 0.4 + 0.84 \log(\text{depth})$, $r^2 = 0.74$, $P = <0.01$. We suggest that this relationship may reflect availability of usable dissolved organic matter (UDOM) and/or inorganic nutrients within the particle with increasing water depth. The latter relationship could also be interpreted in relation with time, i.e., be a consequence of the time taken for enzyme induction and solubilization of particulate organic matter (POM) to UDOM and the subsequent incorporation into bacterial protein during the sinking of the particle. These results may help to explain observations that sinking particles are rapidly decomposed between 100 and 500 m. Bacteria associated with particles in the Mediterranean contributed only 0.8–2.8% of total bacterial numbers but contributed 3–12% of total bacterial production in the upper 70 m. However, their contribution to total bacterial production in deeper waters was substantially higher (48% at 380 m). The activity of attached bacteria is, therefore, important and varies with depth, and this may help to explain the particularly low particle flux and hence the impoverished benthic environment found in the deeper waters of the Mediterranean.

A major, often seasonal (Lampitt et al. 1993a), biogeochemical process in the oceans is the formation of aggregates. The aggregation–disaggregation process is dynamic, and aggregates can vary in size from submicrons (Koike et al. 1990) to several centimeters or greater (Herndl 1992). While sticky muco polysaccharides produced by phytoplankton (Mopper et al. 1995; Passow and Alldredge 1995) and animals (Alldredge 1976) are important in aggregate formation, the microbial use of these compounds via hydrolytic ectoenzyme activity is important in disaggregation processes (Smith et al. 1992). Unique internal chemical microenvironments can evolve within large particles (Alldredge and Cohen 1987), which harbor high concentrations of heterotrophic bacteria, cyanobacteria, microalgae, and microflagellates (Alldredge and Silver 1988; Alldredge and Gotschalk 1990; Turley and Mackie 1994). Biogenic aggregates >0.5 mm in diameter are responsible for the majority of vertical particle flux in the oceans (Fowler and Knauer 1986) and can transport large numbers of attached bacteria down to depths of 3,000–4,000 m (Turley and Mackie 1995). These attached bacteria have been implicated in the remineralization and enzymatic

dissolution of particulate organic matter (POM) during its descent (Cho and Azam 1988; Smith et al. 1992). This process may also be an important carbon source for free-living mid- and deep-water bacteria in the Pacific (Cho and Azam 1988; Simon et al. 1992) and Atlantic (Turley and Mackie 1994). Therefore, attached bacteria play an important biogeochemical role in oceanic carbon flux despite comprising $<5\%$ of total bacterial biomass (Cho and Azam 1988). However, on occasions of high aggregate concentration, they can comprise up to 10–34% of total bacterial biomass (Turley and Mackie 1994).

Considerable variation has been found in measurements of bacterial production on aggregates, with cell-specific thymidine incorporation rates equal to, lower than, or 6 times higher than those of free-living bacteria (Alldredge et al. 1986; Alldredge and Gotschalk 1990; Turley 1993; Turley and Mackie 1994; Turley et al. 1995). Such variations have been explained as a function of the age and composition of particles (Biddanda and Pomeroy 1988; Turley and Mackie 1994). Most studies of aggregates in open oceans have occurred in the upper 100 m, where they are generally more concentrated (Lampitt et al. 1993b), and where aggregation–disaggregation processes are dynamic. A study of bacterial DNA synthesis on particles in the Northeast Atlantic indicated some variation with depth showing an increase in cell-specific thymidine incorporation rates on particles collected from 500 m compared to particles collected from 40 m (Turley et al. 1995). However, at 2,000 m cell-specific thymidine incorporation rates on particles were lower than those collected at 500 m (Turley et al. 1995), possibly due to a loss in usable organic carbon (Smith et al. 1992) and/or the inhibitory effect of pressure at these depths (Turley 1993).

Here we explore variation in bacterial cell-specific leucine incorporation rates as a function of depth on particulate and seawater samples from the Northwest Mediterranean.

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Table 1. Station positions, sampling dates, water depth for the cruises in the Northwest Mediterranean Sea.

Cruise	Station	Sampling date	Position		Water column depth (m)
			Latitude (N)	Longitude (E)	
PICNIC	1	9 Apr 1995	43°37.4'	7°26.6'	1,025
Villefranche Bay	Point B	1 Apr 1995	43°41.1'	7°19.0'	80
EUROMARGE	B5	30 Jun 1995	42°24.0'	3°44.0'	1,000
	B2	1 Jul 1995	42°34.0'	3°17.0'	88
	S5	2 Jul 1995	40°09.5'	3°31.5'	970
	S2	3 Jul 1995	40°02.0'	3°38.0'	120
	M3	5 Jul 1995	43°02.0'	5°12.5'	950
	M1	6 Jul 1995	43°10.0'	5°12.5'	85

Seawater and particles were sampled on two cruises in the Northwestern Mediterranean Sea during 1995 at the station positions and dates shown in Table 1. Particles were sampled with a 7.5-liter programmed detritus sampler (PDS) (Gorsky et al. 1996), which is a cable-operated plexiglass sampler with controlled rotating waterproof lids at each end designed to collect intact aggregates, and by self-contained underwater breathing apparatus (SCUBA) divers. Seawater was sampled with 12-liter Niskin bottles and samples taken for estimates of total bacterial numbers and leucine incorporation rates. It is standard practice to use a Niskin or GoFlo to sample water for measurement of total bacterial numbers and production, although most of these will be the free-living bacterial pool as large particles may not be sampled. We will refer to analysis of bacterial variables in seawater sampled by Niskin as total. The seawater and particles sampled by the PDS were gravity filtered through a 10- μ m pore-size, 147-mm diameter, Nuclepore filter. The particles retained by the filter were rinsed off with 20–30 ml of 0.2- μ m pore-size filtered seawater (FSW) and analyzed for particle-associated bacterial numbers and leucine incorporation rates. During April 1995, large visible particles from Villefranche Bay (point B in Table 1) were sampled by SCUBA divers using syringes (Alldredge 1993). These particles were collected from 40 m, pooled, and subsamples taken for bacterial enumeration and determination of leucine incorporation rates.

Both total and particle-associated bacteria were enumerated by a direct count method using sonication (Conan et al. 1999), epifluorescent microscopy (Porter and Feig 1980; Turley and Hughes 1992), and the 4'-6-diamidino-2-phenylindole (DAPI) fluorochrome.

Bacterial protein synthesis was determined by ^3H -leucine incorporation (Kirchman 1993). Optimal incubation times were determined by time series experiments carried out in surface (5–200 m) and deep waters (>200 m) to ensure that incubation periods were both within the period of linearity and exhibited sample counts measurably higher than the dead controls. Incubation times for surface-water (5–10 ml) and deep-water (40 ml) samples were 2–4 h and up to 6 h, respectively, whereas incubation times for particulate samples ranged between 0.5–1.0 h (0.5–2 ml of particle slurry) depending on particle type (fecal pellets or samples collected by PDS or SCUBA).

A ^3H -leucine concentration of 5 nM (final concentration) was routinely used for seawater samples during the PICNIC

cruise because there was no difference in incorporation rates between the addition of 5- and 10-nM (final concentration) additions of radiolabel. However, on-board scintillation counting facilities were not available during the EUROMARGE cruise, so 10 nM (final concentration) of ^3H -leucine was added to ensure excess label and to repress de novo synthesis of intracellular leucine (Kirchman 1993). Both concentrations should be sufficient to saturate uptake in these environments. The use of radiolabels on particles has many uncertainties (Alldredge et al. 1986). Alldredge (1993) found apparent kinetic saturation of marine snow samples at 2 nM (final concentration) but cautiously selected 20 nM (final concentration) in order to reduce the possibility of underestimating bacterial production through intracellular isotope dilution or decreased diffusion rates into the interstitial spaces of the particles. Applying the same rationale, we added 100 nM ^3H -leucine (final concentration; specific activity 154 Ci mmol $^{-1}$) to particulate samples and also incubated for short periods. No additional nonradioactive substrate was added, as this is not recommended in waters where rates are expected to be low, such as deep waters or oligotrophic environments (Kirchman 1993). Our estimates of attached bacterial production will, therefore, be conservative if either isotope dilution or diffusion is occurring. We used two live replicates and one glutaraldehyde killed control for seawater samples and three live replicates and two controls for particulate samples.

For convenient use at sea, we used the ice-cold trichloroacetic acid extraction method for determining ^3H -leucine incorporation (Chin-Leo and Kirchman 1988). Samples were incubated in the dark at in situ temperatures. During the EUROMARGE cruise, typical seawater temperatures were $19 \pm 2^\circ\text{C}$ above the strong thermocline and $13 \pm 1^\circ\text{C}$ below the thermocline. In contrast, on the PICNIC cruise, the onset of stratification was just occurring with a difference of only 0.6°C between water at the surface and 300 m (13.0 – 13.6°C). A single incubation temperature of 13°C was used on this cruise. Live incubations were terminated with glutaraldehyde and all samples were filtered onto 0.2- μ m pore-size, 25-mm diameter Nuclepore filters. In situ extraction in the filter tower with 5% ice-cold TCA for 5 min was followed by five 1-ml rinses with 5% ice-cold TCA. Filters were placed in 6-ml scintillation vials and allowed to dry. Then 5-ml Beckman Ready Safe scintillation cocktail was added, and the radioactivity was counted on a Beckman LS1800 liquid scintillation counter. Counting efficiency was

Table 2. Temporal changes in cell specific thymidine and leucine incorporation rates by bacteria produced on fecal pellets produced by *Salpa fusiformis* and *Thalia democratica*. Rates for total bacteria in seawater and bacteria associated with particles collected by SCUBA are given for comparison (see text for further details). SD is the standard deviation.

Sample	Depth or age	³ H-Tdr Inc rates (mol × 10 ⁻²¹ cell ⁻¹ h ⁻¹)			³ H-Leu Inc rates (mol × 10 ⁻²¹ cell ⁻¹ h ⁻¹)		
		Range	Mean	SD	Range	Mean	SD
SCUBA aggregates from 40 m	40 m				176.6–182.4	179.5	2.92
SCUBA seawater 40 m	40 m	0.65–1.27	0.88	0.34	18.33–22.09	20.58	1.99
Fecal pellets of <i>S. fusiformis</i>	fresh	91.61–99.56	96.88	4.57	1,182.93–1,344.35	1,263.64	114.14
Fecal pellets of <i>S. fusiformis</i>	24 h old	132.25–145.94	139.45	6.88	2,123.01–2,679.57	2,399.18	278.31
Fecal pellets of <i>S. fusiformis</i>	48 h old	22.96–23.89	23.58	0.54	558.48–700.33	646.51	76.86
Fecal pellets of <i>T. democratica</i>	24 h old	7.73–22.02	319.20	7.51	299.76–338.64	16.21	27.49
Fecal pellets of <i>T. democratica</i>	48 h old	64.45–73.78	208.61	5.36	204.07–213.14	70.65	6.42

corrected for quenching by the external standard channels ratio method.

Rates of bacterial production (BP) were calculated from leucine incorporation rates using a conversion factor of 3.1 kgC mol⁻¹ (Kirchman 1993). Incorporation rates are expressed on a per-cell basis by dividing the incorporation rate by the number of bacteria, assuming that all bacteria are actively incorporating the macromolecule.

Fecal pellets of the salps *Salpa fusiformis* and *Thalia democratica* were collected from animals freshly caught in Villefranche Bay, using a 270- μ m vertical net haul over the upper 30 m of the water column and held in tanks with flowing seawater at sea surface temperatures (15°C). Fresh fecal pellets were harvested after 3 h in captivity and held separately in FSW at in situ temperature in the dark. Sub-samples were removed after 0, 24, and 48 h for the determination of bacterial numbers and rates of thymidine and leucine incorporation. This enabled us to examine bacterial numbers and rates of ³H-leucine incorporation on particles (see above) of known age and relate them to the same measurements on particles from a range of depths but unknown age. In addition, and for the fecal pellet experiments only, we measured ³H-thymidine incorporation rates (Fuhrman and Azam 1982) by the addition of 200 nM ³H-thymidine (final concentration; specific activity 81 Ci mmol⁻¹) using the method outlined above for leucine incorporation. Estimates of sinking rates for fecal pellets produced by *S. fusiformis* and *T. democratica* were determined by measuring the time taken for 24 fecal pellets, from each species, to sink 27 cm in an undisturbed 1-liter glass cylinder of seawater held in a constant temperature room at 13°C.

Fecal pellets and SCUBA collected particles—The cell-specific thymidine and leucine incorporation rates measured for the fecal pellets of *S. fusiformis* and *T. democratica* (Table 2) compare well to those for fecal pellets collected by divers off Southern California (27.4 mol thymidine × 10⁻²¹ cell⁻¹ h⁻¹) by Alldredge et al. (1986) and to particles containing many fecal pellets collected by sediment traps (approximately 1,000 mol leucine × 10⁻²¹ cell⁻¹ h⁻¹) by Turley and Mackie (1994) in the Northeast Atlantic.

The age of the fecal pellet was found to influence the activity of the attached bacteria. After 24 h there is an increase in leucine and thymidine incorporation rates per cell

in fecal pellets produced by *S. fusiformis*. However, after 48 h the cell-specific activities of both substrates fall off substantially (a 3.7 and a 5.8 times decrease for thymidine and leucine, respectively) (Table 2). This may be because the labile, easily assimilable components have been used. In contrast to this, the fecal pellets of *T. democratica* have higher cell-specific thymidine incorporation rates after 48 h, while the highest leucine incorporation rates per cell occur after 24 h. The mean sinking rates of fecal pellets produced by *S. fusiformis* and *T. democratica* were 1,800 m d⁻¹ (SD = 876) and 182 m d⁻¹ (SD = 82), respectively. The fecal pellets of the former would, therefore, sink rapidly out of the water column within a day, whereas the latter may take up to 3 d to reach 600 m.

The cell-specific rates of leucine incorporation by bacteria associated with visible particles collected by SCUBA divers in Villefranche were of the same order of magnitude compared to fecal pellets from *T. democratica*, but were substantially higher than those for total bacteria (Table 2).

Contribution of attached bacteria to total bacterial numbers and production—Bacteria associated with particles from surface waters to 380 m contributed 0.5–4.9% (mean = 2.1%) of total bacterial numbers but 2.8–48.3% (mean = 12.1%) of total bacterial production (Table 3).

Although bacteria associated with particles contributed only <5% of total bacterial numbers, they were consistently more metabolically active than the total bacteria. The mean cell-specific leucine incorporation rates were 2–10 times greater in the upper 70 m and 22–53 times greater below this depth for attached bacteria compared to total bacteria (Fig. 1). In the upper 70 m the contribution of attached bacteria to total bacterial production ranged between 3–12% (mean 6%; Table 3). There are few similar data with which to compare these estimates. However, data exist for a small subset of the attached bacterial population associated with macroscopic marine snow particles. Our estimate of the contribution of attached bacterial production (3–12%) in the surface waters is higher than that for bacteria attached to marine snow particles in the subtropical Atlantic (<0.5%) (Alldredge and Youngbluth 1985) and in the temperate North Atlantic (1.8–3.4%) (Turley and Mackie 1994). However, it is similar to estimates in the Pacific off the Southern Californian coast (1–28%, mean 8%) (Alldredge et al. 1986; Alldredge and

Table 3. Contribution of attached bacteria to total bacterial numbers and production. n/a is data not available.

Cruise	Station	Sampling depth (m)	Total bacteria		Attached bacteria		Ratio of attached/total	
			Numbers (cells $\times 10^6 L^{-1}$)	Production ($\mu gC L^{-1} d^{-1}$)	Numbers (cells $\times 10^6 L^{-1}$)	Production ($\mu gC L^{-1} d^{-1}$)	Attached numbers (%)	Attached production (%)
PICNIC	1	40	375.0	n/a	10.6	n/a	2.8	n/a
	1	360	221.0	n/a	5.3	n/a	2.4	n/a
	1	600	113.0	n/a	5.5	n/a	4.9	n/a
EUROMARGE	B5	40	687.0	0.851	14.9	0.051	2.2	6.0
	B5	450	75.6	n/a	3.4	n/a	4.5	n/a
	B2	40	1,295.0	2.427	36.4	0.122	2.8	5.0
	S5	70	406.0	0.539	4.8	0.064	1.2	11.8
	S5	380	133.0	0.058	1.2	0.028	0.9	48.3
	S2	70	1,004.0	1.282	9.7	0.036	1.0	2.8
	M3	70	806.0	0.721	7.9	0.038	1.0	5.3
	M3	160	317.0	0.197	1.7	0.024	0.5	12.2
	M1	50	712.0	0.611	5.7	0.034	0.8	5.6

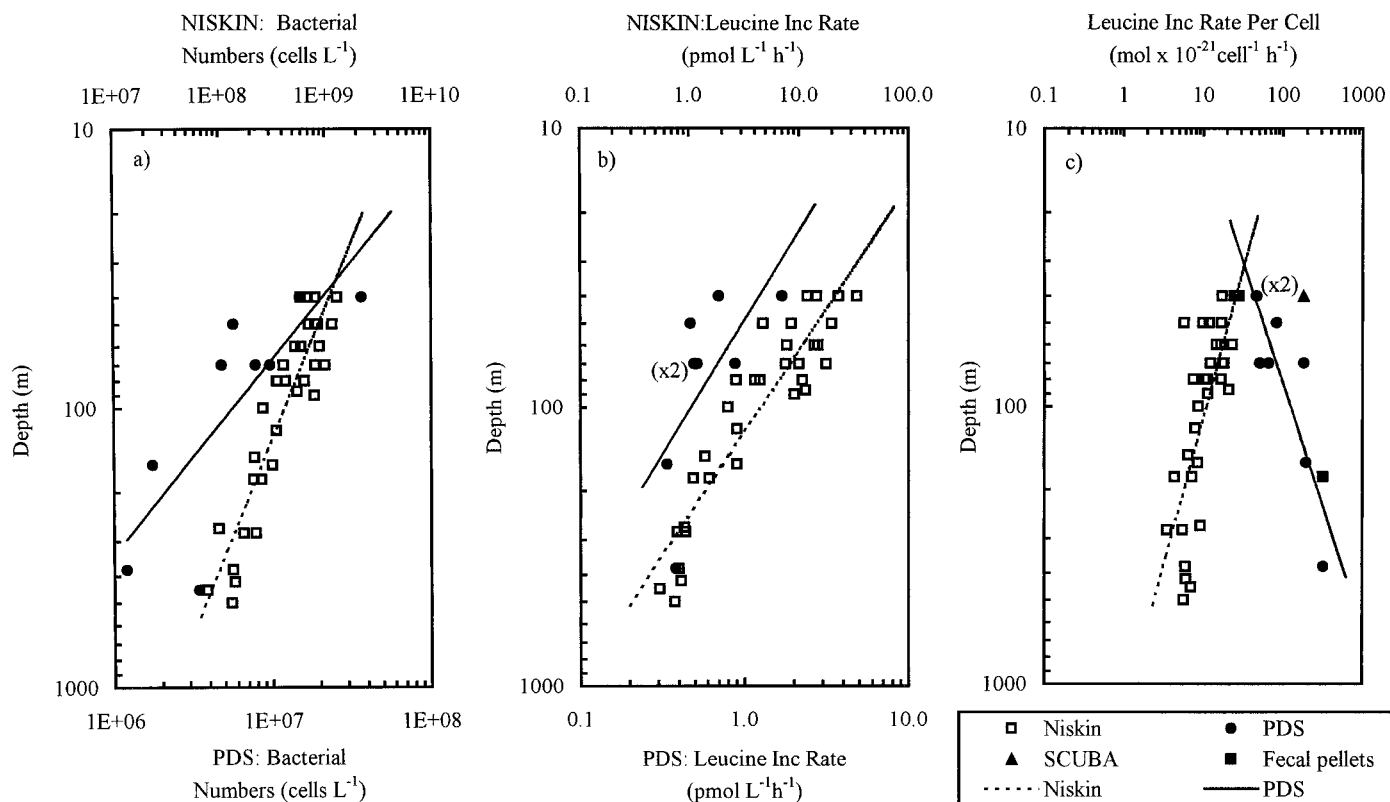


Fig. 1 Depth profiles of (a) log bacterial numbers, (b) log leucine incorporation rates, and (c) log cell-specific leucine incorporation rates for total bacteria in seawater sampled by Niskin bottles and bacteria associated with particles $>10 \mu m$ collected by the programmed detrital sampler (PDS) on the EUROMARGE cruise. Data for macroaggregates collected by SCUBA from Villefranche Bay and fecal pellets from *Thalia democratica* from Villefranche Bay (24 h after their production with a mean measured sinking rate of $180 m d^{-1}$) are given for comparison. Regression lines for Niskin seawater and PDS particles are shown and their formulae and statistics are given in Table 4. (x2) indicates two overlying data points.

Table 4. Regression equations and statistics for total bacteria in seawater sampled by NISKIN and bacteria associated with particles >10 μm sampled by PDS against depth (Fig. 1). The final regression includes data from SCUBA collected macroaggregates and fecal pellets from *T. democratica* with the data from particles collected by PDS. The parameter y is bacterial numbers or rates and x is depth.

Region	Sample type		Formulae	r^2	n	P
A. Bacterial numbers (cells L^{-1})						
	Seawater	(NISKIN)	$\log y = 10.4 - 0.9 \log x$	0.84	33	<0.001
	Particles	(PDS)	$\log y = 8.6 - 0.92 \log x$	0.64	9	<0.01
B. Leucine incorporation rates (pmol $\text{L}^{-1} \text{h}^{-1}$)						
	Seawater	(NISKIN)	$\log y = 3.5 - 1.43 \log x$	0.85	33	<0.001
	Particles	(PDS)	$\log y = 0.6 - 0.44 \log x$	0.42	8	<0.1
C. Cell specific leucine incorporation rates (mol $\times 10^{-21} \text{cell}^{-1} \text{h}^{-1}$)						
	Seawater	(NISKIN)	$\log y = 2.1 - 0.54 \log x$	0.57	33	<0.001
	Particles	(PDS)	$\log y = 0.4 + 0.84 \log x$	0.74	8	<0.01
	Particles	(PDS + SCUBA + fecal pellets)	$\log y = 0.6 + 0.76 \log x$	0.55	10	<0.02

Gotschalk 1990). On one occasion the attached bacterial contribution to total bacterial production was as high as 48%, as shown by the deep-water sample of this study (Table 3). Therefore, this study indicates that bacteria attached to particles in the Mediterranean Sea play an important role in total water column bacterial production.

Relationship of total bacteria and particle-associated bacteria with depth—Total bacterial numbers, leucine incorporation rates, and cell-specific leucine incorporation rates in seawater sampled by Niskin bottles decrease significantly with depth as a power function (Fig. 1a,c; Table 4). Bacterial numbers and rates of leucine incorporation associated with particles also decrease significantly with depth best fitting a power function (Fig. 1a,b; Table 4). However, cell-specific leucine incorporation rates of particle-associated bacteria behave differently to those of total bacteria with a significant increase with depth as a power function (Fig. 1c; Table 4).

The depth distribution of total bacterial numbers and their rates of leucine incorporation in the Mediterranean Sea (Fig. 1a,b) are similar to those found in other oceans (e.g., Ducklow et al. 1993; Li et al. 1993; Turley and Mackie 1994), declining rapidly with depth once below the upper mixed layer. This reflects the decreasing availability of usable dissolved organic matter (UDOM) from photosynthesis. In contrast, deep-sea free-living bacteria rely more on particle-associated bacteria to liberate UDOM from POM via enzymatic hydrolysis (Cho and Azam 1988; Smith et al. 1992). This can result in large-scale transfer of organic matter from sinking particles to the dissolved phase (Smith et al. 1992). Indeed, the carbon demand of mid- and deep-water free-living bacteria is nearly equivalent to the depth-dissipated POC in the north Pacific Gyre (Cho and Azam 1988), subarctic Pacific (Simon et al. 1992), and temperate North-east Atlantic (Turley and Mackie 1994). However, these estimations are based on observations of total bacterial numbers and activities taken at depth rather than on observations of particle-associated bacterial numbers and activity with depth. The results from studying particle-associated bacteria (Fig. 1c) support the preliminary work by Turley et al. (1995) in that the cell-specific activity of particle-associated

cells may increase with depth, at least over the upper 380 m, in direct contrast to that occurring with total bacteria. This may reflect the availability of UDOM within the particle and/or the availability of inorganic nutrients below the thermocline and that these increase with depth over the upper 380 m of the water column. In the upper waters, where the aggregates may on average be younger, the cell-specific leucine activity of particle-associated bacteria is lower and similar to that of free-living bacteria. Presumably, both attached and free-living bacteria respond to the UDOM and/or the inorganic nutrients available in the surface water. In addition, hydrolytic enzymes of bacteria attached to newly formed particles may not have been induced or their production rate may not be fast enough to overcome diffusion rates to such an extent that sufficient concentrations of UDOM are available within the particle to stimulate attached bacterial protein synthesis. In deeper waters the aggregates are presumably older and may, therefore, have had time to hydrolyze POM to UDOM at sufficient rates to form diffusion gradients with sufficiently enriched UDOM microenvironments to support higher rates of attached bacterial protein synthesis. Measurement of the induction time of higher proteolytic activities would assist in determining whether this is a possible explanation. However, if the above hypothesis is true, then the power relationship shown in Fig. 1c, suggesting increasing cell-specific leucine activities with depth, could be viewed as a relationship with time. Bacteria can at least double their biomass in 5 d while decomposing POM (Turley and Lochte 1990), during which time the whole cycle of enzyme induction and production, hydrolysis of POM, UDOM uptake, protein and DNA synthesis, and cell division will have occurred. It is, therefore, possible that particles at 380 m are in the order of 5 d old. Assuming that the particles originated in the surface waters and ignoring that in situ production can occur at depth (e.g., through fecal pellet production by migrating zooplankton; Lampitt et al. 1993b), this would give mean sinking rates of around 75 m d^{-1} . These sinking rates are similar to those obtained from sediment trap studies in the Northwest Mediterranean (92 m d^{-1} ; Miquel et al. 1994), in the Northeast Atlantic (60–125 m d^{-1} ; Newton et al. 1994), and for biogenic particles, aggregates, and

zooplankton fecal pellets (28–150 m d⁻¹; see review in Miquel et al. 1994).

Cell-specific leucine incorporation rates of macroaggregates from 40 m collected by SCUBA and fecal pellets from *T. democratica* after 24 h when placed at 182 m (their mean sinking rate being 182 m d⁻¹) are shown in relation to the power relationship between cell-specific leucine incorporation revealed by the PDS collected data (Fig. 1c; Table 4). When the SCUBA and fecal pellet data are included with the PDS data, the relationship with depth still holds with little change in the gradient, although there is a slight shift of the *x* intercept to the right (due to slightly higher leucine incorporation rates cell⁻¹ on the larger particles) (Table 4). These results further indicate that, although the factors influencing microbial activity on particles are complex and are likely to vary both temporally and spatially at large and small scales, there seems to be a uniform relationship between cell-specific protein synthesis and depth suggesting that the system is in an approximate steady state.

Significance to Mediterranean biogeochemistry—Oligotrophic waters such as the Mediterranean are characterized by a high proportion of regenerated production, the dominance of the microbial loop (Hagström et al. 1988), and a tight coupling between primary and bacterial production (Conan et al. 1999; Turley et al. in press). As a consequence, reduced export production is thought to occur (Heussner and Monaco 1996) resulting in reduced benthic food flux (Duijneld et al. 1996). However, high concentrations (>200 L⁻¹) of particles (>100 μm) are not uncommon in the Mediterranean (Gorsky et al. 1992, 1996).

Sinking particles are rapidly decomposed between 100 and 500 m (Suess 1980; Martin et al. 1987) such that there is an exponential decrease in vertical POC flux (Betzer et al. 1984; Turley et al. 1995) with rapid disappearance of more labile components (Wakeham et al. 1984). In the Eastern Mediterranean, Tselepidis et al. (1996) found that the amount of freshly derived POM reaching the sea bed below 500 m did not vary significantly, whereas there was significant variability at shallower sites (40–200 m), thus implying substantial decomposition of sinking particles in the water column above 500 m. Our results indicate that bacterial activity on these particles, at least to a depth of 380 m, is substantial and varies with depth, and that this may explain the vertical POC flux profiles and hence impoverished benthic environment found in the deeper waters of the Mediterranean.

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