Vol. 115: 191–203, 1994 | MARINE ECOLOGY PROGRESS SERIES
Mar. Ecol. Prog. Ser. | Published December 1

Biogeochemical significance of attached and free-living bacteria and the flux of particles in the NE Atlantic Ocean

C. M. Turley, P. J. Mackie

Plymouth Marine Laboratory, Citadel Hill, Plymouth PL1 2PB, United Kingdom

ABSTRACT: In the NE Atlantic during May 1990, a period of high aggregate abundance, amorphous aggregates contained substantially higher concentrations of bacteria, cyanobacteria and flagellates than the surrounding seawater. Those from 45 to 55 m, at the aggregate maximum just below the seasonal thermocline, contained 2.1 to 25.4 $\times 10^8$ bacteria, 1.0 to 4.7 $\times 10^7$ cyanobacteria and 1.3 to 33.0 $\times 10^6$ flagellates ml^{-1} aggregate. Leucine incorporation rates by bacteria attached to aggregates ranged from 12 to 206 $\times 10^{-21}$ mol $cell^{-1}$ d^{-1}. The concentration of bacteria associated with faecal pellets was generally higher than the concentration on the amorphous aggregates. Bacteria attached to aggregates were equivalent to 10 and 14 % of free-living bacterial carbon integrated through the water column to 100 and 300 m, respectively. This could rise to 25 and 34 % if the different carbon content of attached and free-living bacteria was taken into account. However, this study coincided with the maximum marine snow concentration measured 150 km southwest, so at other times when marine snow concentrations are lower, the proportion of attached bacteria will be less. The contribution of attached bacteria to total bacterial production in the top 100 and 300 m ranges between 1.8 and 3.4 %. The contribution of free-living bacterial carbon to suspended POC (particulate organic carbon) was between 25 and 33 %, and after correcting for their retention on the glass fibre filters, this contribution could be 28 to 40 %. Flux studies during 1989 and 1990 indicated that a smaller proportion of POC flux (9 %) and bacterial carbon flux (10 %) reached 3100 m than mass flux (25 and 35 %), indicating there are processes involved which preferentially utilise or reduce the POC and bacterial components. Bacterial detachment from sinking particles could contribute 2.4 % of the integrated bacterial biomass per annum. The fraction of sinking POC lost between 150 and 3100 m may be an important carbon source to the mid/deep-water bacterial population, capable of supplying around 90 % of the bacterial carbon demand during April to July 1989 at 47° N, 20° W. In the deeper waters, between 600 and 3100 m, there was sufficient depth-dissipated sinking POC to potentially supply the carbon demand of the bacteria. However, above 600 m an additional source of organic carbon is required to support their growth.

KEY WORDS: Aggregates · Bacteria · Cyanobacteria · Flagellates · Bacterial production · Bacterial carbon demand · Particle flux · Particulate organic carbon

INTRODUCTION

Large (>0.5 mm diameter) detrital biogenic aggregates, responsible for the majority of vertical particulate flux in the oceans (Fowler & Knauer 1986), harbour high concentrations of heterotrophic and phototrophic bacteria, phototrophs, microalgae and microflagellates (review by Alldredge & Silver 1988, Alldredge & Gotschalk 1990). During May in the NE Atlantic Ocean, aggregates have been observed in higher concentrations just below the seasonal thermocline (Lampitt et al. 1993a), and at 270 m a strong seasonality in large particle concentration has been observed (Lampitt et al. 1993b). Such seasonality in mass and POC flux events is found even at depths of 3200 m (Newton et al. 1995) and on the seafloor (Theil et al. 1988) in this region. Fluxes of bacteria and cyanobacteria are associated with these seasonal mass flux events (Turley & Mackie 1995) through attachment to, incorporation in and/or growth on sinking particles. Although the attached bacteria contribute < 10 % of the aggregate POC (particulate organic carbon) in surface waters (Simon et al. 1990) intense hydrolytic enzyme activity by these heterotrophs may be important in the

solubilization of the particle (Smith et al. 1992). These workers also found that very little of the hydrolysate was taken up by the attached bacteria and that their results supported the hypothesis that 'uncoupled' hydrolysis is a mechanism for the large-scale transfer of organic matter from sinking particles to the dissolved phase (Cho & Azam 1988). This may be an important route for the supply of carbon to the mid- and deep-water free-living bacteria, the carbon demand of which is almost equivalent to the depth-dissipated POC in the north Pacific Gyre (Cho & Azam 1988) and subarctic Pacific (Simon et al. 1992). Some rapidly sinking particles do however reach great depths (>3000 m), that are rich in POC and bacteria, thus escaping solubilization (Turley 1994, Turley & Mackie 1995).

Here we examine the microbiology of aggregates in the top 20 to 300 m of the NE Atlantic and the flux of bacteria, cyanobacteria and POC on sinking particles collected in sediment traps at 3100 m and relate them to concentrations of suspended POC and the carbon demand of free-living bacteria.

METHODS

Aggregates. Macroscopic aggregates were sampled from 40 to 300 m in the NE Atlantic (Table 1a) using a messenger-operated, 100 l, PVC closing water bottle with 2 large-diameter terminal apertures (Lampitt et al. 1993a). Sampling was carried out from 20 to 29 May 1990 close to a spar buoy attached to a polyester net drogue at a depth of 30 ± 5 m operating in Lagrangian mode. After sampling the aggregates were allowed to settle to the flat bottom of the sampler for 2 h, after which the top 95 l was drained off and the upper section of the sampler detached. Prior to draining, seawater subsamples were removed for the estimation of leucine incorporation rates by free-living bacteria and for their enumeration (see 'Seawater' section below). The bottom section containing the aggregates and 5 l seawater was removed to a room with a constant temperature of 10 °C.

Aggregates were removed using a sterile, wide-bore pipette, and each was gently transferred through a series of wells containing 2.5 ml of 0.2 µm pore-size filtered seawater. Aggregates for bacterial, flagellate and cyanobacterial enumeration were placed in a vial containing 2.5 ml of 2% particle-free glutaraldehyde and stored in the dark at 5 °C for later analysis using epifluorescence direct count techniques. Up to 10 aggregates were placed in each vial, their numbers noted, and their lengths and widths measured using a microscope fitted with an eyepiece micrometer. Aggregate volume was calculated from the length and width of each aggregate by assuming that they were either cylindrical with hemispherical ends or oval. The appropriate formula was used to calculate volumes of the cylinders while the ovals were assumed to be spheres with a diameter equal to the mean of the length and width.

Up to 10 aggregates were placed in a vial containing 1.8 ml of 0.2 µm pore-size filtered seawater for the determination of bacterial protein synthesis. When sufficient aggregates were available several sets of vials containing 10 aggregates were used for the enumeration of microrganisms and the determination of rates of bacterial leucine incorporation. Further samples were taken to describe their composition using the natural fluorescence of cells and structures in the aggregate when viewed under green, blue and UV excitation, and by staining with Acridine Orange (AO), under a range of different magnifications (Lampitt et al. 1993a).

Enumeration of microorganisms: Numbers of bacteria and flagellates were estimated using the AO (Hobbie et al. 1977, Turley & Hughes 1992, Turley 1993a) and DAPI (Porter & Feig 1980) fluorochromes. *Synechococcus*-like chroococcoid cyanobacteria were enumerated by an autofluorescent technique (Johnson & Sieburth 1979). Prior to counting, the aggregates in the glutaraldehyde preservative were ultrasonicated at 20 kHz with a 3 mm tip diameter titanium probe (for details see Turley & Hughes 1992) for 6 periods of 5 s each to break up the particles, disperse the cells, and ensure a good distribution of cells on the filter.

Determination of leucine incorporation: Bacterial incorporation of ^{3}H-leucine (Kirchman et al. 1985, 1986) into the ice-cold trichloroacetic acid (TCA) insoluble macromolecular material was determined by the addition of 50 µl ^{3}H-leucine (final concentration 14 nM) to the vials containing the aggregates and sterilised seawater and incubating them in the dark for 5 h at *in situ* temperature (10 to 14 °C, depending on depth of sample). Incubations were terminated by the addition of 2% glutaraldehyde (final volume), then extracted onto 0.2 µm pore-sized Nuclepore filters using 5% ice cold TCA. The radioactivity incorporated into cellular material was counted on a scintillation counter and incorporation rates were calculated using the procedures, equipment and formula detailed in Turley (1993b). Two controls containing the sterilised seawater were carried out for each group of aggregate analyses.

Sediment trap material. Sinking particles were collected in a series of single-sample drifting sediment traps with mouths of 0.13 m^2 deployed without preservative at 4 depths between 20 and 300 m. The series of traps were deployed in the vicinity of the Lagrangian spar buoy (see above) on 4 different occasions between

Table 1. Sampling positions, dates and depths for (a) aggregates sampled using the large volume marine snow sampler, (b) particulate material sinking into unpoisoned drifting sediment traps and (c) seawater collected by GoFlo bottles attached to a CTD

(a) Aggregates

Sample	Depth (m)	Date	Position
MSC 2	45	20 May 1990	48° 21.9' N, 17° 45.4' W
MSC 4	45	21 May 1990	48° 26.6' N, 17° 49.4' W
MSC 5	55	22 May 1990	48° 29.7' N, 17° 39.2' W
MSC 6	45	22 May 1990	48° 26.8' N, 17° 48.6' W
MSC 7	45	23 May 1990	48° 27.0' N, 17° 45.0' W
MSC 8	300	24 May 1990	48° 25.5' N, 17° 41.5' W
MSC 9	45	24 May 1990	48° 25.6' N, 17° 40.8' W
MSC 10	300	25 May 1990	48° 28.7' N, 17° 34.5' W
MSC 16	45	27 May 1990	48° 28.3' N, 17° 27.0' W
MSC 20	300	29 May 1990	48° 27.2' N, 17° 45.2' W

(b) Sediment trap material

Depth (m)	Deployment date	Deployment position	Recovery date	Recovery position	Deployment duration
50	20 May 1990	48° 25.3' N, 17° 38.2' W	23 May 1990	48° 17.9' N, 17° 35.0' W	79 h 25 min
100	20 May 1990	48° 25.3' N, 17° 38.2' W	23 May 1990	48° 17.9' N, 17° 35.0' W	79 h 25 min
200	20 May 1990	48° 25.3' N, 17° 38.2' W	23 May 1990	48° 17.9' N, 17° 35.0' W	79 h 25 min
300	20 May 1990	48° 25.3' N, 17° 38.2' W	23 May 1990	48° 17.9' N, 17° 35.0' W	79 h 25 min
20	24 May 1990	48° 25.5' N, 17° 37.9' W	26 May 1990	48° 27.3' N, 17° 30.3' W	48 h 50 min
50	24 May 1990	48° 25.5' N, 17° 37.9' W	26 May 1990	48° 27.3' N, 17° 30.3' W	48 h 50 min
100	24 May 1990	48° 25.5' N, 17° 37.9' W	26 May 1990	48° 27.3' N, 17° 30.3' W	48 h 50 min
300	24 May 1990	48° 25.5' N, 17° 37.9' W	26 May 1990	48° 27.3' N, 17° 30.3' W	48 h 50 min
20	26 May 1990	48° 27.3' N, 17° 29.8' W	28 May 1990	48° 26.7' N, 17° 27.1' W	46 h 13 min
50	26 May 1990	48° 27.3' N, 17° 29.8' W	28 May 1990	48° 26.7' N, 17° 27.1' W	46 h 13 min
100	26 May 1990	48° 27.3' N, 17° 29.8' W	28 May 1990	48° 26.7' N, 17° 27.1' W	46 h 13 min
300	26 May 1990	48° 27.3' N, 17° 29.8' W	28 May 1990	48° 26.7' N, 17° 27.1' W	46 h 13 min
50	01 Jun 1990	48° 11.4' N, 16° 57.8' W	03 Jun 1990	47° 45.7' N, 16° 39.8' W	48 h 31 min
100	01 Jun 1990	48° 11.4' N, 16° 57.8' W	03 Jun 1990	47° 45.7' N, 16° 39.8' W	48 h 31 min
200	01 Jun 1990	48° 11.4' N, 16° 57.8' W	03 Jun 1990	47° 45.7' N, 16° 39.8' W	48 h 31 min
300	01 Jun 1990	48° 11.4' N, 16° 57.8' W	03 Jun 1990	47° 45.7' N, 16° 39.8' W	48 h 31 min

(c) Seawater

Date	Position	Depth range (m) Minimum	Maximum
01 Jul 1989	47° 03' N, 20° 21' W	10	300
02 Jul 1989	46° 88' N, 20° 02' W	1500	4200
03 Jul 1989	46° 78' N, 19° 99' W	400	1000
19 May 1990	48° 33' N, 17° 20' W	600	2710
21 May 1990	48° 30' N, 17° 48' W	2	300
23 May 1990	48° 30' N, 17° 47' W	2	300
25 May 1990	48° 28' N, 17° 33' W	2	300
29 May 1990	48° 25' N, 17° 27' W	2	100
29 May 1990	48° 26' N, 17° 28' W	600	4300
31 Aug 1992	49° 00' N, 16° 45' W	3	150
06 Sep 1992	48° 88' N, 16° 48' W	200	4000

20 May and 3 June 1990 (Table 1b). The traps were recovered after 2 to 3 d and the small number of swimmers removed from the sample, using standard sediment trap methods (Knauer & Asper 1989). Subsamples were taken for analysis of mass flux and POC flux using the methods outlined in Newton et al. (1995), and for microbiological analysis. The latter 10 ml subsample was mixed thoroughly on a vortex mixer and subsamples taken for the enumeration of bacteria and the frequency of divided and dividing cells (FDDC; Davis & Sieburth 1984) and for the estimation of bacterial incorporation of leucine.

Enumeration of bacteria: Numbers of bacteria were counted using the AO direct count method on samples stored in 2% glutaraldehyde (final concentration) in the dark at 5 °C for 2 to 6 mo. A loss in epifluorescence-detectable cells can occur during storage of preserved seawater samples (Turley & Hughes 1992, 1994) but

has not been investigated for bacteria associated with particles. Numbers of attached bacteria have therefore not been corrected for cell loss during storage to ensure that we did not unduly bias the importance of attached bacteria. Had we applied the model for cell loss developed for free-living bacteria in preserved seawater, we would have doubled the numbers of attached bacteria (Turley & Hughes 1994). Samples were shaken for 2 min to disperse the particles prior to sample preparation. Four replicate counts were carried out for each sample and >600 cells counted from each replicate and the numbers of divided and dividing cells determined in 40 quadrats (between 20 and 140 couplets counted) from each replicate.

Determination of leucine incorporation: Four 1 to 2 ml replicates of the material from each trap were incubated with 50 to 100 µl ^{3}H-leucine (final concentration 25 nM) at 12°C for 1 h. One of these was the dead control which received glutaraldehyde prior to the addition of ^{3}H-leucine. The extraction and counting methods for estimating ^{3}H-leucine incorporation are in Turley (1993b).

Seawater. Seawater samples were taken throughout the oceanic water column in the NE Atlantic during July 1989, May 1990, and August and September 1992 (Table 1c) using GoFlo water samplers attached to a CTD. In 1990 sampling was carried out close to the spar buoy operating in Lagrangian mode in conjunction with the sampling of aggregates reported in this study (see above). Bacteria and cyanobacteria were enumerated using a AO direct count method outlined in Turley & Hughes (1992). ^{3}H-thymidine (Fuhrman & Azam 1980, 1982, JGOFS 1990) and ^{3}H-leucine (Kirchman et al. 1985, 1986) incorporation rates were determined by adding 5 nM (final concentration) to five 10 to 40 ml replicates (2 of which were glutaraldehyde treated controls) of seawater from each depth and incubating for 1 to 4 h at *in situ* temperatures. Sample size and incubation duration increased with depth. Specific details of these methods are in Turley (1993b). Bacterial production was calculated from thymidine and leucine incorporation rates using conversion factors of 2×10^{18} cells mol^{-1} thymidine (JGOFS 1990) and 0.15×10^{18} cells mol^{-1} leucine (Bjornsen & Kuparinen 1991) and 20 fg C cell^{-1} (JGOFS 1990).

RESULTS

Aggregate composition and microbial activity

The composition of the aggregates collected by the large volume sampler is described in detail in Lampitt et al. (1993a). Briefly, more than 95% of them were of a

Table 2. Bacterial, cyanobacterial and flagellate concentrations and frequency of divided and dividing (bacterial) cells (FDDC) on (a) aggregates and (b) faecal pellets sampled using the large volume marine snow sampler (MSC) and drifting sediment traps (ST). Per unit: no. per aggregate or faecal pellet, respectively; per volume: no. per ml aggregate or faecal pellets, respectively; na: data not available

Sample	Depth (m)	No. of aggregates/ faecal pellets	Concentration per unit			Concentration per volume			FDDC %
			Bacteria $\times 10^5$	Cyanobacteria $\times 10^4$	Flagellates $\times 10^3$	Bacteria $\times 10^8$	Cyanobacteria $\times 10^7$	Flagellates $\times 10^6$	
(a) Aggregates									
MSC 2	45	10	2.1	2.0	na	2.1	2.0	na	7.5
MSC 4	45	16	3.1	na	5.9	17.3	na	33.0	5.5
MSC 5	55	10	2.9	na	3.4	25.4	na	29.9	4.8
MSC 6	45	10	4.3	1.3	1.7	8.2	2.4	3.2	7.1
MSC 7	45	10	2.6	1.0	1.4	2.5	1.0	1.3	7.3
MSC 8	300	3	2.4	1.8	na	0.3	0.2	na	9.5
MSC 9	45	10	3.0	2.5	na	5.7	4.7	na	7.7
MSC 10	300	4	4.9	8.6	na	21.1	37.1	na	6.5
MSC 16	45	10	1.1	0.1	na	6.1	4.5	na	8.8
MSC 20	300	10	1.6	na	1.5	3.0	na	2.9	3.9
ST 1	50	3	9.1	na	10.1	3.4	na	3.8	8.6
ST 2	100	1	126.0	na	99.7	1.3	na	1.0	9.3
ST 3	200	1	41.5	na	36.7	5.1	na	4.5	9.8
ST 4	300	1	110.1	na	130.1	1.3	na	1.5	12.5
(b) Faecal pellets									
ST 1	50	8	3.8	0.5	0.4	37.8	4.7	4.0	11.2
ST 2	100	9	5.7	0.1	0.9	28.6	0.6	4.3	9.2
ST 3	200	7	6.8	0.3	0.5	33.9	1.4	2.5	8.2
ST 4	300	5	14.1	0.8	0.5	28.1	1.5	1.0	4.2
MSC 3	45	10	3.8	0.2	0.0	37.6	1.8	0.2	1.4

similar nature, comprising a dense mucus matrix containing numerous bacteria and cyanobacteria, with less numerous small chlorophytes (2 to 5 µm diameter) and even less numerous inclusions of larger structure such as crustacean moults, faecal pellets, pennate diatoms and lorica of the tintinnid *Dictyosysta* sp. The loricae of *Dictyosysta* sp. were generally intact at 45 m whereas they were badly damaged at 300 m.

The most characteristic components of the aggregates were the high concentrations of bacteria, cyanobacteria and flagellates (Table 2a) Those from 45 to 55 m (0.7 to 1.3 mm diameter), just below the seasonal thermocline where there was a maximum in aggregate density (Lampitt et al. 1993a), contained 2.1 to 4.3×10^5 bacteria, 1.0 to 2.5×10^4 cyanobacteria and 1.4 to 5.9×10^3 flagellates aggregate^{-1}. These are equivalent to 2.1 to 25.4×10^8 bacteria, 1.0 to 4.7×10^7 cyanobacteria and 1.3 to 33.0×10^6 flagellates ml^{-1} aggregate. These concentrations were substantially higher than those found in the surrounding water, and represent a concentration factor on the aggregates of 400 to 5700 for bacteria, 1000 to 7600 for cyanobacteria and 1300 to 33000 for flagellates (Table 3a).

The leucine incorporation rates by aggregates from 45 m ranged from 5 to 62 fmol aggregate^{-1} d^{-1} and taking the mean number of bacteria per aggregate for that 100 l sample represent 12 to 206×10^{-21} mol cell^{-1} d^{-1} (Table 4). These rates of leucine incorporation were 2

Table 3. Ratio of bacteria, cyanobacteria and flagellate numbers and leucine incorporation rates associated with (a) aggregates and (b) faecal pellets to those free-living either in the seawater sampled in the upper 95 l of the large-volume sampler or in seawater samples collected in GoFlo samplers attached to a CTD at the same depth. Flagellate ratios are calculated using the maximum concentration of free-living flagellates (1×10^3 ml^{-1}) found in this area during 1989 (Patterson et al. 1993) and are therefore minimum estimates. Aggregates and faecal pellets were sampled using a large-volume marine snow sampler (MSC) or drifting sediment trap (ST). Leucine incorporation not given for faecal pellets. na: data not available

Sample	Depth (m)	Bacteria	Cyanobacteria	Flagellates	Leucine incorporation per volume	Leucine incorporation per cell
(a) Aggregates						
MSC 2	45	400	3900	na	467.3	1.2
MSC 4	45	3300	na	33000	na	na
MSC 5	55	5200	na	29900	na	na
MSC 6	45	1600	4800	3200	157.7	0.1
MSC 7	45	300	1700	1300	573.9	2.1
MSC 8	300	100	1000	na	na	na
MSC 9	45	5700	7600	na	4296.9	9.3
MSC 10	300	4100	176500	na	na	na
MSC 16	45	1100	7300	na	na	na
MSC 20	300	2100	na	2900	na	na
ST 1	50	6800	na	1000	na	na
ST 2	100	9100	na	10000	na	na
ST 3	200	8200	na	3700	na	na
ST 4	300	5500	na	13000	na	na
(b) Faecal pellets						
ST 1	50	6800	12300	4000		
ST 2	100	9200	1200	4300		
ST 3	200	8300	4100	2500		
ST 4	300	5500	7300	1000		
MSC 3	45	7100	3600	200		

Table 4. Mean leucine incorporation rates associated with aggregates captured using the marine snow sampler (MSC). SE of replicate samples containing 10 aggregates are in parentheses

Sample	Depth (m)	No. of aggregates	Leucine incorporation rate: Per cell (mol $\times 10^{-21}$ d^{-1})	Per aggregate (fmol d^{-1})	Per ml aggregate (pmol d^{-1})
MSC 2	45	10	135	28.9	28.3
MSC 6	45	20	12	5.0 (1.12)	9.5
MSC 7	45	30	80	20.8 (0.18)	20.4
MSC 9	45	50	206	61.7 (0.59)	117.8

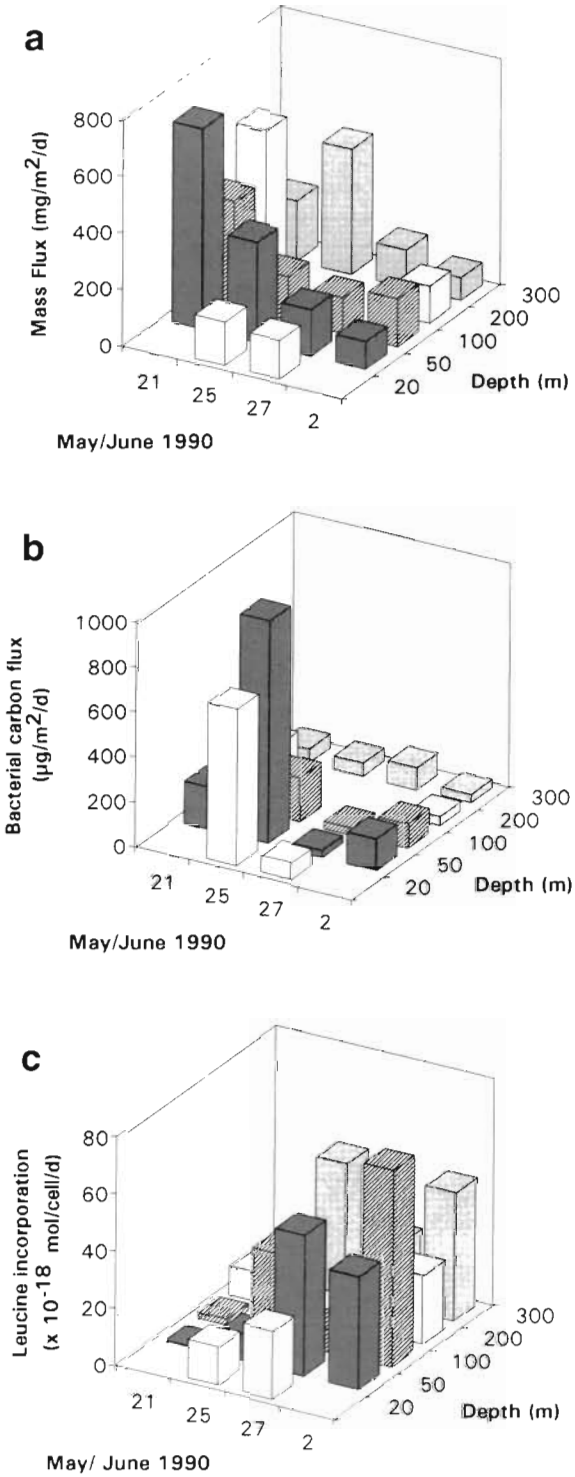

Fig. 1. Change of (a) mass flux, (b) bacterial carbon flux and (c) rate of leucine incorporation into bacteria during 4 deployments of unpoisoned drifting sediment traps, 20 May to 3 June 1990 at 4 depths between 20 and 300 m in the vicinity of a spar buoy with a 30 m drogue operating in Lagrangian mode

to 3 orders of magnitude higher than those in the surrounding water when compared on a per volume basis (Table 3a) but when compared on a per cell basis 2 sets of replicates of bacteria attached to aggregates exhibited 2 to 9 times higher rates and 2 sets of replicates had equal or lower rates of leucine incorporation than the free-living bacteria.

At 300 m, aggregates (1.0 to 2.5 mm diameter) were less numerous and appeared less 'fresh', and tintinnid lorica were crushed, similar to those found in faecal pellets of the amphipod *Thermisto compressa* (Lampitt et al. 1993a). The aggregates contained 1.6 to 4.9×10^5 bacteria, 1.8 to 8.6×10^4 cyanobacteria and 1.5×10^3 flagellates aggregate^{-1}, equivalent to 0.3 to 21.1×10^8 bacteria, 0.2 to 37.1×10^7 cyanobacteria and 2.9×10^6 flagellates ml^{-1} aggregate (Table 2a). Concentration factors were 100 to 4100 for bacteria, 1000 to 176500 for cyanobacteria and 2900 for flagellates (Table 3a).

Bacteria and flagellates on large aggregates (2.3 to 5.8 mm diameter) collected in sediment traps at 50 to 300 m (Table 2a) fell within the lower part of the range for aggregates collected by the large volume sampler when expressed on a per volume basis, but when expressed on a per aggregate basis were all substantially higher than the smaller aggregates.

Faecal pellets (1.2 to 3.3 mm length, 0.3 to 0.4 mm width) sampled by drifting sediment trap or the large volume particle sampler were distinguishable from the 'miscellaneous' aggregates described above and contained generally higher and less variable concentrations of bacteria (29 to 38×10^8 ml^{-1}) while cyanobacteria and flagellates fell within the lower part of the range found in the miscellaneous aggregates (Table 2b). Bacteria, cyanobacteria and flagellates in faecal pellets were respectively 6800 to 9200, 1200 to 12300 and 200 to 4300 times more concentrated than in the same volume of seawater (Table 3b).

Frequency of divided and dividing cells (Table 2) on aggregates and faecal pellets range between 1.4 and 12.5% (mean 7.2%)

Particle flux from the upper mixed layer

Mass flux from the upper mixed layer (Fig. 1a, Table 5a) decreased during the period 20 May to 3 June 1990; at 50 m the flux was approximately 700 mg m^{-2} d^{-1} in the period 20 to 23 May and decreased to about 100 mg m^{-2} d^{-1} during 1 to 3 June. This general decrease in mass flux during the study period could also be seen at 100 and 200 m. At 300 m the peak flux occurred during 24 to 26 May, approximately 4 d after that seen at 50 m. In contrast, bacterial leucine incorporation rate per cell (Fig. 1c, Table 5c) tended to

increase over the study period. Bacterial carbon flux from the upper mixed layer (Fig. 1b, Table 5b) was at a maximum during the period 24 to 26 May with fluxes of around 700 and 1000 µg m^{-2} d^{-1} at 20 and 50 m, respectively. The flux of bacteria and the FDDC (Table 5d) bore no significant relationship to other measured flux variables.

Seawater microbiology

Rates of thymidine (Fig. 2a) and leucine (Fig. 2b) incorporation and numbers of bacterial cells (Fig. 2c) were highest in the upper 20 to 30 m of the water column during the Lagrangian study from 21 to 29 May 1990. Although there were noticeable variations during this study thymidine incorporation, leucine incorporation and bacterial numbers generally ranged between 2 and 4 pmol l^{-1} h^{-1}, 40 and 80 pmol l^{-1} h^{-1} and 2 and 5×10^5 ml^{-1}, respectively.

Integrated bacterial production estimated from either thymidine or leucine incorporation rates in the region of 47° N, 20° W (Fig. 3) was 180 mg C m^{-2} d^{-1} in July 1989, between the estimates of 370 to 580 mg C m^{-2} d^{-1} for May 1990 and 120 to 145 mg C m^{-2} d^{-1} for August and September 1992. The intermediate integrated bacterial production for July 1989 is used in the calculation to estimate the fraction of free-living bacterial carbon demand potentially supplied by the depth-dissipated sinking POC during the same period (see Table 9).

Table 5. Drifting sediment trap flux variables sampled during the 4 deployments of unpoisoned traps at 4 depths between 20 and 300 m between 20 May and 3 June 1990 in the vicinity of a spar buoy with a 30 m drogue operating in Lagrangian mode. SE given in parentheses when available. na: data not available

Depth (m)	Dates of sediment trap deployments (1990) 20–23 May	24–26 May	26–28 May	1–3 Jun
(a) Dry weight (mg m^{-2} d^{-1})				
20	na	152	136	na
50	704	351	162	98
100	368	153	125	167
200	538	na	na	131
300	213	442	133	80
(b) Bacterial carbon (µg m^{-2} d^{-1})				
20	na	696 (0.13)	74 (0.16)	na
50	186 (0.11)	989 (0.10)	34 (0.18)	144 (0.06)
100	164 (0.13)	197 (0.06)	33 (0.16)	110 (0.13)
200	176 (0.01)	na	na	40 (0.15)
300	62 (0.11)	58 (0.19)	95 (0.14)	37 (0.07)
(c) Leucine incorporation ($\times 10^{-18}$ mol $cell^{-1}$ d^{-1})				
20	na	13.3	23.9	na
50	0.3	9.1	49.5	39.7
100	2.2	30.0	8.0	69.1
200	10.3	na	na	24.1
300	2.0	46.0	22.4	45.1
(d) FDDC (%)				
20	na	5.9 (0.14)	6.5 (0.06)	na
50	8.4 (0.19)	9.1 (0.06)	3.7 (0.17)	6.2 (0.58)
100	7.8 (0.07)	5.9 (0.10)	4.1 (0.16)	7.4 (0.17)
200	8.2 (0.30)	na	na	3.8 (0.06)
300	5.6 (0.38)	5.2 (0.19)	6.9 (0.25)	5.9 (0.10)

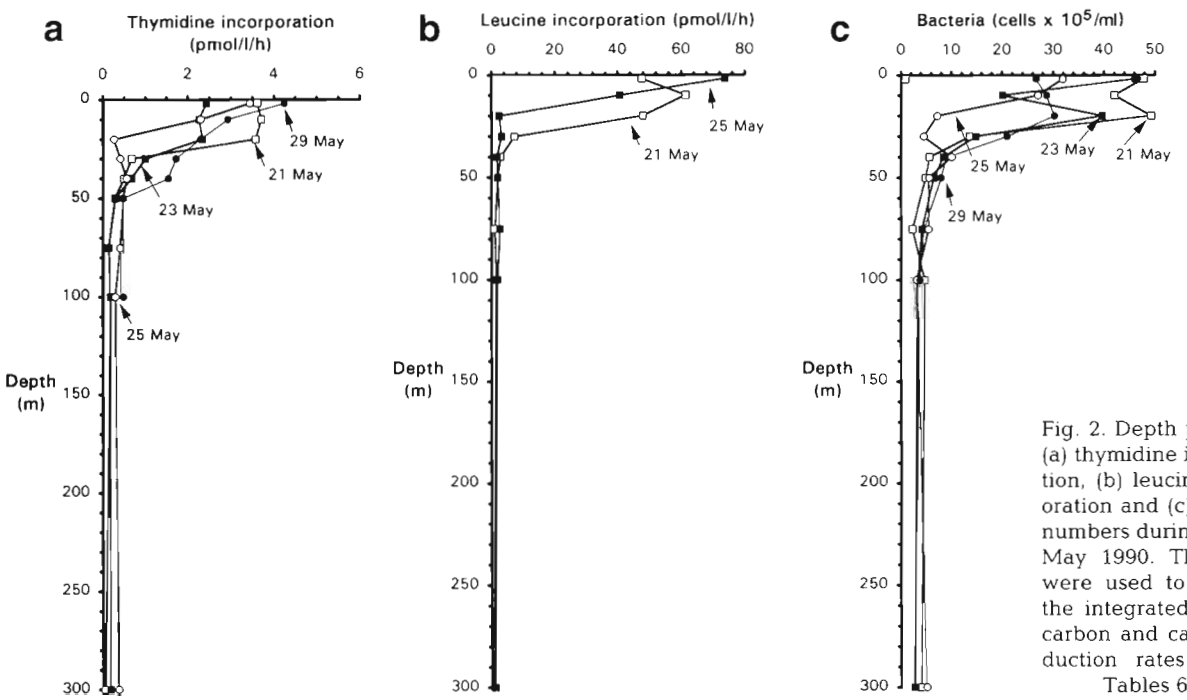

Fig. 2. Depth profiles of (a) thymidine incorporation, (b) leucine incorporation and (c) bacterial numbers during 21 to 29 May 1990. These data were used to calculate the integrated bacterial carbon and carbon production rates used in Tables 6 & 7

DISCUSSION

Microbiology of NE Atlantic aggregates

The aggregates in the top 300 m in the NE Atlantic contained dense bacterial, cyanobacterial and flagellate populations, as was previously shown on aggregates from the western North Atlantic (Caron et al. 1986), with several-fold higher concentrations than in the surrounding seawater (Table 3a). However, bacteria attached to aggregates were equivalent to 10 and 14% of free-living bacterial carbon integrated through the water column to 100 and 300 m, respectively (Table 6). These are a minimum estimates which would increase to 25 and 34% if the different carbon contents of attached and free-living bacteria (Simon et al. 1990) were taken into account (Table 6), and are substantially higher than the <5% found by Cho & Azam (1988). Perhaps this is not surprising as the period of this study coincided with the maximum marine snow concentration (some 20 times higher than at other times of the year) measured at 270 m 150 km southwest of our position (Lampitt et al. 1993b). Thus, at other times when marine snow concentrations are lower, <5% of bacteria may be attached. Our results do show, however, that at times attached bacteria can contribute significantly to the total pool of oceanic bacteria.

Leucine incorporation rates on aggregates from 45 m varied between 12 and 206 $\times 10^{-21}$ mol cell^{-1} d^{-1} (Table 4) during 20 to 24 May. This compares well with the leucine incorporation rate of 300×10^{-21} mol cell^{-1} d^{-1} found in the particulate material from the sediment trap deployed at 50 m from 20 to 23 May (Table 5c). The increase in leucine incorporation rates on material captured in sediment traps deployed after this period (Fig. 1c) may indicate a period of intense activity by the attached bacteria. Substantial variations in the activity of attached cells have been observed before, with thymidine incorporation rates per bacterium equal to, lower than or up to 6 times higher than those of free-living bacteria (Alldredge et al. 1986, Alldredge & Gotschalk 1990, Turley 1993b), and are likely to vary with the age of the aggregate and amount of easily assimilable organic matter within the aggregate. The FDDC of attached bacteria, which can be viewed as another index of bacterial production, varied by 9-fold (Table 2) and is further evidence of the variable production of attached bacteria.

Our estimates of the contribution of attached bacteria to total bacterial production in the top 100 and 300 m range between 1.8 and 3.4% (Table 7). This is higher than the estimates of 0.01 to 0.39% (Alldredge & Youngbluth 1985) but in the lower range of the estimates of 1.0 to 26% (mean 8%) (Alldredge et al. 1986, Alldredge & Gotschalk 1990) previously found on aggregates. All these estimates tend to be low due to the general rarity of aggregates in oceanic waters.

The contribution of free-living bacterial carbon to suspended POC is between 25 and 33% (Table 6), which is lower than the 43% found by Cho & Azam (1988). However, correcting for a 50% retention of bacteria on the glass fibre filters used in the filtration of POC measurements (Lee & Fuhrman 1987) would increase our estimates to betweeen 28 and 40%.

High flagellate concentrations, which have been previously found (Caron et al. 1982, 1986) on aggregates, may play some role in controlling attached bacterial concentration through grazing (100 to 10000 times higher than in the surrounding seawater) (Table 3). Indeed, about 40 species of detrital dwelling flagellates have been isolated and described from this area, most of which were bacterivorous (Patterson et al. 1993).

Aggregates are a potential food resource for zooplankton and nekton and were observed to be

Table 6. Contribution of free-living bacterial carbon (BC_{sw}) to the suspended POC pool (POC_{susp}) and contribution of bacteria attached to marine snow (BC_{att}) to the free-living bacterial carbon pool calculated initially using a conversion factor of 20 fg C cell^{-1} for both BC_{sw} and BC_{att} (JGOFS 1990) and secondly using a conversion factor of 20 fg C cell^{-1} for BC_{sw} (JGOFS 1990) and 50 fg C cell^{-1} for BC_{att} (Simon et al. 1990). Integrated aggregate volume (13.3 l m^{-2} and 30 l m^{-2} for 0 to 100 m and 0 to 300 m, respectively) was estimated from a profile of aggregate volume concentration taken on 22 May 1990 (Lampitt et al. 1993a). Integrated bacterial carbon associated with the aggregates (BC_{att}) was calculated using the integrated aggregate volume and the mean bacterial numbers per ml aggregate (9.6 and 6.8 $\times 10^8$ ml^{-1} for 45 to 55 m and 300 m aggregates, respectively). Bacterial concentration on aggregates taken from 45 and 55 m were used for the 0 to 100 m integration; aggregates from 300 m were included for the 0 to 300 m integration (Table 2a). All measurements of BC_{sw} were carried out during 19 to 29 May 1990. Integrated POC was calculated from depth profiles of POC taken in the region 46 to 50° N, 15 to 19° W during 1 May to 15 June 1990. SE and number of depth profiles (n) are in parentheses. na: data not available

Integration depths (m)	Mean POC_{susp} (g C m^{-2})	Mean BC_{sw} (g C m^{-2})	BC_{sw}/POC_{susp} (×100)	BC_{att}/BC_{sw} (× 100) at 20 fg C cell^{-1}	at 50 fg C cell^{-1}
0–100	10.5 (SE = 0.43, n = 25)	2.6 (SE = 0.19, n = 4)	25	10	25
0–300	12.4 (SE = 0.50, n = 5)	4.1 (SE = 0.16, n = 4)	33	14	34
0–3100	34.4 (SE = 0.31, n = 5)	9.8 (SE = 0.29, n = 2)	28	na	na

Table 7. Estimates of the contribution of attached bacteria to total bacterial production. Integrated aggregate volume (see Table 6 legend) was estimated from a profile of aggregate volume concentration taken on 22 May 1990 (Lampitt et al. 1993a). Integrated bacterial carbon production estimated by leucine incorporation associated with the aggregates ($BCP_{att(leu)}$) was calculated using the integrated aggregate volume and the mean bacterial production per ml aggregate (0.13 µg C d^{-1}, Table 4). The integrated free-living bacterial production $BCP_{sw(thy)}$ and $BCP_{sw(leu)}$ measured by the thymidine and leucine methods respectively were carried out during 21 to 29 May 1990 (see Fig. 2 for original data); values given are the mean of 4 and 2 depth profiles respectively. SE in parentheses

Integration depths (m)	$BCP_{sw(thy)}$ (mg C m^{-2})	$BCP_{sw(leu)}$ (mg C m^{-2})	$BCP_{att(leu)}$ (mg C m^{-2})	$BCP_{att(leu)}/(BCP_{sw(thy)} + BCP_{att(leu)})$ (× 100)	$BCP_{att(leu)}/(BCP_{sw(leu)} + BCP_{att(leu)})$ (× 100)
0–100	98 (0.27)	91 (0.27)	1.8	1.8	1.9
0–300	138 (0.13)	111 (0.20)	3.9	2.7	3.4

ingested by the amphipod *Thermisto compressa*. They may be a food-chain short cut whereby material normally too small for organisms higher in the food chain can be ingested (Lampitt et al. 1993a). Cyanobacteria can survive the passage through zooplankton and nekton guts (Johnson et al. 1982, Lampitt et al. 1993a) while around 30% of attached bacteria may be assimilated (Lawrence et al. 1993). The ability of cyanobacteria to survive gut passage are reflected in the concentrations found in faecal pellets (Table 2b) and may partly account for their flux to the deep NE Atlantic Ocean (Lochte & Turley 1988, Pfannkuche & Lochte 1993, Turley & Mackie 1995).

Flux of attached bacteria and cyanobacteria into the deep ocean

The ratio of bacteria to cyanobacteria on marine snow during 20 to 29 May 1990 in the NE Atlantic from 45 and 300 m was 11 to 34 (mean 21) and 6 & 13 (mean 9), respectively. Assuming a sinking rate of 70 m d^{-1} during this period in 1990 (Newton et al. 1995), these particles would have reached 3100 m between 30 June and 8 July 1990. The ratio of bacteria to cyanobacteria in sediment trap material from 3100 m during 23 June to 7 July 1990 was 160, and was generally above 100 throughout the 17 mo survey (Turley & Mackie 1995), so there is a marked increase in the ratio with depth. This may indicate that free-living bacteria from the mesopelagica and bathypelagica are scavenged by sinking particles in far greater numbers than cyanobacteria. This is not surprising as free-living bacteria are present throughout the oceanic water column whereas there are no detectable free-living cyanobacteria below 300 m (C. M. Turley pers. obs.).

Other explanations may be that bacterial growth on the sinking particles is greater than cyanobacterial growth and/or that other components of particle flux have a higher bacteria:cyanobacteria ratio than that found on marine snow. Indeed, the ratio of bacteria to cyanobacteria on faecal pellets at 45 m from the same period and area was 210 and on faecal pellets from drifting sediment traps at 50 to 300 m depth was 253, substantially greater than that found on the amorphous aggregates (see above). Therefore, if faecal pellets make up a sizeable proportion of the particle flux, the bacteria to cyanobacteria ratio in the deep sediment traps would increase from that expected for flux consisting solely of amorphous aggregates. The concentration of bacteria associated with faecal pellets was generally higher than the concentration on the amorphous aggregates (Table 2) and was in the same range as those found in laboratory-produced faecal pellets from zooplankton fed on bacterized food (10^9 to 10^{10} ml^{-1}). This may be due to the rapid growth of a significant fraction of bacteria which survive gut passage (Lawrence et al. 1993). These investigators also found that a high proportion of aminopeptidase activity was carried out by bacteria in the faecal pellets and proposed that they may be important in faecal pellet solubilization and degradation. Bacteria in naturally occurring oceanic faecal pellets may play a similar role.

Fraction of vertical flux reaching 3100 m

The sharp vertical gradients of marine snow reported during the Lagrangian study (Lampitt et al. 1993a) and the variability seen in the flux of material out of the upper mixed layer in the present study (Fig. 1) imply short time scales of particle production and loss. Losses of particles during sinking are most likely due to biological processes (Alldredge et al. 1990) such as feeding by zooplankton and nekton (Alldredge 1972, 1976, Hamner et al. 1975, Lampitt et al. 1993a) and by enzyme hydrolysis by attached bacteria (Smith et al. 1992).

Comparing fluxes from the upper mixed layer reported here (Fig. 1, Table 5) and from Martin et al. (1993), using sinking rates of 70 and 110 m d^{-1} respec-

Table 8. Comparison of sediment trap fluxes through 150 m (from Martin et al. 1993) during 24 April to 31 May 1989 and through 50 to 300 m during 20 May to 3 June 1990 (Table 5) with sediment trap fluxes at 3100 m (from Newton et al. 1995, Turley & Mackie 1995). The fraction of shallow water flux reaching 3100 m is estimated assuming a sinking rate of 110 and 70 m d^{-1} for the 1989 and the 1990 fluxes respectively (Newton et al. 1995). To be consistent, 50 fg $cell^{-1}$ has been used for estimating bacterial flux in both shallow and deep traps

Year	Flux variable	Flux from UML (mg m^{-2} d^{-1})	Flux to 3100 m (mg m^{-2} d^{-1})	Fraction of shallow flux reaching deep traps
1989	Mass	663	166	0.25
	POC	118	11	0.09
1990	Mass	262	92	0.35
	Bacterial	0.415	0.043	0.10

tively (Newton et al. 1995), with fluxes at 3100 m (Newton et al. 1995, Turley & Mackie 1995), we have been able to estimate the fraction of the flux exiting the upper mixed layer that arrives at 3100 m (Table 8).

A smaller proportion of POC flux (9%) and bacterial carbon flux (10%) reached 3100 m than mass flux (25 and 35%) (Table 8). This suggests that there are processes involved which preferentially utilise or reduce the POC and bacterial components of the flux over the mass flux, and is further support of biological rather than physical processing of particles during sinking. Loss of POC may be attributed to oxidation by mesozooplankton and nekton grazers (Lampitt et al. 1993) and attached bacteria (Cho & Azam 1988) and protozoa (Patterson et al. 1993). In addition, intense hydrolytic enzyme activity has been measured on marine snow and found to rapidly solubilize the aggregate POC, with very little of the hydrolysate taken up by attached bacteria (Karner & Herndl 1992, Smith et al. 1992). The latter would also help meet the supply of carbon demanded by the free-living bacteria (see above).

Contribution of attached bacteria to the free-living bacterial pool

Only 10% (Table 8) of bacterial flux through 50 to 300 m reached 3100 m, indicating that the difference, 372 µg C m^{-2} d^{-1}, is added to the mid/deep water free-living bacterial, DOC or CO_2 pools or biomass of bacterivores. Free-living bacterial carbon integrated through the water column from 300 to 3100 m measured during late May 1990 was 5.7 g C m^{-2} (Table 6). That is, bacterial detachment from sinking particles could contribute 2.4% of the integrated bacterial biomass per annum. It would, therefore, take 42 yr for loss of bacteria from sinking particles to produce the concentration of free-living bacteria found in deep oceanic waters. Although aggregates (Azam & Smith 1991) and copepod faecal pellets (Jacobsen & Azam 1984) were observed to have been a source of bacteria into surrounding water, our observations and calculation would indicate that this is not significant.

Similarily, 9% of POC leaving 150 m reached 3100 m (Table 8), implying that 107 mg C m^{-2} d^{-1} is lost to either the mid/deep water more slowly sinking suspended POC pool or the DOC pool via particle breakup or solubilization, or is biologically mineralized to CO_2. No deep (>300 m) suspended POC measurements are available for this area during April to May 1989. However, in the NE Atlantic during May 1990 and July 1991, suspended POC integrated through the water column from 150 to 3000 m ranged from 23 to 65 g C m^{-2} (R. Harris pers. comm.). If there were no losses to the DOC pool or remineralization to CO_2 then loss of POC from sinking particles could be sufficient to replace the entire mid/deep-water oceanic suspended POC pool annually. However, this is unlikely as there is substantial particle solubilization and remineralization (Smith et al. 1992) and more data are needed of enzyme production and respiration by bacteria attached to sinking particles sampled from greater depths (>300 m) in order to estimate losses of sinking POC due to enzyme hydrolysis to DOC and suspended POC and bacterial remineralization to CO_2.

Our data indicate that the fraction of sinking POC lost between 150 and 3100 m may be an important carbon source to the mid/deep-water bacterial population, capable of supplying between 87% and 90% of the bacterial carbon demand during April to July 1989 at 47° N, 20° W (Table 9). Other research in the subarctic Pacific (Simon et al. 1992) and central N Pacific gyre (Cho & Azam 1988) found that POC can supply 99 and 102% of the bacterial carbon demand, respectively. These studies, however, only looked at fluxes and bacterial production in the top 1000 m. When we examine the contribution of sinking POC to bacterial carbon demand on a finer depth scale in this region, values for lost POC/BCD integrated from 150 to 600, 1000 and 3100 m were 78, 83 and 90%, respectively (Table 9). These are slightly lower than those of Cho & Azam (1988) and the mean value estimates by Simon et al. (1992). It is of interest that below 600 m in the NE Atlantic (Table 9), there was more than sufficient lost POC to supply the carbon demand of the bacteria thus requiring no additional carbon source in these deeper waters. Indeed, between 600 and 3100 m there was double the depth-dissipated POC than that needed to

Table 9. Fraction of free-living bacterial carbon demand (BCD_{sw}) potentially supplied by the depth-dissipated sinking POC (depth differences in fluxes, ΔPOC) calculated from the curve fitted through sediment trap POC fluxes ($12 \times 14.35(z/100)^{-0.946}$ mg C m^{-2} d^{-1}) for 24 April to 6 June 1989 at 47° N, 20° W in the N Atlantic (Martin et al. 1993) and bacterial production by free-living bacteria (BCP_{sw}) measured during 1 to 3 July 1989 at 47° N, 20° W (see Fig. 3). BCD_{sw} is calculated assuming a carbon conversion efficiency of 40% (Bjornsen & Kuparinen 1991). Similar estimates using the POC flux to a fixed sediment trap at 3100 m (ST 3100) during the same period and in the same region (Newton et al. 1995) are included for comparison

Depth (m)	POC flux (mg m^{-2} d^{-1})	Integrated BCP_{sw} (mg m^{-2} d^{-1})	BCD_{sw} (mg m^{-2} d^{-1})	ΔPOC/BCD_{sw} integrated from 150 m (× 100)	ΔPOC/BCD_{sw} integrated between depths (× 100)
150	118	133	333	–	–
600	32	177	443	78	78
1000	19	180	450	83	163
3100	7	182	455	90	240
ST 3100	11	182	455	87	140

meet bacterial carbon demand. However, depth profiles of integrated bacteria production were higher in this region in 1990 than in 1989 (Fig. 3), but mass flux was lower in 1990 than in 1989 (Table 8; Newton et al. 1995), indicating that large interannual variations may exist in the relationship between bacterial carbon demand and depth-dissipated POC.

Our estimates, however, do require that there be another source of organic carbon other than sinking POC in the upper 600 m. The winter mixed layer in this region of the NE Atlantic extends down to around 400 to 600 m (Robinson et al. 1979, Levitus 1982, summarised in Woods 1984) and may enrich deep waters with surface-derived DOC (Toggweiler 1989). In addition, radio isotope modelling studies suggest that POC fluxes derived from sediment traps may be systematically low (Buesseler et al. 1992, Clegg & Whitfield 1993), particularly in shallow traps. Defecation by vertically migrating nekton is another supply of organic carbon but is unlikely to exceed 5% of the passive flux (Lampitt et al. 1993a).

At times deep water bacterial production can be higher than that found during July 1989 (Fig. 3); this and lower carbon conversion efficiencies sometimes found in deep waters (Turley & Lochte 1990) would result in even higher estimates of carbon demand and decrease the lost POC/BCD ratio.

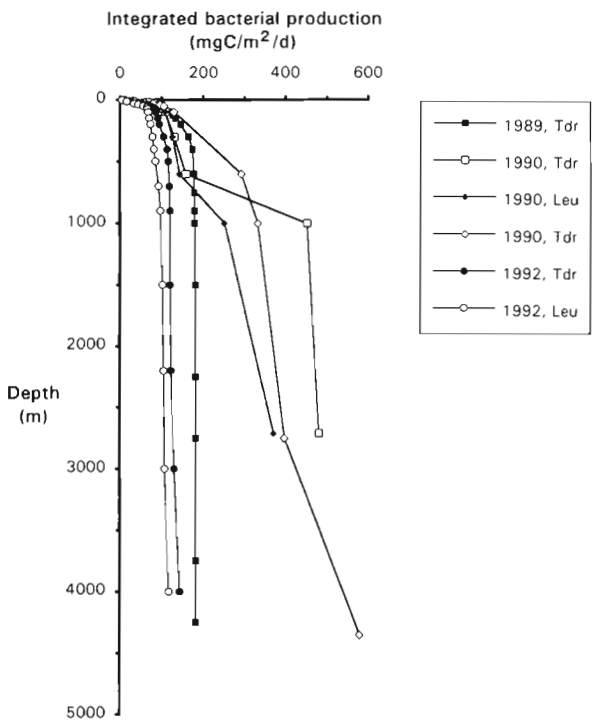

Fig. 3. Depth profiles of integrated bacterial production estimated from thymidine (Tdr) and leucine (Leu) incorporation measured in the sea area around 47° N, 20° W, July 1989, May 1990, and August and September 1992 (See Table 2c for station details)

Acknowledgements. Our thanks to Diane Hughes for technical assistance, to Richard Lampitt for deploying the drifting sediment traps, to Philip Newton for carrying out the mass analysis of the sediment trap material, to Roger Harris for the suspended POC data, to 2 anonomous reviewers for their helpful comments and to the officers and crew of the RRVs 'Discovery' and 'Darwin'. This work was funded by a NERC Biogeochemical Ocean Flux Study (BOFS) Special Topic Award and is BOFS Contribution No 226.

LITERATURE CITED

Alldredge, A. L. (1972). Abandoned larvacean houses: a unique food source in the pelagic environment. Science 177: 885–887

Alldredge, A. L. (1976). Discarded appendicularian houses as sources of food, surface habitats and particulate organic matter in planktonic environments. Limnol. Oceanogr. 21: 14–23

Alldredge, A. L., Cole, J. J., Caron, D. A. (1986). Production of heterotrophic bacteria inhabiting macroscopic organic aggregates (marine snow) from surface waters. Limnol.

Oceanogr. 31: 68–78
Alldredge, A. L., Gotschalk, C. C. (1990). The relative contribution of marine snow of different origins to biological processes in coastal waters. Cont. Shelf Res. 10: 41–58
Alldredge, A. L., Granata, T C., Gotschalk, C. C., Dickey, T D. (1990). The physical strength of marine snow and its implication for particle disaggregation in the ocean. Limnol. Oceanogr. 35: 1415–1428
Alldredge, A. L., Silver, M. W. (1988). Characteristics, dynamics and significance of marine snow. Prog. Oceanogr. 20: 41–82
Alldredge, A. L., Youngbluth, M. J. (1985). The significance of macroscopic aggregates (marine snow) as sites for heterotrophic bacterial production in the mesopelagic zone of the subtropical Atlantic. Deep Sea Res. 32: 1445–1456
Azam, F., Smith, D. C. (1991). Bacterial influence on the variability in the ocean's biogeochemical state: a mechanistic view. In: Demers, S. (ed.) Particle analysis in oceanography. NATO ASI Series, Vol. G27, Springer-Verlag, Berlin, p. 213–236
Bjornsen, P. K., Kuparinen, J. (1991). Determination of bacterioplankton biomass, net production and growth efficiency in the Southern Ocean. Mar. Ecol. Prog. Ser. 71: 185–194
Buesseler, K. O., Bacon, K. C., Cochran, J. K., Livingston, H. D. (1992). Carbon and nitrogen export during the JGOFS North Atlantic Bloom Experiment estimated from ^{234}Th:^{238}U disequilibria. Deep Sea Res. 39: 1115–1137
Caron, D. A., Davis, P. G., Madlin, L. P., Sieburth, J. McN. (1982). Heterotrophic bacteria and bacterivorous protozoa in oceanic macroaggregates. Science 218: 795–797
Caron, D. A., Davis, P. G., Madlin, L. P., Sieburth, J. McN. (1986). Enrichment of microbial populations in macroaggregates (marine snow) from surface waters of the North Atlantic. J. mar. Res. 44: 543–565
Cho, B. C., Azam, F. (1988). Major role of bacteria in biogeochemical fluxes in the ocean's interior. Nature 332: 441–443
Clegg, S. L., Whitfield, M. (1993). Application of a generilized scavenging model to time series ^{234}Th and particle data obtained during the JGOFS North Atlantic Bloom Experiment. Deep Sea Res. II 40: 1529–1545
Davis, P. G., Sieburth, J. McN. (1984). Estuarine and oceanic microflagellate predation of actively growing bacteria: estimation by frequency of dividing-divided bacteria. Mar. Ecol. Prog. Ser. 19: 237–246
Fowler, S. W., Knauer, G. A. (1986). Role of large particles in the transport of elements and organic compounds through the oceanic water column. Prog. Oceanogr. 16: 147–194
Fuhrman, J. A., Azam, F. (1980). Bacterioplankton secondary production estimates for coastal waters of British Columbia. Appl. environ. Microbiol. 39: 1085–1095
Fuhrman, J. A., Azam, F. (1982). Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: evaluation and field results. Mar. Biol. 66: 109–120
Hamner, W. M., Madlin, L. P., Alldredge, A. L. Gilmer, R. W. Hamner, P. P. (1975). Underwater observations of gelatinous zooplankton: sampling problems, feeding biology, and behaviour. Limnol. Oceanogr. 20: 907–917
Hobbie, J. E., Daley, R. J., Jasper, S. (1977). Use of nuclepore filters for counting bacteria by fluorescence microscopy. Appl. environ. Microbiol. 33: 1225–1228
Jacobsen, J. T., Azam, F. (1984). Role of bacteria in copepod fecal pellet decomposition: colonization, growth rates and remineralization. Bull. mar. Sci. 35: 495–502
JGOFS (1990). Bacteria. In: North Atlantic bloom experiment, report of the first workshop. Joint Global Ocean Flux Study (JGOFS) Report No 4. JGOFS Buro, Institut für Meereskunde, Kiel, p. 49–56
Johnson, P. W., Sieburth, J. M. (1979). Chroococcoid cyanobacteria in the sea: a ubiquitous and diverse phototrophic biomass. Limnol. Oceanogr. 24: 928–935
Johnson, P. W., Xu, H. S., Sieburth, J. M. (1982). The utilization of chroococcoid cyanobacteria by marine protozooplankters but not by calanoid copepods. Annls Inst. Océanogr., Paris 58(S): 297–308
Karner, M., Herndl, G. J. (1992). Extracellular enzyme activity and secondary production in free-living and marine-snow-associated bacteria. Mar. Biol. 113: 341–347
Kirchman, D., K'nees, E., Hodson, R. (1985). Leucine incorporation and its potential as a measure of protein synthesis by bacteria in natural aquatic systems. Appl. environ. Microbiol. 49: 599–607
Kirchman, D. L., Newell, S. Y., Hodson, R. (1986). Incorporation versus biosynthesis of leucine: implications for measuring rates of protein synthesis and biomass production by bacteria in marine systems. Mar. Ecol. Prog. Ser. 32: 47–59
Knauer, G., Asper, V. (1989). Sediment trap technology and sampling. In: US GOFS Planning Report, No 10. USGOFS Planning Coordination Office Woods Hole, MA
Lampitt, R. S., Hilier, W. R. Challenor, P. G. (1993b). Seasonal and diel variation in the open ocean concentration of marine snow aggregates. Nature 362: 737–739
Lampitt, R. S., Wishner, K. F., Turley, C. M., Angel, M. V (1993a). Marine snow studies in the Northeast Atlantic: distribution, composition and role as a food source for migrating plankton. Mar. Biol. 116: 689–702
Lawrence, S. G., Ahmad, A., Azam, F. (1993). Fate of particle-bound bacteria ingested by *Calanus pacificus*. Mar. Ecol. Prog. Ser. 97: 299–307
Lee, S., Fuhrman, J. A. (1987) Relationships between biovolume and biomass of naturally derived marine bacterioplankton. Appl. environ. Microbiol. 53, 1298–1303
Levitus, S. (1982). Climatological atlas of the World Ocean. NOAA Technical Paper No 3. Department of Commerce, Rockville, MD
Lochte, K., Turley, C. M. (1988). Bacteria and cyanobacteria associated with phytodetritus in the deep-sea. Nature 333: 67–69
Martin, J. H., Fitzwater, S. E., Gordon, R. M., Hunter, C. N., Tanner, S. J. (1993). Iron primary production and carbon-nitrogen flux studies during the JGOFS North Atlantic Bloom Experiment. Deep Sea Res. II 40: 115–134
Newton, P. R., Lampitt, R. S., Jickells, T. D., King, P., Boutle, C. (1995). Temporal and spatial variability of biogenic particle fluxes during the JGOFS NE Atlantic process studies at 47°N 20°W. Deep Sea Res. (in press)
Patterson, D. J., Nygaard, K., Steinberg, G., Turley, C. M. (1993). Heterotrophic flagellates and other protists associated with oceanic detritus throughout the water column in the mid North Atlantic. J. mar. biol. Ass. U.K. 73: 67–95
Pfannkuche, O., Lochte, K. (1993). Open ocean pelago-benthic coupling: cyanobacteria as tracers of sedimenting salp faeces. Deep Sea Res. I 40: 727–737
Porter, K. G., Feig, Y S. (1980). The use of DAPI for identifying and counting aquatic microflora. Limnol. Oceanogr. 25: 943–948
Robinson, M. K., Bauer, R. A., Schroeder, E. H. (1979). Atlas of North Atlantic-Indian Ocean monthly mean temperatures and mean salinities of the surface layer. Ref. Pub. 18, U.S. Naval Oceanographic Office, Washington, DC
Simon, M., Alldredge, A. L., Azam, F. (1990). Bacterial carbon

dynamics on marine snow. Mar. Ecol. Prog. Ser. 51: 201–213

Simon, M., Welschmeyer, N. A., Kirchman, D. L. (1992). Bacterial production and the sinking flux of particulate organic matter in the subarctic Pacific. Deep Sea Res. 39: 1997–2008

Smith, D. C., Simon, M., Alldredge, A. L., Azam, F. (1992). Intense hydrolytic enzyme activity on marine aggregates and implications for rapid particle dissolution. Nature 359: 139–142

Theil, H., Pfannkucke, O., Schriever, G., Lochte, K., Gooday, A. J., Hemleben, C. H., Mantoura, R. F. C., Turley, C. M., Patching, J. W., Riemann, F. (1988). Phytodetritus on the deep-sea floor in a central oceanic region of the north east Atlantic. Biol. Oceanogr. 6: 137–152

Toggweiler, J. R. (1989). Is the downward dissolved organic matter (DOM) flux important in carbon transport? In: Berger, W. H., Smetacek, V. S. Wefer, G. (eds.) Productivity of the ocean: present and past. Wiley, New York, p. 65–83

Turley, C. M. (1993a). Direct estimates of bacterial numbers in seawater samples without incurring cell loss due to sample storage. In: Kemp, P., Sherr, B., Sherr, E., Cole, J. (eds.) Handbook of methods in aquatic microbial ecology. Boca Raton, Lewis Publishers, p. 143–147

This article was submitted to the editor

Turley, C. M. (1993b). The effect of pressure on leucine and thymidine incorporation by free-living bacteria and by bacteria attached to sinking oceanic particles. Deep Sea Res. 40 (11/12): 2193–2206

Turley, C. M. (1994). Controls of the microbial loop: nutrient limitation and enzyme production, location and control. Microb. Ecol. (in press)

Turley, C. M., Hughes, D. J. (1992). Effects of storage on direct estimates of bacterial numbers of preserved seawater samples. Deep Sea Res. 39: 375–394

Turley, C. M., Hughes, D. J. (1994). The effect of storage temperature on the enumeration of epifluorescence-detectable bacterial cells in preserved sea-water samples. J. mar. biol. Ass. U.K. 74: 259–262

Turley, C. M., Lochte, K. (1990). Microbial response to the input of fresh detritus to the deep-sea bed. In: Labeyrie, L., Jeandel, C. (eds.) Geochemical variability in the oceans, ice and sediments. Palaeogeog. Palaeoclimatol. Palaeoecol. (Global and Planetary Change Section), p. 3–23

Turley, C. M., Mackie, P. J. (1995). Bacterial and cyanobacterial flux to the deep NE Atlantic on sedimenting particles. Deep Sea Res. (in press)

Woods, J. D. (1984). A warmwatersphere of the northeast Atlantic — a miscellany. Ber. Inst. Meerekde 128: 31–34

Manuscript first received: March 31, 1994
Revised version accepted: August 31, 1994