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Downward flux of particulate organic matter in the ocean: a particle decomposition paradox

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Oceanographers now recognize two distinct classes of particles in seawater, broadly categorized as suspended and sinking. The former class dominates the standing stock of particulate matter in the ocean and the latter class dominates the exchange between the surface waters and greater ocean depths[1]. The downward vertical flux of particulate organic matter (POM) in the open ocean exhibits a non-linear decrease with increasing water depth[2–6], and greater than 75% of the net POM loss occurs in the upper 500 m of the water column[6]. Because sinking particles contain viable, metabolically active microorganisms[7–12], the process of microbial decomposition is considered to be an important mechanism controlling POM flux. This model is consistent with the observed correspondence between POM flux and dissolved inorganic carbon concentrations[13], and with the reported selective loss of biochemically labile compounds from sinking particles[14–17]. From our experiments, however, we conclude that the large sinking particles are, in general, poor habitats for bacterial growth and therefore unlikely sites for the active remineralization of organic matter. Our results require a shift in the emphasis of current ideas of particle decomposition from microbes attached to rapidly sinking particles to the microbial populations which are either free-living in the water column or attached to suspended (non-sinking) particulate matter.

Sinking particles were collected during the VERTEX research programme at seven stations in the north Pacific Ocean using a free-floating MULTITRAP system[2]. Three different sediment trap solutions were used in this study: a NaCl–formalin solution for the collection of particulate organic carbon (POC) and nitrogen (PON)[2], a H_3PO_4–NaCl solution for the *in situ* extraction of adenosine-5′-triphosphate (ATP)[18], and a sterile seawater salt solution for the assessment of *in situ* microbial growth[11]. Nitex screens (335 μm mesh) were placed at the base of each sediment trap baffle to minimize contamination by actively mobile zooplankton, which would have seriously compromised data interpretation.

Our experiments were designed to test the hypothesis that microbial (in particular, bacterial) decomposition of sinking organic matter is responsible for maintaining the observed profile of POM flux beneath the euphotic zone. Specifically, we endeavoured to evaluate two ecological predictions which would be consistent with this hypothesis: (1) source term POM (the initial sinking particle pool) contains a low biomass of metabolically-active microorganisms which multiply as particles age (and sink); (2) microorganisms associated with particulate materials collected at the base of the euphotic zone and aged *in situ* consume POC and PON.

At every VERTEX station we observed a significant decrease in the flux of POM (both POC and PON) with increasing water depth (data summarized in refs 5 and 6), a result which is consistent with existing POM flux models[3,4]. The total ATP content of the sinking POM when the particles entered the sediment traps (that is, *in situ* extracted ATP) also decreased with increasing water depth (Table 1). This decrease in particle ATP content could represent either a decrease in total microbial biomass (assuming a constant microbial ATP:biomass-C relationship[19]) or a decrease in the microbial ATP:biomass-C

Table 1 Microbial ATP in association with sediment trap-collected particles at a variety of sites in the north Pacific Ocean

Location (date; deployment period)	Trap depth (m)	*In situ* ATP (μg per trap)	Shipboard ATP (μg per trap)	Shipboard/ *in situ* ATP (×100%)
Manzanillo, Mexico	30	76.7	1.4	2
18° N, 108° W	120	25.0	2.1	8
(10/81; 22 days)	200	10.9	2.5	23
	400	0.8	1.0	125
Pt Sur, California	100	42.1	5.7	14
36°16′ N, 122°57′ W	300	27.9	1.4	5
(6/82: 6 days)				
Hawaii	150	34.0	2.5	7
28° N, 155° W	300	16.2	1.8	11
(8/83; 33 days)	500	15.8	1.7	11
Pt Sur, California	50	30.8	2.7	9
35°40′ N, 123°50′ W	100	9.1	1.3	14
(6/84; 13 days)	225	1.5	0.5	33
	475	0.7	0.1	14
North Pacific Ocean	130	3.4	0.7	21
35° N, 128° W	300	1.0	0.1	10
(6/84; 22 days)	600	0.1	0.1	100
North Pacific Ocean	150	3.7	0.3	8
33° N, 139° W	275	1.0	0.1	10
(6/85; 22 days)	600	0.2	0.1	50

In situ ATP concentrations were determined in sediment traps precharged with a H_3PO_4–NaCl solution[18] and shipboard ATP was measured in unpreserved sediment trap collections[11] after deployment periods indicated above.

Table 2 Effects of *in situ* incubation on the growth of bacteria and zooflagellates and on the decomposition of POC and PON associated with sinking particles

Trap depth (m)	Trap treatment	POC (mg per trap)	PON (mg per trap)	C:N (w/w)	Shipboard ATP (μg/trap)	Shb./*In situ* ATP (×100%)	^{3}H-adenine incorporation (μCi per trap) RNA	DNA	protein
80	live	2.72 (±0.73)	0.46 (±0.14)	6.0 (±0.6)	1.2	27	47.3	3.5	1.1
	live+thiram	3.34 (±0.48)	0.51 (±0.11)	6.5 (±0.5)	1.7	37	40.8	2.4	0.7
	formalin	3.19 (±0.35)	0.48 (±0.08)	6.7 (±0.5)	—	—	—	—	—
175	live	1.30 (±0.36)	0.14 (±0.04)	9.2 (±0.4)	0.4	17	1.9	0.2	0.1
	live+thiram	1.17 (±0.20)	0.14 (±0.04)	10.3 (±2.6)	0.4	17	3.9	0.8	0.1
	formalin	1.67 (±0.13)	0.21 (±0.06)	10.6 (±3.4)	—	—	—	—	—

Sediment traps were deployed at two depths for a period of 12 days off Pt. Sur, CA (35°40′ N; 123°50′ W) during April 1985. All traps were set with 335 μm screens to eliminate contamination by large zooplankton. The trap solutions include: H_3PO4, for the *in situ* extraction of ATP[18]; formalin, for the *in situ* preservation of POC and PON[2]; and two sterile seawater solution traps, without preservative, for the measurement of *in situ* microbial growth and organic matter decomposition[11]. The decomposition measurements were carried out both with and without thiram in order to evaluate the role of protozoans in particle decomposition[12]. The *in situ* extracted ATP concentrations were 4.62 and 2.47 μg ATP per trap for sediment traps deployed at 80 and 175 m, respectively.

ratio with increasing water depth. Direct microscopic measurements of bacterial and zooflagellate biomass made during the VERTEX 5 field experiment[12], however, confirmed that the ATP: biomass-C relationship does not change substantially over the depth range of these *in situ* observations. Consequently, we conclude that there exists a decrease in the flux of living microorganisms with depth beneath the euphotic zone. This observed decrease in particle-associated microbial biomass does not support the original hypothesis regarding the role of microbial decomposition as a primary factor controlling downward POM flux in the ocean. Furthermore, the greatest loss of ATP per unit water depth was consistently observed for the depth stratum immediately beneath the euphotic zone. This is precisely the location where the microbial decomposition model would predict the most intense microbial metabolic activity and growth because the sinking particles would be closest to their source in the surface waters of the ocean.

Several *in situ* microbial growth experiments were performed during the VERTEX programme to complement the *in situ* extracted ATP data. Replicate sediment traps containing sterile seawater salt solutions were used to collect sinking particles which were then allowed to age *in situ* for the duration of the deployment period. The biomass of the particle-associated microbial assemblages which enter these 'live' traps could either increase, decrease or remain the same, depending upon the availability of reduced carbon and energy sources required for net microbial biosynthesis. Following the recovery of the sediment traps the ATP in these unpreserved traps was immediately extracted and these 'shipboard extracted' ATP concentrations were compared with the ATP values derived from the *in situ* extractions, discussed above. The results of this comparison indicate that for all stations investigated, there was net death (that is, net loss of ATP) during the respective incubation periods (Table 1). For the samples collected at the base of the euphotic zone the extent of net community death ranged from 79.5% (North Pacific Ocean, 6/84) to 98.2% (Manzanillo, Mexico, 10/81). Again, these data are inconsistent with the hypothesis that microbial growth and metabolism are responsible for controlling the change in POM flux with depth in the upper water column. If the process of active microbial decomposition was important we would have expected to observe an increased ATP flux with depth and a net positive increase in ATP during the *in situ* sample incubations, both resulting from the hypothesized rapid growth of microorganisms on the sinking particles.

Additional experiments were designed to measure directly the decomposition of sediment trap-collected POC and PON during *in situ* incubation (Table 2). The results indicate that there was no difference between the amount of organic matter collected and preserved *in situ* and that which remained in the sediment traps after the particulate materials were allowed to decompose for 12 days in replicate unpreserved sediment traps either with or without the protozoan inhibitor thiram[12]. The vertical POM flux profile measured at this station would have required a net loss of 60–65% of the POC and PON per day, assuming a sinking rate of 100 m per day. In agreement with the data presented in Table 1, there was no evidence for an increase in microbial biomass with depth or for *in situ* microbial growth on the intercepted particulate materials. The *in situ* metabolic activity of the resident microbial assemblages, as determined by the incorporation of ^{3}H-adenine, indicated a substantial decrease in total metabolic activity with increasing water depth for particles collected in the upper 175 m of the water column, and an order of magnitude decrease in the ATP(biomass)-specific rate of ^{3}H-adenine assimilation.

During the VERTEX 5 field experiment (July–August 1985) we also measured POC and PON flux in 335 μm Nitex-screened sediment traps, in addition to ATP flux, to evaluate the relationship between living and non-living particulate carbon flux in the ocean (Table 3). The biomass (living) carbon flux extrapolated from the *in situ* extracted ATP measurements indicates that the majority of the sinking particulate carbon leaving the euphotic zone (93%, 54.1% and 91.6% for VERTEX-5 STA. 1, 2 and 3, respectively; Table 3) was composed of living microbial biomass. In addition, the ATP content of the collected particulate materials decreased with increasing depth to a greater extent than the content of POC (Table 3). These data imply that the ratio of biomass carbon to total particulate carbon decreases by a factor of 5–10 in the upper 2000 m of the water column. These observations are inconsistent with our initial microbial decomposition model. If rapid microbial growth was responsible for controlling the POC flux profile in the upper 500 m of the water column, we would have expected to observe an increasing trend in microbial biomass per unit POC as the particles were decomposed. Based upon these results we must conclude that sinking particles are, in general, poor habitats for bacterial growth and must be considered unlikely sites for the active remineralization of organic mater. This conclusion, though inconsistent with current hypotheses regarding the decomposition of large particles in the sea, is consistent with direct measurements of heterotrophic microbial activity on freshly collected crustacean faecal pellets[20] and macroscopic organic aggregates (marine snow)[21,22] and with the long time periods (1,500 days) which have been estimated for the microbially-mediated turnover of sediment-trap-collected POC[8].

Our current models of organic matter diagenesis and nutrient regeneration require a balance between the downward flux of biogenic particles and the upward diffusion-advection of dissolved inorganic constituents. These large scale oceanic processes are ultimately dependent upon the production and remineralization of POM through the combined activities of diverse assemblages of marine microorganisms. If the assumption of steady-state is made, then a balance between the downward flux of POC and upward mixing can be used to predict the vertical distribution of dissolved inorganic carbon[13]. The collective data presented here, however, indicate that the relationship between the downward flux of particulate matter and the regeneration

Table 3 Relationship between the flux of total particulate organic carbon (POC) and biomass-carbon in the north Pacific Ocean (VERTEX 5 experiment)

Location and deployment period	Trap depth (m)	Biomass-C flux (mg C m^{-2} per day)	POC flux (mg C m^{-2} per day)	Per cent living
Pt Sur California	50	152	164	93
35°40′ N, 123°50′ W	100	45.0	49.2	92
(22 days)	225	7.5	24.8	30
	475	3.4	9.0	38
	900	1.7	8.5	20
	1,500	1.6	8.7	18
	2,000	1.2	7.1	17
North Pacific Ocean	130	9.8	18.1	54
35° N, 128° W	300	2.9	6.1	48
(22 days)	600	0.4	6.2	7
	750	0.5	5.9	9
	1,000	0.4	4.7	9
	1,500	0.2	5.0	4
	2,000	0.3	4.1	7
North Pacific Ocean	150	10.9	11.9	92
33°06′ N, 139°34′ W	275	2.9	7.8	37
(13 days)	600	0.6	4.9	12
	750	0.5	3.3	15
	1,000	0.5	3.3	15
	1,500	0.4	2.4	17
	2,000	0.1	2.0	5

Three separate sets of sediment traps were deployed during June–July 1984 in a transect from Pt Sur, California, to a station approximately 1,600 km offshore. All sediment traps were configured with screens and contained a sterile seawater solution without preservative. Following recovery, subsamples of each trap were taken for shipboard ATP and for POC (ATP data are given in Table 1). The shipboard ATP values were extrapolated to biomass-C assuming a C: ATP ratio of 250 (ref. 19).

of inorganic nutrients is most likely the result of an indirect coupling rather than being the direct result of microbial decomposition of sinking particles.

Two alternative processes can be invoked to explain the net loss of organic matter as particles sink. First, abiotic particle fragmentation (conversion of sinking particles to smaller non-sinking particles) and solubilization (conversion of sinking particles to dissolved constituents) may be important processes in controlling the net loss of particulate organic matter from the upper regions of the sea. Once the organic matter has been removed from the rapidly sinking particles, the microbial inhabitants of the upper mesopelagic zone (150–500 m) might be responsible for the oxidation of suspended particulate or dissolved organic matter resulting in the consumption of dissolved oxygen, the production of dissolved inorganic carbon and the regeneration of nitrate and phosphate. Although this model requires that heterotrophic microorganisms are ultimately responsible for the active remineralization processes, the site of active microbial growth and decomposition is shifted from microbes attached to rapidly sinking particles to the microbial populations which are either free-living in the water column or attached to suspended (non-sinking) particulate matter. An alternative model invokes particle ingestion by mid-water zooplankton and micronekton as the mechanism responsible for controlling the flux of POM. Decomposition of the particulate matter would then take place within the intestinal tracts of these animals, most likely as a result of the activities of psychrophilic and barophilic bacterial populations[22, 24]. These two decomposition models need not be mutually exclusive.

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