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Vertical distribution, transport, and exchange of carbon in the northeast Pacific Ocean: evidence for multiple zones of biological activity

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Abstract—A sediment trap experiment was conducted to investigate the production, decomposition, and transport of organic matter from 0 to 2000 m at a station 100 km northeast of Point Sur, California. Parameters measured included (1) rates of autotrophic production of carbon, (2) vertical depth distributions of total carbon, nitrogen, and living biomass, and (3) downward flux of organic carbon, nitrogen, ATP, RNA, and fecal pellets. Metabolic activity and microbial growth rates (RNA and DNA synthesis) were also estimated *in situ*, for both the 'suspended' (i.e., samples captured in standard water bottles) and 'sinking' (i.e., samples captured in sediment traps) particles.

Daily depth-integrated rates of primary production averaged 564 mg C m^{-2}, of which 10 to 15% was removed from the euphotic zone by sinking, assuming steady-state conditions. The profiles of suspended carbon, nitrogen, C:N ratios, and ATP conformed to previously published concentration–depth profiles from the region. The vertical flux profiles of organic matter, however, revealed two important features that were not evident in the suspended particulate matter profiles. First, there was an obvious mid-water depth increase (i.e., an increase in organic carbon and nitrogen flux with increasing depth) between 700 and 900 m, suggesting horizontal advection or *in situ* production. Similar flux profiles were also observed for ATP, RNA, and total fecal pellets. Second, the C:N ratios for the sediment trap materials collected at mid-ocean depths (600 to 1200 m) were low compared to values measured for 'suspended' particulate organic materials collected from comparable depths, supporting the *in situ* production hypothesis. An observed maximum in the rate of RNA and DNA synthesis for microorganisms associated with particles collected at 700 m confirmed that the flux anomalies were the result of *in situ* microbiological processes rather than horizontal advection. We hypothesize that the *in situ* activity measured at 700 m is the result of a chemolithotrophic-based carbon production system supported by the presence of reduced inorganic compounds (e.g., NH_4^+, HS^-) found in association with the sinking particles. "New carbon production" (a value equivalent to the increased downward flux of carbon) between 700 and 900 m was 15 mg C m^{-2} d^{-1}, or 2 to 1% of the daily integrated primary production. These regions of intense biological metabolic activity, growth, and organic matter diagenesis may have a profound influence on the oceanic carbon cycle and on the observed steady-state distributions of various non-conservative properties of seawater.

INTRODUCTION

THE production, distribution, transport, and decomposition of organic matter in the ocean are concerns shared by biological oceanographers, marine chemists, and organic geochemists. At present, there exists a substantial data base on the rates of primary production (EPPLEY, 1980; PETERSON, 1980) and on the average concentrations and spatial variations of suspended particulate organic carbon (S-POC; i.e., organic carbon collected using conventional water bottles) and dissolved organic carbon (DOC) in the oceans of the world

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(reviewed by SIMPSON, 1982). By comparison, only limited information is available on the rates of microbial secondary production, the *in situ* size spectrum and morphology of organic particulate matter, and on the specific chemical composition of S-POC and DOC present in seawater.

With the advent and extensive use of particle traps, a new phase of marine organic biogeochemistry has begun. It is becoming clear that the dominant mechanisms for the vertical transport of organic carbon into the deep sea are the fairly rapid settling of large particles such as fecal pellets (URRERE and KNAUER, 1981) and "marine snow" (SHANKS and TRENT, 1980; SILVER and ALLDREDGE, 1981), with the small (<10-μm diameter) numerically more abundant flakes, flocs, and aggregates playing a minor role. Consequently, the interpretation of our historical data base on instantaneous collections of S-POC requires a careful re-evaluation.

The downward vertical flux of organic matter (measured as total organic carbon) appears to exhibit a non-linear decrease with increasing water depth (SUESS, 1980), implying *in situ* decomposition, ingestion, fragmentation, and solubilization en route to the sea floor. SUESS (1980) summarized much of the available oceanic POC flux data obtained using sediment traps and derived an empirical relationship that he used to predict carbon flux as a function of primary production and water depth.

Suess' model is a good beginning, but important refinements are necessary to describe accurately the vertical flux of organic carbon in epi- and mesopelagic ocean waters. As presented, the model fails to differentiate between new and regenerated primary production (EPPLEY and PETERSON, 1979). That is, at steady state there is only a fraction of the total organic carbon production (a value equal to new production) available for export out of the euphotic zone. The ratio of new to regenerated production is known to vary among different marine ecosystems (DUGDALE, 1976; EPPLEY and PETERSON, 1979). In addition, the primary production carbon flux model fails to account for depth-dependent (or discontinuity-layer-dependent) changes in rates of microbial growth and decomposition, which would be expected in most oceanic environments (KARL, 1982a). Coupled with this is the possibility of subsurface inputs of small and large size classes of particulate carbon (i.e., increases in the fast-sinking particle fraction with increasing water depth), as have been observed in some sediment trap experiments (FELLOWS *et al.*, 1981; KNAUER and MARTIN, 1981; URRERE and KNAUER, 1981).

As a further refinement of the generalized carbon flux model, the contribution of heterotrophic particulate carbon production should also be considered in addition to strictly autotrophic processes. It is well known that new soluble organic carbon, capable of supporting the growth of microheterotrophs, is continuously produced during normal phytoplankton metabolism (e.g., through excretion, exudation, death, lysis, and grazing losses). Due to the presence of fairly large exogenous DOC pools, the ^{14}C-DOC produced during experimental incubations would have relatively low specific radioactivities and would not necessarily be coupled to bacterial production during the short intervals used in most productivity studies (i.e., DOC turnover time $\gg$ incubation period). Consequently, bacterial production derived from soluble products of phytoplankton growth, which might channel up to 30% more carbon into microbial cells than currently estimated in some marine environments (POMEROY, 1974), is not adequately considered as a source of particulate carbon for the downward flux system.

The present study was undertaken to evaluate the production, distribution, and downward vertical flux of organic matter at a station approximately 100 km off Point Sur, California. In contrast to several studies concerned with fluxes of carbon to the deep sea (HONJO, 1978,

1980; HINGA *et al.*, 1979; ROWE and GARDNER, 1979), our study was primarily concerned with organic matter transformations in the upper 2000 m, specifically in the vicinity of the oxygen minimum zone. We examined the distribution of particulate organic matter, both S-POC and sediment trap particulate organic carbon (T-POC), in relation to specific particulate organic compounds (e.g., ATP and RNA), which we consider to be indicative of viable microorganisms. Our data indicate the presence of a major zone of intense metabolic activity, growth, and carbon diagenesis at 700 to 900 m (oxygen minimum zone) and a minor zone at 1000 to 1400 m (sub-oxygen minimum zone), which does not appear to be so strongly developed. We also report the results of the first *in situ* sediment trap microbial growth rate experiments and use the data to demonstrate further possible mechanisms for the origin and maintenance of the dissolved oxygen minimum zone.

MATERIALS AND METHODS

Sediment trap experiments

MULTITRAP design and deployment. Sinking particulate materials were intercepted using a free-floating MULTITRAP system as described by KNAUER *et al.* (1979). The MULTITRAP array consisted of 12 individual sediment traps at each of 12 depths ranging from 50 to 1950 m, two current meters, and one inclinometer (Fig. 1). The entire array was deployed for 13.25 days at approximately 100 km off Point Sur, California (123°45′N; 35°45′W) during the VERTEX I (vertical transport and exchange) field experiment (August to September 1980). Details of the current meter data and a comparison with geostrophic flow calculations have been presented elsewhere (BROENKOW, 1982).

Prior to deployment, each trap was cleaned with Micro® and 10% HCl, rinsed thoroughly with sterile de-ionized water, and filled with one of several high density solutions (see below) to prevent flushing. Of the 144 traps deployed, 24 were used for ATP and RNA measurements, 24 for C and N determinations, 12 for *in situ* microbial growth rate estimates, and 12 for fecal pellet collections.

In situ *MULTITRAP ATP and RNA extraction.* At each of 12 depths two cast acrylic collection tubes fitted with baffles at their mouths and 0.8-μm Nuclepore® filters and polyethylene caps at their bases and containing 2.5 l of a high density acid-salt solution (0.5 M H_3PO_4 containing 1.5 M NaCl, $\rho = 1.05$ g cm^{-3}) were used for the *in situ* extraction of trapped ATP (T-ATP) and RNA (T-RNA). The rationale for using the solution was discussed elsewhere (FELLOWS *et al.*, 1981). One of the two traps at each depth was fitted with a 335-μm Nitex® screen at the base of the baffle to discourage the entry of viable zooplankton (swimmers), which are not part of the downward particle flux field. Previous studies emphasized the quantitative significance of contamination by swimmers in the estimation of material fluxes in the ocean (KNAUER *et al.*, 1979; FELLOWS *et al.*, 1981).

Upon recovery the seawater overlying the higher density solutions was removed and the acid-salt mixtures containing the extracted T-ATP and T-RNA were filtered into acid-washed polycarbonate bottles through the Nuclepore filter at the bottom of each trap. The total volume was recorded and triplicate subsamples of the acid-soluble material were processed for total ATP (FELLOWS *et al.*, 1981). The T-ATP concentrations derived from the extraction are subsequently referred to as the "MULTITRAP *in situ* extracted ATP". The Nuclepore filters containing the residual acid-insoluble materials were placed in plastic Petri dishes and stored frozen for shore-based processing and determination of T-RNA.

In the laboratory the surface of each Nuclepore® filter was carefully washed with 5 ml of

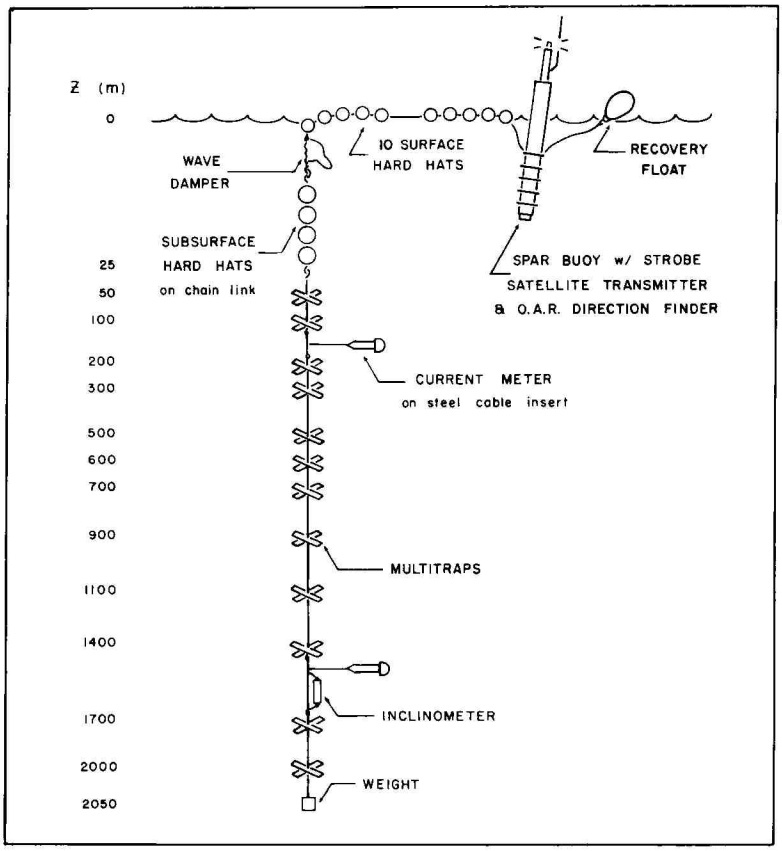


Fig. 1. A schematic representation of the MULTITRAP free-floating sediment trap array used during the VERTEX I experiment.

5% trichloroacetic acid (TCA) and collected materials resuspended. The particulate suspensions were then transferred onto 25-mm glass fiber filters (Whatman GF/F). This step was necessary because the large 90-mm Nuclepore® filters were difficult to process. We evaluated the efficiency of the transfer by analyzing several of the large Nuclepore filters after the cleaning. All such filters retained <1% of the RNA measured on the corresponding GF/F filters. The RNA was isolated, purified, and solubilized as described by KARL *et al.* (1981) and measured spectrophotometrically by the orcinol method (LIN and SCHJEIDE, 1969), using adenosine-5′-monophosphate (AMP) as the primary standard.

Rates of MULTITRAP nucleic acid synthesis. In situ rates of nucleic acid (RNA and DNA) synthesis associated with sinking particles were measured at each of 12 depths. Each cast acrylic collection tube with baffle and bottom closure was cleaned with 70% ethanol and rinsed thoroughly with sterile seawater before filling with 2.5 l of a sterile high density solution consisting of filtered seawater containing 33.8 g NaCl (0.58 M), 14.26 g $MgCl_26H_2O$ (0.07 M), 0.93 g KCl (0.013 M), and 100 μCi[2, ^{3}H]adenine (15 Ci mmol^{-1}; New England Nuclear Co., Boston, MA) per liter ($\rho = 1.065$ g cm^{-3}). Prior to deployment, 1 ml of the solution was removed for determination of total radioactivity (nCi ml^{-1}) and total ^3H_2O as described by KARL *et al.* (1981). Control samples were prepared by removing subsamples of

the solutions into sterile 500-ml polycarbonate bottles for deployment at each depth for the duration of the experiment. No ^{3}H-RNA or ^{3}H-DNA was detected in any of the control samples.

The high density sediment trap solution was decanted into a clean 2-l polycarbonate bottle and gently swirled before subsampling as follows: (1) triplicate 50-ml samples were concentrated onto GF/F filters and extracted in boiling phosphate buffer (60 mM, pH 7.4) for ATP and ^{3}H-ATP as described by KARL *et al.* (1981), and (2) triplicate 50-ml samples were concentrated onto GF/F filters and frozen for ^{3}H-RNA and ^{3}H-DNA (KARL, 1981). In addition, a 320-ml subsample of each collection was passed through a 153-μm Nitex screen and triplicate 50-ml fractions of the filtrate were processed for total ATP, ^{3}H-ATP, and ^{3}H-nucleic acids as described above. In this way, the effects of swimmers on T-ATP pool specific activities and nucleic acid production could be determined because they were quantitatively retained on the 153-μm screens. The T-ATP concentrations (total and <153 μm) measured by the procedure are subsequently referred to as "MULTITRAP shipboard extracted ATP" to distinguish them from the "MULTITRAP *in situ* extracted ATP". *In situ* rates of RNA and DNA syntheses were calculated by the method of KARL (1981).

MULTITRAP organic C and N. Two collector tubes per depth were filled with a reagent grade NaCl solution ($\rho = 1.05$ g cm^{-3}) containing 1% buffered formalin. Upon recovery, the salt solutions were drained through the 0.8-μm Nuclepore filters positioned at the base of the traps and the collected particulate materials were rinsed, picked (to remove swimmers), oven dried, and analyzed for organic C and N (T-POC, T-PON) as described by KNAUER *et al.* (1979) and KNAUER and MARTIN (1981).

MULTITRAP fecal pellet collections. One sediment trap, containing NaCl-formalin (as before), was deployed at each depth for microscopic identification of particles and enumeration of fecal pellets. Upon recovery, the high density formalin solutions were drained through the 0.8-μm Nuclepore filter and the particulate materials transferred to a Petri dish for subsequent microscopic examination. Fecal pellets were sorted by shape (ellipse, cylinder, sphere, or coiled) and size (0.05, 0.1, or 0.15 mm) and enumerated as described by URRERE and KNAUER (1981).

Water column experiments

Suspended ATP, RNA, C, and N concentrations. Seawater samples were collected daily in acid-washed 10-l Niskin bottles throughout the water column (0 to 2000 m). Suspended ATP concentrations (S-ATP) were determined by filtering between 150 and 2000 ml (depending upon water depth) through either Whatman GF/C (nominal pore size, 1.3 μm), Whatman GF/F (nominal pore size, 0.7 μm), or Reeve Angel 984-H (nominal pore size, 0.4 μm) glass fiber filters for comparative purposes. The concentrated particulate materials were extracted in 5 ml of boiling phosphate buffer (60 mM, pH 7.4) and extracts containing ATP were stored frozen (–20°C) for subsequent analyses. S-ATP concentrations were estimated by the firefly bioluminescence reaction described by KARL and HOLM-HANSEN (1978). 'Suspended' RNA (S-RNA) was concentrated from 5 l of Niskin bottle-collected seawater by filtration onto GF/F filters. The samples were stored frozen for later extraction, purification, and colorimetric determination as described above. Total suspended organic C and N (S-POC and S-PON) associated with particulate organic matter (S-POM) were measured as described by SHARP (1974).

Primary production estimates. Primary production was estimated using the metal-free collection and processing techniques developed at Moss Landing Laboratories (KNAUER and

MARTIN, 1981; FITZWATER *et al.*, 1982). Three consecutive 3 to 4-h *in situ* incubations (i.e., morning, noon, and afternoon) were performed each of 4 days for samples collected from the surface to the 1% light level (approximately 50 m). Daily production rates were calculated according to STRICKLAND and PARSONS (1972).

Measurement of rates of RNA and DNA synthesis. Rates of microbial RNA and DNA synthesis were estimated using the methods devised by KARL (1981) and coworkers (KARL *et al.*, 1981). Seawater samples were collected in 10-l Niskin bottles to depths of 2000 m. For each water depth, a 2-l acid-washed polycarbonate bottle was filled to within 5 ml of capacity, 200 μCi[2, ^{3}H]adenine added (in 2.0 ml of sterile seawater), the contents mixed thoroughly, and 1 ml removed for determination of total radioactivity and zero time ^3H_2O content (KARL *et al.*, 1981). In addition, a 500-ml sample was prepared to evaluate the effect of the addition of the salt mixture on the rates of incorporation of ^{3}H-adenine into RNA and DNA at each water depth. The experiment was done to provide a more meaningful interpretation of the *in situ* sediment trap nucleic acid synthesis experiments. Pre-weighed analytical grade NaCl, $MgCl_2$, and KCl were added to each of the 500-ml bottles in proportions identical to those in the MULTITRAPS, followed by the addition of 50 μCi of ^{3}H-adenine. Each set of bottles was then filled to capacity (no air space) with seawater, capped, and returned to its original depth for an *in situ* incubation period of between 13 and 16 h, depending upon the sample depth. For selected experiments, time series analyses were conducted to evaluate the kinetics of uptake and incorporation of ^{3}H-adenine into microbial cells and to strengthen our interpretation of endpoint data.

RESULTS

Distribution and production of suspended organic matter

Suspended concentration–depth profiles for ATP, RNA, POC, and PON from waters adjacent to the free-floating MULTITRAP array are shown in Figs 2 to 5. S-ATP concentrations were not significantly different from day to day, which demonstrates that the steady-state biomass distribution was relatively constant during the period (Fig. 2b). Similar S-ATP concentrations were measured using GF/C, GF/F, and RA-984H filters (Figs 2a and 3). Both S-ATP and S-RNA (Fig. 4) concentrations conformed to values measured previously in samples of coastal oceanic particulate matter.

The depth profiles of C and N in S-POM (Fig. 5) conform qualitatively and quantitatively to values measured in coastal North Pacific waters. The C : N ratios (by atoms) of the suspended materials displayed a general increase with increasing water depth, ranging from 7.6 to 8.7 in the surface waters to a value of 28 at 2000 m (Fig. 5). Based on extrapolations from the S-ATP data, living carbon in the euphotic zone accounted for 75 to 90% of the total S-POC, whereas at 2000 m the value was <5%. The rate of increase in C : N ratios is not constant with depth but appears to have several subsurface anomalies (Fig. 5), which might represent *in situ* injections of fresh organic material, re-consolidation of sinking particles, or interactions between the dissolved and particulate organic matter.

Daily rates of ^{14}C primary production integrated over the euphotic zone (0 to 50 m) ranged from 456 to 647 mg C m^{-2} ($X = 564 \pm 86$ mg C m^{-2}; Fig. 6). Total rates of microbial RNA and DNA synthesis were highest in surface waters and decreased with increasing water depth (Fig. 7). The integrated total microbial carbon production estimate extrapolated from DNA synthesis (KARL and WINN, 1984) was 1.85 g C m^{-2} d^{-1} for the euphotic zone (0 to 50 m).

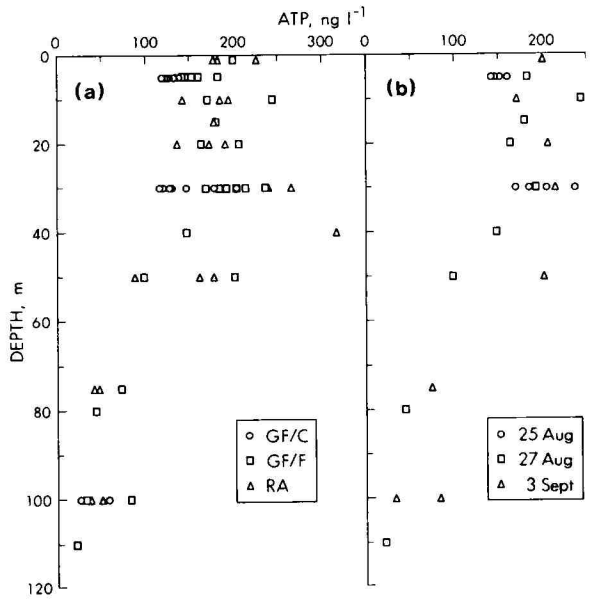


Fig. 2. Vertical distribution of suspended ATP in the surface waters at the VERTEX I station. (a) ATP concentrations as measured with a variety of different glass fibre filters. (b) ATP concentrations (with GF/F filters) on several days during the VERTEX I experiment.

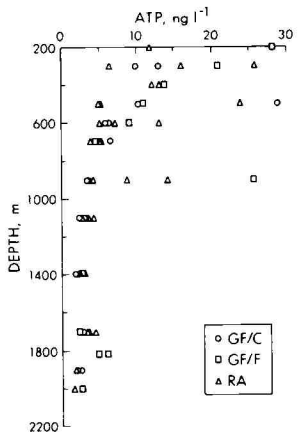


Fig. 3. Vertical distribution of suspended ATP at the VERTEX I station as measured with a variety of different glass fibre filters.

The value is approximately three times the estimate of primary carbon production. The specific radioactivity of the S-ATP pool varied from a minimum of 0.25 nCi(pmol)$^{-1}$ to a maximum of 1.1 nCi(pmol)$^{-1}$, emphasizing the importance of measuring and correcting for extracellular and intracellular dilution of the nucleic acid precursor (KARL *et al.*, 1981; KARL, 1981, 1982b). Despite significant changes in the magnitude of the total rates with depth, the rate per unit biomass (i.e., specific rate of RNA and DNA synthesis) was relatively constant or even increased slightly with increasing water depth (Fig. 7).

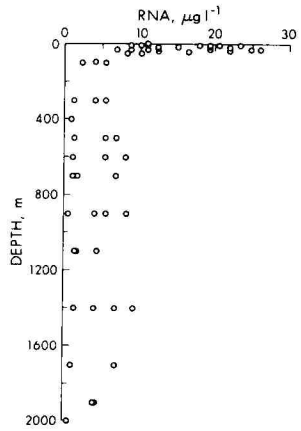


Fig. 4. Vertical distribution of suspended RNA at the VERTEX I station.

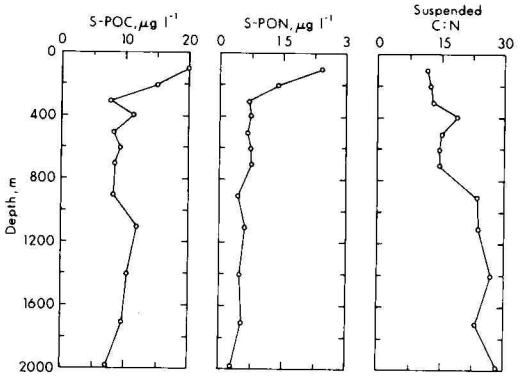


Fig. 5. Vertical distribution of suspended POC and PON and suspended C:N ratios at the VERTEX I station.

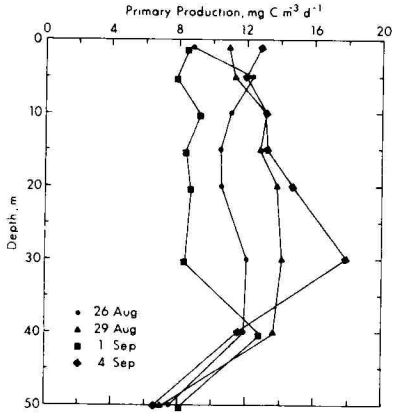


Fig. 6. Vertical profile of daily rates of primary production at the VERTEX I station. Mean daily integrated production was 564 mg C m^{-2} d^{-1}.

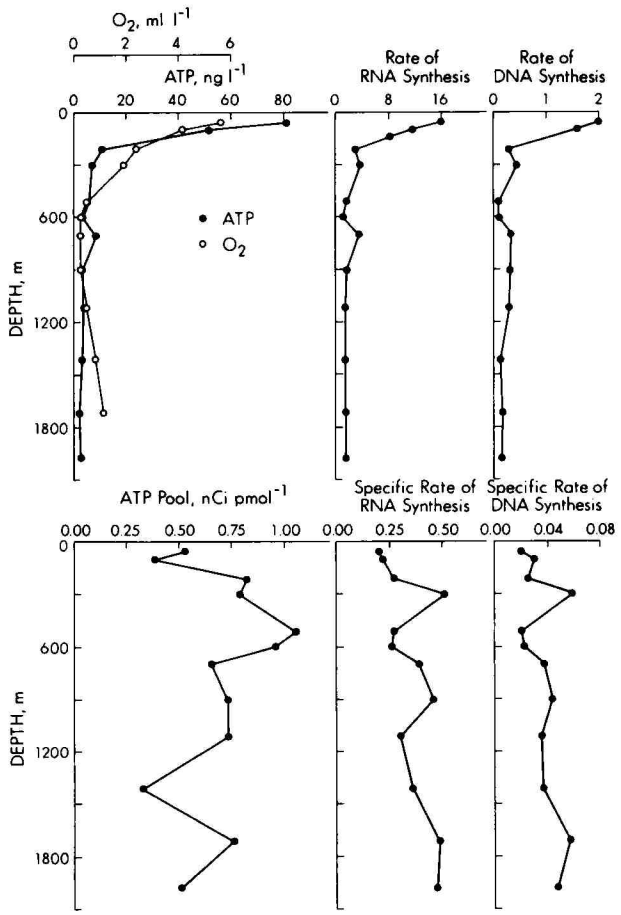


Fig. 7. Vertical distribution of dissolved O_2, ATP, ATP pool specific radioactivity, rates and specific rates of RNA and DNA syntheses for suspended materials collected at the VERTEX I station. The rates of RNA (or DNA) synthesis are expressed as pmol A (or dA) incorporated into RNA (or DNA) l^{-1} h^{-1} and the specific rates are expressed as pmol A (or dA) incorporated into RNA (or DNA) ng ATP^{-1} h^{-1}.

The addition of salts, identical to those used in the *in situ* ^{3}H-adenine MULTITRAP experiment, resulted in a substantial reduction (40 to 75% decrease) in the incorporation of ^{3}H-adenine for surface (0 to 100-m) populations (Fig. 8). However, the effect of adding salt diminished to zero at 600 m and stimulated (10 to 60%) ^{3}H-adenine uptake at greater depths. The effects are undoubtedly complex and can only be indirectly related to the salts. The only conclusion that we wish to draw from the data is that within a maximum factor of two to three, there were no differences in the metabolic activities and growth characteristics of the microbial assemblages with and without salt additions and that the observed effects were negligible (<10 to 20%) between 500 and 900 m. Such information is relevant to the subsequent interpretation of the MULTITRAP experimental data. It should be emphasized that the addition of salts to the sediment traps is necessary to maintain a density discontinuity and to prevent the dissolved materials (e.g., ^{3}H-adenine) from diffusing out of the trap during deployment and from flushing upon recovery. Although sediment trap closures would eliminate the

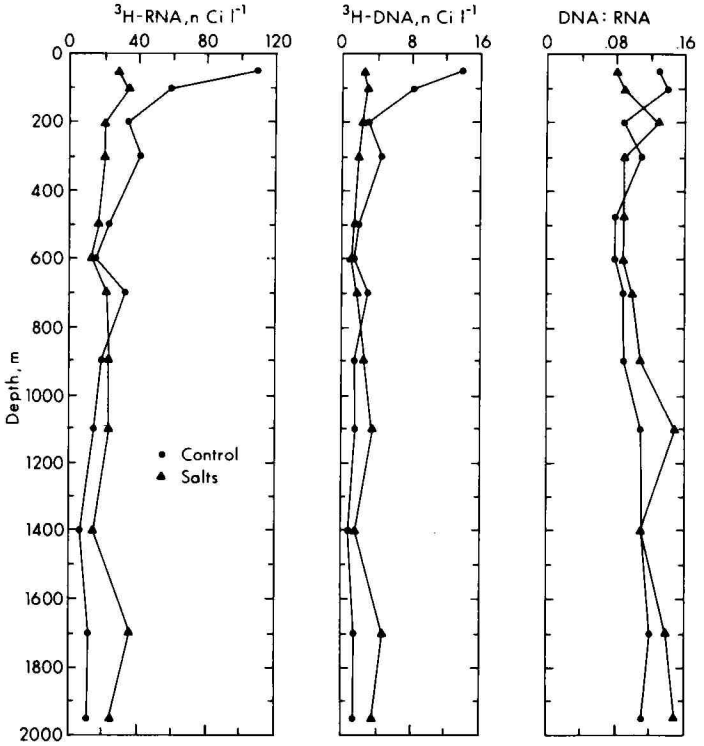


Fig. 8. Effect of salt addition on the incorporation of ^{3}H-adenine into ^{3}H-RNA and ^{3}H-DNA for suspended materials collected at the VERTEX I station.

flushing problem, diffusion out of a trap without added salt would complicate the use of radiotracers.

MULTITRAP collections and flux estimates

The swimmer-free T-POC and T-PON fluxes at the VERTEX I station (Fig. 9) revealed three important features not evident in the water column suspended particulate profiles. First, there was a mid-water depth increase (i.e., an increase in T-POC and T-PON flux with increasing water depth) at 900 m, suggesting a subsurface injection or *in situ* production of T-POC and T-PON in the water column. The second feature was the relatively low C : N ratios (6.2 to 8.7; Fig. 9) in the sediment trap materials compared to the C : N ratios derived from bottle-collected S-POM from comparable depths (Fig. 5). The third was the relative decrease in the sediment trap C : N ratios below the oxygen minimum (900 m) and near 1500 m. The data suggest that the MULTITRAP particles are comprised of materials that differ from S-POM in their nutritional quality and perhaps in their source. Our data support the conclusions of MCCAVE (1975) and FELLOWS *et al.* (1981) emphasizing the differences between S-POM and particles collected in sediment traps.

Similar subsurface flux maxima were observed for T-RNA (Fig. 10) and T-ATP (Fig. 11). The use of the 335-μm Nitex screen was an effective means of eliminating most actively swimming zooplankton at the station, but we cannot determine the extent to which other particles may have been excluded. The mid-depth increases in downward flux of particle-associated

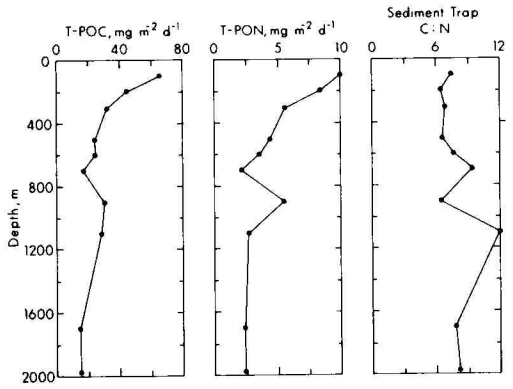


Fig. 9. Downward vertical flux of POC and PON, and sediment trap-collected C : N ratios for particulate materials collected during VERTEX I.

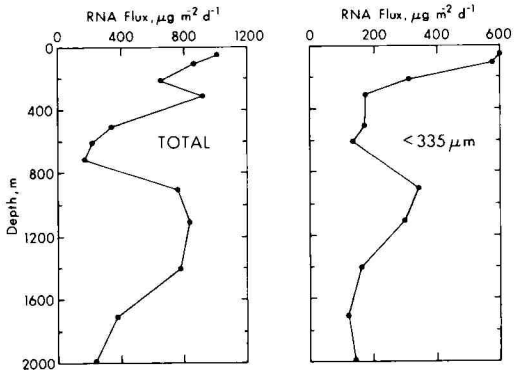


Fig. 10. Downward vertical flux of sediment trap-collected RNA (total and <335 μm fraction) during VERTEX I.

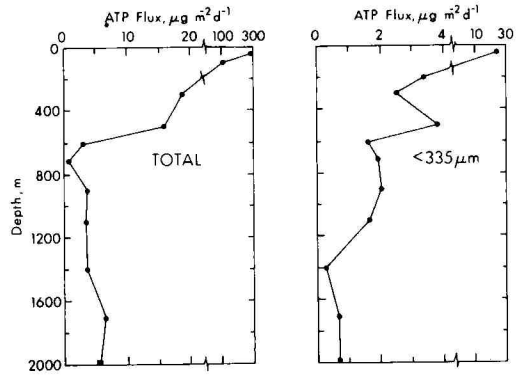


Fig. 11. Downward vertical flux of sediment trap-collected ATP (total and <335 μm fraction) during VERTEX I.

Table 1. Fecal pellet fluxes (total and by size and morphological classes) measured during VERTEX I. All data are expressed as numbers of pellets m^{-2} d^{-1}

Depth (m)	Elliptical pellets (mm) 0.05	0.10	0.15	Cylindrical pellets (mm) 0.05	0.10	0.15	Round pellets	Coiled pellets	Total pellet flux
50	406	348	0	4257	3135	348	1625	348	10469
100	23261	1567	58	2109	1567	813	3677	290	33343
200	46096	23241	116	1258	1974	697	7373	0	80755
300	26705	6192	619	1780	3057	406	3154	0	42883
500	21384	6289	813	1761	1761	252	2206	0	34465
600	31988	11088	658	2652	1819	135	948	0	49289
700	33653	24132	2283	2361	2574	677	2845	0	68757
900	48341	31543	2322	2109	1529	135	2632	0	88611
1100	42632	28679	812	1297	735	310	3213	0	77678
1400	19913	20281	464	774	813	542	948	0	43735
1700	14359	12907	987	406	735	232	697	0	30324
1950	6579	8399	522	464	851	232	213	0	17262

RNA and ATP add credence to the hypothesis of a subsurface injection or *in situ* production of macromolecules and viable microorganisms at intermediate oceanic depths.

Table 1 summarizes the downward vertical flux of various morphological and size classes of fecal pellets analyzed. The total flux of fecal pellets was high in the surface waters (0 to 200 m), decreased with increasing water depths to 500 to 600 m but displayed a distinct subsurface maximum (i.e., increased flux) between 600 and 1100 m, depending upon the size class selected. The data are qualitatively similar to those obtained by URRERE and KNAUER (1981), which suggest that this may be a general feature of the central California coastal region. The increased fecal pellet flux with increasing water depth between 600 and 1100 m was reflected in all morphological and size categories (except coiled pellets), but it was centered at a slightly different depth for each group (see boxes, Table 1). As each class of pellets is presumed to originate from a specific group of zooplankton we suggest that substantial metabolic activity associated with a diverse assemblage of zooplankton species is evident throughout the oxygen minimum zone (600 to 1100 m). The downward vertical flux of discarded larvacean houses also displayed a subsurface peak centered at 900 to 1400 m (Table 2). The number of larvacean house-associated fecal pellets (i.e., contained within the discarded houses) ranged from 10 to 80, with greater densities observed at 900 to 1400 m. Such pellet distributions and increased fluxes relative to depth further support the existence of subsurface zones of intense activity.

Estimates of in situ *MULTITRAP microbial production*

Two independent experiments were performed to estimate the rate of microbial production associated with the sediment trap materials. In the first, we compared MULTITRAP shipboard extracted T-ATP (i.e., total ATP determined in unpreserved sediment traps following recovery) and MULTITRAP *in situ* extracted T-ATP concentrations (Table 3). There are three possible outcomes of the comparison: (1) *in situ* T-ATP could equal the shipboard T-ATP, indicating either that no growth occurred *in situ* or that total microbial growth was

Table 2. Downward vertical flux of larvacean houses and associated fecal pellets

Depth (m)	Flux of larvacean houses (Nos m^{-2} d^{-1})	Flux of 'house-associated' fecal pellets (Nos m^{-2} d^{-1})
50	ND*	—
100	58	716
200	77	658
300	ND	—
500	77	1567
600	58	1393
700	19	174
900	116	2865
1100	194	2110
1400	174	2575
1700	97	1300
1950	19	1570

* No houses detected in subsample examined from this depth.

balanced by death; (2) shipboard T-ATP > *in situ* T-ATP, indicating that net growth occurred during the incubation period, presumably at the expense of the sedimenting organic matter; and (3) *in situ* T-ATP > shipboard T-ATP, indicating that death occurred during the incubation period.

One major disadvantage of the above experimental approach is the requirement for net microbial community growth, which makes it a less sensitive measure of microbial production than the more direct ^{3}H-adenine incorporation procedure to be discussed. For example, even though ATP levels may remain the same or even decrease (indicating zero net community growth), there may still be a substantial level of net growth and biosynthesis on an individual cell or sub-population basis (i.e., cryptic growth). Consequently, the accuracy and reliability of the analysis is greatest where net growth is positive and high (e.g., 700 m). Several interesting features were evident from the data. First, the greatest rate of growth was measured for particulate materials collected at 700 m, immediately above the region where we observed increased fluxes for T-POC, T-PON, T-RNA, T-ATP, fecal pellets, and larvacean houses (Figs 9 to 11, Tables 1 and 2). Second, the two deepest sediment traps (1700 and 1950 m) displayed post-incubation losses of ATP concentration (i.e., death), suggesting that the sedimenting organic materials were incapable of supporting net biomass accumulation (Table 3).

The second way to estimate *in situ* microbial production involved the use of sediment traps charged with a radioisotopic tracer. As the present study was the first to attempt such *in situ* measurements with sediment trap particles, we had to evaluate carefully the assumptions, design, and mechanics of the experiment. Table 4 summarizes data to evaluate the stability of ^{3}H-adenine during the experiment. It is apparent that on the average, 95% (excluding the 1950-m trap) of the initial radioactivity added was recovered following the 13.25-day deployment, indicating that losses from the dense solution by advection, diffusion, and flushing were negligible. The 95% recovery is a minimum value, because only the radioactivity in solution was measured (cell free extract as in KARL *et al.*, 1981), which would underestimate the total if any significant amount had been incorporated into macromolecules.

Table 5 summarizes the results of the *in situ* ^{3}H-adenine uptake experiment. Several important features can be observed in the experiment (Table 5): (1) the uptake and incorporation of exogenous ^{3}H-adenine into ^{3}H-ATP, ^{3}H-RNA, and ^{3}H-DNA were not significantly

Table 3. Comparison of ATP-biomass flux and in situ *carbon production based on two independent procedures for the collection and extraction of particle-associated microorganisms*

Depth (m)	Total ATP flux ($\mu g\ m^{-2}\ d^{-1}$) *In situ* procedure	Shipboard procedure	% change during incubation [(shipboard *in situ*)/*in situ* × 100]	Minimum estimate of μ† (d^{-1})	Estimated carbon production‡ (mg C $m^{-2}\ d^{-1}$)
50	301.9	—	—	—	—
100	104.2	104.5	+0.3	<0.001	0.08
200	—*	74.7	—	—	—
300	19.0	—	—	—	—
500	15.9	32.5	+104	0.078	4.15
600	3.08	6.8	+121	0.086	0.93
700	0.74	65.4	+8738	0.48	16.17
900	3.64	4.05	+11	0.012	0.10
1100	3.39	7.71	+127	0.089	1.08
1400	3.79	—	—	—	—
1700	6.41	1.08	−83	0	0
1950	5.24	1.72	−67	0	0

* Sample not successfully recovered.
† Calculation assumes exponential growth.
‡ Estimated from ΔATP (in mg $m^{-2}\ d^{-1}$) during incubation × 250.

Table 4. *Radiochemical mass balance during* in situ ^{3}H-*adenine experiment*

Sediment trap depth (m)	Launch Total radioactivity (nCi ml^{-1})	Recovery Total radioactivity (nCi ml^{-1})	R : L (×100%)	^3H_2O (nCi ml^{-1})
100	58.6	52.3	89.3	1.48
200	56.8	42.7	75.2	1.60
500	57.7	52.3	90.6	0.45
600	58.2	58.6	100.7	0.07
700	56.4	55.0	97.5	0.27
900	55.9	57.7	103.2	0.09
1100	56.8	56.4	99.3	0.03
1700	55.0	55.9	101.6	0.04
1950	55.5	—*	—	<0.01

* Part of contents lost during recovery.

different between the <153-μm size fraction and the total material collected in the MULTITRAPS, suggesting that the majority of metabolically active microorganisms were associated with particles < 153 μm; (2) the calculated ATP pool specific activities measured on the <153-μm size fractions were generally greater than the total MULTITRAP collections (up to 10 times greater), indicating the occasional presence of large viable (ATP-containing) organisms (presumably zooplankton; i.e., swimmers) or debilitated particle-associated microorganisms incapable of ^{3}H-adenine assimilation. Consequently, we restricted our rate calculations and production estimates to the <153-μm size fractions. The data are summarized in Table 6. (3) All activity parameters measured (^3H_2O production, % utilization of ^{3}H-adenine, ^{3}H-adenine incorporation into RNA and DNA, and *in situ* rates of RNA and DNA syntheses) were larger for the sample collected at 700 m, which corresponded to the dissolved oxygen minimum zone (Fig. 7) and the depth of the greatest difference between shipboard and *in situ* extracted ATP concentrations (Table 3).

DISCUSSION

There is currently controversy over the design and method of sediment trap deployment and over the accuracy and precision of the data obtained from field collections. In the present experiment, we elected to use a free-floating sediment trap array similar to the one described by KNAUER *et al.* (1979). There are several advantages to the design, but the most important consideration is the ability to deploy multiple, replicate traps at several depths. Without the relatively large number of traps we would not have detected the active zones reported. The use of multiple traps at each depth is amenable to *in situ* experimentation with collected materials and allows the use of otherwise incompatible chemical treatments for preservation of rapidly sinking materials. In a separate study (KNAUER *et al.*, 1984), using an identical sediment trap array at the same location, we determined the inter-trap collection variability (at a given depth) to average approximately 10% of the mean (n = 14). Consequently the precision of the Moss Landing sediment traps is probably good and the magnitude of the variations in the present study cannot be attributed to sampling variability. The accuracy of the sediment traps was previously evaluated using ^{210}Pb (KNAUER *et al.*, 1979).

Table 5. In situ *uptake of* ^3H-*adenine and incorporation into* ^3H_2O, ^3H-*ATP*, ^3H-*RNA and* ^3H-*DNA for MULTITRAP experiment*

Depth (m)*	Fraction analyzed	^3H_2O (nCi l^{-1})	ATP pool (pmol l^{-1})	ATP pool (nCi l^{-1})	ATP pool (pCi pmol^{-1})	^3H-RNA (nCi l^{-1})	^3H-DNA (nCi l^{-1})	DNA : RNA (×100%)	% ^3H-adenine used during incubation
100	total	1480	9102	174	19	14259 (±9%)†	926 (±14%)		30.7
	<153 μm		7180	187	26	15175 (±6%)	1160 (±21%)	7.7	
200	total	1596	6586	216	33	12771 (±4%)	1376 (±19%)		31.3
	<153 μm		9811	247	25	14038 (±5%)	1878 (±26%)	13.5	
500	total	455	2872	281	98	3893 (±1%)	890 (±23%)		10.2
	<153 μm		3037	325	107	4117 (±5%)	962 (±7%)	23.4	
600	total	68	565	18.8	33	678	75		1.4
	<153 μm		531	20.4	38	662	76	11.5	
700	total	267	5362	254	47	2077	1096		6.8
	<153 μm		2904	276	95	2199	1041	47.4	
900	total	85	330	4.2	13	105	13		0.4
	<153 μm		60	3.9	65	91	12	13.3	
1100	total	32	616	3.1	5	45.5	4.7		0.2
	<153 μm		43	2.0	47	45.5	6.0	13.2	
1700	total	35	128	1.5	12	3.8	2.4		0.1
	<153 μm		54	1.2	22	4.3	5.6	87.3	
1950	total	5	138	7.9	57	17.1	1.0		0.1
	<153 μm		135	5.8	43	22.2	1.9	9.7	

* MULTITRAPS at 50, 300, and 1400 m were not recovered.
† Values represent mean ± 1 s.d. from the mean based upon 3 to 8 samples; all other data in the table are means of duplicate determinations.

Table 6. In situ *rates of RNA and DNA synthesis and estimated carbon production from* ^{3}H-*adenine MULTITRAP experiment*

Depth (m)	Rates of nucleic acid synthesis (nmol A m^{-2} d^{-1}) RNA	DNA	Estimated carbon production* (mg C m^{-2} d^{-1})
100	12,455	935	62
200	12,067	1575	104
500	868	203	13.4
600	409	48	3.2
700	542	255	16.9
900	36	4.3	0.3
1100	23	3.1	0.2
1700	4.9	6.2	0.4
1950	13.5	1.2	0.08

* Estimated from measured rates of DNA synthesis by assuming: dA = 25 mol% of DNA synthesized and C : DNA ratio = 50.

Our data confirm the results of FELLOWS *et al.* (1981) for an elevated biomass (ATP) of microorganisms associated with rapidly sinking particles and an increased downward flux of biomass and total organic carbon (KNAUER and MARTIN, 1981) beneath the oxygen minimum zone. Furthermore, we demonstrate for the first time that the particle-associated organisms are capable of rapid growth and cell division under *in situ* conditions. The existence of intermediate depth layers of dense metabolically active microbial communities might be expected to have a profound influence on the distribution of non-conservative chemical properties of seawater, on the diagenesis and decomposition of sedimenting organic matter, and on the trophic organization of mesopelagic and deep-sea communities.

It is important that a subsurface layer of active microbial growth and production may be sufficiently large to affect the downward vertical flux of several important and independent measures of organic matter. For example, the downward vertical flux of C, N, RNA, and ATP increased by 100, 164, 363, and 414%, respectively, from the 700 to the 900-m traps (Figs 9 to 11). Despite such elevated *in situ* metabolic activity and growth, there were no detectable depth-related increases in the biomass or productivities of suspended particles collected in Niskin bottles within the same depth interval (Fig. 7). The results confirm that reliance upon bottle collections to define or elucidate the chemical and microbiological properties of particulate matter in the ocean may be misleading.

Utilizable carbon is generally considered to limit both the biomass and metabolic activity of heterotrophic bacteria in the ocean. Consequently, habitats or environments having high fluxes of organic carbon would be expected to exhibit an increased biomass of microorganisms, an elevated rate of community metabolism, or both. To detect such zones in the field, we measured the *in situ* growth and production of microbial cells associated with sediment trap particles by two independent methods. The first was the shipboard vs *in situ* T-ATP experiment. The experiment was equivalent to conducting a microbiological titration of available (labile) carbon and energy, using increases in microbial biomass (i.e., T-ATP) as the metric. The data (Table 3) indicate that the greatest increase in microbial biomass after incubation was at 700 m. The ATP (biomass) associated with the particulate materials entering the 700-m trap was low (as indicated by the *in situ* extracted ATP concentration), but the growth potential was very high (as indicated by the shipboard extracted ATP concentration).

Table 7. Summary of mid-depth downward vertical flux maxima

Station location	Depth of increased flux (m)	Parameter(s) measured	Reference
Sargasso Sea (31°33′N, 55°55′W)	976–3694	Silicates	HONJO (1980)
Demerara Abyssal Plain (13°30′N, 54°00′W)	>389	Silicates	HONJO (1980)
Demerara Abyssal Plain (13°30′N, 54°00′W)	>389	Mn, Ti, V, Sc, La, Co, Si, Al, Fe, K, ^{230}Th, ^{232}Th, ^{210}Pb, clay	BREWER *et al.* (1980)
Demerara Abyssal Plain (13°30′N, 54°00′W)	389–988	Lipid : organic C ratio, free sterols, sterylesters, triacylglycerols	WAKEHAM *et al.* (1980)
Demerara Abyssal Plain (13°30′N, 54°00′W)	389–988	Free sterols (<1 mm), cholesterols (<1 mm)	GAGOSIAN *et al.* (1982)
Panama Basin (5°21′N, 81°53′W)	2265–2869	Total mass flux, organic carbon, nitrogen, and silica	HONJO *et al.* (1982)
Central North Pacific Ocean (18°44′N, 156°50′W)	600–900	ATP	D. KARL and C. LORENZEN (unpublished data)
Central North Pacific Ocean (15°21′N, 151°29′W)	978–2778	Total mass flux, organic carbon, nitrogen, and silica	HONJO *et al.* (1982)
Central North Pacific Ocean (15°21′N, 151°29′W)	978–2778	Total mass flux, carbonates, silicates, organic carbon, nitrogen, hydrogen, and oxygen	HONJO (1980)
Northeast Pacific Ocean (33°50′N, 123°00′W)	750–1500	Organic carbon and nitrogen	KNAUER and MARTIN (1981)
Northeast Pacific Ocean (36°07′N, 122°47′W)	385–1100	ATP	FELLOWS *et al.* (1981)
Northeast Pacific Ocean (33°50′N, 123°00′W)	500–1500	Fecal pellets (total numbers and various size classes)	URRERE and KNAUER (1981)
Northeast Pacific Ocean (35°45′N, 123°45′W)	250–750	$^{239+240}$Pu, ^{241}Am	FOWLER *et al.* (1983)
Northeast Pacific Ocean (35°45′N, 123°45′W)	50–1100	Al	K. BRULAND (unpublished data)
Northeast Pacific Ocean (35°45′N, 123°45′W)	700–1100	Organic carbon, nitrogen, ATP, RNA, fecal pellets (total numbers and various individual size classes), larvacean houses	This study

We suggest that the data are indirect evidence for the input of fresh organic material (or some other utilizable energy source) that has either been produced immediately above the 700-m depth or has short-circuited the normal downward vertical flux pathway. Several interrelated questions must be addressed: (1) is the observed increased flux of organic matter at 900 m the result of *in situ* biological processes below 700 m or is it the result of horizontal advection (i.e., lateral transport along isopycnals)?; (2) what is the source (or are the sources) of carbon or energy required to support such activity and biomass production?; (3) is this a general feature of the mesopelagic realm or does the station represent an anomalous oceanic condition?; and finally (4) what relationships, if any, are there between the increased flux of organic matter at depth and the permanent and ubiquitous intermediate-depth oxygen minimum?

Several sediment trap experiments have also indicated subsurface maxima in the downward vertical fluxes of numerous geochemical and biological variables (Table 7). Many of the data have been interpreted as direct evidence for the horizontal advection of particles (BREWER *et al.*, 1980). The distribution of Al in the suspended and MULTITRAP particles during VERTEX I is evidence for lateral transport of materials from the California coast and was the only variable in the study in which we observed a correspondence between bottle and sediment trap collections (Fig. 12). The Al flux increased from a value of 0.3 mg m^{-2} d^{-1} in the surface waters to >4 mg m^{-2} d^{-1} at 1100 m. Although lateral transport might explain the increased T-POC, T-PON, T-RNA, T-ATP, fecal pellets, and larvacean house fluxes between 700 and 900 m, we are convinced that the biochemical features are the result of *in situ* rather than advective processes. The downward flux of Al exhibited a linear increase with depth between 50 and 1100 m, whereas the fluxes of C, N, RNA, and ATP decreased between 50 and 700 m and then increased at greater depths. Significant but negative correlations were observed for plots of T-POC flux vs T-Al flux ($r = -0.788$) and T-ATP flux vs T-Al flux

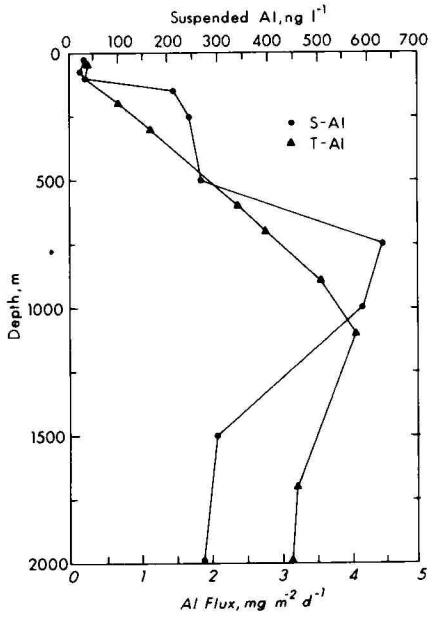


Fig. 12. Vertical distribution of suspended Al (S-Al) and flux of sediment trap-collected Al (T-Al) at the VERTEX I station.

($r = -0.803$). We have also demonstrated by two independent direct *in situ* growth rate and carbon production experiments that the particulate organic matter which entered the 700-m trap was fresh in the sense that it contained a low biomass of microorganisms but had a high potential for supporting further production of cells (Table 3). If the organic matter necessary to support the increased flux below 700 m was transported horizontally from a more productive coastal region, it should be in a more advanced stage of decomposition and would be expected to have a high biomass of microbes and a relatively low potential for supporting additional growth. Furthermore, large particles (e.g., fecal pellets) with sinking rates estimated to be >50 m d^{-1} would have already been removed from the upper 700 m of the water column during the time required to carry surface waters to the station. Lateral transport mechanisms do not appear to be directly responsible for the biological activity and increased fluxes of T-POC, T-PON, R-RNA, T-ATP, and fecal pellets near the oxygen minimum.

A second mechanism that might explain the observed fluxes involves a relaxation of upwelling, followed by a subsequent injection of surface-derived particulate matter into the mesopelagic zone. PACKARD *et al.* (1977) proposed such a model to account for subsurface peaks in suspended ETS activity at intermediate oceanic depths. In our present study we were unable to resolve any subsurface peaks in S-POC, S-PON, S-RNA, or S-ATP over the 700 to 900-m depth interval (Figs 3 to 5), thus it seems unlikely that we observed temporally uncoupled patches of organic matter originating at the surface. Furthermore, the material captured in the 700 and 900-m sediment traps bears little, if any, microscopic similarity to particles collected in surface waters. The interpretation is also supported in a previous study (URRERE and Knauer, 1981), which suggested that fecal pellets collected between 500 and 900 m were produced *in situ* (Tables 1 and 2). Finally, such a mechanism would not explain the low T-ATP, low C : N ratios, and high growth potential of the T-POC collected at 700 m. We conclude that the organic C, N, RNA, and ATP required to sustain the observed flux distributions must have been produced *in situ* between 700 and 900 m.

The source(s) of carbon and energy required to sustain such a substantial level of microbial biosynthesis is important for an understanding of the organic carbon cycle in the sea. By analogy to euphotic zone phytoplankton production we can apply the concept of new carbon production (DUGDALE and GOERING, 1967; EPPLEY and PETERSON, 1979) in defining subeuphotic zone new particulate organic carbon production (NPP) as a value equivalent to the increased downward flux of organic carbon. Thus, NPP between 700 and 900 m is approximately 15 mg C m^{-2} d^{-1}, judging from the T-POC data. If we assume that the production is via heterotrophic growth of microorganisms with a sustained assimilation efficiency of 20%, the NPP would require a minimum flux of 75 mg C m^{-2} d^{-1}, equivalent to 13% of the integrated euphotic zone primary production (Fig. 6). As the measured T-POC flux at 700 m is <20 mg C m^{-2} d^{-1}, it is unlikely that the production of microbial carbon within the oxygen minimum layer can be supported by a process that involves direct sinking of organic carbon out of the euphotic zone.

VINOGRADOV (1962) proposed an hypothesis of food transfer in the mesopelagic zone by overlapping migrations of zooplankton. From Table 1 we know that there is an input of fresh zooplankton feces near the oxygen minimum layer; however, we cannot determine whether it is derived from migrating or indigenous populations. Only a contribution from the former would help to resolve the present carbon budget enigma. If migrating zooplankton and micronekton are important in short circuiting vertical carbon transport, then we may have to re-evaluate the model presented by SUESS (1980) relating surface productivity, carbon flux, and depth. Microscopic examinations of fecal pellets collected at intermediate depths have

generally not supported the hypothesis that the organisms were feeding in the surface waters (HARDING, 1974; URRERE and KNAUER, 1981). Furthermore, if POC derived from fecal pellets were the primary source of carbon for microbial production, we would have expected a peak in T-POC and T-PON flux at 700 m, because the microbial activity and production were maximal for materials collected in the 700-m trap. We conclude that the *in situ* microbial growth and biosynthesis we measured in the sediment traps cannot be derived from strictly heterotrophic microorganisms. The possibility of high rates of chemolithotrophic growth and carbon production in the pelagic realm of the ocean is intriguing but speculative. However, if CO_2 reduction were to occur *in situ* it would have a profound influence on marine organic carbon cycle models. The most likely energy sources necessary to drive such chemolithotrophic processes are NH_4^+ and HS^-, which might be produced within anaerobic microzones.

Carbon production estimates based on the results of the shipboard vs *in situ* extracted T-ATP experiment indicate a sustained production rate of 16.2 mg C m^{-2} d^{-1} for the particulate materials collected at 700 m (Table 1), assuming a carbon : ATP ratio of 250 (KARL, 1980). Based on changes in ATP concentrations at this depth, a minimum community doubling time of approximately 48 h is derived (Table 3), assuming sustained exponential growth. For comparison, carbon production can also be estimated from the *in situ* ^{3}H-adenine experiment. The rates of DNA synthesis can be extrapolated to carbon production by assuming dAMP is 25 mol% of DNA and a carbon : DNA ratio of 50 (HOLM-HANSEN, 1969). Accordingly, an *in situ* production rate of 16.9 mg C m^{-2} d^{-1} is derived (Table 6), which is in agreement with the estimate from the independent *in situ* vs shipboard ATP experiment (Table 1). The rate of new particulate carbon production (16 to 17 mg C m^{-2} d^{-1}) measured for materials intercepted at 700 m is sufficient to account for the increased carbon flux measured for intermediate depths (ΔC flux between 700 to 900 m is 15.5 mg C m^{-2} d^{-1}, Fig. 9). The observation that the increased T-POC, T-PON, T-RNA, and T-ATP fluxes occurred at 900 m rather than at 700 m is consistent with the *in situ* production data, if we assume that growth and sinking occur simultaneously. The fact that little, if any, growth potential remained for the materials collected at 900 m (Tables 3, 5, and 6) suggests that cell growth and carbon production are rapid and complete, being confined to a narrow part of the water column (i.e., within a 200-m zone). This also lends support to the suggestion that the importance of lateral transport of inorganic particles may not be directly coupled to processes involving organic materials because the maximum T-Al flux occurred at 1100 m.

The co-occurrence of a subsurface level of high biological activity and the oxygen minimum zone raises questions concerning the role of *in situ* sediment trap-associated microbiological processes in producing and maintaining the feature. Most oxygen minimum models assume that there is an exponential decrease in microbial metabolism (i.e., oxygen consumption) with increasing water depth. Our data indicate that this is not the case. Microbial activity, growth, and cell division are all intensified on sinking particles collected within the oxygen minimum layer, suggesting that *in situ* utilization of oxygen may be more substantial than previously assumed. WYRTKI (1962) concluded that oxygen minima are ultimately formed biologically but are positioned advectively. The sediment trap experiments suggest that both the origin and position may be the consequence of *in situ* biological activity. One vital datum that is lacking is a direct measure of the rate of *in situ* oxygen consumption.

We have demonstrated that the assessment of total microbial biomass and metabolic activity from water bottle collections may not be valid under all environmental conditions, due to the overwhelming influence of sinking particles (relative to suspended particles) on total

water column metabolism. Estimates of microbial activity and production that rely upon measurements of the steady-state concentrations of soluble constituents (e.g., O_2, CO_2, inorganic and organic nutrients, light, stable isotopes of C, O, and H) although indirect, might yield a more accurate assessment of *in situ* biochemical processes than is generally derived with conventional bottle sampling of suspended particles.

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