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VERTICAL FLUXES OF BIOGENIC PARTICLES AND ASSOCIATED BIOTA IN THE EASTERN NORTH PACIFIC: IMPLICATIONS FOR BIOGEOCHEMICAL CYCLING AND PRODUCTIVITY

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Abstract. Previously published data on vertical fluxes of particulate carbon (PC), nitrogen (PN), organisms (MICRO), and extracted adenosine triphosphate (ATP) into screened sediment traps (335 μm) from the VERTEX 5 and ADIOS I programs are reexamined as they relate to biogeochemical cycling and oceanic productivity. The four stations discussed represent an oligotrophic to mesotrophic gradient in total primary production (P_T), ranging from 245 to 1141 mg C m^{-2} d^{-1} and a gradient in PC flux from the euphotic zone, ranging from 12 to 164 mg C m^{-2} d^{-1} for particles <335 μm in diameter. Vertical fluxes of PC, PN, MICRO, and ATP decreased as negative power functions of depth with significantly higher depth-dependent losses for ATP fluxes. The flux of intact biota (free, particle-associated, and some active "swimmers," measured microscopically and by extracted ATP) decreased rapidly in the upper 200 m, contributing as much as 52.4% at the most productive station and as little as 1.6% to the flux of PC at oligotrophic stations, remaining relatively constant or increasing slightly (to 3.4 - 9.6% PC flux) between 200 and 2000 m. Multiple regression analyses, expressing fluxes as functions of depth and P_T or new production, P_N, demonstrated that MICRO and ATP fluxes were more dependent on P_T, P_N, and depth than bulk PC or PN fluxes. The present analysis illustrates that while sinking particulate organic matter (POM) undergoes rapid attrition in the upper water column, the fluxes of sedimenting biota decrease at even higher rates. Findings support the hypothesis that in oceanic waters, POM sinking from the euphotic zone rapidly becomes a poor habitat for associated microbes, and mechanisms other than remineralization by attached microbes must be invoked to explain observed fluxes and attrition rates. This study also supports the hypothesis that the vertical flux of intact organisms is a more sensitive and less ambiguous record of upper ocean processes than bulk flux measurements of total mass, PC, or PN. Therefore time-resolved measurement of the flux of biota may be useful in estimating P_T and P_N in the overlying waters.

INTRODUCTION

Biogenic particulate organic matter (POM) has a central role in the oceanic carbon cycle and is integral in cycling lithogenic and anthropogenic materials from source to sink through the ocean's interior by sorption and transport processes. Biogenic particles in the water column, which include marine snow, fecal material, feeding structures, carcasses, and molts, are thought to be foci of biomass (microbial and metazoan), metabolic activity (autotrophic and heterotrophic), and biologically mediat-

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ed chemical transformations [Silver et al., 1978; Shanks and Trent, 1979; Caron et al., 1982, 1986, Alldredge and Silver, 1988; Davoll and Youngbluth, 1990]. The importance of POM is illustrated by Goldman's [1984] revised model of planktonic trophodynamics which includes POM as a central locus of chemical and biological exchanges. Knauer et al. [1982], for example, observed that autotrophs associated with marine snow and other biogenic particles could account for 11 to 58% of total primary production in nearshore eastern North Pacific waters. In addition to sites of intensified primary production, Herndl [1988] observed that bacterial growth rates in treatments amended with marine snow were 3 times higher than those of unamended seawater. The oceanographic implications of these studies are that: (1) POM provides a nutrient-replete microenvironment facilitating active microbial growth and biogeochemical cycling in the upper ocean, and (2) microbial populations should proliferate as biogenic particles age until the particles become refractory.

Little direct information about the formation, diagenesis, and microbial ecology of POM in the open ocean is available, although data from a variety of other environments and from laboratory studies for phytoplankton debris and other source materials exist [e.g., Caron et al., 1982, 1986; Alldredge and Silver, 1988; Biddanda and Pomeroy, 1988; Herndl, 1988; Alldredge and Gotschalk, 1989]. Several investigators, such as Shanks and Trent [1979], have observed intensified remineralization in association with microbe-laden marine snow particles. Taylor et al. [1986] observed in situ production of ammonium in sediment traps in the upper 225 m at a neritic station, VERTEX 5-A, Vertical Transport and Exchange Experiment, (VX-1 in the present study). However, no detectable production was evident at greater depths nor at any depth at offshore stations (V5-B and V5-C; VX-2 and VX-4 in the present study). In the VERTEX 5 samples, remineralization accounted for no statistically significant reduction of particulate carbon (PC) or nitrogen (PN) compared with preserved material [Karl et al., 1988].

The preceding evidence leads to the suggestion that while sinking POM in surface waters may be an active microbial habitat, that which sinks from the euphotic zone is not readily remineralized by attached microbes. Examination of POM attrition in the open ocean indicates that POM remains somewhat labile on the order of 3.8 - 7.6 days after leaving the euphotic zone, assuming euphotic zone depth of 120 m, d flux / d Z approaching 0 at 500 m, and sinking rates of 50 - 100 m d^{-1}. The contention that sinking POM is poorly utilized by associated microbes is supported by the following observations for stations in the eastern North Pacific Ocean: (1) the flux of particle-associated organisms diminishes as a negative power function of depth, (2) in unpoisoned traps, living biomass (measured microscopically and by extracted adenosine triphosphate (ATP)) decreases rapidly at all depths as particles age in situ, and (3) although there is measurable nucleic acid synthesis in unpoisoned traps incubated in situ, most assimilated ^{3}H-adenine is respired producing ^3H_2O [Taylor et al., 1986; Karl et al., 1988; Silver and Gowing, 1991]. How then can we resolve the apparent paradox of POM attrition and the suitability of POM as a habitat for open ocean microbes? Review of the literature suggests to us that direct remineralization of sinking POM by attached microorganisms does not dominate decompositional processes below the euphotic zone and that there are fundamental differences between suspended and sinking POM that account for the observations described above. In the ensuing discussion, the term "decomposition" is used in a general, collective sense and includes the processes of physical disaggregation, abiotic solubilization, enzymatic dissolution to labile solutes, and heterotrophic remineralization, which all may contribute to observed attrition rates.

The majority of POM in the water column is believed to be suspended particles and consists of fine and/or neutrally buoyant particles (reviewed by McCave [1984]), whereas sinking POM has been attributed to large, rare particles composed mostly of crustacean feces and macroaggregates (McCave [1984], reviewed by Fowler and Knauer [1986]). Contrary to these earlier descriptions, most of the biogenic flux in offshore waters is not attributable to large, discrete, rapidly sinking crustacean fecal pellets. In fact, $\geq$ 85% of the PC flux in the upper 2000 m of mesotrophic to oligotrophic regions in the eastern North Pacific appears to be amorphous macroaggregates, nondiscrete feces produced by gelatinous zooplankton, molts, as well as intact, free, and particle-associated organisms [Taylor et al., 1986; Asper, 1987; Pilskaln and Honjo, 1987; Taylor, 1989; Silver and Gowing, 1991]. Asper [1987] observed that most of the particles arriving at 380 m in the Panama Basin were large aggregates and not discrete fecal pellets. Similarly, Pilskaln and Honjo [1987] reported that discrete fecal pellets accounted for only 1 - 10% of the PC flux in the upper 5000 m at three oceanographically distinct stations. Practically speaking, PC or biogenic particle flux is usually estimated from material collected in sediment traps and captured on filters and includes debris and intact organisms [Silver and Gowing, 1991]. Therefore PC flux measurements reflect all organic particles, including dead, dying, and viable

biota associated with sinking particles and free-living, i.e., the biotic flux, as well as their by-products.

Not only does the chemical composition of suspended and sinking POM differ in gross C/N ratios, but the relative contributions of specific classes of compounds vary between these two categories of biogenic particles [Fellows et al., 1981; Karl and Knauer, 1984; Wakeham, 1987; Wakeham and Canuel, 1988; Wakeham et al., 1984]. It seems likely that suspended and sinking POM represent a continuum in which young, neutrally buoyant particles are more amenable to biological utilization and that as they age and are transformed, they become more refractory and dense and thereby become part of the sinking flux, which is also composed of young, dense material, such as fecal material, carcasses, and molts. It also must be remembered that rapid delivery of pulses of fresh, even viable, phytoplankton cells to deep sea sediments commonly occurs resulting from blooms of large dense cells or from coagulation of small cells [e.g., Billett et al., 1983; Alldredge and Gotschalk, 1989]. The diverse sources and composition of sinking POM in oceanic provinces confound simple models of vertical transport and decomposition.

Spatial and temporal variations in rates and composition of biogenic fluxes in the upper ocean have been observed in all oceanic provinces examined [e.g., Eppley et al., 1983; Wakeham et al., 1984; Taylor et al., 1986; Laws et al., 1989; Taylor, 1989; Silver and Gowing, 1991]. Biogenic fluxes vary as functions of primary production [e.g., Suess, 1980; Deuser et al., 1981; Betzer et al., 1984; Lee and Cronin, 1984; Lampitt, 1985; Pace et al., 1987], nutrient import [Eppley and Peterson, 1979], and plankton community structure [Michaels and Silver, 1988; Taylor, 1989]. As was demonstrated by Taylor [1989], the biotic flux out of the euphotic zone can provide information on planktonic processes in the overlying waters. In spite of all the nuances and subtleties inherent in the composition of the biotic components [see Taylor, 1989; Silver and Gowing, 1991] and the apparent short-lived fitness of sinking POM as a microbial habitat, several coherent trends, relating biotic flux to biogenic flux, and relating both to total and new production are apparent. Evidence presented below for four stations in the eastern and central North Pacific and six particle trap collections, using internally consistent techniques, demonstrates that the flux of organisms actually has a greater dependence on production and depth than the fluxes of PC or PN. The relationships of the biotic and biogenic fluxes are discussed in the contexts of biogeochemical cycling of bioelements and upper ocean productivity. We suggest that recent data and the observed relationships necessitate reevaluation of existing models of oceanic decompositional processes. Furthermore, we suggest that the functional responses derived in this study, if sufficiently robust, may be exploited to monitor time-resolved primary productivity indirectly with automated sediment traps.

MATERIALS AND METHODS

Sample Collection

Samples were collected using free-floating particle interceptor traps (Multitraps [Knauer et al., 1979]) deployed at one mesotrophic coastal and two oligotrophic offshore stations in the eastern North Pacific (VX-1 = 35°40' N, 123°50' W - 13 day deployment; VX-2 = 35° N, 128°W - 22 days; VX-4 = 33° N, 139° W - 22 days) during the VERTEX 5 research program (June 1984; see Martin et al. [1987] for details). Collections were also obtained from a single oligotrophic station in the central North Pacific north of Hawaii (26° N, 155° W), during the ADIOS I research program (Asian Dust Input to the Ocean System) for three consecutive deployments: AD-A, March 24-31, 1986; AD-B, March 31 to April 12, 1986; AD-C, April 14-17, 1986. Specific details of the trap deployments, experimental designs, and analyses are given by Taylor et al. [1986], Laws et al. [1989], and Taylor [1989]. During VERTEX 5, traps were placed at varying depths, depending on hydrography, from 50 to 2000 m. During the ADIOS I cruise, traps were placed at 30, 120, and 200 m for all three deployments. Data from 30-m traps were used only in analyses of biotic flux composition and not incorporated into regression analyses of flux from the euphotic zone. All traps contained 335-μm Nitex screens between the baffles and the top of the collection tube to exclude "swimmers" [Karl and Knauer, 1989] and were filled with high-density salt solutions whose composition varied depending upon the analysis performed (described below).

Flux Measurements

PC and PN were collected in traps filled with sterile, high-density salt solutions without preservative and analyzed as previously described by Karl and Knauer [1984] and Laws et al. [1989]. Data for PC and PN fluxes for VERTEX 5 were obtained from Karl et al. [1988] and D. M. Karl (unpublished data, 1984). Estimates of primary production, new production, and euphotic zone depths for VERTEX 5 were derived from Martin et al. [1987]. For

ADIOS I, data for PC and PN fluxes, primary production, new production, and euphotic zone depths were obtained from Laws et al. [1989].

Samples for microscopical analyses were collected in traps which contained 2% glutaraldehyde or 1% formalin in high-density salt solutions [Taylor et al., 1986; Taylor, 1989]. Upon recovery, traps were emptied into 2.5-L bottles, and gently agitated, and subsamples were stored for subsequent analyses. In the laboratory, subsamples were enumerated to obtain carbon estimates for microbes including bacteria, zooflagellates, ciliates, phytoplankton, and sarcodines, as well as dormant cysts, zooplankton, and fecal material, using epifluorescence and inverted light microscopy. Details of these analyses are given by Taylor et al. [1986] and Taylor [1989]. Linear dimensions and volume estimates were extrapolated to biomass using the following carbon:volume relationships (in grams C per cubic micron): bacteria, 2.2×10^{-13} [Bratbak and Dundas, 1984]; zooflagellates, ciliates, cysts, dinoflagellates, 8.8×10^{-14} [Heinbokel, 1978]; fecal pellets, 2.68×10^{-14} [Urrere and Knauer, 1981]; diatoms, coccolithophorids, silicoflagellates, 2.5×10^{-14} [Sicko-Goad et al., 1984]; copepods, 8.1×10^{-14} [J. Finn, unpublished data, 1988]. Only intact individuals containing visible cytoplasm were included in the biomass estimates and were considered part of the biotic flux. The terms MICRO and NANO fluxes are defined as the carbon content of all intact organisms collected in screened traps and enumerated and the bacterial-zooflagellate fraction, respectively.

As a metric of total living biomass associated with the passive flux, sedimenting ATP (in situ ATP) was measured in traps that had been precharged with H_3PO_4 (0.5 moles + 88 g NaCl in 1-L dd-H_2O). As organisms entered the acid-salt high-density solution, their cellular ATP was extracted and preserved [Fellows et al., 1981]. After recovery, the cell extracts were processed for total ATP as described by Fellows et al. [1981]. These authors report that this technique yields complete ATP extraction from particles in traps and no measurable loss of extracted ATP within the traps or to the water overlying the density gradient solution.

Statistics

Least squares regressions were run on all data and on $\log_{10}$ transforms of the data to obtain the best fit [Sokal and Rohlf, 1981]. Analysis of covariance (ANCOVA) was employed to test for differences between least squares regression coefficients [Sokal and Rohlf, 1981]. Multiple regression analyses were performed on the $\log_{10}$ transforms of one dependent and two "independent" variables according to Sokal and Rohlf [1981]. Coefficients for all regressions were significant at the 99.9% level ($P < 0.001$), unless otherwise noted.

RESULTS

Depth-Dependent Attrition

Typically, PC flux below the base of the euphotic zone decreases as a negative power function of depth [Martin et al., 1987]. Expressed as percent maximum flux, carbon fluxes of particles < 335 μm, F_{PC}, in all collections, except VX-1, are described by the depth-dependent function, $F_{PC} = B_0 Z^{B1}$, (Figure 1a). PN flux is described equally well in this manner (Figure 1b) and the slopes are not significantly ($P < 0.50$ by ANCOVA) different ($B_1 = -0.590$ and -0.618 for F_{PC} and F_{PN}, respectively). MICRO fluxes (biotic fluxes estimated microscopically) display a trend not significantly ($P < 0.50$ by ANCOVA) different from PC or PN fluxes ($B_1 = -0.543$; Figure 1c). ATP fluxes, however, show a significantly greater depth-dependent decrease than PC, PN, or MICRO fluxes, $B_1 = -1.481$ ($P << 0.001$ for pairwise comparisons of ATP fluxes with PC, PN, and MICRO fluxes by ANCOVA). In all cases, fluxes at the most productive coastal station, VX-1, diminished more rapidly in the upper 500 m than in the other five collections, and the changes in flux with depth approached zero in the underlying 1500 m, indicating slow decomposition, rapid sinking rates, or horizontal advection from the site below the 500-m horizon.

Biotic Contribution to Biogenic Flux

Although biotic and biogenic fluxes decrease as negative power functions of depth, the relative contribution of biomass to the PC fluxes (as percent total PC flux) displays complex behavior (Figure 2). In surface traps (30 - 50 m), biota contribute as much as 52.4% to the total PC flux measured in screened traps, decreasing rapidly in the upper 200 m to as little as 1.6% and remaining relatively constant or slightly increasing to 3.4 - 9.6% over the next 1800 m (Figures 2a & 2b). Similar trends are observed for data obtained either by microscopical survey (Figure 2a) or by in situ ATP collections (Figure 2b). Although the carbon contribution of the ATP collections are based on the assumption of a constant biomass C:ATP conversion factor (derived below) and the percent contribution to the PC flux will depend on the value used (140 in this analysis), coherence in the trends observed microscopically and chemically strengthens our interpretations. The biotic contribution to PN flux in this data set is nearly indistin-

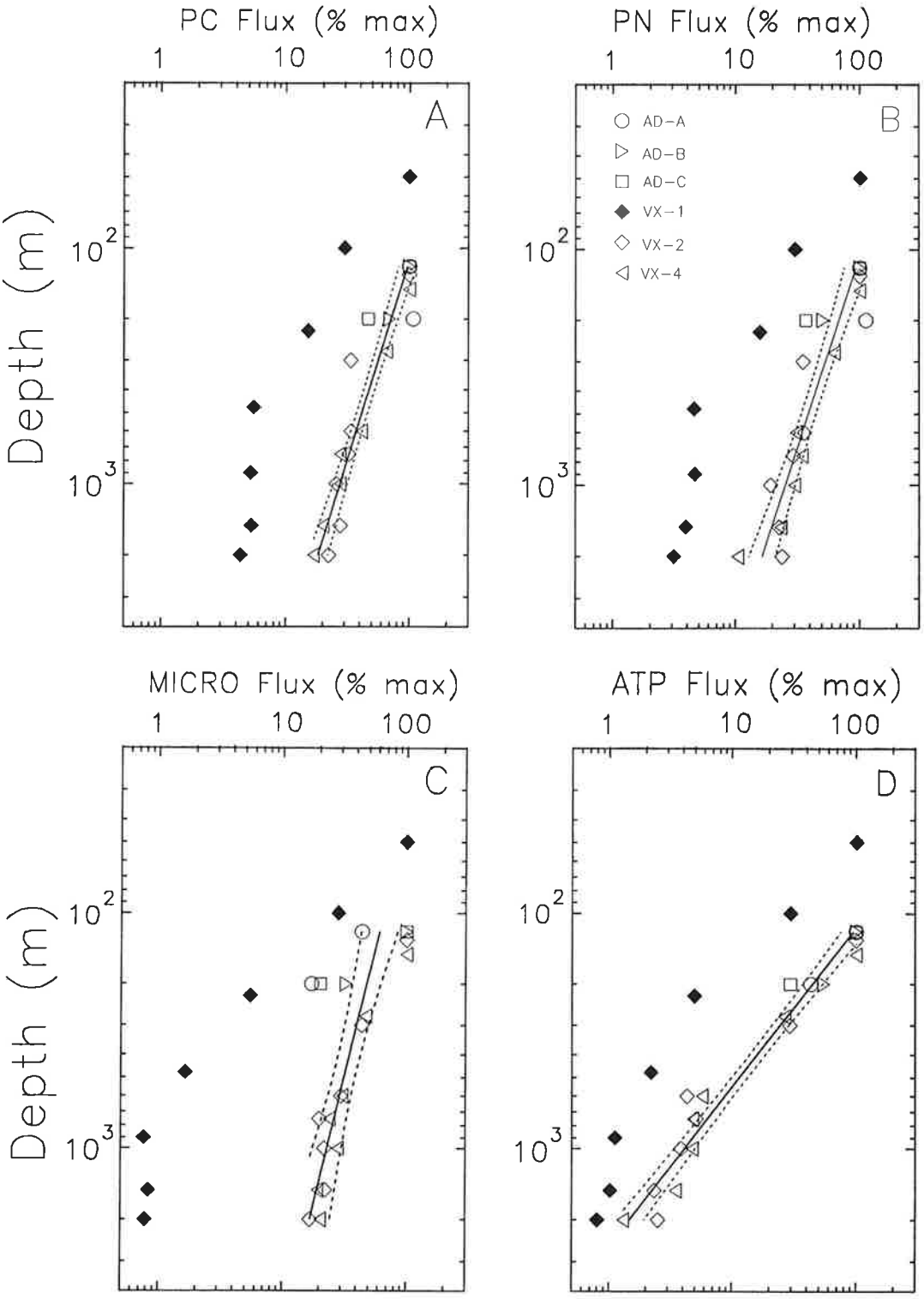


Fig. 1. Fluxes, F_X, of material entering screened sediment traps (335 μm) expressed as percent of maximum flux, corresponding to that measured at the base of the euphotic zone, as functions of depth for (a) particulate carbon, $F_{PC} = 1629\ Z^{-0.590}$, $r^2 = 0.893$, (b) particulate nitrogen, $F_{PN} = 1795\ Z^{-0.618}$, $r^2 = 0.834$, (c) all organisms <335 μm, $F_{MICRO} = 986\ Z^{-0.543}$, $r^2 = 0.718$, and (d) adenosine triphosphate extracted in situ, $F_{ATP} = 113763\ Z^{-1.481}$, $r^2 = 0.961$. All least squares regressions exclude station VX-1, are presented with 95% confidence intervals, and are significant at the $P < 0.001$ level for $n = 20$. Symbols identified in Figure 1b apply to all four graphs.

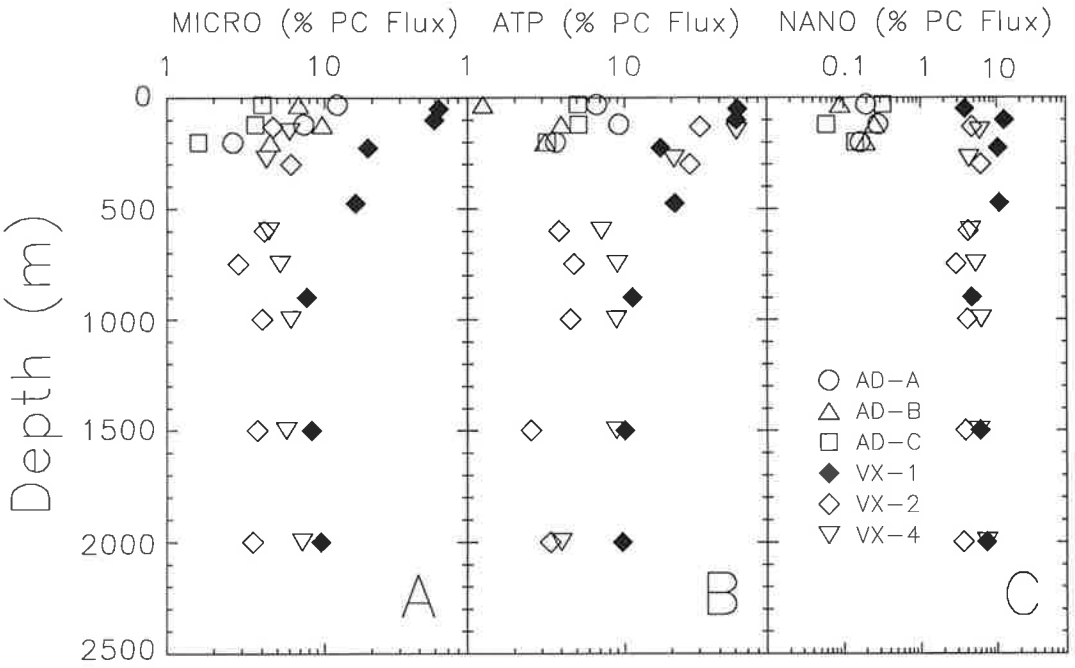


Fig. 2. Depth profiles of fluxes of (a) all organisms < 335 μm, MICRO, (b) ATP extracted in situ from < 335 μm particles, and (c) bacteria and zooflagellates, NANO, expressed as percent of bulk PC flux. A C/ATP conversion factor of 140 is assumed for ATP flux data (see text), and carbon to volume conversion factors for microscopical determination of MICRO and NANO biomass are presented in the Materials and Methods section. Symbols identified in Figure 2c apply to all three graphs.

guishable from that to PC flux, with biota contributing 2.8 to 45.4% to the total PN flux overall (assuming living C/N = 7.1 g/g [Laws et al., 1989]) and a slightly higher contribution at 2000 m (3.5 - 11.6%). The source of the observed complex behavior of these proportions is illustrated by comparing the behavior of the NANO (bacteria and zooflagellates) fluxes alone (Figure 2c) to total biotic flux (Figures 2a and 2b). Although the NANO fraction in the ADIOS I samples apparently contributed less to the PC and PN fluxes than that in the VERTEX 5 samples, small, monotonic increases in the proportions were observed with depth for VX-1 and VX-4. Our microscopic survey confirms that the decreasing biotic contribution observed in the surface waters results from losses of autotrophic and higher trophic level components and the apparent increased proportion with depth is attributable to the relatively constant contribution of lower trophic levels and to attrition of POM.

Dependence of Fluxes on Production

In the current data set, we observed reasonably good correlation of PC and PN fluxes from the base of the euphotic zone (50 - 150 m depending on station) with integrated P_T (Figure 3a; $r^2 = 0.771$ for PC flux; $r^2 = 0.864$ for PN flux, PN flux = $0.63 \times 10^{-4} P_T^{1.887}$, data not presented). PC fluxes out of the euphotic zone account for export of 4.8 to 42.5% of the carbon fixed in the euphotic zone ($\bar{x}$ = 15.8%), and PN fluxes account for 5.2 to 30.8% of the particulate organic nitrogen produced ($\bar{x}$ = 13.5%; assuming living C/N = 7.1 g/g). MICRO flux was observed to have a significantly greater dependence ($B_1 = 3.21$) on and a higher correlation ($r^2 = 0.954$) with integrated P_T than PC or PN flux over the observed production gradient ($P < 0.10$ for ANCOVA of PC and MICRO versus P_T and $P < 0.05$ for ANCOVA of PN and MICRO versus P_T), and the regression intercept is essentially zero ($B_0 = 1.44 \times 10^{-8}$). By interpretation, the regression illustrates the obvious, i.e., as net primary production approaches 0, then the vertical flux of organisms from the euphotic zone approaches 0, and as P_T increases, the export of organisms also increases. Regression analysis of ATP fluxes into single traps at the base of the euphotic zone as a function of P_T was not statistically significant ($P < 0.10$) as the result of two outliers. Exclusion of PC or PN flux data for VX-1 from the regression analysis yields regression coeffi-

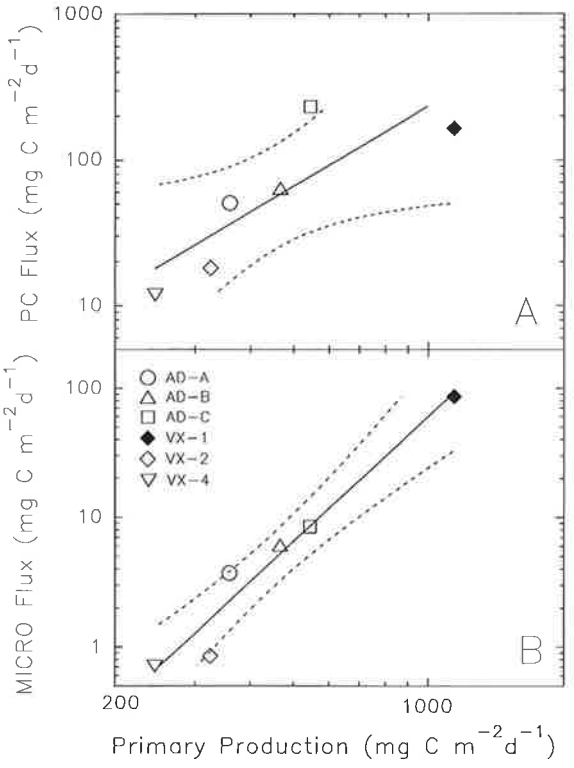


Fig. 3. Covariation of the fluxes of (a) particulate carbon, PC, and (b) all organisms, MICRO, estimated from screened sediment traps (335 μm) deployed at the base of the euphotic zone with integrated daily primary production measured in the water column by ^{14}C incorporation (see text). Symbols identified in Figure 3b apply to both graphs. PC = $4.00 \times 10^{-4}\ P_T^{1.913}$, $r^2 = 0.771$, $P < 0.05$; MICRO = $1.17 \times 10^{-8}\ P_T^{3.210}$, $r^2 = 0.954$, $P < 0.001$.

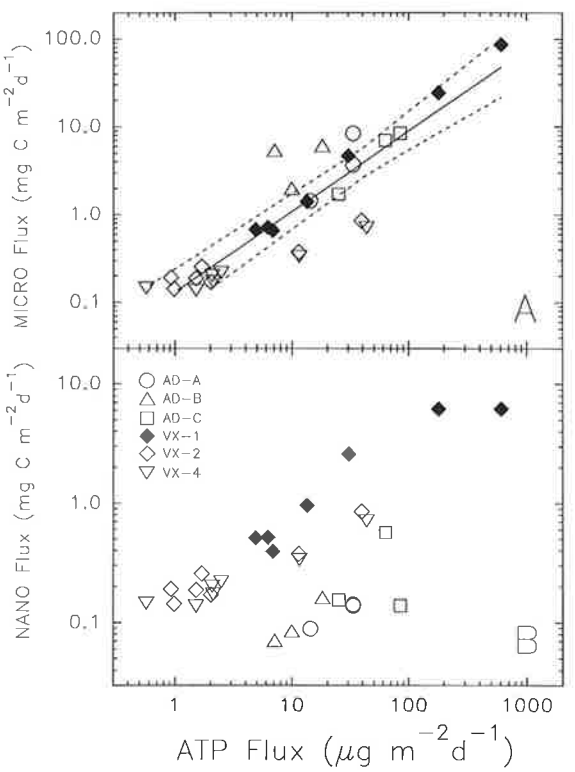


Fig. 4. Covariation of the fluxes of (a) MICRO (all organisms) and (b) NANO (bacteria and zooflagellates) with ATP extracted in situ from particles entering screened traps (335 μm). Data are presented on $\log_{10}$ axes, but least squares regression is for untransformed data. Symbols identified in Figure 4b apply to both graphs, and broken lines represent 95% confidence intervals of the regression coefficients. MICRO = 0.140 ATP - 0.314, $r^2 = 0.984$, $n = 30$, $P < 0.001$.

cients very similar to those of MICRO flux; i.e., PC flux = $4.21 \times 10^{-7}\ P_T^{3.084}$, $r^2 = 0.916$ and PN flux = $1.15 \times 10^{-6}\ P_T^{2.569}$, $r^2 = 0.889$. The lower than predicted values for PC and PN fluxes observed at high P_T may be indicative of two phenomena: (1) inherent time lag between production and export of sinking POM or (2) discrimination against large particles by screened traps. These possibilities are discussed below.

Estimation of Biotic Flux From ATP Measurements

Strong covariation of MICRO fluxes with those of ATP was observed (Figure 4a; $r^2 = 0.984$), in spite of the uncertainties associated with (1) assumed constancy of ATP/biomass relationship, (2) carbon conversion factors for MICRO and NANO estimates, (3) possible inclusion of dead organisms in MICRO and NANO estimates, and (4) underestimates due to small sample size, i.e., oversight of large, rare individuals during enumeration. A C/ATP conversion factor of 140 is obtained from the linear regression of untransformed data (note units in Figure 4a). The y-intercept is likely to be low because larger organisms were probably overlooked in the small sample volumes enumerated microscopically and in situ ATP extraction is likely to be more comprehensive. We believe that these estimates are not severely compromised because the NANO fraction was carefully determined for all collections and accounted for the majority of the biotic flux in the VERTEX 5 data set. Larger sample volumes were available for the VX-1 collection, so bigger, relatively rare organisms (phytoplankton, ciliates, sarcodines, etc.) were included and those data fall on the regression line (Figure 4a). The contribution of the NANO fraction to the biotic

flux is illustrated by comparison with the ATP flux (Figure 4b). The data segregate by trap sets; the NANO fraction for all VERTEX 5 stations accounts for almost 10 times more of the ATP flux than does that from the ADIOS I collections. We believe that these relationships signify that in the VERTEX 5 data set most of the biotic flux is accounted for and that the NANO fraction was a more dominant component of the biotic flux than in the ADIOS I collections.

Multiple Regression Analysis

Variations in the fluxes of PC, PN, MICRO, and ATP have been demonstrated to relate independently to depth, and primary production and to one another (Figures 1 and 3 and Table 1). The functional responses of the fluxes are strengthened by a multiple regression approach [Suess, 1980] that incorporates depth and primary or new production as the "independent" variables (Table 1) and described by a power function [Martin et al., 1987], e.g., PC flux = $53.09\ Z^{-0.942}\ P_T^{0.699}$. Multiple regression analysis illustrates that variations in MICRO and ATP fluxes are more dependent on depth (Table 1, constant B_1) and primary production (constant B_2) than PC or PN fluxes. Variation in the flux of the smallest heterotrophs (NANO) shows negligible depth dependence ($B_1 = -0.282$) and a primary production dependence ($B_2 = 1.018$) comparable to MICRO and ATP, but is poorly explained by regression analysis ($R^2_{Y\,1,2} = 0.425$).

New production (P_N) is estimated as the flux of PC or PN from the base of the euphotic zone, assuming steady state over the appropriate time scale [Eppley and Peterson, 1979]. As expected, variations in the fluxes of PC and PN correlate reasonably well with variations in P_N since determination of P_N is dependent on a flux value at the base of the euphotic zone, but multiple regression analyses of the PC and PN content of < 335 μm particles show weak P_N dependence ($B_2 = 0.427$ and 0.417, respectively; Table 1). Moreover, the independently measured MICRO and ATP variables exhibit significantly higher

TABLE 1. Summary of Multiple Regression Models Describing the Vertical Fluxes of Particulate Carbon (PC), Particulate Nitrogen (PN), All Organisms (MICRO), and Bacteria + Zooflagellates (NANO), as Well as Adenosine Triphosphate (ATP) extracted in Situ From Sinking Particles, as Functions of Depth (Z) and Total Primary Production (P_T) or New Production (P_N)

				Z, m				Production			
Y	B_0	B_1	± 95% CI of B_1[a]	Range	Mean	B_2	± 95% CI of B_2[a]	Range	Mean	$R^2_{Y\,1,2}$	F
Fluxes as a Function of Total Primary Production											
PC	53.090	-0.942	0.239	50-2000	418	0.699	0.428	245-1141	460	0.808	50.5
PN	10.090	-0.938	0.182			0.636	0.328			0.867	78.3
MICRO	0.080	-1.075	0.195			1.442	0.353			0.915	129.3
ATP	47.600	-1.286	0.188			0.986	0.339			0.923	144.7
NANO	0.004	-0.282	0.347			1.018	0.624			0.425	8.9[b]
Fluxes as a Function of New Production											
PC	661.454	-0.981	0.238	50-2000	418	0.427	0.295	54-415	148	0.791	45.3
PN	86.298	-0.970	0.183			0.417	0.227			0.862	74.8
MICRO	11.676	-1.152	0.220			0.922	0.273			0.889	95.7
ATP	789.769	-1.326	0.149			0.742	0.184			0.951	230.7
NANO	0.054	-0.320	0.312			0.795	0.387			0.516	12.8

Fluxes are in mg C m^{-2} d^{-1} except for ATP (μg m^{-2} d^{-1}). Regressions include flux data collected in screened sediment traps (335 μm) from depths equal to or exceeding base of euphotic zone. $Y = B_0 Z^{B1} X^{B2}$, where Y = one of five "dependent" variables; B_0 = y-intercept; Z = depth below ocean's surface; B_1 = slope in Z dimension; X = total or new production (P_T or P_N); B_2 = slope in X dimension; $R^2_{Y\,1,2}$ = coefficient of multiple determination; F = variance ratio.

[a] 95% confidence interval of regression coefficient calculated by adding value to or subtracting value from B_1 or B_2.

[b] Significant at 99.5% level ($P < 0.005$). All other regressions significant at 99.9% level ($F_{0.001[2,24]} = 9.34$).

degrees of new production dependence (B_2 = 0.922 and 0.742, respectively; Table 1), suggesting that the biotic fluxes are more closely coupled to rates of new production, i.e., the introduction of oxidized nutrients from below the euphotic zone and the atmosphere stimulates export of organisms through the intermediary of new production. Export of the NANO-sized biotic fraction appeared to vary with new production (B_2 = 0.795) but is not strongly correlated with depth or P_N ($R^2_{Y\,1,2}$ = 0.516).

DISCUSSION

POM Ecology

As was reviewed in the introduction, suspended and sinking POM appear to differ chemically, as well as physically (size and buoyancy), and potentially represent distinct types of habitats and nutrient resources for microorganisms. Results from the present and previous studies [Taylor et al., 1986; Karl et al., 1988] indicate that sinking POM becomes a poor habitat for microheterotrophs shortly after leaving the euphotic zone. This conclusion is supported by the observations that fluxes of biota decrease more rapidly with depth than fluxes of bulk PC or PN [this study; Taylor et al., 1986; Silver and Gowing, 1991]. Furthermore, as sinking particles age in situ, biomass decreases rapidly because microbial respiration exceeds cellular production [Taylor et al., 1986; Karl et al., 1988]. If sinking POM were a favorable nutrient-replete habitat for microorganisms below the euphotic zone, then the biomass or the biotic contribution to total PC flux would be expected to increase as particles sink and age until some minimum food value were reached when respiration and predation exceed secondary production. We simply do not observe this with the temporal and spatial resolution employed in this and other analyses.

Our observations may be explained by at least five hypotheses: (1) the density gradient trap medium inhibits metabolic activity, thereby suppressing microbially mediated decomposition and microbial growth, (2) association of organisms with particles is purely stochastic, and most are incapable of remineralizing their substratum, (3) microorganisms suspended in the water column dominate decompositional processes, (4) decomposition depends upon physical and chemical processes during vertical transport, and (5) sinking particles and biota are ingested by grazing mesozooplankton and micronekton in the mesopelagic zone. The first hypothesis regarding incubation artifacts has been addressed by Karl and Knauer [1984] and Taylor et al. [1986], who reported that the trap medium did not adversely affect growth or heterotrophic potential (^{14}C-glucose incorporation and respiration) of bacterioplankton nor growth of marine protists. To the contrary, Lee et al. [in press] demonstrated a significant decrease in uptake of ^{14}C-glutamic acid and ^{3}H-thymidine in salt-treated sediment traps. Consequently, we conclude that the potential for sediment trap artifacts exists and the issue requires further resolution.

The second and third hypotheses are interrelated and difficult to demonstrate directly. However, a recent comparison of bacterial biomass and production with suspended and sinking PC below the euphotic zone at a station in the North Pacific central gyre suggests that suspended bacterioplankton in the upper 1000 m could account for as much as 98% remineralization of sinking PC [Cho and Azam, 1988]. In fact, the present study and data synthesized from the entire VERTEX program [Martin et al., 1987] demonstrate that 50 - 60% of the total PC flux from the euphotic zone is remineralized or resuspended in the upper 300 m and 72 - 95% of the <335 μm PC in the upper 1000 m (this study). Particle-associated biota, apparently ineffective at remineralization, may rework large sinking particles, mechanically or chemically, via exoenzymes, causing disaggregation [Biddanda and Pomeroy, 1988; Cho and Azam, 1988; Alldredge et al., 1990]. This being the case, material disaggregated would have a longer residence time in the water column and more opportunity to be acted upon by suspended bacterioplankton, mesozooplankton, or micronekton [Cho and Azam, 1988; Karl et al., 1988; Longhurst et al., 1990; Banse, 1990]. Microscopic evidence to the contrary reveals that some components of the biotic flux, e.g., protists (ciliates and sarcodines), directly consume detritus and presumably remineralize it [Silver and Gowing, 1991], but its significance to PC attrition is unknown.

The net effect of disaggregation is to introduce a time lag between delivery of POM to the mesopelagic and its ultimate remineralization. Therefore "snapshot" comparisons of surface productivity and POM fluxes, both subject to relatively high frequency, stochastic oscillations, with time-averaged oxygen utilization rates (OURs) are not likely to balance. Unfortunately, the processes of disaggregation and resuspension cannot be rigorously examined in our trap collections because of the methods of sampling, handling, and analysis employed. Agitation of the samples will disaggregate fragile particles, and GF/F filters capture all particles larger than 0.7 μm, irrespective of size, i.e., coarse sinking and fine suspended size classes alike. Material disaggregated in the traps would be isolated from many of the physical, chemical, and biological

processes that further decompose it while it is suspended in or transiting through the water column [Banse, 1990]. For example, the diffusive boundary layer around sedimenting POM, which controls chemical solubilization, probably thickens when particles accumulate in the bottom of a trap, thereby slowing dissolution [Banse, 1990]. In the microscopic survey, we observed relatively high proportions of fine-sized particles in the collections, and most microbes were in suspension, not attached to particles, indicating that most trap material is fragile, which supports the disaggregation hypothesis. Recent experimental studies indicate that energy dissipation rates encountered in the bulk field of oceanic regimes are insufficient to physically disaggregate freshly collected marine snow, diatom aggregates, and larvacean houses [Alldredge et al., 1990] and that localized turbulence caused by zooplankton can exceed shear threshold values [Yen et al., 1991]. These findings indicate that chemical erosion of aggregate structure and localized biogenic turbulence may be required for disaggregation and resuspension of macroaggregates.

The fourth hypothesis is actually complementary and may contribute to the disaggregation and dissolution of large particles in the water column. As modeled by Cho and Azam [1988] and Biddanda and Pomeroy [1988], the genesis of the sedimenting biogenic flux in oceanic provinces may progress from (1) suspension of fine particles and dissolved solutes in the euphotic zone to aggregation, via ingestion and egestion, coagulation of densely packed organisms, flocculation of dissolved organic matter (DOM), adsorption and attachment of microbes, etc., to (2) loss of buoyancy, to (3) biological succession on the aggregates with some decomposition, to (iv) chemically and physically mediated disaggregation, resuspension at depth, and remineralization. Finally, upon formation, macroaggregates also may be removed from the water column by grazing mesozooplankton and micronekton, and a portion of the nutrients contained therein may be redistributed in the water column (Karl et al. [1988] and Longhurst et al. [1990], reviewed by Banse [1990]). Resolution of these important biogeochemical processes awaits further experimental data.

Biotic Contribution to Flux

The contribution of whole organisms to the PC flux $< 335\ \mu$m varied from 1.6 to 52.4% of the PC flux over the upper 2000 m, according to our microscopic and ATP-based estimates. The biotic contribution was found to vary with depth and primary production, being highest in shallow and productive waters (VX-1). From their VERTEX traps, Silver and Gowing [1991] reported that 11 - 80% ($\bar{x} = 36\%$) of the PC flux leaving the euphotic zone in the eastern North Pacific is attributable to intact biota; this is within our reported range, but our mean is lower (9.4%). Our MICRO fluxes are likely to be minimal estimates because large, rare individuals, such as some foraminiferans, radiolarians, crustacea, and gelatinous zooplankton, may be underrepresented in the relatively small sample volumes examined and because only organisms with visible cytoplasm were included in the biomass estimates. If we use the in situ ATP flux, which should include all viable organisms, and a C/ATP conversion factor higher than that derived in the present study (250 [Karl, 1980]), the biotic contribution becomes 2.9 - 93.6 ($\bar{x} = 16.8\%$). In spite of uncertainties associated with carbon conversion estimates, the covariation of microbial biomass estimates and in situ ATP estimates demonstrates the internal consistency of the two techniques and supports the contention that few organisms escaped enumeration. Furthermore, the higher proportions reported by Silver and Gowing [1991] may indicate that larger organisms excluded from our traps represent a disproportionately larger contribution to total PC flux than that observed in screened traps. Although these data are not strictly comparable because we employed screened traps and included bacteria and small protists ($< 10\ \mu$m) in our survey and they did not, both data sets illustrate the important and variable contribution of biota to the total PC flux.

As was described by Karl and Knauer [1989], estimates of PC and PN flux derived from screened traps, as in the present study, are likely to be minimal estimates for two reasons: exclusion of large particles from traps and omission of particle-derived dissolved components from the trap inventory. Screens were employed to minimize entry of large active "swimmers" that bias passive flux estimates, but doing so may have also excluded macroaggregates. Screened traps have yielded consistently lower flux estimates than unscreened and "swimmer"-picked traps [Knauer et al., 1984] in the VERTEX experiments [Karl and Knauer, 1989]. However, the higher yields of the unscreened traps may result from contributions of both macroaggregates that are part of the passive flux and so-called "cryptic swimmers," such as gelatinous zooplankton and attendant feeding structures and mesozooplankton ($> 200\ \mu$m) that are technically not part of the passive flux and are not removed from the "swimmer"-picked collections [Michaels et al., 1990]. Viable-appearing "cryptic swimmers" were observed in our screened trap ; copepod adults and nauplii, larvacean bodies, and ostracods were common in the ADIOS I collections but accounted for only a small portion of the PC flux (0.7 - 7.5%, $\bar{x} = 3.7\%$)

and were not detrimental to our regression analyses. It may be inferred that collection of "cryptic swimmers" < 335 μm is as indicative of upper ocean processes as the passive flux. Dissolved organic and inorganic matter released by solubilized POM and organisms in the traps may be a significant fraction of the biogenic flux, which usually goes unquantified and was not accounted for in this study. Experimental means to resolve the problems of "swimmers" and dissolved matter are discussed in detail by Karl and Knauer [1989] and Michaels et al. [1990] and need not be recapitulated here. Suffice it to say that the flux estimates of all components presented in this study, including PC, PN, MICRO, NANO, and ATP, are conservative and internally consistent because all were derived from screened traps. Consequently, we believe that the relationships of the flux components with one another and with depth are valid representations of the biogenic and biotic fluxes, in general.

Attrition of Sinking POM

Despite the differences in species composition and biomass fluxes across gradients in productivity and in biogenic flux represented by our samples, a similar rate of attrition of PC and PN (percent maximum flux versus depth) was observed for all collections, except at the coastal station, VX-1. This observation suggests that attrition of POM over broad oceanic expanses proceeds at a fairly uniform specific rate, independent of the composition or magnitude of the biotic component. The observed departure from this trend, however, suggests that the composition of sinking POM and water column processes at VX-1 differed from the other five collections. Collections from VX-1 traps, deployed during the late stages of a bloom, had the highest biotic contribution of any collection we examined and were dominated by centric diatom frustules (*Actinocyclus sp.* [Silver and Gowing, 1991]) at all depths. Furthermore, the total numbers of diatoms and amount of cytoplasm contained per cell were severely reduced by 2000 m, indicating rapid loss from the water column and die-off or possibly advection from the site at depth. We speculate that mesozooplankton and micronekton grazing pressure in response to the diatom bloom may have played a greater role in POM removal at the mesotrophic VX-1 station than in our other collections. This exception notwithstanding, the trend in PC and PN attrition has an important biogeochemical implication, i.e., most of the biogenic flux (as much as 95% of PC flux) from the euphotic zone is removed in the upper 1000 m, independent of the flux rate. The absolute quantity of material reaching the mesopelagic zone does vary as a function of upper ocean productivity, but depth-dependent attrition rates appear to be uncoupled from the production rates and fluxes.

Trends in biotic fluxes presented here and by Silver and Gowing [1991] indicate (1) that the living component is far more dynamic with respect to depth and more representative of planktonic processes than PC or PN fluxes and (2) that a large proportion of sedimenting organisms (free or particle-associated) die early or are ingested during downward transport. At these stations and times, only 0.3 to 7.5% of the biomass produced in the euphotic zone leaves as intact organisms. The remainder of the fixed carbon contributes to standing stocks, is exuded or lysed, is grazed and repackaged as feces, is removed by migrating grazers, is cycled through the trophic web, is respired, or is excreted as DOM [e.g., Cho and Azam, 1988; Longhurst et al., 1990; Banse, 1990]. Of the biogenic material which becomes part of the passive flux from the euphotic zone, 95.9% + 0.4 (1 SE) of the living biomass (ATP) is lost by 1000 m compared to 72.4% $\pm$ 1.7 and 74.8% $\pm$ 2.7 of the PC and PN flux in offshore waters. At the coastal station (VX-1), the depth-dependent attrition was even higher; by 900 m, 98.9 - 99.1% of the biotic flux and 94.8 and 95.4% of the PC and PN fluxes were lost.

Production and Export

The bulk biogenic flux represents organisms, fecal material, mucus from feeding webs, flocculated DOM, DOM adsorbed to lithogenic and biogenic particles, molts, and partial or complete carcasses. Much of this material is recycled within the euphotic zone before being exported out via the processes of aggregation, ingestion, egestion, disaggregation, dissolution, remineralization, and excretion. As a result, components of the PC and PN fluxes are expected to have inherent time lags in response to changes in primary productivity, e.g., induction of grazing-related processes. We estimate that each atom of C and N cycles 1 to 20 times before leaving the euphotic zone as part of the PC or PN flux, using the relationship of fractional regenerated production to fractional new production ($r = (1 - f) / f$) presented by Eppley et al. [1983]. In contrast, sedimenting microbiota may consist largely of C and N that has cycled only 1 to 6 or 7 times, depending on the length of the trophic chain. Using the functional relationship $T_{POC} = 25.7 \times 10^4 P_T^{-1.50}$ derived by Eppley et al. [1983], we estimate the mean residence times of the total PC pool, T_{POC}, in the euphotic zone at our stations vary from 7 days nearshore to 67 days in the gyre. For the most part, microplankton includes unicellular organisms with physiological response times of minutes to hours and life

spans of days to weeks. Therefore dependence of these flux constituents on nutrient import and primary productivity is far more immediate than bulk POM, and these organisms probably have inherently shorter residence times than bulk POM and DOM.

The differences in the relationships of PC flux and biotic flux to depth and primary productivity derived from multiple regression analysis should be more comprehensible in light of the preceding discussion and are illustrated in Figure 5. The B_1 regression coefficients for PC and PN fluxes (Table 1) are significantly ($P < 0.05$) higher than those presented for unscreened traps from all VERTEX collections and other data sets of Pace et al. [1987]. The B_2 constants for PC and PN, however, are significantly lower than previously reported values and may be influenced by the mode of collection (screened traps). The regression coefficients for MICRO and ATP fluxes reported here are consistent with those reported for PC and PN elsewhere [Suess, 1980; Betzer et al., 1984; Pace et al., 1987], although the responses of MICRO and ATP fluxes are the first of their kind and not strictly comparable with any other published values. PC, MICRO, and ATP fluxes are all power functions of depth with ATP fluxes exhibiting the greatest slope (Table 1 and Figure 5). MICRO flux appears to be most dependent upon P_T, increasing sharply with productivity (Figure 5), while ATP flux is more or less linear with P_T and carbon flux of particles < 335 μm is a hyperbolic function of P_T (Figure 5). Differences between PC and biotic fluxes are accentuated if only nonliving PC ($PC_{detrital}$ = total PC - biotic C) is compared with P_T and Z, e.g., $PC_{detrital} = 76.91\ Z^{-0.884}\ P_T^{0.564}$, $R^2_{Y\,1,2} = 0.742$. Correlation of $PC_{detrital}$ fluxes with Z and P_T is poorer than those of MICRO ($R^2_{Y\,1,2} = 0.915$), ATP ($R^2_{Y\,1,2} = 0.923$) or total PC fluxes ($R^2_{Y\,1,2} = 0.808$). Furthermore, the regression coefficients for $PC_{detrital}$ demonstrate less depth and production dependence than for MICRO, ATP, and total PC fluxes (Table 1).

Consistent with the higher production dependence of the MICRO and ATP fluxes is the increased proportion of primary productivity lost as biotic flux across the productivity gradient: 0.2 - 7.6% of P_T, a factor of 38 compared with PC flux, 4.8 - 38% of P_T, a factor of 8. Analogous trends were observed for particulate amino acid flux which varied from 0.25 - 3.2% of P_T at five eastern North Pacific stations [Lee and Cronin, 1984] and for all organisms entering unscreened traps in VERTEX 1 - 5 [Silver and Gowing, 1991]. The linear relationship of ATP flux to P_T supports the hypothesis that export of living biomass is driven by system productivity. However, the functional response of MICRO to P_T, which is the flux of viable-appearing organisms, some of which may be dead, intact

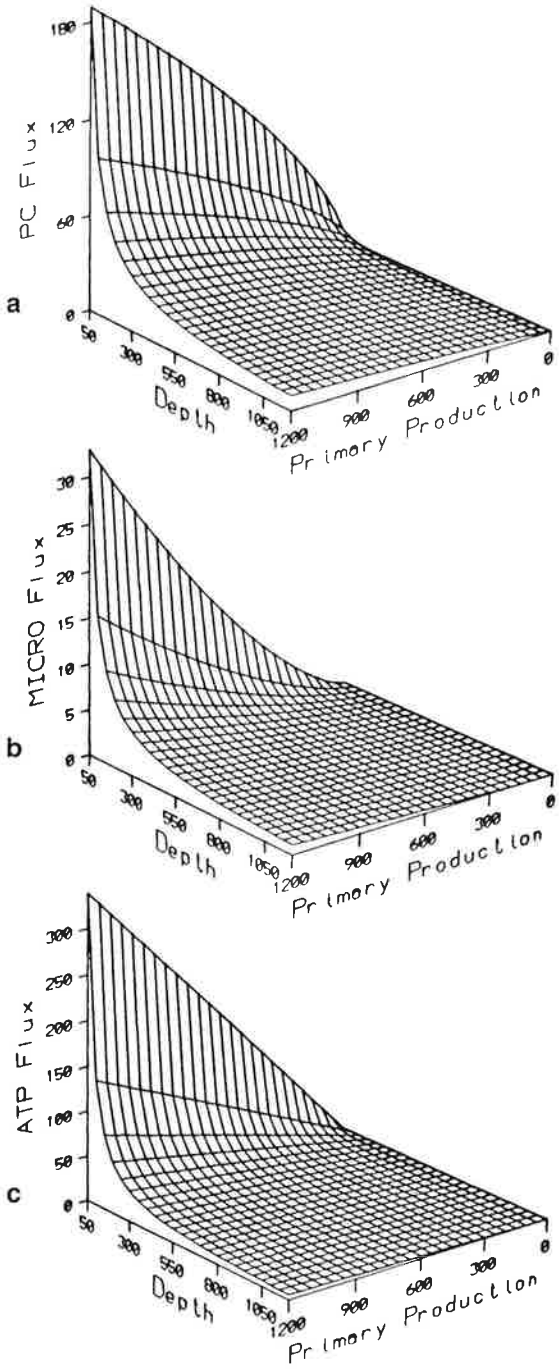


Fig. 5. Interdependence of (a) PC flux, (b) MICRO flux, and (c) ATP flux measured in screened sediment traps (335 μm) on depth and primary productivity. Plots based on the multiple regressions presented in Table 1: $PC = 53.090\ Z^{-0.942}\ P_T^{0.699}$, $R^2_{Y\,1,2} = 0.808$; $MICRO = 0.080\ Z^{-1.075}\ P_T^{1.442}$, $R^2_{Y\,1,2} = 0.915$; and $ATP = 47.600\ Z^{-1.286}\ P_T^{0.986}$, $R^2_{Y\,1,2} = 0.923$. PC, P_T, and MICRO are in mg C m^{-2} d^{-1}, Z is in meters below surface, and ATP is in μg ATP m^{-2} d^{-1}.

individuals, may result from one or more phenomena: variability in the size structure of the planktonic communities, lag between primary production and grazing populations, and aggregation of organisms at high particle concentrations. More productive waters tend to be dominated by larger organisms which have faster sinking rates than the smaller organisms common in oligotrophic regimes [Michaels and Silver, 1988]. The coupling between production and grazing may be undermined during episodic perturbations to nutrient supply, such as upwelling events when higher proportions of primary productivity are lost to the sedimenting flux (reviewed by Taylor [1989]). Finally, as organisms and particles, in general, become more abundant, the likelihood of their coalescing via hydrophobic or adhesive processes and rapidly sinking increases. The processes of mass flocculation and rapid sedimentation of diatoms and other plankters have been observed in many locales [e.g., Billett et al., 1983] and were recently described in detail for the Southern California Bight [Alldredge and Gotschalk, 1989].

The observed dependence of the biotic flux on primary productivity and depth and the potentially faster response of the biotic flux to changes in total and new production discussed above suggest that time-resolved productivity may be better estimated by monitoring the biotic flux into sediment traps. Biotic flux profiles obtained by automated sediment traps precharged with preservative or phosphoric acid and placed at the base of the euphotic and into the mesopelagic zone in quasi-stable hydrographic regions may serve well to estimate production in the overlying waters integrated over the duration of the collection period. Simple algebraic rearrangement of the multiple regressions in Table 1 permits estimation of P_T from flux measurements, e.g., $P_T = (\text{ATP } Z^{1.286} / 47.60)^{1/0.986}$ or $P_T = (\text{MICRO } Z^{1.075} / 0.08)^{1/1.442}$. New production may be estimated by the same method or by comparing export of ATP to the aphotic zone with euphotic zone ATP production rates by measuring d ATP / dt or production of ^{3}H-ATP from the ^{3}H-adenine precursor. ATP production reflects both autotrophic and heterotrophic production in the microplankton and is roughly equivalent to net system productivity, while ATP flux reflects export of a subset of the same organisms. Estimates based on ATP extracted in situ rather than based on microscopy are certainly preferable because of the relative ease of analysis and potential for greater replication. Extracted ATP is contributed by all viable biota, and therefore countermeasures, such as screens, to minimize entry of active "swimmers" must be employed. Entry of small "cryptic swimmers," however, does not appear to hamper this approach. The ATP method has the further advantage of low detection limits; an ATP concentration of 10 ng per 2-L of sediment trap solution is easily measurable [Karl and Holm-Hansen, 1976]. Therefore short collection periods and higher temporal resolution are possible, e.g., < 0.1 day even at our most oligotrophic station. Obviously, routine employment of this approach requires adequate intercalibration of production and flux measurements obtained from the same stations.

SUMMARY

The present study examined gradients in biogenic flux, biotic flux, and primary productivity and found relatively uniform rates of depth-dependent attrition of sedimenting material, with one exception. This and other studies reviewed above illustrate that a wide variety of viable organisms are an integral part of the passive biogenic flux. However, the hypothesis that oceanic POM exiting the euphotic zone is a nutrient-replete habitat that fuels active growth of attendant microbes in the mesopelagic zone is not supported. For sedimenting POM, mechanisms other than heterotrophic remineralization by attached microorganisms must be invoked to explain decomposition of sinking POM in oceanic provinces, such as (1) chemically and physically-mediated disaggregation and resuspension, (2) abiotic solubilization, (3) mechanical and enzymatic attack by attached microbes followed by remineralization by planktonic microbes or microbes associated with suspended POM, and (4) grazing by mesozooplankton and micronekton at depth. A better understanding of the important processes of oceanic decomposition and remineralization of sinking POM awaits further experimental studies.

Evidence has been presented that the flux of organisms is more depth-dependent and representative of water column productivity than that of bulk PC or PN. We suggest that these trends may be used advantageously to perform better time-resolved monitoring of water column productivity indirectly and to provide estimates of new production based on integrated ATP production rates in the upper water column and ATP export from the euphotic zone.

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