Fluxes of particulate carbon, nitrogen, and phosphorus in the upper water column of the northeast Pacific

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Abstract—Concentrations of carbon, nitrogen and phosphorus were determined in particles that passively sank into multi-replicate collectors set at 50, 250, and 700 m in coastal waters, and 75, 575, and 1050 m in the open ocean. Fluxes as high as 36, 4.1, and 0.19 mmoles of C, N, and $P\,m^{-2}\,day^{-1}$ were observed at 50 m under coastal upwelling conditions; at 700 m, upwelling period fluxes (9.6, 0.9, and 0.053 mmoles of C, N and, $P\,m^{-2}\,day^{-1}$) exceeded those measured at 50 and 75 m when samplers were set under low productivity surface waters. ^{210}Pb flux estimates were made on coastal trap particulates. The resulting values were close to the expected and suggest that overall flux estimates are representative of those occurring in the environment.

Atomic ratios of C:N:P under upwelling conditions were similar to values reported for living plankton (~180:18:1), while in the open ocean, atomic ratios of C and N in relation to P were markedly higher (400 to 900:30:1). Fecal pellet fluxes were two orders of magnitude higher under upwelling conditions (~1 to $3 \times 10^5\,m^{-2}\,day^{-1}$) than those in the open ocean (~$1000\,m^{-2}\,day^{-1}$). Quantities of passively sinking particulate C, N, and P appeared to be equal to or in excess of the amounts required to meet the nutritional needs of the mid-water zooplankton.

Rates of change for C, N, and P and inferred rates of oxygen change varied widely in relation to surface productivity. For example, oxygen utilization rates were as high as $790\,\mu l\,l^{-1}\,yr^{-1}$ in near-surface waters under upwelling conditions and as low as $4.4\,\mu l\,l^{-1}\,yr^{-1}$ at mid-depth in the open ocean. Our rates of change, determined by direct measurement, generally agree with previously published estimates from mathematical models.

INTRODUCTION

IN 1888, Agassiz proposed that "... deep-sea organisms are nourished by a 'rain' of organic detritus from overlying surface waters" (p. 141, HARDING, 1974). Most marine scientists agree that this is a logical way for these inhabitants to meet their energy requirements; however, in spite of the enormous biological implications, most attempts at proving the existence of the detrital rain have failed. Marine chemists have also been concerned with this concept, because many elements, radionuclides, and compounds are thought to be transported in association with detrital particles through the water column to the benthos. During transport, elements and compounds may be released from the particles or concentrated in association with them, thus markedly affecting their water column distributions. It is little wonder, then, that there is wide support for MENZEL's contention (p. 675, 1974) that '...the lack of knowledge concerning the mechanisms by which organic matter is transported to depth... [represents] the single most important unresolved problem in the fields of marine biology and chemistry...'

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Because of the magnitude and complexity of this problem, it is obvious that multi-faceted studies must be undertaken using different sampling devices and analytical approaches. A number of studies have been started within the past year or two, and the results of a few have already appeared in the archival literature (WIEBE, BOYD and WINGET, 1976; SOUTAR, KLING, CRILL, DUFFRIN and BRULAND, 1977; BISHOP, EDMOND, KETTEN, BACON and SILKER, 1977).

We have concentrated on measuring the flux of particulate materials in the upper 1000 m of the water column in which three identical trap systems were set simultaneously at various depths under surface waters characterized by low, intermediate, and high rates of primary production. The materials collected in the traps were analyzed for C, N, and P. The purpose of this paper is to present measured particulate C, N, and P fluxes and estimated *in situ* rates of change and to discuss the significance of these data in relation to previous studies of this nature.

<div align="center">METHODS</div>

Material falling through the water column was collected using a trap system consisting of eight individual acrylic tubes mounted on a polyvinylchloride cross frame (Fig. 1). Each tube had an inside diameter of 7.39 cm and was equipped with a baffle system (SOUTAR *et al.*, 1977) that consisted of 16 smaller tubes (length 7.6 cm). The top ends of the baffle tubes had been milled to a wall thickness of 0.06 mm to minimize surface area (about 5% of the cylinder mouth area which is 43 cm^2). We assume that materials hitting these edges fall into the collectors and contribute to the total flux. GARDNER (1977) has shown that open cylinders with a length-to-width ratio of approximately 2 or greater will yield representative fluxes. With our use of a baffle system, an adequate length-to-width ratio (8.4) and density gradients (see below), we assume that our traps sample the vertical flux

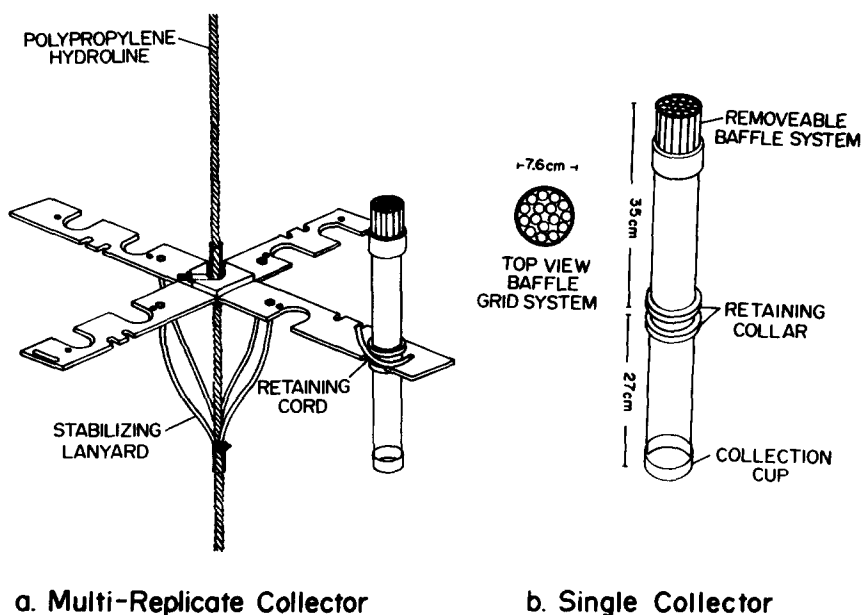**a. Multi-Replicate Collector   b. Single Collector**

Fig. 1.   Multi-replicate collector assembly (a) and top and side views of a single collection tube (b).

of particulate matter with reasonable accuracy. We also have ^{210}Pb data (see below) supporting our assumptions. However, like other investigators attempting to measure vertical fluxes, we presently have no way of definitely knowing whether our supposition is correct. Participation in comparative studies planned for the summer of 1979 (D. Spencer and P. Brewer, personal communication) on various trap and pump systems should help us to evaluate our system better and hopefully, by then, a means of determining absolute accuracy will have been devised.

The use of eight tubes at each depth enabled us to obtain replicate samples for C, N, and P analyses ($n = 2$ to 4) and, at the same time, collect additional samples for other analyses. For example, in most cases, two of the tubes were left undisturbed to insure that delicate flocs and fecal pellets were not disrupted prior to identification. The contents of the other cylinders were reserved for trace element and radionuclide analyses.

All tubes were thoroughly cleaned with Micro$^{®}$ and dilute quartz distilled HNO_3 and filled with a high-density reagent grade NaCl solution ($\rho = 1.07 \, g \, cm^{-3}$). Density stratification was necessary, because dye studies revealed that the traps could be completely flushed during recovery. Although not confirmed, it is also possible that some *in situ* flushing might occur if density stratification were not used. Two identification tubes containing dye were placed at each depth to detect possible flushing. The traps were closed during their descent through the euphotic zone by using plastic sheeting secured by a rubberband and a cherry-flavored Lifesaver$^{®}$ as a soluble link.

To prevent decomposition and microbial growth on the insides of the collectors, buffered formalin was added to yield a 5% concentration. We believed that a preservative was necessary, because we detected the presence of H_2S in unpreserved trap material as well as nitrogen losses in preliminary experiments. In addition, microbial growth on the inside of non-preserved collectors was observed. This is especially undesirable in view of the relatively high surface:volume ratio of our trap cylinders.

We also found various zooplankton species in all collectors. It was apparent that the majority of these animals actively swam into the cylinders and that they were killed by the formalin solution before any *in situ* feeding on the trapped organic matter. Obviously, failure to remove these organisms could lead to serious errors in the C, N, and P analyses on passively sinking detritus; hence, the contents of each collecting cup were viewed under a dissecting microscope and the zooplankton were carefully picked out before freeze-drying. Partially decomposed zooplankton and exuvia were not removed (WHEELER, 1967; HARDING, 1973).

Carbon and nitrogen were determined on freeze-dried samples from two to four tubes taken from each depth using a Hewlett–Packard Model 185-B CHN analyzer after treatment with dilute HCl to remove carbonates. Samples analyzed for phosphorus were digested according to MARTIN and KNAUER (1973) to insure the complete breakdown of phospholipids followed by colorimetric analysis using the method of MURPHY and RILEY (1962).

^{210}Pb was determined in samples from one or two tubes taken from each depth. The digestions, chemical separations, and analyses followed the methods of KOIDE and BRULAND (1975).

Fecal pellets from all identification tubes were enumerated and separated into geometric size classes (i.e. cylinders, spheres, ellipsoids). After class separation, volumes were determined using average geometric dimensions per class (measured with a calibrated ocular micrometer) in conjunction with the appropriate volume equation. The

average class volume was then multiplied by the total number of pellets found in that class. Because of the large number of fecal pellets in the coastal collections, subsamples were taken using the methods outlined in Hopkins (1962). Whole samples were placed in the Hopkins splitter and at least seven subsamples (out of a possible 16) with sample replacement were counted. All identifiable fecal pellets were counted in the collections from the open ocean.

Coastal samples were collected from a station 30 km offshore in Monterey Bay, California (36°42′N; 122°13′W; depth 1000 m) during a period of upwelling when primary production was high and during a non-upwelling period when productivity was low. Moored traps were set for 21 and 19 days, respectively, at depths of 50, 250, and 700 m. Deployment and recovery of the coastal traps was accomplished on the R.V. *Oconostota* and all processing was carried out at the shore-based laboratory. The open ocean samples were collected aboard R.V. *Cayuse* from a station at the eastern edge of the North Pacific Gyre (32°47′N; 144°26′W; depth 5000 m). Three trap arrays were set for 7 days at depths of 75, 575, and 1050 m on a free-floating line buoyed at the surface and weighted at the bottom. Upon recovery, samples were immediately processed for fecal pellet enumeration and then stored in a desiccator to await C, N, and P analyses.

<center>RESULTS AND DISCUSSION</center>

Observed fluxes

It can be assumed that more particulate C, N, and P would be found in waters underlying areas of high productivity than under those in oligotrophic open ocean regions. However, previous attempts using conventional sampling techniques have failed to demonstrate this phenomenon. For example, Menzel and Ryther (1970) found similar mid-depth particulate C concentrations in spite of order-of-magnitude changes in overlying surface waters. This led to the tentative conclusion that most of the particulate C was recycled in the upper 300 m and little was transported to depth. However, recent studies (McCave, 1975) have shown that conventional samplers may not collect fast-sinking particles and it is probable that an important fraction was not included in previous estimates. This sampling problem is one of the more important reasons for using traps specifically designed to collect this fraction. With their use, it becomes apparent that fluxes are indeed much higher in mid-depth waters when conditions promote high rates of primary production at the surface. For example, during periods of high productivity in Monterey Bay, C, N, and P fluxes of 36, 4.1, and 0.19 mmole m^{-2} day^{-1} were observed at 50 m (Table 1). These values decreased with depth, but even at 700 m, substantial amounts were still observed (9.6 C, 0.9 N and 0.053 P mmole m^{-2} day^{-1}). In contrast, fluxes at the same location observed under low productivity conditions were markedly lower. In fact, non-upwelling fluxes at 50 m were lower than those observed at 700 m during upwelling. As expected, fluxes observed in the open ocean were lower still, ranging from 5.7 C, 0.41 N, and 0.014 P at 75 m to 1.0 C, 0.034 N, and 0.0011 P (mmole m^{-2} day^{-1}) at 1050 m (Table 1). These data demonstrate that mid-depth C, N, and P fluxes are related to the rate of primary productivity occurring at the surface.

To the best of our knowledge, there are no other coastal C, N, or P flux rates with which to compare our data. However, there have been two recent estimates for open-ocean conditions. Wiebe et al. (1976) reported organic carbon fluxes in the Tongue of the Ocean, Bahamas, of 0.39 and 0.53 mmole C m^{-2} day^{-1} at a depth of 2150 m. In view of the fact that their trap was set in the Atlantic 1000 m deeper than ours, and that some

Table 1. *Total C, N, and P fluxes and atomic ratios observed under coastal upwelling, non-upwelling, and open-ocean conditions. The fluxes are also expressed as per cent of estimated surface primary productivity using* RYTHER's (1969) *data.* (See text.)

Depth (m)	C	Fluxes N (mmoles m^{-2} day^{-1})	P	Fluxes as % Surface Production C	N (percent)	P	C :	Atomic Ratios N : P		C:N
		COASTAL, UPWELLING								
50	35	3.9	0.20							
	37	4.3	0.18							
	(36)*	(4.1)	(0.19)	53	39	32	190	22	1.0	8.8
250	20	1.8	-							
	22	1.8	0.13							
	(21)	(1.8)	(0.13)	30	18	21	160	14	1.0	12
700	10	0.94	0.055							
	9.1	0.86	0.052							
	(9.6)	(0.90)	(0.053)	14	8.7	8.5	180	17	1.0	11
		COASTAL, NON-UPWELLING								
50	6.4	0.57								
	6.2	0.64								
	8.4	0.90	0.032							
	9.4	0.98	0.026							
	(7.6)	(0.77)	(0.029)	34	23	13	260	27	1.0	9.9
250	4.8	0.41								
	4.3	0.38								
	4.3	0.52	0.013							
	3.8	0.40	0.013							
	(4.3)	(0.43)	(0.013)	19	13	6.3	330	33	1.0	10
700	3.6	0.22								
	4.3	0.41	0.010							
	4.4	0.21	0.012							
	(4.1)	(0.28)	(0.011)	18	8.1	4.9	370	25	1.0	15
		OPEN OCEAN								
75	8.0									
	5.2		0.013							
	4.0	0.41	0.014							
	(5.7)	(0.41)	(0.014)	50	24	13	410	29	1.0	14
575	1.2	0.086	0.0019							
	1.3	0.093	0.0032							
	(1.2)	(0.089)	(0.0026)	11	5.2	2.4	460	34	1.0	13
1,050	1.6	0.034								
	0.75	0.048	0.0016							
	0.77	0.021	0.0006							
	(1.0)	(0.034)	(0.0011)	9	2	1.2	910	31	1.0	29

*Numbers in parenthese indicate averages.

material was lost upon recovery, their C fluxes and ours are comparable. BISHOP *et al.* (1977) also made C flux estimates using a large volume pump system. In spite of the inherent difficulties of attempting to estimate fluxes from pump samples (BISHOP *et al.*, 1977, p. 504, 543), their value of 2.6 mmole C m^{-2} day^{-1} at 388 m also agrees with ours.

This apparent agreement may be fortuitous, and as stated in the Methods section, we have no way of absolutely knowing whether the fluxes in Table 1 are accurate. However, certain natural radionuclides may provide independent estimates for fluxes that can be used to determine accuracy of various measuring systems. An attractive candidate is ^{210}Pb. The principal source of this radionuclide in surface waters is atmospheric input; it is quickly scavenged from surface waters with residence times ranging from a few months to a few years. In addition, there is evidence that little or no regeneration of ^{210}Pb occurs in the water column (BACON, SPENCER and BREWER, 1976) and that scavenging rates in deep waters are one to two orders of magnitude less than those in surface waters (NOZAKI

and TSUNOGAI, 1976; SOMAYAJULU and CRAIG, 1976). Thus, the particulate flux of ^{210}Pb in the upper 1000 m should approximate the atmospheric delivery rate of ^{210}Pb and the fluxes at each depth should be the same or increase only slightly with depth.

Estimates for the average atmospheric input of ^{210}Pb to the northeast Pacific range from 0.5 to 1.0 dpm cm^{-2} yr^{-1} (NOZAKI, THOMSON and TUREKIAN, 1976). The average particulate ^{210}Pb flux we observed under upwelling conditions was 2.0 dpm cm^{-2} yr^{-1} (Table 2); under non-upwelling conditions, the average was 0.25 dpm cm^{-2} yr^{-1} (excluding

Table 2. Coastal ^{210}Pb fluxes observed under upwelling and non-upwelling conditions.

Depth (m)	^{210}Pb Activity dpm gm^{-1}	^{210}Pb Fluxes dpm cm^{-2} year^{-1}
	COASTAL UPWELLING	
50	14.0	2.0
250	23.4	2.2
700	36.1	1.8
	COASTAL NON-UPWELLING	
50	-*	0.27
250	-	0.14
700	-	0.24

* Accurate weight determinations could not be made on these samples because of their low mass and high salt content. Quantities of open ocean particulates were insufficient for ^{210}Pb analysis.

the 250-m value). Thus, the particulate ^{210}Pb fluxes under upwelling conditions are 2 to 4 times the average yearly input estimates, while under non-upwelling conditions, particulate fluxes are lower by a factor of 2 to 4. If these fluxes represent the extremes, then the average flux over a year would be consistent with the estimated atmospheric delivery rate. Both the relatively uniform flux of ^{210}Pb with depth and the absolute fluxes suggest that the traps used in this study yield representative and accurate particulate flux estimates.

Although we cannot demonstrate that our replicate samples are independent for all measured parameters, we have no reason at this time to believe otherwise. The fact that the cylinders were randomly removed from the support frame together with the good replication for C, N, and P we obtained during upwelling (Table 1) suggests independence. Under non-upwelling and open-ocean conditions with associated lower fluxes, less precision was obtained in some cases. This is not unexpected, because one large particle falling into one cylinder and not another could greatly influence the C, N, P results. Nevertheless, the fecal pellet counts (Table 3) observed under all conditions further suggest that excellent precision can be obtained with this sampling system.

It is desirable to relate vertical C fluxes to amounts fixed at the surface via primary production. The best way to obtain these data would be by integrated daily measurements in the surface waters over underlying traps. However, as traps are left out for 1 to 3 weeks, daily primary production measurements would represent a major undertaking well beyond the scope of the present study. The problem is further complicated where vertical current shear may deliver particles to the deeper traps from surface water far from the traps' location. Nevertheless, it is worthwhile to use published estimates for comparative

purposes. RYTHER (1969) provided average rates for three regimes: upwelling areas, coastal zone, and ocean with mean production rates of 25, 8.3, and $4.2\,\text{mole}\,C\,m^{-2}\,yr^{-1}$. We have converted these values to a daily basis and also estimated N and P fixation rates based on FLEMING's (1940) average atomic ratios of 106:16:1 (Table 1). With these estimates, we calculate that, in the open ocean, 50, 24, and 13% of the C, N, and P produced in the surface waters reach a depth of 75 m via sinking. These percentages decrease markedly with depth and only 11, 5, and 2% of the C, N, and P reach 575 m and at 1050 m, the percentages fall to 9, 2, and 1% of the C, N, and P produced at the surface. This same general trend is also observed during coastal upwelling: 53, 39, and 32% of the C, N, and P reach a depth of 50 m. These amounts are halved at 250 m, and at 700 m, the percentages fall to 14, 8.7, and 8.5, respectively. Similar results were observed near the coast during the non-upwelling period. BISHOP et al. (1977) made similar calculations for their 388-m depth open-ocean station. Their values of 13, 9, and 6% of C, N, and P are in agreement with our estimates.

C:N:P ratios

Atomic ratios of C:N:P and C:N were calculated for comparison with the classical average ratios for living plankton of 106:16:1 and 6.6:1.0, respectively (FLEMING, 1940). Little change was noted with depth under upwelling conditions and C:N:P ratios were about 180:18:1, while C:N values were around 10:1 (Table 1). The ratios suggest that, with the exception of the elevated carbon amounts, the materials falling into the traps were similar to living phytoplankton. Under non-upwelling conditions near the coast, C and N increased relative to P; e.g. N:P ratios exceeded 24 and C:P ratios ranged from a low of 260 at 50 m to a high of 370 at 700 m. In contrast, C:N ratios were similar to those observed under upwelling conditions, with the exception of the 700-m sample (15). These results suggest that, relative to the other elements, marked P depletion occurred, while C:N ratios remained nearly constant.

In the open ocean, N:P ratios were similar to those observed under non-upwelling conditions (~ 30), while the C:P ratios were considerably higher (from 410 at 75 m to 910 at 1050 m). Ratios of C:N were also higher at all depths. These ratios suggest that marked losses in both P and N had occurred in the particles, even at the shallowest depth sampled, while comparatively large amounts of C remained in association with them.

BISHOP et al. (1977) also calculated C:N:P ratios for the materials they collected at several depths. The ratios in the large size fraction (> 53 m) increased with depth (50 to 294 m) from 158:19:1 to 490:53:1. At 388 m, their ratios dropped to 218:22:1. Apparently, this occurred because of organic matter recovery problems associated with the 53-μm filters. Nevertheless, in general, the depth trends in their ratios are similar to ours.

The variability in C:N:P noted by us and the authors mentioned above is not unexpected. MENZEL (1974) noted that 90% of the plant matter produced in the ocean is eaten; hence, the vast majority of sinking particles are pieces of detritus that have already passed through an animal's gut. In the process, nutritive compounds such as phospholipids, protein, and carbohydrates are digested, while non-nutritive fractions such as crude fiber are excreted in the feces. The C:N:P ratios in the metabolic by-products will vary in accordance with the quantity and quality of the compounds removed during the digestive process.

Although superfluous feeding is a controversial subject (see BUTLER, CORNER and

MARSHALL, 1970), zooplankton physiologists agree that large amounts of nutritive elements such as P and N remain in the feces when food is abundant. One would expect, then, that ratios in fecal matter would be relatively close to 106C:16N:1P. On the other hand, when food is scarce, consumers would more thoroughly extract the nutritive components while leaving the crude fiber C behind. In this situation, larger amounts of C in relation to N and P would be expected. Our observed increases in C:N with depth can be further explained by continuing microbial decomposition processes, which increase the refractory C pool while ultimately decreasing the N pool (KNAUER and AYERS, 1977).

The material trapped in our collectors reflected these phenomena. In coastal upwelling waters, observed C:N:P ratios were near the theoretical 106:16:1; i.e. about 180:18:1. These ratios also remained relatively constant with depth and the particulate matter had a major fecal pellet component (see below). These results support the contention that superfluous feeding does occur when food is abundant and that these rapidly sinking particles reach mid-depths intact and thus represent a highly nutritive food source for mid-water and benthic organisms living under productive surface waters. Conversely, under open-ocean conditions, with low primary production rates, the sinking particles are depleted in N and P and the result is large amounts of C in relation to N and P, with ratios of 400 to 900:30:1.

Fecal pellets

In addition to measuring C, N, and P fluxes, the number of identifiable fecal pellets at each depth and station were counted (Table 3). In productive upwelling waters, 3.2×10^5 pellets $m^{-2} day^{-1}$ were estimated to reach a depth of 50 m. Rates at 250 and 700 m were 2.2 and $1.2 \times 10^5 m^{-2} day^{-1}$, respectively. Fecal pellet fluxes of this magnitude are reasonable. For example, if we assume that a copepod population $(500 m^{-3})$ migrated to the upper 25 m of the water column and fed at night (12 h) and that these individual animals produced three fecal pellets per hour, the resulting flux for a given day would be 4.5×10^5 fecal pellets m^{-2}. Fluxes in the millions could also be obtained if the herbivore population were doubled and a fecal pellet production rate of 12 $animal^{-1} h^{-1}$ were used (MARSHALL and ORR, 1955). Thus, laboratory studies and our field data indicate that high fluxes of fecal pellets occur in the water column when surface productivity rates are optimal.

During non-upwelling conditions near the coast, fecal pellet fluxes decreased considerably and only 0.17, 0.22, and 0.12×10^5 pellets $m^{-2} day^{-1}$ were observed at the 50-, 250-, and 700-m depth intervals. Open-ocean estimates were lower still: 1.4, 1.1, and 0.7×10^3 pellets $m^{-2} day^{-1}$ at 75, 575, and 1050 m, respectively.

As stated in the Methods section, we can only assume that these fluxes are reasonably accurate. On the other hand, the data in Table 3 suggest that remarkably precise estimates can be obtained with this trap system. This is illustrated by the 575-m open ocean collections where all fecal pellets in six different cylinders were counted and a coefficient of variation of approximately 14% was obtained.

The total volume of fecal pellets in each trap was measured and we calculated the amounts of C, N, and P contributed from this source using the C, N, and P fecal-pellet-content data of JOHANNES and SATOMI (1966). During upwelling, we estimated that 25% of the N and about 60% of the P were carried to midwater depths in association with pellets, while under non-upwelling conditions and in the open ocean, much smaller amounts were observed (Table 3). Nevertheless, in every case, the importance of fecal pellets in terms of C, N, and P increased with depth. This is not unexpected, because these relatively fast-

Table 3. Fecal pellet fluxes and estimates of C, N, *and* P *contributed to the total fluxes from this source.*

Depth (m)	Fecal Pellet Fluxes (numbers m^{-2} day^{-1})	Estimated Contribution* to Total C, N, P Flux		
		C	N (percent)	P
COASTAL, UPWELLING				
50	318,000	9	15	51
250	219,000	11	25	61
700	120,000 122,000 (121,000)†	11	23	65
COASTAL, NON-UPWELLING				
50	16,100 18,100 (17,100)	1	1.9	8.4
250	25,300 18,800 (22,000)	1.7	3.3	18
700	11,600 11,900 (11,700)	1.4	4	18
OPEN OCEAN				
75	1,200 1,520 (1,360)	0.1	0.2	1.1
575	1,280 1,100 1,170 1,030 1,300 900 (1,130)	0.2	0.6	3.9
1,050	620 825 720 (720)	0.25	1.7	7.1

* Calculated from total fecal pellet volume and C, N, P data from JOHANNES and SATOMI (1966); where C = 20%, N = 4.5%, P = 1.7% dry weight. Dry fecal pellet weight = volume × 1.22 g cm^{-3} (WIEBE *et al.*, 1976) × 0.11 (dry:wet ratio).

† Numbers in parentheses indicate averages.

sinking particles, which are enclosed by a protective membrane (SCHRADER, 1971), tend to resist fragmentation and remineralization, while other, slower-sinking material should be recycled more rapidly in the upper 500 m.

Rates of change

Several models of the vertical distribution of solutes contain terms of the form $F = F_0 e^{-\alpha z}$, which have been used to describe a general exponential decrease in non-conservative rate processes; where F is the rate of consumption or regeneration of solute (e.g. O_2, PO_4); F_0 is the flux at zero model depth (not necessarily the surface); z is depth, and α is the exponential decay constant.

Although values of α have been obtained from vertical advection–diffusion models (e.g. WYRTKI, 1962; MUNK, 1966) no direct determinations have been made using field data, to our knowledge. Since we had the minimum number of points necessary to determine α, we felt that it was worth an attempt to compare our field-derived values with those obtained from mathematical models. Using the methods of least squares, we fitted the data from Table 1 to the above equation, where F is the downward flux of particulate C, N, or P

and the other terms are the same. The values of α we obtained varied from 0.8 to 2.7 $\times 10^{-3} \, \mathrm{m}^{-1}$ and generally are near the value of $2.5 \times 10^{-3} \, \mathrm{m}^{-1}$ found by WYRTKI (1962) in modeling oxygen distribution in the North Pacific Ocean. However, plots of $\ln F$ vs z revealed a systematic deviation of the measured flux from the model that was particularly pronounced in the coastal non-upwelling and open ocean samples. This suggests that α is depth-dependent and that larger values will be found in the upper water column where regeneration rates are high and that lower values may be expected for deeper waters. Thus, the use of one model α with our data would result in underestimates of rates of change in the upper portion of the water column and over-estimates in the lower portion. Clearly, more data at closer depth intervals will be needed for the development of an appropriate model.

The best rate-of-change estimates that we can make with our present data are based on $\Delta F / \Delta Z$ calculations, where ΔF is the change of the C, N, or P particle flux over an intervening depth interval, ΔZ. Our values for $\Delta P / \Delta t$ and inferred rates of oxygen consumption, $\Delta O_2 / \Delta t$ (Table 4) calculated using the theoretical ratio of 106 carbon: -276 oxygen (REDFIELD, KETCHUM and RICHARDS, 1963), are generally similar to those given by RILEY (1951): 0.003 to $0.093 \, \mu\mathrm{mol} \, \mathrm{Pl}^{-1} \mathrm{yr}^{-1}$ and 1.6 to $210 \, \mu\mathrm{l} \, \mathrm{O}_2(\mathrm{STP})\mathrm{l}^{-1} \mathrm{yr}^{-1}$, respectively. This is also true of the resulting $\Delta O:\Delta P$ ratios, where Riley obtained values of -170 to -1000 over similar depth intervals. It is also interesting to note that the $\Delta O:\Delta P$ ratios attained for the lower depth intervals all approach the classical expected value of -276 (REDFIELD et al., 1963), while for the upper depths, this ratio is higher by factors of 2 to 4. This is not unexpected. GRILL and RICHARDS (1964), studying phytoplankton decomposition, showed that P is lost faster from the particulate pool than N during early decomposition (upper water column, rapid regeneration), while during latter stages (> 20 days), N and P were released at the expected ratios of $16:1$.

As expected, rates of change were similar under coastal non-upwelling and open-ocean conditions. In both cases, markedly higher values were observed in the upper depth intervals than in the lower. For example, in the upper depth intervals, inferred rates of oxygen consumption were 170 and $96 \, \mu\mathrm{l} \, \mathrm{l}^{-1} \mathrm{yr}^{-1}$, respectively, while at lower depths, they were about $4 \, \mu\mathrm{l} \, \mathrm{l}^{-1} \mathrm{yr}^{-1}$. In contrast, much smaller decreases were observed when the upper and lower upwelling intervals were compared (e.g. 790 versus $270 \, \mu\mathrm{l} \, \mathrm{O}_2 \, \mathrm{l}^{-1} \mathrm{yr}^{-1}$).

The $\Delta N / \Delta t$ values also appear to be reasonable with the exception of the non-upwelling 250- to 700-m value. The rate of change for N almost equaled that of C and both the resulting C:N ratio (1.3) and N:P ratio (75) appear to be out of line with the other values presented in Table 4.

One of the more interesting aspects of studying the vertical flux of particulate matter is its implications in feeding the inhabitants of the deep sea. MENZEL (1974) provided data indicating that the zooplankton respiration requirement at 500 and 1000 m is equivalent to 3.7 and $0.73 \, \mathrm{mg} \, \mathrm{C} \, \mathrm{m}^{-3} \mathrm{yr}^{-1}$, respectively. Our open ocean rate of change estimates for depths of approximately 300 and 800 m are 40 and $1.8 \, \mathrm{mg} \, \mathrm{C}^{-3} \mathrm{yr}^{-1}$, values in the neighborhood of the estimated requirements. Menzel also estimated that a total flux of $3.9 \, \mathrm{g} \, \mathrm{C} \, \mathrm{m}^{-2} \mathrm{yr}^{-1}$ would be required to sustain life in the deep sea. Our values at 575 and 1050 m were 5.5 and $4.5 \, \mathrm{g} \, \mathrm{m}^{-2} \mathrm{yr}^{-1}$, respectively. It appears, then, that adequate energy can be provided to the deep sea via the sinking of detritus. This material is also sufficient in a nutritional sense. If C:N ratios of less than $17:1$ are adquate for animal nutrition (RUSSELL-HUNTER, 1970), then the organic matter sinking to mid-depth (except the 1050-m open-ocean depth) is sufficient to meet the nutritional requirements of higher organisms

Table 4. *Rates of change for* C, N, *and* P *in upper and lower depth intervals from the three sampling periods. Values of* $\Delta O_2/\Delta t$ *and* $\Delta O:\Delta P$ *are inferred from observed values of* $\Delta C/\Delta t$. *Atomic ratios are also shown.*

Depth Interval (m)	$\frac{\Delta C}{\Delta t}$	$\frac{\Delta N}{\Delta t}$	$\frac{\Delta P}{\Delta t}$	$\frac{\Delta O_2}{\Delta t}$	$\frac{\Delta C}{\Delta P}$	$\frac{\Delta N}{\Delta P}$	$\frac{\Delta C}{\Delta N}$	$\frac{\Delta O}{\Delta P}$
		Rates of Change				Regeneration Ratios		
	(μmol liter^{-1} year^{-1})			(μl liter^{-1} year^{-1})	(by atoms)			
COASTAL UPWELLING								
50–250	27	4.2	0.11	−790	250	38	6.4	−640
250–700	9.2	0.73	0.062	−270	150	12	13	−380
COASTAL NON-UPWELLING								
50–250	6.0	0.62	0.029	−170	210	21	9.7	−540
250–700	0.16	0.12	0.0016	−4.6	100	75	1.3	−260
OPEN OCEAN								
75–575	3.3	0.23	0.0064	−96	500	36	14	−1300
575–1050	0.15	0.042	0.0012	−4.4	130	35	3.6	−320

(Table 1). In reality, even lower 'effective' C:N ratios are probably the rule in deep-water particles (KNAUER and AYERS, 1977).

The results of this study, using near-surface and mid-depth particle interceptor traps, demonstrate the feasibility of using such systems to sample rapidly sinking particles. With their use, we have shown that fluxes vary with depth and in relation to the productivity of the overlying surface waters. However, it is also apparent that much better data may be obtained using more traps at more closely spaced depth intervals and by analyzing additional replicates. With these values, it should then be possible to show that the fluxes are consistent with *in situ* dissolved oxygen, nitrogen, and phosphorus rates of change necessary to account for the vertical distributions of these elements.

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