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Particulate organic matter in surface waters off Southern California and its relationship to phytoplankton

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ABSTRACT

Particulate carbon, nitrogen, chlorophyll *a*, adenosine triphosphate, particle count and particle volume were measured in the euphotic zone during six quarterly cruises (between September, 1974, and March, 1976) in the Southern California Bight. The distribution and quantitative relationships among these parameters were examined in an attempt to estimate the relative contributions of plankton to the total particulate matter. Each of the parameters correlated with the others as would be expected if plankton, and especially phytoplankton, contributed significantly to the total particulate organic matter and was dynamically related to the total. Particle volume and number, as determined with a Coulter Counter, apparently measured both living and nonliving organic particulates well. Several methods of estimating the phytoplankton standing stock as carbon agreed in suggesting that phytoplankton carbon accounted for an increasing proportion of the total particulate carbon as the latter increased. Seasonal changes in the estimated carbon:chlorophyll *a* ratio of phytoplankton paralleled changes in the photosynthetic assimilation ratio accompanying seasonal changes in temperature and irradiance. Blooms of diatoms and dinoflagellates were sampled on several occasions allowing approximate determinations of C, N, ATP and chlorophyll *a* per particle and the size of specific dominant organisms and species mixtures in natural samples. The apparent lifetime of the total particulate matter in the euphotic zone, if none were refractory, would be only 1-2 weeks. Its chemical composition apparently resembles that of plankton.

1. Introduction

The purpose of this study was to assess the contribution of plankton to the particulate organic matter in southern California coastal waters. This purpose is related to a set of questions concerning food webs in these waters. First, biological oceanographers want to know the standing stocks of organisms at various levels in the food

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web in order to assess their dynamics and their relationships to physical processes. This is not readily done for phytoplankton by existing chemical methods or other methods suitable for quick, routine use. Second, there is disagreement as to what fraction of the plankton in the Southern California Bight is advected into the area and what fraction is produced within the area. Thus *in situ* growth rates and turnover times are needed. Third, much of the particulate organic matter in seawater is nonliving detritus, but assessments of detritus *v.* plankton have not been made for these waters, save for three inshore stations in 5 months during 1967 off La Jolla (Strickland *et al.*, 1970) and its rate and pathways of formation and loss are unknown.

One expects the particulate matter in the surface waters of the Southern California Bight to be largely autochthonous and largely organic. The inorganic constituents would be largely aluminosilicates and coccolith carbonates. Particulate aluminum in these waters is only 1-3 μg liter^{-1} on average, or 10-30 μg liter^{-1} as aluminosilicates (Sackett and Arrhenius, 1962). There are no major rivers laden with silt and terrigenous organic matter. The main flow of the California Current is well offshore of the Bight, and in fact one or more large eddies exist part of the year (Sverdrup and Fleming, 1941; Reid *et al.*, 1958) with residence time undoubtedly long in comparison with the generation time of the bacteria, phytoplankton and microzooplankton taken in our samples. Other autochthonous sources of particulate organic matter would include elements of the planktonic food web, such as the fecal material, molts, reproductive cells, and secretions of marine animals and macroalgae living in the region. The largest terrestrial inputs would be expected from aerial fallout and sewage, orginating largely from metropolitan areas of Los Angeles, Orange and San Diego counties.

Strickland *et al.* (1970) reported on particulate organic carbon (POC) for three stations sampled for 21 weeks in 1967 off La Jolla. Phytoplankton carbon was estimated microscopically (Reid *et al.*, 1970) and organic detrital carbon was estimated by difference. The detrital organic carbon accounted, on average, for one-half or more of the total POC. Siezen and Mague (1976) found nearly all of the particulate organic nitrogen to consist of protein amino acid-N in near-surface waters sampled in the present study. The carbon associated with this protein amino acid comprised 40-50% of the total POC in the euphotic zone except at a station in Santa Monica Bay near the Hyperion sewage outfall, where the protein fraction was somewhat lower and protein amino acid-N was about 70% of PON.

Beers and Stewart (1970) estimated the particulate organic carbon of microzooplankton to average 148, 138 and 112 mg C m^{-2} in 1967 for the three stations off La Jolla and to comprise 17-21% of the total zooplankton population, as carbon, in the upper 100 m. The phytoplankton crops averaged 2.51, 2.50, and 1.15 g C m^{-2}, respectively, for the three stations (Eppley *et al.*, 1970). The 1967 results suggested that the organisms taken in water bottle samples and filtered through 200

μm mesh netting before analysis would be largely phytoplankton with 5-10% admixture of microzooplankton and the total would comprise $\leqslant$50% of the POC, except in blooms where the living fraction would be greater.

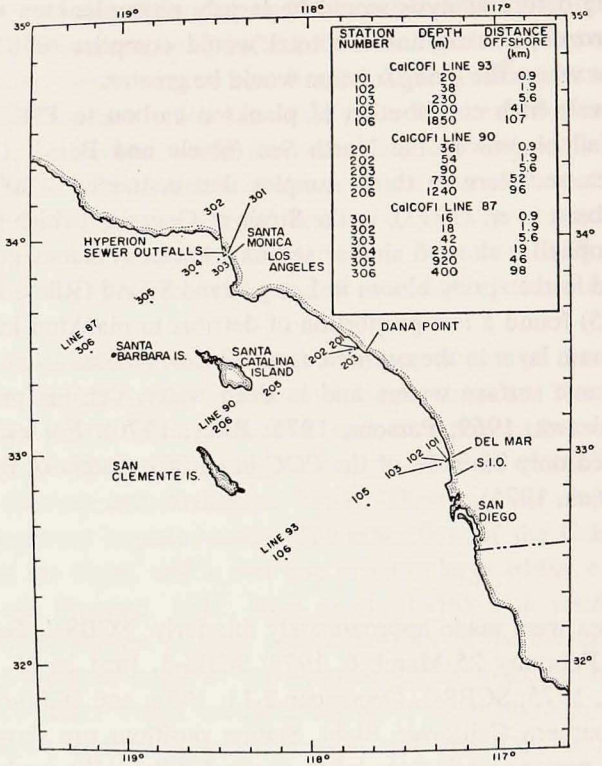
Such a relatively high contribution of plankton carbon to POC was also found in spring and fall blooms in the North Sea (Steele and Baird, 1961, 1962), off southwest Africa and Peru in those samples that contained >200 μg m^{-3} POC reported by Hobson *et al.* (1973), in the Strait of Georgia, British Columbia where POC and chlorophyll *a* showed similar seasonal cycles (Parsons *et al.*, 1969; Parsons, 1975), and in the spring bloom in Long Island Sound (Riley, 1959). Herbland and Pages (1975) found a low proportion of detritus to plankton in the chlorophyll and ATP maximum layer in the euphotic zone off west Africa.

In many oceanic surface waters and in deep water, detritus predominates (see reviews of Nishizawa, 1969; Parsons, 1975; Riley, 1970). For example, plankton carbon comprised only 23-32% of the *POC* in surface waters of the central North Pacific (Beers *et al.*, 1975).

2. Methods

Sampling. Cruises were made approximately quarterly: SCBS-1, September 13-20, 1974; SCBS-2, February 25-March 6, 1975; SCBS-3, June 16-25, 1975; SCBS-4, September 6-17, 1975; SCBS-5, December 2-11, 1976; and SCBS-6, March 13-24, 1976, in the Southern California Bight. Station positions are shown in Figure 1. Samples for the present work were taken at six depths in the euphotic zone. Sampling depths were selected from light penetration measurements, made with a submersible quantum scalar irradiance meter (Booth, 1976), to correspond approximately to 90, 30, 18, 12, 3 and 1 percent of surface irradiance. The depth of the euphotic zone was typically 20 m at the most inshore station and increased with distance offshore to 50-70 m. Sampling devices were 30 and 5 liter Niskin bottles. The water samples were pre-filtered through 183-200 μm mesh nylon netting before analysis.

Chemical analysis. Particulate organic carbon and nitrogen (POC and PON) were measured with a Hewlett-Packard model 184 CHN analyzer with the sample inlet modified (Sharp, 1975). Volumes of 200-1000 ml were filtered directly upon sample collection with pre-combusted glass fiber filters (Whatman GF/C 25 mm diameter) and were stored in a vacuum desiccator for analysis ashore. The filters retain particles $\lesssim$1 μm diameter (Sheldon and Sutcliffe, 1969). Chlorophyll *a* was analyzed on the ship by the fluorometric method, with corrections for phaeopigments (Strickland and Parsons, 1972). Chlorophyll samples were collected on glass fiber filters (Whatman GF/C or Reeve-Angel 984H, 25 mm diameter). Samples for adenosine triphosphate (ATP) analysis were filtered as above and the filters were placed immediately in boiling Tris buffer. The buffer solution and filter were later



LOCATIONS OF STATIONS OCCUPIED DURING QUARTERLY SOUTHERN CALIFORNIA BIGHT CRUISES.

Figure 1. The location of stations occupied during the quarterly Southern California Bight cruises September 1974-March 1976.

frozen and returned to the laboratory for analysis by the luciferin-luciferase method (Holm-Hansen and Booth, 1966).

Particle size distributions were measured for freshly collected samples on the ship for cruises SCBS-2-6 with a 16 channel electronic particle analyzer, Coulter model TA-II. A 280 μm diameter orifice was used to cover the range of particle diameters from 5 to approx. 128 μm. Occasionally, a 50 μm orifice was used to determine particles as small as 1.5 μm diameter.

Particle size analysis. The particle size distribution data were calculated as particles per liter of sample, as the volume of particles as mm^3 $liter^{-1}$ in each of 16 size ranges, and as the carbon content of the particles. The latter was calculated from the equation relating the carbon content of a phytoplankton cell to its volume (Mullin *et al.*, 1966) even though we will subsequently show that detritus as well as phytoplankton was counted. In addition the total particle count and volume of the

sample was recorded. The particle size distributions were also analyzed by a method of characteristic vectors, as used earlier for seawater particulates by Kitchen *et al.* (1975).

Linear regression analysis of the particulate measurements, by pairs, was done using Bartlett's method which assumes variability and error in the measurement of both X and Y variables (Bartlett, 1949). The data were grouped in various ways for these purposes, as described later.

Phytoplankton carbon and carbon:chlorophyll a ratio. The ratio was estimated indirectly by seven methods. In the first method, which we regard as the most reliable of the seven, phytoplankton carbon was calculated as $F \times$ POC where the value of F was 0.158 + 0.00070 (POC). This is equivalent to phytoplankton C = 0.158 (POC) + 0.00070 (POC)^2. It says that phytoplankton constitute an increasing fraction of the POC as POC increases. However, phytoplankton carbon would reach 100% of the POC at POC = 1204 μg liter^{-1} and would exceed 100% at higher POC values. Thus the equation is useful only for POC < 1000 μg liter^{-1}. This equation resulted from comparison of phytoplankton carbon calculated from microscopic cell counts and cell volumes (Reid *et al.*, 1970) and chemically measured POC (Strickland *et al.*, 1970). The 63 samples were for three stations off La Jolla and cover a 21-week period April-September, 1967. The 95% confidence limits for the slope of F on POC were 0.00035-0.00104 and for the intercept, 0.126-0.190. The second method is the equation of Steele (Steele, 1962; Steele and Menzel, 1962) where the C:Chl. *a* ratio = 0.79 (irradiance in ly/day)/(phosphate concentration in μg at liter^{-1}) • (day-length in hours). In method number three, the phytoplankton C:Chl. *a* ratio was estimated from a curve developed by fitting the POC and chlorophyll *a* values to a curvilinear equation POC = a • (Chl. $a + b$)/K + (Chl. $a + b$). The term b allows for a POC intercept on the Y axis when chlorophyll $a = 0$. The slope of the tangent to the curve was taken as the phytoplankton C:Chl. *a* ratio for discrete chlorophyll *a* values. Method four was particulate ATP $\times$ 250, the "living carbon" estimate of Holm-Hansen (1973), divided by chlorophyll *a*. Method five was a linear regression of POC on chlorophyll *a* using Bartlett's method that assumes error in both the X and Y variables. Method six was phytoplankton, C = 0.454 POC where the value 0.454 was the average ratio of all the phytoplankton C:POC comparisons of the 1967 study referred to above, divided by chlorophyll *a*. Method number seven was rather more theoretical, and is based upon the interrelation of specific growth rate, assimilation number, and the C:Chl. *a* ratio of the phytoplankton (Bannister, 1974). A maximum expected specific growth rate (μ) for phytoplankton in continuous light at a given ambient temperature (°C) was calculated as $\log_{10} \mu_m = 0.0275T - 0.070$ (Eppley, 1972). One half this value was taken for growth with natural illumination. Next the maximum observed photosynthetic assimilation number (mg C per mg Chl. *a* per day) measured in the

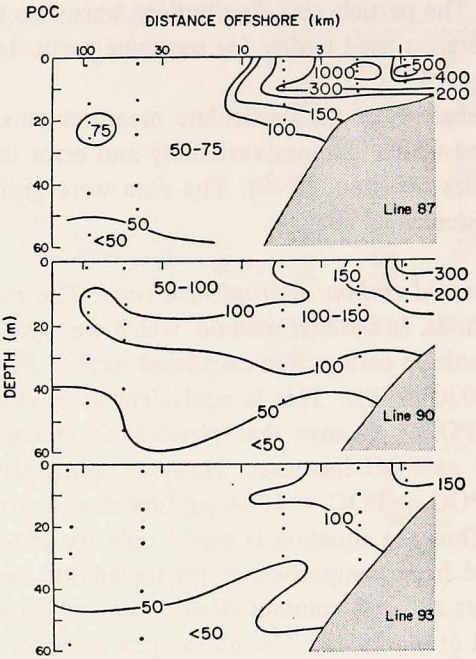


Figure 2. Vertical sections of particulate organic carbon (POC, expressed as μg liter^{-1}) during cruise 4 (September 6-17, 1975). Distance offshore is shown on a logarithmic scale.

water column was recorded. The phytoplankton carbon:chlorophyll *a* ratio (F) was then calculated from the equation $\mu = \ln [(F + \text{max. assim. number})/F]$.

For these comparisons, the measured values were subdivided into groups for all the above methods. Each cruise was treated separately. Within each cruise the stations were divided into three subgroups. Group A consisted of the nearshore stations not adjacent to sewage outfalls (Stations 101, 102, 201, 202 and 303; (Figure 1). Group B consisted of Stations 301 and 302, with high standing stocks, and both nearshore and adjacent to sewage outfalls. Dinoflagellates were usually dominant phytoplankton at these stations. Group C consisted of the more offshore and low standing stock stations (103, 105, 106, 203, 205, 206, 304, 305 and 306). Samples were taken from six depths in the euphotic zone. The present analysis included usually the upper four depths and the depth cut-off was based upon the continuity of photosynthetic assimilation number curves and nutrients with depth.

A nearshore diatom bloom was present during the cruise SCBS-2 (Feb., 1975), even at Stations 301 and 302 which were usually dominated by dinoflagellates. For this cruise, station subgroup A included these stations and Station 304; there was no subgroup B.

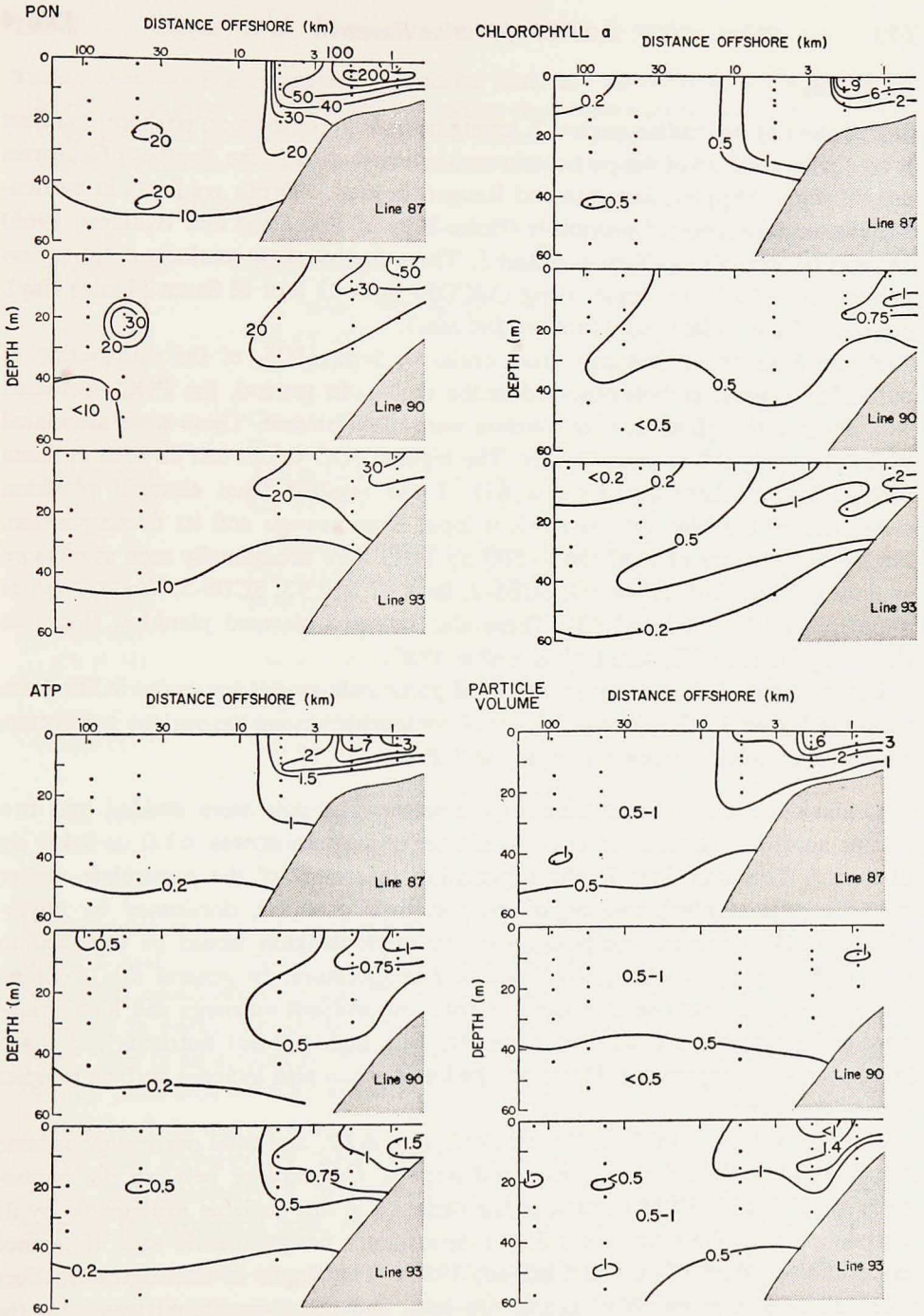


Figure 3a. Vertical sections of particulate organic nitrogen (PON, μg liter^{-1}). Cruise 4, September 6-17, 1975.

Figure 3b. Vertical sections of chlorophyll *a*, μg liter^{-1}. Cruise 4, September 6-17, 1975.

Figure 3c. Vertical sections of adenosine 5'triphosphate (ATP, μg liter^{-1}). Cruise 4, September 6-17, 1975.

Figure 3d. Vertical section of particle volume, mm^3 liter^{-1}. Cruise 4, September 6-17, 1975.

3. Results

Distribution of particulate matter. A strong horizontal (onshore to offshore) gradient is an obvious feature of the particulate matter distribution in the Southern California coastal waters (Eppley, Sapienza and Renger, in prep.). Depth gradients in particulate matter were reported previously (Holm-Hansen, Strickland and Williams, 1966) and can be seen also in Figures 2 and 3. These figures show sections, more or less perpendicular to the coastline, along CalCOFI lines 87 (out of Santa Monica Bay), 90 (out of Dana Point) and 93 (out of Del Mar).

Figure 2 shows an example, from cruise 4, Sept. 1975, of the distribution of particulate organic carbon observed in the region. In general, the POC decreased with depth, although subsurface maxima were often present. These were associated with the chlorophyll maximum layer. The highest POC values can be seen in Santa Monica Bay (inshore stations/line 87). These resulted from elevated plankton stocks due to the high rate of nutrient input from sewage and its decomposition. High concentrations of POC (up to 500 μg/liter) were occasionally seen at offshore stations (cruise SCBS-1, line 90; SCBS-2, lines 87 and 93; SCBS-5, line 87, and at mid-depth on lines 90 and 93). These also reflected elevated plankton stocks as chlorophyll *a* and ATP were high as well as POC.

Comparisons of the various measures of particulate matter for cruise SCBS-4 are shown in Figure 3. The correspondence of contouring among the various parameters suggests a correlation among them and with POC (Fig. 2).

Relationships among the particulate parameters. The data were divided into two groups according to whether ambient nitrate concentration was <1.0 or $\geqslant 1.0$ μg at liter^{-1}. This was done in the expectation that most of the particulate matter would consist of planktonic organisms and their products, dominated by phytoplankton. The chemical composition of the phytoplankton would be expected to vary with nutritional status, irradiance and temperature. In general this grouping method separated near-surface samples with low ambient nutrients and high irradiance and temperature from deeper samples with high ambient nutrients and lower irradiance and temperature. However, the latter group also includes surface samples during upwelling.

Average values of POC, PON, chlorophyll *a*, ATP, and total particulate volume are listed in Table 1 for all cruises and stations. Correlations between the parameters are high with 59-83 percent of the variation in one variable explainable by its correlation with the other according to Spearman's nonparametric rank difference correlation method (Tate and Clelland, 1957). The slopes of the regression lines were all $>$ zero at the 95% confidence level and the Y-intercepts were $<<$ the mean values. Taken at face value this result would support the expectation of a biogenic origin for much of the particulate matter.

The high correlations among the particulates should not be regarded as implying

Table 1. Bartlett's linear regression analysis for particulate matter. Data for all cruises combined. Values in μg liter $^{-1}$ except CV = volume of particulate matter as mm^3 liter^{-1}. SRDF^2 = the square of Spearman's rank difference coefficient expressed as percent. It suggests the degree to which the variability in Y is explained by the variability in X.

Parameter					
Y (mean value)	X (mean value)	Slope	Y-Intercept	SRDF^2 as %	No. Samples
	Waters with nitrate $\geq$ 1 μg at liter^{-1}				
POC (118)	Chl. *a* (1.29)	73.0	23.1	76	200
POC (118)	PON (22.0)	4.95	8.7	83	201
POC (117)	ATP (0.544)	187	15.5	78	202
CV (1.08)	Chl. *a* (1.59)	0.517	0.262	59	134
ATP (0.540)	Chl. *a* (1.28)	0.336	0.110	74	203
PON (22.0)	ATP (0.546)	34.4	3.20	73	201
PON (22.1)	Chl. *a* (1.30)	12.5	5.85	64	199
	Surface waters with nitrate $<$1 μ at liter^{-1}				
POC (211)	Chl. *a* (1.99)	77.0	58.2	77	232
POC (211)	PON (35.4)	5.82	5.36	81	232
POC (211)	ATP (0.998)	193	17.9	82	233
CV (1.74)	Chl. *a* (2.08)	0.654	0.382	61	157
ATP (0.981)	Chl. *a* (1.97)	0.355	0.285	70	246
PON (35.4)	ATP (1.00)	31.6	3.84	78	232
PON (35.5)	Chl. *a* (2.00)	11.8	12.0	64	231
	All data combined				
POC (165)	CV (1.29)	98.4	38.1	67	308
POC (165)	CC (86.9)	1.67	19.9	68	309

homogeneity or uniformity, however, and indeed variability is typical of these waters (Figs. 2 and 3). A result of the temporal and spatial variability appears in the regression equations; they suggest that all living organisms (from ATP) and phytoplankton in particular (from Chl. *a*) comprise about 80 percent of the POC and PON. This is an artifact of the regression analysis as discussed in detail by Banse (1977). Thus little confidence can be placed in the absolute values of the slopes and intercepts of the regressions.

We were surprised by the similarity between the two sample groupings in the slopes and intercepts of the regressions. If differences in chemical composition between the groupings exist, as expected, then this approach fails to reveal them.

Particle volume and size distribution. The analysis was limited to particles of 5 to approximately 128 μm equivalent diameter. Discrete peaks in the size spectra were frequently seen, as noted earlier by Parsons (1969), especially at nearshore stations and in samples from the chlorophyll maximum layer. These were associated with organisms, usually individual dinoflagellate species showing narrow size distribu-

tions, or broader peaks associated with chain diatoms (Fig. 7). The distributions were sometimes featureless when plankton stocks were low, as in samples from offshore stations at the bottom of the euphotic zone.

Both the total particle concentration (numbers liter^{-1}) and the total particle volume (mm^3 liter^{-1}) were correlated with the chemical measures of particulate matter. For example, the Spearman rank-difference coefficient squared was 0.817 for the relation of POC to particle volume and 0.824 for POC to particle count. The correlation was similar between both ATP and chlorophyll *a* and the particle parameters. The high correlations between POC and ATP or chlorophyll *a* and the value of the ratios POC/chlorophyll *a* and particle volume/chlorophyll *a*, imply that large concentrations of inorganic carbonaceous particles, relative to plankton and related organic matter, either were not present or covaried with one or both of those variables.

Kitchen *et al.* (1975) described a method of analyzing particle size distributions by means of characteristic vectors. This method was applied to the present data. The first weighting factor, $W1$, was directly proportional to the total volume of particles and the other particulate measures, such as POC. A Bartlett regression of $W1$ on total particle volume (CV) gave $W1 = -.0449\ (\pm.0013) + .0326\ (\pm.0014)\ CV$, 95% confidence limits in parentheses. The second factor, $W2$, indicated which segment of the size range contained the largest proportion of particulate volume in Kitchen *et al.* (1975). In the present data, high (up to 0.55) positive values of $W2$ were associated with size distribution peaks > 102 μm diameter while large negative values (−0.10 to −0.39) were associated with dramatic peaks at intermediate particle sizes, especially in the range 40-50 μm diameter. Kitchen *et al.* (1975, Fig. 2) presented a graph of $W1$ *v.* $W2$ that shows two clusters or rays of points related to differences in water density (σ_t). Similar clusters or rays of points were present in our data (not shown), but the offshore stations (−04 to −06) provided one cluster, the inshore stations (−01 to −03) the other.

The "percent large particles," defined as particles (20-64 μm/5-64 μm) 100, was correlated with the total particle volume ($p < .05$) implying that large particles (large phytoplankton cells and chains) go along with high crops. There was no correlation between percent large particles and depth or between $W2$ and depth. However, $W1$ decreased with depth as expected of any measure of the standing stock of particulates.

The slope of the regression of particle count (number liter^{-1}) on percent large particles was negative ($p < .05$) implying only that when particles are larger there are fewer of them.

Regression of chlorophyll *a* on particle volume gave a slope of 1.68 μg Chl. *a*:mm^3 particle volume for all data combined; the value would be lower if the volume of 1-5 μm diameter particles were included.

Particulate carbon estimates (abbreviated CC) were calculated from the particle

size distributions using a size-dependent carbon/volume relationship originally derived for phytoplankton (Mullin *et al.*, 1966). Regression of POC on CC for all data gave a slope of 1.67 ± 0.17 and POC intercept of 19.9 ± 9.6 μg C liter^{-1} (95% confidence limits). The slope of the regression implies that the particle counter, counting only particles >5 μm diameter, registered 60 percent of the POC retained on fine filters that retain particles <1 μm. That 40% of the POC is associated with <5 μm particles is consistent with the size fractionation studies we have carried out where 30-50% of chlorophyll *a* passed 5 μm screens and with the size distributions measured when the Coulter Counter was operated with a 50 μm orifice. The average POC/particle volume ratio was 0.0984 mg POC/mm^3 or 0.057 mg/mm^3 if 40% of POC is <5 μm. Sheldon and Parsons (1967) found a ratio 0.050 in Saanich Inlet.

Estimation of carbon content and the carbon/chlorophyll a ratio of the phytoplankton. Several indirect methods were used in these estimates. Since no absolute method exists the relative value of the various indirect methods could be judged only from generalized expectations. These expectations include the following: (1) Phytoplankton carbon will be a variable fraction of the total POC and that fraction is roughly proportional to POC (Hobson *et al.*, 1973). That is, high POC in these waters is usually due to phytoplankton blooms or aggregations where the phytoplankton carbon will often exceed detrital organic carbon. In samples from nutrient impoverished oceanic surface water the phytoplankton carbon will be low and will be a relatively smaller fraction of total POC than in blooms (Hobson *et al.*, 1973). (2) The phytoplankton carbon:chlorophyll *a* ratio will vary as a function of insolation and ambient nutrient levels (Steele, 1962; Steele and Menzel, 1962), as well as with temperature (Eppley, 1972) and the species composition of the phytoplankton assemblage. The ratio in diatom blooms will be low as in spring blooms in temperate waters (Steele and Baird, 1962), the Peruvian upwelling (Lorenzen, 1968; Strickland *et al.*, 1968), or in rich areas of intense vertical mixing (Winter *et al.*, 1975), and of the order 10-40 g/g. Ratios of 100 or more can be expected in mixed assemblages of phytoplankton in summer in stratified surface waters (Steele and Baird, 1962; Eppley, 1968, for local waters). (3) Total POC will be dominated by organic detritus and phytoplankton in these waters (Strickland *et al.*, 1970) as microzooplankton (Beers and Stewart, 1970) and bacterial carbon (Carlucci, pers. comm.) account for only a small fraction on average, of the POC, and carbonate minerals would not be abundant except as coccoliths associated with coccolithophorids.

Results of the seven indirect methods of estimating phytoplankton carbon and the phytoplankton carbon:chlorophyll *a* ratio are shown for the various cruises and station subgroups in Table 2. Total POC and chlorophyll *a*, averaged for the subgroups, are also shown. Perhaps the most striking feature of the table is the large variation in the estimates given by the different methods. The range of estimates

Table 2. Phytoplankton carbon and the phytoplankton carbon:chlorophyll *a* ratio estimated by seven indirect methods for groups of stations and depths. Italicized estimates exceeded POC.

Cruise:	1			2		3			4			5			6		
Date:	Sept. 1974			Feb. 1975		June 1975			Sept. 1975			Dec. 1975			March 1976		
Station Group:	A	B	C	A	C	A	B	C	A	B	C	A	B	C	A	B	C
Method	Phytoplankton carbon (μg liter^{-1})																
1	78	505	22	62	25	75	683	23	56	376	17	66	148	27	76	53	21
2	113	*1800*	24	103	60	91	648	52	36	379	19	59	124	54	94	55	35
3	157	*762*	96	39	114	130	800	30	84	587	48	121	280	89	201	122	58
4	203	592	98	*427*	*192*	*285*	829	*132*	*305*	*1060*	*110*	205	310	*120*	233	*252*	*100*
5	155	—	95	62	109	106	—	33	147	—	55	143	290	92	199	—	61
6	110	338	44	159	70	106	400	45	87	286	36	97	163	52	107	84	43
7	55	220	18	169	29	74	—	39	48	220	19	52	108	19	22	41	10
	Phytoplankton carbon:chlorophyll *a* ratio (g/g)																
1	41	46	37	12	24	45	89	34	47	72	44	32	41	20	31	23	23
2	59	164	40	20	58	54	85	78	30	72	48	28	35	41	39	24	38
3	82	69	159	8	111	77	105	45	70	112	123	58	78	67	183	54	63
4	106	54	163	81	188	170	108	199	256	201	282	98	86	90	96	111	109
5	81	—	158	12	107	63	—	50	124	—	141	68	81	69	82	—	66
6	58	31	74	30	69	63	52	68	73	54	93	46	45	39	44	37	47
7	29	20	30	32	28	44	—	59	40	42	48	25	30	14	9	18	11
	POC (μg liter^{-1})																
	243	749	98	351	155	234	881	99	191	629	80	214	360	114	235	185	95
	Chlorophyll *a* (μg liter^{-1})																
	1.91	11.0	0.60	5.28	1.02	1.68	7.66	0.66	1.19	5.26	0.39	2.09	3.60	1.33	2.42	2.27	0.92
	Maximum growth rate (day^{-1})*																
	1.3	0.7	1.5	2.6	1.2	1.4	0.5	2.4	1.4	0.8	1.6	0.8	0.7	0.8	0.3	0.9	0.5

— Less than 9 samples as required for Bartlett linear regression.
* From maximum assimilation number ÷ C/Chl. *a* ratio by Method #1.

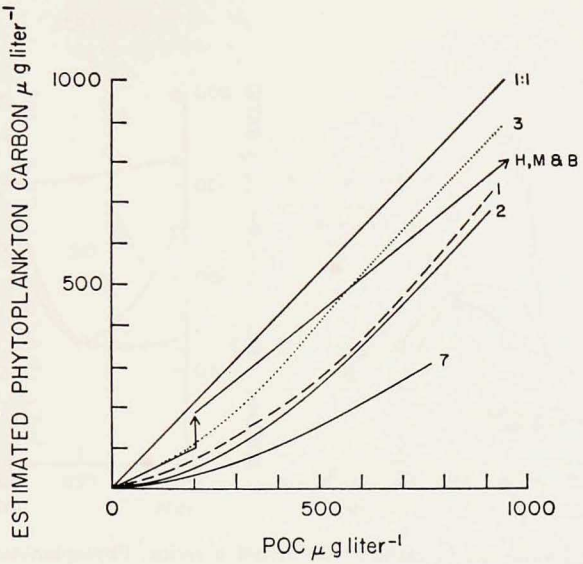


Figure 4. Phytoplankton carbon estimated by methods 1, 2, 3, and 7 (see text) *v.* particulate organic carbon (POC). The lines labelled H, M and B are the regression lines of Hobson, Menzel, and Barber (1973) for phytoplankton and micro-zooplankton carbon *v.* POC. The upper line represents 1:1 correspondence, i.e. phytoplankton carbon = POC.

was 5-10-fold between the highest, usually from method 4 = 250 × ATP, and the lowest, usually method 7 which is based upon maximum assimilation number and expected growth rate. Method 3, the curve fit of POC on chlorophyll *a*, and method 5, Bartlett's linear regression, gave similar and apparently high values. Banse (1977) has discussed the problems of estimating phytoplankton carbon from graphs of POC on chlorophyll *a* and has shown that such methods result in high phytoplankton C:Chl. *a* ratio and low estimates of detrital carbon, as noted here. Method 6, which assumed phytoplankton carbon is 45.4% of POC, gave intermediate and reasonable values, but this method is unattractive because it ignores the probable variation in the phytoplankton carbon:POC ratio. It gave high values when POC was low and low values when POC was high. Because this limitation is overcome in method 1, we regard this estimate as the most reliable one and the standard for comparison for the other estimates.

Method 2, the Steele equation, gave estimates rather similar to method 1 and an unreasonable value only once (cruise 1, group B) when ambient phosphate was unusually low, 0.08 μg at liter^{-1}. This simple method deserves broader application. Figure 4 compares methods 1, 2, 3 and 7 with the results of Hobson *et al.* (1973). These methods suggest the ratio phytoplankton carbon to POC increases as POC increases, a bias assured in method 1 but not methods 2, 3 and 7. This observation

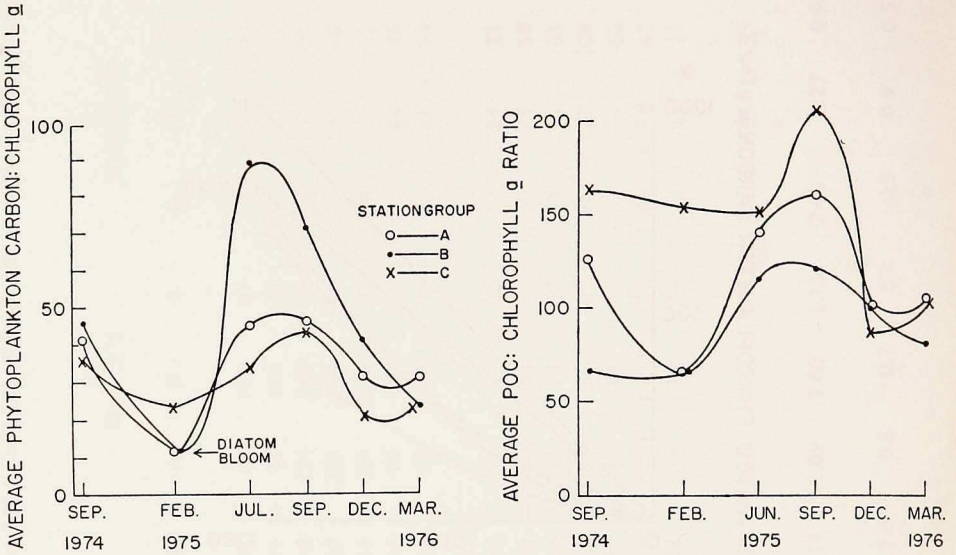


Figure 5a. Seasonal variation in carbon:chlorophyll *a* ratios. Phytoplankton carbon estimated by method 1 (see text). Station groups (described in *Methods*) were A: Stations 101, 102, 201, 202 and 203; B: 301, 302; C: all others.

Figure 5b. Seasonal variation in carbon:chlorophyll *a* ratios—POC. Station groups (described in *Methods*) were A: Stations 101, 102, 201, 202 and 203; B: 301, 302; C: all others.

is also consistent with a comparative study of light transmission and chlorophyll distribution (Kiefer and Austin, 1974). The optical "volume attenuation coefficient" measured with a beam transmissometer was highly correlated with chlorophyll (measured simultaneously in continuous profiles with a fluorometer). From particle scattering theory Kiefer and Austin concluded that the nonphytoplankton material in seawater consisted of one component that was constant with depth and location and another that covaried with the phytoplankton. If both components contained carbon, a curvilinear graph of phytoplankton carbon *v.* POC would result as in Figure 4.

The various methods imply a seasonal variation in the phytoplankton carbon: chlorophyll *a* ratio (Fig. 5a) noted earlier by Steele and Baird (1961) from linear regression of POC on chlorophyll *a* for the North Sea and adjacent waters. A similar variation was noted in the ratio POC/Chl. *a* (Fig. 5b) and in the maximum value of the assimilation number observed in depth profiles of photosynthetic rate (Fig. 6).

Chlorophyll maximum layer. J. D. H. Strickland and colleagues began measuring continuous vertical profiles of *in vivo* chlorophyll fluorescene in 1967 in this area. A subsurface maximum is usually present except during surface blooms (e.g., of diatoms at inshore stations during cruise SCBS-2). The chlorophyll maximum is

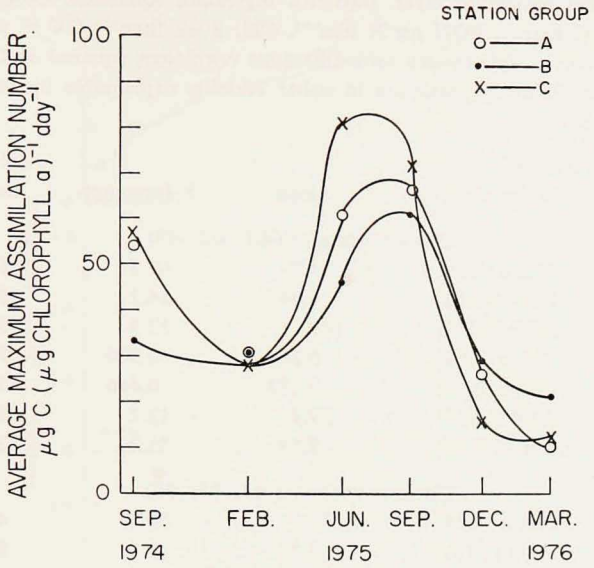


Figure 6. Seasonal variation in the photosynthetic assimilation number (μg carbon assimilated per μg chlorophyll *a* and day).

usually associated with the thermocline, a region of relative stability compared with regions above and below (Pingree *et al.*, 1975).

Results of Bartlett's regression analysis for the particulates of the chlorophyll maximum, taken in pairs, are shown in Table 3. The data were divided into two groups: onshore stations (−01 through −03) and offshore stations (−04 through −06), for all cruises taken together. For data processing purposes the chlorophyll maximum layer was defined as those sampling depths where the chlorophyll concentration was >2 times the surface chlorophyll value, but only the shallowest two such depths were included.

The average chlorophyll *a* concentrations in the layer were 2.65 and 1.04 μg liter^{-1} for the onshore and offshore station groups, respectively (Table 3). As with chlorophyll *a*, the POC, PON, ATP and total particle volume concentrations in the chlorophyll maximum layers were higher onshore than offshore by a factor of 2-3. The phytoplankton C/Chl. *a* ratios implied by the Bartlett's regression analysis are reasonable, compared with those from method 1, Table 2. The ratios POC/ATP and POC/PON were low in the chlorophyll maximum, as would be expected if much of the particulate matter were organisms in that layer (Herbland and Pages, 1975). The largest differences noted in the onshore *v.* offshore chlorophyll maximum layers were in respect to PON. More PON was present per weight of chlorophyll *a*, ATP, and POC offshore than onshore (Table 3) and POC: chlorophyll *a* ratios were lower (Table 3). Such a result would be expected from the increased

Table 3. Chlorophyll maximum layer. Bartlett's regression equations. Cruises 1-6 combined. Units: POC μg C liter^{-1}, PON μg N liter^{-1}, Chl. *a* μg liter^{-1}, CV = particle volume in mm^3 liter^{-1}. SRDF^2 = Spearman's rank-difference coefficient squared and expressed as %, which implies the % of the variation in either variable explainable by its correlation with the other variable.

Variable				SRDF^2	No.
Y (mean value)	*X* (mean value)	Slope	*Y*-Intercept	as %	Samples
		Onshore stations (-01, -02, -03)			
POC (212)	Chl. *a* (2.65)	53.8	69.5	63	23
POC (212)	PON (40.0)	4.94	14.2	58	23
POC (212)	ATP (0.955)	189	32.3	55	23
CV (1.26)	Chl. *a* (2.84)	0.267	0.500	71	15
ATP (0.959)	Chl. *a* (2.66)	0.193	0.446	57	24
PON (40.0)	ATP (0.955)	29.1	12.2	34	23
PON (40.0)	Chl. *a* (2.65)	5.58	25.3	21	23
		Offshore stations (-04, -05, -06)			
POC (91.9)	Chl. *a* (1.04)	39.9	50.2	47	23
POC (91.9)	PON (19.7)	3.34	26.0	81	23
POC (91.9)	ATP (0.498)	148	18.1	80	23
CV (0.917)	Chl. *a* (1.15)	0.519**	0.321	06	17
ATP (0.491)	Chl. *a* (1.02)	0.296	0.187	46	24
PON (19.7)	ATP (0.498)	40.2	—0.351	79	23
PON (19.7)	Chl. *a* (1.04)	10.1	9.19	44	23

** Slope not significantly different from zero ($p > 0.05$).

proportion of blue light reaching the deeper, offshore chlorophyll maximum layers (Wallen and Geen, 1971).

The slopes and intercepts of the Bartlett regression of POC on chlorophyll *a* for the chlorophyll maximum layers imply lower POC/Chl. *a* ratios in the phytoplankton and, in one case, higher "detritus" POC intercepts for this layer (Table 3) than for data grouped in other ways (Table 1).

Phytoplankton blooms. Patches of phytoplankton at the sea surface become apparent to the eye when their chlorophyll *a* content is about 5 μg liter^{-1} (Holmes *et al.*, 1967). Surface chlorophyll exceeded this, and blooms were visually apparent, on several occasions in this study (Fig. 3,) and were present during five of the six visits to Santa Monica Bay.

Particle size distributions in bloom samples were rather broad during the bloom of chain-forming diatoms of cruise SCBS-2 (Fig. 7a). In dinoflagellate blooms, some of which were essentially single species blooms, discrete particle size peaks were seen: a *Prorocentrum micans* bloom (Fig. 7b) and a mixed *Ceratium* spp. (*C. furca, C. fusus, C. dens*) and *Dinophysis* spp. bloom (Fig. 7c) are shown as examples. Particulate carbon estimates from the particle size distributions suggested that as

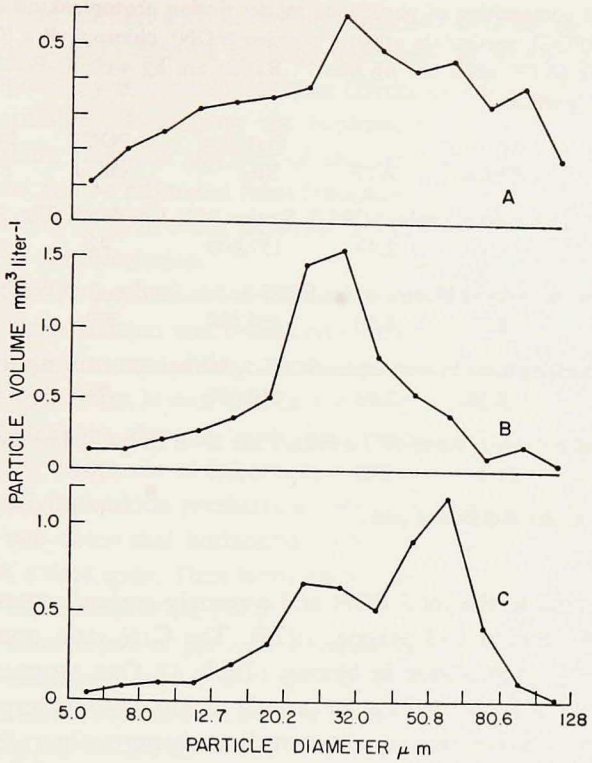


Figure 7. Particle size distributions observed during phytoplankton blooms. A—Mixed assemblage of chain diatoms. B—Bloom of the dinoflagellate *Prorocentrum micans*. C—Mixed assemblage of dinoflagellates dominated by *Ceratium furca, C. fusus, C. dens,* and *Dinophysis* spp.

much as 70 percent of the particulate carbon was associated with the single size distribution peak of *P. micans* (Fig. 7b). About 68 percent of the POC was associated with the peaks of Figure 7c.

The chemical parameters measured for these samples are given in Table 4. The ratio of POC/Chl. *a* was 42 for the diatom bloom and 78-209 for the dinoflagellate blooms. The POC per particle was highest for the diatom chains and follows approximately the average particle size (Fig. 7, Table 4). A dense *Gonyaulax polyedra* bloom, studied by Holmes *et al.* (1967) (Table 4), consisted of particles about 50 μm diameter and only these were counted. The higher POC/particle in that dense bloom refers only to *G. polyedra* rather than total particles >5 μm as in the present samples.

4. Discussion

The particulate matter collected in the present study has a protein amino acid

Table 4. Chemical composition of particulate matter during phytoplankton blooms. Particulate organic carbon (POC), particulate organic nitrogen (PON), chlorophyll *a* (Chl. *a*), and adenosine triphosphate (ATP) units are μg liter^{-1}. Ratios are by weight. POC per particle units are nanogram C/particle.

POC	PON	Chl. *a*	ATP	Particles liter^{-1}*	POC/ chl. *a*	POC/ PON	POC/ particle
Diatom bloom, cruise SCBS-2, Station 302, 1 m depth (Fig. 7a)							
477	77.3	11.4	2.99	157,000	42	6.2	3.0
Prorocentrum micans bloom, cruise SCBS-3, San Onofre, 3 m depth (Fig. 7b)							
1830	302	8.78	8.03	858,000	209	6.1	1.5
Mixed dinoflagellate bloom, cruise SCBS-5, Station 302, 1 m depth (Fig. 7c)							
643	94.4	8.20	2.93	219,000	78	6.8	2.0
Gonyaulax polyedra bloom off La Jolla, June 1965, (from Holmes *et al.*, 1967)							
4000	652	23.4	ND	713,000	170	6.1	5.6

* Particles liter^{-1} in size distribution peak.

content nearly equal to the total PON and a protein carbon content 40-50 percent of the total POC (Siezen and Mague, 1976). The C:N ratio averaged 5-7 (g/g), similar to that of phytoplankton in blooms (Table 4). One assumes the 50-60 percent of the POC, not accounted for by protein amino acids, is largely carbohydrate and lipid. Coccolith carbonate may also contribute importantly to the apparent POC as coccolithophorids are common in this area (Reid *et al.*, 1970). In cultured phytoplankton (Parsons and Takahashi, 1973) protein accounts for 36-68%, carbohydrate 20-42%, and lipid 4-23% of the ash-free dry weight. Similar values for natural phytoplankton grown in large plastic bags were reported by Antia *et al.* (1963). It is difficult to escape the conclusion that the material studied here consists of organisms, mostly phytoplankton, and of organic detritus little altered chemically from its composition in the organisms. Refractory, nonproteinaceous POC levels must be low. This is consistent with current views on particulates found in the euphotic zone, but not for particulate matter in deep water (Parsons and Takahashi, 1973, Chapter 2.4). The decomposition experiments of Menzel and Goering (1966) suggest the refractory POC would be about 20 μg C/l, or about 10-20% of the average POC measured here (Table 1).

The ephemeral nature of the particulate organic matter, including detritus, in the euphotic zone off Southern California is suggested by comparing POC and PON contents with the rates of carbon and nitrogen assimilation of the phytoplankton. If we assume theoretically that all grazing, sinking, and advective loss stopped, then the ratio of content to rate of synthesis would give a replacement time. The average ratio of POC/carbon assimilation observed was 8.2 $\pm$ 6.8 days and the ratio PON/nitrogen assimilation was 13.3 $\pm$ 6.9 days (based upon integrated values under 1 m^2

for the euphotic zone; carbon and nitrogen assimilation data are as yet unpublished.

The fate of the organic detritus remains uncertain. Microbial decomposition *in situ* and consumption by micro-zooplankton (Beers and Stewart, 1970) and salps seem logical possibilities. Loss from the euphotic zone by sinking is difficult to assess. While sinking rates for particles of this size range have been measured in the laboratory, and can be estimated from laboratory results (Smayda, 1970, Fig. 1) the actual trajectories of such small particles in the euphotic zone would be determined primarily by the circulation.

Pingree *et al.* (1975) considered the diffusive time scale of chlorophyll (= phytoplankton) in the water column and estimated characteristic times for a layer to mix above and below with its surroundings. In the upper mixed layer, in the thermocline (and chlorophyll maximum layer), and in the deeper mixed layer estimated times were: unstated but short, about a week, and about an hour, respectively, in the English Channel. A time scale of 1-2 weeks would be appropriate to the POC and PON content *v.* phytoplankton production rate cited above for the entire euphotic zone. However, one notes that horizontal motion would be extensive (many kilometers) over such a time span. Thus temporal studies at a single locality show rapid temporal change (Strickland *et al.*, 1970).

The observed distribution of particulate matter (Figs. 2, 3) reflects primary production and the standing stocks of phytoplankton. Values were high inshore, especially in Santa Monica Bay, and declined with depth in the euphotic zone save for mid-depth chlorophyll maximum layers. The ratio POC:primary production rate of carbon and PON:N-assimilation rate showed no onshore-offshore gradient; standing stocks and production rates changed proportionately. This result implies that loss rates are density-dependent as would be expected if losses resulted from either grazing or sinking (cf. Nakajima and Nishizawa, 1972). The ratios tended to be higher in winter than summer, although this was not statistically significant. If the ratios were interpreted as reflecting residence times of the particulate matter in the euphotic zone, then the longer times in winter could reflect a decline in the rate of biological activity with lower irradiance and temperature, as this seems more likely than seasonal changes in circulation of the sort that would influence particle suspension in the euphotic zone.

Relations among the parameters. "From the great similarity in the chlorophyll and carbon profiles it would seem intuitively reasonable to assume that a large part of the carbon is associated with the chlorophyll and so with the plants" (Steele and Baird, 1962). The rather high correlation between pairs of the parameters measured in this study and in Steele and Baird (1962) is not always to be expected, particularly in areas receiving river discharges and in ocean areas where the temporal changes in POC are out of phase with those in phytoplankton (see Parsons, 1975, p. 370 for a review).

The intercepts of the linear regression equations, taken at face value, suggested that phytoplankton would account for 70-80% of the particulate matter (POC on chlorophyll *a*) and that all organisms would account for 80-90% of the particulates (POC *v.* ATP) leaving only 10% for nonliving organic detritus. Results of other methods of estimating phytoplankton carbon suggest this is an artifact. Banse (1977) has discussed the problems inherent in linear regression analysis to estimate the carbon:chlorophyll *a* ratio of phytoplankton. He noted three sources of error: (1) that detrital organic carbon does not vary independently of phytoplankton carbon, (2) micro-zooplankton carbon does not vary independently of phytoplankton carbon, and (3) if the temporal rate of change of phytoplankton or detrital carbon reverses its sign during the sampling interval and the samples cannot be ordered correctly in space and time. All of these sources of error would be expected to affect the present regressions. Error sources 1 and 3 seem especially important in producing the high slope and low intercept values for this region where microzooplankton (Beers and Stewart, 1970) and bacterial carbon (Carlucci, personal comm.) are relatively low (in fact, Banse used data from the 1967 study off La Jolla among his examples). The errors seem to be less severe for the restricted data set for the chlorophyll maximum layer, in that the POC *v.* chlorophyll *a* regression suggests a lower phytoplankton C:Chl. *a* ratio and higher detritus carbon than the combined data set. However phytoplankton carbon estimated by method 1 (our standard of reference) is still about one-half of that predicted by the chlorophyll maximum regressions.

In principal, the linear regression of POC and ATP would give an intercept POC value reflecting nonliving material and regression of POC on Chl. *a* would give an intercept POC corresponding to nonliving POC plus POC in microheterotrophs. The difference between the two intercepts would be an estimate of the microheterotroph carbon (bacteria and microzooplankton). From Tables 1 and 3 the values of microheterotroph carbon as % of total POC were 6.4 (nitrate >1.0), 19 (nitrate <1), 18 (onshore chlorophyll maximum), and 35 (offshore chlorophyll maximum). While the absolute values are not to be trusted, the trend follows the expected distribution of microzooplankton (Beers and Stewart, 1969; 1970; Beers *et al.*, 1975).

Particle size distribution. Present instrumentation does not distinguish living from dead particles, but the peaks we observed in size distributions were clearly due to organisms. Microscopic examination of the particles was done aboard the ship on several of the cruises and the most dramatic peaks in the size distributions could be associated with particular species of plankton (see also Sheldon and Parsons, 1967).

The total particle volume gave essentially the same information as POC analysis. The average ratio POC:particle volume was about 0.05 mg per mm^3, the same as found by Sheldon and Parsons (1967). When the particle size distribution data were calculated as carbon (>5 μm particle only), using a size-dependent carbon:volume

function derived from phytoplankton (Mullin *et al.*, 1966), this carbon value was about 60% of the POC value. Thus the carbon:volume relationships of the total particulate matter was similar to that of phytoplankton and the 40% difference is likely due to counting only particles >5 μm diameter while the POC analyses were done with filters retaining <1 μm diameter particles.

Ratios of particle volume to chlorophyll *a* were similar to those reported previously. Parsons (1969) found a ratio of 1.0 μg Chl. *a*:mm^3 for microplankton and 3.39 for nanoplankton in Saanich Inlet. Margalef (1974) found an average ratio 2.85 for waters off northwest Africa. Gieskes (1972) reported a value 0.56 off the Dutch coast and Zeitzschel (1970) found 0.8 for the ratio in the Gulf of California. The present mean value was 1.68. The ratio would not be expected to be a constant, but its variation is of some interest to the extent that it reflects variation in phytoplankton composition resulting from species or physiological differences. For example the Chl. *a*:particle volume ratio in the chlorophyll maximum layer was 3.2 and at other depths, 1.6. This implies either less detritus per phytoplankton biomass in the chlorophyll maximum layer or more chlorophyll per volume of phytoplankton, or both.

The particulate size distributions were especially useful in assessing the "purity" of algal blooms and the extent to which the chemical analyses of bloom samples reflected the composition of the dominant phytoplankton species in the samples. For example, the dinoflagellate, *Prorocentrum micans*, contributed as much as 70% of the particle volume, calculated as carbon, in the most nearly uni-algal sample studied here (Fig. 7b, Table 4).

Phytoplankton carbon and carbon:chlorophyll a ratio. As noted by Banse (1977) and others there is no adequate means of estimating phytoplankton carbon in natural seawater samples. Microscopic counting and cell size determination used together with an equation for the cell carbon:cell volume relationship is the best method presently available. This was done, along with POC measurement, in a detailed, weekly plankton study in 1967 off La Jolla. A linear regression of the ratio phytoplankton carbon:POC *v.* POC with the 1967 data gave an equation (see Methods) with the useful feature that phytoplankton carbon would constitute an increasing proportion of the POC as the POC varied from small to large values, as observed elsewhere (Hobson *et al.*, 1973). This is intuitively reasonable if high POC results from plankton blooms. This equation was used here (method 1) as a standard for comparison of other methods of estimating phytoplankton carbon and the carbon:chlorophyll *a* ratio. The other method giving the most similar results was a simple equation developed by Steele (1962; Steele and Menzel, 1962) in which the carbon:chlorophyll *a* ratio of the phytoplankton varies as a function of insolation, daylength and ambient nutrient concentration (phosphate was used here). Some of the other methods gave higher values (POC regression on chlorophyll *a*; a curve

fit of POC to chlorophyll *a*; ATP × 250). Method number 7 (see Methods) gave consistently lower values than method 1 (Fig. 4). Methods 2, 3, and 7 also, as in method 1, indicated that phytoplankton carbon became a greater fraction of total POC as POC increased.

All the estimates, calculated as phytoplankton carbon:chlorophyll *a* ratios, showed a seasonal variation in the ratio as did the POC:chlorophyll *a* ratio (Fig. 5). This paralleled the seasonal change in the photosynthetic rate per chlorophyll (Fig. 6) with lowest values in winter and highest values in summer. These seasonal trends would be expected from studies of phytoplankton growth rate and photosynthesis as functions of irradiance and temperature.

Living particulate matter, as 250 × ATP, gave high values in this study, approximating the total POC (Table 2, method 4). Reasons for this are under study and will be treated in a later publication.

Particulate matter in the chlorophyll maximum layer. The chlorophyll maximum layer is regarded as a plankton habitat of greater physical stability than the surface mixed layer and the waters below (Pingree *et al.*, 1975). For example, Lasker (1975) found a persistent layer for several weeks in the spring of 1974 in this area, dominated by the dinoflagellate *Gymnodinium splendens.* A full discussion of our observations on the chlorophyll maximum layer in these waters will be provided in a separate report. For the present we note that the stability and corresponding homogeneity assumed for the layer would be expected to minimize the sources of error attending linear regression analysis of the particulate parameters. But this was not the case, as discussed earlier. The regression suggested that most of the POC was associated with chlorophyll while the average phytoplankton carbon, estimated by method 1, was only 31 and 21 percent of the POC in the chlorophyll maximum layer, respectively, for the onshore and offshore station groupings of Table 3. These are much smaller proportions than in surface blooms where as much as 70% of the POC could be attributed to a single species of phytoplankton.

The regression slopes suggested that phytoplankton in the chlorophyll maximum layer of offshore stations was relatively richer in chlorophyll and PON than at inshore stations (Table 3). Ambient nutrient concentrations at the depth of the layers did not differ between offshore and onshore, nor did temperature. In both cases the chlorophyll maximum layer was usually located in the upper portion of the vertical nutrient gradient and in the thermocline. But the layer was deeper offshore than onshore. Thus sunlight irradiance would be lower at chlorophyll maximum layer depths offshore. Moreover, the irradiance would be richer in the blue portion of the visible spectrum in offshore layers than in onshore layers. Possibly we are seeing shifts in chemical composition resulting from the blue light, as noted by Wallen and Geen (1971), as well as an intensity effect.

Conclusions. The view that the particulate matter in the euphotic zone of the south-

ern California Bight has a chemical composition not unlike phytoplankton and that it has a short residence time, of the order two weeks, in the theoretical absence of grazing and sinking, allows new hypotheses with respect to the structure and dynamics of the food web and to the related problem of the transfer of pollutants associated with organic particles. For example, the apparent lack of a high background concentration of refractory POC suggests that nonliving POC is either (1) eaten, with micro-zooplankton and salps the most likely grazers, (2) decomposed within the euphotic zone by microbial activities, (3) exported by horizontal currents, or (4) that it sinks to deep water. Future experimental work will be directed at assessing the importance of these routes.

Studies as this, with sampling by water bottles attached to the hydrographic wire, can give misleading results and should be considered with caution. For example, direct observations of particulate matter by divers (e.g. Alldredge, 1976) suggest large aggregates too fragile to be observed in samples taken with water bottles. The water bottle samples presumably included fragments resulting from the mechanical disruption of such aggregates, however, leading perhaps to distortion in particle size determinations, and more seriously, to an erroneous conceptual view of particulate matter in its various biological roles.

The examination of alternative indirect methods for assessing phytoplankton standing stocks as carbon will provide a basis for specific growth rate estimations useful in assessing phytoplankton growth dynamics and yield to herbivores. The particle size information has already been useful in assessing the availability of food particles for anchovy larvae (Lasker, 1975).

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