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THE PHYTOPLANKTON COMPONENT OF SESTON IN SAN FRANCISCO BAY

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ABSTRACT

Phytoplankton biomass (as carbon) was estimated from chlorophyll a concentrations (Chla) and a mean value for the ratio of phytoplankton carbon to chlorophyll a in San Francisco Bay. The ratio was determined as the slope of a Model II regression of POC' against Chla, where POC' is total particulate organic carbon minus sediment-associated non-phytoplankton carbon. Samples from 30 fixed sites in the channel and lateral shoals of San Francisco Bay were collected once or twice a month from April to November 1980, and at irregular intervals in South Bay during 1984 and 1985. For all data the calculated mean value of phytoplankton C:Chl*a* was 51 (95% confidence interval = 47-54). No significant differences were found in the C:Chl*a* ratio between shallow and deep sites (where light availability differs) or between northern and southern San Francisco Bay (where phytoplankton community composition differs). Using the mean C:Chl*a* ratio of 51, we calculated that phytoplankton biomass constitutes about one third of seston carbon under most circumstances, but this fraction ranges from about 95% during phytoplankton blooms to less than 20% during spring periods of low phytoplankton biomass and high suspended sediment concentration.

1. INTRODUCTION

The estimation of phytoplankton biomass is a difficult and important problem in aquatic ecology. Accurate measurement of biomass in terms of photosynthetic pigments is easy, but the pigment content of algal cells is variable and several mechanisms can induce variations in the ratio of chlorophyll to potentially more useful measures of biomass, such as carbon or nitrogen (CULLEN, 1982). Measurement of phytoplankton biomass as carbon (PC) is required in studies of: (1) trophic dynamics, wherein measures of PC as a fraction of total particulate organic carbon (POC) define the relative importance of phytoplankton and detritus as food sources for suspension-feeders, and (2) phytoplankton population dynamics, in which population turnover rate can be calculated from productivity if PC is known.

Determination of PC in natural waters is difficult because there is no quantitative and convenient method of separating it from other components of POC. This problem is especially difficult in turbid estuaries, where non-phytoplankton components of POC can be large and highly variable. Historically, PC has been calculated by either: (1) assuming a constant ratio of phytoplankton carbon:chlorophyll a, with values ranging from about 30 to 60 (MALONE, 1977a; COLIJN, 1982; PETERSON & FESTA, 1984), and then multiplying this conversion factor times Chla; (2) measuring ATP and assuming that the non-algal contribution to ATP is small and that the ratio PC:ATP is constant (HOLM-HANSEN, 1970); (3) counting and measuring algal cells, calculating cell volume, and then using empirical equations (*e.g.,* STRATHMANN, 1967) relating cell volume to cell carbon (EPPLEY *et al.,* 1977; PINGREE *et al.,* 1982; FASHAM *et al.,* 1983; HOLLIGAN *et al.,* 1984): or (4) simultaneously measuring POC and chlorophyll a, then calculating the carbon:chlorophyll a ratio from the slope of the regression of POC against Chla (*e.g.,* MENZEL & RYTHER, 1964; LORENZEN, 1968; MALONE, 1977b; CADEE, 1982; PINGREE *et al.,* 1982). BANSE (1977) has commented on the potential sources of error in this last chemical approach, including interference from zooplankton carbon and tripton carbon.

The purpose of this paper is to use an extension of method (4) to estimate a mean carbon:chlorophyll a ratio for phytoplankton within a

diverse estuarine system, San Francisco Bay. Attempts were made to minimize or correct for the contribution of non-phytoplankton POC by screening out macrozooplankton and large detrital fragments, and subtracting from total POC that fraction associated with suspended sediments. The relative contribution of phytoplankton to seston carbon was then calculated for a range of conditions that typify an annual cycle.

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2. STUDY SITE

The San Francisco Bay system comprises two different estuaries which have been contrasted in detail elsewhere (*e.g.,* CLOERN & NICHOLS, 1985). Northern San Francisco Bay (including Suisun Bay and San Pablo Bay, Fig. 1) is a partially-mixed estuary highly influenced by seasonal inputs of freshwater from the Sacramento and San Joaquin Rivers. Combined river discharge is low ($\simeq$100 to 500 $m^3 \cdot s^{-1}$) during summer-autumn and high (1000 to 10 000 $m^3 \cdot s^{-1}$) during winter freshets. Concentrations of suspended particulate matter (SPM) are high, and can exceed 100 $mg \cdot l^{-1}$ during winter peaks in the riverine influx of suspended sediments or during summer when wind-induced resuspension is most intense (CLOERN & NICHOLS, 1985), and when a turbidity maximum forms in the upper estuary (PETERSON et *al.,* 1975; CONOMOS & PETERSON, 1977; CONOMOS et *al.,* 1985). phytoplankton dynamics are characterized by a spring-summer diatom bloom in San Pablo Bay followed by a summer-autumn bloom in the upstream Suisun Bay (CLOERN et *al.,* 1985).

The South Bay (Fig. 1) is a semi-enclosed basin that is usually well-mixed; exceptions occur

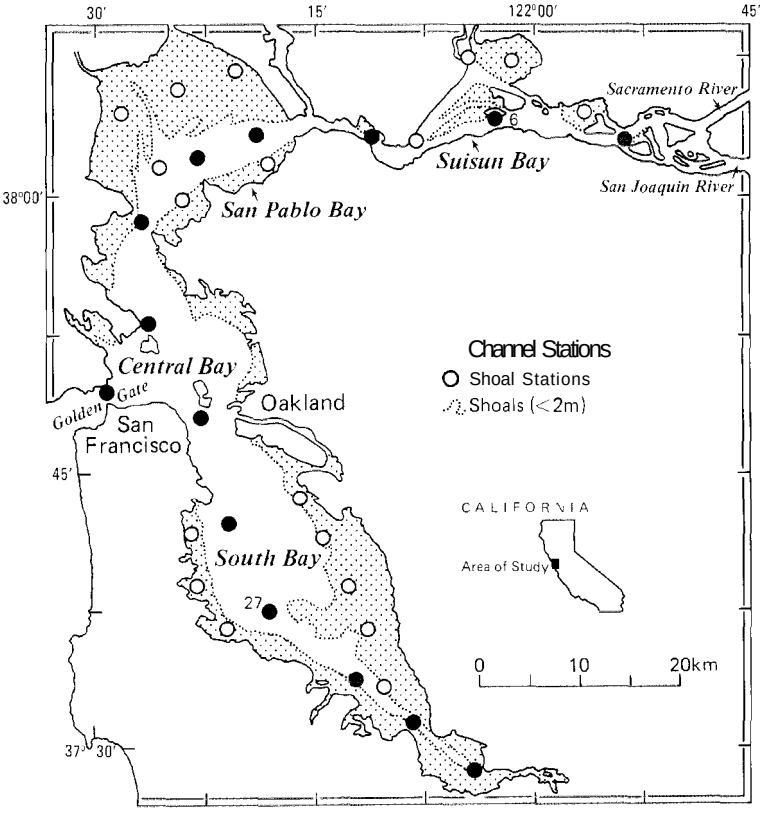

Fig. 1. San Francisco Bay estuary, showing locations of channel and shoal stations where samples were collected. Shaded portions depict areas with water depth of 2 m or less (MLLW).

following peaks in river discharge when freshwater inflow causes density stratification (CLOERN, 1984). Suspended sediment concentrations are lower here, usually less than 50 $mg \cdot l^{-1}$ (CONOMOS et *al.,* 1985). A bloom of nanoplankton (microflagellates and small diatoms) occurs in spring when the water column is stratified, and phytoplankton biomass is low the remainder of the year (CLOERN et *al.,* 1985). Both North and South San Francisco Bay have broad subtidal shoals and a deeper ($\simeq$10 to 30 m) channel (Fig. 1). Typically, suspended sediment concentration and phytoplankton biomass are high in shallow water relative to the channel. Hence, the large-scale spatial variability of seston in San Francisco Bay is characterized by longitudinal gradients away from the riverine source of suspended sediments, and transverse gradients resulting from the influence of bottom topography. This study was designed to include seston samples collected across these spatial gradients as well as over the seasonal cycles of phytoplankton biomass.

3. METHODS

Near-surface water was sampled once or twice a month throughout San Francisco Bay, from April to November 1980, and at irregular intervals in South Bay during 1984 and 1985. During 1980, samples were collected from fixed sites in both the channel and lateral shoals of each embayment (Fig. 1), as well as at the Golden Gate to represent water properties at the seaward end of the estuary. During 1984-85, samples were collected only at the fixed sites in the South Bay channel.

Samples for particulate organic carbon (POC) and chlorophyll a (Chla) were passed through a 60-pm Nitex screen to exclude macrozooplankton and large detrital particles, but to retain most phytoplankton biomass (see COLE & CLOERN, 1984). Then 10 to 75 ml of the screened sample were filtered onto a 13-mm precombusted Gelman AE glass fiber filter. Each filter was dried under vacuum, placed inside a nickel capsule, then stored in a desiccator until analysis. POC was measured with a Perkin-Elmer model 240B elemental analyzer, using acetanilide as a standard. For the 1980 carbon analyses, mean precision among duplicates was 8% (n = 128 sets of duplicates), and the mean for 1984-85 carbon determinations was 5% (n = 25 sets).

For chlorophyll a determinations, 0.1 to 2 liters of screened sample were filtered onto a 47-mm Gelman AE glass fiber filter under light vacuum. Filters were frozen until analyzed. At the time of analysis filters were ground in 90% acetone and extracted overnight prior to measurement with a Varian model 635 spectrophotometer (method from STRICKLAND & PARSONS, 1972). Chlorophyll a concentration was calculated from LORENZEN'S (1967) equations that correct for phaeopigments. For 1980 chlorophyll determinations, mean precision among duplicates was 6% (n = 77), and for 1984-85 samples, 9% (n = 12).

SPM concentration was measured by collecting particulates on preweighed 47-mm silver filters (Selas Flotronics FM-47). Filters were air-dried and reweighed to determine the weight of SPM collected; correction for weight of salts was made from salinity (HAGER & HARMON, 1984). Duplicate samples were taken at most stations, and the mean deviation of SPM measurements made throughout the year was 1.4 $mg \cdot l^{-1}$ (HAGER & HARMON, 1984).

4. RESULTS AND DISCUSSION

A broad range of seston abundance and composition was sampled in this study: SPM concentration ranged from <1 to 297 $mg \cdot l^{-1}$, POC concentration ranged from 94 to >5000 $\mu g \cdot l^{-1}$, and Chla concentration ranged from 0.6 to 57 $\mu g \cdot l^{-1}$. Contrasts between North and South San Francisco Bay are apparent in Fig. 2, which shows the mean and range of values for SPM, POC, and Chla at representative sample sites in each estuary (stations 6 and 27, Fig. 1). Mean SPM concentration was about seven times higher at the North Bay site than at the South Bay site (Fig. 2A), with peaks in spring (following the winter maxima in river flow) and in summer associated with the turbidity maximum. Lowest SPM concentrations occurred in South Bay during stratification events, when suspended sediments presumably sank from the surface mixed layer (CLOERN, 1984). Mean POC concentration was about four times higher at the North Bay site than at the South Bay site (Fig. 2B). Highest POC concentrations were associated with the turbidity-phytoplankton maximum in summer, and minima generally occurred during autumn when phytoplankton biomass, resuspension rate, and the riverine influx of sediments were all low. Mean chlorophyll a concentration was threefold higher in North Bay than in the South

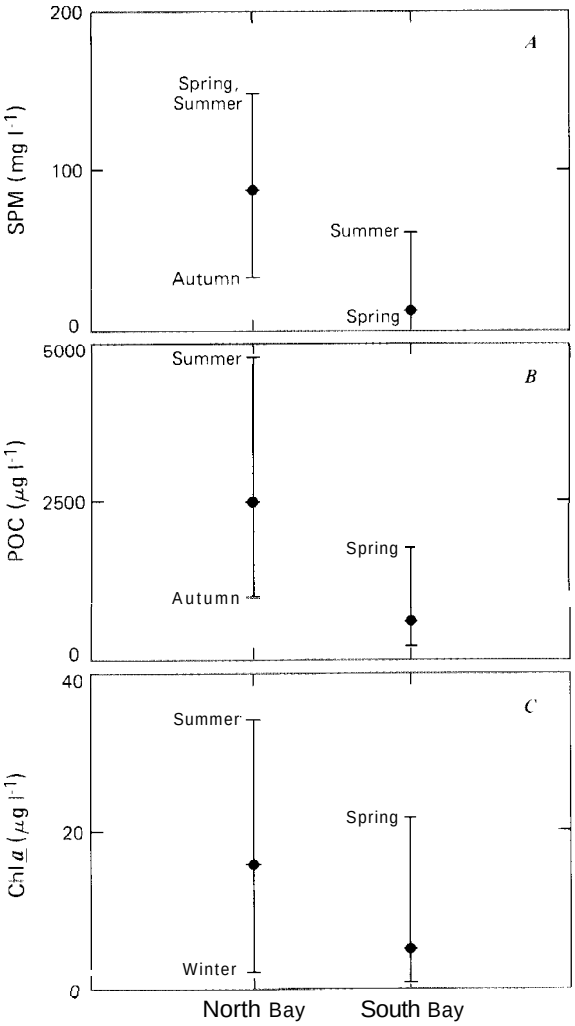

Fig. 2. Mean and range of values for (A) SPM. (B) POC and (C) Chla at Station 6 in North Bay and Station 27 in South Bay.

Bay (Fig. 2C), with maximum concentrations of 35 $\mu g \cdot l^{-1}$ during the summer bloom at station 6, and about 20 $\mu g \cdot l^{-1}$ at station 27 during the spring bloom.

4.1. SEPARATION OF POC INTO PHYTOPLANKTON AND OTHER COMPONENTS

Sources of suspended particulate organic carbon in estuaries are diverse and can include phototrophs (epibenthic microalgae, vascular plants, macroalgae. phytoplankton), sewage-derived POC, zooplankton (molts and live animals), fecal pellets, pseudofaeces of benthic infauna, aggregates of inorganic-organic materials, bacteria, and dissolved organic carbon (DOC) adsorbed onto particles including suspended sediments. Our partitioning of sestonic POC into phytoplankton (PC) and non-phytoplankton (NPC) components is based upon the assumption that measured POC comprises three general classes of organic material:

$$POC = \underbrace{B \times Chla}_{PC} + \underbrace{F \times SPM + D}_{NPC} \qquad (1)$$

where B is the mean carbon:chlorophyll a ratio of phytoplankton; F x SPM represents organic carbon (plus carbonate) bound to or associated with the mineral sediments (F is the carbon content of SPM); and D is the fraction of NPC that is uncorrelated with suspended sediments.

If POC includes a significant component of sediment-associated organic matter, then the traditional approach of estimating B by regression of POC against Chla is inappropriate unless the SPM-associated POC is constant. Thus, this method cannot be used directly in San Francisco Bay because SPM concentration varies over at least two orders of magnitude. However. this inherent complication of turbid estuarine waters can be resolved by partitioning data into subsets according to SPM range (HAGER et *al.*, 1984), then assuming that NPC is constant within each data subset. We divided results from the 249 samples in which SPM < 100 $mg \cdot l^{-1}$ into eight subsets based upon SPM concentration. This partitioning was based on the frequency distribution of SPM measurements such that about 30 values were included in each subset. Then for each subset. we estimated separate values of B from regression of POC against Chla (Table 1). RICKER (1973) explains that Model II linear regression is the appropriate regression model for estimating slopes when both the dependent (POC) and independent (Chla) variables are uncontrolled and subject to measurement error. We used the geometric mean regression of LAWS & ARCHIE (1981).

All eight regressions (Table 1) were significant ($p < 0.01$), although there was a wide range in the goodness of fit among subsets (coefficient of determination, r^2, ranged from 0.24 to 0.85). The eight independent estimates of B ranged from 46 to 101 μg C$\cdot \mu g^{-1}$ Chla and were unrelated to SPM range (Table 1). On the other hand, intercepts of these regressions increased monotonically with mean SPM concentration (Table 1). We interpret these intercept values A

TABLE 1

Geometric mean (Model II) regression of POC against Chla for 8 subsets of data, partitioned according to SPM range. Shown are: mean concentration of SPM within each subset; intercepts (A) and slopes (B) of regressions: coefficient of determination (r^2); and number (n) of POC-Chla data pairs in each subset.

SPM Range ($mg \cdot l^{-1}$)	Mean SPM ($mg \cdot l^{-1}$)	A ($\mu g\ C \cdot l^{-1}$)	B ($\mu g\ C \cdot \mu g^{-1} Chla$)	r^2	n
0- 4	2.6	152	63.0	0.24	34
4- 7	5.8	169	101	0.29	39
7- 10	8.2	236	74.4	0.81	33
10- 13	12.1	329	46.4	0.73	29
13- 17	15.4	438	52.3	0.85	27
17- 26	22.1	462	52.2	0.74	32
26- 63	41.9	748	46.9	0.26	48
63-100	79.7	1469	70.6	0.52	22

as estimates of NPC (*i.e.*, POC when Chla = 0). Regression against mean SPM concentration showed a highly significant linear relation between NPC and suspended sediment concentration (Fig. 3):

$$A = NPC = 106 + 16.8 \times SPM. \quad (2)$$

Equation 2 defines the sediment-associated and residual components of NPC:F = 16.8 μg C·mg^{-1} SPM and D = 106 μg C·l^{-1}. We used equation 2 to correct POC measurements for the large and variable component of non-phytoplankton POC:

$$POC' = POC - NPC = POC - [106 + 16.8 \times SPM]. \quad (3)$$

By definition, the quantity POC' should represent phytoplankton carbon, PC = B x Chla, and thus regression of POC' against Chla should have a zero intercept and a slope equal to the mean C:Chl*a* ratio B. Using equation 3 we calculated 249 values of POC' and regressed these against Chla (Fig. 4). The overall regression was significant (65% of the variation in POC' was correlated with Chla), and yielded a mean C:Chl*a* ratio of 51 (95% confidence interval = 47 – 54, calculated from the approximation of RICKER, 1975). The intercept of the overall regression was small (77 μg C·l^{-1}) and not significantly different from zero (based upon the t-test of a Model I regression of POC' against Chla).

The large residuals around the regression of all data in Fig. 4 are not surprising, considering the variable sources of seston carbon in

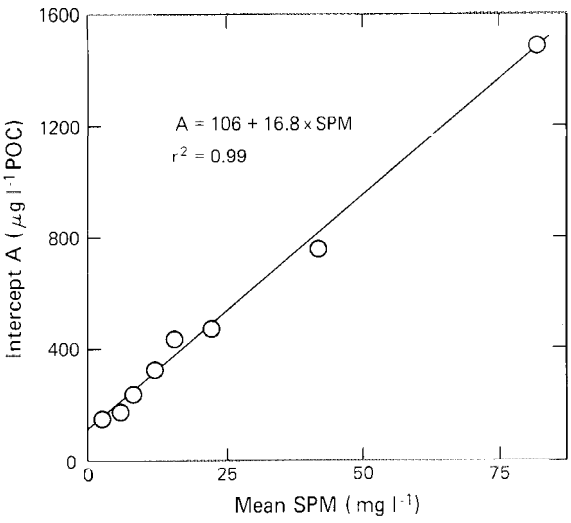

Fig. 3. Linear regression of NPC (intercepts A of the 8 regressions of POC vs Chla; Table 1) against mean SPM concentration in each data subset.

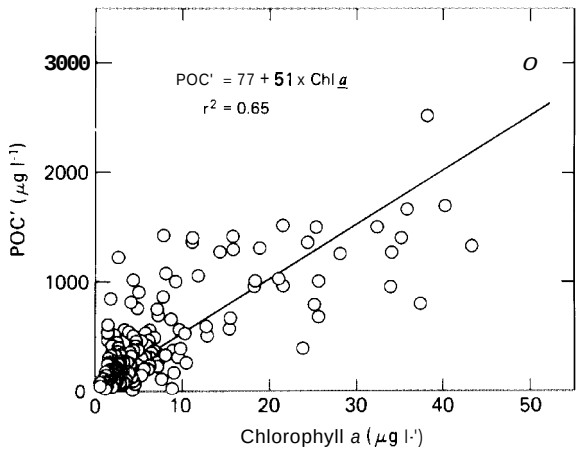

Fig. 4. Plot of all values of sediment-corrected POC against Chla. The line represents the Model II regression of all data: slope = 51, intercept = 77 μgC·l^{-1}.

estuaries, and they represent several sources of error including measurement error which averaged 4 $\mu g \cdot l^{-1}$ for POC and 0.3 $\mu g \cdot l^{-1}$ for Chla. A second source of error is the assumption of a constant C:Chl*a* ratio although planktonic algae have the capacity to regulate cellular quotas of carbon and chlorophyll a in response to variable light environments (LAWS & BANNISTER, 1980; CULLEN, 1982), nutrient concentrations (HUNTER & LAWS, 1981: CADEE, 1982), and growth rates (SAKSHAUG. 1977; HUNTER & LAWS, 1981). Thus much of the scatter in Fig. 4 could result from the constraint of prescribing B as a constant when it truly is a variable ratio. Similarly, use of equation 3 to correct POC for sediment-associated carbon implies that the organic carbon fraction of suspended sediments is constant. THOMSON-BECKER & LUOMA (1985) found that consolidated sediments of San Francisco Bay mudflats have a variable fraction of organic carbon that changes seasonally, and we might expect the same for suspended sediments. Given these known sources of error, we must interpret our overall regression as yielding an estimate of the mean value of B for San Francisco Bay phytoplankton communities, and recognize that the true variance of this ratio is unknown. Remarkably, the mean value of B = 51 is virtually identical to the mean value of B = 52 from phytoplankton enumerations, calculation of biovolume, and application of STRATHMANN'S (1967) equations for subsets of water samples analyzed here (CLOERN et *al.,* 1985).

4.2. SPATIAL VARIATIONS IN THE CARBON: CHLOROPHYLL RATIO

The a *priori* specification of a constant phytoplankton C:Chl*a* ratio in San Francisco Bay is difficult to justify because: (1) phytoplankton community composition varies between the North Bay and South Bay (CLOERN et *al.,* 1985); and (2) the light exposure of phytoplankton (a major environmental control on B; LAWS & BANNISTER, 1980) differs greatly among geographic areas of San Francisco Bay. One measure of light exposure, the ratio of photic depth to water depth, averaged 0.29 for the South Bay channel and 0.08 for the more turbid Suisun Bay channel in 1980 (COLE & CLOERN, 1984). Further, there are transverse gradients in light exposure between the deep channels and lateral shoals. These large-scale spatial variations in light exposure cause parallel variations in the specific productivity (*i.e.,* growth rate) of phytoplankton in San Francisco Bay (CLOERN et *al.,* 1985) and potentially cause similar variability in the cellular ratio of carbon to chlorophyll a in resident phytoplankton. To examine this possibility, we divided all POC'-Chl*a* data pairs (all data in Fig. 4) into subsets by geographic area: first we partitioned data into North Bay and South Bay sites, and then into channel and shoal sites. Separate regressions of POC' against Chla yielded estimates of B that were indistinguishable among geographic areas, with B ranging from 46 to 54 (Table 2). This suggests that (1) large-scale spatial variations in the phytoplankton C:Chl*a* ratio cannot be detected with the approaches used here, even though phytoplankton collected in this study experienced a wide range of light history: and (2) use of a mean value of $B \approx 50$ is justified throughout San Francisco Bay, regardless of phytoplankton community composition or productivity.

4.3. THE PHYTOPLANKTON CONTRIBUTION TO POC

Assuming that phytoplankton biomass can be estimated from measured chlorophyll a concentration and the mean conversion factor B = 51 μg

TABLE 2

Geometric mean (Model II) regressions of POC' against Chla (POC' = A + B x Chla) for data partitioned among North ar South San Francisco Bay; shoal and channel sites (see Fig. 1); and all data Values in parentheses are 95% confidenc intervals of slopes (B), calculated from RICKER (1975).

Area	*A* ($\mu g\ C \cdot l^{-1}$)	*B* ($\mu g\ C \cdot \mu g^{-1} Chla$)	r^2	*n*
North Bay	93	49 (43 - 55)	0.55	107
South Bay	67	53 (48 - 57)	0 75	142
Shoal Sites	118	46 (40 - 53)	0 58	86
Channel Sites	56	54 (49 - 58)	0.70	163
All Data	77	51 (47 - 54)	0.65	249

TABLE 3

Calculated fraction (R) of phytoplankton carbon (= 51 x Chla) to total seston carbon (POC) for data subsets partitioned according to SPM and Chla. Low Chl*a* < 10 $\mu g \cdot l^{-1}$; high Chla > 20 $\mu g \cdot l^{-1}$; low SPM < 20 $mg \cdot l^{-1}$; high SPM > 40 $mg \cdot l^{-1}$.

Seston Properties	*Mean* SPM ($mg \cdot l^{-1}$)	Mean *Chla* ($\mu g \cdot l^{-1}$)	Mean R (%)	*n*
Low SPM-Low Chla	8.4	2.9	33	162
Low SPM-High Chla	13.6	31.0	95	6
High SPM-Low Chla	58.7	5.2	18	26
High SPM-High Chla	70.8	30.0	63	12

$C \cdot \mu g^{-1}$ chlorophyll a, we calculated the phytoplankton component of seston carbon as:

$$R = [(B \times Chla)/POC] \times 100\%. \quad (4)$$

Mean values of R were calculated for conditions when SPM concentration was either low (< 20 $mg \cdot l^{-1}$) or high (> 40 $mg \cdot l^{-1}$), and when Chla concentration was either low (< 10 $\mu g \cdot l^{-1}$) or high (> 20 $\mu g \cdot l^{-1}$). These combinations of SPM-Chla ranges represent the spectrum of seston properties in San Francisco Bay, and allow some generalizations concerning the contribution of phytoplankton biomass to the standing stock of POC. Under most circumstances (*i.e.,* when Chla < 10 $\mu g \cdot l^{-1}$ and SPM < 20 $mg \cdot l^{-1}$), phytoplankton biomass constitutes about one-third of seston carbon in San Francisco Bay (Table 3). Marked deviations from this fraction occur during spring when SPM is high and Chla concentration is low (phytoplankton biomass is less than 20% of seston carbon). Conversely, during the spring bloom of South Bay when SPM < 20 $mg \cdot l^{-1}$ and Chla > 20 $\mu g \cdot l^{-1}$, phytoplankton biomass composes most (mean 95%) of the seston carbon. Hence, the relative importance of phytoplankton as a component of suspended particulate organic matter is highly variable in space and time, ranging from about 20% to 95% during this study period.

5. CONCLUDING REMARKS

We have presented here a simple approach to partition POC in turbid waters among phytoplankton and non-phytoplankton components. Because determination of the phytoplankton component R has been done with a variety of methods, comparison among estuaries is difficult. Our results suggest that in estuaries or coastal waters with high concentrations of suspended sediment, a large fraction of POC is organic material associated with, or bound to, sediments. This implies that regression methods (*e.g.,* POC against Chla) will yield different values for the C:Chl*a* ratio depending on whether the sediment-associated fraction of organic carbon is subtracted from total POC. For our data set, Model II regression of uncorrected POC against Chla yielded a C:Chl*a* ratio of 83, nearly twice as large as the value derived from regression of sediment-corrected values POC' against Chla. Hence, our estimate that $B \simeq 50$ is not comparable, for example, to that of MALONE (1982) for the Hudson River plume and New York Bight, which was based on regression of total POC against Chla. Similarly, calculation of B as the slope of the POC-Chla regression line varies among regression models. By definition, slopes of Model II regressions are greater than slopes of Model I regressions ($B_{II} = B_I/r$; LAWS & ARCHIE. 1981). For our data set, Model I regression of POC' against Chla yielded a value of $B = 41$. Hence, our estimates of the phytoplankton component of POC for San Francisco Bay are not comparable to those based upon Model I regression (*e.g.,* TETT et *al.,* 1975; MALONE & CHERVIN, 1979), which yields smaller estimates of R. Our general understanding of phytoplankton as a carbon or energy source in estuaries is thus dependent upon acceptance of a standard approach for calculating R. Development of a standard approach requires critical analysis of the assumptions and limitations of methods used, and should include a comparison of results from a diversity of techniques. For example, the ^{14}C incubation technique of REDALJE & LAWS (1981) holds promise as a new and independent method for estimating C:Chl*a* ratios of natural phytoplankton communities, and this method should be applied in estuaries.

A more difficult and more important problem is to assess the ecological significance of variations in the phytoplankton component of seston. We perceive estuaries as productive systems, but few generalizations exist concerning the significance of phytoplankton as a food resource in estuaries, particularly as the ratio R varies across the large gradients of SPM and Chla that characterize estuaries. If the phytoplankton fraction of POC ranges from 20 to 95%, what is the significance of this variability to consumers, including bacteria? Do high SPM-low Chla environments select for a different nutritional mode

(and community) of heterotrophs than low SPM-high Chla environments? A related set of questions concerns the large pool of sediment-associated POC: What fractions are adsorbed DOC, inorganic-organic aggregates, or attached bacteria? What are the important sources and sinks, and how do turnover rates of this component compare to turnover rates of phytoplankton POC? These persistent and difficult questions form a basis for our attempt to understand carbon flux and the ecological significance of phytoplankton production in estuaries.

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