Biomass and Productivity of Three Phytoplankton Size Classes in San Francisco Bay

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ABSTRACT: Primary productivity of three **size** classes of phytoplankton ($<$**5** pm, **5-22** pm, $>$**22** pm) was measured monthly at six sites within San Francisco Bay throughout **1980.** These sites in the three principal embayments were chosen to represent a range of environments, phytoplankton communities, and seasonal cycles in the estuary. Temporal variations in productivity for each size class generally followed the seasonality of the **corresponding** fraction of phytoplankton biomass. The **5-22 μm size** class accounted for 40 to 50% of the annual production in each **embayment,** but production by phytoplankton $>$**22** pm ranged from **26%** in the southern reach to **54**% of total phytoplankton production in the landward embayment of the northern reach. A productivity index is derived that predicts daily productivity for each size class as a function of ambient irradiance and integrated chlorophyll a in the photic zone. For the whole phytoplankton community and for each size class, this index was constant and estimated as $\simeq$**0.76 g C m^{-2}** (g chlorophyll a **Einstein**)$^{-1}$. The **annual** means of maximum carbon assimilation numbers were usually similar for the three size classes. Spatial and **temporal** variations in size-fractionated productivity are shown to be primarily due to differences in biomass rather than sire-dependent carbon **assimilation** rates.

Introduction

The predominance of nanoplankton in natural waters has been hypothesized to be due to intrinsically higher growth rates (Williams 1964; Eppley and Sloan 1966), photosynthetic rates ('laguchi 1976). and nutrient uptake rates (Munk and Riley 1952) of small algal cells with high surface-to-volume ratios. However, the evidence from field and laboratory studies for physiological differences associated with cell size is conflicting (Ranse 1976), and the conditions in which one would expect netplankton or nanoplankton to dominate the phytoplankton communities of estuaries are not apparent (Malone 1980).

Year-long studies of estuarine primary productivity by different size classes of phytoplankton are few in number, but they have shown marked variations in the seasonality of productivity by netplankton and nanoplankton. In the Hudson River Estuary (Malone 1977) and Peconic Bay (Bruno et al. 1983), nanoplankton account for the major portion of annual productivity, principally due to their predominance in summer and fall when primary productivity is highest. In Narragansett Bay (Durbin et al. 1975) nanoplankton predominate in summer and netplankton in winter, and the contributions to annual production by the two size classes are essentially equal. In contrast, nanoplankton appear to be responsible for 70 to 90% of phytoplankton productivity in the Chesapeake Bay during all seasons (McCarthy et al. 1974; Van Valkenburg and Flemer 1974).

Annual productivity by the phytoplankton community (Cole and Cloern 1984) and seasonal variations in the biomass of three phytoplankton size classes (Cloern et al. 1985) have been reported for San Francisco Bay. But, the relative importance of these phytoplankton size classes to productivity
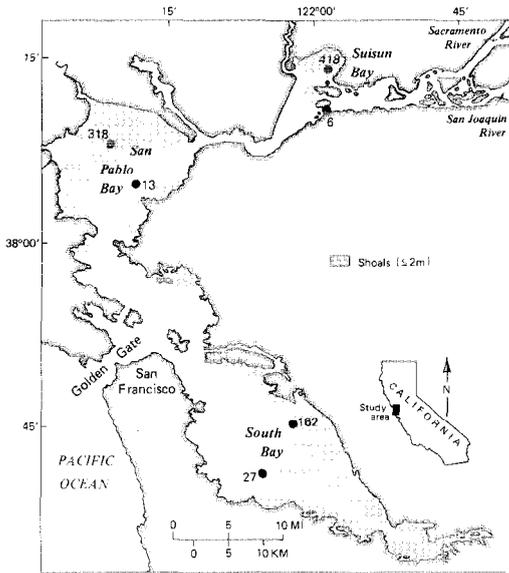
Fig. 1.   Map of San Francisco Bay showing locations of incubation sampling sites. Shaded portions: areas where water depths (MLLW) are less than 2 m.

by the total phytoplankton community is not known for this large estuary. Differential contributions to total productivity by different size phytoplankton can result from either (1) size-dependent rates of photosynthesis (Malone 1980) or (2) differences in the biomass of each size class. Our results suggest that in San Francisco Bay, spatial and temporal variations in the relative contribution of three phytoplankton size classes (<5 pm, 5–22 μm, and >22 pm) to community productivity are controlled primarily by variations in the biomass of the three fractions. This is evidenced by (1) strong correlations between the biomass and productivity of each size class, (2) similar chlorophyll-specific carbon assimilation rates among the size classes, and (3) equal photic zone productivity indices for the three size classes.

Methods

Monthly measurements of size-fractionated chlorophyll a and productivity were made at six sites in San Francisco Bay (Fig. 1) between January 1980 and February 1981. Samples were collected from 2 m at the channel sites (stations 27, 13, and 6) and 1 m at the shoal sites (stations 162, 318,

and 418). A channel and shoal site were selected in each embaymeni because biomass and turbidity vary along horizontal transects from deep to shallow water (Cole and Cloern 1984). Samples for chlorophyll and productivity were prescreened through 59-pm Nitex to exclude macrozooplankton. Shortly after collection, chlorophyll samples were partitioned among netplankton (22–59 pm), nanoplankton (5–22 μm), and ultraplankton (<5 μm). The samples were gravity filtered through a 22-μm Nitex, 5-pm Nuclepore, or a Gelman type A/E glass-fiber filter. The 22-pm and 5-pm filtrates were then passed through Gelman type A/E glass-fiber filters. Chlorophyll a concentration (B) was determined by fluorometry (Strickland and Parsons 1972). Carbon uptake of the whole phytoplankton community was measured using carbon-14 (5 μCi in a 150 ml glass bottle), in 24-h simulated in situ incubations at eight light levels: 100, 55, 30, 15, 8, 3, 1 and 0% of ambient irradiance (I,). Following the incubation, productivity samples were partitioned among the three size classes by gravity filtering 3-ml portions of the sample through a 22-pm Nitex, 5-pm Nucleopore, or a Gelman glass-fiber filter (see Cole and Cloern 1984). Sample activity was determined using a liquid scintillation spectrometer with an external standard to correct for quenching. The CO_2 content of a sample was estimated using the equations proposed by Skirrow (1975) that utilize measures of total alkalinity, determined by a Gran titration, and pH of the water.

Simulated incubation depths were calculated as $\ln(I_i/I_0)/\epsilon$, where I_i/I_0 is the fraction of daily surface insolation received by bottle i. The attenuation coefficient (ϵ) was measured using a submersible LiCor quantum sensor. Net productivity per day in the photic zone was calculated for each size class and for the total assemblage by integrating (trapezoidal quadrature) measured rates of carbon uptake [$mgC\,(m^3\,d)^{-1}$] over the photic layer to Z_p, the depth of 1% ambient irradiance. Net productivity per year in the photic zone was estimated by integrating daily size-fractionated productivity over the year.

Maximum daily carbon assimilation rates ($P_m{}^B$) for each size class were derived from

TABLE 1. Annual mean chlorophyll a concentrations (mg m^{-3}), total community productivity (g C m^{-2}), and percent chlorophyll a and percent production for each phytoplankton size class.

Location	Site	Chl	Prod	Percent Netpl		Percent Yanopl		Percent Ultrapl	
				Chl	Prod	Chl	Prod	Chl	Prod
South Bay	27	4.1	150	20	26	57	47	23	27
	162	5.8	150	18	26	61	46	21	28
San Pablo Bay	13	3.0	140	33	27	41	47	26	26
	318	9.3	130	44	43	41	45	15	12
Suisun Bay	6	13	98	45	58	50	37	4	15
	418	20	93	42	49	55	45	3	6

chlorophyll a normalized photosynthesis-irradiance (P-I) curves. The Gauss-Newton nonlinear least squares technique was used to obtain the best fit of the data to the hyperbolic tangent function (Platt and Jassby 1976).

Results

We measured productivity at locations that reflect the range of temporal and spatial patterns in phytoplankton biomass, productivity, and species diversity typical of San Francisco Bay. Spatial differences in annual means of phytoplankton biomass and productivity are summarized in Table 1. Mean biomass levels differed by nearly seven times, and the relative importance of both size class biomass and productivity varied markedly between embayments. In South Bay, nanoplankton were responsible for the major fraction of both phytoplankton biomass and productivity at both sites. Netplankton and ultraplankton contributions to total biomass and community productivity were nearly equivalent, but only about half the level attributable to nanoplankton. In San Pablo Bay the relative importance of nanoplankton to total phytoplankton biomass (chlorophyll a) and annual productivity levels was similar at the deep and shallow water sites (13 and 318, respectively). However, the relative significance of netplankton and ultraplankton chlorophyll a and productivity levels at the two sites differed both from one another and from those in South Bay. While netplankton and ultraplankton chlorophyll a and productivity contributions were about equal at site 13, about 44% of phytoplankton biomass and productivity could be attributed to netplankton, but only about 14% to ultraplankton. The reduced importance of ultraplankton was even more evident in the landward Suisun Bay. There phytoplankton biomass and production attributable to netplankton and nanoplankton differed slightly between sites 6 and 418, but the ultraplankton contribution was only about 5% of the total.

There were distinct temporal patterns of biomass and productivity for each size class (Figs. 2 and 3). Chlorophyll a maxima were observed during spring and early summer at the lower bay sites and in summer and fall in Suisun Bay. Except for site 13, temporal patterns of phytoplankton community productivity and biomass at an individual site were similar, and the relative importance of the different size classes was similar at both sites within an embayment. Maximum levels of phytoplankton biomass and productivity in the South Bay (Figs. 2A, and 2B, 3A, and 3B, respectively) occurred during early spring when chlorophyll a concentrations reached 25 mg m^{-3}. This bloom was dominated by nanoplankton. Times preceding and following the spring bloom were marked by low levels of chlorophyll a and carbon uptake, so that variations in biomass or productivity for the different size fractions during other seasons had only a small effect on annual totals. In San Pablo Bay, netplankton chlorophyll a (Figs. 2C and 2D) comprised 75% of the late spring biomass maxima. In other seasons netplankton typically comprised only 10% of the total, while to a large degree, nanoplankton and at times ultraplankton accounted for the rest. Consequently, for the annual study period, netplankton and nanoplankton comprised about equal portions of the total phytoplankton biomass. The diversity in seasonal patterns for the three size frac-
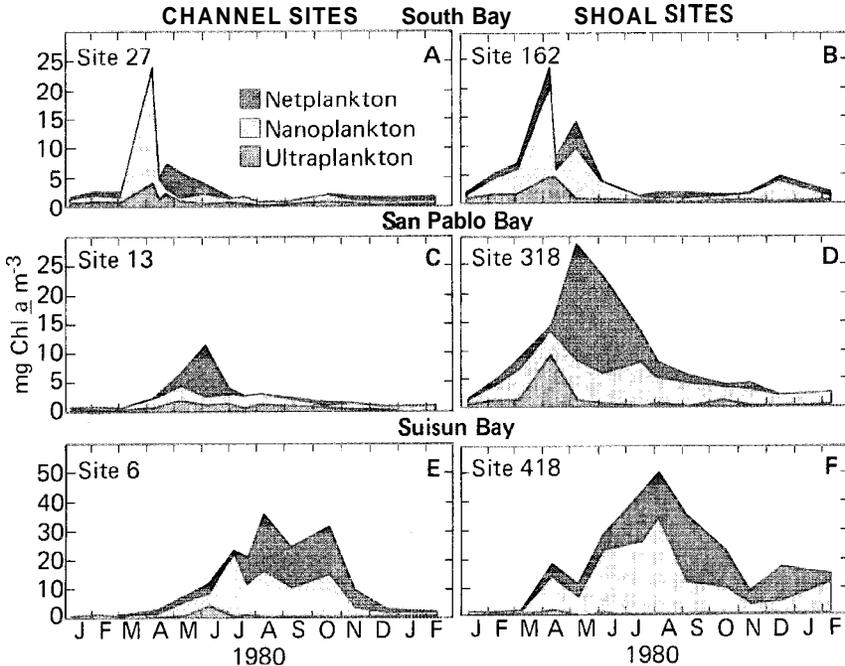
Fig. 2. Seasonal variation of size class chlorophyll *a* at the six incubation sites. Note the scale change for sites-6 and 418.

tions in San Pablo Bay was also due to the greater prominence of ultraplankton at the channel site than at site 318. At site 13, the contribution of biomass and productivity by the <5-μm phytoplankton was relatively consistent throughout the study, while their presence was more episodic at site 318.

Maxima in phytoplankton biomass occurred later in the year in Suisun Bay than in other embayinents (Figs. 2E and 2F; note scale changes), and absolute chlorophyll a concentrations typically exceeded those seen in South Bay or San Pablo Bay. Early in the year the phytoplankton community was dominated by nanoplankton, but by early summer the pattern shifted and netplankton replaced nanoplankton as the dominant form. Ultraplankton never comprised a significant portion of the population, except at the initiation of the bloom. Temporal patterns of photic zone productivity in Suisun Bay (Figs. 3E and 3F) were similar to those of biomass, but the levels of productivity were significantly lower than those measured in the other embayments both for the phytoplankton population as a whole and for each size fraction. This was particularly

evident at site 418 in the shallows. Maximum chlorophyll a levels exceeded 50 mg m^{-3}, but photic zone productivity at the same time was 0.23 g C $(m^2 d)^{-1}$. Although the shallow water and channel sites in each enibayment had similar temporal patterns of relative size class dominance, in terms of absolute chlorophyll a concentrations, the shoals generally had higher levels of phytoplankton biomass than the channel sites. This pattern did not occur with respect to productivity however. Photic zone productivity at each shallow site was equal to or lower than productivity at the nearby deepwater site.

In addition to seasonal differences in biomass and productivity, the diversity of the conditions under which productivity was measured is reflected by differences in the floristic composition of the phytoplankton. Species responsible for the major portion of phytoplankton biomass during bloom and nonbloom periods are listed in Table 2. Microflagellates consistently accounted for a dominant portion of phytoplankton biomass in South Bay. During the bloom period the small diatom *Cyclotella* caspia and
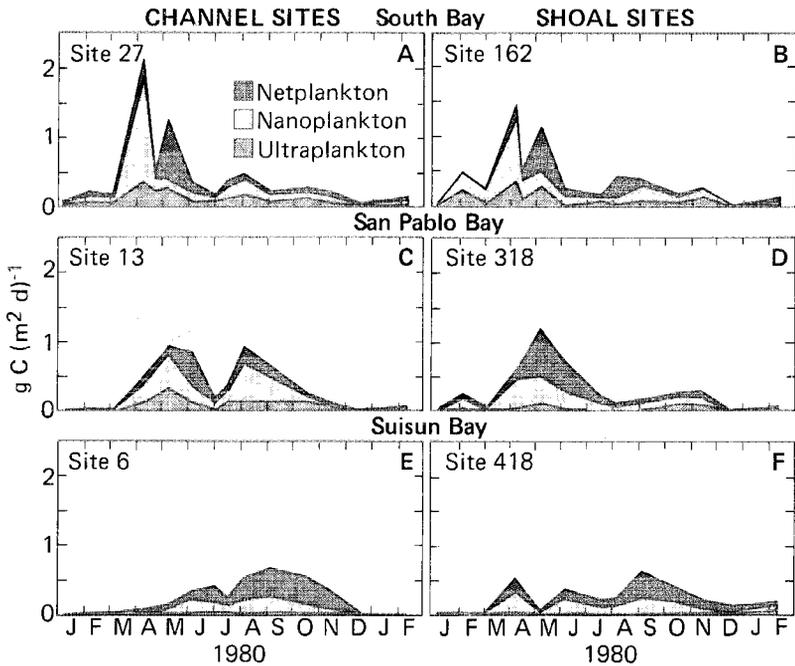
Fig. 3.   Seasonal variation of size class productivity at the six incubation sites.

the larger diatom *Coscinodiscus jonesianus* comprised significant fractions of the biomass, but such forms were not evident during the rest of the study. In San Pablo Bay the phytoplankton population progressed from freshwater taxa before the spring bloom to relatively large diatoms during the bloom,

after which microflagellates predominated. Small freshwater species comprised most of the winter and spring populations in Suisun Bay, whereas diatoms accounted for most of the phytoplankton biomass during the summer bloom and at subsequent times.

Nitex screen (22-μm mesh) was not al-

TABLE 2.   Phytoplankton responsible for the major portion of algal biomass during bloom and nonbloom periods. Cell dimensions are length × width/diameter in μm. The data are taken from Wong and Cloern (1982). Estimates of cell biomass were derived from cell volumes using the conversions of Strathmann (1967).

	South Bay	San Pablo Bay	Suisun Bay
Pre-bloom	*Chroomonas amphioxea* (11 × 6)	*Melosira* spp. (9 × 12)	chlorophytes
	Chroomonas minuta (6 × 4)	*Fragilaria crotenensis* (95 × 3)	*Melosira distans* (12 × 6)
	Cryptomonas testacea (14 × 7)	*Amphora* spp. (74 × 37)	*Cyclotella* spp. (7 × 15)
Bloom	*Cyclotella caspia* (6 × 8)	*Coscinodiscus* spp. >(100 × 150)	*Skeletonema costatum* (8 × 6)
	C. minuta	*Thalassiosira* spp. >(10 × 50)	*Thalassiosira decipiens* (10 × 18)
	C. amphioxea		
	Coscinodiscus jonesianus (48 × 195)		
Post-bloom	*C. minuta*	*C. minuta*	*S. costatum*
	C. amphioxea	*C. amphioxea*	*T. decipiens*
	C. testacea	*C. testacea*	*Cyclotella striata* (10 × 40)

TABLE 3. Annual mean maximum assimilation number [mg C (mg chl d)$^{-1}$] and range for each size class at each incubation site. The number of $P_m{}^B$ values varied because the data would not always converge using the Gauss-Newton curve-fitting routine. Hence, $P_m{}^B$ values could not always be determined.

Location	Site	Size Fraction	$P_m{}^B$	Range	n
South Bay	27	netpl.	150	43–330	7
		nanopl.	98	16–330	12
		ultrapl.	100	43–270	13
	162	netpl.	190	15–410	9
		nanopl.	81	4–160	9
		ultrapl.	120	24–390	11
San Pablo Bay	13	netpl.	110	36–200	5
		nanopl.	88	12–200	12
		ultrapl.	78	29–140	11
	318	netpl.	160	67–300	8
		nanopl.	73	9–130	12
		ultrapl.	98	4–320	12
Suisun Bay	6	netpl.	72	29–160	13
		nanopl.	53	13–110	12
		ultrapl.	86	12–190	14
	418	netpl.	60	10–98	10
		nanopl.	42	6–79	13
		ultrapl.	91	10–290	13

ways appropriate for quantitatively screening the phytoplankton commonly found in Suisun Bay. Based on cell dimensions, *S. costatum* (8 × 6 pm) and *T. decipiens* (10 × 18 μm) would be considered nanoplankton. But, because these algae exist as chains or in aggregates (Cloern et al. 1983) the 22-μm mesh used in this study probably did not completely partition these taxa into either the netplankton or nanoplankton fraction. Undoubtedly a portion of the *S. costatum* and *T. decipiens* community was retained by the screen while the other portion passed through (cf. Bruno et al. 1983; Furnas 1983). Thus, although individuals from these taxa are nominally nanoplankton, they were probably frequently retained by the 22-μm screen.

Maximum carbon assimilation rates for each size class also varied over a broad range at each station and between embayments (Table 3). In South Bay and San Pablo Ray, the annual mean $P_m{}^B$ for netplankton was greater than the mean value for either the nanoplankton or ultraplankton fraction, whereas in Suisun Bay mean $P_m{}^B$ for the ultraplankton was greater than for the other two fractions. However, differences in as-similation rates between size classes were only significant at site 318 where mean $P_m{}^B$ for the netplankton was greater (p < 0.01) than mean $P_m{}^B$ for the nanoplankton and at site 418 where the mean $P_m{}^B$ for the ultraplankton was significantly greater (p < 0.05) than mean $P_m{}^B$ for the nanoplankton. In no other instances were there significant differences in $P_m{}^B$ among size classes at an individual site.

Discussion

Spatial and temporal variations in the relative contributions of three phytoplankton size classes to total phytoplankton productivity in San Francisco Bay result mainly from variations in biomass, rather than physiological differences related to cell size. This conclusion is supported by (1) a direct relation between relative productivity and chlorophyll *a* concentration for each class. (2) a lack of difference in $P_m{}^B$ among size classes, and (3) similarity in photic-zone productivity indices for the different size classes.

An hypothesis that is basic to many studies of productivity by different size classes of phytoplankton is that small cells have higher rates of productivity per unit of chlorophyll *a* than do large cells. If this hypothesis is correct, then the relative contributions of production by small cells should exceed their relative proportion of total phyivplankton biomass. In this study the relative contributions to productivity by the three size classes of phytoplankton were significantly correlated (r   0.56 to 0.80, p < 0.001) with the relative biomass of the respective size class (Fig. 4). But, the slopes of their regressions did not consistently increase with a decrease in cell size as would be anticipated if the smaller cells had higher carbon uptake rates than did large cells. This suggests that for each size class, production is simply proportional to biomass. Similarly, regression analysis of relative netplankton productivity and chlorophyll data from eight estuarine and coastal systems (Malone 1980, Table 12.2) indicates that 85% of the variation in relative productivity by netplankton in those systems is correlated with changes in the relative contribution of netplankton biomass. Likewise, the relative
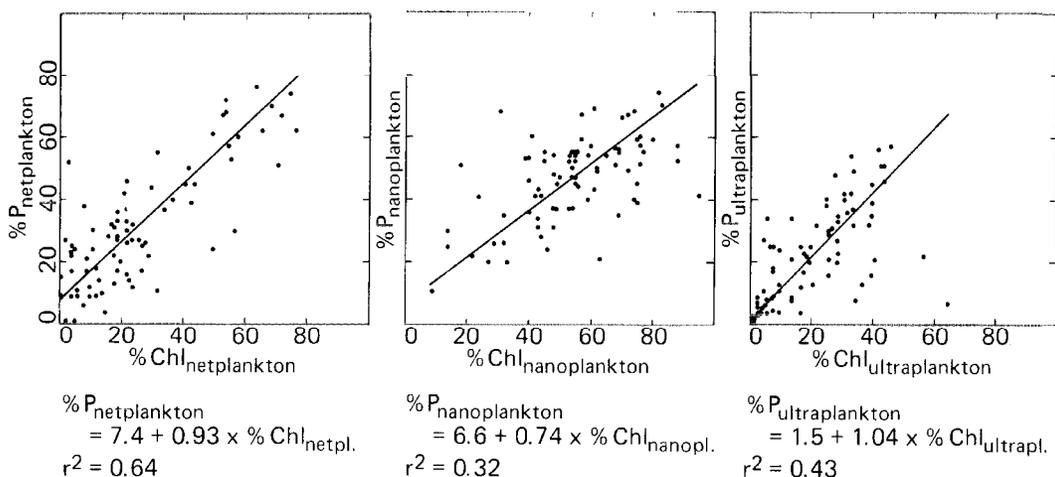
Fig. 4.   Regressions of percent productivity against percent biomass for each phytoplankton size class.

contribution of size-fractionated biomass is an excellent approximation of relative size class production in Peconic Bay (Bruno et al. 1983). Thus, for a variety of estuarine and coastal environments, relative size class productivity is generally proportional to the relative contribution of fractionated phytoplankton biornass. However, scatter in our data and the results of other studies (Furnas 1983) indicate that at times size class productivity is disproportionate to fractionated biornass.

In addition to biomass, productivity in non-nutrient-limiting conditions is dependent on chlorophyll a-specific photosynthetic rates (Falkowski 1981). Culture studies (Williams 1964; Eppley and Sloan 1966; Eppley et al. 1969; Taguchi 1976; Schlesinger et al. 1981) and theoretical considerations (Munk and Riley 1952; Laws 1975) indicate that small cells have inherently high growth rates (assimilation numbers) and thus their productivity should be disproportionate to their biomass. However, the general applicability of this conclusion is challenged by Banse (1976), Durbin (1977), and Chan (1980), who did not find a size-dependence of the chlorophyll-specific growth rate. Additionally, results from field studies are conflicting. No difference in chlorophyll normalized carbon uptake rates for phytoplankton size classes is reported by McCarthy et al. (1974), Van Valkenburg and Flemer (1974), Durbin et al. (1975), and

Bruno et al. (1983). But, Malone (1980) and Malone and Neale (1981) find higher assimilation rates for nanoplankton than for netplankton. In our study there were few significant differences in $P_m{}^B$ among size classes from the same incubation site (Table 3). Neither were there consistent trends in the order of size class $P_m{}^B$ values for the six sites. Consequently, it is not possible to demonstrate that size class productivity in this estuary was greatly influenced by size-dependent differences in photosynthetic rates.

A third piece of evidence that productivity for each size class is primarily a function of biomass is the similar relation between photic-zone productivity and BZ_pI_0 for the three size classes. In the light-limited portion of the photic zone, biomass-specific productivity P^B is a function of photosynthetic efficiency and irradiance (αI). Since irradiance at depth z can be calculated as: $I, - I_0e^{-\epsilon z}$, in systems where B is constant over the photic zone, biomass-specific productivity in the photic zone can be approximated as

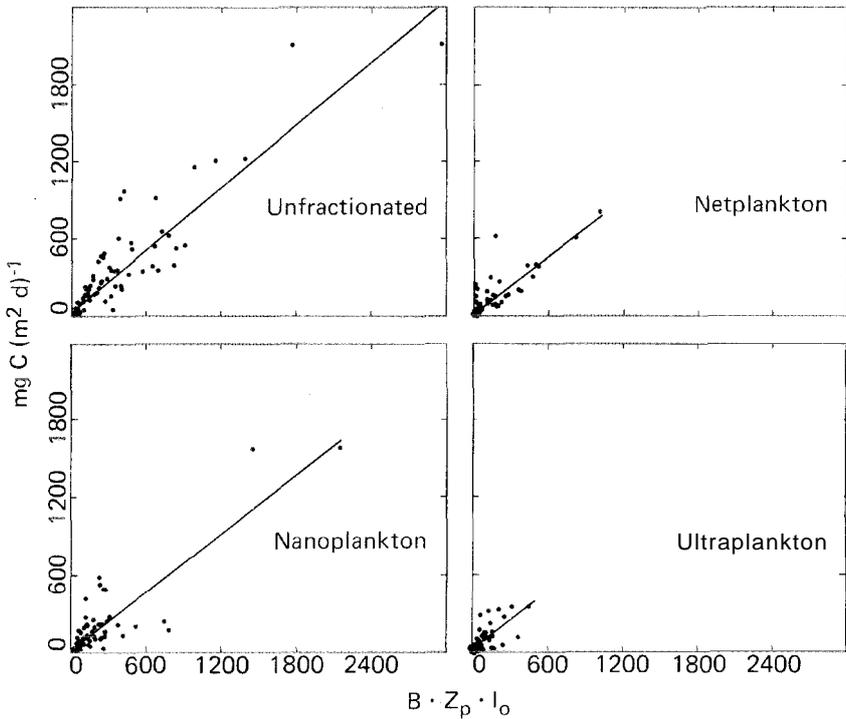$$\int_0^{Z_p} P_z{}^B \, dz = \alpha I_0 \int_0^{Z_p} e^{-\epsilon z} \, dz$$

Fig. 5.   Regression of size-fractionated daily productivity [mg C $(m^2 d)^{-1}$] against the composite parameter BZ_pI_0 for each phytoplankton size class. Regression parameters are given in Table 4. The data for the unfractionated phytoplankton community were originally presented in fig. 5, Cole and Cloern 1984. The figure is included here for comparison with data from size-fractionated samples.

By definition the 1% light depth $Z_p = \ln(100)/\epsilon$ or $4.6/\epsilon$, thus

$$\int_0^{Z_p} P_z^B \, dz = \frac{\alpha I_0 Z_p}{4.6} [1 - e^{-4.6}]$$

$$= \frac{0.99 \alpha I_0 Z_p}{4.6}.$$

If a photic zone productivity index (T) is defined as $0.99\alpha/4.6$ then

$$\int_0^{Z_p} P \, dz = \Upsilon BZ_pI_0. \qquad (2)$$

TABLE 4.   Regression parameters and 95% confidence intervals from regressions of photic zone productivity against BZ_pI_0 for each size class. a = intercept, Υ = slope; n = 82.

Size Class	a	Υ	r^2
Unfractionated	57 ± 50	0.81 + 0.09	0.81
Netplankton	34 ± 20	0.73 ± 0.10	0.73
Nanoplankton	28 + 33	0.73 ± 0.09	0.75
Ultraplankton	25 ± 16	0.76 ± 0.15	0.55

Thus productivity in the photic zone is a function of Υ, irradiance, and photic zone chlorophyll a. Υ is similar to the water-column light utilization index Ψ of Falkowski (1981). However, using equation 2, it can be shown that the two indices (Υ and Ψ) are equivalent only when a values do not vary. This condition is unlikely over an annual study period when species composition and the physiological state of phytoplankton vary.

For 82 measures of productivity by three size classes of phytoplankton, $\int_0^{Z_p} P$ was a linear function of BZ_pI_0 (Fig. 5 and Table 4). For the total phytoplankton community, and each size class: netplankton, nanoplankton, and ultraplankton, 81%, 73%, 75%, and 55% (respectively) of the variance in productivity can be explained simply by variation in BZ_pI_0 (Table 4). The slopes, Υ of the regressions for the three fractions and

the community as a whole ranged from 0.73 to 0.81 g C m^2 (g chl *a* Einstein^{-1}) (Table 4), but these differences were not significant at p < 0.05. Therefore, since I_0 and Z_p were also constant for the three fractions, differences in integral productivity between size classes were primarily a function of differences in biomass between the size classes.

Although species composition, biomass, and primary productivity of the three phytoplankton size classes varied greatly between sites, our results suggest three conclusions. First, differential contributions by the three size classes to productivity by the total phytoplankton community were due largely to differences in biomass. Second, in this study there were no apparent differences in maximum carbon assimilation rate between size fractions. Thus, spatial and temporal variations in size-fractionated production were not related to physiological (carbon assimilation rates) differences associated with cell size. The discrepancy regarding the existence of size-class differences in photosynthetic parameters based on theoretical and laboratory experiments using single species or field experiments with natural phytoplankton populations may be due to the range in physiological responses possible for mixed populations existing in less than optimal growth environments (Banse 1976; Furnas 1983). Differences in physiological response between size classes of phytoplankton may not be generally discernable in field experiments, except when the phytoplankton are dominated by a single species. Third, $\int_0^{Z_p} P$ is the same function of BZ_pI_0 for the whole phytoplankton community and for each of the three size fractions.

Therefore, for San Francisco Bay the question of what controls spatial and temporal variations in productivity by different size fractions of phytoplankton becomes a question of what controls the contribution of each fraction to total biomass. Empirical observations suggest that physical processes (advection, vertical mixing, accumulation at convergences), sinking, and size selective grazing must be important (Cloern et al. 1985). Knowledge of the relative contributions to productivity by different size

classes of algae is growing, but little is yet known about the ecological importance of these results. The significance to higher trophic levels of primary production by large or small algal cells is an inherently much more difficult problem that needs to be addressed.

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