Significance of biomass and light availability to phytoplankton productivity in San Francisco Bay

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ABSTRACT: Primary productivity was measured monthly at 6 sites within San Francisco Bay, USA, throughout 1980. The 6 sites were chosen to represent a range of estuarine environments with respect to salinity, phytoplankton community composition, turbidity, and water depth. Annual net production over the photic zone ranged from 95 to 150 g C m^{-2}, and was highest in regions of lowest turbidity. Daily photic zone net productivity PN_{pd} ranged from 0.05 to 2.2 g C m^{-2} d^{-1}, and was significantly correlated with the composite parameter $B \, I_o/\varepsilon$ (where B = phytoplankton biomass; I_o = daily surface insolation; ε = attenuation coefficient). Linear regression of PN_{pd} against $B \, I_o/\varepsilon$ indicated that most (82 %) of the spatio-temporal variability in primary productivity within this estuary is explained by variations in light availability and phytoplankton biomass. We also calculated annual water-column net productivity PN_{wy} as a fraction of annual gross productivity PG_y. The ratio $PN_{wy} : PG_y$ was inversely related to the ratio of water depth H to annual mean photic depth $\overline{Z}_p$. This linear relation indicates that the water column of San Francisco Bay is a net photosynthetic source of organic carbon only when the ratio $H : \overline{Z}_p < 6$. In deep turbid habitats, where $H : \overline{Z}_p > 6$, respiratory loss exceeds productivity. Thus, 2 empirical formulations allow us to estimate productivity over the photic zone and water column from simple properties that are easily measured.

INTRODUCTION

Estimates of annual phytoplankton productivity in estuaries range between 6.8 g C m^{-2} (Joint and Pomroy, 1981) in very turbid water to 530 g C m^{-2} (Stockner and Cliff, 1979) in a clearer system. However, the study of production by estuarine phytoplankton is in its infancy, and although annual rates of phytoplankton production have been reported for a number of estuaries (Boynton et al., 1982), the processes that control primary and secondary productivity in estuaries are poorly understood. In a review of factors controlling phytoplankton production in 63 estuarine systems, Boynton et al. (1982) note that environmental data are poor predictors of primary productivity. They conclude that in a broad spectrum of estuaries algal production is high in warm periods and that the ratio of nitrogen to phosphorus is low during algal blooms. Otherwise, they find that generalities regarding primary productivity cannot be made when all estuarine systems are considered together.

Spatial and seasonal changes in phytoplankton productivity are described for numerous estuaries (e.g. Williams, 1966; Williams and Murdoch, 1966; Flemer,

1970; Cadée and Hegeman, 1974; Malone, 1977; Cadée, 1978; Colijn, 1978; Stockner and Cliff, 1979; Stockner et al., 1979; Joint and Pomroy, 1981). From such studies we know that productivity in a nutrient replete estuary can vary with phytoplankton biomass, turbidity, daylength, or temperature, but the findings from specific locations cannot be easily related to other estuarine systems. Except for Boynton et al. (1982), there has been little effort in developing a unified theory of what factors control primary productivity in diverse estuarine systems. In simplest terms, primary productivity in nutrient-rich waters is a function of 3 basic variables: phytoplankton biomass, biomass-specific carbon assimilation rate, and light availability. Although these may vary due to changes in phytoplankton community composition, light adaptation, grazing, settling, transport processes, temperature, daylength, or turbulence, if appropriately expressed, productivity should be predictable in terms of the 3 basic variables.

In this paper we present the results of an annual study of phytoplankton production in San Francisco Bay, USA. We show that seasonal variations in productivity differ among geographic regions within the estu-

ary, but that daily net productivity in the photic zone is highly correlated with a simple composite parameter composed of phytoplankton biomass and light availability. We also show that the concept of critical depth : mixed depth ratio, which has become a paradigm of phytoplankton ecology in oceans and lakes (Parsons and Takahashi, 1973; Harris, 1978), has relevance to turbid estuaries such as San Francisco Bay. Using the water depth : photic depth ratio we predict the fraction of gross primary production that is lost to respiration and the fraction that remains for potential consumption by herbivores.

San Francisco Bay (Fig. 1) offers a variety of subenvironments for studying the regulation of primary pro-
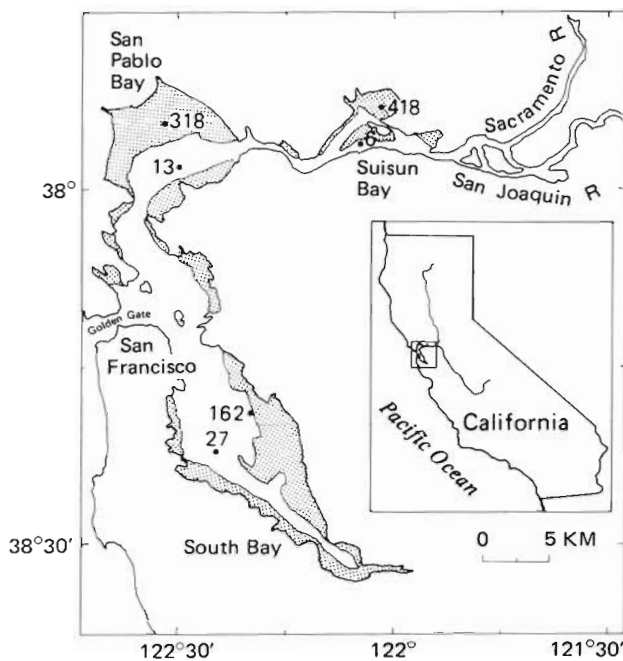

Fig. 1. Map of San Francisco Bay showing locations of incubation sampling sites. Shaded portions: areas where water depths (MLLW) are less than 2 m

duction in nutrient-rich, turbid waters. The northern reach, which includes San Pablo Bay and Suisun Bay, is a river-dominated estuary. It is partially or well mixed (depending on discharge from the Sacramento and San Joaquin Rivers), turbid, and characterized by a large horizontal salinity gradient. In contrast, the southern reach (South Bay) is a brackish embayment that has no large direct riverine source of freshwater, is usually vertically mixed (although salinity stratification occurs in winter–spring; Cloern, 1984), is less turbid than the northern reach, and usually has a small horizontal salinity gradient. Detailed descriptions of the hydrographic, nutrient, and biological character of the San Francisco Bay system are given in Conomos

(1979). Each major embayment (South Bay, San Pablo Bay, Suisun Bay) is composed of a central, relatively deep ($\simeq$ 10 to 15 m) channel where the photic zone is about 10 % of the water depth, bounded by broad expanses of shoals ($\simeq$ 2 m depth) where the photic zone is 50 to 100 % of water depth. Typically, nutrient levels throughout the Bay exceed 10 μM dissolved inorganic nitrogen, 2 μM phosphate, and 50 μM silicate (Conomos et al., 1979). Phytoplankton community composition differs in the three major embayments. The South Bay population is usually dominated by microflagellates (< 15 μm length) and small (< 10 μm diameter) centric diatoms, although *Skeletonema costatum* and larger (> 70 μm diameter) diatoms *Thalassiosira* spp. and *Coscinodiscus* spp. are occasionally abundant. In San Pablo Bay the population comprises marine-brackish diatoms and microflagellates, whereas in Suisun Bay freshwater diatoms usually predominate in winter and *S. costatum* and *T. eccentrica* are dominant during the summer bloom (Wong and Cloern, 1982).

METHODS

Between January 1980 and February 1981 light attenuation, chlorophyll *a*, and phytoplankton production were measured monthly at a deep-water and shallow-water site in each of the 3 major embayments in San Francisco Bay (Fig. 1). Light attenuation coefficient ε (all symbols and units are given in Table 1) was measured using a LiCor model 185 quantum meter coupled to a 192S sensor. Total ambient insolation I_o (photosynthetically active radiation) during the course of an incubation experiment was measured using a LiCor 190 quantum sensor and a recording integrator. Photic depth Z_p (depth of 1 % ambient light energy) was estimated as $\ln(100)/\varepsilon$.

Triplicate chlorophyll *a* samples from each site were prescreened through 59 μm Nitex screen (see below), then filtered onto Gelman type A/E glass-fiber filters. Chlorophyll *a* concentration B, corrected for phaeopigments, was determined by fluorometry (Strickland and Parsons, 1972). Although prescreening with a 59 μm mesh may remove large algal cells or chains, there was never a measurable difference in *in vivo* fluorescence between whole and screened samples, except at Station 318 on May 8 and at Stations 13 and 318 on June 5.

Productivity samples were collected from a single depth, 2 m in the channel and 1 m in the shoals, and also prescreened through a 59 μm Nitex screen. The small mesh was used to eliminate grazing by copepod nauplii and tintinnid ciliates which at times constituted a substantial fraction of zooplankton biomass (Hutchinson, 1981; 1982a, b). Following inoculation with carbon 14 (5 μCi in a 150 ml bottle), 24 h simu-

Table 1. Definitions of variables (and their units)

Variable	Definition	Units
ε	Light attenuation coefficient	m^{-1}
I_o	Ambient photosynthetically active radiation	Einsteins $(m^2 d)^{-1}$
Z_p	Photic-zone depth	m
B	Chlorophyll *a* concentration	mg chl *a* m^{-3}
P_m^B	Maximum carbon assimilation rate	mg C (mg chl *a* $d)^{-1}$
PN_{pd}	Daily photic zone net productivity	g C $(m^2 d)^{-1}$
PN_{py}	Annual photic zone net productivity	g C $(m^2 yr)^{-1}$
R^B	Biomass-specific respiration rate	mg C (mg chl *a* $d)^{-1}$
PG_y	Annual gross productivity	g C $(m^2 yr)^{-1}$
$\bar{Z}_p$	Annual mean photic depth	m
H	Water-column depth	m
PN_{wy}	Annual water column net productivity	g C $(m^2 yr)^{-1}$
R_{wy}	Annual water-column respiration	g C $(m^2 yr)^{-1}$
R_{py}	Annual photic-zone respiration	g C $(m^2 yr)^{-1}$

lated *in situ* incubations were done in a deck incubator. Samples were exposed to natural sunlight of 8 intensities: 100, 55, 30, 15, 8, 3, 1, and 0 % of ambient irradiance. On clear days, light entering the deck incubator was attenuated by an additional 25 to 40 % with a neutral density Plexiglas filter positioned over the samples. Hence, photoinhibition, which is unlikely to occur in turbid well-mixed environments (Marra, 1978; Joint and Pomroy, 1981), was never observed. Irradiance within the incubator was continuously recorded with a submersible quantum sensor.

Following incubation, subsamples from each bottle were filtered by gravity or low pressure (< 110 mm Hg) through Gelman type A/E glass-fiber filters. A 3 ml aliquot of each filtrate and duplicate unfiltered 3 ml aliquots from each bottle were placed in scintillation vials. After adding 0.1 ml of 0.2 N HCl, each aliquot was bubbled under vacuum for 15 min while $^{14}CO_2$ was stripped from the sample (Schindler et al., 1972). The residual activity of the sample was measured using a liquid scintillation spectrometer. All carbon uptake rates were corrected for activity of the filtrate (excretion) and dark-bottle uptake.

Maximum daily carbon assimilation rates P_m^B were derived from 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):

$$P^B = P_m^B \tanh (\alpha I/P_m^B) - R^B \qquad (1)$$

Simulated incubation depths were calculated as $-\ln(I_i/I_o)/\varepsilon$, where I_i/I_o is the fraction of daily surface insolation received by bottle i. Daily photic zone net productivity PN_{pd} was calculated by integrating (trapezoidal quadrature) measured rates of carbon uptake [mg C $(m^3 d)^{-1}$] over the photic depth. Annual

photic zone net productivity PN_{py} was estimated for each site by integrating PN_{pd} over the year. Baywide the specific respiration rate R^B, as the intercept of the P-I curves (Steemann Nielsen and Hansen, 1959), averaged 4.5 % of P_m^B over the year. Since even after a 24 h incubation it is unlikely that samples held at low-light had reached a net productivity rate (Hobson et al., 1976), the intercepts were probably underestimates of the true specific respiration rate (Peterson, 1980). In previous studies in San Francisco Bay (Peterson et al., in press) a typical respiration rate was found to be about 10 % of P_m^B using oxygen light-dark bottle techniques in 24 h incubations. In the analysis presented below, we assumed that R^B was constant and equal to 0.1 P_m^B, and calculated annual gross productivity PG_y as the sum of annual net productivity and integral respiration over the photic zone.

RESULTS

Ambient insolation during the course of the experiments (Fig. 2a, 3a, 4a) was similar for all sites and ranged from 8 to 55 Einsteins $(m^2 d)^{-1}$. Attenuation coefficients varied substantially between embayments and at times between channel and shoal sites within embayments (Fig. 2b, 3b, 4b). Photic depths in South Bay were fairly constant throughout the year and averaged about 3.2 m. In San Pablo Bay large variations in attenuation coefficient resulted in fluctuations of photic depth that ranged from about 0.3 to 6.6 m. Photic depths at both sites in Suisun Bay remained < 1 m throughout most of the year. The annual range of attenuation coefficients was large at most sites, but based on annual mean attenuation coefficients (Table 2) turbidity in South Bay was less than in San Pablo Bay which was less than in Suisun Bay. In
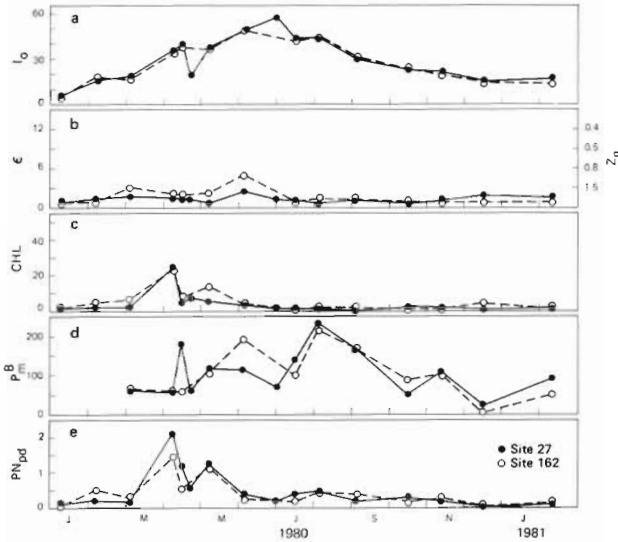
Fig. 2. South Bay. Seasonal variation of (a) ambient irradiance I_o (E m^{-2} d^{-1}); (b) attenuation coefficient ε (m^{-1}) and photic depth Z_p (m); (c) chlorophyll a CHL (mg m^{-3}); (d) maximum carbon assimilation rate P_m^B [mg C (mg chl a d)$^{-1}$]; (e) daily net productivity PN_{pd} [mg C (m^2 d)$^{-1}$] for Incubation Sites 27 (●) and 162 (○)
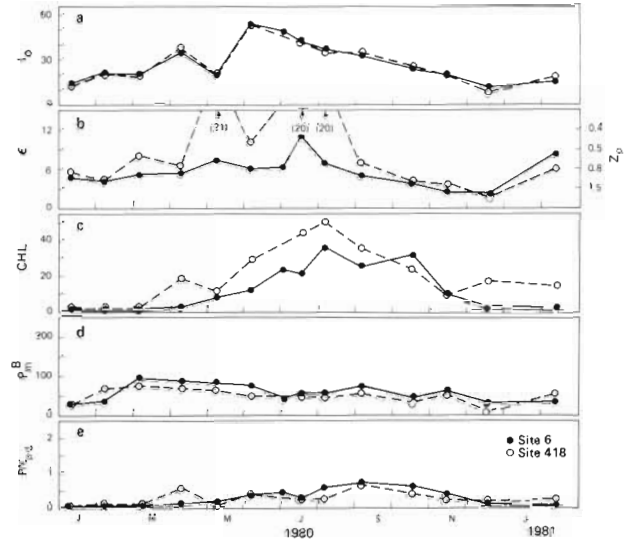

Fig. 4. Suisun Bay. Seasonal variation of (a) ambient irradiance I_o (E m^{-2} d^{-1}); (b) attenuation coefficient ε (m^{-1}) and photic depth Z_p (m); (c) chlorophyll a CHL (mg m^{-3}); (d) maximum carbon assimilation rate P_m^B [mg C (mg chl a d)$^{-1}$]; (e) daily net productivity PN_{pd} [mg C (m^2 d)$^{-1}$] for Incubation Sites 6 (●) and 418 (○)

Fig. 3. San Pablo Bay. Seasonal variation of (a) ambient irradiance I_o (E m^{-2} d^{-1}); (b) attenuation coefficient ε (m^{-1}) and photic depth Z_p (m); (c) chlorophyll a CHL (mg m^{-3}); (d) maximum carbon assimilation rate P_m^B [mg C (mg chl a d)$^{-1}$]; (e) daily net productivity PN_{pd} [mg C (m^2 d)$^{-1}$] for Incubation Sites 13 (●) and 318 (○)
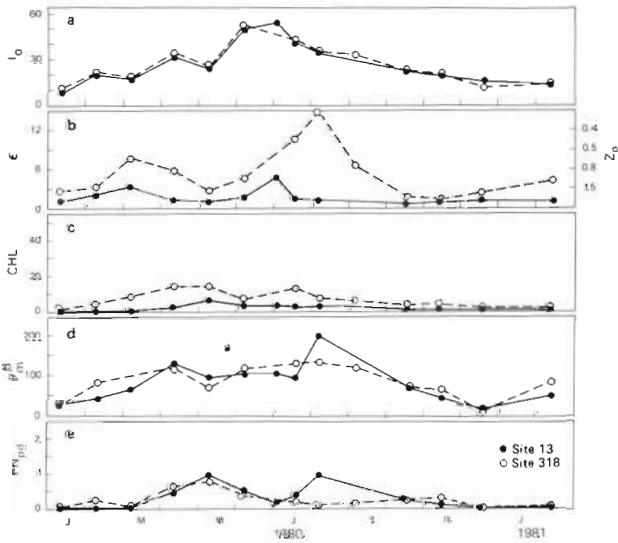
addition, attenuation coefficients were consistently greater in the shoals than the channel of San Pablo Bay and Suisun Bay.

Although the absolute chlorophyll a level for a given date was typically higher at the shallow water incubation site than at the adjacent channel site, the seasonality of chlorophyll a was similar for the 2 incubation

sites within each embayment and distinct from the seasonality in the other two embayments (Fig. 2c, 3c, 4c). In South Bay (Fig. 2c) there was a late winter-early spring chlorophyll a maximum of approximately 24 mg m^{-3} after which chlorophyll a levels remained less than about 2 mg m^{-3}. Maximum chlorophyll a levels in San Pablo Bay (Fig. 3c) were observed in spring. The increase and decline in biomass occurred over a longer period at the shoal site than at the deep-water location. Chlorophyll a concentrations at San Pablo Bay sites ranged from 0.7 to 6.4 mg m^{-3} at Station 13 and from 1.5 to 14.4 mg m^{-3} at Station 318. Maximum concentrations of chlorophyll a at the Suisun Bay incubation sites (Fig. 4c) exceeded those from the other 2 embayments. Winter lows of < 1 mg chl a m^{-3} were followed by a gradual increase to summer maxima of 35 and 50 mg chl a m^{-3} at the deep-water and shallow-water sites respectively.

Daily carbon assimilation rates were usually similar at both incubation sites within each embayment (Fig. 2d, 3d, 4d). Although seasonality in P_m^B was similar at Sites 27, 162, and 13, it differed among the other sampling sites. In South Bay and San Pablo Bay, P_m^B generally increased from winter lows (P_m^B rates in South Bay were not attained in January or February) to maximum rates in midsummer. Low winter P_m^B rates in Suisun Bay were followed by annual maximum values in March after which there was a gradual decline in P_m^B over the year. Baywide, winter minimum P_m^B rates were 25 to 30 mg C (mg chl a d)$^{-1}$, whereas maximum rates ranged from 230 mg C (mg chl a d)$^{-1}$ in South Bay to

Table 2. Annual mean and range of attenuation coefficient (ε), photic depth ($\overline{Z}_p$), water depth (H) [MLLW water depth + 1 m], and $H/\overline{Z}_p$ ratio for the 6 incubation sites

Station		ε (m^{-1})	Range	$\overline{Z}_p$ (m)	H (m)	$H/\overline{Z}_p$
South Bay	27	1.3	0.7– 2.5	3.5	12	3.4
	162	1.7	0.8– 5.1	2.7	3.0	1.1
San Pablo Bay	13	1.8	0.7– 4.7	2.6	11	4.2
	318	5.6	1.4–15	0.8	2.2	2.8
Suisun Bay	6	5.7	2.4–11	0.8	10	12.5
	418	9.6	3.6–21	0.5	1.6	3.2

approximately 170 in San Pablo Bay and 83 mg C (mg chl a d)$^{-1}$ in Suisun Bay.

Although seasonality in daily net productivity (Fig. 2e, 3e, 4e) was generally similar to the pattern observed for chlorophyll a at each of the 6 incubation sites, baywide the levels of productivity had little relation to chlorophyll a concentration. At both sites in South Bay (Fig. 2e) the annual pattern in PN$_{pd}$ was dominated by 2 peaks in early spring of 1.2 to 2.2 g C (m^2 d)$^{-1}$. At all other times during the year productivity was low, not exceeding 0.5 g C (m^2 d)$^{-1}$. In San Pablo Bay low [< 0.05 g C (m^2 d)$^{-1}$] levels of productivity in winter (Fig. 3e) were followed by a peak in spring at both the channel and shoal sites coincident with peaks in chlorophyll a. At the channel site a second peak in productivity, of similar magnitude to the spring peak, occurred simultaneously with a marked increase in P$_m^B$ (Fig. 3d) and decreased turbidity (Fig. 3b). In Suisun Bay extremely low productivity during winter (Fig. 4e) preceded increased PN$_{pd}$ that was coincident with the summer increase of chlorophyll a. Even though biomass in Suisun Bay was the highest observed throughout the San Francisco Bay system, maximum levels of phytoplankton productivity at Stations 6 and 418 did not exceed 0.55 g C (m^2 d)$^{-1}$. Annual net productivity PN$_{py}$ over the photic zone was 150, 110 to 130, and 95 g C m^{-2} for the South Bay, San Pablo Bay, and Suisun Bay sites respectively.

DISCUSSION

Predicting daily productivity

Although the seasonality of parameters that potentially control phytoplankton productivity in San Francisco Bay was diverse, PN$_{pd}$ was primarily a function of phytoplankton biomass and light availability. Falkowski (1981) has also derived an empirical function that relates integral productivity to B and I$_o$ in the New York Bight. Gieskes and Kraay (1977) similarly conclude that the productivity of surface-water samples in

the Southern North Sea can be estimated well from chlorophyll a concentration and incident light. When all measured values of PN$_{pd}$ were regressed against the simple composite parameter B I$_o$/ε (Table 3; Fig. 5), we found that, both within individual embayments and baywide, about 80 % of the seasonal variability in PN$_{pd}$ was correlated with this simple parameter. Therefore, nutrient availability, temperature, and physiological state of the phytoplankton play only minor roles in regulating productivity. All linear regressions were highly significant (r = 0.88 to 0.97, P < 0.001) and indicated that this relation held over a wide range of I$_o$, ε, B, P$_m^B$, and phytoplankton communities.

PN$_{pd}$ was consistently predicted well using this composite parameter, whereas correlations between PN$_{pd}$ and either I$_o$/ε, I$_o$, ε, or P$_m^B$ were weak (Table 3). Because carbon uptake is dependent on phytoplankton biomass, it is common practice to normalize productivity by the chlorophyll a content of the sample. Within a localized area, even normalizing integral productivity to photic zone chlorophyll a at times during the year (Malone, 1977; Bruno et al., 1983) aids in determining the factors regulating phytoplankton production. In San Francisco Bay there was a significant correlation (P < 0.05) between PN$_{pd}$ and phytoplankton biomass (B) at 5 of the 6 incubation sites (Table 3). In each embayment the seasonal pattern in productivity was generally reflective of the seasonality in biomass (Fig. 2c, e; 3c, e; 4c, e). Except at Site 418, variations solely in chlorophyll a accounted for more than 50 % of the variation in observed PN$_{pd}$ (Table 3). Within a restricted environmental setting (i.e. separate embayments), changes in chlorophyll a concentration accounted for most of the variation in productivity. However, only 12 % of the baywide annual variation in productivity was correlated with changes in biomass. Because there was a wide range in slopes (6.5 to 156; data not shown) for regressions between productivity and chlorophyll a at the 6 sites, the single regression of PN$_{pd}$ and B data from all sites accounted for only a small fraction (12 %) of the variation in PN$_{pd}$ baywide (Table 3). Thus, although at a given location phyto-

plankton biomass was indicative of photic-zone productivity, our results suggest that the use of chlorophyll *a* alone is of little value in predicting PN_{pd} among diverse areas. This is consistent with the conclusions of Cadée and Hegeman (1974) and Boynton et al. (1982) that over a wide range of environmental conditions or aquatic environments productivity cannot be estimated from measures of chlorophyll *a* alone.

late well with changes in P_m^B (Table 3). The poor correlation between primary productivity and P_m^B probably results from the fact that productivity is largely determined by biomass, and that spatio-temporal variations in biomass within San Francisco Bay are not controlled by the same processes that regulate growth rate (i.e. P_m^B). For example, the summer biomass maximum in Suisun Bay results from the physical accumulation of

Table 3. Coefficients of determination (r^2) from linear regressions of photic zone productivity (PN_{pd}) against B I_0/ε, chlorophyll *a* (B), I_0/ε, ambient irradiance (I_0), attenuation coefficient (ε), and carbon assimilation rate (P_m^B)

Station		n	B I_0/ε	B	I_0/ε	I_0	ε	P_m^B
Baywide		77	0.82**	0.12*	0.14*	0.15*	0.03	0.08*
South Bay	27	15	0.90**	0.77**	0.08	0.10	0.00	0.01
	162	13	0.89**	0.84**	0.00	0.15	0.06	0.00
San Pablo	13	12	0.78**	0.66**	0.43*	0.17	0.07	0.66**
	318	12	0.94**	0.51*	0.19	0.16	0.03	0.08
Suisun Bay	6	13	0.89**	0.82**	0.36*	0.26	0.00	0.01
	418	12	0.82**	0.29	0.39*	0.37*	0.01	0.01

** $P < 0.001$; * $P < 0.05$

In addition to phytoplankton biomass, productivity in estuaries is commonly believed to be a function of photic-zone irradiance because there is decreased productivity in turbid regions relative to clearer waters (Flemer, 1970; Cadée and Hegeman, 1974; Malone, 1977; Cadée, 1978; Colijn, 1978; Stockner et al., 1979; Joint and Pomroy, 1981). However, the most appropriate means of quantifying the light available to phytoplankton in a photic zone is not obvious. Photosynthetically available light must be related to both ambient light (I_0) and the depth of the photic zone, a measure derived from the attenuation coefficient (ε). We assumed that ε, I_0, and I_0/ε, as indices of light availability, might be useful predictors of daily productivity. At some sites the use of I_0 and I_0/ε increased the predictability of PN_{pd} (Table 3). But neither ε, I_0, or I_0/ε individually accounted for more than 43 % of the variation in daily productivity. The poor relationship between PN_{pd} and ε was surprising because there was a significant relationship between PN_{py} and annual mean photic depth $\overline{Z}_p$, which was calculated from ε (Fig. 6).

Positive correlations are reported between photic zone productivity and P_m^B in some estuaries (Williams and Murdoch, 1966; Malone, 1977), but in San Francisco Bay changes in PN_{pd} were poorly correlated with P_m^B (Table 3). In South Bay and San Pablo Bay, P_m^B generally increased until midsummer, whereas PN_{pd} was maximum in spring. In contrast, maximum PN_{pd} in Suisun Bay was observed in summer, whereas maximum P_m^B was seen in late winter. Over the year-long study, only at Station 13 did variations in PN_{pd} corre-
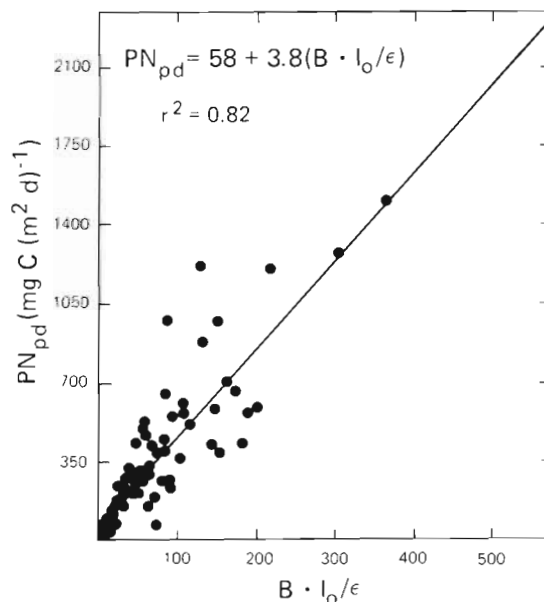

Fig. 5. Regression of daily net productivity PN_{pd} against composite parameter B I_0/ε

phytoplankton by estuarine circulation, rather than from rapid growth rates (Cloern et al., 1983), and the spring bloom in South Bay results partly from decreased benthic grazing pressure when the water column is stratified (Cloern, 1982). Only in estuaries where biomass and carbon assimilation rates are controlled by the same processes (e.g. specific growth rate)
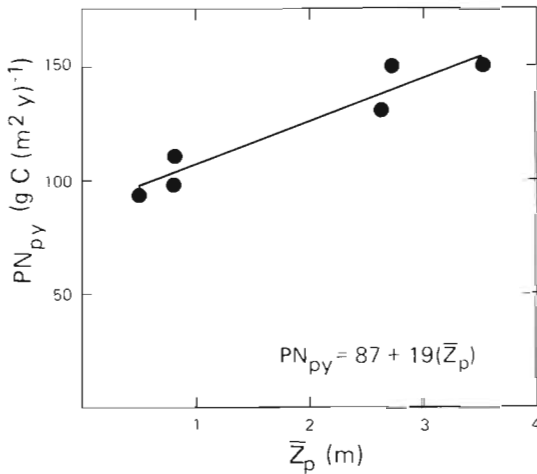
Fig. 6. Annual net productivity PN_{py} as a function of annual mean photic depth $\overline{Z}_p$ at the 6 incubation sites

would a strong correlation between productivity and P_m^B be expected.

Predicting net water-column productivity

The high turbidity of estuaries has a profound impact not only on gross production but also upon the fraction of gross production available to higher trophic levels. Estuaries are generally shallow, but a large portion of the water column is aphotic or exposed to low irradiance. Because photosynthesis is restricted to the photic zone (Z_p), respiratory losses, which occur over the entire water-column depth (H), can greatly reduce net productivity when the ratio H/Z_p becomes large. The importance of the interaction between surface irradiance, mixed depth, photic depth, and production : respiration ratios in regulating productivity was first noted by Gran and Braarud (1935). Their concepts were developed into mathematical models (Sverdrup, 1953; Patten, 1968) to define the 'critical depth' for integral production (i.e. the depth at which respiration in the water column equals carbon production in the photic zone). By examining the mixed depth : photic depth ratio and making assumptions regarding the constancy of the production : respiration ratio (Harris, 1978), one can define conditions which control the seasonality of phytoplankton blooms in marine and freshwater environments (Parsons and Takahashi, 1973; Harris, 1978). Although H/Z_p ratios vary widely in estuaries, the concept of critical depth has not been proposed as an explanation for the differences in productivity observed in different estuaries or the temporal changes in productivity or biomass within an estuarine system. Our data suggest that the concept of critical depth is applicable to estuarine systems and

that the fraction of gross primary production which is potentially available for higher trophic levels can be estimated from the ratio H/Z_p. In these calculations we assume that mixed depth is equal to water depth, a condition which is typical in San Francisco Bay.

Assuming vertical homogeneity and that respiration rate equals $0.1\ P_m^B$, annual water column respiration R_{wy} can be calculated as:

$$R_{wy} = \int_1^{365} (0.1\ P_m^B\ B\ H)\ dt \qquad (2)$$

Similarly, annual respiratory losses in the photic zone R_{py} can be estimated by substituting $\overline{Z}_p$ for H in equation 2. We estimate that annual gross phytoplankton productivity ($PG_y = PN_{py} + R_{py}$) at the 6 sites ranged from 110 to 190 g C m^{-2} and over the year respiration throughout the water column ranged from 49 to 250 g C m^{-2} (Table 4).

Because $\overline{Z}_p$ may be small relative to H, respiratory loss can cause some locations to be a net sink rather than a source of phytoplankton carbon (compare PG_y and R_{wy} for Site 6 in Table 4). The fraction of PG_y remaining after R_{wy} is accounted for is:

$$PN_{wy}/PG_y = (PG_y - R_{wy})/PG_y \qquad (3)$$

The ratio PN_{wy}/PG_y (net productivity : gross productivity) was small or negative at deep (large H) and turbid (small $\overline{Z}_p$) sites (Table 4), which suggests that PN_{wy}/PG_y may be a simple function of the ratio $H/\overline{Z}_p$. Given the constraint that the limit of $PN_{wy}/PG_y = 1$ as R_{wy} (i.e. H) approaches zero (Eq. 3), values of PN_{wy}/PG_y for the 6 sites were, in fact, linearly related to $H/\overline{Z}_p$ (Fig. 7):

$$PN_{wy}/PG_y = 1 - 0.166\ (H/\overline{Z}_p) \qquad (4)$$

The intercept of this function defines that critical ratio $H/\overline{Z}_p$ above which net production becomes negative. On an annual basis for San Francisco Bay, this critical value was $H/\overline{Z}_p = 6$ (Fig. 7). Sverdrup (1953), in describing the conditions necessary for the onset of a spring bloom in the Norwegian Sea, concludes that when the mixed depth exceeds the production zone depth by 5 times the population decreases. In Lake Windermere values of mixed depth : photic depth between 3 and 4 are typical during low chlorophyll a periods, and chlorophyll a levels rise when the ratio decreases (Talling, 1971).

The need for reliable estimates of specific respiration rate has been noted by numerous researchers. Estimates of respiration in the literature range from 4 % (Platt and Jassby, 1976) to 50 % (Eppley and Sharp, 1975) of maximum assimilation rate. In San Francisco Bay R^B is generally 8 to 30 % of P_m^B (Peterson et al., in press). The 10 % respiration value used in these calcu-

Table 4. Annual gross productivity in the photic zone (PG_y), net productivity in the photic zone (PN_{py}), water column respiration (R_{wy}), and ratio of water column net productivity to gross productivity (PN_{wy}/PG_y)

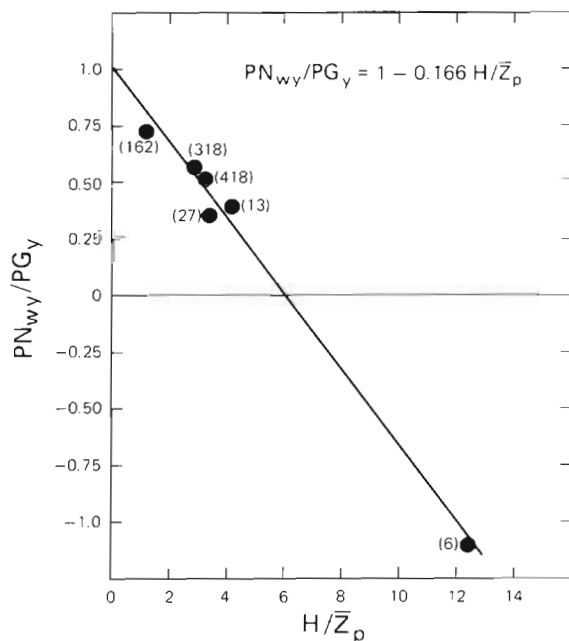| Station		PG_y (g C m^{-2})	PN_{py} (g C m^{-2})	R_{wy} (g C m^{-2})	PN_{wy}/PG_y
South Bay	27	190	150	120	.34
	162	180	150	49	.72
San Pablo	13	160	130	98	.39
	318	140	110	62	.56
Suisun Bay	6	120	98	250	−1.1
	418	110	93	54	.51

Fig. 7. Ratio of water-column net productivity to gross productivity PN_{wy}/PG_y as a function of $H/\bar{Z}_p$

lations is probably reasonable or conservative. If respiration rates are actually higher, say 25 % of P_m^B (Falkowski and Owens, 1978), then water column respiration would be 2.5 times greater and an even smaller fraction of phytoplankton production would be available to grazers (see below).

Carbon available to higher trophic levels

Implications of the critical depth concept also lead to the conclusion that not only do variations in H/Z_p ratios have profound consequences for phytoplankton population dynamics, but also that the availability of phytoplankton carbon to higher trophic levels varies with changes in this ratio. From Equation 4 and as shown in Fig. 7, the fraction of gross phytoplankton production available to herbivores can be estimated from the ratio $H/\bar{Z}_p$. High standing stocks of phytoplankton (chlorophyll a) are often considered to be indicative of abundant food for higher trophic levels. As shown by our results, such a presumption may be misleading. For example, Site 6 in Suisun Bay had the highest concentrations of chlorophyll a, but because the photic zone was only a small fraction of the water-column depth (Table 2), respiratory losses exceeded gross primary production (Table 4). Baywide, there was a greater fraction of production available for herbivores at the shallow-water sites (162, 318, 418), where the ratio $H/\bar{Z}_p$ was smaller (Fig. 7), than at the deep-water sites (27, 13, 6). The extensive shallow areas of San Francisco Bay in general, and Suisun Bay in particular, must be largely responsible for maintaining the system's capacity to support herbivore populations. An estuary's capability to support higher trophic levels should thus depend in part on the size and relative proportion of areas with low and high ratios of H/Z_p rather than solely depend on phytoplankton biomass.

These findings imply 2 general conclusions. First, in deep turbid channels (e.g. Suisun Bay) the requirements for cell maintenance (respiration) are such that phytoplankton populations cannot be maintained by in situ growth. Rather, as postulated by Cloern and Cheng (1981) and Cloern et al. (1983), the populations found in these areas must be advected in from areas with conditions more favorable for growth (i.e. lower H/Z_p ratios). Second, the nutritional mode of herbivores might vary with turbidity. Areal productivity decreases with increasing turbidity (Fig. 6, this paper; Cadée and Hegeman, 1974; Malone, 1977; Cadée, 1978; Colijn, 1978; Joint and Pomroy, 1981), and a large fraction of phytoplankton carbon is lost through respiration in deep, turbid environments. Therefore, either the biomass of herbivores should decline in turbid environments or higher trophic levels in such environments must depend to a large degree on suspended detritus or particulate organic carbon in the sediments. Consumers in a turbid environment may therefore be less dependent upon phytoplankton production as a food source than consumers in clearer waters. Because the nutritional value of detritus is

lower than that of phytoplankton (Kirby-Smith, 1976; Heinle et al., 1977) and there is a negative relation between the percentage of detritus in the diet and growth of copepods (Heinle et al., 1977; Chervin, 1978; Chervin et al., 1981) and scallops (Kirby-Smith, 1976), one might expect to see lower macrofauna biomass in areas where there is a greater dependence on detrital carbon than phytoplankton carbon for food.

The diet for the individual species has not been studied, but distributions of zooplankton and benthic animals in San Francisco Bay support these hypotheses. In the 3 major embayments, biomass of zooplankton and benthic infauna are greater where turbidity is low, the ratio $H/\overline{Z}_p$ is low, and there is a large proportion of phytoplankton carbon available for consumers. The average fraction of gross phytoplankton production available for consumption by herbivores in South Bay, San Pablo Bay, and Suisun Bay was 53, 48, and -29% respectively (mean PN_{wy}/PG_y ratio of channel and shoal sites from Table 4). Mean annual zooplankton biomass during 1980 was 21, 16, and 9.9 mg C m^{-3} in these same embayments (Hutchinson 1982a, b). Similarly, Thompson and Nichols (1981) report that, based on data collected in 1973, wet weight biomass of benthic macrofauna is greatest in South Bay (4800 g m^{-2}) and least in Suisun Bay (100 g m^{-2}) with levels in San Pablo Bay (520 g m^{-2}) being intermediate between the two.

The results of our study show that daily photic zone net primary productivity in San Francisco Bay can be estimated from a simple function: $PN_{pd} = 58 + 3.8$ $(B\, I_o/\varepsilon)$. Moreover, the fraction of phytoplankton carbon production available for higher trophic levels can be estimated from the ratio $H/\overline{Z}_p$. Thus, the capability of this complex ecosystem to support secondary production can be predicted from simple, easily measured parameters. However, it should be noted that the accuracy of calculated net water-column productivity is dependent upon accurate measures of phytoplankton respiration, a process which is not easily measured and which may be variable.

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