Turbidity as a control on phytoplankton biomass and productivity in estuaries

JAMES E. CLOERN*

Abstract—In many coastal plain estuaries light attenuation by suspended sediments confines the photic zone to a small fraction of the water column, such that light limitation is a major control on phytoplankton production and turnover rate. For a variety of estuarine systems (e.g. San Francisco Bay, Puget Sound, Delaware Bay, Hudson River plume), photic-zone productivity can be estimated as a function of phytoplankton biomass times mean irradiance of the photic zone. Net water column productivity also varies with light availability, and in San Francisco Bay net productivity is zero (estimated respiratory loss of phytoplankton balances photosynthesis) when the ratio of photic depth (Z_p) to mixed depth (Z_m) is less than about 0.2. Thus whenever $Z_p:Z_m$ < 0.2, the water column is a sink for phytoplankton production.

Much of the spatial and temporal variability of phytoplankton biomass or productivity in estuaries is explained by variations in the ratio of photic depth to mixed depth. For example, phytoplankton blooms often coincide with stratification events that reduce the depth of the surface mixed layer (increase $Z_p:Z_m$). Shallow estuarine embayments (high $Z_p:Z_m$) are often characterized by high phytoplankton biomass relative to adjacent channels (low $Z_p:Z_m$). Many estuaries have longitudinal gradients in productivity that mirror the distribution of suspended sediments: productivity is low near the riverine source of sediments (low $Z_p:Z_m$) and increases toward the estuary mouth where turbidity decreases. Some of these generalizations are qualitative in nature, and detailed understanding of the interaction between turbidity and estuarine phytoplankton dynamics requires improved understanding of vertical mixing rates and phytoplankton respiration.

INTRODUCTION

Estuaries are perceived as highly productive ecosystems because they are often nutrient-rich and have multiple sources of organic carbon to sustain populations of heterotrophs. including riverine and waste inputs and autochthonous primary production by vascular plants, macroalgae, phytoplankton, and benthic microalgae. However, the perception of high productivity should not necessarily extend to the open water column of estuaries where annual phytoplankton production can be less than that of other marine environments. In their review, BOYNTON *et al.* (1982) calculated a mean annual phytoplankton productivity of 190 g C m^{-2} for 45 estuaries. Although this mean value is higher than productivity of the open ocean, it may not exceed phytoplankton productivity in the nearshore coastal ocean. In those few geographic areas where annual phytoplankton production has been measured in an estuary and in the adjacent coastal zone, productivity generally appears to be highest in the coastal ocean (e.g. Table 1).

Phytoplankton production can be very low in coastal plain and river-dominated estuaries, environments with high turbidity caused by river inputs of suspended particu-

* U.S. Geological Survey, 345 Middlefield Rd., Menlo Park. CA 93025. U.S.A.

Table 1. *Annual phytoplankton production* (g C m^{-2}) *in five estuaries and in the adjacent coastal ocean*

Estuary	Coastal ocean
Ems-Dollard (middle) = 100–140[a]	North Sea coastal zone = 160–240[b]
Hudson River (lower) $\cong$ 180[c]	New York Bight = 370[d]
Wassaw Sound = 90[e]	Shelf waters off Georgia = 285[f]
	Altmaha River plume = 600[f]
Fraser River = 120[g]	Strait of Georgia = 300[h]
Columbia River = 90[i]	Columbia River plume = 125[j]

[a]COLIJN (1983), [b]GIESKES and KRAAY (1975), [c]COLIJN'S (1983) estimate from data of MALONE (1977), [d]MALONE (1976), [e]TURNER *et al* (1979). [f]reported in YODER *et al* (1983), [i]PARSONS *et al* (1970), [h]STOCKNER et ol (1979), [i]SMALL and FREY (1984). [j]ANDERSON (1972)

late matter (SPM) and/or resuspension of bottom sediments. SPM concentrations in these estuaries often exceed *50* mg l^{-1}, such that light is attenuated rapidly in the water column and phytoplankton photosynthesis is confined to a shallow photic zone. As a consequence, phytoplankton dynamics (including productivity and spatial/temporal changes in biomass) are largely controlled by light availability. This conclusion is consistent with results from both theoretical studies and field investigations. For example, WOFSY'S (1983) model indicates that phytoplankton biomass is an inverse function of SPM concentration, and that light limitation prevents phytoplankton blooms when SPM concentration exceeds 50 mg l-'. PETERSON and FESTA (1984) have used numerical simulation experiments to explore the relations between SPM concentration and phytoplankton biomass and productivity. They conclude that estuarine productivity becomes strongly depressed as SPM concentration increases from 10 to 100 mg l^{-1}. In the past two decades there have been numerous studies of individual estuaries supporting the conclusion that light limitation is the major environmental control on primary production. Examples include the Bristol Channel (JOINT and POMROY, 1981), Ems-Dollard (COLIJN, 1983), Wadden Sea (CADÉE and HEGEMAN, 1979), Delaware Bay (PENNOCK and SHARP, 1986), upper Chesapeake Bay (HARDING *et al.* 1986), and the Hudson (MALONE, 1976) and Columbia River (SMALL and FREY, 1984) estuaries.

The purpose of this paper is to review some concepts of how turbidity (SPM) influences estuarine phytoplankton, using results from an ongoing study of San Francisco Bay. Although there are direct interactions between phytoplankton and suspended mineral particles (e.g. adhesion and aggregation; AVNIMELECH *et al.*, 1982), I consider here only the indirect effects of SPM through light attenuation. Most concepts that apply to San Francisco Bay also apply to other turbid estuaries, and results from other studies are used to demonstrate how light availability can regulate estuarine phytoplankton dynamics.

SAN FRANCISCO BAY

San Francisco Bay as a representative estuary

San Francisco Bay has been the site of multidisciplinary research in the past decade, much of which is summarized or referenced in CONOMOS (1979), CLOERN and NICHOLS (1985), and NICHOLS *et al.* (1986). This large estuary of the Sacramento and San Joaquin rivers has a number of features that typify shallow and coastal plain estuaries, including: (1) morphology characterized by a central channel of 10–20 m depth flanked by subtidal

shoals <3 m deep; (2) suspended and consolidated sediments composed primarily of lithogenous materials, mostly silt and clay (CONOMOS and PETERSON, 1977); (3) large seasonal variations in the riverine input of suspended sediments, with maxima during winter storms; and (4) a large spatial gradient in turbidity with highest SPM concentrations in the upper estuary, and lowest SPM concentration at the estuary mouth. Further, San Francisco Bay comprises two distinct estuaries. The northern reach (including San Pablo and Suisun Bays, Fig. 1) is representative of partially mixed estuaries with well-developed gravitational circulation (PETERSON *et al.*, 1975) and a turbidity maximum during summer (CONOMOS and PETERSON, 1977). In contrast, the South Bay (Fig. 1) is a lagoon-type estuary with no large, direct source of freshwater. The South Bay is typically well mixed and has substantially lower SPM concentrations than the upper estuary. Results presented here are from several related studies begun in 1980 and utilizing a network of sample sites (Fig. 1) representing (1) the river–ocean gradients of SPM concentration and phytoplankton biomass, and (2) the transverse gradients between the channel and shallows.
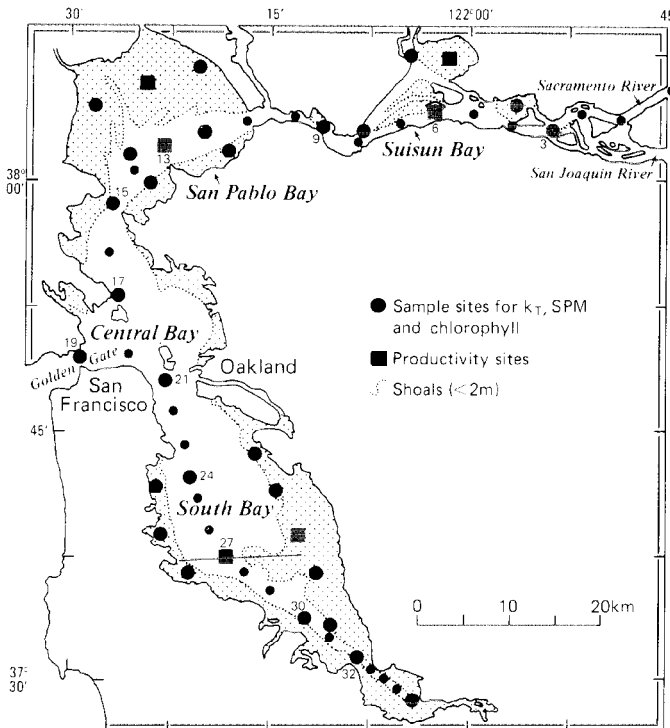

Fig. 1. Map of San Francisco Bay showing sampling sites (large symbols) for biweekly measurement of SPM, k_T, and chlorophyll *a* during 1980. Small circles represent sites where k_T and chlorophyll *a* were estimated from turbidity (nephelometry) and *in vivo* fluorescence. Squares represent sites where primary productivity was measured during 1980 and 1982 (all methods are detailed in CLOERN *et al.*, 1985). Solid line across the South Bay represents the surface transect for continuous measurement of chlorophyll *a* shown in Fig. 7.

TURBIDITY OF ESTUARIES

Turbidity of San Francisco Bay was mapped over an annual cycle by measuring the downwelling light extinction coefficient k_T and SPM concentration, at about 30 fixed sites (Fig. 1) twice monthly during 1980. Regression analysis showed a linear relation between k_T and SPM concentration (Fig. 2). The intercept of this regression (0.77 m^{-1}) represents a mean value for the "background" extinction coefficient due to light attenuation by water, dissolved constituents and the seston uncorrelated with SPM (e.g. phytoplankton). The slope of this regression is a measure of the specific attenuation coefficient (k_s') of suspended sediments in San Francisco Bay. Although the magnitude of k_s' varies among water bodies depending on the nature of their suspensoids (KIRK, 1985), the mean value for San Francisco Bay (0.06 m^2 g^{-1}) is identical to that measured in the New York Bight with comparable methods (MALONE, 1976), and is similar to k_s' measured in the Ems-Dollard Estuary (0.03 m^2 g^{-1}; COLIJN, 1982) and in Delaware Bay (0 075 m^2 g^{-1}; PENNOCK, 1985).

Strong correlations between k_T and SPM (e.g. Fig. 2) imply that light attenuation in estuaries is primarily a function of suspended sediment concentration. This is an important distinction between estuaries and the open ocean where SPM concentration is low and k_T is more strongly correlated with phytoplankton biomass (SMITH and BAKER, 1978). Data in Fig. 2 demonstrate the turbidity range commonly observed in estuaries. In San Francisco Bay, k_T ranges between about 1 m^{-1} in the outer estuary to >10 m^{-1} in the shallows of the inner estuary. Assuming that the photic depth (Z_p) for algal photosynthesis is the depth of 1% surface irradiance (i.e. $Z_p = 4.61/k_T$), this range of k_T is equivalent to photic depths between about 5 and <0.5 m. The photic depth of large rivers and river-dominated estuaries is typically <5 m, and often <1 m during peaks in river discharge, or in the estuarine turbidity maximum, or in shallow embayments where resuspension increases the SPM concentration.
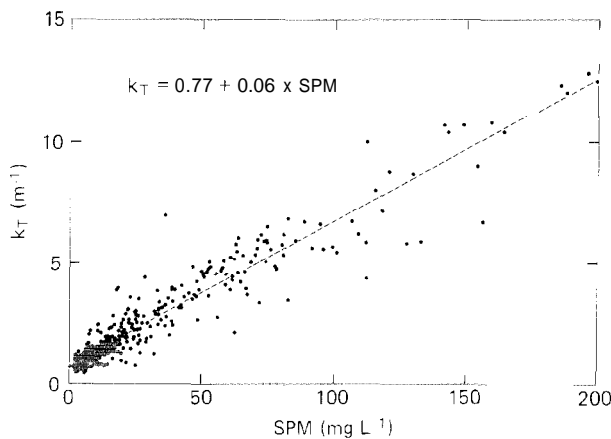

Fig. 2. Linear regression of extinction coefficient k_T against SPM concentration, for measurements made throughout San Francisco Bay during 1980 (n = 417; r^2 = 0.91). SPM concentration was measured gravimetrically and k_T was calculated from depth profiles of irradiance measured with a LiCor 192S quantum sensor [see HAGER and HARMON (1984) and CLOERN et al. (1985) for detailed methods].

Figure 3 summarizes the range of photic depths measured in a variety of estuaries, and compares these with Z_p for some fjords, neritic waters, and the open ocean. The contrast in light penetration between estuaries and other marine systems is obvious, and the extreme shallowness of the photic zone is another fundamental distinction that separates estuaries from coastal and oceanic waters. As a consequence, phytoplankton populations in shallow, turbid estuaries reside in a very different environment than those in deeper, clearer waters of the coastal and open ocean. This distinction has important implications for primary productivity.
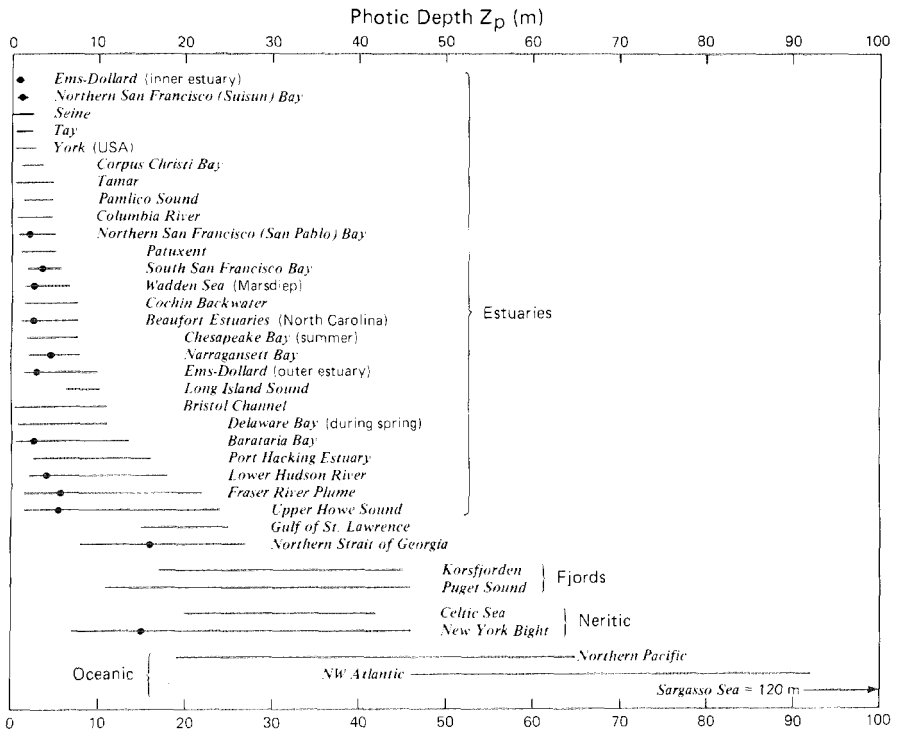

Fig. 3. Photic depths (means shown as circles and ranges shown as horizontal lines) in a variety of estuaries, compared to other marine waters. Photic depths were calculated as $4.61/k_T$ where k_T was either (1) measured directly, (2) estimated as 1.7/Secchi depth, or (3) estimated as $0.06 \times SPM$ where SPM was measured. Data are from the following: Ems-Dollard (COLIJN, 1982), San Francisco Bay (CLOERN et al., 1985), Seine (ROMANA, 1979), Tay (SHOLKOVITZ, 1979), York (MEADE, 1972), Corpus Christi Bay (FLINT, 1984), Tamar (OWENS, 1985), Pamlico (KUENZLER et al., 1979), Columbia River (SMALL and FREY, 1984), Patuxent (STROSS and STOTTLEMEYER, 1965), Wadden Sea (CADÉE and HEGEMAN, 1979), Cochin Backwater (QASIM, 1979), Beaufort estuaries (THAYER, 1971), Chesapeake Bay (CHAMP et al., 1980), Narragansett Bay (OVIATT et al., 1981), Long Island Sound and northwest Atlantic (reported by RYTHER and YENTSCH, 1957), Bristol Channel (JOINT and POMROY, 1981), Delaware Bay (PENNOCK, 1985), Barataria Bay (SKLAR and TURNER, 1981), Port Hacking Estuary (SCOTT, 1978), Hudson River and New York Bight (MALONE, 1980), Fraser River and Strait of Georgia (STOCKNER et al., 1979), Howe Sound (STOCKNER et al., 1977), Gulf of St. Lawrence (SEVIGNY et al., 1979), Korsfjorden (ERGA and HEIMDAL, 1984), Puget Sound (WINTER et al., 1975), Celtic Sea (PINGREE et al., 1976), North Pacific (OTOBE et al., 1977), Sargasso Sea (STEEMANN NIELSEN, 1975).

ESTUARINE PRIMARY PRODUCTIVITY

Most of the spatial and temporal variability of phytoplankton productivity within San Francisco Bay is correlated with variations in biomass B (mg m^{-3} of chlorophyll a) and an index of light availability $Z_p I_0$ (I_0 = surface irradiance in units of Ein m^{-2} d^{-1}, where 1 Ein = 1 mole of photons). For South Bay and northern San Francisco Bay, daily primary productivity in the photic zone (mg C m^{-2} d^{-1}) can be estimated with linear functions of $BZ_p I_0$ (COLE and CLOERN, 1984):

$$\text{South Bay: } P_p = 94 + 0.88[BZ_p I_0], \; n = 29, \; r^2 = 0.88 \tag{1}$$

$$\text{North Bay: } P_p = 63 + 0.67[BZ_p I_0], \; n = 53, \; r^2 = 0.72. \tag{2}$$

Similar analysis of productivity measurements for other estuaries suggests that such relations may apply universally (COLE and CLOERN, 1987). For example, in four estuarine/coastal environments where methods were comparable (Puget Sound, New York Bight, South and North San Francisco Bay), measures of daily productivity fit one linear function:

$$P_p = 146 + 0.73[BZ_p I_0], \; n = 210, \; r^2 = 0.82. \tag{3}$$
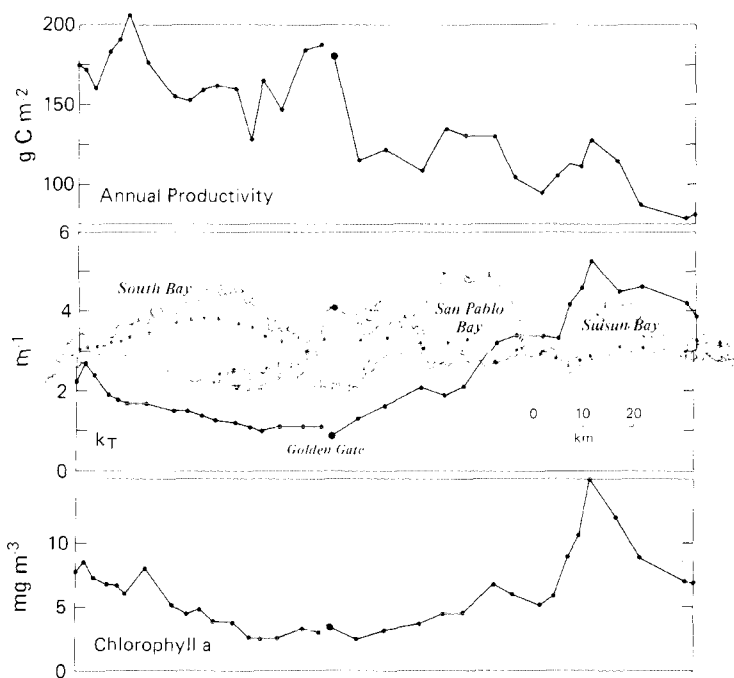

Fig. 4.   Longitudinal profiles of estimated annual primary productivity, mean extinction coefficient k_T, and mean chlorophyll a concentration in San Francisco Bay during 1980. Overlay map shows the location of sampling stations. Daily productivity (P_p) was estimated at each sampling site in the channel using equations (1)–(2), surface B determined from *in vivo* fluorescence, Z_p from estimates of k_T by nephelometry, and I_0 measured with LiCor 190S quantum sensors placed in mid-South Bay and in San Pablo Bay throughout 1980. Interpolated values of B and Z_p were used between the biweekly sampling dates. For each site, daily P_p estimates were then summed to yield annual photic zone productivity.

This relation implies that biomass-specific productivity in estuaries is controlled primarily by light availability. Although it is premature to suggest that one empirical model describes P_p for all estuaries, we do know that biomass-specific productivity (P_p/B) is a linear function of light availability in a wide range of estuarine environments including the Ems-Dollard (COLIJN, 1983), western Wadden Sea (CADÉE and HEGEMAN, 1979), Delaware Bay (PENNOCK and SHARP, 1986), Peconic Bay (BRUNO et al., 1983), Great South Bay (LIVELY et al., 1983). and the lower Hudson River Estuary (MALONE, 1977).

Empirical functions such as equations (1)–(3) can be used to estimate primary productivity whenever B, Z_p, and I_0 are known. This approach was used to map predicted annual production along the main axis of San Francisco Bay from the Sacramento River to the estuary mouth at Golden Gate and into the South Bay (Fig. 4). Estimated annual production ranged from about 80 g C m^{-2} in Suisun Bay near the
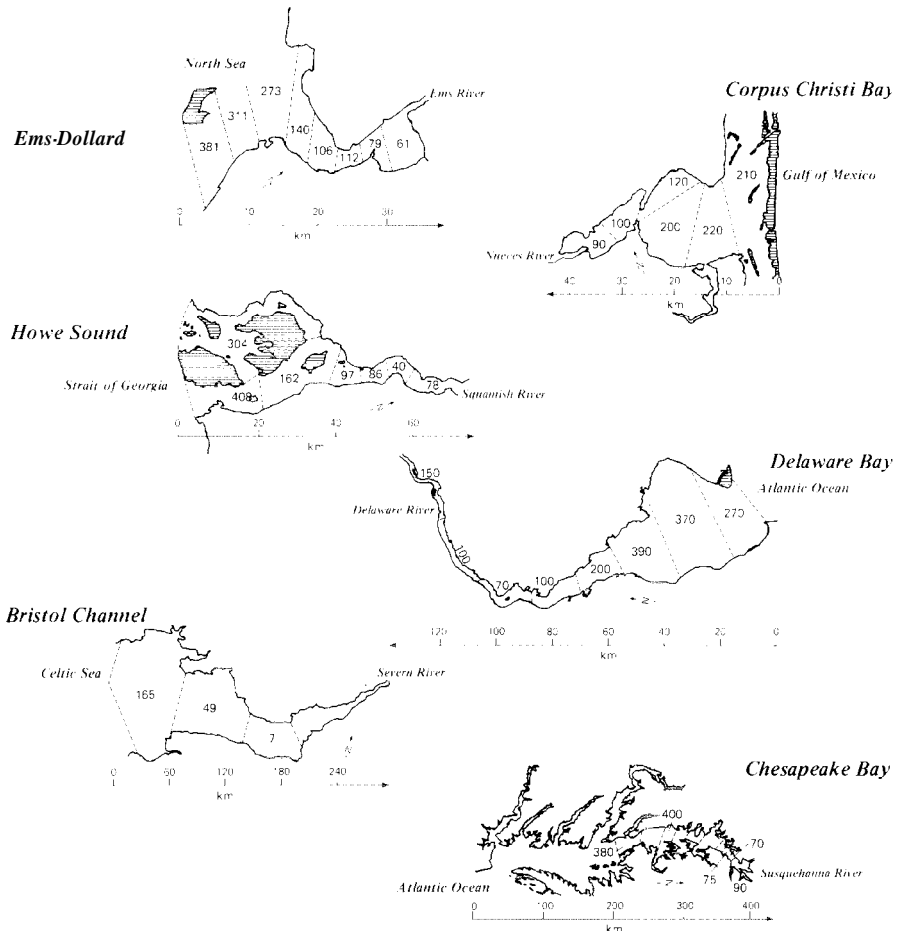

Fig. 5. Horizontal distributions of annual primary productivity in six estuaries, showing spatial gradients between the river and coastal ocean. Data are from COLIJN (1983), FLINT (1984), STOCKNER et al. (1977), PENNOCK and SHARP (1986). JOINT and POMROY (1981). and FLEMER (1970).

Sacramento River, to about 210 g C m^{-2} in the lower South Bay (Fig. 4). Hence the large-scale spatial variability in San Francisco Bay is characterized by increasing productivity away from the riverine source of suspended sediments. This distribution of annual production differs from that of phytoplankton biomass, which is highest in the upper estuary (Fig. 4). However, the spatial variability of annual production is related to photic depth, and generally mirrors the distribution of turbidity measured as k_T. Mean values of k_T decrease from the turbidity maximum in Suisun Bay toward the estuary mouth, and are lower in South Bay than in the upper estuary (Fig. 4).

Distributions shown in Fig. 4 indicate that San Francisco Bay is characterized by a longitudinal gradient in primary productivity, that productivity (unlike biomass) increases seaward, and that the overriding control on the distribution of annual production is the longitudinal gradient of photic depth (i.e. k_T) which reflects the distribution of river-derived suspended sediments. These features were observed over 20 years ago in the Patuxent River Estuary (STROSS and STOTTLEMEYER, 1965), and recent investigations have demonstrated similar spatial patterns in other estuaries. Figure 5 shows the large-scale horizontal distribution of annual phytoplankton production in six estuaries. In all cases, production is highest near the estuary mouth, lowest in the upper estuary (or in the turbidity maximum), and mirrors the distribution of k_T. This spatial pattern apparently continues into the coastal zone, where productivity can increase further. For example, annual production in the adjacent coastal ocean exceeds that of the Ems-Dollard, Wassaw Sound, and Hudson, Fraser, and Columbia River estuaries (Table 1). Hence our perception of estuaries as highly productive ecosystems should be qualified with the observation that phytoplankton productivity can be higher in nearby coastal waters where the photic zone is deeper and nutrient concentrations are still sufficient to sustain algal growth.

SIGNIFICANCE OF THE PHOTIC DEPTH:MIXED DEPTH

Net water column productivity

Because the photic depth (Z_p) can be a small fraction of the water column (or surface mixed layer depth. Z_m) in estuaries, measures of photic zone productivity (P_p) do not necessarily reflect the importance of phytoplankton production as a food resource for herbivores. Net production in the water column or mixed layer (P,,) is a more useful measure for understanding carbon or energy flow to grazers, and P, is less than P_p whenever $Z_p < Z_m$. The difference between P_p and P, is the respiratory loss of assimilated carbon by phytoplankton in the aphotic zone, which can be substantial. The measurement of phytoplankton respiration persists as a difficult problem, but from laboratory studies of algal cultures we can infer bounds on this loss to illustrate the distinction between net production in the photic zone (P_p) and water column (P,,,).

Photosynthetic rate p (mg C m^{-3} d^{-1}) is described by several empirical functions of irradiance $\mathbf{I}$, including the formulation of PLATI and JASSBY (1976):

$$p = p_{\max}[\tanh(aI) - rp_{\max}, \tag{4}$$

where $p_{\max}$ is maximum gross photosynthetic rate, a defines photosynthetic efficiency at low irradiance, and r is the respiratory loss rate as a fraction of $p_{\max}$. Equation (4) can be used to calculate relative productivity ($p/p_{\max}$) at any depth z in the water column:

$$p' = p/p_{\max} = \tanh(aI_z) - r \tag{5}$$

$$p' = \tanh[aI_0 \exp(-k_T z)] - r. \qquad (6)$$

Integration of equation (6) over the mixed depth Z_m yields a relative productivity in the water column:

$$P'_m = \int_0^{Z_m} [\tanh(aI_0 \exp\{-k_T z\}) - r]\, dz. \qquad (7)$$

To illustrate the significance of respiratory losses when $Z_p < Z_m$, equation (7) was solved numerically using different values for k_T (i.e. Z_p) and fixed values for a $(= 0.1 \text{ m}^2 \text{ d Ein}^{-1})$, I_0 $(= 40 \text{ Ein m}^{-2} \text{ d}^{-1})$, and Z_m $(= 10 \text{ m})$ representing the San Francisco Bay channel during summer. Relative productivity was then plotted against the ratio of photic depth to mixed depth in Fig. 6, comparing solutions for three values of the specific phytoplankton respiration rate r. This figure shows that net water column production decreases rapidly when $Z_p:Z_m < 1$, and it approaches zero as $Z_p:Z_m$ approaches a critical ratio of between 0.1 and 0.5 (depending on r). Physiological studies suggest that r can range between about 0.05 and 0.25 (e.g. VERITY, 1982), and that a representative value may be around 0.1.

The functions shown in Fig. 6 demonstrate a fundamental property of estuaries and other turbid environments. Regardless of phytoplankton biomass, net water column production is negative whenever the photic depth is less than about 20% of the mixed depth (as in the ocean; SVERDRUP, 1953). This situation occurs, for example, in upper San Francisco Bay during summer. The mean value of $Z_p:Z_m$ in the channel of Suisun Bay is about 0.1 (CLOEKN et al., 1985), indicating that this part of the estuary is a net respiratory sink for phytoplankton production. Hence the biomass maximum in San Francisco Bay (Fig. 4) occurs in a region where net production may be less than zero. The distinction between water column (or mixed layer) production and photic-zone production is therefore critical in turbid estuaries. and measures confined to the photic zone (e.g. Fig. 4) can grossly misrepresent the net production of organic matter that is available to support populations of heterotrophs.
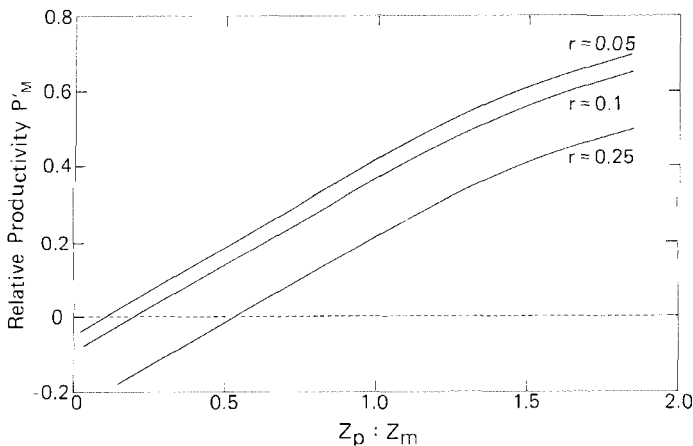

Fig. 6. Relative primary productivity P'_m (equation 7) vs the ratio of photic depth:mixed depth. for three values of the specific respiration rate r.

Spatial distribution of phytoplankton biomass

Because light availability controls productivity it must also play a major role in determining the population growth rate of estuarine phytoplankton, and we expect that biomass should vary across spatial gradients in the ratio of photic depth to mixed depth. For example, in well-mixed estuaries the ratio $Z_p:Z_m$ follows contours of bathymetry and highest phytoplankton biomass is expected to occur over subtidal shoals where Z_m is small and light availability is maximal. To demonstrate this, phytoplankton biomass (calculated chlorophyll *a* from *in-vivo* fluorescence) was measured continuously along transects between the deep channel and subtidal shoals of South San Francisco Bay during March 1985, when the water column was well mixed. A representative profile is given in Fig. 7 showing that biomass increased almost exponentially between the channel and eastern shoals. Biomass was low in the channel where calculated $Z_p:Z_m$ was less than 0.5, and it increased five-fold across the shoals where $Z_p:Z_m$ approached 1.

Yhis horizontal distribution of biomass is consistent with spatial patterns inferred from point samples collected previously. During 1980, mean annual biomass in the shallow embayments of San Francisco Bay was 2–3 times higher than in the nearby channel (CLOERN *et al.* 1985). During the 1980 summer bloom in Suisun Bay. high resolution mapping by remote sensing showed that chlorophyll *a* concentration consistently exceeded 60 mg m^{-3} in the shoals, and was <30 mg m^{-3} in the adjacent channel (CAI-IS *et al.*, 1985). Hence, in San Francisco Bay, the large-scale spatial variability of phytoplankton biomass is characterized by large transverse gradients, and:hi" -ariability is caused at least partly by horizontal gradients in light availability and phytoplankton growth rate. Similar spatial patterns have been observed in other estuaries such as Delaware Bay (PENNOCK, 1985), Chesapeake Bay (MALONE *et al.*, 1986), and the Hudson Estuary (SIROIS and FREDERICK. 1978). and are predicted from WOFSY's (1083) model of phytoplankton growth as a function of k_T and Z_m.

Temporal variability of phytoplankton biomass

Much of the temporal variability of estuarine phytoplankton biomass is also related to variations in light availability. For example, HITCHCOCK and SMAYDA (1977) attribute
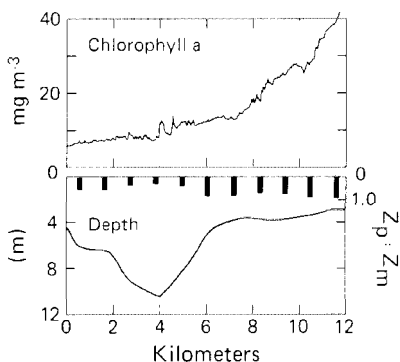

Fig. 7.   Profile of near-surface chlorophyll a, calculated $Z_p:Z_m$ (vertical bars), and bathymetry along a transverse transect in mid-South San Francisco Bay (see Fig. 1). 21 March 1985. Chlorophyll a was estimated from *in vivo* fluorescence [see POWELL *et* al. (1986) for methods]. Water depth (Z,) was recorded at 11 positions along the transect with a fathometer. and photic depth (Z_p) was estimated at these sites from values of k_T derived from nephelometry.

annual variations in the timing of the Narragansett Bay winter bloom to annual variations in mean water column irradiance $\bar{I}$; the winter bloom commences only when $\bar{I}$ exceeds about 40 langleys d^{-1} (19 W m^{-2}). Seasonal variations in SPM concentration can also influence light penetration and phytoplankton dynamics. In San Francisco Bay, bottom resuspension intensifies during mid-summer when wind speed and mean tidal current speed are both rapid. As a consequence, SPM concentration increases, Z_p decreases, growth rates (P_m/B) are near zero, and phytoplankton biomass is low in the upper estuary during mid-summer (CLOERN et al., 1985).

Another important mechanism of temporal variability in $Z_p:Z_m$ is the establishment of density stratification which reduces the mixed layer depth (Z_m) and increases light availability to phytoplankton retained above the pycnocline. Density stratification in estuaries is maintained primarily by buoyancy input from freshwater inflow and is eroded by tidal stirring. Hence stratification events can follow pulsed inputs of freshwater and can respond to changes in tidal current speed (HAAS, 1977: CLOERN , 1984). In South San Francisco Bay, the spring phytoplankton bloom is usually associated with salinity stratification. Two mechanisms may support the spring bloom during stratification events: (1) reduced grazing losses to benthic suspension feeders (CLOERN, 1982), and (2) increased growth rates of phytoplankton in the surface layer as Z_m decreases. For example, an extreme stratification event occurred in early April 1983 when phytoplankton biomass increased rapidly in the surface layer (big. 8). On 29 March 1983 (during a spring tide), the water column of lower South Bay was well mixed and phytoplankton biomass was low. By 8 April 1983 (during a neap tide), a sharp pycnocline had formed at about 6 m and phytoplankton biomass increased four-fold in the surface layer. Similar phytoplankton blooms accompany stratification events in other estuarine systems, including the York River (HAAS et al., 1981), St. Lawrence River (SINCLAIR, 1978), Delaware Bay (PENNOCK, 1985), the Strait of Georgia (STOCKNER et al., 1979), the Korsfjorden (ERGA and HEIMDAL, 1984), and Puget Sound (WINTER et al., 1975). Because estuarine phytoplankton are light-limited, temporal variability in vertical mixing (i.e. Z_m) is a primary mechanism of temporal variability in biomass.
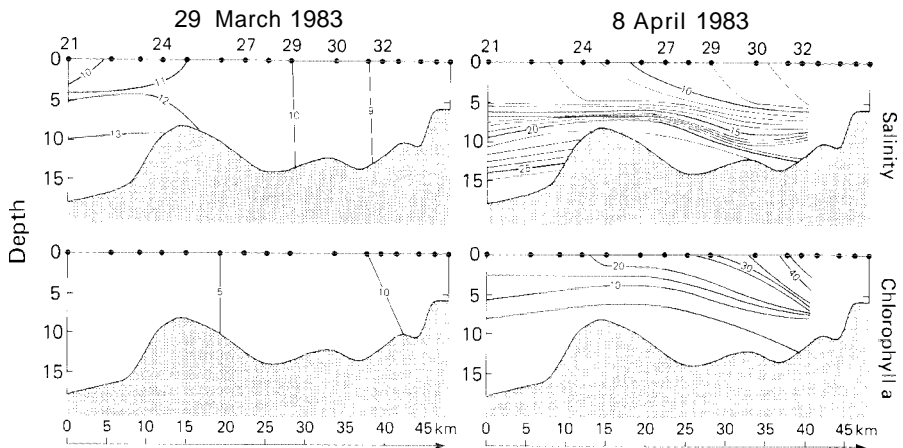

Fig. 8. Salinity and chlorophyll a contours along the South San Francisco Bay channel on 29 March and 8 April 1983. Sample sites correspond to those shown in Fig. 1.

CONCLUSIONS

Results from San Francisco Bay and other estuaries support the generalization that light availability is the critical environmental control on estuarine phytoplankton dynamics. Photic-zone productivity is strongly correlated with light availability, and in many estuaries the spatial distribution of phytoplankton production mirrors the distribution of suspended sediments, i.e. production is highest at the estuary mouth. The growth rate of phytoplankton populations is presumably also a function of light availability, and much of the spatial and temporal variability in biomass can be explained by variations in light exposure. Large-scale horizontal variability of phytoplankton biomass follows distributions of the photic depth: mixed depth ratio $(Z_p:Z_m)$, and phytoplankton blooms occur when $Z_p:Z_m$ increases (e.g. through reduction of Z_m by salinity stratification).

Studies of estuarine productivity also suggest, but cannot yet confirm, two important hypotheses. First, depth profiles of algal photosynthesis indicate that the water column of turbid estuaries can be a respiratory sink (P, < 0), even when phytoplankton biomass is high. This conclusion is based upon assumptions concerning the rates of two processes: vertical mixing (to define Z_m), and phytoplankton dark respiration. Neither process has been studied rigorously in estuaries, and our estimates of net water column production will remain tenuous until simultaneous measures of vertical mixing and respiratory loss are done across a spectrum of estuary types. Second, horizontal profiles suggest that phytoplankton productivity in estuaries may be less than in the adjacent coastal ocean. Our perception of estuaries as highly productive ecosystems should be placed in a broader geographic context, and this requires measurement of production along the continuum from rivers into the coastal ocean. Both hypotheses form a basis for the future research that is needed to better define the role of estuaries as sources of organic matter for consumer organisms.

REFERENCES

ANDERSON G. C. (1972) Aspects of marine phytoplankton studies near the Columbia River, with special reference to a subsurface chlorophyll maximum. In: *The Columbia River estuary and adjacent ocean waters,* A. T. PRUTER and D. L. ALVERSON, editors, University of Washington, Seattle.

AVNIMELECH Y., B. W. TROEGER and L. W. REED (1982) Mutual flocculation of algae and clay: Evidence and implications. *Science,* **216,** 63–65.

BOYNTON W. R., W. M. KEMP and C. W. KEEFE (1982) A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. In: *Estuarine comparisons,* V. S. KENNEDY, editor, Academic Press, New York, pp. 69–90.

BRUNO S. F., R. D. STAKER, G. M. SHARMA and J. T. TURNER (1983) Primary productivity and phytoplankton size fraction dominance in a temperate north Atlantic estuary. *Estuaries,* **6,** 200–211.

CADÉE G. C. and J. HEGEMAN (1979) Phytoplankton primary production, chlorophyll and composition in an inlet of the western Wadden Sea (Marsdiep). *Netherlands Journal of Sea Research,* **13,** 224–241.

CATTS G. P., S. KHORRAM, J. E. CLOERN, A. W. KNIGHT and S. D. DeGLORIA (1985) Remote sensing of tidal chlorophyll *a* variations in estuaries. *International Journal of Remote Sensing,* **6,** 1685–1706.

CHAMP M. A., G. A. GOULD III, W. E. BOZZO, S. E. ACKLESON and K. C. VIERRA (1980) Characterization of light extinction and attenuation in Chesapeake Bay, August, 1977. In: *Estuarine perspectives,* V. S. KENNEDY, editor, Academic Press, New York, pp. 262–277.

CLOERN J. E. (1982) Does the benthos control phytoplankton biomass in South San Francisco Bay (USA)? *Marine Ecology Progress Series,* **9,** 191–202.

CLOERN J. E. (1984) Temporal dynamics and ecological significance of salinity stratification in an estuary (South San Francisco Bay, USA). *Oceanologica Acta,* 7, 137–141.

CLOERN J. E. and F. H. NICHOLS, editors (1985) *Temporal dynamics of an estuary: San Francisco Bay.* Dr. W. Junk Publishers, Dordrecht, 237 pp.

CLOERN J. E.. B. E. COLE. R. L. J. WONG and A. E. ALPINE (1985) Iemporal dynamics of estuarine phytoplankton. A case study of San Francisco Bay. *Hydrobiologia,* **129,** 153–176.

COLE B. E. and J. E. CLOERN (1984) Significance of biomass and light availability to phytoplankton productivity in San Francisco Bay. *Marine Ecology Progress Series, 17,* 15–24.

COLE B. E. and J. E. CLOERN (1987) An empirical model for estimating phytoplankton productivity in estuaries. *Marine Ecology Progress Series,* **36.** 299–305.

COLIJN F. (1982) Light absorption in the waters of the Ems-Dollard Estuary and its consequences for the growth of phytoplankton and microphytobenthos. *Netherlands Journal of Sea Research.* **15,** 196–216.

COLIJN F. (1983) Primary production of phytoplankton in the Ems-Dollard Estuary. Ph.D thesis. University of Groningen, BOEDE-Publicaties en Verslagen, 123 pp.

CONOMOS T. J., editor (1979) *San Francisco Bay: The urbanized estuary,* Pacific Division American Association for the Advancement of Science, San Francisco, 413 pp.

CONOMOS T. J. and D. H. PETERSON (1977) Suspended-particle transport and circulation in San Francisco Bay: An overview. In: *Estuarine processes.* M. WILEY, editor, Academic Press, New York, pp. 82–97.

ERGA S. R. and B. R. HEIMDAL (1984) Ecological studies on the phytoplankton of Korsfjorden, western Norway. The dynamics of a spring bloom seen in relation to hydrographical conditions and light regime. *Journal of Plankton Research.* **6,** 67–90.

FLEMER D. A. (1970) Primary production in the Chesapeake Bay. *Chesapeake Science, 11,* 117–129.

FLINT R. W. (1984) Phytoplankton production in the Corpus Christi Bay Estuary. *Contributions in Marine Science.* **27.** 65–83.

GIESKES W. W. C. and G. W. KRAAY (1975) The phytoplankton spring bloom in Dutch coastal waters of the North Sea. *Netherlands Journal of Sea Research, 9,* 166–196.

HAAS L. W. (1977) The effect of the spring–neap tidal cycle on the vertical salinity structure of the James, York and Rappahannock Rivers, Virginia, USA. *Estuarine, Coastal and Marine Science, 5,* 485–496.

HAAS L. W.. S. J. HASTINGS and K. L. WEBB (1981) Phytoplankton response to a stratification-mixing cycle in the York River Estuary during late summer. In: *Nutrients and estuaries, B. J. NIELSON* and L. E. CRONIN, editors, Humana Press, pp. 619-636.

HAGER S. W. and D. D. HARMON (1984) Chemical determination of particulate nitrogen in San Francisco Bay. A comparison of two estimates. *Estuarine, Coastal and Shelf Science,* **19.** 181–191.

HARDING L. W. Jr. B. W. MEESON and T. R. FISHER Jr (1986) Phytoplankton production in two East coast estuaries: Photosynthesis–light functions and patterns of carbon assimilation in Chesapeake and Delaware Bays. *Estuarine, Coastal and Shelf Science, 23,* 737–806.

HITCHCOCK G. L. and T. J. SMAYDA (1977) The importance of light in the initiation of the 1972–1973 winter-spring diatom bloom in Narragansett Bay. *Limnology and Oceanography.* **22,** 126–131.

JOINT I. R. and A. J. POMROY (1981) Primary production in a turbid estuary. *Estuarine, Coastal and Shelf Science, 13,* 303–316.

KIRK J. T. O . (1985) Effect of suspensoids (turbidity) on penetration of solar radiation in aquatic ecosystems. *Hydrobiologia,* **125,** 195–208.

KUENZLER E. J.. D. W. STANLEY and J. P. KOENINGS (1979) *Nutrient kinetics of phytoplankton in the Pamlico River, North Carolina.* University of North Carolina Water Resources Research Institute Report No. 139, 163 pp.

LIVELY J. S., Z. KAUFMAN and E. J. CARPENTER (1983) Phytoplankton ecology of a barrier island estuary: Great South Bay, New York. *Estuarine, Coastal and Shelf Science,* **16,** 51–68.

MALONE T. C. (1976) Phytoplankton productivity in the apex of the New York Bight: Environmental regulation of productivity/chlorophyll *a.* In: *The middle Atlantic Shelf and New York Bight, M.* G. GROSS, editor, Limnology and Oceanography Special Symposium **2,** 260–272.

MALONE T. C. (1977) Environmental regulation of phytoplankton productivity in the lower Hudson Estuary. *Estuarine, Coastal and Marine Science, 5,* 157–171.

MALONE T. C. (1980) Size-fractionated primary productivity of marine phytoplankton. In: *Primary productivity in the sea,* P. G. FALKOWSKI, editor, Plenum Press, New York. pp. 301–319.

MALONE T. C., W. M. KEMP, H. W. DUCKLOW, W. R. BOYNTON, J. H. TUTTLE and R. B. JONAS (1986) Lateral variation in the production and fate of phytoplankton in a partially stratified estuary. *Marine Ecology Progress Series, 32,* 149–160.

MEADE R. H. (1972) Transport and deposition of sediments in estuaries. In: *Environmental framework of coastal plain estuaries,* B. W. NELSON, editor, Geological Society of America Memoirs, 133, pp. 91–120.

NICHOLS F. H.. J. E. CLOERN. S. N. LUOMA and D. H. PETERSON (1986) The modification of an estuary. *Science,* **231,** 567–573.

OTOBE H., T. NAKAI and A. HATTORI (1977) Underwater irradiance and Secchi disk depth in the Bering Sea and the northern North Pacific in summer. *Marine Science Communications, 3,* 255–270.

OVIATI C., B. BUCKLEY and S. NIXON (1981) Annual phytoplankton metabolism in Narragansett Bay calculated from survey field measurements and microcosm observations. *Estuaries,* 4, 167–175.

OWENS N. J. P. (1985) Variations in the natural abundance of ^{15}N in estuarine suspended particulate matter: A specific indicator of biological processing. *Estuarine, Coastal and Shelf Science*, **20**, 505–510.

PARSONS T. R., R. J. LeBRASSEUR and W. E. BARRACLOUGH (1970) Levels of production in the pelagic environment of the Strait of Georgia, British Columbia: A review. *Journal of the Fisheries Research Board of Canada*, **27**, 1251–1264.

PENNOCK J. R. (1985) Chlorophyll distributions in the Delaware Estuary: Regulation by light-limitation. *Estuarine, Coastal and Shelf Science*, **21**, 711–725.

PENNOCK J. R. and J. H. SHARP (1986) Phytoplankton production in the Delaware Estuary: Temporal and spatial variability. *Marine Ecology Progress Series*, **34**, 143–155.

PETERSON D. H. and J. P. FESTA (1984) Numerical simulation of phytoplankton productivity in partially mixed estuaries. *Estuarine, Coastal and Shelf Science*, **19**, 563–589.

PETERSON D. H., T. J. CONOMOS, W. W. BROENKOW and P. C. DOHERTY (1975) Location of the non-tidal current null zone in northern San Francisco Bay. *Estuarine and Coastal Marine Science*, **3**, 1–11.

PINGREE R. D., P. M. HOLLIGAN, G. 7'. MARDELL and R. N. HEAD (1976) The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic Sea. *Journal of the Marine Biological Association of the United Kingdom*, **56**, 845–873.

PLATT T. and A. D. JASSBY (1976)The relationship between photosynthesis and light to natural assemblages of coastal marine phytoplankton. *Journal of Phycology*, **12**, 421–430.

POWELL T. M., J. E. CLOERN and R. A. WALTERS (1986) Phytoplankton spatial distribution in South San Francisco Bay: Mesoscale and small-scale variability. In: *Estuarine variability*, D. A. WOLFE, editor, Academic Press, New York, pp. 369–383.

QASIM S. Z. (1979) Primary production in some tropical environments. In: *Marine production mechanisms*. M. J. DUNBAR, editor, Cambridge University Press, Cambridge, pp. 31–70.

ROMANA L. A. (1979) Role du bouchon vaseaux dans un ecosysteme estuarien. *2es Journees de la thermoecologie,* Institute Scientifique et Technique des Peches Maritimes, pp. 121–140.

RYTHER J. H. and C. S. YENTSCH (1957) The estimation of phytoplankton production in the ocean from chlorophyll and light data. *Limnology and Oceanography*, **2**, 281–286.

SCOTT B. D. (1978) Phytoplankton distribution and light attenuation in Port Hacking Estuary. *Australian Journal of Marine and Freshwater Research*, **29**, 31–44.

SEVIGNY J.-M., M. SINCLAIR, M. I. EL-SABH, S. POULET and A. COOTE (1979) Summer plankton distributions associated with the physical and nutrient properties of the northwestern Gulf of St. Lawrence. *Journal of the Fisheries Research Board of Canada*, **36**, 187–203.

SHOLKOVITZ E. R. (1979) Chemical and physical processes controlling the chemical composition of suspended material in the River Tay Estuary. *Estuarine and Coastal Marine Science*, **8**, 523–545.

SINCLAIR M. (1978) Summer phytoplankton variability in the lower St. Lawrence Estuary. *Journal of the Fisheries Research Board of Canada*, **35**, 1171–1185.

SIROIS D. L. and S. W. FREDRICK (1978) Phytoplankton and primary production in the lower Hudson River Estuary. *Estuarine and Coastal Marine Science*, **7**, 413–423.

SKLAR F. H. and R. E. TURNER (1981) Characteristics of phytoplankton production off Barataria Bay in an area influenced by the Mississippi River. *Contributions in Marine Science*, **24**, 43–106.

SMALL L. F. and B. E. FREY (1984) Water column primary production in the Columbia River Estuary. Final Report, Columbia River Estuary Data Development program, Astoria, Oregon, 133 pp.

SMITH R. C. and K. S. BAKER (1978) The bio-optical state of ocean waters and remote sensing. *Limnology and Oceanography*, **23**, 247–259.

STEEMANN NIELSEN E. (1975) *Marine photosynthesis with special emphasis on the ecological aspects,* Elsevier, Amsterdam, 141 pp.

STOCKNER J. G., D. D. CLIFF and D. B. BUCHANON (1977) Phytoplankton production and distribution in Howe Sound, British Columbia: A coastal marine embayment-fjord under stress. *Journal of the Fisheries Research Board of Canada*, **34**, 907–917.

STOCKNER J. G., D. D. CLIFF and K. R. S. SHORTREED (1979) Phytoplankton ecology of the Strait of Georgia, British Columbia. *Journal of the Fisheries Research Board of Canada*, **36**, 657–666.

STROSS R. G. and J. R. STOTTLEMEYER (1965) Primary production in the Patuxent River. *Chesapeake Science*, **6**, 125–140.

SVERDRUP H. U. (1953) On conditions for the vernal blooming of phytoplankton. *Journal du Conseil, Conseil International pour l'Exploration de la Mer*, 18, 287–295.

THAYER G. W. (1981) Phytoplankton production and the distribution of nutrients in a shallow unstratified estuarine system near Beaufort, N.C. *Chesapeake Science*, 12, 240–253.

TURNER R. E., S. W. WOO and H. R. JITTS (1979) Phytoplankton production in a turbid, temperate salt-marsh estuary. *Estuarine and Coastal Marine Science*. **9**. 603–613.

VERITY P. G. (1982) Effects of temperature, irradiance, and daylength on the marine diatom *Leptocylindricus danicus* Cleve. III, Dark respiration. *Journal of Experimental Marine Biology and Ecology*, **60**, 197–207.

WINTER D. F., K. BANSE and G. C. ANDERSON (1975) The dynamics of phytoplankton blooms in Puget Sound, a fjord in the northwestern United States. *Marine Biology*, **29**, 139–176.

WOFSY S C (1983) A simple model to predict extinction coefficients and phytoplankton biomass in eutrophic waters *Limnology and Oceanography,* **28,** 1144–1155.

YODER J A , L P ATKINSON, S S BISHOP, E E HOFMANN and T N LEE (1983) Effect of upwelling on phytoplankton productivity of the outer southeastern United States continental shelf *Continental Shelf Research,* **1,** *385404*