Temporal dynamics of estuarine phytoplankton: A case study of San Francisco Bay

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Abstract

Detailed surveys throughout San Francisco Bay over an annual cycle (1980) show that seasonal variations of phytoplankton biomass, community composition, and productivity can differ markedly among estuarine habitat types. For example. in the river-dominated northern reach (Suisun Bay) phytoplankton seasonality is characterized by a prolonged summer bloom of netplanktonic diatoms that results from the accumulation of suspended particulates at the convergence of nontidal currents (i.e. where residence time is long). Here turbidity is persistently high such that phytoplankton growth and productivity are severely limited by light availability, the phytoplankton population turns over slowly, and biological processes appear to be less important mechanisms of temporal change than physical processes associated with freshwater inflow and turbulent mixing. The South Bay, in contrast, is a lagoon-type estuary less directly coupled to the influence of river discharge. Residence time is long (months) in this estuary, turbidity is lower and estimated rates of population growth are high (up to 1–2 doublings d^{-1}), but the rapid production of phytoplankton biomass is presumably balanced by grazing losses to benthic herbivores. Exceptions occur for brief intervals (days to weeks) during spring when the water column stratifies so that algae retained in the surface layer are uncoupled from benthic grazing, and phytoplankton blooms develop. The degree of stratification varies over the neap-spring tidal cycle, so the South Bay represents an estuary where (1) biological processes (growth, grazing) and a physical process (vertical mixing) interact to cause temporal variability of phytoplankton biomass, and (2) temporal variability is highly dynamic because of the short-term variability of tides. Other mechanisms of temporal variability in estuarine phytoplankton include: zooplankton grazing. exchanges of microalgae between the sediment and water column. and horizontal dispersion which transports phytoplankton from regions of high productivity (shallows) to regions of low productivity (deep channels).

Multi-year records of phytoplankton biomass show that large deviations from the typical annual cycles observed in 1980 can occur, and that interannual variability is driven by variability of annual precipitation and river discharge. Here, too, the nature of this variability differs among estuary types. Blooms occur only in the northern reach when river discharge falls within a narrow range, and the summer biomass increase was absent during years of extreme drought (1977) or years of exceptionally high discharge (1982). In South Bay, however, there is a direct relationship between phytoplankton biomass and river discharge. As discharge increases so does the buoyancy input required for density stratification, and wet years are characterized by persistent and intense spring blooms.

Introduction

The relatively long history of lake studies has produced a set of paradigms that explain the gener-al features of phytoplankton ecology in a diversity of lakes, and serve as working models for the design of new research. For example, the development of a phytoplankton bloom is a common response to the

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spring overturn and mixing of nutrients to the surface of temperate lakes (Goldman & Horne, 1983). Empirical models using simple measures of hydrology and nutrient loading have some utility for predicting, at least qualitatively, the expected biomass of phytoplankton in lakes (e.g. Dillon & Rigler. 1974). And there is even promise that phytoplankton community composition (i.e. relative abundance of blue-green algae) may be a function of nutrient (N:P) ratios in lakes (Smith, 1983). Equivalent paradigms are rare for estuaries. This is in part a consequence of the extreme diversity of estuary types, ranging from large deep fjords to shallow tidal creeks, and the extreme complexity of estuaries that have unique circulation, complex bathymetry, large horizontal and vertical gradients of prop-

erties, and distinct temporal dynamics at the seaward and riverine boundaries.

Temporal dynamics of estuarine phytoplankton exhibit a wide range of seasonal patterns. For example, winter diatom blooms occur in Narragansett Bay (Pratt, 1965) and the Peel-Harvey estuary (McComb *et al.,* 1981), and winter blooms of dinoflagellates occur in the Pamlico River (Hobbie *et al.,* 1975) and Niantic River estuaries (Marshall & Wheeler, 1965). Spring diatom blooms are common seasonal events in the Wadden Sea (Cadée & Hegeman, 1979), Columbia River (Small & Frey, 1984), Barataria Bay (Sklar & Turner, 1981) and Bristol Channel (Joint & Pomroy, 1981). Phytoplankton biomass is seasonally maximal during autumn in the Patuxent River (Stross & Stottlerneyer.
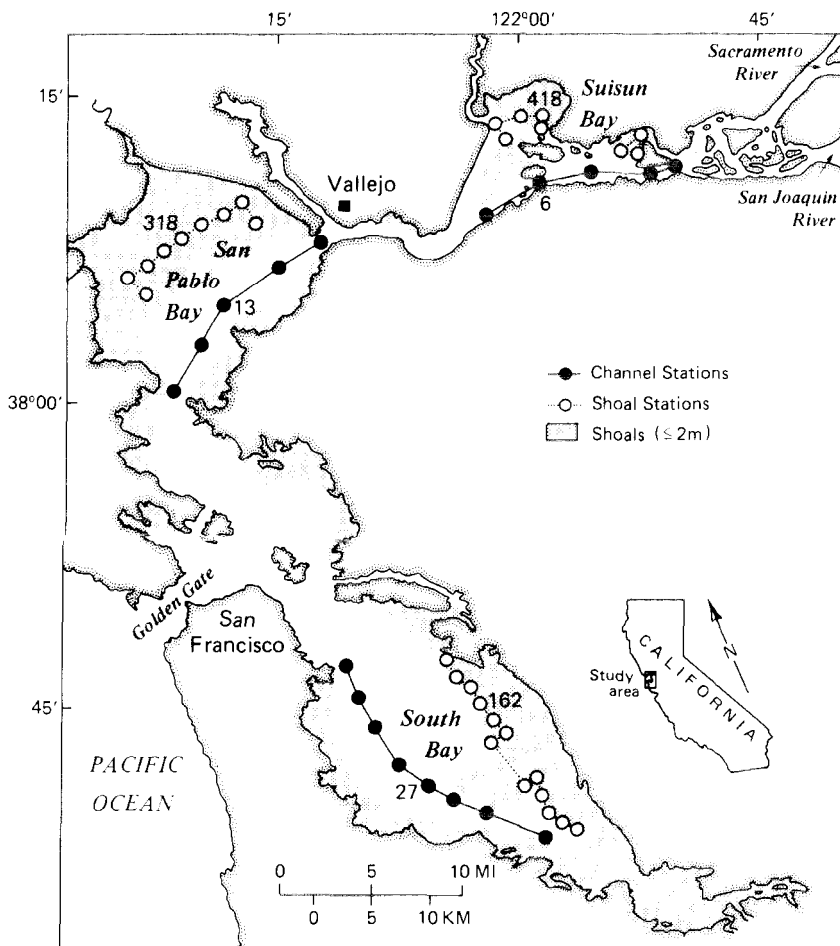

Fig. 1. Map of San Francisco Bay showing locations of sampling sites in the channel (●) and across the shoals (○) of South Bay. San Pablo Bay, and Suisun Bay.

1965), and some estuaries have no clear or consistent seasonal variations in phytoplankton biomass (e.g. Beaufort Channel, Williams & Murdoch, 1966; Chesapeake Bay, Seliger & Loftus, 1974; Lower Hudson River, Malone, 1977a). Annual phytoplankton productivity is also highly variable among estuaries, ranging from <10 g C m^2 (Naiman & Sibert, 1979; Joint & Pomroy, 1981) to >500 g C m^{-2} (Stockner *et al.,* 1979; Kuenzler *et al.,* 1979; Boynton *et al.,* 1982; Mann, 1982), and seasonal maxima in productivity can occur in spring (Gilmartin, 1964; Sklar & Turner, 1981; Small & Frey, 1984) or summer (Williams & Murdoch, 1966; Furnas *et al.,* 1976; Sirois & Fredrick, 1978; Sinclair, 1978; Cadée & Hegeman, 1979; Taft *et al.,* 1980).

This diversity of temporal patterns suggests that different mechanisms may control phytoplankton dynamics and productivity among estuaries, a fact that complicates the development of paradigms of estuarine phytoplankton ecology (Boynton *et al.,* 1982). The evolution of universal concepts is further impeded by the relatively short history of multi-disciplinary investigations in estuaries. Only a handful of studies have elicited mechanisms that

control the distribution, abundance or community composition of phytoplankton in estuaries (e.g. Winter *et al.,* 1975; Malone 1977a, b; Tyler & Seliger, 1978; Sinclair, 1978; Haas *et al.,* 1981; Seliger *et al.,* 1981; Tyler, 1984). Most of these process-oriented studies are recent, and the evolution of paradigms for estuaries will require studies specifically designed to test the general significance of these mechanisms for a variety of estuary types.

San Francisco Bay is a useful system for studying estuarine processes because it comprises several different estuarine habitats. The northern reach is a partially mixed estuary of the Sacramento-San Joaquin Rivers that has two shallow bays (San Pablo Bay, Suisun Bay, Fig. I), and the southern reach (South Bay) is a brackish lagoon. Each of these bays has unique phytoplankton communities and unique temporal variations in phytoplankton biomass and primary productivity. For example, phytoplankton biomass is seasonally maximal during spring in South Bay, during early summer in San Pablo Bay, and during late summer in Suisun Bay (Fig. 2). Biomass maxima are composed of nanoplankton (<22 μm) in South Bay but netplankton in the northern reach. These distinct vari-
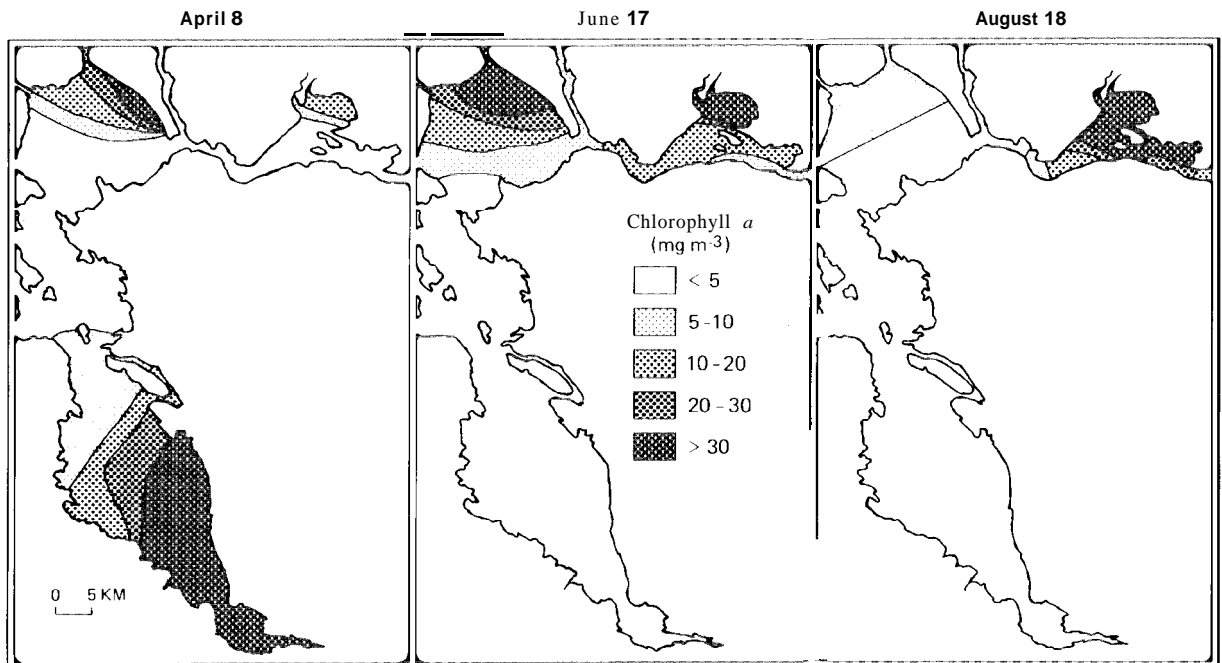

Fig. 2. Contours of near-surface chlorophyll *a* in San Francisco Bay during April, June, and August 1980. Contours are hand-drawn from measurements (in *vivo* fluorescence) made at 106 sites.
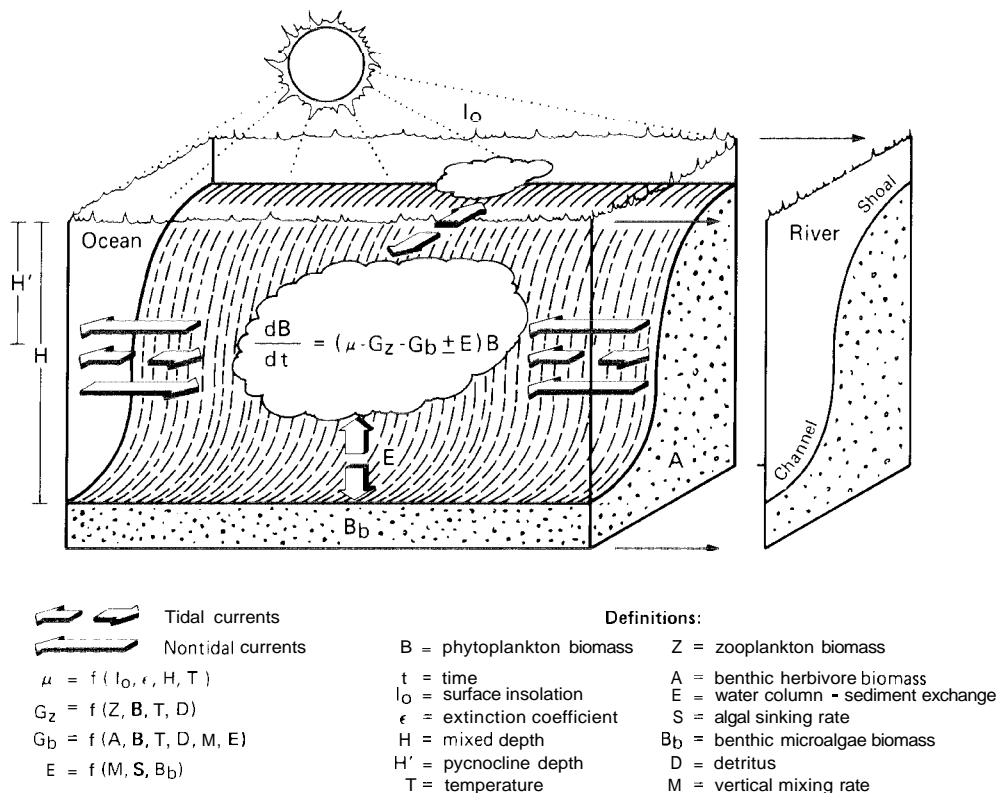
$$\frac{dB}{dt} = (\mu \cdot G_z - G_b \pm E)B$$

Tidal currents
Nontidal currents

Definitions:

B = phytoplankton biomass	Z = zooplankton biomass

$\mu = f(I_o, \epsilon, H, T)$

$G_z = f(Z, B, T, D)$

$G_b = f(A, B, T, D, M, E)$

$E = f(M, S, B_b)$

t = time
I_o = surface insolation
ϵ = extinction coefficient
H = mixed depth
H' = pycnocline depth
T = temperature

A = benthic herbivore biomass
E = water column - sediment exchange
S = algal sinking rate
B_b = benthic microalgae biomass
D = detritus
M = vertical mixing rate

Fig. 3. Schematic of a hypothetical estuary showing processes that control phytoplankton population dynamics within water parcels, and physical processes that move or mix water parcels.

ations within one estuary are intriguing, and suggest that each embayment may have a unique set of physical-chemical-biological controls on phytoplankton dynamics. The purpose of this paper is to examine, in detail, the temporal dynamics of phytoplankton biomass, community composition, and productivity within each sub-environment of San Francisco Bay. with an emphasis on the seasonal (i.e. monthly) time scale (results are mostly from 1980, and methods are given in the Appendix). We then present hypotheses concerning mechanisms that generate distinct temporal patterns within each system, and conclude with generalizations about controls on phytoplankton dynamics that may apply to other estuaries. We begin with a generalized conceptual model of processes that potentially influence phytoplankton populations in estuaries.

A conceptual model

From a Lagrangian reference phytoplankton populations can be influenced by two kinds of pro-

cesses, those that operate within a water parcel and those that mix or move water parcels (Fig. 3). Within a water parcel, phytoplankton biomass can change by (1) population growth (or death) from cell division (lysis or microbial decomposition), (2) losses to herbivorous zooplankton, (3) losses to benthic herbivores, and (4) exchanges (i.e. sinking or resuspension) of microalgal biomass between the water column and sediments. Concentrations of dissolved inorganic nutrients (N, P, Si) generally exceed rate-limiting levels in San Francisco Bay (Peterson et al., 1985a), and specific growth rate μ (d^{-1}) of phytoplankton in this turbid estuary is presumably a function of light availability (Cloern *et* al., 1983; Peterson & Festa, 1984) and perhaps temperature. Hence, μ varies with daily surface insolation I,, light attenuation in the water column ϵ, and mixed depth H, which is either water column depth during periods of vertical mixing or pycnocline depth H' during periods of density (salinity) stratification. The specific loss rate of phytoplankton to zooplankton grazing G_z (d^{-1}) is a function of zooplankton biomass Z and community composi-

tion, phytoplankton biomass B and size distribution, temperature, and perhaps the availability of non-phytoplankton food sources D. Similarly, specific loss rate to benthic grazers G_b is a function of the biomass A and community composition of benthic suspension-feeders (and perhaps surface deposit-feeders), T, B, D, thickness of the layer from which suspension-feeders can collect particles, vertical mixing rate, and sinking rate of phytoplankton. Finally, the exchange E of microalgae between the planktonic and epibenthic communities varies with turbulent mixing rate, sinking rate of phytoplankton S (a function of physiological condition, cell size and morphology, motility, formation of organic aggregates or attachment of inorganic particles), and biomass of the epibenthic community of microalgae B_b.

In addition to these in *situ* processes, circulation and mixing can change phytoplankton biomass and influence community composition (Fig. 3). Over short (hourly) time scales, tidal currents displace and mix water masses, generate surface convergences, and cause vertical mixing: the tidal excursion in San Francisco Bay is about 10 km, and tidal current speeds reach 140 cm s^{-1} (Walters *et al.*, 1985). Over longer time scales, tidal currents cause horizontal dispersion that transports phytoplankton longitudinally (along the length of the estuary), and laterally so that phytoplankton resident in the deeper channels mix with those resident over the adjacent shallows (Fig. 3). Of particular relevance to phytoplankton seasonality are the fortnightly neap-spring and semi-annual components of tidal current speed (Fig. 4), which cause daily to monthly variations in the rates of horizontal dispersion and vertical mixing. Residual (i.e. tidally averaged) circulation also influences the biomass and distribution of phytoplankton in estuaries. Residual currents, which in San Francisco Bay are on the order of 2–20 cm s^{-1} (Walters *et al.*, 1985), are generated by four processes: (1) freshwater inflow (i.e. river currents landward of salt intrusion), (2) wind stress, (3) density-driven currents (i.e. estuarine circulation) that cause net seaward advection in the surface layer and net landward advection in the bottom layer (Fig. 3), and (4) interactions between bottom topography and tidal circulation. Spatial and temporal variations in residual circulation of estuaries are complex and, as yet, poorly-quantified functions of meteorological conditions, river discharge, basin

morphometry, and tidal circulation (Walters *et al.*, 1985).

Our conceptual model indicates that estuarine phytoplankton dynamics are potentially controlled by about a dozen physical or biological processes, many of which have unique temporal variability. For example, daily variations in river discharge (which influences salinity distribution, residual circulation, turbidity, and density stratification), tidal current speed (which influences vertical mixing and horizontal dispersion), surface insolation, temperature, and wind speed exhibit distinct temporal patterns within San Francisco Bay (Fig. 4). Time series analyses of these records would show that each property has characteristic frequencies of change. Each also has an obvious seasonal component: (1) San Francisco Bay generally receives the largest
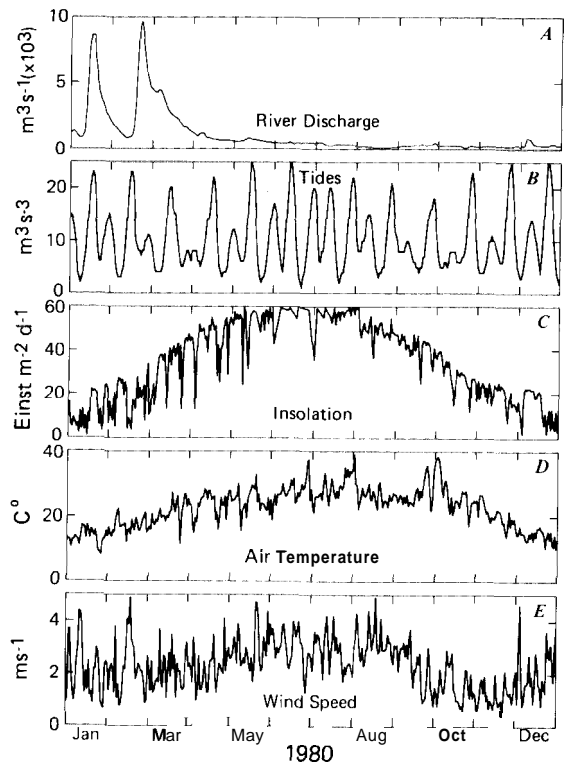

Fig. 4. Daily variations throughout 1980 of: (**A**) freshwater discharge to San Francisco Bay from the Sacramento-San Joaquin Rivers (from U. S. Bureau of Reclamation, Sacramento, Ca.); (**B**) seven-day running mean of u_m^3, where u_m is maximum predicted tidal current speed at Golden Gate (NOAA, 1979); (C) photosynthetically available radiation in San Pablo Bay (R. T. Cheng, personal communication); (D) mean daily air temperature, and (E) wind speed at Vallejo (from Bay Area Air Pollution Control District).

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influx of freshwater during the period from December through March (Fig. 4A); (2) tidal amplitude (and current speed) has a semi-annual periodicity such that maximum spring tides occur in summer and winter, and minimum tidal range occurs during spring and autumn (Fig. 4B); (3) total daily insolation is variable around the bay, but generally reaches a maximum of about 60 Einst m^{-2} d^{-1} (PAR) during summer (Fig. 4C); (4) air and water temperatures have a small annual range relative to other temperate estuaries, but are generally highest from July through September (Fig. 4D); and (5) winds are characteristically strongest in midsummer and calm in fall (Fig. 4E).

Our objective is to use measured temporal changes in the phytoplankton community to deduce which processes exert a primary control on phytoplankton dynamics. The task of identifying dominant processes, then quantifying the response of phytoplankton populations to those processes, is not straightforward and ideally requires detailed information about rates of all processes comprising our conceptual model. At this point, our experimental and field measurements allow us to estimate the rates of only a few biological processes (specific phytoplankton growth rate μ, from primary productivity, and zooplankton grazing rate G_z, from zooplankton biomass), and only to deduce the relative importance of all other mechanisms that potentially govern seasonal phytoplankton dynamics. Our analytical approach is to estimate rates of population growth in the water column μ_g ($= \mu - G_z$), and to compare these values with observed temporal variations in biomass ($\Delta B/\Delta t$). When calculated rates of population growth are consistent with observed seasonal changes in phytoplankton biomass, we infer that phytoplankton dynamics are controlled simply by in situ growth and grazing losses to zooplankton. Conversely, when calculated μ_g differs from measured changes in biomass, we infer that other processes (benthic grazing, transport processes, sinking) must be important. This analysis is done separately for the shallow and deep environments of South Bay, San Pablo Bay, and Suisun Bay, and we emphasize generalizations that emerge from these six different environments.
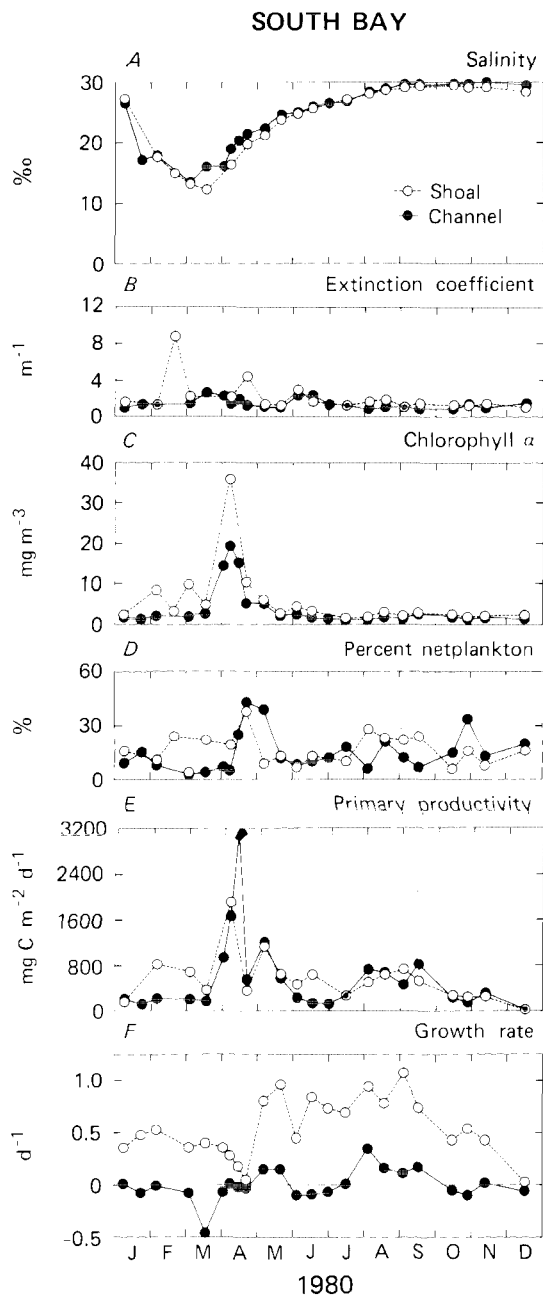

Fig. 5. Mean values of (A) salinity, (B) extinction coefficient, (C) near-surface chlorophyll a, (D) percent netplankton, (E) daily net productivity, and (F) calculated growth rate (corrected for zooplankton grazing) at stations comprising the channel (●) and shoal (○) transects in South San Francisco Bay. See Appendix for methods.

South San Francisco Bay: A lagoon-type estuary

Seasonality

The South Bay is a shallow embayment having a narrow channel (7 to 20 m deep) that widens at the mouth. Surface measurements were made semi-monthly during 1980 along separate transects in the channel and eastern shoals (Fig. 1), and mean values of chlorophyll a, percent netplankton (based upon fraction of *in vivo* fluorescence retained by a 22-μm mesh), extinction coefficient ϵ, and salinity were calculated for each transect (see Appendix for details). Phytoplankton samples were collected from at least one station (numbered stations, Fig. 1) per transect for microscopic examination, and primary productivity was measured monthly at these sites.

Local inputs of freshwater are small, but freshwater is advected into South Bay from the Sacramento-San Joaquin Rivers by tidal and residual currents during peak discharge of winter (Walters et al., 1985; Conomos et al., 1985). During 1980 surface salinity was seasonally minimal (12‰) in March and increased through summer to about 30‰ (Fig. 5A). The water column was well-mixed, except during brief (daily to weekly) stratification events that occurred during the winter-spring 'wet' season. Salinity stratification was most pronounced (9‰ over 10 m) during the two-week period of neap tides in late March-early April (Fig. 4B). Annual variations in turbidity were small in South Bay (Fig. 5B) and the extinction coefficient was consistently higher over the shoals than in the channel (Table 1).

Phytoplankton biomass B, measured as chlorophyll a, was low in South Bay (<3 mg chl a m^{-3}) except for small increases over the shoals during February and March and the large increase that occurred, both in the surface layer of the channel and over the shoals, in April (Fig. 5C). During this spring bloom, which lasted for about a month, phytoplankton biomass was highest (>50 mg chl a m^{-3}) in the southern extremity of South Bay and over the eastern shoals. Size fractionation of *in vivo* fluorescence (Alpine 1983) showed that netplankton constituted a small fraction (usually $<20\%$) of total phytoplankton biomass in South Bay throughout the year (Fig. 5D). During the spring bloom, the phytoplankton community was dominated throughout South Bay by the small (6 μm $\times$ 8 μm) diatom *Cyclotella caspia* and an assemblage of microflagellates *(Chroomonas minuta, C. amphioxeia, Cryptomonas testacea, Pyramimonas micron)*. Large centric diatoms *(Thalassiosira* spp., *Coscinodiscus* spp., *Cyclotella* spp.) were present the remainder of the year, but their biomass was small relative to that of the microflagellates, which accounted for the large nanoplankton fraction throughout the year (common phytoplankton taxa in San Francisco Bay are listed in Tables A1 and A2 in the Appendix). Daily primary productivity in the photic zone ranged from 20 to 3 100 mg C m^{-2} d^{-1}, and was maximal during the spring bloom; season-

Table 1. Depth, mean turbidity (ϵ) and phytoplankton biomass (B), and mean annual rates of processes relevant to phytoplankton dynamics along six transects of San Francisco Bay during 1980.

	South Bay		San Pablo Bay		Suisun Bay	
	Channel	Shoals	Channel	Shoals	Channel	Shoals
Depth at mean tide (m)	12.7	2.7	12.8	2.0	11.1	2.2
ϵ (m^{-1})	1.3	2.1	2.4	6.0	4.7	8.6
B (mg chl a m^{-3})	3.9	5.6	3.8	12.0	8.5	20.0
μ (d^{-1})	0.12	0.62	0.04	0.27	-0.05	0.10
G_z (d^{-1})	0.12	0.09	0.08	0.10	0.04	0.01
G_z/μ (%)	100%	15%	200%	37%	–	10%
Net Primary Production in the Photic Zone (g C m^{-2})	160	190	180	170	80	100
Respiration in the Aphotic Zone (g C m^{-2})	90	60	140	50	160	50
Net Production Over Depth H (g C m^{-2})	70	130	40	120	-80	50

al variations in productivity were similar for the channel and shoal transect (Fig. 5E).

Calculated growth rates μ (see Appendix) were always positive over the shoals and were very high (0.5 – 1.2 d^{-1}) from May through September. Growth rates were lower in the channel, reflecting the smaller ratio of photic depth:mixed depth there, but usually were positive. Calculated zooplankton grazing rate G, (see Appendix) ranged from 0.03 to 0.46 d^{-1} (mean annual values are shown in Table 1), and was never greater than μ in the shoals. Hence, net growth rate μ_g ($= \mu$ – *Gz*) was positive year-round in the shallows of South Bay (Fig. 5F). In the channel, μ_g was positive only in May and August-September.

Mechanisms of seasonality

Calculated values of μ_g suggest that phytoplankton biomass should increase in the South Bay channel during spring and late summer and that the phytoplankton population should grow continuously over the shoals at very high rates from May through September ($\mu_g = 1$ d^{-1} corresponds to 1.4 doublings per day). The discrepancy between observed and calculated population dynamics has been addressed previously (Cloern, 1982), and seasonality in South Bay involves two questions: (1) why is biomass low in summer-fall when μ_g is high?, and (2) why does biomass increase in spring, when calculated μ_g is small?

Residual currents in South Bay are usually slow (several cm per s; Walters *et al.,* 1985), and preliminary estimates of transport rates in South Bay indicate that low phytoplankton biomass is not caused by rapid advection or dispersion in summer. Rather, the high biomass of benthic invertebrates, including suspension-feeding bivalve mollusks, suggests that this community may consume phytoplankton

biomass at a rate equal to μ (i.e. on the order of 1 d^{-1}; Cloern, 1982). The South Bay has modest seasonal variations in salinity, temperature (Conomos *et al.,* 1985). and turbidity, and high rates of primary productivity compared to northern San Francisco Bay (see below). Hence, this stable and relatively productive embayment may be conducive to the maintenance of perennial populations of benthic herbivores. Thompson & Nichols' (1981) bay-wide survey of infauna showed that the biomass of benthic invertebrates is high in South Bay relative to the less stable, less productive northern San Francisco Bay (Table 2).

The occurrence of a spring bloom is not inconsistent with the hypothesis that benthic grazing is an important control in South Bay, because phytoplankton biomass increased only in the surface layer (in the channel) and blooms occurred only during the period of maximum water column stability (salinity stratification; Fig. 5C). During periods of stratification, algal cells above the pycnocline are not mixed throughout the water column and are therefore not subjected to grazing pressure from the benthos. Moreover, those algal cells retained in the shallow (<5 m) surface layer are exposed to greater irradiance than when the water column mixes, and during periods of stratification μ is actually higher than calculated here. Dynamics of the spring bloom in South Bay are therefore related to temporal changes in vertical mixing, and work subsequent to 1980 has shown that the channel of South Bay is highly stratified when (1) there is sufficient influx of freshwater to establish a vertical density gradient, and (2) turbulent mixing induced by tidal currents is insufficient to overcome buoyancy forces (Cloern, 1984). These two conditions are met when the influx of freshwater is high and during that phase of the semi-annual and neap-spring tidal cycles (Fig. 4B; Walters *et al.,* 1985) when tidal currents and vertical mixing are slow.

Table 2. Mean biomass (g m^{-2} wet weight) of benthic invertebrates along six transects of San Francisco Bay, during winter (January. February) and summer (August) of 1973 (from Thompson & Nichols, 1981).

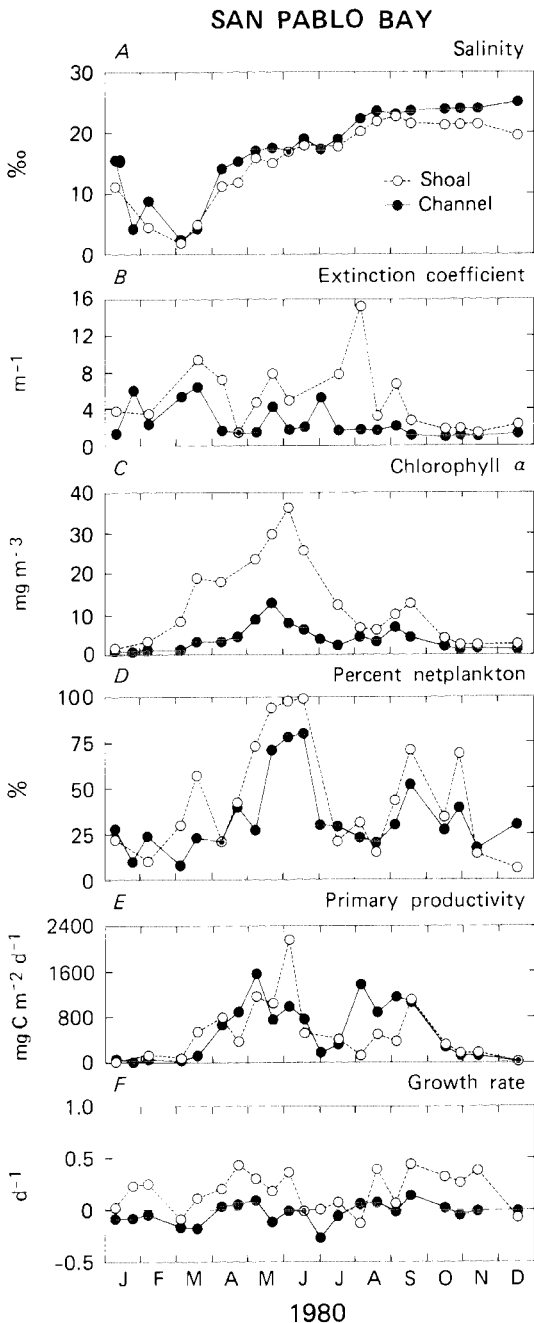| Season	South Bay		San Pablo Bay		Suisun Bay	
	Channel	Shoal	Channel	Shoal	Channel	Shoal
Winter	1153	134	17	49	25	30
Summer	910	132	4	142	34	6

Fig. 6. Mean values of (A) salinity, (B) extinction coefficient, (C) near-surface chlorophyll a, (D) percent netplankton, (E) daily net productivity, and (F) calculated growth rate (corrected for zooplankton grazing) at stations comprising the channel (●) and shoal (○) transects in San Pablo Bay.

In summary, the phytoplankton community of South Bay turns over quickly, especially over the shoals and during summer-fall, and it may be consumed at an equal rate by benthos when the water column mixes. Zooplankton grazing is an important process in the channel, but not in the shoals where depth-integrated zooplankton biomass is small. During the brief periods of stratification that occur in spring, phytoplankton biomass increases rapidly in the surface layer and a bloom occurs. Nanoplankton (microflagellates and small diatoms) may be selected because their rate of sinking from the surface layer is slow relative to growth rate; conversely, large diatoms may sink below the pycnocline at a rate faster than μ (Malone & Chervin, 1979). These generalities are consistent with observations in the South Bay channel, but the mechanism through which phytoplankton biomass increases in the shallows during spring is not yet understood. We presume that loss rate to benthic grazers is slow then, either because of reduced filtration rates by infauna during the colder seasons or because of reduced availability of phytoplankton to filter-feeders as vertical mixing slows.

San Pablo Bay: A seaward embayment of a partially-mixed estuary

Seasonality

San Pablo Bay is a very different estuarine environment from South Bay, although it has a similar morphometric feature of a deep (8–22 m) channel and expansive lateral shoals (Fig. 1). Physical properties of this estuary are more directly influenced by freshwater inflow from the Sacramento-San Joaquin Rivers. Surface salinity during 1980 was seasonally minimal (2‰) in early March when river discharge peaked, and it increased through summer to a maximum of 25‰ (Fig. 6A). Turbidity was persistently higher than in South Bay (compare mean values of ϵ, Table 1), and was always higher over the shoals than in the channel (Fig. 6B). Temporal changes in turbidity appeared to result from either (1) peaks in discharge and the riverine influx of suspended sediments (early March, Fig. 6B), or (2) accelerated resuspension in mid-summer (Fig. 6B) when wind speed and tidal current speed were both rapid (Fig. 4).

Seasonal changes in phytoplankton biomass followed similar patterns in the channel and shoals, but biomass peaks were more pronounced along the shoal transect. Biomass was low (1 mg chl a m $^{-3}$) in winter, increased to 35 mg chl a m^{-3} from March through May, declined in summer, and increased again in September (Fig. 6C). Netplankton composed a higher fraction (usually >20%) of phytoplankton biomass in San Pablo Bay than in South Bay, and the large spring bloom and smaller fall bloom both resulted from increased abundances of netplankton (up to 100% of total chlorophyll a; Fig. 6D). The low winter biomass was composed of freshwater taxa *(Melosira* spp., *Fragilaria crotonensis, Amphora* sp.) as well as *Skeletonema costatum* and *Thalassiosira rotula.* The spring netplankton bloom was composed of a succession from freshwater to marine diatoms that culminated in a community dominated by marine centric diatoms *(Thalassiosira* spp., *Coscinodiscus* spp.), and the June netplankton bloom in the shoals was composed of very large (>100 μm diam) *Coscinodiscus* spp. These large diatoms disappeared from San Pablo Bay in midsummer when the community was dominated numerically by microflagellates. The smaller biomass increase in September included increased abundances of *Skeletonema costatum* in the channel, but *Pleurosigma* spp. in the shoals. Daily primary productivity ranged from 10 to 2 160 mg C m^{-2} d^{-1}, was highest during the spring and fall blooms. and had similar seasonal variations between the shoal and channel transects (Fig. 6E).

Calculated phytoplankton growth rates were smaller in San Pablo Bay than in the less turbid South Bay, and μ was always smaller (−0.13 to 0.21 d^{-1}) for the channel transect that the shoal transect (−0.08 to 0.60 d^{-1}). For both transects, μ was highest in spring and fall when turbidity was lowest. Estimated zooplankton grazing rate was almost always sufficient to balance phytoplankton growth rate in the channel; exceptions occurred in April-May and August-September (Fig. 6F), which were the times of observed biomass increase. Mean G_z was twice the mean value of μ in the channel (Table 1). suggesting that on an annual basis zooplankton grazing is sufficient to consume all net production in the channel. This was not true for the shallows of San Pablo Bay where μ was large and (depth-integrated) zooplankton biomass was smaller. Here, μ_g was usually positive (Fig. 6F) and was high during the spring and fall periods of observed biomass increase; μ_g was negative in the shoals during mid-summer when turbidity increased.

Mechanisms of seasonality

The low phytoplankton biomass in San Pablo Bay during winter appears to result simply from rapid advective losses when freshwater species move through the bay faster than they divide. Nontidal current speed is on the order of 10–20 cm s^{-1} during peak winter discharge (Peterson *et al.,* 1975a; Walters *et al.,* 1985), so residence time in the channel of San Pablo Bay is about one or two days, which is shorter than the calculated doubling time in winter. However when river discharge declines in spring, the advective residence time exceeds algal doubling times and biomass can increase in San Pablo Bay. From March through December, calculated rates of phytoplankton growth agreed qualitatively with observed population dynamics. In the channel, for example, μ_g was positive only during April-May and August-September (Fig. 6F), and these were the times of observed biomass increase (Fig. 6C). Similarly, calculated μ_g over the shoals was positive in spring, small or negative during mid-summer, and increased again in the fall, consistent with seasonal changes in biomass. Small (or negative) rates of growth in mid-summer correspond to periods of high turbidity (Fig. 6B) that apparently resulted from heightened resuspension of sediments by wind waves and strong tidal currents (Fig. 4; Nichols & Thompson, 1985). Hence, the decline of phytoplankton biomass and productivity in summer can be attributed to light limitation that resulted from accelerated inputs of energy to resuspend sediments.

Qualitative agreement between μ_g and seasonal changes in biomass in San Pablo Bay is misleading, however, because the magnitude of calculated growth rate in the shoals (about 0.2 d^{-1} during spring and fall) was much higher than observed rates of population growth based upon chlorophyll changes (about 0.02 d^{-1}). Therefore, the phytoplankton population in the shallows of San Pablo Bay turns over at a moderate rate and must be removed by some process(es) other than zooplankton grazing at a rate of about 0.2 d^{-1}. Our conceptual model includes three potential sinks for phyto-

plankton biomass in shallow waters: (1) sinking and accumulation of phytoplankton biomass in the sediments; (2) consumption by benthos (as in South Bay); or, (3) net advective-dispersive losses to the channel. Bimonthly measurements of benthic chlorophyll a in San Pablo Bay did show accumulation of algal biomass in the shoal sediments from August to October (Thompson *et al.*, 1981) when wind speed, maximum tidal current speed, and presumably resuspension rate slowed. However, the observed rate of chlorophyll accumulation in the sediments during this period ($\cong 0.6$ mg chl a m^{-2} d^{-1}) was slow relative to the calculated production rate of chlorophyll (μ_g BH $\cong 1.9$ mg chl a m^{-2} d^{-1}), and more importantly the dominant species of microalgae associated with the sediments then (*Thalassiosira deripiens, Paralia sulcata*) differed from those of the plankton (Thompson & Laws, 1982). Moreover, there was no obvious increase in chlorophyll concentration in the sediments of San Pablo Bay during spring, the other season when μ_g exceeded observed rates of biomass increase. Therefore, although there may be times when there is a net flux of planktonic microalgae to the sediments, this process alone does not explain the discrepancy between observed and calculated rates of population growth over the shoals.

It is possible, however, that consumption by benthic infauna may play a role in controlling phytoplankton biomass over the shoals of San Pablo Bay, although to a lesser extent than in South Bay. Thompson & Nichols (1981) found an average benthic biomass of about 100 g m^{-2} wet weight in the shallows of San Pablo Bay (Table 2). Assuming that wet weight of infauna (mostly mollusks) comprises 2% organic carbon, and that animals ingest 10% of their body weight daily from phytoplankton. then the benthos potentially ingest about 200 mg C m^{-2} d^{-1}, or 2 mg m^{-3} d^{-1} chlorophyll a from the water column (assuming H $=$ 2 m; phytoplankton C:chlorophyll a $=$ 50). When phytoplankton biomass is 10 mg chl a m^{-3}, this consumption rate is equivalent to -0.2 d^{-1}, which is of the same order as calculated μ_g. Benthic grazing may also partly explain the differences in phytoplankton biomass between the spring bloom and the smaller fall bloom (Fig. 6C), because benthic biomass apparently increases in summer (Table 2) and ingestion rate of infauna increases with temperature (Walne, 1972). While it is tempting to attribute

discrepancies between calculated μ_g and observed seasonality in San Pablo Bay to the process of benthic grazing, this hypothesis is at present tenuous because (1) most infauna in San Pablo Bay are surface deposit-feeders rather than suspension-feeders (F. H. Nichols, personal communication), and (2) this mechanism is inconsistent with the observation that phytoplankton biomass peaks in San Pablo Bay comprise netplankton (large centric diatoms with rapid sinking rates that, presumably, enhance availability to benthic grazers).

The third potential sink for phytoplankton production in San Pablo Bay is horizontal dispersion which drives a net flux of algal biomass from the shoals into the channel, where phytoplankton are either consumed by zooplankton (recall that mean annual $\mu_g < 0$ in the channel; Table 1) or are advected seaward in the surface layer or landward in the bottom layer. Conceptual models of sediment dynamics suggest that sediments are deposited over the shoals of San Pablo Bay during periods of high river discharge, but are transported from San Pablo Bay upstream toward Suisun Bay by tidal and residual currents during periods of low river discharge. Moreover, the processes of resuspension and tidal mixing between the shoals and channel selectively remove fine inorganic particles, so that sediments become progressively coarser throughout summer and fall (Krone, 1979). These physical processes, which sort inorganic particles on the basis of size or density, may operate in an analogous manner to selectively remove nanoplankton (microflagellates. small diatoms) at a faster rate than large centric diatoms which sink rapidly and may be subjected to slower horizontal transport. Hence, netplankton blooms may be a consequence of physical processes that prolong the average residence time of heavy particles over the shallows of San Pablo Bay. This hypothesis is consistent with the persistent horizontal chlorophyll gradient (Fig. 2) such that phytoplankton biomass is highest away from the channel (i.e. phytoplankton residence time over the shoals increases with distance from the channel), and the observation that community composition of phytoplankton over the shoals is, at times, distinct from the community in the channel.

In summary, the channel of San Pablo Bay is a net sink for phytoplankton biomass, except during brief periods in spring and late summer-fall when turbidity decreases and light availability is suffi-

cient to sustain small net rates of population growth. Residual circulation is a potentially important, but as yet unquantified process that determines average residence time in San Pablo Bay, and on an annual basis zooplankton grazing exceeds net primary productivity in the channel. By contrast, the shoals of San Pablo Bay are generally a net source of phytoplankton biomass; exceptions occur in mid-summer during the period of highest turbidity and light limitation. Processes other than zooplankton grazing are responsible for removing phytoplankton biomass from the shoals, and likely possibilities include horizontal dispersion (which may explain the occurrence of netplankton blooms) or benthic grazing which apparently accelerates in summer.

Suisun Bay: A landward embayment of a partially-mixed estuary

Seasonality

Suisun Bay is the closest embayment to the riverine source of freshwater and suspended sediments, and therefore is the region of lowest salinity and highest turbidity within San Francisco Bay. Salinity was near zero until April, and then increased gradually to a maximum of 8‰ (Fig. 7A). Extinction coefficients were very high in Suisun Bay (Table 1) and, as in San Pablo Bay, ϵ was highest over the shoals and increased in summer (Fig. 7B). Phytoplankton biomass increased continuously, but slowly, from April through August (Fig. 7C). Mean chlorophyll concentrations were low (1 mg chl a m^{-3}) in winter and reached maximum values of 45 mg m^{-3} over the shoals. Biomass decreased from September to December. The gradual increase in biomass was accompanied by a progressive increase in the proportion of netplankton (up to about 95% of total chlorophyll a), indicating that the summer bloom in Suisun Bay was composed of algal cells or chains larger than 22 μm (Fig. 7D). Seasonal succession in Suisun Bay was distinct from that of the other embayments. Freshwater taxa (chlorophytes, *Melosira* spp., *Cyclotella* spp.) were present during periods of high river discharge, and these were replaced by an assemblage of diatoms that was progressively dominated by *Skeletonema costatum* and *Thalassiosira decipiens* ($\cong$20 – 25 μm diam;
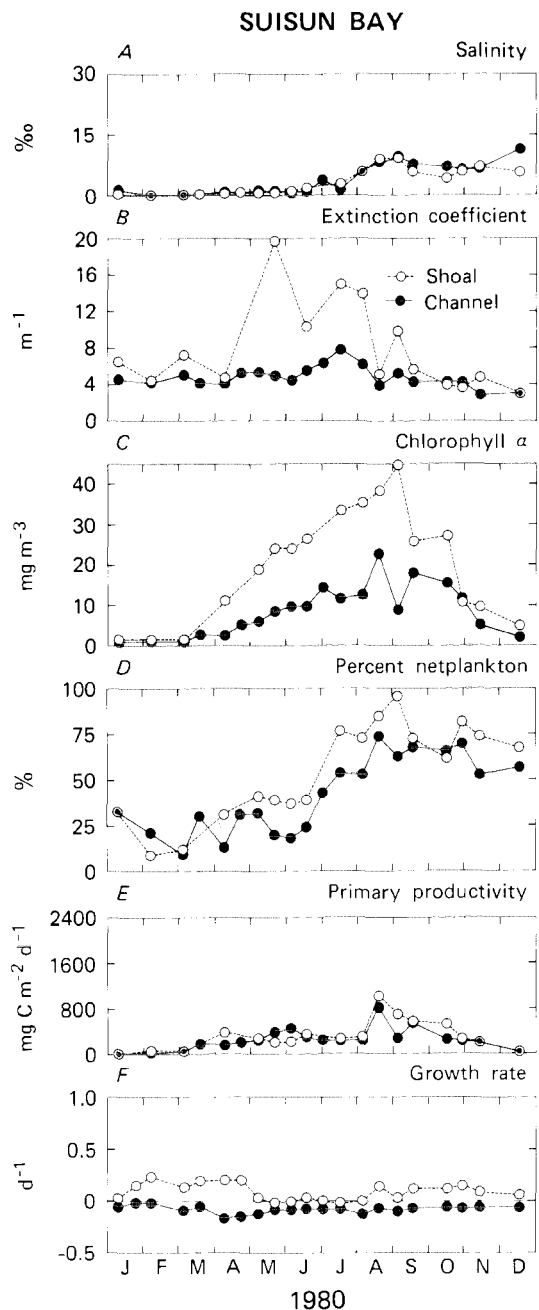

Fig. 7. Mean values of (A) salinity, (B) extinction coefficient, (C) near-surface chlorophyll a, (D) percent netplankton, (E) daily net productivity, and (F) calculated growth rate (corrected for zooplankton grazing) at stations comprising the channel (●) and shoal (○) transects in Suisun Bay.

previously identified as *T. eccentrica*). These species persisted as dominants through the winter (November-December) period of biomass decline and, because they existed as chains or in aggregates (Cloern et *al.*, 1983), they composed the large netplankton fraction. Primary productivity was usually low in Suisun Bay ($9 - 1 020$ mg C m^{-2} d^{-1}) and peaked in August during the biomass maximum (Fig. 7E).

The Suisun Bay channel is usually well mixed (Walters et al., 1985) and the photic zone is a small fraction ($<10\%$) of the mixed depth. Hence, light is not sufficient to sustain net photosynthesis over the mixed depth and calculated growth rates were always negative in the channel during 1980. Specific zooplankton grazing rates ranged from 0.0 to -0.07 d^{-1}, so the Suisun Bay channel was a persistent sink for phytoplankton biomass (Fig. 7F). Although the shoals are more turbid, the ratio of photic depth:mixed depth was usually sufficiently high there to sustain net productivity, and growth rates ranged from -0.02 to 0.24 d^{-1}, with minimal rates in summer when turbidity was highest (Fig. 7B, F). Zooplankton grazing represents a small sink for phytoplankton biomass in the shoals (Table I).

Mechanisms of seasonality

Suisun Bay is an interesting system where phytoplankton biomass increases during that period (summer) when calculated growth rates are seasonally minimal. Furthermore, phytoplankton biomass increases in the channel during summer, even though calculated μ_g is less than zero. Suisun Bay is the site of a localized turbidity maximum during summer (Conomos & Peterson, 1977), and previous papers have presented the hypotheses that (1) accumulation of netplankton in Suisun Bay results from the same physical processes (sinking coupled with estuarine circulation) that cause localized maxima of suspended sediments (Peterson et al., 1975b; Arthur & Ball, 1979), and (2) that algal biomass in the channel is derived from tidal mixing with water over the shoals where growth rates are positive (Cloern & Cheng, 1981). Further, enhanced retention of netplankton in Suisun Bay occurs only when river discharge is in a critical range of about 100 to 400 m^3 s^{-1} (Cloern et *al.*, 1983). At this rate of freshwater inflow, the landward-flowing bottom current and seaward-flowing river current converge in Suisun Bay (Peterson et *al.*, 1975b), thus prolonging the residence time of suspended particulates (including algal cells) in this part of the estuary. When river discharge exceeds this critical range (i.e. during winter or summers of very wet years), advective residence time falls below μ_g and phytoplankton biomass declines.

Seasonal changes in phytoplankton biomass and community composition were consistent with these hypotheses during 1980. Phytoplankton biomass began to increase throughout Suisun Bay in April (Fig. 7C), coincident with the decline of river discharge (Fig. 4A), and it continued to increase at a slow rate throughout the summer when river discharge remained in the critical range. The prolonged summer bloom was composed of netplankton species (*T. decipiens, S. costatum*) and, although biomass was consistently higher over the shoals than in the channel, community composition was similar between the channel and shoal sites. Predicted net growth rates (μ_g) were always negative in the channel, supporting the hypothesis that population growth in the Suisun Bay channel does not result from in situ production. Predicted growth rates over the shoals were small (mean annual $\mu \approx 0.1$ d^{-1}) compared to San Pablo and South Bays, but μ_g was usually positive. As in San Pablo Bay, the summer minimum of μ_g corresponded to the annual maximum turbidity during this season of rapid resuspension from wind and tide mixing. Calculated net growth rates in the shoals were very small from May to August (Fig. 7F), but were of the same order as observed rates of chlorophyll increase ($\cong 0.02$ d^{-1}) from March to September.

Although these observations support our conceptual model of Suisun Bay, the hypothesis that river-induced circulation is the single primary control on phytoplankton dynamics is not supported by observed declines in biomass during fall (Fig. 7C), when river discharge remained within the critical range. Estuarine circulation apparently persisted in Suisun Bay throughout fall, but phytoplankton biomass declined. In a previous paper (Cloern & Cheng, 1981) we speculated that the decline of the summer bloom results from reduced growth rates as surface insolation decreases in fall. However, estimated μ_g was relatively large over the shoals of Suisun Bay from September to November (Fig. 7F) because of decreased turbidity then. Total dissolved inorganic nitrogen (DIN) fell to an annual min-

imum in Suisun Bay during late August, simultaneous with the annual chlorophyll maximum. but mean DIN over the shoals never fell below about $4\,\mu M$ and was consistently near $10\mu M$ in September and October (D. Harmon, personal communication). Therefore, the decline of the summer bloom was not caused by nitrogen depletion (dissolved inorganic Si and P also remained above rate-limiting concentrations; Peterson et al., 1985a).

However, the decline of phytoplankton biomass during September and October did coincide with a large increase in chlorophyll a concentration in the sediments of Suisun Bay (from about 100 to over 200 mg chl a m^{-2}; Thompson et al., 1981), and the decline of the summer bloom may have been the result of increased flux rate of algal biomass from the water column to the sediments. This is a likely possibility because the diatom community in the sediments of Suisun Bay was dominated by *Thalassiosira decipiens* (Thompson & Laws, 1982), a dominant species of the summer phytoplankton bloom. The mechanism(s) responsible for partitioning *T.* decipiens and other diatoms between the benthos and water column is unclear, but increased abundance in the benthos during September and October occurred during the period of reduced wind speed and mean tidal current speed (Fig. 4). Hence, the partitioning of diatoms between these two habitats may simply be a response to seasonal changes in turbulent mixing and resuspension.

Zooplankton grazing is a slow process in Suisun Bay relative to other embayments in San Francisco Bay ('Sable 1). This is especially true for the shoals, where the ratio of zooplankton biomass (Ambler et al., 1985) to phytoplankton biomass is small, and mean annual G_z is only 10% (0.01 d^{-1}) of mean annual μ. Biomass of benthic infauna is normally small in the shallows of Suisun Bay (Table 2; but see below), and it appears that grazing by herbivores usually plays a minor role in controlling phytoplankton dynamics in this embayment.

Suisun Bay therefore represents an estuarine system in which phytoplankton population dynamics are controlled by processes other than growth and grazing. Calculated net growth rates are seasonally maximal in winter, when biomass is low, and algal biomass increases in the channel during summer even though there is insufficient light to sustain net photosynthetic production there. Phytoplankton dynamics in this embayment are influenced by the same physical processes (sinking, resuspension, and concentration by estuarine circulation) that govern the distribution of suspended sediments, and netplankton are selectively retained within the estuarine circulation cell of Suisun Bay on the basis of sinking rates. Unlike the phytoplankton communities of San Pablo Bay, where rapid sinking rates result from large cell size, rapid sinking rates in Suisun Bay (Ball & Arthur, 1981) result from the association of smaller diatoms with inorganic particles or organic aggregates (Cloern et al., 1983). Rapid sinking rates, however, cause a net flux of algal biomass from the water column to the sediments when resuspension rate slows. Chlorophyll a accumulates seasonally in the sediments of Suisun Bay, presumably because biomass of benthic herbivores is smaller there than in other parts of San Francisco Bay.

Interannual variability

Our conceptual model offers a useful starting place for analyzing the seasonal changes in phytoplankton dynamics observed in 1980, but the validation of conceptual (as well as numerical) models requires observations over a sequence of annual cycles, including those having extreme hydrological or meteorological conditions. Long-term records of phytoplankton biomass are available for Suisun Bay where the California Department of Water Resources has monitored chlorophyll concentration since 1969 (Fig. 8A). This record of interannual variability shows that phytoplankton biomass is always low in Suisun Bay during winter when river discharge is high and advective residence time is short, and that the dominant seasonal event is an increase in biomass (to >30 mg chl a m^{-3}) during summer when river discharge is low. Further, the summer bloom has historically been dominated by S. costatum and Coscinodiscus sp. or *Thalassiosira* sp. (presumably *T.* decipiens). so observations made during 1980 are representative of seasonal phytoplankton dynamics in Suisun Bay. This seasonal pattern has occurred over a wide range of annual hydrological cycles, including years when maximum Sacramento-San Joaquin River discharge ranged from <800 to >5 000 m^3 s^{-1} (Fig. 8B).

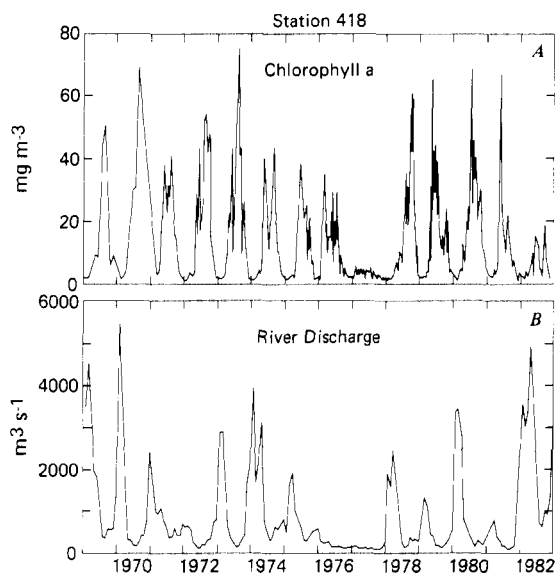However, the typical seasonal cycle was not seen

Fig. 8. Annual variations in (A) near-surface chlorophyll *a* in the shoals of Suisun Bay (station 418), and (B) mean monthly discharge of the Sacramento-San Joaquin Rivers, from 1969 through 1982. Chlorophyll measurements were made by the California Department of Water Resources, and discharge values from the U.S. Bureau of Reclamation.

during hydrologically extreme years, the 1977 drought and in 1982 when river discharge was persistently high (Fig. 8B). Departures from the typical seasonal cycle in 1977 and 1982 substantiate our hypothesis that river-induced gravitational circulation is a primary control on phytoplankton dynamics in northern San Francisco Bay, and confirm our concept of a critical discharge range. During 1977 and 1982 river discharge fell outside the range of $100–400 \ m^3 \ s^{-1}$ required to sustain high biomass, and the summer netplankton bloom was either absent or greatly reduced in magnitude. From 1969 through 1982 the mean annual discharge of freshwater from the Sacramento-San Joaquin Rivers was $29 \ km^3$ and the mean annual chlorophyll *a* concentration was $13.0 \ mg \ m^{-3}$ in the shoals of Suisun Bay. However during 1977 when annual freshwater inflow was reduced to $3 \ km^3$, mean annual chlorophyll *a* concentration fell to $3.1 \ mg \ m^{-3}$ and the phytoplankton community was dominated by microflagellates year-round (Cloern *et al.*, 1983). And in 1982 when total freshwater inflow was $73 \ km^3$, mean annual chlorophyll *a* concentration was only $6.6 \ mg \ m^{-3}$ and the community included

freshwater diatoms (*Melosira granulata, Cyclotella* sp.; California Department of Water Resources 1983) rather than *S. costatum*. Therefore, interannual variability of phytoplankton biomass and community composition in northern San Francisco Bay is highly correlated with interannual variations in the timing and volume of freshwater discharged to the estuary, and the mechanism of this correlation appears to be the accumulation of netplankton by estuarine circulation near the shallows of Suisun Bay when river discharge falls within a specific range.

A second river-driven mechanism of reduced phytoplankton biomass during droughts has been proposed by Nichols (1985), who compiled data showing a 10-fold increase in the abundance of benthic invertebrates in Suisun Bay during the 1977 drought. Prolonged periods of low discharge allow the landward intrusion of salt and the upstream migration of estuarine benthic invertebrates which normally are absent from this part of the estuary. Increased grazing pressure of one species alone, the suspension-feeding bivalve *Mya arenaria*, was apparently sufficient to consume all phytoplankton biomass in the Suisun Bay shallows on the order of once per day ($>\mu_g$). Hence, river discharge has an indirect influence on estuarine phytoplankton dynamics by controlling the distribution and abundance of benthic herbivores, and this is an additional mechanism contributing to interannual variability in San Francisco Bay.

We have also followed changes in phytoplankton biomass and community composition in South San Francisco Bay since 1978, and the spring bloom observed in 1980 appears to be a general seasonal feature in this embayment (Fig. 9). Moreover, spring blooms have occurred during the annual maximum in density stratification when surface chlorophyll *a* concentration exceeded $10 \ mg \ m^{-3}$, and the summer and fall have consistently been periods of vertical mixing and low phytoplankton biomass. Unlike northern San Francisco Bay where blooms are usually composed of the same general assemblage, phytoplankton community composition in South Bay exhibits marked interannual variability. For example, the spring bloom included increased abundance of *S. costatum* in 1978, *Cyclotella caspia* in 1980, *Thalassiosira rotula* in 1981, and a succession of diatoms (*T. rotula, Leptocylindricus danicus, S. costatum*) in 1982. However, all
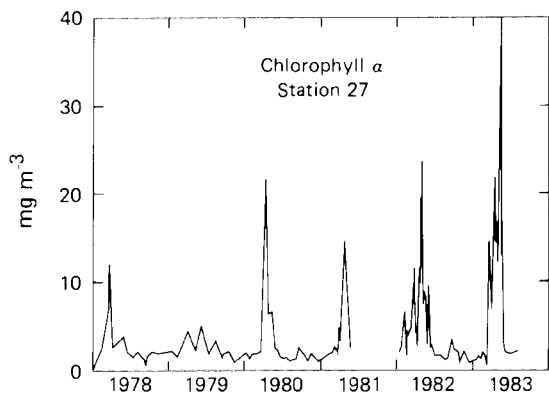
Fig. 9. Near-surface chlorophyll *a* in central South Francisco Bay (station 27) from 1978 through 1983.

biomass (chl *a*) peaks observed in South Bay since 1978 have been dominated by nanoplankton and have included increased abundances of microflagellates.

Because the phytoplankton community responds to changes in vertical mixing, and because stability is a direct response to tidal current speed which varies with high frequency, accurate representation of phytoplankton temporal dynamics in South San Francisco Bay requires frequent sampling during the spring season of alternating stratification-destratification events. Frequent sampling during 1982 and 1983 has shown that phytoplankton biomass can change measurably over short (almost daily) time scales, and the apparent absence of a spring bloom during 1979 (Fig. 9) may be an artifact resulting from insufficient sampling frequency. On the other hand the phytoplankton biomass in South Bay is static from about June through February, and monthly sampling may be adequate to define community dynamics during this period of persistent vertical mixing and low biomass.

Interannual variations of phytoplankton biomass in South Bay suggest a correlation between the volume of freshwater inflow and both the magnitude and duration of biomass increases in spring. For example, blooms during 1978, 1980 and 1981 apparently comprised one event that coincided with the absolute minimum tidal current speed during spring, and they persisted for about a month or less (Fig. 9). These were years of average or below average river discharge (Fig. 8B). However, during 1982 and 1983 when precipitation and freshwater inflow

were much higher than normal, the spring blooms comprised a sequence of biomass increases that apparently had a monthly periodicity correlated with monthly minima in tidal current speed (Fig. 4B). Hence, during years of very high river discharge there is sufficient buoyancy influx to sustain stratification events and phytoplankton blooms for several months. As in northern San Francisco Bay, much of the interannual variability of phytoplankton biomass results from variations in river discharge (Fig. 9), but the mechanism and nature of this relation are very different. In South Bay, river-induced gravitational circulation appears to be less important than water column stability, and phytoplankton biomass increases, rather than decreases, with river discharge.

Some fundamentals

The comparison of phytoplankton dynamics in three very different estuarine habitats, the two river-dominated embayments of northern San Francisco Bay and the lagoon-type South Bay, allows us to make some generalizations about estuarine phytoplankton ecology that may be relevant to other systems. The following generalities summarize our current understanding of processes that regulate phytoplankton dynamics here, and they may be useful for interpreting field observations or designing new field experiments in other shallow estuaries:

1. Phytoplankton growth rate (and primary productivity) in San Francisco Bay is mainly a function of light availability. Calculated specific growth rate μ is highly correlated with the parameter $I_0/\epsilon H$ (Fig. 10), which gives mean irradiance in a totally-absorbing water column ($= \frac{I_0}{H} \int_0^H e^{-\epsilon z} dz$). This correlation has several important implications. First, because turbidity results from the riverine influx of suspended sediments, we might expect a horizontal gradient of increasing μ and primary productivity away from the heads of estuaries. This is true in San Francisco Bay where mean annual growth rate and primary productivity are highest in South Bay, intermediate in San Pablo Bay, and lowest in the landward Suisun Bay (Table 1). Similar horizontal gradients of productivity have been observed in other estuaries including the upper
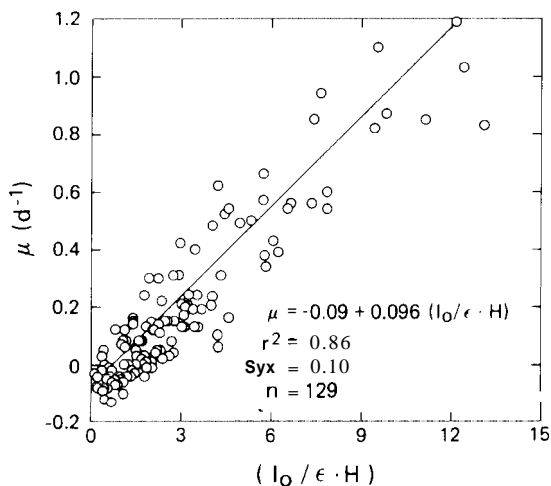
$$\mu = -0.09 + 0.096 \ (I_o/\epsilon \cdot H)$$
$$r^2 = 0.86$$
$$Syx = 0.10$$
$$n = 129$$

Fig. 10. Calculated phytoplankton specific growth rate in San Francisco Bay as a function of mean water column irradiance $I_o/\epsilon H$.

Chesapeake Bay (Flemer, 1970), Wadden Sea (Cadée & Hegeman, 1979), Bristol Channel (Joint & Pomroy, 1981), Barataria Bay (Sklar & Turner, 1981), shallow estuaries near Beaufort, N.C. (Thayer, 1971), and the Columbia River (Small & Frey, 1984). As a corollary, integral productivity over a mixed water column varies inversely with $H\epsilon$ (Cole & Cloern, 1984) such that very deep or turbid systems can be net respiratory sinks for photosynthetically assimilated carbon (e.g. Suisun Bay, Table 1). Similar observations were made in the deep sections of turbid Beaufort Channel (Williams & Murdoch, 1966) where phytoplankton respiration exceeds photosynthesis.

Second, because μ varies inversely with H we expect higher phytoplankton turnover rates in (1) shallow reaches relative to deep channel segments that are vertically mixed, and (2) in the upper layer of deeper waters when a pycnocline is present. This mechanism explains why phytoplankton biomass is consistently higher in shallow embayments than in deeper channels of San Francisco Bay (Table I), Delaware Bay (Pennock, 1985), the Hudson River estuary (Sirois & Fredrick, 1978), Ems-Dollard (Colijn, 1982), and Wadden Sea (Postma & Rommets, 1970). Further, this mechanism explains the occurrence of phytoplankton blooms during periods of enhanced stability in South San Francisco Bay, the York River (Haas et al., 1981), Puget

Sound (Winter et al., 1975), and the lower St. Lawrence (Sinclair, 1978).

And finally. the strong correlation between μ and $I_o/\epsilon H$ demonstrates that spatio-temporal variations in nutrient availability, temperature, and salinity are unimportant as controls on phytoplankton dynamics relative to processes that determine light availability. This general conclusion appears to be valid for a large number of estuaries where phytoplankton biomass increases only when mean irradiance exceeds a critical threshold (Hitchcock & Smayda, 1977; Sinclair et al., 1981; Colijn, 1982) and where productivity is directly proportional to mean irradiance (Malone, 1977a; Lively et al., 1983).

2. 'Iemporal variations in phytoplankton biomass are not necessarily related to temporal variations in specific growth rate μ: physical processes (advective-dispersive transport, resuspension) or grazing losses may occur at a faster rate than cell division. Within San Francisco Bay we have observed cases where phytoplankton biomass is low when calculated growth rate is high. This occurs in South Bay during summer when benthic grazing apparently balances population growth, in the northern reach during winter when advective residence time is short relative to μ, and in Suisun Bay during fall when there may be a net vertical flux of phytoplankton biomass to the sediments. Conversely, we have observed situations in which biomass increases even though calculated values of μ are negative (e.g. the summer bloom in the channel of Suisun Bay). Because physical processes are potentially important sources of spatio-temporal variability, models that incorporate only biological processes (e.g. Wofsy, 1983) can give unrealistic predictions of estuarine phytoplankton biomass. This is true for northern San Francisco Bay where the Wofsy model estimates zero phytoplankton biomass during typical summer conditions.

Physical controls on phytoplankton dynamics are documented for other estuaries. For example, Malone's (1977a) observations suggest that winter netplankton blooms in the lower Hudson River result from the advection of coastal diatoms into the estuary by gravitational circulation. Seliger et al. (1981) presented an interesting example of the Chester River where phytoplankton are locally abundant near the surface convergence of nontidal currents, and Tyler & Seliger (1978) have explained

the significance of estuarine circulation to the seasonality of *Prorocentrurn* in Chesapeake Bay. Persistent low phytoplankton biomass is a general feature of estuaries that have rapid flushing from riverine currents (Malone, 1977a; Small & Frey, 1984) or rapid tidal mixing with coastal waters (Gowen *et al.,* 1983). Zooplankton grazing is inferred to be an important process in other estuaries where phytoplankton biomass is low although indices of growth rate (e.g. P_m^B) are high (Kuenzler *et al.,* 1979; Malone & Chervin, 1979; Deason & Smayda, 1982), and grazing by benthic suspension feeders may be an important process in estuaries other than South San Francisco Bay (Marshall & Wheeler, 1965; Cadée & Hegeman, 1974; Officer *et al.,* 1982).

*3. T*he specific loss rate of phytoplankton biomass to herbivorous zooplankton is directly proportional to ZH. Therefore, we expect that zooplankton grazing is a more important process in a deep water column than in shallows. This mechanism, coupled with large respiratory losses in the deep aphotic zone of channels, suggests that phytoplankton biomass in vertically mixed estuaries should generally be scaled as $1/H$. This is consistently true for all parts of San Francisco Bay (Table 1), and may be a common feature of estuaries.

4. Physical processes appear to play a primary role in determining phytoplankton size distribution or community composition. Netplankton blooms occur when circulation and mixing selectively enhance the residence time of rapidly-sinking cells. This appears to be the situation over the broad shoals of San Pablo Bay and in the estuarine circulation cell of Suisun Bay during summer. Nanoplankton blooms occur in the surface layer of stratified water masses where there is a selective advantage associated with slow sinking. Analogous mechanisms selectively promote winter netplankton and summer nanoplankton blooms in the Hudson River-New York Bight (Malone *et* al., 1980), and the selective accumulation of dinoflagellates in frontal zones is apparently common in some estuaries (Incze & Yentsch, 1981; Seliger *et al.,* 1981).

5. Stable environments (e.g. South Bay) may be more likely to sustain perennial populations of benthic infauna, and therefore are systems in which phytoplankton biomass is controlled by benthic grazing, compared to highly variable environments such as northern San Francisco Bay. In shallow waters having depauperate benthos there may be a close association between the epipelic and planktonic communities of microalgae. In fact, there map be no clear separation of these communities in Suisun Bay where species composition of the benthos and plankton are similar. Here, biomass (chlorophyll a) of microalgae is consistently higher in the sediments than in the water column (Thompson *et* al., 1981), and temporal dynamics of phytoplankton biomass may be related to processes that cause resuspension and therefore alter the partitioning of microalgae between the benthos and water column. On the other hand, in systems having high grazing pressure from infauna (South Bay and perhaps San Pablo Bay) the biomass of microalgae in the sediments is low (Thompson *et* al., 1981). Further, because netplankton generally sink faster than nanoplankton there may be a selective removal of large algal cells from estuarine systems having high biomass of infauna. This mechanism may partly explain the persistent dominance of nanoplankton in South San Francisco Bay and in the Niantic River, another estuary having high biomass of filter-feeders (scallops) (Marshall & Wheeler, 1965).

6. Characteristic frequencies of phytoplankton change in estuaries are determined by the periodicity of the most important physical/biological process(es) (Sinclair *et al.,* 1981). For example, the summer bloom in Suisun Bay persists for months, is characterized by very slow population growth and little successional change, and is dependent upon stable hydrological conditions (i.e. invariant river discharge and estuarine circulation). In contrast the spring bloom in South Bay, which is controlled in part by a higher-frequency process (tidal currents), is much more dynamic and is characterized by changes that occur daily. Therefore intelligent field sampling in estuaries requires *a priori* knowledge about processes that control phytoplankton dynamics as well as characteristic time scales of change for these processes.

7. Although the general pattern of seasonal phytoplankton dynamics may be constant from year-to-year in an estuary, details of seasonality (e.g., successional changes in species composition, timing of blooms) can show a high degree of interannual variability (McComb *et* al., 1981; Boynton *et al.,* 1982; Deason & Smayda, 1982). Further, deviations from the typical seasonal pattern that occur during hydrological extremes (droughts, floods) can be instructive opportunities to test hypotheses

and verify concepts. Thus, a need exists for long term studies of estuarine phytoplankton before useful paradigms will evolve.

Appendix

Field methods

Our sampling program was designed to provide information about seasonal changes of properties and processes within the major geographic divisions of San Francisco Bay, and it included 21 cruises during 1980. Sampling was done on neap tides to minimize variations that occur over a tidal cycle, and each cruise required two consecutive days of sampling from two vessels (one for the shallow embayments and one for the central channel). Near-surface measurements were made at a grid of 115 stations throughout the San Francisco Bay system, and results presented here are mean values for stations composing separate transects (5–15 stations per transect) in the deep and shallow reaches of South Bay, San Pablo Bay, and Suisun Bay (Fig. 1). Vertical profiling was done at selected sites in the channel, but only near-surface values are presented here.

Water was collected by impeller-type pump from 0.25 or 2 m depth, and delivered to instruments for continuous measurement of salinity. temperature, turbidity (by nephelometry), and in vivo fluorescence. Salinity was measured with induction salinometers and temperature with thermistors (Dedini et al., 1982). Extinction coefficients (t) were calculated from depth profiles of irradiance measured with LiCor 192S quantum sensors at 3–4 sites per transect. For each cruise, measured values of ϵ were regressed against turbidity (from Turner Designs Model 10 or Model 40 nephelometers), and the regression equations were used to estimate ϵ at all sites from turbidity. Similarly, chlorophyll a was measured at 3–4 sites per transect and values reported here are calculated from regressions of chlorophyll a against in vivo fluorescence (Turner Designs Model 10 fluorometers). Chlorophyll samples were collected on Gelman A/E glass fiber filters, frozen, and then extracted by grinding with 90% acetone (Alpine et al., 1981). Concentrations were determined spectrophotometrically using the phaeopigment correction of Lorenzen (1967). All data are summarized in Smith et al. (1985).

Phytoplankton biomass was partitioned into netplankton and nanoplankton by measuring the fraction of in vivo fluorescence that passed a 22-μm mesh Nitex screen. Correction was made for soluble fluorescence (passing a Gelmann A/E glass fiber filter) and for the differential fluorescence yield of netplankton and nanoplankton. Hence. percent netplankton was calculated as:

$$\% \text{ Net} = 1.7\,(100)\,\frac{FT - F22}{FT - FS} \tag{A1}$$

where FT is total fluorescence measured in a Turner Designs Model 10 fluorometer, F22 is fluorescence after screening, and FS is soluble fluorescence. The factor 1.7 corrects for the lower fluorescence yield of netplankton than nanoplankton and was determined from a series of simultaneous measurements of chlorophyll a and in vivo fluorescence passing a Nitex screen (Alpine, 1983). Values reported here are means from 3· 4 stations per transect.

Primary productivity was measured monthly at one site per transect (numbered stations, Fig. 1), using simulated in situ incubations with ^{14}C. Samples were incubated for 24 h under natural sunlight that was attenuated with six different neutral density screens, and assimilated ^{14}C was determined with the acid-bubbling technique (see Cole & Cloern, 1984 for details). Measured rates of carbon assimilation P^B (mg C mg^{-1} chl a d^{-1}) were fit by least squares to the hyperbolic tangent function (Platt & Jassby, 1976) of irradiance 1 (Einst m^{-2} d^{-1}):

$$P^B = P_m^B \tanh\,(\alpha I / P_m^B), \tag{A2}$$

giving estimates of the maximum assimilation rate P_m^B and photosynthetic efficiency a . Daily net productivity PN (mg C m^{-}=d^{-}]) was calculated as the mean of estimated values for each station of a transect. given by:

$$PN = B \int_0^{H_p} P_m^B \tanh\,(\alpha I_z / P_m^B)\,dz, \tag{A3}$$

where H_p is depth of 1% surface irradiance I,, and I, $(= I_o e^{-\epsilon z})$ is irradiance at depth z. On dates when primary productivity was not measured. PN was calculated from measured B, ϵ, I_o, and interpolated values of P_m^B and a from the previous and subsequent cruises. For each date, respiratory loss of

Table 3. Common species of phytoplankton in San Francisco Bay during four seasons of 1980: A = January-March; B = April-May; C = June-October; D = November-December. Common species are those that constituted at least 10% of the population (numerically) at least once in a given season. Dominant species (denoted by *) constituted >50% of the population at least once per season or consistently accounted for >25% of the population during a season.

Species	South Bay		San Pablo Bay		Suisun Bay	
	Channel	Shoal	Channel	Shoal	Channel	Shoal
Nondiatoms:						
Mesodinium rubrum		B*				
Pyramimonas plurioculata	B			C		
Ochromonas sp.		A				
Pseudopedinella pyriforme	A					
Pyramimonas micron	A,B,D	A,B,C,D	B	B		
Chrysochromulina kappa	A			D		
Katodinium rotundatum	A,B		A			
Chroomonas minuta	A*,B*,C*,D*	A,B,C*,D*	A,B,C*,D*	A,B*,C*,D*	A,C	A,B
Chroomonas amphioxeia	A,B,C,D	A,B,C,D	A,B,C,D	A,B,C,D	A,B,C,D	A,B,C
Cryptomonas testacea	A,B,C	A,B,C	A,B,C	A,B,D	A	A
Chlamydomonas sp.			A		A	C
Pyramimonas sp.			B			
Merismopedia sp.					C	
Ankistrodesmus falcatus					A	
Scenedesmus sp.					A	
Ankistrodesmus sp.					B	B
Diatoms:						
Nitzschia spp.		A				
Chaetoceros debilis		A				
Thalassiosira rotula	A,B,C		A			
Cyclotella cf. caspia	B*	B*	B			
Cyclotella spp.		C	B	B,C	A,B,C	B,C
Thalassiosira nodulolineata			B	B		
Nitzschia closterium				B		
Nitzschia longissima				C		
Fragilaria crotonensis			A			
Coscinodiscus spp.			C*			
Melosira spp.			A,B	A,C*	C	
Melosira distans var. lirata				A	A*,B*	A,B*
Skeletonema costatum			C	A	B,C*,D*	A,B,C*,D*
Skeletonema potamus				C*	B	B
Melosira dubia				C	C	C
Biddulphia sp.						A
Chaetoceros didymus						A
Cyclotella bodanica					C	
Cyclotella catenata						C
Cyclotella striata					B	
Melosira granulata					A	C
Melosira varians						C
Nitzschia panduriformis					B,C	C
Thalassiosira sp.					A	
Thalassiosira decipiens					C*,D	B,C*,D
Thalassiothrix sp.						C

Table 4 Phytoplankton species that constituted >10% of community biomass in San Francisco Bay during four seasons of 1980 A = January-March, B = April-May; C = June-October, D = November-December Asterisks indicate seasons when a particular species comprised >50% of phytoplankton biomass at least once or >25% of biomass consistently

Species	South Bay		San Pablo Bay		Suisun Bay	
	Channel	Shoal	Channel	Shoal	Channel	Shoal
Nondiatoms:						
Mesodinium rubrum	A,B	A,B*,C	A			
Pseudopedinella pyriforme	A		A			
Katodinium rotundatum	A,C,D		B			
Chroomonas minuta	A,B,C*,D	A,C*	C,D	C,D		
Chroomonas amphioxeia	A,B,C*,D	B,C,D	B,C,D	C,D	D	
Cryptomonas testacea	A,B,C	B,C,D	B,C,D	C,D		A
Heterocapsa triquetra			C	C		
Dinophysis speculum				A*		
Oxytoxum sp.	A					
Diatoms:						
Pleurosigma fasiola	C*					
Thalassiosira spp.		C*				
Thalassiosira cf. baltica	C	C		C		
l'halassiosira nodulolineata	B		B			
Nitzschia sp.		A			A	
Thalassiosira rotula	A,C,D	A*,D	A,D			
Cyclotella caspia	B*	B*	B			
Coscinodiscus sp. (>60 μm)	B,C	C	C	C*		
Coscinodiscus jonesianus		B	C		A*	A*
Coscinodiscus sp.		A*	C*	B*	B*	
Cyclotella spp.		C*	A,B,C	B.C	A,C	B,C
Amphora sp.			A*			
Thalassiosira cf. hendeyi			C	B,C		
Coscinodiscus radiatus			C*			
Coscinodiscus stellaris				A,B		
Pleurosigma spp.				C,D		
Melosira spp.			B	A	C	
Nitzschia longissima				C	A	
Skeletonema costatum				A	C*,D*	C,D*
Thalassiosira sp.			A		A	A
Cyclotella bodanica					C*	B
Cyclotella striata					B*	B,C,D
Melosira distans var. lirata					A,B	B
Nitzschia panduriformis					C	C*
Thalassiosira decipiens					C*,D*'	A,B*,C*,D*
Melosira dubia					C	C

assimilated carbon R (mg C m^{-2} d^{-1}) was estimated for the aphotic zone as:

$$R = B \, (0.1 \, P_m^B) \, (H - Hp), \qquad (A4)$$

assuming that specific respiration rate is 10% of P_m^B (Cole & Cloern, 1984: Peterson et al., 1985b). These values were then subtracted from net productivity in the photic zone and used to calculate net annual productivity over the water column for each transect (Table 1).

Phytoplankton samples were collected from at least one station per transect and preserved in Lugol's solution with acetate. Algal cells were enumerated at 1 000× and 80×, in triplicate aliquots from each sample, using an inverted microscope. Results of enumerations are given in Wong & Cloern (1982), and common taxa are listed in Table 3. During enumeration. algal cells were also measured and assigned a geometric shape for the calculation of total phytoplankton cell volume. Those species comprising a significant fraction of community bi-

omass are listed in Table 4. Phytoplankton biomass as carbon was calculated from estimated cell volumes using the equations of Strathmann (1967), and a mean value for the ratio of phytoplankton carbon:chlorophyll a from these measurements was 52 (n = 120; s — 30).

Growth and grazing rates

Mean values of the phytoplankton specific growth rate μ were estimated for each transect by averaging rates at each site from:

$$\mu = \ln[((PN - R)/H + C)/C], \qquad (A5)$$

where PN is net productivity in the photic zone, R is areal respiration in the aphotic zone (equation A4), H is mean water depth, and C is phytoplankton biomass as carbon (mg C m^{-3}), taken as $52B$. Inherent in this approach are two significant assumptions: (1) that biomass-specific respiration rate is fixed at 10% of P_m^B and (2) that the phytoplankton carbon:chlorophyll ratio is constant and equal to 52. Both assumptions are difficult to justify and for this reason calculated values of μ_g are best interpreted as indices of population turnover rate, rather than accurate measures of absolute growth rate.

Zooplankton grazing rate was calculated from mean zooplankton biomass (averaged over sample depths and along transects; Ambler et al., 1985) and a modified Ivlev function (Parsons & LeBrasseur, 1970) that predicts daily ingestion per animal F (mg C animal^1) as a function of body weight W (μg C animal-'), temperature T, and phytoplankton biomass as carbon C (see Cloern. 1982):

$$F = (9.5 \times 10^{-4})\, W^{0.8}\, e^{0.069(T-10)}\, (1 - e^{-0.01C}). \quad (A6)$$

The zooplankton community was partitioned among 54 taxa, including life stages of all calanoid and harpacticoid copepods, meroplankton (barnacle nauplii and mollusk veligers), and microzooplankton (tintinnid ciliates and rotifers). Then, total daily zooplankton ingestion I (mg C m^{-3}) is:

$$I = \sum_{i=1}^{54} F_i Z_i, \qquad (A7)$$

where Z_i is abundance (m^{-3}) of zooplankton species i, and specific loss rate to zooplankton grazing G_z (d^{-1}) is:

$$G_z = -\ln[(C - I)/C]. \qquad (A8)$$

Net population growth rate of phytoplankton was then calculated as $\mu_g = \mu\text{-}G_z$ for each transect.

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