

River Discharge Controls Phytoplankton Dynamics in the Northern San Francisco Bay Estuary

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Phytoplankton dynamics in the upper reach of the northern San Francisco Bay estuary are usually characterized by low biomass dominated by microflagellates or freshwater diatoms in winter, and high biomass dominated by neritic diatoms in summer. During two successive years of very low river discharge (the drought of 1976-77), the summer diatom bloom was absent. This is consistent with the hypothesis that formation of the diatom population maximum is a consequence of the same physical mechanisms that create local maxima of suspended sediments in partially-mixed estuaries: density-selective retention of particles within an estuarine circulation cell. Because the estuary is turbid, calculated phytoplankton growth rates are small in the central deep channel but are relatively large in lateral shallow embayments where light limitation is less severe. When river discharge falls within a critical range ($100-350 \text{ m}^3 \text{ s}^{-1}$) that positions the suspended particulate maximum adjacent to the productive shallow bays, the population of neritic diatoms increases. However, during periods of high discharge (winter) or during periods of very low discharge (drought), the suspended particulate maximum is less well-defined and is uncoupled (positioned downstream or upstream) from the shallow bays of the upper estuary, and the population of neritic diatoms declines. Hence, the biomass and community composition of phytoplankton in this estuary are controlled by river discharge.

Introduction

Coastal plain estuaries are often characterized by a non-tidal circulation in which a surface layer of low-density (river-derived) water flows seaward over a landward-flowing bottom layer of higher density (ocean-derived) water (Pritchard, 1967). The distribution of suspended particulates is influenced by such estuarine circulation: dense particles sink into the bottom current, which converges with the river current near the landward extent of salinity intrusion (Hansen & Rattray, 1965). Suspended particulates accumulate to form a turbidity maximum near this convergence, or 'null zone', where the tidally-averaged bottom current is zero and upward vertical water velocity is greatest. Because particle concentration

maxima result from a balance between sinking and vertical advection, Postma (1967) speculated that only those suspended particles having appropriate densities will accumulate within the water column of estuaries: light particles are advected seaward in the surface layer and dense particles are not resuspended. The density-selective accumulation of suspended sediments by estuarine circulation is documented in the northern Chesapeake Bay (Schubel, 1969) and Rappahannock Estuary (Nichols & Poor, 1967), and turbidity maxima have been studied in numerous other estuaries (e.g. Simmons, 1955; Postma, 1967; Meade, 1969, 1972; Nichols, 1974), including northern San Francisco Bay (Conomos & Peterson, 1977; Arthur & Ball, 1979a).

Although subsurface upstream transport of phytoplankton has been documented in the Chesapeake Bay (Tyler & Seliger, 1978) and Hudson River estuary (Malone *et al.*, 1980), little is known about the interacting effects of estuarine circulation and sinking on phytoplankton distributions. We have observed a close coupling between river discharge and phytoplankton population dynamics in the northern San Francisco Bay estuary, and believe that such coupling results from the density-selective accumulation of neritic diatoms by estuarine circulation, under specific flow regimes, in a manner analogous to the accumulation of sediments. Whereas the distribution of inorganic particles is governed primarily by transport phenomena, algal cells also grow, divide and decompose or are consumed. Hence, the distribution, abundance and size composition of phytoplankton in partially mixed estuaries are determined by the kinetics of these biological processes in addition to the same transport mechanisms that affect suspended sediments.

Northern San Francisco Bay is a partially-mixed estuary formed at the confluence of California's two longest rivers, the Sacramento and San Joaquin (Figure 1). A narrow channel ($z \approx 10$ m in the upper reach) is bounded by two shallow ($z \approx 1.5$ m) and expansive embay-

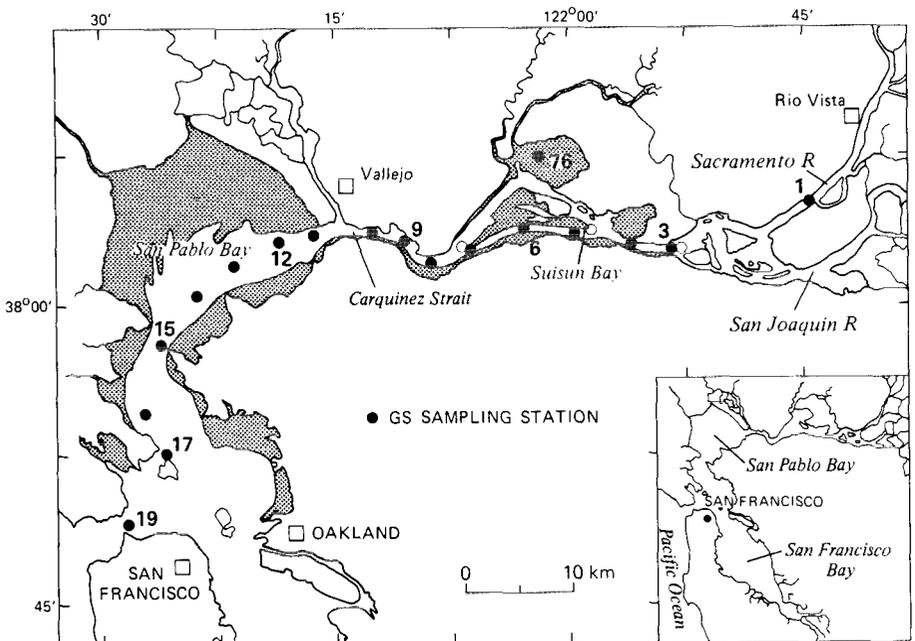


Figure 1. Map of northern San Francisco Bay estuary showing positions of selected GS (●) and FA (○) sampling stations. Shaded areas represent shoals (mean depth < 2 m).

ments—San Pablo Bay and Suisun Bay. Discharge through the Sacramento–San Joaquin Rivers is usually high ($1000\text{--}10\,000\text{ m}^3\text{ s}^{-1}$) during winter–early spring (December–March), then declines in spring early summer (April–June), and is regulated at a reduced summer (July–October) discharge that normally ranges between $100\text{--}300\text{ m}^3\text{ s}^{-1}$. River discharge was severely reduced during the drought of 1976–77. This gave us the opportunity to measure phytoplankton biomass and community composition over a wide range of flow conditions, and to test the hypothesis that phytoplankton dynamics are controlled by river-induced circulation. We emphasize results from the Suisun Bay region (Figure 1), which is the usual site of summer maxima in total suspended particulate matter (Conomos & Peterson, 1977), particulate organic carbon (Schemel & Dedin, 1979), phytoplankton (Storrs *et al.*, 1966; Peterson *et al.*, 1975*b*; Arthur & Ball, 1979*a*; Cloern, 1979), zooplankton (Painter, 1966; Storrs *et al.*, 1966; Orsi & Knutson, 1979) and larval fish (Turner & Chadwick, 1972).

Methods

Data presented here were collected as part of two separate research programmes, one focussed on San Francisco Bay [by the U.S. Geological Survey (GS)] and one focussed on the Sacramento–San Joaquin Rivers and upper estuary, [by the Four Agency Study Program U.S. Bureau of Reclamation, U.S. Fish and Wildlife Service and California Departments of Fish and Game and Water Resources (FA)]. The GS study included near-monthly, continuous underway measurements of salinity, temperature, turbidity and *in vivo* fluorescence in surface water along the longitudinal axis of the channel; vertical profiles were obtained at selected sites in the channel (numbered stations, Figure 1). While profiling, water was pumped to an induction salinometer, thermistor and Turner Designs Model 10 nephelometer and fluorometer. Light extinction coefficient ϵ was calculated from vertical profiles of irradiance measured with a LiCor quantum sensor.

Samples were collected from the outflow of the fluorometer for measurement of extracted chlorophyll *a*, size fractionation of phytoplankton biomass, suspended particulate matter, and phytoplankton taxonomy and enumeration. Discrete samples for these analyses were collected in surface water over the shoals. Concentration of chlorophyll *a* was measured spectrophotometrically (Strickland & Parsons, 1972; Lorenzen, 1967) to calibrate the continuous fluorometer readings. Suspended particulate matter was measured gravimetrically after air-drying filtered samples. Preserved phytoplankton samples were fixed with Lugol's solution and enumerated using the Utermohl method (Lund *et al.*, 1958). The size distribution of phytoplankton was estimated by gravity filtering small volumes ($<50\text{ ml}$) of water through $22\ \mu$ Nitex netting and a Gelman A/E glass fibre filter, and then measuring fluorescence of the filtrates and an unfractionated sample. Total particulate fluorescence was partitioned among netplankton (that fraction of particulate *in vivo* fluorescence retained by the $22\ \mu$ screen) and nanoplankton (passing the $22\ \mu$ screen), after correcting for soluble fluorescence (passing the glass fibre filter).

On selected dates, samples were collected in the channel and shoals for measurement of phytoplankton primary production. Carbon assimilation was measured at 5–7 light intensities with ^{14}C , using the acid-bubbling method (Schindler *et al.*, 1972) after 24 h incubation either *in situ* or in a sunlit water-cooled incubator with neutral density screens. Biomass-specific respiration rate ($\text{mg C mg}^{-1}\text{ chlorophyll } a\text{ day}^{-1}$) was estimated as the intercept of the linear portion of photosynthesis–irradiance curves (Platt & Jassby, 1976). Depth-integrated net production was calculated as the sum of respiration in the aphotic zone and

integral net production in the photic zone. Phytoplankton growth rate (k , = divisions day^{-1}) was calculated as $\log, (C_t + C_0)/C_0$, where C_t is mean net production in the water column ($\text{mg C m}^{-3} \text{ day}^{-1}$) and C_0 is initial phytoplankton carbon (mg C m^{-3}). C_0 was estimated from chlorophyll a concentration, assuming a constant carbon : chlorophyll a ratio of 40 (R. L. J. Wong, unpublished data).

The FA study was comparable, but included biweekly sampling during spring and summer, only spectrophotometric determination of chlorophyll a from bottle samples, and more vertical profiles in Suisun Bay.

Results

During 1975, 1978 and 1979, discharge through the Sacramento–San Joaquin Rivers was representative of normal annual hydrographs (Figure 2). Mean monthly discharge peaked (to over $1000 \text{ m}^3 \text{ s}^{-1}$) in February–March, then declined to relatively constant lower flows

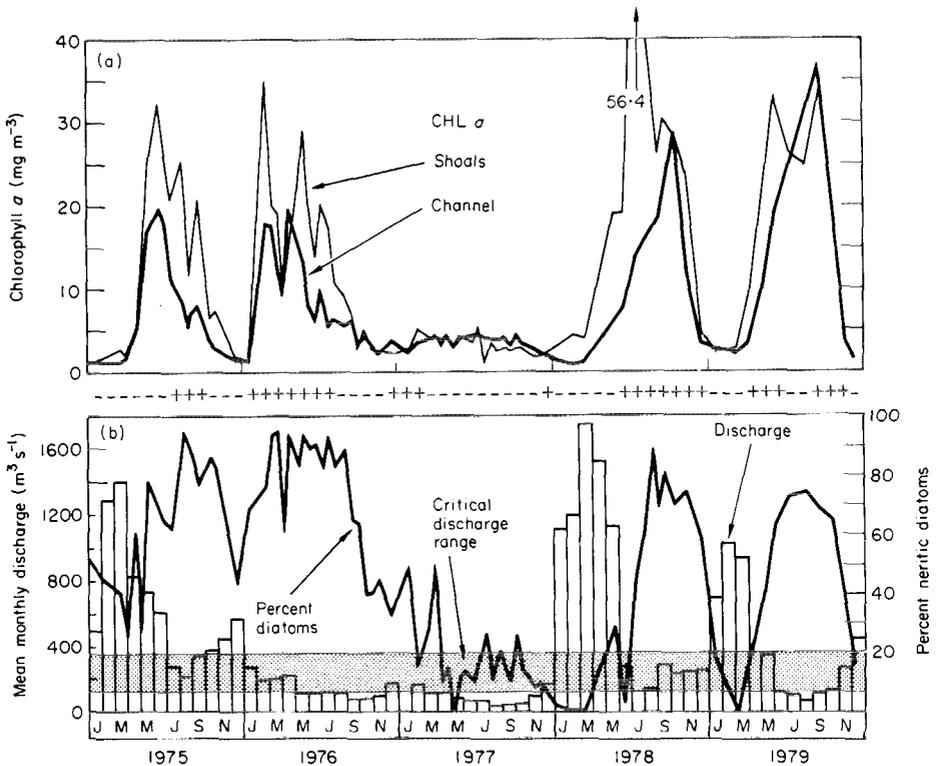


Figure 2. Seasonal changes in (a) chlorophyll a concentration, and (b) mean monthly river discharge (from U.S. Bureau of Reclamation, Sacramento) and percentage of neritic diatoms in Suisun Bay from 1975 to 1979. Chlorophyll a concentrations for 1975–77 are values in near-surface water at three sites (○, Figure 1) in the channel and one site (station 76) in the shoals (data from California Department of Water Resources, 1976, 1977, 1978). Chlorophyll a concentrations for 1978–79 are mean values at four sites (stations 3–6) in the channel and one site (station 76) in the shoals. Percentage of neritic diatoms is from samples taken at one channel station (6) and one shoal station (76). ▨, Critical range of river discharge when diatom biomass increases; symbols between frames represent times when mean monthly discharge fell within ({ }) or outside (-) this range.

(150–400 m³ s⁻¹) from about June through November. During these three years, phytoplankton biomass in Suisun Bay varied inversely with river discharge. Chlorophyll a typically increased when mean monthly discharge fell below about 400 m³ s⁻¹ in the spring, peaked in summer, declined in fall, and reached an annual minimum during peak winter discharge. From January 1976 through December 1977, mean monthly discharge never exceeded 350 m³ s⁻¹ and fell below 50 m³ s⁻¹ during August 1977. During this period, phytoplankton biomass did not vary inversely with discharge: chlorophyll a concentration peaked during February–May 1976, fell to a low level in late summer, and remained low throughout 1977 (Figure 2).

Seasonal changes in phytoplankton biomass from 1975–79 were accompanied by shifts in community composition. The small winter populations during normal hydrological years were dominated numerically by microflagellates (*Chroomonas minuta*, *C. amphioxeia*, *Cryptomonas* spp., *Chrysochromulina kappa*) and freshwater diatoms (*Melosira* spp., *Cyclotella* spp.), while the summer blooms were dominated by neritic diatoms (primarily *Thalassiosira eccentrica* and *Skeletonema costatum*, but also including *Chaetoceros* spp., *Coscinodiscus* spp. and *Cyclotella* spp.). To quantify this observation, we calculated the percentage of algal cells enumerated that were neritic diatoms. With few exceptions, the percentage of neritic diatoms exceeded 50% only during those times when mean monthly river discharge fell within the critical range 100–350 m³ s⁻¹ (Figure 2), and this index was always high (>70%) during the time of the seasonal maximum in chlorophyll a concentration. During normal winters the proportion of neritic diatoms fell below 50%. Seasonal changes in community composition were very different during the drought. The biomass peak of February–May 1976 was dominated by neritic diatoms, and thus appeared to be a typical summer bloom that occurred 3–4 months earlier than normal. Throughout 1977, neritic diatoms were scarce in Suisun Bay and the phytoplankton community was dominated by microflagellates, reminiscent of typical winter populations.

During peak discharge of winter, salinity intruded only up to Carquinez Strait, seaward of Suisun Bay [Figure 3(a)]. The concentration of suspended particulates was uniformly high (due to high sediment influx from the rivers) in the upper reaches of the estuary, and phytoplankton biomass was uniformly low and dominated by nanoplankton (algal cells that passed the 22 μ mesh = microflagellates or small freshwater diatoms); when a localized turbidity maximum was present, it occurred downstream from Suisun Bay near the limits of salinity intrusion. During normal summer river flows, salinity intruded upstream into Suisun Bay, and a well-defined maximum of suspended particulate matter and phytoplankton (chlorophyll a) formed near the upstream zone of salinity intrusion [Figure 3(b)]. Selective accumulation of netplankton (algal cells retained by the 22 μ mesh = neritic diatoms) was evident within the turbidity maximum. Only small maxima of suspended particulates and phytoplankton formed during periods of very low river discharge (drought), when the extent of salinity intrusion and location of the particulate maximum shifted upstream from Suisun Bay into the Sacramento River [Figure 3(c)]; the small chlorophyll peak in the Sacramento River was composed primarily of neritic diatoms.

During summers of normal river discharge, phytoplankton biomass was generally higher in the lateral shallows than in the channel of Suisun Bay, and a local chlorophyll maximum was present in the channel adjacent to the shallows [Figure 4(a)]. During the drought, phytoplankton biomass was greatly reduced throughout Suisun Bay, although chlorophyll concentration was still higher in the shoals than in the channel [Figure 4(b)].

During the summer diatom bloom of 1979, primary production was similar in the photic zone of a representative channel and shoal site (Figure 5). However, because the photic zone

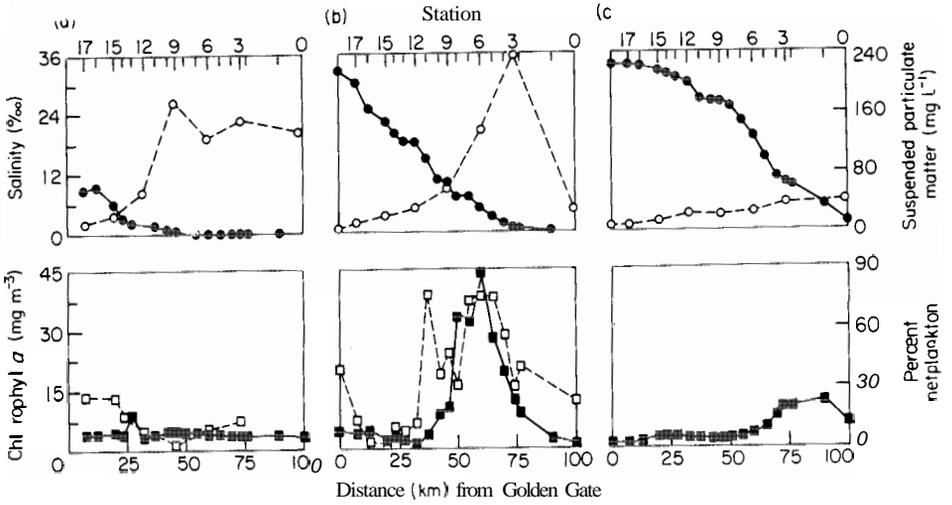


Figure 3. Spatial distributions of salinity and suspended particulate matter (SPM), and chlorophyll a and percent netplankton in near-surface water of northern San Francisco Bay, during periods of river discharge representative of (a) winter (15 March 1978; $Q_5 = 2430 \text{ m}^3 \text{ s}^{-1}$), (b) summer (20 September 1978; $Q_5 = 340 \text{ m}^3 \text{ s}^{-1}$), and (c) drought (27 September 1977; $Q_5 = 50 \text{ m}^3 \text{ s}^{-1}$) conditions. Q_5 is five-day mean river discharge ($\text{m}^3 \text{ s}^{-1}$) prior to the sampling date. \circ , SPM; \bullet , salinity; \square , percent netplankton; \blacksquare , chlorophyll.

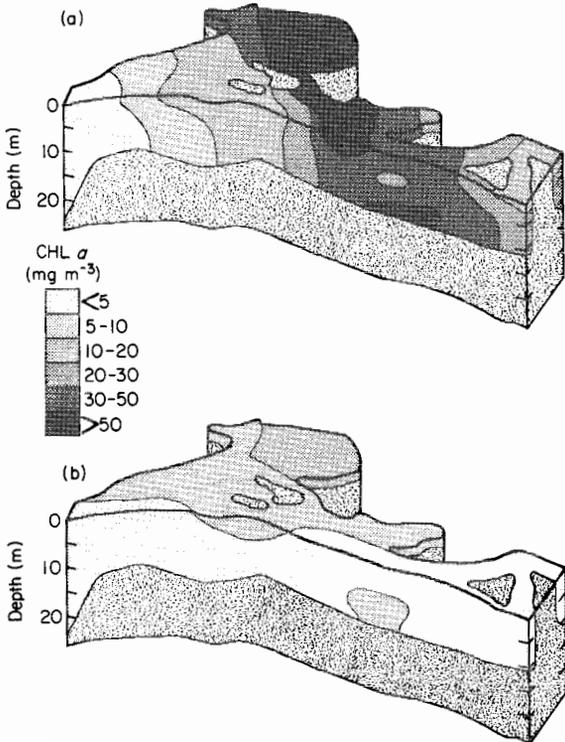


Figure 4. Oblique, mid-channel view of Suisun Bay showing chlorophyll a distribution during periods of river discharge representative of (a) summer (30 August 1978) and (b) drought (6 August 1976).

is a small fraction of mixed depth in the channel, calculated growth rates were small there relative to the shallows. Calculated doubling time of phytoplankton was 2.9 days in the 1.5 m shoals and 27 days in the 8 m channel (Figure 5).

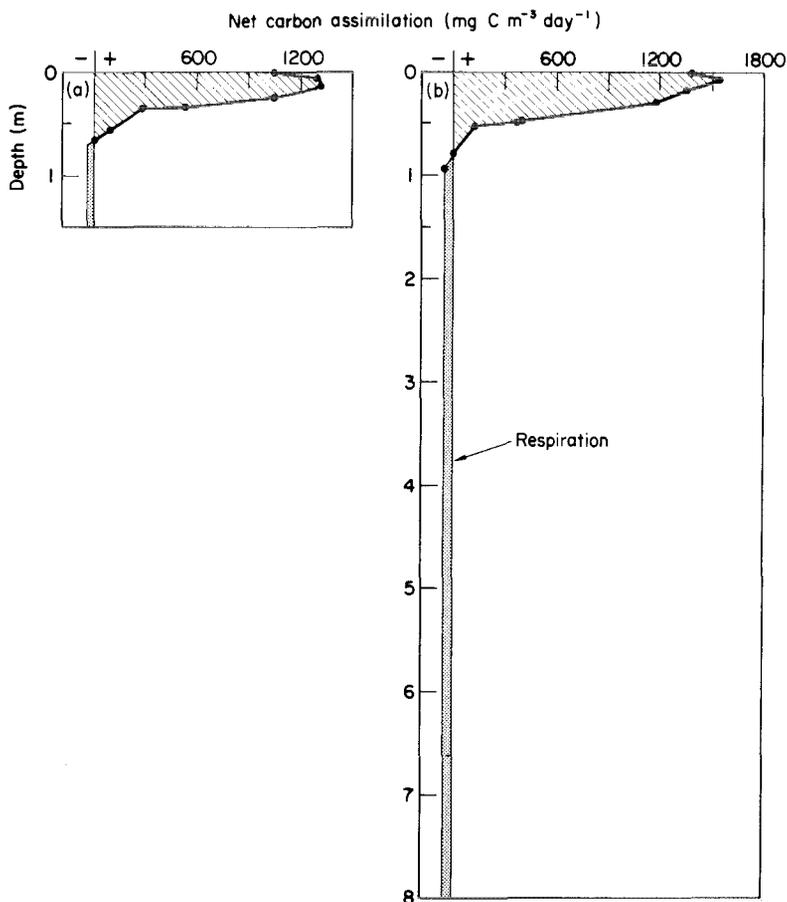


Figure 5. Vertical profiles of carbon assimilation at (a) a shoal station (76) and (b) a channel station (3) during a summer diatom bloom (14 August 1979).

	Shoal	Channel
Chlorophyll <i>a</i> (mg m ⁻³)	24.9	34.3
Phytoplankton C (mg m ⁻³)	996	1372
ϵ (m ⁻¹)	8.2	6.7
k_2 (div. day ⁻¹)	0.35	0.04
Doubling time (days)	2.9	27

Discussion

A conceptual model

Peterson *et al.* (1975a) used current meter records to calculate residual (non-tidal) currents in northern San Francisco Bay over a large range of river discharge (100 to 2300 m³ s⁻¹). Their analysis, supported by a two-dimensional numerical model of circulation (Festa &

Hansen, 1976), provides the framework for a conceptual model (Figure 6) to explain the relationship between river-induced circulation and phytoplankton population dynamics in Suisun Bay.

During periods of high river discharge ($>400 \text{ m}^3 \text{ s}^{-1}$) in winter, salinity is absent, non-tidal currents flow rapidly (up to 50 cm s^{-1}) seaward in the Suisun Bay channel, and the null zone is located seaward of Suisun Bay [Figure 6(a)]. Tidal currents (up to 200 cm s^{-1} ;

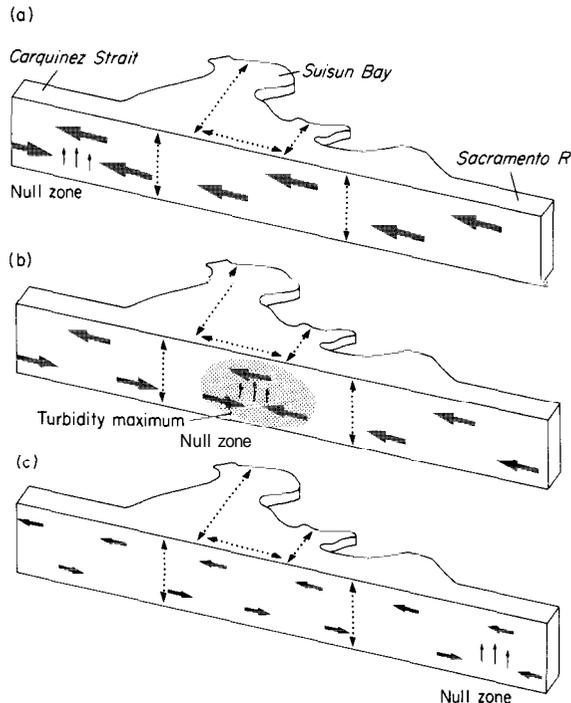


Figure 6. Idealized patterns of circulation in Suisun Bay under three regimes of river discharge: (a) winter ($Q > 400 \text{ m}^3 \text{ s}^{-1}$); (b) summer ($100 \text{ m}^3 \text{ s}^{-1} < Q < 350 \text{ m}^3 \text{ s}^{-1}$); (c) drought ($Q < 100 \text{ m}^3 \text{ s}^{-1}$). Tidal mixing is represented by dotted lines, and non-tidal currents by solid arrows.

Gartner & Cheng, 1981) mix water masses along the channel and between the channel and lateral shoals, and maintain turbulent vertical mixing. Under these conditions, suspended particles are rapidly advected seaward past Suisun Bay. Phytoplankton growth rate is slow relative to advective transport, and biomass remains low. Horizontal tidal mixing between the channel and shoals is sufficiently rapid that residence time over the shoals is also short relative to algal growth rate.

When discharge falls within the critical range of $100\text{--}350 \text{ m}^3 \text{ s}^{-1}$ [summer, Figure 6(b)], salinity intrudes in the bottom layer and the resulting density gradient drives a residual two-layer circulation. The landward-flowing bottom current converges with the river current in the Suisun Bay region. Within the area of convergence (null zone), opposing flows in the surface and bottom layers are balanced by net upward vertical advection having maximum velocity at the null zone [Figure 6(b)]. Under these conditions, suspended particles in the channel are not rapidly advected seaward. Rather, as dense particles (sediments or diatoms) are carried seaward in the surface layer they sink into the bottom current and are then

transported landward toward the null zone again. Turbulent vertical mixing and enhanced vertical advection in the null zone [Figure 6(b)] return diatoms from the bottom layer to the surface layer, thus completing a circular trajectory that traps diatoms in Suisun Bay. Low-density particles (such as microflagellates) are still advected seaward in the surface layer. The entrapment mechanism in the Suisun Bay channel assures that diatoms produced in the shoals and then tidally mixed into the channel will not be rapidly transported from Suisun Bay. Hence, algal biomass can increase.

As discharge falls below $100 \text{ m}^3 \text{ s}^{-1}$ (drought), velocity of the river current falls to $1\text{--}2 \text{ cm s}^{-1}$, salinity intrudes further, and the null zone is positioned upstream of Suisun Bay in the Sacramento River [Figure 6(c)]. Both residual horizontal and vertical water velocities weaken as river discharge decreases (Festa & Hansen, 1976). Under these conditions, the trapping mechanism disappears from Suisun Bay and with it the suspended particulate and chlorophyll maxima (Figure 3). Because residual currents in the bottom layer are directed away from Suisun Bay, tidal exchange between the channel and shoals depletes diatoms from the shoals as in winter.

The presence of an estuarine circulation cell in Suisun Bay is necessary for the formation of diatom population peaks, but the resulting entrapment mechanism is not sufficient in itself to produce high algal biomass in northern San Francisco Bay: high biomass is not associated with the null zone during the very high or very low discharge during winter or droughts (Figure 3).

Phytoplankton in the channel are severely limited by low light availability, and growth rates there are small (Figure 5). A numerical model shows that there is no summer population maximum of *Skeletonema costatum* when growth is restricted to the channel (Cloern & Cheng, 1981). However, phytoplankton do grow rapidly in the lateral shoals of Suisun Bay (Figure 5), and this same model does simulate the summer biomass peak when algal cells produced in the shoals are coupled (by lateral dispersion) with the trapping mechanism in the channel. Hence, we postulate that two mechanisms interact to produce phytoplankton biomass peaks in Suisun Bay: (i) a productive source of algal biomass (the shoals), and (ii) a physical mechanism that retains algal biomass within Suisun Bay. When the null zone is positioned away from the shoals of Suisun Bay, algal biomass declines in the upper estuary.

Our conceptual model is based, in part, upon the premise that neritic diatoms are selectively retained by estuarine circulation because their sinking rates are rapid and of the same magnitude as vertical water velocity in the null zone. Microscopic examination reveals that biomass peaks comprise *Thalassiosira eccentrica* and *Skeletonema costatum*, and that these diatoms exist singly or as aggregates having attached mineral grains [Plate 1; Ernissee & Abbott (1975) reported that *T. eccentrica* also occurs in two South Carolina estuaries with mineral matter attached to the girdle, and Duedall *et al.* (1978) observed diatom-mineral aggregates in the Hudson-Raritan estuary]. During the 1980 summer bloom, Ball & Arthur (1981) measured sinking rates of natural phytoplankton assemblages (dominated by *T. eccentrica* and *S. costatum*) in Suisun Bay by following the time-course of chlorophyll settling in 25 cm tubes. In the area around the turbidity maximum, calculated sinking rates ranged between $2\text{--}6 \text{ m day}^{-1}$ and averaged about 3 m day^{-1} , which is higher than most phytoplankton sinking rates measured in culture (e.g. Smayda & Boleyn, 1966) or *in situ* (e.g. Lannergren, 1979; Bienfang, 1980). However, sinking rates of this magnitude are close to calculated upward vertical water velocity (3.4 m day^{-1}) in the null zone of Suisun Bay during normal summer river discharge (O'Connor & Lung, 1981). Festa & Hansen (1978) have developed a two-dimensional, steady-state model of the turbidity maximum in a hypothetical estuary having dimensions similar to northern San Francisco Bay. Their

theoretical analyses also show that the magnitude of the turbidity maximum increases as particle sinking rate increases up to about 3 m day^{-1} . It appears, then, that neritic diatoms with attached mineral grains (or through the formation of aggregates) have enhanced settling rates that closely balance upward advective flow in the null zone during summer, and thus optimize the likelihood of retention by estuarine circulation. Density-selective retention of diatoms in an area adjacent to productive shoals thus explains: (i) wide variations in diatom abundance in response to river discharge (Figure 2); (ii) the accumulation of netplankton in Suisun Bay during typical summer flows (Figure 3); (iii) the anomalous increase of diatoms during February–May 1976 (when river discharge was typical of summer), and (iv) the reduced abundance of neritic diatoms throughout 1977 (when the turbidity maximum was poorly developed and located about 10 km upstream from the Suisun Bay shoals). Furthermore, our conceptual model indicates that because microflagellates sink slowly (Lannergren, 1979), their biomass should not be controlled by estuarine circulation. Cell density of microflagellates in Suisun Bay was, in fact, comparable during the summers of 1977, 1978 and 1979.

Alternative hypotheses

We have considered other possible explanations for the anomalously small phytoplankton populations in Suisun Bay during 1976–77. The role of nutrient availability in controlling phytoplankton dynamics in northern San Francisco Bay is not yet clear, but concentrations of dissolved inorganic silica, phosphorus and nitrogen generally exceed rate-limiting levels in the channel of Suisun Bay, even during summer blooms (Smith *et al.*, 1979). There is no evidence that nutrient limitation was responsible for the small phytoplankton biomass during 1976–77; dissolved inorganic nitrogen was significantly higher in the Suisun Bay channel during the summers of 1976 and 1977 compared to 1975 and 1978 (Table 1). Decreased river discharge during 1976–77 resulted in a reduced influx of suspended sediment to the estuary, so that transparency was enhanced (Table 1). Since mean daily insolation (at Vallejo, Figure 1) was not different during the drought compared to the previous and subsequent year (Table 1), light availability to planktonic algae was greater during the summers of 1976–77 compared to years of normal river discharge. Temperature was not significantly different between these two periods, and the increased salinity during the drought (Table 1) favoured the growth of neritic diatoms. We conclude, then, that salinity, temperature, and light and nutrient availability during the summers of 1976–77 were more conducive to growth of neritic diatoms compared to conditions that existed during normal summer blooms. Measurements of chlorophyll-specific carbon assimilation (Table 2) further demonstrated that phytoplankton were not physiologically stressed during the 1976–77 drought; mean rates of cell division during the drought may, in fact, have been greater than normal. Population densities of herbivorous zooplankton (mysids and copepods) were lower in Suisun Bay during 1976–77 than in previous and subsequent years (Arthur & Ball, 1979b), and the low biomass of phytoplankton during 1976–77 cannot be attributed to increased grazing pressure.

Unresolved questions

While empirical observations are consistent with our concept of the interaction between river discharge (circulation) and phytoplankton dynamics, important questions remain unresolved. First, was the low diatom biomass during the summers of 1976–77 a consequence of

TABLE 1. Mean values (and standard deviation) of temperature, salinity, dissolved inorganic nutrients, transparency (across a 10 cm path) and chlorophyll *a* in the near-surface water of Suisun Bay (stations 3–6) during the summers (July–September) of 1975 and 1978 compared to 1976 and 1977 (data from Smith *et al.*, 1979, 1980, 1982). Also shown is mean daily insolation (at Vallejo, Figure 1) for the months July–September (data from the Bay Area Air Pollution Control District)

Years	Temperature (°C)	Salinity (‰)	Si (μM)	P (μM)	NO ₃ ⁻ , NO ₂ ⁻ (μM)	NH ₄ ⁺ (μM)	Transparency (%)	Chlorophyll <i>a</i> (mg m ⁻³)	Insolation (Ly day ⁻¹)
1975 and 1978 (<i>n</i> = 8)	20.4 (0.4)	2.2 (0.4)	204 (8)	2.5 (0.1)	12.8 (1.1)	1.4 (0.4)	17 (2)	19.7 (3.7)	468
1976 and 1977 (<i>n</i> = 4)	21.3 (0.5)	9.6 ^a (2.2)	181 (29)	3.3 ^a (0.0)	24.3 ^a (0.6)	1.9 (0.4)	62 ^a (11)	8.5 ^a (3.9)	464

^aSignificant difference between years ($P = 0.01$).

TABLE 2. Maximum assimilation number (P_{\max}^B) of phytoplankton communities in Suisun Bay during summer, both during and subsequent to the 1976-77 drought. Measurements are based upon 24 h incubation either in *situ* (1976-77) or in a sunlit incubator (1979)

Date	P_{\max}^B (mg C mg ⁻¹ chlorophyll a h ⁻¹)	Station	Chlorophyll a (mg m ⁻³)
31 August 1976	1.9	5	8.4
2 September 1976	1.1	5	13.1
12 July 1977	2.2	2	7.7
14 August 1979	1.9	3	34.3
14 August 1979	2.2	76	24.9

primarily (i) displacement of the null zone away from the productive shoals, or (ii) weakened estuarine circulation? As freshwater inflow declined in 1976 and 1977, movement of the null zone upstream may have effectively uncoupled the shoals from the zone of particulate accumulation and therefore precluded population growth of diatoms. On the other hand, because the accumulation of particulates (both sediment and diatoms) depends upon a balance between particle settling rate and upward vertical velocity, absence of the diatom bloom during 1976-77 may have simply been a consequence of hydrodynamic conditions (i.e. reduced vertical water velocity) such that particle sinking rate exceeded the rate of vertical mixing. This response of diatom populations to river discharge is analogous to the behavior of suspended sediments in partially-mixed estuaries. Distinct turbidity maxima occur only during moderate river discharge (Postma, 1967; Meade, 1969; Nichols, 1974), when sediment is trapped within estuaries. During floods (as estuaries approach the salt-wedge type) or during very low discharge (as estuaries approach the vertically-mixed state), sediments escape. The relative importance of null zone position versus intensity of estuarine circulation to the development of diatom blooms is difficult to resolve, but may be elucidated with simulation models that accurately represent the flow field in the channel, tidal exchanges between the channel and shoals, and rates of algal sinking and cell division.

A second and related question concerns the fate of algal cells produced in the shoals of Suisun Bay during 1976-77. We speculate that diatoms produced there were transported tidally into the channel where they sank and were advected upstream or decomposed. During summer, consumptive use of freshwater from the San Joaquin River exceeds the rate of freshwater inflow, and flow reversals occur. Hence, diatoms produced in the shoals during the summers of 1976-77 may have been transported upstream into the San Joaquin River, which behaved as a sink.

Finally, it is important to recognize the potential implications of our results for higher trophic levels. Kost & Knight (1975) demonstrated that centric diatoms are an important component in the diet of the mysid shrimp *Neomysis mercedis*, which in turn is consumed by larvae of striped bass (*Morone saxatilis*) and other fish in the estuary (Orsi & Knutson, 1979). The near-complete collapse of the *Neomysis* population in Suisun Bay during 1977 (Figure 7) may, in part, have resulted from food limitation as the population of neritic diatoms declined during the drought. Furthermore, 1977 was the year of lowest recorded abundance of juvenile striped bass in northern San Francisco Bay (California Department of Fish and Game et al., 1978). River-induced circulation may therefore influence the entire pelagic food web of northern San Francisco Bay, and this hypothesis is a crucial topic for further research.

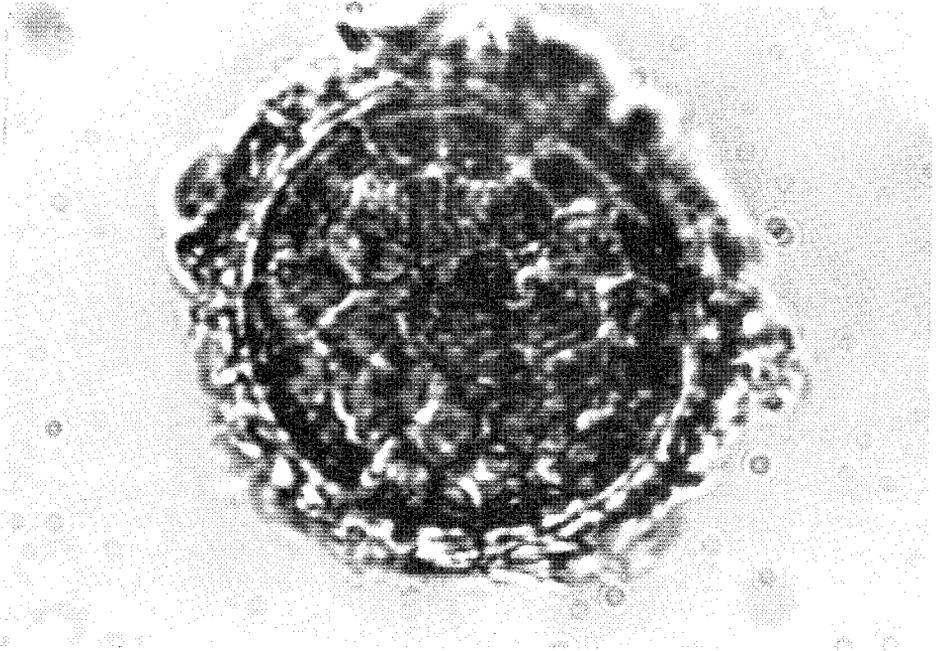


Plate 1. Photomicrograph of *Thalassiosira eccentrica* from Suisun Bay, showing attached inorganic particles. Cell diameter is about 30 μ .

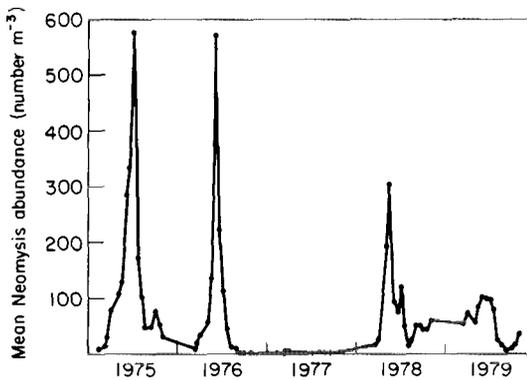


Figure 7. Mean abundance of *Neomysis mercedis* in the channel of Suisun Bay, 1975–79 (data provided by James J. Orsi, California Department of Fish and Game).

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