SAN FRANCISCO BAY: THE URBANIZED ESTUARY
The Pacific Division of the American Association for the Advancement of Science
℅ California Academy of Sciences. San Francisco, California 94118

PHYTOPLANKTON ECOLOGY OF THE SAN FRANCISCO BAY SYSTEM: THE STATUS OF OUR CURRENT UNDERSTANDING

JAMES E. CLOERN
U. S. Geological Survey, 345 Middlefield Road, Menlo Park, CA 94025

Although past studies of phytoplankton dynamics in the San Francisco Bay system are limited in number and scope, they have provided sufficient information to define gross spatial and temporal patterns. Annual changes in the density and composition of phytoplankton populations differ among major geographic areas within the system, and recent studies suggest that phytoplankton dynamics in each major portion of San Francisco Bay are governed by a unique set of environmental factors. The annual maximum abundance of phytoplankton in central San Francisco Bay during spring may be a direct consequence of diatom blooms that occur in coastal waters during the upwelling season. The spring maximum of phytoplankton abundance in South Bay may also result from the dispersion of neritic diatoms from offshore during some years, although the 1978 spring maximum resulted from rapid in *situ* growth of microflagellate populations. Apparently, stratification of the South Bay water column (initiated by movement of Delta-derived low-density water from the northern reach) creates a shallow surface layer where flagellates are given sufficient solar irradiation to maintain rapid growth rates. Phytoplankton populations in the northern reach of San Francisco Bay apparently are most strongly regulated by the physical accumulation of suspended particulates by gravitational circulation, the rapid growth of planktonic algae over shoals, and phytoplankton dynamics in coastal waters and/or tributaries.

Because few research efforts have been implemented to define environmental factors that regulate phytoplankton dynamics, basic unanswered (or unasked) questions remain. There is need (1) to define those functional groups of planktonic algae responsible for fixing inorganic carbon and energy, and then to follow pathways of energy and material transfer from the phytoplankton to other trophic levels, (2) to define the relationships between the physics of water movement and phytoplankton dynamics, and (3) to identify those physical-chemical-biological factors most responsible for regulating phytoplankton population size and composition, and then to quantify the response of algal population growth to changes in these important environmental factors.

The quality of estuarine waters is reflected in and a consequence of the phytoplankton community because the density (i.e. abundance) and composition of plankton populations both respond to environmental stress and can, in turn, cause environmental stress. The species composition and population density of phytoplankton are sensitive to environmental changes, and continual documentation of phytoplankton population dynamics can provide an invaluable record of water quality, can signal if radical changes occur within an estuarine system, and can offer clues to the causes of changes when they do occur. Planktonic algae affect concentrations of dissolved gases (oxygen and carbon dioxide), concentrations of dissolved inorganic and organic substances, and affect pH. Finally, the photosynthetic fixation of inorganic carbon by phytoplankton offers a source of organic carbon and energy for higher trophic levels and ultimately determines the success of fisheries, including those having commercial and recreational value. The understanding of phytoplankton dynamics (i.e. changes in population abundance, composition and distribution, and rates of physiological processes) is, therefore, central to the understanding of how estuarine ecosystems work and how they respond to stresses imposed by man and nature.

Despite the size and economic importance of San Francisco Bay, the biological components of its water column have been meagerly studied. Virtually no baywide phytoplankton studies were done until the University of California's Sanitary Engineering Research Laboratory (SERL) undertook a five-year study in the early 1960's (Storrs et al. 1966). The U. S. Geological Survey initiated a study of water properties of the Bay system in 1969 (Conomos et al. 1978); these surveys included measurements of relative phytoplankton abundance and distribution. In 1970 four agencies (U. S. Bureau of Reclamation [USBR], U. S. Fish and Wildlife Service, and California Departments of Water Resources and Fish and Game) pooled their resources into a cooperative ecological study of the Sacramento-San Joaquin Delta and parts of northern San Francisco Bay. These three major efforts all included descriptive studies of phytoplankton abundance or composition, but with few exceptions (e.g. Peterson et al. 1975a; and Delta studies of Arthur and Ball 1979 and Ball and Arthur 1979) there has been no research effort to define and quantify those environmental factors that regulate phytoplankton dynamics throughout San Francisco Bay. Until this is done, our capability to forecast impacts of proposed perturbations (such as construction of the Peripheral Canal and San Luis Drain and the deepening of the Baldwin Ship Channel; see, e.g. Seckler 1971), and our understanding of factors that determine the success of important fisheries, such as the striped bass (Morone saxatilis) and dungeness crab (Cancer *magister*), will continue to be restricted.

Although our knowledge of dynamic processes affecting the plankton is limited, past studies have provided sufficient information to define gross spatial and temporal patterns of changing phytoplankton abundance that occur over an annual cycle. In this chapter I integrate the results of previous studies into a generalized description of these patterns, then present the results of a recent (1977-78) study that was designed to offer preliminary hypotheses concerning mechanisms that cause these observed patterns. Finally, I point out critical new directions for future research and significant questions that must be addressed before our understanding of the water column of San Francisco Bay will allow for intelligent management decisions in the future.

TEMPORAL AND SPATIAL PATTERNS

Storrs et al. (1966), who first described the seasonal changes of phytoplankton abundance in different portions of the San Francisco Bay system, observed that Suisun Bay (Fig. 1) typically has a maximum phytoplankton standing stock during summer (Fig. 2), whereas all other portions of the Bay system have annual maxima during spring, and that the population maximum in Suisun Bay is at least 10 times greater than the maxima seen elsewhere. Although year-to-year variations exist, subsequent studies (Peterson 1979; Peterson et al. 1975a; Arthur and Ball 1979; Ball and Arthur 1979; Conomos et al. 1979) have confirmed this general pattern. The similarity in both the magnitude and timing of population maxima in San Pablo Bay, Central Bay, and South Bay (Fig. 2) superficially suggests that phytoplankton dynamics in all three embayments are regulated by the same set of environmental factors. However, our recent studies demonstrate that this is not the case. It is appropriate, therefore, that each geographic section of the Bay system be discussed separately.

Central Bay

In the earliest quantitative study of phytoplankton populations in San Francisco Bay, Whedon

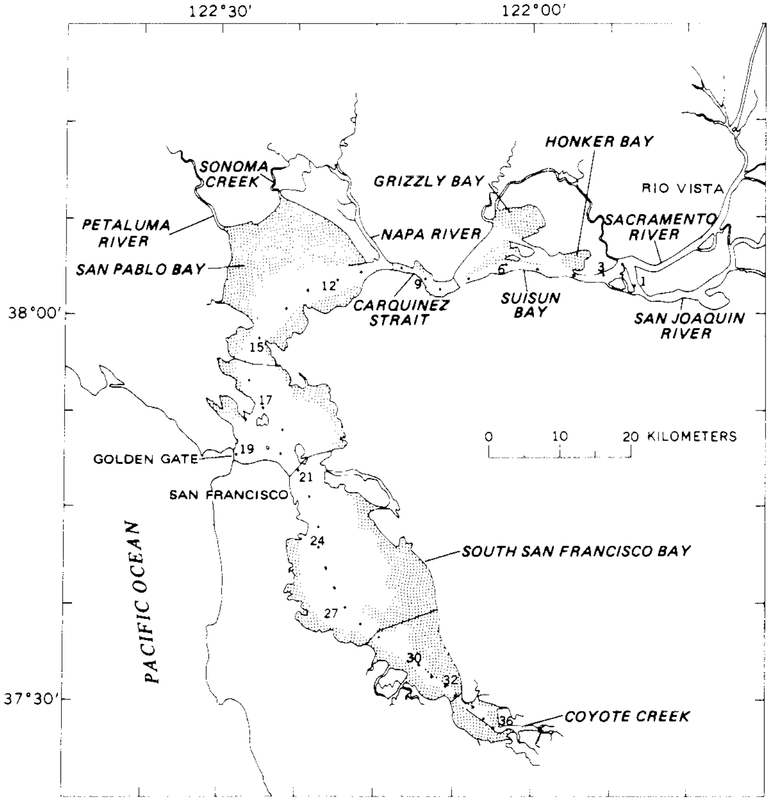

Fig. 1. San Francisco Bay system showing location of major bays, shallows (shaded area with a mean tide depth ⩽ 2 m), central channel (dashed line represents 10-m isobath) and location of sampling stations.

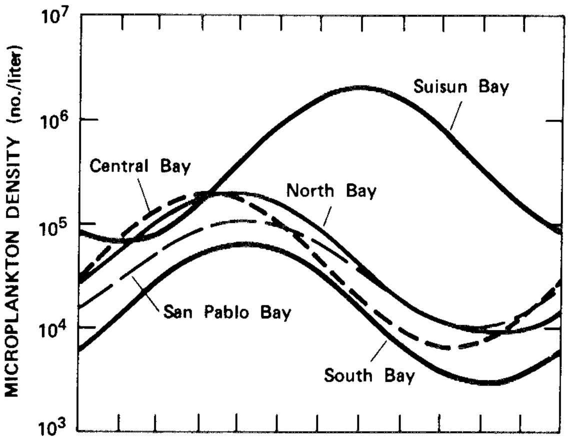

Fig. 2. Seasonal variation of total microplankton density in different parts of the Bay system (redrawn from Storrs et al. 1966).

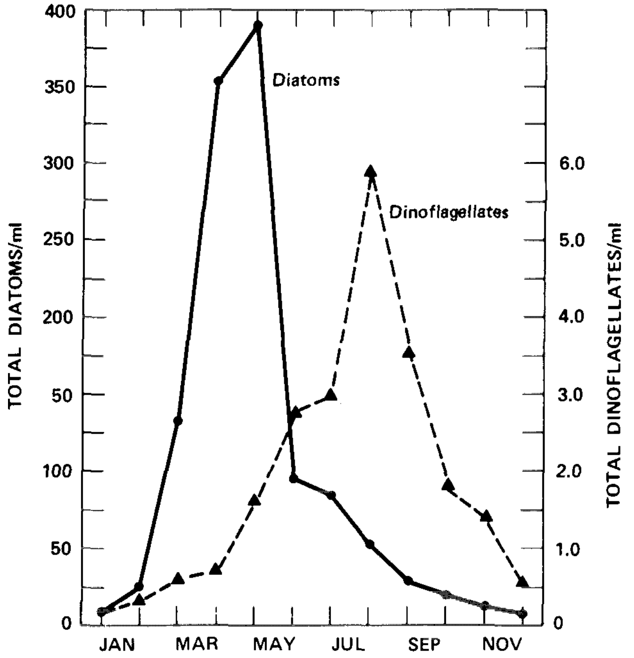

Fig. 3. Monthly mean densities of diatoms and dinoflagellates in surface waters taken from a San Francisco pier, 1933-1935 (data from Whedon 1939).

(1939) found that the Central Bay (bordered by stations 17, 19 and 21 - Fig. 1) has its maximum standing stocks between March and June (Fig. 3), consistent with the observations of Storrs et al. (1966) 30 years later. Results of both studies showed that the spring maximum is a consequence of increased numbers of neritic (i.e. coastal marine) diatoms. From March to as late as September, northerly winds along the California coast generate periods of upwelling that produce episodic blooms of netplankton (single cells or chains larger than about 20 μ) offshore (Bolin and Abbott 1963; Malone 1971). Since these blooms typically are dominated by the same species (Chaetoceros spp., *Nitzschia* spp., Rhizosolenia spp. and *Skeletonema costatum*) as reported by Whedon (1939) and Storrs et al. (1966), it is likely that the spring maximum in Central Bay results from the dispersion of planktonic diatoms into San Francisco Bay from these offshore blooms during the upwelling season.

We did not see a dramatic spring increase in phytoplankton abundance (measured as chlorophyll a concentration) at the Golden Gate during 1978 (Fig. 4), although the modest increases we did measure in the spring resulted from increased numbers of neritic diatoms. Causes of the increased chlorophyll a concentration at the Golden Gate during early December 1977 (Fig. 4) are not known, but microscopic enumeration revealed that this pulse was dominated by the neritic diatom Nitzschia seriata (R. Wong pers. comm.). Conceivably, anomalous meteorological conditions created a winter upwelling event that allowed for rapid population growth of this species offshore, but this hypothesis cannot be tested, and the proposed relationship between coastal upwelling and phytoplankton dynamics in San Francisco Bay will remain speculation until simultaneous studies are done both inside and outside the Golden Gate.

South Bay

Storrs et al. (1963) observed that phytoplankton populations (measured as cell density) are relatively small in South Bay (Fig. 2), and that South Bay, like Central Bay, has its annual maximum during spring (Fig. 5). They also reported a population composition that was dominated by neritic diatoms; this again suggests that the spring maximum results from the importation of marine diatoms from offshore. But our study gave very different results in 1977-78: although phytoplankton density (measured both as chlorophyll a concentration and cell density) was again highest in March (Fig. 4), the partitioning of chlorophyll a into three size classes demonstrated that over 90% of this phytoplankton maximum comprised ultraplankton (very small cells capable of passing through the 5-µ pores of a membrane filter). Microscopic examination of preserved samples confirmed that the South Bay water mass had a large number of microflagellates (primarily cryptophytes, haptophytes and naked dinoflagellates) and relatively few large diatoms (R. Wong pers. comm.). Since offshore blooms are dominated by the large netplankton (Malone 1971; Garrison 1976), the South Bay maximum of March 1978 clearly did not originate from coastal netplankton blooms.

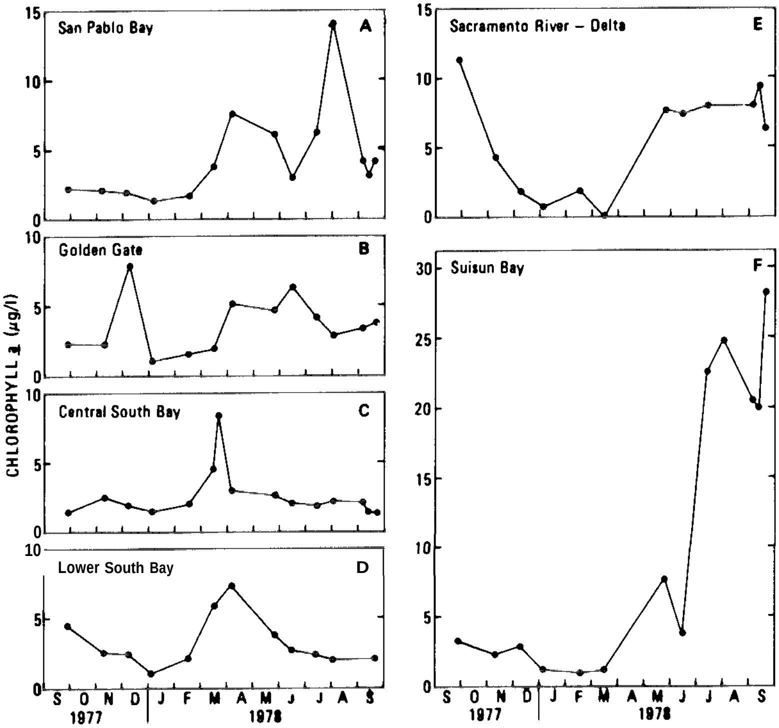

Fig. 4. Mean concentration of chlorophyll a in near-surface waters of the major geographic areas comprising the San Francisco Bay system, between Sept. 1977-Sept. 1978. (San Pablo Bay encompasses the area between stations 9-15; Golden Gate is station 19; Central South Bay lies between stations 24-30; Lower South Bay includes stations 32-36; Suisun Bay lies between stations 4-8.)

Vertical profiles of salinity and chlorophyll a in mid-South Bay (Fig. 6) suggest the cause of rapid phytoplankton population growth during March 1978. On 14 March, vertical distributions of both salinity and chlorophyll a were fairly homogeneous at stations 27 and 30, suggesting that the water column was well mixed; data from station 24 showed pronounced salinity stratification. On 20 March, the entire South Bay showed some degree of salinity stratification, and concentrations of chlorophyll a had increased dramatically in the surface layer (Fig. 6). Apparently, the spring maximum of 1978 occurred under conditions of a salinity stratification which created a shallow surface

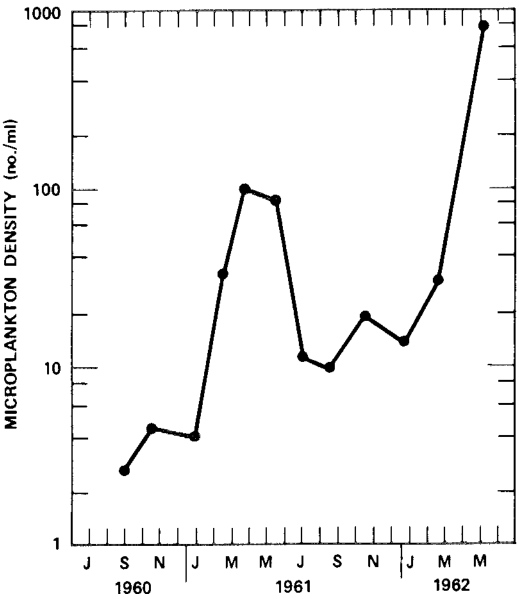

Fig. 5. Average microplankton density in surface waters of South Bay, September 1960 to May 1962 (data from Storrs et al. 1963).

layer where phytoplankton were given sufficient sunlight for rapid growth. When the water column is vertically mixed, planktonic algae spend a majority of time in the lower aphotic (dark) zone of the water column and do not receive sufficient solar irradiation to maintain rapid growth rates.

McCulloch et al. (1970), Imberger et al. (1977) and Conomos (1979) found that pronounced

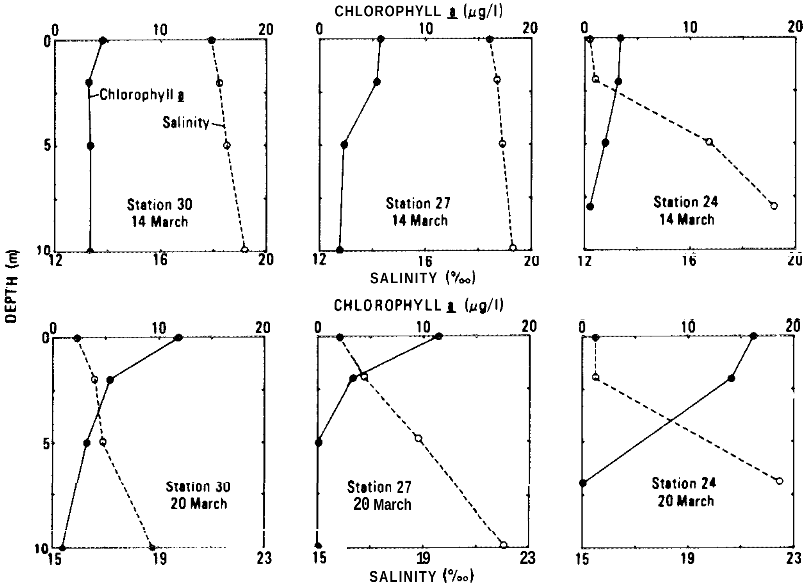

Fig. 6. Vertical distributions of chlorophyll a (solid line) and salinity (dashed line) at three South Bay stations on 14 March 1978 (top frames) and 20 March 1978 (bottom frames).

salinity stratification of South Bay results from the penetration of low-salinity water from the northern reach during periods of rapid freshwater discharge through the Sacramento-San Joaquin Delta. This mechanism explains the salinity stratification of South Bay during March 1978, since Delta outflow increased dramatically between 3-9 March (Fig. 7). Stratification was observed throughout South Bay 16 days after the start of this flood; this is consistent with Imberger et al. (1977) and Conomos (1979) who inferred a time delay of about 1-2 weeks before the South Bay responds to a large flood through the Delta.

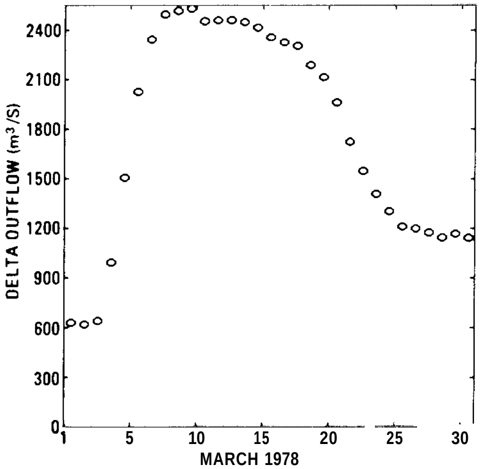

Fig. 7. Net Delta Outflow of the Sacramento-San Joaquin Delta during March 1978 (from USBR, Sacramento, Calif.).

Results of Storrs et al. (1963) study are consistent with the hypothesis that phytoplankton dynamics in coastal waters dominate seasonal patterns in South Bay, and that diatoms predominate. Our results in 1978 demonstrate that spring increases are caused by stratification of the water column during periods of rapid Delta outflow, and that microflagellates dominate the spring increase in phytoplankton biomass. The incongruity between these two studies may reflect the fact that: (1) the methods of Storrs et al. (1963) may have given a severe underestimate of the biomass of microflagellates in South Bay during the 1960's; (2) meteorological conditions in 1978 were not conducive to strong or frequent coastal upwelling events, hence minimizing the importance of neritic netplankton in South Bay during the spring of 1978; or (3) real changes have occurred in the composition of South Bay phytoplankton assemblages since the 1960's. Answers to these basic questions will only come from long term studies that include efforts to determine the relationship between plankton dynamics both in coastal waters and in San Francisco Bay, and studies that provide information about species composition as well as biomass of phytoplankton populations.

Results of previous studies have demonstrated that vertical and longitudinal (north-south) variations in phytoplankton abundance are generally small, implying that South Bay is a fairly homogenous embayment. But examination of the composition of phytoplankton populations in South Bay reveals a different picture. The longitudinal distribution of chlorophyll a on 24 May 1978, for example, was fairly uniform in surface waters of South Bay (Fig. 8a). The relative contribution of ultraplankton (i.e. microflagellates), however, increased rapidly from the Golden Gate to station 24, then declined in mid-South Bay (station 27), increased rapidly again near station 30, and declined again at the southern extremity (Fig. 8b). Reasons for this heterogenity of phytoplankton composition are not yet known but must be related to the complex bathymetry of South

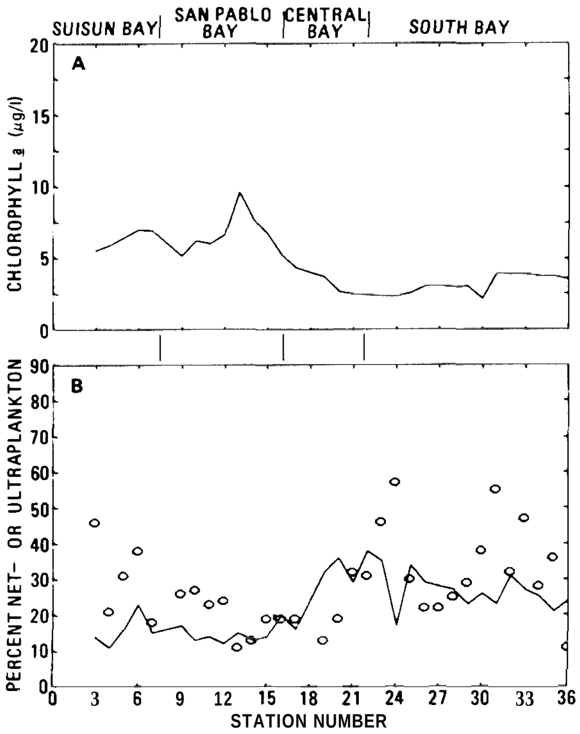

Fig. 8. Longitudinal profiles of near-surface chlorophyll a (A) and size distribution of phytoplankton (B) in the San Francisco Bay system, 24-25 May 1978. Percent netplankton (solid line) is the fraction of chlorophyll a retained by Nitex screens having 22-p mesh, and percent ultraplankton (0) is the fraction passing a Nuclepore filter having 5-p pores.

Bay, influences from local discharges and surface runoff, and the formation of surface lenses of low-density water as Delta-derived water penetrates South Bay on each tidal cycle (Imberger et al. 1977; Conomos 1979). Our initial perception of South Bay as a longitudinally homogeneous embayment changes upon examination of plankton size composition and species composition. Extension of sampling over the lateral shallow areas of South Bay should also offer new insights into spatial patterns observed in the channel.

San Pablo Bay

The northern reach of the San Francisco Bay system (defined here as the area between stations 17 and 1 - Fig. 1) is a partially to well-mixed estuary comprising a central deep channel and two isolated shallow embayments, San Pablo Bay and Grizzly-Honker bays, that contain phytoplankton communities with very different dynamics. Seasonal patterns in the density and composition of phytoplankton populations in San Pablo Bay can vary dramatically from year to year, but Storrs et al. (1966), USBR et al. (1977) and Conomos et al. (1979) all observed annual phytoplankton maxima during spring. Several mechanisms may contribute to the growth of phytoplankton populations in San Pablo Bay during spring, the simplest being the movement of coastal plankton blooms into San Pablo Bay during spring. This hypothesis is consistent with the observation that increased concentrations of chlorophyll *a* between March and May 1978 (Fig. 4) were accompanied by large increases in the population density of *Skeletonema costatum,* a neritic diatom that is dominant in netplankton blooms along the California coast (Bolin and Abbott 1963; Malone 1971). However, the simple dispersion of coastal plankton into San Pablo Bay is not sufficient to explain observed spatial patterns. We consistently measured higher phytoplankton densities in San Pablo Bay than in Central Bay during spring of 1978 (see, for example, Fig. 8a). Therefore, if the spring maximum originates outside the Golden Gate, some additional mechanism causes an accumulation or growth of these coastal-derived populations within San Pablo Bay.

Conomos et al. (1971) demonstrated that surface waters of the northern reach have net (tidally-averaged) advective movement toward the Pacific Ocean, while bottom waters have a net landward movement (see also Conomos 1979). This two-layer flow, caused by longitudinal and vertical salinity gradients characteristic of partially and well-mixed estuaries (e.g. Bowden 1967; Dyer 1973), has a profound influence on the distribution of phytoplankton and other suspended particulates in San Francisco Bay (Conomos and Peterson 1974, 1977; Peterson et al. 1975a; Arthur and Ball 1979). The location along the longitudinal axis of the estuary where net bottom currents are nullified by seaward-flowing river water, the "null zone" is generally characterized by high accumulations of suspended particulates (see, for example, Meade 1972), including planktonic algae, because net advective displacement is relatively slow. Peterson et al. (1975b) demonstrated that the location of this null zone varies seasonally in response to seasonal variations in Delta outflow, and that it is often located near San Pablo Bay during spring, when Delta outflow is high. As marine diatoms enter San Pablo Bay in the bottom density current, they encounter the opposing current from the Sacramento-San Joaquin rivers (Fig. 9), and are either entrained or advected into the surface layer. There, they are either quickly retransported seaward or they disperse laterally into the shallows of San Pablo Bay.

Since waters of the northern reach are generally very turbid, growth rates of planktonic algae are small in the deep (⩾ 10 m) channel where average irradiance is low. However, the shallow

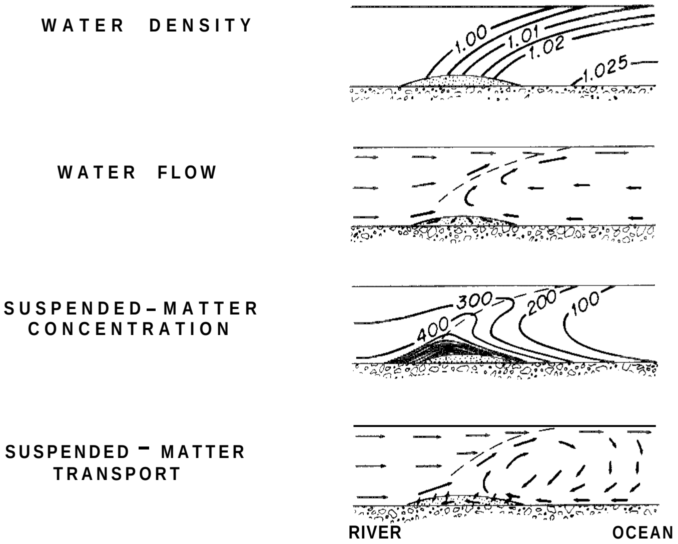

Fig. 9. Schematic representation of the null zone of partially mixed estuaries, showing spatial variations in water density and circulation, concentration of suspended particulates, and the transport of suspended particulates (including dense algal cells). Reproduced with permission from Meade (1972).

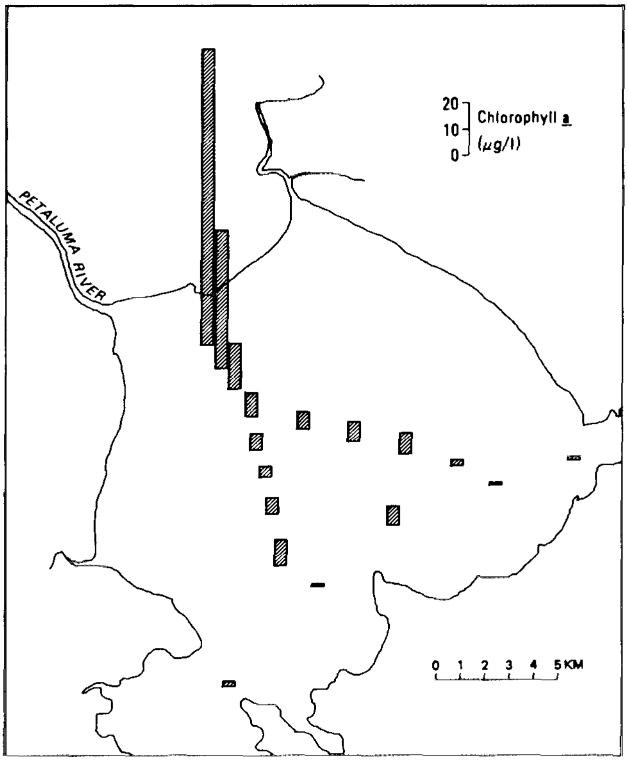

Fig. 10. Distribution of chlorophyll a in surface waters of San Pablo Bay, 15 March 1978.

($\leqslant$ *2* m) depth over San Pablo Bay tidal flats (Fig. 1) provides for increased exposure of the suspended algae to light and thus for rapid growth rates (Cloern 1978). Rapid growth of seed populations that enter San Pablo Bay shallows can maintain large population densities, particularly in northern San Pablo Bay where the exchange rate between the shallows and channel is presumably slow and water residence time is highest. During March 1978, the spatial distribution of phytoplankton biomass (chlorophyll a) in San Pablo Bay (Fig. 10) was consistent with the hypothesis that the shallows are sites of rapid population growth. The extremely high chlorophyll *a* concentrations in northern San Pablo Bay represented a large phytoplankton population that was almost exclusively *Skeletonema costatum.*

The proposed mechanism that causes increased phytoplankton abundance in San Pablo Bay requires: (1) an allochthonous source (in this case, coastal waters) of viable planktonic algae that (2) rapidly disperse over the tidal flats because of location of the null zone, and (3) divide rapidly because of shallow depth (*i.e.*, increased availability of light). The decline of phytoplankton populations during summer (or sometimes as late as fall - Fig. 4) probably results from decreased inputs of marine diatoms in the bottom density current as upwelling frequency declines offshore, and movement of the null zone landward in response to decreased Delta outflow.

Suisun Bay

The most dramatic feature of phytoplankton dynamics in San Francisco Bay is the large standing stock typically seen in the vicinity of Suisun Bay during summer (Figs. 2, 4; see also Ball and Arthur 1979). The rapid population growth seen during most summers is coupled to the timing of decreased freshwater discharge through the Sacramento-San Joaquin Delta (Fig. 11). The null zone is found near Suisun Bay during the summer low flow period (Peterson et al. 1975b; Arthur and Ball 1979) where, as in San Pablo Bay during spring, the presence of an estuarine circulation cell adjacent to a shallow region allows for population growth.

The summer growth of phytoplankton populations in Suisun Bay is accompanied by a dramatic shift in species composition that is reflected in the partitioning of chlorophyll *a* into different size fractions. For example, between September 1977 and July 1978, phytoplankton populations in Suisun Bay had a diverse composition and were not dominated by forms within one size class (e.g. Fig. 8b). However, as the summer maximum developed in 1978, netplankton constituted a growing proportion of total phytoplankton biomass. Between July and September 1978, over 80% of the particles comprising the chlorophyll *a* maximum of Suisun Bay (Fig. 12a) were larger than 22 μ (Fig. 12b). Both upstream and downstream of this chlorophyll maximum, the relative importance of netplankton diminished in more diverse phytoplankton assemblages. Microscopic examination revealed that these large netplankton populations were dominated by several species of neritic diatoms (mainly *Thalassiosira [Coscinodiscus] excentricus*, *Skeletonema costatum* and *Chaetoceros* spp.), and that frustules of these diatoms were coated with a dense layer of clay-size lithogenous material. Adsorption of inorganic particulates onto the silica surface of diatoms is probably governed by the same physicochemical factors that cause aggregation of suspended particulates in estuaries (e.g. Meade 1972; Edzwald et al. 1974; Krone 1978; Zabawa 1978), and clearly is a dominant force in the creation of the phytoplankton maximum in Suisun Bay (Arthur and Ball 1979). Just as dense inorganic particulates accumulate in an estuarine circulation cell (Meade 1972), rapidly-settling diatoms sink into the landward-flowing bottom density current before they can be transported away from Suisun Bay in the surface layer (Fig. 9).

A numerical model of phytoplankton population dynamics in the northern reach (J. Cloern

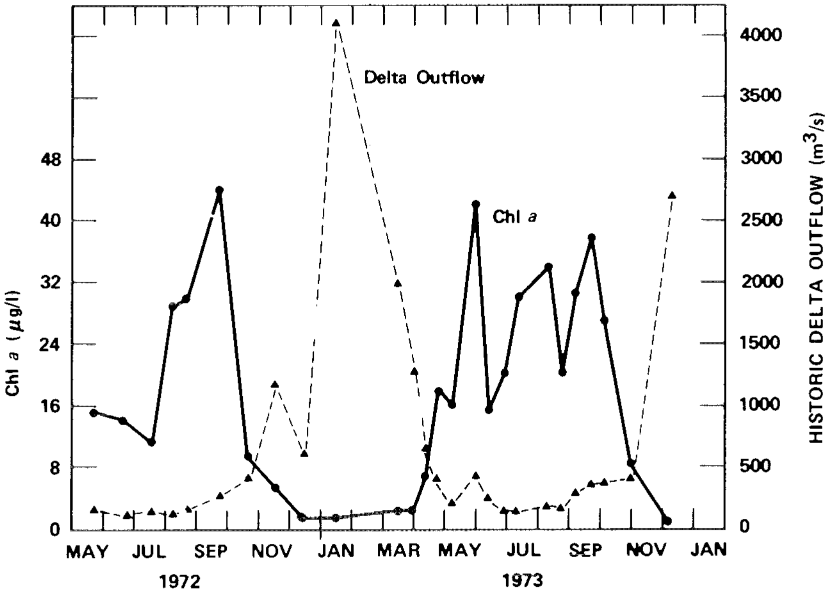

Fig. 11. Historic Delta outflow (from USBR, Sacramento, Calif.) and chlorophyll a concentration in surface waters of Suisun Bay, May 1972 to December 1973 (USBR et al. 1977).

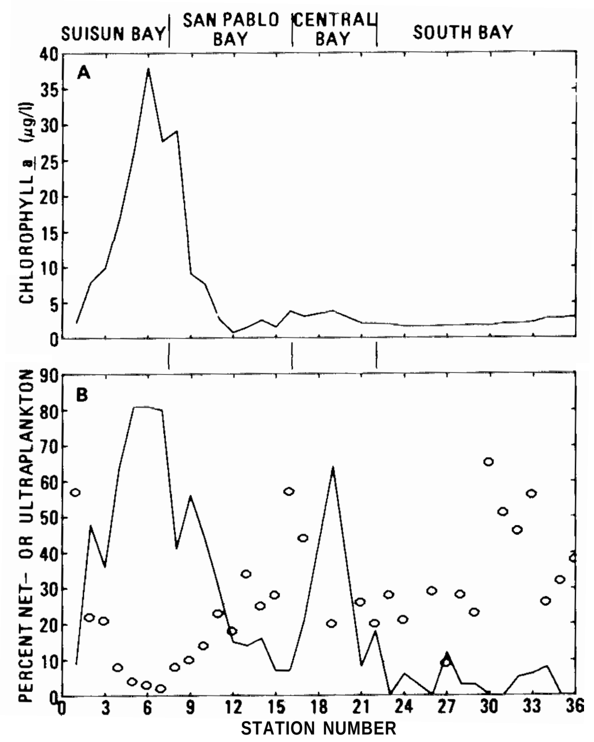

Fig. 12. Longitudinal profiles of surface chlorophyll a **(A)** and size distribution of phytoplankton (B) in the San Francisco Bay system, 19-20 September 1978. See Fig. 8 for details.

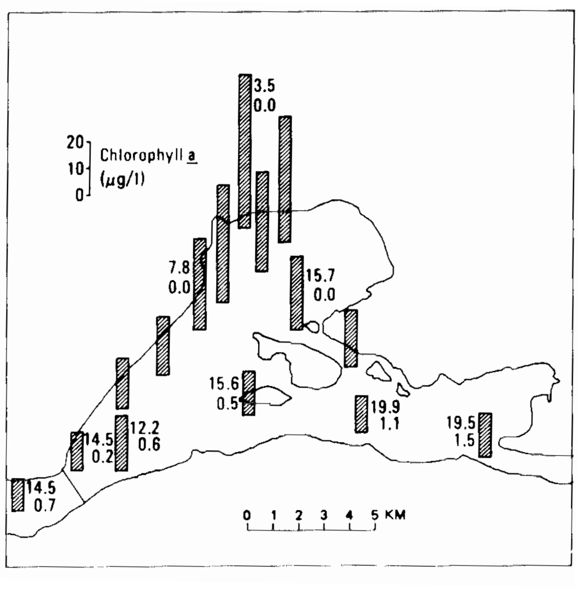

Fig. 13. Distribution of chlorophyll a in surface waters of Grizzly Bay, 13 July 1978. For some stations, concentration (µg-atoms·liter^{-1}) of dissolved nitrate + nitrite (top number) and ammonium (bottom number) are also given.

and R. Cheng unpublished data) suggests that the physical accumulation of diatoms by gravitational circulation is not sufficient in itself to create the very large phytoplankton densities observed in the channel of Suisun Bay. Rather, it is the presence of an estuarine circulation cell in the vicinity of shallow areas where algal growth is rapid that accounts for the high chlorophyll a concentration seen in Suisun Bay. This hypothesis is supported by the observations that phytoplankton densities are consistently higher in the shallow Grizzly Bay than in the Suisun Bay channel (e.g. Fig. 13), and that during summers of unusually high or low Delta outflow (when the null zone is moved downstream or upstream from the Grizzly-Honker Bay shallows), phytoplankton standing stocks are relatively low (Arthur and Ball 1979; Ball and Arthur 1979).

Although phytoplankton standing stocks are typically large in Suisun Bay, net rates of autotrophic carbon assimilation are apparently lower in the Suisun Bay channel than in other parts of the Bay system. During March and August 1976, mean chlorophyll a concentrations were four to five times higher in the Suisun Bay channel than in Central Bay, but areal productivity (i.e. rate of photosynthetic carbon fixation averaged over the day and depth of the water column) was up to 10 times higher in Central Bay than in the channel of Suisun Bay (Table 1). The low net productivity in Suisun Bay seems attributable to the fact that its extreme turbidity restricts the photic zone to a shallow depth, especially since primary productivity is inversely related to extinction coefficient (Table 1). These results suggest, again, that large phytoplankton densities in the channel of Suisun Bay are not a consequence of rapid population growth there.

TABLE 1. MEAN PRIMARY PRODUCTIVITY P ($gC \cdot m^{-2} \cdot d^{-1}$), CHLOROPHYLL *A* CONCENTRATION ($\mu g \cdot liter^{-1}$) AND EXTINCTION COEFFICIENT ϵ (m^{-1}) MEASURED AT THREE LOCATIONS IN SAN FRANCISCO BAY (DATA FROM COLE AND HERNDON 1979)

Location	March 1976				August 1976			
	P	Chla	ϵ	n*	P	Chla	e	n*
Central Bay	0.52	4.6	1.0	4	0.93	2.7	0.7	2
Suisun Bay	.05	22.5	9.0	3	.26	10.8	3.4	2
South Bay					.38	2.4	1.3	2

* number of observations

PERSPECTIVES FOR FUTURE RESEARCH

The capability of San Francisco Bay waters to support or promote the growth of planktonic populations is continually altered by effluents from power generating plants, sewage treatment facilities, chemical, petroleum and other industries, surface runoff from agricultural and urban areas, and oil spills. Further, physical characteristics of San Francisco Bay that affect plankton dynamics (temperature, salinity, concentration of suspended particulates, bathymetry and circulation patterns) change in response to man's activities. Clearly, a detailed understanding of man's impact on plankton dynamics (and, hence, dynamics of other phenomena in the water column) will not be attained until the relationships between important physicochemical factors and phytoplankton growth are better defined. The capability to forecast even gross changes in the density and composition of phytoplankton populations will only be attained if basic studies are implemented that have as major objectives the description and interpretation of natural changes in the phytoplankton community. Our ability to predict the impacts of major perturbations, and our understanding of the variable success of fisheries, will certainly be restricted until such studies are initiated.

Future research programs should give a high priority to basic ecological investigations that attempt to define geographic areas of significant algal carbon assimilation and determine which algal species (or functional groups) are the important primary producers in San Francisco Bay. Most work in the Bay system has been confined to study of surface waters of the main channel. But the limited field work done outside the channel, and results of modeling studies (Cloern 1978), have demonstrated that shallow waters of San Pablo, Grizzly and Honker bays may be the sites of significant autotrophic productivity and population growth by planktonic algae; the same may be true for the shallow areas of South Bay. An intensive effort is needed to measure rates of carbon assimilation both in the waters of the channel and in the shallows, over an annual cycle, to determine the importance of productivity over shoals to the total autotrophic assimilation of carbon within the Bay system. Related studies are needed to define the relative contribution of different communities of planktonic algae to total productivity. Results of previous studies have shown considerable spatial and temporal variation in the relative biomass of nanoplankton and netplankton. But no attempt has yet been made to measure the contribution of different size fractions to total community productivity, and no attempt has been made to determine the relative significance of fresh-water, brackish, and coastal plankton, all of which exist within the Bay system. The expansive tidal flats around the perimeter of San Francisco Bay apparently support a considerable biomass of epibenthic diatoms (F. Nichols pers. comm.). Autotrophic production by this assemblage may be an important source of reduced carbon for benthic invertebrates and ultimately vertebrate predators, but the relative importance of this contribution is yet unknown.

A second major thrust required from the research community is an effort to trace the fate of organic carbon produced in the estuary and to quantify the relative importance of phytoplankton productivity for other trophic levels, especially those having economic value or ecological significance. Central to this effort is the need to integrate results of studies that measure rates of specific processes into a budget of organic carbon transfers in San Francisco Bay. Particularly important processes that require measurement include: (1) the rate of *in situ* autotrophic production by phytoplankton and benthic algae; (2) rates of exportation to the sea and importation of allochthonous plankton and detritus from both coastal waters and tributaries; (3) rates of accrual to the sediments; (4) the rate of bacterial decomposition (mineralization of organic carbon to CO_2) in the water column and sediments; (5) the rate of transformation of particulate carbon to dissolved organic carbon; (6) the rate of organic loading from waste discharges; and (7) the rates of energy and material flow along important pathways between producers and consumers.

Some of these processes have been quantified in San Francisco Bay (see for example Peterson 1979 and Spiker and Scheme1 1979), but plankton ecologists have made little progress in studies of trophic dynamics. Particularly important unanswered questions relate to the interactions between phytoplankton and their consumers (presumably zooplankton and benthic invertebrates), and the link between herbivores and the ultimate consumers that are harvested. Storrs et al. (1964), Painter (1966), Heuback (1969), USBR (1976), Siegfried and Knight (1976) and Orsi and Knutson (1979), in their studies of the northern reach, demonstrated that zooplankton are ubiquitous, that composition of the zooplankton community varies temporally and spatially, and that large standing stocks ($> 5 \times 10^4$ crustaceans·m^{-3}) are common. **A.** Hutchinson (pers. comm.) has measured densities of the copepod *Acartiaclausi* (all life stages) as high as 15×10^4 individuals·m^{-3} in South Bay. We know, then, that zooplankton are abundant in the San Francisco Bay system, but we know nothing about the importance of zooplankton in controlling phytoplankton population growth and species composition. Laboratory studies of Richman et al. (1977) suggest that selective grazing of netphytoplankton by *A. clausi* alone may account for the small biomass of diatoms observed in South Bay during 1978. Hutchinson (pers. comm.) also observed that, at times, South Bay waters contain large numbers of microzooplankton (tintinnid ciliates and rotifers) which, presumably, graze selectively on the microflagellates. A sustained effort is needed (1) to define the impacts of the zooplankton community on regulating the size and composition of phytoplankton populations in the Bay system and, in turn, (2) to define the relationships between phytoplankton abundance and composition and the fluctuating population dynamics of the zooplankton. The impact of benthic filter-feeders has not yet been considered, although their high densities on mudflats of San Pablo and South bays (Nichols 1979) suggest that they may be very important regulators of phytoplankton standing stocks over the shoals.

Of particular interest in the northern reach and Delta is the relationship between algal primary productivity and the success of fisheries, especially the valuable striped bass (Stevens 1979). We know that planktonic invertebrates, primarily the mysid ***Neomysis mercedis*** (Orsi and Knutson 1979) and copepods, are an important food source for larval and juvenile fishes, and that phytoplankton are an important component in the diet of these zooplankters (e.g. Kost and Knight 1975). The correlation between fluctuations in the abundance of striped bass and Delta outflow (Stevens 1979) may be an indirect consequence of the relationship between Delta outflow and standing stock of phytoplankton in Suisun Bay. So, a link between phytoplankton and fisheries dynamics is probable but not quantified. We do not, for example, know what rates of autotrophic production are required to optimize the yield of fisheries. Although we do know that netplanktonic diatoms are important in the diet of ***Neomysis mercedis*** and herbivorous copepods, we do not know if the large standing stock of netphytoplankton in Suisun Bay during summer is a prerequisite for the survival of juvenile striped bass. Therefore, we cannot yet forecast the impacts of potential shifts in the species composition of phytoplankton on fisheries.

Similar questions can be asked of the importance of phytoplankton in Central Bay and San Pablo Bay to the success of the dungeness crab. Crab larval stages are common in coastal waters off San Francisco, and first-year crabs utilize San Pablo Bay as a nursery ground (Tasto 1979). Identification of those planktonic algae that are required by crab zooeae, and determination of environmental factors that regulate primary productivity of these phytoplankters may offer important clues to the solution of the problem of declining dungeness crab catches along central California over the past 15 years (Tasto 1979).

Finally, basic research is needed to determine which physicochemical factors are most important in regulating the composition and productivity of phytoplankton populations in San Francisco Bay. Growth rates of algal cells are governed by light intensity, temperature, water chemistry (including salinity levels and nutrient and toxin concentrations), while population changes result from the net balance between rates of growth, transport and losses. Results of past studies allow us to make gross generalizations about interactions between physicochemical factors and phytoplankton population growth, but we require a higher level of understanding before a predictive capability can be attained. Results of past surveys indicate that light availability (including surface irradiance, water transparency and ratio of photic depth to mixed depth) is a primary factor that limits the growth of planktonic algae in the Bay system. Concentrations of dissolved phosphate and silicate consistently exceed levels that limit algal growth (Peterson et al. 1975a; Conomos et al. 1979), but inorganic nitrogen (nitrate plus ammonium) fell to relatively low levels ($< 1\ \mu$g-atoms·liter^{-1}) in Suisun Bay during the summer phytoplankton maximum of 1972 (Conomos and Peterson 1975), and dissolved ammonium disappeared in Grizzly Bay during periods of summer, when inputs of nitrogen are relatively small and algal densities are large, low nitrogen concentrations may override light availability as a limiting factor for algal growth. We know very little about the existence of toxins and their impacts on phytoplankton population growth. And our understanding of the interactions between physical forces (including algal settling rates, estuarine circulation, longitudinal advective-dispersive processes, and rates of exchange between water masses of the main channel and lateral shoals) and phytoplankton population dynamics is primitive. Answers to these difficult questions are required by decision makers to permit wise choices concerning proposed major perturbations (the Peripheral Canal, for example, will alter the flow regime, salinity distribution, and turbidity of waters in the northern reach; the San Luis Drain will increase nitrogen concentrations near Suisun Bay), and they will come only from long-term interdisciplinary studies based upon cooperative efforts of hydrodynamicists, biologists, chemists and geologists.

ACKNOWLEDGMENTS

I gratefully acknowledge the efforts of A. E. Alpine, B. E. Cole, Anne Hutchinson and R. L. J. Wong who gathered 1977-78 data reported here. Thoughtful manuscript reviews by T. J. Conomos, D. S. McCulloch, F. H. Nichols and D. H. Peterson were very helpful, as were the insights generated by discussions with J. F. Arthur and M. D. Ball.

LITERATURE CITED

Arthur, J. F., and M. D. Ball. 1979. Factors influencing the entrapment of suspended material in the San Francisco Bay-Delta estuary. Pages 143-174 *in* T. J. Conomos, ed. San Francisco Bay: The Urbanized Estuary. Pacific Division, Amer. Assoc. Advance. Sci., San Francisco, Calif.

Ball, M. D., and J. F. Arthur. 1979. Planktonic chlorophyll dynamics in the northern San Francisco Bay and Delta. Pages 265-285 *in* T. J. Conomos, ed. San Francisco Bay: The Urbanized Estuary. Pacific Division, Amer. Assoc. Advance. Sci., San Francisco, Calif.

Bolin, R. L., and D. P. Abbott. 1963. Studies on the marine climate and phytoplankton of the central coastal area of California, 1954-60. Calif. Coop. Ocean. Fish. Invest. Rep. 9:23-45.

Bowden, K. F. 1967. Circulation and diffusion. Pages 15-36 *in* G. H. Lauff, ed. Estuaries. Amer. Assoc. Advance. Sci. Publ. No. 83. Washington, D.C.

Cloern, J. E. 1978. Empirical model of *Skeletonema costatum* photosynthetic rate, with applications in the San Francisco Bay estuary. Advance. Water Res. 1:267-274.

Cole, B. E., and R. E. Herndon. 1979. Hydrographic properties and primary productivity of San Francisco Bay waters, March 1976-July 1977. U. S. Geol. Surv. Open-File Rep. 79-983.

Conomos, T. J., D. S. McCulloch, D. H. Peterson, and P. R. Carlson. 1971. Drift of surface and near-bottom waters of the San Francisco Bay system: March 1970 through April 1971. U. S. Geol. Surv. Open-File Map.

Conomos, T. J., and D. H. Peterson. 1974. Biological and chemical aspects of the San Francisco Bay turbidity maximum. Mem, Inst. Geol. Bassin d'Aquitaine 7:45-52.

Conomos, T. J., and D. H. Peterson. 1975. Longitudinal distribution of selected micronutrients in northern San Francisco Bay during 1972. Pages 103-126 *in* R. L. Brown, ed. Proceedings of a Workshop on Algae Nutrient Relationships in the San Francisco Bay and Delta (8-10 November 1973, Clear Lake, Calif.). San Francisco Bay and Estuarine Assoc., San Francisco, Calif.

Conomos, T. J., and D. H. Peterson. 1977. Suspended-particle transport and circulation in San Francisco Bay: an overview. Pages 82-97 in M. Wiley, ed. Estuarine Processes. Vol. 2. Circulation, sediments, and transfer of material in the estuary. Academic Press, New York.

Conomos, T. J., F. H. Nichols, R. T. Cheng, and D. H. Peterson. 1978. Field and modeling studies of San Francisco Bay. Pages 1917-1927 *in* Coastal Zone '78; Proc. Symp. Technical, Environmental, Socioeconomic and Regulatory Aspects of Coastal Zone Management, ASCE, San Francisco, Calif., March 14-16, 1978.

Conomos, T. J., R. E. Smith, D. H. Peterson, S. W. Hager, and L. E. Schemel. 1979. Processes affecting seasonal distributions of water properties in the San Francisco Bay estuarine system. Pages 115-142 *in* T. J. Conomos, ed. San Francisco Bay: The Urbanized Estuary. Pacific Division, Amer. Assoc. Advance. Sci., San Francisco, Calif.

Conomos, T. J. 1979. Properties and circulation of San Francisco Bay waters. Pages 47-84 *in* T. J. Conomos, ed. San Francisco Bay: The Urbanized Estuary. Pacific Division, Amer. Assoc. Advance. Sci., San Francisco, Calif.

Dyer, K. R. 1973. Estuaries: a physical introduction. Wiley-Interscience, New York. 140 pp.

Edzwald, J, K., J. B. Upchurch, and C. R. O'Melia. 1974. Coagulation in estuaries. Environ. Sci. Technol. 8:58-63.

Garrison, D. L. 1976. Contribution of the net plankton and nanoplankton to the standing stocks and primary productivity in Monterey Bay, California during the upwelling season. Fish. Bull. 74:183-194.

Heuback, W. 1969. *Neomysis awatschensis* in the Sacramento-San Joaquin River estuary. Limnol. Oceanogr. 14:533-546.

Imberger, J., W. B. Kirkland, Jr., and H. B. Fischer. 1977. The effect of Delta outflow on the density stratification in San Francisco Bay. ABAG (Assoc. of Bay Area Governments) Rep. HBF-77/02. 109 pp.

Kost, A. L. B. and A. W. Knight. 1975. The food of *Neomysis mercedis* Holmes in the Sacramento-San Joaquin Delta estuary system. Calif. Fish Game 61:3 4 41.

Krone, R. B. 1978. Aggregation of suspended particles in estuaries. Pages 177-190 *in* B. Kjerfve, ed. Estuarine Transport Processes. Belle W. Baruch Library in Marine Science No. 7. Univ. South Carolina Press, Columbia, S. C.

McCulloch, D. S., D. H. Peterson, P. R. Carlson, and T. J. Conomos. 1970. A preliminary study of the effects of water circulation in the San Francisco Bay estuary--some effects of freshwater inflow on the flushing of South San Francisco Bay. U. S. Geol. Surv. Circ. 637-A. 27 pp.

Malone, T. C. 1971. The relative importance of nanoplankton and netplankton as primary producers in the California current system. Fish. Bull. 69:799-820.

Meade, R. H. 1972. Transport and deposition of sediments in estuaries. Pages 91-120 *in* B. W. Nelson, ed. Environmental Framework of Coastal Plain Estuaries. Geol. Soc. Amer. Mem. 133.

Nichols, F. H. 1979. Natural and anthropogenic influences on benthic community structure in San Francisco Bay. Pages 409-426 *in* T. J. Conomos, ed. San Francisco Bay: The Urbanized Estuary. Pacific Division, Amer. Assoc. Advance. Sci., San Francisco, Calif.

Orsi, J. J., and A. C. Knutson, Jr. 1979. The role of mysid shrimp in the Sacramento-San Joaquin estuary and factors affecting their abundance and distribution. Pages 401-408 *in* T. J. Conomos, ed. San Francisco Bay: The Urbanized Estuary. Pacific Division, Amer. Assoc. Advance. Sci., San Francisco, Calif.

Painter, R. E. 1966. Zooplankton of San Pablo and Suisun Bays. Pages 18-39 *in* D. W. Kelley, ed. Ecological studies of the Sacramento-San Joaquin estuary. Part I. Zooplankton, zoobenthos, and fishes of San Pablo and Suisun Bays, zooplankton and zoobenthos of the Delta. Calif. Fish Game, Fish. Bull. 133.

Peterson, D. H., T. J. Conomos, W. W. Broenkow, and E. P. Scrivani. 1975a. Processes controlling the dissolved silica distribution in San Francisco Bay. Pages 153-187 *in* L. E. Cronin, ed, Estuarine Research. Vol. 1. Chemistry, Biology and the Estuarine System. Academic Press, New York.

Peterson, D. H., T. J. Conomos, W. W. Broenkow, and P. C. Doherty. 1975b. Location of the non-tidal current null zone in northern San Francisco Bay. Estuarine Coastal Mar. Sci. 3:1-11.

Peterson, D. H. 1979. Sources and sinks of biologically reactive oxygen, carbon, nitrogen, and silica in northern San Francisco Bay. Pages 175-193 *in* T. J. Conomos, ed. San Francisco Bay: The Urbanized Estuary. Pacific Division, Amer. Assoc. Advance. Sci., San Francisco, Calif.

Richman, S., D. R. Heinle, and R. Huff. 1977. Grazing by adult estuarine calanoid copepods of the Chesapeake Bay. Mar. Biol. 42:69-84.

Seckler, D., ed. 1971. California water: A study in resource management. University of California Press, Berkeley, Calif. 348 pp.

Siegfried, C. A., and A. W. Knight. 1976. A baseline ecological evaluation of the western Sacramento-San Joaquin Delta. University of California, Davis, Water Science and Engr. Papers, No. 4504.

Spiker, E., and L. E. Schemel. 1979. Distribution and stable-isotope composition of carbon in San Francisco Bay. Pages 195-212 *in* T. J. Conomos, ed. San Francisco Bay: The Urbanized Estuary. Pacific Division, Amer. Assoc. Advance. Sci., San Francisco, Calif.

Stevens, D. E. 1979. Environmental factors affecting striped bass (Morone *saxatilis)* in the Sacramento-San Joaquin estuary. Pages 469-478 *in* T. J. Conomos, ed. San Francisco Bay: The Urbanized Estuary. Pacific Division, Amer. Assoc. Advance. Sci., San Francisco, Calif.

Storrs, P. N., R. E. Selleck, and E. A. Pearson. 1963. A comprehensive study of San Francisco Bay 1961-62. Univ. Calif. Sanit. Engr. Res. Lab. Rep. No. 63-3.

Storrs, P. N., R. E. Selleck, and E. A. Pearson. 1964. A comprehensive study of San Francisco Bay 1962-63. Univ. Calif. Sanit. Engr. Res. Lab. Rep. No. 64-3.

Storrs, P. N., E. A. Pearson, and R. E. Selleck, 1966. A comprehensive study of San Francisco Bay, a final report. Vol. V. Summary of physical, chemical and biological water and sediment data. Univ. Calif. Sanit. Engr. Res. Lab. Rep. No. 67-2.

Tasto, R. N. 1979. San Francisco Bay: Critical to the dungeness crab? Pages 479-490 *in* T. J. Conomos, ed. San Francisco Bay: The Urbanized Estuary. Pacific Division, Amer. Assoc. Advance. Sci., San Francisco, Calif.

U. S. Bureau of Reclamation. 1976. Delta-Suisun Bay ecological studies. A report of water quality in the Sacramento-San Joaquin estuary during the low flow year, 1976. USBR, Water Quality Branch, Sacramento, Calif.

U. S. Bureau of Reclamation, California Department of Water Resources, and California Department of Fish and Game. 1977. Delta-Suisun Bay ecological studies. Biological methods and data for 1968-74. USBR, Water Quality Branch, Sacramento, Calif.

Whedon, W. F. 1939. A three-year survey of the phytoplankton in the region of San Francisco. Int. Rev. Hydrobiol. 38:459-476.

Zabawa, C. F. 1978. Microstructure of agglomerated sediments in northern Chesapeake Bay estuary. Science 202:49-51.