

Organic carbon sources and sinks in San Francisco Bay: variability induced by river flow

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ABSTRACT: Sources and sinks of organic carbon for San Francisco Bay (California, USA) were estimated for 1980. Sources for the southern reach were dominated by phytoplankton and benthic microalgal production. River loading of organic matter was an additional important factor in the northern reach. Tidal marsh export and point sources played a secondary role. Autochthonous production in San Francisco Bay appears to be less than the mean for temperate-zone estuaries, primarily because turbidity limits microalgal production and the development of seagrass beds. Exchange between the Bay and Pacific Ocean plays an unknown but potentially important role in the organic carbon balance. Interannual variability in the organic carbon supply was assessed for Suisun Bay, a northern reach subembayment that provides habitat for important fish species (delta smelt *Hypomesus transpacificus* and larval striped bass *Morone saxatilis*). The total supply fluctuated by an order of magnitude; depending on the year, either autochthonous sources (phytoplankton production) or allochthonous sources (riverine loading) could be dominant. The primary cause of the year-to-year change was variability of freshwater inflows from the Sacramento and San Joaquin rivers, and its magnitude was much larger than long-term changes arising from marsh destruction and point source decreases. Although interannual variability of the total organic carbon supply could not be assessed for the southern reach, year-to-year changes in phytoplankton production were much smaller than in Suisun Bay, reflecting a relative lack of river influence.

INTRODUCTION

The sources of food and energy for estuarine food webs are diverse compared to those of other ecosystems. The diversity arises from several features, including the existence of an intertidal habitat, the supply of materials from rivers, and the waste products of contiguous human communities. In San Francisco Bay (SFB), dramatic changes during the 1970s and 1980s in species composition at higher trophic levels, including fishes and benthic invertebrates (Herbold et al. 1992), have resulted in a strong need for the delineation of food sources. Because San Francisco Bay has been a focus of investigation for over 2 decades (Conomos 1979a, Cloern & Nichols 1985), much relevant information exists. It has never been integrated, however, into an assessment of the total organic matter supply, the relative importance of the different components, and the manner in which the supply is affected by both human activities and natural processes.

Our primary objective here is to synthesize information from a variety of places in order to identify and rank the important sources of organic carbon for the estuary, i.e. to assess the component parts comprising the system metabolism of SFB. Particular attention is paid to the influence of bathymetry on different flux estimates. Organic carbon sinks are also summarized, although the available data are much less comprehensive.

A second objective is based on the recognition that all terms composing an annual carbon budget are dynamic, i.e. they exhibit variability in space and time. We illustrate the variability in space by considering separately the southern and northern reaches of SFB (Fig. 1). Previous work has depicted marked differences for certain materials and processes in the 2 reaches. The southern reach, for example, is only weakly influenced by the Sacramento-San Joaquin Rivers, except during periods of very high river flow (Cloern 1991). In contrast, the northern reach is strongly influenced by river

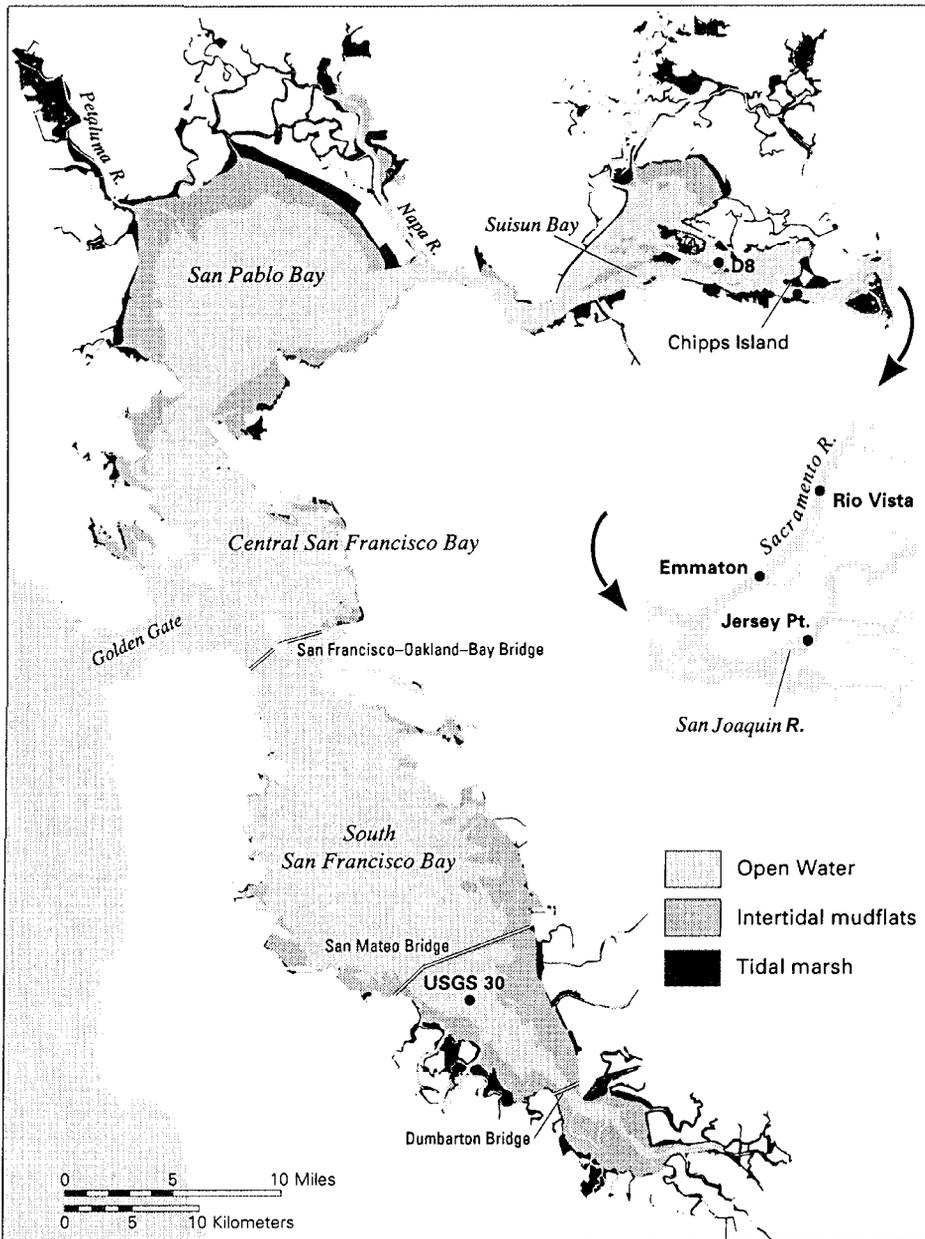


Fig. 1. San Francisco Bay, California, USA, showing the major subembayments and estuarine habitats. Inset shows portions of the Sacramento and San Joaquin rivers just upstream of Suisun Bay

inflows: spatial distributions of salinity, suspended sediments, nutrients, plankton, and benthic communities all respond to seasonal and interannual fluctuations in discharge of the Sacramento-San Joaquin Rivers (Cloern & Nichols 1985). We therefore ask how differently these 2 subembayments are organized on a systemic level, as described by organic carbon sources and sinks. The deep Central Bay, connecting the northern and southern reaches with the coastal ocean, is poorly studied and therefore cannot be included in this analysis.

'The carbon budget is also a function of time, not a collection of static quantities. Here, we focus on how

the annual carbon budget changes from year to year. Although seasonal change in carbon budgets has been a subject of active investigation (Jansson 1988), much less information is available on interannual change. Fluxes contributing to the budget must change from one year to the next, and their relative importance may change as well. Unfortunately, estimates for each flux in SFB are available for only one or a few years, often not overlapping. Nevertheless, many fluxes that appear to dominate the carbon budget were measured during 1980, a year of 'intermediate' river inflow. We use 1980 as a reference

point and estimate a budget for that year; we then examine, insofar as the data permit, how this budget changes over time.

Although various mechanisms underly the spatial and temporal variability in organic carbon fluxes, river inflows are of particular interest. First, as intimated above, many of the known differences between the northern and southern reaches of SFB can be ascribed to different river inflows, and temporal variability on the scale of years to decades in certain estuarine properties has also been attributed to variable inflows (Cloern & Nichols 1985). Changeable inflows are thus likely to have marked effects on net organic carbon fluxes and, consequently, estuarine metabolism. Second, management of river inflows is one of the major means by which humans can exert a direct influence on the estuary; the consequences of this management for organic carbon sources and the resulting supply of food to higher trophic levels is clearly of great practical import. Finally, and in a similar vein, river inflows mediate an important pathway by which climatic fluctuations affect estuarine features; understanding how these inflows affect organic carbon sources may permit some insight into the long-term consequences of climatic trends on estuarine metabolism. We therefore examine spatial and temporal differences in the organic carbon fluxes primarily with regard to Sacramento-San Joaquin River inflows.

San Francisco Bay is a complex estuarine system that is connected to the Pacific Ocean through a narrow deep trough (Golden Gate; Fig. 1), and it receives freshwater inflows primarily from the Sacramento and San Joaquin rivers, which have a combined drainage of 153000 km² (Conomos et al. 1985). These rivers carry runoff produced during winter storms and during spring snowmelt, so riverine inputs are highly seasonal. Riverine inflows are regulated through the collection of runoff in a series of reservoirs on the tributaries; by the diversion of river flow from the estuary, mostly to support irrigated agriculture; and by release of fresh water from the reservoirs during the dry summer-autumn to repel salinity intrusion. Runoff from the smaller local tributaries constitutes only about 10% of the annual source of fresh water to San Francisco Bay (Conomos et al. 1985). The local basin of San Francisco Bay comprises a large metropolitan area (nearly 6 million people) that has expanded to the shoreline, thus eliminating most of the tidal marsh that formed the pristine margin of the open bay in the last century (Atwater et al. 1979). The bay itself includes large expanses of intertidal mudflats and subtidal shallow embayments. These are incised by a narrow channel that is typically 10 to 30 m deep, except in the central basin at the estuary mouth where channel depth reaches ca 100 m.

CALCULATION METHODS AND RESULTS

Morphometric considerations

First, we compiled bathymetric data to define habitat areas and volumes for each subembayment. Data for all open water habitat deeper than mean lower low water (MLLW) were interpolated from nautical charts for the nodes of a 0.25 km grid covering the entire bay (Bureau & Cheng 1989). A hypsographic curve referenced to the MLLW tidal datum was constructed for each major subembayment using these data (Fig. 2; Central Bay is also shown for completeness).

Hypsographic data for areas above MLLW were taken from other sources. First, published values of mean tidal level (MTL) and mean higher high water (MHHW), referenced to the MLLW datum, were averaged for each subembayment (USCOE 1937). Next, the values for MLLW, and thus MTL and MHHW, were referenced to the National Geodetic Vertical Datum (NGVD), again averaged for each subembayment (USCOE 1984). The areas between MLLW and both MTL and MHHW were then determined from tidal stage-area graphs referenced to the NGVD (Morrison 1988) (Table 1).

The hypsographs of South and North bays strongly resemble one another (Fig. 2). Shoal areas, defined here as shallower than 2 m relative to MLLW, occupy a large fraction of each subembayment, 47% in the case

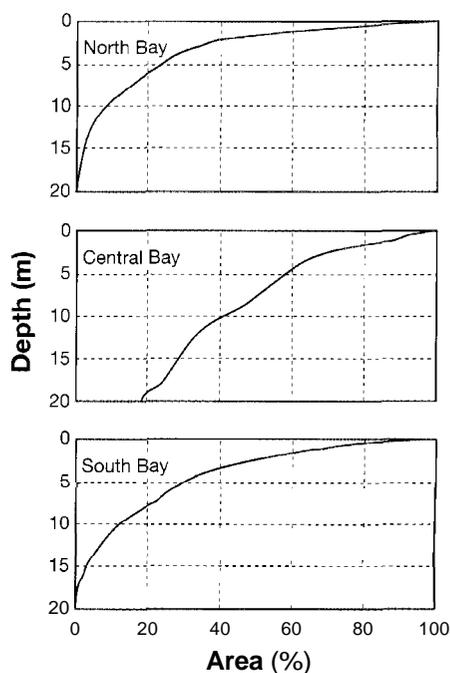


Fig. 2. Hypsographs for South, Central, and North San Francisco Bay down to a depth of 20 m

Table 1. Morphometry of San Francisco Bay's major subembayments. SB: South Bay; CB: Central Bay; NB: North Bay. Data for North Bay are further broken down into results for San Pablo Bay (SP) and Suisun Bay (SU)

Bay	Area ($\times 10^8 \text{ m}^2$)			Volume ($\times 10^9 \text{ m}^3$)	Depth (m)		
	MLLW	MTL	MHHW		MLLW	Mean	Median
SB	4.7	5.5	6.1	1.9	4.0	2.2	29
CB	2.2	2.4	2.5	2.5	11	7.7	99
NB							
SP	2.6	3.2	4.4	0.86	3.3	1.5	29
SU	1.0	1.2	1.7	0.31	3.1	1.8	28
Total	3.6	4.4	6.1	1.2	3.2	1.6	29

of South Bay and 60% for North Bay (cf. median depths, Table 1). Maximum depths are also similar, a consequence of dredging activity to maintain shipping channels. In contrast, the Central Bay has a much smaller shoal area, occupying only 27% of the MLLW area, and a much deeper maximum depth.

Habitat areas within the estuary were determined by a variety of methods, as described in the following sections (Fig. 3). Note that phytoplankton shoal and channel habitat, benthic microalgal habitat, and vegetated tidal marsh are all significant in North Bay, while tidal marsh is relatively small in South Bay. Seagrass

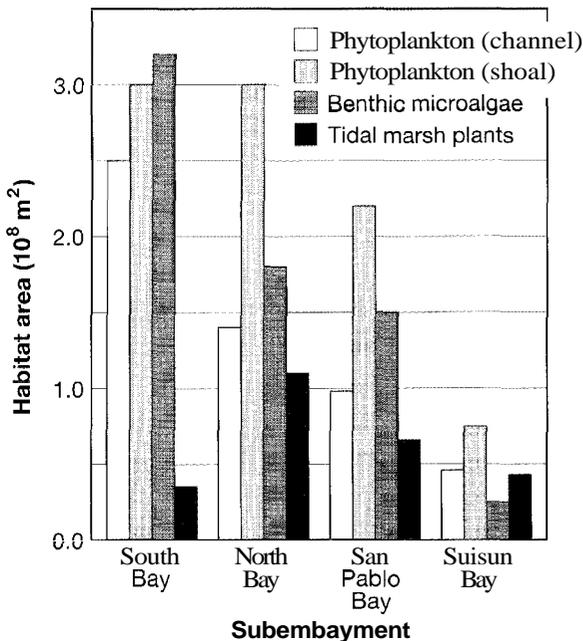


Fig. 3. Habitat areas for the main primary producers of South Bay and North Bay. North Bay can be further subdivided into San Pablo and Suisun bays. Seagrass habitat is too small to appear on this scale, and macroalgal habitat is probably insignificant as well. Habitat areas overlap and therefore do not sum to subembayment areas

stands are insignificant in both subembayments, as is rocky shore habitat for macroalgae. For the purposes of this carbon budget, vegetated tidal marsh was considered external to the system boundaries and an allochthonous source of organic carbon. The budget therefore refers to the entire area bounded by MHHW, exclusive of vegetated tidal marsh.

Autochthonous sources

Phytoplankton. Of the autochthonous organic carbon fluxes in the bay, phytoplankton productivity has been studied in the most detail. During 1980, productivity was determined monthly at 6 representative stations, including a shoal and channel site in each of South Bay, San Pablo Bay and Suisun Bay (Cloern et al. 1985). Samples were incubated in a deck box under natural light attenuated with neutral density filters (including a range of 1 to 100% of surface light). Estimates were based on ^{14}C uptake rates over 24 h. Respiration rates in the dark were assumed to equal 10% of the maximum (light-saturated) ^{14}C uptake determined from these 24 h incubations.

The results for these 6 stations can be converted to estuary-wide estimates of phytoplankton productivity. Because the depth of the euphotic zone – taken here as the depth at which irradiance declines to 1% of the surface value – varies continuously in time and space with changing turbidity, several simplifications were necessary (Fig. 4). First, the water level was assumed to be constant at MTL. Next, each subembayment was divided into a 'shallow' and 'deep' region at 2 m below

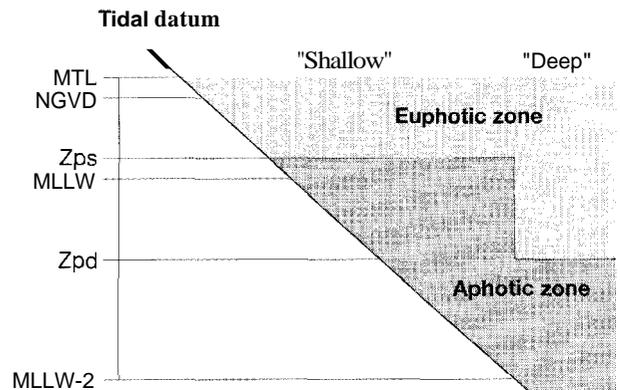


Fig. 4. Schematic cross-section of subembayment illustrating morphometric model used in the estimation of phytoplankton productivity. MLLW: mean lower low water; MTL: mean tidal level; NGVD: National Geodetic Vertical Datum; z_{pd} : 'deep' photic depth; z_s : 'shallow' photic depth

MLLW (ca 3 m below MTL), within each of which net photic zone productivity (P_{np} , $g C m^{-2} d^{-1}$), biomass (b , $mg chl a m^{-3}$), respiration rate below the photic zone (r , $g C m^{-3} d^{-1}$), and photic depth (z_p , m) were assumed to be constant at any given time. Then, P_{np} was integrated over area and year, resulting in estimates of net annual photic zone productivity (π_{np} , $g C yr^{-1}$) for each region. Similarly, using the hypsographic data, the volume below the photic zone was determined for both shallow and deep regions. Phytoplankton respiratory losses were estimated for shallow and deep regions separately, integrated over the year, and subtracted from the corresponding values for π_{np} , resulting in estimates for net annual water column productivity (π_{nw} , $g C yr^{-1}$).

Because phytoplankton respiration rates for the aphotic zone are so uncertain, the phytoplankton productivity data are presented with and without respiration corrections (Table 2). Water column productivity, however, rather than photic zone productivity, represents the true supply of organic matter to consumer organisms. The data clearly demonstrate how aphotic respiration assumptions have a marked effect on water column production estimates, particularly in North Bay where aphotic losses account for a 29% average decrement in net photic zone production. On an areal basis, the productivity values in both South and San Pablo bays are similar, but they are substantially reduced in Suisun Bay and, hence, for North Bay as a whole. Shoal productivity is by far the major component in each subembayment. The shoal contribution of 110% for Suisun Bay reflects a negative channel productivity due to respiratory losses in the deep aphotic zone there. Respiration by autotrophs is therefore a signifi-

cant component in the carbon budget of SFB that we have included implicitly in our estimates of net water column productivity. Similarly, Hopkinson (1988) calculated that autotrophic respiration consumes 13 to 68% of the gross primary production in 6 other coastal estuarine systems.

Benthic microalgae. The benthic microalgal community of SFB has been examined in several studies, most notably in terms of chlorophyll by Thompson et al. (1981) and in terms of species composition by Laws (1983, 1988). Productivity of this community, however, has never been measured in SFB, and we estimated the magnitude of this source based on habitat area and measurements reported for other systems.

Several researchers have tabulated results from benthic primary production studies (Riznyk et al. 1978, Colijn & de Jonge 1984, Knox 1986). We combined these summaries with other recent studies (Thom 1984, Shaffer & Onuf 1985, Varela & Penas 1985, Fielding et al. 1988, Gould & Gallagher 1990) in order to examine the distribution of productivity measurements. We used all locations where an annual production estimate was published, except for the 2 most northerly sites ($>57^\circ N$), which had extremely low values. Multiple estimates for other sites were replaced by their median value, resulting in a total of 28 site estimates. The overall median productivity was $110 g C m^{-2} yr^{-1}$ and the first and third quartiles of the data set were 66 and $180 g C m^{-2} yr^{-1}$, respectively. Because of the large uncertainty inherent in benthic productivity estimates, it would be premature to attribute the differences among studies to habitat or climatic differences (Shaffer & Onuf 1985). We therefore used this median value as the estimate for average areal benthic primary production in the San Francisco estuary.

In order to maintain consistency with the simplifications introduced for estimating phytoplankton production, we defined the habitat for benthic microalgal production as all mudflat and open water areas extending down to a depth of z_p below MTL. The assumption is that, as for phytoplankton, benthic microalgae lying below the mean 1% surface light level do not receive sufficient insolation to grow. The upper boundary for the estimate of habitat area is MHHW, because the hypsographic information extends no further than this tidal datum. The entire area from MHHW to a depth of z_p below MTL was estimated for each subembayment, using the hypsographic curve for MLLW, the areas at MTL and MHHW, and the value of z_p for each subembayment. As tidal marsh habitat is external to the boundaries under consid-

Table 2. Phytoplankton carbon productivity for South Bay (SB) and North Bay (NB) in 1980. Data for North Bay are further broken down into results for San Pablo Bay (SP) and Suisun Bay (SU). All numbers have been rounded to 2 significant digits. π_{np} : net photic zone productivity; π_{nw} : net water column productivity

Bay	$\pi_{np}^{a,b}$ ($g m^{-2} yr^{-1}$)	$\pi_{nw}^{a,c}$ ($g m^{-2} yr^{-1}$)	π_{nw}^c ($Gg yr^{-1}$)	$\frac{\pi_{np} - \pi_{nw}}{\pi_{np}}$ (%)	Shoal π_{nw}^d (%)
SB	150	130	76	13	62
NB	130	90	45	29	78
SP	140	100	39	25	74
SU	87	44	5.6	50	110

^a Based on area at MHHW corrected for tidal marsh habitat
^b Assumes aphotic phytoplankton respiration is negligible
^c Assumes aphotic phytoplankton respiration is 10% of light-saturated ^{14}C uptake
^d Percent of a_r , occurring in water shallower than 2 m referenced to MLLW

eration, it was subtracted from this area. The resulting estimates of benthic microalgal primary production were $36 \times 10^9 \text{ g C yr}^{-1}$ in South Bay and $19 \times 10^9 \text{ g C yr}^{-1}$ in North Bay.

Other autochthonous sources. Eelgrass *Zostera marina* appears to be the only seagrass of significance in the San Francisco estuary (Wyllie Echeverria & Rutten 1989). Its distribution in the bay is limited, covering a total of only 128 ha. No productivity measurements have been made for these eelgrass stands, but temperate eelgrass communities, including those of the subtidal Pacific Coast, have productivities between ca 100 and $500 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Phillips 1974). In the absence of actual measurements, a value of $300 \text{ g C m}^{-2} \text{ yr}^{-1}$ was used here. Because the habitat area is so small, a more careful estimate of eelgrass production is unwarranted; regardless of areal productivity, this source of organic carbon is negligible.

Most macroalgae in the estuary are restricted to Central Bay (Silva 1979, Josselyn & West 1985), but no attempt has been made to assess the total standing crop in any of the major subembayments. The patchy nature of macroalgal distribution reflects both the low availability of suitable locations for attachment and the mobility of drift communities floating along the estuary bottom. The scarcity of suitable locations, however, also limits total macroalgae coverage on an estuary-wide basis, and their contribution to annual primary production is probably not significant (M. Josselyn pers. comm.).

The contribution of epiphytic algae has been included implicitly in estimates for other carbon sources.

We also considered the possibility that bacterial production of organic carbon, including both photo- and chemo-autotrophic processes, might be a significant source term. On the basis of habitat area and substrate concentration, we concluded that these sources must be negligible in SFB. For example, ca $2 \times 10^9 \text{ g yr}^{-1} \text{ NH}_3\text{-N}$ is contributed by the Sacramento-San Joaquin rivers (estimated from Peterson et al. 1985) and $3 \times 10^9 \text{ g yr}^{-1} \text{ NH}_3\text{-N}$ from point source waste loads [estimated by combining NH_3 : Biochemical Oxygen Demand (BOD) ratios from Peterson (1979) with BOD loads from CRWQCB-SFBR (1987)]. If the entire amount were oxidized by nitrifying bacteria within the estuary, and assuming that 35 mol of NH_3 are required for each mol of CO_2 fixed (Atlas & Bartha 1987), the corresponding organic carbon production would be only $0.1 \times 10^9 \text{ g C yr}^{-1}$.

Allochthonous sources

Riverine loading. Based on biweekly flow-weighted measurements of dissolved organic carbon (DOC) at Rio Vista during 1980, Scheme 1 (1984) estimated the

Sacramento River flow of DOC to be $150 \times 10^9 \text{ g yr}^{-1}$, with a mean annual flow-weighted DOC concentration of 5.0 mg l^{-1} . Particulate organic carbon (POC) was measured only from April through December, so an estimate of annual POC transport requires additional assumptions. As there was no apparent seasonal trend in the ratio POC:DOC, based on the 9 mo of overlapping data, the mean of this ratio, 0.10 ± 0.02 (SE), was used to estimate an annual POC load of $15 \times 10^9 \text{ g yr}^{-1}$. In the absence of adequate organic carbon measurements for the San Joaquin River and other smaller tributaries, the annual load of total organic carbon (TOC) into Suisun Bay was estimated by multiplying Sacramento River transport by the ratio of total riverine inflow to Sacramento River flow, a factor of 1.08 in 1980. Summing the estimates for DOC and POC, the 1980 TOC load into Suisun Bay was $180 \times 10^9 \text{ g C yr}^{-1}$.

Tidal marsh export. Because no direct measurements of marsh export to San Francisco Bay have been made, we must turn to results from other estuaries. We combined the tabulations of Nixon (1980) and Borey et al. (1983), including only those sites for which TOC or energy exports were available and converting energy to carbon on the basis of 9 g C kcal^{-1} (Borey et al. 1983). We also included studies by Howarth & Teal (1980), Kjerfve & McKellar (1982), and Roman & Daiber (1989), resulting in a total of 10 sites. The overall median export was $150 \text{ g C m}^{-2} \text{ yr}^{-1}$, which we adopt as a representative value for San Francisco Bay tidal marshes. The first and third quartiles of the data set were 100 and $410 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively. Tidal marsh habitat areas for each subembayment were derived from NWI habitat maps for 1985 (Meiorinet al. 1991). Using the median value for marsh export rate, we estimate this source to contribute $5.2 \times 10^9 \text{ g C yr}^{-1}$ to South Bay and $16 \times 10^9 \text{ g C yr}^{-1}$ to North Bay.

Point sources. Organic carbon data are not part of the required monitoring program for point sources (primarily effluent from sewage treatment plants). As a result, we are compelled to make inferences about carbon loading from the routine measurements of BOD. The California Regional Water Quality Control Board-San Francisco Bay Region (CRWQCB-SFBR) has compiled municipal BOD loading to San Francisco Bay for the period 1955–1985, by subembayment (CRWQCB-SFBR 1987). Industrial discharge, not included in these loading estimates, accounted for only an additional 5% of BOD load, at least in 1985 (T.W. pers. comm.).

The ratio of TOC to BOD is highly variable (Kim 1987), but we can arrive at a lower limit on theoretical grounds. A respiratory coefficient ($\text{C}:\text{O}_2$ molar ratio) of 1, typical of carbohydrates and proteins before nitrification of NH_3 , implies a TOC:BOD mass ratio of 0.38.

Dischargers usually report BOD₅, which is typically two-thirds of the ultimate BOD in domestic sewage (Warren 1971). The corresponding TOC:BOD₅ ratio is thus 0.57. This value would be reduced if some of the ammonia released were oxidized as well. The complete nitrification of NH₃ to NO₃⁻ would result in a TOC:BOD₅ of about 0.43. As nitrification facilities, however, are not integrated into some of the larger treatment plants in the area, an intermediate TOC:BOD₅ ratio is probably appropriate. Accordingly, we chose here a mass ratio of 0.5; a range of 0.5 to 1 is commonly encountered for municipal raw sewage and primary effluent (Meron 1970, Iskandar 1978), where one would expect the lowest values. Based on these assumptions and measured BOD loading for 1980, we estimate point sources of organic carbon to be 6.6×10^9 g C yr⁻¹ for the South Bay and 1.7×10^9 for the North Bay.

Runoff. The category of runoff is defined to be all loads to SFB carried by inflowing waters other than the combined Sacramento-San Joaquin River flow or point sources. The loading from runoff must be assessed through indirect methods, by combining typical TOC concentrations in runoff (8 mg l^{-1} ; Silverman et al. 1985, Smith 1989) with volumetric runoff estimates based on precipitation and land use (Gunther et al. 1987). We estimated urban runoff to contribute 1.8×10^9 g C yr⁻¹ to South Bay and 1.6×10^9 to North Bay in 1980.

An upper limit on nonurban runoff can be estimated by multiplying non-Sacramento-San Joaquin stream flow into the bay (Meiorin et al. 1991) by the characteristic runoff concentration. The resultant loading from the 10 largest streams amounts to 1.8×10^9 g C yr⁻¹ for South Bay and 2.6×10^9 for North Bay, approximately the same as urban runoff. These streams account for 64% of the area that drains directly into the bay, and so the estimates could be scaled upward somewhat. On the other hand, the streams also carry effluent from sewage treatment plants (Coyote Creek), tidal marsh export (Petaluma River), and some urban runoff, so the actual nonurban runoff may be far less.

Other allochthonous sources. We considered a variety of other possible allochthonous sources, but all were found to be negligible. Russell et al. (1982), for example, estimated an aerial fallout of 1.8×10^9 g BOD₅ yr⁻¹ to the surface of SFB in 1978, implying atmospheric deposition of only about 0.90×10^9 g TOC yr⁻¹. On the basis of data for Chesapeake Bay, Gunther et al. (1987) extrapolated a total hydrocarbon deposition of only 0.045×10^9 g yr⁻¹ to San Francisco Bay. Oil spills are also common, although the mass loading from spills was estimated to be only about $0.09 \pm 0.01 \times 10^9$ g yr⁻¹ of petroleum hydrocarbons for 1984–1986 (Gunther et al. 1987) and presumably even

less in terms of TOC. Russell et al. (1982) did not include groundwater among the significant freshwater sources to SFB. If groundwater flow is indeed a minor component of the water budget, then it is probably a negligible term in the organic carbon budget as well.

Exchange across the seaward boundaries is a potentially important source, but we could not assess its magnitude with existing data. The absence of information on exchange is a serious weakness with almost all organic matter balances in estuaries (cf. Wolff 1977; see below for more information).

Carbon sinks

Respiration. Hammond et al. (1985) measured benthic fluxes of total CO₂ at a shoal and a channel station in South Bay. Three replicated measurements were made at each station from June 1980 through February 1981. We integrated these values over time and habitat area to estimate mean annual fluxes for shoal and channel regions. The fluxes were corrected for carbonate dissolution. The corrected fluxes (62×10^9 g C yr⁻¹) were considered to represent the net effects of aerobic plus anaerobic respiration (presumably dominated by sulfate reduction and denitrification).

Additional respiratory losses must take place through planktonic bacteria and zooplankton metabolism. Although no water column measurements of respiration were made in 1980, a few measurements of light and dark O₂ exchange were made in bay waters in 1976–1977 (Cole & Herndon 1979) and again in 1984 (M. Pamatmat pers. comm.). We were unable to distinguish any significant differences among seasons, years, or subembayments, so we simply calculated the mean volumetric respiration rate for 24 hr dark bottle incubations and applied it to both South and North bays. Carbon fluxes were determined by assuming a mean C:O₂ molar ratio of 1 (Hammond et al. 1985). Estimated water column respiration consumed 74×10^9 g C yr⁻¹ in the South Bay and 46×10^9 in the North Bay.

Note that both benthic and water column respiration include contributions from microalgae, so respiratory losses due to heterotrophs are less than implied in the above estimates. As microalgal respiration has been included implicitly in estimates of benthic primary productivity and net photic zone productivity, as well as explicitly in net water column productivity, net system productivity cannot be determined simply by subtracting respiration from allochthonous sources.

Circulation and mixing. No attempt was made to estimate physical transport of organic matter by circulation and mixing across the seaward boundaries

of the 2 reaches. Some of the available evidence indicates that this transport is a net sink, rather than a source. At the seaward boundaries, winter gradients of POC are negative seaward, and summer gradients are small, suggesting that mixing results in net losses from the 2 reaches (Conomos 1979b). Although seabed drifters move from outside the Golden Gate into Central Bay, especially in winter, further landward movement into either South or North Bay is limited (Conomos & Peterson 1977). All the available evidence is circumstantial, however, and this term must be considered unknown in sign, as well as in magnitude. Estuarine circulation or dispersion could conceivably result in net upstream transport, particularly in the northern reach where freshwater inflows are so strong.

Dredging. Dredging and dredged material disposal result in the transport of large quantities of sediment within and between subembayments, and between Bay and ocean. Annual average Federal dredging has been tabulated for the period 1975–1985. Assuming a solids content of 34% (AHI, PWA 1990), a mean TOC:dry weight of 1.4% (Thomson-Becker & Luoma 1985), and non-Federal dredging equal to 38% of the total (AHI & PWA 1990), 7.4×10^9 g C yr⁻¹ was transported from South Bay to the disposal site in Central Bay. In San Pablo and Suisun bays, dredging activity results only in a redistribution of organic carbon within the North Bay segment as defined here.

Permanent burial. Estimates of permanent burial are available only for South Bay. We used Hammond et al.'s (1985) estimate of the organic carbon burial rate, which was based on Fuller's (1982) budget for ²¹⁰Pb, yielding a net loss of 4.4×10^9 g C yr⁻¹.

Active transport. Based on the fact that the major migrating fishes are at least 2 trophic levels higher than primary producers, we would expect them to remove an insignificant fraction of the organic carbon input. In San Francisco Bay, for example, the northern anchovy *Engraulis mordax* is the most abundant fish species. Adults and juveniles enter the bay in late spring and remain until autumn, feeding primarily on zooplankton. Migration back to the ocean removes an estimated 160 t of new anchovy biomass annually (McGowan 1986), or ca 0.016×10^9 g C yr⁻¹. The migratory biomass of piscivorous fish and marine mammals, and the consequent effect on TOC transport, is likely to be even less than for planktivore populations.

Harvest. Harvest losses are also probably negligible. The only commercial fisheries remaining in the bay are for northern anchovy and Pacific herring *Clupeus harengus*. Recent commercial catches of anchovy have stabilized at ca 380 t (Smith & Kato 1979) or only about 0.038×10^9 g C yr⁻¹. San Francisco Bay attracts large

spawning migrations of Pacific herring, with an estimated biomass of 71×10^9 g in 1989–1990 (J. Spratt pers. comm.). Up to 15% of the population can be harvested, which amounts to 1.1×10^9 g C yr⁻¹. In both cases, most of the biomass comes from outside the bay, so the net loss from bay organic carbon pools is much smaller.

Sport' fishing also must account for negligible amounts. The major species of recreational interest, striped bass *Morone saxatilis* and chinook salmon *Oncorhynchus tshawytscha*, are anadromous, and most of the harvested biomass is produced in the ocean. Migrating chinook salmon number between ca 70 000 and 500 000, with a typical wet weight of 5 kg. The equivalent organic carbon is only about 0.1×10^9 g C yr⁻¹ (Gulland 1970), which would have a minor effect on the carbon budget even if it were all harvested from the estuary.

Summary of sources and sinks. Several groups of sources can be distinguished, based on their percentage contribution to the organic carbon supply of both subembayments (Table 3):

(1) The first group consists of those sources that were almost definitely unimportant. This group includes seagrasses, runoff, atmospheric deposition, and spills. These probably contributed less than 10% of the total in both subembayments.

(2) The second group consists of sources that also appear to be insignificant, but the evidence is anecdotal and the conclusion less certain. This group includes macroalgae, bacterial autotrophs, and groundwater.

(3) A third category consists of processes that contributed at least 5% in at least one subembayment. This group includes phytoplankton, benthic microalgae, river loads, tidal marsh export, and point sources.

Of the organic carbon sources, Groups 1 and 2 will be dropped from consideration in what follows. No evidence supports the notion that any of these processes are significant sources for the organic carbon pool, that they were notable in the past, or that they will be in the future (Russell et al. 1982, Silverman et al. 1985).

In South Bay, benthic and water column respiration dominated the organic carbon sinks for which estimates were possible (Table 4). Both dredging transport and permanent burial accounted for minor losses. Active transport and harvest were probably insignificant. In North Bay, benthic respiration and permanent burial could not be estimated from the existing data. Of the remaining sinks, planktonic respiration was dominant, dredging transport was essentially zero, and both active transport and harvest were judged to be unimportant.

Table 3. Organic carbon sources for South Bay (SB) and North Bay (NB), based on data for the indicated years. Estimates (including subtotals and totals) are rounded to the nearest Gg yr^{-1} and then expressed in terms of at most 2 significant digits. *Probably not significant, but no quantitative estimate

	Amount (Gg yr^{-1})		Relative %		Year
	SB	NB	SB	NB	
Autochthonous ^a					
Phytoplankton	76	45	60	17	1980
Benthic microalgae	36	19	28	7	1980
Seagrasses	0	0	0	0	1987
Macroalgae	*	*	*	*	-
Bacterial autotrophs	*	*	*	*	-
Subtotal	110	64	89	25	
Allochthonous ^b					
River inflow					
DOC	0	160	0	62	1980
POC	0	16	0	6	1980
Tidal marsh export	5	16	4	6	1985
Point sources	7	2	5	1	1980
Runoff ^c	2	2	1	1	1979-1982
Atmospheric deposition	0	0	0	0	1978
Spills	0	0	0	0	1986
Groundwater	*	*	*	*	-
Subtotal	14	200	11	75	
Total sources	120	260	100	100	

^aWhere applicable, epiphyte production is implicitly included with host plant production
^bTransport at seaward boundaries not estimated, but could possibly function as a net source, especially for NB (see text)
^cUrban runoff only. Nonurban runoff probably of similar magnitude, at most (see text). NB value includes runoff into the central basin

Table 4. Organic carbon sinks for South Bay (SB) and North Bay (NB), based on data for the indicated years. Estimates were rounded to the nearest Gg yr^{-1} and then expressed in terms of at most 2 significant digits. *Probably not significant, but no quantitative estimate; nd: not determined

	Amount (Gg yr^{-1})		Year
	SB	NB	
Respiration ^a			
Benthic	62	nd	1980
Planktonic	74	46	1976-1977, 1984
Circulation and mixing	nd	nd	-
Dredging	7	0	1975-1985
Burial	4	nd	1980
Active transport			-
Harvest			-

^aIncludes microalgal respiration and therefore overestimates heterotrophic respiration

DISCUSSION

Contrasts between North and South San Francisco Bay

Although there are large uncertainties associated with each carbon flux in SFB, we presume that values shown in Tables 3 & 4 are unbiased estimates that reflect the relative importance of sources and sinks for organic carbon in this estuary. On this basis we conclude that the annual carbon budget for SFB includes 2 prominent source terms: autochthonous primary production by microalgae (mostly phytoplankton), and fluvial inputs of allochthonous organic carbon. The relative contributions of these 2 sources differ markedly between northern and southern SFB. From measurements made in 1980, the ratio of autochthonous to allochthonous sources is 8 for the South Bay but only 0.3 for the North Bay (Table 3). This strong contrast in organic carbon sources is a consequence of the contrasting landscape settings of these 2 subembayments: the South Bay is lagoon-like in character with a small local watershed and small inputs of freshwater from local streams, whereas the North Bay receives discharge from a large river system.

Riverine inputs directly influence the ratio of autochthonous to allochthonous sources in SFB through 2 mechanisms (a third mechanism, riverine supply of inorganic nutrients, may operate in other estuaries where phytoplankton are not light-limited; Malone et al. 1988). First, river flow provides continual input of suspended sediments that attenuate light penetration in the water column, confine z_p to a narrow zone, and therefore suppress autotrophic production by limiting light availability for photosynthesis. As a consequence, spatial gradients of P_{nw} mirror the distributions of river-derived suspended sediments within individual estuaries (Cloern 1987), and much of the difference in P_{nw} among some estuaries is attributable to differences in their mean optical depth or turbidity (Peterson et al. 1988). Secondly, river flow provides an external source of organic carbon and for some estuaries, such as North SFB, fluvial input is the single largest source of organic carbon. The ratio of autochthonous to allochthonous sources is therefore a simple index of the watershed influence on estuarine metabolism, as mediated through riverine inflow (Peterson et al. 1988). In fact this ratio may be a useful basis for com-

parison among estuaries that, on a global scale, exhibit a wide range of influence by external sources. For example, phytoplankton primary production in the Fana Fjord (Norway) is $416 \text{ g C m}^{-2} \text{ yr}^{-1}$ compared to areal averaged riverine inputs of $25 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Pearson 1988), so the ratio of autochthonous to allochthonous sources for this fjord-type estuary is 17. In contrast, the ratio of autochthonous to allochthonous sources is only 0.07 in Grays Harbor estuary, Washington, USA (Thom 1984), where fluvial inputs of organic carbon overwhelm total autochthonous production. The contrasting carbon budgets for North and South SFB illustrate that these 2 subembayments fall near opposite ends of the global scale relating autochthonous and allochthonous sources of organic matter.

Such simple quantitative comparisons of source terms may provide little useful information, however, for comparing metabolism among estuaries because of the diverse qualitative nature of both autochthonous and allochthonous organic matter. A more useful index would be the ratio of utilizable autochthonous to utilizable allochthonous organic carbon, where the utilizable fraction is that component of DOC+POC that can be biochemically oxidized faster than the hydraulic retention time of an estuary. For SFB, perhaps only about 10% of the river-derived organic carbon is utilizable. Based on measurements made by the California Department of Water Resources (DWR) from 1968–1977, the mean BOD, along the Sacramento River between Rio Vista and Chipps Island was $1.3 \pm 0.1 \text{ (SE) mg l}^{-1}$, which corresponds to 0.5 mg l^{-1} organic carbon (assuming respiratory quotient, $\text{RQ} = 1$). This measure of utilizable organic carbon is about 10% of the mean TOC concentration. Due to the organic matter contributions from the Sacramento-San Joaquin rivers, North Bay appears to have a much higher organic carbon supply than South Bay, $520 \text{ vs } 210 \text{ g C m}^{-2} \text{ yr}^{-1}$. But if only 10% of the river contribution is utilizable, then North Bay sources amount to $200 \text{ g C m}^{-2} \text{ yr}^{-1}$, almost the same as South Bay. Freshwater inflow can thus be seen as inducing a tradeoff of indigenous microalgal production for inflows of external supplies of organic matter.

What is the nature of the utilizable fraction of fluvial organic carbon delivered to SFB? Based on measurements of chlorophyll and its degradation products, much of the POC appears to be river-borne phytoplankton and phytoplankton-derived detritus. Along with organic carbon, chlorophyll a and phaeophytin a were measured in the lower Sacramento River at Rio Vista during 1980. The implied POC flux to North SFB was $7 \times 10^9 \text{ g C yr}^{-1}$ for phytoplankton plus phytoplankton-derived detritus (assuming a carbon : pigment ratio of 40, and that phaeophytin a concentrations averaged 50% of chlorophyll a concentrations; Ball

1987). This represents about half of the estimated flux of utilizable TOC. Spiker & Schemel (1979) found that the stable isotope composition of POC just upstream of Suisun Bay was characteristic of riverine phytoplankton, not of land plants. This result is consistent with the estimates presented here as well as observations that upstream phytoplankton blooms are often advected into Suisun Bay when flows exceed $300 \text{ m}^3 \text{ s}^{-1}$ (Ball 1987).

These conclusions do not necessarily apply generally to other estuaries, because the nature and reactivity of fluvial organic matter is highly complex (Degens 1982) and dependent upon hydrologic and landscape setting of the river basin. For some river-estuary systems such as the Columbia River, northwestern USA (Small et al. 1990), perhaps Delaware Bay, Delaware, USA (Cifuentes et al. 1988), and North SFB, a substantial fraction of the utilizable allochthonous organic carbon appears to be derived from freshwater algae. However in other settings, such as the upper St. Lawrence estuary, Quebec, Canada (Lucotte et al. 1991) or Dabob Bay, Washington, USA (Hedges et al. 1988), geochemical markers suggest that the bulk of the allochthonous POC is derived from terrestrial vegetation. A fundamental challenge for deriving useful indices for comparing estuarine metabolism is the development of a systematic approach for characterizing the chemical nature, origin, and reactivity of allochthonous organic matter that is delivered to estuaries from their watersheds. Development of such approaches is necessary before we can understand the ecological or biogeochemical significance of the differing origins of organic matter among estuaries, such as North and South SFB. For example, Smith et al. (1991) suggest that coastal ecosystems are generally 'net heterotrophic'; but what is the origin of the allochthonous organic carbon that supports system respiration at rates faster than in situ primary production? And are the pathways of metabolism different for different sources of organic matter? In this vein, Parsons et al. (1989) hypothesize a distinct 'heterotrophic food chain' based on riverine organic matter, and 'autotrophic food chain' based on phytoplankton production. If this hypothesis were true, then we could expect greatly differing food web dynamics and ecological efficiencies in the production of consumer organisms between North and South SFB, and other estuaries that have contrasting origins of organic matter.

Organic carbon supply rates

Although estuaries are generally perceived as highly productive ecosystems, there is a remarkable range in the areal rates of primary production among estuaries.

Phytoplankton primary production varies about 2 orders of magnitude, from <10 to >600 $\text{g C m}^{-2} \text{yr}^{-1}$ (Knox 1986). The mean P_{np} for temperate-zone estuaries appears to be on the order of about 200 $\text{g C m}^{-2} \text{yr}^{-1}$ (Boynton et al. 1982), so rates of phytoplankton primary production in SFB are relatively small: during 1980, P_{np} was 150 $\text{g C m}^{-2} \text{yr}^{-1}$ for South Bay and 130 for North Bay. These values, however, are consistent with the concept of suppressed autotrophic production in estuarine systems having large riverine inputs of suspended sediments. Along the west coast of North America 2 other large river systems, the Columbia River and Fraser River estuaries, also have low phytoplankton primary production (55 and 120 $\text{g C m}^{-2} \text{yr}^{-1}$, respectively; Small et al. 1990, Parsons et al. 1970).

The effects of turbidity are not limited to phytoplankton productivity. Seagrasses contribute significant amounts of organic matter in many estuarine systems and, because of their potential for much higher productivity than phytoplankton (Zieman & Wetzel 1980), often raise mean estuary-wide productivity. In San Francisco Bay, eelgrass beds are limited to a mere 128 ha, and the main limitation on expansion of seagrass beds appears to be turbidity (Zimmerman et al. 1991). High suspended sediment concentrations therefore play a major role in the low total autotrophic organic carbon supplies for South and North SFB (190 and 130 $\text{g C m}^{-2} \text{yr}^{-1}$, respectively), which are less than the total primary productivity measured in the open-water habitats of other estuaries along the North American west coast: Tomales Bay, 330 $\text{g C m}^{-2} \text{yr}^{-1}$ (Smith et al. 1991); Grays Harbor estuary, 310 $\text{g C m}^{-2} \text{yr}^{-1}$ (Thom 1984); Puget Sound, 465 $\text{g C m}^{-2} \text{yr}^{-1}$ (phytoplankton production only; Winter et al. 1975).

A further factor contributing to the low levels of combined organic matter sources in SFB is the small extent of tidal marsh habitat. When counted as an autochthonous source, the high productivity of tidal marsh vegetation relative to phytoplankton results in a higher estuary-wide areal productivity (2000 $\text{g C m}^{-2} \text{yr}^{-1}$ for Barataria Bay, Louisiana, USA; Hopkinson 1988). When counted as an allochthonous source, it acts as a supplement to autochthonous sources and will also increase the supply of total organic matter. The importance of marsh contributions obviously depends on the ratio of marsh to total estuarine habitat (Nixon 1980). This ratio has been drastically decreased in SFB by marsh leveeing and filling over the past 140 yr (Atwater et al. 1979). According to the NWI wetlands inventory (Fig. 3), SFB tidal marsh in 1985 occupied only 144 km^2 , equivalent to ca 18% of the pre-1850 tidal marsh area. Assuming constant marsh export rates, tidal marsh would have contributed 117×10^9 g C yr^{-1} to SFB if habitat area were the same as in 1850.

The additional material (96×10^9 g C yr^{-1}) represents an increase of 25% over 1980 loading. Tidal marsh contributions were clearly much higher in the last century, and the destruction of marsh habitat is a significant factor in the low organic matter supply to contemporary SFB. The elimination of marsh habitat upstream of the Bay may also have had a long-term effect on the quantity and quality of allochthonous materials carried in by the Sacramento-San Joaquin rivers.

A related issue is the long-term change in point source loading. BOD loads from municipal sources peaked in the 1960s and then decreased at a remarkable rate, particularly since 1972 when the U.S. Federal Clean Water Act required a minimum of secondary treatment for all dischargers (CRWQCB-SFBK 1987). BOD removal efficiency increased from 29% in 1955 to 95% in 1985. The effect of the relatively rapid decrease in BOD loading on the organic carbon budget must have been substantial. In South Bay, for example, BOD loads decreased from 157 to 36×10^6 g d^{-1} between 1965 and 1980, a factor of 4.4 . The additional loading in 1965 was 22×10^9 g C yr^{-1} , or 18% of total organic carbon sources in 1980. North Bay experienced a 2.9 -fold decrease in BOD loading between 1970 (the long-term peak year) and 1980. The contribution to total organic carbon sources was small, though, and the decrease probably did not change the budget substantially.

River flow and interannual variability of organic carbon sources

Each term of the annual carbon budget (Tables 3 & 4) represents the net sum of many complex processes that all vary in time. How much variability might we expect to see from year to year in the total supply of organic carbon to SFB, and where does the 1980 carbon budget fit within this expected range of interannual variability? Fundamental hydrological and ecological changes have occurred in SFB in recent years, including a 5 yr drought and sustained low river flow from 1987 to 1991; invasion of SFR by an exotic suspension-feeding clam (*Potamocorbula amurensis*) that has greatly altered seasonal phytoplankton cycles in the North Bay and caused a 5 -fold decrease in primary production in Suisun Bay (Alpine & Cloern 1992); and large declines in the abundance of virtually all species of fish that either reside in Suisun Bay or use this subembayment as nursery habitat (Herbold et al. 1992). To what extent are these changes related to interannual changes in the magnitude or character of organic matter that is available in SFB to support its food webs?

For South SFB, phytoplankton productivity is the only budget term that can be examined from the view-

point of interannual variability; it does appear, however, to be the major source of organic carbon (60% in 1980; Table 3). Cloern (1991) hypothesized a mechanism contributing to interannual variability in South Bay that acts through the influence of freshwater inflow on density stratification of the water column, which controls the balance between rates of phytoplankton population growth and consumption by the benthos. The long-term biomass record now suggests that this mechanism may be important only during years of extreme flows. The most complete chlorophyll series in South Bay (USGS Stn 30, Fig. 1) includes approximately 300 surface chlorophyll measurements from 1980 to 1991. The annual mean chlorophyll concentrations for this period were compared with mean Sacramento-San Joaquin River flow during February to May (covering the spring bloom period of maximum biomass and primary production). Although the Pearson correlation between chlorophyll concentration and river flow was significant ($r = 0.78$, $p = 0.026$), the Spearman correlation was not ($r = 0.52$, $p = 0.084$), reflecting the fact that a few extreme years (record floods of 1982–1983 and 1986) dominate the relationship. At lower flows, a wide range of chlorophyll concentrations is found. Regardless of the significance of the relation between phytoplankton biomass and river flow, the actual year-to-year variability in phytoplankton productivity is small in South Bay. Estimates of annual mean P_{np} had a coefficient of variation of 26% for the period 1980–1987 (P_{np} data from Cloern 1991). In contrast, annual Sacramento-San Joaquin River inflows during this period had a coefficient of variation of 81%, with a maximum more than 13 times the minimum. We can only conclude that the response of annual organic carbon fluxes in South Bay to interannual river flow variability, insofar as we currently understand, is highly damped and perhaps only significant in years of extreme flow.

Unlike South Bay, riverine loading is a major source term for the North Bay and therefore a potentially important source of variability in its annual organic carbon budget. Data exist for an assessment of year-to-year fluctuations in the phytoplankton-associated carbon carried by river inflows, which may account for much of the TOC loading available for consumption. From DWR measurements, we determined the riverine loading of phytoplankton-derived pigments for 1975 to 1989 by summing flow-weighted chlorophyll *a* and phaeophytin *a* concentrations from the Sacramento and San Joaquin rivers. Pigment loads were converted to organic carbon by assuming a carbon: pigment ratio of 40. Although several long-term changes in upstream biomass and algal community composition have occurred since 1973 (Ball 1987), annual phytoplankton-derived loading during 1975 to 1989 appears to be

largely proportional to annual river inflows, except in years of exceptionally high flows (Fig. 5). The drought period that began in 1987 was therefore a time of highly reduced loading from river inflows and probably of total allochthonous sources to North Bay. Note that this source of organic matter can vary by an order of magnitude among years.

Our understanding of variability in primary productivity in the North Bay rests largely on data for Suisun Bay, where long-term chlorophyll measurements have been sustained. Two main factors underlying interannual variability in biomass (chlorophyll *a*) have been implicated in Suisun Bay. The first is the effect of river inflow on residual circulations that retain phytoplankton biomass in the upper estuary (Ball & Arthur 1979). The second is consumption by benthic herbivores (Nichols 1985), which is indirectly influenced by river inflows: during low flow periods of at least 16 consecutive months, estuarine benthic macroinvertebrates colonize Suisun Bay, leading to a large increase in their biomass and grazing impact (Nichols et al. 1990). As a result of these 2 processes, the interannual variability in P_{np} is much higher for Suisun Bay (and probably North Bay as a whole) than for South Bay. Estimates of annual mean P_{np} from a channel station in Suisun Bay for 1974 to 1990 (Alpine & Cloern 1992) have a coefficient of variation of 47%, almost twice that of South Bay.

Together, phytoplankton production and riverine loading accounted for 85% of the organic carbon sources for North Bay in 1980. Even if only 10% of the riverine loading were available, these 2 sources would account for 62% of the total. The figures are similar for Suisun Bay alone (Table 5). Variability in river flow therefore has a major impact on the total annual organic matter supply to the North Bay. Although we could not examine these impacts quantitatively for the entire northern reach, existing data do permit some

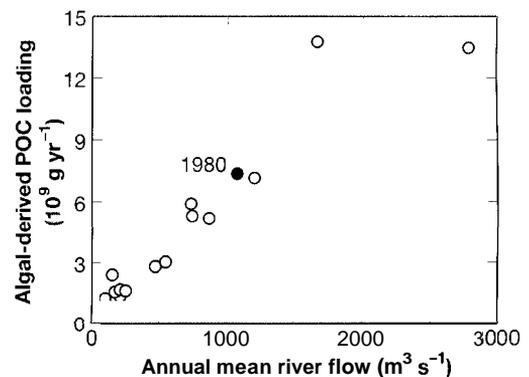


Fig. 5. Algal-derived organic carbon loading into North Bay, 1975 to 1989. Estimates are based on flow-weighted measurements of phytoplankton pigments at Emmatton on the Sacramento River and Jersey Point on the San Joaquin River (see Fig. 1)

Table 5. Organic carbon sources for Suisun Bay, based on data for the indicated years. Estimates were rounded to the nearest Gg yr⁻¹ and then expressed in terms of at most 2 significant digits. *Probably not significant, but no quantitative estimate

	Amount (Gg yr ⁻¹)	Relative %	Year
Autochthonous^a			
Phytoplankton	6	3	1980
Benthic microalgae	3	1	1980
Seagrasses	0	0	1987
Macroalgae	*	*	-
Bacterial autotrophs	*	*	-
Subtotal	8	4	
Allochthonous			
River inflow			
DOC	160	83	1980
POC	16	8	1980
Tidal marsh export	6	3	1985
Point sources	2	1	1980
Runoff ^b	0	0	1979–1982
Atmospheric deposition	0	0	1978
Spills	0	0	1986
Groundwater	*	*	-
Subtotal	180	96	
Total sources	190	100	

^a Where applicable, epiphyte production is implicitly included with host plant production
^b Urban runoff only. Nonurban runoff probably of similar magnitude, at most (see text)

additional conclusions regarding Suisun Bay, which is an important habitat for anadromous (striped bass) and estuarine (delta smelt *Hypomesus transpacificus*) fish species. The annual pigment-associated POC loads from the Sacramento-San Joaquin rivers for 1975 to 1989 (Fig. 6) were assumed to represent the POC loading contributed by upstream phytoplankton. We also used the annual phytoplankton production estimates P_{np} of Alpine & Cloern (1992) for a Suisun Bay station (D8, Fig. 1) and scaled them by the ratio of $\pi_{np}:P_{np}$ for 1980. The scaled values were assumed to represent estimates of annual phytoplankton production in Suisun Bay as a whole for 1975 to 1989. Together, these 2 different series constitute the phytoplankton-associated organic carbon supplied to the food web of Suisun Bay for this 15 yr record.

River inflow has a marked effect on both the total supply of organic carbon from phytoplankton, as well as its relative makeup. Between 1975 and 1989, the total varied by a factor of 7 (Fig. 6a) and the percentage attributable to river loading ranged from 20 to 90% (Fig. 6b). Above 500 m³ s⁻¹ annual mean flow, total supply increases with flow, except perhaps at the highest flows (1983). Similarly, the importance of load-

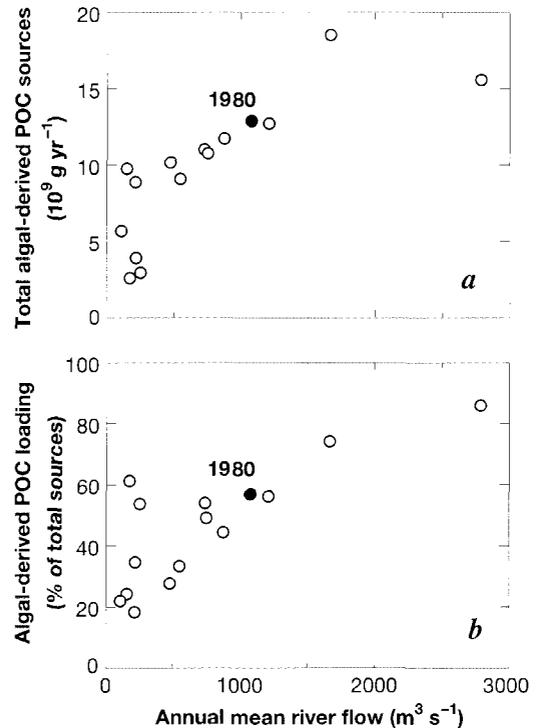


Fig. 6. (a) Organic carbon supplied to Suisun Bay either by *in situ* production of phytoplankton or by loading of phytoplankton and phytoplankton-derived detritus from upstream sources, 1975 to 1989; (b) Ratio of upstream to total sources of phytoplankton carbon in Suisun Bay, 1975 to 1989

ing from upstream systematically increases only above 500 m³ s⁻¹. Another factor comes into play below about 500 m³ s⁻¹, namely herbivory by benthic macroinvertebrates. *In situ* phytoplankton production dominates at these low flows and, as mentioned previously, benthic filter-feeders can depress primary production strongly during prolonged low-flow periods (Nichols et al. 1990, Alpine & Cloern 1992). The close relationship between annual river inflows and the organic matter supply to Suisun Bay, as well as the existence of plausible mechanisms underlying the relationship, clearly indicates a fundamental role for river inflows in the interannual variability of organic matter supplies for this important nursery area. More specifically, the drought that began in 1987 signals a period of greatly impoverished organic matter supplies because of reduced loading from upstream, in addition to the depressed indigenous production. Note, however, that the applicability of these relationships to North Bay as a whole is not known.

The above analysis demonstrates that year-to-year fluctuation in the supply of organic matter can be very large for some estuarine ecosystems. Fundamental questions now remain about the ecological and biogeochemical implications of this variability. We know that rates of nutrient cycling and metabolism and production

by heterotrophs respond to short-term changes in the supply of organic carbon (Hansen & Blackburn 1992). Do processes of element cycling or rates of secondary production also vary from year to year in response to these interannual fluctuations in total organic carbon supply? How much of the year-to-year variability in the production by upper trophic level consumers is attributable to fluctuations in the annual supply of organic carbon to estuaries? Finally, can estuarine ecosystems exhibit year-to-year variability even in their net metabolism, shifting from net heterotrophy to net autotrophy, depending on annual fluctuations in rates of primary production and allochthonous loading? At this stage of estuarine science we know little about the system responses to interannual variability of organic carbon supplies of the magnitude demonstrated here for San Francisco Bay.

SUMMARY

Construction of an annual carbon budget shows that the primary sources of organic carbon to San Francisco Bay are autotrophic production by microalgae (mostly phytoplankton) and fluvial inputs of organic carbon from the Sacramento-San Joaquin rivers, with smaller contributions from point sources and perhaps tidal marshes. The primary sinks for organic carbon in South SFB (apart from possible contributions by circulation and mixing) are pelagic and benthic respiration, which appear to be of comparable magnitude.

The origin of organic matter differs markedly between the 2 subembayments of San Francisco Bay. In the lagoon-like South Bay, autotrophic sources dominate (92% of total). In the river-dominated North Bay, however, most (68%) of the total organic carbon supply is delivered by the Sacramento-San Joaquin rivers. These contrasts among the subembayments of SFB provide a unique opportunity for comparative study in one system to explore the role of fluvial inputs of organic matter on estuarine metabolism and food web dynamics. Here, as elsewhere, there is great uncertainty about the origin, chemical nature, and reactivity of river-derived organic matter.

Total supplies of labile organic carbon to San Francisco Bay are relatively small: 210 g C m⁻² yr⁻¹ for the South Bay and 200 for the North Bay. Autotrophic production is suppressed by high concentrations of suspended sediments that limit habitat for submerged vascular plants and restrict phytoplankton primary production to a shallow photic zone. In addition, total system autotrophy has likely been reduced in the past 140 yr through massive diking and filling of tidal marshes, and organic matter from sewage has decreased dramatically in recent decades.

Annual fluctuations in the total organic carbon supply to North SFB are larger than annual fluctuations in the South Bay, suggesting that river-dominated estuaries may, in general, have large interannual variability in their carbon budgets (and therefore system metabolism). For North SFB, most of this interannual variability is attributable to annual fluctuations in river discharge, which overwhelm variability associated with human activities such as marsh reclamation.

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