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Organic matter sources and rehabilitation of the Sacramento–San Joaquin Delta (California, USA)

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ABSTRACT

1. The Sacramento–San Joaquin River Delta, a complex mosaic of tidal freshwater habitats in California, is the focus of a major ecosystem rehabilitation effort because of significant long-term changes in critical ecosystem functions. One of these functions is the production, transport and transformation of organic matter that constitutes the primary food supply, which may be sub-optimal at trophic levels supporting fish recruitment. A long historical data set is used to define the most important organic matter sources, the factors underlying their variability, and the implications of ecosystem rehabilitation actions for these sources.

2. Tributary-borne loading is the largest organic carbon source on an average annual Delta-wide basis; phytoplankton production and agricultural drainage are secondary; wastewater treatment plant discharge, tidal marsh drainage and possibly aquatic macrophyte production are tertiary; and benthic microalgal production, urban run-off and other sources are negligible.

3. Allochthonous dissolved organic carbon must be converted to particulate form with losses due to hydraulic flushing and to heterotroph growth inefficiency before it becomes available to the metazoan food web. When these losses are accounted for, phytoplankton production plays a much larger role than is evident from a simple accounting of bulk organic carbon sources, especially in seasons critical for larval development and recruitment success. Phytoplankton-derived organic matter is also an important component of particulate loading to the Delta.

4. The Delta is a net producer of organic matter in critically dry years but, because of water diversion from the Delta, transport of organic matter from the Delta to important, downstream nursery areas in San Francisco Bay is always less than transport into the Delta from upstream sources.

5. Of proposed rehabilitation measures, increased use of floodplains probably offers the biggest increase in organic matter sources.

6. An isolated diversion facility channelling water from the Sacramento River around the Delta to the water projects would result in substantial loading increases during winter and autumn, but little change in spring and summer when food availability probably matters most to developing organisms.

7. Flow and fish barriers in the channel could have significant effects, especially on phytoplankton sources and in dry years, by eliminating 'short-circuits' in the transport of organic matter to diversion points.

8. Finally, productivity of intentionally flooded islands probably would exceed that of adjacent channels because of lower turbidity and shallower mean depth, although vascular plants rather than phytoplankton could dominate if depths were too shallow.

KEY WORDS: agricultural drainage; aquatic macrophyte; food web; organic carbon; phytoplankton; restoration; river loading; tidal marsh

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INTRODUCTION

The Sacramento San Joaquin River Delta. a complex mosaic of tidal freshwater habitats in California. is now a focus of ecosystem rehabilitation because of changes in critical functions associated with its geographic location at the land–estuary interface. One of these functions is the production. transport and transformation of organic matter that constitutes the 'primary food supply', i.e. the food supply to the base of the food web. Interest in this function is motivated by evidence for sub-optimal food quantity or quality at the trophic levels that support fish recruitment. Here. we use an unusually long historical data set to examine the magnitudes of the most important organic matter sources, the factors underlying their interannual and longer-term variability. and the implications of ecosystem rehabilitation actions for these sources.

The Delta is the transition zone between San Francisco Bay and its watershed. a 1.63×10^7 ha basin occupying 40% of California's land area (Figure 1). In the Delta. tributaries collecting precipitation from this watershed coalesce and pass through a narrow notch in the coastal range into San Francisco Bay. The Delta is now a focus of ecosystem restoration (CALFED. 1998) because of: (1) loss of the original dominant tule (*Scirpus* spp.) marsh through filling and diking (Atwater *et al.*, 1979): (2) radical changes in the seasonal pattern. magnitude. and routing of flows (Arthur *et al.*, 1996): (3) introductions and invasions of exotic plants and animals (Cohen and Carlton, 1998): and (4) toxic contaminants (Brown and Luoma, 1999). These changes have been accompanied by significant declines in the abundances of many species of fishes that use the Delta as a migration route, nursery, or permanent habitat (Moyle *et al.*, 1992: Jassby *et al.*, 1995). Some endemic species of fish have already become extinct. others are now at risk of extinction. and still others have dramatically reduced populations (Moyle, 1976: Meng and Moyle. 1995; Kohlhorst, 1997: CDWK, 1999). All key components of the zooplankton and epibenthic invertebrates also exhibit significant downtrends (Kimmerer and Orsi. 1996: Orsi and Mecum, 1996; Orsi, 1999). Furthermore, phytoplankton primary production has decreased fivefold in the landward regions of the estuary (Alpine and Cloern. 1992).

As mentioned above. food quantity or quality in the Delta may now be sub-optimal for fish recruitment. The first trophic link is from pools of organic matter allochthonous or autochthonous to primary consumers. Laboratory and field experiments of Foe and Knight (1985) showed that growth of the clam *Corbicula fluminea* is limited in some regions of the Delta because of sub-optimal phytoplankton biomass. Orsi and Mecum (1996) concluded that food limitation, a result of recent decreases in phytoplankton biomass of the upper estuary. is the primary cause of *Neomysis mercedis* decline. Food limitation probably has also contributed to declining abundance of rotifers and cladocerans (Kimmerer and Orsi. 1996). For macrobenthic suspension feeders in general. Heip *et al.* (1995) argue that system-wide biomass and secondary production are limited by planktonic primary production.

A second trophic link is from primary to secondary consumers. including early stages of fishes that are spawned and develop in the Delta. The majority of declining fish species in the Delta are 'recruitment limited'. i.e. they have poor survival through the first year of life (Bennett and Moyle. 1996). Poor recruitment may result in part from changes in the forage base supporting growth of fish in their first year. For example. larval striped bass (*Morone saxatilis*) grow more slowly in the Sacramento–San Joaquin Delta than in the Chesapeake Bay. Other species. such as delta smelt (*Hypomesus transpacificus*), are even more susceptible to food limitation and potential starvation because of limited abundance or quality of invertebrate food resources (Nobriga, 1998). Success of juvenile chinook salmon (*Oncorhynchus tshawytscha*) is also influenced by the food resource (CDWR, 1999).

The uncertainty in quantifying certain organic matter sources is high. Nonetheless. we believe it essential to summarize existing data systematically because important conclusions can be drawn within the constraints of this uncertainty. Specifically, our objectives include: (1) identification of the primary

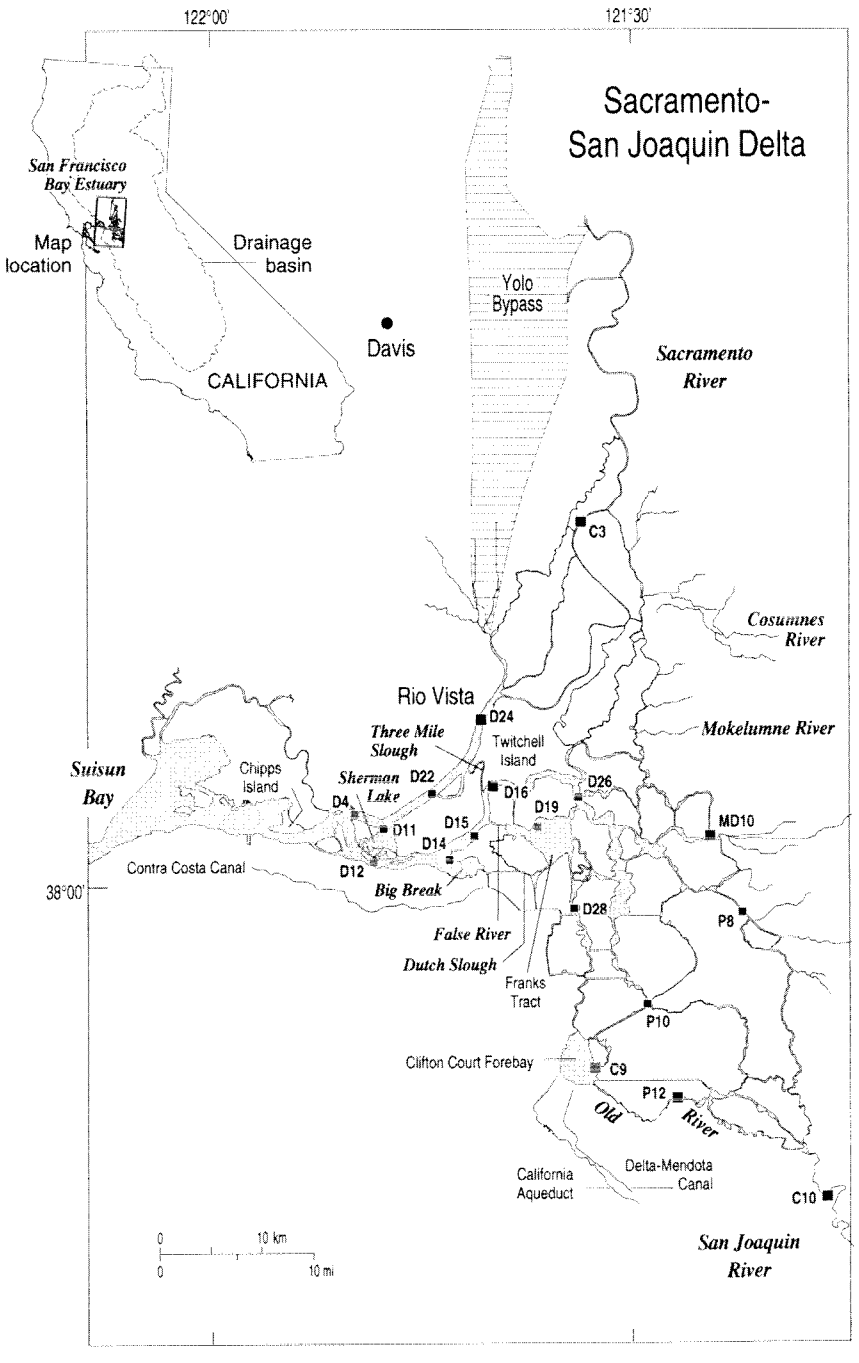

Figure 1. Suisin Bay and the Sacramento San Joaquin Delta. Water quality stations are indicated by filled squares.

sources of organic matter that fuel biological production in the Delta; (2) estimation of organic matter transport from the Delta downstream to the food web of San Francisco Bay; and (3) assessment of how specific restoration actions could influence the supply of organic matter to lower trophic levels.

System description

The Sacramento–San Joaquin River Delta includes a network of linked channels comprising 26000 ha of open-water habitat. Much of the Delta landmass is partitioned into discrete tracts separated from open waters by man-made levees. Through decades of soil erosion, peat decomposition and subsidence. many of these agricultural tracts have fallen up to 10 m below sea level; active maintenance of the levee system is required to protect farmlands from flooding. Some levees have been breached during large floods. creating shallow lake-type habitats (e.g. Franks Tract, Figure 1). Morphometry of the channel-lake network is complex. partly because of natural processes of sediment erosion and deposition and partly because of human activities such as channel dredging. Water depths range from < 1 m in the shallowest lake habitats to > 15 m in the deepest channels.

Hydraulics of the Delta result from four primary forces: riverine inflows. pumping exports. within-Delta water consumption and drainage, and tides. Freshwater is delivered to the Delta by the two largest rivers in California. the Sacramento and San Joaquin. which flow into the north and south Delta. respectively (Figure 1). Delta inflows. on average, comprise 84% Sacramento River flow. 13% San Joaquin River flow, and 3% from smaller rivers (Cosumnes, Mokelumne, and others) that discharge into the east Delta (Arthur *et al.*, 1996). River inflows are highly seasonal. reflecting a climate of wet winters and dry summers. The mean inflow is 1700 ± 300 m^3 s^{-1} during winter and 540 ± 40 m^3 s^{-1} during summer (S.E. among years 1968–1995). Large flood pulses occur in response to warm winter storms that produce rainfall run-off in lower elevations of the watershed and snowmelt run-off at higher elevations. The recent decades have been a period of extreme interannual variability of river inflow. ranging from an average of 230 m^3 s^{-1} during the dry El Niño–Southern Oscillation (ENSO) year 1977 to 2700 m^3 s^{-1} during the wet ENSO year of 1983. During high flow events. part of the Sacramento River discharge is diverted into the Yolo Bypass floodplain (Figure 1). These events occur about once every 3 years. and they persist for weeks or months (CDWR, 1999). When completely flooded, the Yolo Bypass surface area is approximately the same as the Delta.

An estimated $10\% + 1\%$ of the mean annual river inflow is consumed within the Delta. primarily as evapotranspiration. More than 2000 siphons collect water from Delta channels and deliver it to irrigated crops across levees. Irrigation drainage, seepage and precipitation is pumped from farm fields back to the channels at approximately 260 locations. Water is also exported by pumping to the State Water Project (SWP) California Aqueduct and the Central Valley Project (CVP) Delta–Mendota Canal (Figure 1). Smaller amounts are diverted for municipal use through the Contra Costa Canal. Both within-Delta consumption and pumped exports are strongly seasonal. with maximum losses during the dry summer–autumn period of lowest inflow.

The legally defined boundary between the Delta and San Francisco Bay is at the confluence of the Sacramento and San Joaquin Rivers (Chipps Island. Figure 1). Tidal flows propagate through this connection into the network of Delta channels, and the tidal wave becomes damped as it moves inland. Tidal currents are an important mechanism of transport and mixing between the open-water habitats, especially during periods of low river inflow.

The Delta is thus a mosaic of tidal habitats whose hydrology is influenced by seasonally-varying river inflows, local depletions and drainages. exports. and transport between the Delta and San Francisco Bay. The water balance of the Delta is illustrated in Figure 2. which shows inflow as the cumulative discharge of the Sacramento River (Q_{sac}), San Joaquin River (Q_{sjr}), Yolo Bypass (Q_{yolo}) when it is flooded. and the smaller east-side streams (Q_{csmr}, Q_{moke}, Q_{misc}). It shows exports as the sum of pumped flows into the CVP (Q_{cvp}), SWP (Q_{swp}), and smaller aqueducts that deliver water to local municipalities (Q_{out}). These routes of water flow are also routes for transporting organic matter. and we use these flows to calculate the transport of organic matter into the Delta (carried with water inflows). and from the Delta as exports and with outflow (Q_{out}) to the upper San Francisco Bay estuary. We compare these fluxes with internal

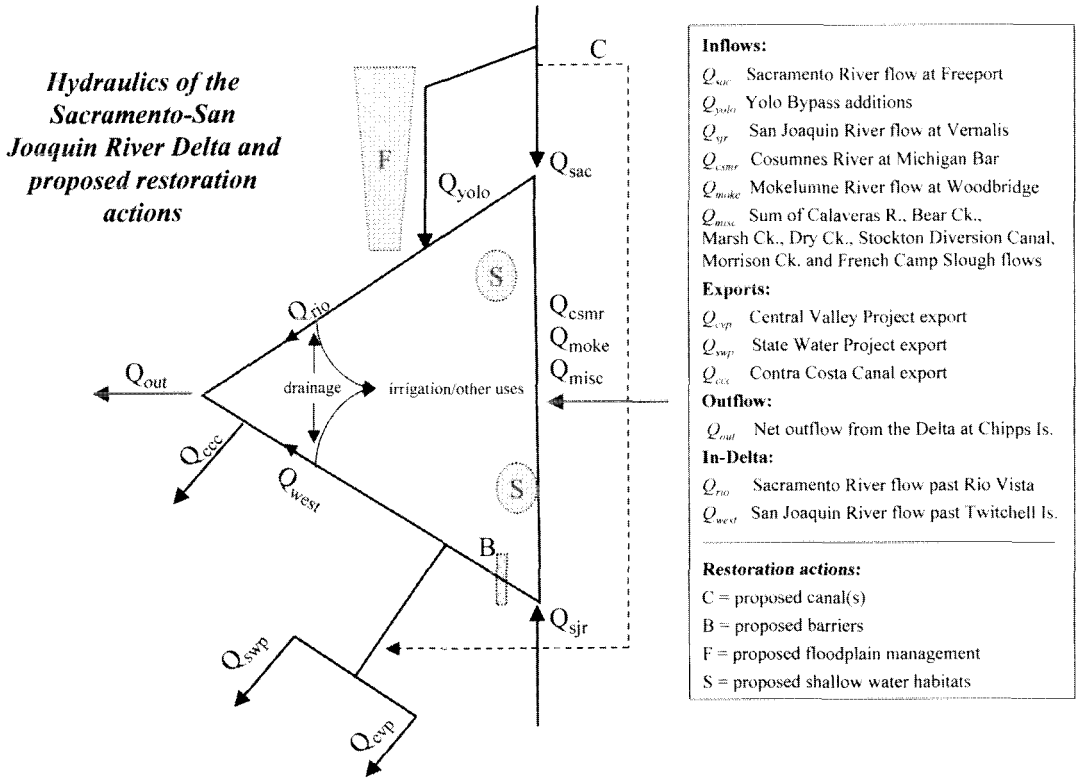

Figure 2. Schematic diagram of main water flows in the Sacramento–San Joaquin Delta (CDWR, 1986).

production of organic matter within the Delta and develop an accounting of the major organic matter sources for the Delta food web. We address four potential actions considered in the ecosystem restoration plan (CALFED, 1998): (1) construction of new canals to facilitate movement of water from the Sacramento River to the pump intakes in the south Delta (see Figure 2); (2) construction of temporary barriers to direct flows away from the pump intakes during periods of juvenile salmon migration; (3) active management of flood plains, such as the Yolo Bypass, to establish seasonal shallow-water habitats for the spawning and rearing of native fishes; and (4) removal of some levees to flood agricultural lands and establish new, permanent shallow-water habitats.

GROSS ORGANIC MATTER SOURCES

Potential sources

In principle, organic matter supplies for estuaries are diverse compared with other aquatic ecosystems. Intertidal habitat, adjacent human activities and the strong influence of rivers all contribute to this diversity. Autochthonous producers include phytoplankton, tidal marsh, seagrasses and other higher aquatic plants, benthic microalgae, and seaweeds. Potential allochthonous sources include inputs by tributaries, agricultural drainage, wastewater treatment plant discharge, urban run-off, atmospheric deposition, fuel spills, bacterial autotrophy using reduced chemical inputs such as ammonium, inputs of dredging spoils, active transport by fish and birds, and groundwater contributions. In practice for any

given estuary, many of these sources are negligible. Some of these can be shown negligible. while others must be assumed so based on qualitative considerations or evidence from other estuaries.

For the Delta primary producers. data exist to consider contributions by (1) phytoplankton. (2) higher aquatic plants and (3) benthic microalgae. Seagrasses and seaweeds are absent. Among the allochthonous sources. data exist to consider (1) tributary contributions, (2) agricultural drainage. (3) tidal marsh export. (4) wastewater treatment plant discharge and (5) urban run-off. Among the remainder, atmospheric deposition, spills. and bacterial autotrophy are certainly negligible based on similar considerations for San Francisco Bay (Jassby *et al.*, 1993). Although dredging is significant for downstreani embayments (Jassby *et ul.*. 1993), all dredging spoils are transported out of the Delta and. if anything. are an organic matter sink (Monroe and Kelly. 1992: table 69). Fish movements also probably represent a sink, although even if all migrating chinook salmon. for example. expired in the Delta, the contribution of organic carbon would be negligible (Jassby *et al.*, 1993). Waterfowl excretion into the Delta is largely a recycling of organic matter and will be ignored. Finally. groundwater inputs are unknown but we assume here that they are small compared with agricultural drainage inputs. Drainage ditches designed to collect surface flow from agricultural tracts will also collect much of the subsurface flow; the latter is therefore included largely in drainage inputs.

Primary producers

Phytoplankton productivity

We reconstructed gross primary productivity using the following relationship:

$$P_g = \left(\frac{4.6\Psi I_0 B}{k}\right)\left(\frac{C}{C_s + C}\right) \quad (1)$$

where P_g is gross primary productivity (mg C m $^{-}$ day^{-1}); I_0 is the surface flux of photosynthetically active radiation (E m $^{-2}$ d^{-1}); B is phytoplankton biomass (mg Chl *a* m^{-3}); k is the attenuation coefficient (m^{-1}); C is conductivity (mS cm^{-1}); and Ψ (mg C [nig Chl *u*]$^{-1}$ [E in^{-2}]$^{-1}$) and C_s (mS cm^{-1}) are constant. The first term is derived from basic theoretical considerations (Platt, 1986) and is known to describe aquatic primary productivity in many light-limited systems (Heip *et al.*, 1995). including San Francisco Bay (Cole and Cloern, 1987). The second term is an empirical one that significantly improves predictions of P_g in the Delta; the exact mechanism is unknown at this time. The constants were estimated, and the model specification verified, using 51 short-term ^{14}C uptake experiments in the Delta. The experiments were conducted for 30 min at nine different stations on 23 different occasions during the period 27 May 13 November 1997 (Brian Cole and Jody Edmonds, USGS, personal communication). In each experiment, the variables of Equation (1) were measured simultaneously. along with other water quality characteristics. The model was estimated using the Gauss–Newton algorithm (Bates and Chambers, 1992).

The estimated value of Ψ is 0.77 ± 0.04 mg C (mg Chl *a*)$^{-1}$ (E m $^{-2}$)$^{-1}$ and the estimate for C_s is 105 ± 23 μS cm^{-1}. Equation (1) describes the 51 experiments with high accuracy: The Pearson correlation between predicted and measured values is 0.98 ($t = 31$, df = 49. p-value < 0.001). This model was therefore used for historical estimates. Further details of this model are beyond the scope of interest here, and will be presented elsewhere.

The water chemistry data used for historical estimates consist of measurements for the period 1968–1995 at 19 stations distributed throughout the upper estuary (Figure 1). Samples were collected and analysed by the US Bureau of Reclamation (USBR) and the California Department of Water Resources (CDWR) using standard methods (CDWR, 1993). The samples were taken approximately monthly, usually from 1 m below the surface during high slack tide. We used solar radiation data collected by the

California Irrigation Management Information System, obtained from the University of California Integrated Pest Management project (UCIPM, 1999). The station closest to the Delta with a daily record spanning the period of interest (1968–1995) is at Davis.

Delta-wide phytoplankton productivity was then estimated by dividing the Delta into regions and averaging water area at mean tidal level (MTL) over the stations within each region. We used essentially the same regionalization as Lehman (1996), but divided the southern region into three smaller regions, based on cluster analysis of the primary productivity data (Table 2). Morphometric data were based on a 25 m grid using the CDWR bathymetry database (CDWR, 1998), with the addition of data from National Oceanographic and Atmospheric Administration (NOAA) surveys in 1990–1992 (N. Monsen, Stanford University, personal communication). These data cover all open water habitats up to MTL but exclude tidal marsh habitat and Clifton Court Forebay, which feeds the export pumps.

Delta-wide phytoplankton productivity could be estimated for most years since 1975 (Figure 3). If data were missing for any station for any month, then a Delta-wide estimate was not made. Delta productivity as a whole appears to lack any long-term pattern. The extreme ENSO periods, 1976–1977 and 1983, do correspond to the highest and lowest productivity periods, respectively, but a decadal-scale trend is absent. Mean seasonal productivity was highest in spring, substantially lower in summer, and lowest in winter and autumn. For those years in which data were available every month, annual Delta-wide production averaged 47 ± 5 t C day^{-1}, or 78 ± 8 g C m^{-2} $year^{-1}$.

Aquatic macrophytes

Estimates for aquatic macrophytes are complicated by the fact that their coverage—the 'effective' habitat area—is in constant flux. Certain species may exhibit complex temporal patterns, with seasonal rise and fall imposed upon longer-term trends. These trends may be positive if the species is a recent invader, or negative if the population is being controlled with herbicides. Further, the limits of distribution at any one time are difficult to assess, as is the population density within these limits. Contributions to primary production are therefore difficult to assess and highly uncertain; only order-of-magnitude estimates are possible.

Two exotic species have proliferated in the Delta during the period of interest, *Eichhornia crassipes* (water hyacinth) and *Egeria densa*. *Eichhornia*, a free-floating macrophyte, reached approximately 200 ha in the early 1980s, when spraying began with 2,4-D (Anderson, 1990). No quantitative distribution data are available, but a record of treated area has been kept since 1983 (P. Thalken, California Department of Water Resources, personal communication). The median area sprayed during 1983–1998 was 302 ha, with first and third quartiles of 152 and 786 ha, respectively. As the treated area includes respraying, it overestimates actual coverage. Floating macrophytes have a high areal productivity. In warm climates, productivity reaches 500–1500 g C m^{-2} $year^{-1}$. Considering that productivity in the Delta is very low

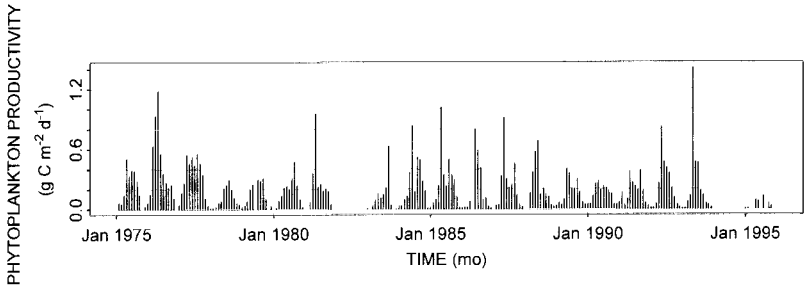

Figure 3. Time series of monthly mean primary productivity for the entire Delta.

during the cold winters, we combined a flux of 600 g C m^{-2} $year^{-1}$ (Westlake. 1963: Sculthorpe. 1985) with the median area sprayed to obtain a representative estimate of primary productivity by *Eichhornia*: 4.9 t C day^{-1}.

Egeria, a submerged macrophyte from Brazil that first appeared in the 1960s. did not reach nuisance levels until the 1990s. The prolonged 1987–1992 drought exposed the weed to additional solar radiation. Its coverage has expanded since then. Based on 1:24000-scale colour infrared aerial photos taken in September 1997. total coverage is estimated at 1830 ha (P. Foschi. California State University at San Francisco. personal communication). Much of the *Egeria* coverage is found at three sites: Franks Tract. Sherman Lake. and Big Break: together they constituted 799 ha or 44% of total coverage in September 1997. We combined a representative productivity of 150 g C m^{-2} year-' (E. Rejmankova. University of California at Davis. personal communication) with the current total coverage as an estimate of maximum primary productivity by *Egeria*: 7.4 t C day^{-1}.

The value for macrophytes is an upper limit and perhaps a large over-estimate, for three reasons. First. the coverage for *Eichhornia* is based on treated area, which includes respraying. Second. the coverage for *Egeria* is based on aerial photographs for September 1997, whereas coverage before the 1990s was negligible. Third. the coverage has a strong seasonality and may be much less during other times of year.

Benthic microalgae

In order to estimate benthic microalgal production and tidal marsh export, we considered the Delta divided into wetland and deepwater habitats based on the 1985 National Wetlands Inventory (Table 1; Meiorin *et al.*, 1991): (1) open water. which includes subtidal estuarine and tidal riverine habitat; (2) intertidal mudflat and rocky shores, which includes intertidal estuarine habitat: (3) tidal salt, brackish and freshwater marsh: and (4) lakes and ponds. In the Delta, open water habitat refers primarily to river

Table I. Habitat areas for aquatic primary producers of the Delta"

Habitat type	Area (ha)	Delta:estuary (%)
Open water (subtidal estuarine and tidal riverine)	18 536	17.2
Intertidal mudflat and rocky shore	130	0.5
Tidal marsh	3328	18.5
Lakes and ponds	5051	42.5[b]

[a] Also shown is the proportion of each habitat category found in the Delta alone. compared with the total for that habitat in the San Francisco Estuary.
[b] Estuary total includes lakes and ponds in San Francisco Bay watershed.

Table 2. Water quality subregions of the Delta and associated sampling stations

Region	Stations
Northern	C3
Lower Sacramento River	D4, D22, D24
Western	D11, D12, D14, D15
San Joaquin River	D16, D19, D26, D28
Eastern	MD10
Southern	
1	P8
2	C9, P10
3	C7, C10, P12

channels. cuts and sloughs. while lake and pond habitat refers primarily to flooded islands. Dominated by diatoms. benthic microalgae are motile cells that emerge from the sediment only when water recedes and light is present (Serôdio *et al.*, 1998). The appropriate habitat is therefore intertidal mudflat. Because of the channelized nature of the Delta. a typical tidal excursion of 1 m results in little change of surface area and so intertidal habitat is small.

We previously compiled primary productivity measurements for benthic microalgae from 28 ecosystems (Jassby *et al.*, 1993). The median value was 110 g C m^{-2} $year^{-1}$, with first and third quartiles of 66 and 180 g C m^{-2} $year^{-1}$, respectively. Benthic microalgal productivity estimates have a large uncertainty and differences among sites cannot be attributed to habitat or climatic differences. Consequently. we used the median value as the characteristic value for benthic microalgae in the Delta. We combined the characteristic productivity value with intertidal habitat area to arrive at an estimate of benthic microalgal contribution: 0.38 t C day^{-1}.

Allochthonous sources

Tributary-borne loading

Monthly mass transports at Delta boundaries were estimated by using monthly mean flow and concentration for the location. The mean flow was based on daily flow estimates from the DAYFLOW database management system (CDWR. 1986). We examined the possibility of using daily concentration estimates as well. by trying to develop a relationship between instantaneous concentration and daily flow: no relationship that explained an adequate amount of the variability could be found, however. We decided. therefore, to use the monthly mean (because at most two measurements were made per month, the monthly mean and median are the same). Sufficient data are not available for estimation of tributary-borne organic carbon contributions. but an excellent record of organic nitrogen data is available. We therefore calculate total organic nitrogen (TON) loads and later convert these to total organic carbon (TOC) based on TOC:TON ratios at the upstream boundary of the Delta. An excellent record also exists for the photosynthetic pigment chlorophyll *a* and its derivative pheophytin *a*. We use the first as an index of phytoplankton biomass. and the second as a conservative index of phytoplankton-derived detritus (phytodetritus). Together. they provide a conservative index of phytoplankton-derived organic matter. By converting them to TOC and TON equivalents using typical values for C:pigment and N:pigment ratios, the contribution of river-borne phytoplankton to organic matter loading can be estimated. Macrophyte and other pigment sources are a potential interference. but no identifiable macrophyte remains can be seen in microscopic samples. and chlorophyll *a* tends to track phytoplankton biovolume (P. Lehman. CDWR. personal communication).

Monthly mean mass transport of TON and phytoplankton-derived pigments were estimated at three different boundaries in the upper estuary: (1) total influx into the Delta: (2) export from the Delta to local. county, state, and federal water systems; and (3) outflow across an approximately north–~0~1th boundary in the Delta passing through the stations at Rio Vista and Twitchell Island (Figure 1, stations D24 and D16). The low salinity zone west of this boundary is the most important larval nursery in the estuary and delivery of organic matter across this boundary from upstream is therefore highly significant. We estimated the general magnitude of dispersive transport at D24 and D16 in order to compare with advective transport. Channel cross-sections were taken from the CDWR Delta Simulation Model (CDWR. 1998) and a characteristic mixing coefficient of 100 m^2 s^{-1} was used (Fischer *et al.*, 1979).

Influx (g s^{-1}) was calculated as follows:

$$\text{influx} = (Q_{\text{sac}} + Q_{\text{yolo}})C_{\text{C3}} + Q_{\text{sjr}}C_{\text{C10}} + (Q_{\text{cosmr}} + Q_{\text{moke}} + Q_{\text{misc}})C_{\text{MD10}} \quad (2)$$

where Q_{sac}, Q_{yolo}, Q_{esmr}, Q_{moke}, and Q_{misc} ($m^3\ s^{-1}$) are monthly mean flow rates for the corresponding DAYFLOW variables (Figure 2) and C_{C3}, C_{C10}, and C_{MD10} ($g\ m^{-3}$) are monthly mean concentrations at the corresponding CDWR stations (Figure 1). Station C3 is on the Sacramento River at Greene's Landing and C10 on the San Joaquin River at Vernalis. Equation (2) implicitly assumes that the quality of water entering the Yolo Bypass is similar to that at Greene's Landing.

Export ($g\ s^{-1}$) into the state and federal water projects. as well as into the local Contra Costa Canal. was calculated as follows:

$$\text{export} = Q_{ccc}C_{D28A} + Q_{swp}C_{C9} + \begin{cases} Q_{cvp}C_{P12} & Q_{sjr} \geq Q_{cvp} \\ Q_{sjr}C_{P12} + (Q_{cvp} - Q_{sjr})C_{C9} & Q_{sjr} < Q_{cvp} \end{cases} \quad (3)$$

The last term describes how more northerly channels are used to supplement the San Joaquin River when flow in the latter is unable to meet the demands of the CVP. Beginning in 1988, a temporary rock barrier was constructed each autumn at the head of Old River channel to divert fish away from the water projects. In some years (1992 and 1994). the barrier was in place in spring as well. The effect of this barrier is to replace some unknown fraction of the water coming directly from the San Joaquin River with water from the northerly channels. In order to assess the effects on mass balances. we made calculations for two extreme conditions: first. the rock barrier formed a perfect seal: and second, the rock barrier had no effect on channel flow.

Outflow ($g\ s^{-1}$) downstream was estimated as follows:

$$\text{outflow} = Q_{rio}C_{D24} + Q_{west}C_{D16} \quad (4)$$

Three main channels join the San Joaquin River downstrearn of station D16 (Figure I). One of these—-Three-Mile Slough– may transport water from the Sacramento River, but its contribution to *outflow* is already accounted for in the first addend of Equation (4). Flows for the other two tributaries False River and Dutch Slough are implicitly included in Q_{west}: the latter is calculated by a water balance and represents all upstream inflows (other than the Sacramento River) corrected for exports and net within-Delta hydrological exchanges (CDWR, 1986).

Efflux ($g\ s^{-1}$) will be used to denote the following sum:

$$\text{efflux} = \text{export} + \text{outflow} \quad (5)$$

Mass loading rates of TON and chlorophyll *a* for the Delta are plotted in Figure 4. No decadal-scale trends are apparent for TON. In the case of chlorophyll *a*. the generally lower values in the second half of the record correspond to the prolonged drought of 1987–1992. Interannual variability also appears to reflect climatic fluctuations, such as the dry ENSO years of 1976–1977 and the wet ENSO year of 1983. The dependence on river inflow can be seen when seasonal averages are plotted against river inflow (Figure 5): higher loading usually occurs at higher inflows. An estimate can also be made of the proportion of TON loading contributed by phytoplankton and phytoplankton-derived detritus (indexed by chlorophyll *a* + pheophytin *a*). Assuming a C:pigment mass ratio of 40 for both chlorophyll and pheophytin. and a C:N (Redfield) mass ratio of 5.7. results in an N:pigment mass ratio of 7.0. On a quarterly basis. then. the phytoplankton-derived N to TON ratio was 18% + 1%. i.e. about 18% on average of the TON entering the Delta was in the form of phytoplankton and phytoplankton-derived detritus. The maximum value of 85% occurred in spring of 1977 when chlorophyll *a* was extremely high in the San Joaquin River.

Mass loading rates of TON and chlorophyll *a* for the Bay and Delta west of Rio Vista and Twitchell Island are plotted in Figure 6. Hydrological impacts are evident. with low values during the 1976–1977 dry ENSO year and the more recent 1987–1992 drought, and high during the 1983 wet ENSO year. Flow patterns in the Delta are controlled primarily by river inflow and by export flow. The dependence of TON

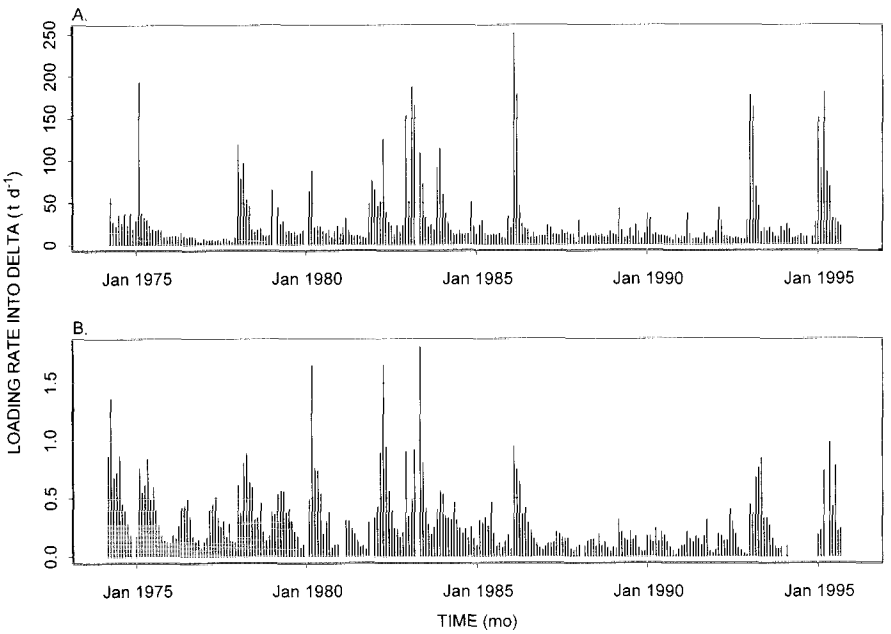

Figure 4. Time series of monthly mean loading rate into Delta for (A) TON and (B) chlorophyll *a*.

loading on these flows can be illustrated with partial residual plots (Figure 7). In the first column, residuals for each variable (TON loading and river inflow) are plotted against each other, after first regressing each variable on export flow. Similarly, in the second column, the variables (TON loading and export flow) have first been regressed on river inflow. Partial residual plots show the individual effects of explanatory variables, by first removing the effects of other explanatory variables. For TON, inflow is important in all seasons, and export in all seasons except winter (Table 3). On a quarterly basis, the phytoplankton-derived N to TON loading ratio was 13% ± 1%. The maximum value of 42% occurred in spring of 1976.

The magnitude of dispersive flux was small at Rio Vista and Twitchell Island compared with advective transport. For TON, the median ratios of dispersion to advection were 0.043 and 0.081, respectively, at the two locations. For chlorophyll *a*, the median ratios were 0.071 and 0.095, respectively. Higher values occur at lower flows (low advection), and therefore have even less effect on mass balances than suggested by the medians. Nonetheless, the estimates are not negligible, especially considering the uncertainty.

Agricultural drainage

Approximately 260 pump stations are situated among 60 Delta islands and farming tracts below sea level. These pumps discharge a mixture of seepage, run-off and irrigation return water into adjacent channels. Because the Delta was once a vast *Scirpus* marsh, the soil — and consequently the drainage water — is rich in organic matter. Estimates are available for monthly average drainage volumes during 1976–1991, and monthly average dissolved organic carbon (DOC) concentrations based on data from 1982 to 1997 (Jung and Tran, 1999). Almost all TOC in drainage water is in the form of DOC. These data can therefore be used to compute monthly average DOC loads to Delta waterways. On a quarterly basis beginning with the winter season, the resulting mass loads of organic carbon are 71, 27, 26 and 23 t C day^{-1}, and average of 36 t C day^{-1} for the year.

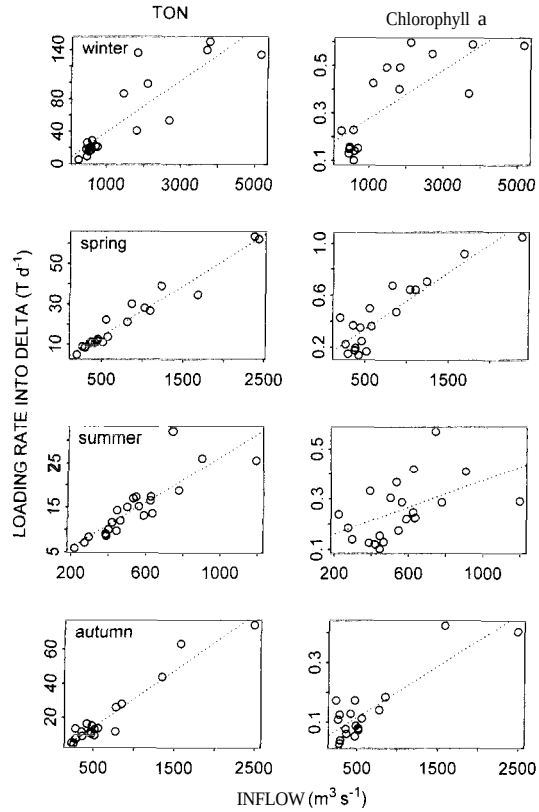

Figure 5. Plots of loading rate into Delta for TON and chlorophyll *a* versus total river inflow. by season. Dotted line. linear regression fit ($p < 0.05$).

Tidal marsh export

For the purposes of our assessment here, vegetated tidal marsh was considered external to the system boundaries. We are therefore concerned not with productivity of the tidal marsh vegetation but with its export of organic matter to adjacent waterways. No comprehensive field measurements of tidal marsh export to adjacent water have been made in the Delta and we therefore turn to results from other estuaries. In a previous study, we compiled data from 10 relevant studies of tidal marsh export (Jassby *et al.*, 1993). The median value was 150 g C m year '. We used this median value for export and National Wetland Inventory (NWI) data for tidal marsh habitat in the Delta (Table 1) to arrive at an estimate for tidal marsh loading: 14 t C day '.

This estimate is perhaps the most uncertain for several reasons. First. the variability in the 10 studies is high. as illustrated by first and third quartiles of 100 and 410 g C m year ', respectively. Second. the channel banks are lined in places with riparian vegetation, above the high tide level but producing litter fall in the waterways and also contributing to TOC run-off. Finally, many tidal channels are bounded by a thin line of marsh (mostly tule and cattail) that is difficult to map from aerial photographs of the scale used by NWI. A 2-m border of marsh lining all the waterways of the Delta is an order-of-magnitude less in area than the NWI tidal marsh habitat. Nonetheless. the export flux from this marginal marsh might be much higher than the median value found in other studies. Studies in the Delta show that essentially no water returns on the ebb tide from the interior reaches of the broad marshlands; only the marginal few metres readily exchange with the channels (Josh Collins, San Francisco Estuary

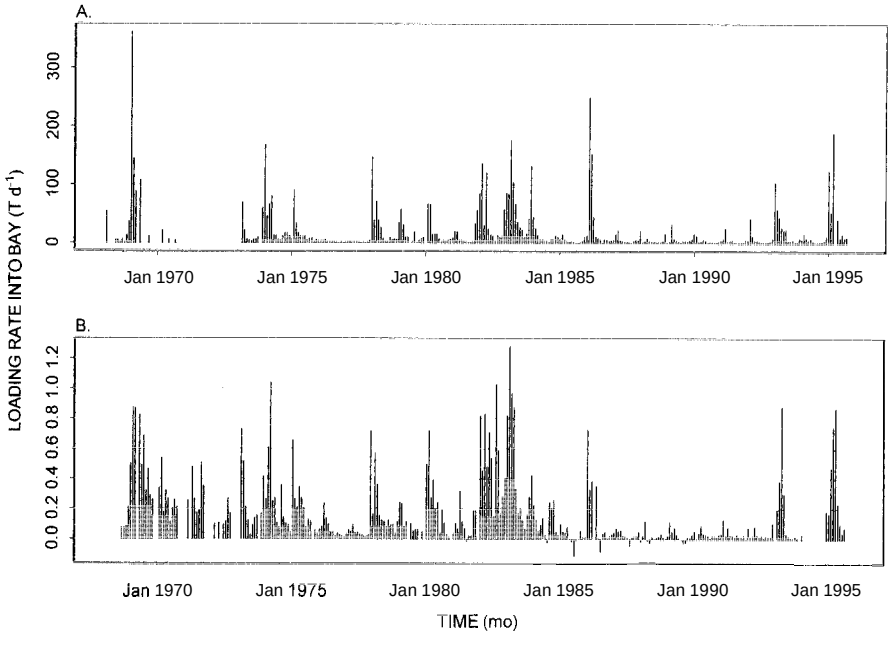

Figure 6. Time series of monthly mean loading rate into Bay for (A) *TON* and *(B)* chlorophyll *a*

Institute, personal communication). The larger channels have very broad natural levees that increase trapping of water on the marsh surface. Furthermore, water percolates rapidly into the peat soils away from the channels or is lost due to high evapotranspiration rates. The marsh interiors may actually be net sinks for organic solutes. The median value of 150 g C m^{-2} $year^{-1}$ may therefore be due to a much higher export flux on the margins, and a much lower or even negative export flux in the interiors of these marshes. As a result, we cannot rule out that these marginal areas are exporting organic matter out of proportion to their area.

Wastewater discharge

The main sewage wastewater contribution to the Delta is the Sacramento Regional Wastewater Treatment plant, although there are many other smaller sources. Baseline flow amounts to 9.52 m^3 s^{-1} total for plants discharging to the Delta (from data of Montoya *et al.*, 1988). An average value of 12.3 mg L^{-1} for the 5-day biochemical oxygen demand (BOD,) was found in a comprehensive assessment of wastewater final effluent discharge to San Francisco Bay (CRWQCB-SFBHK, 1987). Comprehensive TOC data were not available, but TOC is typically similar in magnitude to BOD, in sewage treatment plant effluent. A September 1991–August 1993 study of discharge from the Sacramento Treatment Plant resulted in mean TOC levels of 15 mg L^{-1} TOC (10.8 S.E., $n = 48$), compatible with the more comprehensive data from San Francisco Bay. These two values–flow and concentration were combined to obtain an estimate of organic matter loading in treatment plant discharge: 12 t C day^{-1}.

The Delta is also heavily used by recreational visitors, who produce an unknown amount of sewage waste discharged directly into Delta waterways. If each of the 12 million user-days per year resulted in the discharge of 1 kg excreta into the Delta, the total would amount to only 1.6 t C day^{-1}, affecting our estimate of wastewater sources only slightly.

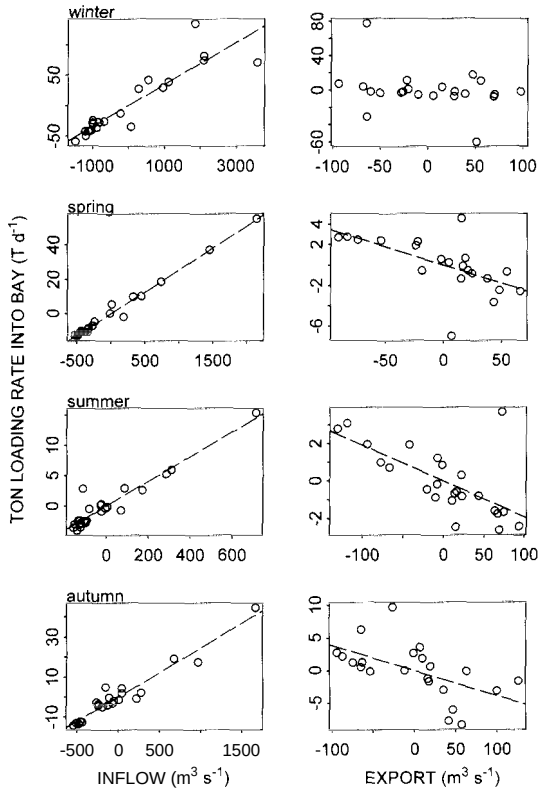

Figure 7. Partial residual plots of TON loading rate into Bay versus total river inflow and total water export, by season. Dotted line. linear regression fit ($p < 0.05$).

Table 3. Coefficients (±S.E.) for total tributary inflow and export flow in the multiple linear regression relating TON outflow into the Bay (t day^{-1}) and these two quantities (m^3 s^{-1})[a]

	Tributary inflow	Export flow	R^2
Winter	0.035 + 0.004	−0.11 + 0.09	0.83
Spring	0.025 ± 0.001	−0.036 ± 0.011	0.99
Summer	0.020 ± 0 001	−0.019 ± 0.005	0.90
Autumn	0.024 ± 0.002	−0.039 ± 0.013	0.94

[a] All coefficients except for export flow in winter are significant at the $p = 0.01$ level. at least

Urban run-off

The loading from urban run-off must be assessed through indirect methods. by combining typical TOC concentrations in run-off with volumetric run-off estimates based on urbanized area. precipitation. and a characteristic run-off coefficient. A TOC concentration characteristic of the region was used (8 mg L^{-1}; Silverman *et al.*, 1985: Smith. 1989). City-specific area and rainfall were obtained from a mass loading assessment of pollutant discharge (Montoya *et al.*. 1988). We used a run-off coefficient of 0.3. The resulting estimate is 2.2 t C day^{-1}.

Summary of sources

Organic matter sources are summarized in Table 4. Riverine loading was expressed in terms of carbon, using the mean C:N mass ratio of 12 ± 2 (S.D.) for the upstream boundary of the Delta obtained in our current study. Comparisons are possible only on an annual basis for most of these sources. Tributary-borne loading is the largest source overall, on this average annual Delta-wide basis. Phytoplankton production and agricultural drainage are secondary sources. Wastewater treatment plant discharge, marsh export and possibly aquatic macrophyte production are tertiary sources. Benthic microalgal production, urban run-off and other sources not explicitly mentioned are negligible. Phytoplankton is clearly the dominant primary producer on a Delta-wide basis, whereas tributary-borne loading is dominant among the allochthonous sources. The ratio of combined primary production to allochthonous sources is only *ca* 0.2. It is important to note that these are sources for benthic habitat and water column combined. An accounting for the water column alone would have to isolate the supply of DOC from the sediments, which can be a significant source for bacterioplankton production (Hopkinson *et al.*, 1998).

For most of the organic matter supply, sufficient data exist to compare based on season and water year classification. A water year extends from 1 October of the previous calendar year to 30 September. Water years in the Sacramento River Basin are classified based on annual stream flow data into (1) wet, (2) above-normal, (3) below-normal, (4) dry, and (5) critical (SWRCB, 1991). We combined (1) and (2) into a category referred to as 'above normal' and (3) to (5) into a category referred to as 'below normal'. For each category, we compared phytoplankton productivity and tributary-borne load, only for those years in which complete data are available for each of these sources. Agricultural drainage is also included, although we have had to assume that the amount is independent of year (Table 5). Phytoplankton production, tributary-borne loading and agricultural drainage together account for 90% of total sources. In above normal years, tributary-borne loading is always dominant. Although phytoplankton productivity is small compared with agricultural drainage in winter, it is similar in autumn and much greater during spring and summer. In the spring of below normal years, phytoplankton productivity increases because of higher hydraulic residence time and the resulting accumulation of phytoplankton biomass. Tributary-borne loading, in contrast, decreases because of lower inflows. Consequently, the two sources are similar in magnitude. Even in the summer of below-normal years, they differ by only a factor of two. The relative importance of sources is therefore clearly dependent on season and on the prevailing climate conditions.

Table 4. Annual average organic carbon sources for the Delta[a]

	TOC (t day^{-1})
Primary producers	
Phytoplankton	47 ± 5 ($n = 9$)
Macrophytes	< 12
Benthic microalgae	0.38
Allochthonous	
Tributary-borne load	270 ± 50 ($n = 16$)
Agricultural drainage	36
Tidal marsh export	14
Wastewater discharge	12
Urban run-off	2.2

[a] Phytoplankton production and riverine load ($\pm$S.E.) are for the n years in which data are available every month. All values are rounded to two significant digits.

Table 5. Major organic carbon sources for the Delta (t C day^{-1}, ± S.E. among years) on the basis of season and water year type (1968–1995)[a]

	Phytoplankton GPP	Tributary load	Agricultural drainage	Number of years
Above normal:				
Autumn	26 ± 7	140 ± 40	23	3
Winter	5.7 ± 2.0	1300 ± 290	70	4
Spring	75 ± 21	310 ± 50	27	5
Summer	69 ± 4	200 ± 19	26	7
Below normal:				
Autumn	19 ± 3	150 ± 32	23	7
Winter	22 ± 7	230 ± 39	70	7
Spring	100 ± 13	120 ± 8	27	10
Summer	62 ± 6	130 ± 14	26	10

[a] The number of years for which data are available to compare phytoplankton and tributary contributions is also shown. Data are not sufficient to describe agricultural drainage contributions on the basis of water year type. Two significant digits are shown.

Many of these sources are also distributed in a spatially heterogeneous manner. This diversity and heterogeneity implies that the relative importance of sources will change as we move from one Delta subregion to another. *Egeria*, for example, covered 35% of Franks Tract in September 1997. If we assume this level of coverage for the year and apply our phytoplankton productivity estimates for station D19 in Franks Tract to the remaining area, then annual *Egeria* and phytoplankton production are within 10% of each other. Similarly, much of the remaining tidal marsh habitat in the Delta is found in the western portion, and so tidal marsh export is bound to be more important in this region. In the San Joaquin River near Vernalis (C10), large phytoplankton blooms occur, sometimes reaching chlorophyll *a* concentrations of over 50 μg L^{-1}. Phytoplankton production is most likely the dominant organic matter source in this part of the Delta during spring and summer.

Finally, these sources differ in their availability to the food web, and a further refinement is necessary before they can be directly compared as food sources.

NET ORGANIC MATTER SOURCES

Primary food resources and the food web

The preceding analysis described sources of organic carbon to the Delta, irrespective of their value to the food web. The issue of food value is a multi-dimensional one, involving chemical composition; particle size and shape; organism needs; and other factors. One of the fundamentally important differences among components of the organic matter supply, however, is whether they are dissolved or particulate, as defined operationally by the ability to pass through a filter of specified pore size (usually on the order of 0.1–1 μm). To examine this in more detail, consider a simplified model of organic matter pools and flows in the Delta (Figure 8). The metazoan food web comprises all multicellular organisms, including those of most concern to the public – fish, waterfowl, large crustaceans and molluscs – as well as the smaller organisms that they feed on, such as crustacean zooplankton in the water column and nematodes in the sediments. It also includes larger detrital particles, such as faeces and vascular plant remains, and their attached microbial communities. This metazoan food web is supplied by three main sources in the Delta: vascular plants (mostly *Egeria densa* and *Eichhornia crassipes*), algae (mostly phytoplankton), and a

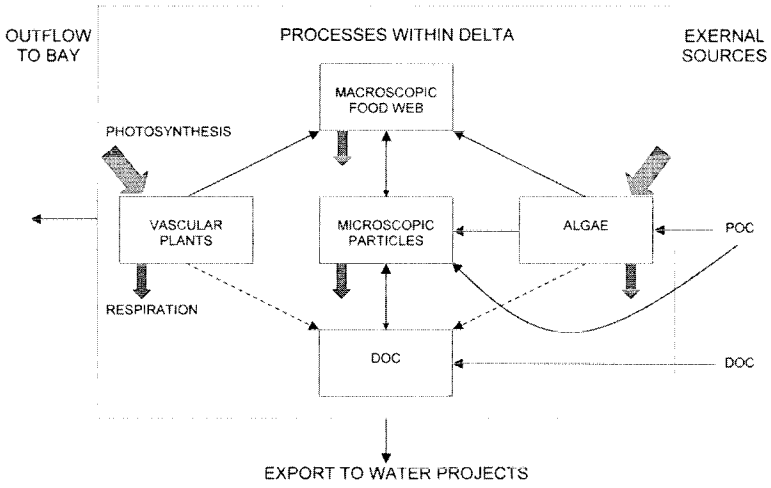

Figure 8. A simplified model of organic carbon pools and flows in the Sacramento–San Joaquin Delta. The thick grey lines represent exchange with the CO_2 pool through photosynthesis or respiration. The dashed lines represent flows of secondary significance.

category called 'microscopic particles'. This latter category consists of free-living unicellular heterotrophs bacteria, ciliates and flagellates—as well as microscopic detrital particles with or without attached microorganisms. Finally, there is a DOC pool. The photosynthetic organisms—vascular plants and algae—leak significant fractions of photosynthetic products into the DOC pool. In addition, the smaller phytoplankton may first be consumed in the microbial loop. Nonetheless, most of their primary production is expected to flow to the metazoan food web, including detritivores in the case of vascular plants, and crustacean zooplankton or benthic suspension-feeders in the case of phytoplankton. The DOC pool can supply the microscopic particle pool through adsorption and flocculation, but assimilation by heterotrophs is considered the major route. A smaller amount is shown flowing back to the DOC pools from particle dissolution and leakage from microheterotrophs. In principle, flows also exist directly connecting the DOC pool and the metazoan food web, although these are probably small compared with the flows explicitly shown.

Particulate organic carbon (POC) enters the Delta from allochthonous sources mostly as phytoplankton and phytoplankton-derived detritus, other microscopic detrital particles, microheterotrophs, and suspended mineral particles with adsorbed organic matter. It is not clear how much the latter form of POC participates in the food web. The remaining POC input immediately becomes part of the microscopic particle or microalgae pool; it should be just as available to the metazoan food web as particulate primary production. In contrast, allochthonous DOC must go through an additional step before it becomes available to the metazoan food web. Conversion to POC does not guarantee incorporation into the metazoan food web, but at least it places DOC input on a par with microscopic food particles. It is essential to consider the losses during this step (see 'Availability of Allochthonous Dissolved Organic Matter'), because most of the allochthonous organic matter enters in dissolved form. Then we can more accurately compare allochthonous sources and primary production in terms of food value.

Net phytoplankton productivity

Because our phytoplankton productivity estimates are based on incubations of 30 min, they probably represent gross rather than net productivity. If we are going to correct DOC inputs for losses during

conversion to particulate form, then we must also correct gross productivity for losses to phytoplankton respiration. We estimated phytoplankton respiration at any location as the sum of a basal biomass-dependent rate (1.5%) and a photosynthesis-dependent rate (15%):

$$R = 0.015BH(C{:}Chl) + 0.15P_g \quad (6)$$

where R is respiration rate (mg C ni ' day^{-1}), B is phytoplankton biomass (mg Chl a m^{-3}); H is water column depth (m), and C:Chl is the C:chlorophyll a ratio of 35 (Cloern *et al.*, 1995). As in the case of P_g, R was estimated for each of the eight subregions monthly and summed for the entire Delta. Net phytoplankton productivity P_n (mg C ni ' day^{-1}) was then estimated by $P_n = P_g - R$. Averaged over all months. respiration amounted to 23% of gross productivity, similar to the results for San Francisco Bay (Jassby *et al.*, 1993).

Availability of allochthonous dissolved organic matter

As pointed out above, most of the allochthonous organic matter is in dissolved form and must be converted to particulate form before it can enter the food web. Utilization by niacroheterotrophs, adsorption to clay particles. and formation of particulate matter from high molecular weight dissolved organic matter (DOM) in salinity gradients (Alberts and Griffin. 1996) may account for some conversion to particulate organic matter (POM). According to current notions. however. most DOM conversion will take place through consumption by bacteria, heterotrophic nanoflagellates and ciliates. and possibly facultative heterotrophic algae. In the process of conversion, a certain fraction will be flushed from the Delta before it can be metabolized. Moreover. even the metabolized material will be converted to particulate form with respiratory losses. depending on its chemical composition and the growth efficiency of microconsumers. The microbial food web may be mostly a respiratory sink for many DOM sources (Ducklow *et al.*, 1986). The contribution of TOC loading to particulate food resources can be expressed as:

$$TOC_p = [\lambda \cdot \varepsilon \cdot f + (1 - f)] \cdot TOC \quad (7)$$

where TOC_p is the TOC loading that ends up in particulate form (t C day^{-1}); λ is the proportion of DOC loading metabolized in the estuary: ε is the proportion of metabolized DOC that ends up as heterotroph biomass; f is the ratio of DOC to TOC loading: and TOC is TOC loading (t C day^{-1}).

First, uhat proportion of DOC ***(i)***s actually metabolized in the estuary? DOC represents a spectrum of organic matter compounds that are metabolized at different rates. The rates depend on the compounds themselves. as well as on the organisms present, physical conditions. and the concentrations of inorganic nutrients. Here. we are not interested in a detailed model of these transformations. only an estimate of their result. This result is sometimes expressed as the proportion of the DOC that is 'labile' and can be decomposed or metabolized. In principle, however. this proportion is time-dependent: what is labile in one system may be refractory in another, depending on the time spent by the material in the system. An appropriate time scale for the Delta is the median residence time, *ca* 25 days. Søndergaard and Middelboe (1995) compiled a database of labile DOC measurements. based on bacterial decomposition of DOC over a time span of one to a few weeks. They found that the proportion of labile DOC was closely related to total DOC. with a mean ($\pm$ S.D.) of 0.14 $\pm$ 0.08 for lakes ($n = 27$) and 0.19 $\pm$ 0.16 for rivers ($n = 16$). The median values were 0.12 and 0.25, respectively. We used a characteristic value of 0.20 for our calculations here.

Second. what proportion of the metabolized DOC (ε) will end up as heterotroph biomass? Bacterial growth efficiency the fraction converted to biomass—is quite varied for aquatic DOC. Based on data compiled from many systems, del Giorgio and Cole (1998) found that the range of the middle 50% of the data was about 0.05–0.32 in rivers and 0.20–0.37 in lakes. with medians of 0.22 and 0.26. respectively.

we used a value of 0.25. the approximate median for lakes and rivers. del Giorgio and Cole (1998) also developed a plot of growth efficiency versus net primary production by combining their results with a related synthesis by Ducklow and Carlson (1992). For the Delta's net primary production rate (60 g m^{-2} $year^{-1}$, or 29 μg L^{-1} day^{-1}), the implied bacterial growth efficiency is only about 0.05-0.10. Our choice of 0.25 may therefore overestimate production of lieterotroph biomass.

Finally, what proportion of TOC loading (f') is in the form of DOC? The tno major loading sources are tributaries and agricultural drainage. For river-borne loading, we used the average from our current study for the Sacramento and San Joaquin rivers near the upstream boundaries of the Delta: $f = 0.67 \pm 0.06$ (S.D.). Agricultural drainage derives primarily from subsurface flow and contains little particulate matter apart from what is picked up in drainage ditches. We used $J' = 0.9$ for agricultural drainage.

Although there are many obvious uncertainties in the estimates of λ and ε above, the estimate for TOC_p depends primarily on f, in which we have the most confidence. For example. the range of TOC_p is only 0.33–0.46 of tributary-borne TOC loading when we vary λ and ε simultaneously by +100%. Conclusions can therefore be drawn that depend only on the general magnitude of our results. Most importantly. except for above-normal hinters. phytoplankton productivity is a significant source in all seasons (Table 6) Moreover, phytoplankton productivity is comparable with and sometimes greater than tributary-borne loading in spring and summer of both above-normal and below-normal water years. Spring and summer are particularly critical seasons for larval development and recruitment success. In contrast, agricultural drainage is almost never significant.

Relative role of allochthonous POM

The above considerations imply that tributary-borne DOM contributes little to the available supply. From the viewpoint of primary food sources. the main function of the tributaries is to deliver POM. What is the value of this allochthonous POM as food for primary consumers? In particular, how does it compare with the food value of phytoplankton produced in the Delta?

First, consider the phytoplankton contribution to this POM load, which we estimated from loading of chlorophyll *a* and pheophytin *a* by converting them to phytoplankton-derived N, assuming a characteristic N:pigment ratio of 7.0. Phytoplankton-derived N is relatively highest in spring. when it averages 27 ± 3% (S.E.) of river TON loading. Values increase markedly only with the lowest flows.

Table 6. 'Net' organic carbon sources for the Delta's food web (t C day^{-1}, ± S.E. among years)[a]

	Phytoplankton NPP	Tributary load	Agricultural drainage
Above normal			
Autumn	20	51	3.3
Winter	3.9	460	10
Spring	58	110	3.9
Summer	54	74	3.8
Below normal			
Autumn	14	53	3.3
Winter	17	82	10
Spring	81	44	3.9
Summer	50	48	3.8

[a] Similar to Table 5. except (1) phytoplankton productivity has been corrected for respiration, and (2) tributary load and agricultural drainage have been corrected for refractor) DOC and losses of labile DOC during conversion to heterotroph biomass.

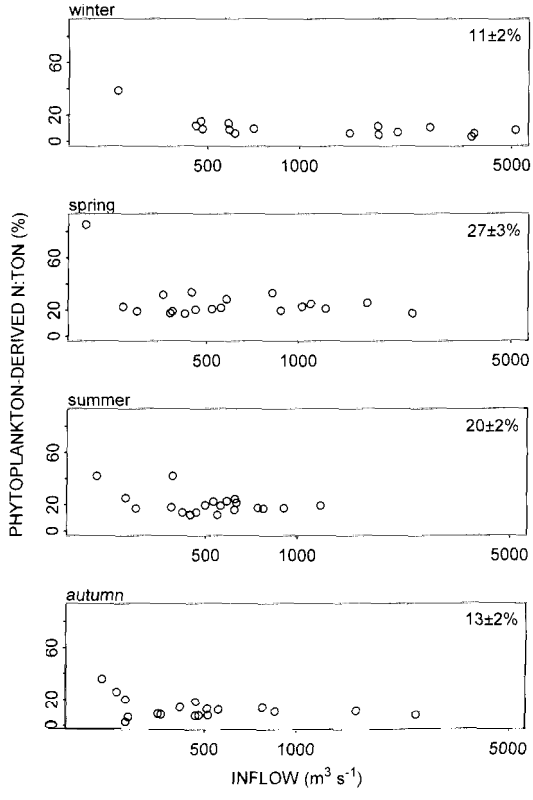

Figure 9. Phytoplankton-derived N loading relative to TON loading. as a function of season and river inflow. Inset values are seasonal means (± S.E. among years).

reaching over 80% in the extreme dry ENSO event of 1977 (Figure 9). How does the supply rate of allochthonous material derived from phytoplankton compare with autochthonous primary productivity? In general. allochthonous contributions are less than autochthonous production rates. but are occasionally greater in spring and frequently greater in winter (Figure 10). The relative contributions are highly dependent on flow; higher flows increase allochthonous contributions but have less effect on Delta-wide productivity. In summary, then. a large fraction of POM loading appears to be phytoplankton and phytoplankton-derived detritus. and it constitutes an important fraction of total phytoplankton-derived materials supplied to the Delta food web (*cf.* Jassby and Powell. 1994).

Some of the remaining portion of the POM load is composed of nonliving organic detritus along with bacteria and other heterotrophs. In a classic study. Darnell (1961) demonstrated the wide occurrence of organic detritus in the gut of lower-level consumers. Detrital particles are important secondary food sources for estuarine mesozooplankton (Heinle and Flemer. 1975). and free-living bacteria for estuarine microzooplankton (Lessard and Swift, 1985; Sherr *et al.*. 1986). Generally. though, the food value of detritus and bacteria is not as high as phytoplankton. The trophic role of phytoplankton is often much higher than its relative role in the organic matter supply. such as in many floodplain lakes that have an enormous biomass of macrophytes (Bunn and Boon. 1993: Forsberg rt *al.*, 1993). Highly unsaturated fatty acids (HUFAs) rather than organic carbon or energy *per se* often limit primary consumers (Brett and Müller-Navarra, 1997). HUFAs are most concentrated in phytoplankton. especially cryptophytes and diatoms; the latter are usually dominant in the Delta. The food value of detritus is therefore enhanced when supplied in combination with phytoplankton (Roman, 1984). which contains higher amounts of

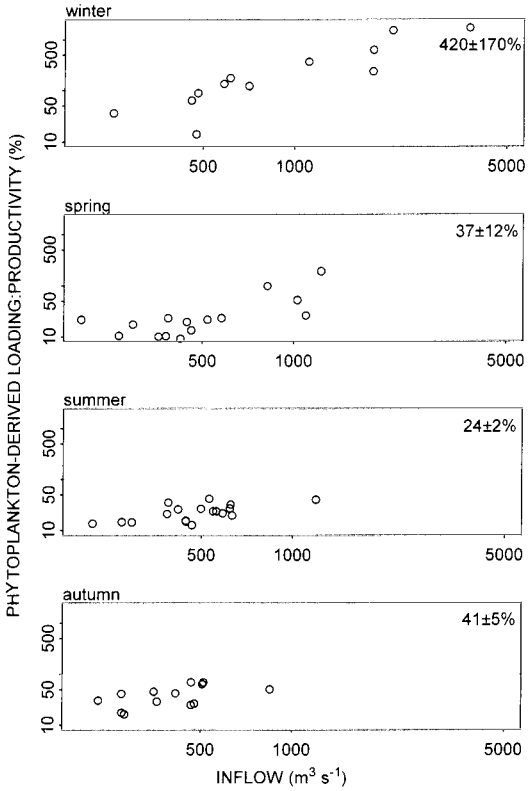

Figure 10. Phytoplankton-derived POC loading into the Delta relative to phytoplankton productivity within the Delta, as a function of season and river inflow. Inset values: seasonal means (± S.E. among years); line, 100%.

essential fatty acids and other substances. The chemical composition of algal-derived materials may therefore determine not only their own food value but also the extent to which the detrital load can be utilized to support the food web.

A final portion of the POM load is organic matter adsorbed to suspended mineral particles. Although a large portion of the load may be in this form at times (Schemel *et al.*, 1996), its value for the food web remains unknown and is a major gap in our understanding of organic matter supply.

How does the 'capture' of POM loading by the Delta compare with DOM loading? In contrast to DOM, much of the POM loading may be consumed within the Delta. Effective hydraulic residence time ranged from 2 to 107 days on an average monthly basis over the time period of interest, with a median of 25 days. If the turnover time of the water column by filter feeders is lower than this value, then a large fraction of the POM should enter the food web of the Delta. Although we do not have estimates of these turnover times for the Delta, turnover times of 1 day due to benthic macroinvertebrates alone are common downstream (Alpine and Cloern, 1992). Evidence from other systems also supports the notion that much of the phytoplankton-derived POM is consumed within the Delta. A study by Admiraal *et al.* (1993), for example, indicated that almost all phytoplankton were utilized in the Rhine delta despite a 2–4-day residence time.

THE DELTA AS A TRANSITION ZONE

Suisun Bay and the western Delta downstream of our boundary at Rio Vista–Twitchell is the site of an important larval fish nursery. The estuarine turbidity maximum with its unique biological characteristics and elevated POC is found in this downstream region. The Delta can be viewed as a kind of transformer. either attenuating or enhancing the mass loading from tributaries before discharging into this region and ultimately San Francisco Bay. This role is a significant one historically, and any changes in it due to restoration activities are of great interest. What net effect does the Delta have on delivery of this material? We examine this question by comparing mass loading ratios for TON in wet versus critically dry water years. The minimum flow for a wet year is approximately double the maximum flow in a critically dry year. The wet and critically dry years were chosen for comparison because they are the most extreme categories and because the necessary data are available.

Table 7 demonstrates that. on the upstream side. the Sacramento River contributed most TON loading. Nonetheless. the San Joaquin River contributed 20–42% of the total on a seasonal basis. much higher than expected based on flow. The San Joaquin receives relatively more agricultural drainage and has higher temperatures and a longer residence time than the Sacramento, and chlorophyll *a* levels are often much higher. The Sacramento was relatively more important than the San Joaquin as a source of TON mass loading in critical versus wet years, especially during winter–summer. This reflects the relatively higher impact that drought has had on the San Joaquin flow. In wet years. the efflux of TON the total leaving the Delta either for the Bay or for export is approximately the same on average as the influx, except for an elevation in winter. The higher winter value may reflect much higher run-off from agricultural and urban lands within the Delta. Critical years have a much stronger seasonality, with elevated efflux in autumn–spring and a distinctly depressed efflux in summer. The elevation is due to the high residence time in critical years, which allows phytoplankton populations to increase sufficiently to affect TON levels. The summer decrease is probably due to temperature-controlled decomposition processes that respond to the high water temperatures of summer, combined with an increase in Delta channel depletions for irrigation. The main difference of note between year types. however. is the proportion flowing downstream—i.e. the outflow:efflux ratio in wet versus critical years. In critical years. the proportion of the efflux flowing out into the ecologically important area just downstream of the Delta drops by almost half. Only 24–47% of the TON, depending on the season. flows downstream into the Bay; the remaining 53–76% is exported from the Bay–Delta for use elsewhere.

Table 7. Mass loading ratios (±S.E. among years) for TON in wet[a] and critically dry[b] years, for water gears in which necessary data are available every month

	Autumn	Winter	Spring	Summer
Wet years				
Sacramento:total influx	0.56 ± 0.04	0.57 ± 0.04	0.41 ± 0.03	0.55 ± 0.04
San Joaquin:total influx	0.30 ± 0.04	0.20 ± 0.04	0.42 ± 0.04	0.37 ± 0.03
Efflux:influx	0.88 ± 0.19	1.14 ± 0.21	0.97 ± 0.08	1.03 ± 0.08
Outflow:efflux	0.60 ± 0.10	0.88 ± 0.03	0.68 ± 0.12	0.36 ± 0.07
Critically dry years				
Sacramento:total influx	0.70 ± 0.05	0.73 ± 0.02	0.66 ± 0.05	0.73 ± 0.04
San Joaquin:total influx	0.27 ± 0.05	0.22 ± 0.02	0.29 ± 0.04	0.25 ± 0.04
Efflux:influx	1.20 ± 0.14	1.18 ± 0.11	1.11 ± 0.05	0.85 ± 0.07
Outflow:efflux	0.34 ± 0.05	0.47 ± 0.06	0.35 ± 0.03	0.24 ± 0.06

[a] 1978, 1982, 1984, 1986.
[b] 1976–1977, 1987–1988, 1990–1991.

Several points implied by the data of Table 7 require emphasis because of their ecological and management importance to Suisun Bay and the rest of San Francisco Bay downstream. First. the Delta more often acts as a net producer rather than net consumer of organic matter in dry years. Second, despite the overall augmentation of organic matter. so much is exported from the system that organic matter outflow into the Bay is much less than inflou from tributaries to the Delta. Export of Delta water thus more than offsets any natural tendency of the Delta to augment organic matter supplies for the Bay. Filially. even with losses to exports. organic matter loading from the Delta to Suisun Bay is still significant compared with sources within the Bay. For example. we previously estimated organic matter sources in Suisun Bay to be 3.9 t day^{-1} TON. exclusive of riverine loading (Jassby *et al.*, 1993. assuming a C:N ratio of 12). In the present study. u e estimate the mean ($\pm$ S.E.) for riverine loading to Suisun Bay. i.e. outflow from the Delta, to be 17 ± 4 t d a y TON. Taken together. these points demonstrate that flow management has profound effects on the supply of organic matter to Suisun Bay and therefore the food supply for larval fish in this important nursery area.

RESTORATION IMPACTS

The above results demonstrate that sources, use. and fate of organic matter varies strongly with flow management and the mix of habitats: changes in either will affect the primary food supply for the Delta *and* San Francisco Bay. As part of the restoration programme for the Bay–Delta. several combinations of alternative actions are under consideration. These include: (1) an isolated diversion channel: (2) fish and flow barriers: (3) increased use of floodplains and flooded islands: (4) channel widening and related modifications; and (5) increased water storage. What effect may these restoration options have on the Delta itself and on its role as a filter for San Francisco Bay'? Although nothing quantitative can be said about (4) and (5). data do exist to explore the first three of these actions, and we do so below.

Isolated diversion channel

Currently, water exported into state and federal water projects flows from tributaries through the Delta to or near Clifton Court Forebay and then into the California Aqueduct and Delta–Mendota Canal (Figure I). One alternative envisions an isolated diversion channel connecting the Sacramento River upstream of the Delta directly with Clifton Court Forebay, bypassing the Delta. If the quantity of water required for export into state and federal water projects were unchanged. an isolated diversion would result in elimination of export flows from the Delta and a concomitant decrease in inflows from the Sacramento River. In view of the results presented here (Figure 7). the change in both export and inflow would have an impact on mass loading rates downstream. but in opposite directions. What would be the net effect of such a change? Much of the variability in mass loading rates downstream can be explained by both total river inflow and export flow (Figure 3). The high multiple R^2 values indicate that a linear model is an adequate specification of the relationship. We can deduce from the coefficients of the model the consequences of decreasing export flow and river inflow by the same amounts. For average hydrological conditions. loading into the Delta would increase by 32% in winter. 10% in spring and 21% in autumn, and decrease 3% in summer. On an annual basis. a substantial increase in mass loading to the Bay would therefore be expected if an isolated diversion channel were constructed.

In fact, this analysis is probably conservative in terms of predicting a mass loading rate. because the decrease in river inflow will not affect all tributaries equally. Rather. the Sacramento River inflow will decrease disproportionately compared with the San Joaquin River. As the San Joaquin River is generally richer in its organic matter load. the mass loading into the Delta will not decrease as much as expected based on the decrease in total inflow: mass loading into the Bay should therefore be even higher than the

model of Table 3 suggests. It is also likely to be of higher food quality. as the San Joaquin typically carries a much higher ratio of phytoplankton-derived N to TON compared with the Sacramento. Operation of the export pumps for the state and federal water projects tends to cause a 'short-circuiting' of the San Joaquin along the Old River channel (Figure 1). This shortened route moves the organic matter-rich water directly out of the system instead of allowing it to follow its traditional course through the Delta into the Bay.

Operation of an isolated diversion channel would therefore trade relatively organic matter-poor water from the Sacramento for richer San Joaquin water. Although influx into the Delta as defined in (2) would decrease. for all practical purposes the elimination of the San Joaquin shunt to the export pumps implies a loading increase. Furthermore. increased chlorophyll loading and increased Delta residence time suggest that phytoplankton biomass and hence productivity would increase. Although not discussed here. N, P and Si are in excess in the Delta and unlikely to limit biomass except in the most extreme cases, such as the dry ENSO of 1976–1977. The supply rate of organic matter to the Delta itself is therefore likely to increase. It is important to note that allowing more San Joaquin River water to enter the Delta may have consequences in addition to increasing organic matter supply. The San Joaquin receives pesticide-laden agricultural drainage. as well as high selenium loads (Hinton, 1998). An increased loading of these materials to the Delta may have unforeseen effects on selected components of the food web.

Fish and flow barriers

The 'short-circuiting' of the San Joaquin River through the export pumps not only redirects organic matter out of the system but can also shunt migrating fish to Clifton Court Forebay. In the Forebay, fish may be entrained in the export pumps. preyed on by subadult striped bass (M. *saxatilis*), or injured during salvage operations. Accidental movement of organisms to the export pumps along other pathways in the Delta is also possible. More than 40 species are affected, including migrating chinook salmon (*O. tschawytscha*) (Brown *et al.*, 1996). As a result, one of the rehabilitation alternatives under consideration is the placement of barriers to force water and migrating organisms along predetermined safe paths. Beginning in 1987. four barriers have been placed in Delta channels. Three of these are agricultural-]-elated. with one-way gates to maintain higher upstream water levels and irrigation supplies. One of them is a rock barrier at the head of Old River. installed in 1988 and operating through 1994. usually in late summer and autumn. The barrier has been modified to include a culvert so farmers can continue to divert irrigation water from the Old River channel. Through 1994. however. no culvert was in place. The barrier results in substitution of Delta water from the north of the Forebay for San Joaquin River water moving down Old River. Although the barrier leaked to some extent. we can use it as a model for determining whether these barriers significantly affect the delivery of organic matter to the Delta.

Data are available to examine the effect of the barrier during the autumns of 1988–1990. The substitution of Delta water for San Joaquin water results in a lower mass loading into the water projects and a higher one into the Delta itself. How much does the presence of a barrier increase the mass loading rate into the Delta? Using Equation (3), we can calculate export with and without a barrier, and consider the difference as an augmentation of the influx. For TON, the augmentation is 8.8–12% in autumn. Because of the rich load of phytoplankton usually carried by the San Joaquin, the augmentation for phytoplankton-derived material is much higher: 36–86%. Two of these years were critically dry and one was below normal. and the applicability of these exact numbers for other year types is uncertain. Nonetheless. the barriers clearly can have a marked effect on organic matter supply to the Delta. and this byproduct needs to be considered carefully when designing such structures for fish protection and other purposes.

Floodplains and flooded islands

A third rehabilitation action is to increase shallow-water habitat. Certain fish require shallow-water habitat for completion of their life cycle or because of their feeding behaviour. but such habitat in general has a higher density of macrobenthos (Nixon, 1988) and probably higher food availability. Expanding shallow-water habitat can be accomplished in several ways. One is to breach the levees of Delta islands. which are largely below sea level and will accordingly fill with water. Breaching has occurred in the past through a combination of levee weakening and flood conditions, and some of the islands such as Franks Tract have been subsequently abandoned to aquatic habitat. To a certain extent. these areas can be used as a model for effects on primary organic matter sources.

The increased aquatic habitat of course implies increased primary productivity. How does the productivity of these areas compare with the Delta as a whole? A comparison of Franks Tract (D19) with a nearby channel station (Twitchell Island. D16) offers some insight. On a seasonal basis. little difference in chlorophyll a can be observed. The ratio of D16 to D19 chlorophyll a is 1.05 ± 0.37 (S.E. among years). 1.04 ± 0.39, 0.96 ± 0.21 and 1.04 ± 0.35 in winter through autumn. respectively. A much larger difference can be seen in turbidity, however. especially in winter and autumn. The corresponding ratios are $.48 = 0.45$, 1.09 ± 0.17, 1.06 ± 0.11 and 1.42 ± 0.24. The higher channel turbidities occur in seasons of higher flow and imply that the differences arise because of contrasting mixing regimes in deep channels compared with shallow-water expanses. These differences are large enough to result in significantly higher productivity in shallow-water areas (Equation (I)).In principle. shallow-water regions will also have lower phytoplankton respiratory losses because the aphotic zone is relatively smaller than in deep waters. Both factors imply a higher supply of organic matter for primary consumers: indeed, cross-sectional studies demonstrate that macrobenthic biomass tends to increase as water depth decreases (Nixon, 1988). A complication arises in that shallow-water habitat is also superior habitat for submerged aquatic plants. As pointed out above, almost half of current *Egeria* coverage is found in three western Delta shallow areas that were formed after levee breaches. As current policy is to maintain these areas navigable by applying herbicides, it should be recognized that an increase in shallow-water habitat probably means increased use of these herbicides.

A separate route to greater shallow-water habitat is by increasing the area and duration of floodplain inundation. The major floodplain of the San Francisco Bay–Delta is the Yolo Bypass, which routes flood flows around the Sacramento metropolitan area. When completely inundated, its area (2.4×10^4 ha) is approximately the same as the rest of the Delta in its entirety. The Bypass floods 1 out of 3 years on average. Inundation-drainage cycles can occur throughout the winter and sometimes in spring. The Bypass supports at least 40 species of fish and appears to give several native species a competitive advantage. such as the federally listed Sacramento splittail (*Pogonichthys macrolepidotus*) (CDWR. 1999). Juvenile chinook salmon migrating seaward through the Yolo Bypass have higher feeding success. growth rate and survival than juveniles migrating seaward in the Sacramento River. Enhanced growth and survival in the Yolo Bypass is partly explained by the higher availability of forage (drift insect larvae) in this shallow flood plain habitat compared with the deep river habitat. Water from the Bypass rejoins the Sacramento River at Rio Vista. and the Bypass has been hypothesized to be an important source of organic matter for the downstream estuary. In view of the Bypass' purported ecological role, both for organisms in the Bypass itself and as a food source for downstream ecosystems, interest has developed in optimizing Bypass management through several options. These include increasing the frequency and duration of Bypass flooding. while still retaining flood cycles resembling historical hydrology. The native fish fauna is adapted to spawn in winter and early spring. emigrating from the floodplain before warmwater exotic species have spawned. Retaining inundation–drainage cycles is therefore essential to providing the native fauna a competitive advantage.

What can be said quantitatively regarding the Bypass' role in the organic matter supply? Certainly. the Bypass is an important addition to phytoplankton habitat in the Delta. at least for limited periods. In the wet winters of 1998 and 1999. for example, the mean inundated Bypass area added an additional 86% and 52%, respectively, to the Delta's area (Ted Sommer, CDWR. personal communication). In spring of 1998. the additional area was 51%. There are no historical time series of chlorophyll *a*. water clarity and conductivity in the Bypass for making phytoplankton productivity estimates. but clearly these inundated areas offer the potential for a very large augmentation of within-Delta phytoplankton productivity. Even on a Delta-wide basis. the augmentation could be especially significant in spring of above-normal years (Table 6). Additional organic matter will enter the aquatic habitat just through suspension and dissolution of soil organic matter. including vascular plant detritus, in inundated areas but the quantitative contributions are unknown.

Although primary production within the Bypass area may be highly significant for native species, organic inatter exports from the Bypass to downstream habitats do not appear to be important. The volumetric addition of Yolo Bypass water to the Sacramento River- can be estimated from the ratio of Yolo Bypass flow to Rio Vista flow. which is just downstream of where Bypass water reenters the river. On a seasonal basis. the median ratios (+ median absolute deviation among years) are 0.10 ± 0.14. 0.010 ± 0.012. 0.0023 ± 0.0018 and 0.0057 ± 0.0071 for winter through autumn. respectively. of 1968 1995. Medians are used because of the distorting effect of extremely wet years such as 1983. an ENSO year. Unless the level of organic matter in Bypass water is an order-of-magnitude greater than river water. Bypass effects on downstream ecosystems are probably small in winter and negligible in other seasons, except perhaps in very wet years. Furthermore. based on the (admittedly sparse) evidence to date (CDWR. 1999), DOC concentrations in the Bypass, although higher than in the Sacramento River. are not remarkably so. Even in the case of extremely wet winters. the impact of any organic matter subsidy from Bypass water will be damped: residence times will be shorter and organic matter availability lower.

CONCLUDING REMARKS

In the Delta itself. tributary-borne loading is the main source of bulk organic carbon. while phytoplankton production and agricultural drainage are important secondary sources. Collectively. tidal marsh export, wastewater discharge and vascular plant production also contribute to bulk organic carbon. Due to the inefficiency with which most DOC is biodegraded and converted into heterotrophic biomass. as well as the short residence time for the Delta. bulk DOC availability is actually small for loading sources: their main net contribution appears to be in the form of POC. As a result. only tributary-borne loading and phytoplankton production are consistently important sources in almost all seasons and water year types. This conclusion reflects the particular configuration of bulk sources in the Delta and the hydraulic residence time. but organic inatter subsidies from external sources are a common feature of many ecosystems (Polis *et al.*, 1997).

Equally significant is the role the Delta plays as a transition zone between fi-eshwater rivers and the critical nursery area of Suisun Bay downstream. The Delta often augments the supply of organic matter from the rivers. especially in critically dry years when it is most needed. More important. the organic matter that is conducted by the Delta into Suisun Bay is a significant portion of the food available there for larval fish. As a result, water management that redistributes the efflux from the Delta between the downstream estuary and various water projects has a profound effect on food availability for these larval fish.

The examples presented here illustrate that proposed actions have at least significant and sometimes very large effects on primary food resources. Increased use of floodplains probably offers the biggest increase in organic matter sources, due to both the area involved and the availability and quality of

phytoplankton POC. The benefits will accrue mostly to those organisms that can use the floodplains directly rather than organisms feeding downstream. An isolated diversion facility channelling water from the Sacramento River around the Delta to the water projects—results in substantial loading increases during winter and autumn, but little change in spring and summer when food availability probably matters most to developing organisms. Flow and fish barriers in the channel can also have significant effects, especially on phytoplankton sources and in dry years, by eliminating 'short-circuits' in the transport of organic matter to diversion points. These effects can rival those of floodplains. Finally, productivity in flooded islands probably exceeds that of channels because of lower turbidity and shallower mean depth, although vascular plants rather than phytoplankton may dominate if the depths are too shallow.

A distinction is often made between restoration and rehabilitation (MacMahon, 1998). *Restoration* refers to attempts to return a disturbed site to its former state. *Rehabilitation* refers to attempts to restore some elements of structure or function to an ecological system. River systems are often sites of major restoration projects. in the sense defined above (Larsen, 1996; Collier *et al.*, 1997; Harwell. 1997). Restoration is undertaken with the assumption that river hydrology drives the ecosystem and that restoring normal hydrological regimes will restore plant and animal communities. Restoration of the Delta hydrograph to, say. a pre-European settlement era is not feasible. Channelization of a vast tule marsh and the subsequent formation of huge agricultural tracts are now intimately connected with the economy of and water availability in California. The current efforts therefore consist of a complex patchwork of rehabilitation programmes. Each of the proposed programmes some of which have been discussed above is devoted to a subset of ecological functions. These programmes cannot be guaranteed to work in concert. and so unusually detailed scientific understanding is required to identify and resolve conflicts. The historical data analysis presented here is part of a larger project in which measurements of stable isotopes and biogeochemical markers. and experiments on organic matter biodegradation and zooplankton growth rates. are being used collectively to define the primary food resources and their quality. Because of potential food limitation. all Delta rehabilitation programmes need to address the impact on primary food resources.

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