Detritus Fuels Ecosystem Metabolism but not Metazoan Food Webs in San Francisco Estuary's Freshwater Delta

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ABSTRACT: Detritus from terrestrial ecosystems is the major source of organic matter in many streams, rivers, and estuaries, yet the role of detritus in supporting pelagic food webs is debated. We examined the importance of detritus to secondary productivity in the Sacramento and San Joaquin River Delta (California, United States), a large complex of tidal freshwater habitats. The Delta ecosystem has low primary productivity but large detrital inputs, so we hypothesized that detritus is the primary energy source fueling production in pelagic food webs. We assessed the sources, quantity, composition, and bioavailability of organic matter among a diversity of habitats (e.g., marsh sloughs, floodplains, tidal lakes, and deep river channels) over two years to test this hypothesis. Our results support the emerging principle that detritus dominates riverine and estuarine organic matter supply and supports the majority of ecosystem metabolism. Yet in contrast to prevailing ideas, we found that detritus was weakly coupled to the Delta's pelagic food web. Results from independent approaches showed that phytoplankton production was the dominant source of organic matter for the Delta's pelagic food web, even though primary production accounts for a small fraction of the Delta's organic matter supply. If these results are general, they suggest that the value of organic matter to higher trophic levels, including species targeted by programs of ecosystem restoration, is a function of phytoplankton production.

Introduction

The question of how organic matter sources move from terrestrial to aquatic ecosystems and within heterogeneous aquatic ecosystems is of fundamental importance to aquatic ecology (Lindeman 1942; Teal 1962). Knowledge of mechanisms that control magnitudes and paths of organic matter flux translates directly into better ways to manage and restore aquatic food webs and ecosystem health (Rabalais et al. 2002). Such knowledge is of basic importance because it helps aquatic ecologists understand how seemingly diverse ecosystems are closely connected (Boyer and Jones 2001; Reiners and Driese 2001) and how diverse habitats within aquatic ecosystems display disproportionate rates of critical ecological functions (Polis et al. 1997; Lewis et al. 2001).

Over the past two decades following publication of the river continuum concept (Vannote et al. 1980) there has been much research on how organic matter processing within streams alters the transport of organic matter to downstream ecosystems (Webster and Meyer 1997a), but less research on the subsequent fate of allochthonous organic matter in large rivers and estuaries (Smith and Hollibaugh 1997; Findlay et al. 1998; Chanton and

Lewis 2002). There also has been much research on the importance of detritus in supporting food webs in low-order streams (Cummins and Klug 1979; Wallace et al. 1999), but the strength of detrital pathways to food webs in large rivers, estuaries, and coastal waters is debated (Haines 1976; Peterson et al. 1986; Deegan and Garritt 1997; Lewis et al. 2001; Murrell et al. 2002). Two underlying difficulties in attempts to develop a general understanding of the role of detrital organic matter in supporting riverine and estuarine food webs are spatial and temporal variation of habitat types within large rivers and estuaries and identification and evaluation of transfers to higher trophic levels.

Heterogeneous ecosystems provide a challenge to aquatic ecologists because it is difficult to ascertain ecosystem-level community structure and function (Levin 1992; Reiners and Driese 2001). Large rivers and estuaries encompass a diversity of habitats that vary in important physical features, such as depth, turbidity, tidal energy, and residence time. Such a range in physical features can result in marked variation in the autochthonous production of phytoplankton (Boyer et al. 1999; Cloern 2001), which results in variable dilution of allochthonous detrital organic matter (Webster and Meyer 1997b). External delivery and retention of allochthonous organic matter also may vary among habitats (Kemp et al. 1997; Findlay et al. 1998,

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2001). Heterogeneity in detrital importance to higher trophic levels is further complicated by uncertainties in trophic transfer efficiencies (Wetzel 2001). Documentation of persistent net ecosystem heterotrophy in inland aquatic ecosystems has expanded to include several riverine and estuarine ecosystems (Smith and Hollibaugh 1997; Raymond et al. 2000), but the importance of detritus in supporting microbial food webs (McCallister et al. 2004) and higher trophic levels is poorly understood (Wetzel 2001). The fate of detrital organic matter is unknown for most rivers and estuaries.

We evaluated the fate of detrital organic matter delivered to the Sacramento-San Joaquin River Delta, California, building from initial findings reported in Sobczak et al. (2002). The Delta is a hydrologically-complex mosaic of habitats connecting the Sacramento and San Joaquin Rivers to San Francisco Bay. We assessed the source, amount, and bioavailability of detrital organic matter among a wide diversity of Delta habitats for 2 yr. We also examined the role of autochthonous phytoplankton productivity in organic matter dynamics among habitats. The Delta, as a whole, has low primary productivity (approximately 70 g C m^{-2} yr^{-1}; Jassby et al. 2002) and allochthonous detrital inputs dominate the Delta-wide organic mass balance (Jassby and Cloern 2000). We hypothesized that detrital organic matter regulates ecosystem metabolism and secondary production by pelagic metazoans. We addressed questions central to understanding the fate of organic matter within the Delta ecosystem. What fraction is transported through the Delta, metabolized by microbes, and harnessed by the pelagic, metazoan food web?

Materials and Methods

STUDY AREA

The Delta's leveed waterways and tidal freshwater habitats receive runoff from a 1.6×10^7 ha watershed (Fig. 1) and carry the majority of river inflow and organic carbon supply to northern San Francisco Bay (Jassby and Cloern 2000). Riverine inputs account for 69% of the organic matter supply to the Delta, while primary producers within the system account for < 15% (Jassby and Cloern 2000). The Sacramento River provides 84% of the Delta's freshwater, and primary production is dominated by phytoplankton photosynthesis (Jassby and Cloern 2000). The Bay-Delta system has experienced 150 yr of intense, human-induced disturbance; declines in abundances of native species of fishes have recently motivated large-scale ecosystem restoration efforts (CALFED http://calfed. ca.gov/current/ROD.html). Declines in food resources, including zooplankton stocks, have been
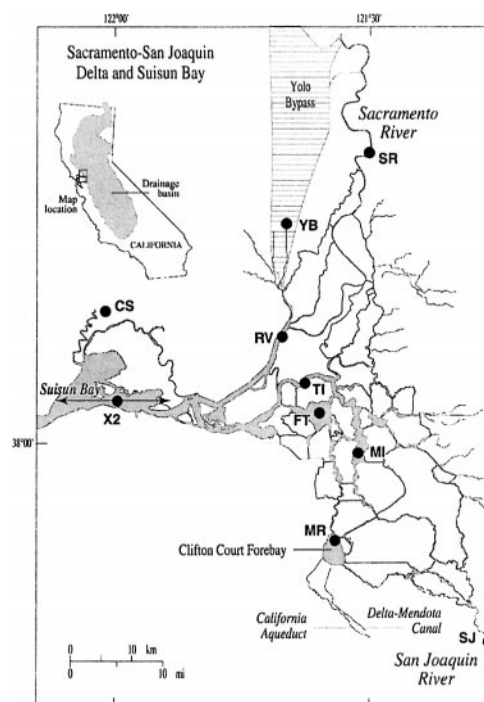

Fig. 1.   Map of the tidal freshwater Sacramento and San Joaquin River Delta in relation to drainage area. Points represent principal sampling sites and an array of sampling locations that are incorporated into the principal sites (see Table 1 for abbreviations).

hypothesized as an important factor in explaining declines of juvenile fish (Bennett and Moyle 1996; Lucas et al. 2002; Sobczak et al. 2002).

EXPERMENTAL APPROACH

This study was designed to compare a wide diversity of Delta habitats, including principal hydrologic inputs and outputs (Fig. 1), and to measure temporal variation in organic matter inputs and outputs by sampling across the seasonal range of hydrologic variability (Fig. 2). This comparative approach aimed to maximize potential variability in the sources, quantity, and quality of organic matter. Ten principal sampling sites were selected to represent the major Delta habitats (Table 1). Spatial variability of physical and chemical attributes is large within all these habitats (Sommer et al. 2001; Lucas et al. 2002), so our sampling design incorporated multiple independent locations (n ≥ 3) within each of the 10 principal sampling sites (Table 1).

Principal sampling sites (hereafter called habitats) included multiple deep river channel and shallow water habitats that span the Delta landscape (Fig. 1). Sacramento River at Hood represents the discharge from the northern Sacramento River drainage basin. Sacramento River at Rio Vista
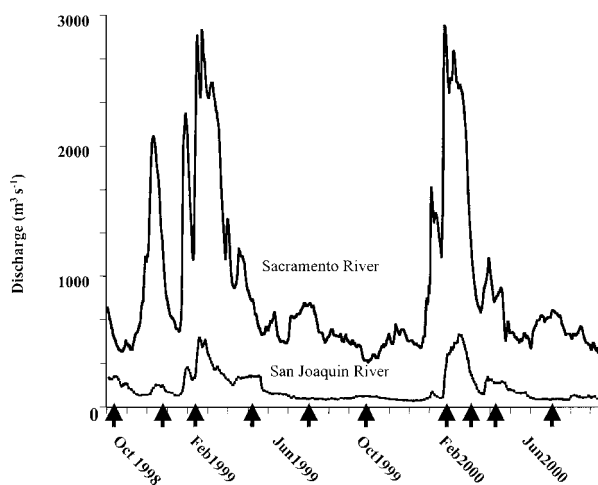
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Fig. 2.   Temporal variation in freshwater discharge into the Delta represented by variation in Sacramento and San Joaquin River discharge between October 1, 1998 and October 1, 2000. Arrows indicate sampling periods. Data are provided by the Interagency Ecological Program of the San Francisco Estuary (http://iep.water.ca.gov/dayflow/).

is a 1-km wide, deep tidal channel that integrates hydrologic inputs from the entire northern Delta. San Joaquin River at Twitchell Island is a highly variable mixture of San Joaquin and Sacramento River water (Monsen 2001). Middle River at Clifton Court Forebay is a variable mixture of Sacramento River, San Joaquin River, and agricultural drainage water that is exported for municipal and irrigation supplies via the California and Delta-Mendota Aqueducts. The saltwater-freshwater interface is operationally defined as the spatially-variable location (X2) where bottom salinity is 2 psu, an index of net freshwater flow to San Francisco Bay that is highly correlated with several measures of biotic resources, including abundances of zooplankton and fish (Jassby et al. 1995). Cutoff Slough in Suisun marsh represents a remnant, tule (*Scirpus*) tidal marsh slough with a dendritic drainage. Suisun marsh is the largest remaining tidal marsh in the Delta and one of the largest tidal marshes in the United States. Yolo Bypass drainage is an agricultural floodplain that is inundated as a flood-protection measure when Sacramento River discharge exceeds 2,000 m³ (Schemel et al. 1996). The Yolo Bypass is 60 km long and extends to 24,000 ha when fully flooded (see Schemel et al. 2003). Sampling locations were located throughout Prospect Slough and Little Holland Tract, which receive Yolo Bypass drainage. Franks Tract is a 12.9 km² lake-like habitat in the central Delta (mean depth = 3 m) that receives water from sources throughout the entire Delta ecosystem (Lucas et al. 2002). Mildred Island is a smaller (4.1 km²), deeper (mean depth = 5 m), lake-like hab-

itat in the eastern Delta that has slower exchanges with surrounding waterways (Lucas et al. 2002). San Joaquin River at Mossdale represents riverine inputs from the San Joaquin River drainage basin, a predominantly agricultural catchment that provides 13% of the Delta's freshwater input (Jassby and Cloern 2000).

SAMPLING AND ANALYSIS OF GASES AND INORGANIC SOLUTES

Water samples were collected during 10 sampling periods from October 1998 through July 2000, spanning a range of hydrologic conditions from summer-autumn low flow (< 500 m³ s⁻¹) to winter flood peaks having combined river inflow $> 3,000$ m³ s⁻¹ (Fig. 2). Water samples were collected 1 m above the bottom with a peristaltic pump, screened through 243-µm Nitex mesh to remove coarse particulate matter, and processed within hours of collection. Depth, temperature, and Secchi depth were measured at each location, and pH was measured in the laboratory using a Cole-Parmer model 59002-00 pH meter. Dissolved oxygen was measured using the Winkler method (Wetzel and Likens 2000). Dissolved inorganic carbon (DIC) was measured using a gas chromatograph interfaced with a hot-wire detector following acidification of samples in serum bottles. Salinity was calculated after measuring specific conductivity by electrode at 25°C. Suspended particulate matter (SPM) was measured gravimetrically using 0.45-µm Nuclepore filters. Ammonium, nitrate, nitrite, soluble reactive phosphorus (SRP), and dissolved silica were measured during selected sampling periods using a Technicon AutoAnalyzer II and modifications of standard methods (Hager 1994).

SAMPLING AND ANALYSIS OF ORGANIC MATTER

Bulk Organic Matter and Bioavailability Bioassays

Particulate organic carbon (POC) and particulate nitrogen were measured by high-temperature combustion following acidification using a Carlo Erba CHN Analyzer. Dissolved organic carbon (DOC) was measured with high-temperature combustion following filtration through an ashed glass-fiber filter (nominal pore size = 1.0 µm), 4°C storage, acidification, and sparging. Dissolved organic nitrogen (DON) was estimated during the first year of the study by measuring total nitrogen (using a high-pressure potassium-persulfate digestion) subtracted by dissolved inorganic nitrogen (DIN). Bioavailable DOC and bioavailable POC were operationally defined as the metabolized fraction during 21-d incubations in the dark at room temperature. This incubation time is the approximate mean transit time across the Delta (Jassby and Cloern 2000). Organic carbon loss was measured

TABLE 1.   List of all sampling locations and mean physical and inorganic chemical characteristics. These locations are grouped within ten principal sampling sites. X2 locations spanned Suisun Bay. LH = Little Holland Tract. PS = Prospect Slough.

Sampling Locations		n	Depth (m)	Salinity (psu)	Secchi (cm)	SMP (mg l^{-1})	SRP (μM)	DIN (μM)
Sacramento River at Hood (SR)		22	9.5	0.1	73	33.4	1.2	24.1
Location 1	SR1	8	9.3					
Location 2	SR2	7	8.6					
Location 3	SR3	7	10.5					
Sacramento River at Rio Vista (RV)		22	9.2	0.1	46	31.8	4.1	92.3
Location 1	RV1	8	10.9					
Location 2	RV2	7	8.9					
Location 3	RV3	7	7.7					
San Joaquin River at Twitchell Island (TI)		19	11.8	0.1	63	24.8	2.0	31.6
Location 1	TI1	7	7.6					
Location 2	TI2	6	16.7					
Location 3	TI3	6	12.0					
Middle River at Clifton Court Forebay (MR)		10	5.7	0.1	59	28.0	2.2	30.0
Location 1	MR1	4	6.7					
Location 2	MR2	3	5.7					
Location 3	MR3	3	2.3					
Export to SF Bay at salinity = 2 psu (X2)		20	11.4	1.7	29	112.7	2.1	76.5
20 Locations	X2	20	11.4					
Cutoff Slough in Susuin Marsh (CS)		20	1.5	1.9	17	88.4	1.7	27.6
Location 1	CS1	8	1.3					
Location 2	CS2	6	1.3					
Location 3	CS3	6	2.1					
Yolo Bypass Drainage (YB)		39	0.9	0.1	15	105.2	2.0	47.8
Location 1	LH1	8	1.0					
Location 2	LH2	3	0.8					
Location 3	LH3	3	0.8					
Location 4	PS1	4	5.0					
Location 5	PS2	6	6.2					
Location 6	PS3	6	6.7					
Location 7	YB	9	12.5					
Franks Tract (FT)		16	3.9	0.1	100	11.6	1.0	10.9
Location 1	FT1	6	5.8					
Location 2	FT2	5	2.7					
Location 3	FT3	5	2.9					
Mildred Island (MI)		16	4.4	0.1	80	13.1	1.1	15.9
Location 1	MI1	5	4.4					
Location 2	MI2	6	4.3					
Location 3	MI3	5	4.5					
San Joaquin River at Mossdale (SJ)		23	4.5	0.2	42	53.0	1.6	24.3
Location 1	SJ1	9	4.5					
Location 2	SJ2	7	4.5					
Location 3	SJ3	7	4.3					

directly in both sets of assays and supported with additional assays that measured 21-d biological oxygen demand and the conversion of POC to DOC.

Analysis of Phytoplankton and Bacterioplankton

Phytoplankton biomass and phytodetritus were measured as chlorophyll *a* (chl *a*) and phaeophytin, using a Turner Model 10 fluorometer and assuming an organic carbon:chl *a* ratio of 35:1 (Cloern et al. 1995). Both total and < 10-μm size

fractions were determined. Additional phytoplankton samples were preserved in acid-Lugol's solution. Identification, enumeration, and measurement of biovolumes of phytoplankton were made using an inverted microscope. Cell volumes were estimated for dominant taxa by measuring 50–100 cells and applying the geometric formulas given by Wetzel and Likens (2000).

Phytoplankton gross primary productivity was calculated as a function of chl *a* and mean water

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TABLE 2.   Total phytoplankton biomass relative to other pools of organic carbon. Phytoplankton biomass was calculated as the sum of chlorophyll a + phaeophytin assuming carbon:pigment ratio of 35:1. BDOC = bioavailable DOC. BPOC = bioavailable POC. Potential protozoan biomass was calculated assuming an efficient transfer of BDOC to bacterial biomass to protozoan biomass using assimilation efficiencies of 0.25. This calculated protozoan biomass is likely an overestimate and used to highlight the role of phytoplankton. Data are given as the median ratio of independent samples. Sample size varied among habitats (see Table 1).

Habitats	Total DOC: Total POC	BDOC:BPOC	Phytoplankton DOC + POC	Phytoplankton on POC	Phytoplankton BPOC	Protozoa: Phytoplankton	Phyto <10 μm: Phytoplankton
SR	3.4	3.6	0.08	0.38	1.28	0.11	0.50
RV	4.2	3.3	0.07	0.36	1.34	0.12	0.84
TI	3.7	2.5	0.05	0.20	0.96	0.14	0.83
MR	4.9	2.8	0.06	0.35	1.41	0.12	0.84
X2	2.2	1.9	0.04	0.13	1.32	0.15	0.66
CS	5.0	2.3	0.04	0.22	0.94	0.15	0.70
YB	2.5	2.7	0.07	0.24	0.80	0.13	0.74
FT	8.4	5.6	0.05	0.47	2.20	0.17	0.68
MI	4.5	2.3	0.07	0.37	1.66	0.10	0.80
SJ	2.6	1.1	0.18	0.61	1.80	0.04	0.38

(Header span: Organic Matter Ratios)

column irradiance, using an empirical model (Eq. 1 in Jassby et al. 2002) built from 51 measurements using a standard $NaH^{14}CO_3$ uptake method. Phytoplankton respiration was calculated as a function of biomass and gross productivity (Eq. 3 in Jassby et al. 2002). Bacterial abundance was measured using direct microscopic counts and converted into biomass assuming bacterial cell mass is 20 fg C cell^{-1} (Hollibaugh and Wong 1996). Whole community respiration was measured as oxygen consumption during 24-h in situ dark incubations, and bacterial respiration was calculated as whole community respiration minus algal respiration. Bacterial productivity was estimated from bacterial respiration assuming growth efficiency is 0.25.

Net Ecosystem Metabolism

The concentrations of dissolved carbon dioxide (CO_2) and oxygen can be powerful indicators of net system metabolism (sensu Smith and Hollibaugh 1997). We calculated CO_2 partial pressure (pCO_2) from DIC, pH, temperature, and salinity (Raymond et al. 1997). Percent saturation dissolved oxygen was calculated from dissolved oxygen concentration and temperature (Wetzel and Likens 2000).

STATISTICAL ANALYSES

Differences among habitats were analyzed with ANOVA using sample groupings outlined in Table 2. Differences among habitats were assessed using unplanned Tukey's post hoc tests and significance was attributed to differences in which $p \leq 0.05$. Spearman rank tests were used to examine relationships between bioavailable pools of organic matter. t-tests were used to compare Delta-wide pools of organic matter.

Results

Delta habitats varied in physical and chemical attributes (Table 1). Water depth varied over an order of magnitude among habitats (mean depth range = 0.9–11.8 m). Delta habitats were generally turbid (mean SPM = 65 mg l^{-1}, n = 220) resulting in low Secchi depths (mean = 46 cm). The shallow lake-like Franks Tract and Mildred Island had lower SPM concentrations and higher Secchi depths (100 and 80 cm, respectively). Inorganic nutrients (DIN and SRP) were high throughout the Delta (mean DIN = 38 μM, mean SRP = 1.9 μM), but somewhat lower concentrations were found in Franks Tract and Mildred Island. The combination of high nutrient concentrations coupled with high SPM concentrations suggests that phytoplankton primary productivity was routinely light limited.

BULK ORGANIC MATTER CONCENTRATIONS AND COMPOSITION

DOC was the dominant form of organic matter in all Delta habitats (overall mean = 3.5 mg l^{-1} ± 0.2 SE, n = 210; Fig. 3). DOC was consistently much higher in Cutoff Slough (mean = 10.1 mg l^{-1} ± 0.6 SE) compared to other habitats (ANOVA, p < 0.001, F = 75.5). Excluding this marsh slough, DOC did not vary markedly among habitats, but was lowest in the Sacramento River habitats. Several high DOC values for the Sacramento River, Rio Vista, Twitchell Island, and X2 habitats were sampled in February 2000 during a winter flood (Fig. 2) and may represent a first flush of soil derived organic matter. Dissolved forms of organic matter were routinely greater than particulate forms, regardless of habitat throughout the study (overall DOC:POC median ratio = 3.6; Table 2). Although POC concentrations were much less than DOC, POC varied more among habitats (Fig. 3).

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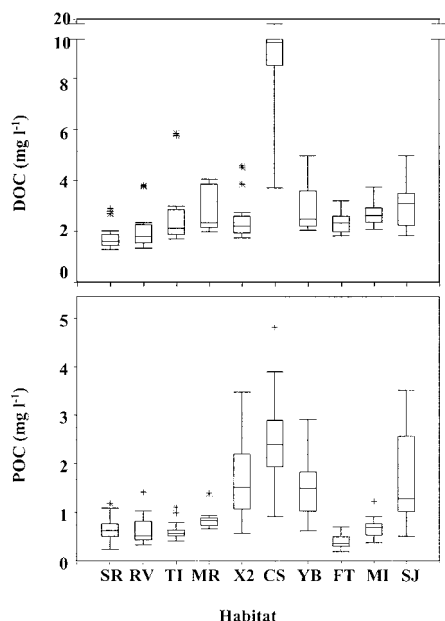Estuarine Organic Matter Bioavailability   **127**

Fig. 3.   Amounts of A) dissolved organic carbon (DOC) and B) particulate organic carbon (POC) among Delta sampling sites. Box plots show median values and box interquartile range. * represent values that exceed ± 1.5 spread of the central box's end members.
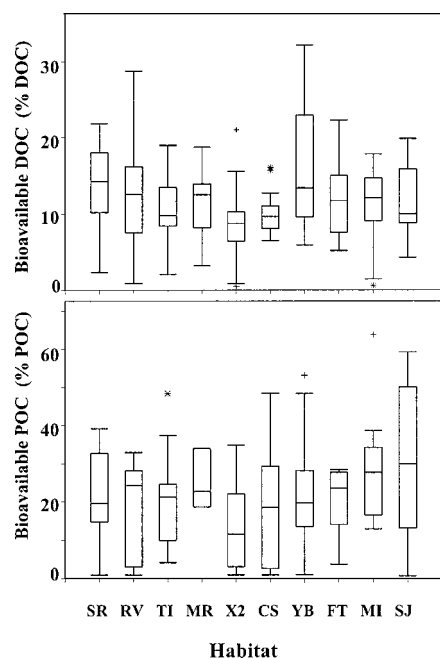

Fig. 4.   A) Bioavailable dissolved organic carbon (DOC) and B) bioavailable particulate organic carbon (POC) among Delta habitats. Box plots show median values and box interquartile range. * represent values that exceed ± 1.5 spread of the central box's end members.

Cutoff Slough had the highest POC (mean = 2.7 mg l^{-1} ± 0.2 SE). Cutoff Slough, X2, Yolo Bypass, and Mossdale POC concentrations were significantly greater than other deep river and shallow water habitats (ANOVA, p < 0.001, F = 22.7). Bulk organic matter composition was generally not different among habitats (data not shown). DOC:DON (overall mean = 17.2 ± 0.14) was consistently and significantly greater than POC:PON (overall mean = 9.0 ± 1.6; t-test, p < 0.001).

BIOAVAILABILITY OF ORGANIC MATTER

Bioassays designed to maximize estimates of potential bioavailablity revealed that only a small fraction of the Delta's organic matter was bioavailable. Relative bioavailable DOC ranged between 10% and 16% among habitats (Fig. 4), so bioavailable DOC concentrations were a function of total DOC concentrations. These findings suggest that the dominant pool of organic matter in all Delta habitats was not readily accessed by heterotrophs, and the bulk of this potential energy was likely exported from Delta habitats to the San Francisco Bay and coastal waters or to Delta aqueducts.

Relative concentrations of bioavailable POC were significantly greater than relative concentrations of bioavailable DOC (t-test; p < 0.001). Bioavailable POC ranges were larger than DOC ranges among habitats (Fig. 4; overall relative median POC concentrations among habitats ranged between 10% and 30%). The disparity in relative bioavailability between dissolved and particulate organic matter resulted in comparable amounts of dissolved and particulate bioavailable organic matter among Delta habitats (Table 2). Bioavailable POC concentrations were a function of phytoplankton biomass (overall Spearman's coefficient rank = 0.66), and this general finding was consistent regardless of habitat. In the absence of phytoplankton biomass, detrital (or nonalgal) biomass had low bioavailability throughout our 2-yr study.

The important contribution of phytoplankton biomass in the Delta's bioavailable POC was surprising because phytoplankton biomass was generally low and accounted for a small component of the Delta's organic matter. Algal biomass was routinely low (median = 102 µg C l^{-1}, n = 210) compared to total POC (median = 983 µg l^{-1}, n = 210), but algal biomass exceeded 350 µg C l^{-1} on selected dates in the X2, Cutoff Slough, Yolo Bypass, Mildred Island, and San Joaquin River-Mossdale habitats (Fig. 5). Excluding isolated bloom events in the San Joaquin River at Mossdale, phytoplankton represented a small proportion (overall median = 5%) of the Delta's organic matter regardless of habitat (Table 2).
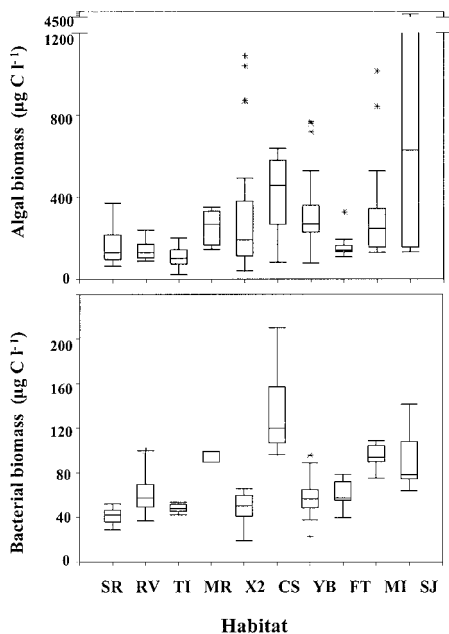
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Fig. 5.   A) Phytoplankton and B) bacterioplankton biomass among Delta habitats. Box plots show median values and box interquartile range. * represent values that exceed ± 1.5 spread of the central box's end members.
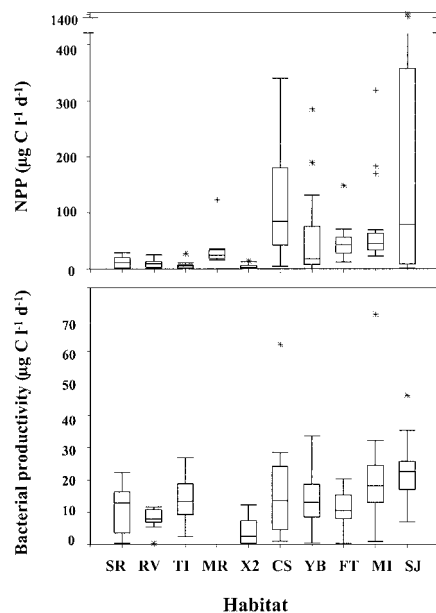

Fig. 6.   A) Phytoplankton net primary production (NPP) and B) bacterioplankton secondary production among Delta habitats. Box plots show median values and box interquartile range. * represent values that exceed ± 1.5 spread of the central box's end members.

PHYTOPLANKTON AND BACTERIOPLANKTON PRODUCTIVITY AND NET ECOSYSTEM METABOLISM

Standing stocks of phytoplankton were much greater than bacterioplankton (Fig. 5). The large discrepancy between phytoplankton and bacterioplankton biomass is most clearly demonstrated by the order of magnitude difference in their y-axes in Fig. 5. Bacterioplankton biomass was generally low in the Sacramento River habitats and was significantly greater in Cutoff Slough relative to other Delta habitats. Phytoplankton net primary productivity was also generally greater than bacterioplankton productivity. The difference between phytoplankton and bacterioplankton productivity is reflected in the order of magnitude difference between y-axis scales in Fig. 6. Net primary productivity was significantly greater in the four shallow water habitats compared to five of the deep water channel habitats (Fig. 6) where aphotic-zone respiration consumes a large fraction of photosynthetic production. Bacterioplankton productivity was generally low throughout the Delta ecosystem and did not vary significantly among habitats.

pCO_2 routinely exceeded atmospheric equilibrium throughout our study (Fig. 7). Eight of the ten habitats had median $pCO_2 > 2$-fold atmospheric pCO_2. Calculated pCO_2 was routinely closer to atmospheric equilibrium at Franks Tract and X2, indicating either more balanced autotrophy and heterotrophy (Franks Tract supports dense stands

Fig. 7.   Independent measures of net ecosystem metabolism: A) partial pressure CO_2 relative to the atmosphere and B) % saturation dissolved oxygen (relative to the atmosphere) among Delta habitats. Box plots show median values and box interquartile range. * represent values that exceed ± 1.5 spread of the central box's end members.
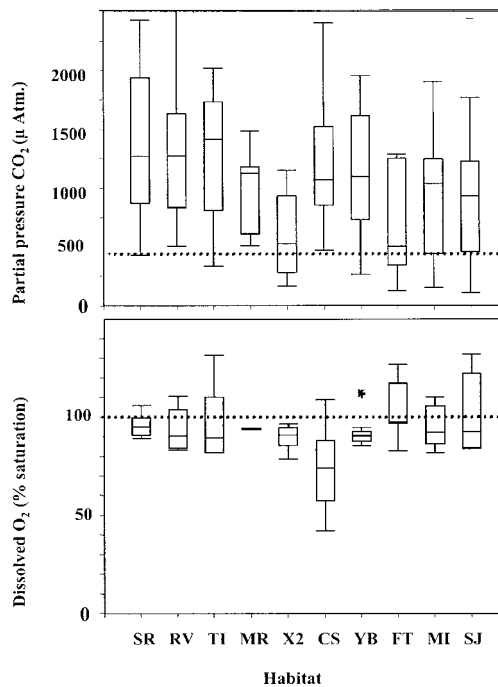
of submerged vascular plants) or more rapid CO_2 flux to the atmosphere (X2 occurs in regions of strong tidal currents and vertical mixing). Dissolved oxygen was routinely less than 100% saturation throughout the Delta ecosystem. Cutoff Slough had the largest in situ dissolved oxygen deficit. Coupled pCO_2 and dissolved oxygen data conclusively demonstrate that the Delta routinely functions as a net heterotrophic ecosystem.

Discussion

"[C]ommonly >90% of the total organic matter produced within [aquatic] ecosystems or imported to [aquatic] ecosystems is metabolized but is never consumed by particulate-ingesting metazoans. Recognition of this reality has been agonizingly slow, or alternatively, it is acknowledged but completely ignored as the predation emphasis continues. Effective management of aquatic ecosystems is difficult and certainly imprecise if most of the metabolism, energetic fluxes, and control mechanisms of that microbial metabolism are poorly understood and separated from higher trophic levels." (Wetzel 2001, p. 732).

DETRITAL SUBSIDIES AND NET ECOSYSTEM METABOLISM

Net ecosystem heterotrophy suggests that allochthonous detritus supports the majority of ecosystem respiration across the Delta (Fig. 7). Two independent measures of ecosystem metabolism (pCO_2 and dissolved oxygen) resulted in similar findings and provided strong support for the hypothesized importance of detrital inputs. This finding contributes to a growing body of research showing that large rivers and estuaries are routinely net heterotrophic (Raymond et al. 1997; Smith and Hollibaugh 1997). Net ecosystem metabolism generally reflects the balance of primarily phytoplankton and bacterioplankton productivity and respiration, but it does not measure the relative importance of allochthonous-detrital subsidies to higher trophic levels such as macrozooplankton (Cole et al. 2002).

Food Web Importance of Detrital and Algal Pathways

Comparisons of bulk pools of organic matter showed that detrital organic matter was the dominant total and bacterial accessible pool of organic matter among all Delta habitats (Table 2). Bioavailable DOC was routinely greater than bioavailable POC, regardless of the detrital or algal component of the bioavailable POC. This discrepancy resulted in a much larger pool of bioavailable organic matter that was directly accessible only by bacteria. This finding is ecologically important because much of the Delta's bioavailable organic mat-

ter must be routed through the microbial loop, resulting in a large respiratory loss of carbon prior to assimilation into pelagic metazoan biomass (Ducklow et al. 1986; Wetzel 2001; Sobczak et al. 2002). Findings from bioavailablity bioassays were consistent with the interpretation of net ecosystem metabolism data, and suggested that Delta habitats were routinely net heterotrophic.

Algal biomass constituted a small fraction of total organic matter among all Delta habitats but was a disproportionately large component of bioavailable organic matter (Table 2). For example, phytoplankton biomass was 8% and 7% (median percentage), respectively, of the organic matter at the Hood and Rio Vista deep-river habitats in the Sacramento River, but accounted for 90% of the bioavailable organic matter available to particle-ingesting rotifers and copepods (hereafter called zooplankton). This finding was based on the knowledge that particulate organic matter (regardless of bioavailability) enters the metazoan food web at a much greater efficiency than dissolved forms that must first be routed through a microbial food web (Jassby and Cloern 2000; Wetzel 2001). This finding was based on comparisons between potential protozoan biomass and measured phytoplankton biomass (i.e., ratios in Table 2). These ratios likely underestimate the importance of algal biomass because potential protozoan biomass was derived using liberal growth efficiency assumptions (i.e., all bioavailable DOC was converted into bacterial biomass with 0.25 growth efficiency and all bacterial biomass was converted into protozoan biomass with 0.25 growth efficiency; see Sanders et al. 1992; del Giorgio and Cole 1998; Sobczak et al. 2002). The purpose of using such liberal assumptions for calculating potential protozoan biomass was to highlight the important role of algal biomass even under optimal conditions for the generation of protozoan biomass.

Overall, our assessment of the potential trophic transfer of organic matter to zooplankton suggests that algal biomass was coupled to zooplankton production even though the Delta ecosystem was net heterotrophic. These results do not support our initial hypothesis regarding the importance of detrital subsidies to the Delta's pelagic, metazoan food web.

In Situ Bacterioplankton and Phytoplankton Activities

Comparisons of bulk and bioavailable pools of organic matter among habitats revealed the potential importance of autochthonous algal biomass as the primary food resource to zooplankton. This finding was based in part on assumptions regarding the transfer of organic matter into bacterioplankton and through the microbial loop. Com-

parisons between bacterioplankton and phytoplankton standing stocks and productivity provided strong and independent evidence in support of the disproportionate importance of phytoplankton. Phytoplankton biomass was routinely several fold greater than bacterial biomass, regardless of habitat (Fig. 5), indicating the disparity in potential energy within the Delta's microbial food web relative to the phytoplankton standing stock. This disparity in biomass was surprising for two reasons: the Delta has low phytoplankton biomass compared to other estuaries (Cloern 1999; Jassby et al. 2002) and an unknown component of the bacterioplankton is likely supported by phytoplankton derived DOC. Low bacterioplankton standing stocks were consistent with previously discussed findings suggesting that detrital inputs supported ecosystem metabolism but not the Delta's zooplankton. A similar decoupling between bacterioplankton and the metazoan food web has been documented in northern San Francisco Bay (Murrell and Hollibaugh 1998) and Pensacola Bay (Murrell et al. 2002).

Comparison of bacterioplankton and phytoplankton productivity were consistent with the finding that standing stocks of bacterioplankton were much less than phytoplankton, suggesting that the turnover rate of bacterioplankton was generally slower than phytoplankton (Fig. 6). This finding is amplified by the fact that bacterial biomass must frequently be transformed through at least one trophic transfer (e.g., bacterial biomass to protozoan biomass) before it would be packaged in a form accessible to many pelagic filter feeders; the realized biomass generated by the microbial food web to higher trophic levels may be less than reported bacterial biomass estimates. Suspension feeders that can filter bacteria directly (e.g., many cladocerans) account for a smaller percentage of the Delta's zooplankton assemblage relative to more selective feeders that generally rely on larger particles (e.g., some copepods and rotifers; Müller-Solger et al. 2002); there are exceptions to these trophic linkages (e.g., Roff et al. 1995).

Nutritional Value and Importance of Phytoplankton

Understanding the relative contribution of detrital and algal resources is of critical importance because Delta zooplankton appear to be food limited. Laboratory-growth assays with the cladoceran *Daphnia magna* (Müller-Solger et al. 2002) showed that Delta zooplankton growth rate and fecundity were strongly related to phytoplankton biomass (chl *a*) and unrelated to the amount of detrital organic matter in samples collected from a subset of the habitats we sampled. The strength of the relationship between zooplankton growth rate and phytoplankton biomass was most pronounced at chl *a* concentrations < 10 μg l^{-1}. This finding suggests that nutritional components associated with phytoplankton, rather than with detritus, regulate zooplankton growth and that Delta zooplankton may be food limited when chl *a* concentration is < 10 μg l^{-1} (Müller-Solger et al. 2002; Sobczak et al. 2002).

Phytoplankton community composition suggested that algal biomass was generally of high nutritional quality. Overall biomass was dominated by diatoms, contributing 66% of the cumulative biovolume in all samples. Key species included *Entomoneis paludosa, Skeletonema subsalum, S. potamos, S. costatum, Cyclotella striata, C. meneghiniana,* and *C. atomus.* The second most important algal component, Cryptophytes, contributed 12% of biomass and included common species *Plagioselmis prolonga, Campylomonas reflexa, C. rostratiformis, Cryptomonas ovata,* and *Teleaulax amphioxeia.* These taxa are in the size range selected by zooplankton consumers and have high nutritional value because they are rich in essential fatty acids (Brett and Müller-Navarra 1997). Our collective findings (Jassby and Cloern 2000; Cloern et al. 2002; Jassby et al. 2002; Müller-Solger et al. 2002; Sobczak et al. 2002) highlight the importance of algal-derived organic matter to the Delta's pelagic food webs.

Energy Flow Conceptual Model Revised

Our findings contribute to a series of recent findings in other large lake, river, and estuarine ecosystems suggesting that small fractions of ecosystem-level organic mass balances support aquatic food webs producing forage for top-level consumers (Lewis et al. 2001; Chanton and Lewis 2002; Cole et al. 2002). Our findings suggest that detrital pathways may support the bulk of heterotrophic metabolism, but may be weakly connected to pelagic food webs in many large riverine and estuarine ecosystems.

Mann's (1988) seminal review of the production and use of detritus in freshwater, estuarine, and marine ecosystems highlighted our lack of understanding of detrital dynamics beyond small streams. Mann (1988, p. 910) hypothesized that detrital pathways were much more important to pelagic food webs in larger downstream ecosystems than previously thought, "There is much circumstantial evidence to suggest that pelagic food webs based on DOM are much more important than previously thought. The conversion of DOM to POM through the microbial loop and its utilization in higher trophic levels is an urgent topic for further study." We applied Mann's conceptual model

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TABLE 3. Organic pools and potential trophic transfers among habitats. Reported values are median values expressed as μg C l^{-1} from the 2-yr study. These values are used to generate the Mann Diagrams presented in Fig. 8. BDOC = bioavailable DOC. BPOC = bioavailable POC. Detrital BPOC was derived from the median BPOC $-$ algal biomass. Protozoan BPOC was derived from the median BDOC value assuming an efficient transfer (i.e., 0.25 assimilation efficiency) into bacterial and protozoan biomass (see Methods). Nonpredatory zooplankton potential was derived assuming complete consumption of bioavailable POC and protozoan biomass with a 0.25 assimilation efficiency. Double ** designates specific sampling periods when bioavailable organic matter was augmented due to episodic or localized phytoplankton blooms: YB** = a falling hydrograph in a fully flooded floodplain (March 2000), MI** = localized phytoplankton bloom in the southern portion of a shallow lake-like habitat (October 1999), and SJ** = a low flow phytoplankton bloom in the San Joaquin River (July 2000).

Habitats	Organic Matter Pools and Potential Trophic Transfers								
	Total OM	Total DOC	BDOC	Total POC	BPOC	Detrital BPOC	Algal Biomass	Protozoan BPOC	Nonpredatory Zooplankton Potential
SR	2,367	1,680	250	687	145	7	130	16	40
RV	2,455	1,883	283	572	155	8	130	18	43
TI	2,861	2,234	245	627	140	7	102	15	39
MR	3,365	2,448	320	917	210	11	268	20	58
X2	3,990	2,321	224	1,669	155	8	192	14	42
CS	12,824	10,145	1,196	2,679	530	32	495	75	151
YB	4,311	2,660	400	1,651	220	44	269	25	61
YB**	7,130	5,030	790	2,100	970	223	747	49	255
FT	2,839	2,445	316	394	80	4	140	20	25
MI	3,520	2,757	391	763	150	8	24	24	44
MI**	4,050	2,690	360	1,360	960	48	1,013	23	246
SJ	4,646	3,241	333	1,405	475	24	627	21	124
SJ**	7,314	3,750	730	3,564	2,300	115	4,329	46	586

summarizing the interrelationships of phytoplankton, allochthonous organic matter, and zooplankton to Delta habitats having different ratios of detrital and algal biomass. We used median values of ecologically important pools of organic matter (Table 3) to construct habitat-specific models of energy flow (Fig. 8) from detrital and algal pathways to support potential zooplankton production.

Comparison of Mann Diagrams representing the deep Sacramento River and tidal-marsh slough (Fig. 8) illustrates variability among habitats in the potential delivery of bioavailable organic matter to zooplankton. Blank areas within the DOC and POC boxes represent recalcitrant organic matter that is unavailable to Delta biota, while shaded areas represent bioavailable organic matter (see Table 3 caption for details). The algal component of bioavailable POC provided the most abundant food resource for zooplankton in both habitats, but the marsh slough supported a potentially larger zooplankton biomass.

LANDSCAPE HETEROGENEITY: IMPORTANCE OF PHYTOPLANKTON PRODUCTION AMONG AND WITHIN HABITATS

A critical finding and subsequent feature of the Mann Diagrams is the critical role of phytoplankton biomass in supporting production of zooplankton consumers. The remaining Mann Diagrams highlight how variation in phytoplankton production within habitats may translate into spatial and temporal variability in potential zooplankton yield.

The Yolo Bypass floodplain is inundated during years of heavy runoff and phytoplankton biomass builds in the shallow floodplain habitat (Sommer et al. 2001). Phytoplankton biomass produced during the flooded period resulted in a large increase in potential zooplankton yield (Table 3, Fig. 8). The tidal lake-like habitats (e.g., Mildred Island) displayed similar periodic increases in potential zooplankton yield following localized phytoplankton blooms. The San Joaquin River at Mossdale consistently had the highest algal biomass, but low-flow blooms may be coupled to localized hypoxia events (Leland et al. 2001) that may not promote secondary productivity.

Phytoplankton biomass may be the critical factor in evaluating the nutritional value of organic matter in most Delta habitats. Annual variation in phytoplankton production among Delta habitats appears to be an important functional distinction in evaluating the value of different habitats in supporting higher trophic levels, such as zooplankton (Müller-Solger et al. 2002) and juvenile fish (Sommer et al. 2001). Our comprehensive assessment showed that deep-river channels in the Sacramento River rarely sustained phytoplankton biomass above the critical threshold of 10 μg l^{-1} chl a reported in Müller-Solger et al. (2002), while marsh slough and shallow lake-like habitats appeared more likely to sustain chl a concentrations that met the proposed nutritional demands of Delta zooplankton (Fig. 9). Phytoplankton biomass in the upper San Joaquin River was also more likely to exceed the proposed food-limitation threshold,

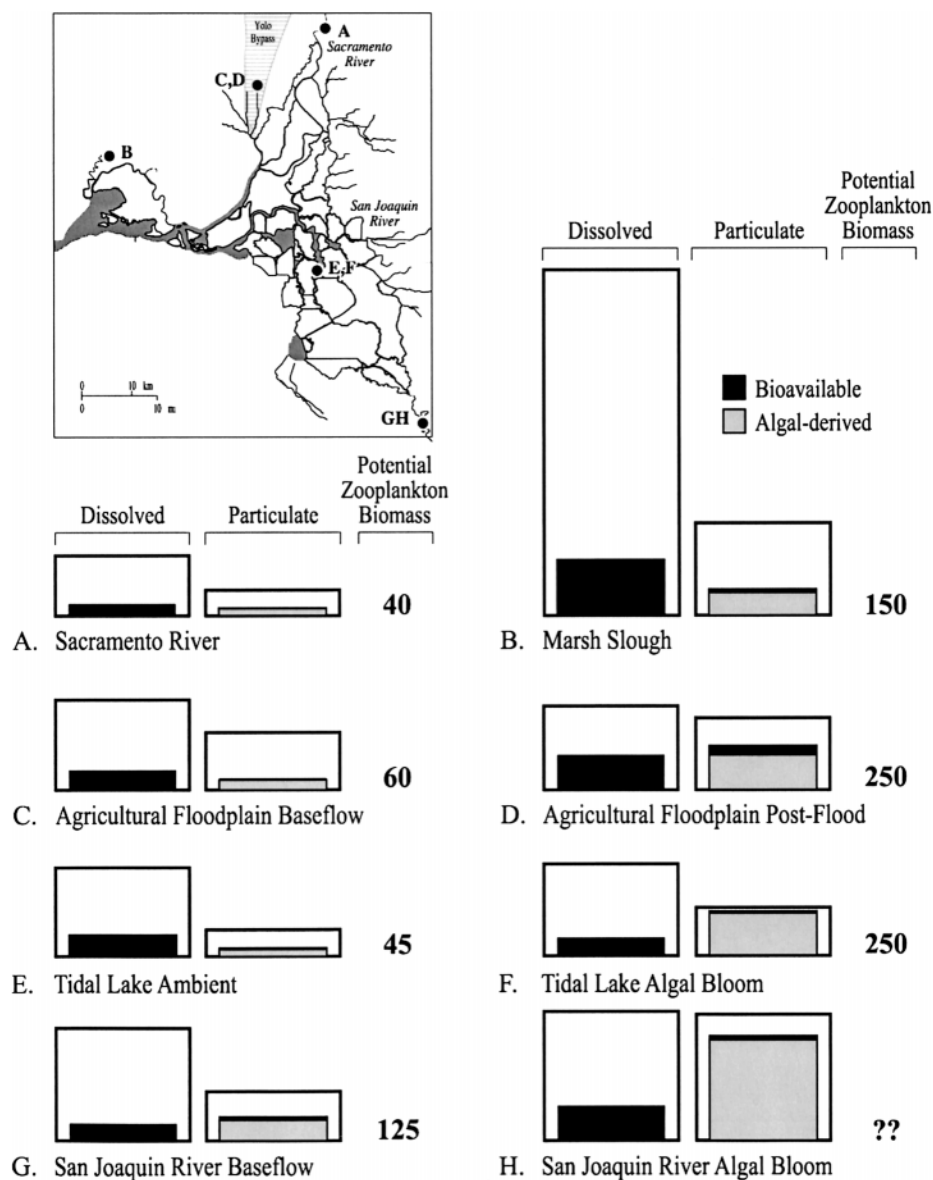**132**   W. V. Sobczak et al.

Fig. 8.   We updated Mann's (1988) conceptual model summarizing the interrelationships of phytoplankton, allochthonous organic matter, and zooplankton in lakes for habitats in the Delta. Cartoons represent pools of organic matter extracted from Table 6. Four contrasts are highlighted: A) deep river channel habitat in the Sacramento River versus B) marsh slough habitat in Suisun Marsh, C) agricultural floodplain habitat at low base flow versus D) postflood, E) tidal lake-like habitat during ambient conditions versus F) during a localized phytoplankton bloom, and G) San Joaquin River upstream of the Delta during normal base flow versus a low flow phytoplankton bloom event. Box sizes can be compared relative to each other (e.g., marsh slough DOC concentrations are much greater than DOC concentrations found in the deep channel habitat in the Sacramento River).

but there is concern that these concentrations may far exceed demand by higher trophic levels and result in detrimental decreases in biological oxygen demand within reaches of the San Joaquin River (Leland et al. 2001).

CONCLUSIONS AND SIGNIFICANCE

Our study of the Sacramento-San Joaquin River Delta supported the emerging principle that allo-

chthonous detritus supports a large component of riverine and estuarine ecosystem metabolism. Our study did not find evidence for detrital pathways significantly contributing to pelagic food webs supporting higher trophic levels. Use of multiple approaches for examining organic matter bioavailability across a wide range of habitats (Table 1) provided strong inference regarding the fate of organic matter at the ecosystem level. Several general
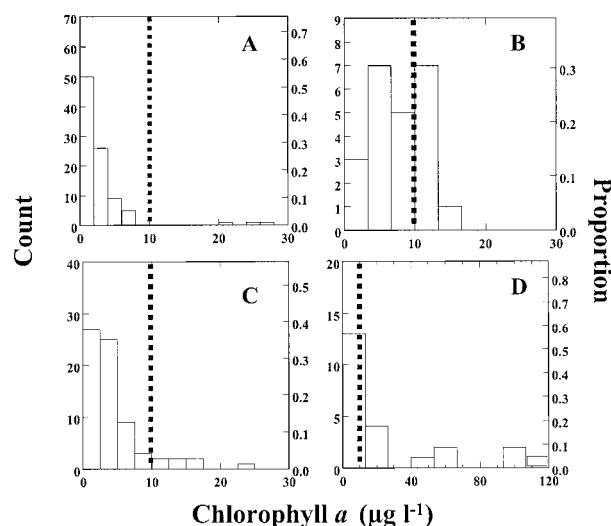
Fig. 9.   Distribution of chlorophyll a among habitat types: A) deep-water channel in the Sacramento River, B) tidal-marsh slough in Suisun Marsh, C) tidal-shallow lakes, and D) San Joaquin River at Mossdale Marina. Dashed vertical lines represent Delta chlorophyll concentrations at which zooplankton-food limitation occurs (Müller-Solger et al. 2002).

findings emerged from our 2-yr bioregional assessment of the Delta's organic matter dynamics.

Only a small fraction of the organic matter was bioavailable, even over the course of 21-d bioassays. This finding suggested that the vast majority of the organic matter delivered to the Delta was transported conservatively to the San Francisco Bay and coastal marine waters. The ultimate fate of this organic matter is unknown.

The Delta ecosystem was routinely net heterotrophic indicating that it respires more organic matter than it produces within the system. This finding indicated that the Delta functions as a sink for organic matter as it moves to coastal waters. A corollary to this finding was that the Delta ecosystem functions as a net source of CO_2 to the atmosphere.

DOC was usually several times $>$ POC. This finding was ecologically significant because DOC and POC enter food webs at different trophic levels; the Delta, a net heterotrophic ecosystem, was microbially coupled to dissolved allochthonous organic matter.

The northern San Francisco Bay and associated Delta is a highly-turbid, light-limited ecosystem with low primary productivity relative to other estuaries (Cloern 2001; Jassby et al. 2002). In spite of this low productivity, our results showed that phytoplankton biomass was a strong predictor of bioavailable POC and was likely the major food resource for the Delta's pelagic metazoans.

Delta habitats functioned differently in terms of potential transfer of organic matter to higher trophic levels. Deep River habitats in the Sacramento River and central Delta, which represent $>$ 50% of the Delta's spatial coverage, provided the lowest potential trophic transfers among Delta habitats. Tidal-marsh sloughs routinely supported the largest potential zooplankton biomass. Several shallow-water habitats throughout the Delta (e.g., an agricultural floodplain and a lake-like habitat) sporadically supported modest algal blooms and these habitats appear to be critical for supplying bioavailable food resources to zooplankton (Schemel et al. 2003). Growth and survival rates of juvenile salmon are higher in the shallow floodplain than adjacent deep river channel (Sommer et al. 2001), so these differences in phytoplankton may propagate to higher trophic levels.

Estuarine-wide organic matter assessments are unusual (Kemp et al. 1997; Smith and Hollibaugh 1997) and have rarely been used in direct support of ecosystem restoration (Rabalais et al. 2002). Improved knowledge about organic matter dynamics in large rivers and estuaries holds the prospect of better management of watersheds connected to these environments and biotic resources within them. We provided a framework for using organic matter dynamics to aid restoration actions that are geared at modifying the supply of bioavailable organic matter to higher trophic levels. We provided a bioregional assessment of a heterogeneous ecosystem's food web base and potential delivery to higher trophic levels. Such an assessment helps provide the basis for understanding the current condition of the Delta's diverse habitats and a basis for forecasting changes in response to planned manipulations of habitat type. Effective restoration of aquatic ecosystems requires knowledge of disparities in the amounts, bioavailability, and food web importance of organic matter delivered from adjacent terrestrial watersheds compared to organic matter produced among diverse habitats within aquatic ecosystems. Bioavailability of organic matter (to microbes and higher trophic levels) is an essential and powerful measure of aquatic ecosystem response to restoration actions aimed at creating habitats within aquatic ecosystems or manipulating land-use features in connected watersheds (Rabalais et al. 2002).

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