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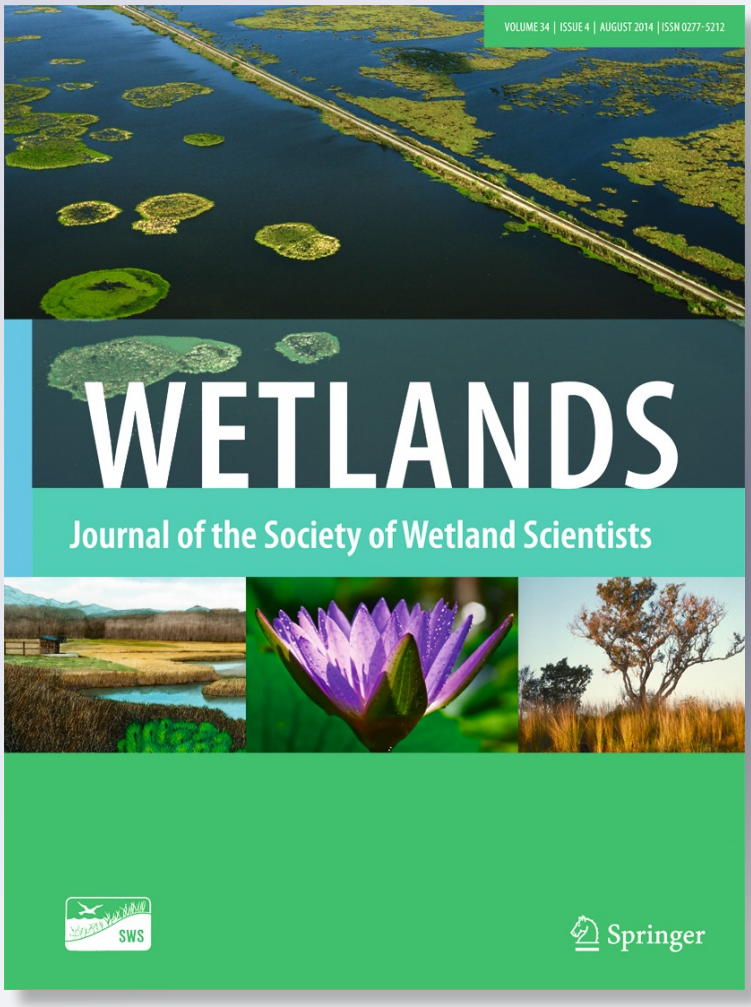
Wetlands
Official Scholarly Journal of the Society of Wetland Scientists

ISSN 0277-5212
Volume 34
Number 4

Wetlands (2014) 34:759-774
DOI 10.1007/s13157-014-0540-3



Springer

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DOI 10.1007/s13157-014-0540-3

ARTICLE

Ecosystem-Scale Rates of Primary Production Within Wetland Habitats of the Northern San Francisco Estuary

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Received: 14 February 2014 / Accepted: 24 April 2014 / Published online: 4 June 2014

Abstract Salt marsh restoration is hypothesized to provide shoreline stabilization, increased fish habitat, and organic carbon subsidies for estuarine food webs. Organic carbon comes from diverse primary producers that differ in carbon fixation rates and areal extent within wetland systems. This study was designed to obtain some of the first estimates of the relative contribution of different primary producers to total organic carbon production within open water and tidally flooded wetlands of the northern San Francisco Estuary (SFE). Carbon fixation rates of phytoplankton, microphytobenthos, and low marsh emergent vegetation were measured in two natural and four restoring wetlands in 2004. Areal (m^2) rates of carbon fixation were greatest for low marsh vegetation, while phytoplankton and microphytobenthos rates were one and two orders of magnitude lower, respectively. However, when areal production rates were scaled to the amount of habitat available for each primary producer group, the relative importance of each group varied by location. Given that each primary producer group supports a different subset of estuarine consumers, the type of food subsidy desired should influence the amount open water channel, mudflat and low marsh area restored. Large-scale wetland restoration activities should consider the types of primary producers likely to occupy restored habitats when estimating future food web impacts.

Keywords Carbon fixation · Microphytobenthos · Nutrients · Phytoplankton · *Spartina foliosa*

Electronic supplementary material The online version of this article (doi:10.1007/s13157-014-0540-3) contains supplementary material, which is available to authorized users.

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Introduction

Estuarine wetlands provide a host of ecosystem services for coastal systems. Wetlands are among the most productive environments on Earth, and as such are hypothesized to be important for shoreline stabilization via sediment accretion (Callaway et al. 2012), carbon sequestration (Whiting and Chanton 2001, Chmura et al. 2003, Callaway et al. 2012), and provide large organic subsidies in support of estuarine consumers (Boesch and Turner 1984, Howe and Simenstad 2011). Assessment of relationships between wetland extent and ecological function is essential on a global scale (Finlayson et al. 1999, Zedler and Kercher 2005). At present, a comprehensive global inventory of wetland habitats is lacking (Finlayson et al. 1999) at the same time that wetland habitats have been degraded at alarming rates (Day et al. 2000, Kennish 2001); for example, approximately 50 % loss has occurred in the US since western settlement (Boyer and Polasky 2004). Large-scale restoration activities are now being implemented worldwide in an effort to re-establish ecosystem functions (e.g. Warren et al. 2002, Espanol et al. 2013). Classically, restoration refers to reversion of a degraded ecosystem to its original condition (i.e. pre-European condition), whereas rehabilitation is used to for situations when an acceptable improvement in ecological condition is the objective. In most US management efforts these words are used interchangeably, since there typically is no record of the original condition.

One goal of wetland restoration (or rehabilitation), is to provide organic carbon subsidies for food webs (e.g. Howe and Simenstad 2011). Organic carbon comes from a combination of riverine and tidal inputs, as well as autochthonous

carbon fixation by multiple groups of autotrophs, including phytoplankton, microphytobenthos, macroalgae, submerged aquatic vegetation and vascular plants (Cloern 1987, Roman et al. 1990, de Jonge and Colijn 1994, Buzzelli and Wetzel 1998, Jassby and Cloern 2000, Sobczak et al. 2002). These diverse primary producers differ in carbon fixation rates, as well as areal extent within wetland systems, likely affecting the magnitude of their contribution to estuarine food webs. Additionally, the way and extent to which carbon from these different primary producers is incorporated in to estuarine food webs varies, with carbon from phytoplankton and microphytobenthos preferred by grazers compared to vascular plant material that typically enters the food web after decomposition. Furthermore, wetland habitat responses to climate change and the implications for restoration will be realized differently on regional and mega-watershed levels (Erwin 2009). Thus, to implement appropriate restoration and management strategies, the overall contribution of autotrophic components to wetland productivity needs to be understood at the landscape scale. California's estuarine wetlands are currently the focus of numerous restoration efforts (Orr et al. 2003); nearly 90 % of the state's wetlands have been altered or destroyed, and these losses are primarily responsible for decreased species diversity and reduced water quality (Zedler 1996). Restoration efforts have the potential to impact inorganic nutrient sources entering estuaries (Bucholz 1982), water and sediment characteristics (Burdick et al. 1989, Zedler 1996) as well as the type of primary producers available to support higher trophic levels (Boesch and Turner 1984).

Within the open water habitats of the northern San Francisco Estuary (SFE), the most important contributor of organic carbon for the food web is thought to be phytoplankton (Jassby et al. 1993, Sobczak et al. 2002), although autotrophs other than pelagic phytoplankton have the potential to be major contributors to organic carbon supply. Variation in phytoplankton standing stocks and rates in this estuary are largely a function of light availability (Cole and Cloern 1984, 1987), while nutrient interactions have recently been shown to be important as well (e.g. Wilkerson et al. 2006, Glibert et al. 2011, Parker et al. 2012). In other temperate estuaries, production rates by benthic microalgae (microphytobenthos) exceed rates of pelagic phytoplankton production (Leach 1970, Varela and Penas 1985), and microphytobenthos can be the dominant source of carbon to grazers in the shallow areas and along mudflats of estuarine wetlands (Gould and Gallagher 1990, Jassby et al. 1993, Pinckney and Zingmark 1993, de Jonge and Colijn 1994). In the low marshes bordering mudflats, the largest contributors to primary productivity are considered to be stands of vascular plants, such as cordgrass (*Spartina* spp.) (Smart 1982). Rates of *Spartina* spp. production can be highly variable within a region (Smart 1982), and have been related to nutrient availability and tidal flushing (Cramer et al. 1981), sediment stability (Smart 1982) and salinity regime (Pearcy and Ustin 1984). Although macrophyte (including macroalgae and submerged and floating aquatic vegetation (SAV)) primary production often exceeds that of phytoplankton, its distribution and abundance in the SFE is highly variable. Macroalgal biomass is generally low (Josselyn and West 1985), and macroalgae are generally not considered major contributors to estuarine production in this area (Jassby et al. 1993). Seaweeds and seagrasses are mostly absent in brackish regions of the SFE (Jassby and Cloern 2000), but submerged, rooted macrophytes, including invasive *Egeria densa* (Grimaldo and Hymanson 1999, Brown 2003a) and *Cabomba caroliniana* (Tu and Randall 2001, Hickson and Keeler-Wolf 2007) are increasing in abundance, and their potential contribution to areal primary production should be evaluated.

Due to the high spatial and temporal variability in different types of autotrophic production (e.g. Pinckney et al. 2003), direct measurements scaled to the ecosystem level are essential. Estimates of primary production by different wetland autotrophs in the SFE have typically been based on indirect measurements such as modeled values (Jassby et al. 1993), biomass (Callaway et al. 2007) or coverage from aerial photographs (Jassby and Cloern 2000). However, direct measures of physiological or photosynthetic rates for low marsh vegetation are necessary not only to evaluate variability in production over a growing season amongst sites in the same region, but also to assess relative contribution of different types of primary producers. Although stable isotopes enable identification of carbon sources to evaluate trophic structure (e.g. Peterson and Howarth 1987, Wainright et al. 2000, Cloern et al. 2002, Howe and Simenstad 2011), the approach indicates which autotrophs may have contributed to total C production without providing their absolute carbon contributions. Information regarding magnitude of total carbon fixed by different primary producers that can be used to rank relative importance of different autotrophs to total C moving through a wetland is less readily available (Galvan et al. 2011).

This study was designed to obtain estimates of the relative contribution of different primary producers to total organic carbon production using directly measured rates of photosynthesis within a variety of estuarine wetland habitats of the northern SFE. We predicted that primary production rates of emergent plants (i.e. low marsh vegetation) would exceed those of either pelagic or benthic microalgae, but overall microalgal contribution to areal wetland production would be greater due to more extensive open water channel habitat and spatial coverage of microphytobenthos. We provide 1) spatially and temporally cohesive measurements of primary production and standing stock for three different autotrophic groups in wetland habitats of the northern SFE and 2) analysis of the relative importance of each group to total carbon supply for the estuarine wetlands. Measurements were made in two natural reference and four restoring estuarine wetlands over

the 2004 growing season. Given that each primary producer group supports a different subset of estuarine consumers, our findings suggest that large-scale wetland restoration activities should consider the types of primary producers likely to occupy restored habitats when estimating future food web impacts.

Methods

Study Area

Six wetland sites were sampled monthly between March and October during 2004 (Fig. 1). One was located in the Petaluma River (Carl's Marsh), three were located in the Napa River (Bull Island, Coon Island, Pond 2A), and two were in Suisun Bay (Brown's Island, Sherman Lake) (Table 1). These sites were sampled as part of the Integrated Regional Wetland Monitoring Project (IRWM) (www.irwm.org) and are described in detail with maps, hydrology, age and degree of restoration in Wetlands and Water Resources Inc (2012). Briefly, Carl's Marsh (38° 07.379 N, 122° 30.566 W), restored in 1994, is a 0.19 km^2 vegetated site with mudflat located near the mouth of the Petaluma River and contains limited channel network complexity. Bull Island (38° 13.277 N, 122° 18. 471 W), restored in the 1950's, is the most upstream location sampled on the Napa River. The 0.44 km^2 site is vegetated, and has exposed areas of mudflat at low tide. Coon Island (38° 11.706 N, 122° 19.178 W) is a 1.6 km^2 natural reference site located 9.5 miles upstream from the mouth of the Napa River. The site is also vegetated with associated mudflat at low tide. Pond 2A (38 ^{o} 09.111 N, 122 ^{o} 18.860 W) is a 2.2 km^2 site restored in 1995, located closest to the mouth of and to the west of the Napa River within the Napa-Sonoma salt pond/marsh complex. The marsh is vegetated, but unvegetated mudflat area is limited due to steep, nearly vertical, channel sides. Brown's Island (38° 02.320 N, 121° 52. 178 W) is a natural reference brackish marsh. The 3.4 km^2 site is vegetated, but lacks developed mudflat. Sherman Lake (38° 02.785 N, 121° 49.032 W), restored in the 1920's, is a 13 km^2 brackish tidal marsh with abundant SAV and little to no mudflat area. The vegetation in the lower elevations of the salt marsh, adapted to daily tidal flooding, is termed the low marsh vegetation. This was dominated by monospecific stands of *Spartina foliosa* (family Poaceae) in all sites except for Brown's Island where there was only *Carex obnupta* (family Cyperaceae). Upper marsh vegetation was not considered in this study.

In each wetland, areal coverage of habitat for each group of primary producers was obtained using Geographic Information System (Wetlands and Water Resources Inc 2012. Phytoplankton habitat was considered open water or channel area. Benthic mudflat habitat (i.e. microphytobenthos habitat) was defined as the sum of intertidal area below mean higher high water, subtidal habitat<2.5 m deep (mean photic zone depth) and the area where low marsh vegetation was present (Pinckney and Zingmark 1993). Submerged aquatic vegetation (SAV) and low marsh vegetation were determined from actual SAV or low marsh vegetation species areal coverage (Table 1). Phytoplankton, microphytobenthos and low marsh vegetation were present at all sites, except for Sherman Lake, where low marsh vegetation was absent and rooted SAV was present. A small amount of macroalgae was occasionally observed at Bull Island, but the high temporal and spatial variability required that we exclude it from quantitative analysis.

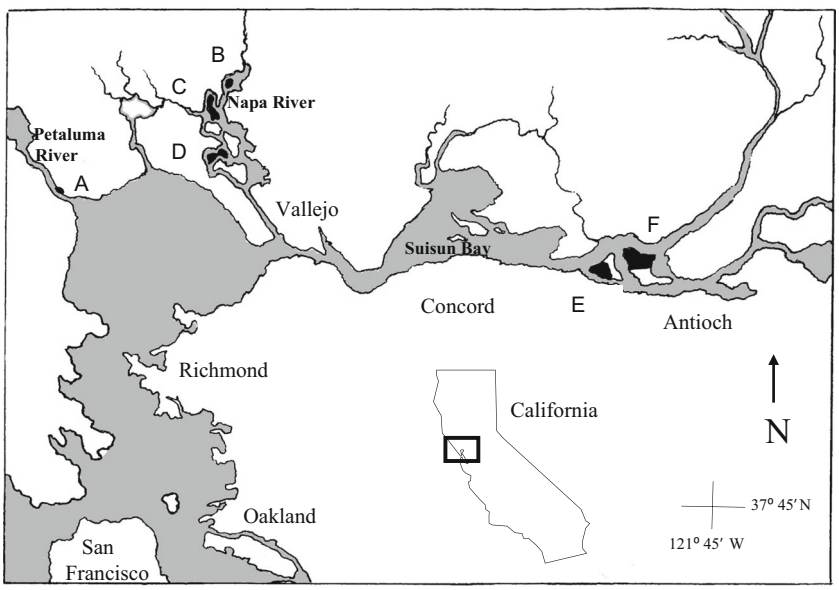

Fig. 1 Map of study sites (in black), **a**) Carl's Marsh, **b**) Bull Island, **c**) Coon Island, **d**) Pond 2A, **e**) Brown's Island and **f**) Sherman Lake

Table 1 Estuarine wetland sites monitored as part of the Integrated Regional Wetland Monitoring Pilot Project (IRWM). Restoring sites were originally estuarine wetland and had tidal flushing returned following breaching of levees in the year listed

	Site	Location	Low marsh vegetation type	Condition	Phytoplankton area, km^2	Microphyto-benthos area, km^2	Low Marsh vegetation. area, km^2	Total autotroph area km^2
A	Carl's Marsh	Petaluma River	*Spartina*	Restoring (1994)	0.02	0.04	0.02	0.07
B	Bull Island	Napa River	*Spartina*	Restoring (1950's)	0.04	0.04	0*	0.07
C	Coon Island	Napa River	*Spartina*	Natural reference	0.08	0.10	0.02	0.19
D	Pond 2A	Napa River	*Spartina*	Restoring (1995)	0.34	0.18	0.18	0.67
E	Brown's Island	Suisun Bay	*Carex*	Natural reference	0.36	0.12	0.11	0.59
F	Sherman Lake	Suisun Bay	*Cabomba* (SAV)	Restoring (1920's)	0.25	0.02	0.02 (SAV)	0.29

*Area=340 m^2

Sampling Design

In each wetland, a permanent 15 m transect was established parallel to the waterline at the border between the high and low marsh vegetation zones. Each month, at each wetland, sampling was carried out between 10:00 and 14:00, around local noon at three random points along each transect within the low marsh zone, on the mudflat, and in the adjacent water column on an incoming tide. All sampling was carried out in dry weather conditions. At each of the three points, low marsh vegetation (n=5) and microphytobenthos (n=3) were sampled for aboveground biomass and C production within 0.25 m^2 quadrats (e.g. Darby and Turner 2008), submerged aquatic vegetation was sampled using a 0.1 m^2 corer (e.g. Madsen 1993), surface water salinity was determined using a refractometer, and water samples for nutrient concentrations (n=3) and pelagic phytoplankton biomass (n=5) and productivity (n=4) were collected as close to the transect as possible. Photosynthetically active radiation (PAR) was measured using a Biospherical Instruments 4π sensor at the water surface and a depth of 0.15 m and used to calculate the light attenuation coefficient (k). Water adjacent to the permanent transects was sampled and filtered through pre-combusted GF/F filters (nominal pore size=0.7 μm). The filtrate was frozen and later analyzed for nitrate (NO_3^-), silicate ($Si(OH)_4$), phosphate (PO_4^{3-}) and ammonium (NH_4^+) using a Bran and Luebbe AutoAnalyzer II [NO_3^- and PO_4^{3-} according to Whitledge et al. (1981), $Si(OH)_4$ using Bran and Luebbe Method G-177–96 (Luebbe AutoAnalyzer Applications 1999)] and spectrophotometer for NH_4^+ (Solorzano 1969). We defined spring as March-May; summer as June-August and fall (or autumn) as September-October, for calculating seasonal averages.

Phytoplankton

Each month from each location, replicate 1 L water samples (n=5) were collected and brought back to the lab in a dark cooler. The ^{14}C light–dark bottle JGOFS protocol (IOC Intergovernmental Oceanographic Commission 1996) was modified to measure SFE phytoplankton primary productivity. A subsample of 250 ml was taken from each individual replicate water sample and incubated with 0.8 μCi of ^{14}C bicarbonate in polycarbonate bottles (four light and one dark). Bottles were incubated for 24 h at ambient bay water temperature and under 50 % ambient surface light conditions to ensure optimal light-saturated production, P_{MAX} (Lorenzi 2006). One hundred ml from each bottle were filtered onto a Whatman GF/F glass fiber filter and ^{14}C incorporation was determined by placing the filter in OptiPhase scintillation cocktail and counting in a low-background liquid scintillation counter (PerkinElmer Winspectral Guardian LSC). Dissolved inorganic carbon (DIC) concentrations were determined with an MBARI clone DIC analyzer (Friederich et al. 2002, Parker et al. 2006). The daily volumetric rates (mg C L^{-1} d^{-1}) were converted to areal rates (mg C m^{-2} d^{-1}) using the photic depth and assuming a linear decrease in photosynthetic activity with depth to the base of the photic zone. Fifty ml from each replicate (n=5) was also filtered onto a GF/F glass fiber filter for chlorophyll *a* analysis. Chlorophyll *a* from each filter was extracted in 8 ml of 90 % acetone at 0 °C in the dark for 24 h, and fluorescence was measured on a Turner Designs 10 AU fluorometer. Seasonal mean areal phytoplankton chlorophyll *a* concentrations were calculated by multiplying seasonal mean chlorophyll *a* (μg l^{-1}) by the mean channel depth (at MHHW, as determined by GIS) for channels in each of the wetland sites.

Microphytobenthos

Benthic primary productivity was measured using a ^{14}C technique developed for marsh sediments (modified from Van Raalte et al. 1974). From each sampling site, 4 cores (2.5 cm diameter, 0.5 cm depth; Admiraal et al. 1982) were collected from random points at low tide, and the golden-brown sheen

on the surface of the sediments suggested that benthic diatoms were the dominant producers (Gould and Gallagher 1990, Sullivan and Currin 2000). The cores (three light and one dark) were incubated intact and upright in 30 ml clear polycarbonate sealed containers in a flow-through water table under 50 % irradiance. The surface of each core was covered with 10 mL of solution containing GF/F filtered water from the collection site and 0.4 μCi of ^{14}C bicarbonate. After 24 h, incubations were terminated with addition of 2 % formalin to stop all photosynthetic activity, and rinsed with dilute hydrochloric acid to remove ^{14}C that was not incorporated. The cores were then digested using full-strength nitric acid to release labeled, fixed ^{14}C into solution and the activity measured using liquid scintillation. We were aware of the potential for underestimation of benthic production associated with the nitric acid digestion method that we employed (Colijn and de Jonge 1984, Gould and Gallagher 1990), however, we are confident that our measured values are useful for cross-site comparisons within this study. The chlorophyll *a* content of the microphytobenthos in mudflat cores was determined by grinding and extraction in 90 % acetone and read on a Turner Designs 10 AU fluorometer.

Low Marsh and Submerged Aquatic Vegetation

To assess primary production in low marsh vegetation (*Spartina foliosa* at all Napa sites and Carl's Marsh, *Carex obnupta* at Brown's Island), we measured CO_2 uptake using an infrared gas exchange technique (Geider and Osborne 1992). Blades of the intact living plants were placed within a chamber with flow-through CO_2 gas flow between the chamber and an infrared gas analyzer (IRGA, CIRAS-1, PP Systems). Carbon fixation was measured directly as the decrease in CO_2. We sampled replicate (n=5 per plot) plants at peak light intensity (points between 10:00 and 14:00 h). Rates were converted to daily rates by allowing for the number of daylight hours minus one hour for sunrise and sunset (Kimmerer et al. 2012). While respiration was accounted for in daytime primary production measurements, no correction was made for overnight respiration that occurs in low marsh vegetation. As a result, these measurements are likely an overestimate of daily net primary production (in contrast to the 24-h incubations for phytoplankton and microphytobenthos, which more closely approximate net primary production (Harding et al. 2002)). Since sampling was carried out only one day a month, to determine how representative the sampling day PAR and extrapolated rates were, the incoming total PAR for each sampling day was compared with the available daily PAR for each month using data available in the California Irrigation Management Information System (CIMIS; cimis.water.ca.gov) available for three stations adjacent to our study sites (Station 170 for Browns Island and Sherman Lake, Station 109 for the Napa sites and station 187 for Carl's Marsh). Photosynthetically active radiation on our sampling days represented 100.2 to 101.2 % of the average monthly PAR means, suggesting that the sampling day values of PAR were representative of the month. At Sherman Lake there was no *S. foliosa* or *C. obnupta*, and the upper marsh plant *Schoenoplectus americanus* occurred. We did not measure *S. americanus* because 1) it was not at an equivalent marsh elevation to *S. foliosa*, and 2) due to its morphology, it could not be analyzed using our IRGA.

At Sherman Lake the macrophyte sampled was exclusively the submerged aquatic vegetation *Cabomba caroliniana*. Production of *C. caroliniana* was determined using the oxygen evolution method and equations of Littler and Littler (1985). Replicate samples were collected and brought back to the lab for incubation under the same temperature and light conditions as the phytoplankton and benthic diatom core samples. Tissue was rinsed to remove epiphytes, invertebrates and debris, and spun in a lettuce spinner for 1 min to remove excess water. One-gram wet-weight samples were placed into each 300 ml BOD bottle with bay water from the collection site. Four light and two dark bottles were incubated in a flow-through water table under 50 % of surface irradiance conditions. After one hour, dissolved oxygen was measured using a WTW 197i meter with self-stirring probe. Oxygen evolution was then converted to carbon fixed using the equations of Littler and Littler (1985). Using the same approach as for low marsh vegetation, daily rates were obtained by multiplying by the number of hours of daylight minus one hour at sunrise and sunset on the sampling day (Kimmerer et al. 2012), and the incoming PAR on the sampling days was representative of the monthly daily average. The daily rates (mg C g^{-1} d^{-1}) were converted to areal productivity rates (mg C m^{-2} d^{-1}) using total grams of wet weight per quadrat. The chlorophyll *a* content of low marsh vegetation and SAV was determined by grinding known areas and wet weights of tissue respectively, extraction of pigments in 90 % acetone, and reading on a Turner Designs 10 AU fluorometer. Chlorophyll *a* content was reported as mg chlorophyll *a* m^{-2} and mg chlorophyll *a* g^{-1} wet weight respectively.

Data Analysis

Comparisons of production across site and time for water column nutrients and chlorophyll *a* concentration and phytoplankton C fixation were performed after testing the data for equal variances using Levene's test and for normality using the Shapiro-Wilk W test. Data not meeting assumptions were either log transformed and analyzed with two-factor ANOVA, or Kruskal-Wallis tests with the Scheirer-Ray-Hare extension (nonparametric analog for a two-factor ANOVA) was used when data could not be transformed. Microphytobenthos and low marsh vegetation chlorophyll *a* and primary production were compared across sites using nested ANOVA with sample

plot nested by site. Differences in the C contribution of each group of producers across different wetland sites over time were analyzed using Friedman's nonparametric test, in which sums of ranks within time blocks were summed across sites, to indicate whether a site effect occurred while controlling for time. Since SAV was only present consistently at Sherman Lake, changes in chlorophyll *a* and production over time were approximated using one-way ANOVA and Kruskal-Wallis nonparametric tests respectively.

Results

Salinity, Light Availability and Nutrients

The Napa sites (Bull and Coon Islands and Pond 2A) all showed similar increasing trends in salinity from spring to fall (autumn) (Table 2). Carl's Marsh, the most seaward wetland, had the highest mean salinity, reaching 26.5 in the fall (autumn). The more landward Suisun Bay sites all had mean

Table 2 Mean (±SEM, n=number of samples) nutrient concentrations and light attenuation (k) measured during spring (Mar-May), summer (June-August) and fall (Sept-October) in 2004

Site	Season 2004	Salinity	k m^{-1}	NO_3^- µmol l^{-1}	$Si(OH)_4$ µmol l^{-1}	PO_4^{3-} µmol l^{-1}	NH_4^+ µmol l^{-1}
Carl's Marsh	Spring	7.3±1.4	4.1±0.3	32.3±7.0	199±16.7	7.7±0.6	13.7±0.8
	n=9	(*n*=3)	(*n*=3)				
	Summer	22±0.6	3.7±1.2	22.2±0.8	162±1.4	6.9±0.3	8.1±2.2
	n=9	(*n*=3)	(*n*=3)				
	Fall	27±0.3	8.2±2.5	10.1±0.2	165±1.6	5.5±0.2	13.1±0.2
	n=6	(*n*=2)	(*n*=2)				
Bull Island	Spring	3.3±0.8	2.0±0.8	34.9±13.0	263±61.1	1.8±0.1	8.0±1.6
	n=9	(*n*=3)	(*n*=2)				
	Summer	12±0.8	2.5±0.6	1.0±0.3	99.9±5.7	2.5±0.1	3.2±0.7
	n=9	(*n*=2)	(*n*=3)				
	Fall	20±0	1.9±0	8.4±0.8	173±0.4	2.8±0.1	8.1±0.2
	n=6	(*n*=2)	(*n*=2)				
Coon Island	Spring	4.0±0.9	2.0±0.3	43.6±11.0	281±44.6	1.9±0.1	9.0±1.5
	n=9	(*n*=3)	(*n*=2)				
	Summer	17±0.6	1.2±0.3	2.4±1.1	98.5±6.1	2.8±0.4	4.3±1.0
	n=9	(*n*=3)	(*n*=3)				
	Fall	20±1.0	1.7±0.2	15.2±2.5	194±15.1	4.0±0.4	12.6±1.1
	n=6	(*n*=2)	(*n*=2)				
Pond 2A	Spring	9.7±1.4	1.9±0.5	3.0±0.9	114±17.2	2.3±0.3	6.5±0.5
	n=9	(*n*=3)	(*n*=3)				
	Summer	19±0.4	1.6±0.1	1.7±0.7	115±7.8	2.7±0.1	6.3±0.8
	n=9	(*n*=3)	(*n*=3)				
	Fall	21±0.3	1.6±0.3	8.1±1.0	177±12.6	4.1±0.2	11.9±0.8
	n=6	(*n*=2)	(*n*=2)				
Brown's Island	Spring	0	1.5±0.6	13.4±1.2	260±14.2	1.6±0.1	3.4±0.2
	n=9	(*n*=3)	(*n*=3)				
	Summer	0	1.4±0.3	9.2±2.5	202±2.5	2.3±0.3	5.7±1.4
	n=9	(*n*=3)	(*n*=3)				
	Fall	2.0±0.5	1.0±0.1	9.9±3.5	174±1.2	2.9±0.4	4.3±1.0
	n=6	(*n*=2)	(*n*=2)				
Sherman Lake	Spring	0	3.4±0.5	1.4±0.3	292±10.5	5.1±0.3	7.8±0.7
	n=9	(*n*=3)	(*n*=3)				
	Summer	0	2.9±0.7	0.5±0.3	311±6.3	3.4±0.6	7.4±0.7
	n=9	(*n*=3)	(*n*=3)				
	Fall	1±0	2.7±1.3	0.2±0.1	323±72.9	2.5±0.1	8.7±0.7
	n=6	(*n*=2)	(*n*=2)				

seasonal salinities≤2 (Table 2). The light attenuation coefficient was greatest at Carl's Marsh (up to 8.2 m^{-1} in fall), followed by Sherman Lake (up to 3.4 m^{-1} in spring). Although k is determined by multiple factors (turbidity, dissolved compounds and intrinsic light adsorption properties of water) low k values seemed to be indicative of turbid water at these locations. The other wetland waters tended to be less turbid, with k ranging from 1.0 to 2.5 m^{-1} (Table 2).

Nitrate, silicate and orthophosphate concentrations differed across site (Sheirer-Ray-Hare, $p<0.001$) and time (Sheirer-Ray-Hare, $p<0.05$), while a significant interaction between site and time occurred for ammonium (Sheirer-Ray-Hare, $H_{35}=75.10$, $p<0.001$) (Electronic Supplementary Material (ESM 1)). Overall nutrient concentrations were generally highest at Carl's Marsh, followed by the Napa wetland marshes, while Suisun wetlands were lowest for all nutrients, except $Si(OH)_4$. Nitrate concentrations tended to be highest in the spring and decreased during the summer. Seasonal mean $Si(OH)_4$ concentrations were> 100 μmol l^{-1} at all sites (Table 2). Orthophosphate concentrations were>1 μmol l^{-1} over all sites and seasons (Table 2) with most sites showing increasing concentrations from spring through fall. Carl's Marsh and Sherman Lake had the highest PO_4^{3-} concentrations. Seasonal mean NH_4^+ concentrations were mostly>4 μmol l^{-1} except at Brown's Island in Suisun Bay, where concentrations were consistently<6 μmol l^{-1}.

Seasonal Changes in Chlorophyll *a* Concentration

A significant interaction between site and time occurred for phytoplankton chlorophyll *a* concentration (Sheirer-Ray-Hare, $H_{35}=97.34$, $p<0.001$, ESM 1) although concentrations appeared to be highest in the spring, with the highest seasonal mean reported for Carl's Marsh (10.9 μg l^{-1} or 10.9 mg m^{-2}) (Table 3). The lowest spring measurements of chlorophyll *a* were made at wetland sites located in Suisun Bay (~4 μg l^{-1}). Phytoplankton chlorophyll *a* concentration generally seemed to decrease from summer to fall (autumn), with the lowest values in the fall at Brown's Island (1.1 μg l^{-1} or 3.2 mg m^{-2}) and Carl's Marsh (1.9 μg l^{-1} or 1.4 mg m^{-2}). On an areal basis (m^2) benthic chlorophyll *a* concentrations were 5.8 to >60-fold higher than pelagic chlorophyll *a* (Table 3) and differed across sites (Nested ANOVA, $F_{5,12}=11.70$, $p=0.0003$). While wetland site explained 17 % of the variance, 82 % was attributed to within-site variation, which is consistent with strong seasonality in chlorophyll *a* concentration. The highest concentrations typically occurred in the summer and fall (e.g. 244 mg m^{-2} at Pond 2A in fall (autumn), except the highest seasonal mean reported was for Brown's Island in the spring (273 mg m^{-2}). Carl's Marsh consistently had the lowest benthic chlorophyll *a* concentration. For all sites where low marsh vegetation was present, chlorophyll *a* concentration differed by location (Nested ANOVA, $F_{4,10}=9.31$, $p=0.0021$). In addition, the high within-site variation (91 %) was likely due to changes in chlorophyll *a* concentration over time; it typically increased throughout the growing season, with the highest values in fall (autumn). Brown's Island had the lowest areal concentration of low marsh vegetation chlorophyll *a*, while the highest was measured at Coon Island (454 mg m^{-2}). Submerged aquatic vegetation was rare at all sites except Sherman Lake (*Cabomba caroliniana*). Concentrations of chlorophyll *a* differed over the growing season (one way ANOVA, $F_{7,31}=3.24$, $p=0.01$), and concentrations were lowest in March, followed by increasing concentrations that peaked in September (Tukey-Kramer HSD, March vs. August ($p=0.048$); March vs. Spetember ($p=0.007$)).

Primary Production by Different Autotrophs at Different Marshes

Areal primary production (g C fixed m^{-2} d^{-1}) patterns across sites and season were complex for all four groups of producers. There was a significant interaction between site and time for phytoplankton production (Two-factor ANOVA, $F_{35}=14.80$, $p<0.0001$), and peaks in phytoplankton production generally seemed to occur in the spring or summer at all sites (Fig. 2). Rates at the Napa locations (Bull, Coon and Pond 2A; Fig. 2b, c, d) were 2–3 times greater than those at Suisun Bay locations (Brown's and Sherman Lake; Fig. 2e, f), with highest rates (~1.5 g C m^{-2} d^{-1}) observed at Bull Island. Microphytobenthos primary production rates differed across wetlands (Nested ANOVA, $F_{5,12}=33.62$, $p<0.0001$) (ESM 1) and were an order of magnitude lower, and more variable than water column phytoplankton production rates (Fig. 3). Site differences accounted for 27 % of the variance with nearly the entire remainder (73 %) attributed to within plot variation, likely due to seasonal changes. Benthic production rates were generally highest in the spring at all sites except Coon Island (Fig. 3c), and several locations exhibited a second peak in the late summer-early fall (Fig. 3b, d, f). The highest rates of benthic production occurred at Pond 2A and Sherman Lake (~0.1 g C m^{-2} d^{-1}). Differences in low marsh vegetation production occurred across wetland sites (Nested ANOVA, $F_{4,10}=41.07$, $p<0.0001$), with 17 % of the explained variation. Production rates for low marsh vegetation appeared to be highest in spring and decrease through the fall (autumn) (Fig. 4a-e). Of the sites with low marsh vegetation, the highest rates of production occurred at Pond 2A (reaching ~10 g C fixed m^{-2} d^{-1}). At Sherman Lake, SAV grew extensively over the course of the growing season, and corresponded to a general increase in production over time (Kruskal-Wallis, $\chi^2=30.15$, $p<0.0001$) (Fig. 4f). Production rates of both low marsh vegetation and SAV were an order of magnitude higher than phytoplankton, and two orders of magnitude greater than rates of microphytobenthos production. Therefore on an areal basis (i.e. per m^2), the order of increasing primary production

Table 3 Mean (±SEM) chlorophyll *a* concentrations measured during spring (Mar-May), summer (June-August) and fall (Sept-Oct) in 2004

Site	Season 2004	Phyto Chl *a* µg l^{-1}	Phyto Chl *a* mg m^{-2}	Benthic Chl *a* mg m^{-2}	Low Veg Chl *a* mg m^{-2}	SAV Chl *a* mg g^{-1} wet tissue	SAV Chl *a* g m^{-2} wet tissue
Carl's Marsh	Spring	10.9±1.6	7.8±1.1	45.1±2.8	200±13.6		
		(*n*=14)	(*n*=14)	(*n*=27)	(*n*=39)		
	Summer	3.0±0.3	2.2±0.2	66.6±2.2	288±12.0		
		(*n*=15)	(*n*=15)	(*n*=27)	(*n*=45)		
	Fall	1.9±0.4	1.4±0.3	44.7±1.6	337±20.6		
		(*n*=12)	(*n*=12)	(*n*=18)	(*n*=30)		
Bull Island	Spring	4.7±0.7	7.6±1.1	79.0±18.3	194±9.9		
		(*n*=15)	(*n*=15)	(*n*=27)	(*n*=30)		
	Summer	4.0±0.4	6.6±0.6	202±25.8	244±12.4		
		(*n*=15)	(*n*=15)	(*n*=27)	(*n*=45)		
	Fall	3.8±0.7	6.2±1.0	207±8.9	363±18.7		
		(*n*=12)	(*n*=12)	(*n*=18)	(*n*=30)		
Coon Island	Spring	6.1±0.5	5.9±0.5	64.8±5.2	135±8.2		
		(*n*=15)	(*n*=15)	(*n*=27)	(*n*=41)		
	Summer	3.2±0.2	3.1±0.2	208±17.1	245±11.0		
		(*n*=15)	(*n*=15)	(*n*=27)	(*n*=45)		
	Fall	3.4±0.3	3.3±0.3	194±19.9	454±22.9		
		(*n*=12)	(*n*=12)	(*n*=18)	(*n*=30)		
Pond 2A	Spring	6.1±0.7	11.5±1.3	152±16.4	267±12.44		
		(*n*=15)	(*n*=15)	(*n*=27)	(*n*=45)		
	Summer	2.6±0.2	4.9±0.4	143±15.0	290±8.5		
		(*n*=15)	(*n*=15)	(*n*=27)	(*n*=45)		
	Fall	3.1±0.6	5.9±1.0	244±8.4	317±20.2		
		(*n*=12)	(*n*=12)	(*n*=18)	(*n*=30)		
Brown's Island	Spring	4.0±0.5	12.1±1.6	273±57.7	203±8.9		
		(*n*=15)	(*n*=15)	(*n*=27)	(*n*=30)		
	Summer	1.6±0.2	4.9±0.5	233±23.0	189±8.1		
		(*n*=15)	(*n*=15)	(*n*=27)	(*n*=45)		
	Fall	1.1±0.1	3.2±0.3	149±17.8	246±18.8		
		(*n*=12)	(*n*=12)	(*n*=18)	(*n*=30)		
Sherman Lake	Spring	4.3±0.5	6.9±0.8	52.8±6.5		31.3±2.3	3.28±0.54
		(*n*=15)	(*n*=15)	(*n*=27)		(*n*=12)	(*n*=12)
	Summer	5.2±0.3	8.4±0.5	123±6.1		42.6±2.6	6.97±0.56
		(*n*=15)	(*n*=15)	(*n*=27)		(*n*=12)	(*n*=12)
	Fall	4.2±0.8	6.9±1.3	177±17.1		43.7±3.6	15.9±1.8
		(*n*=12)	(*n*=12)	(*n*=18)		(*n*=8)	(*n*=8)

is microphytobenthos<phytoplankton<SAV<low marsh vegetation (Figs. 2, 3 and 4).

Ecosystem Scale Primary Production Rates

Areal rates of primary production were multiplied by the wetland area that each group of autotrophs occupied (Table 1) to yield estimates of the contribution that each made to total carbon production within the open water and tidally flooded sites of each wetland (Fig. 5). Not surprisingly, due to the relatively high areal primary production rates (Fig. 4), low marsh vegetation differed across wetlands (Friedman's test, $\chi^2=21.94$, $p<0.001$) and was the largest contributor to carbon production at four of the five wetlands where it was present (Fig. 5a, c, d, e). The exception occurred at Bull Island (Fig. 5b), where low marsh vegetation occupied less than 1 % of the area occupied by the primary producers studied (Table 1). Instead, phytoplankton production (which also differed across site; Friedman's test, $\chi^2=30.18$, $p<0.001$)

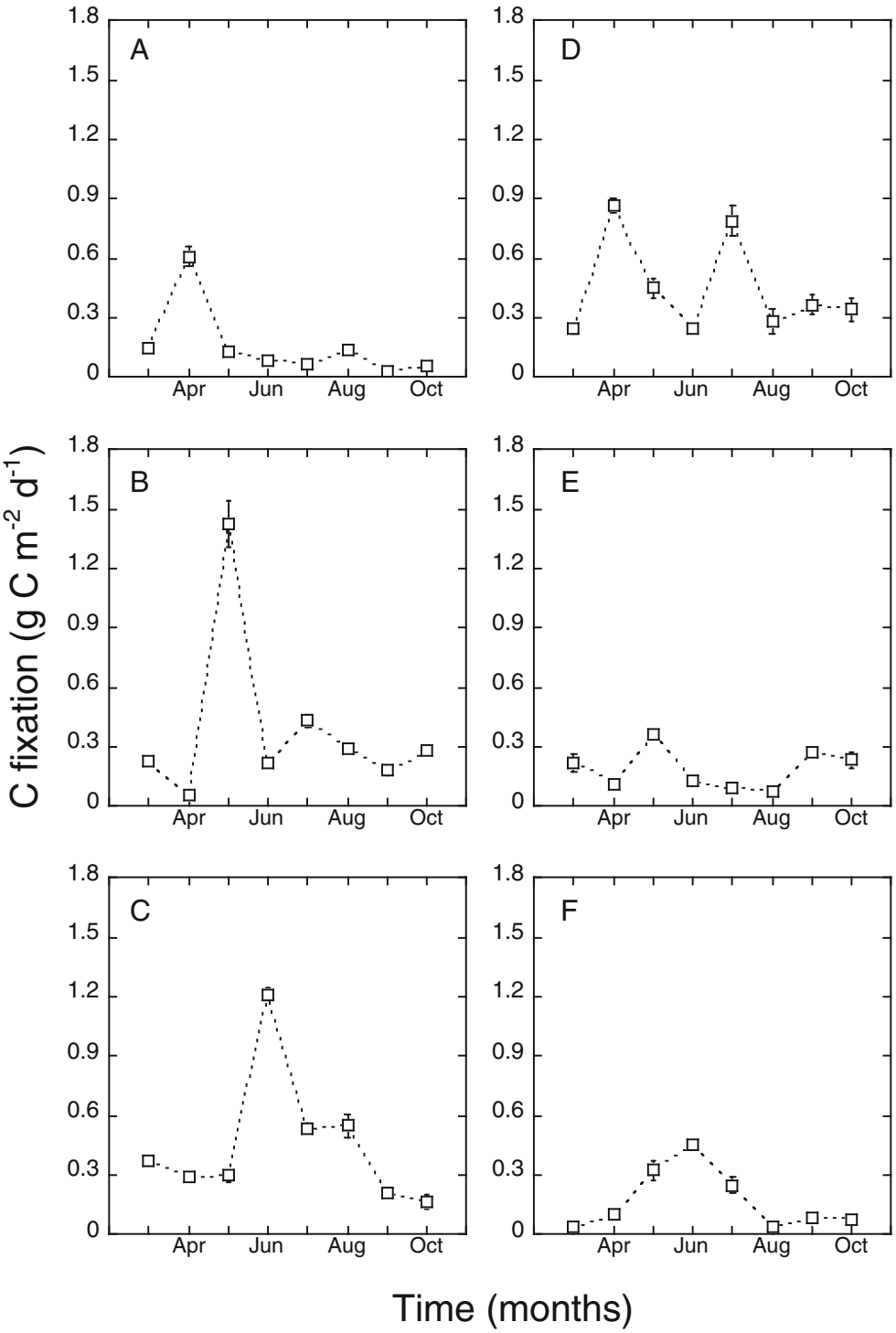

Fig. 2 Phytoplankton productivity at all sites in g C m^{-2} d^{-1} at **a**) Carl's Marsh, **b**) Bull Island, **c**) Coon Island, **d**) Pond 2A, **e**) Brown's Island and **f**) Sherman Lake. Error bars are ± one standard error of the mean (SEM) and n=4

contributed most to carbon production at Bull Island. Microphytobenthos was not a substantial contributor to carbon production at any site when scaled to each wetland (though its contribution differed across sites; Friedman's test, χ^2=27.57, p<0.001), likely a result of relatively low areal primary production rates (Fig. 3) and generally limited areal extent (ranging from <1 % at Pond 2A to nearly half of the area at Bull Island; Table 1). Sherman Lake was the only site with substantial (>5 %) areal coverage of SAV. Due to its relatively high areal primary production (Fig. 4f), and the absence of low marsh vegetation there, SAV accounted for between 16 and 71 % of the carbon production within Sherman Lake. While SAV was the dominant autochthonous carbon source during the fall (autumn) (71 %), phytoplankton contributed greater than 2/3 of the carbon produced during spring and summer in Sherman Lake.

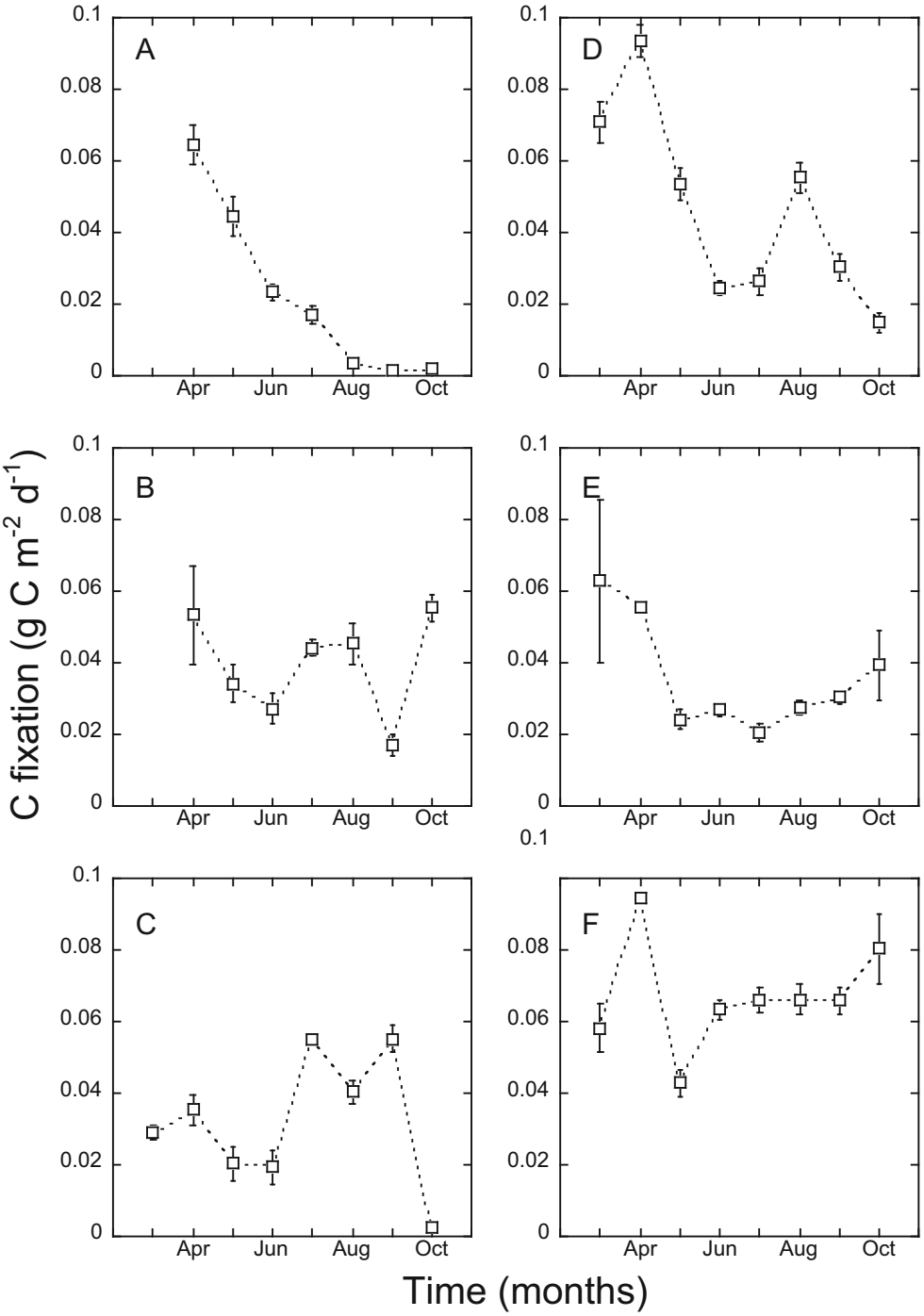

Fig. 3 Microphytobenthos productivity at all sites in g C m^{-2} d^{-1} at **a**) Carl's Marsh, **b**) Bull Island, **c**) Coon Island, **d**) Pond 2A, **e**) Brown's Island and **f**) Sherman Lake. Error bars are ± one SEM and n=9

Discussion

Overview

This study shows that low marsh vegetation and phytoplankton are the major contributors to wetland primary production in these six northern SFE wetlands. When the different primary production rates were compared, our hypothesis that areal production rate of low marsh vegetation would exceed microphytobenthos was met. However, our prediction that pelagic phytoplankton and microphytobenthos production would contribute the most to production within a given wetland, a result of greater areal coverage of extensive open water channel habitat, was only met at the older restored marshes, Bull Island in the Napa River and Sherman Lake in Suisun Bay. Interpreting how different autotrophic components (e.g. low marsh vegetation versus phytoplankton) contribute to landscape level differences in primary production needs consideration if wetland restoration activities are to achieve sufficient subsidies to the food web.

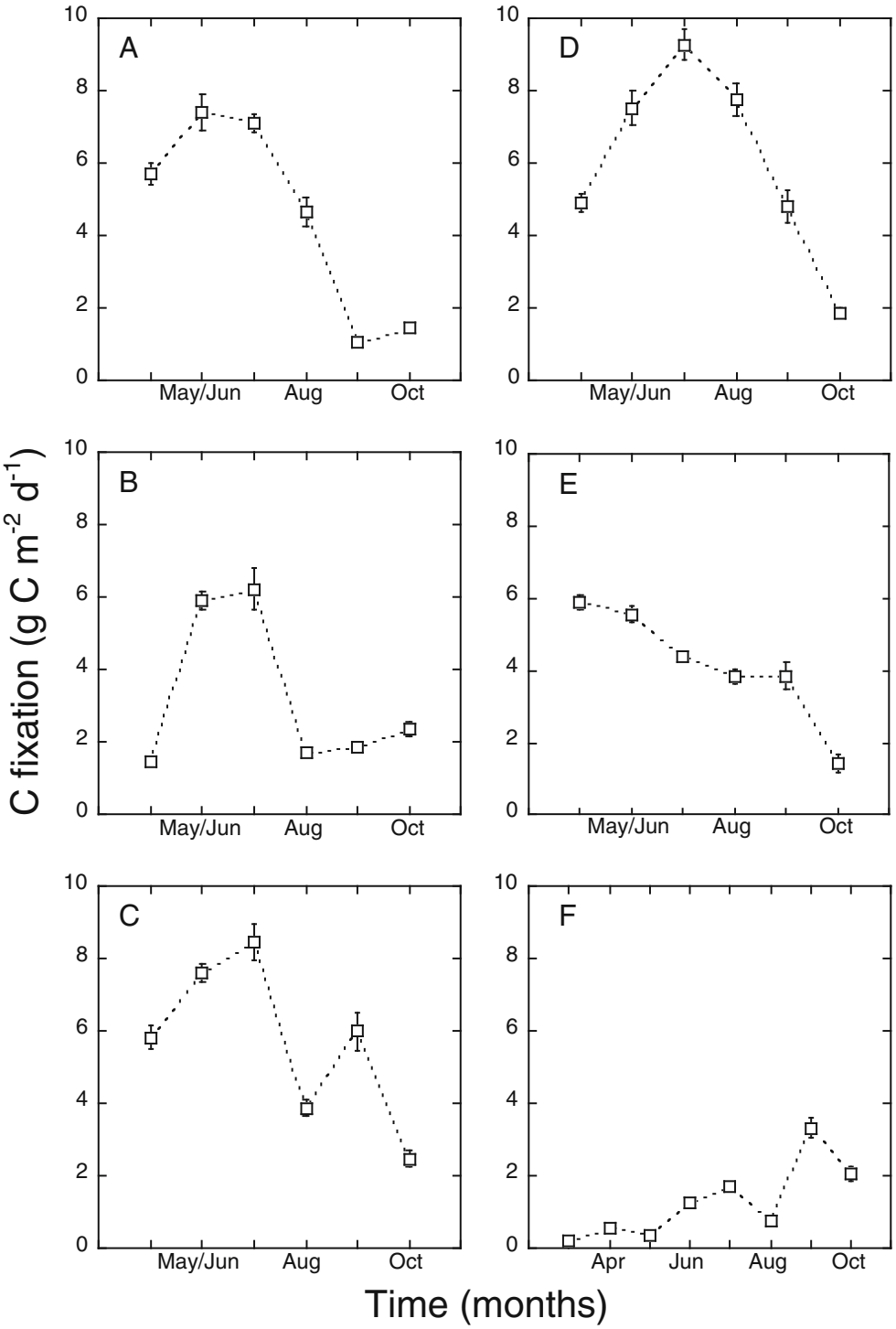

Fig. 4 Low marsh vegetation productivity (n=15) in g C m^{-2} d^{-1} at **a**) Carl's Marsh, **b**) Bull Island, **c**) Coon Island, **d**) Pond 2A, **e**) Brown's Island and **f**) SAV productivity (n=4) in g C m^{-2} d^{-1} at Sherman Lake. Error bars are ± one SEM

Ranking Autotrophs Based on Areal Primary Production and Landscape Scale Contribution to C Production

Rates of areal primary production for the different types of autotrophs varied widely across estuarine wetlands of the northern SFE. In particular, phytoplankton production at Suisun Bay sites (Brown's Island and Sherman Lake) was low relative to the other wetland sites. Lower rates of phytoplankton production have been observed in open water habitats of Suisun Bay when compared to other northern SFE embayments, and have been attributed to relatively low rates of phytoplankton NH_4^+ uptake (Wilkerson et al. 2006; Parker et al., 2012), turbidity and benthic grazing (Alpine and Cloern 1992; Kimmerer et al. 2012).

The microphytobenthos are recognized as important contributors to food web carbon in estuarine systems (e.g. Gould

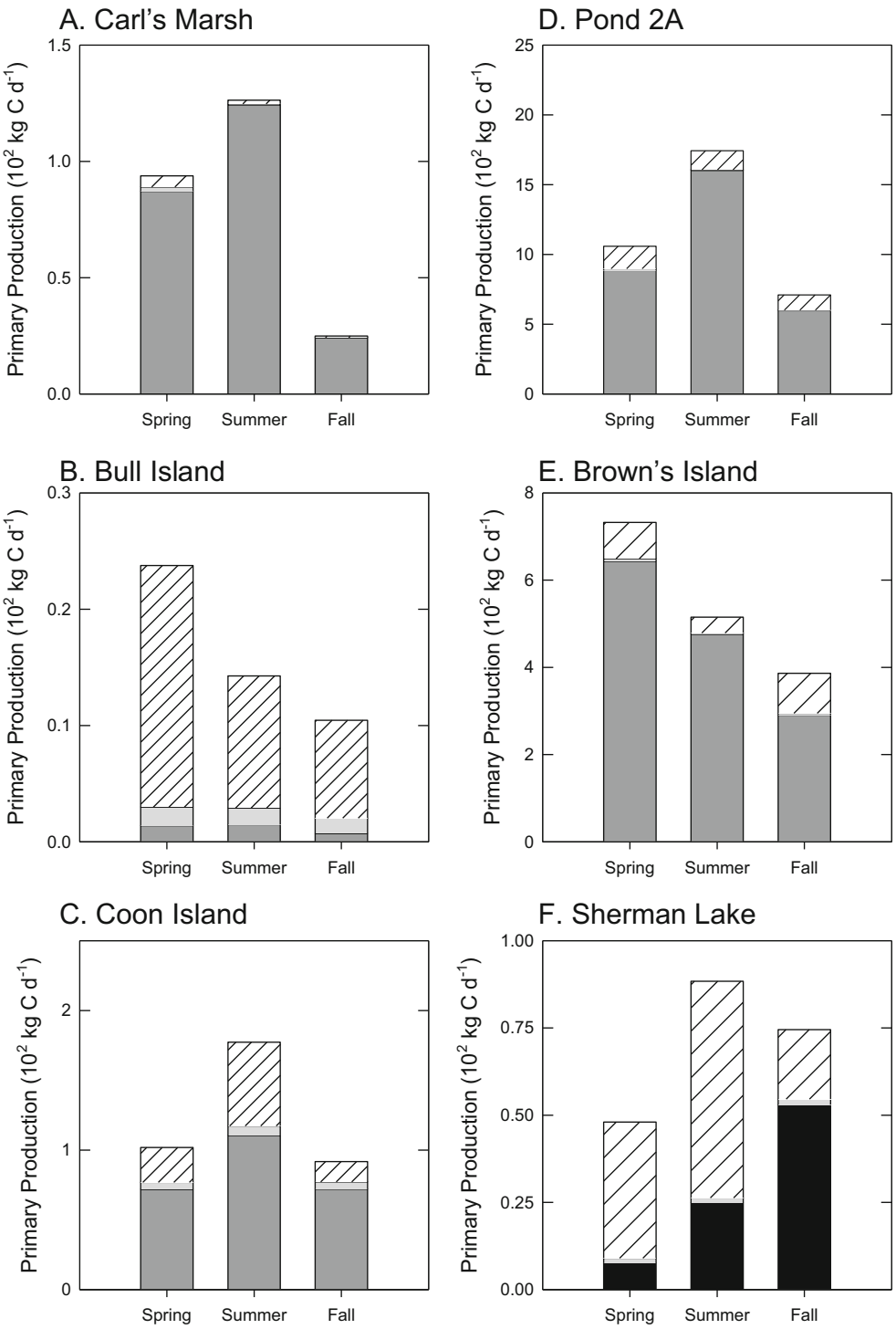

Fig. 5 Comparison of landscape scale productivity (in $*10^2$ kg C d^{-1}) for each wetland for phytoplankton, benthic algae, emergent vegetation and SAV for **a**) Carl's Marsh, **b**) Bull Island, **c**) Coon Island, **d**) Pond 2A, **e**) Brown's Island and **f**) Sherman Lake

and Gallagher 1990; de Jonge and Colijn 1994). However, there are presently few estimates of microphytobenthos production in the SFE. Areal production rates peaked in the spring across all six sites, similar to Van Raalte et al. (1976) who found peaks in benthic production in the early spring in a temperate marsh in the northeastern U.S. However, the microphytobenthos was less productive than phytoplankton overall, and higher variability in the benthic data may reflect patchy distribution (Pinckney and Zingmark 1993). Therefore microphytobenthos production rates should be better constrained as our findings suggest these producers contribute less on areal basis than the overlying water column.

All sites with low marsh vegetation (*Spartina foliosa* or *Carex obnupta*) exhibited the same seasonal pattern of high summer areal primary production rates relative to the other producer groups. That areal production rates were highest for

low marsh vegetation was not surprising given that other *Spartina* species, such as *S. alterniflora* have been shown to produce more than twice as much carbon than microalgae in east coast wetlands (Gallagher and Daiber 1974, Pinckney and Zingmark 1993). Generally this pattern of highest production by low marsh vegetation also held at the landscape level. The exception was at Bull Island, where overall carbon contribution by *S. foliosa* was less than that of phytoplankton, due to low areal coverage (<0.5 % of total autotroph area) (Fig. 5). Thus for the majority of sites sampled in this study, low marsh vegetation was the dominant contributor to overall wetland carbon production.

When present, SAV primary production rates were high, exceeding those for phytoplankton and microphytobenthos, but their importance to wetland productivity appears to be location dependent. Sherman Lake was the only site with abundant SAV, predominantly the invasive fanwort *Cabomba caroliniana*, which filled shallow channels almost completely by mid-summer. It is well known in the limnology literature that lakes tend to exist in alternate stable states, and be either phytoplankton or macrophyte dominated (Scheffer et al. 2003, Peckham et al. 2006). Thus in the extremely shallow channels of Sherman Lake, low phytoplankton productivity would be expected with high biomass of SAV. Furthermore, landscape scale primary production rates for SAV at Sherman Lake were similar in magnitude to low marsh vegetation measurements at Coon Island and Pond 2A. The generally high SAV production rates may have importance for these wetland systems as food and habitat for fish and invertebrate species. For example, Grimaldo et al. (2009) found evidence that fishes in littoral habitats of the SFE rely on food web support from SAV. However, there is the concern that the invasive SAV habitat is not used by native species (Brown 2003b, Nobriga et al. 2005).

Clearly, ranking the relative importance of various wetland primary producers also requires consideration of the spatial scales of analysis. For example, areal (mg C m^{-2} d^{-1}) primary production incorporates the abundance of various taxa within habitat types (i.e. mudflat, open water channel, or low marsh), whereas at the landscape scale (i.e. the entire flooded wetland) considers the relative contribution that each habitat type makes to the estuarine wetland system. Our results show that differences in producer rankings exist across these two spatial scales. At the areal scale, low marsh vegetation and SAV occupy the first and second highest rankings, respectively, followed by phytoplankton and microphytobenthos. At the scale of the wetland landscape, microphytobenthos consistently ranked lowest. For the other groups of producers, the rankings were site-specific, but low marsh vegetation ranked highest in contribution to wetland production at 4 of the 5 sites where it was present. At the fifth site, Bull Island, phytoplankton ranked highest driven by the larger areal cover of open water channel and less coverage of low marsh vegetation. At Sherman Lake (with SAV, but no low marsh vegetation) phytoplankton ranked highest during spring and summer, while SAV ranked highest during the fall (autumn) when open water channel habitat was at a minimum.

Habitat Availability

Habitat availability for primary producer types varied across wetlands. Phytoplankton habitat, defined here as open water or channel area, was the most abundant habitat type (30 to 86 %) while microphytobenthos habitat was 7.5 to 50 % (Table 1). Low marsh vegetation was present at five of the six marshes and occupied between <1 % to approximately 33 % of the area when it was present. Low marsh vegetation at the same elevation as *S. foliosa* or *Carex* sp. was completely absent at Sherman Lake where phytoplankton habitat was 86 % of the wetland productive area. SAV, present only at Sherman Lake (*Cabomba caroliniana*), represented roughly 7 % of the productive area. Based primarily on work in east coast estuarine wetlands, microphytobenthos has been shown to be especially important in young restoring marshes, with low marsh vegetation requiring time for establishment (Underwood 1997). Although our results show that the largest microphytobenthic contribution was in a wetland restored more than 50 years ago, it may be that all of the wetlands we sampled were relatively well established, or that other factors, such as sediment type or salinity, were driving this difference.

Comparison of Carbon Productivity Versus Landscape Size

We expected that the larger the landscape area available for primary production, the greater the overall primary production of the wetland. However, the only sites where the largest autotrophic habitat area also meant the largest areal production were Pond 2A and Brown's Island. This relationship did not hold for the other wetlands, where the ranking for size was Carl's Marsh < Bull Island < Coon Island < Sherman Lake and the ranked areal production was Bull Island < Sherman Lake < Carl's Marsh < Coon Island. In fact, the smallest wetland in terms of total autotrophic coverage, Carl's Marsh, had greater areal productivity than would be expected from the areal coverage of autotrophs alone, and may have been due in part to the high *S. foliosa* coverage (37 %) we observed there. Another small wetland, Coon Island, also had higher productivity than expected from total autotrophic coverage, and was well populated with both *S. foliosa* and phytoplankton habitat. The autotrophic cover of Bull Island was 50 % larger than Carl's Marsh and yet this wetland had the lowest areal production attributed predominantly to phytoplankton production, suggesting that *S. foliosa* coverage may be a good indicator of areal productivity of a wetland, rather than phytoplankton. Howe and Simenstad (2011) suggested that restored sites take 10 years before they reflect similar sources of carbon in their food webs as natural wetlands. Given that

the relatively young sites (Carl's Marsh and Pond 2A) had similar areal production to the natural site (Coon Island) than the older site (Bull Island) suggests that type and amount of habitat available are likely more important determinants of overall production than age post-restoration.

Food Web Implications for Restoration Practices

We found that low marsh vegetation generally contributed the most to overall wetland carbon production on an areal and landscape basis. A number of studies have shown low marsh vegetation (*Spartina* spp.) detritus to have low trophic efficiency, and to be relatively unimportant to estuarine wetland consumers (e.g. Riera et al. 1999; Galvan et al. 2011). In contrast, organic carbon derived from phytoplankton, microphytobenthos and SAV supports the food web through grazer pathways via zooplankton and benthic grazers at relatively high trophic efficiency (e.g. Pinckney and Zingmark 1993; Jassby et al. 1993; Sobczak et al. 2002; Grimaldo et al. 2009). Although generalizations such as these may not apply to all estuarine systems or even to all consumers within wetland habitats (Wainright et al. 2000; Howe and Simenstad 2011), it is essential to know which producer group should be augmented to balance the quantity of carbon produced with trophic efficiency of detrital and grazer pathways. In conclusion, to meet the carbon subsidy requirements for estuarine food webs, the relative contributions of producer types to overall primary production both at the areal (m^2) and landscape scale should be considered when designing large-scale wetland restoration projects.

Acknowledgments This material is based upon work supported by the CALFED Science Program under Grant No. 4600002883 and the Association of Bay Area Governments ERP grant E1083005/ABAG project #102186. Access to sites was granted by CA DFW and the East Bay Regional Park District. Many thanks to A. Marchi for performing water nutrient analyses, and to C. R. Chandler for providing advice on statistical analyses. Assistance with field sampling and laboratory analyses was provided by P. Bouley, S. Govil, J. Hausmann, C. Little, W. Most, A. Slaughter, K. Walker. Comments from P. Glibert, J. Cornwell and two anonymous reviewers greatly improved the quality of the manuscript.

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