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Isotopic Determination of Food Web Origins in Restoring and Ancient Estuarine Wetlands of the San Francisco Bay and Delta

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Abstract We compared the extent to which ancient and restoring wetlands in three estuary regions of San Francisco Bay support estuarine ecosystems through food web contributions. In comparison to mature marshes, we hypothesized that food webs of increasingly younger restoration sites would display increased dependency upon allochthonous subsidies due to nominal internal production. Using multiple stable isotopes ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) in a mixing model, we traced links among primary producers and estuarine consumers. Results indicate that food webs of estuarine marshes are heavily dependent upon autochthonous marsh materials (76±17%), even within the youngest restoration marshes (11 years). Nearly all sampled organisms relied upon autochthonous marsh materials, with the exception of *Neomysis kadiakensis*, a mysid shrimp, which derived the majority of its support from freshwater-produced phytoplankton. Marsh-derived organic matter (OM) support was consistent both temporally throughout the year and spatially along the three estuary regions, but evidence suggests that the specific type of OM supporting estuarine consumers depends on position along the estuarine gradient and on seasonal shifts in freshwater flow. These results indicate that wetland restoration rapidly provides important contributions to marsh consumers and potentially bolsters food web linkages in shallow-water ecosystems.

Keywords Restoration · Food web subsidy · Estuarine marshes · San Francisco Bay · Stable isotopes

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Introduction

Trophic resources often flow from areas of high productivity to those of low productivity, with allochthonous materials subsidizing consumers in adjacent, less productive ecosystems (Polis and Hurd 1995, 1996a, b). One of the most widely acknowledged examples of this phenomenon occurs in estuaries, where high estuarine marsh productivity results in the net outflow of marsh-derived nutrients and organic matter (OM) to coastal ecosystems (Teal 1962; Odum 1980). Food web subsidies have been extensively described among aquatic ecosystems (Duggins et al. 1989; Bustamante and Branch 1996; Menge 2004; Mumby et al. 2004) and across the land–water interface (e.g., Polis and Hurd 1996a; Sanchez-Pinero and Polis 2000; Nakano and Masashi 2001; Winder et al. 2005). The integral resource link across traditional ecosystem boundaries forces the marriage of food web ecology with landscape ecology (Polis et al. 1997) and therefore has unique applicability to restoration ecology. More specifically, recognition of this marriage may help guide decisions about how to increase ecosystem function across broad estuarine and near-coastal ecosystem mosaics.

Considering the link between landscape and food web ecology, it is plausible that significant alterations in land use patterns strongly impact the structure and function of affiliated food webs (Polis et al. 1997; Cloern 2007). Extreme alterations at the landscape scale could potentially disrupt or divert the natural direction of energy flows between adjacent ecosystems, especially if a more productive ecosystem, the traditional "donor", experiences substantial losses in either productivity or connectivity with surrounding environments (Polis et al. 1997; Puth and Wilson 2001). Conversely, strategic restoration and preservation in a complex mosaic of ecosystems may amplify simple additive effects of increasing productivity by

increasing food web interconnectivity among extant and restoring ecosystems.

The estuarine complex of San Francisco Bay and Delta (SFBD) serves as an ideal system in which to examine questions related to food web function and restoration success, as the estuary has experienced extreme structural and hydrological modifications (Conomos 1979; Nichols et al. 1986). During the past 150 years, all but 85 km^2 of the once vast complex (2,200 km^2) of tidal marshes and other wetlands have been disconnected through the construction of levees or eliminated by filling for development projects (Atwater et al. 1979). Until recently, the diminished contributions of tidal wetland ecosystems to SFBD's detritus-based food webs have been considered intractable or even trivialized. However, it is not hard to infer that the tremendous decrease in OM originating in marsh habitats represents a potentially non-trivial shift in subsidy magnitude between estuarine marshes and the open estuarine waters of SFBD, especially considering that large estuaries historically depended upon detrital pathways to fuel the estuarine food web (Teal 1962; Odum 1980). In addition to a shift in subsidy magnitude, the small amount of marsh-derived OM entering SFBD food webs may represent a shift in subsidy direction. As the food web subsidy signal from the once-extensive tidal marshes surrounding the SFBD has potentially faded into the background, evidence from pelagic food web studies suggests that detrital inputs no longer drive the overall SFBD food web (Jassby and Cloern 2000; Jassby et al. 2003). Several studies have shown that particulate organic matter (POM) collected from pelagic waters was largely composed of phytoplankton with minor contributions by vascular plant detritus and bacterial sources and that phytoplankton was the dominant OM type assimilated into some estuarine consumers (Canuel et al. 1995; Sobczak et al. 2005). Thus, as much as these findings conflict with the traditional estuarine outwelling paradigm, it appears that within the SFBD, pelagic production currently exhibits a greater influence on food webs than do estuarine marsh habitats.

Recently, a growing interest and commitment to conserve and restore historically lost wetlands has arisen within the SFBD, such that a mosaic of tidal wetlands, ranging from ancient marshes to currently restoring sites, is now emerging from the recent breaching of levees (Lucas et al. 2002; Simenstad and Bollens 2003). While extensive monitoring has occurred within these restoring marshes, little work has compared the recovery of ecological functions and processes, such as food web linkages among adjacent ecosystems, across this restoring mosaic.

Conceptual Model and Objectives

To test a major tenet of restoration ecology that lost ecological functions caused by disruptions in landscape connectivity and loss of critical ecosystem components can be recovered (Polis et al. 1997; Simenstad et al. 2006), in this study we examined the extent to which tidal marsh production supports estuarine consumers in restoring and ancient marsh ecosystems of SFBD. Specifically, we (1) compared the relative importance of allochthonous versus autochthonous sources of OM assimilated by representative components of the fish and macroinvertebrate assemblages inhabiting SFBD marshes, (2) explored differences in OM food web support between reference and restoring marshes, (3) contrasted diet profiles representing different consumer feeding and life history strategies to elucidate fine-scale food web patterns, and (4) evaluated food web pathways among marshes of varying restoration status (age) to determine whether within-marsh food web supplementation changes from allochthonous (i.e., supplements from the bay's open-water ecosystems) to autochthonous (i.e., in situ marsh production and assumed likely subsidy to comprehensive SFBD food webs) sources with increasing age of restoring wetland due to the recruitment and establishment of wetland autotrophs over time. Thus, we addressed the pragmatic question of "How long does it take a restoring tidal marsh food web to become self-sustaining?"

Methods

Approach

We employed stable carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) isotopes to track linkages between primary producers and consumers in restoring and mature (reference) tidal marshes in northern SFBD. Multiple stable isotope analysis has become a familiar technique to determine food web pathways in aquatic, terrestrial, and marine systems (e.g., Peterson et al. 1986; Hobson 1999) and has likewise proven useful in tracking OM subsidies across discrete ecotones within a system (Deegan and Garritt 1997; Hsieh et al. 2002; Guest et al. 2004). Because stable isotope distributions often vary among different ecosystems within the same estuary, it is often possible to describe the relative contribution of specific ecosystems and sources to the structure and function of food webs.

Study Sites and Sampling Design

Our study sites were embedded in a broader study design under the Integrated Regional Wetland Monitoring project (IRWM; www.irwm.org), an interdisciplinary effort examining wetland restoration in northern SFBD, where both restoring and mature (ancient or centennial) tidal marsh sites exist in close proximity to one another. Sampling was conducted on a quarterly basis in order to capture seasonal

shifts in food web patterns and other marsh processes. Marsh channels chosen for sample collection were consistent among sampling dates. The study was conducted from October 2003 through June 2005.

We conducted this research at eight tidal marshes in three estuary regions of northern San Francisco Bay, California, USA (Fig. 1). Estuary regions in which marsh study sites were located include the Petaluma River, the Napa River, and the confluence of the Sacramento and San Joaquin Rivers (Delta). We categorize sites among three broad ages of SFBD marshes: ancient, centennial, and restoring. Ancient marshes are those still persistent, relatively pristine wetlands that were created following the last glacial period (15,000–18,000 years ago; Atwater 1979), when sea level rise began flooding river valleys adjacent to SFBD, eventually giving rise to these ancient marshes as early as 8,000 years ago (Atwater et al. 1979). Centennial marshes were created as a by-product of hydraulic mining in the Sierras during the California gold rush (1850s), which dramatically increased sediment flows to the bay and created widespread and rapid expansion of tidal marsh area in shallow-water habitats (Atwater et al. 1979). Restoring sites include areas once reclaimed for salt pond evaporation or agricultural purposes, but to which tidal access has now been restored (between 11 and 73 years ago). Study sites for this project include pairs or trios of ancient/centennial and restoring marshes such that ancient/centennial sites serve as reference ecosystems to which restoration efforts can be compared (Table 1).

Food Web Source Collection

We chose primary producers to include the dominant vascular plants present at each study site, as well as benthic diatoms, filamentous algae, and phytoplankton. In June 2006, live plant material was collected from C_4 (*Spartina foliosa*) and C_3 (*Schoenoplectus maritimus*, *Schoenoplectus acutus*, *Salicornia virginica*, *Grindelia stricta*) salt marsh plants, brackish-water emergent marsh vegetation (*Typha* spp., *Juncus* sp.), and submerged aquatic vegetation (*Ceratophyllum demersum*, *Myriophyllum sibiricum*, *Cabomba caroliniana*, *Egeria densa*, *Ludwigia* spp., *Potamogeton crispus*). Four replicates of each available species were sampled at each of the seven primary field sites. Benthic diatoms (edaphic microalgae) were collected at low tide using a method adapted from Cloern et al. (2002); we placed 0.25-m^2 panels of 20-μm Nitex mesh on the sediment surface of exposed mudflats and channel walls (n=12). Screens were removed and rinsed clean with de-ionized water after 2–4 h of exposure

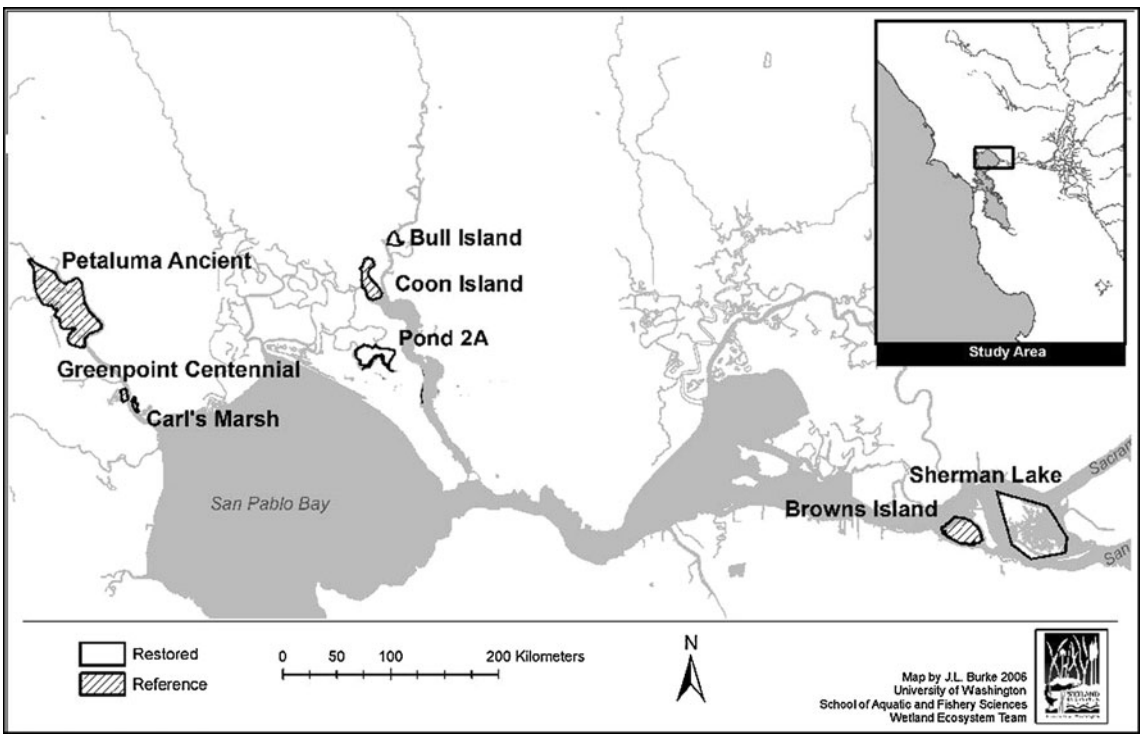

Fig. 1 Study locations, San Francisco Bay, California, USA. Estuarine marsh study sites were organized into three estuarine regions. The Petaluma River estuary region includes Petaluma Ancient, Greenpoint Centennial, and Carl's Marsh*. The Napa River estuary region includes Bull Island*, Coon Island, and Pond 2A*. The Delta estuary region includes Sherman Lake* and Brown's Island. An asterisk denotes restoring marsh sites

Table 1 Characteristics of SFBD marshes included in the study

Variable	Marsh							
	Brown's Island	Sherman Lake	Bull Island	Coon Island	Pond 2A	Greenpoint Centennial	Carl's Marsh	Petaluma Ancient
Region	Delta	Delta	Napa	Napa	Napa	Petaluma	Petaluma	Petaluma
Status	Ancient	Restoring (73 years)	Restoring (25 years)	Ancient	Restoring (11 years)	Centennial	Restoring (15 years)	Ancient
Elevation (m NADV*)	–	–	1.90	2.00	1.75	1.85	1.66	–
Salinity range (psu)	0.1–3.75	0.1–2.45	0.2–21	1.0–21	2.0–22	5–30	5–30	–
Water temp (°C)	9–21	9–21	9–18	8–19	9–19	9–22	9–22	–
% Bare ground	0	0	0	0	6.10	–	12.15	–
% Water	25.50	22.65	24.96	25.03	19.04	–	29.10	–
% Vegetated	74.50	77.35	75.04	74.97	74.40	–	58.75	–
Species richness	117	117	32	37	21	–	10	–
Dominant vegetation	*Scirpus americanus*, *Scirpus acutus*	*Scirpus acutus*	*Salicornia virginica*, *Scirpus maritimus*, *Scirpus* spp.	*Spartina foliosa*, *Salicornia virginica*, *Scirpus maritimus*	*Spartina foliosa*, *Salicornia virginica*, *Scirpus maritimus*	*Spartina foliosa*, *Salicornia virginica*, *Scirpus maritimus*	*Spartina foliosa*, *Salicornia virginica*, *Scirpus maritimus*	*Salicornia virginica*

Cover type percentages and vegetation data were obtained from IRWM's landscape ecology and vegetation teams (Lisa Schile and Karen Tuxin, unpublished data). Temperatures and salinities represent those ranges measured during quarterly collection periods. Many pieces of information are not available for Greenpoint Centennial and Petaluma Ancient, as these sites were not included in the overall IRWM project

**NADV* North American Vertical Datum, the zero surface to which surveyed marsh elevations were referred

to sediments, depending on ambient light levels and visual assessments of diatom migration into the screens from the benthos. Diatoms were filtered onto precombusted (500°C, 4 h) 0.2-μm Whatman GF/F glass fiber filters prior to isotopic analysis.

POM seston was collected at the entrance tidal channel to each marsh site using a 0.25-m-diameter 20-μm mesh Nitex plankton net towed against the current (n=61). Additionally, seston was collected on the USGS R/V *Polaris* cruise in August, 2005, beginning at station 18 in Central Bay near Angel Island and ending at station 649 in the Sacramento River near RioVista (n=12). In order to remove coarse particulate matter and zooplankton, water samples were passed through a 100-μm sieve. Samples were then filtered onto precombusted 0.2-μm Whatman GF/F glass fiber filters and freeze-dried for 24 h before being loaded into tin capsules for isotopic analysis. Corresponding water samples were also obtained and analyzed for chlorophyll α concentration in the water column. Chlorophyll α was extracted from seston samples for 24 h using 90% acetone, then measured using a fluorometer (Holm-Hansen and Reimann 1978). Water samples containing high levels of chlorophyll α and corresponding POM samples exhibiting C/N ratios between 5 and 9 gC g^{-1} N were considered to be phytoplankton-rich seston (Kendall et al. 2001; Jassby et al. 2002). These samples were included in the phytoplankton isotopic signature designation procedure below.

Phytoplankton Isotopic Signature Designation

We used a combination of methods to determine the best estimate for both freshwater and estuarine phytoplankton isotopic values. First, all seston samples were run for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$, C/N ratio, and chlorophyll α concentration. Based on the salinity of their associated collection point at the time of sampling, seston samples were divided into two groups: the Delta region ("Brackish"; <5 psu) and those collected in the bay, lower Napa River estuary, and lower Petaluma River estuary ("Estuarine"). Sixteen seston samples were taken in the Delta. Only four of these samples qualified as "phytoplankton-rich" because their

C/N ratio fell between 5 and 9 gC g^{-1} N. We collected a total of 57 samples in the bay and estuarine marshes, although only 11 qualified as "phytoplankton-rich". Carbon values were extrapolated from a regression line fitting the $\delta^{13}C$ versus C/N ratio ("Brackish": $y=0.2715x-29.683$, $R^2=0.96$; "Estuarine": $y=-2.0045x-9.3705$, $R^2=0.69$). "Pure" phytoplankton was estimated for a C/N ratio of 6.6 based on the Redfield ratio (Redfield 1934). Nitrogen isotope values were estimated using the same technique ("Brackish": $y=-0.7532x+12.735$, $R^2=0.41$; "Estuarine": $y=-0.5949x+13.453$, $R^2=0.53$).

Because pelagic phytoplankton turned out to have negative $\delta^{34}S$ values, we assumed the seston samples to be contaminated with benthic diatoms, which, according to our data, generally have a negative sulfur value in SFBD. We therefore used a more theoretical approach based on seawater sulfate $\delta^{34}S$ scaled by salinity. Pelagic phytoplankton should have a sulfur signature close to that of seawater sulfate, i.e., 20‰ and 22‰ (Stribling and Cornwell 1997). Measured fractionation rates of phytoplankton sulfur uptake are near 1.5‰, making most phytoplankton sulfur values between 18.5‰ and 20.5‰ (Stribling and Cornwell 1997). Having measured the $\delta^{34}S$ of seawater sulfate in the Pacific, Atlantic, and Arctic oceans, Szabo et al. (1950) found that the isotopic ratios of seawater sulfates were remarkably constant across the three oceans, ranging from 21.70±0.02 to 21.80±0.01, with an average $\delta^{34}S$ of 21.75±0.02‰. Sulfate saturation depends on salinity, however. According to Fry (2002), seawater sulfate so dominates a system with a salinity ~1 psu or higher that sulfides do not influence the $\delta^{34}S$ signature of pelagic phytoplankton. Thus, for sites located within the Napa and Petaluma River estuaries, which always had salinities above 1 psu during seston sampling periods, we assumed a fractionated (1.5‰) seawater sulfate signature (20.2‰) was appropriate. The same sulfur value was estimated by Stribling and Cornwell (1997) in a North Carolina estuary after measuring the seawater sulfate of that estuary at 21.7‰. Salinity values at sites located in the Delta, however, were often <1 psu, where sulfides and riverine sulfur begin to play a larger role as they mix with seawater sulfates. According to Weber et al. (2002), freshwater plants uptake water column sulfur with a fractionation rate of −5‰. Using this information, we used our average $\delta^{34}S$ values for submerged vegetation at Brown's Island (13.6‰) and added 5‰ to produce a "brackish" sulfur signature of 18.6‰ for phytoplankton in the Delta.

Consumer Collection

Fish species were chosen for isotope analysis according to feeding guild and life history strategies, representing water column and benthic feeders, marsh residents and transients, and species representing different trophic levels. Additionally, fish were chosen based on their relative numerical prominence and frequency of occurrence (IRWM, unpublished data) in tidal channel samples at each study site. Fishes meeting these criteria included the transient planktivorous inland silverside (*Menidia beryllina*), the resident benthic-feeding shimofuri goby (*Tridentiger bifasciatus*), the resident demersal-feeding yellowfin goby (*Acanthogobius flavimanus*) and Pacific staghorn sculpin (*Leptocottus armatus*), the resident planktivorous rainwater killifish (*Lucania parva*) and mosquito fish (*Gambusia affinis*), and the transient planktivorous/piscivorous striped bass (*Morone saxatilis*).

Fish were collected quarterly from each marsh during the spring tide series between October 2003 and June 2005. Winter and fall sampling periods occurred during the day, while summer and spring sampling occurred overnight. Channel fyke nets (3.2 mm mesh codend, 6.4 mm mesh adjustable wings) were deployed during the post-flood slack tide and recovered the following low slack tide or when the channel dewatered (see Cohen and Bollens 2008). Up to five specimens of each species (minimum of three) captured in each marsh were weighed and measured for fork length and preserved on ice until reaching the laboratory, where they were placed in a −80°C freezer before processing. Because species occurrence in the estuary is patchy, we were neither able to capture all species during each sampling event nor were we able to stratify collections according to size or life history stage.

A suite of invertebrate species representing various feeding guilds were collected at each marsh using a variety of collection methods. Clams (*Macoma balthica* and *Corbicula fluminea*) and mussels (*Ischadium demissum*) were collected by hand, individually removed from channel walls and bottoms inside the mouth of each channel. The tube-dwelling amphipods *Corophium* spp. were collected by sieving the top 5 cm of mud surfaces through a 500-μm sieve. *C. fluminea* and *I. demissum* represent filter feeders, while *M. balthica* and *Corophium* spp. represent benthic deposit and benthic suspension feeders, respectively. Water column zooplankton and neuston were collected during the ebb tide using a 0.5-m-diameter, 73-μm mesh Nitex plankton or floating neuston net, deployed against the current for approximately 15 min. Water column zooplankton analyzed in this study represent those species most abundant in the system at the time of sampling, including cumaceans, decapod shrimp, mysids, and amphipods. Despite this limitation, collected zooplankton and neuston species represent a mix of suspension, epiphyte, and detritus feeders. Based on gut content analysis, the collected species appear in the diets of fish analyzed (IRWM, unpublished data; Cohen and Bollens 2008).

Tissue Preparation for Isotope Analysis

Primary producer, fish, and invertebrate samples were thoroughly rinsed with de-ionized water followed by a rinse of 5% HCl to remove soil carbonates from sediments that coated fauna during sampling. Samples were then rinsed in de-ionized water to neutral pH. Adductor muscles were removed from bivalves, while abdominal muscles were removed from mysid and decapod shrimp exoskeletons. Other invertebrates (cumaceans and amphipods) were analyzed whole without gut evacuation. Frozen muscle tissue from above the lateral line was extracted from fish. For fish ≤40 mm TL, we removed internal body organs and used the remaining entire fish for isotopic analysis. Freeze-dried samples were mechanically homogenized to a fine powder and prepared for carbon (^{13}C), nitrogen (^{15}N), and sulfur (^{34}S) isotope analysis in the same manner as Howe and Simenstad (2007). Carbon and nitrogen analyses were conducted at Oregon State University, while sulfur concentrations were measured at the Coastal Sciences Laboratory in Austin, TX, USA.

Data Analysis

Isotope Ratios

The δ notation indicates the enrichment (+) or depletion (−) of the heavy isotope relative to the light isotope of a particular element relative to the standard as defined by the formula:

$$\delta X\,(‰) = [(R \text{ sample}/ R \text{ standard})\text{-}1] \times 10^3$$

where $X = {}^{13}C$, ^{34}S, or ^{15}N and $R = {}^{13}C/{}^{12}C$, $^{34}S/{}^{32}S$, or $^{15}N/{}^{14}N$. Pee Dee Belemnite and air were the standards for $\delta^{13}C$ and $\delta^{15}N$, respectively; Canyon Diablo troilite was the standard for $\delta^{34}S$. The analytical error, measured as the median difference between triplicate aliquots of plant and animal tissues, was 0.07‰ for $\delta^{13}C$ and 0.25‰ for $\delta^{15}N$ ($n=33$). For $\delta^{34}S$, the median difference between paired aliquots was 0.20‰ ($n=76$). These data indicate a high level of precision and correspond to the level of error reported by others (Cloern et al. 2002; Hsieh et al. 2002).

Multiple-Source Mixing Models

Source partitioning was conducted using the multiple-source mixing model, SOURCE, which allocates a percent contribution to a consumer's food web base for each primary producer group (Lubetkin and Simenstad 2004). This program uses linear programming techniques coupled with multiple tracers to estimate the central tendency of a consumer's direct and indirect uptake of autotrophic sources. Given that the solutions presented herein are only central tendency estimates within the corner-points of solution space, we stress that the results should only be viewed as a characterization of the true solution. Despite this limitation, SOURCE is especially useful because it allows for the accurate estimation of food web source contributions even when the number of potential autotrophic sources or foods exceeds the number of isotopic tracers, a situation particularly pertinent to estuaries.

However, SOURCE requires that the isotopic signatures of primary producers included in model simulations do not overlap. SOURCE thereby uses a nearest neighbor distance measurement (NND^2) to determine whether the isotopic values of included primary producers are distinct enough to be considered individually in model calculations. Plant types with similar isotope values must be pooled if they are not distinguishable according to NND^2 requirements (0.1 NND^2 minimum distance). It is important to note that isotope values that are significantly different from one another using traditional statistics are not necessarily distinguishable according to NND^2 measurements (Lubetkin and Simenstad 2004).

We generated separate mixing models for each of the estuary regions (Napa, Petaluma, and Delta) based on the average isotopic values of each plant species (pooled across marshes within an estuary region). Within each mixing model simulation, fish were treated as individual consumers (i.e., tissues from individual fish were neither combined prior to isotope analysis nor were the isotope values averaged among fish prior to mixing model computations). In contrast, multiple conspecific invertebrate individuals were homogenized in order to obtain enough biomass for isotope analysis, with the exception of *I. demissum* which are large enough to be analyzed individually.

Statistical Analyses

Data were analyzed using SPSS 13.0® (univariate statistics), Microsoft Excel® (univariate statistics), and Primer 6® (multivariate statistics) software. We performed *F* tests to test for equal variance and normality and employed analysis of variance (ANOVA; alpha=0.05) and two-sample *t* tests (assuming equal and unequal variance depending on requirements; alpha=0.05) to distinguish differences in $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values among organisms collected from different marshes and marsh types. These tests were also employed to compare isotopic values among and between organism types. We used Bonferroni post hoc tests to identify specific marsh or organism comparisons contributing to overall significant differences found with ANOVA results.

We employed multivariate data analyses to compare overall consumer isotope values ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$) among sites and dates and also to compare patterns in the OM sources ultimately supporting consumer diets derived from SOURCE mixing models. Consumer isotope and mixing model output data (OM source contributions) were analyzed using Primer's non-metric multidimensional scaling (NMDS) ordination, analysis of similarity (ANOSIM), and similarity percentage (SIMPER) analysis. Prior to NMDS ordination and similarity calculations, all mixing model data were square root-transformed as recommended for percentage data (Schafer et al. 2002). The Bray–Curtis similarity coefficient (mixing model data) and the Euclidean distance coefficient (isotope data) were used to construct similarity matrices (Clarke and Warwick 2001). We used one-way ANOSIM on similarity matrices to determine whether differences existed in isotope values and OM source contributions for specific fish and invertebrate species across sites and among seasons. ANOSIM has been increasingly used to describe community and isotopic differences on spatial, temporal, and organismal scales (Schafer et al. 2002; Lenanton et al. 2003). ANOSIM calculates an R value that is scaled between −1 and +1; as R approaches unity, the biological importance of the difference becomes greater (Clarke and Gorley 2001). ANOSIM also estimates a p value similar to that of ANOVA, with values of $p<0.05$ indicating significant differences. We further examined significant differences found through ANOSIM using SIMPER, which function similarly to ANOVA post hoc tests. We used SIMPER analysis to identify which species or primary producer categories primarily accounted for the differences seen in consumer diets and isotope values among sites, estuarine regions, organism guilds, and marsh types.

Outline of Main Comparisons

We first establish the primary producer baseline for the three estuary regions and then examine the proportion of autochthonous marsh-derived OM sources versus allochthonous (river or bay-derived) OM sources contributing to the overall consumer food webs of each estuary region. We specifically evaluate food web patterns associated with marsh age or restoration status, estuary region, and marsh study sites. Secondly, in order to assess whether the high level of variation across estuary regions and among consumer species masks finer-scale patterns in OM sources contributing to estuarine marsh food webs, we also examine OM source contributions on a per species, per region basis, using three exemplary organisms representing different feeding and life history strategies: (1) *M. beryllina* (inland silversides), thought to be transient planktivores within SFBD, obligated to exit marsh channels on the ebbing tide (Moyle 2002); (2) yellowfin gobies (*A. flavimanus*) considered marsh residents which feed on epibenthic organisms and marsh crustaceans and can remain in marsh channels during low tides (Moyle 2002); and (3) *M. balthica*, a sessile marsh consumer representative of benthic deposit feeders (Olafsson 1986). Enough *M. beryllina* were collected for analysis at all three Napa River estuary sites in January 2005 and September 2004, as well as all three Petaluma River estuary sites in October 2003. Enough *A. flavimanus* were captured for analysis in June 2004 and 2005 and September 2004 in the three Napa sites and in June 2004 at two sites in the Petaluma. In the Delta, enough *A. flavimanus* were collected at Brown's Island in June and September 2004. Finally, enough *M. balthica* were present for analysis in the three Napa River estuary sites in March and June 2005 and in September 2004.

Results

Primary Producer Baseline for Mixing Models

Because we found primary producers in the different estuary regions to be different in species composition and isotope signatures (Table 2), we constructed the isotopic food web base for each estuary region separately (Table 3). Within each estuary region, we pooled certain plant groups due to NND^2 violations. In the Petaluma River estuary, the group "C_3 emergents" includes *S. virginica* and *S. maritimus*. In the Napa River estuary region, *Typha* sp. is also included in "C_3 emergents". In the Delta region, "submerged aquatic vegetation" (SAV) includes *C. demersum*, *E. densa*, *Ludwigia* sp., *M. sibiricum*, *P. crispus*, and algae. The "C_3 emergent" group in the Delta includes *Juncus* sp. and *S. acutus*.

Consumer Isotope Patterns

Consumer isotope values largely fell within three-dimensional boundaries specified by the isotopic values of primary producers collected within each estuary region (Fig. 2), indicating successful characterization of the major primary producers contributing to SFBD food webs. Within the Napa River and Petaluma River estuary regions, macroinvertebrates were grouped into filter feeders (*I. demissum*) and non-filter feeders. Filter feeders tended to be depleted in ^{15}N and ^{13}C in comparison to most other fish and invertebrate species and overlapped most tightly with brackish phytoplankton and some C_3 emergent vascular plants. The remaining fish and macroinvertebrates fell between the isotopic values of the *S. foliosa* and C_3 emergent plants. A similar pattern was observed in the Petaluma River estuary, where both fish

Table 2 Average (± standard deviation) isotope values of primary producers by estuary region prior to mixing model nearest neighbor distance requirements ($n=4$ for each species in a study site. Primary producers were collected from two sites in the Delta Estuary region, three sites in the Napa Estuary, and two sites in the Petaluma Estuary. Within an estuary region, conspecific primary producers from all study sites are pooled)

Estuary region	$\delta^{13}C$		$\delta^{15}N$		$\delta^{34}S$	
	Average	SD	Average	SD	Average	SD
Delta						
Cabomba caroliniana	−35.12	0.41	9.82	0.63	12.53	0.36
Ceratophyllum demersum	−27.34	1.97	10.20	0.56	12.64	0.58
Myriophyllum spicatum	−24.53	2.59	8.67	2.22	13.58	1.22
Egeria densa	−29.42	0.31	10.76	0.43	15.24	0.11
Potamogeton crispus	−22.59	0.87	10.16	0.46	12.93	0.54
Ludwigia sp.	−28.41	0.18	9.45	0.39	11.48	1.42
Algae	−24.80	1.73	9.45	1.41	15.08	0.73
Diatoms	−22.94	1.50	6.09	2.12	5.55	–
Schoenoplectus acutus	−28.08	0.47	5.98	1.33	9.98	1.68
Typha sp.	−29.27	.023	5.71	0.94	5.56	1.40
Juncus sp.	−27.58	0.17	4.24	1.08	10.23	1.39
Napa						
Grindelia stricta	−26.64	0.60	3.89	1.14	17.60	1.00
Typha sp.	−27.44	0.20	6.13	0.50	10.08	1.35
Spartina foliosa	−13.54	0.07	8.51	0.41	17.25	0.37
Schoenoplectus maritimus	−25.47	0.68	8.35	2.03	12.01	2.12
Salicornia virginica	−26.09	1.07	6.96	1.37	14.91	2.10
Algae	−24.19	4.25	9.69	3.15	9.73	5.83
Diatoms	−19.39	2.72	7.42	1.55	−1.18	3.06
Petaluma						
Spartina foliosa	−13.18	0.31	10.30	0.67	15.50	0.86
Schoenoplectus maritimus	−23.81	0.54	8.99	0.45	14.77	0.42
Salicornia virginica	−26.21	0.65	9.14	0.59	15.28	2.96
Algae	−24.19	4.25	9.69	3.15	9.73	5.83
Diatoms	−19.39	2.72	7.42	1.54	−1.18	3.06
Phytoplankton						
Estuarine	−22.60	–	9.53	–	20.20	–
Brackish	−28.14	–	8.44	–	18.60	–

and macroinvertebrates fell between the isotopic values of the C_3 plants and *S. foliosa*. The food web of the Delta was more depleted in ^{13}C in comparison to the Napa and Petaluma systems. Consumers were divided in two loosely associated lobes, one of which focuses around submerged aquatic vegetation, the other around C_3 emergent plants and *Typha* sp.

Consumer Food Web Sources

Due to differences in primary producer species assemblages, cross-regional comparisons of food web source pathways were analyzed by grouping primary producers into three categories after running the SOURCE mixing model: (1) allochthonous bay-produced phytoplankton, (2) autochthonous marsh-derived material, and (3) allochthonous river-produced ("brackish") phytoplankton. With the exception of the mysid *Neomysis kadiakensis*, which was mostly supported by allochthonous brackish phytoplankton (58.7±8.4%), consumers were predominately supported by autochthonous OM from marshes (mean% contribution 76.2±17.4%), including benthic diatoms, filamentous algae, C_3 emergent vascular plants, *S. foliosa*, and submerged aquatic vegetation (Fig. 3).

Multivariate analysis of the collapsed OM source categories supporting SFBD consumers provided an excellent model representation of the consumer group distinction, with a 2D MDS stress level of 0.04. Significant differences in the OM

Table 3 Final isotope values utilized for mixing model input after combining plant groups according to nearest neighbor distance requirements by estuary region

Region	Primary producer	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$
Delta	Bay phytoplankton	−22.60	9.53	20.20
	Brackish phytoplankton	−28.14	8.44	18.60
	Cabomba caroliniana	−35.12	9.82	12.53
	Submerged vegetation	−26.23	9.67	13.34
	Benthic diatoms	−22.94	6.09	5.55
	C3 emergent plants	−27.88	5.39	10.06
	Typha sp.	−29.27	5.71	5.56
Napa	Bay phytoplankton	−22.60	9.53	20.20
	Brackish phytoplankton	−28.14	8.44	18.60
	Benthic diatoms	−19.39	7.42	−1.18
	Filamentous algae	−24.19	9.69	9.73
	Grindelia stricta	−26.64	3.89	17.60
	C3 emergent plants	−26.11	7.33	12.98
	Spartina foliosa	−13.54	8.51	17.25
Petaluma	Bay phytoplankton	−22.60	9.53	20.20
	Brackish phytoplankton	−28.14	8.44	18.60
	Benthic diatoms	−19.39	7.42	−1.18
	Filamentous algae	−24.19	9.69	9.73
	C3 emergent plants	−24.95	9.06	15.04
	Spartina foliosa	−13.18	10.30	18.50

supporting consumers were observed across estuary regions, between restoration and reference marshes, and across study sites (ANOSIM $p<0.001$), as well as across months, across feeding guilds, between fish and invertebrates, and across species (ANOSIM $p<0.001$). However, low R values ($0.049<R<0.227$) for all comparisons indicated that at this broad level of OM source categorization (marsh autochthonous, bay allochthonous, river allochthonous), no strong, biologically important patterns in overall consumer OM support were detected. Additionally, we examined differences in OM support among marshes of varying restoration status (age), finding no significant relationship between marsh age and the type of OM support (Table 4). Combined, these results illustrate the pervasive importance of marsh-derived OM in supporting estuarine consumer food webs within the tidal marsh ecosystem of SFBD.

Somewhat surprisingly, the contribution of each collapsed primary producer group varied little throughout the year (Table 5). Compared to the two phytoplankton types, which rarely contributed more than 15% each, estuarine marsh detritus consistently contributed higher amounts of OM to the food web base. Within the marsh-derived OM category, however, we observed shifts in consumer dependence over time. In the Napa estuary region, consumers relied more heavily on C_3 emergent and *S. foliosa* detritus in all months except for June, when consumers were more supported by filamentous algae and diatoms. In the Petaluma region, consumers were most supported by C3 emergent and *S. foliosa* detritus in all months except for March. In the Delta, the contribution of SAV appears to alternate in importance with emergent marsh plants (C_3 emergent plants and *Typha* sp.). SAV contributions were the highest (37±22%) in September, while combined C_3 emergent and *Typha* sp. contributions were the highest in June 2004 (48±15%) and March 2005 (61±0%).

Individual Consumer Food Web Sources

M. beryllina—Transient Planktivore

Napa River Estuary In contrast to the working hypothesis of greater allochthonous influence in younger marsh sites, inland silversides collected at the older site, Bull Island (BI; 25 years old), were observed to have incorporated significantly greater contributions of bay phytoplankton than those fish collected at the 11-year-old restoration site, Pond 2A ($t=2.26$, $p=0.01$, mean % contribution BI 20.9±8.5%, P2A 15.3±7.2%, Fig. 4). In support of the hypothesis, Bull Island inland silversides had assimilated more OM from phytoplankton than those fish collected at the Coon Island (CI) reference site (mean % contribution CI 19.2±11.8%). However, this difference was not significant.

The food web base supporting inland silversides in the Napa River marshes was dominated by autochthonous production year-round (mean % contribution 82.3±3.4%, min 76%, max 86%, Fig. 4). However, differences in the type of autochthonous OM contributions to *M. beryllina* production were evident among sites (2D MDS stress=0.12, 3D MDS stress=0.06, global $R=0.222$, $p=0.001$), with the main significant difference occurring between the two restoration sites, Bull Island and Pond 2A (ANOSIM pair-wise $R=0.320$, $p=0.009$, NSD between other site pairs). A total of 75.60% of the difference in food web contributions to silversides in Bull Island and Pond 2A can be accounted for by different types of autochthonous marsh materials assimilated by fish. SIMPER results indicate that the difference was mainly driven by saline cordgrass (*S. foliosa*) contributions to fish production (SIMPER test—25.17% of the discrepancy between the two sites due to *S. foliosa*). This matches the isotope data, wherein fish collected in September at Bull Island exhibited more depleted $\delta^{13}C$ values as compared with those fish collected at Pond 2A (Table 6, ANOSIM pair-wise $R=0.251$, $p=0.004$). This also matches the marsh vegetation coverage data, which indicates that Pond 2A exhibits a higher percent cover of *S. foliosa* (10.7%) as compared to Bull Island (4%; unpublished data, IRWM plant group). In contrast to our initial hypothesis, variations in allochthonous phytoplankton contributions to fish production made up only 14.95%

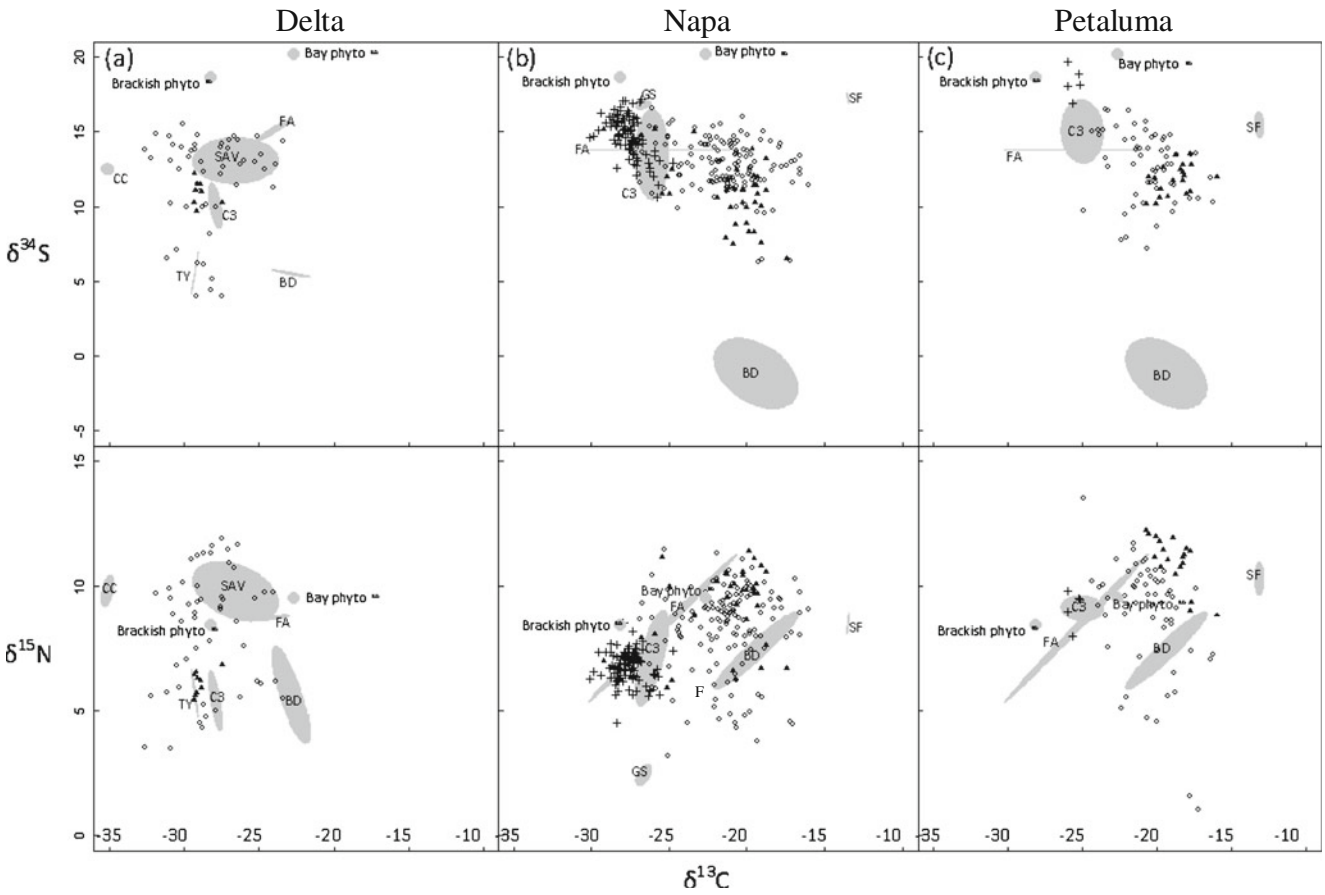

Fig. 2 Dual isotope plots of $\delta^{13}C$ vs $\delta^{15}N$ and $\delta^{13}C$ vs $\delta^{34}S$ in parts per mil for primary producer groups used in the mixing model and consumers in the **a** Delta, **b** Napa, and **c** Petaluma River estuaries of SFBD in parts per mil. Plant producer groups are indicated by *ellipses* outlining the 95% CI around the mean and identified by the following abbreviations: *BD* benthic diatoms, *FA* filamentous algae, *SF S. foliosa*, *C3* C_3 emergent vascular plants, *SAV* submerged aquatic vegetation, *GS G. stricta*, *TY Typha* sp., *CC C. caroliniana*, *Brackish phyto* Brackish phytoplankton <5 psu, *Bay phyto* bay phytoplankton >5 psu. Consumer organisms are indicated by the following *symbols*: *triangle* invertebrates, *circle* fish, *plus sign I. demissum*

of the difference in OM support across marshes of varying restoration status.

In addition to site-based differences, estimated food web source contributions changed seasonally. During high-flow periods (January), silversides from Bull Island and Coon Island were predominantly supported by *S. foliosa* and C_3 emergent plants and roughly equal amounts of bay phytoplankton, algae, diatoms, and brackish phytoplankton (Fig. 4). Diets of silversides in Pond 2A were predominantly supported by *S. foliosa* and benthic diatoms and much lower amounts of C_3 emergent plants. During low-flow periods (September), silverside diets in Coon Island and Pond 2A were more comparable, but silversides in Bull Island fed differently (Fig. 4). During September of 2003, silversides collected at Coon Island and Pond 2A depended primarily upon *S. foliosa*, with secondary contributions from C_3 emergent plants and filamentous algae. In contrast, silversides collected at Bull Island during September 2003 depended most heavily upon C_3 emergent plants and secondarily upon bay-produced phytoplankton and *S. foliosa*. Thus, seasonal changes not only shift the relative importance of particular primary producers to silverside diets but also shift patterns of resemblance in OM food web support among different marsh comparisons.

Petaluma River Estuary Inland silversides from the Petaluma River estuary were predominantly supported by autochthonous tidal wetland production, with observable between-site differences (Fig. 4). Silversides from Carl's Marsh and Petaluma Ancient exhibited strong contributions from *S. foliosa*, secondary contributions from C_3 emergent plants, and very little contribution from phytoplankton, algae, or benthic diatoms. In contrast, the OM supporting silversides at Greenpoint Centennial originated predominantly from benthic diatoms and secondarily from bay-produced phytoplankton and *S. foliosa*. Despite being located directly across the Petaluma River from one

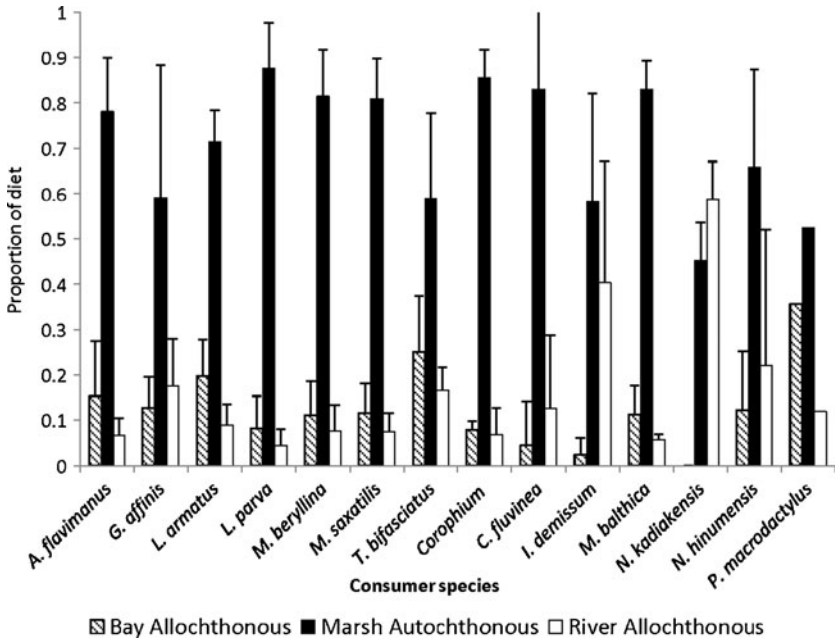

Fig. 3 The average percent contribution of different organic matter sources to estuarine consumer production, originating from bay allochthonous, marsh autochthonous, and river allochthonous sources. *Error bars* represent 1 standard deviation

another, significant differences in the estimated OM sources supporting silverside production were observed between the young (11 years) restoring site, Carl's Marsh, and the reference site, Greenpoint Centennial (MDS results, 2D stress=0.06, ANOSIM pair-wise comparison, R=0.372, p=0.002). SIMPER results indicate that 28.82% of this difference was driven by the amount of diatom support, and 28.50% was due to the amount of *S. foliosa* contributing to silverside production. No significant difference was observed in the sources of OM support between Carl's Marsh and the alternate reference site, Petaluma Ancient (ANOSIM pair-wise R=−0.128, p=0.817), indicating that Petaluma Ancient may be a more appropriate reference for restoration progress in Carl's Marsh. Average dissimilarity in OM support between Petaluma Ancient and Carl's Marsh as measured by SIMPER was much smaller (10.97) than the average dissimilarity between Carl's Marsh and Greenpoint Centennial (17.17). This pattern was further substantiated by multivariate analyses based on isotope values (Table 6, 2D MDS stress=0.04, Global R=0.318, p=0.01), which indicated no significant difference between Carl's Marsh and Petaluma Ancient but a strong difference between Greenpoint Centennial and Carl's Marsh (ANOSIM pair-wise R=0.480, p=0.02).

A. flavimanus—Resident Demersal Feeder

The type of OM supporting yellowfin gobies is largely dominated by autochthonous OM (mean % contribution= 78.0±11.8%, Fig. 5). However, the nature of autochthonous OM assimilated by yellowfin gobies changes among months and across the three estuarine regions.

Napa River Estuary In the Napa River estuary, yellowfin gobies collected in June depended more strongly on algal food web sources (bay phytoplankton, benthic diatoms, filamentous algae), compared to those fish collected in September, which reflected higher proportional inputs of C_3 emergent plants and *S. foliosa* (Fig. 5). Temporal differences, however, were not large enough to be biologically important, although they were significant (global R=0.110, p=0.001). Site-based differences in diets were significant and biologically important (global R=0.535, p=0.001). Similar to that observed for inland silversides, no significant difference in the type of OM supporting goby production was observed between the two downstream sites, Coon Island and Pond 2A, during the summer (ANOSIM pair-wise R=0.168, p=0.17), but both downstream sites were significantly different from the upstream site, Bull Island (CI×BI: R=0.672, p=0.008, P2A×BI: R= 0.740, p=0.008). This pattern was also reflected through the isotope data (Table 6, CI×P2A: R=0.052, p=0.11, CI× BI: R=0.502, p=0.001, P2A×BI: R=0.621, p=0.001). SIMPER analysis indicated that differential assimilation of *S. foliosa* by gobies contributed to 26.88% of the difference in OM support between Bull Island and Pond 2A and 21.34% of the difference between Bull Island and Coon Island.

Petaluma River Estuary Yellowfin gobies collected in June at Greenpoint Centennial and Carl's Marsh were more heavily supported by algal sources (mean % contribution 61.5±7.7%) than C_3 emergent plants (mean% contribution 9.5±3.6%). However, ~30% of assimilated OM in gobies from both sites originated from *S. foliosa* during this time (Fig. 6a). Food web contributions to goby production differed slightly, but

Table 4 Percent contribution of allochthonous bay-produced OM, autochthonous marsh-produced OM, and allochthonous river-produced OM to consumer diets by marsh type

No significant relationship was found between marsh age and the amount of bay-derived OM supporting marsh consumers (R^2 =0.32)

	Bay allochthonous	Marsh autochthonous	River allochthonous
Marsh type			
Restoring	10.52	78.56	11.45
Ancient	12.12	72.32	10.35
Centennial	10.84	73.63	15.93
Marsh age (restoring)			
11 years (Pond 2A)	10.17	83.54	6.69
15 years (Carl's Marsh)	9.66	82.52	7.82
25 years (Bull Island)	10.89	70.44	19.69
73 years (Brown's Island)	11.21	68.78	11.02

not significantly, between Carl's Marsh and Greenpoint (global R=0.250, p=0.09). Isotope values of fish collected at each site also do not differ significantly (global R=0.042, p=0.31), but fish from Carl's Marsh tended to be slightly more depleted in $\delta^{13}C$ and $\delta^{15}N$ as compared to fish collected from Greenpoint Centennial (Table 6).

Delta Yellowfin gobies collected at Brown's Island indicated a different temporal pattern of source contributions compared to fish collected from the Napa and Petaluma river estuaries. Organic matter contributions differed significantly between June and September 2004 (global R= 0.784, p=0.008). In the early summer, goby food web pathways were predominantly supported by vascular plants, but this contribution dropped off by September, when bay-produced phytoplankton and benthic diatoms became more prominent (Fig. 6b). Gobies collected in June were depleted in all three isotopes as compared to those fishes collected in

Table 5 Average temporal (and SD) proportional contributions of primary producers to pooled SFBD consumers

	October 2003	February 2004	June 2004	September 2004	January 2005	March 2005	June 2005	"Annual"
All regions								
Bay source	0.13±0.09	0.09±0.04	0.11±0.08	0.12±0.10	0.11±0.08	0.16±0.10	0.11±0.09	0.11±0.09
Marsh source	0.78±0.13	0.85±0.07	0.83±0.09	0.79±0.19	0.77±0.19	0.76±0.16	0.78±0.21	0.76±0.17
River source	0.07±0.04	0.09±0.06	0.06±0.06	0.10±0.20	0.11±0.21	0.09±0.19	0.06±0.15	0.13±0.16
Napa								
Bay phytoplankton	0.07±0.03	0.09±0.04	0.13±0.08	0.10±0.07	0.10±0.07	0.18±0.10	0.13±0.09	0.12±0.08
Diatoms	0.29±0.14	0.17±0.10	0.25±0.15	0.14±0.09	0.18±0.13	0.19±0.14	0.25±0.14	0.20±0.13
Algae	0.12±0.08	0.20±0.12	0.20±0.11	0.15±0.09	0.15±0.09	0.17±0.10	0.21±0.15	0.17±0.11
C3 emergent	0.13±0.05	0.23±0.16	0.16±0.19	0.20±0.17	0.20±0.52	0.24±0.20	0.17±0.19	0.19±0.27
Spartina foliosa	0.37±0.09	0.24±0.15	0.20±0.11	0.33±0.22	0.30±0.25	0.15±0.11	0.18±0.14	0.25±0.20
Brackish phytoplankton	0.05±0.02	0.09±0.06	0.05±0.09	0.08±0.23	0.08±0.25	0.08±0.21	0.06±0.16	0.07±0.19
Petaluma								
Bay phytoplankton	0.15±0.11	–	0.11±0.09	0.07±0.02	0.13±0.10	0.13±0.09	0.10±0.08	0.13±0.09
Diatoms	0.16±0.13	–	0.15±0.09	0.15±0.06	0.21±0.11	0.16±0.12	0.13±0.05	0.16±0.11
Algae	0.14±0.08	–	0.20±0.08	0.18±0.09	0.13±0.07	0.26±0.20	0.28±0.09	0.18±0.11
C3 emergent	0.12±0.07	–	0.09±0.04	0.06±0.03	0.12±0.10	0.18±0.16	0.09±0.04	0.12±0.09
Spartina foliosa	0.35±0.19	–	0.39±0.13	0.50±0.08	0.33±0.21	0.16±0.13	0.31±0.12	0.33±0.18
Brackish phytoplankton	0.08±0.05	–	0.06±0.02	0.05±0.02	0.07±0.04	0.11±0.05	0.10±0.14	0.08±0.07
Delta								
Bay phytoplankton	–	–	0.04±0.01	0.18±0.16	0.14±0.06	0.08±0.0	0.01±0.01	0.12±0.13
Submerged vegetation	–	–	0.27±0.09	0.37±0.22	0.27±0.12	0.20±0.0	0.16±0.16	0.30±0.18
Diatoms	–	–	0.12±0.03	0.11±0.13	0.08±0.05	0.09±0.0	0.05±0.08	0.09±0.10
C3 emergent	–	–	0.24±0.12	0.10±0.08	0.17±0.07	0.38±0.0	0.03±0.05	0.14±0.11
Typha sp.	–	–	0.24±0.05	0.08±0.08	0.10±0.05	0.23±0.0	0.33±0.04	0.16±0.17
Brackish phytoplankton	–	–	0.09±0.05	0.16±0.08	0.24±0.10	0.04±0.0	0.02±0.02	0.14±0.10

Consumer isotope signatures were run through the mixing model individually and then pooled to obtain means for each month

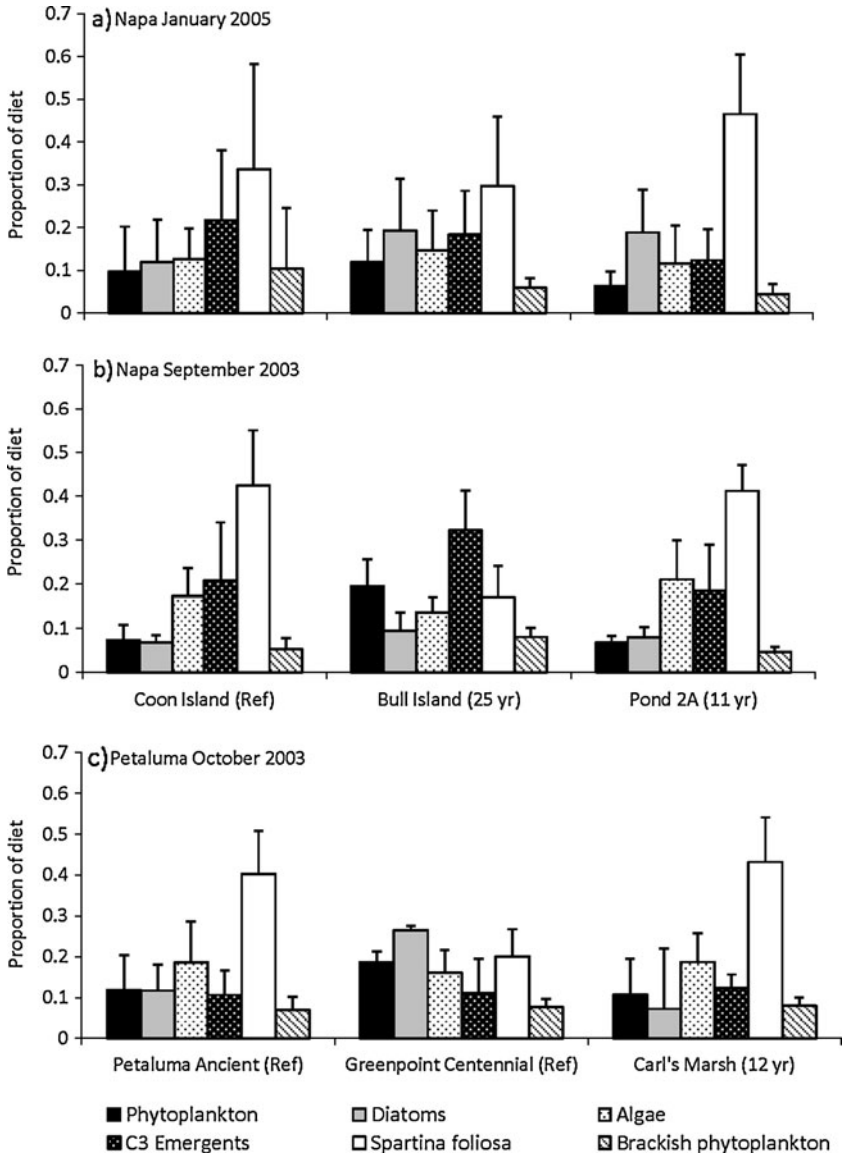

Fig. 4 Site level comparisons of the average estimated organic matter types supporting inland silversides, *M. beryllina*, in Napa River estuary sites in **a** January 2005 (*high flow*) and **b** September 2003 (*low flow*) and the Petaluma River estuary sites in **c** October 2003. *Error bars* represent 1 standard deviation

September (Table 6), indicating a shift from SAV to phytoplankton.

M. balthica—Benthic Deposit Feeder

In the three Napa marsh sites, *M. balthica* largely depended upon a mixture of benthic diatoms, *S. foliosa*, and filamentous algae for support (Fig. 7). Allochthonous inputs from bay phytoplankton were highest in March and June, although contributions neither contributed >20% nor indicated a relationship with marsh restoration status. This pattern was similar in the Petaluma River estuary, where no significant differences in OM support or isotope signatures were observed between Carl's Marsh and Greenpoint Centennial (OM composition: global R=0.099, p=0.228; isotopes: global R=0.005, p=0.365, Table 6), further indicating that clams collected in the restoration site were no more dependent upon pelagic phytoplankton than those collected in the reference site.

Within the Napa River Estuary, significant site-based differences in OM contributions to clam diets were observed (global R=0.416, p=0.001), indicating that the diets of clams collected in Pond 2A and Coon Island were similar, Pond 2A and Bull Island were similar, but that Coon Island and Bull Island differed (P2A×CI: R=0.131, p=0.09, P2A×BI: R=0.124, p=0.20, CI×BI: R=0.488, p=0.01). In addition to site-based differences in diet composition, significant temporal differences in diet composition were observed for clams collected at Bull Island and Coon Island (BI: R=0.393, p=0.008, CI: R= 0.493, p=0.001, NSD at P2A: R=0.145, p=0.16). Temporal differences in OM support were generally attribut-

Table 6 Average isotope values of *M. beryllina*, *A. flavimanus*, and *M. balthica* collected at various sites and dates

Species/region	Site/date	$\delta^{13}C$		$\delta^{15}N$		$\delta^{34}S$		Number
		Mean	SD	Mean	SD	Mean	SD	
Menidia beryllina								
Napa	**January 2005**							
	Bull Island	−16.15	2.23	15.85	0.41	12.59	1.85	5
	Coon Island	−19.01	3.71	15.47	1.31	13.97	1.32	5
	Pond 2A	−16.92	2.12	15.59	0.96	12.88	1.25	5
	September 2004							
	Bull Island	−20.83	0.75	15.55	0.34	14.29	0.73	5
	Coon Island	−17.98	1.60	16.25	0.25	14.42	0.44	5
	Pond 2A	−18.22	0.70	15.36	0.76	13.95	0.79	5
Petaluma	**October 2003**							
	Greenpoint	−19.85	0. 47	17.21	1.08	11.16	1.80	5
	Carl's Marsh	−18.53	0.85	16.65	1.07	13.79	0.90	5
	Petaluma Ancient	−18.66	1.20	15.69	0.50	13.08	1.37	5
Acanthogobius flavimanus								
Napa	**June 2004, 2005**							
	Bull Island	−21.95	1.35	15.05	1.07	12.44	1.34	5
	Coon Island	−19.55	0.39	15.84	0.25	11.95	0.52	4
	Pond 2A	−19.12	0.59	15.14	0.26	12.05	0.34	3
	September 2004							
	Bull Island	−21.80	1.45	14.18	0.81	14.02	0.79	5
	Coon Island	−18.27	1.46	15.75	0.21	13.33	0.80	3
	Pond 2A	−18.27	1.08	15.71	0.29	13.42	1.78	3
Petaluma	Greenpoint (June 2004)	−18.47	1.13	16.74	0.62	12.53	2.01	4
	Carl's Marsh (June 2004)	−19.62	2.08	17.90	1.38	11.37	0.95	5
Delta	Brown's Island (June 2004)	−27.34	1.13	11.20	0.56	10.27	0.44	5
	Brown's Island (Sept 2004)	−23.07	1.11	12.69	0.34	13.64	0.88	5
Macoma balthica								
Napa	**March 2005**							
	Bull Island	−20.75	0.84	13.76	0.17	10.93	0.29	3
	Coon Island	−19.84	0.98	14.41	0.46	8.17	0.23	3
	Pond 2A	−20.04	0.54	13.30	0.08	10.03	0.23	3
	June 2004, 2005							
	Bull Island	−21.50	1.03	13.13	0.49	11.15	0.05	3
	Coon Island	−19.24	0.48	14.21	0.79	10.78	0.62	5
	Pond 2A	−20.66	0.64	12.65	0.49	10.26	0.85	6
	September 2004							
	Bull Island	−18.69	0.78	14.04	0.14	10.77	0.67	3
	Coon Island	−18.75	1.29	14.09	0.31	11.35	0.21	2
	Pond 2A	−20.10	0.87	12.94	0.27	12.10	0.35	3
Petaluma	**January 2005**							
	Greenpoint	−19.39	0.33	14.32	0.23	10.93	0.39	2
	Carl's Marsh	−17.56	0.18	14.86	0.06	10.90	0.14	2
	September 2004							
	Greenpoint	−17.94	0.14	14.43	0.34	12.30	0.28	2
	Carl's Marsh	−18.05	0.28	14.25	0.34	12.67	0.86	3
	March 2005							
	Greenpoint	−19.48	0.84	15.15	0.50	11.87	0.15	3

Table 6 (continued)

Species/region	Site/date	$\delta^{13}C$		$\delta^{15}N$		$\delta^{34}S$		Number
		Mean	SD	Mean	SD	Mean	SD	
	Carl's Marsh	−19.84	0.49	15.42	0.23	10.33	0.23	3
	June 2004, 2005							
	Greenpoint	−19.12	0.22	14.81	0.22	12.78	0.17	4
	Carl's Marsh	−18.93	1.13	14.86	0.54	12.20	0.52	5

able to fluctuating filamentous algae, benthic diatom, and *S. foliosa* inputs (Fig. 7). Vascular plant input tended to increase during the summer months, while algal sources (phytoplankton and benthic algae) increased during the winter and spring months.

Discussion

Our findings imply two notable conclusions: (1) the proportion of allochthonous material entering estuarine marsh food webs at these study sites does not appear to vary greatly across restoring marsh sites of different ages, or between ancient (and centennial) reference marshes and restoring sites and (2) all sites were dominated by autochthonous production, with minimal supplementation from bay-produced phytoplankton. Even those consumer species considered to be transient water-column feeders and therefore expected to reflect inputs principally from phytoplankton (e.g., *M. beryllina*) had assimilated very little OM from phytoplankton in marshes of all ages. Two main explanations can be attributed to these findings. First, every restoring marsh had already established an extensive vegetative assemblage of at least 10 years of age. All sites were composed roughly of 25–30% water and 70–75% vegetation by area (IRWM plant group, unpublished data). Only the two youngest restoration sites, Pond 2A and Carl's Marsh, exhibited bare ground (6% and 12%, respectively). Furthermore, OM contributions to consumers in restoration sites closely aligned with those of ancient and centennial sites, indicating that the food webs of restoration sites function quite similarly to natural sites by the time they reach 10 years of age. The large amounts of autochthonous marsh production by this point in time may overwhelm any early patterns in restoration trajectories with respect to external food web subsidies originating from the bay.

Effects of Landscape Organization on Food Web Linkages

Spatial Proximity The overall similarities in food web sources across sites of varying ages may relate to the landscape position of selected study marshes. External subsidies to younger marshes may be provided by the export of OM from surrounding marsh areas rather than from the open waters of San Francisco Bay. If so, bay phytoplankton would not be expected to play a larger role within younger marshes in comparison to nearby older sites. Additionally, if neighboring marshes subsidize young restoration sites, then marshes in more proximal locations to one another should exhibit greater similarities in food web sources. We observed this phenomenon within the Napa River system, where the two most distal sites, Bull Island (25 years old) and Pond 2A (11 years old), were significantly different from one another, but neither marsh was significantly different from Coon Island (ancient), located intermediate to the two restoring sites. Furthermore, bay-produced OM subsidies are likely to have larger effects in those sites closer to the bay, such that progressively lower contributions of bay-produced phytoplankton could be expected along the estuarine gradient from Pond 2A (11.2 km upstream) to Coon Island (16.1 km) and Bull Island (19.5 km), regardless of marsh age.

Hydraulic Connectivity Detailed examination of food web contributions to *M. beryllina* and *A. flavimanus* further suggests that landscape organization, rather than marsh age, potentially plays a large role in determining food web sources. Contrary to predictions of the estuarine outwelling hypothesis, food web pathways to these consumers are comparatively short and unique, as evidenced by significant site-based differences within a single estuary. Organic matter assimilated by inland silverside and yellowfin goby from the Napa River estuary corresponded to the spatial hypothesis of proximal marshes exhibiting more similar food web contributions, although the degree of similarity likely depends upon hydraulic connectivity. Consumer food web sources at the two upstream sites, Coon Island and Bull Island, were more similar to one another during the winter under high river flow conditions. During this time, freshwater pulsing through the system likely forced salinity intrusion further down-estuary, reducing the input of bay phytoplankton to estuarine consumer production. Such a salinity gradient was evident during the January sampling period, when mean salinity at Bull Island was 1.2 psu,

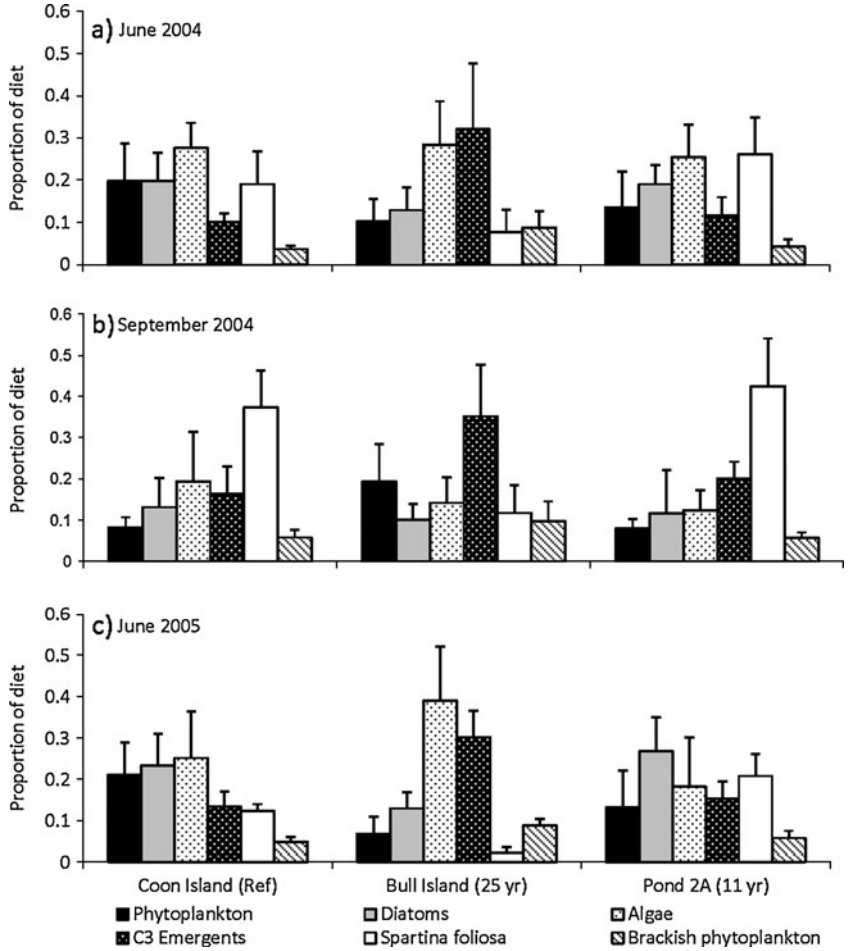

Fig. 5 Average proportion of OM types supporting yellowfin gobies, *A. flavimanus*, collected in the Napa River estuary marshes in **a** June 2004, **b** September 2004, and **c** June 2005. *Error bars* represent 1 standard deviation

3.3 psu at Coon Island, and 4.9 psu at Pond 2A. Perhaps the similarity in OM contributions to inland silverside production between Bull Island and Coon Island arises from their proximity to each other and the strong upstream influence.

The similarity in food web sources between Bull Island and Coon Island shifted during September when river flow was the lowest. During this time, OM contributions to inland silverside and yellowfin goby production at Coon Island resembled that of fish collected downstream at Pond 2A. During low flows, the extent of salinity intrusion shifts upstream; mean salinities at each marsh rose to reach salinities of 21.1 psu (CI), 20.3 psu (BI), and 19.5 psu (P2A), a range of only 1.5 psu. This indicates that, in September, the bay plays a larger role in influencing estuarine marshes than does the river, as evidenced by elevated levels of bay-produced phytoplankton exhibited in the OM contributions to silversides collected at Bull Island.

Further evidence of a shift from a high-flow, river-dominated system to a low-flow, bay-dominated system can be found through *S. foliosa* food web contribution patterns. A large portion of September OM contributions to Pond 2A and Coon Island inland silversides was estimated to originate from *S. foliosa*, an extremely salt-tolerant plant. The scarcity of this plant further upstream at Bull Island suggests that average annual salinities do not support this species at this point along the estuarine gradient and that this in itself is an indicator for the diminished bay influence to this marsh. However, the fact that *S. foliosa* contributes to both inland silverside and yellowfin goby production at Bull Island indicates the occurrence of OM exchange across sites, especially considering that *A. flavimanus* is described as a marsh resident that does not necessarily exit marsh channels on even the lowest of spring tides (personal observation). Alternatively, the presence of OM from *S. foliosa* in Bull Island fish may indicate organism movement (perhaps prey) among marshes, but evidence from *S. foliosa*-supported *M. balthica* from Bull Island and a second study based on sessile mussels (Howe and Simenstad 2007) suggest the movement of OM. In summary, given that OM contributions to Coon Island consumers shift, depending on the net flow direction of the system, to resemble sites located either up- or down-estuary, the Napa River estuary food

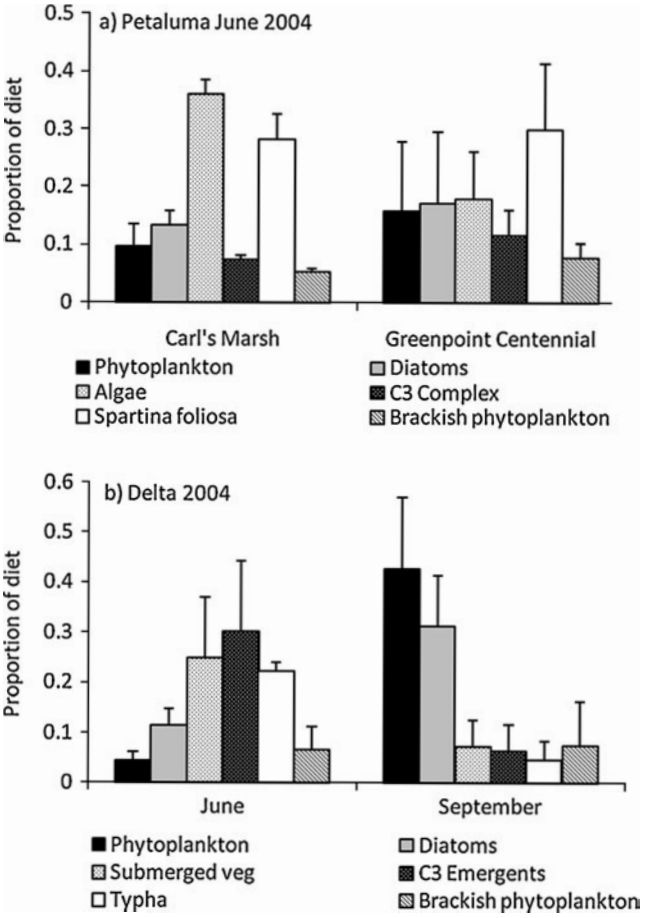

Fig. 6 Average proportion of OM types supporting yellowfin gobies, *A. flavimanus*, collected in **a** Petaluma River estuary marshes in June 2004 and **b** Delta estuary in June and September 2004. *Error bars* represent 1 standard deviation

web provides evidence for inter-marsh subsidies based on spatial proximity and hydraulic connectivity. However, the form of the subsidy, either organism or OM transport, is uncertain.

Channel Geomorphology Patterns of food web contributions to *M. beryllina* in the Petaluma River estuary provide a very different perspective. Differing food web contributions between fish collected at Greenpoint Centennial and Carl's Marsh (located directly across the mainstem of the Petaluma River from one another) indicate that proximity between sites does not necessarily result in similar food web source contributions. However, this difference is likely not a result of differences in marsh age, as we observed a strong resemblance in OM contributions to consumers in Petaluma Ancient and Carl's Marsh. This might suggest that channel geomorphology plays a strong role in determining the amount and type of detritus entering a particular marsh's food web. In Petaluma Ancient, marsh channel patterns are dendritic, with extreme branching and meandering. This complex geomorphology likely inhibits marsh OM exports, trapping autochthonous materials for direct consumption and also allowing microbial communities time to condition emergent plant material for entrance into the food web (Hood 2002). In contrast, Greenpoint, a centennial marsh, is characterized by linear, parallel channels that have little to no branching. Centennial marshes are thus marked by decreased retention periods which likely lead to the absence of microbially conditioned particulate organic carbon (POC), leaving the algal sources of OM to enter and support the internal marsh food web. The prevalence of benthic diatoms supporting inland silversides at Greenpoint aligns with the hypothesis that marsh OM export efficiency influences the autochthonous food web, the mechanism of which could lie in the different geomorphologies of marsh tidal channels. Thus, a difference arises in the mechanism by which different marsh types export autochthonous energy to the estuary: Centennial marshes may do so by directly exporting POC, while ancient sites and some restoring sites, such as Carl's Marsh, are more likely exporting a greater amount of energy to the larger estuary through organismal transport and trophic transfers (Kneib 2000).

Ecosystem Implications

Our findings indicate that estuarine marsh production contributes significant proportions of the OM supporting certain consumer-specific food webs in shallow marsh environments in SFBD. In contrast, allochthonous pelagic phytoplankton production appears to play a very small role in these ecosystems. That both resident and transient consumers relied heavily on this autochthonous macrophyte detritus food web base and both restoring marsh sites (at least 10 years of age) and ancient reference sites relied heavily upon the same autochthonous sources implies that estuarine marsh production at least dominates shallow-water food webs in SFBD. While it is uncertain whether younger sites receive subsidies from nearby marshes or produce enough OM themselves to support the internal food web, it is clear that energy derived from estuarine marsh autotrophs can contribute to the overall SFBD food web either through direct subsidy by OM export or through organism transport and trophic transfers. These results appear to challenge the general paradigm of a phytoplankton-based food web in San Francisco Bay, a paradigm largely built on the extensive investigation of pelagic communities and food webs (Canuel et al. 1995; Jassby and Cloern 2000; Jassby et al. 2003; Sobczak et al. 2005). Our results indicate a parallel and likely integrated macrophyte detritus-supported food web operating in shallow-water habitats

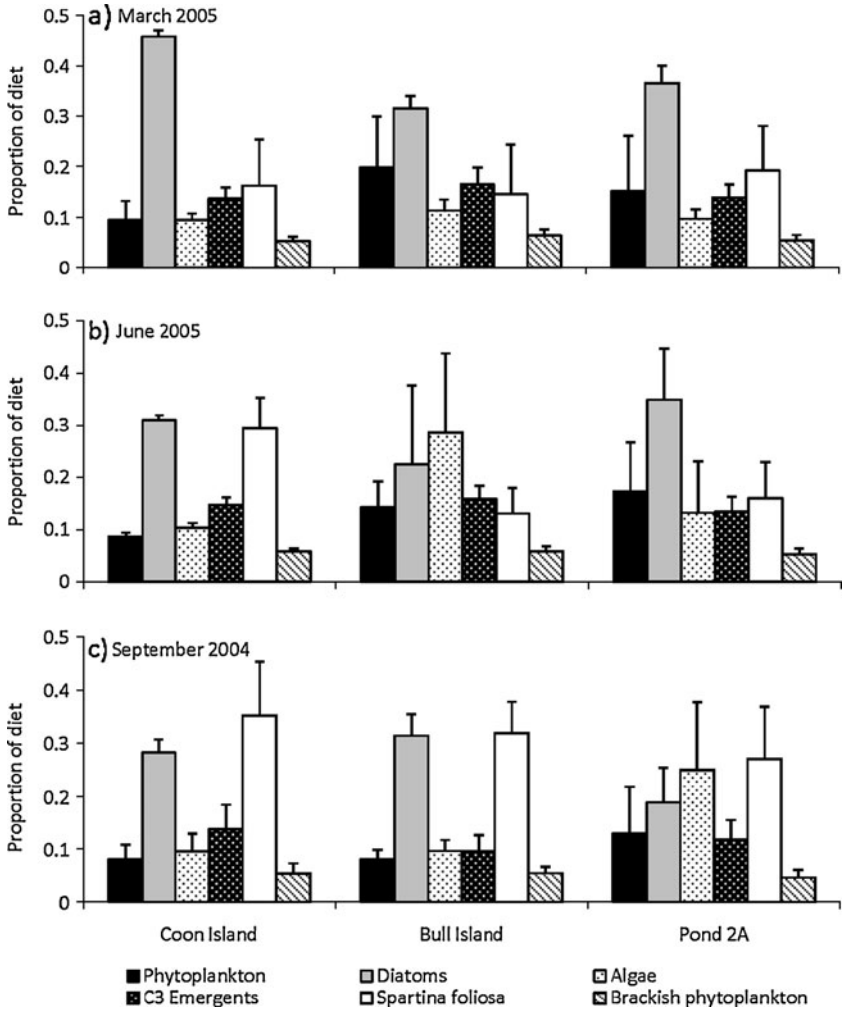

Fig. 7 Average proportion of OM types supporting *M. balthica* collected at Napa River estuary marshes in **a** March 2005, **b** June 2005, and **c** September 2004. *Error bars* represent 1 standard deviation

and vegetated marshes along the northern margin of San Francisco Bay.

Increased food web pathways from autochthonous marsh OM may beneficially complement or even surpass a phytoplankton-based system. The transient nature of phytoplankton production results from a myriad of controlling factors, ranging from freshwater flow, water residence times, nutrient loading, turbidity and light levels, and organism consumption by grazers (Jassby et al. 2003). As a result of these factors, phytoplankton production in SFBD is extremely pulsed, often resulting in chl α concentrations below 10 μm/L, the threshold below which growth of zooplankton may be limiting (Jassby et al. 2003). However, our results indicate that a steady production of autochthonous materials supports the food webs of estuarine marshes, with comparatively smaller pulses of bay-produced phytoplankton occurring in March. An inherent advantage of a detritus-based system is its temporal stability on a seasonal scale (Nakano and Masashi 2001; Takimoto et al. 2002). Because food web linkages reliant upon conditioned detritus have a continual supply of source material and because this extra piece in detrital food webs is therefore not dependent upon seasonality, detrital systems may gain stability despite increasing complexity (Holt 2002).

The importance of diverse food web sources from which estuarine organisms can assimilate OM is illustrated by the estimated OM contributions to *A. flavimanus* in Brown's Island. During peak vegetative growing season, yellowfin goby primarily assimilated vascular emergent and submerged vegetation, with little input from algal sources. This pattern switched by September, when these gobies drew extensively on food webs linked to bay phytoplankton and benthic diatoms, with no apparent change in diet composition based on gut content analyses (unpublished data). This trophic switching contrasts with results from Grimaldo et al. (2009), which show that Delta fishes fall in one of two main categories (although these categories are by no means completely decoupled): (1) edge fishes dependent upon SAV and (2) open-water fishes dependent upon phytoplankton. By focusing efforts between August and November, the study of Grimaldo et al. (2009) perhaps missed an

important temporal shift that our data suggest occurs within the growing season: decreasing nutrient content and increasing toughness as the foliage of vascular plants ages (Newman 1991). As illustrated by the switching of *A. flavimanus* food web sources from vascular plants to algae, which is further reflected in the strong temporal shifts in OM contributions to *M. balthica*, differential availability and lability within primary producers on a seasonal scale may strongly influence food web dynamics. Therefore, increasing diversity of OM sources ensures more consistent availability to the food web base.

In a system as altered as SFBD, where phytoplankton blooms no longer coincide with larval fish recruitment (Nobriga 2002) and key zooplankton blooms (Kimmerer and Orsi 1996), the future success SFBD's estuarine consumers may be more dependent than presently appreciated on the production potential and subsidies of restoring estuarine marshes. However, the contemporary treatment of the SFBD food web and its restoration largely focuses on phytoplankton as the base of estuarine consumer food web pathways (Canuel et al. 1995; Jassby and Cloern 2000; Jassby et al. 2003; Sobczak et al. 2005), and much effort has been put forth to understand the drivers of phytoplankton production in the bay (e.g., Cloern et al. 1985; Jassby et al. 1993, 2002, Cloern and Dufford 2005; Cloern 2007; Lehman et al. 2008). Recently, the ecological value of shallow open-water habitats, as opposed to vegetated marshes, has been targeted by researchers to understand the phytoplankton production potential and consequent forage production potential of these areas, including those in newly restoring estuarine marsh habitats (Lopez et al. 2006; Thebault et al. 2008). Because of the prevailing assumption that the SFBD food web is driven by phytoplankton dynamics, these ecosystem valuation studies fail to examine the same production questions through the detrital food web, thereby potentially missing an important component of estuarine food web pathways and perpetuating uncertainties about the role of shallow-water ecosystem restoration to recovery of the SFBD. While the nutritional content and lability of estuarine marsh detritus may not rival that of pelagic phytoplankton, the consistent availability of marsh-derived detritus to the food web may restore a more stable base on which to rebuild the estuarine fish and invertebrate communities of SFBD. Our results indicate that despite the phytoplankton paradigm of SFBD food webs, detritus-based pathways are nonetheless important year-round to a variety of feeding guilds from lower to higher trophic levels. We thus argue that in light of ecosystem-wide restoration and conservation efforts, vegetated marshlands with dendritic channel systems should not be overlooked in terms of their ability to functionally support estuarine food webs.

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