



Food Web Fuel Differs Across Habitats and Seasons of a Tidal Freshwater Estuary

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Abstract

Estuarine food webs are fueled by multiple different primary producers. However, identifying the relative importance of each producer to consumers is difficult, particularly for fishes that utilize multiple food sources due to both their mobility and their generally high trophic levels. Previous studies have documented broad spatial differences in the importance of primary producers to fishes within the Upper San Francisco Estuary, California, including separation between pelagic and littoral food webs. In this study, we evaluated the importance of primary producers to adult fishes in three closely spaced subregions that represented disparate habitat types (a tidal wetland channel, a turbid backwater channel, and a deep open-water channel), each a potential outcome of local restoration projects. Using stable isotope analysis coupled with a Bayesian mixing model, we identified significant differences in primary-producer contribution to fishes and invertebrates across habitats and seasons, especially in the relative contribution of submersed aquatic vegetation and phytoplankton. Most fishes utilized multiple primary producers and showed little segregation between pelagic and littoral food webs among habitats. Availability of primary producers differs seasonally and across multiple spatial scales, helping to buffer environmental variability and thus enhancing food web resilience. Ecosystem restoration may improve with emphasis on restoring a wide variety of primary producers to support consumers.

Keywords Stable isotopes · Primary producers · Basal resources · Fishes · San Francisco Estuary

Introduction

Many estuarine food webs appear to be fueled by exported wetland detritus (Teal 1962; Odum 1980; Peterson et al. 1985); however, estuarine consumers also use many other organic-matter sources such as phytoplankton (Deegan and

Garritt 1997; Galvan et al. 2008), macroalgae and benthic microalgae (Currin et al. 1995; Kwak and Zedler 1997), submersed aquatic vegetation (SAV; Kitting et al. 1984; Vizzini et al. 2002), and terrestrial vegetation (Chanton and Lewis 2002; Zeug and Winemiller 2008; Tanentzap et al. 2014). Although each source may be an important contributor, the relative importance of each differs substantially across space and time (Peterson et al. 1985; Chanton and Lewis 2002). For example, phytoplankton, benthic microalgae, and marsh vegetation were all important to local consumers in Plum Island Sound, MA, USA, but the relative importance differed depending on location within the estuary (Deegan and Garritt 1997). These spatiotemporal differences stabilize complex food webs (Winemiller 1996; Polis et al. 1997) because diverse sources of productivity maintain consistent support for higher trophic levels (McCann et al. 2005).

Estuaries are particularly complex, with a complicated mix of trophic contributions from marine and freshwater inputs (Fry and Smith 2002; Hoffman et al. 2008; Atwood et al. 2012), with diverse intertidal and subtidal habitats, and with severe human impacts, which include eutrophication, species invasions, and habitat loss (Kennish 2002). Habitat loss can reduce the quantity or availability of different organic matter

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sources to the ecosystem (Cloern et al. 2016). For organisms at lower trophic levels (e.g., invertebrates), a decline or change in productivity can have catastrophic impacts on local populations because their relatively limited mobility and short lifespans bind them to local production (Orsi and Mecum 1996; Kimmerer 2002). Organisms at higher trophic levels, especially mobile omnivores feeding across various habitats (e.g., fishes; Pyke et al. 1977; Pimm and Lawton 1980; Thompson et al. 2007), may be more resilient.

In most estuaries, the habitat type most frequently lost is tidal wetland (Dahl 2011; Brophy et al. 2019), a particularly biologically productive component of the estuary milieu. Dramatic declines in tidal wetland affect the relative abundance of other habitat types (e.g., bays or mudflats make up a higher proportion of remaining habitat), which can influence organisms across multiple trophic levels and in multiple habitats. This phenomenon has been observed in the San Francisco Estuary, where a largely contiguous tidal wetland complex has been converted to a primarily open-water system (Whipple et al. 2012; Robinson et al. 2014), with concomitant trophic impacts.

In some regions of the San Francisco Estuary, the two broad habitat types, tidal wetland and open water, contain distinct trophic pathways that function separately and in parallel (Grimaldo et al. 2009): a food web based primarily on detritus from emergent and submersed vegetation (Howe and Simenstad 2007; Howe and Simenstad 2011; Schroeter et al. 2015), and an adjacent open water, phytoplankton-based food web (Lehman et al. 2010). In these open-water habitats, organic carbon from sources other than phytoplankton is in low quantity (Jassby and Cloern 2000), has low bioavailability (Sobczak et al. 2002), or is otherwise not utilized (Mueller-Solger 2002). However, in habitats where non-phytoplankton organic carbon is abundant, it can readily be incorporated by pelagic zooplankton (Harfmann et al. 2019), suggesting that estuary-wide trophic pathways would have been different prior to habitat modification (Robinson et al. 2014; Cloern et al. 2016). Landscape changes are the likely cause of observed segregation between trophic pathways (Grimaldo et al. 2009), and in the habitat complexity of the historical system, consumers (i.e., invertebrates, fishes) would have likely coupled trophic pathways.

With several plankton-eating fishes nearing extinction in the San Francisco Estuary (Hobbs et al. 2017), efforts are underway to re-create tidal wetland, with the assumption that the new wetland will improve plankton production and food availability. Much effort has been focused on the North Delta, a region in the estuary that has historical habitat features favorable for creation of tidal wetland (e.g., appropriate elevation). While much has been learned about food webs in certain regions of the estuary (Howe and Simenstad 2007; Grimaldo et al. 2009; Howe and Simenstad 2011; Schroeter et al. 2015), little is known about the trophic support provided by different

habitat types in the North Delta. Elucidating the food web structure of this region is thus crucial for informing habitat re-creation. Using stable isotopes of carbon, nitrogen, and sulfur, coupled with diet analysis and a stable-isotope mixing model, we quantified the importance of different primary producers to consumer communities across different subregions, each of which represented a different habitat type (a tidal wetland channel, a turbid backwater channel, and a deep open-water channel), and across seasons. We addressed two primary questions: (1) Does food web support for consumers differ between subregions and seasons?; and (2) Is there evidence for segregation of phytoplankton-based (i.e., pelagic) and vascular macrophyte-based (i.e., littoral) trophic pathways in different subregions? Answering these questions will increase understanding of both trophic impacts of restoration and the role of habitat in supporting estuarine food web resilience in highly disturbed systems.

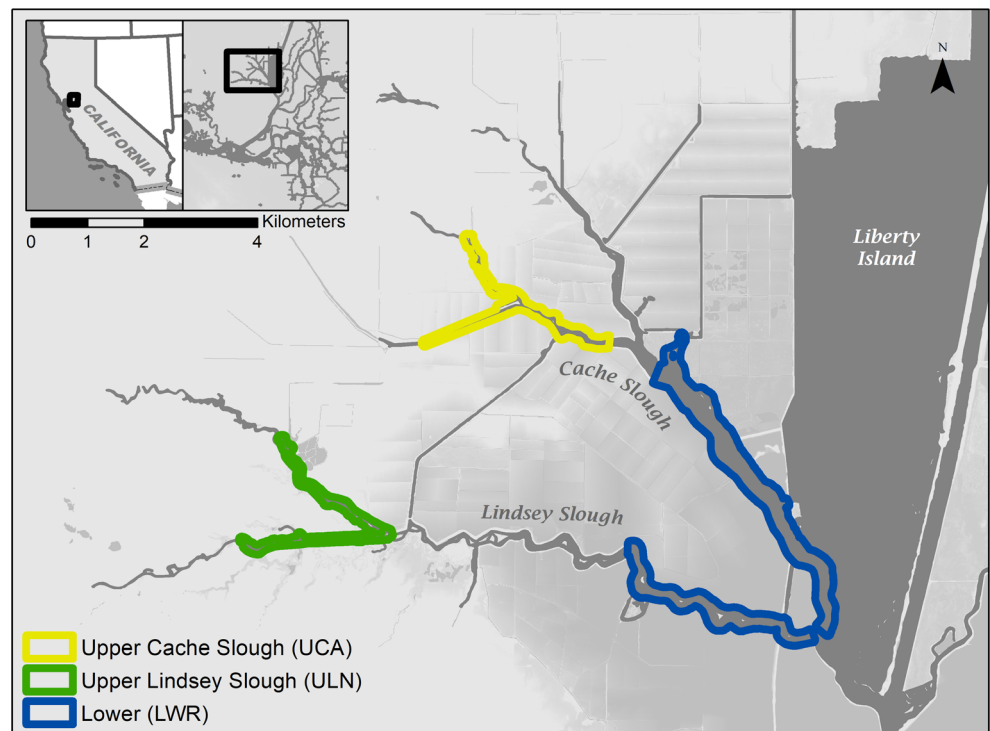
Methods

Study Area

The San Francisco Estuary (SFE), California, USA, the largest estuary on the western coast of North America, historically consisted of dendritic tidal wetland, seasonal floodplain lakes, open-water bays, and sinuous subtidal channels with high variability in salinity and flow (Whipple et al. 2012). After two centuries of intense human use, the contemporary SFE has been altered by species invasions, water diversions, changes to the nutrient regime, and habitat modification (Nichols et al. 1986). Nevertheless, the SFE still encompasses a wide range of physical heterogeneity, such as a patchwork of relict wetlands, channelized tidal sloughs, and restored habitats. The freshwater extent of the SFE, the Sacramento-San Joaquin Delta (Delta), is a 2985-km² network of severely modified habitats. While much of the Delta is devoted to diked farmland, it also includes a patchwork of rock-lined channels, vegetated and unvegetated backwaters, flooded agricultural tracts, and small remnant or restored tidal wetland. Native fishes are most abundant where turbidity is high, where density of submersed aquatic vegetation (SAV) is low, and where water is cool (Moyle et al. 1992; Feyrer and Healey 2003; Brown and Michniuk 2007).

Our study focused on the Cache Slough Complex in the northwest Delta, a region of high fish and habitat diversity in a small geographic area (Young et al. 2015; Fig. 1). We identified three subregions reflecting both historical and contemporary habitats: Upper Lindsey Slough, Upper Cache Slough, and the downstream extent of the complex. Upper Lindsey Slough (ULN) has expansive vegetated tidal wetland, low turbidity, low chlorophyll densities, and large water diversions (Kimmerer and Nobriga 2008). ULN more closely

Fig. 1 Study area. In-lays show sampling location within California, and the Sacramento-San Joaquin Delta, respectively. Subregions are outlined in the main panel



approximates the historical Delta's physical configuration than the other subregions. Upper Cache Slough (UCA) is shallow, with minimal SAV, high turbidity, high chlorophyll densities, minimal emergent wetland vegetation, and represents a possible intermediate state for restoration projects. The lower reaches of Cache and Lindsey Sloughs (collectively the “lower” subregion (LWR)) are deep, wide, rock-lined channels with dense SAV along banks and with low chlorophyll densities, similar to more open-water channels in other Delta regions.

Field Collection

Primary Producers We collected primary producers at every subregion in spring (April 2014) and summer (August 2014). To account for variation within a producer group, we collected multiple samples from each group ($N \geq 3$). We collected the upper stems and leaves of vascular macrophytes (e.g., *Egeria densa*, *Bulboschoenus maritimus*) by hand, as well as green filamentous algae (GFA) when present. We collected benthic diatoms (BD) using methods adapted from Cloern et al. (2002) by using Nitex mesh screens laid atop the sediment surface. Phytoplankton was collected as seston using a 30- μm mesh net towed until clogged. We filtered both seston and benthic diatom samples through 100- μm sieves to remove larger detrital fragments and organisms; we then vacuum filtered them onto pre-combusted GF/F filters. We placed all samples from primary producers on ice in the field and froze them until laboratory analysis.

Invertebrates We collected zooplankton in three separate samples using a 50- μm mesh net with a 0.5-m mouth. The net was towed by boat at the slowest possible forward speed for 10 min or until clogged. We collected zooplankton samples mid-channel on the ebb tide with the assumption that tidal mixing would homogenize zooplankton cross-sectional distribution, allowing us to capture most species. Samples were concentrated into a small volume and placed on ice to limit intra-sample predation. We collected vegetation-associated insects and crustaceans by vigorously shaking SAV and other vegetation types into a 5-gal bucket, which was then rinsed onto a 500- μm sieve for manual transfer into a clean jar. Other invertebrates, including clams and epibenthic invertebrates, were collected via trawl as a byproduct of fish sampling (described below). All macroinvertebrates were kept alive for 24 h in the laboratory to allow for digestive-tract evacuation.

Fishes We collected fishes using multiple gear types (boat electrofishing, otter trawling, and beach seining) to represent the entire local community. Due to a lag in the incorporation of consumed material into fish tissues (Vander Zanden et al. 2015), we sampled fishes in both the same month as plant and invertebrate collections and in the subsequent month (April and May for spring samples, and August and September for summer samples). To minimize ontogenetic diet variation, we identified the size at which a species reached its typical adult diet (Table 1; Moyle 2002) and only fish larger than that size were kept. Electrofishing was conducted using a Smith-Root 5.0 GPP boat-mounted electro-fisher at a constant pulse width

Table 1 Species codes, size cutoff, and sample sizes for all fish species sampled in this study

Species code	Common name	Scientific name	Size cutoff (mm SL)	Spring			Summer		
				LWR	UCA	ULN	LWR	UCA	ULN
BC	Black crappie	<i>Pomoxis nigromaculatus</i>	150	0	3	8	4	13	11
BF	Sacramento blackfish	<i>Orthodon microlepidotus</i>	50	0	1 ^a	0	0	0	0
BG	Bluegill sunfish	<i>Lepomis macrochirus</i>	50	0	1	6	15	6	10
BLB	Black bullhead	<i>Ameiurus melas</i>	100	1	3	0	1	3	0
BLP	Bigscale logperch	<i>Percina macrolepida</i>	70	1	3	2	3	4	4
CCF	Channel catfish	<i>Ictalurus punctatus</i>	200	0	0	0	1 ^a	1	0
CP	Common carp	<i>Cyprinus carpio</i>	100	0	0	5	2	2	0
DS	Delta smelt	<i>Hypomesus transpacificus</i>	60	2	1	0	1	0	2 ^a
GF	Goldfish	<i>Carassius auratus</i>	100	0	2	0	0	0	0
GSF	Green sunfish	<i>Lepomis cyanellus</i>	75	0	0	0	0	0	1
GSH	Golden shiner	<i>Notemigonus crysoleucas</i>	50	6	2	10	15	3	20
HCH	Hitch	<i>Lavinia exilicauda</i>	50	4	2	3	0	2	0
ISS	Mississippi silverside	<i>Menidia audens</i>	60	7	0	1 ^a	18	21	12
LMB	Largemouth bass	<i>Micropterus salmoides</i>	200	11	5	4	17	11	18
MQF	Western mosquitofish	<i>Gambusia affinis</i>	40	0	0	0	0	1	0
RESF	Redear sunfish	<i>Lepomis microlophus</i>	130	6	0	5	8	0	9
SB	Striped bass	<i>Morone saxatilis</i>	200	2	1	0	3	5	1
SCP	Prickly sculpin	<i>Cottus asper</i>	45	13	1	6	11	2	0
SG	Shimofuri goby	<i>Tridentiger bifasciatus</i>	60	8	0	0	12	2	0
SKR	Sacramento sucker	<i>Catostomus occidentalis</i>	90	2	5	0	2	3	2
SPM	Sacramento pikeminnow	<i>Ptychocheilus grandis</i>	200	1	0	0	1	0	1
TFS	Threadfin shad	<i>Dorosoma petenense</i>	55	10	21	8	14	18	22
TP	Tule perch	<i>Hysterocarpus traskii</i>	50	10	19	5	9	7	13
WAK	Wakasagi	<i>Hypomesus nipponensis</i>	60	0	0	0	0	0	1 ^a
WC	White crappie	<i>Pomoxis annularis</i>	150	1	0	3	1	3	1
WCF	White catfish	<i>Ameiurus catus</i>	100	1	12	2	8	5	1
WM	Warmouth sunfish	<i>Lepomis gulosus</i>	75	0	0	0	1	0	1
YFG	Yellowfin goby	<i>Acanthogobius flavimanus</i>	75	0	0	0	14	0	0

^a Subregion/season combinations excluded from mixing model analysis due to missing data

of 60 pulses^{-s} and a variable power so as to maintain a constant electrical current of 8 ± 1 amps. Trawling was conducted using a four-seam otter trawl with a 1.5-m x 4.3-m opening, 5.3-m length, a 35-mm mesh stretch in the main body, and a 6-mm mesh stretch in the cod end. Trawls were towed at 3.5 km/h for 5 min. Beach seines were 10-m bag-less seines with a 6-mm mesh. After capture, we measured all fish and those longer than identified ontogenetic size cutoffs were anesthetized and placed on ice. Up to ten individuals of each species from each subregion and season were kept.

Laboratory Methods

Sample Preparation Primary producers and macroinvertebrates were rinsed with deionized water to remove contamination. Invertebrates were manually sorted and identified to species (Carlton 2007) except for insects, which were

identified to family (Berg et al. 2008). To obtain enough material for stable-isotope analysis, smaller invertebrates were pooled, with up to 300 individual copepods or cladocerans and up to 50 individual macroinvertebrates for each sample. Larger invertebrates (e.g., shrimp, crayfish) and fish were not pooled. All fish were filleted, with left posterior dorsal muscle tissue removed. Fish stomachs were then removed and placed in 10% formalin. Plant and animal tissues for stable-isotope analysis were oven dried for 48–96 h at 60 °C and then ground to a homogeneous powder.

Isotope Analysis We weighed the powdered samples on a microbalance and placed them in tin capsules for isotope analysis. All samples were analyzed for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ at the University of California, Davis, Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass

spectrometer (IRMS; Sercon Ltd., Cheshire, UK). We did not correct for lipid content (Post et al. 2007) as C:N ratios were generally low (~ 3–5).

To estimate a true phytoplankton signature from filtered particulate organic matter (POM), which reflects a broad mixture of detritus, sediments, and phytoplankton cells, we calculated phytoplankton $\delta^{13}\text{C}$ signatures using measured DIC values and an algal fractionation of -26.8‰ (Karlsson et al. 2003). We calculated $\delta^{15}\text{N}$ values using subregion-specific regression equations between POM C:N ratio and POM $\delta^{15}\text{N}$, solving for the Redfield ratio (C:N = 6.625). Phytoplankton $\delta^{34}\text{S}$ signatures can be calculated by adding a fractionation value of -1.5‰ to the $\delta^{34}\text{S}$ signature of dissolved inorganic sulfur (DIS) in water (Stribling and Cornwell 1997). DIS data were unavailable for our study area. We therefore used the mean $\delta^{34}\text{S}$ value of collected POM samples to reflect phytoplankton ($-2.29\text{‰} \pm 1.16$). Our POM phytoplankton proxy value is corroborated by $\delta^{34}\text{S}$ values in juvenile Chinook salmon otoliths (-0.4 ± 1.3), which reflect upstream DIS signatures in the Sacramento River (Weber et al. 2002). When we applied a phytoplankton fractionation value of -1.5‰ to otolith-inferred DIS signatures (-1.9‰), our POM values closely aligned.

Diet Analysis Gut contents from all fishes were identified to the lowest possible taxonomic level (typically family) with a $\times 10$ – 40 dissecting microscope. We counted and weighed all diet items.

Data Analysis

Diets To evaluate diets of fish species across subregions, we calculated the percent Prey-Specific Index of Relative Importance (%PSIRI; Brown et al. 2012) for each prey taxa at each subregion:

$$\%PSIRI = \frac{\%FO_i \times (\%PN_i + \%PW_i)}{2}$$

where %FO equals frequency of occurrence, %PN is the percent numerical abundance divided by the number of stomach samples in which it occurs, and %PW is the percent weight divided by the number of stomach samples in which it occurs. This metric is considered an improvement over conventional indices of relative importance (Pinkas et al. 1970) for two reasons: %PSIRI does not overemphasize abundant prey items, and %PSIRI is additive over taxonomic levels. That is, the %PSIRI of a family will be equivalent to the sum of the %PSIRI of the species within that family, allowing pooling of calculated values for later analyses.

Isotopes We used the package MixSIAR 3.0.0 (Stock and Semmens, 2016) in program R (R Core Team 2019) to

determine the relative proportion of primary source contributions to consumers. This modeling technique incorporates both prior information and uncertainty in source contributions, including trophic-enrichment and diet data (Moore and Semmens 2008; Phillips et al. 2014). We ran each model independently for each subregion and season with species or taxa as a random effect and used all three isotope markers. The model included both process error, by considering source and consumer variation, and residual error except for when the sample size was equal to one. Each model was set to run three chains for 300,000 Markov Chain Monte Carlo simulations, with a burn-in of 200,000.

To minimize under-determination in the mixing models and because of overlap in primary-producer signatures, some primary producers were pooled prior to analysis (Table 2). If ranges of isotope values overlapped, then samples were also pooled across seasons. If a primary producer category was not collected in a region, values from LWR were used in the mixing model. If a primary producer was not collected in a season, this reflected low standing biomass and it was left out of the model. Trophic discrimination factors (TDFs; a measure of isotopic enrichment across trophic levels) were assigned by functional group from McCutchan et al. (2003), with reported standard errors converted to standard deviation per MixSIAR requirements. Enrichment factors for primary consumers (e.g., herbivorous invertebrates) were assigned based on values for aquatic species from McCutchan et al. 2003 (ESM 1). For invertebrate predators, we doubled primary consumer values to account for multiple trophic steps. For invertebrate omnivores, we applied the mean of the pooled invertebrate-herbivores and predators TDFs. We calculated TDFs for fishes by adding the value for fish muscle tissue to that for invertebrate omnivores. Standard errors for all combined TDFs were calculated using the following equation:

$$SE_{\text{Combined}} = \sqrt{SE_1^2 + SE_2^2}$$

We modeled fish and invertebrates from two randomly selected subregion/season combinations using TDFs from Vander Zanden and Rasmussen (1999) to assess the sensitivity of model results to different trophic discrimination factors (ESM 1), a known concern for food web studies (Vander Zanden and Rasmussen 2001). In addition to sensitivity analyses, we compared TDFs used in this study with published values for analogous species to ensure that our chosen values reflected variability in the literature (ESM 1). Sensitivity analyses indicated invertebrate results were robust to use of different TDFs. Fish results were not robust to use of different TDFs, with use of a different TDF affecting results. However, values based on McCutchan et al. (2003) were selected because they more closely approximated trophic enrichment values for largely carnivorous fishes (0.82; Bastos et al. 2017).

Table 2 Mean and standard deviation of isotope values and sample sizes of primary producers

Region	Category	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		$\delta^{34}\text{S}$		n	
		Spring	Summer	Spring	Summer	Spring	Summer		
Upper Cache (UCA)									
Benthic diatoms	BD	-19.54 ± 0.2 ^a	-	7.45 ± 0.2 ^a	-	-0.67 ± 0.4 ^a	-	3	-
<i>Ceratophyllum demersum/Myriophyllum spicatum</i>	SAV	-30.27 ± 0.1	-29.99 ± 1.1	7.06 ± 0.2	12.37 ± 2.3	-3.68 ± 0.3	-3.02 ± 0.3	2	6
Phytoplankton	Phyto	-36.67 ± 0.8 ^a	-	8.12 ± 2.1 ^a	-	-2.29 ± 1.2 ^a	-	3	-
<i>Schoenoplectus californicus</i> (upstream)	EM	-27.72 ± 1.0	-	8.57 ± 4.2	-	-2.12 ± 4.8	-	6	-
<i>S. californicus</i> (downstream)	EM	-29.66 ± 0.2	-	10.50 ± 0.5	-	9.02 ± 4.4	-	3	-
Upper Lindsey (ULN)									
Benthic diatoms	BD	-24.03 ± 0.5	-	5.08 ± 1.7	-	-1.19 ± 0.5	-	3	-
<i>Bulboshoenus maritimus/Schoenoplectus acutus</i>	EM	-26.93 ± 0.8	-	9.03 ± 4.0	-	10.33 ± 2.1	-	3	-
<i>C. demersum/Egeria densa</i>	SAV	-26.19 ± 0.7	-27.49 ± 1.2	11.53 ± 0.3	10.72 ± 1.2	-1.50 ± 0.4	-1.23 ± 1.0	3	6
Green filamentous algae	GFA	-33.94 ± 0.0	-16.46 ± 0.2	8.66 ± 0.1	5.08 ± 0.1	0.27 ± 0.1	8.01 ± 0.7	3	3
<i>Juncus baltica/S. californicus</i>	EM	-28.29 ± 0.7	-27.38 ± 0.2	6.19 ± 0.2	6.77 ± 0.1	-2.08 ± 2.0	0.55 ± 0.4	3	2
<i>M. spicatum</i>	SAV	-18.50 ± 0.0	-24.11 ± 0.8	7.55 ± 0.5	6.74 ± 0.6	-1.24 ± 0.2	1.34 ± 1.0	3	3
Phytoplankton	Phyto	-38.37 ± 0.1	-	6.98 ± 0.8	-	-2.29 ± 1.2	-	7	-
<i>Typha sp./Iris pseudocoras</i>	EM	-30.64 ± 0.5	-28.95 ± 0.7	3.56 ± 0.4	4.93 ± 2.1	-0.69 ± 1.0	-3.11 ± 1.3	2	6
Lower Cache and Lindsey (LWR)									
Benthic diatoms	BD	-19.54 ± 0.2	-	7.45 ± 0.2	-	-0.67 ± 0.4	-	3	-
<i>Cabomba caroliniana/E. densa/Ludwigia peploides</i>	SAV	-27.94 ± 1.5	-25.93 ± 1.1	6.91 ± 0.3	10.76 ± 0.9	-1.59 ± 0.2	-1.31 ± 0.4	2	9
Green filamentous algae	GFA	-17.47 ± 0.1	-17.18 ± 0.6	14.40 ± 0.3	14.22 ± 0.5	0.33 ± 0.3	0.69 ± 0.8	3	4
<i>Juncus baltica</i>	EM	-29.11 ± 0.1	-	3.21 ± 1.2	-	1.60 ± 1.1	-	3	-
<i>C. demersum/M. spicatum</i>	SAV	-25.71 ± 2.1	-	4.27 ± 2.0	-	-0.36 ± 1.4	-	5	-
Phytoplankton	Phyto	-36.67 ± 0.8	-	8.12 ± 2.1	-	-2.29 ± 1.2	-	3	-
<i>Typha sp./S. californicus</i>	EM	-28.00 ± 0.7	-	11.12 ± 0.9	-	-4.09 ± 2.4	-	6	-

Values between the season columns have been pooled across seasons

BD, benthic diatoms; EM, emergent vegetation; GFA, green filamentous algae; Phyto, phytoplankton; SAV, submersed aquatic vegetation

^a Samples pooled with other study regions

Models for invertebrates utilized a generalist prior based on the Dirichlet distribution (Parnell et al. 2013) and only included carbon and nitrogen because sample weights of invertebrates were not high enough to get an accurate sulfur value. Subregion-specific models for each fish species utilized a unique weakly informative prior based on the %PSIRI of diet items and the subregion-specific mixing-model results for that invertebrate. If mixing-model results were unavailable for more than 50% of the fish species' diet, we used a model with a generalist prior. Incorporating the diet data as a prior was intended to help constrain uncertainty associated with TDF selection. Species with a sample size of 1 were excluded from mixing model analysis (Sacramento blackfish *Orthodon microlepidotus*, wakasagi *Hypomesus nipponensis*, and green sunfish *Lepomis cyanellus*).

We tested for differences in average contribution from each primary producer across subregions using a two-way ANOVA with primary producer and season as factors. Pairwise comparisons were conducted across subregions using a Tukey HSD test. To test for differences between pelagic and littoral trophic pathways, we performed a pairwise permutation test on the distribution of phytoplankton contribution to different species in each subregion.

Results

Primary Producer Isotope Values

Primary producer groups had large within- and among-group variation for all three sampled isotopes (Table 2; Fig. 2). Phytoplankton was consistently the most depleted in $\delta^{13}\text{C}$ among primary-producer categories, with mean values across subregion/season combinations ranging from -36 to -38‰ , while benthic diatoms were typically enriched in $\delta^{13}\text{C}$ (-19 to -24‰). Emergent vegetation $\delta^{13}\text{C}$ values exhibited some variability across space and time but were generally intermediate (-26 to -30‰). SAV and epiphytic GFA exhibited the greatest variability of $\delta^{13}\text{C}$ values across space and time (SAV, -18 to -30‰ ; GFA, -16 to -33‰).

Mean benthic diatom $\delta^{15}\text{N}$ values were relatively consistent across all three subregions (5 to 7‰), as were mean phytoplankton $\delta^{15}\text{N}$ values (7 to 8‰). Emergent vegetation (3 to 11‰), SAV (4 to 12‰), and epiphytic GFA (5 to 14‰) $\delta^{15}\text{N}$ values were more variable. Mean $\delta^{15}\text{N}$ values of primary producers were generally enriched in UCA relative to other subregions, and SAV was typically more enriched in summer than in spring, although not in ULN. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of primary producers were consistent with results from other SFE studies (Grimaldo et al. 2009; Schroeter et al. 2015), particularly with respect to the high variability of SAV and emergent vegetation (Cloern et al. 2002).

Most primary-producer categories were intermediate in mean $\delta^{34}\text{S}$ values (between -2 and 1‰), with several prominent exceptions. Two emergent vegetation groups, *Schoenoplectus californicus* from UCA and combined *Bulboshoenus maritimus*/*Schoenoplectus acutus* from ULN, exhibited enriched $\delta^{34}\text{S}$ values ($> 9\text{‰}$). Epiphytic GFA from ULN during summer also had high $\delta^{34}\text{S}$ ($\sim 8\text{‰}$).

Invertebrate and Fish Isotope Values

Generally, the isotopic spread of invertebrate communities was larger in spring compared to summer, when species' signatures became more similar (Fig. 2). Various taxa of zooplankton, cladocerans (mean, -33.23‰ ; standard deviation, 1.71‰) and the copepods *Pseudodiaptomus forbesi* ($-34.30 \pm 1.49\text{‰}$) and *Sinocalanus doerrii* ($-34.76 \pm 0.62\text{‰}$), exhibited the most depleted $\delta^{13}\text{C}$ values of all invertebrates. The amphipod *Hyaella* sp. ($-23.20 \pm 4.03\text{‰}$) and physid snails ($-23.02 \pm 3.74\text{‰}$) exhibited relatively enriched $\delta^{13}\text{C}$ values. The Siberian prawn *Palaemon modestus* ($14.19 \pm 1.39\text{‰}$) had the most enriched $\delta^{15}\text{N}$, along with the two copepod species (*P. forbesi*, $12.82 \pm 1.39\text{‰}$; *S. doerrii*, $13.77 \pm 0.70\text{‰}$) and damselflies of Coenagrionidae ($12.72 \pm 1.08\text{‰}$). Note invertebrate species/group composition and consequent availability for sampling varied by season and subregion, and only zooplankton samples from spring were analyzed due to laboratory error.

Delta smelt *Hypomesus transpacificus* ($-30.46 \pm 1.56\text{‰}$) and wakasagi (-29.64‰ , $n = 1$) exhibited the most depleted $\delta^{13}\text{C}$ values of fish species, while Sacramento blackfish (-22.63‰ , $n = 1$) and warmouth *Lepomis gulosus* ($-24.55 \pm 0.48\text{‰}$) exhibited the most enriched $\delta^{13}\text{C}$ values (Fig. 2). Tule perch *Hysterocarpus traskii*, the most abundant native species, had intermediate $\delta^{13}\text{C}$ values ($-28.08 \pm 0.95\text{‰}$). Largemouth bass *Micropterus salmoides* ($17.20 \pm 0.77\text{‰}$) and white crappie *Pomoxis annularis* ($17.05 \pm 1.57\text{‰}$) had the most enriched $\delta^{15}\text{N}$ values, suggesting they occupied the highest trophic level, while common carp *Cyprinus carpio* ($13.39 \pm 0.34\text{‰}$) and goldfish *Carassius auratus* ($12.86 \pm 1.16\text{‰}$) had the least enriched $\delta^{15}\text{N}$ values (Fig. 2). Striped bass *Morone saxatilis* ($3.95 \pm 0.88\text{‰}$) had the most enriched $\delta^{34}\text{S}$ values, while common carp ($-4.47 \pm 0.13\text{‰}$) had the most depleted $\delta^{34}\text{S}$ values (ESM 2). Variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ across all subregions was consistent, but fish from ULN exhibited the greatest variability in $\delta^{34}\text{S}$ values (-4.80 to 14.42‰), consistent with variability in $\delta^{34}\text{S}$ from reduction-oxidation reactions in tidal wetland (Peterson et al. 1986).

Fish Diets

We examined the stomach contents of 763 individual fish from 30 species. Plant material and detritus had the highest mean %PSIRI values of all gut contents in both seasons (spring 26%, summer 30%), but amphipods (spring 22%,

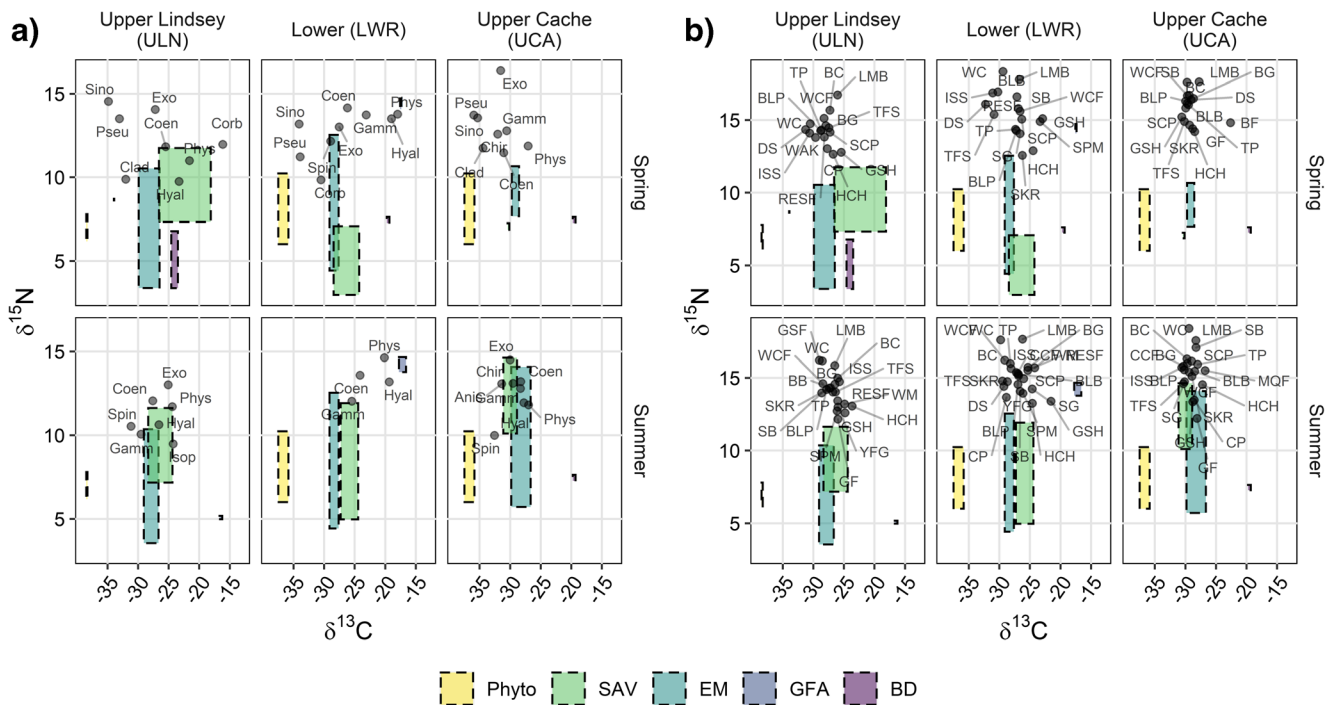


Fig. 2 Biplot of carbon and nitrogen isotopes with taxa means and primary producer category means and standard deviations. **a** Invertebrates: Anisoptera (Anis), Chironomidae (Chir), Cladocera (Clad), Coenogroniidae (Coen), *Corbicula fluminea* (Corb), *Palaemon*

modestus (Exo), *Gammarus daiberi* (Gamm), *Hyaella* sp. (Hyal), Isopoda (Isop), Physidae (Phys), *Pseudodiaptomus forbesi* (Pseu), *Sinocalanus doerrii* (Sino), and *Americorophium spinicorne* (Spin). **b** Fish codes as in Table 1. Biplots including sulfur isotopes are in ESM 2

summer 15%) and other macro-crustaceans (spring 16%, summer 17%) had the highest mean %PSIRI values of all animal prey items in both seasons. No other diet item had a %PSIRI over 10%, although snails, insects, and zooplankton had high %PSIRI values for individual fish species (ESM 3), consistent with recent SFE fish diet studies (Feyrer et al. 2003; Nobriga and Feyrer 2007; Grimaldo et al. 2009; Young et al. 2018a; Weinersmith et al. 2019).

Subregional and Seasonal Differences in Primary Source Contributions to Consumers

We ran mixing models for 13 invertebrate species/groups with eight species/groups present at over half of all site and season combinations. The other five species/groups were either present in only one season or at one location. We ran mixing models for 28 fish species, with 16 species present at over half of all subregion and season combinations. The other 12 species were either present in only one season or at one location.

Mixing-model results showed that zooplankton (cladocerans, *P. forbesi*, and *S. doerrii*) consistently exhibited high contributions from phytoplankton (mean posterior probability >80%) except in ULN, where cladocerans and *P. forbesi* derived significant contributions from emergent vegetation and SAV (Fig. 3; ESM 4). Larger crustaceans (isopods, *Gammarus daiberi*, *Hyaella* sp., *A. spinicorne*, and

P. modestus) exhibited similar trends, relying strongly on phytoplankton in UCA, but relying more strongly on SAV and emergent vegetation elsewhere (Fig. 3). A single primary-producer category dominated mixing-model results (mean posterior probability > 50%) for most invertebrate taxa.

Across spring and summer, invertebrates from UCA had a higher mean contribution from phytoplankton (mean 39%, standard error 8% across all invertebrate taxa) than those from ULN ($14 \pm 5\%$, Tukey HSD adjusted $p = 0.04$), with LWR intermediate (mean, $21 \pm 8\%$). ULN had a higher mean contribution from SAV ($40 \pm 6\%$) than UCA ($16 \pm 4\%$; Tukey HSD adjusted $p = 0.003$). Although LWR had lower average contributions from SAV, they had relatively high contributions from SAV-associated GFA (mean, $26 \pm 7\%$). In aggregate, SAV and epiphytic GFA dominated food webs in LWR (> 50%), SAV and emergent vegetation dominated in ULN (> 75%), and emergent vegetation and phytoplankton dominated in UCA (> 75%). Seasonal differences were primarily driven by an increase in the contribution of SAV in summer (mean 3% increase in UCA and 25% increase in LWR). ULN had minimal seasonal differences.

Unlike the invertebrates, most fish species were supported by more than one primary producer (Fig. 4; ESM 5). Largemouth bass was the only species to show consistent dominance by a single primary-producer category at any given location: either emergent vegetation or SAV comprised

Fig. 3 The contribution of different primary sources to invertebrate taxa across subregions and seasons. Site codes: Upper Lindsey Slough (ULN), Lower (LWR), and Upper Cache Slough (UCA). Primary producer categories: benthic diatoms (BD), emergent vegetation (EM), green filamentous algae (GFA), phytoplankton (Phyto), and submersed aquatic vegetation (SAV). Invertebrate taxa codes as in Fig. 2

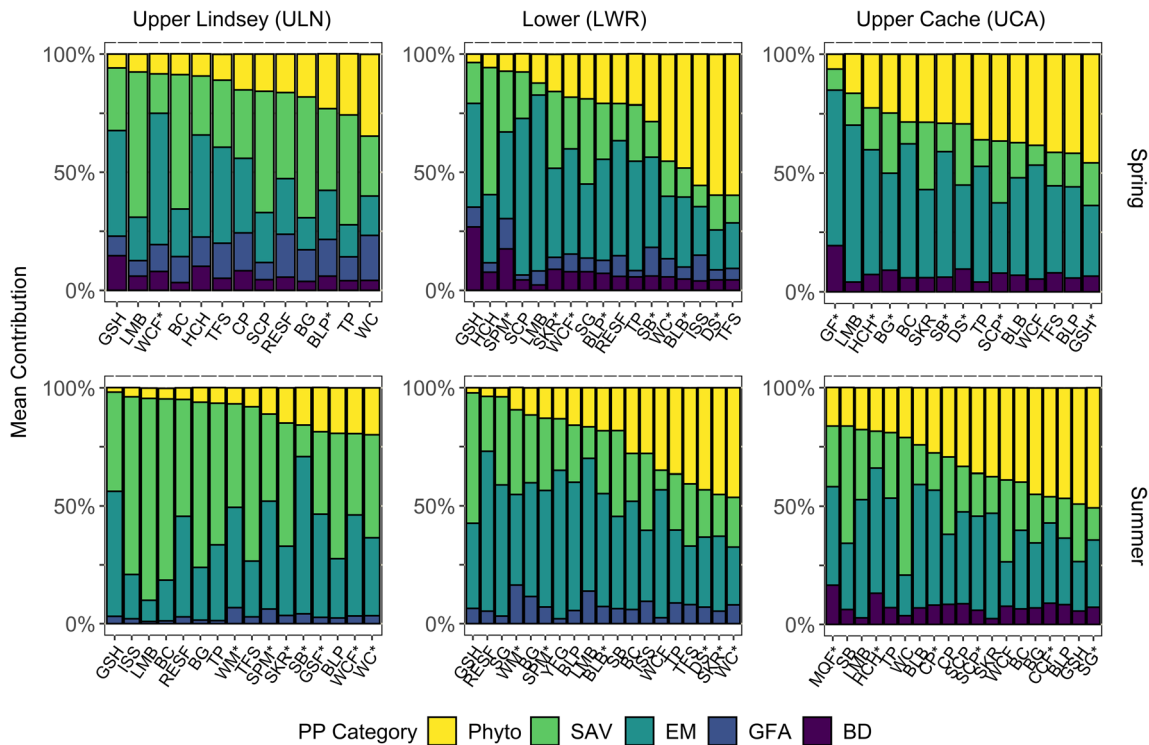
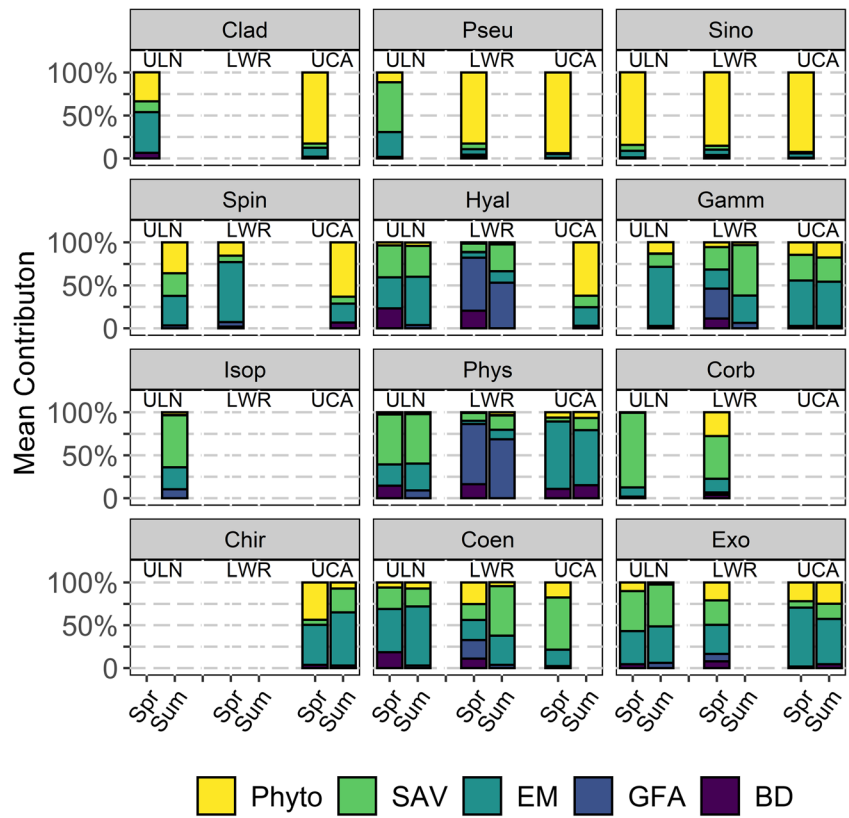


Fig. 4 The contribution of different primary producers to fishes, arranged in order of increasing phytoplankton contribution. Primary producer categories: benthic diatoms (BD), emergent vegetation (EM), green filamentous algae (GFA), phytoplankton (Phyto), and submersed

aquatic vegetation (SAV). Fish codes are in Table 1. Asterisks denote when there were fewer than three samples for subregion/season combination

greater than 50% depending on subregion and season, a result consistent with the littoral associations of largemouth bass diets in this and other systems (Brosseau and Hodgson 2016; Weinersmith et al. 2019). Other fish species typically incorporated a wide variety of primary producers, with individual categories rarely dominating more than one subregion or season for each fish species. For example, black crappie *P. nigromaculatus* were primarily supported by SAV in ULN but not other subregions. Similarly, Mississippi silverside *Menidia audens* support was dominated by phytoplankton in spring months but not summer.

A clear gradient existed in the average contribution of phytoplankton, SAV, and emergent vegetation to fish species across the three subregions (Fig. 5a; ESM 5). Fish from ULN had the highest contribution from SAV across all seasons and species (mean, 45%; standard error, 3%) and the

lowest contribution from phytoplankton ($12 \pm 1\%$). Fish in UCA had the highest contribution from phytoplankton ($31 \pm 2\%$) and the lowest contribution from SAV ($21 \pm 2\%$). Fish from LWR, analogous to most existing Delta littoral habitats, had the highest contribution from emergent vegetation ($41 \pm 2\%$) and intermediate contributions from SAV ($24 \pm 2\%$) and phytoplankton ($24 \pm 3\%$). Benthic diatoms and GFA never averaged more than 10% of the primary-producer contribution.

In addition to strong spatial differences, the contribution of different primary producers to fish differed significantly across seasons (Fig. 5b; ESM 6). From spring to summer, SAV increased by a mean of 8% across all species and subregion ($F(1, 74) = 7.78; p = 0.0067$), while GFA declined ($F(1, 48) = 16.00; p = 0.00022$). Benthic diatoms were not sampled in summer for ULN and LWR, so they were excluded from subregion and season comparisons for fish. The only significant difference between the distributions of phytoplankton contributions was in ULN, where phytoplankton contribution was invariably low ($p < 0.001$). There was no statistical evidence for consistent segregation between pelagic and littoral food webs within the same subregion ($p > 0.8$).

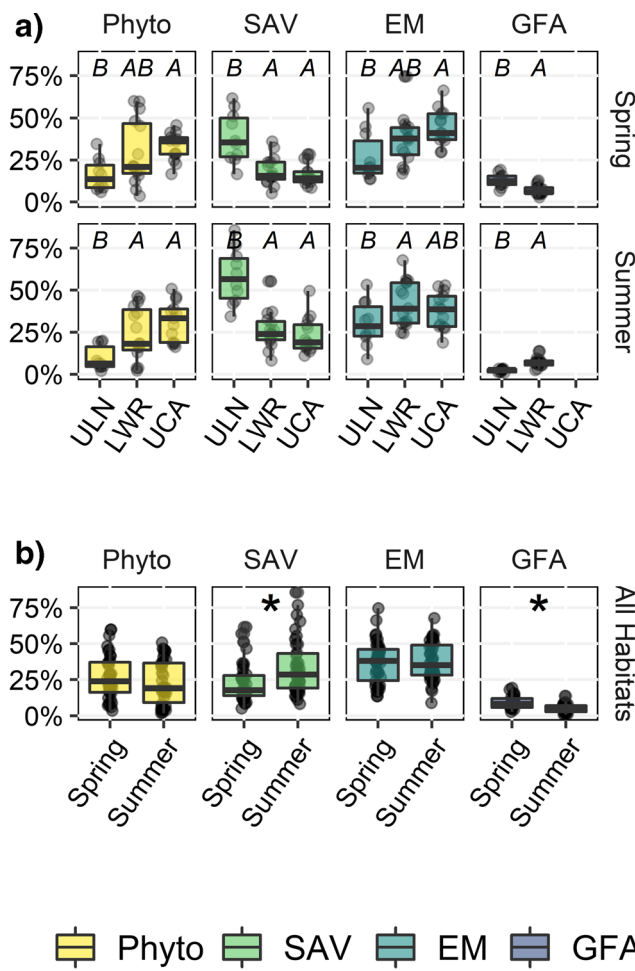


Fig. 5 Boxplots of percent contribution from different primary sources to fishes. Letters in (a) reflect significant differences resulting from Tukey HSD pairwise comparisons across subregions. Asterisks in (b) reflect significant results from ANOVA across seasons. Site codes: Upper Lindsey Slough (ULN), Lower (LWR), and Upper Cache Slough (UCA). Primary producer categories: benthic diatoms (BD), emergent vegetation (EM), green filamentous algae (GFA), phytoplankton (Phyto), and submersed aquatic vegetation (SAV)

Discussion

In general, northern Delta food webs were supported by diverse primary producers, including SAV, emergent vegetation, and phytoplankton. Strong differences existed in sources of primary production that supported consumers across subregions that reflect different habitat types despite close spatial proximity. Similar differences were observed across seasons, with the relative contributions of different primary producers changing from spring to summer. Despite these differences, we observed little consistent segregation between littoral and pelagic trophic pathways. Rather, fishes were reliant on prey that consumed a variety of primary producers and accessed both pelagic and littoral pathways across subregions and seasons. Subregional differences influenced food-web structure, suggesting that small-scale habitat modifications can result in food webs that differ substantially from the surrounding landscape.

Food Web Support in Different Habitat Types

Food webs in the three subregions, despite close spatial proximity, were not supported by the same primary producers. In the tidal wetland (ULN), non-phytoplankton production dominated the food web. SAV contributed more to both invertebrates and fishes in this subregion, likely related to dense SAV stands along slough margins and in nearby shallow sloughs. SAV was less important in the deep channel subregion (LWR) and the turbid backwater (UCA), likely because the deep

channels only exhibited dense SAV along slough margins (Young et al. 2015) and the turbid backwater (UCA) had very little SAV, presumably due to light-limitation as a result of suspended sediment.

The low phytoplankton contribution to the tidal wetland food web can be attributed to water diversions in Upper Lindsey Slough that minimize local pelagic productivity (Lucas et al. 2002). Notably, even the copepod *P. forbesi* and cladocerans, usually classified as grazers on phytoplankton, exhibited low reliance on phytoplankton in the tidal wetland. Although the low phytoplankton contribution was consistent with low chlorophyll levels ($< 4 \mu\text{g/L}$; Montgomery 2017), its lack of importance here highlights the potential for other productivity pathways in tidal wetland. In contrast, the turbid backwater (UCA) had high chlorophyll α concentrations ($> 12 \mu\text{g/L}$) that more consistently supported local consumers. In the deep channels of the lower subregion (LWR), many species utilized phytoplankton; however, chlorophyll α concentration was low ($< 6 \mu\text{g/L}$; Montgomery 2017). LWR likely received phytoplankton tidally transported from Liberty Island, a nearby tidal lake thought to be important for local phytoplankton production (Lehman et al. 2010).

An important caveat to our study is that we did not sample conditioned detritus. Rather, we sampled tissues from living macrophytes, algae, and other primary producers, assuming that the isotopic composition of living tissue approximates the isotopic composition of detritus. Although this assumption is supported in other systems (Currin et al. 1995; Fellerhoff et al. 2003), it may be system- and primary producer dependent. Other studies from the SFE have used methodologies similar to ours to infer detrital contributions to food webs (Howe and Simenstad 2011; Schroeter et al. 2015), as have studies from other estuaries, including Puget Sound (Howe and Simenstad 2015), Botany Bay (Mazumder et al. 2011), and others (Melville and Connolly 2003). Nevertheless, assuming minimal fractionation between living tissue and newly conditioned detritus could have skewed interpretation of our results if the fractionation had been substantially different between live tissue and detritus. Thus findings from this study highlight the value of primary producers other than phytoplankton, either as living tissue or detritus, to consumers. Given the importance of detritus to consumers in other systems (Odum 1980; Peterson et al. 1985; Hyndes et al. 2014), the detrital component probably contributed more than the living tissue, highlighting a next research step: delineating contributions of living tissue and detritus among primary producers to consumers.

Also, the selection of TDFs is crucial for interpreting model results. Given the variability associated with TDF selection observed during sensitivity analyses, future studies should take care in selecting appropriate TDFs. Despite the variability associated with TDF selection in this study, the sensitivity

analyses showed that the qualitative differences in contribution from different primary producers (i.e., macrophytes versus phytoplankton) to local communities were not a result of TDF selection.

Seasonal Shifts in Food Web Support

Submersed aquatic vegetation density is highest in late summer and early fall (Hestir 2010) and is thus more likely to be an important contributor to local food webs during that period. Modest declines in the contribution of emergent vegetation to food webs were seen in all subregions as SAV increased, suggesting that SAV-associated prey is consumed with higher frequency as SAV density increases. SAV typically supports high epiphytic microalgae biomass (Allen 1971) and generally has higher decomposition rates than many types of emergent vegetation (Twilley et al. 1986; Chimney and Pietro 2006), enhancing availability of SAV-associated carbon and other nutrients to food webs. Because this study did not encompass the entire SAV growing season (April–October), SAV contribution to consumers in both late-season SAV growth and senescence periods remains uncertain.

This study was conducted during one of the driest years on record, 2014, and thus does not represent all water-year types. Nevertheless, with probability of drought in California increasing with the changing climate, our results will likely be increasingly applicable in dry seasons (i.e., summer/autumn) and in future years. Although the overall strength of each productivity pathway may differ depending on climatic conditions (e.g., phytoplankton productivity may increase in flooded areas during wet seasons and/or years), fishes will probably continue integrating multiple primary producers across seasons.

Segregation of Trophic Pathways Within Subregions

We found little segregation between littoral and pelagic trophic pathways. Instead, we observed a gradual gradient in the relative importance of pelagic and littoral pathways to fishes across subregions and seasons. Although spatial differences in the importance of phytoplankton or vascular plant-based contributions to consumers were pronounced, most adult fishes did not consistently use a distinct trophic pathway and instead incorporated both primary producer pathways. The only subregion where the fish assemblage exhibited some evidence for separation of littoral and pelagic food webs was the lower deep channel subregion (LWR), and that was not statistically significant ($p > 0.8$). This location resembles other Delta habitats where trophic segregation has been documented (Grimaldo et al. 2009), with a wide, deep channel; narrow SAV and emergent vegetation bands along the banks; and high tidal flow. In this more open-water habitat, phytoplankton strongly supported ($> 40\%$) five fish species and weakly

supported others (< 25%; 13 species), with only one species in between. Such a food web is consistent with the contemporary Delta resembling many freshwater lentic systems in community composition and ecosystem function (Moyle et al. 2012). This is generally similar to some freshwater lakes, where some benthic invertivores (such as pumpkinseed; *Lepomis gibbosus*) and sedentary inter-guild predators (largemouth bass) often show segregation between littoral and pelagic food webs (Vander Zanden and Vadeboncoeur 2002; Eloranta et al. 2011) with only more mobile predators integrating the two.

Aside from lentic habitats, a large body of literature supports the complex interdependencies of pelagic and littoral/benthic food webs (Forbes 1925; Sand-Jensen and Borum 1991; Polis et al. 1997; Vadeboncoeur et al. 2002). Fish typically couple these two habitats because they are both more mobile than most invertebrates and feed at higher trophic levels, resulting in more generalist feeding behavior (Pyke et al. 1977; Petchey et al. 2008). Generalist feeding links disparate food web elements and contributes to overall food web stability (McCann et al. 2005); such food webs are intrinsically more resilient to changing environmental conditions (McMeans et al. 2016). Regions with increased coupling, such as the northern Delta, may have more stable and resilient food webs than other Delta regions where habitat diversity is low and where wetland and turbid backwaters are absent. We acknowledge, however, that possible food web subsidies across subregions/habitats were not addressed in this study. Subsidies across habitats are not uncommon (Odum 1980; Polis et al. 1997) and they could provide additional benefits of restoration projects if scaled appropriately—this is an avenue for future research.

Reconciliation with Previous Findings

For many pelagic fishes (e.g., delta smelt, threadfin shad) phytoplankton was the most valuable primary producer; however, they still utilized other sources, even in subregions such as the turbid backwater (UCA) where zooplankton densities were high (Montgomery 2017). This was unexpected given previous studies that emphasized the importance of phytoplankton for pelagic consumers in the Delta (Jassby and Cloern 2000; Sobczak et al. 2005). The difference may be due to methodology. Our study incorporated $\delta^{34}\text{S}$, which can differentiate primary producers better than using only $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Peterson et al. 1986; Deegan and Garritt 1997; Connolly et al. 2004). Phytoplankton and terrestrial, emergent, and floating vegetation can have similar depleted $\delta^{13}\text{C}$ signatures and are thus difficult to distinguish with just $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Cloern et al. 2002). Based on natural history, previous isotope studies that used only nitrogen and carbon assumed that pelagic fishes aligned with depleted $\delta^{13}\text{C}$ signatures because their main carbon source was phytoplankton rather than other carbon sources such as emergent vegetation

(Grimaldo et al. 2009). Our addition of $\delta^{34}\text{S}$, coupled with advances in modelling software, allowed us to parse out the contribution of phytoplankton versus other primary producers better than previous local isotope studies. Additionally, all fishes included in this study were adults, which feed on a variety of prey, while zooplankton and other small pelagic invertebrates are more important to juvenile and larval fish. Thus, pelagic productivity is likely more important for juvenile fishes than for adults in this region.

Food Webs and Implications for Tidal Wetland Restoration

The landscape matrix affects composition of local food webs (Polis et al. 1997). Uniquely, we found high heterogeneity in primary producers and in diet items within a comparatively small geographic area: the northern Delta. However, tidal wetland food webs in the northern SFE are supported mainly by emergent vegetation (Howe and Simenstad 2007; Howe and Simenstad 2011; Schroeter et al. 2015), while food webs in other habitats are dominated by one other primary producer (Grimaldo et al. 2009). Given historical dominance of dense emergent vegetation and turbid wetland in the Delta (Whipple et al. 2012; Robinson et al. 2014), the basis of the historical food web was likely very different from that of today (Cloern et al. 2016). Trophic pathways currently only available in marginal habitats were likely far more important historically (e.g., terminal tidal backwaters, vegetated off-channel habitat), a notion supported by the prevalence of detrital resources in other large tidal systems (Teal 1962; Odum 1980).

Much of the Delta resembles the deep channels sampled in this study, with off-channel wetland and turbid backwaters being uncommon. The value of wetland and backwaters in today's Delta seems to be low given their small area (Brown et al. 2016). Delta-wide, these habitats probably contribute little to food webs; however, they are locally very important because they occur in areas such as ULN, UCA, and others (e.g., Suisun Marsh, Sherman Lake) that support relatively high densities of native fish (Meng et al. 1994; Moyle et al. 2012; Young et al. 2018b). These areas likely provide other functions for fishes, particularly as rearing and nursery habitats (Colombano et al. 2020). It should also be noted that the sites representing restoration outcomes (i.e., wetland and backwater) better integrated the disparate trophic pathways, which in conjunction with other habitat uses, suggests that habitat restoration could lead to enhanced ecological function.

Extensive habitat restoration is slated for the Delta and considerable uncertainty exists about possible goals and outcomes (Herbold et al. 2014). This study has demonstrated that small-scale habitat differences can greatly alter basal food web structure, so local food webs in restored sites will differ substantially from the surrounding waterways. Many planned restoration projects seek to enhance phytoplankton production to

support pelagic fishes in the Delta, but this study shows that adult fishes are supported by multiple primary producers, particularly in shallow-water habitats. Instead of focusing on a single primary producer, ecosystem restoration efforts should enhance a variety of primary producers to support consumers. Consistent moderate contributions (e.g., from emergent vegetation in tidal wetland) can buffer seasonal declines in SAV and phytoplankton productivity. Availability of diverse sources will differ seasonally and across multiple spatial scales, moderating environmental variability and enhancing resilience of local food webs (Takimoto et al. 2002; Schindler et al. 2015; McMeans et al. 2016).

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