RESEARCH

The Aquatic Trophic Ecology of Suisun Marsh, San Francisco Estuary, California, During Autumn in a Wet Year

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ABSTRACT

Using stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) and mixing models, we investigated the trophic levels and carbon sources of invertebrates and fishes of a large tidal marsh in the San Francisco Estuary. Our goal was to better understand an estuarine food web comprised of native and alien species. We found the following: (1) the food web was based largely on carbon from phytoplankton and emergent-aquatic and terrestrial vegetation, but carbon from submerged aquatic vegetation and phytobenthos was also used; (2) alien species increased the complexity of the food web by altering carbon-flow pathways and by occupying trophic positions different from native species; and (3) most consumers were dietary generalists.

KEY WORDS

food web; San Francisco Estuary; trophic ecology; stable isotope; tidal marsh; Suisun Marsh; *Gammarus daiberi*

INTRODUCTION

The aquatic ecosystem in the San Francisco Estuary (estuary) before European colonization contained a relatively small number of species and a presumably simple food web (Cohen and Carlton 1998; Orsi and Ohtsuka 1999; Kimmerer 2004). Since then, the estuary has undergone major physical and ecological transformation over the last two centuries (Conomos 1979; Nichols et al. 1986; Cohen and Carlton 1998). A substantial part of this transformation has been species introductions, earning the San Francisco Estuary the onerous honor of being the most invaded estuary in the world, at a rate that has been accelerating since the mid-1800s (Cohen and Carlton 1998), and with a new species being established about every 14 weeks during the 1990s. Cohen and Carlton (1998) determined that over 234 species were alien to the estuary, and an additional 125 species were cryptogenic (i.e., place of origin uncertain). New species continue to invade and persist in the system (Emmett et al. 2002; Schroeter and Moyle 2006).

Some of these alien invasions have resulted in significant community and food-web alterations. For example, the overbite clam (*Potamocorbula amurensis*) has reduced pelagic productivity by feeding heavily on both phytoplankton and small zooplankters (Nichols et al. 1990; Alpine and Cloern 1992; Kimmerer et al. 1994; Kimmerer and Orsi 1996). Fishes such as juvenile striped bass (*Morone saxatilis*) that once subsisted primarily on native invertebrates

now have diets dominated by alien species (Feyrer et al. 2003; Bryant and Arnold 2007). The proportion of the inshore fish assemblage comprising alien fishes in the freshwater portion of the estuary has increased substantially from the early 1980s (Brown and Michniuk 2007). Similarly, alien species have become more dominant in both benthic–invertebrate and zoo-plankton assemblages in many parts of the estuary (Peterson and Vayssieres 2010; Winder and Jassby 2011). The full effect of alien species on native fauna, however, remains largely unknown because of igno-rance of the basic ecology of both types of species (Kimmerer 2004; Sommer et al. 2007).

Despite the copious introductions, extinctions of native species in the estuary have been rare (Orsi and Ohtsuka 1999; Moyle 2002). Consequently, the aquatic ecosystem in the estuary is becoming more complex, with an increasingly novel faunal assem-blage (Orsi and Ohtsuka 1999; Kimmerer 2004). To develop effective flow and vegetation management for native species, especially in the context of con-tinuing change (Hobbs et al. 2006; Seastedt et al. 2008; Moyle 2013), this new ecosystem requires bet-ter understanding of the relationships among species.

A few studies in the last decade have shed some light on the trophic structure and function of this new ecosystem. Grimaldo et al. (2009) used both stable isotopes and gut-content analyses to delineate the food web of flooded agricultural islands in the fresh-water portion of the estuary. They found that some fishes, primarily pelagic species, depended heavily on pelagic food sources, but the majority of species mostly ate food supported by submerged aquatic vegetation (SAV) and associated periphyton. Notably, alien and native species both ate each other, forming one integrated food web. Howe and Simenstad (2011) examined aquatic food webs of wetlands along the estuary's salinity gradient using sulfur, carbon, and nitrogen stable isotopes. In contrast to Grimaldo et al. (2009), most of the organisms in Howe and Simenstad's study ultimately derived their food from wetland-produced vegetation, reflecting differences in the dominant vegetation types present. To extend the geographic scope of food-web knowledge of the estu-ary, we performed a study in Suisun Marsh, a region of the estuary slated for large-scale tidal restoration for the benefit of native fishes.

Suisun Marsh, a mosaic of sloughs, tidal wetlands, and managed wetlands in the geographical center of the estuary, is vital habitat for at-risk native species and a major target for future restoration (Moyle et al. 2014). However, the communities of this brackish marsh are similar to the communities found in other areas of the estuary, with alien species accounting for the largest portion of the invertebrate and fish catch (Matern et al. 2002; Schroeter 2008; O'Rear and Moyle 2010). Alien species are not only numerically dominant in Suisun Marsh but are also very diverse, having at least one abundant representative in nearly all taxonomic groups and being the sole members of the classes Hydrozoa and Cirripedia. The trophic ecology of many of these species within the marsh, including six common macroinvertebrate crusta-ceans [the amphipods *Eogammarus confervicolus* and *Gammarus daiberi*, the isopod *Synidotea laticauda*, the mysid *Hyperacanthomysis longirostris*, and the shrimps Siberian prawn (*Exopalaemon modestus*) and oriental shrimp (*Palaemon macrodactylus*)] and three locally abundant clams [Asian clam (*Corbicula flu-minea*), overbite clam (*Potamocorbula amurensis*), and *Macoma petalum*], is largely unknown.

To address this knowledge gap, we used stable isotope ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) to identify the trophic positions and carbon sources of abundant alien and native organisms. Isotope ratios provide time- and space-integrated information about feed-ing relationships and energy flow through food webs; they can be particularly helpful when diet studies are difficult both because of the small size of species and prey maceration by invertebrates. δ^{15}N values are indicators of trophic levels and have been used suc-cessfully in fresh, brackish, and marine environments (Peterson and Fry 1987; Fry 1991; Hansson et al. 1997; Kwak and Zedler 1997). δ^{13}C values are useful in identifying food sources for consumers and thus the energy bases for food webs (Gearing 1991). The combination of δ^{13}C and δ^{15}N yields information on the structure and types of food webs in aquatic com-munities (e.g., Kwak and Zedler 1997).
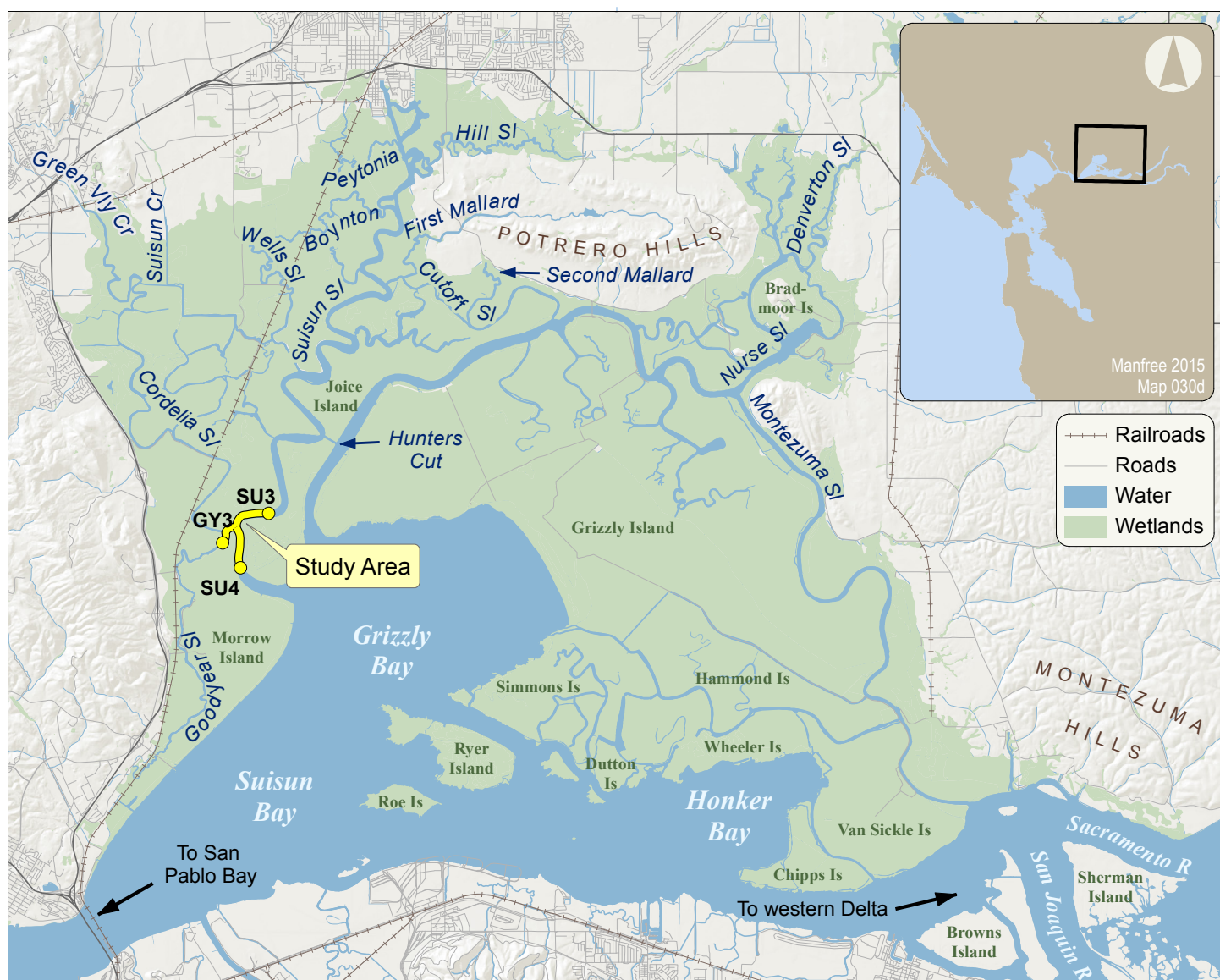
Figure 1 The Suisun Marsh study area; circles show starting locations of trawls, and shaded waterways connecting circles denote sampled reaches of sloughs (map by Amber Manfree).

We therefore used stable isotopes to answer these questions: What is the structure of the Suisun Marsh food web? Do native and alien species play different roles in the food web?

MATERIALS AND METHODS

Study Area

Suisun Marsh is a large brackish marsh (approximately 340 km^2; Figure 1); approximately one-third of the marsh is tidal, and the remainder consists primarily of diked wetlands managed for waterfowl (Moyle et al. 2014). Suisun Marsh occupies a central position in the estuary, being upstream of the saltwater San Francisco Bay and being immediately downstream of the tidal freshwater Delta, the latter of which is Suisun Marsh's major source of fresh water. Environmental conditions within the marsh—including salinity, temperature, water clarity, and dissolved oxygen—vary by season, location, and the amount of inflowing fresh water. Freshwater inflow is usually

highest from February to March and declines towards June, with the lowest inflow occurring between July and November. As freshwater inflow decreases in late spring and early summer, saltier water intrudes and salinity increases, reaching its highest levels in fall before declining after winter rains begin and freshwater inflows from the watershed subsequently increase. These factors strongly influence the diversity of the aquatic community and the abundance of species (Meng and Matern 2001; Matern et al. 2002; Schroeter 2008). Suisun Marsh is generally recognized as being an important low-salinity nursery area for numerous fishes and macroinvertebrates (Meng et al. 1994; Meng and Matern 2001; Matern et al. 2002; Feyrer et al. 2003; Moyle et al. 2014).

Sample Collection

We sampled biota from Suisun Marsh for stable isotope analyses on September 28 and October 26, 2011. We recorded salinity, temperature, dissolved oxygen (DO), and Secchi depth on each sample date at each trawl site (Figure 1), measuring the first three parameters with a Yellow Springs Instruments (YSI) 85 device. Sampling locations were in the southwest region of Suisun Marsh and included the lower reaches of Suisun, Cordelia, and Goodyear sloughs (Figure 1). We selected this area in autumn because of the high taxonomic diversity of fishes and invertebrates that typically reside there (Matern et al. 2002). We intentionally chose a limited area within Suisun Marsh to minimize the variability often encountered with stable isotope analyses along a spatial gradient (e.g., Fry 1999). We specifically targeted abundant species (Table 1) and opportunistically included other species, but the small scope of the study precluded evaluating all organisms captured for isotopes. Taxa from different sites were pooled together because of very similar water-quality conditions among sites (O'Rear, unpublished data).

We collected phytobenthos (benthic algae) samples at low tide when mud flats were fully exposed. To separate phytobenthos from detritus and sediment, we first removed from the mud flat an area of bottom substrate measuring approximately 20 cm × 20 cm and 5-cm deep. We then removed a thin slice of the

surface film (≤1 mm thick). We obtained material for sediment samples from the same bottom substrate but at depths greater than 2 mm to avoid mixing with phytobenthos. We also collected terrestrial and aquatic vegetation. The aquatic plants sampled included three species of SAV: Brazilian waterweed (*Egeria densa*), Eurasian milfoil (*Myriophyllum spicatum*), and sago pondweed (*Stukenia pectinatus*), which we either raked from slough channels or took from otter trawls. We also sampled four species of emergent aquatic vegetation: common reed (*Phragmites australis*), common cattail (*Typha latifolia*), pickleweed (*Salicornia virginica*), and California bulrush (*Schoenoplectus californicus*). We clipped samples from four taxa of terrestrial plants along the slough edges: California rose (*Rosa californica*), *Eucalyptus* sp., perennial pepperweed (*Lepidium latifolium*), and an unknown species of grass.

We sampled benthic invertebrates using a petite ponar dredge that measured 15 cm × 15 cm with a sampling area of 0.023 m². We field-rinsed samples using a 500-μm sieve bucket and further sorted the remaining material in trays. Dip nets were used to sample invertebrates in patches of SAV and emergent aquatic vegetation. Dredging and dip-netting continued until we captured at least 5 individuals of the target species (Table 1).

We collected mysids and copepods with 300-μm and 154-μm mesh conical plankton nets, respectively. Both nets were attached to a weighted bar, lowered into the water column, and then towed twice for approximately 5 minutes at various depths, which yielded the requisite sample sizes for mysids. Water for phytoplankton samples was collected by pump with an inlet positioned approximately 0.75 m below the water surface. The pumped water was pre-filtered through a 100-μm mesh net to remove zooplankton and then further filtered using a low-pressure vacuum pump that pulled the water through an ashed Whatman glass microfiber filter (46-mm diameter) and retained the phytoplankton samples.

Fish, decapod shrimps, and medusae of Black Sea jellyfish (*Maeotias marginata*) were sampled using a four-seam otter trawl 1.5-m high, 4.3-m wide, and 5.3-m long. The trawl was towed at approximately

Table 1 Suisun Marsh taxa analyzed for stable isotope ratios. For animals, the letter superscripts following the animal scientific name indicates the statistical result of the Mann–Whitney rank sum test; unique letters among species in a particular group indicate a significant difference at the $\alpha = 0.05$ significance level (* = too few samples for statistical comparisons; + = targeted animals for study). $\delta^{13}C$ values presented for consumers are the lipid-corrected values.

Group	Scientific name	Common name	Code	Native/Alien?	n	$\delta^{13}C$ (‰) (mean ± SD)	$\delta^{15}N$ (‰) (mean ± SD)
Phytobenthos	N/A	N/A	phytobenth	N/A	6	−22.7 (± 1.5)	7.0 (±0.4)
Phytoplankton	N/A	N/A	phytoplank	N/A	10	−27.6 (±0.6)	3.9 (±1.5)
Terrestrial vegetation	*Eucalyptus globulus*	blue-gum eucalyptus	euc	alien	5	−28.8 (±0.2)	2.0 (±0.4)
	Poaceae	grass	grass	N/A	5	−27.8 (±0.2)	4.6 (±0.5)
	Lepidium latifolium	pepperweed	pep. weed	alien	5	−29.3 (±0.1)	4.9 (±0.1)
	Rosa californica	wild rose	rose	native	5	−25.6 (±0.1)	2.0 (±0.2)
Terrestrial vegetation (all taxa)	N/A	N/A	terrestrial	both	20	−27.9 (±1.5)	3.4 (±1.4)
Emergent aquatic vegetation	*Phragmites australis*	common reed	reed	alien	5	−26.8 (±0.1)	8.0 (±0.2)
	Schoenoplectus californicus	bulrush	rush	native	5	−27.4 (±0.0)	8.8 (±0.2)
	Typha latifolia	cattail	cattai	native	5	−29.1 (±0.1)	6.0 (±0.2)
	Sarcocornia pacifica	pickleweed	pickle	native	5	−28.8 (±0.1)	5.8 (±0.3)
Emergent aquatic vegetation (all species)	N/A	N/A	EAV	both	20	−28.0 (±1.0)	7.2 (±1.4)
Submerged aquatic vegetation	*Egeria densa*	Brazilian waterweed	Egeria	alien	5	−21.8 (±0.1)	9.5 (±0.3)
	Myriophyllum spicatum	Eurasian milfoil	milfoil	alien	5	−19.2 (±0.1)	4.7 (±0.3)
	Stuckenia pectinatus	sago pondweed	sago	alien	5	−17.1 (±0.0)	12.5 (±0.1)
Submerged aquatic vegetation (all species)	N/A	N/A	SAV	alien	15	−19.4 (±2.0)	8.9 (±3.4)
Bryozoa	Bryozoa [+]	moss animal	bry	N/A	5	−25.6 (±0.3)	10.5 (±0.8)
Annelida	Oligochaeta [+]	worms	oligo	N/A	5	−27.9 (±0.4)	9.8 (±1.0)
Insecta	Chironomidae	nonbiting midge	midge	N/A	3	−27.8 (±2.0)	10.2 (±1.6)
Polychaeta	*Laonome* sp. [a, +]	pileworm	Lao	alien	5	−29.1 (±0.9)	7.5 (±0.5)
	*Neanthes limnicola**	pileworm	Neanth	native	1	−26.5	11.6
	Marenzellaria viridis [b, +]	pileworm	Maren	native	20	−26.3 (±0.6)	11.6 (±0.9)
Bivalvia	*Cobicula fluminea* [a, +]	Asian clam	Corbic	alien	15	−28.4 ±(1.4)	10.3 (±0.8)
	Potamocorbula amurensis [a, +]	overbite clam	overbite	alien	21	−27.6 (±1.2)	10.2 (±0.5)
	Macoma petalumb	N/A	macoma	alien	4	−25.1 (±0.7)	13.2 (±2.0)
Copepods	*Copepoda* [+]	N/A	cope	N/A	21	−29.8 (±1.2)	11.0 (±1.1)
Mysida	*Hyperacanthomysis longirostris* [a, +]	opossum shrimp	H. long	alien	23	−28.1 (±2.0)	11.6 (±1.0)
	Neomysis kadiakensis [a, +]	opossum shrimp	N. kad	native	8	−27.8 (±1.3)	10.8 (±0.9)
Amphipoda	*Gammarus daiberi* [a, +]	scud	G. dai	alien	17	−19.4 (±4.8)	12.1 (±1.3)
	Americorophium spinicorne [b, +]	tube-dwelling scud	A. spin	native	19	−26.0 (±4.2)	10.3 (±1.4)
Isopoda	*Synidotea laticauda*	pillbug	S. lat	alien	9	−22.4 (±2.3)	11.7 (±0.9)
Decapoda	*Crangon franciscorum* [a, +]	grass shrimp	b. shrimp	native	28	−22.3 (±2.1)	14.6 (±0.6)
	Exopalaemon modestus [b, +]	ghost shrimp	S. prawn	alien	19	−22.2 (±2.4)	13.4 (±0.9)
	Palaemon macrodactylus [c, +]	ghost shrimp	or. shrimp	alien	15	−23.4 (±2.0)	15.2 (±0.8)
Hydrozoa	*Maeotias marginata* [+]	Black Sea jellyfish	jelly	alien	20	−26.0 (±0.4)	14.5 (±0.4)
Fish	*Cottus asper*	prickly sculpin	SCP	native	2	−24.6 (±2.6)	13.1 (±0.8)
	Morone saxatilis [+]	striped bass	SB	alien	18	−24.5 (±1.1)	15.9 (±0.7)
	Acanthogobius flavimanus	yellowfin goby	YFG	alien	1	−25.0	14.6

$4\,km\,hr^{-1}$ at three spatially fixed sampling locations (SU3, SU4, and GY3; Figure 1) that are part of a monthly monitoring survey of fish and invertebrates in Suisun Marsh that the University of California, Davis, conducts (Matern et al. 2002; Schroeter 2008); a total of six trawls were pulled, three in each month, one per site per month. The trawl mesh was 35-mm fully stretched with a 17-mm rough opening, and the cod-end was lined with a 6-mm fully stretched and 3-mm rough-opening mesh.

Sample Preparation

Fish, vegetation, phytobenthos, phytoplankton, and sediment samples were all frozen on dry ice in the field. Invertebrates were divided by species and were placed live into individual holding containers with marsh water (filtered through 54-μm mesh) for a minimum of 24 hours to allow for gut clearance. We further sorted mall invertebrates in the laboratory using a dissecting microscope to ensure proper species identification. Fish were filleted, and we removed muscle tissue from the left side of the body to the rear of the gut through the caudal peduncle. Clams were taken from their shells prior to drying. We rinsed all animal and plant tissue with de-ionized water before drying it at 60°C. We then used a mortar and pestle to grind all samples into a homogeneous powder, with the exception of small invertebrates weighing between 0.5 and 4 mg and the phytoplankton samples, both of which we analyzed whole. Because of their small sizes, all species of copepods were combined and analyzed together. The omnivores *Acartiella sinensis* and *Acanthocyclops vernalis* (Andreadis and Gere 1992; Kimmerer 2004) together comprised 100% and 91.4% of the September and October catches, respectively; *Limnoithona tetraspina* and *Pseudodiaptomus forbesi* comprised the remainder of the October catch.

Carbon and Nitrogen Stable Isotope Analyses

We analyzed total of 350 samples from Suisun Marsh for stable isotopes (Table 1), including phytobenthos (6), phytoplankton (10), bryozoans (5), hydrozoans (20), clams (40), various invertebrates (193), fish (21), and aquatic and terrestrial plants (55). Twenty-two species of aquatic animals, seven native and 15 alien, were represented (Table 1).

We weighed samples on a microbalance and placed them in tin capsules for isotope processing. All samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ 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). Samples were combusted at 1,000°C in a reactor packed with chromium oxide and copper oxide. After combustion, oxides were removed in a reduction reactor (reduced copper at 650°C) and the helium carrier then passed through a water trap (magnesium perchlorate). N_2 and CO_2 were separated on a carbosieve gas chromatography (GC) column (65°C, 65 ml min^{-1}) before entering the IRMS.

During analysis, samples were interspersed with several replicates of four different laboratory standards: nylon, bovine liver, peach leaves, and glutamic acid. These laboratory standards were previously calibrated against National Institute of Standards and Technology (NIST) Standard Reference Materials (International Atomic Energy Agency [IAEA]-N1, IAEA-N2, IAEA-N3, and U.S. Geological Survey [USGS]-40, and USGS-41). The sample's preliminary isotope ratio was measured relative to reference gases analyzed with each sample. These preliminary values were then finalized by correcting the values for the entire batch based on the known values of the included laboratory standards. The long-term standard deviation for analyses is 0.2 per mil (‰) for $\delta^{13}C$ and and 0.3‰ for $\delta^{15}N$. The final isotope values are expressed relative to international standards Vienna PeeDee Belemnite (V-PDB) and air for carbon and nitrogen, respectively (Sharp 2005).

Data Analyses

We used MixSIAR 2.1.2 (Stock and Semmens 2013) to determine probabilities of carbon sources to consumers. We used the equation provided in Post et al. (2007) to correct $\delta^{13}C$ values for lipid content for animals; no corrections were applied to primary

producers because of the non-significant relation-ship between the C:N ratio and the change in δ^{13}C from lipid content (Post et al. 2007). To reduce under-determined model solutions (Fry 2013), we grouped primary producers by ecological type: emergent aquatic vegetation, SAV, terrestrial plants, phytoplankton, and phytobenthos. Phytoplankton and terrestrial plants were subsequently grouped together because of their similar isotope values (Figure 2). We modeled consumer taxa as random effects and included both process and residual error in the models. We chose the run length "long" for the number of Monte Carlo Markov Chain simula-tions for all models, which comprised three chains of 300,000 simulations each, with a burn-in of 200,000. To assess robustness of the models, we used several sources to assign different discrimination factors to consumers: values from Vander Zanden and Rasmussen (2001, values from McCutchan et al. (2003), and taxonomically grouped values derived from both studies (Appendix A). We ran several mod-els on a subset of consumers with all three types of discrimination factors; results were similar among models (see Appendix A). For example, means and credible intervals of carbon sources with either very high or very low probability (e.g., emergent aquatic vegetation for striped bass and Asian clam, and phytoplankton/terrestrial vegetation for all three animals; see Appendix A) remained either high or low regardless of the discrimination factors used. The means of probabilities that were moderate for three carbon sources of California bay shrimp varied notably among the models, although the phytoplank-ton/terrestrial-vegetation group's probabilities were always lowest (see Appendix A). The models using taxonomically grouped values generally performed best, having the lowest deviation information criteria (DIC) scores (see Appendix A), and so the remainder of consumers was modeled using those discrimination values.

We determined other features of the food-web struc-ture by analyzing a biplot of mean δ^{15}N and δ^{13}C values for all consumers and primary producers. Numerous studies have found a δ^{15}N enrichment from 2.4 to 4.0‰ equivalent to a one-step increase in trophic level (Hansson et al. 1997; Kwak and

Zedler 1997; Peterson 1999; Vander Zanden and Rasmussen 2001; McCutchan et al. 2003), which we used to guide interpretation of the plot and because they encompassed the ranges used in the MixSIAR models. Gut contents of striped bass contained amphipods, mysids, and Siberian prawn, so we were able to constrain possible prey to *G. daiberi*, *A. spin-icorne*, Siberian prawn, and mysids for analysis in MixSIAR. Both mysid species were combined and run as one prey source of striped bass because isotope values between *Neomysis kadiakensis* and *H. longi-rostris* overlapped considerably (Figure 2, Table 1). To explore trophic-level differences between similar native and alien species, we analyzed interspecific differences in δ^{15}N for taxonomic groups that con-tained both alien and native species and with suf-ficient sample sizes using the non-parametric Mann–Whitney rank sum test in SigmaPlot 12.3 (Systat Software, Inc., San Jose, California, USA) given non-normal distributions and unequal variances.

RESULTS

Abiotic Conditions

Water-quality parameters (mean ± SD) on each sam-pling date (September 28 and October 26, 2011) were similar for salinity (4.8 ± 0.0 and 5.1 ± 0.5 ppt), temperature (20.4 ± 0.2 and 17.8 ± 0.4°C), dissolved oxygen (7.0 ± 0.4 and 7.0 ± 0.0 mg L^{-1} O^2), and Secchi depth (30 ± 8 and 29 ± 12 cm).

Primary Producer Isotopic Values

Primary producer groups in Suisun Marsh had large within-group and among-group variation in δ values for both isotopes, although overlap was low among groups except for terrestrial vegetation and phyto-plankton (Table 1, Figure 2). Terrestrial vegetation was depleted in both δ^{13}C (mean ± SD = −28.1 ± 1.3‰) and δ^{15}N (3.9 ± 1.6‰); emergent aquatic vegeta-tion was also depleted in δ^{13}C (−27.8 ± 1.0‰) but more enriched in δ^{15}N (7.6 ± 1.2‰); SAV was much more enriched in δ^{13}C (− 19.4 ± 2‰) and, except for Eurasian milfoil, more enriched in δ^{15}N (8.9 ± 3.4‰). The δ^{13}C and δ^{15}N values for phytoplankton (− 27.6 ± 0.6‰; 3.9 ± 1.5‰) were most similar to
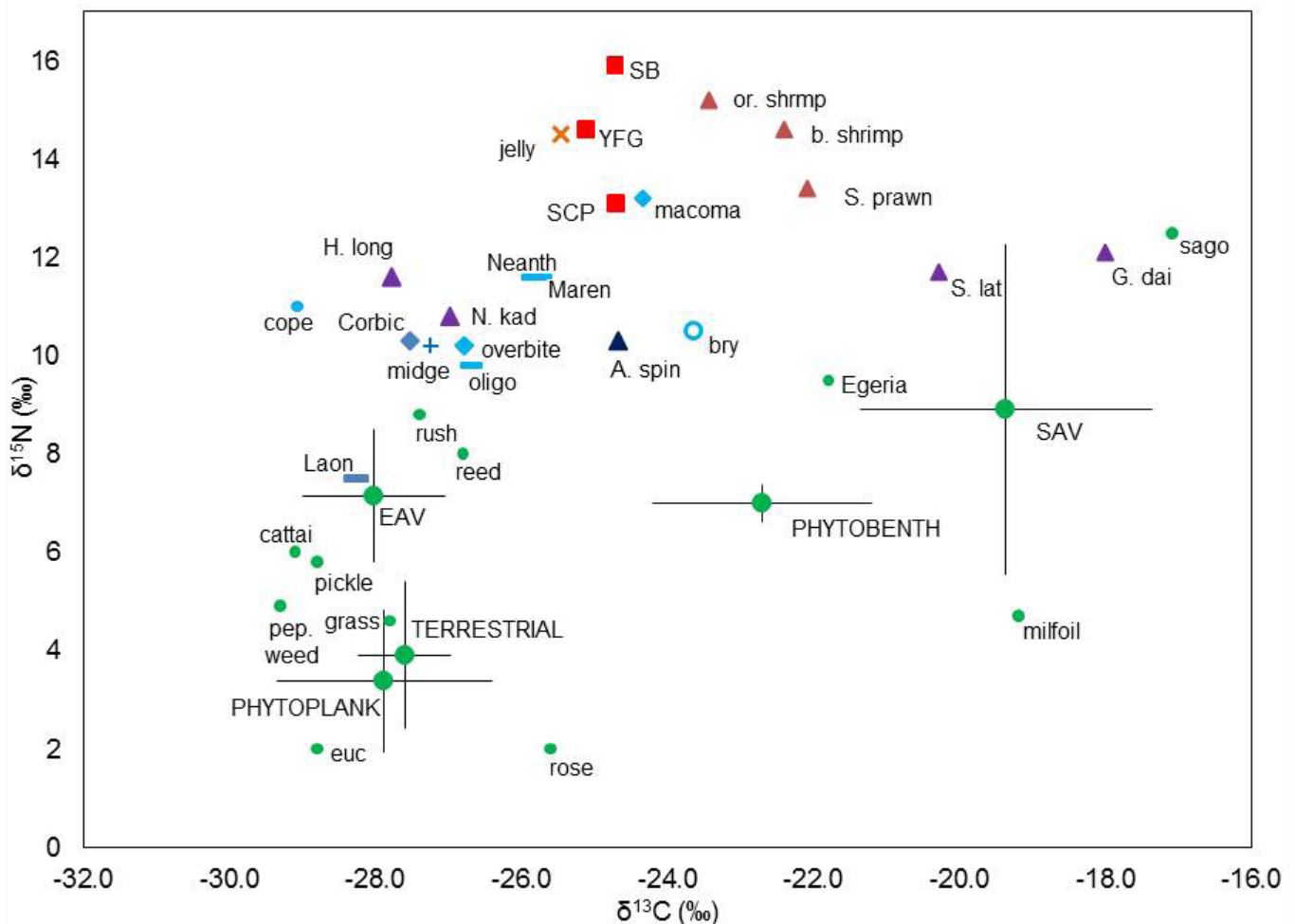
Figure 2 Biplot of mean $\delta^{15}N$ and $\delta^{13}C$ values for organisms captured in Suisun Marsh during autumn 2011 (note that $\delta^{13}C$ values for animals are the lipid-corrected values). Symbols: round = plants/algae, rectangle = annelids, diamonds = clams, triangles = crustaceans, squares = fishes; other symbols denote unique organisms. Colors correspond to animals assigned the same discrimination factors in MixSIAR. Symbols with capitalized labels represent means for primary producer ecological group; error bars are standard deviations. Sample sizes and organism codes are given in Table 1.

terrestrial vegetation; the values for phytobenthos (-22.7 ± 1.5‰; 7.0 ± 0.4‰) were more similar to SAV. Variation within species was much lower than that for the primary producer groups (Table 1). In sum, there were two broad groups of primary producers along the carbon isotope axis: a $\delta^{13}C$-depleted group comprised of phytoplankton, terrestrial vegetation, and emergent aquatic vegetation; and a $\delta^{13}C$-enriched group comprised of phytobenthos and SAV. This isotopic arrangement of carbon sources corresponded well with results of Grimaldo et al. (2009) and with the results of the fresher regions of Cloern

et al. (2002) and Howe and Simenstad (2011). That the Suisun Marsh primary producer isotope values matched up with the fresher regions of both Cloern et al. (2002) and Howe and Simenstad (2011) was probably because 2011 was a wet year, which resulted in lower-than-average salinities in Suisun Marsh for all months of 2011 except December (O'Rear and Moyle 2014).
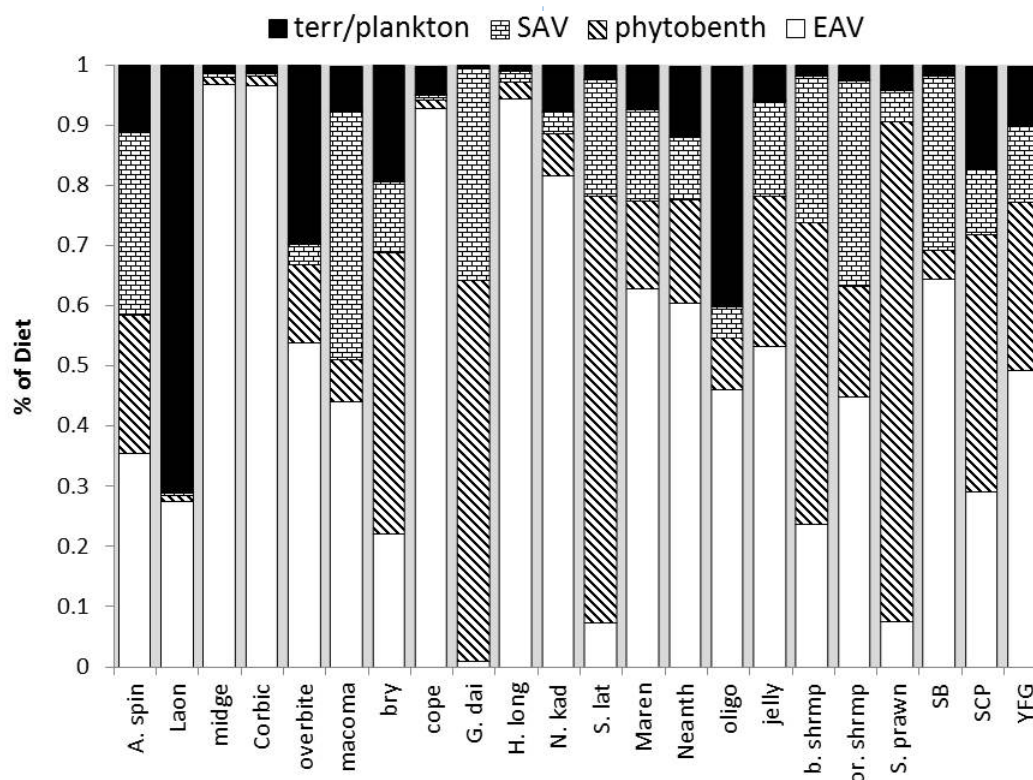
Figure 3 Mean posterior probabilities for four carbon sources of Suisun Marsh animals; codes as in Table 1

Consumer Carbon Sources, Isotopic Values, and Trophic Levels

MixSIAR models suggested that no one carbon source dominated most consumer diets (Figure 3, Table 2). An exception was emergent aquatic vegetation, which appeared to be the greatest source of carbon to midges, Asian clam, copepods, mysids, and—to a lesser extent—two polychaete species and striped bass (Figure 3). Phytobenthos mean probabilities were relatively high for three crustaceans: Siberian prawn, *S. laticauda*, and *G. daiberi*. High mean probabilities for phytoplankton and/or terrestrial vegetation occurred only for two taxa: the worms *Laonome* sp. and oligochaetes. Submerged aquatic vegetation did not dominate the diets of any consumers but was a substantial mean proportion of the diets of the two amphipods, the clam *M. petalum*, oriental and California bay shrimp, and striped bass. Striped bass were modeled as feeding predominantly on mysids and Siberian prawn and less so on amphipods (Figure 4).

Precision of posterior probabilities among animals was highly variable. Standard deviations, which were highly correlated to a width of 95% credible intervals (n = 89, credible-interval width = −5.0213(SD)^2 + 4.7278(SD) − 0.0406, r^2 = 0.98), were especially high for *G. daiberi*, prickly sculpin, and yellowfin goby (Table 2), the latter two of which had very small sample sizes (two and one fish, respectively; Table 1). Precision was quite good for a range of species and carbon sources, although means associated with high precision tended to be very low (Table 2), suggesting that, in general, the MixSIAR models better identified negligible carbon sources than distinguishing among the more important sources.

The trophic arrangement of fauna in Suisun Marsh, based upon mean δ^{15}N values, revealed roughly three consumer trophic levels (Figure 2; Table 1). The lowest-level consumer group contained only one species, the polychaete *Laonome* sp., which had by far the lowest mean δ^{15}N value of any consumer (7.5‰). Centered around a δ^{15}N value of 10.9‰ (3.4‰ above *Laonome* sp.'s mean δ^{15}N value) was

Table 2 Means and standard deviations for posterior probabilities for Suisun Marsh consumers; codes as in Table 1 except for "terr/plankton," which is the combination of the phytoplankton and terrestrial-plant groups.

Taxa	Emergent aquatic vegetation	Phytobenthos	SAV	Terr/Plankton
A. spin	0.355±0.164	0.229±0.172	0.305±0.11	0.111±0.087
b. shrmp	0.236±0.094	0.501±0.127	0.245±0.065	0.018±0.025
bry	0.22±0.105	0.467±0.174	0.12±0.091	0.193±0.097
cope	0.928±0.054	0.014±0.015	0.009±0.01	0.048±0.048
Corbic	0.965±0.054	0.016±0.038	0.008±0.02	0.011±0.028
G. dai	0.009±0.024	0.633±0.393	0.352±0.389	0.006±0.016
H. long	0.943±0.063	0.028±0.047	0.02±0.034	0.009±0.023
jelly	0.531±0.064	0.251±0.092	0.159±0.054	0.059±0.047
Laon	0.275±0.198	0.01±0.03	0.005±0.013	0.71±0.195
macoma	0.441±0.133	0.068±0.068	0.414±0.096	0.076±0.08
Maren	0.627±0.076	0.146±0.092	0.153±0.06	0.075±0.06
midge	0.968±0.064	0.012±0.04	0.009±0.027	0.011±0.038
N. kad	0.816±0.162	0.069±0.096	0.038±0.059	0.077±0.106
Neanth	0.604±0.25	0.171±0.208	0.105±0.114	0.119±0.135
oligo	0.461±0.152	0.084±0.077	0.053±0.047	0.401±0.127
or. shrmp	0.449±0.124	0.182±0.163	0.344±0.088	0.025±0.036
overbite	0.538±0.07	0.129±0.072	0.036±0.029	0.297±0.06
S. lat	0.073±0.11	0.708±0.255	0.196±0.224	0.024±0.049
S. prawn	0.074±0.078	0.832±0.146	0.053±0.064	0.041±0.06
SB	0.644±0.064	0.048±0.066	0.29±0.052	0.018±0.029
SCP	0.29±0.289	0.427±0.368	0.111±0.135	0.171±0.229
YFG	0.493±0.33	0.279±0.345	0.129±0.149	0.098±0.186

a second consumer group comprised of most of the invertebrate species except for the decapod shrimps. Notably, *G. daiberi* and *S. laticauda* were substantially more enriched in $\delta^{13}C$ than other consumers with similar $\delta^{15}N$ values (Figure 2). The taxa with the highest $\delta^{15}N$ values, which tended to have intermediate $\delta^{13}C$ values, were also the largest animals sampled (Figure 2): the fishes, the decapod shrimps, Black Sea jellyfish medusae, and *M. petalum*, the latter of which was generally larger bodied than the other two clam species (Schroeter, unpublished data). The mean $\delta^{15}N$ value for this third group (14.3‰) was about 3.4‰ higher than the mean for the mid-level consumers. These differences in mean $\delta^{15}N$ values among consumer groups corresponded well to enrichment values per trophic level found in the literature (e.g., Vander Zanden and Rasmussen 2001), although

variability was considerable within the groups comprised of many species.

Alien and Native Species Taxonomic Comparisons

In general, $\delta^{15}N$ values between native and alien species differed among taxonomic groups but showed no overall pattern. The three polychaete species exhibited significant differences (Mann–Whitney rank test) in trophic level (Table 1). The alien *M. viridis* and the native *N. limnicola* had $\delta^{15}N$ values 4.1‰ above those of the alien *Laonome* sp. (Figure 2). The mysids *H. longirostris* (alien) and *N. kadiakensis* (native) were both similar trophically, (Figure 2) with no significant differences between their $\delta^{15}N$ values (Table 1). For the amphipods, the alien *G. daiberi* was significantly more enriched in $\delta^{15}N$ than the native
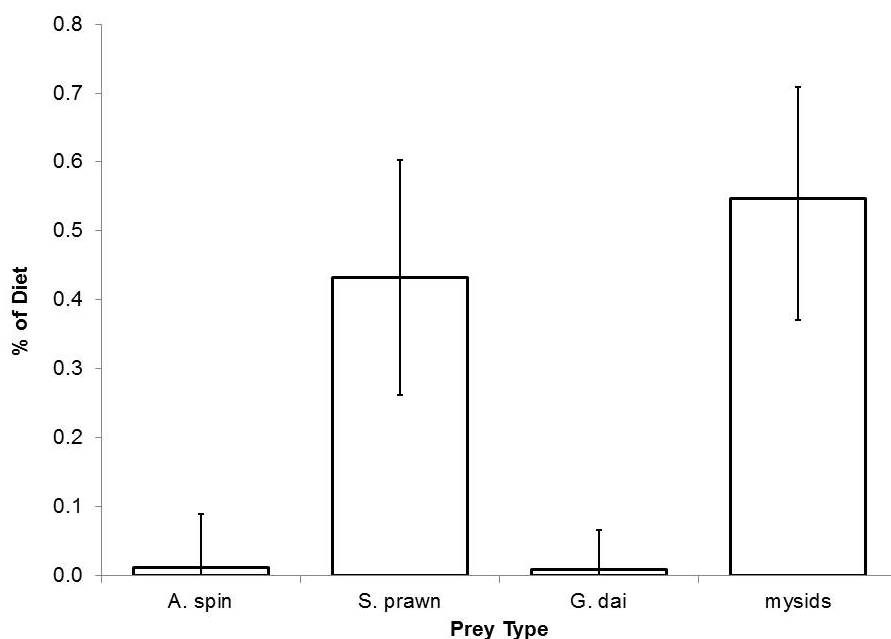
Figure 4 Mean posterior probabilities for four prey sources of striped bass; error bars are 95% credible intervals; codes as in Table 1 except for "mysids," which is the combination of *H. longirostris* and *N. kadiakensis*.

A. spinicorne according to the Mann–Whitney rank sums test (Table 1). Finally, all three decapod shrimp differed significantly from each other in trophic level (Table 1). The alien oriental shrimp had the highest $\delta^{15}N$ values, the native California bay shrimp had intermediate values, and the alien Siberian prawn had the lowest values (Figure 2).

DISCUSSION

What Is the Structure of the Suisun Marsh Food Web?

The MixSIAR models suggested that most consumers gleaned substantial proportions of carbon from more than one primary producer group, although five taxa—midges, Asian clam, the copepods, and the two mysid species—appeared especially to derive their carbon from emergent aquatic vegetation (Figure 3). These findings are curious given the dependence of these animals on phytoplankton noted in the literature (e.g., Boltovsky et al. 1995; Kimmerer 2004; Howe and Simenstad 2011). There are three plausible explanations for this discrepancy. First, phytoplankton may have been the true carbon source for

these consumers, which would have required either (1) very small primary consumers, such as copepod nauplii, that were feeding on phytoplankton and then consumed by Asian clams, mysids, and copepods but were too small to be sampled effectively by our nets; or (2) very little carnivory among these species coupled with abnormally high $\delta^{15}N$ enrichment values ($\sim6‰$). This latter explanation seems unlikely given the omnivory reported for both mysids and the dominant copepod species in the samples (e.g., Kimmerer 2004). Because of the inability to isotopically separate terrestrial vegetation from phytoplankton, the same reasoning could be applied to terrestrial vegetation as the carbon source, although little support exists for terrestrial vegetation fueling such consumers (e.g., Sobczak et al. 2005). Second, emergent aquatic vegetation may be the true carbon source, although it, too, would necessitate absence in our samples of a primary consumer (e.g., protozoans; Sobczak et al. 2002) that processed emergent aquatic vegetation and that had relatively low $\delta^{15}N$ enrichment values. Third, the consumers may have been generalist feeders, eating a range of lower-level,

unsampled consumers that, in turn, fed on a range of carbon sources.

Based upon the δ^{13}C values and MixSIAR results, three invertebrates—*G. daiberi*, *S. laticauda*, and Siberian prawn, and, to a lesser extent, California bay shrimp—gained most of their carbon from phytobenthos and SAV (Figures 2 and 3). Although we did not perform gut-content analyses on the shrimps, and so had no reasonable criteria for constraining the number of prey sources for MixSIAR modeling, it seems sensible based on diet literature in the estuary (Sitts and Knight 1979; Siegfried 1982; Wahle 1985) that the shrimps frequently ate *G. daiberi*. Feeding of the shrimps on *G. daiberi* is likely the reason why SAV probabilities were relatively high for striped bass (Figure 3) even though MixSIAR identified Siberian prawn and mysids as dominant foods (Figure 4): striped bass were probably feeding indiscriminately on all three shrimp species, including oriental and California bay shrimp (Ganssle 1966), despite the presence of only Siberian prawn in the guts of our fish. Thus, *G. daiberi* is likely a major route through which δ^{13}C-enriched carbon can be incorporated by higher-level consumers in Suisun Marsh, similar to the results of Grimaldo et al. (2009) and consistent with the diet study of Bryant and Arnold (2007). The high SAV probabilities for striped bass also may have resulted from their heavier feeding on *G. daiberi* before our sampling in conjunction with inclusion of the larger Siberian prawn in their diets as the fish grew.

δ^{15}N values of Suisun Marsh organisms generally followed predictable patterns, with fish, the three decapod shrimp species, and Black Sea jellyfish at the apex of the food web (Stewart et al. 2004). Given their highly carnivorous diets and relatively large sizes, oriental shrimp and California bay shrimp were expectedly sited high on the biplot (*Figure 2*; Sitts and Knight 1979; Wahle 1985; González–Oretegón et al. 2010); placement of Siberian prawn lower than the other two shrimp species was also not surprising, based on this species' greater omnivory reported in other systems (Shi et al. 1995; Jin et al. 1997; Xu et al. 2008). *Macoma petalum* was located relatively high in the food web but had a wide range of δ^{15}N values, possibly because *M. petalum* was eating small

benthic animals that, in turn, were subsisting partially on detritus from δ^{15}N-enriched SAV; the substantial contribution of SAV to *M. petalum* suggested by the MixSIAR models supports this interpretation. Conversely, *M. petalum*'s relatively high δ^{15}N values may have been from their filter-feeding on zooplankton, a predation similar to other clam species in other brackish regions of the estuary (Kimmerer et al. 1994; Greene et al. 2011), although this is a weaker explanation since congenerics in other estuaries are mainly deposit feeders (Rossi et al. 2004). The mid-level consumers were a diverse group with considerable variation in δ^{15}N. Generalized feeding of animals comprising the middle trophic level of the food web likely contributed to the large range of both isotopes, particularly for the two amphipod species (Table 1).

Do Native and Alien Species Play Different Roles in the Food Web?

Results of the Mann–Whitney rank sum test and MixSIAR models suggests that some alien species may be playing different roles than native species in certain times and places in Suisun Marsh by creating new food-web pathways and by assimilating carbon differently. Relatively new alien species such as *G. daiberi* (and possibly *S. laticauda*; Figure 3) are likely a major route through which carbon from alien SAV enters the food web to higher-level consumers, as appeared to be the case in this study with the shrimps and, to a lesser extent, striped bass, in addition to these alien invertebrates being eaten directly by many native and alien fishes in other regions in the estuary (Feyrer et al. 2003; Bryant and Arnold 2007; Grimaldo et al. 2009). Significant isotopic differences between native and alien species in three taxonomic groups (e.g., polychaetes, decapod shrimp, and amphipods; Table 1) indicate that alien species often occupy slightly different niches, thereby elevating the food web's complexity. However, the lack of isotopic disparity between the two mysids suggests that alien species may compete with native species for food; this could result in less carbon transfer to higher trophic levels since *H. longirostris* is commonly smaller than *Neomysis* spp. (Kimmerer 2004; Bryant and Arnold 2007).

Despite the changes wrought by alien species such as overbite clam on the Suisun Marsh food web (e.g., Feyrer et al. 2003), the function of many alien species appears to be similar to that of native species. Although native corophiid amphipods were a major food of shrimps and small fishes in the estuary before many of the human-caused changes to the system (Turner and Kelley 1966; Sitts and Knight 1979; Wahle 1985), and still continue to be important to some extent currently (e.g., Whitley and Bollens 2013), alien gammaroid amphipods have partially taken over that role today (Figure 3; Feyrer et al. 2003; Grimaldo et al. 2009; O'Rear 2012). The alien mysid *H. longirostris*, in conjunction with *G. daiberi*, has also replaced the once-abundant *N. mercedis* in the diets of many fishes (Feyrer et al. 2003; Bryant and Arnold 2007), which is consistent with the MixSIAR model denoting the importance of mysids to striped bass in this study (Figure 4). Similarly, the recently introduced Siberian prawn has quickly become an important prey of striped bass (Figure 4; Nobriga and Feyrer 2008) like the native California bay shrimp was historically (Ganssle 1966).

In conclusion, the food web of southwestern Suisun Marsh during this high-freshwater-inflow autumn was comprised of two broad groups of primary producers, with most mid-level consumers dependent on δ^{13}C-depleted carbon sources: phytoplankton and detritus from emergent-aquatic and terrestrial plants. Only two mid-level consumers, the alien amphipod *G. daiberi* and the alien isopod S. *laticauda*, relied on phytobenthos and SAV, the δ^{13}C-enriched carbon sources. Nevertheless, both carbon sources appeared to be assimilated by higher-level consumers, given the moderate probabilities for more than one carbon source of the fishes and the shrimps, likely because these animals are relatively generalist feeders. Several alien species occupied different trophic positions than related native species, suggesting that species introductions have increased the complexity of the food web. More importantly, most of these alien species have become integrated into the food web, resulting in a completely novel ecosystem.

A caveat to this study is that it occurred in a small area of Suisun Marsh during an autumn of high freshwater inflows; its scope also did not allow evaluation of all species of the aquatic community, with the fishes especially being under-represented (more than 20 fish species are commonly abundant in Suisun Marsh in most years; O'Rear and Moyle 2014). Consequently, trophic relationships in Suisun Marsh under different flow regimes, in other seasons, and in other areas could be markedly different from those revealed here, although we expect the basic pattern of increased food-web complexity from alien species is consistent through time and space. Nevertheless, this study provides the first use of stable isotopes to both (1) elucidate the aquatic food web structure of this very important part of the estuary for native fishes and (2) provide the first information on several species (e.g., the polychaetes) whose trophic ecology is virtually unknown.

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